

Does predator-driven, biotic resistance limit the northward spread of the non-native green porcelain crab, *Petrolisthes armatus*?

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Abstract Biotic resistance by native predators can limit the geographic range and abundance of non-native species following introduction into an ecosystem. Here we tested the hypothesis that the strength of predation pressure varies with latitude and limits the abundance and northward expansion of the non-native green porcelain crab, *Petrolisthes armatus*, whose northern range is also hypothesized to be limited by physical tolerances to cold temperatures. We quantified the predation risk of *P. armatus* across 400 km of the crab's invasive range along the coastline of the southeastern US. In addition, we measured the density of large *P. armatus*, habitat quality, and other environmental factors that may affect the crab's predation risk. Finally, we conducted a size-selective predator exclusion experiment to determine the predator species and size classes that may be consuming *P. armatus*. Results indicated that neither the density of

large *P. armatus* nor its predation risk varied systematically with latitude. Instead, variation in predation risk was best explained by local site-level differences in habitat quality, the density of large *P. armatus*, and the mean abundance of predators. The predator exclusion experiment indicated that both small and large size classes of predators are capable of equally strong rates of predation on *P. armatus*. Together, our results suggest that although native predators readily consume *P. armatus*, they do not provide biotic resistance against its northward expansion. Instead, it seems likely that other latitudinally differential factors like low winter temperatures that decrease *P. armatus* survival are more influential in limiting the crab's northern expansion.

Keywords Density dependence · Enemy release hypothesis · Limiting factors · Range expansion · Top-down effects · Trophic interactions

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Introduction

The geographic range and abundance of non-native species following introduction often depends on the interaction of multiple factors within a native ecosystem (Sakai et al. 2001; Arim et al. 2006; Hayes and Barry 2008). Abiotic conditions, such as temperature, can often limit the spread of a non-native species

depending upon its thermal tolerance (Ford 1996; Stachowicz et al. 2002; Sorte et al. 2010). Yet if a non-native species can tolerate local environmental conditions, then biotic resistance can play a role in determining invasion success. Biotic resistance through predation by native predators has been frequently shown to limit the local abundance of an invader (Baltz and Moyle 1993; Reusch 1998; Byers 2002; DeRivera et al. 2005; Dumont et al. 2011; Yamanishi et al. 2012). For example, predation by native benthic predators has prevented the establishment of invasive ascidians (*Ciona intestinalis*) and restricted its invasion success to suspended artificial structures in marine systems (Dumont et al. 2011). Given that predation is a strong force that structures marine communities, it is not surprising that this interaction frequently limits invasions in marine systems (Kimbrow et al. 2013; Papacostas et al. 2017). Yet predation pressure may also vary geographically (Trussell and Smith 2000; Hewitt 2002; Ruiz et al. 2009; Freestone et al. 2013) and can frequently depend on the diversity or abundance of predators with which a non-native species co-occurs (DeRivera et al. 2005; Jensen et al. 2007; Dumont et al. 2009). Here, we examine whether variation in biotic resistance through predation may limit the geographic distribution and local abundance of a non-native prey species hypothesized to be limited by physical tolerances.

Differences in the abundance of a native predator or alternative native prey species across a geographic range likely influences the strength of biotic resistance via predation experienced by an invading species (Endler 1977; Fraser and Gilliam 1987; DeRivera et al. 2005). Non-native prey invading sites with higher predator abundance may likely experience stronger biotic resistance through predation than sites with lower predator abundance of the same predator species. For example, higher densities of native predatory ants increased mortality on invasive cane toad metamorphs more than fourfold (Ward-Fear et al. 2010). Similarly, the strength of biotic resistance via predation against invasion of the apple snail, *Pomacea canaliculata*, increased with crayfish predator density (Yamanishi et al. 2012). Consumption of an invasive prey by a native predator has also been shown to be related to prey density (Twardochleb et al. 2012; Charbonnier et al. 2014). Although these factors (e.g., the abundance of a native predator or prey) may be somewhat intuitive, geographic variation in invasion

success has more commonly been studied in the context of whether a predator is present or absent, rather than as a continuous variable (except see MacNeil et al. 2013). Here, we aim to test whether predation pressure by native predators varies along the invaded range of a non-native prey such that it might differentially limit the distribution and abundance of a non-native, invasive prey especially at the present edge of its distribution.

Petrolisthes armatus, the green porcelain crab, is a non-native crab whose northern range is hypothesized to be limited by its susceptibility to cold temperatures (Knott et al. 2000; Stillman and Somero 2000; Hadley et al. 2010; Canning-Clode et al. 2011; Kimball et al. 2014). Specifically, *P. armatus* appears unable to withstand the severe winter temperatures or ‘cold snaps’ associated with northern sites along the eastern US coast (Canning-Clode et al. 2011). Furthermore, although summertime densities of *P. armatus* have been reported as high as several thousand per/m² (Hollebone and Hay 2007a), abundances decline in substantially colder months and at higher latitudinal sites (Hartman and Stancyk 2001). The ephemeral nature of the species’ northern edge has made its northernmost distribution difficult to ascertain, but some evidence suggests it is slowly expanding (Waslick et al. 2017). Though it seems likely temperature has a large influence on the leading edge, there may be other limiting factors affecting the range of this species.

Predation by native predators within invaded oyster reef communities suggests that biotic resistance from predation may be an alternative factor limiting the geographic range of non-native, invasive *P. armatus* (Hollebone and Hay 2008; Pintor and Byers 2015). For example, *Panopeus herbstii*, the Atlantic Mud Crab, is a widespread, important generalist predator that has been shown to readily incorporate *P. armatus* within their diet (Hollebone and Hay 2008; Hostert et al. 2018; Pintor and Byers 2015). Similarly, predatory fish, such as the mummichog, *Fundulus heteroclitus*, has been shown to consume *P. armatus* in a laboratory setting (Hollebone and Hay 2008). Additionally, predator species from the genus *Callinectes* are common predatory crabs within these oyster reef communities and have been suggested to limit the spread of other invasive species (Harding 2003; DeRivera et al. 2005; Carlsson et al. 2011). Although predation by these predators has only been directly

observed under laboratory conditions and field tethering trials at a single invaded site (Hollebone and Hay 2008), we hypothesize that biotic resistance may be another process limiting the spread of this non-native, invasive species.

