Mar Biodiv (2013) 43:7–22
DOI 10.1007/s12526-012-0131-6

Diversity and distribution of azooxanthellate corals in the Colombian Caribbean

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Received: 29 May 2012 / Revised: 31 August 2012 / Accepted: 23 September 2012 / Published online: 23 October 2012

Abstract During the last decade, knowledge of azooxanthellate corals in the Colombian Caribbean has increased through exploration campaigns by the Marine and Coastal Research Institute (INVEMAR). The distribution of 142 species of corals, including hard corals (Scleractinia 64 species), black corals (Antipatharia 18 species), and soft corals (Octocorallia 60 species) is assessed. Statistical analyses were performed to examine the coral species distribution through a geographic gradient (210 stations in 8 sectors) and a bathymetric range (10–520 m depth). Four principal patterns were observed: (1) northeastern distribution (46 species), (2) southwestern distribution (11 species), (3) association with azooxanthellate coral bioherms (37 species), and (4) widespread (44 species). In addition, 4 species were only found around the San Andres Archipelago (insular pattern). Two main oceanographic factors were identified to play a role in the northeast versus southwest coral fauna separation, La Guajira upwelling system and the Magdalena River influx. These patterns appear to be depth-related, since the separation between northeast and southwest was mainly shown by the shallow-water coral fauna, whereas most of the deep-water corals (>200 m depth) were widely distributed along the Colombian Caribbean coastline. These data were also analyzed from a conservation perspective in order to propose new strategies for the protection of the Colombian Caribbean coral fauna.

Keywords Azooxanthellate corals · Colombian Caribbean · Diversity · Scleractinia · Octocorallia · Antipatharia

Electronic supplementary material The online version of this article (doi:10.1007/s12526-012-0131-6) contains supplementary material, which is available to authorized users.

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Introduction

In response to the worldwide decline in marine diversity (Gaston 2000; Pandolfi et al. 2005), a paradigm shift has occurred towards better and more precautionary conservation and management of marine resources (Ludwig et al. 1993; Dayton 1998). These conservation strategies are designed through ecological models (Gering et al. 2003) based on which species occur within a particular area and on what factors control their distribution (Friedlander et al. 2003). The accomplishment of this task receives special attention in Colombia, which is also recognized for its megadiverse terrestrial biota (Mittermeier et al. 1997). Owing to Colombia's position between the Atlantic and the Pacific, each with distinct geological, oceanographic and climatic features, it is one of the countries with the highest marine biological diversity in South America (Díaz and Acero 2003; Miloslavich et al. 2010). Although marine biodiversity research of Colombia has a short history, considerable knowledge has been gathered in the last 10 years, particularly with regard to species inventories and ecosystem characterizations (e.g., Campos et al. 2004; Reyes et al. 2005, 2010; Benavides et al. 2011).

During the last decades, the Colombian continental shelf has been explored through a few research expeditions. The most important ones are those made by the R/V "Oregon" in the 1960s, the R/V "Pillsbury" in 1972, and the B/I "Ancón" in 1995. Consequently, INVEMAR carried out six "Macrofauna" cruises (1998–2002) on board of the B/I "Ancón" to fill the information gap concerning the Colombian soft bottom fauna between 10 and 520 m depth (Saavedra-Díaz et al. 2000; Lattig and Reyes 2001; Borrero-Pérez et al. 2002a, b; Cruz et al. 2002; Gracia et al. 2002, 2004; Reyes and Santodomingo 2002; Roa-Varón et al. 2003; Borrero-Pérez and Benavides-Serrato 2004; Campos et al. 2004; Flórez-Romero et al. 2007). The discovery of azooxanthellate coral communities (Santodomingo et al. 2007) and methane seep ecosystems (Gracia et al. 2012) were among the most interesting results of these expeditions.

Earlier research on scleractinian azooxanthellate corals inhabiting Colombian shallow waters was carried out by von Prahl and Erhardt (1985, 1989), Werding and Sánchez (1989), Sánchez (1995), and Díaz et al. (2000), and regarding deep waters by Cairns (1979, 2000). The most representative studies on the taxonomy and ecology of Colombian octocorals were carried out by Botero (1987), Sánchez (1994, 1998, 1999, 2001), and Sánchez et al. (1997, 1998). Ecological and taxonomic research on antipatharians were performed by Sánchez (1999) and Opresko and Sánchez (1997, 2005). As a result of the recent marine macrofauna expeditions, knowledge about the Colombian coral fauna showed an important growth with three new species for science (Lattig and Cairns 2000; Reyes et al. 2009) and new records for the region (Reyes 2000; Lattig and Reyes 2001; Reyes et al. 2005; Chacón-Gómez et al. 2008, 2010, 2012).

Most results of these expeditions have only been presented in technical reports with no attempt to understand species distribution patterns. Therefore, the main goal of the present study is to analyze and compare the spatial distributions of Colombian Caribbean azooxanthellate anthozoans (orders Scleractinia, Alcyonacea, Pennatulacea, and Antipatharia) along a geographical gradient (210 stations in eight sectors) and a bathymetric range (10–520 m).

Materials and methods

Specimens were collected during the INVEMAR expeditions Macrofauna I (1999), Macrofauna II (2000), Uraba (2003), Corpoguajira (2005), and Marcoral (2005) on board of B/I "Ancón" using an epibenthic trawl net (9×1 m opening; 3 knots by 10 min), a Van Veen grab (60 l, 0.03 m^2), and a heavy chained rocky dredge (1×0.4 m opening; 1.5 knots by 5 min). Specimens collected during previous biodiversity projects and material donated to INVEMAR by the Smithonian Institution's National Museum of Natural History at Washington, DC (NMNH-SI) were also included in the analysis (specimens from San Andres and three stations at depths beyond 520 m). In this way, the study comprised 210 sampling localities primarily covering a depth range from 10 to 520 m depth in the Colombian Caribbean (Table 1; Fig. 1a; ESM 2 Table S1).

Corals with polyps (in 70 or 96 % ethanol) and dry coral skeletons were kept in the collection of the Museo de Historia Natural Marina de Colombia (MHNMC). Specimens were identified to species or to genus level in the case of some octocorals and antipatharians. Some identifications were confirmed by comparison with type material deposited in the NMNH-SI. Identifications were based on: Scleractinia (Cairns 1979, 2000; Zibrowius 1980); Octocorallia (Deichman 1936; Bayer 1961; Bayer et al. 1983; Verseveldt and Bayer 1988; Williams 1995, 1999; Sánchez and Wirshing 2005); and Antipatharia (Brook 1889; Opresko 2001, 2002, 2003, 2004, 2006; Opresko and Sánchez 2005). The database comprised a total of 1,226 records (online at http://siam.invemar.org.co/siam/sibm/index.htm, accessed 30 October 2011).

Systematic surveys carried out by INVEMAR since 1999 along the Colombian Caribbean comprised eight sectors or seascapes (INVEMAR 2000; Díaz and Acero 2003), which are based on the topography and width of the continental shelf, the geomorphology of the coastal zone, upwelling, terrestrial run-off through major river outlets, and the distribution of the main marine ecosystems. These eight sectors are: La Guajira (GUA), Palomino (PAL), Tayrona (TAY), Magdalena (MAG), Coralline Archipelagos (ARCO), Gulf of Morrosquillo (MOR), Southern Colombian Caribbean (DAR), and San Andres and Old Providence islands (SAN). Bathymetric ranges include samples taken at 20, 70, 150, 200, 300, and 500 m depth. Therefore, the data was summarized in a matrix of presence/absence records of species in each sector of the Colombian Caribbean with their respective bathymetric ranges (Appendix 1). Sectors and depth ranges (>2 species) were grouped using group-average clustering based on Bray-Curtis similarities calculated on presence/absence of coral

Table 1 Number of sampling stations of various projects carried out in the Colombian Caribbean

Project	Localities	Methods
Macrofauna I (1)	61	T
Macrofauna II (1)	74	T
Uraba 2003 (1)	9	T
Corpoguajira (1)	31	T
Marcoral (1)	9	T,G,D
Biodiversity	15	S
NMNH-SI (2,3)	11	G,D
Total	210	

Research vessels: *1* B/I "Ancón", *2* R/V "Pillsbury", *3* R/V "Oregon"

