Occurrence and seasonal variations of spiny lobsters, *Panulirus argus* (Latreille), on the shelf outside Bahía de la Ascensión, México

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The spiny lobster, *Panulirus argus*, is one of the most valuable fishery resources on the Mexican Caribbean coast (Secretaría de Pesca, 1987). Lobsters are caught with traps and tangle nets, as well as by SCUBA diving, only on the shelf around Isla Mujeres and Isla Contoy (Fig. 1A), at significantly greater depths than elsewhere on the coast (Seijo et al. 1991). From Puerto Morelos to Xcalak, where the continental shelf is extremely narrow, lobsters are captured mainly by skin diving in the shallow coral reef and lagoon areas (Lozano-Alvarez et al. 1991a).

In Bahía de la Ascensión (Fig. 1B), the fishery for *P. argus* is based on the use of artificial shelters, called "casitas." Casitas are deployed on the bottom and the lobsters sheltering beneath them are caught by skin-diving fishermen. Both casitas and the fishing method are thoroughly described elsewhere (Lozano-Alvarez et al. 1989, 1991a; Briones et al. in press). Casitas are installed only within the bay, but some fishermen also skin dive for lobsters in the shallow coral reefs adjacent to the bay. No lobster fishing is conducted on the coastal shelf outside the bay deeper than 15 m. Only the tails are used. Tails are graded according to weight, packed in 10-pound (4.65 kg) boxes, and frozen. Fishing regulations include a minimum size limit of 13.5 cm tail length (≈74 mm carapace length, CL), a prohibition on the catching of egg-bearing females, and a closed season from 1 March to 30 June.

In 1985–87, results from a tagging program showed that the spiny lobster population within the bay comprised mostly juveniles and subadults (Lozano-Alvarez et al. 1991a). Growth of lobsters in the bay was fast, and they moved from the bay area towards the coral reefs as they grew. No evidence of reproductive activity in bay lobsters was found (Lozano-Alvarez et al. 1991a). Size of onset of sexual maturity is ≈80 mm CL, but females do not become fully mature until approximately 90 mm CL (Fonseca, 1990). This raised the hypothesis of the existence of the reproductive segment of the population on the shelf outside the coral reef, at greater, currently unfished depths. Lozano-Alvarez et al. (1991a) stressed the need to test this hypothesis for future management plans.

In this paper, we present evidence of the occurrence of adult reproductive *P. argus* on the continental shelf outside Bahía de la Ascensión, and discuss seasonal variations in abundance and some biological aspects of this segment of the population, as well as its potential importance as a refugium in space. The fisheries aspects of the study were published elsewhere (Lozano-Alvarez and Negrete-Soto, 1991).

Methods

Bahía de la Ascensión (Fig. 1B) is a large (≈740 km²) and shallow (<6 m deep) bay, bordered by mangroves and grass swamps. A substantial part of the bottom of the bay is covered with seagrass (mainly *Thalassia testudinum*) and dense aggregations of red and green algae (Briones et al., in press). A coral reef tract exists along its mouth, protecting the inner waters of the bay from wave surge. The bay is a nursery area for *P. argus* (Lozano-Alvarez et al. 1991a).

Fishing operations for spiny lobsters were carried out on the continental shelf outside the coral reef tract (Fig. 1B) during two different seasons, summer (11 July–10 September 1989, six fishings), and winter (14 November 1989–27 February 1990, five fishings). Standard lobster traps of the kind used by fishermen at Isla Mujeres were set. The traps were rectangular, measuring 121 × 91 × 40 cm. The frame, built with 12-mm diameter rod, was covered with plastic coated galvanized wire mesh (5 × 2.5 cm), and an entrance was left on one of the small sides. Traps were baited with cow hide.

A maximum of 39 traps was installed in any fishing operation, in lines parallel to the coral reef. The continental shelf in front of the bay is narrow, not exceeding 4 km from the coast. Complex reefs exist in this area at depths of <10 m and from 30 to 40 m (Jordán-Dahlgren et al., in press). After 40 to 60 m the slope becomes very steep, rapidly reaching depths in excess of 400 m. Echosounding was used to

