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Source: Journal of Shellfish Research, 36(1) : 181-188

Published By: National Shellfisheries Association

URL: <https://doi.org/10.2983/035.036.0119>

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## EFFECT OF HABITAT COMPLEXITY ON PREDATOR–PREY RELATIONSHIPS: IMPLICATIONS FOR BLACK MANGROVE RANGE EXPANSION INTO NORTHERN GULF OF MEXICO SALT MARSHES

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**ABSTRACT** The tropically associated black mangrove (*Avicennia germinans*) is experiencing a climate-induced range shift and expanding into salt marshes of northern Florida, southern Louisiana and most recently, Horn Island, MS. To date, little is known about how black mangroves function as nursery habitat for important fishery species such as shrimps or how their increase may affect survival of such species. The main objective of our study was to determine habitat preference and survival rates of common, economically important penaeid shrimps in the presence and absence of the increasingly abundant tropical predator, the gray snapper (*Lutjanus griseus*). We also examined the effects of habitat identity and structure on juvenile white shrimp (*Litopenaeus setiferus*) and brown shrimp (*Farfantepenaeus aztecus*) behavior, using preference experiments in indoor mesocosms both with and without the predatory gray snapper. Results showed that shrimp prefer *Spartina* over *Avicennia* with or without predation risk. Survival of shrimp was lowest in sand and highest in medium-density *Spartina*. Thus, a marsh-to-mangrove habitat conversion could ultimately result in decreased shrimp survival.

**KEY WORDS:** *Avicennia germinans*, *Spartina alterniflora*, range expansion, gray snapper, Penaeid shrimp, predator–prey relationship

### INTRODUCTION

In the northern Gulf of Mexico (GOM), salt marshes are important habitat for the juveniles of fishery species, providing both a refuge from predators and food resources (Boesch & Turner 1984, Hettler 1989, Rozas & Minello 1998, Beck et al. 2001). Dominated by smooth cordgrass (*Spartina alterniflora*) and black needlerush (*Juncus roemerianus*), GOM salt marshes also export large amounts of secondary production, including that of ecologically and economically important shrimp species, to the offshore ecosystem (Boesch & Turner 1984, Zimmerman et al. 2002).

The tropically associated black mangrove (*Avicennia germinans*) has recently been expanding into temperate salt marshes of the GOM (Stevens et al. 2006, Comeaux et al. 2012). Black mangroves are the most cold-tolerant mangrove species, and less frequent and severe frost events have promoted their successful move northward (Pickens & Hester 2011, Cavanaugh et al. 2014, Cook-Patton et al. 2015). Historically, mangroves occur on subtropical and tropical coastlines between 30° N and 40° S latitudes and salt marshes dominate more temperate coastlines (Sherrod & McMillan 1985, Duke et al. 1998). A marsh-to-mangrove conversion has been occurring, however, in some areas along the Texas, Louisiana, and Florida coastlines, and northward expansion is predicted to continue over the next 100 y (Raabe et al. 2012, Osland et al. 2013). Given that black mangrove propagules have the ability to travel long distances and can and do out-compete salt marsh species, the colonization potential of these plants is fairly high (Tomlinson 1986, Nettel & Dodd 2007).

The implications of the shift from estuarine habitat dominated by smooth cordgrass to black mangrove could be large shifts in community structure and ecosystem function. For example, the differences in structure between marsh and black

mangrove species could alter ecosystem processes and the species composition and relative abundances of the animals that use salt marshes. Some research suggests that a combination of *Avicennia germinans* and *Spartina alterniflora* could increase overall habitat structural complexity, which may provide organisms with an additional refuge from predators (Caudill 2005).

The structural complexity of coastal habitats can influence survivorship, predator feeding efficiency, and habitat preference (Crowder & Cooper 1982, Bartholomew et al. 2000). Previous work has shown that prey appear to prefer vertical structure (Meager et al. 2005), but dense structure seems to be preferred when predation risk is high. In freshwater and marine environments, the efficiency of fish predators tends to decrease as vegetation density increases (Crowder & Cooper 1982, Canion & Heck 2009, Scheinin et al. 2012). For example, in laboratory experiments using simulated mangrove habitats with and without fish predators, prawns (shrimp) aggregated in the most complex, heterogeneous habitat composed of mangrove woody debris and branches (Meager et al. 2005). As black mangroves become more abundant in the northern GOM, their pneumatophores may provide more protection from predators than *Spartina* stems, and therefore improve the refuge value of estuarine nursery habitat for fishery species, including penaeid shrimps. Alternatively, black mangroves are typically located higher in the intertidal frame than *Spartina alterniflora*, and therefore mangrove habitat floods for relatively short periods of time during high tide events, which could restrict its use by estuarine organisms (Baker et al. 2015).

