

BLACK CORAL-OCTOCORAL DISTRIBUTION PATTERNS ON IMELDA BANK, A DEEP-WATER REEF, COLOMBIA, CARIBBEAN SEA

Juan A. Sánchez

ABSTRACT

Distribution patterns of black corals and octocorals (Antipatharia and Octocorallia) on a deep-water reef bank off the Caribbean coast of Colombia were studied. In total, 915 colonies of five black coral and 23 octocoral species were counted and identified within 20 stations (four series, each consisting of five 2 × 2 m quadrants). The dominant functional group was black corals followed by azooxanthellate and then by zooxanthellate octocorals. Both classification and ordination analysis separated mid-depth (17–18 m) plateau from deeper slope assemblages (21–27 m). This pattern appeared to be related to the differences in light attenuation (bathymetric input) and substratum inclination (shade). Although the bank exhibits reef-building coral growth (54% of cover) that is similar to other Caribbean reefs, there is a greater proportion of aposymbiotic zooplankton-feeders and deep-water species (black corals and octocorals). This distribution appears to be related to continental run-off, with the combined effect of low transparency and water enrichment allowing this particular community to grow at relatively shallow depths on the reef. Black coral-octocoral densities were positively correlated with depth. Shaded undersides of foliaceous corals on the slope allowed settlement of aposymbiotic species resulting in higher colony densities. Black corals and azooxanthellate octocorals appeared to share the same habitat and resources.

In tropical and subtropical waters black corals (Antipatharia) are predominantly deep reef and deep sea inhabitants. Studies on the community ecology of black corals are scarce (Grigg, 1965; Grange, 1985). Octocorals, and specially gorgonians, on the other hand, are very conspicuous reef inhabitants in shallow Caribbean waters (Bayer, 1961), and comprehensive research on their communities is ever increasing (Goldberg, 1973; Kinzie, 1973; Opresko, 1973; Preston and Preston, 1975; Alcolado, 1981; Muzik, 1982; Lasker and Coffroth, 1983; Botero, 1987; Wheaton and Jaap, 1988; Jordán, 1989; Yoshioka and Yoshioka, 1989; Sánchez et al., 1997, among others). In contrast, the ecology of deep water octocorals is poorly understood. Black coral-octocoral communities have not been described until now.

A number of reef communities including scleractinian corals (Bak and Povel, 1991) and gorgonian octocorals (Yoshioka and Yoshioka, 1989; Sánchez et al., 1997; Sánchez et al., 1998) are distributed along environmental gradients related to wave exposure and topographic relief. Physical disturbance plays an important role among other reef communities, but wave exposure probably does not have an impact on deep banks. Little is known about black coral-octocorals communities; in fact, the major species found in this community have only been mentioned in species lists or taxonomic works. Interestingly this assemblage comprises light-dependent species with symbiotic zooxanthellae (some octocorals) as well as azooxanthellate suspension feeders that are not affected by light attenuation (black corals and other octocorals). Consequently, black coral-octocoral distribution patterns may be governed by the combined effect of light intensity and the availability of suspended food in the water column. The purpose of this work is to study the

distribution patterns of a black coral-octocoral community found on a Caribbean deep water coral reef.

MATERIALS AND METHODS

STUDY AREA.—The study was carried out on a small deep-water bank reef called “Imelda” by divers and “montañita” by local fishermen. It is located 1 km from Barú island (10°15'40"N, 75°37'08"W) off the Caribbean coast of Colombia, South America (Fig. 1). The bank, as well as many others close to Barú island, is surrounded by depths of 50 m and its basement comprises ancient diapiric domes progressively colonized by corals since the early Holocene (Vernette, 1986; see discussion in Sánchez, 1995). The bank has an elongated table shape with a length of 122 m and a width of 63 m. Two geomorphologic features are easily noted: a plateau, the shallow-most zone of the bank at a depth of 15 to 18 m, and the slope drop-off from 18 to 40–50 m (Navas et al., 1992). The bank, as well as Barú island, is located in the path of the Intertropical Convergence Zone with alternating trade winds from the Northwest and Southeast. The average annual sea-water temperature is 27.5°C and the average rainfall is 1013 mm, typical of a dry tropical climate. The main current has the same direction as the northern winds, which are stronger between December and April during the dry season. In the wet season (May–November) the Colombian current flows from the south, and has a periodic influence on the archipelago by carrying continental runoff from Barbacoas Bay and Cartagena Bay (Sánchez, 1995). The average salinity in the area is 35‰ (Martínez and Vernet, 1981).

