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Predator-prey interaction in estuarine bivalves: size selection, effects of salinity, and indirect interactions

Barry Richard Aronhime
Louisiana State University and Agricultural and Mechanical College, baronh1@tigers.lsu.edu

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PREDATOR-PREY INTERACTION IN ESTUARINE BIVALVES: SIZE SELECTION, EFFECTS OF SALINITY, AND INDIRECT INTERACTIONS

A Dissertation
Submitted to the Graduate Faculty of the
Louisiana State University and
Agricultural and Mechanical College
in partial fulfillment of the
requirements for the degree of
Doctor of Philosophy

in

The Department of Biological Sciences

by
Barry Richard Aronhime
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For everyone who believed in me
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ABSTRACT

High stress environments can reduce species diversity. How such stress-induced reduction in predator diversity impacts prey survival is less well studied. Brackish waters in estuaries are stressful, species depauperate areas, but also prime oyster habitat in Louisiana. Surveys revealed reduced bivalve predator diversity at the low salinity (high stress) site. Exclosure experiments indicated highest prey mortality at the high salinity (low stress) site. Predator enclosures corroborated the field study results, with reduced consumption rates at the low salinity site for both stone crabs, *Menippe adina* and oyster drills *Stramonita haemastoma*, but not blue crabs, *Callinectes sapidus*. Blue crab mortality in enclosures was relatively low at all sites, while stone crab and oyster drill mortality were higher at the medium and low salinity sites.

As predator diversity increases, interactions between predators can impact prey mortality. Therefore I studied how the bivalve predators interact, how interactions impact prey survival, and how interactions change with stress. Interactions between blue crabs and stone crabs had an additive effect on bivalve mortality. Videotaping suggested blue crabs fed longer than stone crabs, and that interactions did not impede feeding. Bivalve mortality was however lower than predicted in blue crab-oyster drill combinations, suggesting interference reduced feeding by oyster drills. Salinity did not affect multiple predator interactions or feeding times.

Prey preference by predators also affects prey mortality. Hooked mussels, *Ischadium recurvum*, had higher mortality than oysters, *Crassostrea virginica*, in field and laboratory experiments, possibly because the thinner-shelled mussels were easier to consume. Chapter 4 examined prey preference in two important predator species. Blue crabs preferred small hooked mussels. Because profit did not differ with mussel
size, stone crabs because their stronger claws were less prone to damage showed no
size preference, and large mussels required force generation near levels that can
damage claws, I concluded blue crabs consumed small mussels to reduce risk of claw
damage, or to minimize handling times to limit their own predation risk.
CHAPTER 1

INTRODUCTION
General Introduction

Environmental stress models have long been used to try to explain community structure. Menge and Sutherland’s model (1976, 1987) from the rocky shore predicts that stress will have the greatest impact on community structure at a high level of stress, whereas competition and predation would be most important at medium and low levels of stress, respectively. High levels of stress can also reduce community diversity (Grime 1973, Connell 1978) and reduce predator activity as predators are usually more affected by stressors than their prey (Menge and Sutherland 1976). Additionally, sessile prey are likely to have adapted a greater tolerance to stressors due to their inability to escape the stress (Menge and Sutherland 1976, 1987). I wanted to see how stress impacts predator diversity and consequent prey mortality from predation in a Louisiana estuary.

However, prey mortality is a function of both predator diversity and abundance. In order to tease predator diversity effects from predator abundance effects, I looked into interactions between predators and how those interactions impacted prey mortality. For example, ladybugs and ground beetles feed synergistically on pea aphids (Losey and Denno 1998), meaning that predator diversity is important in the mortality of pea aphids. Multiple predator interactions can impact prey mortality positively when predators interfere with one another or negatively when predators facilitate one another. If predator interactions are additive, predators are functionally substitutable and any increases in prey mortality are the result of increased predator abundance (Sih et al. 1998). A stressor could impact the intensity of the interactions, altering prey mortality as well, so I decided to test these interactions in stressed and unstressed environments.
Another factor that impacts prey mortality is predator behavior (e.g., prey choice). Many predators have been shown to selectively consume prey based on species and size (Stephens and Krebs 1986). This selectivity causes differential prey species survival, and preference for small prey increases mortality at the most sensitive stages in many prey life histories. Prey choice is also known to be altered in multiple predator systems, depending on the interactions between the predators (Siddon and Witman 2004). For example, many crabs prefer small molluscs (Juanes 1992), and I was interested in better understanding the mechanisms that drive size selection. Mechanisms for selection that have been proposed include optimization of energy budgets, minimization of handling times, mechanical limitations, and aversion to chelal damage (Juanes 1992).

To address my basic interests, I picked oyster reefs because they provide a powerful system to test models of the indirect impact of an environmental stressor on prey survival. Estuaries are dynamic systems with large fluctuations in salinity. Salinity and salinity fluctuation are well documented environmental stressors that are thought to explain the generally low species diversity within estuaries (Remane and Schlieper 1971, Attrill 2002). Additionally, within estuaries, highest diversity is found in the coastal and freshwater ends, and lowest diversity in brackish waters near 6 PSU (Remane and Schlieper 1971). Estuarine benthic diversity decreases linearly with fluctuation in salinity (Attrill 2002). In Louisiana, oysters are found in subtidal regions in an optimal salinity band between 5 and 15 PSU (Melancon et al. 1998). The lower salinity limits of this band are based on osmotic stress to the oysters (Heilmayer et al. 2008), while the upper limit of the salinity band is driven by increased predation rates (Melancon et al.)
Because of higher salinities, droughts thus result in increased oyster mortality (Livingston 2000). Oysters or oyster spat are prey to many predators including blue crabs, *Callinectes sapidus*, the Western Gulf stone crab, *Menippe adina*, southern oyster drills, *Stramonita haemastoma*, a variety mud crabs, and a pair of predatory fish, *Pogonias cromis* and *Archosargus probatocephalus*. The oysters, because of their greater tolerance to reduced salinities, have a refuge from some of their predators that are not tolerant of brackish water. However, some predators, such as blue crabs, are as tolerant, or even more so than oysters to salinity.

This system thus provides me with a stressor that limits predator diversity and decreases prey mortality, and allows me to develop and test several hypotheses. My first null hypothesis was that predator diversity, consumption rates, and prey mortality in the field would not vary along a salinity gradient. To test $H_{01}$, I sampled three sites in Barataria Bay at different salinities for oyster predators, and calculated predator diversity indices. I used predator exclusion experiments at these three sites to test for differences in prey mortality with salinity. Predator enclosures were also used to determine differences in specific predator consumption rates with salinity, to further explore the mechanism for the exclusion experiment results. I predicted that predator species richness and predation intensity would be highest in low stress (high salinity) and decrease with increasing stress (decreasing salinity). I further predicted that prey density would be highest at an intermediate level of stress, limited in low stress environments by predation and high stress environments by the stress itself (Figure 1.1). My second null hypothesis ($H_{02}$) was that predator interactions would have an additive effect on prey mortality and that these interactions will not be altered at lower
salinities, increased stress. To test $H_02$, I looked at interactions in feeding rates between some of the primary invertebrate predators of bivalves at 30 PSU (e.g., a salinity where predators were presumably not stressed) and 10 PSU (where predators were likely stressed) in the laboratory.

Finally, crabs feeding on molluscs are again known to be size selective for bivalve prey (Juanes1992). For chapter three, I therefore decided to determine what the mechanism for selection might be for two of these predators. My third null hypothesis ($H_{03}$) was that crabs would not show prey preference. Alternatively, variation in choice might be better explained simply by the relative strength of the crab claws. To test this hypothesis I compared size selection of mussels among three predators: stone crabs with a stronger claw, and large (>10 cm carapace width) and small (<10 cm carapace width) blue crabs with weaker claws. Optimal energy budgets were estimated based on

Figure 1.1 Predictive model of expected relationship between stress, predator diversity, predation intensity and prey density.
Charnov’s (1976) currency, handling times were recorded, and the amount of force needed to damage the chelae of all three predators, as well as the force needed to crush the shells of varying sizes of mussels were determined.

Chapter four was completed first and is published in the *Journal of Experimental Marine Biology and Ecology*. Chapter two has been submitted to, and is under revision for the *Marine Ecology Progress Series*. As part of the revisions, I plan to incorporate the results from chapter three (which suggests that increased feeding rates at coastal sites [shown in chapter two] are probably due to increased predator diversity, and not indirect facilitation among predators) into the revised manuscript resulting from chapter two to make a stronger manuscript.

**Literature Cited**


CHAPTER 2

LOW SALINITY STRESS IN ESTUARIES DECREASES PREDATOR DIVERSITY, CONSUMPTION RATES, AND BIVALVE MORTALITY
Introduction

Environmental stress is important in shaping communities, and theoretical models suggest high levels of stress decrease diversity (Grime 1973, Horn 1975, Connell 1978). Menge and Sutherland’s (1976, 1987) model also suggests that the role of predation in determining community structure is inversely related to the importance of stress. The impact of predator diversity on prey survival is however a factor of both total predator abundance and interactions among predators. Increased predator diversity can dampen (Finke and Denno 2005) or strengthen (Byrnes et al. 2006) trophic cascades if the consumers interfere or facilitate one another respectively.

Salinity is a well known environmental stressor for many estuarine species, and plays a key role in their distribution (St. Amant 1938, Remane and Schlieper 1971, Guillory et al.1995, Melancon et al. 1998, Attrill 2002, Heilmayer et al. 2008). Within an estuary, diversity is highest in the least-stressful, freshwater upper reaches, or in full strength seawater near the mouth of the estuary, and low in brackish waters (Remane and Schlieper 1971). These middle portions of the estuary also have the greatest fluctuation in salinity (Attrill 2002), and increased fluctuations may be as important in reducing diversity as brackish salinities themselves (Attrill 2002).

Louisiana oystermen “seed” their oysters in brackish waters to optimize growth and survival across a salinity range of 5-15 PSU (Melancon et al. 1998). Oysters survive poorly below 5 PSU (Heilmayer et al. 2008), and above 15 PSU in subtidal habitats survival decreases because of an increase in oyster predators (St. Amant 1938, Guillory et al.1995 Melancon et al. 1998, Heilmayer et al. 2008). For example, predation can cause up to 90% of oyster mortality on oyster leases in coastal areas of
Barataria Bay, Louisiana (Brown et al. 2003). Although considered euryhaline, blue crabs also have higher consumption rates in more saline water (Guerin and Stickle 1997). Salinity is more important to the distribution of oysters and mussels than sediment type, dissolved oxygen, or other physical parameters (Montagna et al. 2008). Because estuarine oyster reefs protect coastal wetlands by providing wavebreaks (Meyer et al. 1997, Piazza 2005), their loss could further exacerbate wetland loss occurring along the Louisiana coastline. A better understanding of trophic interactions in estuarine oyster reefs, and how these interactions vary with salinity is therefore needed.