Although the diversity of predators is roughly consistent along the invasive range of *P. armatus*, the abundances of these species is not (Wenner and Wenner 1989; Kimbro et al. 2014; Gehman et al. 2017). Such variation can affect the strength of biotic resistance from predation. This is especially true if different predatory species consume *P. armatus* at different rates (Hollebone and Hay 2008; Pintor and Byers 2015), because variation in their relative abundance will in turn exert highly variable predation pressure on *P. armatus* throughout the invasive range (Wenner and Wenner 1989; Gehman et al. 2017). Hollebone and Hay (2008) compared consumption rates of *P. armatus* within the lab by a suite of predator species thought to function as generalist predators on the reef. *Panopeus herbstii*, *Callinectes similis* (lesser blue crab) and *F. heteroclitus* readily consumed *P. armatus*, while the native fish, *Leiostomus xanthurus* (spot) avoided *P. armatus*. Even within a species, there can be individual variation in consumption of a non-native prey (Réale et al. 2007; Pintor and Byers 2015) that can alter the total strength of predation exerted on a non-native prey population. For instance, female individuals within a single population of *P. herbstii* have been shown to incorporate more *P. armatus* within their diet in comparison to males (Pintor and Byers 2015). Consumption could also be structured by the size class of the native predator (Truemper and Lauer 2005; Toscano and Griffen 2012; Pintor and Byers 2015). For example, smaller *P. herbstii* regularly consumed *P. armatus* more than larger individuals (Pintor and Byers 2015). Because of these known differences in consumption based on predator species and size, it is important to understand the predator composition, including the identity, abundance and demography of predator species.

Finally, additional factors such as habitat availability (Byers 2002; Dumont et al. 2011), the number of alternative prey items (Pyke 1984; Stephens and Krebs 1986; Magoulick and Lewis 2002) and abiotic conditions (Sanford 2002; Ferrari et al. 2015) may mediate the ability of native predators to consume *P. armatus*. In these intertidal communities invaded by *P. armatus*, *Crassostrea virginica*, the Eastern oyster, is an

ecosystem engineer that forms reefs in which higher oyster abundance correlates with higher habitat complexity (Gutierrez et al. 2003; Byers et al. 2015). Specific to this system, *P. armatus* is often found in higher abundances on reefs with higher rugosity, a measure of habitat complexity (Margiotta et al. 2016). If habitat complexity influences predator–prey interactions, then we might expect that predators foraging in habitats with high oyster abundances to exert reduced predation pressure on *P. armatus*. Yet, the consumption of a non-native prey species by native predators is also likely to be influenced by the prey's density on a reef as well as the density of alternative native prey (Krebs and Davies 1981; Pyke 1984; Stephens and Krebs 1986). For example, in the Great Lakes, many native predators have switched to consuming zebra mussels, *Dreissena polymorpha*, as this species becomes very abundant in the freshwater communities it invades (French and Bur 1992; Molloy et al. 1997). Finally, although the physical tolerance to cold temperatures of *P. armatus* has been suggested to limit its spread, temperature can also affect predator metabolism potentially affecting the consumption rate of *P. armatus* by predators (Sanford 2002; Ferrari et al. 2015). Understanding whether temperature affects predation rates on a non-native prey species could elucidate how communities will respond to changing climates (Stachowicz et al. 2002; Sorte et al. 2010).

We set four main objectives to evaluate whether biotic resistance via predation may also limit the current distribution and abundance of *P. armatus* in its non-native range. First we quantified the pattern of density of adult *P. armatus* (i.e., > 4 mm carapace length) along the US Atlantic Coast. We predicted that the density of adult *P. armatus* would decline from southern to northern sites. Second we determined if predation risk changes with latitude and might be a factor that explains the current distribution of *P. armatus*. If predation by native predators helps to limit the spread of *P. armatus* northward, then predation risk should increase with increasing latitude. Third regardless of latitude, we examined whether other environmental factors contribute to explaining predation risk on *P. armatus*. Finally, we determined what predators might be responsible for consuming *P. armatus* in a manipulative field experiment.

Methodology

Study sites

To examine whether density and predation on adult *P. armatus* varied systematically with latitude, we sampled eight replicate estuaries along the invasive range of *P. armatus* from St. Augustine, FL to North Inlet, SC,

SC (Fig. 1). We chose St. Augustine, FL as the southern edge of this sampling range because south of this site estuarine habitat becomes mixed with both oyster and mangrove habitat which could result in different communities (Saintilan et al. 2014). Recent sources cite that the northern most edge of the distribution of *P. armatus* is near Wilmington, NC (Wassick et al. 2017). We also included for informal



Fig. 1 Map of the nine estuaries surveyed in this study along the southeastern United States Atlantic coast. *indicates Morehead City, NC that served as the uninvasive, control site

comparisons, an uninvaded, control site at Morehead City, NC that has no record of *P. armatus* and is well north of its northernmost documentation. These sites were sampled during the summer of 2016 from June 8 to July 27. Within each of the nine estuaries (eight invaded, one control), we selected mid-low intertidal oyster reefs that were a similar distance from the mouth of the estuary and were backed by *Spartina alterniflora* vegetation. To maximize the ability to detect differences in predation pressure across estuaries along the invaded range of *P. armatus*, we sampled reefs (25 total) across the nine estuaries that were similar in habitat quality and abiotic factors based on salinity, tidal range, slope of reef and height of reef (Supplemental Material). When possible, we sampled reefs within the estuaries that were previously sampled in Byers et al. (2015) and considered to be representative healthy reefs within these estuaries. Within each estuary, we sampled a minimum of two reefs, three when available, that were separated by at least 10 m, but similar in location and habitat within the estuary.