The mean coral cover on the bank is high, nearly 54%, with *Montastraea* spp., *Agaricia agaricites* and *Porites astreoides* dominating (Navas et al., 1992). Algae (27% of substratum cover) are also abundant, headed by *Lobophora variegata* and *Dictyota* spp. (Díaz and Rojas, 1992). Sponges are also common (11.02% of substratum cover), among which *Niphates erecta*, *Ulosa rutzleri* and *Rhaphidophylus schoenus* dominate (González, 1992). An assemblage of 102 species of reef fish is present on the bank (Torres et al., 1992). Using SCUBA diving, systematic sampling was performed at 5 depths (17, 18, 21, 24, and 27 m), on each of the bank's four faces (South, North, East and West) for a total of 20 stations. At each station black coral and octocoral colonies were counted and identified on five continuous (2 × 2 m) belt quadrant transects (total of 20 m²). Octacorals were collected, dried and identified according to Bayer (1961; 1991). Black corals were also dried and fixed and identified according to Opresko (1972; 1974; 1996) and Warner (1981). Octocoral and black coral specimens that were difficult to identify were sent to F. M. Bayer (Smithsonian Institution, Washington) and D. M. Opresko (Oak Ridge National Laboratory, Tennessee), respectively, for confirmation. Voucher specimens were deposited in the United States National Museum in Washington (USNM), the Museum of Invertebrates at INVEMAR, Santa Marta, and the Instituto de Ciencias Naturales, Univ. Nacional de Colombia, Santafé de Bogotá DC (ICN-MHN-CO).

To relate recurrent patterns of black coral-octocoral species distributions and abundance to reef zonation and environmental characteristics, stations were grouped by normal (Q-mode) cluster analysis using species density data ($\log_{10} [x+1]$ transformed), the Bray-Curtis dissimilarity index, and the Unweighted Pair Group Method (UPGMA), and to further relate stations and depth, degree 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). Also, the first three axes of a multivariate eigen vector procedure (Canonical Correspondence Analysis-CCA, Ter Braak, 1986) was used to achieve a gradient analysis among stations and depth, the ecological meaning of the CCA axis scores was found through direct correlation to depth for each station (for instance see: Sánchez et al., 1997). Recurrent patterns of abundance, per functional group, related to water depth were tested with simple linear regression (Sokal and Rohlf, 1981).

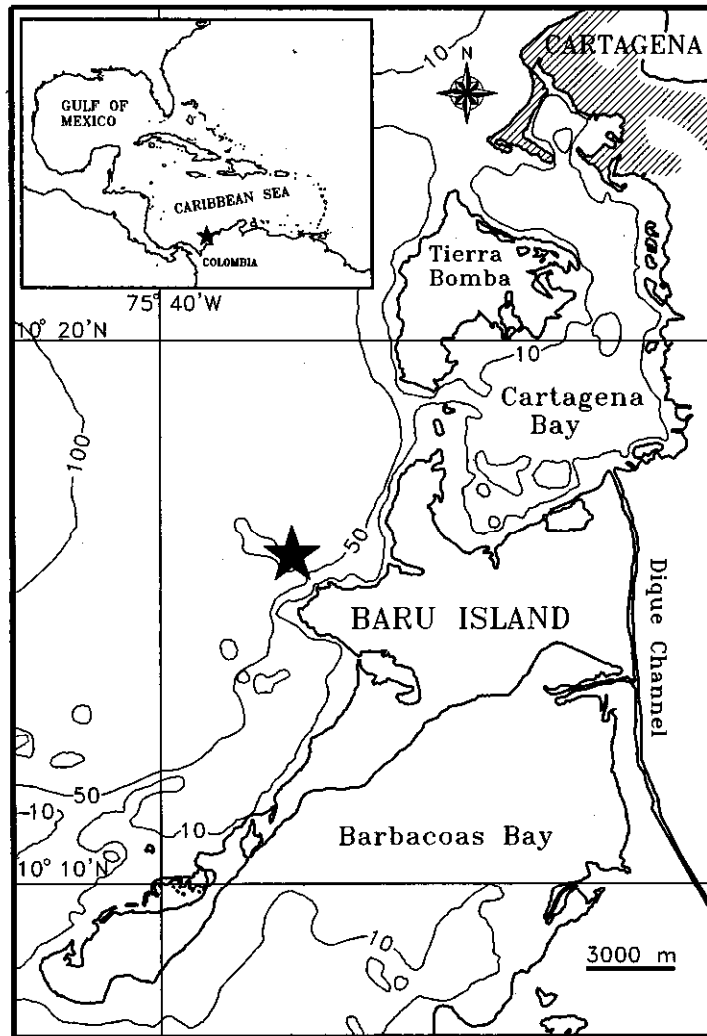


Figure 1. Geographical position of Imelda bank (star) on the Colombian Caribbean.

RESULTS

A total of 915 colonies belonging to 28 species were found. The well-established black coral-octocoral community of the bank can be divided in three functional groups, one group consisting of 13 species of light-dependent octocorals with symbiotic zooxanthellae, another of 10 azooxanthellate octocorals and the third consisting of five species of black corals (Table 1). Also, it is significant that many of the species found are undescribed (*Eunicea*, *Ctenocella*, *Villogorgia* and *Thesea* spp., F. M. Bayer, pers. comm.; *Stichopathes* spp., D. M. Opreško, pers. comm.). Definitive taxonomic positions and systematics of the species will be made available in future publications by the author and will not be discussed in detail in this paper.

Table 1. Mean (min.–max.) density of colonies (col. m⁻²) of species on plateau (8 sites) and slope (12 sites) habitats. (–) = absent; (*) = observed and collected out of transects.

