

## Predation risk predicts use of a novel habitat

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Predator–prey interactions are often highly co-evolved, with selection over time for prey with morphological and behavioral traits that minimize predation risk. Consequently, in many environments prey choose among potential habitats according to their refuge value. It is unclear, however, when presented with new habitats, if prey are able to evaluate the predation risk of these relative to familiar habitats and utilize these in accordance with their value. We tested whether, along the east coast of the USA, native mud crabs *Panopeus herbstii* utilize the non-native alga *Gracilaria vermiculophylla* according to its relative refuge value. Experiments examining predation by blue crabs *Callinectes sapidus* on mud crabs revealed that the non-native alga had an intermediate refuge value relative to native oysters, which were the most protective, and unvegetated sediment, which was the least. In subsequent choice experiments, mud crabs selected oysters over alga over unvegetated sediment, in accordance with habitat refuge values. Further, in field experiments, the use of *Gracilaria* by mud crabs was inversely related to the proximity of the alga to the preferred habitat type, oysters, and was reduced by the presence of a blue crab predator. Consequently, mud crabs are utilizing the non-native alga *Gracilaria* in accordance with its intermediate refuge value. The relative refuge value of non-native vs native habitat-forming species may provide a baseline expectation against which to measure the speed of learning and opportunism in the response of native prey to novel protective habitats.

Predation is a key selective force on morphological and behavioral traits of prey (Abrams 2000). Traits such as armor-ing and chemical defenses, crypsis and behavioral avoidance of predation have a major influence on fitness in environments with high levels of predation (Sih 1987, Abrams 2000). Among these behavioral traits is the ability to select and occupy habitats that minimize predation risk in environments where predator densities are high (Werner et al. 1983, Lima and Dill 1990). Consequently, in environments in which predators are dense and food resources are not constraining, motile organisms should be adapted to select those habitat patches with the greatest refuge value (Gilliam and Fraser 1987). Along with the shape and size of habitat patches, patch structure and location are among those factors that influence the refuge value of habitat patches. In general, prey survival increases with the complexity of habitat and its availability (Heck and Thoman 1981, Crowder and Cooper 1982, Grabowski 2004).

Invasions of foundation species introduce novel biotic habitats to their recipient environments, which may be complex in structure (reviewed by Rodriguez 2006). A growing number of studies indicate that these non-native foundation species can serve as refuges for native prey species (Carroll et al. 2010, Neira et al. 2006, Byers et al. 2010). It is unclear, however, whether native species are able to assess the relative refuge value of these non-native species as compared to native biogenic habitat, and select between these and native biogenic habitats in accordance. Where the

non-native species is morphologically similar to native biogenic habitats, it may be readily recognized as habitat and utilized in accordance with its refuge value. Where the introduced species is morphologically, ecologically, and phylogenetically unrelated to native species, discrimination among habitats based on predation risk may, however, be difficult. In this latter scenario, the non-native species may never be used in accordance with its refuge value, or only after learning or evolutionary change.

The red alga *Gracilaria vermiculophylla* is native to the northwest Pacific, but has established non-native populations on the east and west coasts of the USA and in Europe. Along the mid-Atlantic coast, the coarsely-branched alga that was first recorded in Virginia in 1988 (Nettleton et al. 2013) is commonly associated with the polychaete *Diopatra cuprea* which actively incorporates *G. vermiculophylla* into its tube cap that protrudes above the sediment surface (Thomsen and McGlathery 2005). This facilitation of the alga by the tube worm, along with the alga's ability to tolerate desiccation, burial and grazing (Thomsen and McGlathery 2007), enables it to persist on intertidal mudflats, including those of South Carolina and Georgia that are otherwise devoid of macrophytes, including seagrass and other habitat-forming macroalga (Byers et al. 2012). A diversity of invertebrates and juvenile fish use the alga as habitat (Thomsen et al. 2009, Byers et al. 2012, Wright et al. 2014). Among the species that utilize *G. vermiculophylla* as habitat is the mud crab, *Panopeus herbstii* (Thomsen et al. 2009). Mud

crabs experience reduced rates of predation within complex native biotic substrates, such as oysters and marsh grass (Dittel et al. 1996), and may associate with the non-native alga due to its refuge value.

