

Distribution patterns of spiny lobster (*Panulirus argus*) at Alacranes reef, Yucatan: Spatial analysis and inference of preferential habitat

Veronica Rios-Lara^{a,b,*}, Silvia Salas^b, Bello-Pineda Javier^c, Peniche Irene- Ayora^d

^a Centro de Investigaciones Pesqueras Yucalpeten., I.N.P., Mexico

^b Centro de Investigación y Estudios Avanzados-Mérida, Mexico

^c Universidad Veracruzana, Mexico

^d Facultad de Matemáticas, Universidad Autónoma de Yucatán, Mexico

Abstract

The present study aimed to identify the preferential habitats of spiny lobster (*Panulirus argus*) and associate its density, abundance and biomass to each type of habitat, enable hence prediction of the spatial distribution of the crustacean in the whole area. It also attempted to identify the associated size population structure at different areas of the reef. To do so, a study was undertaken at the National Park “Arrecife Alacranes” in Yucatan, Mexico. First, with the use of geographical information systems (GIS) tools, a thematic map of submerged habitats (bottom type) of the reef area was overlaid to lobster distribution data obtained from 157 diving transects in order to estimate lobster density, abundance and biomass by bottom type. Uncertainty of the analyzed variables was incorporated through Monte Carlo simulation. In addition, the spatial structure of lobster habitat was predicted by using geostatistical tools (kriging) to estimate lobster density from 420 stations sampled by diving in the same reef. Population size structure was obtained from catch data obtained from fishers’ landings and based on records of small individual juveniles collected by fishers. The results show a patchy distribution of lobsters throughout the entire reef, with higher densities predicted in areas of higher habitat complexity. This study supports thus the thesis that structural complexity of habitat has an influence on lobster spatial distribution and emphasizes the relevance of undertaking spatial analysis to study lobster populations.

© 2007 Elsevier B.V. All rights reserved.

Keywords: Alacranes reef; GIS; Habitat; Kriging; *Panulirus argus*; Spatial distribution; Yucatán

1. Introduction

Understanding spatial distribution patterns of marine populations is considered of high importance in the assessment of fishing resources and in defining management schemes of commercially exploited species (Orensanz and Jamieson, 1998; Ehrhardt, 2005; Cochrane et al., 2004). In this context, spatial analysis and its application to fisheries assessment become even more relevant for the understanding of the population dynamics of many species that do not fit the classic models developed for traditional stock assessment (Hilborn, 1986; Caddy and Defeo, 2003; Walters and Martell, 2004).

It has been recognized that spatial distribution and abundance of important fisheries resources depend on the processes that are inherent to their life cycle, as well as on the spatial structure of

the habitats they prefer (Cobb and Wahle, 1994; Polovina et al., 1994; Acosta, 1999; Butler et al., 2006). Consequently, knowledge of these processes can help in predicting more accurately distribution patterns of these resources and defining more viable management schemes for these fisheries.

Given the diverse habitat requirements that lobsters show throughout their life cycles (habitat selection changes during ontogeny), they have been identified among the resources highly dependent on shelter availability (Herrera and Ibarzábal, 1995; Salas et al., 1996; Arce et al., 1997; Davidson et al., 2002; Childress and Jury, 2006). It has also been observed that lobsters seek refuge during the day and tend to search for food at night (Childress and Jury, 2006 and references there in). These patterns of behaviour have also been recognized by fishers and taken into consideration when fishing. In the present study, we assume that the presence of lobsters in their refuges during the day is a good indicator of habitat selection (preferential habitat).

Arrecife Alacranes, was selected for the study, given the importance of this area for lobster fishing’ industry, fisheries managers, and given its condition as protected area, been hence

* Corresponding author at: A.P. 73 Progreso, Yucatan, Mexico.

Tel.: +52 969 9354028; fax: +52 969 9354028.

E-mail address: g.veronicar@yahoo.com (V. Rios-Lara).

one of the less impacted areas by human activities in the region up to now. It was expected that if the identified sites can be spatially located, this information could help characterize the most common habitats for lobster in the sampled area and hence increase knowledge about lobster distribution patterns according to different types of habitats, besides, it serves as important input for the management plan for this area.

It is important to stress that spatial variation of habitat for different organisms (as with many other processes observed in nature) relies on correlated data—i.e., spatial arrangements and phenomena observed in neighboring areas are more similar than those located at further distance; and that spatial dependence is a common phenomenon in environmental studies (Maravelias et al., 1996). Geostatistical techniques, such as kriging, can help analyze regionalized or spatially correlated variables (Keith, 1988). Kriging is considered a powerful tool that allows an estimation of the spatial distribution of lobster habitats, starting from observations of their attributes taken in a finite number of places, quantifying spatial correlation, and making predictions of non-sampled places (Cressie, 1989; Pelletier and Parma, 1994). Some geostatistical applications in fisheries have been used to evaluate spatial structure of populations, to estimate biomass and abundance of populations, and identify cohorts in several areas and resources (Maynou et al., 1998; Roa and Tapia, 2000; Petitgas, 2001; Rueda, 2001; Pérez-Castañeda and Defeo, 2004). Lobster density estimates in the region have been reported by several authors using different approaches (Liceaga et al., 1998; Ríos et al., 1998; Bello-Pineda et al., 2005b). However, to our knowledge, an integrated approach that incorporates different sources of information and several techniques for evaluating the spatial structure of the reef and predicting suitable habitat for lobster has not been considered.

In this study two analytical techniques are used for spatial data, in order to determine the distribution and abundance patterns of lobster population and to infer spatial structure of preferential habitat for lobster. Specifically, the research focused on: (a) identifying lobster habitats using a thematic map of bottom types and, through the use of GIS, associating these to the presence of lobsters and estimate density for each bottom type; (b) predicting spatial structure of lobster preferential habitat taking as attribute lobster density; and (c) describing the size structure of lobster population in different areas throughout the reef. In the following, we provide descriptions of the study area and the lobster fishery in the Yucatan. Next, we describe the methods employed and the results of the analysis. Finally, we conclude by discussing the implications of the observed patterns on the dynamics of the population in the region and implications of fishing activities in the area.

2. Study area

The Arrecife Alacranes reef area is one of the largest and most complex coral reef systems in the Gulf of Mexico, contributing about 25% of lobster landings for the Yucatan State in 2005. This reef is located approximately 130 km north of Progreso (a main fishing port in Yucatan), between 22°21'44" and 22°35'12" North and 89°36'30" and 89°48'00" West (Fig. 1).

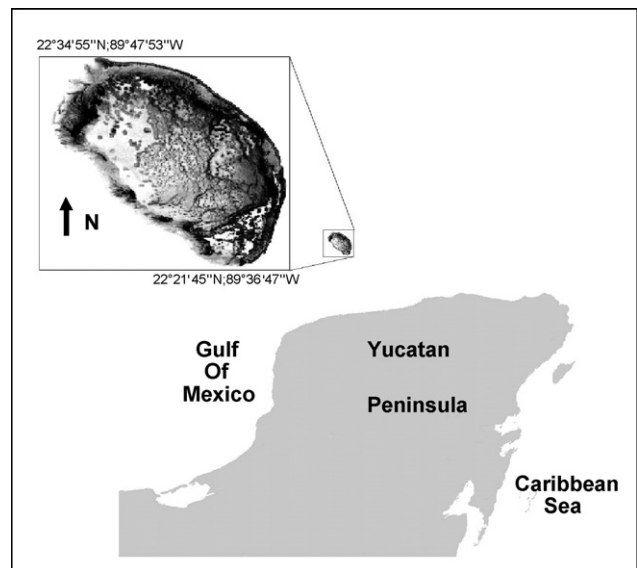


Fig. 1. Location of the National Park Arrecife Alacranes located at the North of the Yucatán Peninsula, México.