Species	Plateau	Slope
Zooxanthellate octocorals		
<i>Eunicea</i> (undescribed species)	0.2 (0–0.4)	0.03 (0–0.5)
<i>Eunicea succinea</i> (Pallas, 1766)	0.006 (0–0.05)	–
<i>Plexaurella tenuis</i> Kunze, 1916	–	0.03 (0–0.15)
<i>P. cf. nutans</i> Verrill, 1912	0.006 (0–0.05)	–
<i>Plexaura flexuosa</i> Lamouroux, 1812	0.1 (0–0.6)	0.1 (0–0.35)
<i>P. nina</i> Bayer and Deichman, 1958	–	0.03 (0–0.15)
<i>Muricea laxa</i> Verrill, 1864	0.05 (0–0.2)	0.03 (0–0.2)
<i>Pseudopterogorgia</i> spp. [including <i>P. americana</i> (Gmelin, 1791), <i>P. acerosa</i> (Pallas, 1766) and <i>P. bipinnata</i> (Verrill, 1864)]	0.06 (0–0.2)	0.1 (0–1.5)
<i>Muriceopsis flavida</i> (Lamarck, 1815)	*	–
<i>Erythropodium caribaeorum</i> (Duch. and Mich., 1860)	*	–
<i>Gorgonia ventalina</i> Linnaeus, 1758	*	–
Azooxanthellate octocorals		
<i>Diodogorgia nodulifera</i> (Hargitt, 1901)	–	0.1 (0–0.5)
<i>Ctenocella (Viminella) cf. barbadensis</i> (Duch. and Mich., 1864)	0.04 (0–0.1)	0.16 (0–0.6)
<i>C. (Viminella) schmitti</i> (Bayer, 1961)	0.03 (0–0.05)	0.4 (0–1.4)
<i>Ctenocella</i> (undescribed species)	–	*
<i>Thelogorgia studeri</i> Bayer, 1991	–	0.01 (0–0.05)
<i>Villogorgia</i> (undescribed species)	–	*
<i>Iciligorgia schrammi</i> (Duch., 1870)	–	*
<i>Thesea</i> (undescribed species)	–	*
<i>Lytrelia plana</i> (Deichmann, 1936)	–	*
<i>Caliacis nutans</i> (Duch. and Mich., 1864)	–	*
Antipatharians		
<i>Stichopathes</i> spp. [including <i>S. lutkeni</i> (Brook)]	0.1 (0.1–0.3)	1.5 (0.4–3.8)
<i>Antipathes caribbeana</i> Opresko, 1996	–	0.1 (0–0.9)
<i>A. atlantica</i> Gray, 1857	0.01 (0–0.05)	0.1 (0–0.5)
<i>A. pennacea</i> (Pallas, 1766)	0.001 (0–0.05)	0.06 (0–0.6)
<i>A. gracilis</i> Gray, 1860	–	0.02 (0–0.1)

The classification analysis based on the population density data of each species showed two detached clusters which correspond to stations located on the plateau (17–18 m in water depth) and on the slope (21–24 m), respectively, with only one exception in 20 stations (Fig. 2A) and corresponding to an intermediate depth (sta. 8: Fig. 2A,C,D). Triangulation plots (Fig. 2B), based on the relative abundance of the three functional groups at each station, and ordination biplot (NMDS two dimensions) of the sampling stations reveals the same distribution pattern seen in the clustering. Slope stations form a compact group in the latter, while the plateau stations form a less coherent group (Fig. 2C), being consistent with the minimum dissimilarity values of each cluster (Fig. 2A) and the proportions of functional groups at plateau and slope (Fig. 2B). There was no pattern related to spatial horizontal distributions on the bank; in fact there was a random mix on the different reef faces in the ordination biplot (data not shown). This pattern dividing the community in two assemblages can be interpreted as the response of community variation to depth gradient (CCA I vs depth, simple linear regression: $r^2 = 0.71$, $F = 44.03$, $P \ll 0.001$). The correlations between each of the other three axes obtained by the CCA and depth were not significant.

