

EASTERN OYSTERS OFFER NO PEARL, BUT THEY MIGHT BE IN PERIL:
UNDERSTANDING HOW LETHAL AND NON LETHAL PREDATOR EFFECTS
INFLUENCE OYSTER DISTRIBUTION AND REEF COMMUNITY

A Dissertation

By

KEITH DARREL JOHNSON

Submitted in Partial Fulfillment of the Requirements for the Degree of

DOCTOR OF PHILOSOPHY

in

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KEITH DARREL JOHNSON

This dissertation meets the standards for scope and quality of
Texas A&M University-Corpus Christi and is hereby approved.

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ABSTRACT

Eastern oysters offer no pearl, but they might be in peril: Understanding how lethal and non lethal predator effects influence oyster distribution and reef community structure

(August 2012)

Keith D. Johnson, B.A., Central College

Chair of Advisory Committee: Dr. Delbert L. Smee

The purpose of this dissertation research was to investigate how predation affects oyster distribution and reef community structure by examining: 1) non lethal predation effects on bivalves by size of prey; 2) the lethal and non lethal effects that influence survival and resource allocation in oysters; 3) predation affects distribution patterns of oysters; 4) top-down forces and seasonal effects on oyster reef community structure.

Although Eastern oysters, *Crassostrea virginica*, are ecologically and economically important, oyster populations are declining in many areas and have decreased 85% worldwide. Like many communities, predation or top-down forces can have significant effects on the structure and function of oyster reef communities. The purpose of this study was to ascertain how oyster recruitment, survival, growth and distribution as well as oyster reef community structure were influenced by lethal and non lethal effects of predators. Results from a series of manipulative field experiments indicate that predators have significant effects on oyster reef community structure and oyster recruitment, but, these effects are significantly more important in the fall than spring. Oyster recruitment and spat survival is strongly affected by the abundance of intermediate consumers, most notably the Atlantic mud crab (*Panopeus herbstii*). In the

absence of higher order predators including blue crabs (*Callinectes sapidus*) and red drum (*Scianops ocellatus*), mud crabs increased in number and preyed more heavily on newly settled oysters. Mud crabs also caused oysters to change their resource allocation to more shell and less tissue at a cost of lowering fecundity. Finally, oysters are limited to intertidal habitats in Corpus Christi Bay, and these results indicate that oysters are restricted to intertidal habitats by predators. This study elucidates how predators have significant lethal and non lethal effects on oysters and their associated fauna and that top-down forces should be considered when developing oyster reef conservation, management, and restoration efforts.

DEDICATION

In dedication to my loving parents Darrel and Joanne Johnson, whose support made this dissertation possible.

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INTRODUCTION

Oyster populations have been declining in many areas, and it is estimated that oyster reefs have decreased 85% worldwide (Rothschild et al. 1994, Seavey et al. 2011). The abundance and diversity of higher-order consumers are declining in many systems (Jackson et al. 2001). Changes in predator abundance can contribute to declines in bivalve fisheries (Myers et al. 2007) and may also contribute to a decline in oyster populations (O'Connor et al. 2008) and in the ecosystem services oyster reefs provide (Grabowski and Peterson 2007).

Eastern oysters, *Crassostrea virginica*, provide numerous ecosystem goods and services reviewed by (Grabowski 2007). Oysters are facilitating species and provide critical habitat for organisms with structure for attachment and with protection from predators (Lenihan 1999, Breitburg et al. 2000, Jackson et al. 2001, Grabowski 2004, Tolley & Volety 2005). They filter water and improve water quality (Nelson et al. 2004) and protect the coast from storms and erosion. Oyster reefs also have a positive effect on commercial and sport fisheries (Breitburg et al. 2000) by providing a safe habitat for juvenile fish (Peterson et al. 2003, Grabowski & Kimbro 2005, Stunz et al. 2010).

Previous studies have shown that top-down forces significantly affect the structure and function of oyster reefs (Lenihan et al. 2001, Grabowski & Kimbro 2005, O'Connor et al. 2008). Mesocosm studies using oyster reefs as a model system have also described strong effects of trophic cascades in higher-order interactions (Grabowski 2004, Grabowski and Kimbro 2005). Grabowski (2004) created an oyster reef system using toadfish (*Opsanus beta*) as a top-predator, which consumed mud crabs (*Panopeus*

herbstii) an intermediate predator, which then consumed newly settled eastern oysters. This study revealed strong positive effects on juvenile oysters from toadfish because this top predator consumed mud crabs and caused mud crabs to remain in refuges, reducing their foraging time. Grabowski (2004) found that both lethal and non lethal effects of top predators were driving the trophic cascade in this system. Grabowski and Kimbro (2005) also noted that the consumption of mud crabs and the suppression of their foraging by toadfish also benefited juvenile hard clams *Mercenaria mercenaria*.

Avoiding predators is often necessary for prey survival, but predator avoidance is costly because it requires prey to allocate resources to defense rather than growth or reproduction (Lively 1986, Harvell 1990, Kats & Dill 1998, Schoeppner & Relyea 2005, Hay 2009). For example, predator-induced behavioral changes such as a reduction of prey foraging time (Turner 2004, Large & Smee 2010) or feeding cessation (Smee & Weissburg 2006, Naddafi et al. 2007) can minimize predation risk, but may ultimately lower growth and fecundity (Relyea 2001, 2002, Fassler & Kaiser 2008, Bourdeau 2010). Constant exposure to risk may also decrease body size and increase the likelihood of being consumed (Edeline et al. 2010). To minimize costs associated with predator avoidance, many prey species use plastic responses to predation risk and change their morphology, behavior, or life-history only when situations pose risk of injury or death (Lively 1986, Crowl & Covich 1990, Harvell 1990, Kats & Dill 1998).

Prey often use chemical cues to evaluate predation risks from predators, injured conspecifics, or heterospecifics, or some combination thereof (Katz and Dill 1998, Hay 2009, Ferrari et al. 2010). Yet, to be cost effective, prey must be able to distinguish the level of risk associated with individual predators based on predator characteristics such as relative

predator size or predator type and then respond appropriately by evaluating differences in chemical cues between predators. Surprisingly, few studies have examined how predator size or biomass influences the propagation of non lethal effects on prey populations (but see Schoeppner and Relyea 2008, Toscano and Griffen 2012, Hill and Weissburg *in review*). Similarly, it is well established that prey size influences risk of being consumed (Micheli 1995, Wong et al. 2010), but few studies have examined whether prey size influences reactions to predation risk (but see Nakaoka 2000).

Oyster abundance and distribution can be influenced by predation, disease, and by stressful abiotic conditions including hypoxia and both excessively low and high salinities that are physiologically stressful and increase disease infection rates (Johnson et al. 2009, Pollack et al. 2011). Predation on both juvenile (newly settled) and adult oysters can be intense and limit oyster reef restoration (O'Beirn et al. 2000). Small, juvenile oysters are vulnerable to a suite of predators including various crabs, oyster drills, and fishes. For example, mud crabs (Xanthidae) inhabit oyster reefs and readily consume newly settled oysters (Grabowski 2004). Oyster drills (*Stramonita haemastoma*) are a common predator for juvenile and adult oysters (Toscano & Griffen 2012) as are black drum (*Pogonias cromis*) (Brown et al. 2008). Predation from multiple predators at various trophic levels can affect juvenile oyster survival (Grabowski 2004, O'Connor et al. 2008) and be important for restoration of oyster reefs.

The purpose of this dissertation research was to investigate how predation affects oyster distribution and reef community structure by examining: 1) non lethal predation effects on bivalves by size of prey; 2) the lethal and non lethal effects that influence

survival and resource allocation in oysters; 3) predation affects distribution patterns of oysters; 4) top-down forces and seasonal effects on oyster reef community structure.

Chapter 1: Size matters for risk assessment and resource allocation in bivalves

ABSTRACT

Predators may affect prey populations by consuming prey (lethal effect) or by causing prey to alter their morphology, behavior, or habitat selection (non lethal effect). In this study, I examined how size relationships between predators and prey influence the expression of non lethal effects. In an empirical field experiment, I assessed how the size and vulnerability to predators would influence expression of non lethal effects in bivalve species common to oyster reefs. I used two size classes of hooked mussels (*Ischadium recurvum*), hard clams (*Mercenaria mercenaria*), and eastern oysters (*Crassostrea virginica*) as prey and compared energy allocation and growth of small vs. large bivalves in the presence of Atlantic mud crabs, *Panopeus herbstii*, a common, resident reef predator.

In laboratory feeding assays, smaller bivalves were more vulnerable to mud crab predators. After 45 days of exposure to crab cues in the field, I observed significant differences in growth among bivalves in response to mud crabs, but, the effects were size and species dependent. In the presence of mud crabs, small clams and small oysters grew significantly less soft-tissue, small mussels grew more shell mass, large clams grew less shell mass, and large mussels grew less tissue and shell mass. Significant differences in the growth of larger oysters were not found. Changes in growth of soft tissue and shell reflect resource allocation differences in response to predators and most likely resulted from costs associated with feeding reductions to minimize release of metabolites attractive to predators, allocation of additional energy for morphological defense, or both

to minimize predation risk. Fecundity is positively correlated with size in bivalves, and the ability to detect predation risk and appropriately allocate resources may be important for future reproductive output of these species. Additionally, bivalve size is inversely related to their susceptibility to mud crabs, and slower growth may lengthen the time these species are vulnerable to these predators and increase their mortality. Results from this study indicate that mud crabs can affect the growth and fecundity of commercially important bivalves by non lethal interactions and that size is an important consideration when investigating the propagation of non lethal predator effects.

INTRODUCTION

Avoiding predators is often necessary for prey survival, but predator avoidance is costly since it requires prey to allocate resources to defense rather than growth or reproduction (Lively 1986, Harvell 1990, Kats & Dill 1998, Schoeppner & Relyea 2005, Hay 2009). For example, predator-induced behavioral changes such as a reduction of prey foraging time (Turner 2004, Large & Smee 2010) or feeding cessation (Smee & Weissburg 2006, Naddafi et al. 2007) can minimize predation risk, but may ultimately reduce growth and fecundity (Relyea 2001, 2002, Fassler & Kaiser 2008, Bourdeau 2010). Constant exposure to risk may also decrease body size and increase the likelihood of being consumed (Edeline et al. 2010). To minimize costs associated with predator avoidance, many prey species use plastic responses to predation risk and change their morphology, behavior, or life history only when situations pose risk of injury or death (Lively 1986, Crowl & Covich 1990, Harvell 1990, Kats & Dill 1998).

Prey often use chemical cues to evaluate predation risk that emanate from predators, injured conspecifics, or some combination thereof (Katz and Dill 1998, Hay 2009, Ferrari et al. 2010). Yet, to be cost effective, prey must be able to distinguish the level of risk associated with individual predators based on predator characteristics such as relative predator size or predator type and then respond appropriately by evaluating differences in chemical cues between predators. Appropriate responses to predators may vary depending on size relationships between predators and prey (Schoeppner and Relyea 2008, Toscano and Griffen 2012, Hill and Weissburg *in review*). It is well established that prey size influences risk of being consumed (Micheli 1995, Wong et al. 2010), and in this study, I examined how prey size influenced reactions to predation risk.

Bivalves have routinely been used in studies of phenotypic plasticity and often produce thicker shells after exposure to predator exudates (Caro & Castilla 2004, Cheung et al. 2004, Leonard et al. 1999, Nakaoka 2000, Smith & Jennings 2000). In addition to increasing shell thickness in the presence of crushing predators (crabs), mussels (*Mytilus edulis*) also increased byssal thread production to increase the force needed by predators to remove them from hard substrates (Cote 1995, Leonard et al. 1999, Shin et al. 2009) and to increase abductor muscle mass for some predators (whelks) (Freeman 2007, Freeman et al. 2009). Hard clams, *Mercenaria mercenaria*, grow more slowly in the presence of knobbed whelk (*Busycon carica*) predators (Nakaoka 2000), possibly because they reduce their feeding (pumping) time in response to them (Irlandi & Peterson 1991, Smee & Weissburg 2006). Changes in morphology, such as increased shell thickness, are a trade-off with soft tissue mass and gonad size. In bivalves, there is a

positive relationship between mass of soft-tissue (including gonads) and fecundity, and a negative relationship between shell thickness and soft-tissue mass (Peterson 1986).

Although numerous studies have examined phenotypic plasticity in mussels, to date, only laboratory studies have examined plastic responses of eastern oysters (*Crassostrea virginica*) to predators (Newell et al. 2007, Lord and Whitlatch 2011). Oysters are an important foundation species in estuaries along the Gulf and East Coasts of the United States, and they provide many ecosystem services (Grabowski and Peterson 2007). Because oysters are an important foundation species, the potential for predators to induce changes in oyster growth and cause reductions in oyster fecundity may potentially have important consequences for oyster populations and estuarine systems by reducing future oyster populations and diminishing the ecosystem services they provide. Additionally, greater complexity on oyster reefs is important for mitigating predation (Grabowski 2004), and reductions in oyster growth could minimize the refuge value of reef habitats.

To determine if predators alter oyster morphology in the field using natural predator densities, I performed a manipulative experiment using mud crabs (*Panopeus herbstii*), Eastern oysters, and two additional common bivalves found on oyster reefs in the Southeastern United States: hard clams (*Mercenaria mercenaria*) and hooked mussels (*Ischadium recurvum*). Mud crabs and associated bivalves were used as a model system for this study because mud crabs are common intermediate predators in oyster reef communities and can consume significant numbers of juvenile oysters and associated bivalves when not regulated by higher-order consumers (Grabowski 2004, Grabowski &

Kimbro 2005). Our results suggest that in addition to consuming these bivalves, mud crab cues affect their growth but the effect is dependent upon bivalve species and size.

METHODS

Study Site

This field experiment was conducted from June 15 to August 15, 2008 near the Skidaway Institute of Oceanography (SkIO) in Savannah, GA, at Priest Landing and Cabbage Island (Fig. 1.1). I measured abiotic conditions in both sites each week during the study using Hydrolab Sondes. Salinity measured on the practical salinity scale (33 ± 0.15 SE) and water temperature (32 ± 0.6 °C SE) were similar between sites. These field sites experience different hydrodynamic regimes. The Wilmington River sites were mostly protected from waves while sites on Cabbage Island were exposed to waves (see Smee et al. 2008, Ferner et al. 2009 for detailed hydrodynamic measurements).

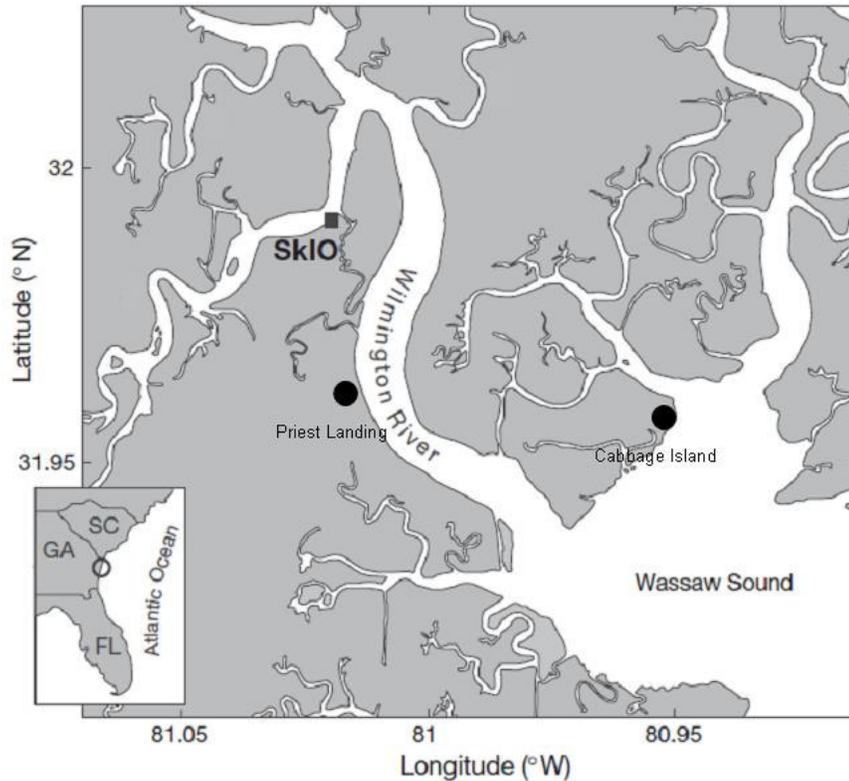


Figure 1.1: Map of the study area with field sites labeled. Skidaway Institute of Oceanography (SkIO) is marked with a square and Priest Landing and Cabbage Island marked as circles.

I measured morphological changes in three of the most common bivalve species on oyster reefs: eastern oysters, hard clams, and hooked mussels when in the presence of mud crab predators (*P. herbstii*). I used two size classes of bivalves and compared the changes in growth of soft tissue and shell as well as the susceptibility to mud crabs from each size. Hatchery-reared eastern oyster larvae (*C. virginica*) were purchased and settled on to grooved sections of polyvinyl chloride pipe (PVC) that were 10 cm in length. These juvenile oysters were allowed to grow for two weeks until they were ~ 2 mm (shell height [SH]), and then thinned so that 10 oysters were present on each piece of PVC. Larger juvenile oysters (10-15 mm SH) were collected from oyster shells placed into the field,

which collected naturally settling individuals in the spring. Two size classes of hard clams, 5-10 mm and 10-15 mm measured from the umbo to outermost edge of the shell, were purchased from a commercial hatchery. Hooked mussels were collected from pilings near SkIO and were separated into size classes: small 5-10 mm and large 10-15 mm. Both large and small bivalves used in this study were relatively small and can grow rapidly in warm conditions with abundant food (Ingle & Dawson 1952). The larger classes were less susceptible to crushing predators like crabs. The mud crabs used in this experiment were *P.herbstii* collected from oyster reefs adjacent to the field sites. Crabs used were 20-30 mm carapace width.

Bivalve Growth

I wanted to ensure that all organisms were growing during the experiment and that changes noted in final tissue and shell weights between predator treatments would reflect changes in resource allocation not starvation or a lack of new growth. To quantify growth on experimental bivalves, I measured initial and final wet weights of clams and mussels. Wet weights can be unreliable and highly variable, so I calculated a regression using final wet weight versus final dry weight to verify that wet weights were reasonable estimates for dry weight and subsequent growth. Values of R^2 were above 0.90 for all relationships, indicating that wet weights were appropriate measurements of respective growth among treatments. I did not measure initial weights of oysters as I was unable to remove them from their attachment points without injury. Changes in wet weights for clams and mussels were compared with t-tests for each size class (Sokal and Rohlf 1995).

Changes in Bivalve Mass after Predator Exposure

Five oysters, clams and mussels from each size class (large and small) of were securely placed in cages (40 x 20 x 15 cm) and these cages were deployed in pairs within oyster reefs in each study site. One member of the pair contained a single mud crab while the other did not to serve as a control. Mud crabs were contained within a 5.0 cm cylindrical cage within the larger cage so that the mud crabs could not contact or consume the bivalves. Ten pairs of cages were placed in each study site. Within pairs, individual cages were placed ~ 1.0 m apart, at ~ 0.5 m above the MLLW line, and pairs were placed ~ 20 m apart. The cylindrical cages were also present in controls but did not contain mud crabs. Cages were checked weekly, at which time mud crabs were fed live, intact clams and mussels and missing or dead crabs were replaced. Drift algae and sediment were also removed from cages during weekly inspections. Cages remained in the field for 45 days, which was sufficient time to observe significant increases in growth of all species and size classes.

After 45 days, the oysters, clams, and mussels were returned to the lab to quantify their final tissue and shell mass. I elected to use mass as a proxy for relative energy allocation in response to predators because individual bivalves, oysters in particular, exhibit great variation in size and shape, making measurements of shell length or width difficult to interpret. In preliminary studies, I noted that measurements of shell length and width were subject to significant measurement errors due to the small size and shell variability, which were avoided by measuring mass. Further, oysters are firmly attached to substrates and their growth patterns vary widely, which make measuring their shell thickness or width/length relationships growth difficult to measure consistently.

Bivalve tissue and shell mass were calculated after the 45-day field experiment using the following protocol. First, all bivalves were placed into a conventional drying oven at 90 °C for 2 days and the dry mass of each individual recorded. This provided a measure of shell and soft tissue weight combined. Then, all bivalves were transferred to a muffle furnace and baked for 2-h at 500 °C to remove all soft tissue. Each bivalve was reweighed to obtain weights of the shell only (ash-free dry mass). The shell weight was subtracted from the dry mass to find the tissue mass.

Two-way ANOVAs were used to examine growth differences between treatments for each size and type of organism with site and predator treatment as fixed factors in the ANOVA model (Sokal 1995). I did not compare tissue or shell weights among different species or sizes of bivalves due to inherent differences in shell thickness and growth rates among species and sizes. Site was not significant ($p > 0.2$) nor was the interaction of site and treatment ($p > 0.3$). I therefore pooled data between sites and used t-tests to compare differences in final mass of tissue and shell for each bivalve size and species between mud crab treatments and controls (Sokal and Rohlf 1995).

Feeding Assays

I performed feeding assays to determine if smaller bivalves were more vulnerable to predation by mud crabs. In these experiments, I placed 1 small and 1 large bivalve in a 2.0 L glass jar containing aerated seawater, and I then measured the time needed for both bivalves to be eaten. Small and large size classes used were the same as those noted above. Time was measured as the number of 1-h periods elapsed before consumption. I covered the sides of the tanks with black paper to minimize visual distractions to the crabs. The assays were stopped after 24-h or when both bivalves were consumed. Sixteen

assays were performed with clams and mussels. I elected not to use oysters for these experiments because I could not remove newly settled oysters from our PVC sticks without injuring them and felt that presenting oysters to predators settled onto a stick would not be a suitable comparison to a single oyster of a slightly larger size. I compared the time until the small vs. large clams or mussels were eaten separately using a nonparametric sign test (Sokal and Rohlf 1995).

RESULTS

Bivalve Growth

Wet weight was highly correlated with dry weight ($R^2 > 0.90$), indicating that wet weight was a reasonable approximation for final dry weight and overall growth. Wet weight increased for both size classes of each species during the experiment, but I did not find significant differences in growth between mud crab treatments and controls: (large clams: $F_{1,43} = 0.88$, $p = 0.37$; small clams: $F_{1,13} = 1.48$, $p = 0.14$; large mussels: $F_{1,21} = 1.68$, $p = 0.10$; small mussels $F_{1,31} = 1.47$, $p = 0.14$; Figs 1.2 & 1.3). Thus, differences in tissue and shell weights between predator treatments and controls resulted from changes in allocation of resources rather than differences in growth rates among bivalve size classes.

