Caribbean Journal of Science, Vol. 34, No. 3-4, 250-264, 1998
Copyright 1998 College of Arts and Sciences
University of Puerto Rico, Mayagüez

Patterns of Octocoral and Black Coral Distribution in the Oceanic Barrier Reef-complex of Providencia Island, Southwestern Caribbean

JUAN A. SÁNCHEZ,[1,2] SVEN ZEA,[1,3] AND JUAN M. DÍAZ[1]

[1]*Instituto de Investigaciones Marinas y Costeras-INVEMAR, AA 1016, Santa Marta Colombia*
szea@santamarta.cetcol.net.co, jmdiaz@ santamarta.cetcol.net.co
[2]*Present address: University at Buffalo, State University of New York, Department of Biological Sciences, 109 Cooke Hall,*
Box 601300, Buffalo, New York, 14260-1300
js15@acsu.buffalo.edu
[3]*Universidad Nacional de Colombia, Departamento de Biología*

ABSTRACT.—**Variation in the composition and density of the soft coral community in Providencia island, an oceanic barrier reef-complex (Caribbean Sea, Colombia), was examined through classification and ordination of per-species density (28 stations; 1-50 m in depth). Forty-seven species were recorded, including 44 octocorals (Gorgonacea), and three black corals (Antipatharia). The stations were grouped in six minimal clusters, represented geomorphological zones, and implied differences in inclination, depth, wave exposure, and relief. The deep (30-50 m) and inclined slope, inhabited by aposymbiotic octocorals and black corals, had a lower species number and colony density, when compared to the shallower (1-30 m) and less inclined upper insular platform dominated by symbiotic octocorals. Changes in community composition, within the upper platform, related to degree of wave exposure were depth-dependent. Shallower (1-8 m) stations did not group in relation to degree of wave exposure. Indeed, the shallower groups differed from the others by the absence or low density of species which were common elsewhere, indicating that historical events of localized impact (e.g., storms, mass mortalities) may play a significant role in the current community. In contrast, deeper stations grouped in relation to the degree of wave exposure. Wave-exposed, low-relief fore-reef terrace stations (25-30 m) had greater species richness, colony density, and cover, when compared with the wave-protected high-relief lagoonal patch-reefs (6-16.5 m) and the leeward terrace margin (17.5-22 m). These differences can be attributed to the greater degree of wave exposure of the former, associated with water flushing and transparency, and hence better oxygen exchange, suspended particle flow, and photosynthetic rates.**

RESUMEN.—**La variación en la composición y la densidad de la comunidad de corales blandos en la isla de Providencia, un complejo arrecifal oceánico de barrera (Mar Caribe, Colombia), fue examinada mediante clasificación y ordenación de datos de densidad por especies, (28 estaciones; 1 a 50 m de profundidad). Cuarenta y siete especies fueron registradas, incluyendo 44 octocorales (Gorgonacea) y tres corales negros (Antipatharia). Las estaciones se agruparon en seis grupos mínimos, representando zonas geomorfológicas, y con diferencias en la inclinación, profundidad, exposición al oleaje y relieve. El talud, profundo (30-50 m) e inclinado, habitado por octocorales sin simbiontes fotosintéticos y corales negros, tuvo menor número de especies y de densidad de colonias, en comparación con la plataforma insular superior, más somera (1-30 m) y menos inclinada, dominada por octocorales con simbiontes. Los cambios en la composición comunitaria, sobre la plataforma superior, en relación con el grado de exposición al oleaje dependieron de la profundidad. Las estaciones someras (1-8 m) no se agruparon en relación con el grado de exposición al oleaje. Es más, los grupos someros difirieron entre sí por la ausencia y baja densidad de especies que eran comunes para todos, indicando que eventos históricos de impacto localizado (p.ej., tormentas, mortalidades masivas) juegan un papel significativo en la comunidad actual. En cambio, las estaciones profundas sí se agruparon en relación con el grado de exposición al oleaje. Estaciones de la terraza prearrecifal (25-30 m), expuestas al oleaje y con bajo relieve, tuvieron mayores valores en cobertura de colonias, riqueza de especies y densidad, en comparación con los arrecifes, protegidos del oleaje y con alto relieve, de la laguna (6-16.5 m) y del margen de la terraza de sotavento (17.5-22 m). Estas diferencias pueden ser atribuidas al mayor grado de exposición al oleaje en las primeras, asociado con flujo de agua y transparencia, y por lo tanto mejor intercambio de oxígeno, flujo de partículas en suspensión y tasas fotosintéticas.**

INTRODUCTION

Caribbean coral reefs are conspicuously and abundantly inhabited by soft corals, particularly octocorals and black corals. Physiognomically and structurally, octocoral and black coral colonies hold most of their biomass well above the substratum, where hydrodynamic forces have a strong influence; their bushy-, tree-, fan- and whip-shaped colonies remain in a vertical layer different for that of corals, algae, and most other sessile organisms that control substratum availability (Jackson, 1977). The success of soft corals is due in part to their ability to withstand physical forces (Vogel, 1983) and their efficiency as colonial photosynthetic suspension feeders of the reef (Lasker et al., 1983; Dai and Lin, 1993). They provide refuge to diverse organisms, such as algae, sponges, copepods, mollusks, polychaetes, and fishes. This is in part brought about by the deterrent activity of secondary metabolites produced by some species and by providing a physical barrier to factors which an organism may encounter in open reef areas.

Providencia island (Old Providence) is located in the Southwestern Caribbean sea, among the oceanic islands, atolls, and banks of the San Andrés and Providencia Archipelago, off the Nicaraguan shelf but belonging to the Republic of Colombia (Fig. 1). The barrier reef-complex of Providencia is an extensive calcareous platform around an extinct Miocene volcano. The present complex consists of a 32 km-long windward barrier reef, the second largest of the Caribbean Sea, enclosing numerous inner reefs. Descriptions of the reef complex of Providencia island are given by Márquez (1987) and Geister (1992). The great geomorphological diversity of the reef complex allows for the existence of different habitats with a wide range of wave energy regimes, depths, and substratum types the most important factors controlling the distribution of soft corals on coral reefs (Kinzie, 1973; Yoshioka and Yoshioka, 1989, 1991). The present study describes quantitatively the soft coral community in terms of species composition and abundance, relating its spatial variation with major environmental factors.

METHODS

To survey the soft coral community, 28 stations were sampled in different reef habitats and zones throughout the reef-complex (Fig. 2). In each station, using SCUBA diving, a rapid quantitative method was used; soft coral colonies in approximately 1 m-wide, 20-50 m-long linear corridors within a homogeneous habitat were counted for 15-30 min. Exact time and length of each corridor varied depending on apparent community complexity (i.e., number of species, density, etc.). This method is similar to others used with gorgonians (Alcolado, 1981) and black corals (Grange, 1985). To account for differences in soft coral density and to minimize the error generated by variation in census duration and swimming speed, absolute total density was estimated at each station counting all colonies in three, 1 m-radius circles (9.424 m^2). Total density was then used to calculate the per-species abundance (colonies per 10 m^2) from the relative abundance of the species in the linear censuses. In addition, the total "cover index" per station, a size estimator of biomass for erect organisms (Müller-Dombois and Ellenberg, 1974; Jordán and Nugent, 1978), was calculated from projected lengths in three dimensions (height, maximal, and minimal diameter in upper-view), measured by a 1 m-long graduated rod in 12 colonies chosen by the wandering quarter method (Catana, 1963).

