

ABSTRACT

RINDONE, RICHARD RYAN. Predator-prey Dynamics between Recently Established Stone Crabs (*Menippe* spp.) and Oyster Prey (*Crassostrea virginica*). (Under the direction of David B. Eggleston).

Range expansion and population establishment of individual species can have significant impacts on previously established food webs and predator-prey dynamics. The stone crab (*Menippe* spp.) is found throughout southwestern North Atlantic waters, from North Carolina through the Gulf of Mexico and the Central American Caribbean, and including the Greater Antilles. Recent observations suggest that stone crabs have become better established on certain oyster reefs in North Carolina than in the early 1900's when they were first observed in NC. To assess the predatory impact of stone crabs on oysters, we (1) quantified stone crab densities on subtidal oyster reefs in Pamlico Sound, NC using scuba diver surveys, and (2) conducted laboratory predation experiments to assess the functional response of stone crabs to varying densities of oysters. We then (3) analyzed previously unpublished functional response data on another important oyster predator, the mud crab *Panopeus herbstii*. Finally, we (4) compared and contrasted potential predatory impacts of stone, mud and blue crabs (*Callinectes sapidus*). The functional response data and analyses for stone crabs was consistent with either a type I or II functional response, whereas mud crabs exhibited a type I functional response. Mud crabs, on a m² basis, inflicted the highest proportional mortality on oysters over a 24 hour period, followed by stone and then blue crabs. Proportional mortality did not vary significantly with oyster size; however, relatively small and large oysters were consumed disproportionately less than medium-sized oysters, likely due to the mechanical inability of stone crabs to handle small oysters, and the inability to crush large oysters. Although stone crabs appear to be established in Pamlico

Sound at densities equivalent to densities in other systems such as the Florida Panhandle, their predatory activities on oysters are not expected to have as significant a negative impact on oyster populations compared to other resident predators such as mud crabs.

Predator-prey Dynamics between Recently Established Stone Crabs (*Menippe* spp.) and Oyster
Prey (*Crassostrea virginica*)

by
Richard Ryan Rindone

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APPROVED BY:

David B. Eggleston
Committee Chair

Geoffrey W. Bell

Kevin Gross

Theresa M. Bert

BIOGRAPHY

Richard Ryan Rindone was born in Charlotte, North Carolina on September 14th, 1985. He grew up in and around the greater Charlotte area, also spending a great deal of time in Florida. Ryan's childhood passions included camping, hiking, swimming, racing, baseball, basketball, and fishing. Ryan has always demonstrated a great deal of creativity, a characteristic eventually leading him into an introductory program in architecture at the University of Miami. While he maintains an enthusiasm for drafting and design to this day, he discovered that he was better suited for work outdoors. Embracing a childhood obsession with the ocean, Ryan decided to pursue an education focusing on marine science. Applying to both North Carolina State University and the University of Miami, it was Ryan's interactions with Dr. Dave Eggleston that eventually led him to select NC State for his undergraduate degree. Beginning his college education in Marine Geology, Ryan quickly discovered he had little interest in the Earth's geologic features and changed degree paths to Natural Resources with a marine and coastal concentration. Earning his BS in 2007, he then went on to work for the Florida Fish and Wildlife Conservation Commission's Division of Marine Fisheries Management where he instructed Florida's marine fisheries stakeholders in ethical angling, marine conservation, and environmental stewardship. During the latter part of his first year working in Florida, Ryan was contacted by Dr. Eggleston about a graduate student position in his lab at NC State which Ryan eagerly accepted. In graduate school, Ryan furthered his passion for marine fisheries, discovering new ways to put his creativity to the test while also working to increase the understanding of predation on oyster reefs.

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TABLE OF CONTENTS

	PAGE
LIST OF TABLES	v
LIST OF FIGURES	vi
INTRODUCTION.....	1
OBJECTIVE	8
HYPOTHESES	9
MATERIALS AND METHODS	10
RESULTS	21
DISCUSSION	24
LITERATURE CITED	32
TABLES	40
FIGURES	42

LIST OF TABLES

	PAGE
Table 1	
Comparison of mean observed stone crab densities from diver surveys of oyster broodstock reserves in Pamlico Sound, NC, during August and September of 2009	40
Table 2	
Comparison of functional response models with respect to mud crab predation on oysters using Akaike's Information Criterion	41

LIST OF FIGURES

	PAGE
Figure 1 Distribution of stone crabs in the Southeastern United States	42
Figure 2 Map of several oyster broodstock reserves in Pamlico Sound, NC	43
Figure 3 Typical layout of an oyster broodstock reserve in Pamlico Sound, NC	44
Figure 4 Graphical depiction of common functional response curves	45
Figure 5 Relative stone crab density by oyster broodstock reserve, reserve salinity and month	46
Figure 6 Number of oysters eaten by stone crabs as a function of oyster density	47
Figure 7 Percent mortality of oysters eaten by stone crabs as a function of oyster density	48
Figure 8 Mean proportional mortality of oysters eaten by stone crabs as a function of oyster density	49
Figure 9 Percent of oysters from each size class offered that were consumed by stone crabs	50

LIST OF FIGURES

	PAGE
Figure 10 Observed mean handling time in minutes by stone crabs as a function of oyster density	51
Figure 11 Number of oysters eaten by mud crabs as a function of oyster density	52
Figure 12 Percent mortality of oysters eaten by mud crabs as a function of oyster density	53
Figure 13 Mean proportional mortality of oysters eaten by mud crabs as a function of oyster density	54
Figure 14 Food web diagram depicting the relative potential predatory impact of crabs on oysters	55

INTRODUCTION

Background

Range expansion and subsequent population establishment of species can have significant impacts to previously established food webs and predator-prey dynamics (Heatwole and Levins 1972, Crawley 1986, Hargeby et al. 1994, Field et al. 2007). Changes in predator-prey dynamics, in turn, often impact population dynamics of both predator and prey species (Holt 1984). For example, the introduction of mosquitofish (*Gambusia affinis*) into habitats plagued by increasing mosquito populations, likely due to warming climates, has, in many cases, resulted in the unintended yet drastic alteration of local ecosystems. The mosquitofish not only prey on mosquito larvae, but the larvae of frogs, newts, fish, and other aquatic organisms, decimating their local populations (Hurlbert et al. 1972). Other interesting examples of changing predator-prey relationships include the introduction and colonization of the Indo-Pacific lionfish (*Pterois volitans*) to Atlantic reef communities (Albins and Hixon 2008). Lionfish predation on native fishes reduced recruitment of those fish species to the reef by an average of 79%. Similarly, the Humboldt squid *Dosidicus gigas* has extended its perennial range in the eastern North Pacific Ocean during a period of ocean-scale warming and the decline of tuna and billfish populations (Zeidberg and Robison 2007). The Humboldt squid may be responsible for the decline of the Pacific hake *Merluccius productus*, as increased observations of squid have coincided with declines in commercial hake landings (Zeidberg and Robison 2007). The common trait shared by these three examples is the broad impact that relatively novel predators have had on their prey and ecosystems.

The stone crab (*Menippe* spp., hereafter “stone crab”) appears to have become better established in several of the sounds in North Carolina (NC), contrary to previous studies and surveys (Hay and Shore 1915, Rathbun 1930) which recognized the stone crab’s presence but did not infer its establishment. During the past decade, commercial crabbers for the blue crab (*Callinectes sapidus*) in NC have reported sharp increases in the bycatch of stone crabs (R. Howell, commercial crabber, Swansboro, NC, pers. comm.). Similarly, research divers visually surveying oyster reefs in Pamlico Sound, NC, have observed stone crabs and their burrows, especially in relatively high salinity estuarine areas (B. Puckett, NC State University, pers. comm.; S. Slade, NC Division of Marine Fisheries [NC DMF], pers. comm.). These diver surveys contradict the currently accepted northern range of the stone crab, presently determined to be Cape Lookout, NC (NOAA 2009). Inquiries to seafood distributors in Virginia indicate that the stone crabs have likely not yet extended their range north of NC since none have been landed north of Cape Hatteras (Sam Rust Seafood, Hampton, VA, pers. comm.). Although anecdotal information suggests that stone crabs are established in North Carolina, there is no quantitative data on their distribution and abundance patterns, nor on their predatory behavior on commercially and ecologically important oysters, which are the subject of large-scale restoration efforts in Pamlico Sound.

Stone crab life history

The stone crab *Menippe* spp. (Say) is a commercially important decapod predator, ranging from North Carolina to Florida and the Caribbean (Bert 1986, Fig. 1; Bert and Harrison 1988, Gerhart and Bert 2008). The predominant species of stone crab include the

Florida stone crab *Menippe mercenaria*, the Gulf stone crab *Menippe adina*, and hybrids between the *M. mercenaria* and *M. adina* species. Juvenile and adult *M. mercenaria* stone crabs are typically light tan or gray in color with white stripes at the joints on the legs, and spotting on the dorsal carapace and claws. They burrow into sand under seagrass beds and excavate holes in hard bottom habitats in higher salinity waters (>25 ppt), and feed primarily on shellfish (Bert 1986). *M. adina* stone crabs are usually dark brown in color, burrow into sandy and hard-bottom habitats, including oyster reefs in low-to-high salinity waters (≥ 15 ppt), and prey primarily on mollusks. Hybrids of these two species can exhibit characteristics representative of both species. NC stone crabs constitute a hybrid population of these two species. They have the mtDNA characteristic of both pure species (T. M. Bert, Florida Fish and Wildlife Conservation Commission [FWC], pers. comm.) and, in general, the allozyme allele frequencies and coloration of introgressed *M. mercenaria*-like hybrids (Bert and Harrison, 1988). The hybrid nature of NC stone crabs is supported by the principally *M. mercenaria* allozyme allele frequencies, the *M. mercenaria*-like to *M. adina*-like coloration (Bert and Harrison, 1988), and the burrowing behavior into hard-bottom oyster habitat (an *M. adina* characteristic) (R. Rindone, pers. obs.). Adult stone crabs have much larger claws than adult blue and mud crabs (R. Rindone, pers. obs.), which may impact the adult stone crab's predatory behavior on NC oysters.

The principal reproductive season for stone crabs occurs between May and September (Williams 1984, Caldwell 1992). Ovigerous females travel from inshore habitats to higher salinity waters offshore to spawn. Hatched larvae develop through two major stages: zoea and megalops. The zoeal stage displays several developmental phases, each lasting ~3 days. The

entire zoeal stage progresses over ~19 days, through successive molts. The megalops stage consists of a single phase lasting approximately 8 days. The megalopal phase is transitional between the planktonic zoeal and benthic juvenile stages. Once megalopae settle to the benthos and molt into the juvenile stage, they reside in benthic cover such as seagrasses, sessile invertebrates, and in hard-bottom habitats such as oyster reefs (Porter 1960, Futch 1966). As molting continues and juveniles become mature adults, molt frequency decreases. Females mate while molting, while males must be in an intermolt phase to mate (Gerhart and Bert 2008). Mature stone crabs utilize a variety of habitats including jetties, shell cultch, mud bottom, seagrass beds, and oyster reefs. Mature crabs dig burrows extending in depth between 30 and 100 cm (Futch 1966, SCDNR 2005; T.M. Bert, FWC, pers. comm.).

Blue crab and mud crab life histories

Two other dominant decapod crustacean predators on oysters are the blue crab (*Callinectes sapidus*) and mud crab (*Panopeus herbstii*) (Sellers and Stanley 1984, Bisker and Castagna 1987, Eggleston 1990, Silliman et al. 2004). Briefly, blue crabs complete their transition from the larval to the megalops stage in approximately one month and to the adult (reproductively mature) stage in eight months to one year, and growth ceases during local winter months (Kennedy and Cronin 2007, and references therein). Blue crabs are considered to be general opportunistic bottom scavengers, preying on a variety of crustaceans, mollusks, finfish, and local flora (Darnell 1959, Lipcius et al. 2007), and can withstand a wide range of temperatures and salinities (Tagatz 1969). Mud crabs are very common in temperate and tropical waters of the Atlantic and the Gulf of Mexico (Dittel et al. 1996). Spawning occurs

during summer months (similar to other Xanthid crabs), and the zoea and megalopae remain within the estuary (Sandifer 1975). Mud crabs serve as important components of benthic food webs in a variety of habitats (Whetstone and Eversole 1981, Meyer 1994, Dittel et al. 1996, Silliman et al. 2004). The predatory behaviors of blue and mud crabs were selected for comparison with stone crab predatory behaviors since all three species live on oyster reefs and consume oysters.

