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ORIGINAL PAPER

# Density-dependent predation and predator preference for native prey may facilitate an invasive crab's escape from natural enemies

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**Abstract** Native predators can confer biotic resistance through consumption of invasive prey. However, early in the invasion process, native predators may initially ignore an invader when it is rare and only increase consumption once it becomes abundant. Furthermore, the willingness of native predators to consume novel invasive prey may be influenced by the similarity of the invader to other native prey species that are favored or familiar. Here we examined whether a native predator (the common mudcrab, *Panopeus herbstii*) consumes the invasive filter-feeding crab, *Petrolisthes armatus* as a function of *P. armatus* abundance relative to native prey and the similarity of *P. armatus* to native prey. Using choice experiments, we quantified consumption of invasive *P. armatus* when its abundance was either rare, equal, or more abundant than native prey that were either taxonomically similar (crab, *Eurypanoepus depressus*) or dissimilar (mussel, *Geukensia demissa*) to the invader. We found that the absolute consumption of invasive *P. armatus* increased as its relative availability increased, but only in treatments where the alternative prey was a native crab. This suggests that prior experience of the native predator with a similar prey may prime the predator to consume more invasive *P. armatus*. A hierarchical Bayesian analysis determined that both native prey species were preferentially consumed by the native predator *P. herbstii* even when native prey were rare or equal in abundance to invasive *P. armatus*. These results suggest that density-dependent predation plus a persistent preference for native prey by native *P. herbstii* predators may help explain how *P. armatus* escapes its natural enemies.

**Keywords** Enemy escape · Non-native species · Novel prey · Predator functional responses · Predator switching

## Introduction

Although many predators forage adaptively in response to changes in the abundance of their prey, predators may be slow to respond to the introduction of a novel, unfamiliar prey. As a result, many invasive species reach high abundances by escaping the control of their natural enemies (Mitchell and Power 2003; Torchin et al. 2003; Shwartz et al. 2009). A slow response by native predators could be due to a variety of causes including lack of evolutionary history, the initial rarity of the novel prey, or constraints to learning (Carlsson et al. 2009; Sih et al. 2010;

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Pintor and Byers 2015b). Regardless, there remains a critical need to identify the mechanisms that influence a predator's interactions with a novel prey and how predators might adapt to a novel prey resource over time.

The relative abundance of prey, along with the value of alternative prey may influence when a native predator incorporates a non-native prey into its diet, leading to at least partial control of the non-native prey population. For example, in the early stages of invasion, the abundance of a non-native prey is often low relative to alternative native prey. If the non-native prey type is of lower value, then it should be ignored relative to the abundant and higher-value native prey (Krebs et al. 1981; Pyke 1984; Stephens and Krebs 1986). The predator may ignore the rarer, less valuable prey and only increase its consumption of the non-native prey as it increases in relative abundance or profitability to native prey (Holling 1959a, b; Krebs et al. 1981; Pyke 1984; Stephens and Krebs 1986). Thus, the effect of a native predator on a non-native prey is expected to change with its abundance and may influence the outcome of an invasion (Holling 1959a, b).

In addition to relative abundance, the value or profitability of a non-native prey may influence how much it is foraged upon, which can be affected by the similarity of the non-native species to a native prey species, especially early on following introduction. Specifically, the retention of learned handling skills for one prey may enhance an individual's ability to transfer skills to a new prey if that prey is similar to the first but may hinder or slow the performance on a new, dissimilar prey (Osgood 1949; Ellis 1965; Tinker et al. 2009). For example, shore crabs trained on a diet of mussels took a shorter time to handle a novel mussel species in comparison to shore crabs trained on dissimilar fish or snails (Hughes and O'Brien 2001). Also, taxonomically similar prey may exhibit similar behaviors or cues to which a predator may already be attuned, e.g., search image (Sih et al. 2010), whereas taxonomically dissimilar prey likely exhibits different behaviors or cues (Binz et al. 2016). This familiarity extends to include traits such as the scents and signals of familiar prey that can prime a predator to target various prey species over others (Cross and Jackson 2010). Therefore, variation in predation rates on a novel prey could be determined both by its relative abundance and taxonomic similarity to the native prey and may drive changes in the adaptive foraging behavior of a native predator.

