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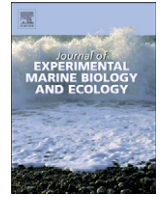
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Contents lists available at ScienceDirect

Journal of Experimental Marine Biology and Ecology

journal homepage: www.elsevier.com/locate/jembe

Predator–prey dynamics between recently established stone crabs (*Menippe* spp.) and oyster prey (*Crassostrea virginica*)

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ARTICLE INFO

Article history:

Received 9 November 2010
 Received in revised form 15 June 2011
 Accepted 17 June 2011
 Available online 16 July 2011

Keywords:

Crassostrea
 Functional response
Menippe
 Oyster
 Predation
 Stone crab

ABSTRACT

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, 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 1900s 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 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 We then (3) analyzed previously unpublished functional response data on another important oyster predator, the mud crab *Panopeus herbstii*.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 both stone crabs and mud crabs were consistent with a type II 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 U.S. 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.

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1. Introduction

Range expansion and subsequent population establishment of species can have significant impacts to previously established food webs and predator–prey dynamics (Crawley, 1986; Field et al., 2007; Heatwole and Levins, 1972; Hargeby et al., 1994). Changes in predator–prey dynamics, in turn, often impact population dynamics of both predator and prey species (Holt, 1984). The introduction and colonization of the Indo-Pacific lionfish (*Pterois volitans*) to Atlantic reef communities (Albins and Hixon, 2008) resulted in predation on native fishes and 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 concurrent declines in

tuna and billfish populations, and may be responsible for the decline of the Pacific hake *Merluccius productus* due to predation (Zeidberg and Robison, 2007). The common trait shared by these 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 sounds in North Carolina (NC), USA contrary to previous studies and surveys (Hay and Shore, 1915; Rathbun, 1930). Commercial crabbers for the blue crab (*Callinectes sapidus*) in NC have recently 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 (B. Puckett, NC State University [NCSU], pers. comm.; S. Slade, NC Division of Marine Fisheries [NC DMF], pers. comm.), contradicting 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 extended their range north of NC since none have been landed north of Cape Hatteras (Sam Rust Seafood, Hampton, VA, pers. comm.).

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Although anecdotal information suggests that stone crabs are established in NC, there is no quantitative data on their abundance, or on their predatory behavior on commercially and ecologically important oysters, which are the subject of large-scale restoration efforts in Pamlico Sound.

1.1. Species characteristics

The stone crab *Menippe* spp. (Say) is a commercially important decapod predator, ranging from North Carolina to Florida and the Caribbean (Bert, 1986). The predominant species of stone crab include the Florida stone crab *Menippe mercenaria* and the Gulf stone crab *Menippe adina*. NC stone crabs constitute a hybrid population of these two species. NC stone crabs have mtDNA characteristic of *M. adina* (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) (Wilber, 1989, R. Rindone, pers. obs.).

Two other dominant decapod crustacean predators on oysters are the blue crab (*C. sapidus*) and mud crab (*Panopeus herbstii*) (Bisker and Castagna, 1987; Eggleston, 1990; Sellers and Stanley, 1984; Silliman et al., 2004). Blue crabs are considered to be opportunistic bottom scavengers, preying on 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). Mud crabs serve as important components of benthic food webs in a variety of habitats (Dittel et al., 1996; Meyer, 1994; Silliman et al., 2004; Whetstone and Eversole, 1981). 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.

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 (Coen et al., 1999; Kennedy and Breisch, 1983). Oyster reefs provide several ecosystem and human services, including improved water quality (Sellers and Stanley, 1984), essential fish habitat, 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. Oyster population declines have initiated widespread restoration efforts (Peterson et al., 2003; Schulte et al., 2009). Predators of oysters include *M. adina* (Baltz and Horst, 1992; Coen et al., 1999; Grabowski et al., 2005; Juanes, 1992; Peterson et al., 2003). In southern Florida, pure-species *M. mercenaria* 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 our pilot studies indicated that stone crabs (*Menippe* spp.) found in intertidal and subtidal communities in NC readily prey on oysters. 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 in this region. Also, stone crab range expansion may significantly impact oyster communities along the East Coast of the United States via predation on oysters.

