Shelter scaling regulates survival of juvenile Caribbean spiny lobster *Panulirus argus*

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ABSTRACT: Marine habitats with limited refugia from predation but adequate food may support increases in prey abundance if artificial shelters placed in these habitats reduce predation-induced mortality. Moreover, the protective capacity of shelters may vary according to the scaling between shelter size and prey size. We tested these hypotheses with field tethering experiments in Bahia de la Ascension, Mexico, by examining the impact of different-sized artificial shelters upon mortality rates of 3 juvenile size-classes of the Caribbean spiny lobster *Panulirus argus* at 2 sites (inner-bay sand-seagrass flat and outer-bay seagrass bed adjacent to coral reefs). The artificial shelters were sunken concrete structures (casitas) that simulate lobster dens. We also quantified potential predators and estimated the physical features of casitas that influence den choice by juvenile spiny lobster. In the tethering experiments, spiny lobster survival was (1) higher in casitas than seagrass meadows, irrespective of casita size; (2) generally higher in smaller than larger casitas, though the effect depended upon the relationship between lobster and shelter size; and (3) independent of site. Thus, spiny lobster survival depends not only upon the availability of shelter, but also on the scaling between shelter size and lobster size. Predator observations indicated that the size range, maximum size and species diversity of predators increased with casita size, thereby imposing higher predation intensity in larger casitas. Furthermore, since shelter appears to limit spiny lobster abundance in habitats such as reefs and seagrass meadows, placement of appropriately-scaled artificial shelters (e.g. casitas) in nursery areas like the study site is likely to augment habitat carrying capacity by increasing protection from predators.

INTRODUCTION

Habitat structural complexity affects predator-prey dynamics by providing refugia from predation (Gause 1934, Huffaker 1958, Smith 1972, Murdoch & Oaten 1975). Reduced predator foraging efficiency in portions of a habitat may provide refugia that are partial (Huffaker 1958, Smith 1972) or absolute (Gause 1934). Recent experiments have emphasized structural complexity within habitats and its impact upon prey survival (Vince et al. 1976, Van Dolah 1978, Brock 1979, Nelson 1979, Coen et al. 1981, Heck & Thoman 1981, Crowder & Cooper 1982, Peterson 1982, Coull & Wells 1983, Ryer 1988, Gotceitas & Colgan 1989). The general conclusion of these studies has been that increasing structural complexity (i.e. density or biomass of plants) decreases predator foraging efficiency. Whereas numerous investigators have examined different physical aspects of aquatic habitats providing structural complexity [e.g. submerged macrophytes (Crowder & Cooper 1982, Coull & Wells 1983), emergent macrophytes (Van Dolah 1978), worm tubes (Bell & Coen 1982), and substrate type (Lipcius & Hines 1986, Smith & Coull 1987)], little work has focused on the effects of scaling of refugia according to prey size.

The geometry of natural surfaces suggests a scaled relationship between shelter dimensions and organism size, such that some specified scaling offers maximal protection to a sheltering individual (Morse et al. 1985, Caddy 1986). An obligate crevice dweller (e.g. spiny lobster, stomatopods, reef fish) is faced for all or part of its life history with a decline in the number of crevices as it grows (Caddy 1986, Moran & Reaka

1988), possibly leading to a population 'bottleneck' (Caddy 1986). Placement of artificial shelters at the appropriate scale could increase the effective number of crevices, thus alleviating the population bottleneck (Caddy 1986). However, a prerequisite to addressing shelter-related bottlenecks is more detailed knowledge of how scaling of refuges affects size-specific survivorship.

Juveniles of the Caribbean spiny lobster *Panulirus argus* (Latreille) inhabit shallow bays throughout the tropical and subtropical Western Atlantic. There they reside in crevices formed by rocky outcrops, coral reefs, sponges, solution holes, and undercut seagrass banks (Herrnkind et al. 1975, Andree 1981, Marx & Herrnkind 1985, Herrnkind & Lipcius in press). Juvenile *P. argus* are nocturnal predators that forage primarily on gastropods, crustaceans, pelecypods, and amphineurans (Lipcius & Herrnkind 1982, Marx & Herrnkind 1985). They reach carapace lengths of 60 to 70 mm after about 2 yr of benthic life (Sweat 1968). During the day they may aggregate in dens (Kanciruk 1980, Herrnkind & Lipcius in press). Gregarious sheltering possibly enhances individual survivorship through communal defense (Berrill 1975, Cobb 1981, Zimmer-Faust & Spanier 1987).

