



Invasive crab positively correlated with native predatory crab species over a regional scale

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Abstract The abundance of an invasive species within an ecosystem after introduction can depend on multiple factors. Although large-scale abiotic data are typically used to model the distribution of invasive species, there may be other fine-scale environmental or biotic factors within the invaded range influencing changes in the species' distribution and abundance. Here, we examined the abundance of the invasive tropical/subtropical green porcelain crab, *Petrolisthes armatus* (Gibbes, 1850), at 33 oyster reef sites along 150 km of coastline within the northerly portion of its invaded range. We measured a suite of biological, physical, and landscape level metrics to examine which factors (other than temperature) were most associated with the abundance of this invasive species. *P. armatus* were present at 32 reefs across our spatial range and densities were highest at the northern sites in our domain. Our results revealed native mud crab density is positively correlated with *P. armatus* density, accounting for 23% of the spatial variation in abundance of *P. armatus* within its invaded range, more than 30 years after initial invasion. We hypothesize that the positive

associations between native predatory mud crabs and this invasive crab may be a result of hydrodynamics aggregating both species within the same areas, or attraction by both crabs for the same fine-scale habitat structural attributes (i.e., interstitial space). These data emphasize the importance of collecting high-resolution survey data to understand the variables that are correlated with the abundance and distribution of invasive species at regional scales within its invaded range.

Keywords Non-native · Community structure · Spatial heterogeneity · *Petrolisthes armatus* · 'Caribbean creep'

Introduction

The expansion of tropical species poleward is being exacerbated by changing climatic conditions (Pinsky et al. 2020) and anthropogenic activities (Johnston et al. 2017). To become established, species must disperse to a new location and withstand a suite of environmental and biotic filters within the new range (Gallien and Carboni 2017). Temperature is a major driver of the ability of non-native or invasive species to expand their range from tropical into temperate regions and persist in the new environment (Cheung et al. 2009; Morley et al. 2018). Within a given region there may be broad reaches with similar temperature regimes. Within such reaches the influences of

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other environmental drivers may be more apparent (González-Moreno et al. 2015). For instance, the lack of suitable habitat (host anemones) is limiting the establishment of tropical anemonefish populations in more temperate locations along the coast of eastern Australia regardless of temperature differences from its native range (Pryor et al. 2022).

Temperature and other abiotic variables collected at broad spatial scales can be used to predict areas of suitable habitat that may facilitate the invasion of species using tools such as species distribution models (Elith et al. 2010; McDowell et al. 2014). However, at smaller regional scales the variance in key abiotic (and biotic) factors may be minimal, making it difficult to predict the distribution of invasive species at high resolutions. Furthermore, on-the-ground survey data from within invaded ranges tend to be sparse, making it difficult to incorporate high-resolution abiotic and biotic variables into these models at smaller spatial scales (Commander et al. 2022; Radomski et al. 2022). Therefore, collecting high-resolution data in the field to complement large-scale abiotic data may provide necessary information to better predict how invasive species redistribute and persist following an invasion.

The green porcelain crab (*Petrolisthes armatus*; Fig. 1) is an invasive filter feeding crab introduced north of Cape Canaveral, along the Atlantic coast of Florida, USA (Wassick et al. 2017). Although the native range of this species is not well defined, there is sufficient evidence that this species was introduced to the southeastern USA coast in the 1980s and has slowly spread up the coast from northern Florida into North Carolina (Hiller and Lessios 2017). As a tropical species, the northern end of this invaded range (currently North Carolina) is likely limited by the crab's susceptibility to cold winter temperatures (Knott et al. 2000; Hartman 2003; Hadley et al. 2010; Canning-Clode et al. 2011; Eash-Loucks et al. 2014). *P. armatus* has planktonic larvae (PLD 17–49 days) released within the estuary in summer and fall with limited dispersal (Tilburg et al. 2010) and limited tolerance to reduced salinities (Shumway 1983). Within its presumed native range, *P. armatus* is found within rocky habitat and mangrove prop roots, while in its invaded range this crab is predominately found within oyster reef habitat (Sheridan 1992; Oliveira & Masunari 1995). Within oyster reef habitat along this invaded coastline, densities of *P. armatus* have



