

Population dynamics of the non-native crab *Petrolisthes armatus* invading the South Atlantic Bight at densities of thousands m^{-2}

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ABSTRACT: The green porcelain crab *Petrolisthes armatus* recently invaded oyster reefs of the South Atlantic Bight. In 2 estuaries of coastal Georgia, USA, crab densities reached peak densities of 4000 to 11 000 crabs m^{-2} in some periods and locations. Densities generally were higher in the low versus the high intertidal and in the lower versus upper regions of the 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. Maximum mean densities of *P. armatus* in Georgia were 37 times the highest densities recorded in the presumptive native 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 Georgia exceeds that of the native range by more than 1 order of magnitude. Densities of native mud crabs in the genera *Panopeus* and *Eurypanopeus* were unrelated to, or positively correlated with, densities of the exotic crabs; correlations were never significantly negative. The impact of *Petrolisthes armatus* on native communities is unclear, but could be considerable if this filter-feeding crab impacts oysters, which are the foundation species of inshore reefs.

KEY WORDS: Marine invasion · Invasive species · Exotic species · Crab densities · Population dynamics · Species boundaries

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INTRODUCTION

Biological invasions threaten natural communities and alter ecosystem structure (Mooney & Drake 1986, Simberloff et al. 1997), so studies of the traits and impacts of exotic species can provide insights into processes affecting community assembly and global change as well as provide management options regarding invasive species (Lodge 1993). Most studies of invasions have focused on terrestrial or freshwater habitats where invaders have strongly impacted native species; studies of marine invasions are less common despite several being well-known and having substantial ecological consequences (Carlton & Geller 1993, Cohen & Carlton 1998, Ruiz et al. 1999).

Oyster reefs are the major hard-substrate communities in coastal areas of the South Atlantic Bight, USA,

and oysters serve as ecosystem engineers that produce the biogenic structure upon which many native species depend (Lenihan & Peterson 1998). These reefs have rarely been affected by invasive macrofauna known to be succeeding in ports and estuaries within other regions of the United States (Ruiz et al. 1997, 1999, Cohen & Carlton 1998). However, sometime in the early 1990s, the green porcelain crab *Petrolisthes armatus* colonized oyster reefs in South Carolina, rapidly increasing from single individuals m^{-2} in 1995 to over 16 000 m^{-2} by August 1999 (South Carolina Department of Natural Resources). The native range of this crab presumably includes the eastern Pacific (Gulf of California to Peru), the western Atlantic (Bermuda, Gulf of Mexico, Caribbean, and Brazil), and western Africa, where the greatest known densities of the crab reach only ≤ 305 individuals m^{-2} (Oliveira & Masunari

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1995). Coen & Heck (1983) listed the crab as occurring in Georgia a decade prior to its discovery in South Carolina, but the basis for this listing is unclear (K. Heck pers. comm.). No other reports of *P. armatus* in Georgia occurred during the 1980s.

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 on rocky shores (Oliveira & Masunari 1995), sand reefs built by sabellid worms (Micheletti-Flores & 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-level effects (but see Sheridan [1992] for density fluctuations in Rookery Bay, Florida, and Oliveira & Masunari [1995] and Micheletti-Flores & Negreiros-Fransozo [1999] for population dynamics in southern Brazil). To provide an initial assessment of the invasion in coastal Georgia, 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. *Petrolisthes armatus* and associated oyster reef crabs were monitored within 2 Georgia estuaries separated by about 75 km (Fig. 1). The southern estuary at Sapelo Island (part of NOAA's National Estuarine Research Reserve System) 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 & 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 3 tidal prisms along its length (Ragotzkie & Bryson 1955). Strong tidal currents at the mouth of the river and the lack of fresh-

water 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 & Bryson 1955, Bahr & Lanier 1981). Thus, waters of the upper and lower regions are hydrologically isolated from one another (Chalmers 1997).

The northern estuary encompasses the rivers, creeks, and marshes near Skidaway Island (Fig. 1). 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 & Lanier 1981). When tidal flow is strong enough to prevent the freshwater source from dominating circulation patterns, a partially mixed estuary with moderate salinity stratification can occur (e.g. Altamaha and Ossabaw Sounds, Georgia) (Bahr & Lanier 1981). The 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

