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Agonistic Behavior and Costs of Aggression in Decapod Crustaceans

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AGONISTIC BEHAVIOR AND COSTS OF AGGRESSION

IN DECAPOD CRUSTACEANS

BY

NIELS-VIGGO SCHOU HOBBS

A DISSERTATION SUBMITTED IN PARTIAL FULFILLMENT OF THE

REQUIREMENTS FOR THE DEGREE OF

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IN

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2016

DOCTOR OF PHILOSOPHY DISSERTATION
OF
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2016

ABSTRACT

Animals that engage in aggressive behavior necessarily incur some costs (e.g., energy expenditure) and risk much greater costs (e.g., injury), both of which are presumably weighed against the potential benefits (e.g., refuge, food, or mates). Such costs and benefits directly impact their distribution, life history, and fitness, so an understanding of the role aggression plays is crucial to a complete understanding of a species' ecological niche. The research presented here evaluates the degree to which aggression has ecological and life history consequences, using several species of co-occurring crabs as models in a combination of laboratory and field experiments. Specifically, we investigated: 1) how conspecific aggressive interactions compare across several ecologically overlapping crab species, 2) the impact exposure to aggression during the juvenile life phase has on the growth, maturity, injury, and survival rates of decapod crustaceans, 3) whether both intra- and interspecific aggression and competition among co-occurring crab species alter habitat selection and play a role in the success of invasive species, and 4) if injury patterns, spatial distribution, and habitat selection across the intertidal zone can be correlated to aggression.

In Chapter One, we present a comparative analysis of the degree to which different species of crabs engage in aggressive behavior. We focused on six species of co-occurring New England crabs, including the invasive *Hemigrapsus sanguineus* and *Carcinus maenas*, and the native *Cancer irroratus*, *Dyspanopeus sayi*, *Libinia emarginata*, and *Ovalipes ocellatus*. We found significant differences in the occurrence of agonistic behavior among species: *O. ocellatus* engaged in prolonged

fighters, and *L. emarginata* showed very little aggressive behavior, while the other four species were intermediate in the instances of, and the amount of time engaged in, aggressive behavior. Our findings shed light on the ecological implications of agonistic behavior in the context of varying life history and ecological strategies, and set a useful benchmark for understanding the role of aggression in the following chapters.

We then studied the costs of aggressive behavior in Chapter Two, focusing particularly on the impact agonism has on growth, maturity, injury, and survival. We selected juvenile *Hemigrapsus sanguineus*, *Carcinus maenas*, and *Cancer irroratus* crabs, three species that directly co-occur and display comparable levels of aggression. Treatments were comprised of conspecific individuals paired together for different lengths of time each day, to simulate encounter rates from post-settlement to the onset of maturity. All three species experienced substantial decreases in survival, significant limb loss, and a decrease in final carapace size. Only time to maturity was not substantially affected, though this may have been partly due to the dramatic mortality rates leading to relatively few crabs surviving to adulthood.

Hemigrapsus sanguineus, one of the species used in all four experiments presented in this dissertation, is a highly successful invasive species whose success stems partly from its ability to exclude established crab species from preferred rocky and cobble intertidal habitat. In Chapter Three, we assessed preference and competition for habitat types (cobble vs. sand) for *H. sanguineus* and two competitor species; the previously established invasive green crab, *Carcinus maenas*, and the native rock crab, *Cancer irroratus*, in New England. We established different

groupings of similarly sized heterospecifics and conspecifics from each species in order to test intra- and inter-specific competition at different densities. While all three species preferred the shelter of cobble substrate in individual trials, *H. sanguineus* invariably displaced the other species, and retained the cobble substrate even when exposed to superior heterospecific numbers. Additionally, multiple *H. sanguineus* would cohabitate in cobble, whereas *C. maenas* and *C. irroratus* individuals each excluded conspecifics from cobble. These patterns illustrate a clear mechanism for overcoming invasion resistance and the exclusion of other intertidal crab species. In addition, despite the aggression seen in Chapter One, this study demonstrates that much of this species' invasion success may stem from its relative lack of intraspecific aggression, when costs and benefits are both present.

One outcome of aggression is often injury, and these intertidal crab species exhibit high occurrences of both claw and leg loss. However, while it is difficult to ascertain the cause of such injuries, the impact on the distribution and demography of injured individuals across habitat types is relatively easy to assess. We found little evidence for differences in the distribution of injured *H. sanguineus* (the sole common species found in surveys) across intertidal zones, with half of all crabs exhibiting loss of at least one limb. Injury also correlated with age and reproductive status which, in turn, did effect distribution.

The results of this series of studies underscore the impact of aggression (and related competition) on shaping many aspects of a species' ecology. Though the outcome of aggressive behavior is not always easy to ascertain, the overall results of

our research serve to further illuminate our understanding of community ecology, invasion biology, life history and fitness, and ethology in general.

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No expression of acknowledgement can correctly convey the depth of gratitude I feel for my advisor, Carol Thornber. After a hiatus from academics, I was given a very welcome home and more top-tier guidance than I could have hoped for. She took a chance on me and, while I haven't always been the easiest student, she always showed grace, patience, and understanding. I am particularly indebted to her for taking a tremendous amount of precious time to help me fashion my over-wrought work into something that can actually contribute to the field. Thank you, Carol.

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I'm incredibly fortunate, too, to have had a superb, supportive committee. I'd like to thank my current committee members, Evan Preisser, David Bengtson, Jason Kolbe, and Susanne Menden-Deuer, as well as previous members, Robert Bullock, Scott McWilliams, and Saran Twombly, who collectively provided me with a great breadth of critical guidance. All took the time to be insightful with in-depth commentary, and constructively critical and supportive in personal meetings. One of the goals of having a diverse committee is to garner the benefits of those broad viewpoints – and from physiology to community ecology, my research has been much improved by having so many different, discerning eyes look keenly upon it. Additionally, I've had these several people to look up to as models for what makes a

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Finally, to my incredible wife, Carmen: I know it's been pretty miserable to see so little of me over the past many months while I was buried behind mountains of papers and the smoke from an overheating laptop, and while I was being cranky from chronic sleep deprivation. I love you so much for having survived it with patience and sweetness – and for all the deliveries of food and tea (or beer, as the need dictated). Of all the people to who probably made this the most possible, I am sure it is you, Carmen. With love, I secondarily dedicate this work to you.

DEDICATION

To Jakobine and Alfred.

I wish you could have stuck around for this one.

Jeg elsker jer.

PREFACE

This dissertation is written in Manuscript Format for submission to various peer-reviewed journals, in accordance with the guidelines set by the Graduate School of the University of Rhode Island. Each of the four chapters present separate research projects that collectively contribute to understanding the role aggression plays in the ecology of decapod crustaceans. Chapter 1 is in preparation for submission to the Journal of Crustacean Biology. Chapter 2 has been submitted to Marine Biology. Chapter 3 is under review by Biological Invasions. Chapter 4 is under review by the Journal of Crustacean Biology.

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CHAPTER 1

COMPARATIVE CONSPECIFIC AGONISTIC BEHAVIOR OF SIX BRACHYURAN SPECIES IN COASTAL SOUTHERN NEW ENGLAND

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ABSTRACT

Studies of aggression frequently utilize crustacean arthropods as effective, simple models to understand within- and among-species interactions. Comparative analysis can provide an understanding of the role of aggression in shaping the ecological interactions of co-occurring species. Here, we investigated conspecific aggressive behavior across six species of co-occurring New England crabs, including the invasive *Hemigrapsus sanguineus* and *Carcinus maenas*, and the native *Cancer irroratus*, *Dyspanopeus sayi*, *Libinia emarginata*, and *Ovalipes ocellatus*. We found significant differences in the occurrence of agonistic behavior among species: *O. ocellatus* engaged in prolonged fights, and *L. emarginata* showed very little aggressive behavior, while the other four species were intermediate in the instances and duration of aggressive behavior. Most interactions did not involve steady escalations, but rather brief periods of escalation punctuated by rapid de-escalations and fluctuations in the aggression, potentially indicating assessment of opponents' fighting ability. We use our findings to assess the ecological implications of agonistic behavior, in the context of varying life history and ecological strategies.

KEY WORDS

Ethogram, conspecific aggression, agonism, Decapoda, Brachyura, *Hemigrapsus sanguineus*, *Carcinus maenas*

INTRODUCTION

A large body of literature explores aggression in animals (Huntingford and Turner, 1987; Hardy and Briffa, 2013), much of it from crustacean arthropods, which are simple models well suited for work on agonistic behavior (Briffa, 2013; Vieira and Peixoto, 2013). In particular, mantis shrimp (Caldwell and Dingle, 1975), lobsters (Briones-Fourzán et al., 2014), and crayfish and other anomurans (Moore, 2007; Ayres-Peres et al., 2011; Palaoro et al., 2014) have been the focus of numerous behavioral studies, and the physiological (Briffa and Sneddon, 2007; Dissanayake et al., 2009) and ecological (Cobb et al., 1986; Reaney and Blackwell, 2007) consequences of such behavior are well studied. Mansour and Lipscius (1992) observed highly aggressive and dangerous competitive interactions between blue crabs, *Callinectes sapidus*, even when resources were plentiful. Likewise, Smith (1990) and Smith and Hines (1991) recorded unusually high occurrences of limb loss in wild populations, attributed to aggressive interactions. The velvet swimming crab, *Necora puber*, has been used extensively to study energetic costs of fighting (Huntingford et al., 1995; Hardy and Briffa, 2013), with these costs applied to a cost/benefit analysis of aggression (Smith et al., 1994; Sneddon et al., 1997). The development of cost/benefit analysis of fighting has its roots in the study of crab aggression and the creation of some of the first behavioral ethograms of aggressive behavior using portunid crabs (Jachowski, 1974; Huntingford and Turner, 1987).

Such ethograms of agonistic behavior are useful tools for analyzing the degree to which a given species is aggressive, how such behavior may be moderated by displays of intent and ability, and how such behavior may show individual variation

(Kravitz and Huber, 2003; Hardy and Briffa, 2013). Given the role that aggression plays in the ecology of a species, quantifying this behavior is important as a baseline for understanding the impact that agonistic behavior might have on a species' ecology, life history, and fitness (Huntingford and Turner, 1987). Ethograms and measures of aggression are particularly relevant when numerous species occupy the same overlapping or neighboring habitats and compete for shared resources (Huntingford et al., 1995; Tierney et al., 2000; Hudina et al., 2011). Additionally, variation in aggression across species, particularly of different genera and families, remains largely unexplored (Hardy & Briffa, 2013).

In southern New England, several crab species inhabit the intertidal and shallow subtidal zones (Williams, 1984; Lohrer and Whitlatch, 2002; Stehlik et al., 2004). Two of these species, the European green crab, *Carcinus maenas*, and the Asian shore crab, *Hemigrapsus sanguineus*, are non-native species that have expanded their ranges along the east coast of North America and beyond (Carlton and Cohen, 2003; Epifanio, 2013). Much work has been done to understand the mechanisms by which both of these species, and invasive species in general, succeed in their new ranges (Holway and Suarez, 1999; Lohrer and Whitlatch, 2002; Snyder and Evans, 2006; Chapple et al., 2012). Some successful invaders are more aggressive than native competitors, actively forcing the native species out of their habitats (Tierney et al., 2000; Dalosto et al., 2015).

A central goal of this study was to compare the degree to which several southern New England crab species engage in aggressive behavior, under identical experimental conditions. Here, we created a generally usable ethogram of aggressive

behaviors, staged conspecific dyadic encounters of six species of crabs, and tested the hypothesis that substantial differences in agonistic acts exist between phylogenetically diverse but geographically and ecologically overlapping decapod species.

Furthermore, by ranking the relative degree to which these crabs display agonistic behavior, we use this information as a framework for the ecological implications of agonism.

MATERIALS AND METHODS

We placed juvenile and young adult crabs in conspecific pairings for 15-minute periods to quantify the relative level of aggressiveness of each species. We used six different crab species collected locally in Narragansett Bay, Rhode Island, including twelve pairs of the Asian shore crab, *Hemigrapsus sanguineus* (de Haan, 1835); eleven pairs of the green crab, *Carcinus maenas* (L., 1758); eight pairs of the rock crab, *Cancer irroratus* Say, 1817; ten pairs of the mud crab, *Dyspanopeus sayi* (Smith, 1869); eight pairs of the spider crab, *Libinia emarginata* Leach, 1815; and five pairs of the lady crab, *Ovalipes ocellatus* (Herbst, 1799). Juveniles and young adult crabs from 10-25 mm carapace width (CW) of all six species were paired by equal CW (to within 3%) and sex (when morphological maturity allowed determination) in glass finger bowls, 100 mm in diameter, so that paired crabs were in close contact for the duration of each bout. Crabs were not fed for two days prior to use in the study, and all were kept in solitary containers prior to use (Johnsson and Aakerman, 1998). The containers were free of any substrate or refugia and were filled with fresh, well-aerated sea water at ~20°C, a typical summer temperature experienced by these crabs

in situ (Williams, 1984). The water was aerated with an airstone until the start of each bout. We then simultaneously placed both crabs into each container and affixed a transparent plastic cover over the top to prevent escape.

