Variation in size and abundance of Caribbean spiny lobster (*Panulirus argus*) with change in hardbottom habitat

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Abstract:
The specific characteristics that make a habitat suitable for an organism vary both between species and between life stages within a single species. Hardbottom habitats in Florida Bay are known as nurseries for a number of commercially and ecologically important species. In this study, we focused on the Caribbean spiny lobster (*Panulirus argus*) and the hardbottom habitats found north of the island of Marathon. We characterized these habitats based on benthic cover (e.g., algae, seagrass) and density of lobster refuge (e.g., coral, sponges, octocorals, solution holes, rocky ledges) to determine how specific habitat characteristics affect lobster abundance and size. We conducted nine benthic surveys and three lobster surveys at each of the three different sites. Dominant benthic cover varied from site to site, as well as the abundance of benthic structures utilized by lobsters. Sponges were the dominant structure type at all sites; however, despite the availability of sponges, corals were the most important habitat type for lobsters. Lobster abundance was statistically equivalent among the three sites, while mean lobster size differed between the sites. We also found an ontogenetic shift in shelter preference: post-larval and juvenile lobsters preferred coral heads, whereas sub-adult and adult lobsters preferentially occupied solution holes and rocky ledges. This study yields classification of benthic habitats within Florida Bay and reveals spiny lobster preference patterns for particular structures and contributes to the overall understanding of the complex life cycle of an economically important fishery species.

INTRODUCTION

The specific characteristics of a habitat that make it suitable for an organism or species will include numerous factors including availability of food resources, protection from predators, and refuge during vulnerable stages of the life cycle (Eggleston and Lipcius 1992).

A major goal in ecology is understanding that the distribution of suitable habitat varies across space as well as the qualities that contribute to a habitat's suitability for a given species (Heck and Wetstone 1997). In many marine ecosystems, more complex habitats tend to harbor larger numbers of animals than do structurally simple environments simply because they are capable of supporting more vital resources that are favored by organisms (Heck and Wetstone 1997). Habitat complexity is defined here as the amount and diversity of physical structures used by animals. For example a critical attribute of complex environments is the amount of refuge afforded to prey from their predators (Beck 1995). Prey species may experience higher survival in areas of high structural complexity (Eggleston and Lipcius 1992). As a result, preference for specific habitat morphologies to avoid predation has been examined in a variety of reef fishes (Kerry and Bellwood 2001) crustaceans (e.g. stone crabs; Beck 1995). The availability of adequate shelters is one of many factors that controls the distribution of species in a given area Eggleston and Lipcius 1992).

Demographic bottlenecks can arise when suitably complex habitats are limited, which in turn affects the size of local populations (Herrnkind and Butler 1994; Beck 1995). However, the specific characteristics that make a habitat suitable will vary between species, and preferences for certain habitat characteristics may change over the life of an organism (Holbrook et al. 2000). Ontogenetic shifts (preferences at different stages of the life cycle) in habitat use are common in marine species where juveniles are found in more protected nursery habitats and adults favor open water or coral reefs. Nursery habitats such as seagrass beds and mangrove prop-roots are essential for the juvenile stages of numerous species including gag (*Mycteroperca microlepis*; Koenig and Coleman 1998) and goliath grouper (*Epinephelus itajara*; Koenig and Coleman 2007), and the Caribbean spiny lobster (*Panulirlus argus*).

"Nursery habitats such as seagrass beds and mangrove prop-roots are essential for the juvenile stages of ... the Caribbean spiny lobster"

In this study we evaluated how hardbottom habitat types within Florida Bay affect the distribution, abundance, and size of juvenile spiny lobster. We first classified three different sites within Florida Bay based on the amount of benthic cover (e.g., red algae, green algae and sea grass). Then we quantified the density of structures within each site that could provide suitable shelter for lobsters (e.g., sponges, corals, and solution holes). We used these factors to determine how lobster size and abundance correlates with specific habitat characteristics.

