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Southern Caribbean azooxanthellate coral communities off Colombia

Javier Reyes, Nadiezhda Santodomingo, Adriana Gracia, Giomar Borrero-Pérez, Gabriel Navas, Luz Marina Mejía-Ladino, Adriana Bermúdez, Milena Benavides

Instituto de Investigaciones Marinas y Costeras, INVEMAR, Cerro Punta Betín, AA 1016, Santa Marta, Colombia
(jreyes@invemar.org.co)

Abstract. As a result of the explorations carried out by the Colombian Marine and Coastal Research Institute (INVEMAR) between 1998-2002 along the Colombian Caribbean continental shelf and upper slope, the occurrence of azooxanthellate coral banks was suspected at three sites (from the northern to southern Colombian Caribbean coast): off La Guajira Peninsula, at a water depth of 70 m; off Santa Marta, at 200 m, and nearby the San Bernardo Archipelago, at 150 m). Each site exhibited particular bottom features (relief and substrate), suggestive of reef structures. The analysis of the fauna collected by bottom trawling at these sites showed that many of the fishes, mollusks, echinoderms, crustaceans, antipatharians, soft corals and bryozoans collected are characteristic dwellers of hard substrates or reef bottoms. At the first site (Guajira) the hard coral *Cladocora debilis*, was the most abundant; a total of 156 species of invertebrates and fishes were identified among the material collected at this site. At the second site (Santa Marta), 13 scleractinian species were collected, but *Madracis myriaster*, was the dominant species; another 102 species of invertebrates and fishes were also found. At the third site (San Bernardo) 19 scleractinian species were found, *M. myriaster* being the dominant. A total of 135 species of invertebrates and fishes were collected at this site. It is presumed that deep-sea coral banks have developed in these three settings, since many of the collected species are known to be hard or reef bottom dwellers.

Keywords. Colombian Caribbean, biodiversity, deep-water communities, azooxanthellate corals, mollusks, echinoderms, fishes, crustaceans

Introduction

The most extensive and unknown ecosystems on earth are on the sea floor (Snelgrove et al. 1997). The majority of marine bottoms are sedimentary plains, showing quite homogeneous features and similar oceanographic characteristics and biota, which are considered cosmopolitan in distribution (Snelgrove et al. 1997). However, within those extensive plains there are small areas like seamounts,

Freiwald A, Roberts JM (eds), 2005, *Cold-water Corals and Ecosystems*. Springer-Verlag Berlin Heidelberg, pp 309-330

deep-sea trenches, reef-forming corals, submarine canyons, and cold seeps, whose characteristics make possible a relative increase of the biodiversity from surrounding soft bottom areas; these ecosystems are remarkable exceptions to the paradigm of the deep sea as one of the most stable, and least productive biospheres on earth (Mortensen et al. 1995; Koslow 1997; Koslow et al. 2001; Korn et al. 2003). They exhibit unique characteristics and support a diverse community of organisms which have been documented in limited biotic inventories and whose ecologic relationships are so far understood (de Forges et al. 2000).

Deep-sea coral communities have been reported throughout the world oceans, and although they seem to be constrained mainly to the North Atlantic and Pacific temperate waters, there are also some other records in tropical waters off the African coast, the Caribbean Antillean, and the Indopacific (Roberts and Hirschfield 2003). Contrasting to shallow-water coral reefs, deep-sea corals do not depend on sunlight to obtain energy, but feed on microscopic organisms from surrounding waters, and their productivity may be related to their association with light hydrocarbon seeps (de Forges et al. 2000). The discovery of these communities has been incidental, and generally made by fishermen (Fosså et al. 2002). Nevertheless, during the last decade the interest in the continental shelf communities has remarkably increased, to the point, that there is current characterization and mapping information available for the North Atlantic and the Pacific (Freiwald et al. 2002).

Although more than one hundred species can be associated with these unique reef habitats, deep-sea coral communities have been classified by the main framework species. Until now four deep-sea coral bank types have been described: *Lophelia pertusa* banks (200-1000 m water depth), *Oculina varicosa* banks (45-150 m water depth), *Primnoa-Paragorgia* forests (35-750 m water depth), and other living habitats colonized not exclusively by corals, but also by sponges, sea anemones, ascidians and bryozoans (Reed and Mikkelsen 1987; Freiwald et al. 2002; Krieger and Wing 2002).

Similar to shallow-water coral reefs, whose high biodiversity is comparable to that of the rain forest (Hubbell 1997), deep-sea corals have demonstrated that coral framework can modify the seabed. Thus, these coral assemblages provide an essential habitat for many species of invertebrates, including sea stars, nudibranchs, octopuses, snails, crinoids, basket stars, sponges, and anemones, by providing shelter, protection from currents and predators, breeding areas, spawning areas, nurseries, food, and resting areas (Krieger 2001; Tunesi et al. 2001). Some of the associated fauna are commercially and recreationally important such as the red porgy, the greater amberjack, the rockfish, the Pacific Ocean perch, the flatfish, the Atka mackerel, many species of snappers and groupers (Robins et al. 1986; Reed and Mikkelsen 1987; Allen and Robertson 1994) and crustaceans like golden king crab and shrimps. In addition, this biodiversity could be a potential source of numerous marine natural products with medical, pharmaceutical and cosmetological value (Bruckner 2002).

The Colombian continental shelf and break areas have been explored through few

expeditions, the most relevant include the R/V Oregon in the 70´s made by BCF, R/V Pillsbury in 1972 made by RSMAS and CIOH-INVEMAR-Smithsonian in 1995 on board at R/V ANCON, from which a systematic survey was done. Based on their results the INVEMAR carried out the 'Macrofauna' cruises (1998-2002) on board at R/V ANCON, whose primary aim was to fill the information gaps in the inventories of the Colombian soft bottom fauna between 20 and 520 m depth. A total of 72400 specimens were collected during the 'Macrofauna' expeditions, of which 50 % of the species were new records for Colombia (Saavedra-Díaz et al. 2000; Lattig and Reyes 2001; Borrero-Pérez et al. 2002a, b; Cruz et al. 2002; Gonzalez et al. 2002; Gracia et al. 2002; Roa-Varón et al. 2003; Borrero-Pérez and Benavides-Serrato 2004; Campos et al. 2004). In total 10 new species have been described (Lattig and Cairns 2000; Lemaitre and Bermúdez 2000; Lemaitre et al. 2001; Saavedra-Díaz et al. 2001; Ardila and Díaz 2002; Saavedra-Díaz et al. 2003).

