AN INVASIVE CRAB IN THE SOUTH ATLANTIC BIGHT: FRIEND OR FOE?

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To my family for their love and encouragement

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TABLE OF CONTENTS

CHAPTER

LIST OF TABLES

LIST OF FIGURES

LIST OF SYMBOLS AND ABBREVIATIONS

~	Approximately
>	Greater than
<	Less than
≥	Greater than or equal to
≤	Less than or equal to
χ^2	Chi Square Test
♂	Male
♀	Female
º , ’	Degree, minute latitude and longitude
ºC	Degrees Celsius
‰	Parts per thousand (salinity)
± SE	Plus or minus the Standard Error
ANOVA	Analysis of Variance
CW	Carapace Width
GPS	Global Positioning System
HPLC	High Performance Liquid Chromatography
PVC	Polyvinyl Chloride

SUMMARY

The green porcelain crab, *Petrolisthes armatus*, recently invaded oyster reefs of the South Atlantic Bight at mean densities of up to several thousand individuals m^{-2}. Despite the crab's tremendous densities, its population dynamics, reasons for successful invasion, and impacts on oyster reefs have remained unknown. Through large-scale monitoring and experimental mesocosm and field studies, we addressed these questions.

We assessed the spatial and temporal population dynamics of *Petrolisthes armatus* by monitoring oyster reefs of the Duplin and Wilmington River estuaries in Georgia, U.S.A. We followed densities, demographics, and reproduction along the rivers (Upper, Middle, and Lower regions) and between tidal heights (high and low) on a quarterly basis from August 2003 to June 2004. Mean densities during warmer months ranged between ~15 to 3900 crabs m^{-2} in the Duplin River and ~790 to 11,200 crabs m^{-2} in the Wilmington River with patches up to 31,390 crabs m^{-2} and maximum mean densities 37 times higher than those reported in the historic range. During colder months, densities declined by ~64 to 95% in the Duplin River and ~89 to >99% in the Wilmington River. Despite these decreases in density, populations of mature adult crabs persisted through the winter, and, by spring, population densities rebounded to levels seen during previous warm periods of the year.

Spatial analyses showed that *Petrolisthes armatus* population density was greatest in the Middle to Lower regions of the rivers during warmer months of the year. Densities were greater in the low versus high intertidal for all 4 monitoring periods in the Duplin

River and significantly or nearly so in the Wilmington River during April and June 2004. These patterns suggest that physical factors set limits on distribution.

A large proportion of the *Petrolisthes armatus* population was composed of recruits and gravid females in warmer months; both recruits and gravid females were nearly absent in colder months. Gravid females were typically found in the low intertidal of the Duplin River but at both tidal heights in the Wilmington River. There was no effect of region on distribution, except in June and July 2004 when we found significantly more gravid crabs in the Upper region of both estuaries. During warmer months, 20 to 85% of mature females were gravid in the Duplin River and 25 to 90% were gravid in the Wilmington River. Gravid females in Georgia were found at one size class smaller than those gravid females in the historic range (3 to 3.9 versus 4 to 4.9 mm CW), suggesting that females reproduce at a smaller size in their new range. This may result in females reproducing at younger ages, and, if survivorship does not differ, have more reproductive events in a lifetime. Despite some changes in the distribution of gravid females, sex ratios remained near 1:1 over space and time. Considerable densities of recruits in warmer months, the ability to reproduce at smaller sizes, and the high percentage of egg-bearing females all attest to the ability of *P. armatus* to increase in number by 10 to 100 fold between seasons. The population fecundity of the crab in Georgia was estimated to exceed that of the historic range by at least an order of magnitude.

Biological factors such as predation or competition may determine the distribution of *Petrolisthes armatus* in oyster reefs of the expanded range. The most likely predators or competitors for space of the invasive crab in Georgia are the native mud crabs,

Panopeus herbstii and *Eurypanopeus depressus*. Mud crab densities were ~580 to 1610 crabs m^{-2} in the Duplin River and ~340 to 1530 crabs m^{-2} in the Wilmington River with higher densities in warmer months. Mud crab distribution was not strongly influenced by region, tidal height, or season; there was only an effect of region in warmer months when more crabs were found in the Middle to Lower estuary. We correlated *P. armatus* densities against mud crab densities to assess potential interactions between the non-native and native crabs. There were no significant negative correlations, but there were several positive ones across different times and regions. The positive correlations could occur because mud crabs consume porcelain crabs and migrate to areas where this prey is most abundant or because both crabs require similar physical or biological conditions and thus co-occur in greater densities where these conditions are present.

Monitoring clearly documented tremendous densities of *Petrolisthes armatus* during warm periods as well as rapid population recovery after declines in colder months. The composition of the habitat itself may be impacting the success of the invasion. Through two field studies we found that *P. armatus* recruitment from the plankton was initially greater onto experimental oyster reef communities with no native species than onto ones with 4 native species, suggesting that native species diversity provided initial resistance to invasion. However, this initial resistance was rapidly overwhelmed by tremendous recruitment that swamped initial biotic resistance. There were no differences among treatments with differing densities of native species beyond 4 weeks, and by 12 weeks recruit densities ranged from 17,000 to 34,000 crabs m^{-2} across all treatments. Presence of the invasive crab stimulated conspecific recruitment from the plankton, creating propagule pressure that resulted in all treatments supporting high densities of the

invasive crab. The initial suppression of recruitment into reefs with more native species could have been due to competition, predation, or the combination of native species. We tested the hypothesis that native mud crabs suppressed *P. armatus* via predation and found densities of the invasive crab increased as rapidly in reefs with mud crabs as those lacking mud crabs; thus, the addition of a mud crab predator did not affect recruitment. The presence of adult crabs due to experimental seeding or through the rapid growth of juvenile settlers enhanced recruitment and caused an intraspecific "invasional meltdown" within our experimental units. Propagule pressure drove invasion success over the longer term.

The densities, recruitment rates, and rapid growth of *Petrolisthes armatus* produced tremendous amounts of new benthic biomass on native oyster reefs. We assessed potential diet shifts of native consumers in light of this biomass by performing laboratory feeding and field tethering assays. Mummichogs, lesser blue crabs, and mud crabs readily consumed the porcelain crab in laboratory assays, whereas spot did not. Mud crabs consumed the invasive crab in preference to large and small native oyster drills and mussels in a laboratory choice assay. *P. armatus* tethered on oyster reefs or mud flats were readily consumed (60% to 95% of tethered crabs), indicating that native consumers will use the invasive crab as food in the field.

Small-scale experiments in mesocosms and the field, indicated that *Petrolisthes armatus* at densities of 750 to 1500 crabs m^{-2} did not suppress the richness of native taxa on oyster reefs but significantly suppressed the growth of smaller adult oysters (<60 mm initial length), benthic microalgal biomass, and native mud crabs from the plankton. In contrast, the presence of the crab significantly enhanced recruitment of total bivalves

(oysters, mussels, and Antillean sphenia clams) as well as macroalgal cover. There was also a trend for enhancing the survivorship of predatory oyster drills. These patterns were consistent with the hypothesis that native crabs, which normally prey on bivalves and gastropods, are shifting their feeding onto the invasive crab, thus lessening predation of the small size classes of native prey.

The enhancement of macroalgae and the suppression of microalgae may be due to the movements or feeding of *Petrolisthes armatus* removing particulates accumulating on oyster surfaces. Microalgae may be consumed, and thus its growth moderated, whereas macroalgae may increase its cover because it is no longer smothered by particulates and is not consumed by the crab. Oysters may suffer depressed growth in the presence of *P. armatus* due to competition among filter-feeders for a shared food or because the movements of the crabs over the oysters causes closing of the shells and, thus, reduced feeding time. Small bivalves often experience greater stress from physical and biological factors. Thus, the depression of oyster growth due to the invasive crab could cause decreased oyster survival. However, the summed effects of the invasive crab during our short-term experiments were positive for bivalves; bivalve recruitment was significantly enhanced. *P. armatus* may increase bivalve recruitment by cleaning oyster surfaces and facilitating attachment of juveniles or by serving as an alternate food for native consumers. The long-term effects of the invasive crab on oyster reefs are unclear. The crabs benefit oysters by enhancing recruitment, but this benefit could be reversed if the crab serves as a food source that contributes to the survivorship and population growth of native predators such as mud crabs and oyster drills.

Overall, our data may be conservative due to comparatively low densities of porcelain crabs and shorter periods of exposure in experimental studies versus in natural reefs, as well as the premature loss of porcelain crab treatments in our mesocosm and field studies. Our experiments suggest that virtually all of the most common native species on oyster reefs are significantly affected by *Petrolisthes armatus*. The presence of the crab has strong implications for the ecology of oysters, the foundation species of the most extensive hard-substrate habitat in coastal Georgia. In the short-term we found depressed growth of oysters, enhanced recruitment of juvenile oysters, as well as rapid and preferential predation of the invasive crab by native consumers. This new source of food may increase the survivorship and population growth of bivalve predators such as mud crabs and oyster drills. The longer-term combined effects of depressed oyster growth, increased oyster settlement, and potentially increased consumer densities could lead to smaller oysters that remain susceptible to predators for longer periods of their life history and decreased growth and survivorship in the longer term.

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CHAPTER 1

POPULATION DYNAMICS OF THE INVASIVE PORCELAIN CRAB *PETROLISTHES ARMATUS* IN OYSTER REEFS OF THE SOUTH ATLANTIC BIGHT, U.S.A.

Abstract

Although the South Atlantic Bight has experienced few invasions of invertebrate macro-fauna, the green porcelain crab, *Petrolisthes armatus*, recently invaded oyster reefs at densities of thousands m^{-2}. We assessed the spatial and temporal dynamics of *P. armatus* densities, sex ratios, sizes, and reproductive patterns via a large-scale monitoring program in two estuaries of coastal Georgia, U.S.A. Exotic crab densities generally were higher in the low versus the high intertidal and in the lower versus upper regions of estuaries. In warmer months, 20 to 90% of adult females were gravid, recruits were dense, and population levels were high. In colder months, densities dropped by 64 to >99%. Male:female ratios were near 1:1 across times and locations. Native mud crab densities were unrelated to, or positively correlated with, densities of exotic crabs; correlations were never significantly negative. These correlations did not lend support to the hypothesis that the invasive crab is negatively affecting native crabs with which it most closely associates. Maximum mean densities of *P. armatus* in Georgia were 37 times the highest densities recorded in the historic range, crabs in the new range reproduced at a smaller size, and the percentage of gravid females was similar between the old and new range. Thus, population fecundity in the new range exceeds that of the native range by more than an order of magnitude. The effects of high density, rapidly

breeding *P. armatus* populations on native communities are unclear, but could be considerable if this filter-feeding crab impacts oysters, which are the foundation species for inshore reefs.

Introduction

Biological invasions threaten natural communities and can alter ecosystem structure (Mooney and Drake 1986, Simberloff *et al.* 1997), but studies of exotic species' traits and impacts can also provide insights into processes affecting community assembly and global change (Lodge 1993). Most studies of invasions have focused on terrestrial or freshwater habitats where successful invaders have had catastrophic impacts on native species (e.g., *Linepithema humile* and *Rattus exulans* in New Zealand, *Bufo marinus* and *Boiga irregularis* in Guam, *Dreissena polymorpha* in the Great Lakes) (Carlton and Geller 1993). Studies of marine invasions are less common despite several being well known and having profound ecological consequences (e.g., *Potamocorbula amurensis* and *Carcinus maenas* in the San Francisco Bay, *Mnemiopsis leidyi* in the Black Sea, and *Caulerpa taxifolia* in the Mediterranean Sea; Carlton and Geller 1993, Cohen and Carlton 1998, Ruiz *et al.* 1999).

Oyster reefs are the major hard-substrate communities in coastal areas of the South Atlantic Bight, U.S.A., and they produce the biogenic structure upon which many native species depend (Lenihan and Peterson 1998). These reefs have rarely been affected by invasive macro-fauna known to be succeeding in ports and estuaries within other regions of the United States (Ruiz *et al.* 1997, 1999, Cohen and Carlton 1998). However, in 1995 the green porcelain crab, *Petrolisthes armatus*, colonized oyster reefs of the South Atlantic Bight and in South Carolina rapidly increased from single individuals m^{-2} to over 16,000 m^{-2} by August 1999 (see the South Carolina Department of Natural Resources website at http://water.dnr.state.sc.us/marine/mrri/shellfish/petro.htm). In its presumptive native range, including the eastern Pacific (Gulf of California to Peru), the western Atlantic (Southern Florida to the Indian River Lagoon, Bermuda, Gulf of Mexico, Caribbean, and Brazil), and western Africa, the crab achieves maximal densities of only ≤305 individuals m^{-2} (Oliveira and Masunari 1995).

In its new range, *Petrolisthes armatus* is found primarily in oyster reef habitats of Georgia and South Carolina. Although this crab has been found across a wide area of the tropical Atlantic and Pacific from rocky shores (Oliveira and Masunari 1995), sand reefs built by sabellid worms (Micheletti-Flores and Negreiros-Fransozo 1999), and even mangrove prop roots (Sheridan 1992), very little is known about the crab's distribution, habitat preference, seasonal fluctuations, population structure, and food web or community effects (but see Sheridan 1992 for density fluctuations in Rookery Bay, Florida and Oliveira and Masunari 1995 and Micheletti-Flores and Negreiros-Fransozo 1999 for population dynamics in southern Brazil). To provide an initial assessment of the invasion, we asked the following questions: (1) what are the spatial and temporal patterns of *P. armatus* densities in tidal creeks of its new range, (2) what are the demographic patterns of the crab (including sex ratios) across seasons, regions, and tidal heights, (3) what are the reproductive patterns of the crab, (4) what are the distributional patterns of co-occurring native crabs, and (5) how do native crab distributions correlate with those of the non-native crab?

Materials and Methods

Study Sites

Monitoring of *Petrolisthes armatus*, as well as associated oyster reef crabs, was performed within two Georgia estuaries separated by about 75 km (Figure 1.1a). The southern estuary at Sapelo Island, Georgia is part of the National Oceanic and Atmospheric Administration's National Estuarine Research Reserve System and includes the Duplin River (~12.5 km in length). The Duplin River does not have a significant freshwater source, and is better described as an elongated tidal embayment (Ragotzkie and Bryson 1955, Chalmers 1997). The transport of materials in the river is primarily diffusive except when there is heavy rainfall at low tide which can nearly replace the water in the upper regions of the river (Chalmers 1997). The Duplin River has three tidal prisms along its length (Ragotzkie and Bryson 1955). Strong tidal currents at the mouth of the river and the lack of freshwater input at the head of the river maintain a well-mixed, vertically homogeneous water column within each defined tidal prism, but the overall impact is little advective transport of water and materials (Ragotzkie and Bryson 1955, Bahr and Lanier 1981). Thus, waters of the upper and lower regions are hydrologically isolated from one another (Chalmers 1997).

Our northern estuary encompasses the rivers, creeks, and marshes near Skidaway Island, Georgia (Figure 1.1a). This is a riverine estuary that is influenced by saline waters at its mouth and freshwater in its upper regions. Such estuaries can show a well-defined vertical salinity stratification where freshwater overrides the higher density salt water, thus forming salt-wedges (Bahr and Lanier 1981). When tidal flow is strong enough to prevent the freshwater source from dominating circulation patterns, a partially

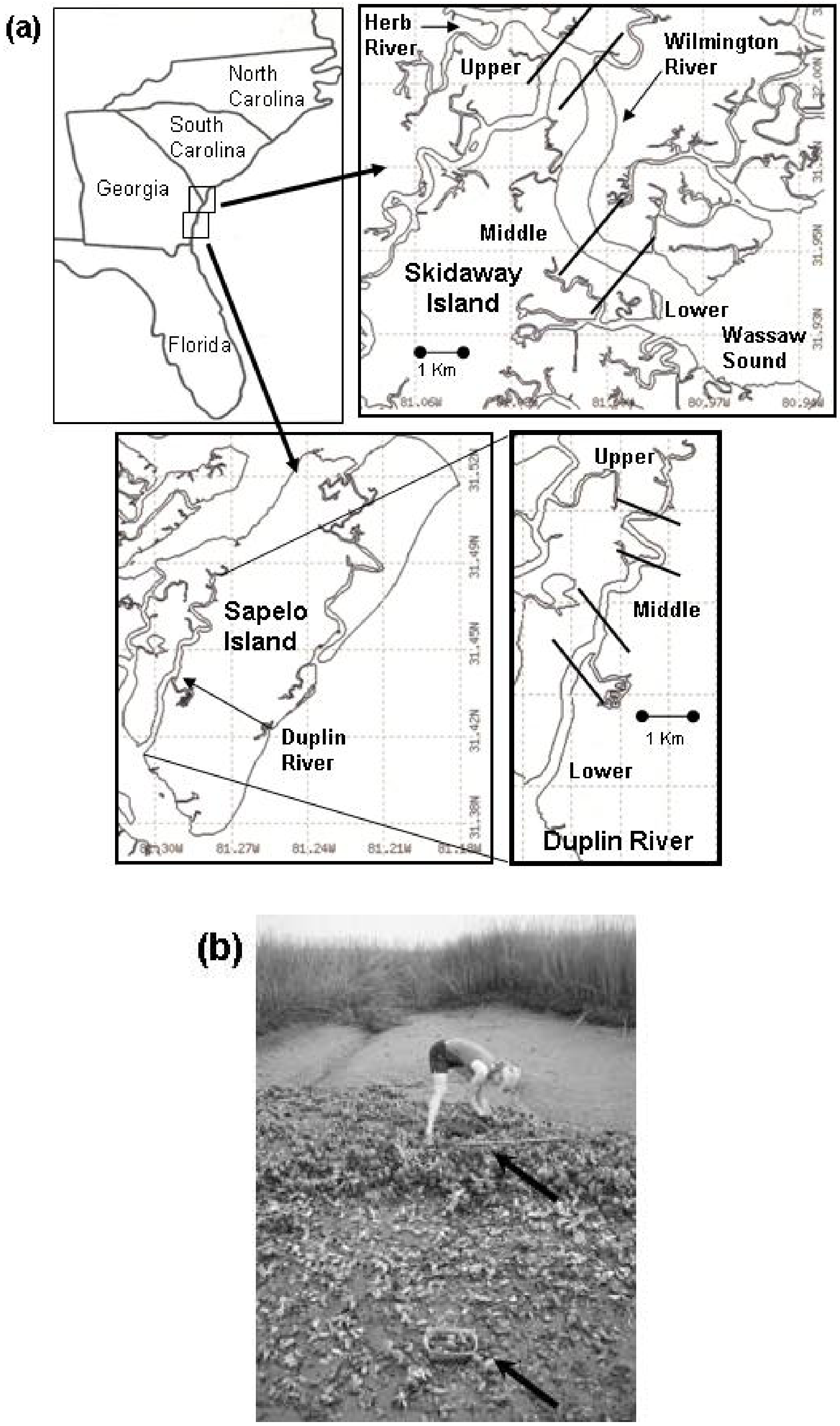


Figure 1.1. (a) Skidaway Island and Sapelo Island, Georgia, U.S.A., showing locations of the monitoring regions (Upper, Middle, Lower) in each estuary. (b) Monitoring baskets at high and low tidal heights are highlighted with an arrow.

mixed estuary with moderate salinity stratification can occur (e.g., Altamaha and Ossabaw Sounds, Georgia) (Bahr and Lanier 1981). Our study area included the mouth of the Wilmington River (where it meets Wassaw Sound) up to its intersection with the Skidaway River (~7 km) and into a large tidal creek (Herb River). There are no known tidal prisms in this region, but recent research shows that frequent gyres of circulating water occur continuously along the river's length (C. Li *personal communication*).

Both estuaries are dominated by marsh cordgrass (*Spartina alterniflora*) in the upper tidal heights, oyster reefs (*Crassostrea virginica*) and associated biota in the middle tidal heights, and muddy sediments in the lower intertidal. The estuaries are subject to semidiurnal tides with a tidal range of 2 to 4 meters (Bahr and Lanier 1981). Thus, depending upon the height of the tide, portions of the middle and/or lower intertidal are exposed on most days.

Despite the hydrodynamic differences between the two estuaries, both appear to have stronger and more frequent physical disturbances in the lower versus upper regions due to wind-wave and tidally generated currents. The middle regions are influenced by both marine and riverine processes, thus these regions are generally more turbid throughout the tides. The upper regions incorporate the network of tidal creeks that drain the surrounding salt marshes and are generally characterized as low-energy, sedimentary environments (Bahr and Lanier 1981).

Monitoring

We monitored crab density, size, and sex along estuarine gradients in our two locations as a function of season and tidal height throughout the year (August 2003 to July 2004). The rivers of both estuaries were divided into three regions: (1) Upper, (2) Middle, and (3) Lower, with unmonitored sections separating each region (see Figure 1.1a). Within each region we marked 20 oyster reef monitoring plots with PVC poles and took GPS coordinates of each location. Monitoring plots were typically separated from each other by ≥20 meters; however, in the Upper region of the Duplin River where reefs became sparse our plots were separated by ~10 meters.

We initiated monitoring in early June 2003 (Wilmington River: June 2-7, Duplin River: June 9-12). At each of the 20 plots within each region, we placed a 22 cm x 15 cm (~0.03 m^2) plastic basket at a high (top edge of the oyster reef, ~1 to 2 meters above mean lower low tide) and low (just above where oysters end and mud begins, ~0 to 0.5 meters above mean lower low tide) tidal height of the oyster reef along the same vertical transect and with similar basket orientation to the water-line (Figure 1.1b). Baskets were nestled into the oyster reef and anchored using rebar stakes. Baskets had perforated sides (nine 5.4 cm long and 1.4 cm tall halfmoon-shaped holes along the length and two along the width) and open tops, allowing movement of crabs into and out of the baskets. Each basket was initially hand-packed to its top with site-specific oyster reef substrate (immediately adjacent to each basket), including any reef-associated organisms in that volume. Crevice size, shape, and number of oysters in each basket appeared visually similar to that of the natural reef.

We monitored crabs in these baskets on a quarterly basis during low tides (2 to 3 hours on either side of the low tide) [Wilmington River: (1) August 25-September 3, 2003, (2) December 2-18, 2003, (3) April 1-15, 2004, (4) July 7-12, 2004; Duplin River: (1) September 5-8, 2003, (2) November 20-22, 2003, (3) March 16-18, 2004, (4) June 30-July 2, 2004]. For the initial sampling, 10 of the 20 plots in each region for each estuary were randomly chosen and sampled. The second set of 10 plots was sampled during the following sampling period. The plots sampled were alternated in this manner throughout the monitoring. In cases where baskets or all material within the baskets were lost due to physical disturbances (this happened for 5 baskets out of a total of 240 possible baskets for the Duplin River and for 30 out of a total of 240 possible baskets for the Wilmington River, mostly in the Lower region during winter storms), the closest alternate basket was sampled. All baskets that were lost or empty were replaced and filled to the top for future sampling. Thus, most individual baskets following the initial sampling were monitored at 6 month intervals, with a few (2 to 9 baskets) from each time-point used after 3 months. In preliminary experiments, baskets achieved a stable density of *Petrolisthes armatus* in one month (A. L. Hollebone *unpublished data*). Thus, the 3 to 6 months between monitoring considerably exceeded the time required for recovery following disturbance due to the previous sampling.

To monitor crab densities, baskets were removed from their anchors and materials within each basket were transferred to a closed container. All material was retrieved and the volume noted for those baskets that were ≤2/3 full (due to physical disturbance). If the baskets were 75% to 100% full, the volume was noted and half of the material was taken. The volume was split by overturning the basket into two plastic shoebox containers (the width of two shoeboxes approximated the length of one monitoring basket). The contents of one shoebox were taken and the contents of the other were returned to the monitoring basket. All baskets were resecured in their original positions and filled to 100% with surrounding oyster substrate.

Upon returning to the lab, all crabs (both native and non-native) were removed, counted, sized (carapace width = CW), sexed (see Oliveira and Masunari 1995), and preserved in 70% ethanol or 10% formalin. If there were less than 40 crabs in a sample, all were sized and sexed. If the sample contained more than 40 crabs, they were subsampled. Subsampling involved: (1) pouring crabs into a sorting tray that had been divided into 12 equal sections, (2) separating crabs from one another, (3) slightly suspending the crabs with a few milliliters of water, and (4) selecting, sexing, and measuring the first 30 crabs encountered in a randomly selected section of the tray (entire carapace had to be within the chosen section). If there were less than 30 crabs in the tray section another section was randomly chosen.

Data Analyses

We determined the estuarine-wide density patterns of non-native porcelain crabs and native mud crabs (*Panopeus herbstii* and *Eurypanopeus depressus* combined) scaled to 1 m^2 (accounting for how much of the basket contents were sampled and how many baskets fit into 1 m^2 of oyster reef, ~30.3 baskets) along the lengths of the two rivers, as a function of tidal height and time period. We included mud crabs because these were the most common native species living at high densities within the oyster reefs, and thus the native crabs that would most commonly interact with the exotic crab. Datasets were tested for normality (Ryan-Joiner W test, $p > 0.050$) and equality of variances (Bartlett's test, $p > 0.050$). Due to non-normality, the data were square root transformed and then analyzed using a two-way ANOVA to assess the overall effect of region, tidal height, and the combination of both factors on densities of *Petrolisthes armatus* and mud crabs throughout the year.

In addition, we evaluated how size classes of *Petrolisthes armatus* (males and females combined; from megalopae and those ≤0.9 mm CW up to those 12 to 12.9 mm CW) were distributed across regions, tidal heights, and seasons by plotting the mean number of crabs (± SE) basket^{-1} in each size class. An overall mean size for each time-region combination was also determined.

We also plotted size classes and mean densities (± SE) for male and female *Petrolisthes armatus* basket^{-1} (scaled as above) across all region, tidal height, and time period combinations. The sex ratio of *P. armatus* for each region x tidal height plot (these calculations ignored megalopae that could not be reliably sexed) was also calculated from the total pooled sample of all males and all females at that region, tidal height, and time period. We did not calculate a ratio for each basket because during some seasons many baskets did not contain any crabs or contained only a few crabs of one sex. We assessed whether the frequency of males within each region and season were significantly different from an expected frequency of 50% by using the χ^2 (Chi square) test.

We also calculated the proportion of all females large enough to be sexually mature (≥3 mm CW) that were ovigerous across sites and seasons. The data were arcsine transformed and tested for normality and equality of variances as described above. The data were then analyzed using a two-way ANOVA. In addition, the proportion of mature females that were gravid across all locations and seasons in both estuaries was calculated for comparison with the overall proportion derived from Oliveira and Masunari's (1995) data for native populations of this crab in Brazil.

To assess the possibility that this invasive crab was suppressing native crabs in oyster reef habitats, we correlated the densities of native mud crabs (dominated by two species, *Panopeus herbstii* and *Eurypanopeus depressus*) against densities of *Petrolisthes armatus* using Fisher's r to z to determine the relation of these crabs among regions, between tidal heights, and over time.

Results

Overall Densities

Densities of *Petrolisthes armatus* in the Duplin River estuary ranged from ~15 to 3900 crabs m^{-2} during warmer months but dropped to maximal mean densities of only 400 crabs m^{-2} after colder portions of the year (March; Figure 1.2). Between the end of the warmest period (November) and the end of the coldest period (March) densities decreased ~64 to 69% in the Upper region, ~85 to 93 % in the Middle region, and ~91 to 95% in the Lower region of the estuary. There was a significant region effect in September, November, and July (two-way ANOVA, $p \leq 0.001$); densities were low in the Upper regions and increased towards the Middle and Lower regions. No significant region effect was detected in March ($p = 0.205$) when densities were low at all sites. Tidal height affected porcelain crab densities across all time periods ($p < 0.001$ for all 4 times), with crabs being most dense in the low intertidal. A significant region x tidal height interaction occurred only in July ($p < 0.001$), when densities in the low intertidal increased with proximity to the sound, whereas those in the upper intertidal did not vary with region.