In this study we examined whether predation by the native mudcrab predator (*Panopeus herbstii*) was affected by the relative abundance of a non-native, filter-feeding crab (*Petrolisthes armatus*, the green porcelain crab) and its taxonomic similarity to two native prey species. *Petrolisthes armatus* has invaded estuarine oyster reef communities along the southeastern coast of the US (Hollebone and Hay 2007). At the time of this study, sources cited that, *P. armatus* was present and abundant from St. Augustine, Florida north to near Wilmington, NC (Saintilan et al. 2014; Kinney et al. 2019). Proportionally, *P. armatus* can compose on average anywhere from 35 to 42% of the most common prey items of *P. herbstii* within invaded oyster reef communities in Georgia (Kinney et al. 2019) and has a caloric value that is similar to many native prey items on the reef (Hostert et al. 2019). *P. herbstii* is a generalist predator that commonly consumes native crabs, mussels, and oysters, as well as non-native *P. armatus* (Pintor and Byers 2015a; Hostert et al. 2019). Thus, upon initial introduction, *P. armatus* might escape much top-down control due to its initial rarity. However, as its abundance increases over time, we would expect that *P. herbstii* should increase its consumption of *P. armatus* and that its consumption might be similar to that of a native crab prey due to its ecological similarity. By creating conditions that simulate the invasion progression from rare to abundant, we can examine whether rarity, as well as dissimilarity, reduce the consumption the invasive *P. armatus*, possibly conferring it protection from strong top-down effects.

Here we tested the hypothesis that the relative abundance of alternative native prey and the taxonomic similarity of native to non-native prey affect the consumption of *P. armatus* by native *P. herbstii* predators. Our first objective was to compare the consumption of *P. armatus* by native *P. herbstii* predators when it was in low, equal, or high abundance relative to native prey. We predicted that if consumption of *P. armatus* is a function of its relative abundance, then *P. herbstii* predators will consume relatively more *P. armatus* as its abundance increases relative to an alternative prey. Our second objective was to examine whether the consumption of *P. armatus* depended upon whether the alternative native prey was taxonomically similar (crab, *Eurypanoepus depressus*) or dissimilar (mussel, *Geukensia demissa*) to *P. armatus*. We predicted that if consumption of *P. armatus* is a function of its similarity to the alternative native prey, then consumption would be greater on *P. armatus* when paired with a more similar mobility prey item (*E. depressus*). Finally, our third objective was to use a Bayesian approach to examine whether native *P. herbstii* predators exhibited a preference for either the native or non-native prey. We predicted that if *P. herbstii* predators exhibited a preference for a particular prey type then it would consume that prey out of proportion to its availability in the environment.

## Methodology

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We used a 3×2 factorial design to test whether consumption and preference on *P. armatus* by *P. herbstii* was dependent on the relative abundance of alternative native prey and the similarity of *P. armatus* to a native prey. We randomly assigned an individual *P. herbstii* predator to one of three treatments that manipulated the relative abundance of native to invasive prey (herein after "abundance treatment"). Specifically, we had 3 treatments with abundance ratios of native: invasive prey individuals at 1:3 (abundant *P. armatus*), 1:1 (equal *P. armatus*), or 3:1 (rare *P. armatus*), while holding the total prey density across all treatments equal at 16 per $0.14\,\mathrm{m}^2$. This density is well within the range of their densities in their natural habitat in the field. Additionally, we manipulated the taxonomic similarity of the alternative native prey offered in the trial (herein after "prey type" treatment) whereby the predator was either offered a similar prey (native crab, *E. depressus*) or a dissimilar prey (native mussel, *G. demissa*) to *P. armatus*. Thus, we had a total of 6 treatment combinations (Fig. 1).

