

Predator size interacts with habitat structure to determine the allometric scaling of the functional response

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While both predator body size and prey refuge provided by habitat structure have been established as major factors influencing the functional response (per capita consumption rate as a function of prey density), potential interactions between these factors have rarely been explored. Using a crab predator (*Panopeus herbstii*) – mussel prey (*Brachidontes exustus*) system, we examined the allometric scaling of the functional response in oyster (*Crassostrea virginica*) reef habitat, where crevices within oyster clusters provide mussels refuge from predation. A field survey of mussel distribution showed that mussels attach closer to the cluster periphery at high mussel density, indicating the potential for saturation of the refuge. In functional response experiments, the consumption rate of large crabs was depressed at low prey density relative to small crabs, while at high prey density the reverse was true. Specifically, the attack rate coefficient and handling time both decreased non-linearly with crab size. An additional manipulation revealed that at low prey densities, the ability of large crabs to maneuver their claws and bodies to extract mussels from crevices was inhibited relative to small crabs by the structured habitat, reducing their attack rate. At high prey densities, crevices were saturated, forcing mussels to the edge of clusters where crabs were only limited by handling time. Our study illuminates a potentially general mechanism where the quality of the prey refuge provided by habitat structure is dependent on the relative size of the predator. Thus anthropogenic influences that alter the natural crab size distribution or degrade reef habitat structure could threaten the long-term stability of the crab – mussel interaction in reefs.

Predator–prey interactions provide structure for communities and the strength of these interactions is a primary determinant of community stability (MacArthur 1955, Paine 1980, Berlow et al. 2004, O’Gorman and Emmerson 2009). Accordingly, understanding the factors that constrain predator–prey interaction strength remains a continual goal in ecology (Berlow et al. 2004). Predator–prey interaction strength is often described by an individual predator’s consumption rate as a function of prey density (Holling 1959, Berlow et al. 2004). This relationship, termed the functional response (Solomon 1949), is dependent on emergent traits related to a predator’s foraging behavior such as attack rate (instantaneous rate of encounter, depending on reactive distance, movement speed and capture success) and handling time (time it takes to capture, subdue, consume and digest an individual prey) (Holling 1959, Jeschke et al. 2002). As a component of predator–prey population models, the functional response allows scaling up from these individual behavioral traits to predict predator and prey population dynamics. At the population level, the precise shape of the functional response, as determined by the predator’s attack rate and handling time, governs the stability of predator–prey dynamics (Murdoch and Oaten 1975, Hammill et al. 2010).

Due to the importance of the functional response for predator–prey population dynamics, considerable work has been conducted on the ecological factors that determine response characteristics (Jeschke et al. 2002). One such factor is the ratio of predator size to prey size. Predator–prey size ratios generally act to constrain the functional response within parameter space due to mechanistic links between body size and foraging behavior traits (Brose 2010). For example, attack rate is predicted to be hump-shaped with respect to the predator–prey body size ratio. When predators are small relative to their prey, their search area and movement speed should be reduced and when predators are large relative to their prey, their capture success should be low with some maximum in between. Indeed, recent work employing simple allometric constraints has had great success in predicting trophic links and their strength in empirical food webs (Otto et al. 2007, Petchey et al. 2008, O’Gorman and Emmerson 2009). However, empirical data on such scaling relationships is sparse, and as a result, common patterns in the size scaling of foraging traits remain unresolved (Brose 2010). Determining the precise allometric scaling of functional response parameters is important because it can have major consequences for the dynamics of size structured populations (Persson et al. 1998, McCoy

et al. 2011). Furthermore, studies documenting allometric scaling of the functional response rarely identify the mechanisms behind empirical scaling relationships (Brose 2010, Vucic-Pestic et al. 2010); identifying these mechanisms is essential in making predictions that extend beyond specific taxonomic groups.

A second ecological factor that can significantly affect the functional response is prey refuge, defined as any strategy that reduces predation risk (Sih 1987). For example, a prey refuge provided by habitat structure is commonly cited as the mechanistic basis of sigmoidal or type III functional responses (Hildrew and Townsend 1977, Anderson 2001). At low prey densities, most prey occupy the structural refuge and are therefore invulnerable to predation. As prey density increases, the refuge becomes saturated and the proportion of prey in the refuge decreases (Sih 1987). This causes density dependent predation (proportional consumption is lowest at the lowest prey densities), and thus a type III response. Because type III functional responses can stabilize predator–prey population dynamics (Murdoch and Oaten 1975, but see Basset et al. 1997), prey refuges are generally assumed to have this effect, but prey refuges can also destabilize interactions under certain circumstances (McNair 1986).