Methods: *T* trawling net, *G* van Veen grab, *D* rock dredge, *S* scuba diving

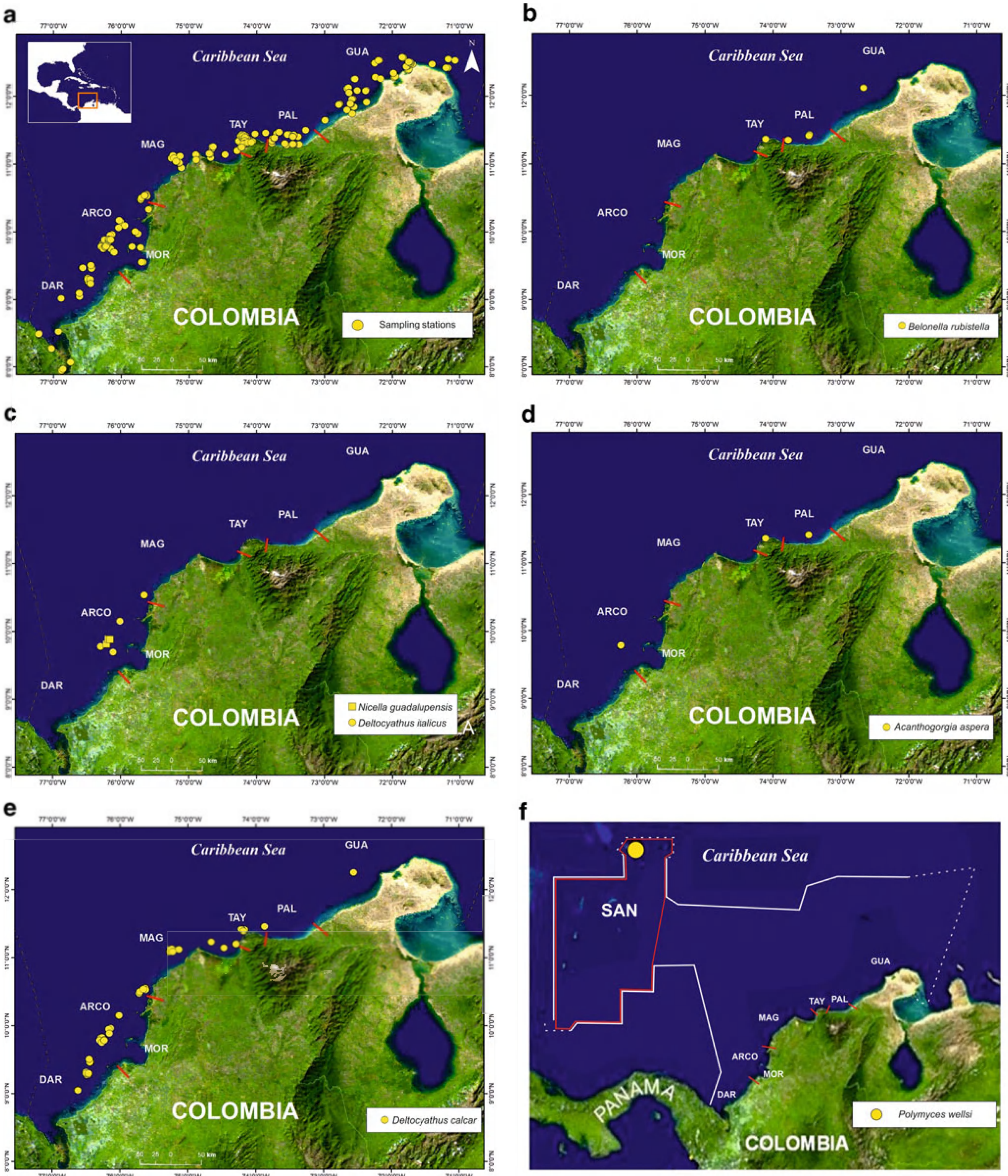

Fig. 1 **a** Distribution of sampling stations in the Colombian Caribbean in the sectors (*red bars*) La Guajira (*GUA*), Palomino (*PAL*), Tayrona (*TAY*), Magdalena (*MAG*), Coralline Archipelagos (*ARCO*), Gulf of Morrosquillo (*MOR*), and Southern Colombian Caribbean (*DAR*). **b**–**f** Example maps of distribution patterns for azooxanthellate corals: **b** northeastern distribution of the octocoral *Bellonella rubistella* (family Alcyoniidae); **c** southwestern distributions of the octocoral *Nicella guadalupensis* (family Ellisellidae) and the free-living scleractinian *Deltocyathus* cf. *italicus* (family Caryophylliidae); **d** associated to coral bioherms: distribution of the octocoral *Acanthogorgia aspera* (family Acanthogorgiidae); **e** widespread: distribution of the hard coral *Deltocyathus calcar* (family Caryophylliidae); **f** insular pattern: distribution of the solitary scleractinian *Polymyces wellsi* (family Flabellidae), from the additional material collected in the sector San Andres and Providencia Archipelago (*SAN*) shown in *red box*; *white line* indicates the Colombian Economic Exclusive Zone (*dotted line*, borders in dispute)

species data using PRIMER 6 software (Clarke and Gorley 2006). This information was sorted using non-metric multidimensional scaling (MDS). The MDS analysis was performed 100 times. Distribution maps of selected species were obtained after the incorporation of the dataset in a georeferenced matrix with ArcGIS™ v.9.3 software.

Results

A total of 142 species was listed (Appendix 1), consisting of 64 Scleractinia (hard corals), 55 Alcyonacea (soft corals and gorgonians), 5 Pennatulacea (sea pens), and 18 Antipatharia (black corals). Over 50 % of the scleractinians belonged to the Caryophylliidae (n=34; ESM 1 Figs. S1–S3), which were followed by the Dendrophylliidae (n=11; Fig. S4), the Flabellidae (n=4), and the Pocilloporidae (n=4; Fig. S5), the Oculinidae (n=3; Fig. S5), the Fungiacyathidae (n=2), and the Turbinoliidae (n=2), and the Gardineriidae, Guyniidae, Rhizangiidae, and Schizocyathidae, each with only 1 species (Fig. S5). Except for *Cladocora arbuscula*, all observed scleractinians were non-symbiotic (azooxanthellate) or facultative symbiotic (apozooxanthellate, see "*" in Appendix 1) (Cairns et al. 1999; Cairns and Kitahara 2012). The antipatharians were represented by 18 species belonging to four families (ESM 1 Fig. S6).

Octocorals (soft corals, gorgonians and sea pens) were represented by 60 species (ESM 1 Figs. S7–S12). The order Alcyonacea was represented by 55 species, belonging to 12 families: Plexauridae (n=19; Fig. S12), Gorgoniidae (n=8; Fig. S10), Ellisellidae (n=7; Fig. S9), Nidaliidae (n=6; Fig. S11), Chrysogorgiidae (n=5; Fig. S8), Acanthogorgiidae (n=4; Fig. S7), and the Alcyoniidae, Anthothellidae, Clavularidae, Nephtheidae, Keroeididae and Primnoidae, each with only 1 species. The order Pennatulacea was represented by 5 species, which belong to three families (Fig. S13). Among the observed alcyonaceans, *Muricea elongata*, *Pterogorgia* sp. and *Eunicea* sp. are recognized as zooxanthellate ("+" in Appendix 1), 9 other species are apozooxanthellate ("*" in Appendix 1), while the remaining 43 species were azooxanthellate (Sánchez and Wirshing 2005).

Bathymetric distribution

The species richness varied along the depth range, reaching a peak of 86 species at the 100–200 m depth range (Fig. 2). The diversity distribution over depth intervals is symmetrical, exhibiting a lower number of species at the shallowest areas (<50 m) and deepest bottoms (>200 m). However, it is important to mention that our knowledge on azooxanthellate corals of the Colombian Caribbean can only be considered as comprehensive down to the 500 m depth, because only a few localities have been sampled below this isobath (Fig. 2, ESM 2 Table S1).

Geographic distribution

A maximum number of 76 species per sector was observed in Tayrona (Fig. 3), 17 of which were only found in this area (Appendix 1). Coralline archipelagos (n=72) were ranked second in species richness. La Guajira (n=62) and Palomino (n=61) showed almost similarly high species numbers, whereas Magdalena (n=21) and Darien (n=19) scored much lower. The lowest diversity was observed in the Gulf of Morrosquillo sector with only 4 species of hard corals, and a total absence of octocorals and black corals (Fig. 3). Although no systematic surveys have been performed by INVEMAR in the sector of San Andres and Old Providence islands (n=8), data retrieved from previous expeditions illustrate the lack of knowledge of this area and the need of filling in this gap.