Here we assess whether mud crabs, which lack an evolutionary history with *G. vermiculophylla*, utilize patches of the non-native alga according to its relative refuge value as compared to surrounding patches of muddy habitat or of the native oyster, *Crassostrea virginica*. First, we conduct predation experiments to assess the relative value of the three types of habitat in protecting the mud crab from the blue crab *Callinectes sapidus*, an abundant intraguild predator of mud crabs on the mud flats of the southeastern USA (Grabowski et al. 2008, Hill and Weissburg 2013), which can also be found in association with oyster reef (Grabowski et al. 2008) and *G. vermiculophylla* (Johnston and Lipcius 2012). Based on the structure of the habitat provided by *G. vermiculophylla*, which is complex but does not provide rigidity, sharp-edged defenses, nor interstices that are as well matched to the body size of mud crabs as oyster reef, we predict that it will be of intermediate refuge value to the oyster and mud flat habitats. Second, we conduct habitat selection experiments, in the presence and absence of blue crabs, to test whether mud crabs select between the three habitat types on the basis of their refuge value, and whether the presence of a predator has stronger effects on habitat occupancy than habitat type. Third, we conduct a field experiment to assess how mud crab utilization of *G. vermiculophylla* varies in the field according to the presence of blue crabs, and the proximity of alternative habitat of greater refuge value. As *G. vermiculophylla* has few to no native analogues on mudflats of the southeastern USA, this system offers the opportunity to rigorously test whether native species are able to utilize non-native invaders in accordance with their refuge value.

## Material and methods

### Refuge value of habitats

To assess the relative refuge value of native and non-native habitats, we compared rates of *Callinectes sapidus* predation on mud crabs, *Panopeus herbstii*, among eastern oyster *Crassostrea virginica*, algal *Gracilaria vermiculophylla* and mud substrates.

Predation experiments were run in replicate 60 cm long  $\times$  40 cm wide  $\times$  23 cm high plastic tubs, filled to a depth of 5 cm with freshly collected sediment from the intertidal mudflat at Priests Landing, Skidaway Island, Georgia (31°96'29"N, 81°01'33"W). Sediment was kept upright and intact to maintain sediment properties. Tub designated to the oyster treatment received 8 l of sun-bleached and hence defaunated *Crassostrea virginica* shell, arranged in small clumps of 8–12 oysters, that was placed on the surface of the mud. This volume of oysters was sufficient to provide 100% cover of oysters, of vertical relief of 10–15 cm, and was based on the mean biomass of oysters at Priests Landing in 0.25 m<sup>2</sup> quadrats with 100% cover. Replicates assigned to the algal treatment received 1.5 l of *G. vermiculophylla* freshly collected from Priests Landing and defaunated by rinsing the alga in fresh water and hand removing remain-

ing invertebrates. The volume of *Gracilaria* provided 100% cover of the mud when the tanks were drained and, as with the oyster treatment, was based on the mean biomass per 0.25 m<sup>2</sup> quadrat of *Gracilaria* on sections of mudflat with 100% cover of algae at low tide. Although at low tide this volume of alga provided minimal vertical relief, at high tide the alga becomes erect due to its buoyancy. The treatments were meant to standardize the percent cover of each habitat-forming species and in realistic quantities that represent the higher end of what is naturally encountered by the mud crabs in the field. By defaunating oysters and algae, the availability of alternative prey items for blue crabs was kept constant across experimental treatments. Tanks were filled with unfiltered, aerated seawater, and covered with 5 mm nylon mesh to prevent escape of crabs.

