Abstract. - In Bahía de la Ascensión, México, the fishery for Panulirus argus is based on artificial shelters called "casitas." Highest catchper-unit-effort (kg tails/boat·day) in the fishery occurs each year immediately after the opening of the fishing season, and declines sharply over the next months. This trend probably reflects combined effects of natural mortality, fishing mortality, and emigration of lobsters from the bay.

In 1985, 3470 tagged lobsters were released during the closed season, and 849 (24.5%) were recaptured by fishermen, mainly during the first three months of the following fishing season. In 1986, an additional 1324 tagged lobsters were released, and 407 (30.7%) were subsequently recaptured. Growth of recaptured lobsters was highly variable, and sexes had different growth rates, that of males being higher. Von Bertalanffy parameters for each sex were calculated using two different techniques: most reasonable estimates were obtained by a maximum likelihood approach. Ninety-nine percent of the recaptured lobsters were caught within the bay, but movements generally tended to be toward the reef in front of the bay. Longest straightline distance moved was 45 km.

The population fished in the bay was composed entirely of juveniles, and we hypothesize that an unfished population of adults exists outside the bay. Testing of this hypothesis would benefit future management plans. In addition, the long-term effects of casitas on the lobster population and on the ecology of the seagrasses and their associated benthic communities need to be understood.

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Fishery Characteristics, Growth, and Movements of the Spiny Lobster *Panulirus argus* in Bahia de la Ascension, Mexico

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Panulirus argus accounts for approximately one-third of México's spiny lobster production of about 2400 t (mean for 1978-87), 80% of which is produced in the state of Quintana Roo (Secretaría de Pesca 1987). The fishery for lobsters in Bahía de la Ascension began in 1965. Initially, traps and skin diving were used, but in 1968 "casitas cubanas" were introduced (Miller 1982). These "casitas" consist of a frame of about $1.8 \times$ 1.2m made of the trunks of a local palm, and a "roof" of the same wood, metal, asbestos or, more recently, ferrocement. Casitas are sunk over seagrass-covered bottom. The fishermen check the casitas by skin diving, and catch the lobsters with a gaff (Lozano et al. 1989). The bottom of the bay suitable for setting casitas has been divided into several parcels of different sizes, alloted to the older fishermen. Miller (1982) suggested that the casitas might increase the fishing pressure on the population and cause overfishing, and Eggleston et al. (1990) propose that casitas provide critical refuge for juvenile lobsters from their predators. The longterm effects of casitas on the lobster population remain to be determined.

Here we report the results of an investigation using tag and recapture methods to study the structure, movements, and growth rates of the spiny lobster population in Bahía de la Ascensión during 1985–87.

Methods

Fishing methods in Quintana Roo

The coast of Quintana Roo can be divided into three areas on the basis of the lobster fisheries (Fig. 1a):

In the northern area, from Holbox to Tulum and especially around Isla Mujeres, the fishery is well developed. Lobsters are caught mainly by traps in depths of 15-60m, and by Scuba and "hookah" diving to depths near 40m. An annual migration of lobsters occurs along the northeastern coast of the Yucatan Peninsula in a southerly direction, at the end of autumn or in winter (Kanciruk and Herrnkind 1978). During this migration, fishermen use lobster bottomnets in areas 2-10m deep. Twelve cooperatives, involving 65% of the 1084 lobster fishermen of the state. operate in the northern area.

In the central area, where Bahía de la Ascensión is located, skin diving and "casitas cubanas" are used. In this area, where three cooperatives



with 21% of the fishermen operate, lobster fishing is limited to a depth of approximately 15m.

In the southern zone, including Chinchorro Bank, three cooperatives involving 14% of the fishermen catch lobsters exclusively by skin diving with a gaff, to a depth of approximately 15 m (Secretaría de Pesca 1987).

Study site

Bahía de la Ascensión (Fig. 1b) is an open, shallow bay (<6m) approximately 740 km^2 in area. Several coral banks follow an ancient shore line along the mouth of the bay (Jordán 1988) and form an interrupted reef. This reef reduces wave surge, and hence the bay has relatively calm waters.

