

SPATIAL VARIATIONS IN DENSITY AND SIZE OF THE ECHINOID *DIADEMA ANTILLARUM* PHILIPPI ON SOME VENEZUELAN CORAL REEFS*

by

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ABSTRACT

The distribution, population density and size structure of *Diadema antillarum* Philippi was found to vary with reef locality, food availability and the structural complexity of the reef. Structural complexity was classified according to the growth morphology and abundance of the coral species found in the different reef zones. Mean urchin density in the reef varied between 2.6 and 3.7 ind. m⁻². High densities (4.0-7.0 ind. m⁻²) were found in the upper reef zone, which was characterized by high structural complexity, and by a dominance of the coral species *Acropora palmata*, *A. cervicornis*, *Montastrea annularis* and the hydrozoans *Millepora alcicornis* and *M. complanata*. Low densities (1.5-4.0 ind. m⁻²) were found in the deep fore reef and flat reef platform, which were characterized by low structural complexity.

A significant and positive correlation was found between urchin density and the cover of dead substrate.

RESUMEN

Se determinó que la distribución, las densidades poblacionales y la estructura de tamaños del erizo negro *Diadema antillarum* Philippi varía según la zona del arrecife, la complejidad estructural de esta y la disponibilidad de alimento. La complejidad estructural de cada zona arrecifal se determinó en función de las formas de crecimiento y abundancias relativas de las especies de coral que allí se desarrollan. Las densidades promedio de erizos variaron entre 2.6 y 3.7 ind. m⁻² en los tres arrecifes estudiados. Densidades altas

(4.0-7.0 ind. m⁻²) se encontraron en las zonas someras y frontales de los arrecifes, caracterizadas por una alta complejidad estructural determinada por la abundancia de los corales *Acropora palmata*, *Montastrea annularis* y los Hidrozoarios *Millepora alcicornis* y *M. complanata*. Densidades bajas (1.5-4.0 ind. m⁻²) fueron características de las zonas profundas y la plataforma arrecifal, conformadas por especies con crecimiento en forma de domo e incrustante y por lo tanto con una complejidad estructural baja e intermedia.

Se determinó una correlación significativamente positiva entre las densidades de erizos y el porcentaje de cobertura de coral muerto (roca de coral) a lo largo de los arrecifes.

INTRODUCTION

The black sea urchin *Diadema antillarum* Philippi is one of the most common and conspicuous animals in Caribbean coral reefs. The geographic distribution of this species ranges from Bermuda to Surinam, but it is also found in the eastern Atlantic, particularly in the Azores, Canaries, Madeira and the Gulf of Guinea (Mortensen, 1940). It inhabits all kinds of marine communities: shallow coral reefs, rocky shores, sea grass beds, sandy bottoms, mangrove roots and even to depths of 400 m (Randall et al., 1964). However, because of its herbivorous habits (Lewis, 1964; Randall et al.,

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1964; Sammarco et al., 1973, 1974; Sammarco, 1972, 1980) it apparently prefers shallow coastal areas with high algal growth.

Lewis (1964) worked on the feeding habits and digestion of *D. antillarum* and was the first to suggest its importance as a source of bioerosion in Caribbean coral reefs. Since then, much attention has been paid to the role of this sea urchin as a regulator of shallow algal and coral reef communities (Sammarco, 1972, 1980; Sammarco et al., 1973, 1974) and to the effect of the bioerosion pressure on Caribbean coral reefs (Hunter, 1977; Stearn et al., 1977; Scoffin et al., 1980; Ogden & Lobel, 1978).

In spite of the numerous investigations on the ecology of this sea urchin, little is known about the variables that control spatial variations in abundance and population size structure. Urich (1977) was the first to find a significant correlation between the mean test diameter of *D. antillarum* and the mean radius of the holes and crevices inhabited by it in a coral reef of La Orchila, Venezuela. He suggested that there is a relationship between the morphological complexity of the reef and the presence or absence of different size classes of sea urchins.

The present paper is part of a major research effort to investigate the ecology of this sea urchin on Venezuelan coral reefs. We report on the different densities of the various size classes of *D. antillarum* found in four main reef zones and on the relationships between these and the structural morphology of the reef, food availability and predation pressure.

STUDY AREA

This study was carried out at the National Park of Morrocoy on the west coast of Venezuela (fig. 1). The Park, with an area of 32,000 ha, is formed by a large number of coral keys, mangrove islands, shallow coral reefs and sand banks, and large sea grass beds dominated by the turtle grass, *Thalassia testudinum*.

Weather conditions vary little during the year. According to Köppen (1900), the area has a tropical savanna climate with a heavy rainy season. Average temperature is 26.5°C,

average rainfall is 1,213 mm and wind direction is mostly from the north-east with an average annual speed of 4.5 km/h (Anonymous, 1978).

