Postlarval Recruitment of the Spiny Lobster, *Panulirus argus* (Latreille), in Southwestern Puerto Rico

OSCAR E. MONTERROSA
Department of Marine Sciences
University of Puerto Rico
Mayagüez, P.R. 00709-5000

ABSTRACT

Post larval recruitment of the commercially important Caribbean spiny lobster (*Panulirus argus*) was monitored at seven stations (each with two Witham collectors) from July 1983 to December 1984. Split-split plot ANOVA showed significant differences among months, stations, and lunar phases ($p < .001$). In addition, all first and second order interactions - stations by month, stations by lunar phase, lunar phase by month, and station by month by lunar phase - proved significant ($p < .001$). Month to month variability was high, but there appears to be a seasonal peak occurring in late summer (July—September). Highest recruitment levels occurred during new and first quarter moon phases. Offshore stations (at patch reefs) consistently caught more postlarvae than nearshore ones (in mangrove channels). Spatial differences in recruitment over time indicated that pre-settlement pueruli were most likely influenced by changes in water circulation.

INTRODUCTION

The spiny lobster *Panulirus argus*, is the most abundant and commercially important of the three West Indian species of this genus. The range of adult *P. argus* encompasses the western Atlantic from the coast of central Brazil, throughout the Caribbean Sea, Bahama Islands, Gulf of Mexico, southeast Florida, and northward to North Carolina and Bermuda (Williams 1965). In addition, two specimens have been captured off western Africa (Marchal 1968).

In the Caribbean, biological or economic aspects of *P. argus* populations have been described for Cuba (Buesa 1965), Belize (Allsop 1968), Jamaica (Munro 1974), U.S. Virgin Islands (Olsen *et al.* 1975), Martinique (Farrugio 1975), Antigua and Barbuda (Peacock 1974), and Venezuela (Cobo de Barany *et al.* 1972). In Puerto Rico, the spiny lobster fishery has been described by Wilcox (1902), Mattox (1952), Iñigo (1952), and Feliciano (1957); Ting (1973) examined spiny lobster resource potential, and Velazco (1981) analyzed parameters of adult farming using sea-cages.

Spiny lobsters have ecologically distinct life-history stages. During daylight, adults and juveniles are found under ledges and coral heads as well as in caves and crevices; at night they emerge to feed. Spawning by gravid females occurs year-round with maximum activity in late spring and early fall (Buesa 1969). The planktonic larval period lasts from 6-12 months (Lewis 1951, Ingle *et al.* 1963, Buesa 1970). During this time, the transparent, leaf-like larvae or phyllosomes molt through 11 larval stages before metamorphosing into transparent, lobster-like, swimming post-larvae or pueruli (Lewis 1951). Pueruli then traverse the insular shelf and settle in shallow coastal waters, beginning a juvenile benthic existence (Lyons 1980).

Witham *et al.* (1964) described the widespread occurrence of *P. argus* pueruli in a southeast Florida estuary. Later, using artificial substrate habitats, Witham *et al.* (1968) showed that recruitment to estuaries occurred year-round. Artificial habitats have been used to monitor puerulus recruitment for *Panulirus longipes cygnus* in western Australia (Phillips 1972), and *P. interruptus* in southern California (Serfling and Ford 1975). Technical aspects of using artificial habitats have been reported by Little and Milano (1980). Data from habitats have been used to measure patterns and relative strengths of recruitment from season to season and year to year (Chittlebourough and Phillips 1975, Serfling and Ford 1975, Little 1977).

The temporal pattern of pueruli settlement in Puerto Rico has not been established by previous studies. Although inshore areas serve as nursery grounds for juvenile *P. argus* (Ting 1973), it is not known whether settlement occurs primarily at offshore reefs or nearshore mangrove areas.

The objective of this study is to determine temporal and spatial patterns in the recruitment of pueruli to artificial habitats in the La Parguera area.

In order to avoid confusion, I define the terms settlement and recruitment according to Connell (1985), with settlement being the instance when a larva (puerulus in this case) first takes up permanent residence on the substratum; recruitment is the combination of settlement with any early mortality encountered on the substratum up to the time of the first census.

