Impacts of Marine Invasive Species on Subtidal and Intertidal Food Web Dynamics

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IMPACTS OF MARINE INVASIVE SPECIES
ON SUBTIDAL AND INTERTIDAL
FOOD WEB DYNAMICS

BY
NICOLE ELISABETH ROHR

A DISSERTATION SUBMITTED IN PARTIAL FULFILLMENT OF THE
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OF

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ABSTRACT

Invasive species can have a variety of impacts on food web structure and interspecific interactions. They can impact recruitment rates of associated marine species, influence behavior of potential prey items, and alter predator-prey relationships. This research is designed to assess 1) the relationship between the recruitment of *Lacuna vincta* and two species of algal epiphytes, the native *Ceramium virgatum* and the invasive *Neosiphonia harveyi*, in the shallow subtidal zone; 2) the spatial and temporal distribution of the invasive *Hemigrapsus sanguineus* in the intertidal zone of cobble beaches; and 3) the top-down effects and predator-prey interactions of *H. sanguineus*.

Through manipulative field experiments, we found that the presence of algal epiphytes facilitated the recruitment rate of *Lacuna vincta*, regardless of the epiphyte species composition. We also found a positive relationship between the number of *L. vincta* present and epiphyte recruitment, which is disproportionately driven by higher recruitment of *Neosiphonia harveyi* than *Ceramium virgatum*.

Long-term monitoring can be used to understand population trends of invasive species. Through monthly surveys in Narragansett Bay, Rhode Island, we determined that *Hemigrapsus sanguineus* densities are highest in the early summer and early fall months. Juvenile *H. sanguineus* are most abundant in June and July and gravid females are most prevalent in August and September. *H. sanguineus* exhibited a density gradient with the highest densities in the northern section of Narragansett Bay and declining toward the mouth at the southern end of Narragansett Bay.

Invasive species can outcompete native and established species, thereby altering food web dynamics through changes in top-down and predator-prey interactions.
Through mesocosm studies, we found that while *Hemigrapsus sanguineus* has an impact on *Littorina littorea* behavior, it does not alter the perwinkles’ grazing rates. By contrast, the combined presence of *H. sanguineus* and *L. littorea* results in a greater decrease in algal biomass than only *L. littorea*. In field tethering experiments, we observed that abiotic but not biotic factors were the dominant force in structuring the vertical distribution of *H. sanguineus*. Overall, we found that *H. sanguineus* does not occupy the same ecological niche as *Carcinus maenas*, the previously dominant crab in the intertidal zone of cobble beaches.

This research provides insight into how invasive species shape the sub- and intertidal zones by influencing the recruitment rate and behavior of native and established species. Given that marine invasions are occurring at an increasing rate due to international marine transportation, human-mediated introductions, and global climate change, fully understanding the impacts of these invasive species is critical to mitigating and adapting to changes in species composition and abundance.
ACKNOWLEDGMENTS

First and foremost, I thank my major professor, Carol Thornber. Through her guidance, support, and training, I became a better researcher, vastly improved my writing skills, and discovered an enjoyment of teaching. Perhaps even more importantly than that, she allowed me the leeway to pursue a nontraditional graduate career that took me from Rhode Island to California and Washington DC. These meandering travels eventually led to my current career path. My committee members Evan Preisser, Graham Forrester, Kenny Raposa, and Scott McWilliams provided honest and insightful recommendations on manuscripts, grant proposals, and scientific presentations. Even though they often did not hear from me for long stretches of time as I went on interdisciplinary excursions, they always knew I would finish the graduate journey. A special thanks to Kenny for working side-by-side with me on Prudence Island each month as we braved all weather to collect, count, and measure tens of thousands of crabs.

There are no words to effectively convey my gratitude to IGERT, which was the single most transformative experience of my graduate career. It exposed me to alternatives to a life in academia and provided the skills I needed to enter into a career in environmental policy. Thank you to Pete August, Q Kellogg, and Judith Swift, who saw something in me during my IGERT interview that inspired them to accept me into the Fellowship program; it was at that point my two roads diverged, and I – I took the one less traveled by, and that has made all the difference. My fellow co-07ers, Carrie Byron, Kim Lellis-Dibble, and Nate Vinhaterio stand out among my support system. We haven’t been CIIPers for three years, but I still seek out their advice over beers and gossip.
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Lastly, but far from least, I thank my family. My Pops, Madre, and Ty were my perpetual cheerleaders who never lost faith that I would complete this journey. I looked forward to trips home to play cards, hang out, and relax. Their love and support are as much responsible for my completion of this degree as my work and research.
PREFACE

This dissertation is presented in manuscript format in accordance with the guidelines set by the Graduate School of the University of Rhode Island. Each of the three chapters are written to stand alone as separate research questions while contributing to the larger body of knowledge regarding the impacts of marine invasive species on sub- and intertidal food web dynamics. Chapter 1 is published in Aquatic Ecology. Chapter 2 is in preparation for Environmental Monitoring and Assessment. Chapter 3 is submitted to Marine Ecology Progress Series.
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CHAPTER 1

EPiphyte and Herbivore Interactions
Impact Recruitment in a Marine Subtidal System

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Abstract

Marine assemblages are influenced by the rate and timing of species settlement and recruitment. Both abiotic factors and biotic interactions can impact recruitment rates of marine species in a variety of systems. However, the impacts of species which recruit at the same time upon each other are less well understood. We investigated the relationship between the recruitment of *Lacuna vincta*, a small (< 6 mm shell diameter) marine snail, and two species of algal epiphytes, the native *Ceramium virgatum* and the invasive *Neosiphonia harveyi*, in the shallow subtidal zone of Narragansett Bay, Rhode Island. All three species exhibit peak recruitment densities during two months in the summer. We found that the presence of algal epiphytes facilitates the recruitment rate of *L. vincta*, regardless of the epiphyte species composition. We also found a positive relationship between the number of *L. vincta* present and epiphyte recruitment, which is disproportionately driven by higher recruitment of *N. harveyi* than *C. virgatum*.

Understanding recruitment dynamics and interactions is vital to effectively mitigate the effects of and adaptations to changes due to the establishment of non-native species.

Introduction

Recruitment is a key process in the population dynamics of many marine species (Bertness et al. 1992, Gaines & Bertness 1992, Miron et al. 1995, White 2007). Abiotic and biotic factors that influence settlement, and subsequent recruitment, have been examined in a variety of marine systems, including coral reefs (Steele et al. 1998, Schmitt & Holbrook 2000, Mumby et al. 2007), intertidal zones (Osman & Whitlatch 1995, Gribben et al. 2009b), and the marine Antarctic (Siegel & Loeb 1995). The presence or
absence of other macrobenthic species on a suitable substratum is one biotic factor that may influence larval settlement dynamics (Rodriguez et al. 1993, Huggett et al. 2005).

One group of macrobenthic species that can influence larval settlement is epiphytic macroalgae (Hall & Bell 1993, Swanson et al. 2006). Epiphytic macroalgae are small, often filamentous species that live attached to larger host macroalgal species. Algal epiphytes can increase the structural complexity of their host algal species, which may, in turn, increase the suitability of the host as habitat for small invertebrates, including herbivores (Martin-Smith 1993). Epiphytes can provide these herbivores protection from predators while also serving as a food source (Pavia et al. 1999). The epiphytes can also buffer the associated herbivores from abiotic stress such as desiccation (Salemaa 1986, Bostrom & Mattila 1999). As a result, these herbivores may benefit the host macroalgae by preventing epibiont overgrowth (Stachowicz & Whitlatch 2005) and/or promoting algal growth via nitrogen excretion (Fong et al. 1997, Bracken et al. 2007).

*Lacuna vincta* (Montagu) is a small (<6 mm shell diameter), ubiquitous, herbivorous snail that feeds and lives on algae within rocky intertidal and subtidal zones of the Northwest Atlantic (Martel & Chia 1991). While *L. vincta* are occasionally found on larger host algae, it has been suggested that the small epiphytes are more accessible and palatable to the herbivores, particularly the newly recruited juveniles (Steneck & Watling 1982, Chavanich & Harris 2002). Adult *L. vincta* tend to move from algal epiphytes to the host macroalga itself.

*Lacuna vincta* is commonly found in shallow rocky subtidal habitats in New England from late spring to early fall (Jones & Thornber 2010). They are found in high densities during juvenile recruitment (>1200 juveniles on algae per cm² of rocky
substrate; Jones 2007). In these shallow subtidal habitats, *L. vincta* often co-occurs with two species of epiphytic filamentous red algae, the native *Ceramium virgatum* (Roth) and the invasive *Neosiphonia harveyi* (J. Bailey). *N. harveyi* has been present in New England for over 120 years (Farlow 1881) and has invaded areas in which *C. virgatum* frequently occurs (Pederson et al. 2003, Mathieson et al. 2008); both are commonly found in Narragansett Bay (Jones & Thornber 2010).