I determined how predator diversity and resulting bivalve survival varied at sites along a salinity gradient in a Louisiana estuary. My first null hypothesis (H₀₂₁) was: predator diversity would not vary along a salinity gradient. Alternatively, I hypothesized that if low salinity was the primary stressor, predator diversity would be lowest at the low salinity site and would increase at the medium and high salinity sites. Bivalve mortality, estimated from predator exclosure experiments, would therefore be highest at the high salinity site, and decrease at the medium and low salinity sites. To state this hypothesis in the null form: Prey mortality would not vary along a salinity gradient (H₀₂₂). I also used enclosures to determine how prey consumption by several predators varied with salinity. My last null hypothesis (H₀₂₃) was that predator consumption rates would not vary along a salinity gradient. Alternatively, I hypothesized that consumption rates should decrease with decreasing salinity. If fluctuation in salinity was instead the primary stressor, I predicted that low predator diversity and consumption rates, and the lowest bivalve mortality, should occur at the medium, but more variable, salinity site.
Materials and Methods

Site Description I worked in Bayou Fourchon Louisiana, part of the Barataria Bay estuarine complex (Figure 2.1), and compared predator diversity and prey survival among sites with varying salinity. Our low salinity site was in Galliano, La (29° 27’25.5” N 90° 21’44.8” W). The average salinity at this site, from YSI measurements, was 6.7 ± 0.9, (N = 6) PSU, and the site was chosen to be close to the lower salinity tolerance limit for oysters (Heilmayer et al. 2008). This site was a brackish Spartina alterniflora salt marsh with soft sediment and a substantial amount of Spartina alterniflora detritus, relative to the other sites. Within two meters from the marsh edge, the sediment was very soft with a shallow redox potential differential (RPD) layer. Experimental cages were placed along the marsh edge, at approximately 1 m depth, where the substrate was more firm.

![Map of LaFourche Parish, La with high, medium and low salinity sites where experiments were carried out indicated.](image)

The second site was along the shoreline of Bayou LaFourche in Leeville, Louisiana (29° 16.1’ 53” N, 90° 12.7’ 80” W). Mean salinity at this “medium” site was 14.8 ± 1.0 PSU (N = 6). The marsh edge had a narrow band of Spartina alterniflora
with a variety of plant species (including *Celtis sp.*) within a meter inland from the shore. This site was chosen to be near the salinity of optimal oyster habitat in Barataria Bay, 15 PSU (Melancon *et al.* 1998). The substrate was soft sediment, with a very dense oyster population. All experiments and sampling occurred within three meters of the marsh edge, in a depth of one m. The “high” salinity site was near Port Fourchon, Louisiana (29° 06' 38.9" N 90° 11' 10.8" W), with a mean salinity of 23.5 ± 1.4 (N = 6) PSU. This site is still well within the physiological tolerance of oysters. The vegetation at the high site was a mix of *Spartina alterniflora* and *Avicennia germinans*. The substrate was soft sediment with patches of oysters and oyster shell. All sampling and experiments occurred with one m of the shore, where the substrate was again more firm.

**Physico-chemical Variables and Bivalve Surveys**  At each site, I measured salinity, temperature, and dissolved oxygen using an YSI 85 probe at each sampling date. Two Hydrolab Datasonde III dataloggers were also used at the medium and low sites during cage experiments in the summer of 2008 to provide long-term, hourly records of salinity, temperature, pH, and dissolved oxygen. For the high salinity site, I used Louisiana Department of Natural Resources Coastwide Reference Monitoring System salinity and temperature data from a nearby coastal site (29° 08' 28" N 90° 13’ 41" W). I analyzed all water chemistry data using one-way ANOVAs contrasting the sites. To compare the ranges in salinity fluctuation among sites, coefficients of variation were calculated for each day at each site, and these data were subjected to a one-way ANOVA testing for differences among sites. To determine bivalve densities, at three times during summer 2008, ten 1 m² quadrats were haphazardly thrown out at each site, and carefully hand
searched for oysters and mussels. Differences in abundances among sites were analyzed with ANOVA.

**Predator Survey** In summer 2007, two baited crab traps were repeatedly set out over night at each site to sample for *Callinectes sapidus* (hereafter referred to as blue crabs) and *Menippe adina* (hereafter stone crabs, N=7 dates), and all crabs were identified and sexed. During predator exclusion and enclosure experiments in summer 2008, crabs were also trapped at each site in the same manner (N = 5 dates). Any *Stramonita haemastoma* (hereafter referred to as oyster drills) found on the cages were also counted, and for oyster drills, a 1 m$^2$ quadrat was also haphazardly tossed ten times to estimate density at each site (N = 5 dates). To sample for smaller xanthid crab predators, such as *Panopeus simpsoni*, *Panopeus obesus*, *Rhithropanopeus harrisii*, and *Eurypanopeus depressus*, three bags made of 2.5 cm Vexar mesh (66 cm X 30.5 cm X 7.5 cm) were filled with oyster shell and left out for two weeks for colonization at each site (Stuck and Perry 1992). These smaller xanthids prey on oyster spat but do not consume adult oysters (McDonald 1982, Stuck and Perry 1992). Sampling for xanthids was repeated three times in summer 2008. Predator sampling data were converted into catch per unit effort (CPUE) to standardize across gear types, and I analyzed differences in CPUE among sites with a one way ANOVA. CPUE for each species at each site were then compiled to calculate Shannon diversity indices for each site.

**Predator Exclosures** For one trial in summer 2007 and three trials in summer 2008, predator exclusion cages were set out at each site. Plastic bread trays (TA Industries, 66 cm x 54.6 cm x 15.2 cm) were lined with 0.5 cm Vexar mesh (Figure 2.2).
Two bread trays were stacked on top of each other and lined on all sides with mesh to make exclosure cages. Three of these cages were placed at each site for four separate trials (total N = 12 cages). A second cage type was designed to control for artifacts of caging (Virnstein 1977) at each site. Two trays were stacked and lined with mesh as above, but two sides were left open (total N = 12 cages). The last three cages were single bread trays lined with Vexar, but left open to allow predator access (total N = 12 trays).

Figure 2.2 Cages used in the predator manipulation experiments: a) open tray allowing predator access, b) closed cage excluding predators, c) cage control with two sides open to allow predator access. The ties used to hold the aggregation of bivalves in place can be seen in a.
In each cage, a single clump of 3.5 ± 0.2 oysters (Mean ± SE), with 24.3 ± 1.2 mussels epizoic on the oysters, was fastened to the bottom center with cable ties. Oyster clumps were collected along Bayou Lafourche near Leeville, La. (29° 17′40.15 N 90° 13′52.72 W). The cages were placed at approximately 1 m depth, and at least 5 meters apart to ensure independence (Virnstein 1977), and left submersed for two weeks. When cages were retrieved, oyster clumps were detached and surviving prey were counted to calculate percent mortality. A two-way ANOVA tested for differences in percent mortality among sites and cage treatments. Trials were treated as blocks, and separate ANOVAs were run for oysters and mussels. If the data were not normally distributed, I used a non parametric two-way ANOVA equivalent to test whether trends in mortality rates among sites differed among cage types.

**Predator Enclosures** For two trials in summer 2008, I also used full cages for predator enclosure experiments. At each site, I placed 3 cages with a stone crab (for two trials, total N = 6), three with a blue crab (N = 6), and three with five (roughly comparable in biomass to one stone crab or one blue crab) oyster drills (N = 6). Stone crabs and blue crabs were trapped in the predator surveys or from traps placed near rock jetties in Belle Pass, La. (29° 05′20.19″ N 90° 13′37.51″W), 5 km east of the high site. Oyster drills were collected from the predator surveys at the high site or from nearby bridge pilings. Cages contained oysters and mussels as described above. To reduce chances of prey exhaustion, cages had two prey clumps and were retrieved after only seven days. Surviving predators and prey were counted and percent mortality calculated for both. A two-way ANOVA tested for differences in prey mortality among predators and sites. Trials did not differ statistically, and the prey data were therefore
pooled in a completely randomized design. Percent predator mortality data were analyzed with a Chi-square test.

**Results**

**Physico-chemical Data and Mollusc Density** There were significant differences in salinity regimes among the three sites ($F_{2, 1,910} = 3,927.2, p < 0.0001$), although the data were not normally distributed ($Kolmogorov Smirnov D = 0.09, p < 0.01$). However, a non-parametric Kruskal Wallis one way analysis of variance also indicated a difference in salinity among sites ($\chi^2 =1450.9, p < 0.0001$). The medium site had the greatest range in salinities, from near freshwater to 22 PSU. In comparison, fluctuation in salinity at the high site ranged from 10.3 – 28.3 PSU. The low site, in contrast, was fairly stable in salinity for much of the study period (0.3 - 9.0 PSU). The low site, however, did reach 16 PSU when Hurricane Ike made landfall in late September, and caused a salt water intrusion (Figure 2.3). The medium site had a greater coefficient of variation in salinity than the high site (Tukey $p = 0.0005$), but not the low site (Tukey $p = 0.05$), nor were the high and low sites different (Tukey $p = 0.20$). Temperatures also differed among all three sites ($F_{2, 4,682} = 26.1, p < 0.0001$). However, mean temperatures for low, medium, and high sites were still fairly similar, at $29.79 \degree C \pm 0.06$ (SE), $29.32 \degree C \pm 0.05$, and $29.82 \degree C \pm 0.07$, respectively. Dissolved oxygen and pH were not normally distributed, and Kruskal –Wallis one way analyses of variance revealed no difference in pH ($\chi^2 = 3.32, p = 0.06$), but that dissolved oxygen differed between medium and low sites ($\chi^2 = 141.37, p < 0.0001$), and was lowest at the low salinity site. Oyster ($F_{2, 6} = 112.9, p < 0.0001$) and mussel ($F_{2, 6} = 68.1, p < 0.0001$) densities differed among sites. Although mussel densities were not normally distributed, a Kruskal-Wallis also indicated
Figure 2.3  Mean (± standard error) daily salinities at the three field sites during predator manipulation experiments.

differences ($\chi^2 = 7.45, p < 0.02$). Oysters were rare at the low salinity site, and mussels were also uncommon (Figure 2.4). The medium salinity site had the greatest density of oysters and mussels. Oysters were only found in lower intertidal zones at the high site and in reduced density than at the medium site (Tukey adjusted $p < 0.0001$), and no mussels occurred at the high site. Oyster density did not differ between the low and high sites (Tukey adjusted $p = 0.36$).