Study Site

Florida Bay is a large open embayment in south Florida bounded by the Everglades to the north and the Florida Keys to the south (Figure 1). The shallow coastal waters of Florida Bay are characterized by approximately 30% hardbottom habitat, which is described as limestone bedrock covered in a sediment layer (Bertelsen et al. 2009). Interspersed among the hardbottom are patches of algae and seagrass. Biogenic structures associated with Florida Bay hardbottom include numerous sponges, large branching octocorals, and stony corals. Solution holes, a common feature of karst limestone geology, are also a common feature of Florida Bay hardbottom.

Study Organism

Caribbean spiny lobsters undergo a 6-9 month planktonic larval period during which their dispersal is primarily regulated by open sea current (Herrnkind and Butler 1994). They then metamorphose into a post-larval phase, migrate inshore, and settle to nursery sites (Bertelsen et al. 2009). Post-larval spiny lobsters (5-25 mm carapace length [CL]) selectively settle in dense benthic cover, particularly red algae of the genus Laurencia (Butler and Herrnkind 1992), with which they remain associated for several more months (Herrnkind and Butler 1986).

Juvenile spiny lobster (26-45 mm CL) emerge from their vegetative sanctuary in search of daytime refuge among various hard bottom structures such as coral heads and sponges (Butler and Herrnkind 1986). The specific types of shelters used in any particular region vary depending primarily on the availability of shelters that make suitable dens (Bertelsen et al. 2009). Sub-adult spiny lobsters (46 -65 mm CL) are found associated with these juvenile shelters as well as in solution holes. Den choice has been shown to be scaled to body size, which minimizes the risk of predation (Eggleston and Lipcius 1992). Mature adult spiny lobsters (> 66 mm CL) migrate toward reefs where they spawn and where their larvae are dispersed with the ocean currents (Bertelsen et al. 2009). In this study, we define four lobster sizes classes: Post-larval (<30 mm CL), Juveniles (31-49 mm CL), Sub-Adult (50-69 mm CL) and Adult (>70 mm CL).

MATERIALS AND METHODS

We first evaluated the characteristics of the benthic habitat at each of three sites. The three study sites were located north of the islands of Marathon in the Florida Keys, Florida, USA (Figure 1). At each site we conducted two types of surveys: a benthic cover survey which quantified the vegetative cover at each site, and a structure survey which quantified the density of structures suitable for lobster. Three sites were chosen for the study: Seven Mile, located approximately 1.9-km from the nearest point of land with a mean depth of 3.5-m; Burnt Point, located approximately 0.5-km from the nearest point of land with a mean depth of 2.5-m; and Hawks Cay, located approximately 5.8-km from the nearest point of land with a mean depth of 2.9-m. Upon arrival at each site we first delineated three 100 x 100 meter sampling stations. Within each of the three sampling stations, three 25 meter transects were laid out at random, a total of 9 transects per site, along which the benthic and structure surveys were conducted. First, a team of two divers swam along the transects and recorded the type of benthic cover at each half meter interval as marked on the transect (see Figure 2). Since early juvenile lobsters are known to associate with certain types of red algae (e.g. Laurencia spp.; Marx and Herrnkind 1986) and to forage in the seagrass (Cox et al. 1997), the benthic cover survey focused on these features. Red algae (Laurencia spp.), green algae (Halimeda spp.Penicillus spp.), and seagrass (Thalassia testudinum and Syringodium filiforme) found directly under the transect were recorded. Points with no vegetative cover were recorded as bare rock or sand. A total of 27 transects were surveyed across all sites.

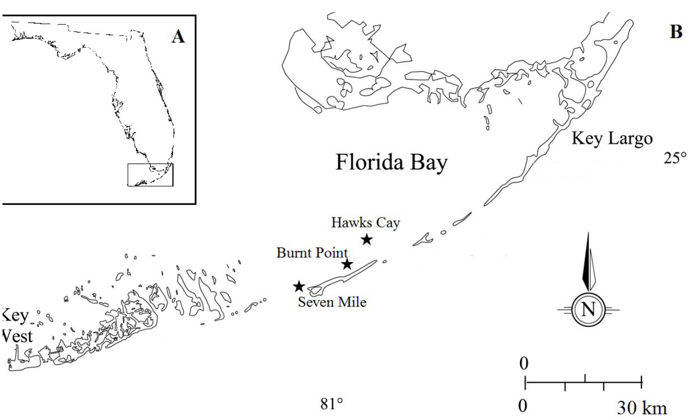

Figure 1. (A) Map of Florida, USA. Study was conducted in Florida Bay,

north of Marathon, FL. (B) Location of the three survey sites in Florida Bay: Seven Mile (approx. 1.9 km from land), Burnt Point (approx. 0.5 km from land), and Hawks Cay (approx. 5.8 km from land).

