Investigating the effect of habitat type on foraging efficiency

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Investigating the effect of habitat type on foraging efficiency

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Benthic predators forage in multiple habitats, each of which can differ in its structure density. Few studies have directly compared foraging across habitat type, and even fewer studies have modified habitat density in a comparable fashion across different habitat types. The focus of this dissertation was to evaluate the effect habitat structure and composition has on the efficiency with which predators find and consume their prey. Two different habitat types, a soft-vegetated and hard-calcified, were compared to determine whether structure density and habitat type were important in changing the consumption rate on the bivalve prey, *Mytilus edulis*. I found that the mesopredator decapod *Dyspanopeus sayi*’s foraging efficiency relates not only to the structure density in its habitat, but also the type of habitat it forages in. Specifically, the soft-vegetated eelgrass (*Zostera marina*) habitat, regardless of density, had no effect on foraging efficiency. In comparison, the hard-bottomed slipper snail (*Crepidula fornicata*) shell hash habitat strongly inhibited predator foraging once a minimum habitat density was reached. I also found that this habitat-linked change in attack rate was a species-specific effect. A different
decapod predator, *Callinectes sapidus*, was not affected by the two tested habitat types regardless of predator size. Considering *D. sayi* can be found in high densities in *Z. marina* and *C. fornicata* environments, I also wanted to examine the effect of structure type on *D. sayi*’s intraspecific competition. Eelgrass did not alleviate intraspecific competition among *D. sayi* individuals, whereas *C. fornicata*’s effect on competition was dependent on predator and prey density. When prey was limiting, increasing predator density reduced the structural benefit of *C. fornicata* on *M. edulis* prey survival. Conversely, when prey was saturated, structural effects could not be overcome by increases in predator density. My dissertation brings an alternative and unique perspective in how habitat type and structure affect predator-prey relations that could be tested in many other ecological settings.
Dedication Page

I would like to dedicate this dissertation to not only my family, who have supported me through every step of my dissertation, but also my life partner and love of my life, Julien Azimzadeh. Nothing expresses my gratitude to you Julien, then this excerpt from our wedding vows I wrote and spoke to you on May 28, 2017 in front of our most treasured friends and family:

Even though we stand before each other vowing to commit to one another till our last breath, I do not need to hear any words from you; you have already committed to me. You have stood by me through my hardest moments in life, never doubting your love for me. I know that our relationship will only grow stronger with the trials life throws at us.
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Chapter 1

Dissertation introduction
Background

Understanding the mechanisms that structure communities is a fundamental goal of ecological research. Initially, bottom-up processes like resource availability, resource competition and disturbance events were considered to be the primary mechanisms regulating community structure (Hairston et al. 1960, Interlandi and Kilham 2001, Wilkinson and Sherratt 2016). However, top-down control by predators has also proven to be an important regulator of community structure (Paine 1966), especially in systems where anthropogenic effects have altered top predator abundance (Estes et al. 1998, Silliman and Zieman 2001, Worm and Myers 2003). Predators play an important role in structuring communities and can have larger-scale implications if their presence can influence the formation of structure by a foundation species, such as eelgrass (Zostera marina), eastern oysters (Crassostrea virginica), or blue mussels (Mytilus edulis).

A predator’s foraging behavior may directly impact top-down control. The steps involved in a predator’s successful capture of prey have been described as the predation cycle (O’Brien 1979): 1) a predator encountering a prey, 2) deciding to attack a prey, 3) successful capture of prey, and 4) successful consumption of prey. Habitat type, habitat structure density, predator competition, and prey density may alter a given part of the predation cycle, increasing or decreasing top-down control by predators. Predator identity can also be an important component that changes how the above factors limit the steps in the predation cycle. Morphological and behavioral differences that exist among predators need to be considered in understanding the major components that regulate top-down control.

No matter the composition or habitat type, structured habitats have repeatedly been shown to enhance prey survival by creating a refuge from predatory attack (Moksnes et al. 1998, Heck et al. 2003, Stoner 2009, Hill and Weissburg 2013a). Structure can impede a predator’s
ability to detect and encounter a prey (step one of the predation cycle) and therefore reduces encounter rate between predator and prey by changing its movement (Ryer et al. 2004) and reducing its ability to visually (Main 1987, Ryer 1988, Hovel et al. 2016) and/or chemically (Ferner et al. 2009) detect the presence of prey. Habitats may differentially affect how structure impedes a predator’s foraging efficiency. A meta-analysis found a difference in habitat quality between submerged aquatic vegetation (SAV) and hard-bottom structured environments, where hard-bottom habitats were more successful nursery habitats for finfish and shellfish juveniles (Heck et al. 2003). Similarly, studies that have compared prey survival in SAV and hard-bottom habitats show prey survival to be greater in hard-bottom habitats (Barshaw and Lavalli 1988, Siddon and Witman 2004). This leads to the hypothesis that hard-bottom habitats may be a better prey refuge compared to vegetated habitats. The habitat-type effects may be different based on how the scaling of interstitial space to the predator’s size (Bartholomew et al. 2000, Bartholomew 2012, Wong 2013). Few studies have compared habitat structure effects across different species (but see Sponaugle and Lawton 1990). Thus, an important next step is to examine whether habitat type effects scale to predator size in a species-dependent manner.

Within a given habitat, there is a range of composition, morphology and structure density that could modify the relationship between structured habitats and prey acquisition by the predator. Habitat composition and density effects have been well-studied in SAV habitats, where typically shoot or thallus density is used as the habitat complexity metric (see review by Heck and Orth 2006). Studies that have examined habitat density effects with a single predator and a constant prey resource level have found that increases in habitat structure non-linearly decrease foraging success in a smooth continuous fashion (Heck and Orth 2006). Structure can either reduce foraging hyperbolically until a single habitat threshold is reached (Nelson 1979,
Carroll et al. 2015b) or in a step-like fashion at multiple thresholds (Nelson and Bonsdorff 1990). Conversely, structure may initially enhance the consumption rate and then decrease it in a parabolic relationship (Crowder and Cooper 1982), where predators are most successful at capturing and consuming prey at intermediate structure densities. All of the above habitat density studies have been performed with a mobile predator; different structure density relationships exist for predators that rely on sit-and-wait strategies (James and Heck 1994, Horinouchi 2007). In hard-bottom habitats, increases in habitat structure also negatively affect predator foraging (Grabowski 2004, Humphries et al. 2011), but it is unclear of the types of non-linear relationships that exist. No studies to my knowledge have compared habitat density effects between a hard-bottom and SAV habitat in the same study, and thus the following question remain unanswered: will hard-bottomed habitats have similar habitat density effects as vegetated habitats, or are there fundamental differences in how structure form interacts with habitat complexity?

In addition to habitat density affecting the predation cycle, competition among predators can affect foraging success. Competition among predators not only reduces resources per predator (exploitative competition), but also reduces per capita foraging rates due to behavioral interactions among individuals (interference competition). These antagonistic interactions among competitors - that range from avoidance, prey stealing, prey switching, body damage, or death (Mansour and Lipcius 1991, Smallegange et al. 2006, Griffen et al. 2011) - can ultimately lead to reduced top-down control. Model simulations predict that antagonistic interactions reduce the likelihood of local extinction of prey populations (DeAngelis et al. 1975, Sih 1979, Anders 2001). Increasing predator density may further stabilize predator and prey populations by increasing the number of antagonistic interactions among predators. Manipulative
experiments have shown that per capita consumption rates non-linearly decrease as predator density increases (Mansour and Lipcius 1991, Mistri 2003, Smallegange et al. 2006). This could be due to increases in the search and handling time (Smallegange et al. 2006, Griffen and Williamson 2008) or a predator becoming less efficient at consuming prey due to body damage (Mansour and Lipcius 1991, Clark et al. 1999b). Structure may alter predator-predator encounter rate in the same way habitat structure reduces a predator’s ability to encounter prey. While structure can alleviate competitive effects among individuals (Grabowski and Powers 2004), there have also been instances where structure increases either did not affect competition (Anholt 1990, Corkum and Cronin 2004, Simkins and Belk 2017) or enhanced competition (Swisher et al. 1998). If structured habitats reduce competitive interactions among predators, then it remains to be determined whether habitat type effects exist and how increases in structure affect competition among individuals.

The habitat structure and competitive effects on the predation cycle (O'Brien 1979) may be modified by prey density. Studies that have examined whether prey density changes the effect of structure have found conflicting results. Increasing prey density either did not change structure effects (Corona et al. 2000, Humphries et al. 2011, Hovel et al. 2016) or it reduced structure’s negative effect on foraging efficiency (Sponaugle and Lawton 1990). Further, the effects of competitive interactions among predators have been suggested to decrease with an increase in resource availability (DeAngelis et al. 1975, Mansour and Lipcius 1991, Smallegange and van der Meer 2006). Therefore, both predator and prey density may interact with structure type and density. In studies that have scaled predator and prey ratios with structure density, increases in structure did not alter total consumption of prey density (Mattila et al. 2008, Canion and Heck 2009, Scheinin et al. 2012). This may mean structure increases may not always
enhance prey refuge and may be dependent on predator and prey density effects. To better understand these co-varying factors, effects of predator and prey increases need to be evaluated separately. Specifically, prey density effects need to be evaluated for individual and multiple predators foraging in structured habitats that vary in form and density.

**Implication of habitat utilization to ecological restoration**

Abiotic and biogenic structured habitats provide multiple ecosystem services. They support extensive commercial shellfish, crustacean, and finfish fisheries (Kirby 2004, Watson et al. 2005), improve water quality through having filter feeding organisms (Grizzle et al. 2008, Nelson et al. 2014), and provide shoreline protection during storm surge (Piazza et al. 2005, Scyphers et al. 2011). In the last century, however, the benthic coverage of these habitats has undergone a dramatic decline. For instance, since at least 1879, seagrass bed coverage worldwide has declined approximately 29% (Waycott et al. 2009). The degradation of these important communities has been linked to increased anthropogenic nutrient levels (de Jonge et al. 2002, Worm and Lotze 2006), overfishing (Newell 1988, Jackson et al. 2001), climate change (Gazeau et al. 2007, Doney et al. 2012, Heath et al. 2012), harmful algal blooms (Shumway 1990, Anderson et al. 2008), and harmful recreational and commercial boating and fishing practices (Lenihan and Peterson 1998, Bishop et al. 2005).

Due to the ecosystem services provided by these structured environments, restoration efforts have focused on rebuilding biogenic habitats. One such effort has been in the creation of eastern oyster (*Crassostrea virginica*) reefs by 1) depositing hard-bottomed structure for colonization of juvenile oysters (spat) and 2) planting adult oysters or hatchery-reared spat. One of the goals of oyster restoration is to create conditions for self-sustaining populations without continually seeding the reefs with hatchery-reared spat. Understanding how predation
contributes to survival of hatchery-reared spat can help refine and enhance current oyster reef management strategies.

Predator size and habitat structure greatly influence foraging success and energy transfer in benthic communities. Xanthid mud crabs are common and abundant resident predators found within *C. virginica* reefs and have been shown to influence juvenile *C. virginica* populations (O'Connor et al. 2008, Johnson et al. 2014, Carroll et al. 2015a). Four out of the five most common xanthid mud crab species (excluding the common mud crab, *Panopeus herbstii*), reach carapace widths (CW) no larger than 27 mm (Ryan 1956). While mud crab individual consumption rates do not rival those of larger decapod individuals, their collective consumption rates may be equivalent to or larger than those of predators with larger body size (Kulp et al. 2011, Rindone and Eggleston 2011). Yet, recorded laboratory consumption rates (Kulp et al. 2011, Rindone and Eggleston 2011) do not incorporate the different habitat landscapes these predators forage within or examine whether predators of different sizes perceive their environments differently. While smaller predators may have the collective potential to consume at rates equivalent to larger predators, they may not have the same foraging success as larger predators among the same habitat landscapes. Field research that focuses partitioning mortality based on predator size can assist in understanding the role these predators have in restoration success and in the benthic communities they inhabit.

**Chapter objectives:**

Few studies have directly compared foraging across habitat type (Barshaw and Lavalli 1988, Siddon and Witman 2004, Griffen and Byers 2006), and even fewer studies have modified habitat density in a comparable fashion across different habitat types (Warfe and Barmuta 2004). In Chapters 2 - 5, I examine how the structure and composition of habitats influence the
efficiency with which predators find and consume their prey. I examined how prey density and predator identity, size and density affect the way in which structured habitats influence foraging efficiency.

I focused on comparing habitat type effects by choosing two very different habitat types: a hard-bottom habitat and a vegetated habitat. I selected slipper snail (*Crepidula fornicata*) shell hash bed and eelgrass (*Zostera marina*) bed to represent the hard-bottom and vegetated habitats because they are both abundant in the Long Island estuarine system where my dissertation was conducted. I scaled experimental habitat densities of each habitat type based on what a predator experiences in the field (shoot density for *Z. marina* and shell hash volume for *C. fornicata*), allowing for ecologically relevant habitat type comparisons to be made even though they offer very different forms of structure.

In Chapter 2, I examined habitat density effects in the *C. fornicata* and *Z. marina* habitats for a model predator that inhabits both habitat types, the mesopredator Sayi mud crab (*Dyspanopeus sayi*). The majority of habitat density studies have been performed in submerged aquatic vegetation habitats (see review by Heck and Orth 2006) with few performed in hard-bottom habitats (except see Grabowski and Powers 2004, Humphries et al. 2011). Chapter 2 is unique in comparing habitat density effects across two habitat types. Habitat structure effects have been shown to be related to predator size (Bartholomew 2002, Wong 2013). Thus, predator size may be more important to habitat structure effects than species-dependent effects. In Chapter 3, I wanted to understand whether equivalently-sized predator species forage similarly or differently in the *C. fornicata* and *Z. marina* habitats, and how predator size may change habitat type effects. I compared habitat type effects between *D. sayi* and sized-matched blue crabs (*Callinectes sapidus*), as well as larger-sized *C. sapidus*. 
In the same way that structure reduces contact between predator and prey (e.g. Ryer et al. 2004, Hovel et al. 2016), structure may also reduce predator-predator encounters with the result of alleviating competitive effects between predators (e.g. Grabowski and Powers 2004). Competitive interactions among conspecifics (mutual interference) have been shown to intensify when predator density increases (e.g. Griffen and Williamson 2008). In Chapters 4 and 5, I examined whether 1) there were predator density effects on top-down control and 2) if increases in structure by *Z. marina* and *C. fornicata* reduces predator density effects. I selected *D. sayi* as the model predator, since they are ubiquitous in Long Island structured habitats (Carroll 2012) and engage in antagonistic interactions (*personal observations*).

In addition to evaluating the effect predator identity, size and density in foraging efficiency in different habitat types, I also wanted to determine how predator size may influence top-down effects from a restoration perspective. In my sixth chapter, I explored how predator utilization of the hard-bottom habitat, eastern oyster (*Crassostrea virginica*) reef, may affect top-down control on juvenile *C. virginica* populations. This work also examined how environmental context could affect how predators of different sizes contribute to top-down control.

*In summary, I had the following expectations:*

1) The hard-bottom habitat, *Crepidula fornicata*, will be a better prey refuge than the vegetated habitat, *Zostera marina*.

2) The habitat type effects will be predator size-dependent and not predator species-dependent.

3) Mutual interference effects will be reduced by increases in habitat structure.
   
   a. *Crepidula fornicata* habitat will reduce mutual interference effects more than *Zostera marina* habitat.
4) Prey density increases will reduce both habitat structure effects and predator density effects.

5) Predator size and environmental context will differentially affect top-down control on juvenile *Crassostrea virginica*. 
Chapter 2

The influence of habitat structure on mesopredator foraging efficiency
Abstract

Benthic predators often inhabit multiple habitats with varying amounts of structure that could differently affect foraging efficiency for prey. Both the complexity and prey density of these habitats determine mobile predators’ ability to encounter and successfully capture prey. However, few studies have examined structure and prey density effects in more than one habitat type at a time. In a series of functional response mesocosm experiments, the foraging efficiency of the mesopredator, *Dyspanopeus sayi*, on *Mytilus edulis* was tested between a soft-bottom structured habitat, *Zostera marina*, and hard-bottom structured habitat, *Crepidula fornicata* shell hash. Increasing *M. edulis* densities were placed in one of four mimicked structure habitat density treatments (no structure, low [-1 SD of field mean], middle [field mean] and high [+1 SD of field mean]). Contrary to results from typical submerged aquatic vegetative habitat density studies, *Z. marina* structure did not have a negative effect on *D. sayi* foraging efficiency regardless of shoot density. Unlike in *Z. marina* structure, *M. edulis* were less likely to be consumed once *C. fornicata* reached the middle habitat density. When prey densities approached saturation, *C. fornicata* structure no longer affected foraging rates. The differential foraging behavior in each habitat type was likely a result of differential prey accessibility in the habitat structure. Further, the lack of a negative structure effect in *Z. marina* may be linked with *M. edulis’* reliance on passive shell defenses rather than physically escaping predation. Perhaps prey mobility may be an important factor in determining the degree structure or structure density reduces prey consumption. Results indicate habitat type and prey mobility need to be considered to understand how habitat complexity alters predator foraging efficiency.
Introduction

Habitat structure modifies foraging efficiency for predators, affecting prey encounter and capture rates. Numerous studies have shown that regardless of habitat type, prey survival is higher in structured versus unstructured habitats (Moksnes et al. 1998, Heck et al. 2003, Stoner 2009, Hill and Weissburg 2013a). While a variety of properties have been studied to better understand the effect of structure, such as habitat morphology (Warfe and Barmuta 2004) and heterogeneity (Stoner 2009), the effect of habitat density has been the most well-studied (see review Heck and Orth 2006). Sentinel habitat density studies, all performed in submerged aquatic vegetative (SAV) habitats, predict that as structure increases, mobile predators start to encounter prey less, decreasing consumption rate in a non-linear relationship (Nelson 1979, Heck and Orth 1980, Crowder and Cooper 1982). Multiple non-linear relationships have been suggested: predation could 1) decrease continuously (Nelson and Bonsdorff 1990), 2) increase to a maximum before decreasing (Crowder and Cooper 1982), 3) decrease to an asymptote at one or multiple threshold densities (Nelson 1979) or 4) increase after decreasing when prey no longer is be able to fit within the interstitial space (Bartholomew et al. 2000). Even though the non-linear relationships between habitat density and prey consumption have been heavily supported and debated in SAV habitats (Lipcius et al. 1998, Canion and Heck 2009, Wong 2013, Carroll et al. 2015b), few studies have examined whether similarities exist in other habitat types (but see Grabowski 2004, Humphries et al. 2011). Examining the effect of habitat type in alternative habitats is important because many predators reside in more than one type of habitat or move between habitats. Those few habitat density studies conducted in non-SAV habitats have generally supported that with structure density increases predation decreases (Grabowski 2004, Humphries et al. 2011), though the types of non-linear relationships remain unclear. Thus, two
important questions remain unanswered: 1) how do predators respond to increased structure in habitat types other than SAV habitats and 2) does habitat type affect a predator’s response to increases in structure?

Most non-SAV structured habitats—such as shellfish, coral, or cobblestone reefs—can be characterized as hard-bottomed structured habitats. Often these habitats do not have a flexible interstitial space above the benthos in the same conformation as a canopy does as in SAV. Instead, these hard-bottomed areas offer a matrix on the benthos of inflexible substrate that provide interstitial spaces in orientations not always present in soft-bottomed structured habitats. While comparative studies have contrasted similar types of structure (Lipcius and Hines 1986, Seitz et al. 2001, Warfe and Barmuta 2004, Carroll et al. 2010) or compared structured to unstructured environments (Olmi and Lipcius 1991, Jordan et al. 1997), few studies have compared between soft- and hard-bottomed structured habitats (but see Barshaw and Lavalli 1988, Griffen and Byers 2006). Though habitat density effects were not evaluated, prey generally had higher mortality in soft- than hard-bottomed structured habitats (Barshaw and Lavalli 1988, Dittel et al. 1996, Griffen and Byers 2006). While dependent on predator and prey size, higher survival in hard-bottomed structured habitats may be related to differences in prey accessibility. For instance, Barshaw and Lavalli (1988) found that cunner (Tautogolabrus adspersus) did not consume any juvenile lobsters (Homarus americanus) in the rock structure treatment. Predators that access prey differently in the different structures may exhibit prey switching, as demonstrated in Griffen and Byers (2006), and could lead to preferentially foraging in soft-bottomed structured habitats. The next steps to continue evaluating prey refuge value would be to evaluate foraging efficiency as structure increases in soft- and hard-bottomed habitats.
The effect soft- and hard-bottom structured habitats have on predator foraging efficiency can be quantified through a predator’s attack rate (i.e. Wong et al. 2006, Toscano and Griffen 2013). Attack rate incorporates the encounter rate and capture success after a capture attempt is made. One way to estimate attack rate other than directly assessing behavior is through fitting functional response curves. There are three standard functional responses: type I, II, or III (Holling 1959). A linear type I functional response occurs in situations where handling the prey does not affect predation and the attack rate is density-independent, typically displayed by filter feeders (Jeschke et al. 2004). In the most common functional response, type II, prey handling affects consumption (Jeschke et al. 2002). Prey handling incorporates the time it takes a predator to capture a prey after an attack is initiated. This results in prey density having a hyperbolic relationship with consumption that reaches an asymptote at high prey densities. The third functional response, type III, occurs when prey handling affects consumption and if prey density affects attack rate, leading to a sigmoidal consumption response to prey density. A shift from type II to III functional response could have important implications on population dynamics. For instance, systems with a type III functional response may be more resilient to local extinction at low prey densities, stabilizing predator-prey populations over time (Oaten and Murdoch 1975). Habitat structure has been suggested to make it more difficult to find prey at low prey densities (Alexander et al. 2012), shifting a predator’s functional response from the destabilizing type II to stabilizing type III functional response.

The primary goal of this study was to understand how habitat type affects predator foraging efficiency using a functional response approach. This study compared two different habitat types—a soft-vegetative to hard-calcified habitat—to determine whether structure density and habitat type were important in changing prey consumption rate. The effect of increasing
prey and structure density on an epibenthic predator’s (*Dyspanopeus sayi*) foraging was examined in a SAV (*Zostera marina*) and shell hash (*Crepidula fornicata*) habitat. Structure in both habitat types was predicted to have an effect on foraging until reaching a structure density threshold. When approaching prey satiation structural effects were expected to decrease. Increases in *C. fornicata* density was expected to have a greater effect on predator foraging than *Z. marina* density increases because of differential material properties that would make smaller crevice spaces in higher *C. fornicata* density. The functional response was also expected to shift from a destabilizing type II to a stabilizing type III functional response when the *C. fornicata* structure increased in density.

**Methods**

**Study System**

Shinnecock Bay, NY contains a variety of structured soft-vegetative and hard-bottomed biogenic habitats: eelgrass (*Z. marina*), blue mussel (*Mytilus edulis*), salt marsh (*Spartina spp*.), and slipper snail (*C. fornicata*) shell hash beds. We selected *Z. marina* and *C. fornicata* shell hash bed habitats as our model soft- and hard-bottomed biogenic habitats because they are the dominant shallow subtidal (<4 m depth) habitat types in our system. Clonal monoecious *Z. marina* beds in Long Island estuaries exist in continuous and patchy stands up to 6 hectares in size with an assortment of patch sizes in shallow, sandy-dominated substrate (Furman et al. 2015). The *C. fornicata* shell hash beds are made-up of protracted suspension-feeding *C. fornicata* limpet gastropods. Individuals stack on top of one another to form clumps that lay on top of loose *C. fornicata* shells in muddy-substrates. Similar to *Z. marina*, *C. fornicata* shell hash beds exist in continuous and patchy sections comparable to native *C. fornicata* beds reported along Rhode Island (Stickney and Stringer 1957, Lindsey et al. 2006) and non-native
beds now existing along northeastern Europe (Blanchard 1997, De Montaudouin and Sauriau 1999).

Field surveys were conducted over the summers of 2014 at representative *Z. marina* and *C. fornicata* sites in Shinnecock Bay (8 *Z. marina* and 3 *C. fornicata* sites) to quantify the range of habitat structure predators encounter (Table 1). One difficulty of comparing between habitat types is determining whether two different habitats offer the same complexity value. Different metrics are often used to quantify structure in soft-vegetative versus hard-bottomed habitat. Shoot, stem or thalli density and surface area is used to quantify soft-bottomed habitats (Crowder and Cooper 1982, Canion and Heck 2009, Hovel et al. 2016), while volume, clump density, height or rugosity is used to quantify hard-bottomed habitat types (Grabowski 2004, Toscano and Griffen 2013). The goal of this study was not to compare habitat types with equivalent habitat structure, but to expose predators to representative conditions they experience. Thus, the surveys used metrics that best represented the habitat type: shoot density for *Z. marina* and clump number and shell hash volume for *C. fornicata*.

Even though a variety of predators exist among *Z. marina* and *C. fornicata* beds (Carroll 2012), the Sayi mud crab (*D. sayi*), an epibenthic decapod, was selected as the model predator. Reaching no larger than 27 mm carapace width (CW; Ryan 1956), the *D. sayi* predators reaches the highest abundance out of crustacean predators in *Z. marina* and *C. fornicata* habitats (Carroll 2012). The *D. sayi* belong to the xanthid mud crab family, made-up of sexually dimorphic individuals who have disproportionally large crusher chelea compared to their body size (Ryan 1956). While no formal diet studies have been performed with *D. sayi*, their gut morphology suggests a high-protein diet (Griffen and Mosblack 2011). Xanthid mud crabs are important predators not only because they are ubiquitous and occur in high abundances (Strieb et al. 1995,
Silliman et al. 2004, Carroll et al. 2015a, Kulp and Peterson 2016), but due to their claw morphology and high mechanical advantage are able to consume shellfish similar in size to larger crustacean predators (Milke and Kennedy 2001, O’Connor et al. 2008, Carroll et al. 2015b). As a shellfish model prey, *M. edulis* was selected because it is widely available in a variety of structured habitats in Shinnecock Bay, easy to collect, readily consumed by *D. sayi* (Breen and Metaxas 2008), and is present in both *Z. marina* and *C. fornicata* habitats in Shinnecock Bay.

**Mesocosm Experiments**

*Zostera marina* habitat structure experiment. Between June and August 2015, the effect of increasing *Z. marina* habitat on *D. sayi* with increasing *M. edulis* prey densities was tested in outdoor continuous flow-through mesocosms (flow rate = $4.73 \pm 1.51$ L/min [mean ± 1 SD]) at the Stony Brook Southampton Marine Station. There were nine *M. edulis* prey densities (10-15 mm shell height [SH]: 2, 4, 6, 8, 10, 15, 20, 30, 40 mussels per mesocosm) placed in one of four habitat treatment levels (no structure, low, medium, and high) with a single male *D. sayi* (18-22 mm CW) for 36 hours. There was one replicate per experimental run for each of the 36 treatment combinations; seven runs were performed in total.