Intra- and interspecific aggression for suitable dens can force smaller juvenile *Panulirus argus* to find another den (Berrill 1975). Information on the physical properties that constitute a suitable den for *P. argus* is limited; however, den preferences of the California spiny lobster *Panulirus interruptus* include structures having shaded cover and multiple den openings (Spanier & Zimmer-Faust 1988). Predation represents a major source of mortality for *P. argus* (Munro 1974, Herrnkind & Butler 1986), and when individuals are displaced or forced to shelter in an inadequate den, they may be subject to increased predation rates (Herrnkind & Butler 1986). Besides affording intermolt lobsters protection from predators and storm surge, dens provide refuge during molting (Lipcius & Herrnkind 1982). Premolt individuals typically seek isolation during ecdysis, a period when they are extremely vulnerable to predation (Lipcius & Herrnkind 1982, D. B. Eggleston unpubl.).

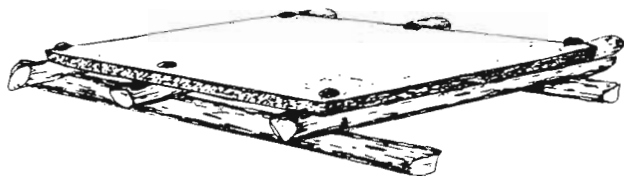Studies on recruitment and population dynamics indicate that habitat may be limiting for some palinurids. For example, recruitment of *Panulirus cygnus* in Western Australian waters is characterized by density-dependent mortality in nursery areas as a consequence of limitations in food or shelter (Chittleborough 1970, Chittleborough & Phillips 1975, Ford et al. 1988). Thus, in areas of adequate food supply but limited shelter, placement of artificial lobster shelters of an appropriate design and size seems a feasible approach for augmenting habitat carrying capacity by increasing protection from predators. Yet, little information exists on the key biological and habitat variables useful in the design, construction, and placement of artificial lobster shelters, particularly with reference to protection from predators. Below we describe a series of field experiments which evaluate the efficacy of scaled artificial shelters in reducing size-specific mortality rates of juvenile *Panulirus argus* within 2 habitats. We also identify potential predators and estimate the physical features of the artificial shelters that influence den choice by juvenile *P. argus* in Bahia de la Ascension, Mexico.

METHODS AND MATERIALS

Shelter scaling. Our design of artificial lobster shelters was based on 'casitas' – sunken wood and concrete structures that simulate crevices in rocks and reefs (Miller 1982, 1989) (Fig. 1) and are used to concentrate lobsters for harvest in Cuba and the Mexican Caribbean (Miller 1982, 1989, Aguilar & Gonzalez 1984, Cruz & Brito 1986). Previous experiments in Bahia de la Ascension, Mexico indicate that casitas provide large juvenile lobsters greater protection from predators than seagrass habitats (Eggleston, Lipcius and Miller unpubl.). Thus, we hypothesized that scaling down the size of existing casitas would enhance the protective attributes of the casita for smaller lobsters (Fig. 1).

Our scaling of smaller casitas began with a reduction in the height of casita openings (Fig. 1). We assumed that existing large casitas (Fig. 1; 177 cm length × 118 cm width × 6 cm height of opening) were suitable for concentrating large juveniles and adults (>65 mm CL: carapace length) entering the fishery. We then assigned casita opening heights of 3.8 cm (medium casita) and 1.9 cm (small casita) to smaller casitas (mini-casitas) to correspond to medium (46 to 55 mm CL) and small (35 to 45 mm CL) juveniles, respectively. Reductions in casita opening height allowed for adequate entry of the targeted lobster size-class, but was also assumed to exclude larger predators.

Next we scaled the 'mini-casita' roofs according to reductions in casita height. A 2-dimensional scaling equation, $R = 1/(N)^{1/2}$ (Eq. 1) (Peitgen & Saupe 1988), was employed to construct casita roofs that were identi-

Fig. 1. A large 'casita' constructed with a frame of thatch palm and roof of cement

cally scaled. The value N was calculated by determining the ratio of large casita height to mini-casita height. For example, N for the medium casita was calculated as 6 cm/3.8 cm = 1.6. R was then computed according to Eq. (1) $[R = 1/(1.6)^{1/2}]$ with the resulting scaling factor (R) multiplied by the area (cm^2) of the large casita roof [i.e. $0.79 \times (177 \text{ cm} \times 118 \text{ cm} = 16499.9 \text{ cm}^2)$]. To determine the final length-width dimension of the mini-casita, a similarity ratio (Schmidt-Nielsen 1984) was calculated based on the ratio of corresponding sides of the large casita with Eqs. (2) and (3):