Figure 2. The first author conducting a transect count at the Burnt Point site north of Marathon, Florida Keys, USA. Note the transect tape laying on the bottom and the presence of two octocorals and a vase sponge.

When the benthic cover survey was complete, the divers swam back along the transect while recording the number of biogenic and physical structures found within 1-m on either side of the transect tape. For this study, “structure” refers to any rigid structure, either biogenic, geologic, or anthropogenic in origin larger than 20-cm in any single dimension. The total area surveyed by the belt transect was 50 square meters. A meter-long PVC pipe was used to determine if a structure was within the appropriate distance from the transect and also used to measure the structure. Structures were measured in three dimensions: maximum height, width, and depth. If a structure was less than 20-cm in any dimension it was not recorded.

Following the benthic and structure surveys, each diver conducted a 30-minute roving diver search within each of the 100-m2 sampling stations (total duration of search = 1 hour per station; 3 hours per site). Lobster size was measured in situ (in their place of hiding) to the nearest centimeter. Total lobster abundance was determined for each site by summing the total number of lobsters encountered by both divers at all three stations. Lobster encounters per hour was calculated for each site and also for each size class.

Data Analysis
Tests for differences between sites in terms of abundance of structure type, lobster encounters per hour, and mean lobster size (CL) were all performed using one-way Analysis of Variance (ANOVA). Dependent variables were total number of each structure type per site, total number of encounters, and size respectively. Shapiro-Wilk tests for normality and equal variance tests were conducted simultaneously and data transformations were performed as needed to conform to the assumptions of ANOVA (e.g. abundance data were all square-root transformed). Post-hoc pairwise comparisons (Tukey HSD tests) were used to test which sites were different when ANOVA results indicated site differences.

A Chi-squared test of independence was used to test whether or not the observed counts of lobsters associated with specific structure types differed between stages. This test compared the frequency of association of each lobster size class to each structure type in proportion to the occurrence of each structure type to determine structure preferences between lobster size classes.

All statistical tests were performed with a Sigma Plot 12.0 (Systat Software Inc., San Jose, California).

RESULTS

Habitat characteristics and lobster abundance within each size class varied between sites. Sponges were the dominant structure type at all sites. Octocorals, which are groups of polyps organized into branching structures, and coral heads which are stony corals, were abundant at both Burnt Point and Seven Mile but were rarely encountered at Hawks Cay. Solution holes were common at all three sites, with similar densities found at Burnt Point and Seven Mile. Ledges were found only at Seven Mile and were the least common shelter overall (see Table 1).

Table 1. Mean (±SE) shelter abundance per hectare at each of the three sites in Florida Bay off Marathon, FL, USA, during June 2012. #/ha is the number of structure type per hectare; +/- SE is the standard error; and the % is the overall percentage of structure type within each of the three study sites.

	Site								
	Burnt Point			Hawks Cay			Seven Mile		
Shelter	#/ha	+/- SE	%	#/ha	+/- SE	%	#/ha	+/- SE	%
Coral	44.44	14.81481	0.02	0.00	0.00	0.00	111.11	19.59816	0.04
Sponge	1355.56	7.407407	0.54	444.44	19.59816	0.95	2244.44	276.46600	0.74
Octocoral	1000.00	38.49002	0.40	0.00	0.00	0.00	466.67	55.92470	0.15
Solution Hole	111.11	19.59816	0.04	22.22	7.40741	0.05	111.11	37.03704	0.04
Ledge	0.00	0.00	0.00	0.00	0.00	0.00	88.89	29.62963	0.03
Total	2511.11	80.31	1.00	466.67	27.01	1.00	3022.22	418.66	1.00

Lobster abundance by size class revealed the highest number of post-larval, juvenile, and sub-adult lobsters was found at Burnt Point and the highest number of adult lobsters at Seven Mile. Lobster abundance was not different between Burnt Point and Seven Mile, but was significantly lower at Hawks Cay, which exhibited very few lobsters overall (see Table 2).