The three habitat structure levels (low, medium, and high) were based off of the mean ± 1 SD shoot density collected during *Z. marina* habitat surveys in Shinnecock Bay (Tables 1 and 2). Thereby, predators were experiencing realistic density treatments. *Z. marina* habitat structure was mimicked using green curling ribbon (0.5 x 25 cm, width x height) attached to a circular 10 mm Vexar® black mesh mat, where each *Z. marina* mimic shoot had four ribbon leaves. The mesh mat was buried under 7.6 cm of sand in black rubber 95 L Tuff Stuff® conical tub (bottom diameter: 0.54 m; bottom area: 0.229 m²) with the mimicked seagrass blades floating upright in
the mesocosm water column. Artificial seagrass units (ASUs) have repetitively been used to standardize seagrass habitat in controlled experiments (Mattila et al. 2008, Canion and Heck 2009, Carroll et al. 2015b, Hovel et al. 2016).

Weekly experimental runs were initiated at dusk with *D. sayi* that have at least 7 legs intact and were previously starved for 24 hours. *D. sayi* were collected from a *C. fornicata* shell hash bed in Shinnecock Bay, NY (40.8596°N 72.4339°W) and held no more than 2 days prior to starvation. Remaining mussels were enumerated after structure was thoroughly searched and sand sieved (3 mm aperture). No-predator controls in no-structure and high-structure treatments with the highest mussel density confirmed mussel mortality was due to predation with a recovery rate of 97.9 % ± 4.7 % in *Z. marina* mesocosms.

The flow-through system followed ambient conditions (temperature: 20 - 31°C; salinity: 26 - 31) in Old Fort Pond, Shinnecock Bay, NY (40.8845°N 72.4419°W). Continuous HoBo® data loggers were placed in mesocosms at the beginning and end of each plumbing line and confirmed temperatures were consistent between mesocosms with a mean difference between tubs of 1.3°C ± 1.0°C.

*Crepidula fornicata* structure experiment. Between June and August 2014, the effect of increasing *C. fornicata* habitat on *D. sayi* with increasing *M. edulis* prey densities was tested in a modified design from the *Z. marina* structure experiment. Instead of nine, there were seven *M. edulis* density treatments (10-14 mm SH: 2, 4, 6, 8, 10, 20, 30 mussels per mesocosm) added to one of four habitat structure treatments (no structure, low, medium, and high), making a total of 28 treatment combinations. Experiments were run biweekly with one replicate per run; ten runs were conducted in total.

The three habitat structure levels (low, medium, and high) were based off of the mean ± 1
SD clump abundance and shell hash density collected during *C. fornicata* habitat surveys in Shinnecock Bay (Tables 1 and 2). *C. fornicata* habitat structure was mimicked using loose *C. fornicata* shell and *C. fornicata* chains artificially glued with ethyl cyanoacrylate. There were 2 and 5 *C. fornicata* shells glued into a chain to mimic typical *C. fornicata* clumps.

A smaller mesocosm was used for the *C. fornicata* experiments than the *Z. marina* experiment due to infeasible time constraint associated with processing the high *C. fornicata* density treatments. The mesocosm was a white plastic conical 18.9 L bucket (bottom diameter: 0.28 m; area: 0.062 m²) that had the bottom removed and covered with a double layer of mesh (2 mm window screen on top of 5 mm Vexar). Additionally, there were 5 mm diameter holes drilled into the side. These buckets were inserted in the 95 L mesocosms used in the *Z. marina* experiment with a 2 cm layer of sand on the bottom. *D. sayi* (18 - 20 mm CW) were collected from a different *C. fornicata* bed in 2014 (40.8370°N 72.5051°W). No-predator controls in no-structure and high-structure treatments with the highest mussel density confirmed mussel mortality was due to predation with a recovery rate of 98.8 ± 4.4 % in *C. fornicata* mesocosms. Remaining experimental conditions followed those used in *Z. marina* experiments.

**Data Analysis**

**Functional Response**

Foraging efficiency was estimated for each structure type and density treatment by fitting a functional response. The type of functional response appropriate for each structure treatment was determined by fitting a polynomial logistic regression between the initial prey density and proportion of prey consumed using R Statistical Software (Juliano 2001, R Core Team 2015). A type II response would have a significantly negative linear term, whereas a type III response would have a significantly positive linear and negative quadratic terms (Juliano 2001). If the
polynomial logistic regression failed to distinguish between type II and III functional responses, then all three functional responses (type I, II, and III) were fit and compared using Akaike information criteria (AIC).

Maximum likelihood estimation assuming binomial errors was used to optimize the functional response parameters (Bolker 2008) using the friar_fit function from the ‘friar’ package (Pritchard et al. 2017). For type II response curve fitting, prey depletion was incorporated by using the Rogers type II random predator equation (equation 1; Rogers 1972)

\[
N_e = N_o \{1 - \exp[a(T_h N_e - T)]\} 
\]

where \(N_e\) is the number of prey eaten per mesocosm, \(N_o\) is the initial prey density per mesocosm, \(a\) is the attack rate, \(T_h\) is the handling time per prey, and \(T\) is the total foraging time. For type III response curve fitting, prey depletion was incorporation by using Hassel’s type III equation, which modifies equation 1 by having the attack rate, \(a\), dependent on prey density (equation 2; Hassell et al. 1977)

\[
a = b N_o / (1 + c N_o) 
\]

To isolate \(N_e\) in equations 1 and 2, the Lambert \(W\) function was used to solve for each parameter (Bolker 2008, Pritchard et al. 2017). The type I functional response was optimized using the equation \(N_e = a N_o\), where the consumption rate was linearly dependent on the attack rate (Hassell et al. 1977, Hassell 1978, Juliano 2001). Prey depletion was not incorporated into the type I functional response model.

Different mesocosm areas between the \(Z.\ marina\) and \(C.\ fornicata\) structure experiments prevented functional response comparison between habitat types. Instead, the functional response parameters were compared in each respective \(Z.\ marina\) and \(C.\ fornicata\) structure treatments. Because there has been much debate on the ability of functional response equations
to mechanistically represent attack rate and handling time (Jeschke et al. 2002) and parameter values were not empirically validated, the optimized parameter values were used for comparative purposes only. Parameter values were compared using biased-corrected and accelerated (BCa) bootstrapped 95% confidence intervals (CIs) obtained through the ‘frair’ and ‘boot’ packages (Pritchard et al. 2017, Canty and Ripley 2017). Confidence intervals have been readily used within the literature, where overlapping 95% CIs denote values likely from the same distribution (Neyman 1937, Steiger and Fouladi 1997, Cumming and Finch 2001).

**Structure Effect Size**

Due to the limitations of mechanistically representing attack rate and handling time parameters through functional response curve fitting, a structure effect size was calculated as a more direct way of quantifying habitat density effects within each structure type

\[
\text{Structure effect} = \bar{X}_{T,m} - \bar{X}_{C,m}
\]

where \(\bar{X}\) is the mean number of mussels consumed, \(T\) the low, middle or high structure treatment group, \(C\) the no structure treatment, and \(m\) the mussel density treatment. Due to differential foraging area between the habitat type experiments, structure effects were compared within each habitat type. For each structure effect, BCa 95% CIs were calculated using the ‘bootES’ package in R (Gerlanc and Kirby 2015). Confidence intervals that include zero signify that structure had no effect on foraging (Neyman 1937, Steiger and Fouladi 1997, Cumming and Finch 2001). Similarly, overlapping confidence intervals between treatment groups indicate structure density increases did not affect foraging (Neyman 1937, Steiger and Fouladi 1997, Cumming and Finch 2001).

**Habitat Type Response Ratio Effect Size**
To compare across habitat types, prey density was standardized by area (\(Z.\ marina\) experiments: 0.229 m\(^2\); \(C.\ fornicata\) experiments: 0.062 m\(^2\)). Only four prey density treatments in \(Z.\ marina\) (8, 15, 30 and 40 mussels per mesocosm) and \(C.\ fornicata\) (2, 4, 8, 10 mussels per mesocosm) experiments had approximately the same prey density (34, 65, 131, and 169 mussels per m\(^2\)). Thus, these four initial prey density treatments were used for comparing \(Z.\ marina\) and \(C.\ fornicata\) habitat type effects. Comparisons were made using response ratios, an effect size commonly used for comparing treatment effects conducted between studies with different experimental conditions (Osenberg et al. 1997, Hedges et al. 1999). We did not perform a logarithm transformation on the response ratio, as is commonly done in meta-analysis studies (Osenberg et al. 1997, Hedges et al. 1999, Borenstein et al. 2009) due to the high occurrence of zeros in the middle and high \(C.\ fornicata\) treatment replicates. The response ratio (RR) was taken as:

\[
Response\ Ratio = \left( \frac{\bar{X}_T}{\bar{X}_C} \right)
\]

(4)

where \(\bar{X}_T\) is the sample mean prey consumed in the low, middle or high structure treatments and \(\bar{X}_C\) is the sample mean prey consumed in the no structure treatment. For each habitat type effect, bootstrapped BCa 95% CIs were calculated using the ‘boot’ package in R (Canty and Ripley 2017). Overlapping confidence intervals with one indicated habitat type did not influence predation rates, whereas overlapping confidence intervals indicated no difference between treatment groups (Neyman 1937, Steiger and Fouladi 1997, Cumming and Finch 2001).

Results

Functional Response

Functional response type. For all \(Z.\ marina\) habitat treatments (Figure 1), as well as \(C.\ fornicata\) no structure and low habitat treatments (Figure 2), the type II functional response was used for
parameter optimization and comparison, as the linear parameter value in the logistic polynomial regression was significantly negative (Figure 3; \( P < 0.01 \)). Conversely, the logistic polynomial regression linear and quadratic terms were not significantly different from zero in the *C. fornicata* middle and high habitat treatments (Figure 4; \( P > 0.3 \)), supporting neither a type II or type III functional response.

To determine the appropriate functional response for the *C. fornicata* middle and high habitat treatments, all three functional response types were fit to the consumption rates and evaluated using AIC model comparisons. The type II functional response best represented the *C. fornicata* middle habitat treatment with \( 0 \Delta AIC_c \) and 71.88% \( wAIC_c \) (Figure 2; Table 3). While the type II functional response had the poorest fit to the *C. fornicata* high habitat treatment with 1.39 \( \Delta AIC_c \) and 20.84% \( wAIC_c \), the type I and III functional response fits were indistinguishable with 0.23 \( \Delta AIC_c \) and approximately 5% \( wAIC_c \). Since neither type I nor type III could be separated as the appropriate model (Burnham and Anderson 2002), *C. fornicata* high habitat treatment was excluded from further functional response analysis. Thus, for the *C. fornicata* habitat treatments, only the no structure, low and middle habitat treatments parameter estimates were compared.

**Functional response parameter comparison.** The type II functional response parameter values in the *Z. marina* habitat treatments were similar in value, unlike those in the *C. fornicata* habitat treatments. In *Z. marina* habitat treatments, all the attack rate (Figure 5A) and handling time (Figure 6A) parameter values had overlapping 95% CIs. This suggests *D. sayi* were not affected by *Z. marina* structure, regardless of the shoot density. Conversely, a structure density effect was demonstrated in the *C. fornicata* functional responses. The attack rate parameter was significantly lower in the *C. fornicata* middle compared to the overlapping no structure and low
habitat structure treatments (Figure 5B). There were no handling time differences between the no, low and middle structure treatments (Figure 6B). Thus, the downward type-II functional response shift exhibited in the middle structure treatment is best characterized by more than a four-fold reduction in attack rate parameter and non-overlapping CIs compared to the no and low structure treatments. From the functional response parameter fitting, structure type and density had different effects on feeding efficiency. *Z. marina* structure and density did not alter feeding rates, whereas *C. fornicata* structure negatively affected feeding rates once reaching the middle structure treatment.

**Structure Effect Size**

*Zostera marina* habitat type. *Zostera marina* structure never had a significantly negative effect on consumption (Figure 7). In fact, there was evidence *Z. marina* structure could have a positive effect on consumption in three treatment combinations: the 4 and 20 mussel densities in *Z. marina* middle structure habitat treatment, as well as the 30 mussel density in *Z. marina* high habitat treatment. Further, the structure effects were not different from each other across the habitat treatments at every mussel density except 20. When 20 mussels were added, the middle structure treatment had an effect size 3 times higher than the high middle structure treatment. Generally, *Z. marina* structure did not influence consumption when prey was limiting or saturated.

*Crepidula fornicata* habitat type. Structure and mussel density effects were seen in *C. fornicata* experiments (Figure 8). While *C. fornicata* low structure habitat treatment never had an effect on consumption, *C. fornicata* had a negative effect on consumption once the middle *C. fornicata* was reached and while mussel density was greater than 2 mussels and less than 30 limiting. As mussel density increased from 4 to 20, the negative effect size increased six-fold, indicating that
until prey approaches saturation *C. fornicata* structure density effect became more negative as mussel density increased. However, the *C. fornicata* structure no longer had an effect on consumption once prey density reached 30 mussels.

Even though the *C. fornicata* middle and high structure treatments negatively impacted foraging while prey was limiting, the *C. fornicata* structure treatments were rarely different from one another. The two exceptions occurred between the *C. fornicata* high and low structure treatments at 2 and 8 mussel densities. Here, the high structure treatment CIs were shifted more negative than the low structure treatment. Thus, while prey was limiting *C. fornicata* structure negatively impacted foraging once a minimal habitat structure density was reached at the middle structure treatment.

**Habitat Type Effect Size**

As shown by the effect size results, only *C. fornicata* and not *Z. marina* habitat structure affected consumption: the middle and high *C. fornicata* density treatments had a significant negative structure effect on foraging (Figure 9). As in the structure effect, there was evidence that *Z. marina* structure positively affected foraging. At the 131 mussels per m² treatment, the highest shoot density positively influenced feeding rates; all other mussel density treatments in *Z. marina* had no effect on consumption. Between habitat types, the low habitat structure treatment had the greatest overlapping response ratio range, with at least 75% of *Z. marina* overlapping with *C. fornicata*. This indicates that habitat type did not affect foraging when structure density remained low. However, for the remaining middle and high structure mussel density treatment combinations, no more than 25% of the response ratio ranges overlapped between habitat types. This suggests a greater difference in foraging between the habitat types in the middle and high structure treatments. In fact, the degree of difference between habitat types depends on both the
mussel and structure density. In two instances, there was a habitat type effect exhibited: 1) the 65 mussel per m² treatment in the middle structure density and 2) the 131 mussel per m² treatment for the middle and high structure densities. Here, *C. fornicata* had a more negative effect on consumption than *Z. marina*. Confirming results from the functional response and effect size analysis, *C. fornicata* was the only structure to negatively affect *D. sayi* foraging when habitat density reached a minimum threshold, whereas *Z. marina* either had no impact or a positive impact on foraging.

**Discussion**

Structure effects on foraging have been heavily studied over the past three decades (Bell et al. 1991, Moksnes et al. 1998, Heck et al. 2003, Stoner 2009, Hill and Weissburg 2013a), where the overwhelming evidence suggests that for mobile predators structure decreases foraging efficiency compared to unstructured habitats. While there have been an extensive number of studies performed in one habitat type, few have compared between soft-and hard-bottomed habitat types (but see Barshaw and Lavalli 1988, Griffen and Byers 2006). This study is unique in being the first to examine the effect increasing habitat density has on predator foraging between either a soft- and hard-habitat type. Unlike previous studies, this is the first to demonstrate that structure does not always affect foraging of a mobile predator. The soft-vegetative habitat (*Z. marina*) did not have a negative effect on foraging efficiency of *D. sayi* consuming the bivalve prey, *M. edulis*, regardless of shoot density. Conversely, the hard-bottomed habitat (*C. fornicata*) negatively affected *D. sayi’s* foraging efficiency once a minimum habitat density threshold was reached.

The lack of a negative *Z. marina* soft-vegetative structure effect at any shoot density does not match the typical predator foraging response shown in other SAV structure density studies.
SAV habitat structure typically has a negative effect on encounter rate by impeding a predator’s movement, slowing down the speed and changing the path trajectory (Stoner 1982, Ryer et al. 2004, Hovel et al. 2016). In this study, the model predator, *D. sayi*, which uses its leg appendages to walk sideways around structural blocks or push structure out of the way while searching for prey (Kulp, personal observation), should have had its encounter rate negatively affected when interstitial eelgrass shoot space decreased as shoot density increased. When applying the interstitial index developed by Bartholomew (2000) to this study, the interstitial space: predator size index decreased from 3.6 to 1.5 (see Table 2 for further details) as shoot density went from low to high *Z. marina* density. This suggests that *D. sayi* movements should have been impacted by the decreasing interstitial space formed by the higher shoot densities, decreasing encounter rate. Further, structure should have also decreased encounter rate by allowing *M. edulis* to move off the sandy bottom and either into the canopy. However, since no negative *Z. marina* structure effect was found in this study, there has to be another feature of the predation cycle occurring in this system that explains these results.

Unlike other SAV habitat structure studies (Bartholomew 2012, Carroll et al. 2015b, Hovel et al. 2016), this study did not use a mobile prey. Mobile prey have been shown to benefit from structure by actively moving behind structure to avoid being detected or to successfully escape before an attack is initiated (Main 1987, Ryer et al. 2004, Stoner 2009). Even though *M. edulis* is able to break its byssal threads and move its position (Lee et al. 1990), *M. edulis* is not able to respond to a predator’s movement quick enough to 1) prevent an encounter or 2) physically escape an encounter. Instead of physical avoidance, *M. edulis* relies on their size, shell thickness, abductor muscle strength, byssal attachment, and aggregation to escape
consumption (Elner 1978, Robles et al. 1990, Leonard et al. 1999, Smith and Jennings 2000). Thus, for a predator to successfully capture a bivalve prey similar to *M. edulis*, it has to isolate prey and break through the shell defenses to access the tissue. As described by O’Brien (1979), in addition to encounter rate the decision to attack a prey and ability to successfully capture the prey are two important components of the predation cycle. Bivalve prey selection has been linked with handling time, claw damage and energetic costs (Elner and Hughes 1978, Juanes and Hartwick 1990, Juanes 1992, Wong and Barbeau 2005), which may mean the limiting factor for determining attack rate on prey with reduced mobility like *M. edulis* is not encounter rate. Instead, the predator’s ability to overcome the bivalve’s prey defenses to successfully capture the prey may be more important than encounter rate in determining the attack rate. Since structure’s effect on foraging has typically been linked with reductions in encounter rate (Stoner 1982, Ryer et al. 2004, Hovel et al. 2016), perhaps structure has to affect the predator’s ability to overcome a prey’s passive defenses for a structure effect to be detected when the prey has limited mobility. Support for this hypothesis comes from a study conducted by Wong (2013). Wong (2013) examined *Carcinus maenas* foraging on infaunal prey, *Mya arenaria* in treatments with decreasing interstitial rhizome space scaled to claw area. Results indicated interference by smaller interstitial rhizomal space increased handling time by limiting *C. maenas*’ ability to manipulate *M. arenaria* through the rhizome mat, leading *C. maenas* to transition from using their claws to leg appendages to handle prey. In this case, structure influenced a predator’s ability to successfully isolate prey and access prey tissue. In a related study, Peterson and Heck (2001) found that the increased survival of the sessile semi-infaunal mussel (*Modiolus americanus*) in *Thalassia testudium* beds was due to the belowground rhizome mat and not the presence of aboveground biomass. Similar to findings by Wong (2013), the belowground
rhizome mat likely influenced predators’ ability to handle and successfully consume *M. americanus* in *T. testudium* beds. Perhaps for prey that have enhanced prey defenses with reduced mobility, structure needs to affect a predator’s capture success and not just predator-prey encounter frequency to have a habitat density effect.

There were three *Z. marina* treatments, the 4 and 20 mussel treatment in the middle structure and 30 mussel treatment in the high structure density treatment, which had a significant positive affect on *D. sayi* consumption of *M. edulis*. Potentially, *Z. marina* shoots impeded *M. edulis* movement, reducing the number and size of aggregated mussels. Given that bivalve clumping prevents interior prey from being handled and increases the time it takes to isolate prey (Wong and Barbeau 2005), *Z. marina* could have decreased handling time by decreasing the number of mussels in a clump, leading to higher prey consumption than in the unstructured treatment. This study did not quantify predator or prey behavior and therefore it is unknown whether structure affected encounter rate or successful tissue access after encounter. Additional behavioral experiments will need to be conducted to validate or refute the hypothesis that *Z. marina* typically does not limit foraging for a mobile predator-sessile prey system because *Z. marina* habitat structure does not affect the likelihood of a successful consumption event after encounter occurs.

Unlike all *Z. marina* treatments, consumption rate was negatively affected at almost every prey density once the middle *C. fornicata* density was reached. Adapting the interstitial index developed by Wong (2013) for this study’s *C. fornicata* density treatments (see Table 2 for further details), the interstitial index was 22.5 to 0.69 to 1.2 for the low to middle to high density treatments. The drastic reduction in interstitial space at the middle and high *C. fornicata* density indicates *D. sayi* movement would have been impeded if attempting to maneuver through the
interstitial spaces formed by the shell matrix. While *D. sayi*’s chelea should not be able to fit within the average space between shells, the shells are not cemented together. *D. sayi* is thus capable of re-positioning shells (*Kulp, personal observation*) and can make the space big enough for them to move between shells at the surface and within the shell matrix. The four-fold reduction in attack rate between the low and middle *C. fornicata* treatments could mean that *C. fornicata* affected the ability for *D. sayi* to successfully overcome *M. edulis*’ prey defenses, as well as encounter rate. For instance, though *D. sayi* has the ability to access *M. edulis* in interstitial spaces between shells in the shell matrix by moving the shells, their range of movement would become restricted and could have affected the efficiency with which they could isolate prey after encountered. In addition to inter-shell spaces, *C. fornicata* creates rigid crevices formed by the shelf on the underside of the limpet shell. When *M. edulis* settled within these rigid crevices, it would either become difficult for an encountered prey to be optimally handled or the crevice may make it impossible for the prey to be handled. Crevice space and predator access have been shown to negatively affect *M. edulis* consumption (*Lee and Kneib 1994, Toscano and Griffen 2013*). Further, once the middle *C. fornicata* structure was reached the shell hash covered 100% of the mesocosm bottom. The increase in shell hash could have increased the surface area for *M. edulis* byssal attachment. Byssal attachment and number has been linked with increased prey survival (*Reimer and Tedengren 1996*) , which could indicate the increase in shell hash could have increased the number of byssal threads attached. Thus, while not directly measured in this study, *C. fornicata* after surpassing a minimum structure density threshold could have not only decreased encounter rates, but also altered the rate of successful prey captures after a prey is encountered.
The similar habitat effect displayed between the middle and high *C. fornicata* treatments suggest that *C. fornicata* habitat effects become redundant after the middle density treatment. Bartholomew (2000) argued that as habitat increases there is overlap between the habitat structure, decreasing the effect additional structure has on obstructing the predator. Perhaps in the high *C. fornicata* structure treatment, the lower portion of shell hash matrix was too difficult for either *M. edulis* or *D. sayi* to access. Both prey and predator may have stayed within the surface matrix layers that existed in the middle and high *C. fornicata* structure treatment. Thus, predators may have encountered similar impedance in both habitat density treatments, causing limited difference in consumption between treatments. Alternatively, the increase in structure may have affected *D. sayi* and *M. edulis* differently, resulting in no effect of increasing structure on overall consumption rates. Hovel et al. (2016) found that increases in structure did not change consumption rate, but was a result of two opposing features. Increases in structure lowered encounter rate between predator and prey in Hovel et al. (2016), but decreased the efficiency of the prey’s mobile escape. This caused the predator to have more successful encounters in the treatment with increased structure. Similarly, if the *M. edulis* was less able to form clumps as the structure density increased beyond the middle density, then perhaps *M. edulis* individuals could have been handled easier making a capture more likely once it was encountered. The idea of a habitat threshold existing has been debated, where multiple thresholds have been shown to exist (Nelson 1979) versus the threshold effect being removed if additional structure treatments were added (Nelson and Bonsdorff 1990). The threshold *C. fornicata* density effect detected in this study has been supported in other hard-bottomed habitat structure density studies such as the *Crassostrea virginica* shell hash structure in Humphries et
al. (2011). Since the high *C. fornicata* structure density represents the upper range of realistic habitat density it is unlikely that the threshold effect exhibited was an experimental artifact.

The *C. fornicata* habitat threshold effect was removed when *M. edulis* prey density approached saturation. The lack of a structure density effect when predator and prey densities increase has been supported in the literature (Mattila et al. 2008, Canion and Heck 2009, Lannin and Hovel 2011, Scheinin et al. 2012), suggesting that structural effects also depend on prey and predator abundance. Fauna density has been shown to be closely tied with structural density (Lee et al. 2001, Hosack et al. 2006, Christie et al. 2009), which may mean that in studies where prey and predators remain constant as habitat density increases (i.e. Heck and Orth 1980, Crowder and Cooper 1982) structure effects could be overestimated. Studies need to continue isolating both predator and prey density affects, along with examining their combined effects, to understand structure effects under realistic predator and prey densities.

In direct comparison between soft-vegetative and hard-bottomed habitats, this study suggests the soft-vegetative *Z. marina* had a less negative effect on foraging compared to hard-bottomed *C. fornicata* shell hash habitat type. Furthermore, *Z. marina* never exhibited a significantly negative effect on consumption, whereas *C. fornicata* middle and high density had a negative effect on consumption until approaching prey saturation. This study indicates that structure type has an important impact on foraging efficiency, where hard-bottomed habitat inhibits foraging more than *Z. marina* with prey that relies on passive rather than active defenses. In other habitat comparison studies (Barshaw and Lavalli 1988, Griffen and Byers 2006), researchers similarly found that habitat type affected foraging. Griffen and Byers (2006) found the inflexible spaces in hard-bottomed substrate led the Asian shore crab (*Hemigrapsis sapidus*) to switch from consuming Gammarid amphipod prey to intraguild green crabs (*Carcinus*
 Compared to soft-bottomed substrate. Similarly, Barshaw and Lavalli (1988) showed a difference between hard and soft-bottomed habitat types for fish predator, *T. adspersus*, where predators could not access *H. americanus* prey in the rocky hard-bottomed habitat. Though it is difficult to compare among habitat types, results from this study suggest that hard-bottomed habitats that form a matrix of crevices may make it more difficult to catch prey that utilize the small crevices than the crevices formed in soft-bottomed vegetative habitats. Other differences besides structural differences not tested in this study may be important in understanding the effect of habitat type of foraging, including prey availability, abundance, alternative prey, and presence of competitors.

**Conclusion**

This study seeks to expand current knowledge on habitat effects not only based on habitat density, but also habitat type. The results from this study does not conform with the majority of published work that shows SAV habitats negatively influence foraging when the predator is actively foraging for prey. A fruitful line of inquiry would be to explore how prey mobility affects these questions, and if the results found in this study are more applicable to bivalve prey with passive defenses. Predators often reside in more than one habitat type either traveling between habitats or permanently residing in one out of multiple potential habitats. Quantifying how habitat type and density affect foraging efficiency may help better explain or predict the proportion of time a mobile predator spends in a given habitat type and future predator abundance and distribution patterns.