**Predator Surveys**  Shannon’s Diversity Indices indicated differences in predator diversity among sites ($F_{2,6} = 13.2, p = 0.006$), with the low site the least diverse (Figure 2.5), and no difference between the medium and high sites (Tukey test, $p = 0.43$). Although the greatest total CPUE of predators was at the low site (Tukey test, $p = 0.04$, Figure 2.6), ninety-eight percent were the small mud crabs, *Rhithropanopeus harrisii*, capable of feeding only on spat. Stone crabs and oyster drills were found only at the high site. Blue crabs occurred at all sites, but were most abundant at the high site.
Predator Exclosures

Exclosure experiments indicated both higher mortality rates at the high salinity site, and differences among cage types. For mussels, I found significant site ($F_{2, 93} = 7.5, p = 0.001$) and cage type ($F_{2, 93} = 42.2, p < 0.0001$) effects, but no interaction ($F_{4, 93} = 2.2, p = 0.08$). Mortality was higher in open trays (Tukey adjusted $p < 0.0001$) and cage controls (Tukey adjusted $p < 0.0001$) than in closed cages. Mortality did not differ between open and cage controls (Tukey adjusted $p = 0.44$). Mortality was higher at the high site than the medium (Tukey adjusted $p = 0.0007$) or low (Tukey adjusted $p = 0.05$) site. Mortality did not differ between medium and low sites (Tukey adjusted $p = 0.31$). The oyster mortality data were not normally distributed ($Shapiro–Wilk’s W = 0.93, p < 0.0001$ so the distribution of the data were compared to a variety of distributions with Proc Genmod (SAS 1997). The data most closely resembled a gamma distribution. The two-way ANOVA equivalent based on a gamma distribution found a significant site effect ($\chi^2_{2} = 11.51, p = 0.003$), but no cage effect ($\chi^2_{2} = 5.61$,
Mortality was higher at the high site than the medium \((p = 0.002)\) and low \((p = 0.006)\) sites. The medium and low sites did not differ \((p = 0.57)\).

![Shannon diversity indices](image)

Figure 2.5 Shannon diversity indices (± standard error) of predators from three sites in Barataria Bay with varying salinity.

**Predator Enclosures** In comparison, enclosure experiments indicated differences in consumption rates with salinity for only one of the bivalves. I did not find a difference between trials \((F_{1,60} = 0.02, p = 0.9)\) and all trials were therefore pooled in a completely randomized design. Consumption rates of mussels differed among sites (Figure 2.8, \(F_{2,38} = 5.11, p = 0.01\)) but neither the predator treatment \((F_{2,38} = 2.54, p = 0.09)\), nor the interaction \((F_{4,38} = 1.48, p = 0.23)\) were significant. Consumption rates at the low site were lower than the medium (Tukey test, \(p = 0.03\)) and high sites \((p = 0.03)\), but consumption rates did not differ between medium and high sites. In comparison, there was not a significant site \((F_{2,38} = 0.8, p = 0.47)\), predator \((F_{2,38} = 2.5, p = 0.10)\), nor interaction effect \((F_{4,38} = 0.2, p = 0.95)\) for consumption rates on oysters. The data
were again not normally distributed (Shapiro-Wilk’s W = 0.85, p < 0.0001), and the non-parametric G test of independence was also insignificant ($\chi^2 = 0.55, p = 0.97$).

![Graph showing mean (± standard error) catch per unit effort for seven oyster predators collected at three sites with varying salinity.](image)

**Figure 2.6** Mean (± standard error) catch per unit effort for seven oyster predators collected at three sites with varying salinity.

Oyster drill mortality was 100% at the low salinity site, but no mortality occurred at the medium and low sites (Figure 2.9). Stone crab mortality was lowest at the high site (0%), and increased at the medium and low sites (33% and 50% respectively). Blue crab mortality rates did not differ among sites and were relatively low (33%). These differences in mortality among sites and predators were significant ($\chi^2 = 132.52, p < 0.0001$).
Figure 2.7  Mean (+ standard error) percent mortality of mussel and oyster from predator manipulations at three sites with varying salinity.

To further examine the impact of blue crabs, stone crabs, and oyster drills on bivalve mortality, I created a predation index. The consumption rates of each of the three predators from the above mentioned enclosure experiments were multiplied by the number of individuals of each predator species at each site at the time of the enclosure experiments ( predator sampling data). The indices for each predator species were then summed within sites and trials. A two-way ANOVA tested for differences in the index among sites and prey species. The ANOVA found a significant site by prey species interaction ( $F_{2,6} = 84.95$, $p < 0.0001$). A posteriori Tukey tests for pairwise comparisons found more mussels should be consumed ( according to the index) than oysters at all
Figure 2.8  Mean (± standard error) number of mussel and oyster consumed per day by three predators in enclosure experiments at three sites with varying salinity.

sites (p < 0.05). Mussel mortality was projected to be highest at the high site followed by the medium and low (p < 0.05). The index predicted no difference in oyster mortality among sites (p > 0.05).

Discussion

Physico-chemical Variables  Our data indicate a strong positive correlation of predator richness, prey consumption rates, and prey mortality with salinity. Although other variables, such as temperature and dissolved oxygen varied among sites, I believe salinity to be the primary stressor at low salinity sites. Water temperatures overlapped quite a bit among sites, and were well within the thermal limits of the oyster predators. Longer periods of hypoxia did however occur at the low site. While hypoxia can
impact the distribution of many organisms (Rabalais 2002), the two common predators at the low salinity site were still *Rhithropanopeus harrisii* and blue crabs, both of which are more sensitive to hypoxia (Stickle et al. 1989) than stone crabs (Ayers 1938) and oyster drills (Stickle et al. 1989), which were absent at the medium and low salinity sites.

**Predator Surveys** Only three predators were found at all three sites:

*Rhithropanopeus harrisii* is common in brackish waters (Tolley et al. 2005), while *Eurypanopeus depressus* is euryhaline and competitively dominant to *Panopeus simpsoni* (Brown et al. 2005). *Panopeus spp.* are typically found in higher salinity waters (Tolley et al. 2005). Blue crabs are also quite euryhaline (Mangum and Towle 1977, Findley et al. 1978, Guerin and Stickle 1997) although reduced foraging occurs at low salinity (Guerin and Stickle 1997). In contrast, oyster drills do not occur in the field...
below 15 PSU (St. Amant 1938), although they survive at 3.5-7.1 PSU in the laboratory (Stickle 1999). Stone crabs survived best between 15 and 35 PSU in the laboratory (Combs et al. 1997) but are rare in upper regions of estuaries (Stuck and Perry 1992, Tolley et al. 2005, Peter Vujnovich, Jr., personal communication).

Ninety –eight percent of the predators at the low site were *Rhithropanopeus harrisii*, which reaches only 35 mm carapace width (McDonald 1982), and does not consume larger mussels. *Panopeus herbstii*, which grow larger than *Rhithropanopeus harrisii*, are capable of cracking *Geukensia demissa* shells 50 mm or greater in length (Seed and Hughes 1995), but prefer mussels 10-20 mm in length. It therefore seems unlikely that large mussels are impacted by *Rhithropanopeus harrisii*. In contrast, the high site had the greatest abundance of large invertebrate predators, such as blue crabs, stone crabs, and oyster drills. Blue crabs consume mussels (Brown and Richardson 1987, Aronhime and Brown 2009) and oyster spat (Lunz 1947, Menzel and Hopkins 1956), but have difficulty with larger oysters (Aronhime, personal observation). Stone crabs consume up to 60 oysters per week (Gunter 1955) and oyster drills can consume 0.12 oysters per day (Garton and Stickle 1980).

**Prey Mortality** The reduction in predator diversity at the low salinity site thus correlates with an increase in prey survival. More important than predator diversity *per se*, is predator identity (O’Connor 2008). Blue crabs are the most important oyster predator in the Gulf of Maine, more so than *Menippe mercenaria* and *Panopeus herbstii*; however O’Connor et al. (2008) used oysters < 20 mm, whereas many of the oysters I used were much larger (> 60 mm in length). Stone crabs and oyster drills are important predators of adult oysters (Powell and Gunter 1968, Richardson and Brown 1987). The low
mortality in exclosures indicates mortality in open trays and cage controls was from predation, probably by crabs. Bivalve shells in the latter two cage types were not crushed into small fragments, an indication of black drum predation (Brown et al. 2003), nor did I find gaping shells, indicative of oyster drill predation (Brown and Richardson 1987). Whole valves were instead pried open, or shell fragments were large, indicative of blue crab (Elner 1978, Aronhime and Brown 2009) and stone crab predation (Powell and Gunter 1968).

At the high salinity site, mortality in the cage controls was higher than in the open trays. Crabs may have used cage controls as a refuge from their own predators, such as redfish and black drum. The absence of reduced oyster mortality at medium and low sites in open trays was surprising, given the absence of stone crabs and oyster drills, and the reduced abundance of blue crabs. On the other hand, mussel mortality at the low site still occurs, apparently because euryhaline blue crabs can consume mussels (Blundon and Kennedy 1982, Aronhime and Brown 2009). Mussels have thinner shells and are easier to open than oysters, and are preferred prey for blue crabs (Aronhime and Brown unpublished data). However, prey mortality did not differ between closed cage controls and open trays, suggesting no cage artifacts.

**Predator Enclosures** The reduced foraging rates for most predators at the medium and low sites also corroborated the increased survival of bivalve prey in the exclosure experiments. The high mortality of oyster drills in enclosures at the low site indicates that salinity restricts their range. In the laboratory, oyster drills can survive salinities as low as 5 PSU (Stickle and Howey 1975), but do have lower prey consumption and scope for growth (Stickle 1985). The low site did reach salinities as low as 0.3 PSU.
The increased mortality of stone crabs at the medium and low sites also indicates these sites are sub-optimal for stone crabs. Blue crab mortality did not differ among sites, although some mortality occurred at each site, suggesting a caging artifact. Blue crabs are sensitive to hypoxia (Stickley et al. 1989) which did occur at the medium and low sites. Blue crabs typically migrate from hypoxic zones (Bell et al. 2003), but were unable to within the enclosures.

**Other Biotic Factors Impacting Oyster Survival** Other important predators in Barataria Bay (Brown et al. 2008) include sheepshead (*Archosargus probatocephalus*) and black drum (*Pogonias chromis*). Salinity tolerances of these predators exceed the tolerance of the invertebrate predators (Perret 1971, Jennings 1985, George 2008) and the oysters themselves, and thus probably do not explain increased survival of prey at low salinity sites (Peter Vujnovich Jr., personal communication). In higher salinity areas of Chesapeake Bay, oyster mortality has also been attributed to MSX and Dermo (Newell 1988), and predation explains only 1% of oyster mortality per month (Brown et al. 2005a). Although Dermo is an important cause of oyster mortality in Louisiana (Melancon et al. 1998), it is less important than in Chesapeake Bay (Encomio et al. 2005) possibly because Louisiana oysters are more resistant to Dermo (Brown et al. 2005 b).

