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EFFECTS OF INDIVIDUAL PHENOTYPIC VARIATION ON PREDATOR-PREY RELATIONSHIPS OF XANTHID CRABS IN NORTH INLET ESTUARY, SOUTH CAROLINA

by

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ABSTRACT

Ecological communities and the biological interactions that regulate community structure are notoriously complex. To make these systems more tractable, ecologists traditionally measure and model communities at the population level, treating individuals as functionally equivalent. While this approach has yielded tremendous insight into the factors governing communities, it remains unclear whether accounting for individual-level variation could improve our capacity to predict the responses of communities to perturbation, a major goal in the midst of unprecedented rates of environmental change.

The objective of this study was to examine the magnitude of individual-level phenotypic variation in predatory crabs (family Xanthidae), and the effects of this variation on crab trophic behavior and the strength of their interactions with bivalve prey in oyster reef communities. Specifically, I measured individual variation in crab body size, behavioral traits and parasite infection. A main aspect of this work was testing how each of these factors affected the crab functional response, i.e. the per capita rate of prey consumption depending on prey density. This response is important in scaling up prey consumption rates to the population level, and to larger spatial scales. I also explored how oyster reef habitat structure and threat from toadfish, a predator of crabs, can mediate the ecological effects of crab phenotype.

The results of this work support the importance of individual-level variation for species interactions that influence the structure of reef communities. The body size distribution of crabs, which is in part dependent on the presence of structurally complex reef habitat, determined their top-down effects on the bivalve prey community. Furthermore, individual behavioral traits scaled with crab body size and were consistent over time in the field. Individual crab behavior also varied independently of crab body size, but could not be predicted by individual metabolic rate. Individual-level variation in crab body size, behavioral traits and parasite infection all influenced the crab functional response to bivalve prey density in different ways. This work provides a general pathway (modification of the functional response) by which the effects of individual phenotypes can scale up to influence predator-prey population dynamics.

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CHAPTER 1

INTRODUCTION

A central goal of ecology is to understand the factors that regulate the abundances of interacting species in a given location (i.e. community structure). Early depictions of communities linked species based on their feeding relationships (Summerhayes and Elton 1923, Hardy 1924, Elton 1927), while natural history observations suggested the importance of predation in limiting the abundances and distributions of prey species (De Bach 1958, Hairston et al. 1960, Pearson 1964, Brooks and Dodson 1965). Brooks and Dodson (1965), for example, observed that large-bodied zooplankton were curiously absent from Connecticut lakes containing a planktivorous fish, the alewife (*Alosa pseudoharengus*). These lakes were instead dominated by an assemblage of smaller-bodied zooplankton species (Brooks and Dodson 1965).

Experimental manipulations, such as predator additions or removals, confirmed the potential for predators to regulate communities. For example, Paine (1966) identified a predatory invertebrate, the ochre seastar (*Pisaster ochraceus*), which governs the diversity of lower trophic levels in the rocky intertidal through preferential predation on the competitively dominant prey species. Ecologists have since demonstrated that such indirect, cascading effects of predators are widespread. Trophic cascades, whereby a predator reduces the abundance of its prey and this in turn enhances the abundance of the prey's resource, have now been detected across wide range of aquatic and terrestrial ecosystems (Terborgh and Estes 2010). Traditional trophic cascades are driven by the direct removal of prey by predators (i.e. consumptive effects), but the mere threat of predation can induce behavioral changes in prey that reduce their feeding rate (i.e. non-consumptive effects: Schmitz et al. 2004). Thus the direct and indirect effects of predation on ecological communities can be strong and wide-reaching.

To predict the effects of predators, ecologists seek a mechanistic understanding of how this behavioral interaction, often occurring between an individual predator and prey, scales up to affect the dynamics of populations and communities over longer time scales. This goal is especially topical today given widespread population declines and extinctions of top predators (Estes et al. 2011), and the introduction of invasive predators around the globe (e.g. Wardle et al. 2009). An ideal model of predator-prey interactions incorporates only the necessary elements of the interaction to be generalizable across species (i.e. the reductionist approach: Lotka 1925, Volterra 1926, Holling 1959). Traditionally, this is accomplished by modelling interactions without regard to the specific traits of individuals, but instead focusing on mean effects and changes in population sizes.

The predator functional response, for example, describes the rate of prey consumption by a single predator individual as a function of prey density (Holling 1959). This response is dependent on the behaviors that a predator and its prey exhibit during an encounter, such as the rate of attack and the time it takes to handle an individual prey item (Holling 1959). A number of mathematical models have been developed to describe this response (Jeschke et al. 2002), and its precise shape is crucial for predictions of population stability (Murdoch and Oaten 1975). In general, the same functional response shape is applied across individuals for use in population models (Lotka-Volterra form) that predict predator-prey dynamics (Okuyama 2008, Bolnick et al. 2011) or the dynamics of multi-trophic systems (Rosenzweig 1973, Oksanen et al. 1981). These models also assume homogeneity of predator and prey life-history traits (e.g. birth rate, death rate). Again, implicit in this approach is the assumption that the traits of individuals are the same, or if variation exists, then it is relatively unimportant.

This “taxonomic approach” to ecology (sensu Rall et al. 2011) is commonly applied in empirical studies as well. In classic food webs, species are depicted as nodes, while feeding links between consumers and their energy sources are based on mean diet data, or solely from the diets of adult individuals (Cohen 1978, Polis 1991). Furthermore, field manipulations, such as predator removal studies, generally remove all predators from an area to test the overall effect of predation on communities. Finally, predation experiments often constrain the body sizes of individuals in order to reduce this potential source of variability, and therefore elucidate the effects of other factors of interest on predator-prey interactions (Polis 1984, Werner et al. 1984). Thus whether, and when, it is worth incorporating individual variation into empirical studies of predation, at a cost of increased complexity, is an important question (Bolnick et al. 2011, Sih et al. 2012).

In reality, conspecific individuals vary greatly in their traits (Hardy 1924, Bolnick et al. 2003). Sex (Shine 1989, Shine 1991) and body size dependent on ontogeny (Polis 1984, Werner and Gilliam 1984) are two of the most studied aspects of individual variation, but there exists further variation *within* sexes and size classes. This includes variation in individual morphology, physiology and behavioral traits (Bolnick et al. 2003, Sih et al. 2004, Nespolo and Franco 2007, Burton et al. 2010). In some communities, individual variation even exceeds variation between species means, with important ecological consequences (Woodward and Hildrew 2002, Arim et al. 2010). Woodward and Hildrew (2002), for example, found that the individual body size of predatory invertebrates in the Broadstone stream (UK) was the best predictor of their niche overlap, even when compared to their species designations, encounter rates with prey, and microhabitat use. Evolutionary biologists have long-recognized individual phenotypic variation as the raw material for natural selection (Darwin 1859). However, it remains unclear how this variation scales up to affect the population dynamics of interacting species and community structure (Bolnick et al. 2011), and in reverse, how the abiotic and biotic environment promotes and maintains individual variation in natural populations (Araujo et al. 2011).

A new focus of ecology examines whether the explicit consideration of individual variation can help better predict population and community dynamics (Bolnick et al. 2003, Bolnick et al. 2011). To address this, traditional ecological models of population dynamics and species interactions have been revisited to incorporate individual variation (Bolnick et al. 2011). One way this has been accomplished is by using a quantitative genetics framework that permits modelling of individual phenotypic variation and heritability in variation (Schreiber et al. 2011). Furthermore, the development of individual-based (Grimm and Railsback 2005) and state-based models (Persson et al. 1998), requiring previously unavailable computational power, allow the simulation of unique individuals and their interactions over time and across space.

Somewhat in parallel, widespread reductions in biological diversity have motivated examination of the importance of functional diversity, i.e. the range of functional traits among species, for ecosystem functions, such as energy transfer, biomass production and nutrient cycling (Hillebrand and Matthiessen 2009). Specifically, studies of the effects of species richness on ecosystem functioning (Loreau et al. 2001) often show that functional diversity, rather than species richness *per se*, drives ecosystem functioning (Tilman et al. 1997, Hillebrand and Matthiessen 2009). A number of indices have been developed to quantify functional diversity (Schleuter et al. 2010), and studies have compared the efficacy of these indices in linking the traits of organisms with their ecological effects (e.g. Petchey et al. 2004).

The goal of my dissertation is to experimentally examine the importance of individual-level phenotypic variation for predator-prey interactions that influence community structure. I accomplish this using a model system of Xanthid crabs (*Panopeus hersbtii* and *Eurypanopeus depressus*) that inhabit intertidal oyster (*Crassostrea virginica*) reefs in North Inlet estuary, South Carolina. Xanthid crabs are important consumers of bivalves in oyster reefs, and my work reveals considerable variation in the traits of crabs, including body size, behavior and parasite load. By examining the drivers of this variation and its effects on crab trophic behavior, this work contributes to the current reassessment of the traditional taxonomic approach to studying predator-prey interactions (Bolnick et al. 2003, Bolnick et al. 2011). My dissertation touches on three main research themes, all of which fall under the umbrella of individual ecology.

1. *Body size constraints on species interactions*

An individual's body size is perhaps its most ecologically important phenotypic trait (Peters 1983, Polis 1984, Werner and Gilliam 1984). Body size influences individual energetic demands (Brown et al. 2004), reproductive capacity (Blueweiss et al. 1978), and the strength of species interactions such as competition or predation (Brose et al. 2010). Individuals often change their diet or habitat use as they grow, and such ontogenetic niche shifts are widespread across animal taxa (Polis 1984, Werner and Gilliam 1984). Human exploitation, such as fishing, impacts the body size distributions of predators by selectively removing the largest individuals (Fisher et al. 2010, Shackell et al. 2012), and a reduction in body size has been deemed a universal response to global warming (Gardner et al. 2011, Forster et al. 2012). Therefore, understanding of the role of body size variation in governing species interactions is necessary to predict the effects of these perturbations on communities.

In Chapter 2, I use a field experiment to test the effects of body size diversity, i.e. the number of size classes present, in *Panopeus herbstii* populations on their consumption of the bivalve community in oyster reefs. Humans are altering organismal diversity at multiple organizational scales, from reduced genetic diversity in threatened populations (Ellstrand and Ellam 1993), to the loss of entire biotic communities (Guerold et al. 2000). Nevertheless, the vast majority of experimental studies have manipulated local species richness as the sole metric of biodiversity (Balvanera et al. 2006). Thus, a major research challenge is to move beyond species richness manipulations for a more holistic understanding of the importance of biodiversity. My work (Chapter 2) shows that large crabs are particularly important in determining top-down effects on the bivalve prey community in reefs, while body crab size diversity *per se*, has little effect on the overall rate of prey consumption. This is due to an increase in prey size and diet breadth with crab body size, making large crabs functionally unique in their ability to consume large bivalves. Furthermore, in a field survey, I show that large crabs tend to inhabit portions of reefs where the height of the surficial oyster shell layer is relatively tall. Because the destructive harvest of oysters by humans reduces the height of this shell layer (Lenihan and Peterson 1998, Lenihan and Micheli 2000, Lenihan and Peterson 2004), oyster harvest could compromise trophic transfer through the loss of large crabs.

A number of studies have tested how the predator functional response scales with the size ratio of a predator to its prey (e.g. Miller et al. 1992, Brose et al. 2010, McCoy et al. 2011, Rall et al. 2011). Furthermore, allometric constraints on predator-prey interactions have been used to successfully predict the structure of natural food webs (Otto et al. 2007, Petchey et al. 2008). Still, it is unclear how the size-dependent functional response interacts with additional ecological factors, such as physical habitat structure. In Chapter 3, I test how the functional response of *Panopeus herbstii* scales with crab body size in structurally complex oyster reef habitat, while keeping mussel prey (*Brachidontes exustus*) size constant. This work shows, counterintuitively, that larger crabs consume less mussel prey than smaller crabs at low mussel prey densities (i.e. a reduced attack rate). In an additional manipulation, I show that this reduced consumption rate is due to the impaired ability of large crabs to extract mussel prey from narrow crevices between oyster shells. Again, through the destruction of oyster reef habitat via fishing (Lenihan and Peterson 1998, Lenihan and Micheli 2000), this work suggests that the loss of structurally complex reef habitat could have major effects on the strength of the crab-bivalve interaction.

2. *Individual behavior, a departure from optimality theory*

Animal personality describes intraspecific variation in the behavioral traits of individuals that is consistent over time and across ecological contexts (Gosling 2001, Sih et al. 2004, Sih et al. 2012). Specifically, behavioral types describe individual variation in single behavioral traits (e.g. boldness or aggression), while behavioral syndromes describe correlations between multiple behavioral traits or the same behavior across multiple ecological contexts (Sih et al. 2004). The concept of animal personality provides a departure from the traditional view that animal behavior is infinitely labile, varying with the organism's internal state as well as the external environment to maximize fitness (i.e. optimality theory: Stephens and Krebs 1986). For example, constraints on individual behavior (i.e. cross-context behavioral correlations) have been used to explain sub-optimal behavior exhibited in natural populations, such as precopulatory mate cannibalism in fishing spiders (*Dolomedes triton*) (Johnson and Sih 2005). Despite the existence of personality in a diversity of animal taxa (Gosling 2001), ecologists have only begun to examine how consistent individual differences in behavior can affect the strength of species interactions (Sih et al. 2012).

In Chapter 4, I measure individual variation in the refuge use behavior of the crab *Panopeus hersbtii*, both in the absence and presence of threat from a major predator of crabs, the oyster toadfish (*Opsanus tau*). This study reveals considerable variation in crab refuge use behavior, a portion of which is dependent on crab body size. I find that, in general, large crabs use the refuge use less than small crabs, spending more time active in both the absence and presence of predation threat. I then use mark-recapture techniques to test for temporal consistency in this behavioral trait (i.e. the existence of a behavioral type). This work shows that crab refuge use behavior is repeatable over time (crabs spent a month in the field on average), and particularly repeatable when measured under the risk of toadfish predation. Studies of personality in invertebrates are relatively rare

(Kralj-Fišer and Schuett 2014), and this is one of the first to test for the consistency of individual behavior in an invertebrate species after time in the field.

Similar to behavior, there is widespread intra-population variation in metabolic rate that is consistent over time, but unexplainable based on size, sex or other easily-measured aspects of the phenotype (Nespolo and Franco 2007, Burton et al. 2010). Individual physiology has been implicated as a key driver of individual behavior (Careau et al. 2008); individuals that exhibit energetically costly behaviors (e.g. high activity level) should require a greater rate of energy metabolism to support these behaviors (Biro and Stamps 2010). In Chapter 5, I examine relationships between individual crab (*Panopeus herbstii*) activity level and standard metabolic rate (O^2 consumption measured via respirometry). To test for context-dependence in the behavior-physiology relationship, I measure these traits of crabs in the absence and presence of water-borne chemical cues from toadfish (*Opsanus tau*). In contrast to my previous measurements of individual crab behavior (Chapter 4), I use a restricted size range of crabs where the effect of crab body size on individual behavior is undetectable. While this study reveals repeatability of both individual activity level and metabolic rate independent of crab body size, I find no relationship between activity level and metabolic rate, either in the absence or presence of predation threat.

Lastly, in Chapter 6, I examine how individual crab behavior, specifically activity level, affects the crab (*Panopeus herbstii*) functional response to mussel prey (*Brachidontes exustus*) density. The form of the functional response is dependent on predator and prey behavior (Holling 1959, Brose 2010), but it remains unclear how consistent individual behaviors (i.e. animal personality) can affect the response. In this

Chapter, I also test how predation threat from toadfish (*Opsanus tau*) influences the functional response by manipulating the presence of toadfish chemical cues during crab foraging. I find that crab activity level affects the functional response of small, but not large crabs, suggesting size-dependent effects of activity level on the crab-mussel interaction. Specifically, small crabs with a high activity level consume more mussel prey across the range of mussel prey densities, reflected in the increased magnitude of their type-2 (hyperbolic) functional response. Toadfish predation threat, in contrast, reduces the magnitude of the crab functional response. Through alteration of the functional response, crab activity level could have important consequences for the population dynamics of crabs and mussels. Considering the ubiquity of behavioral types in predator and prey populations (Gosling 2001), this work has broad implications beyond the crab-mussel system.

3. *Parasite effects on individual ecology*

Parasites often modify the traits of their hosts, including host morphology, behavior and physiology (Holmes and Bethel 1972). Little known is known however, of how these trait changes could alter the species interactions that hosts are involved in (i.e. trait-mediated indirect effects). In Chapter 7, I examine the effect of an invasive barnacle parasite (*Loxothylacus panopaei*) on the foraging behavior and functional response of its host, the Xanthid crab, *Eurypanopeus depressus*. I find that this parasite drastically reduces the magnitude of the crab functional response, and this change in the response is driven by the delayed reaction of infected crabs to mussel prey. Furthermore, individual crabs harboring a greater parasite load exhibit a greater reaction time to mussel prey. This study therefore provides a mechanistic framework whereby the effects of a parasite on individual behavior can scale up to influence predator-prey interaction strength. These effects are particularly relevant considering the high prevalence of parasite infection in *Eurypanopeus depressus* from North Inlet estuary (~20%).

Study system: Xanthid crabs in intertidal oyster reefs

Xanthid crabs are a diverse taxonomic group, containing the most genera of any Brachyuran family (Williams 1984). Along the Atlantic and Gulf coasts of the U.S., Xanthid crabs are some of the most common and ecologically important consumers in estuarine habitats. Specifically, in North Inlet estuary, South Carolina (my dissertation study site), these crabs are the biomass and density-dominant resident consumers in intertidal reefs formed by the Eastern oyster (*Crassostrea virginica*) (Dame 1979). Oyster reefs are critical habitats in North Inlet, covering approximately 5% of its total area and providing the only hard-bottom substrate among a seascape of sand/mud flats (Dame 1979). These reefs host diverse ecological communities (37 resident species) that utilize the surfaces of oyster shells, the interstitial spaces between shells and the underlying mud/shell hash layer for refuge (Dame 1979). While oysters, the dominant filter-feeder, form the foundation of reefs, these habitats support multi-level food webs with major trophic groups (Dame and Patten 1981). Oysters also attract mobile predators (Lenihan et al. 2001) as well as juvenile fishes that use reefs as nursery grounds (Lehnert and Allen 2002).

The bivalves that Xanthid crabs feed upon in reefs, including oysters and several species of mussels, provide critical functions to estuarine ecosystems, such erosion control, benthic-pelagic coupling and water filtration (Dame et al. 1980, Dame and Libes 1993, Beck et al. 2011). North Inlet estuary in particular provides a good example of an estuary in which shellfish reefs play a critical role in cycling materials throughout the larger estuarine system. Work by Dame et al. (1980) shows that due to North Inlet's small size and extremely dense oyster aggregations, the time it takes for oysters to filter the entire water volume is just 0.7 days. By converting phytoplankton to oyster biomass and depositing suspended detritus, oysters effectively couple the pelagic and benthic zones of the estuary (Dame et al. 1980).

Two species of Xanthid crabs, *Panopeus herbstii* and *Eurypanopeus depressus*, co-occur in North Inlet's reefs (McDonald 1982). These crabs are omnivorous, but the larger *Panopeus herbstii* preys in large part on bivalves, such as oysters, ribbed mussels (*Geukensia demissa*) and scorched mussels (*Brachidontes exustus*). The smaller *Eurypanopeus depressus* has a more general diet, but can still consume substantial numbers of recently-settled juvenile bivalves (McDonald 1982, Chapter 7). These crabs have been considered pests for bivalve aquaculture operations in the southeastern U.S. due to their predation on cultured bivalves (Gibbons and Castagna 1985, Bisker et al. 1989), and predation on oyster spat by crabs has been implicated in impacting reef development (Wells 1961). Studies of niche variation between these crabs (McDonald 1982, Meyer 1994) have found that *Panopeus herbstii* tends to inhabit the shell hash/mud layer beneath oyster shells, while *Eurypanopeus depressus* is more often found in the interstitial spaces within the oyster reef matrix.

The work conducted on the community inhabiting oyster reefs in North Inlet has been largely descriptive (e.g. Dame 1979), but several lines of evidence point to the importance of predation in controlling the structure of the reef community. Using data on the biomasses of different trophic groups in North Inlet's reefs, Dame and Patten (1981) developed an energy flow model that predicts levels of control throughout the reef food web. Their results indicate that next to filter-feeders, the predator trophic group, comprised primarily of Xanthid crabs, plays the most important role in controlling the dynamics of the reef community. Specifically, predators control filter-feeders by directly consuming them, which in turn, alters the deposition of detritus in the system, indirectly affecting microbiota and meiofauna components. This result lead the authors to conclude that the data "support the ecological argument for top level consumer control of the environment" (Dame and Patten 1981). Furthermore, several studies have shown that trophic cascades involving Xanthid crabs as mesopredators are major determinants of community structure in reefs (e.g. Grabowski 2004, Grabowksi and Kimbro 2005, Griffen et al. 2012, Kimbro et al. 2014). These cascades are largely mediated by predator-induced changes in Xanthid crab foraging behavior (Grabowski 2004, Kimbro et al. 2014). Taken together, this evidence indicates that the biotic force of predation is important in controlling reef community structure in North Inlet.

In addition to their roles as consumers, Xanthid crabs serve as prey to a variety of vertebrate predators including fish and birds. In particular, the oyster toadfish (*Opsanus tau*) is a voracious predator of mud crabs; in South Carolina waters, mud crabs make up 65% of the diet of toadfish (Wilson et al. 1982). *Eurypanopeus depressus* are also infected by an invasive barnacle parasite (*Loxothylacus panopaei*) that was introduced to the Atlantic coast in the 1960's through shipments of oysters from the Gulf of Mexico (Van Engel et al. 1966). By altering the density and behavior of crabs, these natural enemies release the prey of crabs, namely bivalves, from crab predation (i.e. a trophic cascade) (Grabowski 2004, Grabowksi and Kimbro 2005, Griffen et al. 2012, Chapter 6, Chapter 7).

Several characteristics make these crabs an ideal system for which to test the importance of individual phenotypic variation for species interactions. First, these crabs occur in high densities in North Inlet's reefs (Dame and Vernberg 1982, McDonald 1982), making manipulations of their trait distributions in small experimental areas realistic. Second, these crabs reproduce continuously over the spring and summer months (McDonald 1982), and this pattern of reproduction produces continuous variation in body size. In particular, *Panopeus herbstii* reaches a maximum size of 55 mm (carapace width) in North Inlet (Dame and Vernberg 1982, McDonald 1982), and there is some evidence that larger crabs utilize different food resources compared to smaller crabs (Seed 1980, Whetstone and Eversole 1981). Third, Xanthid crabs have recently been used as a model system to examine animal personality (Hazlett and Bach 2010, Griffen et al. 2012, Gherardi et al. 2012). While most studies of personality have been conducted using vertebrate species, recent work has revealed that invertebrates, such as Xanthid crabs, also exhibit individual variation in behavioral traits that is consistent over time (Kralj-Fišer and Schuett 2014).

CHAPTER 2

PREDATORY CRAB SIZE DIVERSITY AND BIVALVE CONSUMPTION IN OYSTER REEFS[1]

ABSTRACT

Body size is widely recognized as an important functional trait of predators due to its influence on prey consumption rates and diet breadth. Yet it remains unclear how the diversity of this trait within predator populations affects prey communities. To test the effects of intraspecific predator size diversity, we manipulated the number of size classes (i.e. size diversity) in the Xanthid crab *Panopeus herbstii* and measured their consumption of the bivalve community in intertidal oyster (*Crassostrea virginica*) reefs. In the experiment, the presence of large crabs, but not size diversity, significantly affected total prey biomass consumption. The largest size class of crabs effectively consumed all bivalve prey types whereas smaller crabs were restricted in diet breadth. As such, any treatment containing large individuals had significantly greater total prey consumption and more uniform consumption across the prey community than those without. We also investigated the potential for oyster harvest by humans to alter crab population size structure at the study site (North Inlet, South Carolina, USA). Specifically, anthropogenic oyster harvest, which acts to compress the surficial shell layer in reefs, could reduce crab body size by reducing the availability of refuge habitat

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[1] Toscano, B.J. and B.D. Griffen. 2012. *Marine Ecology Progress Series*. 445: 65-74. Reprinted here with permission of publisher.

for large crabs. Therefore, we tested for a relationship between the height of the shell layer and average crab body size in the field. In the field survey, average crab body size decreased with decreasing height of the shell layer. Thus, our data suggests that oyster harvesting practices have the potential to skew crab size structure towards a preponderance of small individuals, thereby compromising the trophic transfer that occurs in unperturbed reefs.

INTRODUCTION

Predator body size is a key functional trait with important consequences for how predators affect prey communities (Elton 1927, Kneib & Stiven 1982, Werner & Gilliam 1984, Woodward et al. 2005, Brose 2010). Predator populations are naturally heterogeneous in body size, and different sized conspecifics often have divergent ecological effects (Polis 1984, Werner & Gilliam 1984, Werner 1992). For example, body size affects individual prey consumption rates due to differing energetic requirements or handling times (Mittelbach 1981, Brose 2010), and can also influence diet diversity or trophic position due to changes in size of the feeding apparatus (Hardy 1924, Arim et al. 2010). Incorporating such intraspecific functional variation in both empirical and theoretical frameworks has major consequences for trophic interactions and food web dynamics (Rudolf 2007, Okuyama 2008, Bolnick et al. 2011, Rudolf & Lafferty 2011).

Body size variation within predators represents a potentially important, yet understudied level of predator biodiversity (i.e. intraspecific diversity). Previous studies of predator biodiversity have focused almost exclusively on predator species richness (i.e. interspecific diversity) (Bruno & Cardinale 2008, Hillebrand & Matthiessen 2009, Reiss et al. 2009, Finke & Snyder 2010). These studies indicate that functional diversity (i.e. the range of functional traits among predator species), rather than richness *per se*, drives ecological processes such as prey suppression (Schmitz 2007, Bruno & Cardinale 2008, Schmitz 2009). For example, crab species that consume different prey types fulfill complimentary functional roles in the rocky intertidal (Griffin et al. 2008). Such resource partitioning allows greater resource use efficiency, thus enhancing ecological process rates (Finke & Snyder 2008, Griffin et al. 2008).

Mechanisms such as resource partitioning could apply similarly to the ecological effects of intraspecific body size diversity. For example, the partitioning of food resources is common within predator species (Polis 1984), where small and large size classes of a predator often have non-overlapping diets (Stoner & Livingston 1984). Such ontogenetic (i.e. growth-related) shifts are widespread throughout fish, amphibians, reptiles and invertebrate taxa (Werner & Gilliam 1984). While some of these species undergo major morphological and habitat transitions that are associated with diet differences (e.g. amphibians), intraspecific partitioning is also common in predators that exhibit simple allometric growth (Werner & Gilliam 1984). Other types of intraspecific phenotypic variation (e.g. morphology, sex, individual specialization; Bolnick et al. 2003) can have similar effects on diet variation within species. In some communities, such niche variation within predator species exceeds variation among predator species means (e.g. Woodward & Hildrew 2002, Arim et al. 2010). Particularly in these communities, intraspecific predator diversity could have ramifications for consumptive effects in food webs.

Furthermore, intraspecific predator size diversity is being altered by anthropogenic stressors. For example, harvesting practices that target the largest individuals in a population (i.e. minimum size limits) skew population size structure towards smaller individuals (Fisher et al. 2010, Shackell et al. 2010), thus reducing body size diversity within predator populations. Harvesting can also indirectly affect predator size structure by decreasing intraspecific competition, which in turn increases growth rates and size-at-age in some harvested populations (Law 2000).

The mud crab, *Panopeus herbstii*, is common along the Atlantic and gulf coasts of the U.S., where it inhabits hard-bottom substrates in the intertidal zone, especially oyster reefs (Williams 1984). Throughout its range, this crab is a major consumer of mollusks (particularly bivalves and gastropods), affecting their local distribution and population structure (McDermott 1960, Seed 1980, Bisker & Castagna 1987, Milke & Kennedy 2001). Within our study site (North Inlet, South Carolina), this crab is the numerically- and biomass-dominant resident predator in intertidal reefs created by the eastern oyster (*Crassostrea virginica*) (Dame 1979). These reefs fringe the banks of tidal creeks throughout North Inlet and provide the only natural hard substrate available, supporting food webs with major trophic levels (e.g. primary producers, primary consumers, predators) (Dame 1979). Here, *P. herbstii* feeds on a community of bivalves including *C. virginica*, scorched mussels (*Brachidontes exustus*) and ribbed mussels (*Geukensia demissa*) (Dame & Patten 1981, Dame & Vernberg 1982). Feeding preference experiments conducted in the laboratory show that larger *P. herbstii* preferentially consume larger bivalves (Seed 1980, Whetstone & Eversole 1981). In North Inlet's reefs, bivalve prey size varies considerably (Figure 2.1), providing opportunity for intraspecific prey resource partitioning. These bivalves in turn provide important ecosystem services to North Inlet including benthic-pelagic coupling and erosion control (Dame & Libes 1993).

While *Panopeus herbstii* is not harvested directly, the harvest of their biogenic habitat (oysters) is potentially altering the size distribution of *P. herbstii* in North Inlet's reefs. Oyster harvest (e.g. tonging, dredging, hand-harvesting) is a destructive practice that reduces the height and structural complexity of subtidal oyster reefs (Lenihan & Peterson 1998, 2004). In North Inlet, recreational oyster harvest has similar impacts on intertidal reefs where oyster removal and concomitant trampling reduces the height of the surficial shell layer (Toscano, *unpublished data*), defined as the extension of live and dead oyster shells above the sediment. Structurally complex reefs provide refuge for *P. herbstii* and crab density is positively correlated with the volume of oyster clusters (Meyer 1994). Because larger crabs require more refuge space than smaller crabs (Meyer 1994), reductions in the height of the surficial shell layer that occur with oyster harvesting could skew crab size structure towards a preponderance of smaller individuals. This reduction in crab body size and the more general loss of size diversity could have important cascading effects on the oyster reef food web.

Here, we tested how altered body size diversity in *Panopeus herbstii* influences their top-down effects on bivalves. To accomplish this we manipulated the number of size classes in *P. herbstii,* treating size classes as units of biodiversity, and measured aggregate and prey-specific consumption of the bivalve community in reefs. We also examined the relationship between the height of the surficial shell layer and *P. herbstii* body size in the field to determine the potential effects of oyster harvest on crab size structure in intertidal reefs.

METHODS

Study site

We conducted the experiment and sampled crabs in tidal creeks within North Inlet estuary (33° 20’ N, 79° 10’ W) in Georgetown, South Carolina USA. North Inlet is an ocean-dominated estuary characterized by high average salinity (34 ppt) and a diurnal tidal cycle (mean tidal height of 1.5 m above MLLW) (Dame et al. 1986). The experiment was run from July-August 2010 and field sampling was conducted during August of 2010 and July of 2011.

Field experiment

In order to test the role of intraspecific body size diversity in mediating the predatory impacts of *Panopeus herbstii*, we manipulated body size diversity, or the number of size classes present in a population. We manipulated size diversity over 3 levels (1, 2 and 3 size classes present) while maintaining a constant total energy demand (Chalcraft & Resetarits 2004) in a substitutive experimental design (Table 2.1). This design allows separation of the effects of population size distribution on consumption rates, without confounding associated allometric changes in metabolic rate that would arise if densities were held constant across size classes. This application of the substitutive design is analogous to that in species richness studies that alter the number of species while maintaining a constant overall density of individuals (e.g. Griffin et al. 2008, Toscano et al. 2010).

We determined densities of each size class that are equivalent in total energy demand using a power-law metabolic rate model where the total energy demand of a population (*T*) of mean body size (*W*) is a function of the metabolic rate (*I*) of individuals times the number of individuals (*N*) (Brown et al. 2004, Chalcraft & Resetarits 2004):

Equation 1.
$$\mathrm{T}_{w} = I \times N$$

Metabolic rate (*I*) scales as a power-law function of body size with a scaling exponent of roughly 0.75 (Leffler 1973, Brown et al. 2004). Thus, populations *i* and *j* of densities *N* and mean body sizes *W* have an equivalent total energy demand when the following equality is satisfied (Chalcraft & Resetarits 2004):

Equation 2.
$$\frac{\ln\left(\frac{N_i}{N_j}\right)}{\ln\left(\frac{W_i}{W_j}\right)} = -0.75$$

This energetic equivalence rule predicts that populations of equivalent total energy demand will have similar impacts on ecological processes related to metabolic rate (e.g. ingestion), without taking into account the roles of density-dependence or size specific foraging abilities (Chalcraft & Resetarits 2004).

Specifically, this model yielded the prediction that 8 small crabs (19-23 mm carapace width [CW]), 4 medium crabs (29-33 mm CW) and 2 large crabs (38-42 mm CW) are approximately equivalent in total energy demand, and so these densities were used in assembling the various treatments (Table 2.1). This inverse relationship between density and body size as well as the overall crab biomass used in this experiment is similar to patterns in natural populations of *Panopeus herbstii* from North Inlet (Dame & Vernberg 1982, McDonald 1982). Here, crabs exhibit fairly distinct size classes due to pulsed recruitment during late spring and summer (Dame & Vernberg 1982, McDonald 1982). The experiment was conducted in a randomized complete block (temporal) design with a total of 5 blocks (N = 5 replicates per treatment).

We conducted the experiment within completely enclosed wire cages (0.5 [L] × 0.6 [W] × 0.3 [H] m) lined with 0.25 cm polyethylene plastic sheet netting to prevent predator emigration or immigration. Each cage received two artificial oyster reefs (0.3 [L] × 0.16 [W] × 0.12 [H] m) to recreate the intertidal oyster reefs inhabited by the study species. We used artificial reefs to precisely control the amount and type of prey in cages, as well as standardize the complexity of the habitat because reef complexity is an important determinant of *Panopeus herbstii* bivalve consumption rates (Grabowski 2004, Grabowski & Powers 2004). We created these reefs using oyster shell that had been dried and cleaned to remove epifauna. Holes were drilled in shell and shell clusters were assembled to mimic natural reef formations using plastic zip-ties. We then mounted the clusters on a fiberglass base and standardized by size as well as volume (measured through water displacement) to create a standardized reef matrix on which bivalve prey could be attached.

Two sizes of *Brachidontes exustus* (small: 0.5-0.9 g wet weight [WW], large: 1-2 g WW) and *Crassostrea virginica* (small: 4-7 g WW, large: 11-14 g WW), and a single size of *Geukensia demissa* (3-6 g WW) were offered to crabs in cages within the range of natural field densities (Figure 2.1; Table 2.1). These species are the most common constituents of the bivalve grazer community in North Inlet's reefs (Dame 1979), and are all commonly found in the stomach contents of *Panopeus herbstii* from the field site (Griffen, *unpublished data*). Bivalve prey were attached to the artificial oyster reefs in the lab prior to trials. Oysters were glued (Gorilla Super Glue) to artificial reefs while mussels attached naturally through byssal thread formation. After attachment, artificial reefs with prey were placed in flow-through seawater tanks and individual bivalves were observed for normal filtering behavior over 24 h. Predators and prey were collected from reefs adjacent to the study site and used only once in the experiment. Crabs were starved for 2 days prior to trials to standardize hunger levels.