We conducted these trials at the Skidaway Island Institute of Oceanography in Savannah, GA between June 1–July 30, 2016, and June 20–July 10, 2017. *Petrolisthes armatus* has been established at this site since 1994 and previous work has shown that *P. herbstii* from this site readily consume *P. armatus* (Hollebone and Hay 2008; Pintor and Byers 2015a; Kinney et al. 2019). We hand-collected individual *P. herbstii* from oyster reefs and housed them in flow-through seawater tanks and fed them frozen shrimp ad libitum. Male and female *P. herbstii* were housed separately. For prey items we collected *P. armatus* (carapace width 7–10 mm), *E. depressus* (carapace width 7–12 mm) and *G. demissa* (shell length 20–30 mm) from the same oyster reefs and housed them in separate flow-through seawater tanks. The size ranges were chosen based on previous work looking at the consumption of these prey species by *P. herbstii* (Hostert et al. 2019).

Before the start of the trial, we placed a single *P. herbstii* in an isolated holding tank (11.75 cm diameter, filled with 0.6 L of aerated seawater) and withheld food for 24-h to standardize hunger levels. After 24-h, we randomly assigned the isolated individuals to one of the six treatment tanks and allowed the predator to acclimate to the testing tank for 8-h (48.2 cm × 29.21 cm × 23.81 cm, filled with 15.9 L of aerated seawater). Fifteen minutes before the start of a trial, we isolated the *P. herbstii* predator within the tank using an inverted and weighted, opaque cup. We then added a total of 16 prey according to the randomly assigned abundance and prey similarity treatment (Fig. 1). The prey species were allowed to acclimate for three minutes and then we released the *P. herbstii* predator from isolation and the experiment began. We checked each individual tank every 30 min over a 4-h period during the evening (19:00–23:00) for a total of 8 nighttime observations to quantify the number of each prey species eaten. We performed these trials in the dark and during evening hours because *P. herbstii* is a nocturnal species and forages most often in the dark. We used red light headlamps to check the tanks to reduce disturbing the trial individuals. We replaced each prey item consumed to maintain prey densities and thus the corresponding prey ratio treatment. At the end of the 4-h trial we summed up the total number of each prey consumed over the eight observations in an individual tank (i.e., 4-h trial was the unit of replication). Individual *P. herbstii* predators were used only once during the experiment. We removed any *P. herbstii* that did not consume any prey items (native or invasive) during the trial from any statistical analyses. Therefore, in the end each treatment was replicated between 15 and 17 times (15–17 reps/treatment, Total N = 98 trials). We followed all applicable institutional and national guidelines for the care and use of animals.