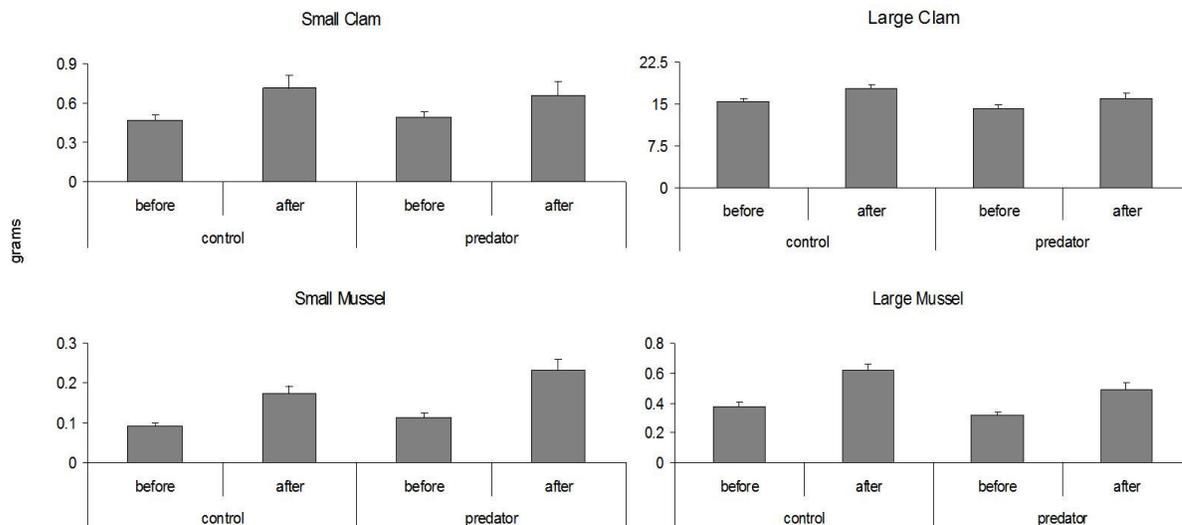


Figure 1.2: Mean wet weight \pm SE of clams and mussels at the beginning and end of the experiment. They are separated into the predator and control (no predator) treatments as well as before and after wet weights. All species and size classes grew during the experiment.

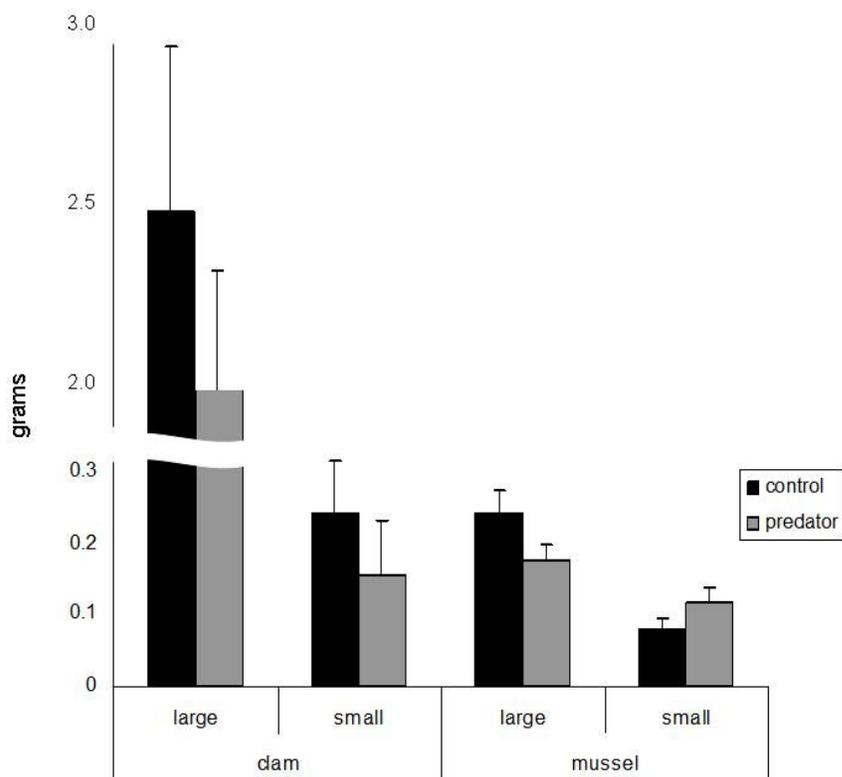


Figure 1.3: Mean wet weight \pm SE gained during the experiment by species, size, and treatment. Significant differences were not found between treatments using a t-test. The control (no predator) treatment is in black and the predator treatment is grey

Changes in Bivalve Mass After Predator Exposure

Tissue and shell weights were not statistically different between predator treatments for the larger size classes of oysters (tissue $F_{1,116}=0.25$, $p=0.61$; shell $F_{1,116}=0.29$, $p=0.58$). Large mussel tissue and shell growth was significantly less in mud crab treatments at $\alpha = 0.1$ (tissue $F_{1,38}=2.91$, $p=0.09$; shell $F_{1,38}=3.44$, $p=0.07$, Fig 1.4). Large clams grew significantly less shell in the presence of mud crabs but their soft tissue growth was not significantly different (tissue $F_{1,85}=0.27$, $p=0.61$; shell $F_{1,85}=1.98$, $p=0.02$). In contrast, mud crabs affected tissue mass but not shell mass in the smaller bivalves since tissue masses were significantly lower for small oysters ($F_{1,60}=13.34$, $p<0.001$) and small clams ($F_{1,46}=5.85$, $p=0.02$, Fig 1.4). I did not observe significant changes in shell mass between mud crabs and controls for either small oysters ($F_{1,60}=0.36$, $p=0.58$) or small clams ($F_{1,46}=0.18$, $p=0.67$, Fig 1.4). There was no significant difference in the tissue ($F_{1,56}=0.10$, $p=0.75$) mass for small mussels with and without mud crabs present. Unlike oysters and clams, small mussels produced more shell mass in response to mud crabs ($F_{1,56}=3.24$, $p=0.07$), which was significant at $\alpha = 0.1$.

Feeding Assays

Smaller clams and mussels were consumed significantly more quickly than larger individuals ($p < 0.05$), indicating that smaller bivalves are more vulnerable to mud crabs. In 12 of the assays with clams, the larger clam was not consumed after 24-h. In the 4 assays where the large clam was consumed, the mud crab ate the smaller clam first. In 8 of the mussel feeding assays, the smaller mussel was consumed first. In 4 assays, large and small mussels were consumed during the same 1-h period, and in the remaining 4 neither mussel was consumed.

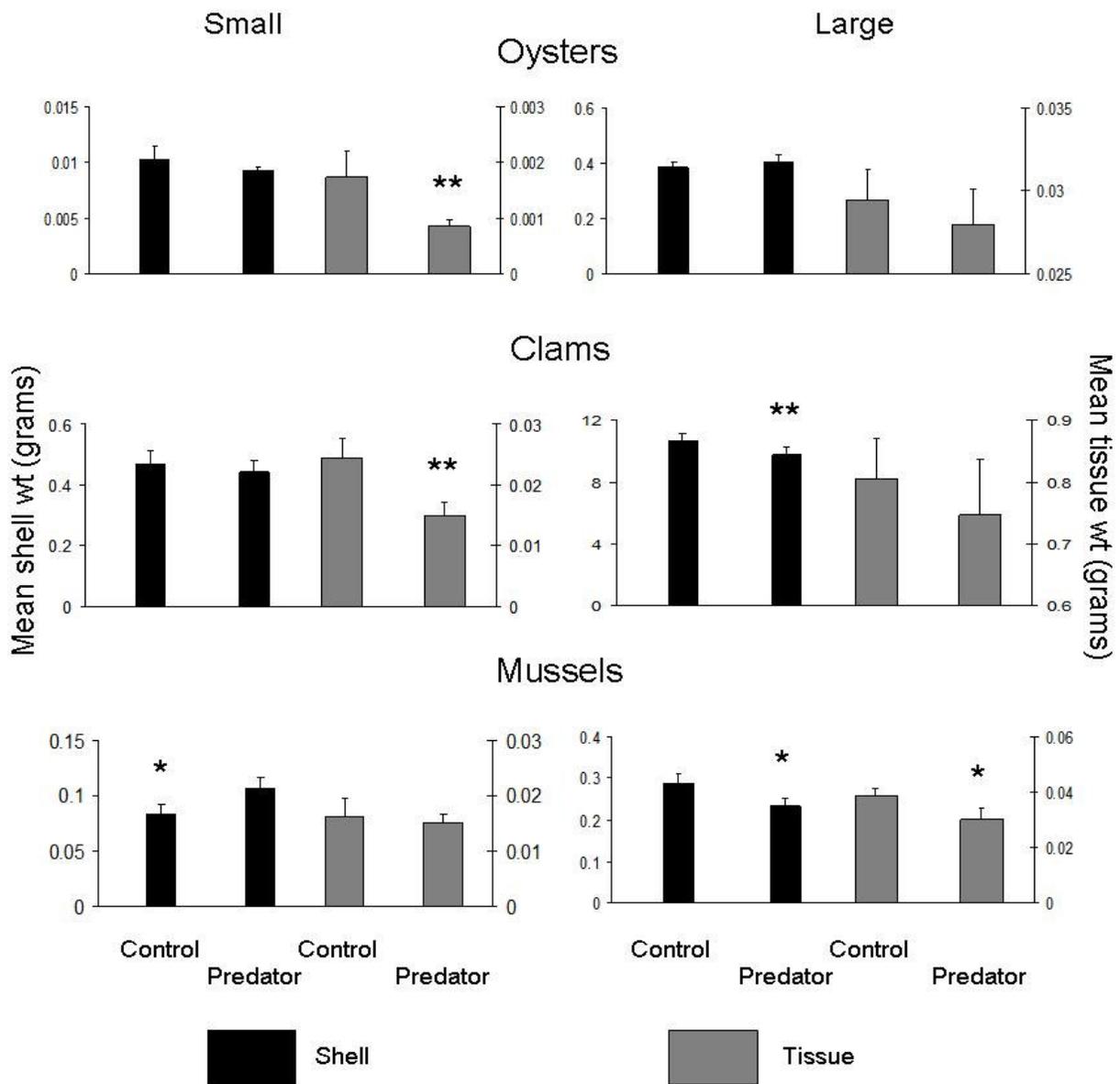


Figure 1.4: Mean change in shell and tissue mass \pm SE for large and small clams, oysters and mussels by control and predator treatment. Error bars represent standard error and ** denotes a significant difference at $p < 0.05$ and * denotes significance at $p < 0.1$ based upon a t-test.

DISCUSSION

Bivalves exhibit both behavioral and morphological defenses against predators, and our results indicate that size influences their predator avoidance responses. Prey size often affects vulnerability to predators and subsequent lethal predator effects in communities (Micheli 1995, Wong et al. 2010). By inducing avoidance responses in prey, predators may initiate trophic cascades that are similar in magnitude to those generated through direct prey consumption (Trussell et al. 2003, Werner and Peacor 2003, Preisser et al. 2009). Our findings indicate that size may also affect if and how prey react to consumers and should be considered in determining the scales of non lethal predator effects and the extent to which predators indirectly affect multiple trophic levels.

Bivalves can reduce predation risk through changes in behavior (Griffiths and Richardson 2006, Smee & Weissburg 2006, Naddafi et al. 2007, Flynn and Smee 2010), morphology (Leonard et al. 1999, Newell et al. 2007, Lord and Whitlatch 2011), or a combination of defensive strategies (Freeman 2007, Naddafi et al. 2007, Freeman et al. 2009). They may build a stronger shell as protection from crushing consumers like crabs (Micheli 1995, Leonard et al. 1999, Nakaoka 2000). Mussels exhibit additional morphological defenses against predators including producing extra byssal threads to more firmly attach themselves to the substrate (Cote 1995, Leonard et al. 1999, Shin et al. 2009) and/or grow thicker abductor muscles to discourage prying predators (Freeman 2007, Freeman et al. 2009). Some bivalves reduce predation risk by reducing their feeding rates to minimize release of cues that attract predators (Smee and Weissburg 2006, Naddafi et al. 2007), while others burrow more deeply to escape from burrowing consumers (Griffiths and Richardson 2006, Flynn and Smee 2010).

Regardless of the mechanism used to reduce predation risk, the expression of defenses incurs costs such as reductions in growth and fecundity as resources are expended (Nakaoka 2000, Relyea 2002). Chronic stress alone can decrease growth rates (Edeline et al. 2010), which may extend the time bivalves are vulnerable to mud crabs and increase their mortality (Micheli 1995, Wong et al. 2010). Additional work is needed to more clearly link reductions in growth to specific predator avoidance responses in the species used in this study as well as to establish long-term effects on mortality, growth, and fecundity.

From our data it is clear that size can influence if and how prey respond to predators (Fig. 1.4). In oysters, smaller individuals produced less soft tissue in response to crabs but larger individuals did not (Fig. 1.4). Laboratory studies have shown oysters to grow stronger shells in response to blue crabs (Newell et al. 2007) and oyster drills (Lord and Whitlatch (2011), and the reduction in soft tissue growth may have occurred as smaller, more vulnerable, oysters allocated more energy to shell strengthening and less to tissue growth.

Mud crabs affected growth of both large and small clams, but did so in different ways. Smaller clams grew less soft tissue while larger individuals grew less shell mass. Hard clams react to crabs by reducing feeding time to minimize release of metabolites that attract predators and close their valves to protect siphons and soft tissues (Smee and Weissburg 2006, Smee et al. 2008). Here, growth reductions in clams may be explained by lost feeding time, but, the costs associated with predator avoidance manifested in different ways based on size. Unlike mud crabs, knobbed whelks tend to forage on larger clams (> 30 mm) (Peterson 1982), and larger clams grew less in response to whelks

while the growth of smaller clams (< 30 mm) that are not eaten by whelks were unaffected by their presence in the field (Nakaoka 2000). Thus, clams respond differently to mud crabs than knobbed whelks in a manner that seems adaptive based upon relative risk of each predator.

Small and large mussels also responded to mud crabs differently. Small mussels increased shell mass in predator treatments, which has been reported for other mussel species (Chuang et al. 2004, Smith & Jennings 2000). Smaller mussels did not reduce soft tissue growth in predator treatments even though they grew a thicker shell. This may have occurred because mussels produce additional byssal threads in response to predators to make it more difficult for predators to dislodge and crush them (Cote 1995, Leonard et al. 1999, Fassler & Kaiser 2008). Soft tissue mass included mass from byssal threads, and thus I were unable to determine if mussels were allocating soft tissue growth differently in predator treatments (Fig. 1.4). Unlike the smaller mussels, larger mussels grew less tissue and shell in predator treatments (Fig. 1.4).

Oysters and clams are commercially important species, and lowering their fecundity may have long-term economic and ecological consequences. Despite their importance as a commercial fishery and as a foundation species in estuaries, oyster populations are declining in many areas of the United States (Rothschild et al. 1994, Jackson et al. 2001, Kirby 2004). Our results, along with earlier studies (Grabowski & Powers 2004, Grabowski et al. 2005), indicate the importance of maintaining sufficient populations of higher-order predators to consume mud crabs and maintain top-down control and alleviate both lethal and non lethal effects propagating from mud crabs to juvenile oysters and other bivalves. Further, larger bivalves are mostly commonly

targeted for harvesting, leaving the smaller individuals which are more vulnerable to predators and more likely to alter growth patterns in response to predators to replenish the population (Fenberg and Roy 2008). Consideration of both lethal and non lethal predator effects at multiple trophic levels should be incorporated into management plans of bivalve fisheries.

ACKNOWLEDGEMENTS

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Chapter 2: Lethal and Non lethal predator effects influence survival and resource allocation of oysters *Crassostrea virginica*

ABSTRACT

Predators often have large effects on prey populations and entire communities, but the role of predator diversity in food webs is often difficult to assess due to consumer interactions such as complementarity, predator interference, and omnivory. Here, I assessed the effects of consumer diversity on oyster reef communities through predator exclusion experiments designed to isolate the effects of predators at different trophic levels. Predators were excluded from oyster reefs using mesh-covered cages with openings of 1.0 cm² to exclude all potential oyster predators, 5.0 cm² to allow intermediate consumers to access oyster reefs, and cage controls accessible to all predators. Natural oyster settlement and survival was greatest in the small mesh cage when oysters were completely protected from consumers. I found *Panopeus herbstii*, the Atlantic mud crab, to be the common intermediate consumer preying on juvenile oysters, and I observed significantly more *P. herbstii* in the 5.0 cm² cage than in other treatments. Oyster survival was not statistically different in the 5.0 cm² mesh cage and controls, indicating that mud crabs alone may consume significant numbers of newly settled oysters. Intermediate oyster consumers such as mud crabs were rare in control treatments, probably because they were consumed by higher-order fish and crab predators. Survival of newly settled oysters was also low in controls because mud crab predators including blue crabs (*Callinectes sapidus*) and sheephead (*Archosargus probatocephalus*) consume mud crabs and juvenile oysters. In subsequent experiments, I found that

predation and not recruitment accounted for oyster survival differences among cage treatments. I also found mud crabs induced oysters to grow thicker shells and less soft tissue, which likely lowers their fitness. Thus, both intermediate and higher-order predators may consume oysters, but, by regulating the numbers of intermediate predators such as mud crabs, higher-order consumers alleviate non lethal effects exerted onto juvenile oysters from intermediate consumers. Our results show that mud crabs exert lethal and non lethal effects on oysters, and that these effects may increase when larger predators are absent.

INTRODUCTION

Many communities are structured by predation or top-down forces (Paine 1966, Estes & Palmisano 1974, Menge 2000, Trussel 2003) exerted on a community from either one species or a guild of consumers that control populations at lower trophic levels (Grabowski 2004). Predators may also affect abundance and distribution of organisms at several trophic levels by initiating trophic cascades (Carpenter et al. 1985). In general, trophic cascades occur when predators prey on intermediate consumers causing a reduction in consumer pressure on lower trophic levels. Top-down forces are important community-structuring agents in terrestrial (Schmitz et al. 1997), freshwater (Carpenter et al. 1985) and marine systems (Paine 1966).

Top-down forces occur via two distinct mechanisms, lethal or consumptive effects where predators consume prey (Trussel 2003) and non lethal or nonconsumptive effects in which predators alter prey traits such as foraging behavior or habitat selection (Trussel 2003, Werner & Peacor 2003, 2006). Non lethal effects can have significant influence on communities that are equal to or greater than those from consumption (Grabowski 2004),

and both lethal and non lethal indirect predator effects are known to affect trophic interactions in oyster reef communities (Grabowski 2004, Grabowski et al. 2005, O'Connor et al. 2008). Specifically, higher-order consumers such as toadfish (*Opsanus tau*) cause mud crabs, an intermediate consumer, to seek refuge and forgo foraging opportunities, which increases oyster survival (Trussel 2003, Grabowski 2004, Grabowski et al. 2005).

Yet, trophic cascades can be dampened when higher-order consumers feed at multiple trophic levels (O'Connor et al. 2008), occurs on oyster reefs when predators such as blue crabs (*Callinectes sapidus*) and sheepshead (*Archosargus probatocephalus*) consume not only mud crabs but juvenile oysters and other bivalves. Using oyster reefs, *Crassostrea virginica*, as a model system, I completed a series of field experiments to ascertain how higher-order consumers influence abundance of intermediate consumers, the extent to which different trophic levels prey on juvenile oysters, and how changes in abundance of intermediate consumers may affect growth of juvenile oysters.

I selected oysters reefs as a model system because they provide numerous ecosystem goods and services (reviewed by Grabowski and Peterson 2007), and because top-down forces significantly affect structure and function of oyster reefs (Lenihan et al. 2001, Grabowski et al. 2005, O'Connor et al. 2008). I performed a field experiment to isolate the effects of intermediate predators on oyster survival using cages with varying mesh sizes since diversity of intermediate predators can play an important role in structuring communities (Stachowicz et al. 2007). Our results suggest predators can significantly affect oyster reef community structure, that mud crab numbers increase in the absence of higher-order consumers, and that mud crabs both consume large numbers

of juvenile oysters and cause oysters to allocate resource to defense rather than tissue growth.

METHODS

Study Site

These experiments were performed in Corpus Christi Bay near Port Aransas, Texas on intertidal oyster reefs. The reefs are bordered by salt marsh and seagrass habitats and are typical of oyster reefs in the general area. These reefs receive little freshwater input and the water is exchanged by tidal changes (~ 0.5 m) through the nearby Port Aransas ship channel. The average water temperature during the experiments was 28.6^c and the average salinity was 31 as measured on the practical salinity scale.

Cage Experiment

First, I used a predator exclusion experiment to ascertain how the absence of higher-order consumers would influence the prevalence of mud crabs and the settlement and survival of juvenile oysters. Predator exclusion cages were constructed from 2x2 lumber, were 1.0 m x 1.0 m x 0.25 m tall, and were completely covered with vexar mesh of one of two mesh sizes (1.0 cm² and 5.0 cm²) to exclude different sizes of predators (Fig. 3.1). Cages with only two sides covered in mesh were used as controls, and I placed one cage control along with one cage covered with each mesh size in the field to create an experimental block of 4 treatments (3 cages + 1 control = 1 block). Within blocks, cages or controls were spaced ~ 5.0 m apart and their placement relative to each other was randomly assigned. Blocks were separated by at least 100 m. Cages were anchored flush with the sediment using rebar.

Trophic levels on Oyster Reefs

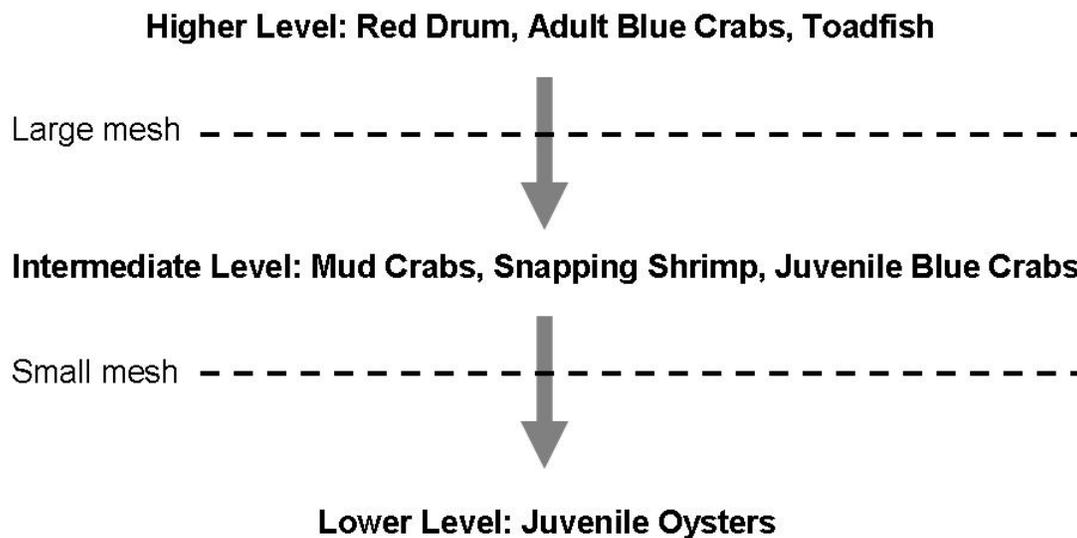


Figure 2.1: Diagram of expected exclusion of predators by cage mesh size.

In the oyster reef community there are larger, transient predators such as adult blue crab (*Callinectes sapidus*), red drum (*Sciaenops ocellatus*), black drum (*Pogonias cromis*), and sheepshead (*Archosargus probatocephalus*). These larger predators would be excluded by both the large and the small mesh cage but would have access to the control. There is also a group of intermediate, resident predators in oyster reef communities including mud crabs (*Xanthidae*), snapping shrimp (*Alpheus heterochaelis*), juvenile blue crab (*C Sapidus*), and stone crabs (*Menippe sp.*). The intermediate predators would only be excluded from the small mesh cage while having access to the control and the larger mesh cage. The large and intermediate predators would all be excluded from the small mesh cage where the juvenile oysters are free from predation pressure (Fig.

2.1). The large predators prey on the intermediate predators and some may feed on the juvenile oysters as well. Some of the intermediate predators prey on the juvenile oysters which are the foundation species in this system. The exclusion by size allowed me to examine what occurred in the absence of different trophic levels in oyster reef communities.

I controlled for cage artifacts using a 2-sided cage. Preliminary data indicated that oyster recruitment and reef fauna collected in two-sided controls and control cages without sides were not significantly different, suggesting that the two-sided control was appropriate to control for caging artifacts. Within each cage and control, I placed 10 L of oyster shells to mimic the structural complexity of natural oyster reefs in the western Gulf of Mexico. Cages were in the field from August – November 2008.