Pattern of abundance of *P. armatus* along the US Atlantic Coast

To quantify the pattern of abundance of *P. armatus* across the US Atlantic Coast we quantified the density of large *P. armatus* and the proportion of large *P. armatus* in the prey base for each reef across the nine estuaries described above. We targeted larger bodied crabs (> 4 mm) because they are reproductively mature and thus contributing most to population growth. We used an excavation method to quantify the density of large *P. armatus* and alternative native prey taxa (Gehman et al. 2017). While other studies have quantified crab densities using recruitment to artificial substrates (e.g., bag and trays), we chose to excavate existing plots because it can be used to quantify absolute, as opposed to relative, density, and it is more efficient at sampling oysters and mussels which require a long time to recruit to artificial substrates. At each reef, we haphazardly placed a 0.25 m² quadrat 1 m up from the bottom (waterward) edge of the reef. We rapidly excavated this area from outside in, using hand shovels to block escapement and hand collecting all material within it, including all the oyster shell down to approximately 5 cm beneath the mud surface. To further reduce escapement, we immediately placed all excavated shell, organisms,

and sediment into a 5 gallon bucket and sealed it with a lid for transportation back to shore for processing. We then rinsed the collected oyster reef material through a 2 mm sieve. To quantify the densities of large *P. armatus* and the dominant native prey species on the reef, we counted the number of individuals of the following epifaunal, reef-based prey species: *P. armatus*, *Geukensia demissa* (ribbed mussel), *C. virginica* (Eastern oyster), and *Eurypanopeus depressus* (depressed mud crab). These are the most conspicuous prey items on the reef and have been shown to be the primary prey items that make up the diet of important generalist predators like *P. herbstii* (Lee and Kneib 1994). Because they often have a size refuge from predation, *G. demissa* and *C. virginica* were separated into two size classes. We considered *G. demissa* and *C. virginica* that were less than 20 mm to be considered prey items. We calculated the relative proportion of *P. armatus* in the representative prey base as the number of *P. armatus* over the total number of all prey items per 0.25 m². In total, we quantified density plots at 25 reefs across the nine estuaries.

We examined the effect of latitude on the density of large *P. armatus* and on the proportion of large *P. armatus* within the prey base using simple linear regressions in the statistical program R 3.4.2 (R Development Core Team 2017). Because our level of replication is at the level of estuary, we averaged the density of large *P. armatus* and the proportion of large *P. armatus* in the prey base across the reefs within each estuary. We used two simple linear regressions weighted by sample size within a site to test for a relationship between latitude and the density of large *P. armatus* and between latitude and the proportion of large *P. armatus* in the prey base for the invaded eight estuaries only (excluding our control site in Morehead City, NC). We also checked for quadratic relationships in these regressions, but removed the quadratic term if it was not significant. We examined the residuals for signs of patterns to ensure that we met model assumptions.

Predation risk on *P. armatus* along its invasive range

To determine whether the risk of predation varies with latitude, we conducted tethering experiments at each of the invaded estuaries (n = 8 replicate estuaries). Tethered crabs are considered at higher risk and can

result in higher predation than natural circumstances (Zimmer-Faust et al. 1994). Thus, this experiment aimed to quantify the relative predation risk across the estuaries invaded by *P. armatus*. Individual *P. armatus* crabs (6–11 mm carapace width) were collected by hand from oyster reefs at the Skidaway Institute of Oceanography (SkIO) in Savannah, GA. We attached an individual crab to 35 cm length of 6.8 kg strength fishing line on the back of the carapace using super glue. We used a higher strength of fishing line to reduce breakage caused by large predators. Any crabs that dropped claws/legs during the set-up process were not used in the experiment. Because this species readily autotomizes its limbs, we used a towel to handle crabs and made sure to cover the eyes and claws while attaching the fishing line with super glue. Handling the crabs in this manner substantially reduced the occurrence of crabs dropping limbs. Because tethers were much longer than the length of a crab, tethered crabs were able to move about the reef and potentially take shelter within the oyster reef habitat to avoid predation. We then attached the line to a roofing nail (8.89 cm) to be used as an anchor point for installment in the reef. Tethered crabs were kept in a flow-through system for a minimum of 24 h before deployment to ensure tether integrity and that no mortality occurred due to tethering.

Tethered crabs were transported to each deployment site in 5 gallon buckets filled with filtered and aerated sea water. At each reef we placed approximately 20 *P. armatus* 1 m apart for 12 h during a nocturnal high tide. We made sure that tethers were underwater during the night hours, so tethers were placed on an incoming tide between 18:00 and 23:00 and picked up no later than 09:00 the next morning during low tide. Predation was determined by counting the number of crabs that were missing (all missing crabs had a piece of carapace remaining on the tether). There were 19 tethers observed with a cut line (5% tethered crabs used in the experiment). Because of the ambiguity of the cause of tether breakage, these cut line tethers were not included in the estimated predation risk and excluded from all further analyses. Therefore, in total we placed 371 tethered crabs across 22 reefs within the eight invaded estuaries.

We examined the effect of latitude on the predation risk of *P. armatus* using a generalized linear mixed effects model (GLMM) using the lme4 package in the statistical program R 3.4.2 (Bates et al. 2014; R

Development Core Team 2017). We coded the dependent variable, predation risk on tethered crabs, as binary data with predation as the success (“1”) and survival as a failure (“0”). Individual tethered *P. armatus* were nested within “estuary” and included in the model as a random factor ($n = 8$ replicate estuaries). Nesting tethered *P. armatus* within “reef”, as well as estuary, did not improve model fit and was excluded from the model. We fitted the latitude of each estuary as the only independent variable.

Environmental factors that contribute to explaining risk of predation on *P. armatus*

To determine other environmental factors, regardless of latitude that contribute to the risk of predation on *P. armatus*, we quantified multiple biotic and physical variables at the sites where the tethering experiments were conducted ($n = 8$ estuaries). Specifically, as outlined in the methods above, we quantified the mean density of large *P. armatus* and the mean density of alternative native prey (small *G. demissa*, small *C. virginica*, and *E. depressus*). Because *C. virginica* is a foundational species (Gutierrez et al. 2003, Byers et al. 2015) that provides habitat for many species including *P. armatus* (Margiotta et al. 2016), we used the mean density of *C. virginica* > 20 mm as an indicator of habitat quality. These variables were included because all could influence predation rates on tethered *P. armatus*.

