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Regional characterisation of hard-bottom nursery habitat for juvenile Caribbean spiny lobster (*Panulirus argus*) using rapid assessment techniques

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Abstract Shallow, hard-bottom habitat constitutes approximately 30% of the coastal waters of south Florida, United States, yet it is a chronically understudied feature of the marine seascape in this region. In this study, we characterised the general biogeographic and structural features of shallow benthic hard-bottom communities in the Florida Keys, and related those to the abundance of juvenile Caribbean spiny lobster (*Panulirus argus*), the target of one of Florida's most economically valuable fisheries. We used rapid assessment techniques to survey more than 100 hard-bottom sites in the Florida Keys to estimate the percentage bottom coverage of vegetation (seagrass and macroalgae) and the abundance of sponges, octocorals, hard corals, and other crevice-bearing structures, as well as the abundance of juvenile lobsters. Using a multivariate statistical approach, we evaluated the relationship between habitat and size-specific juvenile lobster abundance and quantitatively verified the existence of six generally accepted biogeographic subregions. Although the types of hard-bottom shelters used by juvenile lobsters varied somewhat among these subregions, in all regions, branching-candle sponges and octocorals were under-used by lobsters, whereas loggerhead sponges, coral heads, and solution holes were over-used (i.e., used more frequently than expected based on their availability). There was also an ontogenetic transition in the shelter preference of juvenile lobsters; small juveniles tended to occupy a variety of sponges, whereas large juveniles preferred hard structures such as coral heads and solution holes. This study yields the first quantitative biogeographic description of hard-bottom communities of the Florida Keys, and confirms the suspected relationship between the structural features of hard-bottom habitat and the value of these communities as nurseries for juvenile spiny lobster.

Keywords Florida Keys; habitat use; essential habitat

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INTRODUCTION

Hard-bottom habitat is a ubiquitous feature of the Florida Keys, Florida, United States marine ecosystem, covering over 30% of the region's shallow coastal seafloor (Zieman et al. 1989, Herrnkind et al. 1997). Hard-bottom occurs in shallow (<5 m) coastal waters and is characterised by low relief (<0.5 m), limestone bedrock overlain by a thin veneer of sediment and populated by a complex assemblage of sponges, octocorals, corals, and macroalgae (Chiappone 1996). It has been variously referred to as live-bottom habitat, octocoral-dominated hardgrounds, exposed bedrock outcrops, alcyonarian-sponge communities, nearshore rock-bottom habitat, and algal-dominated hard-bottom (see Schomer & Drew 1982; Chiappone 1996). In the shallow waters surrounding the Florida Keys

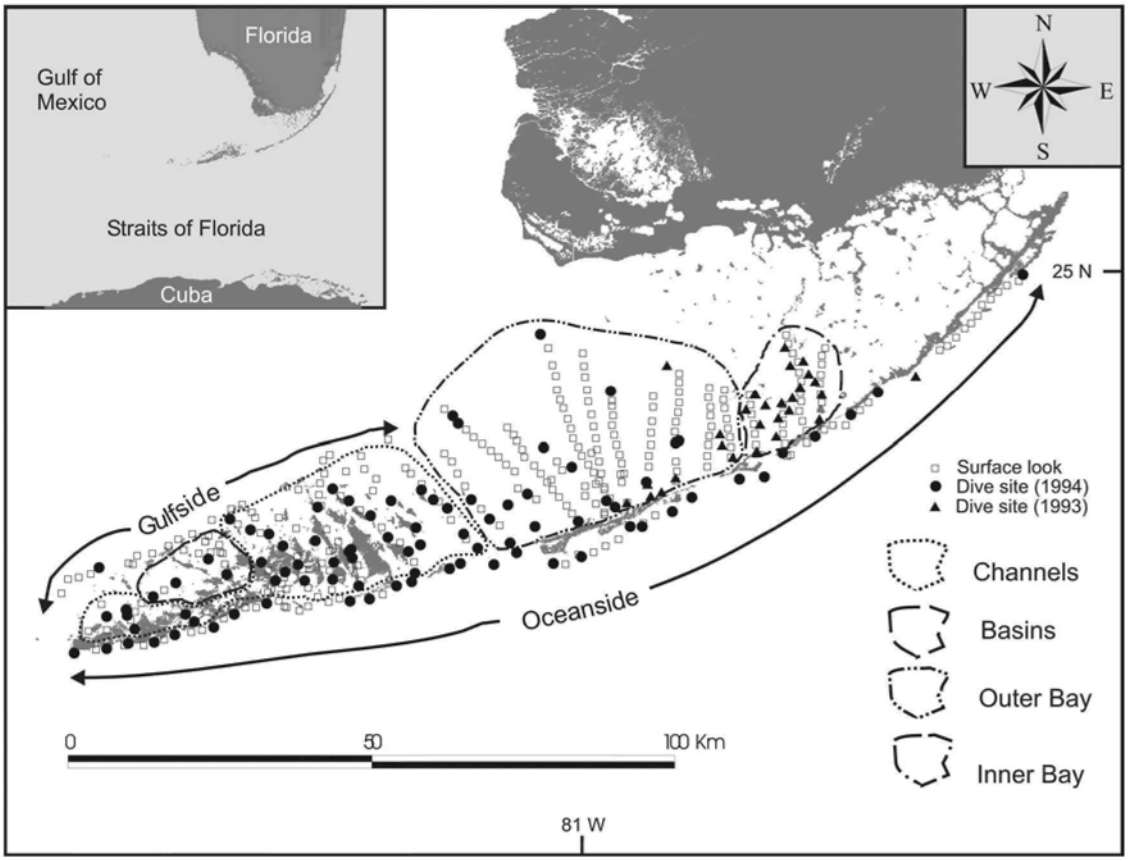

Fig. 1 Location of 355 sites evaluated as potential survey locations (all symbols) and the location of 115 hard-bottom sites (closed symbols), where rapid assessment surveys of benthic habitat structure and lobster population structure were conducted.

off the southern tip of Florida, hard-bottom habitat intersperses with sand, calcareous mud-bottom, and seagrass meadows (primarily *Thalassia testudinum*, *Syringodium filiforme*, and *Halodule wrightii*).

A large but unknown number of motile macrofaunal species dwell in hard-bottom areas of the Florida Keys. Many species use hard-bottom habitat opportunistically (e.g., bonefish, tarpon, sharks, turtles), whereas others are obligate dwellers of hard-bottom and are rarely found elsewhere (e.g., octocorals, many anemones, spider crabs, octopus, and certain fishes; Lindeman & Snyder 1999). A number of fishes use hard-bottom as a nursery before migrating to other habitats, such as coral reefs (Baron et al. 2004). The Caribbean spiny lobster (*Panulirus argus*, Latreille, 1804), which sustains one of the most economically important fisheries in Florida (Hunt 2001), also uses the hard-bottom habitat as a nursery (Herrnkind et al. 1997).