At the conclusion of the cage deployment, the number of oyster recruits and other sessile species (e.g., mussels) were counted and the associated reef fauna collected using a throw trap (for detailed methods refer to Rozas & Minello 1997). The throw trap was constructed using 1.0 m² metal frame covered with fine mesh and fitted with a sharp metal skirt. Immediately prior to cage retrieval, I placed the throw trap over the cage and pressed it into the sediment to trap all mobile organisms in the sampler. I then removed the cage and jostled it in the water to dislodge mud crabs and other organisms and thoroughly searched the shells by hand and collected any remaining mud crabs. Then I swept the throw trap with nets until all organisms were collected. After collection, organisms were placed in 10% formalin, and transported to the lab for sorting, identification, measurement, and enumeration. I also counted the number of oyster recruits that naturally settled on the shells. Because our treatments were deployed in the

field in a block design, I was concerned that drop sampling could disturb other treatments in the block. To account for this potential artifact, I used multiple throw traps so that all cages within a block were covered by a throw trap simultaneously.

Mud crabs were the most common intermediate predator collected and are important predators of newly settled oysters and other bivalves (Fig. 2.2). Abundance of mud crabs and other intermediate predators collected were compared using a one-way blocked ANOVAs with cage treatment as the fixed factor in the model and the group of four (site) as the blocking factor (Sokal et al. 1995). Tukey-Kramer post hoc tests were used to determine pairwise differences among treatments (Day & Quinn 1989). I divided mud crabs into two size classes: < 10 mm carapace width and > 10 mm carapace width and compared abundances of difference sizes as well as species for the larger mud crabs were compared using separate ANOVAs. Larger mud crabs are known predators of oysters and other bivalves while smaller individuals did not consume juvenile oysters in preliminary experiments (Johnson unpublished data).

In addition to intermediate predators, I counted the number of juvenile oysters (<10 mm) that were found on the 10 L of shells in each treatment. The number of juvenile oysters per treatment was compared using a one-way blocked ANOVA with cage treatment as the fixed factor in the model and the group of four as the blocking factor (Sokal et al. 1995). Tukey-Kramer post hoc tests were used to make pairwise comparisons among treatments (Day & Quinn 1989).

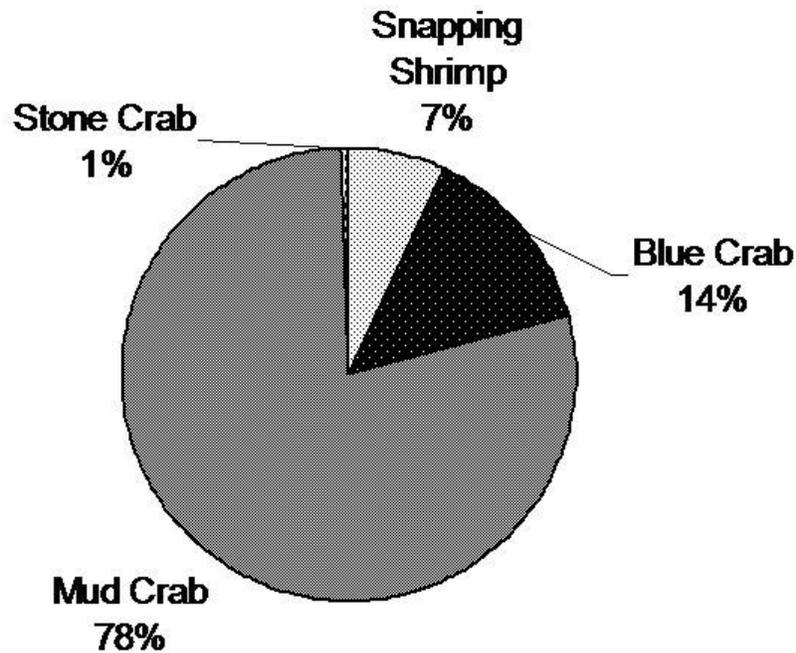


Figure 2.2: Percent abundance of intermediate predators collected in throw traps.

Oyster Predation Experiment

I found more oyster recruits in the cages than the cage controls, and I hypothesized that this could have resulted from either differential oyster recruitment into the cages due to the presence or absence of predators in the cages or from equal oyster recruitment in all treatments followed by different levels of consumption by predators. To test these hypotheses, I performed a mark and recovery experiment on pre-settled juvenile oysters that were protected with cages.

First, I purchased oyster larvae from a local supplier and settled them onto sun-bleached oyster shells. After the larvae settled, they were given ambient seawater and

allowed to grow until they reached ~ 2 mm in diameter. I then removed excess oyster larvae from each shell to reduce the number of juveniles to 10. These shells were then individually attached to rebar and deployed into existing oyster reefs in our study site. The rebar was pressed into the sediment so that the shells were at a similar height as other shells on the reef. I placed these shells in a block design with 4 treatments to correspond to the caging study: no cage (control), 1.0 cm² mesh cage (small) and 5.0 cm² mesh cage (large). Ten blocks were deployed so that treatments within blocks were ~ 5.0 m apart and blocks were ~ 100 m apart. The shells were recovered after 1 week, and the number of juvenile oysters remaining was counted and compared between caging treatments using a one-way blocked ANOVA with cage treatment as a fixed factor in the model and the group of four as the blocking factor (Sokal et al. 1995). Tukey-Kramer post hoc tests were used to make pairwise comparisons among treatments (Day & Quinn 1989).

Non Lethal Effects

I performed a field experiment to elucidate the non lethal effects of mud crabs on juvenile oysters. Preliminary work indicated that oysters would produce thicker shells and less soft tissue in the presence of mud crabs. I used juvenile oysters settled onto oyster shells as previously described and placed these juvenile oysters in the field in a cage near one of 3 treatments: a control with no mud crab predators, a treatment with two mud crabs, and a treatment with six mud crabs. This design permitted us to determine if oysters altered their morphology in the presence of mud crabs and if increasing the amount of predator cue produced greater morphological changes.

The mud crabs were caged on both sides of the cage containing the juvenile oysters to insure that the oysters received predator cues regardless of flow direction. Mud crabs

were fed weekly and any dead crabs replaced. The experiment lasted for 45 days since previous work indicated this time was sufficient to observe morphological changes in oysters.

After 45 days, the oysters were recovered and returned to Texas A & M University – Corpus Christi (TAMU-CC). Individual oysters were placed in a drying oven for 2 days at 90 °C and then weighed to the nearest 0.01 gram to determine total dry weight. The oysters were then transferred into a muffle furnace at baked at 500 °C for 2 hours and reweighed to determine the ash-free dry weight. I then divided the ash-free weight from the total dry weight to obtain a percent shell mass. This percentage represents the relative allocation of growth to shell vs. soft tissue and accounts for growth or size differences among individual oysters (Johnson and Smee *in press*, chapter 1). Higher percent shell mass indicate greater production of shell and less allocation of resources to tissue mass.

Percent shell mass was compared among controls and treatments using a one-way blocked ANOVA with number of mud crabs (0, 2, or 6) as the fixed factor in the model and the group of three as the blocking factor (Sokal et al. 1995). Tukey-Kramer post hoc tests were used to compare pairwise differences among treatments (Day & Quinn 1989).

RESULTS

Intermediate Predator Abundances

I was able to identify six species of intermediate predators that potentially could prey on oysters in our cage and control treatments (Table 2.1). I also found a large number of mud crabs that I were unable to identify to species level, but were small (< 8 mm carapace width) and equally distributed among the cage treatments (Table 2.1). With

the exception the Atlantic mud crab *P. herbstii*, the abundance of all potential oyster predators was not significantly different among cage treatments and controls.

Significantly more *P. herbstii* were present in the 5.0 cm² mesh cage than in the other treatments (Table 2.2), and the *P. herbstii* collected in all treatments were > 12 mm carapace width and clearly capable of consuming juvenile oysters. Snapping shrimp, blue crabs, and other mud crabs were small and did not appear to consume significant numbers of oysters in this experiment, and the abundance of these species could not account for differences in survival of newly settled oysters. The blocking factor was not significant ($F_{20,60}=1.48$, $P=0.12$, Fig. 2.3) and therefore not included in the ANOVA models for each species. The nonsignificant blocking factor indicates that these species are ubiquitous in this habitat.

Table 2.1: Intermediate predators' abundance and average size (mm) by treatments. The Atlantic Mud Crab column is highlighted because it is the only intermediate predator whose abundance was significantly different by treatment.

		Snapping Shrimp	Blue Crab	Stone Crab	Atlantic Mud Crab	Ridgeback Mud Crab	Flatback Mud Crab	Small Mud Crab
		<i>A heterochaelis</i>	<i>C sapidus</i>	<i>M mercenaria</i>	<i>P herbstii</i>	<i>P turgidus</i>	<i>E depressus</i>	<i>Xanthidae</i>
Control	#	77	186	1	5	171	2	656
	ave size	21.43	4.95	28.3	23.52	12.09	9.15	6.7
Small Mesh	#	170	222	11	12	268	39	1102
	ave size	21.88	5.6	14.49	23.92	12.5	13.17	7.23
Large Mesh	#	102	313	2	98	138	0	1298
	ave size	21.37	4.89	9.65	14.63	14.07		6.23
Total	#	349	721	14	115	577	41	3056
	ave size	21.56	5.15	17.48	20.69	12.89	11.16	6.72

Table 2.2: ANOVA table for intermediate predators by treatment. Only *P. Herbstii* was significantly different and is shaded in gray.

		DF	Error	F	p
Snapping Shrimp	<i>A heterochaelis</i>	2	48	2.8691	0.0665
Blue Crab	<i>C sapidus</i>	2	48	0.8173	0.4477
Stone Crab	<i>M mercenaria</i>	2	48	0.9215	0.4049
Atlantic Mud Crab	<i>P herbstii</i>	2	48	6.1091	0.0043
Ridgeback Mud Crab	<i>P turgidus</i>	2	48	2.6807	0.0788
Flatback Mud Crab	<i>E depressus</i>	2	48	1.2306	0.3012
Small Mud Crab	<i>Xanthidae</i>	2	48	0.9415	0.3971

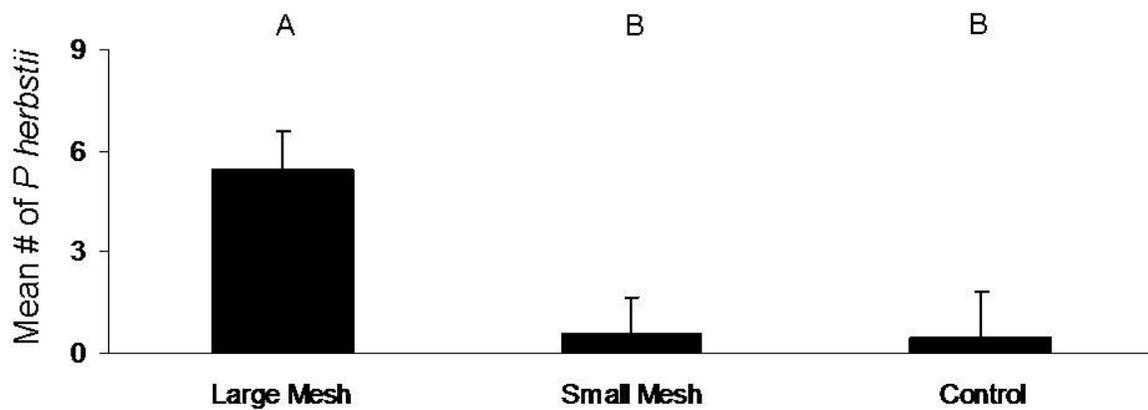


Figure 2.3: Mean abundance of *P. herbstii* (>10mm) ± SE by caging treatment. Error bars represent standard error and letters represent significant differences detected using a Tukey-Kramer post hoc test.

Natural Oyster Settlement and Survival

There were significantly more newly settled oysters in the 1.0 cm² mesh cages than the 5.0 cm² mesh cages and the controls ($F_{2,12} = 6.12$, $P = 0.015$, Fig. 2.4). The blocking factor was significant ($F_{2,12} = 6.01$, $P < 0.01$) and included in the ANOVA model, suggesting patchy settlement and survival of oysters across the study site. The number of surviving, newly settled oysters was not significantly different between controls and cages covered with 5.0 cm² mesh, and in this treatment significantly more *P. herbstii* were collected. This observation suggests that *P. herbstii* is the primary consumer of juvenile oysters at the intermediate trophic level and that they can consume oysters at a rate similar to that of the entire predator field.

Juvenile Oyster Predation

In a mark and recovery experiment, significantly more oysters remained after the experimental period in the 1.0 cm² mesh treatment compared to the other treatments ($F_{2,27} = 19.96$, $P < 0.0001$, Fig 2.5). This finding suggests that the higher oyster survival observed in the 1.0 cm² mesh cage treatment in the predator exclusion experiment resulted from a reduction in predation on newly settled oysters and not on preferential settlement in this treatment.

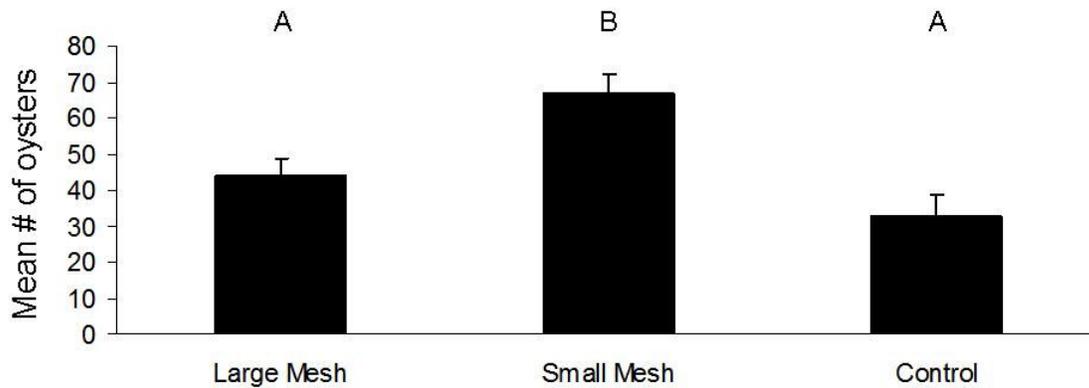


Figure 2.4: Mean abundance of naturally settled juvenile oysters \pm SE by caging treatment. Error bars represent standard error and letters represent significant differences detected using a Tukey-Kramer post hoc test.

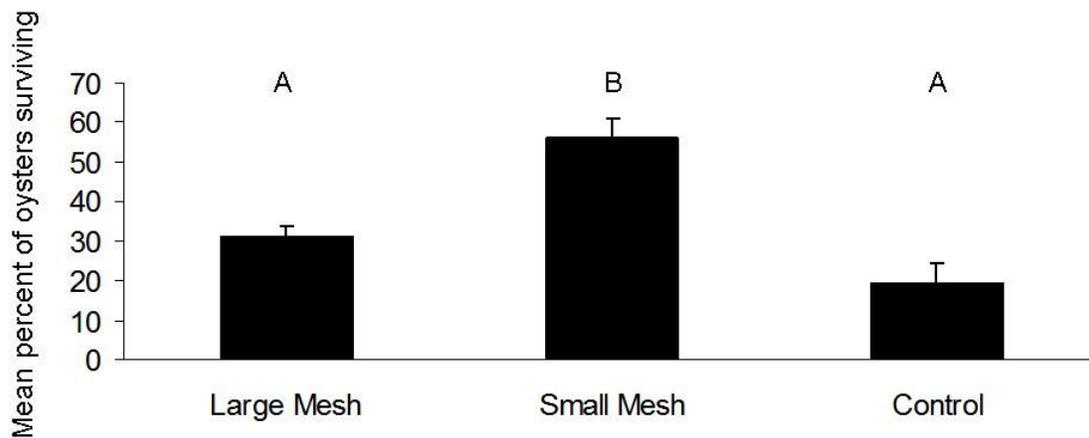


Figure 2.5: Mean percent of juvenile oysters that survived for a week \pm SE by caging treatment. Error bars represent standard error and letters represent significant differences detected using a Tukey-Kramer post hoc test.

Non lethal Effects of Mud Crabs on Juvenile Oysters

When caged near mud crabs in the field, oysters produced significantly more shell mass relative to overall mass as compared to controls ($F_{2,84} = 10.28$, $P < 0.001$, Fig. 2.6). I did not find a significant difference in treatments with 2 vs. 6 mud crabs.

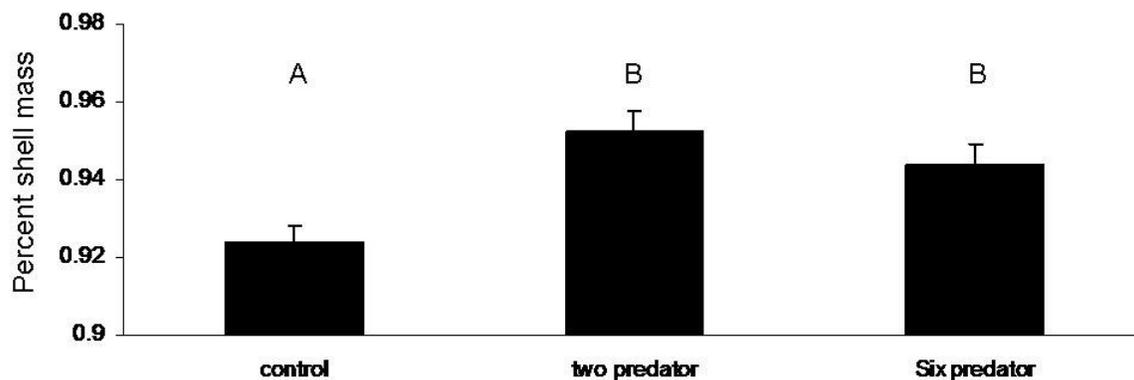


Figure 2.6: Mean percent shell mass \pm SE by treatment. Error bars represent standard error and letters represent significant differences detected using a Tukey-Kramer post hoc test.

DISCUSSION

Oyster populations have been declining in many areas, and it is estimated that oyster reefs have decreased 85% worldwide (Rothschild et al. 1994, Seavey et al. 2011). The abundance and diversity of higher-order consumers are declining in many systems (Jackson et al. 2001). Changes in predator abundance can contribute to declines in bivalve fisheries (Myers et al. 2007) and may also contribute to a decline in oyster populations (O'Connor et al. 2008) and in the ecosystem services oyster reefs provide (Grabowski and Peterson 2007).

In this study, I was able to ascertain how communities associated with oyster reefs would change when different sizes of predators were excluded. When all predators were excluded using a cage covered in mesh with 1.0 cm² openings, juvenile oysters experienced a significant increase in recruitment success (Fig. 2.4). Oyster survival was not significantly different between the 5.0 cm² mesh cage treatment and controls. The only oyster predator that was more abundant in the 5.0 cm² mesh cage than in controls was *P. herbstii* (Tables 2.1 and 2.2), suggesting that this mud crab can consume significant numbers of juvenile oysters when not controlled by higher-order consumers.

By reducing the density or altering the behavior of species in lower trophic levels, predators can induce trophic cascades and increase the abundance of producers or primary consumers (e.g., Estes and Palmisano 1974, Carpenter et al. 1985, Schmitz et al. 1997, Trussell et al. 2003). In this study, I noted a significant increase in *P. herbstii*, an intermediate predator that readily consumes oysters, and a decline in survival of newly settled oysters when this species was abundant. Yet, in control treatments, *P. herbstii* abundance was significantly lower than in 5.0 cm² cage treatments, but, the survival of newly settled oysters was not significantly different (Fig. 2.4). I attribute the reduced oyster survival in control treatments to a diverse array of predators including adult blue crabs (*Callinectes sapidus*), black drum (*Pogonias cromis*) and sheepshead (*Archosargus probatocephalus*) that feed on oysters and on intermediate predators like mud crabs. Tidal changes may also offer a refuge from predation and foraging opportunities for *P. herbstii* when low tides exclude the larger predators from the control treatment (Dittel et al. 1995).

A diverse predator assemblage can increase top-down forcing in communities when predators have complementary diets or facilitate one another or may decrease top-down forcing when predators interfere with one another (reviewed by Stachowicz et al. 2007). In diverse communities, consumers routinely feed at multiple trophic levels, which can dampen trophic cascades (Sih et al. 1998, Casula et al. 2006). Oyster survival increases in assemblages when toadfish (*Opsanus tau*) are present as the top predator and mud crabs (*P. herbstii*) are used as the intermediate consumer because toadfish consume mud crabs, which causes them to seek refuge and cease foraging (Grabowski 2004, Grabowski and Kimbro 2005). In contrast, when blue crabs are used in place of toadfish as the top predator, juvenile oyster survival is not positively affected because blue crabs consume both mud crabs and juvenile oysters (O’Conner et al. 2008). Thus, in oyster reef communities, predator identity and diversity can be important determinants of the magnitude and effects of top-down forcing (O’Conner et al. 2008), but, intermediate predators increase in the absence of higher-order consumers (Fig. 2.3).

Although some higher-order consumers such as blue crabs and sheepshead may consume oysters, they are likely to benefit juvenile oysters because they alleviate both the lethal and non lethal effects of mud crabs (Johnson and Smee *in press*, chapter 1). I found mud crabs to induce oysters to allocate more energy to shell growth than to tissue growth, which likely lowers their fitness (Fig. 2.6). As a resident species on oyster reefs, a persistent and abundant presence of mud crabs may have significant, long term effects on oyster fitness and population size via non lethal effects. In contrast, higher-order consumers that are likely to prey on both oysters and mud crabs are transient and may not be present for sufficient periods to induce morphological changes in oysters. Clearly

more work is required to assess how the type and diversity of predators as well as their transient or resident behavior influences top-down forcing via lethal and non lethal effects in this system.

I did not find significant differences in the number of small mud crabs, small blue crabs, and snapping shrimp among the different cage treatments and controls. Three possible explanations may account for this result. First, oyster reefs are complex habitats that provide many species with a predation refuge (Grabowski and Peterson 2007, (Grabowski 2004). Smaller animals may be able to hide within the reef matrix, and the oysters themselves act to minimize top-down forcing via providing an effective refuge. Second, crabs are cannibalistic (Moksnes et al. 1997, Ferner et al. 2005, Almeida et al. 2011), and when their abundances are high numbers in the absence of top-down forcing, smaller crabs may simply eat one another. Third, some of these species may not be affected by the exclusion of larger predators if they are not prey for the common larger predators found in this system.

I found significantly more juvenile oysters in the 1.0 cm² cage, and hypothesized that this increase resulted from either greater protection from predators or from preferential recruitment into this cage due to either cage artifacts or the absence of predators. Results from the mark and recovery experiment indicated that oyster survival was significantly greater in the smaller mesh cage (Fig. 2.5), suggesting that predation was responsible for differences in juvenile oyster abundance in the cage treatments.

Non lethal effects from the presence of mud crabs changed the resource allocation of juvenile oysters (Fig. 2.6), which may in turn change the reproductive output for the individuals and the oyster population. There were no significant differences in percentage

of new growth devoted to shell between the two mud crab treatment and the six mud crab treatment, and in an earlier field study, oysters responded to a single mud crab (Johnson and Smee *in press*, chapter 1). These findings suggest that individual mud crabs alter oyster growth patterns, and an increase in mud crab abundance likely increases the spatial non lethal effects they have on oysters (Turner & Montgomery 2003).

Exclusion treatments reveal possible community changes that may be attributed to the loss of the higher-order predators. If released from top-down control, mud crabs will increase in abundance and exert more predation pressure on juvenile oysters via lethal and non lethal interactions. The combination of the lethal and non lethal effects that are demonstrated on juvenile oysters in these experiments could be of concern for the future size and health of oyster populations and the habitat they provide. Understanding what the natural suite of intermediate predators include, their abundances, and the role they play in the oyster reef community will allow for proper conservation, management, and restoration projects. Future studies should examine the abundances of higher predators in the area and the projected changes in these abundances to determine the possible effect on future oyster populations via trophic cascades including lethal and non lethal effects.