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Table 1. *Zostera marina* and *Crepidula fornicata* field survey habitat metrics (mean ± 1SD). *Zostera marina* survey was conducted in August 2014 at five different sites in Shinnecock Bay, NY. At each site, shoot density and canopy height was measured in six 1/16 m² quadrats. Additionally, within each of the six quadrats five shoots were selected. Each *Z. marina* eelgrass shoot had the shoot height measured of the tallest leaf. Aboveground and belowground biomass of eelgrass shoots and rhizomes was determined by using the following equation based off of samples taken at three sites in Shinnecock Bay and four sites in an adjacent body of water, Great South Bay, Long Island, NY (aboveground biomass: log(Biomass) = 0.385*log(Shoot Density), R² = 0.880; belowground biomass: log(Biomass) = 0.802*log(Shoot Density), R² = 0.953). The *C. fornicata* field survey was conducted in May 2014 at three different *C. fornicata* shell hash beds in Shinnecock Bay, NY. Using the 18.9 L mesocosm bucket used in the experiment (area: 0.062 m²), *C. fornicata* habitat was excavated at four locations within each site. The water displacement method was used to determine the volume of shell hash and live *C. fornicata* clumps. Each live *C. fornicata* clump was counted and the number of individuals in the longest chain was counted. The number of individuals in a chain ranged from 1 to 12, where the most number of live *C. fornicata* clumps had three in a chain. We listed two different live *C. fornicata* clump number: those with at least three individuals in the main chain and then those with more than three individuals. The biomass of shell hash and live *C. fornicata* clumps was determined by fitting a linear model off of subsamples (shell hash: Biomass = 1.93*Volume, R² =0.994 live clumps: Biomass = 1.03*Volume, R² = 0.997). Additionally, within a 0.25 m² quadrate, the height of the *C. fornicata* habitat was taken in five random locations; four quadrats were performed at each site.

<table>
<thead>
<tr>
<th>Zostera marina</th>
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</tr>
</thead>
<tbody>
<tr>
<td>Shoot Density (per m²)</td>
<td>Aboveground dried biomass (g per m²)</td>
<td>Belowground dried biomass (g per m²)</td>
<td>Canopy Height (mm)</td>
<td>Shoot Height (mm)</td>
<td>Shoot Sheath Width (mm)</td>
</tr>
<tr>
<td>653 ± 386</td>
<td>68.0 ± 55.4</td>
<td>315.0 ± 206.5</td>
<td>426 ± 100</td>
<td>440 ± 128</td>
<td>4 ± 1</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Crepidula fornicata</th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>Shell hash volume (mL per 0.062 m²)</td>
<td>Clump volume (mL per 0.062 m²)</td>
<td>Shell hash dried biomass (g per 0.062 m²)</td>
<td>Clump dried biomass (g per 0.062 m²)</td>
<td>Clump number (≤3 individuals stacked per 0.062 m²)</td>
<td>Clump number (&gt;3 individuals stacked per 0.062 m²)</td>
<td>Height (mm)</td>
</tr>
<tr>
<td>201 ± 258</td>
<td>555 ± 177</td>
<td>389.6 ± 498.6</td>
<td>572.8 ± 182.7</td>
<td>16 ± 16</td>
<td>17 ± 11</td>
<td>367 ± 133</td>
</tr>
</tbody>
</table>
Table 2. *Zostera marina* and *Crepidula fornicata* mesocosm treatment structure conditions and estimated structure indexes. For the *Z. marina* mesocosm treatment (bottom area = 0.229 m²), the number of shoots was determined to approximate the mean ± 1 SD shoot density from the field survey (Table 1). The structure was mimicked with using green curling ribbon (0.5 x 25 cm, width x height) attached to a circular 10 mm Vexar® black mesh mat, where each *Z. marina* mimic shoot had four ribbon leaves. For the *C. fornicata* mesocosm treatments (bottom area = 0.062 m²), the volume of shell hash was determined from the approximate mean ± 1 SD volume of shell hash from the field survey (Table 1). There were 2 and 5 *C. fornicata* shells glued together glued with ethyl cyanoacrylate to mimic the live *C. fornicata* clumps with at least three individuals or greater than three individuals in the main chain. The number of 2 and 5 *C. fornicata* shells glued into a chain was based off of the approximate mean ± 1 SD number of live *C. fornicata* clumps with at least 3 individuals or more than 3 individuals in the main chain from the field survey, respectively. The bottom shell in the mimicked clump was at least 30 mm in shell height (SH), which was within the range of the bottom shell found in the survey (range: 21 - 46 mm SH; mean: 34 ± 6.4 mm SH [SD]). The Bartholomew (2000) interstitial index was calculated by taking the mean distance to closest mimicked *Z. marina* shoot or *C. fornicata* shell and dividing by the mean *D. sayi* carapace length (16.4 mm). The Wong (2013) interstitial index was calculating by taking the mean area of interstitial space formed by *Z. marina* mimicked shoots or *C. fornicata* shells divided by the mean *D. sayi* crusher claw area (56.2 mm²; 18-22 mm CW individuals). The alternative Wong (2013) interstitial index used a different calculation of the crusher claw area calculated from the front instead of the side of the claw (35.0 mm²).

<table>
<thead>
<tr>
<th>Zostera marina</th>
<th>Interstitial Index</th>
</tr>
</thead>
<tbody>
<tr>
<td>Low</td>
<td>44</td>
</tr>
<tr>
<td>Middle</td>
<td>145</td>
</tr>
<tr>
<td>High</td>
<td>220</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Crepidula fornicata</th>
<th>Interstitial Index</th>
</tr>
</thead>
<tbody>
<tr>
<td>Low</td>
<td>0</td>
</tr>
<tr>
<td>Middle</td>
<td>200</td>
</tr>
<tr>
<td>High</td>
<td>460</td>
</tr>
</tbody>
</table>
Table 3. Akaike information criteria model assessment of *Crepidula fornicata* middle and high structure treatments fit to type I, II and III functional responses.

<table>
<thead>
<tr>
<th>Structure Treatment</th>
<th>AICc</th>
<th>ΔAICc</th>
<th>wAICc</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Middle</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Type I</td>
<td>404.52</td>
<td>6.55</td>
<td>2.72%</td>
</tr>
<tr>
<td>Type II</td>
<td>397.97</td>
<td>0</td>
<td>71.88%</td>
</tr>
<tr>
<td>Type III</td>
<td>400.05</td>
<td>2.08</td>
<td>24.41%</td>
</tr>
<tr>
<td><strong>High</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Type I</td>
<td>380.90</td>
<td>0.23</td>
<td>37.33%</td>
</tr>
<tr>
<td>Type II</td>
<td>382.06</td>
<td>1.40</td>
<td>20.84%</td>
</tr>
<tr>
<td>Type III</td>
<td>380.67</td>
<td>0</td>
<td>41.82%</td>
</tr>
</tbody>
</table>
Figure 1. Mean number of *Mytilus edulis* consumed by *Dyspanopeus sayi* when foraging in *Zostera marina* habitat types: no structure (A), low *Z. marina* density treatment (B), middle *Z. marina* density treatment (C), and high *Z. marina* density treatment (D). The points are observed mean consumption rates with SE error bars, the solid line is the fitted type II functional response curve fitted model and the dashed lines are the BCa bootstrapped 95% CI.
Figure 2. Mean number of *Mytilus edulis* consumed by *Dyspanopeus sayi* when foraging in *Crepidula fornicata* habitat types: no structure (A), low *C. fornicata* density treatment (B), middle *C. fornicata* density treatment (C), and high *C. fornicata* density treatment (D). The points are observed mean consumption rates with SE error bars, the solid line is the fitted type II functional response curve fitted model and the dashed lines are the BCa bootstrapped 95% CI. No functional response was fit for *C. fornicata*’s high structure treatment because polynomial logistic regression and AIC model comparisons could not identify the type of functional response.
Figure 3. Proportion of *Mytilus edulis* consumed by *Dyspanopeus sayi* when foraging in *Zostera marina* habitat types: no structure (A), low *Z. marina* density treatment (B), middle *Z. marina* density treatment (C), and high *Z. marina* density treatment (D). The points are observed means with SE error bars.
Figure 4. Proportion of *Mytilus edulis* consumed by *Dyspanopeus sayi* when foraging in *Crepidula fornicata* habitat types: no structure (A), low *C. fornicata* density treatment (B), middle *C. fornicata* density treatment (C), and high *C. fornicata* density treatment (D). The points are observed means with SE error bars.
Figure 5. Optimized attack rate parameter with 95% bootstrapped CI in vegetative habitat (Zostera marina; A) and hard-bottom habitat (Crepidula fornicata; B) by the habitat density treatment. Because the AIC model comparison was inconclusive for the C. fornicata high structure treatment, the attack rate parameter value is not shown (Table 3).
Figure 6. Optimized handling time parameter with 95% bootstrapped CI in vegetative habitat (*Zostera marina*; A) and hard-bottom habitat (*Crepidula fornicata*; B) by the habitat density treatment. Because the AIC model comparison was inconclusive for the *C. fornicata* high structure treatment, the handling time parameter value is not shown (Table 3).
Figure 7. Unstandardized effect size in *Zostera marina* habitat type with 95% bootstrapped CI between density treatment and unstructured treatment by initial prey density. The density treatments are: low structure (A), middle structure (B), and high structure (C). A value of 0 (denoted by the dashed line) is considered to be no effect of structure density.
Figure 8. Unstandardized effect size in *Crepidula fornicata* habitat type with 95% bootstrapped CI between density treatment and unstructured treatment by initial prey density. The density treatments are: low structure (A), middle structure (B), and high structure (C). A value of 0 (denoted by the dashed line) is considered to be no effect of structure density.
Figure 9. Response ratio effect size with 95% bootstrapped CI between structure density treatment and unstructured treatment by habitat types (*Zostera marina*: grey; *Crepidula fornicata*: black). The plots are broken-up by standardized mussel density treatments between habitat types (34, 65, 131 and 169 mussels per m²). A value of 1 (denoted by the dashed line) is considered to be no effect of structure density.
Soft-vegetative and hard-bottomed biogenic habitats alter the foraging efficiency of predators in a species-dependent manner
Abstract

The size, foraging strategy, and morphology of predators may affect how habitat type influences foraging efficiency. However, habitat type effects may be based on predator size, such that species-specific differences may not matter. Sized-matched Sayi mud crab (*Dyspanopeus sayi*) and blue crab (*Callinectes sapidus*) individuals were selected to evaluate whether equivalently sized predators of different species foraged similarly in various habitat types. Larger sized *C. sapidus* individuals were additionally selected to examine whether predator size changes habitat type effects on foraging efficiency. Across these three predator group treatments, consumption rate of a single predator was evaluated in one of three habitat types: sand, eelgrass (*Zostera marina*) and slipper snail (*Crepidula fornicata*) shell hash habitats. Since prey density could affect habitat type effects, *Mytilus edulis* prey was either limiting (low density) or saturated (high density). Prey density had a density-dependent effect among the three predator group treatments and habitat types; a greater proportion of prey was consumed in the low versus high prey density treatment. Habitat type effects were not detected for *C. sapidus* at either size class. In contrast, habitat type affected *D. sayi* foraging for *M. edulis*, where the *C. fornicata* habitat negatively affected *M. edulis* consumption compared to *Z. marina* habitat. Further, the habitat type effect detected for *D. sayi* occurred when prey was limiting or saturated, which suggests that prey density increases may not remove effect of habitat type. This study validates the importance of considering species-specific differences in how predator identity affects habitat type effects and that there may be important habitat type differences in prey refuge between hard-bottom and vegetative habitat types.
Introduction

Habitat structure has important effects on fauna survivorship and utilization. Fauna benefit from structured habitats by having increased food resource availability (e.g. Heithaus and Dill 2002, Ince et al. 2007) and refuge from predator-based mortality (e.g. Heck et al. 2003). Numerous studies have confirmed structure as an important prey refuge; prey survival increases in structured habitats compared to unstructured sediment (Moksnes et al. 1998, Heck et al. 2003, Stoner 2009, Hill and Weissburg 2013a). Studies examining the effect of structure have found that structure can physically (Ryer et al. 2004, Toscano and Griffen 2013), visually (Main 1987), and chemically (Ferner et al. 2009) alter cues mobile predators use to both detect and encounter prey. Structure can also change the predator’s speed and direction (Ryer et al. 2004), thereby increasing prey search time (Wong 2013). These effects of structure have been suggested to decrease a predator’s encounter rate with prey, ultimately increasing prey survival (Stoner 1982, Ryer et al. 2004, Hovel et al. 2016). Further, prey can modify their location to enhance structure’s effect on decreasing prey detection and encounter rate (Main 1987), as well as prey accessibility (Ryer 1988, Stoner 2009). While structure has been shown to decrease prey mortality from predators, there have been examples of prey being unable to successfully escape or detect a predator in structure, decreasing their survival (James and Heck 1994, Hovel et al. 2016).

The habitat refuge value may also be dependent on the habitat type and composition. A meta-analysis comparing the refuge value in aquatic habitats found that hard-bottom structured habitats had higher juvenile fauna survival than submerged aquatic vegetative (SAV) habitats (Heck et al. 2003). Further, in habitat type comparison studies, hard-bottom habitats also displayed a higher survival of the basal prey over SAV habitats (Barshaw and Lavalli 1988,
Different habitat type effects between these hard-bottom and SAV structured habitats could be a result of different 3-dimensional interstitial spaces. Hard-bottom habitats such as coral cobblestone, and oyster reefs tend to have rigid, unmoving crevices on the benthos that vary in volume, shape, size and height. Conversely, in SAV habitats, there is a 3-dimensional canopy formed off the benthos and whose interstitial space depends on stem thickness and branching, leaf morphology, shoot or thalli density. In hard-bottom habitat, predator foraging behavior can be differently affected by the arrangement of the 3-dimensional crevice space. For instance, Hesterberg et al. (2017) found that even though volume was kept constant, the arrangement of oyster valve crevice space differentially affected prey mortality. Reduced prey accessibility has also been shown to lead to prey-switching in hard-bottom habitats (Griffen and Byers 2006). Further, a predator may have different encounter rates with prey based on the difficulty of moving through the habitat material, as Seitz et al. (2001) showed for *Callinectes sapidus* foraging for *Mya arenaria* in sand versus mud environments.

Regardless of the habitat type, fauna density has been shown to be positively related with habitat structure (Lee et al. 2001, Hosack et al. 2006, Christie et al. 2009) and indicates prey resources become more available in structured habitats. This increase in prey resources with structure may either reduce the chance of an individual prey from being encountered (Lannin and Hovel 2011) or change the way structure affects prey encounter (Corona et al. 2000) or capture success (Hovel et al. 2016). Studies that have examined the effect of prey density and structure effects on a single predator have shown conflicting results, sometimes removing or reducing structure effects (Sponaugle and Lawton 1990) or not changing structure effect (Corona et al. 2000, Humphries et al. 2011, Hovel et al. 2016). When researchers scaled predator and prey...
abundances with structure density, they have found that structure density no longer negatively affects feeding rates (Mattila et al. 2008, Canion and Heck 2009, Scheinin et al. 2012).

Considering the importance of resource limitation in foraging rates of predators (i.e. the functional response; Holling 1959), habitat type effects on predator foraging may also be dependent on prey resource density.

Predator size can change the relationship structured habitats have on foraging efficiency. For instance, Toscano and Griffen (2013) found that increased Panopeus herbstii claw size interfered with their ability to reach mussel prey nested inside oyster clump crevices. One way researchers have incorporated predator size in evaluating habitat effects is by scaling interstitial space to predator size (Bartholomew et al. 2000, Wong 2013). Studies applying these interstitial indexes have supported that as the index decreases, predators become less able to enter or maneuver in the interstitial spaces, decreasing consumption rates on their prey (Bartholomew 2002, 2012, Bartholomew et al. 2016). In some cases, predators may have to change their foraging strategy to isolate prey, such as Carcinus maenas using their legs opposed to their claws to manipulate Mercenaria mercenaria through an eelgrass rhizome mat mimic (Wong 2013). If habitat type effect is related to how interstitial space scales to predator size, then equivalently-sized predators of different species may have similar habitat type effects. While one study that compared two decapod predators similar in size and morphology supported this hypothesis (Sponaugle and Lawton 1990), more work is needed.

A previous study (Kulp et al. in preparation; Chapter 2) has indicated that the decapod mesopredator, Sayi mud crab (Dyspanopeus sayi), responds differently to increases in habitat density based on the habitat type. The mimicked vegetative habitat (Zostera marina) had no structural effects, whereas the mimicked hard-bottom shell hash habitat (Crepidula fornicata)
had a negative effect on consumption once a structure density threshold was reached. Further, prey saturation reduced the negative effect of *C. fornicata* and indicates prey density increases could reduce the negative effects that increasing *C. fornicata* structure has on predator foraging.

The current study sought to understand whether *D. sayi*’s relationship to habitat type and prey density is unique to *D. sayi* or is consistent for predators of similar size. Thus, the effect of habitat type (sand, *Z. marina*, and *C. fornicata*) at limiting and non-limiting prey densities was examined between *D. sayi* and a similarly sized second predator, *C. sapidus*. Because *D. sayi* does not grow to a size that likely changes how it interacts with structure, a size-effect was only examined for *C. sapidus* by performing the same experiment with a larger size class of *C. sapidus*. Numerous studies have shown that larger decapod predators consume shellfish of the same size as smaller decapod predators, but at higher per capita rates (Juanes 1992, O’Connor et al. 2008). Thus, *D. sayi* and sized-matched or larger sized *C. sapidus* likely target the same sized shellfish prey, allowing for habitat type effects to be examined using the same sized bivalve prey, *Mytilus edulis*. The sized-matched predators were expected to have the same relationship with habitat type and prey density as shown in the previous study (Kulp et al. *in preparation*, Chapter 2). Conversely, the larger sized *C. sapidus* was expected to become inhibited by both *Z. marina* and *C. fornicata* at low prey density, but not display any structure effects at high prey density.

**Methods**

*Mesocosm Experiments*

The species- and size-dependent effects of prey availability and habitat type on foraging efficiency was tested across two experimental periods. The species-dependent effect was tested between size-matched *D. sayi* (18 - 22 carapace width [CW]) and juvenile *C. sapidus* (hereafter
termed small *C. sapidus*; 24 - 45 mm CW). The selected sizes of *D. sayi* and small *C. sapidus* were based on equivalent dried biomass (1.3 ± 0.4 g). The size-dependent effect was tested using *C. sapidus* individuals approximately eight times the dried biomass of the individuals used in the species-dependent experiment (hereafter termed large *C. sapidus*; 60 - 86 mm CW, 10.8 ± 2.8 g). See Tables 1 and 2 for additional morphological measurements. The species-dependent effect was tested in September 2016 when small *C. sapidus* individuals were easily collected and the size-dependent effect with the large *C. sapidus* individuals were performed in July 2016 when feeding rates would be maximized.

In both experimental periods, a single predator was exposed to one of two *M. edulis* prey density treatments (low and high; 10-15 mm shell height) and one of three habitat type treatments (sand, *Z. marina*, and *C. fornicata*). The low and high *M. edulis* prey density treatments represented conditions when prey was either limiting or non-limiting. The size-matched *D. sayi* and *C. sapidus* had either 10 or 40 mussels; the large *C. sapidus* had either 8 or 200 mussels. The experimental runs were performed in 95 L Tuff Stuff tubs (bottom diameter: 0.54 m; bottom area: 0.229 m²) with a flow-through water system (flow rate = 7.2 ± 1.3 L/min [mean ± 1 SD]) at the Stony Brook University Marine Station, Southampton, NY (40.8845N 72.4418W). Thus, water conditions followed ambient conditions (July temperature: 25°C - 29°C, September temperature: 18°C - 27°C; salinity: 26 - 31).

There was 7.6 cm of sand placed into each habitat type treatment. The *Z. marina* and *C. fornicata* habitat treatment levels were mimicked using either artificial seagrass units or *C. fornicata* clumps and shell hash. The artificial seagrass units were made by tying green curling ribbon (0.5 x 25 cm [width x height]) to a circular Vexar® black mesh mat with 10 mm aperture, and then buried under the 7.6 cm of sand. Each mimic of *Z. marina* shoot had four leaves, which
floated upright in the water column. Artificial seagrass structure offers the best method to
standardize seagrass, and not only has been widely used (Bologna and Heck 1999, Canion and
Heck 2009, Carroll et al. 2012) but also demonstrated to not alter fauna behavior (Healey and
Hovel 2004). *Crepidula fornicata* clumps were mimicked using two or five sun-bleached *C.
forncata* shells stacked on top of one another using ethyl cyanoacrylate. Shell hash consisted of
loose *C. fornicata* shells collected from resident *C. fornicata* beds or beaches. The habitat
density used in the *Z. marina* and *C. fornicata* habitat type treatments reflected the mean
structure density experienced by predators in Shinnecock Bay (Tables 3 and 4). Thus, the two
habitat types can be compared even though the habitat density is not equivalent.

The *D. sayi* were hand collected from a *C. fornicata* shell hash bed in Shinnecock Bay
(40.8596°N 72.4339°W). The small *C. sapidus* were either collected with a seine in Great South
Bay (40.7485°N 72.9967°W) or by hand in a seagrass bed in Shinnecock Bay (40.8583°N
72.4503°W). The large *C. sapidus* were collected through crab traps deployed off the Marine
Station docks. Only individuals with both chelipeds and no more than 2 legs missing were used
in the experimental trials. Only males *D. sayi* were used while both genders of *C. sapidus* were
used. Both genders were used for *C. sapidus* in order to obtain enough individuals for an
experimental run. Further, preliminary runs indicated no gender-based differences in
consumption rates of *M. edulis*. After being collected, individuals were held no more than a
week in flow-through seatables. *Dyspanopeus sayi* could move among *M. edulis* and *C.
forncata* clumps distributed along the bottom of seatables, which served as both food and
structure. *Callinectes sapidus* were kept in perforated plastic Zipblock® storage containers that
floated in the seatables. *Mytilus edulis* and *C. fornicata* clumps were placed into the containers
and remnants of consumed food was removed every day the animals were held.
The *M. edulis* prey were added at least one hour prior to the initiation of each experimental run close to dusk. Predators that had been starved for 24 hours were added individually to mesocosm tubs. After 36 hours, remaining mussels were enumerated by thoroughly searching the structure and sieving the sand (3 mm aperture). There were controls performed in each habitat type at the highest mussel density. The controls did not have a predator added allowing for natural mussel mortality and recovery success to be estimated. Controls confirmed mussel mortality was due to predation with natural mortality never being higher than 6% per mesocosm (2.1 ± 2.1 % in July and 0.4 ± 1.4 % in September) and a percent recovery above 99% (99.6 ± 1.3% in July and 100 ± 3.0% in September). Continuous HoBo® data loggers in mesocosms located at the end of each plumbing line confirmed temperatures were similar among mesocosms with a maximum mean difference in July of 1.8°C ± 2.2°C and September of 0.9°C ± 1.2°C. In between experimental runs, the tubs were drained to prevent faunal colonization into the tubs. Across the two experimental periods, treatment replication varied among the experimental runs (see Table 5 for replicate numbers per experimental run). Any replicate where a predator died, molted, or could not be recovered was removed from the analysis.

There was a harmful red algal bloom caused by *Cochlodinium polykrikoides* during the first three runs of the September 2016 experimental period. This harmful algal bloom has been shown to have multiple adverse effects on faunal populations (see review by Kudela and Gobler 2012). The third run was the only time a thin layer of rust-colored debris (< 5 mm thick) settled on the bottom of the tubs, presumably from the red tide. This layer was siphoned-off on the morning of the second day in each mesocosm. Considering decapod predators tend to be crepuscular and active during the night (e.g. Clark et al. 1999a), it is unlikely the siphoning had
major impacts on feeding rates. Further, while *C. polykrikoides* has been shown to negatively affect shellfish (Tang and Gobler 2009), little to no mussel mortality occurred (0.4 % ± 1.4%). However, any negative effect has been accounted in the analysis by including experimental run as a random variable.

*Data Analysis*

The statistical analysis was performed using R Statistical Software version 3.4.1 (R Core Team 2017). Predator group (*D. sayi*, small *C. sapidus* and large *C. sapidus*), mussel density (low and high) and habitat type (sand, *Z. marina*, and *C. fornicata*) effects on the proportion of *M. edulis* consumed were examined. Due to different environmental conditions of each experimental run among the two experimental periods, experimental run was treated as a random variable and a mixed model used for the analysis. In addition, predator size was added as a covariate in the model to account for the chance that differently sized individuals were distributed among the habitat type and mussel density treatments. Reasons for including a predator size covariate were: 1) there was a large range of sizes used for the small and large *C. sapidus* predator group treatments and 2) *C. sapidus* carapace width was positively related with the proportion of *M. edulis* consumed (Table 6). In order to account for the different carapace morphologies between *D. sayi* and *C. sapidus* (*C. sapidus* has longer carapace spines), dried biomass estimates were used as the size metric opposed to carapace width. To estimate dried biomass, a subsample of individuals of each predator group had their carapace width and dried weights taken, and a linear regression built for each predator group (see Table 7 for the models’ estimated coefficients).

Two model approaches were used to model the proportion of mussels consumed in a 3-factorial design (predator group x mussel density x habitat type) with predator size as a covariate
and experimental run as a random effect. Both approaches used the package ‘lme4’ (Bates et al. 2015) for building the mixed model. In the first model approach, a generalized linear mixed model (GLMM) assuming a Poisson error distribution (hereafter termed Poisson regression) was fit to the number of mussels consumed with a log-transformed offset of the initial number of mussels. In the second model approach, a GLMM assuming binomial error distribution (hereafter termed binomial regression) was fit to the proportion of mussels consumed. Overdispersion in the two GLMMs was corrected by adding individual observations as a random effect (Bolker et al. 2009). The models converged when the optimization was bounded by quadratic approximation with 20,000 iterations and the three-way main effect interaction removed. The binomial regression had a lower corrected Akaike information criteria (AICc) value and higher weighted AICc value compared to the Poisson regression (AICc: 694.9 vs 802.2; w: 1 vs 0). Thus, the binomial regression was used in evaluating main and interactive effects.

Main effects were evaluated using a type III Wald chi-square test in the ‘car’ package (Fox and Weisberg 2011). The type III test was used to address unequal sample sizes and because there were significant interactions. Pairwise post-hoc chi-square tests were performed on the highest-order significant terms with multiple comparisons corrected by using the Holm-Bonferroni method in the ‘phia’ package (De Rosario-Martinez 2015). Appropriate model diagnostics were run to assess model fit; statistical significance α was set at 0.05.