Petrolisthes armatus densities in the Wilmington River estuary ranged between ~790 to 11,200 crabs m^{-2} during warmer months, but during colder months (reflected in

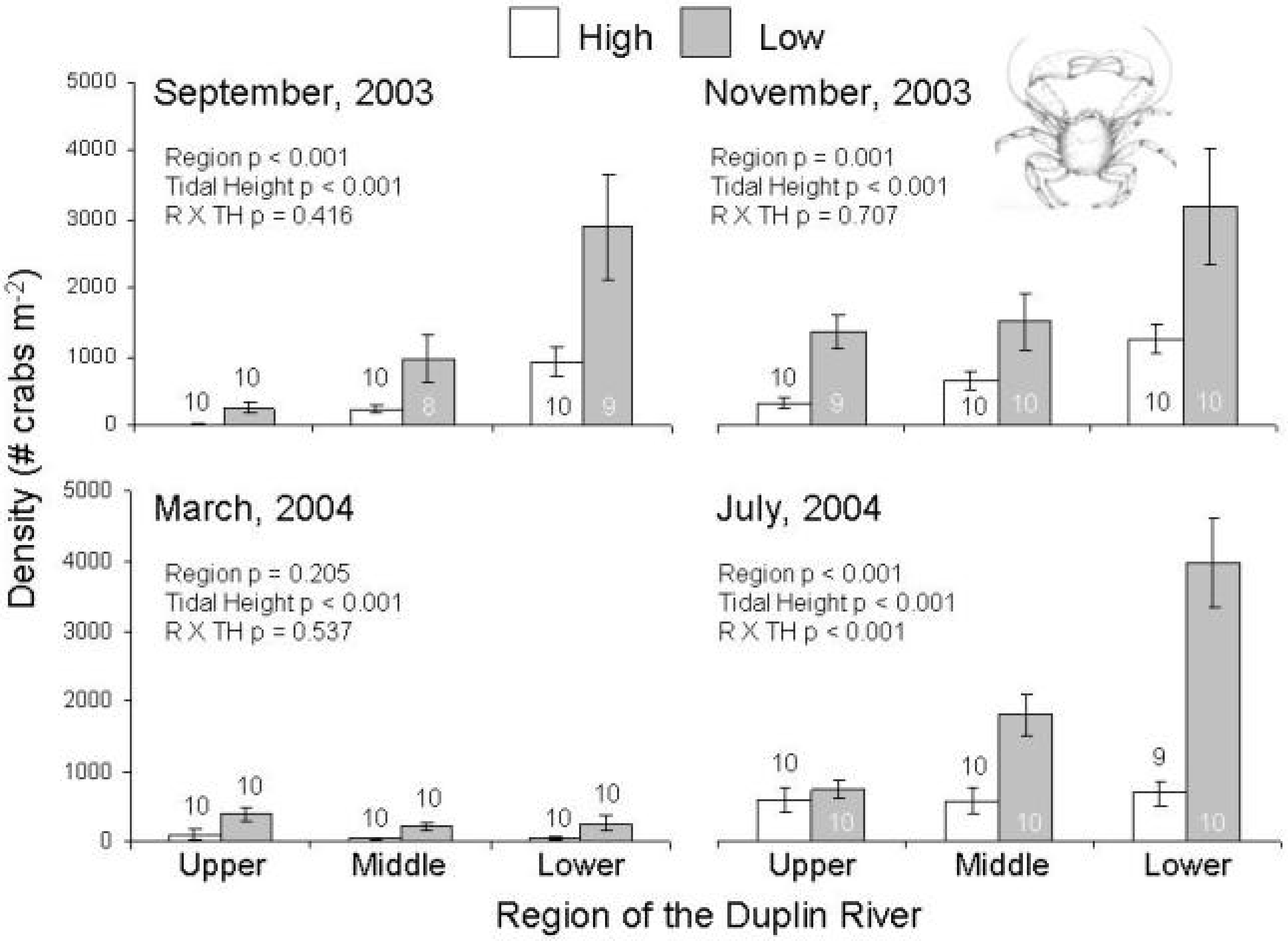


Figure 1.2. Densities of *Petrolisthes armatus* (mean ± SE, scaled to 1 m^2) in the Duplin River across regions, tidal heights (white: high intertidal; grey: low intertidal), and sampling periods. Numbers within or above bars indicate the number of replicate baskets sampled. P values derived from a two-way ANOVA following square root transformation.

the April 2004 data; Figure 1.3), densities decreased by 89 to >99% (averaging only ~20 to 165 crabs m^{-2} across all regions compared to the December 2003 densities). Significant region effects occurred in August, June ($p \leq 0.010$), and nearly in December ($p = 0.070$) due to greater densities occurring in the Middle region of the Wilmington River estuary. Tidal height significantly affected densities in April ($p = 0.010$) and almost in June ($p = 0.057$), but not during the other monitoring periods. In this estuary there was never a significant region x tidal height interaction on porcelain crab densities.

Demographics

Recruitment (appearance of crabs <3 mm CW) in both estuaries occurred primarily during the warmer months of June to September (Figures 1.4 and 1.5). Recruits (megalopae), juvenile crabs, and gravid females (Figures 1.4 to 1.9) were essentially absent following the coldest months of the year (March and April). Some crabs of reproductive size (≥3 mm CW) persisted through the winter months. Although crabs were generally more abundant in the low versus high intertidal, size class distributions were crudely similar for the two tidal habitats with the exception that the largest size classes tended to occur in the low tidal zone.

We sexed over 5500 crabs. Regardless of the estuary, time, region, or tidal height, sex ratios rarely differed significantly from an expected ratio of 1:1 (Figures 1.6 and 1.7; summarized in Table 1.1, χ^2 test, $p > 0.050$). This analysis entailed 48 separate statistical tests. One could expect 2 to 3 significant differences with $p = 0.050$ by chance alone (i.e., 48 x 0.05 = 2.4 significant differences expected), so we do not interpret the three differences we detected as meaningful.

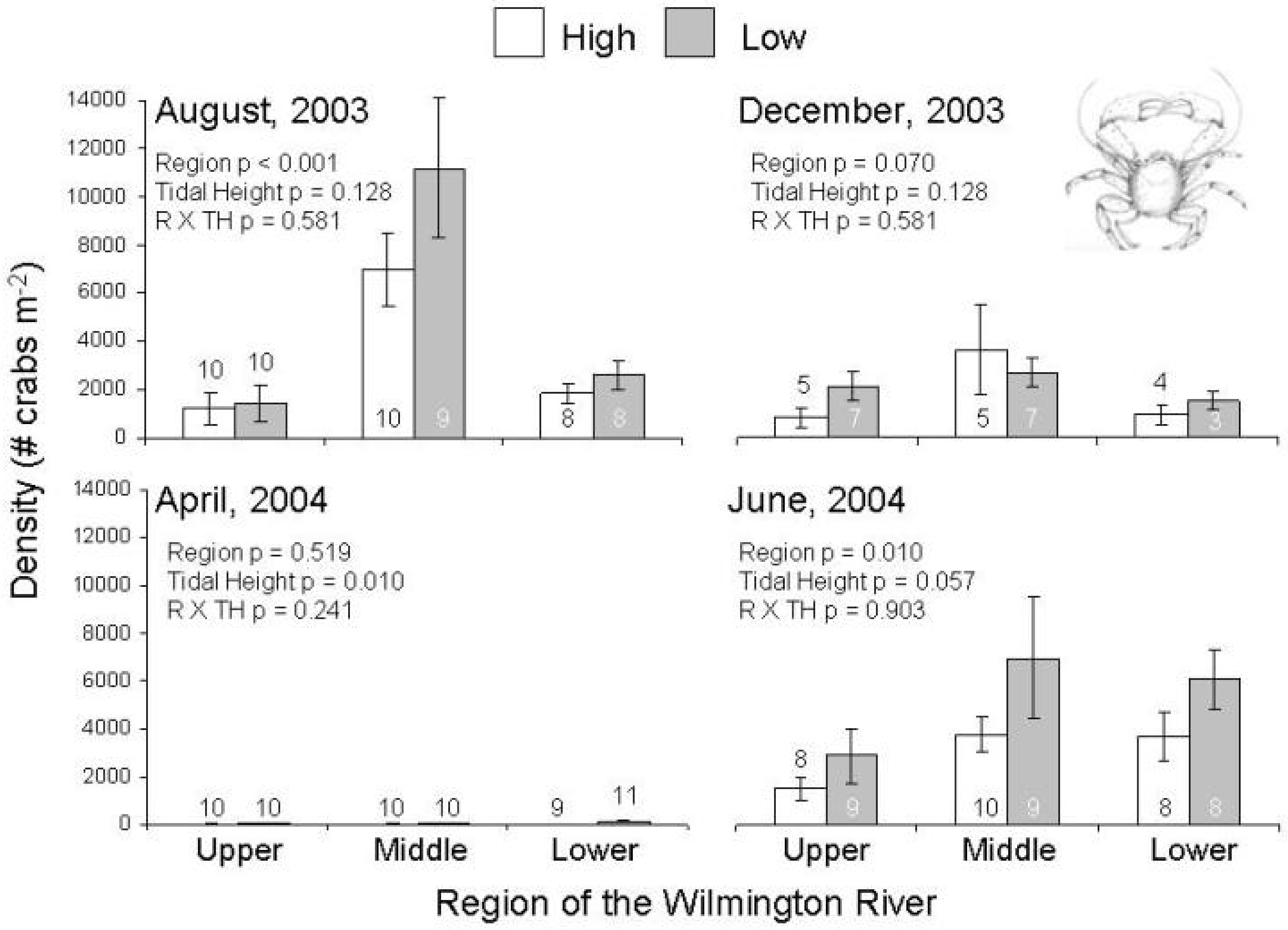


Figure 1.3. Densities of *Petrolisthes armatus* (mean ± SE, scaled to 1 m^2) in the Wilmington River across regions, tidal heights, and sampling periods. Analyses and symbols as in Figure 1.2.

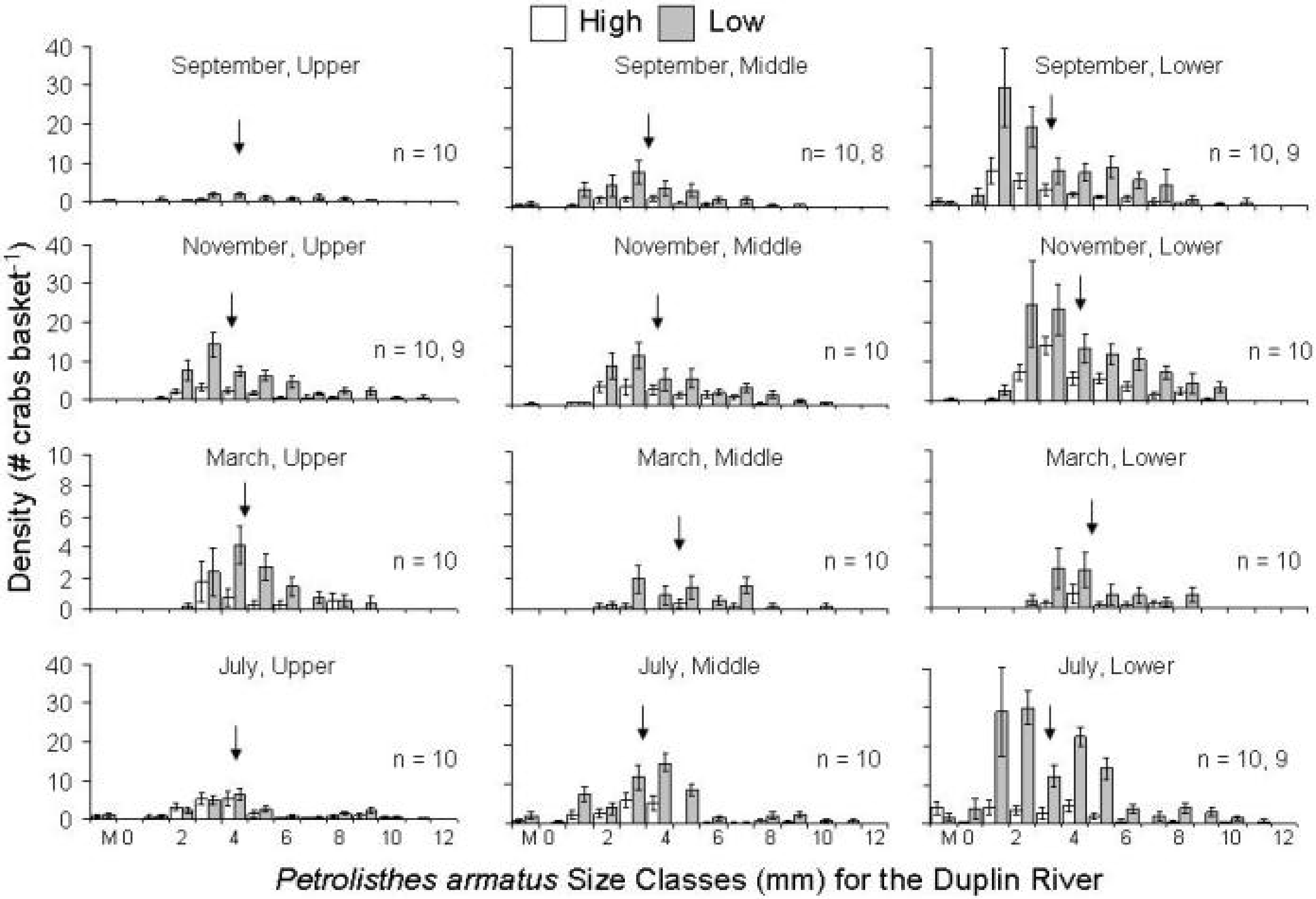


Figure 1.4. Densities of *Petrolisthes armatus* (mean ± SE basket^{-1}) by size class (M: Megalopae, 0: 0 to 0.9 mm CW, 2: 2 to 2.9 mm CW, 4: 4 to 4.9 mm CW, 6: 6 to 6.9 mm CW, 8: 8 to 8.9 mm CW, 10: 10 to 10.9 mm CW, 12: 12 to 12.9 mm CW) in the Duplin River across regions, tidal heights (white: high intertidal; grey: low intertidal), and sampling periods. Megalopae are newly settled crabs. Arrows indicate mean size for all crabs represented.

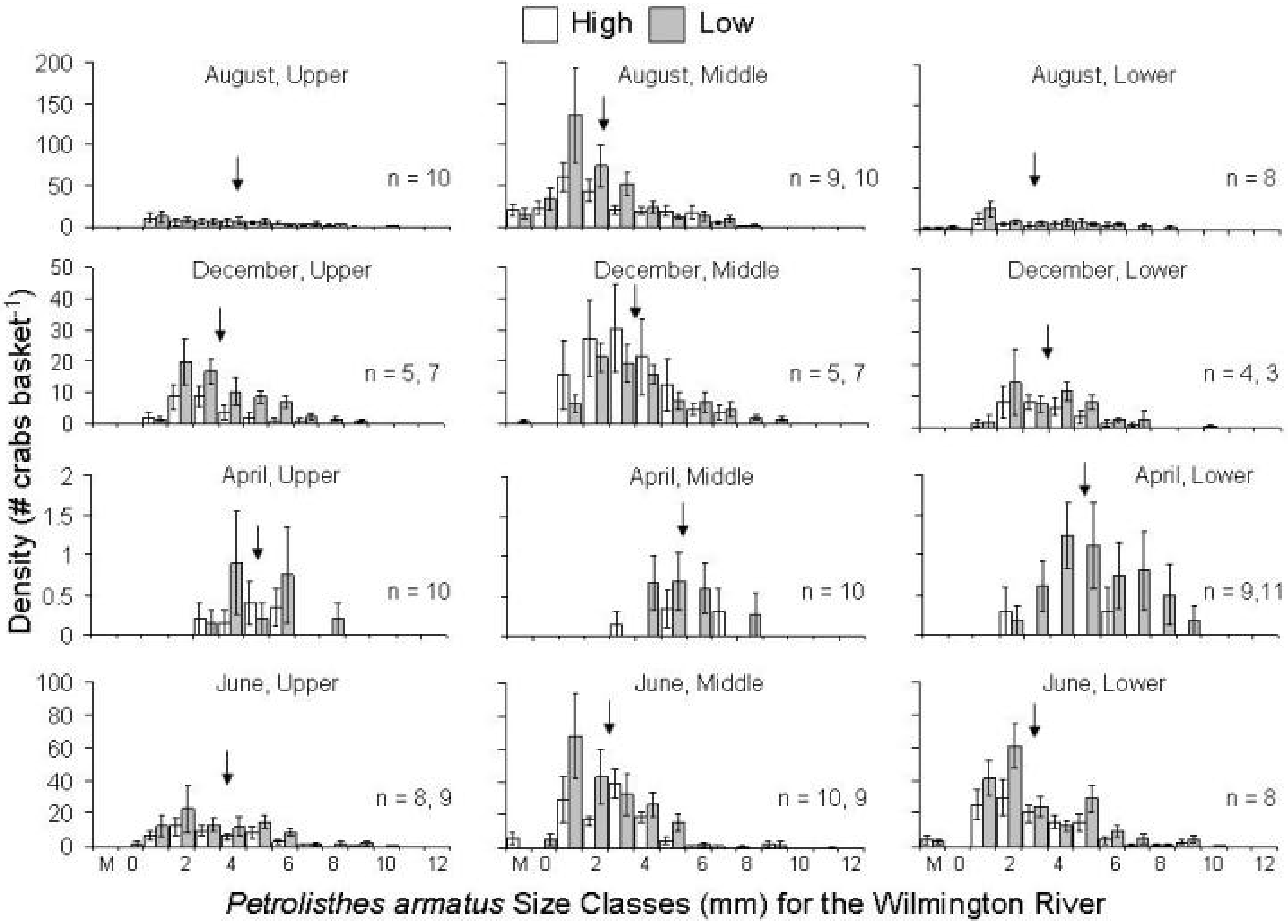


Figure 1.5. Densities of *Petrolisthes armatus* (mean ± SE basket^{-1}) by size class in the Wilmington River. Symbols as described in Figure 1.4.

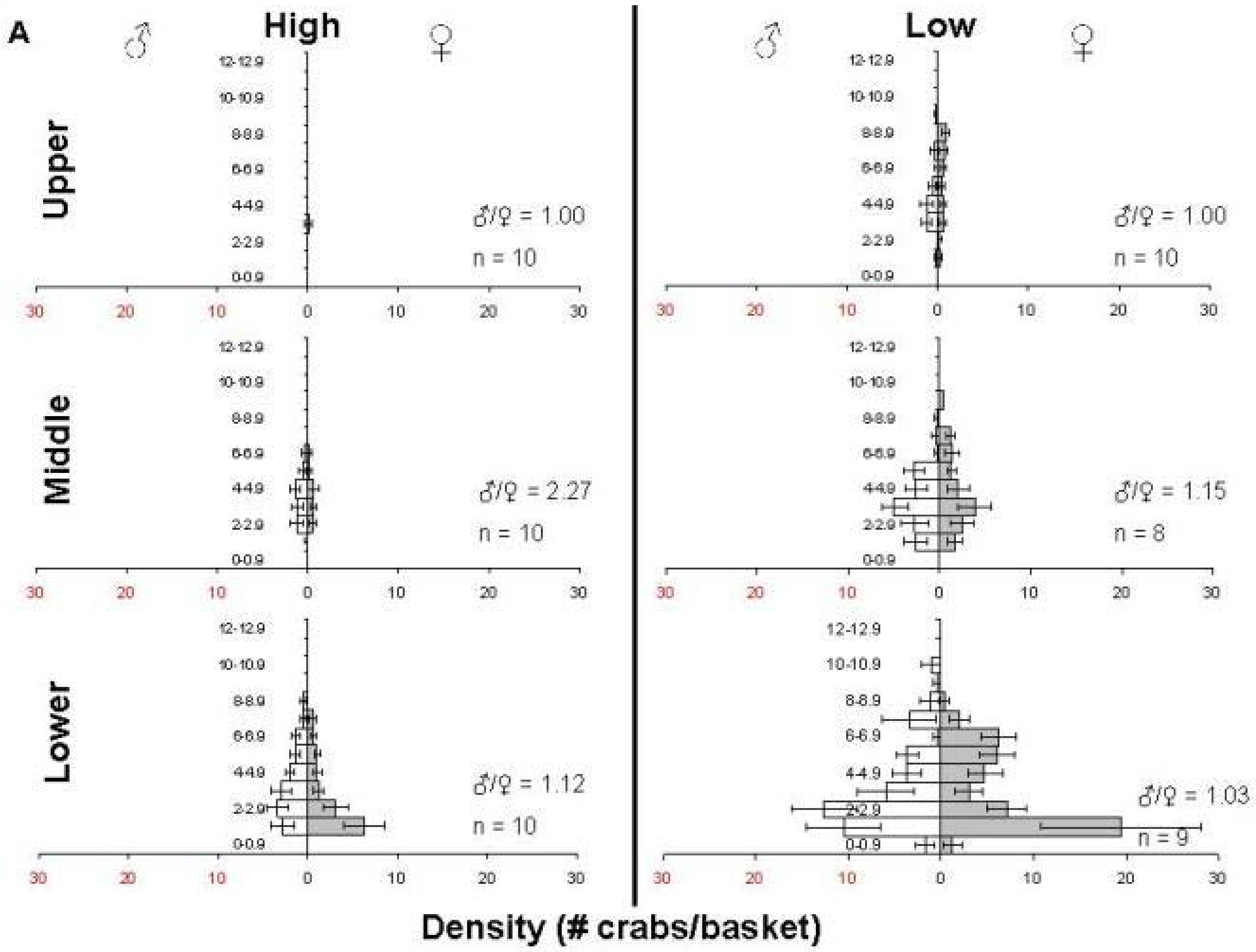
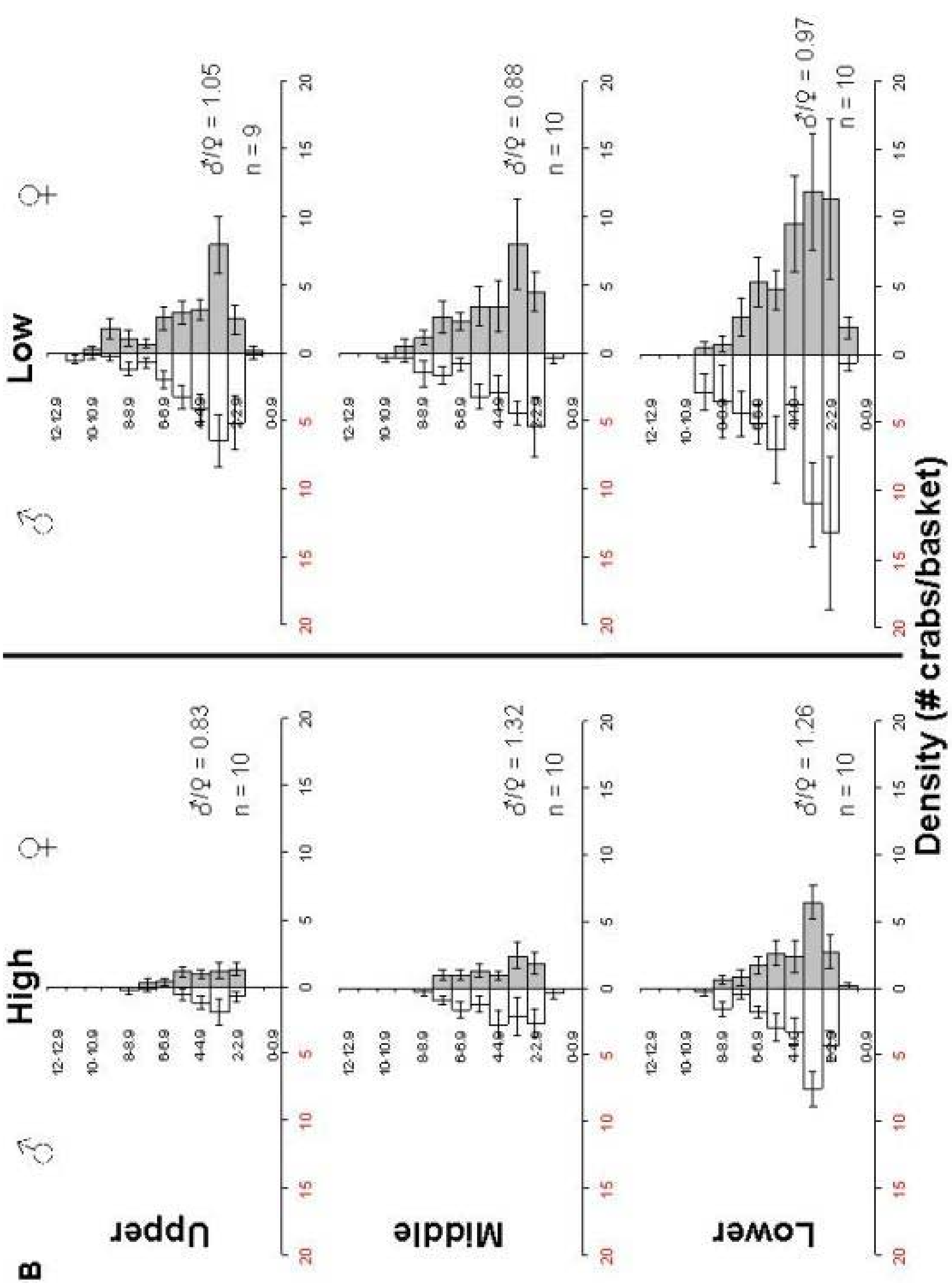
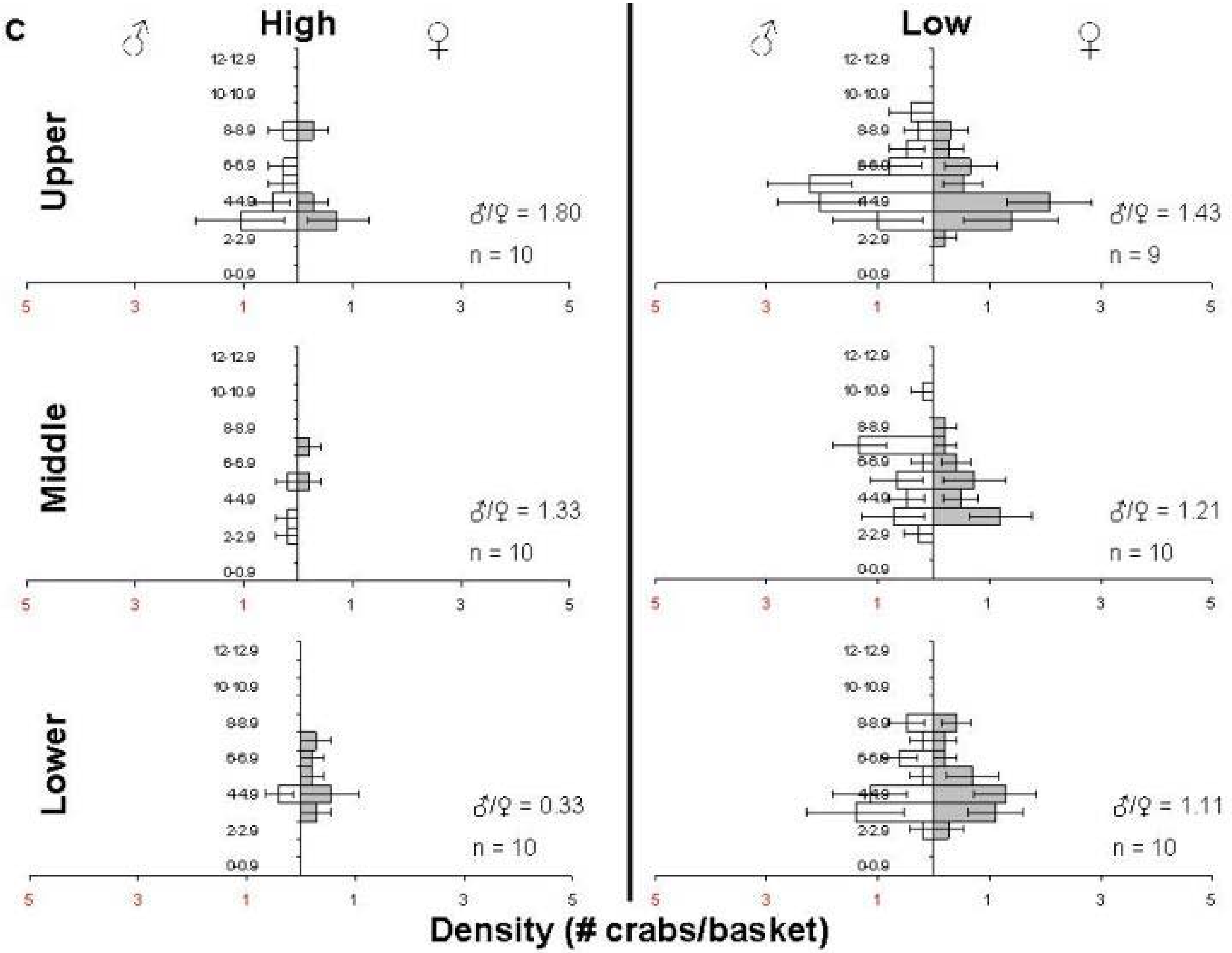
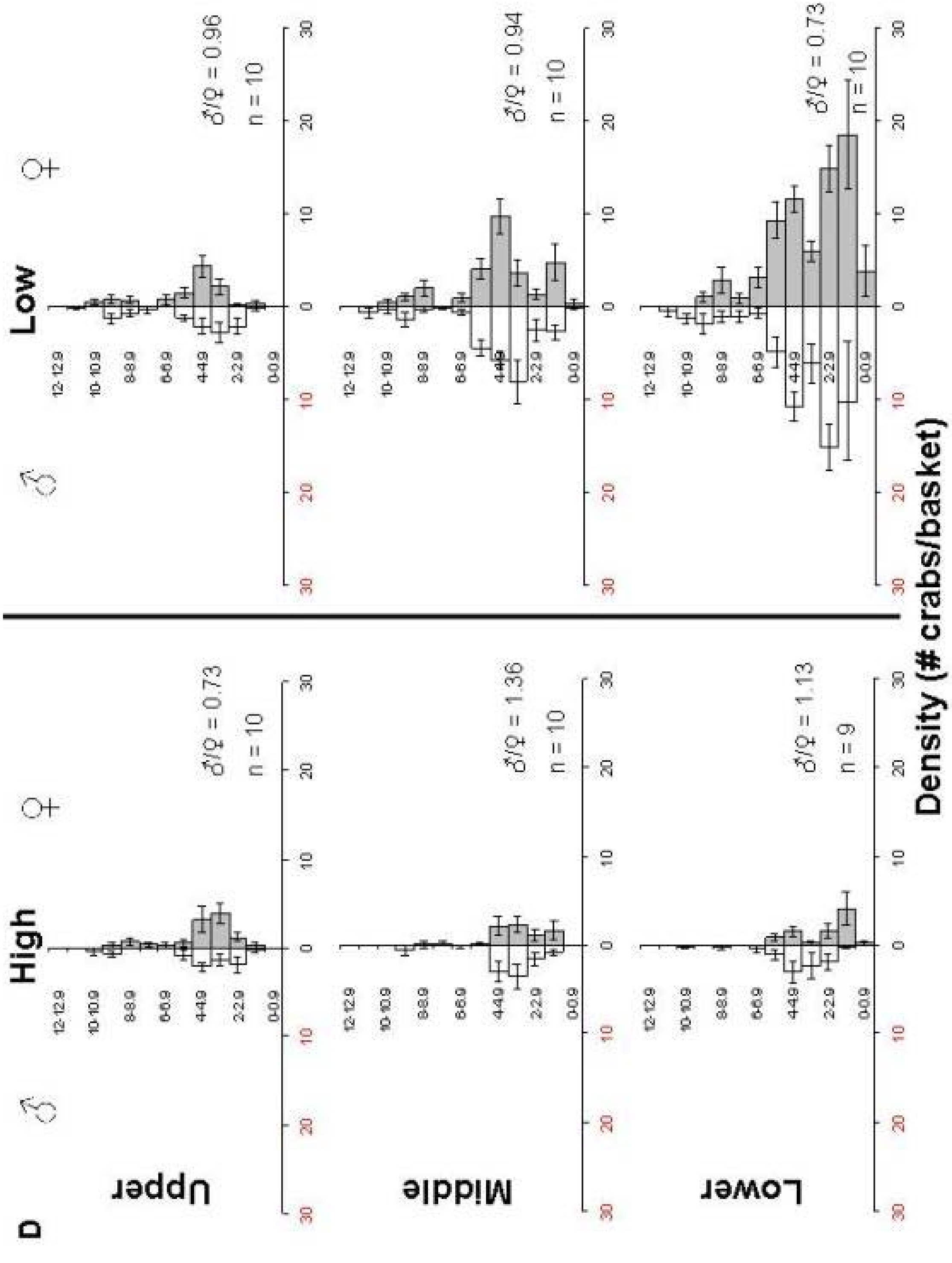


Figure 1.6. Densities of *Petrolisthes armatus* (mean ± SE basket^{-1}) by size class (mm CW) of male (white bars, ♂) and female (grey bars, ♀) crabs in the Duplin River across regions and tidal heights. Sampling periods are: (A) September 2003, (B) November 2003, (C) March 2004, and July 2004.