The overarching goal of this study was to examine habitat preference and survival of penaeid shrimps in both the presence and absence of the increasingly abundant and predatory gray snapper (*Lutjanus griseus*). Using a series of laboratory experiments, we compared the habitat preference of shrimp when offered a choice among *S. alterniflora* (*Spartina*), simulated black mangrove (*Avicennia*), or bare sand. In addition, we determined

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DOI: 10.2983/035.036.0119

if shrimp behavior changed in the presence of a predator and if survival rates varied among bare sand, sparse and dense simulated mangrove pneumatophores, and salt marsh stems.

## MATERIALS AND METHODS

### Experimental Prey

Because penaeid shrimps comprise over 60% of the gray snapper diet (Harrigan et al. 1989, Hettler 1989), juvenile stage white (*Litopenaeus setiferus*) and brown (*Farfantepenaeus aztecus*) shrimps were used in the habitat-selection experiments. These are the two most common penaeid shrimp species found in salt marshes of the northern GOM (Minello & Webb 1997, Howe et al. 1999). These species also support a valuable U.S. fishery that is centered in the northern GOM (Zimmerman et al. 2002, NMFS 2016). In addition, the species are ecologically important in coastal ecosystems. As a major component in the diets of many predators, juvenile penaeid shrimps are an important constituent of the estuarine food web (Minello & Zimmerman 1983, Harrigan et al. 1989, Rozas & Minello 1998). In migrating from estuaries to join the adult population offshore and complete their life cycle, penaeid shrimps also translocate secondary production derived from estuarine habitats to the GOM (Zimmerman et al. 2002).

We collected juvenile [30- to 50-mm total length (TL)] brown shrimp and white shrimp at West Point aux Pins, AL, and Dauphin Island, AL, between September and November 2014 using a small bag seine (3-mm mesh) and a beam plankton trawl (0.2-mm mesh). Individuals were measured, placed into aerated coolers, and transported to the Dauphin Island Sea Laboratory, where they were kept in holding tanks.

### Experimental Predator

The predator used in this study, gray snapper, is a subtropical and tropically associated species with a distribution along coastlines of the Atlantic Ocean, the Caribbean Sea, and throughout the GOM (Johnson et al. 1994, Allman & Grimes 2002). The gray snapper supports both recreational and commercial fisheries. Juveniles occupy structurally complex habitats such as seagrass, salt marsh, and mangroves that occur in nearshore nursery areas (Chester & Thayer 1990, Burton 2000, Tzeng et al. 2003). The abundance of juvenile gray snapper has increased in northern GOM seagrass meadows more than 100-fold since the 1970s, making it one of the 10 most abundant demersal fish species (Fodrie et al. 2010).

Juvenile gray snapper (65- to 100-mm TL) were collected using a standard 5-m otter trawl in various seagrass beds spanning from St. Joseph Bay, FL, to the Chandeleur Islands, LA, in the fall of 2014. Individuals were measured, placed into aerated coolers, and transported to the Dauphin Island Sea Laboratory, where they were kept separately in holding tanks.

### Experimental Design

Experiments were conducted from October 2014 to February 2015 in six cylindrical indoor mesocosms (110-cm diameter; 70-cm deep) at the Dauphin Island Sea Laboratory, Dauphin Island, AL. Each mesocosm was filled to a depth of 30 cm with filtered seawater and aerated to maintain good water quality. A temperature range of 20–25°C was maintained throughout the

experiments, and salinity was kept at 15 psu to reduce the risk of parasites that are often present at higher salinities. Each mesocosm was filled with 5 cm of clean sand and divided into three habitat types: salt marsh (*Spartina*), black mangrove (*Avicennia*), and bare sand (control). Salt marsh habitat was simulated using *Spartina* shoots collected from nearby marshes on Dauphin Island. The shoots were transported to the laboratory and rinsed of all epifauna and epiphytes, which could provide food for the experimental shrimp. The cleaned shoots were attached to Vexar mesh to ensure they remained upright as natural marsh habitat. Black mangrove habitat (pneumatophores) was simulated using untreated wooden dowels (30 cm length and 0.9 cm diameter) placed vertically in holes of precut pieces of gray Plexiglass, which was buried beneath the sand. Before trials began, dowel rod panels were placed into each experimental tank to fully soak for a week to remove any unnatural odors. Previous manipulative studies have used similar artificial mangrove pneumatophores in laboratory and field experiments investigating habitat preference (Laegsgaard & Johnson 2001, de la Morinière et al. 2004, Meager et al. 2005). Densities of plant stems and pneumatophores (dowels) matched those previously recorded locally in the field at Horn Island, MS and the Chandeleur Islands, LA (Scheffel et al. 2013, Scheffel 2015). The average densities of pneumatophores and *Spartina* shoots at Horn Island were 50/m<sup>2</sup> and 150/m<sup>2</sup>, respectively. Shoot density of *Spartina* was similar at the Chandeleur Islands and Horn Island, but pneumatophore density at the Chandeleurs was much higher (mean = 250/m<sup>2</sup>). Therefore, one density of *Spartina* stems (150/m<sup>2</sup>) and two densities of pneumatophores (50/m<sup>2</sup> and 250/m<sup>2</sup>) were used to simulate colonizing versus established stands of black mangroves.

