

Reproductive performance of the marine green porcelain crab *Petrolisthes armatus* Gibbes, 1850 in its introduced range favors further range expansion

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Abstract

Invasive marine crustaceans can exhibit population-level variation in reproductive traits that are consistent with a response to stressful conditions near the range edge, or alternatively, that may favor establishing new exotic populations. Reproductive characteristics of the green porcelain crab *Petrolisthes armatus* Gibbes, 1850 were not previously known in its invasive range in the Atlantic waters of the southeastern USA. We compared fecundity estimates, size at sexual maturity, and various other morphological aspects among crabs collected from two sites at each of four locations spanning approximately 230 km from North Inlet, South Carolina (SC), to Savannah, Georgia (GA), USA. Reproductive output and smallest ovigerous female sizes within the invaded range also were compared to those in the native range, which extends from the Gulf of Mexico and the Caribbean to Brazil in the Western Atlantic Ocean. Reproductive output and egg number were higher and female size at maturity was smaller for crabs from more northern locations (North Inlet and Charleston, SC). Crabs were sexually dimorphic, but population-level differences in overall morphology (e.g., dimensions of the carapace, chelipeds, and secondary sexual characteristics) were not evident in two populations examined (North Inlet, SC, and Bluffton, SC). Secondary sexual characteristics (i.e., abdomen length, abdomen width and pleopod length) contributed the most to the morphological differences between males and females. Using allometric methods, size at sexual maturity was estimated to be 3.99 mm carapace width (CW) for males at North Inlet and 2.96 mm CW for males at Bluffton. Minimum sizes of ovigerous females at our study sites were smaller (3.0 mm to 4.2 mm CW) than a published value for a native population (4.0 mm CW). Reproductive output also was higher in the introduced range (0.05–0.11) than in native populations (0.03–0.07). Along a latitudinal gradient at the northern extent of the invaded range, females allocated more energy to producing offspring at range-edge locations. These results indicate that both within the introduced range and compared to the native range, *P. armatus* exhibits considerable variation in reproductive performance, which may have assisted in the species' successful invasion and may aid the species in continuing its range expansion.

Key words: allometry, fecundity, invasive, Porcellanidae, reproduction, sexual maturity, Atlantic waters of the southeastern USA

Introduction

Species invasions occur worldwide and can have negative impacts on native communities (Grosholz 2002; Hanfling et al. 2011). For instance, invasive

crustaceans, a species-rich clade of marine invertebrates (Galil et al. 2011), can act as consumers or an alternative prey resource, thus altering trophic interactions (e.g., MacDonald et al. 2007; Jorgensen and Primicerio 2007; Hollebone and Hay 2008). Invasive

species can have complex impacts on the structure of native communities based on habitat availability (Gribben et al. 2015) and recruitment success that may be facilitated by native ecosystem engineers (Wright et al. 2016). Historical barriers to successful marine invasions, such as unsuitable temperature regimes, may be weakened by climate change. For example, range expansion into higher latitudes may be facilitated by less frequent or milder cold temperatures (Stachowicz et al. 2002; Sorte et al. 2010; Canning-Clode et al. 2011). Crustaceans are among the more prominent taxa of marine invaders (Galil et al. 2011) and commonly possess traits characterizing successful invaders, such as gregarious behavior, omnivorous suspension feeding, and high reproductive output potential (van der Velde et al. 2000), the latter of which is a key component of invasion success. For instance, colonization by individuals with high reproductive output can increase the chances of establishing self-sustaining populations to a new location (Lodge 1993; Williamson and Fitter 1996; Morton 1997; Sakai et al. 2001).

Predicting the ability of an invasive species to continue expanding its range can be aided by comparing reproductive characteristics, such as size at sexual maturity and fecundity, between native and introduced populations (e.g., Fowler and McLay 2013) as well as among populations within the introduced range. Early onset of sexual maturity in introduced populations is a characteristic of a successful invader because it increases the number of reproducing individuals, which can accelerate the establishment of permanent populations (Ricciardi and Rasmussen 1998; van der Velde et al. 2000). Size (but, not necessarily age) at sexual maturity can be assessed in crabs as the minimum size at which females carry eggs and through allometric analyses of certain reproductive structures (e.g., Gerhart and Bert 2008; Bueno and Shimizu 2009; Fowler and McLay 2013; Lira et al. 2015). Reproductive characteristics also may vary among populations within an introduced range, as observed in other crabs (Jones and Simons 1982; Lardies and Castilla 2001; Lira et al. 2015). Limited expansion potential may be indicated if organisms are physiologically stressed near their range limits due to exposure to suboptimal environmental conditions (Sorte and Hofmann 2004). Females may be more vulnerable to physiological stress due to higher energetic investment in egg production (Rivadeneira et al. 2010). Suboptimal conditions toward range edges can limit reproductive output, thus shaping the higher latitudinal boundaries of species and overall population dynamics (Brown 1984; Rivadeneira et al. 2010). In Crustacea, lower fecundity and higher organic content per dry mass of

eggs may signal physiological stress (Lardies and Wehrmann 2001). Low temperatures are likely a stressor for individuals near poleward range limits (e.g., Canning-Clode et al. 2011), just as high temperatures negatively affect porcelain crabs (Stillman and Somero 2000; Stillman 2004). Alternatively, high reproductive output in populations near range edges would suggest effects from environmental stresses are limited and that continued expansion might be possible.

Porcellanid crabs are important decapods in intertidal and shallow-water habitats of tropical and subtropical regions (Mantelatto et al. 2011). Several porcelain crab species are invasive with measurable impacts on receiving ecosystems. For example, *Petrolisthes elongatus* H. Milne-Edwards, 1837 was introduced to Tasmania from its native range in New Zealand in the early 1900s, and it is now widespread at high densities in its invasive range where it is better able to inhabit rocky habitat in the low intertidal zone (Gribben et al. 2013). In the southeastern USA, the green porcelain crab, *Petrolisthes armatus* Gibbes, 1850 was introduced into the Atlantic waters of the southeastern USA in the mid-1990s (Knott et al. 2000) from a native range extending from the Gulf of Mexico, through the Caribbean south to Brazil (Oliveira and Masunari 1995). This species has spread north of Cape Canaveral, Florida, establishing dense populations on intertidal oyster reefs in Georgia (Hollebone and Hay 2007) and as far north as South Carolina (Knott et al. 2000; Hadley et al. 2010). It is speculated that *P. armatus* was introduced into the Atlantic waters of the southeastern USA either by ballast water or as a hitchhiker on shellfish for aquaculture or seafood stores (Knott et al. 2000). This species is gregarious and, like most porcelain crabs, is a filter feeder although benthic microalgae also may be a major food resource (Zimba et al. 2016). At high crab densities, this crab can interfere with oyster growth, not through competition for food (Byers et al. 2014), but by disturbing oysters and decreasing their feeding time (Hollebone and Hay 2008). *Petrolisthes armatus* decreases in abundance with increasing latitude in the introduced range and, as of 2004, was not recorded on intertidal oyster reefs near the northern border of South Carolina (Hadley et al. 2010). In 2008, however, this species was observed on intertidal oyster reefs farther north in Wilmington, North Carolina, (Troy Alphin, University of North Carolina Wilmington, personal communication), although it is not clear that it has become established. Although ecological impacts have been studied, little is known about the species' reproductive biology; therefore, it is unclear whether its reproductive characteristics may facilitate further range expansion.

