

# An invasive crab alters interaction webs in a marine community

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**Abstract** Over the last decade, the non-native, filter-feeding crab *Petrolisthes armatus* invaded oyster reefs of the South Atlantic Bight at densities of thousands  $\text{m}^{-2}$ . Mesocosm and field experiments demonstrated that *P. armatus* at  $\sim 10\text{--}75\%$  of mean summer densities: (1) suppressed growth of small oysters, biomass of benthic microalgae, and recruitment of native mud crabs, (2) enhanced oyster, mussel, and total bivalve recruitment, macroalgal cover, and survivorship of predatory oyster drills, but (3) did not affect native taxonomic richness. Laboratory feeding assays, field tethering experiments, and population changes in field and mesocosm experiments suggest that *P. armatus* is a preferred prey for native mud crabs and other consumers, thus relieving predation on native species and enhancing recruitment or survival of bivalves and oyster drills. In contrast, the invasive crab can consume crustacean larvae and via this

feeding may suppress recruitment of native mud crabs. Our findings should be conservative given the low densities of *P. armatus* seeded into experimental plots and our inability to run longer-term experiments due to controls rapidly being colonized by non-native crabs recruiting from the plankton. Invasive crabs commonly impact native communities via predation, but community impacts of this invasive crab may be as much due to its role as a preferred prey of native consumers as to its predation on native prey. Given that oysters are foundation species for shallow reefs in the South Atlantic Bight, the long-term effects of this invasion could be considerable.

**Keywords** Consumer–prey interactions · Invasive species · Oyster reefs · *Petrolisthes armatus* · South Atlantic Bight

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## Introduction

Species invasions are natural processes that shape communities over both ecological and evolutionary time (Vermeij 2005). Although, invasions have historically been impeded by natural barriers (Elton 1958), human activities have reduced these barriers, produced unparalleled rates of introductions, and caused serious threats to community structure and function (Sanders et al. 2003; Gurevitch and Padilla 2004).

Non-native species disrupt natural communities by establishing new ecological relationships and altering evolutionary pathways via competition (Callaway and Aschehoug 2000), genetic hybridization and introgression (Rhymer and Simberloff 1996; Lambrianos 2004), predation (Savidge 1987), facilitation (Simberloff and Von Holle 1999; Parker et al. 2006), or introducing new pathogens (Juliano and Lounibos 2005). Invasions can also displace or completely disassemble native communities (Nichols et al. 1990; Sanders et al. 2003). However, interactions between native and exotic species are not always destabilizing or detrimental. Invaders can form mutualisms with native species, contributing to the success of both parties (Mooney and Cleland 2001). Introduced species may also act as a trophic subsidy, providing alternative food to native consumers and altering food web dynamics (Maerz et al. 2005; King et al. 2006; Migge-Klein et al. 2006). Thus, invasions can produce a range of ecological and evolutionary responses from minimal to dramatic (Sax et al. 2005).

Non-native species are rapidly invading marine habitats worldwide, with some fundamentally altering native communities (Ruiz et al. 1997). Although marine systems are among the most heavily invaded (Carlton and Geller 1993), research on non-indigenous species in these habitats has developed more slowly than studies in terrestrial and freshwater systems (Groszholz 2002). Thus, less is known about the biotic interactions affecting invasions, or the consequences of invasions, within marine communities (Stachowicz et al. 2002). In this investigation we studied interactions between native species and a non-native crab invading oyster reefs in coastal Georgia, USA.

The green porcelain crab, *Petrolisthes armatus*, historically occurred in the tropical eastern Pacific, tropical western Atlantic, and off west Africa (Oliveira and Masunari 1995). In 1994, the crab progressed north of Cape Canaveral, Florida into estuaries of the South Atlantic Bight, and its densities increased rapidly within only months of this colonization (Knott et al. 2000; <http://www.dnr.sc.gov/marine/serc/P%20armatus%20SOM.pdf>). In 2004, mean densities of *P. armatus* in oyster reefs of Georgia and South Carolina were commonly several thousand crabs  $m^{-2}$  (Hollebone and Hay 2007a, b).

Despite their broad distribution, recent invasion, and high densities, little is known about the ecology

of *P. armatus* as an invader or its effects on native communities. Through mesocosm and field experiments, we explored the potential impacts of *P. armatus* on native oyster reef biota. We asked whether the presence of the crab affected: (1) native species richness, (2) the recruitment, growth or survivorship of native foundation species (e.g., oysters) and other common invertebrates and seaweeds, and (3) interactions among native species by serving as a trophic subsidy for native consumers?

## Methods

### Native and non-native consumer–prey interactions

*Petrolisthes armatus* is a filter-feeder that consumes detritus, algae, and zooplankton (Caine 1975). To determine if *P. armatus* would consume large planktonic prey and conspecific larvae, we placed seven adults *P. armatus* in separate 470 ml plastic containers and offered each a brine shrimp of about 7–10 mm in length followed by a conspecific larva (zoea) of similar size. Each item was placed into the crabs' mouth parts and observed for ~5 min to record consumption or rejection. If the conspecific larva was not consumed, the crab was offered another brine shrimp to test for possible satiation. Data on acceptance versus rejection were analyzed using a Fisher's Exact test with Yates correction (Zar 1999).

To see if common native predators would consume adult *P. armatus*, the fishes *Fundulus heteroclitus* [mummichog (40–60 mm SL),  $n = 16$ ] and *Leiostomus xanthurus* [spot (50–80 mm SL),  $n = 10$ ] and the crabs *Callinectes similis* [lesser blue crab (58–63.5 mm CW),  $n = 7$ ] and *Panopeus herbstii* [common mud crab (18–32 mm CW),  $n = 10$ ] were each offered a palatable control food (brine shrimp, commercial fish food, squid or oyster tissue) and then an adult *P. armatus*. If *P. armatus* was not eaten within 2 min of the food being offered, the consumer was offered a second palatable food to exclude rejection due to satiation. Acceptance was defined as the complete consumption of the crab. We used *P. armatus* of 4–6 mm CW for the mummichog, spot, and mud crab assays, and in five different size classes (<5, 5–6, 6.1–8, 8.1–9, and >9 mm CW) in the blue crab assays. Acceptance-rejection data were analyzed

by Fisher's Exact tests with Yates correction for continuity. Mud crabs fed slowly, so porcelain crabs were left in containers with mud crabs and standing seawater for 24 h and consumption was monitored periodically. For all other assays, consumers were individually held in 3.8 or 7.6 l perforated containers within a flow-through seawater table in the lab.