Results

Habitat type effects was species-dependent and not size-dependent (Figure 1), where the predator group treatment effects were dependent on both habitat type and mussel density treatments (significant interactive effects, Table 8). Only D. sayi displayed a habitat type effect,
where a significant difference occurred between the *Z. marina* and *C. fornicata* habitat types ($X^2 = 10.2, P = 0.012$). *Dyspanopeus sayi* consumed approximately 2.5 times as many mussels when foraging in *Z. marina* compared to *C. fornicata*, suggesting that *C. fornicata* structure offers better prey refuge to *M. edulis* than *Z. marina* structure. However, *D. sayi* had similar foraging rates of *M. edulis* in *Z. marina* and *C. fornicata* structured habitat treatments compared to the sand habitat type. There was approximately 7% fewer mussels consumed in *C. fornicata* than the sand habitat type. While *D. sayi* consumed approximately two times as many mussels as in *Z. marina* compared to the sand habitat type, the high variability led this difference to not be significant (Figure 1 C and D; *Z. marina* vs no structure: $0.28 \pm 0.19$ vs $0.12 \pm 0.14$ proportion of mussels eaten per g of predator [mean $\pm$ 1 SD]). Unlike *D. sayi*, there was not a habitat type effect displayed by either the small or large *C. sapidus* ($P = 1$).

Comparing among the predator treatment groups, the small *C. sapidus* consumed about twice the proportion of mussels than *D. sayi* at both mussel densities, though these differences were driven by the sand and *C. fornicata* habitat type treatments ($P < 0.001$). There was no difference in proportion of *M. edulis* consumed between *D. sayi* and small *C. sapidus* when individuals foraged in *Z. marina* habitat type ($P = 0.51$). While similar habitat type treatments occurred for small and large *C. sapidus*, there was a significant difference detected in the proportion of mussels consumed in the high mussel treatment among *C. sapidus* size classes ($X^2 = 7.75, P = 0.021$). After standardizing feeding rates by predator biomass, the small *C. sapidus* consumed approximately four times the proportion of mussels consumed by large *C. sapidus* in the high mussel treatment (Figure 1 C and D).

For each of the predator group treatments, a greater proportion of mussels were consumed in the low-mussel treatment compared to the high-mussel treatment ($P < 0.005$).
However, there were no interactive effects detected between mussel density and structure habitat type. This suggests *M. edulis* prey were not more difficult to find when prey was limiting. Results support the hypothesis that habitat structure effects were species-specific. The hard-bottom *C. fornicata* habitat had a negative effect on *D. sayi*’s feeding rate of *M. edulis* compared to vegetative *Z. marina* habitat, whereas neither structured habitat influenced *C. sapidus*’ feeding rate of *M. edulis*.

**Discussion**

Hard-bottom and vegetative habitats may offer prey different refuge based on fundamental differences in interstitial space formation. Part of the difficulty in studying habitat type effects is using a standardized form of defining the habitat type density. This study’s approach of using a structure density that the predator regularly experiences in the field (Tables 3 and 4) allows for habitat type comparisons to be made. This study sought to understand whether the crustacean mesopredator *D. sayi*’s habitat type relationship displayed previously (Kulp et al. *in preparation*, Chapter 2) was unique to *D. sayi* or be generally applied to other crustacean predators of similar size. This study confirms that the hard-bottom *C. fornicata* habitat provides a better prey refuge than the vegetative *Z. marina* habitat. However, the habitat type differences displayed by *D. sayi* were unique to *D. sayi*. Regardless of the size, the *C. sapidus* individuals did not display a habitat type effect at either prey density treatment. Therefore, the habitat type effect displayed in this study and the earlier study (Kulp et al. *in preparation*, Chapter 2) by *D. sayi* is a result of a species-specific difference between *D. sayi* and *C. sapidus*.

The lack of *D. sayi*’s habitat type effect between the sand and hard-bottom *C. fornicata* treatments does not match previous results (Kulp et al. *in preparation*, Chapter 2), where *C. fornicata* significantly reduced *D. sayi*’s feeding rate compared to an unstructured environment.
Conversely, there was evidence to support the habitat type differences between *C. fornicata* and *Z. marina* that was previously displayed by *D. sayi*. In the current study, the proportion of *M. edulis* consumed was significantly less in the *C. fornicata* habitat compared to the *Z. marina* habitat. Habitat type effects have been demonstrated in other studies, where hard-bottom habitats have offered greater prey refuge than submerged aquatic vegetative habitats (Barshaw and Lavalli 1988, Siddon and Witman 2004, Griffen and Byers 2006). The habitat type effects in this experiment similarly indicates hard-bottom habitats enhance prey refuge compared to a vegetated habitat. Structured environments have been shown to reduce foraging by reducing movement speed and direction (Ryer et al. 2004), decreasing prey detection rate (Main 1987, Hovel et al. 2016), and altering prey accessibility (Ryer 1988, Toscano and Griffen 2013, Hesterberg et al. 2017). While follow-up behavioral-based experiments are needed to determine the mechanisms leading to the habitat type differences in foraging efficiency, two hypotheses can be proposed. First, *C. fornicata*’s 3-dimensional shell matrix likely offered a greater number of interstitial spaces than the 2-dimensional interstitial spaces formed between the base of *Z. marina* mimicked shoots. This likely reduced encounter rate more between predator and prey in *C. fornicata* than *Z. marina*. Second, the interstitial spaces were smaller and more numerous in *C. fornicata* than *Z. marina* (see Table 4), as well as offered robust attachment sites for byssal thread attachment. This could have made *M. edulis* prey more difficult to access in *C. fornicata* than *Z. marina*, increasing *D. sayi*’s prey rejection in the *C. fornicata* habitat type. The differential effects of hard-bottom and vegetative habitats described above could have differently affected prey encounter and accessibility and led to the habitat type effect displayed by *D. sayi*.

In contrast to expectations, the habitat type effects displayed by *D. sayi* were not dependent on prey density. Other studies, including results in Kulp et al. (*in preparation*,
Chapter 2), have suggested that increases in prey density dilutes structural effects (Sponaugle and Lawton 1990) or that scaled increases in predator to prey densities removes structural density effects (Mattila et al. 2008, Canion and Heck 2009, Scheinin et al. 2012). One explanation is that *M. edulis* needed to be at a higher density than used in this study to remove the negative effect of *C. fornicata* structure on feeding rates. Even though the number of mussels used between this study and Kulp et al. (*in preparation*, Chapter 2) were similar (40 vs 30 mussels), the mussels were distributed across difference volumes of *C. fornicata* shell hash. This meant that the highest *M. edulis* density treatment in this study was 175 mussels per m$^2$ compared to 480 mussels per m$^2$. Additional experiments focusing on increasing prey density are needed to determine if there is a prey density at which *C. fornicata* structure no longer negatively affects *D. sayi*’s consumption.

While *D. sayi* displayed a habitat type effect, there were no habitat type effects detected for *C. sapidus* at either size class. The species-specific habitat type effect was likely due to two morphological differences between *D. sayi* and small *C. sapidus*: 1) different claw dimensions and 2) swimmer appendages in *C. sapidus*. Two researchers have scaled interstitial space formed by structure to either predator width (Bartholomew et al. 2000) or the claw surface area (Wong 2013). The interstitial space indices scaled for each of the tested predator group treatments is displayed in Table 4. The Bartholomew (2000) index between *D. sayi* and small *C. sapidus* is similar in both structures. This suggests that small *C. sapidus* movement through structure will be similarly inhibited as *D. sayi*. Conversely, the Wong (2013) index indicates that *C. sapidus* claw movement will be less impacted in both habits than *D. sayi*. The small *C. sapidus*’ crusher claws are longer in length, shorter in height and thinner in width than *D. sayi* (Table 2). These differences in claw dimensions may allow small *C. sapidus* to access *M. edulis*
prey in *C. fornicata* spaces that *D. sayi* is not able to access. Further, the ability of small *C. sapidus* to use their swimmer appendages may provide greater propulsion through the shell hash structure or orient themselves to successfully access *M. edulis* in the shell matrix formed by *C. fornicata*.

Even though the large *C. sapidus* had reduced interstitial space indexes compared to *D. sayi* and small *C. sapidus*, there were no effects of habitat type. The large *C. sapidus* claws likely made some *M. edulis* inaccessible in narrow crevices formed by *C. fornicata*. However, *C. sapidus*’ longer and larger appendages and ability to swim may allow *C. sapidus* to overcome the small spaces formed by the shell hash matrix by moving the loose shells out of the way. Further, the large *C. sapidus* may use appendages other than their claws to isolate *M. edulis* prey similar to the *C. maenas* using their legs to isolate *M. mercenaria* (Wong 2013). On the other hand, the large *C. sapidus* may have eaten the *M. edulis* mussels sooner than *D. sayi* or small *C. sapidus*. The *M. edulis* prey has the ability to change its orientation, position and byssal thread attachment (Lee et al. 1990, Reimer and Tedengren 1996). If given less time, *M. edulis* individuals may have had fewer and weaker byssal threads and may not have moved as deep within the shell matrix, decreasing the prey refuge benefits of *C. fornicata* structure from large *C. sapidus*.

Both *D. sayi* and *C. sapidus* displayed a prey density effect on the proportion of *M. edulis* consumed. This suggests these predators do not have a type I functional response when foraging for bivalve prey (Holling 1959), as has been indicated in functional response experiments for both species (Kulp et al *in preparation*, Chapter 2, Eggleston 1990, Mansour and Lipcius 1991). However, there was an interesting effect of prey density based on predator size. When prey was limiting, large *C. sapidus* consumed almost every available *M. edulis* prey (exception: two out of the 45 replicates ate 6 and 7 mussels instead of 8 mussels). Conversely, even though the small
C. sapidus and D. sayi demonstrated themselves capable of consuming more than 10 mussels (see Figure 1), they never consumed all the M. edulis in the low-prey treatments. The reason for the difference likely lies in the different energetic costs (Elner and Hughes 1978) and claw damage risk (Juanes and Hartwick 1990, Juanes 1992) for D. sayi and small C. sapidus compared to the large C. sapidus. Even though the size range was within the preferred size class for each predator group treatment (10-15 mm; Juanes 1992), there likely exists variation in the shell thickness and likelihood of a M. edulis prey to aggregate and attach themselves in an unfavorable orientation. This could lead to important prey-density effects, where there could be a greater number of the prey in the high-prey treatment with lower energetic costs and risk to claw damage. Thus, prey may have a greater refuge from D. sayi and small C. sapidus at lower prey densities than large C. sapidus. There was also a significant difference detected in proportion of mussels consumed between small and large C. sapidus when prey was saturated. However, this difference detected was likely a result of the way in which the statistical model corrected for differences in the initial number of mussels and predator size, and thus not be ecologically relevant. Assuming the small or large C. sapidus consumption rates would not change with additional mussels, the number of mussels consumed in the high mussel treatment can be directly compared between small and large C. sapidus. After standardizing the number of mussels consumed by predator biomass, the large C. sapidus consumed 35% more mussels than small C. sapidus per gram of body mass. This indicates that the C. sapidus size difference detected in the feeding rate was likely due to the proportion of mussels consumed (bounded between 0 and 1) being more affected by differences in predator biomass than number of mussels consumed.
Results from this experiment suggest that the hard bottom and vegetative structured habitat types did not offer greater prey refuge than the unstructured sand habitat. This contrasts with literature that has indicated structure’s presence enhances prey survival for a variety of bivalve prey in the field (Bertness and Grosholz 1985, Sponaugle and Lawton 1990, Peterson and Heck 2001). Byssal thread attachment and position either in a clump or in a crevice are important defenses *M. edulis* employs to reduce their susceptibility to predation (Reimer and Tedengren 1996). One limitation of this study is that *M. edulis* were given approximately an hour to select their position and orientation, aggregate and attach their byssal threads to the structure. The *M. edulis* prey defenses may not be interacting with *Z. marina* or *C. fornicata* in the same manner they do in the field. While *M. edulis*’s behavioral response is dampened by time and structure benefits likely reduced, this study still demonstrates the effect structure has on *D. sayi* and *C. sapidus* foraging for a prey species that does not rely on movement for escaping predation. Specifically, 1) how *D. sayi* and *C. sapidus* could be affected by different structured habitat types to encounter prey and 2) how a predator’s claw morphology interacts with crevice space in structure to affect prey accessibility. Additional experiments are needed to evaluate how transferrable these results are to the field.

**Conclusion**

This study suggests that both *Z. marina* and *C. fornicata* do not sufficiently impede *C. sapidus* movement or prey accessibility if *M. edulis* is limited by time to select a refuge location and form byssal threads. This study also confirms that *D. sayi* is negatively affected by *C. fornicata* compared to *Z. marina*, supporting other studies that have suggested hard-bottom habitats enhance prey survival over vegetative habitats (Barshaw and Lavalli 1988, Siddon and Witman 2004, Griffen and Byers 2006). This study also illuminates the importance of
considering a prey’s defense strategy against predators, and how structure may enhance, dampen or have no effect on the strategy. For *M. edulis*, who rely on passive prey defenses like byssal thread attachment, interstitial space accessibility and clump formation (Elner 1978, Robles et al. 1990, Leonard et al. 1999, Smith and Jennings 2000), structure may need to enhance these features for the structured habitats to serve as a prey refuge. Habitat refuge value depended on predator-identity and was likely a result of how predator morphology affected prey access within interstitial spaces.

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Table 1. The carapace morphology measurements of the three predator groups: Sayi mud crab (*Dyspanopeus sayi*) and small and large blue crab (*Callinectes sapidus*). A subsample of individuals had their carapace width, carapace length, claw morphology (Table 2) and dried weight taken. The mean ± 1 SD are displayed in the cells.

<table>
<thead>
<tr>
<th>Predator Group</th>
<th>Carapace Width (mm)</th>
<th>Carapace Length (mm)</th>
<th>Biomass (g)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mud</td>
<td>20 ± 0.8</td>
<td>16.4 ± 0.8</td>
<td>1.3 ± 0.2</td>
</tr>
<tr>
<td>Small Blue</td>
<td>35 ± 4.3</td>
<td>19.3 ± 2.6</td>
<td>1.3 ± 0.5</td>
</tr>
<tr>
<td>Large Blue</td>
<td>72 ± 6.2</td>
<td>39.2 ± 3.3</td>
<td>10.9 ± 2.9</td>
</tr>
</tbody>
</table>
Two estimates of claw area were taken. Claw area$^{1}$ was calculated using the same method as Warner and Jones (1976). Two estimates of claw area were taken. Claw area$^{1}$ was calculated using the same method as Warner and Jones (1976). In addition, the mechanical advantage was calculated for each claw type by dividing L1 (length of the finger to the pivot point) by L2 (length from the pivot point to the closer apodeme muscle attachment point; Warner and Jones 1976). Table 2. The claw morphology measurements of the three predator groups: Sayi mud crab (*Dyspanopeus sayi*) and small and large blue crab (*Callinectes sapidus*). A subsample of individuals had their claw length (from the joint to the tip of the dactyl), claw height (tallest point from the base to top of the claw), and claw width (widest point on either side of the claw) measured of both their crusher and slasher claws. In addition, the mechanical advantage was calculated for each claw type by dividing L1 (length of the finger to the pivot point) by L2 (length from the pivot point to the closer apodeme muscle attachment point; Warner and Jones 1976). Two estimates of claw area were taken. Claw area$^{1}$ was calculated using the same method as Wong (2013), where the claw length (not including the dactyl) was multiplied by claw height. Claw area$^{2}$ calculated the cross-section area (if viewing the claw from the front) as an ellipse, using $\frac{1}{2}$ the claw height and width as the two radius measurements. The mean ± 1 SD are displayed in the cells.

<table>
<thead>
<tr>
<th>Predator Group</th>
<th>Mechanical Advantage (L1/L2)</th>
<th>Claw length (mm)</th>
<th>Claw height (mm)</th>
<th>Claw width (mm)</th>
<th>Claw Area$^{1}$</th>
<th>Claw Area$^{2}$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mud</td>
<td>Crusher: 0.404 ± 0.084</td>
<td>15.4 ± 0.7</td>
<td>8.4 ± 1.0</td>
<td>5.3 ± 0.5</td>
<td>56.2 ± 10.9</td>
<td>35.0 ± 6.8</td>
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<tr>
<td></td>
<td>Slasher: 0.352 ± 0.047</td>
<td>13.6 ± 0.9</td>
<td>6.4 ± 0.5</td>
<td>4.0 ± 0.2</td>
<td>36.5 ± 5.1</td>
<td>20.5 ± 2.7</td>
</tr>
<tr>
<td>Small Blue</td>
<td>Crusher: 0.234 ± 0.061</td>
<td>17.2 ± 2.5</td>
<td>4.9 ± 0.7</td>
<td>4.0 ± 0.7</td>
<td>45.6 ± 13.5</td>
<td>15.8 ± 4.9</td>
</tr>
<tr>
<td></td>
<td>Slasher: 0.215 ± 0.069</td>
<td>16.4 ± 2.2</td>
<td>4.5 ± 0.7</td>
<td>3.8 ± 0.7</td>
<td>34.0 ± 34.7</td>
<td>13.9 ± 4.4</td>
</tr>
<tr>
<td>Large Blue</td>
<td>Crusher: 0.253 ± 0.030</td>
<td>38.7 ± 3.9</td>
<td>11.4 ± 1.6</td>
<td>9.1 ± 1.0</td>
<td>230.7 ± 52.1</td>
<td>82.0 ± 19.4</td>
</tr>
<tr>
<td></td>
<td>Slasher: 0.218 ± 0.030</td>
<td>37.6 ± 4.4</td>
<td>10.2 ± 1.0</td>
<td>8.6 ± 1.0</td>
<td>196.6 ± 40.0</td>
<td>68.9 ± 14.0</td>
</tr>
</tbody>
</table>
Table 3. *Zostera marina* and *Crepidula fornicata* field survey habitat metrics (mean ± 1SD).

*Zostera marina* survey was conducted in August 2014 at five different sites in Shinnecock Bay, NY. At each site, shoot density and canopy height was measured in six 1/16 m² quadrats. Additionally, within each of the six quadrats five shoots were selected. Each *Z. marina* eelgrass shoot had the sheath width and shoot height measured. Aboveground and belowground biomass of eelgrass shoots and rhizomes was determined by applying conversion coefficients from a model fit to eelgrass biomass samples taken at three sites in Shinnecock Bay and four sites in an adjacent body of water, Great South Bay, Long Island, NY (aboveground biomass: log(Biomass) = 0.385*log(Shoot Density), R² = 0.880; belowground biomass: log(Biomass) = 0.802*log(Shoot Density), R² = 0.953). The *C. fornicata* field survey was conducted in May 2014 at three different *C. fornicata* shell hash beds in Shinnecock Bay, NY. *Crepidula fornicata* habitat was excavated out of four 0.25 m² quadrat samples taken at each site. The water displacement method was used to determine the volume of shell hash and live *C. fornicata* clumps. Each live *C. fornicata* clump was counted and the number of individuals in the longest chain counted. The number of individuals in a chain ranged from 1 to 12, where the most number of live *C. fornicata* clumps had three in a chain. The number of live *C. fornicata* clump was categorized by either those with at least three individuals in the longest chain or those with more than three individuals. The biomass of shell hash and live *C. fornicata* clumps was determined by fitting a linear model off of subsamples (shell hash: Biomass = 1.93*Volume, R² =0.994 live clumps: Biomass = 1.03*Volume, R² = 0.997). Additionally, within each quadrate, the height of the *C. fornicata* habitat was taken in five random locations.

<table>
<thead>
<tr>
<th></th>
<th>Shoot Density (per m²)</th>
<th>Aboveground dried biomass (g per m²)</th>
<th>Belowground dried biomass (g per m²)</th>
<th>Canopy Height (mm)</th>
<th>Shoot Height (mm)</th>
<th>Shoot Sheath Width (mm)</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Zostera marina</em></td>
<td>653 ± 386</td>
<td>68.0 ± 55.4</td>
<td>315.0 ± 206.5</td>
<td>426 ± 100</td>
<td>440 ± 128</td>
<td>4 ± 1</td>
</tr>
<tr>
<td><em>Crepidula fornicata</em></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Shell hash volume (mL per 0.25 m²)</td>
<td>720 ± 1073</td>
<td>3156 ± 937</td>
<td>1395 ± 2077</td>
<td>3260 ± 968</td>
<td>74 ± 33</td>
<td>84 ± 59</td>
</tr>
<tr>
<td>Clump volume (mL per 0.25 m²)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Shell hash dried biomass (g per 0.25 m²)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Clump dried biomass (g per 0.25 m²)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Clump number (3 individuals stacked per 0.25 m²)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Clump number (&gt;3 individuals stacked per 0.25 m²)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Height (mm)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>367 ± 133</td>
</tr>
</tbody>
</table>
Table 4. *Zostera marina* and *Crepidula fornicata* mesocosm (bottom area = 0.229 m²) treatment structure conditions and estimated structure indexes. For the *Z. marina* habitat treatment, the number of shoots was determined to approximate the mean shoot density from the field survey (Table 3). The structure was mimicked with using green curling ribbon (0.5 x 25 cm, width x height) attached to a circular 10 mm Vexar® black mesh mat, where each *Z. marina* mimic shoot had four ribbon leaves. For the *C. fornicata* habitat treatment, the volume of shell hash was determined from the approximate mean volume of shell hash from the field survey (Table 3). There were 2 and 5 *C. fornicata* shells glued together glued with ethyl cyanoacrylate to mimic the live *C. fornicata* clumps with at least three individuals or greater than three individuals in the longest chain. The number of 2 and 5 *C. fornicata* shells glued into a chain was based off of the approximate mean ± 1 SD number of live *C. fornicata* clumps with at least 3 individuals or more than 3 individuals stacked from the field survey, respectively. The bottom shell in the mimicked clumps was at least 30 mm in shell height (SH), which was within the range of the bottom shell found in the survey (range: 21 - 46 mm SH; mean: 34 ± 6.4 mm SH). The Bartholomew (2000) interstitial index was calculated by taking the mean distance between mimicked *Z. marina* shoots or *C. fornicata* shells and dividing by the mean Sayi mud crab (*Dyspanopeus sayi*) and small and large blue crab (*Callinectes sapidus*) carapace lengths (Table 1). The Wong (2013) interstitial index was calculated by taking the mean area of interstitial space formed by *Z. marina* mimicked shoots or *C. fornicata* shells divided by the mean *D. sayi* and small and large *C. sapidus* crusher claw area1 (Table 2). The modified Wong (2013) interstitial index was calculating by taking the mean area of interstitial space formed by *Z. marina* mimicked shoots or *C. fornicata* shells divided by the mean *D. sayi* and small and large *C. sapidus* crusher claw area2 (Table 2).

<table>
<thead>
<tr>
<th><em>Zostera marina</em></th>
<th>Interstitial Index</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Density Treatment</strong></td>
<td><strong>Shoot number (per mesocosm)</strong></td>
</tr>
<tr>
<td>Middle</td>
<td>145</td>
</tr>
<tr>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th><em>Crepidula fornicata</em></th>
<th>Interstitial Index</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Density Treatment</strong></td>
<td><strong>Shell hash volume (mL per mesocosm)</strong></td>
</tr>
<tr>
<td>Middle</td>
<td>700</td>
</tr>
<tr>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Table 5. Replicate numbers for the three predator group treatments: Sayi mud crab (*Dyspanopeus sayi*) and small and large blue crab (*Callinectes sapidus*). There were four experimental runs conducted in September 2016 with the size-matched *D. sayi* and small *C. sapidus*. There were three experimental runs conducted in July 2016 with the large *C. sapidus*. The number in the parenthesis is the number of the replicates that were not included in the analysis because the crab either molted or was missing from the tub at the end of the experiment. In the experimental runs conducted in September 2016, there was greater replication of the small *C. sapidus* treatments to account for their higher molting rate compared to *D. sayi*.

<table>
<thead>
<tr>
<th></th>
<th>Run 1</th>
<th></th>
<th>Run 2</th>
<th></th>
<th>Run 3</th>
<th></th>
<th>Run 4</th>
<th></th>
<th>Replicate Total</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Low</td>
<td>High</td>
<td>Low</td>
<td>High</td>
<td>Low</td>
<td>High</td>
<td>Low</td>
<td>High</td>
<td>Low</td>
</tr>
<tr>
<td><strong>No Structure</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mud:</td>
<td>2</td>
<td>2 (1)</td>
<td>2</td>
<td>2</td>
<td>1</td>
<td>1</td>
<td>4</td>
<td>4</td>
<td>9</td>
</tr>
<tr>
<td>Small Blue:</td>
<td>2 (1)</td>
<td>2</td>
<td>2 (1)</td>
<td>2</td>
<td>3 (3)</td>
<td>3 (1)</td>
<td>5</td>
<td>4 (1)</td>
<td>12 (5)</td>
</tr>
<tr>
<td>Large Blue:</td>
<td>3</td>
<td>2</td>
<td>3</td>
<td>3</td>
<td>2</td>
<td>3</td>
<td>NA</td>
<td>NA</td>
<td>8</td>
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<tr>
<td><strong>Shell Hash</strong></td>
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<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mud:</td>
<td>2</td>
<td>2</td>
<td>2</td>
<td>2</td>
<td>1</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>5</td>
</tr>
<tr>
<td>Small Blue:</td>
<td>2</td>
<td>2</td>
<td>2</td>
<td>2 (2)</td>
<td>3</td>
<td>3</td>
<td>2</td>
<td>2</td>
<td>9</td>
</tr>
<tr>
<td>Large Blue:</td>
<td>2</td>
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<td>3</td>
<td>3</td>
<td>2</td>
<td>2</td>
<td>NA</td>
<td>NA</td>
<td>7</td>
</tr>
<tr>
<td><strong>Seagrass</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
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<tr>
<td>Mud:</td>
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<td>2</td>
<td>2</td>
<td>2</td>
<td>1</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>5</td>
</tr>
<tr>
<td>Small Blue:</td>
<td>2</td>
<td>2 (1)</td>
<td>2 (1)</td>
<td>2 (1)</td>
<td>3</td>
<td>3 (1)</td>
<td>1</td>
<td>3</td>
<td>8 (1)</td>
</tr>
<tr>
<td>Large Blue:</td>
<td>3</td>
<td>2</td>
<td>3</td>
<td>3</td>
<td>2 (1)</td>
<td>3</td>
<td>NA</td>
<td>NA</td>
<td>8 (1)</td>
</tr>
</tbody>
</table>
Table 6. Generalized linear model assuming quasibinomial error distribution used to test for an effect of predator size on proportion of *Mytilus edulis* consumed. The predator size was modeled with carapace width measurements. A separate model was fit for each predator group: Sayi mud crab (*Dyspanopeus sayi*) and small and large blue crabs (*Callinectes sapidus*).

