SPATIAL AND TEMPORAL VARIABILITY IN MARINE INVASION AND TROPHIC DYNAMICS

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By
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ABSTRACT

Species interactions are central to the study of community ecology, but these interactions can change with context. For instance, predator-prey interactions can vary with species introductions, spatial scale and temporal scale, and we are still learning how such factors can influence the strength of these interactions. Studying species interactions via multifaceted approaches and at different scales aids in the understanding of local and large scale processes, and can lead to predictions of how our ecosystems will persist in the face of continued anthropogenic alteration of the globe. The present series of studies sought to explore spatial and temporal variability in marine predator-prey interactions and invasion dynamics. The first objective assessed biogeographic variability in predator invasions. The second examined spatial variation in niche breadth and the third examined temporal variability in native and non-native behavioral interactions.

Specifically for the first objective, I examined the strength of marine invasive species-induced trophic cascades across latitude, hypothesizing that a non-native tertiary consumer could facilitate non-native basal prey establishment through the consumption of a native secondary consumer. I further predicted that the ecological importance of this cascade may be reduced in the subtropics relative to the temperate zone due to stronger predation pressure at lower latitudes. I found evidence of a trophic cascade in both regions, but it was only maintained under ambient predation pressure in the temperate zone. My results also suggest that strong predation pressure on the non-native intermediate predators in the subtropics may explain the weakened cascade under ambient conditions.

For the second objective, I tested the hypothesis of increased specialization at lower latitudes using brachyuran crabs as a model system and diet as my measure for niche breadth, while controlling for range size, body size and evolutionary relatedness. I compiled a dataset on 39 crab species' diets from existing studies and conducted my own diet analyses on species collected in a temperate, subtropical and tropical region, resulting in a global comparison. I found that latitude was correlated with range size for temperate species, but not for tropical species, and found no correlation between the other focal variables and latitude. These results suggest that ecological mechanisms (i.e. competition strength) may be driving patterns of niche breadth in the temperate zone, while evolutionary mechanisms may be more important in predicting niche breadth patterns in tropical systems.

For the third objective, I examined the influence of native and non-native prey naiveté on intermediate predator invasion success. I hypothesized that 1) naïveté is greatest in earlier stages of invasion across all trophic levels, decreasing the longer a non-native species is established in a system, 2) Native prey naïveté results in resource effects which increases invasion success, or 3) predator effects on non-native species would prevent non-native population growth. Through laboratory trials, I found support for naïveté being stronger at earlier stages of invasion, for both native basal prey and non-native intermediate predators. I also found weak predation on the more recently established intermediate predator in the field. However, my population model predicted that growth independent of basal prey naïveté. The results suggest that physiological traits, such as conversion efficiency and growth rates of the invasive crab may be driving its population growth more-so than foraging benefits.

My studies surrounding the variability of species interactions are the first to examine the strength of invasive species-induced trophic cascades across latitude, one of very few marine empirical studies to examine diet breadth at a large spatial scale, and the first to examine multi-trophic behavioral effects on invasion success respectively. They highlight the importance of studying multi-trophic interactions, as examining more pieces of the food web is increasingly important in developing a broader understanding of interactions and adaptations within invaded communities. My research also highlights the importance of studying interactions from a macroecological perspective. Tracking both invasions and native species interactions through space and time provides insight into marine community dynamics and may elucidate possible mechanisms of species coexistence.

DEDICATION

For my father, Frank and late mother, Julia,

who both inspired me to be who I've become,

and to always shoot for the stars.

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CHAPTER 1

INTRODUCTION

Habitat destruction, climate change and species invasions have caused historically unprecedented biodiversity loss and rapid ecological change throughout the world (Vitousek et al. 1996, Mack et al. 2000, Dirzo and Raven 2003, Butchart et al. 2010). While our communities and ecosystems are continually altered and we are faced with growing challenges to sustainability (Jerneck et al. 2011), the field of ecology still has many gaps about large scale (Agrawal et al. 2007, Schemske et al. 2009) and multi-trophic dynamics (Finke and Denno 2004, Hooper et al. 2005, O'Connor and Donohue 2013). Species interactions, which are central to the study of community ecology, can vary considerably with context (Agrawal et al. 2007). For instance predator-prey interactions can change depending on environmental conditions (Fairweather and Underwood 1991, Hammerschlag et al. 2006), evolutionary context (Pratt and Grason 2004, Friman et al. 2008), and both spatial (Freestone et al. 2011) and temporal scale (Oro et al. 2006, Sih et al. 2010), and we are still learning how such factors can influence trophic dynamics and the strength of these species interactions (Agrawal *et al.* 2007). Studying species interactions via multifaceted approaches and at different scales aids in the understanding of local and large scale processes, and can lead to predictions of how our ecosystems will adapt to global change. A thorough theoretical understanding of ecological communities and ecosystems can provide a basis for the most effective and well informed conservation efforts and is often called for in the decision making process (Sneddon 2000). Thus, understanding both local and large scale processes can lead to

predictions of how our ecosystems will persist in the face of continued anthropogenic alteration of the globe, and may help us learn how best to mitigate these impacts.

1.1 Marine Species Invasions

The anthropogenic transport and subsequent introduction of non-native species into new areas is the one of the leading causes of species diversity declines (Butchart et al. 2010). Invasive species have been shown to alter ecosystem function, and can affect economies and human health (Stachowicz et al. 2002, Blackburn et al. 2011, Gurevitch et al. 2011). Invasions have been examined rigorously in terrestrial systems (Catford et al. 2009), yet recent syntheses are lacking in marine systems (but see Ruiz et al. 2000). This fundamental gap in the literature is likely due to the more recent acknowledgement of invasive species in marine systems, and the uncertainty surrounding the taxonomy and native ranges of many marine species (Ruiz et al. 2000). With the majority of world trade occurring by sea and trade volume predicted to sharply increase in coming years (Kaluza et al. 2010), invasive species are a growing conservation threat in marine systems (Molnar et al. 2008), making an understanding of the mechanisms underlying marine invasions increasingly urgent.

There have been many attempts at developing a theoretical framework for invasion biology (e.g. Barney and Whitlow 2008, Catford et al. 2009, Blackburn et al. 2011, Foxcroft et al. 2011, Gurevitch et al. 2011). While these frameworks differ, have their limitations, and range from simple to complex, there are two main points of

agreement. First, invasions occur in stages: (1) transport, when species and/or propagules move from one area to another, (2) introduction, when species/propagules are released into a new system, (3) establishment, when a population of introduced organisms becomes self-sustaining, and (4) spread, when the introduced population undergoes range expansion. Second, success in any of these four stages of invasion depends on one or more of three primary factors: (1) propagule supply, which can be strongly influenced by trade frequency, (2) biological factors, including characteristics of the non-native species and the nature of their interactions with the recipient community, and 3) abiotic characteristics of the recipient ecosystem. A large majority of invasion hypotheses, which often form the foundation of the these frameworks, focus on biological factors (23 of the 29 leading invasion hypotheses reviewed in Catford et al. 2009) as opposed to propagule pressure and abiotic factors, though all three factors often operate in conjunction. This focus most likely occurs because propagule pressure is inherently difficult to examine in an invasion context (Levine et al. 2004), and although resource availability is one of the main abiotic characteristics that can promote invasion success (Davis et al. 2000), the responses of species to the abiotic environment often hinge on biological factors. Therefore, biological factors are not only tractable to study, but also critical to the invasion process.

Important predator-prey interactions are disrupted by invasions (Elton 1958, Williamson and Fitter 1996, Kimbro et al. 2009). Studies have begun to outline that non-native trophic interactions vary spatially and temporally. For instance, strong predation pressures at lower latitudes have been documented to hinder invasion success more than at higher latitudes (Freestone et al. 2013, Kimbro et al. 2013), and native prey have been

shown to undergo evolutionary change (Freeman and Byers 2006) and behavioral modification (Bool et al. 2011) with prolonged exposure to non-native predators. Predator-prey interactions are often attributed to coevolutionary history (Barrio et al. 2010, Sih et al. 2010), and it is unclear how the lack of coevolutionary history between native and non-native species influences these interactions and contributes to the success of non-native species. If a non-native species survives initial introduction, how the native community interacts with it may influence how rapidly that non-native population is able to establish and spread (Sih et al. 2010).

Studying invasive predator species impacts across spatial and temporal scales can aid in predicting areas where invasions will be more high-impact or low-impact. However, existing marine invasion studies at large spatial scales tend to focus on invasive prey species (e.g. Freestone et al. 2013) and not predators (but see deRivera et al. 2005). Additionally, both spatial and temporal invasion studies do not typically examine multi-trophic interactions, leaving invasive species-induced alterations to native trophic structure overlooked. Many invasive species are predators that establish in various levels of the food web (Ruiz et al. 2000), and how they affect the native community could be dependent on what native competitors or predators are present in that system (Levine et al. 2004, Liu and Stiling 2006, Kimbro et al. 2013). It is also rare for a system to have only one invasive species, therefore studies that examine interactions across multiple levels of the food web, involving multiple native and non-native species, are becoming increasingly important in developing a more holistic understanding of interactions and adaptations within invaded communities.

1.2 Global Species Diversity Patterns and Species Interaction Strength

The latitudinal diversity gradient is a widely observed biogeographic phenomenon encompassing many terrestrial and marine taxonomic groups (Hillebrand 2004a) where species diversity peaks in the tropics and then declines closer to the poles (Dobzhansky 1950, Pianka 1966, Silvertown 1985, Gaston 2000, Jablonski et al. 2006). Many ecological and evolutionary hypotheses have been proposed to explain the pattern. Evolutionary explanations of large-scale diversity patterns use speciation rates, extinction rates and immigration rates of species, and one of the most popular hypotheses, the out of the tropics model (Jablonski et al. 2006), suggests that high tropical diversity is maintained because taxa originate in the tropics and extend to the poles while maintaining their tropical presence. Ecological explanations involve climate (Araujo et al. 2008), habitat heterogeneity (Kreft and Jetz 2007) metabolic theory (Bailly et al. 2014), and multiple hypotheses tie large-scale diversity patterns to a gradient in biotic interaction strength, which is predicted to be strongest at low latitudes (Schemske et al. 2009).

A proposed pattern that may strongly relate to the latitudinal diversity gradient is a latitudinal gradient in niche breadth (Hutchinson 1959). Ecological specialization, defined as narrowed niche breadth (Devictor et al. 2010), evolves from strong species interactions (Araujo et al. 2011). As species interactions are predicted to be strongest at low latitudes, it has been hypothesized that niche breadth decreases with decreasing latitude (Hutchinson 1959). A higher prevalence of specialist species at low latitudes

then may enable more species coexistence, allowing for higher diversity. However, other factors besides, or in conjunction with, latitude may also relate to niche breadth, such as geographical range size (Slove and Janz 2010), phylogenetic conservatism (Barnagaud et al. 2014) and body size (Ashmole 1968, Gaston 1988, Novotny and Basset 1999), which may confound detecting a true niche breadth-latitude relationship. Although long hypothesized and widely accepted, research on this topic remains inconclusive. Terrestrial studies have shown mixed results (Vazquez and Stevens 2004), with some supporting a latitudinal gradient in niche breadth (e.g. Eeley and Foley 1999, Dyer et al. 2007, Krasnov et al. 2008) and some refuting (e.g. Beaver 1979, Fiedler 1998, Slove and Janz 2010). In the marine realm, examinations of latitudinal gradients in specialization are rare (but see Rohde 1978) and it is unclear how niche breadth relates to latitude in marine species.

1.3 Focal Research Questions

Examining species interactions via multifaceted approaches can aid in the understanding of multi-scale processes; understanding such processes can then lead to predictions of how our ecosystems will adapt to continued anthropogenic alteration, and may help us learn how best to mitigate our impacts on our living resources. I therefore sought out to address three objectives surrounding the trophic dynamics of marine species, targeting how invasive predator interactions change across space and time, and examining predictors of native species dietary niche breadth at a global scale. I chose invasions topics that have broad implications for both invasion ecology as well as

community ecology, and as resource usage has a large hypothesized influence on species distribution patterns (MacArthur 1972), I felt that deciphering large scale predictors of niche breadth would elucidate potential native species coexistence mechanisms, which could then also have further implications for invasive species distribution patterns. These studies used marine invertebrates as a model system, specifically crustaceans, mollusks and epifaunal species, and consisted of field experiments, surveys, collections, laboratory behavioral observation and experimentation, database development, and population modeling. The following chapters outline the three studies designed to address these objectives.

Specifically, the first objective was to examine how intermediate predator introductions affect communities in different biogeographic regions. This study consisted of large-scale field experiments, and tested longstanding biogeographic hypotheses on species interactions, both in the context of species invasions and community ecology more broadly, that are only just beginning to be empirically examined (Schemske et al. 2009, Freestone et al. 2011, Freestone et al. 2013). Chapter two describes this study in detail.

Chapter three discussed my second objective, which was to determine how latitude influences niche breadth in marine consumers. Using diet as a metric for niche breadth, I compiled a global dataset on brachyuran crab species from existing studies and from my own diet analyses conducted on species collected in temperate, subtropical and tropical North America. This study was unique in that it is one of very few large-scale empirical studies on diet breadth in marine systems and controlled for key latitudinal

covariates, including latitudinal range size (Stevens 1989) , body size (Bergmann 1848), and phylogenetic relatedness (Barnagaud et al 2014). Although a latitude-niche breadth relationship has been a widely proposed mechanism for the maintenance of high species diversity at low latitudes, existing research to date is inconclusive (Vazquez and Stevens 2004, Krasnov et al. 2008, Slove and Janz 2010). As such, this study advances marine macroecology research, and also controls for three important covariates that very few existing terrestrial studies to my knowledge take into account when testing for this global trend.

My third and final objective was to examine temporal variation in marine invasion dynamics and the relative importance of native and non-native anti-predator behavior on the population of an intermediate non-native predator. To address this goal, I tested the prey naïveté hypothesis, which predicts limited anti-predator behavior when a prey organism lacks coevolutionary history with a predator (Sih et al. 2010), across three trophic levels by conducting a series of laboratory behavioral experiments, assessing predation pressure on focal consumers in the field, and modeling the effects of these tritrophic behavioral interactions on the population of a recently introduced intermediate predator. This study provided some of the first insight into prey naïveté across multiple trophic levels and how naïve behavior may affect invasion success at the population level. Chapter four describes this research in detail, and chapter five discusses the general results, overarching conclusions, implications, and potential future directions for this suite of projects.

CHAPTER 2

STRONGER PREDATION AT SUBTROPICAL LATITUDES DAMPENS INVASIVE SPECIES-INDUCED TROPHIC CASCADES

2.1 Abstract:

Invasive predators can disrupt important predator-prey dynamics in multi-trophic systems and thereby facilitate invasions into prey communities. Lower latitude food webs can have strong consumer pressure and top-down control due to trophic complexity, however, and thus could be more robust to alterations by introduced predators than higher latitude food webs. I examined the strength of marine invasive species-induced trophic cascades across latitude, hypothesizing that a non-native tertiary consumer could facilitate non-native basal prey establishment through the consumption of a native secondary consumer. I further predicted that the ecological importance of this cascade may be reduced in the subtropics relative to the temperate zone due to stronger predation pressure by top predators at lower latitudes. Experiments were conducted in temperate Long Island Sound, Connecticut and subtropical Indian River Lagoon, Florida to test my hypothesis using marine invertebrates, specifically non-native Portunid crabs (tertiary consumers), native Columbellid gastropods (secondary consumers), and non-native tunicates (basal prey), as a model system. Additionally, predation pressure was examined on my tertiary consumers in order to assess any top-down control of the invasive species-induced cascade from higher trophic levels. There was evidence of a trophic cascade in both regions, but it was only maintained under ambient predation pressure in the temperate region. The results also suggest that strong predation pressure on the non-

native Portunid crabs in the subtropics may help explain the weakened cascade under ambient conditions. This study is the first to examine variation in the strength of invasive species-induced trophic cascades at different latitudes. Studying predator invasions in the context of full communities and from a macroecological perspective can be used to predict both local and large scale patterns of invasion and lead to identifying locations where high-impact invasions are more likely to occur.

2.2 Introduction:

Invasive predators have been well documented to impact native communities (e.g. Elton 1958, Williamson and Fitter 1996) by disrupting important native predator-prey dynamics (Kimbro et al. 2009). These disruptions can be caused by the direct consumption of native species (e.g. Sih et al. 2010), but a direct consumer effect can also result in indirect facilitation of both native (Rodriguez 2006) and non-native prey species (Grosholz 2005). A potential example is a trophic cascade, where top consumers suppress the abundances of an intermediate consumer, thus alleviating predation on basal prey populations (Strong 1992, Pace et al. 1999, Shurin et al. 2002). Trophic cascades have been widely observed across ecosystems and the relative strength of these cascades are mediated by factors such as climate (Wagner et al. 2013), habitat complexity (Grabowski et al. 2008), species diversity (Finke and Denno 2004, Byrnes et al. 2006), and food web complexity (Philpott et al. 2012). Overall however, trophic cascades are reported to be stronger in aquatic systems, particularly in lakes and the marine benthos (Strong 1992, Shurin et al. 2002).

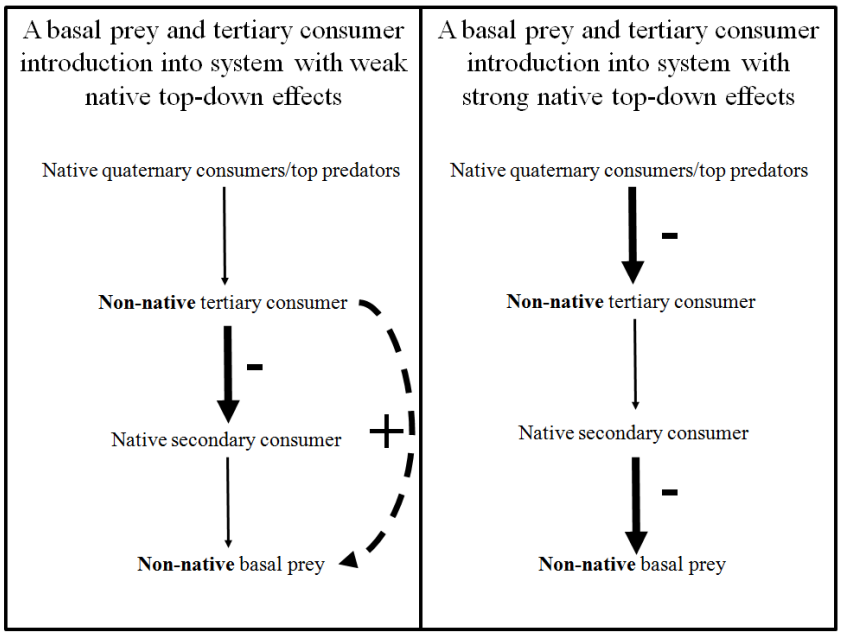


Figure 2.1: Conceptual diagram of indirect facilitation between a non-native predator and a non-native prey in the context of increased native predation pressure: Solid arrows indicate predation, dashed arrows indicate facilitation and arrow thickness indicates strength of the interaction (thicker arrows indicate stronger interaction). The net effect of strong interactions is further highlighted using plus (for positive) and minus (for negative) signs. When native predation pressure from top predators is weak (which could be due to low top predator diversity and/or reduced trophic complexity), the introduction of a non-native tertiary consumer can create a trophic cascade and indirectly facilitate invasive basal prey (first panel). When native predation pressure from top predators is strong (i.e. where predator diversity and/or trophic complexity is high), non-native predators have less of an impact and the strength of facilitative interaction with non-native basal prey is diminished (second panel).

While invasive species can interrupt native trophic cascades (e.g. Kimbro et al. 2009), they could also introduce trophic cascades that did not previously exist in the native system. These invasive species-induced trophic cascades could then allow other non-native species to become more abundant in the basal prey community ([(Locke et al. 2007)] Figure 2.1, first panel). As trophic cascades in general are more likely to occur in systems with low diversity (Strong 1992), trophic cascades involving invasive species should theoretically also occur in areas of low species richness and simple foodwebs (Figure 2.1, first panel). In these systems, an invasive predator may encounter lower competition with other consumers and lower predation pressure on itself. Therefore, this invasive species could potentially establish as a top predator, introduce a cascading effect on the rest of the community, and facilitate basal prey.

Ecosystem processes can be sensitive to changes in trophic diversity and structure (Hines and Gessner 2012); however, some food webs are more resistant to change than others (Dunne et al. 2007), and thus may be less impacted by invasions. For example, native trophic complexity (characterized by trophic diversity, number of trophic levels and the number of links in the food web [(Dunne et al. 2007, Cooper and Wissel 2012)]) and predation pressure can be greater at lower latitudes (Paine 1966, Bertness et al. 1981, Menge and Lubchenco 1981, Freestone et al. 2011), and both terrestrial and marine evidence points to these regions being more resistant to invasions (Sax 2001, Freestone et al. 2013, Kimbro et al. 2013). Previous marine research also suggests that lower latitude trophic cascades are more regulated by top-down pressure due to greater variation in top consumers than at higher latitudes (Marczak et al. 2011). Stronger predation pressure and more complex interactions expected at lower latitudes could diminish the ecological

importance of invader-invader facilitations resulting from trophic cascades in these regions. When native predation pressure is strong and a native community contains robust top consumers, non-native predator populations may be reduced. Smaller non-native predator populations would lead to a reduced relative impact on lower trophic levels, diminishing the strength of facilitative interactions with non-native basal prey (Fig. 2.1, second panel).

Studying impacts of invasive predators in different biogeographic regions can aid in predicting areas where invasions will have the greatest impact. This is becoming increasingly important in marine systems, with growing global trade volume (Kaluza et al. 2010) and ballast water transport introducing both predator and prey larvae (Ruiz et al. 1997). However, large scale experimental marine invasion studies, particularly biogeographic studies, remain rare in the literature despite their importance for understanding how community structure varies across regions with environmental and biotic variability (deRivera et al. 2005, Freestone et al. 2013), and have not yet examined invasive species alterations to native trophic structure. There are very few marine examples of invasive species-induced trophic cascades (but see Locke et al. 2007) and none to my knowledge have explored how this dynamic varies in different biogeographic regions.

