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The Effects of Seagrass Species and Trophic Interactions in Experimental Seagrass Communities

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THE EFFECTS OF SEAGRASS SPECIES AND TROPHIC INTERACTIONS IN EXPERIMENTAL SEAGRASS COMMUNITIES

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In Partial Fulfillment

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Master of Science

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by

Althea F. P. Moore

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This thesis is submitted in partial fulfillment of

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ABSTRACT

Increasing environmental stressors in rapidly changing marine environments are expected to favor more stress tolerant species. Changes in the abundance or distribution of foundation species may have particularly important consequences for the communities they support. Thus it is increasingly vital to determine how habitat-forming species differ in their abilities to provide structure and mediate important interactions. Seagrasses act as foundation species, modifying the environment and providing habitat for trophically important prey. In the Chesapeake Bay, increasing water temperatures are associated with declines in the seagrass *Zostera marina*, and may benefit the temperature-tolerant seagrass *Ruppia maritima.* I used manipulative experiments to compare predator-prey interactions, recruiting species, and the effect of food chain length between these two seagrasses.

To test for differences in predator-prey interactions between foundation species, I observed a common seagrass predator, pipefish *Syngnathus fuscus*, preying on several crustacean prey species in the two seagrasses in controlled laboratory trials. Predators foraged more effectively in *Ruppia*, with significantly higher rates of encounter with prey, attacks on prey, and captures of prey than in *Zostera* at equivalent biomass. This pattern was driven primarily by a greater probability of amphipod prey detection in *Ruppia*, apparently due to its thin leaf structure and lower canopy. These results suggest that these seagrasses can have distinct effects in mediating predator-prey interactions.

I addressed the effects of food chain length and recruiting assemblage on the communities associated with the two seagrass species in an eight-week, factorial mesocosm experiment, which manipulated seagrass species and number of trophic levels at each of six seagrass densities. Trophic levels included no consumers, and small crustacean mesograzers alone or with fish and shrimp predators. I examined the algal and invertebrate assemblages that recruited to the mesocosm tanks. Consumers decreased diversity of recruiting taxa, likely due to consumption by or competition with mesograzers. Predators decreased grazing on algae through an apparent trophic cascade. Individual prey characteristics seemed to determine predation levels, rather than the relative refuge value of the seagrasses. All but one of the most abundant recruiting species were more abundant in *Zostera.*

The laboratory experiment suggests that trophic transfer of mesograzer prey to a small fish predator is greater in *Ruppia*, however such differences were not observed in the mesocosm experiment, perhaps due to the effects of two predators and additional structure of the tanks and macroalgae. Differences in recruiting assemblages between seagrasses could affect higher trophic levels that rely on these epibionts in seagrass beds. Changes in the composition or relative abundances of these seagrass species will likely have important consequences for associated fauna, as these seagrasses may differ in mediating predator-prey interactions and providing habitat for epifauna. Additionally, established differences in the morphology, distribution, and phenology of *Ruppia* and *Zostera* would also be likely to affect important functions in the Chesapeake Bay if species loss or changes in abundance occur.

THE EFFECTS OF SEAGRASS SPECIES AND TROPHIC INTERACTIONS IN EXPERIMENTAL SEAGRASS COMMUNITIES

CHAPTER 1. SEAGRASS SPECIES INFLUENCES THE FORAGING SUCCESS OF A COMMON FISH PREDATOR

ABSTRACT

Increasing environmental stressors in rapidly changing marine environments are expected to favor more stress tolerant or opportunistic species. Changes in the abundance or distribution of habitat-forming foundation species may have particularly important consequences for the communities they support. Thus it is increasingly vital to determine specifically how such foundation species differ in their abilities to provide habitat and mediate important interactions. Seagrasses are important foundation species, modifying the environment and providing habitat for trophically important prey species. In the Chesapeake Bay, increasing water temperatures have been associated with declines in the seagrass *Zostera marina*, and may benefit the temperature-tolerant seagrass *Ruppia maritima.* To test for differences in predator-prey interactions between morphologically distinct foundation species, I used controlled experiments to observe a common seagrass predator, pipefish *Syngnathus fuscus*, preying on several epifaunal crustacean prey species in *Ruppia maritima* and *Zostera marina.* Predators foraged more effectively in *Ruppia*, with significantly higher rates of encounter with prey, attacks on prey, and captures of prey than in *Zostera* at equivalent biomass. This pattern was driven primarily by a greater probability of amphipod prey detection in *Ruppia*, apparently due to its thin leaf structure and lower canopy. One thin-bodied isopod prey species, *Erichsonella attenuata*, was not vulnerable to predator detection in either seagrass species, suggesting a possible mechanism for its high field densities during times of greatest small predator abundance. These results suggest that these foundation species can have distinct effects in mediating predator-prey interactions. Alterations in the composition or relative abundances of foundation species will likely have important consequences for associated fauna, and caution should be exercised in assuming equivalency of foundation species in mediating predator-prey interactions.

INTRODUCTION

Anthropogenic stressors, including the effects of climate change, have the potential to alter communities by creating environmental conditions that favor more stress-tolerant or opportunistic species. Species near the limits of their physiological tolerances are expected to contract their ranges (Parmesan, 2006), while more stress-tolerant or opportunistic species may either increase in abundance or in their relative importance, as sensitive species decline (Chapin et al., 1998). Thus it is increasingly vital to determine whether similar species are equivalent in their ecological roles, and whether more stress-tolerant species will be able to provide some degree of functional redundancy for the species they may replace.

In particular, changes in the relative abundance of habitat-forming, 'foundation' species (*sensu* Dayton, 1972) can alter important processes. Foundation species can provide refuge from predation and ameliorate stressful environmental conditions, having important and cascading impacts on the communities they form (Bruno & Bertness, 2001; Ellison et al., 2005). Changing abundances of key taxa in altered systems can cause cascading effects on species composition and interactions, ultimately helping to determine the effects of environmental change on community structure (Walther et al., 2002; Schiel, 2004; Micheli et al., 2008). Species redundancy in important ecological roles may determine the reliability of ecological functions as species composition changes (Walker, 1992; Walker, 1995; Naeem, 1998).

Seagrasses are a unique group of marine angiosperms which act as foundation species, creating a refuge and modifying the environment by affecting water flow, nutrient cycling, and community structure (Heminga & Duarte, 2000). Seagrass beds also provide numerous valuable ecosystem services to humans. Seagrass contributions to nutrient cycling alone have considerable value economically (Costanza, 1997). Seagrasses also provide coastal protection (Koch et al., 2006), carbon storage (Duarte & Chiscano, 1999), and fisheries production (Gillanders, 2006), thus playing an important role in coastal ecosystems. Seagrass beds are also some of the most threatened coastal habitats, with stressors, such as nutrient and sediment run-off, physical disturbance, and temperature stress, causing large-scale declines (Duarte, 2002; Orth et al., 2006; Waycott et al., 2009) and changes in species composition (Johnson et al., 2003; Micheli et al., 2008). More stress tolerant species are expected to increase relative to more sensitive species, if stressful conditions are intensified. To the extent that seagrasses differ functionally, species loss or alteration in the composition of foundation species would likely have important consequences for the ecosystem services provided by these communities. Thus, it is important to determine specifically how foundation species differ in their abilities to provide habitat and mediate important interactions.

Seagrasses provide structural complexity and food resources for the highly abundant fauna that utilize these important habitats, and are thought to contribute considerably to the production of coastal fisheries through refuge and trophic support (Kikuchi, 1974; Heck & Orth, 1980; Orth & Heck, 1980; Heck et al., 2003; Gillanders, 2006). Epiphytic algae growing on the seagrass provides an accessible source of primary production, which is utilized by a host of small epifaunal grazers inhabiting seagrass beds, including crustacean mesograzers such as isopods and amphipods. Thus, the primary production in seagrass beds is transferred to small grazers, creating biomass available for transfer to higher trophic levels (Williams & Heck, 2001). Indeed, crustacean grazers are an important trophic link, with the majority of seagrass fish feeding primarily on small crustaceans, including copepods, amphipods and decapods (Klumpp et al., 1989; Edgar & Shaw, 1995). Adams (1979) estimated that food produced in seagrass beds accounted for approximately 56% by weight of the diet of seagrass fishes.

Seagrass habitats apparently attract and maintain high abundances of fauna by providing physical structure, which creates habitat and serves as a visual and tactile barrier between potentially interacting predators and prey (Main, 1985; Main, 1987). Many studies have supported the hypothesis that increasing the density of refuge structure or habitat complexity leads to lower predation rates. When the density or biomass of seagrass (or an artificial analogue) is increased experimentally with predator and prey densities held constant, predation rates tend to decrease (Nelson, 1979; Stoner, 1982; Heck & Thoman, 1981; Nelson & Bonsdorf, 1990 and studies listed therein; reviewed in Heck & Orth, 2006). It is less clear whether the specific type or morphology of structure in a community greatly affects interactions. A meta-analysis by Heck et al. (2003) found no significant average differences across studies in important functions, such as the provision of structural refuge and trophic support for juvenile fishes, between seagrass beds and other structured habitats such as macroalgal mats. However, other studies have indicated that the specific morphology of vegetation can have a significant impact on small-scale predator-prey interactions. Experimental manipulations of aquatic macrophytes showed that while vegetation density had no effect on refuge, predation was significantly reduced in the most structurally complex vegetation, which possessed whorls of highly dissected leaves (Warfe & Barmuta, 2004). The size of a structural refuge relative to predator and prey sizes can also be important for refuge and foraging efficiency (Ryer, 1988; Bartholomew, 2002).

To test for differences in predator-prey interactions between morphologically distinct foundation species, I used controlled experiments to observe a common seagrass predator, pipefish *Syngnathus fuscus*, preying on three epifaunal crustacean grazers, in two species of seagrass, *Ruppia maritima* and *Zostera marina*. These seagrasses will hereafter be referred to by their genus names. During timed trials, I recorded the number of encounters between predators and prey, attacks on prey, and captures of prey in each of the two seagrasses. Thus I was able to determine whether seagrass species affected predation, and whether differences were due to greater detection of prey (indicated by the encounter rate), or an increased probability of attack or capture by predators. I expected that plant morphology would affect predator-prey interactions, with thinner-leaved plants providing less effective refuge for epifaunal prey. However, I also hypothesized that the influence of plant species on predator-prey interactions might differ by prey species, depending on the prey's morphology and behavior.

METHODS

Study system

The Chesapeake Bay is an estuary with historically abundant seagrass beds, which have declined greatly over a period of decades, reaching an all-time low in the early 1980s (Orth & Moore, 1983; Orth & Moore, 1984) and recovering to some extent in subsequent years (Moore et al., 2000) with abundance patterns correlated with water quality throughout the Bay (Orth et al., 2010). In addition to the stress of poor water quality, increasingly high summer water temperatures in the Chesapeake Bay have the potential to change the relative abundance of seagrass species in this system (Moore & Jarvis, 2008; Johnson et al., 2003). Of the two species of seagrasses found in polyhaline waters of the Chesapeake Bay, *Zostera marina* seems likely to decrease relative to *Ruppia maritima*, due to *Zostera's* more narrow range of physiological tolerances. The Chesapeake Bay is near the southern limit of *Zostera* in the northern hemisphere (Moore & Short, 2006). High water temperatures during the summer of 2005 (approximately 1-2°C above normal) apparently contributed to a severe dieback of *Zostera*, suggesting that *Zostera* is close to its physiological limits in this region and may be significantly impacted by climate change (Moore & Jarvis, 2008). While some marine species may adapt to warming by to deeper water depths (Fields et al., 1993), species such as seagrasses, which are restricted in their vertical distribution by light requirements, may be more susceptible to range contraction near their limits (Harley et al., 2006; Micheli et al., 2008). *Ruppia*, in contrast to *Zostera*, has broad physiological tolerances, which allow it to survive in stressful environments, contributing to its nearly cosmopolitan distribution (Setchell, 1924; Kantrud, 1991). *Zostera* has historically been more abundant than *Ruppia* in the Chesapeake Bay, reaching double its biomass during peak growing season (Moore et al., 2000), and may be able to competitively exclude *Ruppia* through shading (Orth, 1977). *Ruppia* may be able to increase opportunistically if *Zostera* declines with higher water temperatures. *Ruppia* would also be expected to increase relative to *Zostera* with declining water quality (Dennison et al., 1993; Burkholder et al. 1992; Burkholder et al., 1994) or decreases in salinity (Moore et al., 2000; Kahn & Durako, 2005) due to *Ruppia's* greater tolerance of shading, excess nutrients, and low salinities.

Ruppia and *Zostera* also differ morphologically. Because seagrasses are an important source of structure in marine environments, the morphological differences between *Ruppia* and *Zostera* may result in differing abilities to provide habitat and mediate predator-prey interactions. In the Chesapeake Bay *Zostera* has flat, strap-like blades with rounded tips, typically about 80 cm long and 3-12 mm wide, though morphology can vary greatly with environmental conditions (Moore & Short, 2006). *Ruppia* has much shorter and thinner leaves than *Zostera*. The leaves of *Ruppia* extend from rounded sheaths and are typically about 1 mm wide by 5-20 cm long, with pointed tips (Kantrud, 1991). *Ruppia* also has a four fold greater surface area to biomass ratio, than *Zostera* (Parker et al., 2001). I expected that the distinct leaf structures of *Ruppia* and *Zostera* would cause predator-prey interactions to differ between these species, due to differences in protection they provide to crustacean prey.

Study animals

I selected predator and prey species common in seagrass meadows throughout the Chesapeake Bay for use in this experiment. The northern pipefish, *Syngnathus fuscus*, is an abundant predator in seagrass habitats (Orth & Heck, 1980) that primarily feeds on small crustaceans, including copepods, amphipods and isopods (Adams, 1976; Ryer & Orth, 1987). Small crustacean mesograzers are both important sources of food for fishes (Klumpp et al., 1989; Edgar & Shaw, 1995) and highly abundant, at times accounting for over half the total secondary production in Chesapeake Bay seagrass beds (Fredette & Diaz, 1990). Thus crsuteacean mesograzers are important vectors for transfer of primary production to higher trophic levels.

Syngnathus fuscus possesses a long snout with a small mouth and is gape limited in its prey consumption (Nelson, 1979; Ryer & Orth, 1987; Ryer, 1988). Pipefish are visual predators, foraging actively by searching for prey through continuous movement (Ryer, 1988). My qualitative field observations of *Syngnathus* foraging behavior were consistent with this description. *Syngnathus* generally moves slowly through the vegetation, resting a portion of its body or prehensile tail against seagrass leaves as it moves. Its eyes move constantly, in a circular motion. When a potential prey is encountered, the fish moves within striking distance, and attempts to capture it in a sudden forward movement. Pipefish and other syngnathids are 'pipette' or 'pivot' feeders, using a dorsal rotation (lifting) of the head to rapidly approach and draw prey into the mouth using suction (Bergert & Wainwright, 1997; de Lussanet & Muller, 2007).

The three crustacean mesograzers included as prey species in the experiment were abundant in the field as seagrass epifauna at the time of experimentation, and are distinct in their morphology and behavior. *Cymadusa compta* and *Gammarus mucronatus* are amphipods, with similar rounded, laterally flattened body shapes, whereas the isopod *Erichsonella attenuata* is ventrally flattened, with an elongated body. *Erichsonella* is the most sedentary of the three species, while *Gammarus* is the most active (personal observation; Duffy & Hay, 1994). *Cymadusa* builds small tube-like nests that it uses for refuge, while the other species do not (Nelson, 1979). I included multiple prey species to create the most realistic assemblage feasible, and to determine whether predator-prey interactions differ between seagrass species for the numerous prey species that utilize this vegetation as habitat.

Experimental design and procedures

To evaluate differences in predator-prey interactions between foundation species, I observed *Syngnathus* in controlled experiments, preying on the three crustacean grazers during timed trials in *Ruppia* and *Zostera* vegetation. Experiments were conducted between August 24th and September 15th, 2009, at the Virginia Institute of Marine Science, Seawater Research Laboratory. Experimental plants and animals were collected from seagrass beds within Mobjack Bay on the western shore of the Chesapeake Bay. Seagrasses were defaunated through a series of freshwater rinses before being planted in experimental tanks (Duffy & Harvilicz 2001; Duffy et al., 2001). The two seagrass species were standardized to approximately the same above-ground biomass per tank, based on known ratios of average above- to below-ground biomass for *Ruppia* and *Zostera* (Kantrud, 1991; J.E. Duffy, unpublished data). Seagrass was planted at the wet equivalent of 25 g dry weight per m^2. This density is below the lowest mean field density of *Zostera* in the Chesapeake Bay (which falls between 50-225 g dry weight per m^2), and is equal to the lowest mean field density of *Ruppia* in the Chesapeake Bay, which is observed though the winter and early summer (Moore et al., 2000).

Experimental animals were kept in 0.28 m^2 outdoor, flow-though tank arrays until their use in the experiment. *Syngnathus fuscus* individuals were between 11-15 cm in length. The mean size of fish used in the trials did not differ between *Ruppia* and *Zostera* treatments (t-test, $t = -0.80$, $df = 13$, $P = 0.43$). Crustacean prey individuals were identified to species in a laboratory using light microscopy. A natural size distribution of prey was used in the experiment, except for the exclusion of individuals (usually *Erichsonella*) estimated to be greater than 1 cm in length, which may not be consumed by *Syngnathus fuscus* (Ryer & Orth, 1987; Ryer, 1988).

The experiment was conducted in 18.93 l (5-gallon) clear, glass tanks with either *Ruppia* or *Zostera* vegetation planted at the wet weight equivalent density of 25 g dry wt./m^2 in equal amounts of sand sufficient to cover the seagrass roots and rhizomes completely. Experimental tanks were filled with water pumped from the York River estuary (approximately 20 ppt salinity), filtered at 100 μm. Aquarium circulator pumps were used to ensure adequate aeration. One predator was added to each tank. *Syngnathus fuscus* individuals were allowed to acclimate in experimental tanks for 24 hours prior to each trial, during which time they were also starved, allowing for complete gastric evacuation at room temperature (Ryer & Boehlert, 1983). Each tank was stocked with 10 individuals of each of the three crustacean prey species. Prey animals were added to tanks with pipefish 12 hours prior to experimentation. Tanks were covered immediately with black, opaque covers, which blocked light completely from the tanks. This allowed acclimation of the prey without the possibility of being visually detected by predators (Ryer, 1988). Treatments were randomly assigned to tank locations within the laboratory, to account for any differences in ambient conditions.

