Artificial shelters and survival of juvenile Caribbean spiny lobster *Panulirus argus*: Spatial, habitat, and lobster size effects*

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Abstract.–A principal mechanism underlying a production hypothesis that artifical reefs increase environmental carrying capacity and eventually the biomass of reef-associated organisms is that these structures reduce predation on reef residents. We tested this predation mechanism with a series of field experiments at two sites (inner-bay sand-seagrass flat, and outer-bay seagrass bed adjacent to coral reefs) in Bahia de la Ascension, Mexico. We examined survival of two size-classes of juvenile Caribbean spiny lobster *Panulirus argus* tethered in seagrass beds with and without access to artificial lobster shelters, and at different distances from the shelters. The artificial shelters were concrete structures (casitas) that simulate lobster dens. Large juvenile lobsters (56–65 mm CL) attained a relative size refuge when tethered 60 m away from casitas compared with smaller (46–55 mm CL) lobsters. Conversely, the small lobsters survived better beneath casitas than did large lobsters. Small juveniles also survived better at casitas or 30 m away from casitas than at 15 m or 70 m away. Observations indicated that the daytime predator guild, composed primarily of snappers (family Lutjanidae), seldom foraged more than 60 m from casitas and were typically within 15 m of casitas. There was also a significant positive correlation between predation-induced lobster mortality and numbers of snapper associated with casitas at the inner-bay site. Thus, tethering lobsters 70 m away from casitas appeared adequate to examine survival of lobsters in an environment uninfluenced by daytime predators aggregating to casitas. These results indicate that (1) the relative importance of a lobster-size refuge from predators varies according to shelter availability, and (2) that there is a nonlinear relationship between predation risk and distance from an artifical shelter. Our results demonstrate that casitas increase survival of small juvenile lobsters but reduce survival of larger juveniles. Small casitas scaled according to body size may enhance survival of large juvenile lobsters in nursery habitats where large conspecifics are removed from large casitas.

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Artificial reefs are in use worldwide as a means of increasing local abundance of finfish and invertebrates (see reviews by Bohnsack and Sutherland 1985, Grove and Sonu 1985, Mottet 1985, Bohnsack 1989). The use of artificial reefs to increase fisheries production remains controversial because it is unknown whether these structures (1) provide critical resources that increase the environmental carrying capacity and eventually the biomass of reef-associated organisms (production hypothesis), or (2) merely attract and aggregate organisms from surrounding areas without increasing total biomass (attraction hypothesis) (Bohnsack 1989). The attraction hypothesis is an important consideration for artificial-reef-based fisheries that may be vulnerable to overexploitation. Thus, there is a need for ecological investigations capable of assessing the impact of artificial reefs upon species distribution, abundance, and survival patterns, and the processes underlying these patterns.

Artificial reef technology has traditionally been based on the assumption that obligate reef dwellers (e.g., reef fishes and lobsters) are limited locally or regionally by the availability of shelter (Bohnsack 1989, Hixon and Beets 1989, Eggleston et al. 1990 and references therein). Conversely, artificial reefs also concentrate numerous potential predators (Hixon and Beets 1989, Eggleston et al. 1990); increased predation pressure at or near these structures could outweigh the benefits from increases in production. For instance, fishes and lobsters normally dispersed over a wide area could be concentrated and consumed by predators more rapidly in a smaller area. Thus, artificial shelters may either enhance or reduce the survival of their inhabitants, depending upon predator responses. In this paper, we present the results of a series of field experiments comparing survival rates of two size-classes of juvenile Caribbean spiny lobster *Panulirus argus*

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Latreille, with and without access to artificial shelters at different spatial scales in seagrass beds. We then discuss these mortality patterns in terms of the relative importance of lobster size, shelter availability, and distance of lobsters from the artifical shelter. Moreover, we use daytime abundance and foraging ranges of shelter-associated predators to speculate on the mechanisms underlying these mortality patterns.

Juvenile *P. argus* inhabit shallow bays throughout the tropical and subtropical western Atlantic where they frequently aggregate during the day in crevices of coral and rocky reefs (Berrill 1975, Herrnkind et al. 1975). Gregarious behavior within dens probably enhances individual survivorship because spiny lobsters collectively use their spinose antennae to fend off diurnally active predators (Berrill 1975, Cobb 1981, Zimmer-Faust and Spanier 1987, Eggleston and Lipcius 1992). However, intra- and interspecific competition for suitable dens can force smaller juvenile *P. argus* out of these dens (Berrill 1975). Predation represents a major source of mortality for juvenile spiny lobsters (Munro 1974, Herrnkind and Butler 1986, Howard 1988, Smith and Herrnkind 1992), and when individuals are displaced or forced to shelter in an inadequate den they may be subject to increased predation rates (Herrnkind and Butler 1986, Eggleston et al. 1990).

Large juvenile and adult spiny lobsters are the focus of intense commercial and recreational fisheries in south Florida and the Caribbean, with the possibility of regional overexploitation of spiny lobster fisheries (U.S. Agency for International Development 1987). Several Caribbean nations have met increased market demand with the large-scale use of artificial shelters to concentrate lobsters and facilitate harvest (e.g., Mexico—Miller 1989, Lozano-Alvarez et al. 1991; Cuba—Cruz and Brito 1986; Bahamas—R.W. Thompson, Dep. Fish., Nassau, Bahamas, pers. commun., May 1991). These artificial shelters, commonly referred to as "casitas Cubanas" (see Fig. 1), attract and concentrate a broad size-spectrum of juvenile *P. argus*, particularly in nursery areas (Eggleston et al. 1990, Lozano-Alvarez et al. 1991).

