

INFLUENCE OF HABITAT COMPLEXITY IN STRUCTURING SPECIES-SPECIFIC
INTERACTIONS AND TROPHIC LINKAGES ON OYSTER REEFS OF
SOUTHEASTERN NORTH CAROLINA

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ABSTRACT

Species interactions influencing the strength of trophic linkages play a key role in structuring communities. Although the importance of these interactions has been recognized, currently there are relatively few studies characterizing the role of habitat in moderating these interactions, especially in marine environments. Habitat complexity that provides refuge for some organisms may alter interactions between species with consequences for community composition. Recently created oyster reefs of differing complexity in southeastern North Carolina provide an excellent opportunity to test the hypothesis that increased habitat complexity modifies predator-prey interactions leading to direct and indirect effects in the oyster reef community. The common mud crab, *Panopeus herbstii*, is an abundant intermediate predator living within oyster reefs feeding on bivalves such as oyster spat, *Crassostrea virginica*, and ribbed mussels, *Geukensia demissa*, and is prey for other species such as blue crabs, *Callinectes sapidus*, and larger fishes. The goal of this study was to determine the direct and indirect effects of oyster complexity on mud crab populations (density, distribution, feeding, and survival) in a field setting and mud crab: bivalve (predator-prey) dynamics in the presence and absence of a top predator, the blue crab in a laboratory setting. Mud crab density was significantly greater in areas of high habitat complexity during both field and lab studies. Tethering trials indicated predation on mud crabs increased as oyster reef complexity decreased with highest predation rates in open sand. However, highest predation on mud crabs occurred in open sand areas along the edge of high complexity reefs compared to sand areas distant from a reef. Laboratory studies indicated mud crab predation on oyster spat and mussels was greater in high complexity oyster patches, but mussels were

preferred over oyster spat. The presence of a top predator had differing effects on mud crab predation of oyster spat and ribbed mussels. Predation on oyster spat was reduced in high complexity patches, whereas predation on ribbed mussels was reduced in low complexity patches when blue crabs were present. A potential positive feedback was observed where high complexity oyster habitat provide increased settlement habitat for mussels and mussels provide an alternate, preferred prey source reducing predation pressure on oyster spat. This study demonstrated the multifaceted role of habitat complexity in modifying trophic interaction within a multi-prey system.

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INTRODUCTION

The eastern oyster, *Crassostrea virginica*, exists intertidally throughout large portions of the southeastern and Gulf coasts of the United States (Bahr and Lanier 1981) and is of importance not only as a direct fishery resource but also as critical habitat for other important fishery and forage species (Ortega and Sutherland 1992, Posey et al. 1999, Meyer and Townsend 2000). Oysters predominantly occur in small clusters attached to hard substrates such as large shells, pilings, and rock jetties or more commonly as aggregated groups forming extensive reef structures (Wells 1961, Bahr and Lanier 1981). Oyster reefs may be composed of low complexity oyster shell, high complexity oyster shell, or varying combinations of the two. Low complexity reefs are composed of flat unaggregated shell and individual live oysters that do not provide much vertical or three dimensional structure. High complexity reefs are dominated by shell aggregates, forming upright clumps of live oysters with articulated shell offering vertical relief and a complex three dimensional structure. Habitat complexity in intertidal *C. virginica* oyster reefs has two components: rugosity and vertical relief. Rugosity refers to variability in surface topography (roughness) while relief refers to the height of the reef relative to surrounding substrate. Complexity is maximized when both rugosity and relief of an oyster reef are high. For intertidal oyster reefs in southeastern North Carolina, high vertical relief tends to correlate with high rugosity and therefore high complexity.

Oyster reefs serve important ecological roles in nearshore estuarine ecosystems. They reduce local shoreline erosion and stabilize marsh edges (Meyer et al. 1997), increase sedimentation by slowing the overlying water flow (Dame et al. 1984) and

through biodeposition of feces and pseudofeces. Increased sedimentation along with the oyster's active filtration of the overlying water decreases turbidity (Newell 1988, Powell et al. 1992) and improves aspects of water quality (Nelson et al. 2004). Oyster reefs, as a physical structure support a high diversity of life, providing both refuge and foraging area to many resident and transient species of finfish and decapods (Wells 1961, Bahr and Lanier 1981, Coen et al. 1999, Griffitt et al. 1999, Posey et al. 1999, Meyer and Townsend 2000, Harding and Mann 2001, Peterson et al. 2003) as well as many infaunal and epifaunal species. Intertidal oyster reefs are considered trophic hot spots as they occur commonly on unstructured mud flats. The structure offered by oyster reefs support greater densities of a wide variety of species compared to unstructured mudflats. These various ecosystem functions (provided by healthy oyster populations) underscore the importance of understanding inter-relationships between oysters and their environment and factors affecting this relationship.

With the decline of oyster populations throughout much of their range (due to pressures from overharvesting, disease, and eutrophication) conservation and restoration of these systems is becoming an increasingly important management issue (Rothschild et al. 1994, Luckenbach et al. 1996, Meyer and Townsend 2000, Breitburg et al. 2000, O'Beirn et al. 2000, Peterson et al. 2003). Oyster restoration strategies now incorporate multiple goals, including enhancement of water quality, fisheries, and/or habitat (Luckenbach et al. 1996, Breitburg et al. 2000, Peterson et al. 2003), but the goal of restoring degraded oyster populations in environmentally disturbed areas to historic levels is the common focus of most restoration efforts. However, little is known as to how reef morphology, including microhabitat complexity, affects settlement of oyster

spat and reef development (O'Beirn et al. 2000), or the role reef structural complexity plays in modifying predator-prey interactions and determining habitat use by other fauna. If more oyster settlement is occurring within lower complexity regions of oyster reefs in southeastern North Carolina (Posey and Alphin manuscript in prep) due to the indirect effects of higher predation, the translocation and relocation of high complexity oyster aggregates, an approach suggested for restoration, might have short-term negative effects relative to the spreading of flat, disarticulated shell to promote reef growth. Awareness of these potential factors is of particular significance to managers who are continually faced with decisions on efficient means in which to create and promote subsequent growth of sustainable oyster reefs.

Among the dominant species in the oyster-dependent epifaunal community are the xanthid crabs, *Panopeus herbstii* (common mud crab) and *Eurypanopeus depressus* (flat mud crab), which are both found abundantly in intertidal oyster reefs along the southeastern coast of the U.S. (Grant and McDonald 1979, McDonald 1982, Day and Lawton 1988, Meyer 1994). These crabs are considered reef resident fauna and use the reef to escape desiccation at low tide (Grant and McDonald 1979) and as a refuge from predators and foraging habitat at high tide (Seed 1980, Whetstone and Eversole 1981, McDonald 1982, Lin 1990, Powell 1994). Although crab use of oyster reefs is well documented, there have been relatively few studies of xanthid crab microhabitat preference within reefs or how reef landscape may affect occurrence and behavior. Meyer (1994) showed *P. herbstii* was positively associated with surface shell cover (flat shell) and, to a lesser degree, cluster volume. However, his study may have underestimated the strength of the association because *P. herbstii* that occurred

underneath culms were not considered associated with these structures, but rather with flat shell. If overlying structure is considered, mud crab association with cluster volume and complexity may be stronger than initially suggested.

Mud crabs, mainly *P. herbstii*, play an important intermediate trophic role within oyster reefs (Wells 1961, Powell 1994). They are voracious predators on bivalves such as oyster spat (McDonald 1982, Bisker and Castagna 1987, Lin 1990, Abbe and Breitburg 1992, Grabowski 2004), ribbed mussels, *Geukensia demissa* (Seed 1980, McDonald 1982, Lin 1990), and hard clams, *Mercenaria mercenaria* (Whetstone and Eversole 1981, McDonald 1982, Day and Lawton 1988, Lin 1990, Micheli 1997, Grabowski 2004). They have a mechanical advantage for shell crushing over other crabs, in the form of a large molariform tooth on the dactyl of the major claw (Vermeij 1977, Bisker and Castagna 1987), allowing more efficient predation on larger individuals. Adult mud crabs can consume oyster spat as large as 25mm long (MacKenzie 1981, Bisker and Castagna 1987), with some studies reporting consumption up to 54mm (McDermott and Flower 1952). In addition to being important predators on bivalves, mud crabs are also prey for other species such as adult blue crabs, *Callinectes sapidus*, (Powell 1994) and fish such as oyster toadfish, *Opsanus tau* (Abbe and Breitburg 1992, Grabowski 2004). Although both adult and juvenile blue crabs are known predators on bivalves (Seed 1980, Bisker and Castagna 1987, Abbe and Breitburg 1992, Micheli 1997, Clark et al. 1999, Clark et al. 2000), predation on mud crabs would seem to offer greater yield per unit effort compared to smaller bivalves such as oyster spat and ribbed mussels. Previous tethering studies have shown predation on mud crabs by transient predators, like adult blue crabs, to be higher within the oyster reef compared to adjacent sand areas

(Powell 1994). Although lower predation rates were observed in sand areas adjacent to a reef, mud crabs were never found on the sandflat suggesting predators may actively target oyster reefs as foraging grounds (Powell 1994). While the importance of predation on mud crabs in oyster reefs compared to adjacent sand areas has been shown, studies are lacking on the predation pressure among reefs of varying complexity. If there is significant predation on mud crabs in lower complexity oyster habitat compared to high complexity reefs there may be critical indirect implications for mud crab prey. The refuge offered by more complex reefs might inhibit foraging by mud crab predators, allowing for higher bivalve predation by mud crabs. Conversely, in lower complexity reefs higher predators may have easier access to mud crabs, which may provide bivalves with a release from predation by mud crabs and promote higher oyster spat survival rates. Implications of such interactions suggest lower complexity reefs could potentially develop faster than higher complexity reefs, at least initially. Habitat complexity can have significant ecological implications through behavioral or density changes in intermediate predators (Grabowski 2004).

The overall goal of this study was to examine trophic interactions of xanthid crab predation on bivalves and how it is moderated by habitat complexity and higher predators. More specifically, major objectives were to determine the effect of oyster reef complexity on mud crab distribution, feeding and survival as well as to assess potential direct and/or indirect effects of oyster reef complexity on mud crab: bivalve predator-prey dynamics.

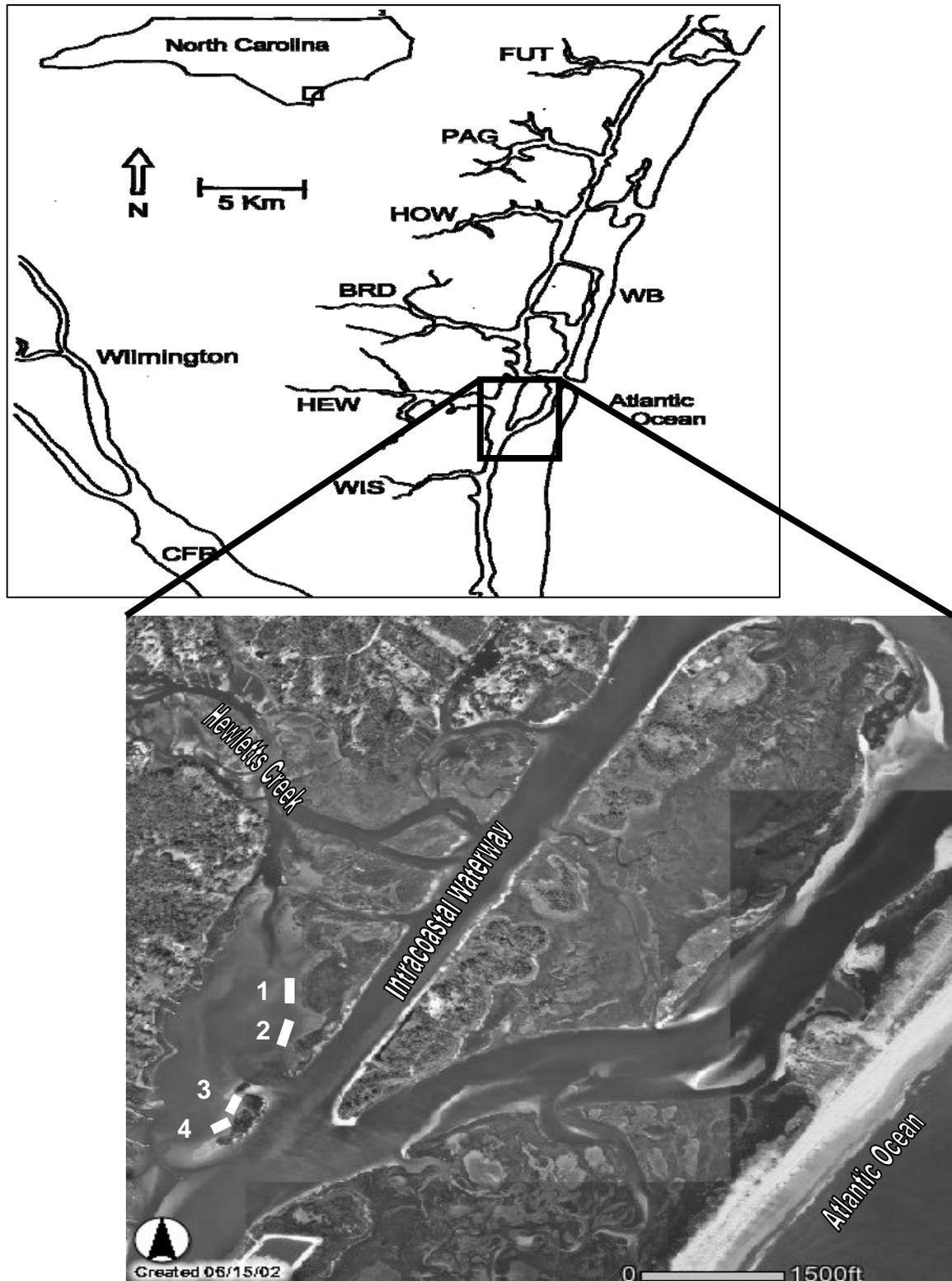
METHODOLOGY

This study consisted of both lab and field components. Field studies consisted of oyster reef excavations to determine ambient density and distribution, tethering of mud crabs to examine mud crab survival, and a recruitment study to examine interactions between complexity and initial spat survival. Field studies on created experimental and natural reefs were conducted intertidally in Masonboro Sound near Wrightsville Beach, North Carolina, on the University of North Carolina Wilmington (UNCW) research lease as well as on natural reefs in Hewlett's Creek, a tidal creek system located just north of the Masonboro site (Figure 1). These areas consist of extensive intertidal mud flats with natural oyster reefs in the mid intertidal and bordered by *Spartina* marshes in the upper intertidal. These field areas have been the sites of several previous studies (Powell 1994, Molesky 2003, Harwell 2004). Laboratory studies were conducted at the UNCW Center for Marine Science in order to examine direct and indirect predator-prey interactions among varying trophic levels and reef complexity treatments using blocked experimental conditions.

