



Spatial and Temporal Associations Between Native Crabs and the Invading Green Porcelain Crab, *Petrolisthes armatus*, Throughout Its Northernmost Invaded Range

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Abstract

Increasing ocean temperatures have led to poleward range expansions of many marine organisms. The green porcelain crab, *Petrolisthes armatus*, was first reported on intertidal oyster reefs near Charleston, South Carolina in the mid-1990s, an expansion from its tropical to sub-tropical native range. In order to investigate the relative abundances of this introduced crab and a portion of the native crab community, resident crab assemblages were sampled on intertidal oyster reefs across four seasons from 2015 to 2016. Sampling occurred at five locations extending from Savannah, Georgia where *P. armatus* is now well-established, to Wilmington, North Carolina, where its inter-annual presence is intermittent. *Petrolisthes armatus* was the numerically dominant crab species at all locations except Wilmington, where the species was not collected in the winter. Differences between northern and southern sample locations in the taxonomic composition of crab assemblages were most pronounced in the summer (June–September) and fall (October–January), with dissimilarities largely attributed to high abundances of *P. armatus* at southern locations. Crab abundances of all species peaked in the summer and were lowest in the winter (February–March). *Petrolisthes armatus* was less abundant toward the northern range edge, whereas native crabs did not differ in abundance throughout the sampling range. Throughout the study area, adult *P. armatus* sex ratios shifted from unbiased or female-biased in the summer to male-biased in the fall. Adults were collected in the spring (April–June), indicating they had overwintered. While native crab densities (*Panopeus herbstii*, *Eurypanopeus depressus*) stayed relatively constant across locations, *P. armatus* densities varied greatly, suggesting that resources, such as shelter and food, are not limiting factors for the coexistence of these native and invading crabs.

Keywords Range expansion · Oyster reef ecology · *Eurypanopeus* · *Panopeus*

Introduction

Changing ocean temperatures are associated with altered distributions of marine species, in many cases resulting in poleward expansion (Sorte et al. 2010; Canning-Clode et al. 2011; Canning-Clode and Carlton 2017). In the mid-1990s, intertidal

oyster reef habitats in Atlantic waters of the southeastern US (hereafter referred to as South Atlantic Bight, or SAB) were invaded by the green porcelain crab, *Petrolisthes armatus* (Porcellanidae; Knott et al. 2000; Hartman 2003, Hollebone and Hay 2008). The northern range of this species has likely been limited by intolerance of cold water temperatures (Canning-Clode et al. 2011; Eash-Loucks et al. 2014), but could expand further with warming ocean waters (Hartman 2003). In both its native and invaded range, *P. armatus* can occur at high abundances and has the potential to alter trophic interactions in novel communities (Hollebone and Hay 2008; Pintor and Byers 2015a). However, relatively little is known about the extent of this species' range expansion or its potential impacts on native crab assemblages in the SAB.

Within the Western Atlantic, *Petrolisthes armatus* is native from the Indian River, Florida south through the Caribbean to Brazil (Fig. 1; Knott et al. 2000; Werding et al. 2003). Its initial introduction to Charleston, South Carolina, likely

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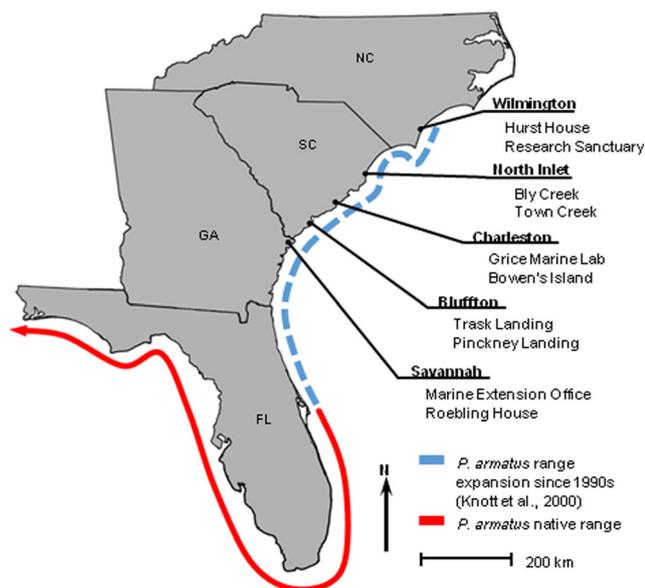


Fig. 1 Five sampling locations (and sites therein) within northernmost invaded range of *Petrolisthes armatus*. From south to north: Savannah, Georgia (Marine Extension Office and Roebbling House), Bluffton, South Carolina (Trask Landing and Pinckney Landing), Charleston, South Carolina (Grice Marine Lab and Bowen's Island), Baruch, South Carolina (Bly Creek and Town Creek), and Wilmington, North Carolina (Hurst House and Research Sanctuary). Portion of native range of *P. armatus* indicated by solid line, invaded range by dashed line. See Table 1 for distances between sites at same location. Adapted from Knott et al. 2000

involved inadvertent transportation from Florida alongside oysters and seed clams for use in the aquaculture industry (Knott et al. 2000; Wally Jenkins, South Carolina Department of Natural Resources, pers. comm.). Warm water temperatures and mild winters coincided with further northward expansion in the early 2000s (Hartman 2003), potentially through dispersal of planktonic larvae (sensu Tilburg et al. 2010). In a 2004 survey of intertidal oyster reefs that sampled resident crab assemblages, the species was not found in northern South Carolina (Hadley et al. 2010). *Petrolisthes armatus* was found in oyster samples from intertidal reefs in Wilmington, North Carolina as early as 2008, but is not observed there every year and, when present, occurs in low numbers (Troy Alphin, University of North Carolina Wilmington, pers. comm.). While the species' northern range limit is apparently shifting poleward, the exact dynamics involved remain unclear. Genetic evidence indicates that populations in Georgia and South Carolina were established by a large number of initial propagules, with a likely origin in Florida (Hiller and Lessios 2017). These populations belong to a different clade from more southerly populations in Yucatan and Brazil, with the separation occurring over hundreds of years ago followed by limited gene flow (Hiller and Lessios 2017). *Petrolisthes armatus* has two zoeal stages and a megalopal stage (Gore 1969) and can reach the first juvenile crab stage in 15–17 days under laboratory conditions

(Hollebone and Hay 2007). Larvae migrate to deeper water, which aids their retention in natal estuaries (Tilburg et al. 2010) and are recognized as having low dispersal (Hiller and Lessios 2017). Continued poleward expansion may depend on movement into new habitat and subsequent overwintering of adults.