Although most species were identified in the field, fragments of all were collected, fixed in ethanol 70%, and examined for external and spicular characteristics according to Bayer (1961). Erect sponges and hydroid species reaching up to the soft coral layer were not recorded. Stations were assigned a level of wave-exposure (low, mid-low, mid-high, high) according to the reef zone, depth, and the pattern of wave refraction shown in panchromatic aerial photographs. To relate patterns of soft coral species distribution and abundance to reef types and zones, and to their predominant environment, the 28 quantitative stations were grouped by a hierarchical cluster analysis using species density data ($\log_{10}$ X+1 transformed), the Bray-Curtis

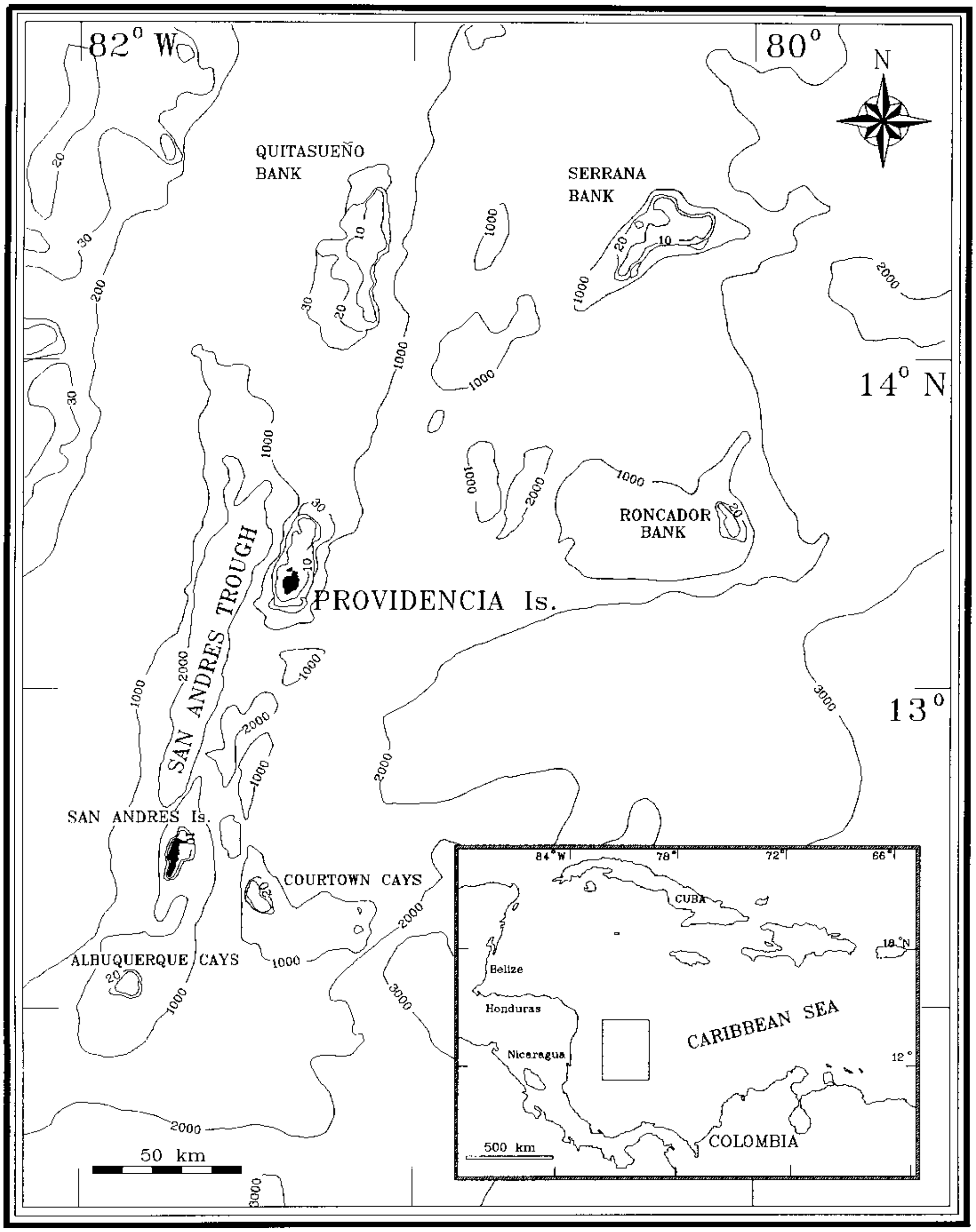

FIG. 1. Southwestern Caribbean and the location of the archipelago of San Andrés and Providencia, Colombia.

dissimilarity index (Bray and Curtis, 1957), and the unweighted pair group dendrogram construction method (UPGMA: Field et al., 1982). Groups of stations for further community characterization were delimited within the dendrogram as those minimal clusters having the best internal consistency in terms of the sampling scheme (i.e., reef type or zone, depth, degree of wave exposure). Species charac-