Following an extended period of larval dispersal in the open sea, Caribbean spiny lobster postlarvae arrive inshore every month on new moon flood tides (Acosta et al. 1997), seeking structurally complex vegetation in which to settle. In south Florida, they preferentially settle in clumps of red macroalgae within hard-bottom habitat (Marx & Herrnkind 1985; Herrnkind & Butler 1986; Herrnkind et al. 1994; Butler et al. 1997), but highly-fouled mangrove roots (Marx 1986; Acosta & Butler 1997), seagrass (Herrnkind et al. 1994; Acosta & Butler 1997) and possibly other complex substrates may also harbour newly settled lobsters in other regions (Briones-Fourzan & Lozano-Alvarez 2001). After a few months, juveniles emerge from their vegetated settlement sites and take up daytime refuge under hard-bottom structures (e.g., sponges, solution holes, corals) that provide them with suitable shelter from predators (Eggleston et al. 1990; Forcucci et al. 1994;

Butler et al. 1995). Later, as subadults, they migrate to coral reefs to join the adult population (Lyons & Kennedy 1981). To complete their complex life cycle, lobsters therefore use most of the region's marine habitats beginning with the hard-bottom nursery.

Characterising the regional biogeography of hard-bottom habitat and understanding the interaction between shelter availability and its usage by lobsters may help us determine the regions and features of nursery habitat most critical to juvenile lobster. We therefore surveyed juvenile lobster abundance and selected structural features of hard-bottom habitat at more than 100 sites throughout Florida Keys to detail regional patterns in hard-bottom habitat structure, juvenile lobster abundance, and their interrelationship.

MATERIALS AND METHODS

Field surveys

Field surveys of benthic habitat and surface visual assessments were conducted at 381 sites throughout the Florida Keys during May–July of 1993 and 1994 (Fig. 1). In 1993, we used SCUBA to survey the benthos and lobsters at 26 sites, whereas in 1994 we assessed the habitat types of 355 sites, 89 of which included SCUBA-based benthos and lobster abundance estimates, and the remainder were visual assessments from the surface. When this study began, GIS-based benthic habitat type maps were not yet available for use in our selection of survey sites, so survey sites could not be stratified by habitat. Also, the distribution of various shallow benthic habitats was unknown. Therefore, we used a uniform sampling protocol wherein the basic criterion guiding our selection of survey locations was to maintain a more-or-less even separation of one nautical mile (1.85 km) between sites along transect lines running approximately north-south. However, in some areas, the complex topography of islands and shallow water in the Florida Keys precluded exact north-south transects and one nautical mile inter-site distances (Fig. 1).

Depending on the initial characterisation of bottom type, up to four types of data were collected at each site. Upon arrival at each pre-determined site location, we first noted our exact position (latitude and longitude) and then characterised the site into one of three broad habitat types (sand, seagrass, or hard-bottom) based on visual inspection of the bottom. If the site was predominantly sand or seagrass, no further data were collected. If the site was hard-bottom and thus contained large sponges, octocorals, or other potential juvenile lobster shelters, we then proceeded with quantitative surveys conducted by divers. These included surveys of the abundance of: (1) general vegetation types (i.e., seagrass, red macroalgae, and green algae) that influence lobster settlement; (2) prominent benthic structural features that are potential lobster shelters (i.e., sponges, corals, solution holes); and (3) juvenile lobsters. At each dive site, percentage cover of bottom vegetation was determined from three, non-overlapping 25 m long tape transects (four transects in 1993) placed haphazardly along the bottom at each site. Transects containing more than 20% seagrass were rejected and repositioned. Divers travelled along each tape and recorded the size and positions of all patches of seagrass, green macroalgae (e.g., *Halimeda* spp., *Penicillus* spp.) and red macroalgae (*Laurencia* spp.) larger than 5 cm.

Sponges, octocorals, and other crevice-bearing structures large enough to be potential shelter for juvenile lobster (Childress 1995) were surveyed using three 2 m □ 25 m belt transects using the same transect positions as for the vegetation surveys. Within each 50 m^2 belt transect, divers enumerated all of the loggerhead sponges (*Speciospongia vesparium*), vase sponges (*Ircinia campana*), branching-candle sponges (*Ircinia* sp.), hard coral (primarily *Solenastrea bourgani*), miscellaneous sponges, solution holes, and octocorals (sea plumes, primarily *Pseudopterogorgia* spp.; sea whips, *Pterogorgia anceps*; and sea rods, primarily *Plexaurella* spp.). These benthic structures were characterised as "large" (>20 cm diam.) or "small" (<20 cm diam.); structures <20 cm do not shelter juvenile lobster (Childress 1995). For octocorals, only those whose holdfast fell within the belt were counted. Though not living benthos, solution holes large enough (>20 cm) to accommodate juvenile lobster were also counted.

The relative abundance of juvenile lobster was estimated with a 1 h timed search (i.e., catch-per-unit-effort, CPUE). Typically two divers searched separate portions of the survey site for 30 min each. The search time included the time to capture the lobster and record the shelter type used by the lobster. If a capture was missed, divers recorded a shelter type and estimated lobster size. At the end of the search, divers returned the captured lobsters to the boat where carapace length (CL) to the nearest 0.1 mm, sex, moult condition, injuries, and shelter type were recorded. For the 1994 sites, lobsters larger than 50 mm CL were not captured although their

abundance was recorded. For many of the analyses, juvenile lobsters were divided into either three size classes (<25 mm, 25–35 mm, and 35–50 mm CL) or four size classes (15–25 mm CL, 25–35 mm CL, 35–45 mm CL, 45–65 mm CL) similar to other studies (e.g., Herrnkind & Butler 1986; Field & Butler 1994; Childress & Herrnkind 1996).

Data analysis

Descriptive statistics for surface assessments were based on the 355 survey sites in 1994 (surface assessments had not been formalised in 1993), and those for benthic surveys were based on 113 of the 115 benthic survey sites (data from two sites were omitted because of errors in the collection of data). Multivariate analyses for biogeographic characterisations of subregions were based on 108 benthic survey sites covering four subregions with approximately equal sample size (28 sites in Oceanside; 22 sites in Outer Bay; 21 sites in Inner Bay; and 37 sites in Channel). Gulf (1 site) and Basin (4 sites) subregions were retained for descriptive statistics, but were inadequately sampled for reliable mulitivariate analysis (e.g., the inclusion of the Gulf site would introduce a singularity).

The subregions of the Florida Keys were defined *ad hoc* based on topography and hydrology categorisations described by Browder (1976) and Schomer & Drew (1982), and confirmed by our own field observations. The Inner Bay comprises a series of shallow basins surrounded by banks that restrict waterflow. Fresh water enters this subregion from the Florida mainland. Freshwater input and rapid evaporation create dramatically changeable salinities in this subregion, particularly in the north (10–60 PSU; Chiappone 1996), however; our surveys were conducted in the southern portion (Fig. 1) where salinities range between 30 and 42 PSU. The Outer Bay subregion covers an open water area north of the middle Keys. This subregion receives little fresh water from the mainland and, lacking the intensive banks of the Inner Bay, water flow between the Gulf of Mexico and Straits of Florida are impeded only by the islands in the middle Keys (Schomer & Drew 1982). Salinities in the Outer Bay thus vary little: typically between 32 and 39 PSU (D'Sa et al. 2001). The Channel subregion (Fig. 1) comprises north-west to south-east channels bordered by islands. These channels range from 14 to 26 km in length by approximately 1 km in width and correspond to a habitat zonation referred to as "high velocity channel" by Browder et al. (1973) or "tidal channels" by Department of Commerce (1996). Rainfall is the only freshwater input to this subregion and salinities are usually between 34 to 36 PSU (D'Sa et al. 2001). The Gulfside and Oceanside subregions are nearshore areas adjacent to the open ocean waters of the Gulf of Mexico and Straits of Florida, respectively. Salinities in these two subregions reflect their open connection to offshore waters and, like the Outer Bay subregion, vary little from 35 PSU. Our use of these subregions also follows the conventions used by Herrnkind et al. (1997) with only minor exception.