Predation intensity in and around artificial shelters is affected by numerous factors including the sizes of predator, prey, and shelter (Hixon and Beets 1989, Eggleston et al. 1990), and distance from the reef (Shulman 1985). Moreover, since most crustaceans have indeterminate growth (Hartnoll 1982), they must continually search for larger shelters as they grow, a process that involves predation risk that is inversely related to body size (e.g., Scully 1983, Reaka 1987, Vermeij 1987). Hence, we hypothesized that (1) the relative importance of a lobster size refuge would vary according to shelter availability, and (2) that the impact of artificial shelters upon predation-induced mortality of juvenile lobsters would vary according to the distance of unprotected lobsters from these shelters. We tested these hypotheses experimentally in the field by quantifying the survival of tethered spiny lobster juveniles in seagrass beds of Bahia de la Ascension, Mexico. This bay is a productive nursery for juvenile *Panulirus argus* and supports a commercial fishery for large juveniles and adults (Miller 1989, Lozano-Alvarez et al. 1991). Experimental factors included (1) presence or absence of artificial shelter, i.e., casitas Cubanas, (2) lobster size, (3) site, and (4) distance between tethered, unprotected lobsters and artificial shelters.

Methods and materials

Study site

Tethering experiments were conducted in Bahia de la Ascension, a large bay (~740 km^2) within the Sian Ka'an Biosphere Reserve, Mexico (19°45'N, 87°29'W) (Fig. 2). Two experimental sites with contrasting

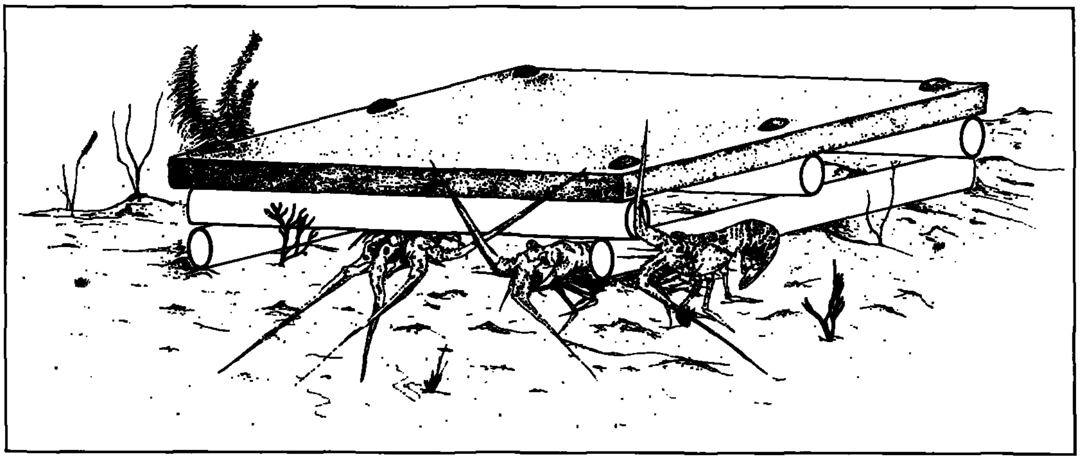

Figure 1
A large "casita Cubana" constructed with a frame of PVC-pipe and roof of cement (177 cm length × 118 cm width × 6 cm height of opening).

habitats were chosen to compare relative rates of predation: an inner-bay sand-seagrass (*Thalassia testudinum*) flat located at the northwestern portion of the bay, and an outer-bay seagrass meadow adjacent to a coral reef (Fig. 2). Seagrass and algal habitats likely provide the only natural daytime refuge for juvenile *P. argus* in this system because of an apparent lack of crevices (formed by rocky outcrops, patch coral reefs, sponges, solution holes, or undercut seagrass banks). Anecdotal information from lobster fishermen present in Bahia de la Ascension prior to the introduction of casitas (around 1974) indicated that juvenile lobsters commonly resided solitarily under dense stands of *Thalassia* or complex red algae (e.g., *Laurencia*), or aggregated around existing structures such as sponges or cobble. Moreover, previous tethering experiments with juvenile *P. argus* in this system demonstrated that seagrass and algae provide some protection for spiny lobster juveniles from predators (R.N. Lipcius et al., unpubl. data).

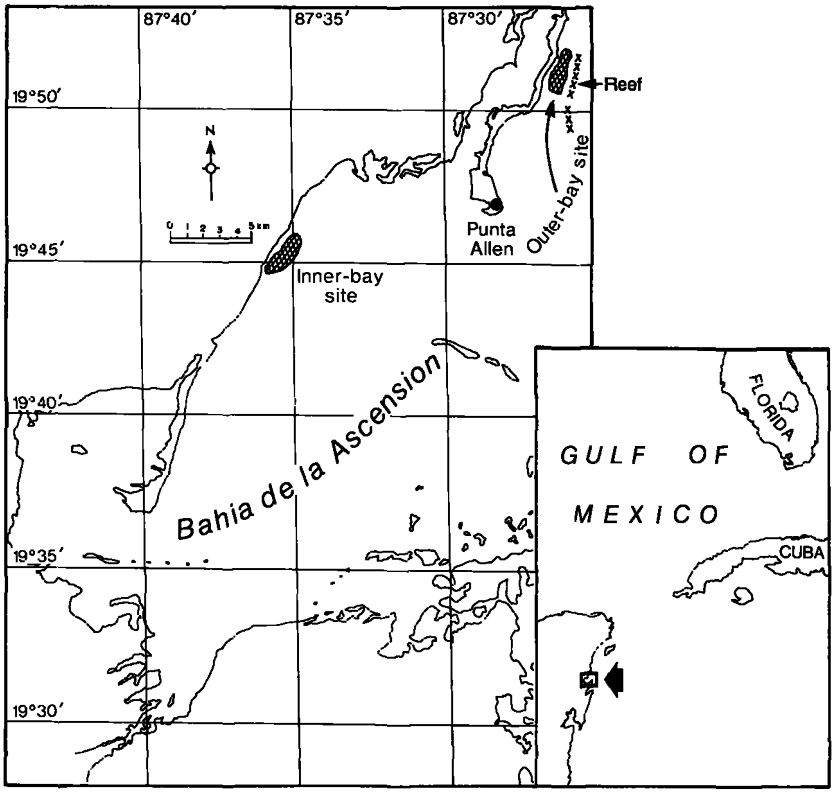

Figure 2
Study sites at Bahia de la Ascension, Mexico.