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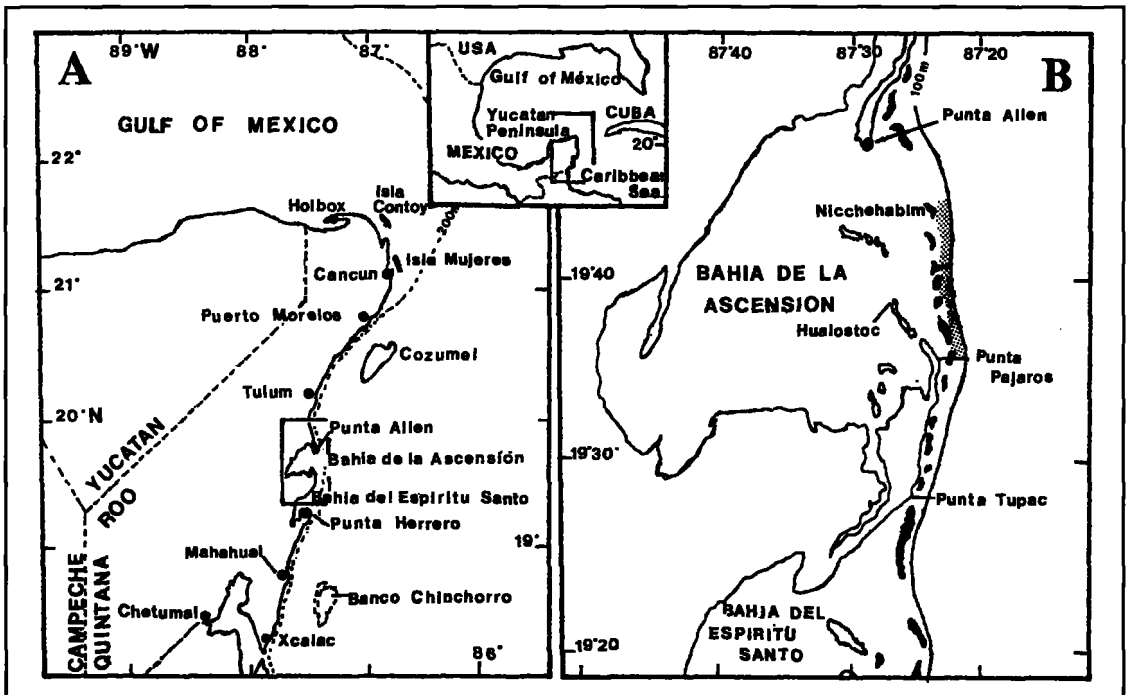

Figure 1

(A) The coast of Quintana Roo, showing the main fishing localities for *Panulirus argus*. (B) Bahía de la Ascensión. Black areas denote coral reef tracts; shaded areas show the sector of the shelf where exploratory fishings with traps were carried out. Casitas for lobster fishing were used coastward from the coral reef.

locate suitable bottoms for installing traps to minimize trap loss. In certain areas where the deep reefs are well developed (e.g., offshore from Punta Allen, Fig. 1B), no suitable bottoms were found. Thus, fishing operations were constrained to a range of depths between 15 and 30 m, from Nicchehabim Reef to Punta Pájaros (Fig. 1B).

Because soak time does not affect catch rate of the traps (Lozano-Alvarez et al., 1991b, Lozano-Alvarez and Negrete-Soto, 1991), we considered the number of lobsters per trap-lift as a gross index of abundance. Carapace length (CL) of lobsters was measured (±0.1 mm) from between the rostral horns to the posterior dorsal edge of the cephalotorax. Carapace state of lobsters was recorded following an arbitrary scale from 1 (newly molted and completely clean) to 4 (heavily fouled), as a relative indicator of the time elapsed since the last molt (Kanciruk and Herrnkind, 1976). Females were considered non-reproductive (NR) when eggs were absent, the carapace was clean, and no traces of spermatophores were found on the sternum. Reproductive females comprised those that presented a new spermatophore attached to the sternum (SP); external eggs attached to the pleopods (EE); or empty egg capsules remaining on the pleopods (EC).

To compare the size distribution and general features of the lobsters found on the shelf outside the bay with those from the bay, two different groups of data were obtained from the bay area. Throughout the fishing season, July 1989–February 1990, monthly data from a number of boxes of lobster tails, categorized by tail weight (TW, g) class, were obtained from a local processing plant. This plant receives all the catch from the bay area. The data were transformed to CL by applying the following equation: Log TW (g)= 2.550 log CL (mm) –2.69298 (Lozano-Alvarez et al., 1989). However, because the size structure of the catch is constrained by the minimum size limit and includes lobsters caught on the fore-reef down to a depth of 15 m, and the catch data gives no information on sex or reproductive activity, we also used data from Lozano-Alvarez et al. (1991a) taken during a tagging operation carried out in May–June 1986, which comprised lobsters found solely beneath casitas throughout the bay, as a less biased estimate of size structure, sex ratio, and carapace state of lobsters in the bay.