Three different reefs were selected for the study (fig. 1):

Pescadores: A fringing reef located at the west side of Pescadores, in the extreme northern section of the Park. The reef protects a mangrove area named Costa de los Muertos and it is separated from the key by a channel 70 m wide and 25 m deep. The reef reaches a maximum depth of 17 m.

Playuela: A small bay located at the north-eastern coast of Animas key, in the eastern section of the Park. The reef is U-shaped with a narrow channel which divides it into two separate sampling zones, PL-1 and PL-2. The reef reaches a maximum depth of 17 m as well.

Cayman: A semi-protected fringing reef on the main coast bordering the interior lagoon of the Park. The reef protects a small, shallow bay and has a narrow channel that divides it into two sampling zones (Cy-1 and Cy-2). It reaches a maximum depth of 8 m.

METHODS

Population density and size structure

Population density was estimated during day and night by two similar methods. The first method involved counting every urchin (including the ones hidden in the reef crevices) in a 4 m wide transect extended perpendicularly to the shore along the entire reef.

The second method involved dividing the reef into four zones (fig. 2):

- (1) The inner reef flat (IRF), extending from the edge of the grass bed to the back limit of the surf zone and characterized by a flat platform of dead coral, covered by zoanthids (*Zoanthus sociatus* and *Palythoa mamillosa*), some algae, and dispersed coral colonies of *Diploria strigosa*, *D. clivosa*, *Porites astreoides*, and *Agaricia agaricites*.
- (2) The outer reef flat (ORF), the shallow surf zone, characterized by dispersed colonies of *Acropora palmata*, *Diploria strigosa*, *D. clivosa*, and *Montastrea annularis*.

