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Fauna diversity in *Madracis* spp. coral patches in the Colombian Caribbean

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Abstract

Fauna diversity in Madracis *spp. coral patches in the Colombian Caribbean. Madracis* spp. coral patches are the main deep–sea framework builder observed on the shelf–break scarp of the Colombian Caribbean, between 107 and 230 m depth. The Marine Protected Area, Corales de Profundidad National Natural Park, was established in 2013 to protect a site of high biodiversity associated with *Madracis* communities. Our research summarizes the advances in knowledge of its biodiversity as the result of four expeditions and offers insights into the state of its associated fauna. *Madracis* colonies occur in five areas of the park but corals thrive and build coral patches in only two of the five, both in the southwest area. Our surveys have resulted in the inventory of 337 species. Mollusca (116) dominated the fauna, followed by Bryozoa (70), Cnidaria (50), Echinodermata (39), Arthropoda (14), Annelida (13), Brachiopoda (3), and Chordata (32 fishes). Store voucher specimens at the Museo de Historia Natural Marina de Colombia–Makuriwa and metadata are available online in the SiBM database.

Checklist published through GBIF (DOI: 10.15470/vqshir)

Key words: Marine Protected Area, Benthic, Deep–sea corals, Macrofauna, Megafauna, New records

Resumen

Diversidad faunística en los parches de coral aislados de Madracis *spp. del Caribe colombiano.* El coral *Madracis* spp. es el principal bioconstructor de las aguas profundas del borde de la plataforma continental del Caribe colombiano, entre 107 y 230 m de profundidad. El Área Marina Protegida Parque Nacional Natural Corales de Profundidad se estableció en 2013 a fin de proteger una zona de alta biodiversidad asociada a estas comunidades. Nuestra investigación resume los avances en el conocimiento de su biodiversidad como resultado de cuatro expediciones y ofrece una visión del estado de la fauna asociada. Las colonias de *Madracis* están presentes en cinco zonas del Parque, pero solo en dos de ellas, situadas en la zona suroeste, construye parches de coral aislados. Nuestros estudios

han dado como resultado un inventario de 337 especies. El filo Mollusca (116) domina la fauna, seguido de Bryozoa (70), Cnidaria (50), Echinodermata (39), Arthropoda (14), Annelida (13), Brachiopoda (3) y Chrordata (32 peces). Los especímenes se encuentran en el Museo de Historia Natural Marina de Colombia y los metadatos están disponibles en línea en la base de datos del SiBM.

Lista de datos publicada en GBIF (DOI: 10.15470/vqshir)

Palabras clave: Área Marina Protegida, Bentos, Corales de profundidad, Macrofauna, Megafauna, Nuevos registros

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Resum

Diversitat faunística als esculls de corall aïllats de Madracis *spp. del Carib colombià*. El corall *Madracis* spp. és el principal bioconstructor de les aigües profundes de la vora de la plataforma continental del Carib colombià, entre 107 i 230 m de profunditat. L'Àrea Marina Protegida Parc Nacional Natural Coralls de Profunditat es va establir l'any 2013 per tal de protegir una zona d'alta biodiversitat associada a aquestes comunitats. La nostra recerca resumeix els avenços en el coneixement de la biodiversitat com a resultat de quatre expedicions i ofereix una visió de l'estat de la fauna associada. Les colònies de *Madracis* es troben presents en cinc zones del Parc, però només en dues, situades a la zona sud–oest, construeix esculls de corall aïllats. Els nostres estudis han donat com a resultat un inventari de 337 espècies. El fílum Mollusca (116) domina la fauna, seguit de Bryozoa (70), Cnidaria (50), Echinodermata (39), Arthropoda (14), Annelida (13), Brachiopoda (3) i Chrordata (32 peixos). Els espècimens es troben al Museu d'Història Natural Marina de Colòmbia i les metadades estan disponibles en línea a la base de dades del SiBM.

Llista de dades publicada a GBIF (DOI: 10.15470/vqshir)

Paraules clau: Àrea Marina Protegida, Bentos, Coralls de profunditat, Macrofauna, Megafauna, Nous registres

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Introduction

Like their analogs from shallow waters, deep–sea coral communities are a reservoir of ecological, biological and chemical resources and home to a great biodiversity, including species of commercial interest and potential new species for science (Roberts et al., 2009). In the Caribbean region, knowledge of this valuable ecosystem remains understudied, and vast areas are still unexplored (Lutz and Ginsburg, 2007; Hernández–Ávila, 2014). Due to their vulnerability to environmental disturbances and anthropogenic activities, several global efforts have been oriented to protect and study these unique habitats (Fuller et al., 2008; Hourigan, 2009; Zimmerman et al., 2020).

The Corales de Profundidad National Natural Park (CPNNP) was declared by the Resolution 0339 of 2013 (MADS, 2013) according to IUCN category II, and hosts one of the three deep–sea corals areas identified in the Colombian Caribbean (Reyes et al., 2005; Flórez and Santodomingo, 2010; Santodomingo et al., 2013; Alonso et al., 2021). The highly diverse communities that inhabit the CPNNP are mainly supported by habitat–forming species of *Madracis* (Santodomingo et al., 2007). In 2001 these communities were accidentally discovered during the 'Macrofauna II' expeditions using epibenthic trawl nets (Reyes et al., 2005). The area was later mapped and characterized in 2005 during the 'Marcoral' expedition, using Van Veen dredge and rock dredges (Santodomingo et al., 2007, 2013). Detailed maps, the first footage and the description of macro–habitats were obtained using ROV and multipurpose drift–cam (CADEM) during the expeditions carried out in 2015 (Alonso et al., 2015; Cedeño–Posso et al., 2022) and 2016 in campaigns 'PNN Corales de Profundidad' and 'PNN *Madracis'*, respectively.

During the campaign PNN Corales de Profundidad (2015), eleven areas of potential development of *Madracis* were explored and mapped using a digital elevation model of bathymetry and ROV surveys. *Madracis* colonies were observed in five of the eleven areas surveyed. However, *Madracis* corals thrive and sustain a large concentration of marine fauna only in two of the areas, both in the southwest where they were discovered (Santodomingo et al., 2007) (Alonso et al., 2015; Cedeño–Posso et al., 2022). These two coral patches were targeted for additional multipurpose drift–cam surveys during the PNN *Madracis* expedition in 2016.

This paper describes and summarizes the state–of–the art of the biodiversity associated with these *Madracis* spp. coral patches. Here, we integrate the information obtained in four expeditions using several methods in order to provide a physical description of the patches, their distribution, and an inventory of cnidarians, mollusks, bryozoans, brachiopods, annelids, arthropods, echinoderms and fishes that inhabit these important deep–sea coral communities in the CPNNP.

Material and methods

The CPNNP is located in the Colombian Caribbean (fig. 1) on the continental margin off the Gulf of Morrosquillo and the Archipelago of San Bernardo, approximately 12 km from one of the areas with major development of shallow–water coral reefs in Colombia, Corales del Rosario y de San Bernardo National Natural Park, and 32 km from the nearest point on the continent (Barú Peninsula). The area is characterized by a strong influence of continental inputs, relatively transparent waters, and large mosaics combining bio–clastic sediment plains and extensive development of coral reefs (Díaz et al., 2000).

The work circumscribed biodiversity data where *Madracis* spp. coral patches occur southwest of the CPNNP, at depths of 107 and 230 m. These patches are located within the coordinates 9º 46' 18.208" N–9º 50' 33.101" N and 76º 11' 10.099" W–76º 14' 39.688" W (fig. 1). *Madracis* colonies have been identified as a species complex that includes *M. myriaster* (the most abundant), *M. asperula* and *M. brueggemanni* (Santodomingo et al., 2007) (fig. 2) given the difficulty to differentiate *M. myriaster* from its sister species *M. brueggemanni*

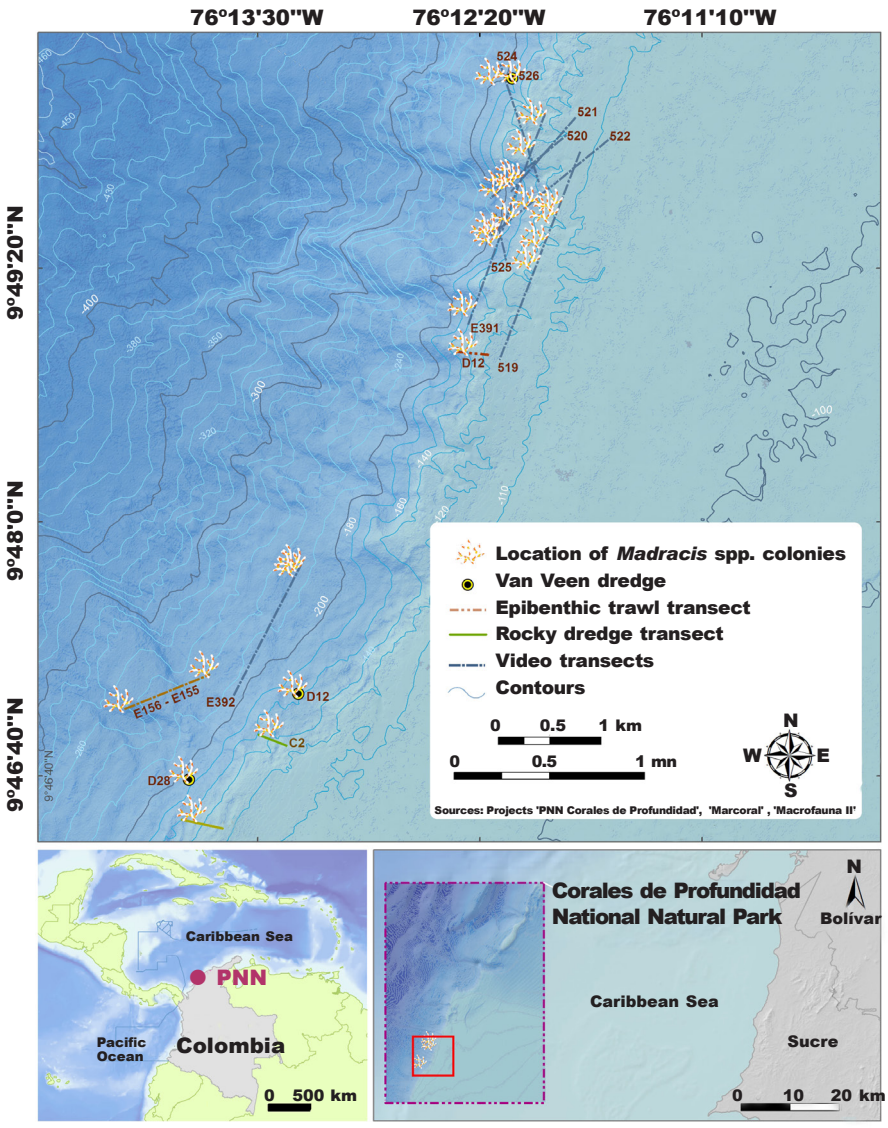

Fig. 1. Location of the Corales de Profundidad National Natural Park in the Colombian Caribbean (bottom left), showing collection stations with Van Veen dredge, rocky dredge, epibenthic trawl, and video–transects analyzed during this study (top). Violet dashed lines represent the limits of the CPNNP and the red box indicates the area where *Madracis* spp. coral patches thrive (bottom right).

