



Predator density, not structure, influences intraspecific competition in the mud crab *Dyspanopeus sayi*

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ABSTRACT: Structured habitats can offer prey refuge by reducing the encounter rates between predators and prey. However, structured habitats can also reduce predator–predator encounters, thereby dampening intraspecific interactions and increasing overall prey consumption. In this study, we tested whether intraspecific competition among Sayi mud crabs *Dyspanopeus sayi* foraging on mussel *Mytilus edulis* prey was modified by the density of mimicked eelgrass *Zostera marina* shoots. Predation was measured in 3 predator densities (1, 3, or 6 predators) and 1 of 5 levels of shoot density. We found no impact of *Z. marina* on intraspecific competition, regardless of predator density. Intraspecific competition was weak; per capita crab consumption decreased as predator density increased and became significantly reduced when predator density increased from 1 to 6. However, there was no evidence of non-additive predator density effects when predator abundance doubled from 3 to 6 predators. Our results also indicate that eelgrass structure may not offer the sessile prey *M. edulis* refuge when one or more *D. sayi* predators are present. Further exploration is needed to understand whether the lack of a structure effect is due to our use of sessile rather than mobile prey as used in other studies. Predator density and not structural density influenced intraspecific competition among *D. sayi* predators when they were foraging for *M. edulis* in mimicked *Z. marina* shoots.

KEY WORDS: Habitat complexity · Predator density · Mutual interference · *Zostera marina* · *Dyspanopeus sayi*

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1. INTRODUCTION

Habitat structure can directly alter how a predator encounters its prey (Main 1987, Ryer 1988, Hovel et al. 2016) and competitors (Finke & Denno 2002, Griffen & Byers 2006). Habitat structure often acts as a prey refuge, reducing the encounter and capture rate between predators and prey (Nelson 1979, Heck & Orth 1980, Crowder & Cooper 1982) as well as reducing predator movement (Ryer et al. 2004, Hovel et al. 2016) and visually obstructing the prey's location (Main 1987, Ryer 1988). Habitat structure also reduces the encounter rate between predators (both conspecific and heterospecific), altering how preda-

tors forage and interact with their shared environment (Finke & Denno 2002, Grabowski & Powers 2004, Griffen & Byers 2006, Hughes & Grabowski 2006, Janssen et al. 2007). Thus, habitat directly influences how a predator competes with members of its own species and the broader ecological network existing within a given community.

In addition to reducing prey populations, a predator can interfere with the ability of another predator to consume a targeted prey through interference competition (i.e. Clark et al. 1999, Smallegange et al. 2007). Interference often occurs through antagonistic interactions, which range in severity from avoidance to lethal physical contact. Non- or sub-lethal ener-

getic costs from antagonistic interactions include increased foraging and handling time (Clark et al. 1999, Griffen & Delaney 2007, Smallegange et al. 2007), decreased foraging efficiency (Crowley et al. 1987), and selection of suboptimal prey (Smallegange & van der Meer 2009, Griffen et al. 2011, Peterson et al. 2014). Long-term effects of these energetic costs can lead to negative impacts on growth and reproduction (Griffen et al. 2011). Extreme forms of interference competition directly reduce predator populations by intraguild predation (Finke & Denno 2002) or cannibalism (Mansour & Lipcius 1991, Moksnes et al. 1997, Wildy et al. 2001, Rudolf 2007). Further, studies comparing and contrasting conspecific and heterospecific predators have demonstrated how conspecific interference competition is often greater (Griffen & Williamson 2008, de Villemereuil & López-Sepulcre 2011, Peterson et al. 2014).

Per capita consumption tends to decline as conspecific predator density increases, though often in a non-linear or non-additive relationship (Mansour & Lipcius 1991, Abrams 1993, Mistri 2003, Griffen & Byers 2009). Body damage, prey search time, handling time, and time spent in antagonistic interactions often increase with conspecific predator abundance (Mansour & Lipcius 1991, Smallegange & van der Meer 2007, Griffen & Williamson 2008) and may contribute to the decreasing per capita consumption rates often detected. At high predator densities, interference competition can reduce predator capture rates, stabilizing predator–prey population dynamics (DeAngelis et al. 1975, Sih 1979, Anders Nilsson 2001). However, because these antagonistic interactions can be dampened by the presence of structure (Corkum & Cronin 2004, Grabowski & Powers 2004, Finke & Denno 2006), increases in structure—up to the level of saturation—may lead to no capture rate decreases as predator densities increase.