*Ceramium virgatum* and *Neosiphonia harveyi* individuals are present year-round but their peak recruitment period overlaps substantially (early- to mid-summer; Jones & Thornber 2010). They can account for 50-80% of algal epiphytic biomass during the summer months, a period that coincides with peak *Lacuna vincta* recruitment. The remaining biomass was composed of a variety of epiphyte species with no single species accounting for more than of 15% of the algal epiphyte biomass, on average (Jones 2007). This synchronization of recruitment events may be beneficial to *L. vincta* and host macroalgae (including the native species *Chondrus crispus* and *Fucus vesiculosus* and the invasive species *Grateloupia turuturu* and *Codium fragile ssp. tomentosoides*) and detrimental to the epiphytes; at present, however, the relationship between these epiphytes and *L. vincta* recruitment is not well described.

In this study, we investigated interactions between *Lacuna vincta* and the two epiphytes *Ceramium virgatum*, and *Neosiphonia harveyi*. Through a series of field-based manipulations conducted in Narragansett Bay, Rhode Island, we investigated three possible relationships: (1) if the presence of species specific epiphytes influences *L. vincta* recruitment and, alternatively (2) if the presence of *L. vincta* influences species specific epiphytes in terms of their recruitment and/or biomass.
Materials and Methods

Study location

We conducted our experiments in the shallow (<1m below MLLW) rocky subtidal at the University of Rhode Island’s Graduate School of Oceanography during the summer of 2008. This zone is characterized by dense stands of macroalgae, primarily Chondrus crispsus, Polysiphonia spp., and Codium fragile. We wanted to assess new epiphyte and Lacuna vincta recruitment to macroalgae; thus, we used green, nylon rope 0.5 cm in diameter and 13 cm in length (total surface area of 42.4 cm²) to mimic natural macroalgae; this rope has been shown to work well for settlement and colonization by algal epiphytes and invertebrates in this system (Jones & Thornber 2010).

We previously conducted a pilot experiment during the summer of 2007; these results indicated that there was no significant caging effect of containers (open or closed) on the recruitment of epiphytes to macroalgal mimics ($F_{2, 29} = 0.78$, $p = 0.47$, n=10).

Impacts of epiphytes on Lacuna vincta recruitment

During May of 2008, before recruitment of Ceramium virgatum and Neosiphonia harveyi occurred, we secured 60 macroalgal mimics by zip-tie to PVC rings that had been attached to the shallow subtidal with marine epoxy (A-788 Splash Zone Compound). We left the mimics in the field for one month to allow for epiphyte recruitment. One month later, when the first L. vincta appeared as recruits in the field, we removed the mimics from the intertidal and brought them to the lab in order to manipulate the epiphyte abundance and composition prior to L. vincta recruitment. We divided the 60 mimics evenly into six groups of ten each. Three groups were used for epiphyte abundance
experiments and three for epiphyte composition experiments. Mimics were removed from the field for a maximum of twelve hours and were stored in ambient temperature, flow-through seawater systems at the URI Graduate School of Oceanography when not being processed.

Within the epiphyte abundance experiments, ten mimics retained a high epiphyte density (75% - 100% of mimic surface area covered with epiphytes), ten were pruned to have a low epiphyte density (25% - 50% of mimic surface area covered with epiphytes), and ten were pruned to remove all visible epiphytes. Within the epiphyte composition experiments, we selectively pruned the mimics such that ten mimics contained only *Ceramium virgatum* epiphytes, ten had only *Neosiphonia harveyi* epiphytes, and ten had a mixture of half *C. virgatum* and half *N. harveyi* epiphytes.

We photographed each mimic and measured its wet mass after blotting off excess moisture. We then reattached the mimics in the shallow subtidal to allow for natural *Lacuna vincta* recruitment. After two weeks, we removed the mimics and brought them to the lab for analysis. We photographed each mimic, measured the total wet mass (after blotting the mimics), removed and identified all of the epiphytes, and measured the mass of each epiphyte species. We also removed and counted the *L. vincta* found on each of the mimics. Data were log transformed and analyzed for differences in *L. vincta* recruitment among epiphyte abundance and composition with one-way ANOVAs and post-hoc Tukey tests (JMP v. 7; www.sas.com).
Impacts of *Lacuna vineta* on epiphyte recruitment

During May of 2008, before yearly *Lacuna vineta* recruitment occurred, we placed one macroalgal mimic in each of 30 one-liter semi-transparent plastic containers with one-mm mesh sides and lids. These containers were then secured directly to the rocky subtidal, using the same method as described above. In the same manner, we also attached mimics in ten open containers, and ten mimics without containers, to additional PVC rings, as controls. Following the recruitment of *L. vineta* in mid June 2008, we placed 200 *L. vineta* individuals in each of ten closed containers (‘high’ treatment), 40 *L. vineta* individuals in each of ten closed containers (‘low’ treatment), and no *L. vineta* in each of ten closed containers (‘none’ treatment). These treatments were based on *L. vineta* recruitment densities measured during the summer of 2006 (Jones & Thornber 2010). *L. vineta* had free access to the mimics in the open containers and the mimics with no containers.

After *L. vineta* were added, we left the containers and mimics in the field for two weeks (this duration was based on pilot data collected in the summer of 2007) to allow for epiphyte recruitment. After these two weeks, we removed the mimics and containers, placed them in individual plastic bags to retain all *L. vineta*, and brought them to the lab. We photographed each mimic, measured its wet mass (mimics were first blotted to remove excess moisture), removed and indentified all of the epiphytes, and measured the mass of each epiphyte species. We also removed and counted the *Lacuna vineta* in the closed containers, on the mimics in the open containers, and on mimics with no
containers. Data were analyzed for a relationship between *Lacuna* density and epiphyte biomass using correlation techniques (JMP v. 7; www.sas.com).

**Results and Discussion**

Across all of our treatments, we found a significant positive correlation between the proportion of *Neosiphonia harveyi* (0.02 ± 0.006 grams per cm$^2$ of macroalgal mimic) and the total epiphyte mass ($r = 0.92$, $p > 0.0001$). *Ceramium virgatum* densities were never greater than 0.005 grams per cm$^2$ of macroalgal mimic regardless of total epiphyte mass, indicating that recruitment densities of *C. virgatum* were low, or that the *C. virgatum* that did recruit to the mimics was rapidly consumed by *L. vincta*.

There was no significant effect of epiphyte composition (*Ceramium virgatum, Neosiphonia harveyi/C. virgatum, N. harveyi*) on *Lacuna vincta* recruitment (Figure 1A, $F_{2,17} = 2.24$, $p = 0.14$); *L. vincta* recruited to all three epiphyte composition types at similar rates (mean *L. vincta* density = 0.47 ± 0.08 per cm$^2$ of macroalgal mimic). However, there was an effect of epiphyte presence (high density, low density, and no epiphyte treatments) on *L. vincta* recruitment (Figure 1B, $F_{2,23} = 9.58$, $p = 0.0009$).

Macroalgal mimics containing high or low epiphyte densities had significantly more *L. vincta* (4.10 ± 1.16 per cm$^2$ macroalgal mimic and 3.86 ± 0.88 per cm$^2$ macroalgal mimic respectively) than mimics with no epiphytes present (0.67 ± 0.30 *L. vincta* per cm$^2$ macroalgal mimic; post hoc Tukey Kramer test), and there was no significant difference between the high and low epiphyte densities. Data are means ± 1 SE.
Figure 1. Effect of epiphytes on recruitment of *L. vincta*. (A) There was no difference in *L. vincta* recruitment among epiphyte composition treatments: *C. virgatum, N. harveyi/C. virgatum*, and *N. harveyi* (p = 0.1336). (B) There is a significant difference in *L. vincta* recruitment among macroalgal mimics with varying densities (p = 0.0009, post hoc Tukey Kramer tests); significant results are indicated. All data are means ± 1 SE.

Overall, we found a significant positive correlation between the number of *Lacuna vincta* present and the total mass of epiphytes (the most abundant species being *Neosiphonia harveyi* and a mix of juvenile and cryptic *Polysiphonia* spp. that could not be identified to the species level) that recruited to macroalgal mimics in all treatments (Figure 2A, r = 0.5, p = 0.0058). Unknowingly, some extremely small planktonic *L. vincta* larvae were able to pass through the mesh covering of the containers: recruitment
by these ‘accidental’ individuals produced a range of *L. vincta* densities in our closed buckets that reached 5x’s the level of our stocking density. Due to this, we examined the relationship between the number of *L. vincta* and epiphyte density in all of the treatments. When *N. harveyi* and *Ceramium virgatum* were analyzed individually, we found a weak but significant, positive relationship between the number of *L. vincta* and *N. harveyi* recruitment (Figure 2B, $r = 0.46, p = 0.0026$) but no significant relationship between *L. vincta* and *C. virgatum* (Figure 2C, $r = 0.26, p = 0.14$).