Fig. 1 Image of *Petrolisthes armatus* (11 mm; carapace width) collected from an oyster reef along the coast of Georgia, United States in June 2022 (image credit: S.L. Ziegler)

reached >2000 individuals m^{-2} (within collection trays; Hollebone and Hay 2007) and *P. armatus* abundances tend to decline at higher latitudes near the leading edge of its invasion (Hadley et al. 2010). Previous studies within the invaded range indicate that the densities of *P. armatus* are positively correlated with oyster reef structure and overall habitat complexity (Margiotta et al. 2016; Kinney et al. 2019), in part because of nearly 100% mortality outside of reef habitat (Hollebone and Hay 2008). These invasive crabs have been found to be readily consumed by native crab species (e.g., the Atlantic mud crab, *Panopeus herbstii*; Hollebone and Hay 2007, Pintor and Byers 2015a, Kinney et al. 2019) which could influence the abundance on reefs across the invaded range. Furthermore, high *P. armatus* densities have been shown to reduce the recruitment of native species to reef habitat (Hollebone and Hay 2008), although the relationship between native crabs and this invasive is still unclear (Hadley et al. 2010).

In this study, we quantified the spatial variation in density of the invasive green porcelain crab (*P. armatus*) at 33 oyster reefs within a 150 km reach of its invaded range. To better understand how fine-scale environmental conditions influence the crab's abundance, we also quantified several abiotic and biotic variables at each reef. We analyzed the effects of these variables to determine which are most

strongly associated with the density of the invader. We hypothesized *P. armatus* densities would be highest at lower latitudes in warmer waters that are more similar to its native tropical/subtropical range. We predicted that *P. armatus* densities would be highest near urbanized areas with greater potential for invasion (Ruiz et al. 2000). Previous studies have found variables of road density and shoreline armoring to affect the distribution and abundance of intertidal and subtidal estuarine species (Urban 2006; Altman and Byers 2014; Laurino et al. 2022). Specifically, hardened shorelines have been recognized to facilitate invasive species that utilize hard substrates such as *P. armatus* (Dugan et al. 2018). We also expected higher densities near oceanic inlets where water has higher salinity and where flow rates and flushing are higher, increasing the potential for delivery of coastal planktonic larvae to reefs (Pineda et al. 2007). We also hypothesized that *P. armatus* densities would be highest at oyster reef sites with high structural complexity (reef rugosity; Margiotta et al. 2016) and with low densities of resident predatory crabs (e.g., mud crabs) across its invaded range.

Methods

Site selection

We selected 33 oyster reefs grouped into 11 spatially distinct clusters spread systematically across the 150 km coastline of Georgia, United States. Each reef was 1) directly adjacent to salt marsh (< 1 m from the reef's landward edge), 2) had an intertidal area of at least 3 m wide × 3 m long, 3) had a density of at least 30 adult (> 30 mm) oysters m⁻², 4) had a reef slope between 15 and 30%. At each reef, we sampled habitat structural complexity (oyster density and reef rugosity), predators and competitors (resident crab fauna), and abiotic environmental conditions (salinity) known to influence *P. armatus* abundance.

Field sampling

In June 2022, we sampled 33 intertidal oyster reefs over the course of 10 days with each reef sampled within 1 h on either side of low tide. We haphazardly placed a single 0.25 m² quadrat along the upper edge of our designated intertidal oyster reef 1 m from

the edge of the adjacent marsh cordgrass (*Spartina alterniflora*) to ensure all samples were representative of low tide resident faunal densities. Within the quadrat, we quickly excavated all oysters down to the surface of the mud by hand, placing contents into a tub to retain any resident fauna. Adjacent to each quadrat we measured reef rugosity (a metric of structural complexity) via the chain method (Aronson and Precht 1995) where a 4-m chain was conformed to the reef topography parallel to the marsh-reef edge, and a rugosity index, R was calculated as $R = 1 - (d / l)$, where d is the horizontal distance from the start of the chain to its end, and l is the length of the chain. At each reef, we recorded latitude and longitude and with a YSI meter measured point source temperature (°C) and salinity (ppt) at 0.2 m water depth within 3 m of the subtidal edge of the reef.

Biological variables Upon returning to shore, we rinsed oysters of mud in a sieve (1 mm) to retain all organisms for processing. To calculate oyster density, we counted all living oysters. We identified all resident crustaceans down to species level with particular focus on the invasive green porcelain crab (*P. armatus*) and the native mud crabs (*Eurypanopeus depressus* and *P. herbstii*) and counted all individuals.