Habitats formed by eelgrass *Zostera marina* are well studied (Heck & Orth 2006, Hovel et al. 2021, Murphy et al. 2021) and provide vital ecosystem services for coastal communities (Heck et al. 2003, Mtwana Nordlund et al. 2016, Orth et al. 2020). Habitat studies with *Z. marina* consistently show that prey survival increases in *Z. marina* compared to unstructured habitats (Heck et al. 2003, Lannin & Hovel 2011, Carroll et al. 2015). We used *Z. marina* as a study system to refine our understanding of how structure informs intraspecific competition. We tested how submerged aquatic vegetation influences intraspecific competition in the crustacean predator *Dyspanopeus sayi* while foraging for the blue mussel *Mytilus edulis*. We compared collective and per

capita consumption rates across increasing densities of *D. sayi* and *Z. marina* to answer the following questions: (1) How do shoot and predator density affect overall mussel mortality? (2) How is intraspecific competition affected by increased shoot and predator density? We expected shoot density to impede the foraging of a single predator, supporting previously documented habitat complexity relationships (Nelson 1979, Heck & Orth 1980, Crowder & Cooper 1982). Yet when the number of predators increases concurrently with the complexity of the habitat, we expected structure to no longer enhance prey survival by reducing intraspecific competition among conspecifics. These relationships were statistically evaluated by examining (1) the combined effects of shoot density and predator density on overall mussel mortality and (2) potential intraspecific competition effects through per capita consumption rates. To further explore intraspecific competition, we compared the number of mussels eaten in the highest crab density to a null model that assumed multiplicative effects across shoot density treatments.

2. MATERIALS AND METHODS

2.1. Experimental design

To test the effect of *Zostera marina* structure on intraspecific interactions between *Dyspanopeus sayi* individuals, we used a factorial (3×5) randomized experimental design. There were 3 levels of *D. sayi* abundance and 5 levels of shoot density structure treatments. Each abundance \times structure combination was set up in a separate 95 l mesocosm (bottom diameter: 0.54 m; bottom area: 0.229 m²). We chose the levels of predator and structure densities to reflect densities found during field surveys conducted in Shinnecock Bay, New York (Table S1 in the Supplement at www.int-res.com/articles/suppl/m709p045_supp.pdf). The 3 *D. sayi* abundance levels were 1, 3, and 6 crabs mesocosm⁻¹, equating to 4.4, 13.1, and 26.2 ind. m⁻². For reference, *in situ* mud crab densities averaged 21 ± 9 m⁻² (mean \pm SD). Artificial *Z. marina* treatment levels corresponded to 0, 100, 200, 800, and 1200 eelgrass shoots m⁻² compared to an *in situ* density of 447 ± 223 shoots m⁻². The full experiment (15 combinations) was replicated 10 times over a 5 wk period (Jul to Aug 2014) at Stony Brook University's Southampton Marine Station, Southampton, NY (40° 53.13' N, 72° 26.53' W).

D. sayi are small, intermediate predators (carapace width maximum: ~25 mm) ubiquitously found within

Z. marina, *Crepidula fornicata*, and *Mytilus edulis* mixed shell hash beds in our study system in Shinnecock Bay, NY. We have observed them engaging in the following antagonistic interactions in the field and holding tanks: attacks that can result in body damage, kleptoparasitism, and cannibalism. Crabs were collected from *C. fornicata* and *M. edulis* mixed shell hash beds in Shinnecock Bay (40° 51.61' N, 72° 25.94' W) and held for no more than 2 d prior to being starved for 24 h and used in experimental runs. We used male *D. sayi* individuals with at least 7 legs that had both claws intact and were 14–16 mm carapace width. We excluded from the analysis any replicate in which a crab molted or died during the experimental run. This reduced the replicate numbers in some of the treatment groups. Replicate numbers thus ranged from 7 to 10 in each treatment level combination (139 out of 150 possible replicates).