**Comparison with Theoretical Models** The predator exclosure results were also as predicted by Menge and Sutherland (1976, 1987), when the absolute level of salinity is considered the stressor. Because the high salinity site was the least stressful, predation had the greatest impact at this site. The reduced foraging in enclosures at lower salinities also supported Menge and Sutherland’s model. Decreased consumption by
oyster drills and M. adina could have been caused by mortality, or reduced feeding rates (Garton and Stickle 1980). In contrast, blue crab consumption rates did not vary among sites, because of their greater salinity tolerance (Mangum and Towle 1977).

My results thus suggest that the upper regions of estuaries are refuges where bivalve prey are subjected to lower predation rates, especially by stone crabs and oyster drills. As the Louisiana coastline erodes, these upper estuaries may face higher or more variable salinity regimes due to salt water intrusion, and predators will likely extend their ranges and impacts into the refugia. Thus the optimal spatial zone for oyster production in Louisiana estuaries will likely decrease unless coastal erosion can be halted.

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CHAPTER 3

MULTIPLE PREDATOR AND SALINITY DEPENDENT EFFECTS ARE RARE IN ESTUARINE BIVALVE PREDATORS
Introduction

Estuaries have dynamic salinity regimes, and salinity is believed to limit the distribution of several oyster predators (Melancon et al. 1999, Brown and Stickle 2002, Hulathduwa et al. 2007). Subtidal oysters, *Crassostrea virginica* (hereafter referred to as oysters), are rarely found at high salinity (Melancon et al. 1998) due to the diverse suite of predators, including blue crabs, *Callinectes sapidus* (hereafter referred to as blue crabs), Western Gulf stone crab, *Menippe adina* (hereafter referred to as stone crabs), and southern oyster drills (hereafter referred to as oyster drills), *Stramonita haemastoma* (Menzel and Hopkins 1956, Brown and Richardson 1987, Brown and Haight 1992, Tolley et al. 2005). In Barataria Bay, Louisiana, up to 90% of oyster mortality on subtidal oyster leases can be from predation (Brown et al. 2008), and oyster drills consume up to 80% of oyster spat in reefs in Mobile Bay, Alabama (Hofstetter 1977). Blue crabs can also exert top down control on *Macoma* (Seitz and Lipcius 2001) in Chesapeake Bay, and have a Type II or Type III functional response on oysters (Eggleston 1990).

Increased predator diversity at higher salinities could also result in indirect increases or decreases in prey mortality from density mediated indirect interactions (DMII), and trait mediated indirect interactions (TMII) (Schmitz et al. 2004). Increased diversity can strengthen or dampen trophic cascades if predators facilitate (Byrnes et al. 2006) or interfere (Finke and Denno 2005) with one another, respectively. Trophic cascades occur on oyster reefs (Grabowski 2004) and indirect interactions can thus impact bivalve survival and the productivity of oyster reefs. In earlier work, higher bivalve mortality occurred in field experiments at coastal sites with higher predator
diversity, suggesting either an additive effect or facilitation between predators (Aronhime and Brown, *in prep*, see Chapter 2).

The eastern oyster, *Crassostrea virginica*, is a commercially important species worth $38.8 million in Louisiana harvests in 2008 (National Marine Fisheries 2008). Oyster reefs also provide important ecological services such as filtering nutrients to prevent eutrophication (Dame *et al.* 1989, Nelson *et al.* 2004), providing wave breaks (Meyer *et al.* 1997, Piazza 2005), and providing structure and habitat for commensal organisms (Guitierez *et al.* 2003, Soniat *et al.* 2004), including hooked mussels. Hooked mussels can reach densities greater than 3,000 /m$^2$ on oyster reefs (Rodney and Paynter 2006) and are considered a nuisance species by oystermen (Louisiana Department of Wildlife and Fisheries 2000).

The experiments described below were designed to test the following null hypotheses: H$_{031}$) Interactions between bivalve predators will have no effect on prey mortality. Alternatively, bivalve predator interactions can lead to increased bivalve mortality; H$_{032}$) Reduced salinity will have no effect on predator interactions. Alternatively, bivalve consumption rates and predator activity will decline at reduced salinity.

**Materials and Methods**

**Collecting and Holding** I collected at Belle Pass, Louisiana (29° 05’20.19” N 90° 13’37.51”W) using baited crab traps during the summers of 2007-2009, and placed in 93 L coolers in layered wet burlap sacks for transport to the laboratory. Crabs were held individually in the laboratory in 38 L aquaria with under-gravel filters at 30 PSU. Crabs were fed on bivalves and then starved for 24 hours before the start of an
experiment to standardize hunger levels. Oyster drills were collected at the Louisiana Universities Marine Consortium laboratory (29° 06’49.59” N 90° 11’04.64” W) near Port Fourchon, Louisiana, and held in 38 L aquaria at 30 PSU with under gravel filters in the laboratory. Salinities in the Belle Pass, Port Fourchon area range from 10-30 PSU (Aronhime and Brown, unpublished data). For low salinity experiments (10 PSU), predators were stepwise acclimated (5 PSU per day) from 30 PSU to 10 PSU and acclimated at 10 PSU for 48 hours prior to the start of the experiment.

Bivalves were hand collected from intertidal oyster reefs 21 Km northwest of Port Fourchon, near Leeville, Louisiana (29° 17’40.15 N 90° 13’52.72 W). Mussels are much more common in these brackish waters than at Port Fourchon. Bivalves were placed in 19 L buckets covered with wet burlap sacks and brought back to the laboratory where they were kept in 56 L aquaria with under-gravel filters at 30 PSU and fed dried marine phytoplankton.

**Experimental Design**  Three 495 L water tables were arranged vertically (Figure 3.1) and covered with 2 cm Vexar mesh to prevent predators from escaping. Each water table was divided in half with a Vexar mesh partition. A clump of two to five oysters and 12 to 30 mussels were placed on the side of the water table with a filter box filled with oyster chips through which water was re-circulated and filtered by a pump. These clumps served as controls for accidental mortality. In the other half of two of the water tables one clump of bivalves was placed with either one blue crab, one stone crab, or five oyster drills (to roughly standardize predator biomass). The last water table contained bivalves and both one stone crab and one blue crab, or one blue crab and five oyster drills. Treatments were temporally paired so that treatments with both blue
crabs and stone crabs were concurrent with individual predator treatments. All predators were measured (carapace width to the nearest cm for crabs and total length to the nearest mm for oyster drills). Sex of crabs and any noticeable chelal damage were also recorded. I weighed bivalve clumps to the nearest gram, and measured individual bivalves (to the nearest mm), and tagged clumps using cable ties and tree tags. All other fouling organisms, such as barnacles, nereid polychaetes, xanthid crabs, encrusting sponges, and amphipods were removed from the aggregations so there were no alternative prey. Experiments were run for 48 hours under a 12:12 photoperiod in 30 and 10 PSU seawater (to test $H_{0.32}$). Prey mortality data were analyzed with eight
separate two-way (predator treatment x prey species) ANOVAs. To test $H_{031}$, the null model for no multiple predator effects in each of these analyses is:

\[ P = p_a + p_b - (p_a p_b) \]

Where $P$ is the expected proportion of prey consumed in combined predator treatments, $p_a$ is the proportion of prey consumed by predator $a$, and $p_b$ is the proportion of prey consumed by predator $b$ (Soluk and Collins 1988). In instances where normality could not be achieved after transforming the data, I used Proc Genmod (SAS 1987) to find the distribution that the data most closely resembled based on deviance of the data from the given distribution. Among the distributions examined and tested were normal, Poisson, negative binomial, binomial, and gamma. After the distribution was chosen, an ANOVA equivalent was used based on the distribution most resembling the data, rather than a normal distribution.

**Predator Interaction and Identifying Mortality from Predation** In the combined predator treatments, I wanted to see how the predators interact and identify which predator had the greater impact on prey mortality. A time-lapse video recorder and camera were used during the 12 hours of light for the blue crab – stone crab combined predator treatments to determine the frequency and duration of behaviors (advances, retreats, meral spreads, and feeding bouts). Separate two way ANOVAs analyzed differences in frequency for each behavior between predators and salinities ($H_{032}$), as well as differences in feeding times. In the blue crab – oyster drill pairings, shell damage was used as an indicator of the responsible predator. Gaping shells represented predation by oyster drills (Brown and Richardson 1987), while shells broken or pried apart were consumed by blue crabs (Elner 1978). Gaping shell data
were compared to mortality data from oyster drills alone to see if oyster drill consumption declined in the presence of blue crabs.

**Results**

**Multiple Predator and Salinity Effects** Comparing mortality of mussels consumed by blue crabs and stone crabs (Figure 3.2), the data were not normally distributed (Shapiro-Wilk W = 0.93, p = 0.0002). Goodness of fit analyses (Proc Genmod) suggested the distribution most closely resembled a gamma distribution, and a two-way ANOVA equivalent test based on a gamma distribution showed no effects of salinity ($\chi^2_1 = 0.19, p = 0.66$), predator treatment ($\chi^2_3 = 0.59, p = 0.90$), or predator*salinity interaction ($\chi^2_3 = 1.44, p = 0.70$), thus supporting $H_{031}$ and $H_{032}$.

For oyster mortality, data were also not normally distributed (Shapiro-Wilk W = 0.91, p = 0.0006). Proc Genmod again suggested the distribution most closely resembled a gamma distribution, and a two-way ANOVA equivalent test showed no effects of salinity ($\chi^2_1 = 0.14, p = 0.71$), predator treatment ($\chi^2_3 = 1.74, p = 0.63$), or predator*salinity interaction ($\chi^2_3 = 0.12, p = 0.99$), thus supporting $H_{031}$ and $H_{032}$.

Regarding the comparison to controls in each table, mortality of mussels and oysters in each of the predator treatments differed from their respective controls at both salinities ($p < 0.05$). In the blue crab and oyster drill combinations (Figure 3.3), the mussel mortality data were also not normally distributed (Shapiro-Wilk W = 0.95, p = 0.02). Proc Genmod again suggested that the mussel mortality distribution most closely resembled a gamma distribution, and a two-way ANOVA equivalent test showed no effect of salinity ($\chi^2_1 = 0.68, p = 0.41$) or predator*salinity interaction ($\chi^2_3 = 5.54, p = 0.14$), but a significant predator treatment effect ($\chi^2_3 = 58.10, p < 0.0001$). Mussel
mortality was significantly lower in the combined predator treatment than the predicted model, suggesting interference between predators, and rejecting H_{031}. Regarding the predation controls in each water table, mortality of mussels in each of the predator treatments differed from their respective controls in both salinities (p < 0.05). Oyster mortality data with both blue crabs and oyster drills were normally distributed (Shapiro Wilk W = 0.98, p=0.19) and there was a predator-salinity interaction (F_{2,54} = 2.98, p = 0.04). The combined predator treatments and the null model did not differ at 10 (Tukey adjusted p = 0.76) or 30 PSU (Tukey adjusted p = 0.99), suggesting no multiple
predator effect. There was no difference between salinities within predator treatments (Tukey adjusted $p > 0.05$), supporting $H_{032}$. Oyster mortality in the 10 PSU multiple predator treatment ($\chi^2_1 = 1.37$, $p = 0.24$) did not differ from its control. In all other predator treatments at both salinities, oyster mortality differed from controls ($p < 0.05$).

