**COMMUNITY ECOLOGY – ORIGINAL RESEARCH** 



# Polymorphism promotes edge utilization by marsh crabs

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#### Abstract

Understanding how habitat edges affect ecological processes is crucial given widespread and increasing modifications to natural landscapes. Resource specialization is a key factor affecting among-species edge responses, but we know little about how intraspecific resource use variation mediates edge utilization. Here, we integrate stomach content analysis, geometric morphometrics and feeding experiments to explore the role of resource polymorphism in mediating marsh crab (*Panopeus obesus*) foraging within the marsh-oyster reef boundary. Stomachs of edge individuals contained a greater proportion of morphologically defended edge prey (bivalves) compared to core marsh individuals, and edge individuals possessed relatively tall and robust claw morphology for manipulating such prey. We further show experimentally that phenotypic changes of edge *P. obesus* are associated with enhanced feeding efficiency on small, but not large edge prey. Morphological and ecological traits of edge *P. obesus* overlapped with the edge-occurring congener, *P. herbstii*, suggesting some degree of functional convergence despite the potential for interspecific competition within edges. Though this polymorphism is likely plastic, the success of *P. obesus* along edges could subsidize predator production within marshes and alter top–down pressure across mosaic estuarine landscapes. More generally, our study reveals polymorphism as a driver of edge utilization, while yielding new insight into the processes that maintain or erode spatial niche differentiation within predator guilds.

Keywords Edge effects · Food web · Intraspecific variation · Predation · Niche specialization

# Introduction

Studies of edge effects examine how boundaries between habitats modify ecological processes (Fagan et al. 1999). Regarding species interactions, the role of edges in mediating consumer–resource (or predator–prey) relationships has received substantial research attention (Hartley and Hunter

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1998; Lahti 2001; Paton 1994), with recent focus on predicting differences in edge sensitivity among consumer species or functional groups (Ewers and Didham 2006; Ries et al. 2017). Resource-based models have been particularly successful towards this goal, predicting declines of resource specialist species towards edges, but positive or neutral responses of resource generalists (Ries and Sisk 2004; Wimp et al. 2019). Yet despite the importance of resource use in determining among-species edge responses, we know relatively little about how intraspecific variation in resource use mediates edge utilization. Because intraspecific variation shapes the success of species in heterogenous environments (Bolnick et al. 2011, 2003), the prevalence of this phenomenon could explain mixed support for among-species models (Ries et al. 2017). Exploring the effects of intraspecific variation on edge utilization could also expand our understanding of the mechanistic basis of edge effects, an important research goal (Ewers and Didham 2006).

One potential mechanism that can affect edge responses is resource (or trophic) polymorphism, defined as covariance between aspects of phenotype (e.g., morphology, behavior) and resource use within a population (Anthony et al. 2008; Maerz et al. 2006). Resource-based models predict that resource specialists should be relatively vulnerable to habitat fragmentation because their foraging is restricted to a single habitat type, whereas generalists can exploit resources across adjoining habitats or greater spatial scales (Ries and Sisk 2004). While this framework assumes that phenotypic tradeoffs limit the foraging success of specialists across habitats, resource polymorphism can relax tradeoffs to promote edge utilization (Wilson 1998). Resource polymorphism is generally assumed adaptive, enhancing trophic efficiency and driving some degree of intraspecific specialization (Ehlinger and Wilson 1988; Skúlason et al. 1993). Phenotypic changes associated with resource use can be plastic if, for example, individuals incorporate a new resource over the course of their ontogenetic development (Ruehl and DeWitt 2005), or have genetic underpinning if phenotypic or habitat differentiation drives some degree of reproductive isolation (Whiteman and Semlitsch 2005). Due to this latter effect, most studies approach resource polymorphism from an evolutionary perspective (Smith and Skúlason 1996), while the ecological ramifications of resource polymorphism and its relation to edge utilization are less studied.