The platform reef rises up from 50 m depth. The most conspicuous morphologic features include the reef shelf, the windward barrier, the north reef ridge, the leeward reef ridge, the reef plateau, and six small sandy islands known as Pérez, Pájaros (Bird Island), Chica (Little Island), Muertos (Island of the Dead), Desterrada (Shunned Island) and Desaparecida (Disappeared Island). For more details on the reef features of Alacranes reef see Ardisson et al. (1996) and Bello-Pineda et al. (2005a).

3. The lobster fishery in Yucatan

In the Yucatan Peninsula, the spiny lobster (*P. argus*) contributes high revenues to fishers and it is considered among the most important fisheries in the region. This fishery was initiated informally in the 1950s at Arrecife Alacranes, with the operation of three sailboats of about 13 m in length. Each boat carried three “alijos” (small boats without motor, approximately 3 m long). Formal lobster fishery started towards the end of the 1970s with the creation of the Fish Production Cooperative Associations (FPCA). Today this species is caught mainly near the coastal area and only few boats fish in Arrecife Alacranes. More than 936 fishers organized in 17 fishing cooperatives, plus another 1872 independent people benefit from the capture of the crustacean in the Yucatan State. A total of 25 large boats (between 12 and 19 m long) and 420 small boats (approximately 8 m in length with outboard motors between 40 and 75 HP) comprise the lobster fleet. From those only few have a fishing permit to fish around or within the protected area. Regulatory measures include legal minimum size of 135 mm tail length (TL) which is equivalent to 76 mm carapace length (CL), closed season (from March to June), and prohibition to capture berried females (Salas et al., 2005).

In 1994, Arrecife Alacranes was officially designated as protected areas, allowing access to the area only to 14 large boats,

based on traditional fishing rights. In principle, no more boats are allowed to enter this fishery in the State. Fishing is undertaken using traps around the reef area and by diving within the reef. The boats take about 10 trips during a fishing season (15 days per trip) which goes from the beginning of July to the end of February.

Despite the existence of a management plan for the reef area (Ardisson et al., 1996) and regulatory measures set for the lobster fishery, several unregistered boats have been caught fishing around or in the reef area. Furthermore, there is a concern on the potential impact that this type of fishing may have on the resource in the long term (Salas et al., 2005). The lack of knowledge on the lobster population structure and its distribution patterns in the area have represented limitations for the implementation of viable management policies, especially given the high value of these species and the potential production that many fishers perceive as available in the zone.

4. Methods

4.1. Sources of information

Two main sources of information are used in this study: (a) direct observations of lobsters in the area recorded between 1997 and 2000 by diving transects undertaken in 23 field surveys, and (b) size frequency data obtained from the landings of commercial boats and direct sampling in selected locations within the reef, which were referred by fishers as lobster nursery areas.

Regular and irregular transects were surveyed by diving to record number of lobsters around the reef area. A total of 420 transects of the same size (100 m long and 10 m wide) were surveyed. In addition, surveys of 157 transects of different sizes were also conducted. The sampled area at each of the irregular transects was calculated taking into account the initial and final position of the diver, diving time, the average speed of the diver and the estimated visibility. In this case, data collection was undertaken in areas where fishers operate (diver followed fishers on their regular fishing trips). When the ground was flat, the longitude of transects was calculated through initial and final position of the diver. When transects were not regular, due to the ground complexity, the transect length was calculated taking into account the average speed of the diver (mean speed of 750 m/h) and diving time (between 15 and 30 min). The location in the reef area was registered using a geographical positioning system (GPS). In both cases, the number of lobsters caught was recorded by site.

Size frequency data used to estimate the structure of the population in the reef was estimated sampling animals from commercial catches. Given that in Yucatan, lobsters are landed and sold as tails exclusively, hence length was recorded as tail length (TL) in cm and tail weight (TW) in grams. Afterwards, the records were transformed into total length (TotL) based on the function reported by Zetina et al. (1996) for spiny lobster for the Yucatan region (Eq. (1)).

$$\text{TotL} = 1.91 + 1.39(\text{TL}) \quad (1)$$

A total of 5261 lobsters obtained from the commercial landings were measured during the sampling period as follows: July (540), August (1369), September (575), October (491), November (117), December (626), January (579) and February (964). In order to account for organisms smaller than commercial size (<13.5 cm TL), small lobsters were collected between the end of the fall and the beginning of the winter (the period indicated by fishers when small lobsters are more abundant). A total of 896 small animals were obtained (231 in November, 337 in December and 328 in January) and measured for total length (TotL).

4.2. Lobster density estimates

For the first part of the study, a thematic map of bottom type in Arrecife Alacranes was used for the analysis. The map was obtained through Landsat TM images, aerial photos in black and white, and digitalized aerial video (for details see Bello-Pineda et al., 2005b).

Lobster abundance and density estimates were obtained using geo-referenced data collected during July and August (i.e., in the beginning of the fishing season) from 1997 to 2000. The abundance and density estimates were related to the bottom types depicted in the map. The assumption here was that observations in this period could give the best estimates given that lobsters have been inaccessible to fishers during the closed season (March–June). This condition allows concentration of lobsters in their refuges, thus a major presence of lobsters was expected, as usually by the end of the fishing season the areas have been swept by fishers.

A vector file was created; representing the coordinates of the 157 irregular transects sampled using the “IDRISI” software from GIS (Eastman, 1993). The vector file was then overlaid on top of the thematic map to show the correspondence of each site with the respective bottom type in the map. The characteristics of each bottom type are depicted in Table 1, which covers the depth of different habitats ranging from 1 to 30 m and the area, varying in size between 1 and 90 km².

For the lobster abundance and density estimates for each bottom type, it was necessary to estimate the total area of preferential habitat for lobster in the reef. To do so, information provided by fishers and from literature (for example, Arce et al., 1997; Bello-Pineda et al., 2005a) were compiled. On the whole, lobsters prefer areas that provide refuge, such as hard structures with holes and complex structure like hard coral, coral heads, dead coral, and coral covered with algae. Hence, using the same database employed to generate the map of bottom type, the area corresponding to the lobster preferential habitat was estimated, based on the total area for each habitat type and the proportion of every area for the corresponding benthic element.