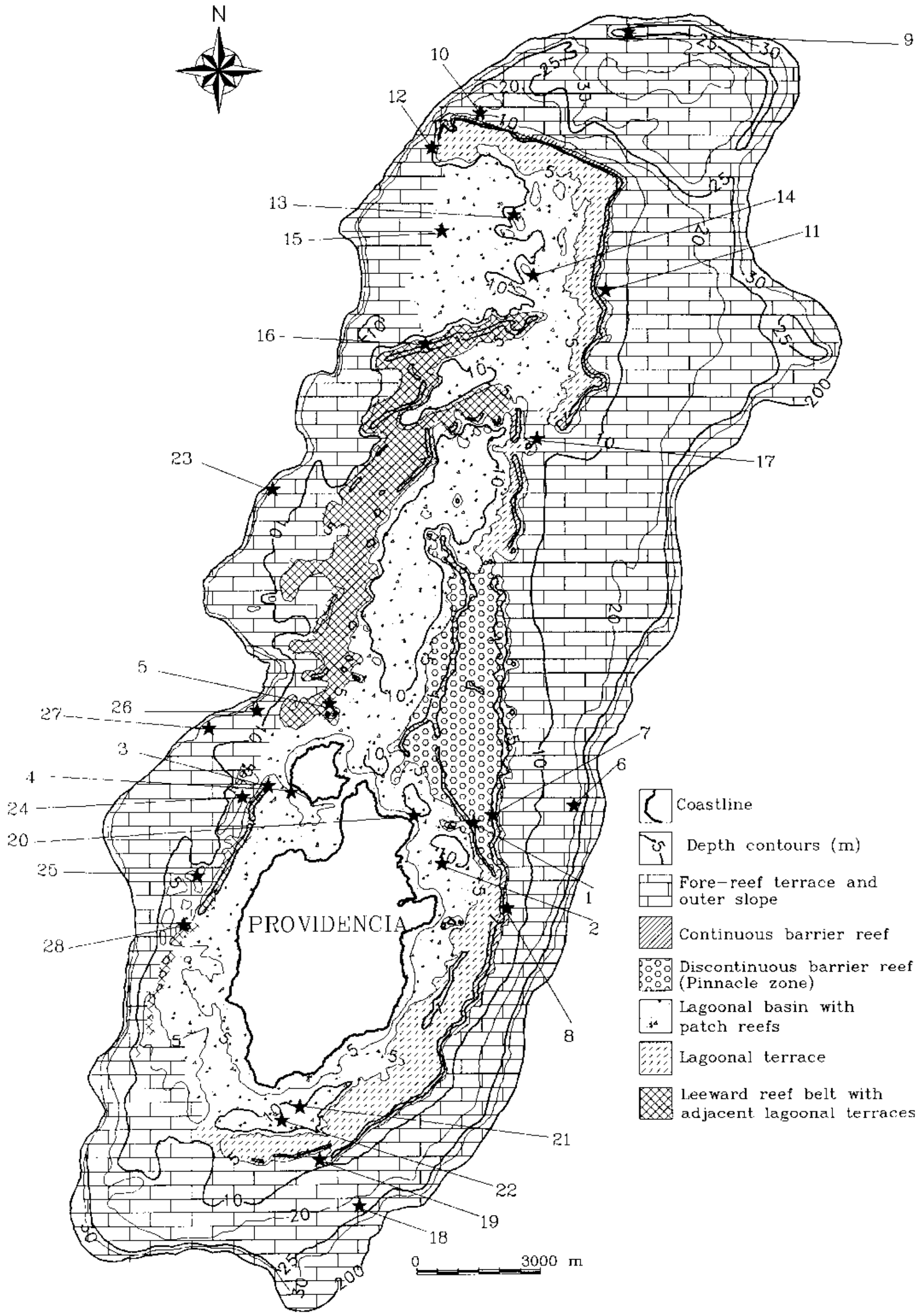

FIG. 2. Geomorphological features of the barrier reef-complex of Providencia island. Numbers and stars correspond to sampling stations.

teristic of each successively nested cluster within the dendrogram were determined by recalculating mean species density for each minimal cluster, then accumulating their density from higher to lower and successively marking those minimal clusters which contained at least 90% of the species' total abundance. Species were then recorded and grouped according to membership within a given cluster or nest of clusters (Kaandorp, 1986). To further relate station species composition to community (i.e., total density, number of species, cover index) and environmental parameters (i.e., depth, degree of wave exposure), the magnitudes of the latter were superimposed on nonmetrical multidimensional scaling (NMDS, 2 dimensions) station ordination plots obtained from the Bray-Curtis dissimilarity index matrix (Field et al., 1982).

RESULTS

Forty-four species of octocorals (Octocorallia, mainly Gorgonacea) and three of black corals (Antipatharia) comprised the soft coral community. Thirty-five species of octocorals are described species while 11 are possibly undescribed plexaurid gorgonians (complete list and abundance per species in Table 2). Number of species per station varied between 4 and 26 (mean 11.9). Total density per station varied between 2.0 col.[10 m]$^{-2}$ and 99.8 col.[10 m]$^{-2}$ (mean 32.1 col.[10 m]$^{-2}$), while the highest density that a single species reached in a given station was 20.5 col.[10 m]$^{-2}$. The 28 sampling stations were grouped into six minimal clusters, at dissimilarities lower than about 0.7 (Fig. 3). Non-metric Multidimensional Scaling ordination (Fig. 4) also segregated stations according to classification clusters. Most clusters represented single or combined reef types or reef zones (Table 1). All upper platform stations separated from the only station quantified on the steeply inclined (>45°) and deep outer slope (cluster F, station 27, 30-50 m, Fig. 1, Fig. 4, Table 1). Within the upper platform, shallow and mid-depth clusters A, B and C, segregated from the generally deeper clusters D and E (Figs. 3 and 4). Cluster A represented stations located on the shallow (1-4 m) pinnacles of the discontinuous barrier reef and on the spur-and-groove system of the continuous barrier reef (stations 1, 7, 11). Cluster B grouped stations 21 and 22, located on the mid-depth (4-8 m) patch reefs of the southern lagoon.

The remaining shallow and mid-depth (1-8 m) stations were grouped in Cluster C, and located in a mixture of reef types and zones with varied degrees of wave exposure (Fig. 4), i.e., on shallow lagoonal and coastal reefs (stations 2, 3, 4, 5, 20, see Fig. 5a), on the leeward reef belt (stations 3, 16, 24, 25, 28[Fig. 5b]) and on the windward inner fore-reef terrace off the barrier reef (stations 8, 10, 17, 19). Deeper stations on the upper platform were clustered in two groups according to degree of wave exposure and bottom relief (Fig. 4). The first (Cluster D) was composed of the stations located on the deep (25-30 m), low-relief windward fore-reef terrace (stations 6, 9, 18 [Fig. 5c], and including station 12, an outlier located in a shallower, ca. 3 m depth site in the inner windward fore-reef terrace off an algal ridge); the second (Cluster E) was composed of those stations located on the high-relief, mid-depth, and deep (6-16.5 m) patch reefs of the northern lagoon (stations 13, 14, 15, see Fig. 5d), and the deep (17.5-22 m), leeward terrace margin (stations 23 and 26). There were general differences in soft coral community structure and composition between reef types and zones, whose distribution follow the main geomorphology of the island reef-complex, which in turn depends mainly on a combination of overall substratum inclination, depth, degree of wave exposure and bottom relief. These relations are described below.

Relation to depth and overall substratum inclination: upper insular platform vs. outer slope

There were consistent differences in the composition of the soft coral community between the insular platform and the outer slope, which can be related to depth and overall substratum inclination. The less inclined and shallower (up to 30 m) upper insular platform (clusters A to E) held more