Although the subregions described above are generally accepted, their habitat or biogeography have not been quantitatively defined. Therefore, we used a multivariate statistical approach to: (1) characterise subregions within the Florida Keys with respect to general features of hard-bottom habitat that are likely to influence recruitment of juvenile spiny lobster; and (2) examine the association between juvenile lobster abundance and various features of hard-bottom habitat within each biogeographic region. Spatial presentation of data was plotted onto south Florida Arc/Info coverage information provided by the Florida Fish and Wildlife Conservation Commission (FKNMS 2000). For use in these analyses, the raw data from the field surveys were summarised in the following ways. The percentage cover of red macroalgae and seagrass was determined by summing patch sizes for each taxon and dividing by total transect length (200 m in 1993 and 150 m in 1994) for each site. The density of hard-bottom structures was determined by summing the counts of large structures by type and converting them to number per hectare. The three taxa of octocorals were grouped into a single variable owing to inconsistencies in field discrimination of species. The relative abundance of juvenile lobster abundance was defined as the count of lobsters <50 mm CL found within 60 min.

We examined juvenile lobster preference for shelter in the different subregions using a log-likelihood chi-squared test described by Neu et al. (1974). This procedure is robust to scaling changes and Type II errors, and permits the determination of confidence limits for the indices (Allredge & Ratti 1992 a,b; McClean et al. 1998).

Discriminant analysis was used to examine the most parsimonious combination of shelter and lobster size class information that best described the various regions. For the analysis, we used a data matrix that included the density of all types of

structure and the abundance of three size classes of juvenile lobsters using subregion as the grouping variable.

Non-linear canonical correlation analysis was used to examine the relationships of the shelters and lobster size classes (Meulan & Heiser. 2004). The advantages of the non-linear canonical correlation is that it is robust to many zeros, ordinal and nominal variables can both be used in a single analysis, and highly correlated variables can be placed into a single variable set that prevents those correlations from dominating the analysis and masking other relationships (Gifi 1990). Categorical variables were first formulated from lobster abundance by size, the abundance of each type of structure, and percentage cover. Then, an equal membership technique was used to define categories wherein observations were ranked then divided into bins of equal size with the first and last member in a bin defining the bounds of a category. This technique is useful when data contain widely divergent distributions and ranges. The number of individuals in each of three lobster size classes was then placed into a single variable set to examine the differences between the size classes and to reduce the high correlations between these variables. All shelter types were placed into different single variable sets.

RESULTS

Distribution of hard-bottom habitat and juvenile lobsters

Of the 355 surface assessments performed during the spring of 1994 throughout the Florida Keys region, 25% were characterised as hard-bottom, and thus surveyed in detail by divers. This result compared well with a *post hoc* spatial analysis of the Arc/Info benthic coverages in which 31% of the region was designated as hard-bottom. Within subregions, the comparison between the percentage of hard-bottom from the benthic cover data and percentage from our surface assessments was weaker. For example, in the Channels subregion, the GIS benthic cover data estimated that 29% of this subregion comprised hard-bottom, whereas 44% of our field surveys were over hard-bottom.

The first two discriminant functions described 97% of the variation in the data matrix and comprised the abundance of corals, octocorals, solution holes, three sponge taxa, and three size classes of juvenile lobsters. The first discriminant function was dominated by hard shelter structures (solution holes and coral) plus octocoral densities. The second function comprised vase sponges, miscellaneous sponges, and the three size classes of juvenile lobsters. The configuration of the confidence ellipses (Fig. 2) mirror in many ways the geographical configuration of the *ad hoc* topographic and hydrological subregions. For example, the subregion Outer Bay occupied an undifferentiated position in the discriminant analysis, suggesting that it constitutes a subset of the Ocean subregion. The Outer Bay shares two broad waterway connections with the Ocean subregion through the Long Key bridge (>3 km) and Seven Mile bridge (10 km). The Channel and Inner Bay subregions are the most differentiated pair of subregions and they are also the most geographically separated. Although discriminant analysis suggests that the Inner Bay and the Channel subregions have the greatest differentiation, they shared a similar distribution of discriminant function 2 scores. All three lobster sizes classes correlated best with discriminant function 2 and both subregions contained the highest juvenile lobster densities.

The abundance of structures of potential importance to lobsters as shelter varied by several orders of magnitude among the four subregions (Fig. 3, Table 1). Octocorals were the most common structure throughout all of the subregions except the Channels. Sponges were most common in the Channels followed by the Outer Bay. Solution holes and coral heads, although not common, reached their highest densities in the Inner Bay. Juvenile lobsters of all sizes were most abundant in the Channels and Inner Bay and least abundant along the Oceanside.

Unlike shelter density, discriminant analysis could not differentiate the subregions based solely on the percentage of different potential settlement substrates (i.e., seagrass, red macroalgae, and green algae) and the abundance of lobsters by size class. Likewise, the non-linear canonical correlation analysis produced non-specific results. For example, when we added one settlement substrate at a time into the shelter and lobster size class model, each loaded positively on the first dimension with the sponges and smallest size class of lobsters. So none of the settlement substrates added any additional discriminatory power exceeding that already attributable to the abundance of hard-bottom structure or lobster size class.

Hard-bottom structure—lobster relationships

Disregarding any differences in shelter use among subregions, a more general analysis of juvenile lobster shelter preference using the entire data set revealed

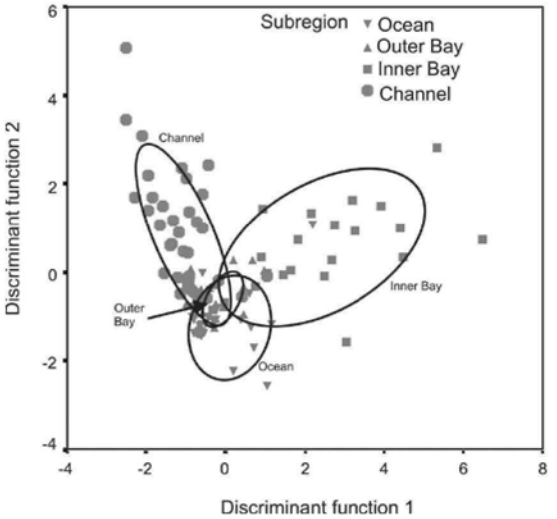

Fig. 2 Site loadings for two discriminant functions for each survey site grouped *a priori* into four subregions (represented by different symbols). The ellipses represent 95% confidence intervals for the subregions as defined by the discriminant function model.