The principal aim of the present study is to show and discuss the occurrence of azooxanthellate coral banks in three localities of the southwestern Caribbean sampled by the 'Macrofauna' cruises (INVEMAR 1998-2002). The results of this study represent new evidence of coralline banks constructed by different azooxanthellate corals species than those already reported (Freiwald et al. 2002). The associated faunas are quite different in each one of the three coral settings, represented primarily by anthozoans, crustaceans, mollusks, echinoderms and fishes. In this way, these three unique azooxanthellate coral communities sustain one of the highest species diversities found along the Colombian continental shelf. Due to the fact that the sampling performed by the Macrofauna cruises focused on macrobenthic fauna living on soft bottoms, the discovery of these three localities rich in azooxanthellate corals and their associated fauna was an unexpected result.

Abbreviations

AC: Azooxanthellate corals
BCF: Bureau of Commercial Fisheries, U.S. Department of Interior
DSC: Deep-sea corals
INVEMAR: Instituto de investigaciones Marinas y costeras
GIS-SR Lab: Geographic information systems and remote sensors laboratory at INVEMAR
MCZ: Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts
MHNMC: Museo de Historia Natural Marina de Colombia
NMNH: National Museum of Natural History, Washington
SIBM: Colombian marine biodiversity database
RMNH: Nationaal Natuurhistorische Museum, Leiden, The Netherlands
RSMAS: Rosenstiel School of Marine and Atmospheric Science, Miami
Senckenberg: Senckenberg Museum Frankfurt, Germany

Materials and methods

The sampling was carried out on board the R/V ANCON in two phases: Macrofauna I (October 1998 - April 1999) and Macrofauna II (March - April 2001). In total 80 trawling stations were included between off La Guajira Peninsula (12º 34'N 71º 50' W) and off Gulf of Urabá (09º 02' N 76º 02' W) at five depth ranks (20, 70, 150, 300 and 500 m). A bottom area of about 25000 m^2 was swept at each station by using a semi-balloon trawl net (ca. 9 x 1 m opening) during 20 min, and at a vessel speed of about 3 knots (5.5 km/h). Sea-bottom relief was differentiated using a FURUNO FE 824 echo sounder (200 kHz). On board, the samples were washed through a sieve, sorted and preserved in 70 % and 96 % ethanol (invertebrates) and 10 % formalin (fishes). The locations of the three sites where a significant abundance of azooxanthellate corals and their associated organisms were collected are shown in Table 1 and Figure 1. The specimens were identified to species level by consulting group specific monographs and through direct examination of museum repositories from the NMNH, MCZ, RMNH, RSMAS, Senckenberg, and MHNMC collections. Species relevant information was stored in the SIBM data base, hosted at http://web.invemar.org.co/redcostera1/invemar/sib.jsp.

Results

During the expeditions, three localities with a significant abundance of AC and associated organisms were discovered unexpectedly; however, AC species in other localities have recorded in small amounts. The AC stations were located along the Colombian continental shelf (Fig. 1), off La Guajira Peninsula, off Santa Marta, and off San Bernardo Islands (Table 1). Unlike other sampled bottoms of continental shelves and upper slope, the species richness found for these three AC stations (338 species) was relatively high, with a value representing around 40 % of the species collected throughout the whole study. Species list is shown in Appendix 1. Although the most abundant AC and dwellers found in the three settings belong to different species (in terms of taxonomic identification)**,** the number of species observed in each station was similar, the species common to all sectors remains low (11 species). The most diverse and abundant group sampled corresponds to mollusks (Fig. 2). Some of the echinoderms collected from these three coralline formations constitute

Table 1 Station list, samples collected in each of the coralline communities. Locality (INVEMAR Macrofauna project station name), depth range, and initial (superior coordinates) and final (inferior coordinates) trawl position are shown

Station	Depth (m)	Lat (N)	Long (W)
La Guajira (INV 048)	70-71	11º 23.53'	73º27.78'
		11º24.40'	73º27.62'
Santa Marta (INV 019)	200–220	11º23.25'	74º12.46'
		11º23.61'	74º12.37'
San Bernardo (INV 073)	155-160	9º47.12'	76º13.45'
		9º46.61'	76º13.72'

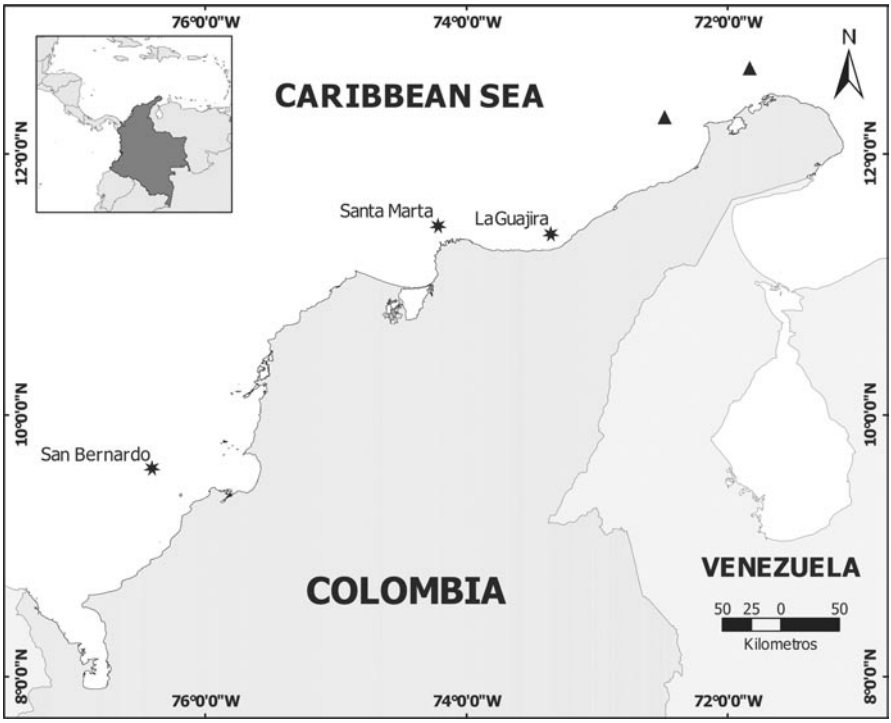


Fig. 1 Map of the Colombian Caribbean showing the three localities where the coral communities were discovered (stars), and where *Lophelia pertusa* was recorded (triangles)

the first records for the Colombian Caribbean. Many fish species associated with coral reef and rocky bottoms were also collected in the areas mentioned.