B
High
Low
Upper
Middle
Lower
♂
♀
♂/♀ = 0.83
n = 10
♂/♀ = 1.32
n = 10
♂/♀ = 1.26
n = 10
♂/♀ = 1.05
n = 9
♂/♀ = 0.88
n = 10
♂/♀ = 0.97
n = 10
12-12.9
10-10.9
8-8.9
6-6.9
4-4.9
2-2.9
0-0.9
20
15
10
5
0
5
10
15
20
Density (# crabs/basket)


c
High
Low
♂
♀
Upper
Middle
Lower
12-12.9
10-10.9
8-8.9
6-6.9
4-4.9
2-2.9
0-0.9
♂/♀ = 1.80
n = 10
♂/♀ = 1.43
n = 9
♂/♀ = 1.33
n = 10
♂/♀ = 1.21
n = 10
♂/♀ = 0.33
n = 10
♂/♀ = 1.11
n = 10
5
3
1
1
3
5
Density (# crabs/basket)


D
High
Low
Upper
Middle
Lower
♂
♀
12-12.9
10-10.9
8-8.9
6-6.9
4-4.9
2-2.9
0-0.9
♂/♀ = 0.73
n = 10
♂/♀ = 1.36
n = 10
♂/♀ = 1.13
n = 9
♂/♀ = 0.96
n = 10
♂/♀ = 0.94
n = 10
♂/♀ = 0.73
n = 10
30
20
10
0
Density (# crabs/basket)

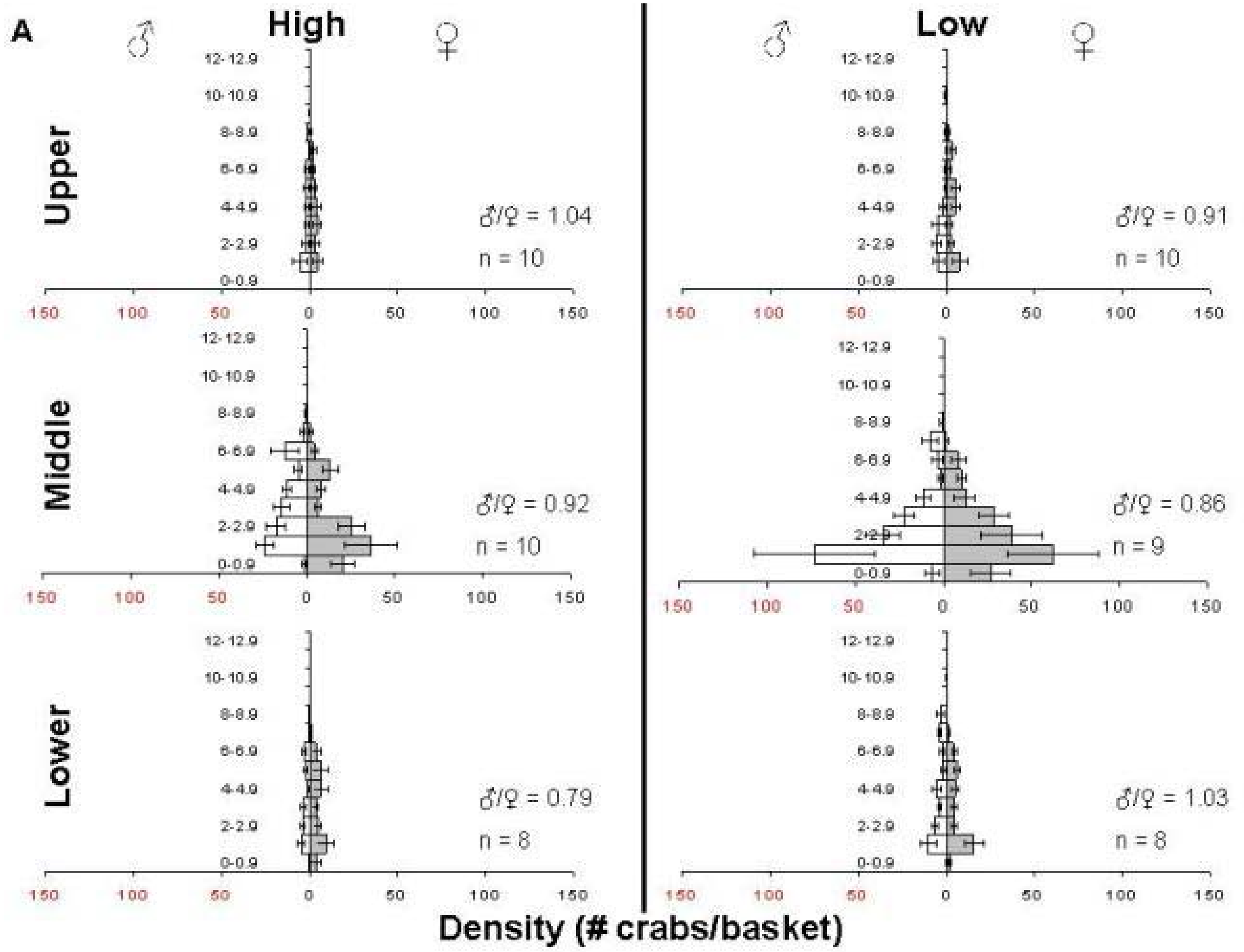
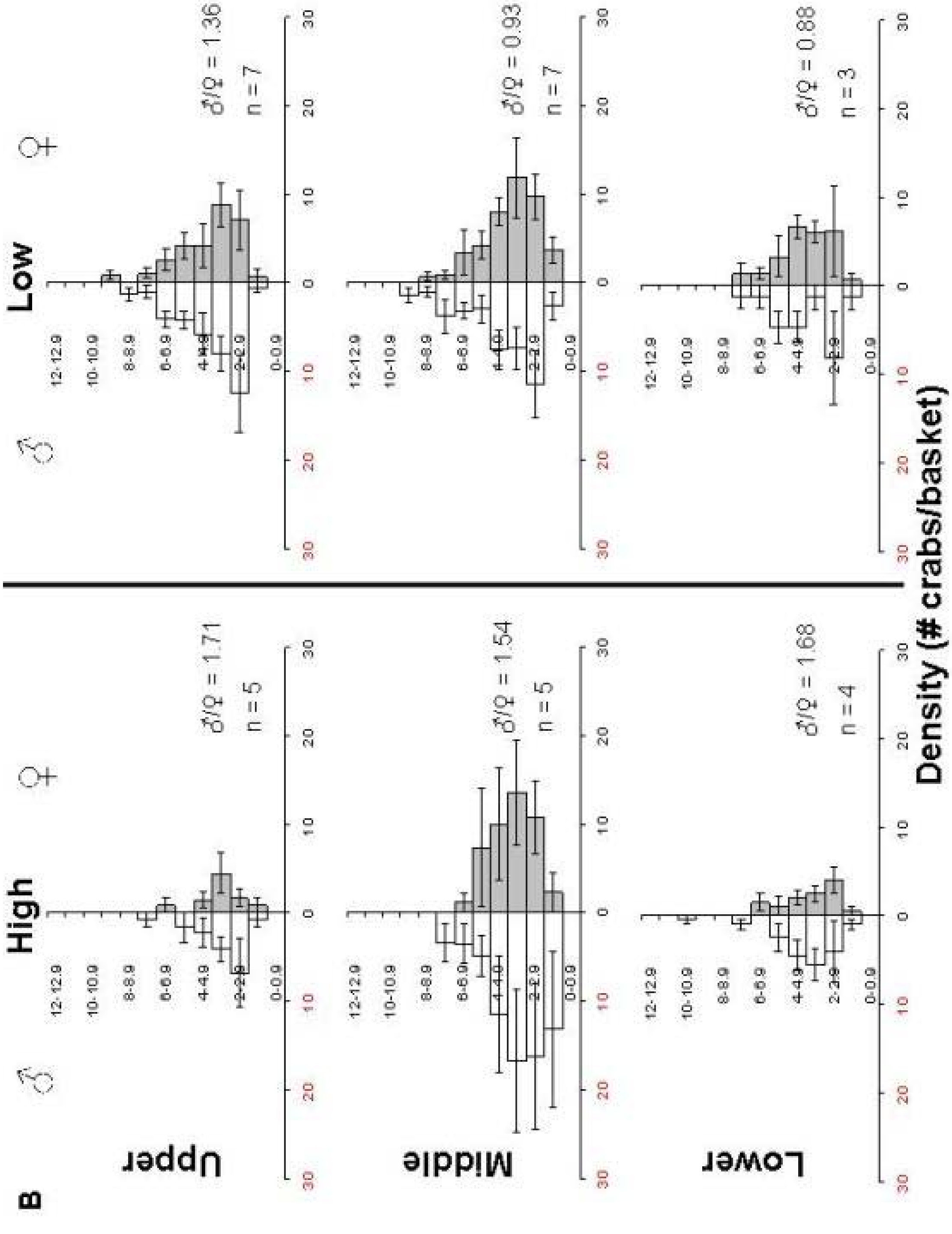
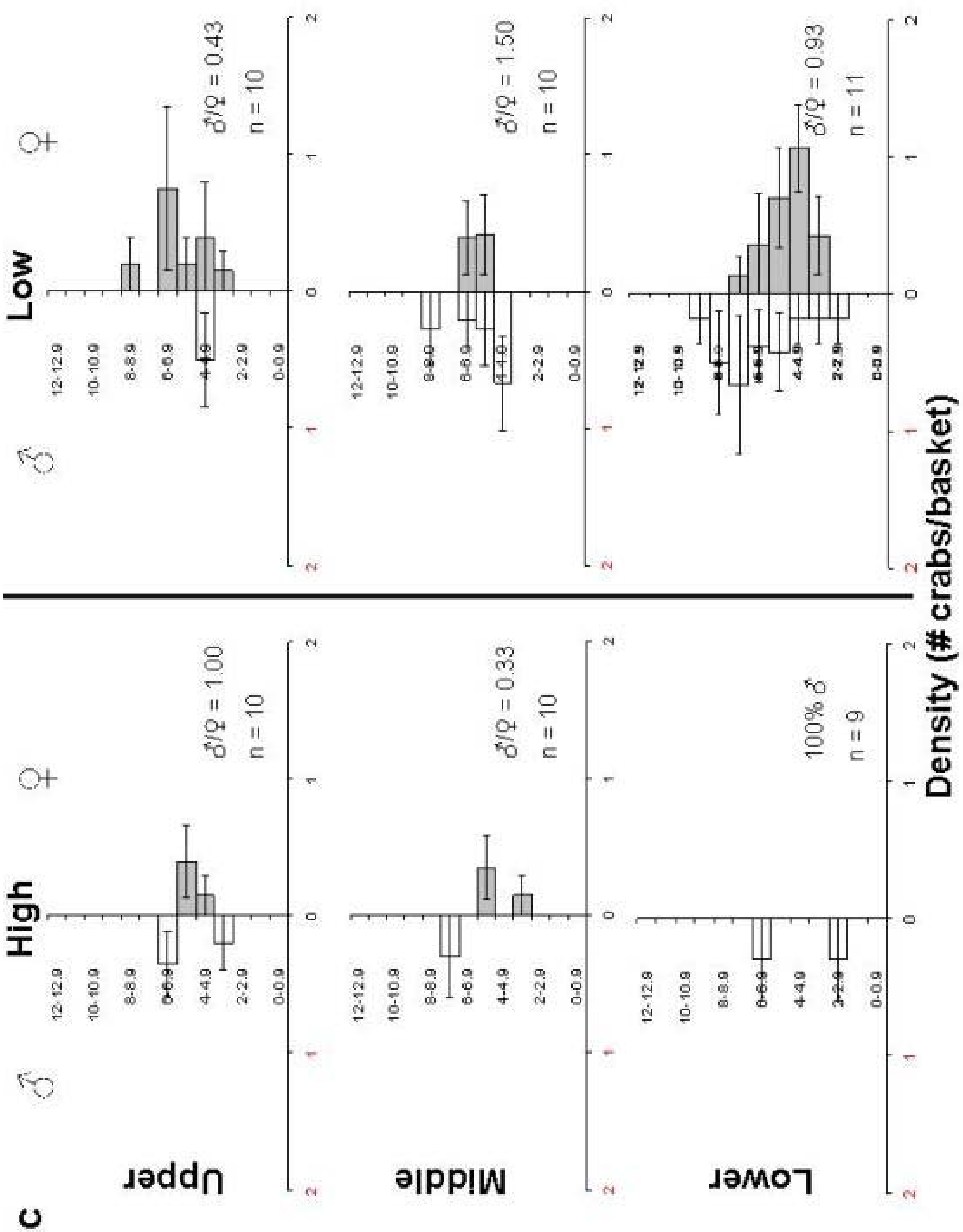
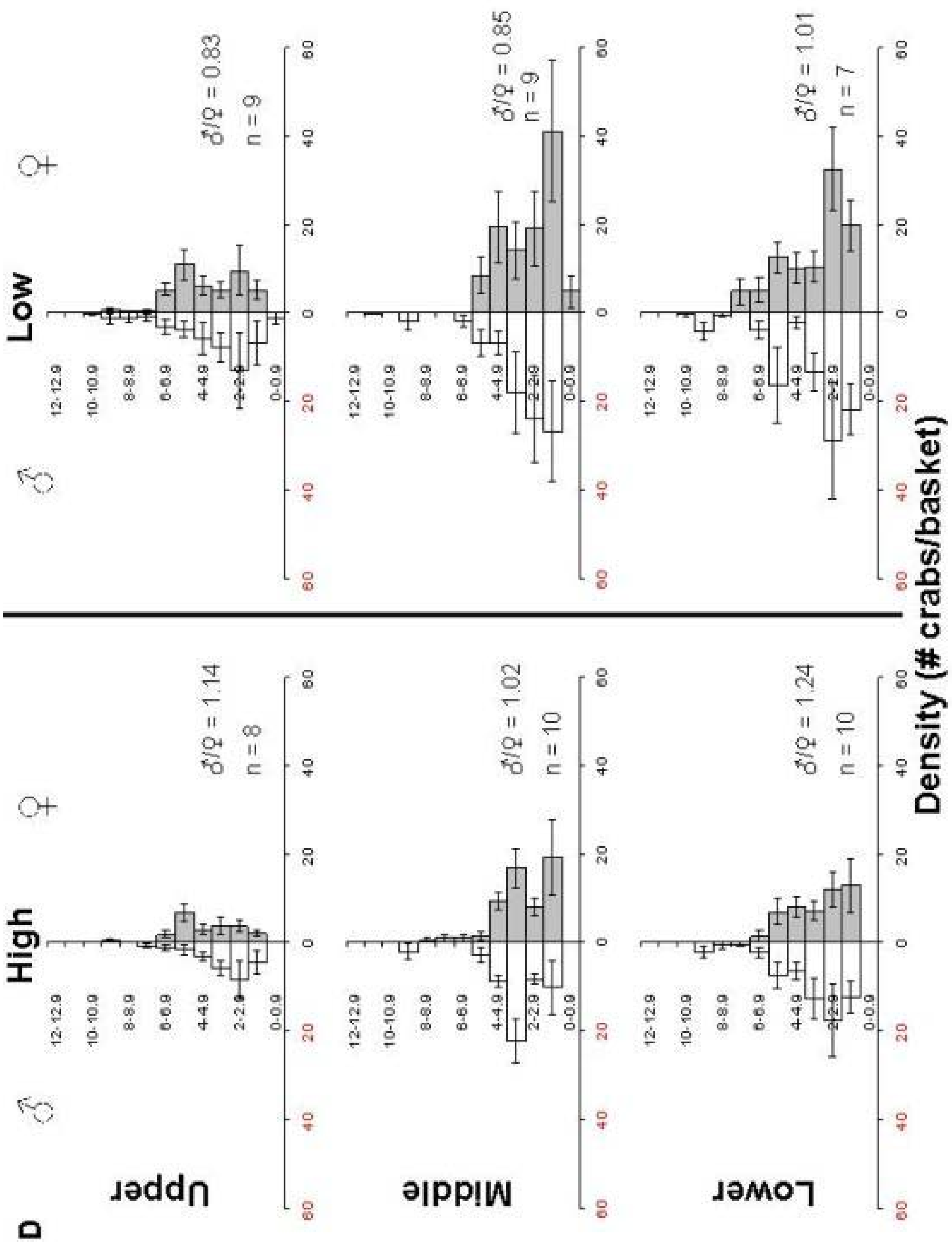


Figure 1.7. Densities of *Petrolisthes armatus* (mean ± SE basket^{-1}) by size class (mm CW) of male (white bars, ♂) and female (grey bars, ♀) crabs in the Wilmington River across regions and tidal heights. Sampling periods are: (A) August 2003, (B) December 2003, (C) April 2004, and June 2004.


B
High
Low
Upper
Middle
Lower
♂
♀
♂/♀ = 1.71
n = 5
♂/♀ = 1.54
n = 5
♂/♀ = 1.68
n = 4
♂/♀ = 1.36
n = 7
♂/♀ = 0.93
n = 7
♂/♀ = 0.88
n = 3
12-12.9
10-10.9
8-8.9
6-6.9
4-4.9
2-2.9
0-0.9
30
20
10
0
10
20
30
Density (# crabs/basket)


c
High
Low
Upper
Middle
Lower
♂
♀
♂
♀
12-12.9
10-10.9
8-8.9
6-6.9
4-4.9
2-2.9
0-0.9
♂/♀ = 1.00
n = 10
♂/♀ = 0.33
n = 10
100% ♂
n = 9
♂/♀ = 0.43
n = 10
♂/♀ = 1.50
n = 10
♂/♀ = 0.93
n = 11
2
1
0
1
2
Density (# crabs/basket)



D
High
Low
Upper
Middle
Lower
♂
♀
♂/♀ = 1.14
n = 8
♂/♀ = 1.02
n = 10
♂/♀ = 1.24
n = 10
♂/♀ = 0.83
n = 9
♂/♀ = 0.85
n = 9
♂/♀ = 1.01
n = 7
12-12.9
10-10.9
8-8.9
6-6.9
4-4.9
2-2.9
0-0.9
60
40
20
0
20
40
60
Density (# crabs/basket)

Table 1.1. Sex ratios (male:female) of *Petrolisthes armatus* >1 mm CW analyzed by χ^2 tests, *: $0.025 < p < 0.050$, **: $p < 0.010$.

Sampling Period	Duplin River		Wilmington River	
August - September 2003	Male:Female	Ratio	Male:Female	Ratio
Upper High	1:1	1.00	53:51	1.04
Upper Low	20:20	1.00	60:66	0.91
Middle High	25:11	2.27*	122:132	0.92
Middle Low	53:46	1.15	114:133	0.86
Lower High	76:68	1.12	88:112	0.79
Lower Low	113:110	1.03	115:112	1.03
November - December 2003				
Upper High	20:24	0.83	24:14	1.71
Upper Low	98:93	1.05	83:61	1.36
Middle High	49:37	1.32	60:39	1.54*
Middle High	82:93	0.88	97:104	0.93
Lower High	98:78	1.26	37:22	1.68
Lower Low	106:109	0.97	28:32	0.88
March - April 2004				
Upper High	9:5	1.80	3:3	1.00
Upper Low	30:21	1.43	3:7	0.43
Middle High	4:3	1.33	1:3	0.33
Middle Low	17:14	1.21	6:4	1.50
Lower High	2:6	0.33	2:0	100% ♂
Lower Low	21:19	1.11	14:15	0.93
June - July 2004				
Upper High	33:45	0.73	73:64	1.14
Upper Low	49:51	0.96	72:87	0.83
Middle High	49:36	1.36	142:139	1.02
Middle Low	109:116	0.94	112:132	0.85
Lower High	34:30	1.13	138:111	1.24
Lower Low	135:186	0.73**	100:99	1.01

A large proportion of mature females (≥3 mm CW) were gravid in the warm months of the year (Duplin River: ~40 to 85% in September and ~20 to 70% in July, Wilmington River: ~70 to 90% in August and ~25 to 75% in June). Females were rarely gravid during the colder months (Duplin River: ~0 to 10% in November and March, Wilmington River: ~0 to 15% in December and April) (Figures 1.8 and 1.9). The proportion of mature females that were gravid across all locations and seasons was 30.5% in the Duplin River and 48.1% in the Wilmington River.

In the Duplin River, a larger proportion of mature females were gravid in the low versus the high tidal habitats during all sampling periods when gravid females were present ($p \leq 0.012$ for November and July and nearly significant with $p = 0.065$ in September). Region had a significant effect in July ($p = 0.025$) when a larger proportion of females were gravid in the Upper versus Middle or Lower region of the estuary (Figure 1.8). In the Wilmington River estuary, tidal height never significantly affected the percentage of gravid females. In June, more females in the Upper estuary tended to be gravid ($p = 0.039$ for region; Figure 1.9). There was never a significant region x tidal height interaction for either estuary.

Biological Factors

The two most common native mud crabs within the oyster reefs we monitored, *Panopeus herbstii* and *Eurypanopeus depressus*, were abundant in both the low and high tidal areas and varied less than *Petrolisthes armatus* as a function of time period or location within the estuary (Figure 1.10 and 1.11). Throughout the year, mud crab densities were ~580 to 1610 crabs m^{-2} in the Duplin River and ~340 to 1530 crabs m^{-2} in the Wilmington River. While *P. armatus* were 10 to 100 times more common in warmer

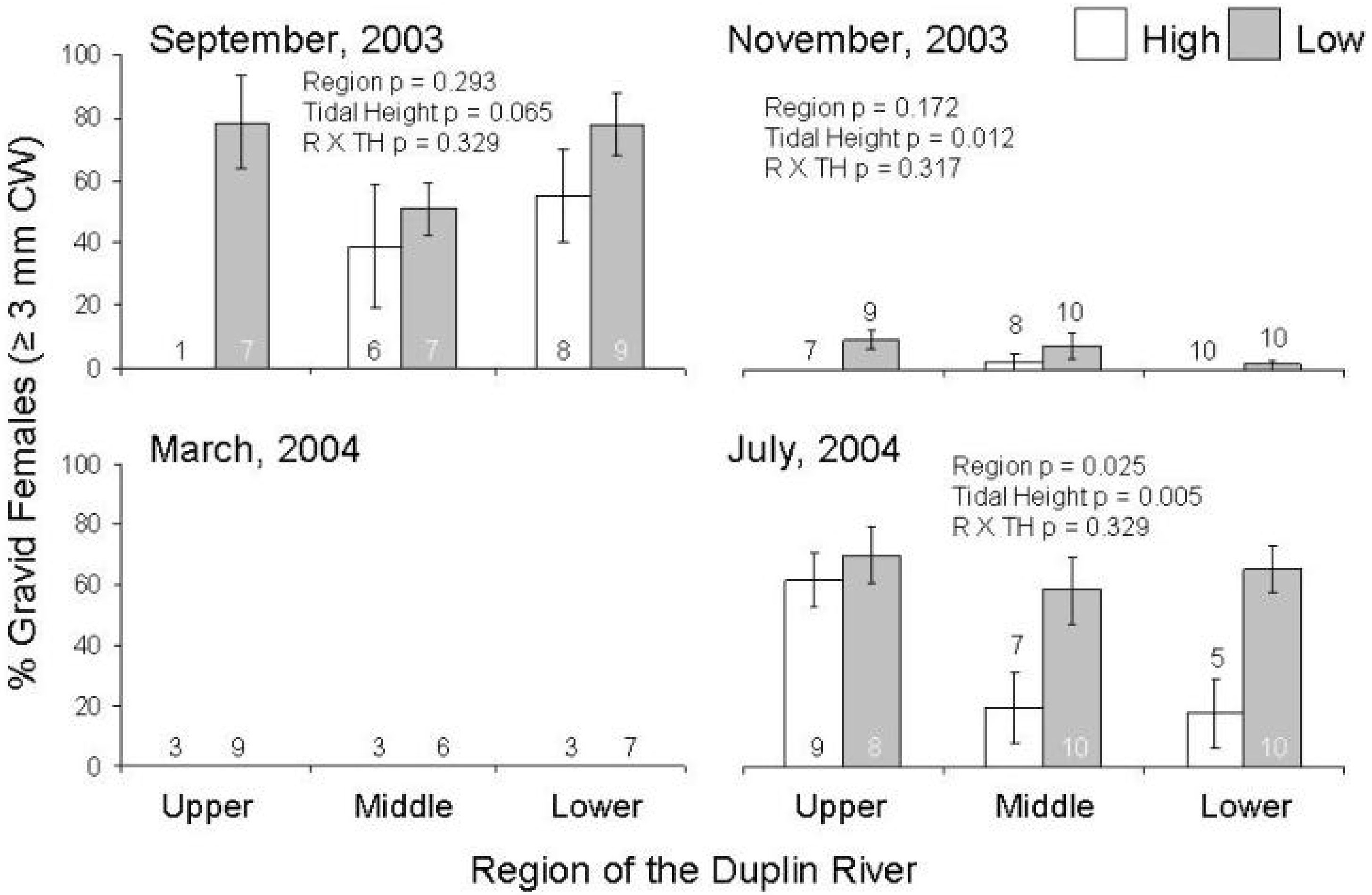


Figure 1.8. The proportion of mature *Petrolisthes armatus* females (≥ 3 mm CW; mean ± SE) that were gravid in the Duplin River across regions, tidal heights (white: high intertidal; grey: low intertidal), and sampling periods. Sampling size was commonly lower than for overall densities due to reproductively mature females being absent from some baskets. Numbers within or above bars indicate the number of replicate baskets sampled. P values derived from a two-way ANOVA following arcsine transformation of the data.