While resource polymorphism can facilitate edge utilization, this process could be constrained by the degree of consumer species overlap. Consumer overlap within edges occurs in part due to cross-habitat spillover (Rand et al. 2006), making edges well-known sites of species mixing and novel species interactions (Ewers and Didham 2006; Fagan et al. 1999; Ries et al. 2017). If an edge is unoccupied, then phenotypic modifications should proceed unabated, barring additional, counteracting selection pressures or functional constraints. Yet in occupied edges, predator resource polymorphism could be constrained by interspecific competition, particularly with closely related (e.g., congeneric) consumers that occupy similar functional roles (Bøhn and Amundsen 2001; Robinson et al. 1993; Schluter and McPhail 1992; Werner 1977). These effects might further depend on resource availability. Under high resource environments, predators may undergo phenotypic convergence, while resource limitation and thus strong interspecific competition could cause predators to retain or develop distinct phenotypes (sensu character displacement) that minimize niche overlap (Bøhn and Amundsen 2001; Robinson et al. 1993; Schluter and McPhail 1992). Thus, while the role of resource polymorphism in reducing intraspecific competition is well recognized (Swanson et al. 2003), the importance of this process within edges may be constrained by the degree of interspecific competition with functionally similar predators.

Here, we explore how resource polymorphism affects edge utilization by a key estuarine predator. The saltmarsh mud crab, *Panopeus obesus*, is well known from the low intertidal salt marsh (characterized by salt marsh grasses) but has also been detected in the boundary between low intertidal marsh and oyster reefs (Menendez 1987; the present study). Differences in prey assemblages between core marsh (mostly other crabs and snails) and edge (bivalves) suggest that P. obesus may undergo phenotypic modification to enhance resource use efficiency, particularly given previously recorded plasticity (Smith 2004; Smith and Palmer 1994) and intraspecific variation (Schenk and Wainwright 2001) in crab trophic morphology. Yet, edges also experience spillover of a congeneric crab predator, P. herbstii, that specializes in consuming morphologically defended edge prey, i.e., hard-shelled bivalves. Such consumer overlap introduces the potential for interspecific competition to modify P. obesus phenotype within edges. This scenario allows addressing whether a purported marsh habitat specialist (P. obesus) occupying edge: (1) retains its characteristic foraging phenotype; (2) converges on the foraging phenotype of a closely related predator; or (3) undergoes phenotypic differentiation (sensu character displacement) to partition resources with a closely related predator.

Our study integrated diet analysis, geometric morphometrics, and feeding experiments to map these potential niche shifts. We utilized a comparative approach, measuring the phenotypes of P. obesus within core marsh vs. edge, and comparing these phenotypes to P. herbstii, the edge prey specialist. We first tested for prey resource use differences using stomach contents analysis and morphological differentiation by means of geometric morphometrics (Bookstein 1991; Mitteroecker and Gunz 2009). We hypothesized that, due to high resource availability and low competitor density within edges, marsh crabs would shift to edge prey and converge on the phenotype of the congeneric edge prey specialist. Then, to examine potential consequences of this polymorphism for estuarine food webs, we compared crab feeding efficiency on two species of edge prey across a range of prey sizes. We predicted that polymorphism would enhance feeding performance on edge prey. Broadly, our study reveals resource polymorphism as an important factor which promotes niche establishment within heterogeneous environments such as edges.

# Methods

#### Study system

The Xanthid crabs *Panopeus obesus and P. herbstii* (Family: Panopeidae) are important meso-predators within estuaries along the Southeastern U.S. and U.S. Gulf of Mexico coasts (Williams 1984). These congeneric crabs are known to partition estuarine habitats: *P. obesus* excavates U-shaped burrows in cordgrass (*Spartina alterniflora*) salt marshes (Griffin et al. 2015; Reames and Williams 1983; Silliman et al. 2004), while *P. herbstii* builds burrows within intertidal oyster (*Crassostrea virginica*) reefs (Kimbro et al. 2014; Williams 1984). Marsh habitats support several species of fiddler crab (*Uca* spp.), the purple marsh crab (*Sesarma reticulatum*) and the marsh periwinkle (*Littorina irrorata*), all of which are consumed by marsh-dwelling *P. obesus* (Griffin et al. 2015; Reames and Williams 1983; Silliman et al. 2004). In contrast, *P. herbstii* exploit the bivalve prey community present in reefs, most notably oysters (*Crassostrea virginica*) and scorched mussels (*Brachidontes exustus*) (Toscano and Griffen 2012). Thus, while both crab species could be considered generalist foragers, their habitat preferences typically limit diet overlap within estuarine ecosystems.