We also characterized and quantified the invertivore predator community at each of the eight replicate estuaries using a combination of trapping and plot sampling. Specifically, we set out 1 crab trap (standard size 61 cm \times 61 cm \times 28 cm) and 1 minnow trap (standard 42 cm \times 22.9 cm with 2.54 cm openings) at each reef within the sampled estuary. Traps were set at low tide, 1 m up from the edge of the reef (waterward) and retrieved approximately 6 h later at high tide. Each of the minnow traps were baited with ~ 132 g of frozen shrimp. Each crab trap was baited with ~ 1500 g of frozen chicken. Additionally, the common mud crab predator, *Panopeus herbstii* was quantified using the 0.25 m² plot excavation method described in “Methodology” section, sub-section “Pattern of abundance of *P. armatus* along the US Atlantic coast” section. Captured fish species were identified and classified as potential predators if they were listed as having “decapods” in their diets on

fishbase.org (Froese and Pauly 2017). This included *F. heteroclitus* (mummichog), *Lagodon rhomboides* (pinfish), *Orthopristis chrysoptera* (pigfish), and *Bairdiella chrysoura* (American silver perch). Although our trapping methods cannot quantify the abundance of larger fish predators that might consume *P. armatus*, it does quantify predators that are consistently in the reef and that have definitively been shown to consume *P. armatus* in the lab (Hollebone and Hay 2008; Pintor and Byers 2015; Hostert et al. 2018). We summed the total number of predators of all species quantified in the trapping regime and density plots for each reef, and then averaged across the reefs to yield the mean abundance of native predators per reef within each estuary.

Because temperature can affect the metabolic rates of predators, we also included the water temperature for each estuary in our analyses. We measured the water temperature in degrees Celsius during the night time high tide using iButtons placed in protective waterproof glass jars installed in the reef (Hubbart et al. 2005). For sites where we were able to retrieve more than one iButton logger, we averaged the temperature readings to include in the analyses. All of the iButton loggers were lost during the tidal cycle at our North Inlet, SC site. Therefore we used the reports filed in the National Estuarine Research Reserve Data Export System (NERR DES) to find the high tide water temperature at Oyster Landing, North Inlet-Winyah Bay, SC during the night we placed tethered crabs.

To determine whether predation risk could be explained by environmental variables, regardless of latitude, we conducted a GLMM using the lme4 package in the statistical program R 3.4.2 (Bates et al. 2014; R Development Core Team 2017). We coded the dependent variable, predation risk, as binary data with predation as the success (“1”) and survival as a failure (“0”). Individual tethered *P. armatus* were nested within “estuary” and included in the model as a random factor ($n = 8$ estuaries). Within our model the unit of replication is the eight estuaries therefore the density and abundance measurements taken at the reef level were averaged for inclusion as the mean of each estuary. We fitted the mean density of alternative native prey, the mean density of large *P. armatus*, the mean density of oysters > 20 mm, the mean abundance of all native predators, and the water temperature. We used the package MuMin in R 3.4.2 to run an

exhaustive search of all possible models (with 5 candidate independent variables: $2^5 = 32$ possible models) and determine the best model using Akaike information criterion (AIC) including calculating the corrected AIC (AICc), delta AIC (Δ AIC) and Akaike weight (w) (Burnham and Anderson 2002; Symonds and Moussalli 2011). For those models with Δ AIC less than 1, we ran an Analysis of Variance likelihood ratio test to determine whether these models statistically differed. If they did not, we promoted the most parsimonious model, i.e., with the fewest degrees of freedom. We also determined the relative variable importance (RVI) of each of the five independent variables by adding the w 's for each of the models that include that variable (Burnham and Anderson 2002; Symonds and Moussalli 2011).

Identifying predators responsible for *P. armatus* predation

To more directly determine predator species or size classes that might be consuming *P. armatus*, we designed a caging experiment to differentially exclude predators based on size and feeding ecology and quantified predation on tethered *P. armatus*. We conducted this experiment at SkIO during 6 nocturnal high tides from June 28–30 and July 12–14, 2017. SkIO was one of the 8 invaded sites previously surveyed and is known to have all the predatory species quantified in the trapping regime (McFarlin and Alber 2005). Individual *P. armatus* were tethered using the same methodology as described above, but instead super glued to 17 mm length of 6.8 kg strength fishing line. The length of the tether did not allow *P. armatus* to reach any side of the cage. We then attached the line to a roofing nail for installment in the reef substrate, placing one crab every meter. Next we applied one of five predator exclusion treatments to each tethered crab. The basic exclusion cage was made out of wire shelving grids that were 35.5 cm \times 35.5 cm \times 35.5 cm with 40 mm mesh. This cage treatment excluded all but small/medium crabs and small fish. We modified this basic cage design to create three other treatments. Specifically, for one of the treatments we covered the cages with 17 mm birding mesh to exclude all but small crabs and small fish. For another treatment we covered the cages with 6 mm birding mesh to exclude all predators. This total exclusion treatment also allowed us to confirm that

mortality of *P. armatus* was due to predation as opposed to another factor such as water flow over the reef. A fourth treatment consisted of a 35.5 cm × 35.5 cm × 5 cm roof covered with 6 mm bird mesh (i.e., sides of the cage free of mesh and open) to allow all crab and small fish predators to enter from the sides close to the substratum but not from the top. Thus, this treatment prevented large predatory fish, such as red drum and wading birds from accessing the tethered crab, but allowed all other benthic predators to enter from the sides. Finally, a cage-less control treatment was an exposed tether with no caging structure that allowed all predators' access including crabs and fish of all sizes.

Replicates of each treatment were blocked over space and time. Spatial blocks were established in areas with similar mud substrate type including shell hash for refuge but was muddy enough to allow the cages to be pushed ~ 2.5 cm into the substrate to ensure no predators could enter through the bottom. Spatial blocks were at least 10 m apart and contained one of each of the five treatments placed in random order within the block. Replicates were also blocked over time (i.e., a single evening tide), such that there were between 3 and 6 spatial blocks within a time block. We placed the tethers during an evening tide and left them for approximately 12 h until the morning tide. We then removed all cages and quantified predation events during the morning low tide. New spatial blocks were established following each time period. In total, there were 32 spatial blocks that were nested within 6 temporal blocks. The treatment “Small Crabs and Small Fish” was only replicated over 11 spatial blocks and three nights. Thus, across all blocks there were a total of 139 tethered *P. armatus*. Treatment cages within four spatial blocks were compromised because of a storm event. Two of the “No Predator Control” treatments in two additional spatial blocks were found to contain a small *P. herbstii* predator. After removing these six compromised blocks, each treatment was replicated for a total of 26 blocks except the “Small Crabs and Small Fish” treatment which had 5 replicate blocks. We ran analyses with and without these compromised blocks and found that results did not differ.

