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Survival of juvenile Caribbean spiny lobster: effects of shelter size, geographic location and conspecific abundance

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ABSTRACT: The Caribbean spiny lobster *Panulirus argus* seeks structured shelter throughout its benthic phase, often forming aggregations within shelters. Casitas — concrete, low-relief, artificial shelters — are effective in aggregating lobsters, and are used to harvest spiny lobster in the Caribbean. However, casitas may also enhance populations of *P. argus*, by providing shelter from predation. In this study we examined the effects of various shelter features upon the survival of juvenile *P. argus*. Juvenile lobsters were tethered at several artificial shelter treatments in Florida Bay, Florida, USA, to test the efficacy of casitas as refuge from predation. Survival of juveniles was analyzed with respect to 4 shelter types (2 casita sizes, a simulated natural shelter and a no-shelter control) within 2 locations in Florida Bay. In general, casita availability significantly increased survival. The geographic location of artificial shelter placement also significantly affected survival; the degree of survival enhancement was apparently linked to the availability of natural shelter. Furthermore, there was a quantitative relationship between lobster survival and lobster abundance within shelters, which was tempered by local predation pressure. Survival of tethered individuals was highest when the number of conspecifics was high and predator abundance was low. While larger shelters allowed for larger lobster aggregations and usually contained more lobsters, lobsters tethered to large shelters that contained relatively few conspecifics sustained higher mortality, probably due to their increased vulnerability to larger casita-associated predators. Thus, the survival of juvenile *P. argus* is controlled not only by physical features of the shelter, but also by the relative abundance of conspecifics and predators in shelter-providing habitats.

KEY WORDS: Spiny lobster · *Panulirus argus* · Predation · Shelter · Artificial reefs · Gregarious behavior

INTRODUCTION

Throughout its benthic phase, the Caribbean spiny lobster *Panulirus argus* relies upon structured habitats for shelter (Lipcius & Cobb 1994). After several months of planktonic existence in oceanic waters, postlarvae migrate inshore via oceanic currents (Phillips 1981), where they settle on structurally complex microhabitats such as the red alga *Laurencia* spp. (Marx & Herrnkind 1985). As they grow, juveniles utilize small crevices provided by sponges and soft corals. Larger juveniles and adults inhabit the larger crevices of reefs, boulders and limestone ledges, and often form aggregations (Kanciruk 1980, Herrnkind & Lipcius 1989).

The propensity of spiny lobsters (Palinuridae) to aggregate is well documented (*Panulirus cygnus*: Cobb 1981; *P. interruptus*: Zimmer-Faust & Spanier 1987; *P. argus*: Berrill 1975, Herrnkind et al. 1975, Herrnkind & Lipcius 1989, Eggleston & Lipcius 1992). This behavioral phenomenon influences harvesting practices. For instance, lobster fishermen in Florida, USA, use live conspecifics as attractants (Heatwole et al. 1988), while Mexican, Cuban and Bahamian fishermen line seagrass beds with specially designed artificial shelters ('casitas') (Miller 1982, Cruz et al. 1986, Lozano-Alvarez et al. 1991, Eggleston et al. 1992) that provide sufficient space for lobster aggregations in excess of 250 individuals (R. N. Lipcius & D. B. Eggleston unpubl.). Although casitas provide short-term

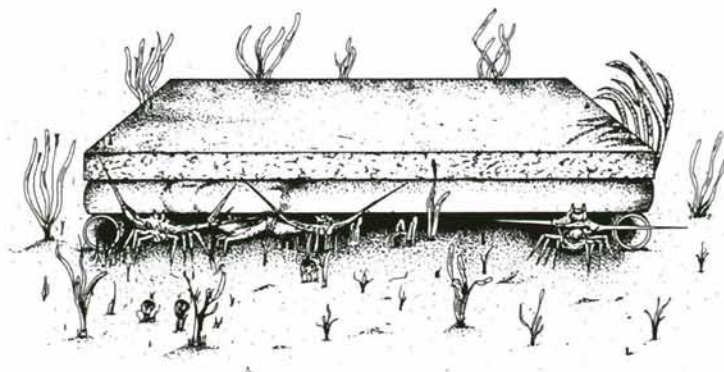


Fig. 1. Large casita (177 cm length \times 118 cm width \times 6 cm opening height) constructed of a reinforced concrete roof bolted to a supporting PVC-pipe frame. Medium casitas are smaller in area and leave a smaller opening height for entry (157.3 cm length \times 105 cm width \times 3.8 cm opening height)

benefits for fishermen by increasing harvesting efficiency (Miller 1982), the long-term effects of casita use on lobster populations are uncertain. Miller (1982) suggested that fisherman harvesting lobsters from casitas might eventually decrease the stock by not allowing enough *P. argus* to spawn. Conversely, Eggleston et al. (1990) proposed that casitas scaled according to lobster size could provide lobsters with critical refuge from predators and thereby enhance the local population.

Artificial reefs are employed worldwide by commercial and recreational fishermen to increase catch while decreasing effort (Seaman et al. 1989). However, it is unknown whether the presence of an artificial reef actually increases production of reef residents — by providing additional critical habitat that increases local environmental carrying capacity of reef fish and invertebrates — or merely concentrates individuals (Bohnsack 1989). The distinction is critical for fisheries management: if artificial reefs merely concentrate individuals, a fishery based on their use may be depleted rapidly because of the increased catchability of reef residents. It has been suggested, though, that artificial reefs may enhance populations of resident species by increasing their feeding efficiency, providing recruitment habitat or providing residents with shelter from predation (Bohnsack 1989). This study focuses on the last mechanism — the relative value of artificial shelters (casitas) as refuges from predation for juvenile Caribbean spiny lobster.