The bay is bordered by mangrove and grass swamps and has several mangrove keys in its central and southern parts. The outer half of the bay is dominated by hard, sandy substrates with extended seagrass areas, whereas the inner half of the bay is shallow (<2m), with mostly soft, unconsolidated sediments.

The fishery

Up to a maximum of 108 lobster fishermen in the area belong to a cooperative named "Pescadores de Vigía Chico," based at Punta Allen. A team that fishes the casitas in an owner's parcel during the fishing season consists of two or three fishermen (the parcel owner and one or two assistants). The number of casitas per parcel varies, and some owners claim to have more than 1000. The total number of casitas in the entire fishing ground of the cooperative was estimated at approximately 20,000, based on interviews of all fishermen in the cooperative. The fishermen catch lobsters mainly in the outer half of the bay, where seagrass is more abundant. There are no parcels in the inner half because the bottom is not suitable for casitas and the water is usually too turbid for diving. Regulations for this fishery include a closed season from 16 March to 15 July, a minimum size limit of 135mm tail length (\approx 74mm carapace length), and a prohibition on the catching of egg-bearing females. Only the tails are utilized. Tails are graded according to weight, packed in 10-pound (4.650kg) boxes, and frozen.

Detailed data on monthly production (in boxes) of the cooperative during the 1985–86 fishing season were obtained from the processing plant. The relationship between tail weight (TW, in g) and carapace length (CL, in mm) was estimated by linear regression expressed as a power equation,

TW (g) = 0.00203 CL (mm)^{2.5503}

where N = 98, $r^2 = 0.98$, CL range = 44.7-137.9 mm.

Data on catch in kg/tail weight of each fishing team were available since 1981 and converted to catch-perunit-effort (CPUE, catch/boat \cdot day). A Leslie analysis (Leslie and Davis 1939) was applied to the CPUE data to estimate the fishing mortality (F).

Tagging

Lobsters were tagged in Bahía de la Ascensión during 16 April-14 May 1985, and 18 May-30 June 1986, i.e., during the closed season. The area of the bay where casitas are distributed was divided into six sampling zones (Fig. 1b). Lobsters were tagged in all zones during 1985, and in zones II-VI in 1986. Chittleborough's (1974) western rock lobster tags were used. Only animals \geq 44 mm CL were tagged in order to reduce incidental mortality which might occur on smaller animals (Chittleborough 1974). Tags were inserted into the dorsolateral extensor muscle between the cephalothorax and first abdominal segment. After tagging, the lobsters were immediately released where they had been caught. Underwater observations revealed that after a few minutes, the tagged lobsters returned under the same casita.

Tag number, date, release location, sex, reproductive state, and CL (± 0.1 mm measured from between the rostral horns to the posterior dorsal edge of the carapace) were recorded. Fishermen were requested to keep the head of a recaptured lobster with its tag so the CL could be measured, and to provide the recapture date and location. The tagging program was advertised widely, and a reward was offered in the form of a lottery to encourage tag returns.

Analyses of growth data

The analysis of growth using capture-recapture data was performed using Fabens' method (1965), and a technique developed by M. Palmer (CSIRO Div. Math. Stat., Floreat Park, W.A. 6014, Australia). This technique assumes an individual lobster grows exponentially with time:

$$y = a (1 - e^{bt}) + E$$

where y = CL (mm), a = asymptotic CL (mm), b = agrowth coefficient, t = time, and E = residuals. A mean value of 6mm CL obtained from 50 settling pueruli was introduced as a starting size (zero age) into the model.

Parameters for the model, including variability of individual growth, were estimated using a multivariate Gaussian distribution. The residuals around an individual's curve (E) were assumed to be independent Gaussian normal with constant variance. The likelihood estimate, assuming that individual coefficients are known for an individual, was

$$L_i = p (y | a, b) p (a, b)$$

where $L_i = initial$ length, and p(.|.) denotes a probability distribution.