Student's *t*-test (Zar, 1984) was used to compare log-transformed data on seasonal abundance of lobsters (number of lobsters per trap-lift), mean sizes between males and females, and mean sizes between shelf and bay lobsters. Sex-ratios were compared with a χ^2 test. Mean sizes of summer and winter lobster catches taken on the shelf outside the bay were compared with a

Table 1

Number of traps lifted, number of lobsters (*Panulirus argus*) caught, and number of lobsters obtained per trap-lift during exploratory fishings with traps (summer 1989 and winter 1989–1990), on the continental shelf outside Bahía de la Ascensión, México.

Date of trap-lifting		No. of traps lifted	No. of lobsters	Lobsters per trap-lift
Summer				
	Jul 19, 1989	36	0	0
	Jul 24	21	16	0.76
	Aug 10	18	23	1.28
	Aug 16	13	5	0.38
	Aug 22	34	14	0.41
	Sep 05	34	9	0.26
	Total summer	156	67	0.43
Winter				
	Nov 23, 1989	39	106	2.72
	Nov 26	30	29	0.97
	Dec 05	39	204	5.23
	Dec 08	13	21	1.62
	Feb 27, 1990	39	35	0.90
	Total winter	160	395	2.47

Table 2

Catch composition of *Panulirus argus* caught on the shelf outside Bahía de la Ascensión during the exploratory fishings with traps (summer 1989 and winter 1989–1990), and of those obtained from beneath casitas in the bay during May–June 1986 (M=males, F=females, CL=carapace length in mm).

	Offshore		
	Summer	Winter	Bay[a]
N	67	395	1402
Male: Female	1.31:1	1.04:1	1.04:1
Mean CL, F.	89.3	78.9	64.4
CL range, F.	55.0–156.9	52.4–117.2	22.0–100.3
Mean CL, M.	111.0	88.7	65.9
CL range, M.	76.5–162.1	56.0–134.0	29.8–113.1

[a] Data from Lozano-Alvarez et al. (1991a).

Table 3

Percentage of *Panulirus argus* in each of the four carapace states, caught on the shelf outside Bahía de la Ascensión during the exploratory fishings with traps (summer 1989 and winter 1989–1990), and of those obtained from beneath casitas in May–June 1986. Carapace states 1–4 represent a range from newly molted and completely clean to heavily fouled.

	Offshore		
Carapace state	Summer (*N*=67)	Winter (*N*=395)	Bay (*N*=1402)
1	35.82	74.43	55.99
2	37.31	18.99	37.44
3	17.91	6.07	6.13
4	8.95	0.50	0.42

non-parametric Mann-Whitney *U*-test with normal approximation (Zar, 1984). The level of significance considered throughout this paper is $P = 0.05$.

Results

Size structure and catch composition of lobsters on the shelf outside the bay

A total of 462 lobsters, 239 (52%) males and 223 (48%) females, were caught during fishing operations outside the bay. The observed sex ratio was not significantly different from the expected value (χ^2=0.554, df=1). Males were significantly larger than females (t=25.06, df=460, P<0.001). Mean CL for males was 92.2 mm (range: 56.0–162.1 mm) and for females was 80.4 mm (range: 52.4–156.9 mm).

Of the total catch obtained outside the bay, only 67 individuals (29 females and 38 males) were caught during the summer, while 395 (194 females and 201 males) were captured in the winter. Abundance of lobsters on the shelf outside the bay, expressed as number of lobsters per trap-lift, was significantly higher

Table 4

Reproductive state by size class of female *Panulirus argus* caught on the shelf outside Bahía de la Ascensión during exploratory fishings with traps (summer 1989 and winter 1989–1990). NR=non-reproductive; SP=new spermatophore on sternum; EE=external eggs on pleopods; EC= empty egg capsules on pleopods. Reproductive females comprise states SP, EE and EC.