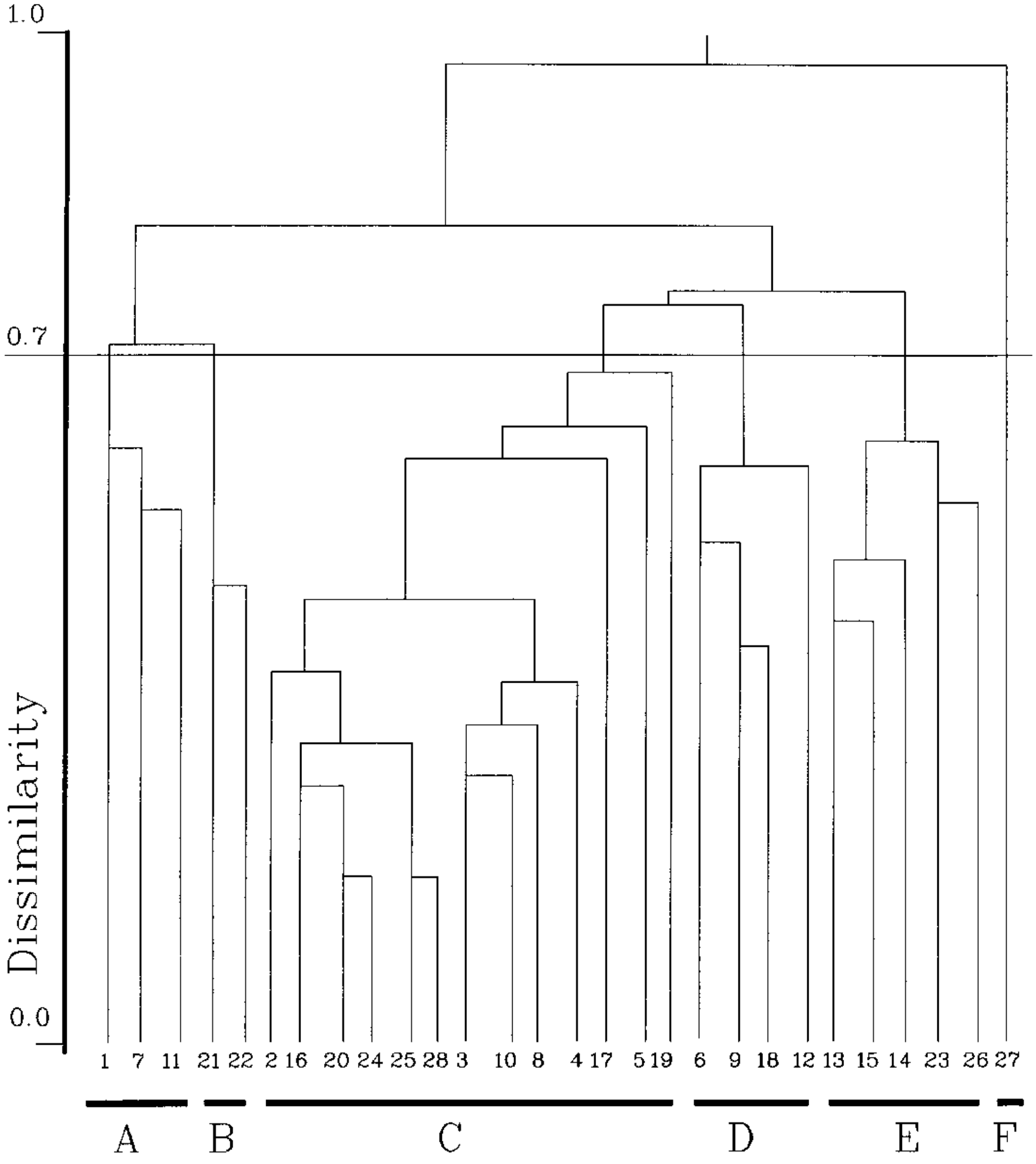

FIG. 3. Cluster analysis: dendrogram of the 28 stations. Data were Log_{10} (X+1) transformed density (cols.[10 m]$^{-2}$). Minimal clusters are marked by capital letters. (Cophenetic Correlation Coefficient = 0.59).

gorgonian octocoral species (41) in relation to the deeper and steeply inclined outer slope (cluster F, 10 species, quantified in a single station), although mean number of species (10) and total density (28.8 col.[10 m]$^{-2}$) of the latter (Table 1) were near the overall average (11.9 species and 32.1 col.[10 m]$^{-2}$ respectively). The upper platform had several widespread species; *Briareum asbestinum* (Pallas, 1766) and *Plexaura flexuosa* Lamoroux, 1821 were present throughout the upper platform, in varying densities among clusters. In contrast, only 2 of the 39 species characteristic of any one cluster of the upper platform were also characteristic of the outer slope, being present only on the deeper platform zones (clusters D, E and F, *Eunicea* sp. 1, *Eunicea*

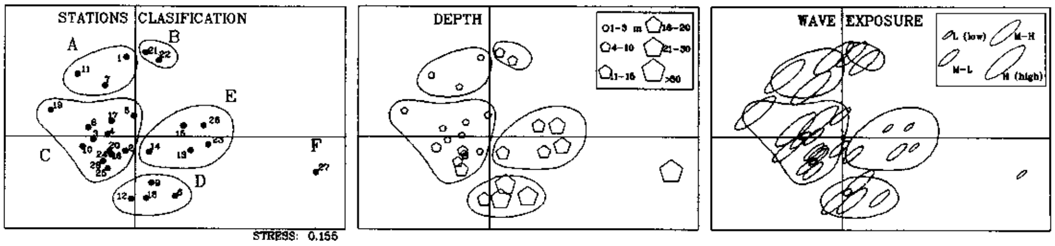

FIG. 4. Nonmetrical multi-dimensional scaling (NMDS) ordination of stations (data as in Fig. 3). Stations encircled correspond to dendrogram (Fig. 3) clusters.

sp. 4, see Table 2). The outer slope had eight characteristic species, the most abundant being the antipatharian *Stichopates* spp. and the gorgonian octocoral *Pseudoplexaura* sp. 2. In contrast to the upper platform, in which all species were zooxanthellated octocorals, the most abundant species of the outer slope (*Ctenocella schmitti* [Bayer, 1961], *C. barbadensis* [Duch. & Mich. 1864], *Antipathes atlantica* Gray, 1857, *A. caribbeana* Opresko, 1996 and *Stichopathes* spp.) were exclusive to this zone and were either aposymbiotic octocorals or antipatharians (Table 2).

Relation to depth, degree of wave exposure and bottom relief within the upper insular platform

Depth. Soft coral community composition varied partly in relation to depth within the upper insular platform. Clusters D and E included a few mid-depth stations and all the deepest had a greater number of species (38 combined) and mean number of species per stations (>11.5), when compared to clusters A, B and C. The latter included all shallow and the remaining mid-depth stations (24 species combined, <11.5 species per station) (Table 1). Density and cover indexes did not follow the same depth pattern (Table 1).

Degree of wave exposure: shallow and mid-depth reefs. Differences in soft coral community composition related to degree of wave exposure were depth-dependent. Shallower clusters (A, B and C) showed no consistent differences in community composition in relation to location within the insular shelf, which in turn determines the overall degree of wave exposure. Although clusters A and B correspond to stations located in particular reef types with consistent differences in degree of wave exposure (highly surf-exposed *Millepora* spp. pinnacles and spurs for A, *Montastraea* spp. more wave-protected and slightly deeper (4-8 m) patch reefs of the southern lagoon for B), cluster C was represented by various types of coastal, lagoonal, leeward and windward reef types and zones, from the surf down to 8 m in depth. Differences in composition and density between these three shallower clusters were due to the absence and low density of certain soft coral species in clusters A and B which were otherwise common and widespread on shallow areas or on the entire upper platform. For example, *Pseudoplexaura porosa* (Houttuyn, 1772), *Gorgonia ventalina* L. 1758, *Plexaura* sp., *Eunicea mammosa* Lamoroux, 1816, and *Plexaura dichotoma* (Esper, 1791), although widely distributed on the upper platform, were characteristic of (i.e., at least 90% of their abundance was contained in) cluster C-D-E (Table 2). Furthermore, *Pseudoplexaura flagellosa* (Houttuyn, 1772), *Eunicea succinea* (Pallas, 1766), *Plexaurella grisea* Kunze, 1916, *Plexaura* sp., *Plexaurella* sp., *Pseudopterogorgia americana* (Gmelin, 1791), *Muriceopsis flavida* (Lamarck, 1815) and *Eunicea* sp. 2, were widespread or characteristic on the upper platform except for their absence or low density on clusters A and B (Table 2).

