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Foundation species identity and trophic complexity affect experimental seagrass communities

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ABSTRACT: The abundance and species composition of marine foundation species is changing due to range expansion or contraction, with potentially important ecosystem-level consequences. In Chesapeake Bay, USA, warming is likely to favor the more heat and stress-tolerant *Ruppia maritima* (widgeongrass) over *Zostera marina* (eelgrass). Because of the key role of seagrasses in providing habitat and trophic support, it is important to determine whether the more stress-tolerant seagrass provides similar ecological functions to the species it may replace. We addressed how trophic control differs between communities associated with the 2 seagrass species in a mesocosm experiment. Grazing of epiphytic algae can benefit seagrasses over competing algae, and crustacean mesograzers are an important link for higher trophic levels. We manipulated seagrass density, species identity, and presence of grazers and predators, and examined the resulting communities of recruiting algae and invertebrates. Overall, predation was higher in *Ruppia* than in *Zostera*, although mesograzer species individually differed in their susceptibility to predation and response to seagrass species. The presence of grazers and predators had a greater overall effect on multivariate metrics of fouling community development than did seagrass species identity. Initial densities of seagrass and grazer species had interactive effects on some recruiting microalgae and tunicates. Differences in grazer composition and predation between seagrass species could have consequences for higher trophic levels that rely on fauna in seagrass beds. However, given the considerable effects of manipulated seagrass and mesograzer density on trophic interactions and the fouling community, it may be most important to consider the overall density and distribution of seagrass present, rather than seagrass species identity. Our results highlight the importance of testing redundancy in ecological functions among habitat-forming species.

KEY WORDS: Chesapeake Bay · Ecosystem engineer · Foundation species · Functional redundancy · *Ruppia maritima* · Seagrass · Species redundancy · *Zostera marina*

INTRODUCTION

Climate change and anthropogenic stressors are altering abundances and distributions of species, often by favoring stress-tolerant or opportunistic species. Under these conditions, species near the limits of their physiological tolerances are expected to contract their ranges (Parmesan 2006), while more stress-tolerant or opportunistic species may increase in abundance or relative importance as sensitive species decline (Chapin et al. 1998, Walther 2010). The pace of climate change appears to be more rapid in marine than terrestrial ecosystems, leading to faster shifts in species ranges (Sorte et al. 2010, Burrows et al. 2011) with many ecosystems undergoing rapid changes, consistent with climate change predictions (Fodrie et al. 2010, Pinsky et al. 2013, Poloczanska et al. 2013). Range shifts due to climate change are leading to novel assemblages of species that may result in unpredictable changes in ecological functions (Williams

& Jackson 2007). Thus, it is increasingly important to understand how such changes in species composition affect species interactions in marine communities (Van der Putten et al. 2010, Walther 2010).

While some marine animals can adapt to warming by shifting to deeper water depths (Fields et al. 1993), seagrasses are restricted in their vertical distribution by light requirements and may be more susceptible to range contraction near their limits (Harley et al. 2006, Micheli et al. 2008). In addition, seagrass beds are also threatened by nutrient and sediment run-off and physical disturbance, which can cause 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). Stress-tolerant species are expected to increase relative to more sensitive species, if stressful conditions are intensified.

The composition and abundance of habitat-forming, 'foundation' species (sensu Dayton 1972) such as seagrasses can have important and cascading impacts on the communities they form (Bruno & Bertness 2001, Bruno et al. 2003, Ellison et al. 2005, Altieri & van de Koppel 2014). Seagrasses create refuge from predation and affect water flow, nutrient cycling, and community structure (Heck & Thoman 1984, Hemminga & Duarte 2000). Seagrass beds also provide numerous valuable ecosystem services to humans, including nutrient cycling (Costanza et al. 1997), coastal protection (Koch et al. 2009), carbon storage (Duarte & Chiscano 1999), and production of coastal fisheries through refuge and trophic support (Kikuchi 1974, Heck & Orth 1980, Orth & Heck 1980, Heck et al. 2003, Gillanders 2006). A primary source of food supporting higher trophic levels in seagrass beds comes from epiphytic algae growing on seagrass, which is consumed by mesograzers such as isopods and amphipods. Small crustacean grazers provide an important trophic link as the primary food source for the majority of seagrass-associated fishes (Adams 1976, Klumpp et al. 1989, Edgar & Shaw 1995). The grazing of epiphytic algae and sessile fouling epifauna can also benefit the seagrass by preventing overgrowth of these epibionts, which can shade the seagrass leaves (Hughes et al. 2004, Valentine & Duffy 2006, Duffy et al. 2015). Thus, trophic interactions can be important both for maintaining seagrass dominance and for the provision of ecosystem services in these systems, and it is vital to investigate how anthropogenic changes in seagrass ecosystems may influence habitat provision and the related transfer of biomass to higher trophic levels.

Because of their key ecological roles, it is important to understand whether stress-tolerant foundation species provide similar ecological functions to those they may replace. The degree of such functional redundancy may determine the reliability of ecological functions as species composition changes (Walker 1992, 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 coastal vegetated ecosystems such as seagrass and salt marsh can influence faunal density (Brusati & Grosholz 2006, Chaplin & Valentine 2009, Holsman et al. 2010) and cause shifts in associated food webs (Levin et al. 2006, Valinoti et al. 2011), as they replace native foundation species. To the extent that seagrasses differ functionally, species loss or altered composition could have important consequences for ecosystem services. Thus, it is important to determine specifically how foundation species differ in their abilities to provide habitat and mediate important interactions.

The Chesapeake Bay, USA, is an estuary with historically abundant seagrass beds. These beds have declined greatly, reaching the lowest levels in the 1930s and early 1980s (Orth & Moore 1983). They have recovered to some extent in subsequent years (Moore et al. 2000), although seagrass beds in the Bay are still threatened by poor water quality (Orth et al. 2010). Currently, *Zostera marina* (hereafter referred to as *Zostera*) is more abundant than *Ruppia maritima* (hereafter referred to as *Ruppia*) in the Chesapeake Bay, reaching double *Ruppia*'s biomass during peak growing season (Moore et al. 2000). The 2 species typically show a pattern of zonation, with *Ruppia* dominating a narrower band in the shallows, *Zostera* dominating deeper areas, and a mixed zone at intermediate depths. Depth distributions on the western shore of the Chesapeake Bay for *Ruppia* and *Zostera* are 10 to −80 cm and 10 to −110 cm mean low water, respectively (Orth & Moore 1988). *Zostera* may be able to competitively exclude *Ruppia* through shading (Orth 1977); however, *Ruppia* may be able to increase opportunistically if *Zostera* declines with higher water temperatures (Moore et al. 2014). High water temperatures during the summers of 2005 and 2010 (approximately 1 to 2 and 4 to 5°C above normal, respectively) contributed to a severe dieback of *Zostera* (Moore & Jarvis 2008, Moore et al. 2014), suggesting that *Zostera* is close to its physiological limits in this area and may be significantly affected by climate change. Further, the *Zostera* decline in 2010 was accompanied by a concomitant increase in *Ruppia* (Moore et al. 2014), which has broad physiological tolerances, allowing it to survive in stressful environments (Setchell

1924, Kantrud 1991). *Ruppia* is also expected to increase relative to *Zostera* with declining water quality (Burkholder et al. 1992, 1994, Dennison et al. 1993) or decreases in salinity (Moore et al. 2000, Kahn & Durako 2005) due to *Ruppia*'s greater tolerance to shading, excess nutrients, and low salinities.

We tested the effects of varying trophic structure on the communities associated with *Zostera* and *Ruppia* in an 8 wk factorial mesocosm experiment in which we manipulated seagrass species, seagrass density, and number of trophic levels. Specifically, we sought to address whether seagrass species identity and density would affect predation on several crustacean mesograzers, given that vegetation density can affect trophic interactions in seagrass ecosystems by altering predator behavior and prey refuge (Heck & Crowder 1991, James & Heck 1994). We also aimed to determine whether seagrass density, grazing, and predation interactively affect the structure of the fouling community between *Ruppia* and *Zostera*. Morphological differences between *Ruppia* and *Zostera* may result in differing abilities to provide habitat and support higher trophic levels due to the importance of their structure-providing role (e.g. Martin & Valentine 2011). *Zostera* has flat, strap-like blades with rounded tips, and thick, extensive below-ground structures, though morphology can vary greatly with environmental conditions (Moore & Short 2006). *Ruppia* has much shorter and thinner leaves than *Zostera*, more shallow below-ground structures (Kantrud 1991, Moore & Short 2006), and approximately a 4 times greater surface area to biomass ratio (Parker et al. 2001). We expected that *Ruppia* might provide less refuge from predation for epifauna than *Zostera* due to its smaller, thinner leaves, resulting in differences in faunal community development, grazing, and predation effects.