Trials were run individually and sequentially, so that predators and prey could be observed during each 50-minute trial. All trials were run between 0800 and 1500, Eastern Standard Time, with a maximum of four trials per day. Trials were conducted in a dimly lit laboratory with ambient light from a window, and a small LED light positioned between the observer and tank, facing the tank under observation. The fish did not appear to respond to the presence of the observer. During the trials I recorded the occurrence of specific interactions between predators and prey species, including encounters between predators and prey, attacks on prey, and successful captures of prey. To determine whether predators or prey were using vegetation differently in the two seagrasses, I recorded the location within an experimental tank where interactions occurred, which I defined as microhabitat. I grouped these locations as being above the sediment surface in the canopy, at the sediment surface, at an amphipod nest, or outside of the vegetation. An encounter between pipefish and prey was defined by fixation of both eyes on the prey individual by the pipefish. I considered that an attack had occurred when the pipefish attempted to capture the prey through a forward thrusting of the head and concurrent inward sucking with the mouth. A capture was defined as successful consumption of the prey individual. These behavioral descriptions follow those of Ryer (1988).

Statistical analyses

Eight trials in which fish did not forage or displayed abnormal behavior, such as rapid swimming against tank walls throughout a trial, were excluded from analysis. Differences in response variables between seagrass species were analyzed using generalized linear models. Poisson regressions were used for counts, including the effects of seagrass species on summed encounters, attacks and captures per trial. Logistic regression was used to test for the effect of seagrass species on binomial responses, including the probability of attack (given an encounter) and the probability of capture (given an attack). Over-dispersion was corrected by the use of a quasi-Poisson regression when testing for the effects of seagrass on summed encounters per trial.

Log-likelihood (G) tests were used to determine whether the proportions of interactions differed by prey, seagrass species, or microhabitat location. I addressed whether some prey are more vulnerable than others in one seagrass compared to the other, based on whether the proportion of predator-prey interactions with each prey species differed by seagrass species. I also determined whether predators and prey were more likely to interact in certain microhabitats in one seagrass species compared to the other, based on the proportion of interactions occurring in certain microhabitat locations in each seagrass species. Additionally I asked whether a given prey species was more likely to interact with a predator in some microhabitat locations compared to others, based on the proportion of interactions occurring in various microhabitat locations for each prey species. As *Cymadusa* was the only nest-building species used in the experiment, this microhabitat could not be analyzed for all prey species. As the nests observed in the experiment were all located at sediment interface, the microhabitat location “nest” was combined with “sediment surface” in statistical tests in order to compare interactions among prey species. Interactions with prey individuals that could not be positively identified were excluded from analyses of differences between prey species (excluded encounters n= 14, attacks n=8, captures n=2). Statistical analyses were conducted using R version 2.10.1 (Copyright 2009, The R Foundation for Statistical Computing, www.r-project.org).

RESULTS

Pipefish predators foraged more effectively on small crustacean mesograzers in *Ruppia maritima* than in *Zostera marina.* There were significantly higher rates of encounters with prey, attacks on prey, and captures of prey in *Ruppia maritima* (Fig. 1, Table 1). The higher rate of attack and capture in *Ruppia* appears to be driven primarily by the greater probability of detection in terms of encounter rate in this seagrass. *Syngnathus* was not significantly more likely to attack encountered prey or successfully capture attacked prey in *Ruppia*, as there was no significant difference between the two seagrasses in the probability of attack given an encounter, or the probability of capture given an attack (Fig. 2, Table 1). It is worth noting however, that there was a trend toward higher attack probability in *Ruppia,* which may also contribute to predator success in this seagrass.

Pipefish encountered amphipods *Cymadusa* and *Gammarus* more often than the isopod *Erichsonella* in both seagrass species, with approximately twice as many encounters in *Ruppia* as in *Zostera* with each prey species. Thus the *proportion* of total encounters occurring with each of the three prey species was essentially identical between seagrass species (Fig. 3A, Log-likelihood ratio statistic (G) = 0.08, Chi-square df = 2, P = 0.96). The same pattern was evident for the rate of attacks on and captures of amphipods (Fig. 3B, 3C). Both amphipods were more vulnerable to attack and capture in *Ruppia*, and in both cases *Cymadusa* was more vulnerable than *Gammarus*, as there was no significant difference in the proportion of attacks (Fig. 3B, Log-likelihood ratio statistic (G) = 0, Chi-square df = 1, P = 1.0) or captures (Fig. 3C, Log-likelihood ratio statistic (G) = 0.17, Chi-square df = 1, P = 0.68) that occurred with each amphipod between the two seagrass species. The isopod *Erichsonella* was never attacked or captured in either seagrass species. *Erichsonella* was encountered very rarely (twice in *Ruppia* and once in *Zostera*), which accounts for the lack of attacks and captures. Interactions with prey individuals that could not be positively identified were excluded from analysis of differences between prey species. However, the pattern of an approximately two-fold higher interaction rate in *Ruppia* compared to *Zostera* held true for excluded observations as well, which was evident when interactions were pooled across species (Fig. 4).

I examined whether the proportion of predator-prey interactions occurring in each microhabitat location (canopy, sediment surface, amphipod nest, not in vegetation) differed between the two seagrass species. There was no difference between seagrass species in the proportion of encounters between predators and prey occurring in the various microhabitat locations (Fig. 5A, Log-likelihood ratio statistic (G) = 0.99, Chi-square df = 3, P = 0.80). In the case of attacks on prey, however, there was a significant difference between *Ruppia* and *Zostera*, with a higher proportion of attacks occurring at the sediment surface in *Ruppia* (Fig. 5B, Log-likelihood ratio statistic (G) = 9.75, Chi-square df = 3, P = 0.02). There was no significant difference between the two seagrasses in the proportion of captures occurring in different locations (Fig. 5C, Log-likelihood ratio statistic (G) = 2.74, Chi-square df = 3, P = 0.43).

I also compared the proportions of predator-prey interactions occurring in each microhabitat location between each of the prey species, to determine whether some prey were more likely to interact with predators in certain microhabitats. As *Cymadusa* was the only nest-building species used in the experiment, the microhabitat location “nest” was combined with “sediment surface” in statistical tests to compare interactions among prey species. The proportion of total encounters occurring in each microhabitat location did not differ significantly among the three prey species (Fig. 6A, Log-likelihood ratio statistic (G) = 8.3739, Chi-square df = 4, P = 0.079). However, there was a trend toward *Cymadusa* being encountered more often in the vegetation and rarely outside of it, whereas interactions with *Gammarus* were more evenly distributed between the two locations within the vegetation (“sediment surface” and “canopy”) and the area outside of the vegetation. The few encounters with *Erichsonella* all occurred in the canopy. As *Erichsonella* was never attacked or captured, it was excluded from analyses of these responses. The proportion of attacks occurring in different microhabitat locations was significantly different between the two amphipods that were attacked, with *Cymadusa* being attacked more frequently within the vegetation than *Gammarus* (Fig. 6B, Log-likelihood ratio statistic (G) = 7.8074, Chi-square df = 2, P = 0.020). The proportion of captures occurring in different locations did not differ for the two amphipod species that were captured (Fig. 6C, Log-likelihood ratio statistic (G) = 6.7659, Chi-square df = 4, P = 0.149). Prey individuals were never captured in nests when attacks occurred in this location. However, the number of captures occurring in this experiment were very low, so tests of this response variable have relatively low power to detect differences.

DISCUSSION

The higher rates of encounters, attacks and captures in *Ruppia* compared to *Zostera* indicates that there is indeed a difference in the ability of these two seagrasses to mediate predator-prey interactions between these predator and prey species (Figure 1, Table 1). The data suggest that the higher rates of attacks and captures were driven primarily by the higher encounter rate in *Ruppia*, though the probability of attack and capture may have had some influence as well (Figure 2, Table 1).

A central question of this experiment was whether these seagrass species could be considered equivalent in providing refuge when standardized to biomass, or whether their distinct leaf morphology would affect interactions. I found that prey individuals were more visible in *Ruppia*, which has greater surface area per biomass than *Zostera*, but thinner, shorter leaves. Vegetation surface area has been posited to affect predator-prey interactions and their outcome, to the extent that it provides usable refuge for prey species (Heck & Orth, 1980b). However, greater surface area itself does not necessarily indicate an effective barrier between predators and prey. For example, Stoner (1982) compared fish predation on amphipods in three seagrass species and found that at a given biomass, *Halodule wrightii*, the species with the narrowest blades and highest surface area per biomass, provided the poorest refuge from predation. The two other seagrasses *Thalassia testudinum* and *Syringodium filiforme* which have wider, strap-like blades, were more effective in reducing predation.

Similarly, an experiment manipulating leaf width of artificial seagrass vegetation demonstrated that amphipod prey were only protected from predation by *Syngnathus fuscus* when they were able to fit into the refuge spaces between leaves, and wider artificial leaves afforded better refuge for amphipods than thin leaves, although interactions depended on the relative size of the structure, predator, and prey (Ryer, 1988). Thus, the greater encounter rates in *Ruppia* may be due to its thinner blades, which provide less structural refuge from detection for small crustacean prey.

The lower canopy height of *Ruppia* may also have influenced the predator-prey interactions observed in this experiment. Both fish and prey tended to stay within the seagrass vegetation during the trials (personal observation). *Syngnathus fuscus* seemed to spend more time closer to the sediment surface in *Ruppia* and utilized more vertical space in *Zostera*. This may explain why I observed a trend toward more interactions near the sediment surface in *Ruppia*, with a significantly higher proportion of attacks occurring in this location compared to *Zostera* (Fig. 6). Alternately, prey may be utilizing vegetation differently in *Ruppia* and *Zostera*. Small shrimp can avoid predation in seagrass using behaviors that obscure them from the view of visual predators, such as moving behind seagrass blades and choosing microhabitats in the canopy that make them less accessible to predators (Main, 1987; Main, 1987). Since I did not observe the locations of predators or prey in the absence of one another, patterns in the location of interactions may be due to either the foraging behavior of the predator, or the habitat preference or vulnerability of prey species in various locations. This difference in attack location suggests a difference in habitat use or foraging of *Syngnathus fuscus* in the two habitats, as there was no significant difference in the number of encounters occurring in these environments. Because *Ruppia* has a shorter canopy, the three-dimensional space in which predators and prey were interacting may be reduced, potentially increasing the probability of interactions in this vegetation.

I intentionally tested similar densities of *Zostera* and *Ruppia* in this experiment. However, the seagrass density used is slightly lower than even the lowest mean field density of *Zostera*, and approximately equal to the lowest mean field density of *Ruppia* in the Chesapeake Bay (Moore et al., 2000). Because seagrass density can influence predation rates (Nelson, 1979; Stoner, 1982; Heck & Thoman, 1981; Nelson & Bonsdorf, 1990 and studies listed therein; reviewed in Heck & Orth, 2006), this experiment may underestimate the natural refuge provided by *Zostera*, as its field densities will rarely be as low as those used in the experiment. Likewise, the prey densities I used experimentally are considerably lower than field densities per unit of vegetation (Douglass et al., 2010). Thus I might expect encounter and predation rates to be higher in the field than those I observed experimentally. However at least one experiment has found no significant difference between vegetation density treatments when the ratio of predator to prey to vegetative surface area was kept constant (Matilla et al., 2008), which may be explained by higher rates of encounter at higher faunal densities.

The abundance or distribution of epifaunal assemblages in the field can provide indirect evidence that a particular vegetation type provides superior food resources, habitat or refuge. Seagrass epifauna are highly mobile (Virnstein & Curran, 1986) and may select substrates based on either abundance or morphology, as it affects important aspects of their survival (Bell & Westoby, 1986; Schneider & Mann, 1991b). Predation by pipefish and other small predators appears to have a large effect on the field abundance of seagrass epifauna (Virnstein & Howard 1987a; Virnstein & Howard, 1987b; Ryer & Orth, 1987;

Schneider & Mann, 1991). Higher predation rates in *Ruppia* or habitat selection would not necessarily translate to differences in mesograzer composition or abundance in the field. Previous field surveys found no overall differences in abundance and species composition of crustacean mesograzers in *Ruppia* and *Zostera* although species abundances did differ at certain points in time (Parker et al., 2001). These small crustacean prey species likely move between contiguous areas of *Ruppia* and *Zostera* vegetation responding to complex, interacting factors, including predation, habitat selection, and competition for living space and refuge.

While amphipods *Cymadusa* and *Gammarus* were encountered much more often than the isopod *Erichsonella*, the proportion of total encounters, attacks and captures that occurred with each prey species was essentially identical between grass species. Thus it appears that the increased vulnerability of prey in *Ruppia* is not due to a disproportionate effect on any one species, but rather that *Ruppia* has a similar effect on multiple prey species. Because amphipods are laterally flattened with a rounded body shape it may be more difficult for these prey to obscure their entire bodies behind a *Ruppia* blade, whereas this is likely to be easier in *Zostera*. The fact that *Cymadusa* was never captured in nests corroborates previous findings that tube-building amphipods are well protected in these structures (Nelson, 1979). *Cymadusa* may have been better protected in this experiment if given a longer acclimation period in which to build these protective structures. The amphipods also moved by swimming at times during the experiment, and did not necessarily remain attached to seagrass blades (personal observation), behaviors that may have made them more vulnerable to detection, compared with *Erichsonella*. Thus, the distinct morphology and behavior of the prey may account for differences in their detection in this experiment.

Erichsonella was rarely encountered and never attacked or captured in either seagrass. This prey species may be less detectable by predators due to its elongated and dorso-ventrally flattened body shape and tendency to remain attached to seagrass leaves, while moving relatively little and generally in parallel with the leaf surface (personal observation). Ryer (1987) also observed that *Syngnathus fuscus* had difficulty consuming even small *Erichsonella* individuals, likely due to the isopod's enlongated body and clinging behavior. *Syngnathus fuscus* does consume *Erichsonella* in the field, but this isopod is an important part of its diet only during the fall months, when other more desirable prey species are less abundant (Ryer, 1987). Additionally, Douglass et al. (2010) found that *Erichsonella* dominated the seagrass epifaunal assemblage in the western Chesapeake Bay during the late summer when small predators are most abundant. The low encounter rate with *Erichsonella* in my study suggests that difficulty in detection may also decrease the consumption of this isopod when more easily encountered prey species are available, suggesting a mechanism for its seasonal patterns of field abundance.

The fact that seagrasses did not differ greatly in the probability of attack given an encounter may indicate that predators are not altering their attack behavior between the two seagrasses. The relative size of prey and available refuge can influence the attack probability for *Syngnathus fuscus*, possibly due to size refuge of prey, or ability of the fish to position its snout close to the prey (Ryer, 1988). The small difference in attack probability between grasses here indicates that fish are not much more likely to encounter larger, less attackable prey in *Ruppia*. However, it is possible that the non-significant trend toward increased attack probability in *Ruppia* may represent a biologically important pattern that would be statistically significant with greater replication to increase statistical power. The smaller difference between the two seagrasses in the capture probability given an attack also indicates that predators may encounter prey too large to be consumed at equal rates in the two grasses. This result also suggests that prey are equally capable of utilizing escape strategies once attacked in the two seagrass species. The low overall capture rate may be due in part to the gape limitation of *Syngnathus fuscus*, which usually selects small prey (Nelson, 1979; Ryer & Orth, 1987; Ryer, 1988). As I used a natural size distribution of prey, some were likely too large to be successfully consumed by the predator. While *Syngnathus fuscus* will sometimes attempt to consume large prey, these individuals often escape (Ryer & Orth, 1987).

If greater detection rate in *Ruppia* is due to greater visibility of prey against the thin leaf, then this effect may hold true for a whole assemblage of small crustacean mesograzers in these systems. This generality could lead to higher trophic transfer in *Ruppia* compared to *Zostera*, particularly at times of year when gammarid amphipods are most abundant. Small crustacean mesograzers including isopods and amphipods can account for over half the total secondary production in Chesapeake Bay seagrass beds (Fredette & Diaz, 1990) and provide an important trophic link, with the majority of seagrass fish feeding primarily on small crustaceans (Klumpp et al., 1989; Edgar & Shaw, 1995). The interactions between crustacean mesograzers and small predators may be an important mechanism of energy transfer from the primary production of epiphytic algae to higher trophic levels, including resident and transient tertiary predators. In the Chesapeake Bay for example, *Syngnathus fuscus* appears to be a large component of the diet of summer flounder (*Paralichthys dentatus*) at certain life stages (Lascara, 1981). As an intermediate predator, *Syngnathus fuscus* is presumably seeking refuge from predation as well. Although it is difficult to say whether the seagrasses are equal in this respect, I would expect pipefish to find more effective refuge from predation in *Zostera*, as they are very cryptic in this environment (personal observation). If *Syngnathus* is able to forage more effectively in *Ruppia*, there may be a trade-off between food and protection in utilizing these two environments (Werner & Hall, 1988). However, if the greater rate of predator-prey interactions I observed translates to higher predation rates in *Ruppia*, this may result in more rapid transfer of secondary production to higher trophic levels in these seagrass communities.

My results suggest that similar foundation species may have distinct effects in mediating predator-prey interactions. Increasing environmental stressors in rapidly changing marine environments are expected to cause changes in the abundance and distribution of seagrasses, favoring stress tolerant species over competitive dominants. In the Chesapeake Bay, it seems likely that the abundance of *Ruppia maritima* may increase and *Zostera marina* may decline, particularly if water temperatures increase during the summer, surpassing the temperature tolerance of *Zostera*. The timing and severity of such changes in seagrass abundance and distribution are difficult to predict. Thus, it is vital to determine how such changes may affect seagrass communities, to predict the impacts and provide insight for future management decisions. Species loss or alteration in the composition of foundation species will likely have important consequences for associated fauna, and caution should be exercised in assuming equivalency of foundation species in mediating predator-prey interactions.