Fig. 1. Localización del Parque Nacional Natural Corales de Profundidad en el Caribe colombiano (abajo a la izquierda), mostrando las zonas de recolección con draga Van Veen, caja de rocas y red de arrastre epibentónica, así como los vídeo–transectos analizados durante este estudio (arriba). Las líneas discontinuas violetas representan los límites del PNNCP y el recuadro rojo indica la zona donde se desarrollan los parches de coral Madracis *spp. (abajo a la derecha).*

Fig. 2. *Madracis* spp. coral patches at the southwest of the Corales de Profundidad National Natural Park: left, image taken during the 2015 expedition with ROV Diavolo II; right, image taken during the 2016 expedition with multipurpose drift–cam (CADEM).

Fig. 2. Parches de coral Madracis *spp. en el suroeste del Parque Nacional Natural Corales de Profundidad: izquierda, imagen tomada durante la expedición de 2015 con el ROV Diavolo II; derecha, imagen tomada durante la expedición de 2016 con la cámara de deriva multipropósito (CADEM).*

(Ballesteros–Contreras et al., 2022). According to the digital elevation model (DEM), they are on a moderate slope between 4º to 11º in the transition between the continental shelf and the shelf–break scarp, probably covered by recent sediment flows, and over a sliding crown (Santodomingo et al., 2007; Morales et al., 2017). Biodiversity data were compiled from four research expeditions carried out in the southwest area of the CPNNP (table 1): (1) 'Macrofauna II' (2001), a baseline survey on soft bottoms in the Colombian Caribbean with collections made with an epibenthic trawl net (9 × 1 m opening; 3 knots for 10 min) (fig. 3A) (Reyes et al., 2005). (2) 'Marcoral' expedition (2005), a study for mapping and characterizing the occurrence of *Madracis* spp. corals using a single–beam echo sounder, collections with a Van Veen dredge (60 l, 0.03 m^2) (fig. 3B) and a heavy–chained rocky dredge (1 × 0.4 m opening; 1.5 knots for 5 min) (Santodomingo et al., 2007, 2013). (3) 'PNN Corales Profundidad' expedition (2015), to perform detailed geomorphological mapping (Morales et al., 2017) supported by the first footage obtained using ROV Diavolo II (fig. 3C) with a front camera (¼″ CCD 380 l TV–lines, 0.1 Lux/F = 1.2) and 10 cm parallel lasers for scale. Positioning was estimated using an ultra–short baseline (USBL) mounted on the vehicle (Cedeño–Posso et al., 2002). (4) 'PNN *Madracis*' expedition (2016), a complementary expedition for sampling areas using a multipurpose drift–cam (CADEM) with a modified Van Veen grab (0.066 m^2) to collect samples of sediments (fig. 3D). The drift–cam incorporates high–definition cameras capable of acquiring color images with 61º range, 120 x zoom and 2200 lumen LED lights, both with titanium casing resistant up to 4,000 m depth, a multimedia tracking console, and adaptable protection cages for different environments.

The quality of the videos (380 TV–lines) allowed recognition only of common taxa larger than 10 cm (cnidarians, crustaceans, echinoderms and fish), with exceptional cases of fauna > 5–10 cm such as cup corals with extended polyps and crustaceans. Biological samples that remained unsorted from 'Marcoral' and 'PNN *Madracis*' (Bryozoa and Annelida) were identified to the lowest taxonomic level possible. Identifications were confirmed from videos based on specimens deposited in the collections of the Museo de Historia Natural Marina de Colombia (MHNMC)–MAKURIWA of INVEMAR in Santa Marta, Colombia.

Table1. List of projects carried out surrounding *Madracis* spp. coral patches of the Corales de Profundidad National Natural Park, dates, coordinates, depths and methods used per station.

Tabla 1. Lista de proyectos realizados en torno a Madracis *spp. parches de coral del Parque Nacional Natural Corales de Profundidad, fechas, coordenadas, profundidades y métodos utilizados por estación.*

Project				
Sampling date	**Station/transect**	**Coordinates**	**Depth**	**Method**
Macrofauna II				
26/03/2001	E155, E156	9º 47' 12" N, 76º 13' 45" W to 9º 47' 17.9" N, 76º 13' 54" W	155–160	Trawling
Marcoral				
01/05/2005	D3	9º 48' 53" N, 76º 12' 28.5" W	210	Van Veen dredge
01/05/2005	D12	9º 47' 5.8" N, 76º 13' 17.1" W	157	Van Veen dredge
01/05/2005	D28	9º 46' 38.7" N, 76º 13' 51.5" W	181	Van Veen dredge
01/05/2005	C2	9º 46' 52.8" N, 76º 13' 29.6" W to 9º 46' 49.5" N, 76º 13' 21" W	123–151	Rock dredge
01/05/2005	C3	9º 46' 26" N, 76º 13' 53.8" W to 9º 46' 23.3" N, 76º 13' 41" W	117–154	Rock dredge
PNN Corales de Profundidad				
13/10/2015	E391 Sector 8	9º 49' 02.1" N, 76º 12' 23.7" W to 9º 50' 17.2" N 76º 11' 56.4" W	106–197	ROV (1:00:19)
15/10/2015	E392 Sector 9	9º 47' 05.3" N, 76º 13' 37.5" W to 10º 08' 39.0" N 76º 06' 47" W	109–239	ROV (00:32:27)
PNN Madracis				
02/11/2016	E519	09º 48' 51.1" N, 76º 12' 13.8" W to 09º 49' 56.9" N, 76º 11' 48.4" W	110–120	CADEM (1:43:00)
04/11/2016	E521	09º 50' 02.3" N, 76º 11' 52.7" W to 09º 49' 42.0" N, 76º 12' 16.7" W	120–220	CADEM (00:42:50)
04/11/2016	E522	09º50'01.6"N, 76º11'38.3"W to 09º 49' 30.3" N, 76º 12' 16.6" W	110–200	CADEM (1:27.00)
04/11/2016	E524	09º 49' 47.5" N, 76º 12' 01.6" W to 09º 50' 24.4" N, 76º 12' 13.6" W	140–220	CADEM (00:58:41)
04/11/2016	E525	09º 49' 22.4" N, 76º 12' 11.8" W to 09º 49' 37.2" N, 76º 12' 15.1" W	200–220	CADEM (00:22:40)
04/11/2016	E526	9º 50' 19.9" N, 76º 12' 09.8" W	180	CADEM (grab)
Total	14		106–239	

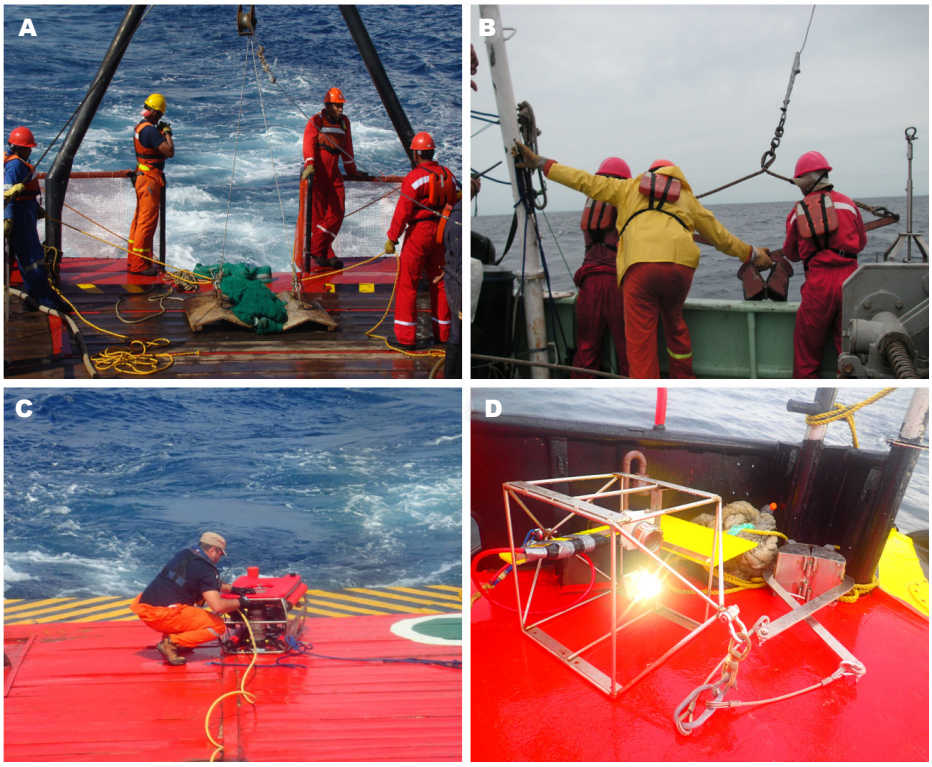

Fig. 3. Images of some methods used for specimen and video collection in the Corales de Profundidad National Natural Park: A, epibenthic trawl net and otter board during Macrofauna II Expedition; B, Van Veen dredge during 'Marcoral' expedition; C, ROV Diavolo II during 2015 expedition; D, multipurpose drift–cam (CADEM) during the 2016 expedition.