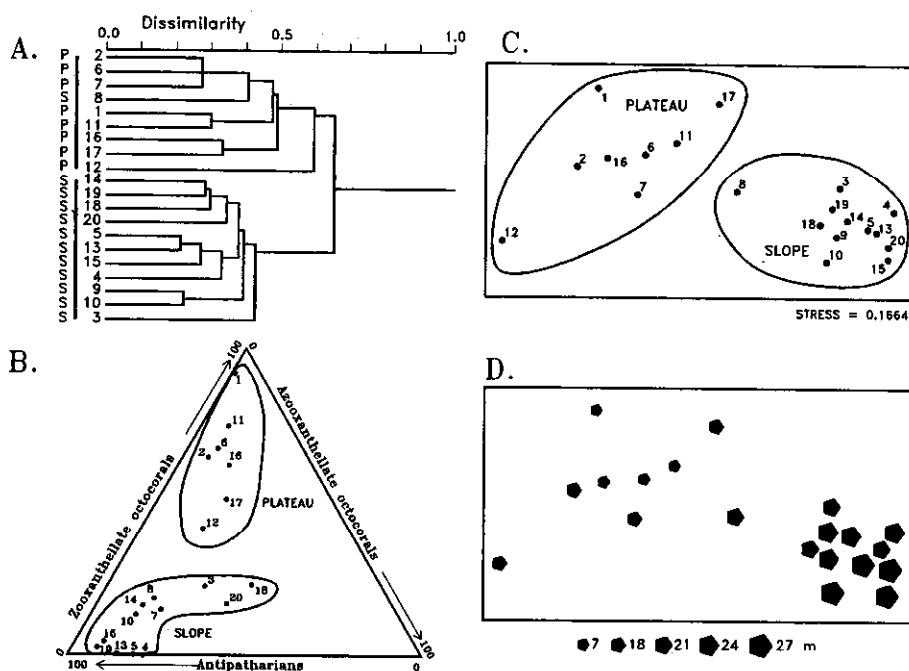


Figure 2. A.- Normal (Q-mode) cluster analysis dendrogram of the 20 sampling stations applying the Bray-Curtis dissimilarity index to $\log_{10}(x+1)$ transformed density of colonies per species (Cophenetic Correlation Coefficient = 0.8122) (P = plateau; S = slope). B.- Triangular diagram of station locations with three coordinates according to the percentage (per station) of black corals (antipatharians), azooxanthellate octocorals, and zooxanthellate octocorals. C.- Nonmetrical multidimensional scaling (NMDS) ordination of stations (data as in A). D.- NMDS when depth values has been superimposed on each station.

The high correlation between CCA axis I and depth implies that there is a progressive change in community composition and structure from mid-depth to deeper stations. For the whole community and for the separate functional groups there is a trend of increasing colony abundance toward deeper sites which is reflected in the decreasing CCA I axis values (Fig. 3). However, it is clear that this progressive change does not occur at the species level because of the distinctive composition and the marked exclusiveness of species in each zone (Table 1). This trend is clearly shared by black corals (antipatharians) and azooxanthellate octocorals, while zooxanthellate octocorals differ from this pattern (Fig. 3). At the community level, the pattern of progressively increased abundance with depth is manifest in the highly significant positive regression between total abundance and depth ($P < 0.001$; Table 2). Abundance of black corals and azooxanthellate octocorals also varied with depth (Table 2). Spatially, density of colonies is higher towards deeper stations, and, although zooxanthellate octocorals did not correlation with depth, both azooxanthellate functional groups increased in abundance with depth (Fig. 4). Octocorals exhibited their highest densities on the deep west face of the reef, which is likely due to the main current flowing from the south-west along the Barú island coast (27 m; Fig. 4).