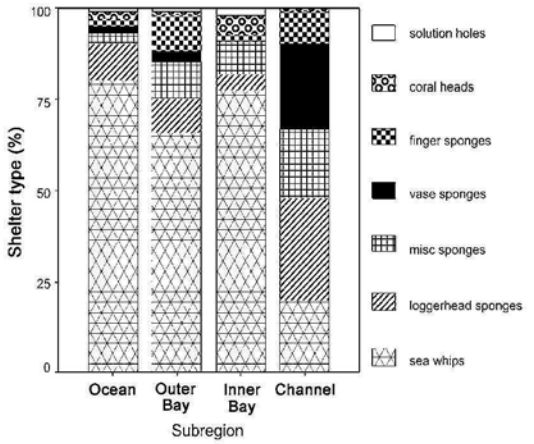

Fig. 3 Mean relative abundance of seven types of hard-bottom structures of potential use as shelter by lobsters within four subregions of the Florida Keys, United States.

distinct ontogenetic differences in shelter preference among lobster size classes. Examination of only shelter use without reference to shelter availability suggests that loggerhead sponges were the single most important shelter for all sizes of juvenile lobsters, becoming increasingly less important as lobsters grew larger and occupied solution holes (Fig. 4). But a different picture emerged when

Table 1 Mean (±SE) density of shelters and mean relative abundance (catch-per-unit-effort) of juvenile lobsters (by size class) for each subregion of the Florida Keys, Florida, United States. Percentages reflect proportions of each shelter or lobster size class within a given subregion.

	Subregion (no. of sites)																	
	Ocean (28)			Outer Bay (22)			Inner Bay (21)			Channel (37)			Basins (4)			Gulf (1)			Overall		
Shelter	No./ha	SE	%	No./ha	SE	%	No./ha	SE	%	No./ha	SE	%	No./ha	±SE	%	No./ha	SE	%	No./ha	±SE	%
Sea whips	2794	±873	82	2156	±443	68	4857	±1219	75	418	±132	20	450	±450	24	1200	na	78	2247	±363	64
Loggerhead sponges	333	±81	10	283	±90	9	278	±119	4	598	±98	28	433	±96	24	133	na	9	408	±48	12
Misc. sponges	82	±36	2	306	±95	10	663	±135	10	405	±78	19	267	±112	14	0	na	0	348	±46	10
Vase sponges	50	±19	1	84	±36	3	7	±4	>1	488	±94	23	350	±110	19	0	na	0	201	±37	6
Finger sponges	54	±24	2	293	±157	9	120	±51	2	197	±45	9	333	±170	18	0	na	0	171	±37	5
Coral	68	±27	2	27	±11	<1	344	±78	5	12	±7	<1	6	±6	<1	200	na	13	101	±20	3
Solution holes	25	±12	1	25	±7	<1	174	±26	3	9	±6	<1	6	±6	<1	0	na	0	47	±9	<1
Total	3406	±927		3174	±519		6441	±1297		2128	±253		1846	±426		1533			3523	±388	
Lobster CPUE																					
<25 mm CL	0.5	±0.2	25	0.9	±0.3	26	1.7	±0.4	20	3.2	±0.7	34	0.5	±0.5	25	0	na	na	1.8	±0.3	29
25–35 mm CL	0.5	±0.2	25	1.4	±0.6	40	3.8	±0.8	44	3.5	±0.6	38	1.0	±0.7	50	0	na	na	2.4	±0.3	38
35–50 mm CL	1.0	±0.3	50	1.2	±0.3	34	3.1	±0.7	36	2.6	±0.5	28	0.5	±0.5	25	0	na	na	2.0	±0.2	33
Total	2.0	±0.5		3.5	±0.8		8.6	±1.5		9.4	±1.3		2.0	±1.7		0	na		6.2	±0.6	

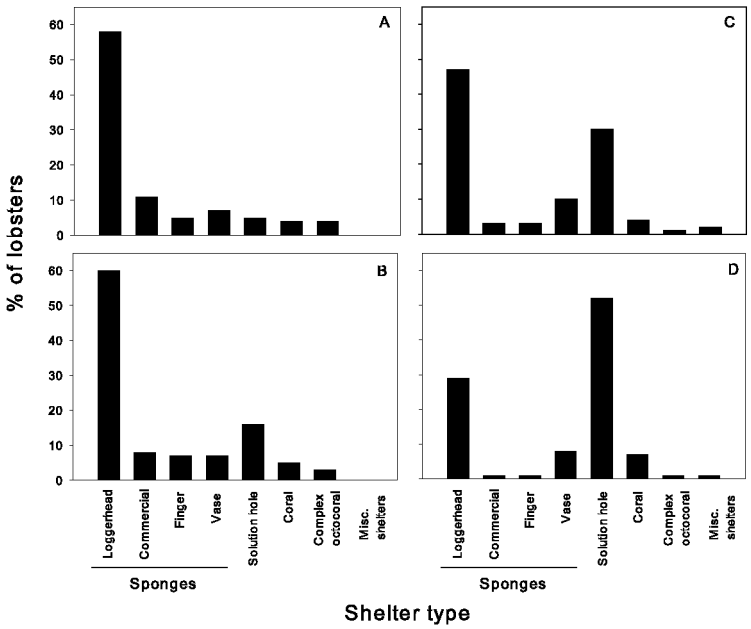

Fig. 4 Percentage of lobsters by size category (**A**, 15–25 mm CL, n = 109; **B**, 25–35 mm CL, n = 186; **C**, 35–45 mm CL, n = 129; **D**, 45–65 mm CL, n = 539) occupying eight different types of shelter.

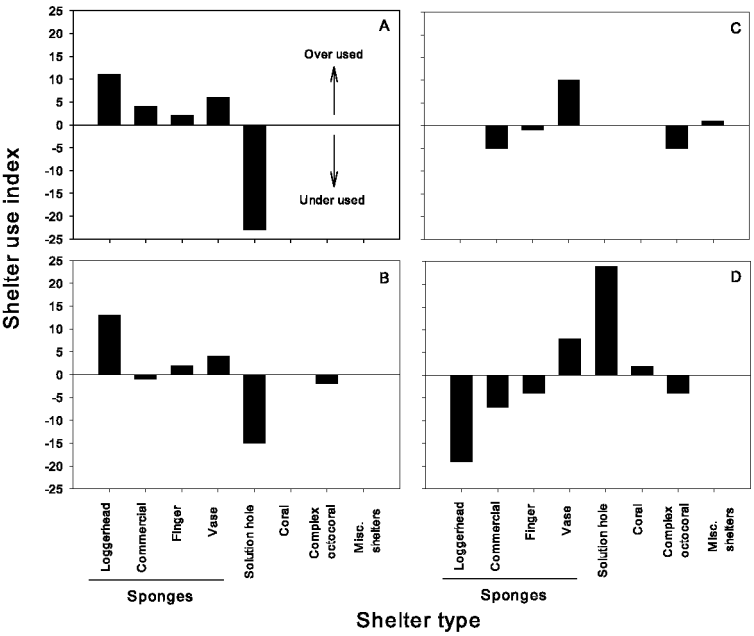

Fig. 5 Use of different types of shelter by lobsters grouped into four size categories (**A**, 15–25 mm CL, n = 109; **B**, 25–35 mm CL, n = 186; **C**, 35–45 mm CL, n = 129; **D**, 45–65 mm CL, n = 539), as determined by a shelter use index: % use – % available for each shelter type. Positive values indicate shelters that were used disproportionate to their abundance, suggesting preference for those types of shelters by lobster; negative values indicate that those habitats were used less frequently than their abundance would imply.

shelter availability was taken into account (Fig. 5). The smallest juvenile lobsters (15–35 mm CL) preferentially used a variety of commercial and non-commercial sponges (including the ubiquitous loggerhead sponge) and avoided hard, rocky substrates such as solutions holes and hard corals. Vase sponges were preferred by juvenile lobsters of intermediate size (35–45 mm CL) and large juvenile lobsters preferred vase sponges, solution holes, and hard coral heads.