Oyster life history

The Eastern oyster, *Crassostrea virginica* (Gmelin), is an economically and ecologically important shellfish found throughout coastal and inland waters from the Gulf of St. Lawrence in Canada south to the West Indies to Venezuela, and west through the Gulf of Mexico (Sellers and Stanley 1984). Oysters are suspension-feeding epibenthic organisms that form complex reef systems of varying size and density in intertidal and subtidal habitats (Kennedy and Breisch 1983, Coen et al. 1999). Oyster reefs provide several ecosystem and human services, including improved water quality (Sellers and Stanley 1984), essential fish habitat via structural refuges for prey from predators, associated prey communities that enhance foraging opportunities for predators (Coen et al. 1999, Lenihan et al. 2001, Peterson et al. 2003), as well as a harvestable resource that supports local, regional, and global economies.

In 2008, commercial oyster harvests in North Carolina totaled 211,176 kg of meat, worth \$2,036,491 US (NC DMF 2008). Oyster population declines throughout its range have initiated widespread restoration efforts in many estuaries to encourage the recovery of this important species (Peterson et al. 2003, Schulte et al. 2009). Examples of oyster restoration

efforts include Chesapeake Bay (MD DNR 2009), Pamlico Sound (NC DMF 2008), and the Pensacola Bay System (FL DEP 2009). Predators of oysters include mobile crustacean species, including the Gulf stone crab (*Menippe adina*) (Baltz and Horst 1992, Juanes 1992, Coen et al. 1999, Peterson et al. 2003, Grabowski et al. 2005). In southern Florida, pure-species *M. mercenaria* stone crabs do not live among or prey upon oysters (T.M. Bert, FWC, pers. comm.); however, recent laboratory studies indicate that stone crabs (*M. mercenaria*, Wong et al. 2010; *M. adina*, Fodrie et al. 2008) readily prey on bivalve mollusks such as hard clams (*Mercenaria mercenaria*) and oysters (*C. virginica*), and pilot studies indicated that stone crabs (*Menippe* spp.) found in intertidal and subtidal communities in NC readily prey on oysters (R. Rindone, NC State University, unpublished data). A recent bio-economic modeling study (Millstein and Eggleston, in review) suggests that restoration of oyster reefs in Atlantic waters of the southeastern United States could significantly increase the overall abundance of stone crabs. Therefore, stone crab range expansion may significantly impact oyster communities along the East Coast of the United States via predation on oysters, as well as other potential indirect effects including crab burrowing and interspecific interactions between stone crabs and other native oyster reef inhabitants.

Predator-prey dynamics and the functional response

A predator's functional response is a measure of the number of prey consumed per predator as a function of prey density (Solomon 1949, Holling 1959), and is a key process underlying predator-prey dynamics. To fully characterize a predator's functional response, the number of prey available and prey handling time must be measured or estimated from

mathematical models (Holling 1959). Understanding the functional response of predators is essential to predicting their impact on prey population dynamics. The type of functional response observed gives researchers insight into the dynamic relationship between predators and varying prey densities. In this study, the functional response was used to understand the underlying behaviors and mechanisms associated with stone and mud crab predation on oysters, and to make relative comparisons of potential predatory impact among crabs.

There are three main forms of functional response: Holling's type I, II and III (Fig. 4). A type I functional response demonstrates a linear increase in the number of prey consumed and constant proportional mortality of prey as prey density increases, reaching an upper asymptote in the number of prey consumed and a linear decrease in proportional mortality of prey as prey density continues to increase. This type of functional response is often representative of filter-feeders (Hassell 1978). The predator is capable of consuming an increasing amount of prey up to a point where the prey's density (or concentration) exceeds the predator's ability to consume more prey items, resulting in the decrease in proportional mortality as prey density (or concentration) continues to increase. This density-independent type of functional response can potentially lead to localized extinction of prey items (Hassell 1978). In a type II functional response, the number of prey consumed increases exponentially to an upper asymptote with proportional mortality decreasing to a lower asymptote as prey density increases. This pattern of inversely density-dependent consumption reflects the increased energetic costs associated with higher consumption rates at higher prey densities. The type II functional response is often indicative of decapod crab predation (Eggleston 1990, Sponaugle and Lawton 1990, Eggleston et al. 1992, 2005, Taylor and Eggleston 2000, Wong and Barbeau 2005). Similar to the type I

response, a type II functional response can also lead to localized extinction of prey items, with the proportional risk of prey mortality increasing with decreasing prey density (Hassell 1978). The type III functional response is sigmoid, revealing density-dependent consumption rates at low to moderate prey densities. This scenario is often observed when the energetic benefit of consumption is not sufficient enough to offset the energetic costs of foraging. Unlike type II, the risk of prey mortality in a type III functional response decreases as prey density decreases. The number of prey consumed at low densities is relatively low, followed by a sharp increase up to an upper asymptote. Similarly, the proportional mortality of prey in a type III response increases, peaks, and then decreases as prey density continues to increase. These patterns likely arise as a function of the predator learning to search more for a given prey item as prey density increases, eventually becoming satiated as prey density continues to increase. The type III functional response, unlike types I and II, can result in a relative prey refuge at low prey densities (Hassell 1978). A type III functional response is often the result of predator learning, prey switching, and prey inaccessibility or refuge (Lipcius and Hines 1986, Eggleston et al. 1992).

Objectives

The objectives of this study were to:

1. Quantify abundance patterns of stone crabs in subtidal oyster reefs in Pamlico Sound, NC.
2. Quantify the functional response of stone crabs to varying densities and sizes of eastern oysters.
3. Quantify the functional response of mud crabs on oysters, by statistically analyzing previously unpublished data.

4. Use information from 1-3 above, in combination with previously published functional response data for blue crabs preying on oysters, to assess the potential predatory impact of stone crabs on oysters relative to predation by mud and blue crabs.

HYPOTHESES

We tested four hypotheses using a combination of field surveys, laboratory feeding studies, and statistical analyses of previously unpublished functional response data for mud crabs:

- H₁: Mean stone crab densities will not vary significantly according to month and oyster broodstock reserve.
- H₂: The proportion of oysters eaten/adult stone crab or adult mud crab/unit time will vary with oyster density, irrespective of mean oyster size, and will increase with decreasing oyster density, indicative of a type II functional response (based on the preponderance of type II functional responses for other crab-bivalve predator-prey systems: Eggleston 1990, Sponaugle and Lawton 1990, Wong and Barbeau 2005).
- H₃: The observed handling time (T_h) of oysters by adult stone crabs will not vary with oyster density.
- H₄: Oysters measuring less than 25 mm in left valve length will have a relative size refuge from predation by adult stone crabs.

MATERIALS AND METHODS

Study Area

Pamlico Sound is the largest water body in the Croatan-Albemarle-Pamlico Sound Estuarine System (CAPES), which constitutes the largest lagoonal system and the second largest estuarine system in the United States (Pietrafesa et al. 1986, Xie and Eggleston 1999). Pamlico Sound is a wind-driven, shallow, lagoonal estuary that is separated from the Atlantic Ocean by a string of barrier islands. Three major inlets connect the estuarine waters with the Atlantic Ocean (Pietrafesa et al. 1986). In North Carolina, ten oyster broodstock reserves have been created by the NC Division of Marine Fisheries (NC DMF) in Pamlico Sound (Fig. 2) in the hopes that these reserves will be self-sustaining, as well as supply larvae to other areas in Pamlico Sound that are still open to harvest (NC DMF 2006). These high relief mounds are each constructed with ~ 150 tons of limestone rip-rap material to a height of approximately two meters above the seafloor and two meters below the water's surface (Fig. 3). Mounds are spaced equidistantly and ~ 15 m apart. The areas containing the mounds have been established as reserves in which the harvest of oysters is strictly prohibited. Natural oyster reefs in Pamlico Sound primarily fringe the sound in relatively shallow waters near the mainland or barrier islands, and are often intertidal. Previous field research in Pamlico Sound oyster broodstock reserves has identified potentially increasing numbers of stone crabs at relatively high-salinity reserves such as Ocracoke, Hatteras, and West Bay (R. Rindone, NC State University, unpublished data). We quantified stone crab distribution and abundance in four of these 10 reserves during 2009 (see below).

Objective 1. Quantify abundance patterns of stone crabs in subtidal oyster reefs in Pamlico Sound, NC.

The distribution and abundance of stone crabs in Pamlico Sound, as well as in the oyster broodstock reserves, is currently unknown. Oyster broodstock reserves in Pamlico Sound provide oyster settlement habitat that is protected from oyster harvest. Of the ten available oyster broodstock reserves, four were selected for assessment of stone crab abundance: West Bay, Ocracoke, Hatteras, and Crab Hole (Fig. 2), based on their relatively similar mound composition and similar construction dates in 2006 or earlier (NC DMF 2008).

One of every 10 mounds created in 2006 or earlier within each oyster reserve was chosen randomly to survey for stone crabs using scuba divers, and a minimum of three mounds were selected in each reserve. Scuba-diver surveys for stone crabs were repeated in early August and early September of 2009 at randomly chosen oyster mounds each month. Mound area measurements were averaged and standardized for all mounds surveyed at each reserve based on previous side-scan-sonar mapping of these oyster reserves (Ballance 2006) to facilitate measures of stone crab density. Average mound area at each reserve was: Ocracoke: 109.6 m², Hatteras: 222.4 m², West Bay: 194.7 m², and Crab Hole: 170.6 m² (Ballance 2006). A two-person team of SCUBA divers descended on each mound and conducted one-meter visual transects using a marker line with marks every meter in the vertical direction. Divers swam in a “corkscrew” manner from the top of a mound to the bottom searching for stone crabs within each 1 m vertical “bin”. The same two-person dive team surveyed all selected mounds in all reserves to decrease any variability due to diver skill, such as an individual diver’s ability to discern a stone crab burrow from a rock crevice while underwater, and the ability to detect and

correctly identify stone crabs on/in oyster reef habitat. When stone crabs were not visible from burrow entrances, divers used 1 m long aluminum rods (“tickle sticks”) to determine whether a stone crab burrow was occupied or vacant by inserting the rod into the burrow, then rotating the rod around while moving it back and forth in a sweeping motion. Using this method, it was possible to detect the presence of stone crabs within burrows because the rod would come into contact with the crab, which would usually grab the rod once it was touched (R. Rindone, pers. obs.). Both the total number of burrows observed and the number of burrows occupied by stone crabs were recorded during diver surveys, as well as discernable prey debris and depth. Temperature, salinity, and dissolved oxygen measurements were taken once at each reserve at an approximate depth of 2 meters. Stone crab surveys were conducted in early August and early September when water temperatures were warm. Surveying stone crabs during these months may have increased the likelihood of observing stone crabs occupying burrows on the mounds, as these months are within the time of the year when commercial crabbers cite noticeable stone crab activity (R. Howell, commercial crabber, Swansboro, NC, pers. comm.). All surveys took place during daylight hours and no specimens were taken from reserves.

Statistical analyses of field observation data

Comparisons of mean stone crab density across months and among reserves (H_1) were conducted using a two-way ANOVA with month (August, September) and oyster reserve (West Bay, Ocracoke, Hatteras, and Crab Hole) as factors. Subsequent multiple comparison tests were conducted using Tukey’s Honestly Significant Difference (HSD) test, since

comparisons between means using either Bonferroni's or Scheffe's tests could potentially have been too conservative (J. Thompson, NC State University, pers. comm.).

Objective 2. Quantify the functional response of stone crabs to varying densities and sizes of eastern oysters.