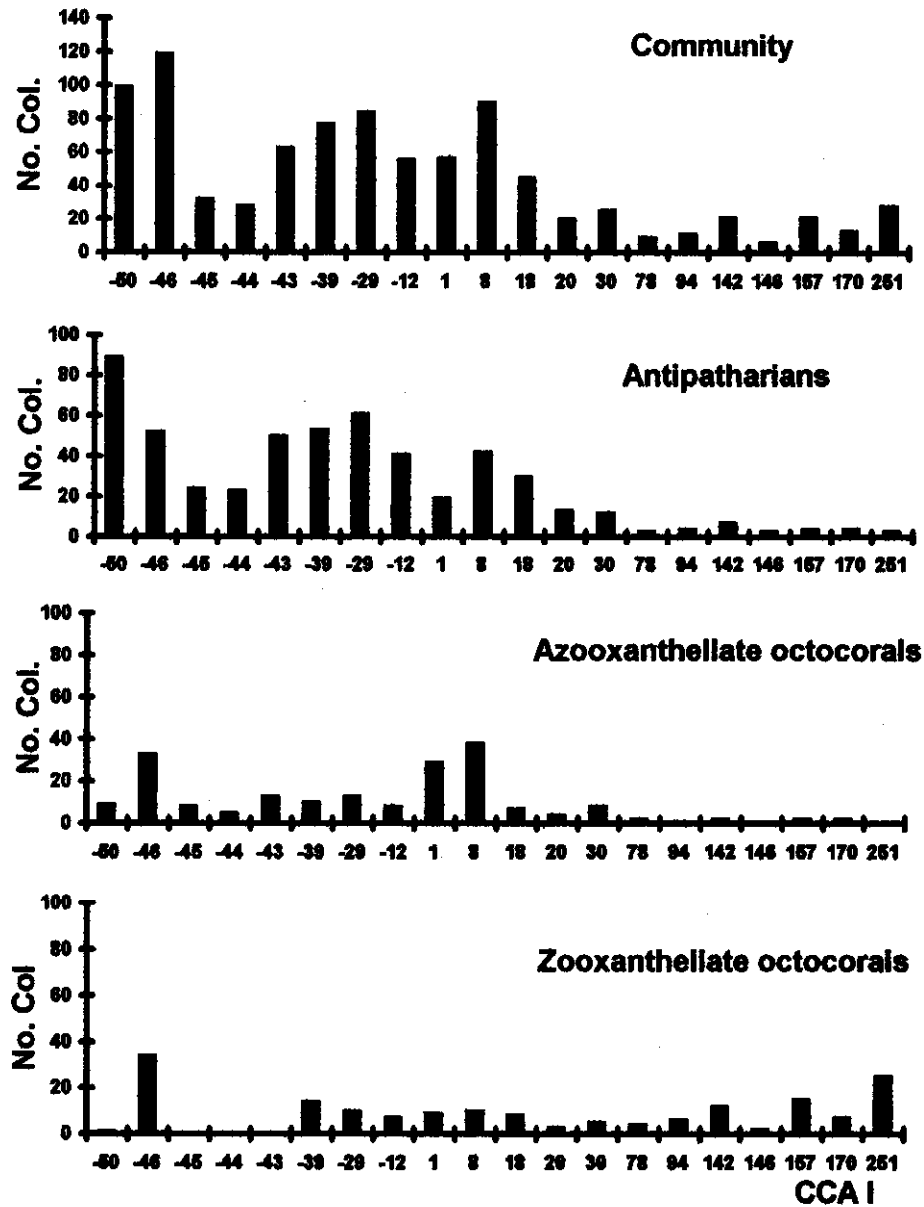


Figure 3. Total number colonies per station sorted along ascending CCA axis I values for total community, black corals (antipatharians), azooxanthellate octocorals, and zooxanthellate octocorals.

DISCUSSION

A large portion of the Caribbean coast of Colombia contains luxuriant and dense populations of black corals and octocorals, particularly on deep water banks and reef slopes (Botero, 1987; Ortiz and Sánchez, 1992; Sánchez and Ortiz, 1992; Sánchez, 1992; Zea, 1993; Sánchez, 1995; Opresko and Sánchez, 1997). This is a rare assemblage of species

Table 2. Results of simple linear regression analyses of variance between colony density and depth at each station for black corals, azooxanthellate octocorals, zooxanthellate octocorals, and total community data. (n.s.= non significant, $P > 0.05$)

Factor	df	SS	MS	r^2	F	P
Black corals (Antipatharia)	1	9,390.13300	9,390.13300	0.82	80.701410	<<< 0.001
Residuals	18	2,094.41700	116.35650			
Azooxanthellate octocorals	1	781.15970	781.15970	0.34	9.308198	< 0.010
Residuals	18	1,510.59000	83.92168			
Zooxanthellate octocorals	1	2.29422	2.29422	0.01	0.029529	n.s.
Residuals	18	1,398.50600	77.69477			
Total community	1	15,968.52000	15,968.52000	0.74	52.235130	<< 0.001
Residuals	18	5,502.68200	305.70460			
Corrected total	19	21,471.20000				

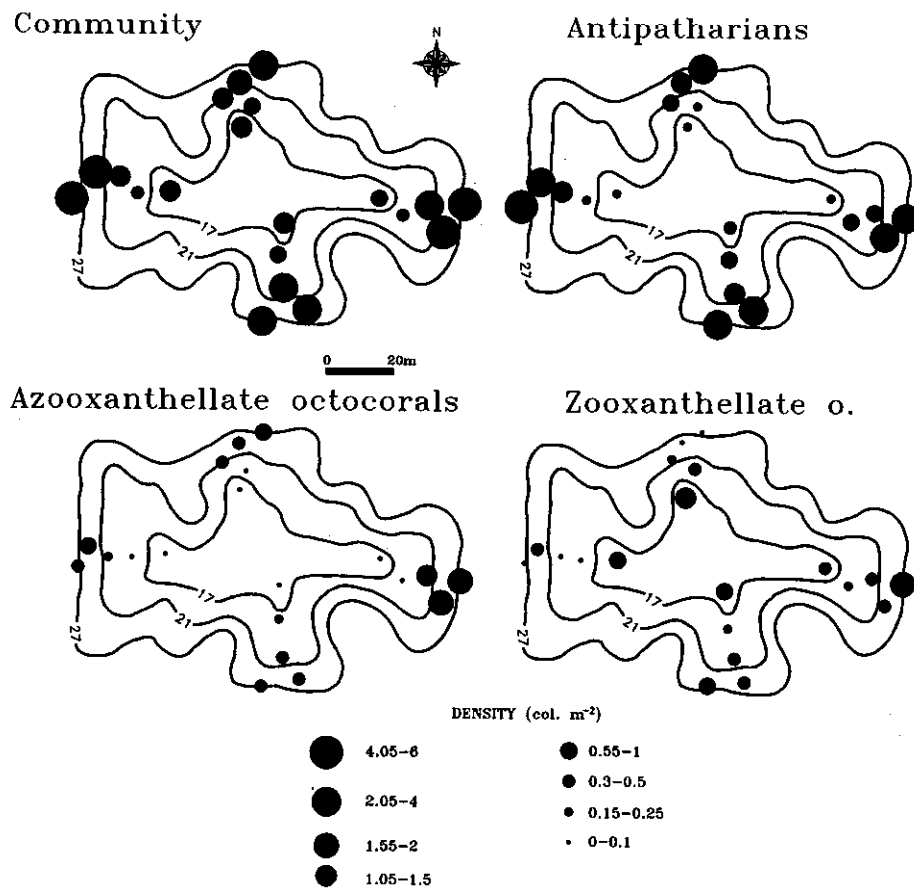


Figure 4. Bathymetric maps of Imelda bank (modified from Navas et al., 1992) with station locations when colony density values has been superimposed on each.