The experimental design consisted of two factors: habitat (four levels; fixed: *Spartina* = medium complexity, sparse *Avicennia* = low complexity, high *Avicennia* = high complexity, and bare sand = none) and predator (two levels; fixed and present or absent). Each mesocosm had two vegetated habitat types, which were opposite each other, and two unvegetated sandy areas (Fig. 1). This design prevented habitat overlap, and forced organisms to occupy only one type of habitat at a time. The habitats were placed haphazardly in each of the quadrants, and the location of each habitat was changed every few trials to control for bias.

Control trials were habitat preference trials without a predator that included 5 shrimp per mesocosm or a density of 10 shrimp/m<sup>2</sup>. Similar densities of brown shrimp and white shrimp are found in natural vegetated habitats (Howe et al. 1999, Rozas et al. 2013, Rozas & Minello 2015). Shrimp size was standardized in each trial by using experimental shrimp that were all of similar length (mean ± SE, TL = 39 ± 0.5 mm). To begin an experiment, shrimp were released into the center of the mesocosm and allowed a 30-min acclimation period. The duration of each trial was set at 1 h (postacclimation), based on previous studies (Mattila et al. 2008, Canion & Heck 2009). Portable Go Pro Hero 3 + cameras recorded all trials, and at the completion of each trial, a Plexiglas divider was dropped to separate each habitat and trap experimental shrimp in place. The sand in each experimental mesocosm was thoroughly sieved after each trial to collect any buried shrimp. Each trial consisted of sparse or dense *Avicennia* each paired with *Spartina* plus bare sand, and each *Avicennia* treatment was replicated 6 times for a total of 12 trials.

An additional set of trials was conducted in a predation experiment to examine the effect of predation risk on shrimp habitat preference and the effect of habitat preference on

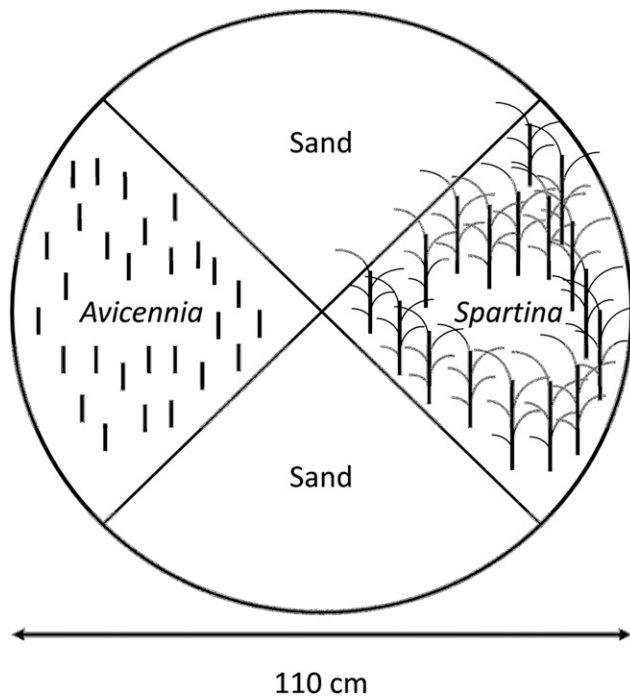


Figure 1. Overhead view of the experimental mesocosm (tank) design showing the arrangement of the three habitat types (*Spartina*, *Avicennia*, and sand) and tank diameter.

shrimp survival. We used the same experimental design as described earlier, but this second experiment differed by the addition of a predator and in duration. Experiments were initiated by placing five shrimp into the center of each tank and allowing them to acclimate for 30 min before introducing a gray snapper (predator). The gray snapper ( $81 \pm 2.31$  mm TL) were between 2 and 2.5 times the size of the prey and large enough to easily consume the juvenile shrimp used in this experiment (Dall et al. 1990, Scharf et al. 1998, Scharf et al. 2000). The duration of each trial was 2 h.

Individual shrimp were marked on the dorsal surface of their carapaces with pink nail polish for ease of detection. A pilot study ( $n = 12$  trials) using marked and unmarked shrimp indicated that this method of marking the experimental shrimp had no effect on survival. The mean number of shrimp eaten by gray snapper in these trials was similar for marked ( $2.22 \pm 0.32$ ) and unmarked ( $2.81 \pm 0.27$ ) shrimp. This result is consistent with that of a previous study, which reported little difference in survival rates between stained and unmarked shrimp (Costello & Allen 1961).