Fig. 3. Imágenes de algunos métodos utilizados para la recolecta de especímenes y grabación de vídeos en el Parque Nacional Natural Corales de Profundidad: A, red de arrastre epibentónica y compuerta de arrastre durante la expedición Macrofauna II; B, draga Van Veen durante la expedición "Marcoral"; C, ROV Diavolo II durante la expedición de 2015; D, cámara de deriva multipropósito (CADEM) durante la expedición de 2016.

Data quality controls were applied to the species previously identified in 'Macrofauna II' and 'Marcoral' campaigns through the validation of their current taxonomic status. Likewise, taxonomic levels higher than family were excluded from the analysis to avoid uncertain identifications and data duplicity, except for specimens identified in the orders Antipatharia, Comatulida and Ophiurida that correspond to unique specimens observed in the ROV videos. Consulted updated taxonomic identities and classifications in the World Register of Marine Species (WoRMS, 2022) and Eschmeyer's Catalog of Fishes (Fricke et al., 2020). All biological data and collections are available in the Marine Biodiversity Information System (SiBM–OBIS Colombia) and it stored voucher specimens at the Museo de Historia Natural Marina de Colombia (MHNMC)–MAKURIWA of INVEMAR in Santa Marta, Colombia. Our analyses use the concept of species diversity in terms of species/morphospecies richness.

Geo references for stations were verified by the Geographic Information Systems Laboratory of INVEMAR (LabSiS) through ArcGIS Desktop–ArcMap 10.6 (2018) Software. Coordinates and sampling methods for the 14 stations analyzed in this review are summarized in table 1.

Results

Structural description and distribution

Madracis spp. are located at the south–west of the CPNNP. They cover an area of approximately 2.1 ha. Their delicate branches form small bushy colonies of about 50–80 cm high and up to 1 m wide. They are situated along the shelf–break scarp at between 107 and 230 m depth, and they are irregularly distributed on the muddy sand substates (fig. 2) forming coral patches. The area is characterized by warm waters with temperatures between 19º and 23ºC, strong currents at the surface between 0.2 and 0.3 m/s, and milder currents near the bottom between 0.1 and 0.2 m/s.

Diversity associated

Our compiled dataset from the SiBM and MARIKUWA Museum collections and imagery resulted in a biodiversity inventory of 337 species belonging to eight phyla (see checklist published through GBIF, DOI: 10.15470/vqshir). Mollusca is the phylum of highest species richness with 116 species (34.4%), followed by Bryozoa with 70 species (20.8%), Cnidaria with 50 species (14.8%), Echinodermata with 39 species (11.6%), Chordata (Fishes) with 32 species (9.5%), Arthropoda with 14 species (4.1%), Annelida with 13 species (3.8%) and Brachiopoda with three species (~1%). Most records come from the early collections of 'Macrofauna II' and 'Marcoral' (87.5%), accounting for almost the total list of species of mollusks, cnidarians, echinoderms, crustaceans, and brachiopods and about three–quarters of the compiled fish list. Although 43 species were identified in the videos, they account only for 10% to additional records of the associated fauna contributed by the collections of the projects PNN Corales de Profundidad and PNN *Madracis*, and 8% correspond mainly to the inventory of bryozoans and annelids. General characteristics of the studied taxa are summarized from the most diverse to the least diverse phylum. A complete list of species is shown in appendix 1.

Mollusca

With 116 morphospecies, mollusks are by far the most diverse. Records mainly come from collections of the 'Macrofauna II' and 'Marcoral' expeditions. The malacofauna comprised four classes: Gastropoda (104 species), Bivalvia (10 species), Cephalopoda (one species) and Scaphopoda (one species). From these morphospecies, 76 were identified at species level, 36 at genus level and four at family level (appendix 1). Gastropoda included seven orders represented by 50 families. Among these, the most diverse were Muricidae with nine species, followed by Fissurellidae and Mangeliidae with seven species each, and Drilliidae with six species. Bivalvia had representatives in five orders, of which Pectinida was the most outstanding with three families. Cephalopoda and Scaphopoda were represented by only one species each, *Semirrossia tennera* and *Dentalium laqueatum*, respectively. The most frequent species were *Arene variabilis, Nassarius* sp*., Olivella myrmecoon, Olivella watermani, Polystira albida, Trivia candidula* and *Vexillum styria*.

Bryozoa

Seventy morphospecies were found (appendix 1), of which 52 were identified at species level and 18 remained with open nomenclature, three in *confer* (cf.) and 15 in genus. It classified the specimens into 34 families belonging to the orders Cheilostomatida (89%) and Cyclostomatida

(11 %). The most diverse families were Cupuladriidae and Phidoloporidae (fig. 4A, 4B) with seven and six species, respectively, followed by Colatooeciidae, Lepraliellidae, Smittinidae and Schizoporellidae with four species each. Within cupuladriids, the genus *Cupuladria* is highlighted as the most diverse with five species, while for phidoloporids it was *Plesiocleidochasma* with three species. Within other families, outstanding genera were *Trematooecia* (2 species), *Celleporaria* (3 species), *Parasmittina* (2 species) and *Stylopoma* (three species). The species *Aimulosia palliolata*, *Celleporaria magnifica*, *Colatooecia serrulata*, *Gemelliporina hastata, Micropora acumminata*, *Steginoporella connexa*, *Stylopoma smitti*, *Trematooecia arborescens*, *Turbicellepora pourtalesi*, and the genera *Drepanophora* and *Metrarabdotos*, are new records for the Colombian Caribbean (appendix 1 indicated by *). Regarding growth type, the majority of species were encrusting colonies (70 %), followed by erect, flexible and rigid forms (17 %) and free–living colonies (11 %). Bryozoans were found with *Madracis* spp. coral patches between 117 m and 217 m depth in six of the seven bottom–sampled locations. Bryozoans form small colonies, from one millimeter to a few centimeters, so none were observable in the video transects.

Cnidaria

Fifty morphospecies were identified, with representatives of five orders, Scleractinia (25 species) Alcyonacea (12 species), Antipatharia (10 species), Zoanthidea (two species) and Stylasterida (one species) (appendix 1). Thirty–three were identified to species level, 14 at genus level, two at family level and one to order. The most diverse families were the scleractinian Caryophylliidae with nine genera, followed by the black corals Antipathidae with five genera (fig. 6B), and the octocorals Ellisellidae with three genera. Besides colonies of the *Madracis* spp. complex (*Madracis myriaster, M. bruggemanni* and *M. asperula)* also identified were other frequent scleractinians from the family Caryophylliidae, *Caryophyllia berteriana*, *Coenosmilia arbuscula*, *Oxysmilia rotundifolia*, from the family Dendrophylliidae, *Balanophyllia cyathoides* and *Eguchipsammia cornucopia* (fig. 4F), and *Javania cailleti* from the family Flabellidae.

Echinodermata

The 39 Echinodermata records are based on the collections made during the 'Macrofauna II' expedition and a few records made with video–transects. Five classes were identified: Ophiuroidea (21 species), Crinoidea (nine species), Echinoidea (seven species), Asteroidea (one species) and Holothuroidea (one species). The expedition identified thirty–five at species level, two at genus level (*Amphilimna* and *Ophiacantha*), one at order level (Comatulida) and one to class (Ophiuroidea) (appendix 1). Ophiuroidea presented 12 families, with Ophiosphalmidae as the richest, with three species, followed by Ophiotomidae with two species, Ophiacanthidae (two species), Amphiuridae (two species) and Gorgonocephalidae (two species). Among Crinoidea, six families have been recorded, of which Comatulidae is the richest with three species (fig. 6D, 6E); the other families each have one species. Echinoidea, on the other hand, presented five families, of which Clypeasteridae and Paleopneustidae were the richest with two species each.

Arthropoda (Crustacea)

Records are based on the collections made during the 'Macrofauna II' expedition (appendix 1). It identified twelve at species level, one at genus level (*Iridopagurus)* and one at family level (Callianassidae). Overall, this phylum comprised 11 families from the Bachyura infraorder: Aethridae, Goneplacidae, Inachidae, Inachoididae, Leucosiidae, Mithracidae, Palicidae, Plagusiidae, Portunidae, Paguridae (Anomura infraorder) and Callianassidae (Axiidea infraorder). Inachidae and Inachoididae were the richest families found with the species *Anomalothir frontalis, Stenorhynchus seticornis, Stenorhynchus yangi, Collodes trispinosus* and *Pyromaia propinqua* (fig. 5H, 5I).