compared to other Caribbean reef communities occurring at similar depths, such as in the Antilles, Belize, Jamaica, oceanic Colombia, and Florida (Kinzie, 1973; Goldberg, 1973; Lasker and Coffroth, 1983; Yoshioka and Yoshioka, 1989; Sánchez et al., in press; among others). However, dense communities of black corals have also been found in other areas of the Caribbean and in the South West Pacific (Warner, 1981; Grange, 1985), and azooxanthellate octocoral communities dominated by ellisellids, have been found in the West Pacific (Goh and Chou, 1994). The high abundance of deep water organisms on the reef banks may be due to high amounts of seston in the surface waters (Warner, 1981). The southern Caribbean, including the whole Colombian coast, has been considered oligotrophic. However, annual discharge from Orinoco and Magdalena rivers and seasonal upwelling provide constant sources of nutrients (Müller-Karger et al., 1989). The waters of Barú island and Rosario islands have been considered as partly eutrophic due to the high content of inorganic nutrients brought by water run-off, and the resulting decrease in water transparency (Alvarado and Corchuelo, 1992). Both black corals and azooxanthellate octocorals are known to feed mainly on zooplankton (Grigg, 1965; Lewis, 1978; Coma et al., 1994). Growth rates of aposymbiotic suspension-feeding animals (i.e., azooxanthellated octocorals and black corals) are strongly associated with the amount of food in the water column and the greater abundance of black corals and azooxanthellate octocorals appears to be related to prevailing enriched waters surrounding the banks. In contrast, growth rates of zooxanthellate animals such as reef corals and some octocorals do not appear to be affected by nutrient input (Birkeland, 1988 and references therein). It is important to note that the waters around Barú island have been exposed to outwelling run-off only since the Spanish conquest four centuries ago, when an artificial arm of Magdalena river (Dique channel) was opened, discharging into Cartagena Bay close to Barú island. Apparently, enough time has passed since then for the nearby coral reef communities to recover and adapt themselves to new outwelling run-off conditions.

The pattern of distribution separating plateau and slope assemblages occurred in spite of the narrow (3 m depth) separation between these zones. This close limit implies there is a strong effect of slope and bottom topography on the community distribution patterns. Black coral larvae settle on a lightly shaded calcareous substrate and then grow towards the source of light (Grigg, 1965). Oakley (1988) assessed the effect of substrate inclination on black-coral larval using artificial substrates, and found that shaded inclined substrates were likely to be settled by black corals. All the black corals and azooxanthellate octocorals were found attached on the shady undersides and crevices of foliaceous and sub-massive scleractinian corals. Foliaceous corals on Imelda bank are present over the entire depth-range (*Agaricia lamarcki*, *A. undata*, *A. grahamae*, *A. agaricites*, and *Leptoseris cucullata*) of the bank while others, such as *Montastraea franksi* and *Porites astreoides*, change from mound-like to a flattened-foliose morphology as a response to light attenuation (Graus and Macintyre, 1982; Hughes and Jackson, 1985; pers. observ.). Navas et al. (1992) found an intermediate zone between 18 and 22 m of water depth with a complex mix of corals, the highest coral cover on the bank, and a mixture of shapes. The abundance of black corals and zooxanthellate octocoral species with depth may be a response to substratum supply which is controlled by light attenuation and/or bathymetric input reflected in the progressive abundance of foliaceous corals. Overall substratum inclination comprises the main factor to determine black coral-octocoral composition at Caribbean oceanic reefs, where slope areas exhibits different black coral-octocoral species than the upper platform (Sánchez et al., in press). Zooxanthellate octocorals such as

Pseudopterogorgia bipinnata and *P. elisabethae* may settle beneath coral crevices (Sánchez et al., 1997), but they do not have the same ability to settle under foliaceous corals, and, because of the oligotrophic conditions of the southwestern Caribbean reefs (Díaz et al., 1996), azooxanthellate octocorals and black corals are poorly represented (Sánchez et al., in press).

To a lesser degree, flow regime can also influence the community distribution. Flow along Barú island and the bank stems from south-west cyclic cells generated by the encounter between the Colombian current and the Rosario islands (Pujos et al., 1986). Although there was no significant pattern in the community related to a given reef face, high densities of both azooxanthellate and zooxanthellate octocorals were evident at west stations, likely in response to this regional flow. In conclusion, clear pattern separating mid-depth plateau and deeper slope black coral-octocoral assemblages on the bank was found and appeared to be related to the differences in light attenuation (bathymetric input) and substratum inclination (shade).

ACKNOWLEDGMENTS

The author expresses his gratitude to V. Ortiz for his help during field work, data collection, and early discussions. To the yacht EL CARACOL and D. Torres for coordination and support during field work. To the Facultad de Biología Marina, Universidad Jorge Tadeo Lozano (Cartagena, Colombia). Special thanks to F. M. Bayer (Smithsonian Institution, Washington) and D. M. Opresko (Oak Ridge National Laboratory, Tennessee) for their identification of specimens and comments. To D. M. Opresko, F. Zapata (Universidad del Valle, Colombia), and two anonymous reviewers for their comments and criticisms on the manuscript. To P. Lecompte, S. Conde, D. Osorio, and C. de la Hoz for his collaboration. To J. M. Díaz (INVEMAR) and S. Zea (Universidad Nacional de Colombia, Sede Santa Marta). Contribution to marine science Nr. 8 of the Centro de Investigaciones Científicas, Universidad de Bogotá Jorge Tadeo Lozano.