Distribution patterns

Our statistical approach clustered the coral fauna into two main groups: (1) coral communities from deep bottoms (>200 m) on the continental slope and (2) coral communities on the continental shelf ≤200 m (Fig. 4a). Within the shallow fauna group, three main clusters were observed: (2a) southwestern, conformed by stations<200 m from sectors MAG, ARCO, and DAR; (2b) northeastern, all the stations <150 m from sectors GUA, PAL and TAY; and (2c) coral fauna associated to the bioherms represented by stations ARCO_150 and TAY_200. Exceptionally, the third azooxanthellate coral bioherm located in the Palomino sector (PAL_70) was more similar to the surrounding shallow-water fauna at the northeastern bioherm than to the other two. These four major groups were also observed in the MDS analysis (Fig. 4b). Based on these clusters, four principal distributional patterns of coral species in the Colombian Caribbean are proposed:

1. *Northeast*: 46 coral species (32 %) with occurrences at sectors GUA/PAL/TAY, mainly in shallow waters (32 species). *Carijoa riisei* (Fig. S9b), *Renilla muelleri* (Fig. S14a–g), and *Stichopathes* sp., which exhibited a GUA/PAL/TAY/MAG distribution, were also included in this category since their records were restricted to a single station at the north of the Magdalena River mouth. The distribution of the soft coral *Bellonella rubistella* is shown as an example (Figs. 1b, 5a).
2. *Southwest*: 11 species (8 %) distributed over sectors MAG/ARCO/DAR. Six species inhabit shallow waters (e.g., *Nidalia occidentalis*, Fig. S11f), while the other five occurred mainly in deep waters (e.g., *Stephanocyathus diadema* Fig. S3a, b). The distributions of *Deltocyathus* cf. *italicus* and *Nicella guadalupensis* are shown as examples (Figs. 1c, 5b).
3. *Azooxanthellate coral bioherms*: 37 coral species (26 %) exclusively living in azooxanthellate coral bioherms

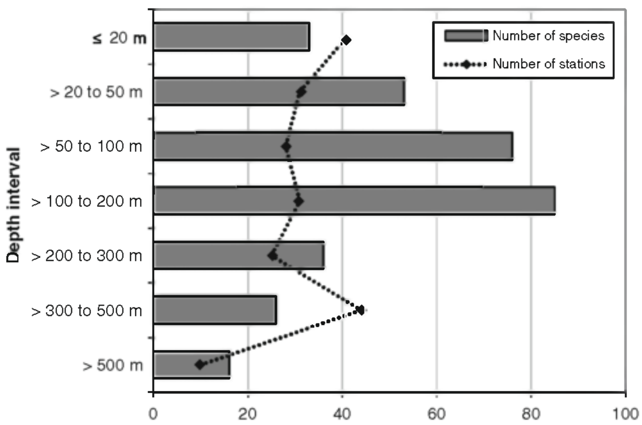

Fig. 2 Species richness distribution of azooxanthellate corals in the Colombian Caribbean over depth intervals. The number of stations sampled (*diamonds*) per depth interval is also indicated

(Reyes et al. 2005; Santodomingo et al. 2007). These bioherms are mainly constructed by *Madracis asperula* (Fig. S5t), *M. myriaster* (Fig. S5u), *Anomocora fecunda* (Fig. S1a, b), *Cladocora debilis* (Fig. S1n), and/or *Eguchipsammia cornucopia* (Fig. S4o), and were found in sectors Tayrona (150 m), Coralline Archipelagos (200 m), and Palomino (70 m). Examples of this distribution are the octocorals *Acanthogorgia aspera* (Figs. 1d, 5c) and *Stereonephthya portoricensis* (Fig. S11b, c), the solitary scleractinian *Coenocyathus parvulus* (Fig. S1o, p), and the antipatharian *Tanacetipathes barbadensis*.

4. *Widespread*: 44 species (31 %), 10 of which are mainly from deep water (e.g., *Stephanocyathus paliferus*, *Schizocyathus fissilis*), 24 mainly from shallow-water (e.g., *Diodogorgia nodulifera*, Fig. S9a, and *Trichogorgia lyra*, Fig. S10e), while the other 10 species occur in both depth ranges (e.g., *Caryophyllia berteriana*, Fig. S1k, l,

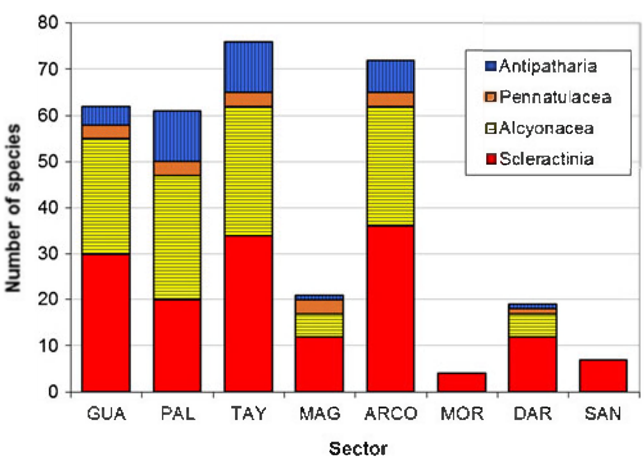

Fig. 3 Number of azooxanthellate species of Scleractinia, Alcyonacea, Pennatulacea, and Antipatharia in eight sectors of the Colombian Caribbean: La Guajira (*GUA*), Palomino (*PAL*), Tayrona (*TAY*), Coralline Archipelagos (*ARCO*), Gulf of Morrosquillo (*MOR*), Darien (*DAR*), and San Andres and Old Providence islands (*SAN*)

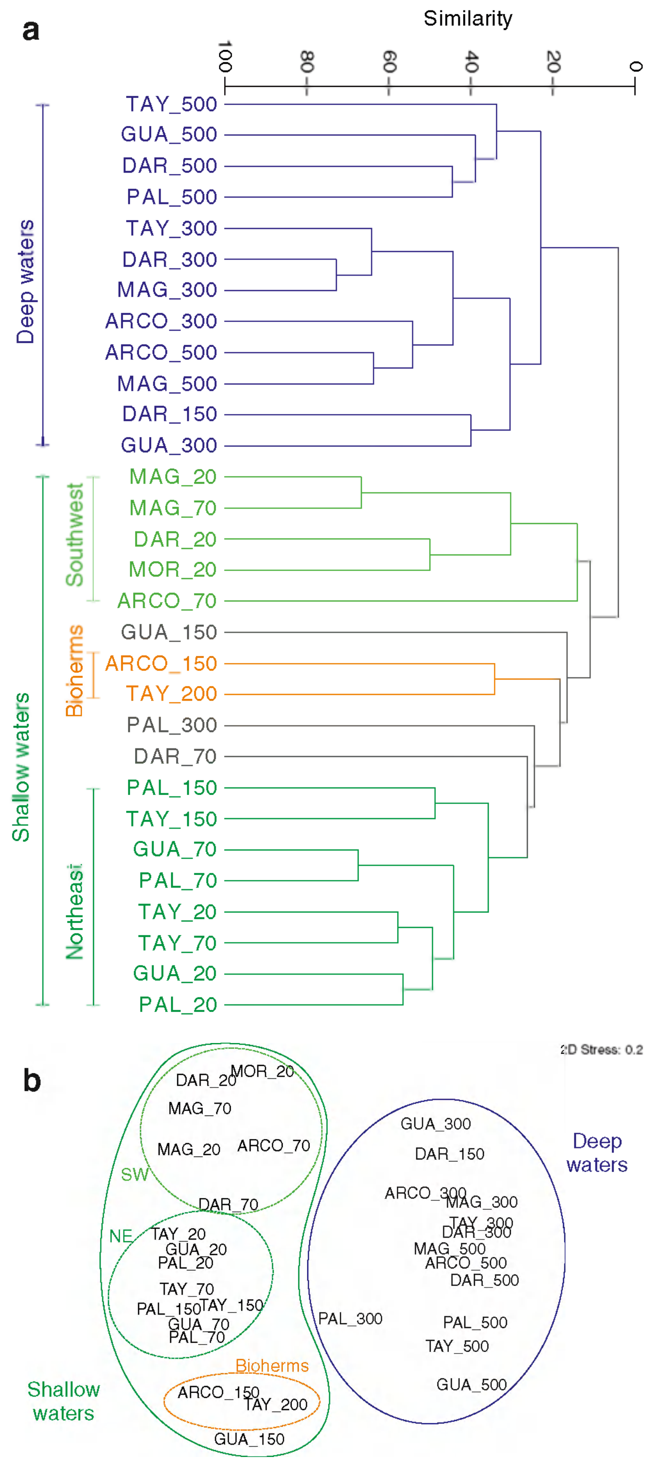

Fig. 4 **a** Bray-Curtis similarity analysis for the Colombian Caribbean sectors based on presence/absence of azooxanthellate corals; **b** MDS analysis based on presence/absence of azooxanthellate corals in the Colombian Caribbean. Codes for sectors were simplified to La Guajira (*GUA*), Palomino (*PAL*), Tayrona (*TAY*), Coralline Archipelagos (*ARCO*), and Darien (*DAR*). Depth is indicated besides the sector code, e.g. Palomino at 500 m = PAL_500

and *Oxysmilia rotundifolia*, Fig. S2j, k). *Deltocyathus calcar* was the most widely distributed species (Figs. 1e,