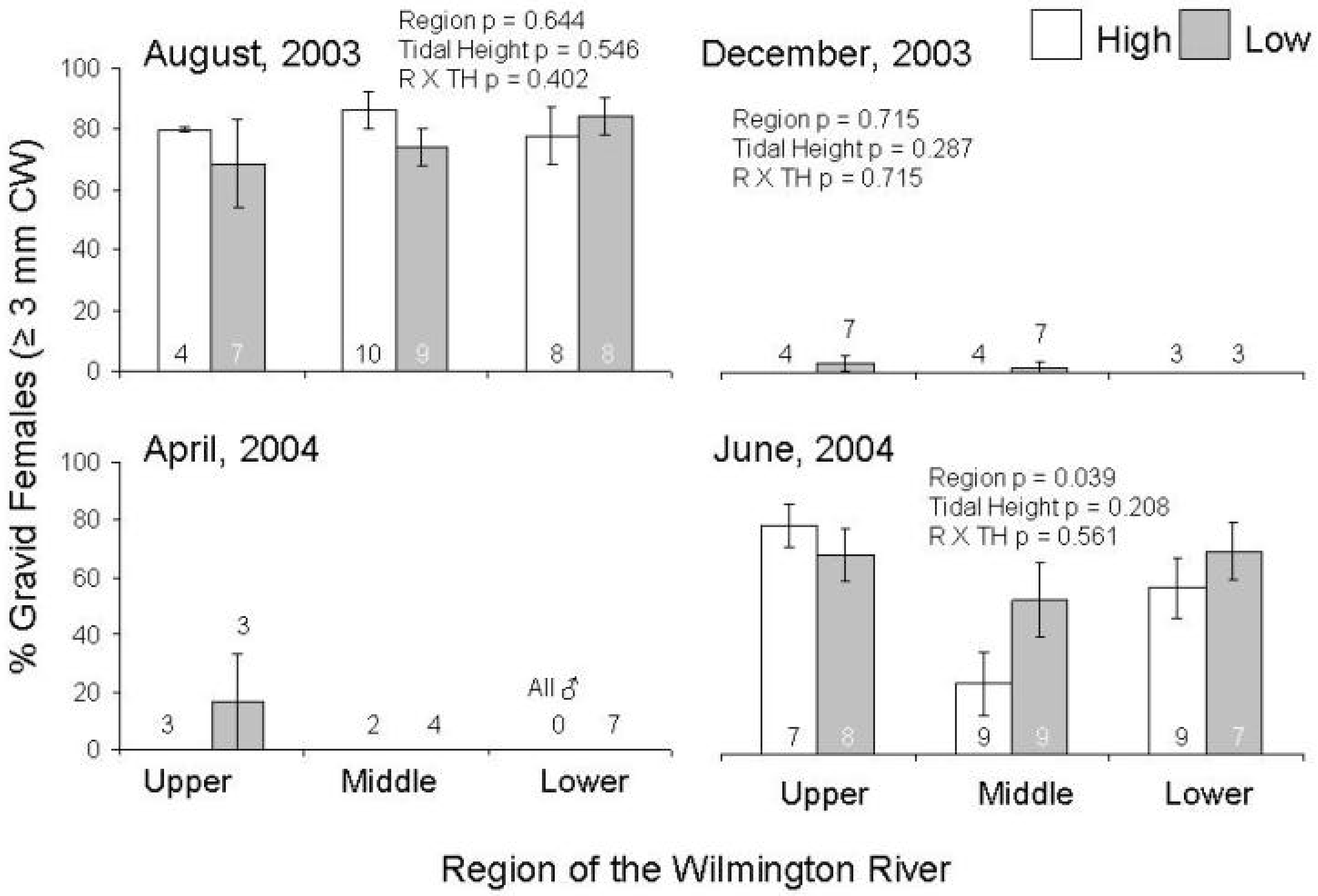


Figure 1.9. The proportion of mature *Petrolisthes armatus* females that were gravid in the Wilmington River. Statistical evaluations not calculated for April due to severe limits of sample size. Analyses, symbols, lowered sample size as described in Figure 1.8.

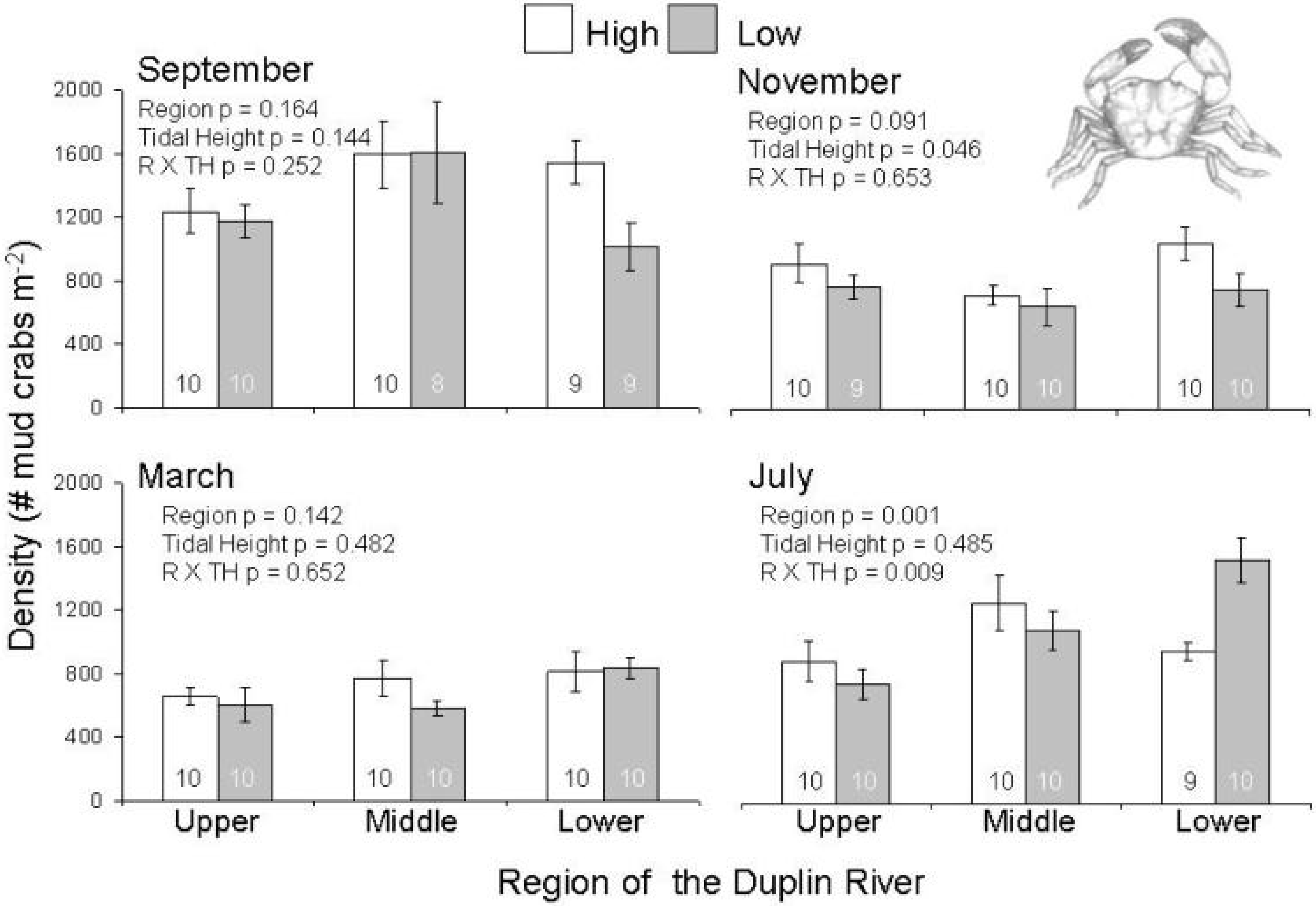


Figure 1.10. Densities of native mud crabs, *Panopeus herbstii* and *Eurypanopeus depressus* (mean ± SE, scaled to 1 m^2) in the Duplin River across regions, tidal heights, and sampling periods. Analyses and symbols as in Figure 1.2.

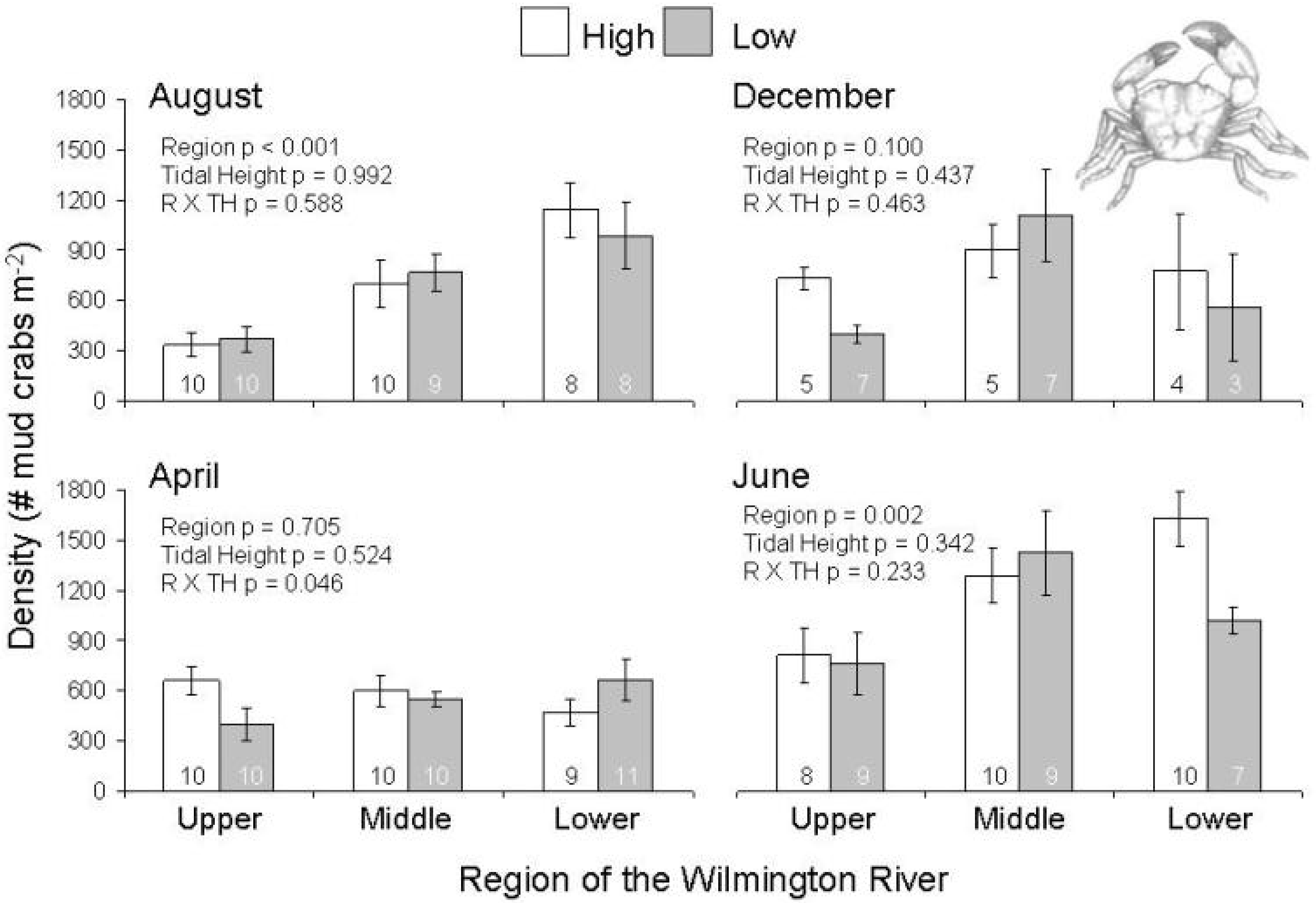


Figure 1.11. Densities of native mud crabs, *Panopeus herbstii* and *Eurypanopeus depressus* (mean ± SE, scaled to 1 m^2) in the Wilmington River across regions, tidal heights, and sampling periods. Analyses and symbols as in Figure 1.2.

months than in the early spring, mud crabs were only 1 to 3 times more common in warm periods. Mud crab densities were suppressed in the Upper Duplin River, compared to the Middle and Lower regions during July ($p = 0.001$), but not during other sampling periods. A significant tidal height effect occurred only in November ($p = 0.046$) when there were slightly more mud crabs in the high versus the low intertidal. There was a significant region x tidal height effect in July ($p = 0.009$) with the Middle and Upper regions having more mud crabs in the high intertidal and the Lower region having more crabs in the low intertidal. For the Wilmington River, a similar regional effect on mud crab densities occurred in August, June ($p \leq 0.002$), and nearly in December ($p = 0.100$) with more mud crabs in the Middle and Lower regions than in the Upper region. There was no significant effect of tidal height or region x tidal height on mud crab densities and distribution in the Wilmington River estuary.

Correlations of mud crab density basket^{-1} with *Petrolisthes armatus* density basket^{-1} across each region, tidal height, and time period, indicated several significant positive relationships but no significant negative relationships (Table 1.2). Of the 24 contrasts in each estuary system, five (Wilmington River) or six (Duplin River) were significantly positive ($p < 0.050$), with all but one of these occurring during the warmer periods of the year (June-July and August-September). No significant negative correlations occurred at any location or time.

Discussion

Invasive species pose serious threats to the function and maintenance of native communities (Carlton and Geller 1993), with recent rates of invasion exceeding all

Table 1.2. Correlations (Fisher's r to z) of native mud crabs (*Panopeus herbstii* and *Eurypanopeus depressus*) versus exotic porcelain crabs (*Petrolisthes armatus*) for the Duplin River estuary and the Wilmington River estuary. Boxed p values indicate significant correlations ($p < 0.050$).

Sampling Period	Duplin River				Wilmington River			
August - September 2003	n	Correlation	z	p	n	Correlation	z	p
Upper High	10	0.079	0.210	0.834	10	0.780	2.769	$\boxed{0.006}$
Upper Low	10	0.269	0.731	0.465	10	0.791	2.842	$\boxed{0.005}$
Middle High	10	0.601	1.838	0.066	10	-0.100	-0.267	0.790
Middle Low	8	0.780	2.339	$\boxed{0.019}$	9	0.164	0.406	0.685
Lower High	9	0.837	2.966	$\boxed{0.003}$	8	0.333	0.774	0.439
Lower Low	9	0.294	0.742	0.458	8	0.712	1.992	$\boxed{0.046}$
November - December 2003								
Upper High	10	0.208	0.557	0.577	5	0.384	0.572	0.568
Upper Low	9	-0.473	-1.260	0.208	7	0.276	0.567	0.571
Middle High	10	0.116	0.309	0.758	5	0.433	0.655	0.513
Middle High	10	0.366	1.015	0.310	7	0.157	0.316	0.752
Lower High	10	-0.247	-0.667	0.505	4	0.638	0.754	0.451
Lower Low	10	0.760	2.636	$\boxed{0.008}$	3	0.494	0.000	>0.999
March - April 2004								
Upper High	10	-0.464	-1.330	0.184	10	-0.423	-1.193	0.233
Upper Low	10	0.306	0.836	0.403	10	0.273	0.742	0.458
Middle High	10	-0.574	-1.728	0.084	10	-0.095	-0.253	0.800
Middle Low	10	-0.136	-0.363	0.716	10	0.467	1.340	0.180
Lower High	10	-0.353	-0.975	0.329	9	0.342	0.872	0.383
Lower Low	10	0.057	0.150	0.880	11	-0.058	-0.164	0.870
June - July 2004								
Upper High	10	0.736	2.492	$\boxed{0.013}$	8	0.717	2.016	$\boxed{0.044}$
Upper Low	10	0.212	0.569	0.569	9	0.355	0.910	0.363
Middle High	10	0.919	4.187	$\boxed{<0.001}$	10	0.244	0.659	0.510
Middle Low	10	0.157	0.419	0.675	9	0.741	2.335	$\boxed{0.020}$
Lower High	9	0.470	1.251	0.211	10	0.302	0.826	0.409
Lower Low	10	0.826	3.111	$\boxed{0.002}$	7	-0.109	-0.219	0.827

known historic levels due to human activities circumventing or breaking down physical and biological barriers to dispersal (Ruiz *et al.* 1997). These invasions have fundamentally changed the community composition of areas such as the San Francisco and the Chesapeake Bays, and they continue to threaten native communities of many coastal marine systems (Ruiz *et al.* 1999). Successful invasions of marine communities have been studied far less than those in terrestrial and freshwater environments but are of such a magnitude that they may be leading to profound ecological changes in the world's oceans (Grosholz 2002).

Marine invaders are not limited to specific taxa or functional groups. Instead, they range from plants such as the salt marsh cordgrass (Ayres *et al.* 2004) and seaweeds (Meinesz and Hesse 1991, Levin *et al.* 2002) to tunicates (Stachowicz *et al.* 1999), clams (Carlton *et al.* 1990), snails (Carlton 1999), and jellyfish (Vindogradov *et al.* 1996). Crabs, in particular, have had wide-ranging impacts on native organisms and communities. Introduced crabs affect the induction of morphological defenses (Trussell and Nicklin 2002), trait-mediated indirect effects on prey (Trussell *et al.* 2002), the evolution of defenses (Vermeij *et al.* 1981), and even the success of bivalve fisheries (Walton *et al.* 2002).

The exotic crab *Petrolisthes armatus* has established in tremendous densities over broad spatial scales of coastal Georgia suggesting that it could significantly impact oyster reef communities throughout the South Atlantic Bight. *P. armatus* was the most abundant crab in oyster reefs at both our northern and more southern sites. At some locations and times, mean densities reached 11,200 crabs m^{-2}, which is 37 times greater than the highest density ever documented through trapping studies performed in the crab's historic range (Oliveira and Masunari 1995). *P. armatus* persisted throughout the year, colonizing, growing, and reproducing rapidly during the warmer months. The highest mean densities of *P. armatus* found at any site during monitoring in the warm months exceeded by ~2 to 10 times the highest combined densities of the two most common native crabs normally found on Georgian oyster reefs, *Panopeus herbstii* and *Eurypanopeus depressus* (compare Figures 1.2 and 1.3 with 1.10 and 1.11). High densities of *P. armatus* are not only found on the Georgia coast; the South Carolina Department of Natural Resources has also reported densities of thousands m^{-2} (http://water.dnr.state.sc.us/marine/mrri/shellfish/petro.htm).

In Georgian estuaries, *Petrolisthes armatus* was found at mean densities of several thousands m^{-2} in warmer portions of the year with localized patches of up to 1036 crabs 0.03 m^{-2} (= 31,390 crabs m^{-2}). Invasive crab densities were generally higher in Middle and Lower regions of the estuaries than in Upper regions (Figures 1.2 and 1.3), and there were more crabs in the low versus the high intertidal during the warmer months. During colder months, crab densities declined by 64 to 95% in the Duplin River and by 89 to 99.7% in the Wilmington River across all region x tidal height combinations compared to maximal mean densities in the previous monitoring time period. Distributions of crab size classes indicated that local populations of adult porcelain crabs persisted throughout the winter for all region x tidal height combinations in both estuaries. These numbers included both males and females of reproductive size, leaving a potentially viable local population year-round. Observations of larval development in the laboratory have indicated that *P. armatus* reach their final molt before settlement within a relatively short period of time (~15 to 17 days, A.L. Hollebone *personal* *observation*). Thus, these two factors suggest that increases in densities in the warm season may not need to rely on propagule input from more southerly populations in the historic range (e.g., Florida).

Tidal Distribution

Spatial and temporal patterns of density and reproduction could be affected by physiological or biological constraints on the crabs. Previous work with the porcelain crabs *Petrolisthes cinctipes* and *Petrolisthes eriomerus* in Washington, U.S.A. and British Columbia, Canada, showed that both biotic (competition and predation) and abiotic (thermal tolerance and substrate composition) factors affected their distribution in the intertidal (Jensen and Armstrong 1991). Both species were susceptible to desiccation, with smaller individuals being at greater risk, and *P. eriomerus* was particularly susceptible to thermal stress during low tides. The higher densities of *P. armatus* in the low intertidal at the sites we monitored, particularly during the warmer months of the year, could be explained by the greater desiccation exposure and increased temperatures at higher elevations. Extreme low tides (the times when we concentrated our sampling) are not sudden events; tides drop increasingly lower for several days prior to the lowest low tide. This may result in crab mortality or the crabs moving down the tidal gradient as the tides progress over time, possibly biasing our tidal height data for greater numbers in the lower intertidal.

Competition with local crabs appears unlikely to regulate tidal height distributions. The abundance of native crabs (Figures 1.10 and 1.11) between tidal heights was not the inverse of *P. armatus* patterns (Figures 1.2 and 1.3) and there were no negative correlations between *P. armatus* and mud crab abundance (Table 1.2).

Additionally, *P. armatus* is a filter-feeder while mud crabs are predators or omnivores. Mud crabs will eat *P. armatus* in laboratory assays (Chapter 3), but, again, the lack of negative correlations (Table 1.2) does not suggest that mud crabs are displacing *P. armatus* into the lower intertidal.

Regional Distribution

Regional patterns of *Petrolisthes armatus* distribution might be affected by the thermal environment of the estuary, which is strongly influenced by hydrography (Bahr and Lanier 1981). Typically, temperature does not show a pronounced vertical gradient in the water column in the Lower regions of the estuary but is subject to daily fluctuations (Bahr and Lanier 1981). During the warmer months of the year, the cooler ocean water temperatures have a moderating effect on the Lower estuary, whereas water temperatures of the marsh creeks and Upper estuary are higher due to the heating of dark sediments during low tides (Bahr and Lanier 1981). Data collected in 2003 (during a portion of the monitoring program) from the Sapelo Island National Estuarine Research Reserve hydrographic monitoring stations (http://gce-lter.marsci.uga.edu/portal/ sinerr_hydro) at Sapelo Island, Georgia (Upper site: Flume Dock; Lower Site: Marsh Landing) support Bahr and Lanier's (1981) generalizations. From June to September 2003, the Upper region of the Duplin River estuary was, in general, warmer (~25 to 32.5ºC) than the Lower region (~25 to 30ºC). By November and December 2003, water temperatures in the Upper region were similar to (~8 to 25ºC) or colder than, those in the Lower region (~10 to 25ºC).

In its native range, *Petrolisthes armatus* thrives under thermal conditions within the range of Spring-Autumn temperatures of the South Atlantic Bight (16 to 29ºC at Farol

Island, Paraná, Brazil [Oliveira and Masunari 1995] and 20.8 to 28.7ºC at Paranapuã Beach, São Vicente, Brazil [Micheletti-Flores and Negreiros-Fransozo 1999]). In Brazil, the highest densities of *P. armatus* occurred during the summer when mean surface water temperatures were above 25ºC (Oliveira and Masunari 1995). Upper thermal tolerance limits of *Petrolisthes spp.* have been shown to be positively correlated with surface water temperatures and with maximal temperatures of microhabitats where they occur (Stillman and Somero 2000). In laboratory studies *P. armatus* has an upper thermal tolerance of 40.5ºC (Stillman and Somero 2000). Therefore, *P. armatus* can likely survive increased temperatures as a result of low tide exposure as long as microhabitats remain below this upper thermal limit.

Water temperatures during the winter in Georgia are well below the minimal 16ºC temperature recorded in the crab's native range (Oliveira and Masunari 1995). Seasonally low temperatures in Georgia may exceed the lower thermal limit of crabs in many habitats, contributing to the drastic decrease in densities we observed during colder months. This effect was documented for blue crabs, *Callinectes sapidus*, at Sapelo Island when water temperatures fell below 15ºC (Fitz and Weigert 1991). Seasonality has also been shown to affect the strata habitation of mud crabs (*Panopeus herbstii* and *Eurypanopeus depressus*) in oyster reefs of North Carolina (Meyer 1994). During warmer months crabs more frequently inhabited the cluster stratum of the oyster reefs, whereas in the colder months they inhabited the subsurface stratum.

Alterations in salinity seem less likely to be determining the distribution or abundance of *Petrolisthes armatus* because in the crab's native range it lives in salinities of 6.7 to 31.5 ‰ (Oliveira and Masunari 1995), which brackets what it would experience at our monitoring sites. Salinities in the Duplin River ranged from 13 to 30 ‰ (see http://gce-lter.marsci.uga.edu/portal/sinerr_hydro), whereas those in the portions of the Wilmington River we monitored ranged from 15 to 31 ‰ (Coastal Georgia Adopt-A-Wetland *unpublished data*) during the time periods we monitored.

Reproduction

The dramatic seasonal change in densities (e.g., from ~60 crabs m^{-2} in the Middle region of the Wilmington River in April 2004 to ~6000 crabs m^{-2} in June 2004), the considerable densities of newly recruited crabs in the warmer months (Figures 1.4 and 1.5), the ability of females to reproduce at sizes as small as 3 mm CW, the high percentage of egg-bearing females (often 50 to 80%, Figures 1.8 and 1.9), and the high densities of *Petrolisthes armatus* zooea we noted in plankton tows during the summers of 2003 and 2005 (A.L. Hollebone and W. Morrison *personal observation*) all attest to the remarkable ability of the crab to rapidly increase from tens or hundreds of crabs m^{-2} in the winter to thousands and tens of thousands of crabs m^{-2} in the summer.

Within the native range of *Petrolisthes armatus* at Farol Island, Brazil, there were about 1.05 males for each female over an entire year (Oliveira and Masunari 1995). Our data were consistent with this ratio in that across all time periods, regions, and tidal heights, *P. armatus* in Georgia maintained a male:female ratio of about 1:1 (Figures 1.6 and 1.7; summarized in Table 1.1).

At the Duplin River sites, 20 to 85% of adult female crabs were ovigerous during the spring and summer; for the Wilmington River sites, 25 to 90% of adult females were ovigerous. At Farol Island, Brazil, Oliveira and Masunari (1995) found that ~48% of all females ≥4 mm CW (or ~34% of all females ≥3 mm CW) were gravid (data combined for all seasons). This figure falls within the range seen in both estuaries we studied as well as an overall proportion calculated for all females ≥3 mm CW at all locations throughout the entire year (Duplin River: 30%; Wilmington River: 48%). Thus, invasion of a more temperate habitat has not constrained reproduction by *P. armatus*. Additionally, Oliveira and Masunari (1995) documented that females in the historic range matured at 4 to 4.9 mm CW, whereas we found mature females at 3 to 3.9 mm CW. Crabs in the new range become sexually mature at a smaller size (potentially increasing the number of broods year^{-1} or breeding lifetime^{-1}), maximal adult densities are commonly 10 to 37 times those seen in Brazil, but the percentage of females that are gravid between new and old range does not differ. Given these contrasts, population fecundity in the invaded range should exceed that in the historic range by at least an order of magnitude. It appears that *P. armatus* is more than capable of sustaining its populations locally without relying on seasonal inputs of propagules from more tropical regions.

Biological Factors

Introduced species often have large impacts on assemblages of native species via predation and competition for resources (e.g., Nichols *et al.* 1990, Lodge and Kershner 1994, MacIsaac 1996), and pre-existing species may repel invasions via the same interactions (e.g., Stachowicz *et al.* 1999, Parker and Hay 2005). Although this study did not experimentally test the impacts of competition and predation on community structure, we correlatively addressed this possibility by evaluating how crab density for both native mud crabs and invasive porcelain crabs covaried over space and time. We saw significant positive relationships in 23% of the 48 possible correlations of mud and porcelain crabs in both estuaries across all region-tidal height combinations and seasons.

Significant negative relationships never occurred. Positive correlations occurred during warmer months (August-September 2003, June-July 2004) when the densities of *Petrolisthes armatus* were increasing dramatically and densities of mud crabs were at their peak. Thus, crabs tended to peak at similar times and places. These are correlations rather than experiments showing cause and effect, but they lend no support to the hypothesis that the invasive crab is negatively affecting the native crabs with which it most closely associates. Other investigations (Chapter 3) show that mud crabs readily consume *P. armatus* in a laboratory setting, thus the positive correlations could occur because mud crabs move within oyster reefs to areas of high *P. armatus* densities to feed. Alternatively, both native and non-native crabs may respond similarly to physical and biological factors in the environment.

Summary

Since its first documentation on oyster reefs of the South Atlantic Bight in 1995 (http://water.dnr.state.sc.us/marine/mrri/shellfish/petro.htm), *Petrolisthes armatus* has increased from single individuals m^{-2} to mean summer densities of up to ~11,200 m^{-2}. Despite these tremendous densities and distribution throughout estuaries of coastal Georgia, there have been no visually apparent impacts of the crabs on native communities to date. We can speculate on a number of reasons why we have not seen any changes. Unlike recent introductions of predatory crab species that have drastically altered the activities of individual species (Trussell and Nicklin 2002) or "reorganized" native and previously invaded assemblages (Lohrer and Whitlach 2002), the invasion of *P. armatus* may be too recent, and its effects too subtle to be seen at a broad scale. Short-term, small-scale studies have suggested that the presence of the crab in oyster reefs can suppress oyster growth, microalgal biomass, and goby densities, while enhancing bivalve recruitment, macroalgal growth, and oyster drill survivorship (Chapter 3). Given that oysters are relatively long-lived and that much of their hard structure persists long after their death, though, effects on this foundation species could take years to show.