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.
- Alvarado, E. and M. Corchuelo. 1992. Los nutrientes, la temperatura y la salinidad provenientes del Canal del Dique como factores de deterioro en el Parque Nacional Natural Corales del Rosario (Cartagena, Colombia). Mem. VIII Sem. Nal. Cienc. Tec. Mar, Santa Marta I: 277-286.
- Bak, R. P. and G. D. E. Povel. 1989. Ecological variables including physiognomic-structural attributes, and classification of Indonesian coral reefs. Netherlands J. Sea Res. 23: 95-106.
- Bayer, F. M. 1961. The shallow water Octocorallia of the west Indian region; Stud. Fauna Curaçao 12(55): 1-373.
- _____. 1991. *Thelogorgia*, a new genus of gorgonacean octocorals, with descriptions of four new species from the western Atlantic. Bull. Mar. Sci. 49: 506-537.
- Birkeland, C. 1988. Second-order ecological effects of nutrient input into coral communities. Galaxea 7: 91-100.
- Botero, L. 1987. Zonación de octocorales gorgonáceos en el área de Santa Marta y Parque Nacional Tayrona, costa caribe colombiana. An. Inst. Inv. Mar. Punta de Betín. 17: 61-80.
- Coma, R., J. M. Gili, M. Zabala and T. Riera. 1994. Feeding and prey capture cycles in the aposymbiotic gorgonian *Paramuricea clavata*. Mar. Ecol. Prog. Ser. 115: 257-270.

- Díaz, G. and M. A. Rojas. 1992. Las comunidades del bajo arrecifal profundo "Imelda", Isla Barú, Caribe colombiano. III. Estructura de la comunidad macroalgal. Mem. VIII Sem. Nal. Cienc. Tec. Mar, Santa Marta I: 304-315.
- Díaz, J. M., J. A. Sánchez, J. Garzón-Ferreira and S. Zea. 1996. Morphology and marine habitats of two Southwestern Caribbean atolls: Albuquerque and Courtown. Atoll Res. Bull. 435: 1-34.
- 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.
- Goh, N. K. and L. M. Chou. 1994. Distribution and biodiversity of Singapore gorgonians (sub-class Octocorallia)—a preliminary survey. Hydrobiologia 285: 101-109.
- Goldberg, W. 1973. The ecology of coral-octocoral communities of southeast Florida coast: geomorphology and species composition. Bull. Mar. Sci. 23: 465-488.
- González, D. 1992. Las comunidades del bajo arrecifal profundo "Imelda", Isla Barú, Caribe colombiano. IV. Evaluación estructural preliminar de las esponjas (Porifera). Mem. VIII Sem. Nal. Cienc. Tec. Mar, Santa Marta I: 316-327.
- Grange, K. R. 1985. Distribution, standing crop, population structure, and growth rates of black corals in the Southern fiord of New Zealand. New Zealand J. Mar. Freshw. Res. 19: 467-475.
- Graus R. R. and I. G. Macintyre. 1982. Variation in growth forms of the reef coral *Montastrea annularis* (Ellis and Solander): a quantitative evaluation of growth response to light distribution using computer simulation. Smithson. Contrib. Mar. Sci. 12: 441-464.
- Grigg, R. W. 1965. Ecological studies of black corals in Hawaii. Pacific Sci. 19: 244-260.
- Hughes T. P. and J. B. C. Jackson. 1985. Population dynamics and life histories of foliaceous corals. Ecol. Monogr. 55: 141-166.
- Jordán, E. 1989. Gorgonian community structure and reef zonation patterns of Yucatán coral reefs. Bull. Mar. Sci. 45: 670-696.
- 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.
- Lewis, J. B. 1978. Feeding mechanisms in black corals (Antipatharia). J. Zool. 186: 393-396.
- Martínez, S. H. and G. Vernet. 1981. El complejo arrecifal de las islas del Rosario, zonación coralina, sedimentos y foraminíferos bentónicos. Rev. CIAF. 6(1-3): 329-345.
- Müller-Karger, F. E., C. R. McClain, T. R. Fisher, W. E. Esaias and R. Varela. 1989. Pigment distribution in the Caribbean sea: observations from space. Oceanog. 23: 23-64.
- Muzik, K. 1982. Octocorallia (Cnidaria) from Carrie Bow Cay, Belize. Pages 303-310 in K. Rützler and I. Macintyre, eds. The Atlantic barrier ecosystem at Carrie Bow Cay. I. Smithson. Contrib. Mar. Sci. 12.
- Navas, G. R., O. D. Solano and D. F. Torres. 1992. Las comunidades del bajo arrecifal profundo "Imelda", Isla Barú, Caribe colombiano. II. Caracterización estructural de la comunidad coralina (Scleractinia). Mem. VIII Sem. Nal. Cienc. Tec. Mar, Santa Marta I: 291-303.
- Oakley, S. G. 1988. Settlement and growth of *Antipathes pennacea* on a shipwreck. Coral Reefs 7: 77-79.
- Opresko, D. M. 1972. Redescriptions of antipatharians described by L.F. Pourtales. Bull. Mar. Sci. 22: 950-1017.
- _____. 1973. Abundance and distribution of shallow water gorgonians in the area of Miami, Florida. Bull. Mar. Sci. 23: 535-558.
- _____. 1974. A study of classification of the Antipatharia (Coelenterata: Anthozoa) with redescriptions of eleven species. Ph.D. dissertation. Univ. Miami. Coral Gables, Florida. 189 p.
- _____. 1996. New species of black coral (Cnidaria: Anthozoa: Antipatharia) from the Caribbean. Bull. Mar. Sci. 58: 289-300.
- _____ and J. A. Sánchez. 1997. A new species of Antipatharian Coral (Cnidaria: Anthozoa) from the Caribbean coast of Colombia. Carib. J. Sci. 33: 75-81.