Comparison of juvenile lobster shelter preferences among subregions were generally consistent with

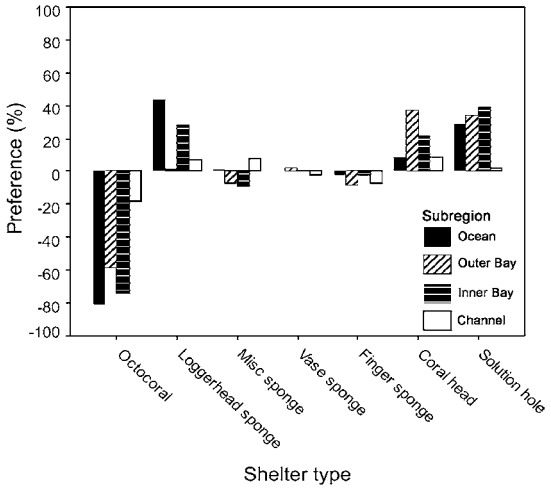

Fig. 6 Preferences of juvenile lobster for seven types of shelter by subregion. Positive values indicate shelters that were used disproportionate to their abundance, suggesting preference for those types of shelters by lobster; negative values mean that those habitats are used less frequently than their abundance would imply.

the more general analysis described above, the exceptions being attributable to differences in shelter availability among subregions (Fig. 6). Branching-candle sponges (*Ircinia* sp.) and octocorals were significantly underused across all subregions. In contrast, solution holes were used significantly above availability in all subregions except the Channels, as were loggerhead sponges, which were used significantly above availability in all subregions except the Outer Bay. Large coral heads were only available in the Inner Bay and Outer Bay, where large juvenile lobsters invariably used them as shelter in disproportion to their abundance. Miscellaneous sponges comprised a variety of sponge taxa of varying shapes (from encrusting to barrel shaped) and all were underused in all subregions except the Channels. In the Channels subregion, we often found small (<25 mm CL), solitary lobsters in the crevices of large sponges (>20 cm diam.) encrusted by the green sponge *Haliclona viridens*.

Non-linear canonical correlation analysis revealed multivariate relationships between lobster abundance by size class and benthic habitat structure that were consistent with the single-variable shelter preference analyses. The component loadings chart (Fig. 7) revealed two basic groups of shelters used by juvenile lobsters. All sponges loaded positively along the first dimension, whereas the other shelters (e.g., octocorals, corals, and solution holes) loaded negatively. The placement of the size classes of lobsters among the shelter types suggests a transitional relationship. The component loadings for the smallest juvenile lobsters (<25 mm CL) placed them among sponge shelters, whereas component loadings for medium sized juveniles (25–35 mm CL) were intermediate between sponges and hard shelters. The component loading for the largest juveniles (35–50 mm CL) was closer to the hard shelters (e.g., corals, solution holes) (Table 2).

DISCUSSION

The results of our rapid assessment survey of the shallow hard-bottom communities of the Florida Keys yields the first quantitative biogeographic description of this ubiquitous, but largely overlooked habitat. Our results also confirm the value of hard-bottom habitat as nurseries for juvenile spiny lobster. We also detail the relationship between the structural features of the habitat and ontogenetic changes in the use of habitat structures as lobsters grow larger.

Hard-bottom characterisation

In general, the biogeographic regions that we subjectively defined at the start of the study based on general topographic features were quantitatively distinguishable by the abundance of juvenile lobster and two classes of hard-bottom structures: (1) octocorals and hard structures (hard corals, octocorals, and rocky solution holes); and (2) large sponges (Fig. 2). We found that large sponges were abundant in the Channel subregion, but octocorals and hard structures were not. The Inner Bay subregion was typified by greater numbers of octocorals and hard structures and fewer sponges. The density of nearly all structures on shallow hard-bottom in the Ocean and Outer Bay subregions were generally low. There were individual sites that deviated from these general patterns and our results do not include hard-bottom areas further offshore that are deeper and more closely associated with the reef tract (see Chiappone & Sullivan 1994b) .

One particularly striking biogeographic pattern was the near absence of juvenile lobsters in the Gulfside and Basin subregions of the Florida Keys, which we suspect reflects an inadequate influx of postlarvae to these subregions. In the Basin subregion, a web-like network of emergent mudbanks and small mangrove islands restricts

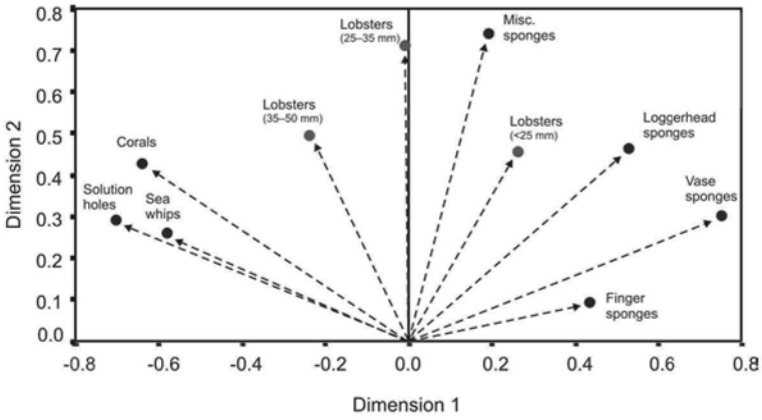

Fig. 7 Component loadings of the variables used in the non-linear canonical correlation (optimal scaling) analysis. Direction from the origin indicates the relationship of each variable in the analysis with the other variables. Distance from the origin (length of the arrow) indicates the strength of the relationships.

Table 2 Discriminant structure matrix for all major shelter abundances and juvenile lobster size classifications. Numbers indicate the pooled within-groups correlations between discriminating variables and standardised canonical discriminant functions. Variables ordered by absolute size of correlation within function. The first function is dominated by hard structures (coral heads and solution holes) along with octocorals, whereas the second function comprises all three size classification of juvenile lobsters, and some sponges.

	Discriminant function		
Shelters/lobster size classes	1	2	3
Solution holes	0.665*	0.205	–0.092
Coral	0.560*	0.155	–0.287
Octocorals	0.353*	–0.132	–0.158
Lobsters (25 to 35 mm CL)	0.081	0.586*	0.141
Vase sponges	–0.328	0.520*	–0.139
Lobsters (<25 mm CL)	–0.111	0.479*	–0.082
Misc. sponges	0.178	0.398*	0.371
Lobsters (35 to 50 mm CL)	0.092	0.386*	–0.140
Finger sponges	–0.046	0.060	0.723*
Loggerhead sponges	–0.133	0.229	–0.285*

*Largest absolute correlation between each variable and any discriminant function.

water flow and offers no direct connection to the sea, the source of lobster postlarvae for settlement. Field & Butler (1994) have shown that a similar situation occurs in the interior of nearby Florida Bay, where mudbanks impede postlarval transport. The Gulfside subregion contains little habitat that is also suitable for lobster settlement and, although open to the Gulf of Mexico to the north, this region is also blocked by islands and mudbanks from the primary source of postlarvae, which arrive from the Straits of Florida to the south of the Florida Keys. No postlarvae have been caught on artificial collectors placed in this subregion to monitor the arrival of postlarvae from the Gulf of Mexico (David Eggleston, North Carolina State University pers. comm.), whereas collectors placed on the oceanside of the Florida Keys are reliable indicators of postlarval supply (Acosta et al. 1997).