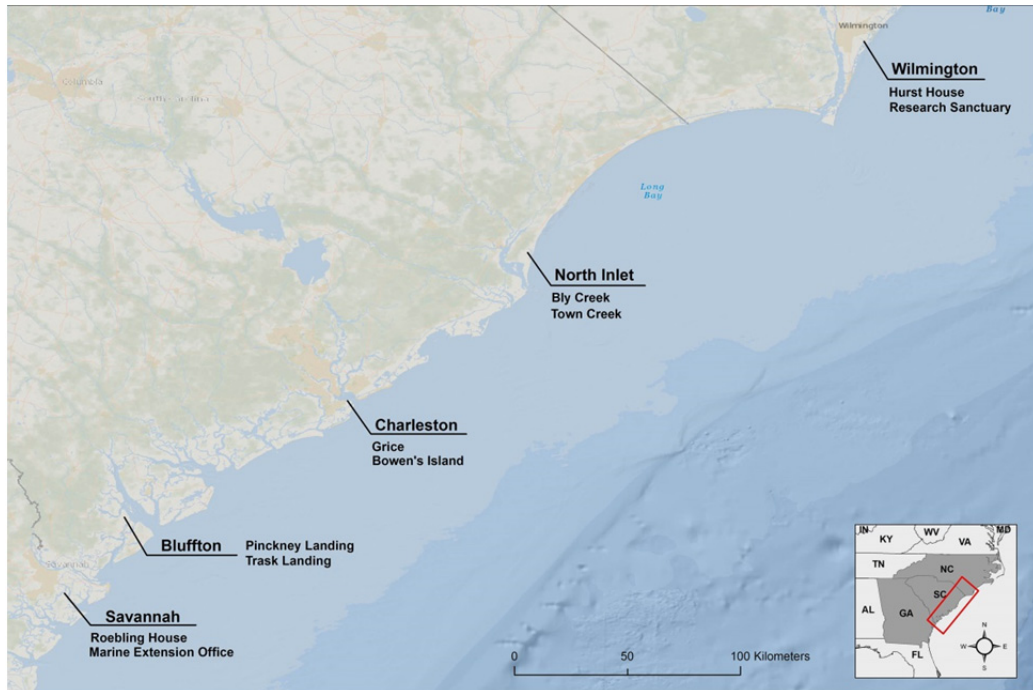


Figure 1. *Petrolisthes armatus* sampling locations for this study. At each location, there were two sites.

The reproductive biology and demography of *P. armatus* are well understood in its native range. For instance, higher fecundity in a Pacific Costa Rican compared to a Brazilian population in the Atlantic Ocean was attributed to a degraded environmental condition in Brazil as well as its closer proximity to the southern edge of the range (Wehrtmann et al. 2012). *P. armatus* reproduces year-round in Brazil and at higher intensity during the rainy season (Pinheiro et al. 2017). Allometric studies of crabs from the same area in Brazil (São Paulo State) found smaller sizes at sexual maturity for the population from a polluted site (Miranda and Mantelatto 2010) compared to males and females inhabiting a pristine area (Pinheiro et al. 2017). Some aspects of reproduction are known for parts of the introduced range. For example, the reproductive period of this species in South Carolina and Georgia ranges from May to November (Coen and McAlister 2001; Hollebne and Hay 2007). In addition, smaller minimum sizes of ovigerous females have been observed in non-native populations compared to native Brazil populations (Hollebone and Hay 2007).

Reproductive characteristics of *P. armatus* among populations at the northern extent of its introduced range have not been examined. In this study, we investigated fecundity, egg quality (egg size and organic content), reproductive output, and allometric

growth of specific body parts in *P. armatus* populations across a four-degree latitudinal gradient in the northern extent of its introduced range. We compared our estimates to those in the native range where possible. If allometric and fecundity analyses indicate signs of high physiological stress near the edge of the introduced range, continued range expansion is unlikely. Alternatively, if these *P. armatus* exhibit high reproductive output and low physiological stress, further range expansion may be expected.

Methods

Crabs were collected from two sites at each of the five locations across a nearly 400-kilometer range in the Atlantic waters of the southeastern USA (Figure 1): 1) Savannah (GA), with Roebing House (31°59'25.3"N; 81°01'16.5"W) and Marine Extension Office (31°59'20.0"N; 81°01'28.7"W); 2) Bluffton (SC), with Trask Landing (32°17'20.4"N; 80°48'33.7"W) and Pinckney Landing (32°13'47.1"N; 80°47'15.1"W); 3) Charleston (SC), with Grice (32°45'09.0"N; 79°53'51.2"W) and Bowen's Island (32°40'31.1"N; 79°57'54.5"W); 4) North Inlet (SC) with Town Creek (33°19'45.6"N; 79°11'19.2"W) and Bly Creek (33°20'28.7"N; 79°10'44.9"W) and Wilmington (NC) with Research Sanctuary (34°10'45.3"N; 77°50'35.5"W) and Hurst House (34°11'16.9"N; 77°51'05.5"W).

Only a few crabs ($n = 14$) were collected at only one Wilmington site (none at the second), precluding inclusion of Wilmington in most analyses.

Collection sites were selected based on the presence of natural, intertidal oyster reefs that were not close to degraded habitats or developed areas. Accessibility of the oyster reefs and known *P. armatus* occurrences in South Carolina Department of Natural Resources sampling (Nancy Hadley, SCDNR, personal communication) also were considerations in site selection. Crabs were collected from four trays (30.5 cm W \times 45 cm L \times 10.5 cm H) lined with window screen and filled with dead oyster shell placed on intertidal oyster reefs at mid-reef locations at each site. Shell configuration in the trays was standardized with tight packing of vertically-oriented shell because oyster habitat rugosity affects the densities of associated resident crabs (Margiotta et al. 2016). Trays were placed approximately 5 m apart and were secured in position with hooked rebar. Netting with 5 cm holes was attached to the top of the trays with zip-ties, which allowed crabs and other fauna to move in and out of the trays, but kept the oyster shell in place. Using trays to collect crabs increased the likelihood that crabs were representatively collected across all size classes and reduced damage to crabs and the oyster habitat that can occur when collecting by hand.

Trays were deployed for three-month durations and were collected in September of 2015, and January, March, and June of 2016 during spring low tides. The reproductive period of *P. armatus* lasts from May to November within the study region (Coen and McAlister 2001; Hollebene and Hay 2007); therefore, the September and June collections were near the end and beginning of the spawning season, respectively. All crabs from each site were frozen until fecundity and allometry parameters were measured. Sex determinations were attempted for all non-ovigerous *P. armatus* > 2.0 mm carapace width (CW) by examining the pleopods: males have one large modified pair of pleopods on the second somite; and females have three pairs of setose pleopods on the third, fourth, and fifth somites. The CW was measured with calipers to the nearest 0.01 mm.

Reproductive output

All females were examined for the presence of eggs, and a female was considered ovigerous even when but a few eggs were present. Thirty females with early-stage eggs and thirty females with late-stage eggs from each site were selected across the size spectrum of ovigerous females for fecundity analyses from the September collection period. Eggs were

considered early-stage if there was a uniform yolk and late-stage if the eyes were clearly visible (Wehrtmann 1990). Eggs were carefully removed from the pleopods and counted using a dissecting microscope. Egg length and width were measured using ImageJ for 20 eggs from each female with early-stage eggs to estimate mean egg volume (EV) using the formula: $EV = 1/6 (\text{egg length} \times \text{egg width} \times \pi)$ (Turner and Lawrence 1979). All of the separated egg masses and the females were dried for 60 hours at 65 °C, and dry weights were measured to the nearest 0.01 mg for females (Mettler AE50 balance) and to the nearest 0.1 μg for egg masses (Cahn C-31 microbalance). Reproductive output was calculated as dry egg mass (mg)/dry female mass (mg). The dried egg masses were then placed in a combustion oven for 6 h at 500 °C and weighed again to the nearest 0.1 μg to obtain an ash weight which represents the inorganic content of the eggs. The organic content (ash-free dry weight) of each egg mass was calculated by subtracting the ash weight from the dry weight.