Cages were deployed over a homogenous substrate of mud/sand adjacent to and at the same tidal level as natural oyster reefs. First, sediment taken from the mud/sand flat adjacent to the experimental site was added to cages (8 cm). Artificial reefs with attached prey were then added. Next, 20 loose shells of similar dimensions, also dried and cleaned of epifauna, were scattered around the artificial reefs in each cage, again to recreate the complex, 3-dimensional habitat of natural oyster reefs. Finally, treatments were randomly assigned to cages and crabs were added. Trials lasted 48 hours (4 tidal cycles) and cages were deployed and retrieved at low tide. At the conclusion of each trial, surviving prey were counted and mortality was determined as the loss of prey between the start and end of trials.

Prey biomass consumption (dry weight prey tissue consumed, g 48 h^{-1}) was used as the response variable in all statistical analyses. Dry weight was determined as follows. First, sub-samples of prey used in the experiment were randomly taken to estimate the mean wet weight of each prey type (Table 2.2). Then, for a range of sizes of each prey type, soft tissue was removed and dried in a drying oven at 60 °C for 24 h to determine the relationship between wet tissue weight and dry tissue weight using linear least-squares regression (*Brachidontes exustus*: $R^2 = 0.84$, *Crassostrea virginica*: $R^2 = 0.69$, *Geukensia demissa*: $R^2 = 0.85$). To estimate prey-specific consumption, the number of individual prey of each type that were missing at the end of trials was multiplied by the mean dry tissue weight for individuals of that prey type (as estimated through linear regression) (Table 2.2). The mean dry tissue weight of each individual prey species consumed by crabs was summed to derive the total consumption by the crab population in each cage.

We used a two-factor analysis of variance (ANOVA) with temporal block and treatment as factors to test for differences in total consumption among the different treatments (treatments A to G, Table 2.1). We then used the following planned linear contrasts to test specific hypotheses regarding the effects of crab size diversity and size composition on total consumption. First, we compared the mean of the three single-size-class treatments (A, B, C) to the most diverse 3-size class treatment (G) to test for the effect of body size diversity on total consumption. Second, we compared treatments with large crabs (C, E, F, G) to treatments without (A, B, D) to test for the importance of large crabs in determining total consumption.

For treatments with 2 size classes present (D-F), we compared actual total consumption to that predicted by a substitutive model (Griffen 2006):

Equation 3. $$E = (C_1 \times C_2)^{0.5}$$

where E is expected total prey consumption and C_1 and C_2 are total consumption by each size class separately. This substitutive model predicts total consumption assuming additive effects (Griffen 2006). Two-tailed paired *t*-tests were used to compare predicted and observed total consumption to determine whether predation by different size classes did in fact combine additively (Griffen 2006). Total consumption data for these analyses were not significantly different from a normal distribution (Shapiro-Wilk normality test: $W = 0.965$, $P = 0.325$) and variances were homogenous among groups (Bartlett's test: test statistic = 11.9719, df = 6, $P = 0.063$).

We used permutational multivariate ANOVAs (PERMANOVA) to test for differences among treatments in their effects on the bivalve prey assemblage. The first PERMANOVA tested for differences in prey resource use between the 3 single-size-class treatments (treatments A to C). The second PERMANOVA tested for differences in prey resource use between the multiple size class treatments (treatments D to G). Similarity percentage (SIMPER) analysis was used to determine which bivalve prey types contributed most to dissimilarity between treatments. SIMPER was conducted using PAST (Hammer et al. 2001). All other statistical analyses were conducted using R (v.2.12.0) (R Core Development Team 2010).

Crab sampling

To examine the relationship between the height of the surficial shell layer and crab body size, we sampled mean shell layer height and mean crab body size in 0.25 m^2 quadrats (N = 29) from intertidal oyster reefs that receive mild harvest pressure (Toscano, *personal observations*). Quadrats were taken from reefs bordering tidal creeks that were roughly equivalent in area (50 m^2) and shape. Mean shell layer height was measured as the distance between the mud layer and tops of shells at the corner of each quadrat (4 measurements for each quadrat were averaged). Crabs from within the quadrat were removed and mean size was determined. Because crab recruitment occurs over the spring and summer months (Dame & Vernberg 1982, McDonald 1982), densities of new recruits were likely higher than if crabs were sampled at other times of the year. Thus, we only sampled crabs over 15 mm CW to reduce the influence of new recruits. Only plots with 100% oyster shell cover were sampled to avoid confounding the known effects of percent shell cover on *Panopeus herbstii* populations (Meyer 1994). Since both variables were sampled with error, model II regression (reduced major axis regression) was used to test for a significant relationship between reef height and crab body size.

RESULTS

Field experiment

Prey mortality in predator-free controls was low (< 3% for all prey species combined), indicating that prey mortality in predator-present treatments was due to predation. Total prey consumption differed across treatments (ANOVA, $F_{6,24} = 5.207$, $P = 0.001$, Figure 2.2) and temporal blocks (ANOVA, $F_{4,24} = 3.939$, $P = 0.013$). Mean total prey consumption of the 3 single-size-class treatments (A to C) did not differ from that when 3 size classes were combined (G) (linear contrast, $F_{1,24} = 0.391$, $P = 0.538$, Figure 2.2), though treatments that included large crabs had greater total consumption than treatments without large crabs (linear contrast, $F_{1,24} = 14.422$, $P = 0.0009$, Figure 2.2).

Small and medium crab combinations (treatment D) and small and large crab combinations (treatment E) had greater total consumption than substitutive model predictions based on consumption by each size class alone (paired *t*-tests, $t_4 = -3.083$, $P = 0.037$ and $t_4 = -3.921$, $P = 0.017$, for treatments D and E respectively, Figure 2.2). Total consumption by medium and large crabs together (treatment F) however, did not differ significantly from the model prediction (paired *t*-test, t_4 = -0.894, *P* = 0.422, Figure 2.2).

Prey-specific consumption of the bivalve assemblage was dependent on treatment in single-size-class treatments (PERMANOVA, $F_{2,12}$ = 16.616, *P* = 0.01, Figure 2.3a). SIMPER analysis revealed that *Geukensia demissa* was the prey type that contributed most to dissimilarity between small and large crab treatments, as well as between medium and large crab treatments (Figure 2.4). Small *Crassostrea virginica* contributed most to dissimilarity between small and medium crabs (Figure 2.4). In general, small crabs restricted their diet to small and large *Brachidontes exustus*. Medium crabs also consumed both size classes of *B. exustus*, while adding *G. demissa* and small *C. virginica* to their diet. Large crabs had the broadest diet and consumed the bivalve prey types most evenly. Specifically, large crabs increased their consumption of *G. demissa* and small *C. virginica*, while further adding large *C. virginica* to their diet and reducing consumption of *B. exustus* (Figure 2.3a).

Treatment had a marginal effect on prey-specific consumption of the bivalve community when multiple size classes of crab were present (perMANOVA, $F_{3,16}$ = 2.232, *P* = 0.06, Figure 2.3b). Consumption of *Brachidontes exustus* remained fairly consistent across multiple size class treatments (Figure 2.3b), while consumption of large *Crassostrea virginica*, a much larger prey item (Table 2.2, Figure 2.1), occurred only in the presence of large crabs (Figure 2.3b).

Crab sampling

The average body size of *Panopeus herbstii* was positively related to the height of the surficial shell layer (model II regression, $P < 0.0001$, $R^2 = 0.479$, Figure 2.5) within intertidal oyster reefs.

DISCUSSION

In the field experiment, crab body size diversity had no effect on total prey consumption when all 3 size classes were combined (Figure 2.2). There was however, some evidence of emergent, positive effects of size diversity in treatments with 2 size classes (Figure 2.2). More important than diversity *per se* was the presence of large crabs. In treatments with large crabs present, total prey consumption was significantly greater than in treatments without large crabs (Figure 2.2). In the field survey, we found a positive relationship between the height of the surficial shell layer and crab body size (Figure 2.5). Because oyster harvest reduces the height of this shell layer, harvest can have substantial indirect effects on crab size structure. Specifically, oyster harvesting practices that reduce shell layer height and structural complexity likely skew crab size structure towards a preponderance of small individuals, thereby reducing mean crab size in reefs. Due to the importance of large crabs in enhancing trophic transfer (Figure 2.2), the loss of large crabs could substantially perturb the oyster reef food web.

Data on prey-specific consumption (Figure 2.3) provides some insight into the mechanisms behind the total consumption results. The lack of a consistent effect of body size diversity was not surprising considering crab size classes did not discretely partition bivalve prey resources. Theoretical work predicts that increasing specialist consumer diversity should enhance aggregate resource use, while increasing generalist consumer diversity should have no effect (Ives et al. 2005). Empirical studies support this prediction, showing that partitioning among foragers can increase resource use efficiency (Finke & Snyder 2008, Griffin et al. 2008). Instead of partitioning among size classes, there was an increase in diet breadth with crab body size (i.e. nested diets, Figure 2.3a). Smaller crabs were restricted in their resource use to the smallest prey types (small and large *Brachidontes exustus*: Figure 2.3a) while larger crabs added larger prey to their diet while still consuming smaller prey, albeit at lower rates (Figure 2.3a).

Positive effects of diversity were seen however, in treatments with 2 size classes present. Both small and medium, as well as small and large crabs together consumed significantly more than the additive prediction (Figure 2.2). In our substitutive experimental design, there is a reduction in size class density in the more diverse treatments (Table 2.1). This could have the effect of releasing crabs from intra-size class competition. This is congruent with the empirical finding that only size ranges that overlap in resource use exhibit density-dependence within species (Polis 1984) and that interference competition between crabs is strongest among similarly-sized conspecifics (Smallegange & van der Meer 2007). This same mechanism has been observed in studies of predator richness, where multispecies predator assemblages have greater effects on ecological processes due to reduced intraspecific densities, and thus reduced resource overlap and interference (Griffin et al. 2008, Takizawa & Snyder 2011). However, only with stomach contents analyses or additional treatments from an additive design (Griffen 2006, Byrnes & Stachowicz 2009) can this hypothesis be assessed with the present system. It also is worth mentioning that while we limited the prey community to bivalves, a major food source for *Panopeus herbstii*, these crabs are omnivorous and will consume other food resources including other invertebrates, algae and detritus (Toscano and Griffen, *unpublished data*). Had these other food resources been incorporated into the study, partitioning between size classes may have been detected.

In treatments with large crabs, total prey consumption was enhanced relative to treatments without large crabs. This was due to the ability of large crabs to consume the larger bivalve prey types (Figure 2.3a) that were not consumed by smaller crabs on the time scale of our experiment. These resource use differences among different sized crabs were likely driven by morphological constraints on foraging, and a trade-off in the foraging capabilities of small and large crabs (Seed & Hughes 1997, Morton & Harper 2008). The major claw of small crabs, the functional organ used to handle prey, is not large and robust enough to crush the large prey types outright, and so these prey gain a size refuge in treatments with small crabs on the time scale of our experiment (Figure 2.3a). However, smaller crabs are more efficient than large crabs at consuming *Brachidontes exustus* in this study (Figure 2.3a). This is supported by functional response data in which small crabs consume more small *B. exustus* at low prey densities (Toscano and Griffen, *unpublished data*). Thus, under predation by large crabs, smaller prey may gain a partial refuge from predation.

While our experiment revealed these short-term changes in predation with crab size structure, size structure could also affect bivalve population dynamics, the long-term stability of the reef community, and the recovery of the community from disturbance. While our data suggests that the loss of large crabs may free larger oysters from predation, higher consumption rates on small, or newly settled bivalves (e.g. oyster spat) by small crabs could impede the recovery of reefs from perturbation. Thus the loss of large crabs (and predominance of smaller crabs) could affect the recruitment and assembly of the bivalve community. These long-term consequences of changes in predator size structure are unknown, but likely important for the management of imperiled reef systems worldwide.

Ontogenetic diet expansion, as detected in the present study, is common in consumers (Polis 1984, Werner & Gilliam 1984, Woodward & Hildrew 2002, Woodward et al. 2005, Arim et al. 2010) and particularly those that are limited by the size of their feeding apparatus (e.g. mouth gape size in fish and amphibians, claw size in crabs). In such consumers, large individuals are functionally unique as they can consume prey that smaller individuals cannot. In these cases, the loss of size structure, and particularly the loss of large individuals, can have important implications for lower trophic levels; without large predator individuals, large prey items will be freed from top-down control. This is an important applied issue because human harvesting practices often remove the largest individuals in a population, skewing population size structure towards smaller individuals and reducing intraspecific body size diversity. Thus understanding how intraspecific size diversity in predator populations mediates their community impacts is critical to ecosystem-based management practices, which in part focus on the community-wide effects of harvesting a species.

Reduced top-down control resulting from the harvesting of large individuals was recently observed by Shackell et al. (2010) who reported that exponential increases in prey abundance over 38 years in a northwest Atlantic fishery are related to declines in the average body size of exploited fish predator species. Total predator biomass remained constant over this time period, but the body mass of predators declined 60% due to the preferential exploitation of large individuals. This loss of large individuals initiated a trophic cascade in which prey were freed from top-down control, in turn reducing zooplankton and increasing phytoplankton abundances. Our study provides a mechanistic basis that elucidates how such a broad-scale effect can transpire with the loss of large size classes from predator populations.

In sum, previous studies document the importance of predator species richness (Bruno & Cardinale 2008), yet aspects of intraspecific predator diversity remain to be fully incorporated into the larger framework of predator biodiversity. Our study has addressed one component of intraspecific phenotypic diversity, though other components of intraspecific diversity are likely also important in driving ecological or even ecosystem level processes (e.g. individual specialization, resource use differences due to polymorphism; Bolnick et al. 2003). As with size diversity, these additional forms of diversity can be altered by human activities. For example, exploitation often targets certain animal personality types where the boldest individuals more frequently approach and are caught in traps (Biro & Post 2008). This removal of particularly bold individuals can alter the intraspecific behavioral diversity of a population. With continued alterations to all organizational levels of biodiversity, the challenge is to move beyond species richness manipulations alone to gain a more holistic understanding of the functional importance of biodiversity.

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Table 2.1 Treatments in a substitutive experimental design used to examine the effects of body size diversity and size composition of *Panopeus herbstii* populations on bivalve prey consumption. Each treatment was replicated 5 times in a randomized complete block design. Total energy demand (*T*) units refer to densities of crabs from each size class that are approximately equivalent in total energy demand. Small crabs were 19-23 mm carapace width (CW), medium crabs 29-33 mm CW and large crabs 38-42 mm CW.

Treatment code	Small no. cage^{-1}	Medium no. cage^{-1}	Large no. cage^{-1}	T units size class^{-1}	Size diversity
A	24	0	0	3	1
B	0	12	0	3	1
C	0	0	6	3	1
D	12	6	0	1.5	2
E	12	0	3	1.5	2
F	0	6	3	1.5	2
G	8	4	2	1	3
H (control)	0	0	0	0	0

Table 2.2 Bivalve prey community offered in all treatments. Numbers of prey were split evenly between the 2 reefs in each cage. Sub-samples of prey used in experiment were randomly taken to estimate mean wet weight for each prey type. See "Methods" for procedure used to estimate dry tissue weight for each prey type.

Prey species	N cage^{-1}	Size class (wet weight; g)	N (sub-sample)	Mean wet weight (g)	SE	Dry tissue weight (g)
Brachidontes exustus						
small (15-18 mm)	20	0.5 - 0.9	201	0.68	0.009	0.027
large (19-24 mm)	10	1.0 - 2.0	154	1.39	0.033	0.055
Crassostrea virginica						
small (35-44 mm)	12	4.0 - 7.0	183	5.73	0.075	0.077
large (53-58 mm)	6	11.0 - 14.0	168	12.34	0.078	0.159
Geukensia demissa (34-44 mm)	4	3.0 - 6.0	74	4.31	0.106	0.131

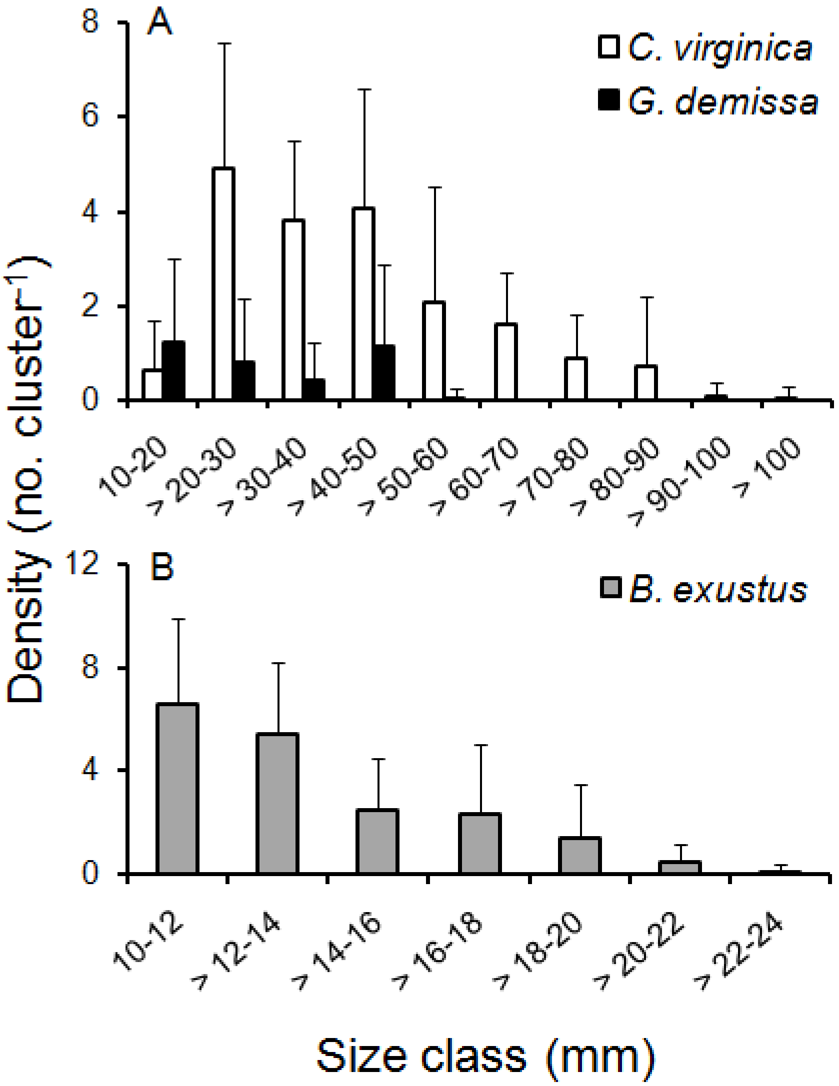

Figure 2.1 Size frequency distributions of bivalves in intertidal oyster reefs in North Inlet, South Carolina: A) Size frequency distributions of oysters, *Crassostrea virginica* (white bars) and the mussel *Geukensia demissa* (black bars). Only oysters on the exterior of the cluster, and thus vulnerable to predation on the time scale of our experiment were enumerated; B) Size frequency distribution of the mussel *Brachidontes exustus* (grey bars). All bars are means ± 1 SD from oyster clusters (N = 13). Clusters were randomly selected from reefs adjacent to the study site. Clusters varied in volume, and so densities here were scaled to the cluster volume (5760 cm^3) used in field cages. Each cage received 2 clusters of this volume (see main text for explanation of field experiment).

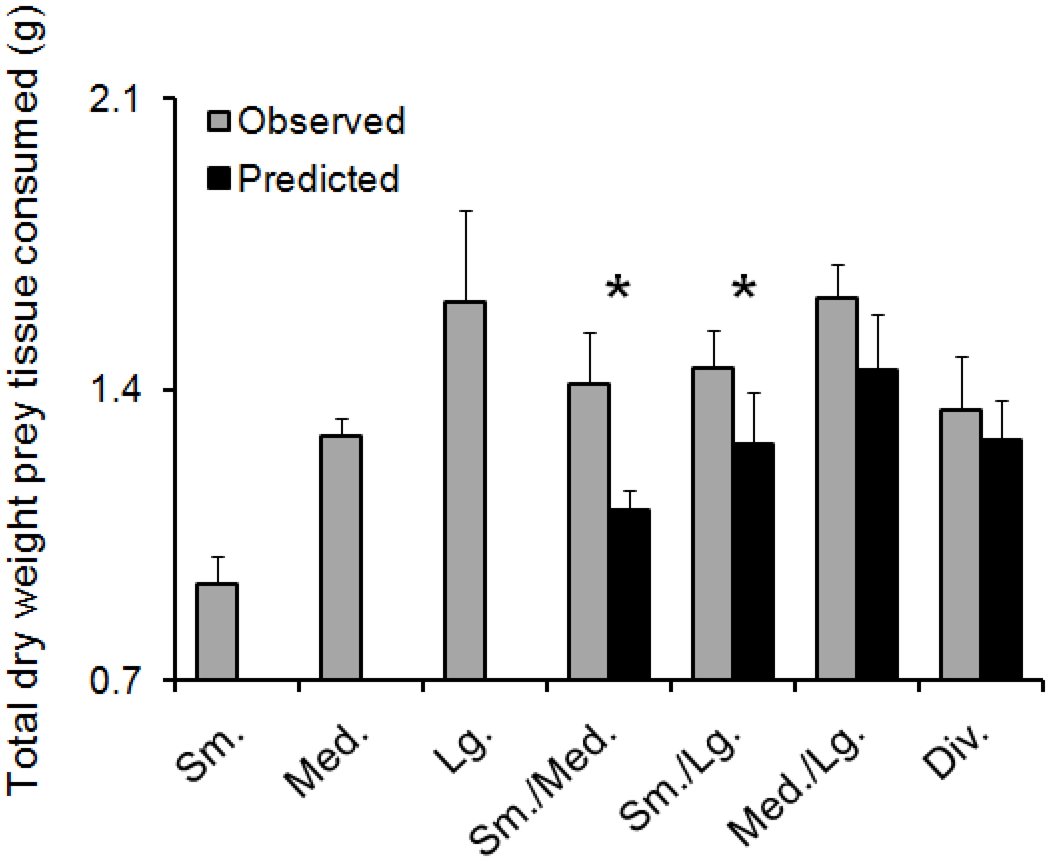

Figure 2.2 Observed total prey consumption by crab population treatments (A-G, Table 2.1) and substitutive model predictions for treatments with 2 crab size classes (D-F, Table 2.1). Values are mean total dry weight tissue consumed, g 48 h^{-1} of 5 replicates ± 1 standard error. Substitutive model predictions were calculated for each trial block separately using eq. 3. * denotes a significant difference between observed and predicted total consumption rate ($\alpha = 0.05$). "Div." refers to the diverse treatment with 3 crab size classes present (treatment G, Table 2.1). See Table 2.1 for densities of different crab size classes within treatments.

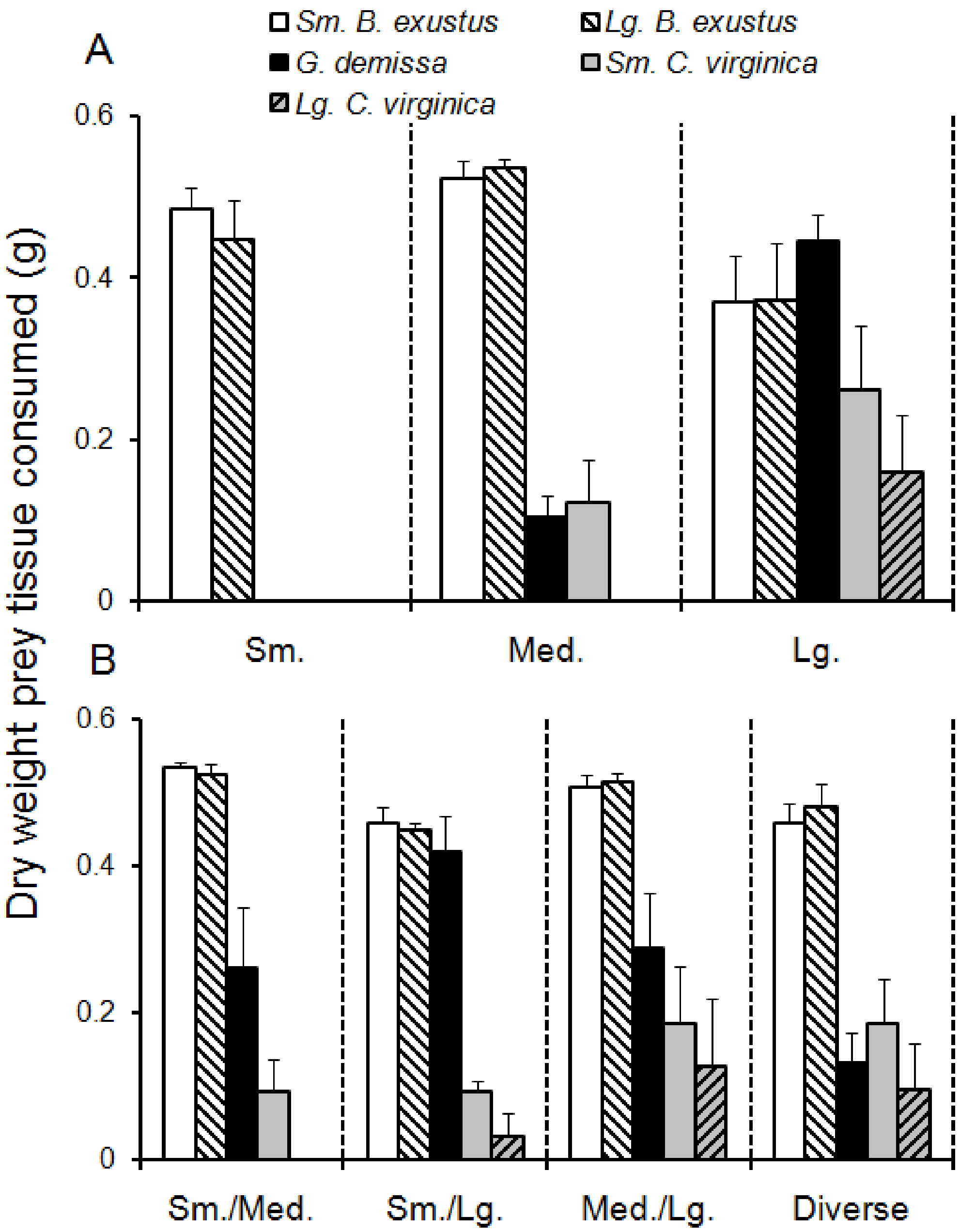

Figure 2.3 Consumption of different bivalve prey types by predator population treatments: A) Consumption by single-size-class treatments (A-C, Table 2.1); B) Consumption by multiple size class treatments (D-G, Table 2.1). Values are mean dry weight tissue consumed, g 48 h^{-1} of 5 replicates ± 1 standard error. See Table 2.2 for prey sizes and densities.

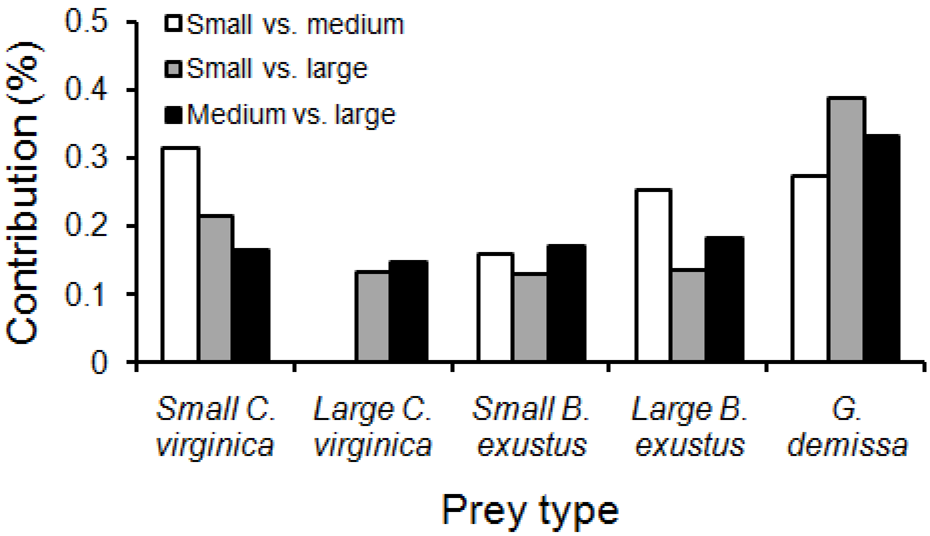

Figure 2.4 Histogram of the contribution of bivalve prey types to dissimilarity between small and medium crab treatments (A vs. B, Table 2.1; white bars), small and large crab treatments (A vs. C, Table 2.1; grey bars), and medium and large crab treatments (B vs. C, Table 2.1; black bars) as determined by SIMPER. See Table 2.2 for prey sizes and densities.

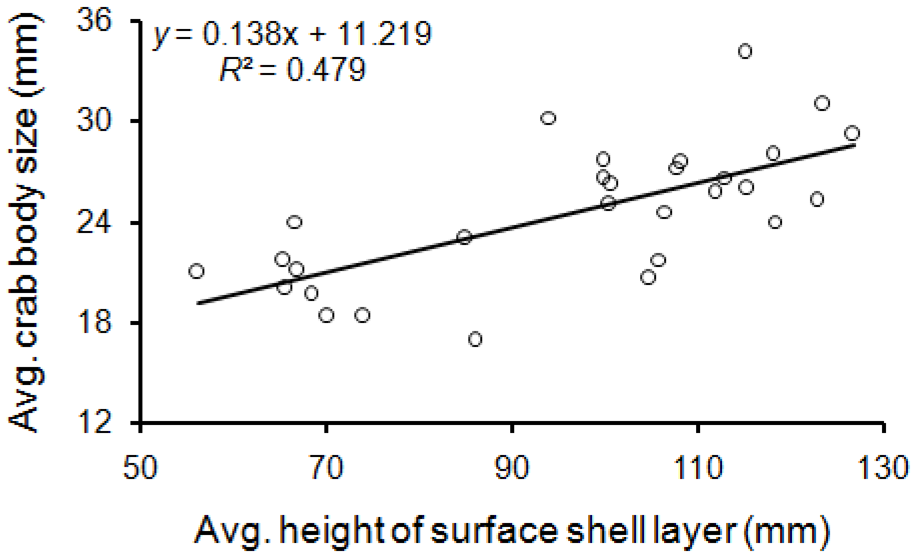

Figure 2.5 Relationship between reef height and body size of *Panopeus herbstii* in intertidal oyster reefs in North Inlet, SC. Each point represents the mean crab body size (mm) and mean reef height (mm) sampled per 0.5 m^2 quadrat (N = 29).

CHAPTER 3

PREDATOR SIZE INTERACTS WITH HABITAT STRUCTURE TO DETERMINE THE ALLOMETRIC SCALING OF THE FUNCTIONAL RESPONSE[2]

ABSTRACT

While both predator body size and prey refuge provided by habitat structure have been established as major factors influencing the functional response (*per capita* consumption rate as a function of prey density), potential interactions between these factors have rarely been explored. Using a crab predator (*Panopeus herbstii*) - mussel prey (*Brachidontes exustus*) system, we examined the allometric scaling of the functional response in oyster (*Crassostrea virginica*) reef habitat, where crevices within oyster clusters provide mussels refuge from predation. A field survey of mussel distribution showed that mussels attach closer to the cluster periphery at high mussel density, indicating the potential for saturation of the refuge. In functional response experiments, the consumption rate of large crabs was depressed at low prey density relative to small crabs, while at high prey density the reverse was true. Specifically, the attack rate coefficient and handling time both decreased non-linearly with crab size. An additional manipulation revealed that at low prey densities, the ability of large crabs to maneuver their claws and bodies to extract mussels from crevices was inhibited relative to small crabs by the structured habitat, reducing their attack rate. At high prey densities, crevices

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[2] Toscano, B.J. and B.D. Griffen. 2013. *Oikos*. 122: 454-462.
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were saturated, forcing mussels to the edge of clusters where crabs were only limited by handling time. Our study illuminates a potentially general mechanism where the quality of the prey refuge provided by habitat structure is dependent on the relative size of the predator. Thus anthropogenic influences that alter the natural crab size distribution or degrade reef habitat structure could threaten the long-term stability of the crab - mussel interaction in reefs.

INTRODUCTION

Predator-prey interactions provide structure for communities and the strength of these interactions is a primary determinant of community stability (MacArthur 1955, Paine 1980, Berlow et al. 2004, O'Gorman and Emmerson 2009). Accordingly, understanding the factors that constrain predator-prey interaction strength remains a continual goal in ecology (Berlow et al. 2004). Predator-prey interaction strength is often described by an individual predator's consumption rate as a function of prey density (Holling 1959, Berlow et al. 2004). This relationship, termed the functional response (Solomon 1949), is dependent on emergent traits related to a predator's foraging behavior such as attack rate (instantaneous rate of encounter, depending on reactive distance, movement speed and capture success) and handling time (time it takes to capture, subdue, consume and digest an individual prey) (Holling 1959, Jeschke et al. 2002). As a component of predator-prey population models, the functional response allows scaling up from these individual behavioral traits to predict predator and prey population dynamics. At the population level, the precise shape of the functional response, as determined by the predator's attack rate and handling time, governs the stability of predator-prey dynamics (Murdoch and Oaten 1975, Hammill et al. 2011).

Due to the importance of the functional response for predator-prey population dynamics, considerable work has been conducted on the ecological factors that determine response characteristics (Jeschke et al. 2002). One such factor is the ratio of predator size to prey size. Predator-prey size ratios generally act to constrain the functional response within parameter space due to mechanistic links between body size and foraging behavior traits (Brose 2010). For example, attack rate is predicted to be hump-shaped with respect to the predator-prey body size ratio. When predators are small relative to their prey, their search area and movement speed should be reduced and when predators are large relative to their prey, their capture success should be low with some maximum in between. Indeed, recent work employing simple allometric constraints has had great success in predicting trophic links and their strength in empirical food webs (Otto et al. 2007, Petchey et al. 2008, O'Gorman and Emmerson 2009). However, empirical data on such scaling relationships is sparse, and as a result, common patterns in the size scaling of foraging traits remain unresolved (Brose 2010). Determining the precise allometric scaling of functional response parameters is important because it can have major consequences for the dynamics of size structured populations (Persson et al. 1998, McCoy et al. 2011). Furthermore, studies documenting allometric scaling of the functional response rarely identify the mechanisms behind empirical scaling relationships (Brose 2010, Vucic-Pestic et al. 2010); identifying these mechanisms is essential in making predictions that extend beyond specific taxonomic groups.