The only species found in all shallow clusters (A to C) were *Plexaura homomalla* (Esper, 1792) and *Pseudoplexaura crucis* Bayer, 1961, but they were characteristic only of cluster C, being sparsely distributed in the other two shallow clusters. Indeed, clusters A and B had only 12-13 species (vs.

TABLE 1. Number of species, density and cover index of soft corals for the clusters defined in Fig. 3. Data are mean ± standard deviation.

	Cluster					
	Shallow barrier reef pinnacles and spurs A	Mid-depth patch reefs S. Lagoon B	Shallow and mid-depth mixture C	Deep windward fore-reef terrace[1] D	Mid-depth reefs N. lagoon and deep leeward terrace E	Outer slope[2] F
Depth	(1-4 m)	(4-8 m)	(1-8 m)	(25-30 m)[1]	(6-22 m)	(30-50 m)
No. stations	3	2	13	4	5	1
No. Species						
Total	12	13	23	30	27	10
Mean	6.7 ± 2.1	11.0 ± 1.4	11.5 ± 3.4	18.0 ± 6.3	11.6 ± 2.9	
Mean density (cols. $[10\ m]^{-2}$)	2.71 ± 0.85	2.11 ± 0.18	41.00 ± 28.69	45.52 ± 33.76	28.78 ± 6.91	28.53
Mean cover index (c.i. $[10\ m]^{-2}$)	2.51 ± 0.52	2.11 ± 0.18	41.15 ± 28.65	45.39 ± 33.81	28.33 ± 6.47	NR[2]

[1] Includes station 12, located in a shallow (1-3 m), inner fore-reef terrace habitat off a wave-swept algal ridge.

[2] NR-not recorder due to limitations in safe diving bottom time.

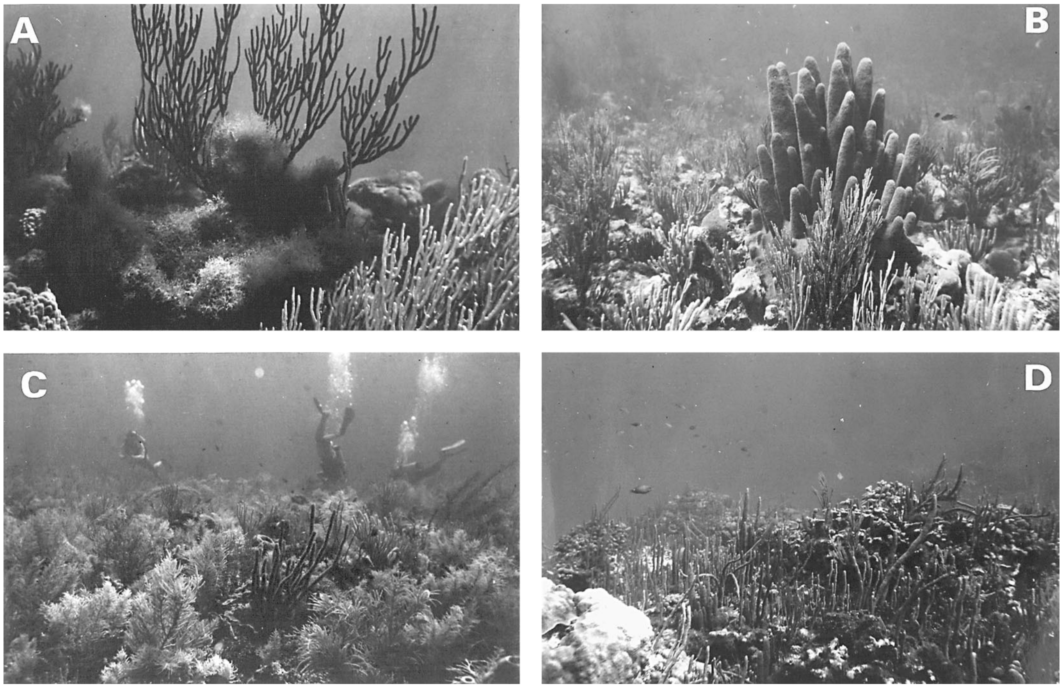

FIG. 5. (A) Mid-depth patch reefs of the southern at lagoon Maracaibo Hill, 1.5 m in depth; *Plexaura homomalla* and *P. flexuosa* with strong invasion of the alga *Ceramiun nitens* (st. 20). (B) Leeward reef belt off Fresh Water Bay, 4 m in depth; coral at center is *Dendrogyra cylindrus* (st. 28). (C) Deep windward fore-reef terrace off Tinkhams Cut, 24 m in depth; luxuriant *Pseudopterogorgia* spp. and *Eunicea* spp. growth (st. 18). (D) *Montastraea* patch reefs of the northern lagoon, 5 m, dense octocoral is *B. asbestinum* with fast vegetative propagation (st. 14).

22 in cluster C), in total densities of up to 2.7 col.$[10\ m]^{-2}$ (vs. 41 col.$[10\ m]^{-2}$ in cluster C) (Table 1). Cluster B stations, located in mid-depth (4-8 m) patch reefs of the southern lagoon, were surprisingly different in terms of soft coral community composition and abundance from the slightly deeper (6-16.5 m) patch reefs of the northern lagoon (part of cluster E), which were otherwise similar in their overall physiognomy, degree of wave protection, and their dominant coral species (*Montastraea* spp.).

Degree of wave exposure and bottom relief: deeper reefs. In contrast to shallower clusters, the generally deeper clusters D and E showed consistent differences in soft coral community composition in relation to a combination of depth, degree of wave exposure and bottom relief. The deep (25-30 m), low reef-relief, windward fore-reef terrace represented the greatest soft coral community development, with the greatest species richness (total of 30 species, mean 18.0 species per station) and the highest total density (mean 45.5 col.$[10\ m]^{-2}$). In comparison, the slightly shallower (6-22 m) but wave-protected and higher relief mid-depth and deep reefs of the northern lagoon and the leeward terrace margin (cluster E), had slightly fewer species (30 in total, 11.6 species per station), and a much lower total density (mean 28.8 col.$[10\ m]^{-2}$).

Windward fore-reef terrace stations had 10 characteristic species, 8 of which were exclusive to them; of these, *Pseudopterogorgia kallos* (Bielchowsky, 1929), *Pterogorgia citrina* (Esper, 1792), *P. anceps* (Esper, 1792) and *Pseudopterogorgia* sp. 1 occurred in mean densities greater than 1 col. $[10\ m]^{-2}$ (Table 2). In contrast, north lagoonal and leeward terrace margin stations had only four characteristic species (three exclusive), two of them (*Pseudopterogorgia bipinnata* [Verrill, 1864], *P. elisabethae* Bayer, 1981) reaching mean densities greater than 1 col. $[10\ m]^{-2}$.