LITERATURE CITED

Adams, S.M. 1976. Feeding ecology of eelgrass fish communities. Transactions of the American Fisheries Society 105: 514-519.

Bartholomew, A. 2002. Total cover and cover quality: predicted and actual effects on a predator's foraging success. Marine Ecology-Progress Series 227: 1-9.

Bell, J.D. & M. Westoby. 1986. Abundance of macrofauna in dense seagrass is due to habitat preference, not predation. Oecologia 86: 205-209.

Bergert, B.A. & P.C. Wainwright. 1997. Morphology and kinematics of prey capture in the syngnathid fishes *Hippocampus erectus* and *Syngnathus floridae*. Marine Biology 127: 563-570.

Bruno, J.F. & M.D. Bertness. 2001. Habitat modification and facilitation in benthic marine communities. In: Bertness, M.D., Hay, M.E. & Gaines S.D. (eds) Marine Community Ecology, pp 131-158. Sinauer Associates. Sunderland, Massachusetts.

Burkholder, J.M., Mason, K.M. & Glasgow, H.B. 1992. Water-column nitrate enrichment promotes decline of eelgrass *Zostera marina* - evidence from seasonal mesocosm experiments. Marine Ecology Progress Series 81: 163-178.

Burkholder, J.M., Glasgow, H.B. & Cooke, J.E. 1994. Comparative effects of water-column nitrate enrichment on eelgrass *Zostera marina*, shoalgrass *Halodule wrightii*, and widgeongrass *Ruppia maritima*. Marine Ecology Progress Series 105: 121-138.

Chapin, F.S., Sala, O.E., Burke, I.C., Grime, J.P., Hooper, D.U., Lauenroth, W.K., Lombard, A., Mooney, H.A., Mosier, A.R., Naeem, S., Pacala, S.W., Roy, J., Steffen, W.L., & DT Tilman. 1998. Ecosystem consequences of changing biodiversity. BioScience 48: 45-52.

Costanza R., Arge R., Groot R., Farber S., Grasso M., Hannon B., Limburg K., Naeem S., ONeill R.V., Paruelo J., Raskin R.G., Sutton P., vandenBelt M. (1997). The value of the world's ecosystem services and natural capital. Nature 387: 253-260.

Dayton, P.K. 1972.Toward an understanding of community resilience and the potential effects of enrichment to the benthos at McMurdo Sound, Antarctica. In: Proceedings of the Colloquium on Conservation Problems in Antarctica, ed. Parker, B.C. Allen Press. Lawrence, Kansas.

de Lussanet, M.H.E. & M. Muller. 2007. The smaller your mouth, the longer your snout: predicting the snout length of Syngnathus acus, Centriscus scutatus and other pipette feeders. Journal Of The Royal Society Interface 4: 561-573.

Dennison, W.C., Orth, R.J., Moore, K.A., Stevenson, J.C., Carter, V., Kollar. S., Bergstrom, P.W. & Batiuk, R.A. 1993. Assessing water-quality with submersed aquatic vegetation. BioScience 43: 86-94.

Duarte, C.M. 2002. The future of seagrass meadows. Environmental Conservation 29: 192-206.

Duarte, C.M. & Chiscano, C.L. 1999. Seagrass biomass and production: a reassessment. Aquatic Botany 65: 159-174

Duffy, J.E. & Harvilicz A.M. 2001. Species-specific impacts of grazing amphipods in an eelgrass-bed community. Marine Ecology Progress Series 223: 201-211.

Duffy, J.E., K.S. Macdonald, J.M. Rhode, & J.D. Parker. 2001. Grazer diversity, functional redundancy, and productivity in seagrass beds: an experimental test. Ecology 82: 2417-2434.

Duffy, JE & Hay, MET. 1994. Herbivore resistance to seaweed chemical defense: the roles of mobility and predation risk. Ecology 75: 1304-1319.

Douglass, J.G., France, K.E., Richardson, J.P. & J.E. Duffy. 2010. Seasonal and interannual change in a Chesapeake Bay eelgrass community: Insights into biotic and abiotic control of community structure. Limnology & Oceanography 55: 1499-1520.

Edgar, G. J. .1990. The use of the size structure of benthic macrofaunal communities to estimate faunal biomass and secondary production. Journal of Experimental Marine Biology and Ecology 137: 195-214.

Ellison, A.M., Bank, M.S., Clinton, B.D., Colburn, E.A., Elliott, K., Ford, C.R. , Foster, D.R., Kloeppel, B.D., Knoepp, J.D. , Lovett, G.M., Mohan, J., Orwig, D.A., Rodenhouse, N.L., Sobczak,W.V., Stinson, K.A., Stone, J.K., Swan, C.M., Thompson, J., Von Holle, B., & J.R. Webster. 2005. Loss of foundation species: consequences for the structure and dynamics of forested ecosystems. Frontiers in Ecology and the Environment 3: 479-486.

Fields, P.A., Graham, J.B., Rosenblatt, R.H., & G.N. Somero. 1993. Effects of expected global climate change on marine faunas. Trends in Ecology & Evolution 8: 361-367.

Gillanders, B.M. 2006. Seagrasses, fish and fisheries. In: Larkum, A.W.D. et al. (eds), Seagrasses: Biology, Ecology and Conservation. Springer, Dordrecht. 503-536.

Harley, C.D.G., Hughes, A.R., Hultgren, K.M., Miner, B.G., Sorte, C.J.B., Thornber, C.S., Rodriguez, L.F., Tomanek, L., & S.L. Williams. 2006. The impacts of climate change in coastal marine systems. Ecology Letters 9: 228-241.

Heck, K..L, Hays G. & Orth, R.J. 2003. Critical evaluation of the nursery role hypothesis for seagrass meadows. Marine Ecology Progress Series 253:123-136.

Heck, K.L. & Orth RJ. (1980a) Structural compenents of Eelgrass (Zostera marina) meadows in the lower Chesapeake Bay-decapod crustacea. Estuaries 3: 289-295.

Heck, K.L. & Orth RJ. (1980b) Seagrass habitats: The roles of habitat complexity, competition and predation in structuring associated fish and motile macroinvertebrate assemblages. In: Kennedy, V.S. (ed) Estuarine Perspectives, pp 449–464. Academic Press, New York.

Heck K.L. & Thoman T.A. 1981. Experiments on predator–prey interactions in vegetated aquatic habitats. J Exp Mar Biol Ecol 53: 125–134

Heck, K.L. & Orth RJ. 2006. Predation in seagrass beds. In: Larkum, A.W.D. et al (eds), Seagrasses: Biology, Ecology and Conservation. Springer, Dordrecht. pp. 537-550.

Hemminga, M.A. & Duarte, C.M., 2000. Seagrass ecology. Cambridge University Press, New York.

Johnson, M.R., Williams, S.L., Lieberman, C.H,. & A. Solbak. 2003. Changes in abundance of the seagrasses *Zostera marina* L. (eelgrass) and *Ruppia maritima* (widgeongrass) in San Diego, California, following an El Nino event. Estuaries 26: 106-115.

Kahn, A.E. & Durako, M.J. 2005. The effect of salinity and ammonium on seed germination in Ruppia maritima from Florida Bay. Bulletin of Marine Science 77: 453-458

Kantrud, H.A. 1991. Wigeongrass (Ruppia maritima L.): A literature Review. U.S. Fish and Wildlife Service, Fish and Wildlife Research 10. Jamestown, ND: Northern Prairie Wildlife Research Center Online. http://www.npwrc.usgs.gov/resource/plants/ruppia/index.htm (Version 16JUL97).

Kikuchi, T. 1974. Japanese contributions and consumer ecology in eelgrass (*Zostera marina* L.) beds, with special reference to trophic relationships and resources in inshore fisheries. Aquaculture 4: 145-160.

Klumpp, D.W., Howard, R.K. & D.A. Pollard. 1989. Trophodynamics and nutritional ecology of seagrass communities. In: Larkum, A.W.D., McComb, A.J. and S.A. Shepherd (eds). Biology of Seagrasses. Elsevier, Amsterdam. 394-457.

Lascara, J. 1981. Fish predator-prey interaction in areas of eelgrass (*Zostera marina*). M.S. Thesis. The College of William and Mary, Williamsburg, VA. 81 p.

Main, K. L. T. 1987. Predator avoidance in seagrass meadows: prey behavior, microhabitat selection, and cryptic coloration. Ecology 68: 170-180.

Main, K. L. T. 1985. The influence of prey identity and size on selection of prey by two marine fishes. Journal of Experimental Marine Biology and Ecology 88: 145-152.

Matilla, J., Heck, K.L., Millstein, E., Miller, E., Gustafsson, C., Williams, S., & D. Byron. 2008. Increased habitat structure does not always provide increased refuge from predation. Marine Ecology Progress Series 361: 15-20.

Micheli, F., Bishop, M.J., Peterson, C.H. & J. Rivera. 2008. Alteration of seagrass species composition and function over two decades. Ecological Monographs 78: 225-244.

Moore K.A., Wilcox, D.J. & R.J. Orth. 2000. Analysis of the abundance of submersed aquatic vegetation communities in the Chesapeake Bay. Estuaries 23: 115-127.

Moore, K.A. & Jarvis J.C. 2008. Environmental factors affecting recent summertime eelgrass diebacks in the lower Chesapeake Bay: implications for long-term persistence. Journal of Coastal Research 55:135-147.

Moore KA & Short FT. 2006. *Zostera*: Biology, ecology, and management. In: Larkum, A.W.D. et al (eds), Seagrasses: Biology, Ecology and Conservation. Springer, Dordrecht. 323-345.

Naeem, S. 1998. Species redundancy and ecosystem reliability. Conservation Biology 12: 39-45.

Nelson, W.G. 1979. Experimental studies of selective predation on amphipods: Consequences for amphipod distribution and abundance. Journal of Experimental Marine Biology and Ecology 38: 225–245.

Nelson, W.G. & Bonsdorff, E. 1990. Fish predation and habitat complexity: are complexity thresholds real? Journal of Experimental Marine Biology and Ecology 141: 183-194.

Orth, R.J. 1977. Effect of nutrient enrichment on growth of the eelgrass *Zostera marina* in the Chesapeake Bay, Virginia, USA. Marine Biology 44:187-194

Orth, R.J. & Heck, K.L. 1980. Structural compenents of Eelgrass (*Zostera marina*) meadows in the lower Chesapeake Bay-fishes. Estuaries 3: 278-288.

Orth, R.J., Carruthers, T.J.B., Dennison W.C., Duarte, C.M, Fourqurean, J.W., Heck, K.L., Hughes, A.R., Kendrick, G.A., Kenworthy, W.J., Olyarnik, S., Short, F.T., Waycott, M., Williams, S.L. 2006. A global crisis for seagrass ecosystems. Bioscience 56: 987-996.

Orth, R.J. & K.A. Moore. 1983. Chesapeake Bay: An unprecedented decline in submerged aquatic vegetation. Science 222: 51-53.

Orth, R.J. & K.A. Moore. 1984. Distribution and abundance of submerged aquatic vegetation in Chesapeake Bay: an historical perspective. Estuaries 7: 531-540.

Orth, R.J., et al. 2010. Long-Term Trends in Submersed Aquatic Vegetation (SAV) in Chesapeake Bay, USA, Related to Water Quality. Estuaries and Coasts 33: 1144-1163.

Parker, J.D., Duffy, J.E. & Orth, R.J. 2001. Plant species diversity and composition: experimental effects on marine epifaunal assemblages. Marine Ecology Progress Series 224: 55-67

Parmesan, C. 2006. Ecological and Evolutionary Responses to Recent Climate Change. Annual Review of Ecology, Evolution, and Systematics. 37: 637-669

Ryer, C.H. & Boehlert, G.W. 1983. Feeding chronology, daily ration, and the effects of temperature upon gastric evacuation in the pipefish, *Syngnathus fuscus*. Environmental Biology of Fishes 9: 301-306.

Ryer, C.H. & Orth, R.J. 1987. Feeding Ecology of the Northern Pipefish, *Syngnathus fuscus*, in a seagrass community in the lower Chesapeake Bay. Estuaries 10: 330-336.

Ryer CH (1988) Pipefish foraging: Effects of fish size, prey size and altered habitat complexity. Marine Ecology Progress Series 48: 37-45.

Schiel, D.R. Steinbeck, J.R., Foster, M.S. 2004. Ten years of induced ocean warming causes comprehensive changes in marine benthic communities. Ecology 85:1833-1839

Setchell, W.A. 1924. *Ruppia* and its environmental factors. Proceedings of the National Academy of Sciences of the United States of America 16: 286-288.

Schneider, F.I. & K.H. Mann. 1991a. Species specific relationships of invertebrates to vegetation in a seagrass bed. I. Correlational studies. Journal of Experimental Marine Biology and Ecology 145: 101-117.

Schneider, F.I. & K.H. Mann. 1991b. Species-specific relationships of invertebrates to vegetation in a seagrass bed. II. Experiments on the importance of macrophyte shape, epiphyte cover and predation. Journal of Experimental Marine Biology and Ecology 145: 119-139.

Stoner, A.W. 1982. The influence of benthic macrophytes on the foraging behavior of pinfish (*Lagodon rhomboides*) (Linnaeus). Journal of Experimental Marine Biology and Ecology 58: 271–284.

Virnstein R.W. & C.M. Curran. 1986. Colonization of artificial seagrass versus time and distance from source. Marine Ecology Progress Series 29: 279-288

Virnstein RW & Howard RK. (1987a) Motile Epifauna of Marine Macrophytes in the Indian River Lagoon, Florida. I. Comparisons among three species of seagrasses from adjacent beds. Bulletin of Marine Science 41: 1-12.

Virnstein RW & Howard RK. (1987b) Motile Epifauna of Marine Macrophytes in the Indian River Lagoon, Florida. II. Comparisons between drift algae and three species of seagrasses. Bulletin of Marine Science 41: 13-26.

Walker, B. 1995. Conserving biological diversity through ecosystem resilience. Conservation Biology 9: 747-752

Walker, B. 1992. Biodiversity and ecological redundancy. Conservation Biology 6: 18-23

Werner, E. E. & Hall, D. J. 1988. Ontogenetic habitat shifts in bluegill: the foraging rate-predation risk trade-off. Ecology 69: 1352-1366.

Walther, G.R., Post, E. Convey, P., Menzel, A., Parmesan, C., Beebee, T.J.C., Fromentin, J.M., Hoegh-Guldberg, O. & F Bairlein. 2002. Ecological responses to recent climate change. Nature 416: 389-395

Warfe, D.M. & Barmuta, L.A. 2004. Habitat structural complexity mediates the foraging success of multiple predator species. Oecologia 141: 171-178.

Waycott, M., CM Duarte, TJB Carruthers, RJ Orth, WC Dennison, S Olyarnik, A Calladine, JW Fourqurean, KL Heck, A Hughes, GA Kendrick, WJ Kenworthy, FT Short, SL Williams. 2009. Accelerating loss of seagrasses across the globe threatens coastal ecosystems. Proceedings of the National Academy of Sciences of the United States of America106: 12377-12381.

Williams, S.W., Heck, K.L. 2001. Seagrass communities. In: Bertness M, Gaines S, Hay M, eds. Marine Community Ecology. pp. 317–37. Sinauer Press, Sunderland, MA.

TABLE 1. Results from generalized linear models of differences between *Ruppia maritima* and *Zostera marina* treatments on the number of encounters, attacks and captures per trial, analyzed with Poisson regression, and attack probability (given an encounter) and success probability (given an attack) analyzed with logistic regression models. The quasi-Poisson distribution was used for encounters per trial to account for over-dispersion of the data. Bold indicates a significant effect at P<0.05.

Response	Residual d.f.	Residual deviance	Std. Error	Z value	P value
Encounters per trial	13	46.708	0.4363	-2.115	**0.0543**
Attacks per trial	13	38.841	0.3005	-4.048	**0.0001**
Captures per trial	13	15.276	0.7905	-2.267	**0.0234**
Aattack probability	13	13.744	0.4684	-1.593	0.1111
Capture probability	10	2.9027	0.4443	-0.265	0.7910

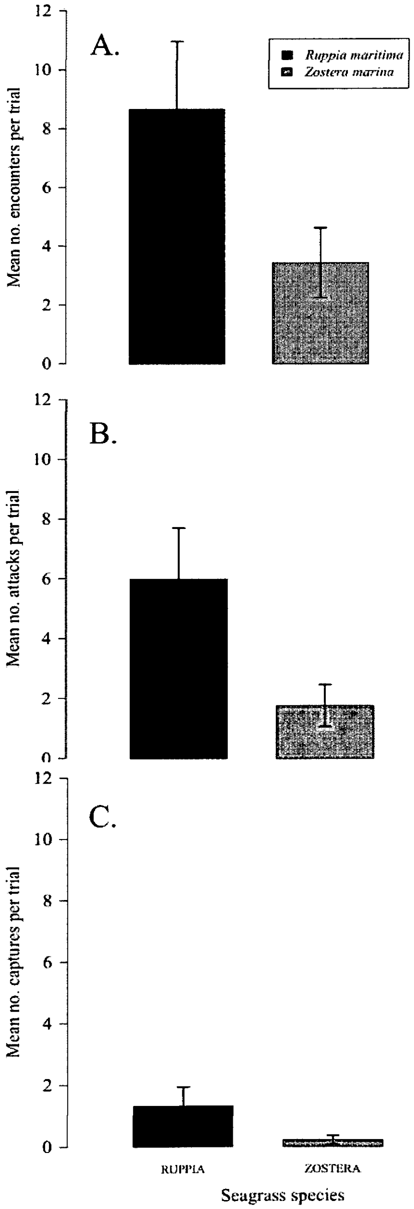

Figure 1. Mean (±SE) number of encounters (a), attacks (b), and captures (c) per trial in *Ruppia maritima* (dark grey bars) and *Zostera marina* (light grey bars).