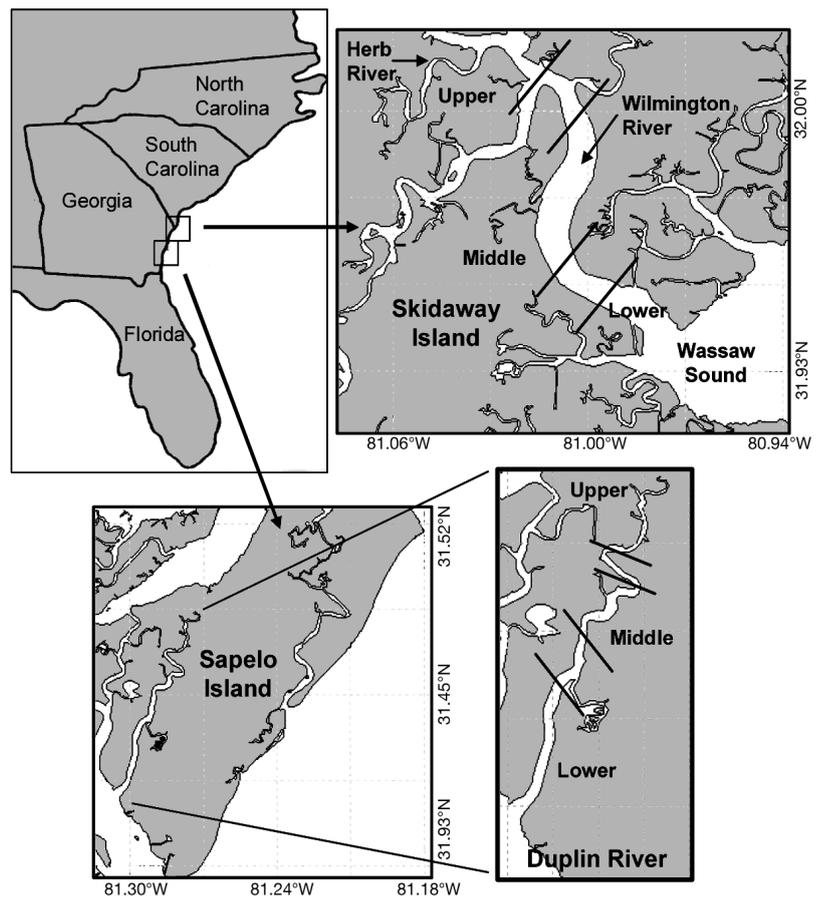


Fig. 1. Skidaway Island and Sapelo Island, Georgia, USA, showing locations of the monitoring regions (Upper, Middle, and Lower) in each estuary

creek (Herb River). There are no known tidal prisms in this region, but frequent gyres of circulating water occur continuously along the river's length (C. Li pers. comm.).

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 m (Bahr & 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 2 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 & Lanier 1981).

Monitoring. We monitored crab density, size, and sex along estuarine gradients in the 2 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 3 regions: (1) Upper, (2) Middle, and (3) Lower, with unmonitored sections separating each region (Fig. 1). 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 m; however, in the Upper region of the Duplin River where reefs became sparse our plots were separated by ~ 10 m.

We initiated monitoring in early June 2003 (Wilmington River: June 2 to 7, Duplin River: June 9 to 12). At each of the 20 plots within each region, we placed a 22×15 cm (~ 0.03 m²) plastic basket at a high (top edge of the oyster reef, ~ 1 to 2 m above mean lower low tide) and low (just above where oysters end and mud begins, ~ 0 to 0.5 m above mean lower low tide) tidal height of the oyster reef along the same vertical transect and with similar basket orientation to the waterline (see inset in Fig. 2). 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 2 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 vol-

ume. 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 h before and after 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, after the initial sampling, most individual baskets were monitored at 6 mo intervals, with a few (2 to 9 baskets) from each time-point used after 3 mo. In preliminary experiments, baskets achieved a stable density of *Petrolisthes armatus* in 1 mo (A. L. Hollebone unpubl. data). Thus, the 3 to 6 mo between monitoring considerably exceeded the time required for recovery following disturbance due to previous sampling.

To monitor crab densities, baskets were removed from their anchors and materials within each basket transferred to a closed container. All material was retrieved and the volume noted for those baskets that were $\leq \frac{2}{3}$ full of oyster habitat (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 over 2 plastic containers (the width of two of these containers approximated the length of one monitoring basket). The content of one container was taken and the content of the other was returned to the monitoring basket. All baskets were resecured in their original positions and filled to 100% with surrounding oyster substrate.

Upon return to the laboratory, all crabs (both native and non-native) were removed, counted, sized (carapace width = CW), sexed (see Oliveira & Masunari 1995), and preserved in 70% ethanol or 10% formalin. If there were < 40 crabs in a sample, all were sized and sexed. Samples containing > 40 crabs were subsampled. This 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 randomly selected sections of the tray (sections were chosen using a random numbers table, and the entire carapace had to be within the section chosen to be counted). Additional sections were sampled until 30 or more crabs had been assessed.

Data analyses. We determined the estuarine-wide density patterns of exotic porcelain crabs and native mud crabs (*Panopeus herbstii* and *Eurypanopeus depressus* combined) scaled to 1 m² along the lengths of the 2 rivers, as a function of tidal height and time period. Because a sampling basket covered 3.3% of a 1 m² area, we multiplied each value by 30.3 to scale densities to 1 m⁻². We included mud crabs because these were the most common native crabs co-occurring with the invasive crabs within the oyster reefs. Data sets were tested for normality (Ryan-Joiner W, $p > 0.050$) and equality of variances (Bartlett's test, $p > 0.050$, Zar 1999). Because of non-normality, the data for *P. armatus* were log-transformed and data for the native mud crabs were square root transformed. These transformations improved the homogeneity of variances for all the monitoring data, but in some cases (e.g. low sample size in the lower region of the Wilmington River in December 2003) equality of variances for the entire data set was not achieved. Following transformation we performed 3-way ANOVAs for porcelain crabs and for mud crabs, with estuary, time period, and tidal height as fixed factors and region of the river nested within estuary.

We evaluated how size classes of *Petrolisthes armatus* (males and females combined) were distributed across regions, tidal heights, and time by plotting mean (\pm SE) density scaled to crabs m⁻² (from newly settled megalopae through the largest adults, with size measured as carapace width in mm). We determined mean size for each time–region combination.

Size classes and mean (\pm SE) densities were determined for male and female *Petrolisthes armatus* basket⁻¹ (scaled as above) across all regional, tidal height, and time period combinations. The sex ratio of *P. armatus* for each region \times tidal height plot (these calculations ignored megalopae that could not be reliably sexed) was calculated from the total pooled sample of all males and all females in that region, tidal height, and season. We did not calculate a ratio for each basket because during some samplings several baskets contained no crabs, or only one or a few of the same sex—such low densities produce large variances in ratios that may not be representative of samples for larger numbers of individuals. We assessed whether the frequency of males within each region and season were significantly different from an expected frequency of 50% by the χ^2 test.