Differences in seagrass density between and within sites were determined prior to experiments by measuring dry-weight biomass (g) of *Thalassia* removed from 0.25m^2 plots. The inner-bay site was composed of sparse seagrass patches ($\bar{x}$ *Thalassia* biomass 62.4 g/m^2, N 6, 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 larger 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* biomass 111.6g/m^2, N 6, SD 13.4, and 210.0g/m^2, N 6, SD 12.6, respectively). Further details of the study site are described in Eggleston et al. (1990).

Artificial shelters

Our design of artificial lobster shelters was based on "casitas Cubanas"—sunken wood and concrete structures that simulate lobster dens (Miller 1989) (Fig. 1). The large casitas used in this study (177x118x6cm) were constructed with a reinforced concrete roof bolted to a supporting PVC-pipe frame. Several physical properties of the casita appear to make it an optimal lobster den: (1) shaded cover provided by the wide concrete roof, (2) a low ceiling that excludes large piscine predators, and (3) multiple den openings which are smaller than the inner roof height of the casita (Fig. 1) (Eggleston et al. 1990). Hence, the use of casitas permitted us to standardize den size and availability in different habitats.

Tethering experiments and predator observations

Spiny lobsters were collected from existing casitas and held in traps for 1–2 days prior to initiation of each experiment. Only intermolt lobsters exhibiting strong "tail flipping" responses 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 cyano-

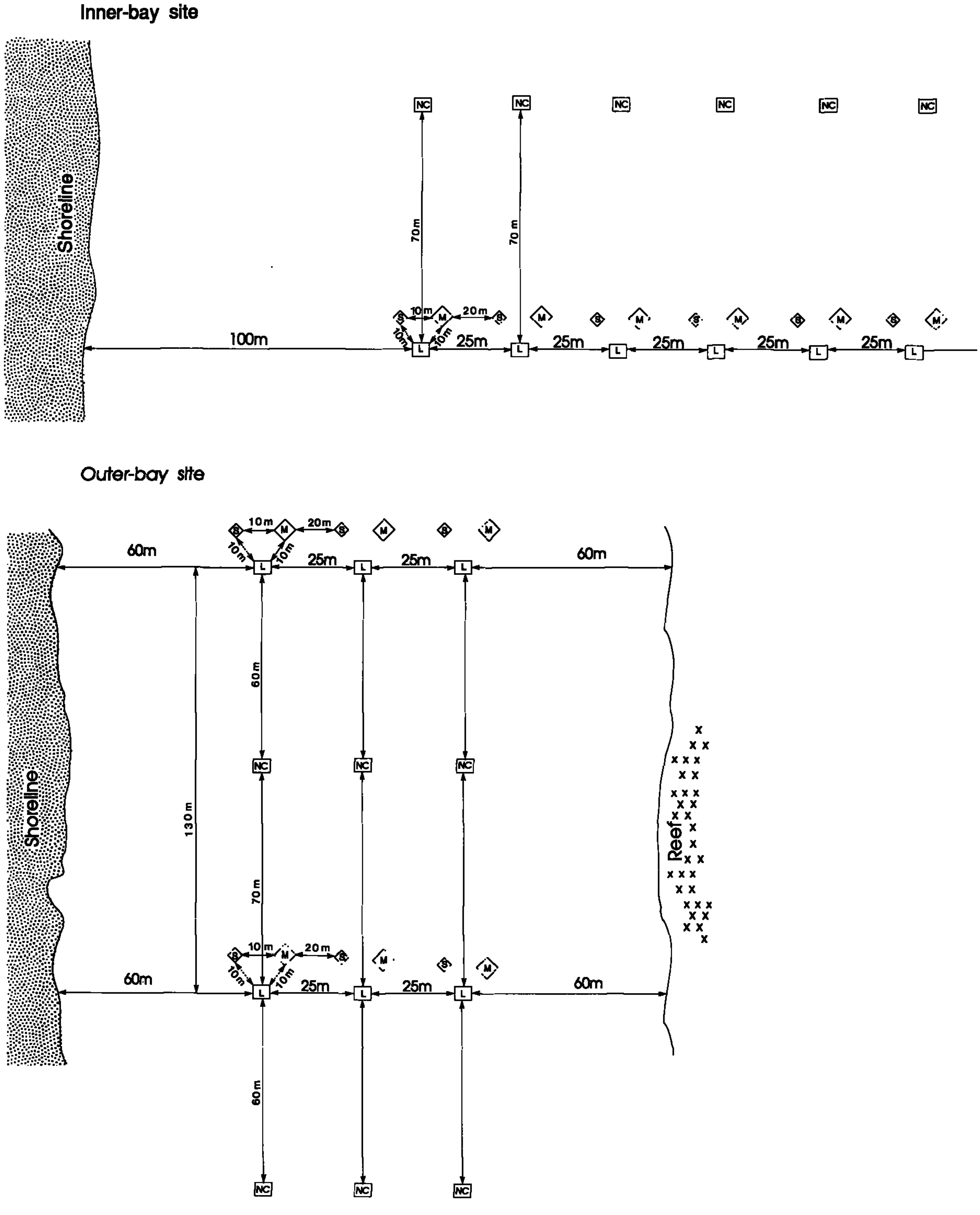

Figure 3

Schematic of casita layout at the (upper) inner-bay and (lower) outer-bay sites for the January 1989 experiment. S = small casita, M = medium casita, L = large casita, and NC = no-casita station.

acrylate cement ensured that a piece of carapace remained on the line as evidence of predator-induced mortality. An empty cable tie without a piece of carapace attached to it was scored as an escape. Each cable-tie was connected with 30 lb test monofilament line either to another cable-tie and attached to a shelter, or attached to a square wire-metal frame that was positioned outside of the triangular casita station (Fig. 3) on the seagrass bed with lead weights. The wire-metal frame had the same length-width dimensions as the large casita but did not provide shelter. The metal frame was chosen over stainless-steel stakes because stakes could not penetrate the underlying carbonate platform at the inner-bay site. The metal frames were visually inconspicuous because they were covered by a thin layer of sediment. Tether lengths of 0.7 m provided a foraging area of about 1.5 m^2 and prevented tangling between adjacent lobsters. Although tethering does not necessarily measure absolute rates of predation, it does measure relative rates of predation (Heck and Thoman 1981), which can serve to compare mortality rates as a function of different experimental treatments.