We mimicked structure of *Z. marina* using artificial seagrass units (ASUs). ASUs are widely used to mimic seagrass habitat (Bologna & Heck 1999, Canon & Heck. 2009, Carroll et al. 2012) to overcome the logistical difficulties of keeping seagrass alive in mesocosms and standardizing structure metrics across replicates. We constructed each ASU by tying artificial eelgrass shoots to a circular Vexar® plastic mesh mat (10 mm aperture). To mimic a *Z. marina* shoot with 4 leaves, each artificial eelgrass shoot consisted of 4 green curling ribbons (0.5 cm wide × 25 cm long) tied in a bundle to the mesh. The artificial shoots were evenly spaced at a density equivalent to the structure treatment. The mat was buried under 7.6 cm of sand with the artificial leaves floating upright in the water column.

M. edulis was selected as the prey item, as it is a common prey resource in Shinnecock Bay *Z. marina* beds (Table S1). New recruits (<40 mm shell height [SH]) can form dense mats in the seagrass canopy; mussels larger than 30 mm SH often form clumps at the base of eelgrass shoots, though not as abundantly. Mussel clumps with mixed sizes of mussels can also form clumps between eelgrass shoots. *D. sayi* have been seen climbing within the seagrass canopy, consuming *M. edulis* as well as foraging for *M. edulis* on the sandy bottom. We added 100 *M. edulis* (8–12 mm SH) to each mesocosm 1 to 4 h before the addition of *D. sayi*. *M. edulis* were not removed until the conclusion of the 36 h experimental period. Preliminary experiments indicated that 100 mussels were never completely consumed by 6 predators in a sandy bottom (0 shoots treatment). For comparison, field densities of *M. edulis* (size class: <40 mm) in *Z. marina* beds averaged $3365 \pm$

2684 m^{-2} . Taking into consideration the size of the experimental mesocosm, this equates to ~840 blue mussels per 0.25 m^2 . Therefore, our saturating density of 17 mussels per mud crab (100 mussels per 6 mud crabs) is well below reported field observations (840 mussels per 21 mud crabs = 40 mussels per mud crab). At the end of an experimental run, ASUs were thoroughly checked for mussel attachment, and the sand was sieved through a 3 mm aperture sieve to recover all live mussels.

In addition to the 15 treatment level combinations, we also tested a non-predator control. A 1200 shoots m^{-2} ASU was used in the non-predator control to determine natural mussel mortality and the processor's ability to recover shellfish. Mussel mortality in controls was $0.6 \pm 0.97 \text{ ind. mesocosm}^{-1}$ and we had $96.3 \pm 0.04\%$ recovery. Therefore, we assumed any mussel not recovered was consumed by a *D. sayi* predator.

The study was conducted in an outdoor flow-through mesocosm system (flow rate: $5.0 \pm 1.4 \text{ l min}^{-1}$). Thus, mesocosm environmental conditions followed ambient conditions (temperature: 21–28°C; salinity: 26–31 PSU). To ensure the plumbing system did not alter water temperature among mesocosm tubs during an experimental run, we placed continuous HoBo® data loggers in the mesocosms located at either end of the 2 plumbing lines ($n = 4$). The temperature variation within each experimental run was small. The average maximum difference in temperature across all 4 mesocosms at any given point was $1.6 \pm 2^\circ\text{C}$.

2.2. Data analysis

We conducted all statistical tests using R statistical software version 4.2.2 (R Core Team 2022) in RStudio version 2022.07.0.548 (RStudio Team 2022). Of the 139 viable replicates, we removed one replicate from the single crab at 1200 shoots m^{-2} treatment from all analyses as an outlier. We believe this was either a counting or recording error. The recorded mussel consumption in this replicate was 63 mussels, which is an unrealistic rate of consumption. This value was almost 4 times greater than the mean number of mussels eaten by a single crab (16.2 ± 1.79) and 19 more mussels consumed than the next closest data point.