To each tub (n = 10 for oyster and algal treatments, n = 9 for mud treatment), we added ten mud crabs of carapace width 10–15 mm that had been collected during the previous two days from intertidal oyster reefs at Priests Landing. This density of mud crabs was within the range observed on the Priests Landing intertidal oyster reef. Mud crabs were given ~30 min to bury into the substrate before a single male blue crab of ~10 cm carapace width was added to each tub. Blue crabs had been trapped in intertidal and shallow subtidal waters at Priests Landing during the two weeks prior to the trial and were fed oyster tissue ad libitum until 48 h prior to the experiment. Tubs were left overnight for 12 h after which the blue crab was removed from each and the remaining contents sieved through a 1 mm mesh so that surviving mud crabs could be enumerated.

To control for any loss of mud crabs from intraspecific predation or escape, we simultaneously ran a second set of trials in which mud crabs, but not blue crabs were added to tubs (n = 4 for oyster and algal treatments, n = 3 for mud treatment). Methods for these were otherwise as described above.

We compared the number of mud crabs remaining in experimental tanks with blue crabs at the end of the experiment using a one-way permutational analysis of variance (PERMANOVA; Anderson et al. 2008), with the single factor habitat. The PERMANOVA used a matrix of Euclidean distances between each of the replicates. A PERMANOVA was chosen over a classical analysis of variance because it does not require that the underlying distribution of the data is normal (Anderson et al. 2008). Where PERMANOVA detected a significant effect of habitat (at  $\alpha = 0.05$ ), the source of habitat differences was assessed by comparing pairs of treatments with a posteriori PERMANOVA tests. These a posteriori tests were corrected for the error rate associated with multiple comparisons using the Bonferroni method.

### Habitat selection

To test the hypothesis that mud crabs select habitat according to its refuge value, but that this selection is modified by predator presence, we conducted a habitat choice experiment in the field.

On the intertidal mudflat of Priests Landing, Skidaway Island, we established twenty-eight 1  $\times$  0.5 m cages at a tidal height of mean spring low water + 0.5 m in June 2013. Cages were cleared of all oysters and macro-algae and divided

into two halves, each of which received one of three habitat types, oyster *C. virginica*, algae *G. vermiculophylla* or bare mud. First, to assess prey selection of habitat in the absence of predators, we established three treatments in which all possible pairings of the three habitat types were offered to mud crabs *P. herbstii*. Second, to assess whether mud crab habitat selection was modified by the presence of a predator in the structured habitat, either as an effect of consumptive or non-consumptive effects, we established treatments in which oyster habitat with a tethered blue crab *C. sapidus* was paired with predator-free algal or mud habitat and where algal habitat with a tethered blue crab was paired with predator-free oyster or mud habitat. Blue crabs were tethered so that their movements could be restricted to a single habitat type, rather than roaming between the paired habitat treatments. This design gave a total of seven treatments, with four replicates of each.

Cages were constructed of 30 cm high, 0.5 cm galvanized mesh, depressed ~7 cm into the sediment to prevent crab escape via burial. A 1 mm mesh was cable-tied across the top of the cage to exclude predator access. The 0.5 × 0.5 m areas assigned to the oyster treatment received 11 litres of dead, sun-bleached oyster shell, arranged in small clumps of 8–12 oysters. The areas assigned to the algal treatment received 2 l of *G. vermiculophylla*, collected from the Priests Landing mudflat and defaunated using the methods described above (Refuge value of habitats experiment). These volumes of biogenic habitat were set based on the biomass per unit area of each of the habitat types in the mesocosm experiment. As with the previously described experiment, the defaunation of algae and oysters ensured that putative prey items for mud crabs did not differ in abundance among habitats at the start of the experiment.

At low tide, we first added blue crabs (males of ~10 cm carapace width) to designated habitats on 25 cm tethers, anchored to the centre of the designated 0.5 × 0.5 m area. The tether, constructed of 700 µm diameter monofilament line, was looped around the lateral spine of the crab, securely tied, and glued to the crab's carapace using cyanoacrylate glue. At the other end, it was secured to a 30 cm high and 10 mm diameter PVC pipe that was depressed 20 cm into the sediment. We then added 12 mud crabs (10–15 mm in carapace width) to each cage, along the central boundary between the two habitat types.