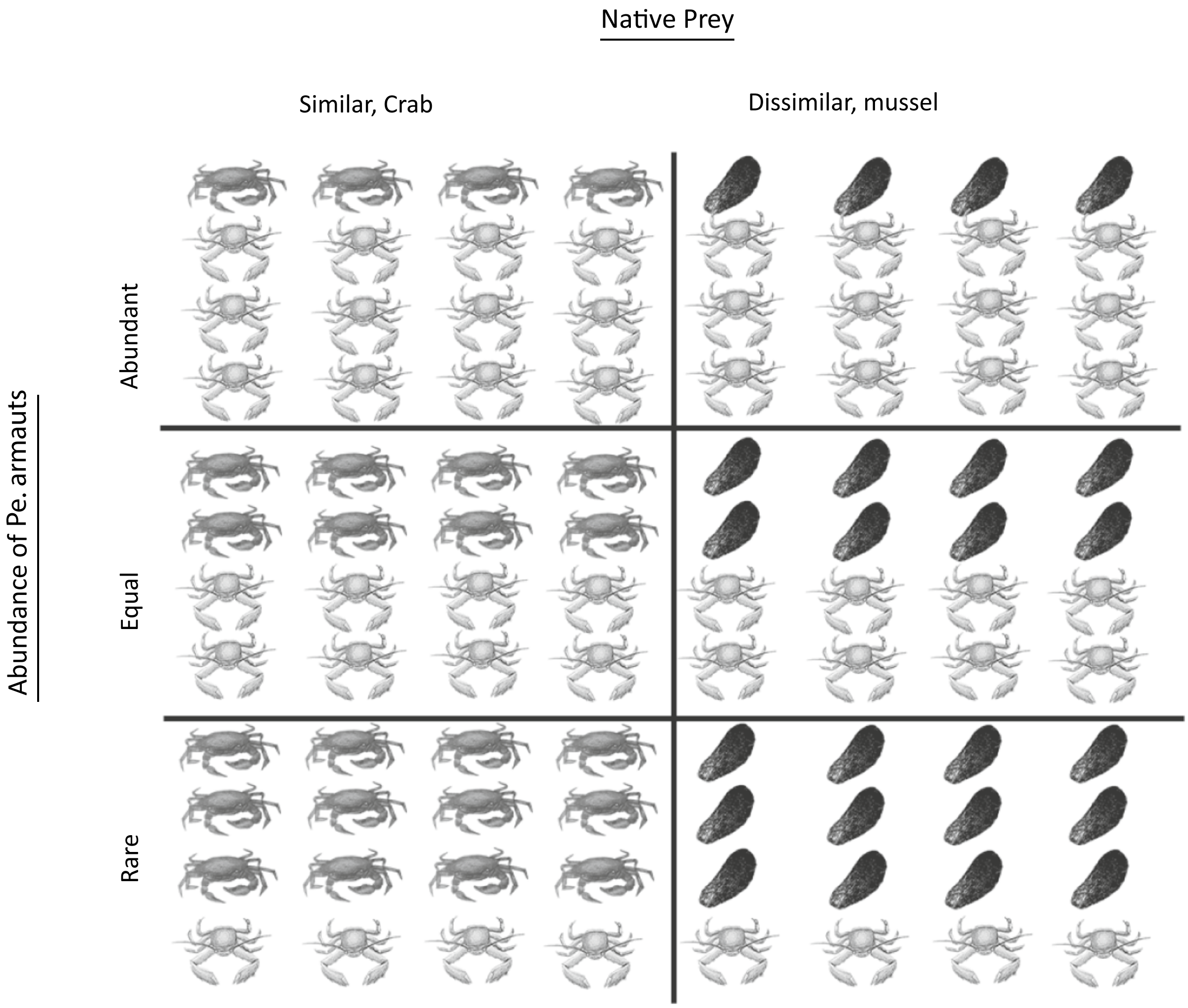

**Fig. 1** Treatment combinations applied in the prey choice assay. In a fully crossed experiment, we manipulated the relative abundance of invasive *P. armatus* (light grey crab) prey, and the taxonomic similarity of the native prey. Native prey were either similar (*E. depressus*, dark grey crab) or dissimilar (*G. demissa*, dark grey mussel) to *P. armatus*

### *Data analysis*

We used a generalized linear model with a Poisson distribution to test for an effect of the abundance and prey type treatments on the number of *P. armatus* eaten. Previous work has suggested that male and female *P. hertbstii* differ in their diet (Pintor and Byers 2015a), therefore, we also included sex in the model. Because replicates of the experiment were run in two different years, we included the year the trial was run as well. We also checked for interaction terms between all variables but removed any non-significant interaction terms at an α level of 0.05 or greater (Spake et al. 2023). We used R 3.4.2 statistical program for all analyses (R Development Core Team 2019).

Although the GLM is useful in understanding whether the mean absolute consumption of *P. armatus* by native predators differed across treatments, it does not tell us whether native predators consume *P. armatus* in proportion to their availability in the tank (i.e., exhibit a preference for a prey type). Therefore, we used a hierarchical Bayesian analysis in the R 3.3.2 package "bayespref" (Fordyce et al. 2011; Haram et al. 2018) to estimate the strength of foraging preference of *P. herbstii* for invasive *P. armatus* or native prey within each abundance treatment. In other words, we tested whether *P. herbstii* were eating prey relative to their abundance in the tank, or whether predators were exhibiting a preference for one prey over another. For example, if the native and invasive prey were equal in abundance and neither were preferred, one would expect both species to be consumed in equal proportion. If the proportion of one prey species consumed was significantly greater than 50%, this would indicate a preference for that species of prey. In each analysis, we ran models for 5000 MCMC steps, with 1000 generation burn-ins, along with a 95% credible margin of error around the mean parameter value. Once we generated the strength of the preferences for each prey species, we compared the credible intervals to the expected consumption values for both invasive and native prey. If the population variance in consumption included the expected value, we concluded that consumption was as expected and *P. herbstii* foraged in proportion to the prey's density. If the population variance did not include the expected value, we concluded that consumption was either higher or lower than expected and that *P. herbstii* is showing a preference or avoidance of a prey item, respectively. We ran separate Bayesian analyses for each individual treatment combination and combined male and female predator responses together since sex was not significant in the GLM.