Body measurements

Crabs from two sites (one more northern, Town Creek, North Inlet, SC, and one more southern, Pinckney Landing, Bluffton, SC) were used to assess size at maturity by allometric analysis. Eight morphometric measurements (carapace width, carapace length, greatest claw width, greatest claw length, fourth walking leg length, abdomen length, abdomen width at the second somite, and first pleopod length) were made based on Miranda and Mantelatto (2010) and used to compare potential population-level differences in crab morphology. One hundred crabs were examined from each site from the September collection period. Fifty males and 50 females were measured from Pinckney Landing, whereas there were fewer intact females available from Town Creek, therefore 28 females and 72 males were measured from this site. All measurements, except pleopod length, were made with calipers to the nearest 0.01 mm. Pleopods were photographed on a dissecting microscope and measured to the nearest 0.01 mm using ImageJ.

Data analysis

Crab abundances and percent ovigerity

Mean crab densities (number m^{-2}) and the sex ratio for each site were determined for all collection periods. Size frequency histograms were created to examine the number of ovigerous and non-ovigerous females in each 1-mm size category (3.00–3.99, 4.00–4.99,

etc.). A two-way Analysis of Variance (ANOVA) was used to compare percent ovigery among sites, using site and sampling period as random factors (September 2015 and June 2016). Tukey's post-hoc tests were used to reveal pairwise differences between sites within a sampling period. Assumptions for all parametric tests were assessed by Shapiro-Wilk's and Levene's tests, and data did not need to be transformed unless otherwise stated. For comparative purposes, sites were grouped as "northern" (North Inlet and Charleston) and "southern" (Bluffton and Savannah).

Size at maturity

Size at maturity was compared among sites using logistic regressions that used the proportion of ovigerous females as the dependent variable and CW as the independent variable. These analyses were conducted separately for the September 2015 and June 2016 collection periods. The size at maturity at each site was defined as the size at which 50% of the females were ovigerous (e.g. Groeneveld and Melville-Smith 1994). A Hosmer-Lemeshow test was used to test the fit of the logistic regression model for each site. A second approach compared the CW of the smallest ovigerous female in each tray among sites using a one-way ANOVA for the September 2015 collection period. The smallest ovigerous females were collectively (using all sites) compared to the smallest ovigerous female observed within the native range (4.0 mm; Ilha do Farol and São Paulo State, Brazil; Oliveira and Masunari 1995; Miranda and Mantelatto 2010) using a two-tailed, one sample Student's t-test to determine if ovigery is initiated at a smaller size in the introduced range. This test allows a population mean to be compared to a single value.

Reproductive output

Reproductive output was compared among sites with ANCOVA using egg mass dry weight as the dependent variable and female dry weight as the covariate. Mean reproductive output at each site also was compared to that of two populations in the native range (0.07 ± 0.02 in Costa Rica and 0.03 ± 0.02 in Brazil; Wehrtmann et al. 2012) with two separate two-tailed Student's t-tests with Bonferroni corrections (significance at $\alpha < 0.00625$).

Egg counts and egg loss

Fecundity was compared among sites with ANCOVA using CW as the covariate. Egg counts were square-root transformed to meet the normality and homogeneity of variance assumptions of the test. Potential

differences among sites in egg loss were examined by comparing the relationship of egg number and female size for early- and late-stage eggs at each site using ANCOVA. Egg organic content and volume were compared among sites with separate ANCOVAs using female CW as the covariate.

Allometry

Multivariate statistical analyses were used to determine whether crab morphology varied by sex or site. The eight morphological traits were standardized by carapace width for each crab. Data were normalized and Euclidean distances used to create similarity matrices and a non-metric multidimensional scaling (nMDS) plot was used to visualize similarities and dissimilarities in crab morphology by site and sex. Analysis of Similarity (ANOSIM; Primer 7.0.10; Clarke et al. 2014; Clarke and Gorley 2015) was used to test for differences in morphology by sex and site. Similarity Percentage (SIMPER) was used to identify the morphological traits that contributed the most to any dissimilarities between sites or sexes. ANOSIM distinguishes potential differences on a scale of $R = 0$ (samples are indistinguishable from each other) to $R = 1$ (no similarity between groups). R values > 0.5 indicate clear differences between groups with some degree of overlap (Clarke and Gorley 2015). In addition, each morphological trait was examined individually using a two-way ANCOVA with carapace width (log-transformed) as the covariate and site and sex as independent categorical factors.

Different relative growth analyses were conducted for crabs collected in September 2015 using carapace width as the reference dimension (X). The power function $Y = aX^b$ was used along with the logarithmic transformation, $\log Y = \log a + b \times \log X$, to detect ontogenetic changes (Lewis 1977). The slope values for each regression were tested (t-test against a constant) against the isometric slope of 1 to determine the relative growth status of each body dimension for the two sexes. A slope significantly less than 1 indicates negative allometry (the dependent variable grows at a lower rate than the carapace width); a slope significantly greater than 1 indicates positive allometry (the dependent variable grows higher than carapace width). A slope that was not significantly different from one indicates isometric growth (Finney and Abele 1981).

Size at maturity was estimated by determining if there are breaks (i.e., changes in slope) in any of the relative growth regressions using a piece-wise regression analysis (George and Morgan 1979; Mantelatto and Garcia 2001). Since the dominant claw for this

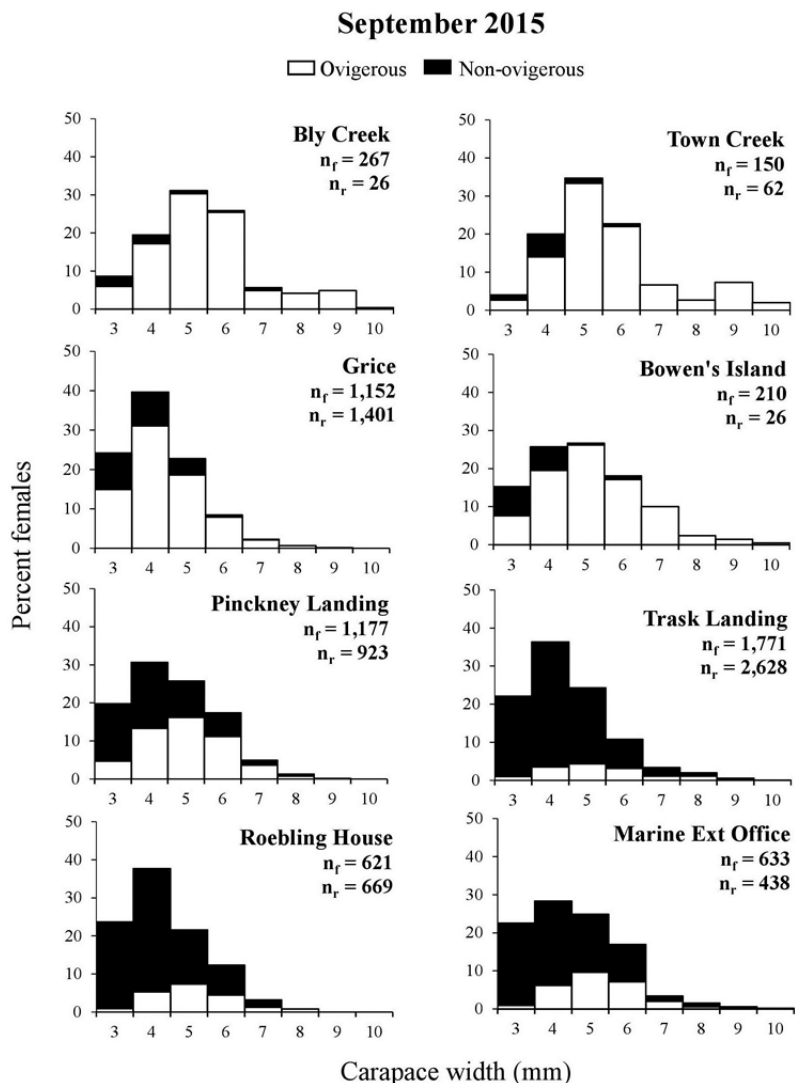


Figure 2. Percent ovigerous (white) and non-ovigerous (black) *Petrolisthes armatus* at each site for the September collection period. Total number of females (n_f) and recruits (any crab < 3 mm CW; n_r) are above the bars for each site. Sites within locations (Wilmington, North Inlet, Charleston, Bluffton, and Savannah) are depicted from top to bottom.

species can be on either side (personal observation), another regression line was created for the largest claw length for each crab to assess whether there was a change in growth for the dominant claw.