Annelida

Records are based exclusively on the collection made during the last expedition using the multipurpose drift–cam (CADEM). Eleven were identified at genus level and two at family level (Enchytraeidae and Opheliidae), belonging to three subclasses, Oligochaeta (one spe-

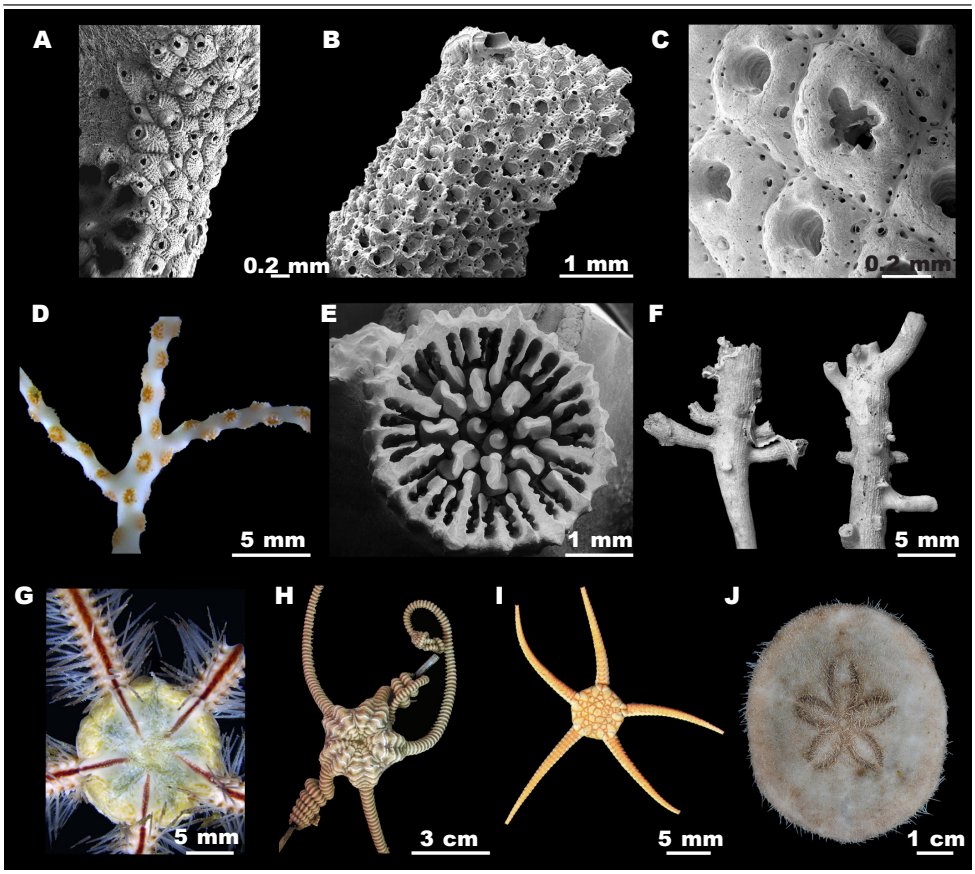

Fig. 4. Images of invertebrate specimens associated with *Madracis* spp. coral patches in the Corales de Profundidad National Natural Park, Colombian southern Caribbean. Bryozoans: A, Family Cribrilinidae, *Cribrilaria smitti* growing on a *Madracis* sp. branch; B, Family Phidoloporidae, *Rhynchozoon spicatum*; C, Family Colatooeciidae, *Trematooecia arborescens.* Cnidarians: D, *Madracis myriaster*; E, Family Caryophylliidae, *Caryophyllia (Caryophyllia) barbadensis*; F, Family Dendrophylliidae, *Eguchipsammia cornucopia*. Echinoderms: G, Family Ophiothrichidae, *Ophiothrix (Acanthophiothrix) suensoni*; H, Family Gorgonocephalidae, *Asteroporpa (Asteroporpa) annulata*; I, Order Amphilepidida, *Ophiothyreus goesi;* J, Family Clypeasteridae, *Clypeaster lamprus*. Note: *O. suensoni* (G) was collected attached to *Madracis myriaster* (D).

Fig. 4. Imágenes de especímenes de invertebrados asociados a parches de coral Madracis *spp. en el Parque Nacional Natural Corales de Profundidad, en el sur del Caribe colombiano. Briozoos: A, familia Cribrilinidae,* Cribrilaria smitti *creciendo en una rama de* Madracis *sp.; B, familia Phidoloporidae,* Rhynchozoon spicatum*; C, familia Colatooeciidae,* Trematooecia arborescens*. Cnidarios: D,* Madracis myriaster*; E, familia Caryophylliidae,* Caryophyllia (Caryophyllia) barbadensis*; F, familia Dendrophylliidae,* Eguchipsammia cornucopia*. Equinodermos: G, familia Ophiothrichidae,* Ophiothrix (Acanthophiothrix) suensoni*; H, familia Gorgonocephalidae,* Asteroporpa (Asteroporpa) annulata*; I, Orden Amphilepidida,* Ophiothyreus goesi*; J, familia Clypeasteridae,* Clypeaster lamprus*. Nota:* O. suensoni *(G) se recolectó adherido a* Madracis myriaster *(D).*

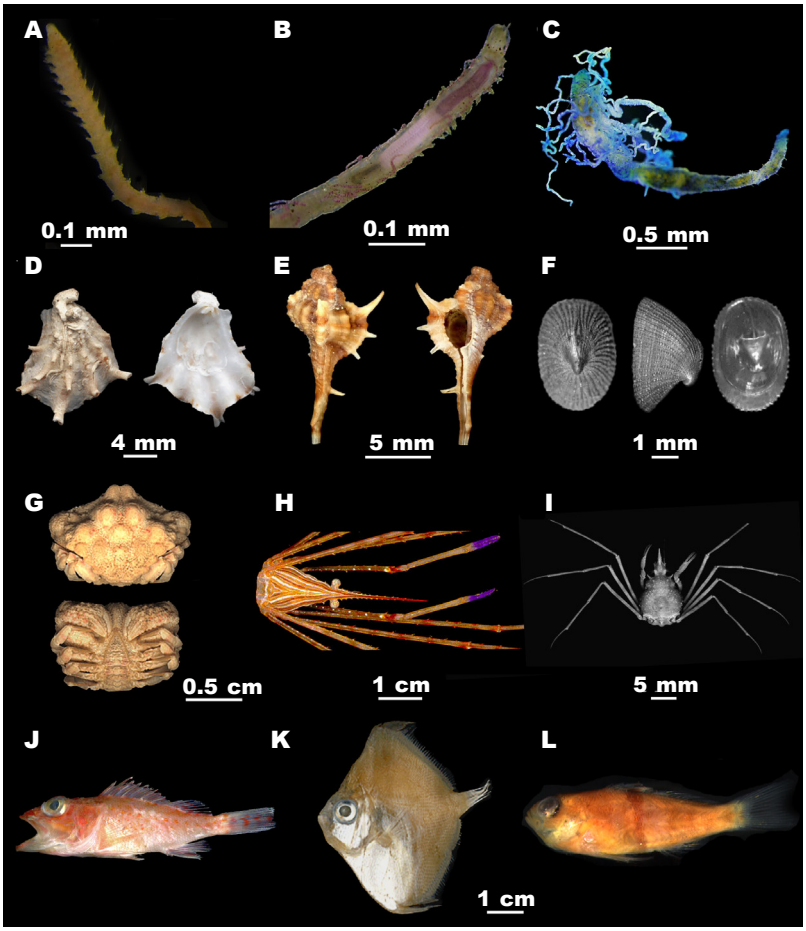

Fig. 5. Images of invertebrate specimens associated with *Madracis* spp. coral patches in the Corales de Profundidad National Natural Park, Colombian southern Caribbean. Annelids: A, Family Spionidae, *Scolelepis (Scolelepis)* sp.; B, Family Syllidae, *Syllis* sp.; C, Family Cirratulidae, *Chaetozone* sp. Mollusks: D, Family Pectinidae, *Plicatula gibbosa*; E, Family Muricidae, *Vokesimurex olssoni*; F, Family Fissurellidae, *Puncturella granulata*. Arthropoda (Crustacea): G, Family Aethridae, *Osachila antillensis*; H, Family Inachoididae, *Stenorhynchus yangi*; I, *Pyromaia propinqua*. Fishes: J, Family Scorpaenidae, *Pontinus nematophthalmus*; K, Family Caproidae, *Antigonia capros*; L, Family Serranidae, *Serranus atrobranchus*.

Fig. 5. Imágenes de especímenes de invertebrados asociados a los parches de coral Madracis *spp. en el Parque Nacional Natural Corales de Profundidad, en el sur del Caribe colombiano. Anélidos: A, familia Spionidae,* Scolelepis (Scolelepis) *sp.; B, familia Syllidae,* Syllis *sp.; C, familia Cirratulidae,* Chaetozone *sp. Moluscos: D, familia Pectinidae,* Plicatula gibbosa*; E, familia Muricidae,* Vokesimurex olssoni*; F, familia Fissurellidae,* Puncturella granulata. *Arthropoda (Crustacea): G, familia Aethridae,* Osachila antillensis*; H, familia Inachoididae,* Stenorhynchus yangi*; I,* Pyromaia propinqua. *Peces: J, familia Scorpaenidae,* Pontinus nematophthalmus*; K, familia Caproidae,* Antigonia capros*; L, familia Serranidae,* Serranus atrobranchus.

cies), Errantia (four species) and Sedentaria (eigth species). Amphinomidae was the richest family found. Two genera are new records for the Colombian Caribbean (*Linopherus* sp. and *Aglaophamus* sp.) and two are new records for the Greater Caribbean (*Galathowenia* sp. and *Eclysippe* sp.) (appendix 1 indicated by *).

Brachiopoda
Records of three species were mainly based on the collections of the 'Marcoral' expedition and some samples of 'Macrofauna II' (appendix 1). The identified species were *Tichosina plicata, Terebratulina cailleti,* and *Argyrotheca barrettiana. Tichosina plicata* and *T. cailleti* were the first records for the Colombian Caribbean (Rojas et al., 2015), increasing the number of brachiopod species known for the Colombian Caribbean Sea to five. The three species represent three families.

Fish (Chordata)
Records are based on the collections made during the 'Macrofauna II' expedition and a few additional observations made with video–transects, as fish are easily disturbed by submersibles**.** Twenty–seven were identified at species level, three at genus level, one at family level and one at order level (Pleuronectiformes) (appendix 1). Findings comprised nine orders, Perciformes (13 species), Scorpaeniformes (six species), Pleuronectiformes (four species), followed by Gadiformes, Lophiiformes and Zeiformes with two species each. And finally, orders with only one species each were Batrachoidiformes, Gasterosteiformes and Tetradontiformes. The families with the highest richness of species were Scorpaenidae with four species (*Neomerinthe beanorum, Pontinus nematophthalmus, Pterois volitans* and *Scorpaena agassizii*) and Serranidae also with four species (*Epinephelus* sp. fig. 6G, *Serranus atrobranchus* fig. 5L*, Pronotogrammus martinicensis* and *Serranus phoebe* fig. 6H).