As different size quadrants were sampled during the dives performed jointly by fishers and the research team, average density (\hat{D}_1), was estimated for each bottom type using Eq. (2), e.g. based on sampling for quadrants of different size (Seber, 1982; Krebs, 1989). The average density was estimated by dividing the total number of observed lobsters ($\sum y_i$) by the total number

Table 1
Characteristics of the bottom ground at the Alacranes reef

Type	Habitat	Depth (m)	Average coverage (%)	Area (km ²)
1	Seagrass beds	1–3	Macro algae and seagrass associations (80); Seagrass: <i>Thalassia testudinum</i> and <i>Syringodium filiform</i> ; Algae: Chlorophytas, Phaeophitas and Rhodophytas	31.1
2	Patches of hard coral and soft coral	1–3	Coral associations (45); Hard coral (Hexacorals) stony corals: (Branching corals) genus: <i>Acropora</i> , <i>Tubastrea</i> , <i>Porites</i> ; (Massive corals) genus: <i>Montastraea (cavernosa, annularis)</i> , <i>Siderastrea</i> , <i>Solenastrea</i> and <i>Porites</i> ; (Brain corals): genus: <i>Diploria</i> and <i>Meandrina</i> ; Soft coral: (Octocorals): genus: <i>Gorgonia</i>	89.8
3	Coral heads of hard and soft coral	1–3	Sand (73) coral associations (15) (Gravel, pieces of dead corals). Hard coral (Hexacorals) stony corals: (Brain corals): genus: <i>Diploria</i> and <i>Meandrina</i> . Soft coral: (Octocorals): genus: <i>Gorgonia</i>	26.1
4	Patches of hard and soft coral	3–8	Coral associations (40); Hard coral (Hexacorals) stony corals: (Branching corals) genus: <i>Acropora</i> , <i>Tubastrea</i> , <i>Porites</i> , <i>Dendrogyra</i> , <i>Oculina</i> and <i>Madracis</i> ; (Massive corals) <i>Montastraea (cavernosa, annularis)</i> , <i>Siderastrea</i> , <i>Solenastrea</i> ; (Brain corals): genus: <i>Diploria</i> and <i>Meandrina</i> ; (Hydrocorals) <i>Millepora</i> ; Soft coral: (Octocorals): genus: <i>Gorgonia</i>	94.6
5	Bare substrate	1–5	Bare substrate (97); (Gravel, pieces of dead coral)	11.2
6	Patches of hard and soft coral	8–15	Coral associations (45); Hard coral (Hexacorals) stony corals: (Branching corals) genus: <i>Acropora</i> , <i>Tubastrea</i> , <i>Porites</i> ; (Massive corals) genus: <i>Montastraea (cavernosa, annularis)</i> , <i>Siderastrea</i> and <i>Solenastrea</i> ; (Brain corals): genus: <i>Diploria</i> and <i>Meandrina</i> ; Soft coral: (Octocorals): genus: <i>Gorgonia</i> , <i>Eunicea</i> , <i>Plexaura</i> , <i>Pseudoplexaura</i> , <i>Plexaurella</i> , <i>Muricia</i> , <i>Pterogorgia</i> , <i>Pseudopterogorgia</i>	3.1
7	Hard coral and walls	15–25	Coral associations (61); Deep water of the Leeward shelf: Hard coral (Hexacorals) stony corals: (Massive corals) genus: <i>Montastraea (cavernosa, annularis)</i> , <i>Siderastrea</i> ; (Brain corals): genus: <i>Diploria</i> , <i>Meandrina</i> , <i>Manicina</i> ; (leaf, plate and sheet corals) genus: <i>Leptocoris</i> and <i>Agaricia</i> ; (fleshy corals) genus: <i>Mycetophyllia</i> ; Soft coral: (Octocorals): genus: <i>Gorgonia</i>	14.9
8	Bare substrate	8–20	Bare substrate (98); Gravel, pieces of dead coral.	38.6
9	Patches of hard coral	20–30	Coral associations (46); Windward: Hard coral (Hexacorals) stony corals: (Massive corals) genus: <i>Montastraea (cavernosa, annularis)</i> and <i>Siderastrea</i> ; (Brain corals): genus: <i>Diploria</i> and <i>Meandrina</i> . (Leaf, plate and sheet corals) genus: <i>Leptocoris</i> , <i>Agaricia</i> ; (Fleshy corals) genus: <i>Mycetophyllia</i>	12.6
10	Mixed substrate sand/hard coral walls	<1	Coral associations (47); Gravel, pieces of dead coral; Hard coral (Hexacorals) stony corals: (Massive corals) genus: <i>Montastraea (cavernosa, annularis)</i> and <i>Siderastrea</i> ; (Brain corals): genus: <i>Diploria</i> and <i>Meandrina</i>	1.4
11	Bare substrate	5–8	Bare substrate (97); Gravel, pieces of dead coral	3.0
12	Deep water	>30	Information not available	8.1

Source: Modified from Bello-Pineda et al. (2005a). Corals identification review in Humann (1993).

of areas visited ($\sum w_i l_i p_i$)

$$\hat{D}1 = \frac{\sum y_i}{\sum w_i l_i p_i} \quad (2)$$

where w_i is the width of the transect, l_i the length of the transect and p_i is the probability of detecting lobsters. The first element was estimated (as shown in Eq. (3)) considering the

width of the transect reported by the diver w_0 and the appreciation error E_a (with normal distribution, mean w_0 and coefficient of variation = 20%):

$$w_i = w_0 + E_a \quad (3)$$

The length of the transect l_i was obtained according to $l_i = L_0 + E_p$; where L_0 = calculated length from the position

recorded with the GPS in the transect, and E_p = error from 0 to 50 m regarding the initial and final position of the transects with uniform distribution.

Monte Carlo simulation was applied to obtain density estimates (considering a uniform distribution) assuming uncertainty from different sources may affect observations during the diving process. Among those sources we considered: geographic position, transect width, and the probability of detecting lobsters. Regarding the later, detection of animals depends highly on divers' skills, as this species usually are not easily located, but by diving at the opening of the fishing season, detection was assumed in between 80% and 99% favored by colonization of shelters during the close season. It was also assumed that some error could come from diving observations regarding the transect length owing to potential bias on the geographic position of the GPS. Hence, to determine geographic position and transect length, a random error of ± 50 m was considered (Magellan Systems Co.).

The biomass estimate for each bottom type resulting from the product of the total number of organisms in the area of interest (\hat{Y}) and lobster average weight (AW) (Eq. (4)) equals to 0.18 kg. This value was calculated from lobsters captured on Arrecife Alacranes during the opening of the fishing season (July–August) in the same period (1997–2000).

$$B = \hat{Y} \times AW \quad (4)$$

Finally, the total number of organisms in each area was used to estimate lobster average densities and their variances. Ten thousand simulations were run using Visual-Basic as implemented in EXCEL (V5).

4.3. Spatial structure of lobster habitat

In the second part of the analysis the spatial structure of lobster habitat was modeled using geostatistical tools. Lobster density ($\hat{D}2_i$) was considered as the indicator variable of the habitat for each of the 420 regular transects in the sampled sites, defined as $x[Z(x_i)]$, where x represents the latitude and longitude in two spatial dimensions. The density estimator by each site was then defined by Eq. (5):

$$\hat{D}2_i = \frac{n_i}{a_i} \quad (5)$$

where $\hat{D}2_i$ is the density in the sampled area i , n_i is the number of organisms observed in the transect, and a_i is the area surveyed by the diver.

An exploratory analysis was performed on density data (defined as the number of lobsters per ha)—the mean, variance, and probability density function were estimated. Modelling the spatial structure of lobster habitat based on the presence of lobsters in the sites sampled in Arrecife Alacranes was performed through variograms. These diagrams help to define the coefficients of an optimal lineal predictor (Cressie, 1989), so that it can provide an indicator of the nature of space-dependency of lobster density, and indicate an increase or decrease in correlation between data when the lag distance between them changes.