Though *P. obesus* is traditionally considered a marsh habitat specialist (Williams 1984), this species has also been detected within the salt marsh-oyster reef transition (Menendez 1987; the present study), a common estuarine edge habitat. This edge shares characteristics of marsh and reef habitats: tidal inundation is reduced compared to core oyster reef, Spartina is less dense than in marsh, and hard-shelled oyster reef bivalves (oysters and scorched mussels) are abundant. Previous work described the edge occurrence of P. obesus as an ontogenetic habitat shift (Menendez 1987), and our own sampling within North Inlet Estuary (South Carolina, USA) supports this. Specifically, due to the preponderance of large, adult P. obesus and lack of juveniles within edges, we suspect that adults migrate to edge, as opposed to settling there as larvae. In contrast, the oyster reef specialist P. herbstii is relatively rare within edges (Menendez 1987), but an efficient consumer of common edge prey (Toscano and Griffen 2012). Notably, these crab species, P. obesus and P. herbstii, appear similar to the untrained eye (to the point where (Menendez 1987) suggests that previous studies have misidentified them), suggesting these species could face similar mechanical or morphological constraints on phenotypic change. This scenario invites detailed analysis of P. obesus edge utilization, particularly in the presence of a morphologically similar congeneric predator, which could constrain phenotypic change and thus edge utilization.

#### **Study design**

Our study explored differences in trophic niches and phenotypes of the three crab groups: core marsh *P. obesus* (1) served as a baseline in this comparison from which edge *P. obesus* (2) could diverge, while *P. herbstii* (3) served as a foraging phenotype adapted to exploit bivalve prey that occur within edges. We first tested for diet differences among these crab groups using stomach contents analysis. We then applied geometric morphometrics to test for *P. obesus* morphological differentiation between marsh and edge. Last, to provide insight into the functional consequences of *P. obesus'* edge occupancy, we compared the feeding efficiency of all crab groups on edge prey across a range of prey sizes.

#### Diet

We collected crabs by hand during low tides from intertidal habitats within North Inlet estuary, South Carolina, USA during the summer of 2010. Crabs are active nighttime foragers, and thus we collected at night to minimize the chances of sampling crabs with empty stomachs. While the sampling period covered several months, environmental conditions in North Inlet are relatively stable over this period with minimal change in prey resource availability (Dame 1979). Crabs were identified to the species level using to previously established morphological characteristics (Williams 1983). Crabs (marsh *P. obesus:* n = 30, edge *P. obesus:* n = 30, *P. herbstii:* n = 103) were frozen within 1 h of collection to preserve stomach contents prior to stomach dissection and content analysis.

We examined the stomach contents of each crab under a dissecting microscope and measured percent composition of contents following (Griffen and Mosblack 2011). In crabs, ingested food is ground by the gastric mill located within the foregut, producing a slurry of particles that are relatively consistent in size. Accordingly, we emptied crab stomachs and separated contents by food type into a single layer of uniform height on a gridded Petri dish. We then counted the number of grid cells (or portions of grid cells) that each food type occupied to determine proportional contribution of each food type (Griffen and Mosblack 2011). Due to the largely pulverized nature of stomach contents, we categorized food types into seven groups: algae, crustaceans, oysters [C. virginica], mussels, Spartina, unidentified plants, and unidentified shells. The hard parts of crustaceans (exoskeleton), oysters and mussels (shells) were readily distinguishable through texture and color, as were clumped algae and Spartina fibers.

We visualized differences in diet composition across marsh *P. obesus*, edge *P. obesus* and *P. herbstii* using non-metric multidimensional scaling (nMDS) applied to the Bray–Curtis distance matrix of proportional stomach contents data using the R package *vegan* (Oksanen et al. 2020). To test for differences in diet composition among crab groups, we ran an Analysis of Similarities (ANOSIM, 9999 permutations), also in the R package *vegan*. Last, to quantify trophic niche similarity across each pair of crab groups, we computed the degree of niche overlap with bootstrap-generated confidence intervals using the R package *indicspecies* (De Cáceres et al. 2011).

#### Shape

We used landmark-based Geometric Morphometrics (Bookstein 1991) to perform shape analysis of carapace, major claw and minor claw. Carapace shape is only indirectly related to resource use (Idaszkin et al. 2013) and thus we did not expect carapace shape change between core marsh vs. edge *P. obesus*. In contrast, major and minor claws are used directly in prey capture, manipulation and feeding (Schenk and Wainwright 2001; Seed and Hughes 1995; Smith and Palmer 1994), and we hypothesized major and minor claw shape divergence. We further expected shape divergence of edge *P. obesus* claws to occur in the direction of *P. herbstii* which regularly consumes hard-shelled edge prey.