- Ortiz, V. and J. A. Sánchez. 1992. Las comunidades del bajo arrecifal profundo "Imelda", Isla Barú, Caribe colombiano. VI. Estructura de la comunidad de corales negros (Antipatharia, Antipathidae). Mem. VIII Sem. Nal. Cienc. Tec. Mar, Santa Marta I: 341-349.
- Preston, M. and J. L. Preston. 1975. Ecological structure in a West Indian gorgonian fauna. Bull. Mar. Sci. 25: 535-558.
- Pujos, M., J. L. Pagliardini, R. Steer, G. Vernet and O. Weber. 1986. Influencia de la contracorriente norte colombiana para la circulación de las aguas en la plataforma continental: su acción sobre la dispersión de los efluentes en suspensión del río Magdalena. Bol. Cient. CIOH 6: 3-15.
- Sánchez, J. A. 1992. Las comunidades del bajo arrecifal "Imelda" Isla Barú, Caribe colombiano. V. Estructura de la comunidad de gorgonáceos (Cnidaria: Octocorallia). Mem. VIII Sem. Nal. Cienc. Tec. Mar. Santa Marta. Colombia I: 328-340.
- _____. 1995. Benthic communities and geomorphology of the Tesoro Island reef, Colombian Caribbean. An. Inst. Invest. Mar. Punta Betín 24: 55-77.
- _____. and V. Ortiz. 1992. Distribución de los corales negros (Antipatharia: Antipathidae) de arrecifes coralinos entre Cartagena y el Golfo de Urabá, Caribe colombiano. Mem. VIII Sem. Nal. Cienc. Tec. Mar. Santa Marta. Colombia I: 362-369.
- _____. J. M. Díaz and S. Zea. 1997. Gorgonian communities in two contrasting environments on oceanic atolls of the southwestern Caribbean. Bull. Mar. Sci. 61: 453-465.
- _____. S. Zea and J. M. Díaz. (in press) Patterns of octocoral and black coral distribution in the oceanic barrier reef-complex of Providencia island, Southwestern Caribbean. Carib. J. Sci.
- Sokal, R. R. and F. J. Rohlf. 1981. Biometry. The principles and practice of statistics in biological research. W. H. Freeman and Company, New York.
- Ter Braak, C. J. F. 1986. Canonical correspondence analysis a new eigenvector technique for multivariate direct analysis. Ecology 67: 1167-1179
- Torres, D., E. A. Rodríguez, L.E. Mejía and C. A. Buitrago. 1992. Las comunidades del bajo arrecifal profundo "Imelda", Isla Barú, Caribe colombiano. VII. Evaluación preliminar de la Ictiofauna. Mem. VIII Sem. Nal. Cienc. Tec. Mar, Santa Marta I: 350-361.
- Vernette, G. 1986. La plate-forme continentale Caraïbe du Colombie. Importance du diapirisme argileux sur le morphologie, et la sédimentation. Thèse doctorale. Mém. del Inst. Géol. Bassin d'Aquitaine, 20: 1-387.
- Warner, G. F. 1981. Species descriptions and ecological observations of black corals (Antipatharia) from Trinidad. Bull. Mar. Sci. 31: 147-163.
- Wheaton, J. L. and W. C. Jaap. 1988. Corals and other prominent benthic Cnidaria of Looe Key National Marine Sanctuary, Florida; Fla. Mar. Res. Publ. 43: 1-25.
- Yoshioka, P. M. and B. B. Yoshioka. 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.
- Zea, S. 1993. Cover of sponges and other sessile organisms in rocky and coral reef habitats of Santa Marta, Colombian Caribbean Sea. Carib. J. Sci. 29(1-2): 75-88.

DATE SUBMITTED: August 20, 1997.

DATE ACCEPTED: March 2, 1998.

ADDRESS: Museo del Mar—Centro de Investigaciones Científicas, Universidad de Bogotá Jorge Tadeo Lozano, Calle 22 # 3-30, A.A. 78353, Santafé de Bogotá DC, Colombia. E-mail: <jsanchez@ciencias.ciencias.unal.edu.co>. CURRENT ADDRESS: Department of Biological Sciences, State University of New York at Buffalo, Cooke Hall 109, Buffalo, New York 14260. E-mail: <js15@acsu.buffalo.edu>.