While numerous studies demonstrate the independent importance and ubiquity of predator–prey body size ratios and structural prey refuges in determining the functional response, interactions between these two factors, though rarely explored, may be fundamental to determining the functional response in many systems. Habitat structure is intrinsically size-dependent, as different sized individuals perceive habitat structure differently based on their own body size (sensu MacArthur and Levins 1964). For example, habitat structure could act as a filter that restricts large predators more effectively than small predators from accessing prey due to the greater maneuverability of smaller predators through structurally complex habitats (Denno et al. 2004, Brose 2010). This effect could be particularly strong at low prey densities when a greater proportion of prey are located within the refuge (Sih 1987). Such an interaction of predator size and a prey structural refuge could lead to changes in the attack rate, driving a shift from a hyperbolic, type II (no prey refuge) to a type III response (prey refuge) with increasing predator–prey size ratio (Brose 2010).

In the present study, we examined potential interactions between predator body size and a structural refuge for prey in determining the functional response of a crab (*Panopeus herbstii*) foraging on mussels (*Brachidontes exustus*) in oyster *Crassostrea virginica* reef habitat. Here, mussels use crevices within oyster clusters as a refuge from crab predation. We first tested for density dependence in refuge use by mussels in the field, an important criterion for the stabilizing effects of the refuge on predator–prey dynamics (Sih 1987). We then examined how the functional response scales with predator body size within this structured habitat. We hypothesized that the crab functional response would shift from type II to type III with increasing crab size. *Panopeus herbstii* exhibits a type II response when foraging on another bivalve (loose oysters) in a simple, unstructured laboratory setting (Rindone and Eggleston 2011). Therefore we expected small *P. herbstii*

to exhibit a type II response when foraging on mussels because they are not restricted by habitat structure in accessing mussels. Large crabs, in contrast, should be more restricted in accessing mussels, eliciting a type III response. Finally, we performed a manipulation to determine the degree to which habitat structure hampers the ability of large versus small crabs to extract prey from the refuge.

Methods

Study system

We used a crab predator (*Panopeus herbstii*) – mussel prey (*Brachidontes exustus*) system to examine the effects of predator body size and a structural refuge for prey on the functional response. *Panopeus herbstii* (Xanthidae) inhabits a range of habitats in the intertidal zone along the eastern and Gulf coasts of the US (Williams 1984). Within our study site (North Inlet estuary, SC, USA), this crab is the numerically dominant resident predator in structurally complex intertidal oyster *Crassostrea virginica* reefs (Dame 1979). Here, *P. herbstii* feeds on a number of bivalve species including *B. exustus* (Toscano and Griffen 2012).

The *P. herbstii* – bivalve body size ratio is important in determining their predator–prey relationships in reefs. For example, there is evidence that larger *P. herbstii* individuals (> 30 mm carapace width, CW) preferentially consume larger bivalves (Seed 1980, Whetstone and Eversole 1981), while smaller individuals are restricted to consuming smaller bivalves (Seed 1980, Toscano and Griffen 2012). These shifts in prey choice may be related to size specific differences in the foraging abilities of different sized crabs. Furthermore, because populations of *P. herbstii* in North Inlet include a broad size range of individuals (Dame and Vernberg 1982, McDonald 1982), size dependent foraging traits could determine the population-level impacts of *P. herbstii* on bivalves (Toscano and Griffen 2012).

The importance of reef habitat structure and the complexity of this structure (e.g. aggregated versus unaggregated oyster shells, Grabowski and Powers 2004) for trophic interactions involving *P. herbstii* has also received attention. Experimental manipulations show that oyster reef structural complexity reduces interference between foraging *P. herbstii* conspecifics at high crab densities, enhancing their consumption of the hard clam *Mercenaria mercenaria* (Grabowski and Powers 2004). In contrast, ribbed mussel *Geukensia demissa* prey appear to take some refuge in structurally complex oyster clusters from *P. herbstii* predation (Lee and Kneib 1994). Similarly, the mussel *B. exustus* is found almost exclusively in crevices within oyster clusters in intertidal oyster reefs in North Inlet. When placed on oyster shell in flow-through tanks, these mussels tend to seek out (‘walking’ with their muscular foot) and attach preferentially to crevices between shells (Toscano unpubl.). Living within protective crevices could limit the capture success of their relatively larger crab predator, thus serving as a refuge from otherwise intense crab predation in reefs.

All animals used in experiments as well as oyster clusters for the survey of mussel distribution within clusters were

collected from intertidal oyster reefs in North Inlet estuary (33°20'N, 79°10'W), Georgetown, South Carolina, USA. We conducted our study during May–September in 2010 and 2011, and experiments were run in a screened-in wet laboratory at the Belle W. Baruch Inst. for Marine and Coastal Sciences.

Field survey of mussel distribution in oyster clusters

We first surveyed the distribution of individual mussels within oyster clusters ($n = 35$) from the field to examine potential density-dependence in their use of this refuge habitat. An oyster cluster is a conglomeration of live oysters and dead shells that is detached, but still resting on the surface of the reef. These clusters contain a network of interstitial spaces that are occupied primarily by mussels. For our survey, we selected oyster clusters of roughly equal size from intertidal reefs (~50 m²) that border tidal creeks in North Inlet. Clusters selected were from the same tidal height and spaced at least 1 m apart in reefs. We measured the weight of each cluster, the depth of individual mussels within the cluster (cm from cluster edge), as well as the number of mussels in each cluster. Only mussels that were visible from the cluster exterior and thus presumably accessible to crabs were measured.