We assessed all females ≥ 3 mm CW (the smallest size at which we noted ovigerous females) to determine the proportion of ovigerous females across sites and seasons. Data were arcsine transformed, tested for normality and equality of variances, and then analyzed using a 2-way ANOVA with fixed factors of region and tidal height. Time was not included as a fixed factor because gravid females were not present during each monitoring period. To determine the potential population-level fecundity of crabs in the invaded range versus the presumptive native range, we determined the proportion of mature females that were gravid across all locations and seasons in both estuaries and compared this proportion with the overall proportion derived from Oliveira & Masunari's (1995) data for populations in Brazil.

To assess how this invasive crab might be interacting with native crabs in oyster reef habitats, we correlated the densities of native mud crabs (dominated by 2 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; Fig. 2A). Between the end of the warmest period (November) and the end of the coldest period (March), densities decreased by ~ 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. *P. armatus* densities in the Wilmington River estuary ranged between ~ 790 and 11 200 crabs m⁻² during warmer months, but during colder months (reflected in the April 2004 data; Fig. 2B), densities decreased by 89 to $>99\%$ (averaging only ~ 20 to 165 crabs m⁻² across all regions compared to the December 2003 densities). The 3-way ANOVA indicated that estuary, time period, and tidal height, as well as the nested factor of region in estuary, all significantly affected *P. armatus* density ($p \leq 0.015$, Table 1). There were significant time \times estuary, time \times region nested in the estuary, and tidal height \times estuary interactions ($p \leq 0.020$). The time \times tidal height interaction was nearly significant ($p = 0.068$), but other higher order interactions were not significant ($p \geq 0.215$, Table 1).

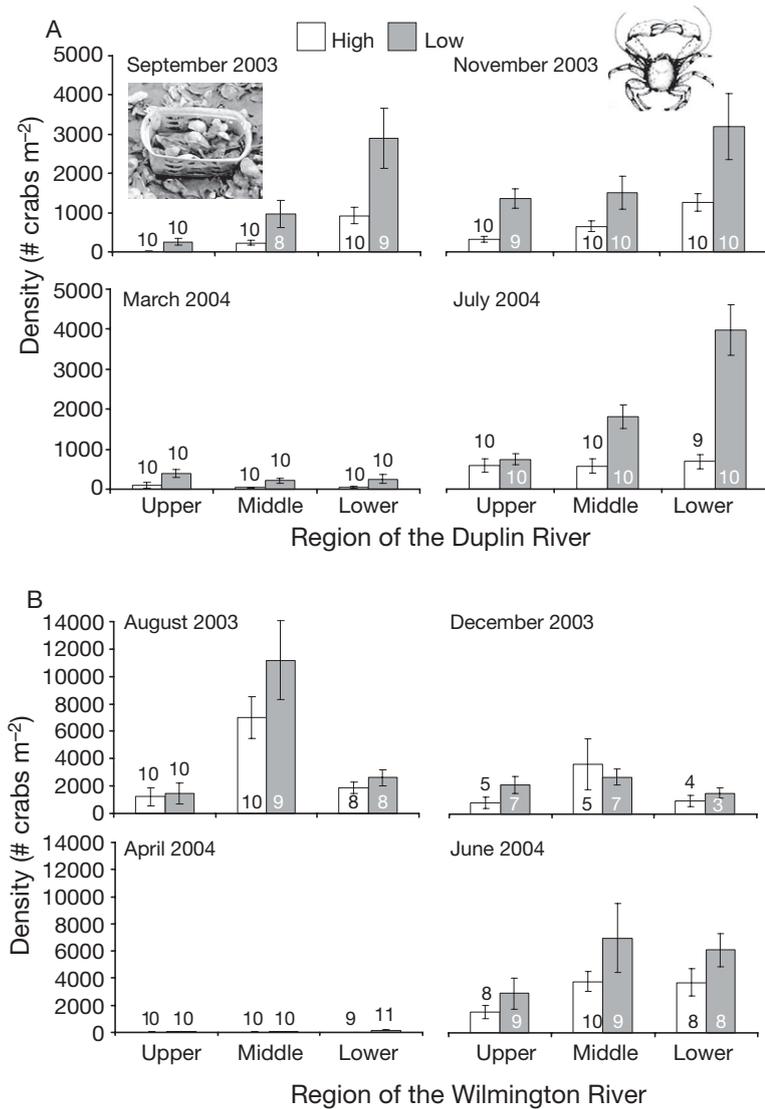


Fig. 2. *Petrolisthes armatus*. Densities (mean \pm SE, scaled to 1 m²) in (A) Duplin River and (B) Wilmington River across regions, tidal heights (high and low intertidal), and sampling periods. Numbers within or above bars indicate number of replicate baskets sampled. For statistical analyses see Table 1. Inset in (A) shows an oyster basket

Sex ratios rarely differed significantly from an expected ratio of 1:1 regardless of estuary, time, region, or tidal height, (Table 2, 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. $48 \times 0.05 = 2.4$ significant differences expected), so we do not interpret the 3 differences we detected as meaningful.

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) (Fig. 5). The proportion of mature females that were gravid across all locations and times 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 (Fig. 5A). In the Wilmington River estuary, tidal height never significantly affected the percentage of females that were gravid. In June, more females in the upper estuary tended to be gravid ($p = 0.039$ for region; Fig. 5B). There was never a significant region \times tidal height interaction for either estuary.

Demographics

Recruitment (appearance of crabs < 3 mm CW) in both estuaries occurred primarily during the warmer months of June to September (Figs. 3 & 4). Recruits (megalopae), juvenile crabs, and gravid females (Figs. 3 to 5) were absent, or nearly so, 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 roughly similar for the 2 tidal heights with the exception that the largest size classes tended to occur in the low tidal zone.