After 24 h, we placed a 0.5 mm mesh divider between the two habitat types within each cage, so as to prevent further crab migration, and enumerated the number of mud crabs within each of the two habitat pairings.

For each enclosure, a  $\chi^2$ -test was done to test for a significant (at  $\alpha = 0.05$ ) difference in the proportion of crabs in each of the two habitats. We then used Fisher's (1954) method to combine probabilities across replicate, independent enclosures of a given treatment.

## Colonization experiment

To assess how in a natural field setting, habitat configuration influences mud crab utilization of *G. vermiculophylla*, we conducted a colonization experiment in May 2013. The experiment tested the hypotheses that: 1) the number of mud crabs colonizing *G. vermiculophylla* would increase

with distance from the preferred oyster habitat; and 2) colonization would be negatively affected by the presence of blue crabs. Experimental deployments of defaunated *G. vermiculophylla* were made along a section of the Wilmington River (31°96'36"N, 80°95'60"W) near Savannah, Georgia with continuous oyster reef on the high shore and an intertidal mudflat that was devoid of *G. vermiculophylla*. Use of a field site without *G. vermiculophylla* enabled us to test hypotheses about how proximity to oyster reef influences colonization of the alga, without pre-existing algae confounding results by acting as stepping-stones for mud crab colonization.

At distances of 3, 6 and 9 m from the oyster reef, we deployed at low tide replicate 75 g clumps of defaunated *G. vermiculophylla* tethered to the centre of 45 cm diameter ring crab traps (0.16 m<sup>2</sup>). The traps were constructed of two wire rings that formed the top and bottom of a collapsible basket that was lined with 1 mm mesh. The collapsed traps were buried flat just below the sediment surface, with the *G. vermiculophylla* sitting above the trap on the sediment surface, so that organisms could freely colonize the alga. By tethering the *Gracilaria* to buried crab traps, we could retrieve algae and the associated phytal community at high tide, when habitat utilization by mobile organisms is greatest (J. L. DeVore unpubl.). When pulled by an attached rope, the traps form a basket, lined with the 1-mm mesh, that retains macrofauna and does not lead to significant by-catch from the water column above (J. L. DeVore unpubl.).

The alga was tethered to the underlying net using 10 cm long pieces of braided nylon rope through which the alga was threaded at one end, and a cable tie was threaded at the other, to secure the nylon rope to the centre of the trap. By threading the alga through the rope, rather than directly cable tying it to the trap, we were able to minimise algal breakage caused by abrasion. Furthermore, we were able to mimic the alga's natural method of retention on intertidal mudflats, which requires incorporation into *Diopatra cuprea* worm tubes, which are of similar length and width to the braided rope. The braided rope with attached algae was positioned so that it sat just above the surface of the mud, as would a *D. cuprea* worm tube with incorporated algae. Adjacent lift nets (n = 8 per distance) were separated by at least 9 m so that the distance between the alga and the oyster reef was less than between adjacent algal clumps.

We randomly assigned four of the eight algal clumps per distance to receive a single tethered male blue crab of ~10 cm carapace width. The tethers were 20 cm long and constructed of the same monofilament line and secured in the same manner as described above (Habitat selection experiment). These were anchored at the end to the base of the braided nylon rope, at the other end of which the alga was also attached.

The crab traps, containing the alga and associated faunal communities, were collected by boat on a slack high tide (~2 m water depth), 3 days after deployment. The positions of crab traps were identified by attached buoys, and using the connecting rope, we carefully and swiftly pulled each from the substrate. The contents of each trap was transferred to a tub and, back at the lab, washed through a 1mm-mesh sieve so that mud crabs could be identified and enumerated.