The effect of predator abundance and shoot density on overall mussel mortality was evaluated by examining the total number of mussels consumed in a given treatment. We evaluated the effects of crab abundance on intraspecific competition by looking at per capita consumption rates. Because temperature

affects feeding rates (Newell & Branch 1980, Whetstone & Eversole 1981), we treated experimental run as a random variable in the statistical models to account for temperature differences across the experimental runs. In both cases, we fitted a 2-way linear mixed model (LMM) using the R package 'lme4' (Bates et al. 2015) with restricted maximum likelihood estimation. We evaluated the LMM diagnostics by visually examining the residuals (Logan 2010); statistical significance was set at $\alpha = 0.05$. To remove LMM residual structure, per capita consumption rates were square-root transformed.

We evaluated the main effects of crab abundance and shoot density and their interaction using a type II Wald chi-squared test in the 'car' package (Fox & Weisberg 2019), which accounts for unequal sample sizes. A significant interaction would provide evidence that structure alters intraspecific competition among *D. sayi* predators. If an interaction was significant, pairwise post hoc *t*-tests were performed within the levels of a factor while holding the other factor levels constant. Otherwise, main effect groups were evaluated across a level. Multiple comparisons were corrected by the Tukey method in the 'emmeans' package (Lenth 2022).

We also evaluated the effect *Z. marina* shoot density has on intraspecific competition by comparing the collective feeding rate of the 6-predator treatment against a null model that assumes no change in feeding rates when the predator density doubles. The null model was calculated by modifying the multiplicative risk model (Eq. 1) that has typically been used to calculate multiple predator effects between 2 species (Soluk & Collins 1988, Soluk 1993, Sih et al. 1998):

$$P_{e_{s1+s2}} = P_{s1} + P_{s2} - (P_{s1} + P_{s2}) \quad (1)$$

where P_{s1} and P_{s2} are the proportions of prey consumed by species 1 and 2 in isolation and $P_{e_{s1+s2}}$ is the estimated proportion of prey consumed if species 1 and 2 have multiplicative predation effects. The equation also accounts for the number of prey removed by the other species, preventing an estimate greater than 100% of prey being consumed.

The multiplicative risk model was modified to calculate the estimated proportion of prey consumed for the predator treatment with 6 crabs ($P_{e_{c6}}$, assuming multiplicative predation effects by using the proportion of prey consumed when 3 crabs were present P_{C3j} ; Eq. 2):

$$P_{e_{c6}} = 2(P_{C3}) - P_{C3}^2 \quad (2)$$

We used Eq. (2) to calculate the estimated consumption for 6 crabs at each shoot density level for

each experimental run. If the conspecific predator effects are multiplicative, then the observed consumption would not be different from the null model. To test this assumption, we built a 2-way LMM with the null model and observed consumption rates treated as levels of one factor and shoot density treated as a second factor (null or observed \times shoot density). We evaluated the main and interactive effects as well as post hoc comparisons using the same procedure as the LMMs described above.

3. RESULTS

3.1. Evaluating effects on overall mussel mortality

There was a significant interaction between predator density and shoot density on the number of *Mytilus edulis* consumed ($p = 0.045$; Fig. 1a-c, Fig. S1a, Table S2). However, shoot density did not alter feeding rates. Within crab density treatments, pairwise comparisons among shoot density treatments were not significantly different from one another (for all pairwise comparisons, $p > 0.068$; Table S3). Conversely, all pairwise comparisons among predator density treatments within each level of shoot density were significantly different (for all pairwise comparisons, $p < 0.03$). The size of the difference among predator density treatments depended on the shoot density treatment, though no clear pattern emerged based on shoot density. Thus, the significant interaction was likely driven by the different effect size magnitudes between crab density treatments.

Consumption approximately doubled when crab density increased from 1 to 3 individuals and approximately quadrupled when increased from 1 to 6 individuals. Results indicated there was a positive predator density effect on collective feeding rates, which was unaffected by *Zostera marina* shoot density.