<table>
<thead>
<tr>
<th>Predator Group</th>
<th>Predator Size Coefficient</th>
<th>z</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mud</td>
<td>0.323</td>
<td>1.9*</td>
</tr>
<tr>
<td>Small Blue</td>
<td>0.082</td>
<td>2.1*</td>
</tr>
<tr>
<td>Large Blue</td>
<td>0.083</td>
<td>4.7***</td>
</tr>
</tbody>
</table>

*** < 0.0001 ** < 0.01 * < 0.05 * < 0.1
**Table 7.** Regression models used to predict dried weights from carapace width values for each predator group: Sayi mud crab (*Dyspanopeus sayi*) and small and large blue crabs (*Callinectes sapidus*). A subsample of each predator group had both their dried weight and carapace measured and incorporated into the following linear model: DriedBiomass = \(X\) * CarapaceWidth.

<table>
<thead>
<tr>
<th>Predator Group</th>
<th>Coefficient Estimate (X)</th>
<th>(R^2)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mud</td>
<td>0.0667***</td>
<td>0.947</td>
</tr>
<tr>
<td>Small Blue</td>
<td>0.037***</td>
<td>0.939</td>
</tr>
<tr>
<td>Large Blue</td>
<td>0.153***</td>
<td>0.965</td>
</tr>
</tbody>
</table>

\(t\) value: *** < 0.0001 ** < 0.01 * < 0.05
Table 8. Type III Wald chi-square test results for the generalized linear mixed model assuming binomial error distribution of the proportion of *Mytilus edulis* consumed.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>df</th>
<th>$\chi^2$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Habitat Type</td>
<td>2</td>
<td>2.30</td>
</tr>
<tr>
<td>Predator Group</td>
<td>2</td>
<td>19.9***</td>
</tr>
<tr>
<td>Mussel Density</td>
<td>1</td>
<td>31.5***</td>
</tr>
<tr>
<td>Predator Size Covariate</td>
<td>1</td>
<td>13.8***</td>
</tr>
<tr>
<td>Habitat Type: Predator Group</td>
<td>4</td>
<td>9.82*</td>
</tr>
<tr>
<td>Predator Group: Mussel Density</td>
<td>2</td>
<td>16.7***</td>
</tr>
<tr>
<td>Habitat Type: Mussel Density</td>
<td>2</td>
<td>2.79</td>
</tr>
</tbody>
</table>

*** < 0.0001 ** < 0.01 * < 0.05
Figure 1. Boxplot of proportion of mussels consumed across the three habitat type treatments: sand, mimicked eelgrass (*Zostera marina*), and mimicked slipper snail (*Crepidula fornicata*) shell hash. The predator group, Sayi mud crab (*Dyspanopeus sayi*) and small and large blue crabs (*Callinectes sapidus*), were differentiated by an increasing gradient from light to dark grey. The unstandardized feeding rate (A, B) was calculated as the proportion of mussels consumed per individual; the standardized feeding rate (C, D) was calculated as the proportion of mussels consumed divided by the dried biomass of the individual. Dried biomass was estimated using the regression models displayed in Table 7. The low *Mytilus edulis* prey density treatment (A, C) and high *M. edulis* prey density treatment (B, D) had different initial starting values depending on the predator group. The *D. sayi* and small *C. sapidus* had either 10 or 40 initial number of mussels, whereas the large *C. sapidus* had either 8 or 200 initial number of mussels.
Chapter 4

Investigating whether *Zostera marina* alleviates intraspecific competition in mesopredators
Abstract

Intraspecific competition among foragers become more pronounced as species population density increases and may be mediated by habitat structure. The role of habitat structure on foraging by omnivorous crabs was assessed across increasing mimicked *Zostera marina* habitat densities. Competition between one, three, and six *Dyspanopeus sayi* individuals was compared across five levels of increasing seagrass habitat density: 0, 100, 200, 800, and 1200 shoots m\(^{-2}\). *Zostera marina* had no effect on foraging at any predator density. Further, no emergent effects of predator density were detected when predator density doubled from three to six predators. Additional experimentation is needed in order to determine whether intraspecific competition occurring among three individuals negatively affects individual feeding rates. If interference among predators does not affect foraging rates, then predator-prey populations could become destabilized above a predator density threshold. Future studies quantifying predator behavior as predator density increases will assist in clarifying the mechanisms that lead intraspecific competition to either not change *D. sayi* feeding rates or not increase when predator density increases past three predators. Further, this study indicates that eelgrass structure may not alter *M. edulis* prey risk with one or multiple predators present.
Introduction

Competition is an important ecological process that leads to shifts in population distributions, morphological features, and species compositions. In addition to reducing prey resources by exploitative competition, a predator can interfere with the ability of another predator to consume a targeted prey resource through interference competition (i.e. Clark et al. 1999b, Smallegange et al. 2007). Depending on the form of antagonistic interaction and resource availability, interference competition could have greater impacts than exploitative (Amarasekare 2002, Holdridge et al. 2016). Further, interference competition, which can affect predator capture rates at high predator densities, has been shown to stabilize predator-prey population dynamics (DeAngelis et al. 1975, Sih 1979, Anders 2001), making interference an important ecological feature to understand.

The type of antagonistic interaction ranges in severity from avoidance to lethal physical contact. Non- or sub-lethal energetic costs from antagonistic interactions include increased foraging and handling time (Clark et al. 1999b, Griffen and Delaney 2007, Smallegange et al. 2007), decreased foraging efficiency (Crowley et al. 1987), and selection of suboptimal prey (Smallegange and van der Meer 2009, Griffen et al. 2011, Peterson et al. 2014). Long-term effects of these energetic costs can lead to negative effects on growth and reproduction (Griffen et al. 2011). Extreme forms of interference competition can cause intraguild predation (Finke and Denno 2002) or cannibalism (Mansour and Lipcius 1991, Moksnes et al. 1997, Wildy et al. 2001, Rudolf 2007) that directly reduce predator populations.

Interference competition among similarly matched individuals tends to be greater than asymmetric competitors (i.e. Smallegange and van der Meer 2006). Conspecifics have similar dietary demands and feeding apparatus and therefore interference effects should be greater than
among heterospecifics. Studies comparing and contrasting between conspecific and heterospecific predators have confirmed that conspecific interference competition is usually greater (Griffen and Williamson 2008, de Villemereuil and López-Sepulcre 2011, Peterson et al. 2014). Predator density may also modify intraspecific competition. Numerous studies have shown that per capita consumption rates tend to decline as conspecific predator density increases, though often in a non-linear or non-additive relationship (Mansour and Lipcius 1991, Abrams 1993, Mistri 2003, Griffen and Williamson 2008). Body damage, prey search time, handling time, and time spent in antagonistic interactions have been shown to increase with conspecific predator abundance (Mansour and Lipcius 1991, Smallegange et al. 2006, Griffen and Williamson 2008) and could contribute to the decreasing per capita consumption rates often detected.

Even though increasing conspecific density has been linked with increasing competition effects, the habitat landscape in which conspecifics forage may alleviate predator density effects. Structure has been shown to reduce the encounter and capture rate between predator and prey (Nelson 1979, Heck and Orth 1980, Crowder and Cooper 1982) by reducing predator movement, altering the path trajectory (Ryer et al. 2004, Hovel et al. 2016), and visually obstructing the prey’s location (Main 1987, Ryer 1988). Mutual interference (i.e. conspecific antagonistic interactions) may similarly be impacted by structure and reduce predator density consumptive effects. Structure has been shown to alter higher-order interactions that occur among multiple predator species foraging (Finke and Denno 2002, Griffen and Byers 2006, Hughes and Grabowski 2006, Janssen et al. 2007), reducing the predator interference and increasing prey risk (Grabowski and Powers 2004). Further, predator and prey abundances need to be considered to better understand the role of habitat complexity because often faunal densities positively
correlate with structure density (see Mattila et al. 2008 for further discussion). For instance, in studies that scaled predator and prey abundances with habitat density either no longer had an effect of habitat density on collective consumption rates or the pattern changed (Mattila et al. 2008, Canion and Heck 2009, Scheinin et al. 2012). An important next step is to isolate predator density effects from prey density effects, which will in turn assist in understanding whether predator density increases lead to the removal of structure density effects.

The focus of this study was to test the effect of submerged aquatic vegetation on intraspecific competition in the crustacean predator *Dyspanopeus sayi*. *Dyspanopeus sayi* was selected because they are ubiquitous predators (Carroll 2012) that engage in antagonistic interactions (R. Kulp pers. obs.). Consumption rates were compared across increasing *D. sayi* density when mimicked eelgrass, *Zostera marina*, shoot density was also increased to test the following questions: 1) how does habitat density alter intraspecific competition? and 2) how does habitat density affect predator-prey relationships when predator density is increased? Structure density was expected to impede foraging of a single-predator, supporting previously documented habitat complexity relationships (Nelson 1979, Heck and Orth 1980, Crowder and Cooper 1982). However, as predator-density increased, increases in structure density was expected to reduce structure’s positive effect on prey survival by reducing intraspecific competition among conspecifics.

**Methods**

**Mesocosm experiments**

Over five weeks in July and August 2014, mesocosm experiments were conducted testing the effect of *Z. marina* structure on intraspecific interactions between *D. sayi* individuals. The study was conducted in an outdoor flow-through mesocosm system (flow rate = 5.0 ± 1.4 L/min
[mean ± 1 SD]) at the Stony Brook University Marine Station, Southampton, NY (40.8845°N,72.4418°W). A 95 L Tuff Stuff tub (bottom diameter: 0.54 m; bottom area: 0.229 m²) was used for each mesocosm replicate. There were three different D. sayi abundances (14 - 16 mm carapace width; 1, 3 and 6 individuals per mesocosm) tested in one of five Z. marina structure treatment levels (0, 200, 400, 800, and 1200 eelgrass shoots m⁻²). There was one replicate of each treatment level combination in the nine experimental runs conducted. To ensure relevant structure and predator densities, treatment levels were chosen to match densities found in Shinnecock Bay, the body of water closest to the Marine Station. Table 1 provides a summary of habitat structure metrics and D. sayi densities from one of the surveys conducted in Shinnecock Bay eelgrass beds. Male D. sayi individuals with at least 7 legs and both claws intact were collected from Crepidula fornicata and Mytilus edulis mixed shell hash beds in Shinnecock Bay (40.8370°N,72.5051°W) and held no more than 2 days prior to being starved for 24 hours and used in experimental runs. Any replicates where a crab molted or died during the experimental run were removed from analysis.

Structure of Z. marina habitat was mimicked using artificial seagrass units (ASUs), which had green curling ribbon (0.5 x 25 cm [width x height]) tied to a circular Vexar® black mesh mat with 10 mm aperture; the mat was buried under 7.6 cm of sand. Each mimic of Z. marina shoot had four leaves, which floated upright in the water column. Artificial seagrass structure has been commonly used to mimic seagrass habitat (Bologna and Heck 1999, Canion and Heck 2009, Carroll et al. 2012). Fauna has also been shown to behave similarly in ASUs as seagrass beds (Healey and Hovel 2004).

Mytilus edulis was selected as the prey item, as it is a common prey resource in Shinnecock Bay seagrass beds (Table 1). There were 100 M. edulis (8 - 12 mm shell height)
added to each mesocosm for a 36-hour experimental period that was initiated at dusk. Preliminary experiments indicated 100 mussels were never completely consumed by six predators, suggesting prey was saturated at the greatest predator density. In addition to having one replicate for each of the 15 treatment level combinations, a control with the 1200 shoot density ASU was also tested with no predator added. The control was used to determine natural mussel mortality and the processor’s ability to recover shellfish. The ASUs were thoroughly checked for mussel attachment and the sand was sieved through a 3-mm aperture sieve to recover all live mussels. Any mussels not recovered were assumed consumed. Mussel mortality in controls was 0.6 ± 0.97 individuals per mesocosm and we had a 96.3 ± 0.04 % recovery. Environmental conditions followed ambient conditions (temperature: 21 - 28°C; salinity: 26 - 31). HoBo® data loggers were placed in mesocosms located at the ends of each plumbing line. Temperatures between mesocosms had small variation with a maximum mean difference of 1.6°C ± 1.4°C. Considering the effect temperature has on metabolism and feeding rates (Newell and Branch 1980, Whetstone and Eversole 1981), the temperature range across mesocosms and experiments likely impacted feeding rates.

*Data analysis*

All statistical tests were conducted using R Statistical Software version 3.4.1 (R Core Team 2017). A two-way factorial (predator density x *Z. marina* shoot density) linear mixed model (LMM) with experimental block treated as a random variable (Logan 2010) was fitted using the ‘lme4’ package (Bates et al. 2015) with restricted maximum likelihood estimation to determine if structure density effects on collective consumption rates changed as predator density increased. Main and interactive effects were evaluated using a type III Wald chi-square test in the ‘car’ package (Fox and Weisberg 2011). Pairwise post-hoc chi-square tests were performed
on the highest-order significant groups with multiple comparisons corrected by using the Holm-Bonferroni method in the ‘phia’ package (De Rosario-Martinez 2015).

Effects of structure and predator density were additionally evaluated using per capita feeding rates. Per capita feeding rates that change with predator density provide evidence that intraspecific competition is altering top-down control by predators. Because LMM model assumptions of normality and homogeneity were violated even after transformations, per capita consumption rates were compared using the bias-corrected Hedges’ $g$ effects size (Hedges and Olkin 1985 equation 1)

$$g = \frac{\bar{x}_T - \bar{x}_C}{s} J$$

(1)

where $\bar{X}$ is the mean number of mussels consumed, $T$ the treatment groups, and $C$ the comparison group treatment. The term $S$ is the pooled standard deviation between the 2 groups being compared. The term $J$ corrects for small-size bias. There were three sets of bias corrected Hedges’ $g$ calculations made to determine whether 1) three and six predators reduced per capita consumption rate compared to a single predator when grouped by shoot density, 2) increases in shoot density above 0 changes foraging without considering predator density and 3) increases in predator density above one changes foraging without considering shoot density. For each of the three calculations, the $T$ and $C$ groups were as following: 1) $T$ the three and six predator density treatments grouped by shoot density and $C$ the single predator density treatment grouped by shoot density, 2) $T$ the 100, 200, 800 and 1200 shoots per m$^2$ treatment groups and $C$ the 0 shoot per m$^2$ treatment group, and 3) $T$ the three and six predator treatment groups and $C$ the single predator group. Biased-corrected and accelerated (BCa) bootstrapped 95% confidence intervals (CIs) were calculated for each Hedges’ $g$ effect size using the ‘bootES’ package in R (Gerlanc and Kirby 2015).
To further evaluate intraspecific competition, an expected feeding rate assuming no competitive interactions was calculated and then compared to observed feeding rates. The expected feeding rate of six crabs was determined by modifying the multiplicative risk model (equation 2) that has typically been used to calculate multiple predator effects between two species (Soluk and Collins 1988, Soluk 1993, Sih et al. 1998):

\[ P_{e_{s1+s2}} = P_s1 + P_s2 - (P_s1 * P_s2) \]  

where \( P_s1 \) and \( P_s2 \) is the proportion of prey consumed by species 1 and 2 in isolation and \( P_{e_{s1+s2}} \) is the expected proportion of prey consumed when species 1 and 2 are together and have multiplicative predation effects. The equation also takes into account reduced prey consumption caused by the other species’ consumption.

The expected proportion of prey consumed for the predator treatment with six crabs \( (P_{e_{c6}}) \) was calculated using the proportion of prey consumed when three crabs were present \( (P_{c3}; \text{equation } 3) \).

\[ P_{e_{c6}} = 2(P_{c3}) - P_{c3}^2 \]  

Equation 3 was used to calculate the expected consumption for six crabs at each shoot density level for each experimental run. If the conspecific predator effects are multiplicative, then the expected consumption would not be different from the observed consumption. A two-way LMM was built with expected and observed consumption rates treated as levels of one factor and shoot density treated as a second factor. Experimental run was treated as a random factor. The main and interactive effects, as well as post-hoc comparisons were evaluated using the same procedure as the LMM described above.

Appropriate model diagnostics were run on each analysis to assess models; statistical significance \( \alpha \) was set at 0.05.
Results

There was a significant interaction between predator density and habitat density on the number of *M. edulis* consumed (Fig. 1; $\chi^2 = 16.1$, $P = 0.041$), though all pairwise comparisons among predator density treatments with shoot density fixed were significantly different ($P < 0.01$). Further, shoot density did not have any effect on predator foraging at any predator density (pairwise comparison among shoot density with predator density fixed: $P > 0.3$). Thus, habitat density did not impede foraging (main effect: $\chi^2 = 4.78$, $P = 0.311$); mean feeding rates were less than 16% different among shoot density treatment levels. However, as predator density increased, consumption significantly increased (main effect: $\chi^2 = 70.3$, $P < 0.001$). Consumption approximately doubled when crab density increased from 1 to 3 individuals and approximately quadrupled when increased from 1 to 6 individuals, leading to different consumption amounts among predator density treatment levels (orthogonal pairwise comparisons: $P < 0.001$).

When three and six predators were present, the per capita consumption rates were no different within each shoot density treatment group compared to when a single predator foraged (Fig. 2A). There was also not an overall effect of mimicked *Z. marina* structure at any shoot density above zero shoots (Fig. 2B). However, when per capita consumption rates were grouped by only the predator density treatments, the three and six predator treatments were less than a single predator’s per capita consumption rate (Fig. 2C). One *Dyspanopeus sayi* consumed 34% and 58% more mussels when by itself than with two or five additional predators present, respectively. Along with the mean per capita consumption rates, the standard deviation also declined with predator additions (one crab: 12.6 mussels per predator, three crabs: 5.3 mussels per predator, and six crabs: 2.9 mussels per predator). The decrease in mean per capita consumption when more than one predator was present may indicate prey risk is enhanced from intraspecific
competitive effects. Conversely, the observed and expected consumption rate for six predators were not different from one another (Fig. 3; $\chi^2 = 0.290, P = 0.590$). Thus, predator density doubling from three to six predators did not produce emergent effects on top-down control. The lack of 1) a predator density effect within each shoot density treatment and 2) any emergent effects from predator density doubling suggests predator additions may linearly increase top-down control.

**Discussion**

This study sought to examine whether 1) the submerged aquatic vegetation, *Z. marina*, reduces intraspecific competition among the crustacean predator *Dyspanopeus sayi* and 2) if the presence of structure reduces intraspecific competition as predator density increases. Results indicate that mimicked *Z. marina* presence and shoot density had no effect on a *D. sayi* foraging on *M. edulis* regardless of predator density. Further, the intraspecific competition effects on top-down control did not change between three and six predators, such that no emergent effects were detected due to predator density doubling. However, it is unclear whether intraspecific competition was occurring among three individuals since no differences in per capita consumption rates were detected between three or six predators when feeding rates were compared within the mimicked *Z. marina* treatments.

A lack of a statistical effect for the mimicked *Z. marina* treatment does not necessarily indicate there was no effect of *Z. 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 indicated that the LMM’s power was less than 0.5 due to the low replication of each of the 15 treatment groups. However, when a Hedges’ *g* effect size (Hedges and Olkin
1985 equation 1) was calculated for each Z. marina treatment group with shoots compared to the no-structure (0 shoots per m$^2$), the BCa bootstrapped 95% CIs included zero. This supports that eelgrass structure did not negatively affect D. sayi’s top-down control on M. edulis in a laboratory setting, even if the LMM statistical output cannot confirm no effect of eelgrass structure.

Results from this study amplify a recent functional response laboratory study, where the type II functional response parameters were unchanged by the mimicked Z. marina shoot density (R. Kulp unpubl. data). The lack of a Z. marina habitat structure density effect on a single D. sayi’s foraging on M. edulis in both studies contrasts with trends typically shown in habitat complexity studies (Nelson 1979, Heck and Orth 1980, Crowder and Cooper 1982), which have consistently demonstrated that habitat structure impedes predators like D. sayi with a mobile foraging. For these predators, structure has been shown to visually and physically limit the predator (Main 1987, Ryer 1988, Lee and Kneib 1994, Wong 2013), altering their search and capture patterns (Ryer et al. 2004, Lannin and Hovel 2011, Hovel et al. 2016). Further, mobile prey has been shown to additionally enhance the habitat refuge value by behaviorally modifying their location in the structure to decrease the number of predator-prey encounters (Main 1987, Ryer 1988, Stoner 2009). An additional contrast between this study and others is that D. sayi and similar crustacean species have been 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. 2015b).

One explanation for the difference in results between this study and others is that M. edulis prey defenses may not have been enhanced or complemented by mimicked Z. marina structure under the laboratory 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). Rather than mobile defenses, *M. edulis* relies on shell thickness, orientation, byssal attachment, and clumping to deter predation (Elner 1978, Bertness and Grosholz 1985, Robles et al. 1990, Smith and Jennings 2000). *D. sayi* is likely able to cover the surface area of the mesocosm even when impeded by eelgrass shoots and consistently find *M. edulis* before the end of the experiment. This leads to a new hypothesis that the limiting factor of a successful predation capture on *M. edulis* may be in the steps that occur after a prey 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 requirement of opening the shell to access tissue after the prey is isolated that may lead to a prey being rejected.

Structure has been shown to amplify the passive prey features in other shellfish species. For instance, the bay scallop (*Argopecten irradians*) benefits from attaching to shoots above the sediment within the seagrass canopy (Pohle et al. 1991, Ambrose and Irlandi 1992) and the semifaunal mussel (*Modiolus americanus*) benefit from rhizomal attachment (Peterson and Heck 2001). Even though there were occasions where *M. edulis* was found byssally attached to mimicked shoots, the majority were found in various sized clumps in-between shoots on the sediment surface. In the field, *M. edulis* may benefit from *Z. marina* presence. However, in this study, mussels may not have had enough time to distribute themselves among the *Z. marina* structure before predators were added one to four hours later, preventing beneficial habitat refuge from being detected. Regardless, this study suggests that any effect mimicked *Z. marina* had on *D. sayi*’s ability to encounter and successfully capture *M. edulis* was not enough to lower consumption rate. Follow-up behavioral studies focusing on quantifying *M. edulis*’ use of the *Z.*
marina are needed to determine if there are situations where *M. edulis* can benefit from mimicked *Z. marina* presence, as well as whether *M. edulis* benefit from eelgrass beds in the field.

Predators, particularly decapod predators, have been shown to engage in antagonistic interactions that can lead to prolonged handling time, kleptoparasitism, body damage, and less time spent searching for food (Mansour and Lipcius 1991, Smallegange et al. 2006, Griffen and Delaney 2007, Griffen and Williamson 2008). Further, as predator density increased, handling time increased, along with the total time spent in aggressive interactions (Mansour and Lipcius 1991, Clark et al. 1999b, Smallegange et al. 2006, Griffen and Delaney 2007, Griffen and Williamson 2008). This than led to non-linear decreases in per capita consumption rates. However, in this study, there was no evidence intraspecific competition altered the potential of top-down control when predator density doubled from three to six predators. To determine whether the lack of a difference between observed and expected consumption rates was due to low replication, a power analysis was conducted using the effect size calculated by the LMM. The simulated power value was less than the suggested 0.8, indicating that there was not a high enough replication to detect a difference. Alternatively, when BCa bootstrapped 95% CIs were calculated for the Hedges’ *g* effect size (Hedges and Olkin 1985 equation 1) between the expected and observed consumption rate of *M. edulis* by six predators with or without grouping by shoot density treatment the 95% CIs included zero. This suggests that any intraspecific interactions that were occurring among three predators did not lead to emergent predator density effects when predator density doubled to six.

While the multiplicative risk model suggests intraspecific competition did not change when predation density doubled to six, determining whether intraspecific competition occurred
among the three predators is difficult without direct observations of individual consumption rates and aggressive behaviors. Outside of this study, the *D. sayi* have been observed stealing food from one another, engaging in fights, demonstrating avoidance behavior, cannibalism after a conspecific molted, and removing limbs when in close proximity (R. Kulp pers. obs.). Thus, it was expected that top-down control of multiple *D. sayi* would be reduced due to mutual interference occurring. Even though the mean per capita consumption rates declined with more than one predator present, the lack of a Hedges’ *g* effect size between multiple predators and a single predator across any of the shoot density treatments negates the conclusion that intraspecific competition reduced the top-down control of three *D. sayi* on *M. edulis*. Further, the lack of an effect of shoot density among the predator density treatments suggests either that 1) eelgrass did not alter intraspecific competition or 2) intraspecific competition was not strong enough to be affecting top-down control. The per capita feeding rates calculated in this study assumes equal consumption among all individuals and will not be able to detect unequal consumption rates due to aggressive interactions. In addition, there may be long-term energetic costs associated with potential body damage from encounters or reduced intake rate not able to be detected in this study. Thus, while it is likely intraspecific competition is occurring among individuals, there is not strong enough evidence from this study to determine whether intraspecific competition among three predators led to a reduction in top-down control.

**Conclusion**

In this study, *Z. marina* presence did not improve *M. edulis*’s survival, a result different from previous habitat studies (Nelson 1979, Heck and Orth 1980, Crowder and Cooper 1982). Further, mutual interference did not change when three or six predators were present. Since it is unclear whether intraspecific competition occurred among three predators, no conclusions about
whether or not *Z. marina* altered intraspecific competition can be made. Antagonistic competitive interactions among conspecifics have been suggested to stabilize predator-prey relationships by reducing top-down effects (DeAngelis et al. 1975, Sih 1979, Anders 2001). If mutual interference remains constant regardless of predator density doubling, or does not alter top-down control, then predator additions could de-stabilize predator-prey populations. Prey that do not benefit from habitat structure could be driven to local extinction in systems where mutual interference among predators does not change with predator density increases.

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A field survey was conducted in *Zostera marina* beds in July 2014 in Shinnecock Bay, NY to evaluate natural *Dyspanopeus sayi*, *Mytilus edulis* and *Z. marina* shoot densities. Three different *Z. marina* beds were evaluated. At each eelgrass bed, three 1 m² quadrats were suction sampled and *D. sayi* individuals greater than 10 mm in carapace width (CW) were measured and sexed. Adjacent to the 1 m² quadrats, six 0.625 m² quadrats measuring *Z. marina* shoot were taken. Additionally, mussels were excavated from the quadrat and mussels were counted. Shell heights (SH) were measured for mussels greater than 40 mm SH. Of the remaining mussels less than 40 mm SH, 30 mussels were randomly selected to obtain a SH range. Values displayed are the mean ± 1 SD.