## Results

Although predators increased consumption of *P. armatus* as they became more abundant (Abundance; L-R ChiSquare = 16.83, $p = 0.0002$), this was dependent on the native prey species in the treatment (Abundance × Prey Type; L-R ChiSquare = 11.61, $p = 0.003$; Fig. 2). Specifically, there were increasingly more *P. armatus* consumed as its

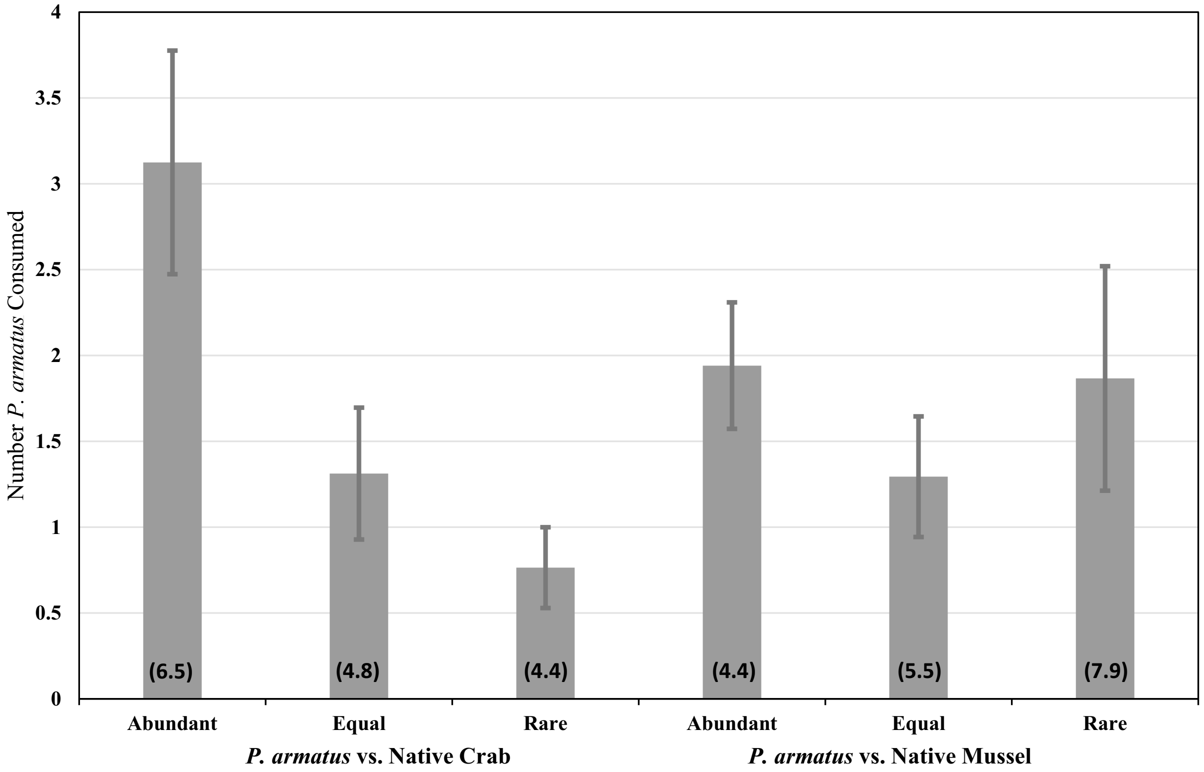

**Fig. 2** Number of *P. armatus* consumed by *P. herbstii* over 4 h across treatments that manipulated the relative abundance of invasive *P. armatus* prey paired with two different native prey—one that was taxonomically similar (crab, *E. depressus*) and one that was dissimilar (mussel, *G. demissa*) to the invader. The average total number of both prey consumed in each treatment is noted in bold in parentheses within the bar

abundance increased when it was paired with the native crab prey, but not the native mussel prey. There was no effect of prey type alone on the number of *P. armatus* consumed (L-R ChiSquare = 0.77 df = 1, $p$ = 0.38). There was no effect of sex on the number of *P. armatus* eaten (L-R ChiSquare = 1.79, df = 1, $p$ = 0.18), nor an effect of the year the trial was run (L-R ChiSquare = 3.69, df = 1, $p$ = 0.06).