Landscape variables To assess the landscape context of each reef we extracted landscape variables in ArcGIS Pro 3.0.2 (ESRI) with data layers downloaded from the Georgia Coastal and Marine Planner (GCAMP: <https://geospatial.gatech.edu/GCAMP/>) and Georgia Wetlands Restoration Access Portal (G-WRAP: <https://geospatial.gatech.edu/G-WRAP/>). We calculated the shortest linear distance by water to the nearest oceanic inlet from each reef as a proxy for recruitment potential and flushing rates. To assess variation in the level of urbanization, we calculated the distance of each reef to the nearest road and the distance from each reef to the nearest armored shoreline.

Data analysis

For analysis, we considered reef the level of replication to maximize the breadth of sampling across the 150 km coastline. To examine the spatial patterns in *P. armatus* densities, we first visualized density data by mapping data across the coast of Georgia in ArcGIS Pro 3.0.1 (ESRI 2022). We then determined the proper distribution of the data for

analysis using the `Ord_plot()` function in the `veclust` package (Meyer et al. 2023) in R version 4.3.0 (R Development Core Team 2023) and verified it using the compare distribution function in JMP (version 17). Both methods indicated a negative binomial distribution best described the data's distribution ($X^2=3.24$, $df=3$, $p=0.36$). We then ran a negative binomial model with the `MASS` package (Venables and Ripley 2002) in R to determine the relationship between *P. armatus* density and latitude.

Prior to additional analyses, we tested for collinearity among biological and landscape variables. We examined cross-correlations using a Pearson correlation matrix. If correlation coefficients were greater than 0.7, we selected the variable that was most likely to influence *P. armatus* density based on previously published studies. There was a high correlation between distance to the nearest road and distance to nearest armored shoreline ($r=0.75$). Due to the importance of roads in driving the distribution of other intertidal estuarine taxa (Urban 2006; Altman and Byers 2014), we removed distance from armored shoreline from statistical models. To determine the variables associated with *P. armatus* density across our spatial range, we conducted negative binomial models with predictor variables of salinity, reef rugosity, oyster density, mud crab density, distance to the nearest road and distance to the nearest oceanic inlet using the `MASS` package. All predictor variables included in the models were scaled by their mean and standard deviation $[(x-\text{mean})/\text{sd}]$ to better compare the relative importance of predictors in model outputs. We then identified all possible model combinations ($n=64$) and examined the Akaike information criterion corrected for small sample sizes (AICc) with the `dredge` function, and pseudo- R^2 values were calculated with the `r.squaredGLMM` function in the `MuMIn` package (Bartoń 2023). We considered the top models with ΔAICc less than 2. We then conducted model averaging (as described in Burnham and Anderson 2002) with the `model.avg` function in the `MuMIn` package for the top models ($\Delta\text{AICc} < 2$) to determine the relative importance of the explanatory factors.

To ensure the robustness of our results, we conducted the same procedure as described above with any potential outliers ($n=2$) removed (mud crab densities > 140). We also examined the relationship between all variables and *P. armatus* density with

mud crab density divided into large (> 10 mm) and small (< 10 mm). We did this categorization because large mud crabs are exclusively *P. herbstii* and are more likely to have a predatory and competitive role. Small mud crabs are a mix of *P. herbstii* and *E. depressus* and are more likely to correlate with *P. armatus* due to general shared proclivities for environmental properties as opposed to strong interactive effects.

Results

A total of 1781 *P. armatus* were collected at 32 of 33 reefs sampled within estuaries along the 150 km coastline of Georgia (Fig. 2). When present, *P. armatus* densities averaged 59.3 (± 9.1 SE) individuals 0.25 m^{-2} across all reefs and ranged from 1 to 239 individuals 0.25 m^{-2} . Across reefs, *P. armatus* ranged in size from 1.9 mm to 12.0 mm in carapace width (7.3 ± 0.1 SE). Total oyster density was lowest at one of our most southern reefs (CM3; 233 oysters 0.25 m^{-2}) and peaked at 3,217 oysters 0.25 m^{-2} (including juveniles and spat) at reef HP2 located at 31.53°N (Table 1). A total of 2123 native crabs (*P. herbstii* and *E. depressus*) were collected and native mud crab densities varied across the reefs