Oyster Reef Excavations

To assess the relationship between oyster habitat complexity and resident fauna, experimental reefs of high (reefs containing oyster culms that provide vertical relief) and low (reefs containing flat disarticulated shell) complexity were sampled using excavations. This was carried out quarterly from summer 2002 through summer 2005. The experimental reefs used in this study were circular structures providing two treatments: high complexity reefs that included both high and low vertical relief patches

Figure 1. Map of the four experimental oyster reef sites (bottom); white rectangles denote the four sites. Oyster reef sites at Masonboro Sound were located just south of the mouth of Hewletts Creek (HEW).



in equal proportions set up in a checkerboard fashion creating high surface rugosity and low complexity reefs composed of unarticulated shell. The experimental reefs were designed to approximate characteristics of natural patch reefs. Maximum vertical relief (top of structure to the underlying substrate) was used to objectively quantify and standardize microhabitat complexity in the field. Low complexity maximum heights were under 5cm whereas high complexity maximum heights exceeded 15cm with most ranging from 20-25cm. These reefs were created in summer 2002 as part of a broader project examining reef complexity relative to reef function (Molesky 2003, Harwell 2004). Eight experimental reefs, four of high and four of low complexity (one pair of each reef type at each of the four sites), were used in the field studies. Eight natural reefs (four from adjacent areas near the experimental reefs and four within Hewlett's Creek) of both high (containing microhabitats of high and low relief) and low complexity were also selected as natural references in the field studies. These reefs were selected to have a size and shape approximating the experimental reefs.

Mud crab density was assessed with low-tide excavations using one 20cm x 20cm quadrat per low complexity reef, while two quadrats were used for high complexity reefs, (one quadrat for each microhabitat), for a total of 26 quadrats per sampling period. Mud crabs were identified to species, measured (carapace width), and sex was recorded. Total xanthid crab densities were analyzed alone, as well as by *Panopeus herbstii* (by far the dominant species recorded) and all other xanthid crabs (mainly the flat mud crab, *Eurypanopeus depressus*) to assess mud crab distribution patterns. The significant local predators on mud crabs were ascertained primarily through a literature review as well as personal observation (shallow-water sightings, seine nets, as well as sweep net samples)

in the field. Previous studies have examined predation on mud crabs or have provided data on stomach contents from potential predators (Abbe and Breitburg 1992, Powell 1994, Grabowski 2004).

Field Mud Crab Predation Risk

Relative predation rates on the mud crab, *Panopeus herbstii*, were determined through tethering experiments on and adjacent to experimental reefs during the summer of 2005. The high complexity reef used for this study consisted of all high complexity culms as this reef was originally created as a low complexity reef in 2002 but received so much recruitment over the past three years that it essentially became a high complexity reef containing greater than 15cm vertical relief. *P. herbstii* was used exclusively because they were the numerically dominant mud crab within oyster reefs of this area. Tethering provides useful insights on relative predation rates among habitat types. There are some concerns regarding tethering as a methodology especially for more mobile species (Zimmer-Faust et al. 1994), but for less vagile species such as mud crabs, which seldom leave the reef, artifacts should be minimal. Concerns notwithstanding, tethering is the most practical approach for direct comparisons of the effects of high and low oyster reef complexity on relative predation rates in the field.

Crabs used for this experiment were hard shell non-ovigerous mud crabs ranging from 20-30mm carapace width, collected from the field and kept in laboratory tanks no greater than two weeks. The tethering apparatus was applied using modifications to procedures described by Powell (1994). The carapace was cleaned and dried with acetone and a wire loop was then attached to the carapace using a drop of clear superglue

gel to secure the loop in a manner that does not hinder the crab's movement. Crabs were observed in the laboratory for 24hrs prior to field deployment to ensure that the tether apparatus was secure and handling mortality did not occur. A 20cm segment of monofilament line (40lb test) was secured to the loop and then attached to the top of an 20cm 60-penny nail that was pressed into the substrate. A small float was attached to the nail by a 1.0m segment of monofilament line to aid in retrieval. Crabs were placed in one high and one low complexity reef as well as a sand control. Ten tethered mud crabs were used for each treatment and control. The crabs were tethered in the interior regions of each reef (no closer than 0.5m from the edge). Five additional mud crabs were tethered in the sand 5cm outside the edge of the high and low complexity reefs with 10cm of monofilament to assess potential reef edge effects. The tethered crabs were deployed on an incoming tide and left for 2hrs after the reef became inundated and was replicated three times. A predation event was recorded for crabs if a portion of the carapace was still attached to the apparatus. If no carapace was remaining and there was no sign of the line being cut, the crab was not included in mortality assessments because of the possibility of crab escape.

Oyster Recruitment

Field surveys assessing oyster recruitment were performed on the same eight reefs (four high and four low) used for excavations as well as on natural reefs in Masonboro Sound. Recruitment was recorded as scars, dead and live newly settled oyster spat (measured shell height) as a function of complexity. Oyster recruitment was recorded by placing 20cm x 20cm baskets (made from 1cm wire mesh) for shell treatments (culms

and flat shell) on both natural and experimental reefs. In order to monitor recruitment, defaunated shell/culms matching appropriate reef structure were set out and buried to a level that was consistent with the height of the reef and marked by flags. One basket containing the shell type that corresponded to the microhabitat complexity treatment was used for each reef. For oyster reefs containing both high and low vertical complexity, two baskets were used (one for each microhabitat type). The defaunated shell/culms were placed in the field late July 2004 and recruitment was measured in early January 2005.

Preliminary Laboratory Predation Trials

A preliminary study of maximum consumption by small and large size classes of mud crabs, *Panopeus herbstii*, was conducted to determine the maximum amount of bivalves mud crabs of different sizes could consume in one day. The tanks used for this and subsequent laboratory studies were 90cm x 150cm and filled with approximately 8cm of beach sand across the bottom. In separate trials, two mud crabs (held without food for 48h) ranging from 20-21mm carapace width (CW) and two ranging from 29-30mm (CW) received either 10 or 30 bivalves not attached to shell (either oyster or mussels). This was a fully blocked experiment that examined crab size, prey number, and prey type influences on prey consumption with the objective of defining optimum prey density and crab size for trophic interaction and complexity studies. Bivalves, ranging from 10-20mm shell height, were randomly placed on top of the sand for each treatment so that each mud crab had easy access to the prey. This was repeated 3 times for both oyster

spat, *C. virginica*, and mussels, *G. demissa*. The number of bivalves consumed was recorded for each treatment.

Mud crabs ranging from 29-30mm (carapace width) consumed on average 8 of the 10 oyster spat given to them over a 24hr period. This size class of mud crabs consumed 21 out of the 30 spat given to them over a 24hr period (consumption for 2 crabs per trial). Smaller mud crabs (20-21mm) on average consumed 4 out of 10 oyster spat and an average of 14 out of 30 oyster spat. Both size classes of mud crabs generally chipped open the shell (~ 65%) compared to crushing the shell (~35%) when consuming spat. Larger mud crabs (29-30mm) consumed all mussels when offered 10 over 24hrs and an average of 25 out of 30 mussels. Mud crabs ranging from 20-21mm on average consumed 7 out of 10 mussels over 24hrs and when given 30 mussels, they consumed approximately 18 of them. When consuming mussels, the larger mud crabs more often crushed the entire shell whereas smaller mud crabs tended to either chip open the shell or crush them with similar frequencies. These results indicated a minimum number of 10 bivalves per crab was optimum for 24hr laboratory trials, with some variability in crab consumption with varying crab size.

Laboratory Bivalve Predation

A laboratory study was conducted to determine the relationship between oyster habitat complexity and presence of a predator on mud crab distribution and prey survival. The laboratory study also evaluated whether prey distribution interacts with predator presence in affecting mud crab distribution. Laboratory trials consisted of a high complexity and a low complexity 20cm x 20cm oyster patch offered in a 90cm x 150cm

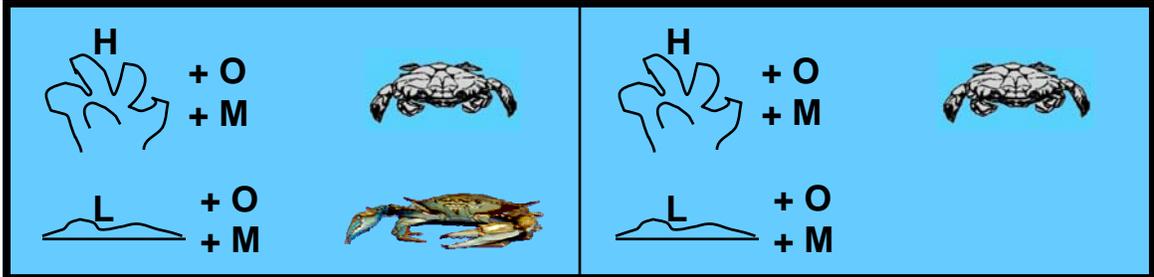
mesocosm. High complexity patches were made from culms collected from the field, defaunated and cleaned thoroughly to remove any biofilms. The high complexity habitats ranged in volume from 800-900mL and height ranged from 20-26cm (base to highest point). Low complexity patches consisted of flat, unarticulated shell arranged in a manner that was consistent with field observations and ranged from 500-550mL in volume. These patches provided less than 5cm vertical height. Mud crabs, 20-30mm carapace width, and oyster spat and ribbed mussels, 10-20mm shell height (umbo to outer edge), were used in the laboratory study. Based on preliminary trials and other studies, this size class of mud crabs was expected to be able to consume 5-20 bivalves of the size range offered over a 24hr period (Castagna and Bisker 1987, Lin 1990). The presence of a mud crab predator (blue crab) and prey (oyster spat and ribbed mussels) was varied among eight treatments in this lab study. There were 30 bivalves of each species per habitat complexity type (for trials containing bivalves), and 3 mud crabs (held without food for 48hrs) in each trial, with half the trials including a single blue crab. Bivalves were affixed to the under side (concave portion) of an oyster shell using super glue gel (Grabowski 2004) with 5 oyster spat and 5 mussels attached per shell. Adult blue crabs used for this experiment ranged from 130 to 150mm carapace width, which is a known size range of blue crabs preying on mud crabs. The claws of the blue crab were tied using Tygon tubing to prevent possible destruction of the oyster patches or actual predation on mud crabs or bivalves since the primary focus of this study was on behavioral changes in the presence of a top predator. All crabs used in this experiment were hard-shelled non-ovigerous individuals. All treatments were run simultaneously with treatments assigned at random among the eight experimental tanks for all five

replicates. Standing water was used to minimize any potential confounding effects associated with inflow of fresh saline water. High and low complexity habitat patches were randomly assigned to either end of each tank.