Table 2. Encounter rate of Caribbean spiny lobster (Panulirus argus) abundance by size class (post-larval = <2-cm; juvenile = 3-4 cm; sub-adult = 5-6 cm; adult = >7-cm) counted by divers at each of three sites in outer Florida Bay. #/ha is the number of lobsters per hectare; +/- SE is the standard error; and % is the overall percentage of each life stage within each of the three study sites.

	Site		
		Burnt Point	
Lobster encounter rate	#/ha	+/- SE	%
Post larval	4.00	--	0.22
Juvenile	6.00	--	0.33
Sub-Adult	5.00	--	0.27
Adult	3.33	--	0.18
Total	18.33	2.03	1.00

Site(cont'd)					
Hawks Cay			Seven Mile		
#/ha	+/-SE	%	#/ha	+/-SE	%
0.67	--	0.08	0.67	--	0.04
2.67	--	0.31	1.00	--	0.05
3.00	--	0.35	3.33	--	0.18
2.33	--	0.27	13.33	--	0.73
8.67	3.71	1.00	18.33	9.21	1.00
466.67	27.01	1.00	3022.22	418.66	1.00

Habitat classification

The dominant benthic cover type differed between the three sites: at Burnt Point the most abundant cover was red algae, at Seven Mile the most abundant cover was green algae, and Hawks Cay had essentially equal amounts of red algae and green algae. Sea grass was rare overall, but most abundant at the Hawks Cay site (Fig. 3).

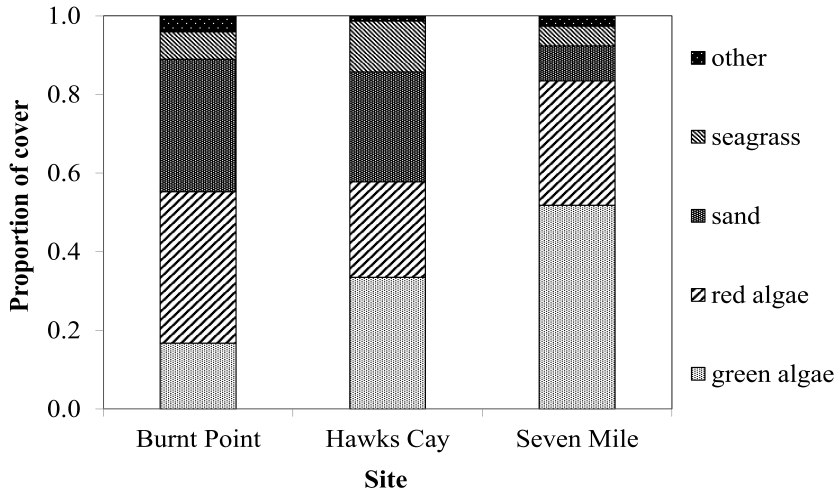

Figure 3. Proportion of benthic cover found at three study sites located north of Marathon, Florida Keys, USA. "Other" group includes any biogenic, geologic or anthropogenic feature including sponges, sea biscuits, and bare rock.

The abundance of structures differed between sites (one-way ANOVA; $p= 0.002$), with Hawks Cay having significantly fewer structures compared to the other two sites (Tukey HSD; Hawks Cay vs. Seven Mile: $p=0.002$; Hawks Cay vs. Burnt Point: $p=0.006$). There was no significant difference in structure abundance between Seven Mile and Burnt Point (Tukey HSD; $p= 0.48$). Sponges were the dominant structure type at all three sites, but each site differed in the relative proportion of sponges present (Fig. 4). The Seven Mile site was the only site with all structure types present and also had the highest total number of structures (see Table 1).