<table>
<thead>
<tr>
<th>Mud Crab Density (per m²)</th>
<th>Mussel Less than 40 mm Density (per m²)</th>
<th>Mussel Greater than 40 mm Density (per m²)</th>
<th>Mussel Size Range (less than 40 mm)</th>
<th>Mussel Size (greater than 40)</th>
<th>Shoot Density (per m²)</th>
<th>Shoot Density Range (per m²)</th>
<th>Aboveground Dried Biomass (g per m²)</th>
<th>Belowground Dried Biomass (g per m²)</th>
</tr>
</thead>
<tbody>
<tr>
<td>21 ± 9</td>
<td>3365 ± 2684</td>
<td>133 ± 264</td>
<td>3 - 39</td>
<td>6.5 ± 3.1</td>
<td>447 ± 223</td>
<td>192-1024</td>
<td>58.7 ± 44.7</td>
<td>231.0 ± 133.1</td>
</tr>
</tbody>
</table>
Figure 1. Total number of mussels consumed by *Dyspanopeus sayi* across increasing mimicked *Zostera marina* shoot density when predator density was 1 crab (A), 3 crabs (B), or 6 crabs (C). Shoot density increased from 0 to 1200 shoots per m². The least square mean estimated from the LMM are shown by the black dots and the error bars are 1 SE estimated from the LMM. The grey x’s are the raw data values. Only predator density affected total consumption rates (main effect: $\chi^2 = 70.3$, $P < 0.001$) such that consumption rates significantly increased as predator density increased (pairwise comparison: $P < 0.001$).
Figure 2. Hedges’ $g$ effect sizes (equation 1) of per capita mussel consumed by *Dyspanopeus sayi* when examining predator density effects across shoot density (A), only examining shoot density effects (B), or only predator density (C). The dashed grey line at zero indicates no effect of A) shoot density within each predator density, B) shoot density or C) predator density.
Figure 3. Expected versus observed consumption rates for six predators using the multiplicative risk model (Soluk and Collins 1988, Soluk 1993, Sih et al. 1998). The least square mean estimated from the LMM are shown by the black dots and the error bars are 1 SE estimated from the LMM. The grey x’s are the raw data values. Values were grouped by Zostera marina shoot density because the interaction and shoot density did not affect consumption rates. Expected and observed feeding rates were not different from one another ($\chi^2 = 0.294$, $P = 0.588$).
Chapter 5

The effect of a shell hash habitat (*Crepidula fornicata*) on intraspecific competition among mesopredator crustacean *Dyspanopeus sayi* predators
Abstract

Small predators can reach high densities in structured habitats, likely increasing intraspecific competition. However, this increase in competition may be less than expected due to habitat structure reducing predator-predator encounters. The crustacean mesopredator Sayi mud crab (*Dyspanopeus sayi*) can reach densities that exceed 60 individuals per m² in the hard-bottomed slipper snail (*Crepidula fornicata*) shell hash habitat, making this an ideal system to study structure’s effect on conspecific competition. Competition among two or four *D. sayi* predators were compared across increasing *C. fornicata* habitat structure density (low and high) using a functional response approach. Prey density effects on consumption were predator-dependent. Thus, the per capita consumption rates were best explained by the ratio-dependent functional response, which accounts for predator density in the initial number of prey available. Further, there was no evidence that mutual interference increased with predator density increase or that structure increase alleviated mutual interference effects. Habitat structure increases reduced per capita feeding rate, though this inverse relationship depended on predator and prey density. Habitat structure increases did not significantly reduce per capita feeding rate when prey was limiting and predator density doubled. As such, an increase in structural complexity may not increase the prey refuge value at low prey densities if predator density is high enough. Conversely, predator density increase did not reduce the negative structure effect when prey was saturated and may have led *D. sayi* and prey to interact with *C. fornicata* differently. This study suggests that saturating the system with prey may not overcome habitat complexity effects if multiple conspecifics are present.
Introduction

Mutual interference can be an important process in regulating top-down control on prey populations. Mutual interference results from antagonistic interactions that occur from conspecifics interacting with one another or simply being present. Mutual interference effects can range in severity from non-lethal body damage or reduced time spent foraging (Clark et al. 1999b, Griffen and Delaney 2007, Smallegange et al. 2007) to lethal body damage or cannibalism (Mansour and Lipcius 1991, Moksnes et al. 1997, Wildy et al. 2001, Rudolf 2007). Predator-prey population model simulations have indicated that mutual interference stabilizes predator and prey populations, and may be an important feature in preventing local species extinction (DeAngelis et al. 1975, Sih 1979, Anders 2001). Experimental manipulation has validated that mutual interference among antagonistic conspecifics leads to prey risk reduction (e.g. Griffen and Williamson 2008), supporting that mutual interference could stabilize predator and prey populations. Mutual interference may also depend on predator density, as predator density increases can lead to non-linear reductions in per capita feeding rates (Mansour and Lipcius 1991, Mistri 2003, Smallegange et al. 2006). Further, increased in conspecific density has been linked with increased search and handling time (Smallegange et al. 2006, Griffen and Williamson 2008), as well as increased predator-predator encounters that result in body damage or cannibalism (Mansour and Lipcius 1991, Clark et al. 1999b) that can reduce individual foraging efficiency.

An additional consideration when examining predator density effects on mutual interference is that interfering predators often encounter one another within a structured environment. Habitat structure has been repetitively shown to interfere with mobile predators’ ability to find their prey (see review by Heck and Orth 2006), leading to habitat structure being
considered an important prey refuge from predation. Habitat structure decreases the encounter rate between predator and prey through visually or physically impeding the predator as they forage for food (Main 1987, Ryer 1988, Ryer et al. 2004, Hovel et al. 2016). In the same way, structure could visually or physically prevent conspecifics from encountering one another, alleviating mutual interference effects. Studies examining the effect of structure on multiple predators have supported that habitat structure can reduce antagonistic interactions, increasing prey mortality (Finke and Denno 2002, Grabowski and Powers 2004, Hughes and Grabowski 2006).

While habitat structure effects on competition has been examined, the effect habitat structure density has on predator density effects is less well understood. Studies examining predator density effects in increasing habitat complexity have found that structure density increases can have a positive (Swisher et al. 1998), negative (Grabowski and Powers 2004), or neutral effect (Anholt 1990, Corkum and Cronin 2004, Simkins and Belk 2017) on prey survival. The variability in the possible effects of structural increases on competitive interactions likely depends on the mechanism by which structure alters a predators’ ability to detect or interact with another predator and species-specific aggression. Another important consideration regarding habitat density effects on competition is that prey density may modify interference effects. Prey density has been shown to alleviate antagonistic interaction effects (DeAngelis et al. 1975, Mansour and Lipcius 1991, Smallegange and van der Meer 2006). Thus, structure’s effect on mutual interference may also be conditional on prey saturation level. Studies that have scaled the predator and prey density with increases in habitat density (Mattila et al. 2008, Canion and Heck 2009, Scheinin et al. 2012) have either found no effect of habitat density or a different relationship between habitat density and consumption rate than when predator and prey
abundances were kept constant. However, in scaling predator to prey ratios with habitat complexity, it is difficult to disentangle the effects that habitat structure and prey density each have on intraspecific competition.

One way to examine how prey density affects habitat density and predator density is through a predator’s functional response (Holling 1959), which examines how prey density affects per capita feeding rate. If predator density effects such as interference affect per capita feeding rate, then the functional response may be better represented by a predator-dependent instead of a prey-dependent model (Hassell and Varley 1969, DeAngelis et al. 1975, Abrams and Ginzburg 2000). While controversy exists as the correct way to incorporate predator-density effects in a predator’s functional response (Abrams 2015), there is empirical evidence that a predator-dependent functional response can be used to assess predator density effects (Kratina et al. 2009, Hossie and Murray 2016, Prokopenko et al. 2017). Intraspecific competition among the crustacean mesopredator *Dyspanopeus sayi* was evaluated across increasing shell hash (*Crepidula fornicata*) habitat through a functional response approach. This study sought to evaluate 1) if increases in habitat structure reduces competitive effects among conspecifics and 2) whether prey density changes the relationship between habitat density and intraspecific competition. Previous experiments indicate that increases in *C. fornicata* shell hash impede a single predator’s foraging and is more pronounced when prey is limited (Kulp et al. *in preparation*, Chapter 2). Similarly, increases in *C. fornicata* habitat are expected to negatively affect consumption rates when prey is limiting. Further, the system is expected to have a predator-dependent functional response. However, structure increases are expected to reduce mutual interference effects among *D. sayi*, which will be more pronounced when prey is limiting.
Methods

Mesocosm experiments

From June to August 2015, the effect *C. fornicata* shell hash habitat has on intraspecific competition was tested in outdoor mesocosms. Mesocosm experiments were conducted using a continuous flow-through water system (flow rate = 4.3 ± 1.58 L/min [mean ± 1 SD]) at the Stony Brook University Southampton Marine Station (40.8845°N 72.4418°W). Two different predator density treatments (two and four *D. sayi* individuals, 18-22 mm carapace width) were tested across two *C. fornicata* habitat densities (low and high). *Dyspanopeus sayi* predator densities used in this study were within the range of the predator densities found in *C. fornicata* shell hash beds in Shinnecock Bay, NY (Table 1). There were eight *M. edulis* prey (10-15 mm shell height) density treatments (2, 4, 6, 8, 10, 25, 40, and 70 mussels per 0.062 m² mesocosm). Across 34 mesocosm tubs, one replicate of the 32 treatments were tested during each of the nine experimental runs, along with two no-predator controls. The no-predator controls had the highest prey density added to either low or high *C. fornicata* habitat densities. These were used to both quantify natural mussel mortality, as well as the processor’s ability to recover all mussels placed into the mesocosm.

The low and high *C. fornicata* shell hash habitat treatments represented 1 SD below and above the mean clump abundance and loose shell volume found in Shinnecock Bay *C. fornicata* shell hash beds (Tables 1 and 2). Previous experiments (Kulp et al. *in preparation*, Chapter 2) indicated that a single *D. sayi* had similar consumption in no-structure as low *C. fornicata* habitat treatment and middle as high *C. fornicata* habitat treatment. Thus, to limit the number of treatment combinations only the low and high *C. fornicata* habitat treatments were tested to reflect the two extreme habitat densities *D. sayi* may be exposed to in the field. *Crepidula*
fornicata clumps were mimicked using sun-bleached C. fornicata shells artificially stacked with two or five shells using ethyl cyanoacrylate. Shell hash consisted of loose C. fornicata shells collected from resident C. fornicata beds or beaches.

Due to the logistical constraints with processing high C. fornicata habitat density treatments, an 18.9 L white conical bucket (bottom diameter: 0.28 m; bottom area: 0.062 m²) that sat in the middle of a plumbed 95 L Tuff Stuff conical tub (bottom diameter: 0.54 m; bottom area: 0.229 m²). The bottom of the bucket was cut-off and covered with 2 layers of mesh (2 mm window screen on top of 5 mm Vexar). There was 2 cm of sand added to the bottom of the 18.9 L conical bucket prior to the start of the experiment. Continuous water (temperature: 20°C - 30°C; salinity: 26 - 31) flowed into the side of the 95 L conical tub through a submerged 1.9 cm diameter PVC pipe and out through a stand pipe positioned on the side of the tub. Water diffused into the 18.9 L bucket mesocosm through 5 mm diameter holes lining the side of the bucket. The rim of the 18.9 L experimental mesocosm was approximately 1 cm below the water surface. In preliminary tests, the water column had unchanging temperature and salinity measurements, demonstrating the water was well-mixed. Continuous HoBo® data loggers were placed in mesocosms located at the end of each plumbing line to determine whether temperatures were consistent across tubs with different flow rates. Temperatures were similar among these mesocosms with a maximum mean difference of 1.2°C ± 0.9°C. Water was drained from the 95 L tubs in-between experimental runs to prevent colonization within the tub.

Only male D. sayi individuals that had at least 7 legs and both chelipeds intact were used in the study. Individuals were starved for 24 hours prior to the initiation of the experiment. Dyspanopeus sayi were collected from a C. fornicata shell hash bed in Shinnecock Bay, NY (40.8596°N 72.4339°W) no more than two days prior to starvation. Mytilus edulis prey were
added to mesocosms at least one hour prior to the initiation of an experimental run at dusk. After
36 hours, remaining mussels were enumerated by thoroughly searching the structure and sieving
the sand through the two-layers of mesh that covered the mesocosm bucket bottom. No-predator
controls confirmed mussel mortality was due to predation with a natural mortality of 2.4 % ± 5.1
% per mesocosm and a mussel recovery rate of 98.4 % ± 1.8 % per mesocosm.

Data Analysis

Functional Response

All statistical tests were conducted using R Statistical Software version 3.4.1 (R Core
Team 2017). Foraging efficiency was estimated for each structure and predator density
treatment by fitting a functional response to the per capita feeding rates. The appropriate
functional response can by determined by first fitting a polynomial logistic regression between
the initial prey density and proportion of prey consumed. If the linear term is significantly
negative, then a type II response is the best fit. Conversely, significantly positive linear and
negative quadratic terms signifies a type III functional response (Juliano 2001). Considering that
logistic regression models integers, the proportion of mussels consumed per capita was rounded
to the nearest integer prior to model fitting. In situations where per capita feeding rate was
between zero and 0.5, the feeding rate was rounded to up to a feeding rate of one mussel.

After fitting a polynomial logistic regression to the per capita proportion of mussels
consumed for each treatment combination, a type II functional response fit the best (negative
linear term, P < 0.0001 for all habitat and density treatments). Since prey depletion occurred, the
per capital feeding rates were fit with a Rogers type II random predator equation (equation 1;
Rogers 1972).

\[ N_e = N_0 \left(1 - \exp\left[a(T_h N_e - T)\right]\right) \]  (1)
In equation 1, \( N_e \) is the number of prey eaten per mesocosm, \( N_o \) is the initial prey density per mesocosm, \( a \) is the attack rate, \( T_h \) is the handling time per prey, and \( T \) is the total foraging time. Parameters were optimized using maximum likelihood estimation with binomial errors (Bolker 2008) through the friar_fit function from the ‘friar’ package (Pritchard et al. 2017). To isolate \( N_e \) in equation 1, the Lambert \( W \) function was used to solve for each parameter (Bolker 2008, Pritchard et al. 2017). Since the parameter values were not empirically validated and limitations exist on the equation’s ability to mechanistically represent handling time (Jeschke et al. 2002), the optimized parameter values were used for comparative purposes only. Bias-corrected and accelerated (BCa) bootstrapped 95% confidence intervals (CIs) were compared among the parameter values.

Fitting a Roger’s type II functional response assumes that the predator’s feeding rate is prey-dependent and does not incorporate predator density. However, a variety of modifications have been made to incorporate predator density effects into the functional response (Hassell and Varley 1969, DeAngelis et al. 1975, Arditi and Ginzburg 1989), though there is still much debate on the appropriate approach (Abrams 2015). One way to determine if predator-density needs to be incorporated in the functional response is to compare prey-dependent, predator-dependent, or ratio-dependent models. The initial prey density \( (N_o) \) from equation 1 was modified to incorporate predator density effects using the Hassel and Varley (1969) approach (equation 2; see Griffen and Delaney 2007).

\[
N_e = \left( \frac{N_o}{P^m} \right) \{1 - \exp[a(T_hN_e - T)]\} \quad (2)
\]

The parameter \( P \) is the number of predators in the mesocosm and \( m \) is the interference coefficient, which represents the degree to which predator density effects per capita feeding rates. An \( m \) value of 0 denotes that the functional response is prey-dependent, whereas a value
of 1 indicates ratio-dependent. Conversely, if the $m$ value is between 0 and 1, then the functional response is predator-dependent. To determine whether the functional response was predator-dependent, competing functional response models of per capita feeding rates were fit with different $m$ values that increased in 0.1 increments from 0 to 1. Per capita feeding rates of both predator density treatments were grouped by habitat structure, so the predator-dependency was evaluated separately for low and high structure treatments. The best-fit model was determined using Akaike’s information criterion corrected for small sample size (AICc). Habitat structure effects were evaluated by comparing the 95% BCa CIs of the attack rate and handling time parameters from the best-fit model between the low and high habitat structure treatment levels.

**Generalized Mixed Models**

Given the limitations of functional response curve fitting in estimating foraging efficiency, the effects structure, predator and prey density have on proportion of mussels consumed for the collective and per capita feeding rate were modeled using generalized linear mixed models (GLMMs) assuming a binomial error distribution. Prey density was treated as a continuous variable, whereas the habitat structure and predator density were treated as categorical factors. Experimental block was treated as a random variable (Logan 2010) and modeled using the ‘lme4’ package (Bates et al. 2015). As in the functional response curve fitting, the number of mussels successfully or not successfully eaten were rounded to the nearest integer since a binomial distribution is discrete. Optimization was only possible after each mussel density treatment was scaled by subtracting the mean mussel density (20.6 mussels) and dividing by the SD (23.7 mussels). Further, the GLMM fitting the total proportion of mussels consumed per mesocosm was overdispersed and corrected by modeling individual observations
as a random factor (Bolker et al. 2009). Further, the optimization of this GLMM was bounded by quadratic approximation with a maximum 100,000 iterations. Unlike the GLMM for the proportion of mussels consumed, the GLMM for the per capita proportion of mussels consumed was not overdispersed and the default optimization technique was used.

To quantify the effect structure had on intraspecific competition, observed consumption rates of the four-predator treatment was compared to an expected per capita feeding rate. The expected feeding rate was estimated by modifying the multiplicative risk model (equation 3) that has typically been used to calculate multiple predator effects between two species (Soluk and Collins 1988, Soluk 1993, Sih et al. 1998):

\[ P_{e_{s1+s2}} = P_{s1} + P_{s2} - (P_{s1} \times P_{s2}) \]  

(3)

where \( P_{s1} \) and \( P_{s2} \) is the proportion of prey consumed by species 1 and 2 in isolation and \( P_{e_{s1+s2}} \) is the expected proportion of prey consumed when species 1 and 2 are together and have independent predator effects. The equation also takes into account that either predator could eat the same prey item, so the number consumed does not exceed the number available.

The expected proportion of prey consumed for the four-crab treatment (\( P_{eC_4} \)) was calculated using the proportion of prey consumed by the two-crab treatment (\( P_{C_2} \); equation 4).

\[ P_{eC_4} = 2(P_{C_2}) - P_{C_2}^2 \]

(4)

The expected and observed feeding rates were compared using a GLMM with binomial error distribution with prey and habitat density as main effects and experimental block as a random effect. As the GLMM model fitting the proportion of mussels consumed in each treatment, the mussel density predictor variable was scaled, the model was corrected for overdispersion and the bound optimization model fitting technique was used.
Across all fitted GLMMs, a type III Wald chi-square test was used to address unequal sample sizes (Logan 2010) using the ‘car’ package (Fox and Weisberg 2011). Pairwise post-hoc chi-square tests were performed on the highest-order significant terms with multiple comparisons corrected by using the Holm-Bonferroni method in the ‘phia’ package (De Rosario-Martinez 2015). Appropriate model diagnostics were run on each analysis to assess models; statistical significance $\alpha$ was set at 0.05.

**Results:**

*Functional Response*

Increased *C. fornicata* structure reduced per capita feeding rates regardless of *D. sayi* predator density (Figures 1 and 2). However, habitat density effects on the attack rate and handling time parameters depended on predator density (Figure 3). The attack rate 95% confidence intervals did not overlap when two predators were present and overlapped when four predators were present (Figure 3A). This could suggest that the four predators were able to collectively find prey at low densities, even though increased structure made it more difficult to successfully find and consume prey. Further, the decrease in attack rate when four rather than two predators were present suggests that intraspecific competition among individuals was higher in the four rather than the two-predator treatment level. Predator-density had a different relationship in the handling time parameter compared to the attack rate parameter (Figure 3B). At each habitat density level, predator density did not alter handling time. While predator density did not affect handling time, increases in *C. fornicata* structure increased handling time only in the four-predator treatment.

The ratio-dependent type II functional response model fit both habitat treatment levels the best (Table 3 and Figure 4). This suggests that the decrease in attack rate detected between the
four versus two predators in the prey-dependent functional response is due to prey limitation among individuals. Further, the increased habitat structure reduced per capita feeding rates by lowering the attack rate parameter and increasing the handling time parameter (Figure 5). This suggests that the negative effect habitat structure has on per capita feeding rates depends on prey and predator densities.

*Generalized Mixed Models*

The GLMMs show that there were variable significant interactions depending on the response variable modeled (Tables 4 and 5). When proportion of mussels consumed were modeled, there was a significant interaction between mussel and habitat density (Table 4). At low mussel densities, a smaller proportion of mussels were consumed in the high versus low structure treatment level ($\chi^2 = 24.4, p < 0.0001$). Conversely, the mussel density effect on proportion of mussels consumed per capita was dependent on predator density and not habitat density, as indicated by the significant interaction between mussel and predator density (Table 4). At lower mussel densities, the *D. sayi* in the two-predator treatment consumed a greater proportion of mussels per capita than the four-predator treatment across both habitat treatments ($\chi^2 = 11.6, p < 0.0001$). Thus, predator density effects on individual feeding rates depended on prey density. The expected and observed feeding rates in the four-predator treatment were not different from one another (Table 5 and Figure 6). As such, the predator density main effects detected in both models (Table 4) was due to the multiplicative effect of predator density doubling. This would also mean that intraspecific competition increases from two to four-predators when prey is limited, reducing per capita consumption rates. While there was a clear negative effect of increased structure on feeding rates, the lack of an interactive effect between structure, predator, and mussel density indicates structure increase did not remove intraspecific
competition.

**Discussion**

The effects habitat structure density has on competition among *D. sayi* individuals was evaluated using a functional response approach. Results indicated that both predator and prey density need to be considered in evaluating the functional response; the per capita consumption rates were best explained by a ratio-dependent type II functional response. Competition among individuals increased with predator density only when prey was limiting, indicated by the reduced per capita consumption rates among four vs two predators. Further, there was a strong habitat structure effect that was maintained even when prey density approached saturated per capita feeding rates. This implies that *C. fornicata* beds may offer prey refuge even at high prey to predator ratios. While there were strong negative effects of increased structure, increased structure did not alleviate mutual interference among individuals. However, there was evidence that increased structure reduced competition among individuals when prey was limiting. Results reaffirm that competitive interactions can be important when prey is limited and in low-structured environments.

There was a negative effect of increasing *C. fornicata* habitat density on per capita feeding rates. The negative effect of habitat density occurred across all prey densities, shown by a reduced attack rate parameter and increased handling time parameter in the ratio-dependent functional response. Structure increases have been suggested to negatively affect encounter rate between predator and prey (Bell et al. 1991, Heck and Orth 2006). One way that habitat structure has been suggested to decrease encounter rate is by the prey modifying their location within the structure (Main 1987, Ryer et al. 2004, Stoner 2009). The prey used in this study, *M. edulis*, can change attachment position even after byssally attaching to a surface (Lee et al.
At the end of the experiment, *M. edulis* individuals were rarely found on top of the shell matrix in the high structure density treatment, suggesting individuals selected attachment locations within the habitat matrix. By modifying their position in the shell matrix, predators had to also move through the shell matrix to encounter these individuals. As shown in other habitat studies (Sponaugle and Lawton 1990, Ryer et al. 2004, Lannin and Hovel 2011), moving through the shell matrix likely reduced their speed and increased searching time compared to foraging on top of the shell matrix. Further, *M. edulis* may have preferentially attached in the interstitial space formed by the *C. fornicata* shell shelf and as a result affected *D. sayi*’s ability to isolate prey, similar to the inability of other decapod predators to access bivalve in oyster reef crevices (Toscano and Griffen 2013, Hesterberg et al. 2017). In a pilot study comparing *D. sayi*’s consumption of *M. edulis* attached inside or outside the *C. fornicata* shelf, any mussel that had byssally attached inside *C. fornicata*’s shelf was uneaten. This suggests that *D. sayi* is physically impeded by the crevice formed by the *C. fornicata* shelf, potentially reducing the attack rate by making prey inaccessible after being encountered. In addition to the prey modifying their location, increased *C. fornicata* structure most likely enhanced *M. eduilis*’ predator defense strategy of using byssal threads (Reimer and Tedengren 1996) by offering robust attachment sites. An increase in the number of byssal threads could not only limit *D. sayi*’s ability to access prey, but also increase the time it takes to handle prey. An increase in prey handling may alter the rate of prey rejection, which can affect feeding rate (Wong and Barbeau 2005). The shell hash matrix in the high *C. fornicata* treatment likely negatively affected attack rate through increasing refuge locations, physically impeding *D. sayi* movement, and providing robust byssal thread attachment sites.

In addition to increased structure affecting the attack rate parameter, increased structure
also negatively influenced the handling time parameter. This implies that prey saturation did not remove the effect of increased structure, unlike results in a previous study examining the effect of C. fornicata habitat complexity on a single D. sayi’s predator foraging efficiency (Kulp et al. in preparation, Chapter 2). The effect of increased structure on handling time for D. sayi in this study is likely dependent on having more than one predator present. Considering that expected and observed consumption rates were consistent across the same structure density, the increase in handling time cannot be explained by increased antagonistic encounters between individuals as displayed by other decapod species (Clark et al. 1999b, Griffen and Delaney 2007, Smallegange et al. 2007). Instead, in the presence of more than one predator D. sayi may change its behavior on where it handles M. edulis after it has been successfully isolated. Perhaps, in the high C. fornicata structure treatment D. sayi is more likely to forage and consume M. edulis inside the shell matrix when more than one predator is present in an attempt to avoid interacting with other individuals. Being surrounded by shells in the shell matrix could have affected the claw movement and an individual’s ability to access M. edulis’ tissue. On the other hand, greater prey depletion caused by a higher predator density may mean that a greater proportion of uneaten mussels have better defended themselves against predation in the shell matrix, making them suboptimal prey with a greater handling time cost (Elner and Hughes 1978). Similar to other prey, M. edulis may be behaviorally responding to an increase in predator density (Lin 1991, Leonard et al. 1999, Flynn and Smee 2010). These behavioral responses could negatively affect D. sayi’s foraging efficiency. For instance, M. edulis prey may preferentially attach inside the C. fornicata shell shelf or increase the number of attachment points to shells, increasing handling time. Behavioral follow-up studies are needed to validate or reject these hypothesized mechanisms of why increased structure lowered the per capita feeding rates when prey was
saturated.

Intraspecific competition was important at low prey densities and became diluted at high densities, supporting a ratio-dependent type II functional response. The predator density effect only occurred when prey was limiting, leading to the attack rate parameter being negatively affected by predator density. There were no emergent effects of predator density detected in this study; though this does not mean that interference was not occurring. In a previous study (Kulp et al. *in preparation*, Chapter 4), there was a significant decrease in per capita consumption rate when more than one *D. sayi* predator was present even though no emergent effects were detected when predator density increased from three to six individuals. This may mean that *D. sayi* is not like other crustacean predators whose interference effects increase when predator density increases above two (Mansour and Lipcius 1991, Clark et al. 1999b, Smallegange et al. 2006, Griffen and Delaney 2007, Griffen and Williamson 2008). Instead, mutual interference among *D. sayi* is likely independent of predator density, remaining constant no matter the predator density.