Biological factors

The 2 most common mud crabs, *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 (Fig. 6). 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 months than in the early spring, mud crabs were only 1 to 3 times more common in warm periods. As with porcelain crab densities, mud crab densities exhibited significant effects

Table 1. *Petrolisthes armatus*. 3-way ANOVA of density with estuary, time period, and tidal height as fixed factors and region nested within estuary

Source	df	Seq SS	Adj SS	Adj MS	F	p
Estuary	1	3.6338	3.8152	3.8152	5.97	0.015
Time period	3	266.5887	268.9672	89.6557	140.24	≤0.001
Tidal height	1	36.1261	32.8580	32.8580	51.40	≤0.001
Region (Estuary)	4	46.1801	42.1820	10.5455	16.50	≤0.001
Estuary × Time	3	30.3143	30.5927	10.1976	15.95	≤0.001
Estuary × Tidal height	3	4.1075	3.4697	3.4697	5.43	0.020
Time period × Tidal height	3	4.3730	4.5976	1.5325	2.40	0.068
Time period × Region (Estuary)	12	42.6752	42.1898	3.5158	5.50	≤0.001
Tidal height × Region (Estuary)	4	3.2927	3.3043	0.8261	1.29	0.272
Estuary × Time period × Tidal height	3	1.0211	0.8654	0.2885	0.45	0.717
Time period × Tidal height × Region (Estuary)	12	9.9775	9.9775	0.8315	1.30	0.215
Error	386	246.7701	246.7701	0.6393		
Total	433	695.0600				

of the 3 fixed factors in the model (estuary, time period, and tidal height) as well as region nested within estuary ($p \leq 0.029$, Table 3). The time × estuary and time × region in the estuary interactions had significant effects on mud crab densities ($p < 0.001$), but time ×

tidal height, tidal height × estuary, and tidal height × region in the estuary did not ($p \geq 0.267$). The interaction of all 3 fixed factors was not significant ($p = 0.445$), but nesting region into the estuary factor did significantly affect densities ($p = 0.049$, Table 3).

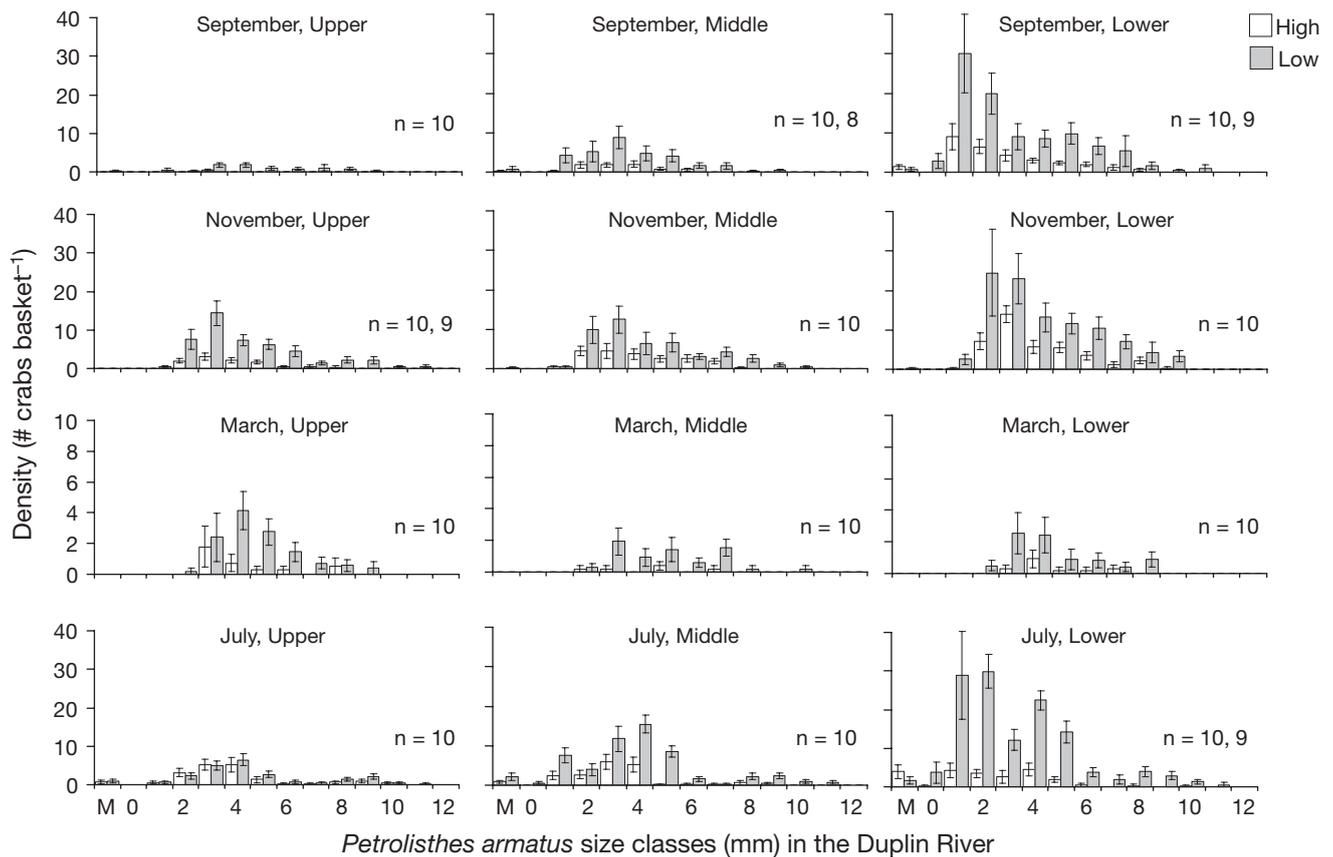


Fig. 3. *Petrolisthes armatus*. Densities (mean \pm SE m^{-2}) by size class in the Duplin River across regions, tidal heights (high and low intertidal) and sampling periods. M = megalopae (newly settled crabs); 0 = 0–0.9 mm CW; 2 = 2–2.9 mm CW; etc. Note different y-axis scale for March