Similar to the models described above, we conducted GLMM models using the lme4 package in R (Bates et al. 2014) to test whether the predation risk of *P. armatus* differed under the five predator exclusion

treatments: (1) “No Predator Control”, (2) “Small Crabs and Small Fish”, (3) “Small/Medium Crabs and Small Fish”, (4) “All Crabs and Small Fish”, and (5) “All-Predators”. These treatment names refer to which sizes and taxa of predators should have had access to *P. armatus*. As described above, we coded the response variable, predation risk, as binary data with predation as the success (“1”) and survival as a failure (“0”). For statistical purposes, we coded a single “dummy” predation event for the “No Predator” treatment because there was no variation in predation (all crabs survived) which allowed us to determine statistical significance between other treatments. We included spatial block nested within the temporal block as a random factor. Predator exclusion treatment was fitted as a fixed effect. Since “treatment” is a categorical variable, model output reports how each group differed from the “reference” group. To determine significant differences between all the groups, we ran separate models changing the reference group of the model to compare against each of the other treatments. We then used the estimates of beta and the associated *p* values to determine whether post hoc differences between treatments were significant.

Results

Pattern of abundance of *P. armatus* along the US Atlantic Coast

The mean density of large *P. armatus* across the eight surveyed invaded estuaries ranged between 0 and 21 individuals per 0.25 m² (Table 1). We found 0 individuals per 0.25 m² at all reefs for the uninhabited estuary in Morehead City, NC. Within sites, the coefficient of variation in large *P. armatus* density at sites that had at least 3 reefs ranged between 0.42 and 0.74. Results of the weighted regression indicated there was no relationship between latitude and the density of large *P. armatus* ($R^2 = 0.09$, $p = 0.48$, $n = 8$, Fig. 2). The quadratic term was not significant ($p = 0.132$) and removed. The mean proportion of large *P. armatus* in the prey base across the eight surveyed estuaries ranged between 0 and 42% of the prey base. Within sites, the coefficient of variation in the proportion of large *P. armatus* in the prey base at sites that had at least 3 reefs was low, ranging between 0.30 and 0.74. Results of the weighted regression

Table 1 Average values of each predictor variable included in the GLMM model examining which environmental factors affect predation risk on *P. armatus* regardless of latitude

Estuary	Number of reefs	Mean density of oysters > 20 mm (#/0.25 m ²)	Mean density of large <i>P. armatus</i> (#/0.25 m ²)	Mean density of native prey (#/0.25 m ²)	Mean abundance of native predators	Water temperature (°C)
North Inlet, SC	3	91.67	0.00	174.33	10.0	29.1*
Charleston, SC	3	133	14.67	151.00	36.67	28
ACE Basin, SC	3	36	3.33	8.33	6.33	30.25
SkIO, GA	3	94.33	21.00	38.33	18.67	27.5
St. Catherine's Island, GA	3	47	10.67	14.33	7.67	30.25
Sapelo Island, GA	2	153	11.00	56.50	25.50	30.25
Jacksonville, FL	3	119.67	17.33	120.67	13.67	30
St. Augustine, FL	2	66	4.50	123.50	26.50	30

Densities reflect the number per 0.25 m² from the excavated plots. Native Prey is the total number of *C. virginica* < 20 mm, *G. demissa* < 20 mm, and *E. depressus*. Native Predators included the abundance of *Panopeus herbstii*, *Callinectes* sp., *Fundulus heteroclitus*, *Lagodon rhomboides*, *Orthopristis chrysoptera*, and *Bairdiella chrysoura*. Water temperature is the night time high tide water temperature calculated using iButton loggers placed in the reef

*iButton loggers were lost during the tidal cycle for this site. Reported temperature value comes from the National Estuarine Research Reserve Data Export System (NERR DES) for night time high tide temperature at Oyster Landing, North-Inlet Winyah Bay, SC

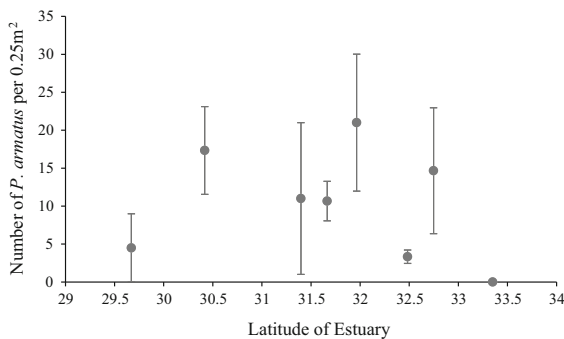


Fig. 2 Mean density of large *P. armatus* (\pm SE) across the sampled range. Each dot represents the average number of large *P. armatus* per 0.25 m² across the reefs within each estuary. *P. armatus* was not found in density plots at our most northern site and thus there is no estimate for standard error. There was no relationship between the density of large *P. armatus* and latitude ($R^2 = 0.09$, $p = 0.48$, $n = 8$)

indicated that the quadratic term was significant ($p = 0.025$) for the relationship between the latitude and proportion of large *P. armatus* in the prey base and thus was retained in the full model ($R^2 = 0.67$, $p = 0.064$, $n = 8$, Fig. 3).

Finally, the observed density and proportion of large *P. armatus* at the southernmost site sampled (i.e., St. Augustine, FL) was surprisingly low relative to other sites where *P. armatus* has been established for a

shorter period of time. We examined the influence of this site on the relationship between latitude and the density and proportion of large *P. armatus* by removing it from the weighted linear regressions. We found that exclusion of the St. Augustine site did not affect the relationship between latitude and the density of large *P. armatus*, with results continuing to indicate a non-significant relationship for both linear ($R^2 = 0.37$, $p = 0.14$, $n = 7$) and quadratic models ($R^2 = 0.45$, $p = 0.23$, $n = 7$). However, latitude no longer explained the proportion of *P. armatus* in the prey base once the St. Augustine site was removed (quadratic term: 0.09, overall model: $R^2 = 0.62$, $p = 0.14$, $n = 7$). Because all of the habitat variables measured at the St. Augustine site were within the range of other sites (Supplemental Material) we continued to include this site in further analyses.