Predation is recognized as a major force shaping prey community structure (e.g. Paine 1969), population dynamics (e.g. Connell 1961), and behavior (e.g. Sih 1987, Sazima & Machado 1990). Casitas harbor known and potential lobster predators, such as snappers (Lutjanidae), groupers (Serranidae), portunid crabs (Portunidae) and stone crabs *Menippe mercenaria* (Eggleston et al. 1990, pers. obs.), possibly due to their

concentration in areas of higher prey (i.e. lobster) density (Cowie & Krebs 1979). During the day, each casita harbors a distinct group of predators which disperses shortly after sunset (Mexico: Eggleston et al. 1990; Florida Bay, Florida: pers. obs.).

Lobster aggregations within casitas (Eggleston et al. 1990, 1992) may themselves provide residents with protection from predators. It has been suggested that gregarious behavior is a defense mechanism for spiny lobsters either through earlier predator detection (Berrill 1975, Zimmerfaust et al. 1985) or the collective, defensive use of their spinose antennae (Berrill 1975, Cobb 1981). Thus, low lobster abundance in certain habitats may limit the protective capacity of shelters by reducing the potential for gregarious interactions (Eggleston & Lipcius 1992). However, experimental evidence correlating lobster group size with lobster survival is lacking.

Below we describe a field experiment that examined how *Panulirus argus* survival varied according to shelter type and location. We also provide evidence that lobster survival is influenced by the abundance of conspecifics and predators within a given shelter.

METHODS AND MATERIALS

Study sites. Casitas, which are described in detail in Eggleston et al. (1990), are flat concrete structures, supported by PVC, that mimic rock and reef crevices (Fig. 1). These casitas were placed at 2 locations, Arsnicker Keys and Twin Keys, within Everglades National Park in Florida Bay in July 1990. Two types of casitas were deployed: large casitas (177 cm length \times 118 cm width) are lifted approximately 12 cm off the substrate, with an opening height of 6 cm on all sides. Medium casitas (157.3 cm \times 105.1 cm) leave a 3.8 cm opening height. Terminology of casita sizes has been kept consistent with previous studies. 'Small' casitas (Eggleston et al. 1990) were not used in this study.

Florida Bay is a 1500 km² lagoonal estuary, subdivided into shallow basins by seagrass-covered mudbanks which restrict circulation within the bay (Holmquist et al. 1989). Expansive seagrass *Thalassia testudinum* beds, red algae *Laurencia* spp., gorgonians and sponges are common throughout the bay, providing nursery habitat for diverse finfish and invertebrate populations (Marx & Herrnkind 1985). However, on a smaller scale (e.g. km², ha), bottom features such as seagrass beds, macroalgal mats, sponges and limestone ledges can differ greatly in distribution and density (pers. obs.).

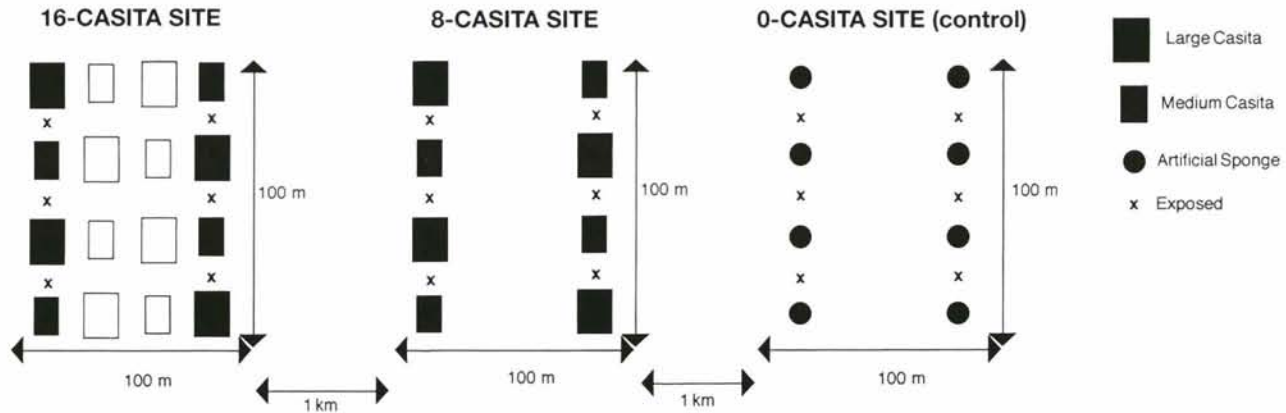


Fig. 2. Approximate layout of an experimental location, consisting of 16-casita, 8-casita and 0-casita (control) sites. Darkened areas are potential tethering stations for the tethering experiments (see 'Methods and materials: Tethering experiments')

Each of the 2 experimental locations (Arnsnicker Keys and Twin Keys) was divided into 3 sites, approximately 1 km apart: a 16-casita site, an 8-casita site, and a control (0-casita) site (Fig. 2). All sites were approximately 1 ha in area, with *Laurencia* spp. and a thin layer of silt covering a hard bottom with *Thalassia testudinum* and *Penicillus* spp. interspersed throughout soft-bottom areas. *Laurencia* spp. exists in dense mats at the Arnsnicker Keys, often spanning several m², while being sparsely distributed at Twin Keys (pers. obs.).

Assessment of lobster and predator abundances. The casita sites were visually censused by SCUBA monthly for 1 yr after deployment, and bimonthly thereafter, always during the new moon phase. Daytime surveys consisted of inventories of each casita, with abundances and sizes of all lobsters, fish and crabs recorded. Nighttime surveys consisted of diagonal transects across each site (approximately 141 m), to observe foraging predators in the seagrass beds. Each diagonal transect was run twice just after sunset and twice 2 h later. This procedure was repeated later the same week for a total of (2 transects site⁻¹ × 2 transects evening⁻¹ × 2 evenings =) 8 transects per site.