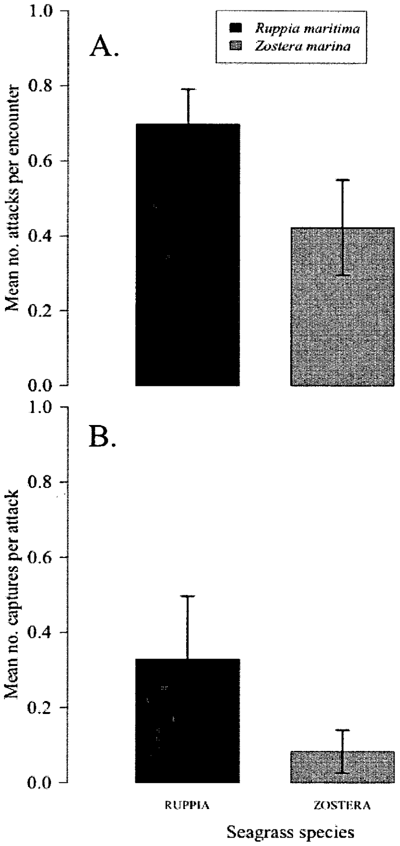

Figure 2. Mean (±SE) attack probability, as attacks per encounter (a), and capture probability, as captures per attack (b) in *Ruppia maritima* (dark grey bars) and *Zostera marina* (light grey bars).

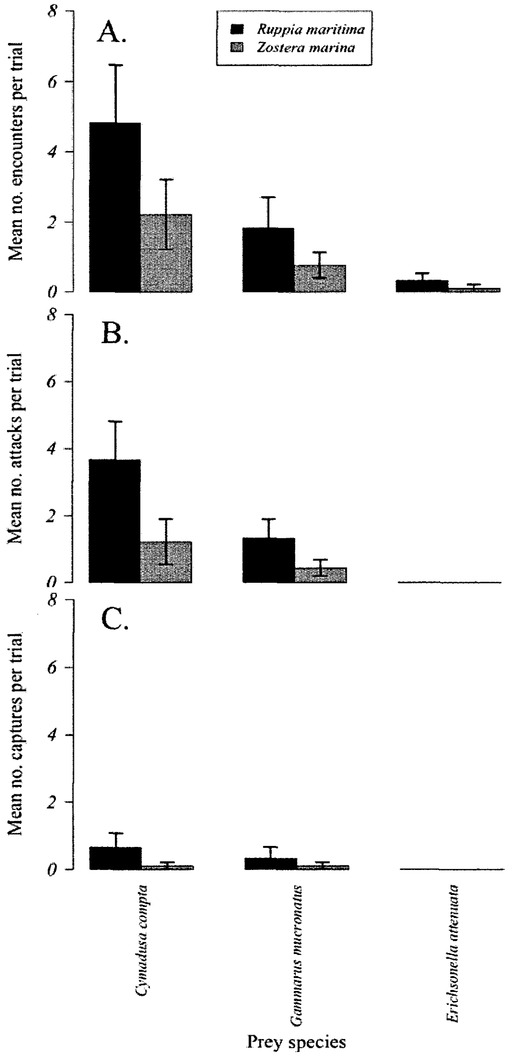

Figure 3. Mean (±SE) number of encounters (a), attacks (b), and captures (c) per trial in *Ruppia maritima* (dark grey bars) and *Zostera marina* (light grey bars) on each prey species.

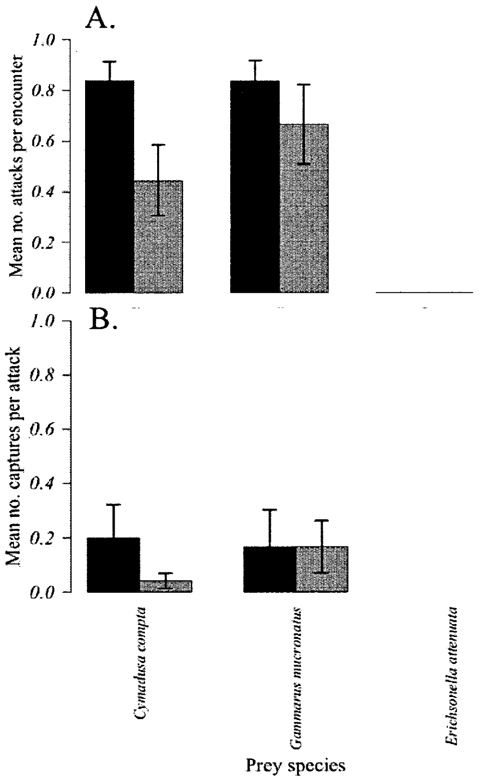

Figure 4. Mean (±SE) attack probability, as attacks per encounter (a), and capture probability, as captures per attack (b) in *Ruppia maritima* (dark grey bars) and *Zostera marina* (light grey bars) for each prey species.

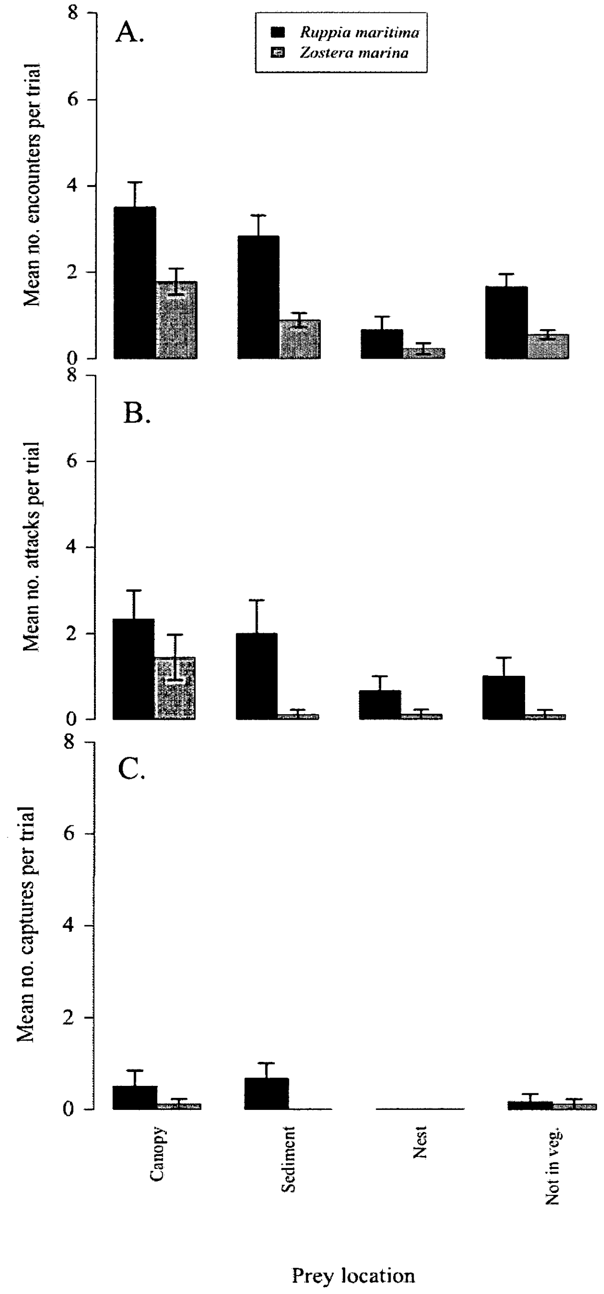

Figure 5. Mean (±SE) number of encounters (a), attacks (b), and captures (c) per trial in *Ruppia maritima* (dark grey bars) and *Zostera marina* (light grey bars) in each microhabitat location.

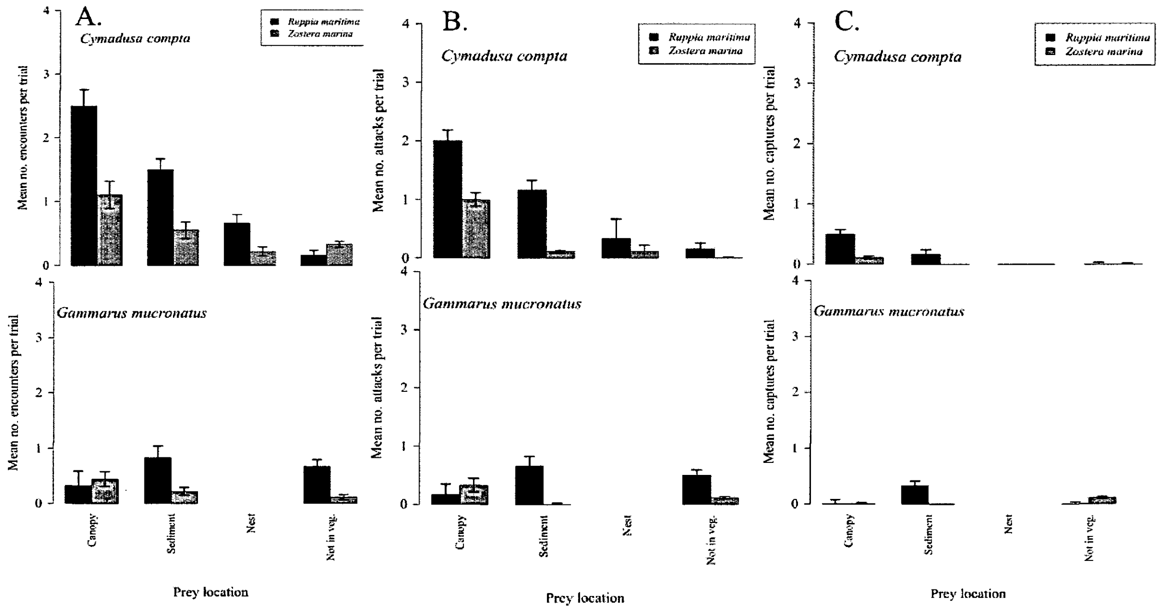

Figure 6. Mean (±SE) number of encounters (a), attacks (b), and captures (c) per trial in *Ruppia maritima* (dark grey bars) and *Zostera marina* (light grey bars) in each microhabitat location for amphipods *Cymadusa compta* (upper panel) and *Gammarus mucronatus* (lower panel). The isopod *Erichsonella Attenuata* is not included here, as it was encountered only rarely and was never attacked or captured.

CHAPTER 2. THE EFFECTS OF TROPHIC LEVEL AND FOUNDATION SPECIES IN EXPERIMENTAL SEAGRASS COMMUNITIES

ABSTRACT

Increasing summer water temperatures in the Chesapeake Bay have the potential to change the relative abundance of seagrass species in this system, favoring the more heat and stress tolerant *Ruppia maritima* over *Zostera marina*. Because of the key role of seagrasses in providing habitat and trophic support, it is important to determine whether the more stress tolerant seagrass may be able to provide similar ecological functions for the more sensitive species it may replace. In particular, trophic interactions in seagrass ecosystems can be important, as grazing of epiphytic algae can release seagrass from competition for light, and predation on crustacean mesograzers by small fish predators is an important link for higher trophic levels. I addressed the effects of food chain length on the communities associated with two Chesapeake Bay seagrass species in an eight-week, factorial mesocosm experiment, which manipulated seagrass species and number of trophic levels at each of six seagrass densities. Trophic levels included no added consumers, and small crustacean mesograzers alone and with fish predators. I examined the communities that developed, as algae and invertebrates recruited to the mesocosm tanks through the flow-through water system. The number of trophic levels had a greater overall effect on community development than did seagrass species. Consumers tended to decrease diversity of recruiting algae and invertebrates, likely due to direct consumption by or competition with mesograzers. Grazing controlled algal abundance, but predators decreased this effect through an apparent trophic cascade. For the most part, the effects of grazing did not vary by seagrass species, though *Ruppia* leaves appeared to be more susceptible to direct grazing than *Zostera*. Predators decreased the abundance of grazers across seagrass species, but some mesograzer species were more vulnerable to predation than others. Thus, the individual prey characteristics seemed to determine predation levels, rather than the relative refuge value of the seagrasses. The composition of recruiting invertebrate species differed by seagrass species, with all but one of the most abundant recruiting species having greater abundance in *Zostera*. These idiosyncratic differences in community development between seagrass species could have consequences for higher trophic levels that rely on sessile fouling species or infauna in seagrass beds. Established differences in the morphology, distribution, and phenology of *Ruppia* and *Zostera* would also be likely to affect important functions in the Chesapeake Bay if species loss or changes in relative abundance occur.

INTRODUCTION

Climate change and anthropogenic stressors have the potential to alter the abundance or distribution of key species by creating environmental conditions that favor more stress-tolerant or opportunistic species. Species near the limits of their physiological tolerances are expected to contract their ranges (Parmesan, 2006), while more stress-tolerant or opportunistic species may either increase in abundance or in their relative importance, as sensitive species decline (Chapin et al., 1998). While some marine species may adapt to warming by shifting to deeper water depths (Fields et al., 1993), species such as seagrasses, which are restricted in their vertical distribution by light requirements, may be more susceptible to range contraction near their limits (Harley et al., 2006; Micheli et al., 2008). Because of the key role of foundation species in many systems, it is increasingly important to determine whether more stress-tolerant foundation species may be able to provide similar ecological functions to those they may replace.

The composition and abundance of habitat-forming, 'foundation' species (*sensu* Dayton, 1972) such as seagrasses, can alter important processes. Foundation species can provide refuge from predation and ameliorate stressful environmental conditions, having important and cascading impacts on the communities they form (Bruno & Bertness, 2001; Ellison et al., 2005). Seagrasses create refuge and modify the environment by affecting water flow, nutrient cycling, and community structure (Heminga & Duarte, 2000). Seagrass beds also provide numerous valuable ecosystem services to humans. Seagrass contributions to nutrient cycling alone have considerable value economically (Costanza, 1997). Seagrasses also provide coastal protection (Koch et al., 2006), carbon storage (Duarte & Chiscano, 1999), and fisheries production (Gillanders, 2006), thus playing an important role in coastal ecosystems.

Trophic interactions in seagrass ecosystems can be important for seagrasses and the ecosystem services they provide. Seagrasses provide structural complexity and food resources for the highly abundant fauna that utilize these important habitats, and are thought to contribute considerably to the production of coastal fisheries through refuge and trophic support (Kikuchi, 1974; Heck & Orth, 1980; Orth & Heck, 1980; Heck et al., 2003; Gillanders, 2006). Epiphytic algae growing on the seagrass provide an accessible source of primary production, which is utilized by a host of small epifaunal grazers inhabiting seagrass beds, including crustacean mesograzers such as isopods and amphipods. Consumption of algal primary production in seagrass beds by small grazers also produces biomass available for transfer to higher trophic levels (Williams & Heck, 2001). Indeed, crustacean grazers are an important trophic link, with the majority of seagrass fishes feeding primarily on small crustaceans, including copepods, amphipods and decapods (Klumpp et al., 1989; Edgar and Shaw, 1995; Adams, 1979). Trophic interactions can also have important effects on seagrass beds themselves. The grazing of epiphytic algae and sessile fouling epifauna can prevent shading of seagrass due to overgrowth of these epibionts on seagrass leaves (Neckles et al., 1993; Short et al., 1995; Williams & Ruckelshaus, 1993).

Seagrass beds are also some of the most threatened coastal habitats, with stressors, such as nutrient and sediment run-off, physical disturbance, and temperature stress, causing large-scale declines (Duarte, 2002; Orth et al., 2006; Waycott et al., 2009) and changes in species composition (Johnson et al., 2003, Micheli et al., 2008). More stress tolerant species are expected to increase relative to more sensitive species, if stressful conditions are intensified. Changing abundances of key taxa in altered systems can cause cascading effects on species composition and interactions, ultimately helping to determine the effects of environmental change on community structure (Walther et al. 2002; Schiel, 2004; Micheli et al., 2008). Species redundancy, or the ability to perform similar ecological roles, may determine the reliability of ecological functions as species composition changes (Walker 1992; Walker 1995; Naeem 1998). However, even superficially similar foundation species can differ in important characteristics that affect associated communities. For example, the physical structure of invasive foundation species in wetland systems can influence faunal density (Brusati & Grosholz, 2006) and cause shifts in associated food webs (Levin et al., 2006), as they replace native foundation species. To the extent that seagrasses differ functionally, species loss or alteration in the composition of foundation species would likely have important consequences for the ecosystem services provided by these communities. Thus, it is important to determine specifically how foundation species differ in their abilities to provide habitat and mediate important interactions.

The Chesapeake Bay is an estuary with historically abundant seagrass beds, which have declined greatly over a period of decades, reaching an all-time low in the early 1980s (Orth & Moore, 1983; Orth & Moore, 1984) and recovering to some extent in subsequent years (Moore et al., 2000) with abundance patterns correlated with water quality throughout the bay (Orth et al., 2010). In addition to the stress of poor water quality, increasingly high summer water temperatures in the Chesapeake Bay may have the potential to change the relative abundance of seagrass species in this system (Moore & Jarvis, 2008; Johnson et al., 2003). Of the two species of seagrasses found in higher-salinity waters of the Chesapeake Bay, *Zostera marina* seems likely to decrease relative to *Ruppia maritima*, due to *Zostera marina's* more narrow range of physiological tolerances. I will hereafter refer to these species by their genus names. The Chesapeake Bay is near the southern limit of *Zostera* in the northern hemisphere (Moore & Short, 2006). High water temperatures during the summer of 2005 (approximately 1-2 °C above normal) apparently contributed to a severe dieback of *Zostera*, suggesting that *Zostera* is close to its physiological limits in this area and may be significantly impacted by climate change (Moore & Jarvis, 2008). *Ruppia*, in contrast to *Zostera*, has broad physiological tolerances, which allow it to survive in stressful environments, contributing to its nearly cosmopolitan distribution (Setchell, 1924; Kantrud, 1991). *Zostera* is more abundant than *Ruppia* in the Chesapeake Bay, reaching double *Ruppia's* biomass during peak growing season (Moore et al., 2000), and may be able to competitively exclude *Ruppia* through shading (Orth, 1977). *Ruppia* may be able to increase opportunistically if *Zostera* declines with higher water temperatures. *Ruppia* would also be expected to increase relative to *Zostera* with declining water quality (Dennison et al., 1993; Burkholder et al. 1992; Burkholder et al., 1994) or decreases in salinity (Moore et al., 2000; Kahn & Durako, 2005) due to *Ruppia's* greater tolerance to shading, excess nutrients, and low salinities.