Stone crabs were captured with blue crab pots along the central NC coast in Bogue Sound, as well as the North and White Oak Rivers, NC and transferred to holding tanks at the Center for Marine Science and Technology (CMAST) in Morehead City, NC. Crabs were fed fish, squid and bivalves *ad libitum* prior to feeding trials. Only large (80 – 130 mm carapace width, CW- Mean CW: 96 mm, SD: 12.02 mm), male, inter-molt stone crabs, representative of the dominant size class on oyster reefs in Pamlico Sound (R. Rindone, pers. obs.), were used in feeding trials because adult male stone crabs are typically larger and have thicker chelae than their adult female counterparts (T. M. Bert, FWC, pers. comm.), which may increase the adult male's ability to attack a larger size range of molluscan prey items.

Oysters were hand-collected haphazardly from subtidal and intertidal habitats in Bogue Sound, NC. Most oysters were attached to cultch material such as larger oyster shells, rocks, or limestone rip-rap. Oysters were grouped into five density categories to facilitate treatment applications and some statistical analyses for functional response (L: <100/m², M: 100-250/m², H: 250-400/m², VH: 400-800/m², VVH: >800/m²). These density groupings are representative of naturally occurring densities found in oyster broodstock reserves where stone crabs were surveyed (B. Puckett and D. Eggleston, unpubl. data). In addition to density groupings, each oyster was measured by left valve length (LVL mm) and placed into one of four size categories

(0-25mm, 25-40mm, 40-70mm, 70+mm), representative of naturally occurring shell valve lengths found at the oyster broodstock reserves in Pamlico Sound, NC (B. Puckett and D. Eggleston, unpubl. data). Prior to use in experimental feeding trials, oysters were stored in a flow-through tank of filtered seawater (30 μ m) at Carteret Community College (adjacent to CMAST) with flow rates of 90 l/min. Prior to the start of a feeding trial, the size and location of each oyster on the cultch pieces were recorded (mm LVL) and mapped by hand, after which a given oyster density was placed into a single randomly selected tank. Oyster LVL was measured to determine if predation varied with oyster size class (H_4). Oysters were mapped to facilitate quantifying the number and percent of oysters consumed during each feeding trial, as well as those sizes that were eaten upon the termination of a feeding trial. No fouling organisms, which could serve as alternative prey, were found on the oysters used in feeding trials.

Laboratory experiments were performed from May to July 2009 at CMAST's wet-laboratory facilities to determine the functional response of adult stone crabs to varying densities and sizes of oysters. Twelve experimental tanks (measuring 31.5 cm wide, 45 cm long, and 42 cm deep; filled to ~60 l) were positioned in an identical manner to ensure homogeneity with respect to extraneous variables, such as laboratory foot traffic and lighting, and were visually isolated from one another. Tanks were supplied with a steady flow of filtered seawater (30 μ m) at a rate of 90 l/hr. Inflow tubes were regulated by polyvinyl chloride ball valves with inflow pipes terminating at subsurface levels to allow for clear viewing of specimens within tanks, and to eliminate any altered crab behavior as a result of

surface water disruption/turbulence. This tank layout allowed for concurrent feeding trials and random interspersions of oyster density treatments.

A single, randomly selected stone crab was measured (mm CW) and then placed into a randomly assigned tank after being starved for 48 hours to ensure total digestion of stomach contents (e.g., Eggleston 1990). A randomly selected oyster density treatment was then placed in the treatment tank during late evening hours. Crabs were placed in tanks approximately 2 hours prior to oyster density treatments to allow each crab time to acclimate to the tank environment. The subsequent feeding trial lasted ~12 hr, after which time the remaining prey items were removed, and the numbers and sizes of oysters eaten versus live oysters remaining were recorded. Time-trial data was then extrapolated out to be equivalent to a 24-hr time period, since NC State scientific divers have not observed any evidence of variation in daytime or nighttime feeding behavior in laboratory pilot studies (Rindone, pers. obs.) or in the wild (Rindone, pers. obs.; D. Eggleston and G. Plaia, pers. comm.). The same procedure was repeated 12 times for each of the 5 oyster density groupings for a total of 60 trials.

A total of 16 stone crabs were used in the study due to logistical and live specimen storage constraints. No crab was subjected to the same oyster density treatment more than once. To ensure that experimental treatments were independent, I assessed the potential for certain individual crabs to be better (or worse) at feeding under laboratory conditions than others, as well as the potential for crabs to “learn” to more efficiently prey on oysters over time. To assess possible crab effects on oyster predation, the number of oysters eaten and the percent of oysters consumed were analyzed separately using a 2-way ANOVA with individual crab (blocking factor) and oyster density as the explanatory variables using a partially

balanced, incomplete block ANOVA model. To assess possible time effects on crab predation, the number of oysters eaten and the percent of oysters consumed were analyzed separately using a linear regression model with the Julian Day of the laboratory trial as the explanatory variable. The mean number and percent mortality of oysters eaten did not vary significantly according to either the crab blocking factor or time (both $p > 0.16$), suggesting that each laboratory predation trial be viewed as an independent replicate.

Behavioral observations

The continuous-time type II functional response model, which was the model chosen in this study to fit to the crab predation data (see justification below), employs the basic components of predation,

$$N_e = \frac{a' T N_t}{1 + (a' T_h N_t)}$$

where the number of prey eaten per predator (N_e) equals a function of the instantaneous attack rate (a'), total time available for foraging (T), the number of prey available (N_t), and prey handling time (T_h). The instantaneous attack rate (a') is a measure of encounter success with prey, and is equivalent to the area a predator searches for prey per unit time. Handling time (T_h) is the time from the initial encounter between predator and prey, through prey capture and manipulation, ingestion and digestion of the prey item, to when the predator resumes foraging behavior (Hassell 1978). Since a' and T_h can vary with the functional response model chosen, reliable parameter estimates are typically chosen from the most parsimonious model that provided a statistically significant fit to the data (e.g., Eggleston et al. 2008).

Stone crab prey handling time and behavior were observed (H_3) during the first hour of feeding to avoid possible satiation effects, which can increase handling time and reduce attack rates (Eggleston 1990). Prey handling time was quantified in 7 of 12 feeding trials at the lowest three oyster density groupings. These densities were used because pilot studies indicated that the greatest amount of change in percent mortality of oysters occurred at these density levels (consistent with Lipcius and Hines 1986, Eggleston 1990, Eggleston et al. 1992). “Foraging” was characterized as movement by crabs around the tank and use of legs and chelae to probe oyster cultch and oysters. An “oyster attack” was characterized by a stone crab selecting an oyster prey item, attempting or succeeding to dislodge the prey item and break open the shell, potentially consuming the prey item, and discarding the remains of, or ignoring, the prey item.

Statistical analyses of laboratory feeding data

Our goal concerning the functional response of stone crabs (and mud crabs, see below) to oysters was to determine if predation rates were density-independent or –dependent, and if density-dependent, to objectively determine if the functional response was type II or III. First, we determined if proportional mortality varied with oyster density with a one-way ANCOVA model, with oyster density as the independent variable and oyster LVL as the covariate. Pair-wise comparisons between mean proportional mortality rates and oyster density were then conducted using Tukey’s Honestly Significant Difference (HSD) test. If the relationship between proportional mortality and oyster density was not statistically significant across all levels of oyster density, or at the lowest oyster density treatment levels followed by a decline in

proportional mortality with increasing oyster density, this would indicate density-independent mortality (type I functional response, Hassell 1978). If proportional mortality was significantly lowest at the lowest oyster density treatments, followed by an increase as oyster density increased, this would indicate a type III functional response. If proportional mortality was significantly highest at the lowest oyster density treatment levels and then declined as oyster density increased, this would indicate a type II functional response. The results of statistical testing of stone crab laboratory functional response data indicated no support for a type III functional response, and evidence in support of both type I and type II functional responses (see Results below). Given that both type I and II functional responses can be destabilizing to predator-prey dynamics (Eggleston et al. 2008), I fit the data to both discrete- and continuous-time type II functional response models to generate estimates of a' and T_h that could be compared to decapod predators of oysters:

Discrete-time type II:

$$N_e = N_t * (1 - \text{EXP}(-a' * (t - (T_h * N_e))))$$

Continuous-time type II:

$$N_e = \frac{(t * N_t * a')}{(1 + (a' * T_h * N_t))}$$

where a' is the instantaneous attack rate, T_h is the prey handling time, N_t is the total number of prey available for predation, N_e is the total number of prey consumed by a single predator, and t is the time available for foraging by the predator. The purpose of testing both discrete- and continuous-time models was to determine the most accurate estimates of instantaneous attack rate and prey handling time. Testing revealed that the continuous-time model best fit the data (see Results). Estimated values for attack rate (a') and handling time (T_h) from the continuous-

time type II functional response model were then used to make relative comparisons of potential predatory impact among crabs (see below).

*Objective 3. Quantify the functional response of mud crabs (*Panopeus herbstii*), another key decapod predator on oysters, by statistically analyzing previously unpublished data*

In July and August of 1985, D. Eggleston (NC State University [NCSU]) examined the predatory behavior of the mud crab *Panopeus herbstii* on eastern oysters within a flow-through seawater system at the Virginia Institute of Marine Science, Gloucester Point, Virginia. The laboratory system and feeding protocols observed were similar to those described in Eggleston (1990) and Eggleston et al. (1992). Briefly, predation trials were conducted in 0.33m² experimental tanks. Oyster density treatments were set to 5, 10, 20, 30, 40, and 50 oysters per tank (or 15, 30, 61, 91, 121, and 152 oysters/m²) due to logistical constraints with testing additional levels of oyster density, and to test low prey density levels to detect changes in predation to facilitate functional response evaluation (D. Eggleston, NCSU, pers. comm.). Mud crab carapace width in millimeters was also recorded. No mud crabs were subjected to the same oyster density treatment twice, and only one mud crab was present in each tank for each density trial. Predation trials were conducted over 48 hours since pilot studies indicated that mud crab predation occurred at a slower rate when compared with other decapod predators such as blue crabs. Mud crabs often use their chelae as a type of “ice-pick” to punch a hole in the oyster’s umbo, followed by insertion of the chelae into the exposed oyster and cutting the adductor muscle, or simply prying the oyster apart (D. Eggleston, NCSU, pers. obs.). For comparison with this study, predation results for mud crabs have been adjusted to a 24-hour-

feeding period for comparison to stone and blue crab functional response experiments by dividing the number of oysters consumed by a mud crab in each trial by 2. The mud crab predation data were then statistically analyzed as described above to determine the type of functional response (H_2) and estimate behavioral parameters. Observed values for T_h were not recorded for mud crabs.

Objective 4. Use information from objectives 1-3 above, in combination with previously published functional response data for blue crabs preying on oysters, to assess the potential predatory impact of stone crabs on oysters relative to predation by mud and blue crabs.

I estimated the relative potential predatory impact of stone, blue and mud crabs on oysters by combining laboratory functional response data on stone and mud crabs with previously published data on blue crab functional response (Eggleston 1990). Next, field observations of stone crab density in this study were combined with density data for blue and mud crabs. This allowed for an estimate of maximum predatory potential among the three decapod crabs and oysters (i.e., maximum feeding rate/crab X number of crabs/m² in field). Stone crab density (0.13 crabs/m²) data were provided via field surveys at the Ocracoke oyster broodstock reserve in Pamlico Sound, where densities were highest (this study). Since no data were available for blue crab density in oyster broodstock reserves in Pamlico Sound, blue crab density (0.09 crabs/m²) was based on surveys of Snow's Cut in the Cape Fear River estuary in North Carolina (Cammen 1976). Mud crab density for oyster broodstock reserves in Pamlico

Sound was also unavailable; therefore, mud crab density was set to 20 crabs/m² based on data for estuaries in southeastern NC (Harwell 2004).

RESULTS

Objective 1. Quantify abundance patterns of stone crabs in subtidal oyster reefs in Pamlico Sound, NC.

The mean density of stone crabs per m² in a given reserve varied significantly according to the location of an oyster broodstock reserve, but not between months (2-way ANOVA; Reserve: $F = 23.34$, $df = 6$, $p < 0.0001$; Month: $F = 0.26$, $df = 1, 23$, $p = 0.6148$) (Table 1). There was no significant Reserve X Month interaction effect ($p = 0.2418$). Stone crab densities on oyster broodstock reserves in Pamlico Sound ranged from 0.02 to 0.127/ m². Highest mean densities of stone crabs were found at Ocracoke, followed by West Bay, Hatteras, and Crab Hole (Tukey's HSD; Fig. 5).