1.2. 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; Fig. 1), and is a key process underlying predator–prey dynamics. To fully characterize a predator's functional response, factors such as the number of prey available and prey handling time must be measured or estimated from mathematical models (Holling, 1959). Functional response gives researchers insight into the relationship between predators and varying prey densities. In this study, functional response was used to understand the underlying behaviors and mechanisms associated with stone, blue and mud crab predation on oysters, and to make relative comparisons of potential predatory impact among crabs.

1.3. Objectives

The objectives of this study were: to quantify abundance patterns of stone crabs in subtidal oyster reefs in Pamlico Sound, NC; to quantify the functional response of stone crabs to varying densities and sizes of oysters, as well as quantify the functional response of mud crabs on oysters; to use information from the above objectives, 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.

2. Materials and methods

This study was conducted in Pamlico Sound, a wind-driven, shallow, lagoonal estuary that is separated from the Atlantic Ocean by barrier islands. Three major inlets connect the estuarine waters with the Atlantic Ocean (Pietrafesa et al., 1986). In NC, ten oyster broodstock reserves have been created by the NC Division of Marine Fisheries (NC DMF) in Pamlico Sound. Our previous field research at these reserves identified potentially increasing numbers of stone crabs at Ocracoke, Hatteras, and West Bay (R. Rindone, NCSU, pers. obs.). We quantified stone crab abundance in four of these ten reserves during 2009.

2.1. Quantify abundance patterns of stone crabs

Of the ten available oyster broodstock reserves, four were selected for assessment of stone crab abundance: West Bay, Ocracoke, Hatteras, and Crab Hole, based on their relatively similar mound composition and similar construction dates in 2006 or earlier (NC DMF, 2008). One of every ten mounds created in 2006 or earlier within each selected oyster reserve was chosen randomly to survey for stone crabs by 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. To facilitate measures of stone crab density, mound area measurements were averaged and standardized for all mounds surveyed at each respective reserve based on previous side-scan-sonar mapping (Ballance and Eggleston, 2008). 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 and Eggleston, 2008). A two-person team of SCUBA divers descended on each mound during daylight hours and conducted one-meter wide 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”. Both the number of burrows observed and the number of burrows occupied by stone crabs were recorded during diver surveys, as well as discernable prey debris. Surveying stone crabs during August and September may have increased the likelihood of observing stone crabs occupying burrows on the mounds, as these months are within the

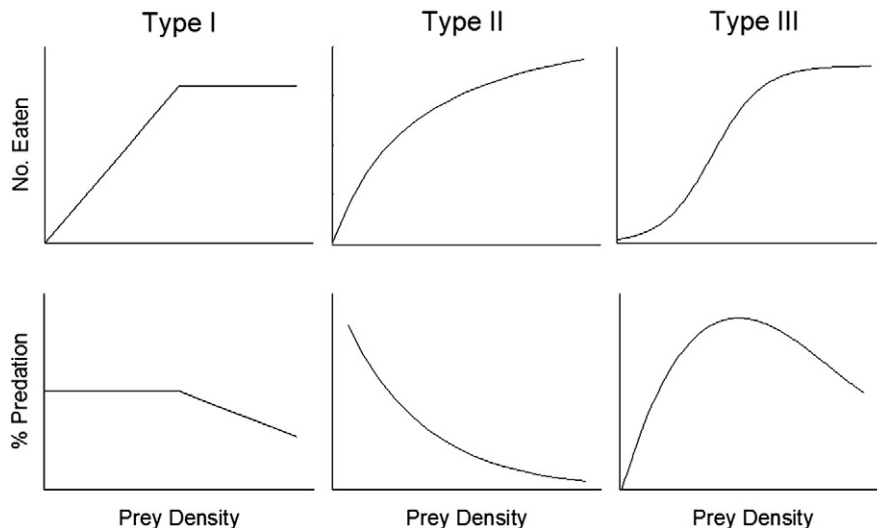


Fig. 1. Depiction of the three main types of functional response with respect to both the number of prey eaten and the percent of prey consumed (y-axes) over prey density (x-axes). Both types I and II are destabilizing, and can lead to localized extinction of prey at low prey densities. Type III is stabilizing, and results in a low density refuge for prey.

time of the year when commercial crabbers cite noticeable stone crab activity (R. Howell, commercial crabber, Swansboro, NC, pers. comm.).