This study compared the strength of invasive predator facilitation of non-native prey between a temperate and subtropical region as a first order test of biogeographic variation in multi-trophic interactions among native and non-native species. Marine invertebrates served as a model system, specifically non-native Portunid crabs, non-

native tunicate species, and native gastropod intermediate predators. This tri-trophic system and focal non-native species were experimentally tractable and also ecologically important, as tunicates are documented as some of the most widespread non-native sessile species (Whitlatch and Bullard 2007) and crustaceans are one of the most diverse taxonomic groups of non-native species across the globe (Galil 2011, Hanfling et al. 2011), both serving as important models for marine invasions in general. I hypothesized that non-native predators can alter trophic dynamics by creating cascades that facilitate basal non-native prey establishment, but that this impact is dampened in the subtropics due to higher trophic levels strengthening native top-down control at lower latitudes.

2.3 Methods:

2.3.1 Study System:

Subtidal invertebrate communities in both temperate Long Island Sound (Connecticut, 41°N) and subtropical Indian River Lagoon (Florida, 27°N) were used to test my hypothesis about biogeographic variation in invasive species-induced trophic cascades. These regions were chosen because they are two of the largest estuaries in the US, with Long Island Sound spanning 177 kilometers in length across several northeastern states (Rinebold 2003), and Indian River Lagoon spanning 251 kilometers in length, approximately 30% of Florida's east coast (Dineen et al. 2010) and thus support many habitats (Rinebold 2003, Dineen et al. 2010) and species typical of temperate and subtropical coastal systems of the west Atlantic. These two ecosystems were,

furthermore, ideal representatives of my factors of interest, including biogeographic differences in diversity and food web complexity in the temperate zone compared to the subtropics. Long Island Sound contains >1000 marine species while Indian River Lagoon (Rinebold 2003) contains >3500 species of animals, plants, fungi and protists (Dineen et al. 2010), as well as high predator diversity and a highly complex food web (Dineen et al. 2010). These areas were also chosen due to the parallel invasions occurring in both systems. Both communities contain non-native tunicates as well as native predatory gastropods in the family Collumbellidae (*Anachis* spp.). Collumbellid gastropods can consume over 200 recruits, or juvenile sessile invertebrates, per day, and have a preference for tunicates (Osman and Whitlatch 2004). Each estuarine community also contains a non-native, tertiary consumer Portunid crab; the European green crab *Carcinus maenas* in Long Island Sound and the Indo-Pacific swimming crab *Charybdis hellerii* in Indian River Lagoon. Although *C. maenas* has been established in the west Atlantic since 1817 (Roman 2006) and *C. hellerii* was only recently established in Indian River Lagoon in 1995 (Lemaitre 1995), both crabs have similar ecology (Lemaitre 1995, Dineen et al. 2001, Baeta et al. 2005) and consume Collumbellid gastropods (Berger 1998, Rogers 1998 Papacostas, personal observation). Thus, these two ecosystems varied greatly in the diversity and food web complexity representative of temperate and subtropical systems, both had parallel subsets of functionally similar species, and also contained potential trophic cascades induced by invasive species within the invertebrate community (Figure 2.1), making them ideal models for a temperate-subtropical comparison of cascade strength.

2.3.2 Facilitated invasion via trophic cascades:

We examined trophic cascades created by non-native Portunid crabs that facilitate non-native tunicates by conducting predator enclosure experiments at one site in Long Island Sound, Connecticut in July of 2010 and two sites in Indian River Lagoon, Florida in July of 2011 (Figure 2.2). Sessile invertebrate recruitment was allowed to occur for one week under reduced predation on 100cm^2 polyvinyl chloride (PVC) panels at each site to allow juvenile tunicates to settle and develop. In Long Island Sound, predation was reduced by suspending panels from a floating dock to allow only fish predation, which is low on the focal sessile species at this site (Osman and Whitlatch 2004). In the Indian River Lagoon, cages were used with a mesh size of 1.7mm x 1.4mm to exclude both fish and benthic predators, which is a mesh size that has been shown to exclude most predation but also allows sessile invertebrate recruitment to occur without difficulty (Freestone et al. 2011). Tunicates were then exposed to one of five predation treatments at each site. Treatments included 1) a control predation exclosure (no predation), 2) a control open to the full suite of predators, 3) *Anachis* snails only, 4) a non-native Portunid crab only (*C. maenas* in Long Island Sound and *C. hellerii* in Indian River Lagoon), and 5) *Anachis* and an invasive Portunid crab (*C. maenas* in Long Island Sound and *C. hellerii* in Indian River Lagoon). All enclosures were 15.24x15.24x15.24cm cages with a 1.7mm x 1.4mm mesh size, which were effective in containing focal predators and giving them mobility but still excluding other predators. It is possible that caging in marine experiments can affect flow in subtidal environments (Miller and Gaylord 2007), but as trials were short (communities exposed to predators for 3 days), and I was primarily interested in the effects of my focal benthic predators within the cage enclosures,

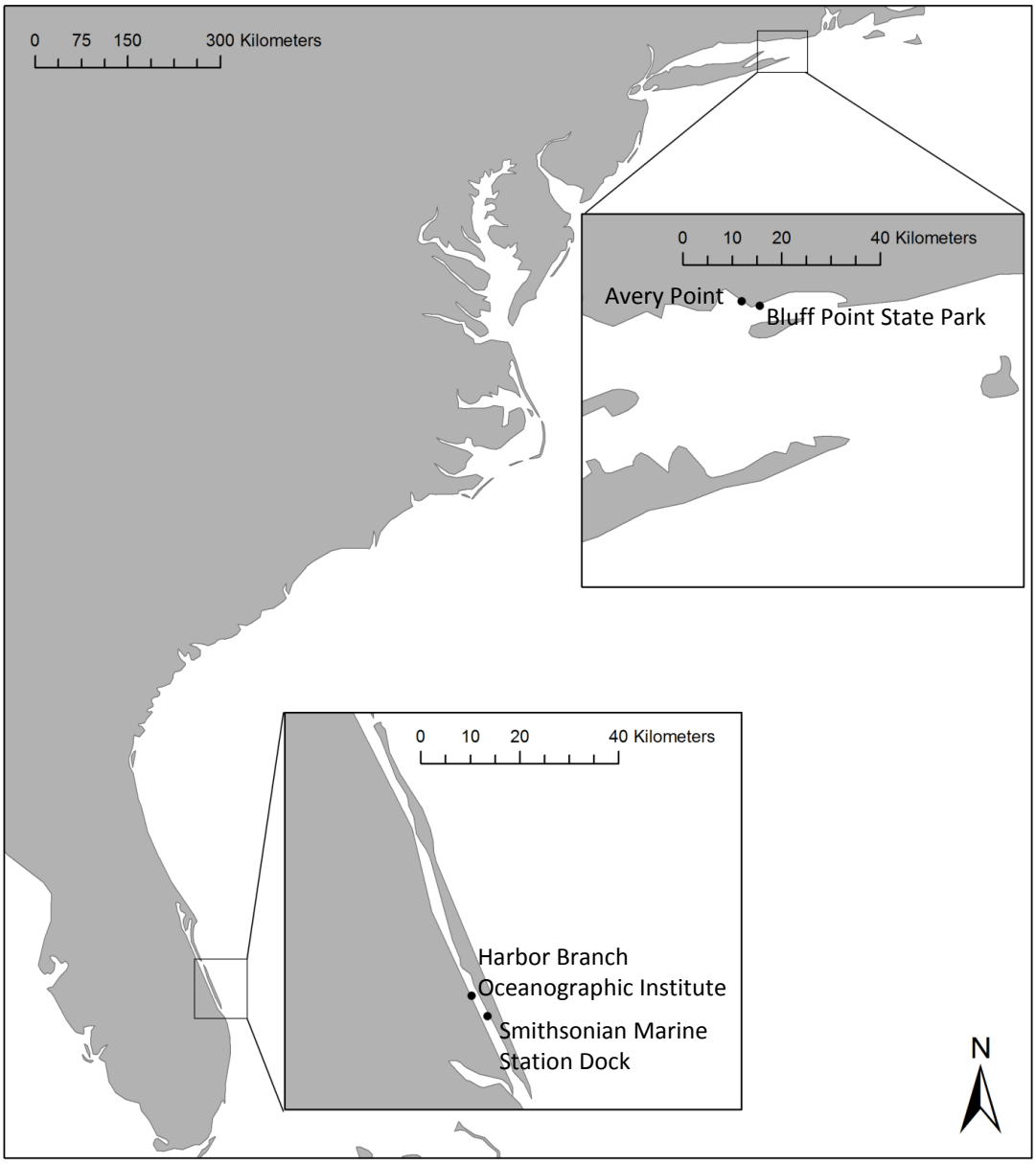


Figure 2.2: Map of study regions Long Island Sound and Indian River Lagoon, and sites used within study regions: Four sites total were used for experiments, including Avery Point in Groton, CT (41°18'57.72"N, 72° 3'39.78"W), Bluff Point State Park in Groton, CT (41°20'12.41"N, 72° 2'5.40"W), Harbor Branch Oceanographic Institution in Fort Pierce, FL (27°32'6.55"N, 80°20'51.25"W), and the Smithsonian Marine Station Dock in Fort Pierce, FL (27°27'21.83"N, 80°18'34.74"W).

a control for caging artifacts was not included. *Anachis* snail treatments were stocked at natural densities in each location (14 snails per enclosure in Long Island Sound; three snails per enclosure at site one in IRL and two snails per enclosure at the second [Table 2.1]). Densities were determined from the literature for Long Island Sound (Rogers 1998) and via core sampling (7.5cm in diameter and 11cm in height, conducted directly before experiment) in Indian River Lagoon (Table 2.1). One crab was used in each of the crab treatment enclosures to conform to natural densities and because of the cannibalistic nature of crabs (Moksnes 2004, Baeta et al. 2006), which would have confounded the testing of the hypotheses of interest. Additionally, 79 individuals and 35 individuals of *C. maenas* and *C. hellerii* respectively were collected and their carapace width measured at each site prior to the experiment to determine a size range of crab to use that was representative of the crab's average size range at the site to make the enclosures as realistic as possible (*C. maenas* with carapace widths of 38-59mm in Long Island Sound and *C. hellerii* with carapace widths of 22-42mm in Indian River Lagoon). While crabs used in Long Island Sound were slightly larger than those used in Indian River Lagoon, using these size classes ensured the most ecologically relevant representation of the trophic interactions occurring within each system. Treatments were weighted down subtidally in Long Island Sound using a blocked design (deployed haphazardly on cinderblocks with 1 replicate of each treatment per cinderblock), and in Indian River Lagoon replicates were weighted down independently. In Long Island Sound there were between eight and ten replicates per treatment, resulting in a sample size of 46, and in Indian River Lagoon due to the low abundances of *C. hellerii*, I had a minimum of four replicates per treatment at two sites for a total sample size of 75.

Table 2.1: Results from snail surveys at Indian River Lagoon Sites

Site	Number of core samples taken	Average density of *Anachis* spp/core (core base area = 45.6cm^2)	Average density of *Anachis* spp. scaled to experimental enclosures (enclosure base area = 232.3cm)
1 (Smithsonian Marine Station Dock)	30	0.53	2.72
2 (Harbor Branch Oceanographic Institute)	20	0.35	1.78

After three day trials, I recorded non-native tunicate and *Anachis* abundances in treatments. I also observed native tunicate recruitment in both regions and thus collected data on native abundances as well for comparison purposes. Tunicate abundances in each region were square-root transformed and analyzed using mixed model ANOVAs (REML method) in JMP Statistical Software, with treatment as a fixed factor and a random effect (a blocking effect in Long Island Sound to account for deploying the treatments in groups, and a random effect of site in Indian River Lagoon to account for the use of two sites in the region). There was high variation in richness and relative abundance of tunicates in Long Island Sound compared to Indian River Lagoon, and I also had to use different sample sizes between regions due to unanticipated low abundances of *C. hellerii* in the lagoon. The data for both regions were therefore analyzed separately rather than pooled into one model due to heteroscedasticity caused by the differences in variance between subtropical and temperate sites.

2.3.3 Ecological relevance of cascade - quantifying the effects of the full predator community on focal native and non-native predators:

To detect top-down pressure from higher trophic levels that could affect the cascades created by focal non-native crabs in each region (Fig. 2.1), I examined ambient predation pressures on both the non-native crabs and the native snail involved in the cascade in Long Island Sound and in Indian River Lagoon. Predation rates on focal predators (*C. maenas* in Long Island Sound, *C. hellerii* in Indian River Lagoon, and *Anachis* species in both regions) were quantified in August of 2011 (Indian River Lagoon) and 2012 (Long Island Sound) in the field. All focal predators were tethered using braided microfilament line and cyanoacrylate adhesive. Tethered animals were attached to a 1.5 ft stake in sediment and placed in the field 10 feet apart to minimize multiple predation events caused by a single predator. Additionally, half of the tethered animals were deployed in cages to control for tether failure. A total of 80 *Anachis* snails were used in the experiments (10 replicates per treatment [open or caged] with two sites per region for a total of four sites [Fig. 2.2]). *C. hellerii* abundances were unexpectedly low in the Indian River Lagoon, thus 10 crabs (five open, five caged) were used for tethering at one site in Indian River Lagoon and 10 *C. maenas* individuals (five open, five caged) were tethered at one site in Long Island Sound to have equal sample sizes. Animals were tethered for two days in the field, and then predation rates (expressed as lost individuals over two days) were quantified. *Anachis* and non-native crab individuals lost in each region were analyzed with Pearson's Chi square tests. All experiments, including both the enclosure and tethering experiments, were conducted in open sand near rocky areas in order to standardize experimental environment.

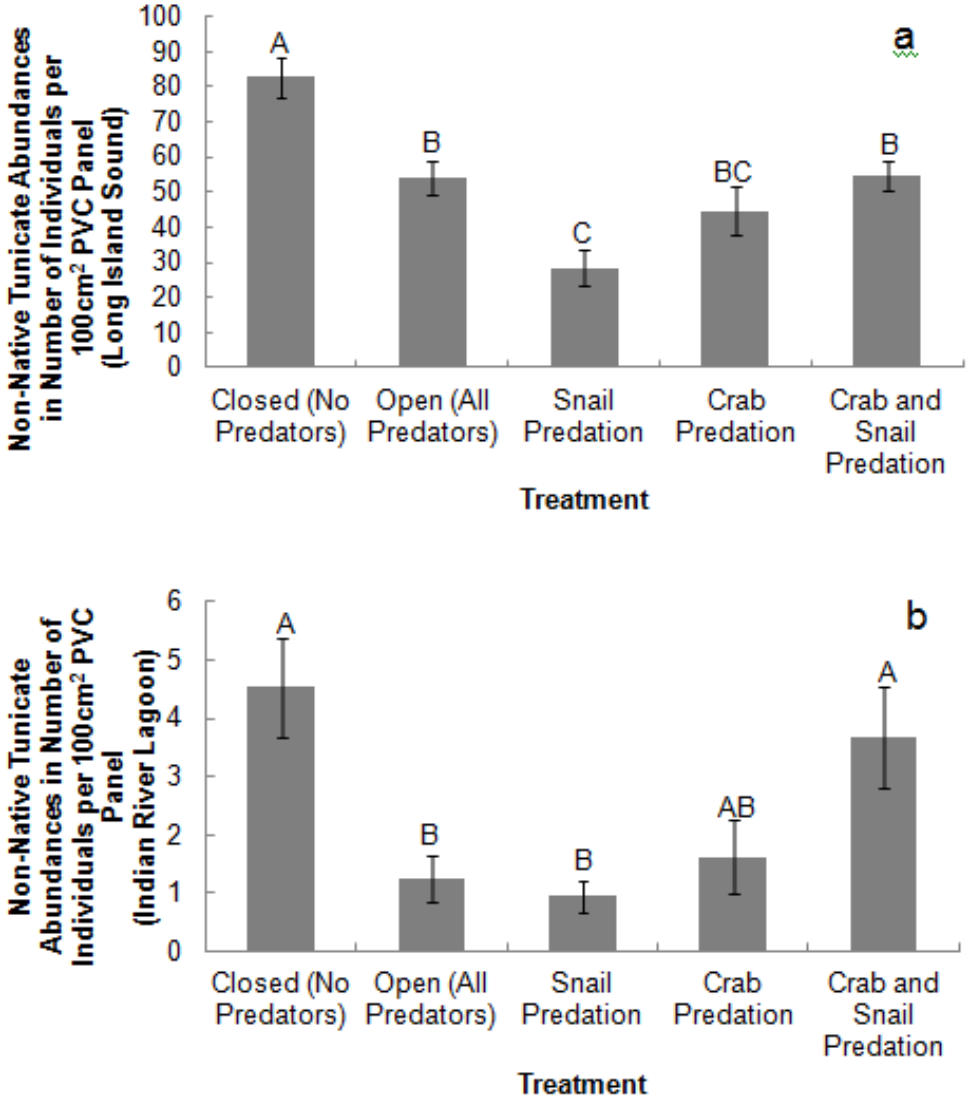


Figure 2.3: Results of Long Island Sound and Indian River Lagoon Trophic Cascade Experiments (Non-native Tunicates): Abundance expressed as number of individuals of (a) Long Island Sound non-native tunicates and (b) Indian River Lagoon non-native tunicates across five predation treatments. Untransformed data are shown. Error bars indicate standard error and different letters above bars indicate significant differences between treatments, as determined using a Tukey's HSD test.

2.4 Results:

2.4.1 Facilitated invasion via trophic cascades:

Our results support the hypothesis that non-native predators can create trophic cascades that facilitate non-native basal prey in the temperate zone. *C. maenas* in Long Island Sound indirectly facilitated non-native tunicate abundances through consumption of the secondary consumer *Anachis*. Six species of non-native tunicates were observed in experimental communities, including the colonial *Botryllus schlosseri, Botrylloides violaceus, Diplosoma listerianum* and *Didemnum vexillum,* and the solitary *Ascidiella aspersa, Styela clava* and *Ciona intestinalis*. Predation by *Anachis* reduced non-native tunicate abundances, while the inclusion

of *C. maenas* weakened this predation effect (Figure 2.3a, ANOVA full model: R^2_{adj}=0.49, N=46, $F_{4/34}$=12.23, p<0.0001). Exposure to *C. maenas* resulted in a moderate predation effect on tunicates, however with *Anachis* present, *C. maenas* consumed ~40% of the snails (Figure 2.4) within the enclosures, resulting in reduced predation on tunicates (Figure 2.2a). This facilitative effect was not only seen within an enclosure, but was also maintained by the full predator community, where tunicate abundances were the same as those exposed to both crab and snail predation.

Although the non-native crab *C. hellerii* in Indian River Lagoon also had the potential to induce a trophic cascade, the effect was weakened by the full predator community. The subtropical epifaunal communities contained only three species of non-native tunicate (*Diplosoma listerianum, Styela canopus* and *Styela plicata*) in much lower

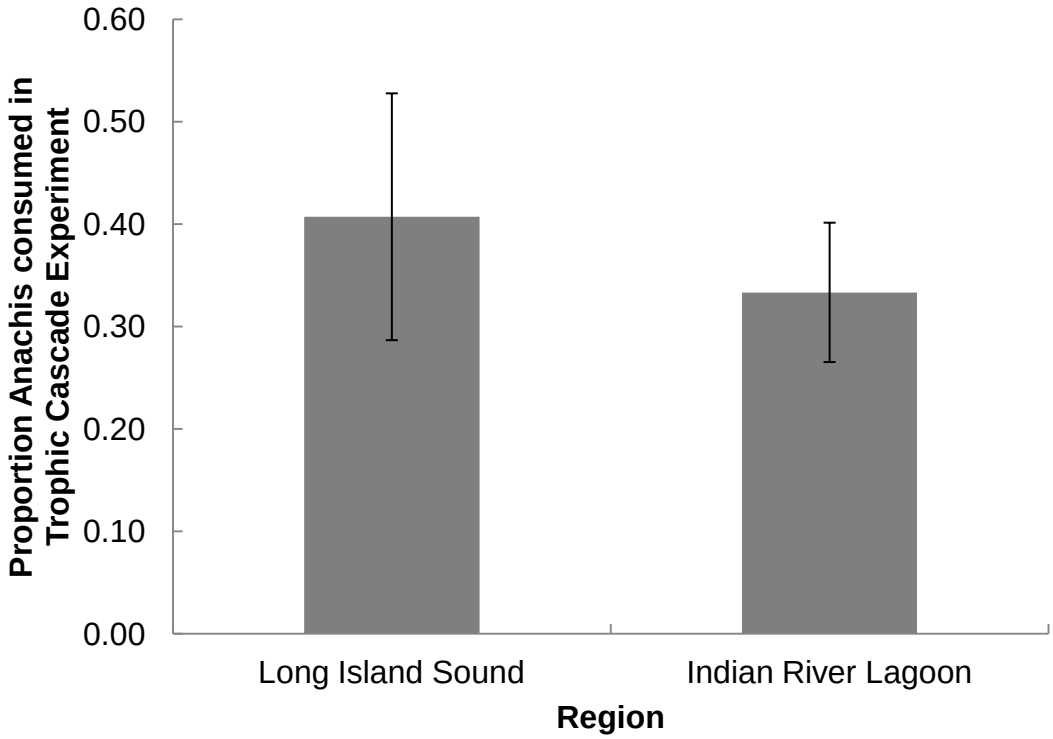


Figure 2.4: Results of Long Island Sound and Indian River Lagoon Trophic Cascade Experiments (Snails): *Anachis* dovesnail consumption over the course of the trophic cascade experiments, resulting from *Carcinus maenas* predation in Long Island Sound and *Charybdis hellerii* predation in Indian River Lagoon. Error bars indicate standard error and results showed no significant difference in consumption of snails between regions.

abundances than in Long Island Sound (average of 5 individuals per predator exclosure panel in Indian River Lagoon compared to 83 individuals per predator exclosure panel in Long Island Sound). Similar to Long Island Sound, *Anachis* had a strong predation effect on non-native tunicate abundances (Figure 2.3b, ANOVA full model: R^2_{adj}=0.37, N=75,

$F_{4/69}$=9.53, p<0.0001), but *C. hellerii* weakened that effect by reducing predation on tunicates, consuming ~30% of the snails within the enclosures (Figure 2.4). However, panels exposed to the full predator community all had low non-native tunicate abundances, indicating that the facilitation between invasive crab and non-native tunicates was not maintained when exposed to the full predator community.