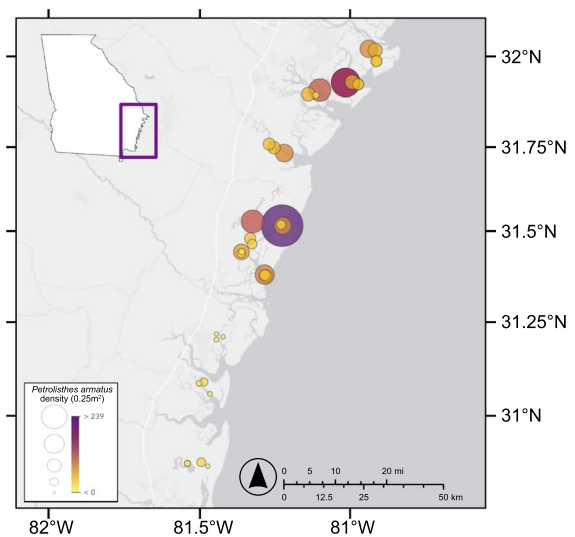


Fig. 2 Oyster reefs sampled across the 150 km coast of Georgia, United States. Color and size of the circles indicate *P. armatus* density (individuals 0.25 m^{-2})

Table 1 The distribution of measured variables across the 33 reefs sampled along the coast of Georgia, United States ordered by latitude from north to south

Cluster	Reef	Latitude	Longitude	Oyster density	Mud crab density	<i>P. armatus</i> density	Reef rugosity	Salinity	Temperature	Distance to nearest inlet (km)	Distance to nearest road (km)	Distance to nearest armored shoreline (km)
Tybee	TB1	32.02	-80.94	717	47	85	0.188	23.8	27.9	11.59	0.74	0.63
	TB2	32.02	-80.92	426	54	64	0.175	25.8	27.9	10.68	0.91	0.91
	TB3	31.99	-80.92	490	85	43	0.25	27.6	28.1	7.32	3.75	3.80
Romerly Marsh	RM2	31.93	-81.00	599	52	63	0.35	27.9	28.4	7.01	3.00	3.05
	RM1	31.93	-81.02	691	75	156	0.425	27.8	28.4	8.98	1.19	1.25
	RM3	31.92	-80.98	471	39	44	0.45	29.3	28.6	5.16	5.02	4.79
Little Ogeechee	LO3	31.91	-81.10	2969	93	115	0.425	24.2	29.6	11.09	2.15	2.14
	LO1	31.90	-81.14	1634	70	59	0.25	22.3	29.1	13.37	3.69	3.94
	LO2	31.89	-81.12	984	33	14	0.175	22.6	29	11.03	5.66	4.79
Liberty-Sunbury	SB3	31.76	-81.27	339	38	49	0.195	28.6	31.1	14.63	0.87	1.00
	SB2	31.75	-81.26	928	76	53	0.188	28.5	31.1	12.72	1.62	1.71
	SB1	31.73	-81.22	279	54	87	0.25	29	31.4	9.28	1.33	1.59
High Point	HP1	31.53	-81.23	1136	41	33	0.212	29.7	32.6	4.95	11.91	4.09
	HP3	31.53	-81.23	1070	102	82	0.142	29.7	32.6	4.46	11.47	4.65
	HP2	31.53	-81.23	3217	143	239	0.167	29.7	32.6	4.66	11.42	4.49
McIntosh	MI3	31.54	-81.33	409	51	119	0.15	26.3	32.3	13.62	1.17	1.10
	MI2	31.49	-81.33	256	32	45	0.25	25.9	31.1	15.74	0.75	0.71
	MI1	31.48	-81.33	730	66	35	0.3	25.5	30.2	15.84	1.39	1.48
Meridian	MD3	31.45	-81.36	424	28	14	0.049	27.4	32.6	13.01	0.35	0.08
	MD1	31.45	-81.36	494	74	74	0.505	27.4	32.6	13.06	0.45	0.04
	MD2	31.45	-81.36	1277	37	28	0.335	27.4	32.6	13.81	0.39	0.57
Dean Creek	DC3	31.39	-81.29	1159	109	96	0.113	30.1	31.3	2.04	1.39	2.25
	DC2	31.39	-81.29	978	74	42	0.054	30.1	31.3	1.96	1.43	2.38
	DC1	31.39	-81.28	2898	204	54	0.089	30.1	31.3	1.68	1.33	2.78
MacKay River	MR2	31.22	-81.45	788	56	0	0.125	16.4	29.8	11.37	0.15	0.13
	MR1	31.21	-81.42	1045	48	1	0.1	18	30.6	9.84	2.74	2.36
	MR3	31.21	-81.45	1230	47	5	0.283	17.8	30.9	9.89	1.53	1.17
Glynn-Jointer Creek	JC1	31.09	-81.49	544	41	25	0.39	30.1	29.2	9.99	0.62	0.66
	JC2	31.08	-81.50	923	36	9	0.323	29.2	30.3	10.62	2.15	2.16
	JC3	31.05	-81.47	1190	66	5	0.275	29.9	29.8	5.8	1.72	1.72