2.1.1. Statistical analyses of stone crab abundance patterns

Comparisons of mean stone crab density across months and among reserves 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, NCSU, pers. comm.).

2.2. Quantify the functional response of stone crabs on 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, intermolt 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.).

Oysters were hand-collected haphazardly from subtidal and intertidal habitats in Bogue Sound, NC. Most oysters were attached to cultch material. 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, unpublished data). In addition to density groupings, each oyster was measured by left valve length (LVL mm) and placed into one of four size categories (0–25 mm, 25–40 mm, 40–70 mm, 70+ mm), representative of naturally occurring shell valve lengths found at oyster broodstock reserves in Pamlico Sound, NC (Puckett and Eggleston, in review). Prior to the start of feeding trials, the size and location of each oyster relative to its substrata was recorded (mm LVL) and mapped by hand, after which a given oyster density was placed into a single, randomly selected tank. 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 µm) at a rate of 90 l/h. This tank layout allowed for concurrent feeding trials and random interspersed 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 h 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 h prior to oyster density treatments to allow each crab time to acclimate to the tank environment. The subsequent feeding trial lasted ~12 h, after which time the remaining prey items were removed, and the numbers and sizes of oysters eaten versus live oysters remaining were recorded. To allow comparisons with mud- and blue-crab feeding data, time-trial data for stone crabs was then extrapolated out to be equivalent to a 24-h time period, since no evidence of variation in daytime or nighttime feeding behavior had been observed in laboratory pilot studies (Rindone, pers. obs.) or in the wild (R. Rindone and D. Eggleston, 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.

Stone crab prey handling time and behavior were observed 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 and use of legs and chelae to probe oyster cultch and oysters. An "oyster attack" was characterized by a stone crab selecting an oyster, attempting or

succeeding to dislodge the oyster and break open the shell, potentially consuming the oyster, and subsequently discarding the remains of, or ignoring, the oyster.

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. Crabs were completely removed from the experiment after being subjected to each level of density. We did not test the relationship between crab CW and size of oysters consumed because crabs were prone to molting, and were occasionally rotated out of experimental trials after becoming afflicted with black spot disease, both of which likely confounded the relationship between crab CW and size of oysters consumed (e.g., large crabs that did not eat large oysters due to molting or emergence of disease). To ensure that experimental treatments were independent, we 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.

2.2.1. Statistical analyses of laboratory feeding data

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). Our goal concerning the functional response of stone crabs (and mud crabs, see below) to oysters was to determine if predation rates were types I, II or III (Fig. 1). First, we determined if proportional mortality varied with oyster density with a one-way ANCOVA model, with oyster density as the independent variable and mean 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 (Fig. 1). 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 types I and II functional responses can be destabilizing to predator–prey dynamics (Eggleston et al., 2008), we fit the data to type I, and discrete- and continuous-time type II functional response models to generate estimates of a' and T_h that could be compared to other decapod predators of oysters:

Type I:

$$N_e = (t * N_t * a')$$

Discrete-time type II:

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

Continuous-time type II:

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

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. Continuous-time models relate the number of both successful and unsuccessful encounters of a predator with prey to a function of prey density (Nt). Discrete-time models relate the number of prey eaten to prey density (Lipcius and Hines, 1986). Testing revealed that both type I and the continuous-time type II model 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.

2.3. Quantify the functional response of mud crabs on oysters

In July and August of 1985, D. Eggleston (NCSU) examined the predatory behavior of the mud crab *P. 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). Predation trials were conducted in 0.33 m² 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. 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 h since pilot studies indicated that mud crab predation occurred at a slower rate when compared with other decapod predators such as blue crabs. 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 and estimate behavioral parameters.

2.4. Assess and compare the relative potential predatory impact of crabs on oysters

We 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, 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). Estimates for each crab species were then multiplied by the respective field density of each crab species to determine the number of oysters that could potentially be consumed by the specified density of that crab species. These estimates do not account for other interactions between crabs and other oyster predators, physical environmental variables, or anthropogenic influences. 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). This comparison assumes constant feeding throughout previously described feeding periods.