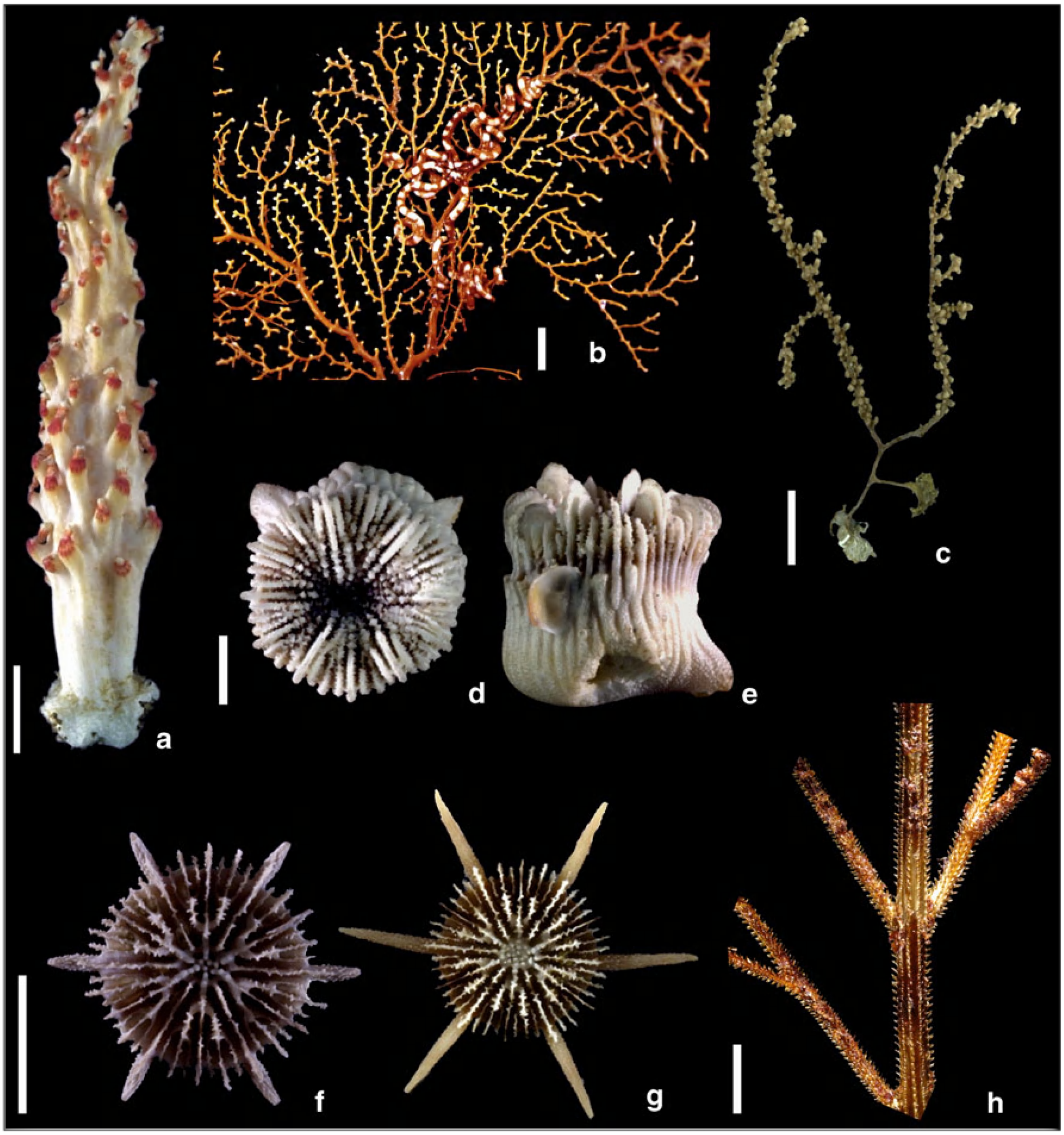

Fig. 5 Diversity of azooxanthellate corals of the Colombian Caribbean. Octocorals: **a** *Bellonella rubistella*, **b** *Nicella guadalupensis*, and **c** *Acanthogorgia aspera*. Scleractinians: **d**, **e** the endemic species *Heterocyathus antoniae*, and **f**, **g** morphological variability of *Deltocyathus calcar*. Antipatharian: **h** *Aphanipathes salix*. *Scales* (**a**–**c**) 1 cm, (**d**–**g**) 5 mm, (**h**) 2 mm. More illustrations in ESM 1

5f-g), followed by *Caryophyllia ambrosia caribbeana* (Figs. S1g, h), and *Deltocyathus eccentricus* (Fig. S2c, d).

Despite a lack of systematic sampling around San Andres and Old Providence Archipelago, four of the eight species from here represent a distribution restricted to these islands: i.e. *Stephanocyathus* (*Odontocyathus*) *coronatus* (Fig. S3g, h), *Balanophyllia hadros*, *Polymyces wellsi* (Figs. 1f, S5g, h), and *Fungiacyathus symmetricus* (Fig. S5k). These islands consist of oceanic atolls that are located near Jamaica.

Endemism and similarities with the Pacific fauna

Heterocyathus antoniae (Fig. 5d, e), the only Colombian Caribbean scleractinian endemic, has a northeastern distribution pattern. This species is remarkable since congeneric extant species were only known from the Pacific, mainly on sandy bottoms adjacent to coral reefs in the eastern Pacific and Indian oceans, from Mozambique to Japan (Hoeksema and Best 1991; Cairns and Zibrowius 1997; Zibrowius 1998; Cairns 1999) and the Gulf of California (Durham and Barnard 1952). The last occurrence of *Heterocyathus* in the Tethys Ocean is known from the Miocene (20–15 MYA, Burdigalian) based on fossils recovered in southwestern France (Stolarski et al. 2001).

Tethocyathus prahli represents an interesting case of shared biota with the Pacific. This scleractinian species is an exclusive trans-isthmic species that does not exhibit a cosmopolitan distribution. It has been found off the Magdalena River delta (Colombia), Cocos Island (Costa Rica), and the northern coast of the Colombian Pacific (Lattig and Cairns 2000; Reyes et al. 2009). Concerning octocorals, it is noteworthy that *Muricella* (ESM 1 Fig. S7c, d) and *Astrogorgia* (ESM 1 Fig. S12a, b) were hitherto only known from the Indo-Pacific. In addition, specimens of *Verrucella* and *Ctenocella*, known from Pacific shallow waters (Hoeksema and van Ofwegen 2008) and western Atlantic deep waters (Bayer and Grasshoff 1995), are reported here for the first time in southern Caribbean shallow waters. Detailed taxonomic revisions of these four genera and the subsequent description of potentially new Colombian species are still needed to address further discussion on the similarities and divergences between the Tropical Eastern Pacific and Caribbean fauna.

Discussion

Corals thrive in shallow waters, mainly on coral reefs, which harbor the highest diversity of species known in the marine realm (Veron 2000; Fabricius and Aldersdale 2001), especially in the center of maximum marine species richness, the so-called Coral Triangle (Hoeksema 2007). The construction of reef structures is assisted by the symbiotic relationship with zooxanthellae. However, almost 66 % of the scleractinian coral species lack this symbiosis and are found deeper than 50 m (Cairns et al. 1999; Cairns 2007), some of which form reefs on cold and deep-sea bottoms (Roberts et al. 2006). Only a few zooxanthellate coral species can be found deeper than 50 m in tropical seas, on so-called mesophotic reefs (Bongaerts et al. 2010).

During the present study, a high diversity of exclusively azooxanthellate coral species (138 spp.) was found exploiting a wider range of marine habitats such as soft-bottoms, hard-grounds, and deep-sea coral bioherms, far beyond the boundaries of shallow coral reefs. Thus, a higher species richness of azooxanthellate scleractinian corals (n=63) in contrast to their zooxanthellate reef-dwelling counterparts (n=54) has been observed in the Colombian Caribbean (Díaz et al. 2000; Reyes 2000; Reyes et al. 2010). The difference in species richness is even more remarkable for the antipatharians, with almost twice (n=18) the number for mesophotic and aphotic deep waters (≤520 m) in comparison with the 10 species previously known in shallow-water Colombian reefs (Sánchez 1999; Opresko and Sánchez 1997, 2005). Regarding octocorals, around 70 species were known from studies on reef communities, with about half of the species belonging to only four zooxanthellate genera *Eunicea* (n=12), *Pseudopterogorgia* (n=10), *Plexaura* (n=5), and *Pseudoplexaura* (n=5) (Botero 1987; Sánchez 1994, 1998, 1999, 2001; Sánchez et al. 1997, 1998); although the number of azooxanthellate octocoral species is lower (n=57), it is remarkable that most of the 33 genera were represented by one or two species, and only a few genera by more than four (e.g. *Chrysogorgia*, *Nidalia*, and *Leptogorgia*).

Diversity with depth

Depth has been recognized as one of the major parameters controlling coral species distribution (Houston 1985; Adjeroud 1997; Dawson 2002). In this study, the coral fauna varies in the bathymetric gradient, showing the lowest diversities in the shallowest and deepest bottoms, and a peak of high diversity at 100 to 200 m depth (Fig. 2). This pattern resembles those observed in other biogeographic provinces, where high species richness occurs on the border of continental margins between 100 and 300 m depth, as for example in azooxanthellate scleractinians of the Indo-Pacific (Cairns and Zibrowius 1997) and Brazil (Kitahara 2007), and octocorals of Japan (Matsumoto et al. 2007). The bathymetric pattern of Colombian azooxanthellate corals is also similar to that exhibited by azooxanthellate scleractinians at a global scale, which shows a high species richness at 50–200 m depth (Cairns 2007). Despite the global diversity peak for this group at 200–1,000 m depth (Cairns 2007), more surveys would be required to attempt direct comparisons of our data with those ranges, as faunas >500 m are still poorly sampled (Fig. 2).