Size class (CL, mm)	Summer				Winter			
	NR	SP	EE	EC	NR	SP	EE	EC
<80	8	0	0	0	112	0	0	0
80-85	3	1	1	0	21	0	1	6
85-90	1	1	0	1	27	1	0	4
90-95	5	0	0	1	1	2	0	5
95-100	0	0	0	1	2	0	0	3
100-105	0	0	0	2	1	0	0	2
105-110	0	0	0	1	1	2	0	0
110-115	1	0	1	0	0	0	0	1
>115	0	1	0	0	1	0	0	1
Total	18	3	2	6	166	5	1	22

during the winter than during the summer (t=4.21, df=9, P< 0.01) (Table 1). No significant differences in sex ratio were found between the two seasons (χ^2=1.332, df=1). The mean CL of the whole catch (Z=8.25, df=460, P<0.001), and of both males (Z=5.99, df=237, P< 0.001) and females (Z=4.15, df=222, P<0.001), was significantly greater in summer than in winter (Table 2).

Newly molted lobsters (carapace state 1) were more abundant in winter (74.4%) than in summer (35.8%), whereas lobsters with old, heavily fouled exoskeletons were more evident in summer (8.95%) than in winter (0.5%) (Table 3). During the summer, 11 (38%) of the 29 females were reproductive, while only 28 (14%) of the 194 females caught in winter were in this condition (Table 4). In both seasons, reproductive females measured over 80 mm CL, and most were in stage EC (Table 4). Only 2 females in summer and 1 in winter were actually carrying eggs (EE).

Size structure and catch composition of lobsters from casitas within the bay

The 1,402 lobsters caught beneath the casitas during May–June 1986 comprised 713 (51%) males and 688 (49%) females. No significant difference from unity was found in sex ratio. Mean CL of males (65.9 mm) was significantly larger (t=2.50, df= 1000, P<0.01) than that of females (64.4 mm) (Table 2, data from Lozano-Alvarez et al., 1991a). Most of the lobsters within the bay were in carapace states 1 and 2, i.e., recently molted (Table 3). Only five of the 688 females from within the bay were reproductive (stage EC), but these were among the largest in size (87.0–100.3 mm CL), and were found in sites close to the reef (Lozano-Alvarez et al. 1991a).

Comparison of size distribution between the shelf and bay segments of the population

Figure 2 shows the size distribution of a) the sample taken from casitas within the bay (modified from Lozano-Alvarez et al. 1991, a and b) the total sample taken on the shelf outside the bay. Both males and females were significantly larger on the shelf than in the bay (t=25.88, df=948, P<0.001 for males, and t=18.47, df=917, P<0.001 for females), but females composed a small proportion of shelf lobsters ≥90.0 mm CL (Fig. 2B).

Size structure of lobsters in the commercial catch from the bay and adjacent shallow reefs

Table 5 shows the monthly size distribution of the catch taken by the fishermen. Peak catches occurred in the 69.3–76.3 mm CL size class (which includes the minimum legal size) throughout the fishing season, except in July, where the peak was located in the 76.3–82.4 mm CL class. Lobsters ≥102.2 mm CL probably represented the catch from the adjacent shallow reefs, and represented a small proportion of the catch during most of the fishing season.