MATERIALS AND METHODS

We tested the effects of varying trophic structure on the development of communities associated with 2 Chesapeake Bay seagrass species in a fully factorial mesocosm experiment that manipulated seagrass species and number of trophic levels. We ran the experiment for 8 wk, from September to November 2008. We planted monospecific treatments of the 2 seagrass species at each of 6 densities, crossed with 3 trophic level treatments (no added fauna, crustacean mesograzers, and crustacean mesograzers + predators). We used an analysis of covariance design in which all treatments were represented at each sea-

grass density, but there was no replication of treatments within a given density.

The experiment was conducted in 113 l cylindrical outdoor mesocosms, arranged in larger tanks with up to 8 mesocosms tank^{-1}. We assigned treatments randomly to mesocosms. Each mesocosm 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. We controlled for artefacts of tank experiments as the regular inflow of water ensured circulation and aeration of water, shade cloths covering each mesocosm reduced light levels, and the larger tanks containing our mesocosms were partially filled with water to reduce temperature fluctuations, as described previously for similar experiments (Spivak et al. 2007, Blake & Duffy 2012). The filtering prevented most mesograzers from colonizing, but allowed natural recruitment of microscopic propagules of other invertebrates and algae. One tank was colonized by a few individuals each of the amphipod grazers *Elasmopus levis* and *Ampithoe longimana*, but because this tank was assigned to a grazer treatment, we do not expect this minor contamination to have influenced our results. We filled mesocosms 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. We defaunated the seagrass through a series of freshwater rinses before planting it in mesocosms (Duffy & Harvilicz 2001, Duffy et al. 2001). We standardized the 2 seagrass species to approximately the same above-ground biomass per mesocosm in each density treatment, based on known ratios of average above- to below-ground biomass for *Ruppia* and *Zostera* (Kantrud 1991, J. E. Duffy unpubl. data). We did not use reproductive seagrass shoots, as reproduction alters the structure of both *Ruppia* and *Zostera* (Kantrud 1991, Moore & Short 2006). We planted seagrass treatments at the wet equivalent of 17 to 100 g m^{-2} dry above-ground biomass (see Table S1 in the Supplement at www.int-res.com/articles/suppl/m556 p105_supp.pdf), 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). We chose this density range to include realistic field densities of both seagrass species while controlling for biomass between the 2 seagrass species. Vegetation density is known to affect trophic interactions in seagrass ecosystems by altering predator behavior and refuge availability for prey species (Heck & Crowder 1991, James & Heck 1994), depending on the relative densities of vegetation and prey

(Mattila et al. 2008). Thus, manipulating trophic interactions across a range of seagrass densities provides a more realistic comparison of trophic function between the 2 seagrass species.

We added the 3 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*) to mesocosms in a ratio of 1:1:2, which was representative of their relative field abundances at that time. Total mesograzer abundance was kept in proportion with seagrass biomass, at a density of approximately 4 individuals per wet equivalent of 1 g dry weight above-ground mass seagrass, and mesograzer density ranged from 20 to 120 ind. mesocosm^{-1} (Table S1 in the Supplement). We used the same densities of mesograzers on *Ruppia* and *Zostera*, since their densities do not differ by seagrass species in the field (Parker et al. 2001). 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 a more realistic representation of trophic interactions in seagrass than using a single grazer density (Mattila et al. 2008, Canion & Heck 2009).

In our predator present treatments, we included 2 abundant and common seagrass predators: the pipefish *Syngnathus fuscus* and the grass shrimp *Palaemonetes vulgaris*. Pipefish feed on crustacean mesograzers in the field (Adams 1976, Ryer & Orth 1987). Grass shrimp are also effective predators on small crustacean mesograzers, as demonstrated by experimental trials using seagrass amphipods (Nelson 1979), yet they also facultatively feed on microalgae (McCall & Rakocinski 2007). Predator treatments each contained 1 pipefish and 2 grass shrimp, which falls within the range of realistic predator field densities (Douglass et al. 2010). We checked for predator presence at least once per week, and dead predators were replaced as necessary. All organisms used in our study were collected from seagrass beds in the York River estuary on the western shore of the Chesapeake Bay. Between collection and initiation of the experiment, study organisms were kept in outdoor tanks with flow-through water and food available. The mesograzers were identified and counted in the laboratory during the several days prior to experiment initiation in containers with seagrass leaves and ambient seawater changed daily. We sub-sampled the stocked mesograzer species non-destructively at the midpoint of the experiment to estimate abundances by sweeping a small aquarium net through each mesocosm 10 times in a figure eight pattern and counting the individuals collected by the net, which were then returned to the mesocosm. This time point gave us the opportunity to quantify grazer abundances after the experimental treatments had ample time to influence grazer populations, while allowing us to understand faunal dynamics before the end of the experiment. We counted the sampled grazers and identified individuals to species where possible. The grazer estimates from this midpoint sampling are reported as number of individuals. Some juvenile amphipods were too small to identify non-destructively to the species level, so counts of these individuals were only included in the analysis of the total counts of all species combined.

At the end of the experiment, we removed all vegetation and macrofauna from each mesocosm, washed it over a 500 µm sieve, and preserved it by freezing. Samples retained on a 500 µm sieve were separated by taxon. We dried separated taxa at 60°C, and then combusted at 400°C to determine ash-free dry mass (AFDM), excluding stocked crustacean mesograzers, which were not combusted (see below). We separated final seagrass biomass into above-ground, below-ground, and detrital vegetation. Seagrass pieces that were completely brown and no longer attached to shoots were considered detrital. Algae and fauna that recruited to the experiment through the flow-through seawater system were identified to the lowest taxonomic level feasible. We used established equations (Edgar 1990) to estimate biomass (expressed as AFDM) of the crustacean mesograzers at the end of the experiment based on their abundance and the size distribution, following previous methodology necessary to separate and identify small crustacean grazers (e.g. Duffy et al. 2001, Blake & Duffy 2012). We separated crustacean mesograzers from the other taxa, preserved them in 70% ethanol and sub-sampled the individuals into one-eighth of the total abundance using a plankton splitter. Thus, the estimated grazer biomasses reported here are appropriate for comparison between treatments but do not represent absolute biomass. We then sieved the mesograzers (using mesh sizes of 8.0, 5.6, 4.0, 2.8, 2.0, 1.4, 1.0, 0.71, and 0.05 mm), identified them to species using light microscopy, and counted them by size class.

We analyzed the effects of seagrass species identity, seagrass and mesograzer density, and predator treatment on the final biomass (AFDM) of seagrass, stocked grazers, recruited algae and invertebrates, and diversity indices, with full models including all possible interactions among factors (seagrass species identity, trophic treatment, and seagrass density), with the flow-through tank where the mesocosm was

located as a random factor, using the 'lmer' function in the 'lme4' package (Bates et al. 2015) in R v.3.1.3 (R Development Core Team 2015) and 'anova' function in the 'lmerTest' (Kuznetsova et al. 2014). We Box-Cox transformed response variables to improve normality and homogeneity of variances when necessary and a small number (0.0001) was added to zero values to allow transformation. To determine the response of mesograzer counts to treatments at the experiment midpoint, we used generalized linear mixed models with the full model described above with the 'glmer' function in the 'lme4' package and the 'anova' function in the 'car' package (Fox & Weisberg 2011) in R using a Poisson distribution. Only the most abundant recruiting algal and invertebrate species, which cumulatively accounted for over 99% of the final biomass in the experiment (see Table S2 in the Supplement), were analyzed individually. For recruiting taxa that showed a significant main or interactive effect of trophic treatment, we also ran the full model with final total mesograzer biomass as a covariate to clarify the role of grazing specifically, as final grazer biomass did not correspond to the initial abundances represented by the density treatments. For recruiting taxa that appeared as though they may have a non-linear relationship with seagrass density, we ran the full statistical model including a quadratic term; however, it was not significant in any case. We used Tukey's HSD tests to make multiple comparisons between treatments using the 'glht' function in the 'multcomp' package (Hothorn et al. 2008) when seagrass species and trophic level treatments did not interact significantly with seagrass density. For responses that showed a significant effect of initial seagrass density, we used the 'lm' function in the base R statistics package to calculate the R^2 value and equation describing the relationship (y = intercept + slope × x + residual standard error) using responses transformed as described above.