Following the initial invasion, *P. armatus* occurred at high densities that varied with latitude from ~ 300 crabs m^{-2} in South Carolina (Hartman 2003; Hadley et al. 2010) to over several thousand crabs m^{-2} in Georgia (Hollebone and Hay 2007). Population densities also vary by season, with highest densities in the invaded range during summer (June–September) followed by a drastic reduction in density in the winter (Hartman 2003; Hollebone and Hay 2007). The species' low tolerance of cold winter temperatures may explain latitudinal and seasonal differences in abundance (Canning-Clode et al. 2011; Eash-Loucks et al. 2014).

In its invaded range, *P. armatus* occupies interstitial space on intertidal oyster reefs. The Eastern oyster, *Crassostrea virginica*, is an ecosystem engineer (Jones et al. 1994) that forms vertically complex reefs that stabilize shorelines (Meyer et al. 1997; Piazza et al. 2005) and provide habitat for other resident and transient organisms (Menzel and Nichy 1958; Leinhert and Allen 2002; Tolley and Voley 2005; Shervette and Gelwick 2008; Hadley et al. 2010). Oysters also provide ecosystem services, such as coupling benthic producers with pelagic consumers (Dame and Libes 1993) and improved water clarity (Nelson et al. 2004; Porter et al. 2004). Two of the most common native crabs on intertidal oyster reefs along the SAB are the panopeid mud crabs *Panopeus herbstii* and *Eurypanopeus depressus*. These species exhibit different life history traits that lead to microhabitat partitioning within oyster reefs (McDonald 1982; Meyer 1994; Margiotta et al. 2016). Both species have important roles in trophic relationships within intertidal oyster reef communities; *P. herbstii* is larger and primarily carnivorous, consuming molluscs, crustaceans, and annelids (McDermott 1960; Meyer 1994; Silliman et al. 2004), whereas *E. depressus* consumes algae and detritus (McDonald 1977; McDonald 1982), and both species prey on oyster spat (McDonald 1982; Kulp et al. 2011). Historically, the two species had similar densities, with lower numbers in winter (McDonald 1982). Recently, a decline in *E. depressus* abundance in at least one area of the SAB was attributed to parasitism by the invasive rhizocephalan barnacle *Loxothylacus panopaei* (Eash-Loucks et al. 2014). However, inherent host-parasite abundance cycles are predicted to favor crab populations under projected warming conditions because infected crab survival is reduced at higher temperatures (Gehman et al. 2018), limiting the parasite's long-term impact on its host.

The invasion of intertidal oyster reefs along the SAB by *Petrolisthes armatus* could alter trophic interactions (Menzel

and Nichy 1958; Kimbro et al. 2014), leading to altered crab assemblages. In other systems, invasive predatory crabs have altered community composition within invaded areas (Grosholz and Ruiz 1995; Grosholz et al. 2000; Lohrer and Whitlatch 2002). *Petrolisthes armatus*, however, is a primary consumer as it both suspension and deposit feeds (Kropp 1981; Zimba et al. 2016). Thus, it is less likely to compete with, and more likely to serve as a food source for native crabs, altering the trophic structure in these communities (Hollebone and Hay 2008; Pintor and Byers 2015b). Oysters and clams filter more effectively when *P. armatus* is present, possibly because the predatory threat of the native crab, *P. herbstii*, on these bivalves is reduced because *P. armatus* provides an alternative prey item (Byers et al. 2014).

Intertidal oyster reef habitat in the SAB supports ecologically important resident crab communities that may have changed in response to the northern expansion of *P. armatus*. The potential impacts to native resident crabs and capacity for further range expansion of *P. armatus* populations are not fully understood. Here, we examine spatial and temporal trends in *P. armatus* abundances, size distributions, and sex ratios, which when female-biased, can be advantageous to the invasion process (e.g., Devin et al. 2004; Rumbold et al. 2016). We also assess associations between *P. armatus* and resident crab assemblages on oyster reefs in the northernmost invaded range of *P. armatus*. We pose the following questions pertaining to this species and co-occurring native crabs on oyster reefs in the SAB: (1) Are there differences in resident crab assemblages between locations where *P. armatus* is well-established and those near its expanded range edge? (2) Do population characteristics (abundance, size, and sex ratio) of *P. armatus* and native crabs vary with latitude and season?

Methods

Study Locations

Five locations, each with two oyster reef sites (Fig. 1), were sampled across a latitudinal range spanning ~400 km within the northernmost invaded range of *Petrolisthes armatus*. Sampling locations and oyster reef sites within those locations in the SAB (Table 1) were selected based on prior reporting of *P. armatus* (Hartman 2003; Hadley et al. 2010) as well as access to natural, non-degraded, intertidal oyster reefs. The SAB is a biogeographic region characterized by similar salinities and semi-diurnal tides of varying amplitude (Byers et al. 2015). The abundance of *P. armatus* is positively related to vertical complexity of intertidal oyster reef habitat (Margiotta et al. 2016). Within the study area, vertical relief of oyster reefs peaks in Georgia and southern South Carolina estuaries, where oysters achieve high density, biomass, and recruitment (Byers et al. 2015). Sites sampled (from south to north) were

located in Savannah (Georgia); Bluffton, Charleston, and North Inlet (South Carolina); and Wilmington (North Carolina; Table 1). For the purposes of this study, “southern” locations are comprised of Savannah and Bluffton and “northern” locations by Charleston, North Inlet, and Wilmington.