The northward movement and drastic increase in density of this tropical crab could be due to increasing water temperatures associated with global climate change. Previous studies have documented shifts of tropical fishes onto temperate reefs off of North Carolina (Parker and Dixon 1998), and southern species of intertidal invertebrates have shifted northward in California (Barry *et al.* 1995). Although we cannot connect global warming with regional shifts in porcelain crabs, the crab is clearly finding new habitats that fit its needs, and allow for dramatic increases in crab densities. The long-term ecological effects of this exotic crab on oyster reef communities are yet to be determined.

CHAPTER 2

THE INVASIVE CRAB *PETROLISTHES ARMATUS* OVERWHELMS BIOTIC RESISTANCE BY RECRUITING AT THOUSANDS M^{-2}

Abstract

To address the effects of native species richness and composition on the susceptibility of oyster reefs to invasion by the exotic crab, *Petrolisthes armatus*, we constructed isolated oyster-reef communities that varied in native species richness (0, 2, or 4 native species) and in the density of adult invasive crabs seeded in the most species rich community. We monitored recruitment of juvenile *P. armatus* to these communities over a 12 week period. A similar study the following year assessed the shorter-term (4 weeks) effects of adult conspecifics and of a predatory mud crab on recruitment. At week 4 of the first experiment, recruitment to physical structure lacking native species was significantly 3.75 times greater than to the community having 4 native species. Recruitment to structure alone was ~2.75 times that of recruitment to the 2 native species treatment, but this difference was not statistically significant. Adding adult conspecifics (at 750 crabs m^{-2}) to the community with 4 native species enhanced recruitment of the exotic crab ~3 times, overwhelming biotic resistance and making recruitment similar to that occurring in areas with no native species. These short-term (4 weeks) differences were lost over the longer term (12 weeks) due to recruitment (~17,000 to 35,000 recruits m^{-2}) that swamped the initial ability of native species to slow invasion. In the second study, adult conspecifics again stimulated settlement, while the predatory mud crab had no effect. Although native species richness slowed initial invasion, early colonists

stimulated the settlement of later ones, and this behavior coupled to tremendous recruitment rates overwhelmed the initial effects of biotic resistance and allowed this invasive crab to establish rapidly at densities of thousands m^{-2}.

Introduction

Species invasions historically have played an integral role in the structuring of biological communities (Vermeij 2001, 2005). However, natural processes of invasion occurred relatively slowly, while human activities have exponentially increased invasion rates (e.g., Cohen and Carlton 1998, Mooney and Cleland 2001). Invasions mediated by anthropogenic introductions or breakdown of barriers to dispersal not only alter local community composition and function but also lead to homogenization of biota (Olden *et al.* 2004) and the growing global biodiversity crisis (Stachowicz *et al.* 2002). Thus, there is a critical need to predict how, why, and where invasions are most likely to occur. In particular, what traits make communities more susceptible to invasion and what traits make particular species so invasive?

Numerous assessments of the processes determining invasion success have been driven by Elton's diversity-resistance hypothesis (1958) positing that a community's resistance to invasion is proportional to the richness of its native components. Several theoretical and empirical studies, predominantly in grassland communities or mesocosms, have supported the idea that increased native biodiversity has a negative impact on invasion success (e.g., Tilman 1997, Stachowicz *et al.* 1999, Naeem *et al.* 2000, Kennedy *et al.* 2002). In sharp contrast to this historic and widely-accepted view, recent models as well as observational and experimental studies have challenged this hypothesis, demonstrating that the probability of invasion increases with increasing species richness (e.g., Moore *et al.* 2001, Sax 2002, Gilbert and Lechowicz 2005). More importantly, this dichotomy of results has been explained by the spatial scale of the observations and experimentation (Levine 2000, Knight and Reich 2005), the dominance of the species involved (Smith *et al.* 2004), resource availability (Tilman 2004), environmental heterogeneity in productivity (Cleland *et al.* 2004), or the density of invaders (Von Holle and Simberloff 2005).

Despite recent developments in our understanding of marine invasions, there have been relatively few experimental studies quantifying the direct, indirect, or cumulative effects of invasions (Ruiz *et al.* 1999). In addition, little is known about the mechanisms underlying increases in an invader's densities and spread in marine habitats (but see Stachowicz *et al.* 1999, 2002, Dunstan and Johnson 2004). Experimental studies assessing the effects of community composition on invasibility in marine systems have primarily focused on sessile invertebrates, largely in observational or microcosm-based studies. It is unclear whether such studies predict how more mobile invaders in a three dimensional environment will respond to native community composition under field conditions.

In the past decade the green porcelain crab, *Petrolisthes armatus*, has invaded shallow oyster reefs of Georgia and South Carolina, U.S.A. This crab was found in South Carolina at densities of single individuals m^{-2} in 1995 (http://water.dnr.state.sc.us/marine/mrri/shellfish/petro.htm) and increased to mean densities of several thousand crabs m^{-2} by 2004 (Hollebone and Hay *in review*). A similar high density invasion (exceeding 10,000 individuals m^{-2} at some sites) of the filter-feeding Asian clam, *Potamocorbula amurensis*, into San Francisco Bay altered the composition and seasonality of plankton in the Bay (Carlton *et al.* 1990, Nichols *et al.* 1990). Thus, the invasion of *P. armatus* with its comparatively high densities and similar filter-feeding strategy could drastically impact oyster reefs of the South Atlantic Bight.

The tremendous densities and widespread occurrence of *Petrolisthes armatus* in coastal Georgia (Hollebone and Hay *in review*) make this crab a readily available candidate species for assessing how and why invasions into oyster reef communities succeed. In this paper, we examine the impacts of native community composition and intraspecific cueing on the colonization and short-term versus longer-term recruitment of *Petrolisthes armatus*. Our approach focused on field studies in which we assembled oyster reef communities with differing levels of native species richness. We addressed how native species may be acting as a form of biotic resistance to invasion at both the horizontal (within feeding guild, i.e., competing filter feeders) and the vertical (consumers, i.e., predatory mud crabs) levels of diversity and also addressed whether presence of adult invasive crabs stimulated more larval recruitment, possibly overwhelming native biotic resistance once a few exotic crabs established.

Materials and Methods

Study Organisms

Oyster reefs are the major hard-substrate communities in estuarine ecosystems of the South Atlantic Bight (Bahr and Lanier 1981). These communities are primarily composed of the foundation species, the oyster *Crassostrea virginica*, as well as numerous other vertebrates and invertebrates that use oysters as settlement substrate, habitat, and feeding grounds during tidal inundation (i.e., barnacles, bryozoans, mussels, gobies and blennies, worms, amphipods, mud crabs, blue crabs, mummichogs, oyster drills) (Bahr and Lanier 1981). The green porcelain crab, *Petrolisthes armatus*, is one of the most recent additions to these communities and is found during warmer months at densities of thousands m^{-2}, or ~2 to 10 times those of native mud crabs (*Panopeus herbstii* and *Eurypanopeus depressus* combined) (Hollebone and Hay *in review*). Some of the most common and most effectively manipulated macrofauna in these oyster reefs include oysters, mussels (*Brachidontes exustus*), mud crabs, oyster drills (*Urosalpinx cinerea*), and porcelain crabs. We, therefore, focused on these organisms in our studies.

Initial Field Study: Summer 2004

We assessed the effect of habitat composition on the density of colonizing *Petrolisthes armatus* by performing a constructed community study (Levine and D'Antonio 1999) in which we manipulated the native species richness of spatially isolated oyster reef communities and monitored larval recruitment of *P. armatus* to these communities during the peak recruitment season (summer months, Hollebone and Hay *in review*). We established 12 replicated blocks of 5 community types including: (1) a 0 native species treatment composed of only sun-bleached oyster shells, (2) a 2 native species, filter-feeding community composed of natural densities of live oysters and mussels, (3) a 4 native species community composed of live oysters, mussels, mud crabs (potential bivalve and gastropod predators), and oyster drills (oyster predators), (4) a 4 native species community composed of live oysters, mussels, mud crabs, oyster drills, seeded with the equivalent of 225 adult (>5.5 mm CW) *P. armatus* m^{-2} (~16.5 to 22.5 grams basket^{-1}), and (5) the same 4 native species treatment as above seeded with the equivalent of 750 adult *P. armatus* m^{-2} (~55 to 75 grams basket^{-1}).

Each community was established in plastic baskets (29 cm long x 23 cm wide) with perforated sides (twelve 6 cm long and 1.5 cm tall halfmoon-shaped holes along the lengths and four holes plus one 10.5 cm long and 3 cm tall hand hold along the widths) and open tops allowing movement of organisms into and out of the basket. Within each basket, we included three randomly distributed subsamplers (Figure 2.1b) that were periodically removed to assess community dynamics without disturbing the entire community. These subsamplers were constructed from the lower 2.0 cm of a plastic deli container (radius = 4.0 cm; bottom area = 50.3 cm^2) and PVC-coated chicken wire (hexagonal shape, 4.0 x 2.5 cm). The chicken wire was cut to a height of 16.0 cm and formed into a cylinder that could be inserted into the container and secured (volume = 804.8 cm^3).

Prior to experimentation, all oysters and mussels were defaunated (all visible organisms manually removed from the shell surface), and all mud crabs and porcelain crabs for seeded treatments were measured (carapace width: CW). We established our communities with natural densities of each organism using data obtained from monitoring studies conducted near our experimental plots (Hollebone and Hay *in review*). Each basket contained ~1.5 liters of live oysters or sun-bleached oyster shells as the underlying substrate and 10 mussels (~150 m^{-2}), 15 oyster drills (~225 m^{-2}), and 3 large (>18 mm CW; 45 m^{-2}) and 5 small (10-18 mm CW; 75 m^{-2}) mud crabs (*Panopeus herbstii*; comparable to the mean densities from Spring 2004), according to the assigned treatment.

All spatially blocked communities were placed on three isolated mud flats near Skidaway Island, Georgia, U.S.A. (Figure 2.1a, sites #1-3). Mud flats were used because we wanted to assess crab recruitment from the plankton and thus needed to preclude migration of post-settlement crabs from nearby oyster reefs. All blocks were established ≥20 m from the edge of the nearest oyster reef or from another experimental block, and each basket was 5 m from its nearest neighbor. Treatment types were randomly assigned

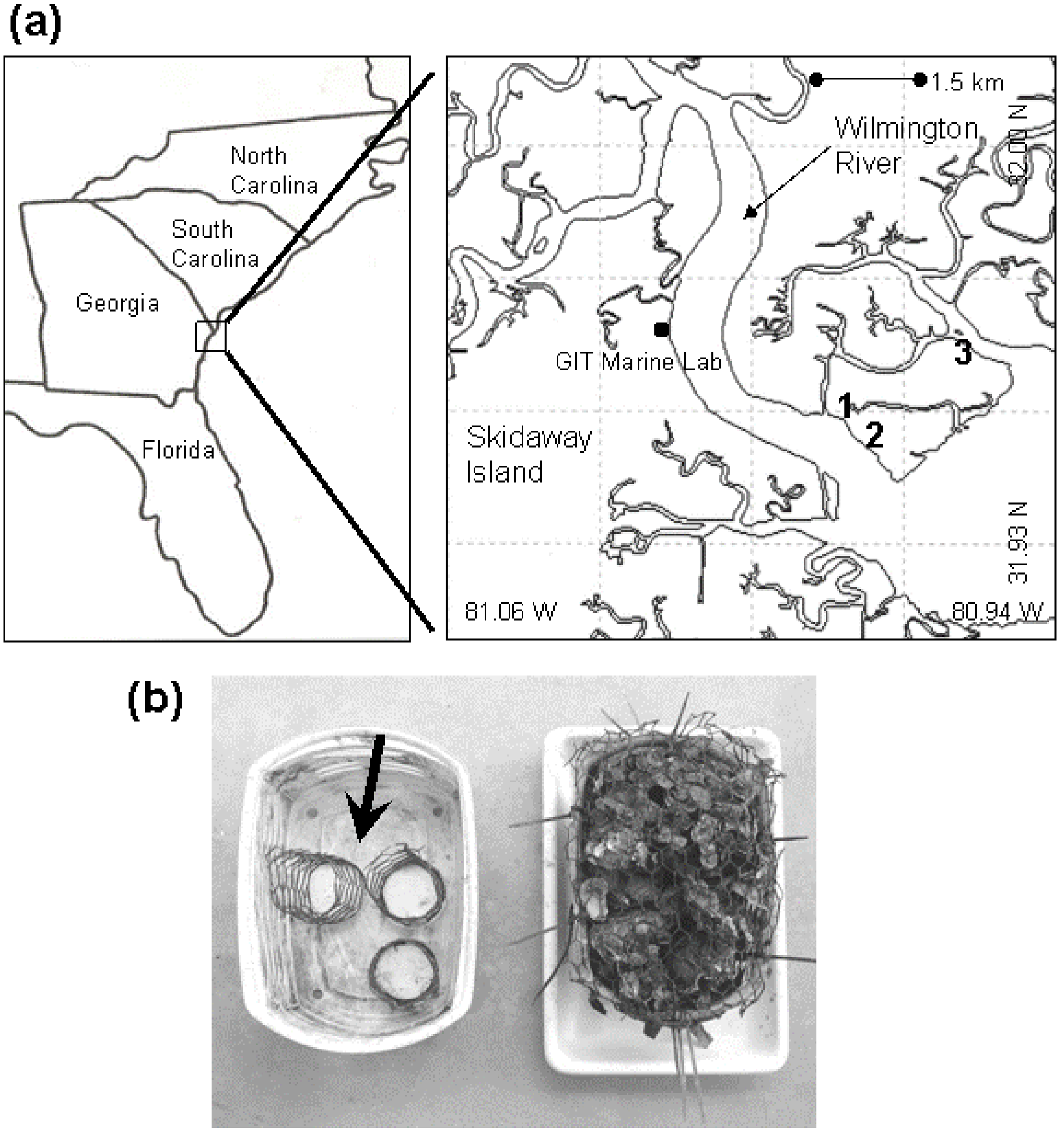


Figure 2.1. (a) Skidaway Island, Georgia and surrounding areas. Mud flat sites where field studies were performed are labeled as 1, 2, and 3. (b) Plastic baskets with and without oysters. Subsampling devices highlighted with an arrow.

to a position within each blocked array. The baskets were anchored on top of the sediment with four rebar stakes (~46 cm long, one on each side) and oriented lengthwise to the incoming tide along one transect parallel to the shore (0.3 to 0.5 m above mean lower low). During the initial set-up, we brought all defaunated, measured, and sorted organisms from the laboratory to each mud flat site and distributed them among the baskets. Once secured, the baskets were covered with PVC-coated chicken wire to avoid oyster wash-out by wave action due to storms or heavy boating activity.

Sampling and Data Analysis

The recruitment of *Petrolisthes armatus* to the constructed communities was monitored at weeks 2, 4, 8, and 12. The length of each low tide allowed for only partial sampling of the 12 blocks. Thus, we sampled only six of the original twelve blocks at week 2. We sampled every other block so that representatives from all three mud flats were included and no two blocks directly next to one another were sampled. During the 1 to 3 hours before and after the low tide, we removed one randomly selected subsampler from each community treatment. All organisms within the subsampler were manually extracted or separated from sediments using a 500 micrometer sieve and recorded. All crabs were identified, counted, sized, and sexed as visibility in the field and length of tidal exposure allowed. In particular, we noted the sizes of *Petrolisthes armatus* as ≥5.5 mm CW (seeded adult size) or <5.5 mm CW (unseeded recruit). All material and organisms were returned to their original sampler, and this was returned to the basket. At 4 weeks we sampled the second set of six blocks in the same fashion, and at 8 weeks we sampled the original set of six again. At 12 weeks we brought all baskets back to the laboratory (except two blocks from mudflat site #3 on Figure 2.1a because of sediment movement that covered the baskets), preserved all organisms within the final selected sampler in 70% ethanol, and performed the assessments described above.

Recruit densities were scaled to recruits m^{-2}. Data were square root transformed to meet the requirements of normality (Ryan-Joiner W test, $p > 0.050$, one violation remained following transformation with the oyster and mussel treatment at 12 weeks) and equality of variances (F test, $p > 0.050$). Effects of time and treatment on recruitment were then assessed via repeated-measures ANOVA. We further analyzed the short-term effect of community composition on differential recruitment of *Petrolisthes armatus* using a one-way ANOVA and Tukey-Kramer post hoc test ($p \leq 0.050$) on the week 4 data.

Follow-up Field Study: Summer 2005

Our initial field study suggested that biotic resistance and conspecific cueing may be contributing to how *Petrolisthes armatus* invaded oyster reef communities within the first 4 weeks. Therefore, we further assessed the local-scale, short-term effects of community composition (e.g., predation, competition, and cueing on adult conspecifics) on recruitment, by establishing communities of varying oyster reef composition on mud flats during summer 2005. To minimize sorting effort, the baskets used in the initial study were divided in half by securing 0.64 cm plastic vexar mesh across the inner width of the basket. Half of each basket was then filled with defaunated live oyster substrate as well as treatment-specific crabs. The other half remained empty. The treatments consisted of: (1) live, defaunated oysters, (2) oysters spiked with adult porcelain crabs (≥5.5 mm CW, 40 crabs $basket^{-1}$ or ~1200 crabs m^{-2}), or (3) live oysters with mud crabs (two >18 mm CW, 60 crabs $basket^{-1}$ and three 10 to 18 mm CW, 90 crabs $basket^{-1}$) and adult porcelain crabs (same density as above). We increased the density of porcelain crabs in this follow-up study compared to the initial study (1200 versus 750 crabs m^{-2}) in an attempt to elicit stronger signals and because densities of porcelain crabs in the field commonly range from 1000 to 10,000 m^{-2}. In both studies, we were limited by our ability to collect large numbers of porcelain crabs, therefore experimental densities fell towards the lower end of natural densities during the warmer months (Hollebone and Hay *in review*).

The three treatment baskets were randomly assigned a position in 10 linear blocked arrays over two mud flats (sites 1 and 2 in Figure 2.1a; site 3 was not used because of physical disturbances). Placement and arrangement were the same as described previously. The experiment ran for 4 weeks. Baskets were then returned to the laboratory where all organisms were preserved in 70% ethanol. Porcelain crabs were counted and identified as recruits (<5.5 mm CW) or seeded adults (≥5.5 mm CW). All data were scaled up to 1 m^2 (30 baskets m^{-2}), tested for normality (Ryan Joiner W test, $p > 0.050$) and equality of variances (F test, $p > 0.050$), and analyzed with a one-way ANOVA and Tukey-Kramer post hoc test ($p \leq 0.050$).

Results

Over the 12 week duration of the initial study, *Petrolisthes armatus* densities rose from zero to mean densities of ~17,000 to 34,000 crabs m^{-2} (Figure 2.2). Densities were ~2000 to 2500 crabs m^{-2} for all treatments after only 2 weeks. There was a significant effect of time on recruitment over the course of the entire experiment (repeated-measures ANOVA, $p < 0.001$), but no significant effect of treatment or treatment x time interaction ($p = 0.396$ and $p = 0.309$, respectively). By 12 weeks mean recruit densities exceeded

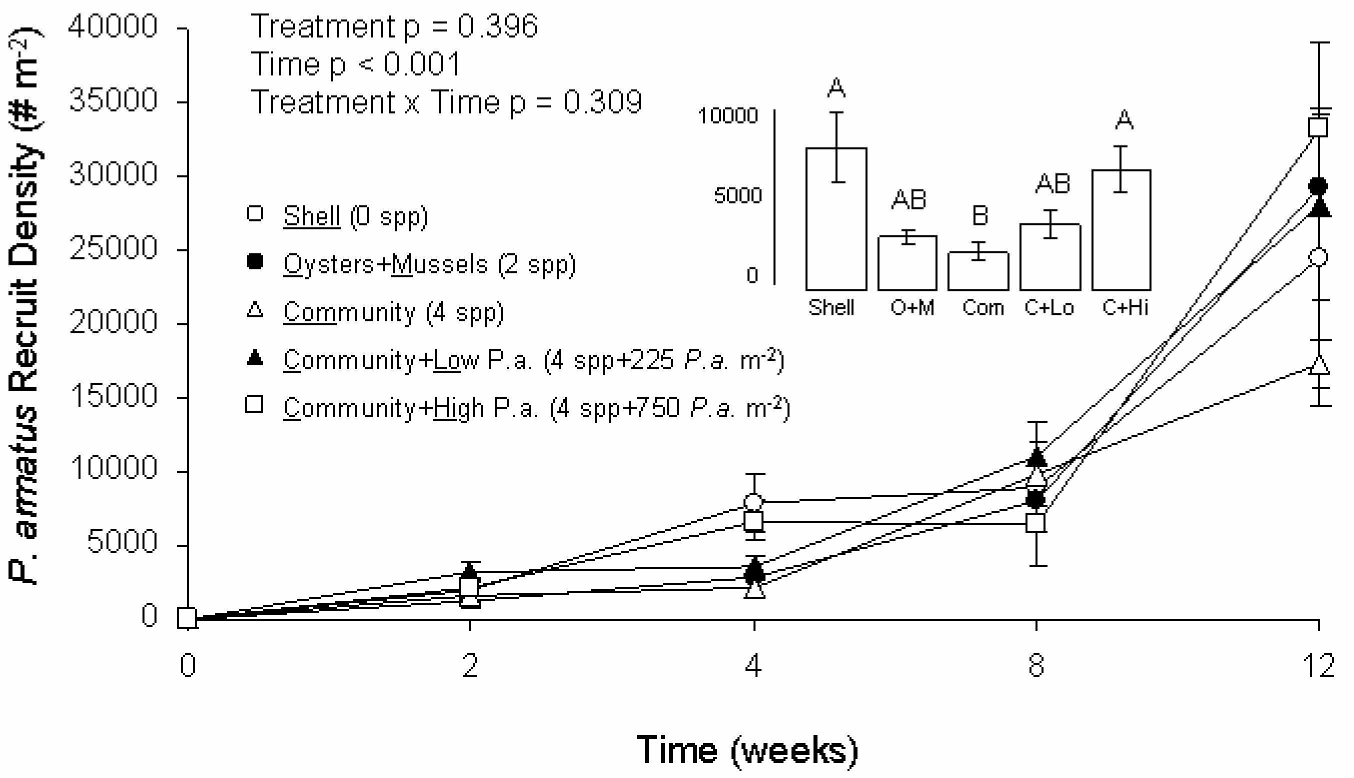


Figure 2.2. 2004 field experiment. Mean densities (± SE) of *Petrolisthes armatus* recruits over 12 weeks in constructed oyster reefs that differed in species composition. P values derived from a repeated-measures ANOVA following transformation of the data. Inset shows data for 4 weeks only. Letters indicate significant differences (ANOVA, Tukey-Kramer, p ≤ 0.050) among treatments.

15,000 crabs m^{-2} in all treatments with some individual baskets scaling to nearly 60,000 crabs m^{-2}.

Because some of our treatments involved the absence of invasive crabs and because crab recruitment was so rapid, we were concerned that the treatments without the invasive crab may have initially differed in their attraction to recruits but that this effect was quickly overwhelmed. As one way of assessing this, we evaluated our week 4 data separately. At the week 4 sampling, recruitment to the shell only treatment (0 native species) significantly exceeded recruitment to the treatment with 4 native species alone (Figure 2.2 inset, ANOVA, Tukey-Kramer $p \leq 0.050$). However, when the 4 native species community was seeded with the equivalent of 750 adult porcelain crabs m^{-2} recruitment increased significantly and attained levels equivalent to those seen in the treatment lacking all native species (Figure 2.2 inset). The treatment seeded with the equivalent of 225 adult porcelain crabs m^{-2} recruited intermediate densities of juveniles, not significantly different from the equivalent community without adult porcelain crabs or the community with the higher density of adult *P. armatus*.

The additional experiment in 2005 also demonstrated that *Petrolisthes armatus* recruited significantly more rapidly to treatments containing adult conspecifics; in contrast, mud crabs (a potential predator) had no effect on recruitment (Figure 2.3). Again, recruitment was very high. After 4 weeks, there were 70% more recruits in communities with adult conspecifics then those without (~17,000 recruits m^{-2} versus ~10,000 recruits m^{-2}).

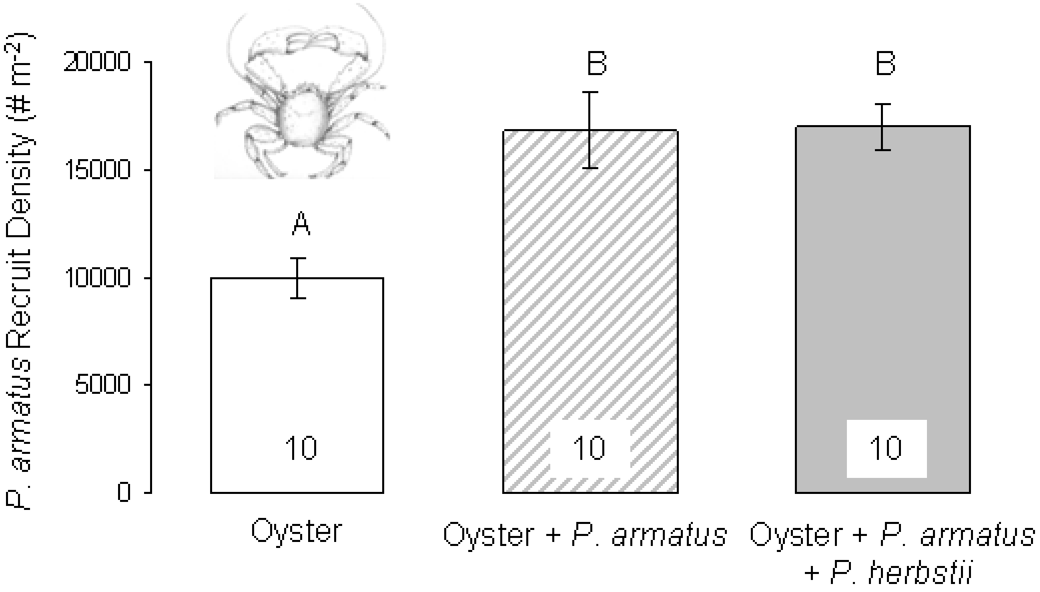


Figure 2.3. 2005 field experiment. Mean densities (± SE) of *Petrolisthes armatus* recruits in three constructed community types after 4 weeks. Treatment labels indicate the following: Oyster - live oysters, Oyster + *P. armatus* - live oysters with 1200 porcelain crabs m^{-2}, and Oyster + *P. armatus* + *P. herbstii* - live oysters with 1200 porcelain crabs m^{-2} and 60 large (>18 mm CW) and 90 small (10 to 18 mm CW) mud crabs m^{-2}. Letters indicate significant differences (ANOVA, Tukey-Kramer, $p \leq 0.050$) among treatments.

Discussion

Human activities have dramatically increased biotic invasions, causing both loss and homogenization of global biodiversity. These changes necessitate a better understanding of the ecosystem traits and species traits affecting invasion success (Stachowicz *et al.* 2002). Historically, most experimental assessments of invasion patterns have focused on small-scale manipulations in terrestrial systems or microcosms (e.g., Tilman 1997, Naeem *et al.* 2000, Hector *et al.* 2001). Similar studies in marine systems have been limited primarily to sessile invertebrates in two dimensional environments that are more persistent through time and, thus, more readily manipulated (e.g., Stachowicz *et al.* 1999, 2002). Our investigation assessed the invasion of a highly mobile crustacean in a three dimensional field setting where colonization was limited to recruitment from the plankton.

In the initial field experiment, we did not detect an effect of native species richness or the presence of adult *Petrolisthes armatus* on densities of recruits after 12 weeks of colonization (Figure 2.2). Levels of recruitment were exceedingly high with mean densities of ~17,000 to 34,000 crabs m^{-2} across treatments after 12 weeks. Given these recruitment rates, we were concerned that our treatment of added conspecifics would quickly have been negated by recruits of the invasive crab being added across all treatments. Therefore, we separately evaluated recruitment after only 4 weeks as a way of assessing early patterns. We found that the shell only treatment with no native species and the 4 species community treatment seeded with the equivalent of 750 seeded adult *P. armatus* m^{-2} had significantly more porcelain crab recruits than the 4 native species community that had not been seeded with adult *P. armatus* (Figure 2.2). Communities with 2 native species and those with 4 species plus the equivalent of 225 adult *P. armatus* m^{-2} were intermediate in the recruitment of juvenile crabs. Thus, *P. armatus* selectively recruited to adult conspecifics despite potential competition with and predation from native species; however, presence of conspecifics was not mandatory, recruitment to physical structure alone (sun-bleached oyster shells) was as high as to any other treatment (Figure 2.2).

Increased short-term recruitment to the sun-bleached oyster shell treatment was consistent with the hypothesis that native species richness suppresses invasion; this treatment had no native species and thus no initial biotic resistance. However, the large influx of recruits across all community types overwhelmed this initial pattern and quickly allowed conspecifics to stimulate settlement across all treatments (Figures 2.2 and 2.3).