Our results support the hypothesis that *Lacuna vincta* recruitment is influenced by the presence of epiphytes, and lend support to the growing body of evidence on the importance of biotic interactions in recruitment dynamics. This relationship may be explained, in part, by protection from predators provided by the epiphytes’ three-dimensional structure (Williams et al. 2002, Henninger et al. 2009). There may be additional interactions taking place on a shorter time frame than our two-week experiments, but we are primarily concerned with longer-scale, community-wide impacts that persist and ultimately shape the intertidal algal community.

Alternatively, epiphytes may provide a source of food for *L. vincta*. Prior feeding studies in our study location have shown that *L. vincta* preferentially consume native *Ceramium virgatum* over invasive *Neosiphonia harveyi* (Jones & Thornber 2010), even though we found that *L. vincta* recruit to both at the same rates. Chemical defenses in algae can also play a role in herbivore food preferences and selection (Hay & Fenical 1988, Erickson et al. 2006, Lyons et al. 2007); whether defense compounds are present in *Ceramium virgatum* and *Neosiphonia harveyi* is, however, currently unknown. Our data
show correlative support that there is no reciprocal effect of *L. vineta* on epiphyte recruitment, but further research is needed in this area.

**Figure 2** Relationship between *Lacuna vineta* density and epiphyte recruitment. There is a significant positive correlation between the number of *L. vineta* present and (A) the mass of all epiphytes on each macroalgal mimic (*r* = 0.50, *p* = 0.0058) as well as (B) the mass of *N. harveyi* (*r* = 0.46, *p* = 0.0026) on each macroalgal mimic in closed containers.
Grazers play an important role in controlling epiphyte densities in many marine habitats, including subtidal rocky reefs (Heck Jr. & Valentine 2006, Jaschinski & Sommer 2008). On rocky shores, grazers are also important in controlling algal growth, and elevated levels of herbivory can increase species diversity (Benedetti-Cecchi 2000, Noel et al. 2008). In coastal areas with subtidal seagrass beds, epiphytes settling on seagrass blades can outcompete the seagrass for resources and eventually cause a decline of seagrass beds (Valiela et al. 1997, Drake et al. 2003, Hauxwell et al. 2003, Brush & Nixon 2004, Hays 2005). As non-native species continue to become established in coastal marine communities at unprecedented rates (Cohen & Carlton 1998, Grosholz et al. 2000, Grosholz 2002), it is important to understand how these new species could influence recruitment and survival rates of native and other non-native species (Bownes & McQuaid 2009, Gribben et al. 2009b).

It is generally assumed that invasive algae have negative effects on native communities and biodiversity, which is true in many cases (Williams & Smith 2007), but there are instances where invasive algae have either had positive or no effects on native organisms (Gribben & Wright 2006, Gribben et al. 2009a, Jones & Thornber 2010). We found that Lacuna vincta recruit in higher densities to macroalgal mimics where epiphytes are present. We also found a positive correlation between the abundance of L. vincta and the density of the invasive Neosiphonia harveyi, but no correlation between abundance of L. vincta and the density of the native Ceramium virgatum. When L. vincta were present, we found low densities of C. virgatum and evidence of severe grazer damage; this is likely because L. vincta preferentially consume C. virgatum (Jones & Thornber 2010). Thus, our data indicate that N. harveyi may facilitate L. vincta
populations by providing a more complex habitat structure; this may then have a
negative, indirect impact on *C. virgatum* density. Determining specific interactions for
individual species and communities can be critical to properly mitigating the effects of
these species and adapting to the constantly changing marine environment.
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CHAPTER 2

SPATIAL AND TEMPORAL DISTRIBUTIONS OF THE INVASIVE CRAB
HEMIGRAPSUS SANGUINEUS AND RECOMMENDATIONS FOR LONG-TERM
SAMPLING METHODS

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Abstract

Invasive species are becoming established in coastal estuaries at high rates and can create severe consequences for their associated abiotic and biotic environments, as well as the coastal communities that depend on them. Long-term monitoring can be used to search for introduced and invasive species and, if containment is not possible, to understand the invasive population's trends, including their interaction with other organisms. As an example, *Hemigrapsus sanguineus* is a highly invasive crab that is abundant on intertidal cobble beaches from North Carolina to Maine. We used a series of monthly surveys in Narragansett Bay, RI, to determine that using quadrats to sample intertidal crabs is more accurate and efficient than using semi-permanent trays buried in the substrate. We found peak densities of *H. sanguineus* in the early summer and early fall months, with the summer peak driven by small, juvenile crabs. Densities also tended to be highest in the northern section of Narragansett Bay and declined toward the mouth of this estuary. These surveys provide a solid foundation for long-term monitoring of this invasive species and can provide valuable context for future scientific experiments.

Introduction

Marine invasive species commonly occur in coastal waters, where they can have serious ecological and economic impacts (Carlton 1992, Carlton & Geller 1993, Cohen & Carlton 1998, Carlton & Cohen 2003, Molnar et al. 2008). Invasive species may experience lower rates of predation than native species, be superior competitors, and may cause declines in native biodiversity (Mack et al. 2000, Keane & Crawley 2002, Callaway & Ridenour 2004, Vermeij et al. 2009). Invasive species can also facilitate the
recruitment and survival of native species, but the long-term benefits of these facilitative interactions are unclear (Gribben & Wright 2006, Rodriguez 2006). The most effective manner to avoid the negative impacts of invasive species is to prevent their introduction and spread. This can be accomplished through regulation of the procurement, maintenance, and disposal of nonnative organisms that are intentionally brought into new areas for accepted uses (such as the aquarium trade; Cohen & Carlton 1997, Padilla & Williams 2004, Weigle et al. 2005), and treatment of known vectors such as open ocean ballast water for ships. However, even a combination of these prevention measures is not 100% effective, and the next line of defense against the establishment and spread of invasive species is monitoring and early detection (Simberloff et al. 2005).

Invasive species surveillance typically occurs in areas where species are most likely to become established (Buchan & Padilla 2000), but this method is only effective when there is sufficient knowledge of environmental factors that can impact invasive species and may overlook additional locations that introduced species can inhabit. Long-term environmental monitoring can provide information on the biotic and abiotic characteristics of potential invasion sites. Researchers consistently conducting surveys are more likely to notice changes to the biotic community and identify nonnative species before they become established, making control and/or eradication viable options (Mehta et al. 2007). However, the impacts of eradication should be carefully assessed in order to avoid unintended consequences (Bergstrom et al. 2009). Even if eradication does not occur, continuation of long-term monitoring can provide critical information on how the invasive species interacts with and impacts the native community, and changes can be
better anticipated and/or mitigated (Lovett et al. 2007, Henry et al. 2008, Lindenmayer & Likens 2010).

Long-term environmental monitoring can provide extremely useful information but is often quite costly (Caughlan & Oakley 2001) and difficult to fund (Lodge et al. 2006, Lovett et al. 2007). Even so, federal agency mandates prioritize long-term data collection, and state and local agencies frequently incorporate long-term monitoring into their environmental management plans. For example, the Aquatic Nuisance Species Task Force was formed in Rhode Island by the Department of Environmental Management in response to the Nonindigenous Aquatic Nuisance Prevention and Control Act of 1990 (P.L. 101-646). The Task Force developed the Rhode Island Aquatic Invasive Species Management Plan. Monitoring is one of the seven strategies of this plan, and RIDEM partners with other agencies, including the Narragansett Bay National Estuarine Research Reserve (NBNERR), and non-governmental organizations to carry out the plan (Rhode Island Aquatic Invasive Species Management Plan, 2007).

The Asian shore crab, *Hemigrapsus sanguineus*, is a highly invasive marine species that is too abundant to control or eradicate in its invaded range. *H. sanguineus* was first discovered off the coast of New Jersey in 1988 (McDermott 1991) and has since become common along the east coast of the United States from North Carolina to Maine (Stephenson et al. 2009). *H. sanguineus* overlaps with the invasive European green crab, *Carcinus maenas*, on cobble beaches. *C. maenas* has been present on U.S. Atlantic shorelines for approximately 200 years and has become an important predator (Carlton & Cohen 2003). *C. maenas* has been a key species in New England intertidal and shallow subtidal communities and has both lethal and non-lethal impacts on *Littorina littorea*, an
abundant herbivore (Menge 1976, Lubchenco & Menge 1978, Trussell et al. 2003, Bertness et al. 2004, Trussell et al. 2006).

*Hemigrapsus sanguineus* frequently outcompetes *Carcinus maenas* for both available habitat and preferred prey (Jensen et al. 2002, Griffen 2007, 2011), and it may have a lower mortality rate due to predators a lack of predators and/or the substrate complexity of cobble beaches, which provides refuge from predators (Kim & O'Connell 2007, Brousseau et al. 2008, Heinonen & Auster 2012). Within the past decade, *H. sanguineus* has replaced *C. maenas* as the most abundant crab in coastal New England, including Narragansett Bay, RI (Lohrer & Whitlatch 2002, N. Rohr unpubl. data).