Common species

The stony coral *Madracis myriaster* (Fig. 3a), common in Santa Marta and San Bernardo, but rare in La Guajira (the shallowest site), appears to be the main coralline matrix builder in the two first areas. Other species common to all localities were the stony coral *Anomocora fecunda* (Fig. 3c), the black coral *Antipathes lenta*, the alcyonarian *Stereonephthya portorricensis* (Fig. 3k) and the brittle-star *Ophiothrix suensonii*, both of them coralline ground dwellers. *Paracyathus pulchellus* (Scleractinia) was commonly found attached to other stony corals skeletons; crabs belonging to the genera *Mithrax* and *Stenorhyncus*, and the fishes *Synagrops bella* and *Antigonia capros* were also recorded.

Associated biota, general characteristics

La Guajira. Water depth 70 m. *Cladocora debilis* (thin tube coral; Fig. 3b) was the main coral matrix builder, its sympodial budding and recumbent shapes provide more surfaces on which sponges, bryozoans, octocorals and tunicates can settle. Other scleractinian species such as *Madracis myriaster* (Fig. 3a),

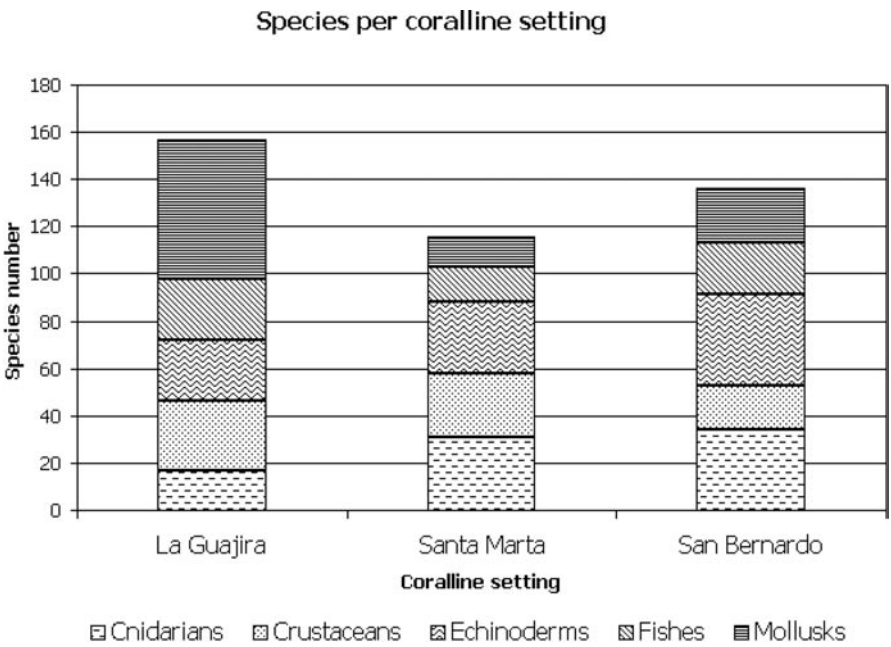
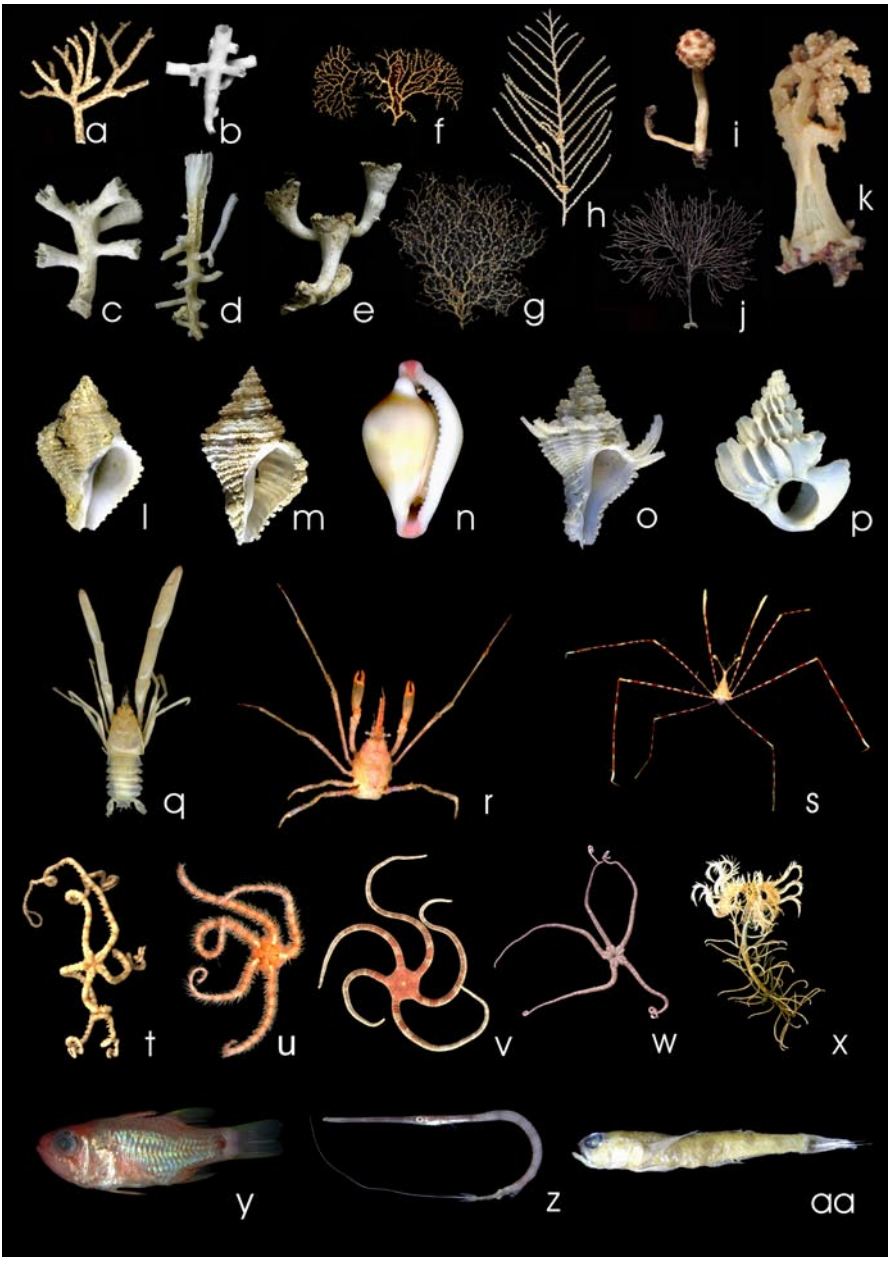