We tested for the effects of mussel density on the location of individual mussels within oyster clusters using generalized linear mixed effects modeling (function *glmer*, package *lme4* in R ver. 2.12.0). We first regressed the number of mussels per cluster on cluster weight to determine the residual variation in mussel number not due to cluster size (i.e. mussel density). We then used these residuals as well as cluster weight as fixed factors, and cluster number as a random factor (to control for pseudoreplication), with the distance of individual mussels from the edge of the cluster as the response variable in a generalized linear mixed model (GLMM) fit by the Laplace approximation. Because mussel location data contained zeros and behaved like count data, we assumed Poisson distributed errors with a log link (Bolker et al. 2009). To correct for overdispersion, we included an additional random factor at the level of the individual observation (the number of data points) (Elston et al. 2001, Bolker et al. 2009), which has the effect of converting the Poisson distribution to a lognormal-Poisson distribution (similar to the negative binomial distribution typically used to model overdispersion). We fit models with and without fixed factors (while retaining the random factors) and compared models using Akaike's information criterion corrected for small sample sizes (AIC_c) to determine whether adding factors significantly improved the fit of models, while taking into account the added model complexity.

Functional response experiments

We determined the functional response for six crab size classes (18–21 mm carapace width (CW), 23–26 mm CW, 28–31 mm CW, 33–36 mm CW, 38–41 mm CW and 43–46 mm CW) foraging in oyster reef habitat. The smallest crab size class (18–21 mm CW) is around the minimum size capable of consuming the size of *B. exustus*

used in the present study (12–16 mm shell length) (Toscano unpubl.), and the largest size class is near the maximum body size of *P. herbstii* from North Inlet (Dame and Vernberg 1982, McDonald 1982). We offered *B. exustus* to crabs in 10 densities within oyster clusters: 1, 2, 4, 6, 8, 10, 14, 20, 30 and 40 mussels per tank. Smaller increments between lower prey densities allowed detection of subtle curvature in the functional response. Trials were run in a randomized block design. All treatments were replicated at least three times, with treatments showing particularly high variance replicated up to nine times.

Artificial oyster clusters were used to approximate the structure of natural reefs, while providing a relatively standardized reef habitat on which mussels could attach. Clusters were created using oyster shell that had been dried and cleaned to ensure removal of any epifauna. Holes were drilled in shell and shell clusters were assembled to mimic natural reef formations using plastic zip-ties. Clusters were standardized by the number of shells (five shells per cluster) as well as volume (measured through water displacement). The necessary number of mussels for a given treatment were placed evenly on two oyster clusters in a flow-through seawater table and allowed to attach through byssal thread formation overnight. During this period, mussels moved within the clusters to find an appropriate anchoring location. Crevice space was limiting in these clusters at high mussel densities, forcing some mussels to attach towards the cluster periphery.

We ran the functional response experiments in glass mesocosms (50 × 28 × 30 cm) that were completely enclosed in black plastic to reduce light entry, thus mimicking the low-light conditions of North Inlet estuary during summer months (Dame et al. 1986). Each tank received a single crab, which scales up to a density of approximately seven crabs per m². Crab population density during summer months averages 13.08 ± 6.23 (mean \pm 1 SD) crabs > 18 mm CW (Toscano unpubl.), and thus our experimental density falls within this range. We established mesocosms as follows. First, a 3 cm layer of sand/mud substrate taken from the estuary was added to the bottom of the tanks. Next, two artificial oyster clusters with attached mussel prey of a certain density were added. Last, eight large oyster shells (dried and cleaned of epifauna) of approximately equal size were scattered around the oyster clusters within each mesocosm, again to mimic natural reef habitat. Each tank received a constant flow of unfiltered seawater throughout trials.

Only crabs with two fully developed and functional claws (i.e. no re-growing or damaged claws) were used and individual crabs were only used once (i.e. for 1 prey density). Crabs were starved for one day prior to trials to standardize hunger levels. Crabs were placed in tanks at the start of trials and given 24 h to forage, after which the sand substrate was sieved and oyster clusters and loose shell were checked for remaining mussels. We used 24 h trials to prevent high levels of prey depletion based on consumption rates determined in preliminary trials.

Functional responses were estimated separately for each predator size class ($n = 6$). We applied a generalized functional response model to consumption data (Real 1977, Hammill et al. 2010):

$$N_e = \frac{PT}{b + (1/bN_0^q N_0)} \quad (1)$$

Where N_e is the number of prey eaten, N_0 is initial prey density, P is the number of predator individuals, T is the experimental duration, b is handling time and bN_0^q describes the attack rate (Real 1977, Hammill et al. 2010). This attack rate term (bN_0^q) allows density-dependence in the functional response, where b is a coefficient that describes the scaling of attack rate with prey density (Vucic-Pestic et al. 2010), and q is an exponent that allows the response type to vary between a type II response ($q = 0$) and a type III response ($q > 0$) (Hammill et al. 2010). Because prey were consumed and not replaced over the 24 h duration of our experiment, declining prey density was integrated over the experimental duration to find the number of prey eaten (Hammill et al. 2010). To estimate parameters, the functional response model was fit using maximum likelihood with binomial errors. We only assumed a type III response when q was significantly greater than zero and confirmed the response type by fitting traditional type II and type III functional response models to each crab size class and comparing fits using Akaike's information criterion (AIC).