The kriging interpolation method was used to define the coefficients. From Eq. (6), variograms for different directions (0, 45, 90 and 135°) and angles of tolerance were tested in order to find directions of the continuity, maximum and minimum, and to find the lag distance or more appropriate intervals that fit best the variogram

$$\hat{\gamma}(h) = \frac{1}{2} \text{media}[\{z(x) - z(x+h)\}^2] \quad (6)$$

where $z(x)$ and $z(x+h)$ represent real values of lobster density ($\hat{D}2_i$), in separated sites by h (distance lag), such that, for a group of data $z(x_i)$, $i = 1, 2, \dots$, calculated through Eq. (7):

$$\hat{\gamma}(h) = \frac{1}{2m(h)} \sum_{i=1}^{m(h)} \{z(x_i) - z(x_i+h)\}^2 \quad (7)$$

where $m(h)$ is the number of data pairs of the attribute value for z separated by each h vector.

The coefficient of determination (R^2) and residual sum of squares (RSS) were defined as criteria for goodness of fit. This model is represented by Eq. (8):

$$\hat{\gamma}(h) = C_0 + C(1 - \exp\left(\frac{-h^2}{A_0^2}\right)) \quad (8)$$

where C_0 is nugget variance, C is structural variance and A_0 is the range.

Ordinary kriging was used to predict the spatial structure of lobster habitat in the reef. The values of the theoretical variogram are coefficients of a series of lineal equations that are used to obtain the weight (λ) needed for the interpolation in the estimate (Eq. (9)), which is unbiased (Cressie, 1989).

$$\hat{Z}(\mathbf{x}_0) = \sum_{i=1}^N \lambda_i z(\mathbf{x}_i) \quad (9)$$

where $\hat{Z}(\mathbf{x}_0)$ is a parameter predicted for a non-sampled site. The maps generated show the spatial distribution of lobster (defined by its density) associated with the spatial structure of the habitat in Arrecife Alacranes. To test the goodness of fit of the model, cross-validation was applied by excluding a sampling point and re-estimating it by kriging (Isaaks and Srivastava, 1989). The geostatistical analysis was implemented with GS+ (V5. 1).

5. Results

5.1. Identification of preferential habitat for lobster and estimation of lobster density, abundance and biomass

Density ($\hat{D}1$), abundance (A) and biomass (B) estimates by bottom type throughout the reef based on the map obtained with GIS are depicted in Table 2. The map includes 12 bottom types, 10 of which were identified as preferred lobster habitats. From these, eight types had high densities (between 9.39 and 28.42 lobsters/ha). These sites are located at depths between 1 and 25 m and they present some degree of common coverage of coral reef associations, ranging from 15 to 60% (Table 1).

Table 2
Density, abundance and biomass of lobster estimated for each type of bottom at Arrecife Alacranes. A = abundance (total number of organisms), D = density (lobsters/Ha), B = biomass (tons), LL (lower limit at 95%), UL (upper limit at 95%), minimum and maximum (estimated values for the analyzed variable)

Type	Variable	Mean	LL	UL	Minimum	Maximum
1	A	848.00			762.00	946.00
	D	0.60	00.59	0.61	0.54	0.67
	B	0.48			0.43	0.54
2	A	115,952.00			103,409.00	129,359.00
	D	28.42	28.40	28.45	25.35	31.71
	B	65.75			58.63	73.35
3	A	14,515.00			13,056.00	16,182.00
	D	12.25	12.19	12.30	11.02	13.65
	B	8.23			7.40	9.17
4	A	57,328.00			51,438.00	63,868.00
	D	13.39	13.37	13.40	12.01	14.91
	B	32.51			29.17	36.21
5	A	1,710.00			1,523.00	1,923.00
	D	3.36	3.31	3.41	2.99	3.78
	B	0.97			0.86	1.09
6	A	3,014.00			2,586.00	3,434.00
	D	21.38	21.28	21.48	18.34	24.36
	B	1.71			1.47	1.95
7	A	5,649.00			5.08	6,317.00
	D	17.42	17.32	17.51	15.65	19.47
	B	3.2			2.88	3.58
8	A	19,624.00			17,659.00	21,885.00
	D	9.39	9.37	9.42	8.45	10.47
	B	11.13			10.01	12.41
9	D	0	0	0	0	0
10	A	724.00			606.00	809.00
	D	11.75	11.63	11.86	9.83	13.13
	B	0.41			0.35	0.46
11	D	0	0	0	0	0
12	A	6,367.00			5,527.00	7,101.00
	D	17.57	17.53	17.61	15.25	19.59
	B	3.61			3.14	4.03

Bottom types 5, 8 and 11 had a large coverage of sand (bare substrate), but only in the first two (5 and 8) some lobsters were spotted. These sites had some kind of crevices that offer shelter to lobsters, including caves on the base of coral heads or some other areas. On the other hand, bottom type 7 (with depths ranging between 15 and 25 m) and type 9 (between 20 and 30 m) comprise dense coverage of coral reef associations, e.g. 61% and 46%, respectively (Table 1). Despite similarities between these sites, the presence of lobsters was recorded only in site 7. It was assumed that location of the reef and its exposure to currents influenced the ability of divers to spot lobsters more than the total absence of lobsters in the refuges. Bottom type 7 was located leeward (west side of the reef), where currents are less strong and the structure of the coral reef seems less complex, while bottom type 9 was windward (east side of the reef), where stronger currents hit the reef and the refuges present a more complex structure making it more difficult to spot the lobsters. In deep areas (>30 m), high density of lobsters was estimated,

although it was not possible to contrast this information with data from map for bottom type.

Mean total abundance of lobsters was estimated at $225,732 \pm 25,000$ organisms, which corresponds to an average total biomass of 128 ± 15 t of lobsters in total weight (TotW), equivalent to 42.7 t of lobster tails weight. This value falls between the estimated range of landings reported for this fishing area during the analyzed period (between 38 and 50 t, with a mean value of 45 t of lobster tails weight).

5.2. Prediction of the spatial distribution of preferential habitat for lobster

Results from variographic analysis show that preferential habitat for lobster is spatially structured. From the tested models – Gaussian, esferic, lineal and exponential – the first one fits the data best (Fig. 2), showing a smooth variation. The variogram parameters are:

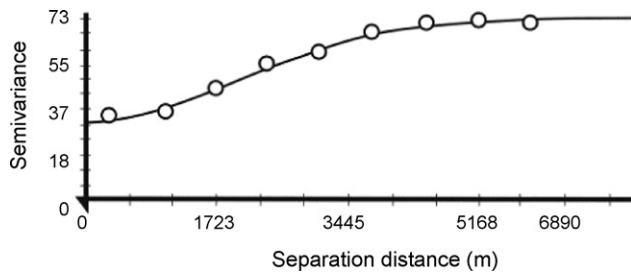


Fig. 2. Variogram for lobster density at Alacranes reef. Separation distance is estimated in meters. The range $A_0 = 2.82$ km, the nugget variance $C_0 = 32.3$, the structural variation plus a short scale variation ($C_0 + C$) = 73.2.