MATERIALS AND METHODS

Study Area

The study area is located adjacent to the fishing village of La Parguera (17° 58.5' N, 67° 3.8' W), in southwest Puerto Rico (Figure 1). The insular shelf in this region is 8-10 km wide, with an average depth of 19 m. Southeast trade winds prevail, resulting in a westerly surface waterflow. Tides are diurnal with an average and maximum range of 20 and 40 cm respectively (Glynn 1973). Emergent coral reefs comprise approximately 20% of the shelf area. They are arranged in outer and inner reef lines that are parallel to the coastline, thus reducing shoreward wave energy (Morelock *et al.* 1977). The coastline is dominated by the mangrove *Rhizophora mangle*, with many channels leading to semi-enclosed lagoons. Inshore surface temperatures and salinities were obtained from the U.S. Coast and Geodetic Survey tide station on the west end of the Isla Magueyes (Dept. Marine Sciences, U.P.R. field station).

FIGURE NOT RECEIVED FROM AUTHOR AT PRESS TIME

Stations

Seven stations were established in offshore and nearshore areas (Figure 1). Each station consisted of two floating artificial habitats coupled 2-3 m apart and, as a set, arranged perpendicular to the direction of the mean water flow.

Nearshore stations

Station I, Cueva Lagoon, is a large, 218,315 m^2 ,mangrove-lined lagoon. Habitats were located along the side opposite the main lagoonal entrance. Water depth was 1.5 m, and the bottom consisted of fine sediment with sparse turtlegrass (*Thalassia testudinum*).

Station II, Isla Cueva, is located along the mangrove coastline west of La Parguera. Habitats were near a channel entrance, floating in water of 2.0 m depth over a fine sediment bottom.

Station III, Burkholder Bay, is a mangrove-lined embayment, 6,541 m^2, off the northeast corner of Isla Magueyes. Habitats were near the southernmost portion of the shoreline over water 1.5 m deep with a fine-sediment mud bottom.

Offshore stations

Station IV, Tres Pelotas, is a group of three mangrove islands. Habitats were located on the leeward side of the easternmost island (approximately 20 m in diameter). Water depth was 1.0 m with a turtlegrass bottom.

Station V, Caballo Blanco , is a mangrove island approximately 100 m by 60 m. Habitats lay on the island's leeward side in water 1.0 m deep over a sand bottom.

Station VI, Enrique Reef, is a 1200 m long reef, parallel to the shoreline. Forereef and reef crest are dominated by living corals and coral rubble (predominantly *Acropora palmata* and *Porites porites*). Backreef areas consist mostly of turtlegrass, sand patches, coral rubble, and mangrove outcroppings. Most of the reef crest is submerged under 0.10 to 0.25 m water. Emergent portions consist of coral rubble and mangrove patches. Habitats were placed on the leeward side of the westernmost mangrove outcrop in water 1.0 m deep over a turtlegrass bed.

Station VII, San Cristobal Reef, is an "L-shaped" coral reef, 600 m in total length (exposed). The reef crest and backreef are dominated by coral rubble. Habitats were situated in the backreef zone in water 1.5 m deep.

Artificial Habitats

The general design for artificial-habitat devices followed that of Witham *et al.* (1968). Each habitat consisted of a float and substrate. From this floating platform hung eight "pages" of nylon-webbed unbacked carpet matting (NOMAD™, 3M Co. Inc.). One piece of carpet matting measured 62.4 x 44.2 x 0.5 cm. Four pieces were attached along their respective transverse midlines, resulting in eight pages hanging approximately 31 cm into the water. Habitats were anchored by polyproplene line tied to concrete blocks.

A visual survey of the area adjacent to each station showed that biological growth on artificial habitats (fouling) was consistent with local flora and fauna. It was decided to permit fouling so that settlement surfaces would more closely reflect that of the adjacent natural environment. Only when a habitat page became 50% overgrown was fouling partially removed (approximately 4-5 and 9-12 weeks for nearshore and offshore stations respectively).