In order to better understand the population dynamics of *Hemigrapsus sanguineus*, we conducted monthly crab surveys in the intertidal zone of cobble beaches at numerous sites in Narragansett Bay, Rhode Island. We investigated: 1) two sampling methods (trays and quadrats) to determine which was more reliable, unbiased, and cost-effective; 2) the patterns of the abundance and size distribution of *H. sanguineus* in NBNERR on Prudence Island, RI; and 3) the patterns of the abundance and size distribution of *H. sanguineus* throughout Narragansett Bay. Our findings clarify spatial and temporal patterns of *H. sanguineus* in Narragansett Bay, help develop effective monitoring strategies, and serve as a baseline for continued long-term monitoring efforts. Detailed demographic profiles such as these can also provide context for manipulative experiments by scientific researchers, and inform decisions by local resource managers who strive to protect native species while containing invasives.
Material and Methods

General survey methods

We conducted all surveys on intertidal cobble and small boulder beaches (diameter 20-60 cm; hereafter referred to as ‘cobble’) in Narragansett Bay, RI (see subsequent sections for particular survey descriptions). All sites were readily accessible from the landward side and were open to the general public. Surveys were conducted monthly during spring low tides ± two hours along a transect parallel to, and just above, the low water line, and sample areas (see subsequent sections) were randomly selected along a 30m transect using a random number generator. We collected all crabs ≥ 4mm carapace width from each sample area. We identified each crab to the species level, measured its carapace width (mm), recorded its sex, and, if the crab was female, recorded whether or not it was gravid. For *Hemigrapsus sanguineus*, all crabs 4mm to 9mm carapace width were recorded as juveniles (for this size range, sex was not able to be determined visually), while crabs ≥ 10 mm carapace width were recorded as adult and either male or female based on sexual dimorphism in the abdomen. Over 99% of the crabs collected from each site were *H. sanguineus* (N. Rohr, unpubl. data); therefore, we only analyzed data on this species.

Survey methods comparison

In conjunction with NBNERR’s ongoing long-term biological monitoring program (Raposa & Durant 2011), we established long-term monitoring sites in May 2007 at four intertidal cobble beaches on Prudence Island in Narragansett Bay, RI: Bear Point, Nag Creek, Stone Wharf, and T-Wharf (Figure 1). At each site, we randomly
selected three sample areas along a 30m transect at the spring low tide line, parallel to the shore. We buried one plastic bread tray (65cm x 55cm, 0.36m²) lined with 3mm mesh at each of the sample areas. To bury the trays, we removed all of the cobble from the area, dug 10cm deep into the underlying sand/silt substrate, placed the tray in the hole so that the end edges of the tray were visible, and then replaced the displaced sediment and cobble in the tray (Riggs 2003). We visited each site monthly from June 2007 through June 2008. Each month, after the crabs were collected from the trays, we returned the cobbles to the tray and released the crabs back onto the beach.

We conducted a concurrent survey using quadrat sampling in June and July 2007 at the same four sites. This was to determine any potential sampling bias due to monthly cobble removal and re-addition. Each month, we sampled three 1m² quadrats per site randomly placed along a 30m transect parallel to the water line during spring low tides. We removed all of the crabs from the sampling area by removing all cobble from the quadrat until the underlying coarse sand substrate was completely revealed. After we removed the cobble and captured and measured the crabs (see General Survey Methods), we replaced the cobbles and released the crabs in the same location.

The number of *Hemigrapsus sanguineus* collected from each tray was standardized to crabs m⁻². *H. sanguineus* density data was square root transformed. Data were analyzed for differences in density and mean carapace width between method types (tray and quadrat), among sites, and among months using three-way fixed factor ANOVAs (JMP v.9, www.sas.com). Significant differences were analyzed using a Student’s *t* or Tukey post-hoc analysis, as appropriate.
Figure 1 Mean *Hemigrapsus sanguineus* density on cobble intertidal beaches throughout Narragansett Bay, Rhode Island, in August 2008

Prudence Island surveys

To quantify the variability of the density and body size of *Hemigrapsus sanguineus*, we conducted quadrat surveys (described above) at our four Prudence Island sites from June through October 2008 and June through November 2009. We selected
these months based on our observed crab density patterns from June 2007 through June 2008; we included months that typically had the greatest densities of *H. sanguineus*. Data were analyzed for differences in density and mean carapace width among months and sites using two-way fixed factor ANOVAs. Significant differences were analyzed using Tukey post-hoc analyses.

**Narragansett Bay surveys**

In May 2008, we established 12 survey sites throughout Narragansett Bay, including our prior four Prudence Island sites: Bear Point, Colt State Park, Freebody Street, Fort Wetherill, Low Lane, Mackerel Cove, Nag Creek, Potter Cove, Roger Williams University, Sabin Point, and Save The Bay (Figure 1). These sites were randomly selected from known, publically accessible, cobble intertidal sites. We conducted monthly quadrat surveys (described above) at each site during spring low tides, through October 2008. Data were analyzed for differences in density and mean carapace width among months and sites using two-way fixed factor ANOVAs. Significant differences were analyzed using Tukey post-hoc analyses.

**Population demographics**

We analyzed the data from our ‘‘Narragansett Bay Surveys’’ for differences between numbers of males and females, adults and juveniles, and gravid and not gravid females to better understand intrapopulation patterns. Data were analyzed using contingency analyses among months and sites with correspondence analyses to evaluate groupings. Results are expressed as percentages to more clearly show comparisons.
Results

Survey methods comparison

The density of *H. sanguineus* was significantly higher when sampled with the tray method than the quadrat method (52 ± 7 vs. 23 ± 3 crabs m\(^{-2}\); Figure 2, Table 1). We found higher densities of *H. sanguineus* in June 2007 than July 2007, which is consistent with temporal patterns seen across additional sites and years (described below). When combined across survey methods, we also significantly fewer *H. sanguineus* at T-Wharf (16 ± 4 crabs m\(^{-2}\)) than at Nag Creek or Stone Wharf (41 ± 6 crabs m\(^{-2}\) and 55 ± 10 crabs m\(^{-2}\), respectively).

**Table 1** ANOVA results for analyses examining the impact of month, site, and sampling method on *Hemigrapsus sanguineus* density and carapace width.

| Treatment Effect         | df | SS     | F-value | P-value |
|--------------------------|----|--------|---------|---------|
| Density                  |    |        |         |         |
| Month                    | 1  | 2365.39| 5.94    | 0.0208  |
| Site                     | 2  | 9247.54| 11.60   | 0.0002  |
| Method                   | 1  | 8743.85| 21.95   | < 0.0001|
| Month*Site               | 2  | 112.65 | 0.14    | 0.8687  |
| Month*Method             | 1  | 2795.38| 7.02    | 0.0126  |
| Site*Method              | 2  | 2421.89| 3.04    | 0.0623  |
| Month*Site*Method        | 2  | 190.73 | 0.2394  | 0.7886  |
| Error                    | 31 | 12351.60|        |         |

| Carapace With            |    |        |         |         |
|--------------------------|----|--------|---------|---------|
| Month                    | 1  | 2.05   | 0.42    | 0.5234  |
| Site                     | 2  | 37.27  | 3.78    | 0.0339  |
| Method                   | 1  | 53.77  | 10.91   | 0.0024  |
| Month*Site               | 2  | 19.14  | 1.94    | 0.1605  |
| Month*Method             | 1  | 9.51   | 1.93    | 0.1746  |
| Site*Method              | 2  | 9.45   | 0.96    | 0.3943  |
| Month*Site*Method        | 2  | 19.57  | 1.99    | 0.1544  |
| Error                    | 31 | 152.75 |         |         |

*Hemigrapsus sanguineus* in trays had a significantly larger mean carapace width (15.64 ± 0.23 mm) than from quadrats (14.13 ± 0.21 mm; Figure 2, Table 1). The mean
carapace width did not differ between months, and there were no significant interaction effects. We found smaller *H. sanguineus* at Stone Wharf (13.93 ± 0.24 mm) than at either Nag Creek (15.23 ± 0.21 mm) or T-Wharf (16.05 ± 0.56 mm).

![Graph showing comparison of tray and quadrat survey sampling methods for *Hemigrapsus sanguineus*](image)

**Figure 2** Comparison of 2007 tray and quadrat survey sampling methods for *Hemigrapsus sanguineus*: A) density and B) mean carapace width. A * indicates a significant difference of $p < 0.05$.