$$K_l = L_1/L_2 \qquad (2)$$

$$K_w = L_2/L_1 \qquad (3)$$

where K_l = the similarity ratio for length; K_w = the similarity ratio for width; L_1 = large casita length; and L_2 = large casita width. This was then multiplied by the area of the mini-casita roof as determined from Eq. (1). For example, the length-width dimensions of the medium casita were determined as: K_l = 177/118 cm = $1.5 \times 16499.9 \text{ cm}^2 = 24749.9 \text{ cm}^2$ and $(24749.9 \text{ cm}^2)^{1/2}$ = 157.3 cm. Similarly, K_w = 118/177 cm = 0.67 $\times$ $16499.9 \text{ cm}^2 = 11054.9 \text{ cm}^2$ and $(11054.9 \text{ cm}^2)^{1/2}$ = 105.1 cm. Thus, our calculations resulted in the construction of medium (157.3 $\times$ 105.1 $\times$ 3.8 cm) and small (132.3 $\times$ 88.4 $\times$ 1.9 cm) casitas. Shelters were constructed with a reinforced concrete roof connected to a PVC pipe frame with plastic cable-ties and wire.

Study site and tethering experiments. Tethering experiments were conducted in Bahia de la Ascension, Mexico (19.45°N; 87.29°W) (Fig. 2). This large bay (ca 260 km^2) is an important nursery area for juvenile spiny lobsters and supports a commercial fishery for large

Fig. 2. Study sites at Bahia de la Ascension, Mexico

juveniles and adults (Montes 1983, Miller 1989). Two experimental sites of contrasting habitat type were chosen to compare relative rates of predation: an inner-bay sand-seagrass flat located at the northwest portion of the bay, and an outer-bay seagrass (*Thalassia testudinum*) meadow adjacent to a coral reef (Fig. 2). Differences in density of seagrass between and within sites were determined at the beginning of the study by measuring dry weight biomass (g) of *Thalassia* removed from 0.25 m^2 plots. Six samples were taken from 3 seagrass densities (dense, moderate, and sparse) and dry weights measured after drying at 100°C for 24 h. The inner-bay site was composed of sparse seagrass patches ($\bar{x}$ *Thalassia* = 15.6 g 0.25m^{-2}, SD = 10.7) interspersed among coarse calcareous sand and coral rubble. The coral rubble was covered mostly by green and red algae (*Dasycladus* spp. and *Laurencia* spp., respectively), but also supported various sponges. The outer-bay site was located shoreward of a fringing coral reef and composed of sand patches and patch corals interspersed among moderate to dense seagrass beds ($\bar{x}$ *Thalassia* = 27.9 g 0.25m^{-2}, SD = 13.4 and $\bar{x}$ *Thalassia* = 52.5 g 0.25m^{-2}, SD = 12.6, respectively). The seagrass beds are comparable in *Thalassia* biomass to other moderate-dense seagrass beds in the Caribbean (e.g. Bahamas: ca 25 to 30 g 0.25m^{-2}; Stoner 1989).

Spiny lobsters were collected from existing casitas and held in traps for 1 to 2 d prior to initiation of each experiment. Only intermolt lobsters were used in tethering experiments. Tethers were constructed by locking a plastic cable-tie around the cephalothorax of a lobster, between the second and third walking legs, and securing the cable-tie with cyanoacrylate cement. The cable-tie was connected with 30-lb-test (14 kg) monifilament line either to another cable-tie and attached to a shelter, or attached to a J-shaped, stainless steel stake pushed into the sediment. The cyanoacrylate cement ensured that a piece of carapace remained on the line as evidence of predator-induced mortality (Herrnkind & Butler 1986). Although tethering does not necessarily measure absolute rates of predation, it does measure relative rates of predation (Heck & Thoman 1981), which can serve to compare mortality rates as a function of different experimental treatments.