Light is not a determinant factor in the distribution of azooxanthellate corals, whereas changes in salinity, temperature, nutrients, and sediments across the depth gradient can play a significant role in the presence and richness of species (Reyes-Bonilla and Cruz-Piñón 2000; Kitahara 2007). Oceanographic data reported for the Colombian Caribbean indicate that at 100–200 m depth, where the highest coral diversity is observed (61 %), the salinity is around 36.5 psu and temperatures oscillate between 18 and 21 °C (Andrade and Barton 2000, 2005; Andrade et al. 2003).

Some studies have suggested that seawater calcium carbonate could play a major role in the biogeography of corals, as scleractinians deposit aragonite to build their skeletons and octocorals use calcite to form their sclerites (Buddemeier and Fautin 1996; Buddemeier and Smith 1999). Although this hypothesis is supported by a major development of species-rich coral reefs in saturated waters above the aragonite saturation horizon (Guinotte et al. 2006; Cairns 2007), some corals with unique microstructural adaptations can live below carbonate saturation levels, such as micrabaciids, up to 5,000 m depth (Janiszewska et al. 2011) and *Fungiacyathus*, up to 6,000 m (Cairns 2007). So far, all Colombian corals have been surveyed above the aragonite saturation horizon, including records for *Fungiacyathus crispus* (up to 318 m) and *F. symmetricus* (up to 842 m). There are no records for micrabaciid corals, and *Stephanocyathus diadema*, the deepest-living coral (up to 1,257 m) in this area.

The distinction between shallow and deep waters is arbitrary and its extent depends on the scope of each study. According to Cairns (2007), deep-water species are those occurring >50 m depth based on the argument that few zooxanthellate coral species are present below this depth (but see Kahng and Maragos 2006; Bongaerts et al. 2010; Kahng et al. 2010). This limit was supported by Lindner et al. (2008) arguing that a 50-m wave disturbance boundary is used to determine the division between 'onshore' and 'offshore' environments in the fossil record (Bottjer and Jablonski 1988), and this corresponds approximately with the maximum depth at which regular storm-generated waves may cause sediment resuspension and disturbance to the benthos. In this study, a 200-m boundary was adopted to distinguish shallow- from deep-water, based on scleractinian studies by Cairns (1979, 2000) and because it corresponds with the continental shelf edge (Lakewood 1999; Stewart 2008). In this sense, the presence of an ecotone area with fauna elements of the continental shelf and the upper shelf slope may explain the maximum species diversity at 100–200 m depth.

Biogeographic patterns

The coral faunas of the northeastern (GUA, PAL, and TAY) and the southwestern (MAG, MOR, and DAR) sectors differ in terms of species richness and composition due to the synergy of two ecological factors. First, the cold-water upwelling off La Guajira increases the concentration of nutrients (Andrade et al. 2003; Andrade and Barton 2005) and therefore creates suitable conditions to the occurrence of suspension feeders such as corals. Second, the presence of the Magdalena River Delta and its freshwater and sediment discharge (Restrepo et al. 2006) could act as a barrier for the larval dispersion of coral species.

Coral fauna in shallow waters (<200 m) seem to follow this distribution pattern (northeastern vs. southeastern), while most of the deep-water species are widely distributed in the Colombian Caribbean. The relative constancy of deep-sea environmental conditions might explain the more homogeneous distribution of species in deep bottoms (Grassle 1991).

The diversity of scleractinian corals, solitary ones in particular, together with octocorals and antipatharians, was higher in areas where azooxanthellate coral bioherms occur (Roberts et al. 2006, 2009). This relationship is partly explained by the presence of hard-bottom substrates where solitary coral species and many other sessile suspension feeders live. It is evident that branching azooxanthellate corals (e.g., *Madracis* spp. *Cladocora debilis*, *Thalamophyllia riisei*, among others) are the principal components of such hard substrates as either living colonies or accumulated debris (Santodomingo et al. 2007).

It is remarkable that the Morrosquillo sector has only four species, including two common dwellers of artificial substrates, *Phyllangia americana americana* and *Astrangia solitaria*. This low diversity could be due to natural factors such as high sedimentation rates on shallow (<40 m) sea floors inside the Gulf of Morrosquillo, or to destructive fisheries, with the latter being the most plausible. The Gulf of Morrosquillo has been swept by shrimp trawling nets over more than 30 years. The primary gears have been trawling nets, both demersal and pelagic, that on average operate for about 9 h/day (Herazo et al. 2006). Octocorals are included in their bycatch (García et al. 2008). Consequently, it is possible that coral diversity and abundances were higher in the past. Unfortunately, there are no historical coral collections to support this hypothesis (see Hoeksema et al. 2011).

Relationship with the Pacific fauna

The closure of the Central American Isthmus (12–2.8 MYA) led to a great schism in the marine realm resulting in the extinction of some species and the development of two separate and distinctive marine faunas: the Tropical Eastern Atlantic from the Caribbean (Collins et al. 1996; Knowlton and Weigt 1998; Lessios 2008). Therefore, the occurrence of *Tethocyathus prahli* at both the Atlantic and Pacific Colombian coastal areas is remarkable (Lattig and Cairns 2000; Reyes et al. 2009) as a relict of the trans-isthmian fauna in deep waters and could be used in further phylogeographic studies.

The presence of a center of endemism in the Colombian Caribbean is suggested for the area surrounding La Aguja Canyon, located between sectors PAL and TAY. This hypothesis is based on the occurrence of the free-living coral *Heterocyathus antoniae* (Reyes et al. 2009), belonging to a genus previously only known from the Indo-Pacific (Hoeksema and Best 1991), as well as the fish *Quadratus ancon* (Mok et al. 2001), belonging to a West Pacific genus, and the ophiuroid *Ophiosizygus disacanthus* (Borrero-Pérez and Benavides-Serrato 2004), described from Japan. In addition, the particular distribution of these taxa suggests that they probably belong to an Atlantic relict fauna in this specific area of the Colombian Caribbean.

Colombian corals in the regional context

The geographic distribution patterns of azooxanthellate scleractinian corals described by Cairns (1979, 2000) based on geopolitical regions were successfully tested by using statistical analyses (see fig. 1 in Dawson 2002). However, those analyses were carried out on only the 42 Colombian azooxanthellate coral species known at that time. The recent addition of 17 new species records and 3 new species (Reyes 2000; Lattig and Reyes 2001; Reyes et al. 2005; Santodomingo et al. 2007) significatively increased the knowledge on azooxanthellate scleractinians in the Colombian Caribbean, which appears to have one of the most diverse coral faunas in the region with representatives of almost 50 % of the described species in the western Atlantic region. Thus, although the patterns proposed by Cairns (1979, 2000) and Dawson (2002) explain general trends of scleractinian distribution in the Caribbean region, they do not resemble the patterns observed in the present study. Furthermore, distributions of octocorals and antipatharians are also included in the present analysis as an effort to cover the main groups of azooxanthellate anthozoans.

The current geographic distribution patterns revealed by Colombian azooxanthellate corals seem to correspond better with the delimitation of Marine Ecoregions of the World (MEOW) proposed by Spalding et al. (2007). In their proposal, the southern Caribbean MEOW (=northeastern Colombia) only includes La Guajira sector, while the remaining sectors, Palomino, Tayrona, Magdalena, Morrosquillo, Coralline Archipelagos and Darien, belong to the southwestern Caribbean MEOW (=southwestern Colombia). Based on the criteria used to define MEOWs as “areas of relatively homogeneous species composition, clearly distinct from adjacent systems” (Spalding et al. 2007), our results could contribute to a more precise delineation of MEOWs at the Colombian Caribbean. Consequently, a new proposal for the delimitation of MEOWs would include sectors under the influence of La Guajira upwelling system (La Guajira, Palomino and Tayrona sectors) within the southern Caribbean MEOW (=northeastern Colombia), and would include the remaining sectors (Magdalena, Morrosquillo, Coralline Archipelagos and Darien) within the southwestern Caribbean MEOW (=southwestern Colombia), also establishing the Magdalena River delta as a barrier.

Our comprehensive analysis highlights not only the importance of rigorous taxonomic studies but also indicates the need for more faunistic sampling in poorly studied areas in order to overcome Linnean and Wallacean shortfalls (Brown and Lomolino 1998; Lomolino 2004) and to better understand distribution patterns in the marine realm.