Each gray snapper used in a trial was starved for 24 h before being measured and placed into the center of a mesocosm. When predators were not being used in an experiment, they were fed frozen grass shrimp. Field densities (mean  $\pm$  1 SE) of gray snapper have been reported to range from  $0.3 \pm 0.3$  to  $1.6 \pm 0.3$  individuals/m<sup>2</sup> (Hammerschlag et al. 2010). Therefore, a single different gray snapper was used in each trial.

Shrimp survival rate was calculated for each mesocosm by dividing the number of shrimp remaining at the end of a trial by the total ( $n = 5$ ) placed in the mesocosm initially. Predation attempts were enumerated by viewing the video recording during each trial: a successful attempt was defined as a capture and consumption of a shrimp; a failed attempt was defined as

a strike immediately followed by the escape of that shrimp. Capture efficiency or feeding efficiency was defined as the proportion of successful to total predation attempts that occurred in each habitat.

Each of the treatment combinations described earlier for the control experiment was replicated six times in this predation experiment for a total of 24 trials. These trials included both marked ( $n = 12$ ) and unmarked shrimp ( $n = 12$ ).

#### Behavioral Observations

Predator and prey behaviors during control and predation experiments were recorded. Observations were recorded every 5 min beginning at time zero (start of trial) through the end of each trial for a total of 13 observation periods for each control trial and 26 for each predator trial. At 5-min intervals, the number of shrimp and fish in each habitat and predation attempts were recorded. Gray snapper movement among habitats and their maneuverability over the bare sand and within the habitat structure were recorded. In control and predation trials, shrimp movement among and within habitats, the approximate time spent in a particular habitat, and any abnormal behavior were noted. Shrimp position within a habitat, whether they were utilizing the base of *Spartina* or *Avicennia* structure or clinging to leaves or pneumatophores, was also recorded.

#### Statistical Analysis

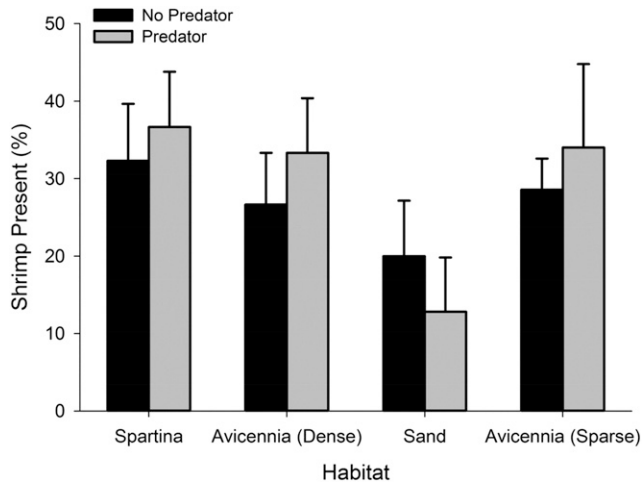
Shrimp habitat preference was evaluated by comparing the mean proportion of shrimp present in each habitat over time using a three-way repeated measures analysis of variance (ANOVA) in R (R Core Team 2015). The ANOVA model included habitat type, predator (presence or absence), and time as fixed factors. Comparisons of feeding efficiency (the proportion of successful predation attempts) among habitats were made using a one-way ANOVA with habitat type as a fixed factor and using SigmaStat statistical software.

Shrimp survival in each habitat was compared using a Cox proportional hazards (CPH) analysis in R (R Core Team 2015). This analytical method is a type of logistic regression with a Z-test statistic ( $df = 3$ ) that compares rates instead of proportions and uses an exponential equation to fit the model. The proportions of shrimp present in each habitat during each time interval were used to compare survival rates across habitats. The hazard ratio calculated in this analysis can be translated to relative death rate. A Pearson correlation coefficient was used to evaluate the relationship between predator size and number of shrimp consumed in each trial.