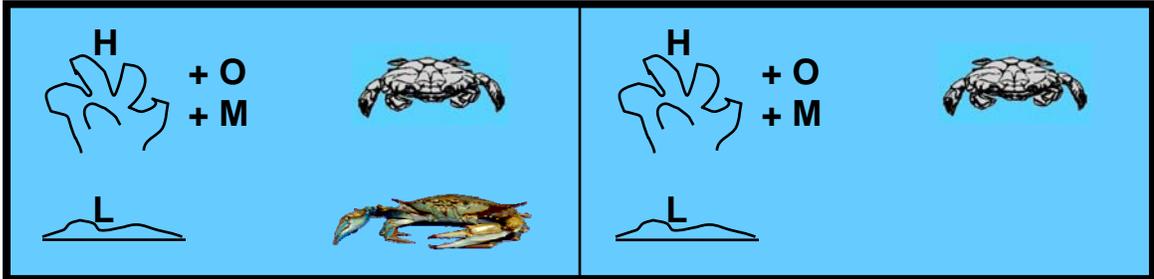
The first two treatments assessed the relationship between oyster vertical complexity and presence/absence of a predator (blue crab) on mud crab distribution and prey survival in high and low complexity habitats (Figure 1a). Treatment 1 had bivalve prey present in both oyster habitats along with a blue crab and mud crabs, and assessed the relationship between mud crab occurrence and predation on bivalves with a higher predator in the system (Figure 1a). The second treatment had bivalves present in both habitats and mud crabs but no blue crab (Figure 1a). Treatments 3, 4, 5, and 6 when compared with treatments 1 and 2 evaluated how the availability of bivalve prey in high and low complexity oyster patches affected mud crab distribution and predation on bivalves in the presence/absence of a higher predator (Figure 1a, b, c). Treatment 3 had bivalves exclusively located in the high relief with the top predator present and treatment 4 was identical except it had no blue crab (Figure 1b). For treatments 5 and 6 bivalves were limited to only the low relief with the higher predator present in treatment 5 and absent in trial 6 (Figure 1c). Treatment 5, when compared to treatment 6, assessed if the presence of prey in only low complexity areas mediated mud crab distribution with a predator in the system in such a way that foraging ability outweighs the protection of high complexity areas that offer no prey. Treatments 7 and 8 offered no bivalve prey and examined mud crab distribution in high and low complexity in the presence or absence of a higher predator (Figure 1d).

Figure 2. Diagram of the lab treatments; each letter represents two treatments. H = high complexity patch, L = low complexity patch, +O (oyster) and +M (mussel) = bivalve prey present, mud crab picture (top crab on all 8 treatments) = mud crab present, blue crab picture (bottom crab on treatments 1, 3, 5, and 7) = blue crab present.

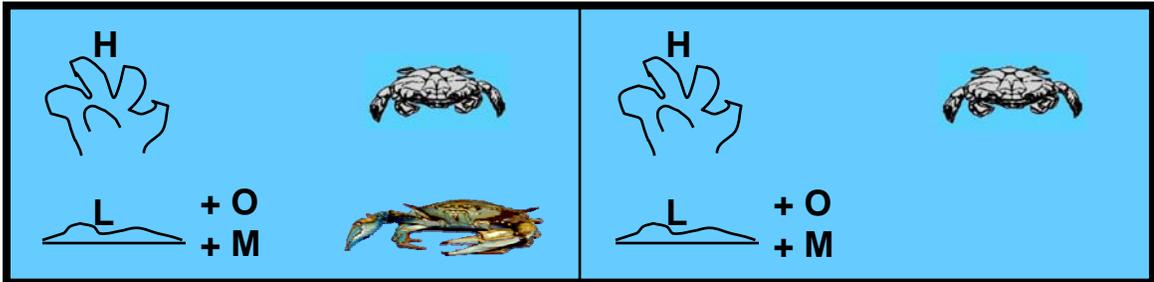
a.) Treatments 1 and 2.



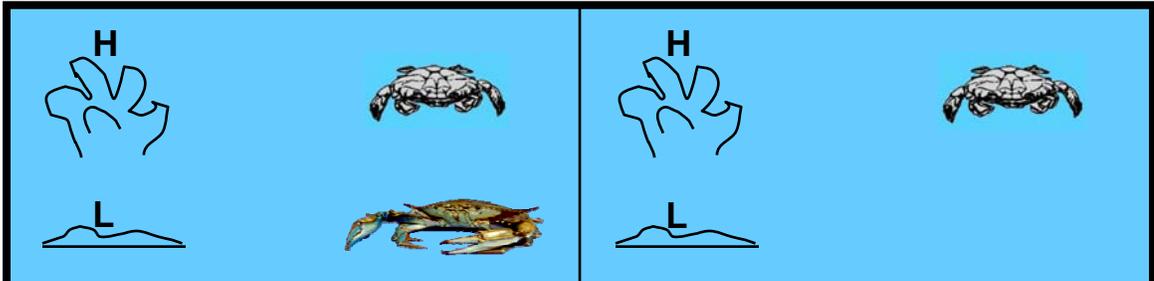
b.) Treatments 3 and 4.



c.) Treatments 5 and 6.



d.) Treatments 7 and 8.



Statistical Analysis

Analysis of variance (ANOVA) was used to examine density and size distribution from excavations, field predation from tethering, oyster recruitment, and lab bivalve predation data (SAS PROC GLM). Data was not log transformed and met assumptions of homogeneity of variance (F-max test). To compare densities of xanthid crabs and *Geukensia demissa* as well as mean sizes (CW) of xanthids collected from field excavations among different treatments, a 2-way ANOVA was run with complexity (microhabitat type) and season as main effects, along with complexity*season interactions. To analyze the mortality data from tethering, an arcsine square root transformation was performed. A 2-way ANOVA, with complexity and date as main effects, was used to compare proportional mortality of tethered mud crabs among different treatments (including complexity, edge/interior, and date). When ANOVA indicated a significant effect, the Student-Newman-Keul (SNK) test was used to detect differences among treatments. Oyster recruitment density and spat shell height was compared among complexity treatments using a 1-way ANOVA. The laboratory bivalve predation data showed significant trial differences for predation on both species of bivalves. To minimize trial variability, raw predation on both *C. virginica* and *G. demissa* was converted (independently) to the proportion of the most consumed for each trial. For each trial run, the treatment(s) with the greatest spat and mussel predation was standardized to 1. *C. virginica* and *G. demissa* predation for all the other treatments were scaled relative to this treatment. An arcsine square root transformation was performed on this new proportion data. A 2-way ANOVA compared predation on each bivalve species with complexity and blue crab presence along with complexity*blue crab interactions.

To test the effect of bivalve location on predation, predation on both bivalves occurring in high complexity was analyzed using a 2-way ANOVA with bivalve location and blue crab presence as main effects for all treatments containing bivalves in high complexity patches. This was also done for bivalves occurring in low complexity. To compare predation on *C. virginica* and *G. demissa* by mud crabs over all treatments and trials during the laboratory study, a 1-way ANOVA was run. Chi-square was used to examine mud crab locations (total number for each habitat) during the laboratory study at the start and end of a trial. The effect of treatment and blue crab presence on mud crab presence in high relief was analyzed using Chi-square.

RESULTS

Excavation Densities

A total of 27 taxa were collected over the course of the excavation studies. Most of the organisms collected were resident species that occur commonly in intertidal oyster reefs throughout southeastern North Carolina (Table 1). Dominant species were mud crabs, *Panopeus herbstii* and *Eurypanopeus depressus*, ribbed mussels, *Geukensia demissa*, oyster drills, *Urosalpinx cinerea*, polychaetes and amphipods. These species compromised greater than 95% of total abundance.

There was a significant complexity effect for mean total xanthid crab densities in the experimental reefs, but no significant season or complexity*season interaction (Table 2). Densities of total xanthids were higher in high complexity reefs than in low complexity reefs ($F=34.42$, $p=0.0001$, Figure 3). This held true for both *Panopeus herbstii* ($F=14.76$, $p=0.0003$) and all other xanthid crabs ($F=39.86$, $p=0.0001$) (Figure 3).

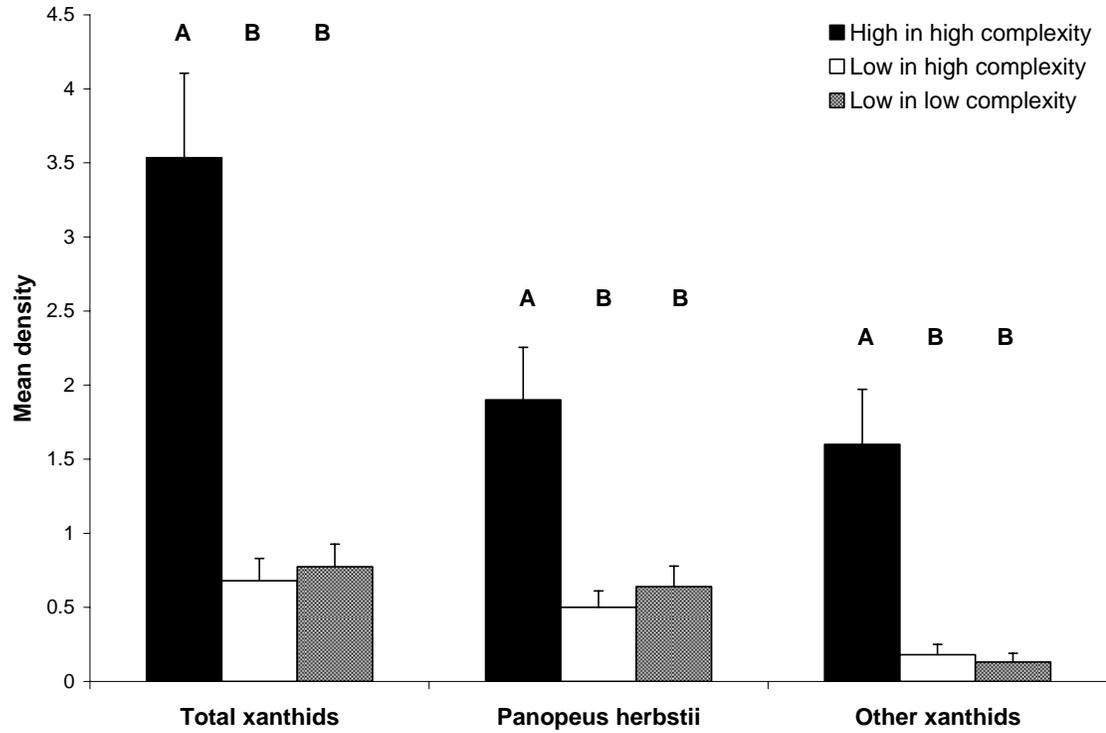
Table 1. Mean density per quadrat (20cm x 20cm) for all species collected during the excavation studies.

Species	Mean density per 0.04m ²
<i>Alpheus heterochaelis</i>	0.0229
<i>Alpheus normanni</i>	0.0153
Amphipod spp.	0.9618
Anemone sp.	0.0534
Bivalve spp.	0.0840
<i>Chione cancellata</i>	0.0229
<i>Clibanarius vittatus</i>	0.0076
<i>Crepidala</i> sp.	0.0916
Decapod spp.	0.0382
<i>Eurypanopeus depressus</i>	0.6183
<i>Fasciolaria tulipa</i>	0.0076
Gastropod sp.	0.0229
<i>Geukensia demissa</i>	5.6870
<i>Hexapanopeus angustifrons</i>	0.0076
<i>Ilyanassa obsoleta</i>	0.0611
<i>Menippe mercenaria</i>	0.0229
<i>Mercenaria mercenaria</i>	0.0157
<i>Mulinia lateralis</i>	0.0076
<i>Opsanus tau</i>	0.0076
<i>Palaemonetes pugio</i>	0.0229
<i>Panopeus herbstii</i>	1.5649
<i>Planes minutus</i>	0.0076
Polychaete spp.	1.5954
<i>Rhithropanopeus harrisii</i>	0.0229
Urochordate sp.	0.0076
<i>Uca pugnax</i>	0.0763
<i>Urosalpinx cinerea</i>	6.5344

Table 2. 2-way ANOVA results for mean density of dominant species collected by excavations. High (H) and low (L) complexity reefs as well as high and low complexity areas on the same reef were analyzed for both the experimental reefs and natural reefs in Hewletts Creek. Shown below are F-values and (p-values) with significant differences designated by an asterisk (*p≤0.05, **p≤0.01, ***p≤0.001).

Species/contrast	Complexity	Season	Complexity*Season
Experimental reefs (H vs L reefs)			
All xanthid crabs	34.42*** (0.0001)***	0.53 (0.664)	0.28 (0.842)
<i>Panopeus herbstii</i>	14.76*** (0.0003)***	0.66 (0.579)	0.83 (0.481)
Other xanthid crabs	39.86*** (0.0001)***	0.33 (0.886)	0.25 (0.921)
<i>Geukensia demissa</i>	40.04*** (0.0001)***	0.73 (0.537)	1.84 (0.148)
Experimental reefs (H vs L on same reef)			
All xanthid crabs	21.67*** (0.0001)***	0.21 (0.890)	0.17 (0.918)
<i>Panopeus herbstii</i>	14.07*** (0.0005)***	0.62 (0.605)	0.59 (0.622)
Other xanthid crabs	12.78*** (0.0008)***	0.15 (0.928)	0.06 (0.979)
<i>Geukensia demissa</i>	16.52*** (0.0002)***	0.97 (0.415)	0.75 (0.530)
Hewletts Creek natural reefs (H vs L reefs)			
All xanthid crabs	2.71 (0.134)	1.66 (0.243)	2.05 (0.186)
<i>Panopeus herbstii</i>	2.45 (0.152)	1.04 (0.392)	0.49 (0.502)
Other xanthid crabs	2.27 (0.166)	2.97 (0.103)	4.43 (0.065)
<i>Geukensia demissa</i>	2.10 (0.181)	3.46 (0.077)	1.52 (0.249)
Hewletts Creek natural reefs (H vs L on same reef)			
All xanthid crabs	9.96** (0.007)**	2.60 (0.110)	1.63 (0.232)
<i>Panopeus herbstii</i>	11.0** (0.005)**	1.42 (0.275)	0.77 (0.484)
Other xanthid crabs	6.18* (0.026)*	4.03* (0.041)*	4.03* (0.041)*
<i>Geukensia demissa</i>	5.24* (0.038)*	3.19 (0.072)	3.34 (0.065)

Figure 3. Mean density (number/0.04m²) of total xanthids, *Panopeus herbstii*, and other xanthids (not including *P. herbstii*) in high (containing high and low complexity microhabitats) and low complexity experimental reefs. Bars with the same letter designation do not differ significantly. Error bars indicate +1 SE.