We gathered behavioral data via video of encounters between conspecifics; video cameras were positioned directly over the containers. The particular species used in each bout were haphazardly selected and assigned a number with no reference to species, in order to minimize observer bias during video observation. Two independent observers recorded instances of all behaviors and the time duration of each instance (in seconds), with discrepancies double-checked and corrected. Behaviors were then categorized and ranked on an ordinal scale of 1 to 5 (Table 1); inactivity defined the low score of 1, actual physical combat (sustained clawing and wrestling) defined 5, and behaviors such as general movement, meral spreads and lunges, were in between (*sensu* Huber and Kravitz, 1995 and Karavanich and Atema, 1998). Our goal was to group associated behaviors with similar costs and risks to interacting individuals and to minimize the subjectivity that accompanies the ranking of individual behaviors.

We analyzed the instances and duration of specific behaviors within and among species. To do so, we pooled the data from each pair of crabs; thus, the total for duration of behaviors in a pair is 30 (not 15) minutes. We used Kruskal-Wallis analyses for each species separately to determine differences in both instances and duration of behaviors using chi-square approximation. *Post-hoc* Steel-Dwass analyses of conspecific differences were then performed for all pair-wise comparisons. All data were analyzed using JMP v.12 (www.jmp.com).

Finally, we recorded the behavior sets observed in each ten-second increment of each bout (90 increments total, combining both individuals in a single bout), and then averaged the behavior set for each individual in each species. This gave a mean aggressive score between 1 and 5 for each individual. The mean aggressive score of all increments were compared by ANOVA with *post-hoc* Tukey HSD tests at 95% C.I. for all pair-wise species comparisons. In order to test for evidence of the establishment of dominance, the mean aggressive score for the first half of each trial was compared to the second half by paired t-test at 95% C.I.

RESULTS

We observed fifteen different distinct behaviors (Table 1), grouped into five behavioral sets. Passive behaviors (set 1) included “stand” and “sit;” Non-Aggressive Action (set 2) included “walk” and “run;” Non-Contact Aggression (set 3) included “meral spread,” “reach,” “close approach,” and “lunge;” Contact Aggression (set 4) included “touch,” “side push,” “front push,” “grab,” and “lock;” and Fighting (set 5) included “grapple” and “sustained fight.” All species displayed all behavior sets, with the exception of *Libinia emarginata*, which never displayed any Fighting behaviors (set 5). For ease of discussion and analysis, we refer to the five sets of behavior and not their constituent behaviors (*sensu* Karavanich & Atema, 1998).

Ovalipes ocellatus

This species had a strong tendency to escalate quickly to Contact Aggression and Fighting behaviors and sustained those behaviors for large portions of the trial period (Figs. 1, 2), with both opponents highly responsive to increasing aggressive behavior. There was no difference among mean instances of different behavior sets for *O. ocellatus* ($\chi^2_4 = 7.2837$, $p = 0.12$), but crabs did display significant variation in the duration of behaviors ($\chi^2_4 = 14.2085$, $p = 0.0067$), spending more time engaging in Fighting (12.2 minutes) than any other behavior. *Ovalipes ocellatus* displayed a mean aggression score of 3.15 out of a possible 5, with 40% of bout duration engaged in Fighting behaviors.

Cancer irroratus

Overall, *C. irroratus* showed a significant difference among instances of behavior sets (Fig. 1; $\chi^2_4 = 26.6201$, $p < 0.0001$), with instances of Fighting and Passive behaviors significantly lower than Non-Aggressive Action, Non-Contact Aggression, and Contact Aggression behaviors ($p < 0.05$ for all). There was a significant difference among duration of behavior sets for *C. irroratus* (Fig. 2; $\chi^2_4 = 11.8629$, $p = 0.0184$), although there were no significant post-hoc comparisons. *Cancer irroratus* had a mean cumulative behavioral score of 2.60.

Carcinus maenas

Carcinus maenas displayed an overall significant difference among instances of behavior sets (Fig. 1; $\chi^2_4 = 27.7482$, $p < 0.0001$), with Fighting and Passive

behaviors occurring less than half as often as the other behavior sets ($p < 0.05$ for all). The duration of behaviors varied significantly ($\chi^2_4 = 22.9660$, $p < 0.0001$), with Fighting lower than Passive, Non-Aggressive Action, and Non-Contact Aggression behaviors ($p < 0.05$ for all). *Carcinus maenas* had a mean cumulative behavioral score 2.587, similar to *Cancer irroratus*.

Hemigrapsus sanguineus

Overall, *H. sanguineus* behavior significantly varied among instances of behaviors (Fig. 1; $\chi^2_4 = 19.6514$, $p = 0.0006$), with Fighting behaviors occurring less often than Non-Aggressive Action and Contact Aggression behaviors ($p < 0.05$ for both). Likewise, duration varied significantly (Fig. 2; $\chi^2_4 = 26.0645$, $p < 0.0001$), with Non-Aggressive Action behaviors occurring at least twice as long as any other behavior set. *Hemigrapsus sanguineus* had a mean cumulative behavioral score of 2.462, similar to *Carcinus maenas* and *Cancer irroratus*.

Dyspanopeus sayi

As a whole, *D. sayi* did not significantly vary among instances of behaviors (Fig. 1; $\chi^2_4 = 5.3988$, $p = 0.2488$), though duration did vary significantly (Fig. 2; $\chi^2_4 = 23.6796$, $p < 0.0001$), with the majority of time spent in less aggressive behavior sets. Overall, *D. sayi* had a mean cumulative behavioral score of 2.031.

Libinia emarginata

Libinia emarginata was the least aggressive of all six species. Instances of behaviors differed significantly (Fig. 1; $\chi^2_4 = 24.4045$, $p < 0.0001$), with instances of Passive behaviors occurring more than all other behavior sets combined. Overall duration of behaviors in *L. emarginata* varied significantly (Fig. 2; $\chi^2_4 = 28.8223$, $p < 0.0001$), with the duration of Passive behaviors significantly greater than all other behavior sets. As the least aggressive crab species observed in this study, *L. emarginata* tallied a mean cumulative behavioral score of 1.115. Overall, *L. emarginata* spent 91.4% of its time in extended periods of Passive behavior (Fig. 2), occasionally moving around the container but only engaging in agonistic behaviors 1% of the time.

Comparisons among species

We found significant variation among species in their mean cumulative behavior score, ($F_{5, 59.75} = 59.78$, $p < 0.0001$). Crabs were more aggressive in the first half than the second half of trials (Table 2) for *Cancer irroratus* ($p = 0.0053$), *Carcinus maenas* ($p < 0.0001$) and *L. emarginata* ($p < 0.0001$), potentially indicating the establishment of dominance.

DISCUSSION

All six species showed differences among both the instances and duration of agonistic behavior sets (Figs. 1 and 2), though significantly low aggression by *L.*

emarginata and high aggression by *O. ocellatus* accounted for most of the variation. We observed that most crabs escalated from passive or low aggression to high aggression behaviors in line with game theory models (Maynard-Smith, 1982; Smith et al., 1994), though they were generally not steady escalations and included numerous de-escalations and fluctuations. Similar non-linear escalation patterns have been observed in the velvet swimming crab *Necora puber* (Smith et al., 1994), the American lobster *Homarus americanus* (Huber and Kravitz, 1995), and in several species of crayfish (Tierney et al., 2000; Dalosto et al., 2015).

The observed behaviors are in line with game theory predictions such that combatants will go through a process of escalation through more aggressive behaviors prior to engaging in actual fights (Huntingford et al., 1995; Smallegange et al., 2007). Such ritualized display serves to minimize the likelihood of fights with the receiver and the inherent risks of aggressive interactions for the signaler (Clutton-Brock and Albon, 1979; Berman and Moore, 2003; Reichmuth et al., 2011). The signals themselves carry a cost, including the energy needed both to grow and use claws (Dingle, 1983; Smith and Taylor, 1992; Briffa and Elwood, 2002). The stronger the signal the higher the cost (Briffa and Elwood, 2001), but this is offset by the greater cost incurred by sustained fighting without the benefit of such ritualized signals (Juanes and Smith, 1995; Rillich et al., 2007; Arnott and Elwood, 2009). Therefore, it is not surprising that most of the species in this study spent the majority of time engaged in displays and aggressive behaviors short of fighting (Fig. 2).

Another method by which animals can decrease the costs of aggressive behavior is by the establishment of dominance hierarchies (Atema and Cobb, 1980;

Moore, 2007; Yasuda et al., 2014), which override the impetus for aggression because of the perceived greater fighting capacity of an opponent. We found a decrease in mean cumulative behavioral scores between the first and second halves of the trials for *Cancer irroratus*, *Carcinus maenas*, and *L. emarginata* (Table 2), consistent with the formation of dominance hierarchies in these three species, similar to other crustaceans (Dingle and Caldwell, 1969). *Hemigrapsus sanguineus* did not appear to form dominance hierarchies, although it is typically observed in very high densities in the rocky intertidal (Epifanio, 2013). *Hemigrapsus sanguineus* often engaged in non-aggressive physical contact as they moved about the container without initial aggressive displays. This may provide some insight into the mechanism behind this species' capacity to exist in relatively high densities (Lohrer, 2001; Epifanio, 2013) compared to the other two ecologically overlapping species. Unlike the other species, the aggressive nature of *O. ocellatus* meant that fighting did not cease over the 15-minute bouts (Table 2), offering a possible explanation for their highly dispersed distribution in nature (Williams, 1984).

Ovalipes ocellatus, the most aggressive crab in this study, belongs to the Portunidae, the family of swimming crabs that also includes *Callinectes sapidus*, a species that geographically overlaps with the species in this study and is comparably aggressive to *O. ocellatus* (Clark et al., 1999; Reichmuth et al., 2011), nearly to the point of the behavior posing a substantial risk to fitness (Mansour and Lipscius, 1992). Another member of the family, *Necora puber*, has been the model species for much of the primary work on the energetic costs of fighting (Smith and Taylor, 1992; Smith et al., 1994a; Smith et al., 1994b) and the effects of perceived resource value on strategic

decisions (Maynard-Smith, 1982; Smallegange et al., 2007; Palaoro et al., 2014).

Carcinus maenas, a member of the Carcinidae which is closely related to the Portunidae, is not as aggressive yet ranked second among the six species in the study. Conversely, *L. emarginata*, the least agonistic of the six study species and not closely related to the other five species, forms gregarious assemblages (De Goursey and Auster, 1992), particularly during mating events. Such mating aggregations are unlike the highly aggressive interactions that are associated with other decapod species (Bergman and Moore, 2003; Smallegange et al., 2007).

While not closely related, the Asian shore crab, *H. sanguineus*, and the European shore crab, *Carcinus maenas*, are both highly successful non-native species in New England waters (Lohrer and Whitlatch, 2002; Carlton and Cohen, 2003; Klassen and Locke, 2007; Epifanio, 2013) and, increasingly, globally (Carlton and Cohen, 2003; Epifanio, 2013). The ecological costs associated with biological invasion (Ruiz and Carlton, 2003; Carlton, 2011; Ruiz et al., 2011) necessitate study of the potential mechanisms by which invaders are successful, such as agonistic capabilities. However, though aggression has been correlated to invasion success in other studies (Hudina et al., 2011; Chapple et al., 2012; Dalosto et al., 2015), aggressive behavior may not be a primary factor in the invasion success of these two species. By contrast, of the six species studied here, two of the least aggressive ones, *H. sanguineus* and *L. emarginata*, are two of the most abundant species found in New England coastal habitats (Williams, 1984; Epifanio, 2013).

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Table 1. Generalized ethogram of crab behaviors. Behavior sets group separate behaviors according to a proposed ranking of physiological cost and risk.