To compare the overall composition of recruiting taxa by treatment, we used permutational multivariate analysis of variance (PERMANOVA), including the full model of explanatory variables described above. We used the 'adonis' function in the 'vegan' package in R with 999 permutations, constrained by flow-through tank location. We tested multivariate homogeneity of variance for recruited taxa using the 'betadisper' function in the 'vegan' package in R and determined that the assumption was met (p > 0.29). To visualize the relationship between recruited taxa and treatments, we performed non-metric multidimensional scaling (NMDS) using Bray-Curtis dissimilarities on log-transformed data, using PRIMER v.6

(Clarke & Gorley 2006). We included all recruiting taxa in multivariate analyses. We conducted statistical analyses using general and generalized linear mixed models and PERMANOVA using R v.3.1.3 (www.r-project.org).

RESULTS

Seagrass biomass

Both *Zostera* and *Ruppia* 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 (Fig. 1, Table 1). Below-ground biomass was positively correlated with initial biomass for *Zostera* (y = 0.458 + 0.0382x + 0.463, adjusted R^2 = 0.852) but not for *Ruppia* (Fig. 1, Table 1), and overall, more *Zostera* remained at the end of the experiment than *Ruppia* (Fig. 1, Table 1). This difference was primarily due to senescence of *Ruppia* during the last week of the experiment (A. Moore pers. obs.). The total amount of detrital seagrass corresponded to initial density across both seagrass species, suggesting that much of the lost seagrass biomass became detrital (across both seagrasses, y = 0.112 + 0.0230x + 1.643, adjusted R^2 = 0.118; Fig. 1, Table 1).

Effects of seagrass and predators on mesograzers

We included estimates of grazer abundances from the experiment midpoint, which was after the experimental treatments had ample time to influence grazer populations but well before seagrass senescence at the end of the experiment would have influenced faunal dynamics. At the midpoint of the experiment, seagrass species identity affected mesograzer abundances, yet these effects depended on the presence of predators and the initial seagrass density. *Cymadusa compta* was more abundant in *Zostera* vegetation overall (Fig. 2A, Table 2), with a slight tendency for predators to have different effects between the 2 seagrass species (Fig. 2A). *Gammarus mucronatus* was greatly reduced in the presence of predators, particularly in denser *Zostera* vegetation, but not *Ruppia*, as shown by a significant 3-way interaction with seagrass species and density (Fig. 2B, Table 2). *Erichsonella attenuata* was more abundant in *Ruppia* than in *Zostera*, and its abundance increased with planted density of *Zostera* more strongly than for *Ruppia* (Fig. 2C, Table 2).
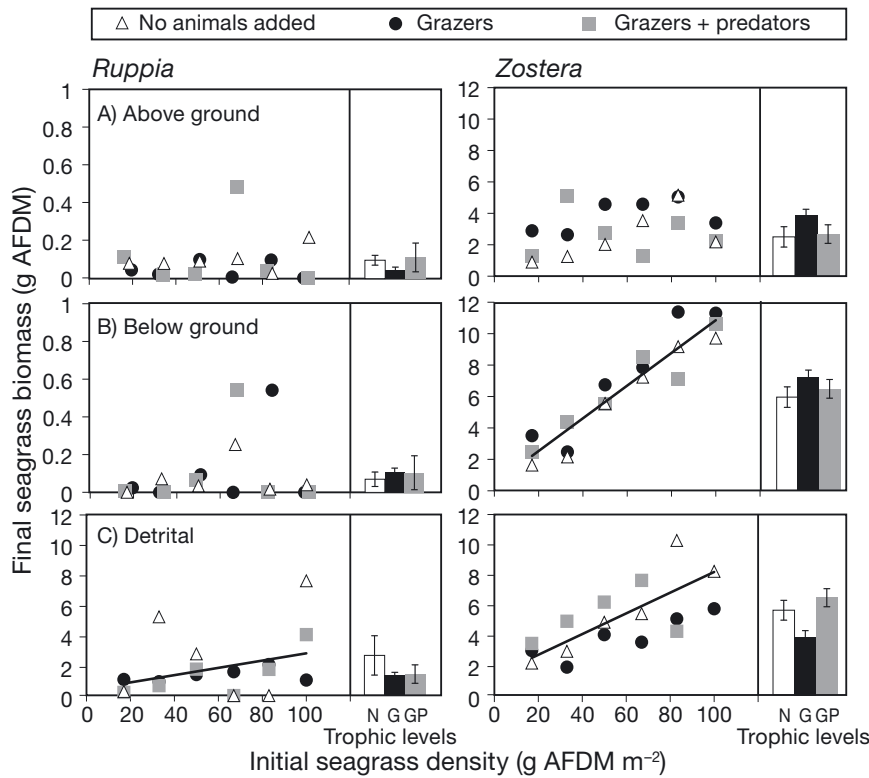
Fig. 1. Final biomass (g ash-free dry mass, AFDM) of planted seagrass species *Ruppia maritima* (left panels) and *Zostera marina* (right panels) remaining (A) above ground, (B) below ground, and (C) as detritus. Symbols indicate trophic treatments: no animals added (open triangle), grazers (black circles), and both grazers and predators added (grey squares). Scatter plots show total biomass per mesocosm vs. initial seagrass density, while adjacent bar plots give mean (±SE) across seagrass densities by trophic treatment. Letters below bar plots indicate trophic level treatments: no animals added (N, white bar), grazers (G, black bar), and both grazers and predators added (G+P, grey bar), respectively. Solid lines on scatter plots show a significant effect of density for all treatments combined. Note the differing *y*-axes for the 2 seagrass species

Table 1. Results from linear mixed models of seagrass species and predator treatment effects on final abundance (in g ash-free dry weight, AFDW) of seagrass and detrital matter including flow-through tank location as a random factor. Abundances were Box-Cox transformed to improve normality and homogeneity of variances. df_N: numerator degrees of freedom; df_D: denominator degrees of freedom. **Bold** indicates significance at p < 0.05

Factors	Above-ground seagrass				Below-ground seagrass				Detrital seagrass			
	MS	df_N, df_D	F	p	MS	df_N, df_D	F	p	MS	df_N, df_D	F	p
Seagrass species	73.421	1, 23.829	20.890	**<0.001**	135.762	1, 23.146	18.427	**<0.001**	43.738	1, 23.998	1.530	0.228
Trophic treatment	0.049	2, 21.075	0.635	0.540	0.138	2, 20.235	0.045	0.956	0.929	2, 23.998	0.071	0.932
Seagrass density	0.001	1, 23.98	0.004	0.948	5.802	1, 22.349	35.250	**<0.001**	15.353	1, 23.998	9.493	**0.005**
Species × Treatment	1.022	2, 22.338	0.364	0.699	0.159	2, 21.024	0.276	0.761	1.394	2, 23.998	0.632	0.540
Species × Density	1.249	1, 23.971	3.596	0.070	9.914	1, 22.866	48.322	**<0.001**	2.161	1, 23.998	1.336	0.259
Treatment × Density	0.292	2, 21.719	0.946	0.404	0.035	2, 20.587	0.195	0.824	0.710	2, 23.998	0.439	0.650
Species × Density × Treatment	0.057	2, 22.064	0.175	0.840	0.024	2, 21.017	0.118	0.889	0.504	2, 23.998	0.312	0.735

Unlike the other grazers, *E. attenuata* was more abundant where predators were present, regardless of seagrass species and initial seagrass densities. Overall, mesograzer abundance was reduced by predation, but this effect was stronger and depended more on initial seagrass density in *Ruppia* than in *Zostera* (Fig. 2D, Table 2). Although the effects of initial density on mesograzers depended on other treatments, none of the individual regressions with density showed significant patterns.