3.2. Evaluating intraspecific competition

3.2.1. Per capita consumption analysis

There was no interaction detected between shoot and crab density on per capita consumption rates ($p = 0.34$; Fig. 1d-f, Fig. S1b, Table S4). Similar to collective feeding rates, there was no main effect of shoot density on feeding rates ($p = 0.82$), indicating that structure did not alter competition among predators. There was a weak effect of the number of crabs present in a mesocosm ($p =$

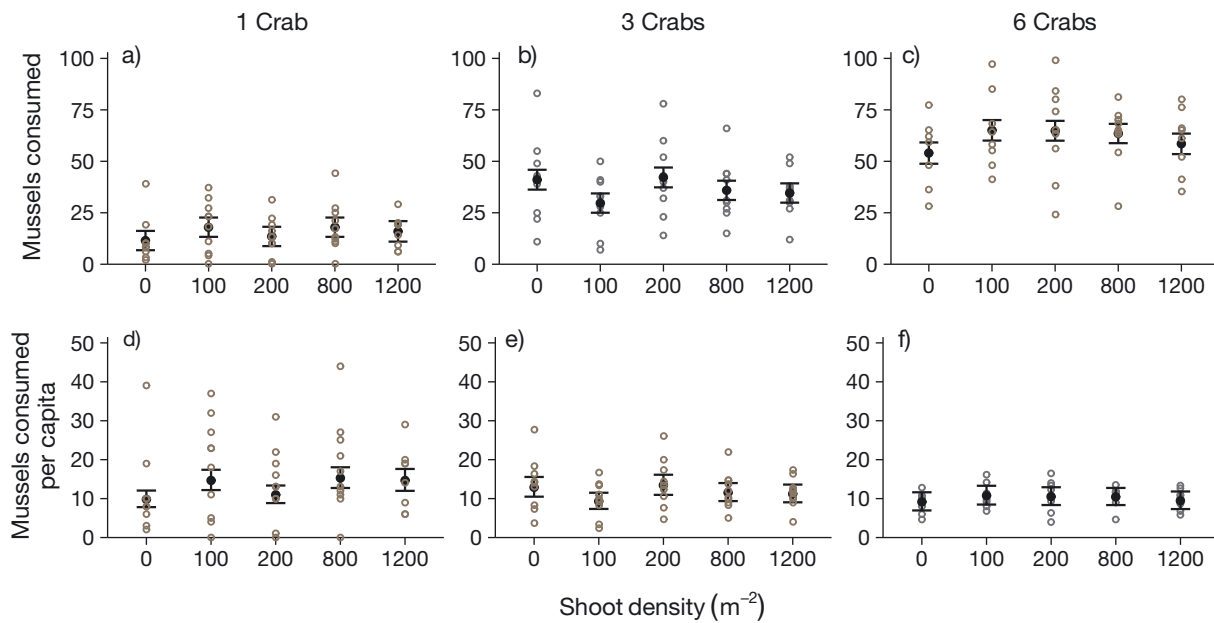


Fig. 1. (a,b,c) Total and (d,e,f) per capita number of mussels *Mytilus edulis* consumed by mud crabs *Dyspanopeus sayi* across increasing mimicked eelgrass *Zostera marina* shoot density treatments when predator density was 1 crab (a,d), 3 crabs (b,e), or 6 crabs (c,f) per mesocosm. Shoot density increased from 0 to 1200 shoots m^{-2} . Black circles: least square means estimated from the linear mixed model (LMM); error bars: ± 1 SE estimated from the LMM; grey open circles: raw data values

0.056); the per capita consumption rate was significantly lower when 6 predators were present as opposed to one ($p = 0.046$; Fig. 2, Table S5). Even though there was no significant difference in per

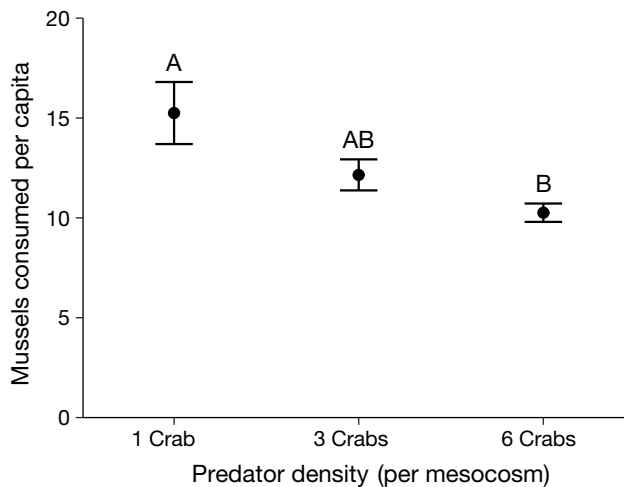


Fig. 2. Mean (± 1 SE) number of mussels *Mytilus edulis* consumed per capita by *Dyspanopeus sayi* across increasing predator abundance. Values were grouped by crab density because the interaction and eelgrass *Zostera marina* shoot density did not affect consumption rates (type II Wald chi-squared test, $p > 0.05$). Capital letters represent significantly different groups; the 6-crab treatment had significantly lower per capita consumption than the single-crab treatment (Tukey method, $p = 0.046$)