Behavior Sets	Constituent behavioral units	Description of behaviors
1. Passive	Sitting	Crab sits low to ground, motionless, claws close to body
	Standing	Crab is raised off ground, motionless, claws close to body
2. Non-Aggressive action	Walking	Crab walks slowly, usually sideways, claws close to body
	Running	Crab walks rapidly, usually sideways, claws close to body
3. Non-Contact aggression	Meral spread	Crab spreads claws out and forward from body, generally farther apart than width of carapace; pincers often spread open
	Reach	Crab reaches one claw directly out toward another crab, typically with pincers spread open and other claw in meral spread
	Close approach	Crab moves directly forward, closing distance with another crab; generally combined with meral spread
	Lunge	Crab moves forward and rapidly toward another crab, coming close to reach; generally displaying meral spread; if contact does not occur as a result, a final slight movement away is common
4. Contact aggression	Touch	Crab reaches out with one or both claws, touching tip against another crab
	Side push	Crab exerts force against another crab, pushing sideways with one or more walking legs; claws may be extended out from body; pincers may be open
	Front push	Crab exerts force against another crab, pushing forward with one or both claws; claws extended out from body; pincers may or may not be open
	Grab	Crab briefly pinches onto another crab's body, with one or both claws immediately letting go
5. Fighting	Lock	Crab pinches onto the body of another crab; pincers remain closed on other crab's body
	Grapple	Crab actively exerts force against another crab, claws pushing and locking on opponent; moving against or being pushed away from opponent
	Sustained fight	More strenuous and lengthy than previous behavioral unit, involving a large degree of claw pinching and pulling; injury common

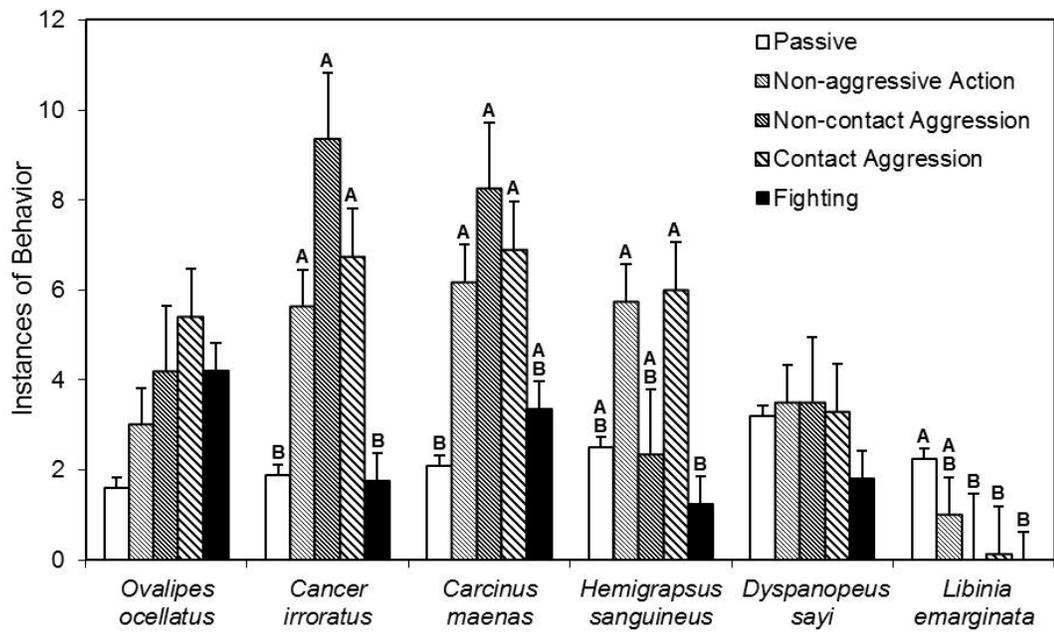
Table 2. Results of paired t-test (at 99% CI) analyzing behavioral differences between mean observed behavioral levels in first half and second half of paired bouts

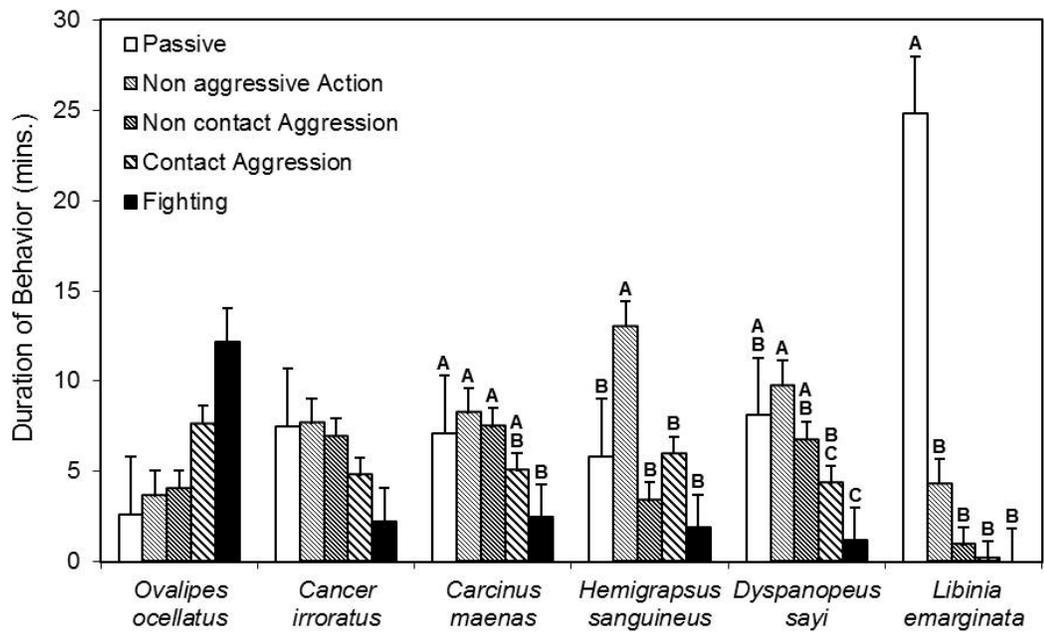
Species	1st half mean	2nd half mean	t statistic	DF	2-tailed p
<i>O. ocellatus</i>	3.78	3.651	0.71	9	0.4975
<i>H. sanguineus</i>	2.598	2.326	1.76	23	0.0918
<i>C. maenas</i>	3.19	1.984	9.93	21	<0.0001
<i>C. irroratus</i>	2.931	2.269	3.25	15	0.0053
<i>D. sayi</i>	2.097	1.964	1.24	19	0.2294
<i>L. emarginata</i>	1.226	1.004	4.25	15	0.0007

FIGURE LEGENDS

Fig. 1. The mean total instances of the five different types of behavior sets occurring for all six species. Data combines the behavior for both individuals in each bout. Error bars are one standard error. Letters denote significantly different treatments within each species.

Fig. 2. The mean total duration of the five different types of behavior sets for all six species. Data combines the behavior for both individuals in each bout. Error bars are one standard error. Letters denote significantly different treatments within each species.





CHAPTER 2

LIFE HISTORY COSTS OF CONSPECIFIC AGONISM IN THREE DECAPOD CRUSTACEAN SPECIES

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ABSTRACT

Aggression in decapod Crustacea is well studied, but the associated long-term costs have not been fully explored. To identify how aggression impacts growth, maturity, injury, and survival, we conducted a growth study of juvenile *Hemigrapsus sanguineus*, *Carcinus maenas*, and *Cancer irroratus* crabs. Treatments were comprised of individuals paired together for different lengths of time each day, to simulate encounter rates from post-settlement to the onset of maturity. All three species experienced at least a 50% decrease in survival, loss of up to an average of 2.24 legs and 0.34 claws per crab, and 14% to 21.6% smaller mean carapace width compared to controls. Although there was a trend toward decreased gonadal development among experimental treatments, the difference was not significant. Our study provides important evidence for the cost of agonism on life history and fitness characteristics, data crucial to understanding the role that aggression plays in shaping the population dynamics of animals.

KEY WORDS

Aggression, agonism, growth, maturity, injury, survival, *Hemigrapsus sanguineus*, *Carcinus maenas*, *Cancer irroratus*

INTRODUCTION

The consequences of agonistic behavior for individual animals have been studied since the inception of ethology (Maynard-Smith and Price 1973; Parker 1974; Huntingford and Turner 1987). Contestant growth, reproduction, and survivorship can

be strongly affected by agonistic interactions (Hardy and Briffa 2013), and the fitness of losing individuals is often lowered via aggression-related physiological changes (Sneddon et al. 1999; Matsumasa and Murai 2006) or denial of access to preferred mates, habitats, or food resources (Clutton-Brock and Albon 1979; Cobb et al. 1986; Amaral et al. 2009). Relatively few investigations, however, have looked specifically at the life history costs of aggression over a substantial portion of an organism's life (but see Romano 1990; Frisch and Hobbs 2011; Nesto et al. 2012).

The majority of research on aggression and its consequences has been performed with vertebrate animals (Huntingford and Turner 1987; Hardy and Briffa 2013). Decapod Crustacea are one of the few groups of invertebrates that have been well studied (Huntingford et al. 1995; Godsall and Smallegange 2011; Reichmuth et al. 2011), and several species exhibit some of the most aggressive behaviors observed in the metazoa (Mansour and Lipscius 1991; Reichmuth et al. 2011; Weaver et al. 2012). Relatively little research, however, has been done on the impact of aggression on life history parameters, including fitness (Juanes and Smith 1995; Hardy and Briffa 2013). By contrast, short-term proxies for fitness such as energy expenditure, heart rate, and the build-up of tissue metabolites are well studied (Huntingford et al. 1995; Sneddon et al. 1999; Matsumasa and Murai 2005). Most long-term growth and survival studies have been focused on the role of factors such as feeding and temperature (e.g., Hartnoll and Bryant 2001; Baeza et al. 2012), or the impact of injury on growth (Juanes and Smith 1995; He et al. 2016). Smith (1990) demonstrates the detrimental effect of aggression- and fighting-related limb loss on long-term growth.

We assessed the costs of agonistic behaviors on crab life history parameters. Because such costs can result from both the external physical impacts of aggression and the internal stresses of being aggressive (Hardy and Briffa 2013), both winners and losers of agonistic encounters may be negatively affected. Apart from increased energy expenditure, however, aggression appears to have either mixed or little to no short-term physical cost (Thorpe et al. 1995; Sneddon et al. 1999). The impact of physiological stresses over weeks or months still remains relatively untested (but see Li and Brocksen 1977; Vollestad and Quinn 2003).

Here, we address agonistic interactions in ecologically overlapping species, to assess potential trade-offs in the allocation of metabolic resources that impact maintenance, regeneration, growth and/or reproduction (Hardy and Briffa 2013; Hogan and Griffen 2014). In terms of direct effects, there is likely to be an increase in injury and mortality among aggressive crabs encountering conspecifics.

MATERIALS AND METHODS

Post-settlement juveniles of three crab species, *Hemigrapsus sanguineus* (De Haan, 1835), and *Carcinus maenas* (L., 1758), and *Cancer irroratus* Say, 1817, were collected at several rocky shore sites around the mouth of Narragansett Bay, Rhode Island, USA, in late summer 2000 and 2001, the seasonal peak of natural recruitment for most local crab species (Williams, 1984). All three species were raised in 200ml cylindrical growth chambers from post-settlement to the onset of maturity as young

adults. The walls of the growth chambers were made of a perforated plastic that allowed temperature-regulated (~18-20°C) seawater to flow through.

We had four experimental treatments for each species, each involving paired crabs of similar sizes: control, two-hour, six-hour, and constant. These different treatments manipulated the daily interaction time crabs had with conspecifics in order to test the impact of aggression on life history parameters. Control crabs were kept physically isolated in separate growth chambers for the duration of the study. Each day, conspecifics were haphazardly paired together in growth chambers for a two, six, or twenty-four hour trials, depending on which treatment they were in. At the end of each pairing period, depending on treatment, the crabs were placed alone into containers or switched into a new pairing to prevent the establishment of dominance hierarchies. Olfactory cues were not blocked in any treatments. We conducted conspecific pairings because these are generally the most common form of inter-individual interaction (*sensu* Connell 1980).

Tracking the identity of individual crabs was logistically not possible. While we could easily keep track of individuals with lost limbs and avoid over-counting injuries, it was not feasible to follow the growth rates of individual crabs. Therefore, we could neither randomly pair nor schedule pairings of crabs, necessitating the daily haphazard shuffling of individuals in treatments. This shuffling was also necessary due to the rapid pace at which dominance hierarchies can develop and persist (Karavanich and Atema 1998), which serves to minimize aggressive behavior. There was no significant difference in size among within-species treatment groups at the start of the experiments.

Crabs were checked daily for mortality and injury, recording both claw and leg loss and noting any carapace damage. Carapace width (CW), measured at the widest point, was recorded bi-monthly, regardless of molt status, using manual Vernier calipers. The carapaces of recently molted crabs were given 2-3 days to harden before measurement to minimize injury. All crabs were free of injury at the start of the study, but were continually used regardless of injury. However, crabs that were known to have just molted were isolated for 24-48 hours to minimize cannibalism.

Individuals were fed a slurry made from a frozen *Artemia* brine shrimp applied with a plastic pipette, first ~0.5 mL twice weekly and increasing to ~1.0 mL as the crabs grew larger. Feedings took place while crabs were kept separately; those crabs that were constantly housed together were fed both crabs' rations simultaneously. Additionally, each crab was fed a ~2cm² portion of fresh marine algae (primarily *Ulva* spp.) on a weekly basis to allow for a more complete diet, even for species generally identified as carnivorous (Jensen and Asplen 1998). A separate *ad libitum* feeding control for each species was fed twice as much *Artemia* as all the primary treatments in order to determine if experimental crabs were experiencing limited dietary intake, necessitating allocation of limited metabolic resources.

We concluded experiments for each species when morphological maturity was first detected in any crab during group measurement. We determined maturity by using species-specific assessments of size (Williams 1984; Epifanio 2013) that we compared to measurements of external physical characters tied to maturity (Campbell and Eagles 1984; Pinheiro and Fransozo 1998), i.e. relative chela volume (height x width at thickest part of claw – CV) in males and width of the fifth abdominal somite

(AW) in females. Measurements of these external morphological characteristics were conducted using manual Vernier calipers during the routine measurement of carapace size. Gonadal tissue was collected from all crabs, fixed in neutral buffered formalin and then stained and preserved using methylene blue in 70% isopropyl alcohol. Using a protocol simplified from Campbell and Eagles (1983), development of male and female gonadal tissue was assessed on a scale of 1) absent- no development visible; 2) immature- some signs of immature gonadal development; and 3) mature- presence of any gonads in mature state.