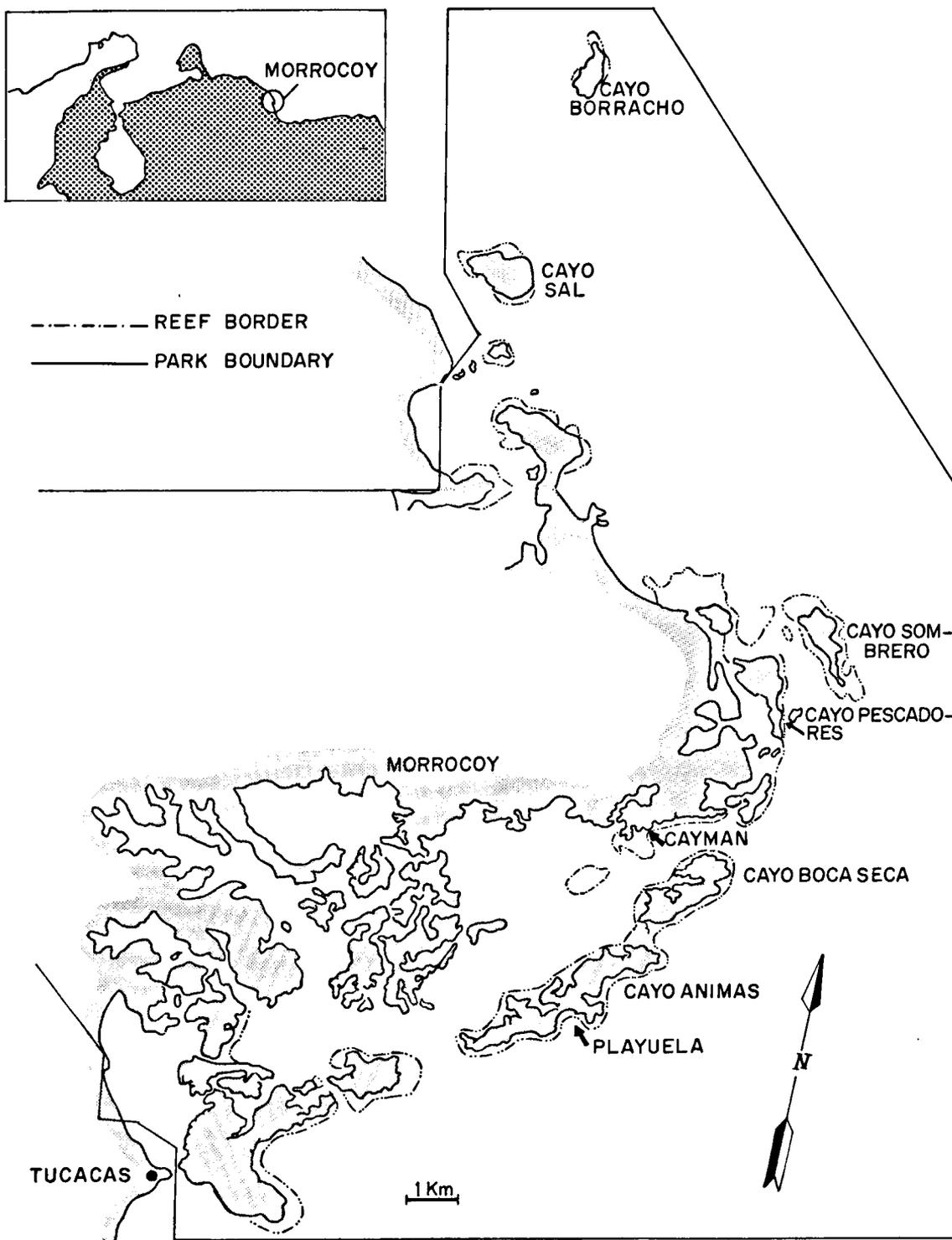


Fig. 1. Study area indicating sampling sites in Cayo Pescadores, Playuela, and Cayman, at the National Park of Morrocoy, Venezuela.

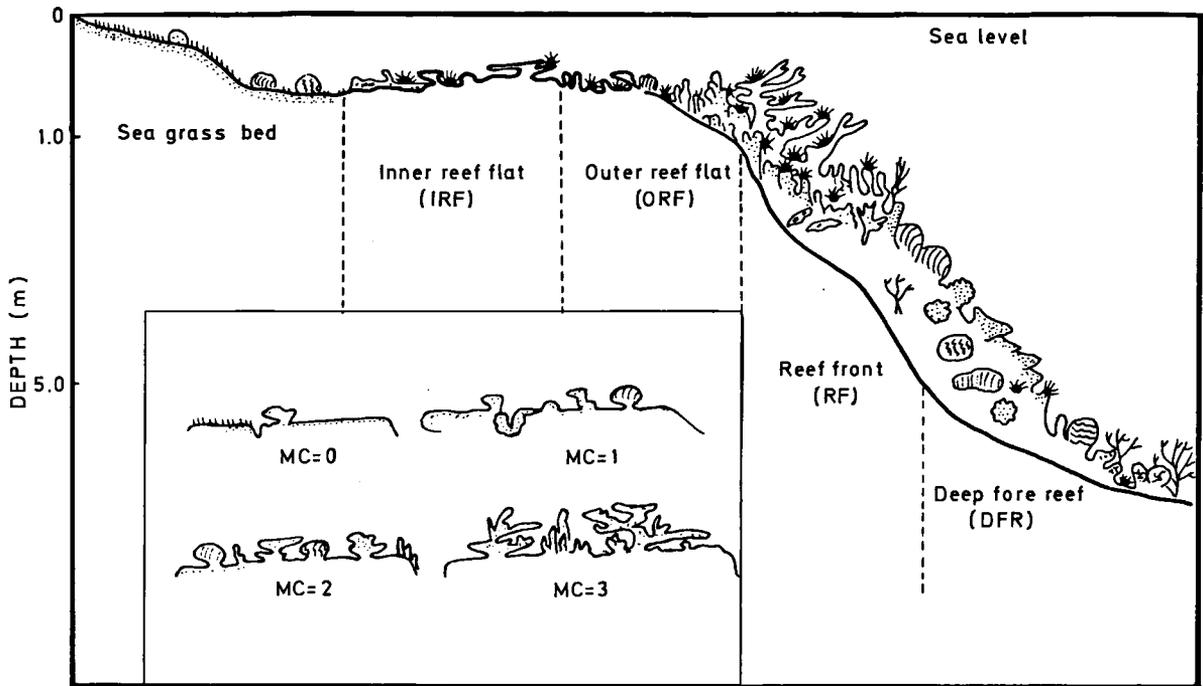


Fig. 2. Reef profile showing the different reef zones. The insert shows the arbitrary classification utilized to identify the morphological complexity of the reef.

(3) The reef front (RF), the upper slope of the deep surf zone with depths ranging from 1 to 5 m, dominated by *Acropora palmata*, *Montastrea annularis*, and the hydrocorals *Millepora alcicornis* and *M. complanata*.

(4) The deep fore reef (DFR), the deepest zone of the reef, characterized by a high coral diversity with dominance of *Montastrea annularis*, *Colpophyllia natans*, *Solenastrea bournoni*, and *Diploria strigosa*.

In each zone we arbitrarily selected sampling areas of 200 m² (4.0 × 50.0 m), parallel to the shore line, where all urchins were counted. In addition, 80 to 140 urchins were removed at random from each reef zone for size determination. Test diameter was measured with calipers.

Structural complexity

Structural complexity was determined by noting the growth morphology and abundance of the coral species at each zone. Thus we ar-

bitrarily classified the reef's morphological complexity (MC) as (fig. 2):

MC = 0. Sandy substrate, grass beds and/or flat platforms of dead coral with few incrusting species such as *Agaricia agaricites*.