Conservation topics

Concerning the shallow-water coral reefs of Colombia, most reef areas have been included within Marine Protected Areas MPAs (Díaz et al. 2000), and the conservation status of nine coral species from Colombia was emphasized in the IUCN Red List of endangered species of Colombia (Ardila et al. 2002). The recent discovery of three azooxanthellate coral communities of the Colombian Caribbean and their high associated diversity of molluscs, crustaceans, echinoderms, bryozoans, and fishes (Reyes et al. 2005; Santodomingo et al. 2007) has promoted the inclusion of this ecosystem in the conservation priorities for the design and management of some MPAs (Alonso et al. 2008a, b). For instance, the establishment of the 200-m isobath border for the Rosario and San Bernardo Coralline Archipelagos MPA was supported by the presence of azooxanthellate *Madracis* coral bioherms between 150 and 160 m depth within its boundaries (MAVDT 2005). Although the second azooxanthellate coral bioherm is located in the area adjacent to the Tayrona National Park, the management plans of this MPA do not so far include this ecosystem. Moreover, the high coral diversity found in La Guajira and Palomino sectors could be affected by the current increment of trawling fishing registered in these sectors (Viaña et al. 2002). Some strategies have been designed for the future establishment of an MPA network in this area (Alonso et al. 2008b), including the Palomino sector, which contains the third azooxanthellate coral community.

The need for conservation of many reef coral species has been established because they are relatively well known and relatively few species are considered data-deficient (Carpenter et al. 2008). The present study indicates that information about the deep-water coral fauna is scarce. Future campaigns in areas with special biodiversity values, such as La Aguja Canyon in the Tayrona sector (down to 3,000 m depth) or around the *Lophelia pertusa* records of La Guajira (500–1,000 m), would not only provide important information to the knowledge of the Colombian coral fauna and its deep-water coral communities but also increase our knowledge on the global deep-water coral fauna, which may be important for its protection.

Acknowledgements Special thanks to S. Cairns for his advice, support, and allowing the use of the National Museum of Natural History coral collection. Thanks to D. Opresko (Oak Ridge National Laboratory) and G. Williams (California Academy of Science) for giving advice and literature for the identification of antipatharians and pennatulaceans, respectively. Thanks to J. Sánchez (Universidad de Los Andes) for fruitful discussions. Thanks to P. Lattig for her help on identifications. G. Navas, A. Gracia, L. S. Mejia, N. Ardila, G. Borrero, N. Cruz, M. Benavides, A. Polanco, A. Bermudez, A. Roa, M. Díaz, and E. Montoya participated in the expeditions (INVEMAR). T. López and B. Rodriguez provided some pictures of corals. S. Braden (Smithsonian Institution) helped during SEM sessions of Guyniidae and Pennatulacea specimens, and A. Freiwald facilitated the use of the SEM laboratory at the Institute of Palaeontology (Erlangen-Nuremberg University). J. Bohórquez, L. Arias and C. Garcia (LAB-SI, INVEMAR) facilitated the access to the marine biodiversity database. The study of deep-sea corals of the Colombian Caribbean was possible thanks to the financial and logistic support of INVEMAR and the Instituto Colombiano para el Desarrollo de la Ciencia y la Tecnología “Francisco José de Caldas (COLCIENCIAS) given to the projects Macrofauna I, Macrofauna II (2105-13-07997) and MARCORAL (2115-09-16649). The MSc study of NS was funded by the Alβan Programme (code E07M402757CO). The valuable comments of S.E.T. van der Meij and three anonymous reviewers helped to improve this manuscript.

Appendix

Table 2 Distribution of 142 species of azooxanthellate corals: 64 Scleractinia, 18 Antipatharia, 55 Alcy\onacea, and 5 Pennatulacea collected during INVEMAR expeditions in the Colombian Caribbean. Sectors: La Guajira (*GUA*), Palomino (*PAL*), Tayrona (*TAY*), Coralline Archipelagos (*ARCO*), Darien (*DAR*) and San Andres and Old Providence islands (*SAN*); exclusive species to one of the sectors (Ex.=•). Geographical distribution pattern (*GeoP*): Widespread (*Wide*), Northeast mainly in sectors GUA/PAL/TAY (*NE*), Southwest mainly in sectors MAG/ARCO/DAR (*SW*), associated to azooxanthellate coral bioherms present in the sectors PAL, TAY and ARCO (*Bioherm*), Insular (*Is*) and Endemic to the Colombian Caribbean (*Endemic*). Bathymetric range (*BatR*): (*1*) shallow waters, (*2*) shallow and deep waters, (*3*) deep waters. Most are azooxanthellate species (unmarked), except for (+) zooxanthellate and (*) apozooxanthellate

Species	Code	GUA	PAL	TAY	MAG	ARCO	MOR	DAR	SAN	Ex.	GeoP	BatR	Depth
Order Scleractinia													
Family Caryophylliidae													
Anomocora fecunda (Pourtalès, 1871)	Afec	GUA	PAL	TAY	–	ARCO	–	DAR	–		Wide	1	10–200 m
Anomocora marchadi (Chevalier, 1966)	Amar	GUA	PAL	–	–	–	–	–	–		NE	1	50 m
Anomocora prolifera (Pourtalès, 1871)	Apro	GUA	PAL	TAY	–	ARCO	–	–	–		Wide	1	50–200 m
Caryophyllia ambrossia caribbeana Cairns, 1979	Caca	–	PAL	TAY	MAG	ARCO	–	DAR	–		Wide	3	200–510 m
Caryophyllia barbadensis Cairns, 1979	Cbar	–	–	–	–	ARCO	–	–	–	•	Bioherm	1	160 m
Caryophyllia berteriana Duchassaing, 1850	Cber	GUA	–	TAY	–	ARCO	–	–	SAN		Wide	2	22–293 m
Caryophyllia crypta Cairns, 2000	Ccry	–	–	TAY	–	–	–	–	–	•	NE	1	17 m
Cladocora arbuscula (Lesueur, 1821) +	Carb	GUA	PAL	TAY	–	–	–	–	–		NE	1	10–60 m
Cladocora debilis Milne Edwards and Haime, 1849	Cdeb	GUA	PAL	TAY	MAG	ARCO	–	–	–		Wide	1	10–153 m
Coenocyathus parvulus (Cairns, 1979)	Cpar	–	PAL	–	–	ARCO	–	–	–		Bioherm	1	21–160 m
Coenosmilia arbuscula Pourtalès, 1874	Coar	–	–	TAY	–	ARCO	–	–	–		Bioherm	1	72–218 m
Colangia immersa Pourtalès, 1871	Cimm	GUA	–	–	–	–	–	–	–	•	NE	1	73 m
Deltocyathus calcar Pourtalès, 1874	Dcal	GUA	PAL	TAY	MAG	ARCO	–	DAR	–		Wide	2(3)	107–520 m
Deltocyathus eccentricus Cairns, 1979	Decc	GUA	–	TAY	MAG	ARCO	–	DAR	–		Wide	3	270–507 m
Deltocyathus italicus (Michelotti, 1838)	Dita	–	–	–	MAG	ARCO	–	–	–		SW	2(3)	70.9–500 m
Heterocyathus antoniae Reyes, Santodomingo and Cairns, 2009	Hant	–	PAL	TAY	–	–	–	–	–		Endemic	1	21–76 m
Lophelia pertusa (Linnaeus, 1758)	Lper	GUA	–	–	–	–	–	–	–	•	NE	3	305–314 m
Oxysmilia rotundifolia (Milne Edwards and Haime, 1848)	Orot	–	–	TAY	–	ARCO	–	–	SAN		Wide	2	107–238 m
Paracyathus pulchellus (Philippi, 1842)	Ppul	GUA	PAL	–	–	ARCO	–	–	–		Wide	2	10–269 m
Phacelocyathus flos (Pourtalès, 1878)	Pflo	–	–	–	–	ARCO	–	–	–		SW	1	150–180 m
Phyllangia americana (Milne Edwards and Haime, 1848)	Pame	GUA	PAL	TAY	–	–	MOR	DAR	–		Wide	1	10–73 m
Polycyathus mayae Cairns, 2000	Pmay	–	–	–	–	ARCO	–	–	–	•	Bioherm	1	113–160 m
Polycyathus senegalensis Chevalier, 1966	Psen	GUA	–	–	–	–	–	–	–	•	NE	1	73–152 m
Rhizosmilia maculata (Pourtalès, 1874)	Rmac	–	–	TAY	–	–	–	–	–	•	NE	1	15–42 m
Stephanocyathus (*S.*) *diadema* (Moseley, 1876)	Sdia	–	–	–	MAG	ARCO	–	–	–		SW	3	502–1,257 m
Stephanocyathus (*S.*) *isabellae* Reyes, Santodomingo and Cairns 2009	Sisa	GUA	PAL	–	–	ARCO	–	–	–		Wide	3	493–504 m
Stephanocyathus (*S.*) *paliferus* Cairns, 1977	Spal	GUA	–	–	MAG	ARCO	–	DAR	–		Wide	3	269–510 m
Stephanocyathus (*S.*) *laevifundus* Cairns, 1977	Slae	–	–	–	–	–	–	DAR	–	•	SW	3	1,158–1,225 m
Stephanocyathus (*O.*) *coronatus* Cairns, 1977	Scor	–	–	–	–	–	–	–	SAN	•	Is	3	750–768 m
Tethocyathus prahli Lattig and Cairns, 2000	Tprah	GUA	–	–	MAG	–	–	–	–		Wide	3	152–310 m
Tethocyathus variabilis Cairns, 1979	Tvar	–	–	–	–	ARCO	–	–	–	•	Bioherm	1	113–160 m
Thalamophyllia riisei (Duchassaing and Michelotti, 1864)	Trii	–	–	–	–	ARCO	MOR	–	SAN		Wide	1	22–160 m
Trochocyathus cf. *fasciatus* Cairns, 1979	Tfas	–	–	TAY	–	–	–	–	–	•	NE	2	218 m
Trochocyathus rawsonii Pourtalès, 1874	Traw	GUA	PAL	–	–	ARCO	–	–	–		Wide	2	70–308 m
Family Dendrophylliidae													
Balanophyllia bayeri Cairns, 1979	Bbay	–	–	TAY	–	–	–	–	–	•	Bioherm	1	200 m
Balanophyllia caribbeana Cairns, 1977	Bcar	GUA	–	TAY	–	ARCO	–	–	–		Wide	1	20.4–107 m
Balanophyllia cyathoides (Pourtalès, 1871)	Bcya	GUA	–	TAY	–	ARCO	–	–	–		Wide	1	70.5–200 m
Balanophyllia dineta Cairns, 1977	Bdin	GUA	–	–	–	–	–	–	–	•	NE	1	151 m
Balanophyllia hadros Cairns, 1979	Bhad	–	–	–	–	–	–	–	SAN	•	Is	3	238–247 m
Balanophyllia palifera Pourtalès, 1878	Bpal	GUA	–	TAY	–	ARCO	–	–	–		Wide	1	22–218 m
Balanophyllia pittieri (Cairns, 1977)	Bpit	GUA	–	TAY	–	–	–	–	–		NE	1	70.1–200 m
Balanophyllia wellsi Cairns, 1977	Bwel	GUA	–	–	–	ARCO	–	–	–		Wide	1	73–160 m