By the end of the experiment, the final biomass of grazers (g AFDW) did not differ by seagrass species

identity (Fig. 3, Table 3), in contrast with grazer counts at the midpoint of the experiment (Fig. 2, Table 2). Final biomass of *C. compta* was not related to any experimental treatment. *E. attenuata* biomass was higher in plots with higher initial seagrass density, but it was not affected by seagrass species identity or predation (across treatments, $y = 1.529 \times 10^{-3} + 1.836 \times 10^{-4} x + 0.00837$, adjusted $R^2 = 0.265$; Fig. 3A,C, Table 3). The final biomass of *G. mucronatus* was reduced by predation, and this predator effect was stronger at low initial seagrass density than high initial seagrass density (with predators,
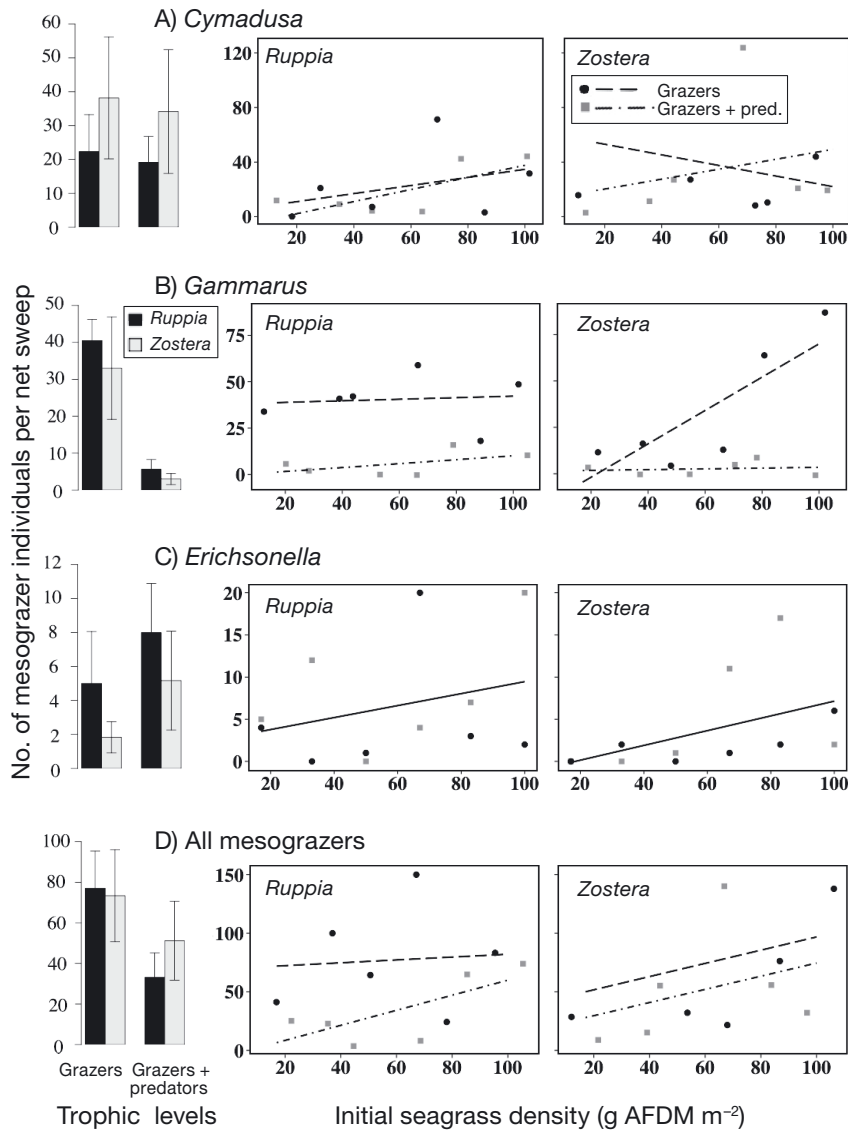
Fig. 2. Abundance of crustacean mesograzer species (A) *Cymadusa compta*, (B) *Gammarus mucronatus*, and (C) *Erichsonella attenuata*, and (D) all species sampled non-destructively at the midpoint of the experiment. Bar plots give mean (±SE) number of mesograzer individuals by trophic treatment with either grazers added or grazers and predators added, with seagrass treatments shown as *Ruppia maritima* in black and *Zostera marina* in light grey. Scatter plots show the count of individuals sampled per mesocosm vs. initial seagrass density in *R. maritima* (left panels) and *Z. marina* (right panels). Solid lines show a significant main effect of density for all treatments combined. Other lines show statistically significant interactions between density and trophic treatments for treatments that had a significant relationship with density

$y = -1.941 + 0.00498x + 0.208$, adjusted $R^2 = 0.294$; Fig. 3B, Table 3). Total biomass of mesograzers across species showed a similar pattern to that of *G. mucronatus*, with biomass positively related to initial seagrass density in predator treatments, but negatively related to initial density in grazer-only treatments (Fig. 3D, Table 3).

Effects of seagrass and predators on the fouling community

The community structure of recruited algae and sessile invertebrates was primarily affected by trophic interactions and did not differ strongly between the 2 seagrass species (Table 4, p = 0.064). NMDS ordination illustrated that the fouling assemblages separated most clearly by trophic treatment rather than by seagrass species, with grazer-only treatments being most different from no grazer treatments, and grazer + predator treatments having intermediate assemblage structure (Fig. 4). The no-grazer treatment and grazer + predator assemblages were also less variable in composition than the grazer-only treatment. Grazers and predators generally decreased diversity of the recruiting assemblage. Shannon-Wiener diversity declined with initial seagrass density in the grazer + predator treatment but showed a positive trend or no trend in the other trophic treatments (trophic treatment × density, MS = 0.31, F = 4.47, p = 0.02; Fig. 5A, Table S3 in the Supplement at www.int-res.com/articles/suppl/m556 p105_supp.pdf). Evenness showed a very similar pattern (trophic treatment × density, MS = 0.008, F = 3.67, p = 0.04; Fig. 5B, Table S3). Diversity trends were roughly inverse to those of final grazer biomass, being lower at high initial seagrass densities where final grazer biomass was higher (Fig. 3D). When added as a covariate in the full statistical model, final total grazer biomass was a significant predictor of species evenness (MS = 0.018, F = 5.30, p = 0.033), but not Shannon-Wiener diversity (p > 0.4). Species richness did not differ significantly among any treatments (Table S3).

Mesograzers reduced accumulation of both macro- and microalgae. Microalgal biomass was more strongly reduced by grazers than was the macroalga *Ulva* sp. (Fig. 6, Table 5). The effect of grazing on *Ulva* sp. was eliminated in predator treatments, likely through a trophic cascade (Fig. 6B, Table 5). Mesograzers reduced microalgal biomass, but this effect

Table 2. Results from generalized linear mixed models of seagrass species and predator treatment effects on the abundance of amphipod and isopod crustacean mesograzers (as counts of individuals) sampled non-destructively at the experiment mid-point. Models used the Poisson distribution and included flow-through tank location as a random factor. Analysis excludes treatments without vegetation and to which grazers were not added. **Bold** indicates significance at p < 0.05