Crabs used in shape analysis (marsh *P. obesus*: n = 33, edge *P. obesus*: n = 31, *P. herbstii* n = 94) were largely overlapping with individuals used for diet analysis. We chose landmarks (n = 8 for carapace [Fig. 2B], n = 7 for major claw [Fig. 2D], n = 6 for minor claw [Fig. 2F]) that were easily identifiable across crab species and captured general shape differences (Schenk and Wainwright 2001). Crab carapaces and claws were removed before photography to facilitate standardized positioning. Claws were manually opened at maximum gape before being photographed in a lateral–distal view, while carapaces were photographed in top–down (i.e., dorsal) view. Landmarks were digitized using TpsDig2 (Rohlf 2006) and shape data were analyzed using the *geomorph* package in R (Adams and Otárola-Castillo 2013).

We used Procrustes ANOVA (*procD.lm* function) to test for morphological divergence between marsh and edge *P. obesus*. Edge individuals were on average larger than marsh individuals (ANOVAs of centroid size: P < 0.001 for each anatomical feature). Accordingly, we accounted for allometry throughout our analyses to ascertain that shape differences were not just a manifestation of shape allometry. The full model for each anatomical feature contained log centroid size, habitat type (marsh vs. edge), and their interaction as fixed effects. Crab sex and handedness (i.e., left vs. right) had no effect on shape (Procrustes ANOVA: P > 0.05 for each anatomical feature) and were thus excluded from full models.

The log centroid size × habitat type interaction was insignificant for carapace (Procrustes ANOVA: F=0.2042, P=0.989) and minor claw (Procrustes ANOVA: F=0.2156, P=0.936), supporting a common allometric scaling relationship while testing the effect of crab habitat type. Despite a significant log centroid size × habitat type interaction for major claw shape (Procrustes ANOVA: F=3.0125, P=0.035), the explanatory power of this effect was weak (Z-score = 1.802) and visual inspection of common allometric component plots (Online Resource, Mitteroecker et al. 2004) supported a common allometric scaling model. Accordingly, for all three anatomical features, we assumed a common allometric scaling relationship (i.e., additive effects of log centroid size and habitat type) in testing the effect of crab habitat type.

To visualize shape variation between marsh and edge *P. obesus* independent of allometry, we applied Principal Components Analysis (PCA) to size-corrected shape data using the *plotTangentSpace* function. Size-corrected shape data were residuals from an allometric model with log centroid size as the independent variable (*procD.lm* function). To visualize shape change of *P. obesus* relative to *P. herbstii*, we calculated Procrustes coordinates for all three crab groups together and used PCA to visualize major axes of shape variation (*plotTangentSpace* function). Because *P. herbstii* exhibited significantly different allometry than *P. obesus*, we could not correct for allometry and instead interpret shape with the effect of allometry included.

#### **Feeding efficiency**

We used mesocosm experiments to test for differences in feeding efficiency of the three crab groups on edge prey covering a range of prey sizes. Feeding experiments featured the most abundant bivalve prey species found within edges as well as oyster reefs: eastern oysters and scorched mussels (Dame 1979). We offered crabs adult oysters (45–60 mm shell length) and three size classes of scorched mussels (small: 13–16 mm shell length, medium: 17–20 mm shell length, large: 21–24 mm shell length) to explore whether prey size mediated the feeding efficiency of crabs.

For oyster feeding trials, we manipulated predator type, resulting in 3 treatments: marsh *P. obesus* (n=9; mean carapace width  $\pm 1$  standard deviation =  $35.38 \pm 2.88$  mm), edge *P. obesus* (n=9;  $35.89 \pm 2.05$  mm) and *P. herbstii* (n=9;  $33.81 \pm 1.91$  mm). Trials were run in a randomized complete block design with 3 treatment replicates per block and a total of 3 blocks (n=9 replicates per treatment). For mussel feeding trials, we crossed predator type with mussel size resulting in a  $3 \times 3$  factorial design. Again, we utilized a randomized complete block design with 1 replicate per treatment per block and a total of 6 blocks (n=6 replicates per treatment). Sizes of crabs used in mussel feeding trials were marsh *P. obesus* (n=18) =  $32.47 \pm 2.09$  mm, edge *P. obesus* (n=18) =  $34.29 \pm 1.94$  mm, and *P. herbstii* (n=18) =  $34.11 \pm 2.11$  mm.