We tested for effects of distance from the oyster reef and presence of blue crabs on colonization of *G. vermiculophylla*

by mud crabs using a two-way fully orthogonal univariate PERMANOVA (see Habitat selection experiment for a full description). This was followed by a posteriori pair-wise PERMANOVAs to assess differences among levels of factors identified by the PERMANOVA as significant. As with the Habitat selection experiment, we corrected for the error rate associated with multiple pairwise a posteriori comparisons using the Bonferroni method.

## Results

### Refuge value of habitats

In the absence of blue crabs and irrespective of habitat treatment, 100% of mud crabs were retrieved from experimental tubs at the end of the 12 h experimental period. Hence, in tubs with blue crabs, loss of mud crabs was interpreted as predatory mortality.

Among tubs with blue crabs, survivorship of mud crabs varied according to habitat treatment (Fig. 1). Almost all of the mud crabs survived the 12 h period with a blue crab in tubs with oysters. This survivorship was significantly greater than in tubs with *Gracilaria vermiculophylla* or with mud, and survivorship of mud crabs was in, turn, greater in the *G. vermiculophylla* than in the mud (oyster > alga > mud; a posteriori tests, sig. PERMANOVA, pseudo- $F_{2,19} = 12.2$ ,  $p = 0.001$ ).

### Habitat selection

There was no significant difference in the number of mud crabs recovered from enclosures with or without blue crabs (two-sample t-test:  $t_{23} = -0.5$ ,  $p = 0.311$ ). Hence, differences in the occupation of habitats could be interpreted as the outcome of habitat selection rather than consumptive effects.

When offered a choice, significantly more mud crabs were found in the oyster habitat than in either of the algal or mud

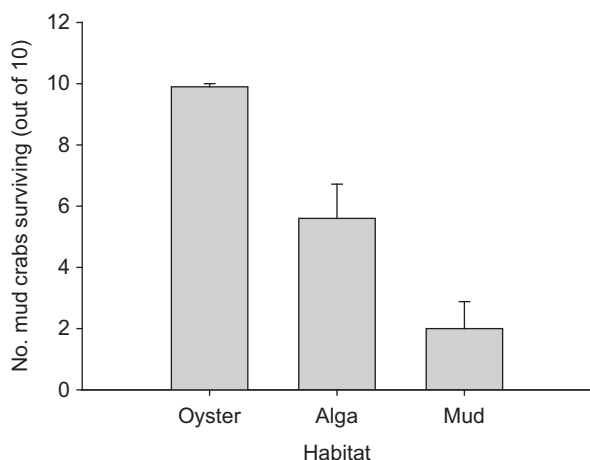


Figure 1. Mean (+ SE) number (out of ten) of *Panopeus herbstii* mud crabs surviving across 10 replicates in each of three habitats (oyster = *Crassostrea virginica*, alga = *Gracilaria vermiculophylla*, mud = bare) over 12 h of deployment with a blue crab.

habitats, and in the algal than in the mud habitat (Table 1). These differences persisted even when a blue crab was present in the oyster or in the algal habitat. Instead, the presence of a blue crab in the oyster habitat acted to increase mud crab occupancy of oysters over the mud or the algal habitat. Although the presence of blue crabs in the algal habitat also acted to strengthen the selection of oyster over algal habitat, it weakened, to a small degree, the mud crabs' selection of the algal over the mud habitat (Table 1).

### Colonization experiment

There was no interactive effect of the distance of *G. vermiculophylla* from the oyster reef and blue crab presence on the number of mud crabs colonizing the alga (PERMANOVA, pseudo- $F_{2,17} = 0.3$ ,  $p = 0.849$ ), allowing the interpretation of main effects. As hypothesised, the number of mud crabs colonizing *G. vermiculophylla* increased with distance from the oyster reef (PERMANOVA, sig. effect of distance pseudo- $F_{2,17} = 4.0$ ,  $p = 0.031$ ; Fig. 2). Also as expected, there were significantly fewer mud crabs in algal patches with than without a blue crab (PERMANOVA, sig. effect of predator distance pseudo- $F_{1,17} = 4.4$ ,  $p = 0.041$ ; Fig. 2).