Objective 2. Quantify the functional response of stone crabs to varying densities and sizes of eastern oysters.

In general, the number of oysters eaten per stone crab increased with oyster density, but with considerable variation at intermediate densities (Fig. 6). The percent mortality of oysters increased sharply with decreasing oyster density (Fig. 7), indicative of either a type I or type II functional response. The percent mortality of oysters varied significantly with oyster density, but not oyster size (ANCOVA; oyster density: $F = 16.62$, $df = 1, 59$, $p < 0.0001$; oyster size: $F = 0.18$, $df = 1, 59$, $p = 0.67$). There was no statistically significant oyster density X oyster size

interaction effect ($F = 0.65$, $df = 1$, 59 , $p = 0.42$). Mean percent mortality of oysters was not significantly different between the three lowest oyster density treatments, nor between the third lowest treatment and the next highest oyster density treatment (Tukey's HSD multiple comparisons test; Fig. 8). Thus, according to our *a priori* criteria for determining the type of functional response, there was equivocal support for either type I or type II, and no strong evidence in support of a type III functional response. Both type I and II functional responses have similar implications regarding predator-prey dynamics, in that both demonstrate high levels of proportional mortality at low prey densities, potentially resulting in localized extinction of prey (Hassell 1978, Eggleston et al. 2008). Subsequent examination of the fit of both discrete- and continuous-time type II functional response models to the data indicated that only the continuous-time, type II functional response model provided a statistically significant fit to the data (SAS Proc Nlin: Gauss-Newton: $F = 24.06$, $df = 2$, $p < 0.0001$; discrete-time, type II functional response model $p > 0.24$).

Oysters appeared to have a relative prey refuge in size to adult male stone crabs at both small (< 25 mm LVL) and large (> 70 mm LVL) sizes (Fig. 9). Observations of prey handling time (T_h) by stone crabs increased with increasing oyster density (Fig. 10).

Objective 3. Quantify the functional response of mud crabs (Panopeus herbstii), another key decapod predator on oysters, by statistically analyzing previously unpublished data.

The number of oysters eaten per mud crab increased with oyster density up to an asymptote as oyster density continued to increase (Fig. 11). The percent oyster mortality due to mud crabs was highest at low oyster densities, and decreased sharply with increasing oyster

density (Fig. 12). The percent mortality of oysters varied significantly with oyster density (ANOVA: $F = 33.63$, $df = 5$, $p < 0.0001$). Data were not available to test the relationship between mud crab predation and oyster size because all oysters offered during feeding trials were within the same general size range (31.5 ± 8 mm LVL). Mean percent mortality of oysters was not significantly different between the two lowest oyster density treatments, which were significantly different from successively higher oyster density treatments (Tukey's HSD multiple comparisons test; Fig. 13). This pattern in percent mortality with oyster density is consistent with both a type I and II functional response. Models with a large number of parameters are often more flexible and provide a more accurate description of the data than those with few parameters. In practice, it is not desirable to always accept the most complex model from a candidate set, and it is generally accepted that the best model is one that provides an adequate predictive capability with the fewest parameters (Myung & Pitt 1997). We chose AIC (Akaike 1973) for model selection, a commonly used approach which provides an objective method for selecting the most parsimonious model that still provides an adequate fit to the data. To determine the most appropriate model of predation, we statistically measured the relationship between the numbers of oysters eaten by mud crabs and oyster density using linear regression, as well as discrete- and continuous-time type II functional response models in SAS (proc nlin for type II models). The functional response of mud crabs to oyster prey was best explained by a type I functional response model (Linear regression: $F=52.16$, $df=1$, $p<0.0001$, Table 2).

Objective 4. Use information from objectives 1-3 above, in combination with previously published functional response data for blue crabs preying on oysters, to assess the potential predatory impact of stone crabs on oysters relative to predation by mud and blue crabs.

Although stone crabs displayed the highest attack rates and shortest prey handling times of the three crabs examined, mud crabs appear to be the dominant decapod predator of oysters based on their approximately two-order of magnitude higher density per m² on oyster reefs compared to either stone or blue crabs (Fig. 14).

DISCUSSION

Stone crabs appear to have extended their range from Cape Lookout, NC as far north as Cape Hatteras. This range expansion could result in increased vulnerability of higher salinity oyster reefs (≥ 15 ppt) to stone crab predation. Diver surveys found that stone crabs were abundant on relatively high-salinity oyster reefs in Pamlico Sound, NC, though future research should examine stone crab distribution and abundance on oyster reefs across a varying range of salinities to better understand the effects of salinity on their ecology. Stone crabs may exhibit either type I or type II functional response, in which proportional mortality rates increased sharply at the lowest oyster densities. Similarly, blue crabs exhibited an inversely density-dependent, type II functional response when preying on oysters (Eggleston 1990). Mud crabs exhibited density-independent type I functional response, where proportional mortality remains high at low oyster densities. The demonstration of type I and II functional responses by these crab species indicates that oyster reefs at low prey densities may be vulnerable to localized extinction by crab predators. By multiplying the maximum potential number of oysters

consumed per crab from functional response experiments (i.e., asymptote of the functional response) by the best estimates of the density of a given crab in the field, mud crabs were determined potentially to be the dominant decapod predators of oysters, followed by stone and blue crabs. These results suggest that although stone crabs appear to have become better established on some high salinity oyster reefs in Pamlico Sound than originally thought, they are not expected to greatly alter oyster abundance due to predation at current levels of oyster and stone crab densities, especially when compared with mud crabs at current best estimates of mud crab densities.

Field abundance patterns of stone crabs

Observed densities of stone crabs in Pamlico Sound oyster broodstock reserves (0.13 crabs/m²) are in the range of those found in the Florida Panhandle (Apalachee Bay: ~0.1 crabs/m², St. Joseph Bay: ~0.16 crabs/m², Lanark Reef: ~0.17 crabs/m²; *Menippe* spp., Beck 1997), and are orders of magnitude higher than those found in southwestern Florida (mean: 0.001 crab/m², or 1 crab/hectare; Bert 1985). The similarities between stone crab densities in Pamlico Sound and the Florida Panhandle, as well as observations of stone crabs spawning in nearby Bogue Sound, NC (M. Hooper, commercial diver, per. obs.), suggest that stone crab populations in some areas of Pamlico Sound may be sufficiently established to support local stone crab fisheries if preliminary stock assessments can set sustainable catch limits (Muller et al. 2006).

Stone crab densities within Pamlico Sound were three times higher at Ocracoke than other oyster broodstock reserves, despite the lack of significant differences in mean salinities

between reserves. Conversely, the salinity at Crab Hole was ~ 10 ppt, which is below the lower salinity tolerance for both juvenile and adult stone crabs (Brown and Bert 1992), and we never observed stone crabs there. In addition to salinity, mean annual temperature appears to be another important factor influencing stone crab distribution patterns. For example, anecdotal evidence indicates that no stone crab claws have ever been landed at one of the largest seafood dealers in North Carolina and Virginia (Sam Rust Seafood, Inc.) from fishermen fishing north of Cape Hatteras. Additional stone crab surveys in other possible habitats north of Cape Hatteras, including relic oyster reefs and man-made hard-bottom structures like jetties, should be conducted to validate or refute the inference that Cape Hatteras represents the current biogeographic northern limit of stone crab establishment. In addition to salinity and temperature, other variables may influence stone crab distribution and abundance patterns in North Carolina, such as structural aspects of oyster and rubble habitat (Beck 1995, 1997), available prey, and predation risk. The similarities between observed stone crab densities in Pamlico Sound and those of historically established stocks observed by Beck (1995, 1997) in the Florida Panhandle suggest that NC stone crabs are comparably established in Pamlico Sound. The use of scuba diver surveys and the resulting stone crab density data should be useful to fishery management agencies such as the NC DMF, as it begins to assess the status of the stone crab stock in the face of an emerging fishery for it in North Carolina.

Laboratory predator-prey experiments

The results of laboratory functional response experiments suggest that adult, male stone crabs exhibit either destabilizing type I or II functional responses when preying on eastern

oysters. These types of functional responses can result in localized extinction of prey species at low prey densities (Hassell 1978). Given the varied densities of oysters observed in Pamlico Sound, it is possible that low density oyster reefs with established stone crab populations could be subjected to localized extinction if stone crab predators do not emigrate or exhibit prey-switching behavior as the abundance of oyster prey items decreases. It should be noted, however, that stone crab foraging decreased and handling time with prey increased as oyster densities reached higher levels (> 800 oysters/m²). This potential prey refuge from stone crabs at high oyster densities could be due, in part, to mechanical hindrances experienced by large adult stone crabs trying to prey on tightly packed oysters at high densities. This mechanical limitation could result in more time spent foraging and handling prey and less time spent actually consuming prey at high prey densities. Future studies should assess how the proximity of oysters to one another and the orientation of oysters to the substrate influence foraging efficiency of adult stone crabs on oysters.

The observed values for prey handling time mentioned in this study comply with one of the assumptions of type II functional response, which states that prey handling time increases as prey density increases because a predator cannot capture additional prey while already handling a prey item, causing predation to proceed more slowly than it may at lower prey densities (Abrams 1990). Likewise, this limitation in the ability to handle multiple prey items may also result in a decrease in instantaneous attack rate as prey density increases, as predators are not likely to search for additional prey whilst already handling a single prey item (e.g. Hassell et al. 1977, Murdoch et al. 1984).

Oysters measuring less than 25 mm LVL and greater than 70 mm LVL were preyed upon significantly less than oysters measuring between 25 and 70 mm LVL. For oysters measuring less than 25 mm, the decreased level of predation by stone crabs was likely due to the inaccessibility of these smaller prey items to the crab as a result of the crab's general lack of dexterity (Rindone, pers. obs.). The stone crab's claws are not as pointed as the claw tips of other decapods such as portunids, nor are they as small as smaller xanthids, which may help to explain decreased foraging on relatively small oysters. Reduced predation on smaller oysters is not necessarily due to low prey profitability (prey size-specific dry tissue mass divided by prey handling time) because prey profitability is generally uniform across oyster size classes, indicating that increased handling times may be balanced by increases in size-specific oyster dry tissue mass (*M. adina*, Brown and Haight 1992). Similarly, greatly reduced feeding on relatively large oysters > 70 mm LVL may be due to mechanical difficulty when attempting to crush their relatively large shells (*M. adina*, Brown and Haight 1992). Size refuges for larger prey items are not uncommon in crustacean-molluscan predator-prey interactions (Robles et al. 1990, Brown and Haight 1992, this study).

Mud Crab Predation Trials

Mud crabs exhibited a type I functional response to varying densities of oysters. The higher quantity of oysters (albeit smaller in LVL) consumed by mud crabs per 24 hours compared to blue and stone crabs may be due to two distinct reasons. First, since the adult mud crabs used in Eggleston's study were smaller than the adult stone crabs used in the present study, they could conceivably prey upon the more numerous, smaller oysters. Second, the

claw tips of mud crabs are typically more pointed than those of stone crabs (Rindone, pers. obs.), and likely aid mud crabs in achieving improved dexterity and relatively low prey handling times with smaller oyster prey items. Thus, it appears that the <25mm LVL size refuge for oysters observed to exist under stone crab predation in this study is compromised in the presence of predatory mud crabs. This conclusion should be further investigated, since O'Connor et al. (2008) showed that juvenile mud crabs (10-20mm CW) consumed fewer oysters than juvenile blue crabs (30-70mm CW), and that the presence of only juvenile mud crab predators on oyster habitat resulted in higher recruitment of oysters than in the presence of juvenile blue and/or stone crabs. Higher oyster recruitment in the presence of juvenile mud crabs may be explained, however, by mud crab predation on freshly settled barnacles in late spring/early summer months (G. Plaia, pers. comm.), potentially drawing predation away from juvenile oysters while simultaneously clearing off settlement substrate for the oyster larvae. This explanation is supported by empirical evidence that verifies mud crab predation on barnacles (McDermott 1960, Bahr 1974), but should be tested experimentally. Further study should also examine the predatory relationship between mud crabs and oysters at oyster densities higher than those used in this study, to determine at what oyster density (or range of densities) the number of oysters consumed by mud crabs plateaus and remains constant as oyster density continues to increase (e.g., Fig. 4).