Experimental design. Separate tethering experiments were performed during July and October 1988 and July 1989. In July 1988 we examined the survival of 2 sizes of juveniles in 2 casita sizes at the inner-bay nursery site. A row of large casitas was positioned ca 100 m from shore extending in an easterly direction towards the bay mouth (Fig. 2). Large casitas were placed 20 to 25 m apart; medium and small casitas were placed 10 m away from the large casitas. Each of
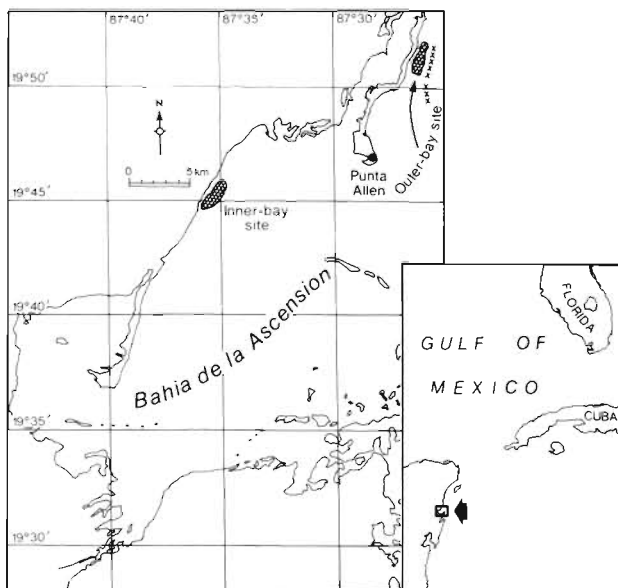
6 stations consisted of the 3 casita sizes arranged in a triangular pattern. Juvenile lobsters were divided into 2 size-classes: medium (45 to 55 mm CL) and large (56 to 65 mm CL), and tethered for 7 d to large and medium casitas. Each large and medium casita had 6 tethered lobsters from either of the size classes giving a total of 72 tethered lobsters (6 lobsters × 6 stations × 2 casita sizes).

In October 1988, the previously described experiment was repeated at the inner-bay site, and an additional experiment was performed at the outer-bay reef-seagrass site. The experiment at the outer-bay site used only medium-sized juveniles (56 to 65 mm CL) tethered to stakes either in dense seagrass without shelter or to large and medium casitas. Casitas were positioned equidistant between the shore and reef line and arranged in 2 rows, each containing 3 triangular stations. As above, the small casitas at each station were not used in these tethering experiments. Six lobsters were tethered to large and medium casitas at each station for 8 d. Three additional stations were nonfunctional because of damage associated with Hurricane Gilbert. Lobsters in seagrass were tethered to single stakes arranged in the same order as the length-width dimensions of the large casita. The 3 seagrass stations without shelter were positioned 15 m away and perpendicular to the large casitas. Thus, in October we tethered 72 medium juvenile lobsters at the outer-bay site [6 lobsters × 3 stations × (2 casita sizes + 2 seagrass sites)], and 36 large and 36 medium juveniles at the inner-bay site (6 lobsters × 6 stations × 2 casita sizes).

In July 1989, we examined the survival of 2 size classes of juveniles in 3 casita sizes at the inner-bay site. Juvenile lobsters were classified as small (35 to 45 mm CL) or medium (46 to 55 mm CL) and tethered for 9 d at each of 6 stations containing small, medium, and large casitas. Each casita had 6 tethered lobsters of either size class, for a total of 108 lobsters (6 lobsters × 6 stations × 3 casita sizes).

To avoid tangling, tether lengths of 70, 50, and 30 cm were used with lobsters tethered to large, medium, and small casitas, respectively. Lobster size treatments were systematically interspersed between stations (sensu Hurlbert 1984), with 3 replicates for each lobster size and casita size combination.

Predation losses were scored and a visual census of potential predators taken every 1 to 2 d during experiments. Cumulative losses were converted to proportional mortality casita^{-1} d^{-1}. Proportions were analyzed as a function of shelter quality [casita size (large, medium, small) and no shelter], lobster size (large, medium, small), site (bay, reef), and date (July and October 1988) with 1-, 2-, and 3-way fixed-factor analyses of variance (ANOVA) models (after pro-

cedures in Underwood 1981). Proportional mortality was arc-sine square-root transformed to meet assumptions of normality and homogeneity of variance (Underwood 1981). In all cases, either the variances were homogeneous as determined by Cochran's C-test, or the hypotheses were rejected at alpha values lower than the p-values of the test for homogeneity of variance (Underwood 1981). Differences among means were revealed by use of Student-Newman-Keuls (SNK) tests on the means (Underwood 1981).

During July and October 1988, the presence of potential lobster predators was only casually observed. In July 1989 we used a stationary visual census technique (Bohnsack & Bannerot 1986) to quantify the community structure of potential predators associated with each of the 3 casita sizes during the experimental period. The visual census was usually performed between 10:00 and 14:00 h with 3 replicate samples taken during the experimental period. One night-time census was performed during the July 1989 experiment.

RESULTS

Tethering experiments

The inner-bay site was generally inhabited by small juvenile lobsters (30 to 80 mm CL; Fig. 3a), whereas the outer-bay site was inhabited by large juvenile and adult lobsters (60 to 100 mm CL; Fig. 3b). At the inner-bay site during July and October 1988, casita and lobster size affected proportional mortality of juvenile spiny lobsters, with significantly lower mortality rates in medium casitas than large casitas, and for medium lobsters than large lobsters (Fig. 4; 3-way ANOVA; shelter size: $F = 17.79$, df = 1,16, $p < 0.01$; lobster size: $F = 8.86$, df = 1,16, $p < 0.009$). Predation rates were not significantly affected by date (July vs October 1988), nor were there any interaction effects (Fig. 4; 3-way ANOVA, $p > 0.1$).