There was also a significant microhabitat difference within the high complexity experimental reefs, with higher densities of xanthid crabs in the high complexity compared to low complexity microhabitats and little difference among low complexity areas whether isolated or in mixed areas. The oyster reefs at Hewletts Creek showed no significant effect on xanthid crab density comparing separate high and low complexity reefs (Table 2). When comparing high and low complexity areas on the same natural reef, a significant complexity effect occurred, with greater densities of total xanthid crabs ($F=9.96$, $p=0.007$), *Panopeus herbstii*, ($F=11.0$, $p=0.005$), and other xanthid crabs ($F=6.18$, $p=0.026$) in high complexity over low complexity areas (Figure 4).

Geukensia demissa densities showed a significant complexity effect but no season or complexity*season interactive effects for the experimental reefs (Table 2). Densities were higher in high complexity reefs compared to low complexity reefs ($F=40.04$, $p=0.0001$, Figure 5). For high and low complexity microhabitats on the same natural reef, mussel density was significantly greater in the high complexity areas (Table 2). Pairwise comparisons examining *G. demissa* densities in high and low complexity microhabitats on the same reef at Hewletts Creek yielded a significant microhabitat complexity effect in high complexity reefs but no season or complexity*season interactive effects. Densities of *G. demissa* were greater in high complexity areas ($F=5.24$, $p=0.038$, Figure 6).

Mean Sizes (carapace width) of Xanthid Crabs from Excavations

No analyses of crab size were conducted for natural reefs in Hewletts Creek due to low catch numbers. Xanthid crabs in the experimental reefs were collected with

Figure 4. Mean density (number/0.04m²) of total xanthids, *Panopeus herbstii*, and other xanthids in high (containing high and low complexity microhabitats) and low complexity areas on the same reef at Hewletts Creek. Bars with the same letter designation do not differ significantly. Error bars indicate +1 SE.

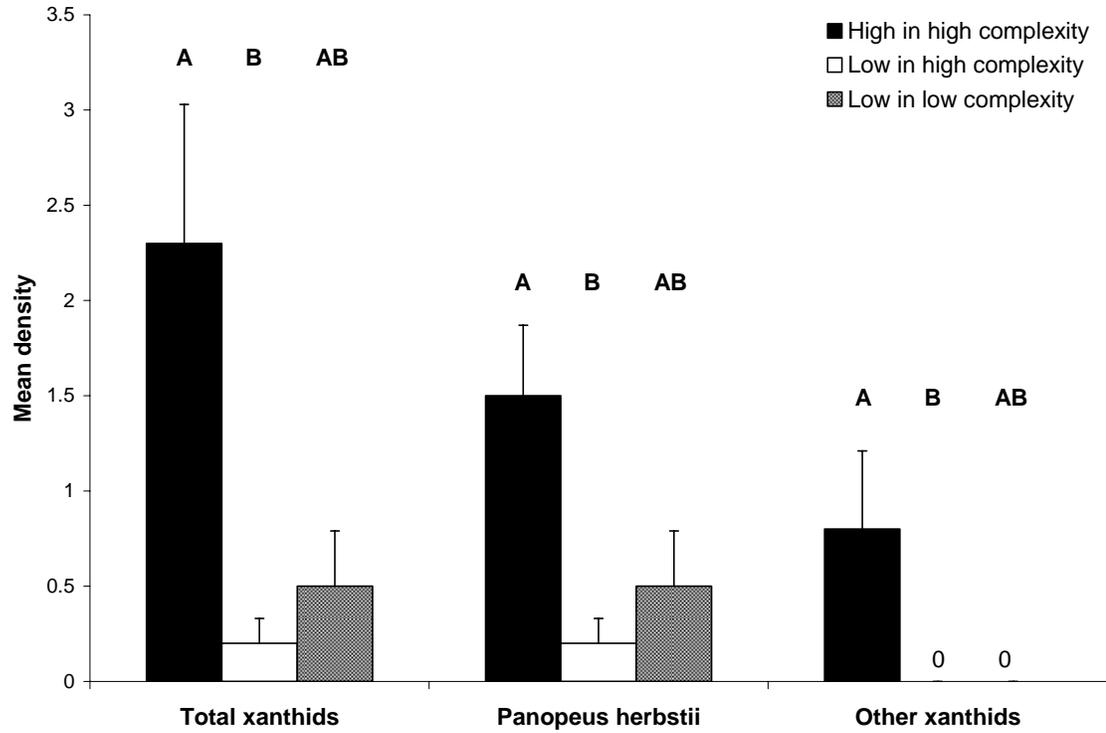


Figure 5. Mean density (number/0.04m²) of *Geukensia demissa* in high (containing high and low complexity microhabitats) and low complexity experimental reefs. Bars with the same letter designation do not differ significantly. Error bars indicate +1 SE.

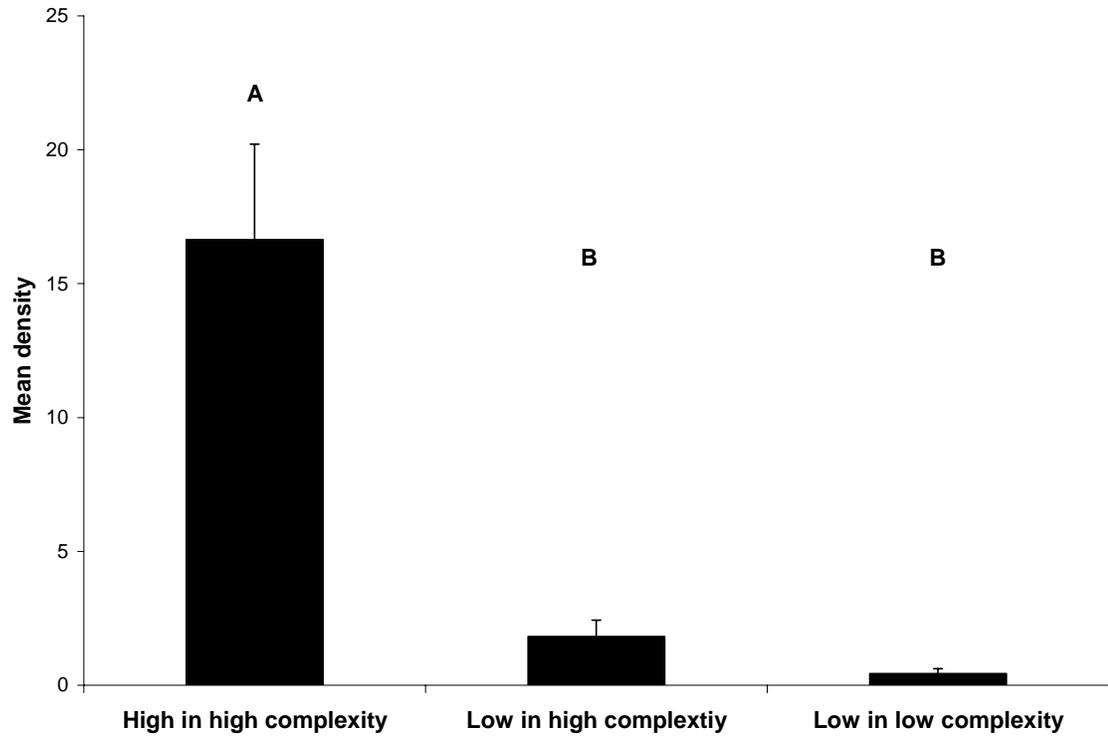
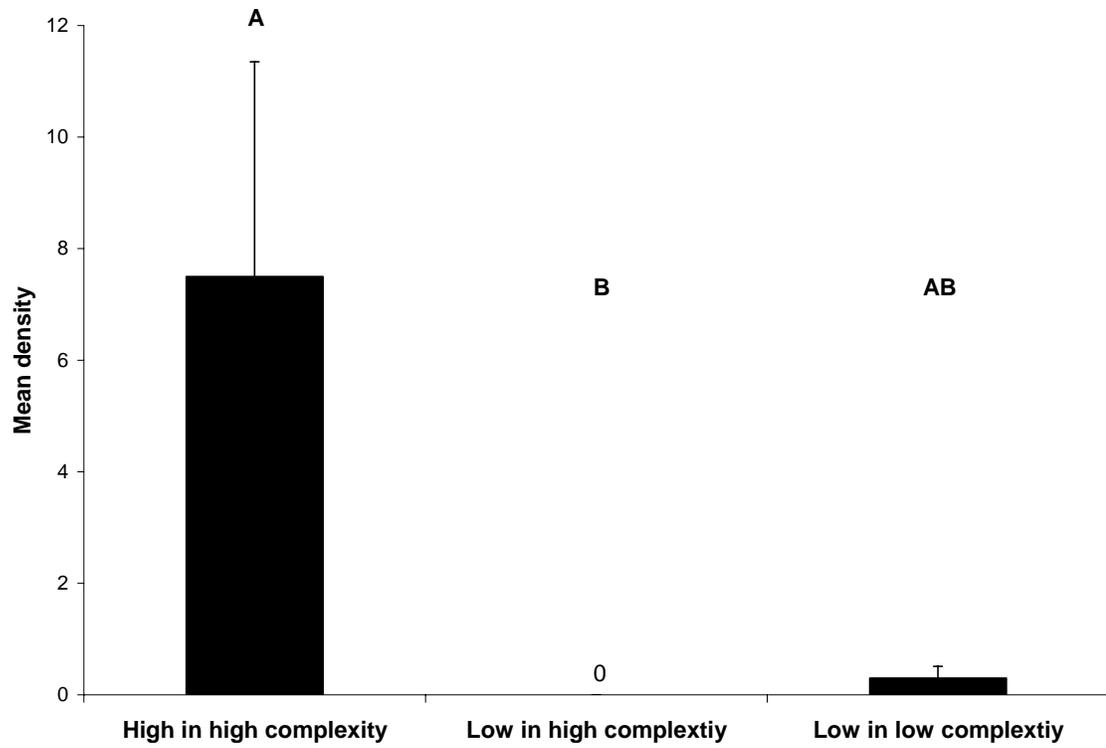


Figure 6. Mean density (number/0.04m²) of *Geukensia demissa* in high (containing high and low complexity microhabitats) and low complexity natural reefs at Hewletts Creek. Bars with the same letter designation do not differ significantly. Error bars indicate +1 SE.



enough frequency to allow for mean size analysis to be conducted. Mean carapace width for all xanthids and for *Panopeus herbstii* showed a significant complexity effect, but no season or complexity*season interactive effects for the comparison of high and low complexity reefs (Table 3). Mean carapace width for total xanthid crabs ($F=4.58$, $p=0.038$) inclusive of *P. herbstii* ($F=5.78$, $p=0.024$) were significantly larger in the high complexity experimental reefs (Figure 7). Other xanthid crabs, excluding *P. herbstii*, showed similar patterns of mean size as *P. herbstii* but this trend was not significant (Table 3). Microhabitats in the high complexity reefs yielded no significant effects for xanthid crab carapace width (Table 3).

Mean Mortality of *Panopeus herbstii* from Tethering

There was a significant treatment and date effect for mean percent mortality of *Panopeus herbstii* (Table 4). High complexity reefs, although not significantly different from low complexity reefs, had lower percent mortality of *P. herbstii* compared to open sand controls ($F=11.41$, $p=0.022$, Figure 8). The date effect was primarily driven by a single sampling event that had much higher mortality, although it did have the same general pattern as the other sampling events ($F=13.09$, $p=0.018$). There were greater numbers of adult blue crabs observed on that day in small tide pools on the mud flat, possibly explaining the overall increased predation on *P. herbstii*.

Comparisons of mortality along the edges of the high and low complexity reefs for *P. herbstii* indicated significant treatment effects (Table 4). The edge of the high complexity reef had significantly greater predation than the interior region ($F=4.77$, $p=0.05$, Figure 9). Although, the interior of the high complexity reef had the lowest

Table 3. 2-way ANOVA results for mean size (carapace width) of mud crabs collected by excavations. High (H) and low (L) complexity reefs as well as high and low complexity areas on the same reef were analyzed for the experimental reefs. Shown are F-values and (p-values) with significant differences designated by an asterisk (* $p \leq 0.05$, ** $p \leq 0.01$, *** $p \leq 0.001$).