A second ecological factor that can significantly affect the functional response is prey refuge, defined as any strategy that reduces predation risk (Sih 1987). For example, a prey refuge provided by habitat structure is commonly cited as the mechanistic basis of sigmoidal or type III functional responses (Hildrew and Townsend 1977, Anderson 2001). At low prey densities, most prey occupy the structural refuge and are therefore invulnerable to predation. As prey density increases, the refuge becomes saturated and the proportion of prey in the refuge decreases (Sih 1987). This causes density dependent predation (proportional consumption is lowest at the lowest prey densities), and thus a type III response. Because type III functional responses can stabilize predator-prey population dynamics (Murdoch and Oaten 1975, but see Basset et al. 1997), prey refuges are generally assumed to have this effect, but prey refuges can also destabilize interactions under certain circumstances (McNair 1986).

While numerous studies demonstrate the independent importance and ubiquity of predator-prey body size ratios and structural prey refuges in determining the functional response, interactions between these two factors, though rarely explored, may be fundamental to determining the functional response in many systems. Habitat structure is intrinsically size-dependent, as different sized individuals perceive habitat structure differently based on their own body size (*sensu* MacArthur and Levins 1964). For example, habitat structure could act as a filter that restricts large predators more effectively than small predators from accessing prey due to the greater maneuverability of smaller predators through structurally complex habitats (Denno et al. 2004, Brose 2010). This effect could be particularly strong at low prey densities when a greater proportion of prey are located within the refuge (Sih 1987). Such an interaction of predator size and a prey structural refuge could lead to changes in the attack rate, driving a shift from a hyperbolic, type II (no prey refuge) to a type III response (prey refuge) with increasing predator-prey size ratio (Brose 2010).

In the present study, we examined potential interactions between predator body size and a structural refuge for prey in determining the functional response of a crab (*Panopeus herbstii*) foraging on mussels (*Brachidontes exustus*) in oyster (*Crassostrea virginica*) reef habitat. Here, mussels use crevices within oyster clusters as a refuge from crab predation. We first tested for density dependence in refuge use by mussels in the field, an important criterion for the stabilizing effects of the refuge on predator-prey dynamics (Sih 1987). We then examined how the functional response scales with predator body size within this structured habitat. We hypothesized that the crab functional response would shift from type II to type III with increasing crab size. *P. herbstii* exhibits a type II response when foraging on another bivalve (loose oysters) in a simple, unstructured laboratory setting (Rindone and Eggleston 2011). Therefore we expected small *P. herbstii* to exhibit a type II response when foraging on mussels because they are not restricted by habitat structure in accessing mussels. Large crabs, in contrast, should be more restricted in accessing mussels, eliciting a type III response. Finally, we performed a manipulation to determine the degree to which habitat structure hampers the ability of large verses small crabs to extract prey from the refuge.

METHODS

Study system

We used a crab predator (*Panopeus herbstii*) – mussel prey (*Brachidontes exustus*) system to examine the effects of predator body size and a structural refuge for prey on the functional response. *P. herbstii* (Family: Xanthidae) inhabits a range of habitats in the intertidal zone along the eastern and Gulf coasts of the U.S. (Williams 1984). Within our study site (North Inlet estuary, SC, USA), this crab is the numerically dominant resident predator in structurally complex intertidal oyster (*Crassostrea virginica*) reefs (Dame 1979). Here, *P. herbstii* feeds on a number of bivalve species including *B. exustus* (Toscano and Griffen 2012).

The *P. herbstii* – bivalve body size ratio is important in determining their predator-prey relationships in reefs. For example, there is evidence that larger *P. herbstii* individuals (>30 mm carapace width, CW) preferentially consume larger bivalves (Seed 1980, Whetstone and Eversole 1981), while smaller individuals are restricted to consuming smaller bivalves (Seed 1980, Toscano and Griffen 2012). These shifts in prey choice may be related to size specific differences in the foraging abilities of different sized crabs. Furthermore, because populations of *P. herbstii* in North Inlet include a broad size range of individuals (Dame and Vernberg 1982, McDonald 1982), size dependent foraging traits could determine the population-level impacts of *P. herbstii* on bivalves (Toscano and Griffen 2012).

The importance of reef habitat structure and the complexity of this structure (e.g. aggregated vs. unaggregated oyster shells [Grabowski and Powers 2004]) for trophic interactions involving *P. herbstii* has also received attention. Experimental manipulations show that oyster reef structural complexity reduces interference between foraging *P. herbstii* conspecifics at high crab densities, enhancing their consumption of the hard clam (*Mercenaria mercenaria)* (Grabowski and Powers 2004). In contrast, ribbed mussel (*Geukensia demissa*) prey appear to take some refuge in structurally complex oyster clusters from *P. herbstii* predation (Lee and Kneib 1994). Similarly, the mussel *B. exustus* is found almost exclusively in crevices within oyster clusters in intertidal oyster reefs in North Inlet. When placed on oyster shell in flow-through tanks, these mussels tend to seek out (“walking” with their muscular foot) and attach preferentially to crevices between shells (Toscano personal observation). Living within protective crevices could limit the capture success of their relatively larger crab predator, thus serving as a refuge from otherwise intense crab predation in reefs.

All animals used in experiments as well as oyster clusters for the survey of mussel distribution within clusters were collected from intertidal oyster reefs in North Inlet estuary (33° 20’ N, 79° 10’ W), Georgetown, South Carolina, USA. We conducted our study during May-September in 2010 and 2011, and experiments were run in a screened-in wet laboratory at the Belle W. Baruch Institute for Marine and Coastal Sciences.

Field survey of mussel distribution in oyster clusters

We first surveyed the distribution of individual mussels within oyster clusters (N = 35) from the field to examine potential density-dependence in their use of this refuge habitat. An oyster cluster is a conglomeration of live oysters and dead shells that is detached, but still resting on the surface of the reef. These clusters contain a network of interstitial spaces that are occupied primarily by mussels. For our survey, we selected oyster clusters of roughly equal size from intertidal reefs (~50 m^2) that border tidal creeks in North Inlet. Clusters selected were from the same tidal height and spaced at least 1 m apart in reefs. We measured the weight of each cluster, the depth of individual mussels within the cluster (cm from cluster edge), as well as the number of mussels in each cluster. Only mussels that were visible from the cluster exterior and thus presumably accessible to crabs were measured.

We tested for the effects of mussel density on the location of individual mussels within oyster clusters using generalized linear mixed effects modeling (function g*lmer*, package *lme4* in R [v.2.12.0]). We first regressed the number of mussels per cluster on cluster weight to determine the residual variation in mussel number not due to cluster size (i.e. mussel density). We then used these residuals as well as cluster weight as fixed factors, and cluster number as a random factor (to control for pseudoreplication), with the distance of individual mussels from the edge of the cluster as the response variable in a generalized linear mixed model (GLMM) fit by the Laplace approximation. Because mussel location data contained zeros and behaved like count data, we assumed Poisson distributed errors with a log link (Bolker et al. 2009). To correct for overdispersion, we included an additional random factor at the level of the individual observation (the number of data points) (Elston et al. 2001, Bolker et al. 2009), which has the effect of converting the Poisson distribution to a lognormal-Poisson distribution (similar to the negative binomial distribution typically used to model overdispersion). We fit models with and without fixed factors (while retaining the random factors) and compared models using Akaike's information criterion corrected for small sample sizes (AIC_C) to determine whether adding factors significantly improved the fit of models, while taking into account the added model complexity.

Functional response experiments

We determined the functional response for 6 crab size classes (18-21 mm carapace width [CW], 23-26 mm CW, 28-31 mm CW, 33-36 mm CW, 38-41 mm CW and 43-46 mm CW) foraging in oyster reef habitat. The smallest crab size class (18-21 mm CW) is around the minimum size capable of consuming the size of *B. exustus* used in the present study (12-16 mm shell length) (Toscano unpublished data), and the largest size class is near the maximum body size of *P. herbstii* from North Inlet (Dame and

Vernberg 1982, McDonald 1982). We offered *B. exustus* to crabs in 10 densities within oyster clusters: 1, 2, 4, 6, 8, 10, 14, 20, 30 and 40 mussels per tank. Smaller increments between lower prey densities allowed detection of subtle curvature in the functional response. Trials were run in a randomized block design. All treatments were replicated at least 3 times, with treatments showing particularly high variance replicated up to 9 times.

Artificial oyster clusters were used to approximate the structure of natural reefs, while providing a relatively standardized reef habitat on which mussels could attach. Clusters were created using oyster shell that had been dried and cleaned to ensure removal of any epifauna. Holes were drilled in shell and shell clusters were assembled to mimic natural reef formations using plastic zip-ties. Clusters were standardized by the number of shells (5 shell per cluster) as well as volume (measured through water displacement). The necessary number of mussels for a given treatment were placed evenly on 2 oyster clusters in a flow-through seawater table and allowed to attach through byssal thread formation overnight. During this period, mussels moved within the clusters to find an appropriate anchoring location. Crevice space was limiting in these clusters at high mussel densities, forcing some mussels to attach towards the cluster periphery.

We ran the functional response experiments in glass mesocosms (50 × 28 × 30 cm) that were completely enclosed in black plastic to reduce light entry, thus mimicking the low-light conditions of North Inlet estuary during summer months (Dame et al. 1986). Each tank received a single crab, which scales up to a density of approximately 7 crabs per m^2. Crab population density during summer months averages 13.08 ± 6.23 (mean ± 1 standard deviation) crabs >18 mm CW (Toscano unpublished data), and thus our experimental density falls within this range. We established mesocosms as follows. First, a 3 cm layer of sand/mud substrate taken from the estuary was added to the bottom of the tanks. Next, 2 artificial oyster clusters with attached mussel prey of a certain density were added. Last, 8 large oyster shells (dried and cleaned of epifauna) of approximately equal size were scattered around the oyster clusters within each mesocosms, again to mimic natural reef habitat. Each tank received a constant flow of unfiltered seawater throughout trials.

Only crabs with two fully developed and functional claws (i.e. no re-growing or damaged claws) were used and individual crabs were only used once (i.e. for 1 prey density). Crabs were starved for 1 day prior to trials to standardize hunger levels. Crabs were placed in tanks at the start of trials and given 24 h to forage, after which the sand substrate was sieved and oyster clusters and loose shell were checked for remaining mussels. We used 24 h trials to prevent high levels of prey depletion based on consumption rates determined in preliminary trials.

Functional responses were estimated separately for each predator size class (N = 6). We applied a generalized functional response model to consumption data (Real 1977; Hammill et al. 2011):

$$N_e = \frac{PT}{h+\,(1/bN_0{}^{q}N_0)}\,, \qquad \text{eqn 1}$$

Where N_e is the number of prey eaten, N_0 is initial prey density, P is the number of predator individuals, T is the experimental duration, h is handling time and bN_0^q describes the attack rate (Real 1977, Hammill et al. 2011). This attack rate term (bN_0^q) allows density-dependence in the functional response, where b is a coefficient that describes the scaling of attack rate with prey density (Vucic-Pestic et al. 2010), and q is an exponent that allows the response type to vary between a type II response ($q = 0$) and a type III response ($q > 0$) (Hammill et al. 2011). Because prey were consumed and not replaced over the 24 hour duration of our experiment, declining prey density was integrated over the experimental duration to find the number of prey eaten (Hammill et al. 2011). To estimate parameters, the functional response model was fit using maximum likelihood with binomial errors. We only assumed a type III response when q was significantly greater than zero and confirmed the response type by fitting traditional type II and type III functional response models to each crab size class and comparing fits using Akaike's information criterion (AIC).

Manipulation of mussel distribution within oyster clusters

During functional response experiments, we observed that mussels not eaten by large crabs at low mussel densities tended to be located within crevices in clusters, rather than exposed. This led us to hypothesize that large crabs are less efficient foragers at low mussel densities because their larger claws are less dexterous within crevices, resulting in a lower attack rate than small crabs. To test this interaction of habitat structure and predator size, we crossed mussel distribution (0, 3 and 6 cm from the cluster exterior) with crab size (23-26 mm CW, 33-36 mm CW and 43-46 mm CW), resulting in 9 unique treatments, each replicated 6 times. Trials were run in a randomized block design with 6 treatments per temporal block. Mussel distribution was manipulated by gluing 8 mussels within a standardized cluster at a set distance from the exterior of the cluster (0, 3 or 6 cm). A density of 8 mussels was used because all size classes 23-26 mm CW and larger showed the ability to consume this number of prey over 24 h (Figure 3.2), allowing us to attribute any differences in predation efficiency to capture success, rather than handling time. Observations confirmed that mussels continued normal filtering activity after being glued to clusters.

Artificial clusters used in this additional manipulation were different from those used in the functional response experiment and were created as follows. Five rectangular sheets (12 × 5 × 0.2 cm, roughly the size of an oyster shell) of acrylic Plexiglas were glued together at one end in the configuration of an open book. This design allowed us to hold the angle between Plexiglas sheets constant (not possible with irregularly shaped oyster shells) and precisely control the distribution of mussels within the cluster. This experiment was run in smaller plastic mesocosms (30 × 18 × 12 cm). Experimental conditions (e.g. mesocosm setup and experimental duration) were otherwise the same as in the functional response experiments.

We tested for the fixed effects of mussel distribution (distance from the edge of the cluster), crab size, and their interaction, with temporal block as a random factor on mussel consumption in a GLMM. Again, we fit the model using the Laplace approximation and assumed Poisson distributed errors with a log link for count data (Bolker et al. 2009). Fixed factors and the interaction term were dropped sequentially while retaining the random factor. We determined the most parsimonious model using AIC_C comparisons. All statistical analyses were conducted using R (v.2.12.0) (R Core Development Team 2010).

RESULTS

Field survey of mussel distribution in oyster clusters

Mussel density was an important predictor of individual mussel location; the model including this factor provided a better fit than the null model of the random factor (cluster number) only ($\Delta AIC_C = 4.81$), as well as the next best model including the additional factor of cluster weight ($\Delta AIC_C = 2.01$) (Table 3.1). Mussel density was negatively associated (coefficient ± SE: -0.062 ± 0.0227, $P = 0.006$) with mussel location within clusters (distance from cluster edge) (Figure 3.1).

Functional response experiments

In contrast to our hypothesis that crabs would transition from a type II to a type III functional response with crab size, we found that all crab sizes exhibited type III functional responses (q significantly greater than 0; Table 3.2, Figure 3.2, Figure 3.3b), except for 23-26 mm and 43-46 mm size classes, in which q was greater than, but not significantly different from zero (Table 3.2). AIC comparison of type II and type III models fit to each size class generally supported these results; a type III response better explained consumption rate data than a type II response for all predator size classes. Attack rate coefficient and handling time parameters declined non-linearly with predator body size (Figure 3.3a, 3.3c). Specifically, the attack rate declined abruptly between 28-31 mm and 33-36 mm crab size classes (Figure 3.3a). Handling time declined as a power-law function of crab size, as indicated by the linear relationship after log-transformation (Figure 3.3c). A simple power-law function fit to the handling time data yielded the equation $h = 1.718(\text{body size})^{-0.87}$.

Manipulation of mussel distribution within oyster clusters

In the test of the mechanism behind the shift in attack rate (Figure 3.3a), the model including crab size and mussel distribution as factors, as well as their interaction, performed much better than the next best model ($\Delta AIC_C = 20.44$) (Table 3.1). Regarding the interaction between these factors, the mussel consumption of small crabs (23-26 mm) was not affected by mussel location within the artificial cluster, while the consumption of larger crabs (33-36 mm, 43-46 mm) decreased when mussels were located deeper within the cluster (3, 6 cm) (Figure 3.4).

DISCUSSION

The relative sizes of predator and prey constrain trophic interactions at an individual level (Brose 2010), and studies employing these allometric constraints have had great success in predicting the properties of natural food webs (Otto et al. 2007, Petchey et al. 2008, O'Gorman and Emmerson 2009). In the present study, we examined how habitat structure affects the allometric scaling of the functional response, thus extending our understanding of size-based foraging constraints to more realistic habitats that include prey refugia. While all crab sizes exhibited roughly type III functional responses in the structurally complex habitat (Figure 3.2, Figure 3.3b), crab sizes differed in functional response parameter estimates. These parameter estimates and their size scaling have major implications for predator and prey population stability (Persson et al. 1998, Hammill et al. 2011, McCoy et al. 2011). In particular, we observed a decline in the attack rate coefficient with crab size, separating the 3 smaller and 3 larger size classes into functional groups (Table 3.2, Figure 3.3a). We hypothesized that this reduction in attack rate with predator size was due to larger crabs being limited in their ability to reach into tight spaces within clusters to remove mussels, resulting in a prey refuge that is dependent on predator size. This hypothesis was supported by our experiment that manipulated the location of mussels within artificial clusters and measured the consumption efficiency of crabs of different body sizes (Figure 3.4). Furthermore, our survey of mussel distribution within clusters from the field showed that mussels attached closer to the edge of clusters with increasing mussel density (Figure 3.1). This is probably because the deeper, more protected spaces in clusters were already occupied, forcing newly settling mussels to attach where they are more vulnerable to crab predation. Thus crevice space could be a limiting resource in the field.

While an abundance of studies show that habitat structure and the complexity of this structure can reduce foraging efficiency (Orth et al. 1984), the precise mechanism by which this occurs is rarely identified. Decreased foraging efficiency in structured habitats is usually attributed to increased search and pursuit time of predators (Crowder and Cooper 1982). The interaction between predator size and habitat structure shown here (Figure 3.4) provides an alternative or additional mechanism behind the commonly reported negative relationship between habitat structure and predation success. This mechanism is potentially widespread, occurring wherever relatively larger predators must enter or reach into tight spaces to capture prey. For example, this mechanism has been implicated in driving the predation refuge for small or juvenile resident fish in corals reefs (Hixon and Beets 1993, Holbrook and Schmitt 2002, Almany 2004), where sheltered holes in high complexity reefs limit the foraging success of large transient predators. This mechanism was also suggested to operate in decreasing the foraging success of large, but not small pipefish foraging on amphipods that took refuge in crevices between seagrass shoots (Ryer 1988), as well as smallmouth bass foraging on crayfish that use interstitial spaces between cobble substrate as a refuge from predation (Stein 1977). While these studies have implicated the mechanism shown here, ours is one of few to demonstrate this mechanism (see also Holbrook and Schmitt 2002, Sarty et al. 2006), as made possible by our ability to manipulate the distribution of prey within the refuge. In general, reductions in predation rate associated with prey refuges reduce interaction strengths and enhance population stability (McCann et al. 1998, Berlow 1999). Thus, the size dependent prey refuge revealed in the present study could have important implications for the dynamics of predator and prey populations and food webs more broadly.

Past studies have reported hump-shaped relationships between predator-prey size ratio and the attack rate (Spitze 1985, Vucic-Pestic et al. 2010, McCoy et al. 2011), although linear relationships have also been shown (Thompson 1975, Hassell et al. 1976). Proposed mechanisms behind hump-shaped attack rates include reduced consumer movement and reactive distance at a low size ratio, decreased capture success at a high size ratio, and a high attack rate due to improved movement and capture success at some intermediate predator-prey size ratio (Brose 2010), though these hypothesized mechanisms await empirical confirmation. While the scaling of the attack rate with predator size in our study could be interpreted as the middle-right region of a hump-shaped relationship (Figure 3.3a), and thus the result of previously suggested, habitat structure-independent mechanisms, several lines of evidence indicate that these mechanisms do not apply to the present system. First, while a predator’s attack rate is dependent on predator and prey speeds of movement, prey movement speed can be ignored in the present study because mussels are relatively sessile. Increases in crab size (and thus the length of walking legs) should increase movement speed and the amount of prey encountered, thereby increasing the attack rate. We however, observed a decrease in attack rate with crab size (Figure 3.3a). Second, while a predator's attack rate is also dependent on predator and prey reactive distances, reactive distance is probably of limited importance in our experiment due to mussel distribution; because mussel prey were located in a central patch (the oyster cluster), other mussels are within reach of the predator after a single mussel is detected. Lastly, a predator's attack rate is dependent on capture success, which we have shown is highly dependent on habitat structure (Figure 3.4) but may also depend on factors independent of structure. Because crabs of different sizes still exhibited some variation in consumption efficiency when all mussels were at the edge of the cluster and thus completely vulnerable (0 cm: Figure 3.4), this indicates that some factor is operating to reduce the attack rate independently of the prey refuge. For example, larger crabs could have a reduced ability, again independent of habitat structure, to grasp mussels in order to remove them from the cluster. Alternatively, optimal foraging theory predicts that consumers will choose prey that maximize their energy intake. If large crabs, relative to small crabs, do not perceive mussels as profitable prey (*sensu* Basset et al. 2012), they may be conditioned to passing up mussels at low densities in the field in lieu of more profitable prey. Again, this could cause variation in consumption efficiency when mussels are completely vulnerable. This also indicates that in a field setting where alternate prey types are available (Toscano and Griffen 2012), the interaction strength between crabs and mussels could be reduced.

Handling time declined nonlinearly with predator body size (Figure 3.3c). Although we lack the replication and coverage along axes necessary to determine the true shape of this function, handling time appears to follow a negative power-law decline with crab size (Figure 3.3c). This result is consistent with theoretical predictions based on metabolic theory (Brose 2010). When prey are dense (highest N_0) there is no search required, and so predators are only limited by their handling time. Thus, a predator's maximum consumption rate is equivalent to the inverse of its handling time. Because maximum consumption rate is roughly proportional to body size (Peters 1983), handling time should follow a ¾ power-law decline with increasing predator-prey body size ratio (Brose 2010). Handling time in the present study declined with body size at a scaling exponent of -0.87, indicating fairly good agreement with this theory.

The type III response in our study is consistent with that in other studies where a general prey refuge is included (Hildrew and Townsend 1977, Anderson 2001). *P. herbstii* exhibits a type II response when foraging on oysters in an unstructured laboratory setting (Rindone and Eggleston 2011), although a comparison of the response type in an unstructured habitat in our study is needed to identify the prey refuge as the mechanism behind the type III response. Only one other study has tested the size scaling of the exponent that allows the response to vary between a type II and type III. This study found that the scaling exponent generally increased with relative predator size (a shift from type II to type III responses) (Vucic-Pestic et al. 2010). This result however, was species-specific: beetle predators displayed a significant shift, though spiders did not. Furthermore, this comparison by Vucic-Pestic et al. (2010) was confounded by the use of different prey species for the 2 different sizes of prey. We did not find strong evidence for change in response type with crab body size.

Our results may have important implications for community dynamics in oyster reefs that experience substantial fishing pressure. Destructive fishing practices are a major source of physical disturbance for marine communities and common ecological effects of fishing include habitat degradation (Thrush and Dayton 2002) and changes to the size structure of harvested species (Law 2000, Shackell et al. 2010). Oysters, in particular, are heavily exploited worldwide (Beck et al. 2011) and oyster harvesting tends to diminish the height and structural complexity of oyster reefs (Lenihan and Peterson 2004). In addition to these effects on reef habitat, oyster harvest also potentially alters crab size structure at our study site (North Inlet, SC, USA). Specifically, by reducing the height of the surficial shell layer in intertidal reefs (Toscano unpublished data) and thus the availability of refuge space for large (>30 mm CW) crabs, harvest can skew crab population size structure towards a preponderance of small individuals relative to the natural crab size distribution (Toscano and Griffen 2012). Thus, changes to both habitat structural complexity and crab size structure are occurring at our study site, and the interaction between these factors revealed in our study could play a major role in the dynamics of crabs and mussels in the face of this anthropogenic influence. Based on the results of the present study, high densities of small crabs and an elimination of refugia for mussels could reduce mussel densities or even eliminate local populations. Comparing mussel population dynamics in heavily harvested vs. unharvested reefs could provide some test of the general effects of harvest on community dynamics and the importance of the mechanism revealed in the present study.

Finally, though traditional functional response models assume predator conspecifics to be functionally equivalent (Jeschke et al. 2002), intraspecific variation in the functional response is probably widespread in nature. Understanding how different individual functional responses combine and scale up to influence prey over larger spatial scales is a major remaining research challenge. Scaling up could be complicated by errors due to the averaging of non-linear responses (i.e. Jensen's inequality: Okuyama 2008), differential interference between different sized predator individuals (Smallegange and van der Meer 2007), and prey preferences that vary with individual predator size (Kalinkat et al. 2011). Despite these inherent complexities, the allometric scaling of the functional response and its scaling to population and community levels is essential to effectively modeling and managing the dynamics of size-structured populations (Hunsicker et al. 2011), and is thus deserving of focused attention.

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Table 3.1 Comparison of competing models used to predict individual mussel location within oyster clusters from the field survey (see "Methods: Field survey of mussel distribution in oyster clusters"), and models used to predict mussel consumption in the experiment (see "Methods: Manipulation of mussel distribution within oyster clusters").

Model parameters	*K*	AIC_C	ΔAIC_C	*W*
Response: individual mussel location within oyster clusters (field survey)				
Mussel density + cluster number + observation number	3	315.5	0.00	0.67
Mussel density + cluster weight + cluster number + observation number	4	317.5	2.01	0.25
Cluster number + observation number	2	320.3	4.81	0.06
Cluster weight + cluster number + observation number	3	322.2	6.70	0.02
Response: mussel consumption (experiment)				
Crab size + mussel location + crab size*mussel location + temporal block	4	86.88	0.00	1.00
Crab size + mussel location + temporal block	3	107.3	20.44	0.00
Mussel location + temporal block	2	117.1	30.20	0.00
Crab size + temporal block	2	133.9	47.03	0.00

K is the number of parameters, ΔAIC_C is the difference between AIC_C values for each model and the model with the lowest AIC_C, and *W* is the AIC_C weight.

Table 3.2 Parameter estimates, their standard errors, and statistical significance levels for the functional response model (eq. 1) fit to each predator size class. Model parameters are the attack rate coefficient (*b*), a scaling exponent parameter (*q*) indicating the type (i.e. type II or type III) of response, and handling time (*h*).

Size class	*b*	SE (*b*)	*q*	SE (*q*)	*h*	SE (*h*)
18-21 mm	1.5340***	0.0372	0.6547***	0.0160	0.1414***	0.0034
23-26 mm	1.6706	1.0612	0.9374	0.8038	0.1251***	0.0126
28-31 mm	1.5043*	0.5978	1.4522*	0.6395	0.0823***	0.0053
33-36 mm	0.3961*	0.1918	0.7588*	0.3193	0.0729***	0.0091
38-41 mm	0.2545*	0.1127	0.5960*	0.2904	0.0786***	0.0162
43-46 mm	0.1399	0.1017	0.6953$^{\#}$	0.3887	0.0689***	0.0191

Level of significance: $P < 0.001$: ***; $P < 0.01$: **; $P < 0.05$: *; $P < 0.1$: $^{\#}$

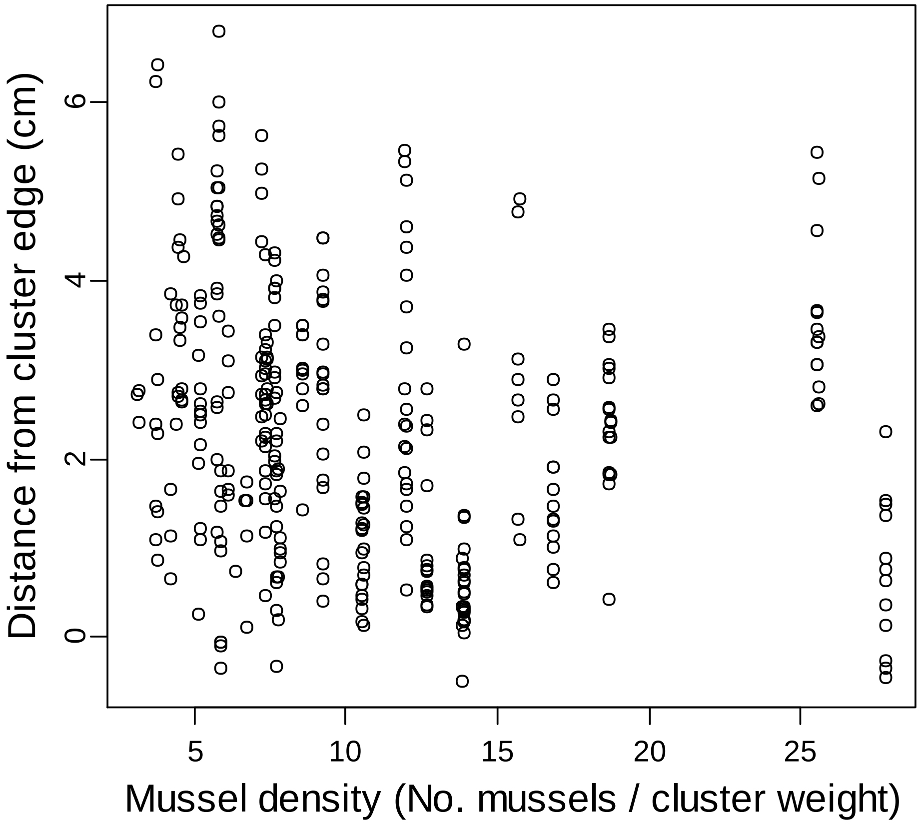

Figure 3.1 Relationship between mussel density and individual mussel location from oyster clusters collected from intertidal oyster reefs in North Inlet, SC. Each point represents an individual mussel's location (distance from the edge of the cluster [cm]) as a function of the mussel density (no. of mussels / cluster weight [kg]) in that cluster. Small amounts of horizontal and vertical displacement were added to points for clarity.

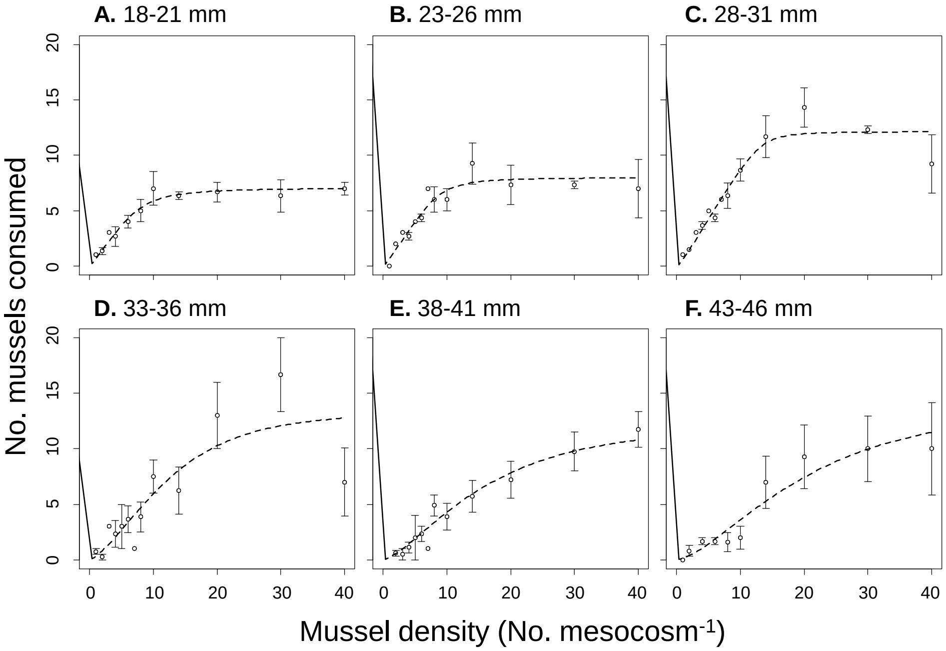

Figure 3.2 Mean consumption ± 1 standard error with functional response model (eq. 1) fits for 6 crab size classes foraging on mussels across a range of mussel densities: A) 18-21 mm carapace width (CW); B) 23-26 mm CW; C) 28-31 mm CW; D) 33-36 mm CW; E) 38-41 mm CW; F) 43-46 mm CW.

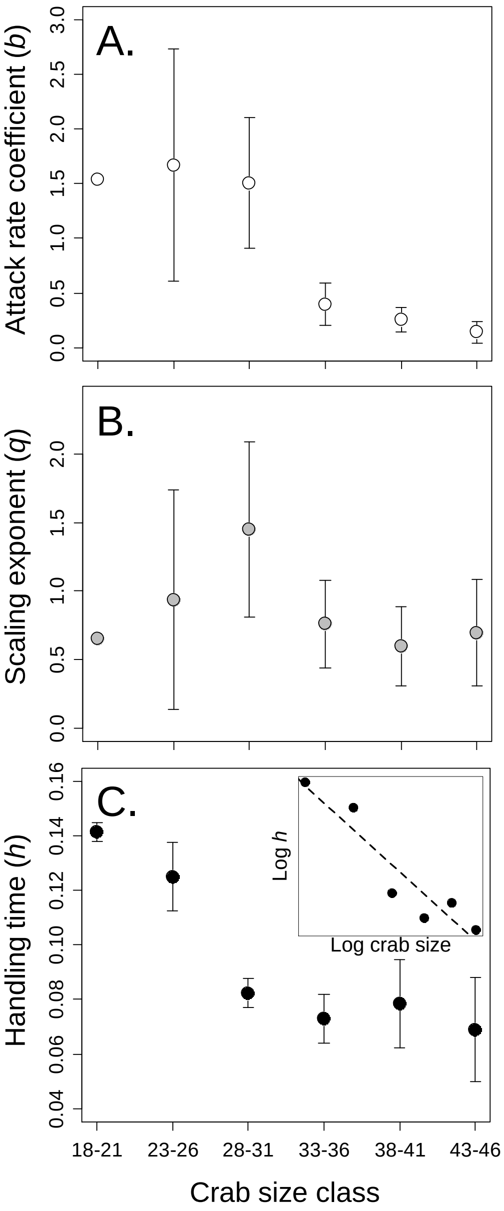

Figure 3.3 The scaling of functional response parameters with crab predator body size: A) *b* = attack rate coefficient (white points); B) *q* = scaling exponent parameter indicating the response type (gray points); C) *h* = handling time (day ind.$^{-1}$) (black points). Points indicate parameters estimates ± 1 standard error. Inset graph in panel C depicts the roughly linear relationship between size $\log_{10}$ and handling time $\log_{10}$, indicative of a power-law function. The equation of a power-law function fit to the handling time data is $h = 1.718(\text{body size})^{-0.87}$.