Discussion

Biodiversity data that settled the basis for the creation of the Marine Protected Area (MPA), include the first description of the *Madracis* communities by Reyes et al. (2005) and the series of papers to compile the status of knowledge of the anthozoan fauna of 'Marcoral'expedition by Santodomingo et al. (2007, 2013). The initial report of the fauna associated from one locality (two samples between 155 m and 160 m depth) recorded a total of 134 species of fishes (20 species) and invertebrates, including four main taxa Cnidaria (34 species), Mollusca (23 species), Echinodermata (38l species) and Crustacea (19 species) (Reyes et al., 2005). Subsequently, during the 'Marcora' expeditions, the record of invertebrate richness increased to 333 species for the MPA, including both coral associated fauna and their adjacent soft bottoms: Cnidaria (40 species) (Santodomingo et al., 2007, 2013), Mollusca (215 species), Bryozoa (33 species), Echinodermata (14 species) and Crustacea (27 species). Under the framework of the 'Marcoral' project, one of the main goals was to identify biological criteria to support the creation of the MPA, so a more comprehensive study by Urriago et al. (2011) compiled the available biodiversity data of the shelf–break scarp in the MPA that resulted in a total of 528 species: 154 species of mollusks, 129 species of fishes, 110 species of crustaceans, 97 species of echinoderms and 38 species of cnidarians. Differences in the species numbers vary depending on the number of taxonomic groups at family or genera level included in the compilations, the number of localities, the type of habitat (coral, soft bottoms, hard grounds, etc.) considered in the analyses and multi–gear sampling (Reyes et al., 2005; Urriago et al., 2011 for methods). Within this context, the outcomes of our research are constrained to the specific localities in which *Madracis* spp. coral patches were found in abundance, in the sense that we have more certainty that we can refer to them as the biodiversity directly associated with the coral patches they build. As a result, a comparison between the original report of Reyes et al. (2005) where *Madracis* communities were discovered (one locality)

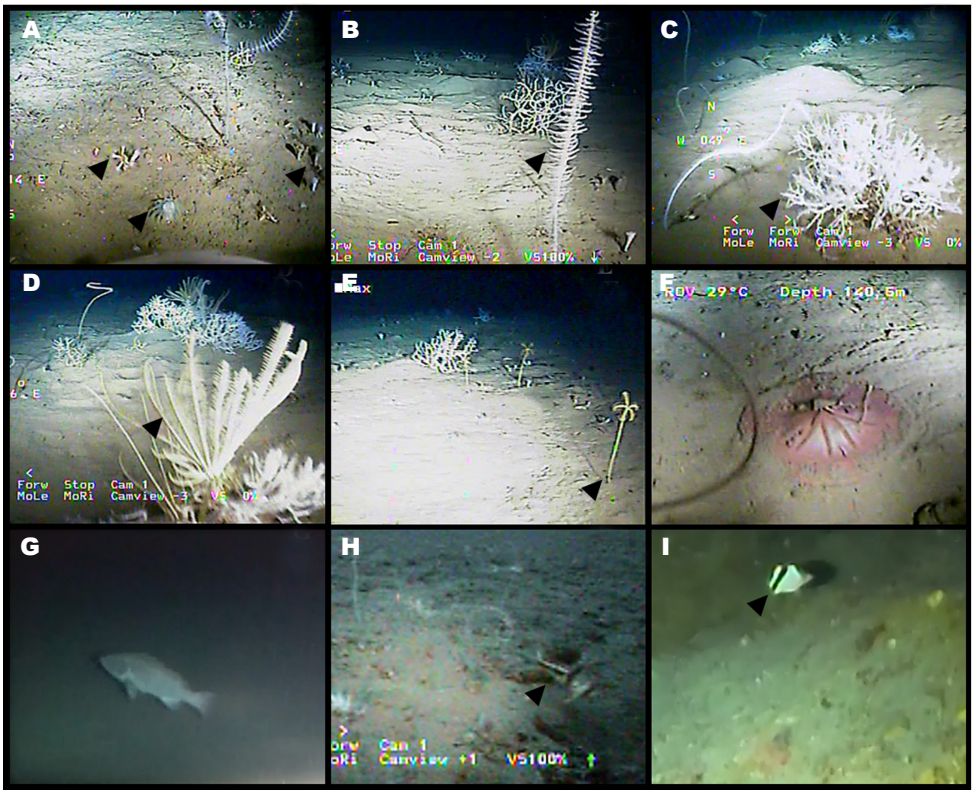

Fig. 6. Images taken by the ROV Diavolo II and multipurpose drift-cam (CADEM). (Laser pointers = 10 cm). Fauna associated with *Madracis* spp. coral patches in the Corales de Profundidad National Natural Park, Colombian southern Caribbean. Cnidarians: A, cup corals from the family Caryophylliidae; B, Family Antipathidae, *Elatopathes abietina;* C, *Madracis* colony; D, echinoderm comatulid over *Madracis* colonies; E, Family Comatulidae, *Democrinus conifer*; F, Family Clypeasteridae, *Clypeaster euclastus*; G, *Epinephelus* sp.; H, *Serranus phoebe*; I, *Prognathodes guyanensis.*

Fig. 6. Imágenes tomadas por el ROV Diavolo II y la cámara de deriva polivalente (CADEM). (Punteros láser = 10 cm). Fauna asociada a los parches de coral Madracis *spp. en el Parque Nacional Natural Corales de Profundidad, en el sur del Caribe colombiano. Cnidarios: A, corales copa de la familia Caryophylliidae; B, familia Antipathidae,* Elatopathes abietina*; C, colonia de* Madracis*; D, equinodermo comatúlido sobre colonias de* Madracis*; E, familia Comatulidae,* Democrinus conifer*; F, familia Clypeasteridae,* Clypeaster euclastus*; G,* Epinephelus *sp.; H,* Serranus phoebe*; I,* Prognathodes guyanensis.

and our up–to–date compilation (14 localities) evidenced an increase of more than two–fold for the species record from 134 species (Reyes et al., 2005) to 337 species (this review). New data include new 96 mollusks, 25 cnidarians, six echinoderms, three crustaceans, and 12 fish species, plus 70 species of bryozoans, 14 annelids, and three brachiopods that were not initially listed. This increase has been achieved thanks to the all the different collection methods and sampling efforts invested in exploring this area.

Regarding the physical environment where *Madracis* spp. corals patches develop, evidence from echo sounder profiles and video footage suggests that coral colonies are in low mounds (10 to 20 m high), and therefore they may be able to participate in the construction of coral mounds (Santodomingo et al., 2007). Regional geological characterizations have shown that mounds in this area are related to active mud diapirism and tectonism, which in turns result in a complex diversity of geoforms (Reyes et al., 2005; Rangel–Buitrago and Idárraga–García, 2010). More detailed mapping supported by geological sampling is still needed to better understand the geomorphology of *Madracis* spp. coral patches occur and to what extent they may be able to build up bioherms on the seafloor. Independently of their ability to construct bioherms, there is no doubt that *Madracis* species are habitat–forming providing ecological niches for associated species (Rogers, 1999) and in this study we have found that their occurrence is related to a high number of species. As proposed for deep–sea coral frameworks, the construction of a three–dimensional structure is favored by sediment inputs that enhance the vertical growth, providing physical support around the corals (Wheeler et al., 2005, 2011). Sediment inputs also allow the delivery of organic particulate material to the epifaunal suspension–feeders (Wheeler et al., 2005, 2011; Mastrototaro et al., 2010). Most of the invertebrate fauna found here are suspension–feeders (scleractinians, octocorals, bryozoans, brachiopods, bivalves, crinoids, ophiurans, and polychaetes) inhabiting the mud/sand substrate where the colonies of *Madracis* settle. Sediment samples from the seafloor are mainly composed of mixed sand–mud sediments and coral rubble (Santodomingo et al., 2007) which also offer suitable substrates and nutrients for the colonization of sessile invertebrates (Buhl–Mortensen and Fosså, 2006; Henry and Roberts, 2007; Mastrototaro et al., 2010; Buhl–Mortensen et al., 2016; Winston, 2016).

Sampling and museum collections

Our outcomes highlight the importance of systematic sampling and museum collections (Funk, 2018) because most knowledge on the biodiversity of *Madracis* spp. coral patches is based on identifications of voucher specimens. Indeed, 97 % of the species listed is based on museum specimens with accurate accompanying metadata. To date, footage collected with ROV and CADEM has provided a valuable overview of the seascapes where *Madracis* colonies occur –including growth forms, colony sizes, distribution and relation to some of the associated fauna. However, these data have been limited by the quality of the images and low–tech manipulator arm for collections. Underwater footage has shown about 12.9 % of the morphospecies have been identified as they show diagnostic characters that can be recognized (mostly megafauna > 5 cm), yet they only add 28 morphospecies to our collection–based inventory. In general, studies of deep–water coral fauna have also found that images and videos alone are only useful to identify common taxa, and for most organisms access to physical samples for taxonomic purposes or fragments for molecular studies are recommended (Etnoyer et al., 2006; Henry and Roberts, 2016). Such is the case of Arthropoda, which we consider an underestimated group in the samples, either because of its mobility, which makes it difficult to capture, or because of its small sizes. Future collections will surely increase the number significantly. Further surveys with ROVs equipped with high–definition cameras and high–tech manipulator arms for the collection of target fauna are still needed to gain more insight into the extension and structure of these important communities.