Sampling

Artificial habitats were deployed on 2 July 1983; pre-sampling to assess habitat efficiency and station locale was performed in July and August 1983. Stations were examined weekly from September 1983 to December 1983; to decrease the margin between settlement and recruitment, sampling frequency was changed to every four days from January 1984 to December 1984. All stations were sampled consecutively using a small outboard motorboat. Inspection of habitats involved turning the habitat over and individually examining each page, then repeating the process (second inspections rarely revealed additional pueruli). Pueruli were counted and removed from the habitat. I define pueruli as pre-molt postlarvae with a dorsoventrally flattened carapace. Body pigmentation ranges from none (0-5 days after settlement) to fully pigmented (brown and white) with no internal organs visible (3-8 days after settlement). True postlarvae (or early juveniles) result from the molt of a puerulus (> 6 days after settlement) and are characterized by a well-rounded carapace with numerous small spines and hairs on antennae and pereopods. Coloration is as in the puerulus except brown-colored portions are darker (these definitions are based on personal observations).

Lunar periods (new moon, first quarter, full moon, and last quarter) were defined as 3 days before and after the actual date of the lunar phase. A sampling date was assigned to the nearest lunar phase.

Since station sites and sampling sequence were not completely selected at random, a split-split plot ANOVA design - with a log (x + 1) transformation to equalize variances - was applied (Steel and Torrie 1980). The response variable was the number of postlarvae per habitat. Three treatment levels were examined:

1. Among months, stations, and lunar phases (whole units).
2. Among stations within months, stations within lunar phases, and months within lunar phases (sub-units).
3. Among stations within months within lunar phases (sub-sub-unit).

Data were analyzed using the MANOVA program (Hull and Nie 1981) of SPSS-X (Statistical Package for the Social Sciences) on an IBM-4381. A T-method unplanned comparison (Sokal and Rholf 1981) was used for aposteriori analysis of selected means. Significance was set at the 95% ($p = 0.05$) confidence level.

RESULTS

During the course of the study, surface temperatures ranged from 25.6 to 30.0°C, and salinity varied from 32.9% to 37.5%.

Seven stations, each with two artificial habitats sampled from 6 September 1983 to 29 December 1984, yielded a total of 166 postlarvae. Of these, 158 (95%) were pueruli and eight (5%) were true postlarvae or early juveniles. The postlarval specimens (5%) captured in this study most likely had been overlooked in previous samplings, or they entered the habitats after having settled in nearby natural substrates; therefore, sampling frequency was changed from weekly to every 4 days on 23 January 1984. Overall significance of results was not affected by including these specimens in final calculations.

Split-split plot ANOVA showed significant differences ($p < .001$) among months, stations, and lunar phases. In addition, all first and second order interactions – stations by month, stations by lunar phase, lunar phase by month, and station by month by lunar phase – proved significant ($p < .001$). An a posteriori examination of the monthly means of recruits, using an unplanned comparison or T-method (Sokal and Rholf 1981) of least significant differences between means, indicate a significant amount of variation in month to month recruitment levels; nevertheless, there appears to be a seasonal pattern.

Temporal Recruitment

Pre-sampling on 29 July and 24 August 1983 resulted in 16 pueruli, 3 postlarvae (full moon, 25 July), and 17 pueruli, 7 postlarvae (full moon, 23 Aug.) respectively. These points are included in Figures 2 and 4 but were not included in the statistical analysis. Since sampling on these dates occurred late in their respective months, and the duration of a puerulus is approximately from 0 to 8 days after settlement, the points on Figure 2 representing the mean number of pueruli for July and August 1983 can be considered as minimum values of recruitment for those months. However, when viewed over the course of the entire study period, these points contribute to one of two relatively high peaks. The second peak corresponds to the same period, July and August, of the following year. Thus it is apparent that peak recruitment took place in late summer to early fall. .