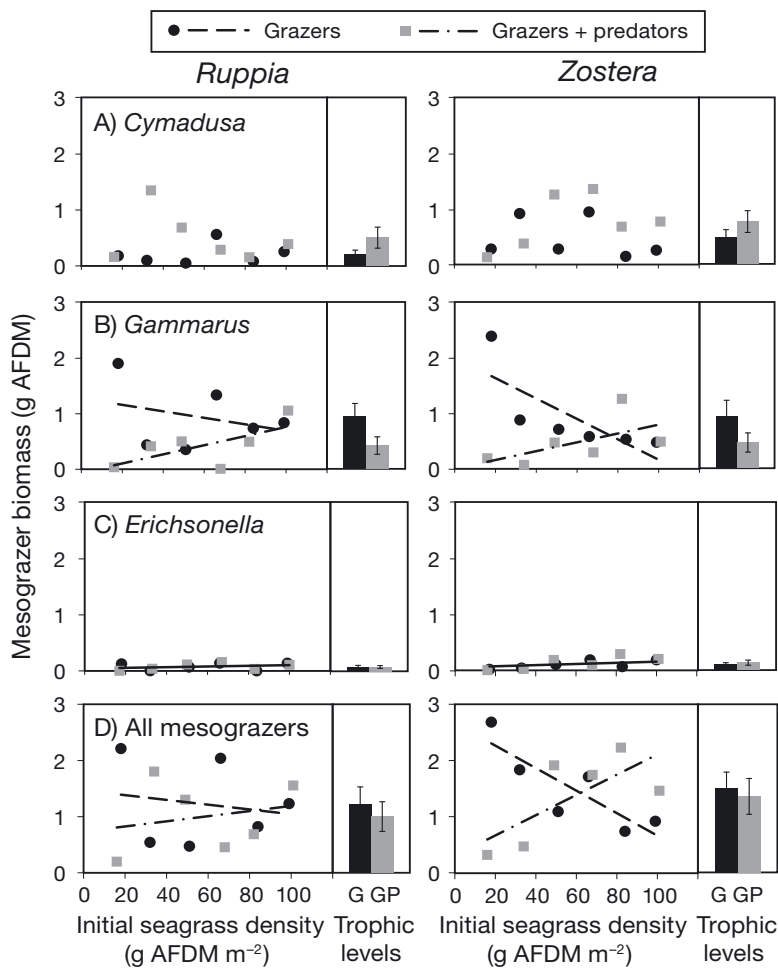| Factors	Cymadusa compta			Gammarus mucronatus			Erichsonella attenuata			All grazers		
	χ^2	df	p	χ^2	df	p	χ^2	df	p	χ^2	df	p
Seagrass species	96.544	1	**<0.0001**	18.633	1	**<0.0001**	8.335	1	**0.0039**	18.200	1	**<0.0001**
Seagrass density	47.189	1	**<0.0001**	59.657	1	**<0.0001**	11.860	1	**0.0006**	87.181	1	**<0.0001**
Trophic treatment	1.450	1	0.2285	158.030	1	**<0.0001**	10.798	1	**0.0010**	86.301	1	**<0.0001**
Species × Density	61.736	1	**<0.0001**	8.905	1	**0.0028**	3.961	1	**0.0466**	4.660	1	**0.0309**
Treatment × Density	14.967	1	**0.0001**	0.493	1	0.4827	0.107	1	0.7432	6.082	1	**0.0137**
Species × Treatment	8.030	1	**0.0046**	0.165	1	0.6844	1.405	1	0.2358	32.813	1	**<0.0001**
Species × Density × Treatment	0.193	1	0.6607	4.524	1	**0.0334**	0.328	1	0.5670	8.436	1	**0.0037**

Fig. 3. Final biomass (g ash-free dry mass, AFDM) of stocked crustacean mesograzer species (A) *Cymadusa compta*, (B) *Gammarus mucronatus*, and (C) *Erichsonella attenuata*, and (D) all species in seagrass treatments *Ruppia maritima* (left panels) and *Zostera marina* (right panels). Scatter plots show total biomass per mesocosm vs. initial seagrass density, while adjacent bar plots give mean (±SE) across grass densities by trophic treatment. Solid lines show a significant main effect of density for all treatments combined. Other lines show statistically significant interactions between density and trophic treatments for treatments that had a significant relationship with density

depended on seagrass species identity and initial seagrass density (Fig. 6A, Table 5). In *Ruppia*, grazers reduced microalgae less when predators were present, whereas in *Zostera*, microalgal biomass was uniformly low in both treatments with stocked grazers (Fig. 6A). The relationship between microalgal biomass and initial seagrass density also differed by seagrass species and trophic level treatment (Fig. 6), driven most strongly by the relationships in *Zostera* with no stocked mesograzers ($y = 2.356 + -0.0343 + 0.867$, adjusted $R^2 = 0.568$) and in *Ruppia* with mesograzers only ($y = -2.1717 + -0.0511x + 1.419$, adjusted $R^2 = 0.513$) and mesograzers and predators ($y = 1.327 + -0.0861x + 2.277$, adjusted $R^2 = 0.542$).

When analyzed by species, the biomass of several abundant fouling invertebrates differed by initial seagrass and grazer density or trophic treatment (Fig. 7, Table 5). Only barnacles, *Balanus* spp., differed strongly between seagrass species, having higher biomass in *Zostera* than in *Ruppia* (Fig. 7A, Table 5). Mesograzers decreased the biomass of the solitary tunicate *Molgula manhattensis*, and this effect depended marginally on seagrass species identity and density, being stronger in *Zostera* than in *Ruppia* (Fig. 7D, Table 5). The only strong relationship between *M. manhattensis* and seagrass density occurred in *Ruppia* with predators ($y = 2.372 + -0.0189 + 0.450$, adjusted $R^2 = 0.601$). The biomasses of the other most

Table 3. Results from general linear mixed models of seagrass species and predator treatment effects on final abundance (g ash-free dry weight, AFDW) of amphipod and isopod crustaceans, including flow-through tank location as a random factor. Analysis excludes treatments without vegetation and to which grazers were not added. Biomass was estimated 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 *E. attenuata*, which did not require transformation. df_N: numerator degrees of freedom; df_D: denominator degrees of freedom. **Bold** indicates significance at p < 0.05

Factors	*Cymadusa compta*				*Gammarus mucronatus*				*Erichsonella attenuata*				All grazers			
	MS	df_N, df_D	F	p	MS	df_N, df_D	F	p	MS	df_N, df_D	F	p	MS	df_N, df_D	F	p
Seagrass species	2.765	1, 15.998	0.273	0.609	0.023	1, 15.997	0.701	0.415	0.010	1, 15.975	0.992	0.334	0.621	1, 15.998	0.343	0.566
Seagrass density	0.149	1, 15.998	0.211	0.652	0.040	1, 15.997	0.120	0.733	0.042	1, 15.975	9.900	**0.006**	0.001	1, 15.998	0.002	0.965
Trophic treatment	2.779	1, 15.998	0.105	0.750	2.775	1, 15.997	14.842	**0.001**	0.001	1, 15.975	0.468	0.504	0.194	1, 15.998	6.292	**0.023**
Species × Density	0.104	1, 15.998	0.148	0.706	0.211	1, 15.997	0.644	0.434	0.014	1, 15.975	3.398	0.084	0.002	1, 15.998	0.005	0.946
Treatment × Density	0.259	1, 15.998	0.369	0.552	2.699	1, 15.997	8.230	**0.011**	0.004	1, 15.975	1.067	0.317	2.632	1, 15.998	6.072	**0.025**
Species × Treatment	0.264	1, 15.998	2.718	0.119	0.041	1, 15.997	0.324	0.577	0.002	1, 15.975	0.007	0.936	0.010	1, 15.998	1.820	0.196
Species × Density × Treatment	1.657	1, 15.998	2.357	0.144	0.213	1, 15.997	0.649	0.432	0.000	1, 15.975	0.054	0.819	1.074	1, 15.998	2.476	0.135

Table 4. Results from permutational multivariate analysis of variance (PERMANOVA) model of seagrass species and predator treatment effects on abundance (g ash-free dry weight, AFDW) of all recruiting taxa in treatments with vegetation. Permutations were constrained by flow-through tank location. **Bold** indicates significance at p < 0.05

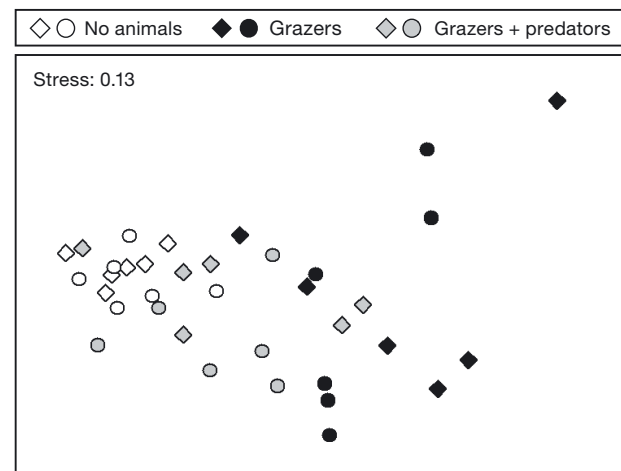| Factors	Recruited assemblage			
	MS	df	F	p
Seagrass species	0.298	1	2.190	0.064
Trophic treatment	1.108	2	8.132	**0.001**
Seagrass density	0.417	1	3.059	**0.011**
Species × Treatment	0.088	2	0.650	0.785
Species × Density	0.182	1	1.339	0.102
Treatment × Density	0.150	2	1.104	0.284
Species × Density × Treatment	0.193	2	1.416	0.112
Residuals	0.136	24		