At the outer-bay site in October 1988, mortality rates of medium juvenile lobsters were significantly affected by the presence or absence of artificial shelter (1-way ANOVA; $F = 12.3$, df = 2,8, $p < 0.008$). Medium and large casitas provided significantly more protection from predation than seagrass (Fig. 5; SNK test, experimentwise error rate = 0.05). During October 1988 predation rates on medium juvenile lobsters did not differ significantly between sites (inner-bay vs outer-bay: ANOVA, $F = 4.72$; df = 1,8; $p = 0.328$).

Mortality rates of juvenile lobsters at the inner-bay site during July 1989 differed significantly by shelter size but not by lobster size (Table 1a). The interaction effect between shelter size and lobster size was significant (Table 1a), precluding contrasts among treatment

A

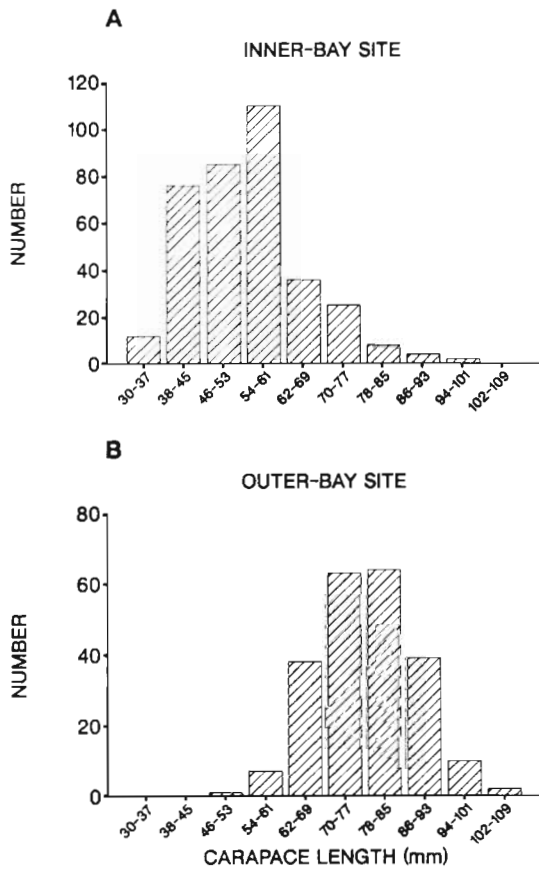INNER-BAY SITE

B

OUTER-BAY SITE

Fig. 3. *Panulirus argus*. Size-frequency of lobsters captured from large casitas at the 2 field sites. (A) Inner-bay site; mean = 53.9 mm CL, range = 31 to 100 mm CL (15 casitas sampled). (B) Outer-bay site; mean = 77.8 mm CL, range = 47 to 118 mm CL (20 casitas sampled)

means (Underwood 1981). Thus, we examined treatment effects within each lobster and shelter size. The interaction effect was due to mortality differences between casita sizes within each lobster size class. Small lobsters had significantly higher survivorship in small shelters followed in decreasing order by medium and large shelters (Fig. 6; Table 1b). Although medium shelters afforded more protection to medium lobsters than either large or small shelters (Fig. 6), as in the previous experiments (Figs. 4 and 5), the trend was not significant (Table 1b).

Predator observations

Casitas also attracted or concentrated numerous reef fish, especially at the inner-bay site. Potential piscine predators of juvenile lobsters at the inner-bay site during July and October 1988 included gray snapper *Lutjanus griseus*, schoolmaster snapper *L. apodus*, mutton snapper *L. analis*, barracuda *Sphyraena barracuda*,