Predation risk on *P. armatus* along its invasive range

Although predation risk across the eight invaded estuaries was high (range from 68.2 to 98.2%), there was a significant difference in predation risk across estuaries ($\chi^2 = 38.549$, $df = 7$, $p < 0.001$). However, the results of the GLMM indicated that predation risk

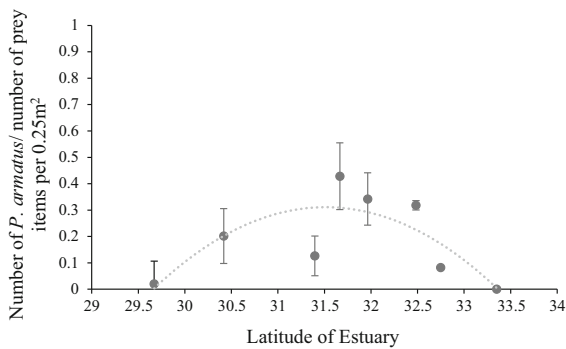


Fig. 3 Mean proportion of large *P. armatus* (\pm SE) within the prey base across the sampled estuaries. Each dot represents the average number of large *P. armatus* over the number of total common prey items (*C. virginica*, *G. demissa*, *E. depressus*, and *P. armatus*) per 0.25 m² plot across each reef within the estuary. *P. armatus* was not found in density plots at our northernmost site and thus there is no estimate for standard error. There was a significant quadratic relationship between the proportion of large *P. armatus* of the prey base and latitude ($R^2 = 0.67$, $p = 0.025$, $n = 8$)

across the estuaries did not differ systematically with respect to latitude ($R^2 = 0.02$, $p = 0.43$, $n = 8$, Fig. 4).

Environmental factors that contribute to predation risk on *P. armatus*

Using AIC criteria, the model that best predicted predation risk on *P. armatus* included the density of oysters > 20 mm, the density of large *P. armatus*, and the mean abundance of native predators ($R^2 = 0.26$, Table 2). However, this model and the second ranked AIC model differed in Δ AIC by less than 1, and the subsequent Analysis of Variance likelihood ratio test showed that these models did not statistically differ ($\chi^2 = 2.69$, $df = 1$, $p = 0.10$). Thus, the more parsimonious model (#2 in Table 2), with four degrees of freedom, that included only the density of oysters > 20 mm and the density of large *P. armatus* was promoted as the top model. Specifically, predation on tethered *P. armatus* was negatively associated with the number of oysters > 20 mm (i.e., a proxy for habitat quality; $z = -5.007$, $p < 0.001$, $n = 8$) and positively associated with the natural densities of *P. armatus* ($z = 2.327$, $p = 0.02$, $n = 8$). Looking across all models, these same two variables also had the highest RVI's by a wide margin: the density of oysters > 20 mm (RVI = 0.95) and the density of large *P. armatus* (RVI = 0.81).

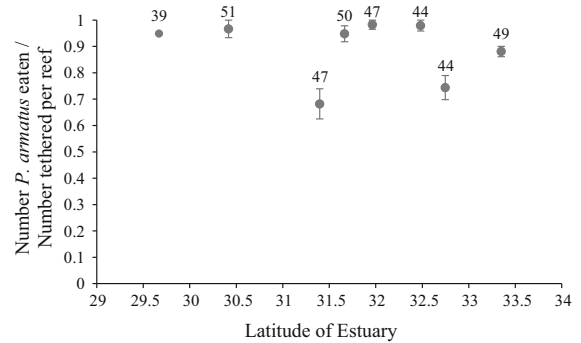


Fig. 4 The mean predation risk on *P. armatus* (\pm SE) across the 8 estuaries invaded by *P. armatus*. Predation was quantified over a nocturnal high tide, with tethered crabs placed on evening low tide and retrieved during low tide the following morning to ensure that tethers were underwater the entire trial. Each dot represents the mean number of *P. armatus* eaten out of the number placed per reef across each estuary. The standard error for our most southern site, St. Augustine, FL was very small at 0.0013. The number of replicate tethers per estuary are shown above each dot. There was no relationship between predation risk and latitude ($R^2 = 0.02$, $p = 0.43$, $n = 8$)

Identifying predators responsible for *P. armatus* predation

Results of the caging experiment indicated that there was an overall treatment effect on the predation of tethered crabs ($p < 0.001$, Fig. 5). The “No Predator Control” treatment experienced no predation and was significantly different from all the other predator access treatments ($p < 0.001$ for all comparisons). There was no difference between the “All Predators” and the “Small Crabs and Small Fish” treatment ($p = 0.818$), however all other treatments had lower predation risk compared to the “All Predators” (“Small/Medium Crabs and Small Fish”: $p = 0.041$ and “All Crabs and Small Fish”: $p = 0.013$). There were no differences between the “Small/Medium Crabs and Small Fish” and the “All Crabs and Small Fish” treatments ($p = 0.762$), the “Small Crabs and Small Fish” and the “Small/Medium Crabs and Small Fish” treatments ($p = 0.181$), and finally the “Small Crabs and Small Fish” and the “All Crabs and Small Fish” treatments ($p = 0.122$).