While the experimental trophic cascades facilitated non-native tunicates in both regions, this effect was not observed for native tunicates. Long Island Sound panels only contained one native solitary tunicate species *Mogula manhattensis,* while Indian River Lagoon experimental epifaunal communities contained 20 native tunicate species. In both regions, only removal of all predators resulted in alleviated consumer pressure on native tunicates (Figure 2.5a, ANOVA full model: R^2_{adj}=0.42, N=46, $F_{4/33}$=7.63 p=0.0002, Figure 2.5b, ANOVA full model: R^2_{adj}=0.21, N=75, $F_{4/69}$=5.76, p=0.0005).

2.4.2 Ecological Relevance of Cascade - Quantifying the effects of the full predator community on focal native and non-native predators:

Predation rates on the non-native crabs in Long Island Sound were much lower than in Indian River Lagoon. All *C. maenas* individuals survived in the Long Island Sound experiment over the course of 2 days, while all *C. hellerii* individuals exposed to predators were consumed (Pearson's Chi Square: p<0.0016). In Indian River Lagoon, some tethers were completely empty, while others had pieces of carapace still attached. All caged *C. maenas* and *C. hellerii* were alive and tethered with no sign of damage

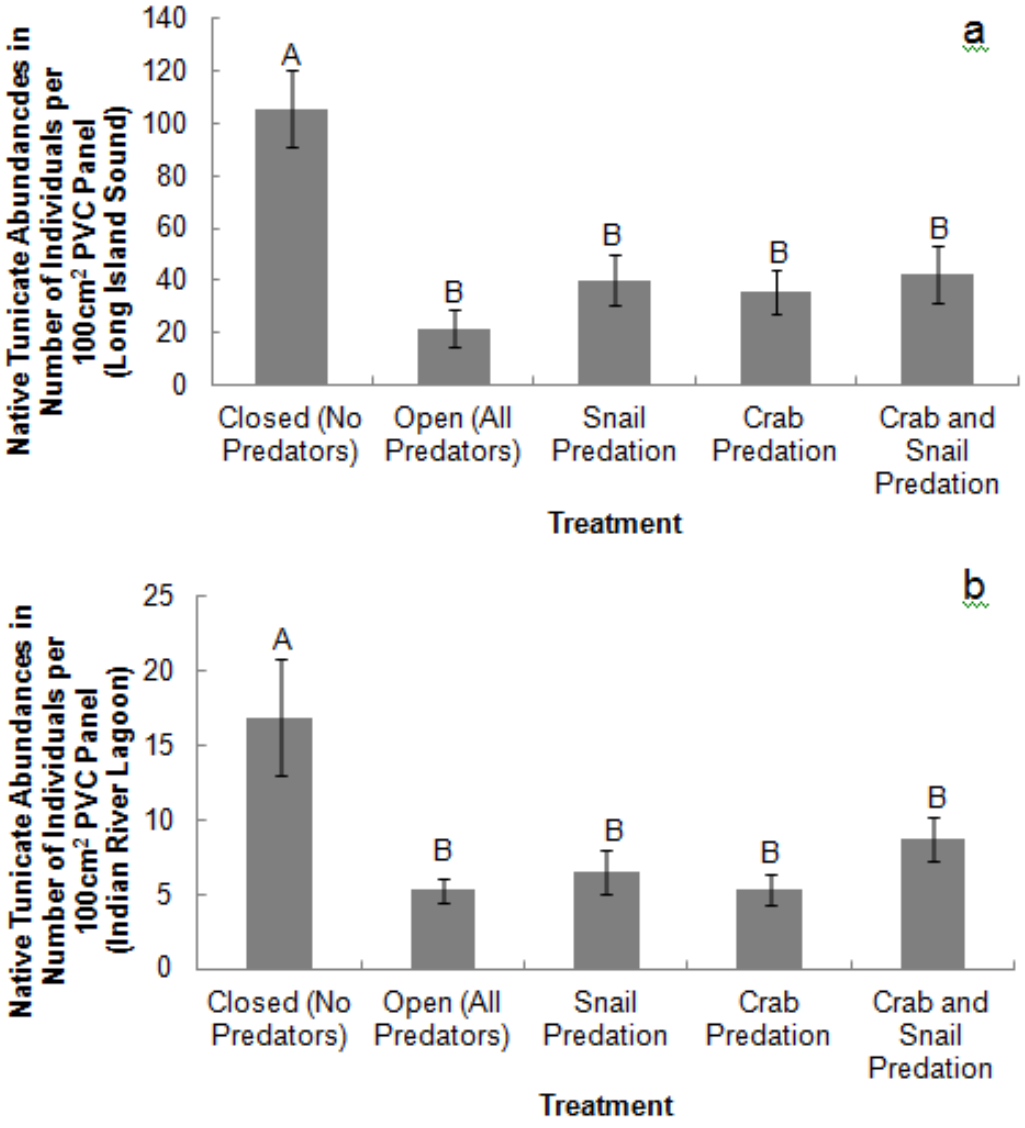


Figure 2.5: Results of Long Island Sound and Indian River Lagoon Trophic Cascade Experiments (Native Tunicates): Abundance expressed as number of individuals of (a) Long Island Sound native tunicates and (b) Indian River Lagoon native tunicates across five predation treatments. Untransformed data are shown. Error bars indicate standard error and different letters above bars indicate significant differences between treatments, as determined using a Tukey's HSD test.

except one *C. hellerii*, which had escaped from the cage and was then consumed (indicated by the tether protruding from the cage with a piece of carapace still attached). Thus, loss of tethered *C. hellerii* that were exposed to predators was most likely due to consumption rather than abiotic factors or escape.

In contrast to the observed difference in consumer pressure on the non-native crabs, predation rates on snails in both Long Island Sound and Indian River Lagoon did not differ from each other, with ~50% of the snails consumed over the course of 2 days. As with the crabs, all snails in the caged control treatments were still alive and securely tethered at the end of the experiments, supporting the interpretation that the snail loss in the predator-exposure treatments was due to consumption rather than abiotic factors or escape.

2.5 Discussion:

In both the temperate and subtropical regions, non-native tertiary consumers created trophic cascades, facilitating non-native basal prey through consumption of a native secondary consumer. Non-native tunicates (basal prey) were more abundant in treatments with non-native crabs (tertiary consumer) and *Anachis* (secondary consumer) than with just *Anachis*, which have been previously shown to heavily prey upon and even prefer certain non-native tunicate species (Osman and Whitlatch 1995, 2004). In treatments containing all three trophic levels, non-native crabs reduced snail abundances by ~40% and alleviated snail predation on the non-native tunicates partially in Long

Island Sound, and completely in Indian River Lagoon. Given the short duration of the predation experiments and the fast consumption of snails, it is likely that these non-native crabs have a significant impact on *Anachis* abundances over longer periods of time. Surviving snails could also reduce their consumption rates, as gastropods often alter foraging behavior in response to chemical cues emitted from predators and crushed conspecifics (Schmitt 1981, Cotton et al. 2004), which would enhance cascading effects.

Despite observed invasion facilitation in my experimental communities, the trophic cascade was only maintained by the full predator community in the temperate region, but not in the subtropical region, highlighting the importance of studying multi-trophic interactions at a biogeographic scale. In Long Island Sound, tunicate abundances were not different when exposed to the full predator community compared to those exposed to only *C. maenas* and *Anachis* predation, indicating that the facilitative effects of the non-native tertiary consumer may be maintained under ambient predation pressure in this temperate region. In subtropical Indian River Lagoon, however, a trophic cascade was not observed in the context of the full predator community, as non-native tunicate abundances were lower when exposed to ambient predation than just *C. hellerii* and *Anachis* predation.

Top-down effects from top predators may be a primary mechanism weakening this non-native trophic cascade in Indian River Lagoon. *C. hellerii* is low in abundance in the lagoon (Papacostas, *unpublished data*, Dineen et al. 2001), and results show strong predation pressure on *C. hellerii* in comparison to no observed predation on *C. maenas* in Long Island Sound. Thus, strong benthic predation by top predators could be removing

the cascading effect on non-native tunicates by reducing *C. hellerii* abundances. In contrast, predation pressure by top predators appears to be minimal or absent in the temperate region, which is consistent with previous studies that have also documented fewer predators and lower predation rates on *C. maenas* in higher temperate latitudes in comparison to southern portions of their range, likely contributing to their high abundances in these regions (deRivera et al. 2005).

Predation pressure from a single or few top predators alone could be reducing the invasion success (deRivera et al. 2005, Jensen et al. 2007, Carlsson et al. 2011) and the cascading effects of *C. hellerii*, but Indian River Lagoon's very diverse predator community (Dineen et al. 2010) could also be a mechanism of the weakened cascade of the subtropical species; trophic cascades have been shown to be removed by food web complexity (Shurin et al. 2002) and also to be dampened by predator diversity in terrestrial systems (Finke and Denno 2004). The predator community observed in Indian River Lagoon was more diverse and contained predators that were absent at the Long Island Sound site. Octopuses, and other larger crabs (e.g. the Florida stone crab *Menippe mercenaria* and the blue crab *C. sapidus*) readily consume *C. hellerii* (Papacostas, *personal observation*) and are abundant in the lagoon, along with other potential predators such as various species of fish and rays (Dineen et al. 2010).

The weakened trophic cascade in the subtropical region could also have been due to a variety of other factors in addition to top-down effects. For instance, the effect of the full predator community on tunicate abundances was no different in Indian River Lagoon than the effect of *Anachis* alone, suggesting that the snails may maintain this effect in

nature. Other species within the full predator community, however, may also reduce tunicate abundances. It is unknown what other species in Indian River Lagoon consume tunicates, but there are many species of predatory gastropods, flatworms, fish, crabs and other invertebrate and vertebrate species that may be other natural enemies (Dineen et al. 2010).

Our observed higher predation rates on the non-native Portunid in Indian River Lagoon is consistent with existing hypotheses that consumer pressure is stronger at lower latitudes than at higher latitudes (Jeanne 1979, Pennings and Silliman 2005, Freestone et al. 2011). I also found equal predation rates on snails in both regions, however, which is contradictory to a previous study that has shown strong predation pressures on snails at lower latitudes due to the high abundance of more specialized crushing predators (Bertness et al. 1981). In Long Island Sound, previous research indicates that the non-native *C. maenas* exerts strong predation on *Anachis* species, and even shapes their abundances and distribution (Berger 1998, Rogers 1998). Thus, while other species may consume Anachis in temperate areas, *C. maenas* may be a key cause of ambient predation on *Anachis* being higher than expected in Long Island Sound. This strong pressure from *C. maenas* on *Anachis* could be what drives the discrepancy between this study and the previous study (Bertness et al. 1981), particularly given that I found no predation on *C. maenas*.

Non-native tunicates were generally more successful in Long Island Sound than in Indian River Lagoon, as non-native richness was double that of Indian River Lagoon and there was roughly a twenty-fold difference in abundance. Stronger facilitative

interactions with the non-native Portunids in Long Island Sound likely promote invasion success, but other factors may also contribute to high abundances of non-natives tunicates in the temperate zone. For example, propagule pressure of non-native tunicates may be higher in the temperate zone in comparison to lower latitude systems; similarly, lower propagule pressure may help explain reduced success of lower latitude invasions (Fine 2002). Commercial shipping is the primary vector for marine invasions (Ruiz et al. 2013) and 14 of the top 20 central ports of the global shipping network are located at temperate latitudes (Kaluza et al. 2010), making strong propagule pressure to those temperate areas highly likely. In terms of these sites specifically, the area surrounding Long Island Sound has a higher frequency of global shipping than southern Florida, with New York serving as the 13th most central port of the global network (Kaluza et al. 2010). Therefore, geographic variation in propagule supply likely provides different invasion potential in different regions, with multi-trophic species interactions further facilitating or limiting the success of these introductions.

Marine systems are perpetually threatened by rising numbers of invasions which can cause significant ecological and economic impacts (Ruiz et al. 2000, Sax 2001, Grosholz 2002). In the temperate zone, I found that non-native tertiary consumers create trophic cascades that facilitate non-native basal prey through consumption of a native secondary consumer. In the subtropics however, my results demonstrated that invasive species-induced trophic cascades were weaker under ambient conditions that include the full food web. These conclusions are drawn with caution, as a limited number of study sites in only two regions were used, and encourage further research examining community-level interactions surrounding invasive species at large scales. However,

these results are consistent with longstanding biogeographic hypotheses on species interactions, both in the context of species invasions and community ecology more broadly, that are only just beginning to be tested empirically (Schemske et al. 2009, Freestone et al. 2011, Freestone et al. 2013). As systems become more invaded, understanding interactions among multiple invasive species and in a multi-trophic context is becoming increasingly essential and can help target management plans for areas where invasives may have the highest impact. Additionally, examining invasions from a macroecological perspective can help predict global patterns of native system persistence with continued anthropogenic alteration.

CHAPTER 3

LATITUDINAL GRADIENT IN NICHE BREADTH OF BRACHYURAN CRABS

3.1 Abstract:

Niche breadth has been long hypothesized to decrease at low latitudes and contribute to global species diversity patterns. Range size, phylogenetic relatedness, and body size also have hypothesized relationships with latitude, which may further affect patterns of niche breadth. Existing terrestrial data is inconclusive and little data exist examining a latitudinal gradient in niche breadth in the marine realm. I tested the relationship between latitude and niche breadth in a marine system, while accounting for variation in range size, phylogenetic relatedness and body size. A global dataset was compiled on 39 brachyuran crab species' dietary niche breadth from existing studies and my own analyses on species collected in Connecticut and Florida, USA and Bocas del Toro, Panama. Estimates of latitude, range size, phylogenetic group, and body size were obtained for each species. I then tested for relationships among the focal variables and used model selection to detect their relative importance in predicting diet breadth. Both latitude and range were associated with niche breadth in temperate species, and the latitude-niche breadth relationship was particularly strong for large-bodied species. For tropical species, the only factor predictive of niche breadth was phylogenetic relatedness. I found that latitudinal position was correlated with range size for temperate species, but not for tropical species, and found no correlation between the other focal variables and latitude. I found an interesting division in niche breadth predictors for temperate and tropical species, with temperate species' diets being related to latitude, range size and

body size and tropical species' diets only being related to clade. These results suggest that ecological mechanisms (i.e. competition strength) may be driving patterns of niche breadth in the temperate zone, while evolutionary mechanisms may be more important in predicting niche breadth patterns in tropical systems.

3.2 Introduction:

Niche breadth is defined as the range of environmental conditions and resources a species can utilize, and can range from very broad (i.e., generalist species) to very narrow (i.e., specialist species) (Sa-Oliveira et al. 2014). Species interaction strength, such as competition, may determine niche breadth according to classic ecological theory; weaker species interactions should allow for species to evolve a broader niche (Bolnick et al. 2010). Strong interactions should, over time, drive species to utilize fewer resources and have greater specialization, which in turn should reduce interspecific competition (Bolnick et al. 2010).

It has been long hypothesized that niche breadth varies with latitude (MacArthur 1972). Species diversity peaks in the tropics (Hillebrand 2004a) and studies have shown that species interaction strength varies spatially, being strongest at lower latitudes (Schemske et al. 2009, Freestone et al. 2011). These strong species interactions could drive a higher prevalence of specialist species at lower latitudes, enabling species coexistence and allowing for higher diversity. Although long hypothesized and widely accepted, research on this topic remains inconclusive. Terrestrial studies have shown mixed results (Vazquez and Stevens 2004), with approximately half of existing studies

supporting a latitudinal gradient in niche breadth (e.g. Krasnov et al. 2008, Belmaker et al. 2012 [who specifically examined richness-specialization patterns]) and half refuting (e.g. Fiedler 1998, Slove and Janz 2010). In the marine realm, examination of latitudinal gradients in specialization are rare (but see Rohde 1978, Sunday et al. 2011) and it is unclear how niche breadth relates to latitude in marine species.

Other factors may also be related to niche breadth either alone, or in conjunction with, latitude. Geographical range size, for instance, may be associated with the range of resources a species can utilize (Slatyer et al. 2013), with generalist species having larger ranges and specialist species having narrower ranges. However, range size may also be correlated with latitude; Rapoport's rule predicts that species at higher latitudes have larger ranges on average than species restricted to lower latitudes (Stevens 1989), potentially due to the increased seasonal variability at higher latitudes selecting for broader climatic tolerances (Fernandez and Vrba 2005). Both latitude and range size thus have a hypothesized relationship with niche breadth, but may also be related and could interactively influence niche breadth. For instance, recent research suggests that narrow dietary niche breadth at lower latitudes may be related to smaller range size of low latitude species (Slove and Janz 2010). Phylogenetic conservatism can also affect consumer-resource associations, shaping both niche breadth and species distributions (Barnagaud et al. 2014). Specifically, very closely related species are expected to be more ecologically similar due to niche conservatism (Kerkhoff et al. 2014), thus niche breadth of such species may also be similar. Phylogenetic relatedness may, therefore, limit detectable differences in temperate versus tropical species niche breadth (e.g. Fiedler 1998, Krasnov et al. 2008). Furthermore, conflicting hypotheses exist for the

distribution of related clades across latitude. The 'out of the tropics' model suggests that more species originate in the tropics and then spread towards the poles (Jablonski et al. 2006), in which case newer clades should be more prevalent in the tropics. In contrast, the 'tropical niche conservatism' hypothesis posits that older, more basal clades remain closer to the tropics, and newer derived clades that have overcome the cold winter temperature barrier are more prevalent at higher latitudes (Hawkins and DeVries 2009). Finally, body size has also been proposed to contribute to diet breadth; large species have been suggested to be more generalist, and able to utilize a wider variety of prey resources than smaller species (Ashmole 1968, Novotny and Basset 1999). Support for this hypothesis is mixed, however, and other more recent studies of vertebrate and invertebrate taxa suggest that larger bodied animals may target larger, more energetically profitable prey and thus may be more specialized (Bergmann 1848, Costa et al. 2008, Krasnov et al. 2013). Body size is also predicted by Bergmann's Rule to increase with latitude (Bergmann 1848, Timofeev 2001), with lower average temperatures being a hypothesized driver of larger cell growth (vanVoorhies 1996), resulting in another potentially confounding factor in the niche breadth-latitude relationship.

We therefore examined latitudinal trends in niche breadth using brachyuran crabs as a model system and diet as a measure of niche breadth, while accounting for variation in latitudinal range size, phylogenetic relatedness and body size. Due to limited phylogenetic variation in the brachyuran crab group, and due to mixed support for body size as an important predictor of niche breadth, I hypothesized that these covariates would have limited importance in understanding niche-breadth-latitude relationships in

brachyuran crabs. I therefore predicted that niche breadth would increase with latitude, due solely or in part to a positive range size-latitude relationship.

3.3 Methods:

We conducted a global analysis of brachyuran crab diet by compiling published datasets (n = 30 species) and completing field collections and diet analyses on temperate, subtropical and tropical crabs (n=10 species, one species whose diet had been analyzed in numerous other studies and nine species whose diets had not been previously analyzed). I searched ISI Web of Science for relevant studies using the broad search string 'crab' AND 'marine' AND 'diet.' I then included data from studies that conducted gut content analyses on a population of crabs of one or more species in their native range, and reported the average diet composition of those species as either volumetric proportion (%V) data or frequency of occurrence data (%O). Volumetric proportion (%V) is defined as the estimated volume per prey item in an individual's gut, averaged across all the analyzed guts of that species (total n=100%). Frequency of occurrence (%O) is defined as the number of times a prey item is found in a crab stomach (N_i; for i = category 1 to n), divided by the total number of analyzed guts, multiplied by 100 (total n > 100%).

To supplement the dataset obtained from the literature, gut content analyses were conducted on animals collected from Connecticut and Florida, USA (n=2 native crab species) and Bocas del Toro, Panama (n=8 native crab species). Specimens in each region were gathered at the same time of day (morning), and during the late summer/fall in each region to minimize seasonal and diurnal variability in diet within species.

Specimens were preserved within two hours of collection. For each crab I noted the sex and size, measuring the carapace width to the nearest mm. I then removed the carapace, extracted the stomach with forceps and measured the width of the cardiac stomach (posterior ventral edge) to the nearest mm (Griffen & Mosblack 2011). Using a dissection microscope, I visually identified gut contents for individuals of each species (4-16 individuals per species, N=88) to the lowest possible taxonomic level (Table 3.1). Gut contents were separated by food type into grid cells on a Petri dish. I determined proportional contribution of each food type from the number of grid cells (or portions of grid cells) that each occupied. This provided an estimate of the percent of each food type in the diet (Griffen and Mosblack 2011). I used these data to calculate both volumetric proportion (%V) and frequency of occurrence (%O) of prey items for each species.