Field Collections

Resident crabs were sampled at each site using five plastic trays per site placed ~25 m apart at mid-reef locations within the oyster shell matrix. Trays dimensions (in cm) were 45.0 L × 30.5 W × 10.5 H. Each tray had perforated sides and bottom for water drainage, were lined with 2-mm nylon mesh screen, and packed tightly with dead oyster shells oriented vertically to standardize vertical habitat complexity (Margiotta et al. 2016). Trays were secured flush to the substrate with hooked rebar, so the height of shells within the trays approximated the height of some oyster habitat on surrounding reefs. Plastic netting with 5 × 2 cm holes was secured over each tray with zip-ties to keep oyster shell in place and to exclude large predators while allowing crabs to move in and out of the trays. One tray at each site contained a HOBO temperature datalogger (Onset UA-001-64) that recorded temperature every 30 min for the duration of deployment.

Trays were collected in September 2015 and January, March and June 2016 (summer, fall, winter, and spring, respectively) and new trays were deployed at the time of collection. The trays collected in September were first deployed in June 2015. Trays from all sites were collected within a 5-day time period for each season. Quarterly sampling permitted seasonal comparison among populations. Individual *P. armatus* from a single tray at each site were kept alive for use in cold tolerance experiments (Mack 2017), whereas all other trays were placed in large plastic bags and transported to Grice Marine Laboratory, Charleston, South Carolina for processing. Each tray was emptied and rinsed over a 0.5-mm mesh sieve to separate macrofauna from sediment and oyster-shell hash. All crabs were identified to the lowest taxonomic level possible using Abele and Kim (1986) as a reference for identifications. Crabs were counted, sexed, and measured for carapace width (CW) to the nearest 0.01 mm with digital calipers. Sex identification was not attempted on *P. armatus* < 2 mm CW. Small *Panopeus herbstii* and *Eurypanopeus depressus* (< 4 mm CW) were not identified to the species level and were classified as “panopeid spp.” Parasitism by the invasive rhizocephalan barnacle *Loxothylacus panopaei* was noted when mature externa were visible on the abdomen of native crabs. Sizes and numbers of mature parasite externa per individual were not measured. All samples collected were frozen and stored at Grice Marine Lab through the duration of the study.

Temperature data were downloaded from loggers when trays were collected, and then re-deployed. Data quality was

Table 1 Five sampling locations and two sites sampled within each location. Approximate river kilometer (km) distances from each site to the Atlantic Ocean within each estuary estimated using Google Earth's "measure distance" tool

Location	Site	Latitude (°N)	Longitude (°W)	Estuary	Sediment type	Estuary width (m)	Distance to Atlantic (km)
Savannah	Marine Extension Office	31.988	81.024	Skidaway River	Fragmented oyster reef	50+	18.1
	Roebing House	31.990	81.021				
Bluffton	Trask Landing	32.289	80.809	Harbor River	Mud and oyster reef	50+	21.5
	Pinckney Landing	32.229	80.787		Oyster shell hash	50+	16.1
Charleston	Grice Marine Lab	32.752	79.897	Charleston Harbor	Rocky cobble	3000+	4.5
	Bowen's Island	32.675	79.965	Folly River	Oyster shell hash	100+	7.4
North Inlet	Bly Creek	33.341	79.179	Winyah Bay	Mud and fragmented reef	15	2.7
	Town Creek	33.329	79.188			100+	3.4
Wilmington	Hurst House	34.188	77.851	Masonboro Sound	Mud and fragmented reef	200+	6.3
	Research Sanctuary	34.179	77.843			200+	4.3

assessed and erroneous or anomalous temperature readings were excluded. Using tide height data, times when trays could have been exposed to air temperatures were determined. Infrequently, our temperature data showed drastic changes during these times, confirming that trays were exposed. In those instances, air temperature data were excluded. Water temperatures were the focus of this study because trays were mostly submerged, and because focal resident crab species are mobile enough to avoid air exposure at low tide.

Statistical Analyses

To determine variation in temperature experienced by crabs, spatial (among locations) and temporal (seasonal) differences in mean daily water temperature were analyzed with a linear mixed effects model (LMM). Spatial and temporal differences in abundance, male frequency, and crab size were analyzed for the two most abundant resident crabs: the invading *P. armatus* and the native *Panopeus herbstii*. *Eurypanopeus depressus* was omitted from sex frequency analyses because of low sample sizes, but was included in abundance and size analyses. Small panopeids (<4 mm) were used only in the analysis of abundance. For *P. armatus*, *P. herbstii*, and small panopeids, abundance was analyzed with a LMM. Because recruitment events could substantially influence abundance and average size estimates, *P. armatus* <4 mm CW were excluded from abundance and crab size analyses. A minimum size of 4 mm CW was used because this is the size at which females reach sexual maturity in our study area (Wassick et al. 2017). Abundance data (crabs tray⁻¹) were log-transformed for *P. armatus* and square-root transformed for *P. herbstii* and the panopeids in order to meet test assumptions of normality and homogeneity of variance. Because *E. depressus* was abundant at some sites but not collected at others (i.e., patchy distribution), a generalized linear mixed effects model (GLMM) with a Gaussian distribution and log-link function was used to

analyze its abundance. Sex ratio was analyzed as the number of males/total crab number for all species using a GLMM with a binomial distribution. Carapace width was analyzed for all species with a LMM, though separate analyses were conducted for males and females in *P. armatus* due to sexual dimorphism in the species. Size data for all species were square-root transformed to meet normality and homogeneity of variance assumptions. Spatial and temporal differences in the occurrence of the castrating barnacle *Loxothylacus panopaei* on *E. depressus* were analyzed using a GLMM with a binomial distribution using crab size as a covariate.