Fig. 2 Species number by major taxa (cnidarians, mollusks, crustaceans, echinoderms and fishes) in each of the coral communities: La Guajira, Santa Marta, and San Bernardo

Anomocora fecunda (Fig. 3c), *Anomocora prolifera*, and *Paracyathus pulchellus* also occasionally occur.

A total of 156 species were collected in this locality, where mollusks were the most diverse taxon (59 species). Bivalves like *Chlamys munda* and *Arca zebra,* and gastropods like *Petaloconchus erectus*, and *Vermicularia spirata* were the most abundant mollusk species. *V. spirata* was often found attached to sponges and to *C. debilis* in small clusters with bryozoans. *V. spirata* is a facultative coral associate, using it as refuge or preying on it (Reed and Mikkelsen 1987). Echinoderms were the most abundant taxon, with 1367 specimens (Fig. 2). The crinoid *Analcidometra armata* was the dominant echinoderm, it has been reported as a common species attached to the gorgonians in the Caribbean Sea (Meyer 1973; Hendler et al. 1995). *Ophiothrix angulata* (Fig. 3u) was found in several stations along the sampling area,

Fig. 3 Invertebrates and fishes collected in the Southern Caribbean deep-sea coral banks off Colombia. The measures given in parenthesis following the species names correspond to the specimen approximate height (invertebrates) and length (fishes). The species shown in this figure were selected to be hard bottom dwellers or associated to their surrounding areas. Cnidarians: **a** *Madracis myriaster* [10 cm]; **b** *Cladocora debilis* [3 cm]; **c** *Anomocora fecunda* [3 cm]; **d** *Thalamophyllia riisei* [5 cm]; **e** *Caryophyllia berteriana* [5 cm]; **f** *Nicella* cf. *guadalupensis* [4 cm]; **g** *Chrysogorgia desbonni* [8 cm]; **h** *Callogorgia* sp. [11 cm]; **i** *Nidalia rubripunctata* [7 cm]; **j** *Antipathes* n. sp. [4 cm]; **k** *Stereonephthya portorricensis* [11 cm]. Mollusks: **l** *Coralliophila caribaea* [2 cm]; **m** *Coralliophila squamosa* [2 cm];



n *Pseudosimnia vanhyningi* [1.3 cm]; **o** *Babelomurex dalli* [2.4 cm]; **p** *Sthenorytis pernobilis* [1.6 cm]. Crustaceans: **q** *Uroptychus uncifer*; **r** *Anomalothir frontalis*; **s** *Latreillia elegans*. Echinoderms: **t** *Asteroschema* cf. *oligactes* [3 cm]; **u** *Ophiothrix angulata* [4 cm]; **v** *Ophioderma rubicundum* [6 cm]; **w** *Astrocnida* cf. *isidis* [10 cm]; **x** *Pentacrinus* sp. [14 cm]. Fishes: **y** *Apogon pseudomaculatus* [3 cm]; **z** *Fistularia petimba* [15 cm]; **aa** *Bollmannia* sp. [2 cm]

but it was especially abundant in the La Guajira community. *O. angulata* has also been reported on *Oculina varicosa* banks off Florida (Reed and Mikkelsen 1987).

In the La Guajira setting, coral reef dweller fishes such as the family Apogonidae (*Apogon affinis*, *A. quadrisquamatus* and *A. pseudomaculatus*) were common (Palacio 1974; Uyeno et al. 1983; Böhlke and Chaplin 1993; Cervigón 1993; Allen and Robertson 1994). Seagrass-inhabitant species like *Paradiplogrammus bairdi*, were also found there.

Santa Marta. Water depth 200 m. 13 scleractinian species were collected. *Madracis myriaster* (Fig. 3a), *Coenosmilia arbuscula, Anomocora fecunda* and the solitary *Polymices fragilis*, were the most abundant species. Here, the stony corals are characterized by bushy shaped colonies (*M. myriaster*, *A. fecunda* and *C. arbuscula*) or individual polyps (*Polymices fragilis* and *Javania cailleti*), both forms have strong bases attached directly to the rock.

Another 102 species of fishes, echinoderms, mollusks, crustaceans, and cnidarians were also found. However, in contrast to La Guajira, other organisms did not significantly encrust the coral skeletons. The species of black corals and octocorals were also numerous, especially *Antipathes columnaris*, *Aphanipates abietina*; and species of the genus *Stichopathes*, and the octocorals *Chrysogorgia desbonni* (Fig. 3g), *Trychogorgia lyra*, *Nidalia* sp. (Fig. 3i) and *Nicella* cf. *guadalupensis* (Fig. 3f). The abundance of mollusks was low; the gastropods found were anthozoan´s dwellers, which usually prey on it; *Sthenorytis pernobilis* (Epitonidae) (Fig. 3p) on sea anemones; *Pseudosimnia vanhyningi* (Ovulidae) (Fig. 3n) on octocorals; and *Babelomurex dalli* (Fig. 3o), and *Coralliophila squamosa* (Fig. 3m) (Coralliophilidae) on stony corals (Keen 1971; Cate 1972; Reed and Mikkelsen 1987), all of these constitute first records for the Colombian Caribbean (Gracia et al. 2004).