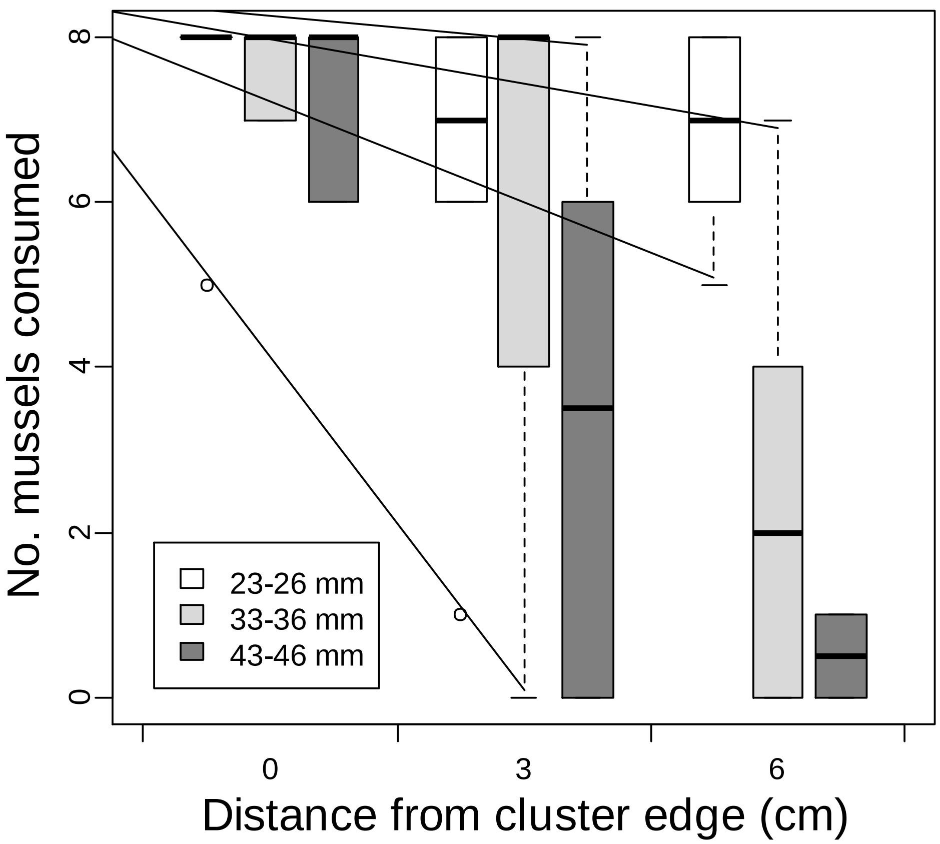

Figure 3.4 Mussel consumption by small crabs (23-26 mm carapace width [CW]; white bars), medium crabs (33-36 mm CW; light gray bars) and large crabs (43-46 mm CW; dark gray bars) foraging on 8 mussels glued at 3 distances (0, 3 and 6 cm) from the edge of a standardized cluster.

CHAPTER 4

EFFECT OF PREDATION THREAT ON REPEATABILITY OF INDIVIDUAL CRAB BEHAVIOR REVEALED BY MARK-RECAPTURE[3]

ABSTRACT

The persistence of behavioral types *in situ* and the drivers of persistence are central to predicting the ecological effects of intraspecific behavioral variation. We surveyed individual refuge use of mud crabs (*Panopeus herbstii*), a behavior related to the strength of a trait-mediated trophic cascade in oyster reefs, in the absence and presence of toadfish (*Opsanus tau*) predation threat. We then released these crabs into the field and using mark-recapture, measured the repeatability of this behavior in the absence and presence of threat, and how behavioral change was affected by time in the field (a month on average, up to 81 days), crab size, and sex. Because crabs exhibited some evidence of a circatidal rhythm in refuge use, we also tested how tidal height during observation influenced behavioral change. Predation threat increased refuge use and small crabs used the refuge more than large crabs, particularly under threat. In recaptured crabs, refuge use was more repeatable under threat. Neither time in the field, crab size, crab sex nor tidal height had any effect on behavioral change. Our results support the non-mutually exclusive hypotheses that (1) prey organisms in the presence, rather than absence, of predation threat should exhibit less behavioral variability because the fear of

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dying (a severe fitness consequence) should take precedence over less immediately important influences on behavior (e.g. hunger); and that (2) individual behaviors tied to fixed traits (e.g. the body size dependence of refuge use under threat in this study), rather than variable traits, should be more repeatable over time.

INTRODUCTION

Consistent variation in behavior between conspecific individuals, variously referred to as behavioral types, behavioral syndromes, coping styles, animal personality and/or temperament, is a common and taxonomically widespread phenomenon that has fundamentally changed the way ecologists view behavior (Gosling 2001; Sih et al. 2004). Here we define consistent behavioral variants as behavioral types (BTs), and correlations between multiple behavioral traits or the same behavior across multiple contexts as behavioral syndromes following the terminology of Sih et al. (2004). Traditionally, animal behavior was considered highly plastic, shaped by both the organism's internal state as well as the external environment to maximize fitness (Emlen 1966; Stephens and Krebs 1986). Yet increasingly, the importance of constraint imposed by individual BTs on behavioral flexibility is recognized as a common aspect of behavior. Accordingly, a new research front explores the effects of BTs, as well as other aspects of individual-level variation more broadly (Bolnick et al. 2003; Bolnick et al. 2011), on population and community dynamics (Sih et al. 2012). Individual constraints on animal behavior have recently been used to successfully predict the form and strength of intra- and interspecific interactions that ultimately determine community structure (e.g. Pruitt and Ferrari 2011; Griffen et al. 2012; Pruitt et al. 2012). For example, Pruitt and Ferrari (2011) found that the proportion of aggressive vs. docile BTs in spider (*Anelosimus studiosus*) colonies determines the nature of their interactions (commensal vs. mutualistic) with other spider species that inhabit their webs.

Determining both the long-term persistence of ecologically-relevant BTs and the drivers of persistence in wild animals is critical to understanding the ecological and evolutionary consequences of BTs (Bell et al. 2009; Archard and Braithwaite 2010). If the behavioral traits of individuals change over time in the field, then the ecological effects of these traits will also change accordingly. At one extreme, traits that prove highly variable (i.e. non-persistent) in the field will offer little predictive power in ecology. Furthermore, measuring the persistence of BTs, particularly in natural field situations, can shed light on the internal and environmental drivers of BTs (Stamps and Groothuis 2010), and is necessary to fully understand the timing and overall effects of BTs on individual fitness (Dingemanse and Réale 2005).

Two methodologies common to BT studies currently impede our ability to assess the long-term persistence and thus ecological relevance of BTs. First, many studies of BTs assess repeatability (i.e. proportion of total phenotypic variation due to between-individual variation, a measurement of the temporal consistency of individual behavior) over relatively short time intervals of a few days or less, and second, studies commonly house animals in the lab between longitudinal behavioral measurements (Bell et al. 2009; Archard and Braithwaite 2010; but see e.g. Réale et al. 2000; Wilson and Godin 2009, Ferrari et al. 2013). These approaches exacerbate the difficulty of extrapolating to field situations. For example, repeatability can decline over time (Bell et al. 2009), and so traits that are shown to be repeatable over a few days should not be assumed repeatable over longer periods. Furthermore, short repeatability estimates can be strongly influenced by stochastic variation in environmental conditions during behavioral measurement (Dingemanse et al. 2002; Gabriel and Black 2010). Repeatability of wild vs. lab-held animals may differ because the field generally provides a more dynamic environment, and therefore traits with any environmental dependence should change at a faster rate (Hoffman 2000). Holding animals in the lab for long periods of time between behavioral measurements (e.g. weeks or months) can also impede learning and development dependent on field conditions or experiences which may drive behavioral change in the field (Archard and Braithwaite 2010). Lastly, because the lab is foreign to animals, they may become acclimated to the lab when held for long periods of time, distorting measurements of repeatability and potentially yielding behavioral patterns that are inconsistent with those of animals accustomed to field conditions (Butler et al. 2006; Biro 2012; but see Herborn et al. 2010).

Short duration experiments on animals housed in the lab are particularly common with invertebrates that have become important model systems for studying the ecological effects of BTs (Mather 2013; more specifically, decapods: Gherardi et al. 2012; spiders: Pruitt and Riechert 2012; anenomes: e.g. Rudin and Briffa 2012). Indeed, the majority of studies measuring repeatability of invertebrate behavior do so over a period of a few days, and few studies have measured the persistence of individual behavior for invertebrates living under natural field conditions, as opposed to being held in the lab, between behavioral measurements (but see recent studies of anemones: Briffa and Greenway 2011; Hensley et al. 2012). This dependence on the lab is understandable because the small size and cryptic nature of invertebrates make them difficult to follow or relocate in the field. Yet the longer-term repeatability and thus the ecological relevance of

BTs in this important group of model organisms remains understudied. Measuring the persistence of BTs in invertebrates is also important for evaluating the welfare of invertebrates in animal research, which has been overlooked in comparison to the welfare of vertebrate species (Horvath et al. 2013).

In the present study, we assessed the long-term (a month on average, up to 81 days) repeatability of individual refuge use behavior in mud crabs (*Panopeus herbstii*) measured in the absence and presence of toadfish (*Opsanus tau*) predation threat. Specifically, we measured crab refuge use behavior in the lab, marked and released crabs into the field, and then recaptured crabs and measured behavior once again in the lab to assess repeatability. Refuge use behavior of mud crabs has important ecological consequences for oyster (*Crassostrea virginica*) reef community dynamics (Griffen et al. 2012). Individual refuge use mediates the strength of an indirect species interaction common in reefs along the Atlantic and Gulf coasts of the United States. Mud crabs that feed on scorched mussels (*Brachidontes exustus*) and juvenile oysters respond to chemical cues from predatory toadfish by taking refuge under oyster shells, and this increased refuge use reduces their bivalve consumption rate (Grabowski 2004; Grabowski and Kimbro 2005). Yet individual crabs differ in their response to toadfish threat along a shy-bold continuum (Griffen et al. 2012; this study). Accordingly, individual refuge use by crabs helps predict their mussel consumption in the presence of toadfish threat, mediating the strength of the indirect interaction (Griffen et al. 2012). While some variation in crab refuge use behavior can be explained by crab size, there is additional variation in refuge use not explained by size or other crab characteristics that is important in determining the consumption rate of crabs (Griffen et al. 2012). Here, in addition to measuring the repeatability of refuge use behavior in the absence and presence of threat, we tested how duration in the field between behavioral measurements and individual crab traits (body size and sex) influenced change in refuge use behavior over time.

We formulated several hypotheses regarding the persistence of individual crab refuge use behavior. First, we hypothesized that refuge use under toadfish predation threat would be more repeatable than refuge use in the absence of predation threat. This is because the fear of dying should take precedence over an organism’s current energetic state (e.g. hunger level) or other environmental conditions (e.g. social situation) that influence behavior, but have less immediate fitness consequences (termed here ‘the predation hypothesis’; Fodrie et al. 2012). Therefore, behavioral variability derived from these less important behavioral influences should be reduced. Second, it is likely that large *P. herbstii* reach a size refuge from predation in the field (Hill 2011; Heinonen and Auster 2012; Toscano unpublished data), and therefore may have little reason to fear and avoid toadfish. By the opposite reasoning behind our first hypothesis, we expected that larger crabs should exhibit greater flexibility in refuge use due to a size refuge that reduces the importance of predator avoidance, thus elevating the relative importance of their current internal state and environmental conditions. Lastly, we hypothesized that repeatability of refuge use would decline with time spent in the field due to greater opportunity for environmental effects, learning, development and conditioning: processes which have been demonstrated to drive behavioral change (Bell et al. 2009). Furthermore, individuals for whom repeatability is measured over a long time interval are more likely to change physiological state (e.g. hunger level) between measurements compared to individuals measured over shorter time intervals (Bell et al. 2009), which again should decrease repeatability over time.

METHODS

We first surveyed the individual refuge use of 247 mud crabs in the absence of a toadfish chemical cue and the refuge use of 224 separate crabs in the presence of the cue (i.e. under predation threat) from May-August 2012. All crabs were collected by hand from an oyster reef known as Oyster Landing in North Inlet estuary, Georgetown, SC, USA (33°20′N, 79°10′W). Crabs were collected within a 20 × 20 m area at the center of the reef. Behavioral measurements were made in a screened-in wet laboratory at the adjacent Belle W. Baruch Institute for Marine and Coastal Sciences. Measuring crab refuge use behavior in the field was not possible due to the high turbidity of water in North Inlet during the summer months that limits visibility (Dame et al. 1986).

Initial behavioral measurements

The following describes our procedure for a single observational block. Thirty-two observational blocks were run over the course of the study (May-August). Sixteen crabs were collected between 20 and 30 mm carapace width (CW) from Oyster Landing reef and we attempted to ensure that each collection reflected the entire crab size range (20 – 30 mm CW). We randomly assigned 8 of these 16 crabs to the toadfish cue absent treatment and the other 8 to the toadfish cue present treatment. Due to constraints on the number of crabs a single person could observe in a night, we observed 8 crabs per night over 2 consecutive nights, generally from 2000-2300 h. During each night, 4 crabs receiving the no cue treatment and 4 crabs receiving the cue treatment were observed. The night measured (first or second) had no effect on refuge use behavior (ANOVA: $p >$

0.05), so the blocking factor used in our analyses was the 2 day span over which 16 crabs were measured. Any crabs molting, carrying eggs or dying during their time in the lab were removed from the data set.

Refuge use was measured following the behavioral assay protocol used in Griffen et al. (2012). All crabs were starved for 24 h before their refuge use behavior was measured. Each crab was observed in a separate glass mesocosm (50 × 28 × 30 cm) containing a 3 cm layer of sand/mud substrate and 5 L of oyster shell (8 – 12 cm shell length) that had been dried and cleaned to remove epifauna. This amount of shell ensured that crabs had ample refuge to hide completely. Mesocosms were completely filled with a continuous supply of seawater. Eight large scorched mussels were suspended near the water surface in a mesh bag to release prey chemical cues and induce crab searching behavior while remaining out of reach of crabs. To create the toadfish cue treatment, crabs received a continuous supply of seawater that was first pumped through a holding chamber that contained a single adult oyster toadfish. Crabs assigned the no cue treatment received a continuous supply of seawater pumped through a holding chamber without a toadfish.

Crabs were observed under red light with the observer located behind a blind to minimize crab disturbance. Crabs were first given a 15 minute acclimation period in the observation tanks, after which their refuge use was observed once every 6 minutes over 3 hours (30 observations in total for each crab). Refuge use was measured as the proportion of the 30 observations where crabs were completely in the oyster shell refuge and thus invisible to the observer. The refuge was a matrix of shells, so crabs could be hiding under a single shell or multiple shells (i.e. at the bottom of the matrix).When crabs were observed out of the refuge, they were usually walking on top of the shell substrate (i.e. were active). In addition to refuge use behavior, we measured the carapace width and sex of each crab.

Repeatability and behavioral change

After refuge use behavior was measured, each crab was marked with a unique ID number and released back into the field. To mark crabs, we glued (with super glue) a piece of laboratory labeling tape numbered with permanent marker to the center of the crab's carapace (Stachowicz and Hay 1999).We realized during the middle of the study that these hand-written numbers were becoming illegible over time in the field, and so the last 80 crabs from the survey were marked using plastic bee tags (queen marking kit: the Bee Works, Orillia, Ontario) that did not wear over time. All marked crabs were released in a 10 × 10 m area at the center of Oyster Landing reef. To assess the persistence of refuge use behavior for crabs released into the field, we recaptured crabs and measured their refuge use for a second time using the same behavioral assay procedure in the lab. Recaptured crabs were observed under the same treatment (toadfish cue absent or present) that they were observed under before release. We recaptured crabs by hand within the release area of Oyster Landing reef. We searched the reef over two separate search periods (end of July, end of August) until no more marked crabs were recovered at each search period. Because crabs were released regularly over the duration of the study (after each block) but resampled just twice, individual crabs were recaptured after different durations in the field, allowing us to test the effects of duration in the field on behavioral change over time.

Statistical analysis

Initial graphical exploration of refuge use behavior over the course of the study revealed persistent oscillations in mean refuge use observed each night with approximately a 14 day period. These oscillations in behavior appeared to be negatively correlated with the mean tidal level at Oyster Landing (the collection site of crabs) at the time of observation in the lab. Crabs used the refuge most while it was low tide (when they are generally inactive in the field), indicative of a circatidal rhythm in refuge use. We tested for this influence of the tidal cycle on refuge use behavior, among other factors affecting crab refuge use behavior, in the following analysis.

To explore factors influencing crab refuge use behavior (pre-release), we tested the effects of toadfish predation threat, crab carapace width, an interaction between threat and carapace width, and mean tidal level during observation on refuge use with generalized linear mixed models (GLMM, lme4 package in the statistical software R). Female crabs were smaller than male crabs (Welch two-sample *t*-test: $t = -8.267$, $p < 0.001$), which confounded crab sex with crab size. Therefore, we tested the effects of these factors on refuge use separately for males and females. Observational block was modeled as a random factor in both GLMM. Because crab refuge use (the response variable) was proportional, we modeled this behavior using a binomial distribution and logit link (Bolker et al. 2009).

After recapturing a portion of these original crabs (108 crabs recaptured), we calculated the repeatability of their refuge use behavior using pre-release and post-recapture behavioral measurements. Repeatability (*r)* is defined as the proportion of the total variation that occurs within individuals as opposed to between individuals and is calculated as $r = s^2_A / (s^2 + s^2_A)$, where s^2_A is the among-individual variance and s^2 is the within-individual variance (Bell et al. 2009; Nakagawa and Schielzeth 2010). Thus repeatability provides a metric of the amount of behavioral variation between relative to within individuals, where a higher repeatability value indicates a higher level of individual behavioral consistency between measurements. Again, due to the proportional behavioral measure (refuge use), we used GLMM-based repeatability estimation (rptR package in R, Nakagawa and Schielzeth 2010) with a binomial distribution and logit link. Repeatability was calculated separately for crab refuge use in the absence and presence of the toadfish cue, and confidence intervals (95%) and statistical significance (*p* values) were estimated using parametric bootstrapping with 1000 resamplings.

Next, we explored factors driving change in refuge use behavior (i.e. deviation from perfect repeatability) of recaptured crabs after time in the field. We calculated behavioral change by subtracting the value of the 1st behavioral measurement (pre-release) from the 2nd behavioral measurement (post-recapture). Behavioral change was log-transformed to meet assumptions of linear regression. To test for a predominant direction in behavioral change, we first tested whether behavioral change was significantly different than zero in the absence and presence of toadfish predation threat using one-sample *t*-tests. We then used general linear models testing the fixed effects of duration (days) in the field, crab carapace width and crab sex on individual behavioral change of recaptured crabs. Two separate linear models were used to test the effects of these factors in the absence and presence of toadfish predation threat.

As previously mentioned, crab refuge use behavior oscillated with a circatidal rhythm over the course of the study. This means that if a recaptured crab was originally observed (pre-release) during one tidal height, and observed a second time (post-recapture) at a different tidal height, then behavioral change would be generated. We tested for this tidal influence on behavioral change as follows. We first subtracted for each individual crab the tidal height when the pre-release observation was made from the tidal height when the post-recapture observation was made. We then used the absolute value of this difference as a factor (termed ‘tidal influence’) in general linear models testing the effects of duration in the field, carapace width, sex and the tidal influence on the absolute value of behavioral change in the absence and presence of predation threat. This analysis allowed us to explore the relative influences of these factors on the overall magnitude of behavioral change.

Lastly, we tested for the differential recapture of crabs with low vs. high refuge use (i.e. a sampling bias). We did this by comparing the recapture rate of crabs from the lower and upper quartiles of refuge use behavior using Fisher’s exact tests. We conducted this analysis separately for crabs with refuge use measured in the absence and presence of toadfish predation threat.

RESULTS

The presence of toadfish predation threat caused crabs to spend more time in the oyster shell refuge (Table 4.1, Figure 4.1). Large crabs spent less time in refuge than small crabs (Table 4.1, Figure 4.1), and this negative effect of crab size on refuge use was enhanced in the presence of predation threat (Table 4.1, Figure 4.1). Mean tidal level in the field during behavioral observation in the lab reduced the refuge use of male crabs but not female crabs (Table 4.1).

We recaptured 108 crabs out of the 484 crabs that were released over the course of the study. However, thirty of these crabs had labels where the ID number had faded beyond recognition, leaving 78 identifiable crabs. Thirty-five of these crabs had been assayed for refuge use in the absence of toadfish predation threat, while the other 43 had been assayed for refuge use in the presence of toadfish predation threat. The duration that these recaptured crabs spent in the field ranged from 11 to 81 days, with a mean of about a month (mean ± 1 SD: 32 ± 16 days).

Refuge use both in the absence ($r = 0.021$, 95% CI: 0 – 0.066, $p = 0.032$, Figure 4.2a) and presence of toadfish predation threat ($r = 0.173$, 95% CI: 0.084 – 0.304, $p = 0.001$, Figure 4.2b) was repeatable over time, though repeatability was approximately 8 times higher in the presence of threat. Furthermore, the significance of repeatability in the absence of predation threat was driven by an influential data point (Figure 4.2a, see figure caption); when removed, repeatability was reduced substantially ($r = 0.011$, 95% CI: 0 – 0.048) and was no longer significant ($p = 0.139$).

Neither behavioral change in the absence (one-sample *t*-test: $t = -1.245$, $p = 0.222$) or presence (one-sample *t*-test: $t = 1.541$, $p = 0.131$) of toadfish predation threat was significantly different from zero, indicating no predominant direction of behavioral change. None of the factors tested including time in the field, crab size or crab sex had any effect on directional behavioral change in recaptured crabs (Table 4.2). We also tested whether these same factors, as well as the ‘tidal influence’ factor, affected the overall magnitude of behavioral change regardless of direction. Again none of these factors (duration in the field, crab size, crab sex, or the tidal influence) had a significant effect on absolute behavioral change, either in the absence or presence of toadfish predation threat (general linear models: $p > 0.526$).

Lastly, the recapture rate of crabs with low refuge use vs. high refuge use did not differ. This was true of crabs with refuge use measured in the absence (Fisher's exact test: $p = 0.459$) and presence (Fisher's exact test: $p = 0.285$) of toadfish predation threat.

DISCUSSION

Our study revealed repeatability of crab refuge use behavior after substantial time in the field (a month on average, up to 81 days) and strong size-scaling of this behavioral trait. Most interestingly, the presence of predation threat during behavioral observation increased the repeatability and size-dependence of individual crab refuge use behavior. Furthermore, contrary to our hypotheses, we found that time in the field between behavioral measurements and crab body size did not influence change in refuge use behavior over time in wild crabs. Below we discuss potential reasons for these effects of predation threat on the repeatability and size-scaling of refuge use behavior, as well as the implications of these results for the community ecology of oyster reefs.

Factors driving crab refuge use behavior

By measuring crab behavior daily over 3 months, we were able to detect a persistent effect of the tidal cycle on crab refuge use behavior measured in the lab. Had our study been conducted over a shorter duration (and thus over fewer oscillations of the tidal cycle), we likely would have overlooked this tidal influence on behavior. Male crabs used the refuge less (i.e. were most active) when they were observed during high tides at the Oyster Landing reef where crabs were collected. Though the influence of the tidal cycle on the behavior of other crabs species (e.g. Barnwell 1966; Saigusa 1992) and marine invertebrates in general (Palmer 1973) has been shown to dissipate with time in the lab, the crabs used in this experiment were collected from the field just 24 - 48 h before behavioral observations. This lack of a substantial acclimation period could explain the remaining tidal influence on refuge use behavior shown here. We discuss the potential effects of the tidal cycle on measuring the persistence of crab behavior below in ‘Repeatability and behavioral change’.

In line with previous work (Griffen et al. 2012), we found that individual refuge use in *P. herbstii* is negatively related to crab body size and positively related to toadfish predation threat. However, the study by Griffen et al. (2012) differed from ours in that they used larger crabs (>30 mm), and found that the size-scaling of refuge use behavior was the same in the absence and presence of toadfish predation threat. In contrast, using smaller crabs (<30 mm), we found that the effect of body size on refuge use was more pronounced in the presence than absence of predation threat for both male and female crabs (Figure 4.1); smaller crabs in particular spent more time in refuge and less time active in the presence of threat. The enhanced size scaling of refuge use under predation threat shown here is most likely the result of the heighted vulnerability of small crabs to predation. Toadfish, a major consumer of mud crabs in South Carolina (Wilson et al. 1982), are gape-limited predators (Gudger 1910), and the resident toadfish that inhabit North Inlet’s reefs are generally small (<15 cm, Toscano personal observations). Though not confirmed, it’s likely that larger crabs gain a size refuge from predation by resident toadfish in the field, as has been observed in other systems (Hill 2011; Heinonen and Auster 2012). This is supported by feeding trials in the lab (Toscano unpublished), where toadfish (mean total length ± 1 SD: 14.73 ± 2.58 cm) not limited by their gape size were averse to eating larger crabs (>22 mm carapace width), perhaps due to the damage these crabs can inflict with their claws. Thus smaller crabs below this size refuge have reason to be more responsive to predation threat, while large crabs, safe from toadfish predation, would gain no benefit and instead lose foraging opportunities by modifying their behavior in the presence of a toadfish risk cue, particularly when foraging opportunities are limited (these intertidal crabs can only forage during high tides).

The mesococosoms where behavior was measured contained live mussels that released prey cues, stimulating crab foraging behavior. Thus refuge use in this study was a measure of the risk that a crab is willing to take (i.e. its boldness) in order to gain energy through foraging. Numerous studies have detected such a link between individual body size and boldness, but both positive and negative relationships have been reported (Dowling and Godin 2002; Brown and Braithwaite 2004). In situations where prey reach a size refuge from predation (e.g. the present study), it should be expected that boldness is positively related to body size. Alternatively, small individuals may be less averse to risk when foraging under predation threat due to their proportionally higher metabolic rates and thus greater energy requirements (Dowling and Godin 2002; Brown and Braithwaite 2004). This indicates that the relationship between body size and boldness can depend on both individual-level (i.e. prey metabolic rate) and community-level processes such as predator prey dynamics.

Repeatability and behavioral change

Our recapture rate of marked *P. herbstii* was fairly high: ~22% of crabs released were recaptured within the 10 × 10 m release area. This rate of recapture is in general accord with a previous study (Stachowicz and Hay 1999), in which 20 *P. herbstii* were marked and released into an intertidal oyster reef and 6 individuals were recovered within a 5 m^2 search area after 48 h. While our recovery rate was similar, the duration of time that crabs spent in the field here was much greater (a month on average, but up to 81 days). This suggest that *P. herbstii* movement rates within and between North Inlet's reefs are fairly low, considering that we failed to recapture crabs that molted or died during the course of the study yet still recaptured a substantial portion of crabs released.

We hypothesized that crab refuge use would be more repeatable in the presence vs. absence of predation threat because the fear of dying, a severe fitness consequence, should take precedence over other influences on behavior (e.g. current energetic state or social situation) that can introduce behavioral variability (termed here 'the predation hypothesis'). A related explanation is that higher repeatability of refuge use under predation threat is driven by the stronger size dependence of refuge use in the presence vs. absence of threat (Figure 4.1). Crab body size was fixed over the duration of this study (none of the recaptured crabs had molted), and behaviors that are dependent on some fixed property of the individual should be more consistent over time than behaviors that depend on shorter-term changes in an individual's internal state or environmental conditions (termed here 'the fixed-trait hypothesis') (Bell et al. 2009). Either or both of these non-mutually exclusive drivers of behavioral trait persistence could be operating in the present study. The predation hypothesis could be tested by manipulating crab energetic state (e.g. hunger level) and testing repeatability in the presence and absence of predation threat, with the expectation that repeatability should decrease faster in the absence of predation threat with increasing hunger level (Dowling and Godin 2002). The fixed-trait hypothesis could be tested by measuring the behavioral change of crabs over successive molts, with the expectation that behavior will change with increasing body size.

In a meta-analysis of repeatability estimates from a wide range of both invertebrate and vertebrate species, Bell et al. (2009) found that repeatability generally decreased with time between behavioral measurements. Contrary to our hypothesis, we found no evidence of behavioral change dependent on time. This is despite crabs spending up to 81 days in the field, and for reference, the lifespan of *P. herbstii* has been estimated at 2.3 years (McDonald 1982). However, we cannot discount the possibility that we tended to recapture crabs which were more consistent in their behavior over time, though we detected no bias regarding the differential recapture of crabs with low vs. high refuge use behavior. Clearly, crabs change their refuge use behavior over ontogeny (Figure 4.1), but the lack of behavioral change with time in the present study suggests that most behavioral change happens during molting when crabs grow or at other times of the year. This consistency of behavior over time while crab body size was fixed again suggests high repeatability of individual behavior when that behavioral trait is dependent on a fixed trait of the individual.

As previously mentioned, we detected an influence of the tidal cycle on crab refuge use behavior over the course of the study. Measuring an individual crab at 2 different tidal levels (pre-release, post-recapture) in this tidally-influenced behavioral cycle should reduce behavioral consistency, even if the individual’s actual BT relative to other crabs is not changing. Our analysis however did not detect any effect of the tidal cycle on behavioral change. This could be due to individual variation in responsiveness to the tidal rhythm, as has been shown in other marine invertebrates (Palmer 1973). Still, such persistent circatidal rhythms in activity have been observed in a variety of intertidal marine invertebrates (Palmer 1973) and biological temporal rhythms are taxonomically widespread (Dunlap et al. 2004). Thus behavioral ecologists should be cognizant of such endogenous temporal rhythms in behavior, particularly when taking repeated longitudinal behavioral measurements to assess behavioral consistency (Koski 2011).

Implications for oyster reef community ecology

Individual crab refuge use behavior and body size, as studied here, have previously been shown to mediate the consumption rate of crabs foraging on mussels in the presence of toadfish predation threat (Griffen et al. 2012), thereby determining the strength of indirect interactions that are a major community-structuring force in oyster reefs (Grabowski 2004; Grabowksi and Kimbro 2005). The repeatability of refuge use revealed here suggests that this crab behavioral trait is relatively stable over time in the field. Thus any ecological effects of crab refuge use are not just a transient feature of the reef food web. Rather, if individual crabs remain on the same reef, or within the same location within a reef for long periods of time, then their individual refuge use behavior could drive spatial variation in ecological interactions (Griffen et al. 2012). Such testable predictions can only be made by measuring the persistence of BTs and the drivers of persistence in natural field situations, thus advancing mechanistic study of the ecology of individual behavior (Sih et al. 2012).

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ETHICAL STANDARDS

This research complies with the current laws of the United States.

CONFLICT OF INTEREST

We declare no conflict of interest.

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Table 4.1 Results of generalized linear mixed models (GLMM) testing the effects of fixed factors on pre-release refuge use behavior of male and female crabs. *P* values of significant model factors (α = 0.05) are shown in bold. Observational block was modeled as a random factor in these models.

Model factors	Estimate	SE	*z*	*P*
Response: pre-release refuge use behavior of male crabs				
Predation threat	-3.652	0.438	-8.336	**<0.001**
Crab size	-0.224	0.013	-17.626	**<0.001**
Tidal level	-0.359	0.120	-2.984	**0.003**
Predation threat × crab size	0.115	0.016	6.962	**<0.001**
Response: pre-release refuge use behavior of female crabs				
Predation threat	-3.718	0.909	-4.089	**<0.001**
Crab size	-0.374	0.028	-13.203	**<0.001**
Tidal level	0.101	0.283	0.358	0.721
Predation threat × crab size	0.106	0.037	2.898	**0.004**

Table 4.2 Results of general linear models testing the effects of fixed factors on directional behavioral change measured in the absence and presence of toadfish predation threat.

Model factors	β	SE	*t*	*P*
Response: directional behavioral change (toadfish cue absent)				
Duration (days) in the field	0.003	0.003	0.907	0.371
Crab size	-0.006	0.016	-0.344	0.733
Crab sex	0.128	0.113	1.131	0.267
Response: directional behavioral change (toadfish cue present)				
Duration (days) in the field	-0.003	0.002	-1.141	0.261
Crab size	-0.013	0.008	-1.522	0.136
Crab sex	0.004	0.060	0.063	0.950

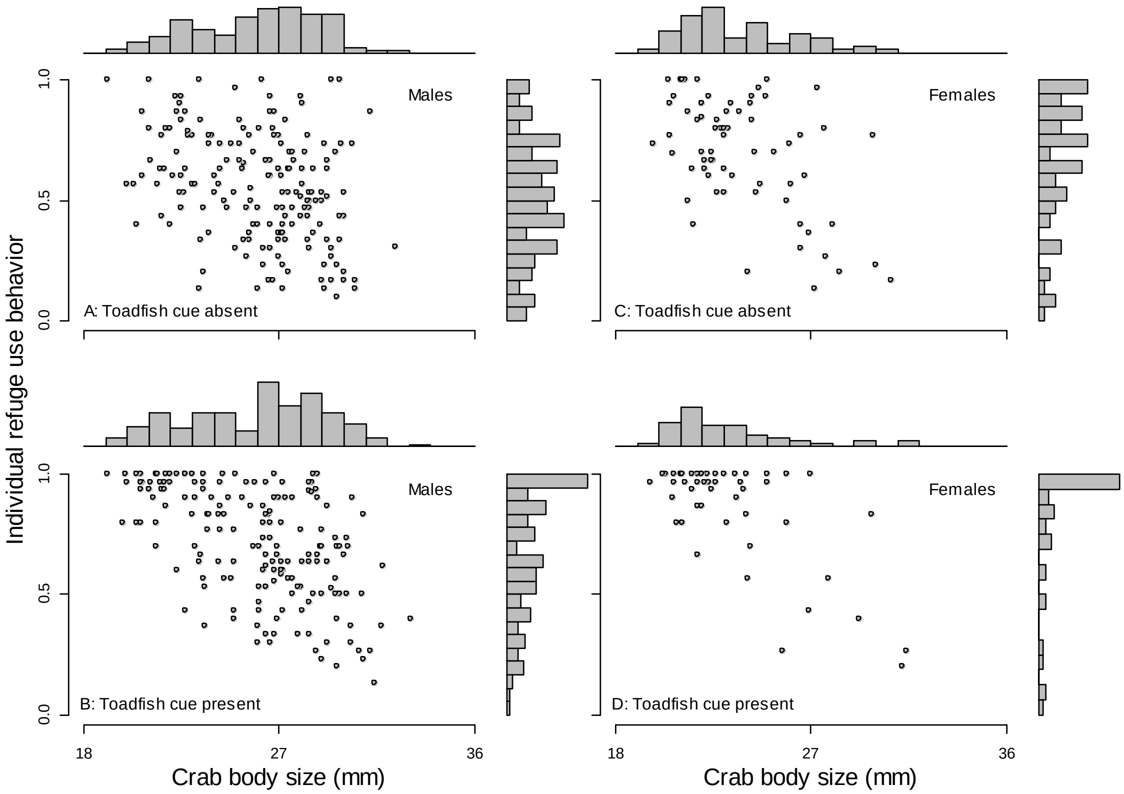

Figure 4.1 Size scaling of individual refuge use behavior in male and female mud crabs (*Panopeus herbstii*) with histograms of body size and behavior distributions: A) Male crab refuge use in the absence of toadfish (*Opsanus tau*) predation threat, measured as the proportion of observations over 3 h where a crab was observed taking refuge under oyster shell; B) Male crab refuge use in the presence of toadfish predation threat, measured in the same way but in the presence of chemical cues from toadfish; C) Female crab refuge use in the absence of toadfish predation threat; D) Female crab refuge use in the presence of toadfish predation threat

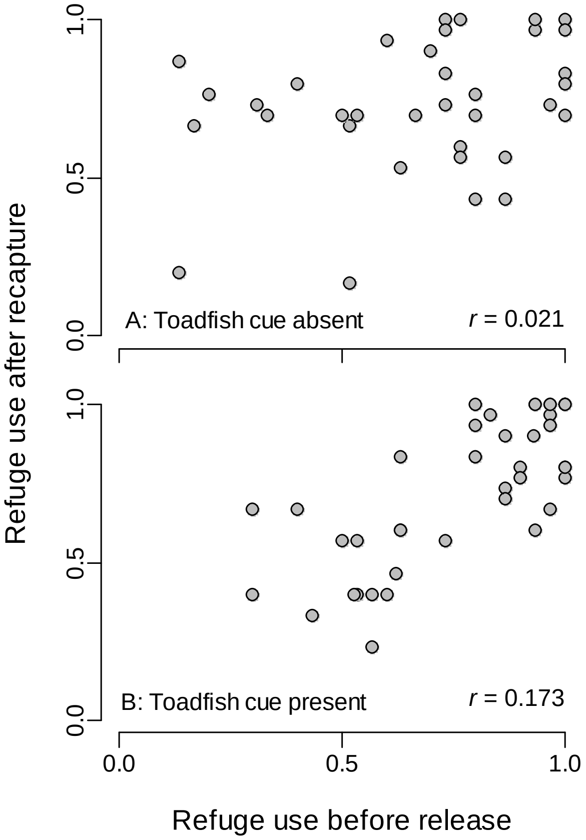

Figure 4.2 Individual refuge use behavior of marked and recaptured mud crabs (*Panopeus herbstii*) measured in the absence (A) and presence (B) of toadfish (*Opsanus tau*) predation threat; repeatability (*r*) of refuge use was statistically significant in both cases ($\alpha = 0.05$), however significance of repeatability of refuge use in the absence of predation threat was dependent on an influential data point (bottom left corner of panel A)

CHAPTER 5

TESTING FOR RELATIONSHIPS BETWEEN INDIVIDUAL CRAB BEHAVIOR AND METABOLIC RATE ACROSS ECOLOGICAL CONTEXTS[4]

ABSTRACT

Two hypotheses have been proposed to explain covariation between activity and metabolic rate among conspecifics. First, individual-level variation in activity exhibited *during* the measurement of metabolic rate should covary with metabolic rate (e.g. O_2 consumption measured via respirometry). Second, the 'pace-of-life' syndrome hypothesis posits a persistent positive relationship between individual activity level measured under more natural conditions and metabolic rate, among other behavioral, physiological and life-history traits. Here, we examined these potential relationships between individual behavior and standard metabolic rate (SMR) in the mud crab (*Panopeus herbstii*). Specifically, we recorded (1) crab movement in metabolic chambers during the measurement of SMR, and (2) crab activity level in a more natural situation where laboratory mesocosms mimicked field conditions. To test for context-dependency, we assessed behavior-SMR relationships in the absence and presence of predation threat from toadfish (*Opsanus tau*) in the form of waterborne chemical cues. We first measured the repeatability (i.e. proportion of phenotypic variation due to between-individual variation) of crab activity level and SMR and found these traits to be repeatable. Crabs

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increased movement in metabolic chambers in the presence of threat, but decreased activity level under more natural conditions. Interestingly, crabs with an initially low SMR increased SMR in the presence of threat, while crabs with an initially high SMR showed the opposite response. Individual differences in SMR were partially explained by crab movement during the measurement of SMR (i.e. a methodological relationship). We did not however, detect a relationship between crab activity level and SMR in the absence or presence of toadfish predation threat, even after accounting for the direct effect of movement on SMR. Thus despite repeatability of activity level and SMR, our study does not support covariance between activity level and SMR as a ‘pace-of-life’ syndrome in mud crabs.