Results

Crab abundances and percent ovigery

Petrolisthes armatus densities were generally highest in September, with a maximum density of 11,542 individuals m^{-2} estimated at Trask Landing (Bluffton). Many of these crabs were new recruits (< 2 mm CW) of unknown sex. The smallest crab in which sex could be determined was a male with carapace width of 1.98 mm. Crab abundance declined in January, and the lowest numbers occurred in March at all

sites (data are presented in Supplementary material Table S1) following the coldest months of the year. Native resident crabs collected at each site included *Panopeus herbstii* H. Milne Edwards, 1834, *Eurypanopeus depressus* Smith, 1869, and *Menippe mercenaria* Say, 1818.

Ovigerous *P. armatus* were present at all sites in September and at higher proportions in all size classes at the northern locations (North Inlet and Charleston; Figure 2) except the most northern location (Wilmington) due to low sample size. Only one ovigerous female was collected in January, and this female (9.37 mm CW) was from Bluffton (Bly Creek). No ovigerous females were collected in March. In June, most females carried eggs underneath the abdomen (Figure 3). Ovigerity rates were higher at the

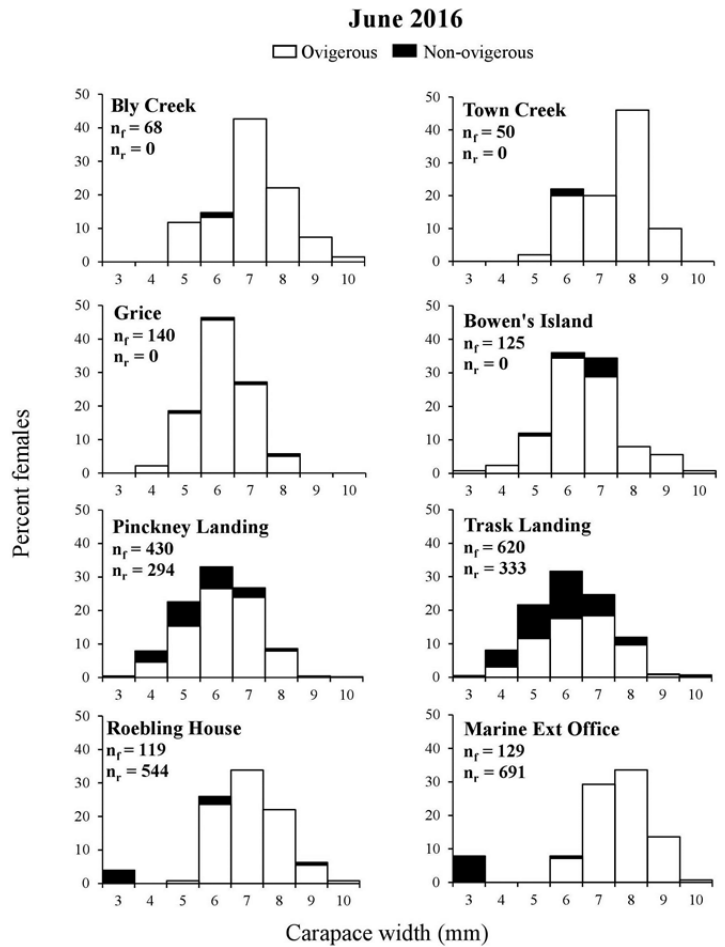


Figure 3. Percent ovigerous (white) and non-ovigerous (black) *Petrolisthes armatus* at each site for the June collection period. Total number of females (n_r) and recruits (any crab < 3 mm CW; n_r) are above the bars for each site.

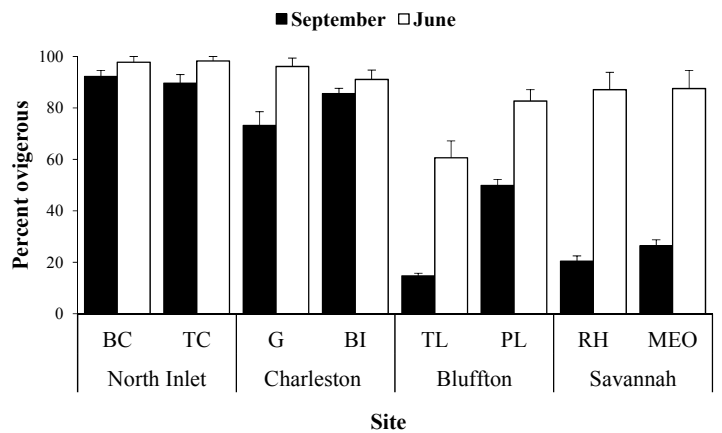


Figure 4. Mean (+ standard error) percent ovigerous *Petrolisthes armatus* females at each site within locations (see Figure 1 for site names).

southern locations (Bluffton and Savannah) in June (60.6–87.5%) when compared to September (14.7–49.8%) and were relatively consistent between time periods (73.2–98.2%) at northern locations (North Inlet and Charleston), resulting in a significant time period × site interaction in the statistical analysis

($F_{7,46} = 17.8$, $p < 0.001$, Figure 4). In September, percent ovigery was lower at southern compared to northern locations, whereas in June, ovigery was relatively consistent across sites. Opaque, white eggs that lacked developmental features, were present on females collected in September at the southern sites where

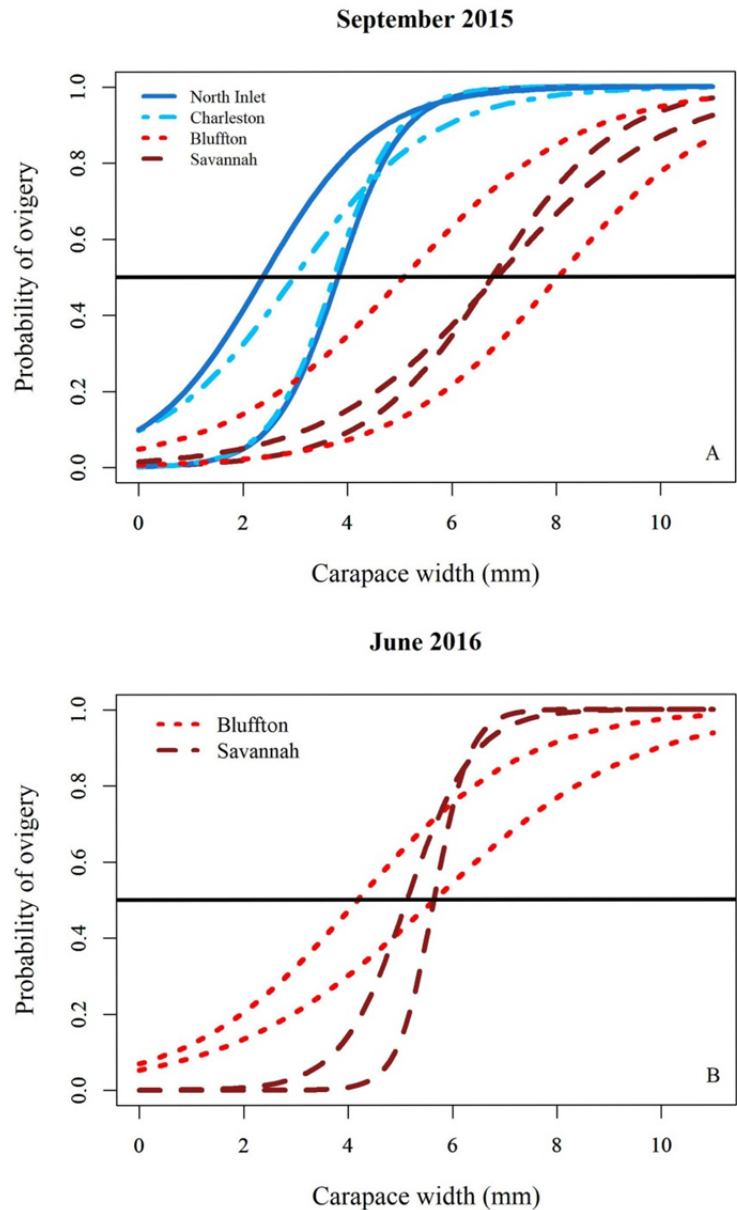


Figure 5. Logistic regression to calculate size at maturity for *Petrolisthes armatus* females at each site for the September (A) and June (B) collection periods. Northern locations are depicted in blue (North Inlet sites are solid lines and Charleston sites are dash/dot lines), while southern sites are depicted in red (Bluffton sites are dot lines and Savannah sites are dash lines).

ovigery rates were lowest. Females with opaque eggs were counted as ovigerous, but were not used in analyses of egg quality.