To supplement the predator observations, some representative predators were caught by spearfishing and checked for the presence of *Panulirus argus* in stomach contents. In an attempt to catch nocturnal predators, 10 lobsters were tethered overnight with treble hooks attached to 125 lb (ca 57 kg) steel-plated monofilament.

Tethering experiments. To assess relative predation rates across location and casita size, juvenile lobsters were tethered at several shelter-treatment combinations during the summer months (July–August 1991), when lobster and predator populations at the casita sites are greatest (Lipcius & Eggleston unpubl.). Tethering is an effective technique for assessing relative rates of predation between treatments, having been used successfully with blue crabs (Wilson et al. 1987), xanthid, mud and

hermit crabs (Heck & Wilson 1987), juvenile American lobster (Barshaw & Able 1990), and juvenile Caribbean spiny lobster (Herrnkind & Butler 1986, Eggleston et al. 1990, 1992, Smith & Herrnkind 1992).

Four types of tethering stations were established in this experiment (Fig. 2). Individual *Panulirus argus* were tethered to medium and large casitas. Two additional types of tethering stations were then constructed: artificial sponges and exposed stations. The artificial sponges were designed to mimic the common loggerhead sponge *Spheciospongia vesparium*, thereby simulating natural *P. argus* habitat without attracting the lobster and fish aggregations associated with casitas (Eggleston et al. 1990). These were constructed by filling the rim of a standard automobile tire with cement block pieces (to insure stability), and then wrapping in fine-mesh shade cloth (to smoothen surface area). Artificial sponges were deployed at the control (0-casita) sites to match the layout of the casitas at the 8-casita sites. Exposed stations, each consisting of a PVC stake driven completely into the sediment, were placed within all sites to assess lobster survival in the absence of shelter (Fig. 2).

Tethers were constructed by tying 60 lb (ca 27 kg) monofilament around the cephalothorax of a lobster, between the second and third walking legs, and securing the knot with cyanoacrylate cement. Intermolt juvenile spiny lobsters, 30 to 55 mm CL (carapace length, the distance from the anterior margin of the carapace between the rostral horns to the posterior margin of the cephalothorax), were collected, fitted with 10 cm tethers and held in tanks for 24 to 48 h (to minimize handling-related effects) prior to placement in the field.

At the 16-casita sites, tethering was confined to the outer rows to standardize spacing among all sites. Thus, each casita site had 8 casitas (4 large and 4 medium) that served as tethering stations, and control sites had 8 artificial sponges that served as tethering

stations. Each site had 6 designated exposed stations that were kept equidistant (approximately 12.5 m) from neighboring casitas or artificial sponges (Fig. 2).

The experiments were performed as a series of 48 h trials. Of the 8 casitas designated as tethering stations at each casita site, 2 large and 2 medium were randomly selected for each trial. At each control site, 4 artificial sponges were randomly selected for each trial. Of the 6 exposed stations at each of the 6 sites (sites: 16, 8 and 0 at 2 locations), 4 were randomly selected for each trial. For each trial, a single lobster was tethered to each of 48 randomly selected stations [$2 \text{ locations} \times 3 \text{ sites location}^{-1} \times (4 \text{ shelter stations} + 4 \text{ exposed stations site}^{-1})$]. Tethered lobsters were checked for survival after 48 h. Seven trials were run between July 13 and August 9, 1991 ($48 \times 7 = 336$ lobsters). An additional trial with the 24 exposed stations was run shortly thereafter, to compensate for uprooted stations from earlier trials.

Statistical analysis involved time as a blocking factor in a log-linear analysis of frequencies (*G*-test; Sokal & Rohlf 1981); when time was not found to be significant, data from the separate trials were pooled (Sokal & Rohlf 1981). Data from the exposed stations were analyzed first, to determine if there were any differences in survival associated with location or site at each location, using a 2-way *G*-test with location as a blocking factor and density (i.e. 16-casita, 8-casita and 0-casita) as a fixed factor. Second, differences in survival associated with shelter types were determined using separate *G*-tests for each site type with location as a blocking factor. Lobster survival (alive or dead) was the dependent variable, with shelter type (large casita, medium casita, exposed station, artificial sponge) as the independent variable. Differences between frequencies were deter-

mined using lower-level *G*-tests. The CATMOD module of SAS statistical software (SAS Institute, Inc., Cary, NC, USA) was used in the log-linear analyses.

We also examined the relationship between lobster survival and relevant continuous variables (e.g. abundances of the different predators, abundance of lobsters within a shelter) with linear least-squares multiple regression models using proportional lobster survival per treatment as the response variable. Residuals from these analyses were analyzed visually to detect departures from randomness.