JULY-1988
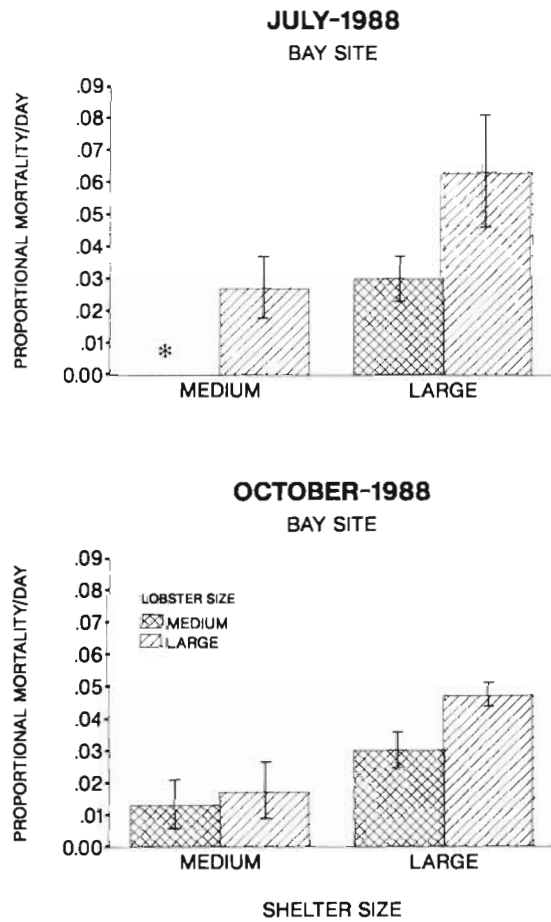
BAY SITE

OCTOBER-1988

BAY SITE

Fig. 4. *Panulirus argus*. Results of field tethering experiments at the inner-bay nursery site comparing predation as a function of juvenile lobster size (medium: 46 to 55 mm CL and large: 56 to 65 mm CL), shelter size (medium and large), and date (July and October 1988). Values are mean proportional mortality casita^{-1} d^{-1}. Vertical bars are 1 SE. *No mortalities observed
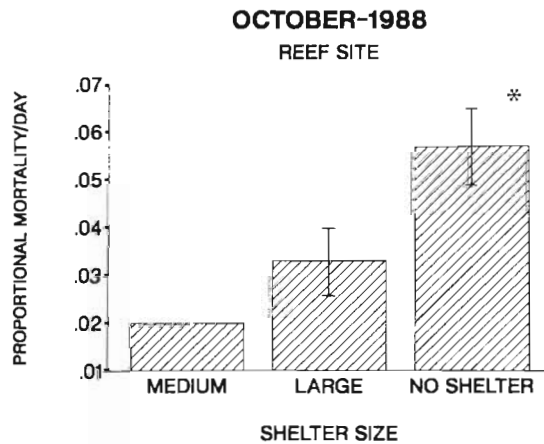
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Fig. 5. *Panulirus argus*. Results of field tethering experiments at the outer-bay seagrass site with medium juveniles (46 to 55 mm CL), comparing predation in medium and large size shelters, and without shelter. Values are mean proportional mortality station^{-1} d^{-1}. Vertical bars are 1 SE. *Significantly different, p < 0.05
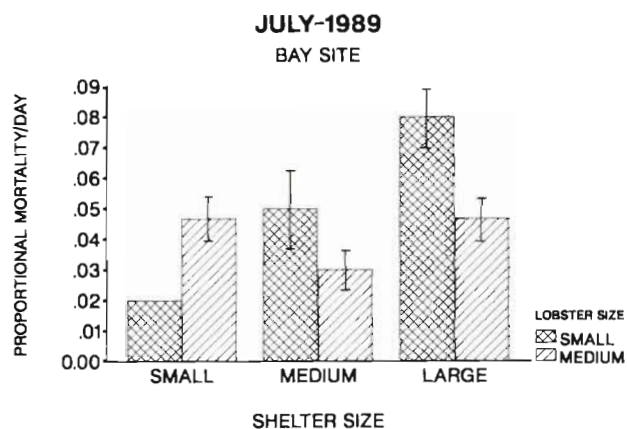
JULY-1989
BAY SITE

Fig. 6. Results of field tethering experiments at the inner-bay nursery site during July 1989 comparing predation as a function of juvenile lobster size (small: 35 to 45 mm CL and medium: 46 to 55 mm CL) and shelter size (small, medium, and large). Values are mean proportional mortality casita^{-1} d^{-1}. Vertical bars are 1 SE

green moray eel *Gymnothorax funebris*, nurse shark *Ginglyostoma cirratum* and bottlenose dolphin *Tursiops truncatus*. Other potential predators at the inner-bay site included the loggerhead turtle *Caretta caretta*, stone crab *Menippe mercenaria* and portunid crabs. Potential predators at the outer-bay site included mutton snapper, yellowtail snapper *Ocyurus chrysurus*,

Table 1. (a) Two-way analysis of variance of arc-sine square-root transformed proportional mortality rates (proportional mortality casita^{-1} d^{-1}) at the inner-bay nursery site during July 1989, examining the effects of shelter size (small, medium, large) and lobster size (small and medium)

Experimental condition	df	MS	F	p<
Shelter size	2	0.008	9.20	0.004
Lobster size	1	0.001	1.07	0.321
Shelter size × lobster size	2	0.009	10.04	0.003
Error	12	0.001		

gray snapper, barracuda, green moray eel, spotted moray eel *Gymnothorax moringa*, and octopus. The visual census of potential predators at the inner-bay site during July 1989 indicated that total abundance, mean number of individuals per casita per sample, and mean length increased with casita size (Table 2). Large casitas concentrated more species of potential predators followed in decreasing order by medium and small casitas (Table 2). Gray snapper was the predominant potential predator, irrespective of casita size (Table 2). The night-time visual census indicated that the predator guild observed during the day had dispersed within 1 h after dusk.