- range (A_0), that indicates a spatial dependence of 2.82 km
- small scale variation, represented by the nugget (C_0) equal to 32.3
- the sill ($C_0 + C$), that defines the structural variation plus the short scale variation valued on 73.2.

The regression coefficient estimated in $R^2 = 0.97$ and the residual sum of squares $RSS = 44.6$, confirm a good fit.

Maps obtained by kriging (Fig. 3a and b), show that lobsters are distributed around the whole reef, but patches of higher densities were associated with areas of higher complexity, where the reef structure is intricate and includes a higher number of crevices or hidden sites for lobsters. These areas are mainly present in the central and northeast part of the reef. From direct observations we notice that these areas are also attractive for other organisms like fishes, mollusks, and other crustaceans.

5.3. Lobster population structure associated to Alacranes reef

A wide range of lobster sizes was registered in the reef area, dominated by juveniles and sub-adults, while in the surrounding deeper waters, larger animals have been reported. For instance, lobsters obtained from commercial catches include animals between 110 and 230 mm TL, equivalent to 170 and 350 mm of TotL and 60 and 120 mm of carapace length (CL) (Fig. 4). It is worth mentioning that the minimal legal size in the region is 13.5 cm TL, so according to the data gathered, about 10% of animals fall below legal size.

Observations during the sampling period did not report high abundance of mature females inside the reef. Nonetheless, high density of large animals has been reported in deeper waters (40–50 m) and at the windward reef. For instance, Ríos et al. (2004) reported that mature females represented 38% of landed females in February 2000. Fishers also have reported high incidence of mature females at the beginning of the fishing season (e.g. between 50% and 80% in July).

Lobsters collected independently of catches include a range between 25 and 100 mm TotL, equivalent to 13 and 50 mm CL (Fig. 5). The small animals were found in areas dominated by seagrass and microalgae such as *Thalassia testudinum*, *Syringodium filiforme*, and other algae (chlorophytes, phaeophytes and rhodophytes). Some animals were also found on the borders of the internal lagoons around 7 m deep.

We recognize that there is an information gap on the population structure between the data on juveniles collected directly in the area and those sampled from commercial catches (animals between 11 and 16 cm TL). However, we can assume that this is generated more by the sampling approach rather than by the total absence of animals in this size range.

6. Discussion

In recent years, several scientists (Orensanz and Jamieson, 1998; Freire et al., 2002; Pauly et al., 2003; Pérez-Castañeda and Defeo, 2004; Cochrane et al., 2004) have emphasized the need to incorporate spatial analysis into stock and fisheries assessment, in order to understand the dynamics of natural resources in general and fisheries in particular. Nonetheless, in practice this type of analysis has been limited, among other things, due to the economic and logistical costs (sampling effort) and availability of data, especially in developing nations. This paper undertakes an integrated spatial analysis of spiny lobster (*P. argus*) in a protected area, incorporating different sources of information, as well as two analytical techniques in order to predict the lobster distribution patterns in the reef area according to its structure and associated to preferential habitat of this crustacean. The participation of fishers in the collection of data was critical. It is expected that our results can both contribute to an improved understanding of the dynamics of this resource, and illustrate the advantages of the employed approaches to incorporate spatial analysis in the evaluation of marine resources, including fisher's participation in the field work.

Spatial techniques used in this research provide an integrated view of the reef ecosystem and lobster distribution at Arrecife Alacranes. For instance, GIS helped obtain an approximation of the proportion of the area occupied by lobster relative to the total area of the reef. This information can help provide better estimates of the distribution of the resource and evaluate stock densities (Green et al., 1996; Jones and Stoner, 1997). Kriging, on the other hand, was used to model the spatial structure of the most suitable habitat for lobster. The maps generated by kriging show patches with differential density among areas in the reef, indicating that the spatial distribution of habitats preferred by lobster is not homogeneous. These results, when contrasted with those obtained with GIS, showing similar patterns, e.g. the map of different types of bottom shows high densities ($\hat{D}1$) in areas that correspond with those of higher lobster densities ($\hat{D}2$) obtained by kriging. In both cases, these sites present high complexity within the reef area.

The use of the bottom type map and density estimates allowed us to evaluate lobster abundance at the beginning of the fishing season in a protected area. This situation give confidence to our results, even though one of the surveys was undertaken guided by fishers, which could have the risk of direct the survey to areas of higher density. But, by taking information at the opening of the fishing season, it was assumed that lobsters were distributed according to their preferences for particular habitats, e.g. lobsters colonized the most suitable habitats available for them in the reef area during the closed season (without the presence of perturbations by human). Hence lob-