INTRODUCTION

Individual-level phenotypic variation in behavioral and energetic traits is ubiquitous in animal populations (Careau and Garland 2012). For example, behavioral traits such as activity level, boldness and aggressiveness can vary substantially between conspecifics and this variation is often consistent over time (referred to as behavioral types; Sih et al. 2004, Bell et al. 2009). Furthermore, single behavioral traits are often consistent across ecological contexts, and multiple behavioral traits may be correlated at the individual-level (referred to as behavioral syndromes; Sih et al. 2004, Bell and Sih 2007). Such consistent individual differences (CIDs) in behavior have now been detected across a wide range of animal taxa (Gosling 2001).

Similarly, measures of baseline metabolic rate, including basal, standard and resting metabolic rate, can vary threefold among conspecifics of the same size, age and sex (Speakman et al. 2004, Burton et al. 2011). Such residual variation in metabolic rate had been considered noise around populations' or species' means and treated analytically as measurement error (Careau et al. 2008), but researchers have since demonstrated that individual differences in metabolic rate can persist over the lifetime of individuals (Nespolo and Franco 2007, Burton et al. 2011). Current work illuminates the ecological and evolutionary consequences of CIDs in behavioral (Sih et al. 2012) and energetic traits (Burton et al. 2011), though the maintenance of variation in these traits within populations remains unresolved (Careau and Garland 2012).

Recent work suggests potential links between CIDs in behavior and energetics that could shed light on the maintenance of these traits (Careau et al. 2008, Biro and Stamps 2010, Careau and Garland 2012). First, covariation between behavioral and energetic traits is expected based on methodological grounds (Careau et al. 2008). Measurements of baseline metabolic rate (e.g. O_2 consumption via respirometry) assume animals are at rest within metabolic chambers designed to restrict movement, yet individual animals often vary in the amount of activity or stress exhibited during the measurement of metabolic rate. Active individuals are expected to consume more O_2 than resting individuals, and so measurements from excessively active individuals are often discarded and metabolic rate re-measured at another time (Careau et al. 2008). Nevertheless, individual differences in behavior expressed during the measurement of metabolic rate are potentially repeatable (i.e. a behavioral type), and correlated with other behaviors in more natural contexts (i.e. a behavioral syndrome). Therefore, removal of excessively active individuals can bias the population sample (Careau et al. 2008).

A functional link between behavioral and energetic traits has also been hypothesized (Careau et al. 2008, Biro and Stamps 2010, Careau and Garland 2012).

Individuals that exhibit energetically costly behaviors (e.g. high activity level) should require a greater rate of energy metabolism to support these behaviors (Biro and Stamps 2010). In reverse, individual behaviors that increase energy intake (e.g. foraging activity) should enhance metabolic rate (Biro and Stamps 2010). As such, the direction of causality in this relationship is dependent on the mechanism at work (Killen et al. 2013). The link between individual behavior and energetics is potentially part of a broader covariation of behavioral, physiological and life-history traits referred to as the 'pace-of-life' syndrome (Biro and Stamps 2008, Réale et al. 2010). The 'pace-of-life' syndrome has been studied at the population and species levels (Ricklefs and Wikelski 2002), but more recently applied at the individual level (Réale et al. 2010). At the individual level, conspecifics range from a reactive to a proactive pace of life; reactive individuals are characterized by lower activity, boldness and aggression, and this lifestyle is associated with reduced energy expenditure, growth and fecundity. In contrast, proactive individuals are characterized by the opposite traits and pace of life. Covariation of these traits could be maintained by common hormonal control (e.g. testosterone: Buchanan et al. 2001) or correlational selection (Galliard et al. 2013).

Support for the 'pace-of-life' syndrome hypothesis at the individual level, and more specifically relationships between CIDs in behavioral and energetic traits, has been mixed (Bouwhuis et al. 2013), though adequate tests are few (Careau and Garland 2012). In a recent review, Killen et al. (2013) suggested the importance of environmental stressors (i.e. abiotic and biotic factors that "challenge" individuals to adjust their behavior or physiology in order to cope) in mediating behavior-energetic relationships, and potentially explaining this mixed support. Environmental stressors can modify the relationship between CIDs in behavior and energetics by modifying the distribution of one or both of these types of traits, and having differential effects on the traits of certain phenotypes (i.e. different individual reaction norms). Studying the context-dependence of energetic-behavior relationships is important because it can yield insight into the mechanisms behind relationships, as well as the effects of environmental change on these relationships (Killen et al. 2013).

In the present study, we tested for relationships between individual behavior and standard metabolic rate (SMR) in a geographically widespread and abundant marine invertebrate, the common mud crab (*Panopeus herbstii*). We measured crab behavior both in metabolic rate chambers (crab movement) and in laboratory mesocosms that mimicked natural oyster (*Crassostrea virginica*) reef habitat (crab activity level). We further examined how behavior-energetics relationships were affected by the presence of threat from a major predator of mud crabs, the toadfish (*Opsanus tau*). Predation is a powerful agent of selection (Svanbäck and Eklöv 2011, Siepielski et al. 2013) and the threat of predation in the form of visual or chemical cues is a widespread biotic stressor (Lima and Dill 1990). Nevertheless, the effects of predation threat on the relationship between CIDs in behavioral and energetic traits are unclear (Killen et al. 2013).

Previous work established CIDs in *P. herbstii* refuge use behavior (Toscano et al. 2014). Refuge use in this study (Toscano et al. 2014) was measured as the proportion of observations where crabs were observed in an oyster shell refuge and inactive. Crab activity level is the inverse of this measurement, and is referred to as such in the present study. Toscano et al. (2014) however, measured the repeatability of crab refuge use with a wide size range of crabs, where body size explains a substantial portion of the variation in refuge use behavior and therefore temporal consistency in refuge use behavior. Here, we build upon this work by testing for a physiological link with crab activity level within a more restricted size range of crabs, where the influence of body size on behavior is undetectable.

We hypothesized that crab movement in metabolic chambers would be positively related to SMR (i.e. a methodological relationship), and SMR would be further related to crab activity level in a more natural setting (i.e. a functional relationship). We further expected predation threat from toadfish to modify relationships between behavior and SMR, because toadfish predation threat reduces crab activity level, but individual crabs differ in the magnitude of their response to threat (Griffen et al. 2012). More specifically, it could be expected that crabs with higher SMRs should exhibit riskier behaviors (i.e. higher activity) under threat to satisfy their energetic demands, whereas the relationship between activity level and SMR would be less apparent in the absence of threat due to the lack of this constraint on activity (Killen et al. 2011, 2012).

METHODS

We first tested for CIDs in crab activity level and SMR by measuring the repeatability (i.e. proportion of phenotypic variation due to between-individual variation) of these traits. We then tested for relationships between crab behavior (crab movement during the measurement of SMR and activity level) and SMR in the absence and presence of predation threat from toadfish (*Opsanus tau*). In doing so, we were also able to examine the direct effects of predation threat on individual crab traits (crab movement during the measurement of SMR, activity level, and SMR). Experiments were conducted from May through August 2013 in the wet laboratory at the Baruch Marine Field

Laboratory, Georgetown, South Carolina, which is adjacent to North Inlet estuary (33°20’N, 79°10’W). All animals used in the study were collected by hand from the high intertidal portion of oyster reefs in North Inlet.

Repeatability of activity level and SMR

Repeatability of activity level and SMR was measured for separate groups of crabs (*n* = 24 crabs for activity level, *n* = 38 crabs for SMR) from the same size range (mean carapace width [CW] ± 1 SE: 29.03 ± 0.24 mm, 28.53 ± 0.28 mm, respectively). We exclusively used male crabs to remove the potential influence of sex on both activity level (Toscano et al. 2014) and metabolic rate (Niewiarowski and Waldschmidt 1992). To determine the repeatability of activity level and SMR, these traits were measured twice per crab with 48 h between measurements. All crabs were fed with hard clams (*Mercenaria mercenaria*) and starved for 24 h before the measurement of either activity level or SMR to standardize hunger levels.

Individual crab activity level was measured following similar methods to those used in previous studies of *P. herbstii* refuge use behavior (Griffen et al. 2012, Toscano et al. 2014), where crab activity level is the inverse of refuge use as measured in these studies. Each crab was housed in a plastic mesocosm (43 cm length × 31 cm width × 18 cm height) during the measurement of activity level. Mesocosms were set up to mimic the physical structure of a natural oyster reef; each mesocosm received a sand substrate (1 cm deep) and a matrix of loose oyster shell (6 cm deep) that had been dried and cleaned to remove epifauna. Activity level was measured at night from approximately 2000 to 2300 h and mesocosms received flow-through, unfiltered seawater throughout the measurement of activity level. The activity level of crabs was observed under red light and behind a blind to minimize disturbance to crabs (Griffen et al. 2012, Toscano et al. 2014).

To measure activity level, we first placed crabs in mesocosms and allowed them to acclimate for 15 minutes. After this acclimation period, the behavior of crabs was observed once every 9 minutes over 3 hours (20 observations in total per crab). During each observation, we recorded whether crabs were active and moving (usually on top of the oyster shell matrix) or inactive (usually within the matrix). Crab activity level was calculated as the proportion of observations where crabs were observed active out of 20 total observations.

We quantified the repeatability of *P. herbstii* SMR to examine CIDs in the energetic requirements of crabs. Prior to all measurements, crabs were individually housed in small tackle box compartments (3 cm length × 3 cm width) to prevent excessive activity. We measured SMR at night (generally from 2100 to 2400 h) and under red light to minimize disturbance to crabs. SMR was measured in a climate-controlled room to maintain water temperatures between 20 and 22˚C throughout the duration of measurements.

We began trials by placing individual crabs in 0.7 L acrylic chambers (14 cm length × 7 cm width × 7 cm height) filled with 1-µm filtered, O_2 saturated (air-bubbled) seawater (100% O_2 saturation). Each container received a magnetic stir-bar to ensure mixing. Chambers were then sealed and a Clark-type dissolved oxygen sensor (HANNA, model HI-9146; HANNA instruments, USA) was inserted. We recorded the O_2 concentration in chambers every 10 minutes for 60 minutes. Preliminary trials revealed that crabs normalized their O_2 consumption rate after less than 10 minutes in the chamber; therefore, only data collected after 10 minutes was used in statistical analyses. Trials were terminated early if oxygen concentration dropped below 70% of the O_2 saturation level. After each trial, we measured the water volume in chambers with a graduated cylinder. We also measured the O_2 concentration in two crab-free chambers to control for background changes in dissolved O_2. We calculated individual O_2 consumption from the average of the five 10 minute interval measurements. We standardized SMR by crab dry weight (dried for 48 h at 70 °C) in all of our analyses, though doing so did not qualitatively alter our results.

We analyzed the repeatability of activity level and SMR using the methods of Nakagawa and Schlereth 2010 and the associated rptR package in the statistical software R (ver. 2.15.2, R Core Team 2012). Repeatability is the proportion of total phenotypic variation due to between-subject, as opposed to within-subject variation (Lessells and Boag 1987, Bell et al. 2009). Due to the proportional measurement of activity level, we used a generalized linear mixed model (GLMM) with a binomial error distribution to calculate the repeatability of activity level. Confidence intervals (95%) and statistical significance (*p*-values) of the repeatability of activity level were estimated using parametric bootstrapping with 1000 resamplings. Mass-specific SMR data met the assumption of normality (Shapiro-Wilk normality test: $W = 0.973$, $p = 0.330$), and therefore, we calculated the repeatability of SMR using the ANOVA method in the rptR package.

Testing for relationships between crab behavior and SMR

Next, we tested for relationships between crab behavior (the movement of crabs during the measurement of SMR and crab activity level) and SMR, and how these relationships were affected by predation threat from toadfish in the form of waterborne chemical cues. This experiment also allowed us to test the effects of predation threat on crab behavioral traits and SMR. Activity level and SMR were measured as described previously in '*Repeatability of activity level and SMR*'. In addition, we recorded the movement of crabs during the measurement of SMR. Specifically, we recorded whether crabs were moving or still (i.e. resting) at 10 minute intervals corresponding with regular measurements of O_2 concentration in chambers (6 observations per crab). Movement during SMR was quantified as the proportion of observations where crabs were observed moving. We also manipulated the presence of chemical cues from toadfish during the measurement of both activity level and SMR in this experiment. Thus, we measured movement during the measurement of SMR, activity level, and SMR of individual crabs in the absence and presence of predation threat, yielding 6 measurements per crab.

This experiment was run in a randomized complete block design ($n = 8$ crabs per block) using a different group of crabs (mean CW ± 1 SE: 30.22 ± 0.22 mm) from those used in the repeatability experiments. Three blocks were run in total, and each block lasted 5 days. Crab movement during the measurement of SMR was recorded during the last 2 blocks (i.e. $n = 16$ crabs), and so all analyses which include crab movement use these 16 crabs. The following describes our procedure for a single block. On the first day, we collected 8 male crabs from North Inlet. Crabs were housed in tackle box compartments (3 cm length × 3 cm width) between measurements of activity level and SMR, and fed daily with *M. mercenaria* and then starved for 24 h standardize hunger levels at 24 h before all measurements. On the second day, the SMR of these 8 crabs was measured either in the absence or presence of predation threat (this order was alternated for blocks). SMR in the absence of predation threat was measured as described previously (‘*Repeatability of activity level and SMR’*). To measure SMR in the presence of toadfish predation threat, we first treated 1-μm filtered seawater by soaking a single toadfish (25 cm total length [TL]) in 5.65 L of water for 1.5 h. We then sieved the treated water through a 10-μm filter bag to remove traces of fish slime, and aerated it to saturate with O_2. This water was otherwise treated in the same way as seawater used to measure SMR in the absence of predation threat. The SMR of crabs was then measured in this treated water.

On the third day, we measured the activity level of these 8 crabs. We measured the activity level of 4 crabs in the absence of predation threat and the activity level of the other 4 in the presence of threat. Activity level in the absence of predation threat was measured as described previously (‘*Repeatability of activity level and SMR’*). Activity level in the presence of predation threat was measured the same as in the absence of threat , except the seawater which fed mesocosm tanks was first directed through a holding chamber that contained a single toadfish (30 cm TL). On the fourth day, the activity level of this same group of 8 crabs was measured again, but in the alternate treatment (e.g. crabs receiving the predation threat treatment received the predation threat absent treatment). Finally, on the fifth day, the SMR of all 8 crabs was measured again but under the alternate treatment.

We used 2 linear mixed models (LMM) to examine relationships between (1) crab movement assessed during SMR measurements and SMR (i.e. a methodological relationship), and (2) crab activity level and SMR (i.e. a functional relationship). We further tested whether crab activity level influenced SMR after removing the effect of movement on SMR. We did this by first regressing movement on SMR, and using the residuals from this regression in a LMM testing the effect of activity level on movement-corrected SMR. We used generalized linear mixed models (GLMM) to examine the relationship between movement assessed during SMR measurements and crab activity level. Mass-specific SMR data was modeled with a Gaussian error distribution, while movement and activity level (proportional data) were modelled with a binomial error distribution and logit link (Bolker et al. 2009).

To test for each of these relationships, we first constructed models that included all potential predictor terms. Models included toadfish predation threat and crab carapace width as additional fixed factors because behavioral and energetic traits were measured in the absence and presence of predation threat, and crab size could potentially influence both mass-specific metabolic rate and behavior (Toscano et al. 2014). Including predation threat as a factor in models allowed us to test the effect of predation threat on both behavioral traits and SMR. We also tested for an interaction between the predictor trait (crab movement, crab activity and SMR) and toadfish predation threat in each model, to test whether trait relationships were altered by the presence of predation threat. Initial visual inspection of the effect of predation threat on SMR (Figure 5.2c) suggested that predation threat increased the SMR of crabs with initially low SMR, and decreased the SMR of crabs with initially high SMR (though we lacked a proper control in this experiment, where crabs would receive the same treatment twice). To test for this pattern, we tested the effect of SMR in the absence of threat on the change in SMR (SMR in the presence of threat – SMR in the absent of threat) in a LMM.

In all models, crab identity and experimental block were treated as random factors to control for pseudoreplication. For LMM, we tested for the significance of terms by dropping fixed factors (while retaining random factors) and comparing nested models using F tests (Crawley 2009). For GLMM, we used z-values (i.e. the Wald statistic) and associated p-values to examine whether factor coefficients were significantly different from zero. All statistical analyses were conducted using R (ver. 2.15.2, R Core Team 2012).

RESULTS

Both individual activity level (r [link scale] ± 1 SE = 0.047 ± 0.027, 95% CI: 0.005 – 0.11, $p = 0.002$; Figure 5.1a) and SMR (r ± 1 SE = 0.533 ± 0.148, 95% CI: 0.227 – 0.838, $p = 0.005$; Figure 5.1b) were significantly repeatable over time, indicating temporal consistency in these traits.

Predation threat increased crab movement in metabolic rate chambers (GLMM: effect of threat ± 1 SE = 1.435 ± 0.355, $z = -4.044$, $p < 0.001$; Figure 5.2a), but reduced the activity level of crabs (GLMM: effect of threat ± 1 SE = -1.183 ± 0.186, $z = -6.376$, $p < 0.001$; Figure 5.2b). Predation threat had no consistent linear effect on SMR (F test: LMM with threat as a fixed factor vs. null model [random factors only], $p = 0.707$; Figure 5.2c). Instead, crabs with initially low SMRs increased SMR in the presence of threat, while crabs with initially high SMRs decreased SMR in the presence of threat (F test: LMM with SMR measured in the absence of threat as a fixed factor vs. null model [random factor only], $p < 0.001$; Figure 5.2c). Crab body size (carapace width) did not affect crab movement in metabolic rate chambers (GLMM: effect of crab size ± 1 SE = -

0.397 ± 0.234, $z = -1.701$, $p = 0.089$) or crab activity level (GLMM: effect of crab size ± 1 SE = 0.002 ± 0.272, $z = 0.008$, $p = 0.994$).

Individual crab movement, observed during the measurement of crab SMR, was positively related (effect of movement ± 1 SE = 8.688 ± 2.378) to crab SMR (*F* test: model with crab movement as a fixed factor vs. null model [random factors only], $p = 0.002$; Figure 5.3). The relationship between crab movement and SMR was best described by a second-order polynomial model (*F* test: polynomial term, $F_{2, 29} = 12.582$, $p < 0.001$; Figure 5.3). Movement and threat did not interact to predict crab SMR (*F* test: LMM with movement × threat interaction vs. model with independent factors, $p = 0.263$; Figure 5.3).

In contrast, crab activity level, observed under more natural conditions, had no effect on crab SMR (*F* test: LMM with crab activity level as a fixed factor vs. null model [random factors only], $p = 0.551$; Figure 5.4), nor did the interaction between activity level and threat (*F* test: LMM with activity × threat interaction vs. model with independent factors, $p = 0.816$; Figure 5.4). This was true even after removing the effect of crab movement in metabolic rate chambers on SMR prior to analysis (*F* test: LMM with activity × threat interaction vs. model with independent factors, $p = 0.069$).

Lastly, crab movement measured during SMR did not predict activity level measured under more natural conditions (GLMM: effect of movement ± 1 SE = -0.016 ± 0.815, $z = -0.020$, $p = 0.984$), either in the absence or presence of toadfish predation threat (GLMM: effect of movement × predation threat interaction ± 1 SE = 1.191 ± 0.827, $z = 1.441$, $p = 0.150$).

DISCUSSION

In the present study, we found repeatable individual-level variation (i.e. CIDs) in crab activity level and mass-specific SMR with 48 h between longitudinal measurements. Though activity level is typically less repeatable than other behaviors (e.g. aggression or exploration; Bell et al. 2009), the significant repeatability of crab activity level detected here qualifies this trait as a behavioral type of *P. herbstii*. A previous study (Toscano et al. 2014) also found repeatability of individual *P. herbstii* behavior (referred to as refuge use in Toscano et al. [2014], which is the inverse of activity level), though this study used a wide size range of crabs (20-30 mm CW) in which crab body size had a large negative effect on refuge use (Toscano et al. 2014). In the present study, we demonstrated significant repeatability using a much smaller size range of crabs where body size had no effect on behavior. Furthermore, in line with other studies of CIDs in metabolic rate and SMR in particular (reviewed in Nespolo and Franco 2007), our data indicate that crab SMR is a temporally consistent trait at the individual level. The repeatability of SMR in the present study ($r \pm 1$ SE = 0.533 ± 0.148) was close to the range of previously reported repeatability values for SMR (mean $r \pm 1$ SE = 0.645 ± 0.076) in other taxa (Nespolo and Franco 2007).

Waterborne chemical cues from toadfish influenced crab movement (measured in metabolic rate chambers), crab activity level and crab SMR in different ways. Predation threat increased the movement of crabs in metabolic rate chambers, but decreased crab activity level measured under more natural conditions. We attribute these different behavioral responses to the lack of refuge habitat in the containers where crab SMR was measured and presence of refuge habitat in mesocosms where activity level was measured. Increased movement in the presence of predation threat likely reflects attempts to hide or escape the metabolic rate chamber (i.e. stress). In contrast, crabs that reduced activity level in the presence of threat often took refuge under oyster shells, consistent with other studies on the effects of predation threat on *P. herbstii* behavior (Grabowski 2004, Griffen et al. 2012, Toscano et al. 2014). Reduced activity is a taxonomically widespread response to predation threat and an effective mechanism of predator avoidance (Krupa and Sih 1998, Anholt et al. 2000, Grabowski 2004).

Interestingly, crabs with an initially low SMR increased SMR in response to predation threat, while crabs with an initially high SMR decreased SMR. While the influence of predation threat on metabolic rate has received little attention (Woodley and Peterson 2003), metabolic rates, or correlates of metabolic rate (e.g. opercular rate in fish), generally increase in the presence of threat (Woodley and Peterson 2003, Hawkins et al. 2004, Steiner and Van Buskirk 2009, Hawlena and Schmitz 2010), though decreases with threat have also been detected (Cooke et al. 2003). For example, Cooke et al. (2003) found that largemouth bass (*Micropterus salmoides*) heart rate decreased in the presence of threat from bird predators but increased after simulated attack, suggesting an initial hiding response and heightened stress after attack. Our findings that crabs with an initially low SMR increased SMR but only up to ~20 µmol/h/g DW oxygen consumption, and that crabs with an initially high SMR did not increase their SMR past this rate, suggests that this is an approximate upper limit for the mass-specific SMR of *P. hersbtii* in our study. The increase in SMR of crabs with initially low SMRs could be indicative of preparation for an escape response such as a sudden movement away from the source of threat (Höjesjö et al. 1999, Killen et al. 2013). This also suggests that increased energy expenditure is a nonlethal cost of predation threat for crabs with low SMR, although it is unknown whether crabs can compensate for this cost after threat has passed (Cooke et al. 2003). In contrast, the reduction in SMR of crabs with initially high SMR could be associated with a hiding response during attack, though this prediction remains to be tested.

Our data supported the hypothesis that crab movement in metabolic chambers would be positively related to SMR (i.e. a methodological relationship; Careau et al. 2008), suggesting that crabs which move more in metabolic rate chambers also respire more. This relationship was best described by a polynomial model which peaked at approximately 18 µmol/h/g DW oxygen consumption. Again, this suggests an upper limit to mass-specific SMR in our study beyond which additional movement had little effect on SMR. Methodological relationships between metabolic rate and behavior make it difficult to effectively separate the effects of individual behavioral variation from metabolic rate (Careau et al. 2008). Preventing animal movement via restraint could eliminate individual differences in movement, though this would likely induce further stress and thereby modify metabolic rates in unrealistic ways. While other studies have failed to detect a methodological relationship between behavior and energetics (e.g. Bouwhuis et al. 2013), this likely depends on the behavioral response of the particular study species to the method of metabolic rate measurement. It has been previously suggested that discarding metabolic rate data from individuals which exhibit excessive activity during the measurement of metabolic rate can bias the population sample in favor of inactive individuals (Careau et al. 2008), and our results suggest this is true with *P. herbstii*.

We further hypothesized that crab activity level measured in a relatively more natural setting would be related to SMR (i.e. a functional relationship). Arguments in support of functional relationships between individual behavior and baseline metabolic rate posit that high levels of activity, boldness and aggressiveness are required to gain energy in support of a high metabolic rate, or vice versa (i.e. the pace-of-life-syndrome hypothesis). Despite CIDs in crab activity level and metabolic rate and the aforementioned methodological relationship, we failed to detect a relationship between crab activity level measured under more natural conditions and SMR, even after removing the direct effect of crab movement on SMR. The lack of a functional relationship is not particularly surprising, given that individual crab movement, which predicted some variation in SMR, was not related to crab activity level. Both crab activity levels and SMR were measured over relatively short time periods (3 h and 1 h, respectively) in the lab, and while repeatable, it is possible that these assays do not capture natural variation in traits such as daily foraging activity and energy expenditure over longer time scales. Measuring such traits in the field is relatively labor-intensive (e.g. via the doubly labeled water technique) but a crucial next step in rigorously examining the pace-of-life syndrome hypothesis (Bouwhuis et al. 2013).

The lack of relationship between crab activity level and SMR was consistent across the absence and presence predation threat from toadfish in the form of waterborne chemical cues, a widespread biotic stressor. In a recent review, Careau and Garland (2012) reported that 9 of 21 studies detected significant relationships between behavior and metabolic traits, providing mixed support for individual-level behavior-energetics relationships (Biro and Stamps 2010, Careau and Garland 2012, Bouwhuis et al. 2013).

Killen et al. (2013) proposed context-dependence as one reason for this mixed support. Evidence for the importance of context-dependence is provided by work on juvenile European sea bass *Dicentrarchus labrax* (Killen et al. 2011, 2012). These studies show that relationships between risk-taking behavior and metabolic rate only emerge in food deprived fish (Killen et al. 2011), or fish experiencing hypoxic environmental conditions (Killen et al. 2012). This is because these stressors cause fish with higher metabolic rates to undertake risky behaviors which are unnecessary under normal conditions. Based on this work, we hypothesized that crabs with higher SMRs would exhibit higher activity under threat in order to satisfy their energetic demands, whereas the relationship between activity level and SMR in the absence of threat would be less apparent. It is possible that this influence of crab SMR on activity did not emerge due to the relatively short duration of the activity level assay and starvation period used (24 h) in our study. Alternatively, differences in risk perception among individuals could drive variation in crab activity level that is independent of variation in SMR in the presence of predation threat (Stankowich and Blumstein 2005).

While our study did not support a pace-of-life syndrome between activity level and SMR in *P. herbstii*, it is one of few studies to test for such a syndrome in an invertebrate species (Careau and Garland 2012, Krams et al. 2013). Krams et al. (2013) found that mealworm beetles (*Tenebrio molitor*) with lower metabolic rates also displayed higher durations of immobility, a behavior that reduces predation risk, providing rare support for a pace-of-life syndrome in an invertebrate species. Ectothermic invertebrates could be expected to show different individual-level relationships between behavior and energetics compared to endotherms (Kralj-Fišer and Schuett 2014) due to

(1) the importance of environmental temperature in determining both behavior (e.g. Briffa et al. 2013) and metabolic rate in ectotherms (e.g. Clarke and Johnston 1999), and (2) the importance of metabolism in maintaining endothermy (Galliard et al. 2013). We suggest that additional research on CIDs in the behavioral and physiological traits of invertebrates will provide insight into the commonness of individual-level behavior-energetics relationships across taxonomic groups, and therefore the mechanisms behind relationships. This information is critical in refining our understanding of the maintenance of individual-level phenotypic variation in natural populations.

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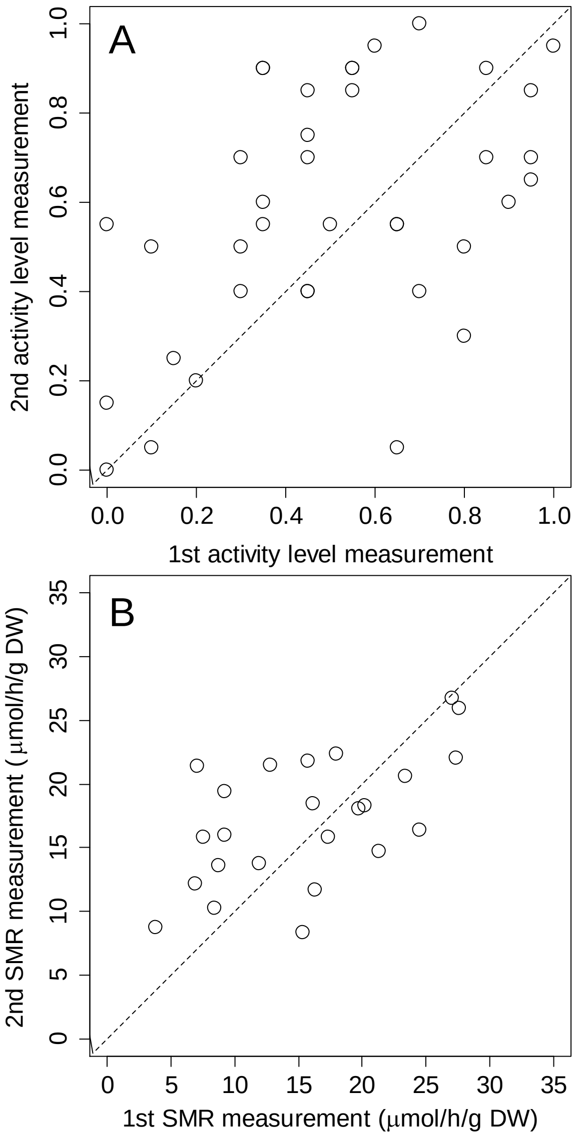

Figure 5.1 Individual activity level (panel A) and standard metabolic rate (SMR) (panel B) of mud crabs (*Panopeus herbstii*) measured twice over a period of 3 days with 48 h between measurements. Dotted lines indicate a 1:1 relationship (i.e. perfect consistency) for comparison to the distribution of data points.

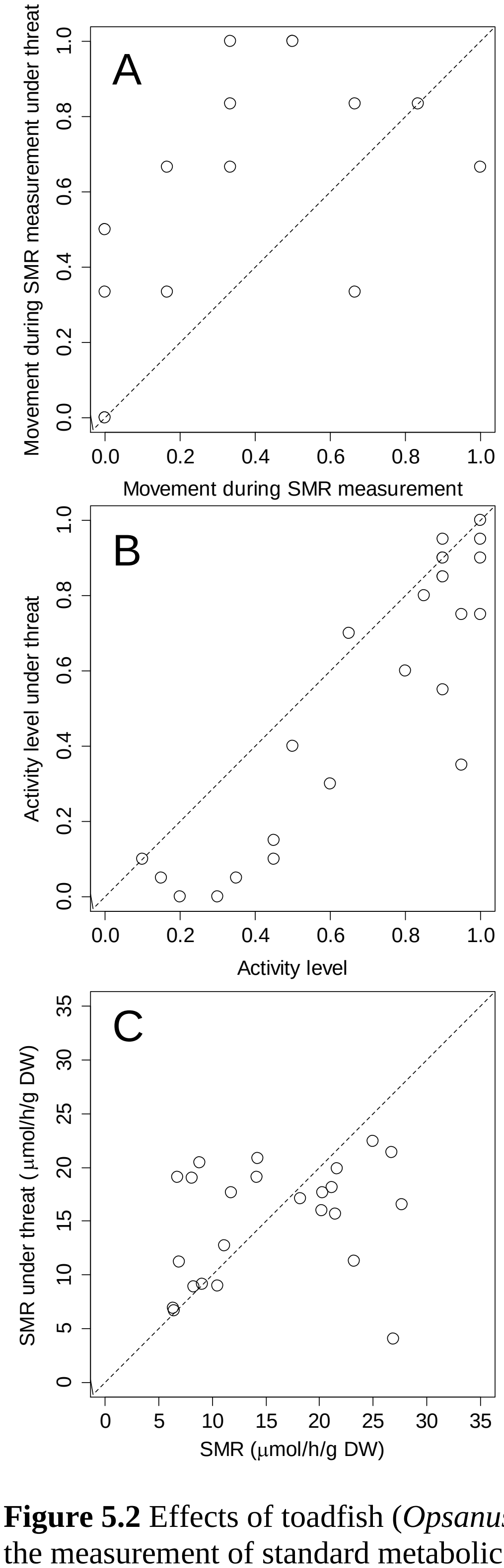

Figure 5.2 Effects of toadfish (*Opsanus tau*) predation threat on crab movement during the measurement of standard metabolic rate (SMR) (panel A), activity level (panel B), and SMR (panel C) of mud crabs (*Panopeus herbstii*). Dotted lines indicate a 1:1 relationship for comparison to the distribution of data points.