Two smaller peaks were recorded for December 1983 and April 1984. During the course of the study, there were two measurements for the month of December. Figure 2 shows the large differences in the mean number of postlarvae recruited between December 1983 and 1984 thus indicating that the December 1983 peak is not a seasonal peak; instead, it is an indication of the high variability possible in year to year recruitment levels. In 1984, there was a small spring recruitment peak (relative to the late summer peak). Whether or

FIGURE NOT RECEIVED FROM AUTHOR AT PRESS TIME

FIGURE NOT RECEIVED FROM AUTHOR AT PRESS TIME

not this is a "true" seasonal peak is unknown because there is no repeated measurement for the month of April, and this peak may be due to yearly variation (as in Dec. 1983, 1984).

Spatial Recruitment

Recruitment was significantly different among stations (p < .001) with highest levels occurring at offshore sites (IV, V, VI, VII). Figure 3 shows that the highest number of collected postlarvae occurred at station VI, Enrique Reef. The next highest was station V, Caballo Blanco, followed by stations VII, San Cristobal; IV, Tres Pelotas; III, Burkholder Bay; and I, Cueva Lagoon. No postlarvae were collected at station II, Isla Cueva, throughout the course of the study.

The mean number of postlarvae per offshore station plotted for each month (Figure 4) shows that collections varied among stations and among months (recruitment at nearshore stations were too low for comparison). The high significance of the station by month interaction term (p < .001) indicates that not all stations followed the same recruitment pattern throughout the study period. Figure 4 shows that most offshore stations peak at the same time; however, in December 1983, there was an influx of recruits mainly at station V, Caballo Blanco.

Significant differences (p < .001) among lunar periods exist. Figure 5 shows that collections were higher during first quarter and new moon lunar periods compared to full moon and last quarter.

DISCUSSION

The roles of biological and physical factors in larval recruitment of *P. argus* are poorly understood. Variations (short and long term) in spatial and temporal patterns of recruitment could be influenced by factors acting independently and in combination.

Considering the long larval period (6-12 months), and observations of spring through fall spawnings, it seems logical that late-stage larvae are available for recruitment year-round and should be present in offshore waters in moderate quantities during any month. Late-stage phyllosome larvae have been reported in all months off Florida and Cuba (Lewis 1951, Sims and Ingle 1966, Baisre 1976, Richards and Potthoff 1980). Abundances have been low; consequently, no seasonal pattern of larval abundance has been observed.

Environmental factors such as light, temperature, salinity, and water circulation could affect recruitment levels. Little (1977) postulated on these effects, but was not able to establish any direct correlations with South Florida's recruitment levels. Johnson (1971) hypothesized that palinurid recruitment peaks result from intermittent arrival of favorable ocean eddies and that these eddies are therefore ultimately responsible for stock fluctuations in southern

FIGURE NOT RECEIVED FROM AUTHOR AT PRESS TIME

FIGURE NOT RECEIVED FROM AUTHOR AT PRESS TIME

California. Water transport must figure prominently in providing competent late-stage larvae access to the insular shelf. Local offshore processes such as currents, eddies and gyres, upwelling and downwelling, island mass effects, and oceanic fronts possibly account for much monthly and yearly variation. Yoshioka *et al.* (1985) gave a review of such processes and how they could affect spatial and temporal patterns of zooplankton abundance off southern Puerto Rico. They reported for the month of July (1980), a relatively uniform eastward surface flow (depths < 200 m), constituting a reversal in the prevailing westward geostrophic surface flow maintained by easterly trade winds. They associated this reversal to the periphery of cyclonic flows induced by a large-scale low salinity lens originating from Amazon and Orinoco river runoffs. Similarly, Froelich *et al.* (1978) reported seasonal intrusions of low-salinity water off the south coast of Puerto Rico for the months of October and November (1971-1973). Thus, Yoshioka *et al.* (1985) conclude that variations in zooplankton abundance throughout the eastern Caribbean are forced by such a large-scale, seasonal, physical process.