3. Results

3.1. Quantify abundance patterns of stone crabs

The mean density of stone crabs per m² in a given reserve varied significantly according to the location of an oyster broodstock reserve, but did not vary 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. 2).

3.2. Quantify the functional response of stone crabs on eastern oysters

In general, the number of oysters eaten per stone crab increased with oyster density, but with considerable variation at intermediate densities (Fig. 3). The percent mortality of oysters increased sharply with decreasing oyster density (Fig. 4), indicative of either a type I or type II functional response. The percent mortality of oysters varied

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 m ²)	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

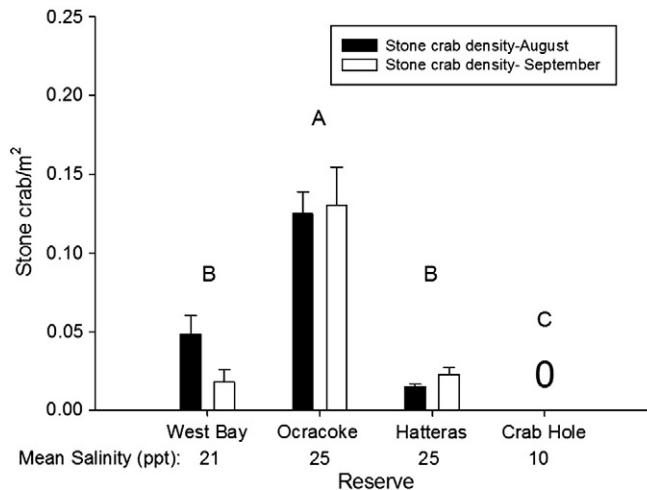


Fig. 2. Mean (+ 1 SE) stone crab density in Pamlico Sound, NC as a function of oyster broodstock reserves, with corresponding mean salinity (ppt) on the x-axis. Differences in means determined via Tukey's HSD test are denoted by capitalized letters above data bars, with similar letters indicating no significant difference between reserves (see text for further results of statistical analyses).

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 among 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. 5). Thus, according to our a priori criteria for determining the type of functional response, there was equivocal support for either a type I or type II functional response, and no strong evidence in support of a type III. Both types 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 (Eggleston et al., 2008; Hassell, 1978). Subsequent examination of the fit of type I and both discrete- and continuous-time type II functional response models to the data indicated that both

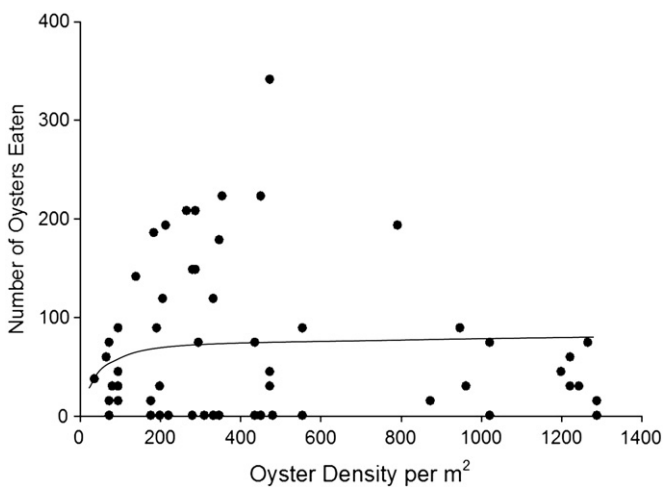


Fig. 3. Relationship between the number of oysters eaten (y-axis) per predator per 24 h and oyster density (x-axis). Line fit to data is from a non-linear, continuous-time type II functional response model (see text for statistical results to determine the type of functional response, and the best fitting 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, R² = 0.01).