RESULTS

Lobster abundances

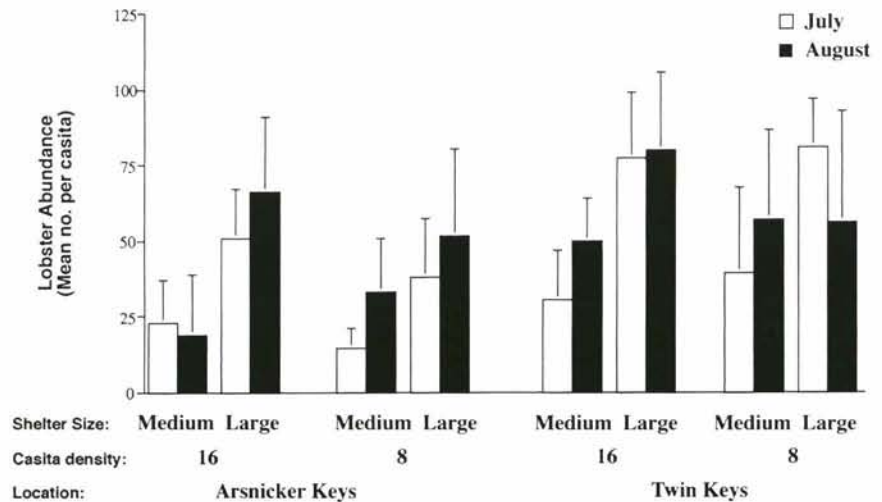
Panulirus argus colonized the casitas shortly after they were deployed in July 1990. By summer 1991, several casitas appeared to be filled to capacity with juvenile to adult lobsters. Mean lobster abundances for the separate treatments (combinations of location, casita density and casita size) are given in Table 1 and shown in Fig. 3.

Throughout the summer, there were many more lobsters at the Twin Keys casitas than at Arsnicker Keys, and many more lobsters inhabiting large casitas than medium casitas, with the sole exception at the Twin Keys 8-casita site in August. Total abundance at each 16-casita site was approximately double that of the 8-casita site within the same location; thus the mean number of lobsters per casita did not differ greatly between 16-casita and 8-casita sites within each location (Table 1, Fig. 3). These observations are consistent with those of Lipcius & Eggleston (unpubl.), who found

Table 1. *Panulirus argus*. Abundances and sizes (mm carapace length, CL) of Caribbean spiny lobster observed during the study

Location	Casita density	Casita size	July 1991			August 1991		
			Total	Avg./casita	Mean size (mm CL)	Total	Avg./casita	Mean size (mm CL)
Arsnicker Keys	16	Medium	185	23.1	43.1	152	19.0	59.7
		Large	405	50.6	53.5	530	66.3	62.5
		Total	590	36.9	50.2	681	42.6	62.0
	8	Medium	58	14.5	41.7	133	33.3	52.9
		Large	151	37.8	52.6	206	51.5	61.7
		Total	209	26.1	49.6	339	42.4	58.2
Twin Keys	16	Medium	242	30.3	57.4	399	49.9	64.4
		Large	618	77.3	64.6	639	79.9	69.1
		Total	860	53.8	62.6	1038	64.9	67.3
	8	Medium	158	39.5	46.5	228	57.0	55.2
		Large	324	81.0	57.3	225	56.3	52.3
		Total	482	60.3	53.8	453	56.6	53.8

Fig. 3. *Panulirus argus*. Mean numbers of spiny lobster found within each casita treatment (treatment: combination of location/casita density/casita size, e.g. Arsnicker Keys 16 Large) during July and August 1991. Error bars represent 1 SD



significantly more lobsters inhabiting the casitas at Twin Keys than at Arsnicker Keys throughout the year, and significantly more lobsters inhabiting large casitas than medium.

Predator observations

A species observed during the surveys was considered a potential predator if it fit at least 1 of the following criteria: (1) previously found with lobsters in gut contents [e.g. nurse shark *Ginglymostoma cirratum* (Cruz et al. 1986), bonnethead shark *Sphyrna tiburo*

(Smith & Herrnkind 1992), southern stingray *Dasyatis americana* (Smith & Herrnkind 1992), snappers *Lutjanus* spp. (Starck & Schroeder 1971, this study), and groupers *Epinephelus* spp. (Randall 1967, this study)]; (2) those that we have observed eating *Panulirus argus* during related studies (e.g. stone crab *Menippe mercenaria*, and octopus *Octopus vulgaris*); or (3) those identified by Randall (1967) as either 'shelled-invertebrate feeders' or 'generalized carnivores' [e.g. hogfish *Lachnolaimus maximus*, and spiny puffers (Diodontidae)].

The casitas placed in Florida Bay attracted numerous potential juvenile lobster predators (Tables 2 to 4). Grey

Table 2. *Lutjanus griseus*. Abundances and sizes (cm total length) of grey snapper observed during July and August daytime surveys. Speared snappers were taken approximately 1 wk prior to August surveys. Associated casita sizes of speared snappers are not known, thus abundances and sizes of speared snappers are only included in the totals for each site

Location	Casita density	Casita size	July 1991				August 1991					
			Abundance		Size (cm)		Abundance		Size (cm)			
			Total	Avg./casita	Mean	Min.	Max.	Total	Avg./casita	Mean	Min.	Max.
Arsnicker Keys	16	Medium	82	10.3	9.3	6	20	56	7.0	11.1	10	15
		Large	78	9.8	10.9	8	25	82	10.3	11.2	8	30
		Total	160	10.1	10.0	6	25	140	8.8	11.4	8	30 ^a
	8	Medium	22	5.5	10.7	8	18	31	7.8	14.4	10	30
		Large	24	6.0	11.2	8	20	17	4.3	13.2	10	25
		Total	46	5.8	11.0	8	20	55	6.9	15.0	10	35 ^b
Twin Keys	16	Medium	144	18.0	12.7	7	35	72	9.0	11.2	8	25
		Large	212	26.5	13.0	10	35	177	22.1	10.9	8	20
		Total	356	22.3	12.9	7	35	260	16.3	11.5	8	30 ^c
	8	Medium	146	36.5	12.0	7	25	198	49.5	12.5	8	25
		Large	159	39.8	12.2	8	25	268	67.0	13.0	8	30
		Total	305	38.1	12.1	7	25	466	58.3	12.8	8	30