Lobster surveys

Lobster association with specific structures differed between sites (Fig. 5). At Burnt Point most lobsters were found under corals or in solution holes, at Hawks Cay most lobsters were found in solution holes, and at Seven Mile more lobsters were found under rocky ledges compared to all other structure types. The Seven Mile site also had the largest diversity of structures utilized by lobsters of the three sites (e.g. corals, sponges, solution holes). No lobsters were found associated with octocorals at any site.

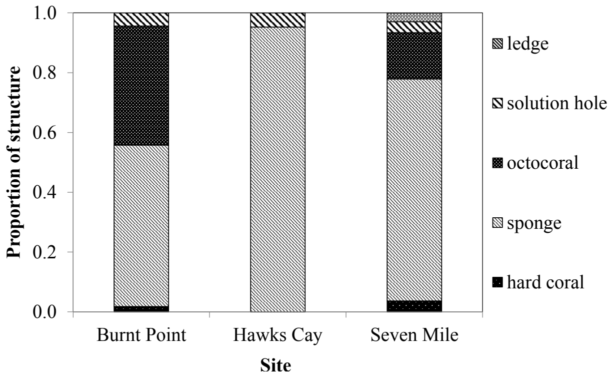

Figure 4. Proportion of five structure types potentially used by juvenile lobsters at three study sites located north of Marathon, Florida Keys, USA.

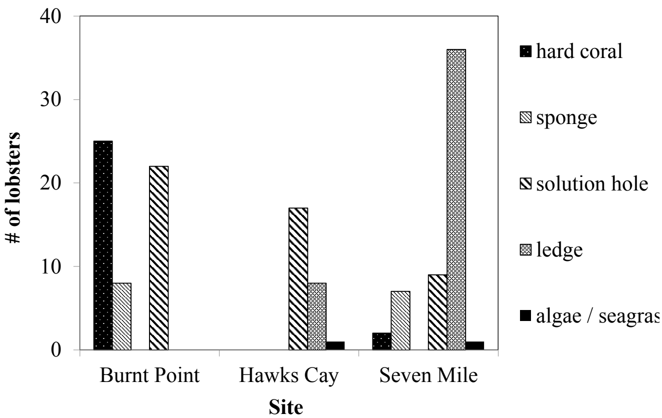

Figure 5. Total number of lobsters found associated with different structures during half-hour roving diver surveys at each of three sites located north of Marathon, Florida Keys, USA.

The number of lobsters encountered per hour was similar among all three sites (Fig. 6). A one-way ANOVA showed that there was no significant difference in the lobster encounter rate between the three sites ($p=0.452$).

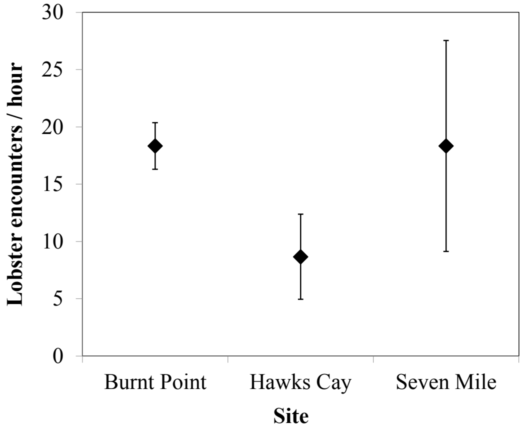

Figure 6. Mean number of lobsters encountered per hour of searching (total search time = 3 hours per site) during roving diver surveys conducted at three sites located north of Marathon, Florida Keys, USA. Error bars ± SEM.

Mean lobster size differed significantly between the three sites (one-way ANOVA; $p = 0.007$; Fig. 7). The largest lobsters were recorded at Seven Mile followed by Hawks Cay and then Burnt Point. Pairwise comparisons showed that Seven Mile differed significantly from the other two sites (Tukey HSD; Seven Mile vs. Burnt Point: $p = 0.008$; Seven Mile vs. Hawks Cay: $p = 0.023$), but the mean size of lobsters found at Hawks Cay and Burnt Point were not significantly different (Tukey HSD; $p = 0.579$).