While interference was likely occurring between individuals, there was also no evidence that increased structure alleviated mutual interferences. The expected and observed feeding rates for the four-predator density treatment level were not different from one another when *C. fornicata* habitat density remained constant. Further, increased predator density did not lower per capita feeding rates at saturated prey levels within a given habitat density treatment level. These results do not match other studies that have shown increases in structure reduces interference among predators by reducing antagonistic encounters between predators (Moksnes et al. 1998, Finke and Denno 2002, Griffen and Byers 2006, Grabowski et al. 2008). In particular, Grabowski and Powers (2004) found that increased *Crassostrea virginica* shell hash...
reduced antagonistic interactions among individuals of another mud crab species, *Panopeus herbstii*. However, the *P. herbstii* individuals used in their study were at least 30 mm in carapace width. Perhaps for *D. sayi*, who rarely grow larger than 24 mm in carapace width, conspecifics are more likely to avoid one another than engage in antagonistic encounters. Smallange et al. (2006) found that conspecific *Carcinus maenas* predators encounter rate was influenced by predator size, where smaller individuals were more likely to avoid one another than engage in aggressive interactions. If mutual interference among *D. sayi* does not rely on encounters but avoidance, then the mutual interference may not have been affected by increased structure because the individuals were still able to detect one another’s presence. While there was no evidence that increased structure altered mutual interference effects, there was evidence that increases in predator density can overcome increased structure effects when prey density is low. Unlike when two-predators were present, habitat structure did not decrease the attack rate parameter when four-predators were present. This could imply that while increased structure makes scarce prey more difficult to find and successfully consume, an increase in predator density could increase the chance of 1) dispersed prey being encountered by a predator or 2) rejected prey being later consumed by a different predator. Results indicate then that predator density increases will reduce structural benefits to prey at low densities.

**Conclusion**

While disagreement remains on how to incorporate predator density into a predator’s functional response (Abrams 2015), this study supports using a ratio-dependent functional response. Predator density and structure density had different effects when prey was limiting or saturated. When prey was limiting, increasing predator density reduced the structural benefit of *C. fornicata* on *M. edulis* prey survival. Conversely, when prey was saturated, structural effects
could not be overcome by increases in predator density. Predators and prey may behaviorally change how they interact with *C. fornicata* structure when more than one predator is present. These results emphasize the need to incorporate predator and prey density to understand the relationship between structure complexity and foraging efficiency.

**Acknowledgments**

Technical assistance for the mesocosm set-up was provided by the staff at the Stony Brook University Southampton Marine Station: C. Paparo, B. Gagliardi, and A. Brosnan. Data collection was made possible through the help of the following research assistants: N. Floros, M. Cashin, T. Vlasak, K. O’Toole, T. Palmer, S. Milea, T. Apter, W. Wied, S. Growth, L. Howlett, N. Kriefall, and C. Fernandes. Assistance with experimental design, data analysis, and interpretation was provided by R. Kulp’s dissertation committee: P. Petraitis, J. Levinton, B. Griffen, and J. Nye. Funding was supported by the Shinnecock Bay Restoration Program (SHiRP) and the Sigma XI Grants-in-Aid Research Program.
Table 1. *Crepidula fornicata* field survey habitat metrics (mean ± 1 SD). The field survey was conducted in May 2014 at three different *C. fornicata* shell hash beds in Shinnecock Bay, NY. Using the 18.9 L bucket in the experiment (area: 0.062 m$^2$), *C. fornicata* habitat was excavated to the sediment layer in four locations. Samples were rinsed down through a 500-micron sieve, and all the live crustacean predators were separated and frozen for later processing. The frozen crustaceans were processed for abundance, gender and carapace width (CW) to the nearest mm. The mud crab density includes *Dyspanopeus sayi* individuals that were at least 10 mm in CW. The water displacement method was used to determine the volume of shell hash and live *C. fornicata* clumps. Each live *C. fornicata* clump was counted and the number of individuals in the longest chain was counted. The number of individuals in a chain ranged from 1 to 12, where the most number of live *C. fornicata* clumps had three in a chain. We listed two different live *C. fornicata* clump numbers: those with at least three individuals in the longest chain and then those with more than three individuals. The biomass of shell hash and live *C. fornicata* clumps was estimated from a fitted linear model (shell hash: Biomass = 1.93*Volume, $R^2 = 0.994$ live clumps: Biomass = 1.03*Volume, $R^2 = 0.997$). Additionally, within a 0.25 m$^2$ quadrate, the height of the *C. fornicata* habitat was taken in five random locations.

<table>
<thead>
<tr>
<th>Mud crab density (per 0.062 m$^2$)</th>
<th>Shell hash volume (ml per 0.062 m$^2$)</th>
<th>Clump volume (ml per 0.062 m$^2$)</th>
<th>Shell hash dried biomass (g per 0.062 m$^2$)</th>
<th>Clump dried biomass (g per 0.062 m$^2$)</th>
<th>Clump number (≤3 individuals stacked per 0.062 m$^2$)</th>
<th>Clump number (&gt;3 individuals stacked per 0.062 m$^2$)</th>
<th>Height (mm)</th>
</tr>
</thead>
<tbody>
<tr>
<td>4 ± 3</td>
<td>201 ± 258</td>
<td>555 ± 177</td>
<td>389.6 ± 498.6</td>
<td>572.8 ± 182.7</td>
<td>16 ± 16</td>
<td>17 ± 11</td>
<td>367 ± 133</td>
</tr>
</tbody>
</table>
Table 2. *Crepidula fornicata* density treatments added to the 18.9 L mesocosm tubs (bottom area = 0.062 m²). The volume of shell hash in the low and high structure treatments were approximately 1 SD below or above the mean volume of shell hash from the field survey (Table 1). There were 2 and 5 *C. fornicata* shells glued together with ethyl cyanoacrylate to mimic the live *C. fornicata* clumps with at least three individuals or greater than three individuals in the main chain. The number of 2 and 5 *C. fornicata* shells glued into a chain in the low and high structure treatments were approximately 1 SD below or above the mean number of live *C. fornicata* clumps with at least 3 individuals stacked or more than 3 individuals stacked from the field survey, respectively (Table 1). The shell at the base of the mimicked clump was at least 30 mm in shell height (SH), which was within the range of the bottom shell found in the survey (range: 21 - 46 mm SH; mean: 34 ± 6.4 mm SH [SD]).

<table>
<thead>
<tr>
<th>Density Treatments</th>
<th>Shell hash volume (mL per mesocosm)</th>
<th>Mimicked clump (2 shells stacked per mesocosm)</th>
<th>Mimicked clump (5 shells stacked per mesocosm)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Low</td>
<td>0</td>
<td>0</td>
<td>6</td>
</tr>
<tr>
<td>High</td>
<td>460</td>
<td>32</td>
<td>34</td>
</tr>
</tbody>
</table>
Table 3. Comparing prey dependent, predator-dependent and ratio-dependent functional response models. The two and four crab feeding rates were separately fit to the Hassel and Valey (1969) functional response (equation 2) with an increasing interference coefficient (m). Models increased m from 0 to 1 in 0.1 increments. A model was fit for each Crepidula fornicata habitat structure treatment (low and high). AICc is the corrected Akaike’s information criterion, ΔAICc is the difference in the AICc from the selected model and the model with the smallest AICc value, and w is the weighted AICc value.

<table>
<thead>
<tr>
<th>m</th>
<th>Low Structure Treatment</th>
<th>High Structure Treatment</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>AICc</td>
<td>ΔAICc</td>
</tr>
<tr>
<td>0</td>
<td>454.3</td>
<td>194.2</td>
</tr>
<tr>
<td>0.1</td>
<td>444.5</td>
<td>184.4</td>
</tr>
<tr>
<td>0.2</td>
<td>436.4</td>
<td>176.3</td>
</tr>
<tr>
<td>0.3</td>
<td>426.8</td>
<td>166.7</td>
</tr>
<tr>
<td>0.4</td>
<td>411.4</td>
<td>151.3</td>
</tr>
<tr>
<td>0.5</td>
<td>391.3</td>
<td>131.2</td>
</tr>
<tr>
<td>0.6</td>
<td>391.3</td>
<td>131.2</td>
</tr>
<tr>
<td>0.7</td>
<td>365.3</td>
<td>105.2</td>
</tr>
<tr>
<td>0.8</td>
<td>328.0</td>
<td>67.9</td>
</tr>
<tr>
<td>0.9</td>
<td>295.3</td>
<td>35.2</td>
</tr>
<tr>
<td>1.0</td>
<td>260.1</td>
<td>0</td>
</tr>
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</table>
Table 4. Type III Wald chi-square test results for the generalized linear mixed models of the proportion of mussels consumed per mesocosm and the proportion of mussels consumed per capita.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>df</th>
<th>$X^2$</th>
<th>$X^2$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Predator Density</td>
<td>1</td>
<td>19.9 ***</td>
<td>34.5 ***</td>
</tr>
<tr>
<td>Structure Density</td>
<td>1</td>
<td>64.0 ***</td>
<td>36.5 ***</td>
</tr>
<tr>
<td>Mussel Density</td>
<td>1</td>
<td>59.3 ***</td>
<td>63.4 ***</td>
</tr>
<tr>
<td>Predator Density: Structure Density</td>
<td>1</td>
<td>3.0 *</td>
<td>1.05</td>
</tr>
<tr>
<td>Predator Density: Mussel Density</td>
<td>1</td>
<td>0.04</td>
<td>11.0 **</td>
</tr>
<tr>
<td>Structure Density: Mussel Density</td>
<td>1</td>
<td>13.8 **</td>
<td>0.76</td>
</tr>
<tr>
<td>Predator Density: Structure Density: Mussel Density</td>
<td>1</td>
<td>0.003</td>
<td>0.54</td>
</tr>
</tbody>
</table>

*** < 0.0001  ** < 0.01  * < 0.05  *<0.1
Table 5. Type III Wald chi-square test results for the generalized linear mixed models of the proportion of mussels consumed per mesocosm of the expected and observed feeding rates.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>df</th>
<th>$X^2$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Expected vs Observed</td>
<td>1</td>
<td>1.6</td>
</tr>
<tr>
<td>Structure Density</td>
<td>1</td>
<td>49.7 **</td>
</tr>
<tr>
<td>Mussel Density</td>
<td>1</td>
<td>34.9 ***</td>
</tr>
<tr>
<td>ExpvsObs: Structure Density</td>
<td>1</td>
<td>1.5</td>
</tr>
<tr>
<td>ExpvsObs: Mussel Density</td>
<td>1</td>
<td>0.02</td>
</tr>
<tr>
<td>Structure Density: Mussel Density</td>
<td>1</td>
<td>11.1***</td>
</tr>
<tr>
<td>Predator Density: Structure Density: Mussel Density</td>
<td>1</td>
<td>0.003</td>
</tr>
</tbody>
</table>

*** $< 0.0001$ ** $< 0.01$ * $< 0.05$ *$<0.1$
Figure 1. Type II functional response curves for four treatment combinations: two and four crabs in low *Crepidula fornicata* structure (A, C) and two and four crabs in high *C. fornicata* structure (B, D). The points (2 crabs: triangles; 4 crabs: circles) are observed mean consumption rates with SE error bars, the solid line is the fitted model and the dashed lines are the BCa bootstrapped 95% CI.
Figure 2. Proportion mussels consumed per capita by the initial number of mussels (per 0.062 m²) for four treatment combinations: two and four crabs in low *Crepidula fornicata* structure (A, C) and two and four crabs in high *C. fornicata* structure (B, D). The points (2 crabs: triangles; 4 crabs: circles) are observed means with SE error bars.
Figure 3. Comparing estimated attack rate (A) and handling time (B) parameters from functional response model fitting across the four treatment combinations: two and four crabs in low Crepidula fornicata structure and two and four crabs in high C. fornicata structure. The points (two crabs: triangle; four crabs: circles) represent optimized parameter values and the error bars are the 95% BCa confidence intervals.
Figure 4. Comparing the best-fit ratio-dependent (A, B) and worst-fit prey-dependent (C, D) type II functional response model fits (Table 3) to the observed per capita consumption rates when predators were exposed to low (A, C) or high (B, D) *Crepidula fornicata* habitat density. The two crab (triangles) and four crab (circles) feeding rates were fit to the ratio-dependent and prey-dependent model with the Hassel and Valey (1969) functional response (equation 2) with an interference coefficient ($m$) value of 1 or 0. The points are observed mean consumption rates with SE error bars, the solid line is the fitted model and the dashed lines are the BCa bootstrapped 95% CI.
Figure 5. Comparing estimated attack rate (A) and handling time (B) parameters from functional response model fitting across increasing *Crepidula fornicata* habitat structure (low and high). The points represent optimized parameter values and the error bars are the 95% BCa confidence intervals.
Figure 6. Expected (A, B) and observed (C, D) proportion mussels consumed by four *Dyspanopeus sayi* predators as mussel density increases when foraging in either low (A, C) or high (B, D) *Crepidula fornicata* habitat structure treatment levels. The points (expected: triangles; observed: circles) are means with SE error bars. The expected consumption was calculated using the multiplicative risk model (Soluk and Collins 1988, Soluk 1993, Sih et al. 1998).
Chapter 6

Evaluating the impact of mesopredators on oyster restoration in the New York Metropolitan Region

A version of this chapter has been published as:

Abstract

Predation of newly settled juvenile *Crassostrea virginica* often dominates post-settlement mortality. Resident mesopredators such as the xanthid mud crabs are abundant (> 200 m⁻²) on constructed subtidal oyster reefs in the New York Metropolitan Region and may contribute to post-settlement oyster mortality. Two study sites with differing mesopredator species, Hastings and Soundview Park, were selected to examine the role of small crustacean predators in post-settlement mortality. The white-fingered mud crab (*Rhithropanopeus harrisii*) inhabits Hastings, while the flat mud crab (*Eurypanopeus depressus*) and Sayi mud crab (*Dyspanopeus sayi*) inhabit Soundview Park. Using size selective mesh cages to exclude predators, the effects of predator size on oyster predation and recruitment at Hastings and Soundview Park were examined. Overall, Soundview Park had higher consumption rates than Hastings. The highest consumption at Soundview Park occurred when predators of all sizes had access to the oyster prey. Larger-sized predators were likely responsible for oyster mortality, as oyster mortality was not different between the mesopredator and no-predator treatments at Soundview Park. Few oysters recruited at Soundview Park; thus predator size effects on oyster recruitment could not be effectively evaluated between sites. Recruitment at Hastings was not affected by predator exclusion treatments, in agreement with the oyster predation experiments. Though abundant, no mud crab mesopredator recovered at either site was greater than 22 mm in carapace width. Mesopredators were likely not of sufficient size to be dominant predators of newly settled juvenile oysters at Hastings or Soundview Park. Instead, predation pressure at Soundview Park was likely due to larger mobile predators such as blue (*Callinectes sapidus*) and spider crabs (*Libinia* spp.). Mesopredator size is an important factor to consider when evaluating mesopredator roles on oyster reefs.
Introduction

Predator size and habitat structure greatly influence foraging success and energy transfer in benthic communities. Species abundance, growth, and diversity tend to be higher in structured than unstructured habitats (Edgar 1990, Lee et al. 2001, Heck et al. 2003, Tolley and Volety 2005). This is likely because structured habitats provide increased prey refuge from predation (Lee and Kneib 1994, Beukers and Jones 1997, Hill and Weissburg 2013a, Bishop and Byers 2015) by increasing searching and handling time (Stoner 2009, Alexander et al. 2012), decreasing the accessibility of prey located in crevices (Toscano and Griffen 2013), and altering olfactory cue detection (Ferner et al. 2009). Decapod predators, which are important in regulating bivalve populations (Hines et al. 1990, Seitz et al. 2001, Lohrer and Whitlatch 2002), tend to be mobile, actively scavenging and foraging within a structured habitat. Small decapod predators may have an advantage over larger decapod predators in their ability to access prey in hard to reach crevices (Toscano and Griffen 2013). Small decapod predators may also travel less than transient predators such as adult blue crabs (*Callinectes sapidus* (Rathbun, 1896)), which have the potential to move large distances daily (Hines et al. 1995, Carr et al. 2004). Thus, unlike transient predators, smaller resident predators may apply consistent predation pressure in a given structured habitat. Additionally, numerous studies have shown that larger decapod predators, such as *C. sapidus* and green crabs (*Carcinus maenas* (Linnaeus, 1758)), consume shellfish of the same size as smaller decapod predators, but at higher per capita rates (Juanes 1992, O'Connor et al. 2008). While individual decapod mesopredators consumption rates do not rival those of larger transient decapods, their collective consumption rates may be equivalent to or greater than those of larger transient predators due to their high abundances (Kulp et al. 2011, Rindone and Eggleston 2011, Carroll et al. 2015a).
One group of potentially important decapod mesopredators includes the xanthid mud crabs, ubiquitously found in high densities in salt marsh (Silliman et al. 2004), seagrass beds (Strieb et al. 1995), and oyster reefs (Meyer 1994) along the Eastern coast of the United States. Xanthid mud crabs have been suggested to be important predators of juvenile *Crassostrea virginica* (Gmelin, 1791) on oyster reefs (Kulp et al. 2011, Rindone and Eggleston 2011). One of these, the Atlantic mud crab (*Panopeus herbstii* (Edwards, 1834)), has the largest carapace width of the xanthid mud crabs (Ryan 1956), the highest per capita juvenile oyster predation rate (Bisker & Castagna 1987), and is abundant in high salinity sites (>20) (McDonald 1982, Meyer 1994) coincident with the highest oyster growth rates (Paynter and Burreson 1991). Due to these listed traits, most mud crab mesopredator studies have focused on the influence of *P. herbstii* on juvenile oysters (Grabowski 2004, Toscano and Griffen 2012, Hill and Weissburg 2013a). Yet, in the locations of some oyster reef restoration projects, such as those in the New York Metropolitan Region, *P. herbstii* is not abundant (Kulp, *personal observation*). Instead, xanthid mesopredators such as the flat mud crab (*Eurypanopeus depressus* (Smith, 1834)), Sayi mud crab (*Dyspanopeus sayi* (Smith, 1869)), and white-fingered mud crab (*Rhithropanopeus harrisii* (Gould, 1841)) dominate.

Efforts to restore oyster reefs have increased in recent years, with a goal of enhancing oyster fisheries and the ecosystem benefits provided by oyster reefs (Wells 1961, Tolley and Volety 2005, Grizzle et al. 2008). The Hudson River Foundation constructed preliminary oyster reefs throughout the New York Metropolitan Region in 2010 with the goal of expanding reef sites in the future. Two of the five oyster restoration sites, Soundview Park and Hastings, were selected to examine the collective contribution of mesopredators to post-settlement oyster mortality. These sites were selected because they have different mud crab species present. At
Soundview Park, *E. depressus* and *D. sayi* have been found, while only *R. harrisii* has been observed at Hastings (Peterson and Kulp 2015). Although mud crabs can be found in high abundances at both sites (> 200 m²), the two sites may have different predation pressures due to the different mud crab species present. Kulp et al. (2011) found that *E. depressus* consumed four times more juvenile oysters than *R. harrisii* in a laboratory environment. Thereby, *R. harrisii* may not consume oyster prey in the field as readily as other mesopredators such as *E. depressus* and *D. sayi*, which could result in lower predation pressure at Hastings than Soundview Park. As such, there may be important site-specific differences in the impact of mud crabs on juvenile oyster survival rates.

The main goal of this study was to clarify species-specific roles of mud crabs on restored oyster reefs by using predator exclusion cages. While Soundview Park and Hastings reefs were expected to have similar mud crab abundances, their differential mud crab species compositions were expected to lead to higher predation at Soundview Park than Hastings. Understanding these site-specific differences could help with future restoration site selection not only in New York, but also at locations that have a similar composition of mesopredator species present.

**Methods**

*Site selection*

Experiments were conducted at two constructed preliminary oyster reefs in the New York Metropolitan Region: Hastings (41°0.032'N, 73°53.068'W) and Soundview Park (40°48.576'N, 73°51.860'W). In 2010, the Hudson River Foundation and partners built the two continuous oyster reefs by laying shell veneer on top of a transplanted bedrock base. The footprints of the Hastings and Soundview Park oyster reefs are approximately 69 m² and 40 m², respectively. Hatchery-reared juvenile oysters that settled on shell were planted at both sites in three
installments: October 2010, November 2010 and June 2011. The sediment at Soundview Park was a mixture of gravel and sand, while the sediment at Hastings was unconsolidated mud. The two sites have different salinity regimes (Soundview Park: salinity of ca. 20-25; Hastings: salinity of ca. 5-10) and different resident mud crab species (Soundview Park: D. sayi and E. depressus; Hastings: R. harrisii). Additionally, at the higher salinity site, Soundview Park, adult C. sapidus and spider crabs have been regularly observed (Libinia spp.; (Peterson and Kulp 2015). Conversely, while not regularly caught or observed, oyster toadfish (Opsanus tau (Linnaeus, 1766)) and adult C. sapidus have been observed at the Hastings site (Peterson and Kulp 2015). Overall, fewer large juvenile oyster predators are present at Hastings than Soundview Park.

**Predator abundances**

To estimate resident mesopredator abundances, four replicate trays (44 x 30 x 12 cm) lined with fiberglass window screen were placed across the longest axis of the Hastings and Soundview Park reefs for five and six weeks in July and September 2012, respectively. Trays were filled with veneer Atlantic surf clam (Spisula solidissima (Dillwyn, 1817)) shell prior to being inserted into the reef. After retrieval, mesopredators in each tray were identified, measured, and counted. Not all trays were recoverable in July and September. One tray was missing from Hastings in July and one tray was missing from both sites in September.

To determine presence of large mobile predators, one baited fish trap (ca. 120 x 50 x 40 cm with 20 cm diameter doors) was deployed at Hastings and Soundview Park for 48 hours in August 2012.

**Predator-exclusion experiments**
A randomized two-factorial design comparing predator exclusion (3 levels: all predators, mesopredators, and no predators) and oyster reef site (Hastings and Soundview Park) was used to test the effects of mud crab species identity and predator size on post-settlement juvenile oyster (spat) mortality. Spat mortality was measured using two different experiments: a short-term predation experiment and a long-term recruitment experiment.

There are multiple limitations to using naturally settled oyster spat for consumption studies, including different settling densities, variable growth rates, and orientation (Hidu 1969, Newell et al. 2007, Kulp et al. 2011). Therefore, the number, size, and arrangement of oysters were standardized by artificially attaching individual oyster spat onto 12 x 12 cm unglazed terracotta tiles using ethyl cyanoacrylate glue in the short-term predation experiment. Hatchery-reared oyster singles (5 to 8 mm shell height (SH)) used for the artificially adhered oyster tiles were provided by the East Hampton Town Shellfish Hatchery in East Hampton, NY. Artificially adhered oysters were given at least one week to grow in a flow-through indoor seawater system at Stony Brook University’s Marine Station, Southampton, NY. Individuals that died after the gluing process were replaced at least one day prior to deployment. Oysters less than 5 mm SH were not used due to increased mortality post-gluing. At the time of deployment, oysters had grown to between 10 and 20 mm SH, a range that mud crabs are capable of consuming (Newell et al. 2007, Kulp et al. 2011).

While using artificially adhered oysters has become a regular practice in predation studies (Kimbro et al. 2014, Carroll et al. 2015a), the artifacts on predation remains unknown. Therefore, a mesocosm experiment was conducted to quantify the difference between artificially adhering oysters versus naturally recruited oysters. Oysters were adhered to unglazed terracotta tiles (n = 13) or naturally settled on oyster cultch (n = 12). The oyster treatments were offered to
male *D. sayi* (15 to 23 mm carapace width) in mesocosms for 72 hours. Results from this experiment suggests that artificially adhering oysters to tiles inflates predation rates (Two sample t-test: $t = 2.67$, df = 23, $p = 0.014$), so caution should be used when interpreting consumption rates from the short-term experiment.

Because mud crabs may prefer smaller-sized oyster spat (< 10 mm SH; Newell et al. 2007, Kulp et al. 2011), there is the potential that fewer oysters were consumed by mesopredators during the field experiment than would be expected with smaller spat. In an effort to address this concern, a long-term recruitment study was conducted to evaluate predation during early settlement and at oyster sizes that were not represented in the short-term experiment. The long-term recruitment experiment measured oyster recruitment onto the top and side of 12 x 12 cm unglazed terracotta tiles in August 2012. Recruitment was defined as the number of settled spat present after six weeks. The number and size of live oysters (with tissue), oyster scars (valve imprint), and oyster boxes (articulated valves with no tissue) on the top and side of each tile were recorded after retrieval. The oyster scars and boxes were used as a proxy for post-settlement oyster mortality.

In the short- and long-term experiments, each terracotta tile was haphazardly assigned to one of three predator-exclusion treatments - all predators (AP), mesopredators (MP), and no predators (NP) - that offered varying levels of protection from predation. The AP treatments offered no protection from predation; tiles were attached to a 25 mm aperture vinyl-coated lobster wire panel (20 x 35 cm). The MP treatments consisted of 20 x 10 x 35 cm cages made from 25 mm aperture vinyl-coated lobster wire so that predators larger than 25 mm could not access the prey. The NP treatments were also made from 25 mm aperture vinyl-coated lobster wire, but with Vexar® polyethylene netting lining the cage interior to prevent entry of predators.
larger than 5 mm. To test for potential cage artifacts (Steele 1996), a cage control was used. The cage control had two of the six sides missing and was lined with 5 mm Vexar® polyethylene netting. In all treatments, tiles were zip-tied to the wire frame and a brick was attached on the bottom for cage stability. Four replicates of each treatment were randomized across two rows; each row had two replicates of each treatment.

In the short-term predation experiment, terracotta tiles were deployed for one week during one of two consecutive experimental runs in July 2012. The second deployment at Hastings was removed after five days instead of seven days due to logistical constraints. For this experimental trial, consumption was scaled to a 7-day predation rate to account for differing experimental length between sites. Any oysters missing at retrieval were assumed to have been consumed.

Data Analysis

All statistical analyses were performed in R (R Core Team 2015). A two-way factorial general linear model (GLM) with quasipoisson residual errors was used to determine whether site and retrieval month affected mud crab abundance (Logan 2010).

For the short-term predation study, a two-way GLM with quasibinomial residual errors was used to determine site and predator exclusion effects (AP, MP, and NP) on oyster mortality. The 7-day scaled predation rate for the 5-day Hastings experimental run was rounded to the nearest integer prior to being analyzed. Tukey’s HSD post-hoc tests were performed comparing within-site cage treatment effects using the package “multcomp.”

For the long-term recruitment experiment, only the Hastings site was analyzed due to the low recruitment at Soundview Park (<2 oysters per tile). To examine the effects of predator treatment (AP, MP, and NP) on oyster recruitment, a one-way factorial GLM with quasipoisson
residual errors was used. As above, Tukey’s HSD post-hoc tests were used to distinguish between-treatment effects. Appropriate model diagnostics were run on each analysis to assess models; statistical significance $\alpha$ was set at 0.05.

**Results**

*Predator abundances*

Mud crab abundance of individuals depended on both site location and retrieval month (interaction term: $F_{1,12} = 7.08$, $p = 0.026$). While there was no main retrieval month effect ($F_{1,12} = 0.99$, $p = 0.35$), there was a main site location effect ($F_{1,12} = 24.6$, $p = 0.0008$). In both July and September, the Hastings site contained twice as many mud crabs as Soundview Park. The abundance of Hastings’ resident species, *R. harrisii*, was similar in July and August. At Soundview Park, however, the abundances of *D. sayi* and *E. depressus* decreased by 50% in August. Abundances at Soundview Park were dominated by *D. sayi* with densities four and ten times greater than *E. depressus* in July and August, respectively. Thus, *D. sayi* could be a more important mesopredator than *E. depressus* at Soundview Park.