Discussion

Density of large *P. armatus* varied substantially across the sampled range, but did not vary systematically

Table 2 Top GLMM models examining which environmental factors affect predation risk on *P. armatus* regardless of latitude. Only models with a Δ AIC score less than five are shown

Model rank	Intercept	Water temperature (°C)	Density of native prey (#/0.25 m ²)	Density of oysters > 20 mm (#/0.25 m ²)	Density of large <i>P. armatus</i> (#/0.25 m ²)	Abundance of native predators	df	AICc	Δ AIC	<i>w</i>	R ²
1	2.50			− 0.92	0.58	− 0.36	5	234.69	0.00	0.23	0.26
2	2.45			− 1.11	0.49		4	235.33	0.63	0.17	0.23
3	2.47		0.16	− 0.90	0.65	− 0.42	6	236.23	1.54	0.11	0.23
4	2.50	− 0.02		− 0.91	0.58	− 0.37	6	236.75	2.06	0.08	0.26
5	2.48	0.13		− 1.15	0.53		5	236.95	2.25	0.07	0.25
6	2.44		0.05	− 1.11	0.50		5	237.32	2.63	0.06	0.22
7	2.43			− 0.87			3	237.66	2.97	0.05	0.18
8	2.47	0.15	0.26	− 0.96	0.74	− 0.38	7	238.06	3.36	0.04	0.23
9	2.45	0.27	0.23	− 1.20	0.68		6	238.27	3.58	0.04	0.23
10	2.42			− 0.71		− 0.24	4	239.00	4.31	0.03	0.19
11	2.44		− 0.11	− 0.85			4	239.54	4.85	0.02	0.19
12	2.42	− 0.10		− 0.88			4	239.55	4.86	0.02	0.17
	RVI	0.30	0.31	0.95	0.81	0.55					

The bold font for model 2 signifies that it was not-significantly different from model 1 in an analysis of variance likelihood ratio test, and thus promoted as the best model due to its higher parsimony. The possible variables included: Density of Native Prey (total number of *C. virginica* < 20 mm, *G. demissa* < 20 mm, and *E. depressus* per 0.25 m²), Density of Oysters > 20 mm (the number of *C. virginica* > 20 mm per 0.25 m²), Density of large *P. armatus* (the number of *P. armatus* per 0.25 m²), Abundance of Native Predators per reef (the total number of native predators caught in the trapping regime and density plots averaged across reefs), and Water Temperature (the night time high tide water temperature in Celsius). The RVI calculations are calculated for the full set of models. The top model is seen in bold

with latitude. Although density dramatically dropped off at the northernmost site at the edge of the range of *P. armatus*, this decline does not appear to be attributable to differentially higher predation rates. Specifically, standardized measurements of predation risk of tethered crabs were relatively similar (and high) across all sites and did not systematically vary with latitude. Also, predation rates scaled positively with *P. armatus* density, indicating that low densities of crabs should experience lower than average predation risk. Together, our results suggest that native predators do not provide stronger biotic resistance against *P. armatus* at the northward edge of its expansion than they do along the rest of its range along the southeastern coast of the U.S. where the crab is highly abundant. Instead, it seems likely that other factors like low winter temperatures have detrimental effects on *P. armatus* survival and are more influential in limiting the crab's northern distribution (Canning-Clode et al. 2011).

Variation in predation risk was best explained by differences in habitat quality and the density of large *P. armatus*. Increasing habitat quality had a protective effect on *P. armatus* and increasing the ambient density of large *P. armatus* increased predation risk, suggesting density dependent foraging by predators. Habitat properties can heavily influence the vulnerability of non-native species to predation (Byers 2002). Here we found that although predation risk was high across invaded sites, habitat quality (measured as the number of oysters > 20 mm) significantly reduced predation risk, suggesting that high quality habitat (i.e., increased refuge habitat) may increase survival of *P. armatus*. Because oysters are the foundational species within this community, their density and structure creates complex reefs that allow species to hide among the interstitial spaces in the otherwise simplistic landscape of mudflats (Gutierrez et al. 2003; Byers et al. 2015, 2017). However, the dynamics between habitat quality and predation rates on *P. armatus* will likely change due to continued harvest

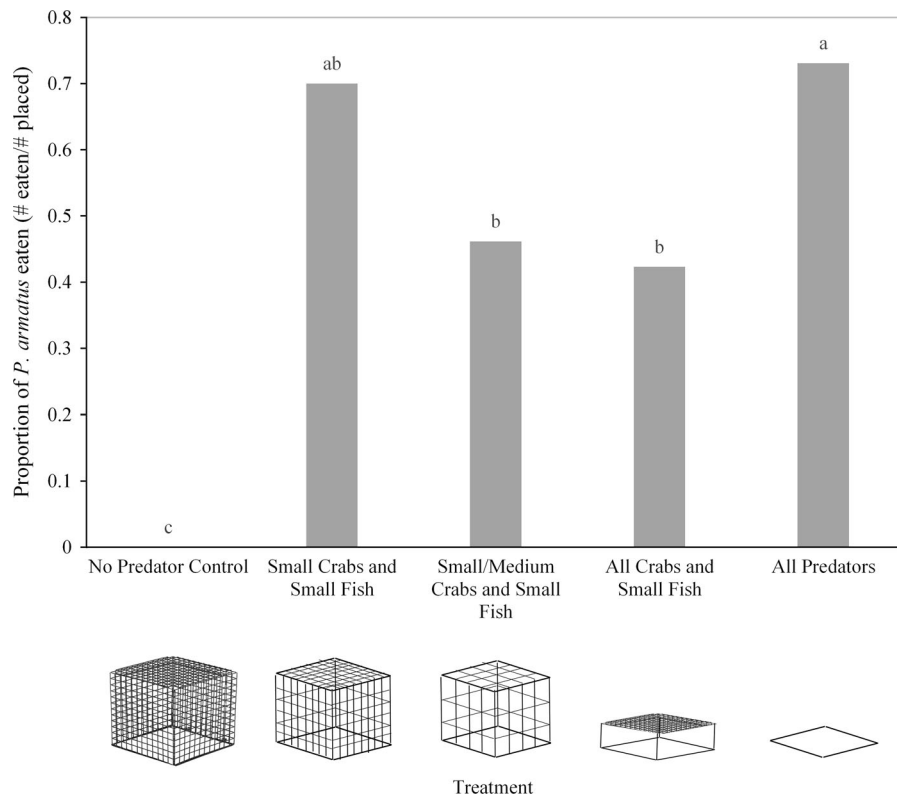


Fig. 5 Proportion of large *P. armatus* eaten by predators across the five different cage treatments. Treatments are named to reflect which predators could potentially access the tethered crab placed in the cage. Because the graph shows the proportion of large *P. armatus* eaten across the entire trial period, there are no

error bars. The letters above each treatment indicate significant differences between treatments at $\alpha = 0.05$ determined by a generalized linear mixed effects model. The number of replicate blocks was $n = 26$ for all treatments except “Small Crabs and Small Fish” treatment which had $n = 5$ replicates

practices of oysters, along with climate-induced changes in sea level (Beck et al. 2011). Thus, as habitat quality changes, we may expect the trophic interactions between *P. armatus* and native predators to change as well.