^aIncludes 2 snappers (27 and 29 cm) speared August 13, 1991

^bIncludes 7 snappers (mean 22 cm, min. 15 cm, max. 35 cm) speared August 13, 1991

^cIncludes 11 snappers (mean 26 cm, min. 24 cm, max. 30 cm) speared August 14, 1991

Table 3. Potential predators of juvenile *Panulirus argus* observed during July and August daytime casita surveys (not including grey snapper *Lutjanus griseus*)

Location	Casita density	Casita size	Species	July 1991				August 1991			
				Abundance		Size (cm)		Abundance		Size (cm)	
				Total	Avg./casita	Mean	Max.	Total	Avg./casita	Mean	Max.
Arnsnicker Keys	16	Medium	Stone crab <i>Menippe mercenaria</i>	1	0.125	8	8	1	0.125	8	8
			Stone crab	3	0.375	12	11	1	0.125	11	13
			Nurse shark <i>Ginglymostoma cirratum</i>					1	0.125	130	
			Octopus <i>Octopus vulgaris</i>					1	0.125		
Twin Keys	16	Medium	Stone crab					1	0.250	8	8
			Grey triggerfish <i>Balistes capricus</i>					1	0.250	15	15
			Stone crab	2	0.500	11	9				
			Hogfish <i>Lachnolaimus maximus</i>	1	0.250	15	15				
Twin Keys	16	Medium	Stone crab	4	0.500	8	7				
			Spiny puffer <i>Diodon</i> sp.					1	0.125	12	12
			Stone crab	2	0.250	8	7	1	0.125	5	5
			Red grouper <i>Epinephelus morio</i>					1	0.125	36	36
Twin Keys	8	Medium	Stone crab	2	0.500	8	6	3	0.750	7	7
			Stone crab	3	0.750	7	5			10	10

^aCarapace width for crabs, total length for fish

snapper *Lutjanus griseus* was the most abundant predator during the daytime surveys (Table 2), though many of the *L. griseus* were smaller than 15 cm total length and probably could not feed on lobsters of the experimental size range (Starck & Schroeder 1971, Smith & Herrnkind 1992). *L. griseus* larger than 15 cm in total length were significantly more abundant at Twin Keys than at Arsnicker Keys (3-way ANOVA, $F = 7.58$, $p < 0.01$), and were most numerous at the Twin Keys 8-casita site, especially in August (Fig. 4). Other potential predators observed during the casita surveys included stone crab *Menippe mercenaria* and red grouper *Epinephelus morio* (Table 2). A more diverse group of predators was observed foraging during the night surveys (Table 2), including many predators that were not observed during daytime surveys (e.g. bonnethead shark *Sphyrna tiburo* and southern stingray *Dasyatis americana*). Other potential predators observed during tethering runs, but not seen during the surveys, included 5 bottlenose dolphins *Tursiops truncatus* at the Twin Keys 16-casita site.

Of the 10 lobsters tethered overnight with treble hooks, only 3 were recovered alive — the rest were missing with at least 1 of the hooks straightened. Gut contents of 20 large (>15 cm) grey snapper and 1 red grouper (36 cm) were checked for presence of *Panulirus argus*; lobster parts were found in 1 snapper (30 cm) and the grouper.

Tethering experiments

Tethered lobsters that could not be recovered, mostly at uprooted exposed stations, were considered as lost data points. Of 7 trials, 2 were eliminated as they contained several lost stations. The remaining trials were not found to be hetero-

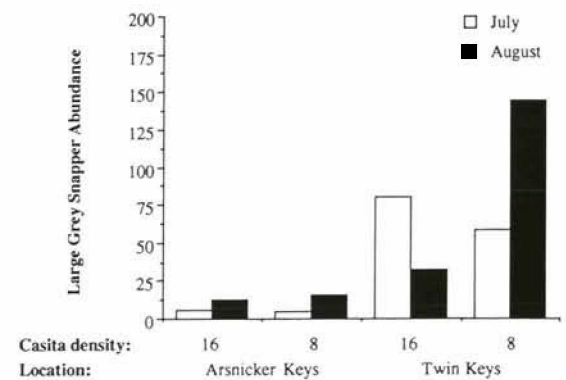


Fig. 4. *Lutjanus griseus*. Abundances of large (≥ 15 cm) grey snapper) in the casita sites during July and August

Table 4. Potential predators of *Panulirus argus* observed during night surveys

Location	Casita density	Species	Abundance	Size (cm)			
				Mean	Min.	Max.	
Arnsnicker Keys	16	Grey snapper <i>Lutjanus griseus</i>	7	22	18	30	
		Porgy <i>Calamus</i> spp.	3	18	15	20	
		Hardhead catfish <i>Arius felis</i>	1	25			
		Nurse shark <i>Ginglymostoma cirratum</i>	1	130			
		Tarpon <i>Megalops atlanticus</i>	1	30			
		Yellowfin mojarra <i>Gerres cinereus</i>	1	20			
		Portunid crab	1	8			
	8	Grey snapper	13	23	15	35	
		Porgy	2	20	15	25	
		Yellow stingray <i>Urolophus jamaicensis</i>	1	30			
	0	Grey snapper	5	21	15	35	
		Hardhead catfish	1	35			
		Lane snapper <i>Lutjanus synagrus</i>	1	15			
		Mutton snapper <i>Lutjanus analis</i>	1	15			
		Porcupinefish <i>Diodon hystrix</i>	1	25			
		Porgy	4	23	18	30	
		Yellow stingray	1	30			
		Stone crab <i>Menippe mercenaria</i>	3	15	15	15	
	Twin Keys	16	Black grouper <i>Mycteroperca bonaci</i>	1	35		
			Grey snapper	4	21	15	30
			Red grouper <i>Epinephelus morio</i>	1	40		
Southern stringray <i>Dasyatis americana</i>			1	75			
Portunid crab			2	7	7	7	
Stone crab			4	8	6	10	
8		Bonnethead shark <i>Sphyrna tiburo</i>	1	100			
		Grey snapper	16	18	15	35	
		Porgy	1	30			
		Sea robin <i>Prionotus</i> sp.	1	35			
		Portunid crab	1	5			
0		Stone crab	7	5	4	7	
		Grey snapper	7	21	15	30	
		Sea robin	1	20			
	Striped burrfish <i>Chilomycterus schoepfi</i>	1	10				
	Portunid crab	1	3				
	Stone crab	4	6	4	9		

geneous (G -test, $G = 6.648$, $p = 1.6666$; Sokal & Rohlf 1981); thus, the data from these trials were pooled.