Statistical analysis

Differences in the final sizes for all surviving crabs for each treatment were tested by analysis of variance (ANOVA), with all pair-wise comparisons carried out by Tukey HSD with $\alpha = 0.05$. Physiological maturity was analyzed using chi-square analysis of gonadal development, and as there were no between-sex differences in any treatment, sexes were pooled together for analyses. Within-species limb loss (legs and claws) was analyzed by likelihood-ratio goodness of fit tests. Comparisons of *ad libitum* feeding with limited feeding controls were conducted by paired t-tests for each species. Survival analysis was conducted with Cox proportional hazards tests.

Analysis of interspecific growth compared the constant treatments for the three species. In order to normalize for inherent interspecific growth differences, the percent difference between carapace widths of surviving constant treatment crabs and control crabs was calculated for each species. After an arc-sign square root transformation of the percent data, we carried out an ANOVA with a Tukey HSD test with $\alpha = 0.05$ for

all pair-wise comparisons. All data were analyzed using JMP v. 12 (www.jmp.com), with the exception of Cox proportional hazards tests, which were performed using XLSTAT (www.xlstat.com).

RESULTS

Hemigrapsus sanguineus

The final size of *H. sanguineus* was significantly different among treatments (Fig. 1; ANOVA, $F(3,77) = 5.07$, $p = 0.0029$), with the constant treatment 17.1% smaller than the 2-hour treatment and 19.4% smaller than the control. The final mean size of the *ad libitum* feeding treatment was significantly larger than the corresponding limited feeding control (paired t-test, $T = 5.50$, $p = 0.0066$). Gonadal maturity was not different among treatments (Fig. 2a; pooled Chi-square test, $\chi^2 = 8.42$, $p = 0.21$).

Leg loss frequency among *H. sanguineus* experimental treatments was significantly different (Fig. 3a; likelihood-ratio goodness-of-fit test, $\chi^2 = 82.294$, $p < 0.0001$), though claw loss was not ($\chi^2 = 7.030$, $p = 0.071$). The mortality rate differed among treatments (Fig. 4a; Cox proportional hazards, $\chi^2 = 14.8661$, $p = 0.0001$), ranging from 100% survival of control crabs to 44% survival of constant treatment crabs.

Carcinus maenas

Similar to *H. sanguineus*, the final size of *C. maenas* was significantly different among treatments (Fig. 1; ANOVA, $F(3,72) = 5.63$, $p = 0.0016$) with the constant treatment 14.0% smaller than the 2-hour treatment and 21.6% smaller than the control. The final mean size of the *ad libitum* feeding treatment was significantly larger than the corresponding limited feeding control (paired t-test, $t = 4.12$, $p = 0.0213$). As with *H. sanguineus*, gonadal maturity was not different among treatments (Fig. 2b; pooled Chi-square test, $\chi^2 = 10.96$, $p = 0.09$).

Leg loss and claw loss among *C. maenas* experimental treatments were significantly different (Fig. 3b; leg loss: likelihood-ratio goodness-of-fit test, $\chi^2 = 80.626$, $p < 0.0001$; claw loss: $\chi^2 = 12.603$, $p = 0.0056$). The mortality rate differed among treatments (Fig. 4b; Cox proportional hazards test, $\chi^2 = 6.8757$, $p = 0.0087$), ranging from 100% survival of control crabs to 38% survival of constant treatment crabs.

Cancer irroratus

As with the other two species, the final size of *C. irroratus* was significantly different among treatments (Fig. 1; ANOVA, $F(3, 88) = 7.15$, $p = 0.0002$) with the control group 19.3% larger than the 6-hour treatment and 20.0% larger than the constant treatment. The final mean size of the *ad libitum* feeding treatment was significantly larger than the corresponding limited feeding control (paired t-test, $t = 5.50$, $p = 0.0066$). Similar to the other two species, gonadal maturity was not different among treatments (Fig. 2c, Chi-square test, $\chi^2 = 10.96$, $p = 0.09$).

Leg loss and claw loss among *C. irroratus* experimental treatments were significantly different (Fig. 3c; leg loss: likelihood-ratio goodness-of-fit test, $\chi^2 = 78.407$, $p < 0.0001$; claw loss: $\chi^2 = 12.036$, $p = 0.0073$). The mortality rate differed among treatments (Fig. 4c; Cox proportional hazards test, $\chi^2 = 7.4406$, $p = 0.0064$), ranging from a 100% survival in control crabs to a 50% survival in constant treatment crabs.

Interspecific Comparison

The final (normalized) size of the three species' constant treatments did not differ significantly (Fig. 1; ANOVA, $F(2, 63) = 1.18$, $p = 0.31$). Pooled gonadal data showed no significant differences among the control treatments (Chi-square test, $\chi^2 = 2.56$, $p = 0.63$) or among the constant treatments (Chi-square test, $\chi^2 = 6.98$, $p = 0.14$). Survival among any experimental treatments across all three species did not differ (Cox proportional hazards test, $\chi^2 = 1.6301$, $p = 0.20$ for overall model fit).

DISCUSSION

We found that agonistic behavior incurs clear life history and fitness costs on growth, injury, and survival, but not maturation. Similarity of limb loss across all three treatments for each species (Fig. 3) indicates that decreased final body size (Fig. 1), especially in longer duration treatments, is a product of more than just injury. The establishment of dominance hierarchies may minimize the relative proportion of additional injuries in longer-duration treatments (Juanes and Smith 1995; Hardy and

Briffa 2013), though this may not explain the discrepancy between differences in growth and differences in injuries. Since crabs were fed limited amounts of food, such discrepancy is evidence for a long-term physiological cost to aggression beyond that resulting from injury. Our results are consistent with comparable long-term studies of aggression showing a clear negative correlation between aggression and growth in fish (Wang et al. 2002; Vollestad and Quinn 2003), and invertebrates (Romano 1990; He et al. 2016).

Although there was a trend for paired treatment crabs to be less physically mature than control crabs, these differences were not significant. One potential explanation is that crabs may be selectively allocating limited resources to repair and regeneration. Norman and Jones (1993) found smaller brood sizes in field-collected females of the crab, *Necora puber*, that were missing limbs; they suggested that this was likely due to an aggression-based trade-off. Hogan and Griffen (2014) found similar energetic trade-offs affecting reproduction in commercial stone crabs, *Menippe* spp., which are routinely declawed as part of their fishery.

Survival of the crabs in this study suffered due to aggressive encounters, with each species experiencing significant rates of mortality (Fig. 4). Mansour and Lipschus (1991) showed that the blue crab, *Callinectes sapidus*, engages in highly aggressive bouts over food *in situ*, often to the point of serious injury and possible mortality, even when food is not limiting. Although crabs are soft-shelled for only one to two days per molt cycle (which varied from 6 to more than 27 days over the course of the study), 20 of 46 *H. sanguineus* deaths, 27 of 71 *C. maenas* deaths, and 16 of 57 *C. irroratus* deaths occurred to newly molted individuals. Newly molted crabs are inherently

lacking in defenses, but they can display extensive agonistic behaviors (Adams and Caldwell 1990; Amaral et al. 2009), as have injured Crustacea (Berzins and Caldwell 1983; Briones-Fourzán et al. 2014; Maginnis et al. 2015).

Given such comparable costs, when placed in the context of game theory, these three species may be equally likely to escalate to fighting and risk injury when faced with the same rewards and competing for the same resources (e.g., refuge, mates, food). Subordinate or losing individuals are commonly relegated to poor-quality habitats that reinforce the life history costs of aggression (Aguilera and Navarrete 2012; Hardy and Briffa 2013). Haller et al. (1996) found that the fish *Macropodus opercularis* modifies its behavior in response to aggression, with subordinate individuals choosing to live in low-oxygen environments rather than risk fighting. Larval damselflies selectively avoid areas of low predation, specifically because these desirable sites subject them to increased intraspecific aggression (Elkin and Baker 2000). Iribarne et al. (1994) demonstrated that aggressive competition for space can cause a demographic bottleneck in juveniles of the Dungeness crab *Cancer magister*. The mechanism for this and other ecological consequences becomes quite clear in studies of the highly aggressive blue crab, *C. sapidus*, where they are known to engage in interference competition to the point of mortal injury, even when food is plentiful (Mansour and Lipscius 1991; Reichmuth et al. 2011).

Two of the species used in this study, *H. sanguineus* and *C. maenas*, are invasive species that compete with each other and the native *C. irroratus* for space in the rocky intertidal habitats of the northeastern United States (Epifanio 2013; Griffen and Riley 2015). The very high densities at which *H. sanguineus* is found (up to 120

crabs/m²; Kraemer et al. 2007) relative to other co-occurring species may attenuate intraspecific aggression (Lohrer and Whitlatch 2000; Hobbs unpublished data) and thus facilitate the species' invasion success. Decreased aggression at high densities is well documented in several fish species (Siikavuopio and Jobling 1994; Wang et al. 2002), but not commonly found in Crustacea (Moyle et al. 2009). Since the cost of aggression for *H. sanguineus* is comparable to the other two species, and behavioral observations of these crab species show comparable patterns of agonistic behavior (Hobbs unpublished data), there may be inherent mechanisms for minimizing agonism in this species.

Here, we focused on aggression in juvenile decapods, a period in their life of significant competition for limited resources after the ontogenetic shift from the water column to the benthos (Amaral et al. 2009; Viviani et al. 2010). A demographic bottleneck has been implicated in past decapod work (Moksnes et al. 1998; Amaral et al. 2009), which agonism makes more challenging. Past studies have shown that the cost at this age is substantially greater than at older ages, both in increased mortality and injury and in decreased growth (Juanes and Smith 1995; Smith 1995; Amaral et al. 2009).

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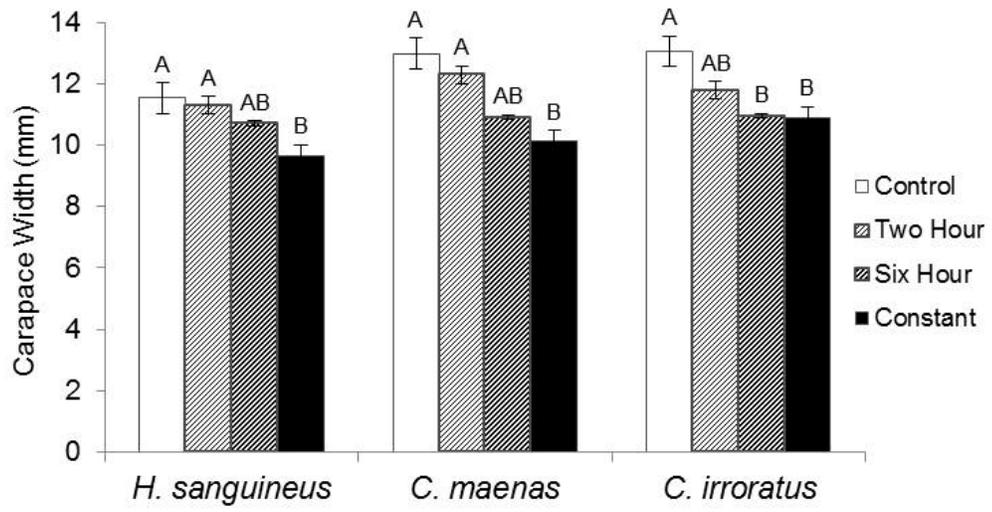
FIGURE LEGENDS