capita consumption rates among the 2 remaining pairwise comparisons ($p > 0.37$), there was a general decline in per capita feeding rates as predator density increased. A single *Dyspanopeus sayi* individual consumed 22% more available prey by itself than when in the presence of additional predators. Further, claw and limb damage were detected in a portion of the 3 and 6 predator treatment replicates (Table S6). Therefore, even though intraspecific competition occurring among predators became detectable at the 6 predator density treatment, there was evidence of intraspecific competition occurring at the 3 and 6 predator densities.

3.2.2. Null model analysis

A weak interaction was detected ($p = 0.059$; Fig. 3, Table S7) between the null model comparison of observed feeding rates and shoot density. The observed consumption rate for 6 predators was not different from the null model at all shoot densities ($p > 0.23$; Table S8) except at the 100 shoots m^{-2} density treatment ($p = 0.004$). It is unlikely that the observed proportion of mussels consumed at this density treatment (0.16 ± 0.008 values higher than the null model's proportion of mussels consumed) was due to a multiplicative effect. The post hoc t -test comparing

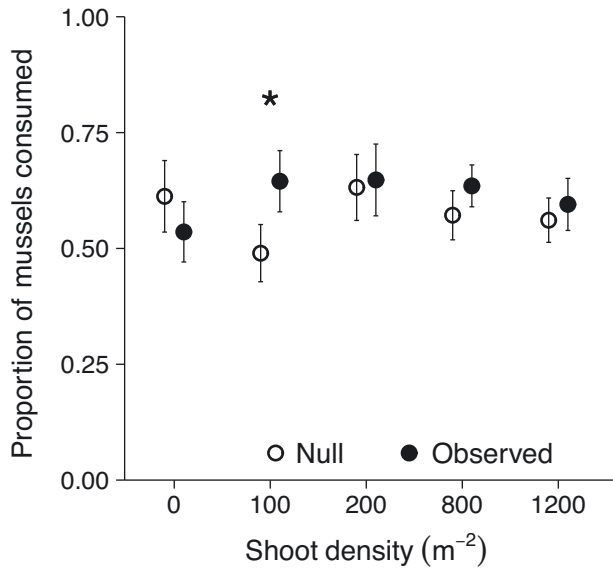


Fig. 3. Comparing mean (± 1 SE) observed (filled circles) consumption rates for 6 *Dyspanopeus sayi* predators against a null model (open circles) to test for multiplicative predator effects. The null model was modified from the multiplicative risk model (Eq. 2; Soluk & Collins 1988, Soluk 1993, Sih et al. 1998). There was a weak interactive effect (type II Wald chi-squared test, $p = 0.059$) of eelgrass *Zostera marina* shoot density on the null/observed consumption rate driven by a significantly higher observed mussel *Mytilus edulis* consumption rate compared to the null mussel consumption rate at the 100 shoots m^{-2} density treatment (Tukey method, $p = 0.004$, marked by an asterisk). There were no differences between null and observed consumption rates at the other shoot density treatments

the per capita consumption rate between 3 and 6 predators at the 100 shoots m^{-2} density treatment was not significantly different ($t_{114} = -0.56$, $p = 0.84$). Further, even though shoot density did not significantly affect the collective consumption rates with 3 or 6 predators (Fig. 1), the 3-crab treatment uniquely had a lower consumption rate at the 100 shoots m^{-2} density treatment compared to the other treatments. This is likely due to random chance and small sample size ($n = 7-10$ treatment replicates) and not evidence of interference competition changing in the 100 shoots m^{-2} density treatment.