In Santa Marta, *Ophiothrix suensonii*, commonly found on gorgonians, recorded by Hendler et al. (1995) from shallow to deep reef zones and the sea cucumber *Holothuria lentiginosa enodis* previously recorded off Florida from *Oculina varicosa* banks (Pawson et al. 1982), were found (Borrero-Pérez et al. 2003). Another 14 species were found exclusively in this area; three of them, *Stephanasterias* cf. *albula*, *Trigonocidaris albida*, and *Palaeobrissus hilgardi* were the first records for the southern Caribbean.

The crustacean fauna found in the three coralline formations presents no major exclusive coral associations, however, in Santa Marta species of the family Chyrostilidae like *Uroptychus* sp., were recorded as hosted in octocorals of the *Chysogorgia* genus (Pequegnat and Pequegnat 1970). Some crab species collected, like those of the genera *Anomalothir* and *Latreillia*, are known to be common inhabitants of rubble shells and sandy bottoms (Williams 1984). *Palicus affinis, P. alternatus, P. gracilipes* and *P. sicus*, exhibit no particular habitat preferences (Rathbun 1918), but were found associated with coral grounds only in the Santa Marta and San Bernardo areas.

Rocky-bottom fishes like *Gymnothorax poligonius*, *Chlorophthalmus agassizi*, *Bellator egretta*, *Antigonia capros*, *Antigonia combatia*, and *Pontinus nematophthalmus* were the first records for the Colombian Caribbean.

San Bernardo. Water depth: 155-160 m. 19 scleractinian species were found, among which, *Anomocora fecunda*, *Coenosmilia arbuscula*, *Thalamophyllia riisei* (Fig. 3d) and *Madracis myriaster* were dominant. *Eguchipsammia cornucopia*, mostly devoid of living tissue, was also common. Other less abundant scleractinians were also found attached to the four species mentioned above. Three different growth forms of stony corals were present: recumbent (*T. riisei* and *E. cornucopia*); bushy (*M. myriaster* and *A. fecunda*); and solitary (*Caryophyllia berteriana*, Fig. 3e, and *Coenocyathus parvulus*). The San Bernardo site corresponds to an extensive carbonate deposit formed during the Pleistocene epoch over older strata deformed by tectonism and diapiric intrusion (Vernette 1989a).

Beside corals, a total of 115 species of invertebrates and fishes were collected at this site. San Bernardo was the most diverse sector in echinoderms with 38 species (Fig. 2); brittle stars such as *Ophioderma appressum*, *Astrocnida* cf. *isidis* (Fig. 3w), *Asteroporpa* cf. *annulata, Asteroschema* cf. *laeve* and *Asteroschema* cf. *oligactes* (Fig. 3t) were found attached to stony corals and gorgonians. Also, rare species, like *Ophiosyzygus disacanthus*, previously recorded as dwelling in hard bottoms (Turner and Heyman 1995; Borrero-Pérez and Benavides-Serrato in press), the pedunculate crinoids *Democrinus conifer* (Macurda and Meyer 1976), and the coral reef crinoid *Nemaster rubiginosus* (Hendler et al. 1995) were also present in San Bernardo. The mollusk fauna here has no restricted coral dwellers, except the gastropod *Coralliophila caribaea*, 10 species of bivalves were found.

In San Bernardo, five fish species associated with coral reefs (Allen and Robertson 1994; Cervigón 1994) were caught. *Fistularia petimba*, *Bollmannia* sp., *Serranus atrobranchus, Decodon puellaris* and *Pristigenys alta*, although they were not the most abundant species collected (Fig. 3). While *Citharichthys cornutus, Lipogramma evides* and *Neomerinthe beanorum* were the most frequent species caught.

Discussion

The Colombian seabed still remains poorly known. The efforts addressed to the study the shallow-water coral reefs and seagrasses during the last three decades have been increased, and data about characterization and mapping of them are already available (Díaz et al. 2000, 2003), but shallow-coral reefs and seagrasses, represent only less than 1 % of the Colombian marine bottoms (SIG-SR Lab). Recently, other complex ecosystems occurring on the continental shelf and slope around the world are being discovered and studied mainly in North Atlantic and Pacific oceans. DSC banks belong to those recently described ecosystems (Mortensen et al. 1995; Freiwald et al. 2002; Korn et al. 2003). According to the results of this study, three new records of azooxanthellate coral communities occurring on the Colombian continental shelf are documented. The records registered off La Guajira, Santa Marta and San Bernardo were fortuitous, because the Macrofauna expeditions were focused to explore the soft bottoms of the continental shelf and slope between 20 and 500 m. In 77 of the 80 stations sampled no major amounts of corals on hard

substrates were found. Occasionally, in some sampling areas, where rough relief was observed, trawling was avoided to prevent net damage; for that reason, more areas where deep-sea coral communities occur would be expected. Further research aiming to map and study their biodiversity is necessary to assess the value of these deep-sea coral ecosystems and to propose conservation measures.

The results suggest that the deep-sea coral communities observed on the Colombian continental shelf have a similar ecological role (in terms of dwelling and food supply) to those reported in temperate regions. The fauna composition of the stony coral framework here however is different. *Lophelia* spp., *Oculina* spp. and *Madrepora* spp. were uncommon species; *Madracis myriaster* and *Cladocora debilis* seem to be the main frame building species found. *M. myriaster* belongs to the apozooxanthellate coral group defined by Best (2001), which developed adaptive strategies to survive in colder waters; this adaptive response could derive from the facultative presence of zooxanthellae, followed by the migration to deep waters. This kind of adaptation explains the extensive bathymetric range of *M. myriaster* namely 20-700 m in the West Atlantic (Best 2001).

On the other hand, the *Lophelia pertusa* records in the Oceana Report (Roberts and Hirschfield 2003) give some evidence of the possible occurrence of *Lophelia* banks off Venezuela. In addition, some other non-living *Lophelia* records from the R/V Pillsbury (Cairns 1979) and INVEMAR expeditions in Colombian waters at 500 m depth, suggest that *Lophelia* could have occurred there in the recent past, or could be alive there now and forming coral banks in the surrounding waters.