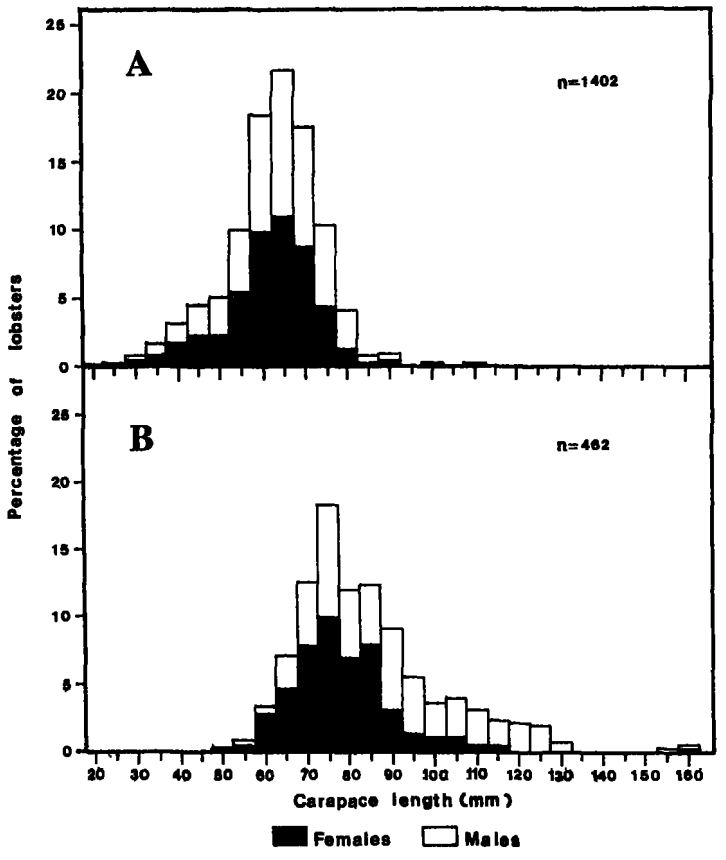

Figure 2

Size-frequency distribution of male and female *Panulirus argus* caught (**A**) beneath casitas within Bahía de la Ascensión (modified from Lozano et al. 1991a), and (**B**) in traps on the continental shelf outside the bay.

Discussion

The occurrence of a reproductive segment of the population of *Panulirus argus* on the shelf outside Bahía de la Ascensión has been documented in this study. The large sizes of lobsters and the evidence of mating and spawning activity on the continental shelf indicate that reproduction takes place in this deeper, unfished habitat, as opposed to the smaller sized, non-reproductive segment of the population within the bay.

Munro (1974) suggested that in coralline areas it is unlikely that the amount of shelter would be a limiting factor for spiny lobsters, but that this might be important in shelf areas with sparse coral cover. The deep and complex reef formations on the shelf outside Bahía de la Ascensión (Jordán-Dahlgren et al., in press) likely offer abundant natural shelters for *P. argus*. Lobsters are attracted to traps for refuge rather than for food (Heatwole et al., 1988), and traps apparently fail to adequately sample resident individuals (Herrnkind, 1980). Thus, the poor catches obtained during our summer fishings probably reflected the occupation of the available natural shelters by resident adult lobsters. The resident nature of these lobsters seems to be further supported by the large proportion of reproductive females and the high incidence of lobsters with fouled carapaces. The existence of resi-

Table 5

Monthly size-frequency distribution of the commercial catch (July 1989–March 1990) of *Panulirus argus* in Bahia de la Ascension, obtained by converting tail weight (TW, g) to carapace length (CL, mm)*.

Commercial category (TW, g)	Size range (CL,mm)	Number of lobsters							
		Jul	Aug	Sep	Oct	Nov	Dec	Jan	Feb
60–100	56.7–69.3	1,484	848	636	1,274	636	424	0	371
100–128	69.3–76.3	17,720	6,680	5,240	4,640	3,200	2,680	2,401	1,600
128–156	76.3–82.4	18,464	5,408	3,680	3,456	2,144	1,760	2,240	1,184
156–185	82.4–88.1	12,717	3,672	2,592	2,241	1,431	1,134	540	621
185–213	88.1–93.2	6,785	2,461	1,656	1,472	897	690	690	391
213–241	93.2–97.8	3,480	1,460	960	880	560	420	402	240
241–270	97.8–102.2	1,692	900	612	468	306	342	180	162
270–298	102.2–106.3	944	432	352	288	160	240	0	128
298–340	106.3–111.9	810	480	285	255	150	180	0	105
340–397	111.9–118.9	572	338	195	195	117	156	130	91
≥397	≥118.9	486	348	191	110	81	171	190	91
Total		65,154	23,027	16,399	15,279	9,682	8,197	6,773	4,984

* Log TW = 2.55 Log CL –2.69298 (Lozano-Alvarez et al., 1989).

dent populations of *P. argus* has been suggested in the Bahamas (Kanciruk and Herrnkind, 1978; Herrnkind and Lipcius, 1989) and the Dry Tortugas (Davis, 1974).

In contrast, the greater abundance of lobsters on the shelf during the winter, in addition to their smaller mean size and recently molted carapaces, indicates a recent recruitment of subadult lobsters to the deep habitat. The recruits likely originated in the bay, from where they exited in pulses, as suggested by the large number of lobsters caught in two fishings (Table 1). These two fishings were conducted immediately after the passage of two severe cold fronts. Offshore movements of *P. argus* associated with cold fronts have been documented in other parts of the Caribbean and Florida (Herrnkind, 1980). Moreover, catches increase notably in winter in the deep fishery off Isla Mujeres, whereas catches from more shallow areas, such as Bahía de la Ascensión and Banco Chinchorro (Fig. 1A) decline at that time of year (Lozano-Alvarez, 1992). However, lobsters moving along the coast (Davis, 1979; Gregory and Labisky, 1986; Fonteles-Filho and Corréa-Ivo, 1980; Herrnkind, 1980) could also account for the greater abundance found on the shelf. Some lobsters tagged in Bahía de la Ascensión were recovered at locations several kilometers to the north and south of the bay (Lozano-Alvarez et al. 1991a). The extent of these movements along the offshore depth contours remains unknown, and warrants further investigation.