Native mud crabs (*Eurypanopeus depressus* and *P. herbstii*) occur at high densities within oyster reefs occupied by *P. armatus* (Hollebone and Hay 2007a). To assess mud crab preference for the invasive crab relative to native prey, 13 *P. herbstii* (21–36.5 mm CW) were housed individually in 470 ml containers (filled with ~200 ml seawater) with small (length: 12–19.5 mm) and large (24–34.5 mm) oyster drills (*Urosalpinx cinerea*), small (10.5–24.5 mm) and large (27–45 mm) mussels (*Brachidontes exustus*), and an adult porcelain crab (5–9 mm CW). Perforated lids prevented animal escape. Containers were monitored over 24 h to document which prey were consumed first by each crab. Data were analyzed using a *G* test.

To assess consumption of *P. armatus* in the field, we tethered porcelain crabs in oyster reefs and nearby mud flats during both night and day tidal inundation (~12 h). For each time and habitat, 15–20 porcelain crabs (4.5–11 mm CW) were tethered to separate 10 cm nails using 45 cm of monofilament line and superglue. Just prior to an incoming tide, nails with tethered crabs were pushed into the substrate; remaining crabs were retrieved ~12 h later as the tide receded. Survivorship was analyzed using a *G* test. Before this experiment, 20 tethered crabs were placed in a laboratory flume at a flow of  $\geq 5 \text{ cm s}^{-1}$  to assess tether failure and crab survivorship for 18 h. No tethers failed and survivorship was 95%, suggesting that crabs missing from the field tethers were eaten rather than dislodged.

## Mesocosms

Effects of *P. armatus* on growth and survivorship of oysters and mussels, and on recruitment of oyster-reef biota, were assessed in ten outdoor mesocosms ( $1.2 \times 1.2 \times 0.8 \text{ m}^3$ ) at the Georgia Institute of Technology's laboratory on Skidaway Island, GA. Mesocosms received unfiltered, flow-through seawater from the adjacent sound via a wave-generator at ~60 s intervals. Mesocosms were under a partially

transparent awning that lowered direct sunlight and prevented excessive heating. We simulated tidal exposure by draining tanks for 2.5–4 h  $\text{day}^{-1}$ .

Within each mesocosm, we placed three separate 23 cm wide  $\times$  30 cm long  $\times$  13 cm tall plastic containers filled with a 2 l volume of live oysters that were manually defaunated of other macro-organisms. These containers held *P. armatus* at densities of 0, 1,500 (100 crabs or ~55–75 g wet mass of crabs  $\text{container}^{-1}$ ), or 1,500+ crabs  $\text{m}^{-2}$  (100 crabs  $\text{container}^{-1}$  + 10 extra crabs  $\text{week}^{-1}$  for several weeks). In contrast, mean field densities of *P. armatus* occur at up to 11,000 crabs  $\text{m}^{-2}$  (Hollebone and Hay 2007a). We were unable to maintain crab densities above 1,500  $\text{m}^{-2}$ , and thus pooled data for the 1,500 and 1,500+ treatments. Each treatment also received ten measured (length) and individually labeled (Floy<sup>TM</sup> fish tags) oysters and mussels to assess impacts of *P. armatus* on the growth and survivorship of co-occurring filter-feeders. Growth was measured as change in length.

Blocking all treatments within each tank prevented confounding treatment- and tank-effects. Each treatment was randomly assigned an initial position in each tank, and the array was rotated counterclockwise every 2–3 days to avoid spatial bias. Each container had 47 cm tall walls of 0.17 cm mesh hardware cloth secured inside each container, making a wire basket that extended several cm above the surface of the water to prevent crab escape. Each basket was secured on a 20 cm tall concrete block to raise it above the anoxic mud that accumulated in the bottom of the tank, and small holes drilled in the bottom of each basket allowed slow drainage of water during simulated low tides. We included three randomly placed cylindrical subsamplers within each basket to allow minimally disruptive sampling of the communities. Subsamplers were constructed from the lower 2 cm of a plastic container (4 cm radius) and PVC-coated chicken wire (hexagonal shape,  $4.0 \times 2.5 \text{ cm}^2$ ). The chicken wire was cut to a height of 16 cm, formed into a cylinder, inserted into the container, and secured.

At weeks 2, 3, 4, 6, 7, 9, and 12, we randomly selected one subsampler from each basket, counted adult porcelain crabs, and returned the sampler and its contents to the original position. Each sampling period we rotated to a different sampler and returned to the original cylinder by week 6. Crabs were replenished

during the first 7 weeks if densities were low based on the mean density across all tanks for the addition treatment. For analyses, data were scaled to  $1 \text{ m}^2$  ( $14.5 \text{ baskets m}^{-2}$ ), assessed for normality (Ryan–Joiner test,  $P > 0.050$ ) and equality of variances ( $F$  test,  $P > 0.050$ ), and then analyzed using a repeated-measures ANOVA. Using the mean densities ( $\pm$ SE) of porcelain crabs at 3 weeks in the  $1,500 \text{ crabs m}^{-2}$  treatment ( $1,413.5 \pm 147.9 \text{ crabs m}^{-2}$ ) and  $0 \text{ crabs m}^{-2}$  in the 0 crab treatment as a benchmark against which to compare means at other time points, we performed individual two-tailed paired  $t$  tests to determine when crab density departed significantly from our treatment density goals.