All trials were run in plastic mesocosms  $(15 \text{ cm} \times 13 \text{ cm} \times 8 \text{ cm})$  containing 3 cm sand substrate and sparse oyster shell habitat as found along edges. We first drilled holes in the sides of mesocosms and then submerged them within a larger cylindrical tank that received a constant flow of unfiltered seawater pumped in from North Inlet. Each mesocosm contained 4 clusters of oyster shells assembled with plastic zip ties. These clusters were standardized by size as well as volume (measured through water displacement)



**Fig. 1** A Frequency of occurrence of food items in the stomach contents of marsh *P. obesus* (OM; n=30), edge *P. obesus* (OE; n=30), and *P. herbstii* (H; n=103). B Non-metric multidimensional scaling

to create a standardized matrix on which bivalve prey could attach. Bivalves were added at densities of 10 oysters or 20 mussels per mesocosm. Oysters were fixed to shell clusters using cyanoacrylate, while mussels were given time to attach naturally through byssal thread formation. After attachment, bivalves were observed for normal filtering behavior for 24 h to ensure good health before the start of feeding trials. Crabs were starved for 48 h to standardize hunger levels. A single crab was placed in each mesocosm and left undisturbed for 24 h after which surviving bivalves were counted. Crabs and bivalves were never reused.

We tested whether marsh P. obesus, edge P. obesus and P. herbstii differed in their feeding efficiency of edge prey using mixed models in the R package *lme4* (Bates et al. 2014). We constructed separate models for oysters and mussels. For oysters, we modelled proportional consumption with a binomial error distribution, including crab type and crab size (carapace width) as fixed effects with temporal block as a random effect. Proportional mussel consumption did not differ significantly from a normal distribution, and binomial model fits failed to converge and were over-dispersed. Therefore, we modelled proportional mussel consumption with a Gaussian error distribution, including crab type, prey size (small, medium or large) and crab size as fixed effects with temporal block as a random effect. We further included an interaction term between crab type and prey size to test whether potential consumption differences among marsh P. obesus, edge P. obesus and P. herbstii depended on mussel size. For both oyster and mussel models, the significance of fixed effects was tested by dropping fixed effects from full

(nMDS) of the Bray–Curtis distances computed on trophic data (two dimensions, stress=0.074). Standard ellipses represent core trophic niche areas (containing approximately 40% of the data)

models and comparing nested models using likelihood ratio tests. We used Tukey's contrasts in the R package *multcomp* (Hothorn et al. 2016) to make pairwise comparisons of foraging efficiency across crab groups.

# Results

# Diet

Resource use, measured via stomach contents, differed among the three crab groups (ANOSIM, R = 0.12, P = 0.0001) (Fig. 1). While marsh *P. obesus* exhibited a more omnivorous diet composed of plants (including *Spartina*), crustaceans and unidentified shells, edge *P. obesus* and *P. herbstii* diets were dominated by oysters (Fig. 1A). Accordingly, trophic niche overlap was higher between edge *P. obesus* and *P. herbstii* (overlap = 84.08%; CI 56.98–98.06%) than between marsh and edge *P. obesus* (53.58%, CI 27.55–87.97%) (Fig. 1B). Despite this general pattern, *P. obesus* from both edge and marsh habitats fed considerably on crustaceans, while crustacean prey made up just a small fraction of *P. herbstii* diet (Fig. 1A).

#### Shape: carapace

After accounting for the shared effect of size on shape (centroid size: F = 71.0426, P = 0.001), carapace shape was indistinguishable between marsh and edge *P. obesus* (crab type: F = 2.1253, P = 0.071; Fig. 2A, B). In

Fig. 2 Shape variation between marsh and edge P. obesus. Principal component analysis plots of carapace shape (A), major claw shape (C), and minor claw shape (E). OM: marsh P. obesus (n=33), white points; OE: edge *P. obesus* (n=31), grey points. Principal components analysis was applied to shape data which had been corrected for the effect of allometry (residuals from a centroid size model). Reference (grey) and target (black) shapes relative to the extremes of PC1 for carapace (B), major claw (D), and minor claw (F)



the 2-species (*P. obesus* and *P. herbstii*) PCA ordination plot, both types of *P. obesus* shared a wider, triangular carapace shape (positive portion of PC1—64.8% of

variance explained), while *P. herbstii* was characterized by a relatively rounded carapace (negative portion of PC1) (Fig. 3A, B).