TABLE 2. Density of soft coral species in each cluster defined in Fig. 3. Data are mean ± standard deviation (col. [10 m]$^{-2}$). Boldfaced density values mark all the minimal clusters which contain at least 90% of a species' total density, accumulated from greater to lower, defining to which clusters the species is characteristic. Boxes mark all the species characteristic of each successively nested cluster. (—) = Absent. (A) = Antipatharia, black corals.

	Cluster					
Cluster(s)/Species	Shallow barrier reef pinnacles and spurs A	Mid-depth patch reefs S. Lagoon B	Shallow and mid-depth mixture C	Deep windward fore-reef terrace[1] D	Mid-depth reefs N. lagoon and deep leeward terrace E	Outer slope F
A-B-C-D-E						
Briareum asbestinum (Pallas, 1766)	0.34 ± 0.35	**0.92 ± 0.71**	**2.90 ± 3.31**	0.79 ± 0.46	**8.40 ± 9.44**	—
Plexaura flexuosa Lamoroux, 1821	**0.94 ± 0.22**	0.05 ± 0.03	**5.05 ± 4.53**	**3.04 ± 2.31**	0.14 ± 0.31	—
Plexaura kuna Lasker et al., 1996	—	**0.21 ± 0.20**	**0.68 ± 1.11**	—	**0.74 ± 1.18**	—
Briareum polyanthes Duch. & Mich., 1869	**0.12 ± 0.21**	—	**0.21 ± 0.39**	0.04 ± 0.08	**0.32 ± 0.38**	—
C-D-E						
Pseudoplexaura porosa (Houttuyn, 1772)	0.29 — 0.29	0.22 ± 0.21	**5.28 ± 4.89**	**1.08 ± 1.39**	**0.34 ± 0.75**	—
Gorgonia ventalina L. 1758	0.30 ± 0.39	0.02 ± 0.02	**1.71 ± 3.34**	**4.84 ± 4.41**	**0.82 ± 0.92**	—
Plexaura sp.	0.11 ± 0.19	0.02 ± 0.02	**3.59 ± 4.61**	**0.44 ± 0.67**	**0.80 ± 1.16**	—
Eunicea mamosa Lamoroux, 1816	0.03 ± 0.05	0.09 ± 0.08	**2.49 ± 2.60**	**0.72 ± 0.83**	**0.42 ± 0.94**	—
Plexaurella dichotoma (Esper, 1791)	0.04 ± 0.04	0.04 ± 0.05	**1.17 ± 1.37**	**1.24 ± 1.25**	**0.42 ± 0.94**	—
Pseudoplexaura flagellosa (Houttuyn, 1772)	—	0.27 ± 0.13	**3.04 ± 5.03**	**0.54 ± 0.68**	**0.74 ± 1.24**	—
Eunicea succinea (Pallas, 1766)	—	0.07 ± 0.00	**0.96 ± 1.45**	**1.09 ± 2.18**	**0.38 ± 0.35**	—
Plexaurella grisea Kunze, 1916	—	—	**0.64 ± 1.55**	**1.03 ± 0.85**	**0.87 ± 1.86**	—
Plexaurella sp.	—	—	**0.02 ± 0.07**	—	**0.14 ± 0.31**	—
Pseudopterogorgia americana (Gmelin, 1791)	—	—	0.71 ± 1.10	**5.88 ± 2.57**	**2.34 ± 2.27**	—
Muriceopsis flavida (Lamarck, 1815)	—	—	0.14 ± 0.44	**2.76 ± 4.02**	**1.33 ± 1.05**	—
Eunicea sp. 2	—	—	0.07 ± 0.25	**0.87 ± 0.37**	**0.36 ± 0.53**	—
C-D						
Eunicea tourneforti Milne, Edwards & Haime, 1857	0.03 ± 0.05	0.02 ± 0.02	**0.72 ± 1.09**	**2.62 ± 3.23**	—	—
C						
Plexaura homomalla (Esper, 1792	0.37 ± 0.56	0.14 ± 0.10	**7.25 ± 4.93**	—	0.20 ± 0.31	—
Pseudoplexaura crucis Bayer, 1961	0.11 ± 0.13	0.07 ± 0.00	**3.73 ± 2.88**	—	—	—
Pseudopterogorgia acerosa (Pallas, 1766)	—	—	**0.15 ± 0.50**	—	—	—
Eunicea cf. *laxipisca* Lamarck, 1816	—	—	**0.12 ± 0.44**	—	—	—

[1] Includes station 12, located in a shallow (1-3m), inner fore-reef terrace habitat off a wave-swept algal ridge.

TABLE 2. Continued.

	Cluster					
Cluster(s)/Species	Shallow barrier reef pinnacles and spurs A	Mid-depth patch reefs S. Lagoon B	Shallow and mid-depth mixture C	Deep windward fore-reef terrace[1] D	Mid-depth reefs N. lagoon and deep leeward terrace E	Outer slope F
D						
Pseudopterogorgia kallos (Bielchowsky, 1929)	—	—	—	**6.80 ± 9.32**	0.29 ± 0.40	—
Pterogorgia citrina (Esper, 1792)	0.03 ± 0.05	—	—	**2.50 ± 1.94**	—	—
Pterogorgia anceps (Esper, 1792)	—	—	—	**1.78 ± 1.26**	—	—
Pseudopterogorgia sp. 1	—	—	—	**1.46 ± 2.92**	—	—
Plexaurella fusifera (Kunze, 1916	—	—	0.06 ± 0.21	**0.92 ± 1.39**	—	—
Plexaurella sp. 2	—	—	—	**0.73 ± 1.47**	—	—
Pseudopterogorgia sp. 2	—	—	—	**0.35 ± 0.71**	—	—
Pseudoplexaura sp. 1	—	—	—	**0.35 ± 0.71**	—	—
Eunicea laciniata Duch. & Mich. 1860	—	—	—	**0.35 ± 0.71**	—	—
Eunicea calyculata (Ellis & Solander, 1786)	—	—	—	**0.69 ± 0.58**	—	—
E						
Pseudopterogorgia bipinnata (Verrill, 1864)	—	—	0.30 ± 1.09	—	**6.29 ± 2.20**	—
P. elisabethae Bayer, 1961	—	—	—	—	**1.00 ± 2.24**	—
P. cf. albatrossae Bayer, 1961	—	—	—	—	**0.50 ± 1.11**	—
P. cf. *hystrix* Bayer, 1961	—	—	—	—	**0.45 ± 0.73**	—
F						
Stichopates spp. including *S. lutkeni* (Brook) (**A**)	—	—	—	—	0.68 ± 1.53	**7.32**
Pseudoplexaura sp. 2	—	—	—	—	—	**7.32**
Ctenocella schmitti (Bayer, 1961)	—	—	—	—	—	**2.94**
Eunicea sp. 3	—	—	—	0.04 ± 0.08	—	**2.19**
Antipathes caribbeana Opresko, 1996 (**A**)	—	—	—	—	—	**2.19**
Ctenocella cf. *barbadensis* (Duch. & Mich. 1864)	—	—	—	—	—	**2.19**
Antipathes cf. *atlantica* Gray, 1857 (**A**)	—	—	—	—	—	**1.47**
Gorgonia cf. *mariae* Bayer, 1961	—	—	—	—	—	**1.47**
D to F (off cluster)						
Eunicea sp. 1	—	—	—	**1.25 ± 1.25**	0.03 ± 0.08	**0.72**

[1] Includes station 12, located in a shallow (1-3m), inner fore-reef terrace habitat off a wave-swept algal ridge.