To assess porcelain crab effects on native species recruitment, we noted native taxonomic richness during the assessment of porcelain crab densities at weeks 3, 6, 9, and 12. Richness data were analyzed as above using a two-way ANOVA.

To assess the effects of *P. armatus* on growth of native filter feeders at week 4, we measured all live, labeled mussels and oysters that could be acquired without disturbing the contents of the baskets. At week 12, we retrieved all labeled oysters and mussels and performed the same assessments. Data on growth and survivorship were analyzed using one-tailed  $t$  tests because we expected *P. armatus* to compete with native filter-feeders. If needed, data were arc-sine transformed to achieve normality and equality of variances. If variances were heterogeneous after transformation, we used Welch's modification to the  $t$  test.

*Petrolisthes armatus* filter-feeds, but also scrapes benthic surfaces (Caine 1975). Crab impact on benthic microalgae was assessed at weeks 2, 4, 6, 8, and 12 by scraping three randomly selected  $1 \text{ cm}^2$  areas on oyster surfaces from each mesocosm and using chlorophyll *a* as a proxy for biomass (modification of Parsons et al. 1984). Chlorophyll *a* measurements were log transformed and treatments compared via a two-way ANOVA.

At week 8, macroalgae (*Ulva* and *Enteromorpha* spp.) became abundant, so we quantified macroalgal cover at weeks 8 and 12 using a quadrat that fit the length and width of the basket and had 100 randomly located points. Treatment effects were compared using a two-tailed  $t$  test or Welch's modification, if appropriate after arc sine transformation.

#### Initial field study: summer 2004

We assessed the impact of *P. armatus* on oyster reef communities in a more natural setting by constructing experimental communities in the field. We constructed 12 replicated blocks of four community types as part of a larger study (Hollebone and Hay 2007b). Here we focus on two of these treatments: (1) a four native species community composed of oysters (*Crassostrea virginica*), mussels (*B. exustus*), mud crabs (*P. herbstii*), and oyster drills (*U. cinerea*) and (2) the same four native species community with the addition of the equivalent of 750 *P. armatus* adults ( $\geq 5.5 \text{ mm CW}$ )  $\text{m}^{-2}$ . Each community was established in  $29 \times 23 \text{ cm}$  plastic baskets with six 1.5 cm holes in their sides and an open top that was covered with PVC-coated wire mesh (2.5 cm openings) to prevent oyster wash-out by physical disturbance. Three subsamplers within each basket allowed periodic sampling with minimal disruption of the community.

Before placing communities in the field, all oysters and mussels were manually defaunated of macroorganisms, and the CW of all seeded mud and porcelain crabs were measured. Communities were established with natural densities of native organisms, determined from local monitoring efforts (Hollebone and Hay 2007a). Each community was composed of 1.5 l of live oysters, 10 mussels, 15 oyster drills (labeled with red paint on upper edge of aperture), and three large ( $>18 \text{ mm CW}$ ) and five small (10–18 mm CW) mud crabs. Ten labeled and measured oysters and mussels were included in each community.

We placed the spatially blocked communities on three mud flats near Savannah, GA (locations: N  $31^\circ 57.042'$ , W  $80^\circ 58.982'$ ; N  $31^\circ 56.739'$ , W  $80^\circ 58.641'$ ; N  $31^\circ 57.618'$ , W  $80^\circ 57.006'$ ). These mud flats lacked oyster reefs, thus limiting colonization to recruitment from the plankton. All blocks were  $\geq 20 \text{ m}$  from the nearest oyster reef or other replicate blocks, and each basket was 5 m from its within-block neighbor. Community types were randomly allocated within each block, baskets anchored with rebar stakes along a transect 0.3–0.5 m above mean lower low tide, and oriented lengthwise to the incoming tide.

Communities were monitored at weeks 2, 4, 8, and 12. Due to the 2–4 h of working time at low

tide, only 6 of the 12 blocks were sampled each period. Every other block was sampled so that representative blocks from all three mud flats were assessed and no two adjacent blocks were used. Sampled blocks were alternated for the next sampling period.

We followed juvenile recruitment, densities of adult *P. armatus*, and native taxonomic richness over time by randomly selecting one subsampler per basket each assessment period. Organisms within the subsampler were retained using a 500  $\mu\text{m}$  sieve; porcelain crabs were counted, sized (as  $\geq 5.5$  or  $< 5.5$  mm CW), and sexed (those crabs  $\geq 5.5$  mm CW), and all materials and organisms returned to the basket within the original sampler. We also obtained benthic microalgae for chlorophyll *a* analysis, as described previously.

At week 12, baskets were collected (except for two blocks that had been covered by shifting sediments), smaller organisms from one of the subsamplers enumerated, and macrofauna sorted from the remainder of each basket. Growth and survivorship of labeled oysters and mussels were assessed. Crabs were counted, sexed, and measured (CW). Marked oyster drills were identified as alive or dead, and growth was measured as the distance between the red paint and the aperture. Oyster recruitment was assessed as the number of juvenile oysters per area of each labeled (previously defaunated) oyster. Oyster shell surface area was determined by wrapping the animal in aluminum foil, cutting this to size, removing and flattening the foil, and measuring its area five times with a LI-COR, LI-3100 area meter.

One-tailed *t* tests assessed these data when we anticipated that *P. armatus* would suppress native species due to competition, consumption or disturbance of settling larvae. Two-tailed tests were used when there was no basis to predict a direction of change. Changes in density of non-native crabs, and of non-native crab effects on native species richness and microalgal biomass over time, were assessed via two-way ANOVA. Recruitment of all bivalves combined and of individual bivalve species, as well as the survivorship of oyster drills (arc-sine transformed) between communities initially with and without *P. armatus* was assessed using one-tailed *t* tests or the Mann–Whitney non-parametric test (clams) depending on distribution of the data.