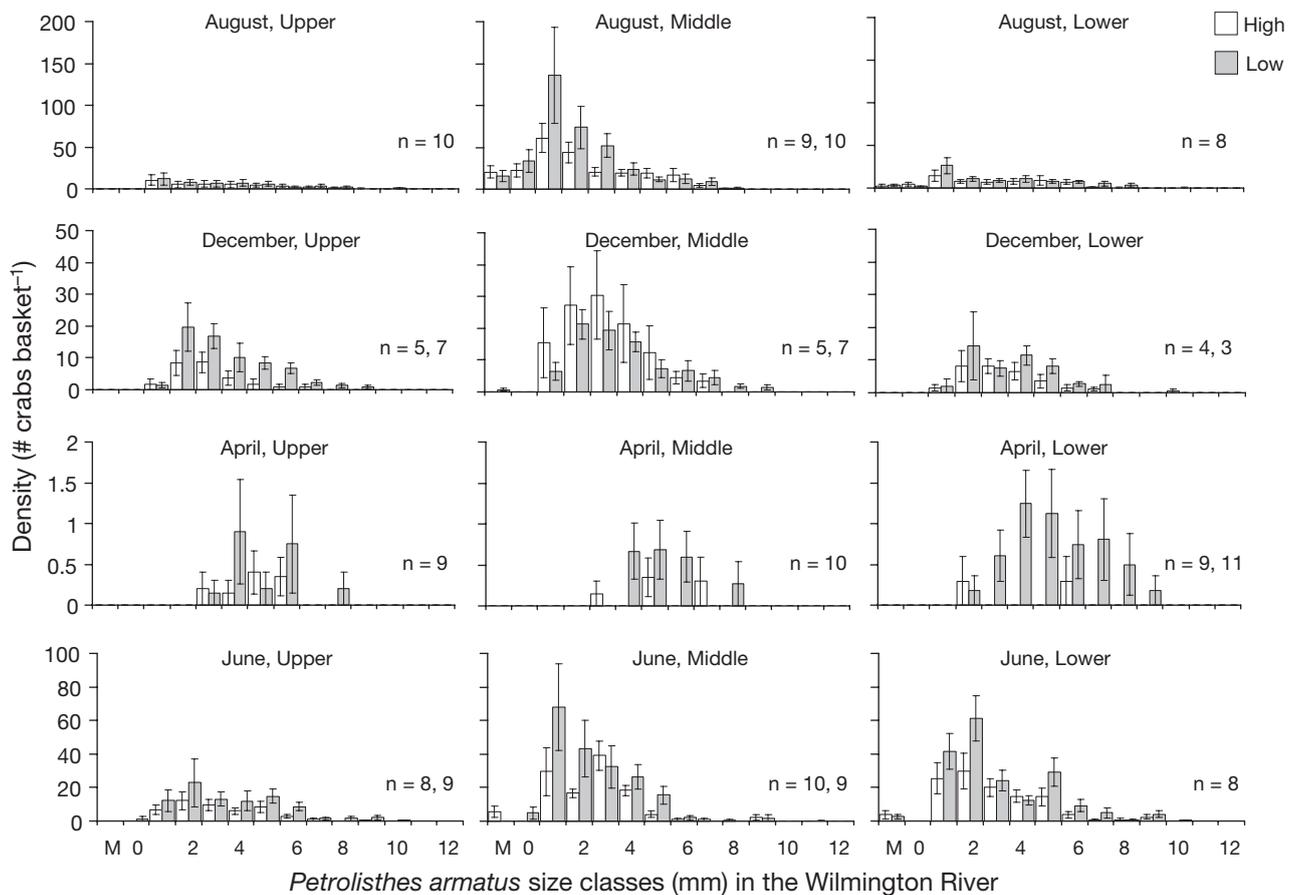


Fig. 4. *Petrolisthes armatus*. Densities (mean \pm SE m^{-2}) by size class in the Wilmington River. Note different scales for all y-axes. Further details as in Fig. 3

Correlations of mud crab density basket^{-1} with *Petrolisthes armatus* density basket^{-1} across each region, tidal height, and season, indicated several significant positive relationships but no significant negative relationships (Table 4). Of the 24 contrasts in each estuary system, 5 (Wilmington River) or 6 (Duplin River) were significantly positive ($p < 0.050$), with all but one of these occurring during the warmer periods of the year (June and July, August and September).

DISCUSSION

Invasive species pose serious threats to native communities (Carlton & Geller 1993). 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 magnitude that they may

lead to profound ecological changes in the world's oceans (Grosholz 2002).