Since the individual animal's coefficients were unknown, we consider them as "nuisance" parameters and integrate them out of the likelihood, giving

$$l_i = \int_{-\infty}^{\infty} p(y \mid a, b) p(a, b) dadb$$

where l_i is the likelihood for the ith individual. Then the product of the individual likelihood must be maximized to find the estimates of the population parameters. A convenient algorithm to use in this case is the EM algorithm (Dempster et al. 1977). Details of its application in this context are in Laird et al. (1987), Palmer (1986), and Palmer et al. (1988).

Although the time between subsequent captures was known, the age at first capture was unknown. A probability distribution for this unknown parameter was also assumed, but now the initial time is treated as "missing" and is removed from the likelihood by integrating it out. The likelihood for the ith animal is now of the form

$$l_i = \int_0^\infty \int_{-\infty}^\infty p(y \mid a, b, t_1) p(a, b) \, da \, db \, dt_1.$$

Maximum likelihood is used to estimate both the growth parameters and the distribution of initial ages. The method of constructing and maximizing the likelihood is described in Palmer et al. (1988).

Mean weekly growth rates (Hunt and Lyons 1986) of recaptured lobsters were analysed to determine if there were significant changes in growth rate along their size range. la Ascensión, obtained by converting tail weight (g) to carapace length (mm).

Results

Commercial catch and size composition

The total catch of lobster tails in Bahía de la Ascensión for 1985-86 was 42.5t, and for 1986-87, 63.0t. The size composition of the commercial catch for July 1985-February 1986 is shown in Figure 2. Data for March were insufficient and not included. There was a mode around the minimum legal size throughout the fishing season, except in July.

The CPUE (catch/boat · day) data trends were similar each year (Fig. 3). The highest CPUE occurred during 16 July-15 August, i.e., immediately after the opening of the fishing season, followed by a sharp decline over the next few months. This trend probably reflected both fishing and natural mortality, as well as emigration.

The values of F (fishing mortality), between 1.25 and 2.80, derived using a Leslie analysis (Leslie and Davis 1939) were highly influenced by the July data, which were the annual peaks (Fig. 3), implying a different F for that month. Therefore, the results of the analysis were biased and could not be considered a good estimate of mortality.

Tagging results

Of the total 3893 lobsters caught in 1985, 3470 were large enough to be tagged (Fig. 4a). The male:female ratio of the captured population was 1.14:1, and that of the tagged population was 1.13:1. Of the total 1403 lobsters caught during 1986, 1324 were tagged (Fig. 4b). The male:female ratios of both the captured and tagged populations were 1.04:1. The size range of both sexes was similar for both years.

A total of 849 tagged lobsters were recaptured during the 1985-86 fishing season (24.5% of total tagged in 1985). None of the animals tagged in 1985 were recaptured during the 1986 tagging period. However, four lobsters tagged in 1985 were recaptured during the 1986-87 fishing season. The male:female ratio of recaptured animals was 1.14:1. Lobsters were recaptured in all sampling zones in the bay, as well as at some localities outside of the bay.

A total of 407 lobsters were recaptured during the 1986-87 fishing season (30.7% of total tagged in 1986); the male:female ratio was 1.08:1. In this season, no lobsters were recaptured outside the cooperative's fishing grounds.

In both fishing seasons, nearly all the recoveries occurred during the first three months of the season (e.g., Fig. 5).

Population structure

The mean CL (61.4mm, range 10.2-142.4mm) of lobsters caught in the Bay during 1985 was significantly smaller (z test, Hoel 1976; z = 10.4, P < 0.05) than that of lobsters caught during 1986 (65.2mm,







range 22.0 - 113.1 mm). However, the tagging operation in 1985 occurred one full month earlier than in 1986.

The means of CL of lobsters caught in each of the six sampling zones during 1985 and 1986 (Figs. 6, 7) were significantly different (P < 0.05, approximate test of equality of means when the variances are heterogeneous; Sokal and Rohlf 1981, Box 13.2). An unplanned comparison among pairs of means (Sokal and Rohlf 1981) shows three groups of mean sizes in each year (Table 1). This result implies that the distribution of lobsters by size in the bay is not random. Smaller lobsters occupied the more interior of the six sampling zones (zones II, III, and IV), and larger lobsters occupied zones closer to the reef (zones I, V, and VI).