In order to standardize the dataset (total n=100%), I converted frequency of occurrence to relative frequency of prey items (Safi and Kerth 2004) using the following equation:

$$\%F = (\%O_i) / \Sigma^{n}_{i=1}(\%O_i).$$

We then calculated Levins' standardized measure of niche breadth (Hurlbert, 1978) using %V and %F data for each species (n=39) as follows:

$$B_A = (B - 1)/(n - 1),$$

where B_A is Levins' standardized niche breadth, B is Levins' measure of niche breadth and n is a constant that reflects the total number of prey resources used across all species. Levins' measure of niche breadth (Levins' B) (Safi and Kerth 2004) was calculated as

$$B = 1 / \Sigma^{n}_{i=1}(\%F_i^2) \text{ or } B = 1 / \Sigma^{n}_{i=1}(\%V_i^2).$$

Standardizing Levins' B puts the measure of niche breadth on a scale from zero to one. Those species with a Levins' B closer to zero have a narrower diet and are more specialized, and those with a Levins' B closer to one have a broader diet and are more generalist. When multiple studies examined the same crab species, I calculated a standardized Levins' B from the average %V or %F of prey items across the studies examining that particular species in order to have one Levins' B per crab species. Most studies had unidentifiable prey items (usually labeled 'detritus' or 'unidentifiable remains'), which were excluded from analyses. Additionally, the way volumetric proportion (%V) values and relative frequency (%F) values are inferred from stomach contents differs fundamentally, so I tested for a relationship between standardized Levins' B values calculated using both %V and %F values, using my own data. Calculations of standardized Levins' B using %V data and %F data had a strong linear relationship ($R^2 = 0.86$, N=10, $p<0.0001$) and Levins' B values using %F data were converted to Levins' B values using %V data using the following equation prior to other analyses:

$$\mathbf{B_{A(from\ \%V\ data)} = 0.5944 * B_{A(from\ \%F\ data)} - 0.0044.}$$

After diet breadth for each species was calculated, I obtained estimates for the focal predictor variables. For each crab species, latitudinal range size and latitudinal position were estimated primarily through species distributions data and species occurrence maps found on the World Register of Marine Species database (WoRMS, http://www.marinespecies.org/). I calculated latitudinal range size (hereafter referred to as range size) by subtracting the degree of latitude of the lowest latitude observations of the species in its native range from the highest latitude extent of the species in either the

northern or southern hemisphere, and then used this data to determine the midpoint of each species' geographic range (hereafter termed latitude). This midpoint approach is generally accepted for use in biogeographic studies (e.g. Johnson 1998, Rohde 1999, Krasnov et al. 2008) justified by the idea that species are likely to have originated near the midpoint of their latitudinal distribution and then spread to adjacent latitudes rather than originating at the limits of their latitudinal distributions (Rohde 1999). Only one species lacked distribution information on WoRMS and for that species I consulted the literature directly to determine its latitudinal distribution (see Table 3.2). Each crab species was then categorized by phylogenetic group; while brachyura is a monophyletic group, it can be divided into seven clades of increasing distance from the ancestral species (Brosing et al. 2007). The 39 species studied fell into three clades: 1) Majoidea, 2) Cancridae/Portunidae/Xanthoidea, and 3) Neobrachyura, with Majoidea being closest to the ancestral species (Brosing et al. 2007). Average body sizes for each species were obtained from the literature (see Table 3.2).

We tested for linear relationships between 1) latitude and range size, as predicted by Rapoport's Rule (Stevens 1989), 2) latitude and clade and 3) latitude and average body size as predicted by Bergmann's Rule (Timofeev 2001) to detect any potential multicollinearity in the dataset. Approximately half of the data was for tropical species (n=18) and the other half was temperate species (n=21), and in these preliminary analyses I found an interesting division in latitude-range size relationships between tropical and temperate species (see Figure 3.1 and results). I therefore proceeded by analyzing tropical and temperate species separately. I examined important predictors of diet breadth for both temperate and tropical species by conducting a backward stepwise

(Neter et al. 1996) model selection using the corrected Akaike Information criterion (AICc) which is an adjusted AIC for small sample size (Burnham and Anderson 2002, Johnson and Omland 2004, Kim et al. 2014). I further calculated Akaike weights (w_i) and evidence ratios (w_j/w_i) for each model for comparison purposes. The predictor variables included in the two full models were as follows: latitude, range size, clade, average body size, body size range of individuals dissected (to control for sample bias in the dataset), sample size for each species (to control for sample bias in the dataset), and interactions between latitude and the focal covariates (see Tables 3.3 and 3.4). One outlier was identified in the dataset, *Callinectes sapidus*, (average body size of 12.2cm, size range 0.1-24cm and sample size of 4117 individuals which was four, eight and 40 times greater than those values for all other crabs respectively [Table 3.2]) and was removed prior to analyses.

Table 3.1: Diets of Crabs Collected in Connecticut, Florida, and Panama: Data is shown as average %V of prey items in diet. Abbreviations are as follows: *A.a. = Armases americanum, C.s. = Callinectes sapidus, M.t. = Macrocoeloma trispinosum, M.b. = Microphrys bicornutus, M.f. = Mithrax forceps, M.s. = Mithrax sculptus, P.h. = Panopeus herbstii, P. lac = Panopeus lacustris, P. lhe = Pitho lherminieri,* and *U.b. = Uca burgersi.*

Prey Categories	*A. a*	*C. s*	*M. t*	*M. b*	*M. f*	*M. s*	*P. h*	*P. lac*	*P. lhe*	*U. b*
Mollusca:										
Class Bivalvia	-	0.168	0.030	-	-	-	0.160	-	-	-
Class Gastropoda	-	0.232	-	-	-	-	0.068	-	0.068	-
Class Cephalopoda	-	-	-	-	-	-	-	-	-	-
Class Polyplacophora	-	-	-	-	-	-	-	-	-	-
Arthropoda:										
Class Insecta	-	-	-	-	-	-	-	-	-	-
Infraorder Brachyura	-	0.040	-	-	-	-	0.013	-	-	-
Infraorder Anomura	-	-	-	-	-	-	-	-	-	-
Suborder Dendrobranchiata	-	0.142	0.018	0.054	0.034	-	0.017	0.082	-	0.003
Infraclass Cirripedia	-	0.032	-	-	-	-	0.044	-	-	-
Subclass Copepoda	-	-	-	-	-	-	-	-	-	-
Order Amphipoda	-		0.060	0.142	0.016	0.023	-	-	-	0.001
Echinodermata:										
Class Ophiuroidea	-		-	-	-	-	-	-	-	-
Class Echinoidea	-	-	-	-	-	-	-	-	-	-
Class Holothuroidea	-	-	-	-	-	-	-	-	-	-
Class Asteroidea	-	-	-	-	-	-	-	-	-	-
Bryozoa	-	-	-	0.029	-	-	0.022	0.029	-	-
Polychaeta	-	0.222	0.352	0.091	0.105	-	0.033	0.000	0.018	-
Fish	-	0.036	-	-	-	-	0.017	0.705	-	-
Foraminifera	-		-	-	-	-	-	-	-	-
Porifera	-	-	0.023	0.047	0.023	0.250	-	-	-	0.006
Urochordata	-	-	0.016	0.029	0.051	-	-	-	-	-
Cnidaria	-	-	0.046	0.077	0.023	-	-	-	0.134	-
Algae	0.496	0.075	0.314	0.484	0.628	0.497	0.145	0.219	0.437	0.099
Vascular plant	0.313	0.024	0.148	0.077	0.037	0.230	0.128	0.018	0.317	0.323
Inorganic Materials	0.169	0.157	0.029	0.035	0.129	-	0.243	0.029	0.027	0.591

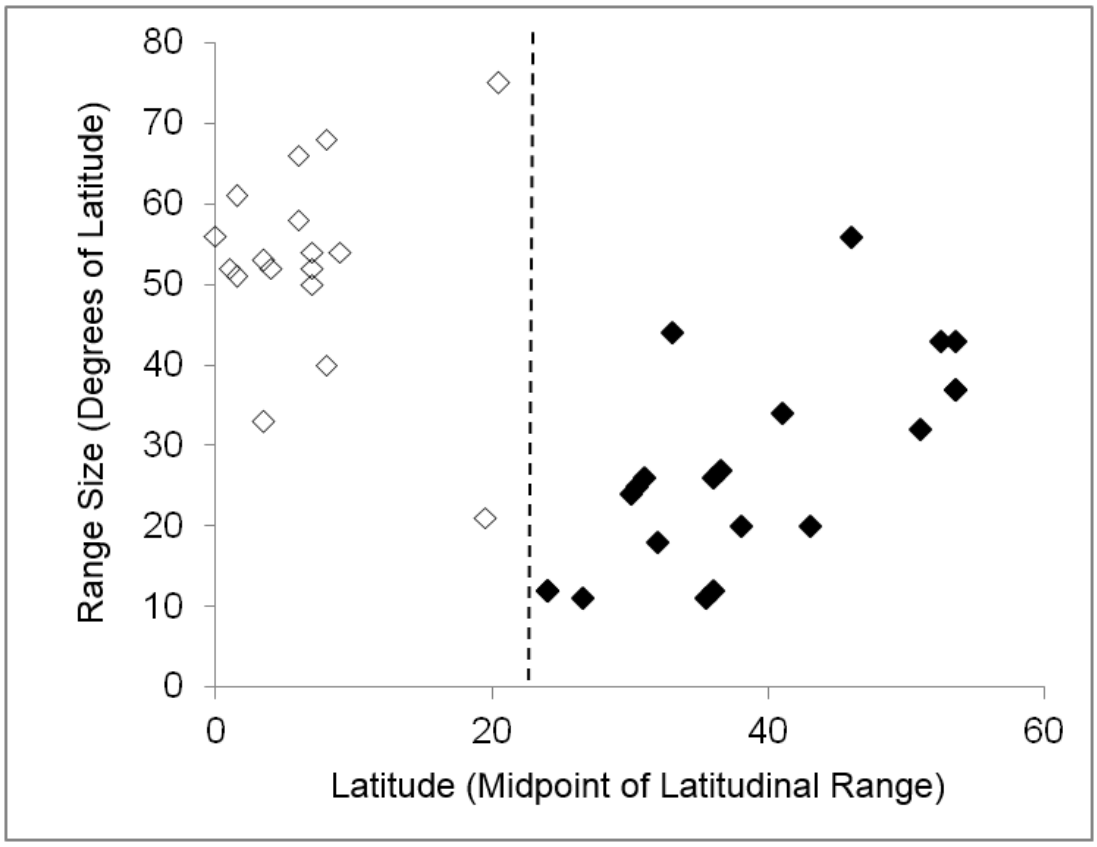


Figure 3.1: Relationship between latitude and range size: Scatter plot of latitude (midpoint of latitudinal range) by range size for both tropical and temperate species. Each point is a brachyuran crab species and the dotted line is at 23.5° which delineates species found in the tropics (open points) from species found in the temperate zone (closed points).

Table 3.2: Full list of species and data included in analyses, and corresponding references: Table is organized by species in alphabetical order. All sample sizes and size ranges are those reported in the respective studies (if not reported, listed as NR), Average sizes were either those reported in corresponding studies or, in the case of

(Table 3.2 Continued)
multiple studies for one species, averaging the reported sizes across those studies. Average sizes for additional species collected in CT, FL and Panama were calculated based on the individuals collected in each region. I was able to obtain sample sizes for 38 of the 39 species analyzed and body size ranges and averages for 37 of the 39 species. Midpoint of latitudinal ranges and range sizes of each species were obtained from the World Register of Marine Species Database (http://www.marinespecies.org/). Only one species, *Chionoecetes japonicas*, was not in the database, therefore latitudinal and range size data for this species were obtained from the reference listed in the table. Species were categorized by clade based on findings from Brosing *et. al, 2007*.

Brachyuran crab species examined	Reference for diet	Sample size (number of non-empty stomachs dissected)	Size range of crab (cm)	Average body size	Midpoint of latitudinal range	Range	Clade
Armases americanum	**Table 3.1**	4	1.2-1.8	1.05	24°N	12	Neobrachyura
Arenaeus cribrarius	(Carmona-Suarez and Conde 2005)	450	0.29-9.89	6.39	30°N	24°	Cancridae, Portunidae, Xanthoidea
Cancer borealis	(Stehlik 1993)	85	7-12.9	9.95	36°N	26°	Cancridae, Portunidae, Xanthoidea
Cancer irroratus	(Stehlik 1993)	142	3.0-12.9	7.95	36.5°N	27°	Cancridae, Portunidae, Xanthoidea
Callinectes sapidus	(Epifanio et al. 2003) (Laughlin 1982) (Meise and Stehlik 2003) (Ropes 1988) (Seitz et al. 2011) **Table 3.1**	52 3200 661 190 NR 14	0.1-3.0 3-13.1 0.5-20 2.6-16.0 0.4-4.0 4.6-10.2	12.2	3°N	84°	Cancridae, Portunidae, Xanthoidea

(Table 3.2 Continued)

Chionoecetes japonicas	(Chuchukalo et al. 2011)	169	7.0-12	9.50	53.5°N (Jadamec *et al.*, 1999)	37° (Jadamec et al. 1999)	Majoidea
Chionoecetes opilio	(Chuchukalo et al. 2011)	147	6.5-10.5	8.50	53,5°N	37° (Jadamec et al. 1999)	Majoidea
Erimacrus isenbeckii	(Chuchukalo et al. 2011)	37	7.0-14.5	10.75	51°N	32°	Cancridae, Portunidae, Xanthoidea
Eurypanopeus depressus	(Lohrer et al. 2000)	30	0.1-2.5	1.30	30.5°N	25°	Cancridae, Portunidae, Xanthoidea
Eurytium limosum	(Kneib and Weeks 1990)	399	1.1-3.7	2.40	24°N	12°	Cancridae, Portunidae, Xanthoidea
Grapsus albolineatus	(Kennish et al. 1996)	190	3.0-5.6	4.30	4°S	52°	Neobrachyura
Libinia emarginata	(Ropes 1988)	30	1.3-9.3	5.30	31°N	26°	Majoidea
Liocarcinus arcuatus	(Freire et al. 1996)	NR	0.1-3	1.55	46°N	56°	Cancridae, Portunidae, Xanthoidea
Liocarcinus depurator	(Chartosia et al. 2010)	278	1.03-3.16	2.10	52.5°N	43°	Cancridae, Portunidae, Xanthoidea
Macrocoeloma trispinosum	**Table 3.1**	9	2.2-3.2	2.7	7°N	54°	Majoidea
Maja squinado	(Bernardez et al. 2000)	308	NR	NR	20.5°N	75°	Majoidea
Metopograpsus thukuhar	(Fratini et al. 2000)	89	0.8-2.2	1.5	8°S	40°	Neobrachyura
Microphrys bicornutus	**Table 3.1**	16	1.0-1.7	1.35	3.5°N	53°	Majoidea
Mithrax forceps (accepted name *Mithraculus forceps*)	**Table 3.1**	9	1.2-1.8	1.5	7°N	52°	Majoidea
Mithrax sculptus (accepted name *Mithraculus sculptus*)	**Table 3.1**	5	1.1-1.6	1.35	19.5°N	21°	Majoidea
Necora puber	(Freire and Gonzalezgurriaran 1995)	575	4.0-7.9	5.95	53.5°N	43°	Cancridae, Portunidae, Xanthoidea
Neopanopeus texana	(Ropes 1988)	56	0.3-1.2	0.75	36°N	12°	Cancridae, Portunidae, Xanthoidea
Ocypode cursor	(Chartosia et al. 2010)	66	NR	NR	9°N	54°	Neobrachyura
Ovalipes	(Ropes 1988)	31	2.7-	6.95	38°N	20°	Cancridae,

(Table 3.2 Continued)

ocellatus	(Stehlik 1993)	73	8.3 5-8.9				Portunidae, Xanthoidea
Pachygrapsus marmoratus	(Chartosia et al. 2010)	176	0.84-1.81	1.33	43°N	20°	Neobrachyura
Plagusia squamosa	(Frick et al. 2011)	5	1.08-1.94	1.51	1°N	52°	Neobrachyura
Panopeus herbstii	**Table 3.1**	4	2.0-5.0	3.5	8°N	68°	Cancridae, Portunidae, Xanthoidea
Panopeus lacustris	**Table 3.1**	4	1.0-2.8	1.9	7°N	50°	Cancridae, Portunidae, Xanthoidea
Pitho lherminieri	**Table 3.1**	10	0.8-1.8	1.3	6°N	58°	Majoidea
Planes major	(Frick et al. 2011)	52	0.43-2.56	1.50	1.5°N	61°	Neobrachyura
Planes marinus	(Frick et al. 2011)	54	1.0-2.15	1.58	33°S	44°	Neobrachyura
Portumnus latipes	(Chartosia et al. 2010)	31	0.81-2.14	1.48	41°N	34°	Cancridae, Portunidae, Xanthoidea
Portumnus lysianassa	(Chartosia et al. 2010)	57	0.46-1.51	0.99	35.5°N	11°	Cancridae, Portunidae, Xanthoidea
Portunus pelagicus	(de Lestang et al. 2000)	465	1.2-15.9	8.55	6°S	66°	Cancridae, Portunidae, Xanthoidea
Selatium elongatum	(Cannicci et al. 1999)	20	2.0-3.6	2.8	3.5°S	33°	Neobrachyura
Sesarum cinereum (accepted name: *Armases cinereum)*	(Seiple and Salmon 1982)	12	1.28-1.95	1.62	26.5°N	11°	Neobrachyura
Sesarma reticulatum	(Seiple and Salmon 1982)	20	1.24-2.06	1.65	32°N	18°	Neobrachyura
Thalamita crenata	(Cannicci et al. 1996)	211	2.5-5.0	3.75	0°S	56°	Cancridae, Portunidae, Xanthoidea
Uca burgersi	**Table 3.1**	13	1.1-1.7	1.4	1.5°N	51°	Neobrachyura

3.4 Results:

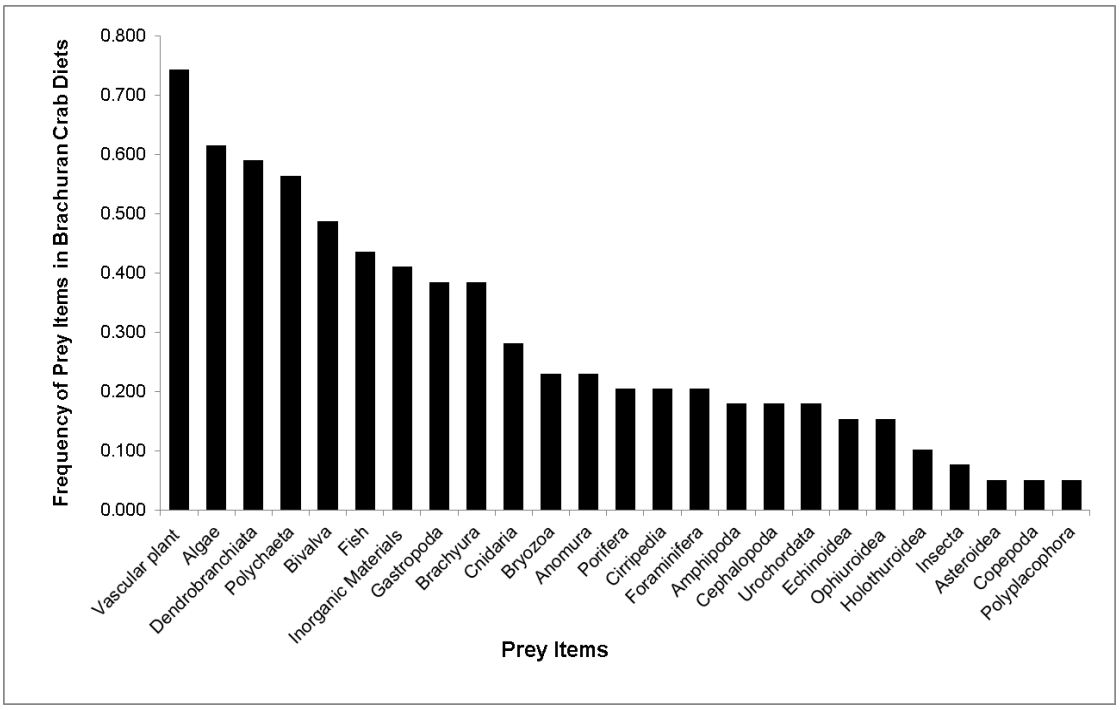


Figure 3.2: Frequency of prey items consumed across all species analyzed: Data calculated by dividing the number of species found to consume each prey item over the total number of species analyzed (n= 39 species).

Overall, brachyuran crabs have broad diets characteristic of generalist species, using prey resources from 25 taxonomic categories (Figure 3.2). Most crabs were found to utilize both plant and animal resources, with crustaceans and mollusks being the dominant animal food groups (Figure 3.2). Plant and algal matter were the dominant prey items used across species, with over 70% of the individuals examined consuming some type of vascular plant and over 60% consuming algal material (Figure 3.2).

Table 3.3: Results of model selection for tropical species: Comparison of the best fit model to the six other models, listing the corrected Akaike information criterion (AICc), the difference from the 'best fit' model (ΔAICc), the Akaike weight (w_i) and the evidence ratio (w_j/w_i) for each model. Main effects are Midpoint of latitudinal range (MLR), Range size (RS), Clade (C), Average Body Size of crabs sampled (ABS), Sample Size for each crab species (SS), and Body size range of crabs within sample (BSR).

Model	# Parameters	Variables Included in Model	AICc	ΔAICc	w_i	w_j/w_i
M7 (Best Fit)	1	*Main effects*: C	**-53.3**	**0**	**0.9**	**1.0**
M6	2	*Main Effects:* RS, C	-48.5	4.5	0.09	9.49
M5	3	*Main Effects:* RS, C, SS	-43.7	9.3	0.009	104.5
M4	4	*Main Effects:* RS, C, ABS, SS	-20.2	32.8	6.77E-08	1.33E+07
M3	6	*Main Effects:* MLR, RS, C, SS *Interactions:* MLR*RS, MLR*C	-2.2	50.8	8.35E-12	1.07E+11
M2	8	*Main Effects:* All *Interactions:* MLR*RS, MLR*C	93.0	146	1.78E-32	5.05E+31
M1 (Full)	9	*Main Effects:* MLR, RS, C, ABS, SS, BSR *Interactions:* MLR*RS, MLR*C, MLR*ABS	301.4	354.4	9.90E-78	9.06E+76

My hypothesis of positive latitude/range size relationships with diet breadth was supported only by temperate species, and not tropical species. Latitude and range size relationships differed significantly for tropical and temperate species (Figure 3.1, Tables 3.3 and 3.4, Figure 3.3). I found no relationship between latitude and range size for tropical species (linear regression: p=0.75, Figure 1a, Appendix S4), but those species found at temperate latitudes had range sizes that increased with latitude (linear regression: p=0.0005, R^2_{adj} = 0.46, Figure 3.1, Figure 3.3b). Latitude and range size were

not strong predictors of tropical species diet breadth (see Table 3.3 for model selection results, Figure 3.3c and 3,3e), however both factors were strong predictors of temperate species diet breadth (see Table 3.4 for model selection results, Figure 3.3d and 3.3f). Species with larger ranges as well as those found at higher temperate latitudes had the broadest diets, while lower latitude temperate species with smaller ranges had narrower diets.