Ruppia and *Zostera* also differ morphologically. Because seagrasses are an important source of structure in marine environments, the morphological differences between *Ruppia* and *Zostera* may result in differing abilities to provide habitat and support higher trophic levels. In the Chesapeake Bay *Zostera* has flat, strap-like blades with rounded tips, about 80 cm long on average and 3-12 mm wide, though morphology can vary greatly with environmental conditions (Moore & Short, 2006). *Ruppia* has much shorter and thinner leaves than *Zostera.* The leaves of *Ruppia* extend from rounded sheaths and are typically about 1 mm wide by 5-20 cm long, with pointed tips (Kantrud, 1991). *Ruppia* also has an approximately four times greater surface area to biomass ratio, compared to *Zostera* (Parker et al., 2001). *Zostera* also has a more extensive below ground structure, with thicker rhizomes that extend deeper into the sediment than those of *Ruppia* (Kantrud, 1991; Moore & Short, 2006). I expected that structural differences between these two species might result in the development of differences in community development, grazing, and predation effects in these vegetation types.

I addressed the effects of varying trophic structure on the communities associated with two Chesapeake Bay seagrass species in an eight-week, factorial mesocosm experiment, which manipulated seagrass species and number of trophic levels. Specifically, I sought to address whether the potentially interactive effects of seagrass density, grazing, and predation would differ between *Ruppia* and *Zostera.* I also asked whether the effects of number of trophic levels and seagrass species would affect the structure of the recruiting assemblage of algae and invertebrates, in terms of diversity, abundance, and species composition.

METHODS

I addressed the effects of varying trophic structure on the communities associated with two Chesapeake Bay seagrass species in an eight-week, factorial mesocosm experiment, which manipulated seagrass species and number of trophic levels. The experiment was conducted using 0.28 m^2 cylindrical mesocosms, arranged in larger tanks with up to eight mesocosms per tank. Treatments were randomly assigned to mesocosms within the larger tanks. Each tank received constant flow-through of sand-filtered water from the York River estuary that was further filtered through 500 μm mesh bags at each tank inflow. This filtering generally prevented unwanted mesograzers from colonizing the experimental treatments, but it allowed recruitment of other invertebrates and algae. Mesocosms were filled with a mixture of sand and mud, which was sieved with 2 mm mesh and allowed to become anoxic before being added to tanks, to eliminate live infaunal invertebrates. Seagrass was defaunated through a series of freshwater rinses before being added to vegetated treatments (Duffy & Harvilicz 2001; Duffy et al., 2001). Monospecific treatments of the two seagrasses planted at each of six densities were crossed with three trophic level treatments (no added fauna, crustacean mesograzers, and crustacean mesograzers + predators). All treatments were represented at each density, but there was no replication of treatments within a given seagrass density. I also tested each of the trophic level treatments in unvegetated mesocosms.

Plants and animals used in experimental treatments were collected from seagrass beds in the York River estuary on the western shore of the Chesapeake Bay. I included a range of seagrass densities to determine whether the two seagrasses had different effects across this range. Each density treatment was planted with equivalent above ground biomass across the two seagrass species treatments. The two seagrass species were standardized to approximately the same above ground biomass per tank, based on known ratios of average above- to below-ground biomass for *Ruppia* and *Zostera* (Kantrud, 1991; J. E. Duffy, unpublished data). Seagrass treatments were planted at the wet equivalent of 17-100 g m^{-2} dry above ground biomass (Table 1), which represents the upper range of *Ruppia* field density and is near the lower range of *Zostera* density in the Chesapeake Bay (Moore et al., 2000). The three most abundant crustacean mesograzers in the field at the time of the experiment, the amphipods *Cymadusa compta* and *Gammarus mucronatus*, and the isopod *Erichsonella attenuata*, were added in a ratio (1:1:2) representative of their relative field abundances at that time. Total mesograzer abundance was kept in proportion with seagrass biomass, at a density of approximately four individuals per wet equivalent of 1 g dry weight above ground mass seagrass, and ranged from 20-120 individuals per tank (Table 1). This pattern of increasing faunal density with increasing seagrass biomass is consistent with natural seagrass communities (Heck & Wetstone, 1977; Stoner, 1980; Orth et al., 1984), and is more likely to reflect realistic predator-prey dynamics (Matilla et al., 2008; and references therein). The unvegetated treatment received the same number of mesograzers as the lowest seagrass density treatment. The mesograzers were allowed to acclimate to the tanks for one week before predators were added. I used two abundant and common seagrass predators, the pipefish *Syngnathus fuscus*, which commonly feeds on crustacean mesograzers in the field

(Adams, 1976; Ryer & Orth, 1987), and the grass shrimp *Palaemonetes vulgaris*, which is also abundant in Chesapeake Bay seagrass beds (Heck & Orth, 1980). Although grass shrimp are omnivorous, sometimes considered facultative grazers (McCall & Rakocinski, 2007) or detritivores (Welsh, 1975), they also feed on small crustaceans such as amphipods (Nelson, 1979). Predator treatments each contained one pipefish and two grass shrimp. Predator treatments were systematically examined approximately once per week, to determine whether each contained a living pipefish, and dead individuals were replaced. Although it was not possible to locate the shrimp in the tanks during the course of the experiment, all grass shrimp were recovered successfully at the end of the experiment.

At the end of the experiment, all vegetation and macrofauna were removed from each tank and preserved by freezing. Samples were separated by taxon, including all organisms retained on a 500 μm sieve. Microalgae were separated from larger taxa by sieving and rinsing with freshwater. However, the biomass I have defined as microalgae may also contain other microscopic organisms mixed with the algal biofilm. Separated taxa were dried at 60°C, and then combusted at 400°C to determine ash free dry mass (AFDM). Final seagrass biomass was separated into above ground, below ground and detrital vegetation. Seagrass pieces that were no longer attached to shoots and had been detached long enough to turn completely brown were considered detrital. Biomass of the crustacean mesograzers was estimated based on their abundance and the size distribution using established equations (Edgar, 1990). Algae and fauna that recruited to the experiment through the flow-through seawater system were identified to the lowest taxonomic level feasible.

The effects of seagrass species, seagrass and mesograzer density treatment, and trophic treatment on the final biomass (AFDM) of seagrass, stocked grazers, and recruited algae and invertebrates, were analyzed using linear models including all variables and interactions. Diversity indices, including taxon richness, evenness, and Shannon-Weiner (H') diversity were analyzed in the same manner for recruiting taxa. Data were Box-Cox transformed to improve normality and homogeneity of variances when necessary. The most abundant recruiting algae and invertebrates, which cumulatively accounted for over 99% of the final biomass in the experiment, were analyzed individually. All recruiting taxa were included in multivariate analyses. Statistical analyses using linear models were conducted using R version 2.10.1 (Copyright 2009, The R Foundation for Statistical Computing, www.r-project.org). To compare the composition of recruiting taxa by treatment, Non-metric multidimensional scaling (NMDS) was performed using Bray-Curtis resemblances on log-transformed data, using PRIMER v6 (Clarke & Gorley, 2006). The NMDS minimum 2D stress of 0.13 occurred 20 times in 50 iterations.

RESULTS

Seagrass biomass

Both seagrass species lost above ground biomass across all density treatments, as evidenced by the lack of correlation between remaining seagrass above ground biomass and initial density treatments (Table 2, Fig. 1). Below ground biomass was significantly correlated with initial biomass for *Zostera* but not for *Ruppia* (Table 2, Fig. 1). Overall, a greater proportion of the initial above- and below-ground biomass of *Zostera* remained at the end of the experiment relative to *Ruppia maritima* (Table 2, Fig. 1). This difference was primarily due to senescence of *Ruppia* during the last week of the experiment (personal observation). There was a marginally significant interaction between the effect of seagrass species and trophic treatment on final above ground seagrass biomass (P=0.07), due to contrasting effects of the grazer only treatment across the two seagrass species: *Ruppia* above ground biomass was lower in the presence of grazers, whereas *Zostera* biomass did not differ among the trophic treatments. Detrital seagrass, which consisted primarily of pieces of brown, detached seagrass leaf and root, was more abundant overall in *Zostera* treatments, and increased proportionally with initial density treatments in this seagrass (Table 2, Fig. 1).

Grazer abundance and trophic transfer

The final abundance of total stocked crustacean mesograzers seemed to increase with greater initial density in predator treatments, but decrease slightly with density in grazer treatments, as indicated by a significant interaction between trophic treatment and initial seagrass and grazer density treatment. There was no significant difference in the final abundance of total stocked mesograzers between the two seagrass species (Table 3, Fig. 2). The individual grazer species varied in their responses to predation. In particular, the two amphipod species appeared to differ in their relative competitive ability and resistance to predation: *Gammarus mucronatus* declined in predator treatments relative to grazer only treatments, particularly at low seagrass density, whereas *Cymadusa compta* increased in predator treatments relative to grazer only treatments (Table 3, Fig. 2). These differences resulted in lower overall abundance of *Cymadusa* than *Gammarus* in grazer only treatments (Fig. 2). *Cymadusa* showed a marginally non-significant trend towards higher overall abundance in *Zostera* compared to *Ruppia.* The isopod *Erichsonella attenuata* remained at low densities relative to the other species, and did not differ between trophic treatments, indicating resistance to predation. Final *Erichsonella* abundance was significantly correlated with its initial abundance (Table 3, Fig. 2). The effects of predation on mesograzers did not differ by seagrass species.

Community development and grazing effects on recruited taxa

The specific faunal taxa that recruited to the experiment via the flow-through seawater system differed between the two seagrass species. Grazers generally decreased the diversity (Shannon-Weiner index, H') of recruiting algal and invertebrate taxa, particularly at higher initial densities of seagrass and grazers, as evidenced by the significant interaction between these two factors (Table 4, Figure 3). Taxon diversity increased with seagrass and grazer density in grazer-only treatments, whereas this trend was not apparent in grazer +

predator or no animal treatments. Diversity of recruiting taxa did not differ between seagrass species. Species richness and evenness did not differ significantly among treatments (Table 4, data not shown). The results of non-metric multidimensional scaling (NMDS) demonstrate that the assemblages of recruiting species separate most clearly by trophic treatment rather than seagrass species, with grazer-only treatments being most different from no grazer treatments, and grazer + predator treatments having intermediate assemblages (Fig. 8). There also appears to be lower variation within the no grazer control and grazer + predator assemblages than in the grazer-only treatment.

Mesograzers strongly reduced the alga *Ulva sp.* in grazer-only treatments, but this effect was reduced through a trophic cascade in predator treatments (Table 5, Fig. 4). Grazers alone also reduced microalgae abundance, with predators causing a trophic cascade (Table 4, Fig. 4), however the effects of trophic treatment and density on microalgae differed by seagrass species, based on a three-way interaction between these factors (Table 5). In *Ruppia* treatments, microalgae abundance decreased with increasing seagrass and grazer density in both grazer only and grazer + predator treatments, but showed no relationship with density in no grazer controls (Fig. 4). In *Zostera* vegetation, however, microalgae abundance was uniformly reduced across densities in the grazer only treatments, but decreased with increasing seagrass/grazer density treatments in both no animal controls and grazer + predator treatments (Fig. 4).

Grazers significantly reduced the abundance of the sessile tunicate *Molgula manhattensis* in grazer only treatments across seagrass species (Table 5, Fig.5). The recruiting amphipod *Corophium sp.* was also lower when grazers were present, yet it increased in abundance with increasing seagrass and grazer density, perhaps due to interactions with *Gammarus*, which had a lower final abundance in treatments with higher initial abundance (Table 5, Fig. 6). The abundance of the gastropod *Haminoea solitaria* was lower in the presence of grazers, and decreased significantly with increasing seagrass and grazer density (Table 5, Fig. 6). *Haminoea* was more abundant overall in *Ruppia* (Table 4, Fig. 6). Several of the recruiting fauna were more abundant in *Zostera* than in *Ruppia.* Barnacles *Balanus spp.* (Fig.5) and Nereid worms (Fig. 6) were significantly more abundant in *Zostera* (Table 5). Maldanid worms were more abundant in *Zostera* than *Ruppia*, and more abundant with grazers than without (Table 5, Fig. 7). Spiochaetopterid worms were more abundant in *Zostera*, and increased with increasing density in *Zostera*, but decreased with increasing density in *Ruppia* (Table 5, Fig. 7).

DISCUSSION

Consumers had a larger impact on the overall diversity and composition of recruiting algae and invertebrates than did seagrass species. For the most part, the effects of mesograzers on recruiting fouling organisms did not differ between seagrass species and there were no differences in the effects of predation between the two seagrasses. However, the composition of recruiting invertebrate species differed by seagrass species. Five of the most abundant recruiting species differed significantly by seagrass species, with all but one having higher abundances in *Zostera* than in *Ruppia.*

Consumers tended to decrease diversity of recruiting taxa in both seagrass species, though this effect depended on seagrass and mesograzer density. This is not a surprising result, as previous mesocosm experiments have shown that crustacean mesograzers can have large effects on the abundance and composition of algae and fouling organisms in benthic communities (Duffy & Hay, 2000; Duffy & Harvilicz, 2001; Hughes et al., 2004; Duffy & Valentine, 2006). Non-metric multidimensional scaling (NMDS) also indicates that grazers determine the community structure of recruited fouling organisms (Fig. 8). The fact that the recruiting assemblages in the grazer-only treatment were more variable than within the no grazer control and grazer + predator assemblages suggests that grazing effects are more variable without predator control. The variable abundance of *Gammarus* across grazer only treatment tanks may have contributed to variation in the composition of the recruiting assemblages in this treatment. The significant effect of grazers on algae (Table 5, Fig. 4) is consistent with previous demonstrations of the importance of crustacean mesograzers in controlling algal abundance in seagrass communities (Duffy & Hay, 2000; Duffy & Harvilicz, 2001). Top-down effects of grazing are considered to be important in seagrass systems, because grazing of epiphytic algae on leaves can release seagrass from competition for light (Hughes et al., 2004; Duffy & Valentine, 2006). However, the evidence for top-down or bottom-up control in the western Chesapeake Bay based on field data is inconsistent, and predator abundance does not appear to depress mesograzers in this system, as it may in other locations (Douglass et al., 2010 and references therein). The nature of my experiment may have exaggerated cascading effects of predation and grazing, as the use of mesocosms created a relatively closed system with respect to mesograzers, and did not allow mesograzers to subsequently colonize to the experiment, or disperse from it, as would likely occur in natural seagrass beds (Virnstein & Curran, 1986).

Mesograzers also affected several of the most abundant recruiting invertebrate species. Grazing appeared to be the primary process determining abundance of the sessile tunicate *Molgula manhattensis* (Table 5, Fig. 5). The gastropod *Haminoea solitaria* was decreased in the presence of grazers and with increasing grazer and seagrass abundance (Table 4, Fig. 6), perhaps because they are outcompeted by mesograzers, which use some of the same food resources (Chester, 1993). Another explanation may be consumption of these snails by mesograzers. *Haminoea* has a well-developed mantle, which envelops their relatively thin shells. Thus it seems reasonable that these snails may be vulnerable to consumption, at least as juveniles when they are smaller in size relative to mesograzers. The recruiting amphipod *Corophium sp.* was also decreased in the presence of grazers, though its abundance was positively correlated with seagrass and grazer density (Table 5, Fig. 6). *Corophium sp.* is not considered to be an epifaunal grazer, but is primarily a filter-feeding detritivore (Gaston & Nasci, 1988). As both mesograzers and *Corophium sp.* may have been utilizing detritus as a food resource, the lower abundance in grazer treatments may reflect a competitive relationship with stocked grazers, particularly *Gammarus*, which had lower final abundance in higher initial density treatments. The greater abundance of *Corophium sp.* in higher initial seagrass density treatments may also have been due to a greater availability of plant-based detrital food with increasing initial seagrass biomass.

The significant interaction between trophic treatment and initial density for final abundance of total mesograzers (Table 3, Fig. 2) may have been due to different effects of predation at different seagrass and grazer densities. Mesograzers seemed to increase with greater initial density in predator treatments, but decrease with initial density in grazer treatments, an effect attributable to the final abundance of *Gammarus* in particular. Apparently cannibalism or other density dependent population processes cause a reduction in overall biomass of this grazer. The differences in predation effects among mesograzers (Table 3, Fig. 2) are consistent with morphological and behavioral differences between these species. *Erichsonella* has a long, thin body form, and relatively sedentary behavior (personal observation), which make it highly cryptic, potentially explaining the lack of predation effect on this species. Interestingly, this may suggest a mechanism for particularly high abundances of *Erichsonella* in the field during late summer, when small predator abundance is at its highest (Douglass et al., 2010). There appears to be a trade-off between competitive ability and predator avoidance in the interaction between *Gammarus* and *Cymadusa*, as predators reduced the abundance of *Gammarus*, but increased the abundance of *Cymadusa*.

Previous work has suggested that these mesograzers compete for common resources (Duffy & Harvilicz, 2001; Duffy et al., 2005), and it appears that *Gammarus* may be competitively dominant, but more vulnerable to predation, relative to *Cymadusa*. *Cymadusa* is a tube-dwelling species of amphipod, and is highly protected in the small nests that it builds (Nelson, 1979). In contrast, *Gammarus* does not build tubes, and is relatively active compared to the other species (personal observation), potentially increasing its vulnerability to predation.

There were no differences in predator effects on grazers between the two seagrass species, despite morphological differences that could influence predation rates. *Ruppia* has much thinner, shorter leaves, which I would expect to provide less refuge to crustacean mesograzers. The same amphipod species used in this experiment were more vulnerable to predation in *Ruppia* relative to *Zostera* in a set of controlled laboratory experiments (Moore, unpublished data). This greater vulnerability appeared to be due primarily to a higher encounter rate in *Ruppia,* likely attributable to its thin leaf structure. Any effects of such structural differences between seagrasses may be overshadowed in this experiment by the effect of the artificial structure of the mesocosms themselves, or by the use of recruiting macroalgae as refuge.