In all models, the variables season and location were included as fixed effects, and sites were treated as a random effect nested within location. Hypothesis testing was conducted with a likelihood ratio test fit by restricted maximum likelihood in the case of the LMM, and by maximum likelihood in the case of the GLMM. Tukey post-hoc pairwise comparisons were conducted for each season within each location, and each location within each season. The statistical package R (version 3.2.3; R Core Team 2015) was used for all LMM and GLMM analyses and post-hoc tests. The lmer (Pinheiro et al. 2017) package was used for the LMM and the lme4 (Bates et al. 2015), MASS (Venables and Ripley 2002), and car (Fox and Weisberg 2011) packages were used for the GLMM. All post-hoc comparisons were conducted using the multcomp (Hothorn et al. 2008) and lsmeans (Lenth 2016) packages.

Differences in the taxonomic composition of resident crab assemblages among locations ($N = 4$) were analyzed using analysis of similarity (ANOSIM) tests for each season. Low crab sample sizes at the Wilmington location precluded using that location in all assemblage-related statistical analyses. Crab abundances were log-transformed to increase the contribution of the less abundant crab taxa. Analyses used ranked similarity matrices based on Bray-Curtis similarity measures and were distinguished on a scale of $R = 0$ (groups were indistinguishable) to $R = 1$ (no similarity; Clarke and Gorley 2015).

Non-metric multidimensional scaling (nMDS) plots were used to visualize dissimilarities in crab assemblages among locations. Similarity percentage (SIMPER) analysis was used to determine which crab species contributed most to the observed differences in taxonomic assemblages among locations. ANOSIM, nMDS plotting, and SIMPER were conducted in Primer 7.0 (Clarke et al. 2014).

Results

Temperature Variation

Mean daily water temperature differed among seasons and locations (Fig. 2). In the summer, temperatures did not differ among locations (likelihood ratio $X^2(4) = 1.54$, $p = 0.343$); however, southern locations were warmer than northern locations in the fall ($X^2(4) = 22.54$, $p = 0.002$), winter ($X^2(4) = 28.47$, $p = 0.001$), and spring ($X^2(4) = 19.32$, $p = 0.007$). In summer, water temperatures were warmest and fluctuated from 25 to 32 °C. During the fall, temperatures dropped at all locations to between 9.5–13.0 °C in the north and 12–14 °C in the south. In the winter, the coldest days occurred in late February, when field sites experienced eight consecutive days of cold water temperatures, near 10 °C at southern locations and as cold as 8 °C at northern locations. Differences among locations persisted in the spring when water temperatures rose from approximately 17 °C at the end of winter to 25 °C immediately before collection in June.

Abundance by Species

Petrolisthes armatus adults (> 4 mm CW) were most abundant in the summer, ranging from 4 to 782 tray⁻¹, and declined through the winter (likelihood ratio $X^2(3) = 117.76$, $p < 0.001$;

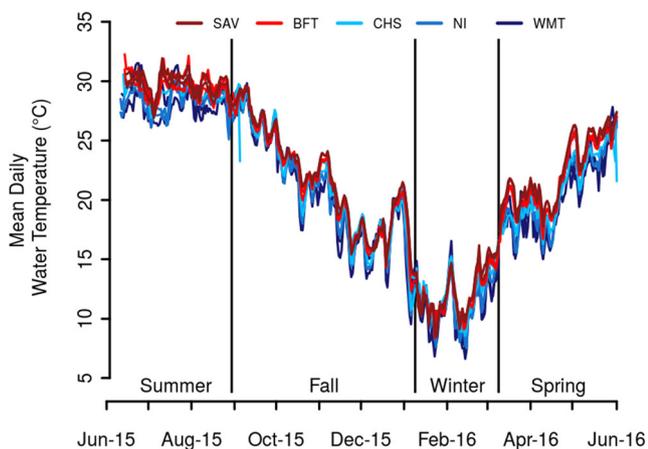


Fig. 2 Mean daily water temperature (°C) recorded in sampling trays on intertidal oyster habitat at five locations within the northernmost invaded range of *Petrolisthes armatus*. Southern locations (Savanna, Bluffton) in red, northern locations (Charleston, North Inlet, Wilmington) in blue

Fig. 3). At all locations except Wilmington, abundances in the fall were comparable to those in summer, and increased from winter into spring. Abundances differed by location within a given season ($X^2(4) = 453.42$, $p < 0.001$) and were generally higher at the southern locations (Fig. 3a). Intermediate abundances occurred further north, with very low abundances in Wilmington, the most northward location. There was no significant interaction between season and location.