Potential predatory impact of stone crabs on oysters in broodstock reserves

Mud crabs exhibited the highest potential predatory impact of the three decapod crabs examined in this study, which was likely due to the approximately two-order of magnitude

higher density of mud crabs than stone or blue crabs on oyster reefs. Though stone crabs appear to be better established in certain parts of Pamlico Sound than in decades past, they do not seem to be more important predators on oysters when compared to mud crabs, despite the stone crab's higher value for instantaneous attack rate and lower value for prey handling time when compared with the mud crab.

In conclusion, the present study is the first to examine the functional response of stone crabs on a prey item. Collectively, stone crabs (*M. mercenaria*, *M. adina*, and the *Menippe* hybrids examined in this study) throughout the southwestern North Atlantic ocean eat a wide variety of prey items including oysters (Fodrie et al. 2008, O'Connor et al. 2008, this study), other bivalves and gastropods (Wong et al. 2010), and sea urchins (R. Rindone, pers. obs.). Recent investigations of the direct and indirect effects of stone crabs on food webs have emphasized facilitation or inhibition of predation by stone crabs within multiple predator, single prey systems (Fodrie et al. 2008, O'Connor et al. 2008, Brodeur et al. 2010, Griffin and Silliman 2010, Johnson and Smee 2010, Wong et al. 2010). For example, oyster predation by oyster drills (*Stramonita haemastoma*) was partially facilitated by the crushing/opening of oyster shells by stone crabs, which periodically consumed oyster drills in addition to oysters (Fodrie et al. 2008). Also, the size refuge from blue crab predation experienced by clams (*Mercenaria mercenaria*) was reduced in the presence of stone crab predation (Wong et al. 2010). Likewise, examinations of predator extinctions indicated that stone crabs may serve as redundant predators of juvenile oysters when cohabitating on oyster reef habitat with blue and mud crabs (O'Connor et al. 2008). Further information regarding stone crab food web dynamics should help to better parameterize food-web models for those fishery managers

applying ecosystem-based fishery management concepts to recently established stone crab populations (e.g., NMFS EPA Panel 1999, Pikitich et al. 2004, Smith et al. 2007).

The results of this study have many other applications. Understanding crab predation on oysters offers resource managers a way to predict and plan for approximate losses of local oyster populations, and these predictions can be adjusted as both oyster and crab populations change with time. Changes in the crab's diet may serve as an indicator of the health and abundance of the oyster population should crabs cease to prey on oysters, justifying the need for additional studies on the prey preference of crab predators. Stock assessments of oyster reef habitat with respect to foraging predators, oyster density and oyster size may reveal which reefs are most susceptible to short- and long-term effects due to crab predation. Lastly, increased understanding regarding the role of oyster density and oyster reef architecture on crab foraging efficiency may help in the design of oyster restoration efforts.

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TABLES

Table 1: Comparison of mean stone crab densities observed during diver surveys of oyster broodstock reserves in Pamlico Sound inhabited by stone crabs during August and September 2009. Data for Crab Hole has been excluded, since no stone crabs were observed at that site.

Month	Reserve	Mean Density (per m²)	Standard Deviation
August	West Bay	0.048	0.021
	Ocracoke	0.125	0.035
	Hatteras	0.015	0.003
September	West Bay	0.012	0.013
	Ocracoke	0.130	0.049
	Hatteras	0.022	0.008

Table 2: Comparison of mud crab functional response predation models using Akaike’s (1973) Information Criterion (AIC). The lowest “ ΔAIC ” value represents the model measured to have the most support in representing the data, while the highest “ W_i ” value represents the probability that the error distribution for the corresponding model is the best among the models tested.

Model	# of parameters	n	df	F	SSR	AICc	ΔAIC	W_i
Linear Regression	2	40	1	52.2	10.36	-49.71	0.00	0.955
Discrete-time type II FR	2	40	1	269.4	20.18	-23.04	26.67	0.000
Continuous-time type II FR	2	40	2	238.9	12.07	-43.61	6.11	0.045

FIGURES

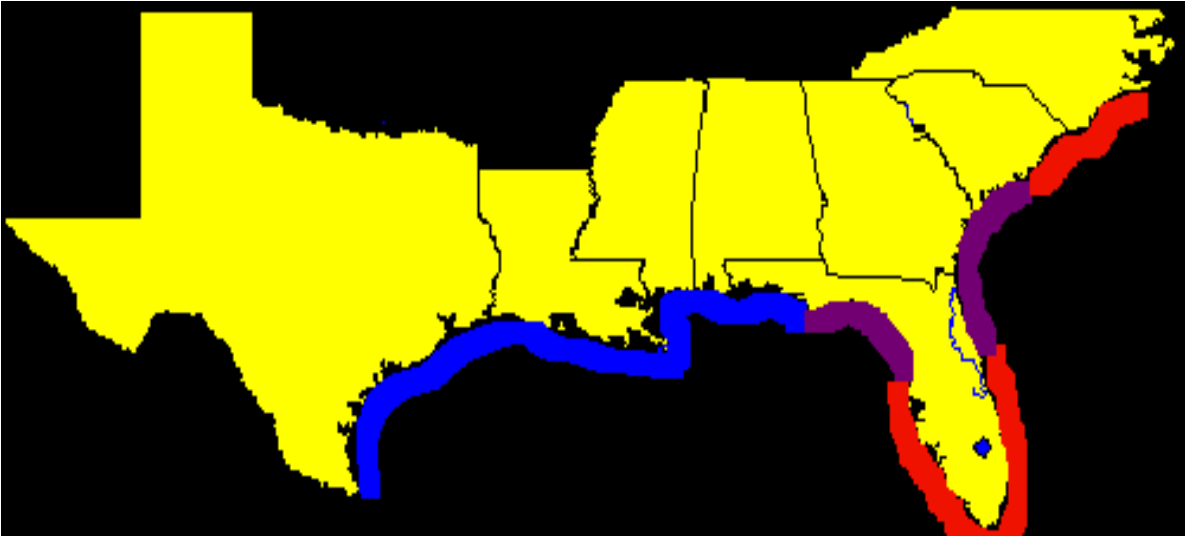


Figure 1: Distribution of stone crabs at present. Blue = *Menippe adina* range, red = *Menippe mercenaria* range, purple = hybrid zones (T. M. Bert, FWC).



Figure 2: Six oyster broodstock reserves in Pamlico Sound, NC. Reserves used to determine relative stone crab abundance in this study include West Bay, Ocracoke (AR-298), Hatteras (AR-296), and Crab Hole.

Oyster Sanctuary

The typical sanctuary consists of mounds of rip rap, with each mound containing about 150 tons of material.

7-foot
clearance

6-foot
mounds
of rip rap

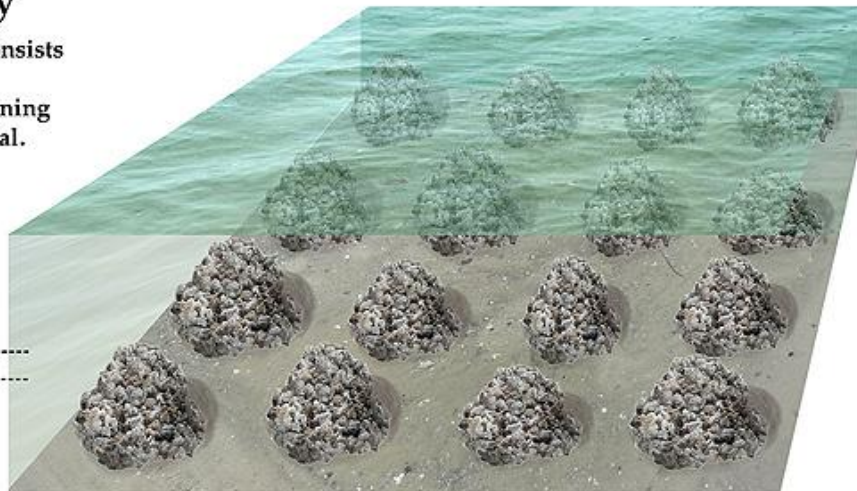


Figure 3: Typical layout of a subtidal oyster broodstock reserve in Pamlico Sound, NC (NCDMF 2009). Each oyster mound is constructed from approximately 100-150 tons of limestone rip-rap material and is spaced equidistant from the surrounding oyster mounds (NCDMF 2009). Actual distance between sea surface and oyster mound peak varies from mound to mound and reserve to reserve (Rindone, pers. obs.).

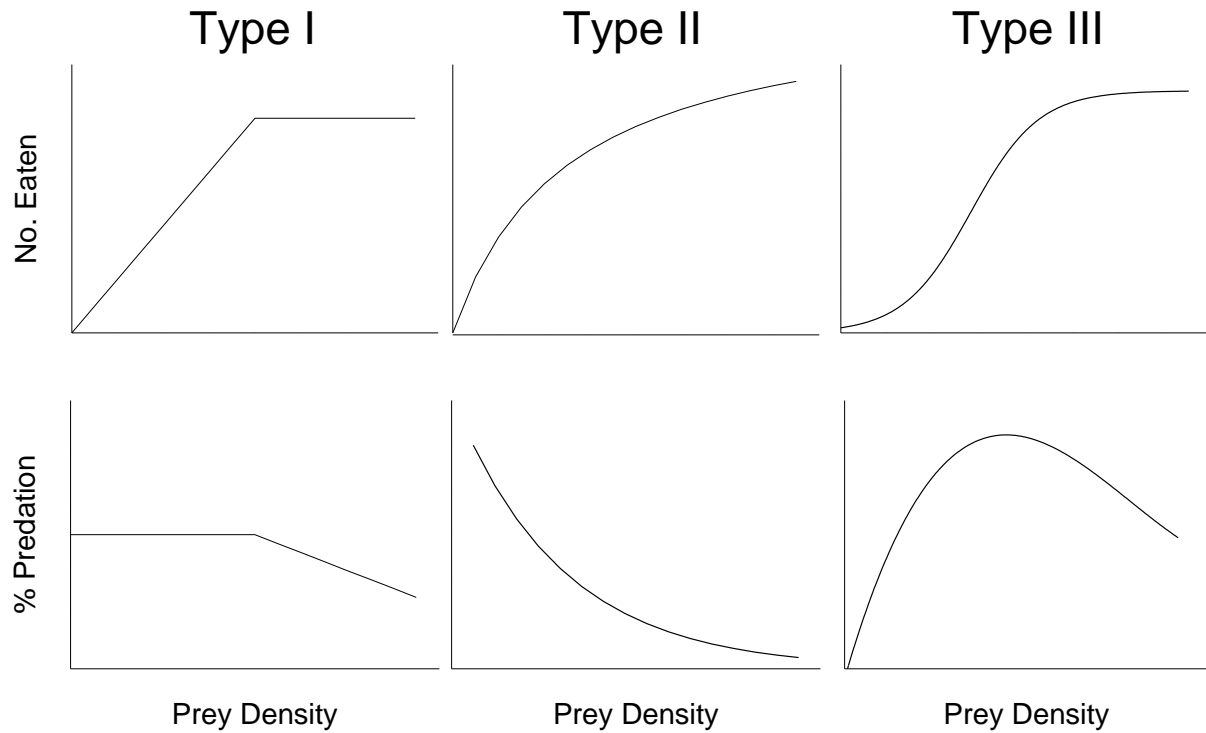


Figure 4: Graphical depictions of the three main types of functional response, with the relationship between the number of prey eaten and prey density on the top row and the relationship between the percent predation of prey and prey density on the bottom row (after Hassell 1978).