The differences in stony coral species composition found among the surveyed localities indicate some differences in environmental conditions. *Cladocora debilis* is the most important coral established in La Guajira formation. This suggests that the growth of recumbent species is favored of a homogeneous non-consolidated bottom in this locality. In fact, sedimentary data sets indicate that deposited material on the coast off La Guajira comes from upper Tertiary and Quaternary alluviums (Thomas and MacDonald 1969). Metamorphic rocks from the Sierra Nevada de Santa Marta mountain system (Gonzáles and Rodríguez 2003) form a favourable substrate for the corals settled at Santa Marta site. There, the coralline fauna was mainly represented by species with corallums showing an extended base attached to the rock (*Polymices fragilis* and *M. myriaster*). In San Bernardo both corallum shapes were common, suggesting a heterogeneous substrate that probably promoted the variability in the corallum forms settled there. Apparently, the attached species grow on limestone substrate, which is composed mainly of a fossil reef terrace built during the last marine regression about 20 ky ago when the sea level was 120 m below the current one (Vernette 1989b). This fossil reef terrace has developed on diapiric domes or mud vulcanoes which can be related to the active plate tectonics off the Colombian Caribbean continental margin (Vernette 1989c).

Although the hard corals that build framework belonged to different species, they exhibit a similar shape characterized by recumbent growth with secondary corallites located both sides of the principal axis (see Figs. 3a-e). The branching pattern displayed by *Anomocora fecunda* (Fig. 3c) and *Coenosmilia arbuscula*,

was quite similar, and sometimes establishing differences between them was very difficult. Some specimens exhibit a transitional form, which indicates a possible hybridization process, analogous to that described for shallow coral reefs (Vollmer and Palumbi 2002). Other evidence suggests that corallum shape convergence is a common phenomenon; species previously described by Cairns (2000) as reptoid colonies (*Thalamophyllia riisei*; Fig. 3d) or as individual polyps (*Caryophyllia berteriana*; Fig. 3e), showed a branching pattern similar to that of *Cladocora debilis* (Fig. 3b). Such convergence suggests an environmental factor response, analogous to those corallum-shape changes showed by some species in shallow coral reefs, responding to hydrodynamic factors.

The differences among the faunas associated with the three DSC communities give some hints about the environmental conditions of the surrounding waters. At La Guajira site, sponges and ascidians (suspension feeders) were abundant; this fact indicates an environment enriched with suspension material, perhaps produced by the upwelling conditions typical of the area. Epizoic fauna was common in La Guajira coral community; sponges, ascidians, bryozoans, antipatharians, octocorals, and scleractinians were settled on *Cladocora debilis* (Fig. 3b) skeletons. Sponges also provide substrates to other fauna; the scleractinian *Paracyathus pulchellus* which was often observed settled on them. In San Bernardo some epizoites were noticed whereas in Santa Marta the epizoites were rare.

Tropical coral reefs present a fragmented distribution due to their specific ecological requirements to develop complex structures (Birkeland 1997). Some typical shallow reef species were found associated with these deep-sea coral communities. The brittle star *Ophioderma* spp., the gobiid fish *Bollmannia* spp. and *Apogon* spp. increased their bathymetric range to deeper waters, suggesting that there may be an ecological relationship (i.e. breeding areas) between shallow-water reef habitats and their deep-water continental shelf counterparts. This example suggests that distributional patterns of some coral reef species may be characterized by a continuum rather than by isolated populations, using these deep-water environments as stepping stone habitats between shallow reefs in order to disperse.

Different facultative or obligate epizoic interactions within these communities were observed, including stony corals, gorgonians and sponges as substrates for bryozoans, mollusks, echinoderms, other stony corals and sponges. Some studies on invertebrate fauna associated with corals have demonstrated that while corals play an important role in framework building, crinoids, sea anemones, bryozoans, sponges, and other scleractinians, participate in the accumulation of carbonate sediments and the accretion of coralline matrix (Sulak and Ross 2003).

Further investigation will be focused on studying the biological and ecological relationships in these settings. It is necessary to carry out research on habitat characterization and mapping, as well as on the assessment of impacts caused by trawl fishing in order to support arguments for the sustainable use and conservation of these unique biological communities.

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Appendix 1

Species list of invertebrates and fishes collected in the coralline settings off Colombia. La Guajira (GUA), Santa Marta (SMA) and San Bernardo (SBE). The new records (NR) for Colombian Caribbean are shown

Group	Species	Coral Setting			NR
		GUA	SMA	SBE	
Cnidarians	*Acanthogorgia schrammi*	×		×	+
	Acryptolaria conferta		×		+
	Amphiantus caribaea		×		+
	Anomocora fecunda	×	×	×	
	Anomocora prolifera	×	×		
	Antipathes atlantica	×			
	Antipathes cf. *salix*		×		+
	Antipathes columnaris		×	×	+
	Antipathes furcata	×			
	Antipathes gracilis	×		×	
	Antipathes lenta	×	×	×	
	Antipathes n. sp.		×		
	Aphanipathes abietina			×	+
	Balanophyllia bayeri		×		+
	Balanophyllia cyathoides		×	×	+
	Balanophyllia palifera		×	×	+
	Balanophyllia pittieri		×		
	Balanophyllia wellsi			×	+
	Bellonella rubistella	×			+
	Callogorgia sp.		×		+
	Caryophyllia ambrossia		×		
	Caryophyllia barbadensis			×	+
	Caryophyllia berteriana		×	×	
	Caryophyllia sp.		×	×	
	Chrysogorgia desbonni			×	+
	Chrysogorgia sp.			×	
	Cladocora debilis	×			
	Coenocyathus parvulus			×	+
	Coenosmilia arbuscula		×	×	
	Deltocyathus calcar			×	
	Diodogorgia sp.			×	
	Eguchipsammia cornucopia			×	+
	Javania cailleti		×	×	
	Leipsiceras pollens		×		
	Madracis asperula	×			
	Madracis myriaster	×	×	×	
	Madracis pharensis			×	
	Madrepora carolina			×	+
	Nicella guadalupensis			×	+
	Nicella sp.1		×		
	Nicella sp.2		×		
	Nidalia cf. *occidentalis*	×			+
	Nidalia dissidens		×	×	+
	Oxysmilia rotundifolia			×	
	Paracyathus pulchellus	×		×	
	Placogorgia tenuis		×		+
	Polycyathus mayae			×	+
	Polymyces fragilis		×		+
	Renilla muelleri	×			
	Riisea sp.		×		
	Stereonephthya portorricensis	×	×	×	+