Fig. 4. 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. *Ruppia maritima* (diamonds); *Zostera marina* (circles)

abundant recruiting fauna were related to initial seagrass and mesograzer density. *Haminoea soliatria* was negatively associated with initial seagrass density across treatments ($y = -0.0493 + -0.0153x + 0.756$, adjusted $R^2 = 0.238$), as was *Corophium* sp., though not as strongly ($y = -3.746 + 0.0200x + 1.615$, adjusted $R^2 = 0.0900$). Spiochaetopterid worms were only significantly related to initial seagrass density in *Zostera* ($y = -2.0171 + 0.00554x + 0.0817$, adjusted $R^2 = 0.795$; Fig. 7G, Table 5).
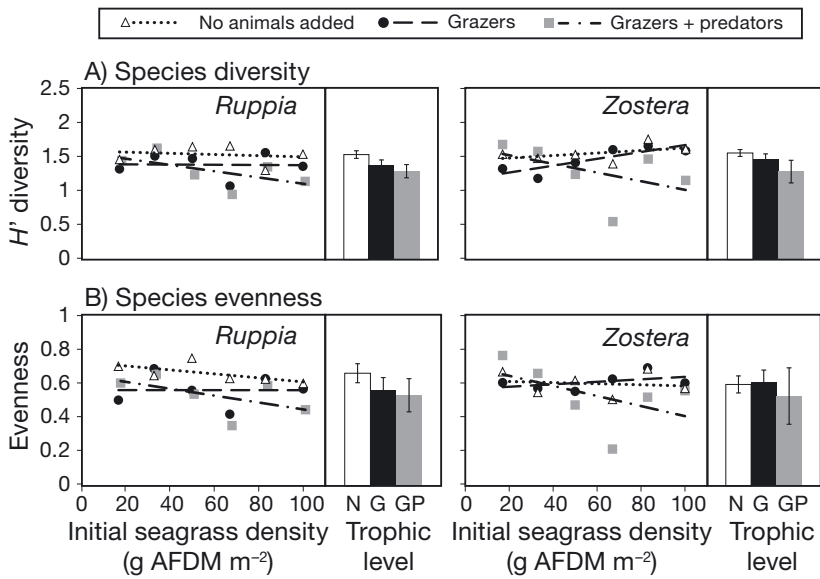
Fig. 5. Final Shannon-Wiener (H') diversity of invertebrates and algae recruiting to mesocosms. Bar plots give mean (±SE) across grass densities by trophic treatment while adjacent scatter plots show diversity of taxa per mesocosm vs. initial seagrass density, for seagrass treatments *Ruppia maritima* (left panels) and *Zostera marina* (right panels). Lines show statistically significant interactions between density and each trophic treatment
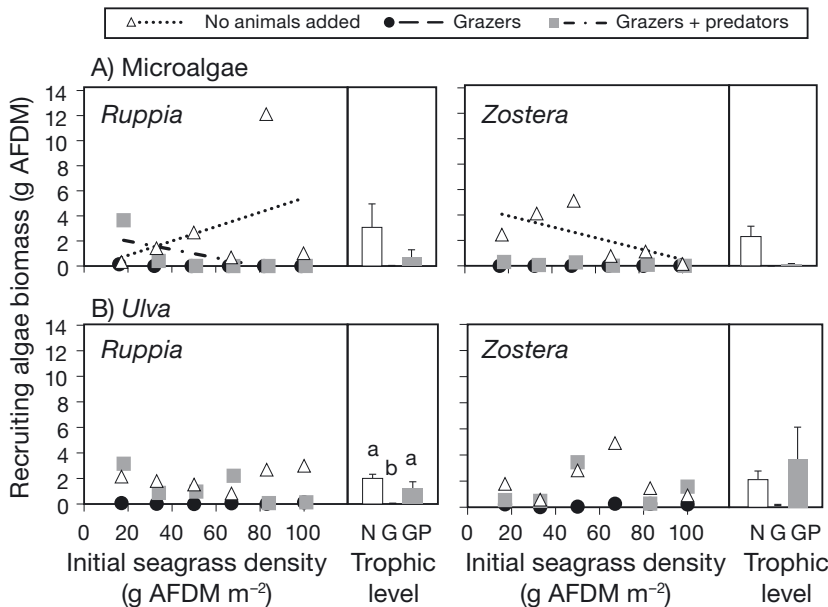

Fig. 6. Final biomass (g ash-free dry mass, AFDM) of algae recruiting to mesocosms. Shown in seagrass treatments *Ruppia maritima* (left panels) and *Zostera marina* (right panels). Scatter plots show total biomass per mesocosm vs. initial seagrass density, while adjacent bar plots give mean (±SE) across grass densities by trophic treatment. Letters above bars in (B) *Ruppia* show main effects of trophic level for *Ulva* sp. Different letters indicate significant differences between treatments at p < 0.05 based on Tukey's HSD tests. Lines show statistically significant interactions between density and each trophic treatment

DISCUSSION

We hypothesized that the 2 seagrass species *Ruppia* and *Zostera* would differ in their ability to mediate trophic interactions, leading to differences in the abundance of crustacean mesograzers and in the algae and fouling organisms that colonized our experimental mesocosms. We found that the total number of sampled mesograzers was lower when predators were present, but this effect was greater for *Ruppia* and depended on initial seagrass density (Fig. 2). The mesograzers differed in their susceptibility to predation (Fig. 2) in a manner consistent with morphological and behavioral differences between these species. The final biomass of mesograzers was largely dependent on initial density and predator presence (Fig. 3). The total biomass across all mesograzer species increased with greater initial seagrass and mesograzer density in predator treatments, but it decreased with initial density in grazer-only treatments. Grazing and predation had a much greater influence on overall community structure and diversity of the recruited fouling community than seagrass species identity, which only marginally affected composition (Table 4) and had no effect on diversity. However, the initial density of stocked seagrass and mesograzers did have an important influence on the fouling community. For seagrass epifaunal assemblages, it may be most important to consider the overall density and distribution of seagrass, rather than seagrass species identity, which seems to have a lesser effect at the mesocosm scale of our experiment. Our results suggest that while species-specific effects of seagrass and mesograzers are important for predator–prey interactions, seagrass density also influences trophic interactions and community structure. Thus, the overall abundance of any seagrass species present is likely to be a crucial factor in determining

Table 5. Results from linear mixed models of seagrass species and predator treatment effects on abundance (g ash-free dry weight, AFDW) of recruiting taxa in treatments with vegetation, including flow-through tank location as a random factor. Abundances were Box-Cox transformed to improve normality and homogeneity of variances. df_N: numerator degrees of freedom; df_D: denominator degrees of freedom. **Bold** indicates significance at $p < 0.05$