## RESULTS

#### Habitat Preference

As expected, shrimp preferred structure over bare sand throughout the experimental trials and showed the greatest preference for *Spartina*, regardless of predator presence. The proportion of experimental shrimp on sand was significantly greater in trials without predators than those with predators (Fig. 2;  $P = 0.03$ ). Approximately 30%–40% of the experimental shrimp moved freely between *Avicennia* and sand during predator-free trials (Fig. 3). A repeated measures ANOVA

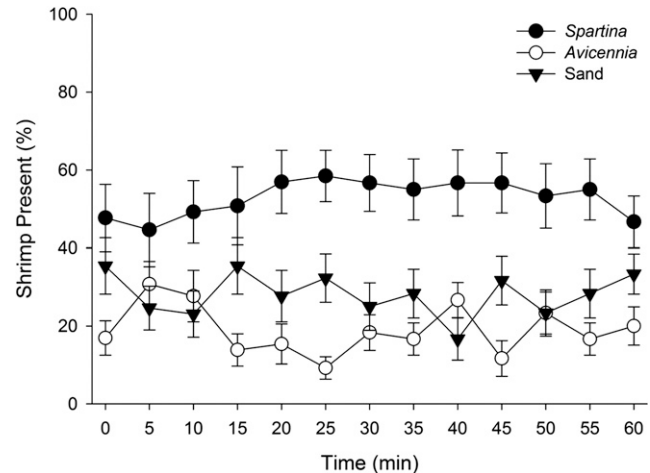


**Figure 2.** Percentage of shrimp present in each habitat type ( $\pm$  SE) at the end of each trial ( $n = 38$ ). The mean for the sand habitat was divided in half to account for fact that the sand habitat was twice the area of either vegetated habitat.

showed that time was not a significant factor in either predator-free or predator-present trials when comparing proportions of shrimp in each habitat (Table 1). On average, more shrimp occupied vegetated habitats than bare sand when a predator was present, although this difference was not significant (Figs. 2 and 3). In trials with a predator, shrimp showed a significant affinity for *Spartina* (Figs. 2 and 4A, Table 1); however, there was a significant interaction between habitat and predator, indicating that the proportion of shrimp in each habitat was dependent on the presence of a predator (Table 1, Fig. 2).

Individuals often moved along the perimeter of the tank when there was no threat of predation. A small proportion of shrimp remained in *Spartina* for extended periods of time, but they too eventually moved over bare sand. In contrast, during the predator trials, shrimp displayed more cautious behaviors and remained in dense vegetation or burrowed in sand (Fig. 4A). Shrimp that occupied sparse and dense *Avicennia* clung to the artificial pneumatophores, seemingly in an attempt to make themselves invisible when predators passed through the habitat.

The pattern for fish predators, higher occupancy over bare sand than within vegetation, was opposite that of shrimp (Fig. 4). A greater percentage of gray snapper began occupying *Spartina*,



**Figure 3.** Average percent shrimp present ( $\pm$  SE) in each habitat over time with no predator present ( $n = 13$ ).

but as time advanced, they spent more time over bare sand, apparently lying in wait to capture exposed shrimp (Fig. 4B). Overall, gray snapper alternated between roving among habitats and waiting in sand for shrimp to move among habitats. Fish also chased shrimp out of vegetation onto bare sand where odds of a successful predation attempt increased.

#### Shrimp Survival

Shrimp survival rates (mean  $\pm$  SE) in the predation trials were 48% ( $\pm 4.3$ ). A mean of 2.6 ( $\pm 0.27$  SE) shrimp was eaten in these trials, whereas 100% of the experimental shrimp survived in control trials. Most shrimp were eaten over bare sand (mean  $\pm$  SE = 1.1  $\pm$  0.16), whereas fewest shrimp were eaten in sparse *Avicennia* (0.45  $\pm$  0.28). Gray snapper spent the least amount of time in *Avicennia*, which may partially explain this finding (Figs. 4B and 5). Based on the proportion of shrimp remaining in each habitat at the end of the trial, survival was highest in *Spartina* and lowest in bare sand (Fig. 2). The sparse and dense *Avicennia* habitats had similar percentages of successful predation attempts (Fig. 5), but success was suppressed in all structured habitats compared with sand, and the mean percentages of successful attempts were significantly different among habitats (Fig. 5, Table 2). Although gray snapper had more failures than successes in all habitats, the largest difference

**TABLE 1.**

**Results of a three-way repeated measures ANOVA test comparing proportions of shrimp among habitats, over time and with or without a predator present.**

Source of variation	df	Sum of squares	Mean square	F-value	P
Habitat	2	54.68	27.338	407.357	0.000***
Time	24	0.09	0.000	0.057	1.000
Predator	1	0.00	0.001	0.011	0.918
Habitat $\times$ time	48	2.88	0.060	0.895	0.677
Habitat $\times$ predator	2	0.92	0.460	6.854	0.001**
Time $\times$ predator	12	0.01	0.001	0.009	1.000
Habitat $\times$ time $\times$ predator	24	0.96	0.040	0.594	0.940
Residuals	2,059	138.18	0.067		

An asterisk indicates level of significance. \*\*\* $P$  value = 0, \*\* $P$  value < 0.001).