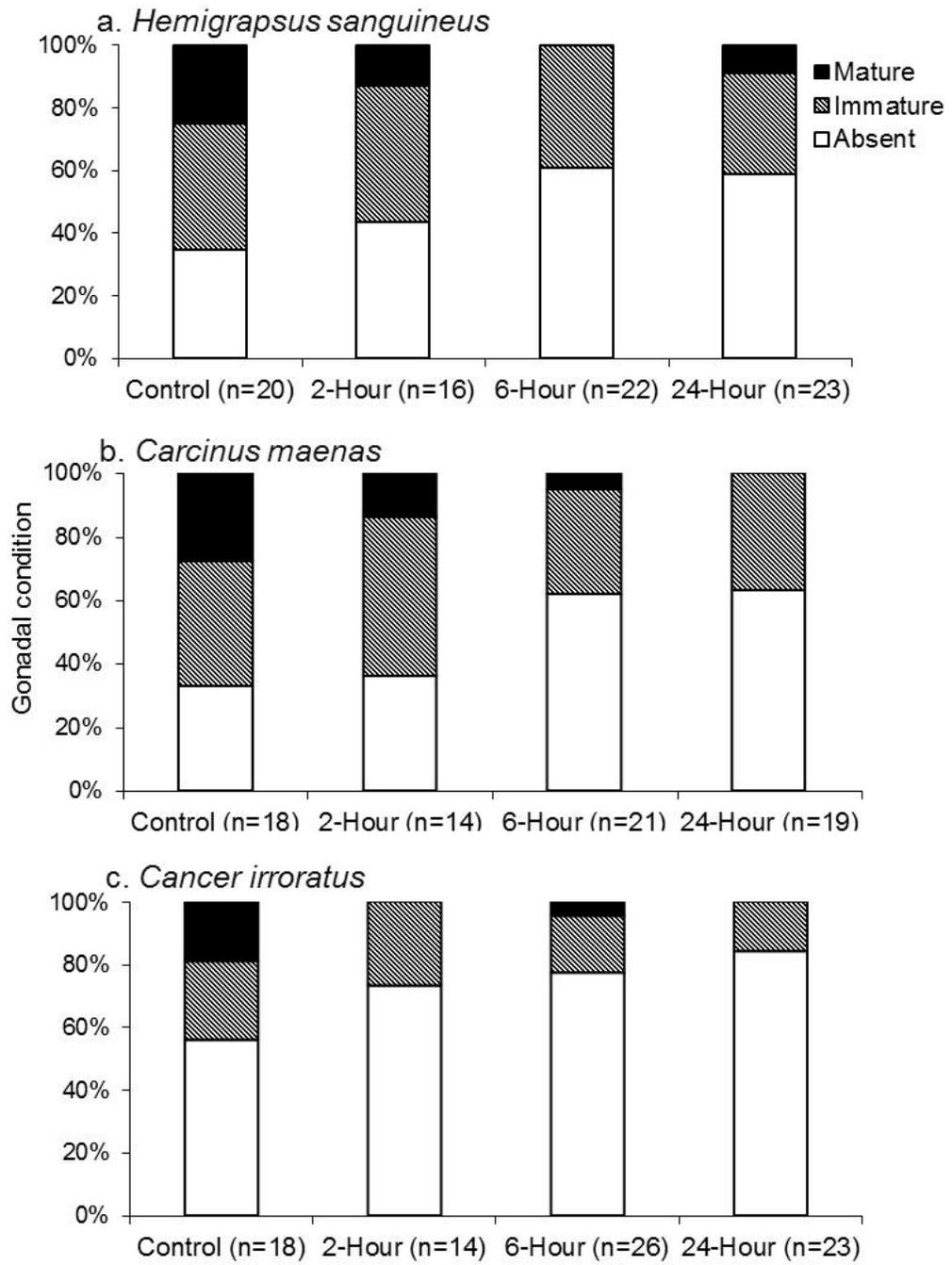
Fig. 1. Final carapace widths (CW) ($\text{mm} \pm 1 \text{ SE}$) of all treatments of *Hemigrapsus sanguineus*, *Carcinus maenas*, and *Cancer irroratus*. Letters signify significantly different treatments within each species, using Steel-Dwass test.

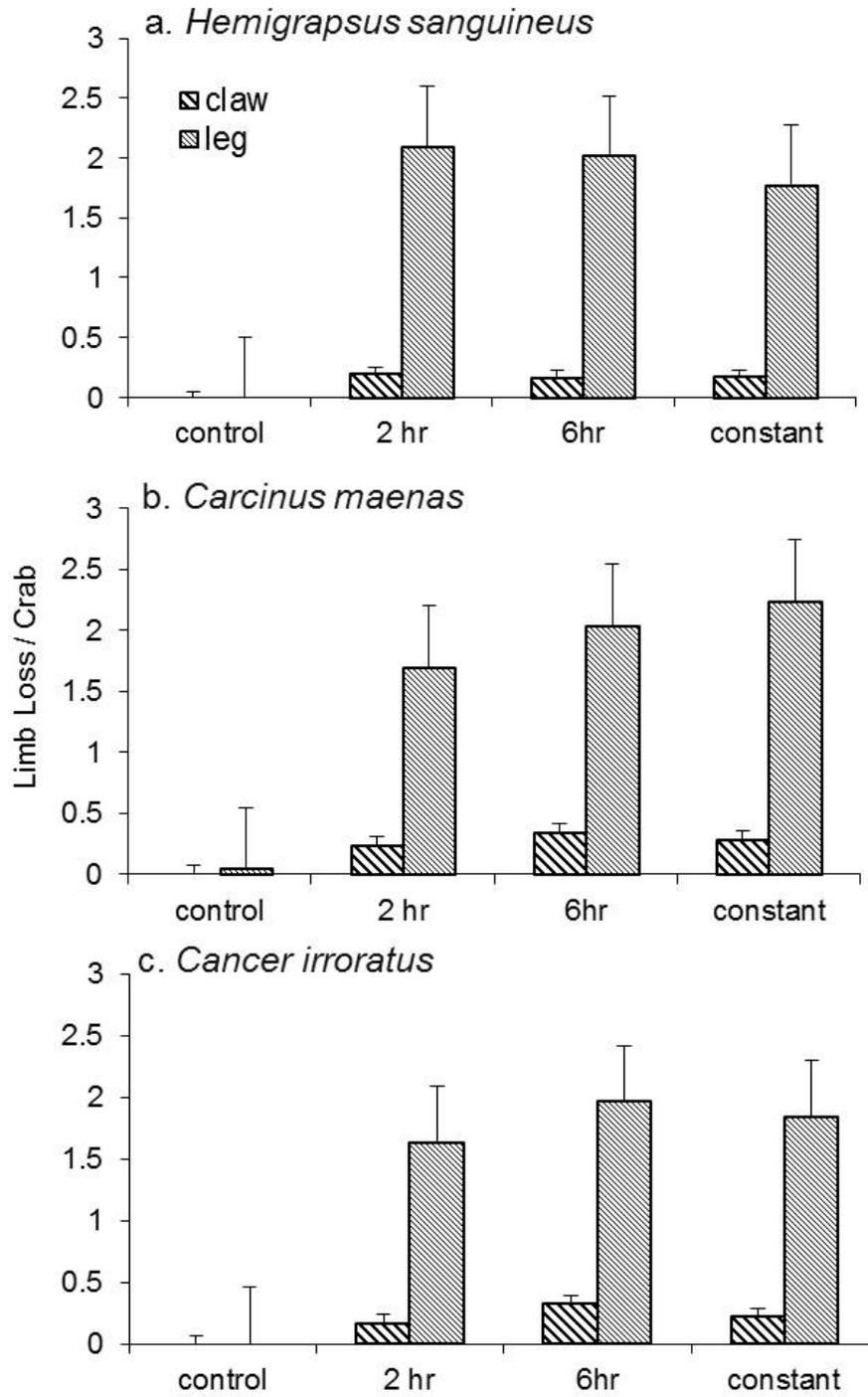
Figure 2: Pooled final gonadal condition of both sexes of all surviving crabs in all treatments of a) *Hemigrapsus sanguineus*, b) *Carcinus maenas*, and c) *Cancer irroratus*. Each bar represents the percentage of crabs whose gonadal condition was scored as either absent, immature, or mature.

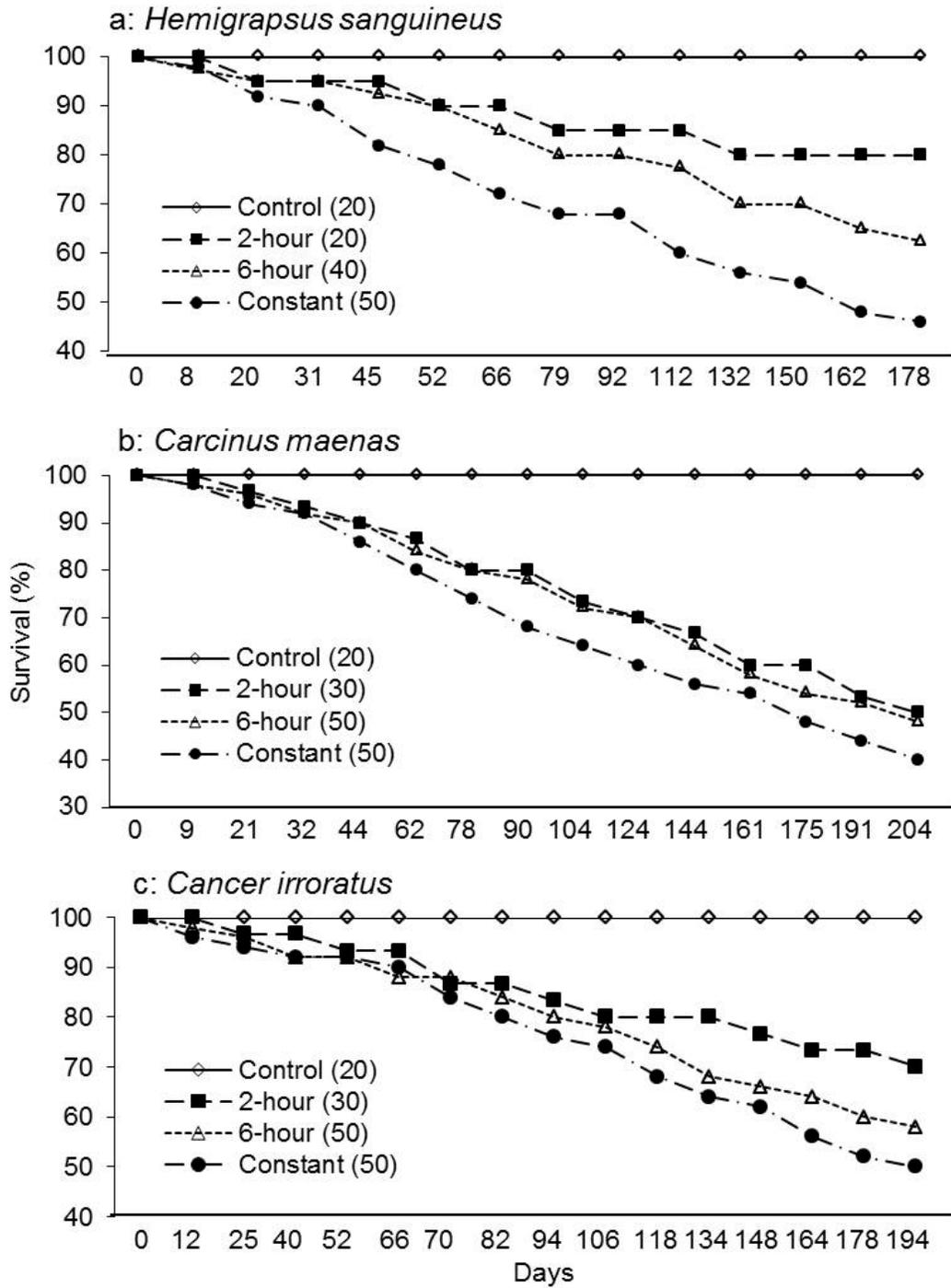
Fig. 3. Mean injuries ($\pm 1 \text{ SE}$) sustained per crab for all treatments of a) *Hemigrapsus sanguineus*, b) *Carcinus maenas*, and c) *Cancer irroratus*

Fig. 4. Percent survival plotted for all treatments of a) *Hemigrapsus sanguineus*, b) *Carcinus maenas*, and c) *Cancer irroratus*. Numbers in parentheses are initial sample size for each treatment. All treatments for each species ended at first detection of morphological maturity.









CHAPTER 3

CONSPECIFIC TOLERANCE AND HETEROSPECIFIC COMPETITION AS MECHANISMS FOR OVERCOMING RESISTANCE TO INVASION BY THE ASIAN SHORE CRAB, *HEMIGRAPSUS SANGUINEUS*

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Abstract

The success of the invasive Asian shore crab, *Hemigrapsus sanguineus*, stems partly from its ability to exclude established crab species from preferred rocky and cobble intertidal habitat. Here, we assessed preference and competition for habitat types (cobble vs. sand) for *H. sanguineus* and two competitor species; the previous invasive green crab, *Carcinus maenas*, and the native rock crab, *Cancer irroratus*, in New England. We paired similarly sized heterospecifics and conspecifics from each species, and also grouped combinations of *C. maenas* and *H. sanguineus* in a series of four-individual sets in order to test intra- and inter-specific competition at different densities. Individually, all three species preferred cobble substrate. With paired conspecifics, *H. sanguineus* individuals would cohabitate in cobble, whereas *C. maenas* and *C. irroratus* individuals each excluded conspecifics from cobble. In heterospecific pairs, *H. sanguineus* excluded both *C. maenas* and *C. irroratus* from cobble. *C. maenas* and *C. irroratus*, were equally likely to exclude the other species, but rarely excluded *H. sanguineus*. In larger assemblages, *H. sanguineus* preferentially grouped under cobble, whereas *C. maenas* were more evenly distributed among habitat types. These patterns illustrate a clear mechanism for overcoming invasion resistance and the exclusion of other intertidal crab species following the introduction of *H. sanguineus* in New England coastal systems.