Appendix 1 continued

Group	Species	Coral Setting			NR
		GUA	SMA	SBE	
...Cnidarians	*Stichopathes* cf. *lutkeni*			×	+
	Stichopathes cf. *occidentalis*			×	
	Stichopathes pourtalessi			×	+
	Stichopathes n. sp.		×		
	Swiftia sp.			×	
	Thalamophyllia riisei			×	+
	Thelogorgia vossi		×		
	Thesea sp.1	×			
	Trichogorgia lyra	×			
	Villogorgia nigrensis		×		+
	Viminella sp.		×		+
Crustaceans	*Aepinus septemspinosus*	×			+
	Agaricochirus alexandri		×		
	Anasimus latus	×			
	Anomalothir frontalis		×	×	+
	Anomalothir furcillatus		×		+
	Anomalothir sp.		×		
	Arachnopsis sp.	×			
	Batrachonotus fragosus	×			
	Calappa sulcata	×	×		
	Callidactylus asper	×			
	Chasmocarcinus cylindricus		×	×	
	Chyrostilidae sp.2			×	
	Chyrostilidae sp.3			×	
	Clythrocerus moreirai		×		+
	Collodes trispinosus			×	+
	Cyclodorippe antenaria		×		+
	Ethusa mascarone	×			
	Euchirograpsus americanus	×		×	
	Eucratopsis crassimanus	×			+
	Euphrognata rastellifera		×		
	Homola barbata	×			+
	Iliacantha subglobosa	×			
	Latreilliia elegans		×		+
	Macrocoeloma eutheca	×			+
	Macrocoeloma septemspinosus	×			+
	Mesorhoea sexspinosa	×			
	Mithrax cornutus	×		×	
	Munida benedicti			×	+
	Munida evermani			×	+
	Munida flinti			×	+
	Munida sp.3	×			
	Munida sp.4	×			
	Munidopsis platirostris		×		+
	Munidopsis sp.1			×	
	Osachila antillensis			×	
	Paguristes sp.1		×		
	Palicus affinis	×			+
	Palicus alternatus	×			
	Palicus gracilipes		×		+
	Palicus sicus		×	×	+
	Panoplax depressa	×			
	Pantomus sp.	×		×	
	Parapontophylus gracilis		×		+
	Parthenope agona	×			
	Parthenope fraterculus	×			
	Parthenope pourtalessi		×		+

Appendix 1 continued

Group	Species	Coral Setting			NR
		GUA	SMA	SBE	
...Crustaceans	*Persephona crinita*			×	+
	Petrochirus diogenes	×			
	Plesionika acanthonotus		×		+
	Plesionika longicauda	×			+
	Plesionika longipes		×		+
	Plesionika miles		×		+
	Plesionika tenuipes		×		+
	Podochela gracilipes	×			
	Pylopaguropsis atlantica		×		+
	Pylopagurus discoidalis		×	×	+
	Pyromaia acanthina		×		
	Pyromaia propinqua			×	+
	Rhodochirus rosaceus		×		
	Stenocionops furcata	×			
	Stenorhynchus seticornis	×		×	
	Stenorhynchus yangii	×	×	×	+
	Uroptychus sp.		×		
	Xylopagus tayrona		×		
Echinoderms	*Agassizia excentrica*	×		×	
	Amphioplus sp.1	×			
	Amphioplus sp.2			×	
	Analcidometra armata	×			
	Asteroporpa cf. *annulata*			×	
	Asteroschema cf. *laeve*			×	
	Asteroschema cf. *oligactes*		×	×	
	Astrocnida cf. *isidis*			×	
	Astropecten alligator		×		
	Bathyplotes natans		×		+
	Brissopsis elongata	×			
	Centrostephanus sp.	×			
	Clypeaster euclastus			×	
	Clypeaster lamprus			×	
	Coccometra sp.			×	
	Coelopleurus floridanus		×	×	
	Comactinia meridionalis	×		×	
	Coronaster sp.		×		
	Crinometra brevipinna			×	
	Democrinus conifer			×	
	Dipsacaster sp.		×		
	Pentacrinus sp.		×	×	
	Eucidaris tribuloides	×			
	Genocidaris maculata	×			
	Histampica cf. *duplicata*		×	×	
	Holothuria lentiginosa enodis		×		+
	Holothuria occidentalis			×	
	Hypalometra defecta	×			
	Leptonemaster venustus	×		×	
	Marginaster cf. *pectinatus*		×		
	Mediaster sp.	×			
	Nemaster discoidea	×			
	Nemaster rubiginosus			×	
	Neocomatella cf. *pulchella*		×		
	Ophiacantha sp.1	×			
	Ophiacantha sp.2			×	
	Ophiacantha sp.3			×	
	Ophiactis algicola	×			
	Ophiactis savignyi	×			