Table 2 (continued)

Species	Code	GUA	PAL	TAY	MAG	ARCO	MOR	DAR	SAN	Ex.	GeoP	BatR	Depth
Eguchipsammia cornucopia Pourtalès, 1871	Ecor	–	–	–	–	ARCO	–	–	–	•	Bioherm	1	117–160 m
Rhizopsammia goesi (Lindstroem, 1877)	Rgoe	GUA	–	–	–	–	–	–	–	•	NE	1	73–152 m
Tubastraea coccinea Lesson, 1829	Tcoc	GUA	PAL	TAY	–	ARCO	–	–	–		Wide	1	10 m
Family Flabellidae													
Flabellum moseleyi Pourtalès, 1880	Fmos	–	PAL	TAY	MAG	ARCO	–	DAR	–		Wide	3	304–520 m
Javania cailleti (Duchassaing and Michelotti, 1864)	Jcai	GUA	–	TAY	–	ARCO	–	–	SAN		Wide	2	113–238 m
Polymyces fragilis Pourtalès, 1868	Pfrag	–	–	TAY	–	–	–	–	–	•	Bioherm	2	200–218 m
Polymyces wellsi Cairns, 1991	Pwel	–	–	–	–	–	–	–	SAN	•	Is	3	548 m
Family Fungiacyathidae													
Fungiacyathus crispus (Pourtalès, 1871)	Fcri	–	PAL	TAY	MAG	–	–	DAR	–		Wide	3	276–318 m
Fungiacyathus symmetricus (Pourtalès, 1871)	Fsym	–	–	–	–	–	–	–	SAN	•	Is	3	576–842 m
Family Gardineriidae													
Gardineria minor Wells, 1973	Gmin	–	–	TAY	–	ARCO	–	–	–		Bioherm	1	17–107 m
Family Guyniidae													
Guynia annulata Duncan, 1872	Gann	–	PAL	TAY	–	–	–	–	–		NE	1	150–153 m
Family Oculinidae													
Madrepora carolina (Pourtalès, 1871)	Mcar	–	–	–	–	ARCO	–	–	–	•	Bioherm	1	108–155 m
Madrepora oculata Linnaeus, 1758	Mocu	–	–	–	–	ARCO	–	–	–	•	SW	3	924–950 m
Oculina tenella Pourtalès, 1871	Oten	GUA	PAL	TAY	–	–	–	–	–		NE	1	21.4–150 m
Family Pocilloporidae													
Madracis asperula Milne Edwards and Haime, 1849	Masp	GUA	PAL	–	–	ARCO	–	–	–		Wide	1	20–153 m
Madracis brueggemanni (Ridley, 1881)	Mbru	–	–	–	–	ARCO	–	–	–	•	Bioherm	1	107–160 m
Madracis myriaster (Milne Edwards and Haime, 1849)	Mmyr	GUA	–	TAY	–	ARCO	MOR	DAR	–		Wide	2	21.4–300 m
Madracis pharensis (Heller, 1868)*	Mpha	–	–	TAY	–	ARCO	–	–	–		Bioherm	1	20–107 m
Family Rhizangiidae													
Astrangia solitaria (Lesueur, 1817)	Asol	GUA	PAL	TAY	MAG	–	MOR	DAR	–		Wide	1	10–154 m
Family Schizocyathidae													
Schizocyathus fissilis Pourtalès, 1874	Sfis	–	–	TAY	MAG	ARCO	–	DAR	–		Wide	2(3)	158–507 m
Family Turbinoliidae													
Sphenotrochus auritus Pourtalès, 1874	Saur	–	–	TAY	–	–	–	–	–	•	NE	1	10 m
Sphenotrochus lindstroemi Cairns, 2000	Slind	–	–	TAY	–	–	–	–	–	•	NE	1	10 m
Order Antipatharia													
Family Antipathidae													
Antipathes atlantica Gray, 1857	Atla	–	PAL	–	–	–	–	–	–	•	Bioherm	1	71.6 m
Antipathes furcata Gray, 1857	Afur	–	PAL	–	–	–	–	–	–	•	NE	1	50–70 m
Antipathes gracilis Gray, 1860	Agra	–	PAL	TAY	–	ARCO	–	–	–		Bioherm	1	21–160 m
Antipathes lenta Pourtalès, 1871	Alen	GUA	PAL	TAY	–	–	–	–	–		NE	2	20–300 m
Antipathes sp.	Atsp	–	–	TAY	–	–	–	–	–	•	NE	2	200–494 m
Cirripathes paucispina (Brook, 1889)	Cpau	–	–	TAY	–	–	–	–	–	•	NE	1	150 m
Stichopathes filiformis (Gray, 1860)	Sfil	–	PAL	–	–	–	–	–	–	•	NE	1	150 m
Stichopathes luetkeni (Brook, 1889)	Slue	–	PAL	–	–	ARCO	–	–	–		Bioherm	2	160–300 m
Stichopathes occidentalis (Gray, 1860)	Socc	–	PAL	TAY	–	ARCO	–	–	–		Bioherm	1	70–160 m
Stichopathes pourtalesi Brook, 1889	Spou	GUA	PAL	TAY	–	–	–	–	–		NE	2	70–300 m
Stichopathes sp.	Stich	GUA	PAL	TAY	MAG	–	–	–	–		NE	2	50–502 m
Family Aphanipathidae													
Aphanipathes salix (Pourtalès, 1880)	Asal	–	–	TAY	–	–	–	DAR	–		Wide	1	160–200 m
Elatopathes abietina (Pourtalès, 1874)	Aabi	–	–	–	–	ARCO	–	–	–	•	Bioherm	1	155–160 m
Rhipidipathes colombiana (Opresko and Sánchez, 1997)	Aclm	–	–	TAY	–	–	–	–	–	•	NE	3	296 m
Family Myriopathidae													
Tanacetipathes barbadensis (Brook, 1889)	Tbar	–	PAL	TAY	–	ARCO	–	–	–		Bioherm	1	50–160 m
Tanacetipathes spinescens (Gray, 1860)	Aspi	–	–	–	–	ARCO	–	–	–	•	Bioherm	1	160 m
Tanacetipathes tanacetum (Pourtalès, 1880)	Ttan	GUA	–	–	–	–	–	–	–	•	NE	3	305 m
Family Stylopathidae													
Stylopathes columnaris (Duchassaing, 1870)	Acol	–	PAL	TAY	–	ARCO	–	–	–		Bioherm	2	150–520 m
Order Alcyonacea													
Family Acanthogorgiidae													

Table 2 (continued)