The patterns of above ground seagrass biomass at the end of the experiment do not reflect the planted biomass, most likely because of senescence during the final week of the experiment (Table 2, Fig. 1). This senescence was particularly pronounced for *Ruppia.* However, I did not observe similar senescence in the field, suggesting that this result was an artifact of the experimental conditions. The marginally significant trend toward lower above ground *Ruppia* biomass in treatments with grazers (Table 2, Fig. 1) suggests that *Ruppia* leaf tissue is more easily grazed than that of *Zostera*, but further experimentation is needed to confirm this pattern. *Ruppia maritima* can be subject to direct grazing by invertebrates (Verhoeven, 1978, In: Kantrud, 1991), as can its structurally similar congener *Ruppia cirrhosa*, which is grazed by gammarid amphipods (Menendez, 1989, In: Kantrud, 1991). Grazers effectively controlled microalgae abundance in *Zostera* in the absence of predators, regardless of seagrass and grazer density (Table 4, Fig. 4). In contrast, microalgae abundance decreased with increasing seagrass and grazer density when grazers were present in *Ruppia*. This may have been due to greater grazing of seagrass tissue and detritus in *Ruppia* (and therefore, presumably less grazing of microalgae), or may be related to behavioral differences in the way the mesograzers utilized the available habitat.

While seagrass species did not strongly affect community composition by multivariate measures (Table 4, Fig. 3, Fig. 8), seagrass species did affect several of the most abundant recruiting species, with all but the motile gastropod *Haminoea* having greater abundance in *Zostera* compared to *Ruppia*. The significantly greater abundance of barnacles *Balanus spp.* in *Zostera* (Table 5, Fig. 5) may have been due to the wide, flat leaves of *Zostera,* which are better equipped to support barnacles, whereas *Ruppia* has thinner leaves that may not support barnacles as they grow. This may have consequences for consumers of barnacles, in particular, the diamondback terrapin, *Malaclemys terrapin*, which appears to consume large amounts of barnacles in seagrass beds (D. Tulipani & R. Lipcius, unpublished data). This apparent difference in barnacle success between seagrass species suggests that the differing structure of the two seagrasses may affect community structure in trophically important ways.

Infaunal maldanid and spiochaetopterid worms were also more abundant in *Zostera* than *Ruppia* (Table 5, Fig. 7). There was a significant interaction between seagrass species and seagrass and grazer density for spiochaetopterid worm abundance, with abundance increasing with density in *Zostera* but not in *Ruppia*. As both maldanid and spiochaetopterid worms were largely among the seagrass rhizomes (personal observation), the larger rhizomes and more complex root structure of *Zostera* may provide better habitat for the these worms. The positive correlation between initial density treatments of *Zostera* and spiochaetopterid worms would support the importance of the below ground structure in *Zostera*, as the final below ground biomass of this seagrass was significantly correlated with the initial density treatments (Table 2, Fig. 1). The significantly greater nereid worm abundance in *Zostera* treatments (Table 5, Fig. 6) may be another indication of differences in habitat provision between the two seagrasses.

In natural systems, the related effects of seagrass density, patch size, flow dynamics and sediment characteristics tend to influence infaunal diversity and abundance (Webster et al., 1998; Bowden et al., 2001). Thus, differences in faunal communities between *Ruppia* and *Zostera* may be more influenced by bed and canopy structure, rather than below ground structures. Seagrass beds experience higher larval settlement in general than unvegetated areas due to their ability to dampen flow velocity in marine environments (Koch et al., 2006), and seagrass species differ in their abilities to alter water flow, depending on their canopy structure (Fonseca & Fisher, 1986). Because *Zostera* has a taller canopy than *Ruppia* during most of the year (Orth & Moore, 1988; Moore et al., 2000), it seems probable that *Zostera* would have a greater baffling effect on water flow, perhaps leading to greater larval deposition, relative to *Ruppia*. Since altered water flow and deposition are unlikely to have played a role in the present experiment, it seems more likely that the increased rhizome structure present in *Zostera* provided a better habitat for the infauna recruiting to this experiment. A field experiment comparing infaunal colonization in artificial *Ruppia* and *Zostera* vegetation in the Baltic Sea indicates that colonization depends on complex interactions between seagrass species, density, and physical disturbance, such that loss of either seagrass would decrease faunal diversity in this system (Boström and Bonsdorff, 2000).

The specific characteristics of foundation species in various systems can influence their roles in ameliorating environmental conditions and influencing community composition (Bruno & Bertness, 2001, and references therein). Studies investigating the roles of invasive foundation species have demonstrated that differences in the physical structure of foundation species can influence faunal density (Brusati & Grosholz, 2006) and shifts in associated food webs (Levin et al., 2006). The loss of foundation species also impacts communities by altering nutrient cycling, trophic processes, and biodiversity (Ellison et al., 2005). Thus it seems likely that even if *Ruppia* and *Zostera* do have similar roles in supporting higher trophic levels, species loss or changes in relative abundance would affect seagrass ecosystems at a broader level. If *Zostera* were to decrease relative to *Ruppia* in the Chesapeake Bay, established differences in the morphology, distribution, and phenology of these species may affect their use by associated fauna, and alter ecosystem processes such as sediment stabilization and water flow. To the extent that overall seagrass biomass may be decreased by a reduction or loss of *Zostera*, it is unclear whether *Ruppia* would be able to compensate significantly to the overall functioning of these systems.

LITERATURE CITED

Adams, S.M. 1976. Feeding ecology of eelgrass fish communities. Transactions of the American Fisheries Society 105: 514-519.

Bell, J.D. & M. Westoby. 1986. Abundance of macrofauna in dense seagrass is due to habitat preference, not predation. Oecologia 86: 205-209.

Boström, C. & E. Bonsdorff. 2000. Zoobenthic community establishment and habitat complexity: the importance of seagrass shoot-density, morphology and physical disturbance for faunal recruitment. Marine Ecology Progress Series 205: 123-138.

Bowden, D.A., Rowden, A. A. & M.J. Attrill. 2001. Effect of patch size and in-patch location on the infaunal macroinvertebrate assemblages of Zostera marina seagrass beds. Journal of Experimental Marine Biology and Ecology 259: 133-154.

Bruno, J.F. & M.D. Bertness. 2001. Habitat modification and facilitation in benthic marine communities. In: Bertness M.D., Hay M.E. and Gaines S.D. (eds) Marine Community Ecology, pp. 131–158. Sinauer Associates. Sunderland, Massachusetts.

Burkholder, J.M., Mason, K.M. & H.B. Glasgow. 1992. Water-column nitrate enrichment promotes decline of eelgrass Zostera marina - evidence from seasonal mesocosm experiments. Marine Ecology Progress Series 81: 163-178.

Burkholder, J.M., Glasgow, H.B. & Cooke, J.E. 1994. Comparative effects of water-column nitrate enrichment on eelgrass *Zostera marina*, shoalgrass *Halodule wrightii*, and widgeongrass *Ruppia maritima*. Marine Ecology Progress Series 105: 121-138.

Chapin, F.S., Sala, O.E., Burke, I.C., Grime, J.P., Hooper, D.U., Lauenroth, W.K., Lombard, A., Mooney, H.A., Mosier, A.R., Naeem, S., Pacala, S.W., Roy, J., Steffen, W.L., & DT Tilman. 1998. Ecosystem consequences of changing biodiversity. BioScience 48: 45-52.

Chester, C. M. 1993. Comparative feeding biology of Acteocina canniculata and Haminoea solitaria (Say, 1822) (Opistobranchia: Cephalaspidea). American Malacological Bulletin 10:93-101.

Costanza R., Arge R., Groot R., Farber S., Grasso M., Hannon B., Limburg K., Naeem S., ONeill R.V., Paruelo J., Raskin R.G., Sutton P., vandenBelt M. (1997). The value of the world's ecosystem services and natural capital. Nature 387: 253-260.

Dayton, P.K. 1972.Toward an understanding of community resilience and the potential effects of enrichment to the benthos at McMurdo Sound, Antarctica. In: Proceedings of the Colloquium on Conservation Problems in Antarctica, ed. Parker, B.C. Allen Press. Lawrence, Kansas.

Dennison, W.C., Orth, R.J., Moore, K.A., Stevenson, J.C., Carter, V., Kollar. S., Bergstrom, P.W. & Batiuk, R.A. 1993. Assessing water-quality with submersed aquatic vegetation. BioScience 43: 86-94.

Duarte, C.M. 2002. The future of seagrass meadows. Environmental Conservation 29: 192-206.

Duarte, C.M. & Chiscano, C.L. 1999. Seagrass biomass and production: a reassessment. Aquatic Botany 65: 159-174

Duffy, J.E. & Harvilicz A.M. 2001. Species-specific impacts of grazing amphipods in an eelgrass-bed community. Marine Ecology Progress Series 223: 201-211.

Duffy, J.E., K.S. Macdonald, J.M. Rhode, & J.D. Parker. 2001. Grazer diversity, functional redundancy, and productivity in seagrass beds: an experimental test. Ecology 82: 2417-2434.

Duffy, JE & Hay, M.E.T. 1994. Herbivore Resistance to Seaweed Chemical Defense: The Roles of Mobility and Predation Risk. Ecology 75: 1304-1319.

Duffy, JE & Hay, M.E.T. 2000. Strong impacts of grazing amphipods on the organization of a benthic community. Ecological Monographs 70: 237-263.

Duffy, J.E., Richardson, J.P. & K.E. France. 2005. Ecosystem consequences of diversity depend on food chain length in estuarine vegetation. Ecology Letters 8: 301-309.

Duffy, J.E. & Valentine J.F. 2006. The central role of grazing in seagrass ecology. In: Larkum, A.W.D. et al (eds), Seagrasses: Biology, Ecology and Conservation. Springer, Dordrecht. 463–501.

Douglass, J.G., France, K.E., Richardson, J.P. & J.E. Duffy. 2010. Seasonal and interannual change in a Chesapeake Bay eelgrass community: Insights into biotic and abiotic control of community structure. Limnology & Oceanography 55: 1499-1520.

Douglass, J.G., France, K.E., Richardson, J.P. & J.E. Duffy. 2010. Seasonal and interannual change in a Chesapeake Bay eelgrass community: Insights into biotic and abiotic control of community structure. Limnology & Oceanography 55: 1499-1520.

Ellison, A.M., Bank, M.S., Clinton, B.D., Colburn, E.A., Elliott, K., Ford, C.R. , Foster, D.R., Kloeppel, B.D., Knoepp, J.D. , Lovett, G.M., Mohan, J., Orwig, D.A., Rodenhouse, N.L., Sobczak,W.V., Stinson, K.A., Stone, J.K., Swan, C.M., Thompson, J., Von Holle, B., & J.R. Webster. 2005. Loss of foundation species: consequences for the structure and dynamics of forested ecosystems. Frontiers in Ecology and the Environment 3: 479-486.

Fields, P.A., Graham, J.B., Rosenblatt, R.H., & G.N. Somero. 1993. Effects of expected global climate change on marine faunas. Trends in Ecology & Evolution 8: 361-367.

Fonseca, MS & Fisher, JS. A comparison of canopy friction and sediment movement between 4 species of seagrass with reference to their ecology and restoration. Marine Ecology-Progress Series (1986) vol. 29 (1) pp. 15-22

Gaston, GR, & Nasci, JCT. (1988) Trophic Structure of Macrobenthic Communities in the Calcasieu Estuary, Louisiana. Estuaries 11: 201-211

Gillanders, B.M. (2006) Seagrasses, Fish and Fisheries. In: Larkum, A.W.D. et al (eds), Seagrasses: Biology, Ecology and Conservation. Springer, Dordrecht. 503-536.

Harley, C.D.G., Hughes, A.R., Hultgren, K.M., Miner, B.G., Sorte, C.J.B., Thornber, C.S., Rodriguez, L.F., Tomanek, L., & S.L. Williams. 2006. The impacts of climate change in coastal marine systems. Ecology Letters 9: 228-241.

Fields, P.A., Graham, J.B., Rosenblatt, R.H., & G.N. Somero. 1993. Effects of expected global climate change on marine faunas. Trends in Ecology & Evolution 8: 361-367.

Hughes, A.R., Jun Bando, KJ, Rodriguez, LF, Williams, SL. 2004. Relative effects of grazers and nutrients on seagrasses: a meta-analysis approach. Marine Ecology Progress Series 282: 87-99.

Johnson, M.R., Williams, S.L., Lieberman, C.H,. & A. Solbak. 2003. Changes in abundance of the seagrasses *Zostera marina* L. (eelgrass) and *Ruppia maritima* (widgeongrass) in San Diego, California, following an El Nino event. Estuaries 26: 106-115.

Kahn, A.E. & Durako, M.J. 2005. The effect of salinity and ammonium on seed germination in *Ruppia maritima* from Florida Bay. Bulletin of Marine Science 77: 453-458

Kantrud, H.A. 1991. Wigeongrass (Ruppia maritima L.): A literature Review. U.S. Fish and Wildlife Service, Fish and Wildlife Research 10. Jamestown, ND: Northern Prairie Wildlife Research Center Online. http://www.npwrc.usgs.gov/resource/plants/ruppia/index.htm (Version 16JUL97).

Klumpp, D.W., Howard, R.K. & D.A. Pollard. 1989. Trophodynamics and nutritional ecology of seagrass communities. In: Larkum, A.W.D., McComb, A.J. and S.A. Shepherd (eds). Biology of Seagrasses. Elsevier, Amsterdam. 394-457.

Matilla, J., Heck, K.L., Millstein, E., Miller, E., Gustafsson, C., Williams, S., & D. Byron. 2008. Increased habitat structure does not always provide increased refuge from predation. Marine Ecology Progress Series 361: 15-20.

Menendez, M., E. Fores, and F.A. Comin. 1989. *Ruppia cirrhosa* - Decomposition in a coastal temperate lagoon as affected by macroinvertebrates. Arch. Hydrobiol. 117:39-48. In: Kantrud, HA. 1991. Wigeongrass (*Ruppia maritima* L.): A literature Review. U.S. Fish and Wildlife Service, Fish and Wildlife Research 10. Jamestown, ND: Northern Prairie Wildlife Research Center Online. http://www.npwrc.usgs.gov/resource/plants/ruppia/index.htm (Version 16JUL97).

Micheli, F., Bishop, M.J., Peterson, C.H. & J. Rivera. 2008. Alteration of seagrass species composition and function over two decades. Ecological Monographs 78: 225-244.

Moore K.A., Wilcox, D.J. & R.J. Orth. 2000. Analysis of the abundance of submersed aquatic vegetation communities in the Chesapeake Bay. Estuaries 23: 115-127.

Moore, K.A. & Jarvis J.C. 2008. Environmental factors affecting recent summertime eelgrass diebacks in the lower Chesapeake Bay: implications for long-term persistence. Journal of Coastal Research 55:135-147.

Moore KA & Short F.T. 2006. *Zostera*: Biology, ecology, and management. In: Larkum, A.W.D. et al (eds), Seagrasses: Biology, Ecology and Conservation. Springer, Dordrecht. 323-345.

Naeem, S. 1998. Species redundancy and ecosystem reliability. Conservation Biology 12: 39-45.

Nelson, W.G. 1979. Experimental studies of selective predation on amphipods: Consequences for amphipod distribution and abundance. Journal of Experimental Marine Biology and Ecology 38: 225–245.

Orth, R.J. 1977. Effect of nutrient enrichment on growth of the eelgrass *Zostera marina* in the Chesapeake Bay, Virginia, USA. Marine Biology 44:187-194

Orth, R.J. & Heck, K.L. 1980. Structural compenents of Eelgrass (*Zostera marina*) meadows in the lower Chesapeake Bay-fishes. Estuaries 3: 278-288.

Orth, R.J., Carruthers, T.J.B., Dennison W.C., Duarte, C.M, Fourqurean, J.W., Heck, K.L., Hughes, A.R., Kendrick, G.A., Kenworthy, W.J., Olyarnik, S., Short, F.T., Waycott, M., Williams, S.L. 2006. A global crisis for seagrass ecosystems. Bioscience 56: 987-996.

Orth, R.J. & K.A. Moore. 1983. Chesapeake Bay: An unprecedented decline in submerged aquatic vegetation. Science 222: 51-53.

Orth, R.J., et al. 2010. Long-Term Trends in Submersed Aquatic Vegetation (SAV) in Chesapeake Bay, USA, Related to Water Quality. Estuaries and Coasts 33: 1144-1163.

Parker, J.D., Duffy, J.E. & Orth, R.J. 2001. Plant species diversity and composition: experimental effects on marine epifaunal assemblages. Marine Ecology Progress Series 224: 55-67.

Parmesan, C. 2006. Ecological and Evolutionary Responses to Recent Climate Change. Annual Review of Ecology, Evolution, and Systematics. 37: 637-669 .

Ryer, C.H. & Orth, R.J. 1987. Feeding Ecology of the Northern Pipefish, *Syngnathus fuscus*, in a seagrass community in the lower Chesapeake Bay. Estuaries 10: 330-336.

Parmesan, C. 2006. Ecological and Evolutionary Responses to Recent Climate Change. Annual Review of Ecology, Evolution, and Systematics. 37: 637-669

Setchell, W.A. 1924. *Ruppia* and its environmental factors. Proceedings of the National Academy of Sciences of the United States of America 16: 286-288.

Short, F. T., D. M. Burdick, and J. E. Kaldy. 1995. Mesocosm experiments quantify the effects of eutrophication on eelgrass, Zostera marina. Limnology and Oceanography 40:740 –749.

Verhoeven, J.T.A. 1978. Natural regulation of plant biomass in a *Ruppia*-dominated system. Pages 53-61 in Proceedings of the European Weed Research Society Symposium on Aquatic Weeds. In: Kantrud, HA. 1991. Wigeongrass (*Ruppia maritima* L.): A literature Review. U.S. Fish and Wildlife Service, Fish and Wildlife Research 10. Jamestown, ND: Northern Prairie Wildlife Research Center Online. http://www.npwrc.usgs.gov/resource/plants/ruppia/index.htm (Version 16JUL97).