Key words

habitat competition, conspecific tolerance, invasion resistance, *Hemigrapsus sanguineus*, *Carcinus maenas*, *Cancer irroratus*, rocky intertidal

Introduction

The distribution of species across their habitats is influenced by numerous positive and negative ecological interactions (e.g. Connell 1961; Boulangeat et al. 2012; Dijkstra et al. 2012; He et al. 2013; Wisz et al. 2013). Research over the past two decades has illustrated the ubiquity of positive interactions, from some forms of short-term facilitations (Bruno et al. 2003) to longer-term mutualisms (Stachowicz 2001), and other direct and indirect interactions (Menge 1995; Holmgren and Scheffer 2010; He et al. 2013). Additionally, simple tolerance of conspecifics, and occasionally heterospecifics, may help to shape population and community dynamics (Ritz 1993; Aguilera and Navarrete 2012; Kintzing and Butler 2014). Given the ubiquity of competition in the natural world (Menge and Sutherland 1987; Steinberg and Epifanio 2011; Aguilera and Navarrete 2012), and its importance in shaping species and community ecology (Best et al. 2013; Mittelbach and Schemske 2015), the selective advantages of non-competitive behavior, such as group living (Alexander 1974) or facilitation (He and Bertness 2014), may be comparably strong.

Extensive work has been done on the role of tolerance and cooperative behavior among group-living species in taxa such as primates (Melis et al. 2010), other mammals (Smith 2014), birds (Dickinson et al. 2009), and invertebrates (Bilde 2007; Komdeur et al. 2013). Much of this work has addressed the role of Hamiltonian kin selection in such interactions; group living, and inherent tolerance and cooperation, occurs most often among related individuals (Sigmund and Nowack 2001). Aggregations of unrelated individuals may simply be the outcome of factors such as sharing patchy shelter to avoid abiotic stressors (Menge and Sutherland 1987),

gaining access to and courting mates (Dubuc et al. 2012; Komdeur et al. 2013), increased foraging success (Hare et al. 2007), or by the dilution effect (Foster and Treherne 1981). Given these potential benefits, tolerance of, or even cooperation with, conspecifics can be just as powerful a force shaping population dynamics and community structure as interspecific competition.

The pressure to aggregate under shelters in the marine intertidal zone in order to avoid predation (Ory et al. 2012) and mitigate physical stresses such as desiccation (Aguilera and Navarrete 2012) conflicts with the pressure to disperse to avoid predation, cannibalism, and competition (Griffen and Byers 2009; Januario and Navarrete 2013). The success of an invasive species is often linked to their ability to outcompete native species for habitat and other resources (Molnar et al. 2008), as well as experiencing enemy release (Torchin et al. 2001; Snyder and Evans, 2006; Sheath et al. 2015). The Asian shore crab, *Hemigrapsus sanguineus* (De Haan, 1825), is a particularly successful invader in the northeastern U.S. that can exclude other crab species from preferred rocky intertidal habitat (Lohrer and Whitlatch 2002; Epifanio 2013). Following the introduction of *H. sanguineus*, densities of both the native rock crab *Cancer irroratus* Say, 1817, and an earlier invader, the European green crab *Carcinus maenas* (L, 1758), have decreased in southern New England rocky intertidal habitats (Jensen et al. 2002; Epifanio 2013). Rocky intertidal densities of *H. sanguineus* are generally much higher than those previously reached by the other two species (Griffen and Byers 2009; Epifanio 2013; Griffen and Riley 2015), suggesting that intraspecific competition may be weaker for this species. The invasion resistance hypothesis (Stachowicz et al. 1999; Kennedy et al. 2002; Marraffini and Geller 2015)

would suggest that the prior presence of the native *Cancer irroratus* and the invasive *Carcinus maenas* was not enough of a barrier to prevent the successful invasion by *H. sanguineus*. Given this, we sought to understand some of the factors that may be at play to overcome this resistance.

Here, we tested how intertidal habitat use by different native and invasive crab species is shaped by both intra- and interspecific competition and intraspecific tolerance, via manipulative experiments. Our results help explain why *H. sanguineus* in complex cobble intertidal habitats reaches much higher densities than either *Carcinus maenas* or *Cancer irroratus* (Epifanio 2013), overcoming the New England rocky shore community's resistance to invasion.

Methods

Study species and experimental protocol

We tested habitat selection and competition with a series of experiments using three focal species, the invasive crabs *Hemigrapsus sanguineus* and *Carcinus maenas*, and the native *Cancer irroratus*. These three species are the most common intertidal decapod crabs along coastal New England and beyond (Lohrer and Whitlatch 2002; Hobbs unpublished data). We collected uninjured crabs along the rocky shoreline south of the town beach in Narragansett, Rhode Island (41.431039 N, 71.455196 W). Crabs from 12 to 27mm carapace width were placed together in experimental trials with similarly sized individuals (within 1mm) and the same sex. No crabs were used more than once in any of the experiments. Individuals were kept in separate containers

in seawater flow-through aquaria at the University of Rhode Island's Narragansett Bay Campus for no more than three days prior to use in experiments. Crabs were not fed for one day prior to, or during, the experiment. Each trial began when study crabs were placed in different densities, as detailed below, in 38l (50cm L x 25cm W x 30cm H) glass tanks filled with continually aerated recirculating seawater (~32-33psu salinity) and kept in a climate-controlled (18-20°C) room on a 12hrL:12hrD light regime. The sides of each tank were covered with dark paper in order to minimize the impact of external stimuli on crab behavior. The bottom of each tank was covered in ~3mm sand substrate; one end of the tank contained a small pile of 10-15 mixed-size cobble (10-25cm long) pieces stacked at least two cobbles high to create crevices big enough to provide shelter. At the start of each trial, crabs were placed on the sand substrate at the center of each tank. Over the course of 24 hours, experimental tanks were observed every three hours to record the location of each crab (in cobble, near cobble, or on sand) and otherwise were not disturbed, in order to minimize outside stimuli. Any crab that was found directly adjacent to the cobble (within 1cm) was ranked as being "near cobble." Due to the scarcity of *Cancer* crabs during field collections, our experimental replicate numbers are lower for this species.

For our control experiment, we placed single individuals of each species, *H. sanguineus* (n = 15), *C. maenas* (n = 12), and *C. irroratus* (n = 12), into separate aquaria for 24hrs, and recorded their location as described above. To test for the impact of intraspecific competition on habitat selection and distribution, we used twelve size-matched pairs of *H. sanguineus* and *C. maenas* each and nine pairs of *C.*

irroratus. The lower number of *C. irroratus* replicates reflects their rarity in our field collections. To assess the impact of interspecific competition, we tested equivalently-sized heterospecific pairs of all potential species combinations: *H. sanguineus* v. *C. maenas* (12 pairs), *H. sanguineus* v. *C. maenas* (7 pairs), and *C. maenas* v. *C. irroratus* (6 pairs). For all assays, we observed individual distributions every three hours during each 24-hour treatment.

To assess how higher conspecific and heterospecific crab densities affect habitat selection, we ran five separate experiments on groups of four equivalently sized crabs. These experiments only included *H. sanguineus* and *C. maenas*; the scarcity of *C. irroratus* precluded their inclusion. Our first two experiments placed four conspecifics together; the *H. sanguineus*-alone experiment was replicated seven times (=28 total crabs) and the *C. maenas*-alone experiment was replicated five times (=20 total crabs). In our third experiment, the four equivalently sized crabs consisted of two *H. sanguineus* and two *C. maenas*; this experiment was replicated six times. In our fourth experiment, the four equivalently sized crabs consisted of one *H. sanguineus* and three *C. maenas*; this experiment was replicated seven times. In our fifth experiment, the four equivalently sized crabs consisted of three *H. sanguineus* and one *C. maenas*; this experiment was replicated eight times.

We analyzed our data for habitat preference using 2x2 Fisher's Exact Test comparisons in JMP 11 (www.jmp.com). Fisher's Exact Tests for 2x3 and 3x3 tests were analyzed with the Freeman-Halton extension (Freeman and Halton 1951) using VassarStats (vassarstats.net). We used the more conservative P_A value for these two-tailed tests, where the probability of the observed cell frequencies and the sum of the probabilities of all other cell-frequencies are equal to or less than the probability of the observed array (Freeman and Halton 1951, VassarStats 2015).

Results

Individual habitat preference

Over 75% of individual *Hemigrapsus sanguineus*, *Carcinus maenas*, and *Cancer irroratus* crabs chose the cobble substrate, with no difference in distribution among the three species (Fig. 1; 3x3 Fisher's Exact Test $P = 0.86$), indicating a strong preference for cobble among individuals of all three species.

Habitat selection – paired crabs

The distribution of conspecific pairs among the three species was significantly different (Fig. 2; 3x3 Fisher's Exact Test $P = 0.0499$). Individuals in the conspecific pairings of *H. sanguineus* were observed in the cobble 79% of the time. By contrast, in pairings of either *C. maenas* or *C. irroratus*, individuals would segregate between the preferred cobble substrate (50% of the time for both species) and sand (44.4% and 37.5% of the time, respectively), so that only one individual was observed in the cobble at any given time for these two species.

When *H. sanguineus* and *C. maenas* were paired together, *H. sanguineus* selected cobble substrate 83.3% of the time. Conversely, *C. maenas* were never found in the preferred cobble substrate, instead being observed on sandy substrate 75% of the time and near cobble 25% of the time (Fig. 3a; 2x3 Fisher's Exact Test $P < 0.0001$). We found similar results when *H. sanguineus* were paired with *C. irroratus*: 85.7% of *H. sanguineus* in cobble, with no *C. irroratus* observed in cobble, and *C. irroratus* on sand 71.4% of the time (Fig. 3b; 2x3 Fisher's Exact Test $P = 0.0008$).

However, when *C. maenas* and *C. irroratus* were paired together, individuals of both species were statistically just as likely to be in cobble (50% and 33.3%, respectively) as on sand (33.3% and 50%, respectively, Fig. 3c; 2x3 Fisher's Exact Test $P = 0.99$).

Habitat selection – grouped crabs

Among groups of four similarly sized crabs of the same species, *H. sanguineus* individuals were observed in the cobble substrate 71.4% and on sand 7.1% of the time, while *C. maenas* was evenly distributed across all three substrates (Figure 4a; 2x3 Fisher's Exact Test $P = 0.01$). In symmetric groups of two *H. sanguineus* and two *C. maenas*, 91.7% of *H. sanguineus* were observed in cobble while *C. maenas* were in cobble only 8.3% of the time, instead of sand 66.7% (Fig. 4b; 2x3 Fisher's Exact Test $P < 0.0001$). In asymmetric groups of one *H. sanguineus* and three *C. maenas*, *H. sanguineus* was observed only 57.1% in cobble, and *C. maenas* 19% in cobble (Fig. 4c; 2x3 Fisher's Exact Test $P = 0.08$). Conversely, when three *H. sanguineus* were grouped with a single *C. maenas*, *H. sanguineus* were observed in the cobble 83.3% of the time, where *C. maenas* were never found, instead being observed 87.5% in sand (Fig. 4d; 2x3 Fisher's Exact Test $P < 0.0001$).

Discussion

Our results indicate that *Hemigrapsus sanguineus* can cohabitate in preferred substrate with conspecifics (Figs. 2 and 4a), and remain in its preferred substrate even when interspecific competitors have a numerical advantage (Fig. 4d). In contrast,

intraspecific avoidance/antagonism in both *Carcinus maenas* and *Cancer irroratus* was great enough to prevent conspecific cohabitation (Fig. 2). The intraspecific avoidance or agonism displayed by these species likely provides an indirect benefit to *H. sanguineus* by decreasing the heterospecific competitor densities in its preferred substrate. Conversely, the ability of *H. sanguineus* to tolerate high conspecific densities and exclude heterospecifics likely underlies this species' success in Southern New England. The success of *H. sanguineus* is demonstrated by the fact that although 3:1 *Carcinus:Hemigrapsus* ratios are not seen in natural habitats, 1:3 *Carcinus:Hemigrapsus* ratios are far more common (Lohrer and Whitlatch 2002; Jensen et al. 2002; Epifanio 2013).

The global spread of *H. sanguineus* is now well documented (Jensen et al. 2002; Epifanio 2013), and the mechanisms which allow for its ecological success include tolerance of temperature and salinity extremes, high rates of reproduction, a generalist diet (Epifanio, 2013), and, as demonstrated here, a degree of conspecific tolerance higher than that of other competing crab species (Lohrer and Whitlatch 2002). While *H. sanguineus* and *C. maenas* (Carlton and Cohen 2003) share most of these characteristics, which are considered classic attributes of successful invaders (Elton 1958; Marchetti et al. 2004; Carlton 2011), the two species differ substantially in their conspecific tolerance. This trait may explain why this species has largely replaced native crabs such as *C. irroratus* and the well-established invasive *C. maenas*; neither species are tolerant of either heterospecific or conspecific crabs, engaging in exclusionary competitive interactions when shelter resources are limited.

In addition to identifying the characteristics that make an introduced species

successful, much work on invasion biology has sought to understand the factors that make that new range more susceptible to introduction and invasion in the first place (Carlton 2011; Marraffini and Geller 2015). Long-standing thinking generally suggests that species-rich areas with robust native communities are less invasible (Stachowicz et al. 1999; Kennedy et al. 2002), but the field evidence has been mixed (Jackson 2015; Marraffini and Geller 2015). Recent work suggests that a more complex and dynamic community, which includes introduced species, is more resistant to future invasions (Jackson 2015; Marraffini and Geller 2015). It is unclear if the New England coastline currently contains such a robust community, as *H. sanguineus* has nearly eliminated both a native and formerly successful invasive species of crab (Kraemer et al. 2007; Lohrer and Whitlatch 2002).