MC = 1. Zones of low structural complexity formed by a flat platform of dead coral, with few crevices and few dispersed colonies of *Agaricia agaricites*, *Diploria clivosa*, and *D. labyrinthiformis*, of the incrusting and dome growth types.

MC = 2. Intermediate structural complexity with more crevices and/or refuges. The upper reef zone with low cover of the columnar forms of *Montastrea annularis*, and the hydrocorals *Millepora complanata* and *M. alcicornis*, or the deep reef with high cover and abundance of the coral species with a dome form such as *Colpophyllia natans*, *Diploria strigosa*, *D. labyrinthiformis*, *Solenastrea bournoni*, and plate and incrusting forms such as *Agaricia tenuifolia*, *A. lamarcki*, *A. grahamae*, *Madracis decactis*, and other species.

MC = 3. Highest structural complexity,

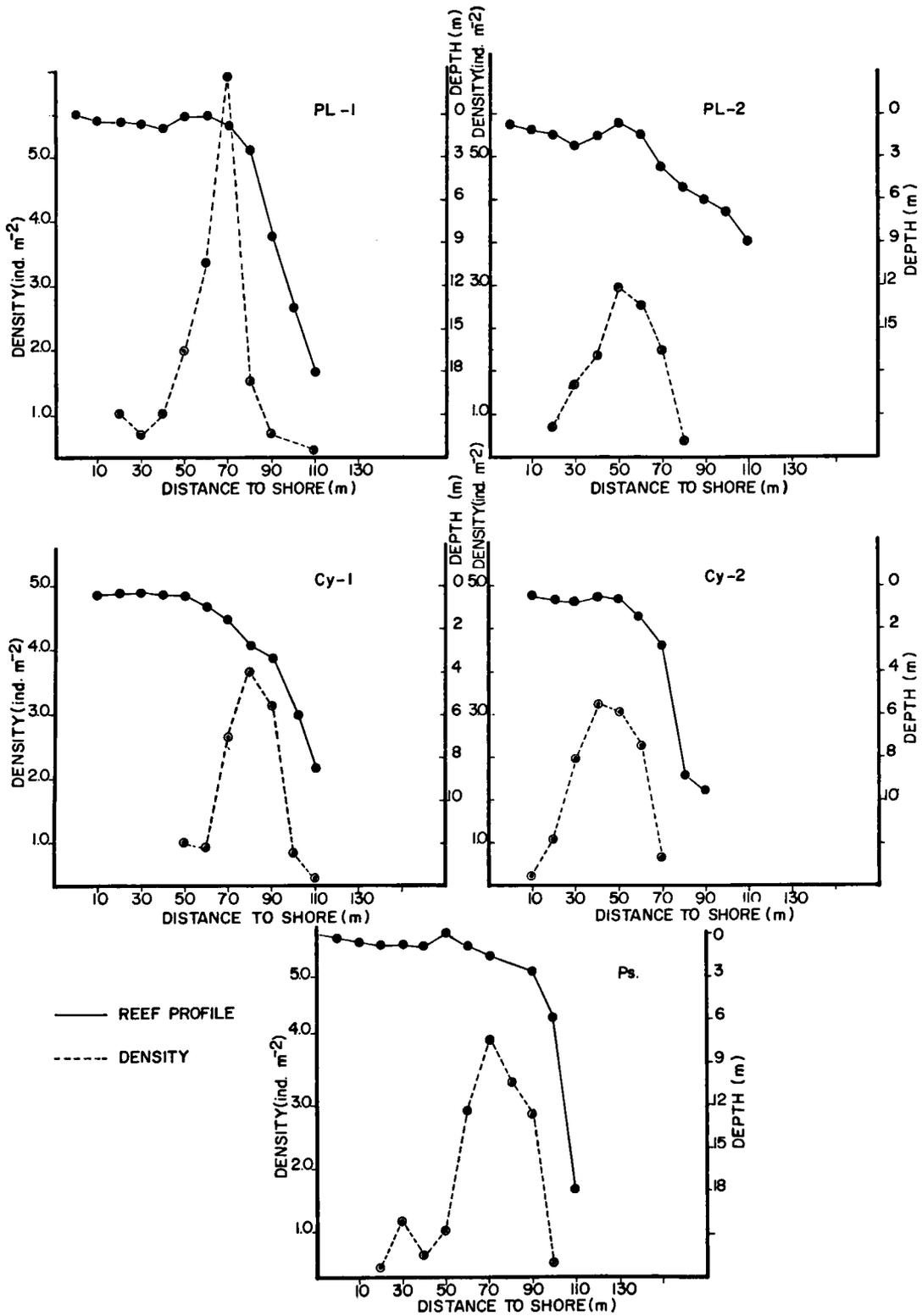


Fig. 3. Densities of *D. antillarum* along the reef profiles of the five sampling sites. (PL = Playuela, Cy = Cayman, and Ps = Pescadores.)