We used a stationary visual census technique (Bohnsack and Bannerot 1986) to quantify the community structure of potential predators associated with casita and no-casita stations during the experimental period (January and August 1989). Visual censuses were performed between 10:00 and 14:00 hours with three replicate samples taken during the experimental period. By performing the visual censuses during midday, we maximized the visibility available for species identification. Nighttime observations were not performed because our previous study (Eggleston et al. 1990) indicated that the predator guild normally associated with the casitas dispersed widely over the seagrass bed at night. However, predator movements were observed during one dawn and dusk crepuscular period.

We examined the daytime foraging ranges of casita-associated predators by swimming along a transect perpendicular to each casita. When potential predators were observed, a float was set to mark the location, whereupon a scuba diver then followed the predators to assure that they were associated with the casita. Our initial observations indicated that piscine predators associated with casitas seldom moved more than 30–40 m away from a casita.

Experimental design

Before initiating the tethering experiments in 1989, we deployed casitas at the inner-bay and outer-bay sites during 1988. During July 1988 at the inner-bay site, we positioned a row of six large casitas 25 m apart from one another (Fig. 3). Each large casita had one medium and one small casita placed 10 m away, yielding six stations with one small, medium, and large casita arranged in a triangle (Fig. 3). At the outer-bay site during August 1988, we positioned six small, medium and large casitas equidistant between the shore and reef line and arranged these in two rows, each containing three triangular stations (Fig. 3b). See Eggleston et al. (1990) and Eggleston and Lipcius (1992) for a complete description of the small and medium casitas and their use in other field experiments. Two separate tethering experiments were then performed during January and August 1989.

The first experiment was performed during January 1989. In this study we examined the survival of two sizes of juvenile lobsters with and without access to shelter at both the inner-bay and outer-bay sites. Six metal-frame, no-casita stations were placed 60–70 m away and perpendicular to the casitas in sparse-to-moderate-density *Thalassia* at both sites (Fig. 3). Juvenile lobsters were divided into two size-classes: small, 46–55 mm carapace length (CL) as measured dorsally from the base of the supraorbital spines to the posterior border of the cephalothorax; and large, 56–65 mm CL. Lobsters were tethered for 7 days. Each casita and no-casita station at both sites had six tethered lobsters from either of two size-classes for a total of 144 tethered lobsters (2 sites × 6 lobsters × 2 sizes × 2 treatments (casita vs. no-casita) × 3 replicate stations).

Based on our initial observations of predator foraging ranges (see above), we assumed that our choice of 60–70 m for the no-casita station was well beyond the foraging range of diurnally active predators, thereby providing unbiased estimates of lobster survival in the absence of artificial shelters (i.e., mortality estimates were not biased towards finding significantly higher predation rates on lobsters tethered within the foraging range of casita-associated predators). However, our observations during the January 1989 experiment indicated that some predators moved nearly 60 m from the casitas (see Results). Thus, although the 70 m distance from the large casitas was probably beyond the foraging range of casita-associated predators, the 60 m distance from the small and medium casitas was probably not.

Before initiating the second tethering experiment, we positioned a row of three large casitas equidistant between the shore and reef line in July 1989 at the outer-bay site (Fig. 4). In August 1989 we examined how lobster survival varied with distance from the casitas. Three metal-frame no-casita stations were placed 15, 30, and 70 m away and perpendicular to the large casitas (Fig. 4). Based on the foraging ranges of predators during the January experiment (see above), we assumed that 70 m was an adequate distance to

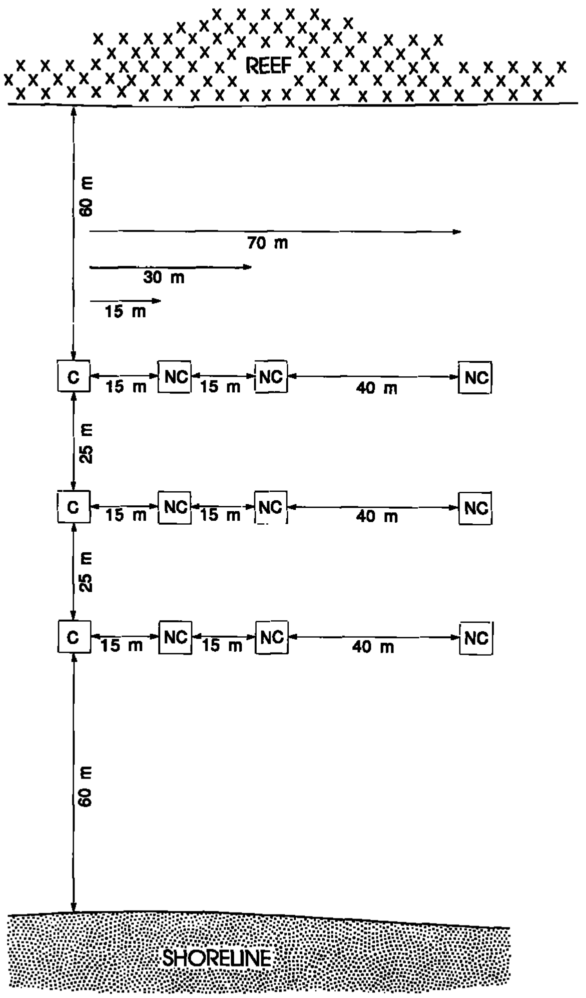

Figure 4

Schematic of casita layout at the outer-bay site for the August 1989 experiment. S = small casita, M = medium casita, L = large casita, and NC = no-casita station.

assess predation in an environment uninfluenced by the casitas. This assumption held true for the diurnal predator guild during August 1989 (see Results). Only juvenile lobsters approximating the small size-class ($\bar{x}$ 53.2 mm CL, range 45.2–59.0 mm CL, N 72, SD 4.1) were tethered for 7 days. We chose only small lobsters in the second experiment because logistical considerations limited us to one size-class, and we wanted to verify that survival of small lobsters was enhanced when residing beneath casitas (See Results for first experiment below). Each casita and no-casita (i.e., metal frame) station contained 6 tethered lobsters for a total of 72 tethered lobsters (6 lobsters × 4 distances (0, 15, 30, and 70 m) × 3 replicate stations).