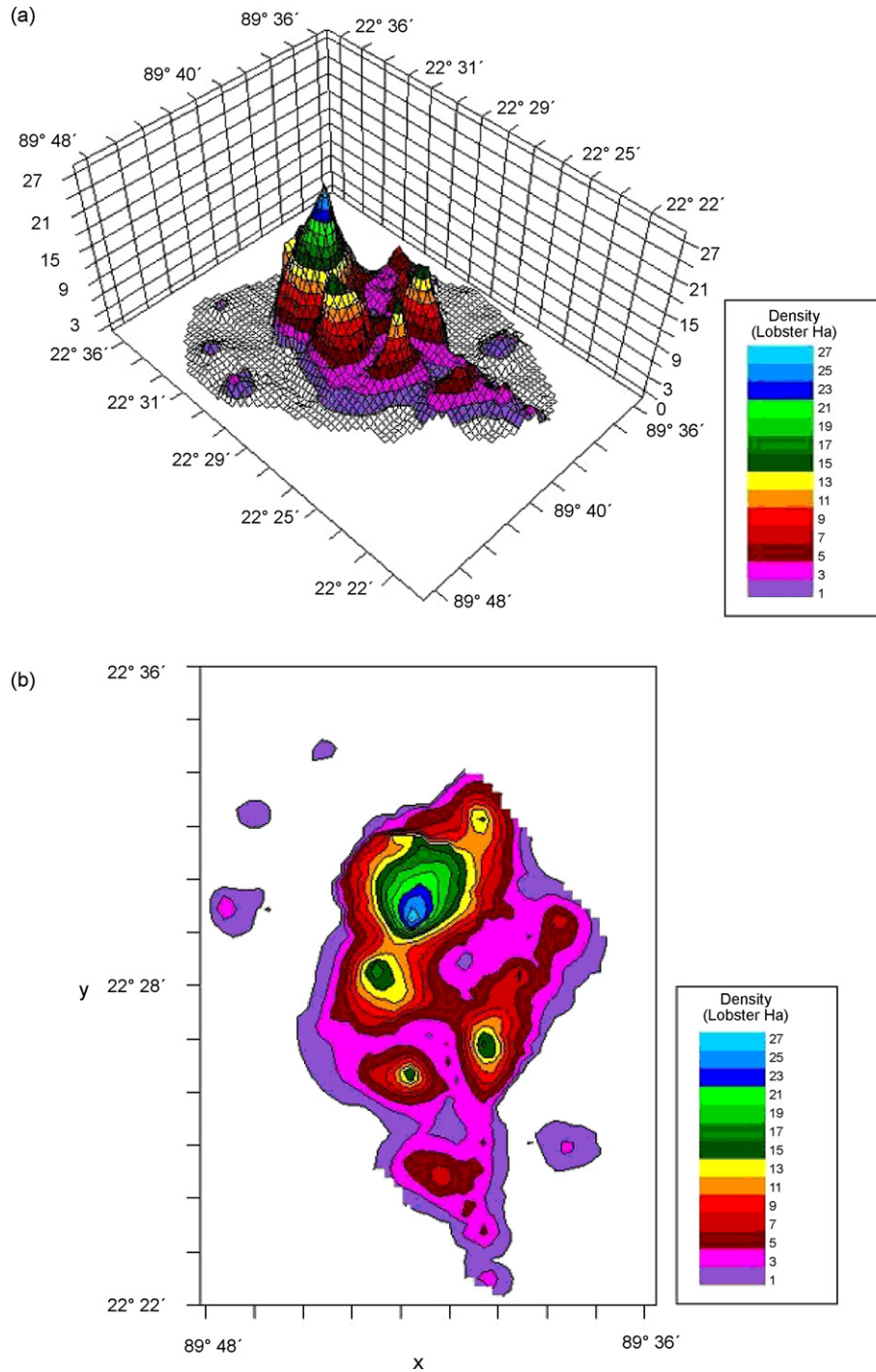


Fig. 3. Lobster density map at Alacranes reef generated by kriging: (a) three-D map of lobster density by Ha distributed along the reef and (b) two dimensions map showing contours of lobster density in the same units.

ster density estimates and abundance can be considered as good estimates.

The biomass value obtained in this study ($128 \text{ t} \pm 15$) is similar to the values estimated by Bello-Pineda et al. (2005a) evaluated in 114 t (considering the confidence intervals), even though the map employed by Bello-Pineda et al. (2005a) considered 10 bottom types, while in the present study, the map was classified into 12 bottom types, in the search of higher resolution.

The values estimated in this study, plus observed trends in catches along each fishing season, showing a decrease towards the end of the season (Ríos et al., 1998; Bello-Pineda et al., 2005a), suggest that, due to the fact that grounds are practically swept by fishers during the fishing season in many fishing areas around, lobster production in the reef area is highly dependent on recruitment (re-colonization) during the closed fishing season. Hence fishing effort control in the zone is mandatory for the resource to be viable in the long term. Special atten-

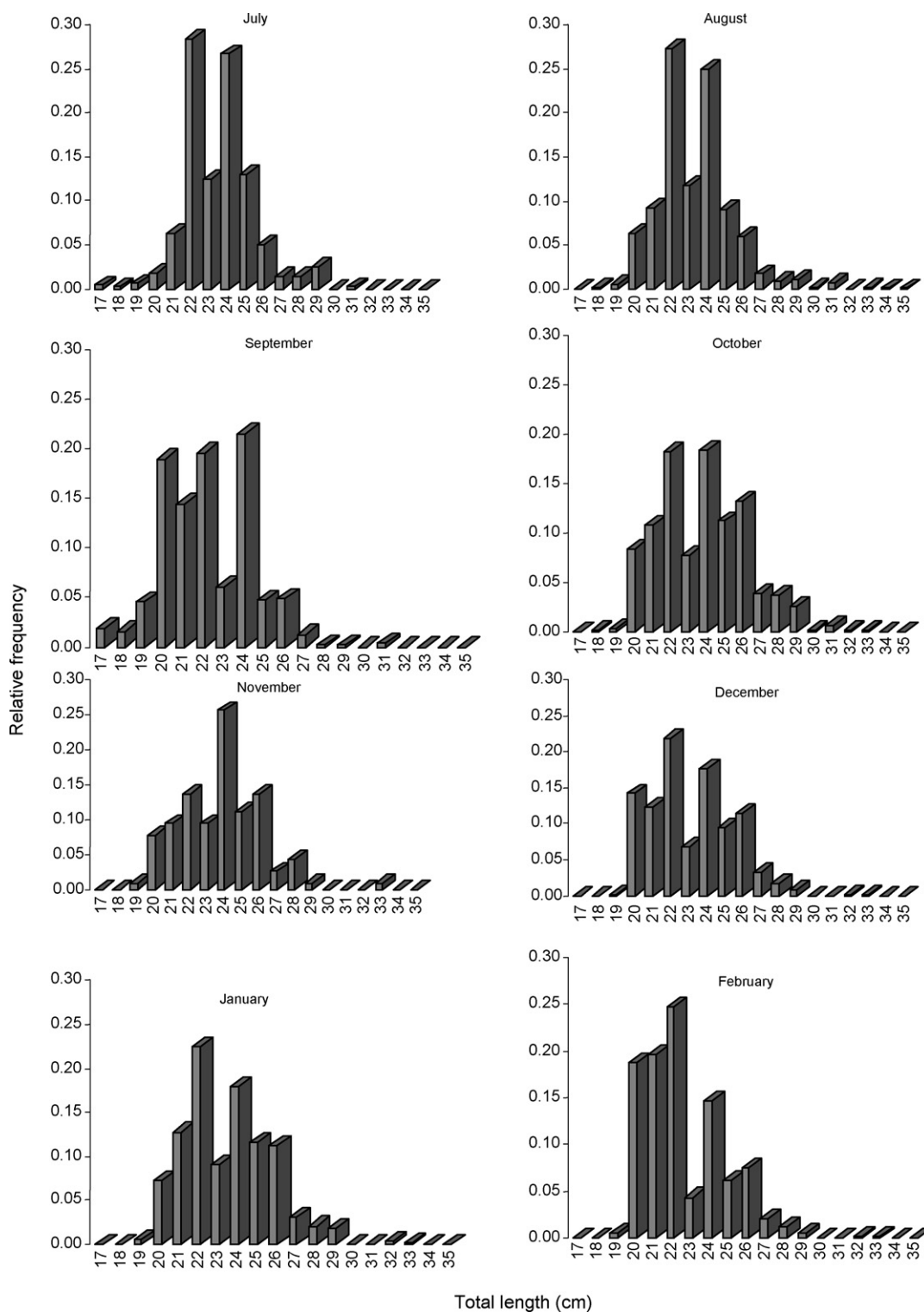


Fig. 4. Relative size frequency distribution of lobster *Panulirus argus* caught at Arrecife Alacranes recorded between July and February in the analyzed period. Mean values of lobster length fluctuated between 220 and 240 mm of total length (TotL), equivalent to 145–160 mm of tail length (TL), respectively. Values in the figure are presented in cm.

tion is required on nursery areas and areas where spawners are present.