Studies with the Pacific congener *Petrolisthes cinctipes* showed that juveniles of that species also preferentially settled with adult conspecifics; benefits of this behavior include habitat cueing, reduced predation risks, facilitation, and access to mates (Donahue 2004). Adult crabs protected settlers from predation by fishes, and by settling with conspecifics, juveniles chose habitats that were successfully supporting adult populations (Jensen and Armstrong 1991). Similar benefits of conspecific cueing may exist for *P. armatus* in oyster reefs of the South Atlantic Bight. The term “invasional meltdown” has been coined to describe the situation where one exotic species enhances the probability of invasion or spread of another (Simberloff and Von Holle 1999, Parker *et al.* 2006). To some extent, *P. armatus* achieved this intraspecifically. It invaded many community types to some extent despite biotic resistance from native species, and once a few adults were in the community, they rapidly stimulated settlement by thousands of larval recruits. This stimulatory effect quickly overwhelmed the negative effects of biotic resistance (Figure 2.2, inset).

The ecological role of specific native species can affect the establishment of exotic invaders (e.g., Baltz and Moyle 1993, D'Antonio 1993, Case and Crawley 2000, Keane and Crawley 2002). In our system, we expected that recruitment of *Petrolisthes armatus* might be diminished in areas occupied by the predatory mud crab *Panopeus herbstii*, a known consumer of adult *P. armatus* (Chapter 3). We were unable to detect any such effect in either our 2004 or 2005 experiments, but the presence of conspecific *P. armatus* did increase settlement in both years (Figures 2.2 and 2.3). Recruitment to treatments with seeded adult *P. armatus* was approximately 70% greater than to an equal, unseeded habitat. This relationship was not altered by the presence of the potential predator.

Petrolisthes armatus recruitment to our experimental baskets in both studies reached ~2000 to 17,000 crabs m^{-2} after only 4 weeks. In the longer duration 2004 experiment, densities of recruits reached ~17,000 to 34,000 crabs m^{-2} after 12 weeks. These densities could be higher than natural densities if our spatially isolated baskets attracted large numbers of recruits into a habitat (i.e., mud flat) that is otherwise lacking in adequate settlement sites or if the baskets themselves attracted recruits regardless of the treatments assigned to them. We did not rigorously test this last hypothesis, but in preliminary experiments, recruitment was very low to baskets where shell hash or oysters were washed out by waves, suggesting that the baskets themselves attracted few recruits. Additionally, the high recruitment we observed to our experimental habitats also occurred in natural oyster reef communities near our study sites. Seasonal monitoring of oyster reefs over >100 km section of the Georgia coast demonstrated that densities of *P. armatus* fell to 10s to 100s crabs m^{-2} in the winter but rapidly increased to mean densities of 1000s to ≥10,000s crabs m^{-2} in the warmer months (Hollebone and Hay *in review*).

Timing can be a major factor in determining an invader's establishment and success. Although we observed local-scale, community composition effects (e.g., preferential recruitment to areas with minimal biotic resistance or to areas with adult conspecifics) in the short-term (4 weeks), the rapid increase and convergence of recruit densities within 12 weeks demonstrated that invaded communities were influenced by both local and regional (e.g., propagule pressure) processes. Within a single summer season, all initial local-scale determinants of differential recruitment were overwhelmed by the tremendous propagule pressure. In summer, the availability of hard, multi-dimensional substrate alone allowed *Petrolisthes armatus* invasion in the estuary we studied. In colder periods of the year, when larval settlement is very low (Hollebone and Hay *in review*), the settlement patterns we observed only in the short-term may be more persistent and the presence of predators may actually influence crab densities. Therefore, fluctuations in demographics for both the native and invasive species across seasons could play an important role in how the community is structured or "resists" invasion over longer periods of time (Stachowicz 1999, 2002).

Although native species richness and interactions with specific native consumers or competitors affects invasion success in some communities (e.g., Tilman 1997, Stachowicz *et al.* 1999, Kennedy *et al.* 2002, Parker *et al.* 2006), the tremendous rates of recruitment that we documented across all treatments in our studies suggests that propagule availability coupled with recruitment stimulation by conspecifics overwhelmed all forms of resistance to invasion by *Petrolisthes armatus* within this system. Adult densities of *P. armatus* in its new range exceed by 10 to 37 times the highest densities ever reported in its native range, and the proportion of gravid females in the new range equals those in the native range (Hollebone and Hay *in review*). Thus, reproductive output of *P. armatus* populations in the South Atlantic Bight will exceed those populations in the native range by at least an order of magnitude. These tremendous densities of potential recruits coupled with conspecific cueing make it likely that high propagule pressure will continue to allow *P. armatus* to overwhelm local biotic resistance to recruitment.

CHAPTER 3

IMPACTS OF THE INVASIVE CRAB *PETROLISTHES ARMATUS* ON NATIVE OYSTER REEF COMMUNITIES OF THE SOUTH ATLANTIC BIGHT, U.S.A.

Abstract

The green porcelain crab, *Petrolisthes armatus*, has recently invaded oyster reefs of the South Atlantic Bight at mean densities of up to several thousand individuals m^{-2}. Despite these densities, its impacts on native species and communities are unknown. We assessed impacts through mesocosm and field experiments in which we simulated oyster reef habitat with and without porcelain crabs. Tremendous recruitment of *P. armatus* to all communities in the field limited the duration of effective treatments to periods of 2 to 4 weeks, but impacts on many species were still apparent at 12 weeks. Despite this limitation, we found that *P. armatus* at densities of 750 to 1500 individuals m^{-2} (~10% to 75% of summer densities near our study site): (1) suppressed growth of small oysters, biomass of benthic microalgae, recruitment of native mud crabs, and possibly densities of the native goby *Gobiosoma bosci*, (2) enhanced bivalve settlement, macroalgal cover, and survivorship of the predatory oyster drill *Urosalpinx cinerea*, but (3) did not affect native taxonomic richness. Laboratory feeding assays, field tethering experiments, and population changes in our field and mesocosm experiments suggest that the high densities of *P. armatus* are serving as alternative and preferred prey for native mud crabs, thus relieving predation on native reef biota such as bivalves and oyster drills. *P. armatus* commonly reaches summer densities of ~1000 to 11,000 m^{-2} on oyster reefs near our study sites. At these densities, impacts may be stronger than those noted above. Without natural controls, reefs lacking *P. armatus*, we cannot rigorously assess how oyster reef

communities are impacted by this invasion over the longer term. However, the large direct and indirect effects of the invasive crabs on growth, survivorship, and recruitment of common native species over only 4 to 12 weeks in small-scale experimental studies indicate the possibility of considerable long-term consequences for one of the major hard-substrate community types in the South Atlantic Bight.

Introduction

Species invasions have played an integral, and natural, role in shaping biological communities over both ecological and evolutionary time (Vermeij 2001, 2005). Although species continually adjust their ranges in response to environmental change or accidents of dispersal, their movements have historically been impeded by natural barriers (Darwin 1859, Elton 1958). Biological invasions as a result of recent reductions in these barriers due to human activities and global climate change pose serious threats to community structure and ecosystem functioning, their impacts being more pervasive than just the homogenization of species and the potential reduction of native species richness (Sanders *et al.* 2003, Gurevitch and Padilla 2004).

Non-indigenous species disrupt natural community interactions, establish new ecological relationships, and alter evolutionary pathways of native species (Mooney and Cleland 2001). Invaders can affect native species through: interspecific competition (e.g., Callaway and Aschehoug 2000, Cole *et al.* 2005), genetic hybridization and introgression (e.g., Rhymer and Simberloff 1996, Lambrinos 2004, Wares *et al.* 2005), predation (e.g., Savidge 1987, Schoener and Spiller 1999), facilitation or "invasional meltdown" (e.g., Simberloff and Von Holle 1999, O'Dowd *et al*. 2003, Parker *et al.* 2006), or the introduction of new pathogens and diseases (e.g., Juliano and Lounibos 2005, Woodworth *et al.* 2005). Invasions can lead to the displacement or even complete disassembly of native communities (e.g., Nichols *et* al. 1990, Sanders *et al.* 2003). However, interactions between native and exotic species are not always destabilizing or obviously disruptive. Invaders can form mutualisms with native species, contributing to the success of both natives and exotics (Mooney and Cleland 2001). Some invader-native species associations can be so intimate as to appear coevolved despite the pair not having co-occurred over evolutionary time (e.g., herbivorous molluscs and marine algal hosts, Vermeij 1992). Thus, the successful colonization of non-native species in new habitats can produce a range of ecological and evolutionary responses from minimal to dramatic (Vermeij 1996, Sax *et al.* 2005).

Exotic species are rapidly invading marine and estuarine habitats worldwide, and several invasions have caused fundamental, and sometimes devastating, effects on native communities and ecosystems (Ruiz *et al.* 1997, 1999). Although marine systems are among the most heavily invaded (Carlton and Geller 1993), research on non-indigenous species in these habitats has lagged behind studies in terrestrial and freshwater systems (Grosholz 2002). Comparatively little is known about the biotic interactions affecting invasions or the consequences of invasions within many marine communities (Stachowicz *et al.* 2002). Thus, there is a need to address the effects of exotic species, the processes facilitating or deterring invasions, and which types of exotic species are most likely to become invasive (Byers *et al.* 2002, Bruno *et al.* 2005).

Petrolisthes armatus in the South Atlantic Bight

Within the past decade, the filter-feeding green porcelain crab, *Petrolisthes armatus*, has invaded intertidal oyster reefs of the South Atlantic Bight, USA. Although historically found in the tropical waters of the eastern Pacific (Gulf of California to Peru), western Atlantic (Southern Florida to the Indian River Lagoon, Bermuda, Caribbean, Gulf of Mexico, and Brazil), and western Africa (Oliveira and Masunari 1995), the crab has become well-established in its new northern range increasing from single individuals m^{-2} in 1995 (http://water.dnr.state.sc.us/marine/mrri/shellfish/petro.htm) to mean densities of several thousand crabs m^{-2} in the warmer months of 2004 (Hollebone and Hay *in review*). Mean densities (up to ~11,000 m^{-2}) in the new range of coastal Georgia can exceed by 37 fold the highest densities ever reported from the native range (Hollebone and Hay *in review*).

Despite their broad distribution, recent invasion, and high densities, little is known about the ecology of *Petrolisthes armatus* in its new range or about its effects on native communities. Previous studies in the historic range provide data on the population demographics and densities of the crab (Sheridan 1992, Oliveira and Masunari 1995, Micheletti-Flores and Negreiros-Fransozo 1999), but the potential impacts of *P. armatus* on oyster reef communities in the expanded range have not been documented. Through mesocosm and field experiments, we assessed the impacts of *P. armatus* adults on oyster reef communities in the South Atlantic Bight. We asked whether the presence of the invasive crab: (1) resulted in lower species richness of native species, (2) affected the growth or recruitment of native foundation species (oysters), (3) affected the recruitment or growth of other common bivalves, fishes, crabs, or seaweeds within the community, or (4) served as an abundant alternative prey for native consumers, thus lessening consumer impact on native prey?

Materials and Methods

Native and Non-native Consumer Interactions

We conducted several observations and laboratory feeding assays to evaluate potential consumer-prey interactions between *Petrolisthes armatus* and native species. *P.*

armatus is known to be primarily a filter-feeder that consumes detritus, algae, and zooplankton (Caine 1975), but we also directly observed its feeding in outdoor mesocosms to see if the crab could harvest materials from oyster surfaces as well. To evaluate the upper size of prey that *P. armatus* might consume, we offered adult *P. armatus* (~5 to 10 mm carapace width, CW) brine shrimp of about 7 to 10 mm in length by placing brine shrimp into the crabs' mouth parts and observing consumption or rejection (n = 11 individual crabs). To evaluate the willingness of *P. armatus* to consume its own larvae, we offered 7 adult crabs a brine shrimp followed by a conspecific larva (zoea) of similar size (8 to 9 mm long). Procedures were as described above, and data were analyzed using a Fisher's Exact test with Yates correction for continuity (Zar 1999).

We also offered *P. armatus* larvae to 8 adult oysters by using a pipette to place live zoea into the feeding currents of each oyster while it actively pumped. Each oyster was then observed for a few minutes to ensure that the larva was entrained in the feeding currents and the valves closed around it. We continued to watch the oyster to see if it expelled the zoea before it began filtering again. To determine if pelagic predators would consume *P. armatus* larvae, we placed 10 zoea in each of 15 separate 1 liter containers of filtered seawater with one juvenile pompano (*Trachinotus carolinus*) in each container. At the end of 1 hour, the fish was removed and surviving zoea counted.

We conducted several laboratory feeding assays followed by a field tethering assay to see if native predators would consume adult *Petrolisthes armatus* and whether the crab was preferred or avoided relative to native prey. The fishes *Fundulus heteroclitus* (mummichog [40 to 60 mm standard length], n = 16) and *Leiostomus xanthurus* (spot [50 to 80 mm standard length], n = 10) and the crabs *Callinectes similis* (lesser blue crab [58 to 63.5 mm CW], n = 7) and *Panopeus herbstii* (the common mud crab [18 to 32 mm CW], n = 10) were each offered a palatable control food (e.g., brine shrimp, commercial fish food, squid or oyster tissue) and then an adult *P. armatus*. If the invasive crab was not eaten, the consumer was offered a second piece of palatable food to determine if rejection was due to consumer satiation. We used *P. armatus* in the range of 4 to 6 mm CW for the mummichog, spot, and mud crab assays, and we used a number of size classes (<5 mm, 5 to 6 mm, 6.1 to 8 mm, 8.1 to 9 mm, and >9 mm CW) in the blue crab assays. Frequency of consumption was analyzed by a Fisher's Exact test with Yates correction for continuity. The mud crabs did not immediately consume the porcelain crabs; therefore, we could not perform feeding assays within a period of several minutes. For the mud crab assays, porcelain crabs were left in containers with mud crabs for 24 hours and consumption was monitored periodically.

Because native mud crabs (*Eurypanopeus depressus* and *Panopeus herbstii*) and *Petrolisthes armatus* co-occur at high densities within oyster reefs (Hollebone and Hay *in review*), mud crabs could be an important predator on the invasive crab. We therefore performed a laboratory choice assay to see if mud crabs preferred or avoided the invasive crab relative to native prey. We confined individual mud crabs (CW = 21 to 36.5 mm) in 13 separate 470 milliliter containers with small (length: 12 to 19.5 mm) and large (24 to 34.5 mm) oyster drills (*Urosalpinx cinerea*), small (length: 10.5 to 24.5 mm) and large (27 to 45 mm) mussels (*Brachidontes exustus*), and an adult porcelain crab (5 to 9 mm CW). Perforated lids prevented animal escape. We documented the prey first eaten by each crab over 24 hours. Data were analyzed using a G test (Zar 1999).

As a final assay to confirm that consumption of *Petrolisthes armatus* occurred under field conditions, we conducted field tethering assays during both day and night tidal inundation (12 hours) and in both oyster reefs and mud flats (within 5 meters of the oyster reefs). Porcelain crabs (4.5 to 11 mm CW) were tethered by their carapaces using superglue and ~45 cm of thin fishing line attached to a nail (10 cm long). Crabs were tethered and held in seawater for several hours before release into the field. In some cases the porcelain crabs died on their tethers before release. The total numbers of crabs placed in the field were n = 19 for mudflats at night, n = 15 for oysters at night, and n = 20 for both mudflats and oysters during the day. Tethering sites were marked with flagging tape so that tethers could be quickly recovered at the end of 12 hours as the tide receded. Survivorship of the crabs exposed to the four conditions described above was analyzed using a G test (Zar 1999). We believe that the loss of crabs in the field was primarily due to predation and not due to tether failure. Preliminary laboratory assays suggested that the tethers hold well. Survivorship of crabs (5.5 to 10 mm CW) tethered inside (n = 10) or outside (n = 10) oysters within a flowing seawater table for 18 hours was 90% and 100%, respectively.

Mesocosms

We used outdoor mesocosms at the Georgia Institute of Technology's marine laboratory at the Skidaway Institute of Oceanography (near Savannah, Georgia) during the summer of 2003 to gain an understanding of how *Petrolisthes armatus* impacts the growth and survivorship of oysters (*Crassostrea virginica*) and mussels (*Brachidontes exustus*) as well as the recruitment of other oyster reef-related biota. We used ten 1.2 m x 1.2 m x 0.8 m deep tanks that received flow-through seawater from Wassaw Sound via a wave-generating bucket that became unstable when full, dumping its contents into the tank at 30 to 60 second intervals and creating wave motion. These mesocosms were under a partially transparent awning that lowered direct sunlight and prevented excessive heating. They allowed us to manipulate porcelain crab densities in a semi-natural outdoor setting but did not replicate normal changes in tidal height and the full complement of natural predators (e.g., blue crabs, fishes). In addition, some larvae were probably killed or prevented from colonizing due to the pumps and pipes supplying seawater. We simulated tidal exposure by draining the tanks for 2.5 to 4 hours day^{-1} during the late morning to avoid the afternoon heat.

We established three oyster reef communities in plastic containers in these tanks. Each container (23 cm wide and 30 cm long) was filled with 2 liters of live oysters that had been manually defaunated of other macro-organisms. Two of the three treatments in each tank were spiked with ecologically relevant densities (Hollebone and Hay *in review*) and biomass of adult porcelain crabs (≥6 mm carapace width, CW). The final array of treatments included the equivalent of: (1) 0 crabs m^{-2}, (2) 1500 crabs m^{-2} (100 crabs or ~55-75 g wet mass of crabs container^{-1}), or (3) 1500+ crabs m^{-2} (100 crabs container^{-1} + ~10 extra crabs week^{-1} for several weeks). Porcelain crab collection was a limiting step in establishing the experimental communities, therefore over a period of 12 days the number of crabs was proportionally added to attain the desired densities. We were unable to maintain crab densities above 1500 m^{-2} in the mesocosms over time; therefore, upon final assessment of crab densities we pooled data for the 1500 and 1500+ treatments. In addition to the exotic crab, each treatment received 10 measured (longest length) and individually labeled (with numbered Floy™ fish tags) oysters and mussels in order to assess impacts of porcelain crabs on the growth and survivorship of co-occurring filter-feeders. Growth was measured as change in length for both oysters and mussels. Change in wet mass was not used as a growth parameter because many organisms settled on bivalves, falsely elevating their mass.

All treatments were blocked within each tank so as not to confound treatment effects with tank-specific effects. Each treatment was randomly assigned an initial position in each tank, and the array was rotated counterclockwise in space every 2 to 3 days to avoid spatial bias. Each container had walls (47 cm tall) of 0.17 cm mesh hardware cloth glued to the inner sides of the container, essentially making a wire basket that extended several centimeters above the surface of the water to prevent crabs from escaping. An open top allowed easy sampling. Each basket was secured on top of a 20 cm tall concrete block to raise it above the anoxic mud that accumulated in the bottom of the tank. Small holes drilled in the bottom of each basket allowed slow drainage of water during simulated low tides. We included within each basket three randomly placed cylindrical subsamplers that allowed for minimally disruptive sampling of the communities. Subsamplers were constructed from the lower 2 cm of a plastic container (radius = 4.0 cm) and PVC-coated chicken wire (hexagonal shape, 4.0 x 2.5 cm^2). The chicken wire was cut to a height of 16 cm and formed into a cylinder that could be inserted into the container and secured.

We evaluated porcelain crab densities at 2, 3, 4, 6, 7, 9, and 12 weeks to determine how well our treatments of 0 and 1500 crabs m^{-2} were maintained. One of the subsamplers from each basket was randomly selected, adult porcelain crabs were counted, and the sampler and contents were returned to the original position. Each sampling period we rotated to a different sampler and returned to the original cylinder by week 6. Crab density in each sampler was scaled to basket size and porcelain crabs were replenished for ~7 weeks if densities were low based on the mean density for that treatment across all tanks. For analyses, data were scaled to 1 m^2 (14.5 baskets m^{-2}), assessed for normality (Ryan-Joiner test W, $p > 0.050$) and equality of variances (F test, $p > 0.050$), and then analyzed using a repeated-measures ANOVA. Using the mean densities (± SE) of porcelain crabs at 3 weeks in the 1500 crabs m^{-2} treatment (1413.5 ± 147.9 crabs m^{-2}) and 0 crabs m^{-2} in the 0 crab treatment as a benchmark against which to compare means at other time points, we performed individual two-tailed paired t tests to determine when crab density departed significantly from our treatment density goals (0 or 1500 crabs m^{-2}).

At weeks 3, 6, 9, and 12, we noted native taxonomic richness during the assessment of porcelain crab densities. These data allowed for the tracking of porcelain crab impact on the recruitment of native taxa. Richness data were analyzed as above using a repeated-measures ANOVA.

We assessed effects of the exotic crab on the growth and survivorship of live oysters and mussels in the communities. At 4 weeks, we measured the length of all live, labeled mussels and oysters that could be acquired without disturbing other contents in the baskets. Upon completion of the experiment at 12 weeks, we retrieved all labeled oysters and mussels (many tags had detached by this time) and performed the same assessments. We determined the impact of the invasive crab on growth and survivorship of both oysters and mussels growth by arcsine transforming the percent survivorship data to achieve normality (Ryan-Joiner W test, $p > 0.050$) and equality of variance (F test, p >

0.050), and performing one-tailed t tests (paired for the mussels). One-tailed tests were used because we expected *Petrolisthes armatus* to compete or interfere with the feeding of native filter-feeders, thus having a negative impact on growth of these bivalves. If variances remained heterogeneous even after transformation, as for the week 4 oyster growth data, we used the Welch's modification to the t test (Zar 1999).

Petrolisthes armatus lives in close association with oysters and has been observed scraping the surface of shells, feeding on the particles removed, as well as clipping and consuming small algal fronds (Caine 1975, Kropp 1981, A.L. Hollebone *personal observation*). We determined the impact of *P. armatus* activities on microalgal growth at weeks 2, 4, 6, 8 and 12 by collecting material growing on oyster surfaces and using chlorophyll *a* as a proxy for biomass (see also Duffy *et al.* 2001). During a period of simulated low tide we scraped three randomly selected 1 cm^2 areas using a metal spatula. The three scrapings from each basket were pooled, stored at 4º C for no more than 24 hours, and then filtered onto a glass microfiber GF/F filter, which was stored in the dark at -20º C for ≤30 days before assessing chlorophyll.

We extracted chlorophylls in 90% acetone (HPLC grade) for ~24 hours at -20º C. Following extraction, samples were sonicated for 30 to 60 seconds, allowed to extract on ice for 20 to 30 additional minutes, and then centrifuged. The high concentrations of pigments in our samples were diluted with 90% acetone so as not to overwhelm the fluorometer readings (Turner Designs 10-AU Fluorometer). Periphyton (chlorophyll *a*) and phaeophyton (following the addition of 1 drop of 2 molar hydrochloric acid) content were calculated by an adaptation of Parsons *et al.* (1984). Chlorophyll *a* measurements were log transformed to achieve normality and equality of variances, and treatments were compared over time using a repeated-measures ANOVA.

At 8 weeks, green macroalgae (*Ulva sp.* and *Enteromorpha sp.*) became commonly seen in the mesocosms. At this time, we quantified algal cover using a quadrat that fit the length and width of the basket and had 100 randomly selected points. We assessed algal cover in the same manner upon completion of the experiment at week 12. A comparison of algal cover in treatments with 0 versus 1500 crabs m^{-2} was performed using a two-tailed t test following arcsine transformation of the data. We used the Welch's modification of the t test for the 12 week data due to heterogeneous variances.

Initial Field Study: Summer 2004

We assessed the impact of *Petrolisthes armatus* on oyster reef communities in a more natural setting by constructing a series of isolated oyster reef communities in the field, adding natural densities of invasive crabs to half of these communities, and sampling throughout peak periods of crab recruitment during the summer of 2004 (Hollebone and Hay *in review*). Twelve replicated blocks of five community types were established as part of a larger study (see Chapter 2). We only used two community types for this particular study: (1) a 4 native species community composed of live oysters, mussels, mud crabs (potential predator), and oyster drills (oyster predator) and (2) the same 4 native species community but with the equivalent of 750 *P. armatus* adults (≥5.5 mm CW) m^{-2}.

Each community was established in plastic baskets (0.29 m x 0.23 m) with perforated sides (twelve 6 cm long and 1.5 cm tall half-moon shaped holes along the lengths, four of the same holes plus one 10.5 cm long and 3 cm tall hand hold on both ends) and an open top that allowed for the movement of organisms into and out of the basket. We included three subsamplers within each basket, as described previously, for periodic, minimally disruptive assessment of community composition.

Before placing communities in the field, all oysters and mussels were manually defaunated of macro-organisms, and the carapace width (CW) of all mud crabs and porcelain crabs seeded in the communities were measured. We established our communities with natural densities of each organism, using data obtained from local monitoring efforts during the spring of 2004 (Hollebone and Hay *in review*). Each community was composed of approximately 1.5 liters of live oysters and 10 mussels, 15 oyster drills (labeled by painting the upper edge of the aperture with red nail polish), and 3 large (>18 mm CW) and 5 small (10 to 18 mm CW) mud crabs. We also incorporated 10 measured and individually labeled oysters and mussels, as described previously.

We placed the blocked communities on three isolated mud flats near Savannah, Georgia ([1] N 31º 57.042’, W 80º 58.982’, [2] N 31º 56.739’, W 80º 58.641’, [3] N 31º 57.618’, W 80º 57.006’). These mud flats lacked oyster reefs, thus preventing adult crab migration from nearby habitats and limiting recruitment to colonization from the plankton. All blocks were established ≥20 meters from the edge of the nearest oyster reef or from other replicates and each basket was 5 meters from its neighbor. All community types were randomly placed within each blocked array. The baskets were anchored on top of the sediment (using 46 cm rebar stakes on each side) along a transect 0.3 to 0.5 meters above mean lower low tide and oriented lengthwise to the incoming tide. All baskets were covered with PVC-coated chicken wire (same material used for subsamplers) to avoid oyster wash-out by physical disturbance.

We monitored the communities at 2, 4, 8, and 12 weeks. During each sampling period only six of the original twelve blocks were sampled due to limited working time during the low tides (~2 to 4 hours). Every other block was sampled so that representative blocks from all three mud flats were assessed and no two blocks directly next to one another were visited. The baskets sampled were alternated for each sampling period.

We followed recruitment and adult crab dynamics of *Petrolisthes armatus* as well as native taxonomic richness over time by randomly selecting one subsampler from each basket in the 6 blocks sampled at each assessment period. All organisms within the subsampler were separated from sediments using a 500 micrometer sieve and recorded. All porcelain crabs were counted, sized (those ≥5.5 mm CW or <5.5 mm CW), and sexed (those crabs ≥5.5 mm CW). All materials and organisms were returned to the basket within their original sampler as quickly as possible. We also obtained microalgal samples for chlorophyll *a* analysis, as described previously. In most cases, though, we had low replication (n = 3 or 4) because of time limitations due to the duration of low tides.

At week 12, we brought all baskets to the laboratory. Two of the three blocks established at mudflat site 3 had been filled with shifting sediments, so these blocks were eliminated. During this final sampling we assayed the more numerous, smaller organisms from one of the subsamplers and sorted through the remainder of each basket to assess more sparsely distributed macrofauna such as crabs, fishes, oysters, mussels, and oyster drills. Measurement of oysters and mussels to determine growth and survivorship was performed as described previously. Crabs were identified, counted, sexed, and measured (CW). Fish were identified and counted. Oyster drills were identified as those with or without markings and as alive or dead. For live drills with markings, growth was measured as the distance between the edge of the red marking and the aperture, taking into account shell curvature. Oyster recruitment was determined by counting the number of juvenile oysters on each labeled (previously defaunated) oyster. Surface area of these marked oysters was determined by wrapping the animal in aluminum foil and cutting the foil to size, removing and flattening the foil, and measuring the foil with an area meter (LI-COR, LI-3100) 5 times to determine a mean surface area. The number of juvenile oysters cm^{-2} was then calculated.

Data from this field experiment were analyzed similarly to the analyses described for the mesocosm experiments. In most contrasts between communities initially with porcelain crabs and communities initially without porcelain crabs, we anticipated that *P. armatus* would suppress local species due to competition (e.g., bivalve growth) or physical disturbance; for these contrasts we used one-tailed t tests. We used two-tailed tests in cases where we were uncertain of the response *a priori* due to many possible direct and indirect interactions. We determined shifts in mean adult porcelain crab densities over time by log transforming the data, and performing a repeated-measures ANOVA. We assessed effects of the introduced crab on native taxonomic richness and microalgal biomass over 12 weeks using repeated-measures ANOVAs after testing for normality and equality of variances. We compared the settlement of juvenile bivalves (oysters, mussels, and Antillean sphenia clams [*Sphenia antillensis*]) both combined and separately as well as oyster drill survivorship between communities initially with and without *P. armatus*. For all of these comparisons we used two-tailed t tests (paired for the mussel and drill data) with the exception of the clams which were compared using a Mann-Whitney non-parametric test. Oyster drill survivorship data were arcsine transformed prior to statistical comparison. The impact of the introduced crab on goby densities was assessed using a two-tailed t test with Welch's modification (Zar 1999).