**Predator Interactions and Identifying Mortality from Predation** During daylight hours, blue crabs were far more active in general, and specifically in feeding than stone crabs (Figure 3.4). A series of two way ANOVA equivalent tests, with gamma distributions due to a lack of normality, did not suggest any salinity dependent effects on

![Graph showing mortality of two bivalves (mean ± SE) as a function of salinity and predator treatment in oyster drill – blue crab multiple predator studies with letters above histograms indicating differences as suggested by *a posteriori* pairwise comparisons. “Predicted” refers to the predicted mortality values based on a null model using mortality from individual predator treatments. “Actual” refers to the mortality of bivalves in the treatment with both predators.]

Figure 3.3. Mortality of two bivalves (mean ± SE) as a function of salinity and predator treatment in oyster drill – blue crab multiple predator studies with letters above histograms indicating differences as suggested by *a posteriori* pairwise comparisons. “Predicted” refers to the predicted mortality values based on a null model using mortality from individual predator treatments. “Actual” refers to the mortality of bivalves in the treatment with both predators.
the number of advances ($\chi^2_1 = 1.31, p = 0.25$), meral spreads ($\chi^2_1 = 2.63, p = 0.10$), or retreats ($\chi^2_1, p = 0.43$), supporting H\textsubscript{032}. There was also no difference in the number of advances ($\chi^2_1 = 0.22, p = 0.64$), meral spreads ($\chi^2_1 = 0.78, p = 0.38$), nor retreats ($\chi^2_1 = 0.01, p = 0.92$) between blue crabs and stone crabs. I also did not find any salinity-predator interactions in any of the predator interaction behaviors ($p > 0.05$). Blue crabs had significantly higher feeding interval lengths ($\chi^2_1 = 4.22, p < 0.04$) but feeding times did not differ with salinity ($\chi^2_1 = 0.10, p = 0.75$) nor was there a predator*salinity interaction ($\chi^2_1 = 0.11, p = 0.74$).

Figure 3.4. Behavioral data I obtained from the stone crab – blue crab combined predator treatment using a time lapse video recorder. The number of instances each predator initiated each behavior (mean ± SE) are indicated. An asterisk indicates differences between the two crabs.
In the oyster drill-blue crab combined treatment, mortality from drill predation accounted for 17.14% ± 14.09 of oyster mortality and 6.63% ± 3.89 of mussel mortality at 10 PSU. At 30 PSU, drills accounted for 2.22% ± 2.22 of oyster mortality and 12.03% ± 5.67 of mussel mortality. While there was no salinity main effect on oyster drill predation on oysters ($\chi^2_{1} = 0.31$, $p = 0.58$), I did find a predator main effect ($\chi^2_{1} = 9.96$, $p = 0.002$) and a salinity*predator interaction ($\chi^2_{1} = 6.23$, $p = 0.01$) again with the gamma distribution. *A posteriori* comparisons showed the presence of a blue crab decreased the feeding of oyster drills on oysters at 30 PSU ($p < 0.0001$) but not at 10 PSU ($p = 0.34$). Consumption of mussels by oyster drills was also significantly reduced in the presence of a blue crab ($\chi^2_{1} = 7.54$, $p = 0.006$). Salinity did not affect mussel mortality ($\chi^2_{1} = 0.00$, $p = 0.95$) nor was there an interaction ($\chi^2_{1} = 1.31$, $p = 0.25$).

**Discussion**

**Multiple Predator Effects and Behavioral Interactions** Field studies have shown highest bivalve mortality in coastal waters with higher bivalve predator diversity (Aronhime and Brown, *in prep*, see Chapter 2). My laboratory studies presented here show no facilitation among any of the predators, suggesting the increased field mortality is a direct function of increased predator density, and that there is functional redundancy between blue crabs and stone crabs. When predators have a broad habitat domain such as blue crabs, Schmitz (2007) predicted either facilitation between predators or substitutable effects when the prey have narrow or broad habitat domains, respectively. Since oysters have a broad habitat domain relative to stone crabs, our results of substitutable effects in blue crab – stone crab combinations are in line with Schmitz’s predictions. Our blue crab and stone crab combined data agree with those of
O’Connor et al. (2008), who found blue crab alone to have as great an impact on oyster survival than any stone crab or mud crab combinations. While O’Connor et al. (2008) used only oyster spat, and did not use mussels, my results also show bivalve mortality from combined predator treatments to equal mortality from blue crabs alone. The video recordings of predator interactions elucidate the importance of blue crabs further, by demonstrating that most of the foraging was by blue crabs. Although blue crabs were quite active behaviorally, including initiating meral spreads and advances, when stone crabs responded by advancing on the blue crab, the blue crab typically retreated, abandoning the bivalves, indicating they were aggressively subordinate. Further analysis however showed that the differences in the number of retreats between predators were not significant. In contrast, stone crabs were mostly inactive, regardless of salinity. Blue crabs live in a variety of estuarine habitats including marsh edge (Peterson and Turner 1994), course woody debris (Everett and Ruiz 1993), seagrasses (Moore et al. 1996) and oyster reefs (Galstoff 1964). Stone crabs are only found in this last category. While both species are omnivorous, molluscs compose a large portion of the diets of each, especially adults (Bucci et al. 2007, Powell and Gunter 1968). It is possible that the two may interact on oyster reefs for food resources. Little previous work has been done on dominance hierarchies between blue crabs and stone crabs, although stone crabs have been listed as predators of blue crabs (Powell and Gunter 1968). My data suggest that their interactions do not affect bivalve mortality.

I did however find interference between oyster drills and blue crabs for mussels and a non-significant trend for oysters. Oyster drill oyster handling times are considerably larger than for blue crabs (Garton and Stickle 1980, Richardson and
Brown 1990). In fact, relatively few bivalves were consumed by oyster drills, with oyster mortality from drills not differing from controls in the 10 PSU treatment. However, even fewer bivalves were consumed by oyster drills in the presence of blue crabs. Oyster drills are known to climb out of water in laboratory experiments to avoid stone crabs (Richardson and Brown 1992) and may respond to a similar cue from blue crabs; I did observe that oyster drills had crawled out of the water on some occasions. There was also one instance of predation on oyster drills by a blue crab. Although blue crabs prefer to consume thinner shelled molluscs (Aronhime and Brown 2009, see Chapter 4) and are unlikely to consume oyster drills, oyster drill juveniles may be susceptible to blue crab predation, given the prevalence of molluscs in the diet of blue crabs. Although mortality of bivalves was lower than predicted based on our null model, mussel mortality in combined predator treatments did not differ from mortality by blue crabs alone. This also supports the work of O’Connor et al. (2008), and further emphasizes the importance of blue crabs in determining bivalve mortality.

Salinity Effects There were few main effects of salinity in the multiple predator experiments. Although all oyster drills transferred directly from 30 PSU to 10 PSU died, no mortality occurred for oyster drills or other predators when they were stepwise acclimated. The high survival of oyster drills after stepwise acclimation is in accordance with other laboratory experiments involving oyster drills (Stickle and Howey 1975), although they are not found below 15 PSU in Barataria Bay (St. Amant 1938). The lack of at least reduced oyster drill foraging at low salinity was thus not expected (Garton and Stickle 1980). Since our experiments only ran for 48 hours, very few bivalves were consumed by oyster drills alone, even in the 30 PSU treatment, and salinity dependent
changes in foraging activity may not have therefore been identified. Additionally, Garton and Stickle (1980) found decreases in foraging at 7.5 PSU and lower, as opposed to 10 PSU used in our experiments at room temperature. Stone crabs also appear to be restricted to higher salinities in the field (Menzel et al. 1958), although tolerance increases ontogenetically (Guillory et al. 1995), perhaps explaining the lack of reduced foraging at low salinity. Blue crabs are well known for their osmoregulatory abilities (Mangum and Towle 1977), surviving even in freshwater (White et al. 2006), thus explaining lack of changes in blue crab foraging in our study.

**Conclusions** My results suggest that increased bivalve mortality in coastal areas with higher salinities in the Gulf of Mexico is likely due to increased predator density, not any indirect effects like facilitation among predators. My data also indicate that periodic episodes of decreased salinity are not likely to impact interactions between these bivalve predators or dramatically decrease predator foraging, since I found few salinity main effects.

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CHAPTER 4

THE ROLES OF PROFIT AND CLAW STRENGTH IN DETERMINING MUSSEL SIZE SELECTION BY CRABS*

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Introduction

Preference for smaller mussel prey by molluscivorous crabs is well documented (Juanes 1992, Ebersole and Kennedy 1994, 1995, Micheli 1995, Rovero et al. 2000, Smallegange and Van der Meer 2003) but the mechanism remains unclear. Optimal foraging theory predicts that crabs should select prey based on profitability (Charnov 1976), although various “currencies” exist (Stephens and Krebs 1986, Juanes 1992, Rovero et al. 2000, Smallegange and Van der Meer 2003). Juanes (1992) reviewed size selection by crabs, and since a considerable number of studies indicated smaller than optimal prey were selected, suggested that crabs selected smaller bivalves to avert chelal damage. Smallegange and Van der Meer (2003) also found shore crabs (*Carcinus maenas*) selected small blue mussels (*Mytilus edulis*). While the chela wear hypothesis is popular, relatively few studies have attempted to test it (Kaiser et al. 1990, Seed and Hughes 1995). Seed and Hughes (1995) reviewed size selection of molluscs for crabs with varying chelal morphology, and found crabs with larger chelae selected for larger bivalves. However, they also found smaller mussels were more profitable for crabs with smaller chelae, like *C. sapidus*, and that larger mussels were more profitable for crabs with larger chelae, like *Cancer magister*. They mentioned chela wear as a factor in size selection, but did not consider it a major factor since some crabs select for medium size prey (Elner and Hughes 1978), and small mussels are sometimes the optimal prey (Hughes and Seed 1981). Kaiser et al. (1990) studied red and green forms of *Carcinus maenas* and found the red form crabs had greater chelal masses and selected for larger mussels. However, none of these studies looked directly at chelal wear.
I examine the effect of chelal morphology in a comparative study using *Callinectes sapidus* and *Menippe adina*, and the hooked mussel *Ischadium recurvum* as prey. I refer to the force exerted by the crab as the “crushing force”, and the force needed to damage the crab chelae or mussel shell as “resistance to breakage.” *Menippe adina* has a larger crusher chela (Figure 4.1) with greater mechanical advantage (Yamada and Boulding 1998) and force generation than *C. sapidus* (Schenk and Wainwright 2001). I hypothesized that stronger crabs can crush and consume larger prey, and tested whether this hypothesis explains differences in selective behavior between crabs with differing chelal morphologies. I tested three potential mechanisms explaining selection: i. optimization of profit (energy gained/ handling time);
ii. crushing force; and iii. resistance to breakage. I predicted *M. adina* would consume larger mussels than *C. sapidus*. Crushing force in *C. sapidus* is positively correlated with crab size (Hughes and Seed 1981), so I also predicted small *C. sapidus* would select smaller prey than large blue crabs. To specifically determine the force necessary to crush mussel shells, and its relationship to the force necessary to damage the chelae of both predators, I also determined the loads necessary to crush mussel shells and chelae.