Field study: summer 2005

During the 12 weeks field experiment of 2004, we could not assess *P. armatus* effects on oyster growth because the crab recruited to our controls at high densities in only 2–4 weeks. In 2005, we repeated the field experiment for only 4 weeks using baskets composed of: (1) defaunated oysters or (2) similar oysters seeded with adult porcelain crabs ( $\geq 5.5$  mm CW,  $\sim 1,200$  crabs  $\text{m}^{-2}$ ). This higher density ( $1,200$  crabs  $\text{m}^{-2}$  vs.  $750$  crabs  $\text{m}^{-2}$ ) more closely approximated summer field densities ( $\sim 1,000$ – $11,000$   $\text{m}^{-2}$ ; Hollebone and Hay 2007a).

To limit sorting time, we halved the size of baskets by securing 0.6 cm plastic mesh across their center. Half of each basket was filled with defaunated live oysters and treatment-specific crabs; the other half remained empty. Treatments were assigned randomly to a position in each of 10 pairs arrayed linearly along the intertidal. Each array was  $\geq 20$  m from the nearest oyster reef,  $\geq 10$  m from neighboring arrays, and baskets within a pair were 5 m from each other. All treatments were  $\sim 0.5$  m above mean lower low tide. After 4 weeks, labeled oysters were measured to assess growth, and treatment effect was assessed via a one-tailed paired *t* test because the mesocosm study indicated that porcelain crabs suppressed oyster growth.

## Results

In mesocosms, we observed *P. armatus* both scraping benthic surfaces and filter feeding. When offered similar sized brine shrimp and conspecific zoea, all *P. armatus* consumed brine shrimp but only 2 of 7 consumed conspecific zoea ( $P = 0.020$ , Fisher's Exact test, Yates correction for continuity).

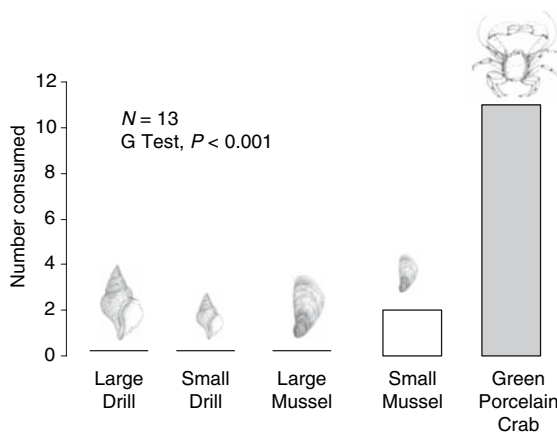
All native consumers except spot readily ate adult *P. armatus*. Sixteen of 16 mummichogs, seven of seven lesser blue crabs, and seven of ten mud crabs consumed the invasive crabs (the blue crabs doing this across all size ranges). Only one of ten spot consumed the invasive crab, but all consumed the control food, both just before and after rejecting the crab ( $P < 0.001$ , Fisher's Exact test, Yates correction for continuity).

The native mud crab *P. herbstii* co-occurs with the invasive crab in oyster reefs (Hollebone and Hay

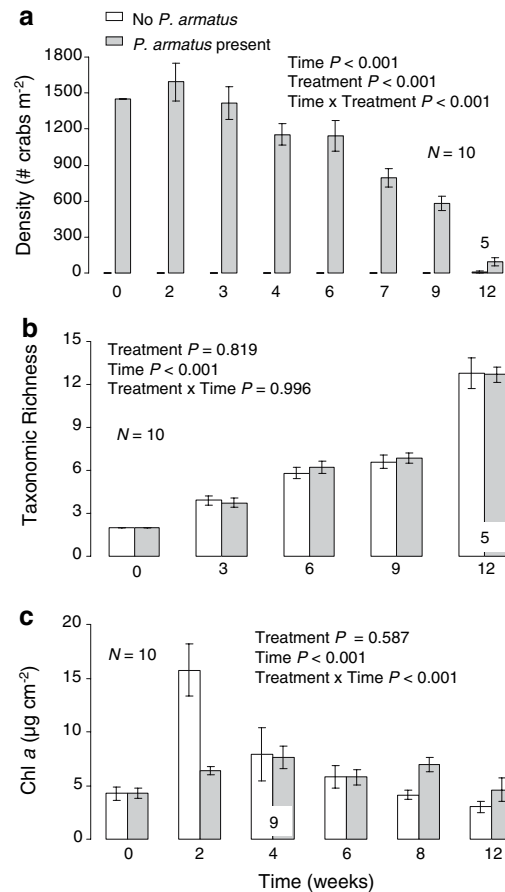
2007a). In laboratory assays, the native crab consumed the invasive crab in preference to native mussels and oyster drills ( $P < 0.001$ ,  $G$  test, Fig. 1). The invasive crab was also consumed when tethered in the field. Ninety and 95% of crabs on mudflats were consumed during the day and night, respectively, whereas 95 and 60% of crabs in oyster reefs were consumed during the day and night, respectively ( $P = 0.023$ ,  $G$  test).

In our mesocosm experiment, non-native *P. armatus* did not recruit to the 0 crabs  $m^{-2}$  treatment during the first 9 weeks, and recruited only  $9 \pm 6$  (mean  $\pm$  SE) crabs  $m^{-2}$  by week 12. Mean density in the 1,500 crabs  $m^{-2}$  treatment held relatively steady at  $\sim 1,200$ – $1,600$  crabs  $m^{-2}$  for the first 6 weeks (likely aided by crab additions during early weeks), but then declined considerably (Fig. 2a). Densities in the crab addition treatments always exceeded those in the control ( $P < 0.001$ , Fig. 2a), but dropped significantly by week 7 when compared with week 3 ( $P = 0.002$ , two-tailed paired  $t$  test).