Fig. 3 Shape variation between marsh and edge P. obesus relative to P. herbstii. Principal component analysis plot of carapace shape (A), major claw shape (C), and minor claw shape (E). OM: marsh P. obesus (n=33), white points; OE: edge *P. obesus* (n=31), grey points; H: P. herbstii (n = 94), black points. Principal components analysis was applied to raw shape data which had not been corrected for allometry. Reference (grey) and target (black) shapes relative to the extremes of PC1 for carapace (B), major claw (**D**), and minor claw (**F**)



# Shape: major claw

Major claw shape differed between marsh and edge P. obesus (crab type: F = 5.9034, P = 0.004; Fig. 2C, D) while

PC 2: 26.98%

accounting for a shared effect of allometry (centroid size: F = 6.9188, P = 0.002). Compared to marsh P. obesus (positive portion of PC1-59.4% of variance explained), edge individuals exhibited a taller, more robust major claw (negative portion of PC1) (Fig. 2D). Additionally, the major claw of edge *P. obesus* featured a dactyl (i.e., moveable finger) that: (1) sloped downward more steeply (landmarks 3, 4); and (2) featured an extended proximal tooth (landmark 5) (Fig. 2D). In the 2-species (*P. obesus* and *P. herbstii*) PCA ordination plot, edge *P. obesus* occupied an intermediate position along PC1 (50.8% of variance explained) (Fig. 3C, D). That is, edge *P. obesus* major claw shape trended towards the tall, robust claw shape of *P. herbstii*, while marsh *P. obesus* exhibited a slender major claw (Fig. 3D).

#### Shape: minor claw

Minor claw shape also differed between marsh vs. edge *P. obesus* (crab type: F = 17.169, P = 0.001; Fig. 2E) after accounting for a common allometry (centroid size: F = 20.273, P = 0.001). Like major claw, edge *P. obesus* exhibited a taller, more robust minor claw (negative portion of PC1—69.1% of variance explained) relative to marsh *P. obesus* (positive portion of PC1) (Fig. 2E, F). In contrast to patterns of major claw variation across crab species, edge *P. obesus* and *P. herbstii* were widely dispersed along PC1 (68.2% of variance explained) in the 2-species PCA ordination of minor claw shape, while marsh *P. obesus* almost exclusively occupied the positive region of this axis (Fig. 3E, F).

# **Feeding efficiency**

Edge *P. obesus* were roughly intermediate in their consumption rates of adult oysters (Fig. 4A), and not significantly different in feeding rate compared to either marsh *P. obesus* (Tukey's contrast: P = 0.625) or *P. herbstii* (Tukey's contrast: P = 0.292). As expected, marsh *P. obesus* consumed fewer oysters than the oyster specialist *P. herbstii* (Tukey's contrast: P = 0.036), driving a significant overall effect of predator type (likelihood ratio test:  $\chi^2 = 6.565$ , P = 0.038; Fig. 4A). Crab size (carapace width) had no effect on oyster consumption efficiency (likelihood ratio test:  $\chi^2 = 0.011$ , P = 0.917).

In contrast, edge *P. obesus* consumed a significantly greater proportion of mussels than marsh *P. obesus* (Tukey's contrast: P = 0.043) but not *P. herbstii* (Tukey's contrast: P = 0.982). The overall effect of crab type on mussel consumption (likelihood ratio test:  $\chi^2 = 0.698$ , P = 0.030) was further consistent across all three mussel size classes (likelihood ratio test:  $\chi^2 = 0.601$ , P = 0.963; Fig. 4B). Crabs consumed fewer large mussels overall, driving a significant independent effect of prey size on consumption efficiency (likelihood ratio test:  $\chi^2 = 15.86$ , P < 0.001; Fig. 4B). Again, crab size had no effect on consumption efficiency (likelihood ratio test:  $\chi^2 = 0.111$ , P = 0.740).