TABLE 2. Continued.

	Cluster					
Cluster(s)/Species	Shallow barrier reef pinnacles and spurs A	Mid-depth patch reefs S. Lagoon B	Shallow and mid-depth mixture C	Deep windward fore-reef terrace[1] D	Mid-depth reefs N. lagoon and deep leeward terrace E	Outer slope F
Eunicea sp. 4	—	—	—	**0.35 ± 0.71**	**0.45 ± 0.73**	**0.72**
Plexaurella nutans (Duch. & Mich. 1860)	—	—	—	**0.58 ± 0.64**	**0.17 ± 0.38**	—
Pseudopterogorgia rigida (Bielchowsky, 1929)	—	—	—	**0.37 ± 0.73**	**0.17 ± 0.38**	—

[1] Includes station 12, located in a shallow (1-3m), inner fore-reef terrace habitat off a wave-swept algal ridge.

DISCUSSION

Species composition

The soft coral fauna of Providencia island may be considered as the richest from the Western part of the Caribbean Sea, with 44 species as compared to 39 found previously in Belize (Muzik, 1982; Lasker and Coffroth, 1983; Keith, 1992). Following Florida (46 spp.), it is the second richest locality in Western Atlantic reefs (Goldberg, 1973; Opresko, 1973; Jordán, 1989). It is also important to note the presence of undescribed species at Providencia island.

Possible causes of variation in the Providencia soft coral community

The greatest variation in the octocoral and black coral community composition of Providencia was related to the combination of depth and overall substratum when comparing upper platform vs. outer slope. Low illumination has been considered the main factor controlling the depth distribution of light-dependent zooxanthellate octocorals (Kinzie, 1973). On the other hand, ellisellid octocorals and black corals are azooxanthellate suspension feeders that are not affected by light attenuation; also, shaded undersides of foliaceous corals, abundant in the slope, allow settlement of these aposymbiotic species, making them more successful space colonizer than light-dependent species, which need open and lighted spaces to settle (Sánchez, 1998). In fact, shaded inclined substrata are more likely to be settled by black corals (Grigg, 1965; Oakley, 1988). This explains the rare occurrence of ellisellid octocorals or black corals on the upper platform and the poor representation of zooxanthellate octocorals on the slope.

Depth and degree of wave exposure within the upper platform of Providencia were the main factors related to variation in soft coral community composition and abundance. Shallower areas lacked a consistent pattern of species distribution with degree of wave exposure, mainly due to the low density or absence in certain reef types or areas, of species which were otherwise widespread. This may be explained by localized impact historical events such as storms, hurricanes or past mass mortalities, which may eliminate some species in a discontinuous manner.

Providencia island lies in the hurricane belt, with four hurricane records during this century; the last two of which occurred in 1967 and 1988 (Geister, 1992). It is probable that shallow and exposed sites would be more directly damaged by storms than deeper or sheltered areas, but the effect of hurricanes on soft coral communities may be unpredictable (Yoshioka and Yoshioka, 1987), provoking in consequence a patchy damage within the shallow areas. Mass mortalities of keystone species have also had a major impact on shallow areas of the Caribbean.

On several shallow habitats of the Providencia island reef-complex, the substratum is now widely covered by fleshy algae, mainly *Turbinaria, Dictyota* and *Lobophora* (Geister, 1992; Díaz et al., unpubl. data), which seem to have bloomed after the herbivore pressure release resulting from the mass mortality of the long-spined sea urchin *Diadema antillarum* L. throughout the Caribbean in 1983-84 (Lessios et al., 1984). This mass mortality was recorded on Providencia island by Geister (1992). Like in other Caribbean sites (Liddell and Ohlhorst, 1987; Jordán, 1989), this algal bloom could have prevented soft coral larval settlement in Providencia, thus decreasing their abundance or preventing their recolonization after hurricanes or mass mortality events. The sea-fan mass mortality event recorded on the continental coast of South America and nearby San Andrés island (Garzón-Ferreira and Zea, 1992; Díaz et al., 1995), also reached Providencia (Geister, 1992), and seems to have been responsible for its current patchy distribution in shallow areas.

Deeper reef areas within the insular platform varied in soft coral composition and abundance in relation to overall degree of wave exposure. A greater and relatively more constant degree of wave exposure in the windward fore-reef terrace causes greater water transparency and flushing, when compared to the leeward fore-reef terrace and deep lagoonal patch reefs. The conditions of the former imply better oxygen exchange, greater suspended particle flow, and greater photosynthetic rates, which produce lush octocoral growth (Sánchez et al., 1997). Soft corals in the windward fore-reef terrace are adapted to strong turbulence and currents; their axial cores vary in the content of elastic fibers and carbonates to produce a rigidity tuned to the turbulence regime (Lewis et al., 1992). In contrast, leeward and lagoonal habitats are dominated by tiny colonies of the gorgonian *Pseudopterogorgia bipinnata* and of dense stands of *Briareum asbestinum*, the latter devoid of a gorgonin axis. In lagoonal habitats there is also a greater incidence of overgrowing of soft corals by *Millepora*, and of injuries and a lower degree of regeneration (Wahle, 1983, 1985). This may explain a less developed and highly adapted octocoral growth at lagoonal and leeward habitats when compared to windward ones at the same depths. In fact, in nearby atolls of Courtown and Albuquerque, it has been found that there is a gradual transition in terms of species distributions and abundance, from calm, deep lagoonal patch reefs, to slightly more exposed deeper leeward terrace, to the strongly wave-exposed, deeper windward fore-reef terrace (Sánchez et al., 1997).

In a wide geographical context we may conclude that recurrent soft coral (octocoral and black corals) assemblages respond to a combination of major environmental factors, such as overall substratum inclination, depth, and degree of wave exposure, rather than to a particular reef type. Historical events such as storms and mass mortalities may bring about changes in soft coral composition, especially in shallow areas.

Acknowledgments.—The authors express their gratitude to Dr. J. Geister (Geologishes Institut U.Bern, Switzerland) for his kindness, knowledge, and collaboration during field work at Providencia island, and to E. Taylor and the people of Providencia island for their hospitality. The Instituto Nacional de Pesca y Acuicultura-INPA provided transportation and SCUBA facilities. Thanks to C. García-Llano for collaboration in data digitizing and to P. M. Yoshioka and A. Borden-Kerby for their comments and criticisms on the manuscript. This study has been funded by the Instituto Colombiano de Ciencia y Tecnología (COLCIENCIAS, Grant No. 2105-09-023-93), the Instituto de Investigaciones Marinas y Costeras (INVEMAR, Santa Marta) and the Universidad Nacional de Colombia (Facultad de Ciencias). Contribution 592 of the Instituto de Investigaciones Marinas y Costeras 'José Benito Vives de Andreis'-INVEMAR, and 143 of the Marine Biology Graduate Program of the Universidad Nacional de Colombia, Faculty or Sciences.