Manipulation of mussel distribution within oyster clusters

During functional response experiments, we observed that mussels not eaten by large crabs at low mussel densities tended to be located within crevices in clusters, rather than exposed. This led us to hypothesize that large crabs are less efficient foragers at low mussel densities because their larger claws are less dexterous within crevices, resulting in a lower attack rate than small crabs. To test this interaction of habitat structure and predator size, we crossed mussel distribution (0, 3 and 6 cm from the cluster exterior) with crab size (23–26 mm CW, 33–36 mm CW and 43–46 mm CW), resulting in nine unique treatments, each replicated six times. Trials were run in a randomized block design with six treatments per temporal block. Mussel distribution was manipulated by gluing eight mussels within a standardized cluster at a set distance from the exterior of the cluster (0, 3 or 6 cm). A density of eight mussels was used because all size classes 23–26 mm CW and larger showed the ability to

consume this number of prey over 24 h (Fig. 2), allowing us to attribute any differences in predation efficiency to capture success, rather than handling time. Observations confirmed that mussels continued normal filtering activity after being glued to clusters.

Artificial clusters used in this additional manipulation were different from those used in the functional response experiment and were created as follows. Five rectangular sheets ($12 \times 5 \times 0.2$ cm, roughly the size of an oyster shell) of acrylic plexiglas were glued together at one end in the configuration of an open book. This design allowed us to hold the angle between plexiglas sheets constant (not possible with irregularly shaped oyster shells) and precisely control the distribution of mussels within the cluster. This experiment was run in smaller plastic mesocosms ($30 \times 18 \times 12$ cm). Experimental conditions (e.g. mesocosm setup and experimental duration) were otherwise the same as in the functional response experiments.

We tested for the fixed effects of mussel distribution (distance from the edge of the cluster), crab size, and their interaction, with temporal block as a random factor on mussel consumption in a GLMM. Again, we fit the model using the Laplace approximation and assumed Poisson distributed errors with a log link for count data (Bolker et al. 2009). Fixed factors and the interaction term were dropped sequentially while retaining the random factor. We determined the most parsimonious model using AIC_C comparisons. All statistical analyses were conducted using R (ver. 2.12.0, R Core Development Team).

Results

Field survey of mussel distribution in oyster clusters

Mussel density was an important predictor of individual mussel location; the model including this factor provided a better fit than the null model of the random factor (cluster number) only ($\Delta AIC_C = 4.81$), as well as the next best model including the additional factor of cluster weight ($\Delta AIC_C = 2.01$) (Table 1). Mussel density was negatively associated (coefficient \pm SE: -0.062 ± 0.0227 , $p = 0.006$) with mussel location within clusters (distance from cluster edge) (Fig. 1).

Table 1. Comparison of competing models used to predict individual mussel location within oyster clusters from the field survey (see 'Methods: Field survey of mussel distribution in oyster clusters'), and models used to predict mussel consumption in the experiment (see 'Methods: Manipulation of mussel distribution within oyster clusters').

Model parameters	K	AIC_C	ΔAIC_C	W
Response: individual mussel location within oyster clusters (field survey)				
Mussel density + cluster number + observation number	3	315.5	0.00	0.67
Mussel density + cluster weight + cluster number + observation number	4	317.5	2.01	0.25
Cluster number + observation number	2	320.3	4.81	0.06
Cluster weight + cluster number + observation number	3	322.2	6.70	0.02
Response: mussel consumption (experiment)				
Crab size + mussel location + crab size \times mussel location + temporal block	4	86.9	0.00	1.00
Crab size + mussel location + temporal block	3	107.3	20.44	0.00
Mussel location + temporal block	2	117.1	30.20	0.00
Crab size + temporal block	2	133.9	47.03	0.00

K is the number of parameters, ΔAIC_C is the difference between AIC_C values for each model and the model with the lowest AIC_C , and W is the AIC_C weight.