This study must be understood as an effort to review the state–of–the art of our knowledge on the diverse fauna associated with *Madracis* spp. coral patches in the CPNNP. The collections of Makuriwa Museum hold an extensive number of specimens collected in other environments of the CPNNP, such as soft substrate, rubble, solitary corals, rock/ledges and rugged stones, other hard grounds and pockmarks, from 46 to 354 m depth (Cedeño–Posso et al., 2022). Moreover, specimens of important taxa such as sponges, foraminifera, tunicates and other cnidaria (Actiniaria and Hydrozoa), and tunicates are yet to be identified. In addition, greater efforts are underway to complete the inventories of Annelida, Bryozoa

and Arthropoda (Crustacea), and the study of the food supply for the deep–sea corals, zooplankton (copepods, euphasian, cumaceans and chaetognaths) (Freiwald et al., 2002). Although mollusks are a more well–known group than other invertebrates, some of the collected material also requires further identification; for some morphospecies, it is essential to include an integrative approach. A full assessment of these collections is needed and will contribute to the planning and better management of this MPA.

Diversity and ecology of associated fauna

The habitat provided by *Madracis* offers shelter and food to an abundant and diverse fauna, as has been described for deep–sea coral communities (Lutz and Ginsburg, 2007). Fauna can be (1) intimately associated with the coral, or (2) associated with the substrate where the coral is established, or (3) in the case of demersal fauna, it can move between the coral patches and the rocky macro–habitats that surround them. Among the eight phyla recorded here, most species benefit from the habitat in these three different ways, while others, such as demersal fishes, fall mainly into the third category.

Mollusca

The high nutrient availability in this deep–sea environment is suitable for the establishment of mollusks because it supports a great diversity of detritivorous gastropods and bivalves, greatly surpassing the species record for other taxa (Janssen and Taviani, 2015). About one third of species that occur in the *Madracis* habitats belong to the class Gastropoda (104 species). Many deep–sea gastropods are detritivorous and may contribute to nutrient recirculation on the seafloor of the CPNNP because of their ecological traits (Ponder et al., 2019). One finding was the high frequency of snails with different feeding specializations, such as the spongivorous snail *Calliostoma* sp., detritivores like *Nassarius* sp, *Olivella myrmecoön*, *Olivella watermani,* and *Euchelus* sp., the carnivorous *Conus* sp., *Trivia candidula, Antillophos chazaliei, Polystira albida* and *Cosmioconcha nitens* and interestingly, the molluscivore *Vexillum styria.*

Bryozoa

Bryozoans are the second most diverse group associated with *Madracis* spp. coral patches. Their ability to colonize diverse substrates and to cope with environmental fluctuations such as temperature, salinity, turbidity and depth, have conferred them an adaptive success over other benthic marine competitors (O'Dea and Okamura, 1999). The relatively high species richness in these habitats and the notable prevalence of encrusting forms can be explained by the ability of bryozoan colonies to settle on the high availability of substrates provided by dead *Madracis* branches, coral rubble, and mollusk shells, similarly that have been described for Florida *Oculina* reefs (Winston, 2016). For example, in samples of the National Natural Park, specimens of *Cribrilaria*, *Plesiocleidochasma*, *Celleporaria*, and *Stylopoma* were observed attached to the branches of dead *Madracis* corals. On the other hand, the mud/sand sediments that surround *Madracis* spp. coral patches allow the development of free–living colonies (O'Dea, 2009), such as *Cupuladria,* the most diverse genus in this study and common and abundant in the Colombian Caribbean, up to 500 m depth (Flórez et al., 2007; Montoya–Cadavid and Flórez, 2010). It is worth mentioning that some bryozoan specimens reported here were found without tissues or opercula (appendix 1 indicated by +), suggesting that they may have been transported here through sediment flows from surrounding environments.

The high species richness of bryozoans associated with *Madracis* becomes more significant if it is compared with similar deep–sea coral environments of the continental shelf of Colombia (Flórez et al., 2007) and Florida (Winston, 2016). Even in the Mediterranean (Spain and France), where the sampling effort has been greater and included several localities, the richness estimate only reaches 74 species (Zabala et al., 1993; Rueda et al., 2019). The new records found in this MPA complement the Bryozoa inventory in the Colombian Caribbean (Osburn, 1947; Flórez et al., 2007; Montoya–Cadavid et al., 2007; Montoya–Cadavid and Flórez, 2010; Delgadillo–G. and Flórez, 2015; Gracia et al., 2018), encouraging the research of this group in this region.

Cnidaria

Represent the third most diverse fauna found in the area. They include solitary corals, octocorals, antipatharians, hydrozoans and zoanthids, characteristically associated with deep–sea coral habitats, where they can find suitable substrates to attach to such as broken branches of hard corals and shells. It seems that *Madracis* habitats also enhance the presence of other azooxanthellate scleractinians, as their abundance and richness are also higher than in other localities where they do not occur (Roberts et al., 2006, 2009; Santodomingo et al., 2013). For example, from the Colombian record of scleractinian species, *Caryophyllia* (*Caryophyllia*) *barbadensis* (fig. 4E) and *Eguchipsammia cornucopia* (fig. 4F) have only been found in these localities (Reyes et al., 2009, 2010; Santodomingo et al., 2013). Among other habitat–forming taxa, it is important to highlight that octocorals and antipatharians also offer shelter to other invertebrates found living in their colonies (Buhl–Mortensen and Buhl–Mortensen, 2005; Chacón–Gómez et al., 2012). Therefore, part of the high diversity of ophiurans, crustaceans and annelids is closely related not only to *Madracis* colonies but also to the presence of these other colonial anthozoans.

Echinodermata

A significant new diversity of echinoderms has also been observed in these *Madracis* spp. coral patches, as 21 out of 39 species found here were recorded for the first time in Colombia (Borrero–Pérez et al., 2002; Borrero–Pérez and Benavides–Serrato, 2004; Reyes et al., 2005; Borrero–Pérez et al., 2008; Benavides–Serrato et al., 2011). Among the most common ophiurans found attached to the coral branches is *Ophiothrix* (*Acanthophiothrix*) *suensoni* (fig. 4G). Currently, this location represents the only one in Colombia where five echinoderm species occur, the crinoids *Coccometra nigrolineata* and *Stylometra spinifera* and the brittle stars *Asteroporpa* (*Asteroporpa*) *annulata, Ophiotreta valenciennesi* and *Ophiosyzygus disacanthus*. The latter is also a first record for the Caribbean Sea, being previously reported for the Gulf of Mexico and the southwestern coast of Japan (Borrero–Pérez and Benavides–Serrato, 2004). In addition, it is important to highlight that the crinoid *Endoxocrinus (Endoxocrinus) parrae,* and the brittle stars *Astrocnida isidis*, *Ophiothyreus goesi*, *Ophiopaepale goesiana*, *Ophiomitrella laevipellis*, *Ophiopristis hirsuta* and *Ophiomusa testudo* have only been recorded in *Madracis* spp. coral patches located in the National Natural Park, La Guajira Peninsula (70 m depth) and Santa Marta (200 m depth) (Reyes et al., 2005). Other echinoderms species are typical of soft bottoms mixed with deep–sea corals, including the Asteroidea (*Plutonaster agassizi agassizi*) and Holothuroidea (*Holothuria (Cystipus) occidentalis*), some Ophiuroidea (i.e., *Ophiomusa* spp.) and most of the Echinoidea. Sea urchins are represented by five species of irregular echinoids in the orders Clypeasteroida and Spatangoida, with burrowers and detritivores habits. Regarding the ecology of this phylum, the crinoids and some brittle stars reported here are suspension–feeders (Gorgonocephalidae, Amphiuridae and Ophiothrichidae) (Birkeland, 1989; Hendler et al., 1995) and inhabit different microhabitats, such as buried in the muddy bottoms (i.e. Amphiuridae) or they may spend most of their life stages on larger organisms such as corals or crinoids stems, extending their arms to catch organic particles, like copepods and other microscopic organisms, as shown by Hendler et al. (1995) for *Asteroporpa* (*Asteroporpa*) *annulata* (fig. 4H).

Arthropoda (Crustacea)

This Phylum has a low diversity, with 4.2 % of the total species found in this study. The infra–order Brachyura is one of the most successful groups of marine organisms worldwide. They can be found in all habitat types, from terrestrial to deep–sea (Ariza et al., 2008), although only a few species are present in the *Madracis* spp. coral patches. Key aspects for their success are perhaps the adaptation of their photoreceptors which allows most of them to be visually competent in a high variety of marine habitats, including deep–sea ecosystems (Frank et al., 2012) and their strictly benthic habits allow them to inhabit close within the coral framework of the colonies (Mastrototaro et al., 2010). One of the ecological features evidenced by crustaceans in the *Madracis* rubble is the presence of coral–symbiont predators

such as the arrow crab *Stenorhynchus seticornis Stenorhynchus yangi* and the spider crab *Pyromaia propinqua* typically found in shallower reef environments (Lemaitre et al., 2009; Antunes et al., 2018) and in the case of *Palicus sicus*, that is the only species of the family Palicidae found in Colombia in substrates with a predominance of deep–sea corals at 200 m depth (Bermúdez et al., 2005).

Annelida

Even though polychaetes showed a low number of species in this study (13 species) they represented a high number of families (12 families), suggesting that community assessments at family level may be sufficient in marine biodiversity studies of this group (Olsgard et al., 2003). Their abundance was relatively high; most individuals were found in the soft sediment around the coral patch and others were directly associated with *Madracis* branches in a symbiotic interaction, as previously described by López et al. (2008) for the families Eunicidae (*Paramarphysa* sp.) and Sabellidae (subfamily Fabricinae). Polychaetes are among the most diverse and perhaps the least studied taxa of coral symbionts (Molodtsova et al., 2016), especially in deep–sea coral communities. Recent studies suggest that these habitats are hidden hotspots for annelid diversity, with many species still undescribed (Molodtsova et al., 2016). They are commonly found associated with sponges, echinoderms, crustaceans, cnidarians, mollusks and even other polychaetes (Martin and Britayev, 1998) in shallower areas. Detritivorous worms such as *Linopherus* sp. *Galathowenia* sp. and *Eclysippe* sp. and the active predator *Aglaophamus* sp. are new records for the Colombian Caribbean. Commensalism is likely to be another common form of interaction between polychaetes and azooxanthellate corals (Morales de Anda, et al. 2014; Pitacco and Karhan, 2019). Close association and inter–relation of highly host–specific symbionts and cnidarian hosts often lead to dramatic changes in the host morphology (Molodtsova et al., 2016). A recently updated review on symbiotic polychaetes (Martin and Britayev, 2018) identified more than 600 species involved in symbiotic relationships, a number that has almost doubled since the most recent review on the topic 20 years ago (Martin and Britayev, 1998).