## Discussion

Non-native foundation species can serve as refuges for native prey species (Carroll et al. 2010, Neira et al. 2006, Byers et al. 2010), but is unclear whether native species that lack an evolutionary history with non-native habitats are able to utilize them in accordance with their refuge value. In combination, our mesocosm and field experiments provide evidence that on mudflats of Georgia, USA, mud crabs, *Panopeus herbstii*, are utilizing the non-native alga, *Gracilaria vermiculophylla*, in accordance with its refuge value relative to mudflat and native biogenic habitat. Mesocosm experiments revealed that the alga was of intermediate value to mud crabs as a refuge from blue crab predation, relative to high value oyster reef and low value mudflat habitat patches. In the field, the utilization by mud crabs of *G. vermiculophylla* increased with distance from the more favorable oyster habitat, and

Table 1. Habitat selection by mud crabs when offered a simultaneous pairwise choice of two habitat types. Oyster = *Crassostrea virginica*; Alga = *Gracilaria vermiculophylla*; Mud = bare; (+ crab) = with tethered blue crab. Mean (and standard error; SE) percentages are calculated from four replicates with 10 crabs each. Separate  $\chi^2$ -tests for each replicate cage tested for a difference in mud crab occupation of the two habitats. These individual  $\chi^2$ -tests were combined across the four replicates per treatment using Fisher's method.

Comparison	Mean ( $\pm$ SE) percentage of mud crabs in each habitat			Fisher's combined probability	
	Oyster	Alga	Mud	$\chi^2$	p
Oyster – Alga	89 $\pm$ 5	11 $\pm$ 5		24.8	0.002
Oyster (+ crab) – Alga	93 $\pm$ 5	7 $\pm$ 5		22.5	0.004
Oyster – Alga (+ crab)	97 $\pm$ 2	3 $\pm$ 2		24.9	0.002
Oyster – Mud	80 $\pm$ 10		20 $\pm$ 10	18.9	0.015
Oyster (+ crab) – Mud	100 $\pm$ 0		0 $\pm$ 0	24.5	0.002
Alga – Mud		93 $\pm$ 5	7 $\pm$ 5	15.6	0.048
Alga (+ crab) – Mud		82 $\pm$ 7	18 $\pm$ 7	33.8	<0.001

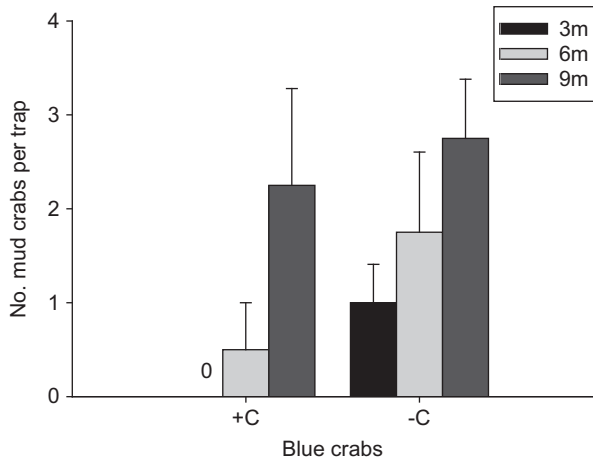


Figure 2. Mean (+ SE) number of *Panopeus herbstii* mud crabs colonizing replicate patches (0.16 m<sup>2</sup> crab traps) of *Gracilaria vermiculophylla* with (+ C) and without (-C) a predatory blue crab and placed at distances 3 m (black bars), 6 m (light grey bars) or 9 m (dark grey bars) from an oyster reef (n = 4).

was diminished by the presence of blue crab predators. The utilization by mud crabs of *G. vermiculophylla* was despite the absence of structurally similar native macrophytes along the Georgia coastline.