The survival patterns of juvenile *Panulirus argus* without access to shelter (i.e. exposed) provided a control for the various shelter treatments. Lobster survival was significantly higher at Arnsnicker Keys than at

Twin Keys, but did not differ by site within location (Table 5). Individuals recovered at the Arnsnicker Keys location were often clutching clumps of *Laurencia* spp. and associated debris, which may have served as camouflage (Herrnkind & Butler 1986). Passing debris and *Laurencia* spp. were not available to tethered individuals at Twin Keys.

In nearly every situation, juvenile lobsters tethered to any type of shelter (medium or large casita or artificial sponge) had higher survivorship than exposed individuals (Fig. 5A to C). The highest survivorship at exposed stations was 56% — survivorship fell below that level at only 1 of the 12 shelter treatments (Twin Keys 8 large casitas, Fig. 5C). Overall, survival pat-

Table 5. *Panulirus argus*. G -test on survival of juvenile spiny lobster tethered to exposed stations only

Source of variation	df	G	p
Location	1	5.63	0.0177
Density	2	1.31	0.5184

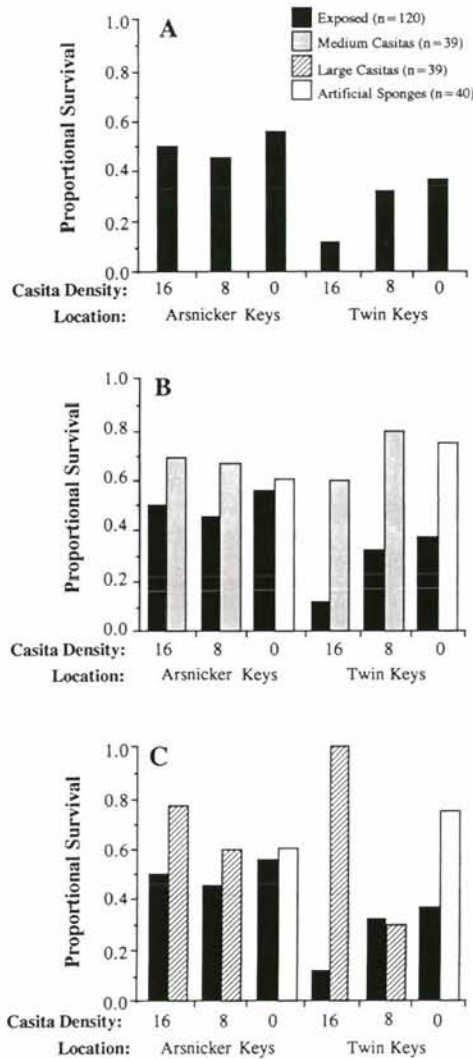


Fig. 5. *Panulirus argus*. Results of tethering experiments. Proportional survival of tethered lobsters is plotted against treatment for (A) exposed stations only, (B) medium casitas vs exposed stations vs artificial sponges, and (C) large casitas vs exposed stations vs artificial sponges

terns across shelter treatments were similar between the 2 locations, with greater differences occurring at Twin Keys (Fig. 5B, C).

16-casita sites. No significant difference in lobster survival was detected across location (G -test, $G = 2.31$, $p = 0.1287$). Shelter type significantly affected survival (G -test, $G = 9.53$, $p = 0.0085$) — lower-level tests indicated that survival was significantly higher at large casitas than at exposed stations (G -test, $G = 11.91$, $p = 0.0006$), and higher at medium casitas than at exposed stations (G -test, $G = 5.14$, $p = 0.0234$). Survival was higher at large casitas than at medium casitas, although a significant difference was not detected at this sample size (G -test, $G = 2.97$, $p = 0.0847$).

8-casita sites. No significant difference in lobster survival was detected across location (G -test, $G = 1.12$, $p = 0.2890$). No significant difference was detected across shelter (G -test, $G = 3.31$, $p = 0.0615$), however the low p -value may indicate low power. Lower-level tests indicated significantly higher survival at medium casitas than at exposed stations (G -test, $G = 6.06$, $p = 0.0138$). No significant difference was detected between large casitas and exposed stations (G -test, $G = 0.23$, $p = 0.6313$), or between medium and large casitas (G -test, $G = 3.20$, $p = 0.0738$), although the sample size in the latter test might have been insufficient to detect a significant difference. At Twin Keys, the higher survival at medium casitas than at large casitas was found to be significant (G -test, $G = 4.53$, $p = 0.0333$).

Control (0-casita) sites. No significant difference in lobster survival was detected across location (G -test, $G = 0.01$, $p = 0.9428$). There was also no significant difference detected across shelter at the 0.05 level (G -test, $G = 3.58$, $p = 0.0586$), although the p -value may indicate that the power of the test was low. Lower-level tests indicated a significant difference at Twin Keys (G -test, $G = 5.44$, $p = 0.0197$), with higher survival at the artificial sponges. No significant difference was detected at Arsnicker Keys (G -test, $G = 0.08$, $p = 0.7818$).