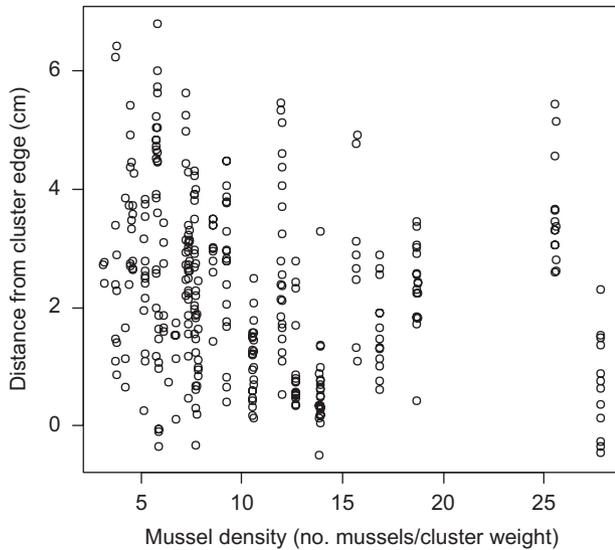


Figure 1. Relationship between mussel density and individual mussel location from oyster clusters collected from intertidal oyster reefs in North Inlet, SC. Each point represents an individual mussel's location (distance from the edge of the cluster [cm]) as a function of the mussel density (no. of mussels/cluster weight [kg]) in that cluster. Small amounts of horizontal and vertical displacement were added to points for clarity.

Functional response experiments

In contrast to our hypothesis that crabs would transition from a type II to a type III functional response with crab size, we found that all crab sizes exhibited type III functional responses (q significantly greater than 0; Table 2, Fig. 2, 3B), except for 23–26 mm and 43–46 mm size classes, in which q was greater than, but not significantly different from zero (Table 2). AIC comparison of type II and type III models fit to each size class generally supported these results; a type III response better explained consumption rate data than a type II response for all predator size classes. Attack rate coefficient and handling time parameters declined non-linearly with predator body size (Fig. 3A, 3C). Specifically, the attack rate declined abruptly between 28–31 mm and 33–36 mm crab size classes (Fig. 3A). Handling time declined as a power-law function of crab size, as indicated by the linear relationship after log-transformation (Fig. 3C). A simple power-law function fit to the handling time data yielded the equation $h = 1.718(\text{body size})^{-0.87}$.

Manipulation of mussel distribution within oyster clusters

In the test of the mechanism behind the shift in attack rate (Fig. 3A), the model including crab size and mussel distribution as factors, as well as their interaction, performed much better than the next best model ($\Delta\text{AIC}_C = 20.44$) (Table 1). Regarding the interaction between these factors, the mussel consumption of small crabs (23–26 mm) was not affected by mussel location within the artificial cluster, while the consumption of larger crabs (33–36 mm, 43–46 mm) decreased when mussels were located deeper within the cluster (3, 6 cm) (Fig. 4).

Discussion

The relative sizes of predator and prey constrain trophic interactions at an individual level (Brose 2010), and studies employing these allometric constraints have had great success in predicting the properties of natural food webs (Otto et al. 2007, Petchey et al. 2008, O'Gorman and Emmerson 2009). In the present study, we examined how habitat structure affects the allometric scaling of the functional response, thus extending our understanding of size-based foraging constraints to more realistic habitats that include prey refugia. While all crab sizes exhibited roughly type III functional responses in the structurally complex habitat (Fig. 2, 3B), crab sizes differed in functional response parameter estimates. These parameter estimates and their size scaling have major implications for predator and prey population stability (Persson et al. 1998, Hammill et al. 2010, McCoy et al. 2011). In particular, we observed a decline in the attack rate coefficient with crab size, separating the three smaller and three larger size classes into functional groups (Table 2, Fig. 3A). We hypothesized that this reduction in attack rate with predator size was due to larger crabs being limited in their ability to reach into tight spaces within clusters to remove mussels, resulting in a prey refuge that is dependent on predator size. This hypothesis was supported by our experiment that manipulated the location of mussels within artificial clusters and measured the consumption efficiency of crabs of different body sizes (Fig. 4). Furthermore, our survey of mussel distribution within clusters from the field showed that mussels attached closer to the edge of clusters with increasing mussel density (Fig. 1). This is probably because the deeper, more protected spaces

Table 2. Parameter estimates, their standard errors, and statistical significance levels for the functional response model (Eq. 1) fit to each predator size class. Model parameters are the attack rate coefficient (b), a scaling exponent parameter (q) indicating the type (i.e. type II or type III) of response, and handling time (h).

Size class	b	SE (b)	q	SE (q)	h	SE (h)
18–21 mm	1.5340***	0.0372	0.6547***	0.0160	0.1414***	0.0034
23–26 mm	1.6706	1.0612	0.9374	0.8038	0.1251***	0.0126
28–31 mm	1.5043*	0.5978	1.4522*	0.6395	0.0823***	0.0053
33–36 mm	0.3961*	0.1918	0.7588*	0.3193	0.0729***	0.0091
38–41 mm	0.2545*	0.1127	0.5960*	0.2904	0.0786***	0.0162
43–46 mm	0.1399	0.1017	0.6953#	0.3887	0.0689***	0.0191

Level of significance: $p < 0.001$: ***; $p < 0.01$: **; $p < 0.05$: *; $p < 0.1$: #