In contrast to the sex-ratio in our shelf samples, females outnumbered males in offshore *P. argus* populations in Florida (Davis, 1974; Lyons et al., 1981; Hunt et al., 1991[1]). Although in the Mexican Caribbean the reproductive season spans from March to November, with significant peaks in August–September (Fuentes-Castellanos, 1988), fully mature females, particularly those bearing eggs, were very scarce in our shelf samples. However, considerable evidence exists suggesting that traps fail to sample gravid females in several species of spiny lobsters (Herrnkind, 1980). We believe that gravid females were underestimated in our shelf samples owing to the availability of natural shelter.

The distribution of lobsters in and outside Bahía de la Ascensión seems to conform to the known size-related distribution of *P. argus*, that is to say juveniles inhabite shallow habitats (lagoons, bays) and adults dwelling on deeper reef habitats. However, some large adult lobsters were found in the bay and shallow adjacent reefs (Fig. 2A, Table 5). This fact suggests that some adult lobsters return to inshore habitats after their ontogenetic migration to deeper habitats. Inshore movements of large *P. argus* have been documented in Antigua and Barbuda (Peacock, 1974), Brazil (Fonteles-Filho and Corréa-Ivo, 1980) and Florida (Gregory and Labisky, 1986; Hunt et al., 1991). Hunt et al. (1991) suggested that these inshore movements are controlled by changes in behavior associated with reproduction.

The *P. argus* population in Bahía de la Ascensión and adjacent offshore areas is highly dynamic. Fishing pressure on juveniles in the bay and near shallow reefs is heavy (Lozano-Alvarez, 1992), but the closed season is strictly observed, and no lobster fishing is conducted offshore. Developing an alternative trap fishery off Bahía de la Ascensión would be impractical and costly, because of the narrowness of the shelf, the complex morphology of the bottom, the strong currents encountered in the zone, and the small and variable CPUE of legal-sized lobsters obtained (Lozano-Alvarez and Negrete-Soto, 1991). Consequently, the fishery will continue to be focused on the small-sized lobsters in the shallow areas.

Despite heavy fishing in the bay, we found evidence of a winter offshore migration. Lozano-Alvarez (1992) estimated a high emigration rate from the bay throughout the year, so other offshore recruitment pulses may occur at other times of the year (e.g., the closed season). Because of their large sizes, the resident females on the shelf outside the bay have high indices of egg productivity (Fonseca, 1990), and spawn more than once in the reproductive season (Lipcius, 1986). Thus, the unfished deep habitat outside the bay may bear importance as a refugium in space (Campbell, 1989; Caddy, 1990) for reproductive lobsters.

Other deep, currently unfished lobster areas were found offshore from Puerto Morelos (Lozano-Alvarez et al., 1991b) and probably exist elsewhere along the coast of Quintana Roo, particularly on the narrow shelf from Puerto Morelos to Xcalak (see Fig. 1A), and in many other areas of the Caribbean as well (e.g. Cuba, González et al., 1990). Their existence might serve to mitigate, through the production of larvae, the pressure exerted on more heavily fished stocks. We propose that the deep habitats on the shelf outside Bahía de la Ascensión should be left undisturbed as a nucleus of protected spawning stock, regardless of the unknown final destination of the larvae. We similarly encourage the protection of other deep, currently unfished areas throughout the Caribbean, as a means to preserve groups of reproductive lobsters that contribute larvae to the regional pool.

[1] Hunt, J. H., T. R. Matthews, D. Forcucci, B. S. Hedin, and R. D. Bertelsen. 1991. Management implications of trends in the population dynamics of the Caribbean spiny lobster, *Panulirus argus*, at Looe Key National Marine Sanctuary. Final Rep., NOAA Office of Ocean and Coastal Resource Management, Sanctuary Programs Div., Contract 50-DGNC-6-00093, 81 p.

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