Table 1 (continued)

Cluster	Reef	Latitude	Longitude	Oyster density	Mud crab density	<i>P. armatus</i> density	Reef rugosity	Salinity	Temperature	Distance to nearest inlet (km)	Distance to nearest road (km)	Distance to nearest armored shoreline (km)
Camden	CM1	30.86	-81.50	423	85	29	0.15	32.6	30.2	16.75	2.29	3.37
	CM3	30.86	-81.54	233	29	12	0.165	32.2	30	19.01	1.38	2.29
	CM2	30.85	-81.47	445	38	2	0.215	32.2	29.4	16.93	4.73	0.82

Variables include latitude, longitude, total oyster density (individuals 0.25 m⁻²), total mud crab density (individuals 0.25 m⁻²), *P. armatus* density (individuals 0.25 m⁻²), reef rugosity, salinity, water temperature (°C), distance to nearest inlet (km), distance to nearest road (km), and distance to nearest armored shoreline (km)

sampled (28–204 individuals 0.25 m⁻²; 64.3 ± 6.3 SE) (Table 1).

There was little variation in temperature across the reefs sampled in summer June 2022 (29.9 ± 0.28 SE). There was a greater range in salinities across reefs with the lowest at 16.7 at reef MR2 near 31.2°N and highest at 32.6 at reef CM1 located at the southern end of the sampling range (~30.9° N) (Table 1). Rugosity also varied greatly across the reefs sampled ranging from 0.049 to 0.505 within the same sampling cluster near the center of our sampling regime. For the distribution of all other variables see Table 1.

There was a strong positive relationship between *P. armatus* density and latitude ($\beta=1.78$, $z=4.0$, $p<0.001$, $R^2=0.34$) with the highest densities of *P. armatus* occurring in the northern portion of sampling region (higher than 31.3°N; Fig. 2). The best fit model included only resident mud crab density ($\beta=0.50$, $R^2=0.23$). The second-best performing model ($\Delta AICc=0.92$) included a positive relationship between *P. armatus* density and reef rugosity ($\beta=0.20$) as well as resident mud crab density ($\beta=0.51$, $R^2=0.26$; Fig. 3). No other model had $\Delta AICc < 2$ (Table 2). Model averaging of the top fit models suggested that mud crab density ($\beta=0.50$, $SE_{adj}=0.16$) was the strongest predictor of *P. armatus* density across all reefs. When outliers were removed from the analysis (removed mud crab densities > 140), we found that mud crab density was still the best predictor of *P. armatus* density ($\beta=0.42$, $R^2=0.18$; Online Resource 1). When we separated out large (> 10 mm) and small mud crabs (< 10 mm) in our analysis, we found that the density of large mud crabs (likely exclusively *P. herbstii*) had a greater effect on *P. armatus* density ($\beta=0.38$; Online Resource 2) compared to small mud crabs (*P. herbstii* and *E. depressus*). However, the strength of the relationship of large crabs on *P. armatus* was less ($R^2=0.16$) than the effect of all mud crabs combined.

Discussion

We found a positive relationship between *P. armatus* density and latitude within its invaded range. However, this pattern was opposite to what we expected based on a tropical species expanding poleward (Morley et al. 2018). Specifically, we

Fig. 3 Influence of environmental variables on *P. armatus* density (individuals 0.25 m⁻²) for 33 reefs along the GA coast from the model averaged output (with a negative binomial distribution). *P. armatus* density is a function of total mud crab density (no. 0.25 m⁻²) and reef rugosity. Densities represent partial residuals for each variable accounting for the influence of the other fixed variables in the model. Trend lines indicate predicted conditional fit of the model