Table 1

(a) Three-way ANOVA table (model I) describing the effects of site (inner-bay sand-seagrass flat, and outer-bay seagrass bed adjacent to coral reefs), lobster *Panulirus argus* size (small 46–55 mm CL; large 56–65 mm CL) and shelter availability (casita vs. no-casita station 60 m away) on proportional mortality rates (arc-sine square-root transformed) of tethered lobsters during January 1989. $^{*}P<0.05$, $^{**}P<0.01$, ns $P>0.05$.

Source of variation	SS	df	MS	F
Site	0.002	1	0.002	0.402 ns
Lobster size	0.040	1	0.040	7.174**
Shelter availability	0.001	1	0.001	0.006 ns
Site × lobster size	0.001	1	0.001	0.112 ns
Site × shelter availability	0.001	1	0.001	0.235 ns
Lobster size × shelter availability	0.023	1	0.023	4.179*
Site × lobster size × shelter availability	0.001	1	0.001	0.187 ns
Error	0.089	16	0.006	

(b) Ryan's Q tests of mean proportional mortality rates (arc-sine square-root transformed) of tethered lobsters for the interaction effect of lobster size × shelter availability. Treatment levels not significantly different at the 0.05 level share an underline. Treatment levels are arranged in increasing order of proportional mortality.

Interaction	
Shelter availability	Lobster size
Casita	$\underline{\text{large}\qquad\qquad\text{small}}$
No Casita	$\underline{\text{large}}\qquad\qquad\underline{\text{small}}$
Lobster size	Shelter availability
Small	$\underline{\text{Casita}\qquad\qquad\text{No Casita}}$
Large	$\underline{\text{No Casita}}\qquad\qquad\underline{\text{Casita}}$

Lobsters were checked and predation losses scored every 1–2 days during experiments. Fewer than 4% of tethered lobsters escaped, and these were not used in subsequent statistical analyses. Lobsters that were eaten or missing were not replaced. Cumulative losses were converted to proportional mortality/day/casita (or station). Proportions were analyzed as a function of shelter availability (casita vs. no casita), distance from the casita (0, 15, 30, and 70 m), lobster size (small vs. large), and site (inner-bay vs. outer-bay) with two- and three-way, fixed-factor analyses of variance (ANOVA) models (after procedures 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, the variances were homogeneous as determined by Cochran's C-test. Differences among means were revealed by use of

Ryan's Q multiple comparison test (Einot and Gabriel 1975) as recommended by Day and Quinn (1989).

Results

Tethering experiments

During January 1989, mortality of juvenile lobsters varied significantly as a function of lobster size but not according to site or shelter availability (i.e., tethered to casitas or 60–70 m away in seagrass) (Table 1a, Fig. 5). However, the interaction effect of lobster size by shelter availability was significant; this interaction effect was due to the significantly higher mortality of small vs. large lobsters tethered in seagrass, and by the significantly higher mortality of large lobsters in casitas compared with those tethered in seagrass (Table 1b).

At the outer-bay site in August 1989, mortality rates of small juvenile lobsters varied significantly according to distance from the casita (i.e., 0, 15, 30, and 70 m away from the casita) (Fig. 6; one-way ANOVA; F 5.89, df 3, $P<0.02$). Lobsters suffered significantly higher mortality rates when tethered 15 and 70 m away from casitas than when tethered to casitas or 30 m away from casitas (Fig. 6; Q Ryan's test, experiment-wise error rate 0.05).

Predator observations

The visual census of potential lobster predators at the inner-bay site during January 1989 indicated two predatory crab species (stone crab *Menippe mercenaria*, and a portunid *Portunus spinimanus*) and two piscine predators (gray snapper *Lutjanus griseus*, and schoolmaster snapper *L. apodus*) associated with the casitas (Table 2). No potential predators were observed in the vicinity of the no-casita stations. Mixed schools of gray snapper and schoolmaster snapper were typically found within 10 m of large casitas. Schools associated with small and medium casitas were usually located within 5 m of the casitas. Observed movements of snappers were seldom more than 15–20 m from the shelters. Similarly, two snapper species predominated at the outer-bay site during January 1989: mutton snapper *L. analis* and yellowtail snapper *Ocyurus chrysurus* (Table 2). Casitas at the outer-bay site also attracted octopus (*Octopus* spp.), green moray eel *Gymnothorax funebris*, the stone crab