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Chapter 3: Predation affects distribution patterns of oysters (*Crassostrea virginica*) across tidal zones

ABSTRACT

Biotic and abiotic conditions can separately and synergistically influence the presence, abundance, and distribution of species in time and space. In Corpus Christi Bay Texas, eastern oysters (*Crassostrea virginica*) are limited to intertidal habitats while in other areas of the Gulf of Mexico, including adjacent estuaries, oysters not only grow subtidally but thrive in these areas to the extent they are a viable commercially fishery. Previous work suggests that abiotic conditions, primarily hypoxia and salinity, as well as oyster disease limits oysters to intertidal areas. Yet, in Corpus Christi Bay, Texas, oysters are absent from subtidal areas where hypoxia is not known to occur. Disease, particular Dermo, is rampant among intertidal oysters making it unlikely to be a factor limiting oyster tidal distribution. I investigated oyster tidal distributions in this system by transplanting newly settled oysters into intertidal and subtidal areas. I found that predation on oysters was significantly greater in subtidal as compared to intertidal habitats and that oysters grew significantly more in subtidal areas and survival was higher when protected from consumers with a cage. These findings suggest that abiotic conditions and disease were not adversely affecting oysters in this area. Further, oysters in subtidal areas devoted significantly more growth to shell growth than did those in intertidal areas, and oysters are known to grow thicker shells in response to predators at a cost of lowering their fecundity. Abiotic conditions measured during the study did not exceed known tolerance limits for oysters. Earlier studies have shown abiotic conditions to influence oyster mortality and the success of restored oyster reefs, and these results,

along with those from this study, suggest that predators as well as abiotic factors can affect oyster distribution and must be evaluated when developing plans for oyster management and restoration.

INTRODUCTION

Classic models of community organization note that physical stress and consumers can have large effects on the spatial and temporal distribution of organisms (Menge and Sutherland 1987). Physical stress may include conditions that pose risk of injury or death, such as wave-energy that limits the abundance of mobile consumers on windward shores (Menge 1976), or conditions including salinity, temperature, or oxygen levels that exceed tolerance levels of sessile species (Menge and Olson 1990). Consumers may also affect the distribution of species by consuming them (Pawlik 1998) or by altering their habitat selection (Turner & Mittelbach 1990). The effects predators have on prey distribution may also be influenced by physical stress that either enhances or diminishes predator foraging ability and the ability of prey to detect and avoid consumers (Leonard et al. 1998, Smee et al. 2010). Abiotic conditions can also increase disease rates by imposing physiological stress increasing susceptibility of target organisms or by benefiting the disease causing organisms (La Peyre et al. 2009).

Oyster abundance and distribution can be influenced by predation, disease, and by stressful abiotic conditions including hypoxia and both excessively low and high salinity that are physiologically stressful and increase disease infection rates (Johnson et al. 2009, Pollack et al. 2011). Predation on both juvenile (newly settled) and adult oysters can be intense and limit oyster reef restoration (O'Beirn et al. 2000). Small, juvenile oysters are vulnerable to a suite of predators including various crabs, oyster drills, and fishes. For

example, mud crabs (*Xanthidae*) inhabit oyster reefs and readily consume newly settled oysters (Grabowski 2004). Oyster drills (*Stramonita haemastoma*) are a common predator of juvenile and adult oysters (Toscano & Griffen 2012) as are black drum (*Pogonias cromis*) (Brown et al. 2008). Predation from multiple predators at various trophic levels can affect juvenile oyster survival (Grabowski 2004, O'Connor et al. 2008) and be important for restoration of oyster reefs.

Besides predators, oyster distribution can be limited by abiotic factors such as dissolved oxygen, salinity, and temperature (Johnson et al. 2009). Hypoxia can cause mortality and reduce growth rates in oysters (Lenihan 1999) and in general is very detrimental to sessile animals (Widdows et al. 1989). Hypoxia can decrease oyster settlement, increase mortality (Baker & Mann 1992), and stunt juvenile oyster development (Baker & Mann 1994). Reduction of reef height from dredging may increase the incidence of hypoxia and length of hypoxic events on subtidal oyster reefs (Lenihan et al. 2001). Other abiotic factors like temperature and salinity have ranges within which oysters are able to survive and grow (Saoud et al. 2000), and high salinity can also increase the susceptibility of oysters to disease (Dermo) (Chu et al. 1993a). Dermo is caused by the protozoa *Perkinsus marinus* (Ray 1996) and infection rates are linked to high salinity and temperature (Powell et al. 1992, Chu & Lapeyre 1993, Chu et al. 1993b). In oysters, disease is often more prevalent in the warmer months when temperature and salinity are higher (Andrews 1988, Ewart 1993). In Texas, infection by *P. marinus* has recently been linked to reduced freshwater inflow and high salinity in some bay systems and has been suggested to limit oyster abundance and distribution (Culbertson et al. 2011a, Culbertson et al. 2011b, Pollack et al. 2012).

In Corpus Christi Bay, Texas, eastern oysters (*Crassostrea virginica*) are only found in intertidal habitats, but, in the northern Texas bays and throughout much of the Gulf of Mexico (GoM), oysters are commonly found in both intertidal and subtidal areas. Subtidal oysters are of sufficient abundance to be commercially harvested using oyster dredges and are an economically viable fishery in Texas and the GoM. In this study, I sought to examine the factors limiting oysters in Corpus Christi Bay to intertidal habitats. In addition to being a viable fishery, oysters provide numerous ecosystem services (Grabowski and Peterson 2007) and these services are lost when oyster populations decrease. Oyster reef habitats have declined by more than 85% worldwide, and there is considerable interest in understanding factors that contribute to oyster population decline as well as affect successfully establishment of new oyster habitats (Beck et al. 2011). In this study, I performed a transplant experiment and compared oyster mortality and growth in intertidal and subtidal areas of Corpus Christi Bay, Texas, while measuring abiotic conditions.

METHODS

Study Site

This experiment was conducted in East Flats, an area in the northeast corner of Corpus Christi Bay, near Port Aransas, Texas (Fig. 3.1). The reefs are bordered by salt marsh (*Spartina alterniflora*) and seagrass (*Halodule wrightii*, *Syringodium filiforme*, and *Thalassia testudinum*) habitats and are typical of oyster reefs in the general area. These reefs receive little freshwater input and the water is exchanged by tides (~ 0.5 m) through the nearby Port Aransas ship channel.

Oyster Larvae

I purchased oyster larvae from a local supplier and settled them onto sun-bleached oyster shells. After the larvae settled, they were given ambient seawater and allowed to grow until they reached ~ 2 mm in diameter. I then removed excess oyster larvae from each shell to reduce the number of juveniles to 10. These shells were then individually attached to rebar and deployed near existing oyster reefs in our study site. The rebar was pressed into the sediment so that the shells were at a similar height as other shells on natural reefs (~ 2.0 cm above the substrate).

Tidal Heights and Cage Treatments

I used predator exclusion cages to protect half of the shells with newly settled oysters to assess how oyster survival was affected by predators vs. other factors. Cages were made from vexar mesh (1.0 cm² openings), and were securely attached to the rebar pole so that they completely enclosed the shell containing the oyster spat. I placed these shells in a block design with 2 treatments: no cage (control) and 1.0 cm² mesh cage deployed at two tidal heights: subtidal and intertidal. Intertidal treatments were placed at ~MLLW, which was the lowest tidal elevation where oysters were naturally found. Subtidal treatments were placed 0.5 m from the intertidal treatments in the subtidal zone so that they were ~ 20-25 cm lower than the intertidal oyster reefs. Eight blocks (each containing 4 treatments: subtidal cage, subtidal control, intertidal cage, and intertidal control) were deployed so that treatments within blocks were ~ 0.5 m apart and blocks were separated by at least 50 m.

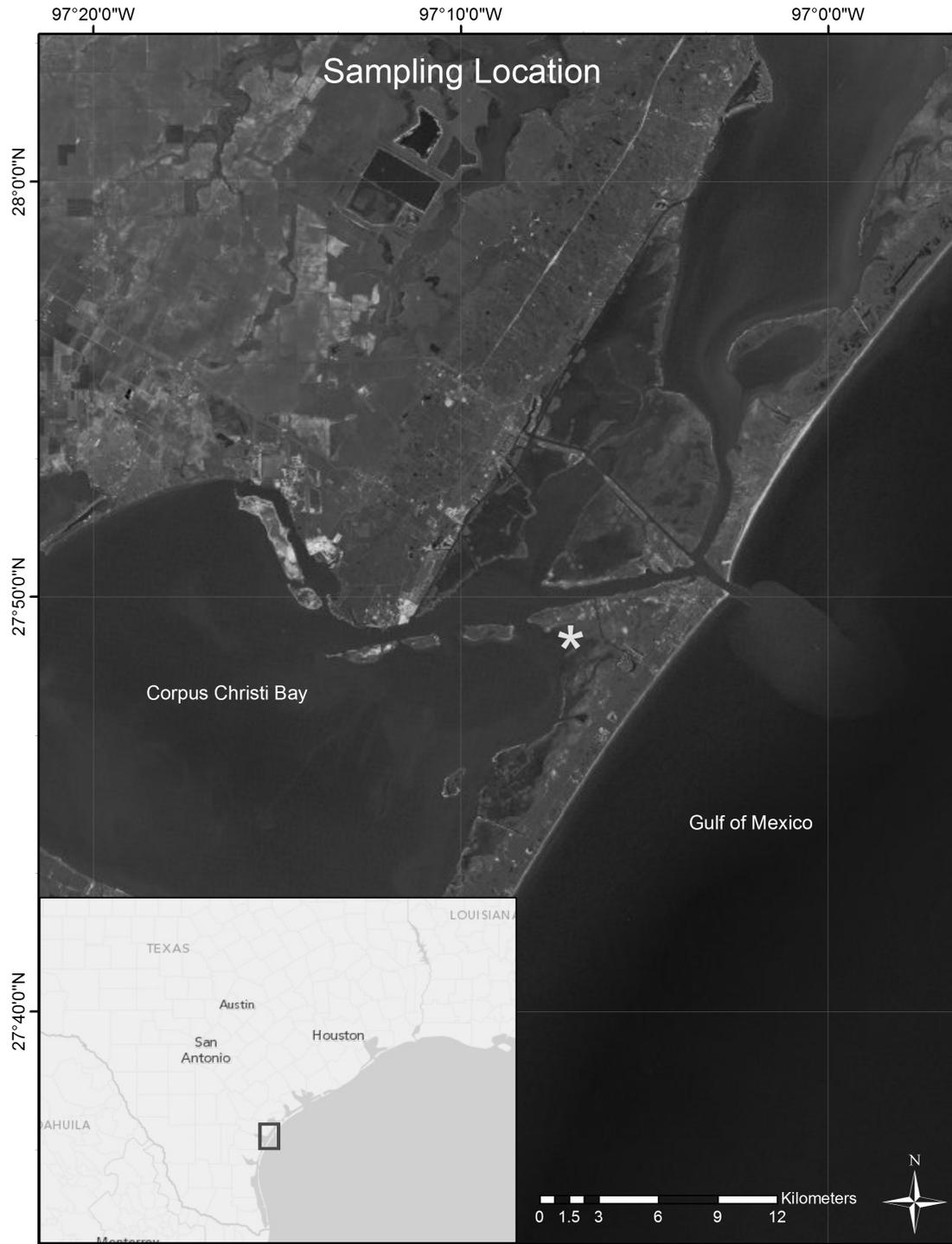


Figure 3.1: Map of the study location in East Flats (Corpus Christi Bay) near Port Aransas, Texas. The site is marked by an asterisk.

Oyster Survival

Oyster survival was measured after 70 days in the field by counting the number of living oyster spat remaining on each shell. Mortality data were compared between cage treatments and tidal heights using a blocked, two-way ANOVA with cage presence/absence and tidal elevation (intertidal or subtidal) as fixed, main effects and the site each experimental block was placed as the blocking factor (Sokal and Rohlf 1995). I found a significant interaction between the main effects and used a simple main effects test to compare pair wise differences among each cage treatment and tidal elevation combination (Kirk 1982).

Oyster Growth

After 70 days, all living oyster spat were returned to Texas A & M University – Corpus Christi (TAMU-CC). Individual oyster spat were placed in a drying oven for 48 hours at 90 °C and then weighed to the nearest 0.01 gram to determine total dry weight. The oyster spat were then burned in a muffle furnace at 500 °C for 2 hours and reweighed to determine ash-free dry weight. Mass was determined for both shell (ash-free dry weight) and tissue (dry weight – ash-free dry weight) for all samples. As with mortality, blocked, two-way ANOVAs were used to compare differences in tissue growth and shell growth using cage treatment and tidal elevation as fixed, main effects, and the site each experimental block was placed as the blocking factor (Sokal & Rohlf 1995). All of the oysters were spawned and settled at the same time and were the same size (~ 2 mm) when they were deployed allowing us to attribute differences in final weights to growth during the experiment. These analyses revealed that subtidal oysters grew significantly more than intertidal oysters and that the caging treatment did not affect growth.

Response to Predators

In addition to growth, I also quantified the percentage of new growth devoted to shell as oysters increase shell growth in response to predators (Newell et al. 2007, Lord & Whitlatch 2012, Johnson and Smee *In Press*, Chapter1) and performed a final analysis to compare resource allocation between oysters in intertidal vs. subtidal habitats. The metric was calculated by dividing the shell weight (ash-free dry weight) by the total dry weight and was compared between intertidal and subtidal habitats using an ANOVA (Sokal & Rohlf 1995).

Abiotic Conditions

Abiotic conditions including water temperature, salinity, and dissolved oxygen were measured during oyster deployment at both tidal heights using Hydolab DX5s Sondes. Data were collected continuously for 60 sec every hr at 1 Hz for 15 days (October 6-20, 2010) during the field experiment. Differences between each abiotic factor were compared using one-way ANOVAs with tidal elevation as the main effect (Sokal & Rohlf 1995).

RESULTS

Oyster Survival

I did not find a significant effect of tidal height ($F_{3,24} = .24$, $p = .6335$) or cage treatment ($F_{3,24} = 3.14$, $p = .0893$) on oyster survival, but did find a significant interaction between the main effects ($F_{3,24} = 5.08$, $p = 0.0336$, Fig. 3.2). The significant interaction term likely resulted because oyster survival increased in the caging treatments in subtidal areas but was not statistically different between cages and controls in the intertidal

habitat. Post hoc tests indicated oyster survival was highest in the subtidal area when protected by a cage, lowest in the subtidal area when not protected by a cage, and cage and control treatments in the intertidal area were not significantly different (Fig. 3.2). This suggests predators exerted a strong effect on oyster survival in subtidal areas but not intertidal ones.

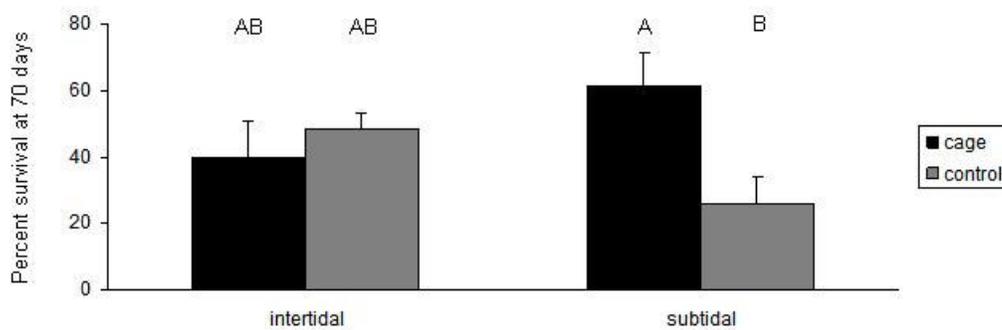


Figure 3.2: Mean oyster survival \pm SE for caged and uncaged juvenile oysters in subtidal and intertidal habitats. Letters represent significant pairwise differences based upon Tukey-Kramer post hoc analysis.

Oyster Growth

Oysters placed subtidally grew significantly more soft tissue than those placed in the intertidal zone ($F_{9,117} = 15.20$, $p < 0.001$, Fig. 3.3). I did not find significant differences in soft tissue growth between cage and control treatments ($F_{9,117} = 0.06$, $p = 0.81$) or a significant interaction between these factors ($F_{9,117} = 0.01$, $p = 0.95$). The mass of shell was also significantly higher for subtidal when compared to intertidal oysters ($F_{9,117} = 21.15$, $p < 0.001$, Fig. 3.3) but not different between the cage and control

treatments ($F_{9,117} = 0.01$, $p = 0.95$). The interaction between these factors was not significant ($F_{9,117} = 0.29$, $p = 0.59$).

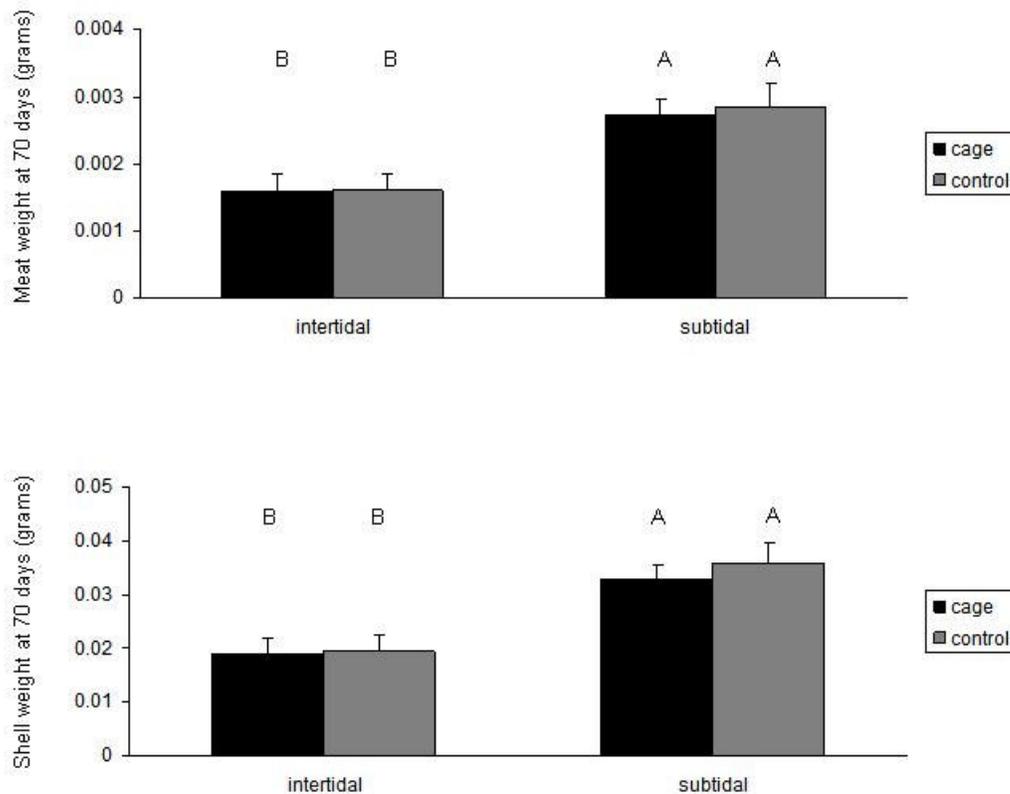


Figure 3.3: Mean tissue and shell weights \pm SE for caged and uncaged juvenile oysters after 70 days in subtidal or intertidal. Letters represent significant pairwise differences based upon Tukey-Kramer post hoc analysis.

Response to Predators

The percentage of new growth devoted to shell in the subtidal was significantly higher than intertidal oysters ($F_{9,117} = 4.83$, $p = 0.03$, Fig. 3.4). This higher rate of shell to total mass indicates a difference in allocation of resources between tidal heights.

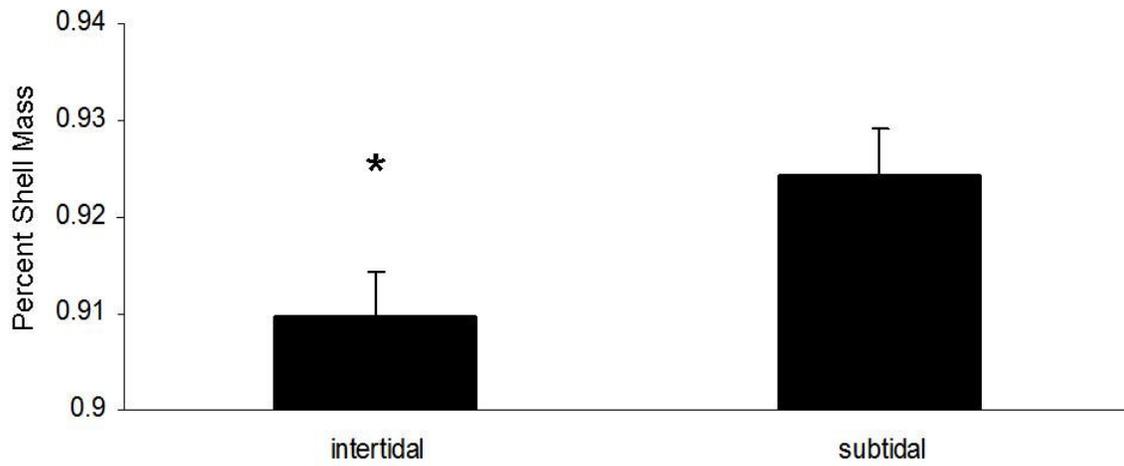


Figure 3.4: Mean percent shell mass \pm SE for intertidal and subtidal oysters after 70 days. The intertidal mean percent shell mass as significantly different from the subtidal (marked by *).

Abiotic Conditions

Abiotic measurements from subtidal and intertidal locations in the study site were significantly different for temperature ($F_{1,498} = 529.24$, $p < 0.0001$), salinity ($F_{1,498} = 351.69$, $p < 0.0001$), and DO ($F_{1,498} = 2143.83$, $p < 0.0001$, Table 1), but I did not observe any of the factors to be outside the tolerance range for eastern oysters.

Table 3.1: Abiotic measurements from East Flats.

Variable	Intertidal				Subtidal				Significant
	Mean	SD	Min	Max	Mean	SD	Min	Max	
Temperature (C°)	27.54	2.29	23.42	31.11	22.84	2.27	19.17	26.45	Yes, $P < 0.0001$
Salinity	35.66	3.62	22.23	38.06	41.65	3.52	21.06	43.27	Yes, $P < 0.0001$
Dissolved Oxygen (mg/l)	13.79	2.05	10.28	20.64	6.23	1.57	3.8	8.81	Yes, $P < 0.0001$

DISCUSSION

Distribution patterns can be driven by abiotic conditions as well as predators in different habitats (Menge & Sutherland 1987). In estuarine systems, hypoxia can affect the presence and distribution of organisms in some habitats (Jung & Houde 2003) while predators may control distribution patterns in other habitats by consuming prey (Pawlik 1998) or altering prey habitat selection (Turner & Mittelbach 1990). My results suggest that by consuming oysters, predators affect their distribution in Corpus Christi Bay, Texas, (Fig. 3.2) as well as the resource allocation of oysters in intertidal vs. subtidal areas (Figs. 3.3 & 3.4).

On subtidal oyster reefs, predation pressure can determine overall oyster abundance and distribution (Obeirn et al. 1995). Protection from predation using mesh bags or cages lowers predation on oysters (Obeirn et al. 1996, Bartol et al. 1999). In this study, oyster mortality was significantly lower in subtidal habitats when oysters were protected from consumers using cages while differences in oyster survival between cages and controls were not different in intertidal habitats (Fig. 3.2). Our cages were effective at excluding predators but would not have protected oysters from disease or from adverse abiotic conditions like hypoxia. Thus, higher survival in cage treatments indicates that predation on subtidal oysters is significant.