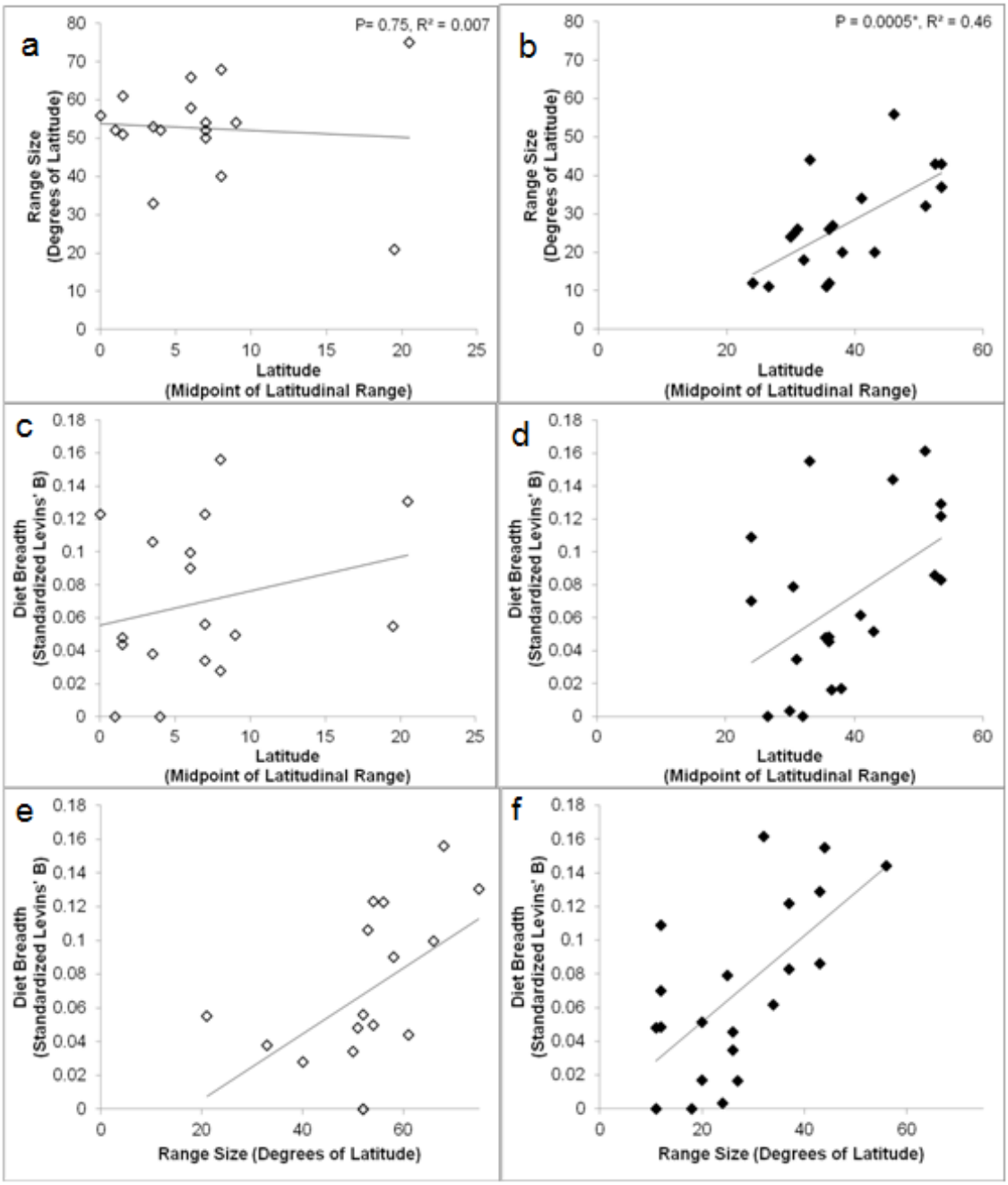
Table 3.4: Results of model selection for temperate species: Comparison of the best fit model to the six other models, listing the corrected Akaike information criterion (AICc), the difference from the 'best fit' model (ΔAICc), the Akaike weight (w_i) and the evidence ratio (w_j/w_i) for each model. Main effects are Midpoint of latitudinal range (MLR), Range size (RS), Clade (C), Average Body Size of crabs sampled (ABS), Sample Size for each crab species (SS), and Body size range of crabs within sample (BSR).

Model	# Parameters	Variables Included in Model	AICc	ΔAICc	w_i	w_j/w_i
M6 (Best fit)	4	*Main Effects:* MLR, RS, ABS *Interactions:* MLR*ABS	**-65.3**	**0**	**0.82**	**1.00**
M7	2	*Main Effects:* MLR, RS	-62.2	3.1	0.17	4.71
M5	5	*Main Effects:* MLR, RS, C, ABS *Interactions:* MLR*ABS	-56.5	8.8	0.01	81.45
M4	6	*Main Effects:* MLR, RS, C, ABS *Interactions:* MLR*C, MLR*ABS	-49.8	15.5	3.52E-04	2.32E+03
M3	7	*Main Effects:* MLR, RS, C, SS, BSR *Interactions:* MLR*C, MLR*ABS	-41.9	23.4	6.77E-06	1.21E+05
M2	8	*Main Effects:* MLR, RS, C, ABS, BSR *Interactions:* All	-30.3	35	2.05E-08	3.98E+07
M1 (Full)	9	*Main Effects:* MLR, RS, C, ABS, SS, BSR *Interactions:* MLR*RS, MLR*C, MLR*ABS	-12.4	52.9	2.66E-12	3.07E+11

No strong relationship was found between clade and latitude for neither temperate nor tropical species (ANOVA for temperate species: R^2_{adj}=0.11, N=21, $F_{2/18}$=2.35, p=0.1, ANOVA for tropical species: R^2_{adj}=0.18, N = 17, $F_{2/14}$ = 2.73, p = 0.1) or range size (temperate species: p=0.4, tropical species: p=0.4). Interestingly, clade was the strongest predictor of diet breadth for tropical species, while it was not retained in the best-fit model for temperate species (Tables 3.3 and 3.4). Those tropical species belonging to the most evolutionarily recent clade, Neobrachyura, had considerably narrower diets than the two older brachyuran clades represented in the dataset (Table 3.3, Figure 3.4).

Figure 3.3: Comparison of the relationships between latitude, range size and diet breadth in tropical and temperate brachyuran crab species: Linear relationships between a) latitude (midpoint of latitudinal range) and range size (degrees of latitude) for tropical species, b) latitude and range size for temperate species, c) latitude and diet breadth for tropical species, d) latitude and diet breadth for temperate species, e) range size and diet breadth for tropical species, and f) range size and diet breadth for temperate species. Each point is a brachyuran crab species. Open points represent tropical species and closed points represent temperate species. Linear regressions were used to analyze relationships between latitude and range size (panels a-b) and model selection was used to test the strength of latitude and diet breadth relationships (panels c-d), and range size and diet breadth relationships (panels e-f). Diet breadth was calculated from the

(Figure 3.3 Continued)
published literature and from my diet analyses on crab species collected in Connecticut, Florida, and Panama (n=21 temperate species, and 17 tropical species). Latitude and range size were both related to diet breadth (as represented by standardized Levins' B values) for temperate species, but neither factor was retained in the best fit model for tropical species.



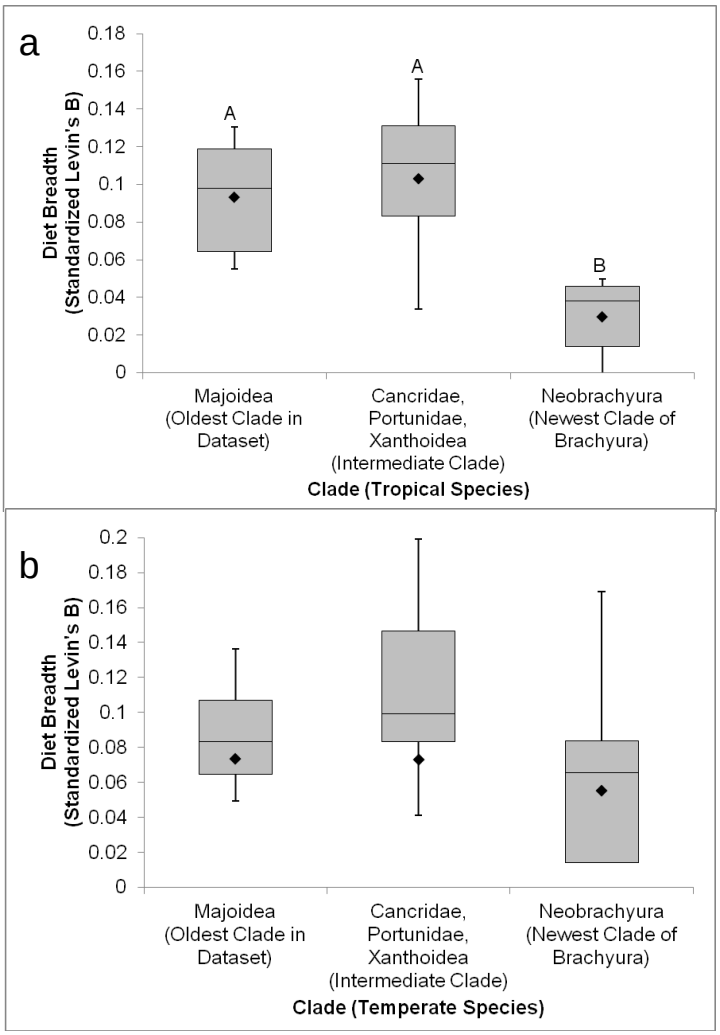


Figure 3.4: Comparison of the relationship between clade and diet breadth for tropical and temperate species: Majoidea is closest to the ancestral species (oldest clade represented in dataset) and Neobrachyura is furthest (newest clade). Data are presented as box plots for (a) tropical species and (b) temperate species; the lower boundaries of the boxes represent the 2nd quartile, the line within the box represents the median, and the upper boundary of the box indicates the 3rd quartile. The bar below the box spans the 1st quartile, and the bar above the box spans the 4th quartile. The means are indicated with individual data points. Different letters above boxes indicate significant differences between groups, as determined using a Tukey's HSD test.

In addition to latitude and range size predicting temperate species diet breadth, the best fit model for the temperate dataset also retained body size and a body size*latitude interaction term (Table 3.3, Figure 3.5). Latitude had a weak relationship with average body size for temperate species, with larger individuals being found at higher latitudes and smaller individuals being found at lower latitudes (linear regression: $R^2_{adj} = 0.16$, N =21, p=0.04, Figure 3.5a). There was not a strong relationship between body size alone and diet breadth (Figure 3.5b), however, the interaction term suggests that the latitude-diet breadth relationship was stronger in the larger-bodied crabs; small-bodied crab diets were not strongly influenced by latitude, while large bodied crabs had broader diets at higher latitudes in comparison to lower latitudes (Figure 3.5c).

Sample size and body size range of crabs used to calculate diet breadth were not included in the best fit models for either the tropical or temperate datasets, indicating that my results are robust to these potentially biasing factors. Evidence ratios indicate that the models including sample sizes were over 100 times and over 12,000 times less likely to predict diet breadth than the best fit model for tropical and temperate species respectively (Tables 3.3 and 3.4). Models including body size ranges were also eliminated early in the selection process (see Akaike weights and evidence ratios in Tables 3.3 and 3.4).

3.5 Discussion:

Increased specialization at lower latitudes was observed for temperate brachyuran crabs, but in contrast, I found no latitude-niche breadth relationship for tropical species. Temperate species niche breadth increased with both increasing midpoint of latitudinal range and range size. I also found that body size and midpoint of latitudinal range had an

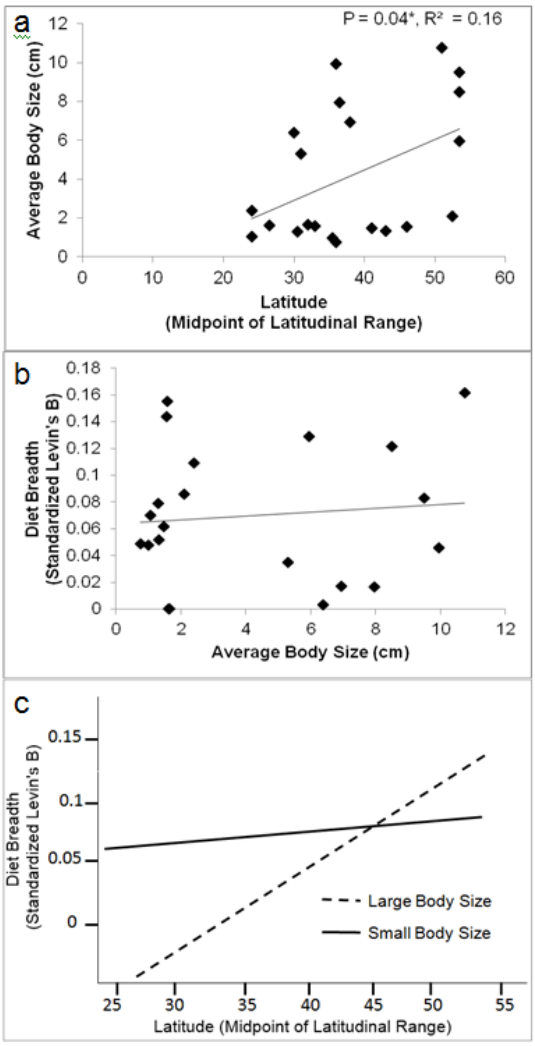


Figure 3.5: Relationships among body size, latitude and diet breadth for temperate crab species: Linear relationships between a) average body size and Levins' B, and b) latitude (midpoint of latitudinal range) and average body size, with each point represents a Brachyuran crab species and c) body size*latitude interaction plot demonstrating both factors' combined effect on diet breadth. Linear regression was used to analyze the relationship between latitude and average body size, and model selection was used to test the strength the average body size relationship with diet breadth, and the body size*latitude interaction relationship with diet breadth.

latitudes in comparison to lower latitudes. The strongest single predictor of diet breadth in tropical species was clade, with the most recent clade having the narrowest diet. There is little marine research exploring latitude-niche breadth relationships. One study examines host-specificity in parasites across latitude (Rohde 1978) and two examine breadth of thermal tolerance with latitude (Sunday et al. 2011) and latitudinal range size (Sunday et al. 2012). In these studies, other possible explanatory variables such as body size and phylogenetic relationships are not examined in conjunction with latitude. By controlling for these other important variables, my results highlight several key mechanisms that may be differentially driving large scale niche breadth patterns in tropical and temperate species.

Clade as the sole factor associated with diet breadth in the tropical dataset suggests evolutionary history may be a key predictor of niche breadth in tropical species. In the tropics, species diversity has been found to be greater than at higher latitudes potentially due to climatic stability, high diversification rates, and/or historical factors (Pianka 1966, Hillebrand 2004a, Jablonski et al. 2006, Mittelbach et al. 2007). New clades in high diversity systems therefore may evolve as specialists as a coexistence mechanism to increase the efficiency of their resource useage and minimize competition with older, more generalist clades. These findings are consistent with evolutionary hypotheses that phylogenetic clustering can lead to ecological divergence of closely related sympatric species (Webb et al. 2002, Losos 2008).

In contrast, evolutionary history was not a strong predictor of diet breadth for temperate species, rather latitude, range size, body size, and a latitude-body size

interaction were found to be important. Body size alone did not strongly influence diet breadth, but the positive relationship between latitude and diet breadth was strongest in large-bodied species. Although it has been suggested that large-bodied species are able to consume a broader range of prey sizes and thus a wider diversity of prey than smaller species (Peters 1983, Diaz 1994), some studies demonstrate that larger-bodied species preferentially target few larger, more energy efficient organisms (e.g. Costa et al. 2008, Costa 2009). These results may suggest that large-bodied crabs utilize these alternative foraging strategies depending on their latitudinal position; large-bodied species at high latitudes may be able to target a wider range of prey due to lower predator diversity (Paine 1966, Hillebrand 2004a, b) and reduced competition (Schemske et al. 2009). As both predator diversity and competition strength are hypothesized to increase at lower latitudes (Paine 1966, Pianka 1966, Coley and Barone 1996, Schemske et al. 2009), specialization may allow more efficient foraging in low-temperate/subtropical large-bodied species.

Brachyuran crabs are considered a generalist taxon (Griffen and Mosblack 2011) and were found to use a wide variety of resources. These results report a conservative estimate of diet breadth, given the course taxonomic resolution (Shkedy and Safriel 1992) of prey items reported in the literature and the lack of data on prey availability (Petraitis 1979). Due to the feeding mode of crabs (McGaw and Reiber 2000) it is challenging to obtain good taxonomic resolution via visual gut content analysis. However, visual gut content analysis was the most commonly used method to examine crab diet and provides a useful but conservative estimate of diet breadth. Additionally, knowing prey availability allows for a more accurate estimate of diet breadth (Petraitis 1979); although

this data was unavailable, based on basic known patterns of species richness (Carr et al. 2003, Hillebrand 2004a) more prey species should be found both at low latitudes and across large ranges. Thus, if prey availability was strongly confounding the observed patterns, large-ranged tropical species should have had the broadest diets in the dataset. However, the high latitude species were found to have the broadest diets overall, and much broader diets on average than tropical species of equivalent range sizes. It is therefore unlikely that prey availability is the major driver of the observed niche breadth patterns.

I found differential support for Rapoport's rule in the dataset, finding no relationship between range size and latitude for tropical species, but a significant positive correlation when examining temperate species. Support for Rapoport's rule varies in the literature (Stevens 1989, Rohde 1999); strong support exists in studies conducted in the northern hemisphere but previous global analyses have found weak patterns (see Ruggiero and Werenkraut 2007). Existing marine studies have found little support for the hypothesis (e.g. Rohde and Heap 1996, Macpherson 2003), and it has been suggested that Rapoport's rule may be weaker in marine systems in comparison to terrestrial systems (Ruggiero and Werenkraut 2007), potentially due to variation in propagule dispersal (Byers and Pringle 2006), larger average scales of connectivity in marine systems (Carr et al. 2003), less temperature variability than terrestrial systems (Sunday et al. 2012) or currents having strong influences on marine species range sizes (Gaylord and Gaines 2000). My results, however, suggest that tropical species with large ranges could also obscure the pattern. Variation in tropical and temperate range patterns may be driven by differences in the abiotic and biotic factors to which they are exposed. For

instance, tropical species ranges are likely restricted by cold boundaries (Sunday et al. 2011, Sunday et al. 2012). As climate is less spatially and temporally variable at low latitudes (Pianka 1966), and the tropics span a wide geographical area (47° of latitude), the entire tropics could be within a tropical species' thermal tolerances. Temperate species ranges are also set by cold boundaries, although they experience more temperature extremes and likely to have broader thermal tolerances (Sunday et al. 2011, Sunday et al. 2012). However, their low latitude range limits are likely set by biotic boundaries such as competitive exclusion from tropical species; species interactions are also determinants of range sizes (Briers 2003, Holt and Barfield 2009) and low-temperate species may have the smallest ranges because they experience these abiotic and biotic limitations on both ends of their ranges.

Overall, only temperate species supported my original hypotheses about latitude and range size relationships with niche breadth. There was a stark division in predictors of temperate and tropical species diet breadths, with temperate species' diets being influenced by latitude, range size and a latitude-body size interaction and tropical species' diets being influenced primarily by evolutionary history. Further research comparing marine and terrestrial, temperate and tropical dynamics is encouraged, as these results suggest that ecological mechanisms (i.e. competition strength) may be driving patterns of niche breadth in the temperate zone, while evolutionary mechanisms may be more predictive of niche breadth patterns in tropical, high diversity areas. These differing mechanisms driving niche breadth may also contribute to large-scale diversity maintenance in both temperate and tropical systems.

CHAPTER 4

RELATIVE IMPORTANCE OF NATIVE AND NON-NATIVE PREY NAIVETE IN MARINE INVERTEBRATE INVASION SUCCESS

4.1 Abstract:

Prey naïveté, which predicts a lack of anti-predator behavior when a prey organism has no evolutionary history with a predator, may be important in early stages of invasion, influencing how quickly an invader is able to spread. Naïveté could act where non-native predators consume more naïve native prey resources leading to resource-driven population growth, or where non-native prey are naïve to native predators, and their population is prevented from growing or undergoes a predator-driven decline. However, an understanding of these behavioral interactions across multiple trophic levels is lacking. I examined the relative importance of prey naïveté across three trophic levels, using marine invertebrates as a model system, specifically native hard clams as basal prey, two invasive crabs (one recent and one long established) as intermediate predators, and a native crab as both an intermediate and top predator in New Jersey, testing two hypotheses: 1) naïveté is greatest in earlier stages of invasion across all trophic levels, decreasing the longer a non-native species is established in a system, and 2) naiveté leads to either a resource-driven increase in invasion success or a negative top predator-driven reduction in invasion success. I conducted a series of laboratory behavioral experiments, assessed predation pressure on focal consumers in the field, and modeled the effects of these tritrophic behavioral interactions on the population of an intermediate predator, a recently-introduced invasive crab species. I found support for naïveté being stronger at

earlier stages of invasion, finding a gradient of antipredator behavior in basal native prey, with naïveté being strongest to the most recent invasive predator. I also observed some naïve anti-predator behavior in the most recent invasive crab in the laboratory, and it was preyed upon more in the field than the long-established invasive and native counterpart. I found little evidence for my second hypothesis, as the model predicted population growth that is independent of basal prey naïveté. These results suggest that physiological traits, such as conversion efficiency and growth rates of the invasive crab may be driving its population growth more-so than foraging benefits. Examining additional components of the food web will be increasingly important in developing a broader understanding of interactions and adaptations within invaded communities.