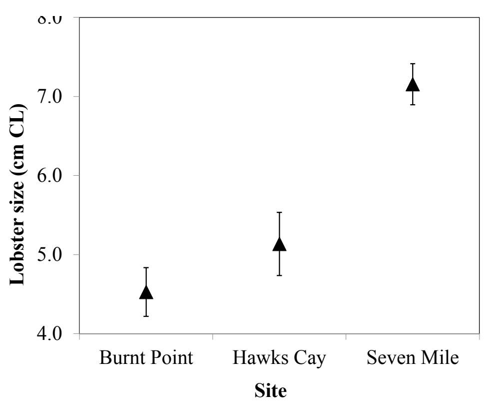

Figure 7. Mean size of lobsters (measured as Cl [cm]) encountered

during roving diver surveys at three sites (Burnt Point, Hawks Cay, and Seven Mile) located north of Marathon, Florida Keys, USA. Error bars ± SEM.

The size of lobsters found associated with shelters varied between sites. At Burnt Point, larger lobsters were found in solution holes and smaller lobsters were found among corals and sponges. At Hawks Cay, larger lobsters were found among solution holes and ledges while smaller lobsters were found among red algae. At Seven Mile, the largest lobsters were found amongst solution holes and rocks and ledges, followed by slightly smaller lobsters around sponges (with the exception of one large lobster [CL = 9-cm] that was encountered out in the seagrass; Fig. 8).

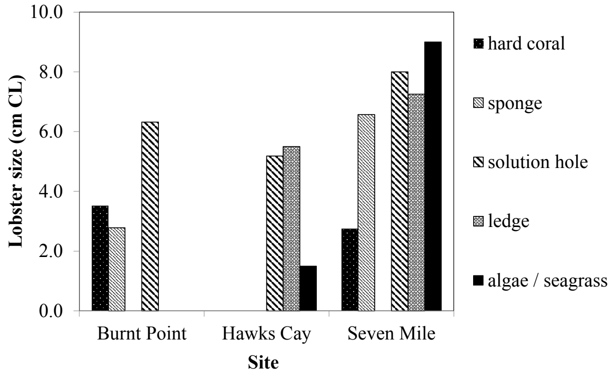

Figure 8. Mean spiny lobster size (carapace length [CL] measured in centimeters) associated with each type of structure at each of the three sites: Burnt Point, Hawks Cay, and Seven Mile near Marathon, Florida Keys, USA. Habitat codes: COR = coral; SPO = sponge; SOL = solution hole; LED = ledge; RA/SG = red algae / seagrass.

Lobster preference for shelter at each site varied between size classes indicating a distinct ontogenetic shift in preference for specific structure types. Post-larval phase lobsters were found mostly associated with stony corals; juvenile spiny lobsters were found on all types of structure except octocorals; sub-adult and adult lobsters were found associated with solution holes and ledges. Tests for structure type preference between size classes showed a shift from corals during early life stages to solution holes and rocky ledges during later life stages.

When we included availability of structure types in the environment, this ontogenetic shift of structure association was clearly evident (Fig. 9). Smaller lobsters (post-larval and juvenile) showed significant positive selection for corals, while sub-adult and adult lobsters showed no preference for corals. Larger lobsters (sub-adult and adult) showed significant positive selection for geologic features like solution holes and rocky ledges, while these structures were not selected for by smaller lobsters. All size classes showed significant negative selection for sponges and octocorals.