Presence of *P. armatus* had no effect on the richness of recruiting native taxa ( $P = 0.819$ , Fig. 2b), but did suppress a microalgal bloom at week 2 ( $P < 0.001$  for the interaction term, Fig. 2c) and facilitated macroalgae (*Ulva* and *Enteromorpha spp.*) by 1.6 $\times$  and 9.4 $\times$  at weeks 8 and 12, respectively ( $P \leq 0.001$ , Fig. 3). Presence of *P. armatus* suppressed mud crab recruitment by 35–66% ( $P = 0.041$ , Fig. 4a) during weeks 3–6, with native



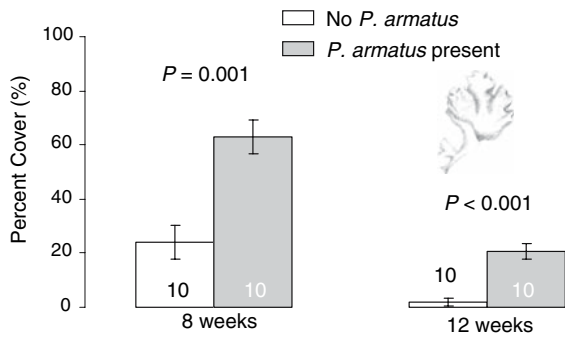
**Fig. 1** Laboratory choice feeding assay showing the number of prey consumed first by 13 separate *Panopeus herbstii*.  $P$ -value from the  $G$  test



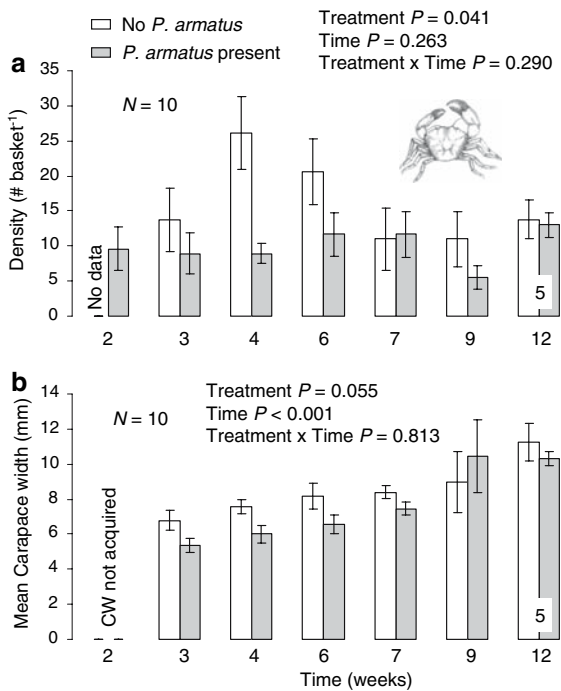
**Fig. 2** **a** Mean densities (scaled to 1  $m^2$ ,  $\pm$ SE) of adult *Petrolisthes armatus* in the mesocosm treatments over 12 weeks. **b** Mean native taxonomic richness ( $\pm$ SE). **c** Mean microalgal biomass ( $\pm$ SE) on oyster surfaces.  $N = 10$  unless otherwise indicated at the base or just above the bars.  $P$ -values from two-way ANOVAs

crabs also tending to be smaller in the presence of *P. armatus* ( $P = 0.055$ , Fig. 4b).

*Petrolisthes armatus* suppressed growth of small oysters (initial length  $\leq 60$  mm) by 84% during the first 4 weeks of the mesocosm experiment ( $P = 0.048$ , Fig. 5a). They had no effect on growth of small ( $\leq 30$  mm) mussels ( $P = 0.231$ , one-tailed  $t$  test, Fig. 5b). Growth of a larger size range of oysters (30–90 mm) decreased by a non-significant 51% (mean  $\pm$  SE,  $1.7 \pm 0.9$  mm without crabs and  $0.8 \pm 0.4$  mm with crabs;  $P = 0.204$ , one-tailed  $t$  test with Welch's modification). Growth across larger size classes of mussels (22–42 mm) was also unaffected by crabs at either 4 weeks ( $1.6 \pm 0.2$  mm both with and without porcelain crabs) or 12 weeks

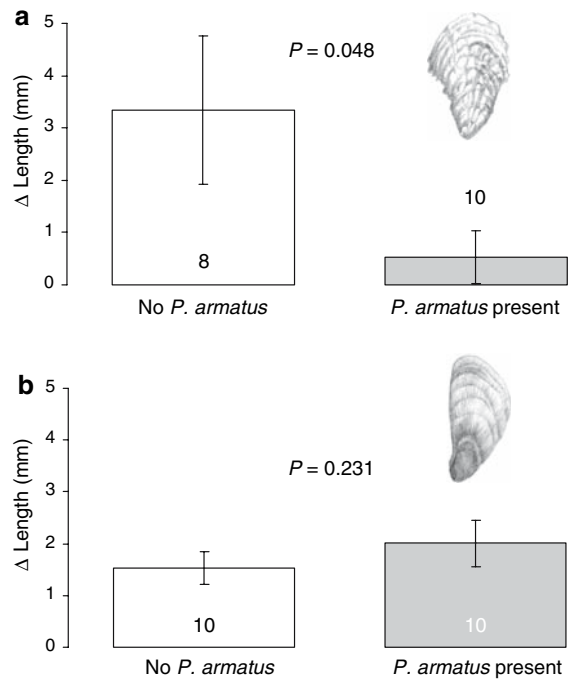


**Fig. 3** Macroalgal cover (mean  $\pm$  SE) at 8 and 12 weeks in the mesocosm experiment. *N* shown within or directly above the bars. *P*-values from two-tailed *t* tests with Welch’s modification to the 12 weeks data



**Fig. 4** **a** Mean density (scaled to one basket,  $\pm$ SE) of newly recruited mud crabs in the mesocosm experiment over 12 weeks. **b** Mean carapace width ( $\pm$ SE) of mud crabs. *N* = 10 unless indicated at the base of the bars. *P*-values from two-way ANOVAs