4.2 Introduction

Species invasions have been long shown to alter ecosystems and are one of the top causes of diversity loss, second only to habitat destruction (Stachowicz et al. 2002). Marine invasions are of particular concern as introductions are increasing with growing trade volume conducted by sea (Kaluza et al. 2010). Once established, non-native species can interact with natives through competition (Byers 2000), facilitation (Altieri et al. 2010) and predation (Sih et al. 2010). Invasive marine predators can alter native food web dynamics, and have a wide range of impacts on native prey communities (Barrio et al. 2010). Understanding native and non-native species interactions is important not only from a management perspective, but this knowledge also enables the study of ecological interactions from a unique evolutionary perspective. Predator-prey interactions are often attributed to coevolutionary history (Barrio et al. 2010, Sih et al. 2010), and it is unclear

how the lack of coevolutionary history between native and non-native species influences these interactions and contributes to the success of non-native species.

Prey naïveté may be important in early stages of invasion, influencing how quickly an invader is able to spread (Sih et al. 2010). This hypothesis predicts a lack of anti-predator behavior when a prey organism lacks coevolutionary history with a predator (Diamond and Case 1986, Freeman and Byers 2006). Prey naïveté is often examined in terms of native prey naïveté to a non-native predator (Sih et al. 2010), and if present, naïveté should increase foraging success, and potentially population growth, of non-native predators. Naïveté can contribute to the lag time of an invasion, and whether or not an invasive species becomes successful (Cox and Lima 2006). Naïveté however is not a permanent phenomenon, and can change temporally as a community adapts to an invasive species (Bool et al. 2011). The length of time for an anti-predator adaptation is dependent on factors such as the prey species and the frequency of encounter with the non-native. These adaptations can occur evolutionarily over several generations (Strauss et al. 2006), or rapidly within a generation through learning (Caller and Brown 2013). Thus, although naïveté may initially boost invasive predator populations, if the native prey survives their initial encounters with the non-native and learns or evolves rapidly, coexistence with the non-native may be possible.

As non-native consumers are often prey themselves, they also face predation risk from higher trophic level consumers and can be at a disadvantage due to their own naïveté (Barrio et al. 2010). While naïveté can act where non-native predators consume more naïve native prey resources, potentially facilitating establishment and leading to

population growth (a resource driven effect), non-native prey could also be naïve to native predators, which could limit population growth (a predator driven effect). This multi-trophic naïveté likely occurs in ecological communities, but the relative importance of native and non-native prey naïveté has not been examined rigorously in either terrestrial or marine systems (Sih et al. 2010). Past studies have primarily examined two trophic levels, either a naïve non-native prey and native predator or a naïve native prey and non-native predator (e.g. Freeman and Byers 2006, Hirvonen et al. 2007, Webb et al. 2008, Barrio et al. 2010, Polo-Cavia et al. 2010, Pease and Wayne 2011). While such studies are extremely valuable, they may limit the ability to extrapolate findings from individuals to the population level as well as to the full community. Multifaceted approaches that incorporate more of the food web and examine multiple angles of naïveté aid in developing a more holistic understanding of interactions and adaptations within invaded communities.

The aim of this study was to determine the relative importance of naïveté across multiple trophic levels, examining naïveté in a native prey and a non-native intermediate predator species. I used a marine invertebrate model system, using a native hard clam as basal prey, two invasive crabs (one recent and one long established) as intermediate predators, and a native crab as both an intermediate and top predator. I tested two main hypotheses. First, naïveté is strongest in earlier stages of invasion across all trophic levels and decreases the longer a non-native species is established in a system. For my second hypothesis, I considered two alternatives: either native basal prey naïveté would result in a resource-driven increase in non-native intermediate predator population growth and invasion success, or predator-driven effects on non-native intermediate predators

would outweigh the importance of basal native prey naïveté, thereby limiting non-native intermediate predator population growth.

4.3 Methods:

4.3.1 Study System:

A marine invertebrate system in Tuckerton, NJ was used to test my hypotheses about temporal variation in prey naïveté and the relative importance of naïveté across trophic levels (Figure 4.1). The community contains two invasive intermediate predator species that differ in time since establishment; the most recent is the Asian shore crab *Hemigrapsus sanguineus* (Fofonoff 2003) which was first sighted in my study area approximately 25 years ago (McDermott 1991). The other invasive, the European green crab *Carcinus maenas,* has been established in the ecosystem for approximately 200 years (Audet et al. 2008). The system also contains the native blue crab *Callinectes sapidus,* the juvenile of the species being an intermediate predator and adults being important top benthic predators in the area (Reichmuth et al. 2009) that are known to structure communities (e.g. Clark et al. 1999). The native clam *Mercenaria mercenaria*, is an important shared prey resource of the three crabs (Arnold 1984, Eggleston et al. 1992, Brousseau and Baglivo 2005, Whitlow 2010) and burrows in the presence of predator chemical cues (Doering 1982), thus serving as an excellent model

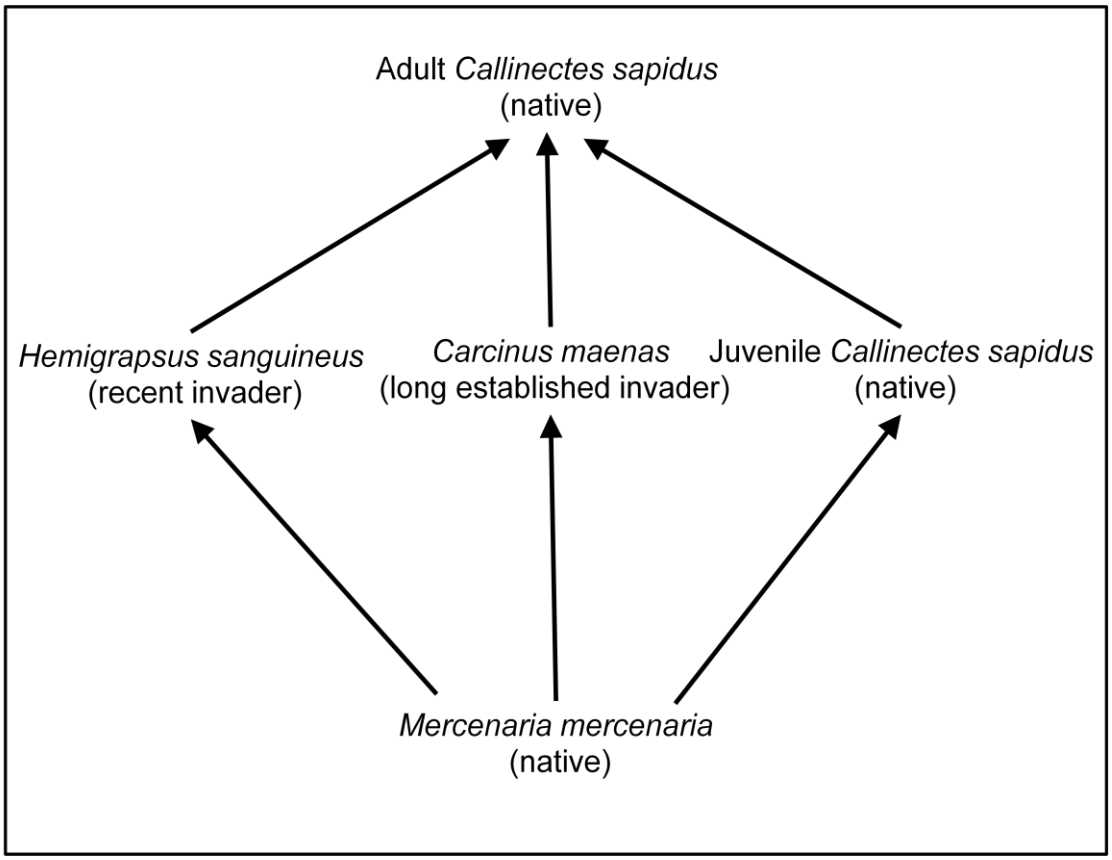


Figure 4.1: Conceptual diagram of feeding interactions examined among focal species: Arrows indicate predation and height on food web indicates trophic level. All predators are crab species. The basal prey species is a clam.

native basal prey. Adult *C. sapidus* readily consume the two non-native crabs (deRivera et al. 2005, K. Papacostas, personal observation). Adult *C. sapidus* are also cannibalistic and can be a major cause of juvenile *C. sapidus* mortality (Hines and Ruiz 1995). This tritrophic system allowed for conducting a temporal comparison of anti-predator behaviors among native (juvenile *C. sapidus*), recent invasive (*H. sanguineus*) and long established invasive (*C. maenas*) intermediate predators, and allowed for a comparison of resource and predation effects on the recent invasive *H. sanguineus.*

Three suites of laboratory experiments, a field experiment, and a population model were used to examine the importance of prey naïveté across multiple trophic levels. In all laboratory experiments, juvenile *M. mercenaria* were 6-18mm in size (average 10.7mm), a size range that all three crab species are able to crush (Arnold 1984, Bourdeau and O'Connor 2003, Miron et al. 2005). *H. sanguineus* size ranged from 16-30mm (average 24mm), *C. maenas* individuals ranged from 40-78mm (average 60mm), *C. sapidus* juveniles ranged from 50-100mm (average 66mm), and *C. sapidus* adults ranged from 110-150mm (average 128mm). All crab species were collected both by hand and through trapping in Little Egg Harbor and Barnegat Bay, NJ and clams were supplied by local hatcheries (see Acknowledgements). All experimental animals were maintained in filtered, aerated laboratory aquaria until use. Clams were fed regularly with cultured phytoplankton. Crabs were fed a mixed diet of clams, mussels and algae, except for those that were used in experiments with live clams, which were instead fed a purely algal diet in order to remove any bivalve chemical cues that may have influenced the clams' behavior over predator scent (Smee and Weissburg 2006). Crabs were not fed for a period of 48 hours prior to experiments to standardize hunger levels. All experiments were run at room temperature (~23°C), using artificial seawater with a salinity of 30ppt, which removed any possibility of external scents or chemical residues from other species in the water.

4.3.2 Detecting native basal prey naïveté - M. mercenaria burrowing experiments:

The first laboratory experiment consisted of burrowing experiments, conducted in the summer of 2012, which examined *M. mercenaria* responses to the intermediate

invasive predator *H. sanguineus* in comparison to the invasive *C. maenas* and the native *C. sapidus*. Clams were introduced into aerated cylindrical mesocosms (30cm in diameter, 37 cm in depth) of sieved locally-collected sediment (15 cm in depth) and artificial seawater and given 24 hours to acclimate, with one clam per mesocosm. After acclimation, clams were subjected to one of four treatments with 10 replicates per treatment: 1) no predator 2) one *H. sanguineus* individual 3) one *C. maenas* individual 4) one juvenile *C. sapidus* individual. Crabs in predator treatments were caged to prevent consumption of clams and the releasing of chemical cues from crushed conspecifics. Trials ran for one week. Burrowing depth was recorded daily, averaged for the week for each replicate. Due to space constraints in the laboratory, two replicates of each treatment (8 mesocosms) were run at a time, resulting in the full experiment being five weeks in duration. At the end of each week, the mesocosms were emptied and thoroughly rinsed with freshwater and allowed to air dry. They were then refilled with sediment and fresh artificial seawater for the next set of trials. The results were analyzed with a mixed model ANOVA in JMP Statistical Software using the REML method, with treatment as a fixed effect and a random blocking effect (trial).

4.3.3 Detecting foraging benefits to invasive intermediate predator from naïve native prey - H. sanguineus foraging experiments:

A second laboratory experiment was conducted in summer 2013 to examine the effects of *M. mercenaria* naïveté on *H. sanguineus* foraging success. *M. mercenaria* were placed within 20 gallon-tanks (base dimensions of 76cm X 32 cm) at densities of 7 clams per tank, which was within the range of natural densities of hard clams in Little

Egg Harbor and Barnegat Bay, NJ (Bricelj et al. 2012). Experimental tanks were aerated and contained 12 cm of water (5cm above the 7cm layer of sieved sediment). *M. mercenaria* were placed in tanks the night before trials to allow them to acclimate. They were then exposed to *H. sanguineus* predation for a 24 hour period, with one crab per mesocosm. Twenty trials were run consisting of 10 trials per treatment: 1) *H. sanguineus* foraging on *M. mercenaria* allowed to burrow naturally (shallower, naïve depth) and 2) *H. sanguineus* foraging on *M. mercenaria* placed at an experienced (deep) burrowing depth of 2.3cm. Experienced depth was determined from the 2012 burrowing experiments, and preliminary trials confirmed that *M. mercenaria* did not move substantially over the 24 hour period. Mesocosms were kept in the dark, and I used red light-illuminated video surveillance to observe the first hour of each trial, recording whether or not prey was detected during that time. After 24 hours, percent mortality of *M. mercenaria* was assessed. Ability to detect prey within the first hour of the trial was compared among treatments with a chi square test, and total *M. mercenaria* consumption after 24 hours was compared among treatments with a t-test.

4.3.4 Detecting invasive intermediate predator naïveté to benthic top predator - intermediate predator behavioral comparisons:

The third set of laboratory experiments, occurring in the summers of 2012 and 2013, examined invasive intermediate predator naïveté to adult *C. sapidus*. These experiments compared *H. sanguineus* and *C. maenas* foraging behavior to that of native juvenile *C. sapidus* when experiencing simulated predation risk through olfactory cues from adult *C. sapidus* (Byrnes et al. 2006). Experiments were conducted in 10 gallon

aerated tanks (32 cm X 26cm X 21cm) which contained 12 cm of water (10cm above the 2cm layer of gravel substrate). The two invasive and one native intermediate predators were exposed to one of two treatments: 1) a control tank with a single food item, an open middle neck clam (width of ~50-60mm), and an empty translucent container next to the food item and 2) a tank containing an adult *C. sapidus* caged in a translucent container next to the food item. Intermediate predators were first introduced into translucent containers at opposite ends of the tank, where they were allowed to acclimate for 10 min prior to trials with the aeration on to disperse scents throughout the tank (MacDonald et al. 2007). Then, aerators were turned off, focal intermediate predators were released from their containers, and observations were taken over a 15 minute period for each replicate with 10 replicates per treatment (top predator present or top predator absent) per species (*H. sanguineus, C. maenas, or* juvenile *C. sapidus*) for a total of 60 trials. Observations included 1) the time it took for each crab to find the food, 2) the time spent consuming food, and 3) the amount of still time where the crab remained unmoving. Data were analyzed using an ANOVA with fixed effects of treatment, species and the interaction term species*treatment. Planned comparisons were used to compare *H. sanguineus* responses to *C. maenas* and *C. sapidus* responses.

4.3.5 Detecting consumer pressure on focal intermediate predators - tethering experiment:

To extrapolate findings from the laboratory to what may occur in nature, predation rates were compared on *H. sanguineus, C. maenas,* and *C. sapidus* in the field in the summer of 2013. Since the three species vary in the average size of adults

(Grosholz and Ruiz 1996, McDermott 1998, Chenery 2002) the experiment was standardized by collecting individuals of each species and matching them by weight (8g-42g). Intermediate predators (3-4 individuals/species) tethered using braided microfilament line and cyanoacrylate adhesive, were attached to 1.5 ft stakes and placed in open, soft sediment habitats 10 feet apart to minimize multiple predation events caused by a single predator. I confirmed in previous experiments that, when using this method, the removal of crabs are indicative of predation events and not tether failure (see Chapter 3). Intermediate predators were tethered for a 24 hour period and mortality of the individuals of each species was assessed and analyzed using a Pearson's chi square test.

4.3.6 Modeling population growth of most recent invasive intermediate top predator:

Finally, in order to detect the importance of resource naïveté and predation effects for the local population growth rate of *H. sanguineus*, a deterministic model was employed based on parameters obtained from the literature and determined through field surveys and laboratory observations. In simplest terms, the predator-prey dynamics of an intermediate predator species in a food chain can be modeled as

$$dY/dt = Y(e_{XY}A_{XY}X - e_{YZ}A_{YZ}Z), \quad (1)$$

where *Y, X* and *Z* are the densities of the intermediate predator (*H. sanguineus*), the intermediate predator's prey (*M. mercenaria*) and the top consumer of the intermediate predator (*C. sapidus*) respectively (derived from Wollrab et al. 2012). Conversion efficiency of consumed prey *X* into intermediate predator *Y* is represented by e_{XY} and conversion efficiency of consumed intermediate predator Y into top predator Z is represented by e_{YZ}. A_{XY} and A_{YZ} are type 2 functional responses of consumer (*Y* in the

case of A_{XY} and Z in the case of A_{YZ}) feeding on its prey resource (X in the case of A_{XY} and Y in the case of A_{YZ}). A_{XY} and is described by

$$\boldsymbol{A_{XY} = a_{XY} / (1 + a_{XY} h_{XY} X)}, \qquad \textbf{(2)}$$

and A_{YZ} is described by

$$\boldsymbol{A_{YZ} = a_{YZ} / (1 + a_{YZ} h_{YZ} Y)}, \qquad \textbf{(3)}$$

where a_{XY} and a_{YZ} are attack rates of the intermediate predator Y and top consumer Z on their prey respectively, and h_{XY} and h_{YZ} are the intermediate predator and top predator handling time of their prey resource respectively (Wollrab et al. 2012).

To parameterize this model, four parameters were derived from existing literature (X (Tarnowski and Bussell 2011), Z (Jivoff 2011), e_{XY} (Lin et al. 2010) and e_{YZ} (Jin et al. 2013), three parameters were empirically determined (Y, a_{XY}, a_{YZ}), and two parameters were both empirically determined and derived from the literature (h_{XY} and h_{YZ}). To determine Y (population density of non-native intermediate predator *H. sanguineus*), two surveys were conducted in Tuckerton, NJ, one using 0.3x0.3m quadrats (n=15) and one using 0.6x0.6m quadrats (n=21) during the summer of 2013. Attack rate (a_{XY}) of *H. sanguineus* on its prey *M. mercenaria* was determined in the laboratory by recording successful attack events per day on *M. mercenaria* (a_{XY}) at natural densities (Bricelj et al. 2012) allowed to burrow naturally to their naïve depth (10 trials) and artificially placed at their experienced burrowing depth (10 trials). These data were collected during the *H. sanguineus* foraging experiments described above. Handling time (h_{XY}), which is defined as the time taken to process prey (Wollrab et al. 2012) was estimated by adding known digestion rates (McGaw and Curtis 2013) to observed consumption rates in the lab. Consumption rate was estimated by observing the videos recorded during *H. sanguineus*

foraging experiments described above, and averaging the time taken for a *H. sanguineus* individual to consume a *M. mercenaria* individual across the ten trials. This consumption rate was then added to the digestion rate of a closely related crab species *Hemigrapsus nudus* (McGaw and Curtis 2013) in order to estimate handling time (h_{XY}).

Attack rate of *C. sapidus* on its prey *H. sanguineus* (a_{YZ}) was determined similarly, by recording successful attack events per day on *H. sanguineus* at natural densities; handling time (h_{YZ}) was estimated by adding the observed consumption rate to the known digestion rate for *C. sapidus* obtained from the literature (McGaw and Curtis 2013). To observe consumption rate and estimate *C. sapidus* attack rates, *H. sanguineus* individuals were placed within 20 gallon tanks (base dimensions of 76 X 32 cm) at densities of two crabs per tank, which was the natural density scaled to the tank as determined from the *H. sanguineus* field surveys described above. Experimental tanks were aerated and contained 12 cm of water (5cm above the 7cm layer of sieved sediment). *H. sanguineus* was exposed to *C. sapidus* predation for a 24 hour period, with one adult *C. sapidus* crab per tank. During the trials (10 total), mesocosms were kept in the dark and I used red light-illuminated video surveillance to observe the first hour of each trial, recording how long *C. sapidus* took to detect and consume prey. After 24 hours, attack rate was assessed as successful attack events per day.

Conversion efficiencies e_{XY} and e_{YZ} were derived from the literature of related species, *Eriochier sinensis* (Lin et al. 2010), which is in the same family, Grapsidae, as *H. sanguineus* (Board 2014) and *Portunus trituberculatus* (Jin et al. 2013), which is in the same family, Portunidae, as *C. sapidus* (Board 2014). Conversion efficiencies were reported as grams of prey intake/grams of predator wet weight gain. To standardize the

units of the model, e_{XY} and e_{YZ} were converted to predator individuals gained/prey individuals consumed; for *H. sanguineus* individuals gained/*M. mercenaria* individuals consumed, I averaged the carapace widths of both males and females from the field surveys (n=76), and then converted average carapace width to wet weight using known carapace width-wet weight relationships for both male and female *H. sanguineus* (Klassen 2012) to determine the average weight per individual. I then found the average wet weight of *M. mercenaria* of the size class used in this study from the literature (Power et al. 2003), and used this weight in grams of an average individual *H. sanguineus* and weight in grams of an average individual *M. mercenaria* to convert the e_{XY} from gram/gram to the desired individual/individual units. E_{YZ} was converted in the same manner; carapace width was converted to wet weight using known carapace width-wet weight relationships for *C. sapidus* (Muffley et al. 2007) and *H. sanguineus* (Klassen 2012). Using these data, two simulations were run using the two different *H. sanguineus* attack rates on clams at a naïve depth versus clams at an experienced depth determined from the laboratory trials (see Table 4.1 for full list of parameter values). I then compared population doubling times in naïve and experienced prey scenarios.