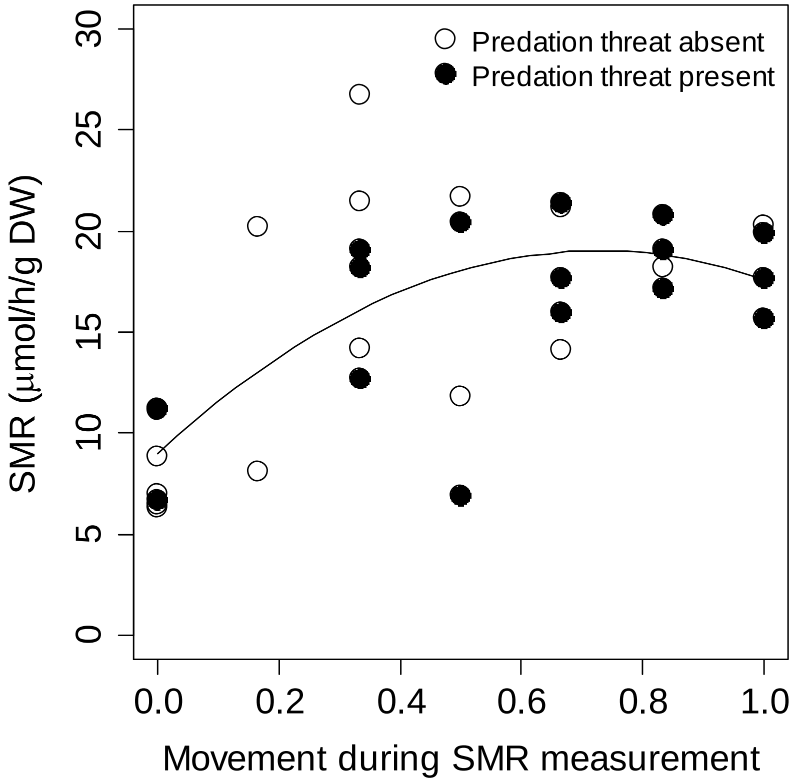

Figure 5.3 Relationship between individual crab (*Panopeus herbstii*) movements assessed during standard metabolic rate (SMR) measurements and SMR in the absence (white circles) and presence (black circles) of toadfish (*Opsanus tau*) predation threat. Black line depicts polynomial model fit to data.

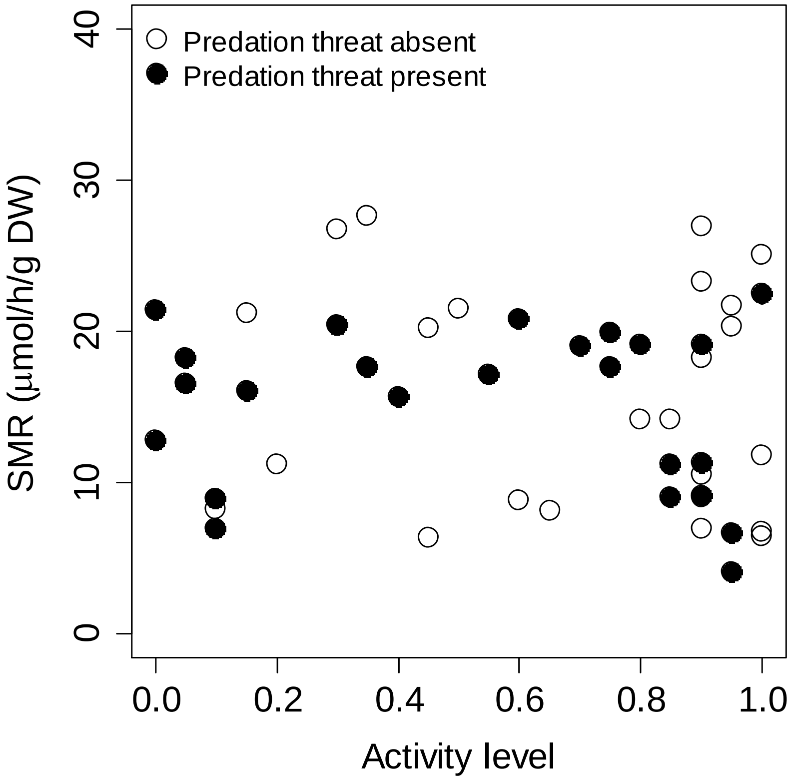

Figure 5.4 Relationship between individual crab (*Panopeus herbstii*) activity level and SMR in the absence (white circles) and presence (black circles) of toadfish (*Opsanus tau*) predation threat.

CHAPTER 6

TRAIT-MEDIATED FUNCTIONAL RESPONSES: PREDATOR BEHAVIORAL TYPE MEDIATES PREY CONSUMPTION[5]

ABSTRACT

1. The predator functional response (i.e. per capita consumption rate as a function of prey density) is central to our understanding of predator-prey population dynamics. This response is behavioral, depending on the rate of attack and time it takes to handle prey.
2. Consistent behavioral differences among conspecific individuals, termed behavioral types, are a widespread feature of predator and prey populations but the effects of behavioral types on the functional response remain unexplored.
3. We tested the effects of crab (*Panopeus herbstii*) behavioral type, specifically individual activity level, on the crab functional response to mussel (*Brachidontes exustus*) prey. We further tested whether the effects of activity level on the response are mediated by the presence of toadfish (*Opsanus tau*) predation threat in the form of waterborne chemical cues known to reduce crab activity level.
4. The effects of crab activity level on the functional response were dependent on crab body size. Individual activity level increased the magnitude (i.e. slope and asymptote) of the type II functional response of small crabs, potentially through an increase in

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time spent foraging, but had no effect on the functional response of large crabs. Predation threat did not interact with activity level to influence mussel consumption, but independently reduced the slope of the type II functional response.

5. Overall, this study demonstrates size-specific effects of a behavioral type on a predator-prey interaction, as well as a general pathway (modification of the functional response) by which the effects of individual behavioral types can scale up to influence predator-prey population dynamics.

INTRODUCTION

Predator-prey interactions have traditionally been described, measured and modeled at the population or species levels. For example, classic food webs are depicted with species as nodes and feeding links determined with mean trophic data from species or solely from adults (Cohen 1978; Polis 1991). Similarly, the functional response, i.e. per capita prey consumption dependent on prey density, is generally averaged across predator individuals for use in models that predict predator-prey population dynamics (Okuyama 2008; Bolnick *et al.* 2011) or the dynamics of multi-trophic systems (e.g. Rosenzweig 1973; Oksanen *et al.* 1981). This is a decidedly taxonomic approach (sensu Rall *et al.* 2011) to studying predator-prey interactions that obscures individual-level variation and assumes interactions can be understood by mean values of populations or species (Bolnick *et al.* 2011).

Recent empirical work has illuminated extensive individual-level phenotypic variation in predator and prey populations with important ecological consequences (reviewed by Bolnick *et al.* 2003; Araujo, Bolnick & Layman 2011; Bolnick *et al.* 2011; Sih *et al.* 2012). For example, conspecific individuals often differ in their behavioral traits (e.g. activity, boldness or aggression) and these differences are consistent over time (termed behavioral types, BTs; Sih, Bell & Johnson 2004, Carter *et al.* 2013). Furthermore, behavioral syndromes describe correlations between different BTs (e.g. boldness and aggression; Bell & Sih 2007), or correlations of a single BT measured across ecological contexts (Sih *et al.* 2004, Carter *et al.* 2013). BTs can influence various aspects of predator-prey interactions including consumption rates (Pruitt & Krauel 2010), predator foraging tactics (Coleman & Wilson 1998; Kurvers *et al.* 2010), predator diet breadth (Riechert 1991), and predator-prey spatial distributions (Cote *et al.* 2010; Griffen, Toscano & Gatto 2012). Nevertheless, it remains unclear whether accounting for such individual-level behavioral variation in traditional models of predator-prey interactions could help explain patterns or alter predictions at the population and community levels (Okuyama 2008; Bolnick *et al.* 2011).

The functional response is central to our understanding of predator-prey population dynamics (Holling 1959; Murdoch & Oaten 1975) and co-evolutionary theory (Abrams 2000). This response is dependent on behavioral traits, including an individual predator’s rate of attack, determined by its reactive distance, movement speed, capture success, and the behavior of its prey, as well as its handling time, i.e. the time it takes to capture, subdue and consume an individual prey (Jeschke, Kopp & Tollrian 2002; Tully, Cassey & Ferriere 2005); these model characteristics affect the long- and short-term stability of predator-prey dynamics (Murdoch & Oaten 1975; Abrams 2000). If predator or prey BTs can influence these emergent behavioral traits (attack rate and handling time), then BTs can alter the functional response and potentially scale up to influence population dynamics. Accounting for BTs in the functional response could be especially important if there is a spatial structure to behavioral types (e.g. Boon, Réale & Boutin 2008; Griffen *et al.* 2012), or when combining different functional responses to make predictions at the population level (Jensen's inequality; for discussion see Okuyama 2008; Bolnick *et al.* 2011).

Activity level is one of the most well-studied behavioral traits (Careau *et al.* 2008), and numerous studies have shown that activity level differs consistently between conspecifics (i.e. a BT; Sih *et al.* 2004). Activity level is typically measured by placing an individual animal in a familiar environment and measuring either the distance moved over a period of time (e.g. Harcourt *et al.* 2009; Pruitt, Stachowicz & Sih 2012) or the frequency or duration of movement (e.g. Wilson *et al.* 2010; Mafli, Wakamatsu & Roulin 2011; Beckmann & Biro 2013). In a foraging context, these measures of activity level should influence predator-prey encounters (although this also could depend on the activity of prey; Sweeney et al. 2013), particularly when prey are at low densities, thus modifying the attack rate (i.e. initial slope) in functional response models. Furthermore, while greater predator activity increases encounters with prey, it also heightens the risk of being eaten by higher order predators (Werner & Anholt 1993; Anholt, Werner & Skelly 2000). Therefore, intermediate predators often modify their activity level to balance foraging demands with the threat of being eaten. While this tradeoff is traditionally studied from an optimization perspective (i.e. activity level is modified to maximize fitness), it has been suggested that individual BTs impose limits on behavioral plasticity, thereby precluding perfect optimization (Sih *et al.* 2004). Thus predation threat from a higher order predator could modify the effects of activity level on the intermediate predator functional response, depending on whether or not individuals respond behaviorally to predation threat, and the degree to which they respond.

In the present study, we explored the hypothesis that individual predator activity level can modify the predator functional response and further examined how predation threat could mediate the effects of activity level on the response. This is an important first step in determining whether accounting for individual predator behavior in the functional response could improve our predictive capacity regarding consumption rate and predator-prey interaction strength. We used a well-studied tri-trophic system consisting of toadfish (*Opsanus tau* Linnaeus) as a top predator, mud crabs (*Panopeus herbstii* Milne-Edwards) as an intermediate predator, and scorched mussels (*Brachidontes exustus* Linnaeus) as prey of crabs (Grabowski & Kimbro 2005; Griffen *et al.* 2012). Previous work in this system indicates that individual differences in crab activity level are consistent over time, validating activity level as a BT of mud crabs (see Methods: *Study system* for further discussion). Furthermore, smaller crabs generally have lower activity levels than large crabs (Griffen *et al.* 2012, Toscano, Gatto & Griffen 2014), likely due to their greater susceptibility to toadfish predation (Toscano unpublished data). Therefore, due to the importance of crab body size in determining activity level as well as the outcome of predator-prey interactions more broadly (e.g. Aljetlawi, Sparrevik & Leonardsson 2004; McCoy *et al.* 2011), we used a wide size range of crabs to test whether effects of activity level further depend on crab body size. In short, our study found that the effects of crab activity level on the crab functional response were indeed size-dependent, while toadfish predation threat had effects independent of crab activity level and body size on the crab functional response.

METHODS

Study system

Toadfish, mud crabs and scorched mussels are common inhabitants of oyster (*Crassostrea virginica* Gmelin) reefs along the Atlantic and Gulf coasts of the United States. Previous work has shown that individual mud crabs differ in their use of oyster shell refuge habitat (Griffen *et al.* 2012), and that these behavioral differences are consistent over months in the field (Toscano *et al.* 2014). Refuge use is negatively related to crab body size, but there is additional consistent variation in refuge use that is not explained by size (Griffen *et al.* 2012; Toscano *et al.* 2014). Furthermore, mud crabs increase refuge use in the presence of toadfish chemical cues (Grabowski & Kimbro 2005), a widespread response to predation threat. This anti-predatory behavior reduces the mussel consumption rate of crabs, thereby modifying the strength of the trait-mediated trophic cascade involving these species (Griffen *et al.* 2012). This trophic cascade is a major determinant of community structure in oyster reefs (Grabowski & Kimbro 2005; Griffen *et al.* 2012). Refuge use in these studies (Griffen *et al.* 2012; Toscano *et al.* 2014) was measured as the proportion of behavioral observations where an individual crab was under oyster shell and inactive. In the present study, we use the inverse of this behavioral measurement (i.e. the proportion of observations where crabs are observed active), as measured in other studies of individual activity level as a BT (e.g. Wilson *et al.* 2010; Mafli *et al.* 2011; Beckmann & Biro 2013), to test the hypothesis that crab activity level influences the crab functional response to mussel prey density.

Experimental setup

The experiment was run from May through August 2012 in a screened-in wet laboratory at the Baruch Marine Field Lab in Georgetown, South Carolina, USA. Organisms used in the experiment were collected from the adjacent Oyster Landing intertidal oyster reef in North Inlet estuary (33°20′N, 79°10′W).

To examine the effects of individual crab activity level on the functional response, we measured both the activity level and mussel consumption rate of individual crabs. Activity level was measured prior to consumption rate trials. We manipulated the presence of chemical cues from toadfish during measurements of both activity level and consumption rate to test how the presence of predation threat directly affects the functional response, and how threat could mediate the effects of activity level on the functional response. Specifically, both the activity level and consumption rate of individual crabs were measured under 1 of 2 predation threat treatments: toadfish chemical cue absent (n = 240 crabs) or toadfish chemical cue present (n = 207 crabs). Activity level measured under predation threat is a measure of boldness as defined in the animal personality literature (Carter *et al.* 2013). The consumption rate of individual crabs was measured at a single prey density rather than a range of prey densities to minimize the duration crabs were held in the lab, which could modify individual behavior through conditioning (Butler *et al.* 2006). We ran the experiment in a complete block design and the following methods pertain to a single block of 4 day duration.

On the first day, 16 crabs (20-30 mm carapace width, CW) were collected from the high intertidal portion of the Oyster Landing reef. Mud crabs become important predators of adult bivalves in oyster reefs in North Inlet estuary when they reach ~20 mm

CW (Toscano & Griffen 2012), and attain a maximum size of 55 mm CW at this site (McDonald 1982). All crabs were fed with mussels *ad libitum* as soon as they were brought into the lab. Eight of these 16 crabs were then randomly assigned to the toadfish cue absent treatment while the other 8 were assigned to the toadfish cue present treatment, and these treatments were maintained for both activity level and consumption rate trials (methods for activity level and consumption rate trials are detailed below). To create the toadfish cue present treatment, we pumped seawater through a holding chamber that contained a single adult toadfish (~ 30 cm total length) fed *ad libitum* with mud crabs in between experimental trials. This seawater was then divided equally among mesocosms containing crabs to keep the amount of chemical cue consistent within blocks. Crabs assigned the cue absent treatment received seawater that did not first pass by a toadfish, but was otherwise distributed using the same seawater system. Mesocosms receiving the toadfish cue absent and cue present treatments were always alternated spatially.

On the second day, 4 crabs receiving the toadfish cue absent treatment and 4 crabs receiving the cue present treatment (8 of the 16 crabs) were observed to measure their activity level, and on the third day, the other 8 crabs were observed in the same manner. This second group of 8 crabs was fed again on the 2nd day to keep their starvation time before activity level measurement (24 h) consistent with the first group of 8 crabs, and on the third day, all crabs were fed to maintain starvation consistency before consumption rate trials. On the fourth day, the consumption rate of all 16 crabs was measured in a 24 h feeding trial. All crabs were held in the lab for an additional 2 days after consumption rate trials to ensure that crabs were not approaching a molt cycle or female crabs were not becoming reproductive. This procedure for a single experimental block was repeated 33 times over the course of the summer (May through August). Any crabs molting, carrying eggs or dying during their time in the lab were removed from the final data set. Additionally, the toadfish chemical cue treatment failed during the measurement of crab consumption rate for 5 blocks and these crabs were therefore removed from the final data set. However, complete removal of these blocks (i.e. both cue absent and present treatments) from the final data set did not alter our results.

Measurement of crab activity level

The activity level of individual crabs was measured using a similar behavioral assay to that used in previous studies of mud crab BTs (Griffen *et al.* 2012; Toscano *et al.* 2014). Each crab was observed in a glass mesocosm (50 × 28 × 30 cm) containing a 3 cm layer of sand/mud substrate and 5 L of oyster shell that had been dried and cleaned to remove epifauna. This experimental crab density (1 crab per 0.14 m^2) is within the range of densities previously reported in North Inlet (McDonald 1982, Toscano unpublished data). Oyster shell was placed on top of the substrate to mimic natural reef habitat. This amount of shell ensured that crabs had ample space to hide completely. In each tank, eight large mussels (~25 mm shell length, SL) were suspended in a mesh bag near the surface of the water to release chemical cues and induce crab foraging behavior while remaining out of reach of crabs.

Crabs were observed at night (from ~2000-2300 h) under dim red light and from behind a blind to minimize disturbance. Over a period of 3 hours, we observed whether crabs were exposed and active (vs. hiding and remaining motionless) every 6 minutes (30 observations per crab in total). Activity level was measured as the proportion of 30 observations that crabs were visible to the observer and moving. In addition to activity level, we recorded the carapace width, major claw width and sex of each crab.

Measurement of crab consumption rate

Eight mussel (12-16 mm SL) prey densities (2, 4, 6, 8, 12, 16, 24 and 36 mussels per mesocosm) were randomly assigned to the 8 crabs receiving the toadfish cue absent treatment as well as the 8 crabs receiving the cue present treatment for each block. These mussel densities fall within the range of recorded mussel densities within a single large oyster cluster from the study site (Toscano & Griffen 2012). This created a total of 16 unique treatment combinations in each block. These trials were conducted in glass mesocosms of the same dimensions that we used to observe crab activity level. Mesocosms contained a 3 cm layer of sand/mud substrate and 10 large oyster shells, and were enclosed in black plastic to mimic the low-light conditions of North Inlet estuary during summer months (Dame *et al.* 1986; Toscano & Griffen 2013). Mussels were scattered evenly on oyster shells throughout each mesocosm and allowed to attach to oyster shells for 6 h prior to the start of trials. Crabs were allowed to forage for 24 h (starting and ending at ~1500 h) and the number of mussels remaining as well as the water temperature was recorded at the end of trials.

Analysis

We first tested the factors influencing individual mussel consumption by crabs with a generalized linear mixed model (GLMM) using the complete data set (n = 447 crabs). After establishing the importance of these factors, we then fit functional response models to subsets of the data set and compared the parameter estimates of functional response model fits to test for the effects of specific factors of interest (notably toadfish predation threat and crab activity level) on the crab functional response. All analyses were conducted using the statistical software R (R Core Team 2012).

We used a GLMM (lme4 package) with a binomial error distribution to examine the effects of crab activity level, crab claw width, experimental treatments (toadfish cue absence/presence, mussel prey density) and temperature, as well as all potential two-way interactions between these factors on the proportional mussel consumption of individual crabs. Claw width, which was strongly related to crab carapace width (linear regression: $R^2 = 0.855$), was used in this model because it is mechanistically tied to mussel consumption in oyster shell habitat (Toscano & Griffen 2013). To correct for overdispersion in this model, we included an observation-level random effect (Browne *et al.* 2005). Experimental block was also included as a random effect to control for pseudoreplication. Our original GLMM included all main factors, as well as all potential two-way interactions. This original model was simplified by dropping non-significant interaction terms.

We then fit functional response models to subsets of the complete data set to test the effects of specific factors of interest (toadfish predation threat and crab activity level) on the shape and parameter estimates of the functional response. To test how toadfish predation threat affected the functional response, we fit models separately to crabs with consumption measured in the absence versus presence of the toadfish chemical cue (2 separate functional response models). To test how crab activity level affected the functional response, models were fit to the consumption rates of small crabs (< 24 mm CW; activity level had no effect on the mussel consumption of large crabs, see Figure 6.1) with low activity (≤ 0.22) versus high activity (> 0.22) (2 separate functional response models). Based on visual inspection of the data, this threshold adequately demonstrated the effect of activity level on the functional response of small crabs, though using other threshold values (0.15-0.3 activity level) did not qualitatively alter our results. We included both small crabs receiving the toadfish cue absent and present treatments because there was no interaction between the toadfish chemical cue and crab activity level on mussel consumption (Table 6.1). Thus we fit a total of 4 functional response models in total to subsets of the data.

Our approach to fitting each functional response model was as follows. First, to determine the proper type (i.e. type I, type II, or type III) of functional response, we plotted proportional mussel consumption as a function of prey density and analyzed these data using a polynomial logistic regression (Juliano 2001). In all cases, these plots showed decreasing proportional consumption with prey density and a significantly negative first-order term, indicative of type II functional responses (Juliano 2001). Because prey were depleted over the 24 h that crabs foraged and not replaced, a Rogers type II functional response model that accounts for prey depletion was used (Rogers 1972; Kalinkat, Brose & Rall 2013):

$$N_e = N_o\,(1 - \exp(\alpha(N_e T_h - PT))) \qquad \text{eqn. 1}$$

Where N_e is the number of prey eaten, N_0 is the initial prey density, α is attack rate, T_h is handling time, P is the number of predator individuals (set to 1 in all models), and T is the experimental duration (24 h). This functional response model was fit using maximum likelihood estimation (bbmle package) in the statistical software R.

We used bootstrapping to test whether toadfish predation threat and crab activity level influenced functional response parameters (α and T_h). Specifically, we randomly subdivided the data into 2 subsets of the same size as the actual treatment groups (e.g. absence of predation threat: $n = 240$, presence of threat: $n = 207$). We then fit the functional response model (eq. 1) to each of these random subsets and calculated the difference in parameter estimates between random subsets. We repeated this procedure 10,000 times to generate a distribution of random differences in parameter estimates. We then compared the actual differences in parameter estimates (i.e. between predation threat absence vs. presence and small crabs with low vs. high activity) to these bootstrapped null distributions of differences to test whether the actual differences fell outside of 95% of null distributions.

RESULTS

Crab activity level and crab claw width interacted to influence proportional mussel consumption (Table 6.1); small crabs that exhibited a higher activity level during behavioral observation ate more mussels during consumption rate trials (Figure 6.1a), while crab activity level had no effect on the mussel consumption of large crabs (Figure 6.1b). Due to the interaction between crab activity and claw width, we could only interpret the conditional effect of crab claw width (i.e. the effect of claw width when activity level was zero) (Brambor, Clark & Golder 2006). At zero activity level, crab claw width increased mussel consumption (Table 6.1). Temperature, which varied between 23 and 33°C over the course of the study, also increased mussel consumption by crabs (Table 6.1). In contrast, the presence of chemical cues from toadfish reduced the mussel consumption of crabs (Table 6.1). Mussel prey density also reduced proportional mussel consumption by crabs (Table 6.1), resulting in saturating functional responses (Figures 6.2 and 6.3).

Crabs exhibited type II functional responses (Figures 6.2 and 6.3), identified by uniformly decreasing proportional mussel consumption with mussel density. The presence of the toadfish chemical cue reduced the initial slope of the crab functional response (Figure 6.2). Specifically, the presence of the cue decreased the attack rate parameter (observed difference between cue and no cue $\alpha = -0.029$, < 97.8% of the bootstrapped parameter differences in α), but had little effect on the handling time parameter (observed difference in $T_h = 0.273$, > 78.2% of the bootstrapped parameter differences) in type II functional response models (Figure 6.2). In contrast, activity level increased the overall magnitude of the functional response of small crabs (Figure 6.3), specifically increasing the attack rate parameter (observed difference between high activity and low activity $\alpha = 0.029$, > 97% of the bootstrapped parameter differences) and reducing the handling time parameter (observed difference in $T_h = -1.096$, < 99.9% of the bootstrapped parameter differences).

DISCUSSION

In the present study, we found that crab predator activity level increased both the initial slope and asymptote of the functional response of small crabs to mussel prey density. In contrast, activity level had no effect on the mussel consumption of large crabs. This shows that the effects of individual behavior on ecological dynamics can further vary within species depending on individual body size or population size structure. Similarly, sex-dependence of the ecological effects of BTs has been observed in great tits (*Parus major*), where individual exploratory behavior had opposite effects on the survival of males and female birds depending on year-to year variation in resource levels (Dingemanse *et al.* 2004; Dingemanse & Réale 2005).

The functional response is a major determinant of predator-prey population dynamics and stability (Murdoch & Oaten 1975), and therefore changes in the response driven by individual crab activity level could scale up to influence the crab-mussel interaction at the population level. Individual-level variation in activity level is taxonomically widespread (Careau *et al.* 2008), and activity level is common mechanism mediating species interactions (Anholt *et al.* 2000). Models of size-dependent functional responses are typically built upon mechanistic or phenomenological links between predator-prey body sizes and attack rate and handling time parameters (e.g. Aljetlawi *et al.* 2004; Rall *et al.* 2011; McCoy *et al.* 2012). Our work shows that functional response models for actively foraging predators could be modified to include the influences of additional size-dependent behavioral variation and predation threat to more accurately predict predation rates in heterogeneous populations.

Our observations of crab activity level in a foraging situation allowed us to indirectly examine the mechanisms by which crab activity level increased the functional response of small, but not large crabs. Despite the presence of mussel prey chemical cues in observational tanks, small crabs were often observed inactive and remaining in the same location over the entire 3 h behavioral observation period (Figure 6.1a; see also Toscano *et al.* 2014). Large crabs exhibited relatively higher levels of activity in comparison (Figure 6.1b). This increase in activity level with crab size is likely driven by a size refuge reached by large crabs from predators in the field (Shervette *et al.* 2004; Hill & Weissburg 2013; Toscano unpublished data), where large crabs have little reason to remain inactive and forgo foraging opportunities (see also Krause *et al.* 1998). If we assume that crabs can only find and consume mussel prey when they are active, then it is possible that a certain level of activity is needed to reach the maximum possible consumption rate over 24 h. Further increases in activity beyond this level should have little effect on mussel consumption. This level of activity was likely reached by most large crabs but very few small crabs, thus limiting their mussel consumption rate.

This suggests that an overall increase in time spent foraging is the mechanism behind the positive effect of activity level on the mussel consumption of small crabs, and this is supported by functional response modeling. We investigated whether an increase in time spent foraging could explain the positive effect of activity level by varying the experimental duration factor (T) in the type II functional response model (eqn. 1) fit to the consumption data of small crabs with low activity (activity level ≤ 0.22). Specifically, we fit a functional response model to consumption data from these crabs in which the attack rate (α) and handling time parameters (T_h) were set to values from the functional response model fit to small crabs with a *high* activity level (activity level > 0.22; $\alpha = 0.083$, $T_h = 2.943$). We then estimated T by fitting this model to the data. The experimental duration, T, in this model was reduced from 24 (as set in our original model) to 16.818 h, and this model provided an equally good fit to the consumption data of small crabs with low activity when compared to the model in which experimental duration was set to 24 h, and attack rate and handling time were allowed to vary (ΔAIC = 1.729). This indicates that a simple reduction in the time parameter in the functional response model effectively captures the effect of activity level on the response.

Though we hypothesized that activity level would primarily influence prey consumption at low prey densities and thus the attack rate parameter, our results suggest that activity level does not change the nature of crab foraging behavior (i.e. a shift in the type of response or relative changes in parameter estimates). It is worth noting however, that the reduction in activity between small crabs exhibiting high vs. low activity (~80% reduction in mean activity level), was much greater than the magnitude of reduction in the time parameter, T, in the functional response model (30% reduction). This indicates that our behavioral observations of activity level underestimated actual activity level in consumption rate trials. This is made clear when considering that small crabs with zero activity during behavioral observation still consumed a substantial proportion of mussel prey (Figure 6.1a), which could happen if crabs observed inactive during the 3 h behavioral observation eventually became active over the course of 24 h consumption rate trials. The underestimation of activity level in consumption rate trials is even more apparent when considering that large crabs with a low level of activity (< 0.2) measured in behavioral observations consumed up to 90% of prey (Figure 6.1b). This further suggests that individual crabs could have a different timing of activity over consumption rate trials that were not fully captured in the 3 hour behavioral observation.

Griffen *et al.* (2012) found that the presence of toadfish predation threat enhanced the effect of crab activity level (referred to as refuge use, the inverse of activity level, in this study) on mussel consumption, but detected no significant effect of activity level on mussel consumption in the presence of threat at an alpha level of 0.05. Griffen *et al.* (2012) however used larger crabs (30-42 mm CW) than in the present study, which may explain our different results (i.e. a significant effect of activity level on mussel consumption for small crabs only). Though we did not detect such an interaction between predation threat and activity level as hypothesized, our study provides some of the first empirical evidence of the effects of predation threat from a higher order predator on the functional response of an intermediate predator (see also Alexander, Dick & O'Connor 2013). The majority of studies on trait-mediated trophic cascades test for a significant effect of trait change on intermediate predator consumption rate at a single prey density, rather than the range of prey densities needed to estimate the functional response (Bolker *et al.* 2003). As expected, the presence of the toadfish chemical cue reduced the crab functional response, but did not change the type of response (functional response remained type II). Similarly, Alexander *et al.* (2013) found that a fish predator chemical cue reduced the magnitude of an amphipod's functional response to isopod prey, but did not change the type of response. Further study is needed before broad conclusions can be drawn on the general effects of predation threat from a higher order predator on the functional response of an intermediate predator.

In general, hyperbolic type II functional responses that predict declining proportional prey consumption destabilize predator-prey population dynamics, while sigmoidal type III responses, that predict initially increasing and then decreasing proportional prey consumption, stabilize predator-prey dynamics (Murdoch & Oaten 1975; Juliano 2001). Previous work with the present study system showed that mud crabs exhibit type III functional responses when foraging in a more complex oyster shell habitat than used in the present study (Toscano & Griffen 2013). Furthermore, Toscano and Griffen (2013) demonstrated that oyster shell habitat structure limits large crabs (> 26 mm carapace width) from accessing mussel prey at low prey densities, thus driving differences in the attack rate parameter in the functional responses of small vs. large crabs. In the present study, the direct effects of crab body size on mussel consumption were likely minimized by our use of a less complex oyster shell habitat, and these differences in mesocosm setup can explain the difference in functional response type measured in this study compared to Toscano and Griffen (2013).

Several additional factors could influence predator activity level and functional responses that our lab experiment did not incorporate. First, interference between conspecific predators or other forms of predator-dependence are important in determining functional responses (Abrams & Ginzburg 2000), and in particular the prey consumption rates of crabs (Grabowski & Powers 2004, Griffen & Delaney 2007). Furthermore, the presence of additional non-prey species has been shown to modify consumption rates (Kratina, Vos & Anholt 2007). Lastly, our experiment used a single predator (toadfish), and it is unclear how predator diversity might affect the functional responses of mesopredators. All these influences could modify individual activity levels. Thus further work should test the importance of individual predator behavior for the functional response under more natural conditions with additional ecological complexity.

Finally, while using a non-mobile prey (mussels) allowed us to isolate the effects of individual predator behavior on the functional response, many predators are faced with the task of capturing mobile prey that exhibit their own individual behaviors (Sih & Christensen 2001). Thus the BTs of predators and prey can interact to determine prey consumption (Pruitt *et al.* 2012; McGhee, Pintor & Bell 2013; Sweeney *et al.* 2013). This has been demonstrated in a marine predator-prey system, where turban snails (*Chlorostoma funebralis*) that exhibit greater predator avoidance behavior have higher survivorship in the presence of active ocher sea stars (*Pisaster ochraceus*), while snails that exhibit reduced predator avoidance have higher survivorship in the presence of inactive seastars (Pruitt *et al.* 2012). Such interactions between predator and prey BTs are likely widespread in nature, and their effects on predator functional responses warrant research attention. Ultimately, measuring such BT-dependent functional responses and combining these measurements with ecological theory (e.g. individual-based models: Grimm & Railsback 2005; or state-dependent predator-prey models: e.g. Persson *et al.* 1998) offer a promising avenue whereby the long-term effects of individual behavior on population and community dynamics can be explored (Bolnick *et al.* 2011).

DATA ACCESSIBILITY

Data from this study is archived in the public archive Dryad (http://datadryad.org) at the DOI: doi:10.5061/dryad.vr14v.

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Table 6.1 Generalized linear mixed model (GLMM) testing the effects of fixed factors on the proportional mussel consumption of mud crabs (*n* = 447). Experimental block and an observation-level factor were included as random effects. Consumption was measured over 24 h in glass mesocosms set up to mimic oyster reef habitat. Eight levels of mussel prey density (2, 4, 6, 8, 12, 16, 24 and 36 mussels per tank) were offered to crabs.