Stone Crab Density by Reserve with Salinity

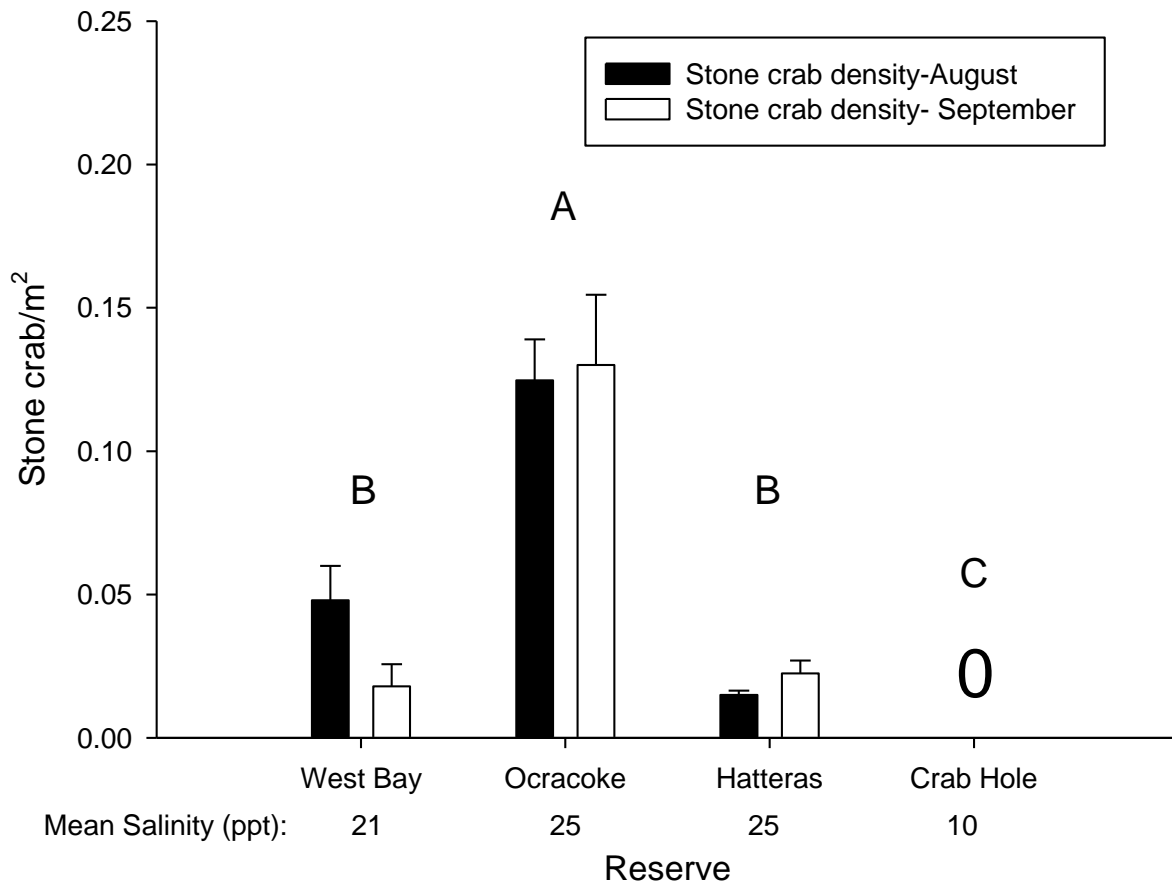


Figure 5: Mean (+ 1 SE) stone crab density in Pamlico Sound, NC as a function of oyster broodstock reserves, with corresponding mean salinity (ppt) on the x-axis. Differences in means determined via Tukey's HSD test are denoted by capitalized letters above data bars, with similar letters indicating no significant difference between reserves (see text for further results of statistical analyses).

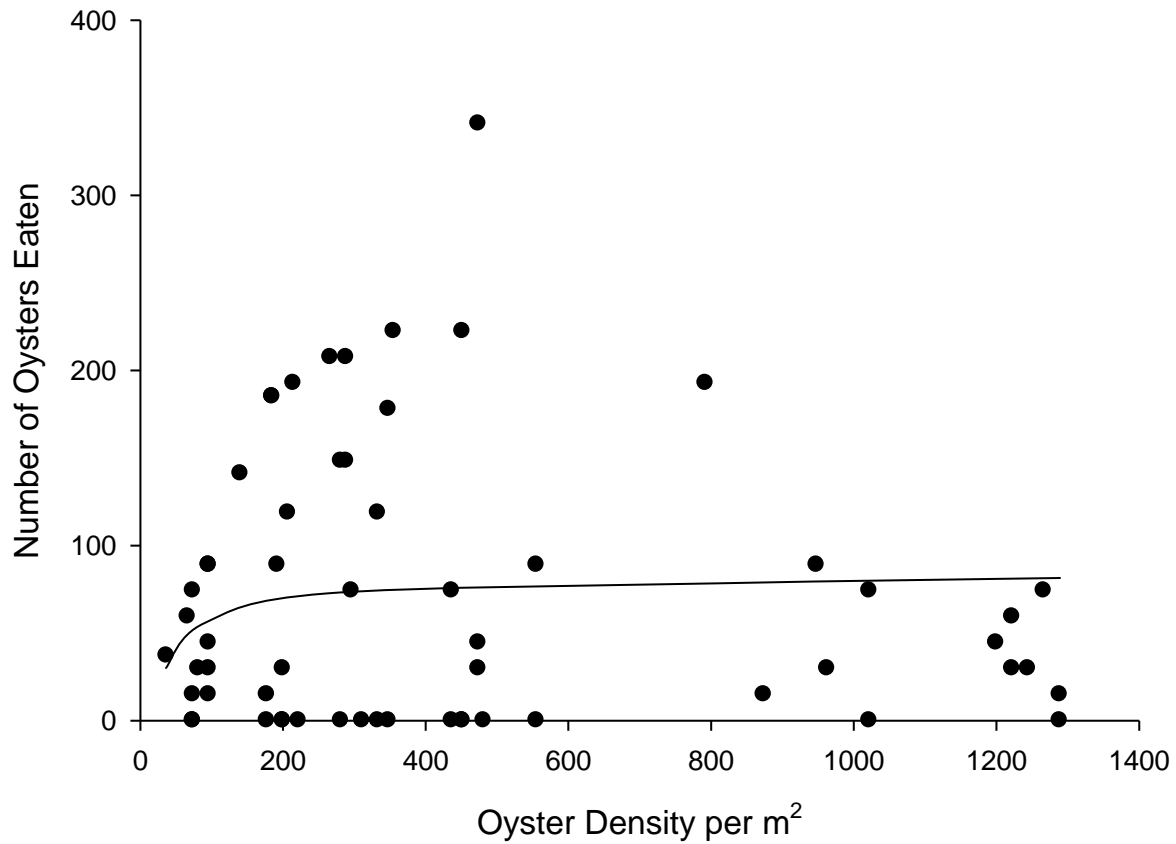


Figure 6: Relationship between the number of oysters eaten (y-axis) per predator per 24 hours and oyster density (x-axis). Line fit to data is from a non-linear, continuous-time type II functional response model (see text for statistical results to determine the type of functional response, and the best fitting functional response model). Linear regression modeling of the number of oysters eaten by stone crabs as a function of oyster density was not significant (Linear regression: $F = 0.69$, $df = 1$, $p = 0.41$, $R^2 = 0.01$).

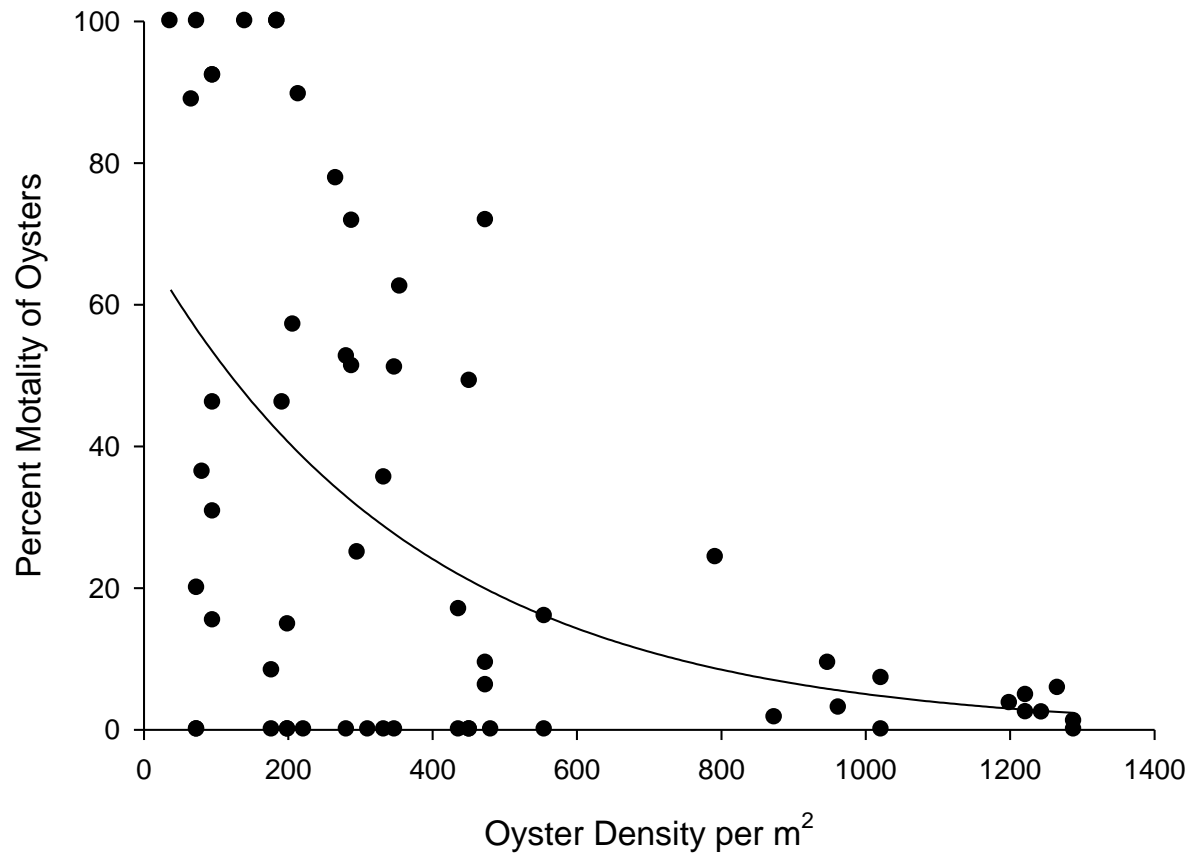


Figure 7: Relationship between percent of oysters consumed per stone crab per 24 hours and oyster density. Line fit to data is from an exponential decay regression model (ANOVA: $F = 21.01$, $df = 1$, $p < 0.0001$).

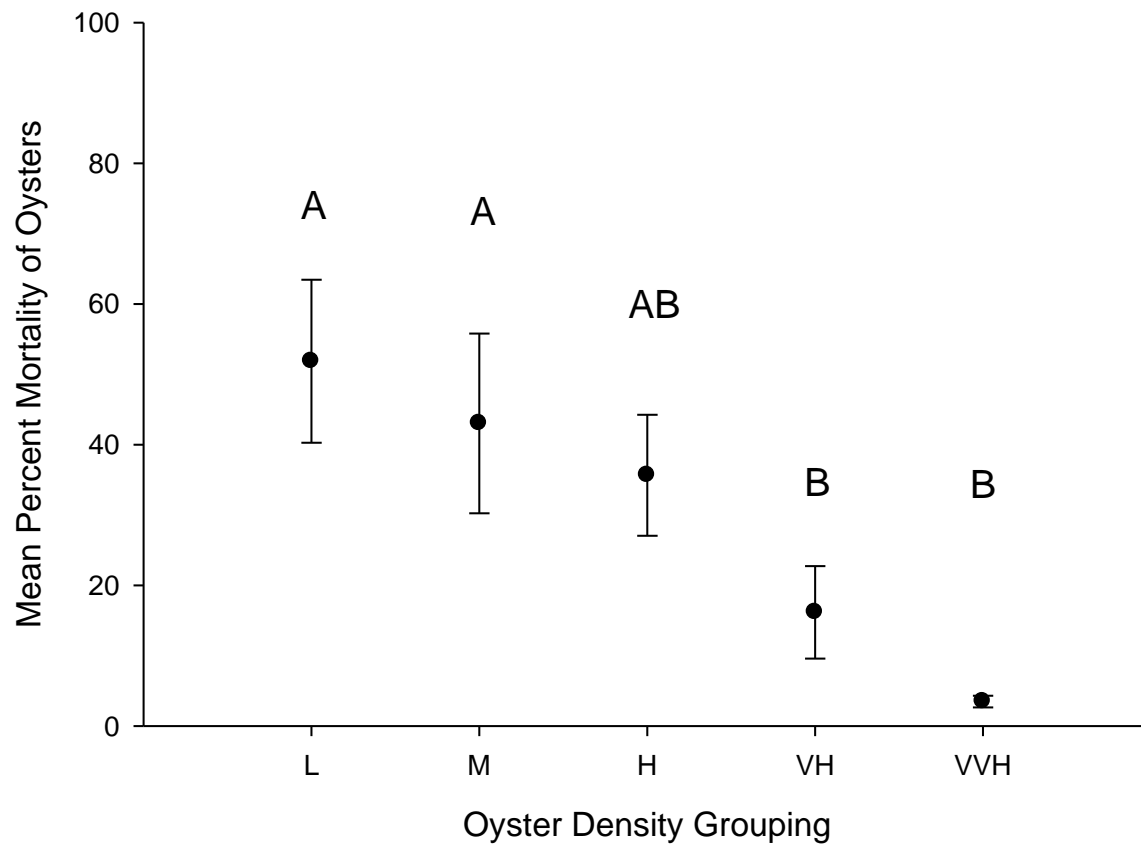


Figure 8: Relationship between mean percent mortality (± 1 SE) and oyster density for data shown in Figure 7. Means testing was performed using Tukey's HSD, where means with the same letter are not significantly different.