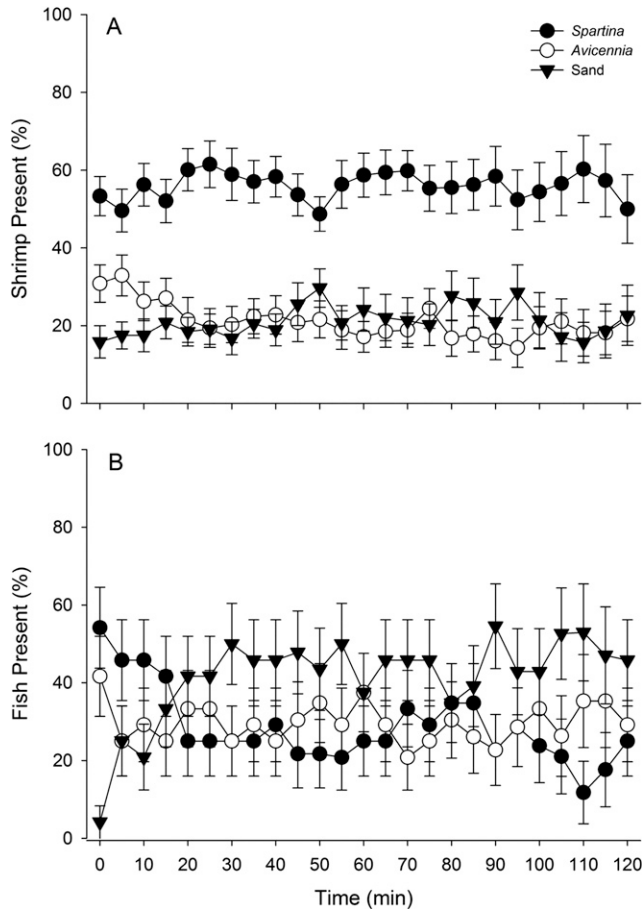


Figure 4. (A) Average percent shrimp present ( $\pm$ SE) and (B) average percent of fish present ( $\pm$ SE) in each habitat across time during predation trials ( $n = 24$ ).

between these outcomes occurred in dense *Avicennia*, where failures were much greater than successes (Fig. 5). Gray snapper actively foraged in all habitats, but the bare sand habitat facilitated predation success. Most failed attempts over bare sand occurred at the water surface, where shrimp propelled themselves out of the water and into another habitat causing fish to retreat. The majority of successful attempts over bare sand occurred as the fish approached from one of the vegetated habitats and captured shrimp at the sediment surface.

Predation attempts by gray snapper were most successful over bare sand and within sparse structure. The mean ( $\pm$ SE) capture efficiency in each habitat was 55.3% ( $\pm$ 0.12) in sparse *Avicennia*, 41.4% ( $\pm$ 0.06) over bare sand, 39.1% ( $\pm$ 0.07) in *Spartina*, and 38.2% ( $\pm$ 0.10) in dense *Avicennia*. Overall, proportions of shrimp remaining over time leveled off after 90 min. Based on results from the CPH model, the rate of shrimp survival was lowest over bare sand and highest in *Spartina*, but the differences among habitats were not significant (Fig. 6). The rate of survival in each habitat was dependent on the number of shrimp available (alive) at each time interval, and the greatest differences in shrimp survival among habitats were observed at the end of each trial (Table 3;  $P < 0.001$ ).

No significant relationship was detected between the size of predators and the proportion of shrimp eaten using linear regression analysis ( $R^2 = 0.0002$ ,  $P = 0.473$ ). Thus, over the

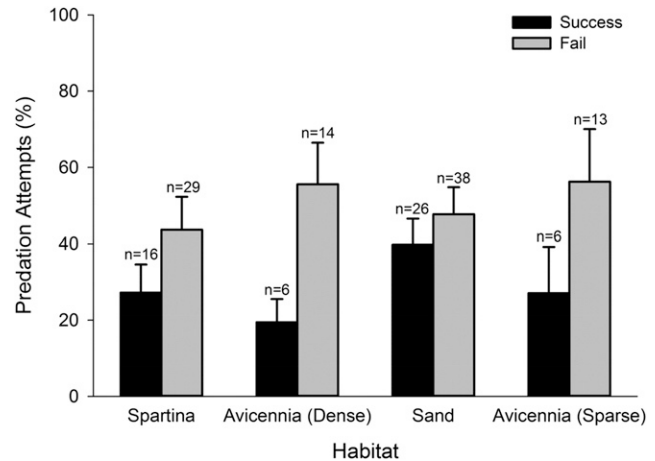


Figure 5. Average percentages ( $\pm$ SE) of successful and failed predation attempts in each of the habitat types ( $n = 24$ ).

range of sizes used in the experiments, predator size did not significantly affect the number of shrimp consumed (Fig. 7).