LITERATURE CITED

Alcolado, P. 1981. Zonación de los gorgonáceos someros de Cuba y su posible uso como indicadores comparativos de tensión hidrodinámica. Informe científico-técnico. Academia de Ciencias de Cuba, La Habana. 187:1-43.

Bayer, F. M. 1961. The shallow water Octocorallia of the West Indian region. Stud. Fauna Curaçao 12:1-373.

Bray, J. R., and J. T. Curtis. 1957. Ordination of the Upland forest communities of Southern Wisconsin. Ecol. Monogr. 27:325-349.

Catana, A. J. 1963. The wandering quarter method of estimating population density. Ecology, 44:349-360.

Dai, C. F., and M. C. Lin. 1993. The effects of flow on feeding of three gorgonians from southern Taiwan. J. Exp. Mar. Biol. Ecol. 173:57-69.

Díaz, J. M., J. Garzón-Ferreira, and S. Zea. 1995. Los arrecifes coralinos de la isla de San Andrés, Caribe colombiano: estado actual y perspectivas para su conservación. Acad. Col. Cienc. Exact. Fis. Nat., Col. 'Jorge Alvarez Lleras', No. 7. Bogotá. 150 pp.

Field, J. G., K. R. Clarke, and R. M. Warwick. 1982. A practical strategy for analyzing multispecies distribution patterns. Mar. Ecol. Prog. Ser. 8:37-52.

Garzón-Ferreira, J., and S. Zea. 1992. A mass mortality of *Gorgonia ventalina* (Cnidaria: Gorgoniidae) in the Santa Marta area, Caribbean coast of Colombia. Bull. Mar. Sci. 50:523-526.

Geister, J. 1992. Modern reef development and Cenozoic evolution of an oceanic island/reef complex: Isla de Providencia (Western Caribbean Sea). Facies 27:1-70.

Goldberg, W. 1973. The ecology of coral-octocoral communities of southeast Florida coast: geomorphology and species composition. Bull. Mar. Sci. 23:465-488.

Grange, K. R. 1985. Distribution, standing crop, population structure, and growth rates of black coral in the southern fiords of New Zealand. New Zealand J. Mar. Freshw. Res. 19:467-475.

Grigg, R. W. 1965. Ecological studies of black corals in Hawaii. Pacific Sci. 19:244-260.

Jackson, J. B. C. 1977. Morphological strategies of sessile animals. *In* G. Larwood and B. R. Rosen (eds.), Biology and systematics of colonial organisms, pp. 499-555. Academic Press, London.

Jordán, E. 1989. Gorgonian community structure and reef zonation patterns of Yucatán coral reefs. Bull. Mar. Sci. 45:670-696.

_______, and R. S. Nugent. 1978. Evaluación poblacional de *Plexaura homomalla* (Esper) en la costa noroeste de la península de Yucatán (Octocorallia). An. Cent. Cienc. Mar Limnol. Univ. Nal. Autón. México 5(1):189-200.

Kaandorp, J. A. 1986. Rocky substrate communities of the infralittoral fringe of the Boulonnais coast, NW France. A quantitative survey using cluster analysis. Mar. Biol. 92:255-265.

Keith, D. E. 1992. Shallow-water gorgonians of Roatan, Honduras. Bull. Mar. Sci. 50(1):212-226.

Kinzie, R. A. 1973. The zonation of West Indian gorgonians. Bull. Mar. Sci. 23:93-155.

Lasker, H. R., and M.A. Coffroth. 1983. Octocoral distributions at Carrie Bow Cay, Belize. Mar. Ecol. Prog. Ser. 13:21-28.

_______, M. D. Gottfried, and M. A. Coffroth. 1983. Effects of depth on the feeding capabilities of two octocorals. Mar. Biol. 73:73-78.

Lessios, H. A., J. D. Cubit, R. D. Robertson, M. J. Shulman, M. R. Parker, S. D. Garrity, and S. C. Levings. 1984. Mass mortality of *Diadema antillarum* on the Caribbean coast of Panama. Coral Reefs 3:173-182.

Lewis, J. C., T. F. Barnowski, and G. J. Telesnicki. 1992. Characteristics of carbonates of gorgonian axes (Coelenterata, Octocorallia). Biol. Bull. 183:278-296.

Liddell, W. D., and S. L. Ohlhorst. 1987. Patterns of reef community structure North Jamaica. Bull. Mar. Sci. 40:311-329.

Márquez, G. 1987. Las islas de Providencia y Santa Catalina. Fondo Fen-Univ. Nacional de Colombia, Bogotá. 110 pp.

Müller-Dombois, D., and H. Ellenberg. 1974. Aims and Methods of Vegetation Ecology. John Wiley & Sons N.Y. 583 pp.

Muzik, K. 1982. Octocorallia (Cnidaria) from Carrie Bow Cay, Belize. *In* K. Rützler and I. Macintyre (eds.), pp. 303-310. The Atlantic barrier ecosystem at Carrie Bow Cay. I. Smith. Contrib. Mar. Sci. 12.

Oakley, S. G. 1988. Settlement and growth of *Antipathes pennacea* on a shipwreck. Coral Reefs 7:77-79.

Opresko, D. M. 1973. Abundance and distribution of shallow water gorgonians in the area of Miami, Florida. Bull. Mar. Sci. 23:535-558.

Sánchez, J. A. (1998). Black Coral-Octocoral distribution patterns on Imelda Bank, a deep-water reef, Colombia, Caribbean sea. Bull. Mar. Sci., in press.

_______, J. M. Díaz, and S. Zea. 1997. Gorgonian communities in two contrasting environments on oceanic atolls of the southwestern Caribbean. Bull. Mar. Sci. 61(2):61-72.

Vogel, S. 1983. Life in moving fluids: the physical biology of flow. Princeton University Press, Princenton, New Jersey. 352 pp.

Whale, C. M. 1983. Regeneration of injuries among Jamaican gorgonians: the roles of colony physiology and environment. Biol. Bull. 165:778-790.

_______. 1985. Habitat-related patterns of injury and mortality among Jamaican gorgonians. Bull. Mar. Sci. 37(3):905-927.

Yoshioka, P. M., and B. B. Yoshioka. 1987. Variable effects of hurricane David on the shallow water gorgonians of Puerto Rico. Bull. Mar. Sci. 40:132-144.

_______, and _______. 1989. Effects of wave energy, topographic relief and sediment transport on the distribution of shallow-water gorgonians of Puerto Rico. Coral Reefs 8:145-152.

_______, and _______. 1991. A comparison of the survivorship and growth of shallow-water gorgonian species of Puerto Rico. Mar. Ecol. Prog. Ser. 69:253-260.