Size at maturity

Size at maturity based on logistic regression and 50% ovigery rates in September differed among sites ($z_6 = 22.4$, $p < 0.001$) and was smaller for females from the northern (North Inlet and Charleston; 2.4–3.7 mm CW) compared to the southern (Bluffton and

Savannah; 5.1–8.0 mm CW; Figure 5a) sites. The Hosmer-Lemeshow test indicated that the logistic model used for comparison among sites had a good fit ($p = 0.08$), however there were a few sites that individually had a poor fit. Given the large size at maturity estimates for the southern sites in September, a second logistic regression was used with crabs collected in June at sites with a sufficient number of non-ovigerous females (i.e., more than 10). A second logistic regression could not be performed for Bly Creek, the only northern site with poor fit,

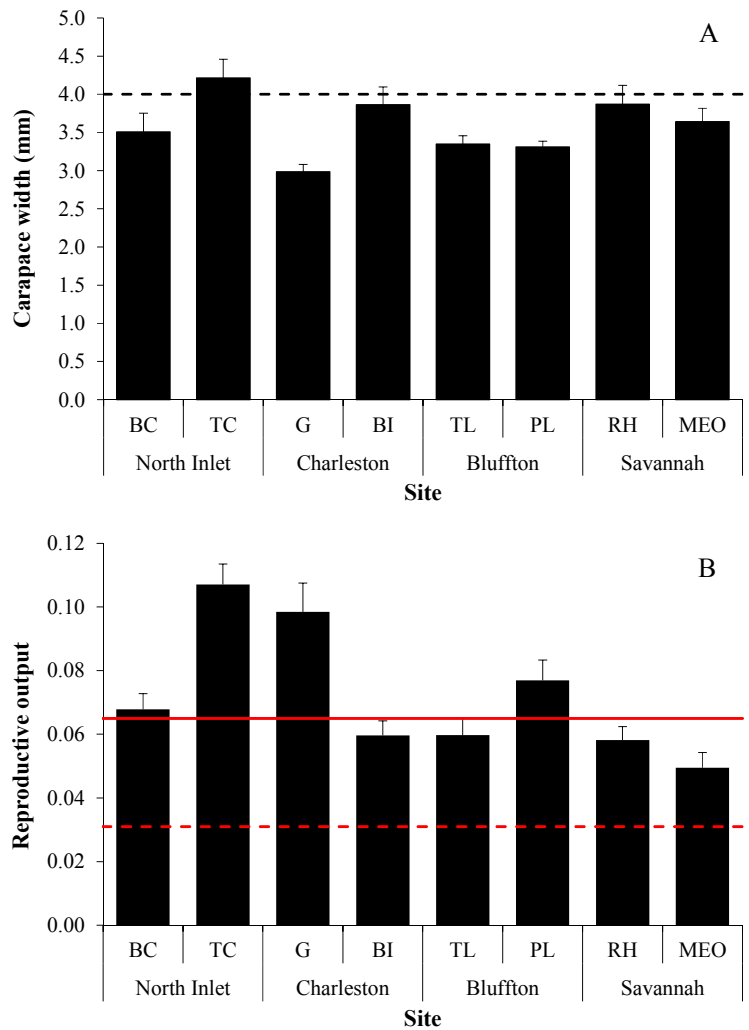


Figure 6. Mean (+ standard error) carapace width (mm) of the smallest ovigerous female in each tray (A) and reproductive output for *Petrolisthes armatus* (B) at each site. The smallest ovigerous female noted in the native range (Ilha do Farol and São Paulo State, Brazil; Oliveira and Masunari 1995; Miranda and Mantelatto 2010) is denoted by a black-dashed line. Reproductive output values for the native range (Wehrmann et al. 2012) are denoted by red-dashed (São Sebastião, Brazil) and red-solid (Punta Morales, Costa Rica) lines.

due to its high ovigery rate in June (Figure 3). Size at maturity estimates in June (4.2–5.7 mm CW) for the southern sites were smaller than September estimates. Size at first maturity for females at Trask Landing (4.2 mm CW) in Bluffton was significantly smaller compared to females at the other southern sites (all p -values < 0.001; Figure 5b).

Smallest ovigerous female size did not exhibit a strong latitudinal trend, but differed among sites ($F_{7,24} = 4.1$, $p = 0.004$; Figure 6A), reflecting a significantly smaller size at Grice (3.0 mm CW) compared to Town Creek (4.2 mm CW), Bowen’s Island (3.9 mm CW) and Roebing House (3.9 mm CW). The smallest ovigerous females were larger at Town Creek (North Inlet) compared to Pinckney Landing (Bluffton) measuring 3.3 mm CW (Tukey post-hoc comparisons, all p -values < 0.05).

Reproductive output

Mean reproductive output for females ranged between 0.06–0.11 at northern sites and between 0.05–0.08 at southern sites (Figure 6B). There was a significant interaction between female dry weight and site, indicating that there were differences in the relationships between egg mass dry weight and female dry weight among the sites ($F_{7,222} = 7.2$, $p < 0.001$). There was no clear latitudinal pattern for these relationships, but at all locations, the egg dry mass increased with female dry mass. The highest reproductive output was observed at two northern sites, namely Town Creek (0.11 ± 0.01) and Grice (0.10 ± 0.01), whereas the lowest reproductive output was observed at a southern site, Marine Extension Office (0.05 ± 0.01 ; Figure 6B).

Figure 7. Square-root (sqrt) transformed egg number vs. carapace width (mm) for *Petrolisthes armatus* females at each site (n = 30 for each site) depicted by location. Northern locations are depicted in blue (North Inlet – solid lines and Charleston – dash/dot lines), whereas southern sites are depicted in red (Bluffton – dot lines and Savannah – dash lines).