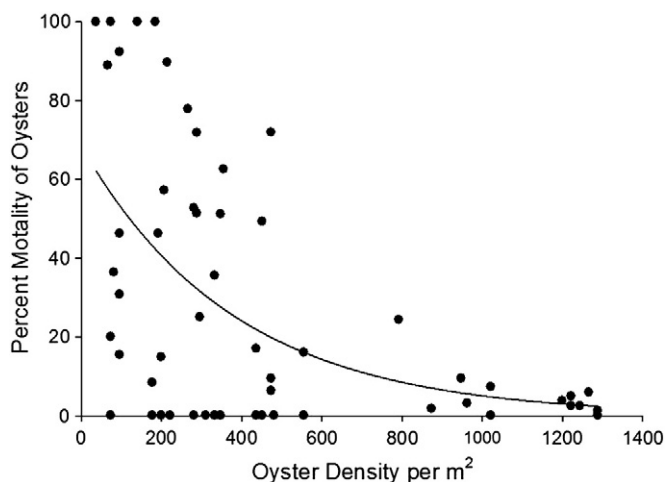


Fig. 4. Relationship between percent of oysters consumed per stone crab per 24 h and oyster density. Line fit to data is from an exponential decay regression model (ANOVA: $F = 21.01$, $df = 1$, $p < 0.0001$).

type I and continuous-time type II functional response models provided a statistically significant fit to the data (type I: SAS Proc Nlin: Newton: $F = 15.47$, $df = 1$, $p > 0.0002$; continuous time type II: SAS Proc Nlin: Gauss–Newton: $F = 24.06$, $df = 2$, $p < 0.0001$; discrete-time type II functional response model $p > 0.24$). 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 and Pitt, 1997). We chose Akaike’s Information Criterion (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. Comparison of type I and continuous-time type II functional response models for stone crab predation on oysters was facilitated through AIC; however, biases may exist in this analysis, as the iterative methods used in the analysis of each type differed (type I: Newton; continuous-time type II: Gauss–Newton). AIC comparisons revealed that the data were best explained by the continuous-time type II functional response model (Table 2). Oysters appeared to have a

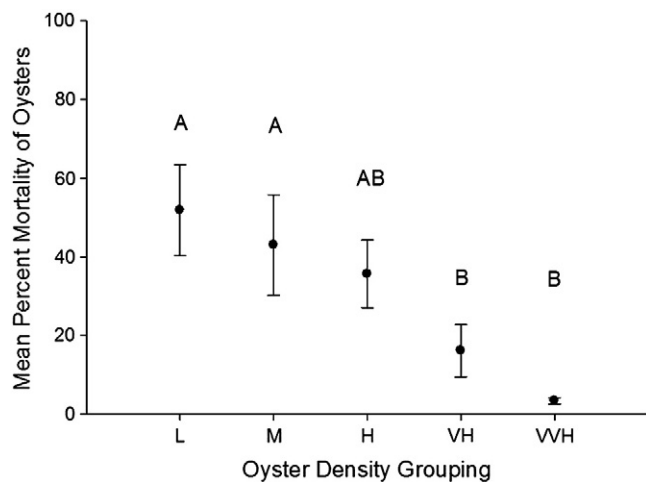


Fig. 5. Relationship between mean percent mortality (± 1 SE) and oyster density for data shown in Fig. 4. Means testing was performed using Tukey’s HSD, where means with the same letter are not significantly different. Oyster Density Groupings are defined as: L = 0–100 oysters/ m^2 , M = 100–250 oysters/ m^2 , H = 250–400 oysters/ m^2 , VH = 400–800 oysters/ m^2 , VVH = 800+ oysters/ m^2 .

Table 2

Comparison of stone 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
Type I FR	1	60	1	15.47	8805.4	301.40	19.11	0.000
Continuous-time type II FR	2	60	2	24.06	6178.9	282.28	0.00	1.000

relative prey refuge in size at both small (<25 mm LVL) and large (>70 mm LVL) sizes (Fig. 6). Observations of prey handling time (T_h) by stone crabs increased with increasing oyster density (Fig. 7).

3.3. Quantify the functional response of mud crabs on oysters

The number of oysters eaten per mud crab increased with oyster density up to an asymptote as oyster density continued to increase (Fig. 8). The percent oyster mortality due to mud crabs was highest at low oyster densities, and decreased sharply with increasing oyster density (Fig. 9). 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. 10). This pattern in percent mortality with oyster density is consistent with both type I and type II functional responses. 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 type I, discrete-time and continuous-time type II functional response models (SAS Proc Nlin). Though all three models were statistically significant (all p ’s < 0.0001), AIC comparison determined that the functional response of mud crabs to oysters was best explained by continuous-time type II functional response (SAS Proc Nlin: Newton: $F = 238.87$, $df = 2$, $p < 0.0001$, Table 3), indicating potential localized extinction of oyster prey at low prey densities by mud crab predators. Although stone crabs displayed the highest attack rates and shortest prey handling times of the three crabs examined, mud crabs appear to be