Oyster spat were able to survive and grow in subtidal areas, but, only when protected from consumers, suggesting that predators and not abiotic conditions restrict oysters to intertidal habitats in this area (Fig. 3.2). Numerous oyster predators including mud crabs, oyster drills, and black drum are abundant in Corpus Christi Bay, but oyster drills are the only resident predators restricted to subtidal areas (Brown & Stickle 2002).

Mud crabs are ubiquitous on oyster reefs at all tidal heights and are important intermediate consumers on oyster reefs and can affect restoration (Grabowski & Kimbro 2005, Hadley et al. 2010) and I collected mud crabs from both subtidal and intertidal reefs in this study site (Johnson unpublished data). Oyster drills are more abundant and forage more on subtidal oyster reefs, which can provide intertidal oysters with a refuge from predation (Brown & Stickle 2002). They also have higher growth rates and fecundity on subtidal oyster reefs (Brown et al. 2004). During the past 5 years, I have collected hundreds of oyster drills from this study site for behavioral experiments (e.g., Byron & Smee 2012), but I have never collected a single oyster drill on intertidal reefs. Thus, oyster drills are the most likely predators that prevent establishment of subtidal oyster reefs in Corpus Christi Bay.

Differences in growth (Moroney & Walker 1999) and survival have been well documented for subtidal and intertidal oysters in various regions of the United States (Roegner & Mann 1995). In general, subtidal oysters grow larger and faster than intertidal oysters because they spend more time underwater and feeding (Ingle & Dawson Jr 1952, Bishop & Peterson 2006). Our results are consistent with these findings as tissue and shell growth were significantly greater in subtidal oysters. Although subtidal oysters grew significantly more than intertidal oysters, they devoted a significantly greater portion of new growth to shell rather than to tissue (Fig. 3.4). Oysters are known to increase shell growth in the presence of blue crabs (Newell et al. 2007), oyster drills (Lord and Whitlatch 2011), and mud crabs (Johnson and Smee *In Press*, Chapter 1) to deter these consumers. But, increased shell growth results in lower tissue growth in bivalves and ultimately lower fecundity (Peterson 1986). The greater amount of relative

shell growth in subtidal oysters suggests a greater abundance of predators in this area (Fig. 3.4), which is consistent with our mortality results (Fig. 3.2).

The abiotic conditions in our study site were significantly different between subtidal and intertidal locations (Table 3.1), but they did not exceed levels that cause oyster mortality (Widdows et al. 1989). Further, oysters grew more and had higher survival in subtidal habitats when caged, suggesting that abiotic conditions are not responsible for limiting oyster distribution in our study site, even though they have been shown to contribute to oyster presence, abundance, and distribution in other locations (Baker & Mann 1992, Lenihan 1999, Johnson et al. 2009). Dermo (infection by *P. marinus*) is routinely high among existing intertidal oysters in Corpus Christi Bay (Reece et al. 2001, Ray 2012) and is known to slow oyster growth and cause mortality in oysters. Cages do not exclude disease, and thus disease is not a likely explanation for the absence of subtidal oysters given the higher growth and survival rate observed in cages when oysters were placed subtidal. In Corpus Christi Bay, the presence of predators, most likely oyster drills, in the subtidal zone, may explain why oysters only exist in the intertidal zone. Understanding what factors, biotic or abiotic, affect natural oyster distribution is very important for future reef restoration and conservation. Our results, along with that from previous studies (e.g., Lenihan et al. 1999, Johnson et al. 2009) suggest that both biotic and abiotic factors can influence oyster distribution and should be carefully evaluated before selecting areas for reef restoration or developing reef management and conservation plans.

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Chapter 4: Top-down forces and seasonal effects on oyster reef communities in Corpus Christi Bay, Texas

ABSTRACT

Oyster reef community structure can be strongly influenced by top-down forces. In simplest terms, large predators consume intermediate predators and alter their behavior, which alleviates predation pressure on juvenile oysters, the foundation species. Here, I examined how top-down forces change oyster reef communities when predators of different sizes are excluded over two seasons, spring and fall, using caging treatments with different mesh sizes. Cage mesh sizes used were 1.0 cm², 2.5 cm², 5.0 cm², and controls (no cage) to allow varying degrees of predator access to the experimental reefs. After three months in the field, I collected all of the species living on and around the oyster reefs for the caging treatments. I also examined ambient densities of predators from collections made by Texas Parks and Wildlife Department (TPWD). Together, these data sets suggest that larger predators were generally significantly more abundant in the spring compared to fall, and historical TPWD data revealed this pattern to be consistent over 10 years prior to and during our experiment 1998-2008. Despite the greater number of predators in the spring, I found top-down control had larger effects on communities in the fall. Crabs were more abundant in the fall compared to the spring and large mud crabs were significantly higher in some cage treatments. The higher abundance of large mud crabs may have been responsible for the significantly different number of juvenile oysters found between caging treatments. I then completed a mesocosm experiment to determine if predator diversity would influence top-down forcing and trophic cascades in this system by blue crabs, red drum, or both as top predators and examining the cascading

effects of these treatments on mud crab consumption of juvenile oysters. I found blue crabs to increase juvenile oyster survival, and together with results from the field experiment, suggest that blue crabs may be important higher-order consumers in this system and benefit juvenile oysters by controlling mud crab. Most species were more abundant in the spring, suggesting that recruitment may have greater effects on reef communities in the spring, and predation then greater effects on reef community structure in the fall.

INTRODUCTION

Many communities are structured by predation or top-down forces (Paine 1966, Estes & Palmisano 1974, Menge 2000, Trussel 2003) exerted on a community from either one species or a guild of consumers that control the populations at lower trophic levels. Predators may also affect abundance and distribution of organisms at several trophic levels by initiating trophic cascades (Carpenter et al. 1985). In general, trophic cascades occur when predators prey on intermediate consumers causing a reduction in consumer pressure on lower trophic levels. Although top-down forces are important community-structuring agents in terrestrial (Schmitz et al. 1997), freshwater (Carpenter et al. 1985) and marine systems (Paine 1966), the effects of biodiversity on community function remain unclear (Stachowicz et al. 2007). Specifically the relationships between temporal and spatial variation in consumer pressure and biodiversity have not been thoroughly tested (Stachowicz et al. 2007).

Top-down forces can be strongly affected by biodiversity, but these effects are often unpredictable and can either magnify or reduce the effects of predators in a given

community (Stachowicz et al. 2007). A diverse prey assemblage is more likely to contain one or more species resistant to certain predators that can thrive in the presence of consumers such that biomass at the prey level may remain unchanged when consumer pressure increases (Duffy 2003). Because the functional roles of prey vary, ecosystem processes could shift when prey species dominance is altered by consumers (Duffy 2003, Thebault & Loreau 2006). In general, a more diverse prey assemblage tends to reduce the effects of consumers in communities (Hillebrand & Cardinale 2004), although the effects of prey diversity vary greatly among systems and requires further investigation (Duffy et al. 2007, Stachowicz et al. 2007, Bruno & Cardinale 2008).

Predator diversity can increase or decrease the amount of top-down control depending upon the types of interactions among predators. For example, predator interference may alleviate predation pressure and increase the abundance of lower trophic levels while complementary foraging may increase predator effects (Long et al. 2007, Stachowicz et al. 2007). Bluegill and salamanders are both predators of isopods in lakes but predator interference lowers the expected predation on isopods when both predators are present because the salamanders seek forage to avoid the bluegill (Huang & Sih 1991). In contrast, complementary feeding occurs between herbivorous fish species that employ different feeding strategies on macroalgae in coral reef systems decreasing macroalgae coverage allowing more space for coral to grow (Burkepile & Hay 2008).

The loss of species can affect functioning of trophic groups (Cardinale et al. 2006) and the ecosystem services they provide (Worm et al. 2006) and may cause a trophic skew. Trophic skew is the shift of trophic structure with the loss or removal of certain species (Duffy 2003). The change in diversity and abundance (removal) of many of the

large predators in a system can indirectly impact the lower levels of the trophic system. In some systems this loss of resources creates a greater loss of biodiversity in the system through competition. Top-down control of a system is sometimes limited when environmental conditions (abiotic factors) prevent predators from foraging successfully (Menge & Sutherland 1987b). This can occur when physical conditions prevent predators from occupying a habitat, such as on windward shores (Menge & Sutherland 1987b) or when conditions compromise the ability of predators to forage (Weissburg & Zimmerfaust 1993, Leonard et al. 1998) or increase prey vulnerability to consumers (Smee & Weissburg 2006, Smee et al. 2008).

Using eastern oysters, *Crassostrea virginica*, and their diverse community as a model system, I examined how changes in consumer diversity would affect reef community structure. Oysters are an ideal model system for several reasons. First, they provide numerous ecosystem goods and services (reviewed by Grabowski 2007) and second, they are influenced strongly by top-down forces. Oysters are facilitating species and provide critical habitat for soft sediment organisms with structure for attachment and with protection from predators (Lenihan 1999, Breitburg et al. 2000, Jackson et al. 2001, Grabowski 2004, Tolley & Volety 2005). They filter water and improve water quality (Nelson et al. 2004) and protect the coast from storms and erosion. Oyster reefs also have a positive effect on commercial and sport fisheries (Breitburg et al. 2000) by providing a safe habitat for the juvenile fish (Peterson et al. 2003, Grabowski & Kimbro 2005, Stunz et al. 2010). Further, previous studies have shown that top-down forces can significantly affect the structure and function of oyster reefs (Lenihan et al. 2001, Grabowski & Kimbro 2005, O'Connor et al. 2008). While many studies have shown

predation by individual predators to strongly influence oyster reef communities, the present study addresses how predator diversity influences oyster reef communities. Mesocosm studies using oyster reefs as a model system have also noted strong effects of trophic cascades in higher-order interactions (Grabowski 2004, Grabowski and Kimbro 2005).

The presence of multiple predators can have varying effects on top-down forcing depending upon complex food web interactions such as complementary feeding, apparent competition, or predator interference. On oyster reefs, trophic cascades are dependent upon the top predator(s) present in a given system. For example, Grabowski (2004) created an oyster reef system using toadfish as a top-predator, which consumed mud crabs (*Panopeus herbstii*) an intermediate predator, which then consumed newly settled eastern oysters. Results from this study revealed strong positive effects on juvenile oysters from toadfish because this top predator both consumed mud crabs and caused mud crabs to remain in refuges and reduce their foraging time. Grabowski (2004) found that both lethal and non lethal effects of top predators were driving the trophic cascade in this system. Grabowski and Kimbro (2005) also noted that the consumption of mud crabs and the suppression of their foraging by toadfish also benefited juvenile hard clams *Mercenaria mercenaria*.

Later studies using field enclosures on oyster reefs revealed that the trophic cascade noted by Grabowski (2004) and Grabowski and Kimbro (2005) was dampened when blue crabs *Callinectes sapidus* were used as the top predator (O'Conner et al. 2008). Blue crabs are opportunistic predators that consume not only mud crabs, but also juvenile oysters, other bivalves, and themselves. Thus, the trophic cascade demonstrated

by Grabowski (2004) and Grabowski and Kimbro (2005) was strongly dependent on the predator species present. Moreover, O'Conner et al. (2008) manipulated the presence and absence of stone crabs (*Menippe mercenaria*) and mud crabs in addition to blue crabs and found that the effects of blue crabs on oyster reefs were stronger than either of the other predators, although some level of function redundancy between these predators was noted.

The purpose of this study was to understand how predator identity, abundance, and diversity structure natural communities. Using oyster reefs as a model system, I examined how exclusion of various sizes of consumers can change the diversity, species present, and abundances across multiple seasons. The exclusion of various sizes of predators, as well as the collection of all of the smaller species on the artificial reefs allowed the analysis of affect on the oyster reef communities. Our empirical data, coupled with ten-year data sets of gill net and trawl data in the area allowed us to examine how different predators affect oyster reef community structure. The changes in the communities when species are excluded may mimic what could happen if there are declines in some of the common larger predators that influence oyster reefs.

METHODS

These experiments were performed in Corpus Christi Bay near Port Aransas, Texas on intertidal oyster reefs (Fig. 4.1). The reefs are bordered by salt marsh and seagrass habitats and are typical of oyster reefs in the general area. These reefs receive little freshwater input and the water is exchanged by tidal changes (~ 0.5 m) through the

nearby Port Aransas ship channel. The average water temperature during the experiments was 28.6 °C and the average salinity was 31 as measured on the practical salinity scale.

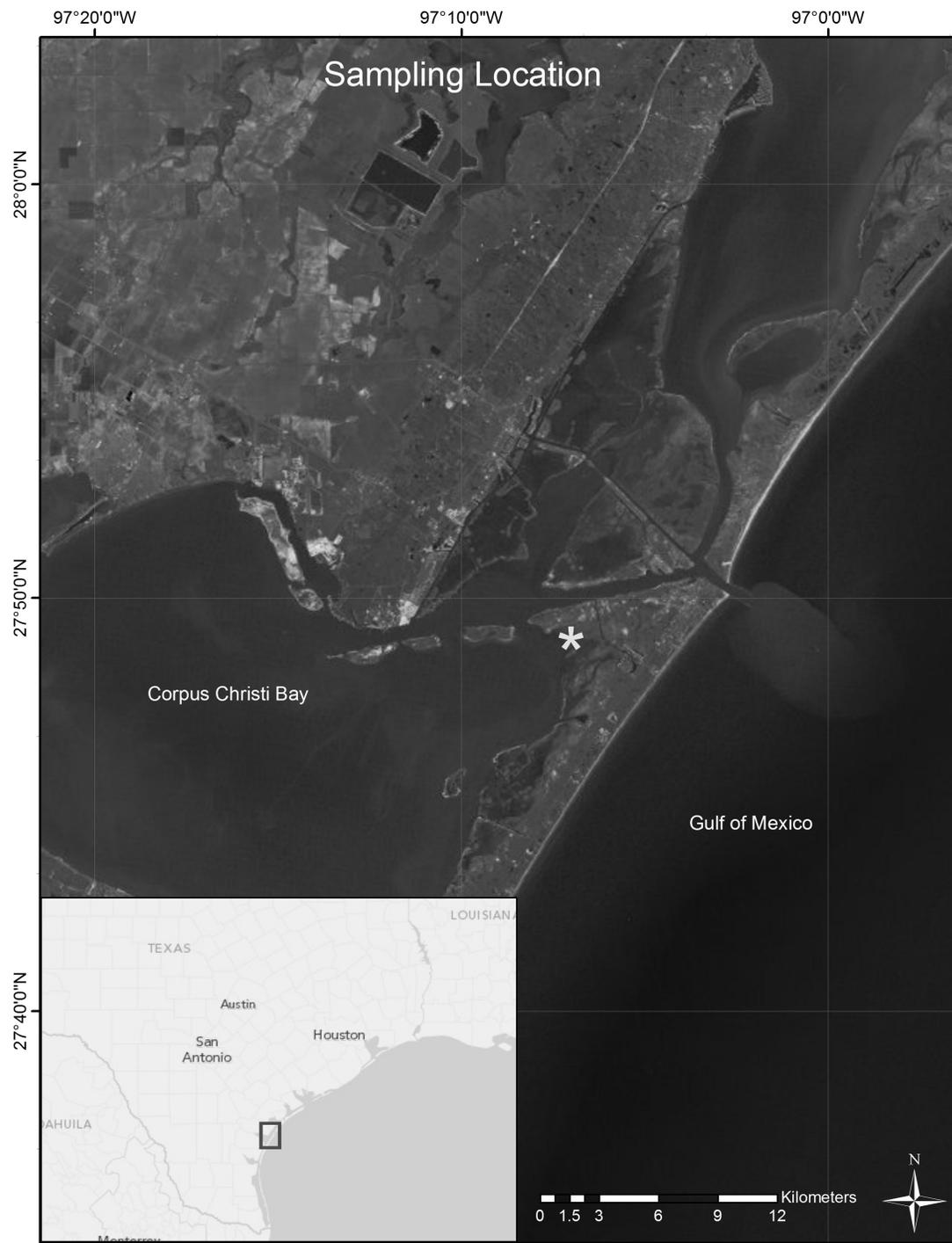


Figure 4.1: Map of study site in East Flats, Corpus Christi Bay, TX. The location of the research site is marked by *.

Cage Experiment

I used a predator exclusion experiment to ascertain how the absence of higher-order consumers would influence the prevalence of mud crabs and the settlement and survival of juvenile oysters. Predator exclusion cages were constructed from 2x2 lumber, were 1.0 m x 1.0 m x 0.25 m tall, and were completely covered with vexar mesh of one of three mesh sizes (1.0 cm², 2.5 cm², and 5.0 cm²) to exclude different sizes of predators (Fig. 4.2). I controlled for cage artifacts using a 2-sided cage. Preliminary data indicated that oyster recruitment and reef fauna collected in two-sided controls and control cages without sides were not significantly different, suggesting that the two-sided control is appropriate to control for caging artifacts. Cages with only two sides covered in mesh were used as controls, and I placed one cage control along with one cage covered with each mesh size in the field to create an experimental block of 4 treatments (3 cages + 1 control = 1 block). I placed 10 L of oyster shells into each cage and control to mimic the structural complexity of natural oyster reefs in the western Gulf of Mexico. Within blocks, cages or controls were spaced ~ 5.0 m apart and their placement relative to each other was randomly assigned. Blocks were separated by at least 100 m. Cages were anchored flush with the sediment using rebar. Cages were in the field from April-July 2008 and August – November 2008 to coincide with the two oyster settlement seasons.

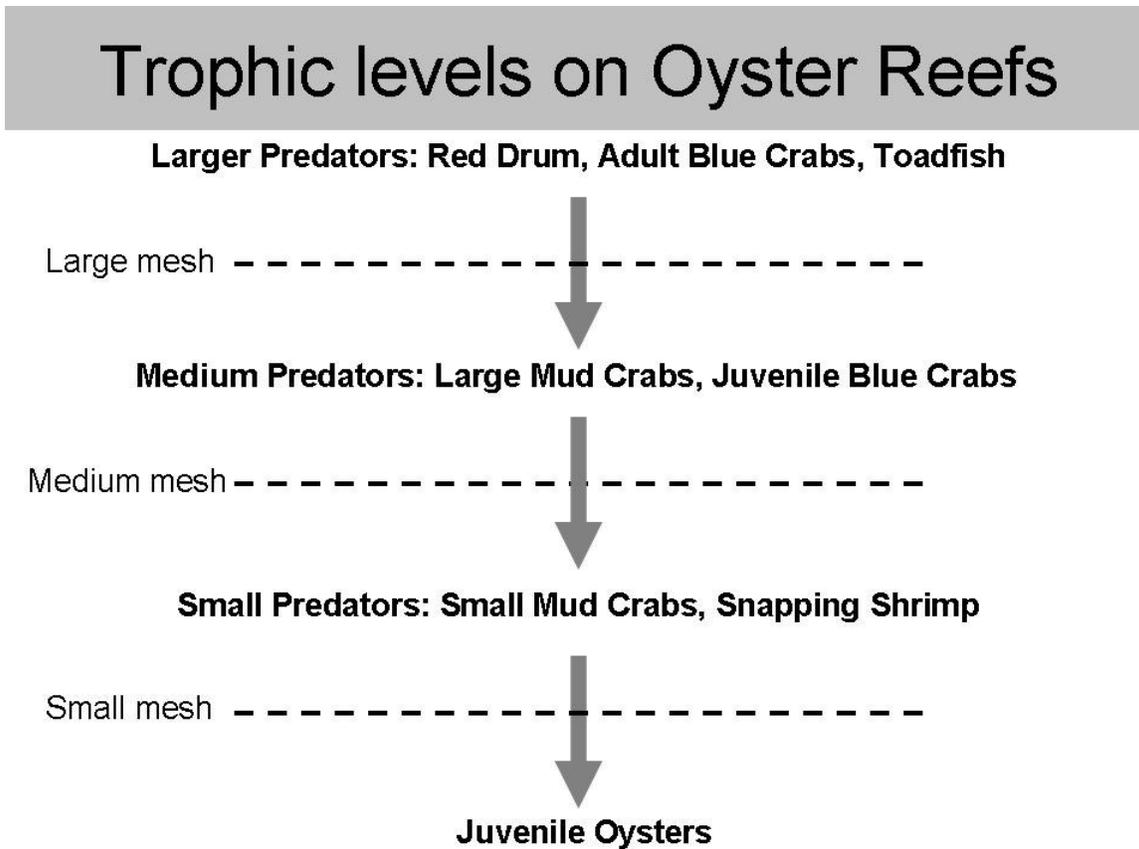


Figure 4.2: Diagram of species expected to be excluded by caging treatments.

In the oyster reef community there are larger, transient predators such as adult blue crab (*Callinectes sapidus*), red drum (*Sciaenops ocellatus*), black drum (*Pogonias cromis*), and sheepshead (*Archosargus probatocephalus*). These larger predators would be excluded by the large, medium and small mesh cage but would have access to the control. There is also a group of intermediate, resident predators in oyster reef communities including mud crabs, snapping shrimp, juvenile blue crab, and stone crabs. The intermediate predators would only be excluded from the small mesh cage while having access to the control and the larger mesh cage. The large and intermediate predators would all be excluded from the small mesh cage where the juvenile oysters are

free from predation pressure (Fig. 4.2). The large predators prey on the intermediate predators and some may feed on the juvenile oysters as well. Some of the intermediate predators prey on the juvenile oysters which are the foundation species in this system. The exclusion by size allows us to examine what occurs in the absence of different trophic levels in oyster reef communities. I expect to see an increase in abundance of intermediate predators in the large and medium mesh cage treatments which will decrease the number of juvenile oysters. I also expect that the small mesh cage treatment will exclude all predators (large and intermediate) and therefore have a higher abundance of surviving juvenile oysters. The control allows us to see what happens on natural reefs when all species have access to the reef.

At the conclusion of the cage deployment, the number of oyster recruits and other sessile species (e.g., mussels) were counted and the associated reef fauna collected using a throw trap (for detailed methods refer to Rozas & Minello 1997). The throw trap was constructed using 1.0 m² metal frame covered with fine mesh and fitted with a sharp metal skirt. Immediately prior to cage retrieval, I placed the throw trap over the cage and pressed it into the sediment to trap all mobile organisms in the sampler. I then removed the cage and jostled it in the water to dislodge mud crabs and other organisms and thoroughly searched the shells by hand and collected any remaining organisms. Then, I swept the throw trap with nets until all organisms were collected. After collection, organisms were placed in 10% formalin, and transported to the lab for sorting, identification, measurement, and enumeration. I also counted the number of oyster recruits that naturally settled on the shells. Since our treatments were deployed in the field in a block design, I were concerned that drop sampling could disturb other

treatments in the block. To account for this potential artifact, I used multiple throw traps so that all cages within a block were covered by a throw trap simultaneously.

The sample data on species was compared using PRIMER 6 to test for similarities and differences between seasons and treatments. The data was fourth root transformed and used in a Bray Curtis similarity matrix. Then multi-dimensional scaling (MDS) was used to examine differences for seasons (spring and fall) and caging treatments.

Diversity between treatments was calculated using PRIMER 6 to run Shannon-Weiner and Simpson indexes and JMP 9 was used to compare the diversity results between treatments in a one-way ANOVAs between caging treatments for spring and fall. Diversity scores were compared using a one-way blocked ANOVAs with cage treatment as the fixed factor in the model and the group of four as the blocking factor (Sokal et al. 1995). Tukey-Kramer post hoc tests were used to compare pairwise differences among treatments (Day & Quinn 1989).