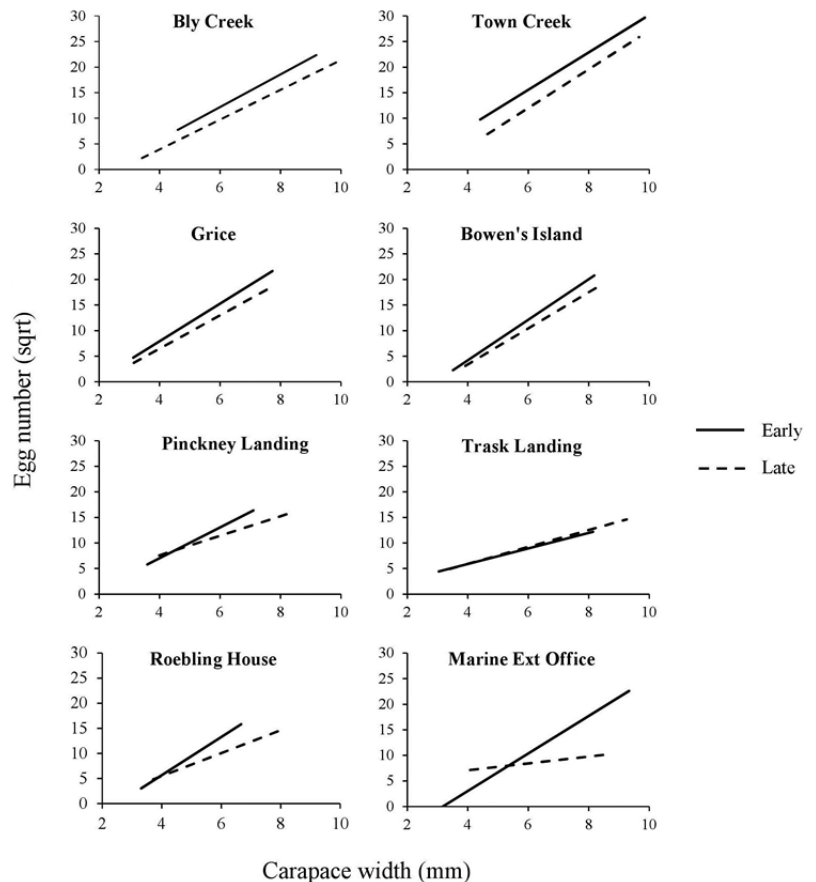
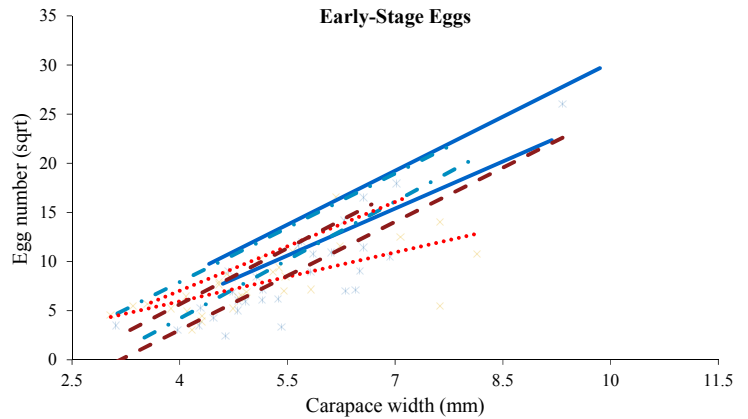


Figure 8. Carapace width (mm) vs. square root (sqrt) egg number for each site for *Petrolisthes armatus* females (n = 30 for each site) with early-stage eggs (solid) and late-stage eggs (dashed).

Egg count, loss, and quality

Egg number was positively related to female size (Figure 7), with a weaker relationship at Trask Landing resulting in a significant interaction between CW and location ($F_{7,225} = 4.0, p < 0.001$). An analysis omitting Trask Landing indicated egg counts differed among the remaining sites ($F_{6,198} = 17.2, p < 0.001$),

with the greatest egg number relative to female CW for females at two northern sites (Town Creek and Grice; Figure 7), averaging 311 and 219 eggs/female, respectively. Lowest egg production (70 eggs/female) occurred at a southern site (Trask Landing), with no clear spatial pattern among the remaining sites.

In general, egg loss at the northern sites (North Inlet and Charleston sites) was consistent across crab

size, while at the southern sites (Bluffton and Savannah sites) egg loss was more common for larger females (Figure 8). Egg number, therefore, differed significantly by the carapace width \times stage \times location interaction ($F_{7,435} = 2.7$, $p < 0.05$). For organic content, there was a significant interaction between site and female CW ($F_{7,225} = 2.6$, $p = 0.1$), and female CW was a significant covariate ($F_{1,225} = 5.1$, $p = 0.03$). However, there was no consistent pattern among sites.

Organic content was fairly consistent among sites ranging from 0.018 to 0.029 mg/egg, with differences in the organic content ($F_{7,233} = 2.1$, $p = 0.04$) resulting from lower organic content at Roebeling House (0.02 ± 0.002 mg/egg) compared to Marine Extension Office (0.03 ± 0.003 mg/egg). There was not a significant relationship between egg volume and female CW ($F_{7,224} = 2.2$, $p = 0.1$) but there were differences in egg volume among the sites ($F_{7,224} = 15.6$, $p < 0.001$). Overall egg volume averaged 0.06 ± 0.001 mm³ and among site averages ranged from 0.04 to 0.07 mm³. Site-related differences were due to smaller eggs produced by Grice females (0.04 ± 0.002 mm³).

Allometry

Overall, crab morphology differed significantly between males and females ($R = 0.68$, $p = 0.001$), with no differences between sites for either males ($R = 0.10$) or females ($R = 0.01$). Pleopod length contributed the most to dissimilarities in crab morphology between the sexes, followed by abdomen length and abdomen width (Table 1). The relative growth of all body measurements differed between males and females (all p -values < 0.05). For any given size, males were larger than females and had a higher growth rate for all measurements except for abdomen width and length. There were significant between-site differences for carapace length, walking leg length, abdomen width and pleopod length (all p -values < 0.05), and the relative growth of right claw length and width differed between the sites (p -values < 0.05). Claw growth rate was higher and abdomen width was larger at Pinckney Landing (Bluffton), while carapace length, walking leg length and pleopod length were larger at Town Creek (North Inlet).

Male body measurements were larger at Pinckney Landing (Bluffton) compared to Town Creek (North Inlet), whereas the inverse pattern was true for females (Table 2), which may reflect the uneven sample sizes of males and females at Town Creek rather than population differences between the sites. There were no morphological characters with break points for females at either Town Creek or Pinckney Landing; therefore, female size at maturity

Table 1. SIMPER results identifying the relative contribution of each morphological trait to the observed dissimilarity in morphology between male and female *Petrolisthes armatus*.

Trait	% Contribution	Cumulative %
Pleopod Length	16.53	16.53
Abdomen Length	14.54	31.07
Abdomen Width	14.26	45.34
Right Claw Length	9.65	54.99
Left Claw Length	9.46	64.45
Carapace Length	9.44	73.89
Right Claw Width	9.25	83.13
Left Claw Width	9.07	92.21
Walking Leg Length	7.79	100.00

could not be predicted using an allometric approach. There was a break in the regression line for pleopod length in males. The linear piecewise regression calculated that break in the regression line (size at maturity) was at 3.99 mm CW for males at Town Creek (northern site) and 2.96 mm for males at Pinckney Landing (southern site).

Males exhibited positive allometric growth for all claw measurements and negative allometric growth for carapace length, walking leg length, both abdomen measurements and pleopod length. This pattern was similar at both sites except at Pinckney Landing there was isometric growth for pleopod length. In contrast, females showed positive allometric growth for all claw measurements, both abdomen measurements and pleopod length and negative allometric growth for carapace length and walking leg length. These relationships were also similar between sites except at Town Creek there was isometric growth for left claw width and abdomen length. The most important difference was that males exhibited a negative allometric relationship between abdomen width, abdomen length and pleopod length compared to CW, whereas females exhibited positive allometric relationships for these same characters (Table 3).

Comparison to native populations

Overall, the smallest ovigerous female in this study was 2.8 mm CW, and the mean size of smallest ovigerous females (3.6 mm CW) was significantly smaller than the smallest ovigerous female (4.0 mm CW) observed in Ilha do Farol and São Paulo State, Brazil ($t_{31} = -4.6$, $p < 0.001$; Figure 6A). Reproductive output was greater at Town Creek (0.1) and Grice (0.09) and lower at Marine Extension Office (0.05) compared to a site in Costa Rica (0.07; all p -values < 0.006). Crabs at all the sites, except Marine Extension Office, had a higher reproductive output compared to a site in Brazil (0.03; all p -values < 0.006 ; Figure 6B).

Table 2. Mean (\pm standard error), minimum and maximum values (mm) of body measurements analyzed for *Petrolisthes armatus* males and females at a northern site (Town Creek) and a southern site (Pinckney Landing).