Species/contrast	Complexity	Season	Complexity*Season
Experimental reefs (H vs L reefs)			
All xanthid crabs	4.58* (0.038)*	1.77 (0.167)	0.15 (0.932)
<i>Panopeus herbstii</i>	5.78* (0.024)*	1.15 (0.341)	0.06 (0.980)
Other xanthid crabs	2.58 (0.128)	1.02 (0.410)	0.08 (0.786)
Experimental reefs (H vs L on same reef)			
All xanthid crabs	3.20 (0.084)	0.87 (0.468)	0.37 (0.775)
<i>Panopeus herbstii</i>	2.90 (0.100)	0.53 (0.664)	0.13 (0.944)
Other xanthid crabs	3.09 (0.099)	0.72 (0.558)	1.17 (0.296)

Figure 7. Mean carapace width for total xanthids, *Panopeus herbstii*, and other xanthids in high (containing high and low complexity microhabitats) and low complexity experimental reefs. Bars with the same letter designation do not differ significantly. Error bars indicate +1 SE.

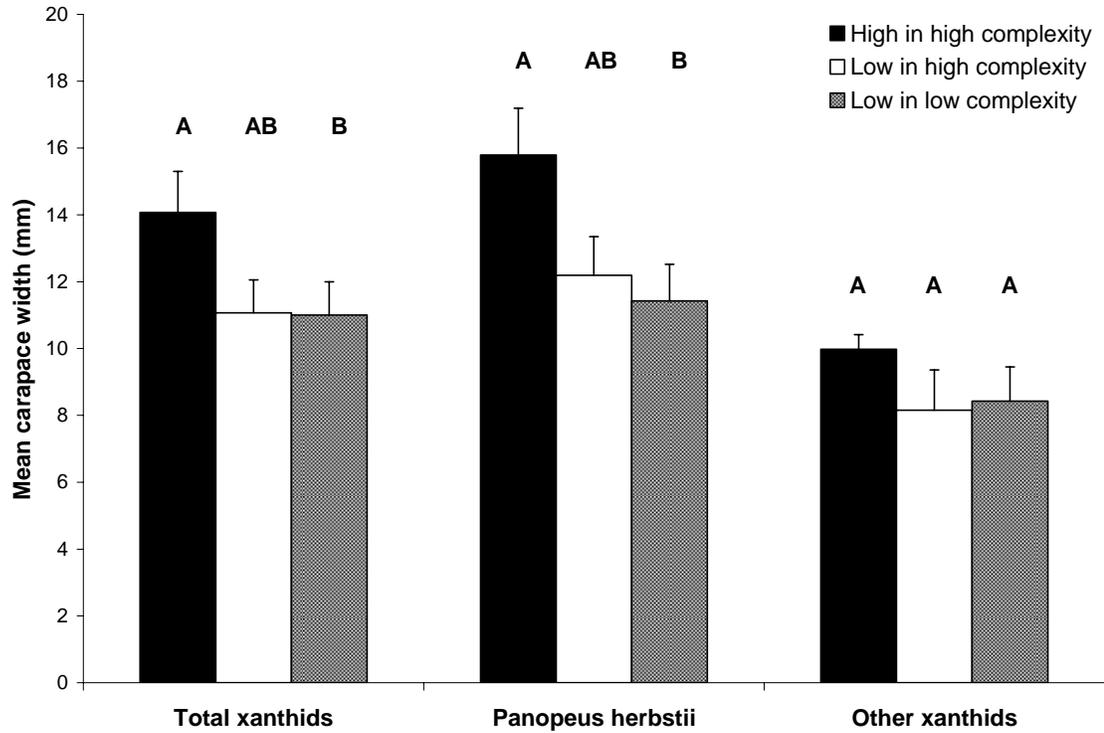


Table 4. 2-way ANOVA results for mean percent mortality on *Panopeus herbstii* from tethering on the experimental reefs. Shown below are F-values and (p-values) with significant differences indicated by an asterisk (*p≤0.05, **p≤0.01, ***p≤0.001). Where significant treatment effects occurred, SNK rankings are shown in decreasing order with differing treatment effects denoted by different superscripts. S=sand, L=low complexity, H=high complexity, HI=high complexity interior, HE=high complexity edge, LI=low complexity interior, and LE=low complexity edge.

Comparison	Treatment	Date
High vs Low vs Sand	11.41* (0.022)* H ^a , L ^{ab} , S ^b	13.09* (0.018)*
Interior vs Edge	4.77* (0.050)* HE ^a , LE ^{ab} , LI ^{ab} , HI ^b	1.15 (0.377)

Figure 8. Mean percent mortality from tethering *Panopeus herbstii* in high and low complexity reefs as well as open sand. Bars with the same letter designation do not differ significantly. Error bars represent +1 SE.

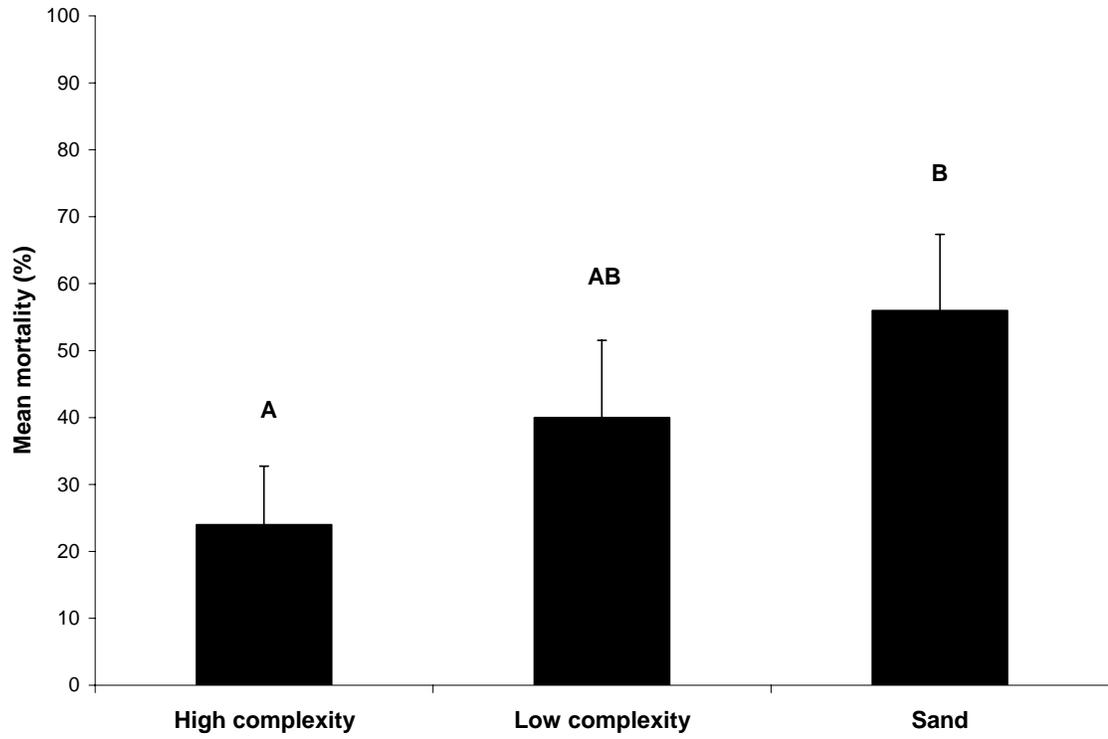
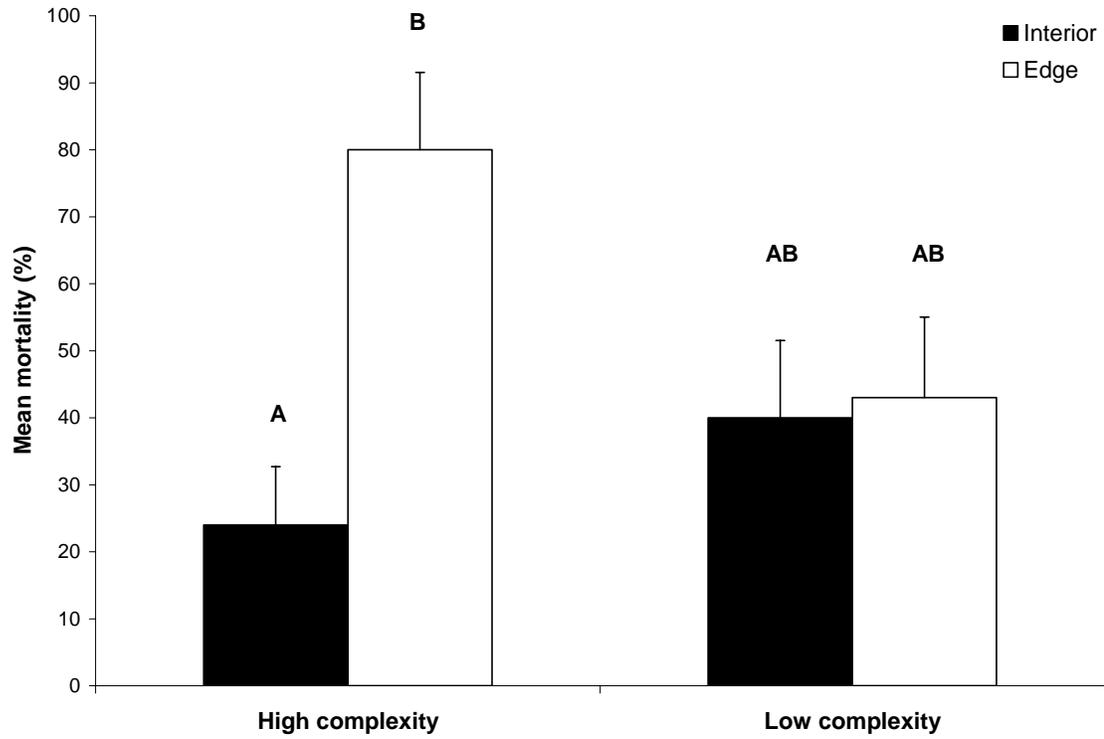


Figure 9. Edge and interior comparisons of mean percent mortality of tethered *Panopeus herbstii* in high and low complexity experimental reefs. Bars with the same letter designation do not differ significantly. Errors bars represent +1 SE.



mean predation on *P. herbstii* of all treatments, the edge of the high complexity reef had the greatest mean predation. There was no difference in mean predation for the edge and interior areas of the low complexity reef.

Oyster Spat Recruitment Densities

Significant complexity effects were found for live oyster spat density among high and low complexity experimental reefs (Table 5). High complexity reefs had greater densities of oyster spat compared to low complexity reefs ($F=52.74$, $p=0.0001$, Figure 10). High complexity areas had greater oyster spat density than low complexity areas on the same reef ($F=36.15$, $p=0.001$, Table 5). Natural reefs with high surface rugosity in Masonboro Sound, located in the vicinity of the experimental reefs, showed significant complexity effects for live spat density (Table 5), where high complexity regions had greater densities compared to low complexity regions ($F=24.22$, $p=0.003$, Figure 11).

Oyster Spat Recruitment Mean Sizes

No significant differences in mean size (shell height) were observed among treatments for live oyster spat in the experimental reefs (Table 6). A significant complexity effect did occur in the natural reefs, with significantly larger spat occurring in trays in high complexity areas versus low complexity areas on the same reef ($F=12.05$, $p=0.026$).

Bivalve Predation from Lab Experiment

There were significant differences in consumption of both *Crassostrea virginica*

Table 5. 1-way ANOVA results for oyster spat abundance in high and low complexity experimental reefs as well as high (H) and low (L) complexity regions on the same reef, for both experimental and natural reefs in Masonboro Sound. Shown below are F-values and (p-values) with significant differences indicated by an asterisk (* $p \leq 0.05$, ** $p \leq 0.01$, *** $p \leq 0.001$).

Comparison	Complexity
Experimental reefs	
H vs L reefs	52.74*** (0.0001)***
H vs L on same reef	36.15*** (0.001)***
Masonboro Sound natural reefs	
H vs L on same reef	24.22** (0.003)**

Figure 10. Mean density (number/0.04m²) of live and dead oyster spat as well as scars (evidence of oyster spat mortality) per area on high and low complexity experimental reefs. Bars with the same letter designation do not differ significantly. Spat shell (dead) and spat shell scars (scar) were not analyzed statistically. Error bars represent +1 SE.