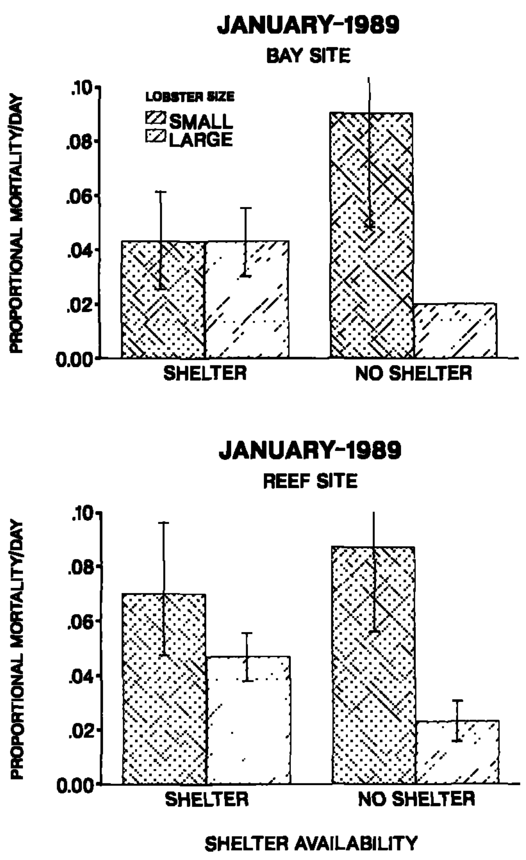

Figure 5
Results of field tethering of *Panulirus argus* at the inner-bay and outer-bay sites during January 1989, describing mortality as a function of lobster size (small 46–55 mm CL; large 56–65 mm CL) and shelter availability (casita vs. no casita). Values are mean proportional mortality · casita^{-1} · d^{-1} resulting from a total of 18 lobsters tested. Vertical bars are 1 SE.

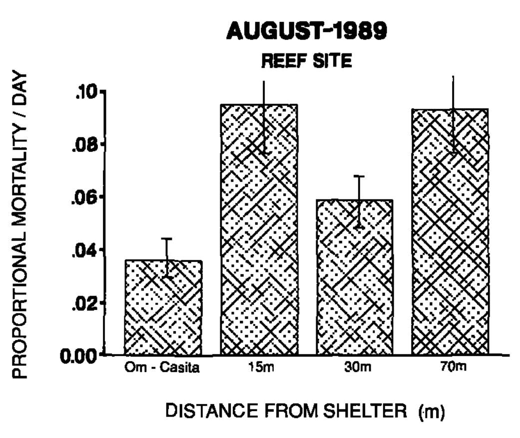

Figure 6
Results of field tethering of *Panulirus argus* at the outer-bay site during August 1989, describing mortality of small juvenile lobsters (46–55 mm CL) as a function of distance from the casita (i.e., 0, 15, 30, and 70 m away from the casita). Values are mean proportional mortality · casita^{-1} · d^{-1} resulting from a total of 18 lobsters tested. Vertical bars are 1 SE.

Table 2

Summary of results from visual census of potential lobster *Panulirus argus* predators associated with 18 casitas of three sizes (small, medium, large) at two sites (inner-bay, outer-bay) during 10–16 January 1989 at Bahia de la Ascension, Mexico. Results below are pooled from censusing 18 casitas on three different sampling dates. Fish size is fork length (cm) and crab size is carapace width (cm).

Species	Total abundance	Mean individuals/ sample/casita	Frequency/ casita size (N 18)	Percent frequency	Size (cm) Mean	Min.	Max.
		Inner-bay site					
Large Casita							
Lutjanus griseus (gray snapper)	213	11.8	18	100.0	23.4	9	37
Lutjanus apodus (schoolmaster snapper)	27	1.50	6	33.3	10.0	8	11
Menippe mercenaria (stone crab)	3	0.17	3	16.7	11.0	11	11
Medium Casita							
Lutjanus griseus	12	0.66	12	66.7	7.5	6	10
Menippe mercenaria	2	0.13	2	11.1	7.0	4	10
Portunis spinimanus (portunid crab)	2	0.11	2	11.1	8.0	8	8
Small Casita							
Lutjanus griseus	30	1.67	12	66.7	7.5	6	10
Lutjanus apodus	2	0.11	1	5.6	9.0	9	9
Menippe mercenaria	1	0.06	1	5.6	4.0	—	—
Portunis spinimanus	4	0.22	2	0.1	8.5	7	12
		Outer-bay site					
Large Casita							
Lutjanus analis (mutton snapper)	15	0.83	6	33.3	25.3	20	40
Ocyurus chrysurus (yellowtail snapper)	24	1.30	6	33.3	22.0	19	25
Menippe mercenaria	3	0.17	3	16.7	10.0	10	10
Octopus	3	0.16	3	16.7	—	—	—
Medium Casita							
Lutjanus analis	4	0.22	4	22.2	12.8	10	15
Portunis spinimanus	2	0.11	2	11.1	9.5	6	13
Small Casita							
Lutjanus analis	3	0.16	2	11.1	8.0	8	8
Gymnothorax funebris (green moray eel)	3	0.16	3	16.7	50.0	50	50
Portunis spinimanus	3	0.16	3	16.7	7.5	6	11

M. mercenaria, and the portunid crab *P. spinimanus* (Table 2). As above, no potential predators were observed in the vicinity of the no-casita stations, and mixed schools of snapper seldom strayed more than 15–20 m from casitas. However, several large snapper of both species (*L. griseus* at the inner-bay site and *L. analis* at the outer-bay site) were observed ~60 m from the casitas. We also witnessed a stone crab feeding on a lobster tethered beneath a casita, and on two separate occasions observed octopus feeding on tethered lobsters beneath a casita.

During January 1989 at the inner-bay site, there was a significant positive correlation between mean lobster proportional mortality per day at a particular casita station and the mean number of potential predators occupying the same casita station (r 0.92, n 6, $P<0.01$; Fig. 7). Conversely, there was no significant correlation between lobster proportional mortality and numbers of predators inhabiting casitas at the outer-bay site (r 0.11, n 6, NS), nor between proportional mortality and the sizes of piscine predators (mm total length; TL) at both sites (inner-bay: r 0.64, n 6, NS; outer-bay: r 0.59, n 6, NS).

Predator observations at the outer-bay site in August demonstrated a more diverse predator guild than that observed during January (compare Tables 2 and 3). Although mutton snapper and yellowtail snapper were abundant at large casitas, they were joined by larger predators, including Nassau grouper *Epinephelus striatus* and a great barracuda *Sphyraena barracuda*. One barracuda was identified by particular scars near the mouth and a broken tooth. This barracuda roamed the entire experimental area. We also observed one Nassau grouper that moved between the 70 m no-casita stations and the reef (see Fig. 4 for geography). Another slightly smaller grouper moved back and forth between the casitas, the 15 m no-casita stations, and the reef.