Trait	Sex	Northern Site (Town Creek) M (n = 72) and F (n = 28)			Southern Site Pinckney Landing M (n = 72) and F (n = 28)		
		Mean \pm SE	Minimum	Maximum	Mean \pm SE	Minimum	Maximum
Carapace width	M	5.71 \pm 0.22	2.93	10.73	6.37 \pm 0.37	2.43	10.83
	F	5.98 \pm 0.30	3.24	9.39	5.23 \pm 0.26	2.31	9.00
Carapace length	M	6.31 \pm 0.24	3.35	12.26	6.86 \pm 0.38	2.76	11.28
	F	6.35 \pm 0.30	3.70	9.76	5.50 \pm 0.26	2.83	9.27
Left claw length	M	9.23 \pm 0.50	3.52	22.75	10.79 \pm 0.80	2.75	20.66
	F	8.32 \pm 0.52	4.12	15.23	7.05 \pm 0.42	2.52	12.89
Left claw width	M	3.13 \pm 0.17	1.16	7.88	3.66 \pm 0.26	0.93	6.95
	F	2.79 \pm 0.17	1.47	4.89	2.45 \pm 0.14	0.88	4.46
Right claw length	M	8.95 \pm 0.44	3.67	20.13	10.72 \pm 0.81	2.85	20.21
	F	8.23 \pm 0.47	4.01	13.71	7.02 \pm 0.43	2.80	13.49
Right claw width	M	3.02 \pm 0.14	1.21	6.68	3.65 \pm 0.27	1.03	7.15
	F	2.78 \pm 0.15	1.35	4.49	2.45 \pm 0.15	0.91	4.49
Walking leg length	M	8.80 \pm 0.31	4.84	16.32	9.06 \pm 0.49	3.65	15.33
	F	8.75 \pm 0.42	5.04	14.02	7.48 \pm 0.37	3.65	12.20
Abdomen width	M	4.12 \pm 0.15	2.17	8.01	4.45 \pm 0.25	1.64	9.00
	F	5.32 \pm 0.31	2.59	9.13	4.52 \pm 0.26	1.68	8.14
Abdomen Length	M	5.63 \pm 0.20	3.06	10.15	6.23 \pm 0.35	2.46	10.72
	F	7.36 \pm 0.41	3.87	12.74	6.41 \pm 0.37	2.36	11.60
Pleopod length	M	2.59 \pm 0.095	1.30	5.04	2.75 \pm 0.16	0.60	4.37
	F	0.90 \pm 0.074	0.38	2.11	0.77 \pm 0.057	0.22	1.51

Discussion

Variability of reproductive characteristics

There was considerable site-specific variability in reproductive characteristics of *Petrolisthes armatus*; however, there was no evidence that crabs on the leading edge of the range expansion were stressed (e.g., these females did not exhibit lower fecundity or carry eggs with higher organic content), which could limit additional range expansion. In some cases, spatial trends in reproductive characteristics were consistent with the attributes of successful crustacean invaders; for example, fecundity was higher in populations in the introduced compared to populations in the native range (Hollebone and Hay 2007; present study). However, these results should be taken with caution as the invasive vs. native range comparisons involve only a few studies from a few areas and are furthermore confounded by temporal differences when studies were conducted. Therefore, further study is needed to better determine whether reproductive characteristics differ between native and invasive populations. Within the invaded range, populations with characteristics favorable for additional range expansion were from more northern locations. For example, when differences occurred, reproductive output and egg number were highest at our two northern sites, i.e., Town Creek and Grice. Female size at maturity also was smaller at two northern sites, which would be advantageous if size

is consistently related to age throughout the study area, i.e., if smaller females are younger and presumably reproduce over more of their lifespans than females with a larger size at maturity. However, more information concerning the size-age relationship for this species in the invaded range is needed to assess this. Females allocated more energy to reproduction to produce more offspring at northern locations. Two native *P. armatus* populations also exhibit intra-specific plasticity in egg number and reproductive output, as well as differences in egg volume (Wehrmann et al. 2012), which did not vary much among populations in our study.

Geographic variability in reproductive characteristics may reflect different life history strategies. Latitudinal trends in female size at maturity, egg number, egg volume, allometric relationships, and reproductive output have been reported in other crustacean species (Jones and Simons 1982; Lardies and Castilla 2001; Lira et al. 2015). Changes in life history strategies due to different selection pressures between range-edge populations compared to established populations near the center of their distribution have been demonstrated through stochastic simulation models (Burton et al. 2010). In the model, simulated populations at the range edge consistently favored characteristics for dispersal by investing more energy into reproduction, while more established populations invested more energy into individual survival. Increases in energy allocation for reproduction at the expansion front have been demonstrated at a fine spatial and temporal scale for an invasive freshwater

Table 3. Relative growth relationships of all the body measurements (CL: carapace length, LCL: left claw length, LCW: left claw width, RCL: right claw length, RCW: right claw width, WL: walking leg, AW: abdomen width, AL: abdomen length and PL: pleopod length) compared to carapace width (CW) for males and females at both sites.

Northern Site (Town Creek)						
M (n = 72) and F (n = 28)						
	Sex	Y = aX ^b	r ²	t-statistic	p-value	Relative growth
CL vs CW	M	Y = 1.16X ^{0.97}	0.99	-2.02	< 0.05	-
	F	Y = 1.23X ^{0.92}	0.99	-3.78	< 0.001	-
LCL vs CW	M	Y = 0.80X ^{1.38}	0.95	10.16	< 0.001	+
	F	Y = 0.95X ^{1.21}	0.95	4.05	< 0.001	+
LCW vs CW	M	Y = 0.27X ^{1.38}	0.92	7.96	< 0.001	+
	F	Y = 0.37X ^{1.13}	0.87	1.55	NS	0
RCL vs CW	M	Y = 1.017X ^{1.24}	0.95	7.17	< 0.001	+
	F	Y = 1.067X ^{1.14}	0.98	4.18	< 0.001	+
RCW vs CW	M	Y = 0.35X ^{1.22}	0.93	5.68	< 0.001	+
	F	Y = 0.38X ^{1.10}	0.94	1.86	< 0.05	+
WL vs CW	M	Y = 1.80X ^{0.91}	0.98	-6.15	< 0.001	-
	F	Y = 1.66X ^{0.93}	0.98	-2.56	< 0.05	-
AW vs CW	M	Y = 0.77X ^{0.96}	0.98	-2.32	< 0.05	-
	F	Y = 0.64X ^{1.18}	0.97	4.28	< 0.001	+
AL vs CW	M	Y = 1.10X ^{0.94}	0.96	-2.76	< 0.05	-
	F	Y = 1.04X ^{1.09}	0.94	1.71	NS	0
PL vs CW	M	Y = 0.47X ^{0.96}	0.98	-1.93	< 0.05	-
	F	Y = 0.067X ^{1.43}	0.81	3.17	< 0.05	+
Southern Site (Pinckney Landing)						
M (n = 50) and F (n = 50)						
CL vs CW	M	Y = 1.18X ^{0.95}	0.99	-5.60	< 0.001	-
	F	Y = 1.21X ^{0.92}	0.99	-7.6	< 0.001	-
LCL vs CW	M	Y = 0.86X ^{1.34}	0.99	15.96	< 0.001	+
	F	Y = 0.94X ^{1.21}	0.99	12.49	< 0.001	+
LCW vs CW	M	Y = 0.31X ^{1.32}	0.97	10.23	< 0.001	+
	F	Y = 0.33X ^{1.20}	0.97	6.96	< 0.001	+
RCL vs CW	M	Y = 0.82X ^{1.36}	0.98	14.84	< 0.001	+
	F	Y = 0.90X ^{1.23}	0.95	9.5	< 0.001	+
RCW vs CW	M	Y = 0.31X ^{1.32}	0.97	9.92	< 0.001	+
	F	Y = 0.32X ^{1.21}	0.97	6.51	< 0.001	+
WL vs CW	M	Y = 1.84X ^{0.86}	0.89	-3.17	< 0.05	-
	F	Y = 1.51X ^{0.97}	0.99	-2.68	< 0.05	-
AW vs CW	M	Y = 0.74X ^{0.97}	0.99	-1.93	< 0.05	-
	F	Y = 0.61X ^{1.20}	0.99	10.92	< 0.001	+
AL vs CW	M	Y = 1.07X ^{0.95}	0.99	-3.63	< 0.05	-
	F	Y = 0.90X ^{1.18}	0.98	7.64	< 0.001	+
PL vs CW	M	Y = 0.41X ^{1.03}	0.94	0.88	NS	0
	F	Y = 0.062X ^{1.49}	0.93	8.58	< 0.001	+