Growth and recruitment

Of the 849 lobsters recaptured during 1985–86 and the 407 recaptured during 1986–87, only 372 and 268, respectively, were returned with accurate CL information. All but two showed growth between tagging and recapture.

During the first three months of the 1985–86 season, the modal CL of recaptured males increased 10mm. Growth of individuals was highly variable (Fig. 8) and in some cases indicates more than one molt occurred. For females (data not illustrated), the mode increased 8mm.

Fabens' method (1965) for estimating growth parameters was used for both sexes and both years separately (Table 2a). The estimates of asymptotic length and the growth coefficient k by this method show great variability.

On the other hand, the EM algorithm needs some initial estimates before it can begin iterating, and the Fabens estimates were used for this. A set of data for males and females for each year was thus obtained (Table 2b). Combining the data over both years, for each sex, did not lead to a significant increase in the



Figure 6

Size-frequency distribution of *Panulirus* argus caught in each sampling zone during the 1985 tagging operation in Bahía de la Ascensión.

log-likelihood ratio, indicating that it was valid to pool the data over the two years, i.e., there was no difference in growth between years. However, combining the male and female data led to a significant increase in the log-likelihood ratio, indicating different growth rates for males and females. Males grew faster and larger than females, similar to other panulirid species (Kanciruk 1980). The final set of data is shown in Table 2c. Estimated mean growth curves for males and females, combined for both years, are shown in Figure 9.

The algorithm also predicts the age at which each animal was initially caught. The estimated non-parametric density function of age at first capture for the 1985 and 1986 data showed a clear mode around 525 days from settlement.

Growth of the lobsters in Bahía de la Ascensión was rapid. Males and females enter the fishery at 74 mm CL, 1.65 and 1.7 years, respectively, after settling. Allowing for a six-month larval period (Lewis 1951), males and females enter the fishery at approximately 2.15 and 2.2 years of age, respectively.

The analysis of mean weekly growth rates (Hunt and Lyons 1986) combining the 1985 and 1986 data (not illustrated) did not show any points of inflection, suggesting that there is no marked decrease in the growth rate of the lobsters in the bay.

Movements

Most of the recaptured lobsters were caught within the boundaries of the cooperative's fishing ground. Lobsters that

Figure 7

Size-frequency distribution of *Panulirus* argus caught in sampling zones II, III, IV, and VI during the 1986 tagging operation in Bahía de la Ascensión.

Table 1

Mean carapace length (\bar{x} CL mm) of *Panulirus argus* caught in each of the six sampling zones. In 1986, no sampling was performed in zone I, and only five individuals were obtained in zone V. Mean CL's followed by corresponding letter in row are not significantly different (P > 0.05). Means with different letter in row are significantly different (P < 0.05), using test for unplanned comparisons among pairs of means.

	Zone					
	IV	III	II	VI	v	I
(a) 1985	60.14 ^a	60.89ª	62.34ª	67.63 ^b	70.63 ^b	78.73
	Zone					
	IV	II	III	VI		
(b) 1986	63.34ª	64.85 ^{ab}	66.41 ^b	78.14°		



Figure 8

(a) Size at initial capture of 148 male *Panulirus* argus tagged at Bahía de la Ascensión, and (b) size of same males at recapture during first three months of 1985-86 fishing season. Shadings denote individual lobters and show carapace length increment by selected size cohorts, to emphasize variability in growth. It is possible that more than one molt is involved in some cases.

Table 2

Estimates of mean growth parameters for *Panulirus argus* form. $\hat{\Gamma}$ = dispersion matrix of the coefficients of the growth curve; $\hat{\sigma}^2$ = variability around an individual curve.