Follow-up Field Study: Summer 2005

In the 2004 field experiment, we determined that we could not exclude the invasive crabs from our control reefs for more than 2 to 4 weeks due to their rapid recruitment from the plankton and their rapid post-settlement growth. The 12 week experiment therefore did not allow an assessment of oyster growth with and without high densities of *Petrolisthes armatus* because high densities of the crab were in both treatments after 4 weeks. To determine the impact of *P. armatus* on the growth of oysters in a field setting, we again established communities with and without *P. armatus* in mud flats near Savannah, Georgia during the summer of 2005. The experimental design included three community types (see Chapter 2), but we were interested in only two of these three treatments for this particular study. These communities of interest contained: (1) live, defaunated oyster substrate or (2) oyster substrate seeded with adult porcelain crabs (≥5.5 mm CW, 40 crabs basket^{-1} or ~1200 crabs m^{-2}). We increased the density of porcelain crabs in this follow-up study compared with the initial study (1200 versus 750 crabs m^{-2}) in an attempt to more closely approximate field densities, which commonly ranged from ~1,000 to 11,000 *P. armatus* m^{-2} in the summer (Hollebone and Hay *in review*). The final density we used fell towards the lower end of natural densities during warmer months (Hollebone and Hay *in review*), but our use of larger crabs (more easily seen and captured) resulted in an estimated biomass of ~1320 to 1800 grams wet mass m^{-2} which was large relative to mean levels normally noted during field monitoring (~800 grams wet mass m^{-2}).

We minimized sorting effort by halving the size of the baskets used in the summer of 2004 by securing 0.6 cm plastic vexar across the center width of the basket. Half of each basket was filled with defaunated live oyster substrate and treatment-specific crabs; the other half remained empty. The treatment basket types were randomly assigned a position in each of 10 blocks arrayed linearly along the intertidal. Each array was ≥20 m from the nearest oyster reef and ≥10 m from neighboring arrays. Baskets within an array were 5 m from each other at ~0.5 m above mean lower low. The baskets were secured in the sediment and covered with PVC-coated chicken wire as described previously. The experiment ran for only 4 weeks so as to minimize invasive crab recruitment to, and growth to adult size in, our control treatments. All live, labeled oysters were measured upon termination of the experiment. A comparison of oyster growth between treatments without *Petrolisthes armatus* and those with ~1200 *P. armatus* m^{-2} was performed using a one-tailed paired t test due to a suggestion from the mesocosm study that porcelain crabs suppress oyster growth.

Results

Who eats whom?

In the mesocosms, we observed *Petrolisthes armatus* both filter feeding and scraping benthic surfaces. *P. armatus* scraped surfaces using the ventral margin of its chelipeds (claws) which were brought near the mouth, cleaned by the second maxillipeds, and then food particles were inserted into the mouth. When 11 adult *P. armatus* were offered brine shrimp of ~7 to 10 mm in length in the lab, all were rapidly consumed, indicating the capacity to feed on crustacean larvae of this size. However, when adult *P. armatus* were offered conspecific zoea of a similar size, only 2 of the 7 crabs consumed these larvae despite all 7 consuming the brine shrimp ($p = 0.020$, Fisher's Exact test with Yates correction for continuity). This suggests a reluctance of *P. armatus* to consume its own young.

When *Petrolisthes armatus* zoea were offered to 8 actively filtering oysters, each oyster ingested the larva (closed their valves and stopped filtering), but within minutes opened and released the larva live and intact. In contrast to this rejection by a dominant, benthic filter feeder, most native fishes and crabs readily consumed *P. armatus* larvae or adults. When 15 juvenile pompano (*Trachinotus carolinus*) were each confined with 10 *P. armatus* zoea for 1 hour, 75 ± 8% (mean ± SE) of all zoea were consumed. Adult *P. armatus* offered to native fish, mummichog (*Fundulus heteroclitus*) and spot (*Leiostomus xanthurus*), suffered different fates. Sixteen of 16 mummichogs immediately consumed the invasive crab, while only 1 of 10 spot did so despite all spot readily consuming a paired piece of commercial fish food offered just after rejecting the crab ($p < 0.001$, Fisher's Exact test with Yates correction for continuity). When adult *P. armatus* were confined with mud crabs (*Panopeus herbstii*) for 24 hours, 7 of 10 mud crabs consumed the invasive crab. Seven individual lesser blue crabs (*Callinectes similis*) rapidly consumed *P. armatus* across all size ranges offered. Thus, with the exception of small spot (50 to 80 mm standard length), all local consumers we tested readily consumed the invasive crab.

Panopeus herbstii, the common mud crab, is the native consumer most closely associated with *Petrolisthes armatus* due to their co-occurrence at high densities within the same oyster reefs (Hollebone and Hay *in review*). When confined with adult *P. armatus*, as well as both large and small mussels and oyster drills, the native crab consumed the invasive crab in preference to all other prey ($p < 0.001$, G test, Figure 3.1). The invasive crab was also rapidly consumed when tethered in the field. Of the 15 to 20 *P. armatus* adults tethered in oyster reefs or on nearby mudflats for one complete high tide cycle (12 hours), 90% and 95% of crabs on mudflats were consumed during the day and night, respectively, whereas 95% and 60% of crabs in oysters were consumed during the day and night, respectively. Survivorship in these assays differed significantly among the 4 conditions ($p = 0.023$, G test). This result may be most strongly influenced by decreased consumption in the oysters at night.

Mesocosm Experiments

Petrolisthes armatus did not recruit to the 0 crabs m^{-2} treatment during the first 9 weeks of our mesocosm experiment and appeared at a mean density (± SE) of only 8.7 ± 5.8 crabs m^{-2} at 12 weeks. Mean density in the 1500 crabs m^{-2} treatment held relatively steady at ~1200 to 1600 crabs m^{-2} for the first 6 weeks of the experiment (likely aided by crab additions following sampling at weeks 2, 3, 4, and 6), but then declined considerably (Figure 3.2A). Densities in the treatments with seeded porcelain crabs always exceeded those in the control ($p < 0.001$, Figure 3.2A), but densities in the crab addition treatment at week 7 were significantly lower than densities in this treatment at week 3 ($p = 0.002$, two-tailed paired t test).

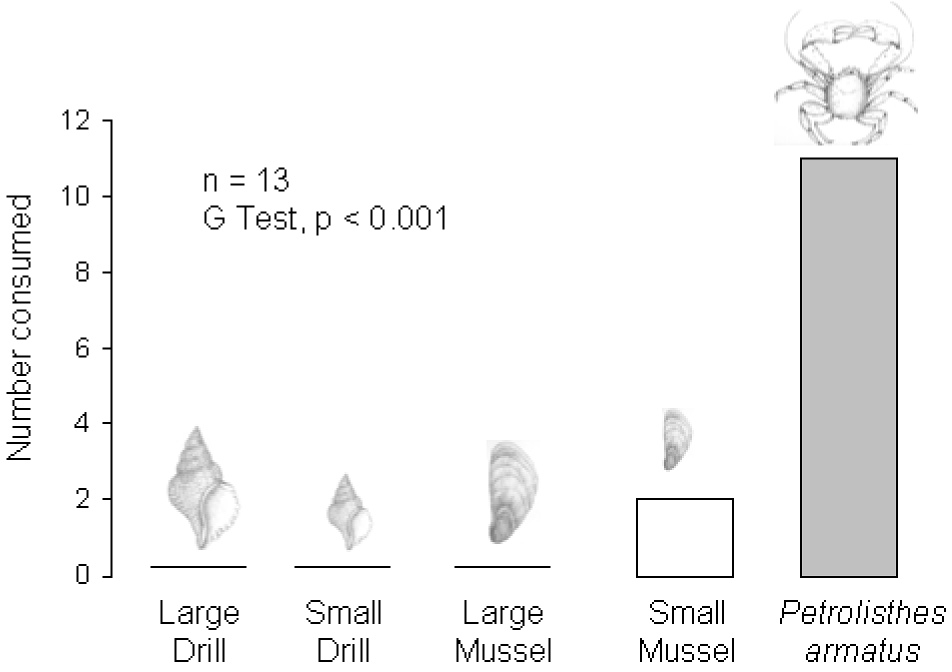


Figure 3.1. Laboratory choice feeding assay. Bars show the number of available prey consumed first by a single *Panopeus herbstii* within a 24 hour period. P value derived from a G test.

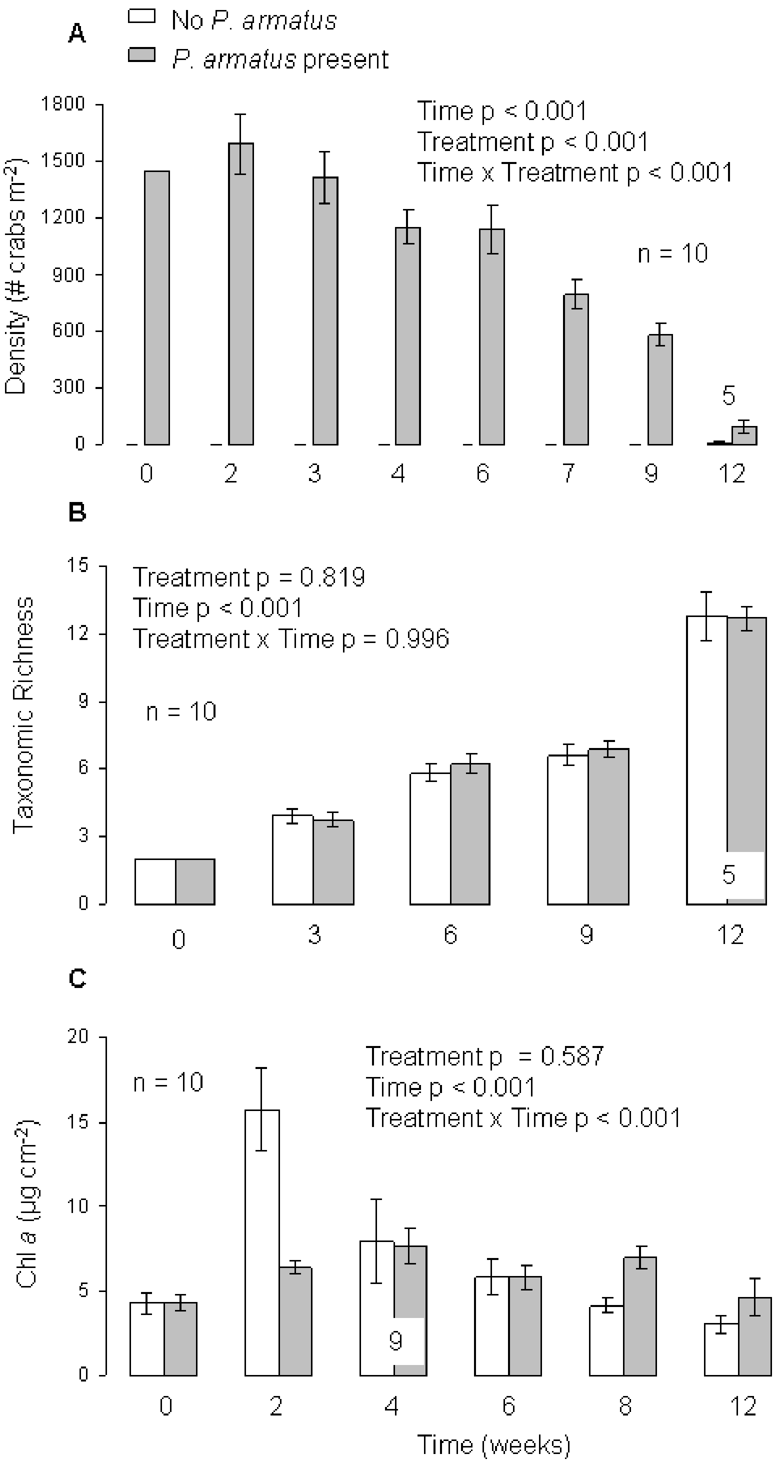


Figure 3.2. (A) Mean densities (scaled to 1 m^2, ± SE) of adult *Petrolisthes armatus* in our mesocosm treatments over 12 weeks. (B) Mean native taxonomic richness (± SE) in mesocosm tanks over 12 weeks. (C) Mean microalgal biomass (± SE) on oyster surfaces during the mesocosm experiment. N = 10 unless otherwise indicated at the base of the bars. P values derived from a repeated-measures ANOVA for all of the above.

Presence of *Petrolisthes armatus* had no effect on the number of native taxa recruiting ($p = 0.819$, Figure 3.2B). The number of native taxonomic groups, or species if identifiable under field conditions, increased over time across all treatments with a maximal mean number of ~13 basket^{-1} at 12 weeks (with the most common taxa being: *Boonea impressa*, *Panopeus herbstii*, *Eurypanopeus depressus*, *Sesarma cinereum*, *Cliona spp.*, *Brachidontes exustus*, Amphipoda, Tannaidacea, Polychaeta). The invasive crab had a modest effect on abundance of microalgae; it suppressed a bloom of microalgae that occurred only in the control treatments by week 2 ($p < 0.001$ for the interaction of treatment with time, Figure 3.2C). Although the invasive crabs initially suppressed microalgal abundance, *P. armatus* significantly enhanced the abundance of macroalgae (primarily green seaweeds in the genera *Ulva* and *Enteromorpha*) later in the experiment (weeks 8 and 12; $p \leq 0.001$ for both periods, Figure 3.3). At 8 weeks, the *Ulva* and *Enteromorpha* covered 24.0 ± 6.4% (mean ± SE) of the area in treatments without porcelain crabs and 63.0 ± 6.2% in areas with crabs. At 12 weeks, the same contrast was 2.0 ± 1.4% and 20.8 ± 2.9%, respectively.

Although *Petrolisthes armatus* rejected conspecific larvae as food, our mesocosm data suggested that the invasive crab may have consumed settling mud crab larvae (*Eurypanopeus depressus* and *Panopeus herbstii*) or suppressed their recruitment in some other way. Recruitment of mud crabs was significantly higher to mesocosm baskets lacking the invasive crab than to baskets containing the crab ($p = 0.041$, Figure 3.4A). During weeks 3 to 6, mud crab densities were 54 to 192% higher in treatments without the invasive crab than in those with the invasive crab. Sizes of newly recruited mud crabs also tended to be smaller in the presence of *P. armatus* ($p = 0.055$, Figure 3.4B),

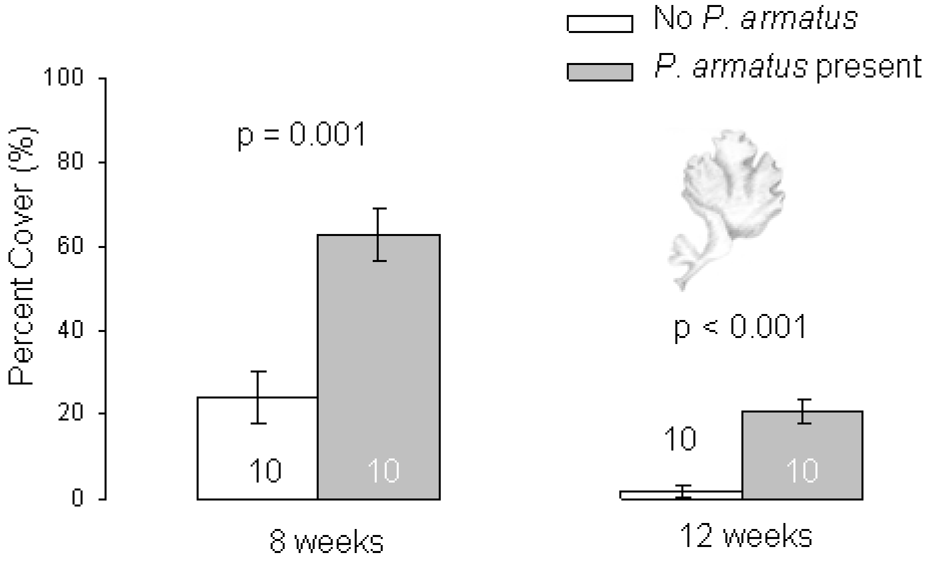


Figure 3.3. Macroalgal cover (mean ± SE) at 8 and 12 weeks in the mesocosm experiment. N shown within or directly above the bars. P values derived from two-tailed t tests with Welch's modification to the 12 week data.

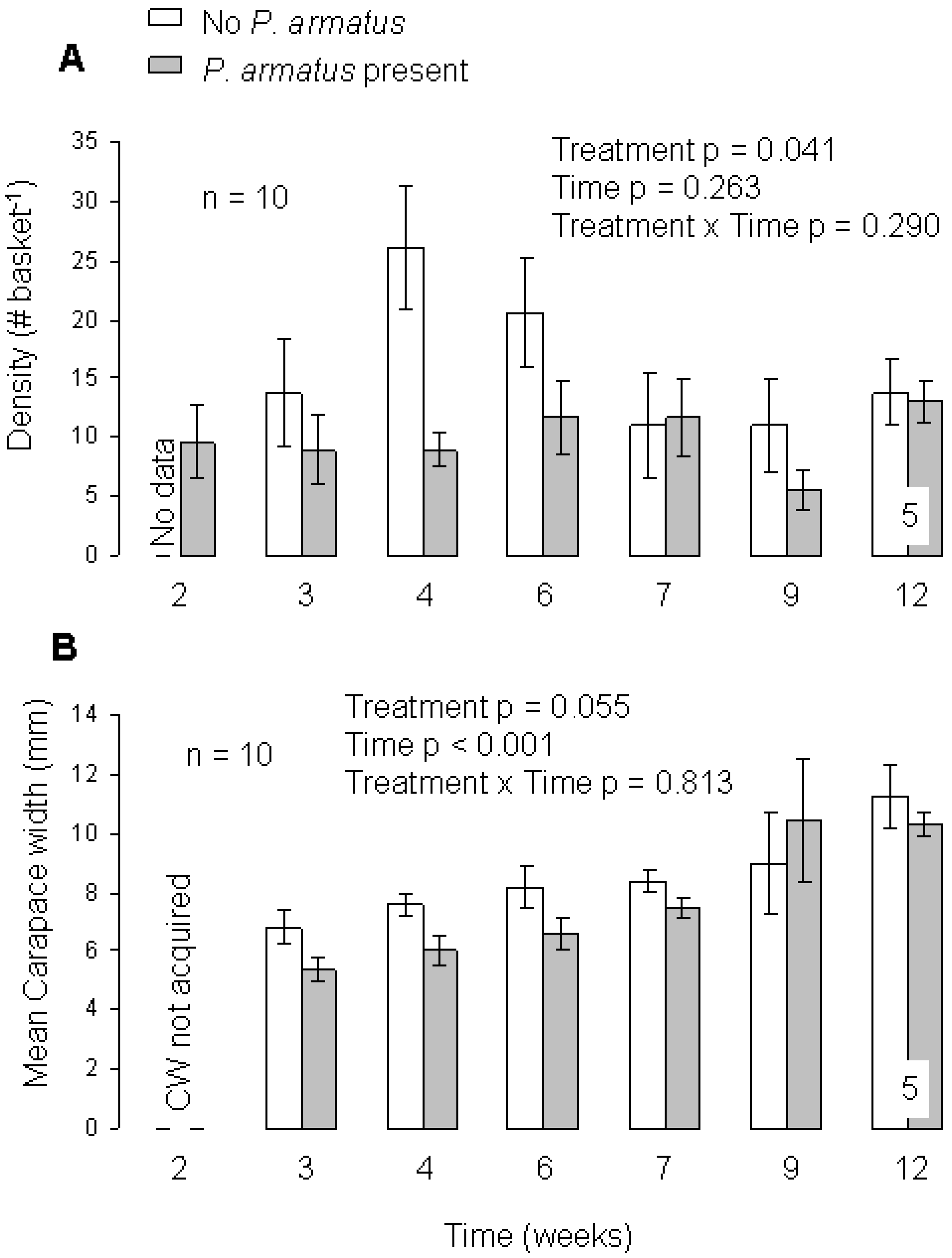


Figure 3.4. (A) Mean density (scaled to 1 basket, ± SE) of newly recruited mud crabs in the mesocosm experiment over 12 weeks. (B) Mean carapace width (± SE) of mud crabs in the mesocosm experiment over 12 weeks. N = 10 unless otherwise indicated at the base of the bars. P values derived from a repeated-measures ANOVA for both analyses.

suggesting suppression of growth as well.

The growth of small oysters (initial length ≤60 mm) in the presence of *P. armatus* was suppressed by a significant 84% ($p = 0.048$, Figure 3.5A) at week 4 of the mesocosm experiment. Growth of oysters across a larger range of initial lengths (30 to 90 mm) decreased by 51% in the presence of crabs (mean growth ± SE, 1.7 ± 0.9 mm without crabs and 0.8 ± 0.4 mm with crabs), but this difference was not significant ($p = 0.204$, one-tailed t test with Welch's modification), possibly due to relative growth decreasing with increasing size, thus lessening our ability to detect differences over the 4 week period. Alternatively, the invasive crab may suppress growth of smaller but not larger oysters. At week 12, we recovered only (mean ± SE) 16.0 ± 4.0% and 21.5 ± 3.3% of all labeled oysters from treatments without and with *P. armatus*, respectively. Survivorship was not significantly different between the two treatments over 12 weeks ($p = 0.175$, arcsine transformed, one-tailed paired t test). It was not clear whether lack of recovery was due to death or to detachment of the numbered tags from the oyster valves. This low rate of recovery and our focus on smaller oysters led to low replication, preventing meaningful analysis of oyster growth over the 12 week period.

Effects on mussels differed from the effects on oysters. There was no effect of the invasive crab on smaller mussels at 4 weeks (initial length ≤30 mm; $p = 0.231$, one-tailed t test, Figure 3.5B). The presence of *Petrolisthes armatus* also did not affect mussel growth (mean ± SE) across an entire range of size classes (22 to 42 mm initial length) at either 4 weeks (1.6 ± 0.2 mm without porcelain crabs and 1.6 ± 0.2 with porcelain crabs present) or 12 weeks (4.2 ± 0.5 mm without porcelain crabs and 4.0 ± 0.4 mm with porcelain crabs) ($p \geq 0.204$ for 4 and 12 weeks, one-tailed paired t test). Mean

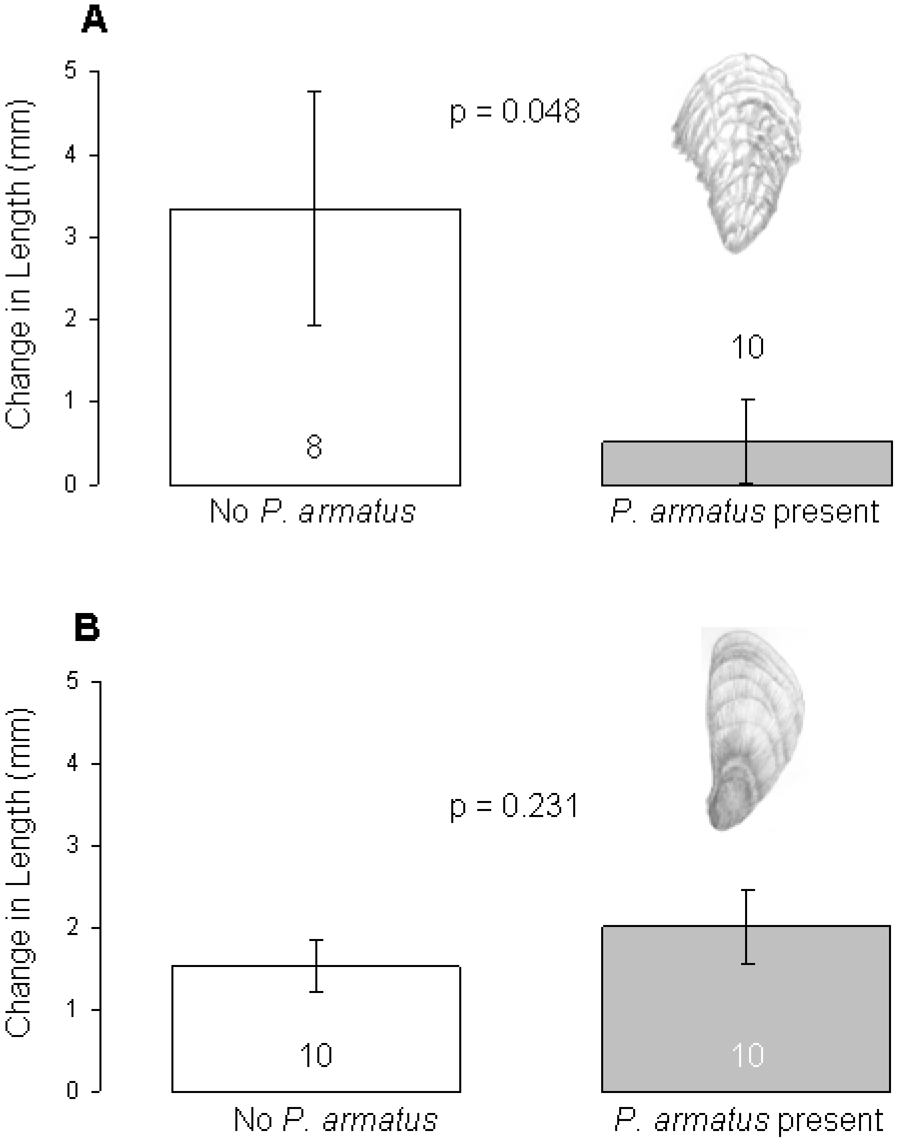


Figure 3.5. (A) Mean growth (± SE) of small oysters (initial length ≤ 60 mm) in the mesocosm experiment after 4 weeks. (B) Mean growth (± SE) of small mussels (initial length ≤ 30 mm) in the mesocosm experiment after 4 weeks. N is shown within or directly above the bars. P value for the oysters derived from a one-tailed t test with Welch's modification. P value for the mussels derived from a one-tailed paired t test.

survivorship (± SE) for mussels over the 12 weeks was higher than for oysters (69.0 ± 5.9% without the invasive crab and 74.0 ± 4.1% with the crab) and did not differ as a function of invasive crab presence ($p = 0.400$, arcsine transformed, one-tailed paired t test).

The decline of *Petrolisthes armatus* starting at about week 7 of the mesocosm experiment coincided with recruiting mud crabs growing to mean sizes of 7.5 to 11.5 mm CW, but with some sampled crabs at week 7 being 13 mm CW, some at 9 weeks being 18 to 24 mm CW, and many at 12 weeks being 18 to 32 mm CW. We suspect that mud crabs within the above-mentioned size ranges would be able to prey on adult *P. armatus*. Thus, the decline in densities of *P. armatus*, as well as the loss of many marked oysters could be related to the recruitment and growth of these predators into the mesocosm system. If predation by this crab is a reason for low oyster survival, then they prefer oysters to mussels, because mussel survival was considerably higher than that of oysters in these assays.