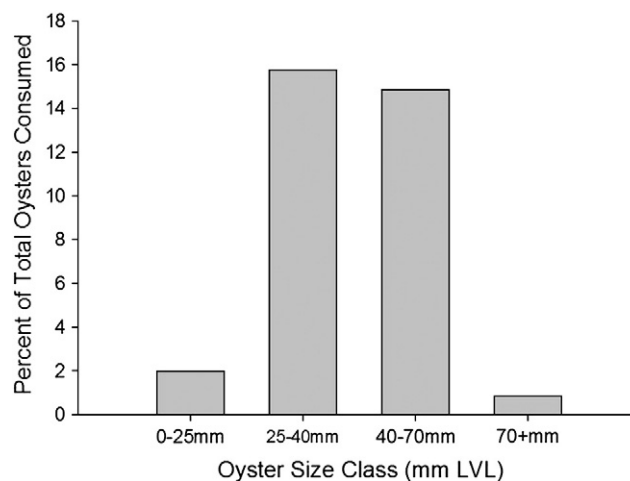


Fig. 6. Relationship between the percent of total oysters consumed by stone crab predators in laboratory predation trials and oyster size class.

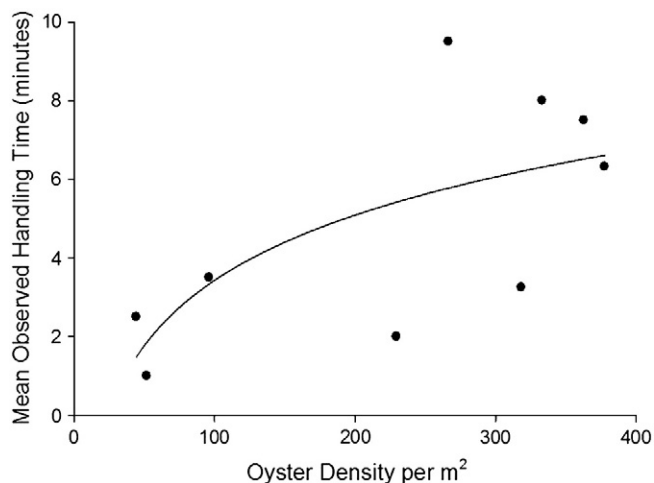


Fig. 7. Relationship between mean observed prey handling time (T_h) in minutes by stone crab predators and oyster density. All zero values for handling time (indicating no stone crab predation, and as such no measurable handling time) have been omitted from this plot. Relationship best described by a logarithmic, 2-parameter regression model (ANOVA: $F = 5.89$, $df = 1$, $p = 0.0456$, $R^2 = 0.46$).

the dominant decapod predator of oysters based on their approximately two-order of magnitude higher density per m^2 on oyster reefs compared to either stone or blue crabs (Fig. 11). Based on the fit of a continuous-time type II 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). 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).

4. Discussion

Stone crabs appear to have extended their range from Cape Lookout, NC as far north as Cape Hatteras. This range expansion could theoretically result in increased vulnerability of 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 abundance on

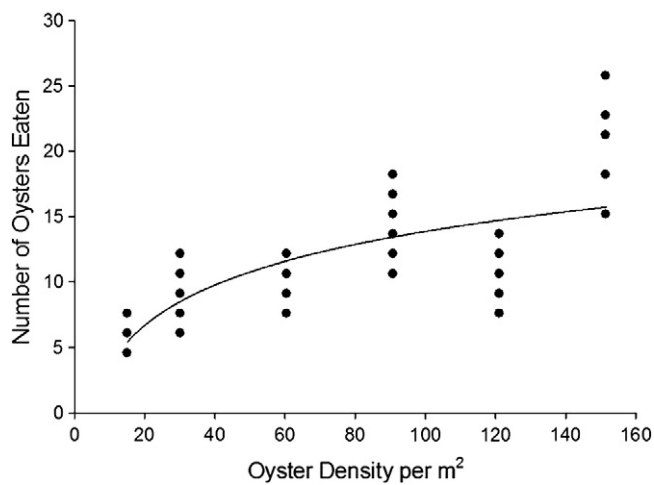


Fig. 8. Relationship between the number of oysters eaten (y-axis) per predator per 24 h and oyster density (x-axis). Line fit to data is from a non-linear, continuous-time type II functional response model (see text for statistical results to determine the type of functional response, and the best fitting 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: $F = 52.16$, $df = 1, 27$, $p < 0.001$, $R^2 = 0.58$).