Ses	Year	L _∞	k
(a) Fabens'	(1965) app	proach	
Males	1985	101.898	-0.0059
Males	1986	113.815	-0.0049
Females	1985	85.970	-0.0109
Females	1986	148.284	-0.0018
(b) Maximu	ım likeliho	od approach	
(Palmer	• et al. 198	8)	
Males	1985	255.464	-0.00057
Males	1985	261.501	-0.00054
Females	1985	222.807	-0.00065
Females	1986	218.149	-0.00067
		$\hat{\Gamma}$ = (10.295	-0.00004
		$\Gamma = \left(\begin{array}{c} 10.295 \\ \end{array} \right)$	2.16×10^{-10}
		$\hat{\sigma}^2 = 25.426$	
(c) Maximu	m likeliho	od approach	
(1985 aı	nd 1986 con	mbined)	
Males		257.204	-0.00056
Females		215.605	-0.00068
		~ / 10.349	-0.000047
			2.19×10^{-10}
		$\hat{\sigma}^2 = 25.421$	
		5 - 20.421	



dispersed from their zones of initial capture tended to move toward and along the reef in both years (Figs. 10, 11). As an example, of the 79 recaptured lobsters that had been tagged in zone III in 1985 (total number tagged in zone III = 581), 29 remained in zone III



and 42 moved to areas nearer or at the outer reef (Fig. 10b). However, because no lobster fishing was conducted in the inner half of the bay, no data have been obtained to indicate the possible movement of lobsters to that area.

In the 1985-86 fishing season, eleven lobsters were recaptured outside of the bay by fishermen of other cooperatives. Of these, ten had traveled south, while only one had gone north (Fig. 10). The longest straightline distance traveled by an animal was 45km. All the recaptured lobsters that were tagged in 1986 were caught in the fishing grounds of the cooperative "Pescadores de Vigía Chico." The longest distance traveled by any of these was 23km (Fig. 11b). No animals were caught north of Boca Paila or south of Punta Herrero (Fig. 10). However, fishing effort immediately outside the bay was restricted to skin diving on the reef to depths of about 15m, so any lobsters that moved beyond that depth would not be recaptured.

Reproduction

During the 1985 tagging program, only four individuals (67.2, 82.5, 83.7, and 116.8 mm CL) of 1819 females had spermatophores attached, and only one individual (76.0 mm CL) carried eggs. In the 1986 program, five individuals (87.0, 90.2, 94.2, 94.9, and 100.3 mm CL)

of 689 females were found with remains of empty egg capsules and/or eroded spermatophores. In both years, all of the females that showed signs of reproductive activity were caught on the edge of the reef (zones II and V, Fig. 1b). No other evidence of reproductive activity was observed.

Discussion

A decline of CPUE from the beginning until the end of the fishing season has been reported for other Panulirus argus fisheries (Warner et al. 1977, Lyons et al. 1981). However, in the fishery of Bahía de la Ascensión, the decline from the first month of the season to the second is sharp. Eggleston et al. (1990) suggest that casitas enhance survivorship of juvenile lobsters by protecting them from their predators, hence increasing lobster production. Thus, during the closed season, in the absence of fishing mortality, it is possible that the aggregation effect of casitas on juvenile lobsters, in conjunction with recruitment by rapid growth, result in the catch from a casita being greater during the first month of the season than during the remainder of the season.

The high level of recaptures during both the 1985–86 and 1986–87 seasons suggests a high level of fishing mortality on the population in Bahía de la Ascensión. The failure to recapture any of the animals tagged in 1985 during the tagging program in 1986, and the fact that only four were recaptured during the fishing season in 1986–87, may reflect tag loss, high natural mortality, or a strong emigration from the bay. The latter is supported by the movements of the recaptured lobsters.

We could not separate fishing mortality from natural mortality because there appeared to be both recruitment by growth of small lobsters throughout the season as well as immigration onto the casitas from other areas. This is sustained by the monthly size composition of the catch by the fishery (Fig. 2). Those catches showed a nearly constant size distribution, with a mode near the minimum size limit, indicating recruitment by growth to the fishery throughout the fishing season.



The estimates of the growth parameters by the Fabens' method showed great variability (Table 2a), which could be interpreted in two ways: (1) Lobster growth differed greatly interanually, or (2) the procedure yielded unreliable estimates. Palmer et al. (1988) suggested that the Fabens method does not explicitly model individual variability in growth (e.g., Fig. 8), and that it produces inconsistent estimates of the asymptote of growth.