The prior invasion by *C. maenas* may have acted to facilitate *H. sanguineus* invasion by decreasing the densities of native decapod species (Carlton and Cohen 2003; Grosholz and Ruiz 1996) which would otherwise have competed with *H. sanguineus*. Since our study shows that neither *C. irroratus* nor *C. maenas* tend to share habitat with other crabs, both species may have indirectly facilitated the establishment and spread of *H. sanguineus* by keeping potential competitor crab densities low and limited shelter available. In addition, *H. sanguineus* mainly overwinters in the intertidal and shallow subtidal zones (Epifanio 2013), whereas both *C. maenas* and *C. irroratus* migrate subtidally to avoid cold stress (Reilly and Saila 1978; Hunter and Naylor 1993), which provides *H. sanguineus* with an additional competitive advantage when the other species attempt to migrate back into the intertidal in spring.

Some supporting evidence for the roles of both conspecific tolerance and species richness in modifying invasion success comes from other portions of the expanded range of *H. sanguineus*. On the west coast of the United States, Steinberg and Epifanio (2011) found that two native *Hemigrapsus* species, *H. nudus* and *H. oregonensis*, outcompete *H. sanguineus* for shelter use. Their observations suggest that both native species are similarly tolerant of conspecifics; if they also share a similar tolerance for conspecific cohabitation, this could help resist *H. sanguineus* establishment and spread. This pattern supports the prevailing thinking on the nature of invasion resistance where species richness, and particularly redundancy in guild members, serves to mitigate invasions (Stachowicz et al. 1999; Jackson 2015; Marraffini and Geller 2015). In other words, the preexistence of conspecific-tolerant congeners may deprive *H. sanguineus* of a critical advantage when invading new habitats.

Conspecific tolerance confers a clear advantage for avoiding predation (Hamilton 1971; Turner and Pitcher 1986), increasing group foraging efficiency (Hare et al. 2007), and acquiring greater access to mates (DeGoursey and Auster 1992; Dubuc et al. 2012). In this study, we demonstrate the role it has in securing limited refugia, allowing conspecifics to survive and thrive in an otherwise physically stressful and ecologically demanding environment. For *H. sanguineus*, the coupling of conspecific tolerance with heterospecific dominance creates a suite of tactics that allow it to successfully invade habitats already populated by guild members that don't display the same tactics. Given the right combination of novel tactics such as these, an invasive species may be able to overcome community resistance.

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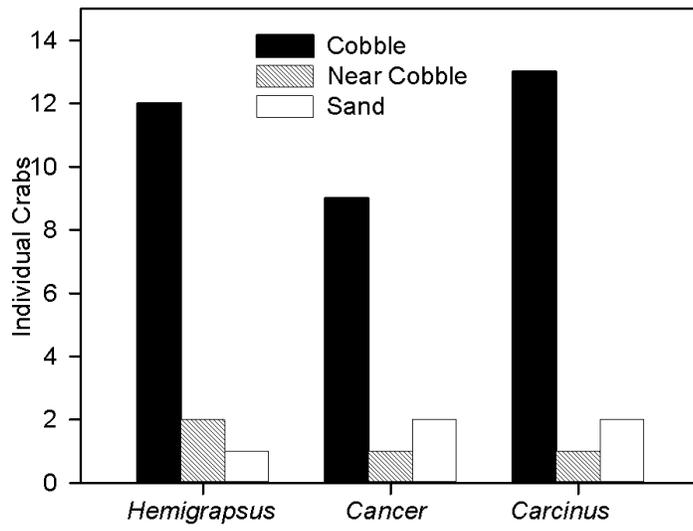
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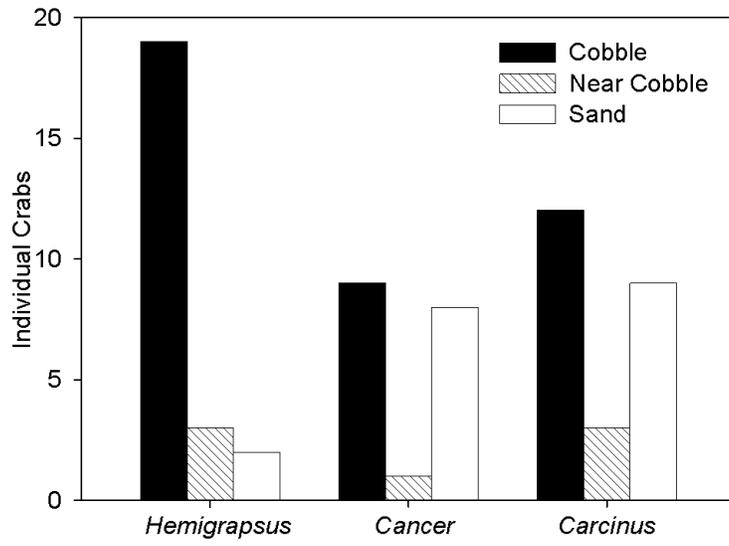
Fig. 1 The distribution of solitary individuals of the three crabs, *Hemigrapsus sanguineus*, *Cancer irroratus*, and *Carcinus maenas*, across cobble (black bars), near cobble (hatched bars), and sand (white bars) substrates. Numbers represent individual crabs.

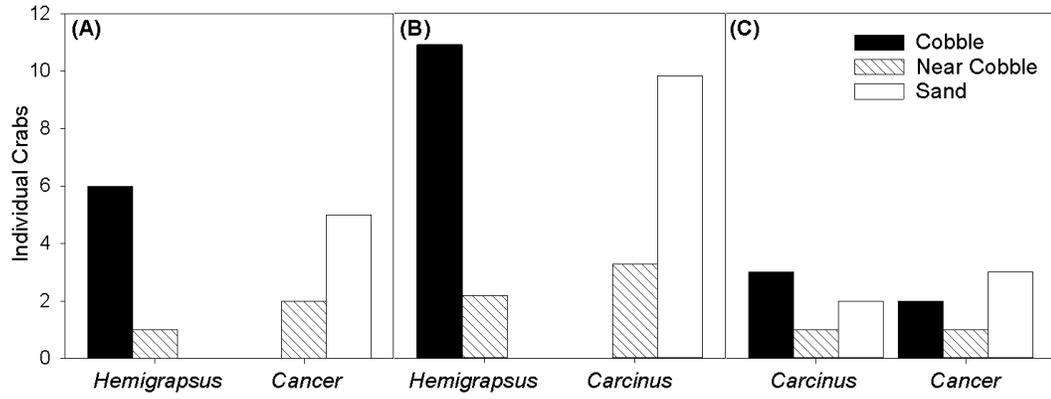
Fig. 2 The distribution of individual crabs within conspecific pairings of *Hemigrapsus sanguineus*, *Cancer irroratus*, and *Carcinus maenas*, across cobble (black bars), near cobble (hatched bars), and sand (white bars) substrates. Numbers represent individual crabs.

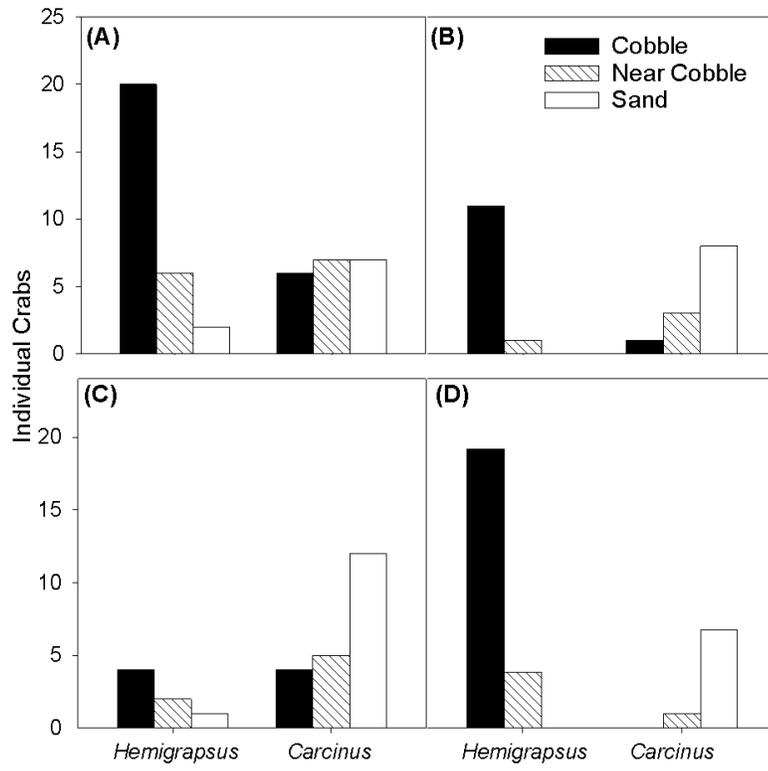
Fig. 3 The distribution of individual crabs within heterospecific pairings of *Hemigrapsus sanguineus* and *Carcinus maenas* (**a**), *H. sanguineus* and *Cancer irroratus* (**b**), and *C. maenas* and *C. irroratus* (**c**), across cobble (black bars), near cobble (hatched bars), and sand (white bars) substrates. Numbers represent individual crabs.

Fig. 4 The distribution of individual crabs in conspecific groups of four *Hemigrapsus sanguineus* or four *Carcinus maenas* (**a**), heterospecific groups of two *H. sanguineus* with two *C. maenas* (**b**), one *H. sanguineus* grouped with three *C. maenas* (**c**), and three *H. sanguineus* grouped with one *C. maenas* (**d**) across cobble (black bars), near cobble (hatched bars), and sand (white bars) substrates. Numbers represent individual crabs.









CHAPTER 4

INJURY, REPRODUCTIVE STATUS, AND DISTRIBUTION OF *HEMIGRAPUS* *SANGUINEUS* (DE HAAN, 1835) IN THE ROCKY INTERTIDAL SHORES OF RHODE ISLAND

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ABSTRACT

Intertidal crabs exhibit high occurrences of injury, including claw and leg loss. While it can be challenging to determine the specific cause of such injuries, the resulting distribution of injured individuals across habitat types is relatively easy to assess. We surveyed rocky intertidal crab populations along Rhode Island USA rocky shorelines to determine the distribution of injured vs. uninjured crabs. We found that the invasive Asian shore crab *Hemigrapsus sanguineus* dominated the surveys, with few other crab species found across our sites. We found little evidence for differences in the distribution of injuries across intertidal zones, with half of all crabs exhibiting loss of at least one limb. There were no differences in claw loss across the sampled populations, though mature crabs were 22% more likely than juveniles to be missing legs. Gravid females had the lowest frequency of injury of all crabs, being three times less likely to be injured than non-gravid females. Relative to other crabs, gravid females and juveniles were also less likely to be found in the high intertidal zone. Our results underscore the complexity of patterns of injury and resulting demographics, and help illuminate the role these patterns play in the ecology of intertidal organisms.

KEY WORDS

Injury, rocky intertidal, competition, predation, *Hemigrapsus sanguineus*, invasive species

INTRODUCTION

Intertidal animals are subject to physical stresses and ecological interactions that make them susceptible to injury (Juanes and Smith, 1995; Lindsay, 2010). Many crustaceans can autotomize limbs to escape predators or speed recovery from injury, and several studies have found that roughly half of intertidal crab individuals are missing at least one limb at any given time (Davis et al., 2005; Dvoretzky and Dvoretzky, 2009; Maginnis et al., 2014). Such field studies often record high rates of claw loss (Juanes and Smith, 1995; Frisch and Hobbs, 2011; Tummon Flynn et al., 2015), an injury which puts the individual at a substantial disadvantage for defense and feeding (Lindsay, 2010). Male crabs are particularly susceptible to claw loss (Maginnis et al., 2014), which has been linked to greater rates of aggressive behavior in decapods (Briones Fourzan et al., 2014). In general, larger crabs are also more likely to be missing a limb, either because they engage in more risky behaviors such as aggressive contests with intra-guild decapods or because they are better able to survive predation events (Davis et al., 2005; Mathews et al., 1999). While injury is preferable to death, and autotomy confers a survival benefit to the crabs (Knopé and Larson, 2014), they nonetheless incur several potential costs including reduced growth, fecundity, and competitive ability (Maginnis, 2006; Lindsay, 2010).

While it can be difficult to ascertain the cause of a particular limb loss, chela loss is most commonly due to injuries sustained in intra-guild contests, rather than from predation attempts (Juanes and Smith, 1995; Lindsay, 2010). Chela loss in crayfish increases with increasing densities (Figiel and Miller, 1995), supporting the notion that it is often a result of aggressive encounters. More important, individuals

that lost at least one chela had higher mortality rates and grew much slower than intact individuals, regardless of density or refuge availability (Figiel and Miller, 1995). Sekkelsten (1988) observed that *Carcinus maenas* males missing a claw were rarely observed to mate and were not capable of retaining mates when confronted with competing males. Limb loss, especially the loss of a claw, can thus significantly affect fitness (Juanes and Smith, 1995; Lindsay, 2010; Frisch and Hobbs, 2011). In response, most decapods are capable of regenerating limbs within one or two molts (Juanes and Smith, 1995). Yasuda et al. (2014) found that autotomized hermit crabs were able to accelerate molting and produce an entirely new claw in one molt. However, such regenerated claws are typically not as robust as the original (Juanes and Smith, 1995; Yasuda et al., 2014), though they may suffice for feeding and defense (Briones Fourzan et al., 2014; Maginnis et al., 2014).