The greater refuge value of oyster than *G. vermiculophylla*, and of *G. vermiculophylla* than mudflat corresponded to differences in the structure of the three habitats. The introduction of *G. vermiculophylla* adds structural habitat to relatively homogeneous soft-bottom systems (Thomsen et al. 2006), but does not replicate the type of habitat attributes provided by oyster reefs, which provide a rigid three dimensional structure, with persistent interstices between shells, in contrast to the alga's more malleable form that collapses at low tide, when the alga is emmersed. Hence, our finding that blue crab predation on mud crabs was greatest in mud, intermediate in *G. vermiculophylla* and least in oyster is consistent with previous observations that prey survival is a function of habitat structure (Heck and Thoman 1981, Crowder and Cooper 1982, Grabowski 2004). Although we did not consider whether *G. vermiculophylla*, relative to oysters and mudflat, also provided mud crabs with intermediate protection from other benthic predators such as fish and, at low tide, wading shore birds, given the generality of effects of habitat structure on predation, we expect this would be the case. Other intermediate predators, such as grass shrimp *Palaemonetes* sp. and the dwarf crab *Rhithropanopeus harrisii*, at the same trophic level as *P. herbstii*, are also common in *G. vermiculophylla* (Wright et al. 2014). In the field experiment, we observed that these intermediate predators also colonized *G. vermiculophylla* (Bishop unpubl.) along with *P. herbstii*.

In small-scale field experiments, the selection by mud crabs of oyster over *G. vermiculophylla* over mud occurred irrespective of whether a blue crab predator was present. This was contrary to our prediction that the presence of a predator would have a greater effect on habitat occupancy than habitat identity. In enclosures in which mud crabs were offered a choice between oyster and one of either the algae or mud, the preference for oyster was strengthened by the presence of a blue crab predator, even when the blue crab was

tethered in the oyster habitat. This is presumably because cues from the predator swamped our small cage size, and upon sensing a predator cue, mud crabs selected the safest habitat (at least in the case of the oysters). As indicated by our predation experiments, predators and prey can live together in the structured oyster habitat because they can partition space. In the larger-scale colonization experiment, in which plots with and without blue crabs were separated by at least 9 m, there were fewer mud crabs in plots with than without blue crab predators. At this scale, at which predator cues did not swamp the predator-free replicates, it is possible mud crabs may avoid habitat patches with blue crabs. Alternatively, in the colonization experiment, fewer mud crabs in patches with blue crabs may result from blue crabs consuming mud crabs.

Independent of the presence of blue crab predators, mud crab colonization of patches of *G. vermiculophylla* increased with distance from the oyster reef. Mud crabs, which may be found from the intertidal to depths of 22 m, display low site fidelity (Lee and Kneib 1994, Stachowicz and Hay 1999), foraging on a variety of prey resources distributed across a broad range of habitats (Lee and Kneib 1994, Stachowicz and Hay 1999) and responding to competitive interactions (Brown et al. 2005). We posit that when foraging in areas where they commonly encounter both oyster reef and *G. vermiculophylla* patches, mud crabs choose oyster reef over *G. vermiculophylla* as their primary refuge habitat, in accordance with the greater refuge value of oysters. However, as the encounter rate with oyster reef decreases, mud crabs increasingly utilize *G. vermiculophylla* as their primary refuge. Hence, the utilization of the non-native species is dependent on the availability/proximity of native biogenic habitat.

Our pattern of colonization was the reverse of what would be predicted if mud crabs were merely spilling over from oyster reefs to the alga, in which case to reach more distant *G. vermiculophylla* patches crabs must travel increasing distances through low complexity, and hence risky mud habitat. Although proximity to oyster reef was confounded with tidal elevation, the pattern of mud crab colonization could not be explained by tidal inundation alone. The mudflat was of extremely low gradient, such that the difference in inundation between *G. vermiculophylla* patches closest to and furthest from oyster reefs was < 15 min. Sampling on an adjacent mudflat without oyster reef revealed that there was no difference in the abundance of mud crabs between unvegetated sediments at heights lower and higher on the shore (two-sample t-test:  $t_8 = -0.75$ ,  $p = 0.356$ ). It is, however, possible that predators such as oyster toadfish *Opsanus tau* and sheepshead *Archosargus probatocephalus* that forage on oyster reefs (Lenihan et al. 2001) contributed to reduced densities of mud crabs in *G. vermiculophylla* close to oyster reefs.