Panopeus herbstii was significantly more abundant in the summer at all locations, ranging from 20 to 50 tray⁻¹, and declined seasonally through the winter ($X^2(3) = 166.76$, $p < 0.001$, Fig. 4). Abundances also differed among locations within a given season ($X^2(4) = 10.34$, $p = 0.012$), but no clear latitudinal trend was present (Fig. 3b). *Eurypanopeus depressus* was not collected at all sites each season, and no significant differences were detected in abundances among seasons ($X^2(3) = 5.91$, $p = 0.115$, Fig. 3c) or locations ($X^2(4) = 0.527$, $p = 0.970$). Small panopeid crab abundance was

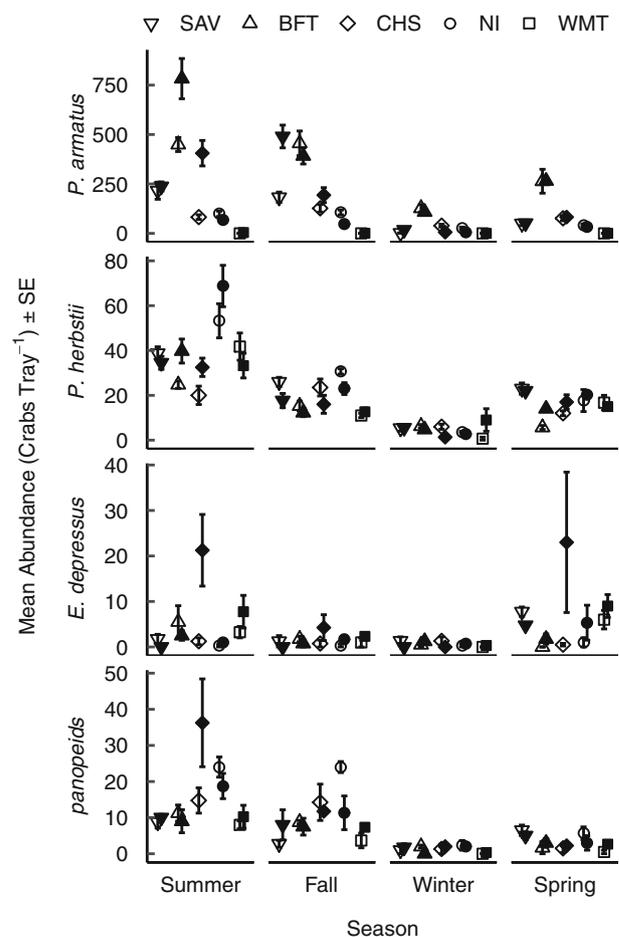
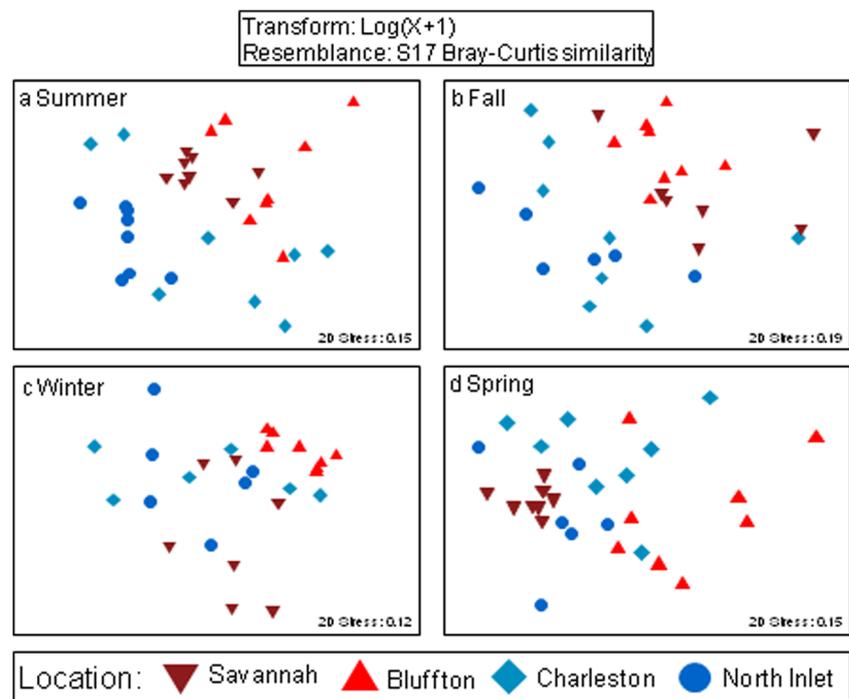


Fig. 3 Mean abundance tray⁻¹ of adult (> 4 mm CW) *Petrolisthes armatus* (a), *Panopeus herbstii* (b), *Eurypanopeus depressus* (c), and panopeids (< 4 mm CW) (d) collected each season at each location. Shapes differentiate between locations. Fill differentiates between sites within a location. Tray dimensions were 45.0 L × 30.5 W × 10.5 H (cm). Panopeids (d) are *Panopeus herbstii* and *Eurypanopeus depressus* which were too small (< 4 mm CW) to be identified to the species level

Fig. 4 nMDS ordination showing grouping of resident crab assemblages by taxonomic abundance in the summer (a), fall (b), winter (c), and spring (d). Symbols differentiate among four locations and each symbol represents an individual tray. Southern locations in red, northern locations in blue



significantly higher in the summer, ranging from 8 to 24 tray⁻¹ ($\chi^2(3) = 68.58$, $p < 0.001$, Fig. 3d) and did not differ among locations within a given season ($\chi^2(4) = 3.02$, $P = 0.128$).

Community Assemblages

Petrolisthes armatus was the numerically dominant crab at all locations except Wilmington. *Panopeus herbstii* and *Eurypanopeus depressus* were the next most abundant species and were common at all locations. Other resident crabs present in small numbers included *Rhithropanopeus harrisi*, *Menippe* spp., and juvenile *Callinectes sapidus*. Although the panopeid crab *Dyspanopeus sayi* (formerly *Neopanope sayi*) was not identified in this study, it has been reported in low abundances within the study area (Hartman 2003; Eash-Loucks et al. 2014).

Within each season, the taxonomic composition of crab assemblages differed among locations, with the greatest dissimilarities between northern and southern locations in the summer and fall (Fig. 4a, b, Table 2). In the summer, higher abundances of *P. armatus* and lower abundances of *P. herbstii* in the south relative to the north contributed to the dissimilarities. Likewise, in the fall, *P. armatus* abundances were higher in southern compared to northern locations. Winter assemblages did not exhibit strong differences between northern and southern locations (Fig. 4c); however, relatively high *P. armatus* abundances at Bluffton (Table 2) resulted in pairwise differences between locations. Similarly, in the spring (Fig. 4d), north-south distinctions were not apparent but overall

dissimilarities among locations were present, driven primarily by high *P. armatus* abundances at Bluffton.