To test the mechanisms outlined above, both *M. adina* and *C. sapidus* in two size groups (carapace width > 10 cm and < 10 cm), were offered mussels in five size classes. To determine if mussel size selection was predicted by profit, I calculated dry mass in tissue per mussel and divided it by observed handling times to estimate profitability as

\[
\text{Profit} = \frac{E}{h},
\]

following Charnov (1976) and Rovero et al. (2000).

**Study Organisms** *Ischadium recurvum*, or hooked mussels, are thin shelled, estuarine bivalves in the family Mytilidae, reaching densities over 3000 per m² as epizoics on oyster reefs (Rodney and Paynter 2006). Planktonic larvae recruit to oyster reefs and attach by byssal threads. Hooked mussels may compete with oysters (*Crassostrea virginica*) for space and food resources, and are considered nuisance species (Louisiana Department of Wildlife and Fisheries 2000, Coleman 2003). They range in size from micrometers as larvae to > 60 mm as adults.

Although blue crabs are omnivorous, molluscs can compose half the *C. sapidus* diet (Darnell 1958, Tagatz 1968, Laughlin 1982, Alexander 1986, Hines et al. 1990,
Callinectes sapidus co-occur with hooked mussels throughout marshes occurring in estuarine systems, and also consume oyster spat (Lunz 1947) and small oysters (Eggleston 1990). *Menippe adina* are more stenohaline than *C. sapidus* and are considered shellfish specialists (Yamada and Boulding 1998), consuming 60 oysters a week (Gunter 1955, Menzel and Nichy 1958, Powell and Gunter 1968). Both crabs are known to consume hooked mussels, based on laboratory studies (Blundon and Kennedy 1982, Brown and Haight 1992).

**Materials and Methods**

**Collecting and Holding Methods** Adult *C. sapidus* (mean carapace width 12.7 ± 0.49 cm) and *M. adina* (mean carapace width 9.45 ± 0.35 cm) were captured using baited crab traps at the Louisiana Universities Marine Consortium laboratory near Port Fourchon, LA (29° 06’04.59” N 90° 11’04.64” W). Smaller blue crabs (mean carapace width 6.02 ± 0.49 cm) were captured with long-handle dip nets from tidal creeks in brackish waters near Leeville, LA. *Ischadium recurvum* were hand collected from intertidal oyster reefs 21 km northwest of Port Fourchon near Leeville (29° 17’40.15 N 90° 13’52.72 W). All sites had soft sediment substrata, and the salinity at Port Fourchon was approximately 25 -30 PSU, and at Leeville 10 -20 PSU. Mussels were placed in 19 L buckets covered with wet burlap sacks for transport back to our laboratory. Crabs were placed in a 93 L cooler and layered with wet burlap sacks. At our Louisiana State University laboratory, crabs were held and starved individually in 38 L aquaria with under-gravel filters at 25 PSU for 48 hours before experiments began. Prior to experiments, bivalves were held in two 56 L aquaria with under gravel filters at 25 PSU.

**Dry Tissue Mass, Handling Time and Resistance to Breakage** To calculate dry
tissue mass per individual for *I. recurvum*, 102 mussels ranging in length from 14.7 mm to 57.6 mm (from umbo to farthest edge) were dissected and all tissue carefully removed and placed in a drying oven at 60° C for 24 h. The tissues were then weighed, and an exponential model was fit between shell length and dry tissue mass using Proc Reg (SAS 1997).

Handling times were recorded with a time-lapse video recorder with lights on continuously (Brown and Haight 1992). A 38 L tank at 25 PSU (average salinity at collection sites) was lined on all sides by opaque paper to prevent visual distractions. The top of the tank was covered with 2 cm Vexar mesh to prevent predator escape. A mirror above the tank, angled at 45°, reflected the image to the camera and video recorder. One mussel was placed in each corner of the tank. Two were greater than or equal to 31 mm in length and two mussels were less than 31 mm, the average mussel size on the oyster reefs. The smaller mussels ranged from 12.5-30.6 mm and the larger mussels ranged from 31.4 mm – 61.9 mm. Carapace width was measured, and a single crab was added to the tank, and the recorder was set to record for 24 hours. Any time period that the crab handled a mussel was recorded, and all times were summed to estimate total handling time in seconds. Handling time ended when the mussel had been cracked and consumed.

I performed curvilinear regressions to examine the relationship between shell length and handling time separately for large blue crabs, small blue crabs, and stone crabs (Table 4.1). Forty-seven mussels were consumed in 20 experiments with large blue crabs. In 14 experiments with small blue crabs, 34 mussels were consumed. There were 13 experiments for stone crabs in which 36 mussels were consumed.
Handling time data were log$_{10}$ transformed, and an Analysis of Covariance was performed to examine differences in handling times between predators with mussel size as the covariate. A one-way ANOVA tested for differences in mean handling times among mussel size classes (11-20 mm, 21-30 mm, 31-40 mm, 41-50 mm, and 51-60 mm) within each predator treatment. When possible, the method with which the predator gained access to mussel tissue was also noted during the experiments. When only fragments of shell were left, mussels were classified as “crushed.” If the valves were pried apart and mostly intact, they were classified as “pried apart.”

Table 4.1. Equations and r-squared values of regressions of handling time against mussel size for three predators.

<table>
<thead>
<tr>
<th>Predator</th>
<th>Equation</th>
<th>$r^2$</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>C. sapidus &lt; 10 cm</td>
<td>$y = 5.40x^{0.01}$</td>
<td>0.48</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>C. sapidus &gt; 10 cm</td>
<td>$y = 5.05x^{0.01}$</td>
<td>0.15</td>
<td>0.02</td>
</tr>
<tr>
<td>M. adina</td>
<td>$y = 0.05x + 4.73$</td>
<td>0.45</td>
<td>0.01</td>
</tr>
</tbody>
</table>

To determine forces necessary to crush shells, five mussels in each of the five size classes were placed in an INSTRON 4411 press (Figure 4.2), and were positioned between two aluminum plates with a diameter of 3 mm (comparable to the diameter of the denticles of large C. sapidus). I used the INSTRON Series IX Program software to collect the data, and a compression rate of 50 mm / min (comparable to rates exerted by crabs, B. Aronhime, personal observation) was used to record the maximum resistance to breakage. To determine the force necessary to crush the chelae, the crusher chelae of M. adina and two size classes of C. sapidus (<10 cm, > 10 cm) were collected from crabs caught using baited crab traps as described above. The crusher chelae were kept on ice for transportation to Louisiana State University. Chelae were placed in a water bath at room temperature for two hours prior to crushing. The
movable dactyls were removed from the chelae. The chelae including the immobile dactyls (pollices) were embedded in fiberglass resin along the base of the pollex to hold chelae in place. The pollices were used because they could more easily be positioned and fixed to the crushing plate. The chelae were positioned so the press exerted force directly on the largest tooth on the pollex nearest the junction of the pollex and the chela (Figure 4.3), where crabs typically crush mussel shells (Elner 1978, B. Aronhime personal observation). A compression rate of 50 mm / min was used to record the maximum force needed to fracture the pollex.

Figure 4.2 Photograph of (A) INSTRON 4411 press setup for mussel crushing experiments and (B) positioning of mussel in pressure plates. The scale bar is 10 mm.
Profit Dry tissue masses estimated from the dry mass to shell length regression were divided by the estimated handling times from curvi-linear models to estimate profit. Profit values were $\log_{10}$ transformed and tested for normality and homoscedasticity using Proc Univariate (SAS 1997). Because no mussels > 50 mm were consumed by *C. sapidus* <10 cm (see results), the experimental design was unbalanced, and 2 two-way ANOVAs were performed. All ANOVAs were preformed with Proc Mixed (SAS 1997) with predator treatment, mussel size and the interaction as the fixed effects. I used Proc Mixed because it is more robust to normality issues than Proc GLM or ANOVA (SAS 1997). Since estimating variation in profit between predators and
different mussel size classes was so crucial to our hypotheses, I also compared linear regressions of profit on mussel size for each predator treatment.

**Size Selection** Selection experiments were conducted in 38 L aquaria at 25 PSU with under gravel filters and a 12:12 photoperiod. Forty mussels were added in 5 size classes (6-10 mm, 11-20 mm, 21-30 mm, 31-40 mm, and 41-50 mm, and 1-2 from 51-60 mm) with 20 mussels always greater than 30 mm, and 20 less than or equal to 30 mm in length. Mussels were held with one crab for 48 hours, or until roughly half of the mussels were consumed (Brown and Haight 1992). The number of mussels consumed in each size class \( r \) and the number of mussels offered in that size class \( n \) were recorded. Chesson’s (1978) \( \alpha \) for each size class was calculated as an estimate of electivity:

\[
\alpha = \frac{(r/n)_i}{\Sigma (r/n)},
\]

where \( r \) is number of prey items consumed and \( n \) is number of prey items offered in size class \( i \). The index ranges from 0 to 1 with the null hypothesis that the proportion of each size class consumed would equal 0.2 since there were five mussel size classes. Due to the lack of independence among size classes in preference experiments (e.g., where several prey size classes are offered to a predator in the same experimental unit), a simple two way ANOVA could not be performed (Peterson and Renaud 1989). A MANOVA was therefore used to test for differences in \( \alpha \) among the size classes of mussels as well as among predator treatments. Since one degree of freedom is lost because the electivity of the last prey size class is known when \( \alpha \) is calculated, one prey size class must be excluded from the analysis (Chesson 1978, 1983), and I excluded the largest size class. *A posteriori* tests for MANOVAs are not available, and I therefore
performed separate one-way MANOVAs for each predator treatment to examine size selection, because a significant interaction occurred between mussel size and predator treatment (see results).