Factor	Algae		Sessile fauna		Motile fauna			Infauna	
	Microalgae	*Ulva* sp.	*Balanus* sp.	*Molgula manhattensis*	*Haminoea solitaria*	*Corophium* sp.	Nereid worms	Maldanidae worms	Spiochaetoptera worms
Seagrass species									
MS	1.371	3.325	1.139	0.245	0.178	0.905	4.856	12.243	0.111
df_N, df_D	1, 22.998	1, 22.982	1, 23.992	1, 22.987	1, 23.96	1, 15.999	1, 23.996	1, 22.146	1, 23.983
F	1.959	0.490	7.372	6.742	0.034	0.661	0.016	0.028	2.329
p	0.175	0.491	**0.012**	0.016	0.854	0.428	0.901	0.868	0.140
Seagrass density									
MS	33.941	0.245	0.176	0.856	4.849	10.253	0.139	0.200	0.288
df_N, df_D	1, 22.998	1, 22.644	1, 23.992	1, 22.71	1, 23.536	1, 15.999	1, 23.996	1, 23.493	1, 23.983
F	21.583	0.000	2.022	3.688	19.123	6.819	0.351	0.144	13.906
p	**0.0001**	0.995	0.168	0.067	**<0.001**	**0.019**	0.559	0.708	**0.001**
Trophic treatment									
MS	124.259	34.569	0.035	1.542	5.779	5.222	0.539	8.008	0.032
df_N, df_D	2, 22.998	2, 19.681	2, 23.992	2, 20.005	2, 20.706	1, 15.999	2, 23.996	2, 20.035	2, 23.983
F	18.154	11.251	0.628	3.015	2.706	2.333	2.349	1.200	0.114
p	**<0.0001**	**0.001**	0.542	0.072	0.090	0.146	0.117	0.322	0.893
Species × Density									
MS	0.803	1.951	0.138	0.550	0.020	2.472	1.347	2.181	0.166
df_N, df_D	1, 22.998	1, 22.875	1, 23.992	1, 22.904	1, 23.838	1, 15.999	1, 23.996	1, 22.969	1, 23.983
F	0.560	2.073	1.583	3.575	0.085	1.644	3.396	2.034	7.987
p	0.462	0.164	0.220	0.071	0.774	0.218	0.078	0.167	**0.009**
Species × Trophic treatment									
MS	4.295	0.340	0.052	0.601	0.088	0.801	0.291	4.285	0.007
df_N, df_D	2, 22.998	2, 20.898	2, 23.992	2, 21.133	2, 21.797	1, 15.999	2, 23.996	2, 22.151	2, 23.983
F	8.044	0.610	0.578	6.294	0.672	0.133	0.424	1.262	0.288
p	**0.002**	0.553	0.569	**0.007**	0.521	0.720	0.659	0.303	0.752
Trophic treatment × Density									
MS	14.681	2.581	0.040	0.367	0.328	0.942	0.539	0.266	0.014
df_N, df_D	2, 22.998	2, 20.116	2, 23.992	2, 20.41	2, 21.235	1, 15.999	2, 23.996	2, 21.129	2, 23.983
F	10.416	2.623	0.454	1.844	1.707	0.627	1.360	0.196	0.677
p	**0.001**	0.097	0.640	0.184	0.205	0.440	0.276	0.824	0.518
Species × Density × Trophic treatment									
MS	9.715	0.917	0.104	0.581	0.061	0.004	0.037	3.434	0.013
df_N, df_D	2, 22.998	2, 20.786	2, 23.992	2, 21.027	2, 21.678	1, 15.999	2, 23.996	2, 21.321	2, 23.983
F	6.239	0.976	1.190	3.408	0.335	0.003	0.094	2.333	0.623
p	**0.007**	0.394	0.321	**0.052**	0.719	0.960	0.910	0.121	0.545
Total final mesograzer biomass									
MS	1.429	1.162		1.116					
df_N, df_D	1, 22.998	1, 18.725		1, 19.107					
F	9.269	4.125		8.305					
p	**0.006**	**0.057**		**0.010**					

community processes if the relative abundances of seagrass species change.

We observed widespread senescence of seagrass in the last week of the experiment that had a particularly pronounced effect on *Ruppia* biomass. We did not observe similar senescence in the field, suggesting that this result was an artefact of the experimental conditions. Interestingly, our non-destructive sampling of crustacean mesograzers from the midpoint of the experiment, approximately 4 wk before noticeable seagrass senescence, did provide some evidence for differences in trophic interactions between the 2 seagrasses. We might have expected that the crustacean biomass results from the end of the experiment would be more likely to show an effect of seagrass species identity, as these data were col-
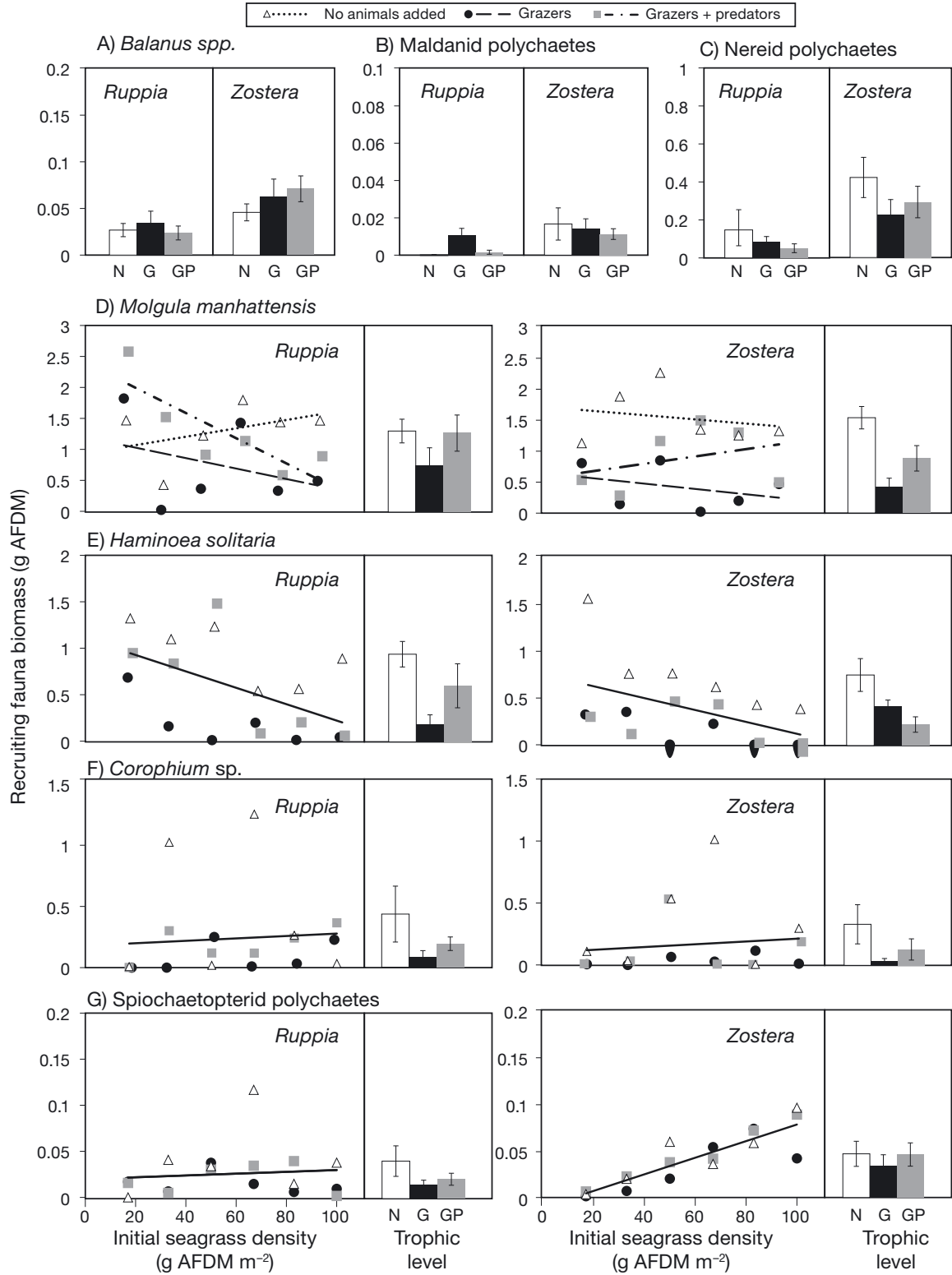
Fig. 7. Final biomasses (g ash-free dry mass, AFDM) of invertebrates recruiting to mesocosms, including (A) *Balanus* spp. (B) Maldanid polychaetes, (C) Nereid polychaetes, (D) *Molgula manhattensis*, (E) *Haminoea solitaria,* (F) *Corophium* sp. and (G) Spiochaetopterid polychaetes. Bar plots give mean (±SE) across grass densities by trophic treatment while adjacent scatter plots show total biomass of taxon per mesocosm vs. initial seagrass density, for seagrass treatments *Ruppia maritima* (left panel of each section) and *Zostera marina* (right panel of each section). Scatter plots are only shown for taxa that were significantly influenced by initial seagrass and grazer density treatments. Solid lines show significant main effect of density for all treatments combined. Other lines show statistically significant interactions between density and trophic treatment for treatments that had a significant relationship with density

lected after noticeable seagrass senescence had occurred, and there may have been greater differences between the 2 treatments in terms of seagrass structure available for mesograzers to evade predators or as habitat for recruited taxa. However, the final biomass data do not provide strong evidence for differences between seagrasses, and results from the end of the experiment may have been more influenced by initial seagrass and grazer densities, detrital seagrass, and density-dependent population processes at high mesograzer densities.