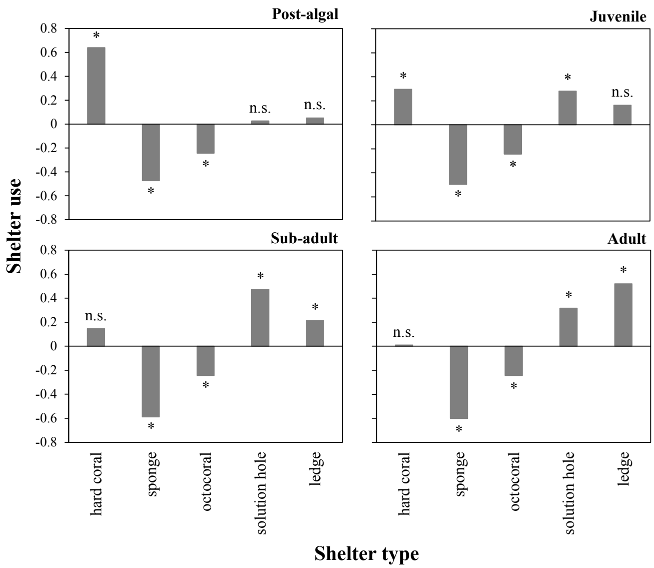

Figure 9. Shelter use in proportion to availability for lobsters of each of the four life stages found in the study; * = values differ significantly from zero (positive or negative selection); "n.s." = values do not differ significantly from zero (no selection). Shelter use is defined as [proportion used – proportion available] for each type of shelter. Positive values indicate that a given shelter type was over used relative to its availability, suggesting positive selection; negative values indicate a given shelter type was under used relative to its availability, suggesting negative selection.

DISCUSSION

The results of our survey of the hardbottom habitats found in Florida Bay suggest that spiny lobster size, rather than abundance, was most sensitive to changes in habitat characteristics between the sites we surveyed. We found the largest lobsters at Seven Mile, the site with the most abundant structures favored by large lobster. We found the smallest lobsters at Burnt Point, which was also the site with the most structures preferred by smaller lobster. Compared to other areas in Florida Bay surveyed in the past using similar techniques, the sites we surveyed generally had fewer structures used by spiny lobster (Bertelsen et al. 2009). This finding is significant, given that population bottlenecks are known to have occurred in this species in the past, driven in part by the loss of suitable habitat (Butler et al. 2001).

The mean size of lobsters recorded at Seven Mile were larger than those found at the other two sites, and at over 7-cm CL suggests that mainly adult lobsters are present at this site. The Seven Mile site was located along the Seven Mile Bridge, on the edge of where Florida Bay meets the open ocean. The ocean side of the Florida Keys are dominated by coral reefs where spiny lobsters are known to migrate towards once mature and which support adults spawning events (Bertelsen et al. 2009). Because the Seven Mile site was the closest site to these reefs, perhaps the observed difference in size could be caused by migration of adults towards coral reefs. Mature adult lobsters may choose to compete for suitable shelter around the edge of the bay, close to the reefs, possibly as a mating advantage.

We observed shelter preferences that were life-stage dependent and that shifted with ontogeny. As lobsters grew and matured from the post-larval stage through to adulthood, the corresponding preference for shelter shifted from corals to solution holes and rocky ledges. These findings corroborate previous research that has shown such shelter use preference changes through ontogeny of spiny lobster (Bertelsen et al. 2009). Where our study differed from previous research was in the shelter preference of small lobsters. Bertelsen and colleagues found the preference of post-larval and juvenile lobsters was primarily for sponges, whereas we found the same size classes to show strong preference for corals. In their surveys (conducted in 1994), Bertelsen et al. found that sponges dominated lobster preference during all stages except the adult stage. However, we did not find any preference for sponges, and in fact found that sponges were under-utilized in comparison to their availability. In 1995, a mass sponge die off occurred in Florida Bay that was attributed to extensive cyanobacteria blooms in the bay (Herrnkind et al. 1997). The results of our study suggest that there may have been a shift in shelter preference by small lobsters in Florida Bay away from sponges to the more stable biogenic structures provided by stony corals, possibly in response to the loss of sponges as suitable habitat. Despite the reappearance of sponges in the area, the small lobsters observed in our study do not seem to use them for shelter. Further research is needed to determine if our results indicate an actual shift in preference or if other factors contribute to shelter use preference by lobsters in Florida Bay. Future changes in shelter availability in Florida Bay could have detrimental effects on the population of spiny lobsters, which supports important commercial and recreational fisheries. Our study highlights the importance of understanding the specific ways in which species interact with their habitats and how changes in habitat characteristics may result in changes in population structure.

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Amie Lentner came to Florida State University in the hopes of pursuing a degree in marine biology in 2009. After declaring her major in biological sciences, she joined the marine certificate program under Felicia Coleman. In the summer of 2012, she partook in an internship in the Florida Keys which was the basis for this article. She hopes to use this experience to fuel future endeavors in marine biology and hopefully make it a career.