Species	Code	GUA	PAL	TAY	MAG	ARCO	MOR	DAR	SAN	Ex.	GeoP	BatR	Depth
Acanthogorgia aspera Pourtalès, 1867	Aasp	–	PAL	TAY	–	ARCO	–	–	–		Bioherm	1	70–160 m
Acanthogorgia schrammi Duchassaing and Michelotti, 1864	Asch	–	PAL	TAY	–	–	–	–	–		NE	2	70–304 m
Acanthogorgia sp.	Acsp	GUA	PAL	–	–	–	–	–	–		NE	1	50–50 m
Muricella sp.	Muri	–	PAL	TAY	–	ARCO	–	–	–		Bioherm	2	20–504 m
Family Alcyoniidae													
Bellonella rubistella (Deichmann, 1936)	Brub	GUA	PAL	TAY	–	–	–	–	–		NE	1	70–152 m
Family Anthothelidae													
Diodogorgia nodulifera (Hargitt and Rogers, 1901)	Dnod	GUA	PAL	TAY	–	–	–	DAR	–		Wide	2	10–300 m
Family Chrysogorgiidae													
Chrysogorgia desbonni Duchassaing and Michelotti, 1864	Cdes	–	–	–	–	ARCO	–	–	–	•	SW	3	296–296 m
Chrysogorgia elegans Verrill, 1883	Cele	GUA	PAL	TAY	–	ARCO	–	–	–		Wide	3	484–510 m
Chrysogorgia sp.	Chry	–	–	–	MAG	ARCO	–	–	–		Wide	2	70.5–475 m
Chrysogorgia thyrsiformis Deichmann, 1936	Cthy	–	–	–	–	ARCO	–	–	–	•	Bioherm	1	160–160 m
Trichogorgia lyra Bayer and Muzik, 1976	Tlyr	GUA	PAL	TAY	MAG	ARCO	–	DAR	–		Wide	1	20–150 m
Family Clavulariidae													
Carijoa riisei Duchassaing and Michelotti, 1860[*]	Crii	GUA	PAL	TAY	MAG	–	–	–	–		NE	2	21.4–500 m
Family Ellisellidae													
Ctenocella sp.1 [*a]	Cteno	GUA	PAL	–	–	–	–	–	–		NE	1	20–152 m
Ellisella barbadensis (Duchassaing and Michelotti, 1864)[*]	Ebar	GUA	–	–	–	–	–	–	–	•	NE	1	50 m
Nicella guadalupensis (Duchassaing and Michelotti, 1860)	Ngua	–	–	–	–	ARCO	–	–	–	•	SW	1	107–160 m
Nicella sp.	Nicel	–	–	TAY	–	ARCO	–	–	–		Bioherm	1	107–200 m
Riisea paniculata Duchassaing and Michelotti, 1860	Rpan	–	–	TAY	–	ARCO	–	–	–		Bioherm	1	160–200 m
Verrucella sp.[a]	Verru	GUA	PAL	TAY	–	ARCO	–	–	–		Wide	1	50–200 m
Viminella sp.	Vimin	GUA	PAL	TAY	–	ARCO	–	DAR	–		Wide	2	20–300 m
Family Gorgoniidae													
Leptogorgia cardinalis (Bayer, 1961)[*]	Lcar	GUA	PAL	–	–	–	–	–	–		NE	2	50–498 m
Leptogorgia medusa Bayer, 1952[*]	Lmed	–	PAL	–	–	–	–	–	–	•	NE	1	70 m
Leptogorgia punicea (Milne Edwards and Haime, 1857)[*]	Lpun	GUA	–	–	MAG	–	–	–	–		Wide	1	10–20.9 m
Leptogorgia setacea Pallas, 1766[*]	Lset	GUA	PAL	TAY	–	–	–	DAR	–		Wide	1	10–152 m
Leptogorgia sp. 1[*]	Lepto	GUA	–	–	–	–	–	–	–	•	NE	1	50 m
Leptogorgia sp. 2[*]	Lopho	GUA	PAL	–	MAG	–	–	–	–		Wide	2	10–475 m
Pterogorgia sp.[+]	Ptero	GUA	–	–	–	–	–	–	–	•	NE	1	10 m
Tobagogorgia hardyi Sánchez and Acosta de Sánchez, 2004	Thar	GUA	PAL	TAY	–	–	–	–	–		NE	1	26.6–76 m
Family Keroeididae													
Thelogorgia vossi Bayer, 1991	Tvos	–	–	TAY	–	–	–	–	–	•	Bioherm	1	200 m
Family Nephtheidae													
Stereonephthya portoricensis (Hargitt, 1901)	Spor	–	PAL	TAY	–	ARCO	–	–	–		Bioherm	1	20–200 m
Family Nidaliidae													
Nidalia deichmannae Utinomi, 1954	Ndei	–	–	–	–	ARCO	–	–	–	•	SW	1	107 m
Nidalia dissidens Verseveldt and Bayer, 1988	Ndis	–	–	TAY	–	–	–	–	–	•	Bioherm	1	200 m
Nidalia occidentalis Gray, 1835	Nocc	–	–	–	–	ARCO	–	–	–	•	SW	1	107–160 m
Nidalia rubripunctata Verseveldt and Bayer, 1988	Nrub	GUA	PAL	TAY	–	ARCO	–	–	–		Wide	1	20–155 m
Nidalia sp.	Nidal	GUA	PAL	–	–	–	–	–	–		NE	1	50–70 m
Siphonogorgia agassizii (Deichmann, 1936)	Saga	–	–	–	–	ARCO	–	–	–	•	SW	1	107 m
Family Plexauridae													
Astrogorgia sp.	Amsp	GUA	–	TAY	–	–	–	–	–		NE	1	73–152 m
Eunicea sp.[+]	Eunic	GUA	–	–	–	–	–	–	–	•	NE	1	10 m
Hypnogorgia pendula Duchassaing and Michelotti, 1864	Hpen	–	–	–	–	ARCO	–	–	–	•	Bioherm	1	160 m
Lytreia plana (Deichmann, 1936)	Lplan	–	–	–	–	ARCO	–	–	–	•	Bioherm	1	98 m
Muricea elongata (Lamouroux, 1821)[+]	Melo	–	–	TAY	–	–	–	–	–	•	NE	1	35 m
Paracis sp.	Parsp	GUA	PAL	–	–	ARCO	–	–	–		Wide	1	50–160 m
Placogorgia atlantica Wright and Studer, 1889	Patl	–	–	TAY	–	–	–	–	–	•	NE	1	72.3–200 m
Placogorgia tenuis (Verrill, 1883)	Pten	–	–	TAY	–	ARCO	–	–	–		Bioherm	1	155–200 m
Scleracis guadaloupensis Duchassaing and Michelotti, 1860	Sgua	–	–	TAY	–	ARCO	–	–	–		Bioherm	1	113–200 m
Scleracis pumila Reiss, 1919	Spum	–	–	–	–	ARCO	–	–	–	•	Bioherm	1	113–160 m
Scleracis sp.	Scler	GUA	PAL	–	–	ARCO	–	–	–		Wide	1	50–127 m

Table 2 (continued)

Species	Code	GUA	PAL	TAY	MAG	ARCO	MOR	DAR	SAN	Ex.	GeoP	BatR	Depth
Swiftia exserta Duchassaing and Michelotti, 1864	Sexe	–	PAL	–	–	–	–	DAR	–		Wide	1	20–70 m
Thesea bicolor Deichamnn, 1936	Tbic	–	PAL	–	–	–	–	–	–	•	NE	1	70 m
Thesea nutans (Duchassaing and Michelotti, 1864)	Cnut	–	–	–	–	ARCO	–	–	–	•	Bioherm	1	98–160 m
Thesea parviflora Deichmann, 1936	Tpar	GUA	PAL	TAY	–	–	–	–	–		NE	2	20–300 m
Thesea solitaria Pourtalès, 1868	Tsol	–	–	TAY	–	–	–	–	–	•	Bioherm	1	200 m
Thesea sp.	These	GUA	PAL	TAY	–	–	–	–	–		NE	1	20–154 m
Villogorgia nigrescens Duchassaing and Michelotti, 1860	Vnig	–	–	TAY	–	–	–	–	–	•	Bioherm	1	200 m
Villogorgia sp.	Villog	–	PAL	–	–	–	–	–	–	•	NE	3	300 m
Family Primnoidae													
Callogorgia sp.	Callo	–	–	TAY	–	–	–	–	–	•	Bioherm	1	200 m
Order Pennatulacea													
Family Kophobelemnidae													
Sclerobelemnon theseus Bayer, 1959	Sthe	GUA	PAL	TAY	MAG	ARCO	–	–	–		Wide	1	20–153 m
Family Renillidae													
Renilla muelleri Kölliker, 1872	Rmue	GUA	PAL	TAY	MAG	–	–	–	–		NE	1	10–76 m
Renilla reniformis (Pallas, 1766)	Rren	–	PAL	–	MAG	–	–	DAR	–		Wide	1	10–70.4 m
Family Virgulariidae													
Acanthoptilum sp.	Almsp	GUA	–	TAY	–	ARCO	–	–	–		Wide	1	50–151 m
Stylatula diadema Bayer, 1959[a]	Stdia	–	–	–	–	ARCO	–	–	–	•	SW	1	20 m

[a] Specimens were identified as belonging to the genera *Ctenocella* and *Verrucella* according to Bayer and Grasshoff (1995)

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