Results

Handling Times, Foraging Mode and Resistance to Breakage Handling times increased exponentially with increasing mussel size (Figure 4.4), although the fit equations and R-squared values for the curves differed among predator treatments (Table 1). The ANCOVA indicated a significant effect of mussel size ($F_{1, 119} = 8.48, p < 0.0001$) and predator treatment ($F_{2, 119} = 20.19, p < 0.0001$) but no interaction ($F_{2, 119} = 0.75, p = 0.63$). For the four smaller size classes the small blue crabs did consume, handling times increased with size ($F_{4, 32} = 3.37, p = 0.04$), as they did as well for large *C. sapidus* ($F_{4, 53} = 4.73, p = 0.002$). Handling times for stone crabs showed this pattern as well, although the effect of prey size was not quite significant ($F_{4, 23} = 2.54, p = 0.07$).

![Figure 4.4](image.png)

Figure 4.4 Logarithms of handling times (in seconds) versus mussel size for three predators: *M. adina* (SC); *C. sapidus* > 10 cm carapace width (LBC); *C. sapidus* < 10 cm carapace width (SBC).
I was unable to discriminate between “boring” and “edge chipping” techniques on videotapes and they were combined as “pried apart,” but was able to distinguish between “crushed” and “pried apart.” Foraging methods differed among predators (Figure 4.5). Stone crabs crushed all mussels regardless of size. Small blue crabs did not crush any mussels and did not consume any greater than 50 mm. Large blue crabs crushed the smallest two size classes of mussels, but pried apart mussels greater than 30 mm.

A one way ANOVA indicated differences in resistance to crushing between different size mussel prey and predator categories (Figure 4.6, F₄,₅₉ = 82.66, p < 0.001). Comparison of Tukey a posteriori tests indicated forces needed to crush mussel shells were not significantly lower than the crushing resistance of chelae of both small and large blue crabs, while much more force was necessary to damage the
chelae of stone crabs. In some cases the force needed to crush the stone crab chelae was greater than 2 kN, which was the maximum force the press could exert.

**Profit** The two way ANOVA comparing profit of mussels (g/s) of all mussel sizes between large *C. sapidus* and *M. adina* indicated no predator effect (*F*$_{2,86}$ = 1.42, *p* = 0.24), mussel size effect (*F*$_{5,86}$ = 2.32, *p* = 0.07), or interaction (*F*$_{5,86}$ = 0.31, *p* = 0.87). Data were normally distributed (Shapiro-Wilk’s *W* = 0.98, *p* = 0.61) and homoscedastic ($\chi^2$ = 7.06, *p* = 0.63). Although the size effect was close to significance in this analysis, separate linear regressions (Figure 4.7) indicated only weak positive trends, and that profit did not differ significantly with mussel size in small *C. sapidus* (*F*$_{1,32}$ = 0.17, *p* = 0.68), large *C. sapidus* (*F*$_{1,60}$ = 0.02, *p* = 0.88) nor *M. adina* (*F*$_{1,25}$ = 2.77, *p* = 0.11). In the second two-way ANOVA comparing all three predators with the largest size class of mussels excluded, there was a significant predator effect (*F*$_{3,109}$ = 19.75, *p* < 0.0001),

![Figure 4.6 Forces (+ SE) required to crush small, preferred *Ischadium recurvum* (SM), large, non-preferred mussels (LM), and the chelae of small blue crabs (SBC), large blue crabs (LBC) and stone crabs (SC).](image-url)
but no effect of mussel size ($F_{4, 109} = 1.87, p = 0.14$), nor interaction ($F_{12, 109} = 0.22, p = 0.97$). *A posteriori* Tukey tests indicated that mussel profit values (g/s) were smaller for the small blue crabs than large blue crabs ($p < 0.0001$) and stone crabs ($p < 0.0001$).

Data were normally distributed (Shapiro-Wilk’s $W = 0.99, p = 0.70$) and homoscedastic ($\chi^2 = 12.34, p = 0.26$) after log transformation. Based on these results, I predicted a lack of size preference in all the predators.

![Figure 4.7 Regression of I. recurvum profit (dry tissue mass / handling time) versus mussel size for M. adina (SC); C. sapidus >10 cm carapace width (LBC); and C. sapidus < 10 cm carapace width (SBC).](image)

**Size Selection** There was a significant effect of mussel size on $\alpha$ (MANOVA, $F_{4, 131} = 27.17, p < 0.0001$), an insignificant effect of predator type ($F_{2, 131} = 0.49, p = 0.61$), but a significant mussel size-predator interaction ($F_{8, 131} = 8.20, p < 0.0001$). Since the interaction was significant, I again performed one way MANOVAs that showed no effect of size on $\alpha$ for stone crabs ($F_{4, 35} = 0.09, p = 0.97$), as predicted by our estimates of profit, but a significant effect for large ($F_{4, 55} = 7.05, p = 0.0005$) and small blue crabs.
(F\textsubscript{3,39} = 66.07, p < 0.0001). Judging from deviations from the null model estimate of 0.2 (Figure 4.8A), both small and large C. sapidus showed a clear preference for the 11-30 mm mussel size range, despite the lack of a difference in profit. Comparing the actual number of mussels consumed (Figure 4.8B), more mussels were consumed in the smallest two size classes for blue crabs, while stone crabs consumed all but the largest mussels.

**Discussion**

**Size Selection, Profit and Handling Times** Blue crabs preferred small *I. recurvum*, in contrast to predictions from estimated profits, which were not clearly related to mussel size. Stone crabs on the other hand were not size selective, as predicted by lack of any size-specific trend in profit. Preference for small molluscs is common (Hughes and Elner 1979, Lawton and Hughes 1985, Ameyaw-Akumfi and Hughes 1987, Juanes and Hartwick 1990, Juanes 1992, Smallegange and Van der Meer 2003), and has also been found in previous studies with C. sapidus (Ebersole and Kennedy 1994, 1995). The differences in size selection among our crab predators may be explained by techniques used to open the shells. As with *Carcinus maenas* (Elner 1978), C. sapidus rarely crushed *I. recurvum* larger than 31 mm, and instead pried them apart, spending more time consuming them than that spent in crushing smaller prey (Elner 1978, Elner and Hughes 1978). Blue crabs may select mussels they can crush and consume rapidly (see below). In comparison, when feeding on *Mya arenaria*, with a thin, more globose shell than *I. recurvum*, C. sapidus crushed shells (Blundon and Kennedy 1982). Brown and Haight (1992) found that *M. adina* selected smaller oysters and *Stramonita haemastoma*, but also found no size-specific difference in profit. *Menippe adina* may
Figure 4.8 (A) Chesson’s $\alpha$ (± SE) versus mussel size for *M. adina* (SC); *C. sapidus* >10 cm carapace width (LBC); *C. sapidus* < 10 cm carapace width (SBC). The horizontal line indicates alpha without size selection. (B) Total number of *L. recurvum* consumed in all mussel sizes by *M. adina* (SC); *C. sapidus* >10 cm carapace width (LBC); *C. sapidus* < 10 cm carapace width (SBC).

select smaller oyster drill or oyster prey because of greater mechanical difficulties or chances of claw wear. Hooked mussels on the other hand required the smallest size-specific crushing force of six estuarine bivalves (Blundon and Kennedy 1982). Stone
crabs exert a crushing force of 0.13 kN/mm² (Brown et al. 1979), much greater than that exerted by *C. sapidus* (Schenk and Wainwright 2001). The relatively large crushing resistance of larger hooked mussels may not affect *M. adina*’s foraging strategy, but require *C. sapidus* to use a prying strategy which increases handling times.

**Profit** Although initially surprising, the lack of differences in profit among mussel sizes is fairly common in the literature. Hughes and Elner (1989) found no sized-based differences in profit with *Calappa ocellata* foraging on *Brachiodontes domingensis*. Ebersole and Kennedy (1995) also found no difference in profit among sizes of *I. recurvum* that they used, based on calories divided by handling time. However, because several profit currencies have been suggested, another model of profit could still indicate the smallest size class to be most profitable. For example, Juanes and Hartwick (1990) used oxygen consumption as an estimate of foraging costs with *Cancer magister*. They concluded instead that the energetic efficiency model (Profit = $E_{\text{gained}} / E_{\text{lost}}$) best described mussel size selection, with small bivalves the most profitable.

Charnov’s profit model (energy gained/handling time) has however helped to explain size selection in *C. sapidus* in other studies. For example, *C. sapidus* selected for small, profitable *Geukensia demissa* (Hughes and Seed 1981). Furthermore, when Rovero et al. (2000) used the heartbeat rate of *Carcinus maenas* to measure foraging costs and tested several currencies; they found no difference among mussel sizes classes when incorporating energetic costs. They did find a difference in profits when using gross energy gained over handling time, prompting us to use Charnov’s (1976) model.
Handling times for small *C. sapidus* were significantly higher, and profits lower, than for stone crabs and larger blue crabs. Increased handling times could certainly increase vulnerability to predators, and *Callinectes sapidus* are eaten by Sciaenids (Overstreet and Heard 1982, Guillory and Elliot 2001, Guillory and Prejean 2001, Brown et al. 2008), cobia (Arendt et al. 2001), sheepshead, spotted and white sea trout (Overstreet and Heard 1982), and adult conspecifics (Laughlin 1982, Hines et al. 1990). Post settlement juveniles (Heck and Wilson 1987, Heck et al. 2001, Heck and Spitzer 2001, Moody 2001) are especially susceptible (Zimmer-Faust et al. 1994). Choosing prey that reduce the amount of time the crabs themselves are exposed to predators is likely to be adaptive, and *C. sapidus* may thus be minimizing foraging time rather than maximizing net energy gain (Hughes and Seed 1981).