fish (Masson et al. 2016). Likewise, *P. armatus* may be encountering different selection pressures in northern versus southern locations in our study. For instance, intra-specific competition is likely more intense in southern populations where densities are higher (Table S1) and environmental stresses, such as more frequent and extreme cold winter temperatures, may more strongly affect northern populations. Connectivity between these sites is unknown without genetic analysis; however, connectivity among the four locations may be limited. Californian populations of *P. cinctipes* Randall, 1840 studied across 700 km of shoreline exhibited limited connectivity at distances greater than 30 km (Hameed et al. 2016). Distances between contiguous locations in our study ranged from approximately 40 to 90 km, and the distance between Charleston and Bluffton, the break

between our grouping of northern and southern sites, was approximately 100 km. A biogeographic break within our study area has not been identified (Altman et al. 2013) and although planktonic larval durations can last from one to two months (Gore 1972), the vertical migration of larvae within the water column likely aids larval retention within estuaries and reduces mixing among populations (Tilburg et al. 2010). Therefore, it is unlikely that the populations sampled at different latitudes consistently receive new propagules from other sampled locations.

Size at sexual maturity

Size at sexual maturity (as estimated by 50% ovigery rates) was smaller at our sampled northern locations and, if size and age are consistently correlated

throughout the study area, may reflect range-edge populations facing selection pressures that favor early reproduction in agreement with the simulation models (Burton et al. 2010). Smaller body size of reproductive females at lower densities also may reflect a reduced influence of intra-specific competition on body size that limited reproduction. Regardless, smaller female size at sexual maturity could increase the number of females available to reproduce and increase the population's reproductive output potential. However, the size-age relationship needs to be determined to better understand the influence of size at maturity on range expansion potential. Additionally, at northern sites, selection may favor shorter life span if cold temperatures cause mortality. Latitudinal trends in reproductive characteristics may reflect plasticity of these parameters. Not much could be inferred about male size at sexual maturity because size was only estimated for two sites, and there were few small males. While there were differences between sites, there was not a consistent pattern of one site exhibiting larger body measurements. Inclusion of more sites and larger sample sizes, especially for smaller crabs, may help clarify latitudinal trends or the lack of thereof in male size at sexual maturity and relative growth between sites. Additional samples could also aid in detecting female size at sexual maturity through allometric analysis as seen elsewhere (Miranda and Mantelatto 2010; Pinheiro et al. 2017).

Timing of reproduction

Differences in the timing of reproduction for *P. armatus* along the latitudinal gradient may explain differences in ovigery rates, reproductive output, and the higher incidence of opaque eggs at the southern sites in September. Reproduction begins earlier in the spring at southern sites (Bluffton and Savannah) based on the presence of new recruits exclusively at southern sites in June. By June, however, ovigery rates were similar across all sites, indicating that environmental conditions suitable for reproduction were present throughout the study area by this time. Near the end of the spawning season (September), ovigery rates were lower at southern compared to northern sites, and non-viable eggs were more common at southern sites, possibly because females at southern sites had exhausted energy reserves after a longer spawning season. While opaque eggs could be an indication of reproductive exhaustion, they also may be an indication of parasites (Jensen 2006), pollution (Lee et al. 1996; Zapata et al. 2001; Pinheiro et al. 2017), or sperm limitation (Hines et al. 2003). Sex ratios do not suggest a deficiency of males, thus

sperm limitation seems unlikely. Results of a nearest-neighbor laboratory study were consistent with mate guarding by males (Wassick et al. 2017); therefore, operational sex ratios may differ from abundance ratios. Crab reproductive output is maximal at the beginning of the reproductive season (Bas et al. 2007; Darnell et al. 2009); therefore, an earlier start to reproduction at the southern sites may lead to less energy available to invest in reproduction by September, reflecting reproductive exhaustion (Palacios et al. 1999; Bas et al. 2007) and lower ovigery rates.

In addition to an earlier start to the reproductive season at southern sites, a shortened reproductive season at the northern sites could explain the higher September reproductive output and ovigery rates. Temperate species, especially those occurring over large latitudinal gradients, commonly have compressed reproductive seasons compared to sub-tropical species (Clarke 1987; Bauer 1992; Defeo and Cardoso 2002; Cardoso and Defeo 2003). Lower temperatures at higher latitudes can decrease female metabolism, allowing increases in energy investment in egg production to compensate for a shorter reproductive season (Cardoso and Defeo 2003).

Egg loss

Crab fecundity is often measured by egg counts and clutch volume, with larger females tending to have higher fecundity than smaller individuals (Reid and Corey 1991; Turra and Leite 1999; Bert et al. 2016). *Petrolisthes armatus* egg counts were positively correlated with female size, and egg loss patterns differed between northern and southern sites. Egg loss was consistent across female size at northern sites and was greater for larger females at southern sites. Late-stage egg loss can occur due to developing embryo being more vulnerable to stress as its metabolic activity increases (Oh and Hartnoll 1999). Higher egg loss for large females in the south at the end of the spawning season may reflect depleted energy reserves not experienced by smaller females that were not sexually mature at the beginning of the spawning season. Other reproductive characteristics related to egg quality (e.g., organic content and egg volume) were relatively consistent across sites suggesting that egg quality may be a relatively stable characteristic.

Allometry

Consistent crab morphology between the native and introduced range in a congener (Gribben et al. 2013) was similar to the homogeneous crab morphology between two populations in this study. The differences

in allometric growth between the sexes, the body measurement used to calculate male size at sexual maturity, and the characters that contributed the most to the dissimilarities between the sexes were all secondary sexual characteristics (abdomen width, abdomen length and pleopod length), which is common in other crustaceans (Hartnoll 1974; Schejter and Spivak 2005; Silva et al. 2014). The positive allometric relationship in the secondary sexual characteristics in females is advantageous because larger abdomens allow females to carry more or larger eggs. In comparison, males investing energy into cheliped growth may be advantageous for aggressive or courtship interactions (Hartnoll 1974). Although body and claw size did not contribute the most to the dissimilarity between the sexes, males were larger than females and had larger claws. Sexual dimorphism in body claw size is also present in Brazilian populations (Miranda and Mantelatto 2010; Pinheiro et al. 2017).

Summary

Given that *P. armatus* exhibits several characteristics of a successful crustacean invader (*sensu* van der Velde et al. 2000), this species has the potential for further range expansion as coastal temperatures increase, moving any temperature barrier to higher latitudes. Spatial trends that signal stress for range-edge populations of other porcelain crabs (Rivadeneira et al. 2010) were not evident for *P. armatus* at our northern sites (e.g., lower reproductive output or higher egg organic content). Although timing and length of the reproductive period likely play a role in the spatial patterns seen in some of the reproductive characteristics, it appeared that northern populations are maximizing reproductive output. Females from northern populations, especially Town Creek and Grice, invested more energy into reproduction and produced more eggs. Given that *P. armatus* is at least intermittently present in Wilmington, NC, increases in water temperatures may allow this species to establish a stable population at this northern location in the near future and continue to spread northward along the northwestern Atlantic coast.

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Supplementary material

The following supplementary material is available for this article:

Table S1. Mean of each population parameter of *Petrolisthes armatus* for all sampling periods.

This material is available as part of online article from:

http://www.aquaticinvasions.net/2018/Supplements/A1_2018_Wassick_etal_Table_S1.xlsx