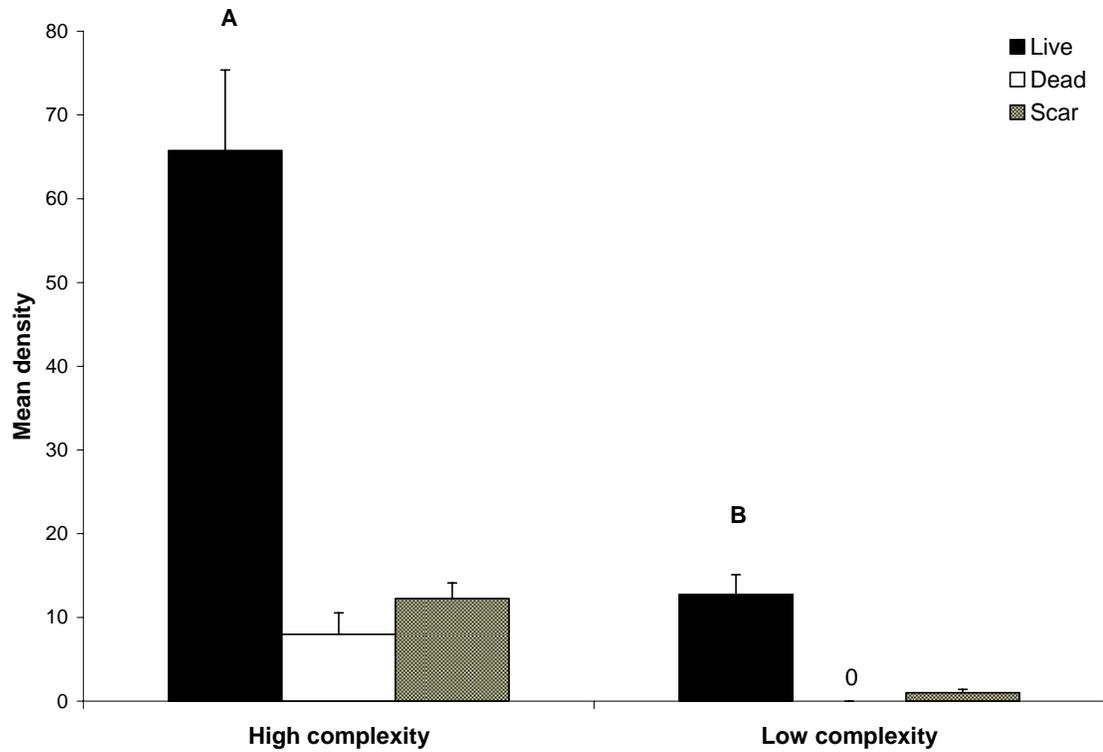


Figure 11. Mean density (number/0.04m²) of live and dead oyster spat as well as scars per area on high and low complexity microhabitats in natural reefs in Masonboro Sound. Bars with the same letter designation do not differ significantly. Spat shell (dead) and spat shell scars (scar) were not analyzed statistically. Error bars represent +1 SE.

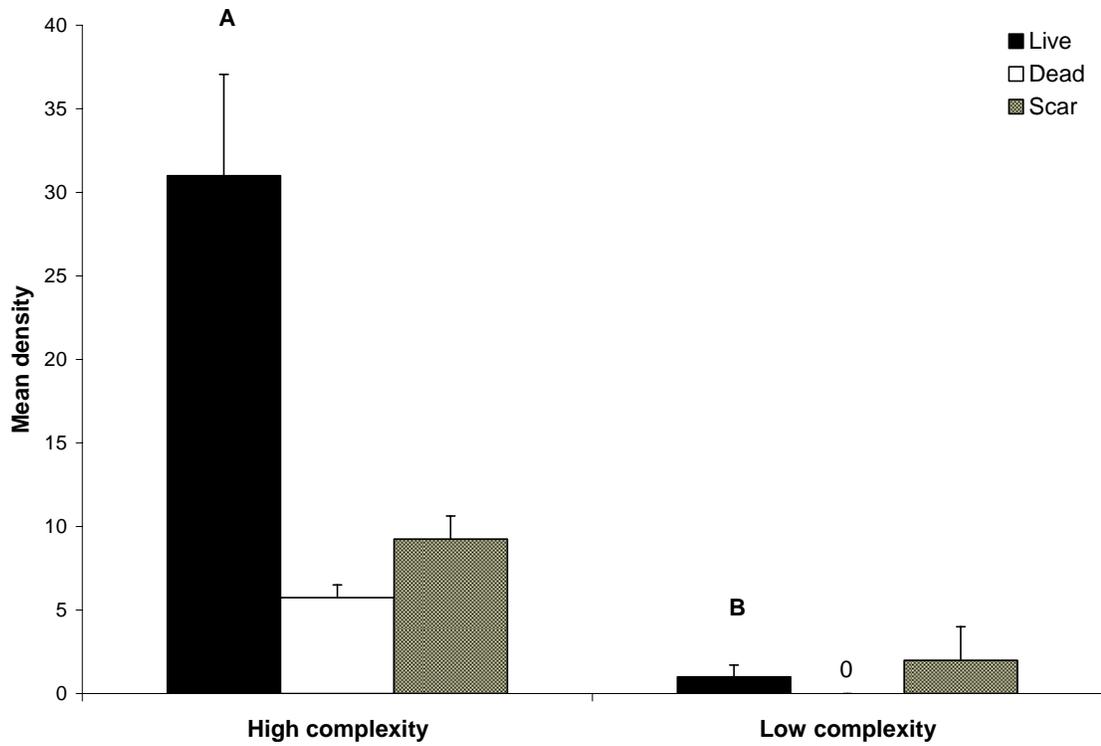


Table 6. 1-way ANOVA results for oyster spat mean size (shell height) in high and low complexity experimental reefs as well as high (H) and low (L) complexity regions on the same reef, for both experimental and natural reefs in Masonboro Sound. Shown below are F-values and (p-values) with significant differences indicated by an asterisk (* $p \leq 0.05$, ** $p \leq 0.01$, *** $p \leq 0.001$).

Comparison	Complexity
Experimental reefs	
H vs L reefs	0.02 (0.891)
H vs L on same reef	0.41 (0.544)
Masonboro Sound natural reefs	
H vs L on same reef	12.05* (0.026)*

and *Geukensia demissa* ($F=5.04$, $p=0.004$; $F=7.56$, $p=0.003$, respectively). As described earlier, the standardization among treatments within a trial relative to highest number consumed was necessary in order to minimize trial effects.

There were significant complexity and blue crab presence effects on *C. virginica* consumption when bivalves were located in both the high and low complexity patches, but there was no complexity*blue crab interactive effect (Table 7), indicating relative patterns did not change with a higher predator, but absolute consumption did. High complexity oyster patches had greater oyster spat predation compared to low complexity patches ($F=17.26$, $p=0.001$) and blue crab presence reduced the predation on spat by *P. herbstii* ($F=4.87$, $p=0.044$) (Figure 12a).

There was a significant complexity effect on *G. demissa* consumption when bivalves were located in both the high and low complexity patches (Table 7). No significant blue crab or complexity*blue crab interactive effects were observed. High complexity oyster patches had greater mussel predation by mud crabs compared to low complexity oyster patches ($F=11.06$, $p=0.005$, Figure 12b).

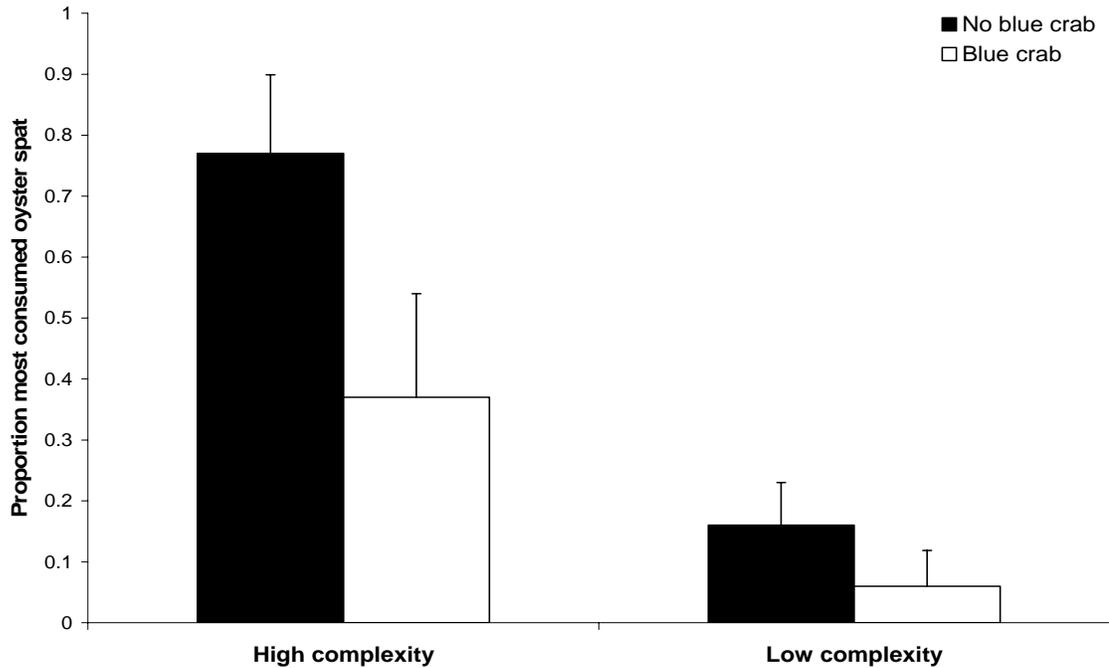
Bivalve location (comparing treatments with bivalves located in both high and low complexity patches to treatments with bivalves located exclusively in high complexity patches) had no effect on *C. virginica* predation in the high complexity patches (Table 8). Blue crab presence did have a significant effect on oyster spat predation in the high complexity patches, where spat predation by mud crabs was significantly reduced when blue crabs were present ($F=13.32$, $p=0.002$, Figure 13a). There were no significant effects of bivalve location (presence in both high and low complexity patches or only in low complexity patches), blue crab presence, or

Table 7. 2-way ANOVA results for bivalve predation by *Panopeus herbstii* when bivalves were located in both the high and low complexity oyster patches during the lab study. Shown below are F-values and (p-values) with significant differences designated by an asterisk (* $p \leq 0.05$, ** $p \leq 0.01$, *** $p \leq 0.001$).

Species	Complexity	BCpresence	Complexity*BCpresence
<i>Crassostrea virginica</i>	17.26*** (0.001)***	4.87* (0.044)*	1.69 (0.214)
<i>Geukensia demissa</i>	11.06** (0.005)**	0.71 (0.415)	0.30 (0.595)

Figure 12. Mean proportion of the most consumed oyster spat (a) and mussels (b) for high and low complexity oyster patches when bivalves were located in both complexity patches (treatments 1 and 2) during the laboratory study. High complexity was significantly greater than low complexity for both bivalves. Error bars represent +1 SE.

a.) Oyster spat



b.) Mussels

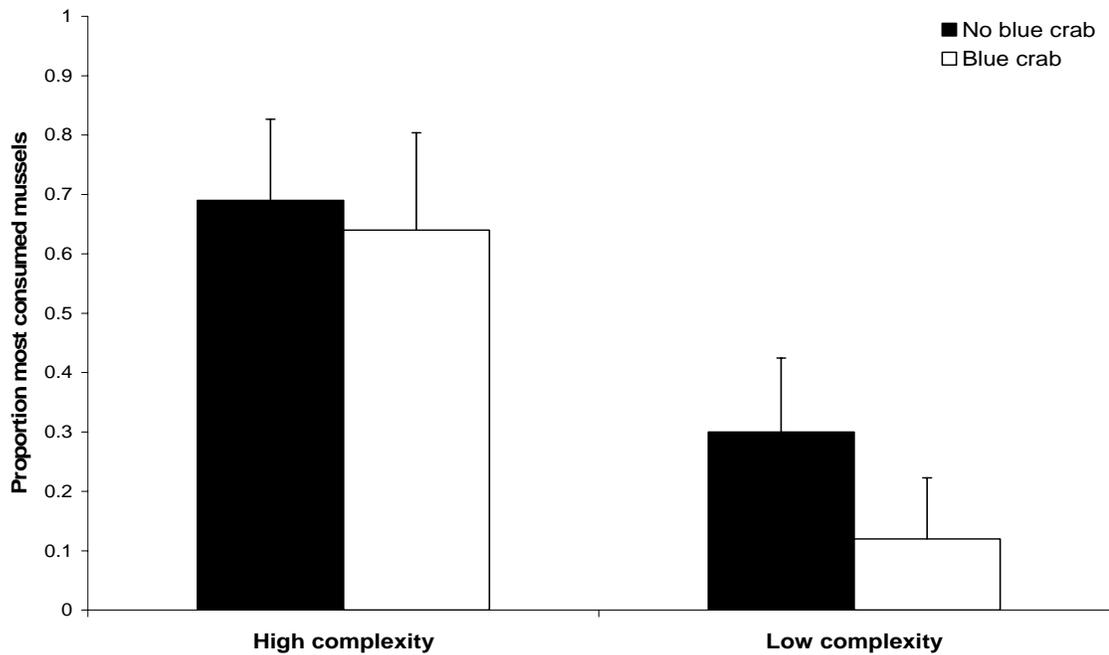
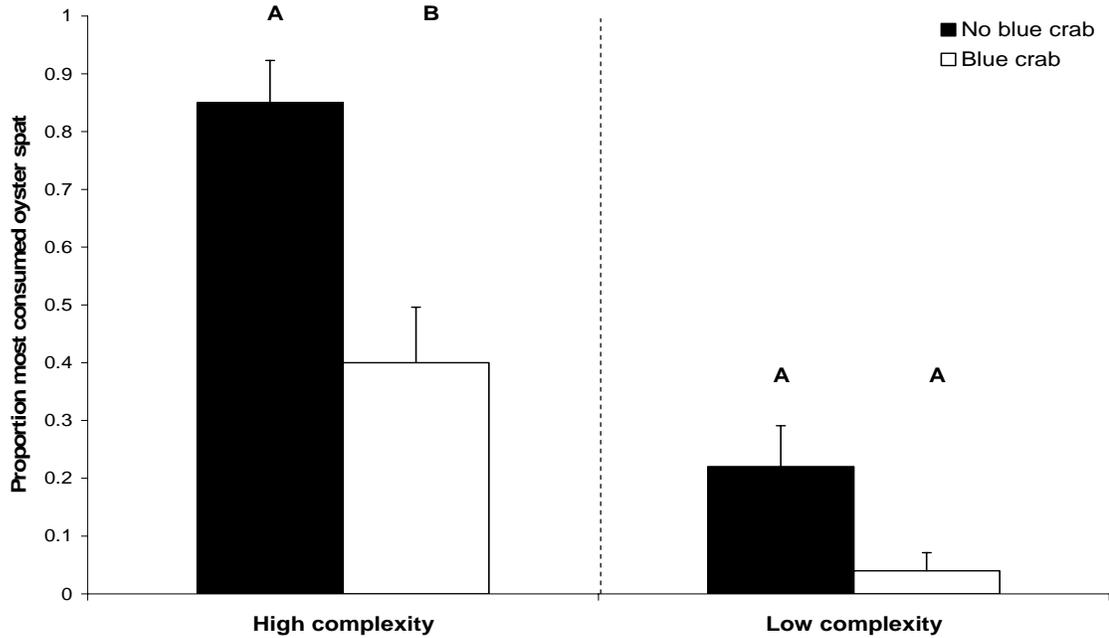


Table 8. 2-way ANOVA results for bivalve predation by *Panopeus herbstii* for bivalves only in the high complexity (H) patches as well as only in the low complexity (L) patches during the lab study. Shown below are F-values and (p-values) with significant differences represented by an asterisk (*p≤0.05, **p≤0.01, ***p≤0.001).