Sex Ratios

Sex ratios of *P. armatus* differed between seasons (likelihood ratio $\chi^2(3) = 69.97$, $p < 0.001$) and locations within a given season ($\chi^2(3) = 18.72$, $p < 0.001$). In the summer, sex ratios were either unbiased or female-biased at all locations (Fig. 5a). In the fall, sex ratios were male-biased at all locations. In the spring, the southern locations, Savannah and Bluffton, were less male-biased than they had been in the fall. Frequencies of male *P. herbstii* did not differ significantly by season ($\chi^2(3) = 1.25$, $p = 0.492$) and only differed between locations in the spring ($\chi^2(4) = 14.38$, $p = 0.006$; Fig. 5b), when the North Inlet location was significantly more male-biased than all other locations.

Body Size

Male and female *P. armatus* body size differed among seasons (likelihood ratio test, males $\chi^2(3) = 331.01$, $p < 0.001$; females $\chi^2(3) = 474.615$, $p < 0.001$), reflecting growth from summer through the following spring (Fig. 6a, b). Average male CW in the summer (mean \pm SE) ranged from 5.52 ± 0.05 mm in Savannah to 6.40 ± 0.16 mm in North Inlet. Female CW ranged from 5.14 ± 0.03 mm in Charleston to 6.21 ± 0.13 mm in North Inlet. Crab sizes increased in fall and winter and were largest in the spring than in any other season; the largest crabs occurred in Savannah at the Marine Extension

Table 2 Analysis of similarity (ANOSIM) results comparing resident crab assemblage composition among locations (Savannah—SAV, Bluffton—BFT, Charleston—CHS, and North Inlet—NI). Mean *Petrolisthes armatus* abundances per tray (45.0 L × 30.5 W × 10.5 H

Season	ANOSIM	Southern		Northern		% Dissimilarity	
		SAV	BFT	CHS	NI	<i>P. armatus</i>	<i>P. herbstii</i>
Summer	$R = 0.51, p = 0.001$	230	619	244	84	65–97	3–22
Fall	$R = 0.37, p = 0.001$	314	423	160	77	77–93	3–9
Winter	$R = 0.35, p = 0.001$	11	118	22	15	61–94	2–19
Spring	$R = 0.41, p = 0.001$	51	238	78	37	53–89	6–21

office (8.70 ± 0.16 mm for males and 8.13 ± 0.08 mm for females). Crab size also differed by location after controlling for season (males $\chi^2(3) = 5.43, p = 0.025$; females $\chi^2(3) = 5.70, p = 0.022$), but no consistent latitudinal trend was apparent.

Native crab sizes did not differ significantly between the sexes and therefore are reported for both sexes combined. Size of *P. herbstii* increased seasonally (likelihood ratio $\chi^2(3) = 66.37, p < 0.001$; Fig. 6c) with the largest mean CW increase occurring from summer through fall. Crabs from southern locations were generally larger than those from northern locations ($\chi^2(4), F = 5.46, p = 0.045$). In the summer, *P. herbstii* CW ranged from 7.76 ± 2.70 mm in North Inlet to 14.45 ± 3.11 mm in Savannah. Mean CW increased in the fall and winter. In the spring, following overwintering, mean CW ranged from 11.25 ± 1.40 mm in North Inlet to 17.51 ± 1.05 mm in Bluffton. Size of *E. depressus* also increased

seasonally from summer to the following spring ($\chi^2(3) = 10.44, p < 0.001$; Fig. 6d), but did not differ among locations within a given season ($\chi^2(4) = 2.156, p = 0.211$). Mean CW of *E. depressus* were smallest at all locations in the summer, ranging from 4.38 ± 0.01 mm in North Inlet to 9.16 ± 0.46 mm in Charleston. Crabs increased in mean CW through the fall and winter and were largest in the spring, ranging from

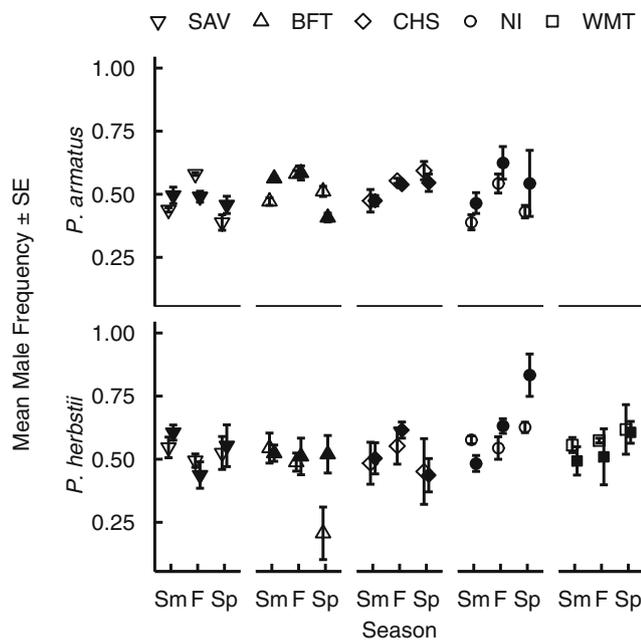


Fig. 5 Proportional frequency of males among adult (>4 mm) *Petrolisthes armatus* (a) and *Panopeus herbstii* (b) collected in trays in each of three seasons at each location. Shapes differentiate locations and fill differentiates sites. Sample sizes at Wilmington too small to permit analysis