Both *C. sapidus* and *M. mercenaria* populations (parameters *X* and *Z*) were assumed constant for the purposes of this model. Densities used were those recorded for Little Egg Harbor, Barnegat Bay and surrounding areas in NJ(Jivoff 2011, Tarnowski and Bussell 2011, Bricelj et al. 2012). *C. sapidus* is the subject of commercial and recreational fisheries

Table 4.1: Full list of model parameters

Parameter	Parameter description	Units of Measure	Value	Estimated empirically (E) or from literature (L)	Source
Y	*H. sanguineus* density	individuals/ meter^2	5.5	E	N/A
X	*M. mercenaria* density	individuals/ meter^2	15	L	(Tarnowski and Bussell 2011)
Z	*C. sapidus* density	individuals/ meter^2	1	L	(Jivoff 2011)
e_{xy}	Y conversion efficiency	originally g/g but converted to individuals Y gained/ individuals X consumed	$2.3x10^{-4}$	L	(Lin et al. 2010) for *E. sinensis*
a_{xy}	Y attack rate on X	average successful feeding events/day	2.1	E	N/A
h_{xy}	Y handling time of X	time (days) from start of feeding to digestion of meal	1.24	E (start to finish of feeding) and L (digestion time)	(McGaw and Curtis 2013) for *H. nudus*
e_{yz}	Z conversion efficiency	originally g/g but converted to individuals Z gained/ individuals Y consumed	$7.70x10^{-5}$	L	(Jin et al. 2013) for *Portunus sp.*
a_{yz}	Z attack rate on Y	average successful feeding events/day	1.44	E	N/A
h_{yz}	Z handling time of Y	time (days) from start of feeding to digestion of meal	1.22	E (start to finish of feeding) and L (digestion time)	(McGaw and Curtis 2013) for *C. sapdius*

throughout the mid-Atlantic United States (Jordan 1998) and the species has experienced declines in certain areas due to overfishing (Muffley et al. 2007). In New Jersey, the population fluctuates (Jivoff 2010), but stock depletion is currently reported to be low (Mizerek 2012). *M. mercenaria* populations underwent declines in NJ and other Atlantic coastal areas in the late 1900s due to overfishing, and other factors, although restoration efforts are in progress to maintain the population and prevent further losses (Bricelj et al. 2012). Assuming *C. sapidus* and *M. mercenaria* populations as constant is a simplification and a limitation to the model, as their population dynamics are complex (Miller 2001, Muffley et al. 2007, Bricelj 2009). However, as public awareness has grown in recent years and monitoring and management projects are in place in NJ and in surrounding states to preserve both species and establish sustainable fishing practices (Bricelj et al. 2012, Mizerek 2012), assuming them as constant is one possible scenario if such efforts are successful. If populations decline, then the results produced by this model would represent both species maximum impact on *H. sanguineus*.

4.4 Results:

4.4.1 Detecting native basal prey naïveté - M. mercenaria burrowing experiments

These results demonstrate naïveté at the level of basal prey; I found that *M. mercenaria* did not change its antipredator behavior when exposed to *H. sanguineus* chemical cues. *M.*

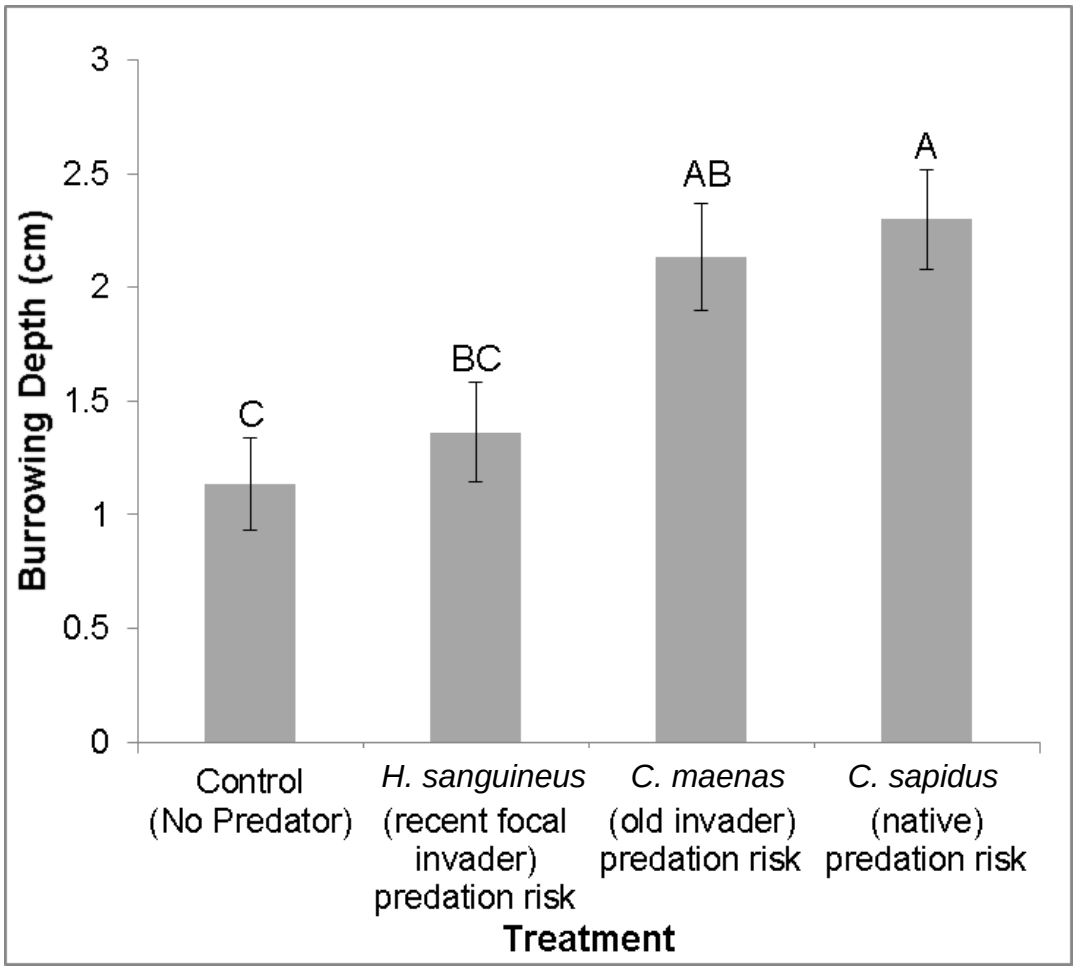


Figure 4.2: Results of *M. mercenaria* burrowing experiments: Mean depth over seven-day trials measured in centimeters. Error bars indicate standard error and different letters above bars indicate significant differences between treatments, as determined using a Tukey's HSD test.

mercenaria burrowing depth was no different in the presence of H. sanguineus than the control treatment with no predators (Figure 4.2, ANOVA full model: R^2_{adj}=0.3, $F_{3/32}$=6.71, N = 40, p<0.0001). It burrowed deepest in the presence of *C. sapidus*, clearly recognizing the native intermediate predator as a threat. In the presence of *C. maenas*, *M. mercenaria* burrowed to an intermediate depth that was not significantly different from either the burrowing response to *C. sapidus* or *H. sanguineus*.

4.4.2 Detecting foraging benefits to invasive intermediate predator from naïve native prey - H. sanguineus foraging experiments

Our results further demonstrate that *H. sanguineus* gains a direct foraging benefit from naïve *M. mercenaria*. Preliminary trials confirmed that *M. mercenaria* individuals did not move significantly over a 24 hour period when placed to a specific depth (n=10), thus I was able to simulate experienced prey in this series of trials. In the filmed first hour of these experiments, *H. sanguineus* was able to detect prey with higher frequency when *M. mercenaria* were at their naïve depth in comparison to their deeper experienced depth (Figure 4.3a, Pearson's Chi Square: p=0.039*, N=19). Furthermore over a 24 hour period, *H. sanguineus* consumed significantly more *M. mercenaria* when they were allowed to burrow naturally to their naïve depth in comparison to those placed at their experienced depth (Figure 4.3b, t-test: R^2_{adj}=0.22, $F_{1/19}$=6.78, N=21, p=0.017*).

4.4.3 Detecting invasive intermediate predator naïveté to benthic top predator and consumer - intermediate predator behavioral comparisons:

I did not find support for naïveté of the recent intermediate non-native predator to a native top predator in terms of altered foraging behavior, but did observe naïve behavior in terms of effective predator avoidance. There was a marginally significant difference in the time it took to find food in the presence or absence of adult *C. sapidus* for all species (ANOVA full model: R^2_{adj}=0.094, N=60, $F_{5/54}$=2.2182, p=0.0657), but no difference among species. There was a significant treatment effect (p<0.0047*), but neither species (p=0.56) nor the interaction between species and treatment (planned comparison: $F_{1/54}$ =0.1, p=0.8) were significant. Additionally, all

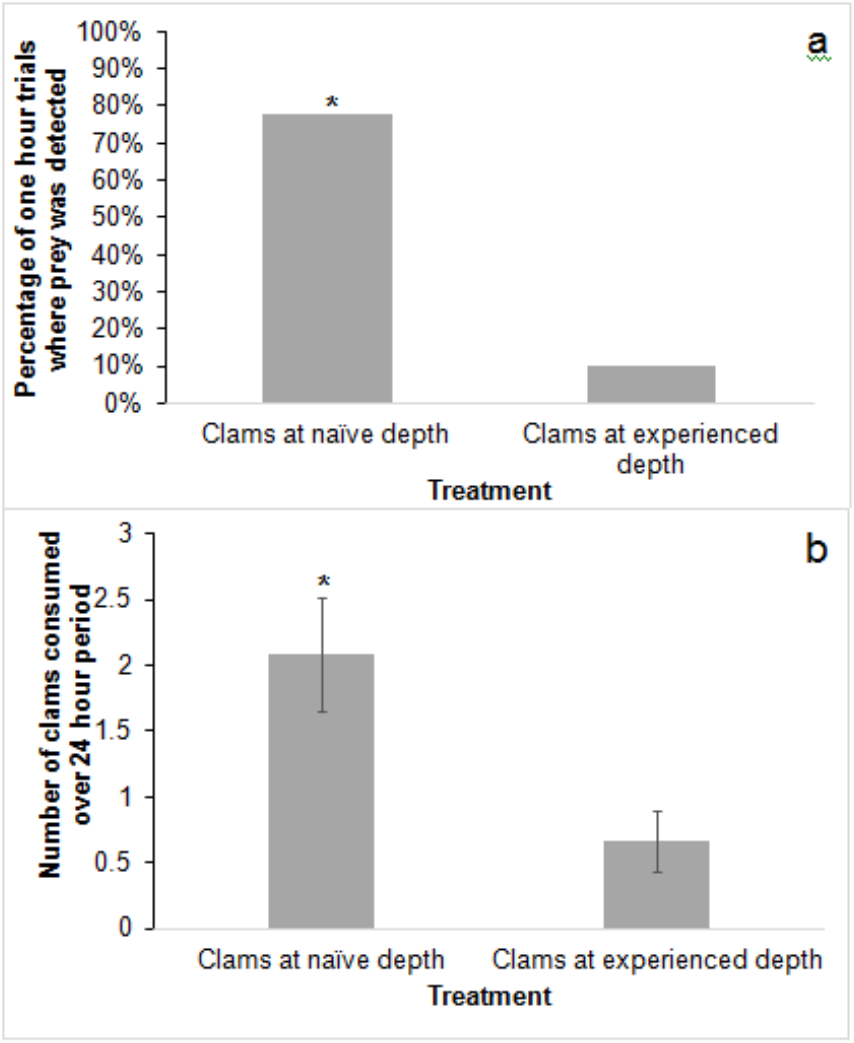


Figure 4.3: Comparison of *H. sanguineus* foraging success on *M. mercenaria* at naïve and experienced burial depths (*H. sanguineus* foraging experiments): a) Detection of *M. mercenaria* when at naïve versus experienced burial depth during the first hour of 24 hour trial and b) total *M. mercenaria* consumption after 24 hours when burrowed at both a naïve and experienced burial depth (error bars indicate standard error). A star indicates a significant difference between treatments. Results show *H. sanguineus* detecting and consuming prey at higher frequencies when *M. mercenaria* are burrowed at a naïve depth.

crabs reduced feeding time in response to predator chemical cues (Figure 4.4a, ANOVA full model: R^2_{adj}=0.22, N=60, $F_{5/54}$=4.23, p=0.003*), and there was no indication of *H. sanguineus* naïveté in terms of altered foraging. There was a highly significant treatment effect (p<0.0001*), but again species (p=0.8) and the interaction between species and treatment (planned comparison: $F_{1/54}$=1.5, p=0.2) were not significant. The average time spent still during the trials, however, did change in the presence and absence of a predator, and depended on the species (Figure 4.4b, ANOVA full model: R^2_{adj}=0.32, N=60, $F_{5/54}$=6.52, p<0.0001*). There was a highly significant treatment effect (p<0.0001*), a significant effect of prey species (p=0.02*), and a significant interaction term (planned comparison: $F_{1/54}$ =4.15, p=0.047*). Juvenile *C. sapidus* and *C. maenas* remained still throughout the majority of the trials in the presence of adult *C. sapidus*, indicating predator avoidance (Figure 4.4b). *H. sanguineus* continued to move in the presence of the predator, providing the first evidence of potential naïveté. Therefore, *H. sanguineus* reduces its foraging time in the presence of adult *C. sapidus* but still remains active, and such behavior could reduce its ability to effectively avoid predation by adult *C. sapidus*.

4.4.4 Detecting consumer pressure on focal intermediate predators - tethering experiments:

In the field, I observed a higher predation rate on the recent intermediate invasive predator in comparison to the long established invasive and the native counterpart (Chi-square test: p=0.03*, N=11). During the 24 hour tethering experiment, all *H. sanguineus*

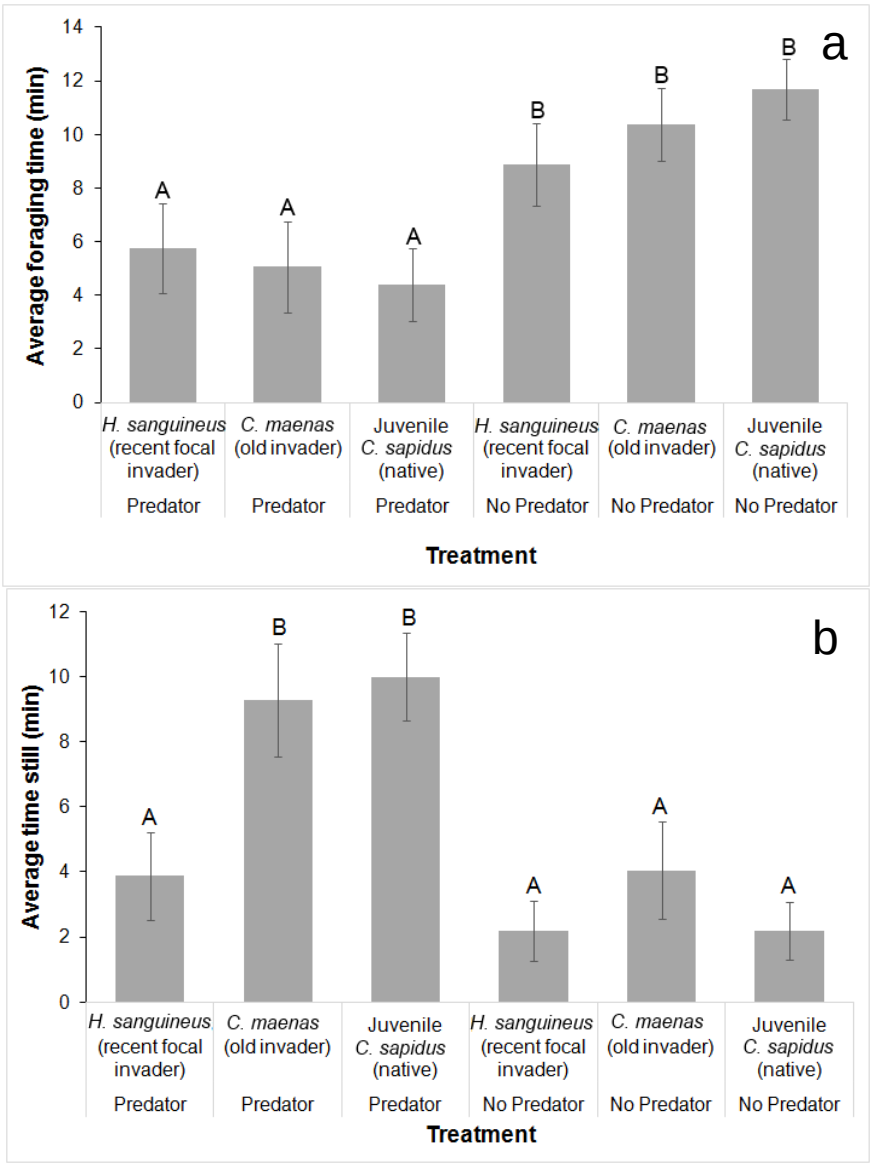


Figure 4.4 Results from intermediate crab behavioral comparisons in the presence or absence of a top predator: Time (in minutes) intermediate predators spent a) foraging and b) unmoving in the presence or absence of top predator. Error bars indicate standard error and different letters above bars indicate significant differences, as indicated by planned comparisons analysis. Results show a) all intermediate predators altered their foraging time in the presence or absence of the top predator but b) *H. sanguineus* continues to move in the presence of the top predator, whereas *C. sapidus and C. maenas* remain still.

individuals were consumed, one juvenile *C. sapidus* was consumed, and one *C. maenas* was consumed.

4.4.5 Modeling population growth of non-native intermediate predator

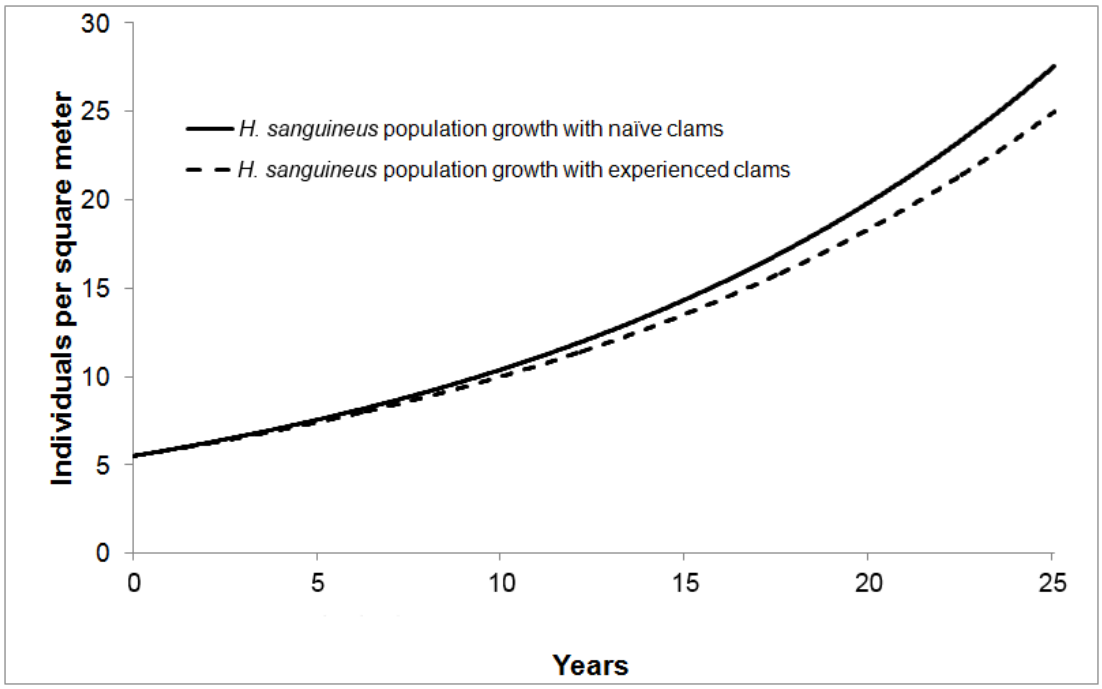


Figure 4.5 Projected population growth of *H. sanguineus* over 20 years: Reported in individuals per square meter when *M. mercenaria* are naïve compared to if *M. mercenaria* are experienced.

Model output showed an increase in the *H. sanguineus* population in both naïve and experienced prey scenarios (Figure 4.5). According to the model, the *H. sanguineus* population would double in 10.8 years if *M. mercenaria* were to continue to exhibit naïve behavior compared to 11.5 years if *M. mercenaria* were experienced or were to rapidly lose their naïveté (Figure 5). The population would double a second time (22 individuals per meter^2) in naïve and experienced prey scenarios in 21.5 and 23 years respectively.