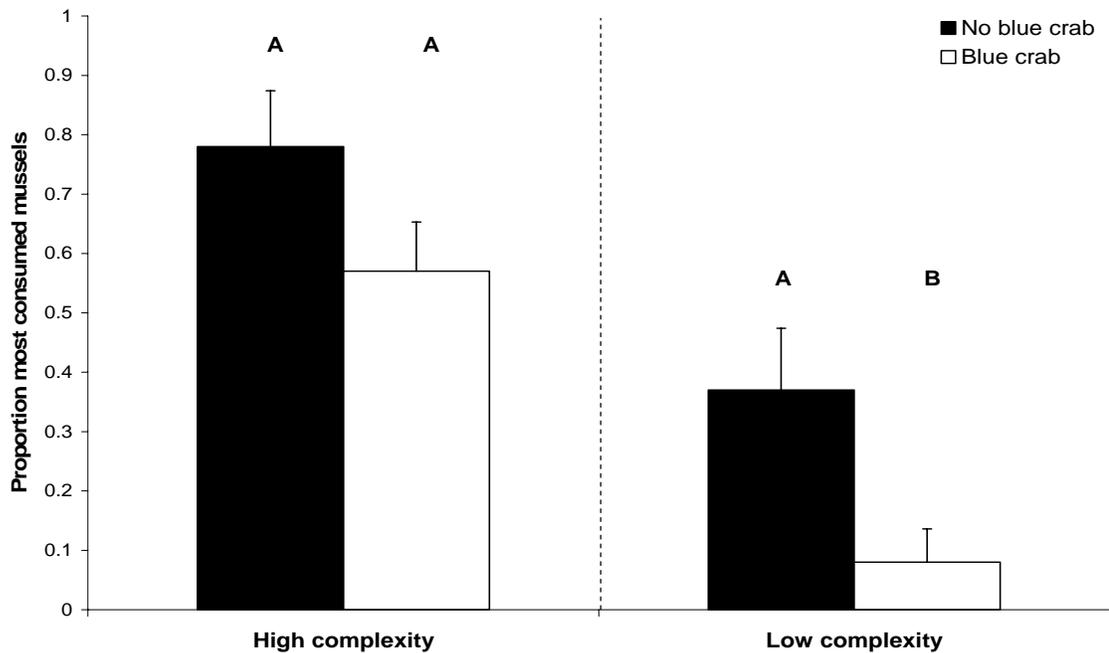
Species	Bivlocation	BCpresence	Bivlocation*BCpresence
Bivalves in H			
<i>Crassostrea virginica</i>	0.53 (0.479)	13.32* (0.002)*	0.13 (0.726)
<i>Geukensia demissa</i>	0.05 (0.833)	2.91 (0.108)	1.72 (0.209)
Bivalves in L			
<i>Crassostrea virginica</i>	0.35 (0.562)	3.74 (0.074)	0.66 (0.429)
<i>Geukensia demissa</i>	0.10 (0.752)	4.84* (0.045)*	0.62 (0.446)

Figure 13. Mean proportion of the most consumed oyster spat (a) and mussels (b) for bivalves only in the high complexity patches (treatments 1, 2, 3, and 4) along with bivalves only in the low complexity patches (treatments 1, 2, 5, and 6) during the lab study. Bars with the same letter designation do not differ significantly. Error bars represent +1 SE.

a.) Oyster spat



b.) Mussels



location*blue crab interaction *C. virginica* consumption by mud crabs in the low complexity patches.

Location of bivalves (presence in both high and low complexity patches or only in high complexity patches), presence of a blue crab, and the interaction between the two had no significant effect on predation of *G. demissa* in the high complexity patches. There was a significant blue crab effect for *G. demissa* consumption in the low complexity patches but there was no effect of location of bivalves (presence in either high and low complexity or only low complexity) or interaction between location and blue crab presence (Table 8). Mussel consumption was significantly reduced in the low complexity patches when blue crabs were present ($F=4.84$, $p=0.045$, Figure 13b).

There was a significant difference in mean consumption of *C. virginica* and *G. demissa* by *P. herbstii* over all treatments and trials. *G. demissa* was consumed to a greater extent compared to *C. virginica* ($F=12.97$, $p=0.0006$, Figure 14). This pattern was evident in all treatments and trials.

Mud Crab Habitat Preference from Lab Experiments

There was a significant habitat effect on mud crab presence at the start and end of each trial. Significantly greater abundances of mud crabs occurred at the start of the trials in the high complexity patch compared to the low complexity patch or sand ($X^2=9.75$, $p<0.05$, Figure 15a). This pattern persisted throughout the trials with greater abundances of mud crabs present in the high complexity patch at the end of the trial ($X^2=40.75$, $p<0.05$, Figure 15b). The number of mud crabs present in the high and low complexity patches increased while the number of crabs in the sand decreased from the start of a trial

Figure 14. Mortality for *C. virginica* and *G. demissa* due to mud crab predation averaged over all treatments and trials during the lab study. Bivalve mortality differed significantly ($F=12.97$, $p=0.0006$). Error bars represent +1 SE.

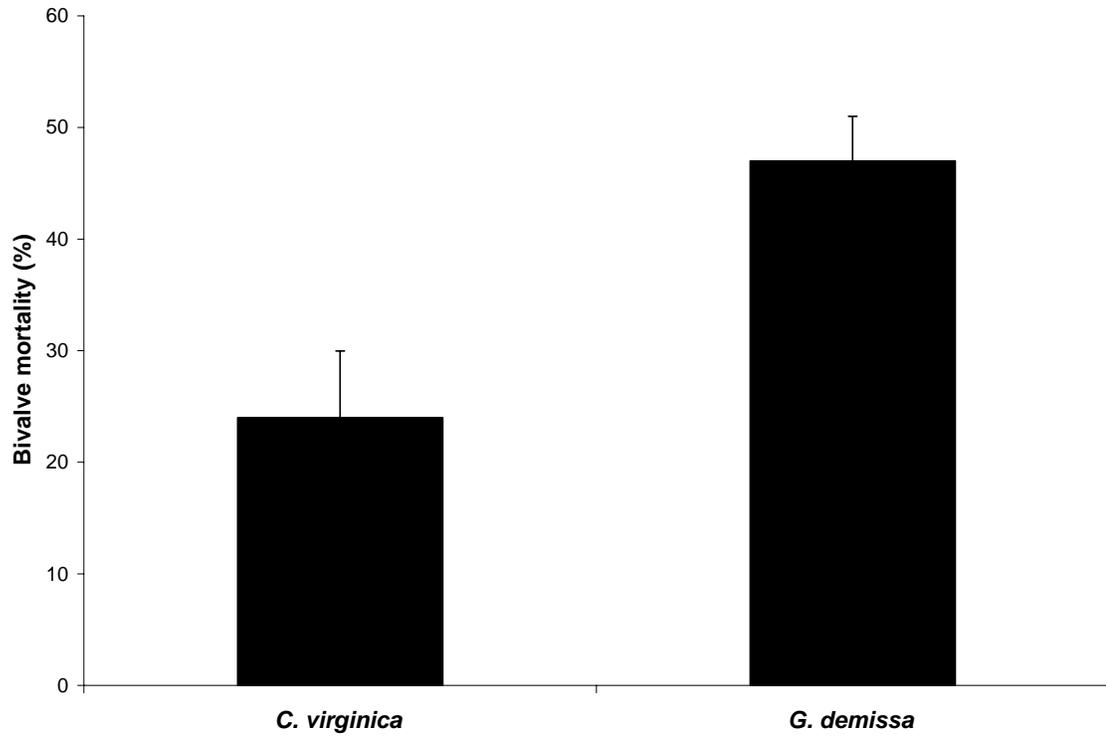
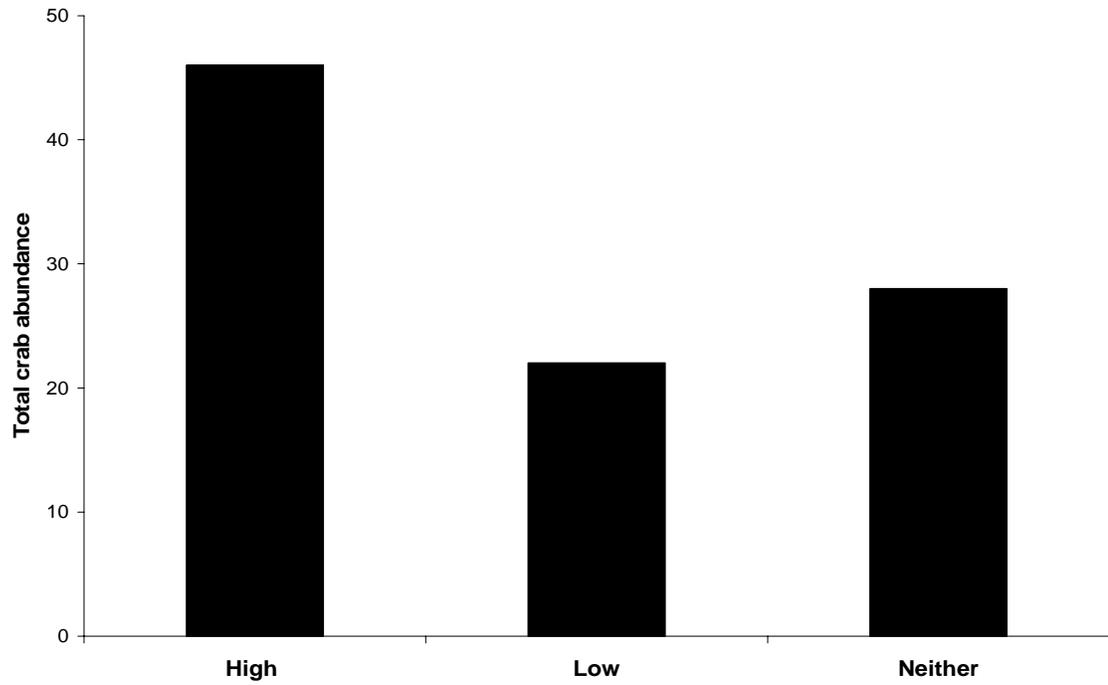
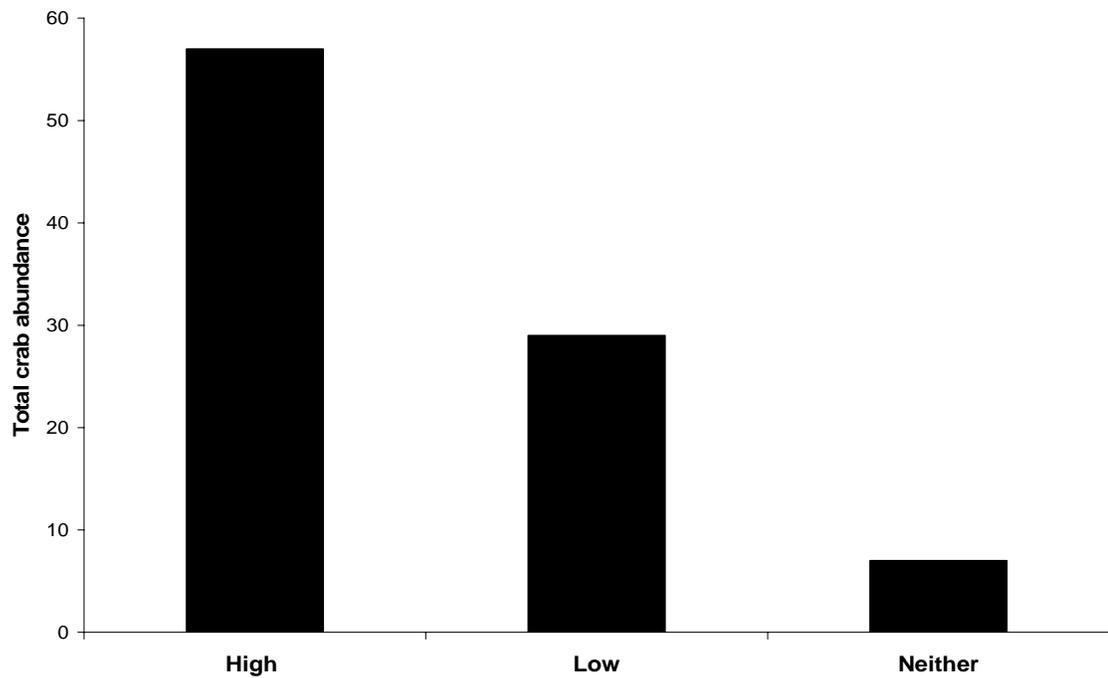


Figure 15. Total *Panopeus herbstii* abundance in each habitat at the start (a) and at the end (b) of the laboratory experiment for all treatments and trials. Abundance of crabs differed significantly among habitats at the start and end of trials.

a.) Start of trial



b.) End of trial



to the end of a trial. There were no treatment or blue crab effects on mud crab presence at the start or at the end of a trial in high complexity patches (Table 9).