The fact that blue crabs select small mussels, although capable of feeding on larger mussels, and that forces required to crush larger mussels are near those that can damage chelae, suggest they might also select prey to minimize claw damage. Stone crabs lack size preference, evidently because their stronger claws allow them to take larger prey without claw damage, since forces required to damage their chelae are well above those required to crush mussel shells. Similarly, Kaiser et al. (1990) found that weaker-clawed green crabs selected smaller mussels than the red form of *Carcinus maenas* which has stronger claws, and crabs with smaller chelae select for smaller bivalves in general (Seed and Hughes 1995). The exact advantage for larger chelae in these studies could be the result of either increased crushing force or resistance to breakage, much like our results. Separating these two mechanisms is difficult as chelae that can exert greater force are also more resistant to breakage.
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CHAPTER 5

SUMMARY AND CONCLUSIONS
Summary

My results from Chapter 2 suggest that environmental stressors can limit the distribution of several predator species of estuarine bivalves, and decrease consumption rates, rejecting \( H_{01} \) (predator diversity, consumption rates, and prey mortality in the field would not vary along a salinity gradient) and support Figure 1.1 presented in the introduction. Predator richness and predation intensity were highest in the low stress environment. Predator richness declined monotonically with increasing stress as predicted. Predation intensity did not differ between the medium and high stress sites, which differs slightly from the predicted model, but predation intensity was still reduced relative to the low stress environment. Specifically, my results suggest reduced predator diversity and consumption rates, along with decreased prey mortality occur at sites with high levels of stress (low salinity). These results agree with Menge and Sutherland’s (1986) model predicting highest predation risk in areas with low stress (high salinity). The predator diversity data also agree with predicted estuarine diversity gradients, with the lowest diversity in waters that approach 6 PSU (Remane and Schlieper 1971) and highest diversity in coastal waters. The decreased consumption rates at low salinity also agree with previous work on *Stramonita haemastoma* (hereafter referred to as oyster drills, Garton and Stickle 1980), *Callinectes sapidus* (hereafter referred to as blue crabs, Guerin and Stickle 1997), and high mortality of *Menippe adina* (hereafter referred to as stone crabs, Guillory et al. 1995). However, the high mortality of oyster drills at the low salinity site was not expected. It may be because oyster drills and stone crabs were not found at the low salinity sites, but were instead collected at the high salinity site and transferred directly to the low salinity field.
experiment site without acclimation. In laboratory settings, oyster drills have survived salinities as low as 5 PSU (Stickle and Howey 1975) after stepwise acclimation, although their feeding rates decline below 7.5 at 30 degrees C (Garton and Stickle 1980).

The increased predation pressure at the coastal site likely explains the absence of subtidal oysters in high salinity, confirming what has been suspected by ecologists (Melancon et al. 1998). These experimental field data however are the first to actually show higher bivalve predator abundance, diversity, and prey mortality at higher salinities in an estuarine gradient. Other studies have shown increased oyster mortality during droughts (Livingston 2000) and a decreased diversity due to salinity (Crain et al. 2004).

The multiple predator interaction experiments clarify the mechanisms behind the increased predation risk at the high salinity field experiment site. That is, increased predation risk could have potentially been due to either increased total predator density, or facilitation between predators. The data I present here, in combination with the work of Richardson and Brown (1992), demonstrated no facilitation between three major invertebrate oyster predators. Blue crabs and stone crabs are thus substitutable predators, according to my results, and the interference between blue crabs and oyster drills certainly does not explain increased mortality at the high salinity (H₀₂: predator interactions would have an additive effect on prey mortality and that these interactions will not be altered at lower salinities, increased stress). The interference between blue crabs and oyster drills appears instead as the result of reduced feeding by oyster drills. Richardson and Brown (1992) also found that oyster drills decreased foraging rates in
the presence of stone crabs in the laboratory, but not in the field. It is therefore possible that the interference between blue crabs and oyster drills may also not occur in the field, requiring further investigation. Furthermore, in both predator combinations, mussel mortality in combined predator treatments did not differ from that in blue crabs alone, suggesting blue crabs are important predators on mussels, as with the case of blue crabs preying on *Macoma balthica* (Seitz and Lipcius 2001). A further examination of the enclosure and predator abundance data predicted that predation intensity would be highest at the high salinity site where total predator abundance was greater. The additional analysis supports the laboratory experiments and demonstrates that total abundance of blue crabs, stone crabs, and oyster drills is primary to bivalve mortality rather than predator diversity.

Salinity did not dramatically impact feeding behaviors, or the interactions between the predators in the multiple predator experiments, rejecting H₀₂. The lack of reduced consumption rates at reduced salinity in the multiple predator experiments was surprising, but perhaps the salinities I used were not low enough. For example, Garton and Stickle (1980) found a reduction in oyster drill feeding at 7.5 PSU at room temperature. In comparison, feeding at 10 PSU was reduced, but the effect was not significant. Blue crabs may also have decreased feeding at extremely low salinity, but again at less than 10 PSU. Stone crabs are less well studied, but should have fed less at the low salinity, given the 100% mortality of juveniles at 10 PSU (Brown and Bert 1993). My results (e.g. lack of feeding reduction) may be because adult stone crabs are more tolerant of low salinities than juveniles (Stuck and Perry 1992).
In general, in both field experiments and multiple predator experiments in the laboratory, the thinner shelled mussels had higher mortality rates than oysters (supporting $H_{03}$: crabs would not show prey preference). Prey preference analysis from the multiple predator studies revealed that mussels were in fact preferred over oysters. I believe this to be the result of two mechanisms: 1) Mussels are epizoic on oyster clumps, making them easier to access by all predators; And 2) Thinner shelled mussels are preferred by these predators because of the ease with which they are consumed, decreasing for example the chance of damage to crab chelae, and likely decreasing handling times as well. Thus blue crabs may be mechanically limited in their ability to consume oysters (Aronhime and Brown 2009). Indeed, blue crabs preferred smaller mussels (rejecting $H_{03}$), while stone crabs with thicker shelled chelae showed no preference. Thus, not surprisingly, blue crab chelae were much more susceptible to damage than stone crab chelae. Of particular interest was that the amount of force required to damage blue crab claws did not differ from the amount of force required to crush a large (> 30 mm) mussel. Blue crabs thus altered their feeding strategies from crushing to prying shells open with mussels > 30 mm, possibly to avoid claw damage. However, such prying techniques are also more time consuming, so whether size selection avoids chelal damage or minimizes handling times and predation risk is still unclear.

My data certainly support the idea that chelal damage could be an important factor in prey preference by blue crabs feeding on mussels. If blue crabs prefer smaller mussels for this reason, they may also prefer mussels over oysters because mussels are easier to crush. More investigation is needed, including the force required to crush
oyster shells. For example, *Menippe mercenaria* do not exert enough force to crush an adult oyster outright, and therefore use a series of slow pulses to fracture the oyster shell (Blundon 1988). Since stone crab claws exert greater force than blue crab claws (Schenk and Wainwright 2001), blue crabs also cannot crush oysters, and instead chip at the shell margins (Eggleston 1990).

In summary, the lower limits of subtidal oyster and mussel populations near the mouth of Louisiana estuaries appears to be set by increased predation risk. In brackish waters (5-15 PSU), stone crabs and oyster drills are rare because of osmoregulatory limitations in larval stages, and blue crab populations are less dense. At high salinity sites, the intense predation pressure restricts oysters and hooked mussels mostly to intertidal zones. However, mussels are rare even in intertidal coastal waters, apparently because of predation risk from crabs and oyster drills. Smaller mussels are especially preferred because of the ease with which they can be crushed. For the blue crabs, more easily consumed mussels may 1) minimize chelal damage, and/or 2) minimize handling times. Damaged chelae will also impede future feeding and long term fitness. Shorter handling times also minimize predation risk from predators such as redfish (*Sciaenops ocellatus*) and black drum (*Pogonias cromis*).

**Conclusions**

The results presented show that predation is a very important source of mortality in these estuarine bivalves. While I did not account for bottom up factors such as nutrient levels, phytoplankton abundance, or larval supply, the literature suggests no shortage of these bottom-up factors in the Barataria Bay system. The bays in southern Louisiana are eutrophic in terms of nutrients and phytoplankton (Turner and Rabalais
1991, Parsons et al. 2006). Additionally, oysters have higher fecundity in more saline environments (Mann et al. 1994). I find it unlikely, therefore, that bottom-up factors limit the distribution of the bivalves discussed in this dissertation in the Barataria Bay system. Predation has been suggested to limit the distribution of these bivalves before (Melancon et al. 1998) although not empirically tested. I present a case that the distribution of these bivalves may be limited by top-down control. Blue crabs exert top down control on Macoma clams in the Chesapeake (Seitz and Lipcius 2001) and may well be important here.

The Mississippi River’s natural flow has been altered by levees contributing to coastal erosion in coastal Louisiana (Abernethy and Turner 1987). To combat the erosion, the state has developed diversions at Caernarvon and Davis Pond. These diversions have been the cause of lawsuits by Louisiana oystermen and do not appear to carry enough sediment to overcome the rapid rates of wetland loss (Blum and Roberts 2009). Furthermore, the diversions make habitat in the headwaters of the estuary more suitable for mussels to foul the oysters. I hypothesize that the diversions will truncate the optimal salinity band for oysters by 1) reducing salinities in the upper estuaries below the tolerances of oysters and 2) burial from sediment deposition. Alternatively, the diversions may result in some relief of predation pressure in areas currently not suitable for oysters. The relief of predation pressure may not be enough to overcome the increased mortality from the diversions, however (Turner 2006).

My results also empirically confirm something that many Louisiana oystermen already believe, that predation intensity decreases in brackish waters. Oystermen often seed their oysters in brackish waters to reduce mortality from predation. My results
show that mortality from predation decreases in brackish waters and that predation is a very important source of mortality for not only oysters, but also mussels in higher saline environments. Furthermore, my results demonstrate that mussels may provide a benefit of being preferred prey by important oyster predators. However, fouling from mussels requires more time and effort in culling oysters and also makes them less marketable (Earl Melancon, Jr., personal communication). The benefit of reduced predation on oysters fouled with mussels may not overcome the costs of low market value and increased effort.

While this dissertation includes substantial work in understating predator prey interactions in estuarine bivalves, there is still much more work that could be done. First, competitive effects between hooked mussels and oysters have not yet been examined. While the presence of hooked mussels may reduce predation on oysters, they may also be competing for space and food resources. Similarities or differences in plankton size preferences between the bivalves may help to clarify any competition or lack thereof. Alternatively, facilitation between organisms has been shown to dampen the effects of a stressor and associative defenses may dampen predation intensity (Bruno et al. 2003). Therefore, facilitative effects between these bivalves are worthy examining to better understand the application of Menge and Sutherland’s model to the estuarine bivalve community. Replicating the field experiments (Chapter 2) with multiple sites per salinity treatment and simultaneously sampling for bottom up factors (nutrient and plankton abundance as well as larval supply) at each site may help to clarify top-down vs. bottom-up control of the distribution of these bivalves. Also looking
into the role of contaminants in oyster distribution may be worthwhile, although hydrocarbon levels were low at all of my sites (William Stickle, unpublished data).

Literature Cited


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APPENDIX: LETTER OF PERMISSION

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Sincerely,--
Barry Aronhime
VITA

Barry Aronhime was born in Louisville, Kentucky, in August 1981, to Bill and Barbara Aronhime. His older brother, Major Ben Aronhime, served as his friend and mentor. He graduated from Trinity High School in May 2000 and earned a bachelor's degree in marine biology (chemistry minor) from the University of North Alabama in May 2004. He spent two summers at Dauphin Island Sea Lab where he took marine behavioral ecology under Dr. Terry Richardson. Dr. Richardson guided him toward Dr. Kenneth Brown and Louisiana State University for research in animal behavior. Currently, he is a candidate for the degree of Doctor of Philosophy in biology.