Lobster survival: effects of lobster and predator abundance

Tethering results showed that both location and shelter features can be significant determinants of lobster survival. However, the results, particularly at Twin Keys, indicated that other factors were involved. Sur-

Table 6. *Panulirus argus*. Multiple regression for proportional survival (angular transformation) of tethered juvenile spiny lobster

Source of variation	df	SS	MS	F
Regression	2	0.515	0.258	39.2***
Residual	5	0.033	0.007	
Total	7	0.548		

Variable	Coefficient	SE	Std coeff.	t
Intercept	0.902			
Lobsters casita ⁻¹	0.013	0.002	0.942	7.08***
Day predators casita ⁻¹	-1.586	0.189	-1.117	8.39***

*** $p < 0.001$

vival of tethered individuals at the large casitas at the Twin Keys 8-casita site was unusually low (Fig. 5C) — nearly identical to the exposed stations at the same site. Abundance of finfish at that site was particularly high (Table 2), and the number of *Panulirus argus* was relatively low (Table 1, Fig. 3). Thus, a multiple regression analysis was conducted to determine if a quantitative relationship existed between lobster survival and the abundances of lobsters and their predators at a given treatment (combination of location/density/shelter size, e.g. Arsnicker Keys × 16-casita × Medium).

Lobster survival varied significantly as a function of the average number of lobsters per casita, calculated as mean number of lobsters per treatment for July and August surveys, and the number of daytime predators per casita (not including *Lutjanus griseus*), calculated similarly (Table 6). The resulting regression equation

$$y = 0.902 + 0.013(\text{Lobsters casita}^{-1}) - 1.586(\text{Daytime predators casita}^{-1})$$

where y = proportional lobster survival (angular transformation) was then algebraically solved for the significant factors and plotted to illustrate their combined effect (Fig. 6A to D). In sum, lobster survival was positively correlated with lobster abundance per casita and inversely correlated with predator abundance per casita (Fig. 6A to D).

DISCUSSION

Spiny lobsters (Palinuridae) aggregate readily, and it has been hypothesized that gregarious behavior enhances lobster survival (*Panulirus cygnus*: Cobb 1981; *P. interruptus*: Zimmer-Faust & Spanier 1987; *P. argus*: Berrill 1975, Herrnkind et al. 1975, Eggleston & Lipcius 1992). Our findings indicate that the probability of survival of a given lobster within a shelter depends on shelter characteristics and a balance between lobster abundance within the shelter and local predation pressure. Specifically, lobster survival was correlated positively with lobster abundance in the shelter.

Tethered lobsters may have been able to cooperate with free-roaming conspecifics to enhance survival of the group (gregarious behavior; e.g. Eggleston & Lipcius 1992). Larger shelters allow for larger lobster aggregations, and, in areas of high lobster abundance, are preferentially selected by *Panulirus argus* over smaller shelters (Eggleston & Lipcius 1992). The large casitas in this study consistently contained more lobsters than medium casitas within the same site, with the exception of those at the Twin Keys 8-casita site (Twin Keys 8), where lobster abundance in large casitas was nearly identical to that in medium casitas. Twin Keys 8 was the only site that showed a slight

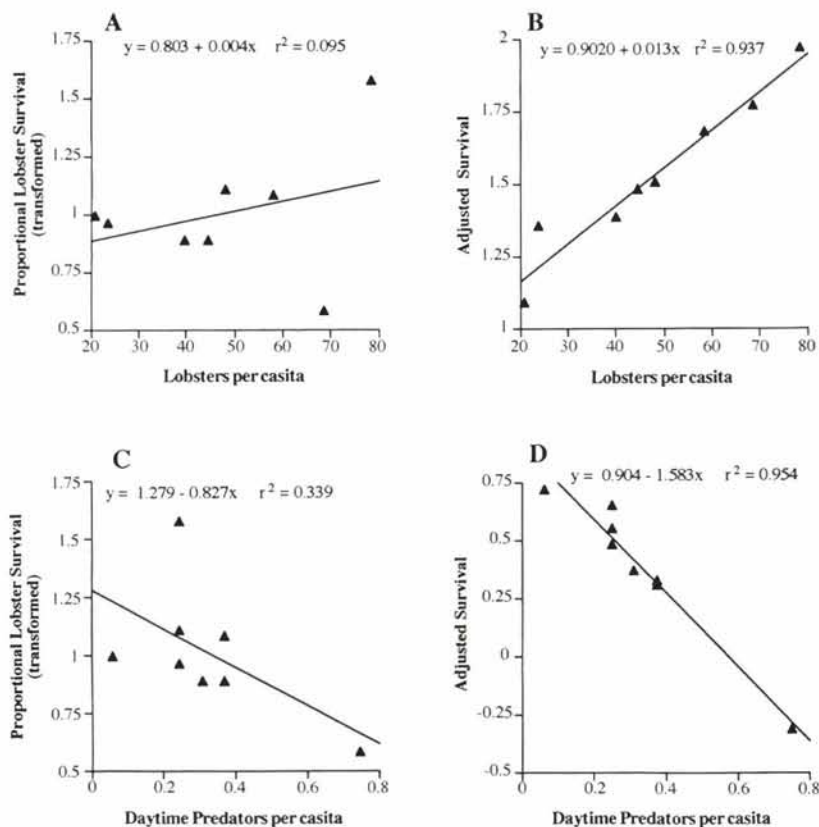


Fig. 6. *Panulirus argus*. Comparison of individual effects of mean lobster abundance per casita and mean daytime predators per casita on lobster survival (A and C, respectively) with their combined effects (B and D). (A) Proportional survival (transformed) vs mean lobster abundance per casita. (B) Adjusted survival [derived by solving regression equation from Table 6 to account for mean daytime predator abundance per casita, i.e. $y = \text{survival} + 1.586(\text{Daytime predators casita}^{-1})$] vs mean lobster abundance per casita. (C) Proportional survival (transformed) vs daytime predator abundance per casita. (D) Adjusted survival [i.e. derived by solving regression equation from Table 6 to account for mean lobster abundance per casita, i.e. $y = \text{survival} - 0.013(\text{Lobsters casita}^{-1})$] vs daytime predator abundance per casita