A table of all species found in the spring samples with averages for each treatment as well as the percent of their group (shrimp, crab, fish, mollusk, and total) was created and one-way ANOVAs were using JMP 9 to look at differences for each species and group by treatment. Abundance of species collected were compared using a one-way blocked ANOVAs with cage treatment as the fixed factor in the model and the group of four as the blocking factor (Sokal et al. 1995).

A table of all species found in the fall samples with averages for each treatment as well as the percent of their group (shrimp, crab, fish, mollusk, and total) was created and one-way ANOVAs were preformed using JMP 9 to look at differences for each species and group by treatment. Abundance of species collected were compared using a one-way

blocked ANOVAs with cage treatment as the fixed factor in the model and the group of four as the blocking factor (Sokal et al. 1995).

Graphs of groups of species for spring and fall were also constructed to visually see how the exclusion of sizes of consumers changed the groups of species. The seasonal differences between fall and spring were compared for the control treatment and the total abundance for all species and groups.

Mud crabs were the most common intermediate predator collected and are known to be important predators of newly settled oysters and other bivalves (Fig. 4.2). Abundance of mud crabs and other intermediate predators collected were compared using a one-way blocked ANOVAs with cage treatment as the fixed factor in the model and the group of four as the blocking factor (Sokal et al. 1995). Tukey-Kramer post hoc tests were used to compare pairwise differences among treatments (Day & Quinn 1989). I divided mud crabs into two size classes: < 10 mm carapace width and > 10 mm carapace width and compared abundances of difference sizes as well as species for the larger mud crabs were compared using separate ANOVAs. Larger mud crabs are known predators of oysters and other bivalves while smaller ones did not consume juvenile oysters in preliminary experiments (Johnson and Smee *In Press*, Chapter 1).

In addition to intermediate predators, I counted the number of juvenile oysters (<10mm) that were found on the 10 L of shells in each treatment. The number of juvenile oysters per treatment was compared using a one-way blocked ANOVA with cage treatment as the fixed factor in the model and the group of four as the blocking factor (Sokal et al. 1995). Tukey-Kramer post hoc tests were used to compare pairwise differences among treatments (Day & Quinn 1989).

TPWD Dataset

The abundance of potential oyster reef predators in the study site was estimated using a ten-year data set from the Texas Parks and Wildlife Department (TPWD). TPWD used both gill net and trawl sampling in Corpus Christi Bay 1998-2008 for collections of resident fauna. The data sets were separated into spring and fall to compare with our sampling times. The gill nets used were 600 feet long and 4 feet deep with separate 150 foot sections of 3 and 4 inch (#12 monofilament), 5 and 6 inch (#18 monofilament) stretched mesh tied together in ascending mesh size. Gill nets were set out overnight with early morning retrieval during the spring and fall seasons. The spring season began in the second full week of April and extended for 10 weeks. The fall season began the second full week of September and extended for 10 weeks. Gill nets were set perpendicular to shore with the smallest mesh shoreward. Nets were set within one hour before sunset and retrieved within four hours after the following sunrise. The TPWD gillnet data was then compared between spring and fall in two-way ANOVA with year and season as factors in JMP 9.

The TPWD trawl sample data was collected was collected 20 times per month in Corpus Christi Bay. I used only the months that were used for the throw trap data and gill net data and split it into spring and fall. The TPWD trawl data was then compared between spring and fall in two-way ANOVA with year and season as factors in JMP 9. Abiotic data including DO, temp, etc. was measured by TPWD and during each trawl and the mean values from these parameters are reported.

Mesocosm Experiment

A mesocosm experiment was conducted at The Texas AgriLife Research Mariculture Laboratory in Port Aransas, TX to measure how the type and diversity of predators affect juvenile oyster survival through lethal and non lethal interactions. The experiment was rotated through 15, 2.25-m diameter tanks to avoid tank effects and allow for cleaning between experiments. The tanks were prepared with two artificial oyster reefs made from sun bleached shells. One reef was built inside a cage (the same as the small mesh treatment from the field experiment) and the second was placed onto tray. On each artificial reef, I placed two oyster shells with a combined 10 juvenile oysters. The juvenile oysters were settled in a separate tank with larvae purchased from a local supplier and allowed to grow until ~ 2 mm and then the number of spat on the shells was reduced for the experiment. There were 4 mud crabs (15-25 mm) tethered to each reef using super glue and fishing line. The treatments for the experiment included: a control (no large predators), 4 blue crab (12-13 cm), 2 red drum (50-65 cm) and 2 blue crab and 1 red drum. The experiment lasted for one week and the number of oysters remaining was recorded after 2 days and again after 7 days. The data was analyzed in a two-way ANOVA in JMP 9 with treatment and cage or control (tray) as factors.

RESULTS

Cage Experiment

MDS analysis in Primer indicated species differences between fall and spring data (Fig. 4.3). I therefore elected to analyze fall and spring samples separately for most of the following statistical analysis.

MDS Diagram

2008 Throw Trap Data

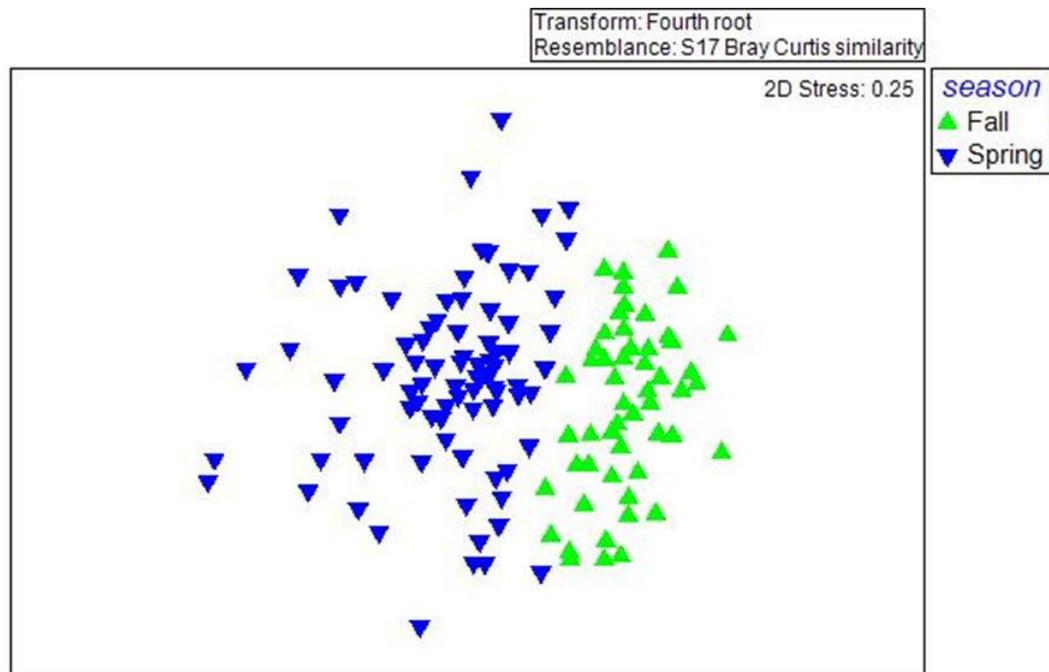


Figure 4.3: MDS diagram showing that fall and spring were different in community assemblage.

Species diversity between caging treatments were significantly different between cage treatments in fall but not in spring (Table 4.1). Post hoc analysis of both diversity indexes revealed that the small mesh cage had significantly lower diversity than the other cage treatments.

Table 4.1: Diversity averages for samples from fall and spring separated out by caging treatment with ANOVA F and p values and Tukey-Kramer post hoc test results.

Season	Sample	Index	Diversity	Tukey	F	p
Spring	2C	Simpson's	0.68	A	1.9435	0.1377
Spring	FL	Simpson's	0.67	A	1.9435	0.1377
Spring	FM	Simpson's	0.7	A	1.9435	0.1377
Spring	FS	Simpson's	0.72	A	1.9435	0.1377
Fall	2C	Simpson's	0.74	A	14.2384	<0.0001
Fall	FL	Simpson's	0.7	A	14.2384	<0.0001
Fall	FM	Simpson's	0.71	A	14.2384	<0.0001
Fall	FS	Simpson's	0.59	B	14.2384	<0.0001

Significant differences were not observed between the caging treatments for the groups of species in the spring, but some individual species were different by treatment in ANOVAs and post hoc analysis (Table 4.2). There were several species that were significantly different between caging treatments including: grass shrimp, ridgeback mud crabs, pinfish, and gastropods. Shrimp abundance was significantly different between caging treatments with higher abundances in the large and medium mesh cages as compared to control and small mesh cages. The total abundance of all organisms was not significantly different between caging treatments (Fig. 4.4).

Table 4.2: Spring 2008 – Throw trap data with caging treatment averages, total in all samples, percent of group (eg shrimp), and one-way ANOVA F and p values. Significant differences between treatments have bold p values. The treatments are the control (2C) and cages with large (FL), medium (FM) and small (FS) mesh sizes.

common name	scientific name	2C Ave	FL Ave	FM Ave	FS Ave	total	%	F	p
Grass shrimp	<i>Palaemonetes spp</i>	121.2	156.7	153.2	110.7	7971	93%	3.0	0.04
Arrow shrimp	<i>Tozeuma carolinense</i>	0.1	0.6	0.0	0.5	17	0%	1.1	0.36
White shrimp	<i>Litopenaeus setiferus</i>	0.0	1.5	0.0	0.0	21	0%	1.1	0.38
Brown / Pink shrimp	<i>Farfantepenaeus spp</i>	5.5	4.8	5.9	4.7	310	4%	0.4	0.76
Snapping shrimp	<i>Alpheus heterochaelis</i>	3.9	3.6	4.2	3.6	227	3%	0.3	0.83
penaeid shrimp	penaeidae	0.0	0.0	0.0	0.1	1	0%	1.0	0.41
shrimp total		130.7	167.3	163.3	119.6	8547	38%	3.0	0.04
Porcelain crab	<i>Petrolisthes galathinus</i>	0.0	0.0	0.1	0.0	2	0%	2.1	0.11
Longnose spider crab	<i>Libinia dubia</i>	0.0	0.1	0.0	0.0	2	0%	2.3	0.09
Blue crab	<i>Callinectes sapidus</i>	1.0	1.1	0.7	1.3	61	2%	0.7	0.56
Mud crabs (Xanthids)	xanthidae	58.5	52.5	53.2	47.8	3128	84%	0.5	0.68
Stone crab	<i>Menippe spp</i>	0.1	1.7	1.0	0.0	40	1%	2.2	0.10
Atlantic mud crab	<i>Panopeus herbstii</i>	0.3	0.5	0.5	0.3	24	1%	0.2	0.92
Ridgeback mud crab	<i>Panopeus turgidus</i>	6.1	2.4	2.9	6.7	269	7%	4.8	0.01
Thinstripe hermit crab	<i>Clibanarius vittatus</i>	1.9	1.5	1.7	2.5	112	3%	0.7	0.56
Hermit Crab	Paguroidea	0.0	2.2	2.1	0.3	68	2%	3.1	0.04
Hermit Crab	Paguroidea	0.0	0.0	0.2	0.0	3	0%	1.0	0.41
Hermit Crab	Paguroidea	0.1	0.0	0.0	0.1	2	0%	0.7	0.59
Dark shore crab	<i>Pachygrapsus gracilis</i>	0.1	0.0	0.0	0.3	6	0%	1.3	0.28
crab total		68.2	62.1	62.4	59.3	3717	17%	0.4	0.77
Atlantic needlefish	<i>Strongylura marina</i>	0.1	0.0	0.0	0.0	1	0%	1.0	0.41
Striped blenny	<i>Chasmodes bosquianus</i>	0.0	0.0	0.1	0.0	1	0%	1.0	0.41
Feather blenny	<i>Hypsoblennius hentz</i>	0.0	0.0	0.0	0.1	1	0%	1.0	0.41
Gulf menhaden	<i>Brevoortia patronus</i>	0.1	0.0	0.0	0.1	2	0%	0.7	0.59
Sheepshead minnow	<i>Cyprinodon variegatus</i>	0.0	0.0	0.1	0.0	1	0%	1.0	0.41
	<i>Eucinostomus</i>								
Spotfin mojarra	<i>argenteus</i>	0.1	0.1	0.0	0.1	5	0%	0.5	0.69
Skilletfish	<i>Gobiosox strumosus</i>	0.0	0.0	0.0	0.1	1	0%	1.0	0.41
Gobies (unknown)	Gobiidae	0.9	0.7	0.4	0.1	31	1%	1.1	0.37
Bathygobius sp.	<i>Bathygobius spp</i>	0.0	0.0	0.0	0.1	2	0%	2.1	0.11
Darter Goby	<i>Gobionellus boleosoma</i>	17.9	24.6	18.1	17.5	1146	50%	1.5	0.23
Naked goby	<i>Gobiosoma bosc</i>	0.1	0.6	0.7	0.1	22	1%	1.3	0.29
Code goby	<i>Gobiosoma robustum</i>	1.9	2.6	4.5	4.9	205	9%	0.9	0.45
Green goby	<i>Microgobius thalassinus</i>	0.0	0.0	0.1	0.0	1	0%	1.0	0.41
Lyre goby	<i>Evorthodus lyricus</i>	0.0	0.1	0.0	0.0	2	0%	2.3	0.09
Pigfish	<i>Orthopristis chrysoptera</i>	1.9	2.8	2.1	2.5	137	6%	0.2	0.92
Mangrove snapper	<i>Lutjanus griseus</i>	0.1	0.0	0.0	0.0	1	0%	1.0	0.41
	<i>Citharichthys</i>								
Bay whiff	<i>spilopterus</i>	0.0	0.1	0.0	0.0	1	0%	1.1	0.38
	<i>Paralichthys</i>								
Southern flounder	<i>lethostigma</i>	0.0	0.1	0.0	0.0	1	0%	1.1	0.38
Silver perch	<i>Bairdiella chrysoura</i>	0.3	0.4	0.2	1.0	29	1%	0.9	0.44

Spot	<i>Leiostomus xanthurus</i>	0.0	0.1	0.0	0.0	1	0%	1.1	0.38
Atlantic croaker	<i>Micropogonias undulatus</i>	0.0	0.1	0.0	0.0	1	0%	1.1	0.38
Sheepshead	<i>Archosargus probatocephalus</i>	0.1	0.0	0.0	0.0	1	0%	1.0	0.41
Pinfish	<i>Lagodon rhomboides</i>	4.2	5.3	11.0	9.3	441	19%	5.7	0.01
Pipefish	<i>Syngnathus spp</i>	0.1	0.3	0.1	0.0	7	0%	2.0	0.12
Gulf toadfish	<i>Opsanus beta</i>	4.5	3.9	3.6	2.6	214	9%	1.2	0.31
Longnose killifish	<i>Fundulus similis</i>	0.0	0.1	0.0	0.0	1	0%	1.1	0.38
Gulf killifish	<i>Fundulus grandis</i>	0.1	0.6	0.5	0.2	19	1%	0.9	0.44
Shrimp eel	<i>Ophichthus gomesii</i>	0.0	0.0	0.1	0.1	3	0%	1.2	0.31
fish total		32.3	42.3	41.5	38.7	2278	10%	1.2	0.33
adult oysters	<i>Crassostrea virginica</i>	45.3	43.3	46.0	47.1	2682		1.1	0.35
juvenile oysters	<i>Crassostrea virginica</i>	8.3	15.1	3.8	14.1	605	8%	0.8	0.48
slipper	<i>Crepidula fornicata</i>	17.9	19.3	24.9	17.1	1167	15%	1.4	0.25
drills	<i>Stramonita haemastoma</i>	0.0	1.6	0.0	0.0	23	0%	1.1	0.38
mussels	<i>Ischadium recurvum</i>	21.2	21.7	23.2	28.1	1392	18%	1.2	0.31
Gastropods		82.4	135.0	56.1	36.0	4508	58%	3.2	0.03
Bivalves		0.9	0.6	0.3	0.8	39	1%	1.3	0.28
mollusc total		130.7	193.4	108.3	96.1	7734	35%	2.2	0.10
grand total		5428.0	6510.0	5633.0	4705.0	22276		2.3	0.09

There were several species that were significantly different between caging treatments including: grass shrimp, ridgeback mud crabs, small mud crabs, hermit crabs, juvenile oysters, and toadfish (Table 4.3). The shrimp group was significantly higher while the crab group was significantly lower in the small mesh cage treatment. The total abundances were significantly different between caging treatments with the small mesh being significantly different from the control and large mesh in post hoc analysis (Fig. 4.5).

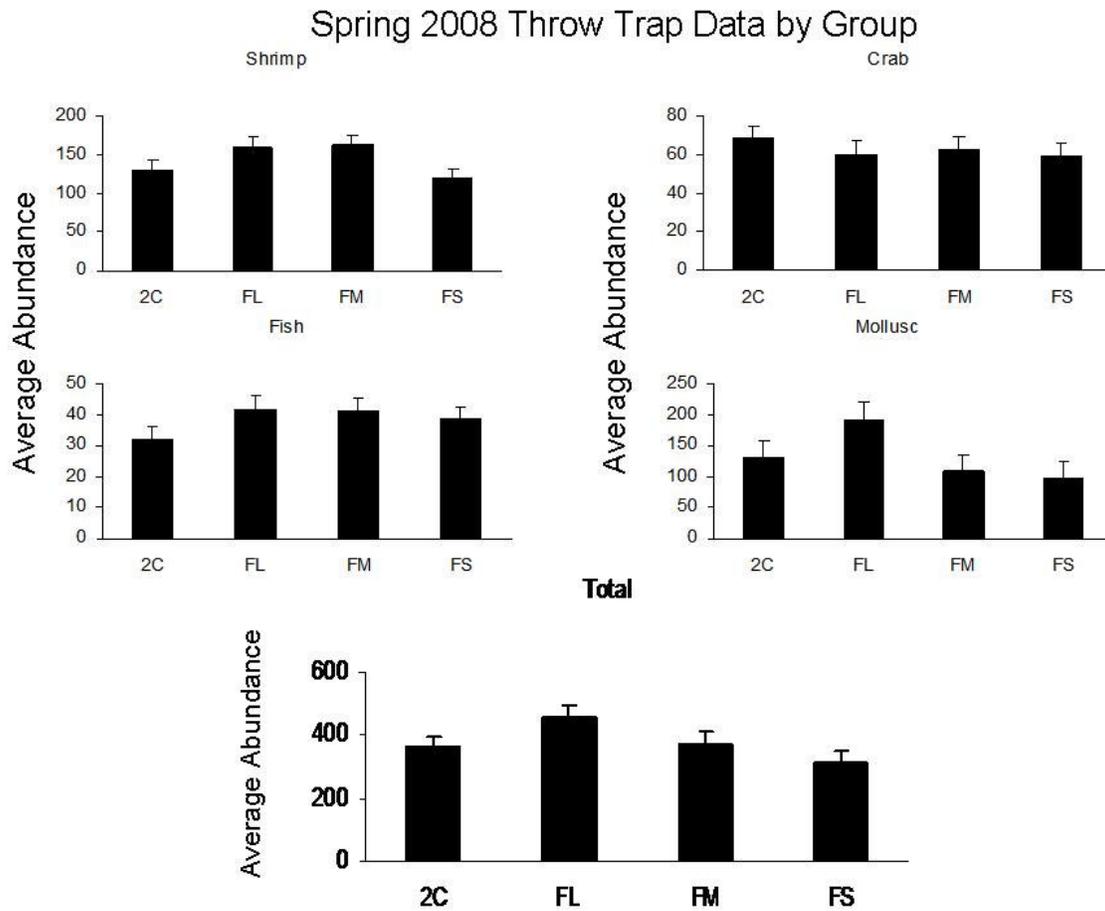


Figure 4.4: Graphs of spring throw trap data by groups and caging treatments. Tukey-Kramer post hoc test found no significant differences by caging treatment. The treatments are the control (2C) and cages with large (FL), medium (FM) and small (FS) mesh sizes.

Table 4.3: Fall 2008 – Throw trap data with caging treatment averages, total in all samples, percent of group (eg shrimp), and one-way ANOVA F and p values. Significant differences between treatments have bold p values. The treatments are the control (2C) and cages with large (FL), medium (FM) and small (FS) mesh sizes.

common name	scientific name	2C Ave	FL Ave	FM Ave	FS Ave	total	%	F	p
Grass shrimp	<i>Palaemonetes spp</i>	76.1	98.0	113.7	287.3	6825	91%	21.9	<0.0001
Arrow shrimp	<i>Tozeuma carolinense</i>	0.8	0.9	1.3	0.7	44	1%	0.6	0.63
White shrimp	<i>Litopenaeus setiferus</i>	0.0	0.1	0.0	0.1	2	0%	0.6	0.63
Brown / Pink shrimp	<i>Farfantepenaeus sp.</i>	2.0	1.1	0.6	1.9	65	0%	1.7	0.19
Mysid shrimp	Mysidae	0.1	0.0	0.0	0.1	2	0%	0.6	0.63
Mantis shrimp	Gonodactylidae	0.0	0.3	0.0	0.0	3	0%	1.0	0.40
Snapping shrimp	<i>Alpheus heterochaelis</i>	12.1	8.3	13.2	9.8	508	7%	3.3	0.04
penaeid shrimp	penaeidae	0.1	0.5	0.9	0.3	21	0%	1.2	0.33
shrimp total		91.2	109.1	129.7	300.2	7470	35%	21.3	<0.0001
Porcelain crab	<i>Petrolisthes galathinus</i>	0.6	3.5	3.7	1.3	108	2%	1.6	0.21
Blue crab	<i>Callinectes sapidus</i>	39.3	26.1	25.0	14.8	1222	17%	2.4	0.09
Mud crabs (Xanthids)	Xanthidae	107.7	95.7	127.3	64.3	4632	66%	3.4	0.03
Stone crab	<i>Menippe spp</i>	0.9	0.1	0.3	0.5	20	0%	0.6	0.59
Atlantic mud crab	<i>Panopeus herbstii</i>	1.8	3.8	2.9	0.8	109	2%	0.9	0.46
Ridgeback mud crab	<i>Panopeus turgidus</i>	15.9	6.5	7.5	15.7	531	8%	3.0	0.05
Thinstripe hermit crab	<i>Clibanarius vittatus</i>	6.4	1.9	12.1	5.6	305	4%	4.1	0.01
Hermit Crab		2.6	3.6	0.6	1.3	94	1%	0.7	0.54
Flatback mud crab	<i>Eurypanopeus depressus</i>	0.0	0.0	0.0	0.0	0	0%	0.0	0.00
Dark shore crab	<i>Pachygrapsus gracilis</i>	0.2	0.2	0.0	0.1	5	0%	0.3	0.79
Gulf Stone Crab	<i>Menippe adina</i>	0.0	0.0	1.0	0.1	13	0%	0.9	0.43
crab total		175.5	141.3	180.3	104.3	7039	33%	4.4	0.01
Striped blenny	<i>Chasmodes bosquianus</i>	0.0	0.0	0.1	0.0	1	0%	1.0	0.43
Blackcheek tonguefish	<i>Symphurus plagiusa</i>	0.0	0.0	0.0	0.1	1	0%	1.0	0.43
Spotfin mojarra	<i>Eucinostomus argenteus</i>	1.8	2.3	2.0	1.2	85	7%	0.2	0.92
Gobies (unknown)	Gobiidae	0.0	1.1	1.4	0.0	30	3%	1.2	0.34
Darter Goby	<i>Gobionellus boleosoma</i>	19.6	14.2	13.9	17.1	758	65%	0.6	0.64
Naked goby	<i>Gobiosoma bosc</i>	0.3	0.4	0.4	0.5	19	2%	0.1	0.94
Code goby	<i>Gobiosoma robustum</i>	0.2	0.3	0.1	0.3	9	1%	0.2	0.86
Green goby	<i>Microgobius thalassinus</i>	0.0	0.0	0.1	0.2	3	0%	0.7	0.59
Lyre goby	<i>Evorthodus lyricus</i>	0.5	0.1	0.3	0.9	22	2%	2.2	0.10
Mangrove snapper	<i>Lutjanus griseus</i>	0.1	0.2	0.3	0.2	8	1%	0.2	0.87
Bay whiff	<i>Citharichthys spilopterus</i>	0.1	0.0	0.1	0.0	2	0%	0.6	0.63
Spotted seatrout	<i>Cynoscion nebulosus</i>	0.0	0.0	0.1	0.0	1	0%	1.0	0.43