Table 3

Summary of results from visual census of potential lobster *Panulirus argus* predators associated with three large casitas at the outer-bay site during 3-10 August 1989 at Bahia de la Ascension, Mexico. Results below are pooled from censusing three casitas on three different sampling dates. Fish size is fork length (cm).

Species	Total abundance	Mean individuals/ sample/casita	Frequency/ casita size (*N* 18)	Percent frequency	Size (cm)		
					Mean	Min.	Max.
Lutjanus analis (mutton snapper)	12	1.33	9	100.0	20.3	15	30
Ocyurus chrysurus (yellowtail snapper)	15	1.67	9	100.0	22.0	19	25
Sphyraena barracuda (great barracuda)	2	0.22	2	22.2	100.0	100	100
Epinephelus striatus (Nassau grouper)	2	0.22	2	22.2	45.0	40	50
Dasyatis americana (southern stingray)	1	0.11	1	11.1	60.0*	—	—

* Measured from wingtip to wingtip (cm).

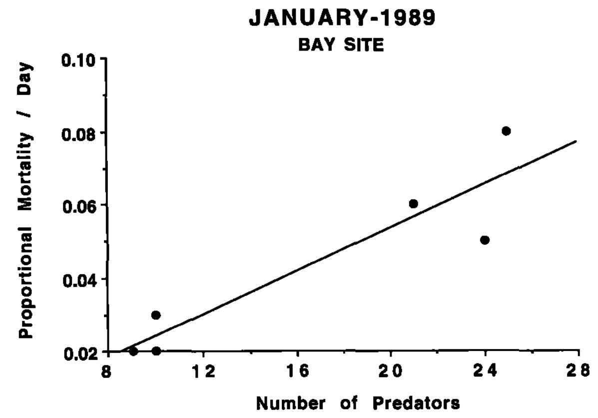

Figure 7

Mean proportional mortality of juvenile lobsters *Panulirus argus* · large casita^{-1} · d^{-1} compared against the mean number of potential predators · casita station^{-1} · d^{-1} at the inner-bay site during January 1989 ($y = -0.0051+0.0029x$; r^2 0.85, *n* 6, $P<0.009$).

Discussion

The impact of artificial shelters upon juvenile spiny lobster survival varied both by lobster size and the distance of unprotected lobsters from shelter. During our January 1989 experiment, which emphasized the effects of lobster size and shelter availability, large lobsters (56–65 mm CL) survived better than small lobsters (46–55 mm CL) in sparse-to-moderate-density seagrass (*Thalassia*) 60 m from casitas. Conversely, small lobsters survived better than large lobsters when tethered beneath casitas. During our August 1989 experiment, small lobsters survived better at casitas or 30 m away from casitas than 15 m or 70 m away. We interpret these patterns in terms of the relative importance of shelter availability and body size upon lobster survival, and then speculate on the influence of artificial-shelter-associated predators and seagrass density relative to these patterns in lobster survival.

We reemphasize that predation estimates based on tethering are likely biased by the technique and may not reflect natural predation rates. For example, lobster dens which are normally abandoned at night may become "traps" for tethered lobsters because they cannot effectively flee and conspecifics are not available to help detect and repel predators. However, predation rates on early juvenile *Panulirus argus* tethered in open sand, seagrass, and algal habitats in Florida Bay were similar both day and night (Herrnkind and Butler 1986, Smith and Herrnkind 1992). Moreover, most casita-associated predators are widely dispersed among the seagrass flats at night in Bahia de la Ascension, Mexico (Eggleston et al. 1990). Thus, we feel that the tethering technique is not only useful for comparing relative rates of predation between different size-classes of juvenile spiny lobster, but also for comparing predation rates between representative benthic habitats (e.g., crevices, algal clumps, seagrass).

Results from our January 1989 experiment support the hypothesis that large juvenile lobsters (56–65 mm CL) attain a relative-size refuge from predation compared with small juvenile lobsters (45–55 mm CL), and that the relative importance of this size refuge varies according to shelter availability. Increased predation on small juvenile lobsters tethered in seagrass suggests that sparse-to-moderate-density *Thalassia* does not provide adequate protection from predators, and that the addition of shelter greatly enhances survival for these smaller juvenile lobsters. Thus, the use of artificial lobster shelters in sparse-to-moderate-density *Thalassia* beds may effectively reduce predation-induced mortality rates of small juvenile lobsters and thereby enhance production of this size-class. However, given the general relationship of increasing survival with habitat complexity for many decapod crustaceans (Heck and Thoman 1981, Wilson et al. 1987, Heck and Crowder 1991 and references therein), the relative importance of shelter availability upon survival of small juvenile lobsters may be reduced in habitats with dense *Thalassia*. Thus, further studies are required to understand the relationship between shelter availability and increasing habitat complexity upon survival of small juvenile lobsters.

The reduced survival of large juvenile lobsters near casitas compared with seagrass 60–70 m away during the January 1989 experiment is consistent with our previous results for this lobster size-class. For example, survival of small lobsters (46–55 mm CL) in large casitas was significantly higher than survival of large lobsters (56–65 mm CL) (Eggleston et al. 1990). Moreover, large lobsters survived better in medium than in large casitas (Eggleston et al. 1990). Eggleston et al. (1990) suggested that medium casitas excluded predators that were able to prey on large lobsters, and postulated that larger predators associated with large casitas may selectively prey upon larger lobsters, due to better visual perception with increasing predator and prey size (Kao et al. 1985, Ryer 1988). The significant positive correlation between the numbers of predators (primarily gray snapper *L. griseus*) occupying specific casita stations and predation rates at these same stations suggests that gray snapper may be the principle predator of juvenile lobsters inhabiting casitas at the inner-bay nursery site. Gray snapper (15 cm TL) have successfully attacked small early-juvenile lobsters tethered in Florida Bay (Herrnkind and Butler 1986).