Results of this study generally agree with those from other areas. In South Florida, Little (1977) reported recruitment peaks in spring and fall, and he also observed relatively high levels throughout summer in the Florida Keys. In Antigua and Barbuda, Peacock (1974) observed relatively small and large recruitment peaks in spring and late summer respectively, for the year of 1973. In Bermuda, Ward (pers. comm.) observed peak recruitment in September of 1983. In this study, seasonal recruitment peaks were unimodal occurring in July-September of 1983 and July-August of 1984. Although slight peaks were observed in December 1983 and April 1984, they cannot be considered seasonal since in the case of December 1983, the peak was not observed the following year, and, in the case of April 1984, there was no repeated measure with which to compare. The late-summer maxima may be correlated with the fall reversal in geostrophic flow along the southcoast of Puerto Rico. This change in surface flow and salinity could either provide more larvae to the study area, facilitate their access to it, or both. However, this process may not explain the summer-fall peaks in Bermuda and Florida, but there may be a similar basis, *i.e.*, a large scale physical phenomenon.

Spatial differences observed in this study showed recruitment predominantly at offshore stations. Factors affecting the density of puerulus settlers between nearshore and offshore stations can be divided into three categories acting sequentially (modified from Connell 1985):

1. Fewer pueruli arrive at nearshore stations than offshore.
2. Conditions in the water adjacent to nearshore habitats more frequently prevents pueruli from settling there.
3. The substratum is less attractive or more adverse at nearshore stations, so fewer pueruli choose to attach, or more are killed during the process of

settling.

The following are physical and biological parameters that potentially influence these density factors:

1. Fewer pueruli arrive at nearshore areas than offshore.

If offshore and nearshore areas are equally suitable for settlement (in all respects), as pueruli migrate shoreward they will settle on the first suitable substrate encountered. Thus offshore patch reefs may filter-out incoming pueruli.

Water circulation, or the lack of, could affect the density of settlers reaching nearshore areas. Water movement throughout the study area is highly complex due to the presence of many offshore patch reefs and variable winds. Pueruli can swim at speeds up to 10 cm/sec in calm water (Calinski and Lyons 1983), but it is unknown to what extent pueruli can orient and manuever in vertical and horizontal planes in response to variable water movements. Spatial differences in recruitment levels over time at offshore stations are best explained by temporal variations in local water circulation. This explanation suggests that incoming pueruli were indeed affected by water movement, and location of stations (*i.e.*, habitats) was the determining factor in detecting this difference. Predation may act as a selective filter as pueruli approach shallow waters. If pre-settlement, swimming pueruli are more susceptible to predation than post-settlement demersal ones, the extra time taken to reach nearshore coastal areas could increase their probability of falling prey.

2. Conditions in the water adjacent to nearshore habitats more frequently prevents pueruli from settling there.

It is apparent that water movement past protected, nearshore stations is less than at exposed offshore stations. However, there is no indication of peculiar hydrodynamics or differences in water quality at nearshore stations which would restrict settlement, based on year-round recruitment of high numbers of crabs and shrimp on artificial habitats (*e.g.*, *Pachygrapsus* sp., *Petrolisthes* sp., *Mithrax* sp., *Periclimenes* sp., *Latreutes* sp.).

Reports of water temperature and salinity differences between nearshore and offshore waters (Glynn 1973, Kimmel 1985) fall within the tolerance range reported for *P. argus* pueruli (Witham *et al.* 1968, Witham 1973). This data suggests that these are not major factors influencing recruitment variability. Turbidity differences between nearshore and offshore stations could influence recruitment, but no information on this factor was gathered in this study.

3. The substratum is less attractive or more adverse at nearshore stations, so fewer pueruli choose to settle, or more of them are killed during the process of settling.

The artificial substrate medium (nylon carpet matting) was uniform for habitats at all stations; therefore any differences in settlement due to environmental cueing can be attributed to differences in either biological or physical fouling, or both, among stations. If this is the case, and, since fouling on a particular habitat corresponded to the biota of the adjacent natural environment, then differences in recruitment between nearshore and offshore stations are thought to reflect natural differences between these areas.

Differential predation intensities upon new settlers may account for variable recruitment between sites. Kimmel (1985) censused approximately three times as many local fish species along the nearshore mangrove coastline as in the lagoonal areas of the offshore patch reefs (representing 45 vs. 73 species respectively). Assuming fish are the primary pueruli predators, such a difference in fish numbers between areas could be significant to settling pueruli.