Our study showed that predation refuge is a sufficient explanation for habitat use by *Panopeus*. Other factors, in particular, differential food availability, could still contribute to patterns of habitat selection by *P. herbstii*. Our experiments utilized defaunated alga and oyster habitat, and were of short duration to minimize differential colonization of the substrates by invertebrate communities. However we expect if anything, that differences in prey availability among the three habitat types would reinforce patterns of habitat selection. Juvenile *P. herbstii* consume a variety of small

invertebrates (McDonald 1977, Dame and Petten 1981), while adults almost exclusively consume molluscs, such as oysters, mussels and hard clams (McDermott and Flower 1952, McDermott 1960, Meyer 1994). Each of *G. vermiculophylla* and oyster reef enhance invertebrate prey abundances relative to unvegetated sediments, with the *G. vermiculophylla* supporting amphipod- and shrimp-dominated communities (Thomsen et al. 2009, Byers et al. 2012, Wright et al. 2014) and oyster reef, higher densities of molluscs and crabs (Wells 1961, Grabowski et al. 2005). Future studies could assess how food provision by *G. vermiculophylla* enhances mud crab population density.

Cumulatively, our results indicate that mud crabs utilize *G. vermiculophylla* as refuge habitat and occupy it in accordance with its relative worth as compared to adjacent native habitats. This is despite a limited history of co-occurrence of the non-native alga and mud crabs along the east coast of the USA (perhaps as short as 15 years in Georgia; Nettleton et al. 2013), and the absence of a native analogue of the non-native alga on Georgia mudflats. Hence, it appears that just as native predators may, in some instances, be able to rapidly respond to non-native prey species (Carlsson et al. 2009), native prey species may be able to rapidly respond to non-native biogenic habitats. At the population level it appears that there are not evolutionary constraints to utilization by mud crabs of non-native habitats as refuges and, to the contrary, the crab may be able to optimally use non-native habitat after only a brief exploratory phase, e.g. through learning and according behavioral shifts. The ability of native species to respond to non-native habitats may, however, depend on the breadth of native habitats they occupy. Here, mud crabs are known to utilize a variety of native habitats as refuge, including oyster reef, saltmarsh, and mussel clumps (Dittel et al. 1996). This facultative use of habitats may provide the plasticity required to capitalize on non-native structural habitat. Species that are habitat-specialists may be less well equipped (or inclined) to capitalize on the habitat provided by non-native species. Ascertaining how habitat breadth corresponds to the ability of native species to identify and respond to non-native species as habitat would be an interesting area of future research.

Our results add to growing evidence that in many instances, native species are able to respond similarly to non-native and native foundation species (Carroll et al. 2010, Johnston and Lipcius 2012, Wilkie et al. 2012). In areas where native habitats have been negatively impacted by human activities and climatic change, these non-native species may provide important refugia to native prey. How a non-native species modifies the physical structure of its novel environment is a primary consideration in evaluating its impact and potential value as habitat (Crooks 2002, Schwindt et al. 2004, Rodriguez 2006). A principal goal of invasion biology is to develop ecological principals that apply generally (Vitousek 1990). Our finding that predator refuge value predicts the utilization of a non-native species as a habitat suggests that trait-based approaches, which are increasingly being used to understand how native species interact, may aid in understanding impacts of species invasions. The relative refuge value of non-native versus native habitat-forming species may provide a baseline expectation of how native prey will utilize novel biogenic habitats, against

which the speed of learning and opportunism of native prey can be assessed.

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