The combined results from this study and previous work in Bahia de la Ascension, Mexico (Eggleston et al. 1990), suggest that juvenile lobsters would survive better by leaving large shelters to take up residence in smaller shelters or nearby seagrass habitats when they reach a body size of ∼56–65 mm CL. This idea of enhancing survival through size-specific emigration from large shelters was partially supported during our recent observations of habitat-specific and size-specific patterns of shelter use by juvenile *P. argus* in Bahia de la Ascension, Mexico. Our recent field observations (Eggleston and Lipcius 1992) indicated that shelter-seeking behavior of *P. argus* is highly flexible to local social conditions (i.e., presence of conspecifics) and shelter scaling. For example, in a habitat containing very few conspecifics (e.g., outer-bay site), large juvenile lobsters chose smaller, safer medium casitas over large casitas as predicted by our tethering results (this study; Eggleston et al. 1990). However, in a habitat containing large numbers of conspecifics (e.g., inner-bay site), large juvenile lobsters occupied large casitas with large conspecifics (Eggleston and Lipcius 1992). The tethering technique in this study did not address the potential benefits of gregarious residency to lobster survival. Gregarious occupancy by more than the six tethered lobsters appeared to be inhibited because of the tethering technique, i.e., lobsters did not colonize casitas containing tethered individuals (pers. observ.). Since gregarious sheltering has been implicated as a mechanism for reducing predator-induced mortality (Berrill 1975, Herrnkind et al. 1975, Eggleston and Lipcius 1992), final conclusions regarding the impact of casitas upon predation-induced mortality rates of large juvenile lobsters must not only consider the size-specific relationship between shelter-associated predators and lobsters, but also the potential benefits of gregarious sheltering.

Results from our August 1989 experiment support the hypothesis that the impact of artificial shelters upon predation-induced mortality of juvenile lobsters varies according to the distance of unprotected lobsters from these shelters. During the August experiment at the outer-bay site, small lobsters survived equally well whether they were tethered beneath casitas or 30 m away. These tethering results, combined with observations on predator movements, suggest that 30 m is beyond the daytime foraging range of most casita-associated predators. However, the lack of a significant correlation between the numbers of potential predators at a specific casita station and predation rates on lobsters at these same stations at the outer-bay site during the January 1989 experiment suggests that transient predators such as jacks (*Caranx* spp.), groupers (*Epinephelus* spp.), sharks (*Ginglymostoma cirratum* and *Sphyrna* spp.), and stingrays (*Dasyatis* spp.) may be moving from the nearby barrier reef (see Figs. 3 and 4 for geography) and preying on tethered lobsters. Gut contents of stingrays (*Dasyatis* spp.) and bonnethead sharks *Sphyrna tiburo*, captured at night in nearshore Florida Bay waters, contained a high proportion of early-juvenile spiny lobsters (Smith and Herrnkind 1992). Nurse sharks *Ginglymostoma cirratum* are also known predators of juvenile *P. argus* (Cruz and Brito 1986). Thus, our observations on the daytime abundance and movements of casita-associated predators (i.e., primarily mutton and yellowtail snapper, *Lutjanus analis* and *O. chrysurus*) at the outer-bay site may not reflect potential predation intensity as previously suggested for the inner-bay site.

Predation risk on artifical reefs usually decreases with distance from a natural, larger reef. For example, mortality of tethered juvenile grunts (family Pomadasyidae) in St. Croix, U.S. Virgin Islands, was 40% higher at the reef edge than 20 m away (Shulman 1985). Our results are somewhat consistent with those of Shulman (1985) in that predation of lobsters decreased from 15 to 30 m from the casitas. However, increased predation rates from 0 to 15 m and from 30 to 70 m indicate that predation risk does not simply decrease linearly with increasing distance from the artificial reef (casita). We hypothesize that the predator guild originating from the nearby barrier reef at the outer-bay site (see Figs. 3 and 4 for geography) forages within the adjacent seagrass habitat and is attracted to the casitas, thereby leaving a relative "gap" in predator abundance between 15 and 60 m from the casitas. Thus, predator encounter rates with lobsters tethered only 15 m from casitas were probably high relative to lobsters tethered 30 m away. The patterns of survival of small *P. argus* within close proximity to casitas (i.e., 15 m) in this study are consistent with our previous work in seagrass habitats of Bahia de la Ascension, Mexico. For example, survival of small lobsters (46–55 mm CL) was significantly higher at medium and large casitas than in seagrass 15 m away (Eggleston et al. 1990). Predation rates also increased from 30 to 70 m, and predators not associated with the casitas, such as Nassau grouper *E. striatus*, were observed moving from nearby natural reefs to the 70 m no-casita stations rather than from the casitas.

Resident piscivores set the upper limit of the number and sizes of prey species that can occupy a given reef (Hixon and Beets 1989, Eggleston et al. 1990). For example, Hixon and Beets (1989) found an inverse relationship between the number of piscivorous fishes on a reef and the maximum number of co-occurring potential prey fishes. The results from our study indicate that large casitas are more effective at reducing mortality on small juvenile lobsters than seagrass habitats, even though seagrass and algal beds provide some refuge for juvenile spiny lobsters (Herrnkind and Butler 1986; R.N. Lipcius et al., unpubl. data). Hence, for small lobsters, our results from both the January and August experiments strongly suggest that artificial lobster shelters such as casitas increase lobster production by enhancing survival in nursery areas. However, our results for the outer-bay site during January indicated that survival of large juvenile lobsters was significantly lower when tethered beneath large casitas compared with nearby seagrass habitats. These results are consistent with the notion of building artificial lobster shelters that are scaled according to body size to enhance survival of larger juveniles in nursery habitats, particularly in areas where large conspecifics are removed from large casitas by the fishery (Eggleston et al. 1990, Eggleston and Lipcius 1992). However, further research on the impact of casitas upon lobster survival, growth rates, local and regional population structure, and benthic community structure will be required to assess the efficacy of this technology as a fisheries enhancement tool.

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