Lunar periodicity in recruitment was observed throughout this study. This pattern agrees with findings in Florida (Witham *et al.* 1968, Sweat 1968, Little 1977) and Cuba (Buesa, pers. comm.) that peak *P. argus* recruitment occurs during new and first quarter moon phases (when moonlight is lowest). Moreover, this correlation has been observed for *P. longipes cygnus* in West Australia (Phillips 1975) but not for *P. interruptus* in southern California (Serfling and Ford 1975). The mechanism supporting this association remains unknown, including the possibility that lunar phase could enhance or conceal environmental factors responsible for inducing pueruli to settle.

The distributional range of *P. argus* is geographically broad, encompassing many continental and insular shelf areas. Coordinated regional sampling could possibly detect correlations among large-scale recruitment variations and large-scale physical processes (*e.g.*, the low-salinity lens affecting most of the Caribbean). On a local scale, hydrological factors influencing settlement and recruitment can be highly complex, and location of artificial habitats can be critical in detecting spatial differences over time and more closely approximating actual recruitment levels. In addition to contributing to the recruitment data pool, future studies could attempt to further correlate local water circulation with recruitment. Additional important features to address are the depth limit of settling pueruli and settlement cues.

As more nations participate in data collection throughout the *P. argus* range, a better understanding of local and regional spiny lobster dynamics will emerge, and this increased understanding will help to preserve critical local habitat and implement harmonized regional fishery management programs.

ACKNOWLEDGEMENTS

My heartfelt thanks to Prof. C. Cutress, committee chairman, who apart from providing outstanding criticism, altruistic assistance, and nutritive elements, was kind enough to adopt this stranded student as one of his own. Drs. R. Cameron and R. Menzies influenced the conception and design of much of the recruitment study; in addition they provided materials without which this study would not be possible. Drs. P. Yoshioka, L. Beaver, J. Carroll and A.

McGinty assisted with different portions of the statistical design. Drs. R. Appeldoorn, P. Yoshioka, I. Boidron Metairon and Mr. K. Lindeman offered helpful criticism of the manuscript and willfully engaged in lively discussion. Dr. R. Buesa shared his vast experience with the Cuban lobster fishery, and Mr. J. Ward provided information on Bermudan recruitment. My sincere thanks to Mr. G. Dennis for presenting this paper at the 40th annual GCFI meeting in Curaçao on my behalf.

This work was supported in part by a Graduate Assistantship from the Department of Marine Sciences, University of Puerto Rico.

REFERENCES

Allsop, W.H.L. 1968. Report to the government of British Honduras on investigations into marine fishery management; research and development policy for spiny lobster fisheries. Food and Agriculture Organization, Rep. FAO/UNDP (TA)**2481**: 1-95 pp.

Baisre, J.A. 1976. Distribución de las larvas de *Panulirus argus* y *Scyllarus americanus* (Crustacea, Decapoda) en aguas alrededor de Cuba. Revista Investigaciones, Inst. Nac. Pesca, Cuba **2**(3): 277-297.

Buesa, R.F. 1965. Biology and fishing of spiny lobsters, *Panulirus argus* (Latreille), pages 62-78. In: Bogdanov, A.S. (ed.). Soviet-Cuban fishery research. Israel Prog. Sci. Transl. Ltd., IPST Cat. No. 5514, U.S. Dept. Commer., Springfield, VA.

----------. 1969. Langosta comun *Panulirus argus* (Latreille), hacia nuevos objetivos en su investigación. *Mar y Pesca* **6:** 5-11.

----------. 1970. Migraciones de la langosta (*Panulirus argus*). *Mar y Pesca* **60**: 22-27.

Calinski, M.D. and W.G. Lyons. 1983. Swimming behavior of the puerulus of the spiny lobster *Panulirus argus* (Latreille, 1804) (Crustacea: Palinuridae). *J. Crust. Biol.* **3**(3): 329-335.