In Bayesian analyses of foraging preferences, in treatments with the native crab prey (*E. depressus*), predators preferred native prey to *P. armatus* (i.e., did not consume prey in proportion to its abundance) when *P. armatus* was more abundant (n = 16) and equal (n = 16) in proportion to the native crab (Table 1; Fig. 3). Predators consumed invasive *P. armatus* and the native crab in proportion to their abundance only when *P. armatus* was rare relative to the native crab (n = 17). Similarly, in treatments with the native mussel prey (*G. demissa*), predators preferred native mussels to *P. armatus* when *P. armatus* was more abundant (n = 17) and equal (n = 17) in proportion to the native mussel. Predators consumed invasive *P. armatus* and the native mussel in proportion to their abundance only when *P. armatus* was rare relative to the native mussel (n = 15).

## Discussion

Native *P. herbstii* predators increased their absolute consumption of *P. armatus* as it became more abundant than the native crab, but not as it became more abundant than the native mussel. Despite the difference in absolute consumption of *P. armatus* between the two native prey treatments (i.e., crab vs. mussel), *P. herbstii* predators' relative consumption of *P. armatus* was significantly less than its available proportion in the environment. That is, *P. herbstii* predators consistently preferred both native prey species relative to *P. armatus*, except when *P. armatus* was rare, and even then, their prey selection was proportional to environmental availability. These results suggest that *P. herbstii* does not always forage on *P. armatus* at rates expected by its relative abundance, and instead exhibits a pronounced preference for native prey. These patterns of foraging by *P. herbstii* predators may contribute to *P. armatus*' escape from natural enemies.

Although *P. herbstii* will consume *P. armatus*, it does not consistently forage on *P. armatus* at rates expected by its relative abundance across all contexts examined in this study. As a non-native prey increases in abundance, native predators should begin to incorporate a larger proportion of the non-native prey if the prey is profitable and encounter rates with native prey

**Table 1** Prey species preferences (and credible intervals) for *P. herbstii*

| Native prey type | Abundance treatment | # Of replicates | Species | Expected consumption | Credible interval (95%) |
|---|---|---|---|---|---|
| *Eurypanopeus depressus* (crab) | Abundant *P. armatus* | *16* | ***P. armatus*** | **0.75** | **0.37–0.59** |
| | | | ***E. depressus*** | **0.25** | **0.41–0.63** |
| | Equal *P. armatus* | 16 | ***P. armatus*** | **0.50** | **0.18–0.44** |
| | | | ***E. depressus*** | **0.50** | **0.56–0.82** |
| | Rare *P. armatus* | 17 | *P. armatus* | 0.25 | 0.11–0.36 |
| | | | *E. depressus* | 0.75 | 0.64–0.89 |
| *Geukensia demissa* (mussel) | Abundant *P. armatus* | 17 | ***P. armatus*** | **0.75** | **0.30–0.61** |
| | | | ***G. demissa*** | **0.25** | **0.39–0.70** |
| | Equal *P. armatus* | 17 | ***P. armatus*** | **0.50** | **0.16–0.42** |
| | | | ***G. demissa*** | **0.50** | **0.58–0.84** |
| | Rare *P. armatus* | 15 | *P. armatus* | 0.25 | 0.16–0.45 |
| | | | *G. demissa* | 0.75 | 0.55–0.85 |

Predator preferences are presented as the proportion of each prey type consumed and was determined using a hierarchical Bayesian model. Credible intervals account for 95% of the variability. If the credible interval did not overlap with the percent of each prey type available, the predator was considered to have demonstrated a "significant" preference, which are represented in bold