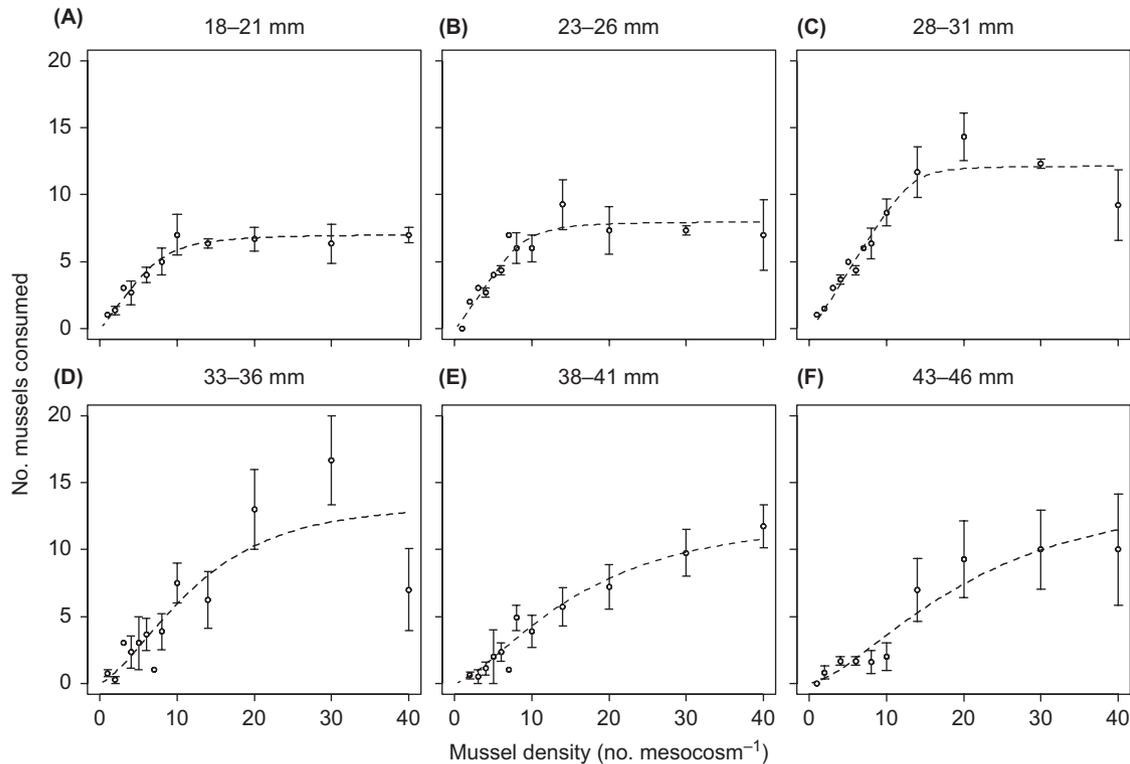


Figure 2. Mean consumption ± 1 SE with functional response model (Eq. 1) fits for six crab size classes foraging on mussels across a range of mussel densities: (A) 18–21 mm carapace width (CW); (B) 23–26 mm CW; (C) 28–31 mm CW; (D) 33–36 mm CW; (E) 38–41 mm CW; (F) 43–46 mm CW.

in clusters were already occupied, forcing newly settling mussels to attach where they are more vulnerable to crab predation. Thus crevice space could be a limiting resource in the field.

While an abundance of studies show that habitat structure and the complexity of this structure can reduce foraging efficiency (Orth et al. 1984), the precise mechanism by which this occurs is rarely identified. Decreased foraging efficiency in structured habitats is usually attributed to increased search and pursuit time of predators (Crowder and Cooper 1982). The interaction between predator size and habitat structure shown here (Fig. 4) provides an alternative or additional mechanism behind the commonly reported negative relationship between habitat structure and predation success. This mechanism is potentially widespread, occurring wherever relatively larger predators must enter or reach into tight spaces to capture prey. For example, this mechanism has been implicated in driving the predation refuge for small or juvenile resident fish in corals reefs (Hixon and Beets 1993, Holbrook and Schmitt 2002, Almany 2004), where sheltered holes in high complexity reefs limit the foraging success of large transient predators. This mechanism was also suggested to operate in decreasing the foraging success of large, but not small pipefish foraging on amphipods that took refuge in crevices between seagrass shoots (Ryer 1988), as well as smallmouth bass foraging on crayfish that use interstitial spaces between cobble substrate as a refuge from predation (Stein 1977). While these studies have implicated the mechanism shown here, ours is one of the few (see also Holbrook and Schmitt 2002, Sarty et al. 2006) to experimentally demonstrate this

mechanism, as made possible by our ability to manipulate the distribution of prey within the refuge. In general, reductions in predation rate associated with prey refuges reduce interaction strengths and enhance population stability (McCann et al. 1998, Berlow 1999). Thus, the size dependent prey refuge revealed in the present study could have important implications for the dynamics of predator and prey populations and food webs more broadly.