Chittleborough, R.G. and B.F. Phillips. 1975. Fluctuations in year class strength and recruitment in the western rock lobster, *Panulirus longipes* (Milne-Edwards). *Australian J. Mar. Freshwater Res.* **26:** 317-328.

Cobo de Barany, T., J. Ewald and E. Cadima. 1972. La pesca de la langosta en el archipiélago de Los Roques, Venezuela. Inform. Tecnico. Proy. Invest. Desarollo Pesq. Venezuela, **43**:1-34.

Connell, J.H. 1985. The consequences of variation in initial settlement vs. post-settlement mortality in rocky intertidal communities. *J. Exp. Mar. Biol. Ecol.* **93**:11-45.

Farrugio, H. 1975. Observations sur deux langoustes de la Martinique: *Panulirus argus* et *Panulirus guttatus*. Premières données biomètriques et étude comparée de leur croissance relatives. *Sci. et peche, Bull. Inst. Peches Marit.* **247**:11-20.

Feliciano, C. 1957. The lobster fishery of Puerto Rico. *Proc. Gulf Caribbean Fish. Inst.* **10**:147-155.

Froelich, P.N., D.K. Atwood and G.S. Giese. 1978. Influence of Amazon River discharge on surface salinity and dissolved silicate concentration in the Caribbean Sea. *Deep Sea Res.* **25**:735-744.

Glynn, P.W. 1973. Ecology of a Caribbean coral reef. The *Porites* reef-flat biotope: Part I. Meteorology and hydrography. *Mar. Biol.* **20**:297-318.

Hull, C.H. and N.H. Nie. 1981. SPSS Update7-9: *New Procedures and Facilities for Releases 7-9.* McGraw-Hill Book Co., New York, N.Y., xxi + 402 pp.

Ingle, R.M., B. Eldred, H.W. Sims, Jr. and E. Eldred. 1963. On the possible Caribbean origin of Florida's spiny lobster populations. Fla. State Bd. Conserv. Tech. Ser. No. 40. 12 pp.

Iñigo, F. 1952. A preliminary report on a survey of the commercial fisheries of Puerto Rico. Rep. Div. Fish. Wildl. Dept. Agric. Commer. Puerto Rico, mimeo: 1-8.

Johnson, M.W. 1971. The palinurid and scyllarid lobster larvae of the tropical eastern Pacific and their distribution as related to the prevailing hydrography. *Bull. Scripps Inst. Oceanogr. Univ. Calif.* **19**:1-36.

Kimmel, J.J. 1985. A characterization of Puerto Rican fish assemblages. Ph.D. Dissertation, Univ. Puerto Rico, Mayagüez, P.R., 106 pp.

Lewis, J.B. 1951. The phyllosome larvae of the spiny lobster, *Panulirus argus.* *Bull. Mar. Sci. Gulf Caribbean* **1**(2): 89-103.

Little, E.J. 1977. Observations on recruitment of post larval spiny lobsters, *Panulirus argus*, to the south Florida coast. Florida Mar. Res. Publ. No. 29. 35 pp.

---------- and G.R. Milano. 1980. Techniques to monitor recruitment of postlarval spiny lobsters, *Panulirus argus*, to the Florida Keys. Florida Mar. Res. Publ. No. 37. 16 pp.

Lyons, W.G. 1980. Possible sources of Florida's spiny lobster population. *Proc. Gulf Caribbean Fish. Inst.* **33**:253-266.

Marchal, E.G. 1968. Sur la capture de long des côtes Africaines de deux specimens de *Panulirus argus* (Latreille). *Bull. Mus. Natl. d'Hist. Nat., 2 Ser.* **39**(5):1120-1122.

Mattox, N.T. 1952. A preliminary report on the biology and economics of the spiny lobster in Puerto Rico. Proc. *Gulf Caribbean Fish. Inst.* **4**:69-70.

Morelock, J., N. Schneidermann and W.R. Bryant. 1977. Shelf reef, Southwestern Puerto Rico. *Am. Assoc. Petroleum Geolog., Studies in Geology* **4**:17-25.