Crabs, in particular, have had wide-ranging impacts on native organisms and communities. Introduced crabs affect the induction of morphological defenses (Trussell & 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 itself in tremendous densities over broad spatial scales in 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 $11\,200 \text{ crabs } m^{-2}$, which is 37 times greater than the highest density ever documented through trapping studies performed in the crab's historic range (Oliveira & Masunari 1995). *P. armatus* persisted throughout the year, colonizing, growing, and reproducing rapidly during the warmer months. The

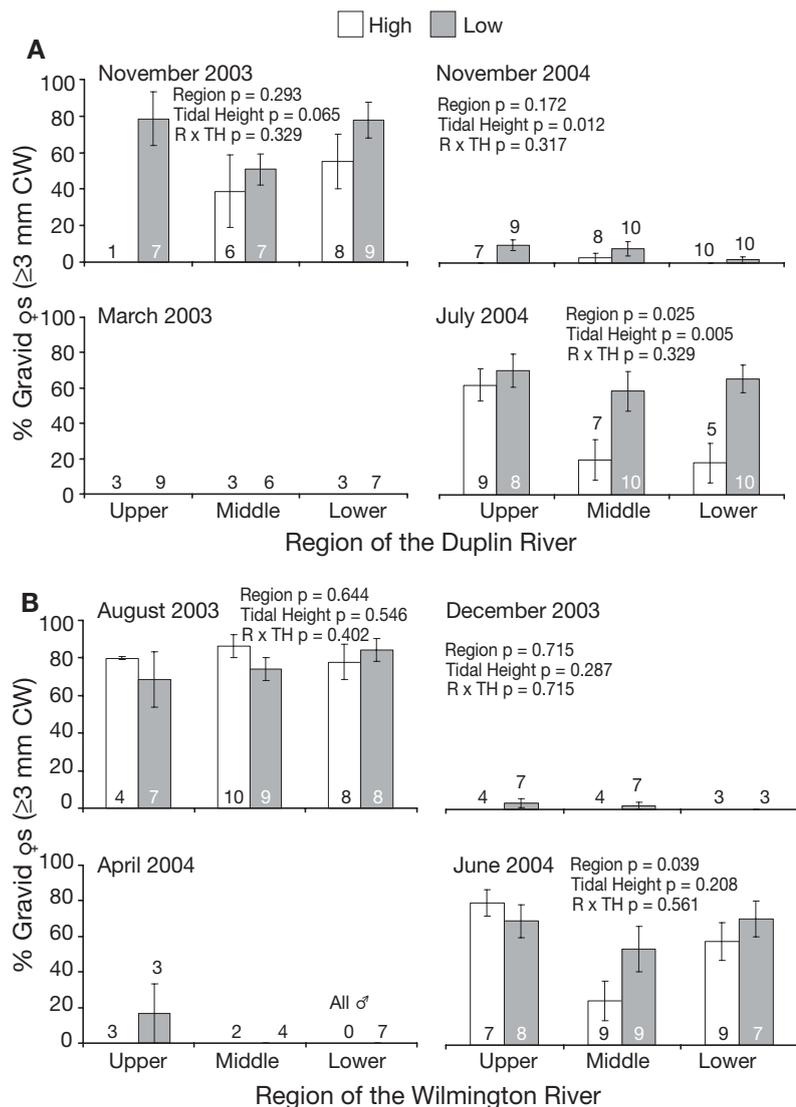


Fig. 5. *Petrolisthes armatus*. Proportion of mature females (≥ 3 mm CW; mean \pm SE) that were gravid in (A) Duplin River and (B) Wilmington River across regions, R, tidal heights, TH (high and low intertidal), and sampling periods. Sampling size was commonly lowered because reproductive, mature females were absent from some baskets. Statistical evaluations not calculated for March and April 2004 because of severely limited sample size. Numbers within or above bars indicate number of replicate baskets sampled. p-values from a 2-way ANOVA following arcsine transformation of data

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 2 most common native crabs normally found on Georgian oyster reefs, *Panopeus herbstii* and *Eurypanopeus depressus*. High densities of *Petrolisthes armatus* are not only found on the Georgia coast, densities of thousands m^{-2} are also reported for South Carolina (South Carolina Department of Natural Resources: www.dnr.sc.gov/marine/sertc/P%20armatus%20SOM.pdf).

In Georgian estuaries, *Petrolisthes armatus* was found at mean densities of 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}). During colder months, crab densities declined dramatically: 64 to 95% in the Duplin River and 89 to >99% in the Wilmington River. Distributions of crab size classes indicated that local populations of adult porcelain crabs persisted throughout the winter for all region \times tidal height combinations in both estuaries. These numbers included both males and females of reproductive size and indicate that *P. armatus* has established a viable local population that persists 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 d, A. L. Hollebone pers. obs.). These 2 factors suggest that warm-season increases in density could result from local reproduction and recruitment, and need not 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. Work with the porcelain crabs *Petrolisthes cinctipes* and *P. eriomerus* in Washington, USA, and British Columbia, Canada, showed that both biotic (competition and predation) and abiotic (thermal tolerance and substrate composition) factors affect their distribution in the intertidal (Jensen & 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 desiccation and heat stress in the high intertidal causing crabs to move to lower 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 could cause crab mortality at high

Table 2. *Petrolisthes armatus*. Sex ratios of crabs >1 mm CW analyzed by χ^2 tests (*0.025 < p < 0.050, **p < 0.010) in 3 regions (Upper, Middle, Lower) of river estuaries at 2 tidal heights (High, Low)

Sampling period	Duplin River		Wilmington River	
	Male:Female	Ratio	Male:Female	Ratio
Aug–Sep 2003				
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
Nov–Dec 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 Low	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
Mar–Apr 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
Jun–Jul 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

tidal heights or the crabs may move down the tidal gradient as the tides progress over time. Despite the potential bias introduced by sampling during the lowest tidal cycles, we still documented densities of up to ~6400 crabs m⁻² in the high intertidal during some periods.

Competition with local crabs appears unlikely to limit tidal height distributions. The abundance of native crabs between tidal heights was not the inverse of *Petrolisthes armatus* patterns and there were no negative correlations between *P. armatus* and mud crab abundance. *P. armatus* is a filter-feeder while mud crabs are predators. Because mud crabs readily consume *P. armatus* in laboratory assays (Hollebone 2006), the positive correlations for the 2 crabs could result from mud crabs accumulating in locations with high densities of favored prey. Alternatively, both native and non-native crabs may have similar physical needs and thus co-occur at high densities in favorable environments. Regardless of the interactions driving these patterns, the lack of negative correlations between native and invasive crabs suggests that mud crabs are not displacing *P. armatus* into the lower intertidal.