Hard-bottom as a nursery habitat for spiny lobster

The pattern of shelter preference by juvenile lobsters that we observed in field surveys conducted over a large spatial scale (i.e., the entire Florida Keys region; c. 10000 km^2) and for a wide range of juvenile lobsters sizes (e.g., approximately 15–50 mm CL), is consistent with those predicted from previous experimental investigations. As juvenile

lobsters grew larger, their preference for shelters changed from sponges to hard substrates such as rocks and corals. However, the specific types of shelters used by lobsters in any particular region varied depending primarily on the availability of shelters that make suitable dens. When natural shelters are limited, suboptimal shelters are readily occupied. For example, Childress & Hunt (2002) examined changes in shelter availability and use by juvenile lobster on sites affected by sponge die-offs (Butler et al. 1995) compared with unaffected areas. They concluded that juvenile lobsters were insensitive to changes in the abundance of hard-bottom structure, because lobsters adjusted their use of shelter in proportion to its availability. Although their analysis did not include lobster size, which our study and those of others show is important for shelter selection (Eggelston & Lipcius 1992; Butler & Herrnkind 1997; Lipcius et al. 1998; Lozano-Alvarez & Briones-Fourzan 2001), it nonetheless demonstrates the plasticity of lobster shelter use. Lobsters respond to the sheltering qualities of objects, not the object *per se*, which is why lobsters will occupy artificial shelters employed for experimental purposes (Butler & Herrnkind 1992, 1997; Lozano-Alvarez et al. 1994), as well as other human-made objects abandoned on the seafloor. Tyres, abandoned lobster traps, oil drums, and other human-made objects housed about 6% of the juvenile lobsters that we observed, indicating the opportunistic nature of shelter use by *P. argus*.

Although lobsters choose many types of objects as dens, certain characteritics of den quality appear to influence their choice. For example, newly settled early benthic juvenile *P. argus* prefer to occupy architecturally complex stands of macroalgae offering a complex network of interstices within which the early benthic juveniles manoeuvre. They choose these shelters over architecturally more simple artificial substrates of similar volume and food quality to natural macroalgae (Herrnkind & Butler 1986; Butler et al. 1997). Experimental studies have shown that the selection of dens by larger juvenile spiny lobsters is driven primarily by size-specific preferences for dens with holes that closely parallel their own dimensions (Eggelston & Lipcius 1992; Lipcius et al. 1998; Lozano-Alvarez & Briones-Fourzan 2001). However, their selection of dens is modified by the chemically attractive cue of conspecifics (Zimmer-Faust et al. 1985; Childress & Herrnkind 1997, 2001; Ratchford & Eggleston 1998; Butler et al. 1999; Nevitt et al. 2000; Lozano-Alvarez & Briones-Fourzan 2001) and their repulsion for diseased conspecifics (Behringer et al 2006) and certain predators, especially octopus (Berger & Butler 2001). Predation itself further modifies the resultant patterns of den occupancy, if not den choice (Eggleston et al. 1990, 1997; Schratwieser 1999).

Although the relationship between the abundance of large juvenile lobsters (>35 mm CL) and the availability of benthic structures is clear, discerning similar patterns for more recently settled juveniles has been elusive. We could not show a strong link between settlement habitat abundance (i.e., red macroalgae) and the abundance of juvenile lobsters (large or small) using data from our Florida Keys-wide surveys, corroborating previous studies conducted at smaller spatial scales. Field & Butler (1994) studied shelter use of post-algal juveniles (15–60 mm CL) within the Inner Bay subregion and examined the relationship between lobster abundance and the density of various structures and settlement substrates with multiple regression. They found that the abundance of larger (>35 mm CL) juvenile lobsters could be predicted by salinity and the density of octocorals, corals, and solution holes. However, they also could not find a predictable relationship between macroalgae and lobsters less than 35 mm CL (Field & Butler 1994). Herrnkind & Butler (1994) also used multiple regression to examine the relationship between juvenile lobster abundance (by size class) within the Inner Bay subregion and a suite of measures, including postlarval supply, macroalgal coverage, and the density of different hard-bottom structures. They found that the best predictor for all lobster size classes was the abundance of sponges (Herrnkind & Butler 1994). The lack of a strong link between macroalgal abundance and juvenile lobsters may be because of the ephemeral nature of the distribution of the macroalgae (Mathieson & Dawes 1975, Butler et al. 1997), or our inability to effectively survey lobsters during their "transitional phase", when they are cryptic, solitary, and transient between macroalgae and benthic structures (Childress & Herrnkind 2001).

Hard-bottom monitoring and protection

One aspect of this study, the regional characterisation of shallow hard-bottom habitat, parallels similar efforts to describe the biogeography of two other major marine habitats in the Florida Keys, namely seagrass (Zieman et al. 1989, 1999) and coral reefs (Florida Fish and Wildlife Conservation Commission & National Oceanic and Atmospheric Administration 2000; Lidz et al. 2006). Our focus in this study was to determine which aspects of hard-bottom

habitat were most relevant as a nursery role for lobsters. Thus, the level of taxonomic detail we used was admittedly coarser and used fewer types of measures of community structure than those used in more detailed studies of fewer sites (Chiappone & Sullivan 1994 a,b). However, this study constituted a first step in hard-bottom characterisation at a time when GIS depictions of habitat coverage were unavailable, and it allowed us to describe general biogeographic patterns in hard-bottom structure by surveying many sites (c. 100) in a short amount of time (c. 1 month)—the very goal of rapid assessment procedures, especially those potentially used in developing nations where GIS-based maps of subtidal habitats may be unavailable.

This project also served to establish a long-term monitoring programme for shallow hard-bottom habitat in the Florida Keys. Like most coastal habitats (Finkle & Charlier 2003; Sale et al. 2008), hard-bottom is threatened by a variety of environmental perturbations, most of which are anthropogenic in origin. Impacts on the abundance of lobster have been documented on hard-bottom areas in Florida affected by siltation (Herrnkind et al. 1988). Declining water quality and harmful algal blooms are the suspected culprits that have triggered massive die-offs of sponges in the Florida Keys and the wholesale reconfiguration of impacted hard-bottom areas (Butler et al. 1995; Phlips et al. 1999). Commercial fishing of sponges removes approximately 7 million sponges from shallow hard-bottom habitat in the Florida Keys each year (Witzel 1999) with unknown consequences, but the indirect effects of other fishing activities may be more severe. For example, commercial trawling for bait shrimp (Eldred et al. 1972; Berkeley et al. 1985) and the use of traps for lobster and crabs (Matthews et al. 2005) damages hard-bottom areas. Lost fishing gear accounts for over 80% of the debris found along the Florida Keys reef tract and associated offshore hard-bottom areas, and it causes over 80% of the physical damage to sessile invertebrates (Chiappone et al. 2005). Damage to juvenile lobsters dwelling in hard-bottom and caught incidentally by commercial and recreational fishers substantially diminishes the recruitment of lobster to the Florida Keys fishery (Lyons & Kennedy 1981; Hunt & Lyons 1986; Forcucci et al. 1994). Compounding these anthropogenic disturbances to hard-bottom habitat are the adverse effects of episodic natural disturbance caused by hurricanes. In short, the importance of hard-bottom habitat in south Florida for economically important species such as spiny lobster, juxtaposed against the suite of human activities that impinge on its sustainability, provides a compelling case for adding shallow hard-bottom to the list of marine habitats deserving more vigilant, regular monitoring and protection.