DISCUSSION

Seagrass meadows provide refuge for small decapods, reduce predation risk, and thereby enhance survival of spiny lobsters (Herrnkind & Butler 1986, Lipcius, Eggleston, Miller and Camarena unpubl.) and crabs (Heck & Thoman 1981, Heck & Wilson 1987). Results from our outer-bay experiment in October suggest that shelter is limited in seagrass meadows and that placement of casitas in these habitats enhances survivorship of juvenile *Panulirus argus*. Placement of casitas in seagrass meadows also places suitable shelter near foraging grounds, and thereby reduces energetic demands associated with movements between sheltering and feeding grounds. Such close coupling of adjacent habitats has been documented between coral reefs and seagrass beds. Reef fish such as grunts, snappers, squirrelfishes *Holocentrus* spp. and cardinalfishes *Apogon* spp. move between diurnal shelter sites on coral reefs and nocturnal feeding grounds in seagrass meadows (Starck & Davis 1966, Ogden & Ziemann 1977, Robblee & Zieman 1984). Ogden & Ziemann (1977) found that the interconnection between these 2 habitats increased fish biomass on reefs.

Table 1 (b) SNK tests of mean arc-sine square-root transformed proportional mortality rates of lobsters for the shelter size × lobster size interaction effect

Treatments						
Lobster size:	Small	Small	Small	Medium	Medium	Medium
Shelter size:	Small	Medium	Large	Small	Medium	Large

* p < 0.05; ** p < 0.01; NS: not significant

Table 2. Summary of results from visual census of potential lobster predators associated with 18 casitas of 3 sizes (small, medium, large) during 22 to 31 July 1989. Results below are pooled from censusing 18 casitas on 3 different sampling dates. Fish size is fork length (cm) and crab size is carapace width (cm)

Species	Total abundance	Mean no. ind. sample^{-1} casita^{-1}	Frequency per casita (N = 18)	Percent frequency	Size (cm)		
					Mean	Min.	Max.
Large casita:							
Lutjanus griseus (gray snapper)	222	12.33	18	100.0	20.4	10	35
Lutjanus apodus (schoolmaster snapper)	64	3.56	11	61.1	18.1	10	25
Lutjanus analis (mutton snapper)	10	0.56	6	33.3	20.3	15	30
Sphyraena barracuda (great barracuda)	3	0.17	3	16.7	103.3	90	120
Epinephelus striatus (Nassau grouper)	1	0.06	1	5.6	45.0	–	–
Epinephelus guttatus (red hind)	1	0.06	1	5.6	12.0	–	–
Dasyatis americana (southern stingray)	1	0.06	1	5.6	50.0*	–	–
Medium casita:							
Lutjanus griseus (gray snapper)	79	4.39	11	61.1	12.7	7	15
Lutjanus analis (mutton snapper)	8	0.44	5	27.8	15.8	10	20
Lutjanus apodus (schoolmaster snapper)	7	0.39	3	16.7	12.5	10	18
Menippe mercenaria (stone crab)	3	0.17	3	16.7	10.0	10	10
Portunus spinimanus (portunid crab)	2	0.11	2	11.1	9.5	6	13
Small casita:							
Lutjanus griseus (gray snapper)	12	0.67	5	27.8	7.6	6	10
Lutjanus apodus (schoolmaster snapper)	2	0.11	1	5.6	7.0	–	–
Portunus spinimanus (portunid crab)	5	0.28	3	16.7	8.5	7	12
Menippe mercenaria (stone crab)	1	0.06	1	5.6	6.0	–	–

* Measured from wingtip to wingtip (cm)

Our field experiments further demonstrate that scaling of refuges according to prey size enhances prey survivorship by providing protection from predators. The likely mechanism producing this pattern is a reduction in accessibility of piscine predators to lobsters in low shelters. These results imply that limitations to the distribution and abundance of spiny lobsters within shelters are a consequence of complex interactions involving lobster density, and the sizes of lobster, shelter, and predator. For instance, the maximum size of a lobster within a particular shelter is limited by the size of the shelter, whereas the minimum size is limited by shelter-associated predators. This relationship is further complicated by (1) social dominance within a shelter, whereby small lobsters may be forced out, or (2) gregarious behavior that might enhance the lower size range of lobsters that can survive.