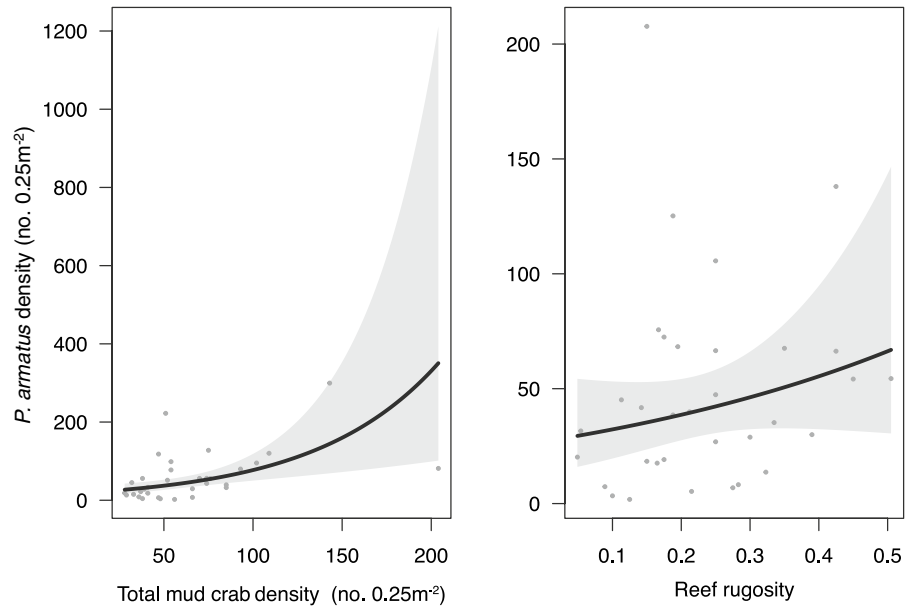


Table 2 The eight best models explaining variation in density of *P. armatus* (individuals 0.25 m⁻²) from 33 oyster reefs in Georgia, United States

Model rank	Distance to the nearest inlet	Distance to the nearest road	Reef rugosity	Salinity	Mud crab density	Oyster density	R ²	df	logLik	ΔAIC _c
1					0.50		0.23	3	-161.30	0
2			0.20		0.51		0.26	4	-160.46	0.92
3					0.41	-0.07	0.26	4	-161.19	2.38
4				0.11	0.48		0.24	4	-161.19	2.38
5		-0.01			0.49		0.24	4	-161.3	2.60
6	-0.01				0.41		0.23	4	-161.30	2.60
7			0.22		0.45	-0.11	0.30	5	-160.22	3.23
8			0.20	0.10	0.49		0.27	5	-160.37	3.54

Explanatory variables include distance to nearest inlet (km), reef rugosity, salinity, total mud crab density (individuals 0.25 m⁻²), and total oyster density (individuals 0.25 m⁻²). The top 8 models from model comparison are shown. The best fitting models (ΔAIC_c value < 2) are in bold. The standardized coefficients associated with each independent variable are shown for each model. For each model, the R², number of model parameters (df), log likelihood (logLik), and ΔAIC_c are shown

expected higher densities in the southern reach of our studies both because those areas would likely be warmer and also because they are closer to the source of the invasion which is moving up from the south. Because *P. armatus* invaded Georgia estuaries likely in the early 1990's (Knott et al. 2000), populations of this species may be more stable than during initial invasion and are fairly well established across our study sites. Although prolonged cold snaps in winter can reduce populations at the leading edge of the

invasion (Canning-Clode et al. 2011), recent winter water temperatures may not be limiting the species across the spatial extent of its invaded range that we examined (NOAA NERR 2024). Therefore, other environmental factors may be driving the distribution and density of this species within a well-established portion of its invaded range.

We also found that mud crab densities and reef rugosity were important variables in predicting patterns of *P. armatus* densities. Reef rugosity,

in particular, has been found to drive increased abundance of *P. armatus* across oyster reefs (Margiotta et al. 2016), and the lack of any type of structured habitat causes high mortality of this invasive species (Hollebone and Hay 2008). In addition to providing increased spatial refuge, oyster reefs with higher vertical complexity are better suited to ameliorate heat stress facilitating resident crab species, including the invasive *P. armatus* (Reeves et al. 2020). However, our metric of reef rugosity was fairly coarse and may not sufficiently capture the highly complex interstitial spaces of the oyster reef utilized by *P. armatus* resulting in its important, but relatively weak correlation.