Walker, B. 1995. Conserving biological diversity through ecosystem resilience. Conservation Biology 9: 747-752.

Walker, B. 1992. Biodiversity and ecological redundancy. Conservation Biology 6: 18-23.

Waycott, M, CM Duarte, TJB Carruthers, RJ Orth, WC Dennison, S Olyarnik, A Calladine, JW Fourqurean, KL Heck, A Hughes, GA Kendrick, WJ Kenworthy, FT Short, SL Williams. 2009. Accelerating loss of seagrasses across the globe threatens coastal ecosystems. Proceedings of the National Academy of Sciences of the United States of America 106: 12377-12381.

Webster, P. J., Rowdena, A. A. & M. J. Attrill. 1998. Effect of shoot density on the infaunal macro-invertebrate community within a *Zostera marina* seagrass bed. Estuarine, Coastal, and Shelf Science 47: 351-357.

Williams, S. L. & M. H. Ruckelshaus. 1993. Effects of nitrogen availability and herbivory on eelgrass (Zostera marina) and its epiphytes. Ecology 74:904 –918.

TABLE 1. Experimental densities of seagrass and crustacean mesograzers. The initial densities of seagrass (added as wet weight equivalent to g dry mass), added to vegetated treatments and mesograzer density (as number of individuals) added to animal treatments. The initial grazer density added was equivalent to approximately 4 individuals per gram dry mass of seagrass.

Density treatment	Grazers added	Seagrass added	Equivalent biomass per square meter
	(no. indiv./tank)	(g dry mass/0.28m2 tank)	(g dry mass/m2)
0	20	0	0
1	20	5	17
2	40	9	33
3	60	14	50
4	80	19	67
5	100	23	83
6	120	28	100

TABLE 2. Results from linear models of seagrass species and predator treatment effects on final abundance (g AFDW) of seagrass and detrital matter. Abundances were Box-Cox transformed to improve normality and homogeneity of variances. Bold indicates significant effect at $p<0.05$. Values in parentheses are df.

Factors	Above ground seagrass			Below ground seagrass			Detrital seagrass			Other Detritus		
	MS	F	p	MS	F	p	MS	F	p	MS	F	p
Seagrass Species (1)	91.311	230.951	**<0.0001**	181.130	541.549	**<0.0001**	43.738	27.043	**<0.0001**	966.620	2.902	0.101
Grass Density (1)	0.137	0.347	0.561	12.068	36.082	**<0.0001**	15.353	9.493	**0.005**	36.960	0.111	0.742
Trophic Treatment (2)	0.103	0.261	0.772	0.133	0.396	0.677	0.929	0.575	0.571	76.240	0.229	0.797
Seagrass Species x Grass density (1)	1.335	3.377	0.079	9.228	27.592	**<0.0001**	2.161	1.336	0.259	108.790	0.327	0.573
Trophic Treatment x Grass Density (2)	0.606	1.533	0.236	0.165	0.493	0.617	0.710	0.439	0.650	104.600	0.314	0.733
Seagrass Species x Trophic Treatment (	1.186	3.000	0.069	0.244	0.731	0.492	1.394	0.862	0.435	248.510	0.746	0.485
Seagrass Species x Grass density x Trophic Treatment (2)	0.039	0.098	0.907	0.028	0.084	0.920	0.504	0.312	0.735	705.240	2.117	0.142
Residual Error	0.395			0.334			1.617			333.090		

TABLE 3. Results from linear models of seagrass species and predator treatment effects on final abundance (g AFDW) of amphipod and isopod crustaceans. Analysis excludes treatments without vegetation and to which grazers were not added. Biomass in g AFDW was calculated from size class abundance of individuals, using established allometric equations (Edgar, 1990). The crustacean mesograzers *Cymadusa compta*, *Gammarus mucronatus* and *Erichsonella attenuata* were added to animal treatments in proportion to initial seagrass density. Abundances were Box-Cox transformed to improve normality and homogeneity of variances with the exception of *Erichsonella attenuata*, which did not require transformation. Bold indicates significant effect at $p<0.05$. Values in parentheses are df.

Factors	*Cymadusa compta*			*Gammarus mucronatus*			*Erichsonella attenuata*			All grazers		
	MS	F	p	MS	F	p	MS	F	p	MS	F	p
Seagrass Species (1)	2.765	3.934	0.065	0.023	0.070	0.795	0.010	2.283	0.150	0.621	1.433	0.249
Grass Density (1)	0.149	0.211	0.652	0.040	0.120	0.733	0.042	9.900	**0.006**	0.001	0.002	0.965
Trophic Treatment (2)	2.779	3.954	0.064	2.775	8.460	**0.010**	0.001	0.312	0.584	0.194	0.448	0.513
Seagrass Species x Grass density (1)	0.104	0.148	0.706	0.211	0.644	0.434	0.014	3.398	0.084	0.002	0.005	0.946
Trophic Treatment x Grass Density (2)	0.259	0.369	0.552	2.699	8.230	**0.011**	0.004	1.067	0.317	2.632	6.072	**0.025**
Seagrass Species x Trophic Treatment (2)	0.264	0.375	0.549	0.041	0.126	0.727	0.002	0.442	0.515	0.010	0.023	0.883
Seagrass Species x Grass density x Trophic Treatment (2)	1.657	2.358	0.144	0.213	0.649	0.432	0.000	0.054	0.819	1.074	2.476	0.135
Residual Error	0.703			0.328			0.004			0.434		

TABLE 4. Results from linear models of seagrass species and predator treatment effects on diversity of recruiting taxa in treatments with vegetation. Shannon-Weiner Diversity and Species Evenness were Box-Cox transformed to improve normality. Bold indicates significant effect at $p<0.05$. Values in parentheses are df.

Factors	Species Richness			Shannon-Weiner Diversity			Species Evenness		
	MS	F	p	MS	F	p	MS	F	p
Seagrass Species (2)	7.111	1.102	0.304	0.035	0.494	0.489	0.000	0.000	0.996
Grass Density (1)	24.070	3.731	0.065	0.025	0.354	0.557	0.009	3.260	0.084
Trophic Treatment (2)	0.750	0.116	0.891	0.317	4.489	**0.022**	0.007	2.562	0.098
Seagrass Species x Grass density (1)	0.000	0.042	0.839	0.069	0.972	0.334	0.000	0.042	0.839
Trophic Treatment x Grass Density (1)	1.712	0.265	0.769	0.305	4.315	**0.025**	0.006	2.295	0.122
Seagrass Species x Trophic Treatment (2)	12.694	1.968	0.162	0.008	0.106	0.900	0.003	1.106	0.347
Seagrass Species x Grass density x Trophic Treatment (2)	2.619	0.406	0.671	0.058	0.823	0.451	0.001	0.428	0.657

TABLE 5. Results from linear models of seagrass species and predator treatment effects on abundance (g AFDW) of recruiting taxa in treatments with vegetation. Abundances were Box-Cox transformed to improve normality and homogeneity of variances. Bold indicates significant effect at $p<0.05$. Values in parentheses are df.

Factor		Algae		Sessile fauna		Motile fauna			Infauna	
		Diatoms	*Ulva sp.*	*Balanus sp.*	*Molgula manhattensis*	*Haminoea solitaria*	*Corophium sp.*	Nereid worms	Maldanidae worms	Spiochaetoptera worms
Seagrass Species (2)	MS	1.371	3.282	1.139	0.237	1.087	0.905	4.856	15.239	0.111
	F	0.655	2.452	13.095	0.874	4.466	0.602	12.240	9.165	5.376
	p	0.426	0.130	**0.001**	0.359	**0.045**	0.449	**0.002**	**0.006**	**0.029**
Grass Density (1)	MS	33.941	0.005	0.176	0.394	6.814	10.253	0.139	0.196	0.288
	F	16.211	0.004	2.022	1.452	28.012	6.819	0.351	0.118	13.906
	p	**<0.001**	0.951	0.168	0.240	**<0.001**	**0.019**	0.559	0.735	**0.001**
Trophic Treatment (2)	MS	124.259	32.692	0.035	2.133	5.755	5.222	0.539	7.950	0.032
	F	59.349	24.430	0.407	7.856	23.656	3.473	1.358	4.781	1.563
	p	**<0.001**	**<0.001**	0.670	**0.002**	**<0.001**	**0.081**	0.276	**0.018**	0.230
Seagrass Species x Grass Density (1)	MS	0.780	1.781	0.138	0.284	<0.001	2.472	1.347	1.082	0.166
	F	0.373	1.331	1.583	1.047	0.001	1.644	3.396	0.651	7.987
	p	0.547	0.260	0.220	0.316	0.979	0.218	**0.078**	0.428	**0.009**
Trophic Treatment x Grass Density (1)	MS	10.251	1.518	0.040	0.201	0.144	0.942	0.539	0.239	0.014
	F	4.896	1.135	0.454	0.740	0.591	0.627	1.360	0.144	0.677
	p	**0.016**	0.338	0.640	0.488	0.561	0.440	0.276	0.867	0.518
Seagrass Species x Trophic Treatment (2)	MS	4.273	1.238	0.052	0.350	0.145	0.801	0.291	4.106	0.007
	F	2.041	0.925	0.602	1.291	0.594	0.533	0.733	2.470	0.349
	p	0.152	0.410	0.556	0.293	0.560	0.476	0.491	0.106	0.709
Seagrass Species x Grass Density x Trophic Treatment (2)	MS	7.676	1.670	0.104	0.705	0.203	0.004	0.037	2.409	0.013
	F	3.666	1.248	1.190	2.597	0.833	0.003	0.094	1.449	0.623
	p	**0.041**	0.305	0.321	0.095	0.447	0.960	0.910	0.255	0.545
Residual Error		2.094	1.338	0.087	0.271	0.243	1.504	0.397	1.663	0.021

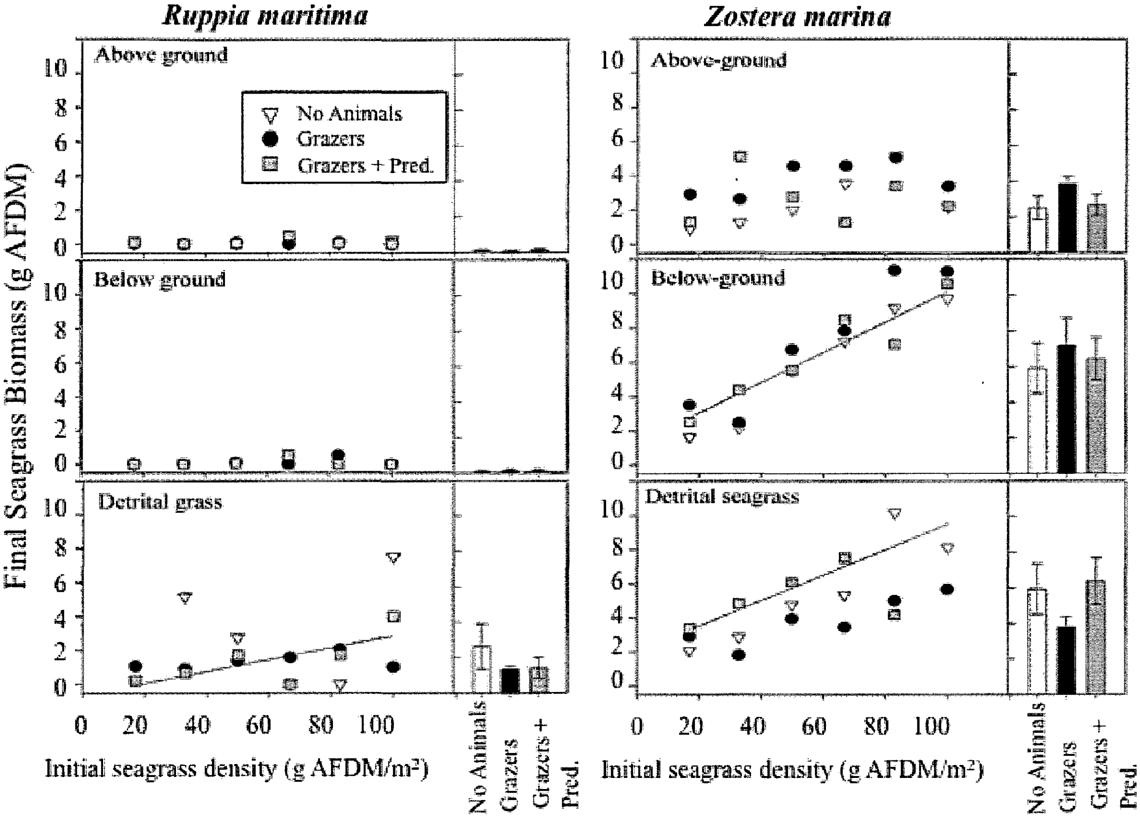

Figure 1. Final abundance of planted seagrass species *Ruppia maritima* (left panel) and *Zostera marina* (right panel) in remaining above ground (a), below ground (b), and detrital (c) biomass (g AFDM). Grass abundance plotted by trophic treatments of: no animals (open triangle), grazers (black circles), and both grazers and predators added (grey squares), respectively. Scatter plots show total biomass per tank vs. initial seagrass density, while adjacent bar plots give mean (± SE) across grass densities by trophic treatment.

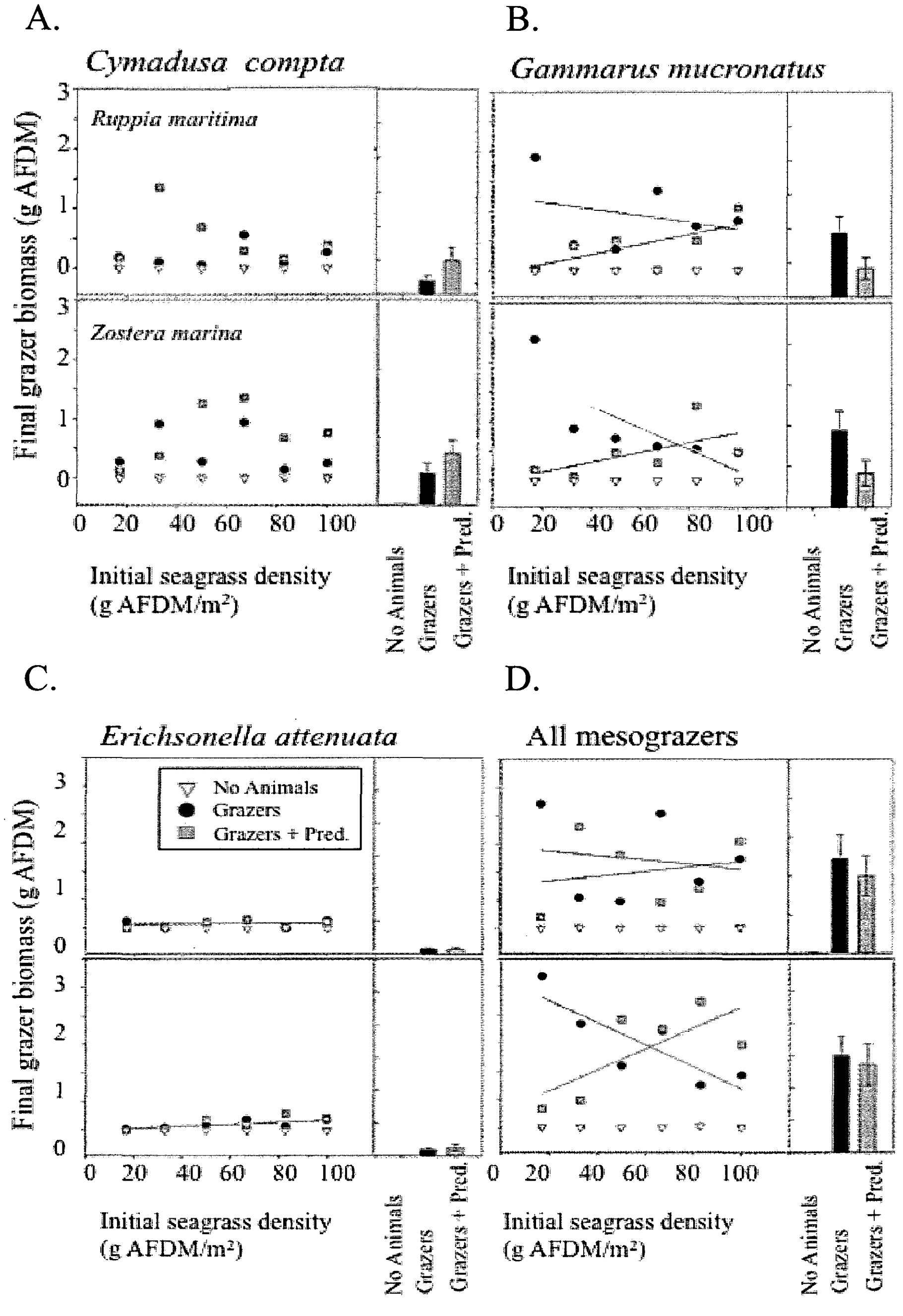

Figure 2. Final abundance (g AFDM) of stocked crustacean mesograzer species *Cymadusa compta* (a), *Gammarus mucronatus* (b), and *Erichsonella attenuata* (c) and all species (d) in seagrass treatments *Ruppia maritima* (upper panel) and *Zostera marina* (lower panel), separated by trophic treatments with: no animals (open triangle), grazers (black circles), and both grazers and predators added (grey squares), respectively. Scatter plots show total biomass per tank vs. initial seagrass density, while adjacent bar plots give mean (± SE) across grass densities by trophic treatment.