Survival of small (35 to 45 mm CL) and medium (46 to 55 mm CL) lobsters was generally dependent on casita size – small and medium casitas afforded the best protection to small and medium lobsters, respectively. Survival of large juveniles (56 to 65 mm CL) did not always depend on shelter size. For instance, large lobsters had higher survivorship in medium casitas than in large casitas, and medium lobsters demonstrated higher survivorship in large casitas than did large lob-

sters. The increased survivorship of large juvenile lobsters in medium casitas compared to large casitas indicates that medium casitas eliminate predators that are able to prey on large juvenile lobsters. Differential survivorship of medium and large juvenile lobsters in large casitas could be a consequence of variations in predator and prey size. The predator observations indicated that a characteristic suite of predator sizes corresponded to each casita size, with large casitas concentrating larger adult fish. Adult fish may become more selective because of better visual perception with age (i.e. size) (Kao et al. 1985), and predator discrimination may become more acute with increasing prey size (Stein 1977). However, more information is needed on the mechanisms of predator choice in this system to discern the precise role of variation in predator and prey sizes in regulating prey survival.

The allometry of predator vulnerability with shelter and body size is fundamental in predicting size-specific asymmetries in species interactions or ontogenetic niche shifts (Werner & Gilliam 1984). Thus, the use of appropriately scaled casitas might be used to examine shelter-related population bottlenecks (sensu Caddy 1986) for juvenile Panulirus argus. In a somewhat analogous study, Reise (1978) examined how mesh size of predator exclusion cages provided differential pro-

tection to infaunal prey. Cages with 5, 2, and 1 mm mesh enhanced macrofaunal survival (sieved through a 0.25 mm mesh) by excluding crabs, shrimp, and gobiid fish, whereas cages with 20 mm mesh did not (Reise 1978). Another possible analogue to our findings may be the use of reef cavities as refuges for reef-dwelling stomatopods. Abundance of stomatopod crustaceans in subtidal reef populations is affected by predation (Reaka 1985), such that the sizes of available reef cavities may limit the body sizes of these stomatopods (Moran & Reaka 1988). Thus, the introduction of artificial reef cavities of the appropriate scale (sensu Caddy 1986) might also be a productive approach for examining shelter-related population bottlenecks of stomatopods and other reef-dwelling species.

The placement of casitas throughout Bahia de la Ascension provides juvenile spiny lobsters with additional, more effective shelter from predators. Various shelter features may be important in reducing predation. For instance, shaded cover provided by dens may decrease encounters with visually directed predators (Spanier & Zimmer-Faust 1988), which for *Panulirus argus* are principally diurnally active fishes (Cruz & Brito 1986, Herrnkind & Butler 1986). However, further experiments are needed to determine differences in the impact of casitas upon lobster survival in the day and night.

Key physical properties of the casita that likely influence den choice and increase survivorship of juvenile *Panulirus argus* are (1) a shaded cover provided by the wide concrete roof, (2) low roof height, which excludes large piscine predators, and (3) multiple den openings that are smaller than the inner roof height of the casita. Recruitment of the slipper lobster *Scyllarides latus* to artificial reefs of different design indicated a preference for lower, horizontal dens with small openings (Spanier et al. 1988). Field surveys in California indicated that dens occupied by *Panulirus interruptus* usually had more than one entrance and that entrances were much smaller than the inner diameter of a den (Spanier & Zimmer-Faust 1988). Furthermore, den preferences of *P. interruptus* depended more on the presence of shaded cover than on den walls, with single, isolated dens having front and rear entrances being selected over dens with only one entrance (Spanier & Zimmer-Faust 1988). Multiple den openings provide alternate escape routes, and may facilitate social grouping with collective anti-predator vigilance. We commonly observed groups of lobsters with their antennae protruding from each opening of a casita, somewhat resembling a defensive pod (Kanciruk 1980) with a roof over it.

The collective evidence from field observations and experiments suggests that shelter is limiting spiny lobster abundance in certain habitats such as reefs (Ford et

al. 1988) and seagrass meadows (this study), with a dynamic interplay between shelter and food availability (Herrnkind 1980). Thus, the placement of appropriately-scaled casitas, which are inexpensive and extremely durable as evidenced by our low loss rate (8 %) of structures in the direct path of Hurricane Gilbert (D. B. Eggleston unpubl.), may be an economical and effective approach for increasing fisheries production in the Caribbean by increasing protection from predators. However, final conclusions regarding the impact of artificial shelters on spiny lobster predator-prey dynamics and production in nursery areas warrant field manipulations that test the aforementioned hypotheses.

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