Red drum	<i>Sciaenops ocellatus</i>	0.0	0.0	0.0	0.3	3	0%	1.7	0.18
Barb fish	<i>Scorpena brasiliensis</i>	0.0	0.0	0.0	0.1	1	0%	1.0	0.43
Pinfish	<i>Lagodon rhomboides</i>	2.7	1.7	3.0	1.8	108	9%	0.4	0.75
Pipefish	<i>Syngnathus spp</i>	0.1	0.0	0.1	0.1	3	0%	0.4	0.78
Gulf toadfish	<i>Opsanus beta</i>	2.9	1.9	2.9	1.3	105	9%	3.4	0.03
Emerald sleeper	<i>Erotelis smaragdus</i>	0.0	0.0	0.0	0.0	0	0%	0.0	0.00
fish total		28.4	22.0	24.8	23.8	1159	5%	0.5	0.71
adult oysters	<i>Crassostrea virginica</i>	0.7	8.0	1.3	0.8	40		1.9	0.16
juvenile oysters	<i>Crassostrea virginica</i>	29.5	33.6	43.8	49.3	1843	31%	5.7	0.00
slipper	<i>Crepidula fornicata</i>	7.5	8.8	11.5	9.5	441	7%	2.4	0.09
mussels	<i>Ischadium recurvum</i>	0.9	0.4	2.0	1.5	57	1%	1.8	0.17
Gastropods		81.7	77.6	75.0	65.8	3519	60%	0.3	0.83
Bivalves		0.5	0.3	1.2	1.0	35	1%	1.1	0.26
mollusc total		120.1	120.8	133.4	127.0	5895	27%	0.1	0.93
grand total		4566.0	4717.0	5617.0	6663.0	21563		4.4	0.01

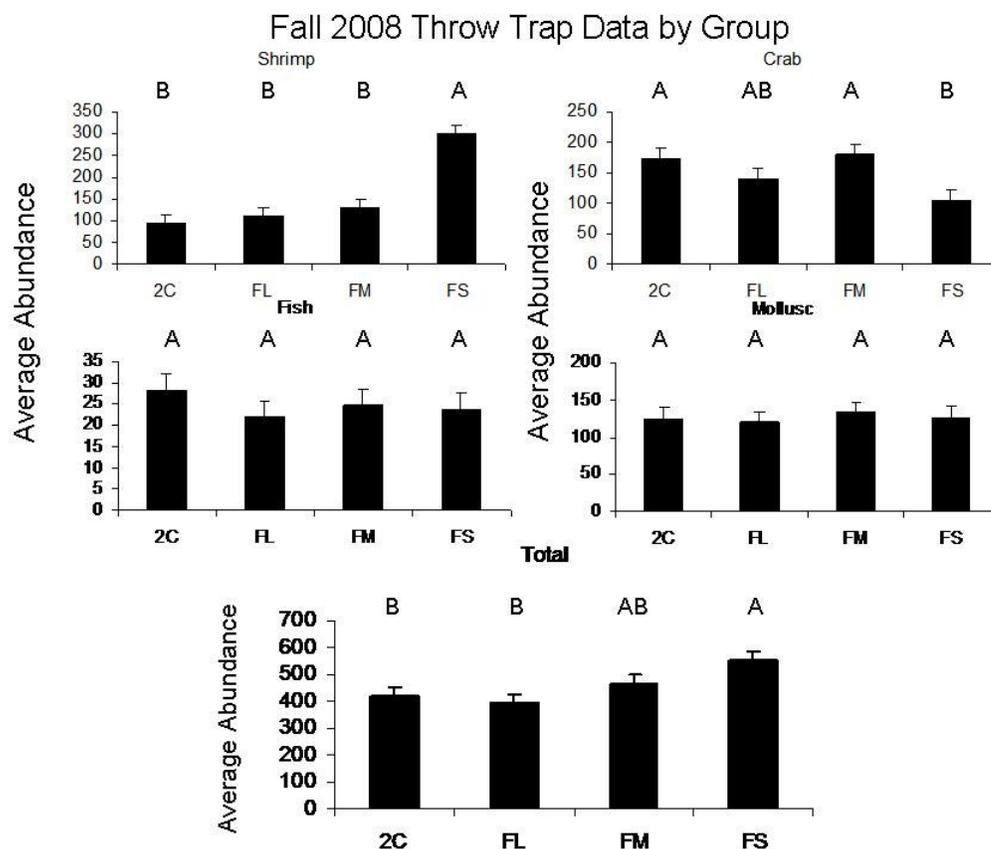


Figure 4.5: Graphs of fall throw trap data by groups and caging treatments. Tukey-Kramer post hoc test for significant differences by caging treatments from ANOVAs marked by letters for each group. The treatments are the control (2C) and cages with large (FL), medium (FM) and small (FS) mesh sizes.

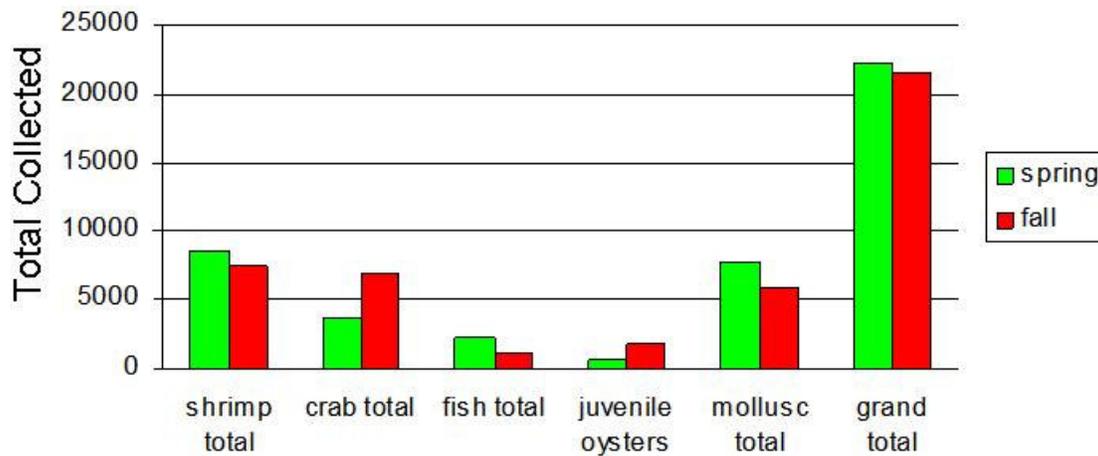
Comparing fall and spring for average abundance in the control treatment and the total in all treatments demonstrated a few species that exist in only one season but they were usually in small amounts (Table 4.4). Groups of types for spring and fall had differences by season with more shrimp, fish, and mollusks in the spring and more crabs and oysters in the fall, but the grand totals for spring and fall were very similar (Fig. 4.6). This was further examined by separating the cage treatments for each season and group (Fig. 4.6). The total abundance of crabs was then compared to the juvenile oysters for the caging treatments and seasons with higher total crab abundance and juvenile oysters in the fall (Fig. 4.7). I wanted to further look at the possible connection between crabs and juvenile oysters so I focused on the larger mud crabs that prey on juvenile oysters.

Table 4.4: Spring and fall averages for control cage treatments and total abundances.

common name	scientific name	spring 2C Ave	Spring total	Fall 2C Ave	Fall total
Grass shrimp	<i>Palaemonetes spp</i>	121.20	7971	76.09	6825
Arrow shrimp	<i>Tozeuma carolinense</i>	0.07	17	0.82	44
White shrimp (<i>Litopenaeus setiferus</i>	0.00	21	0.00	2
Brown / Pink shrimp	<i>Farfantepenaeus spp.</i>	5.53	310	2.00	65
Mysid shrimp	Mysidae	0.00	0	0.09	2
Mantis shrimp	Gonodactylidae	0.00	0	0.00	3
Snapping shrimp	<i>Alpheus heterochaelis</i>	3.93	227	12.09	508
penaeid shrimp	penaeidae	0.00	1	0.09	21
shrimp total		130.73	8547	91.18	7470
Porcelain crab	<i>Petrolisthes galathinus</i>	0.00	2	0.64	108
Longnose spider crab	<i>Libinia dubia</i>	0.00	2	0.00	0
Blue crab	<i>Callinectes sapidus</i>	1.00	61	39.27	1222
Mud crabs (Xanthids)	Xanthidae	58.53	3128	107.73	4632
Stone crab	<i>Menippe spp</i>	0.07	40	0.91	20
Atlantic mud crab	<i>Panopeus herbstii</i>	0.33	24	1.82	109
Ridgeback mud crab	<i>Panopeus turgidus</i>	6.13	269	15.91	531
Thinstripe hermit crab	<i>Clibanarius vittatus</i>	1.93	112	6.36	305
Hermit Crab	Paguroidea	0.00	68	2.64	94
Hermit Crab	Paguroidea	0.00	3	0.00	0
Hermit Crab	Paguroidea	0.07	2	0.00	0
Dark shore crab	<i>Pachygrapsus gracilis</i>	0.13	6	0.18	5

Gulf Stone Crab	<i>Menippe adina</i>	0.00	0	0.00	13
crab total		68.20	3717	175.45	7039
Atlantic needlefish	<i>Strongylura marina</i>	0.07	1	0.00	0
Striped blenny	<i>Chasmodes bosquianus</i>	0.00	1	0.00	1
Feather blenny	<i>Hypsoblennius hentz</i>	0.00	1	0.00	0
Gulf menhaden	<i>Brevoortia patronus</i>	0.07	2	0.00	0
Sheepshead minnow	<i>Cyprinodon variegatus</i>	0.00	1	0.00	0
Blackcheek tonguefish	<i>Symphurus plagiusa</i>	0.00	0	0.00	1
Spotfin mojarra	<i>Eucinostomus argenteus</i>	0.13	5	1.82	85
Skilletfish	<i>Gobiesox strumosus</i>	0.00	1	0.00	0
Gobies (unknown)	Gobiidae	0.93	31	0.00	30
Bathygobius sp.	<i>Bathygobius spp</i>	0.00	2		
Darter Goby	<i>Gobionellus boleosoma</i>	17.87	1146	19.64	758
Naked goby	<i>Gobiosoma bosc</i>	0.07	22	0.27	19
Code goby	<i>Gobiosoma robustum</i>	1.87	205	0.18	9
Green goby	<i>Microgobius thalassinus</i>	0.00	1	0.00	3
Lyre goby	<i>Evorthodus lyricus</i>	0.00	2	0.55	22
Pigfish	<i>Orthopristis chrysoptera</i>	1.93	137	0.00	0
Mangrove snapper	<i>Lutjanus griseus</i>	0.07	1	0.09	8
Bay whiff	<i>Citharichthys spilopterus</i>	0.00	1	0.09	2
Spotted seatrout	<i>Cynoscion nebulosus</i>	0.00	0	0.00	1
Red drum	<i>Sciaenops ocellatus</i>	0.00	0	0.00	3
Barb fish	<i>Scorpena brasiliensis</i>	0.00	0	0.00	1
Southern flounder	<i>Paralichthys lethostigma</i>	0.00	1	0.00	0
Silver perch	<i>Bairdiella chrysoura</i>	0.33	29	0.00	0
Spot	<i>Leiostomus xanthurus</i>	0.00	1	0.00	0
Atlantic croaker	<i>Micropogonias undulatus</i>	0.00	1	0.00	0
Sheepshead	<i>Archosargus probatocephalus</i>	0.07	1	0.00	0
Pinfish	<i>Lagodon rhomboides</i>	4.20	441	2.73	108
Pipefish	<i>Syngnathus spp</i>	0.13	7	0.09	3
Gulf toadfish	<i>Opsanus beta</i>	4.47	214	2.91	105
Emerald sleeper	<i>Erotelis smaragdus</i>	0.00	0	0.00	0
Longnose killifish	<i>Fundulus similis</i>	0.00	1	0.00	0
Gulf killifish	<i>Fundulus grandis</i>	0.07	19	0.00	0
Shrimp eel	<i>Ophichthus gomesii</i>	0.00	3	0.00	0
fish total		32.27	2278	28.36	1159
adult oysters	<i>Crassostrea virginica</i>	45.27	2682	0.73	40
juvenile oysters	<i>Crassostrea virginica</i>	8.33	605	29.45	1843
slipper	<i>Crepidula fornicata</i>	17.87	1167	7.55	441
drills	<i>Stramonita haemastoma</i>	0.00	23	0.00	0
mussels	<i>Ischadium recurvum</i>	21.20	1392	0.91	57
Gastropods		82.40	4508	81.73	3519
Bivalves		0.87	39	0.45	35
mollusc total		130.67	7734	120.09	5895
grand total		5428	22276	4566	21563

2008 Throw Trap Data Totals by Season



2008 Throw Trap Data by Season and Caging Treatment

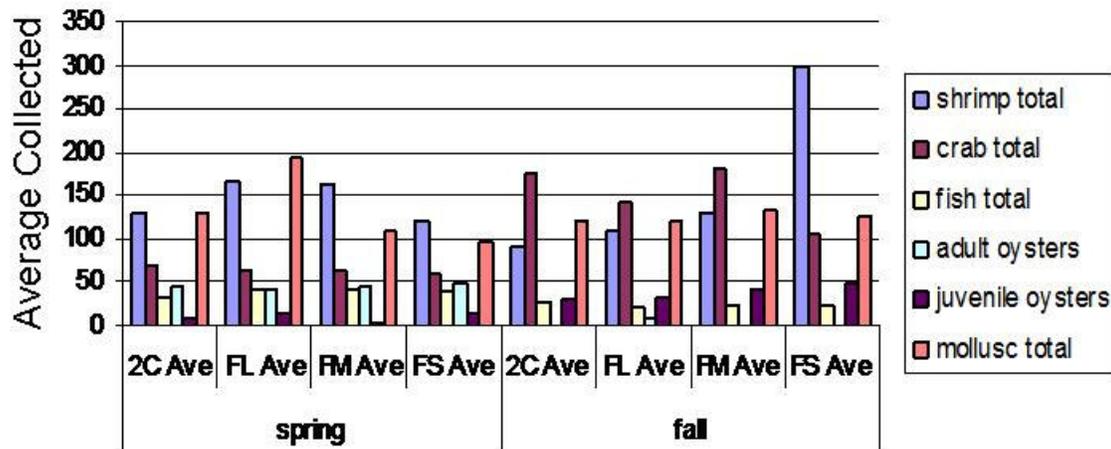


Figure 4.6: 2008 throw trap data with spring and fall groups compared. 2008 drop sampling data with spring and fall groups compared with caging treatments.

2008 Throw Trap Data Juvenile Oyster vs Total Crabs

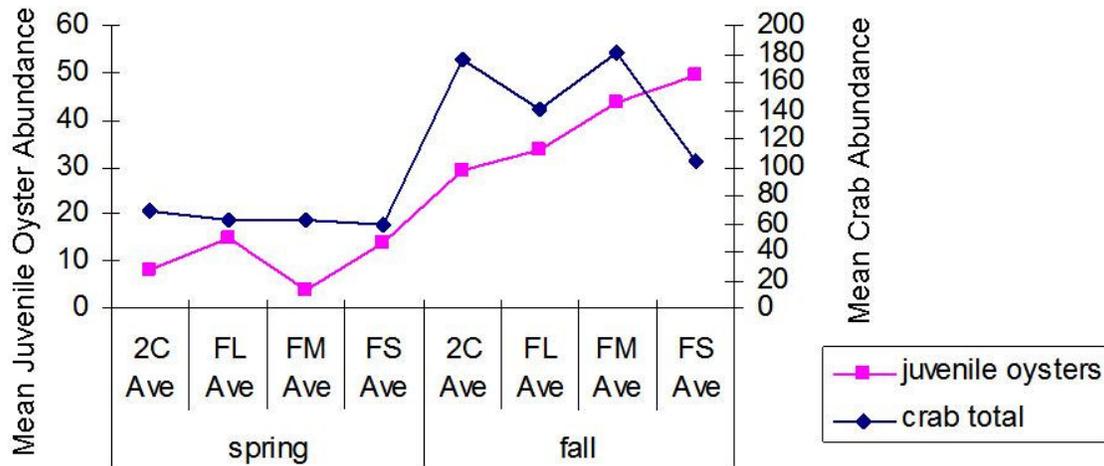


Figure 4.7: 2008 juvenile oysters and total crab abundance by season and treatment.

Mud crabs larger than 10 mm were separated out and analyzed by caging treatment and compared to juvenile oysters by caging treatment for the fall (Fig. 4.8). I found significant differences in the numbers of mud crabs > 10 mm with more of them present in the cage with the largest mesh size ($F_{3,60}=5.12$, $P<0.01$). The blocking factor was not significant ($F_{20,60}=1.48$, $P=0.1248$, Fig. 4.8) and therefore not included in the ANOVA model. Oyster recruitment was significantly higher in the small mesh cage ($F_{3,12}=8.51$, $P<0.01$, Fig. 4.8). The blocking factor was significant ($F_{4,12}=6.01$, $P<0.01$) and included in the ANOVA model, suggesting patchy settlement and survival of oysters across the study site.

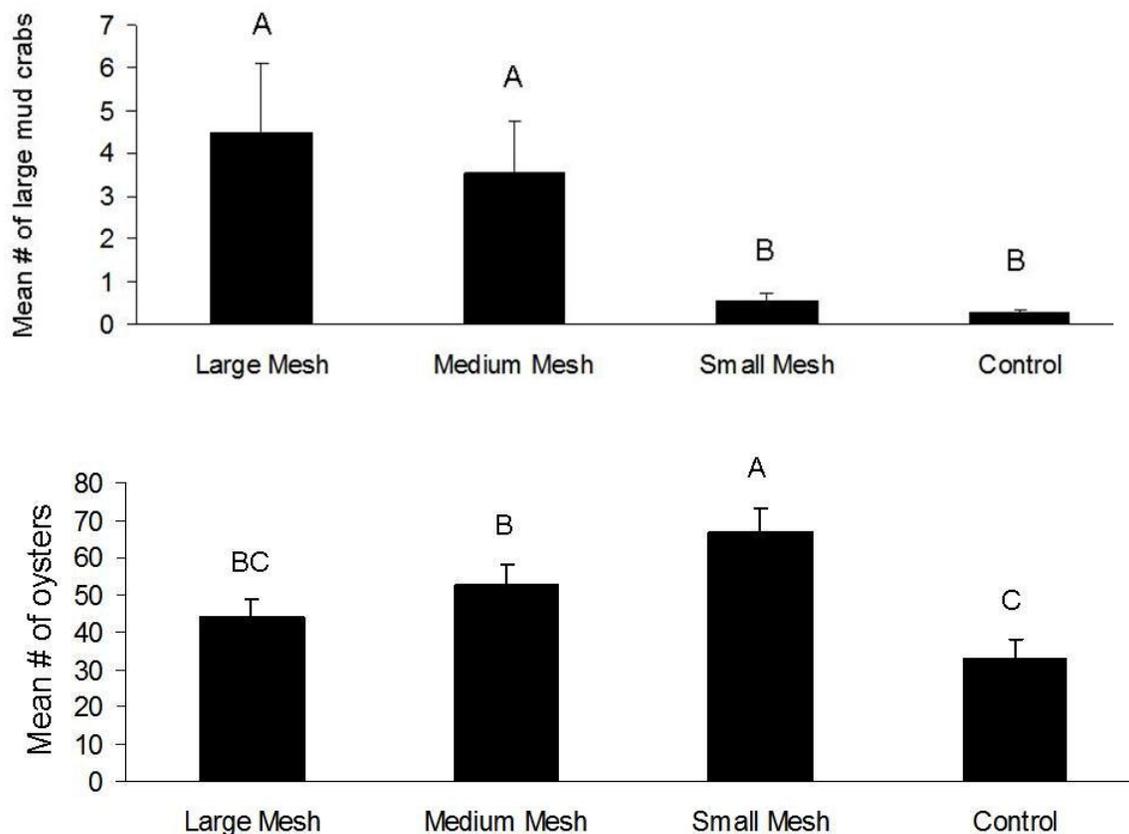


Figure 4.8: Mean (\pm SE) number of Atlantic mud crabs (>10 mm carapace width) and mean (\pm SE) number oyster spat from fall by caging treatment. Significantly more mud crabs of this size were present in medium and large mesh cages ($P < 0.05$), and significantly more surviving juvenile oysters were present in the small mesh cage ($P < 0.05$). Pairwise differences from Tukey-Kramer post hoc test noted by letters.

TPWD Dataset

The TPWD gill net data set from 1998-2008 was separated into years and seasons for some of the larger common predators present in Corpus Christi Bay, Texas and graphs show the seasonal and yearly patterns (Fig. 4.9). Black drum, blue crab and pinfish were not significantly different by season while red drum, sheephead, southern

flounder, and spotted seatrout were significantly different by season and were more abundant in the spring (Table 4.5).

1998-2008 TPWD Gillnet Data by Season For Common Predators

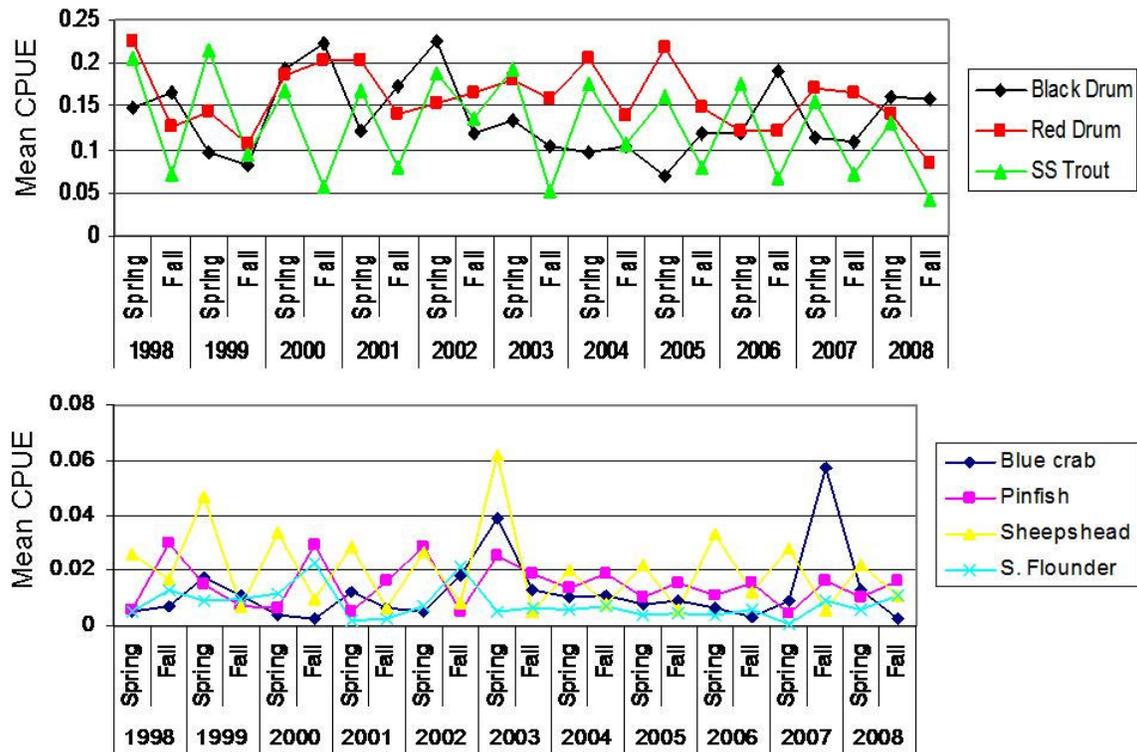


Figure 4.9: TPWD Gill net data from 1998-2008 for predators in Corpus Christi Bay.