Munro, J.L. 1974. The biology, ecology, exploitation, and management of Caribbean reef fishes. V.II. The biology, ecology and bionomics of Caribbean reef fishes: Crustaceans (spiny lobsters and crabs). Scientific report of the ODA/UNI fisheries ecology research project, 1962-1973. Univ. West Indies Zool Dept., Res. Rep. No.3. 57 pp.

Olsen, D., W.F. Herrnkind and R. Cooper. 1975. Population dynamics, ecology, and behavior of spiny lobsters, *Panulirus argus*, of St. John, U.S. Virgin Islands. I. Introduction and general population characteristics. *Bull. Nat. Hist. Mus. Los Angeles County* **20:**11-16.

Peacock, N.A. 1974. A study of the spiny lobster fishery of Antigua and Barbuda. *Proc. Gulf Caribbean Fish. Inst.* **26:**117-130.

Phillips, B.F. 1972. A semi-quantitative collector of the puerulus larvae of the western rock lobster *Panulirus longipes cygnus* George (Decapoda, Palinuridae). *Crustaceana* **22:**147-154.

----------. 1975. The effect of water currents and the intensity of moonlight on catches of the puerulus larval stage of the western rock lobster. CSIRO Australian Div. Fish. Oceanogr. Rep. No. 63. 9 pp.

Richards, W.J. and T. Potthoff. 1980. Distribution and seasonal occurrence of larval pelagic stages of spiny lobsters (Palinuridae, *Panulirus*) in the western tropical Atlantic. *Proc. Gulf Caribbean Fish. Inst.* **33:**244-252.

Serfling, S.A. and R.F. Ford. 1975. Ecological studies of the puerulus larval stage of the California spiny lobster, *Panulirus iinterruptus U.S. Fish. Bull.* **73**(2):360-377.

Sims, H.W. and R.M. Ingle. 1966. Caribbean recruitment of Florida's spiny lobster population. *Q. J. Florida Acad. Sci.* **29**(3):207-242.

Sokal, R.R. and F.J. Rholf. 1981. *Biometry*, 2nd ed. W.H. Freeman and Co., San Francisco, Calif., xviii + 859 pp.

Steel, R.G.D. and J.H. Torrie. 1980. *Principles and procedures of statistics.* McGraw-Hill Inc., New York, N.Y., xxi + 644 pp.

Sweat, D.E. 1968. Growth and tagging studies on *Panulirus argus* (Latreille) in the Florida Keys. Florida State Bd. Conserv. Tech. Ser. No. 57. 30 pp.

Ting, R.Y. 1973. Investigations on the resource potential of the spiny lobster (*Panulirus argus* Latreille) in Puerto Rico. Cont. Agrop. Pesq., Depto. Agric. Puerto Rico **5**(2):1-18.

Velazco, A.T. 1981. Feasibility and desirability of holding juvenile spiny lobsters (*Panulirus argus* Latreille) in wire or tire cages. M.S. Thesis, Univ. Puerto Rico, Mayagüez, P.R., 48 pp.

Wilcox, W.A. 1902. The fisheries and fish trade of Porto Rico. *Bull. U.S. Comm. Fish. and Fish* **20:**27-48.

Williams, A.B. 1965. Marine decapod crustaceans of the Carolinas. *U.S. Fish. Bull.* **65**(1):1- 298.

Witham, R.R. 1973. Preliminary thermal studies on young *Panulirus argus. Florida Sci.* **36**(2-4):154-158.

Witham, R.R., R.M. Ingle and H.W. Sims. 1964. Notes on the postlarvae of *Panulirus argus*. *Q. J. Florida Acad. Sci.* 27(4):289-297.

----------, ---------- and E.A. Joyce, Jr. 1968. Physiological and ecological studies of *Panulirus argus* from the St. Lucie estuary. Florida State Bd. Conserv. Tech. Ser. 53:1-31.

Yoshioka, P.M., G.P. Owen and D. Pesante. 1985. Spatial and temporal variations in Caribbean zooplankton near Puerto Rico. *J. Plankton Res.* 7(6):733-751.