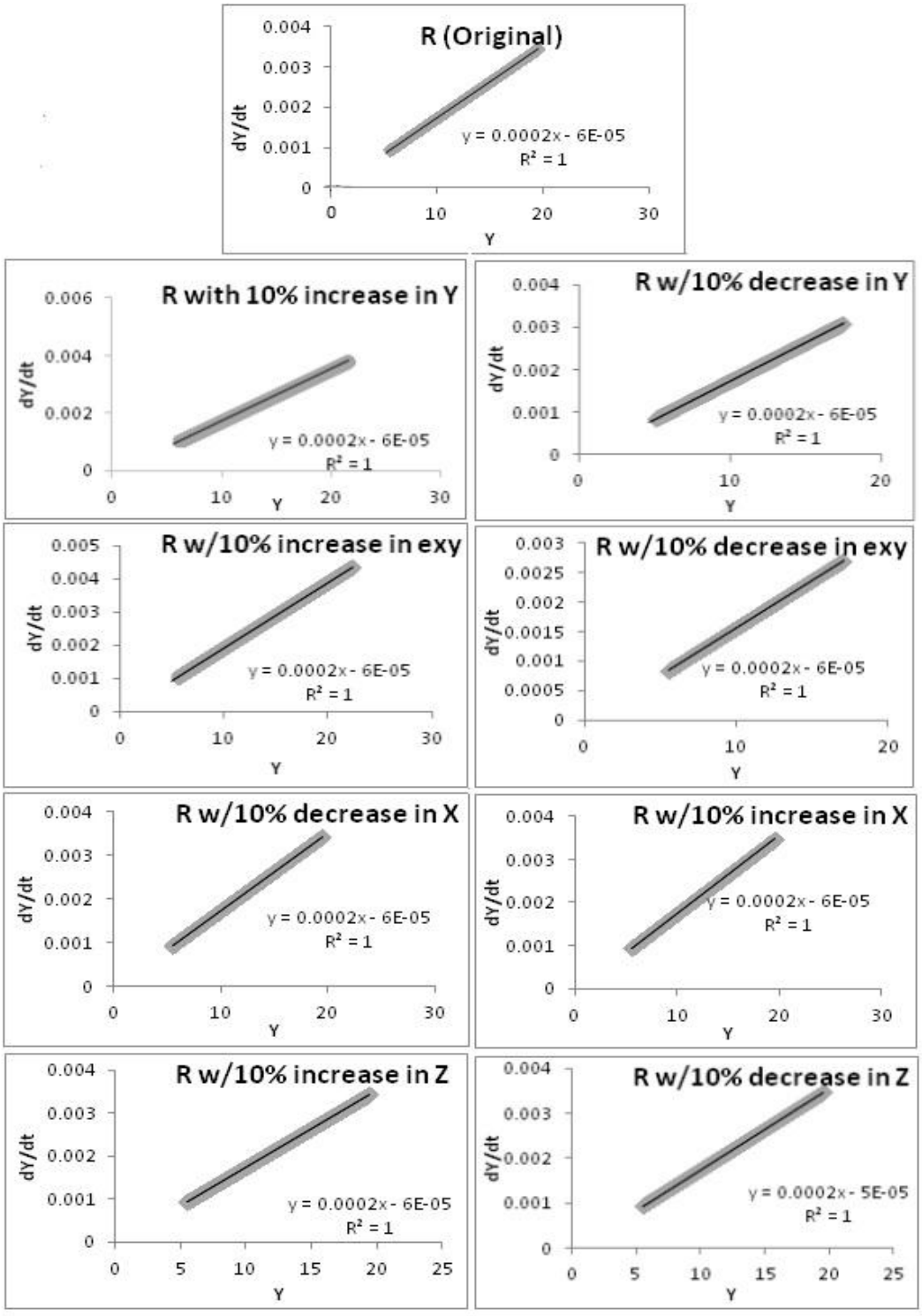
Thus the model predicts that the *H. sanguineus* population would increase with or without prey naïveté, albeit at a slightly slower rate with naïveté.

The model was robust to parameter variation; sensitivity analyses were carried out in order to detect potential effects of uncertainty on *H. sanguineus* population growth (see Appendix B for results of sensitivity analyses). A 10% increase or decrease in parameters X (*M. mercenaria* density), Z (*C. sapidus* density), a_{xy} (*H. sanguineus* attack rate on *M. mercenaria*), a_{yz} (*C. sapidus* attack rate on *H. sanguineus*), h_{yz} (*C. sapidus* handling time of *H. sanguineus*) and e_{yz} (*C. sapidus* estimated prey conversion efficiency) resulted in a maximum of +/- 0.3 years in population doubling time. The only parameters that varied the population doubling time by more than 0.3 years were Y (*H. sanguineus* density), e_{xy} (*H. sanguineus* estimated prey conversion efficiency) and h_{xy} (*H. sanguineus* handling time of clams). Increasing Y by 10% resulted in doubling time occurring 1.3 years earlier and decreasing by 10% resulted in doubling time occurring 1.5 years later than the original model. Increasing and decreasing e_{xy} by 10% resulted in doubling time changing by 0.8 and 1.5 years respectively and increasing and decreasing h_{xy} by 10% resulted in a 1.3 and 0.9 year change in population doubling time respectively. However, all rates of change were proportional to the % change in the parameter, indicating a robust model (Figure 4.6).

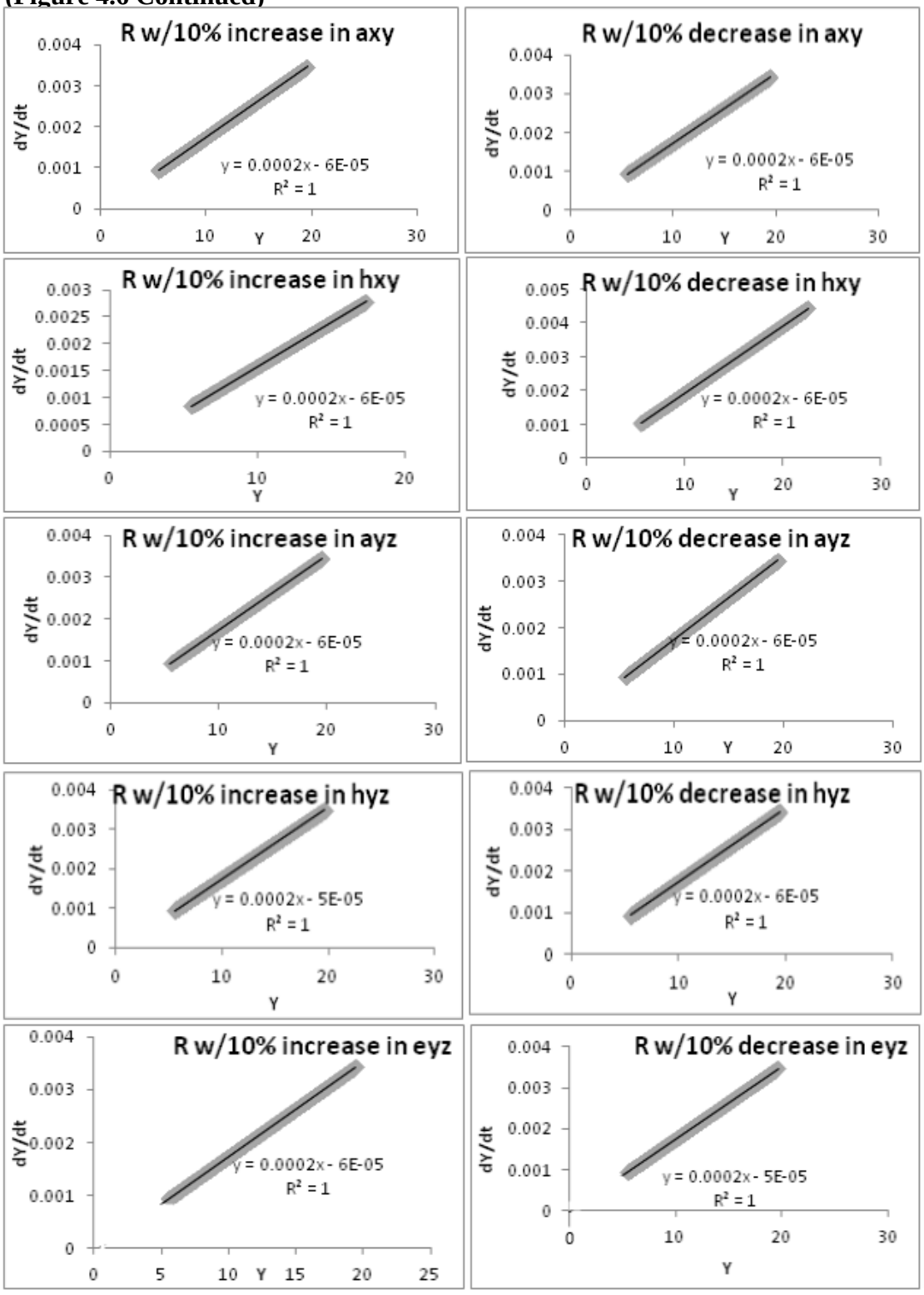
4.5 Discussion:

Based on these results, *M. mercenaria* exhibits naïve behavior to *H. sanguineus* which directly benefits the invasive intermediate predator's foraging success. The basal prey showed a gradient in its behavioral response to predation risk by the three intermediate predators, burrowing deepest in the presence of *C. sapidus* (native species),

Figure 4.6:Sensitivity analyses for population model: Rate of change due to a 10 % increase or decrease of each parameter.



(Figure 4.6 Continued)



an intermediate depth in the presence of *C. maenas* (long-established invasive species), and shallowest in the presence of *H. sanguineus* (newly established invasive species). All three predators are functionally similar toone another as they consume bivalve prey via crushing and prying open of shells (Bourdeau and O'Connor 2003, Moody and Aronson 2012, Schaefer and Zimmer 2013). This gradient in burrowing response could be due to differences in coevolutionary history. It could also be due to the potential chemical similarities between *C. maenas* and *C. sapidus*, as they are phylogenetically and taxonomically more similar to one another than to *H. sanguineus* (Brosing et al. 2007) and may produce similar cues which *M. mercenaria* recognizes. Little research has been done on chemical cue similarities among related species in aquatic systems, so it is unclear whether the burrowing response to *C. maenas* is more likely due to evolutionary history or chemical similarity to the native *C. sapidus*. In New Jersey the only native Grapsid crab (family that includes *H. sanguineus*) is *Sesarma reticulatum* (McDermott 1998); this species has been recorded to primarily consume plant and algal matter, and mollusks have not been found to contribute to their diet (Seiple and Salmon 1982). It is therefore probable that *H. sanguineus* produces chemical cues that *M. mercenaria* does not recognize since it has never had prior exposure to a Grapsid predator. Population turnover of *M. mercenaria* is on the order of 8-10 years in Barnegat Bay and Little Egg Harbor, NJ (Bricelj et al. 2012), so only 1-2 generations of clam have been exposed to *H. sanguineus* compared to 20-25 to *C. maenas*. With several more generations it is likely that the population will adapt its burrowing response as prey often shift to more adaptive antipredator behavior after the initial period of strong predation (Losos et al. 2006, Strauss et al. 2006).

We found some support for *H. sanguineus* naïveté to adult *C. sapidus* predators in that it recognized *C. sapidus* as a predator, but demonstrated an ineffective predator avoidance behavior. *H. sanguineus* reduced its food consumption in the presence of adult *C. sapidus*, which is indicative of predator recognition. However, *H. sanguineus* individuals exhibited a very different predator avoidance strategy than juvenile *C. sapidus* or *C. maenas,* in that they continued to move in the presence of adult *C. sapidus* while the other intermediate predators remained still through the majority of those trials. *C. sapidus* is an excellent visual predator (Baldwin and Johnsen 2011) and this excess movement of *H. sanguineus* could potentially increase the top predator's detection and attack rates on the recent intermediate invasive predator. Furthermore, *C. sapidus* is a fast-moving swimming crab (Woodbury 1986) and likely to outmaneuver smaller, slower prey, such as walking crabs like *H. sanguineus*. Remaining unmoving in an attempt to avoid initial detection, therefore, is a much more effective predator avoidance strategy, which *H. sanguineus* fails to employ. This ineffective predator avoidance behavior may be due to a combination of the short time since establishment, and also because *H. sanguineus* does not have a known Portunid predator in the sea of Japan, its primary native range (Board 2014). In contrast, *C. maenas*, which did exhibit effective predator avoidance behavior to adult *C. sapidus*, has been established in NJ for a longer time period than *H. sanguineus,* but also has two potential Portunid predators in its native range in the eastern Atlantic, *Necora puber* and *Liocarcinus depurator* (Costello et al. 2008). Generation time of *C. maenas* is three years (Berrill 1982), thus over 60 generations have been exposed to *C. sapidus* predation in NJ. Generation time of *H. sanguineus* is only two years (Yasuo 1988) but some crustaceans may be able to develop

learned predator avoidance behavior within a generation (Bool et al. 2011), thus *H. sanguineus* should adapt to *C. sapidus* predation rapidly. It is possible however that the low densities of *H. sanguineus* and *C. sapidus* in NJ have kept *H. sanguineus* from encountering *C. sapidus* with high enough frequency in their time since establishment to develop a fully experienced anti-predatory response.

Predation on *H. sanguineus* in the field was higher than on *C. maenas* or juvenile *C. sapidus*. This supports an increase in top predator effects on the more recent invasive crab, suggesting that *H. sanguineus* is recognized as a resource by higher trophic level predators in the system. Also since I observed *H. sanguineus* movement in the presence of a top predator in the laboratory, *H. sanguineus* may move in the presence of other visual predators, which could be a mechanism of these increased predation rates. Considering the observed rate of loss (all individuals consumed) this pressure may be an important limiting factor for the *H. sanguineus* population. Various species of fish (Able 1992) and other larger omnivorous crabs (Stehlik et al. 1991) are abundant in NJ (Able 1992) and may also consume *H. sanguineus* in addition to *C. sapidus* (Stehlik 1993, Heinonen and Auster 2012).

While *H. sanguineus* foraging success was increased by *M. mercenaria* naïveté and it was also seen to be naïve to adult *C. sapidus* at the individual scale, these behavioral interactions may not have a strong influence on the population. The model predicts that the *H. sanguineus* population will grow despite *H. sanguineus* naïveté to *C. sapidus*, and even after clams develop anti-predator behavior. Development of antipredator behavior only reduced initial population doubling time by 0.7 years and

these results suggest that *H. sanguineus* population growth is not very sensitive to the behavioral benefits of *M. mercenaria* naïveté. Since naïve prey only changes *H. sanguineus* attack rate on *M. mercenaria*, the results indicate that the other model parameters, which are more related to physiology than behavior, may be more important in driving *H. sanguineus* population growth. These conclusions are drawn with caution, as the model only takes into account the interactions of three species' populations within a community. *H. sanguineus* consumes other prey items in addition to *M. mercenaria*, including various mussels, plant and algal matter, annelids and small fish (Lohrer et al. 2000, Ledesma and O'Connor 2001) and the *C. sapidus* may not be its only predator (Heinonen and Auster 2012). The model also does not take into account density dependent mortality, although modeled growth is realistic; documented maxima in the native range of *H. sanguineus* are slightly over 100 crabs per square meter (Fukui 1988) and up to 320 crabs per square meter within its introduced range in the western Atlantic (McDermott 1998). Despite this, the model provides some of the first insight into the predicted relative importance of prey naïveté on invasive predator population growth rates. Further multi-species research is needed to empirically determine the importance of behavior in comparison to physiological traits, and determine how behavioral interactions impact other invasive populations.

Overall, I found evidence for naïveté in basal prey, which directly benefitted the most recent invasive intermediate predator's foraging success. I also found prey naïveté in the invasive intermediate predator and evidence of predation on the species by the native community. However, at the population level, invasive intermediate predator population growth may not be strongly influenced by top predator consumer pressure, nor

the foraging benefit gained from naïve basal prey. These results suggest that physiological traits, such as conversion efficiency of the invasive crab may drive its population growth more-so than foraging benefits. Future work examining how individual prey naïveté translates to the population level in other species, and across trophic levels is encouraged. Examining additional components of food webs will be increasingly important in gaining a more comprehensive understanding of how communities will adapt and persist with increasing species invasions.

CHAPTER 5

CONCLUSION

The overarching goal of this research was to further existing knowledge of invasion and trophic dynamics in coastal systems in light of the drastic anthropogenic change our natural ecosystems are currently facing. Although the field of ecology has made immense progress from beginning as a descriptive science to becoming the more quantitative discipline it is today (McIntosh 1986, Legendre and Legendre 2012), we are only beginning to understand how species interactions change with abiotic and biotic context (Agrawal et al. 2007), which is a crucial piece in being able to predict large scale patterns, how communities will change over time, and where invasive species will be high impact. My results suggest that predation and potentially competition is strongest at low latitudes, supporting longstanding species interactions hypotheses that are rarely tested empirically at large spatial scales (Schemske et al. 2009). More specifically, my results show that strong predation may reduce invasive species impacts, particularly the cascading effects of invasive predators, and highlights a potential mechanism that native species use to adapt to strong competition - narrowed niche breadth. Additionally, my results show that invasive predator individuals can benefit from lack of coevolutionary history with prey, but that this benefit may not scale up to the population level. My three studies highlight and confirm the importance of empirical research at different scales, including across space, across multiple trophic levels, and extrapolating interactions among individuals to the population level. Carrying out such multi-scale studies allows for a broader understanding of population, community and global ecological dynamics.

My first specific objective was to examine trophic cascades created by invasive predators, testing how predation pressure in different biogeographic regions alters these cascades. As discussed in Chapter 2, I found that these invasion dynamics change across biogeographic regions, and that strong predator-prey interactions at low latitudes may temper cascading effects of invasive predators. Marine invasions research lags behind terrestrial invasions research (Ruiz et al. 2000) and the few existing large scale studies focus on non-native prey species (e.g. Freestone et al. 2013), rather than on predators in a multi-trophic context. Therefore, this study contributes to the field of marine invasion ecology, being the first to examine variation in the strength of invasive species-induced trophic cascades at different latitudes. However, to my knowledge this study was also the first experimental field-based study testing the strength of trophic cascades at a biogeographic scale, and thus demonstrates an interesting, more generalizable ecological phenomenon beyond invasion biology. Further research is needed of invasion dynamics across spatial scales and biogeographic regions. In addition, positive interactions and indirect effects (for example, facilitations via trophic cascades) are understudied in the context of invasions (Simberloff and Von Holle 1999) and need further attention. The inclusion of positive interactions in community ecology has lagged behind that of negative interactions more generally (Bruno et al. 2003), and this lag may help explain the more recent appreciation for positive interactions as a driver of invasion success.

Chapter 3 discussed my second specific objective, which was to conduct a global examination of niche breadth patterns within a widespread marine invertebrate taxonomic group. I found an interesting division in niche breadth predictors for temperate and tropical species, with temperate species' diets being related to latitude, range size and

body size and tropical species' diets only being related to clade. Temperate species niche breadth increased with both increasing midpoint of latitudinal range and range size. I also found that body size and midpoint of latitudinal range had an interactive effect on temperate species diet breadth, with larger-bodied species demonstrating a broader diet at higher latitudes in comparison to lower latitudes. In contrast, for tropical species, the only factor predictive of niche breadth was phylogenetic relatedness. As many factors are predicted to change with latitude, examining potential covariates is very important in being able to deduce a true relationship when conducting latitudinal studies. There is little marine research exploring latitude-niche breadth relationships. One study found mixed results for host-specificity in parasites across latitude, with one taxonomic group showing greater specialization at lower latitudes and the other showing no relationship (Rohde 1978). There has since been a study examining breadth of environmental tolerance, which supported a positive relationship between breadth of thermal tolerance and latitude (Sunday et al. 2011). A third study examined predicted versus realized latitudinal ranges of terrestrial and marine species (Sunday et al. 2012), finding that range size increased with thermal tolerance, but did not report whether this explicitly corresponded with latitude (although given their previous 2011 study, this relationship is implied). In these studies, however, other possible explanatory variables such as body size and phylogenetic relationships are not examined in conjunction with latitude. By controlling for these other important variables and also through analyzing our temperate and tropical data separately, our results highlight several key mechanisms that may be differentially driving large scale niche breadth patterns in tropical and temperate species.

My third and final specific objective consisted of comparing predator-prey behavior of species at different stages of their invasion, and also examining how a new invader's population was affected by naïve prey behavior. The results described in Chapter 4 support that prey naïveté is stronger at earlier stages of invasion, although novel chemical cues from introduced taxa, as well as generation time, may also be important factors in predicting naïve behavior of native and non-native species. While naïveté was found to benefit individual foraging in the more recent invasive species, these results suggest that this benefit may not extend to the population as a whole. As such, conversion efficiencies and growth rates may be more important in influencing population growth than anti-predator behavior in this scenario. Despite model limitations, this study provides some of the first insight into how naïve behavior may affect invasion success at the population level. This study confirms the importance of examining how invasions are influenced by multiple trophic levels. Results produced some interesting questions about the influence of physiology versus behavior in predicting invasions success and the implications of individual interactions at the population scale, and further research in those areas is needed. Further work that would also be useful in determining the importance of naïveté in invaded systems would be a comparison of the community dynamics surrounding an invasive species in multiple biogeographic regions of its introduction, which would allow for simultaneous spatial and temporal comparisons of the invasion.

These findings all have interesting implications for the spatial patterns and potential mechanisms of invasion success. I found that strong predation reduces invasion success of basal prey and intermediate consumer species; this result suggests that these

lower-mid trophic level invasions have less of a negative impact on low latitude systems (or in other locations with strong predation pressure). This is not a universal phenomenon , as there are a number of documented cases of invasive species establishments in low latitude systems that have had particularly devastating impacts on ecosystems and economies (e.g. lionfish invasion in the Carribbean [(Black et al. 2014)]). However, my second chapter findings showed that low latitude native species niche breadth is dependent on origin and evolutionary history; if tropical generalist species belonging to older clades, then evolutionary history could also influence, and potentially be used to predict, the success or failure of tropical invasive species. Further, I found that naïveté doesn't largely prevent or enhance population growth in a temperate system and that physiological traits of invasive species may have more of an influence on intermediate predator invasion success. This result may be different in low latitude systems, where species interactions are stronger, and naïveté could result in stronger predation effects, and/or these stronger predation effects could outweigh invasive species physiological advantages. More research is needed on these fronts to further predictability of where and when invasive species will have maximum impacts on ecosystems.

In conclusion, this suite of studies contributed to the growing body of research in marine ecology and invasion biology. When this project commenced in 2009, there had been a recent 'call to arms' for researchers to examine how species interaction strength changes with context, and that this information would advance the field of ecology towards becoming a more predictive discipline (Agrawal et al. 2007). Several important advances have been made on the predictors of species interaction strength

(Hammerschlag et al. 2006, Oro et al. 2006, Friman et al. 2008, Freestone et al. 2011, Wu et al. 2014) yet empirical multi-scale studies are still limited. My three studies highlight and confirm the importance of empirical research at different scales, including across space, across multiple trophic levels, and extrapolating interactions among individuals to the population level. They broadly support that species interactions are of importance in structuring communities at lower latitudes. As subtropical and tropical high diversity systems are the most threatened by global change (Baillie et al. 2004), understanding these mechanisms have implications for conservation, management, and potentially restoration efforts. Further multi-scale studies will allow for a broader understanding of population, community and global ecological dynamics, and better predictions of how our ecosystems will adapt and persist over the coming generations.

NOTES

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