Regional distribution

Regional distribution of *Petrolisthes armatus* might be affected by the thermal environment of the estuary, which is strongly influenced by hydrography (Bahr & 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 & 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 & Lanier 1981). Data collected in 2003 (during a portion of the monitoring program) from the Sapelo Island National Estuarine Research Reserve (SINERR) hydrographic monitoring stations (http://gce-lter.marsci.uga.edu/lter/data/gce_data.htm) at Sapelo Island, Georgia (Upper site: Flume Dock; Lower site: Marsh Landing) support Bahr & Lanier's (1981) generalizations. From June to September 2003, the Upper region of the Duplin River estuary was, in general, warmer (~25 to 32.5°C) than the Lower region (~25 to 30°C). By November and December 2003, water temperatures in the

Upper region were similar to (~8 to 25°C) or colder than, those in the Lower region (~10 to 25°C).

In its native range, *Petrolisthes armatus* thrives under thermal conditions within the range of spring and autumn temperatures of the South Atlantic Bight (16 to 29°C at Farol Island, Paraná, Brazil [Oliveira & Masunari 1995] and 20.8 to 28.7°C at Paranapuã Beach, São Vicente, Brazil [Micheletti-Flores & Negreiros-Franzoso 1999]). In Brazil the highest densities of *P. armatus* occurred during the summer when mean surface water temperatures were above 25°C (Oliveira & Masunari 1995). Upper thermal tolerance limits of *Petrolisthes* spp. are positively correlated with surface water temperatures and with maximal temperatures of microhabitats where crabs occur (Stillman & Somero 2000). In laboratory studies *P. armatus* has an upper thermal tolerance of 40.5°C (Stillman & Somero 2000). Therefore, *P. armatus* can probably 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 16°C temperature recorded in the crab's native range (Oliveira & Masunari 1995).

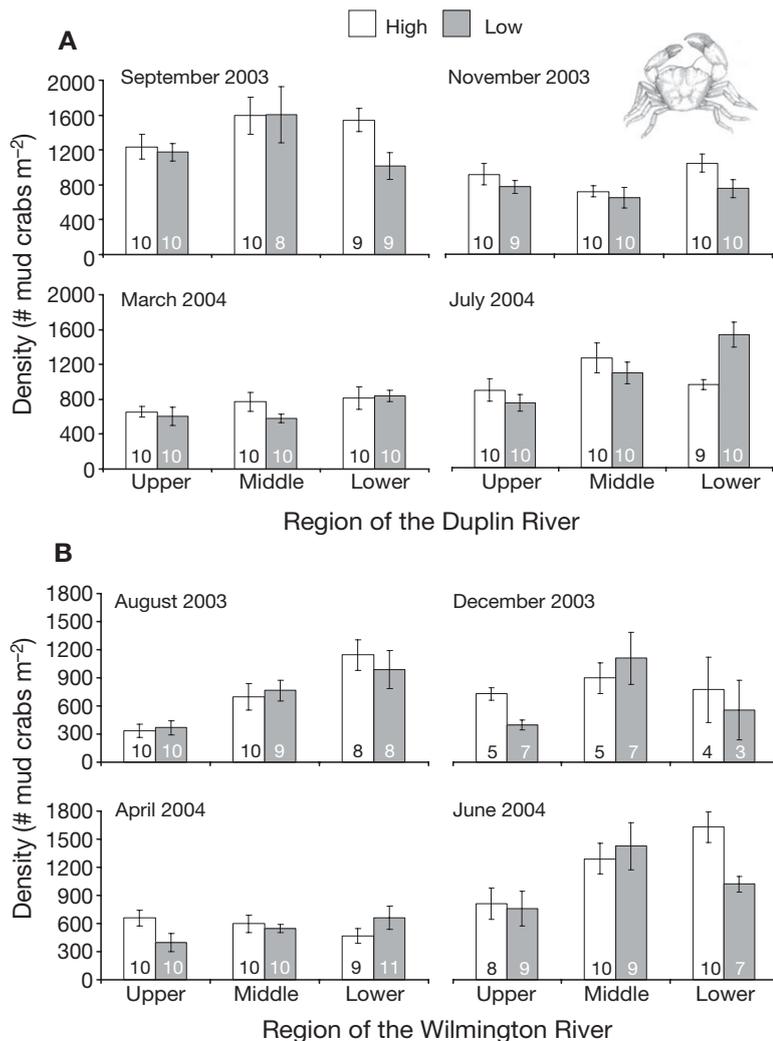


Fig. 6. *Panopeus herbstii* and *Eurypanopeus depressus* (native mud crabs). Densities (mean ± SE, scaled to 1 m²) in (A) Duplin River and (B) Wilmington River across regions, tidal heights, and sampling period. Numbers within bars indicate number of replicate baskets sampled. For statistical analyses see Table 3

Seasonally low temperatures in Georgia may exceed the lower thermal limit of crabs in many habitats, causing the large decrease in densities we observed during colder months. This effect was documented for blue crabs *Callinectes sapidus* at Sapelo Island, Georgia, when water temperatures fell below 15°C (Fitz & Wiegert 1991). Seasonality also affects the strata habitation of the mud crabs *Panopeus herbstii* and *Eurypanopeus depressus* in oyster reefs of North Carolina (Meyer 1994). During warmer months, mud 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 determine the distribution or abundance of *Petrolisthes armatus* at our sites because the crab lives at salinities of 6.7 to 31.5‰ in its native range (Oliveira & Masunari 1995). This salinity range brackets salinities at our monitoring sites. Salinities in the Duplin River ranged from 13 to 30‰ (see http://gce-lter.marsci.uga.edu/lter/data/gce_data.htm), whereas those in the portions of the Wilmington River we monitored ranged from 15 to 31‰ (Coastal Georgia Adopt-A-Wetland unpubl. 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 den-