Field Experiments of 2004 and 2005

When we constructed small oyster reefs on isolated mudflats, adult *Petrolisthes armatus* were only absent from 0 porcelain crab m^{-2} treatment for the first 2 weeks of the experiment. Rapid recruitment to and growth of *P. armatus* within these treatments elevated the density of adult crabs (>5.5 mm CW) in the "control" to 180 to 980 crabs m^{-2} at weeks 4 to 12 (Figure 3.6A). In communities where we initially added the equivalent of 750 adult *P. armatus* m^{-2}, densities declined within the first 2 weeks to about 315 crabs m^{-2}, but then rebounded to 600 to 1350 crabs m^{-2} at weeks 8 and 12. Densities of invasive crabs differed significantly between our treatments for weeks 0 and 2 ($p = 0.007$,

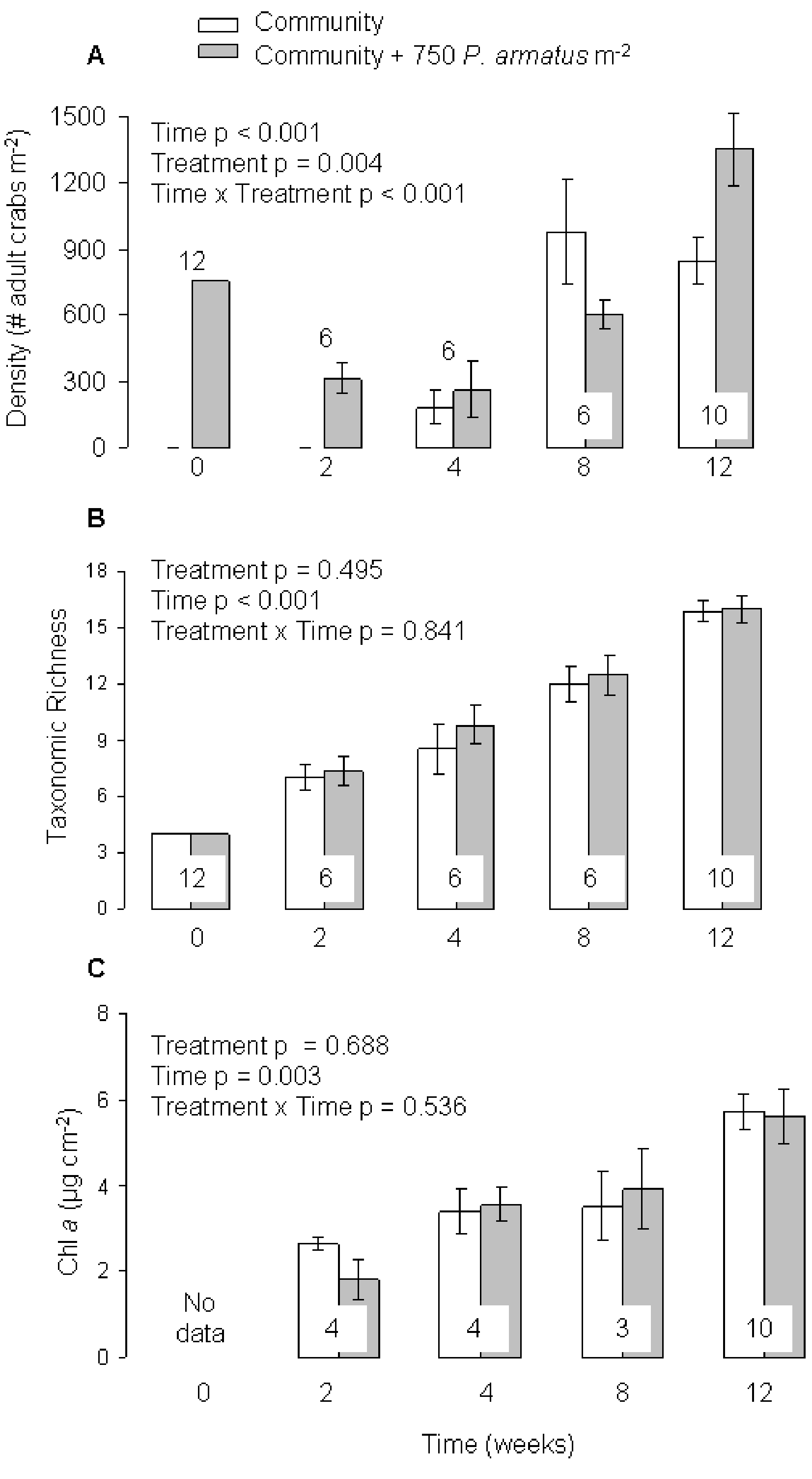


Figure 3.6. (A) Mean densities (± SE) of adult *Petrolisthes armatus* (≥ 5.5 mm CW) in the 2004 field experiment over 12 weeks. (B) Mean native taxonomic richness (± SE) in the 2004 field experiment over 12 weeks. (C) Mean microalgal biomass (± SE) on oyster surfaces during the 2004 field experiment. N is shown within or directly above each set of bars. P values derived from a repeated-measures ANOVA for all of the above.

two-tailed paired t test), but not thereafter ($p > 0.100$, two-tailed paired t tests at each sample interval). Therefore, we only maintained a treatment for 2 to 4 weeks, suggesting that the impacts we observed between 4 and 12 weeks may be conservative.

As we saw in the mesocosm experiment, presence of the invasive crab did not affect the taxonomic richness of natives colonizing our treatments ($p = 0.495$, Figure 3.6B). This could be a result of the loss of treatment at 2 to 4 weeks, but the significant impacts we saw for individual species (see discussion below) suggested a lasting effect of the initial crab addition treatments. The number of native taxa did increase over time across both treatments, with a maximal mean number of 16 species basket^{-1} at week 12 (common taxa included: *B. impressa*, *P. herbstii*, *E. depressus*, *B. exustus*, *Gobiosoma bosci*, *Membranipora tenuis*, *Phyllodoce fragilis*, *Glycera dibranchiate*, *Palaemonetes vulgaris*, *Alpheus heterochaelis*, *Clibanarius vittatus*, *Menippe mercenaria*, *Sphenia antillensis*, *Molgula manhattensis*, *Balanus sp.*, *Sabellaria sp.*, Cephalaspidea, Collumbellidae, Amphipoda, Nereid polychaete, Serpulid worm, Hydroida). In the field we saw no effect of the invasive crab on microalgal abundance ($p = 0.688$, Figure 3.6C), but the limited time for working during the low tides constrained our ability to acquire samples, resulting in a lower sample size and, thus, limited statistical power. However, the general lack of effect of *P. armatus* on microalgal abundance in the field is similar to that seen in the mesocosm experiment with the exception that there was no bloom as seen in the mesocosm controls at week 2 (compare Figures 3.2C and 3.6C).

Recruitment of bivalves was significantly enhanced by the presence of the invasive crab (Figure 3.7). In treatments initially seeded with 750 adult *Petrolisthes armatus* m^{-2} the mean density (± SE) of all juvenile bivalves increased by a significant

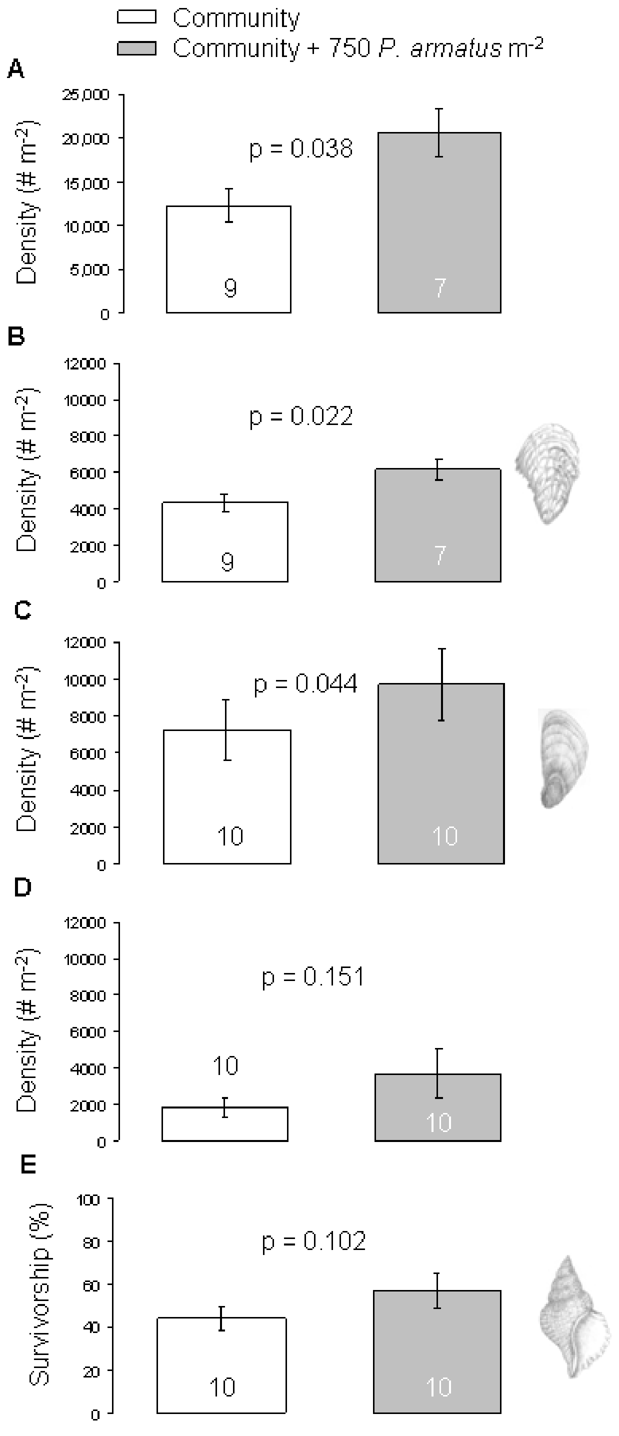


Figure 3.7. Mean density (scaled to 1 m^2, ± SE) of bivalve recruits or survivorship of oyster drills after 12 weeks in the 2004 field experiment: (A) Total bivalves, (B) oyster, (C) mussel, (D) clam, and (E) oyster drill. N is shown within or directly above each bar. P values derived from two-tailed t tests of unequal sample size for (A) and (B), two-tailed paired t test for (C), Mann-Whitney non-parametric test for (D), and arcsine transformed, two-tailed paired t test for (E). Marked oysters were lost from a few replicates, thus lowering the sample size for oyster analyses and total bivalve analyses.

68% (from 12,304.7 ± 1887.5 to 20,638.4 ± 2700.6 individuals m^{-2}, $p = 0.038$, two-tailed t test, Figure 3.7A), of juvenile oysters by a significant 43% (from 4330.3 ± 490.0 to 6182.3 ± 510.0 individuals m^{-2}, $p = 0.022$, two-tailed t test, Figure 3.7B), of juvenile mussels by a significant 34% (from 7256.5 ± 1606.8 to 9701.8 ± 1922.3 individuals m^{-2}, $p = 0.044$, two-tailed paired t test, Figure 3.7C), and of juvenile Antillean sphenia clams by a non-significant 93% (from 1908.5 ± 527.0 to 3677.9 ± 1,351.7 individuals m^{-2}, $p = 0.151$, Mann-Whitney test, Figure 3.7D) compared to the control. Mean survivorship (± SE) of marked oyster drills was also a nearly significant 30% higher in the treatment with seeded *P. armatus* (44.0 ± 5.3% without porcelain crabs and 57.3 ± 8.1% with porcelain crabs, $p = 0.102$, two-tailed paired t test, Figure 3.7E). These observations are consistent with the hypothesis that native mud crabs are diverting their attention from native prey to the more abundant and preferred invasive crab (Figure 3.1), thus reducing their consumption of native bivalves and gastropods. Although *P. armatus* affected the survivorship of marked oyster drills, there was no between-treatment difference in mean growth (± SE) of the drills. Drills grew 7.5 ± 1.4 mm in treatments where there were initially no porcelain crabs and 7.7 ± 1.6 mm where adult porcelain crabs were added ($p = 0.955$, two-tailed paired t test).

During the field study of 2004, mean recovery of marked oysters and mussels was only between 5 and 10% as a result of mortality (possibly due to the inclusion of large mud crab predators or anoxia), loss of labeling tags, or washout from the baskets. This produced too few measurements to adequately assess the effect of porcelain crabs on adult bivalve growth during this 12 week assay.

There was a suggestion that *Petrolisthes armatus* affected recruitment of native fish that live within the oyster reef structure. Naked gobies (*Gobiosoma bosci*) were 34% less numerous in experimental oyster reef communities to which we initially added *P. armatus* (5.7 ± 0.7 fish basket^{-1}) than to communities initially devoid of the invasive crab (8.6 ± 1.7 fish basket^{-1}), but this difference was not significant ($p = 0.134$, two-tailed t test with Welch's modification). This difference may be overly conservative because these densities were obtained at week 12 of the experiment, and the difference in our porcelain crab additions to each treatment was only effective for the first 2 to 4 weeks (Figure 3.6A).

Because we could not maintain treatments for more than 2 to 4 weeks in our 2004 field experiment (Figure 3.6A) and we wanted to ensure that the depression of oyster growth observed in the mesocosm experiment (Figure 3.5A) would occur under field conditions, we conducted a focused 4 week field study in the summer of 2005 to address our concerns. Small marked oysters (initial length ≤50 mm) placed into isolated, experimental oyster reef communities that were not initially seeded with *P. armatus* grew a significant 28% more than oysters in experimental communities initially seeded with the equivalent of 1200 crabs m^{-2} ($p = 0.040$, one-tailed paired t test, Figure 3.8).

Discussion

Biological invasions pose serious threats to the function and maintenance of native communities (Carlton and Geller 1993). In marine systems, non-indigenous species have fundamentally changed community composition in areas such as the San Francisco Bay and the Chesapeake Bay (Ruiz *et al.* 1999). The effects of previous invasions coupled with the densities at which we find *Petrolisthes armatus* in oyster reefs

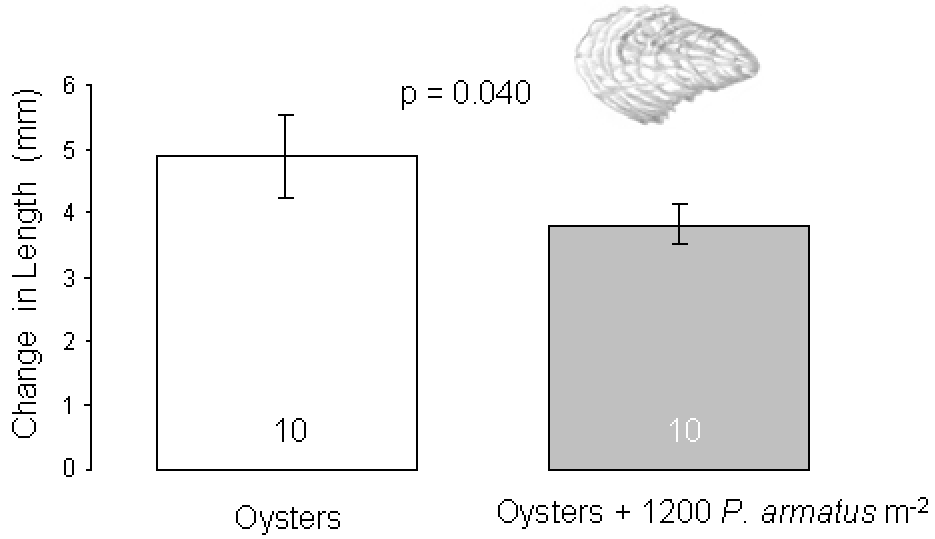


Figure 3.8. Mean growth (± SE) of small oysters (initial length ≤50 mm) in the 2005 field experiment. N shown within each bar. P value derived from a one-tailed paired t test.

of the South Atlantic Bight (mean densities of up to 11,000 crabs m^{-2} or ~3 to 5 billion crabs year-round along Georgia's ~170 km of coast, Hollebone and Hay *in review*) raise concern about the impacts of these invaders on native communities.

Through mesocosm and field experiments, we assessed the impact of the invasive crab on native species and communities. The densities at which we seeded our experimental units (750 to 1500 crabs m^{-2}) were well-within the natural range of densities seen in the field (Hollebone and Hay *in review*), but these densities had no detectable effect on native taxonomic richness, despite richness of native taxa increasing considerably over time in both the field and mesocosm experiments (Figures 3.2B and 3.6B). However, our ability to assess this rigorously in the field was constrained due to rapid recruitment and growth of the invasive crab in our control treatments by 4 weeks (Figure 3.6A). Despite not having an overall impact on native taxonomic richness and our inability to prevent *P. armatus* from colonizing our "control" reefs in the field, our experiments did document strong effects of *P. armatus* on virtually all of the most common native species associated with oyster reefs (e.g., oysters, mussels, clams, mud crabs, oyster drills, seaweeds, and potentially the naked goby) even following a period of several weeks without a porcelain crab treatment.

Bivalve Growth and Recruitment

Oyster populations in the southeastern United States have declined in recent decades as a result of habitat destruction, overharvesting (e.g., Lenihan and Peterson 1998, Kirby 2004, Lenihan and Peterson 2004), and disease (e.g., Bushek *et al.* 1996, Davis and Barber 1999, Ford and Borrero 2001). The recruitment of *P. armatus* at densities of up to several thousand m^{-2}, could add additional stress on this foundation species.

In our mesocosm experiment, the non-native crabs significantly depressed growth of small oysters within the first 4 weeks of exposure (Figure 3.5A), suggesting that porcelain crabs will slow the growth of juvenile oysters and keep oysters in smaller size classes which are more susceptible to both physical (Stanley and Sellers 1986) and biotic stresses (e.g., Brown 1997, Ford and Borrero 2001). Exotic crabs also suppressed juvenile oyster growth in the 2005 field experiment (Figure 3.8), demonstrating that our initial results were not an artifact of the mesocosm experiment. Suppression of oyster growth could occur because (1) oysters and porcelain crabs are both filter feeders and, therefore, compete for a common food resource, and/or (2) the high density of active crabs disturbs oysters, causing frequent closure of shells and resulting in the loss of feeding time.

At 4 weeks, crab densities of 1500 m^{-2} in the mesocosms suppressed growth of small oysters by 84% compared to the treatment without the invasive crab (Figure 3.5A). In the field at crab densities of 1200 m^{-2}, growth was suppressed by 28% (smaller effect size possibly due to the loss of our crab treatment within the first 2 to 4 weeks of the field study; Figure 3.8). This depression of oyster growth in both the mesocosms and the field could be conservative because mean summer densities of *Petrolisthes armatus* on oyster reefs near these sites are commonly in the range of 1000-11,000 crabs m^{-2} (Hollebone and Hay *in review*). Crabs rapidly recruited to our control treatments in the field, precluding our ability to measure oyster growth in the complete absence of the exotic crab and limiting our assays to the first 4 weeks of experimentation. Higher densities of crabs over longer periods of time might more strongly suppress juvenile oyster growth or impact growth of larger size classes; effects we could not demonstrate in this assay. Suppression of oyster growth by *P. armatus* suggests that its invasion could keep annually recruiting oysters in smaller size classes, thus negatively impacting fisheries, aquaculture, and natural areas (Office of Technology Assessment 1993) where oyster reefs constitute the biogenic structure on which many other species rely (Lenihan and Peterson 1998).

In contrast to oysters, growth of mussels was unaffected by *Petrolisthes armatus* (Figure 3.5B). They grew well (~2.5 mm over 12 weeks) and survived at ~70% in both the presence and absence of *P. armatus*. Why the invasive crabs suppressed oyster growth but not mussel growth is not clear.

Although the invasive crabs primarily filter feed on detritus, algae, and zooplankton (Caine 1975) and would consume brine shrimp in the lab (thus indicating that they could potentially prey on larger invertebrate larvae), their presence enhanced, rather than retarded, recruitment of juvenile native bivalves such as oysters, mussels, and the clam *Sphenia antillensis* (Figure 3.7A-D). Thus, they either avoided consuming bivalve larvae, as was the case for avoidance of their own larvae, or their scraping of surfaces and removal of biofilm enhanced oyster recruitment more than their filter feeding removed larvae. Alternatively, and consistent with laboratory feeding assays (Figure 3.1), the invasive crabs may serve as alternate prey for a local consumer that normally consumes juvenile bivalves. Mud crabs commonly prey on native oysters, mussels, and snails (Lee and Kneib 1994, Silliman *et al.* 2004), but selectively consumed *P. armatus* in preference to native species when all were simultaneously available in the lab (Figure 3.1). Given the high density, high palatability, and rapid recruitment of the invasive crab, mud crab feeding may be shifting from native species to this introduced prey, thus increasing the survival and density of native prey species.

The suggestion that *Petrolisthes armatus* is commonly eaten by native consumers is supported by: (1) the rapid and preferential rate at which it is attacked in laboratory assays (Figure 3.1), (2) its rapid decline as predatory mud crabs became larger in the mesocosm experiment (compare Figures 3.2A and 3.4B), and (3) its rapid consumption when tethered in the field. Our tethering procedures could have produced unnaturally high rates of consumption because: (1) the tethers limit mobility of the crabs and/or (2) the tethers attract the attention of consumers. *P. armatus* individuals are thin, fast moving, and easily autotomize their limbs when attacked (A.L. Hollebone *personal observation*). Each of these traits may contribute to the minimization of mortality due to predation as *P. armatus* seek shelter within the interstices of oyster reefs. Tethers may have constrained these movements or visually attracted predators, which then pulled out the sheltered crabs (see crustacean tethering artifacts in Zimmer-Faust *et al.* 1994). However, the high densities of both the invasive crab and native mud crabs in oyster reefs (mean densities of up to ~11,000 and 1600 m^{-2}, respectively; Hollebone and Hay *in review*) suggest that contact in the field would be common.

Additionally, as mud crabs that had recruited to our mesocosm experiment grew to sizes at which they could prey upon the invasive crab, densities of *P. armatus* declined by >90% over a period of 5 weeks (Figure 3.2A). In our field experiment where we seeded the oyster reef communities with both the invasive crabs (≥5.5 mm CW) and adult mud crabs (>10 mm CW), a decline in invasive crab density of ~58% occurred in only 2 weeks (Figure 3.6A). We do not have unambiguous data demonstrating that these declines were due to mud crab predation, but these patterns in addition to the tethering experiment suggest that *P. armatus* may suffer heavy losses to native consumers under field conditions. The ability of the invasive crab to sustain high population densities despite such losses is apparently due to its rapid recruitment from the plankton. In field studies where we placed experimental oyster reef communities in isolated mud flats, *P. armatus* recruited at mean densities of ~17,000 to 35,000 crabs m^{-2} with individual baskets recruiting up to ~60,000 crabs m^{-2} over a 12 week period (Chapter 2).

Algal Biomass

Petrolisthes armatus initially suppressed microalgal biomass on oyster surfaces, but this strong initial effect (at week 2) was short-lived (Figure 3.2C). Porcelain crabs moving over oyster surfaces may have dislodged sediments and particulates that settled out of the water column and accumulated on the benthos. Also, porcelain crabs directly clip and consume microalgae growing on oyster surfaces in addition to filter-feeding. We observed this behavior in our mesocosms, and it has been reported by others as well (Caine 1975, Gabaldon 1979, Kropp 1981). The indirect removal of particulates due to porcelain crabs movements and the crabs' direct consumption of algae may moderate the levels of microalgae on oyster surfaces.

Despite suppressing microalgal biomass, porcelain crabs facilitated larger macrophytes. Abundance of *Ulva sp.* and *Enteromorpha sp.* was ~160% greater in mesocosms with the introduced crab than in those without the crab at week 8 and ~940% greater at week 12 (Figure 3.3). In our mesocosms, porcelain crabs may have been grazing microalgae, removing sediments, and thus making these surfaces more available to settling macrophytes. This has been documented for other small crustacean grazers that facilitate macrophytes by removing filamentous algae (Brawley and Adey 1981). The enhancement of larger algae by porcelain crabs suggests that they do not consume macroalgae. The macrophyte growth we noted in the mesocosms did not occur in our field experiments, suggesting that fishes or other crustaceans missing from our mesocosm treatments may remove macrophytes under field conditions or that some physical stress in the field prevents their accumulation.

Effects on Other Macrofauna

The addition of *Petrolisthes armatus* to native communities was associated with a 30% increase in survivorship of marked oyster drills (p = 0.102, Figure 3.7E). Like with juvenile bivalves, our feeding choice assay (Figure 3.1) suggests that native mud crabs may be attacking *P. armatus* in preference to native oyster drills, thus lessening predation on native prey and enhancing oyster drill survival. Shifts in predator diet from native species such as juvenile oysters, mussels, and oyster drills to non-native porcelain crabs may not only explain the elevated survivorship of oyster drills but also the increased recruitment of juvenile oysters, mussels, and *Sphenia antillensis* clams in the field (Figure 3.7B-D).

Petrolisthes armatus enhanced the recruitment of many potential native mud crab prey, but they suppressed the recruitment of juvenile mud crabs in the mesocosm experiment (p = 0.041, Figure 3.4A), and there was also an indication that the invasive crab suppressed the mean growth of native mud crabs as well (p = 0.055, Figure 3.4B). Thus, adult *P. armatus* significantly suppressed the recruitment of one of their potential predators. The magnitude of suppression ranged from 35 to 66% at weeks 3 to 6. *P.*

armatus densities in the mesocosms at this time were ~1145 to 1415 crabs m^{-2}. *P. armatus* densities in natural oyster reefs during the summer can be considerably higher (Hollebone and Hay *in review*), suggesting that this suppression could be common and potentially stronger in the field. Once mud crabs reach sizes >10 mm CW, we believe they can prey on *P. armatus*. The decline of the porcelain crabs in the mesocosm communities starting at approximately week 7 and the loss of marked oysters could be due to the growth of mud crabs that had recruited into the tanks to a size able to feed on crabs and oysters.

Petrolisthes armatus also tended to suppress recruitment of the naked goby, *Gobiosoma bosci*, during the 2004 field experiment. Goby densities after 12 weeks in the field were 8.6 ± 1.7 (mean ± SE) in baskets initially lacking *P. armatus*, but 5.7 ± 0.7 in baskets initially seeded with the equivalent of 750 *P. armatus* m^{-2} ($p = 0.067$). This 34% difference in goby densities was measured after 12 weeks, even though our *P. armatus* treatments were different from our controls for only the first 2 to 4 weeks of experimentation (Figure 3.6A). The naked goby is one of the most common resident fishes of oyster reefs in the southeastern United States, both hiding and foraging within the structure of the oyster reefs (Lehnert and Allen 2002). The recruitment of large numbers of invasive porcelain crabs into these reefs may lead to competition for space and the suppression of fish densities, or the consumption of settling fishes by *P. armatus*. Overall, the effects of *P. armatus* on native species that we documented in our field experiment could be conservative because our crab addition and removal treatments differed from each other for no more than the first 2 to 4 weeks of the 12 week experiment, whereas our data for juvenile bivalve densities, fish densities, and gastropod survival were collected at 12 weeks.

Summary

Petrolisthes armatus recently established on oyster reefs in the South Atlantic Bight at mean densities of up to several thousand crabs m^{-2}. Their large-scale, long-term effects on these important biogenic habitats have remained unknown. Through both mesocosm and field experimentation we demonstrated that this invasive crab could depress growth of juvenile oysters, microalgal biomass, recruitment of native mud crabs, and possibly density of a native fish, while facilitating bivalve (oyster, mussel, and clam) recruitment, macroalgal growth, and survivorship of predatory oyster drills (see Summary Table 3.1). These impacts occurred in experimental communities with relatively low densities of the introduced crab compared to field densities documented during warmer months of the year (Hollebone and Hay *in review*), and we were unable to maintain control treatments without *P. armatus* for more than 2 to 4 weeks in the field due to its recruitment to all treatments. The effects of greater crab densities in natural reefs over longer time periods could be more intense than the impacts we demonstrated during short-term, small-scale experimentation. Unfortunately, the tremendous recruitment (~2,100 to 7,900 crabs m^{-2} after 4 weeks in the 2004 field study and ~9,900 to 17,000 crabs m^{-2} after 4 weeks in the 2005 field study, Chapter 2) and growth rates of the crab made contrasts with field reefs lacking the crab impossible over longer periods.

Despite our ability to show numerous effects of *Petrolisthes armatus* on the recruitment and/or growth of native oyster-related biota, the overall effect of the invasive crab on oyster reef species or communities is unclear. The suppression of oyster growth

Table 3.1. Summary table of the impacts of *Petrolisthes armatus* on native oyster reef taxa in the mesocosm study and the 2004 and 2005 field studies combined. Symbols are: +/+ for significant ($p \leq 0.050$) positive effects, + for non-significant positive effects ($0.050 < p < 0.160$), +/- for no effect, and -/- for significant ($p \leq 0.050$) negative effects.

Impact	**Mesocosm**	**Field**
Taxonomic Richness (12 weeks)	+/-	+/-
Oyster Growth (4 weeks)	-/-	-/-
Oyster Survivorship (12 weeks)	+/-	+/-
Mussel Growth (4 weeks)	+/-	Not tested
Mussel Survivorship (12 weeks)	+/-	Not tested
Total Juvenile Bivalves	Not tested	+/+
Juvenile Oysters	Not tested	+/+
Juvenile Mussels	Not tested	+/+
Juvenile sphenia clams	Not tested	+
Survivorship of oyster drills	Not tested	+
Gobies	Not tested	+
Juvenile Mud Crabs Recruitment	-/-	Not tested
Juvenile Mud Crab Growth	-/-	Not tested
Macroalga	+/+	Not tested
Microalga	-/-	Not tested

(Figures 3.5A and 3.8) and the enhancement of oyster drill survival (Figure 3.7E) by the presence of *P. armatus* could both undermine the maintenance of oysters, a critical foundation species in estuary systems. However, in addition to these direct and indirect negative effects on oysters, *P. armatus* also produced positive effects for oyster communities, at least in the short-term. Presence of the invasive crab enhanced recruitment of total bivalves as well as oysters and mussels by a significant 34% to 68% (Figure 3.7A-C). This enhancement of recruiting bivalves may be due to *P. armatus* serving as an alternative and preferred prey for predatory mud crabs (Figure 3.1), thus lessening predation on native species. Additionally, *P. armatus* suppressed the recruitment of native mud crabs (Figure 3.4A); mud crabs that might selectively prey on juvenile bivalves.

Whether or not these effects will remain positive over the longer-term is uncertain. Many of these effects could lead to increased growth or survival of bivalve predators (both mud crabs [due to *P. armatus* providing an additional food source] and oyster drills [due to *P. armatus* acting as an alternate food source for drill predators]). If these consumers increase in density, they could eventually have a negative impact on oysters. The combined effect of depressed oyster growth (Figures 3.5A and 3.8), increased oyster settlement (Figure 3.7B), and potentially increased predation of oysters due to increased oyster drill survivorship (Figure 3.7E) could lead to smaller oysters that remain susceptible to predators for longer periods of their life history. Overall, this could decrease oyster growth and survivorship in the longer-term. Rigorously evaluating such ecological interactions in a natural field setting will be challenging, given that *P. armatus* can recruit to experimental "control" reefs at densities of tens of thousands m^{-2} in periods of only a few weeks. This compromises a long-term control to which crab addition treatments can be compared.

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