Predation on tethered *P. armatus* was higher at sites that had higher densities of adult *P. armatus* suggesting that predation on *P. armatus* is density-dependent. Other studies have similarly demonstrated that consumption of non-native prey by a native predator is often a function of the density of the invader (e.g., a predator functional response: Twardochleb et al. 2012; Charbonnier et al. 2014). Predators may avoid a non-native species when it is rare, but may increase consumption as it becomes more abundant relative to native prey (Magoulick and Lewis 2002). Alternatively, native predators might have more opportunity to learn how to capture and consume a non-native prey as it becomes more abundant and encounter rates with

the prey rise. From the perspective of the invasion process, density-dependent predation on non-native prey may be a mechanism that contributes to the invader’s escape from its natural enemies following introduction. For example, if native predators consume *P. armatus* less often when it is in lower densities, there could be a crucial reprieve from predation when *P. armatus* are first arriving at a site and in low abundance. This reprieve could allow *P. armatus* to increase in abundance and establish a population before native predators begin to readily consume *P. armatus*.

The high abundance of *P. armatus* at sites even with high predation suggests that predators may have limited influence to control *P. armatus* populations. Admittedly, tethering methods measure relative and not absolute mortality rates; however, our method tried to minimize artifacts as much as possible by allowing *P. armatus* to still access and use refuge

within the reef and conducting the trials over a short, 12-h timeframe. One way that other invaders have been shown to overcome predation by native predators is by exhibiting high propagule pressure (Colautti et al. 2007; Johnston et al. 2009). Specifically, for *P. armatus*, high recruitment (17,000–34,000 crabs per m²) has been previously suggested to nullify or counteract biotic resistance via competition that is faced by *P. armatus* when it invades a new system (Hollebone and Hay 2007b). Here we suggest that although high recruitment could increase predation risk (e.g., density-dependent predation), recruitment may ultimately be high enough to maintain positive population growth of *P. armatus*. Specifically, predation on *P. armatus* may only increase with density to a point beyond which predators become satiated (e.g., a type 2 or 3 functional response). A type 3 predator functional response has been observed with predation on invasive New Zealand mud snails (*Potamopyrgus antipodarum*) where control by predatory crayfish becomes saturated and unchanging despite higher prey abundances (Twardochleb et al. 2012). Examining how propagule pressure may interact with the native community to structure marine invasions is essential to better our understanding of the potential for biotic resistance of invasive species (Rilov and Crooks 2009).

The abundance of native predators appears in several top models (RVI = 0.55, Table 2), predicting lower rates of predation on *P. armatus* with higher abundance of predators. However, the effect of predator abundance was weak (i.e., low beta coefficient in Table 2 and no significant improvement in model fit with its inclusion), and the variable was not included in the top model. To the extent that this relationship is true, it could be due at least in part to an incomplete sampling of large predators. Or, some of this counterintuitive pattern could have arisen from predator interference. Specifically, increased abundance of predators could lower relative risk to prey due to higher competition among predators for prey resources, and negatively affect the ability of the native predator community to control prey (Sih et al. 1998; Griffen and Byers 2006). For example, the blue crab, *Callinectes sapidus*, alters the foraging behavior and predation rates of meso-predators (e.g., *P. herb-stii*) in the system (Seed 1980; Kneib 1982; Grabowski 2004). Even within a species, especially crabs, larger individuals are known to cannibalize smaller

individuals which can alter patterns of prey consumption (Perkins-Visser et al. 1996; Pintor and Byers 2015). Results from our predator exclusion experiment support that interference may have altered the influence of increasing predator abundance on *P. armatus*. Specifically, there was no linear increase in predation on tethered *P. armatus* when increasingly larger size classes of predators were able to access these prey (Fig. 5). For example, *P. armatus* mortality was equivalent in the small-mesh “Small Crabs and Small Fish” cage treatment where a smaller subset of the predator population had access compared to the open “All Predators” treatment. This may indicate that these smaller predator size classes experience interference from larger predators in treatments where larger individuals have access to the shared prey.

Finally, although we did not find evidence of biotic resistance from predation, the predatory community in salt marshes and mudflats varies seasonally which could lead to different patterns of predation throughout the year (Dahlberg and Odum 1970; McErlean et al. 1973; Hines et al. 1990). Our work was conducted in summer, when predatory pressure is most likely the highest and *P. armatus* is at its highest abundances (Hollebone and Hay 2007a). This means the annualized rate of loss of *P. armatus* due to predation would likely be far lower than the rates measured in our experiment. Although predatory pressure appears similar across this latitudinal range during the summer when temperatures are high and largely similar, there are sharper differences in temperature throughout this region in non-summer months (Byers et al. 2015). Also, there could be differences in timing of migration movements of predators during the cooler months that result in different predation patterns along the coast. If predation is lower in the cooler months, these seasonal differences could create a reprieve for *P. armatus* during the cooler seasons when predators are not around or forage differently. For example, blue catfish exhibit a distinct prey preference based on season, with individuals consuming more invasive zebra mussels during the summer months and native shad during the winter (Magoulick and Lewis 2002). This shift in diet was likely due to changes in prey profitability within the system, with predators switching to the more abundant prey (Magoulick and Lewis 2002).

In summary, our work exemplifies how biotic resistance can be examined experimentally on a large scale and emphasizes that high predation rates alone are not sufficient evidence of effective biotic resistance to an invasive species. Although the density of large *P. armatus* did not vary systematically with latitude, the decline in their abundance at the northern edge indicates that there is some limiting factor preventing *P. armatus* from spreading northward. Our results suggest that biotic resistance through predation although high, is not differentially higher at the northern edge, and thus is not likely limiting the abundance of *P. armatus* there. Instead, low temperatures remain a more likely limiting factor. As previously examined by Canning-Clode et al. 2011, *P. armatus* is a tropical species and so is unable to withstand the colder winter minimum temperatures associated with northern climates (Canning-Clode et al. 2011). As climates change and warmer temperatures extend farther north, we expect *P. armatus* to continue to spread northward (Canning-Clode et al. 2011) uninhibited by biotic resistance.

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