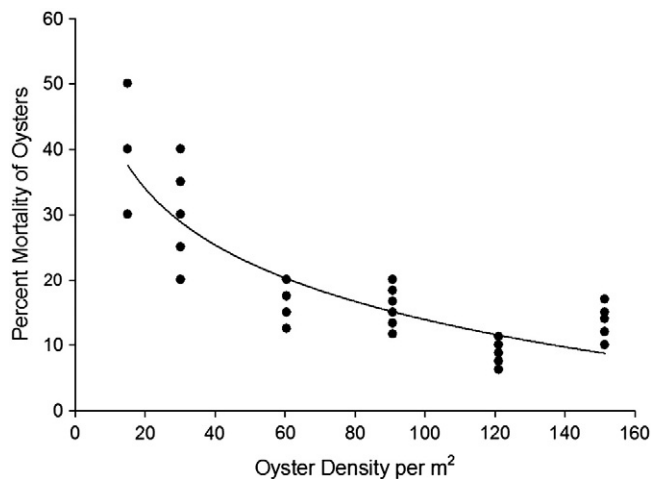


Fig. 9. Relationship between percent of oysters consumed per mud crab per 24 h (adjusted from 48 h) and oyster density. Relationship best described by a logarithmic, 2-parameter regression model (ANOVA: $F = 123.35$, $df = 1$, $p < 0.0001$, $R^2 = 0.76$).

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 also exhibited inversely density-dependent type II functional response when preying on oysters. The demonstration of types 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 (Fig. 1). 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 to potentially 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 oyster and stone crab densities, especially when compared with mud crabs at current best estimates of mud crab densities.

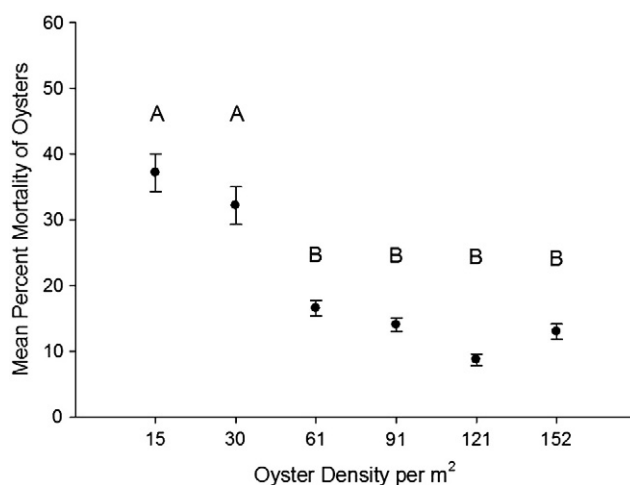


Fig. 10. Relationship between mean percent mortality (± 1 SE) and precise oyster density for data shown in Fig. 8. Means testing was performed using Tukey's HSD, where means with the same letter are not significantly different.

Table 3

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 "Wi" 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	Wi
Type I FR	1	40	1	279.8	19.53	-26.58	17.03	0.000
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	0.00	1.000

4.1. 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; 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. No stone crabs were observed at Crab Hole, likely due to salinities (~10 ppt) that were below the lower salinity tolerance for stone crabs (~15 ppt, Brown et al., 1992). 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. Other variables may also influence stone crab abundance patterns in North Carolina, such as structural aspects of oyster and rubble habitat (Beck, 1995, 1997), available prey, and predation risk and emigration (Lindberg et al., 1990). 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 NC.