Brachiopoda

Brachiopods are not a remarkably diverse group of marine invertebrates in modern faunas. There are roughly 414 species worldwide (WoRMS, 2022). Although the Colombian Caribbean diversity of this group is low, the number of specimens collected suggests that brachiopods in the the Caribbean are probably more abundant offshore than previously thought (Rojas et al., 2009). Some of the species were found within the sediment samples, but it was evident that *Madracis* spp. coral patches has an important role as a habitat–forming species, lending support and colonization substrate to this type of organisms. Specifically, *Tichosina plicata* was observed attached to *Madracis* branches, and in a lower proportion than other corals (Rojas et al., 2022).

Chordata (Fish)

Among the fishes, most of the species are motile between the coral patches and the rocky macro–habitats that surround them. Demersal and bathydemersal species collected in the *Madracis* spp. coral patches include common shallow–reef species such as *Lipogramma evide*s, *Pristigenys alta* and *Decodon puellaris*, with the last two previously reported as new records for the Colombian Caribbean (Polanco et al., 2012). Species observed in video footage are benthopelagic representatives of some highly exploited commercial groups, such as jacks and groupers (fig. 5G). Also, puffers and some reef associated species such as *Pristigenys alta*, *Serranus phoebe*, *Pterois volitans* and *Prognathodes guyanensis* (fig. 6I) that are newly recorded for the Colombian Caribbean were previously known from the Bahamas to Guyana and Venezuela (Robertson and Van Tassell, 2019). The presence of the lionfish, *Pterois volitans*, in these *Madracis* spp. coral patches is noteworthy. The lionfish is a species native to the Indopacific that was introduced in the Caribbean most likely through the aquarium industry via continuous escapes (Schofield, 2009). First documented in Florida

reefs in 1985 (Schofield, 2009), in just a few years its populations expanded south throughout the Caribbean, with records in the Colombian Caribbean in 2009 (Gonzalez et al., 2009), and recent sightings in southern Brazil (Soares et al., 2023). Although lionfish are typically found in highest densities in shallow waters from 30 to 60 m depth (Andradi–Brown, 2019), recent studies have revealed that *P. volitans* has also moved into mesophotic environments in various regions of the Western Atlantic (Andradi–Brown, 2019; Luiz et al., 2021; Sanjuan–Muñoz et al., 2022), and it has even been observed in the upper bathyal zone (Gress et al., 2017). The remarkable adaptability of the lionfish to different habitats and diets has been key in their successful invasion (Cure et al., 2014), both geographically and bathymetrically. Their adaptability may therefore also account for their presence in *Madracis* spp. coral patches, as *P. volitans* tend to aggregate with conspecifics in habitats characterized by high structural complexity (Hunt et al., 2019). Our findings highlight the need to consider deep ecosystems with structural complexity in the management of this invasive species.

The scarce observation of fish in the video–transects is likely because they were easily disturbed by the submersibles, a bias that has previously been suggested to affect results in this type of survey (Trenkel et al., 2004).

Conclusions

The protection of *Madracis* spp. coral patches and their associated high diversity (eight phyla, 337 species) in the CPNNP has an important role in the conservation of marine diversity in the Colombian Caribbean Sea. These protected habitats host species that have only been found in this environment, such as five echinoderms and two cnidarians, plus new records of nine bryozoans, four genera of annelids, and the fish *Prognathodes guyanensis* for the Colombian Caribbean. *Madracis* spp. coral patches are also a refuge for large commercial fish species such as jacks and groupers, highly exploited by artisanal and industrial fisheries. The occurrence of a diverse suspension and filter–feeding invertebrate fauna (scleractinians, octocorals, bryozoans, brachiopods, bivalves, crinoids, ophiurans, and polychaetes) may be related to high availability and retention capacity of food particles supplied to these deep–sea habitats by local hydrodynamics.

Further surveys with advanced ROVs and multibeam bathymetry are strongly recommended to confirm the occurrence of additional patches of these diverse *Madracis* coral communities in the CPNNP. New research using cutting–edge technologies and targeted sampling will enhance our baseline knowledge by providing a better understanding of the extension and structure of the *Madracis* spp. coral patches, as well as aspects of the life history (growth and reproduction) of the main habitat–forming species, their associated fauna, and their possible links (connectivity) with both, shallow–coral reefs and other deep–sea communities in the region. Comprehensive investigations will facilitate the establishment of research priorities and targets for long–term monitoring, which, in turn, will strengthen the planning and management of this MPA.

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Appendix 1. List of the fauna diversity observed/collected in *Madracis* spp. coral patches at the southwest area of the Corales de Profundidad National Natural Park: * new record to Colombian Caribbean; ** new record to Great Caribbean; + bryozoan species without tissues or opercula.

Apéndice 1. Lista de la diversidad faunística observada/recolectada en los parches de coral Madracis *spp. en el área suroccidental del Parque Nacional Natural Corales de Profundidad: + nuevo registro para el Caribe colombiano; ** nuevo registro para el Gran Caribe; + especies de briozoos sin tejidos ni opérculos.*

Phylum	Class	Order	Family	Species
Cnidaria	Anthozoa	Antipatharia	Antipathidae	*Stylopathes columnaris* (Duchassaing, 1870)
				Antipathes gracilis Gray, 1860
				Antipathes sp.
				Elatopathes abietina (Pourtalès, 1874)
				Stichopathes luetkeni Brook, 1889
				Stichopathes occidentalis Gray, 1860
				Stichopathes sp.
			Myriopathidae	*Tanacetipathes barbadensis* (Brook, 1889)
				Tanacetipathes spinescens (Gray, 1857)
				Antipatharia sp.
		Alcyonacea	Acanthogorgiidae	*Acanthogorgia aspera* Pourtalès, 1867
				Muricella sp.
			Chrysogorgiidae	*Chrysogorgia* sp.
				Chrysogorgia thyrsiformis Deichmann, 1936
			Ellisellidae	Ellisellidae Gray, 1859
				Riisea paniculata Duchassaing and Michelotti, 1860
				Verrucella sp.
			Nephtheidae	*Stereonephthya portoricensis* (Hargitt, 1901)
			Nidaliidae	*Nidalia occidentalis* Gray, 1835
				Nidalia rubripunctata Verseveldt and Bayer, 1988
			Plexauridae	*Hypnogorgia pendula* Duchassaing and Michelotti, 1864
				Placogorgia tenuis (Verrill, 1883)
		Scleractinia	Caryophylliidae	*Anomocora fecunda* (Pourtalès, 1871)
				Anomocora sp.
				Caryophyllia (Caryophyllia) barbadensis Cairns, 1979
				Caryophyllia (Caryophyllia) berteriana Duchassaing, 1850
				Caryophyllia sp.
				Coenocyathus parvulus (Cairns, 1979)
				Coenosmilia arbuscula Pourtalès, 1874
				Coenosmilia sp.
				Deltocyathus calcar Pourtalès, 1874
				Oxysmilia rotundifolia (Milne Edwards and Haime, 1848)
				Paracyathus pulchellus (Philippi, 1842)
				Paracyathus sp.
				Polycyathus mayae Cairns, 2000
				Thalamophyllia riisei (Duchassaing and Michelotti, 1864)
				Caryophylliidae Dana, 1846
			Dendrophylliidae	*Balanophyllia (Balanophyllia) cyathoides* (Pourtalès, 1871)
				Balanophyllia (Balanophyllia) palifera Pourtalès, 1878
				Balanophyllia sp.
				Balanophyllia (Balanophyllia) wellsi Cairns, 1977
				Eguchipsammia cornucopia (Pourtalès, 1871)
			Flabellidae	*Javania cailleti* (Duchassaing and Michelotti, 1864)
			Oculinidae	*Madrepora carolina* (Pourtalès, 1871)
			Pocilloporidae	*Madracis brueggemanni* (Ridley, 1881)
				Madracis myriaster (Milne Edwards and Haime, 1850)
				Madracis asperula
		Zoanthidea	Epizoanthidae	*Epizoanthus* sp.
			Zoanthidae	Zoanthidae Rafinesque, 1815
	Hydrozoa	Stylasterida	Stylasteridae	*Stylaster* sp.
Bryozoa	Stenolaemata	Cyclostomatida	Lichenoporidae	+*Patinella radiata* (Audouin, 1826)
				+*Domopora* cf. *floridana* Canu and Bassler, 1928
			Entalophoridae	+*Mecynoecia delicatula* (Busk, 1875)
			Oncousoeciidae	*Proboscina* sp.
			Plagioeciidae	*Entalophoroecia* sp.
			Stomatoporidae	*Stomatopora* sp.
			Tubuliporidae	+*Exidmonea atlantica* (Forbes in Johnston, 1847)
				+*Tubulipora* sp.
	Gymnolaemata	Cheilostomatida	Membraniporidae	+*Biflustra denticulata* (Busk, 1856)
			Adeonidae	*Adeonella* sp.
				+*Adeonellopsis subsulcata* (Smitt, 1873)
			Antroporidae	+*Akatopora leucocypha* (Marcus, 1937)
			Arachnopusiidae	+*Poricella mucronata* (Smitt, 1873)
			Bufonellodidae	*+*Aimulosia palliolata* (Canu and Bassler, 1928)
			Calloporidae	+*Parellisina curvirostris* curvisotris (Hincks, 1862)
			Celleporidae	+*Pourtalesella rugosa* (Osburn, 1940)
				**Turbicellepora pourtalesi* Winston, 2005
			Cleidochasmatidae	+*Gemelliporina glabra* (Smitt, 1873)
				**Gemelliporina hastata* Winston and Woollacott, 2009
			Colatooeciidae	+*Cigclisula turrita* (Smitt, 1873)
				**+Colatooecia serrulata* (Smitt, 1873)
				**+Trematooecia arborescens* (Canu and Bassler, 1928)
				+*Trematooecia aviculifera* (Canu and Bassler, 1923)
			Cribrilinidae	+*Cribrilaria* sp.
			Cupuladriidae	*Cupuladria panamensis* Herrera-Cubilla, Dick, Sanner & Jackson, 2006
				+*Cupuladria surinamensis* Cadée, 1975
				+*Cupuladria* cf. *biporosa* (Canu and Bassler, 1923)
				Cupuladria sp. 1
				Cupuladria sp. 2
				+*Discoporella depressa* (Conrad, 1841)
				+*Vibracellina laxibasis* (Canu and Bassler, 1928)
			Escharinidae	+*Bryopesanser pesanseris* (Smitt, 1873)
				+*Hippomenella fissurata* (Canu and Bassler, 1928)
				+*Therenia porosa* (Smitt, 1873)
			Exechonellidae	+*Exechonella antillea* (Osburn, 1927)
			Hippaliosinidae	+*Hippaliosina rostrigera* (Smitt, 1873)
			Hippoporidridae	*Hippoporella pusilla* (Smitt, 1873)
			Lepraliellidae	**Celleporaria magnifica* (Osburn, 1914)
				+*Celleporaria sherryae* Winston, 2005
				+*Celleporaria* sp.
				**+Drepanophora* sp.
			Mamilloporidae	+*Mamillopora cupula* Smitt, 1873
				Mamillopora sp.
			Marcusadoreidae	+*Marcusadorea tubulosa* (Canu and Bassler, 1928)
			Margarettidae	+*Margaretta cereoide*s (Ellis and Solander, 1786)
				Margaretta sp.
			Metrarabdotosidae	**+Metrarabdotos* sp.
			Microporidae	**Micropora acumminata* Winston, 2005
			Onychocellidae	+*Floridina antiqua* (Smitt, 1873)
				+*Smittipora levinseni* (Canu and Bassler, 1917)
			Petraliidae	+*Petraliella bisinuata* (Smitt, 1873)
			Phidoloporidae	+*Plesiocleidochasma cleidostomum* (Smitt, 1873)
				Plesiocleidochasma porcellanum (Busk, 1860)
				Plesiocleidochasma sp.
				+*Stephanollona asper* (Canu and Bassler, 1923)
				+*Reteporellina evelinae* Marcus, 1955
				+*Rhynchozoon spicatum* Osburn, 1952
			Microporellidae	+*Microporella ciliata* (Pallas, 1766)
				Microporella sp.
			Schizoporellidae	+*Gemelliporidra aculeata* Canu and Bassler, 1928
				Stylopoma projecta Canu and Bassler, 1923
				**Stylopoma smitti* Winston, 2005
				+*Stylopoma spongites* (Pallas, 1766)