TABLE I

Mean density (ind. m⁻²) of *Diadema antillarum* in the four zones of each of the reefs studied in the Morrocoy National Park, Venezuela. \bar{X} is the arithmetic mean for the three reefs, and SD is the standard deviation of the mean.

Reef zone	Pescadores (ind. m ⁻²)	Playuela (ind. m ⁻²)	Cayman (ind. m ⁻²)	\bar{X}	SD
Inner reef flat (IRF)	1.56	2.67	3.99	2.74	0.99
Outer reef flat (ORF)	2.10	3.64	3.57	3.10	0.71
Reef front (RF)	6.96	3.39	6.47	5.60	1.58
Deep fore reef (DFR)	0.52	0.58	0.91	0.67	0.17

characterized by high abundance of the columnar and branch forms of *Montastrea annularis*, *Acropora palmata*, *A. cervicornis* and the hydrocorals *Millepora complanata* and *M. alcicornis*.

Cover of live and dead coral

The percentage of live and dead coral substrate was estimated using the line transect method (Loya, 1972) in exactly the same area where population densities were estimated.

RESULTS

For the three reefs studied, results obtained by both sampling methods showed that density varied according to reef profile and reef zone (fig. 3, table I). High population densities were found in the outer reef flat (ORF) and in the front reef (RF), while lower densities were found in the inner reef flat (IRF) and deep fore reef (DFR). Mean urchin densities in the three reefs were always lower than 4.0 ind. m⁻², but densities up to 13.0 ind. m⁻² were observed in single samples in the front reef zone.

Day and night differences in population densities were not significant (analysis of variance); therefore these data were pooled for further analysis.

The size structures of the urchin populations in the three reefs were similar. Urchins of intermediate sizes (5.0 to 8.0 cm in test diameter) were the most abundant (fig. 4). Small urchins were found mainly in the crevices and narrow holes of the outer reef flat and front reef and

were absent from the deep fore reef. Larger urchins were found in almost every zone.

When the mean size and density of *D. antillarum* were related to the morphological complexity of each zone of the reef, it was found that high mean urchin densities and small mean size classes were found in zones with intermediate and high morphological complexity (MC = 2, MC = 3) and vice versa in zones with

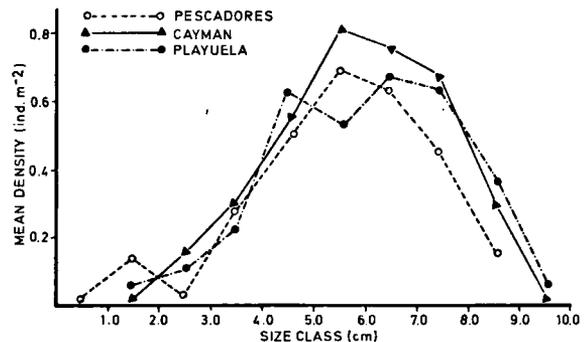


Fig. 4. Size structure of *D. antillarum* in the three reefs studied.

low morphological complexity (MC = 1) (fig. 5). Zones with high structural complexity were inhabited by urchins of all sizes which were hidden in the numerous refuges during daytime and moved out to feed at night. In open areas (IRF) the larger urchins were observed in aggregations during daytime; at night they moved around to feed. The deep fore reef, characterized by intermediate to high morphological complexity, was inhabited by few of the larger urchins (fig. 5).