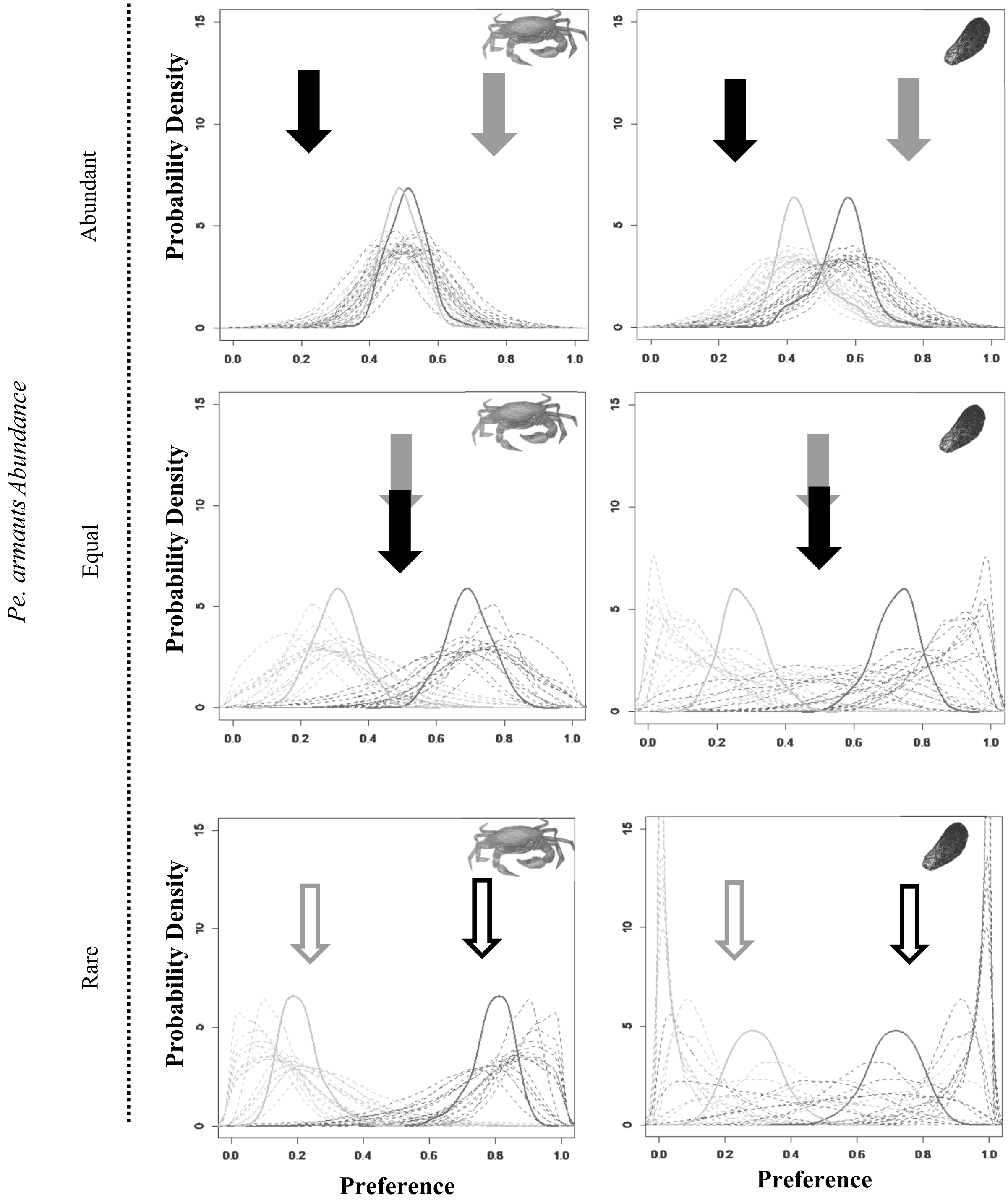

**Fig. 3** Foraging preferences of *P. herbstii* predators during prey choice assays. We analyzed all treatments for individual-level (dotted line) and population-level (solid line) preferences using a Bayesian analysis. Preference curves for the invasive prey are illustrated in grey and for the native prey in black. Arrows indicate the expected proportion of consumption for each prey if *P. herbstii* foraged randomly, given the frequency of prey types available. A filled arrow indicates that the predator foraged differently from expected based on prey availability, whereas an unfilled arrow indicates that the predator foraged as expected