## DISCUSSION

### Habitat Preference

Shrimp exhibited a clear selection for *Spartina* in both the presence and absence of a predator. Juvenile penaeid shrimps are closely associated with *Spartina* in the natural environment and show a preference for *Spartina* marsh over shallow unvegetated bottom in estuaries of the northern GOM (Minello & Zimmerman 1985, Rozas et al. 2007). In our experiments, the search for a refuge by shrimp decreased when a predator was present. This observation is similar to the results of Minello et al. (1990), who reported a 21.2% reduction in penaeid shrimp activity when a predator was present. Habitat selection under natural conditions may be driven by differences in environmental variables (e.g., salinity, temperature, and flooding duration) among habitat types (Ley et al. 1999, Caudill 2005), but this was not the case in our study as we controlled for these variables. Some advantages for shrimp and other nekton using *Spartina* marsh over mangroves may include greater habitat availability and refuge value (Caudill 2005), and perhaps more food (benthic infauna) for shrimp in *Spartina* habitat (Rakocinski et al. 1991, Scheffel 2015). Our research showed that infauna (i.e., tanaids and polychaetes) were least abundant in mangroves when compared with salt marshes and mixed salt marsh/mangrove habitats (Scheffel 2015). Salt marshes are typically available to organisms for greater amounts of time than black mangroves due to their lower position within the intertidal zone (Patterson et al. 1993, Baker et al. 2015). *Spartina* may also provide greater habitat complexity than recently recruited black mangroves by affording prey both stems and leaves as refuge from visual predators. In addition, shrimp in temperate locations may not recognize black mangrove pneumatophores as refuge, and select more familiar habitat. The simulated pneumatophores were inhabited by shrimp in our experiment, and this habitat did provide some refuge from predation. Only ~15%–20% of shrimp occupied either *Avicennia* habitat at any given time during the trials. Based on previous studies, we

**TABLE 2.**  
Results from a one-way ANOVA comparing mean proportions of successful predation attempts among habitat types (fixed factor).

Source of variation	df	Sum of squares	Mean square	F-value	P
Habitat (between groups)	3	3,924.73	1,308.243	20.636	<0.001
Residual	68	4,310.856	63.395		
Total	71	8,235.585			

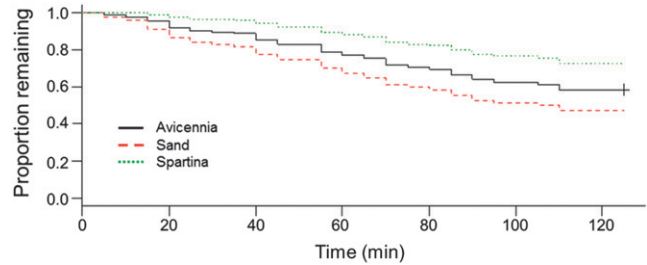
expected shrimp to prefer dense pneumatophore habitat over medium-density *Spartina*, because pneumatophores appeared to be a more complex habitat. Our results did not support this expectation, because 50%–60% of shrimp showed a consistent preference for *Spartina* regardless of predation risk.

Few manipulative studies have compared the relative refuge value of salt marshes and black mangroves because there are relatively few locations where these vegetation types overlap. In our experiment, the addition of predators sharpened the differences in shrimp distribution among habitats. Shrimp shifted from bare sand to dense vegetation, specifically *Spartina*. Similarly, juvenile banana prawns (*Penaeus merguensis*) in Australia preferred greater vertical structure (pneumatophores and mangrove debris) over low vertical structure (bare sand and leaf litter) in both the presence and absence of a fish predator (Meager et al. 2005).

We also expected gray snapper to occupy the same habitats as shrimp because predators typically follow their prey (Minello & Zimmerman 1985). Fish initially occupied *Spartina*, whereas shrimp remained hidden at the base of the stems, at the top of the leaves, or buried in sand. Unlike shrimp, however, snapper made multiple habitat shifts during trials and eventually moved into sand where they were able to capture vulnerable shrimp that shifted habitats. Predators may prefer less complex habitat because their foraging efforts are restricted in high-density vegetation (Crowder & Cooper 1982, Stoner 1982, Bartholomew et al. 2000). Snapper had less maneuverability in dense *Avicennia*, which was demonstrated by the minimal number of predation attempts and the significantly greater number of failed attempts in that habitat. Visual predators, including snappers, exhibit a roving type behavior when searching and rely on visual cues to locate prey (Savino & Stein 1982). If shrimps were buried or out of the line of sight (e.g., clinging to the tops of pneumatophores, stems, or leaves), fish did not seem to recognize the prey and moved to another habitat.