REFERENCES

Acosta CA, Butler IV MJ 1997. Role of mangrove habitat as a nursery for juvenile spiny lobster, *Panulirus argus*, in Belize. Marine and Freshwater Research 48: 721–727.

Acosta CA, Matthews TR, Butler IV MJ 1997. Temporal patterns and transport processes in recruitment of spiny lobster (*Panulirus argus*) postlarvae to south Florida. Marine Biology 129: 79–85.

Alldredge JR, Ratti JT 1992a. Comparison of some statistical techniques for analysis of resource selection. Journal of Wildlife Management 50:157–165.

Alldredge JR, Ratti JT 1992b. Further comparison of some statistical techniques for analysis of resource selection. Journal of Wildlife Management 56: 1–9.

Baron RM, Jordan LKB, Spieler RE 2004. Characterization of the marine fish assemblages associated with the nearshore hardbottom of Broward County, Florida, USA. Estuarine Coastal and Shelf Science 60(3): 431–443.

Behringer DC Jr, Butler MJ IV, Shields J 2006. Avoidance of disease in social lobsters. Nature 441: 421.

Berger DK, Butler IV MJ 2001. Octopuses influence den selection by juvenile Caribbean spiny lobster. Marine and Freshwater Research 52: 1049–1053.

Berkeley SA, Pybas DW, Compos WL 1985. Bait shrimp fishery of Biscayne Bay. Technical Papers of the Florida Sea Grant Program. Florida Sea Grant, Gainsville, Florida, United States. 39 p.

Briones-Fourzán P, Lozano-Alvarez E 2001. Effects of artificial shelters (casitas) on the abundance and biomass of juvenile spiny lobsters *Panulirus argus* in a habitat-limited tropical reef lagoon. Marine Ecology Progress Series 221: 221–232.

Browder J, Littlejohn C, Young D 1976. South Florida: Seeking a balance of man and nature. Center for Wetlands, University of Florida & Florida Division of State Planning, Tallahassee, United States. 117 p.

Butler IV MJ, Herrnkind WF 1992. Spiny lobster recruitment in south Florida: quantitative experiments and management implications. Proceedings of the Gulf and Caribbean Fisheries Institute 41: 508–515.

Butler IV MJ, Herrnkind WF 1997. A test of recruitment limitation and the potential for artificial enhancement of spiny lobster populations in Florida. Canadian Journal of Fisheries and Aquatic Sciences 54: 452–463.

Butler IV MJ, Herrnkind WF, Hunt JH 1997. Factors affecting the recruitment of juvenile Caribbean spiny lobsters dwelling in macroalgae. Bulletin of Marine Science 61: 3–19.

Butler IV MJ, Hunt JH, Herrnkind WF, Childress MJ, Bertelsen RD, Sharp W, Matthews T, Field JM, Marshall HG 1995. Cascading disturbances in Florida Bay, USA: cyanobacteria blooms, sponges mortality, and implications for juvenile spiny lobsters *Panulirus argus*. Marine Ecology Progress Series 129: 119–125.

Butler IV MJ, MacDiarmid AB, Booth JD 1999. Ontogenetic changes in social aggregation and its adaptive value for spiny lobsters in New Zealand. Marine Ecology Progress Series 188: 179–191.

Chiappone M 1996. Marine benthic communities of the Florida Keys, vol. 4. Site Characterization for the Florida Keys National Marine Sanctuary and Environs. Zenda, Wisconsin, Farley Court Publishers. 36 p.

Chiappone M, Dienes H, Swanson DW, Miller SL. 2005. Impacts of lost fishing gear on coral reef sessile invertebrates in the Florida Keys National Marine Sanctuary. Biological Conservation 121: 221–230.

Chiappone M, Sullivan KM 1994a. Ecological structure and dynamics of nearshore hard-bottom communities in the Florida Keys. Bulletin of Marine Science 54: 747–756.

Chiappone M, Sullivan KM 1994b. Patterns of coral abundance defining nearshore hard-bottom communties of the Florida Keys. Florida Scientist 57: 108–125.

Childress MJ 1995. The ontogeny and evolution of gregarious behavior in juvenile Caribbean spiny lobster, *Panulirus argus*. Unpublished PhD thesis, Florida State University, Tallahassee, Florida, United States. 179 p.

Childress MJ, Herrnkind WF 1996. The ontogeny of social behaviour among juvenile Caribbean spiny lobsters. Animal Behaviour 51: 675–687.

Childress M, Herrnkind WF 1997. Den sharing by juvenile spiny lobsters (*Panulirus argus*) in nursery habitat. Marine and Freshwater Research 48: 751–58.

Childress M, Herrnkind WF 2001. The influence of conspecifics on the ontogenetic habitat shift of juvenile Caribbean spiny lobsters. Marine and Freshwater Research 52(8): 1077–1084.

Childress MJ, Hunt JH 2002. The impact of sponge recovery on the abundance and distribution of juvenile Caribbean spiny lobsters in Florida Bay. Final report to Florida Fish and Wildlife Conservation Commission. PO#:S 7701 617012. 29 p.

Department of Commerce 1996. Florida Keys National Marine Sanctuary final management plan/ enviromental impact statement Volume II. National Oceanic and Atmospheric Administration, Silver Spring Maryland, United States. 251 p.

D'Sa EJ, Zaitzeff JB, Yentsch CS, Miller JL, Ives R 2001. Rapid remote assessments of salinity and ocean color in Florida Bay. In: Porter JW, Porter KG ed. Everglades, Florida Bay, and coral reefs of the Florida Keys: an ecosystem sourcebook. Boca Raton, Florida, CRC Press. Pp. 321–334.

Eggleston DB, Lipcius RN 1992. Shelter selection by spiny lobster under variable predation risk, social conditions, and shelter size. Ecology 73: 992–1011.

Eggleston D, Lipcius R, Coba-Centina L, Miller D 1990. Shelter scaling regulates survival of juvenile spiny lobster, *Panulirus argus*. Marine Ecology Progress Series 62: 79–88.

Eggleston D, Lipcius R, Grover JJ 1997. Predator and shelter-size effects on coral reef fish and spiny lobster prey. Marine Ecology Progress Series 149: 43–59.

Eldred B, Futch CR, Ingle RM 1972. Studies on juvenile spiny lobsters, *Panulirus argus*, in Biscayne Bay, Florida. Special scientific report, Florida Department of Natural Resources Vol. 35. Pp. 1–15.

Field JM, Butler IV MJ 1994. The influence of temperature, salinity, and postlarval transport on the distribution of juvenile spiny lobsters, *Panulirus argus* (Latreille, 1804), in Florida Bay. Crustaceana 67: 26–45.

Finkle CW, Charlier RH 2003. Sustainability of subtropical coastal zones in southeastern Florida: challenges for urbanized coastal environments threatened by development, pollution, water supply, and storm hazards. Journal of Coastal Research 19: 934–943.