Appendix 1 continued

Group	Species	Coral Setting			NR
		GUA	SMA	SBE	
…Echinoderms	*Ophiochondrus* cf. *convolutus*		×		
	Ophioderma appressum			×	
	Ophioderma rubicundum	×			
	Ophiomitra cf. *valida*		×		
	Ophiomitrella cf. *laevipellis*			×	
	Ophiomyxa cf. *tumida*		×		
	Ophiomusium acuferum	×	×	×	
	Ophiomusium eburneum		×		
	Ophiomusium cf. *testudo*		×	×	
	Ophiomusium validum			×	
	Ophionereis dolabriformis	×			
	Ophiopaepale cf. *goesiana*			×	
	Ophiophragmus riisei			×	
	Ophioplax cf. *ljungmani*		×	×	
	Ophiopristis cf. *hirsuta*		×	×	
	Ophiopsila hartmeyeri	×			
	Ophiostigma isocanthum	×			
	Ophiosyzygus disacanthus			×	+
	Ophiothrix angulata	×			
	Ophiothrix orstedii	×			
	Ophiothyreus cf. *goesi*			×	
	Ophiothrix suensonii	×	×	×	
	Ophiura cf. *acervata*	×	×	×	
	Palaeobrissus hilgardi		×		+
	Paleopneustes cristatus			×	
	Paleopneustes tholoformis			×	
	Persephonaster echinulatus		×		
	Plutonaster agassizi agassizi	×		×	
	Pteraster sp.		×		
	Rosaster cf. *alexandri*		×		
	Stephanasterias cf. *albula*		×		
	Stylocidaris affinis	×	×		
	Stylocydaris lineata		×	×	+
	Stylometra cf. *spinifera*			×	
	Tamaria cf. *halperni*		×		
	Trigonocidaris albida		×		+
Fishes	*Ancylopsetta cycloidea*			×	
	Antigonia capros	×	×	×	+
	Antigonia combatia		×	×	+
	Apogon affinis	×			
	Apogon pseudomaculatus	×			
	Apogon quadrisquamatus	×			
	Bathyanthias mexicana	×			+
	Bellator brachychir			×	
	Bellator egretta		×		+
	Bembrops anatirostris	×	×		
	Bollmannia sp.			×	
	Bregmaceros atlanticus	×		×	
	Chlorophthalmus agassizi		×		+
	Citharichthys cornutus			×	
	Citharichthys gymnorhinus	×			
	Decodon puellaris			×	
	Engyophrys sentus	×			
	Fistularia petimba			×	
	Gymnothorax polygonius		×		+
	Halieutichthys aculeatus		×		
	Holanthias martinicensis	×		×	

Appendix 1 continued

Group	Species	Coral Setting			NR
		GUA	SMA	SBE	
…Fishes	*Kathetostoma cubana*			×	
	Lipogramma evides			×	+
	Lophiodes reticulatus		×		
	Monacanthus ciliatus	×			
	Pontinus nematophthalmus		×	×	+
	Priacanthus arenatus	×			
	Prionotus beani			×	
	Prionotus stearnsi	×			
	Pristigenys alta			×	
	Saurida brasiliensis	×			
	Saurida caribbaea		×		+
	Scorpaena agassizii			×	
	Scorpaena calcarata	×			
	Serranus atrobranchus	×		×	
	Serranus chionaraia	×			
	Serranus sp.1		×		
	Serranus sp.2	×			
	Serranus tortugarum	×			
	Steindachneria argentea		×		
	Syacium micrurum	×			
	Syacium gunteri	×			
	Symphurus piger	×	×	×	
	Synagrops bella	×	×	×	+
	Synagrops spinosus	×			
	Synodus poeyi	×			
	Thalassophryne maculosa			×	
Mollusks	*Abra* sp.		×		
	Abra longicallis			×	
	Acesta colombiana	×			
	Acteon sp.	×			
	Anadara sp.	×			
	Arca zebra	×			
	Arcopsis adamsi	×			
	Arene sp.	×			
	Babelomurex dalli		×		+
	Barbatia candida	×		×	
	Bellaspira pentagonalis	×			
	Calliostoma fernandezi	×			
	Calliostoma sp.			×	
	Capulus sp.1	×			
	Capulus sp.2	×			
	Cardiomya sp.	×			
	Chama congregata	×			
	Chama macerophylla	×			
	Cheilea equestris			×	
	Chlamys munda	×			
	Circomphalus strigillinus	×			
	Cocculina sp.		×		
	Cochlespira radiata			×	+
	Conus cf. *daucus*	×			
	Conus cf. *granarius*	×			
	Coralliophila caribaea			×	
	Coralliophila squamosa		×		+
	Cosmioconcha nitens	×			
	Crucibulum cf. *marense*	×			
	Crucibulum sp.	×			
	Cuspidaria sp.			×	

Appendix 1 continued

Group	Species	Coral Setting			NR
		GUA	SMA	SBE	
…Mollusks	*Cypraea cassis*			×	
	Cypraea cinerea	×			
	Dentalium sp.			×	
	Dentimargo sp.	×			
	Diodora cayennensis	×	×		
	Diodora sp.1			×	
	Diodora sp.2			×	
	Discotectonica discus		×		+
	Distorsio cf. *mcgintyi*			×	
	Douglassia sp.	×			
	Entodesma beana	×			
	Eratoidea hematita	×			
	Eudolium crosseanum			×	
	Eudollium thompsoni		×		
	Fusinus lightbourni		×		
	Glyphostoma gabbi	×			
	Hypselodoris sp.	×			
	Laevicardium sybariticum	×			
	Laevidentalium callipeplum		×		+
	Limaria sp.		×	×	
	Limopsis antillensis	×			
	Loligo sp.	×			
	Macoma tenta	×			
	Mitrolumna biplicata	×			
	Myrtea prystiphora	×			
	Nassarius scissuratus		×		
	Nassarius hotessieri	×			
	Nemocardium sp.			×	
	Nemocardium tinctum	×			
	Notocrater sp.			×	
	Nuculana cestrota	×			
	Octopus sp.	×			
	Olivella cf. *acteocina*	×			
	Parvamussium pourtalesianum			×	
	Pecten chazaliei	×			
	Persicula pulcherrima	×			
	Petaloconchus erectus	×			
	Pitar albida	×			
	Pitar arestus			×	
	Pitar cf. *albida*	×			
	Pleurobranchus sp.	×			
	Plicatula cf. *gibbosa*			×	
	Polystira tellea	×		×	+
	Poromya rostrata	×		×	
	Prunum marginatum	×			
	Pseudosimnia vanhyningi		×		+
	Pyrgospira sp.	×			
	Semirossia tenera			×	+
	Sthenorytis pernobilis		×		+
	Tellina persica	×			
	Trachipollia didyma	×			
	Tucetona pectinata	×			
	Ventricolaria listeroides	×			
	Vermicularia spirata	×			
	Volvarina cf. *avena*	×			
	Volvarina sp.1	×			
	Volvarina sp.2	×			

Appendix 1 continued

Group	Species	Coral Setting			NR
		GUA	SMA	SBE	
…Mollusks	*Xenophora caribaea*			×	
	Xenophora conchyliophora	×			
TOTAL	**338 species**	**156**	**115**	**134**	**84**