**Prudence Island surveys**

Mean *Hemigrapsus sanguineus* density peaked during June and September 2008 (50 ± 8 crabs/m$^2$ and 54 ± 8 crabs/m$^2$, respectively), and June and August 2009 (26 ± 6 crabs/m$^2$ and 46 ± 11 crabs/m$^2$, respectively) before declining during October/November of each year (Figure 3). There were significant differences in mean *H. sanguineus* densities among months and sites ($F_{9,80} = 5.25$, $p < 0.0001$ and $F_{3,80} = 4.09$, $p = 0.0094$, respectively) with a significant interaction ($F_{27,80} = 2.16$, $p = 0.0043$).
November 2009 had the lowest density (9 ± 3 crabs m⁻²). When averaged across months, Bear Point had the highest mean density of *H. sanguineus* (45 ± 6 crabs m⁻²) and Potter’s Cove had the lowest density (28 ± 6 crabs m⁻²), with Nag Creek and T-Wharf not significantly different from any of the sites (41 ± 4 crabs m⁻² and 31 ± 4 crabs m⁻², respectively).

**Figure 3** *Hemigrapsus sanguineus* density from Prudence Island, Rhode Island at four long-term invasive species monitoring sites

Due to crab growth, mean carapace width of *Hemigrapsus sanguineus* varied significantly among months (*F₉,₈₀ = 30.72, p < 0.0001*) and sites (*F₃,₈₀ = 51.32, p < 0.0001*), with a significant interaction (*F₂₇,₈₀ = 8.09, p < 0.0001*). The mean carapace width in June and July was greatly influenced by a large number of juvenile crabs (4 mm to 9 mm carapace width); this frequency distribution transitioned to more mid-sized crabs in August and September (Figure 4). The largest *H. sanguineus* were found at Potter’s Cove and T-Wharf (13.72 ± 0.14 and 13.44 ± 0.17 mm carapace width), while crabs at
Bear Point and Nag Creek were smaller (10.97 ± 0.11 and 10.51 ± 0.10 mm carapace width, respectively).

![Bar chart showing carapace width distribution for June, July, August, and September 2008](chart.png)

**Figure 4** Mean *Hemigrapsus sanguineus* carapace width, by month, at Bear Point, Prudence Island, Rhode Island.

**Narragansett Bay surveys**

We found similar monthly trends in *Hemigrapsus sanguineus* density across the broad spatial scale of Narragansett Bay. We found significant differences in crab density among months and sites ($F_{4,120} = 13.13$, $p < 0.0001$ and $F_{11,120} = 8.47$, $p < 0.0001$, respectively) with a significant interaction ($F_{44,120} = 3.99$, $p < 0.0001$; Figure 1).

Densities of *H. sanguineus* were highest in June 2008 (59 ± 9 crabs m\(^{-2}\)) and slightly lower during July, August, and September (31 ± 4, 39 ± 4 and 39 ± 6 crabs m\(^{-2}\), respectively). We found the lowest density of *H. sanguineus* in October 2008 at all sites.
(mean 22.80 ± 3.93 crabs m$^{-2}$). When Sabin Point is excluded, which is located in the Providence River at the northern end of the Bay (Figure 1), $H. sanguineus$ densities generally decreased from north to south ($R^2 = 0.5603$, $p = 0.0125$; Figure 5).

**Figure 5** A latitudinal gradient of *Hemigrapsus sanguineus* mean density in Narragansett Bay, averaged from June through October 2008.

We found significant differences in mean carapace width among months ($F_{4,118} = 18.40$, $p < 0.0001$) and sites ($F_{11,118} = 3.27$, $p = 0.0006$) with an interaction ($F_{44,118} = 2.20$, $p = 0.0004$). The mean carapace width of *H. sanguineus* was lowest in June and July ($9.32 ± 0.07, 9.27 ± 0.10$ mm, respectively) and increased monthly thereafter; mean width in October 2008 was $12.59 ± 0.14$ mm (Figure 6).
Figure 6 *Hemigrapsus sanguineus* carapace width histograms at two representative sites, Colt State Park and Freebody Street, during June 2008 and September 2008.

**Population demographics**

We found more male than female *Hemigrapsus sanguineus* during all months across all sites. Males comprised no less than 56% of the population and peaked at 77%
We found significant differences in the ratio of males to females among sites ($\chi^2 = 48.21$, $p < 0.0001$) and months ($\chi^2 = 22.97$, $p = 0.0001$). We found a higher ratio of males to females in June, July, and September 2008 than in August and October. Freebody Street had an average of 77% adult male *H. sanguineus* over all months, which was 10% higher than any other site.

There were significantly more juvenile (60%) *Hemigrapsus sanguineus* than adults (40%) in June and July 2008 ($\chi^2 = 691.02$, $p < 0.0001$, Figure 7B). During the later months, juveniles accounted for 20-30% of the population. We also found significant differences in the ratio of juvenile to total adult *H. sanguineus* among sites ($\chi^2 = 313.33$, $p < 0.0001$). When averaged across months, the percentage of juveniles in the *H. sanguineus* population ranged from 24% at Potter’s Cove to 62% at Freebody Street.

The percentage of gravid female *H. sanguineus* was significantly different among months ($\chi^2 = 207.27$, $p < 0.0001$), with 28% of the female population gravid in August 2008 (Figure 7C). The other four months each had less than 10% gravid females. The percentage of gravid female *H. sanguineus* was also significantly different among sites when averaged across months ($\chi^2 = 150.58$, $p < 0.001$). Colt State Park had 29% gravid females and Save the Bay had 19%. The other sites ranged from zero gravid females at Fort Wetherill to 13% at T-Wharf.
Figure 7  Mean *Hemigrapsus sanguineus* population demographics of A) adult males and females, B) juveniles and total adults, and C) gravid and not gravid adult females. The numbers on the bars represent the total number of *H. sanguineus*
Discussion

Quadrat sampling is widely accepted among scientists for conducting long-term surveys of mobile organisms such as crabs that live on the benthos, (for review, see McIntyre & Eleftherou (eds) 2005). Previous sampling of these species using the quadrat method resulted in a 90-100% sampling efficiency (Lohrer and Whitlatch 2002). While the tray sampling method described here has been used for sampling crabs in other habitat types (Riggs 2003), we do not recommend it for sampling Hemigrapsus sanguineus on cobble intertidal beaches. The tray sampling method inflated crab densities over the quadrat sampling method, and was biased toward larger H. sanguineus, possibly by providing a degree of habitat complexity that protects larger crabs from predators (Lohrer et al. 2000a, Hovel & Lipcius 2001, Lohrer & Whitlatch 2002, Ochwada et al. 2009). Inclement weather also occasionally dislodged trays, and there was evidence of human removal as well. Since uneven sample sizes can inhibit data analysis (Underwood, 2004), it is preferable to utilize a reliable sampling method, such as quadrats, for long-term monitoring. However, if managers are monitoring for H. sanguineus in a previously non-invaded area, a tray may be a better option to attract crabs from a broader area and thereby more likely to detect crabs at a low density.

Along New England shorelines, Hemigrapsus sanguineus have been shown to outcompete the European green crab, Carcinus maenas, which previously was the primary competitor for food resources and space in the rocky intertidal zone (Lohrer et al. 2000b, Jensen et al. 2002, Lohrer & Whitlatch 2002, DeGraaf & Tyrrell 2004, Griffen 2007). While smaller than C. maenas, H. sanguineus can be found at densities up to 30 times higher than C. maenas (Griffen & Delaney 2007) and thus could have a greater
impact on other species. We found that densities of *H. sanguineus* peaked due to an influx of small, juvenile crabs in the early summer. This influx also resulted in a smaller mean carapace width than in later months. In the Middle Atlantic Bight, newly metamorphosed juveniles have a growth rate of approximately $0.06 \text{ mm day}^{-1}$ (Epifanio et al. 1998). This growth rate could explain the peak in 4-9 mm carapace width juveniles, followed approximately 100 days later by a peak in 10-14 mm carapace width crabs.

Gravid females were found in Narragansett Bay, R.I. from June through September, which is consistent with *Hemigrapsus sanguineus* populations found further south (Epifanio et al. 1998, McDermott 1998). We found ovigerous females as small as 10 mm carapace width, but it was not possible to determine if these eggs were viable or successfully metamorphosed. Even though females were gravid in the summer months, we did not see the recruitment of juveniles until the following June. This is due to the cessation of growth during the coldest winter months, and sexual maturity is expected one year after metamorphosis (Epifanio et al. 1998). We found the most gravid females at two of our northern-most sites: Colt State Park and Save the Bay.