Table 4.5: Texas Parks and Wildlife Department gillnet data 1998-2008 for Corpus Christi Bay for spring and fall for species of interest. Spring and fall average catch rates and ANOVA F and p values comparing spring and fall with significant p values bold.

Common name	scientific name	spring ave	spring se	fall ave	fall se	F	p
Black Drum	<i>Pogonias cromis</i>	0.134	0.008	0.1402	0.008	0.2829	0.5847
Blue Crab	<i>Callinectes sapidus</i>	0.0116	0.0012	0.0127	0.0012	0.3681	0.5442
Red Drum	<i>Sciaenops ocellatus</i>	0.1776	0.0075	0.1417	0.0075	11.5441	0.0007
Pinfish	<i>Lagodon rhomboides</i>	0.0124	0.0022	0.0172	0.0022	2.469	0.1165
Sheepshead	<i>Archosargus probatocephalus</i>	0.0317	0.0027	0.0088	0.0027	36.173	<.0001
Southern Flounder	<i>Paralichthys lethostigma</i>	0.0054	0.001	0.0104	0.0009	12.6523	0.0004
Spotted Sea Trout	<i>Cynoscion nebulosus</i>	0.1764	0.006	0.0776	0.006	134.1965	<.0001

The TPWD trawl data set from 1998-2008 was separated into years and seasons for some of the common predators and prey present in Corpus Christi Bay, TX and graphs show the seasonal and yearly patterns (Fig. 4.10). All common predators and prey were significantly different by season in the trawl data (Table 4.6). Blue crab, brown shrimp and pink shrimp were more abundant in the spring while pinfish, white shrimp and striped mullet were more abundant in the fall. Pinfish and blue crabs seemed to follow the salinity levels or rainfall by year.

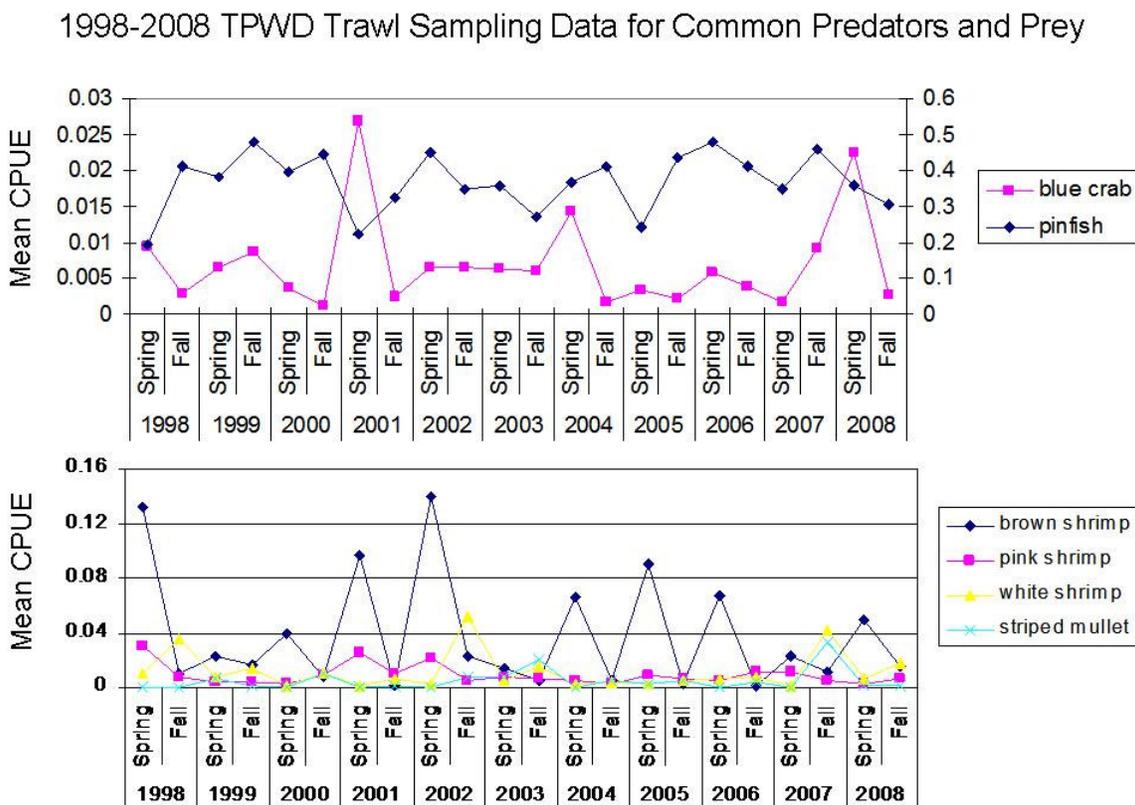


Figure 4.10: TPWD Trawl data from 1998-2008 for predators and abundant prey in Corpus Christi Bay.

Mesocosm Experiment

In the mesocosm experiment the treatment with 4 blue crabs and the treatment with 2 blue crab and 1 red drum had significantly higher oyster survival for the control (tray) compared to the cage treatment (Fig. 4.11). Predator treatment was significant ($F_{3,24} = 4.9675$, $p = .0043$), cage treatment was significant at $\alpha = 0.1$ ($F_{1,24} = 3.0571$, $p = .0865$), and the interaction was not significant ($F_{3,24} = .7288$, $p = .5397$). These results suggest that predator identity and diversity influences mud crab predation on juvenile oysters and that blue crabs can benefit juvenile oyster survival.

Table 4.6: Texas Parks and Wildlife Department trawl data 1998-2008 for Corpus Christi Bay for spring and fall for species of interest. Spring and fall average catch rates and ANOVA F and p values comparing spring and fall with significant p values bold.

Common Name	Scientific Name	Spring mean	spring SE	Fall mean	fall SE	F	p
Predators							
Blue Crab	<i>Callinectes sapidus</i>	0.0097	0.0011	0.0044	0.0011	11.0997	0.0009
Pinfish	<i>Lagodon rhomboides</i>	0.3451	0.011	0.3913	0.0111	8.7423	0.0032
Prey							
Brown Shrimp	<i>Penaeus aztecus</i>	0.0673	0.0034	0.0093	0.0034	141.0111	<.0001
Pink Shrimp	<i>Penaeus duorarum</i>	0.0111	0.0013	0.0069	0.0013	5.3446	0.0209
White Shrimp	<i>Penaeus setiferus</i>	0.0042	0.002	0.0191	0.002	26.9785	<.0001
Striped Mullet	<i>Mugil cephalus</i>	0.0018	0.0015	0.0081	0.0015	8.7797	0.0031

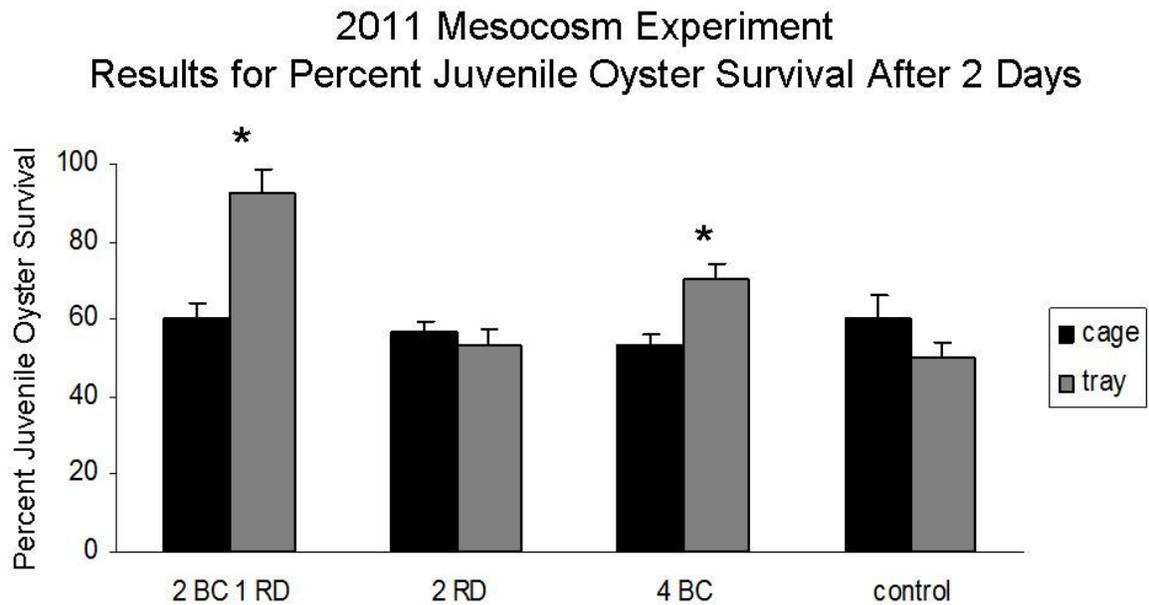


Figure 4.11: 2011 mesocosm experiment results for percent oyster survival after two days by treatment and cage or control (tray). Treatments with significant difference between cage and control are marked by *.

Abiotic Data

Temperature fluctuated by season as expected for the ten year dataset (Fig. 4.12). Salinity changed more by year depending on freshwater inflow from precipitation (Fig. 4.13). Dissolved oxygen also showed a seasonal pattern with lower DO in the warmer summer months and it appeared to also change yearly (Fig. 4.14). Although abiotic conditions fluctuated, predators were consistently more abundant in the spring than the fall.

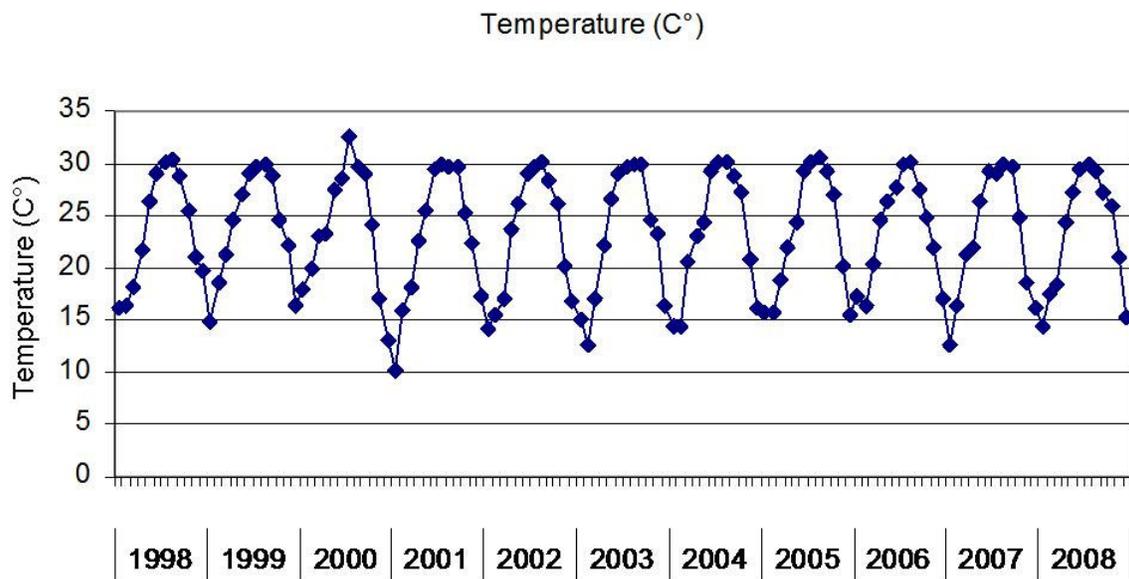


Figure 4.12: TPWD Trawl sampling temperature data from 1998-2008.

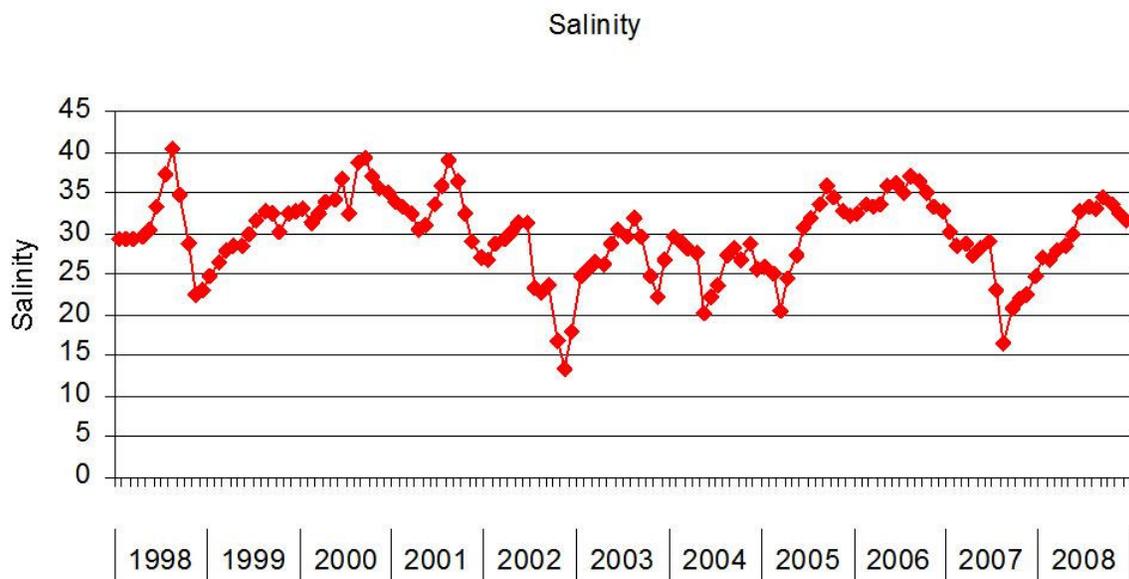


Figure 4.13: TPWD Trawl sampling salinity data from 1998-2008.

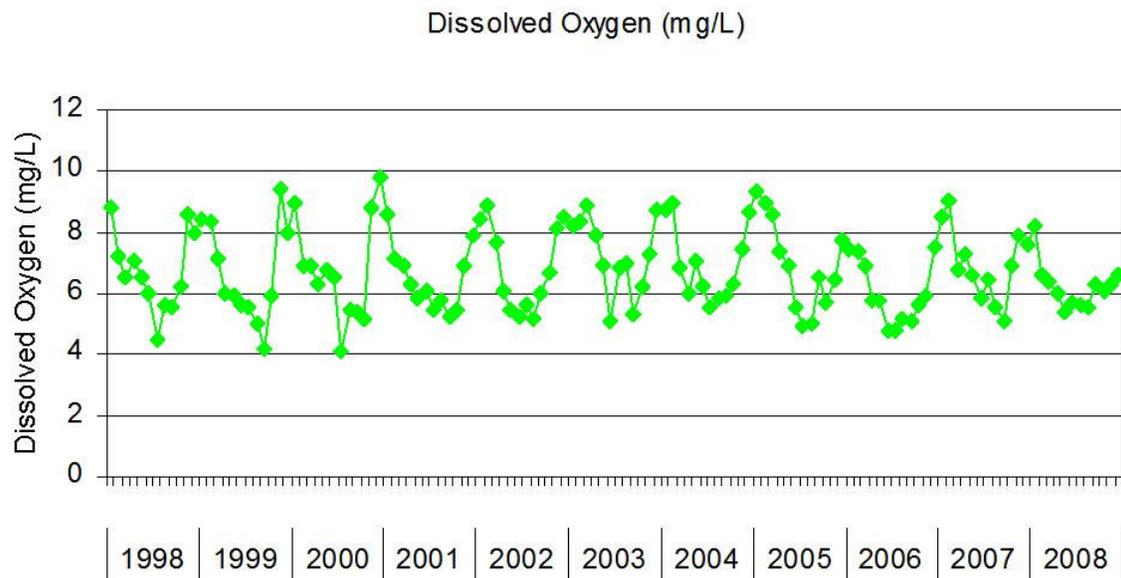


Figure 4.14: TPWD Trawl sampling dissolved oxygen data from 1998-2008.

DISCUSSION

I used the results from this study to analyze the top-down forces on oyster reefs in Texas. The species data from the exclusion of predators of various sizes elucidated changes in community members and abundances. This was compared to the ten-year TPWD datasets to understand which large predators are common and present in the area and how that changes the communities and top-down forces observed in the exclusion experiment. The data from fall and spring was compared to determine how seasonality and different abiotic conditions affect top-down forces and species abundances. The mesocosm study examines the top-down forces of common large predators as they affect juvenile oyster survival.

The diversity was not different between caging treatments for spring and was only different for the small mesh cage treatment in the fall (Table 4.1). The lower average

diversity found in the fall, small mesh cage treatment might be driven by the exclusion of some larger species as well as the very large abundance of grass shrimp compared to other treatments (Fig. 4.6). In many systems, the removal of large predators can reduce diversity when top-down forcing on a few competitively dominant species is removed (Paine 1966). Our findings suggest that the change in diversity is an increase in abundance of a few nekton and use of the oyster reef by a few larval fish species seasonally that created a significant decrease for diversity in just the small mesh cage treatment in the fall.

The overall species present and abundances for spring and fall have very few differences in species that were present in one season and not the other with high abundances (Table 4.2 and 4.3). The difference between seasons is a product of the higher abundances of many species in the spring. In comparing the control cage treatments and the total abundances for all treatments only a few groups stand out as different (Table 4.4). Overall, species were more abundant in spring, but crabs and oysters were more abundant in the fall (Fig. 4.6). The higher abundances for total number of crabs and juvenile oysters in the fall may account for the significant differences between the caging treatments for both in the fall.

Higher total crab abundances and higher juvenile oyster abundances occurred only in the fall (Fig. 4.7). The total crab abundance is lowest in the small mesh cage treatment where the number of juvenile oysters was the highest. This would fit the pattern that was predicted that the small mesh cage would exclude most crabs. There was no significant difference in Atlantic mud crabs between caging treatments. When examining the effects of Atlantic mud crabs by size to isolate those most likely to prey on small

oysters, I found significantly higher abundances of larger mud crabs (>10 mm) in the large and medium mesh cage treatments (Fig. 4.8).

Survival of juvenile oysters was greatest in the treatments that had less of the large mud crabs in the caging experiment or access for all predators (Fig. 4.8). Differences in oyster recruitment among our caging treatments were most likely caused by differences in predation after settlement occurred, not by differences in original oyster settlement rates. The exclusion of the larger predators allowed for the larger mud crabs to be present and foraging in the small mesh and allowed them to be present in the large and medium mesh cages without the larger predators. In the control, all species small and large had access. Thus, mud crabs, particularly large individuals, are most likely to be the primary predators of juvenile oysters in this system. This agrees with early studies that demonstrated mud crabs as the intermediate predator in the trophic cascades in the oyster reef system (Grabowski 2004).

The TPWD gillnet and trawl datasets had most common larger predator fish species significantly more abundant in the spring compared to the fall (Table 4.6 and 4.7). Some intermediate predators like pinfish were significantly more abundant in the fall. Several common predator species like blue crab and black drum were not different by season but seemed more affected by yearly fluctuations (Fig. 4.9). The abundance of larger predator species in both seasons means that the top-down forces from the larger predators on the intermediate predators should exist, but, the effects on the community in spring may have been surpassed by high recruitment of many species. Recruitment can affect communities diversity and abundance based on the abiotic conditions and seasonal patterns for juvenile dispersal and habitat usage (Menge & Sutherland 1987a).

The mesocosm experiment suggested that abundances of blue crab and red drum can affect the predation on juvenile oysters by mud crabs (Fig. 4.11). Isolating the indirect effects of large predators found in the study site on juvenile oyster survival through lethal and non lethal interactions between mud crabs and the large predators were examined. Blue crabs by themselves showed a decrease in oyster predation when the mud crabs were not protected by a cage and blue crab and red drum together had an even greater reduction in consumption of juvenile oysters by mud crabs when not protected by a cage revealing an additive effect of predators. The cage portion of each treatment was not significantly different across treatments but the control (tray) treatments were different by treatment indicating that the risk of predation and consumption for mud crabs increased juvenile oyster survival. This elucidates that the presence of common larger predators can increase juvenile oyster survival, which may benefit oyster populations.

Temperature fluctuated by season as expected for the ten year dataset. Salinity changed more by year depending on freshwater inflow from precipitation each year. Dissolved oxygen also showed a seasonal pattern with lower DO in the warmer summer months and it appeared to also change yearly depending on freshwater inflow. These abiotic conditions seemed to mirror the higher abundances of species observed in the spring for many larger predator species. The season changes in abiotic conditions may have greater affect on the top-down forces in years when the salinity changes the abundance of some of the larger predators that year. These conditions may also affect recruitment, which seems to also play a key role in this system.

A basic understanding of the species that inhabit oyster reefs seasonally in Texas as well as how exclusion of various sizes of consumers is important information for

planning conservation and restoration of the oyster reef communities with some larger species in decline in Texas. Top-down forces do play a role on oyster reefs in Texas, with the magnitude of these forces dependent on seasonal and yearly changes in large predator abundances, oyster spawning rates, and size class of intermediate predator mud crabs.

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SUMMARIES AND CONCLUSIONS

My study demonstrates that top-down forces are important for oysters and oyster reef communities in Texas. However, top-down forcing may vary by season and be rendered less important by other factors such as recruitment. These top-down forces from higher-order predators reduce the density of mud crabs, which increases juvenile oyster survival. Mud crabs also exert non lethal effects on oysters that can lower their fecundity. When oysters detect predation risk, they put more energy into shell growth and less into tissue growth. Oyster response to predation risk is dependent upon the size of the oysters as well as the identity of the predator(s) with smaller oysters being more likely to be eaten and to react to potential consumers.

The strength of top-down forcing is highly dependent on both the presence and identity of consumers. Blue crabs and red drum are common predators in the study system and both prey on mud crabs. Mud crabs reduce their foraging in the presence of predators, and by reducing mud crab foraging activity and abundance, blue crabs and red drum increase the survival of newly settled oysters. Blue crabs have larger effects on mud crabs than do red drum, but together both predators have a greater benefit to oysters than either in isolation. This suggests that a diverse assemblage of higher-order consumers may be important for the long term stability of oyster reef communities. Although some higher predators like blue crabs may consume juvenile oysters, they benefit oysters by alleviating direct predation by mud crabs as well as non lethal effects mud crabs exert on oysters.

I observed that there were no sub tidal oysters in my study site and performed a transplant experiment to ascertain if oysters could grow subtidally. Results indicate

oysters grow more in subtidal areas, but, are much more likely to be eaten. Abiotic conditions are known to affect oyster distribution, and my results suggest that predators can also affect oyster distribution.

Results from this study indicate that: 1) prey size influences their reactions to consumers and the propagation of non lethal predator effects; 2) lethal and non lethal effects that influence survival and resource allocation in oysters; 3) predation affects distribution patterns of oysters; 4) top-down forces and seasonal effects on oyster reef community structure; and 5) top-down forces can be obscured by recruitment and omnivory and are influenced upon abiotic conditions, recruitment levels, and the identify of the predators present.

Oysters are economically and ecologically important. My results indicate that in addition to abiotic conditions, predators can have large effects on oyster reef community structure and the survival of newly settled oysters. Top-down forces should be considered in oyster reef management and conservation.

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BIOGRAPHICAL SKETCH

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