decline following invasion (Krebs et al. 1981; Pyke 1984; Stephens and Krebs 1986). Previous work has shown that predators will switch to consuming an invasive prey when it is abundant (Molloy et al. 1997; French and Bur 1993; Magoulick and Lewis 2002; Carlsson et al. 2009; Charbonnier et al. 2014). In our study, however, no predator switching to the invasive prey was apparent; rather, the proportion of invasive prey consumed relative to native prey was far lower than expected based on environmental availability (Skein et al. 2018). More interaction time between *P. herbstii* predators and invasive *P. armatus* prey might be required for the predator to exhibit prey switching and provide some biological resistance. Although *P. herbstii* did somewhat increase its absolute consumption of *P. armatus*, as the relative abundance of *P. armatus* increased across treatments, its relative consumption was significantly lower than expected based on its environmental availability when the abundance of *P. armatus* was high or equal to that of either native prey. This may suggest that *P. herbstii* is inefficient at consuming *P. armatus* when abundant. Similar results have been previously observed where native signal crayfish were inefficient at consuming the invasive New Zealand mud snail (Twardochleb et al. 2012). Specifically, native signal crayfish increased their consumption rate of mud snails as snail density increased, but when the snail was present at very high densities, crayfish were only able to consume mud snails at a fixed maximal rate, regardless of their increased abundances in the environment (Twardochleb et al. 2012).

Furthermore, our results suggest that strong preferences for native prey may also explain why native predators do not consume *P. armatus* in proportion to its abundance in the environment regardless of the relative profitability of native to non-native prey. For example, *P. herbstii* exhibited a preference for the native crab prey, *E. depressus*, over *P. armatus* despite *E. depressus* having a lower caloric content and presumably requiring similar handling skills (e.g., both are similarly sized, mobile crab prey) (Hostert et al. 2019). Preferences for native prey may be due to naïveté of the native predator. Naivete by prey is often implicated in the large impacts that non-native predators have on native prey (Diamond and Case 1986; Cox and Lima 2006; Freeman and Byers 2006; Sih et al. 2010), yet could equally apply when the prey is the non-native species, and the predators are naive. For example, native predatory west coast rock lobster, *Jasus lalandii*, and starfish, *Marthasterias africana*, preferred native mussels over profitable invasive mussels despite the high relative abundance of invasive mussels following invasion (Skein et al. 2017). As a result, this preference for a native prey can allow invasive species to escape predatory pressure and persist in native environments (Mitchell and Power 2003; Torchin et al. 2003; Shwartz et al. 2009). Here, we suggest that naïveté of native predators may contribute to this preference for native prey despite the caloric profitability of the invasive prey. Native *P. herbstii* predators from the geographic location tested have only interacted with *P. armatus* for a couple of decades relative to when this experience was conducted. Native predator naïveté may require a long timescale to overcome (through evolution and learning) and thus, contribute to a predator's inefficiency in consuming a calorically profitable invasive prey.

Although native *P. herbstii* foraged on *P. armatus* at rates far lower than its relative abundance, it is important to remember that biotic resistance is a community-level process (Elton 1958; Levine et al. 2004). Biotic resistance could still occur through predation by other native predators. *P. herbstii* is only one predator in these coastal oyster reef communities, and although it is one of the dominant predators on *P. armatus* due to its abundance and proximity, there are other native predators species present that will consume invasive *P. armatus* (*Callinectes similis and Fundulus heteroclitus*: Hollebone and Hay 2007). Furthermore, competition from native crabs such as *E. depressus*, although unexplored, could also play a role in biotic resistance. Thus, our results are suggestive, but not definitive, that *P. armatus* experience predator release in a natural community setting.

To conclude, density-dependent predation protects prey when they are rare. Such a mechanism can strongly influence the establishment of non-native species since the definition of a successful invasion is being able to increase when rare (Byers 2000). For *P. armatus*, density-dependent predation, coupled with a strong, persistent preference for native prey by native *P. herbstii* predators, may help to explain how *P. armatus* has become so abundant and well-established within these estuarine communities of the southeastern US.

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**Author contributions** ACM, KAK, JEB and LMP conceived and designed the experiments. ACM and KAK performed the experiments. KAK, LMP, JEB analyzed the data. KAK, LMP, and JEB wrote the manuscript.

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**Data availability** The datasets generated during the current study are available from the corresponding author on reasonable request.

**Declarations**

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

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