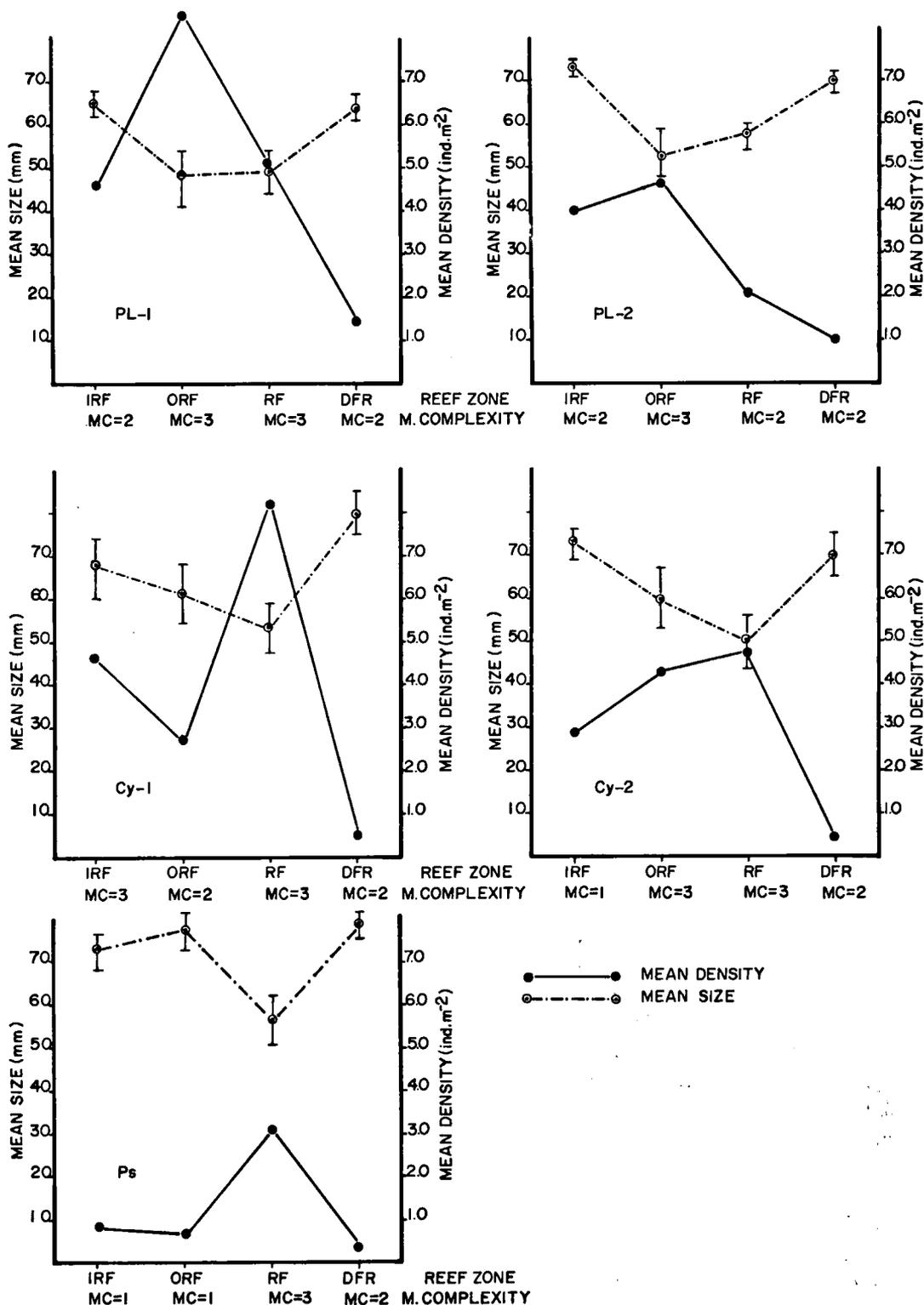


Fig. 5. Mean density and mean size of *D. antillarum* in each of the reef zones sampled for the five sampling sites. The morphological complexity (MC) of each zone is indicated by a value arbitrarily selected by the authors (see fig. 2), and ranges from 0 (lowest) to 3 (highest).

TABLE II
Densities of *Diadema antillarum* reported for different areas of the Caribbean.

Locality	Density (ind. m ⁻²)	Type of reef	Sampling method	Source
Virgin Islands	13.4	Rocky shore	Total removal of population	Randall et al. (1964)
St. Croix	6.0	Patch reef	Line transects	Ogden et al. (1973)
St. Croix	10.40	Patch reef	Total removal of population	Sammarco et al. (1974)
Curaçao	11.5	Fringing reef	Line transects	Bak & Van Eys (1975)
St. Croix	9.00	Patch reef	Total removal of population	Ogden & Zieman (1977)
Barbados	23.0	Fringing reef	Line transects	Stearn et al. (1977)
La Orchila, Venezuela	7.0-13.0	Fringing reef	Transects-quadrats	Urich (1977)
Jamaica	71.0	Fringing reef	Quadrats	Sammarco (1980)
Morrocoy, Venezuela	3.03	Fringing reef	Transects and quadrats	This study

A positive significant correlation ($P \leq 0.05$) was found between the percentage of dead substrate (coral platforms and rocks covered mainly by different algae species), and the mean densities of urchins (fig. 6).

DISCUSSION AND CONCLUSION

The densities of *D. antillarum* in the fringing reefs of Morrocoy are low when compared to those reported for other areas in the Caribbean (table II). In some cases, the great variation in densities reported could reflect the different sampling methods and reef conformations sampled, although even if the data gathered with similar methods and in similar reef conformations are compared, marked differences in population densities are still found. A good example is found in the comparison between the high densities of 23.0 ind. m⁻² reported for Barbados (Stearn et al., 1977) with the intermediate densities of 11.5 ind. m⁻² for Curaçao (Bak & Van Eys, 1975), 7.0-13.0 ind. m⁻² for La Orchila (Urich, 1977) and the relative low densities of 1.6-4.0 ind. m⁻² found in this study.