Within Narragansett Bay, we found a general increase in *Hemigrapsus sanguineus* densities as we moved north. However, this did not hold true at one location, Sabin Point, which is located in the Providence River. This could be due to a number of environmental factors including salinity, cobble size, and wave exposure. The Providence River is more heavily influenced by freshwater input from rivers and precipitation runoff from the surrounding urban areas during storm events; salinities as low as 13 psu have been reported in this area (University of Rhode Island 2001). While *H. sanguineus* can survive in salinities consistently as low as 25 psu, salinities less than 15 psu can be
physiological stressful to these crabs (Ledesma & O'Connor 2001). By contrast, typical salinity ranges in the southern portion of the Bay are 24-32 psu, and match adjacent oceanic salinity regimes (University of Rhode Island 2001). In these locations, *H. sanguineus* may be restricted by higher wave exposure than in the upper bay, either directly by preventing them from inhabiting the area or indirectly by limiting the settlement and growth of prey items (Silva et al. 2010). Sabin Point was also characterized by the smallest cobble, and there may be a positive correlation between cobble diameter and *H. sanguineus* density (K. Raposa, unpubl. data).

Biological factors also may influence the population dynamics of *Hemigrapsus sanguineus*. Settlement of *H. sanguineus* megalopae is facilitated by the presence of adult conspecifics, and developing crabs are attracted by chemical cues from adults as well as from bio-films in rocky intertidal habitats (Kopin et al. 2001, Anderson & Epifaunio 2009). Once a rocky habitat is inhabited by adult *H. sanguineus*, the settlement rate of megalopae can be exponential. Revisiting sites on a regular basis could allow managers to determine if *H. sanguineus* will eventually colonize cobble beaches that currently have low densities of crabs as more adult crabs move onto the beach. If not, then these sites may have restricted recruitment due to ecological and/or physical factors.

Our results provide a solid overview of the temporal and spatial variability in *Hemigrapsus sanguineus* population density and demographics. Because invasive species are contributing to the rapid alteration of coastal ecosystems, expanded monitoring efforts should be implemented in thoughtful and efficient manners in order to capture this change. In addition, targeted experimental research spurred by the survey patterns would also help to determine the finer intricacies of reproduction and recruitment. If the data
collected are managed, analyzed, and reported in a consistent manner, then the return on the effort and investment can be extremely high (Lindenmayer & Likens 2010).

Conclusions

Long-term environmental monitoring serves a critical role in understanding ecosystem trends that occur on yearly or decadal timescales. Our data quantify the temporal and spatial variability, distribution, and life-cycle characteristics of an invasive crab species in a highly impacted estuary. Ongoing monitoring of these sites by NBNERR will increase the knowledge base of this crab's population dynamics, community impacts, and potential for continued spread. There are many cost-effective options to conducting ongoing monitoring studies (Hauser & McCarthy 2009), including recent utilization of citizen science (Delaney et al. 2008, Conrad & Hilchey 2011) and partnering with regional researchers, local agencies, or nongovernmental organizations. This study utilized academic researchers and a local government agency to maximize time, funds, and effort.

The utility of having long-term, robust data sets has been illustrated repeatedly in ecosystems impacted by natural or anthropogenic disasters, such as the Exxon Valdez spill in 1989 or the BP Deepwater Horizon spill in 2010. A major spill occurred at the entrance of Narragansett Bay in 1989, releasing almost 300,000 gallons of home heating oil and costing $567,000 in damage to the natural environment (NOAA 2009). In these instances, long-term data served as a baseline from which to assess the damages in natural resources. In addition, long-term data sets can influence global policy, such as the now-famous ‘Keeling Curve’ that illustrates increasing carbon dioxide concentrations in
the atmosphere and its connection to global climate change (Sundquist & Keeling 2009). While no one could have predicted the significance of – or need for – these data, the commitment of researchers to long-term monitoring proved invaluable.

Invasive species have the ability to reshape intertidal marine food webs (Byrnes et al. 2007, Eastwood et al. 2007, Griffen & Delaney 2007). Prevention of the introduction of novel species is the first line of defense for protecting our coastal and estuarine ecosystems (Simberloff et al. 2005). However, once an introduction occurs, it becomes important to identify new species while there is still the opportunity to prevent their spread, understand the long-term effects of specific invasive species, and prepare for potential impacts (de Rivera et al. 2011, Grosholz et al. 2011).
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CHAPTER 3

IMPACTS OF INVASIVE *HEMIGRAPSUS SANGUINEUS*

ON A NEW ENGLAND FOOD WEB

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ABSTRACT

Invasive species can have a variety of impacts on food web structure and interspecific interactions. On New England rocky shores, the established invasive crab *Carcinus maenas* can exhibit strong lethal and nonlethal effects on the common periwinkle *Littorina littorea*, thereby impacting the abundance and composition of marine algae, which are the lowest trophic level in this system. A more recent invasive crab, *Hemigrapsus sanguineus*, has outcompeted *C. maenas* on cobble beach habitats, but the implications of this replacement on food web dynamics are unknown. Through mesocosm studies, we found that while *H. sanguineus* has an impact on *L. littorea* behavior, it does not alter the periwinkles’ grazing rates. By contrast, the combined presence of *H. sanguineus* and *L. littorea* results in a greater decrease in algal biomass than only *L. littorea*. In field tethering experiments, we observed that abiotic but not biotic factors were the dominant force in structuring the vertical distribution of *H. sanguineus*. Overall, our data support the hypothesis that *H. sanguineus* does not occupy the same ecological niche as *C. maenas*. Thus, the functional replacement of one invasive species by another may have a broad range of impacts on trophic interactions.

INTRODUCTION

Current views on trophic level interactions have been greatly shaped by the concept of trophic cascades (Paine 1966, Carpenter et al. 1987, Kimbro et al. 2009, Newcombe & Taylor 2010, Sieben et al. 2011). Predators can impact community structure either via direct predation, chemical cues that influence the behavior of co-occurring species, and/or the alteration of the physical environment (Paine 1966, Estes et
The disruption of this dynamic through species extirpations or introductions can result in severe consequences that have repercussions for the abiotic (i.e. bioturbidation) and biotic (i.e. loss of predators) environments, as well as the coastal communities that depend on them (Levin et al. 2002, Molnar et al. 2008, Williams & Grosholz 2008, McGeoch et al. 2010, Griffen et al. 2011).

The susceptibility of trophic cascades to disruption is at least partially influenced by biodiversity (Finke & Denno 2004, Duffy et al. 2007, Altieri et al. 2010). A high level of biodiversity increases ecosystem resilience by creating redundant functional roles that promote community renewal following a disturbance (Peterson et al. 1998, Stachowicz et al. 2007). For this reason, biodiversity is an important indicator of healthy and resilient marine ecosystems, and the maintenance of this ecological health indicator has been highlighted as a management goal for ecosystems around the world (Crowder & Norse 2008, Williams & Grosholz 2008, Palumbi et al. 2009). Biodiversity is naturally dynamic but can have enhanced fluctuations due to human-caused extinctions and species introductions (Byrnes et al. 2007).

Introductions of exotic species throughout the world’s coastal and marine ecosystems are widely recognized as serious biological threats with major ecological and anthropological consequences (Carlton & Geller 1993, Cohen & Carlton 1998). For example, San Francisco Bay, CA, is widely recognized as the most invaded estuarine habitat in the world (Cohen & Carlton 1998). Particularly aggressive species such as the Asian clam, *Potamocorbula amurensis*, and shipworms, *Teredo navalis*, cause hundreds of millions of dollars worth of damage a year (Pimentel et al. 2005). In contrast, estuaries
on the northeast coast of the United States do not yet have as high a richness of invasive species, but they are still significantly impacted by nonnative species introductions (see review by Lockwood et al. 2007).

_Carcinus maenas_ (Linnaeus), the European green crab, was introduced to the Atlantic shoreline of the United States approximately 200 years ago (Carlton & Cohen 2003) and became an important predator along shorelines in New England, USA. _C. maenas_ is a key species in structuring intertidal communities of New England through consumptive and non-consumptive impacts on several species, including _Littorina littorea_ (Linnaeus), the marsh periwinkle (Lubchenco & Menge 1978, Trussell et al. 2003, Bertness et al. 2004, Trussell et al. 2006). _L. littorea_ is one of the dominant intertidal invertebrates on northwest Atlantic shorelines (Lubchenco 1978). It preferentially consumes ephemeral green algae such as _Ulva_ (Lubchenco 1978); when the green algae are removed, the algal community shifts towards perennial species such as _Chondrus crispus_. Since its introduction, _C. maenas_ has contributed to the alteration of intertidal algal abundance and composition by changing _L. littorea_ densities and feeding behaviors via both lethal (direct predation) and non-lethal (release of chemical cues) effects (Trussell 1996, Trussell et al. 2002, 2003, Trussell et al. 2006).