Even though intraspecific competition was likely occurring among predators (Fig. 2), consumption rates were not statistically different between the observed consumption rate for 6 predators and the null model ($p = 0.080$). There was also no shoot density main effect ($p = 0.32$). Thus, predator density doubling from 3 to 6 crabs did not produce non-additive or emergent effects on top-down control, regardless of shoot density. Instead, predator density doubling produced multiplicative effects, suggesting

competitive interactions do not increase in intensity regardless of structure presence when predators reach densities beyond 3.

4. DISCUSSION

Results indicate that shoot density had no effect on *Dyspanopeus sayi* foraging on *Mytilus edulis* regardless of predator density. There is evidence that intraspecific competition was occurring among *D. sayi* individuals. However, the effect of predator density doubling from 3 to 6 crabs was multiplicative, indicating that intraspecific competition effects on top-down control did not change with predator density increasing past 3 individuals (or 13.1 ind. m^{-2}). Intraspecific competition among *D. sayi* individuals is likely related to how many individuals a single *D. sayi* can interact with at one time. Thus, as soon as the minimum predator density was reached, intraspecific competition was likely saturated and therefore did not change once more predators were added.

4.1. Evaluating structure and predator density effects

A lack of a statistical effect for the shoot density treatments does not necessarily indicate that there was no effect of *Zostera marina*, since the statistical tests may not have had enough power to detect a difference between treatment levels (Cohen 1988). A power analysis incorporating the sample size and effect size estimated by the LMM on the total *M. edulis* consumption rates suggested the statistical power of the LMM to detect a shoot density main effect was less than 0.5. Given the difficulty of conducting an experiment with 30 mesocosms in one experimental run, having a higher replication was not feasible. Further, this experiment had approximately 10 replicates per treatment; this number is either above or close to the replication number of treatments in other large-scale mesocosm crab experiments (Eggleston 1990, Mansour & Lipcius 1991, Toscano & Griffen 2013). Additional experiments confirmed that increases in mimicked *Z. marina* shoot density would not change feeding behavior (R. E. Kulp unpubl. data). Rather, eelgrass structure does not inhibit top-down control of *M. edulis* in an outdoor, flow-through mesocosm setting.

In contrast to this study, *D. sayi* and similar decapod species were shown to be negatively impacted

by *Z. marina* presence when foraging for prey other than *M. edulis* (Moksnes et al. 1998, Wong 2013, Carroll et al. 2015). One explanation for the difference in results between the finding of this study and others (Moksnes et al. 1998, Wong 2013, Carroll et al. 2015) is that *M. edulis* prey defenses may not have been enhanced by shoot density under the mesocosm conditions. The *M. edulis* prey used in this study, while capable of detaching their byssal threads and changing their position (Lee et al. 1990), are typically unable to physically escape predation after an encounter occurs (exception see Petraitis 1987). *M. edulis* are generally sessile and rely on passive defenses such as shell thickness, orientation, byssal attachment, and clumping to deter predation (Elner 1978, Bertness & Grosholz 1985, Robles et al. 1990, Smith & Jennings 2000). Passive defense may explain the difference in response reported by Carroll et al. (2015) in the same system; bay scallops *Argopectin irradians* are mobile and can actively escape encroaching predators. Further, *D. sayi* are likely able to cover the surface area of the mesocosm before the end of the experiment even when impeded by mimicked eelgrass shoots. This leads to a new hypothesis that the limiting factor of a successful capture may be in the steps that occur after *M. edulis* is encountered. Two of these steps include (1) the likelihood of a successful attack by isolating *M. edulis* from its attachment location and (2) the handling time required to open the shell to access tissue after the prey can be effectively manipulated by the chelae. These 2 steps could make prey rejection an important component of the attack rate. Predators foraging for prey similar to *M. edulis* with passive prey defenses may choose not to complete an attack even though they successfully encountered the prey.