**Fig. 4** Feeding efficiency of marsh *P. obesus* (OM), edge *P. obesus* (OE), and *P. herbstii* (H) on edge prey: oysters (**A**) and scorched mussels (**B**). Individual crabs were offered 10 oysters (45–60 mm shell length) or 20 mussels from three size classes (small: 13–16 mm shell length, medium: 17–20 mm shell length, large: 21–24 mm shell length) in 24 h mesocosm feeding trials. Oyster treatments were replicated 9 times each, while mussel treatments were replicated 6 times each. Bars represent means of proportional consumption and error bars represent ± 1 standard error

# Discussion

Intraspecific variation in resource use is a common property of natural populations (Bolnick et al. 2003; Smith and Skúlason 1996); yet its relation to habitat edges has received scant research attention. We integrated stomach content analysis, geometric morphometrics and feeding experiments to explore the role of resource polymorphism in facilitating edge utilization by a habitat specialist predator. In line with our hypotheses, edge *P. obesus* exhibited dietary and morphological differentiation compared to core marsh individuals as well as enhanced feeding performance on heavily defended edge prey. These phenotypic and functional changes trended towards a closely related edge prey specialist and potential competitor, *P. herbstii*, suggesting a lack of resource limitation and weak interspecific competition within edges (Bøhn and Amundsen 2001; Robinson et al. 1993; Schluter and McPhail 1992). While habitat specialists such as *P. obesus* are expected to decline with proximity to edge based on natural history knowledge alone (Ries et al. 2017; Ries and Sisk 2004), our work suggests resource polymorphism can promote successful edge utilization.

# Correspondence between diet and morphological change: resource polymorphism

The most notable changes in edge P. obesus diet were the increased prevalence of oysters and reduced prevalence of plant matter relative to core marsh individuals. These changes, which could be construed as a shift from omnivory to relative carnivory, yielded a diet which converged on that of the bivalve prey specialist, P. herbstii. Oysters are rare within salt marshes but do occur as patchily distributed clusters (Griffin et al. 2015). Similarly, live Spartina is sparse within edges but dead plants (i.e., "wrack") do wash up during high tides. Thus, the diet shift of P. obesus between marsh and edge appears to track changes in the abundance of food resources across these habitats, perhaps due to prey switching (Murdoch 1969), as opposed to the maintenance of feeding preferences despite shifts in resource abundance. Despite these differences in the diets of edge vs. marsh P. obesus, we did detect one notable similarity: edge P. obesus retained a substantial portion of crustacean prey in their diet, which P. herbstii lacked. While the particular crustacean species that edge P. obesus feeds on are unknown (our stomach content analysis could not distinguish species), it seems likely that edge P. obesus are consuming fiddler crabs (Uca spp.) or Sesarma reticulatum, which are common within edges and consumed by P. obesus in marshes (Griffin et al. 2015; Silliman et al. 2004).

Panopeus obesus' shift to a more bivalve-based diet along edges was accompanied by claw shape differentiation from marsh P. obesus. Notably, shape differentiation occurred independent of size differences (edge individuals were generally larger) which we accounted for in our analysis. Specifically, we found that edge individuals exhibited relatively taller and more robust major and minor claws compared to marsh individuals, while carapace shape was indistinguishable between these two groups. The former finding aligns with previous work comparing claw morphology across crab species that vary in their degree of durophagy, or feeding on hard-shelled prey (Schenk and Wainwright 2001). This study concluded that force generation used to crush hard-shelled prey is largely due to cross-sectional area of the closer muscle and thus differences in the height of claws across species (Schenk and Wainwright 2001). While a number of studies have demonstrated intraspecific variation in crab claw morphology associated with prey resource use over broad geographic scales (Deli et al. 2014; Edgell and Rochette 2007, 2008, 2009; Rebach and Wowor 1997; Silva and Paula 2008; Smith 2004; Taylor et al. 2009), our study demonstrates the importance of polymorphism at small scales where habitats are adjacent.