Model factors	Estimate	SE	*t*	*P*
Response: Proportion of mussels consumed				
Mussel prey density	-0.075	0.004	-16.148	< 0.001
Crab activity level	3.914	1.249	3.133	0.002
Crab claw width	0.482	0.091	5.314	< 0.001
Toadfish cue	-0.314	0.113	-2.786	0.005
Temperature	0.083	0.033	2.503	0.012
Crab activity level × crab claw width	-0.619	0.203	-3.048	0.002

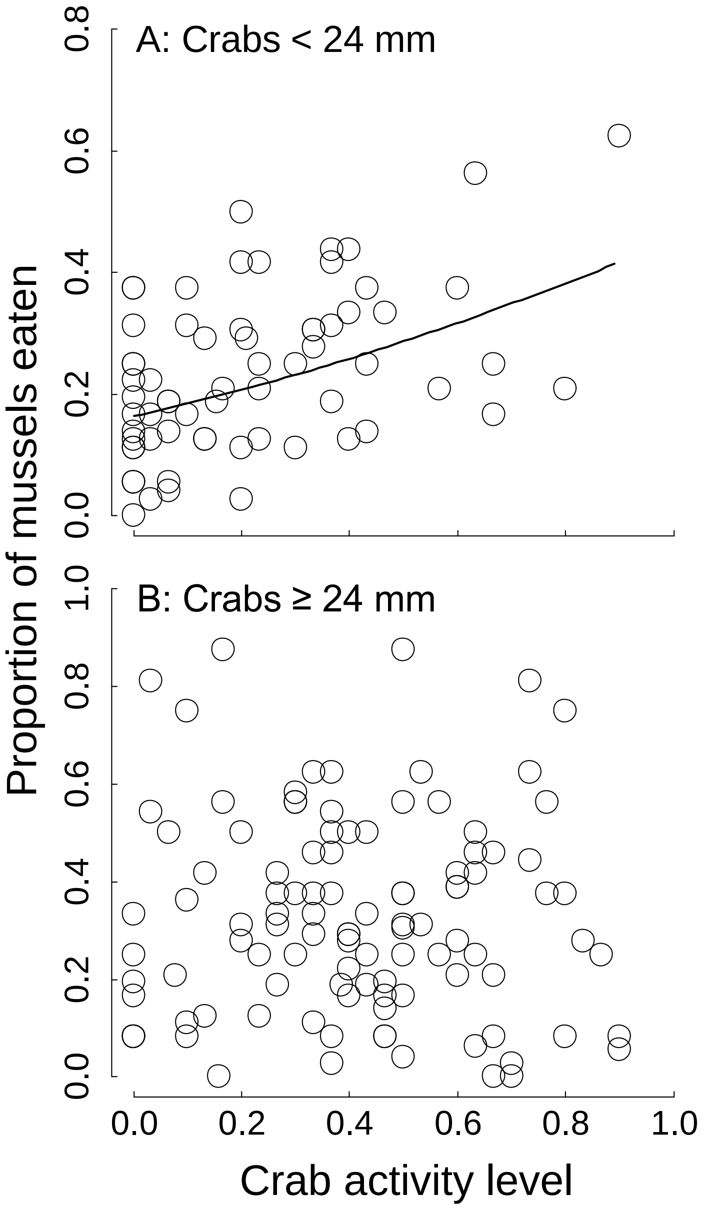

Figure 6.1 Effects of individual crab activity level on proportional mussel consumption by small (< 24 mm carapace width, CW; panel A) and large (≥ 24 mm CW; panel B) crabs at the 3 highest levels of mussel prey density (i.e. where crab consumption was not limited by prey density; 16, 24 and 36 mussels per tank). Line in panel A depicts significant relationship between crab activity level and proportional mussel consumption from binomial model fit to mussel consumption of small crabs at the 3 high mussel prey densities. Removal of the data point in the top-right corner of panel A had no effect on model coefficient estimates or significance of estimates presented in Table 6.1.

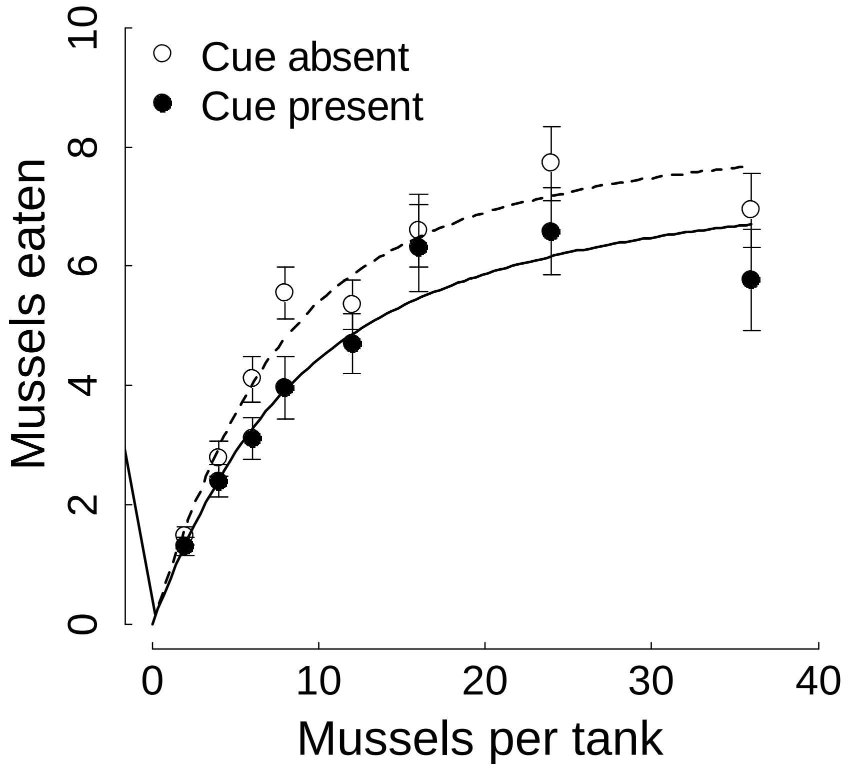

Figure 6.2 Mean number of mussels eaten ± 1 standard error by crabs in the absence (white dots; *n* = 240) and presence (black dots; *n* = 207) of a toadfish predator chemical cue. Sample sizes for the 8 prey density treatments (2, 4, 6, 8, 12, 16, 24 and 36 mussels per mesocosm) in the absence of the chemical cue were: *n* = 27, 32, 28, 29, 30, 30, 32 and 32, respectively. Sample sizes for the 8 prey density treatments in the presence of the chemical cue were: *n* = 26, 27, 26, 25, 27, 26, 24 and 26, respectively. Lines depict functional response model (eqn. 1) fits to the two groups of data (dotted line: model fit to consumption data in the absence of toadfish cue; black line: model fit to consumption data in the presence of toadfish cue).

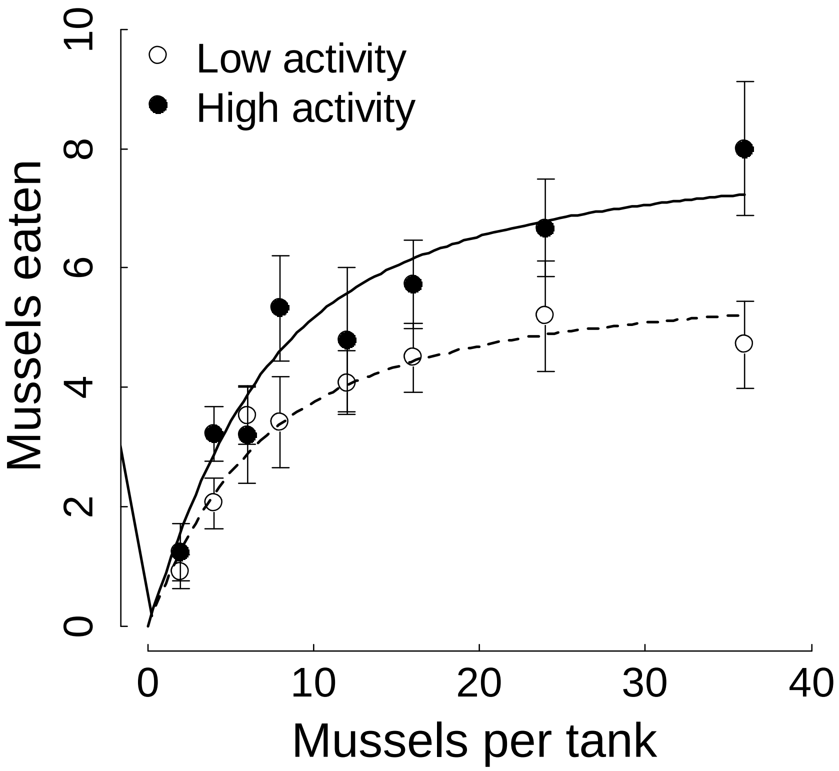

Figure 6.3 Mean number of mussels eaten ± 1 standard error by small crabs (< 24 mm carapace width) that exhibited low activity (≤ 0.22 activity, white dots; *n* = 104) vs. high activity (> 0.22 activity, black dots; *n* = 59). Sample sizes for the 8 prey density treatments (2, 4, 6, 8, 12, 16, 24 and 36 mussels per mesocosm) for crabs with low activity were: *n* = 11, 16, 15, 12, 12, 10, 10 and 18, respectively. Sample sizes for the 8 prey density treatments for crabs with high activity were: *n* = 4, 9, 5, 9, 5, 11, 9 and 7, respectively. Crab activity level was observed prior to measurement of consumption rate. Lines depict functional response model (eq. 1) fits to the two groups of data (dotted line: consumption by small crabs with low activity; black line: consumption by small crabs with high activity).

CHAPTER 7

PARASITE MODIFICATION OF PREDATOR FUNCTIONAL RESPONSE[6]

ABSTRACT

Parasite alteration of the host (predator) functional response provides a mechanism by which parasites can alter predator-prey population dynamics and stability. We tested the hypothesis that parasitic infection of a crab (*Eurypanopeus depressus*) by a rhizocephalan barnacle (*Loxothylacus panopei*) can modify the crab's functional response to mussel (*Brachidontes exustus*) prey and investigated behavioral mechanisms behind a potential change in the response. Infection dramatically reduced mussel consumption by crabs across mussel densities, resulting in a decreased attack rate parameter and a nearly 8-fold reduction in maximum consumption (i.e. the asymptote, or inverse of the handling time parameter) in a type II functional response model. To test whether increased handling time of infected crabs drove the decrease in maximum consumption rate, we independently measured handling time through observation. Infection had no effect on handling time and thus could not explain the reduction in consumption. Infection did however increase the time that it took crabs to begin handling prey after the start of the handling time experiment. Furthermore, crabs harboring relatively larger parasites remained inactive longer before making contact with prey. This behavioral modification likely contributed to the reduced mussel consumption of infected crabs. A field survey

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[6] Toscano, B.J., Newsome, B. and B.D. Griffen. 2014. *Oecologia*. 175: 345-352. Reprinted here with permission of publisher.

revealed that 20% of crabs inhabiting oyster reefs at the study site (North Inlet estuary) are infected by the barnacle parasite, indicating that parasite infection could have a substantial effect on the population level crab-mussel interaction.

INTRODUCTION

Parasites are increasingly recognized for the important roles they play in natural food webs (Minchella and Scott 1991; Wood et al. 2007; Lafferty et al. 2008). Parasites can make up a substantial portion of food web biomass compared to free-living species (Kuris et al. 2008), and their inclusion in food webs as independent nodes modifies patterns of connectance and food chain length (Lafferty et al. 2008). They can also directly alter the reproductive success and survivorship of their hosts (Minchella and Scott 1991; Marzal et al. 2005), thus mediating host population dynamics and the dynamics of communities.

Parasites can also have indirect effects on food webs by modifying the behavior, physiology, morphology and life-history (i.e. the traits) of their hosts (Holmes and Bethel 1972; Poulin and Thomas 1999; Fitze et al. 2004; Wood et al. 2007; Repetto and Griffen 2012). These effects on hosts can cascade to affect the species interactions that hosts are involved in (Minchella and Scott 1991). For example, trematode parasite infection increases the frequency of conspicuous behaviors exhibited by killifish (Lafferty and Morris 1996). Birds, the final hosts of the trematode parasite, preferentially consume infected killifish due to this behavioral modification (Lafferty and Morris 1996). Similarly, infection by an acanthocephalan parasite changes the color and behavior of amphipods, which in turn increases their susceptibility to predation by stickleback fish, the final host of the parasite (Bakker et al. 1997). Despite an abundance of studies on the effects of parasites on host traits, it remains unclear how trait-mediated effects of parasites can scale up to affect the long-term dynamics and stability of predator-prey populations and food webs (Lafferty et al. 2008).

A likely factor that may link parasite impacts on the individual host to broader impacts on predator-prey or food web dynamics is the predator functional response (Dick et al. 2010; Haddaway et al. 2012). The functional response describes how a predator's *per capita* consumption rate of prey changes with the local density of prey (Holling 1959). This response is behavioral, depending on the predator's rate of attack and the time it takes to handle an individual prey (Jeschke et al. 2002). The functional response is a critical component of population models of species interactions, and the precise shape and parameter values of the functional response are major determinants of short and long-term predator-prey population stability in these models (Murdoch and Oaten 1975; Abrams 2000). For example, a hyperbolic response curve (i.e. type II functional response) typically destabilizes predator-prey dynamics, while a sigmoidal response curve (i.e. type III response), often driven by a refuge from predation at low prey densities (Sih 1987), typically stabilizes interactions (Murdoch and Oaten 1975).

Numerous studies have demonstrated strong effects of parasites on predator-prey interactions (Lafferty 1992; Bernot and Lamberti 2008), yet these studies typically examine predation as a mechanism for parasite transmission between hosts, and rarely consider parasites as interaction modifiers (sensu Wootton 1994) of predator-prey systems in a food web context (but see Wood et al. 2007; Bernot and Lamberti 2008). Indeed, only a few studies (Dick et al. 2010; Haddaway et al. 2012) have examined how parasites affect the consumption rates of their predatory hosts across prey densities, i.e.

the predator functional response. Parasite alteration of the host functional response is therefore an understudied pathway by which parasites can indirectly alter the dynamics and stability properties of predator-prey populations. Considering the ubiquity of parasites in food webs and pervasive effects of parasite infection on host behavior (Holmes and Bethel 1972; Poulin and Thomas 1999), parasite modification of host functional responses could be a common trait-mediated indirect interaction in nature.

In the present study, we examined the impact of an invasive rhizocephalan barnacle parasite (*Loxothylacus panopei*) on the functional response of its host, the flat-backed mud crab (*Eurypanopeus depressus*) preying on scorched mussels (*Brachidontes exustus*). Flat-backed mud crabs are important predators of scorched mussels in oyster reefs and other structurally complex habitats along the Gulf and Eastern Coasts of the United States (McDonald 1982; Williams 1984; Lee and Foighil 2004). The parasitic barnacle *L. panopei* was originally restricted to the Gulf of Mexico, but invaded the East coast of the United States in 1964, potentially through shipments of oysters that also carried infected crabs from the Gulf of Mexico (Van Engel et al. 1966). Rhizocephalan barnacles such as *L. panopei* are macroparasites that exclusively infect crustaceans and mainly crabs (Overstreet 1983). Female barnacle cyprid larvae settle on a recently molted crab and produce a system of branching roots throughout the crab's body cavity (O'Brien and van Wyk 1985). After this internal phase is complete, a sac-like externa (the parasite's reproductive body) is extruded under the crab's abdomen. Male cyprid larvae then settle on and fertilize this externa. Common effects of rhizocephalan barnacles on crab hosts include the inhibition or cessation of growth as well as the castration of both female and male crabs (O'Brien and van Wyk 1985). Thus parasite infection precludes reproduction but allows crabs to survive and interact ecologically with conspecifics and other species (Lafferty and Kuris 2009).

We compared the mussel consumption rate of uninfected and infected crabs across mussel densities to examine the hypothesis that parasite infection can alter the predator (host) functional response. We then tested whether increased handling time and/or reaction time (i.e. the time it took crabs to respond to prey) of infected crabs drove the decrease in prey consumption associated with parasite infection. Finally, we surveyed parasite prevalence in the field, providing some insight into the potential population impacts of parasite alteration of the functional response and thus the crab-mussel predator-prey interaction.

METHODS

We tested the effects of barnacle (*Loxothylaccus panopei)* parasite infection on the interaction between the flat-backed mud crab (*Eurypanopeus depressus)* and its prey, the scorched mussel (*Brachidontes exustus*). All animals used in experiments were collected from intertidal oyster reefs in tidal creeks throughout North Inlet estuary (33°20’N, 79°10’W), Georgetown, South Carolina. North Inlet is a relatively pristine salt marsh consisting of ocean-dominated tidal creeks with a high average salinity (~34 ppt) and a diurnal tidal cycle (Dame et al. 1986). We ran experiments in the screened-in, outdoor wet laboratory at the adjacent Baruch Marine Field Laboratory. The field survey of parasite prevalence was also conducted in intertidal reefs throughout North Inlet. Experiments and field sampling were conducted from June through August 2012.

Functional response experiment

We first measured the functional responses of uninfected and infected mud crabs (8-13.5 mm carapace width) foraging on the scorched mussel (4-7 mm shell length). Mussels in this size range are abundant in oyster clusters throughout the study site (Toscano and Newsome, personal observations). We identified infected crabs by the presence of parasite externae, indicative of a mature stage of parasite infection (Alvarez et al. 1995). However, we cannot discount the possibility that uninfected crabs were actually in the immature, internal stage of infection. Mussels were offered to crabs in 8 densities: 2, 4, 6, 8, 10, 16, 24 and 32 mussels per experimental chamber. Trials were run in a randomized complete block design and each treatment was replicated a total of twelve times (12 blocks). Individual crabs were used once in this experiment.

We ran functional response experiments in plastic chambers (15 cm length × 13 cm width × 7.6 cm height) containing oyster shells to simulate the structure of natural oyster reef habitat. Each chamber received five cleaned and dried oyster shells (7-10 cm shell length) to provide a relatively consistent substrate for mussels to attach to. The necessary number of mussels for a given treatment was evenly distributed over the shell throughout each chamber. Experimental chambers were then placed in a larger cylindrical flow-through seawater tank (97 cm diameter × 41 cm depth, water depth: 25 cm) and mussels were allowed to attach to oyster shells over a 12 hour period. Crabs were starved for a 24 hour period before placement in the chambers to standardize hunger levels. After starvation, crabs were allowed to forage for a 13 hour period overnight, generally from 1900-0800 h. Chambers received a constant flow of unfiltered sea water from North Inlet throughout this period. After 13 hours, the number of remaining mussels was recorded. All dead mussels showed signs of being preyed upon by crabs (cracked shells).

Functional response models were fit separately to uninfected and infected crabs, allowing us to examine the effects of parasite infection on the functional response. First, to determine the type of functional response (i.e. type I, II or III), we used polynomial logistic regression on the proportion of prey consumed as a function of prey density (Juliano 2001). For both uninfected and infected crabs, the first order term in this regression was significantly negative (i.e. declining proportion consumed at very low prey densities), indicative of a type II functional response (Juliano 2001). Because prey were depleted over the 24 h that crabs foraged and not replaced, a Rogers type II functional response model that accounts for prey depletion was fit separately to uninfected and infected crabs (Rogers 1972):

$$N_e = N_o\left(1 - \exp\left(\alpha\left(N_e T_h - PT\right)\right)\right) \qquad \text{eqn. 1}$$

where N_e is the number of prey eaten, N_0 is the initial prey density, α is attack rate, T_h is handling time, P is the number of predator individuals (set to 1), and T is the experimental duration (set to 13 h). Eqn. 1 is a recursive function of N_e, and so we used the Lambert W function to implement the model (see Bolker 2008 for details):

$$N_e = N_o \frac{W\left(\alpha T_h N_o \exp^{-\alpha\left(PT - T_h N_o\right)}\right)}{\alpha T_h} \qquad \text{eqn. 2}$$

where *W* is the Lambert W function and all other parameters are the same as in eqn. 1. This functional response model was fit to prey consumption data using maximum likelihood estimation with binomial errors in the statistical software R (package “bblme”).

Handling and reaction time experiment

During the functional response experiment, we noticed that the maximum consumption rate of infected crabs was substantially lower than that of uninfected crabs. In traditional functional response models, maximum consumption rate is equivalent to the inverse of handling time, or the time it takes to capture, subdue and consume an individual prey (Juliano 2001). These models assume that predators forage continuously (Tully et al. 2005; Jeschke et al. 2002), and in such a situation, predators are only limited by handling time at high prey densities. Thus the reduced maximum consumption rate of infected crabs suggested an increase in the handling time of infected crabs. To test this, we observed and compared the handling time of uninfected and infected crabs independently of the functional response experiment.

Crabs and mussels used in this experiment fell within the same size ranges used in the functional response experiment. We recorded the carapace width of each crab and length of each mussel before trials and crabs were starved for 24 hours to standardize hunger levels. The handling time of crabs was observed in cylindrical glass containers (6 cm diameter × 5 cm height) with one crab and one mussel per container. Ten crabs were observed at once and the experiment was conducted over multiple nights. Handling time was observed at night (generally from 1900-2400 h) under a red light to minimize disturbance to crabs (Griffen et al. 2012). Crabs were allowed to acclimate for five minutes before exposure to a mussel. Once a mussel was introduced, we recorded the time it took for a crab to make contact with the mussel (reaction time), as well as the time it took to completely consume the mussel after the first contact (handling time). Crabs were given 1 h to begin handling mussels before the experiment was terminated. Crabs that did not begin handling mussels during this time were excluded from the analysis. The reaction time of uninfected and infected crabs was measured and compared to test whether a longer period of inactivity before reacting to mussel prey contributed to the decreased consumption of infected crabs.

After this experiment, we removed and weighed the parasite externae of infected crabs to test whether the externa mass relative to the crab's body mass influenced the handling or reaction time of infected crabs. This could be expected if the size of the externa is indicative of the level of parasite infection, or acts as a physical impediment to crab handling of mussels. We compared the dry weight of the externa to the dry weight of the remaining crab body to determine relative parasite mass. Both the removed externae and crab bodies were dried in an oven at 60° C for 72 h before measurement of dry weight.

We used linear mixed models (LMM) to test the fixed effects of parasite infection and the crab:mussel size ratio on handling and reaction time. Data were normally distributed, justifying use of a Gaussian distribution. We also used LMM to test the fixed effects of the crab:mussel size ratio and the parasite:crab mass ratio on the handling and reaction time of infected crabs. The day of observation was modeled as a random factor in all models to control for pseudoreplication. We fit models with and without fixed factors while retaining the random factor (day of observation) and compared models using Akaike's information criterion (AIC) to determine whether additional factors improved the fit despite increased model complexity.

Field survey

We surveyed the prevalence of the barnacle parasite in flat-backed mud crabs in the field. This survey allowed us to determine the overall rate of parasite infection in crabs, as well as some intrinsic factors associated with infection. We sampled crabs in haphazardly placed quadrats (0.25 m^2) in intertidal oyster reefs throughout North Inlet. Nine oyster reefs were sampled in total and 6 quadrat samples were taken from each reef (a total of 54 quadrat samples). All quadrat samples were taken from the upper intertidal sections of reefs. Within each quadrat, all *E. depressus* were removed by hand and their carapace width, sex, and infection status was recorded. We recorded the presence of crabs below 5 mm, but were unable to accurately measure the carapace width or discern the sex of these crabs.

We used a generalized linear mixed model (GLMM) with a binomial error distribution to test the effect of crab sex on the probability of parasite infection. A binomial error distribution was used to model binary (presence-absence) data. Crab sex was modeled as a fixed factor and quadrat was modeled as a random factor, with individual infection status (uninfected or infected) as the response variable. We used a non-parametric Kolmogorov-Smirnov test to test for a difference in the size distribution of uninfected and infected crabs. All statistical analyses were conducted in R version 2.15.2 (R Development Core Team).

RESULTS

Functional response

Parasite infection dramatically reduced the mussel consumption rate of crabs across mussel prey densities (Figure 7.1). In a type II functional response model fit to infected crabs, this reduction in mussel consumption was manifested as a ~30% decrease in the attack rate parameter and a nearly 8-fold increase in the handling time parameter compared to uninfected crabs.

Handling time

The predator to prey size ratio was an important predictor of individual crab handling time measured through observation, while parasite infection (i.e. uninfected or infected) had little effect on handling time (Figure 7.2). Handling time was best explained with a model containing the crab:mussel size ratio as a fixed effect (weight = 0.923); the crab:mussel size ratio reduced handling time (estimate ±1 SE = -0.106 ± 0.016; Figure 7.2) in this model. This model was substantially better than the model containing both the crab:mussel size ratio and parasite infection as fixed effects (ΔAIC = 4.96, weight = 0.077), as well as the model containing only parasite infection as a fixed effect (ΔAIC = 32.34, weight = 0.00).

In infected crabs, the predator to prey size ratio was again an important predictor of handling time. The linear model containing this fixed factor (weight = 0.504, crab:mussel size ratio estimate ±1 SE = -0.122 ± 0.029) performed similarly to the model containing both the crab:mussel size ratio and the parasite:crab mass ratio as fixed factors (ΔAIC = 0.10, weight = 0.481, crab:mussel size ratio estimate ±1 SE = -0.121 ± 0.030, parasite:crab mass ratio estimate ±1 SE = -0.251 ± 1.293), and substantially better than the model containing just the parasite:crab mass ratio as a fixed factor (ΔAIC = 7.01, weight = 0.015).

Reaction time

The reaction time of crabs (i.e. latency in responding to mussel prey) was best predicted by a model containing parasite infection as a fixed effect (weight = 0.808, parasite infection estimate ±1 SE = 0.050 ± 0.029; Figure 7.3); this model was substantially better than both the model containing the crab:mussel size ratio as a fixed effect (ΔAIC = 3.11, weight = 0.171) and the model containing both these factors as fixed effects (ΔAIC = 7.26, weight = 0.021). Furthermore, though excluded from the analysis, 23 infected crabs never began handling mussels over the duration of the experiment (1 h) compared to 13 uninfected crabs.

In infected crabs, reaction time was best predicted by a linear model containing the parasite:crab mass ratio as a fixed factor (weight = 0.966). This model performed substantially better than the model containing both the parasite:crab mass ratio and the crab:mussel size ratio as fixed factors (ΔAIC = 7.16, weight = 0.027), and the model containing only the crab:mussel size ratio as a fixed factor (ΔAIC = 9.84, weight = 0.007). In the best fit model, infected crabs with relatively larger parasites took longer to begin handling mussels (parasite:crab mass ratio estimate ±1 SE = 2.590 ± 1.615; Figure 7.3).

Field survey

Nearly 20% of crabs sampled in North Inlet estuary were infected by the barnacle parasite (86 out of 446 crabs). Crab sex had a significant effect (GLMM: estimate ± 1 SE = -0.991 ± 0.299, z = -3.319, p < 0.001) on the probability of infection. Specifically, the sex ratio of infected crabs was heavily skewed towards females (Figure 7.4). The size distribution of infected crabs also differed from that of uninfected crabs (KS-test: $D = 0.486$, $p < 0.001$). The smallest infected crab found was 7.2 mm carapace width, while uninfected crabs below 7 mm carapace width were abundant (Figure 7.4).

DISCUSSION

We found that barnacle parasite infection drastically reduced the magnitude of the crab functional response to mussel prey. The most striking effect of infection was a nearly 8-fold decrease in the maximum consumption rate (i.e. the inverse of the handling time model parameter) of infected crabs. Two other studies (Dick et al. 2010; Haddaway et al. 2012) have tested the effects of parasite infection on the host functional response to prey. Dick et al. (2010) found that acanthocephalan parasite infection actually increased the functional response of an amphipod host foraging on isopods, though the mechanism behind this effect was not investigated. Specifically, infection increased attack rate and handling time parameters in a type II functional response model (Dick et al. 2010). Similar to our study, Haddaway et al. (2012) found that microsporidian parasite infection of crayfish foraging on amphipods reduced attack rate and handling time parameters in a type II functional response model, though neither of these studies found as strong an effect of infection on host prey consumption as in the present study.

We identified infected crabs by the presence of parasite externae and therefore failed to detect whether uninfected crabs were actually in the immature, internal stage of parasite infection. Furthermore, we could not find evidence of the internal portion of the parasite in our dissections of these “uninfected” crabs, and thus could not determine the prevalence of this stage of infection. The internal stage of infection lasts approximately

30 days on average in a different species of Xanthid crab, *Rhithropanopeus harrisii* (Walker et al. 1992; Alvarez et al. 1995). If crabs in the immature stage of infection exhibited reduced prey consumption similar to crabs in the mature stage of infection, our inclusion of these crabs as "uninfected" would reduce the magnitude of the negative effect of infection on the functional response. Our results therefore represent a conservative estimate of the effects of parasite infection on crab consumption rates. However, rhizocephalan parasite effects on the grooming and burrowing behavior of a Portunid crab (*Charybdis longicollis*) were only observed in crabs harboring externae (Innocenti et al. 1998).

We further tested the possibility that increased handling time of infected crabs drove the reduction in consumption by comparing the mussel handling time of uninfected and infected crabs independently of the functional response experiment. Parasite infection had no effect on handling time measured through observation and therefore could not explain the reduction in consumption. Infected crabs did however show some signs of increased latency in reacting to mussel prey in the handling time experiment. Specifically, infection increased the time that it took crabs to begin handling prey after the start of the experiment, and infected crabs with larger parasites took longer to make contact with mussel prey than crabs with relatively smaller parasites. This finding is consistent with behavioral observations indicating that infected crabs spend less time active and more time hiding compared to uninfected crabs (Newsome, personal observations). A similar reduction in activity concomitant with rhizocephalan barnacle infection has been observed in shore crabs (*Carcinus maenas*) (Mouritsen and Jensen 2006). Typical functional response models, including the type II model used here, do not incorporate such non-foraging activities (Jeschke et al. 2002) and instead assume that a predator's time is divided between searching for prey and handling prey, though this assumption is rarely tested (Abrams 1990; Tully et al. 2005). Thus while the type II functional response model described consumption data well in the present study, it did not explain the underlying mechanism behind the reduction in mussel consumption of infected crabs, and we think this reduced consumption is due in part to reduced foraging activity of infected crabs (i.e. violation of the assumption of constant foraging activity).

Several non-mutually exclusive explanations exist for the effects of infection on crab behavior and mussel consumption revealed in the present study. First, parasite infection may reduce the crab's energy demands. Previous work has shown that infection by rhizocephalan barnacles can lead to the reduction or cessation of crab somatic growth, potentially due to the reallocation of energy to the parasite (O'Brien and van Wyk 1985). Thus it is possible that this reduced need for energy for growth could reduce crab foraging effort if the parasite cost is less than the savings of reduced growth. Second, rhizocephalan roots can invade all organs and tissues of the host and the number of rootlets increases over the course of the infection (Bortolini and Alvarez 2008). Therefore, the internal portion of the parasite could compete for space with other internal organs such as the crab's gut, potentially reducing space for food storage before or during digestion. Our dissections of infected crabs however revealed no clear effects of crowding, and so we think this explanation is unlikely. Third, parasite infection could reduce the crab host's digestive capabilities, thereby increasing digestion time and reducing foraging effort and prey consumption (see also Wood et al. 2007). Rhizocephalan parasite infection of blue crabs (*Callinectes sapidus*) damages the crab hepatopancreas and causes significant loss of hepatopancreas tissue (Bortolini and Alvarez 2008). This organ serves multiple functions in digestion, including the secretion of digestive enzymes and absorption of nutrients, and therefore, any damage to the hepatopancreas could reduce the rate of digestion. Lastly, parasite infection could impair the neurosensory capabilities of crabs, altering their behavior and foraging ability.

Potential effects of parasite infection on crab-mussel population dynamics

Twenty percent of crabs sampled harbored parasite externae, indicative of the mature stage of parasitic infection (Alvarez et al. 1995). Again, our survey did not examine the immature, internal stage of parasite infection and therefore likely underestimated actual parasite prevalence. Our survey also revealed that the sex ratio of infected crabs was heavily skewed towards females. This is potentially due to the parasitic feminization of male crabs, a common effect of rhizocephalan barnacles on crab hosts (O'Brien and van Wyk 1985). Furthermore, in accordance with another study (Alvarez et al. 1995), we found that infected crabs were intermediate in body size compared to uninfected crabs (i.e. few crabs < 7 and > 15 mm carapace width). This is likely due to the reduced growth rate or cessation of growth in infected crabs (O'Brien and van Wyk 1985).

Considering the prevalence of parasite infection in flat-backed mud crabs and strong effects of infection on the crab functional response, the parasitic barnacle could have substantial effects on the long-term dynamics of the crab-mussel interaction. Rhizocephalan barnacles castrate their crab hosts, thus precluding reproduction by infected individuals (O'Brien and van Wyk 1985). Therefore, reduced consumption by infected crabs cannot directly feedback to affect the population dynamics of crabs (i.e. the numerical response) as modeled in a typical Lotka-Volterra predator-prey framework.

However, reduced mussel consumption of infected crabs could provide some predation refuge for mussels, allowing mussel density to increase and indirectly enhancing the population growth of uninfected crabs. These predictions are speculative and require further study in the field. Interestingly, the larvae of the parasitic barnacle *L. panopei* cannot tolerate low salinity (Reisser and Forward 1991). Therefore spatial and temporal variation in salinity could mediate barnacle parasite effects on crab-mussel dynamics.

In sum, parasite modification of host behavior and physiology is widespread (Poulin and Thomas 1999), and these trait changes likely influence host functional responses (Dick et al. 2010; Haddaway et al. 2012; the present study), and therefore the dynamics of predator-prey populations and energy flow in food webs. More broadly, parasite modification of the host functional response is part of a general class of trait-mediated indirect interactions driven by parasite alteration of host traits. This class of interactions includes parasite modification of host ecosystem engineering (Thomas et al. 1999), as well as parasite mediation of interspecific competition involving hosts (Park 1948; Schall 1992). Future studies of such parasite-mediated interactions could benefit by measuring the curvature of responses and trade-offs as we have done here, as opposed to two-level experiments (e.g. absence vs. presence, or “low” vs. “high”). Such multi-level experiments allow long-term, population-level prediction in ecological models (Bolker et al. 2003), and will therefore enhance our understanding of the key functional roles of parasites in community and food web ecology (Lafferty et al. 2008).