( $4.0 \pm 0.4$  mm with and  $4.2 \pm 0.5$  mm without porcelain crabs) ( $P \geq 0.204$  for 4 and 12 weeks, one-tailed paired *t* test). At week 12, we recovered only  $22 \pm 3\%$  and  $16 \pm 4\%$  of labeled oysters from treatments with and without *P. armatus*, respectively. Low recovery may be due to either oyster death or tag



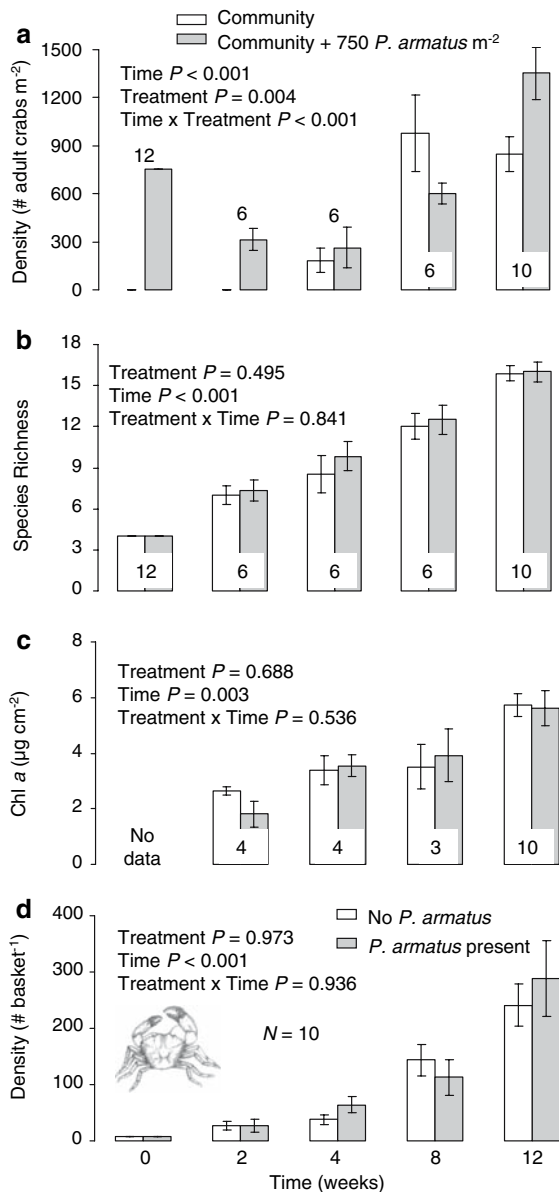
**Fig. 5** **a** Mean growth ( $\pm$ SE) of small oysters (initial length  $\leq 60$  mm) in the mesocosm experiment after 4 weeks. **b** Mean growth ( $\pm$ SE) of small mussels (initial length  $\leq 30$  mm). *N* shown within or directly above the bars. *P*-value for oysters from a one-tailed *t* test with Welch’s modification, for mussels from a one-tailed paired *t* test

detachment. This low recovery prevented analysis of oyster growth over the total 12 weeks. Mussel survivorship over 12 weeks did not differ as a function of *P. armatus* ( $74.0 \pm 4.1\%$  with and  $69.0 \pm 5.9\%$  without the crab;  $P = 0.400$ , one-tailed paired *t* test).

Decline of *P. armatus* in the mesocosms starting at about week 7 (Fig. 2a), coincided with mud crabs growing to mean sizes of 7.5–11.5 mm CW, but with some being 13, 24, and 32 mm CW at weeks 7, 9, and 12, respectively. Such mud crabs will consume invasive crabs and native oysters, possibly producing declines of both *P. armatus* and marked oysters.

When we constructed small oyster reefs on isolated mudflats in the field, rapid recruitment and growth of *P. armatus* compromised our controls within the first 4 weeks. Between weeks 4 and 12, densities of adult crabs ( $>5.5$  mm CW) in control treatments were 180–980 crabs  $m^{-2}$  (Fig. 6a). In communities initially stocked with 750 *P. armatus*  $m^{-2}$ , crab ( $\geq 5.5$  mm CW) densities declined at

weeks 2 and 4 (to about 315 crabs  $m^{-2}$ ) but rebounded to 600–1,350 crabs  $m^{-2}$  at weeks 8 and 12. Densities differed significantly between our treatments until week 2 ( $P = 0.004$ , one-tailed paired  $t$  test) but not thereafter ( $P > 0.050$ ). Despite this loss of treatment, we did observe time-lagged impacts of



**Fig. 6** The 2004 field experiment. **a** Mean densities ( $\pm$ SE) of adult *Petrolisthes armatus* ( $>5.5$  mm CW). **b** Native taxonomic richness. **c** Microalgal biomass on oyster surfaces. **d** Density of newly recruited mud crabs  $basket^{-1}$ . If  $N$  varied, it is shown within or above each set of bars.  $P$ -values from two-way ANOVAs

the crab between weeks 4 and 12; impacts that are likely conservative.