While edge-related morphological change in P. obesus likely has a plastic component, a genetic basis for polymorphism cannot be ruled out. In support of phenotypic plasticity, previous work shows that red rock crabs (Cancer productus) and European green crabs (Carcinus maenas) develop larger and more powerful claws when fed intact vs. crushed mussels between molts, and this morphological change enhances claw crushing force (Baldridge and Smith 2008; Smith and Palmer 1994). We suspect that the same mechanism of phenotypic plasticity occurs when P. obesus enter edges as adults via an ontogenetic habitat shift (Menendez 1987), and thus residence time in edges could determine the degree of marsh vs. edge phenotypic differentiation. While the lack of juvenile P. obesus in edges suggests larval settlement within marshes (Forward et al. 2001; Rodriguez and Epifanio 2000; Weber and Epifanio 1996) and thus incomplete spatial segregation, genetic differentiation between edge and core individuals could still occur via assortative mating. Specifically, if adults with edge-related traits (e.g., enhanced plasticity) mate within edges, then these traits can be passed on to offspring that settle in marshes but migrate to edges later in ontogeny.

#### Effects on estuarine food webs

To test the functional consequences of resource polymorphism, we compared the feeding efficiency of crab groups on edge prey across a range of prey sizes. Supporting the ecological relevance of intraspecific variation (Bolnick et al. 2011; Clegg et al. 2018; Toscano et al. 2016), we demonstrated differences in the predation rates of marsh vs. edge individuals: edge P. obesus consumed more scorched mussels than marsh P. obesus, but did not differ from marsh P. obesus in oyster consumption rate. Adult oysters are significantly larger than scorched mussels and likely reach a partial size refuge from crab predation in the field (Toscano and Griffen 2012). Thus, while bivalve specialists such as P. herbstii often exhibit no preference for bivalves of different sizes (Yamada and Boulding 1998), P. obesus might be limited to small edge prey due to reduced claw strength and thus crushing force. Accordingly, given the prevalence of oysters in edge P. obesus stomachs, we assume that P. obesus are primarily consuming juvenile oysters within edges that are smaller than those used in our feeding experiment.

The difference in edge vs. marsh *P. obesus* feeding rate on scorched mussels is likely a result of morphological rather than behavioral change for two reasons. First, the sessile

nature of bivalves minimizes the importance of capture efficiency relative to mobile prey that can evade predators. Second, we attached bivalves to a fairly simple shell habitat characteristic of edges, a design that should further reduce effects of searching behavior that would arise in a more complex habitat (Toscano and Griffen 2013). Thus, assuming that edge and marsh *P. obesus* spent the same amount of time actively foraging during feeding trials, we suspect that consumption rate differences were mostly due to differences in handling time (i.e., the time it takes to chip open or crush and eat a single bivalve), which should relate strongly to claw morphology.

Despite prey size constraints on the feeding performance of edge *P. obesus*, edge occupancy of *P. obesus* could alter top-down pressure on bivalves across mosaic estuarine landscapes (Minello et al. 1994), though this could further depend on direct interference or even predatory interactions (e.g., intra-guild predation) between *P. obesus* and *P. herbstii*. While increased feeding performance should enhance edge *P. obesus* reproductive output, juvenile crabs would likely settle in marshes due to habitat-specific settlement cues (Forward et al. 2001; Rodriguez and Epifanio 2000; Weber and Epifanio 1996). Through this mechanism, the success of marsh crabs within edges could supplement *P. obesus* population growth within core marsh habitat.

# Conclusion

While species-level, trait-based models have enhanced our understanding of consumer edge responses (Ewers and Didham 2006; Ries and Sisk 2004; Wimp et al. 2019), our study suggests a role for intraspecific trait variation in resource utilization along habitat edges. Specifically, we demonstrated a functional link between habitat edges and predator-prey interactions mediated by resource polymorphism, a widespread but often overlooked feature of natural populations (Bolnick et al. 2003, 2011; Smith and Skúlason 1996). Though resource-based phenotypic changes are often subtle, enhanced feeding efficiency can facilitate niche expansion towards edges, explaining neutral or even positive edge responses of presumed specialist species (Ries et al. 2017). We advocate that further study of the mechanistic basis of edge utilization can be used to refine edge models, thereby increasing our ability to predict ecological patterns and phenomena in an increasingly fragmented world.

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the data. BJT wrote the manuscript; other authors provided editorial advice.

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**Code availability** The code was deposited in Mendeley Data under the reference number https://doi.org/10.17632/8prgdffv92.1.

#### Declarations

**Ethical approval** All applicable institutional and/or national guidelines for the care and use of animals were followed.

Consent to participate No patients were used in this study.

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