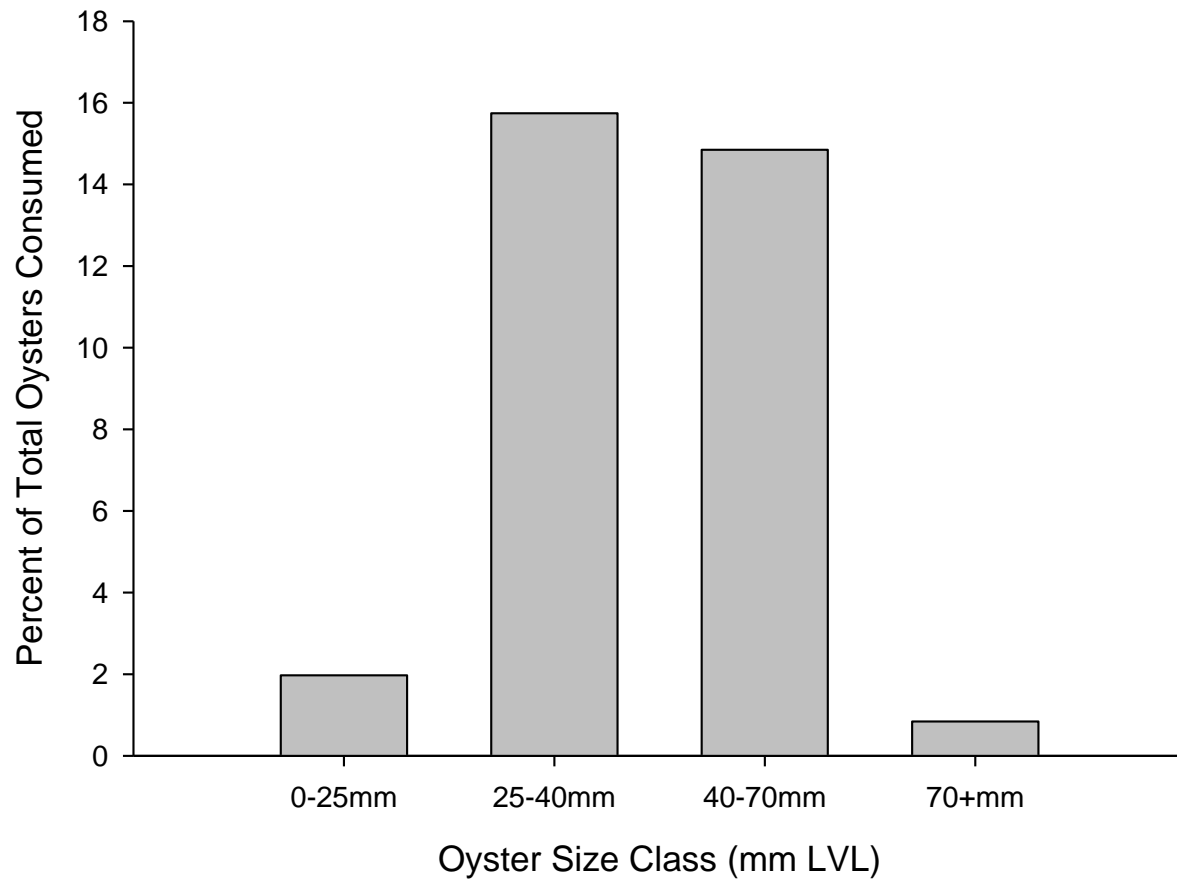


Figure 9: Relationship between the percent of total oysters consumed by stone crab predators in laboratory predation trials and oyster size class.

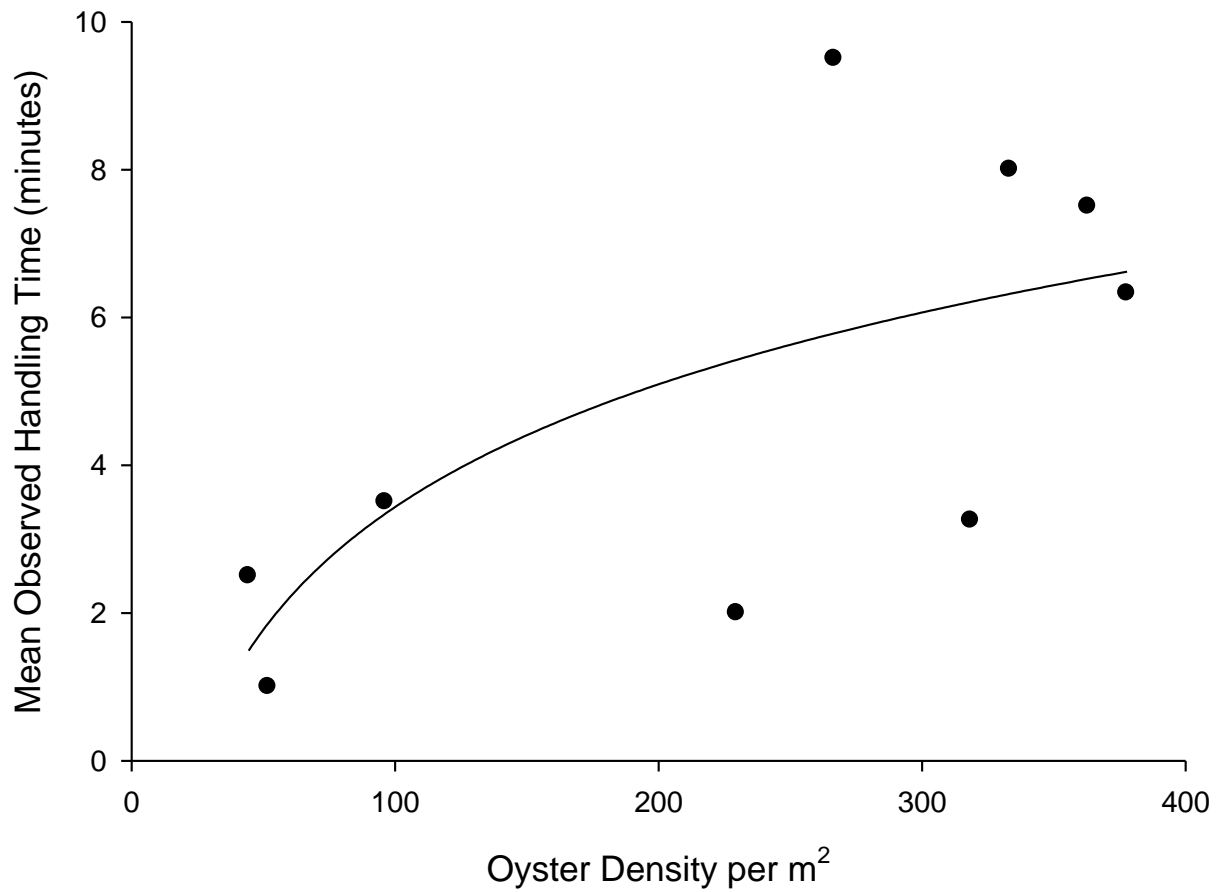


Figure 10: Relationship between mean observed prey handling time (T_h) in minutes by stone crab predators and oyster density. All zero values for handling time (indicating no stone crab predation, and as such no measurable handling time) have been omitted from this plot. Relationship best described by a logarithmic, 2-parameter regression model (ANOVA: $F = 5.89$, $df = 1$, $p = 0.0456$, $R^2 = 0.46$).

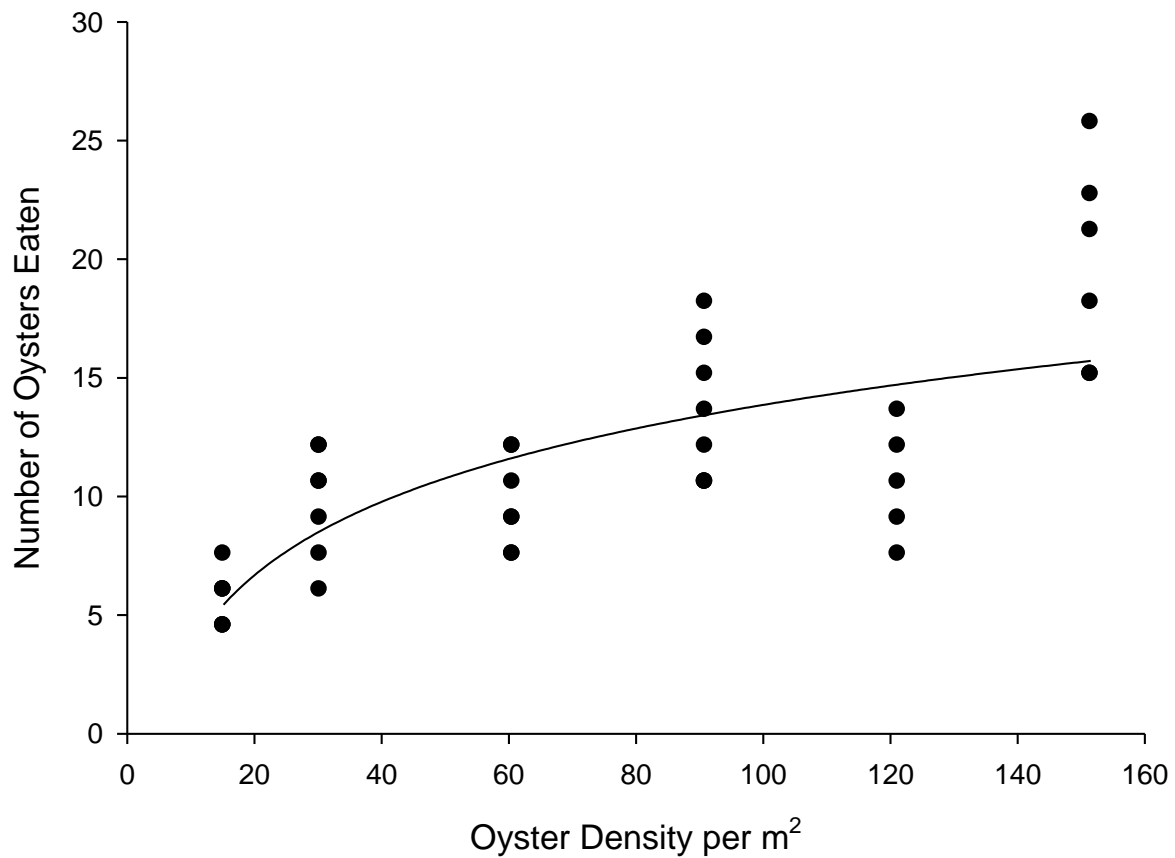


Figure 11: Relationship between the number of oysters eaten (y-axis) per predator per 24 hours and oyster density (x-axis). Line fit to data is from a non-linear, continuous-time type II functional response model (see text for statistical results to determine the type of functional response, and the best fitting functional response model). Linear regression modeling of the number of oysters eaten by mud crabs as a function of oyster density was significant (Linear regression: $F = 52.16$, $df = 1, 27$, $p < 0.001$, $R^2 = 0.58$).