Studies have found that structure amplifies the passive prey features in other shellfish species. For instance, *A. irradians* benefits from attaching to shoots above the sediment within the seagrass canopy (Pohle et al. 1991, Ambrose & Irlandi 1992) and the semi-faunal mussel *Modiolus americanus* benefits from attaching to the rhizome (Peterson & Heck 2001). During field surveys performed in Shinnecock Bay, we observed mussel spat in dense mats attached to eelgrass beds in the canopy (Table S1). In addition to juvenile mussels, adult mussels (>40 mm SH) were found in clumps at the base of eelgrass shoots, resting on the sediment surface. A shortcoming of this experiment is that *M. edulis* mussels did not interact with the eelgrass in the same way as in the field. While there were occasions at the end of the experiment where *M. edulis* had byssally attached to mim-

icked shoots, the majority were found in various sized clumps between shoots on the sediment surface. This was similar in the no-predator controls, which typically had larger clumps of mussels than the rest of the treatments. While *M. edulis* can be found in clumps between seagrass shoots in the field, we did not fully maximize the attachment potential of *M. edulis* over the course of these mesocosm experiments, thereby inhibiting any detectable habitat refuge. Regardless, our results do indicate that the presence of artificial *Z. marina* did not impede *D. sayi*'s ability to encounter and capture *M. edulis*, nor was it enough to lower consumption rate. Additional studies must quantify how *M. edulis* uses *Z. marina* in order to determine whether *M. edulis* can benefit from *Z. marina* either experimentally, *in situ*, or both.

4.2. Evaluating intraspecific competition

Predators, particularly decapod predators, that engage in antagonistic interactions are prone to prolonged handling time, kleptoparasitism, bodily damage, and decreased foraging time (Mansour & Lipcius 1991, Smallegange et al. 2006, Griffen & Delaney 2007, Griffen & Williamson 2008). Increases in predator density coincide with increased time in aggressive interactions (Mansour & Lipcius 1991, Clark et al. 1999, Smallegange et al. 2006, Griffen & Delaney 2007, Griffen & Williamson 2008). Mistri (2004) noted that *D. sayi* engaged in high amounts of antagonistic behavior when encountering a conspecific. This directly translated to decreases in prey mortality. Although we do not have visual confirmation like Mistri (2004), per capita consumption significantly decreased with increased predator density in our mesocosm study (Fig. 2).

In contrast to the other decapod predator density studies (Mansour & Lipcius 1991, Abrams 1993, Mistri 2003, Griffen & Byers 2009), we did not detect multiplicative effects from doubling predator density from 3 to 6 crabs (Fig. 3). This may suggest that antagonistic competitive interactions do not change with predator additions after a 3-predator density threshold. Antagonistic competitive interactions among conspecifics (i.e. mutual interference) may stabilize predator-prey relationships by reducing top-down control (DeAngelis et al. 1975, Sih 1979, Anders Nilsson 2001). If mutual interference remains constant—irrespective of predator density—and does not alter top-down control, then additional predators could destabilize predator-prey interactions. However, because *D. sayi* are intermediate

predators, there are additional ecological features that could modulate this effect for *D. sayi*, such as indirect predator effects (Schmitz et al. 2008) by predators in trophic levels higher than *D. sayi*.

While there are a variety of mechanisms that regulate prey populations, prey that cannot utilize habitat structure may become disproportionately impacted in systems where predators can reach saturation density. Therefore, the magnitude of mutual interference becomes density-independent. We have observed late-spring *M. edulis* sets in Shinnecock Bay *Z. marina* beds being ~90% consumed by mid-summer (evidenced by broken shell fragments) when newly recruited mussels were <25 mm in SH. While *D. sayi* are just one of many *M. edulis* predators and are intermediate predators themselves, perhaps this observation demonstrates an example of how structure and competition among predators do not prevent local large population declines.

5. CONCLUSIONS

We found that artificial *Zostera marina* did not improve the survival of *Mytilus edulis* faced with predation by *Dyspanopeus sayi*. This result differs from previous habitat studies, where both simulated and natural meadows provide prey refuge from prolific marine predators (Nelson 1979, Heck & Orth 1980, Crowder & Cooper 1982). This may be due to a different predator–prey model system used in this study compared to others (i.e. a mobile predator and semi-sessile bivalve prey). Further, even though per capita consumption declined with predator density increases, our results indicate that the intraspecific competition among 6 predators was a multiplicative process. This suggests that competitive interactions among *D. sayi* did not change when predator density increased from 3 to 6 predators. Future behavioral studies are needed to determine whether mutual interference changes when predator density increases and how habitat type and a prey's antipredator strategy alter mutual interference.

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