4.2. Stone crab functional response

The results of laboratory functional response experiments suggest that adult, male stone crabs exhibit continuous-time type II functional response when preying on eastern oysters. This type of functional response 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. It should be noted, however, that we observed a decrease in stone crab foraging and an increase in prey handling time 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

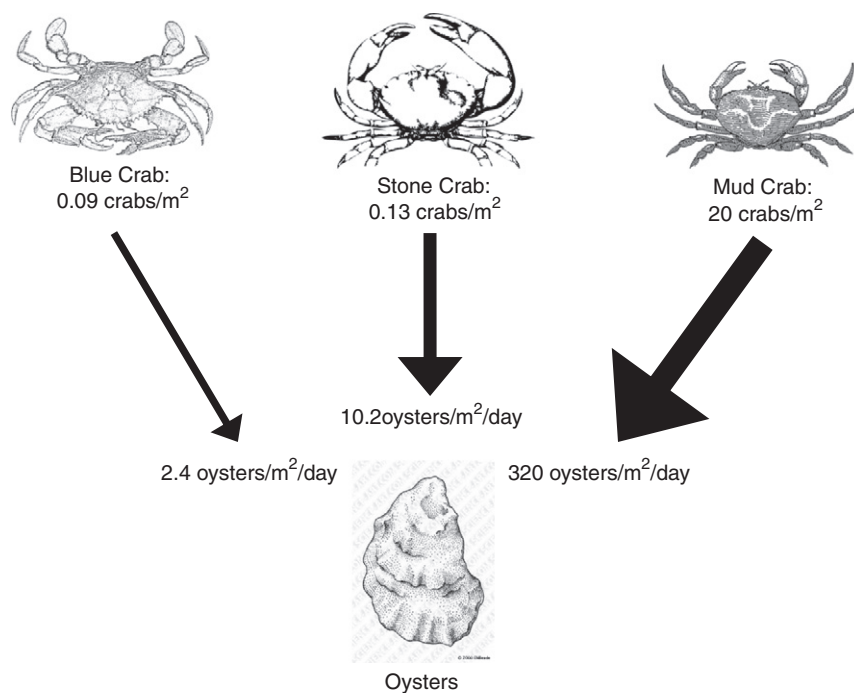


Fig. 11. Schematic of decapod crab–oyster food web depicting the relative maximum predatory potential of blue, stone, and mud crabs preying on oysters. Size of arrow depicts relative potential predatory impact in terms of number oysters eaten per m² per day, which was estimated from the asymptote of 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). Prey handling time (the time taken to break open and eat a prey item, as a decimal fraction of 1 h) 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.

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 increase in prey handling time mentioned in this study supports 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 inability 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 by adult stone crabs than oysters measuring between 25 and 70 mm LVL. For oysters measuring less than 25 mm, the decreased level of predation by adult 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 (R. 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 thick 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).

4.3. Mud crab functional response

Mud crabs exhibited a continuous-time type II functional response to varying densities of oysters. The higher quantity of oysters (albeit smaller in LVL) consumed by mud crabs per 24 h compared to blue and stone crabs may be due to two distinct reasons. First, since adult mud crabs are smaller than adult stone crabs, 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 (R. 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 <25 mm LVL size refuge for oysters observed to exist under stone crab predation in this study could be 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 (10–20 mm CW) consumed fewer oysters than juvenile blue crabs (30–70 mm 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, NCSU, 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 (Bahr, 1974; McDermott, 1960), 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 better compare the predatory

potential of common decapod predators on oyster reefs in Pamlico Sound.

4.4. Relative potential predatory impact of 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 influential predators on oysters when compared to mud crabs.

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 (Brodeur et al., 2010; Fodrie et al., 2008; Griffin and Silliman, 2010; O'Connor et al., 2008; 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 (*M. 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; Pikitch 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.

Acknowledgments

We would like to thank the following people for their valuable help with field surveys and laboratory predation trials: B. Puckett, E. Millstein, A. Haase, A. Lillis, K. Pierson, G. Plaia, M. Barts, and M. McAlister. Special thanks also go to G. Bell, K. Gross, C. Durham, and J. Froeschke for their input on statistical analyses, and to T. Bert and two anonymous reviewers for editing this manuscript. Funding for this project was provided by the American Reinvestment and Recovery Act/National Oceanic and Atmospheric Administration through the North Carolina Coastal Federation, and the Blue Crab Advanced Research Consortium through the University of Maryland to D.B. Eggleston. [RH]

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