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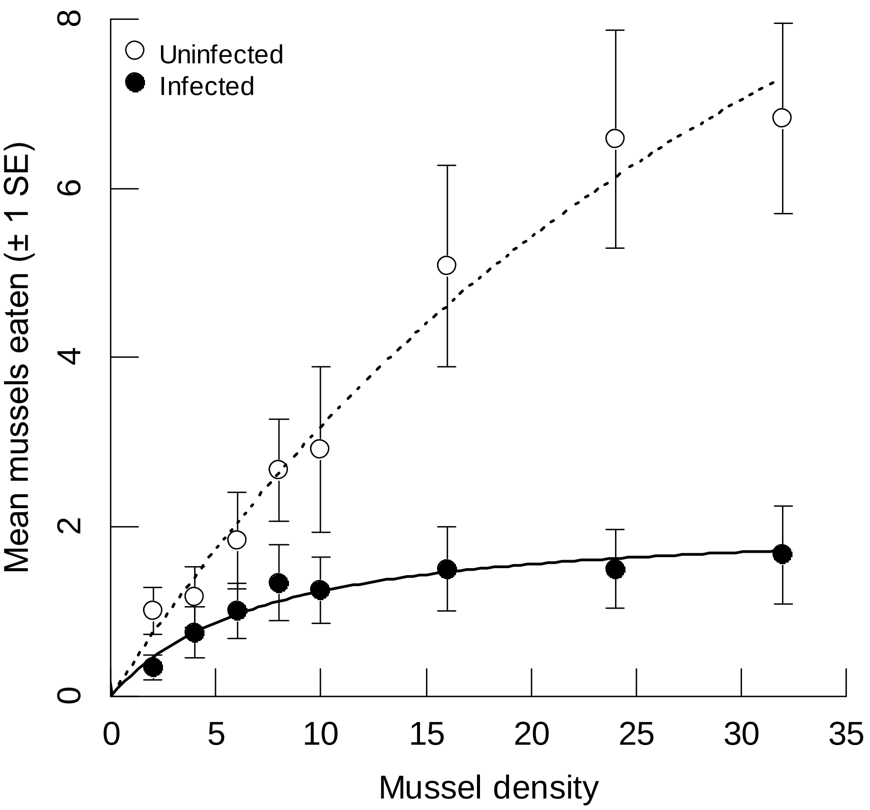

Figure 7.1 Effect of barnacle parasite (*Loxothylaccus panopei*) infection on the functional response of a mud crab predator (*Eurypanopeus depressus)* foraging on mussel (*Brachidontes exustus*) prey. Points indicate mean consumption ± 1 SE of uninfected (white points; n = 96) and infected crabs (black points; n = 96). Lines depict functional response model (Eqn. 1) fits to mussel consumption data of uninfected (dotted line) and infected (black line) crabs. Mussels were offered to crabs in 8 densities (2, 4, 6, 8, 10, 16, 24, and 32 mussels per chamber) and crabs were allowed to forage for 13 h

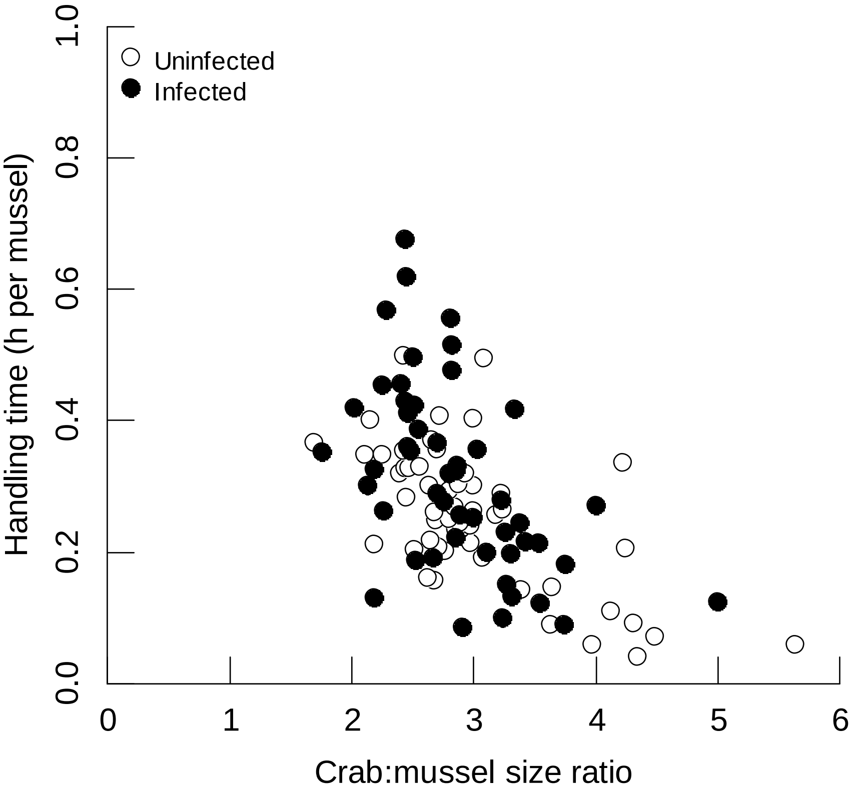

Figure 7.2 The relationship between the crab:mussel size ratio and the handling time of mussel prey by uninfected (white points; n = 53) and infected (black points; n = 55) mud crabs. Handling time was measured through observation of predator-prey interactions

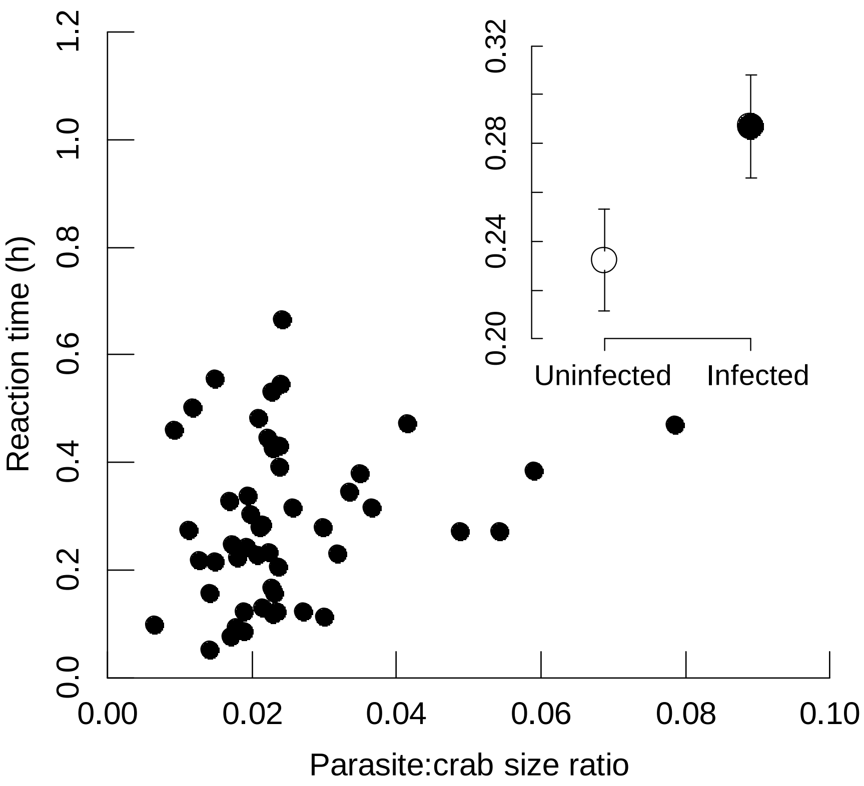

Figure 7.3 Effect of the barnacle parasite on reaction time (i.e. the time it took to begin handling mussels after the start of the handling time experiment) of mud crabs. Main graph depicts the influence of the parasite:crab size ratio on the reaction time of infected crabs (n = 55). Inset graph depicts the influence of parasite infection on the reaction time of uninfected (white points; n = 53) and infected (black points; n = 55) crabs. Reaction time was measured through observation of predator-prey interactions

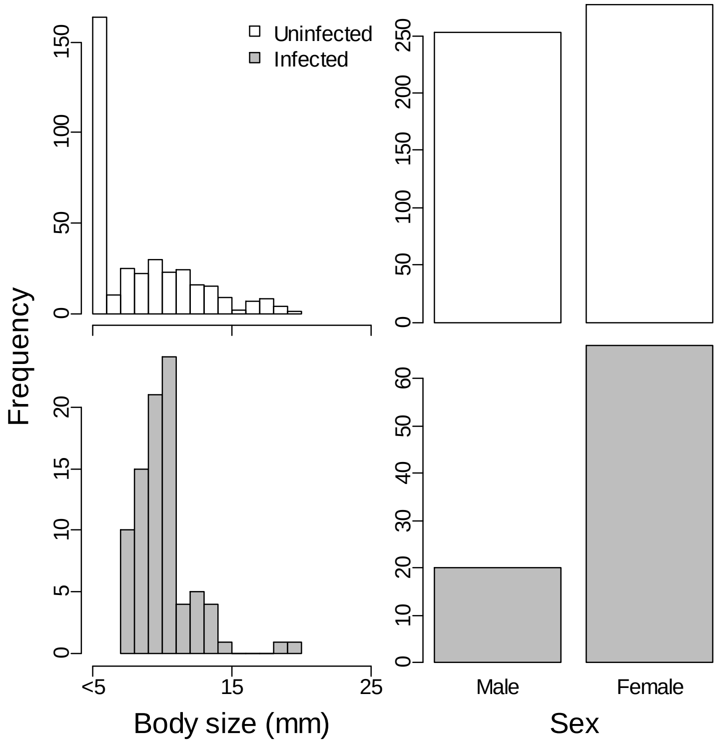

Figure 7.4 Comparison of the size structure and sex ratio of uninfected (white bars; n = 360) and infected (gray bars; n = 86) mud crabs collected from intertidal oyster reefs in North Inlet estuary

CHAPTER 8

CONCLUSION

Predation is a critical process in ecosystems (Terborgh and Estes 2010), and the strength of predator-prey interactions is major determinant of community stability (MacArthur 1955, Paine 1980). Particularly in oyster reefs, trophic cascades between top predators (e.g. fish), mesopredators (e.g. Xanthid crabs), and bivalve prey are a major determinant of community structure (Grabowksi 2004, Kimbro et al. 2014). The strength of trophic cascades in reefs has been shown to vary due to the influences of habitat structure and interactions between multiple predators (Grabowski et al. 2008), as well as resource supply and environmental conditions (Kimbro et al. 2014). Nevertheless, the effects of individual variation on these cascades remain relatively unexplored (but see Griffen et al. 2012).

The objective of this dissertation was to examine the importance of individual-level phenotypic variation for predator-prey interactions that influence community structure in oyster reefs. I accomplished this using a series of experiments testing the effects of individual variation in Xanthid crab body size, behavioral traits and parasite infection on their interactions with natural enemies (e.g. toadfish [*Opsanus tau*] and the barnance parasite [*Loxothylacus panopaei*]) and bivalve prey, including filter-feeding oysters (*Crassostra virginica*) and several species of mussels that inhabit oyster reefs.

My work demonstrates that individual-level variation influences the strength of predator-prey interactions and trophic cascades in intertidal oyster reefs in North Inlet estuary. Body size, for example, varies widely in populations of the Xanthid crab *Panopeus hersbtii* in North Inlet (Dame and Vernberg 1982, McDonald 1982), and humans are potentially influencing the population size distribution of these crabs through the destructive harvest of oysters (Chapter 2). In Chapter 2, I showed that, at the population-level, the size distribution of crabs influences their consumptive effects on the bivalve community in reefs. Furthermore, crab body size interacts with reef habitat structure to determine the individual bivalve consumption rate of crabs (Chapter 3).

Behavioral traits, such as refuge use and activity level, also vary widely among individual crabs, and this variation is consistent after substantial time in the field (Chapter 4). While some variation in behavior is explained by crab body size, there is additional variation that is unexplainable based on aspects of crab phenotype, such as individual physiology (Chapter 5), qualifying crab activity level as a behavioral type (Sih et al. 2004). Importantly, individual variation in activity level influences the mussel consumption rate of small, but not large crabs (Chapter 6), suggesting size-dependent effects of this behavioral type on the crab-mussel predator-prey interaction.

Lastly, a barnacle parasite which infects the Xanthid crab *Eurypanopeus depressus* induces behavioral changes dependent on the size of the parasite relative to the size of the infected crab (Chapter 7). This behavioral modification dramatically reduces the mussel consumption rate of crabs, thereby reducing the strength of the crab-mussel interaction. All three aspects of individual variation (body size, behavioral traits and parasite infection) influence the crab functional response to mussel prey density (Chapters 2, 6 and 7). When combined with the numerical response (i.e. the response of predator density to prey density), the functional response permits scaling up from predator and prey behavioral traits and individual prey consumption rates to the population level (Holling 1959, Murdoch and Oaten 1975, Brose 2010). In sum, my findings suggest that individual phenotypic variation can influence the population dynamics of crabs and the species they interact with in oyster reefs. Specifically, this body of work contributes to the following research themes.

1. *Body size constraints on species interactions*

Increasing prey size and diet breadth with predator size is a common feature of natural food webs (Hardy 1924, Werner and Gilliam 1984). In Chapter 2, I used a field experiment to show that large crabs (*Panopeus hersbtii*) consume larger, adult bivalves, which smaller crabs cannot. Thus large crabs are functionally unique in their ability to consume large bivalves, making their presence critical for top-down control of the bivalve prey community in reefs. Due to the increase in diet breadth with crab size and overlap in resource use among crab size classes, body size diversity had little effect on bivalve prey consumption in this study. However, in a scenario where different size classes partition food resources (Polis 1984, Werner and Gilliam 1984), aggregate prey consumption should increase with size diversity, in part by reducing intra-size class competition (Finke and Snyder 2008, Griffin et al. 2008, Ye et al. 2013). Thus, size diversity, an underappreciated aspect of biodiversity, should be considered when examining the ecological effects of predator populations (Ye et al. 2013).

In Chapter 3, I tested how crab body size affected the crab functional response to mussel prey density in structurally complex oyster reef habitat. Both body size (Kalinkat et al. 2013) and habitat structure (Anderson 2001) are important influences on predator functional responses. Predator-prey size ratios affect attack rate and handling parameters

(Brose 2010), while habitat structure can serve as a refuge for prey at low prey densities, inducing a sigmoidal type-3 functional response that can stabilize predator-prey interactions (Holling 1959, Murdoch and Oaten 1975, Sih 1987). My work showed that these factors can interact to determine the predator functional response. Specifically, reef habitat structure physically restricted large crabs from accessing mussel prey at low prey densities, reducing their mussel consumption rate relative to small crabs. In contrast, mussels saturated the oyster shell refuge at high mussel densities, forcing mussels into areas where they were vulnerable to predation by large crabs.

Furthermore, in a field survey (Chapter 2), I showed that large crabs tend to inhabit portions of reefs where the height of the surficial oyster shell layer is relatively tall. Because the destructive harvest of oysters by humans reduces the height of this shell layer (Lenihan and Peterson 1998, Lenihan and Micheli 2000, Lenihan and Peterson 2004), oyster harvest could compromise trophic transfer through the loss of large crabs, though this prediction remains to be tested in the field.

2. *Individual behavior, a departure from optimality theory*

In Chapter 4, I measured individual variation in crab refuge use behavior. I also examined some internal and external influences on refuge use, and measured the temporal consistency (i.e. repeatability) of this behavioral trait in the field. The majority of studies testing for the temporal consistency of individual behavior do so while holding animals in the lab (Archard and Braithwaite 2010); this approach removes the influences of fluctuating environmental conditions that animals experience in the field (Archard and Braithwaite 2010), and potentially conditions animals to the lab setting, further distorting measurements of repeatability (Butler et al. 2006). I found that refuge use varied widely among crabs, and a considerable portion of this variation was dependent on crab body size. Large crabs used the refuge less than small crabs, likely due to their lower susceptibility to predation in the field (Hill and Weissburg 2013). Using mark-recapture, I demonstrated that crab refuge use behavior is consistent for up to 3 months in the field. Furthermore, time spent in the field had no effect on the consistency of behavior. This work sheds light on some of the drivers of natural variation in crab behavior, and provides rare field evidence for temporal consistency of individual behavior in an invertebrate species, which are underrepresented in studies of animal personality relative to vertebrates (Kralj-Fišer and Schuett 2014).

In Chapter 5, I tested whether the activity level of individual crabs could be predicted by their metabolic rate. Because behavioral traits such as activity and aggressiveness are energetically costly, individual differences in behavior could require different rates of energy metabolism (Careau et al. 2008, Biro and Stamps 2010). This link between individual behavior and energetics is potentially part of a broader covariation of behavioral, physiological and life-history traits referred to as the 'pace-of-life' syndrome (Biro and Stamps 2010). This study was conducted using a much narrower size range of crabs in comparison to Chapter 4, in which the previously demonstrated influence of crab size on behavior was undetectable. Furthermore, to test for context-dependence, I measured individual behavior and metabolic rate in the absence and presence of toadfish (*Opsanus tau*) predation threat in the form of waterborne chemical cues. Support for behavior-physiology relationships at the individual level has been mixed (Bouwhuis et al. 2013), and Killen et al. (2013) suggest context-dependence as one reason for this mixed support. Specifically, environmental stressors that force individuals to modify their behavior or physiology to cope could induce behavior-physiology relationships which are otherwise unapparent (Killen et al. 2013). For example, hypoxic conditions cause European seabass (*Dicentrarchus labrax*) individuals with high metabolic rates to undertake greater risks in the presence of predation threat, driving a positive relationship between individual metabolic rate and risk-taking behavior (Killen et al. 2012). In Chapter 5, I found that both crab activity level and standard metabolic rate were repeatable over time, but were not related, either in the absence or presence of toadfish predation threat.

Animal personality is ubiquitous (Gosling 2001), but there is limited information on how personality can influence the strength of species interactions (Sih et al. 2012). In Chapter 6, I tested how crab activity level affected the crab functional response to mussel prey density. Because predation threat from toadfish causes crabs to reduce activity (Griffen et al. 2012, Chapter 5), I further examined how toadfish predation threat could mediate the effects of activity level on the response. This work showed that activity level enhanced the mussel consumption of small, but not large crabs, presumably through an increase in the amount of time that small crabs spent foraging during consumption rate trials. Specifically, small crabs with a high activity level, as measured in independent behavioral observations, exhibited a type-2 functional response that was greater in both slope and asymptote when compared to the response of less active small crabs. Toadfish predation threat independently reduced the slope, but not the asymptote, of the crab functional response. This study provides important information on how natural behavioral variation in a mesopredator can affect its functional response, thereby providing a framework to connect individual behavior to population and community dynamics.

3. Parasite effects on individual ecology

Parasites were traditionally left out of food web depictions due to their cryptic nature, complex life cycles and the lack of skills necessary for parasite identification (Marcogliese and Cone 1997). Recently, however, there has been a surge of interest in the effects of parasites on energy flow and food web dynamics (Lafferty et al. 2008). One pathway by which parasites can influence food web dynamics is through the modification of species interactions that hosts are involved in. In Chapter 7, I tested the hypothesis that parasite infection can modify the host functional response to prey density. Approximately 20% of flat-backed mud crabs (*Eurypanopeus depressus*) are infected by a barnacle parasite (*Loxothylacus panopaei*) in North Inlet estuary, and this chapter examined the effects of this parasite on the crab functional response to mussel prey density, as well as a potential behavioral mechanism behind these effects. In a lab experiment, I showed that parasite infection increased the time it took for crabs to begin feeding when exposed to a mussel (i.e. increased reaction time). Furthermore, the degree of behavioral alteration was dependent on the size of the parasite relative to the size of the crab; crabs harboring large parasites took longer to respond to mussel prey. The effect of parasite infection on crab consumption rates was dramatic; uninfected crabs consumed approximately 8 times more mussels than infected crabs. This study provides critical evidence that parasites can modify the strength of species interactions in food webs through the modification of host traits (i.e. a trait-mediated indirect interaction).

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APPENDIX A

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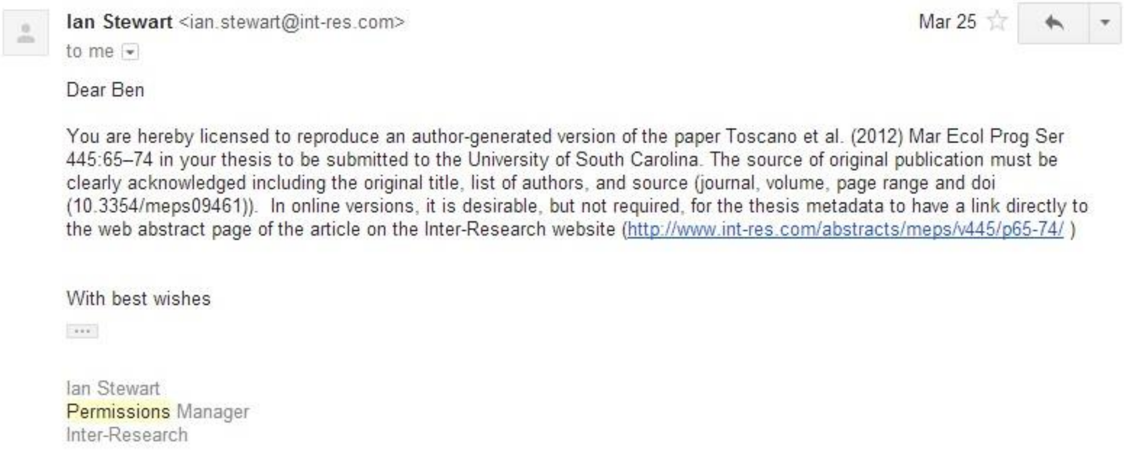

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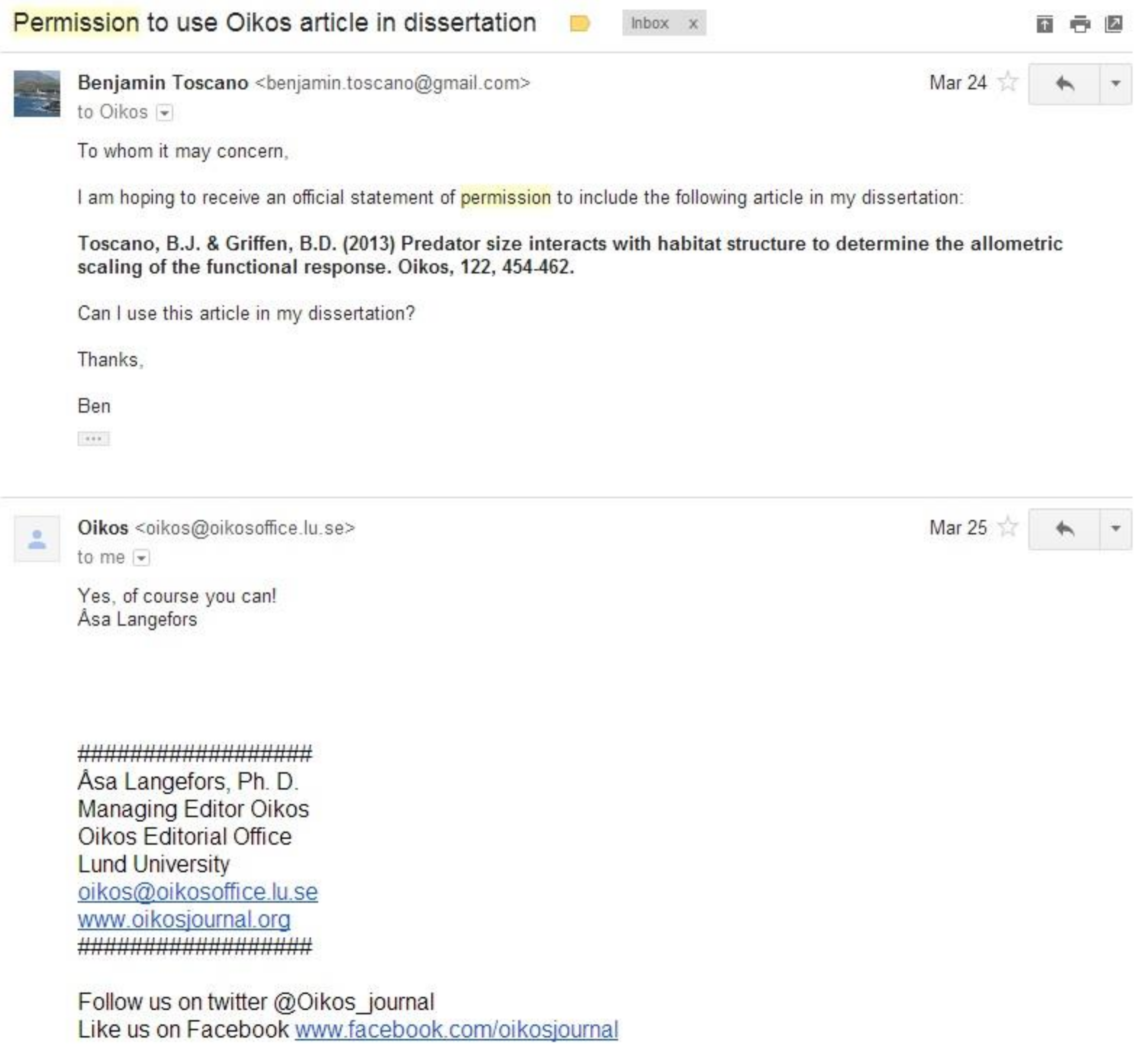

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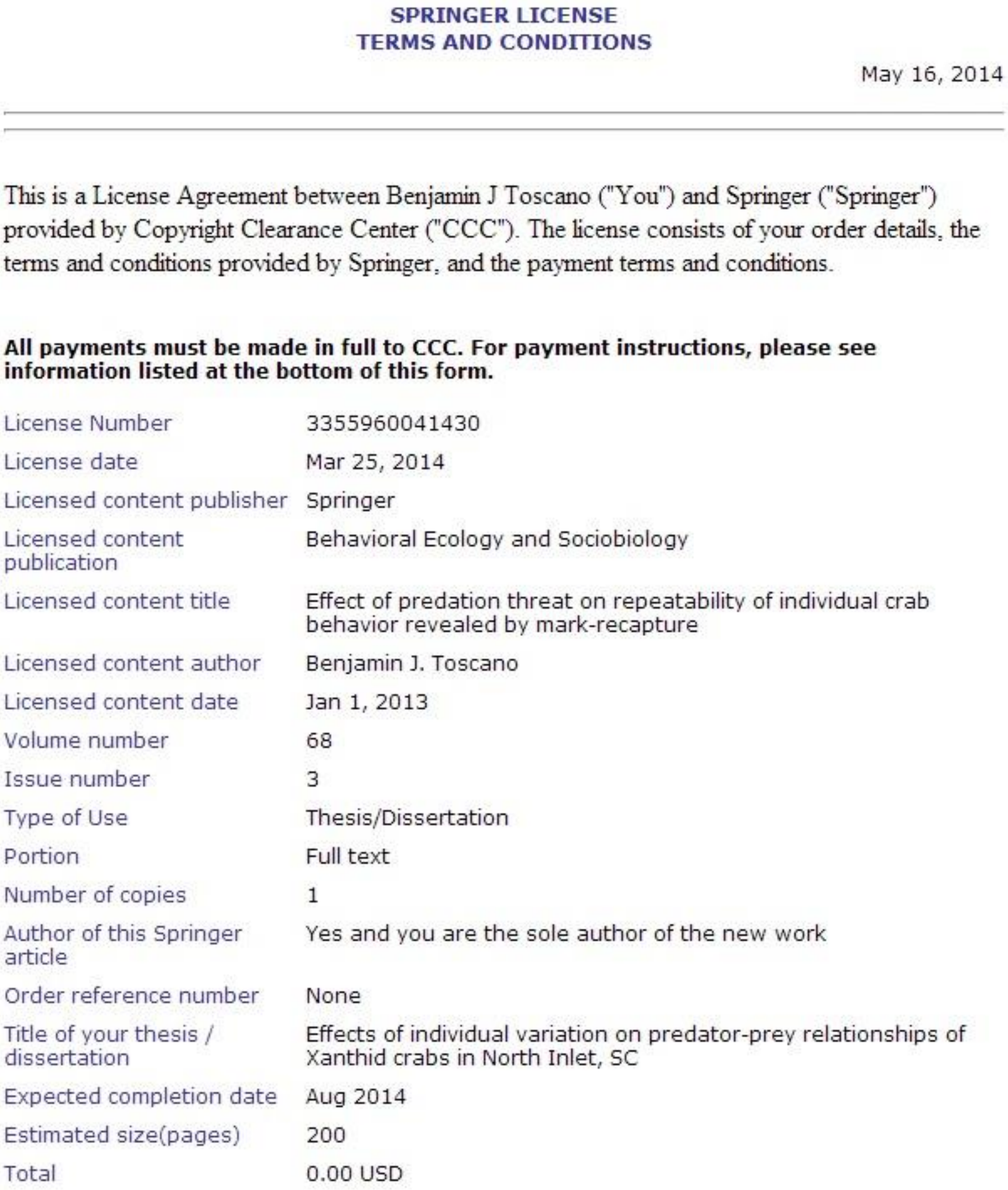

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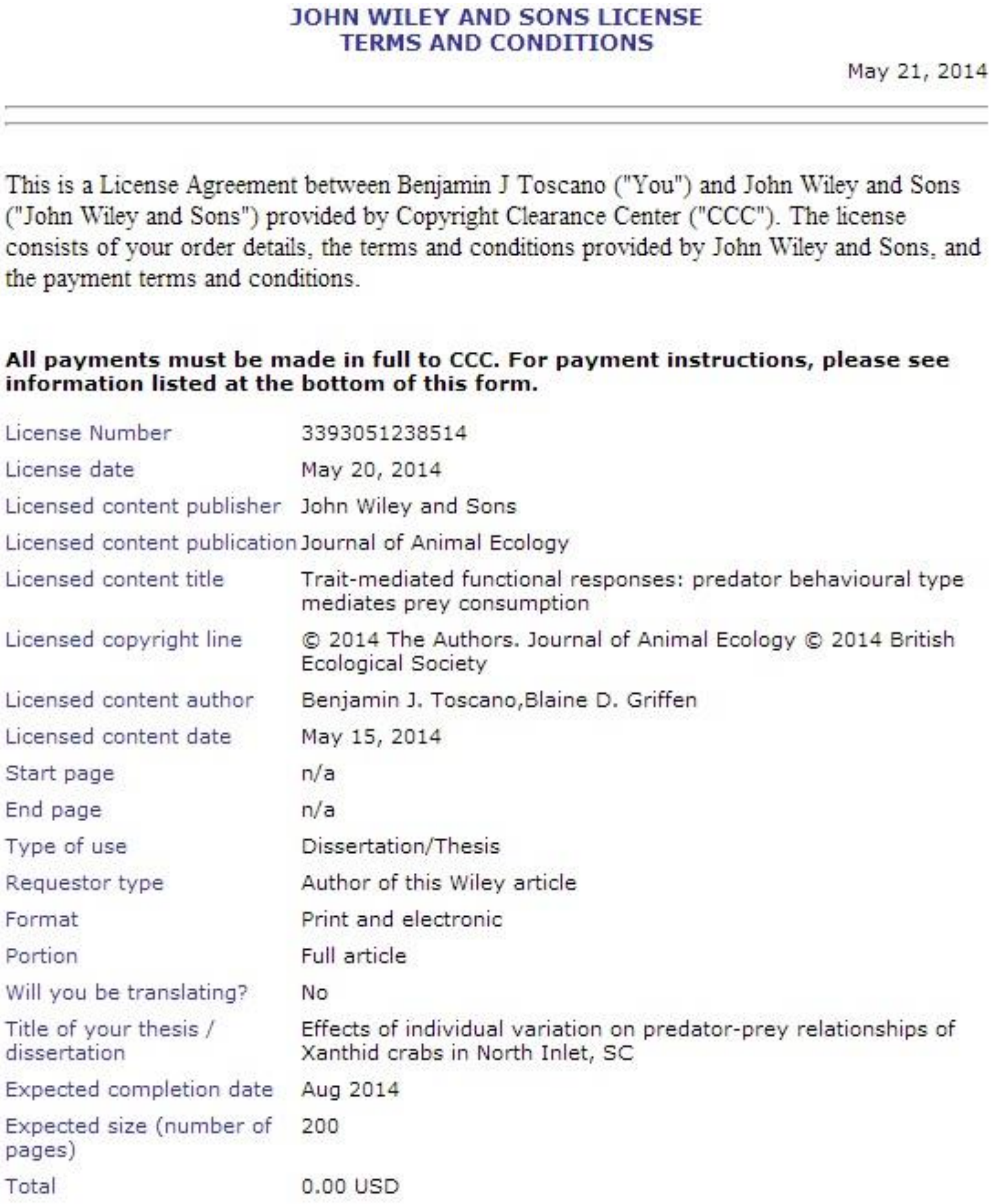

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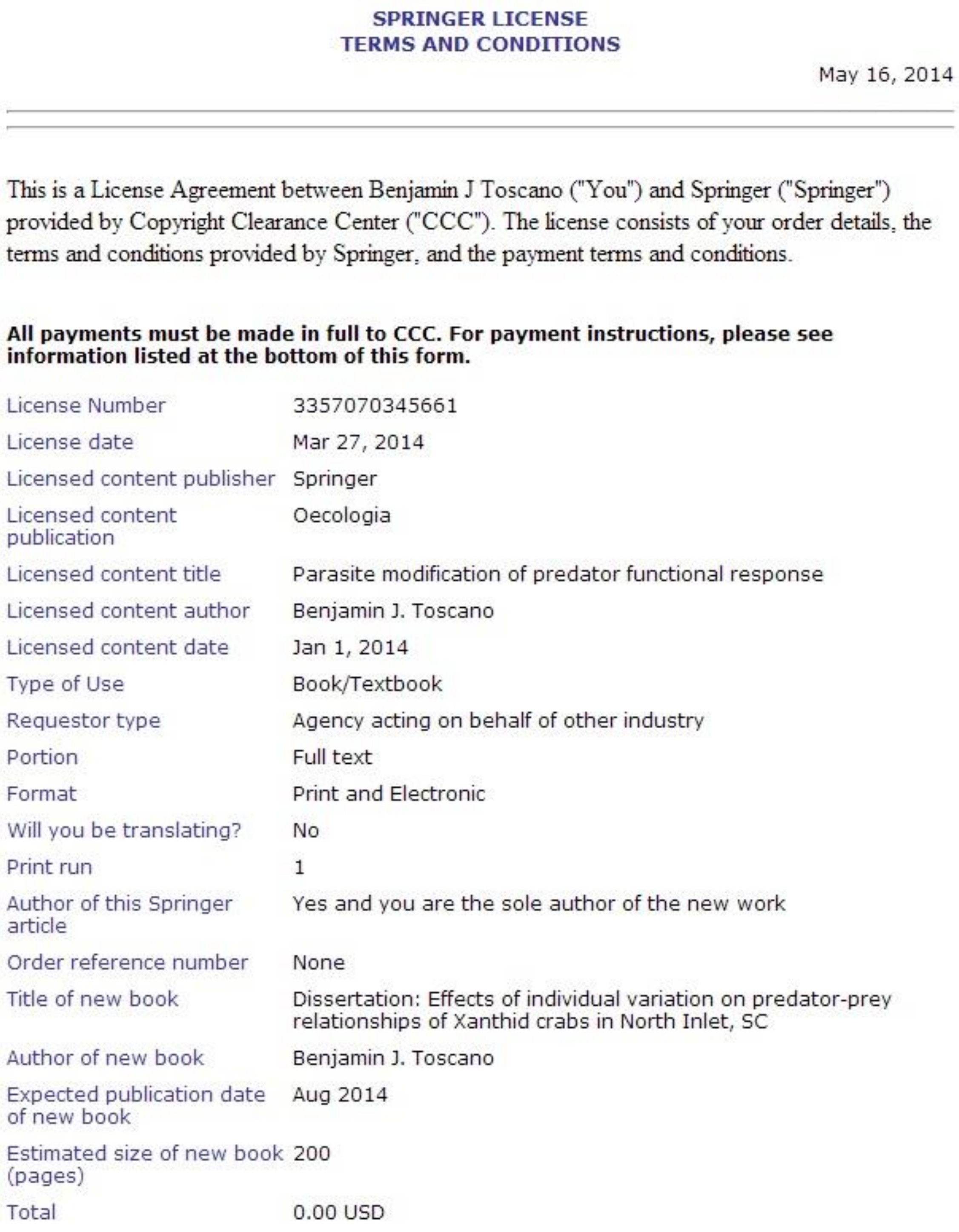

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