Hemigrapsus sanguineus (De Haan, 1835) is the most common rocky intertidal crab in southern New England and is an effective cosmopolitan invader currently expanding its range around the world (Carlton and Cohen, 2003; Epifanio, 2013). *H. sanguineus* arrived in New England in the mid-1990s, nearly two centuries after the arrival of a previous invader, *Carcinus maenas* (L, 1758), the European green crab (Carlton and Cohen, 2003; Williams et al., 2015). Though both species are capable of preying upon each other (Jensen et al. 2002), *H. sanguineus* possesses a competitive advantage in New England rocky intertidal habitats (Epifanio, 2013). This species has largely replaced both *C. maenas* and several native crabs (Jensen et al., 2002; Kraemer et al., 2007) including the rock crab, *Cancer irroratus* Say, 1817, with which both invaders ecologically overlap (Lohrer and Whitlatch, 2002; Matheson and Gagnon,

2012). *H. sanguineus* is found in densities higher than other co-occurring species (Lohrer and Whitlatch, 2002; Epifanio, 2013) and therefore its potential for density-dependent injury from predation and conspecific aggression is increased. A previous study of *H. sanguineus* in New England waters found 42% of individuals had lost at least one limb (Davis et al., 2005), but the impact that such injuries have on the ecology of this invader in terms of their abundance and distribution have not been fully explored.

We sought to determine how injury rates and distribution are structured across the intertidal zone for crabs. If a difference in the distribution of injured crabs across the intertidal zone exists, it may be linked to differences in habitat preference, with injured crabs being less able to defend preferred habitats. Additionally, patterns in injuries across the rocky intertidal habitat may be linked to sex, developmental stage, or reproductive status.

METHODS

We conducted a series of field surveys to investigate the distribution of injury in *Hemigrapsus sanguineus* across the rocky intertidal zone at four sites near the mouth of Narragansett Bay, Rhode Island USA. During spring low tides in the fall of 2003, we surveyed rocky shorelines at Beavertail State Park on Aquidneck Island (41.4525 N, 71.3946 W), at Narragansett Town Beach (41.4310 N, 71.4551 W), at Black Point State Park (41.3955 N, 71.4637 W), and the rocky shore on the northeast side of the Galilee mudflats (41.3843 N, 71.4980 W). At each site, ten 0.25m²

quadrats were laid haphazardly along three different intertidal 10 meter transect lines running parallel to the shoreline, one near the lowest tide mark possible (at peak spring tides), another along the middle of the intertidal zone, and a third along the high intertidal zone (as denoted by the presence of high tide barnacles species) just below the splash zone. Quadrats that landed on bare rock or rock too large to move were repositioned until they landed on rocks and cobble that could be moved. All small rocks and cobbles in a quadrat were cleared and, with the use of 5mm mesh screens, all 5mm carapace width or larger crabs found in each quadrat were collected.

For each crab, we measured the carapace width with digital Vernier calipers and also recorded the species, sex, morphological maturity (of females), and # limbs lost and type (claw-loss versus leg-loss). Using JMP version 11 (www.sas.com), we conducted separate Pearson χ^2 analyses on the proportion of claw loss and leg loss injuries among tidal heights, between sexes, between mature and immature crabs, and between gravid and non-gravid females.

RESULTS

Of the 599 crabs collected, 554 were *Hemigrapsus sanguineus*, twenty-one *Carcinus maenas*, six *Cancer irroratus*, and eighteen panopeid mud crabs (mostly *Dyspanopeus sayi*). Due to this disparity in species abundance, we restricted our analyses to *H. sanguineus*. As we did not find any significant statistical differences among sites (or with site interaction terms) in our response variables, we grouped all sites together for the statistical analyses presented here.

We found no significant difference in the percentage of crabs with claw loss (Pearson $\chi^2 = 2.71$, $p = 0.26$) or leg loss (Pearson $\chi^2 = 0.26$, $p = 0.88$) among intertidal heights (8.6%, 15.6%, and 11.3% claw loss and 50.7%, 52.2%, and 47.1% leg loss at high, middle, and low intertidal, respectively). Across all intertidal heights, there was no significant difference in claw loss or leg loss between mature males (14.4 and 36.6%) and females (11.2 and 36.6%; Pearson $\chi^2 = 0.85$, $p = 0.36$; Pearson $\chi^2 = 0.003$, $p = 0.96$). While sexual maturity was not correlated with claw loss (Pearson $\chi^2 = 2.77$, $p = 0.10$, Figure 1A), mature crabs were 22% more likely than immature crabs to be missing legs (Pearson $\chi^2 = 5.48$, $p = 0.0192$; Figure 1B). Gravid and non-gravid mature females were equally likely to exhibit claw loss (5% and 20.3%, respectively; Pearson $\chi^2 = 2.09$, $p = 0.15$; Figure 2A). However, leg loss was more common among non-gravid females (66.3% as opposed to 20.8% of gravid females; Pearson $\chi^2 = 5.42$, $p = 0.0199$; Figure 2B).

There was no difference in the distribution of mature males vs. mature females across the low, middle, and high intertidal heights, with 31.2% vs. 24.6%, 46.0% vs. 52.4%, and 22.8% vs. 23.0% respectively (Pearson $\chi^2 = 2.31$, $p = 0.32$). However, immature crabs showed significant variation in distribution, with 42.1% in the low intertidal zone, 50.6% in the middle intertidal zone, and only 7.3% in the high intertidal zone (Pearson $\chi^2 = 22.43$, $p < 0.0001$; Figure 3). The proportion of females that were gravid was highest in the low intertidal zone (28.3%), vs. 15.3% in middle intertidal and 2.3% in high intertidal zones (Pearson $\chi^2 = 11.42$, $p = 0.0033$; Figure 4).

DISCUSSION

Many crustaceans are able to autotomize, and later regenerate, limbs after injury or to prevent predation (Juanes and Smith, 1995; Lindsay, 2010), including the invasive crab, *Hemigrapsus sanguineus*. Our study demonstrates that such injuries are found across the intertidal distribution of this species, which may shift the distribution of juvenile and smaller adults to lower intertidal heights (Fig. 3). Additionally, we show that such injuries correlate both with the distribution of gravid females that are likewise found lower in the intertidal zone (Fig 4), and with reproductive status since gravid females had fewer observed injuries (13.6%, compared to 40.8% of non-gravid females). In a previous study in New England, Davis et al. (2005) observed that 42% of *H. sanguineus* had lost at least one limb, which is comparable to our findings and other studies of limb loss for crabs in general (Juanes and Smith, 1995). Often, *H. sanguineus* was missing at least one claw, putting the individual at a substantial disadvantage in terms of defense and feeding. Some studies have shown that larger crabs are more likely to lose a claw (Mathews et al., 1999; Davis et al., 2005), perhaps as a result of risky behaviors such as aggressive contests or competition with other decapods (Amaral et al., 2009; Januario and Navarrete, 2013). While losing a limb of any kind is ultimately better than mortality, limb loss is expensive, incurring diminished growth, fecundity, and/or reduced competitive ability (Maginnis, 2006; Lindsay, 2010). Patterns such as we report here underscore the significance of injury in shaping major aspects of a species' ecology, whether a matter of gravid females being more capable of avoiding injury, or being more likely to suffer outright mortality as a result of predation.

We found no difference in claw loss across size classes, sex, and tidal distribution, similar to a previous study by Davis et al. (2005). The fact that more adult males and non-gravid adult females were missing legs, however, has been suggested as evidence for predation being a greater cause of injury than competition (Juanes and Smith, 1995; Dvoretzky and Dvoretzky, 2009; Maginnis et al., 2014), which may be due to relatively low rates of intraspecific aggression in this species (Hobbs, unpubl. data). Predation risk can be great; Silva et al. (2014) found that different competing predatory crab species forage into the intertidal to hunt at high tide, with variation in their distribution that minimized interference competition among the predators but increased the danger to intertidal prey crabs. As a result, nonconsumptive effects are likely also important as subtidal predators such as fish and larger decapods migrate in to the intertidal during high tide and cause shifts in behavior and distribution of decapod prey species, which reduce activity and remain in shelter until predators depart (Alexander et al., 2013). Given the abundance of observed *H. sanguineus*, and scarcity of other species, *H. sanguineus* may be particularly adept at avoiding predation (Lohrer and Whitlatch, 2002; Epifanio, 2013) via a suite of characteristics including cryptic coloration, effective use of cobble refuge, and anti-predatory behavior, which have been documented in other decapod species (Palma and Steneck, 2001; Lavalli and Spanier, 2015).

Hemigrapsus sanguineus are also effective intertidal predators themselves, feeding on mussels and other bivalves (Bourdeau and O'Connor, 2003; Griffen et al, 2008), as well as other decapods including juvenile lobsters (Demeo and Riley, 2006; Lord and Dalvano, 2015), and co-occurring crabs (e.g., *C. maenas*; Epifanio, 2013;

Griffen and Riley, 2015). Though *H. sanguineus* and *C. maenas* are capable of preying upon the other, the competitive advantage for habitat appears to go to *H. sanguineus* (Hobbs et al., unpubl. data). The functional morphology of *H. sanguineus* chelae indicates they have the capacity to damage other crabs (Payne and Kraemer, 2013), lending credence to the hypothesis that their predation reduces *C. maenas* densities. Regardless of the causative mechanisms, our observations present further documentation for the near monoculture of *H. sanguineus* in rocky and cobble habitat communities that used to be comprised of *C. maenas* and *C. irroratus* (Lohrer and Whitlatch, 2002; Epifanio, 2013).

Much of the threat of predation that intertidal crabs are exposed to comes in the form of cannibalism, particularly following recruitment and settlement, both from within their cohort, and from larger, older conspecifics (Moksnes, 2004; Amaral et al., 2009). Populations of *C. maenas* in Sweden exhibited such strong inter-cohort cannibalism that settlement pulses were typically eliminated from the population over time (Moksnes, 2004). Even with abundant external food sources, this intraspecific predation mitigated positive demographic patterns. Similarly, Januario and Navarrete (2013) found that two different species of crabs on the coast of Chile suffered ~30% mortality from both intra- and inter-cohort cannibals, regardless of density. Research by Amaral et al. (2009) on the coast of Portugal found that the crab *C. pagurus* is both a significant predator on another, smaller co-occurring crab species as well as a cannibal on smaller juveniles. This ontogenetic shift was mitigated by alternative food availability, high cohort density (indicating interference competition within the cohort), and habitat complexity, all of which decreased cannibalism rates significantly.

Given the high numbers of *H. sanguineus* found in our study across all three tidal heights, and the general patterns of observed injury, cannibalism of juveniles may be common (Amaral et al., 2009; Januario and Navarrete, 2013), which may explain the relatively low occurrence of injury observed among juvenile *H. sanguineus* compared to adults. If predation and cannibalism disproportionately affect smaller size classes of *H. sanguineus*, rather than leaving them injured (Juanes and Smith, 1995; Kim and O'Connor, 2007; Amaral et al., 2009; Januario and Navarrete, 2013), it could explain the relatively low occurrence of injuries in the smaller size classes. Some patterns are more difficult to attribute to one particular factor: for example, the relatively low number of gravid females and juveniles in the high tide zone may be due to terrestrial/avian predation pressure, or to abiotic factors causing higher densities of these groups in the lower intertidal (Flores and Paula, 2001; Moksnes, 2002; Weiters et al., 2009).

The occurrence of injury can provide insights into the roles of competition, cannibalism, and predation on shaping population and community dynamics (Juanes and Smith, 1995; Maginnis, 2006; Lindsay, 2010), though it is often difficult to ascertain the specific cause of an observed injury. In our study, greater occurrences of non-lethal injury in adults than juveniles (Figure 1B) may indicate that juveniles either avoid injury or, conversely, suffer higher mortality due to injury or density-dependent cannibalism. The lack of differences in injuries across tidal heights that we found may be due to consistent causative factors across those heights (Pardo et al., 2007; Weiters et al., 2009), or may occur because crabs are highly mobile and quickly migrate across the intertidal zone post-injury. Perhaps the most telling result is that few individuals of

other crab species were found in these surveys, further corroborating previous studies showing *H. sanguineus* dominance of the rocky intertidal shoreline of New England (Epifanio, 2013).

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Figure Legends

Figure 1: Occurrence of claw loss (A) and leg loss (B) among immature and mature

Hemigrapsus sanguineus

Figure 2: Occurrence of claw loss (A) and leg loss (B) among ovigerous and non-

ovigerous mature female *Hemigrapsus sanguineus*

Figure 3: Intertidal distribution of mature and immature *Hemigrapsus sanguineus*

Figure 4: Intertidal distribution of ovigerous and non-ovigerous mature female

Hemigrapsus sanguineus