Past studies have reported hump-shaped relationships between predator–prey size ratio and the attack rate (Spitze 1985, Vucic-Pestic et al. 2010, McCoy et al. 2011), although linear relationships have also been shown (Thompson 1975, Hassell et al. 1976). Proposed mechanisms behind hump-shaped attack rates include reduced consumer movement and reactive distance at a low size ratio, decreased capture success at a high size ratio, and a high attack rate due to improved movement and capture success at some intermediate predator–prey size ratio (Brose 2010), though these hypothesized mechanisms await empirical confirmation. While the scaling of the attack rate with predator size in our study could be interpreted as the middle-right region of a hump-shaped relationship (Fig. 3A), and thus the result of previously suggested, habitat structure-independent mechanisms, several lines of evidence indicate that these mechanisms do not apply to the present system. First, while a predator’s attack rate is dependent on predator and prey speeds of movement, prey movement speed can be ignored in the present study because mussels are relatively sessile. Increases in crab size (and thus the length of walking legs) should increase movement speed and the amount of prey encountered, thereby increasing the attack rate. We

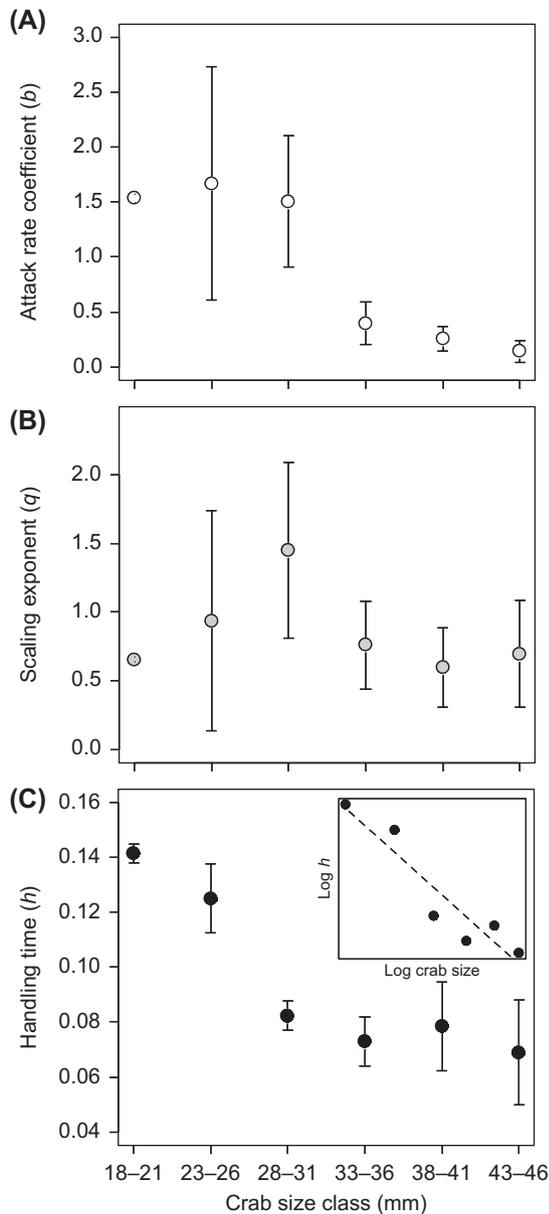


Figure 3. The scaling of functional response parameters with crab predator body size: (A) b = attack rate coefficient (white points); (B) q = scaling exponent parameter indicating the response type (gray points); (C) h = handling time (day ind.^{-1}) (black points). Points indicate parameters estimates ± 1 SE. Inset graph in (C) depicts the roughly linear relationship between size \log_{10} and handling time \log_{10} , indicative of a power-law function. The equation of a power-law function fit to the handling time data is $h = 1.718(\text{body size})^{-0.87}$.

however, observed a decrease in attack rate with crab size (Fig. 3A). Second, while a predator's attack rate is also dependent on predator and prey reactive distances, reactive distance is probably of limited importance in our experiment due to mussel distribution; because mussel prey were located in a central patch (the oyster cluster), other mussels are within reach of the predator after a single mussel is detected. Lastly, a predator's attack rate is dependent on capture success, which we have shown is highly dependent on habitat structure (Fig. 4) but may also depend on factors independent of structure. Because crabs of different sizes

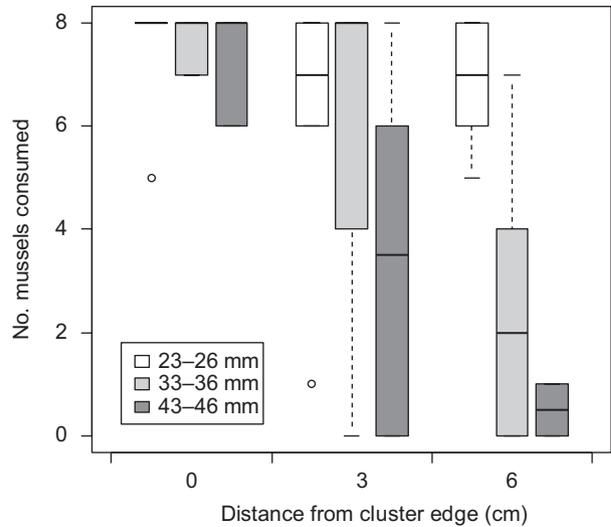


Figure 4. Mussel consumption by small crabs (23–26 mm carapace width CW; white bars), medium crabs (33–36 mm CW; light gray bars) and large crabs (43–46 mm CW; dark gray bars) foraging on eight mussels glued at three distances (0, 3 and 6 cm) from the edge of a standardized cluster.