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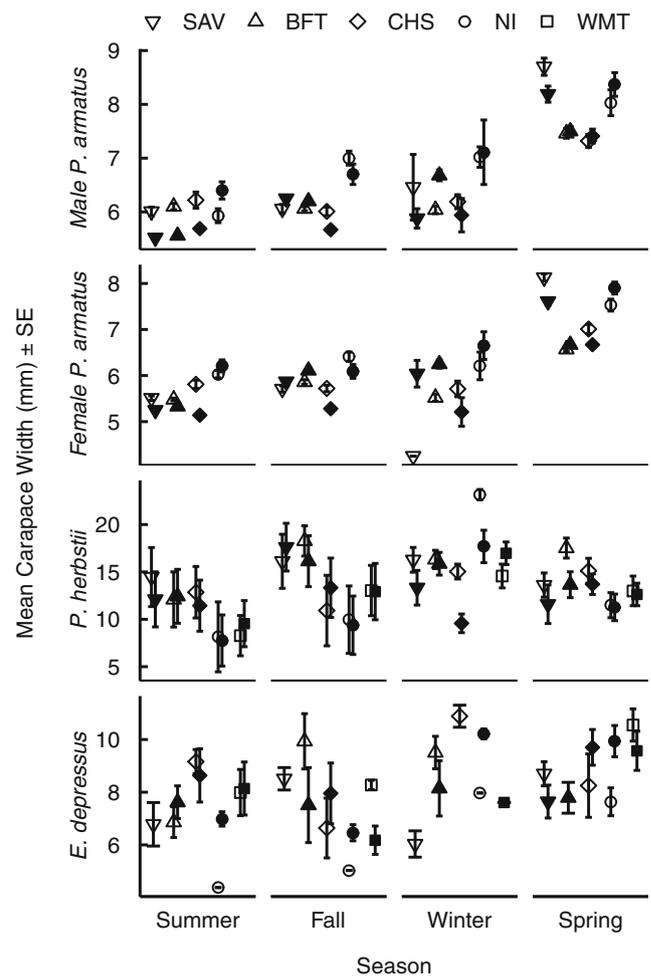


Fig. 6 Mean (\pm SE) carapace width (mm) of adult (>4 mm) *Petrolisthes armatus* males (a), females (b), *Panopeus herbstii* (c), and *Eurypanopeus depressus* (d) collected during each season at each location. Shapes differentiate locations and fill differentiates sites

7.63 ± 0.52 mm in North Inlet to 10.55 ± 0.61 mm in Wilmington.

Rhizocephalan Parasitism

Approximately 40% of *E. depressus* collected showed evidence of infection by the invasive rhizocephalan barnacle *Loxothylacus panopaei*. No infections were found in *P. herbstii* or any other native crab species. Significant differences in parasitism of *E. depressus* were detected among seasons (likelihood ratio $\chi^2(2) = 12.38$, $p = 0.002$) with infection prevalence lower in summer and fall (13 to 27%) than in spring (50%). Across all seasons, infection prevalence was 48% in larger (> 8 mm CW) *E. depressus* compared to 19% in smaller (4–7 mm CW) crabs. Crab size was a significant covariate ($\chi^2(1) = 22.96$, $p < 0.001$), with no significant interactions between season or location, and location was not a significant main effect ($\chi^2(4) = 5.91$, $p = 0.206$).

Discussion

Resident crab assemblages on intertidal oyster reefs varied by latitude in the SAB, largely due to denser populations of the invading porcelain crab, *Petrolisthes armatus*, in the southern portion of the invaded range we studied. Native resident crab abundances were similar across latitudes and there was no evidence that native crab densities changed in response to high *P. armatus* densities. It is not known if the use of collection trays, which excluded large predators, affected the relative abundances of each crab species. For example, oyster toad fish and blue crabs are predators of native resident crabs on oyster reefs (Grabowski et al. 2008), but their relative consumption of *P. armatus* is not known. Size of the native crab, *Panopeus herbstii*, differed geographically, and were larger in southern populations where *Petrolisthes armatus*, a potential food source (Pintor and Byers 2015b), was more abundant. Sizes of *P. armatus* and *E. depressus* did not exhibit a similar latitudinal trend; therefore, further examination of whether the availability of *P. armatus* as prey influences the size of *P. herbstii* is warranted.

The abundance of *P. armatus* varied by both latitude and season, with lowest abundances at the coldest locations and time of the year. Cold water temperatures are associated with seasonal declines in *P. armatus* on intertidal oyster reefs (Hollebone and Hay 2007; Eash-Loucks et al. 2014) and may also limit its northward expansion (Canning-Clode et al. 2011). Temperatures did not differ among locations in the summer, when temperatures were highest, which is consistent with other observations on oyster reefs in our study area (Byers et al. 2015). However, winter and spring water temperatures were colder at northern compared to southern locations and

reached lows in the north (8 °C) that are associated with decreased mobility of *P. armatus* in laboratory experiments (Mack 2017). Temperatures below 6 °C, which result in complete loss of mobility and mortality in this species (Canning-Clode et al. 2011; Mack 2017), were not recorded during the relatively mild winter of 2015–2016. This latitudinal temperature gradient is correlated with several *P. armatus* population characteristics. For instance, crabs from populations on the northern edge of the expanding range tolerated low-temperature extremes better than crabs from southern populations (Mack 2017), suggesting that biological adaptation or acclimation may be facilitating range expansion.