In Morrocoy, as in most fringing reefs in the Caribbean, the upper reef zone, generally subjected to strong wave action, is typically formed by the branching structures of *Acropora palmata*, *A. cervicornis*, the columnar form of *Montastrea*

annularis and the leaf and branch types of the hydrocorals *Millepora complanata* and *M. alcicornis*.

In reefs with less wave action, the upper reef is mainly formed by the columnar and massive forms of *Montastrea annularis*, the branch and fragile forms of *Acropora cervicornis* and the hydrocorals *Millepora alcicornis* and *M. complanata*. Nonetheless, both habitats are struc-

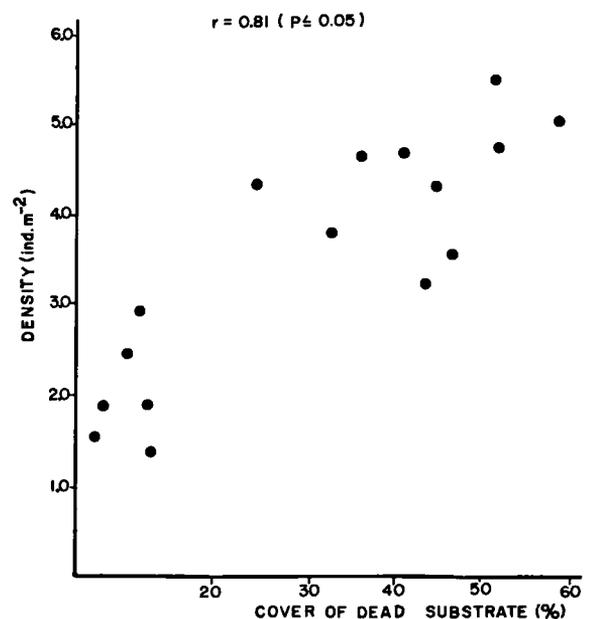


Fig. 6. Correlation (r Pearson) between the mean densities of *D. antillarum* and the cover of dead substrate (%). Data were pooled for the three reefs studied.

turally highly complex and support high population densities of *D. antillarum*, with a wide population size structure.

According to Randall et al. (1964) the spatial complexity of the habitat and the predation pressure are among the main factors affecting the distribution and population parameters of these urchins. Ogden et al. (1973) reported that the high densities of *D. antillarum* found in some areas of the Caribbean reflect the low abundance or absence of its predators which are mainly fish. Fricke (1974) and Glynn et al. (1979) reported that the predator pressure affected the distribution and behaviour of the sea urchins *Diadema setosum* and *Eucidaris thouarsii*, respectively. In areas where the main predators were absent, the urchins did not aggregate and were active throughout the day.

In Morrocoy we have observed high abundances of 10 of the 15 predating fish species reported by Randall et al. (1964), and the lobster *Panulirus argus*, which is considered one of the most important predators of small urchins, was frequently observed. The urchins were aggregated in the open areas or hidden in the refuges provided by the more morphologically complex reef zones during the day; their feeding activity begins in the evening and they return back to the refuges (not necessarily the same ones) or aggregate by the early morning.

A high correlation between the size of *D. antillarum* and the diameter of the holes and crevices where they hide has also been demonstrated (Urich, 1977), which in conjunction with our results suggests that the type and quality of the refuges is an important factor in the distribution of the urchins.

It is also possible that the intraspecific competition in overpopulated reefs might force the urchins to adjacent reef areas or other communities such as *Thalassia* beds (Ogden et al., 1973) and that the numerous aggregations of *Diadema* observed in the wide open areas occur when the population densities exceed the availability of proper refuges in the more complex reef areas.

We found a positive correlation between urchin density and the percentage of dead coral substrate.

The upper illuminated reef zones (RF, IRF) are characterized by large areas of dead substrate which support an abundant community of the fast growing green, red filamentous and calcareous algae which constitute the main food resource of these urchins (Randall et al., 1964; Lewis, 1964; Sammarco et al., 1974; Hawkins, 1981). The contrary is the case on the deep fore reef. According to Bak & Van Eys (1975), the migration of *D. antillarum* from the deep reef to the upper reef during their feeding activity at night may explain the significant differences found only at this period among the three reef zones studied by them.

At dawn, the sea urchins return to the deep reef apparently because there are no available refuges in the upper reef.

In Morrocoy, we did neither observe migrations from one zone to another, nor did we find significant diel differences in urchin density. The main significant differences in density and size structure were found between the different reef zones and even between areas of the same reef zone where the morphological complexity varied.

In conclusion, the density, distribution, and size structure of the *D. antillarum* populations along the reef is the result of the interaction of many variables. The morphological complexity of the reef inhabited, the food availability, and the predation pressure appear to be the main ones.