still exhibited some variation in consumption efficiency when all mussels were at the edge of the cluster and thus completely vulnerable (0 cm: Fig. 4), this indicates that some factor is operating to reduce the attack rate independently of the prey refuge. For example, larger crabs could have a reduced ability, again independent of habitat structure, to grasp mussels in order to remove them from the cluster. Alternatively, optimal foraging theory predicts that consumers will choose prey that maximize their energy intake. If large crabs, relative to small crabs, do not perceive mussels as profitable prey (*sensu* Basset et al. 2012), they may be conditioned to passing up mussels at low densities in the field in lieu of more profitable prey. Again, this could cause variation in consumption efficiency when mussels are completely vulnerable. This also indicates that in a field setting where alternate prey types are available (Toscano and Griffen 2012), the interaction strength between crabs and mussels could be reduced.

Handling time declined nonlinearly with predator body size (Fig. 3C). Although we lack the replication and coverage along axes necessary to determine the true shape of this function, handling time appears to follow a negative power-law decline with crab size (Fig. 3C). This result is consistent with theoretical predictions based on metabolic theory (Brose 2010). When prey are dense (highest N_0) there is no search required, and so predators are only limited by their handling time. Thus, a predator's maximum consumption rate is equivalent to the inverse of its handling time. Because maximum consumption rate is roughly proportional to body size (Peters 1983), handling time should follow a $3/4$ power-law decline with increasing predator-prey body size ratio (Brose 2010). Handling time in the present study declined with body size at a scaling exponent of -0.87 , indicating fairly good agreement with this theory.

The type III response in our study is consistent with that in other studies where a general prey refuge is included (Hildrew and Townsend 1977, Anderson 2001).

Panopeus herbstii exhibits a type II response when foraging on oysters in an unstructured laboratory setting (Rindone and Eggleston 2011), although a comparison of the response type in an unstructured habitat in our study is needed to identify the prey refuge as the mechanism behind the type III response. Only one other study has tested the size scaling of the exponent that allows the response to vary between a type II and type III. This study found that the scaling exponent generally increased with relative predator size (a shift from type II to type III responses) (Vucic-Pestic et al. 2010). This result however, was species-specific: beetle predators displayed a significant shift, though spiders did not. Furthermore, this comparison by Vucic-Pestic et al. (2010) was confounded by the use of different prey species for the two different sizes of prey. We did not find strong evidence for change in response type with crab body size.

Our results may have important implications for community dynamics in oyster reefs that experience substantial fishing pressure. Destructive fishing practices are a major source of physical disturbance for marine communities and common ecological effects of fishing include habitat degradation (Thrush and Dayton 2002) and changes to the size structure of harvested species (Law 2000, Shackell et al. 2010). Oysters, in particular, are heavily exploited worldwide (Beck et al. 2011) and oyster harvesting tends to diminish the height and structural complexity of oyster reefs (Lenihan and Peterson 2004). In addition to these effects on reef habitat, oyster harvest also potentially alters crab size structure at our study site (North Inlet, SC, USA). Specifically, by reducing the height of the surficial shell layer in intertidal reefs (Toscano unpubl.) and thus the availability of refuge space for large (> 30 mm CW) crabs, harvest can skew crab population size structure towards a preponderance of small individuals relative to the natural crab size distribution (Toscano and Griffen 2012). Thus, changes to both habitat structural complexity and crab size structure are occurring at our study site, and the interaction between these factors revealed in our study could play a major role in the dynamics of crabs and mussels in the face of this anthropogenic influence. Based on the results of the present study, high densities of small crabs and an elimination of refugia for mussels could reduce mussel densities or even eliminate local populations. Comparing mussel population dynamics in heavily harvested versus unharvested reefs could provide some test of the general effects of harvest on community dynamics and the importance of the mechanism revealed in the present study.

Finally, though traditional functional response models assume predator conspecifics to be functionally equivalent (Jeschke et al. 2002), intraspecific variation in the functional response is probably widespread in nature. Understanding how different individual functional responses combine and scale up to influence prey over larger spatial scales is a major remaining research challenge. Scaling up could be complicated by errors due to the averaging of non-linear responses (i.e. Jensen's inequality: Okuyama 2008), differential interference between different sized predator individuals (Smallegange and van der Meer 2007), and prey preferences that vary with individual predator size (Kalinkat et al. 2011). Despite these inherent complexities, the

allometric scaling of the functional response and its scaling to population and community levels is essential to effectively modeling and managing the dynamics of size-structured populations (Hunsicker et al. 2011), and is thus deserving of focused attention.

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