Several authors have suggested that recruits in the Caribbean area might come from different locations, while others contend that eddies can contribute to retaining larvae; the presence

of counter currents can return the larvae to their source, and in other cases that populations can contribute with their own recruits (Yeung and Lee, 2002; Ehrhardt, 2005). Even though no specific studies have been conducted up to now to evaluate recruitment (settlement) patterns in the Arrecife Alacranes,

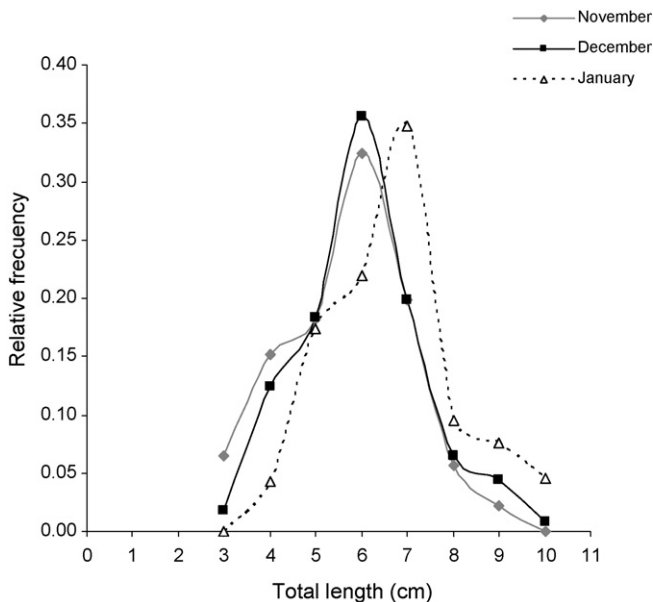


Fig. 5. Relative size frequency distribution of the juvenile lobsters *Panulirus argus* recorded during the period of higher abundance at the National park Arrecife Alacranes (between the end of the fall and the first half of the winter). Mean values fall between 60 and 70 mm of total length (TotL), equivalent to 40–46 mm of tail length (TL), respectively. Values in the figure are presented in cm.

the presence of small juveniles, suggest that the reef has suitable conditions that facilitate settlement in the reef zone, contributing to the renewal of the population every year. The presence of seagrass and algae beds in shallow waters help populate juveniles close to the windward barrier. The observed patterns are consistent with information referred to by several authors who have studied post-larvae settlement patterns and habitat of marine fauna in other areas (Marx and Herrnkind, 1986; Cruz et al., 1987; Butler et al., 1997, 2006; Salas et al., 1996).

We contend that the complex geomorphologic characteristics of Arrecife Alacranes and the presence of eddies (Monreal-Gómez et al., 2004) could favor retention and settlement of larvae in the zone. The elevated frequency of mature females in deep areas surrounding the reef could also contribute to the assumption of annual renewal of the population in the area. These conditions, of course, do not disregard contribution from other Caribbean locations, given the oceanographic conditions prevalent in the peninsula (Ehrhardt, 2005; Cochrane et al., 2004; Monreal-Gómez et al., 2004). Studies that contribute to a better understanding of these processes are highly relevant in order to provide managers with support to develop management strategies to ensure sustainability of the lobster population in this protected area, since some fishing activities in the reef are occurring, including illegal unreported fishing.

From this study it can be concluded that, consistent with the literature, areas with higher geomorphologic complexity provide more suitable habitat for organisms like lobsters. Lobster densities differ according to the complexity of the habitat and the requirements of the animals at any specific life stage. The diversity of habitats as well as the elevated complexity found

at Arrecife Alacranes makes it a suitable zone for settlement and development of lobster at different stages of its life cycle, especially for postlarvae, juveniles and young adults. These conditions make the reef an important nursery and growth zone that deserves special attention to ensure sustainability of lobster for the whole region.

We would like to highlight the importance and utility of collecting spatial data to conduct specific studies on recruitment, movement patterns, and reproduction seasonality, besides the traditionally stock assessment undertaken currently. It is required to improve the knowledge of the population dynamics and fisheries ecology of this crustacean in the area in order to make the corresponding adjustments to the management plan of the reserve if a viable population is expected.

Acknowledgments

This study forms part of the doctoral dissertation of the first author, who acknowledges CONACYT for the grant to undertake her PhD program at CINVESTAV Merida. We thank fishers from Sisal fishing cooperative based in Progreso port for their incredible support during the field work. Luis Capurro, Anthony Charles, and three anonymous referees provided very useful comments to improve this paper.

References

- Acosta, C., 1999. Benthic dispersal of Caribbean spiny lobster among insular habitats: implication for the conservation of exploited marine species. *Conserv. Mar. Biol.* 13 (3), 603–612.
- Arce, A.M., Aguilar-Dávila, W., Sosa-Cordero, E., Caddy, J.F., 1997. Artificial shelters (casitas) as habitats for juvenile spiny lobsters *Panulirus argus* in the Mexican Caribbean. *Mar. Ecol. Prog. Ser.* 158 (1), 217–224.
- Ardisson, H.P., Duncan, J., Aguirre, L., Canela, J., 1996. Programa de manejo del Parque Marino Nacional Arrecife Alacranes, Yucatán, México. CINVESTAV-IPN, Mérida.
- Bello-Pineda, J., Ríos, G.V., Liceaga, M.A., Zetina, C., Cervera, K., Arceo, P., Hernández, H., 2005a. Incorporating spatial analysis of habitat into spiny lobster (*Panulirus argus*) stock assessment at Alacranes reef, Yucatán, México. *Fish. Res.* 73, 37–47.
- Bello-Pineda, J., Liceaga-Correa, M.A., Hernández-Núñez, H., Ponce-Hernández, R., 2005b. Using aerial video to train the supervised classification of landsat TM imagery for coral reef habitats mapping. *Environ. Monit. Ass.* 105, 145–164.
- Butler, M.J., Herrnkind, W.F., Hunt, J.H., 1997. Factors affecting the recruitment of juvenile Caribbean spiny lobsters dwelling in macroalgae. *Bull. Mar. Sci.* 61, 3–19.
- Butler, M.J., Steneck, R.S., Herrnkind, W., 2006. Juvenile and adult ecology. In: Phillips, B. (Ed.), *Lobsters: Biology, Management, Aquaculture and Fisheries*. Blackwell, pp. 263–309.
- Caddy, J., Defeo, O., 2003. Enhancing or restoring the productivity of natural population of shellfish and the other marine invertebrate resources. *FAO Fish. Tech. Rep.* 448, Rome, Italy.
- Childress, M.J., Jury, S.H., 2006. Behaviour. In: Phillips, B. (Ed.), *Lobsters: Biology, Management, Aquaculture and Fisheries*. Blackwell, pp. 78–112.
- Cobb, J.S., Wahle, R.A., 1994. Early life history and recruitment processes of clawed lobsters. *Crustaceana* 67, 1–25.
- Cochrane, K., Chakalall, B., Munro, G., 2004. The whole could be greater than the sum of the parts: the potential benefits of cooperative management of the Caribbean spiny lobster. In: Payne, A., O'Brien C., I.L., Rogers, S. (Eds.), *Management of Shared Stocks*. Blackwell, Oxford, pp. 223–239.
- Cressie, N., 1989. *Geostatistics*. *Am. Stat.* 43 (4), 197–202.