Alternatively, the maximum likelihood estimates of the mean curves did not show great variability, so both years could be pooled to obtain a final set of parameters. The reasonableness of the estimated parameters was further confirmed by the fact that *P. argus* can attain sizes much larger than the asymptotic sizes estimated from the Fabens method (Sutcliffe 1957, Munro 1974, Olsen and Koblic 1975, Farrugio 1975). However, the tagged lobsters were mostly juveniles and young adults as further demonstrated by the lack of an inflection point in their mean weekly growth rate. Thus, the estimated parameters may reflect growth rates of immature lobsters only, and those of reproductive adults could change the last part of the curve (Fig. 9).

Lyons et al. (1981), utilizing a method that involved mean growth rates obtained from several authors. estimated an age of slightly more than two years after settlement as postlarvae for P. argus measuring 76mm CL, allowing for a nine-month larval period. With our maximum likelihood results, and considering the same nine-month larval period, the estimated age for a 76mm CL lobster would be 2.5 years. Munro (1974) produced a growth curve for P. argus based on data from 156 lobsters tagged and recaptured in Florida and Belize. His estimated age of one year after settling as postlarvae for lobsters measuring 45mm CL agrees closely with the estimate obtained in the present study by the maximum likelihood approach. Peacock (1974) tentatively estimated an age of one year for 50 mm CL P. argus, as did Eldred et al. (1972) and Witham et al. (1968).

Therefore, the maximum likelihood approach utilized in this paper seems to have provided a useful set of growth parameters for juvenile and young adult P. argus, with the additional advantage of separating growth data between males and females.

The few signs of reproductive activity in female lobsters near the reef, in conjunction with small carapace length, indicated that the lobster population in Bahía de la Ascensión was probably composed mainly of juveniles. Lyons et al. (1981) found little evidence of mating activity of *P. argus* in the shallow Florida Keys, and they stressed that almost 90% of the spawning occurred at their reef and deep-water stations. Peacock (1974), Davis (1975), and Kanciruk and Herrnkind (1976) also reported an absence of reproductive activity in shallow bank or lagoon areas.

The movements demonstrated by the tagging program indicate a displacement of lobsters from shallows toward deeper habitats offshore. This was also supported by the analysis of the size composition by zones (Figs. 7, 8; Table 1), which indicated that the lobsters were smaller in the innermost sampling zones compared with those caught near or on the reef. Buesa (1970) and Cruz et al. (1986) suggested that juvenile *P. argus* in Cuba live in protected areas with seagrass beds and move towards the outer reefs as they grow. Other authors that mention similar movements for juvenile *P. argus* are Peacock (1974) in Barbuda, Olsen and Koblic (1975) in the U.S. Virgin Islands, Warner et al. (1977), Davis (1979), and Lyons et al. (1981) in Florida.

Although northern and southern movements were made by lobsters which left the bay, southerly movements predominated. In a three-year study of movements of P. argus in Biscavne Bay, Florida, Davis (1979) found southerly movements of tagged lobsters during the first year, northerly movements in the second year, and both northerly and southerly displacements during the third. He concluded that juvenile lobsters from Biscavne Bay are recruited into virtually the entire Florida fishery. The extent of the movements made through deeper water by the lobsters tagged in Bahía de la Ascensión-and their final destination-is still unknown, because from Tulum to Mahahual (Fig. 1a) lobsters are fished only in the bays and on the shallow parts of the reef. A winter migration, similar to that which occurs at the northeastern end of the Yucatán Península (Kanciruk and Herrnkind 1978), may take place in deeper waters outside the coral reef that runs across the front of the bay.

Small size, rapid growth, movements toward the reef areas, and lack of reproductive activity all serve as evidence that the population of lobsters in Bahía de la Ascensión is composed of juveniles. We hypothesize the existence of a population composed of reproductive adults off the coral banks of Bahía de la Ascensión, an area that is not currently being fished.

The existence of adult stocks outside of the bay and the output of lobsters from the bay into offshore deeper areas are issues that need to be assessed for future management plans. In addition, although casitas may provide critical refuge for juvenile lobsters from their natural predators (Eggleston et al. 1990), the long-term effects of the casitas on the lobster populations, as well as on the benthic communities associated with seagrasses and on the stability and structure of the seagrass beds themselves, remain to be determined through future field studies.

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