The mud crab size-distribution patterns were different at Hastings and Soundview Park (Figure 1). Not only were *R. harrisii* smaller in size than *D. sayi* and *E. depressus*, reaching no larger than 15 mm carapace width (CW), but also had a greater proportion of individuals smaller than 10 mm CW. Thus, the difference in the mud crab density between sites was likely driven by high abundance of *R. harrisii* individuals less than 10 mm CW at Hastings. Although more than half of mud crabs at both sites were smaller than 10 mm CW, there was still a formidable density of mud crabs greater than 10 mm CW: $78 \pm 14$ m$^{-2}$ (mean $\pm$ SE) *R. harrisii*, $93 \pm 9$ m$^{-2}$ *D. sayi* and $30 \pm 3$ m$^{-2}$ *E. depressus* individuals in the July recruitment trays. The 15 to 22 mm CW size range also showed a difference in abundance between sites: $33 \pm 2$ m$^{-2}$ *D. sayi* and $15 \pm 4$ m$^{-2}$
2 *E. depressus* individuals at Soundview Park opposed to two *R. harrisii* (both 15 mm CW) collected out of all the recruitment trays at Hastings. Because predator size strongly influences consumption rates, the mud crab abundance data suggests that there was a greater potential for mud crab oyster predation at Soundview Park than at Hastings.

In addition to differential mud crab abundance patterns, there were also different large oyster predator abundances between sites. Four adult *C. sapidus* (between 80 and 180 mm CW) were collected from a fish trap at Soundview Park in September, whereas no predators were collected from the fish trap in July. Even though few individuals were recorded in the fish traps, adult *Libinia* spp. and *C. sapidus* were both regularly observed on the Soundview Park reef during the experimental period. Conversely, no large oyster predators were collected in the fish trap or observed at Hastings. Together, these observations indicate a greater density of large, mobile predators at Soundview Park compared to Hastings.

*Short-term predation experiment*

Consumption rate of oyster spat depended on both site and cage treatment (interaction term: $F_{3,63} = 5.32, p = 0.003$, Figure 2). Consumption was higher at Soundview Park than Hastings ($F_{1,63} = 62.5, p < 0.001$), with 65.0 % ± 14.9% of oysters consumed on tiles accessible to all predators compared to 3.42 % ± 1.60 % in Hastings. Consumption differed significantly between predator exclusion treatments ($F_{3,63} = 20.8, p < 0.001$). Specifically, consumption was more than an order of magnitude higher in the all-predator treatment than the mesopredator treatment at Soundview Park ($p < 0.001$), suggesting that large predators were important oyster consumers. Additionally, consumption in the mesopredator treatment (5.86 % ± 4.0 %) was not significantly different from the no-predator treatment (0.833 % ± 0.546 %; $p = 0.922$), further supporting the importance of large oyster predators at Soundview Park. No significant
differences were observed between all-predator and cage-control treatments at Soundview Park site ($p = 1.00$), indicating there were no cage artifacts affecting consumption. Unlike at Soundview Park, oyster mortality was not significantly different among cage treatments at Hastings ($p > 0.9$). Overall, these results imply that mesopredators have a minimal impact on oyster spat that have reached at least 10 mm SH.

**Long-term recruitment experiment**

Oysters recruited at an average density of 13 to 40 per tile at Hastings and 0 to 1 per tile at Soundview Park in each cage treatment. In addition to being more numerous, the recruited oysters at Hastings were also larger, ranging from 1-20 mm SH, while those at Soundview Park were all less than 5 mm SH. No significant cage-treatment effects ($F_{3,15} = 1.88$, $p = 0.187$, Figure 3) were found at Hastings even though there was a progressive decrease in mean oyster recruitment with decreasing cage protection. While there was a 56% reduction in oysters recruited to the all-predator than no-predator treatment, the high variability in oyster recruitment between tiles likely made detecting statistical differences difficult. For instance, in the no-predator cage treatments, oyster settlement ranged from 17 to 80 oysters per tile. Even if there were biologically significant cage treatment effects, the dearth of oyster scars or boxes found on any of the tiles indicates predation was not contributing to the oyster recruitment cage treatment differences exhibited. An alternative explanation for the decrease in oyster settlement with decreasing protection could be from cage artifact effects on oyster settlement. There were 50% fewer oyster recruited in the all-predator treatment than the cage control, suggesting the cage structure artificially increased recruitment in all cage treatments. Evaluating the role of oyster predators at Hastings becomes difficult due to the high variability in oyster recruitment and
potential cage artifact effects. Regardless, the recruitment results indicate a limited role for oyster predators in oyster settlement and survival at Hastings.

Discussion

Decapod mesopredators have consistently been shown to be important consumers of juvenile oysters (O'Connor et al. 2008, Hill and Weissburg 2013a, Johnson et al. 2014, Carroll et al. 2015a). Yet, few studies have examined the role of mud crabs on oyster reefs north of New Jersey. These northern oyster reefs, unlike those in the Carolinas (Toscano and Griffen 2012, Carroll et al. 2015a), Georgia (Hill and Weissburg 2013a, 2013b) and Texas (Johnson and Smee 2012, Johnson et al. 2014), are often recruitment-limited, entirely subtidal, and do not have abundant *P. herbstii* populations. Therefore, this study sought to understand the mesopredator-imposed top-down control on post-settlement oyster mortality in an understudied system. Two New York Metropolitan restored oyster reef sites, Hastings and Soundview Park, were studied because they had different mud crab species present. Different mesopredator roles were expected at Hastings (*R. harrisii* dominant) and Soundview Park (*D. sayi* and *E. depressus* dominant), as *R. harrisii* has been shown to not consume large quantities of oyster spat (Newell et al. 2007, Kulp et al. 2011). Similar to other mud crab mesopredator studies, *D. sayi* and *E. depressus* were expected to play a critical role in structuring oyster populations on the restored oyster reefs in the New York Metropolitan Region in areas they inhabit. Conversely, *R. harrisii* was expected to have a minimal mesopredator role in areas they inhabit.

Contrary to expectations, there was a minimal mesopredator effect on juvenile oysters in the short-term predation or recruitment experiments. Two studies (Johnson et al. 2014, Carroll et al. 2015a) examined the roles of mesopredators using similar predator-exclusion cages on intertidal oyster reefs in North Carolina and Texas. Unlike results from this study, both studies
found a mesopredator treatment effect. While Carroll et al. (2015a) suggested that mesopredators were likely driving consumption across all treatments, Johnson et al. (2014) suggested that mesopredators were only major contributors in mesopredator treatments. Two major differences existed between this study and previous studies conducted on southern intertidal reefs. First, some mesopredator species present in North Carolina and Texas reach sizes larger than 22 mm, including *P. herbstii*. The highly abundant *P. herbstii* on southern oyster reefs can reach almost 50 mm CW (McDonald 1982). Second, both studies used larger mesh in mesopredator cages than this study, allowing larger mud crab mesopredators to access oyster prey: 37 mm in Carroll et al. (2015a) and 50 mm in Johnson et al. (2014). Although mud crab abundances on the studied New York reefs had high densities of crabs larger than 10 mm CW (approximately 100 individuals m⁻²), there were no mud crab individuals above 15 mm CW at Hastings or 22 mm CW at Soundview Park. Perhaps smaller mesopredators that inhabit northern subtidal oyster reefs do not have the same top-down control on oyster populations as larger mesopredators in southern intertidal oyster reefs.

Predator size affects multiple aspects of predator-prey interactions including prey selection (Toscano and Griffen 2012), foraging rate (Bisker & Castagna 1987), and movement through structure (Bartholomew 2002, 2012). For example, McDonald (1982) suggested that smaller *E. depressus* are able to co-exist with larger *P. herbstii* by foraging within smaller interstitial spaces that are inaccessible to *P. herbstii*. Small predators like mud crabs are also prey for intraguild predators, such as *C. sapidus* and *O. tau* (Grabowski 2004, Hill and Weissburg 2013a). These intraguild predators not only consume mesopredators, but have non-consumptive effects on mesopredators that decrease mesopredator foraging behavior and positively affect oyster spat survival (Grabowski 2004, Griffen et al. 2012). Toscano and Griffen
(2012) further demonstrated that *O. tau* reduces foraging behavior of smaller *P. herbstii* more strongly than larger individuals. Perhaps mud crabs smaller than a certain size were less likely to venture onto experimental tiles, which rested on top of the oyster reef structure, due to habitat partitioning or the fear of being consumed. If smaller predators are less likely to venture on top of the oyster reef due to the presence of larger predators, the role of mud crabs on oyster reefs may have been underestimated using the design in this study. This could be especially important at Soundview Park, which has a more consistent intraguild predator presence than Hastings. Alternatively, as suggested by McDonald (1982), smaller-sized mud crabs may forage primarily in interstitial spaces due to intraguild competition. Although they can readily consume juvenile *C. virginica* under laboratory studies (Kulp et al. 2011), mud crabs are scavengers, consuming multiple bivalve species and other invertebrates and detritus (Lindsey et al. 2006, Griffen 2014). Thus, mud crabs may consume alternative interstitial prey when these are available. There were nine and five alternative prey taxa for mud crabs in recruitment trays at Soundview Park and Hastings, respectively, including amphipods, polychaetes and bivalve prey such as *Mytilus edulis* (Linnaeus, 1758). Future field experiments would benefit by including interstitial oyster treatments and examining whether mud crabs shift from interstitial to reef surface predators once they reach a threshold size.

In contrast to Soundview Park, large predators may not contribute to post-settlement mortality at Hastings. First, there was low consumption of oysters >10 mm exposed to all predators (less than 5% consumed), which should be readily consumed by larger-sized predators. Second, there were few oyster scars or boxes on the tiles, suggesting the lower recruitment on the all-predator oyster tiles was not due to post-settlement mortality. Additionally, few large *C. sapidus* and *O. tau* have been detected at Hastings (Peterson and Kulp 2015), and none were
caught or observed during the experimental period. Due to a reduced predator presence at Hastings, other factors could have influenced initial settlement. Most likely, cage artifact effects artificially increased oyster settlement (Hall et al. 1990, Miller and Gaylord 2007), since the cage controls appeared to have slightly higher recruitment than tiles with all-predator access. Reduced flow induced by the cages could have increased larval supply, as well as alleviated the energy associated with waves (Miller and Gaylord 2007), improving settlement rate. Again, because there were limited oyster scars on tiles after 6 weeks, initial settlement and not post-settlement mortality may have driven the recruitment. Even when oyster larvae settle in controlled environments like hatcheries, they are aggregate settlers (Hidu 1969, Newell et al. 2007, Kulp et al. 2011) with high variability in settlement densities that can range from zero to a hundred per oyster shell (Kulp, personal observation). Thus, the high oyster recruitment variability might also be a result of natural variability in oyster settlement and not due to cage artifact effects. Higher replication in the future would help improve detecting natural settlement variability and potential cage artifact effects.

Results from this study suggest large mobile predators dominate juvenile oyster consumption at the Soundview Park site. Oysters (>10 mm) experienced an order of magnitude higher mortality at Soundview Park than at Hastings. Thereby, mortality of newly settled or seeded *C. virginica* by *C. sapidus* and *Libinia* spp is an important concern for restoration efforts being conducted at sites similar to Soundview Park. The low consumption rate observed at Hastings could be due to a lack of large predatory crabs such as *C. sapidus* and *Libinia* spp. For Hastings, initial settlement density and environmental conditions may be more important factors than predation for the establishment of oyster populations at this site. This study demonstrates
that juvenile oysters experience different predation pressures at Hastings and Soundview Park that can be attributed to the presence or absence of large mobile crustacean predators.

**Conclusion**

This study found that large mobile predators are the dominant consumers of oysters in the New York Metropolitan restored oyster reefs. These results are in contrast to the prior expectations that mesopredators play a dominant role in oyster mortality, as recently suggested by a number of studies (Rindone and Eggleston 2011, Johnson et al. 2014, Carroll et al. 2015a). A fundamental difference may exist between northern and southern oyster reefs due to the different sizes of dominant mud crab species in each region. Mud crab mesopredators of different size classes may utilize different regions of the oyster reef and contribute differently to oyster growth and mortality.

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Figure 1. Average size-frequency distribution of mud crabs at Soundview Park and Hastings in July (A) and September (B) 2012. Four replicate colonization trays (0.13 m²) filled with cultch were inserted into each reef. After six weeks, the number of mud crabs was quantified. At Hastings, *Rhithropanopeus harrisii* were present in trays; at Soundview Park, *Dyspanopeus sayi* and *Eurypanopeus depressus* were present in trays. The mean abundance of mud crabs per m² is shown with ± 1 SE.
Figure 2. Proportion of oysters consumed in short-term predation experiment conducted at Hastings (A) and Soundview Park (B). Tiles with artificially adhered oysters were placed within three predator exclusion treatments, no predators (NP), mesopredators (MP), and all predators (AP), and a cage control (CC) to test for cage artifacts (n = 8 for all treatments). The mean percentage oysters consumed is shown ± 1 SE. Tukey’s HSD post-hoc tests comparing within-site cage treatment are shown above each bar.
Figure 3. Number of oysters recruited onto the top and side of each tile in long-term recruitment experiment at the Hastings site. Bare tiles were placed within three predator exclusion treatment cages (no predators, mesopredators, and all predators) and a cage control to test for cage artifacts (n = 4 for all treatments). The mean number of recruited oysters over six weeks in August 2012 is shown with ± 1 SE. There was no significant difference found between cage treatments ($F_{3,15} = 1.88$, $p = 0.187$).
Chapter 7

Dissertation summary and conclusions
Habitat type and density effects: Conceptual model

There were fundamental differences in prey refuge offered by the hard-bottom \textit{(Crepidula fornicata)} and vegetated \textit{(Zostera marina)} habitats, where the hard-bottom habitat enhanced prey survival. This habitat-type relationship was species-dependent, only occurring when one or multiple Sayi mud crabs \textit{(Dyspanopeus sayi)} foraged for the blue mussel \textit{(Mytilus edulis)}. In contrast, a single blue crab \textit{(Callinectes sapidus)} was not only equally successful at consuming prey in hard-bottom and vegetated structured habitats, but both structured habitats did not enhance prey survival compared to a sand habitat. Chapters 2-5 suggest that structured habitats do not always enhance prey survival; \textit{Zostera marina} structure did not affect foraging for both predator species and \textit{Crepidula fornicata} structure did not affect foraging for \textit{C. sapidus}.

Structure has been typically described as enhancing prey survival by reducing the encounter rate between predator and prey \cite{Moksnes1998, Heck2003, Stoner2009, Hill2013a}, effectively reducing the attack rate \cite{Ryer2004, Wong2013}. Sietz et al. \cite{Sietz2001} introduced a conceptual framework for bivalve prey that related the importance of encounter rate between predator and prey to the strategy a prey uses to avoid being consumed. They proposed encounter rate would be less important for prey that rely on passive defenses (like physical protection) than those that relied on active defenses (like escape). They applied their conceptual framework to two bivalve prey, \textit{Macoma baltica} (an organism that relies more heavily on passive prey defenses) and \textit{Mya arenaria} (relies on active prey defenses), that were found in sand and mud habitat types at different densities. \textit{Macoma baltica} were distributed equally across both habit types, whereas \textit{M. arenaria} populations were reduced in mud compared to sand. Manipulative experiments suggested that habitat type (sand versus mud) did not alter encounter rate between the predator, \textit{Callinectes sapidus}, and \textit{M. baltica}, whereas
sand reduced *C. sapidus’* encounter rate with *M. arenaria*. Researchers proposed that the sand substrate material made it more difficult for *C. sapidus* to detect *M. arenaria* buried deeper in sand compared to mud, lowering its encounter rate and overall mortality.

The conceptual framework introduced in Sietz et al. (2001) can be applied and expanded to understand the results presented in Chapters 2 - 5. Structure’s effect on encounter rate may be less important for prey that rely on passive rather than active prey defenses. The bivalve prey, *Mytilus edulis*, relies on passive prey defenses to avoid being eaten: prey aggregation, byssal thread number and strength, attachment location and orientation, and shell thickness (Elner 1978, Bertness and Grosholz 1985, Robles et al. 1990, Smith and Jennings 2000). Even though habitat type can negatively affect encounter rate, the predator has to still overcome passive prey defenses like separating *M. edulis* from its byssal threads in order to successfully capture prey. For decapods, bivalve prey selection and consumption has been linked with energetic costs and risk of claw damage (Elner 1978, Elner and Hughes 1978, Juanes and Hartwick 1990, Juanes 1992). A predator’s difficulty in overcoming prey’s passive defenses causes the predator to reject prey after encountering, attacking, and/or handling prey (Elner 1978, Wong and Barbeau 2005). Thus, structure may need to limit a consumption event by not only altering encounter rate, but also the number of successful attacks (i.e the bivalve prey isolated and in the predator’s chelae).

Structure could enhance prey survival of sessile bivalve prey with passive prey defenses by 1) increasing the energetic costs associated with consuming prey and/or 2) by increasing the predator’s rejection rate of prey. For instance, the *C. fornicata* structure likely offered robust attachment sites for byssal thread attachment and crevices that would decrease prey accessibility and increase the time until a successful attack occurs. Species-specific differences that were
exhibited between *D. sayi* and *C. sapidus* in Chapter 3 suggests that predator morphology can alter the difficulty in a successful prey capture in structured habitats. For instance, the swimmer appendages may allow *C. sapidus* to move through the material at a different speed than *D. sayi*, and also be impeded differently by the *C. fornicata* shell hash matrix, potentially influencing both the encounter rate and also the likelihood of a successful prey capture.

*Mytilus edulis* must benefit from hard-bottom and vegetated habitats in the field. A major limitation of my experimental set-up is that the *M. edulis* was given an hour to interact with structure. The short time of the experiment probably dampened the benefit both *Z. marina* and *C. fornicata* has on enhancing *M. edulis* survival. However, this dissertation does highlight the importance of understanding how the prey utilizes the structure to enhance its survival. Prey that rely on mobile defense strategies have been shown to continually modify their position within structure to reduce a predator’s encounter rate (Main 1987, Ryer 1988). Perhaps for sessile prey similar to *M. edulis*, structure may also play an important role in enhancing their passive prey defenses. This dissertation shows that structure’s effect on predator’s behavior may not always be enough to impede foraging.

**Mutual interference and structure effects**

Unlike other decapod species (Mansour and Lipcius 1991, Clark et al. 1999b, Smallegange et al. 2006, Griffen and Delaney 2007, Griffen and Williamson 2008), *D. sayi* predator density increases did not change the effect of antagonistic interactions (Chapters 4 and 5). This is similar to another decapod predator, *Hemigrapsus sanguineas*, where predator density increases above two individuals did not alter handling time or searching time even though time spent in antagonistic interactions increased with predator density (Griffen and Delaney 2007, Griffen and Williamson 2008). Without observing the behaviors among *D. sayi*, the reason why
mutual interference effects do not increase when predator density doubled can only be hypothesized. Individuals may have limitations on energetic costs from antagonistic interactions where they need to modify their behavior to off-set interference effects. Some behavioral offsets could include developing territories, prey switching, or increasing their foraging time to maintain a minimum intake rate.

Increases in structure in both *C. fornicata* and *Z. marina* habitats did not alter interference among *D. sayi* (Chapters 4 and 5). This may be related to species-specific differences in the level of aggression among *D. sayi* individuals compared to other decapod species. There may be important habitat type differences in alleviating competitive effects for predators that have higher levels of aggression than *D. sayi*, which remains to be tested.

*Re-evaluation of parameter estimation from functional response curve fitting*

In Chapter 5, the maximum feeding rates were inhibited by increases in *C. fornicata* habitat. This result was dependent on predator density, since maximum feeding rates were similar among *C. fornicata* shell hash treatments when a single predator foraged for *M. edulis* (Chapter 2). Based on the functional response curve fitting, the lowered feeding rates could have been caused by structure increasing handling time. However, a major criticism of using functional response models to estimate attack rate and handling time is that assumptions made in building the models may not apply equally to all species (Jeschke et al. 2002, Tully et al. 2005). For instance, the functional response assumes that the predator is continuously feeding through the entire experimental period. Decapods have been shown to not feed continually, having their highest feeding rates either at night or during crepuscular periods (e.g. Paul 1981, Clark et al. 1999a). A pilot follow-up experiment confirmed that foraging is not constant, and thus it is unlikely *D. sayi* regularly forages for the 36-hour experimental period. Follow-up studies also
D. sayi typically take between 5 to 15 minutes to consume one M. edulis (10 - 15 mm in shell height) prey, which is a shorter time period than the approximate 2-hour handling time period estimated from the functional response curve fitting (Chapters 2 and 5). This would mean the functional response assumption that predators continuously forage is not met for D. sayi. Toscano et al. (2014) found that the observed handling time of the common mud crab (Panopeus herbstii) did not match the estimated handling time estimated from functional response curve optimization. Thus, while the functional response model parameter estimates can be used for comparative purposes, attack and handling time parameters need to be estimated to validate mechanistic relationships between prey density and per capita feeding rates (Jeschke et al. 2002, Tully et al. 2005). In my experimental set-up, quantifying attack rate and handling time through direct observation in C. fornicata and Z. marina is difficult. Predators foraging within the shell matrix cannot be observed and the mimicked Z. marina leaves can obscure an observer from tracking some encounters between predator and prey. Thus, validating the attack rate and handling time through visual observation in the structured treatments used in this dissertation is not possible.

Considering caution needs to be used in interpretation of results based on the attack rate and handling parameters estimated from functional response (Jeschke et al. 2002, Tully et al. 2005), there may be alternative behavioral effects leading to the reduction in maximal feeding rates other than handling time seen in Chapter 5. For instance, unless the presence of multiple predators led an individual predator to change where they consume prey (like staying within the shell matrix, as suggested in Chapter 5), it is unlikely the structure effect on handling time led to the reduced maximum feeding rates. Instead, the presence of additional predators may have enhanced structure’s influence on consumption. Some possible mechanisms include: increasing
the time before an attack is initiated after a prey is encountered and/or preventing an attack from occurring through interference. Without further experimentation, it is unknown as to why increases in *C. fornicata* shell hash reduce the maximum feeding rates when more than one *D. sayi* predator was present (Chapter 5) and not when a single predator was foraging (Chapter 2). While there are limitations to using the functional response curve fitting to mechanistically represent a predator’s attack rate and handling time, they provide a starting point in partitioning the effect of prey density on different steps of the predation cycle (O’Brien 1979) when visual observations are either not possible or cannot be reliably assessed.

**Prey density effects on structure**

Prey density effects were dependent on predator identity, predator density, and whether structure had an effect on foraging. When a single predator was foraging, *D. sayi* exhibited a prey density effect in Chapter 2, but not Chapter 3. In Chapter 2, prey densities reached a saturation level that removed the negative effect increases in *C. fornicata* had on *D. sayi* foraging for *M. edulis*. However, the negative effect of *C. fornicata* still occurred at the high-prey density treatment in Chapter 3. Likely a major difference is that the high-prey density treatment used in Chapter 3 was not saturated enough to dilute habitat structure effects (175 mussels per m² compared to 480 mussels per m² in Chapter 2). Studies have found conflicting results of prey density effects, where prey density has not affected structure effects (Corona et al. 2000, Humphries et al. 2011, Hovel et al. 2016), removed structure density effects (Sponaugle and Lawton 1990) or changed the relationship (Lannin and Hovel 2011). Perhaps the inconsistent effects of prey density and structure is dependent on whether prey exist at a high enough density in the field to remove habitat structure impacts. Prey density effects were different when one versus multiple predators foraged in structured environments (Chapters 2 and 5). This suggests
that predator density could modify the role prey saturation has in reducing structure effects on top-down control. Further work is needed to better understand the conditions that need to exist for habitat structure to negatively or positively affect predator foraging, and how increases in predator and prey densities change this relationship.

**Application of habitat utilization for restoration purposes**

In chapter 6, the background community of predators, in addition to predator size, were important determinants of the top-down control on juvenile *Crassostrea virginica*. At one of the study sites, Soundview Park, there were a greater number of larger-sized decapod predators (*C. sapidus* and *Libinia* sp.) than the second study site, Hastings. This resulted in greater mortality of juvenile *C. virginica* at Soundview Park than Hastings. Further, even though smaller-sized predators (which were predominantly three mud crab species: *Eurypanopeus depressus*, *D. sayi*, and *Rhithropanopeus harrisii*) were more abundant than the larger-sized decapod individuals, they did not significantly contribute to the top-down predation at either site. This contrasts with the more important role another mud crab species, *P. herbstii* has shown in other oyster reef systems (Johnson et al. 2014, Carroll et al. 2015a). Chapter 6 demonstrates top-down control was dependent on both species- and size-specific differences. Restoration of oyster reefs need to consider the predator community, both in terms of predator identity and predator size distribution.

**Conclusions**

This dissertation is unique in examining whether habitats that create different interstitial spaces affect prey refuge in distinct ways. The two habitat types compared, the mimicked hard-bottom slipper snail (*C. fornicata*) shell hash and vegetated eelgrass (*Z. marina*) habitats, did not offer equal levels of prey refuge to *M. edulis* for the predator *D. sayi* (Chapters 2 - 5). In a
species-dependent manner, the slipper snail shell hash habitat was a better prey refuge to *M. edulis* than the eelgrass (Chapter 3). Even though prey density saturation can remove or reduce structure effects on foraging (Sponaugle and Lawton 1990, Mattila et al. 2008, Canion and Heck 2009, Scheinin et al. 2012), it is unclear at what minimum level of prey abundance: shell hash volume is needed for this to consistently occur in the *C. fornicata* model system used in this study (Chapters 2 and 3). When a single *D. sayi* forages in *C. fornicata*, structure effects were removed only when prey density was 480 mussels per m$^2$, which was only offered in Chapter 2. Further, this dissertation highlights that the effects of interference among *D. sayi* did not change when predator density doubled and is not affected by increases in hard-bottom or vegetative habitats when prey is non-limiting (Chapters 4 and 5). However, intraspecific competition among *D. sayi* individuals is important when prey is limiting and structure does not inhibit foraging (Chapter 5). While structure’s role in reducing the encounter rate between predator and prey can positively affect prey survival, perhaps it is also important to consider how prey utilize structure to enhance their own prey defenses. For *M. edulis*, which relies on byssal attachment, orientation, and aggregation (Elner 1978, Bertness and Grosholz 1985, Robles et al. 1990, Smith and Jennings 2000), structured habitats may need to enhance prey rejection for structured habitats to display the well-supported value of habitat refuge (Moksnes et al. 1998, Heck et al. 2003, Stoner 2009, Hill and Weissburg 2013a). This dissertation emphasizes the need to consider how a prey’s defenses modifies the relationship of a habitat’s prey refuge value.
References


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