Florida Fish and Wildlife Conservation Commission & National Oceanic and Atmospheric Administration 2000. Benthic habitats of the Florida Keys. FMRI Technical Report TR-4. 53 p.

Florida Keys National Marine Sanctuary 2000. Florida Keys National Marine Sanctuary Zone Monitoring Program: project locator maps, project metadata, and associated files. CD-ROM. January 2000. Florida Fish and Wildlife Conservation Commission, Florida Marine Research Institute, St. Petersburg, Florida, United States.

Forcucci DM, Butler IV MJ, Hunt JH 1994. Growth and population dynamics of juvenile Caribbean spiny lobster, *Panulirus argus*, in Florida Bay, FL (USA). Bulletin of Marine Science 54: 805–818.

Gifi A 1990. Nonlinear multivariate analysis. New York, John Wiley & Sons. 602 p.

Herrnkind WF, Butler IV MJ 1986. Factors regulating postlarval settlement and juvenile microhabitat use by spiny lobsters *Panulirus argus*. Marine Ecology Progress Series 34: 23–30.

Herrnkind WF, Butler IV MJ 1994. Settlement of spiny lobster, *Panulirus argus* (Latreille, 1804), in Florida: Pattern without predictability? Crustaceana 67: 26–45.

Herrnkind WF, Butler IV MJ, Hunt JH, Childress M 1997. Role of physical refugia: implications from a mass sponge die-off in a lobster nursery in Florida. Marine and Freshwater Research 48: 759–769.

Herrnkind WF, Butler IV MJ, Tankersley RA 1988. The effects of siltation on the recruitment of spiny lobsters (*Panulirus argus*) in south Florida. Fisheries Bulletin 86: 331–338.

Herrnkind WF, Jernakoff P, Butler IV MJ 1994. Puerulus and post-puerulus ecology. In: Phillips B, Cobb S, Kittaka J ed. Spiny lobster management. Oxford, Blackwell Press. Pp. 213–229.

Hunt JH 2001. Status of the fishery for *Panulirus argus* in Florida. In: Phillips B, Cobb S, Kittaka J ed. Spiny lobster management. Oxford, Blackwell Press. Pp. 189–199.

Hunt JH, Lyons WG 1986. Factors affecting growth and maturation of spiny lobsters, *Panulirus argus*, in the Florida Keys. Canadian Journal Fisheries and Aquatic Science 43: 2243–2247.

Lidz BH, Reich CD, Peterson RL, Shinn EA 2006. New maps, new information: coral reefs of the Florida Keys. Journal of Coastal Research 22: 260–282.

Lindeman KC, Snyder DB 1999. Nearshore hardbottom fishes of southeast Florida and effects of habitat burial caused by dredging. Fishery Bulletin 97: 508–525.

Lipcius RN, Eggleston DB, Miller DL, Luhrs TC 1998. The habitat-survival function for Caribbean spiny lobster: an inverted size effect and non-linearity in mixed algal and seagrass habitats. Marine and Freshwater Research 49: 807–816.

Lozano-Alvarez E, Briones-Fourzan P 2001. Den choice and occupation patterns of shelters by two sympatric lobster species, *Panulirus argus* and *Panulirus guttatus*, under experimental conditions. Marine and Freshwater Research 52: 1145–1155.

Lozano-Alvarez E, Briones-Fourzán P, Negrete-Soto F 1994. An evaluation of concrete block structures as shelter for juvenile Caribbean spiny lobsters, *Panulirus argus*. Bulletin of Marine Science 55: 351–362.

Lyons WG, Kennedy Jr. FS 1981. Effects of harvest techniques on sublegal spiny lobsters and on subsequent fishery yield. Proceedings of the Gulf and Caribbean Fisheries Institute 33: 290–300.

Marx JM 1986. Settlement of spiny lobster, *Panulirus argus*, pueruli in south Florida: an evaluation from two perspectives. Canadian Journal of Fisheries and Aquatic Sciences 43: 2221–2227.

Marx JM, Herrnkind WF 1985. Macroalgae (Rhodophyta: *Laurencia* spp.) as habitat for young juvenile spiny lobsters, *Panulirus argus*. Bulletin of Marine Science 36: 423–431.

Mathieson AC, Dawes CJ 1975. Seasonal studies of Florida sublittoral marine algae. Bulletin of Marine Science 25: 46–65.

Matthews TR, Slade S, Moore J 2005. Evaluating trap impacts on essential fish habitat in the Florida Keys. In: Abstracts of the 57th Gulf and Caribbean Fisheries Institute Conference, St. Petersburg, Florida, United States. P. 63.

McClean SA, Rumble MA, King RM, Baker WL 1998. Evaluation of resource selection methods with different definitions of availability. Journal of Wildlife Management 62: 793–801.

Meulman JJ, Heiser WJ 2004. SPSS categories user's manual v14.0. Chicago, SPSS Inc. 355 p.

Neu CW, Byers CR, Peek JM 1974. A technique for analysis of utilization-availability data. Journal of Wildlife Management, 38: 541–545.

Nevitt G, Pentcheff ND, Lohmann KJ, Zimmer RK 2000. Den selection by the spiny lobster *Panulirus argus*: testing attraction to conspecifics odours in the field. Marine Ecology Progress Series 203: 225–231.

Phlips EJ, Badylak S, Lynch TC 1999. Blooms of the picoplanktonic cyanobacterium *Synechococcus* in Florida Bay, a subtropical inner-shelf lagoon. Limnology and Oceanography 44: 1166 –1175.

Ratchford SG, Eggleston DB 1998. Size- and scale-dependent chemical attraction contribute to an ontogenetic shift in sociality. Animal Behavior 56: 1027–1034.

Sale PF, Butler MJ IV, Hooten AG, Kritzer JP, Lindeman KC, Sadovy de Mitcheson YJ, Steneck RS, and van Lavieren H 2008. Stemming decline of the coastal ocean: rethinking environmental management. Policy brief from United Nations University-International Network on Water, Environment, and Health. Hamilton, Canada. 50 p.

Schomer NS, Drew RD 1982. An ecological characterization of the lower Everglades, Florida Bay, and the Florida Keys. Washington D.C., Bureau of Land Management, Fish and Wildlife Service. 246 p.

Schratwieser J 1999. The impact of resident and transient predators on the population dynamics of juvenile Caribbean spiny lobster (*Panulirus argus*) in Florida Bay, Florida. Unpublished MSc thesis, Old Dominion University, Norfolk, VA, United States.

Witzell WN 1999. The origin of the Florida sponge fishery. Quarterly Publication of the Key West Maritime Historical Society 9(3). 4 p.

Zieman JC, Fourqurean JW, Frankovich TA 1999. Seagrass dieoff in Florida Bay: long term trends in abundance and productivity of turtlegrass, *Thalassia testudinum*. Estuaries 22(2B): 460–470.

Zieman JC, Fourqurean JW, Iverson, RL 1989. Distribution, abundance, and productivity of seagrasses and macroalgae in Florida Bay. Bulletin of Marine Science 44: 292–311.

Zimmer-Faust RK, Tyre JE, Case JF 1985. Chemical attraction causing aggregation in the spiny lobster, *Panulirus interruptus* (Randall), and its probable ecological significance. Biological Bulletin 169: 106–118.