Table 3. *Panopeus herbstii* and *Eurypanopeus depressus*. 3-way ANOVA of density with estuary, time period, and tidal height as fixed factors and region nested within estuary

Source	df	Seq SS	Adj SS	Adj MS	F	p
Estuary	1	1890.3600	1798.9700	1798.9700	35.55	≤0.001
Time period	3	4301.8600	4442.7700	1480.9200	29.26	≤0.001
Tidal height	1	257.4800	242.9300	242.9300	4.80	0.029
Region (Estuary)	4	2504.8600	2017.2800	504.3200	9.97	≤0.001
Estuary × Time	3	2038.0400	1773.4900	591.1600	11.68	≤0.001
Estuary × Tidal height	1	0.2800	0.0200	0.0200	0.00	0.985
Time period × Tidal height	3	37.6900	60.3800	20.1300	0.40	0.755
Time period × Region (Estuary)	12	2007.2500	1985.4600	165.4500	3.27	≤0.001
Tidal height × Region (Estuary)	4	231.8200	264.4000	66.1000	1.31	0.267
Estuary × Time period × Tidal height	3	131.2900	135.6600	45.2200	0.89	0.445
Time period × Tidal height × Region (Estuary)	12	1081.8100	1081.8100	90.1500	1.78	0.049
Error	385	19482.7100	19482.7100	50.6000		
Total	432	33965.4200				

Table 4. *Panopeus herbstii*, *Eurypanopeus depressus*, and *Petrolisthes armatus*. Correlations (Fisher's r to z) of densities of native mud crabs versus exotic porcelain crabs in Duplin River estuary and Wilmington River estuary. Bold p-values indicate significant correlations ($p < 0.050$). Further details as in Table 2

Sampling period	Duplin River				Wilmington River			
	n	Correlation	z	p	n	Correlation	z	p
Aug–Sep 2003								
Upper High	10	0.079	0.210	0.834	10	0.780	2.769	0.006
Upper Low	10	0.269	0.731	0.465	10	0.791	2.842	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	0.019	9	0.164	0.406	0.685
Lower High	9	0.837	2.966	0.003	8	0.333	0.774	0.439
Lower Low	9	0.294	0.742	0.458	8	0.712	1.992	0.046
Nov–Dec 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 Low	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	0.008	3	0.494	0.000	>0.999
Mar–Apr 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
Jun–Jul 2004								
Upper High	10	0.736	2.492	0.013	8	0.717	2.016	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	<0.001	10	0.244	0.659	0.510
Middle Low	10	0.157	0.419	0.675	9	0.741	2.335	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	0.002	7	−0.109	−0.219	0.827

sities of newly recruited crabs in the warmer months, 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%), and the high densities of *Petrolisthes armatus* zoea we noted in plankton tows during the summers of 2003 and 2005 (A. L. Hollebone and W. E. Morrison pers. obs.) all attest to the remarkable ability of the crab to rapidly increase from 10s or 100s of crabs m^{-2} in the winter to 1000s of crabs m^{-2} in the summer.

The sex ratio within the native range of *Petrolisthes armatus* at Farol Island, Brazil is about 1.05 males for each female over an entire year (Oliveira & Masunari 1995). Our data are 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.

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 & 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 *Petrolisthes armatus*. Additionally, Oliveira & 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 higher than 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 1 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 native species via predation and competition (e.g. Nichols et al. 1990, Lodge et al. 1994, MacIsaac 1996), and pre-existing species may repel invasions via the same interactions (e.g. Stachowicz et al. 1999, Parker & Hay 2005, Parker et al. 2006). We did not experimentally test the impacts of competition and predation on community structure, but correlatively addressed this possibility by evaluating how crab density for both native mud crabs and exotic 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 the warmer months (August and September 2003, June and 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. We found no negative correlations that one might expect if the invader were having strong negative effects on native crabs; however, correlations alone do not rigorously address cause–effect relationships. Hollebone (2006) showed that mud crabs readily consume *P. armatus* in the laboratory, suggesting that the positive correlations could occur because mud crabs move to areas of high *P. armatus* densities in order to feed.

Summary

Despite densities reaching into 1000s of crabs m^{-2} , the biology and ecological impacts of *Petrolisthes armatus* on native oyster reef communities is relatively unknown. Unlike invasive predatory crabs that change the activities of native species (Trussell & Nicklin 2002) and 'reorganize' native assemblages (Lohrer & Whitlatch 2002), the invasion of *P. armatus* has not produced a dramatic or visually obvious change in the oyster reefs of Georgia. However, the invasion may be too recent, or its effects too subtle, to be visually obvious. Short-term, small-scale studies indicate that the crab may suppress oyster growth, microalgal biomass, and juvenile mud crab densities, while enhancing bivalve recruitment (oysters, mussels, and clams), macroalgal growth, and potentially oyster drill survivorship (Hollebone 2006). The combined, longer-term impacts of these effects are unknown, but the densities, high metabolic rates, and filter feeding activity of the crabs suggest that their feeding could move substantial quantities of water column production to the benthos,

thus altering biogeochemical processes. Because local fishes and crabs readily consume *P. armatus*, its presence could also be altering native food-webs (Hollebone 2006). Given that oysters are long-lived and that much of their hard structure persists for years after their death, effects of *P. armatus* on this foundation species could take years to become obvious.

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