More than 150 years after the invasion of _Carcinus maenas_, another introduced crab has become established in this same region. _Hemigrapsus sanguineus_ (De Haan), the Asian shore crab, was first observed on the coast of New Jersey in 1988 (McDermott 1991) and has since expanded its range from South Carolina through the coast of Maine. _H. sanguineus_ frequently outcompetes _C. maenas_ for both habitat and preferred prey (Jensen et al. 2002), leading to the displacement of _C. maenas_ from the intertidal zone of
cobble beaches (N. Rohr pers. obs., Lohrer & Whitlatch 2002a). The replacement of *C. maenas* by *H. sanguineus* could have significant impacts on the already altered native marine flora and fauna in the coastal northwestern Atlantic (e.g. DeGraaf & Tyrrell 2004, Freeman & Byers 2006, Eastwood et al. 2007, Griffen & Byers 2009).

There is evidence in laboratory settings that *H. sanguineus* consume *L. littorea* up to 13 mm in length (Gerard et al. 1999), but the predation pressure of *H. sanguineus* in the field is unknown. Chemical cues from *H. sanguineus* elicit a shell-thickening response in *Mytilus edulis* in areas of New England where they co-occur, but *M. edulis* outside of the invaded range of *H. sanguineus* fail to express this induced trait (Freeman & Byers 2006). By contrast, the non-lethal effects of *H. sanguineus* on *L. littorea* are unknown. *H. sanguineus* does not consume prey as efficiently as *C. maenas*, but they occur at much higher densities (Lohrer & Whitlatch 2002b, DeGraaf & Tyrrell 2004). If *H. sanguineus* impacts *L. littorea* populations differently than *C. maenas*, this could shift intertidal algal abundance and species composition.

Invasive species can also alter predator-prey interactions. Crabs and other crustaceans are consumed by predators such as fish (Clark et al. 2006, Kim & O'Connor 2007) and seabirds (Ellis et al. 2005). Juvenile *H. sanguineus* are consumed by *Fundulus heteroclitus* and *Fundulus majalis* (Kim & O'Connor 2007, Brousseau et al. 2008). By contrast, field manipulations of *Cancer* spp. and *C. maenas* in New England indicate that gull predation on *H. sanguineus* is unlikely given their small size (J. Ellis pers. comm., Ellis et al. 2007), but they may be potential prey for crows, shorebirds, and/or terrestrial mammals (Carlton & Hodder 2003, Placyk Jr. & Harrington 2004). Currently, there is little known about the predatory pressures on *H. sanguineus* on cobble beaches.
In order to better understand how *Hemigrapsus sanguineus* impacts intertidal and subtidal ecosystems we used a combination of laboratory mesocosm and field experiments to assess: 1) *H. sanguineus* impacts on *Littorina littorea* (via lethal or nonlethal effects) and macroalgae, and 2) predation pressure on *H. sanguineus* from intertidal predators. Our findings yield insight into how invasive species may alter trophic cascades, and how the replacement of one invader by another may further change these dynamics.

**MATERIALS AND METHODS**

*L. littorea* algal consumption rates

To investigate the lethal and nonlethal effects of *Hemigrapsus sanguineus* on the algal consumption rate of *Littorina littorea*, we conducted outdoor mesocosm experiments from June through October 2010 at the University of Rhode Island’s Narragansett Bay Campus in Narragansett, Rhode Island. Mesocosm tanks were supplied with ambient temperature, free flowing filtered seawater from Narragansett Bay. We collected *L. littorea* (> 4mm shell height), *H. sanguineus* (> 10mm carapace width), and *Ulva rigida* (C. Agardh) in Narragansett Bay; the identity of *U. rigida* was confirmed via microscopic analysis in the laboratory with molecular voucher specimens (Hofmann et al. 2010, M. Guidone et al. unpubl. data). *Ulva lactuca* is the algal species typically included in the New England food web based on morphological characteristics (Lubchenco 1978), but recent molecular assessments have determined that *U. rigida* is the most common *Ulva* species from our field sites (Hofmann et al. 2010, M. Guidone et al. unpubl. data).
We used mesh cages (30cm x 30cm x 28cm, mesh size 4mm) placed singly inside mesocosm tanks (60cm in diameter). We installed a 10cm tall (2cm diameter) standpipe in the center of each tank and covered all standpipes with 1mm window screening to prevent the escape of mobile organisms. We placed eight textured PVC tiles (10cm x 10cm) at the bottom of each cage and randomly designated four to have one 2.0-3.0g piece of *Ulva rigida* attached to its center, to simulate algae attached to a hard substrate in the intertidal zone. The remaining four tiles had no algae attached. We then randomly assigned each cage (tank) to one of five treatments: 1) No invertebrates, as a control, 2) 25 *Littorina littorea*, to investigate the algal consumption rate of *L. littorea* in the absence of predators, 3) three *Hemigrapsus sanguineus*, to investigate the impacts of *H. sanguineus* on algal blades, 4) 25 *L. littorea* and three *H. sanguineus*, to determine the effect of *H. sanguineus* on the algal consumption rate of *L. littorea*, and 5) 25 *L. littorea* and three caged *H. sanguineus*, to determine the effect of *H. sanguineus* chemical cue on the algal consumption rate of *L. littorea*. Crab and snail densities were selected based on observed densities at adjacent field sites during the summer months (N. Rohr, unpubl. data).

For each tank, we recorded the initial wet mass (g) of each *Ulva rigida* piece. All algae were spun 20 times in a salad spinner to remove excess water prior to weighing. Each trial ran for four days. Because we only had 10 tanks, we ran six trials during the summer, with two tanks per treatment per trial, using new organisms each time. Trials were ran in sets of two and, after confirming there was no difference between sets, were combined into one treatment with n = 4. The treatments were randomized among tanks over time, and the tanks were scrubbed and allowed to air dry for at least 48 hours.
between trials. At the end of each trial, we measured the final mass (g) of each algal piece; all algae were again spun prior to weighing. We analyzed the change in mass of *U. rigida* with a two-way ANOVA and a post-hoc Tukey analysis (JMP v7.0, www.sas.com) to assess differences in change of algal mass among treatments and time. Data met assumptions for normality and homogeneity of variances.

*L. littorea* feeding behavior

In the same cages as above and concurrent with the previous study, we monitored the behavior of *Littorina littorea* every six hours, beginning at 12:00 AM, for the first 24 hours of each trial. We recorded the number of *L. littorea* that were: 1) on the *Ulva rigida*, consuming it; 2) on the bottom of the tank, neither feeding nor fleeing; and 3) on the sides of the mesh cage, exhibiting a fleeing response by vertically moving out of the reach of the *Hemigrapsus sanguineus*. We analyzed our results using contingency analyses (JMP v7.0, www.sas.com) to assess differences in snail behavior among treatments and across time of day. Results are expressed as percentages to more clearly show comparisons.

Predation rates on *H. sanguineus*

To determine the predation pressure on *Hemigrapsus sanguineus*, we conducted a randomized tethering experiment at Bear Point, Prudence Island, in the Narragansett Bay National Estuarine Research Reserve (NBNERR; 41° 39′.631″ N 71° 20′.527″ W). Bear Point has an intertidal zone with a tidal amplitude of approximately 1.2 m, has low wave disturbance, and the substrate is dominated by cobbles less than 50 cm in diameter.
We constructed predator exclusion cages (25cm x 25cm x 18cm) from 1.3 cm PVC pipe covered with 4mm mesh. Full exclusion cages were covered with mesh on all sides except the bottom; benthic predator exclusion cages were open on the bottom and top, to allow access by pelagic predators; control cages had no mesh covering over the PVC frame to allow access by both benthic and pelagic predators. We conducted experimental trials at three tidal heights: high intertidal, low intertidal, and shallow subtidal, with approximately five meters between tidal heights. However, due to unavoidable complications in the shallow subtidal (i.e. sharp rocks and barnacles that compromised crab tethers), data from this tidal height were excluded from our analyses.

At each tidal height, we secured nine tethered *Hemigrapsus sanguineus* to the cobble substrate. We randomly assigned each crab to one of three treatments: full exclusion cages, benthic predator exclusion cages, and control ‘cages’ (one crab per cage). Each cage was approximately 1m from the next. This was repeated six times during the summer of 2010.

Tethers consisted of a 6lb monofilament harness tied around each *Hemigrapsus sanguineus* between the claws and first walking appendages and secured to the carapace with marine epoxy (Eclectic Products, Marine Goop Adhesive). Each tether was 25cm in length and attached to one side of a 4lb stainless steel double swivel; the other side of the swivel was placed over an 18cm metal stake buried a minimum of 10cm in the substrate. *H. sanguineus* were able to move freely throughout the radius of their tether and were able to conceal themselves beneath cobble. Once crabs were tethered, cages were placed on top of them; the bottom edges of all exclusion cages were then buried in the cobble to prevent organisms from burrowing underneath the mesh and/or frame. After three days,
we removed the cages and recorded all crabs as present, absent, or desiccated (deceased). Results were analyzed contingency analyses (JMP v7.0, www.sas.com) to assess differences among cage types, tidal heights, and time. Results are expressed as percentages to more clearly show comparisons.