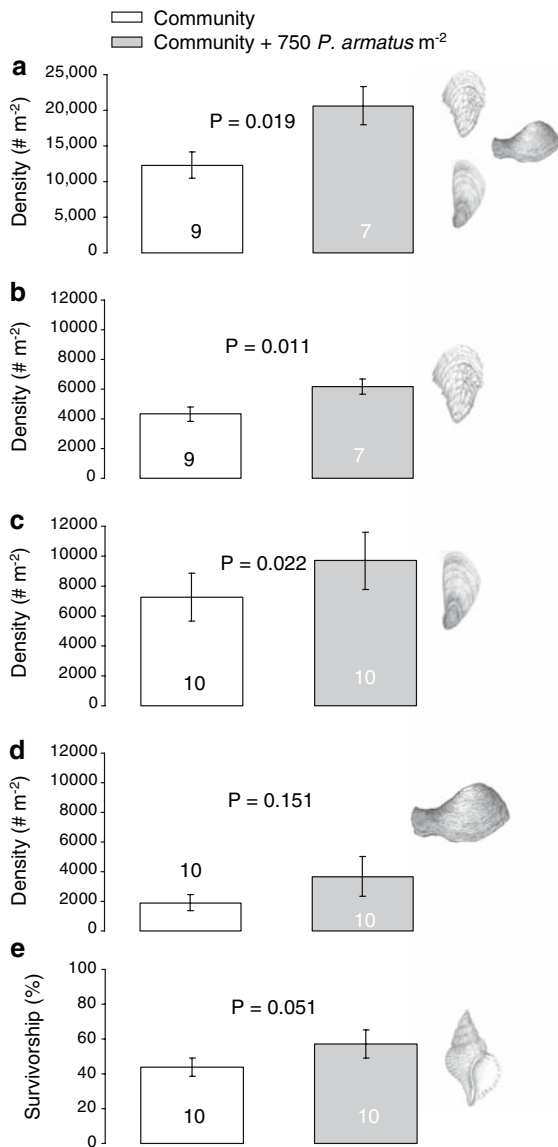
As in the mesocosm experiment, invasive crabs did not affect native taxonomic richness in the field ( $P = 0.495$ , Fig. 6b). Invasive crabs also did not affect microalgal abundance ( $P = 0.688$ , Fig. 6c), but the sample size constrained statistical power. In contrast to mesocosm results, the invasive crab did not affect mud crab recruitment in the field ( $P = 0.973$ , Fig. 6d).

Invasive crabs enhanced the recruitment of bivalves by 68% ( $P = 0.019$ , one-tailed  $t$  test, Fig. 7a), oysters by 43% ( $P = 0.011$ , Fig. 7b), mussels by 34% ( $P = 0.022$ , Fig. 7c), and Antillean sphenia clams by a non-significant 93% ( $P = 0.151$ , Mann–Whitney test, Fig. 7d). Survivorship of oyster drills was 30% higher in the treatment seeded with *P. armatus* ( $P = 0.051$ , one-tailed paired  $t$  test, Fig. 7e). These patterns are consistent with the hypothesis that native mud crabs prey preferentially on invasive crabs (Fig. 1), thus reducing their impact on native prey. *P. armatus* did not affect oyster drill growth; drills grew  $7.7 \pm 1.6$  mm and  $7.5 \pm 1.4$  mm with and without porcelain crabs, respectively ( $P = 0.478$ , one-tailed paired  $t$  test).

Our 4 weeks field experiment in 2005 confirmed our earlier mesocosm results. Small oysters ( $\leq 50$  mm) grew 22% less in the presence of *P. armatus* ( $P = 0.040$ , one-tailed paired  $t$  test, Fig. 8).

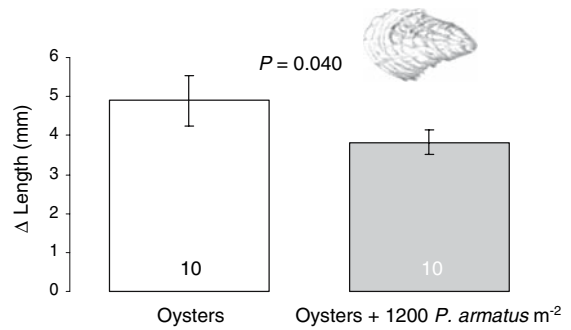
## Discussion

Biological invasion is a natural occurrence affecting the ecology and evolution of all ecosystems (Vermeij 2005); however, the unnatural pace of recent biological invasions threatens the function and maintenance of native communities (Carlton and Geller 1993) and can fundamentally change marine communities over large geographic areas (Ruiz et al. 1997). Over the past decade, *P. armatus* has invaded oyster reefs in the South Atlantic Bight and increased from  $\sim 1$  to as many as 11,000 crabs  $m^{-2}$  (Hollebone and Hay 2007a). Given that oysters are foundation species for inshore, hard-substrate communities of this region and that loss of oyster reefs has caused large-scale ecosystem change in other areas of the Atlantic (e.g., Rothschild et al. 1994; Kurlansky 2006), an invasion at such high densities raises concerns.



**Fig. 7** Density of newly recruited bivalves or survivorship of marked oyster drills after 12 weeks in the 2004 field experiment: **a** Total bivalves, **b** oyster (*Crassostrea virginica*), **c** mussel (*Brachidontes exustus*), **d** clam (*Sphenia antillensis*), and **e** oyster drill (*Urosalpinx cinerea*). *N* shown within or above each bar. *P*-values from one-tailed *t* tests of unequal sample size for (a) and (b), one-tailed paired *t* test for (c), Mann–Whitney non-parametric test for (d), and arc-sine transformed, one-tailed paired *t* test for (e). Oyster settlement could only be followed on marked oyster surfaces cleaned of juvenile bivalves at the experiment’s initiation. Marked oysters were lost from some replicates, thus lowering the sample size for some analyses

Our field and mesocosm studies used *P. armatus* at densities of 750–1,500 crabs m<sup>-2</sup>, which is toward



**Fig. 8** Growth ( $\pm$ SE) of small oysters ( $\leq 50$  mm) in the field with and without the invasive crab. *N* shown within each bar. *P*-value from a one-tailed paired *t* test

the lower end of the natural density range in Georgia and South Carolina (Hollebone and Hay 2007a). Additionally, we could prevent *P. armatus* from invading our controls for only a few weeks; this minimized control—treatment differences and may have limited the impacts detected. Despite these constraints, *P. armatus* significantly impacted almost every common native species. They suppressed the growth of juvenile oysters, the recruitment of mud crabs, and the abundance of microalgae, while enhancing recruitment of total bivalves, oysters, and mussels, the abundance of macroalgae, and the survivorship of oyster drills. For effects on macroalgae, microalgae, and mud crab recruitment, we detected effects in mesocosms but not field experiments; this may be related to our ability to keep mesocosm controls relatively free of *P. armatus* for 12 weeks while rapid recruitment in the field compromised control treatments by week 4.