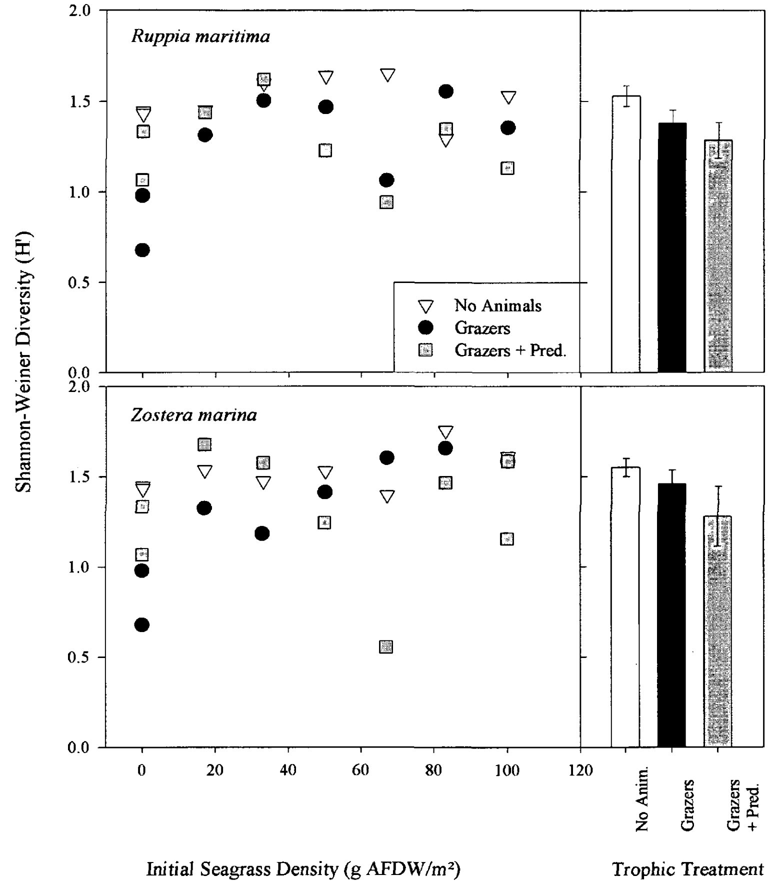

Figure 3. Shannon-Weiner Diversity (H') of recruiting organisms in *Ruppia maritima* (upper panel) and *Zostera marina* (lower panel) by initial grass density and separated by trophic treatments with: no animals (open triangle), grazers (black circles), and both grazers and predators (grey squares) added, respectively. Diversity calculations are based on biomass abundance (g AFDM). Bar plots show means (± SE) across grass densities by trophic treatment.

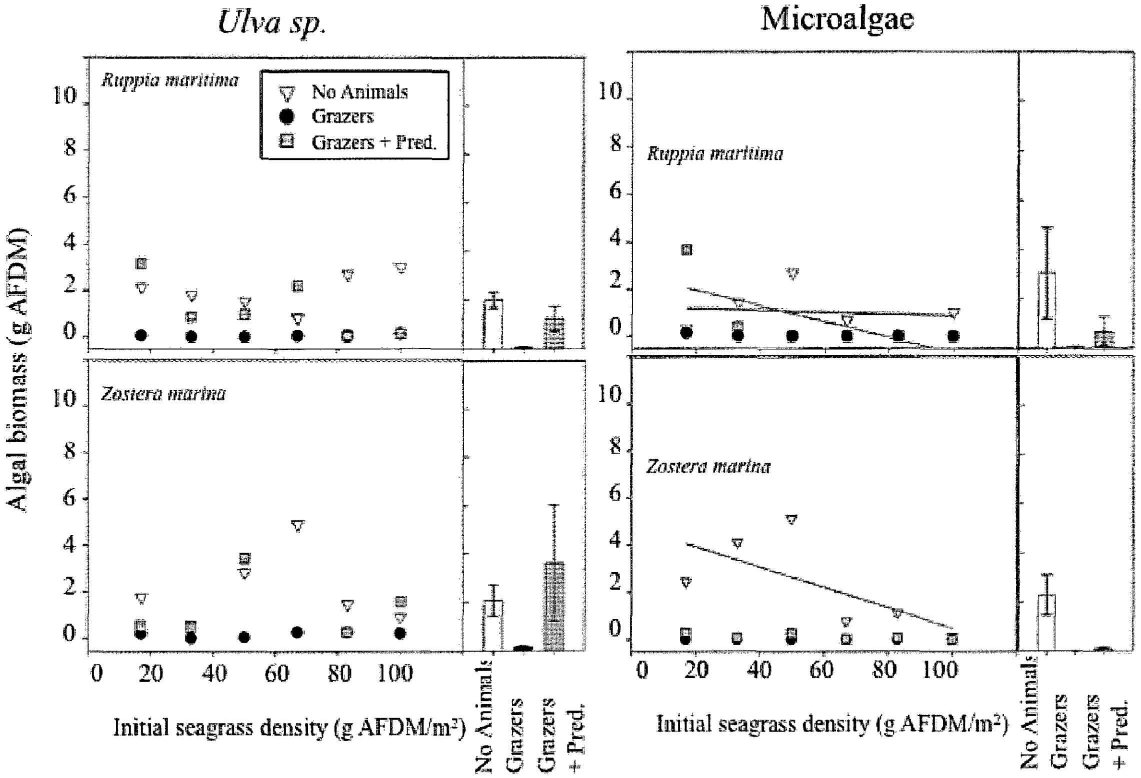

Figure 4. Final abundance (g AFDM) of Algae recruiting to mesocosms. Shown in seagrass treatments *Ruppia maritima* (upper panel) and *Zostera marina* (lower panel), separated by trophic treatments with: no animals (open triangle), grazers (black circles), and both grazers and predators added (grey squares), respectively. Scatter plots show total biomass per tank vs. initial seagrass density, while adjacent bar plots give mean (± SE) across grass densities by trophic treatment.

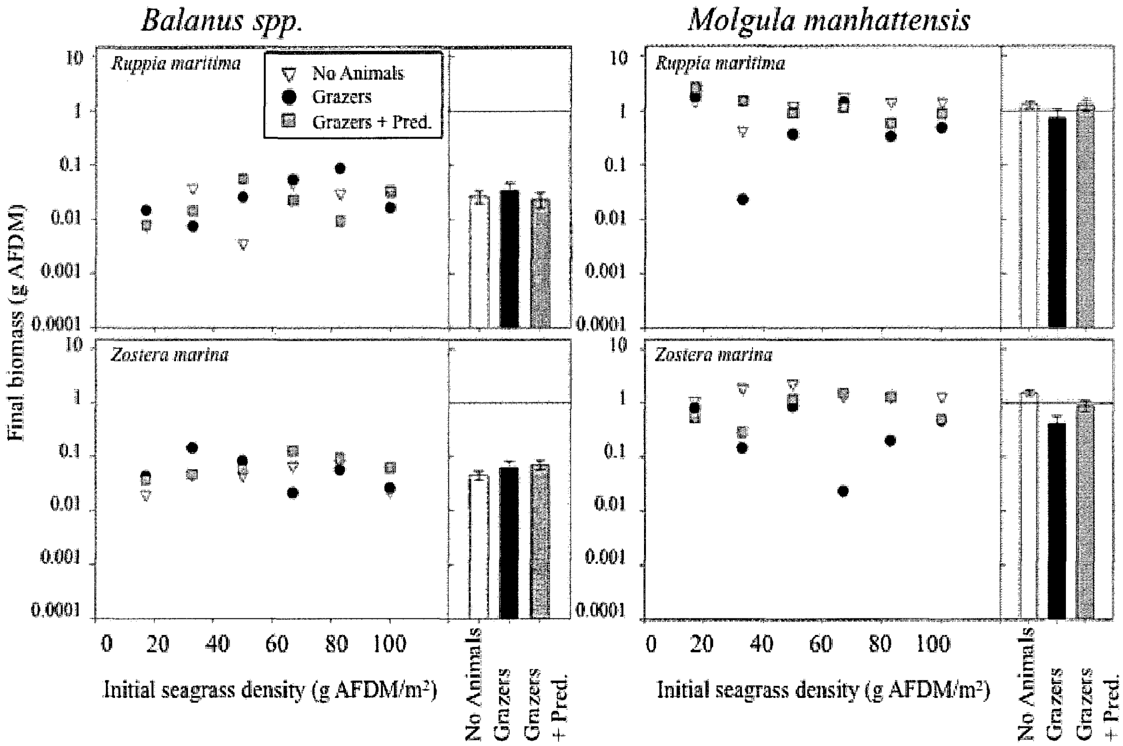

Figure 5. Final abundance (g AFDM) of sessile invertebrates recruiting to mesocosms. Shown in seagrass treatments *Ruppia maritima* (upper panel) and *Zostera marina* (lower panel), separated by trophic treatments with: no animals (open triangle), grazers (black circles), and both grazers and predators added (grey squares), respectively. Scatter plots show total biomass per tank vs. initial seagrass density, while adjacent bar plots give mean (± SE) across grass densities by trophic treatment.

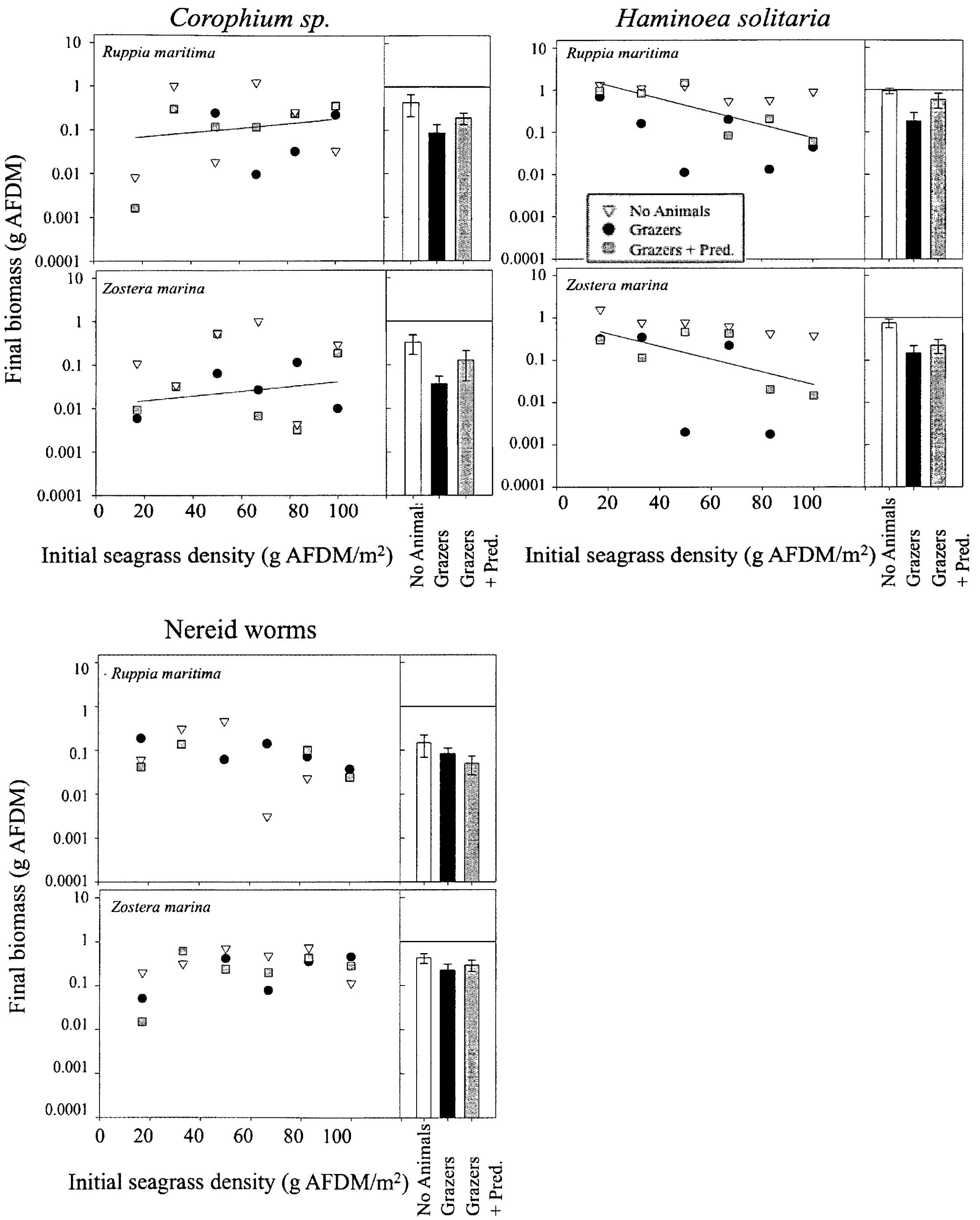

Figure 6. Final abundance (g AFDM) of motile invertebrates recruiting to mesocosms. Shown in seagrass treatments *Ruppia maritima* (upper panel) and *Zostera marina* (lower panel), separated by trophic treatments with: no animals (open triangle), grazers (black circles), and both grazers and predators added (grey squares), respectively. Scatter plots show total biomass per tank vs. initial seagrass density, while adjacent bar plots give mean (± SE) across grass densities by trophic treatment.

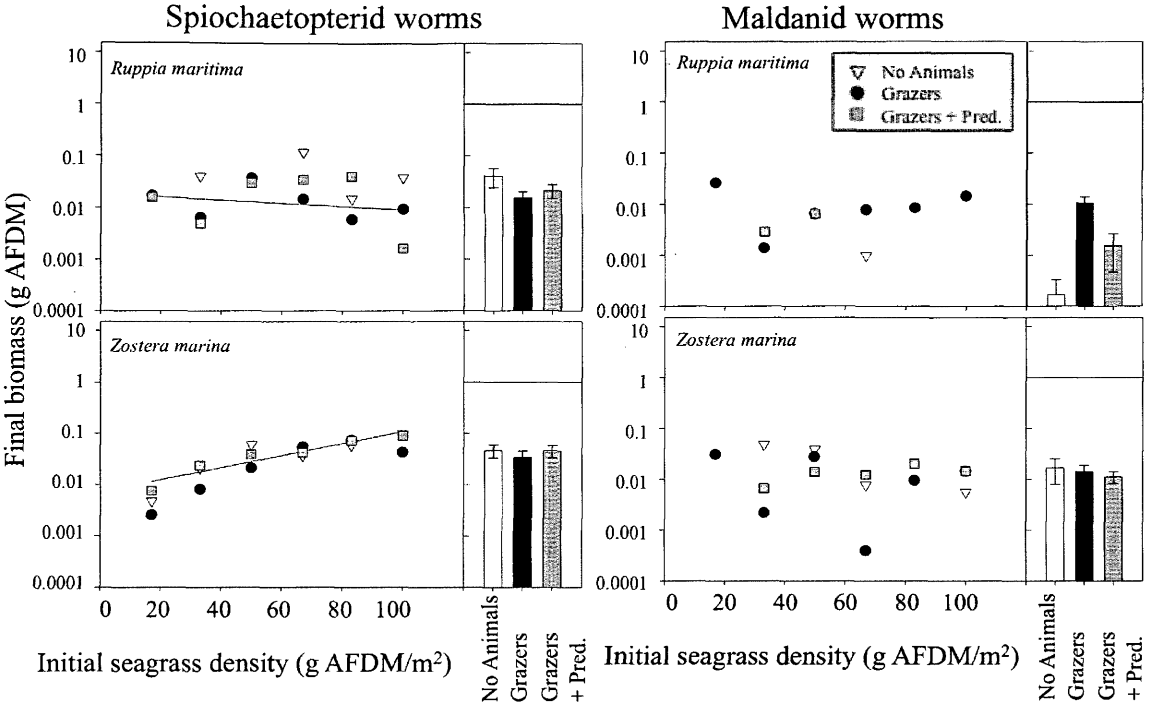

Figure 7. Final abundance (g AFDM) of infaunal invertebrates recruiting to mesocosms. Shown in seagrass treatments *Ruppia maritima* (upper panel) and *Zostera marina* (lower panel), separated by trophic treatments with: no animals (open triangle), grazers (black circles), and both grazers and predators added (grey squares), respectively. Scatter plots show total biomass per tank vs. initial seagrass density, while adjacent bar plots give mean (± SE) across grass densities by trophic treatment.

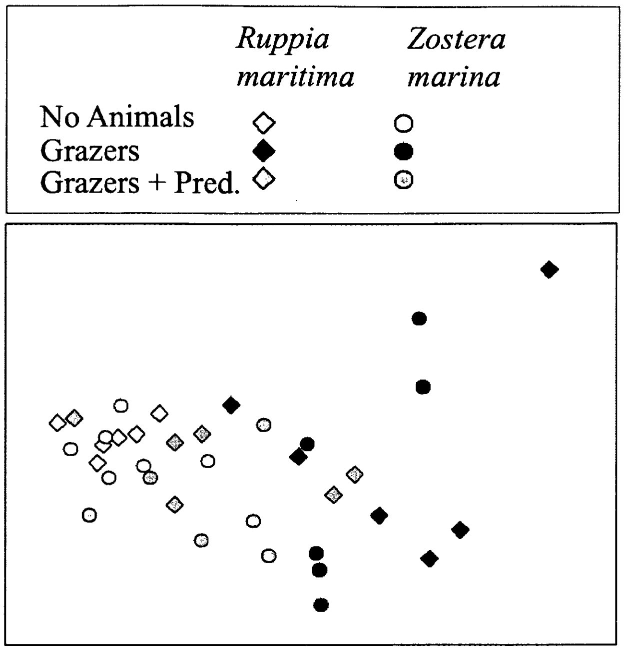

Figure 8. Results from Non-metric multidimensional scaling (NMDS) showing the composition of recruiting algae and invertebrates in experimental seagrass communities as a function of seagrass species and trophic treatment. NMDS was performed using Bray-Curtis resemblances on log-transformed data. The minimum 2D stress of 0.13 occurred 20 times in 50 iterations.

VITA

Althea F. P. Moore was born on December 29th, 1980 in St. Augustine, FL. She graduated from Yellow Springs High School in Yellow Springs, OH in 1999. She graduated from Earlham College with college and departmental honors in 2003. After graduating from college, Althea taught outdoor education at Glen Helen Outdoor Education Center in Yellow Springs, OH, and worked as a research assistant at Brown University. Althea entered the Master of Science program at the School of Marine Science, Virginia Institute of Marine Science, at The College of William and Mary in 2007. At the time of publication Althea had entered a PhD program in biology at Florida State University.