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REFERENCES

- ANONYMOUS, 1978. Parques Nacionales y Monumentos naturales de Venezuela: 1-225 (Instituto Nacional de Parques, Ministerio del Ambiente y de los Recursos Naturales no Renovables, Venezuela).

- BAK, R. P. & G. VAN EYS, 1975. Predations of the sea urchins *Diadema antillarum* Philippi on living coral. *Oecologia*, **20**: 111-115.
- FRIECKE, J. C., 1974. Possible influence of predators on the behavior of *Diadema* sea urchins. *Oecologia*, **18**: 59-62.
- GLYNN, P. W., G. M. WELLINGTON & C. BIRKELAND, 1979. Coral reef growth in the Galápagos: Limitation by sea urchins. *Science*, **203**: 43-49.
- HAWKINS, C. M., 1981. Efficiency of organic matter absorption by the tropical sea echinoid *Diadema antillarum* Philippi fed on macrophytic algae. *J. exp. mar. Biol. Ecol.*, **49**: 245-253.
- HUNTER, U. G., 1977. Sediment production by *Diadema antillarum* Philippi on a Barbados fringing reef. Proc. third int. Coral Reef Symposium, Miami, **2** (Geology): 105-109.
- KÖPPEN, W., 1900. Versuch einer Klassifikation der Klimate, vorzugsweise nach ihren Beziehungen zur Pflanzenwelt. *Geograph. Zeitschr.*, **6**: 593-611; 657-679, pls. 6-7.
- LEWIS, J. R., 1964. Feeding and digestion in the tropical sea urchin *Diadema antillarum* Philippi. *Can. J. Zool.*, **42**: 549-557.
- LOYA, Y., 1972. Community structure and species diversity of hermatypic corals at Eilat, Red Sea. *Mar. Biol.*, **13**: 100-123.
- MORTENSEN, T., 1940. A monograph of the Echinoidea, **3** (1-2). *Aulondonta* (with additions to Vol. 2): 1-370, 1-22 (C. A. Reitzel, Copenhagen).
- OGDEN, J. C., 1976. Some aspects of herbivore-plant relationships on Caribbean reefs and sea grass beds. *Aquatic Bot.*, **2**: 103-116.
- OGDEN, J. C., R. A. BROWN & N. SALESKY, 1973. Grazing by the echinoid *Diadema antillarum* Philippi: formation of halos around West Indian patch reefs. *Science*, **182**: 715-717.
- OGDEN, J. C. & P. S. LOBEL, 1978. The role of herbivorous fishes and urchins in coral reef communities. *Envir. Biol. Fish.*, **3** (1): 49-63.
- OGDEN, J. C. & J. C. ZIEMAN, 1977. Ecological aspects of coral reef — sea grass bed contacts in the Caribbean. Proc. third int. Coral Reef Symp., **1**: 377-383.
- PEARSE, J. C. & S. W. ARCH, 1969. The aggregation behaviour of *Diadema* (Echinodermata: Echinoidea). *Micronesica*, **5**: 165-171.
- RANDALL, J. E., R. E. SCHOEDER & W. STARCK II, 1964. Notes on the biology of the echinoid *Diadema antillarum*. *Caribb. J. Sci.*, **4** (23): 421-433.
- SAMMARCO, P. W., 1972. Some aspects on the ecology of *Diadema antillarum* Philippi: food preference and effect of grazing. Special problems report to the West Indies Laboratory of Fairleigh Dickinson University, Christiansted, St. Croix: 1-47.
- , 1980. *Diadema* and its relationships to coral spat mortality: grazing, competition and biological disturbance. *J. exp. mar. Biol. Ecol.*, **45**: 245-272.
- SAMMARCO, P. W., J. S. LEVINTON & J. C. OGDEN, 1973. Studies on the activity and food of the echinoid *Diadema antillarum* Philippi on a West Indies patch reef. *Publ. West Indies Laboratory, St. Croix*, **2**: 1-65.
- , — & —, 1974. Grazing and control of coral reef community structure by *Diadema antillarum* Philippi. A preliminary study. *J. mar. Res.*, **32** (1): 47-53.
- SCOFFIN, T. P., C. W. STEARN, D. BOUCHER, P. FRYDL, C. M. HAWKINS, I. G. HUNTER & J. K. McGEACHY, 1980. Calcium carbonate budget of a fringing reef on the west coast of Barbados, 2. Erosion, sediments and internal structure. *Bull. mar. Sci.*, **30**: 475-508.
- STEARNS, C. W., T. P. SCOFFIN & W. MARTINDALE, 1977. Calcium carbonate budget on a fringing reef on the west coast of Barbados, 1. Zonation and productivity. *Bull. mar. Sci.*, **27**: 479-510.
- URICH, J., 1977. Estructura comunitaria de un arrecife coralino al sur oeste de La Orchila, Venezuela: 1-147 (Tesis de grado Universidad Central de Venezuela).