- Cruz, R., Baisre, J.A., Díaz, E., Brito, R., García, C., Blanco, W., Carrodegas, C., 1987. Atlas- biológico pesquero de la langosta en el archipiélago cubano. In: Centro de Investigaciones Pesqueras. La Habana, Cuba.
- Davidson, R.J., Villouta, E., Cole, R., Barrier, R.G., 2002. Effects of marine reserve protection on spiny lobster (*Jasus edwardsii*) abundance and size at Tonga Island Marine Reserve, New Zealand. *Aquat. Conserv. Mar. Freshwat. Ecol.* 12, 213–227.
- Eastman, J.R., 1993. IDRISI: A Grid Based Geographical Analysis System—Version 4. 1 Update Manual. Clark University, Massachusetts, USA.
- Ehrhardt, N., 2005. Population dynamic characteristics and sustainability mechanisms in key Western Central Atlantic spiny lobster, *Panulirus argus* fisheries. *Bull. Mar. Sci.* 76 (2), 501–525.
- Freire, J., Bernárdez, C., Corgos, A., Fernández, L., González-Gurriarán, E., Sampedro, M.P., Verísimo, P., 2002. Management strategies for sustainable invertebrate fisheries in coastal ecosystems of Galicia (NW Spain). *Aquat. Ecol.* 36, 41–50.
- Green, E.P., Mumby, P.J., Edward, A.J., Clark, C.D., 1996. A review of remote sensing for assessment and management of tropical coastal resources. *Coast. Manage.* 24, 1–40.
- Herrera, A., Ibarzábal, D., 1995. Aspectos ecológicos de la langosta *Panulirus argus* en los arrecifes de la plataforma cubana. *Rev. Inv. Mar.* 19 (1), 59–63.
- Hilborn, R., 1986. A comparison of alternative harvest tactics for invertebrate fisheries. In: Jamieson, G.S., Bourne, N. (Eds.), North Pacific Workshop on Stock Assessment and Management of Invertebrates, vol. 92. *Can. Special Publ. Fish. Aquatic. Sci.*, pp. 313–317.
- Isaaks, E.H., Srivastava, R.M., 1989. Applied Geostatistics. Oxford University Press, New York.
- Jones, R.L., Stoner, A.W., 1997. The integration of GIS and Remote Sensing in an Ecological Study of queen conch, *Strombus gigas*, nursery habitats. In: Proceedings of the 49th GCFI, pp. 523–530.
- Keith, L.H., 1988. Principles of Environmental Sampling. A.C.S, USA.
- Krebs, C., 1989. Ecological Methodology. Harper Collins Publishers, USA.
- Liceaga, C.M.A., Ríos, L.G.V., Zetina, M.C., Hernández, H., 1998. Clasificación rápida del ambiente arrecifal para la evaluación de los recursos pesqueros. In: Proceedings of the 50th GCFI, pp. 185–189.
- Maravelias, C.D., Reid, D.G., Simmonds, E.J., Haralabous, J., 1996. Spatial analysis and mapping of acoustic survey data in the presence of high local variability: geostatistical application to North Sea herring (*Cuplea harengus*). *Can. J. Fish. Aquat. Sci.* 53, 1497–1505.
- Marx, J.M., Herrnkind, W.F., 1986. Species profiles: life histories and environmental requirements of coastal fishes and invertebrates (south Florida)-Spiny lobster. *U.S. Fish. Wildlife Serv. Biol. Rep.* 82, 11–61.
- Maynou, F.X., Sarda, F., Conan, G.Y., 1998. Assessment of the spatial structure and biomass evaluation of *Nephrops norvegicus* (L.) populations in the northwestern Mediterranean by geostatistics. *ICES J. Mar. Sci.* 55, 102–120.
- Monreal-Gómez, M.A., Salas-de León, D.A., Velasco-Mendoza, H., 2004. Hidrodinámica del Golfo de México. In: Caso, M., Pisanty, I., Ezcurra, E. (compiladores). Diagnóstico Ambiental del Golfo de México. SEMARNAT-INE- Inst. Ecol. A.C., Harte Research Inst. for Gulf of Mex. Studies. Mexico D. F. pp. 47–68.
- Orensanz, J.M., Jamieson, G.S., 1998. The assessment and management of spatially structured stocks: an overview of the North Pacific Symposium on Invertebrate Stock Assessment and Management. In: Jamieson, G.S., Campbell, A. (Eds.), Proceeding of the North Pacific Symposium on Invertebrate Stock Assessment and Management, vol. 125. *Can. Spec. Publ. Fish. Aquat. Sci.*, pp. 441–459.
- Pauly, D., Alder, J., Bennett, E., Christensen, V., Tyedmess, P., Watson, R., 2003. The future of fisheries. *Science* 302 (21), 1359–1361.
- Pelletier, D., Parma, A., 1994. Spatial distribution of Pacific halibut (*Hippoglossus stenolepis*): an application of geostatistics to logline survey data. *Can. J. Fish. Aquat. Sci.* 51, 1506–1518.
- Pérez-Castañeda, R., Defeo, O., 2004. Spatial distribution and structure along ecological gradients: penaeid shrimps in a tropical estuarine habitat of México. *Mar. Ecol. Prog. Ser.* 273, 173–185.
- Petitgas, P., 2001. Geostatistics in fisheries survey design and stock assessment: models, variances and applications. *Fish. Fish.* 2, 231–249.
- Polovina, J.J., Haight, W.R., Moffitt, R.B., Parrish, F.A., 1994. The role of benthic habitat, oceanography and fishing on the population dynamics of the spiny lobster, *Panulirus marginatus* (Decapoda, Palinuridae), in the Hawaiian archipelago. *Crustaceana* 68, 203–212.
- Ríos, L.G.V., Cervera, C.K., Espinoza, M.J.C., Pérez, P.M., Zetina, M.C., Chable, E.F., 1998. Estimación de las densidades de langosta espinosa (*Panulirus argus*) y caracol rosado (*Strombus gigas*) en el área central del arrecife Alacranes, Yucatán México. In: Proceedings of the 50th GCFI, pp. 104–127.
- Ríos, L.G.V., Zetina, M.C., Bello, P.J., Arceo, B.P., Monroy, G.C., 2004. Modelo de distribución geográfica de áreas de reproducción de la langosta (*Panulirus argus*) en zonas arrecifales profundas de la costa de Yucatán. In: Proceedings of the 55th GCFI, pp. 436–449.
- Roa, R., Tapia, F., 2000. Cohorts in space: geostatistical mapping of the age structure of the squat lobster *Pleuroncodes monodon* population off central Chile. *Mar. Ecol. Prog. Ser.* 196, 239–251.
- Rueda, M., 2001. Spatial distribution of fish species in a tropical estuarine lagoon: a geo-statistical appraisal. *Mar. Ecol. Prog. Ser.* 222, 217–226.
- Salas, S., Aguilar, D., Cabrera, M.A., Arceo, P., 1996. Patrones de asentamiento de langosta (*Panulirus argus*) en la costa oriente de Yucatán. In: Proceedings of the 44th GCFI, pp. 536–552.
- Salas, S., Bello-Pineda, J., Ríos, G.V., Cabrera, M.A., Solís, R., Santa María, A., 2005. Programa Maestro del Sistema Producto de la Pesquería de Langosta en Yucatán. CONAPESCA—CINVESTAV (Eds.). Yucatán, México.
- Seber, G.A.F., 1982. The Estimation of Animal Abundance and Related Parameters. Edward Arnold, United Kingdom.
- Walters, C., Martell, S., 2004. Fisheries Ecology and Management. Princeton University Press, Princeton, New Jersey, USA.
- Yeung, C., Lee, T.N., 2002. Larval transport and retention of the spiny lobster, *Panulirus argus*, in the coastal zone of the Florida Keys, USA. *Fish. Oceanogr.* 11 (5), 286–309.
- Zetina, M.C., Ríos, L.G.V., Cervera, C.K., 1996. Relaciones morfométricas de la langosta *Panulirus argus* de las costas de Yucatán, México, vol. 12. Nueva Época, Ciencia Pesquera, Instituto Nacional de la Pesca, SEMARNAP, México, pp. 41–45.