RESULTS

*L. littorea* algal feeding rates

*Littorina littorea* grazing rates were not reduced by the presence of, or chemical cues from, *Hemigrapsus sanguineus*. *Ulva rigida* in the presence of only *L. littorea*, or with both *L. littorea* and *H. sanguineus'* chemical cue, exhibited a four-fold decrease in algal growth compared to the control ($F_{4,90} = 40.41$, $p < 0.0001$; Figure 1). The greatest decrease in algal mass was observed when both consumers were present, with over a six-fold decrease in algal mass versus the control. However, *H. sanguineus* alone also had a negative impact on *U. rigida* biomass (Figure 1). There was also a significant difference in the change in algal mass among trials ($F_{7,90} = 19.63$, $p < 0.0001$) with a significant interaction term ($F_{28,90} = 2.02$, $p = 0.0069$). During the entire experiment, less than 2% of *L. littorea* were unaccounted, with no evidence of snail consumption by a predator (i.e. broken shells).
Figure 1 Effect of Hemigrapsus sanguineus presence and chemical cue on the Littorina littorea consumption rate of Ulva rigida. Letters indicate significant differences. U = Ulva rigida, L = Littorina littorea, H = Hemigrapsus sanguineus, CH = chemical cue of H. sanguineus. Treatments with different letters are significantly different.

L. littorea feeding behavior

The behavior of Littorina littorea in the mesocosm tanks varied significantly among Hemigrapsus sanguineus treatments (presence, absence, or chemical cue; $\chi^2_4 = 13.51, p = 0.0090$) and across daily cycles ($\chi^2_6 = 60.87, p < 0.0001$; Figure 2). L. littorea were found on Ulva rigida most often when no H. sanguineus were present, had the highest fleeing rate in the presence of H. sanguineus chemical cues, and were most often resting on the bottom of the tank when H. sanguineus were present. The presence of crabs decreased the amount of time L. littorea were found on U. rigida by roughly 5% relative to the control. Resting and fleeing were 3.5% and 1% more prevalent, respectively. H. sanguineus chemical cues elicited 4% higher snail fleeing rates than in
control tanks. *L. littorea* activity was also impacted by the time of day, with more periwinkle activity (e.g. presence on algae or fleeing) at midnight, and resting at noon. *L. littorea* behaviors at 6:00 A.M. and 6:00 P.M. were very similar to each other. The number of *L. littorea* observed at 6:00 PM was lower than at the other times of day due to environmental conditions that prevented us from sampling.

![Figure 2](image)

**Figure 2** Effect of *Hemigrapsus sanguineus* chemical cue and presence, and time of day, on the behavior of *Littorina littorea*. The mean response of *L. littorea* behavior was averaged across A) time of day, and B) treatment. The numbers on the bars represent the total number of *L. littorea*.

**Predation rates on *H. sanguineus***

There was a significant difference in the distribution of alive, removed, and desiccated *Hemigrapsus sanguineus* between tidal heights ($\chi^2 = 14.47, p = 0.0007$) but not among cage types ($\chi^2 = 8.75, p = 0.0676$), with no interaction effect ($\chi^2 = 0.39, p = 0.9836$; Figure 3).
When combined across cage types, *Hemigrapsus sanguineus* were more often found alive in the low intertidal than the high intertidal (59% and 41%, respectively). *H. sanguineus* were only found desiccated in the high intertidal zone (28% of crabs desiccated at this tidal height). *H. sanguineus* were removed at the same rate from the low and high intertidal.

When combined across tidal heights, *Hemigrapsus sanguineus* had the highest survival rate in the fully enclosed cages (82% alive), followed by the open top cages (50% alive), and finally the control (45% alive). *H. sanguineus* were most often removed from the control group (44%), while the highest rate of desiccation occurred in the open top cages (23%).

![Figure 3](image-url)

**Figure 3** Effect of tidal height on the predation rate on *Hemigrapsus sanguineus*. FE = fully enclosed cage, OT = open top cage, C = control. The numbers on the bars represent the total number of *H. sanguineus*. 

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DISCUSSION

Our results indicate that *Hemigrapsus sanguineus* and *Carcinus maenas* have different impacts on lower trophic levels. Previous studies indicate that *C. maenas* drastically reduce the feeding rate of *Littorina littorea*. *C. maenas* remove snails via direct consumption (Lubchenco 1978, Hadlock 1980, Trussell et al. 2002, 2003, Eastwood et al. 2007), and their chemical cues cause *L. littorea* to sharply reduce their algal consumption rates (Trussell et al. 2003, Griffen & Byers 2009). Thus, *C. maenas* has an indirect top-down positive effect on algal communities by altering snail density and behavior; *Ulva* growth rates when both *L. littorea* and *C. maenas* are present are similar to when these two species are excluded (Lubchenco 1978, Trussell et al. 2002, 2003, Trussell et al. 2004, Trussell et al. 2006). By contrast, our experiments showed that *H. sanguineus* did not elicit a similar response from *L. littorea*, and their physical presence and/or chemical cue did not significantly reduce the periwinkles' consumption of algae. While *L. littorea* has a negative impact on *Ulva rigida* biomass, this effect is not modified by the presence of *H. sanguineus* chemical cues. The fact that less than 2% of *L. littorea* were unaccounted for during the experiment, and that there was never evidence of consumption by a predator, strongly suggests that *H. sanguineus* did not consume *L. littorea*. *L. littorea* thus appear to not perceive *H. sanguineus* as a predatory threat and continue feeding in their presence.

However, *Hemigrapsus sanguineus* is omnivorous and will consume algae when other prey are not as accessible (Ledesma & O'Connor 2001, Bourdeau & O'Connor 2003). In our mesocosms, *H. sanguineus* had a negative impact on algal biomass, but it was not as strong as the impact from *Littorina littorea* (Figure 1). *H. sanguineus* tore
small pieces from the algal blades; these small pieces then frequently disappeared down
the drainpipe and were lost from the experiment. Because of this shredding behavior, the
ecosystem consequence of *H. sanguineus* on algae is not that of a typical consumer.

*Ulva rigida* biomass decreased the most when both *Littorina littorea* and
*Hemigrapsus sanguineus* were present, and this decrease was greater than would be
expected simply through the combined effects of snails and crabs. This could indicate a
potentially synergistic impact of *L. littorea* and *H. sanguineus*, which further
distinguishes the effects of *H. sanguineus* from those of *Carcinus maenas*.

Unfortunately, *Carcinus maenas* are now extremely rare in the rocky and cobble-
based intertidal habitats in Narragansett Bay and we could not collect sufficient numbers
of *C. maenas* to perform mesocosm experiments using both crab species and snails from
the same environments (N. Rohr, unpubl. survey data). This observation provides support
for the hypothesis that *H. sanguineus* have effectively excluded *C. maenas* from these
intertidal zones.

*Littorina littorea* behavior in the presence of *Hemigrapsus sanguineus* also
differed from previously documented behaviors in the presence of *Carcinus maenas*, as
the snails did not reduce their feeding rate in the presence of *H. sanguineus*. Despite this
response, *L. littorea* still consumed at least as much algae in the presence of *H.
sanguineus* chemical cues as with no crabs present, implying that the periwinkles may
have been influenced by *H. sanguineus* without perceiving them as a potential threat.
Given the mobility and high activity of *H. sanguineus* (Brousseau et al. 2002), it may
disrupt the feeding behavior of *L. littorea* by physically interacting with them.
In the field, the vertical distribution of *Hemigrapsus sanguineus* was influenced by physical factors in the upper-range and biological factors in its lower range, which is the traditional model of species' distributional limits in intertidal habitats (Connell 1961). The lack of significant differences among tethering treatments may have been influenced by similar predation rates on *H. sanguineus* in the open top and control cages in the high intertidal; this similarity could reflect limited removal of *H. sanguineus* by benthic predators (e.g. larger crustaceans).

Replacements of one invasive species by another have the ability to reshape intertidal marine food webs (Byrnes et al. 2007, Griffen & Byers 2009), which can have biological implications through changes to predator-prey interactions, behavior modification of conspecifics, and temporary release from consumption by novel predators (Eastwood et al. 2007, Griffen & Delaney 2007, Griffen et al. 2011, Steinberg & Epifaunio 2011). As globalization increases and maritime transportation becomes more efficient, species are being introduced to new environments at an increasing rate (Ruiz et al. 1997) and, once they are introduced, their establishment and spread is facilitated by the ever-increasing threat of global climate change (Harley et al. 2006, Hellmann et al. 2008, Walther et al. 2009). While prevention of the introduction of novel species is important to protecting the ecologic and economic viability of our coastal and estuarine ecosystems, it is also important to identify the introduction of new species while there is still the opportunity to prevent their spread, understand the long-term effects of specific invasive species, and prepare for the potential economic impact (de Rivera et al. 2011, Grosholz et al. 2011).
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