decrease in total lobster abundance (6%) between the July and August surveys; total abundances at Arsnicker Keys 16, Arsnicker Keys 8, and Twin Keys 16 increased 15, 62 and 20%, respectively. Abundance at the medium casitas at Twin Keys 8 increased 44% from July to August, accompanied by a 44% decrease in lobster abundance at the large casitas. Eggleston & Lipcius (1992) suggest that lobsters preferentially choose smaller shelters at low lobster densities or when perceived predation risk increases. Perceived risk of predation was probably high at Twin Keys 8; the number of large (>15 cm) grey snappers at Twin Keys 8 nearly tripled from July to August (49 to 144), and survival of the tethered lobsters at large casitas at that site was very low. It is unclear whether (1) increased predation at Twin Keys 8 caused lobsters to switch from the large to the medium casitas, or (2) the shifting of free-roaming lobsters to the medium casitas left tethered individuals at large casitas at higher risk. Either scenario is consistent with the shelter utilization model of Eggleston & Lipcius (1992), and is evidence for a relationship between the size of a lobster aggregation and an individual's probability of survival within a shelter.

Lobsters were more abundant in the Twin Keys casitas throughout the summer, possibly indicating fewer natural shelters are available at Twin Keys than at Arsnicker Keys. This was supported in the tethering experiments; although exposed stations were placed in bare sand, many tethered lobsters at Arsnicker Keys appeared to use clumps of *Laurencia* spp. as camouflage. *Laurencia* spp. occurred only in relatively small patches at the Twin Keys sites. Artificial sponges, which are not conducive to lobster aggregations and do not attract predator aggregations, significantly enhanced survival over exposed stations at Twin Keys — another indication that natural shelter was scarce at Twin Keys.

Lobster survival at medium casitas was consistent (60 to 80%) at the 4 sites that had casitas; medium casitas appear to neutralize the apparent higher predation pressure at Twin Keys. Predators that were excluded by the small opening of a medium casita were apparently an important component of the predator guild at Twin Keys, while predators that were capable of fitting beneath medium casitas were equally effective at both locations. The lower survival at the exposed stations at Twin Keys, coupled with the consistent survivorship at medium casitas, indicates that the *degree* of survival enhancement afforded by casitas may also differ greatly between any 2 locations.

Predators appear to be of 2 general types: (1) resident — observed in or near the casita during the daytime (e.g. stone crabs, snappers), and (2) transient — observed foraging on casita sites, but not using the

casitas as shelter (e.g. southern stingray, bonnethead shark). Grey snapper *Lutjanus griseus* were by far the most abundant resident fish species, particularly at Twin Keys. Gut contents confirmed that they are predators of *Panulirus argus*, although samples were too few to determine their impact. Other resident predators observed included red grouper *Epinephelus morio*, stone crabs and octopus, which, despite their low abundance relative to grey snapper, may have been responsible for much of the predation within casitas, particularly since the abundance of grey snapper was not a significant factor in the survival analysis. Despite the apparent vulnerability of lobsters to resident predators, survival of tethered individuals was nearly always higher at casitas than at exposed stations.

The treble hook tests implicate larger, transient predators. Several predators were observed on night surveys that were not seen during daytime surveys. The bonnethead shark *Sphyrna tiburo*, a confirmed predator of juvenile lobster (Smith & Herrnkind 1992), was seen only once at the casita sites. However, these sharks may be more common than observed, possibly shying away from divers and flashlights; Smith & Herrnkind (1992) caught bonnethead sharks readily in trammel nets set in Florida Bay, more than twice as many as nurse sharks, which are commonly observed in the field (pers. obs.).

Variation in rates of predation observed between the 2 locations indicates that site-specific factors (e.g. availability of natural shelter, local predator guild) influence lobster survival and thus would affect the degree of success attainable when attempting to enhance lobster stocks with artificial shelters. Bohnsack (1989) suggests that where natural shelter is scarce, artificial reefs are more likely to enhance production of resident populations. Spiny lobsters colonized the casitas rapidly, probably indicating that adequate shelter is more limited than food (Sale 1980, Bohnsack 1991, Lipcius & Eggleston unpubl.). Similarly, Shulman (1984) found that successful settlement of juvenile coral reef fishes was directly related to the number of available refuges, and that availability of other resources (e.g. food) was a negligible factor.

Our findings suggest that medium casitas placed in areas of low natural shelter availability would enhance lobster survival better than large casitas. However, survival appears to be enhanced maximally when conspecifics within a shelter are numerous and the number of resident predators is low. In the latter situation, large casitas are more appropriate, as they allow for larger aggregations. Although it is not known whether gregarious interactions directly reduce predation, previous studies have suggested that overt communal defense is not required for individuals to benefit from

communal living (e.g. Forbes 1989), or from settling among adult conspecifics (Highsmith 1982, Breen et al. 1985). Some palinurids appear to become more gregarious as they grow (Jernakoff 1990), possibly because they are more vulnerable to predation once they out-grow their algal shelter (Lipcius unpubl.).

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