Because *P. armatus* larvae are largely retained in natal estuaries, their larval dispersal is expected to be low (Tilburg et al. 2010; Hiller and Lessios 2017). Genetic exchange among populations of another porcellanid crab, *Petrolisthes cinctipes* along the coast of California is limited to only 30 km (Hameed et al. 2016). Although circulation patterns may differ between these coastal systems, similar limited connectivity in *P. armatus* also may occur, which would support biological adaptation to cold as a possible mechanism facilitating expansion to more northern locations in the SAB. For instance, populations better able to survive cold winters may contribute to continued poleward range expansion. High larval output (Hollebone and Hay 2007; Wassick et al. 2017) may contribute to the export of some larvae, despite general retention (Tilburg et al. 2010). Recruitment of larvae further north is possible, if winters are mild, resulting in further range expansion. This pattern of adaptation, export, survival, and establishment, could explain the poleward range expansion of this species, especially evidenced by the current low numbers of adult crabs in Wilmington, North Carolina.

Although mechanisms of interaction between *Petrolisthes armatus* and native crabs were not addressed in this study, competition for space and alteration of trophic relationships are both plausible. *Petrolisthes armatus* and the native panopeid crabs share preferences for inhabiting the vertically complex interstitial space of oyster reefs (McDonald 1982; Meyer 1994; Margiotta et al. 2016), raising the potential for space competition. As mentioned, invading *P. armatus* may also provide a novel food source for the native *P. herbstii*. Some (Pintor and Byers 2015a) but not all (Hollebone and Hay 2008) previous studies have shown that *P. herbstii* prefers *P. armatus* over native food sources. A negative interaction with native crabs could exist if *P. armatus* limits recruitment of mud crabs by consuming their larvae (Hollebone and Hay 2008). Abundance data collected in this study, however, did not indicate a density-dependent effect of *P. armatus* on native crab populations.

Understanding how *P. armatus* impacts native crab communities will become increasingly important if the species continues to expand its range poleward. Although a previous

study found a similar trend of lower densities in more poleward populations in South Carolina (Hadley et al. 2010), our study also documents crab assemblages that include this species as far north as Wilmington, North Carolina. Temperature likely helps to explain differences in abundance among seasons (Hartman 2003; Eash-Loucks et al. 2014) as well as among locations across a latitudinal temperature gradient. Previous intertidal sampling at North Inlet and Charleston using identical experimental collection trays also found similar seasonal trends in *P. armatus* populations, with abundances peaking in summer and decreasing significantly in winter (Hartman 2003). Similar reductions from summer to winter abundances as great as 99% have been associated with colder winter water temperatures (Hollebone and Hay 2007). It is unknown if winter reductions in the abundance of *P. armatus* on intertidal oyster reefs are the result of mortality, movement of crabs to deeper habitat, or burial beneath the oyster substrate. The presence of adult-sized crabs on intertidal reefs in the spring is consistent with adults overwintering in the area. Overwintering, however, may have been favored during the relatively mild 2015–2016 winter (Mack 2017). Seasonal changes in intertidal oyster habitat use have been noted in other panopeid (Meyer 1994) and xanthid (Wilber and Hernkind 1986) crabs. *Petrolisthes armatus* may burrow into soft sediments for refuge; however, Hartman (2003) observed higher abundances of *P. armatus* in subtidal oyster trays during winter months, suggesting they may use subtidal areas during the winter. The scarcity of subtidal oyster reefs in South Carolina suggests that adults may move to a different habitat if subtidal migrations occur in winter.

In addition to spatial and temporal differences in abundance, populations of *P. armatus* underwent a shift in sex ratios from summer to fall coincident with the end of the species' reproductive season. In summer, sex ratios were either unbiased or female-biased at all locations, the latter being potentially advantageous for an invading species by increasing its reproduction. Hollebone and Hay (2007) reported a 1:1 sex ratio in summer. The observed shift in sex ratio between seasons could result from differences in habitat use by males and females, where females leave intertidal oyster reefs in summer following reproduction but males stay until colder temperatures arrive in winter. Alternatively, the shift could result from higher mortality in females following reproduction, increasing the proportion of males in the fall.

Although variance in abundance of *P. armatus* most strongly contributed to dissimilarities in resident crab assemblages, the native mud crabs *P. herbstii*, *Eurypanopeus depressus*, and other small panopeids also contributed to differences in crab assemblages among locations. Variation in the abundance of native crabs was most pronounced seasonally, with no clear latitudinal trend. This pattern is consistent with previous

assessments of mud crab populations, which also found decreases in abundance associated with cold water temperatures (McDonald 1982). Seasonal variation in abundance could be explained by crabs burrowing into muddy habitat (Meyer 1994), which would exclude them from sampling trays. The recent relatively low abundance of *E. depressus* could be attributed to parasitism by the invasive rhizocephalan barnacle *Loxothylacus panopaei* similar to Eash-Loucks et al. (2014). However, previous studies have shown that *L. panopaei* prevalence tends to cycle over time in populations of *E. depressus* (Gehman et al. 2018), so the prevalence reported here could be influenced by the temporal design of the survey. We found the highest parasite prevalence in spring and in larger crabs, which could reflect the longer exposure time of larger, sexually mature adults. However, there are several abiotic and biotic factors that also could influence *L. panopaei* prevalences in *E. depressus* populations, including latitude, water temperature, host densities, and host predators (Gehman and Byers 2017; Gehman et al. 2017).

Conclusion

Seasonal assemblages of resident crabs on intertidal oyster habitat differed between northern and southern locations within *Petrolisthes armatus*' northernmost invaded range, largely because of lower abundances near its range edge. Abundances of native crabs were fairly similar among locations. Although it is not known whether *P. armatus* re-establishes populations annually on the leading edge of its range via larval dispersal, the presence of adults in the spring provides the first reported evidence of overwintering in the invaded range, albeit after a relatively mild winter. *Petrolisthes armatus* has the potential to continue its poleward range expansion, especially given the trend of ocean warming. Although there was no sign that *P. armatus* influenced native crab abundances on the temporal and spatial scales examined in this study, this species potentially could affect native resident crab communities via more complex and subtle mechanisms, given the invader's potential contribution to trophic interactions as a high-density prey resource.

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