The variable with the greatest correlation (23%) with *P. armatus* densities was mud crab density, which compete with or directly prey upon *P. armatus* depending on species and size. We suspected the large mud crabs (i.e., *P. herbstii*) would be an associated predator because they have been documented to feed readily upon *P. armatus* and they live in constant close proximity to *P. armatus* on the oyster reefs (Pintor and Byers 2015a; Hostert et al. 2019; Kinney et al. 2023). Furthermore, previous work has shown that the caloric content of *P. armatus* is at least $2.5\times$ higher than that of other similar-sized native prey items consumed by *P. herbstii* on oyster reefs (Hostert et al. 2019), making them an ideal prey item. That said, these large mud crabs are omnivorous and the multiple prey species they have to choose from could dampen or eliminate tight coupling with any single prey species (Coblentz 2020). Nonetheless, based on recorded consumption of *P. armatus* by large mud crabs (*P. herbstii*) and competition for reef habitat with both large and small mud crabs (*P. armatus* and *E. depressus*), we hypothesized these native crabs would negatively correlate with *P. armatus* (Pintor and Byers 2015b; Mack et al. 2019; Tolley et al. 2007). We were thus initially surprised to find a positive relationship between mud crabs and *P. armatus* across our sampling range on the Georgia coast.

There are a number of potential mechanisms by which a species that is expected to directly compete with or prey upon another species may have a positive association. One likely scenario is that the densities of both mud crabs and *P. armatus* positively covary with an unmeasured variable. For instance, the hydrodynamics of the system may play a role allowing

the aggregation of larvae onto the same reefs (Byers et al. 2014). Both species have planktonic larvae and are distributed along the coast via currents and tides (Tolley et al. 2013). Therefore, if recruitment is high in a given area for one of these crab species, it is most likely high for the other as well. Additionally, due to high post-settlement mortality from predation (e.g., Heck et al. 2001), benthic crustacean post-larvae tend to select structurally complex microhabitats (e.g., oyster reefs; Moksnes 2004). Thus, the positive relationship between native mud crabs and invasive *P. armatus* might stem from their joint preference for structurally complex habitats, with the habitat benefit to the prey outweighing the resulting proximity to its predator (Bishop and Byers 2015).

Previous work has also suggested that predator populations will sometimes temporally track their prey (i.e., predator–prey cycles) resulting in a positive relationship in the abundances of a predator and prey species across multiple spatial scales (Colwell and Landrum 1993). These positive associations in abundance are especially pertinent in areas where prey use spatial refuges to hide from predators (Sih 1985, 2010). For instance, Shima and Osenberg (2003), found that juvenile fishes were more likely to settle on patch reefs with high habitat quality, increasing survival and resulting in positive relationships with predatory species. In areas with spatial refuge for prey species, the densities of both predator and prey will increase within that locale; however, the prey species may still be detrimentally affected through reduced feeding rates or reproductive output (Sih 1985). Finally, the system may be regulated by food availability rather than predator density (i.e. bottom-up control; Hairston et al. 1960). In bottom-up resource-controlled systems, resources boost prey population size which in turn supports higher predator population size, resulting in a positive association between predator and prey (Frederiksen et al. 2006).

Petrolisthes armatus is a prominent example of “Caribbean creep”, whereby tropical species, which are often limited by colder temperatures, are moving northward along the southeastern US coastline as a warming climate makes those regions more hospitable (sensu Canning-Clode et al. 2011). As species establish and the leading edge of the invasion advances, it is possible to find relatively large regions within the center of the

invaded range where temperature is less important in driving species abundance. The lower importance of temperature likely stems from the fact that (1) an invading tropical species is presumably buffered from critical temperature minima that are limiting the species at the leading edge of the invasion, and (2) temperature, in general does not vary much over 150 km, and has less explanatory power at this regional scale. In such cases, other variables can take on stronger associations with invasive species abundance. Here, we show that native mud crabs are one such variable and may provide insight into the mechanisms influencing the abundance and distribution of an invasive species. Further, mud crabs explain 23% of the variation across 33 reefs spanning 150 km of coastline emphasizing the importance of including biotic variables into predictive models at small to intermediate spatial scales to better understand the dynamics of species across their invaded range. They also suggest that factors that influence invasive species abundance may differ across locations within their invaded range or if analyzed across different spatial scales.

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Data availability Data and code for this manuscript are publicly available at <https://github.com/sziegler/PetroAnalysis>

Declarations

Conflict of interest The authors have no relevant financial or non-financial interests to disclose.

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