We expected that *Ruppia* might provide less refuge from predation than *Zostera* due to its smaller, thinner leaves and that this effect might differ between grazer species due to variation in their physical and behavioral characteristics. The greater predation effect across all mesograzer species observed in *Ruppia* at the experiment midpoint supports our general prediction that *Ruppia*'s thinner leaf structure might provide less refuge for mesograzers. However, these effects of seagrass species identity differed by mesograzer species and included interactive effects with predation and initial seagrass density. Our results suggest that seagrass species identity might have some effect on mesograzer composition but that this effect will depend on the context of seagrass and mesograzer density.

The differences in susceptibility to predation we observed between the mesograzer species at the experiment midpoint may be due to differences in their morphology and behavior. *Cymadusa compta* abundance was not significantly reduced by predation, and the isopod *Erichsonella attenuata* was actually more abundant in predator treatments than without predators, whereas *Gammarus mucronatus* was strongly reduced by predation. *C. compta* may have been protected by its behavior of building and inhabiting protective tubes, which provide refuge from predation (Nelson 1979). *E. attenuata* appears to be highly cryptic due to its narrow body form and sedentary behavior (A. Moore pers. obs.), potentially explaining the lack of predation effect on this species found here and previously (Douglass et al. 2007). Interestingly, this crypsis may suggest a mechanism for particularly high abundances of *E. attenuata* observed during late summer, when small predator abundance is at its highest (Douglass et al. 2010). These patterns align with results from a set of controlled predation trials using the same mesograzer species, in which *G. mucronatus* was the most susceptible to predation from pipefish and *E. attenuata* the least, with *Zostera* providing greater protection than *Ruppia* (A. Moore unpubl. data). The greater

abundance of *E. attenuata* in predator treatments may be due to competition with *G. mucronatus*, which was less abundant in this treatment. Previous work has suggested that these mesograzers compete for common resources (Duffy & Harvilicz 2001, Duffy et al. 2005), and it appears that *G. mucronatus* has the trade-off of being competitively dominant but more vulnerable to predation relative to the other species.

The pattern of predation and initial density effects on final estimated biomass of all stocked mesograzer species was driven by *G. mucronatus*, which had higher final biomass than the other mesograzers. That biomass increased with greater initial seagrass and grazer density in predator treatments, but decreased with initial density in grazer-only treatments suggests that density-dependent processes in this species, such as cannibalism or competition, apparently caused populations to crash when high densities were added initially. Final *C. compta* biomass was not significantly related to any treatment, and *E. attenuata* biomass was only positively related to initial density, indicating that predation has little effect on the final biomass of these species. These results are in contrast to the results from non-destructive sampling of mesograzers at the experiment midpoint. It may be that later in the experiment different processes were dominating in our model seagrass communities or that treatments converged with respect to mesograzers as many mesocosms became dominated by high *G. mucronatus* densities and detrital seagrass.

Grazing and predation had the strongest influence on overall community structure of fouling species, which is not surprising, given that crustacean mesograzers can have large effects on the abundance and composition of benthic algae and fouling organisms (Duffy & Hay 2000, Duffy & Harvilicz 2001, Hughes et al. 2004, Valentine & Duffy 2006). Mesograzers greatly affected the composition of fouling species, and grazing led to more variable assemblages without predator control (Fig. 4). Mesograzers reduced biomass of the macroalgae *Ulva* sp. in the absence of predators, and they reduced microalgal biomass depending on seagrass species identity and the initial density of seagrass and grazers (Fig. 6A), consistent with numerous previous studies demonstrating the importance of grazing effects in seagrass (Valentine & Duffy 2006). It is worth noting that the grass shrimp *Palaemonetes vulgaris* added in the predator treatments can also be a facultative grazer, so it is possible that the high levels of grazing observed for microalgae in predator treatments could have been influenced by the grass shrimp in addition to the mesograzers. Predation by mesograzers reduced the

biomass of the sessile tunicate *Molgula manhattensis* more strongly in *Zostera* than in *Ruppia,* and there was a marginally significant interaction showing contrasting effects of initial density between the 2 seagrasses (Fig. 7D). The effect of mesograzers on *M. manhattensis* is probably as a result of feeding on newly settled recruits (Duffy & Harvilicz 2001). For *M. manhattensis*, *Zostera* does not provide greater refuge from predation; instead, the wider leaf structure of this seagrass may enhance a grazer's ability to feed on the tunicates. It is also worth noting that the initial density of stocked seagrass and mesograzers had significant influence over the composition and diversity of recruiting taxa (Table 4, Figs. 4 & 5), highlighting the overarching importance of seagrass density on ecological processes in these systems. At the larger scale of natural systems, a number of other characteristics can influence faunal diversity and abundance, including seagrass density, patch size, flow dynamics, and sediment properties (Webster et al. 1998, Bowden et al. 2001), which may be more important than seagrass species identity.

Top-down effects of grazing appear important in many seagrass systems, because grazing of epiphytic algae on leaves can release seagrass from competition for light (Hughes et al. 2004, Valentine & Duffy 2006) and predators can influence the strength of this grazing control, even over 4 links in the food chain (Hughes et al. 2013). If the differences in grazer abundances and predation between the 2 seagrass species at the midpoint of the experiment represent significant ecological processes in the field, shifts in seagrass composition toward *Ruppia* dominance could contribute to changes in these ecosystems. For example, Micheli et al. (2008) found changes in faunal abundance in the field corresponding to changes in seagrass composition over time. Such changes could be significant since effects of grazing may differ depending on the composition of mesograzers (Duffy & Harvilicz 2001). In Chesapeake Bay seagrass beds, however, the interaction between top-down and bottom-up control appears complex. Field observational data generally show positive associations between predator and mesograzer abundances (Douglass et al. 2010 and references therein); however, field experiments show clear evidence of top-down control, and field exclusion of mesograzers leads to large microalgal blooms in Chesapeake seagrass beds (Douglass et al. 2007, Whalen et al. 2013, Reynolds et al. 2014). The nature of our experiment may have exaggerated cascading effects of predation and grazing, as the mesocosms are relatively closed systems 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). However, given that higher grazer diversity tends to enhance grazing effects in natural systems (Duffy et al. 2015), it is possible that our experimental conditions would underestimate grazing relative to the field, where mesograzer diversity is much higher (Douglass et al. 2010). Similarly, predator diversity can increase predation pressure on mesograzers (Douglass et al. 2008). Given the greater diversity of predators in natural systems, predation effects may be much stronger in the field. Conversely, predation on grazers by small predators may be reduced in the field by the higher trophic levels found in seagrass beds (Orth & Heck 1980) that were not represented in our experiment.

Our results suggest that *Ruppia* and *Zostera* may differentially influence the abundance of some grazers; however, support for this effect was modest and depended largely on seagrass density, suggesting that seagrass abundance may have a larger effect on trophic interactions than seagrass species identity. Similarly, a field manipulation of artificial *Ruppia* and *Zostera* vegetation demonstrated that infaunal colonization depended on complex interactions between seagrass species identity, density, and physical disturbance, such that loss of either seagrass would decrease faunal diversity in this system (Boström & Bonsdorff 2000). While some marine foundation species have distinct roles in providing habitat (e.g. Marzinelli et al. 2014), effects of species identity on associated fauna may also depend on the abundance of habitat providers (Maggi et al. 2009). Thus multiple aspects of structural complexity in seagrass communities should be considered in addition to species composition.

Although the 2 seagrass species showed only modest functional differences in regards to trophic support in our experiment, they could have very different effects on other ecosystem processes, such as sediment stabilization and water flow due to variation in their canopy structure (Fonseca & Fisher 1986). Because *Zostera* has a taller canopy than *Ruppia* during most of the year and can grow at a greater range of depths (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 or providing greater coastal protection through wave attenuation. Further tests of the multiple functions of these seagrass species at a range of densities are needed to determine their broader effects on coastal ecosystems.

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