#### Shrimp Survival

Predation in our experiment was more successful over bare sand, as expected, because predators have more difficulty maneuvering in dense vegetation (Bartholomew et al. 2000). Even though shrimp survival was highest in *Spartina*, gray snapper had the most success in sparse *Avicennia* (55.3%). Previous studies suggest that predation success is maximized in habitats of medium complexity (Crowder & Cooper 1982, Gotceitas & Colgan 1989). Gray snapper can change color to match their surroundings (Starck & Schroeder 1971), and this



**Figure 6.** Mean proportion of shrimp remaining (survival) over time in each habitat in predation trials based on results from the CPH survival model ( $n = 106$ ).

species may be best camouflaged against dark mangrove pneumatophores, which enable them to forage efficiently in sparse mangrove habitat. Snapper would also be well camouflaged in dense pneumatophore habitat, but pneumatophore density would likely limit the snapper's mobility.

The CPH model showed higher shrimp survival in *Spartina* than in the other two habitats, and the number of shrimp eaten was dependent on how many shrimp remained at each time interval. Primavera (1997) conducted a similar experiment using a mangrove red snapper predator (*Lutjanus argentimaculatus*) and also showed that predation on shrimp was significantly higher in sand than in medium-density pneumatophores. Survival in their study depended on predator and prey behavior as well as habitat structure type and density.

#### CONCLUSIONS

Salt marsh was the preferred habitat for juvenile brown shrimp and white shrimp when given a choice between *Spartina* and simulated *Avicennia*. This is not surprising because, even though black mangrove pneumatophores provided some refuge from predation, shrimp survival was higher in *Spartina*. If our experimental results are consistent with patterns of habitat use and shrimp survival in the estuaries of the northern GOM, survival rates of juvenile penaeid shrimps may decrease as the climate warms and mangroves outcompete and replace *Spartina* marshes, which also are being converted to shallow open water by a rising sea level. Even though no difference in successful predation attempts was detected between sparse and dense *Avicennia* in our experiment, shrimp survival could be greater in established dense stands of *Avicennia* because predator mobility and success there would likely be hindered. As northern GOM

**TABLE 3.**  
Results from a CPH analysis comparing survival rates over time based on the proportions of shrimp remaining.

Variable	Hazard ratio	95% CI	Standard error	Z	P
Habitat					
<i>Avicennia</i>	Reference				
Sand	1.8422	0.895–3.792	0.358	1.659	0.0972
<i>Spartina</i>	1.2015	0.658–2.194	0.393	0.597	0.5504
Number of shrimp remaining	4.053	2.434–6.747	0.224	5.381	<0.0001

CI, confidence interval.

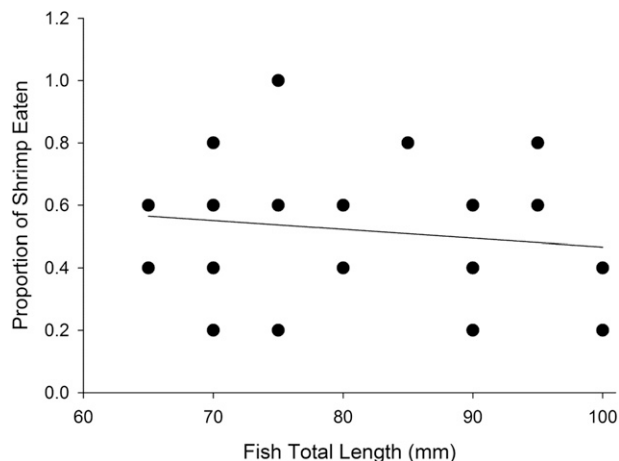


Figure 7. The correlation between fish total length (mm) and proportion of shrimp eaten for all predation trials ( $R^2 = -0.150$ ;  $P = 0.473$ ).

salt marshes transition into black mangrove domination, this habitat will be available for shorter periods of time during the tidal cycle, forcing some organisms to use alternative habitats as refuge (Patterson et al. 1993, Rozas & Minello 1998). It is

important to understand how marsh-associated organisms will use both of these habitats and how the nursery function of estuaries may be altered as black mangroves continue to increase in abundance along the northern GOM.

#### ACKNOWLEDGMENTS

We acknowledge the U.S. Fish and Wildlife Service for funding the field portion of this study that was used in experimental planning, and the financial support of the Dauphin Island Sea Lab (DISL). We thank the DISL maintenance crew, technical support, and Estuarium staff that helped with drop sampler construction, wet lab maintenance, and animal husbandry. Without their assistance, these experiments would have not been successfully conducted. I would like to acknowledge Steven Garner for his assistance in conducting statistical analyses in R. Also, a special thanks to Olivia Caretti and all other interns from the Heck Lab for assisting with experimental set up and break down, and collection of organisms. W. A. Scheffel contributed to the overall project design, all experimental preparation and subsequent analyses, and manuscript preparation. K. L. Heck, Jr. and L. P. Rozas contributed to project design and manuscript preparation. All authors have approved this manuscript for submission.

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