DISCUSSION

Trophic interactions play a key role in structuring communities and are important in understanding community dynamics. Although the importance of trophic interactions has been recognized, there is relatively little work on how habitat type affects or moderates these interactions. Habitat complexity may play a significant role in regulating trophic linkages, and has broad implications for community composition in marine environments (Menge and Lubchenco 1981, Summerson and Peterson 1984, and Grabowski 2004).

Oyster reef habitat complexity had an effect on mud crab densities, with greater densities found in high complexity reefs (Figures 3 and 4). This was true for experimental and natural reefs examined in Masonboro Sound and natural reefs in Hewletts Creek. *P. herbstii* found in high complexity reefs were larger than individuals collected from low complexity reefs, both in natural reefs and in experimental reefs (Figure 7). Larger individuals may be more effective at occupying preferred habitat, strengthening the argument that high complexity oyster habitats may be preferred by mud crabs over low complexity areas. High complexity areas may be the only refuge suitable for larger individuals, possibly indicating low complexity areas may not be a suitable refuge. Complexity had similar effects on ribbed mussels, *G. demissa*, as they were found in much greater abundances in high complexity natural and experimental reefs (Figures 5 and 6). This may be due to greater surface area available for recruitment that

Table 9. Chi-square results for mud crab presence in the high complexity patches and test of independence for habitat type and blue crab presence. Shown below are X^2 -values and ($p_{0.05}$ -values) with significant differences designated by an asterisk.

Time	Treatment	BCpresence	Independence test
Start	1.83	0.78	0.51
	(7.82)	(3.84)	(14.07)
End	0.47	0.44	0.57
	(7.82)	(3.84)	(14.07)

was associated with high complexity habitats, as mussels tend to be located more in the crevices formed by shell aggregates that are not really found in low complexity. Laboratory experiments on mud crabs showed similar patterns to those observed in the field. Mud crabs first placed in the experimental tanks during these experiments were more likely to seek refuge in the high complexity patches compared to the low complexity patches or sand (Figure 15). This trend became more pronounced over the course of a trial, with almost total absence in sand by the end of observations. Mud crabs associated more with high complexity patches regardless of prey (oyster spat and ribbed mussels) or predator presence. This suggests that mud crabs have an inherent attraction to high oyster complexity or structure and will choose high complexity patches over forage location, for at least the 24hr periods observed here, whether or not a predator is present. This is in contrast to more facultative use of refuge patches (Werner et al. 1983, Glasser 1984, Posey et al. 1999). High complexity oyster habitats provide protection from desiccation for mud crabs at low tide (Grant and McDonald 1979) and offer a structurally complex matrix of shell that would normally be a location for prey (Seed 1980, Whetstone and Eversole 1981, McDonald 1982, Lin 1990, Powell 1994), an example of which was the greater densities of *G. demissa* observed in the high complexity oyster reefs. The complex shell matrix also provides mud crabs with refuge from predators. Thus, mud crabs may have an obligate rather than facultative habitat use pattern because of the general lack of favorable alternate habitats.

Relative predation on *P. herbstii* was affected by oyster reef complexity. There was decreasing mud crab mortality with increasing oyster complexity (Figure 8). Tethered mud crabs had the lowest mortality in high complexity oyster reefs compared to

open sand controls which had the greatest relative predation. However, high complexity oyster reefs showed an edge effect, where greater relative predation on *P. herbstii* occurred compared to the interior regions (Figure 9). This utilization of the perimeter of high complexity reefs by predators adds to the concept of halo effects that occur around oyster reefs observed in other studies (Powell 1994, Harwell 2004). Not surprisingly, there was no difference in relative predation on mud crabs around the edge compared to the interior for the low complexity oyster reef. This implies that the edge of a low complexity reef has the same accessibility as the interior regions presumably due to the lack of vertical structure preventing access. The highest relative predation on mud crabs occurred on the edges of the high complexity reef compared to all other treatments. This suggests that predators may be attracted to high complexity reefs and forage heavily around the perimeter but may be inhibited from access to the interior regions. Previous studies have indicated that predators such as *Callinectes sapidus* may actually bypass potential prey in the open mud flat to forage around/on oyster reefs (Powell 1994). High complexity reefs may offer increased abundances of potential prey like *P. herbstii* compared to low complexity reefs and the surrounding mud flat (Posey et al. 1999). The utilization of habitat edges by predatory transient fish and decapods has been shown in other marine systems, where only the first 3m of *Spartina* marsh surfaces is penetrated (Peterson and Turner 1994).

In 2002, when the experimental reefs in Masonboro Sound were first created, the low complexity reefs had greater recruitment of oyster spat compared to the high complexity reefs (Posey and Alphin manuscript in prep). This would seem counterintuitive as high complexity reefs offer greater attachment area compared to low

complexity reefs. Predation on newly settled spat by *P. herbstii* may explain this, as they were first found in the reefs during June 2002 (within a month of reef establishment) and were present throughout the recruitment season in densities similar to current densities for both high and low complexity reefs. Other species such as *G. demissa*, known prey for *P. herbstii* (Seed 1980, McDonald 1982, Lin 1990), were present in the reefs but not in large densities, offering mud crabs limited prey selection. Without alternate prey, mud crabs may have severely reduced oyster spat recruitment success during the first year of reef establishment. A different trend was observed in 2004, where the same high complexity reefs had greater recruitment compared to the low complexity reefs (Figure 10). There was also greater frequency of dead oyster spat and spat scars in the high complexity reefs (Figures 10 and 11). The decrease in the density of oyster recruits in the low complexity reefs in 2004 compared to 2002 may be due to the amount of siltation in the area over the course of two years causing some portions of the low complexity reefs to become buried. However, greater recruitment success in high complexity reefs may reflect indirect trophic effects of higher densities of an alternate prey, mussels. There were also fewer oyster recruits in 2004 compared to 2002. This could be due to normal inter-annual variability in recruitment in the system and it emphasizes the potential importance of first year recruitment to newly created oyster reefs. Natural reefs examined in Masonboro Sound showed similar patterns to the created reefs in 2004, with greater densities of oyster spat in the high complexity areas. Greater densities of dead spat and spat scars were present in the high complexity areas of the surrounding natural reefs as well.

Oyster complexity influenced mud crab predation on oyster spat and ribbed mussels during the lab experiment (Figures 12 and 13). Both oyster spat and ribbed mussels suffered greater mortality in high complexity patches compared to low complexity patches when bivalves were present in both patches (Figure 12). This was probably due to greater numbers of mud crabs present in the high complexity patches. With greater predation on oyster spat in the high complexity patches during the laboratory experiment, one might expect to see oyster recruitment to be less on high complexity reefs in field conditions, contrary to what was seen on the field reefs in 2004 but consistent with 2002 patterns. In addition to complexity effects, the laboratory experiment showed that top predator presence affected mud crab predation on oyster spat in the high complexity reefs whereas predation on ribbed mussels in the high complexity patch was not influenced by the presence of a top predator (Figure 13). This may help explain why there was higher recruitment in low complexity reefs in 2002 (when *G. demissa* was not present but transient top predators like blue crabs were) compared to higher recruitment in high complexity reefs in 2004 (when mussels and transient top predators were present). Oyster vertical complexity directly affected mud crab distribution and behavior (Figure 15), indirectly benefiting oyster spat and ribbed mussel survival in low complexity patches.

Bivalve location did not influence predation on oyster spat and ribbed mussels in laboratory trials. Predation on bivalves in high complexity patches by mud crabs was not affected by the presence or absence of potential bivalve prey in low complexity patches. Likewise, predation on bivalves in low complexity patches was not influenced by the presence or absence of bivalves in high complexity patches. Predation on both oyster

spat and ribbed mussels by mud crabs was influenced by the presence of a top predator, *C. sapidus* (which seldom moved around during the course of a trial), although the bivalves were affected in different ways. Consumption of oyster spat in high complexity patches decreased when *C. sapidus* was present (Figure 13). Blue crabs did not influence predation on oyster spat in low complexity patches. Conversely, the presence of *C. sapidus* only influenced ribbed mussels in low complexity patches where predation by mud crabs was reduced, although the trend still existed in high complexity (Figure 13). A trait-mediated indirect interaction (TMII) occurred during the laboratory experiment, where a higher predator changes the foraging behavior of an intermediate predator, influencing prey abundance (Wootton 1993, Grabowski 2004). In this experiment, the presence of blue crabs, the top predator, influenced the behavior of mud crabs in a way that increased the survival of bivalves due to decreased predation by mud crabs. The strength of these interactions was affected differentially by habitat vertical complexity for the two bivalves, as TMIIIs did not occur in the low complexity patches for oyster spat nor did they occur in the high complexity patches for ribbed mussels. Nevertheless, TMIIIs were observed in both high and low complexity patches showing that although habitat complexity may affect how TMIIIs occur, these interactions were important for both types of microhabitat vertical complexity. Oyster toadfish have been shown to elicit TMIIIs for mud crab predation on oyster spat in laboratory conditions as well, where the presence of toadfish indirectly benefited oyster spat by decreasing predation by mud crabs (Grabowski 2004). TMIIIs are an important structuring component for a wide range of terrestrial and marine communities (Peacor and Werner 2003) and should receive close attention when examining trophic linkages and species interactions. Examining how

habitat complexity affects or moderates these and other types of direct and indirect species interactions will allow for a better understanding of how different communities are structured.

During the lab experiment, both oyster spat and ribbed mussels were present in the same location with the same abundances. Mud crab predation of ribbed mussels was greater than that of oyster spat (Figure 14). This was true for every treatment in every trial, and in some instances all five mussels were consumed while all five oyster spat remained attached and uneaten on the same shell. This indicates that mud crabs preferred ribbed mussels over oyster spat when both prey were available. The preference for ribbed mussels exhibited by mud crabs may be important in further understanding the ecological functioning of oyster reefs that contain these mud crabs, specifically *Panopeus herbstii*, as a dominant epifauna. Adding mussels or enhancing their recruitment to initially created reefs might allow for faster initial growth, an important aspect of oyster reef restoration, by reducing predation on oyster spat by mud crabs.

A positive feedback may be taking place between oysters and ribbed mussels in the intertidal oyster reefs of the southeastern United States. As oyster larvae settle through time, complex aggregates of shell are eventually produced. This provides suitable habitat for ribbed mussels and their densities increase. With the increased density of mussels, specifically in high complexity reefs (where they are located in significantly higher abundances), bivalve predators like *P. herbstii* may target these alternate prey. With both bivalves in the system, oyster spat receive some degree of predation relief and can eventually contribute to increasing habitat complexity. Complex oyster reefs, in turn, benefit mussels by providing suitable habitat. The specific dynamics

of this indirect mutualism may be important to formation and maintenance of small intertidal reef systems.

This study has implications for intertidal oyster reef restoration efforts in the southeastern United States. Newly created low complexity oyster reefs had greater recruitment in the first year of creation compared to created high complexity reefs. This trend was not observed two years later, after the reefs became established (having similar abundances of resident fauna compared to natural reefs in the area). Without mussels present in newly created oyster reefs, oyster spat may be subjected to greater predation pressure from crabs like *P. herbstii*, but in low complexity reefs, where mud crab abundance is reduced, oyster spat might be less affected. Predation on newly settled oyster spat is an extremely important factor accounting for significant oyster mortality in newly created reefs (O'Beirn, et al. 2000). Recruitment may play a more important role in the restoration of oyster reefs as initial growth of the reef allows it to become established more rapidly. Creating oyster reefs that have greater initial recruitment may provide the essential element needed to insure the establishment of healthy self-sustaining oyster habitat in areas that have high sedimentation or abundances of mud crabs.

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