Although it is desirable to understand the mechanisms driving these impacts, we were unable to rigorously investigate these mechanisms under natural conditions due to our inability to maintain controls without invasive crabs in the field. Despite this difficulty, suppression of oyster growth is consistent with (1) oysters and porcelain crabs competing for a common food, and/or (2) the high density of crabs disturbing oysters and causing closure and loss of feeding time. In mesocosms, porcelain crabs suppressed growth of small oysters by 84% within 4 weeks compared to only 22% under field conditions. This difference in effect size could be due to our better ability to maintain controls free of *P. armatus* in mesocosms, or due to differing food

levels or delivery rates between field and mesocosm experiments. However, it is interesting that we did not detect a similar effect on filter feeding mussels. Because mussels can detach and reattach, they may have moved into areas under-utilized by *P. armatus*, thus lessening competition. Our effect sizes are likely conservative because mean summer densities of *P. armatus* can be  $\geq 7\times$  the highest densities we used in our experiments (Hollebone and Hay 2007a). Higher densities of crabs over longer periods of time might more strongly suppress oyster growth or impact larger size classes. Suppression of growth could keep oyster recruits in small size classes which are more susceptible to physical (Stanley and Sellers 1986) and biotic stresses (Brown 1997), potentially limiting the growth of oyster reefs, the biogenic structure upon which many other species rely (Lenihan and Peterson 1998).

Although *P. armatus* can consume larvae as evidenced by their willingness to eat brine shrimp, presence of *P. armatus* enhanced rather than retarded recruitment of native bivalves as a group, and of oysters and mussels specifically (Fig. 7a–d). Thus, the crabs either: (1) avoided consuming bivalve larvae, as appears to be the case for conspecific larvae, or (2) their removal of biofilms from surfaces enhanced bivalve recruitment more than their feeding removed larvae. Additionally, and consistent with laboratory assays (Fig. 1), *P. armatus* may serve as alternate prey for native predators that would typically consume juvenile bivalves and other invertebrates such as oyster drills. Mud crabs commonly prey on native oysters, mussels, and snails (Lee and Kneib 1994), but consumed *P. armatus* in preference to native prey in the lab (Fig. 1). Given the tremendous densities, palatability, and rapid recruitment of *P. armatus*, mud crab consumption may be shifting from native to introduced prey, thus increasing survival of native prey. In contrast to enhancing recruitment of native bivalves, *P. armatus* initially suppressed recruitment and growth of juvenile mud crabs in the mesocosm experiment (Fig. 4). Given their rapid consumption of brine shrimp, it is plausible that adult *P. armatus* are directly consuming mud crab larvae. However, once some settlers grow larger, this relationship may reverse, with mud crabs becoming major consumers of the invasive crabs (Fig. 1).

*Petrolisthes armatus* are eaten by native consumers as evidenced by: (1) the rapid and preferential rate

at which it is attacked in laboratory assays (Fig. 1), (2) its rapid decline as predatory mud crabs increase in number and size in the mesocosm experiment (compare Figs. 2a, 4), and (3) its rapid disappearance when tethered in the field. Our tethering procedures may yield unnaturally high consumption rates because the tethers limit mobility of the crabs and may attract the attention of consumers. *P. armatus* are thin, fast moving, and easily autotomize their limbs when attacked. These traits may minimize predation as *P. armatus* shelters within the interstices of oyster reefs; tethers may have constrained these escape strategies or visually attracted predators. However, the high densities of the invasive crab and native mud crabs in the same zone of oyster reefs (densities up to  $\sim 11,000$  and  $1,600$  crabs  $m^{-2}$ , respectively; Hollebone and Hay 2007a) suggest that contact will be common. *P. armatus* may be able to sustain high losses, due to rapid recruitment and growth. In our 2004 field study, *P. armatus* recruited at mean densities of  $\sim 17,000$ – $35,000$  crabs  $m^{-2}$  in only 12 weeks, with some baskets recruiting up to  $\sim 60,000$  crabs  $m^{-2}$  (Hollebone and Hay 2007b).

In the mesocosm experiment, *P. armatus* initially suppressed microalgal biomass (Fig. 2c), but later facilitated macrophytes such as *Ulva* and *Enteromorpha* spp. whose cover increased by 160–940% (Fig. 3). Similar patterns have been documented for other crustacean grazers that facilitate macrophytes by removing filamentous algae (Brawley and Adey 1981); scraping of surfaces by *P. armatus* could have similar effects. The macrophyte bloom we noted in the mesocosms did not occur in our field experiments, suggesting that herbivores or physical stresses missing from our mesocosm treatments may remove macrophytes in the field.

During the past decade, *P. armatus* invaded oyster reefs in the South Atlantic Bight at mean densities of up to  $11,000$  crabs  $m^{-2}$  (Knott et al. 2000; Hollebone and Hay 2007a). They directly and indirectly affect native foundation species, and nearly all common native species, via both feeding and being fed upon. Their long-term, summed effects on oyster reef communities are unclear. They suppress juvenile oyster growth and enhance survivorship of oyster predators such as oyster drills, but enhance oyster recruitment (potentially due to serving as an alternative, preferred prey for native consumers). Our documented effects should be conservative due to

the relatively low numbers of crabs we seeded into experimental plots and the short duration of our experiments. The summed impacts of the contrasting effects of this invader on natural communities over the long-term under field conditions could not be rigorously determined due to massive recruitment of the invasive crab, which prevented the maintenance of control reefs without the crab.

Invasive crabs commonly alter native community structure and the trajectory of the evolution of prey defenses via their strong impacts as predators (Seeley 1986; Trussell and Smith 2000). Here the crab's impact as prey may rival or exceed its impact as a consumer.

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