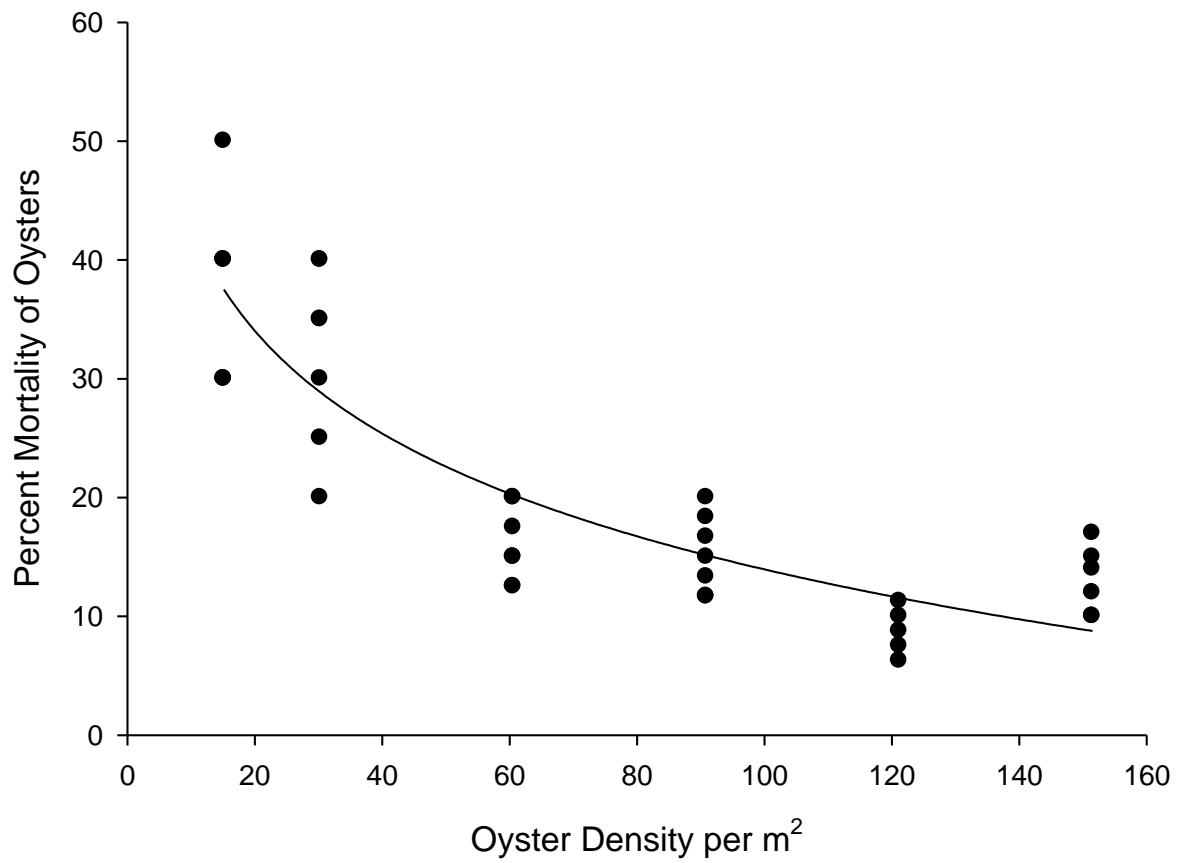


Figure 12: Relationship between percent of oysters consumed per mud crab per 24 hours (adjusted from 48 hours) and oyster density. Relationship best described by a logarithmic, 2-parameter regression model (ANOVA: $F = 123.35$, $df = 1$, $p < 0.0001$, $R^2 = 0.76$).

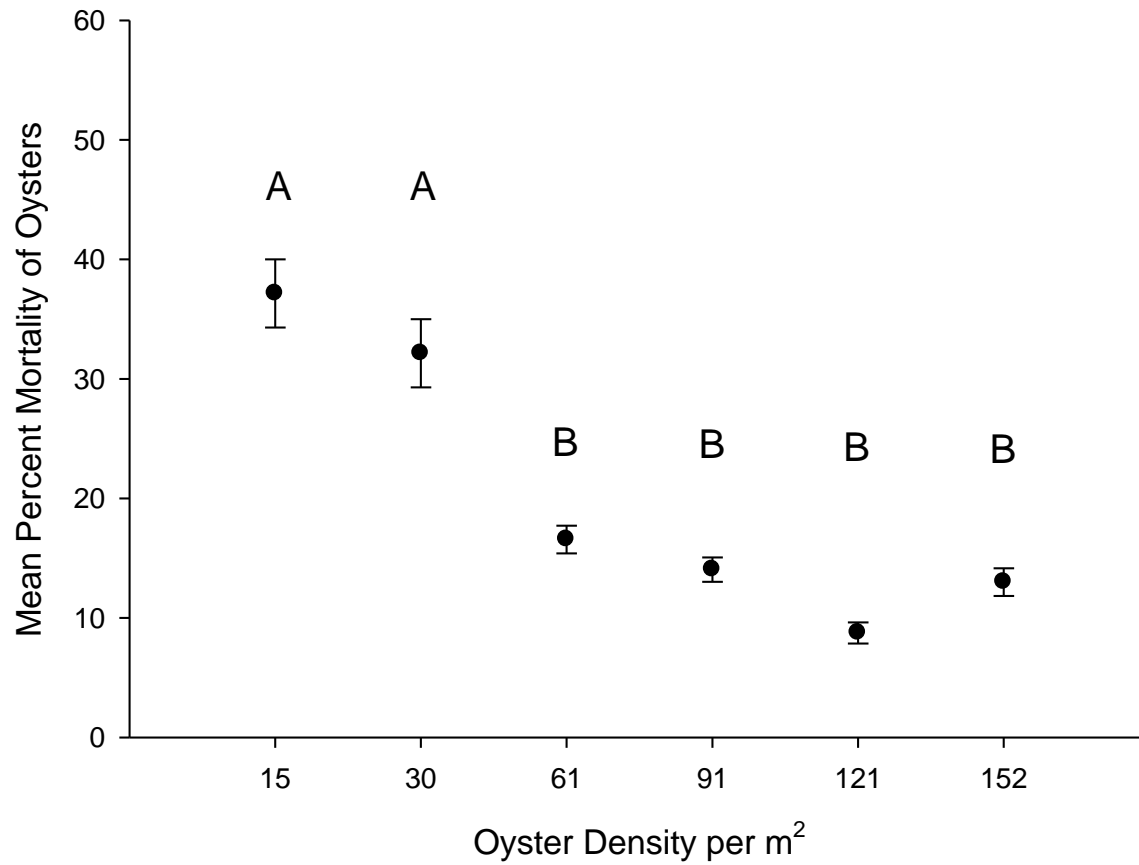


Figure 13: Relationship between mean percent mortality (± 1 SE) and oyster density for data shown in Figure 12. Means testing was performed using Tukey's HSD, where means with the same letter are not significantly different.

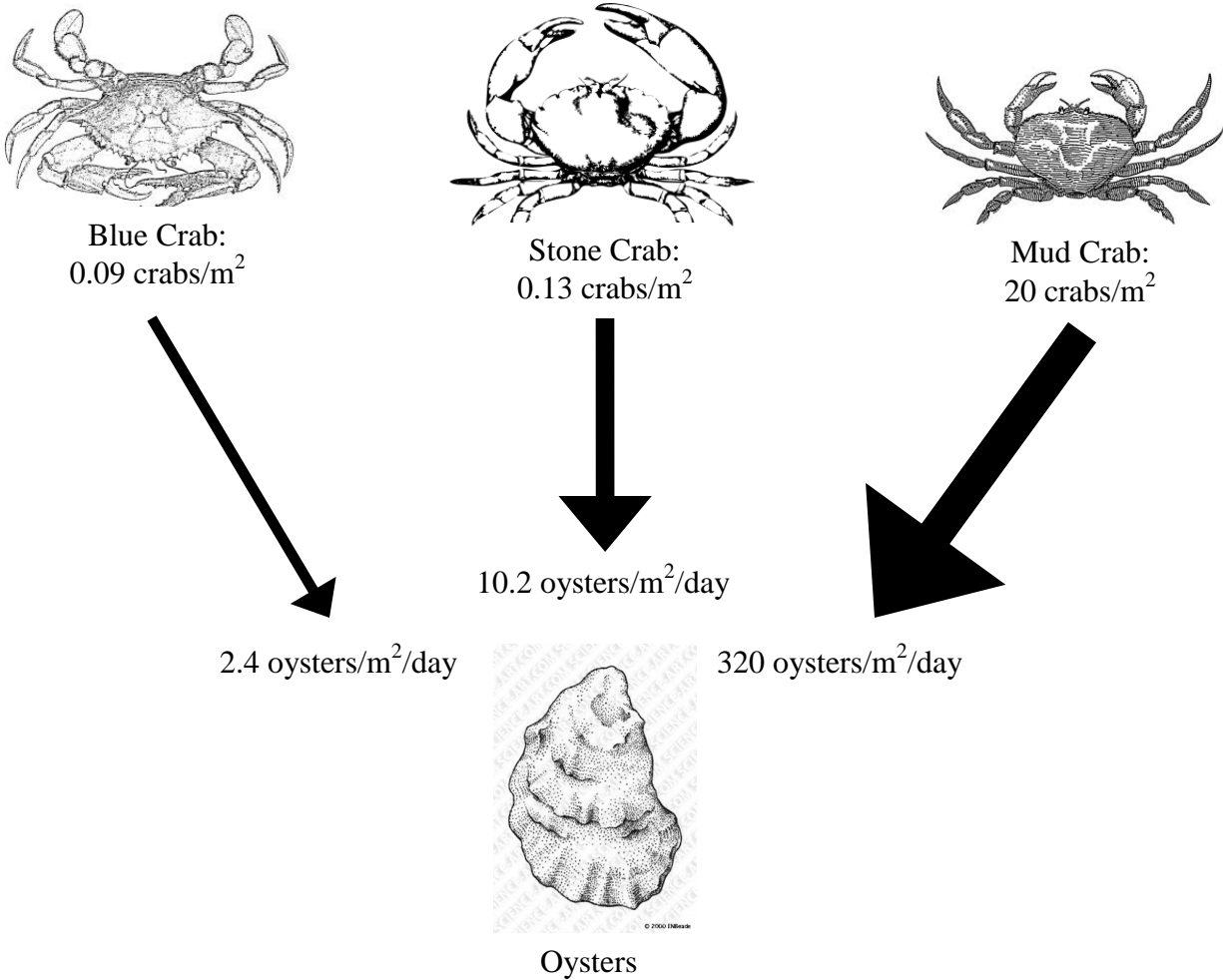


Figure 14: Schematic of decapod crab-oyster food web depicting the relative maximum predatory potential of blue, stone, and mud crabs preying on oysters. Size of arrow depicts relative potential predatory impact in terms of number oysters eaten per m² per day, which was estimated from the asymptote of the functional response from laboratory experiments (i.e., number of oysters eaten/crab/24 h divided by oyster density at asymptote). Based on the fit of a continuous-time functional response model, the instantaneous attack rate (a' ; the percent of the area available for foraging that a predator searches for a prey item per unit time) was: 0.071 (blue crab); 0.123 (stone crab), and 0.02 (mud crab). Although the functional response of mud crabs to oysters was best described with a linear regression model, we chose the next best model (continuous-time type II) as revealed through AIC (see Table 2) to estimate a' and T_h . Prey handling time (the time taken to break open and eat a prey item, as a decimal fraction of one hour) was: 4.000 (blue crab); 0.306 (stone crab), 1.184 (mud crab). Photo credits- blue crab: nbii.gov; stone crab: J. Olsen; mud crab: P. S. Foresman; oyster: E. Beade.