Appendix 1. (Cont.)

Phylum	Class	Order	Family	Species
			Smittinidae	+*Parasmittina nitida* (Verrill, 1875)
				+*Parasmittina* sp.
				+*Smittina* sp.
				+*Pleurocodonellina signata* (Waters, 1889)
			Steginoporellidae	*Siphonoporella dumonti* Canu and Bassler, 1928
				*+*Steginoporella connexa* Harmer, 1900
				+*Steginoporella magnilabris* (Busk, 1854)
Brachiopoda	Rhynchonellata	Terebratulida	Terebratulidae	*Tichosina plicata* Cooper, 1977
			Cancellothyrididae	*Terebratulina cailleti* Crosse, 1865
			Megathyrididae	*Argyrotheca barrettiana* (Davidson, 1866)
Annelida	Clitellata	Enchytraeida	Enchytraeidae	Enchytraeidae Vejdovský, 1879
	Polychaeta	Amphinomida	Amphinomidae	*Chloeia* sp.
				**Linopherus* sp.
		Phyllodocida	Nephtyidae	**Aglaophamus* sp.
			Syllidae	*Syllis* sp.
		Sabellida	Oweniidae	***Galathowenia* sp.
		Spionida	Poecilochaetidae	*Poecilochaetus* sp.
			Spionidae	*Scolelepis (Scolelepis)* sp.
		Terebellida	Ampharetidae	***Eclysippe* sp.
			Cirratulidae	*Chaetozone* sp.
			Chaetopteridae	*Spiochaetopterus* sp.
			Opheliidae	Opheliidae Malmgren, 1867
			Paraonidae	*Aricidea (Acmira)* sp.
Mollusca	Bivalvia			
	Protobranchia	Nuculida	Nuculidae	*Nucula* sp.
	Autobranchia	Arcida	Arcidae	*Barbatia candida* (Helbling, 1779)
		Cardiida	Cardiidae	*Microcardium peramabile* (Dall, 1881)
			Semelidae	*Abra longicallus* (Scacchi, 1835)
		Pectinida	Pectinidae	*Chlamys munda* (Reeve, 1853)
			Plicatulidae	*Plicatula gibbosa* Lamarck, 1801
			Propeamussiidae	*Parvamussium pourtalesianum* (Dall, 1886)
		Venerida	Veneridae	*Pitar arestus* (Dall and Simpson, 1901)
			Cuspidariidae	*Cuspidaria* sp.
			Poromyidae	*Poromya rostrata* Rehder, 1943
Gastropoda	(Neomphaliones)	Cocculinida	Cocculinidae	*Cocculina messingi* McLean and Harasewych, 1995
	(Vetigastropoda)	Lepetellida	Fissurellidae	*Diodora jaumei* Aguayo and Rehder, 1936
				Diodora listeri (d'Orbigny, 1847)
				Diodora sp.
				Emarginula phrixodes Dall, 1927
				Emarginula tuberculosa Libassi, 1859
				Lucapina sp.
				Puncturella granulata (Seguenza, 1863)
			Pseudococculinidae	*Notocrater houbricki* McLean and Harasewych, 1995
		Seguenziida	Chilodontaidae	*Euchelus* sp.
		Trochida	Areneidae	*Arene variabilis* (Dall, 1889)
				Arene sp.
			Calliostomatidae	*Calliostoma* sp.
			Trochidae	*Trochidae* Rafinesque, 1815
			Solariellidae	*Microgaza* sp.
	(Caenogastropoda)	Littorinimorpha	Bursidae	*Bursa cubaniana* (d'Orbigny, 1841)
			Capulidae	*Capulus* sp.
			Eulimidae	*Niso aeglees* Bush, 1885
			Hipponicidae	*Cheilea equestris* (Linnaeus, 1758)
				Hipponix incurvus (Gmelin, 1791)
			Naticidae	*Natica* sp.
			Ovulidae	*Cyphoma intermedium* (G. B. Sowerby I, 1828)
			Personidae	*Distorsio clathrata* (Lamarck, 1816)
				Distorsio mcgintyi Emerson and Puffer, 1953
			Rissoinidae	*Phosinella cancellata* (Philippi, 1847)
				Phosinella sagraiana (d'Orbigny, 1842)
				Rissoina sp.
			Tonnidae	*Eudolium crosseanum* (Monterosato, 1869)
			Triviidae	*Niveria quadripunctata* (J. E. Gray, 1827)
				Niveria suffusa (J. E. Gray, 1827)
				Trivia candidula (Gaskoin, 1836)
			Xenophoridae	*Xenophora conchyliophora* (Born, 1780)
			Zebinidae	*Schwartziella fischeri* (Desjardin, 1949)
		Neogastropoda	Borsoniidae	*Drilliola loprestiana* (Calcara, 1841)
				Drilliola sp.
			Clathurellidae	*Glyphostoma gabbii* (Dall, 1889)
			Columbellidae	*Anachis* sp.
				Cosmioconcha nitens (C. B. Adams, 1850)
				Falsuszafrona pulchella (Blainville, 1829)
				Suturoglypta pretrii (Duclos, 1846)
			Conidae	*Conus* sp.
			Costellariidae	*Vexillum styria* (Dall, 1889)
			Drilliidae	*Bellaspira margaritensis* McLean and L. Poorman, 1970
				Clathrodrillia cf. *solida* (C. B. Adams, 1850)
				Fusiturricula sp.
				Neodrillia sp.
				Splendrillia sp.
				Syntomodrillia lissotropis (Dall, 1881)
			Fasciolariidae	*Fusinus* sp.
			Granulinidae	*Granulina ovuliformis* (d'Orbigny, 1842)
			Mangeliidae	*Cryoturris fargoi* McGinty, 1955
				Cryoturris sp.
				Cryoturris quadrilineata (C. B. Adams, 1850)
				Glyphoturris quadrata (Reeve, 1845)
				Ithycythara cymella (Dall, 1889)
				Ithycythara psila (Bush, 1885)
				Tenaturris bartlettii (Dall, 1889)
			Marginellidae	*Eratoidea hematita* (Kiener, 1834)
				Volvarina sp.
			Mitridae	Mitridae Swainson, 1831
				Subcancilla leonardhilli Petuch, 1987
			Muricidae	*Babelomurex mansfieldi* (McGinty, 1940)
				Coralliophila sp.
				Chicoreus brevifrons (Lamarck, 1822)
				Hirtomurex squamosus (Bivona and Bernardi, 1838)
				Murex sp.
				Muricidae Rafinesque, 1815
				Orania sp.
				Siphonochelus tityrus (Bayer, 1971)
				Vokesimurex olssoni (Vokes, 1967)
			Nassariidae	*Antillophos chazaliei* (Dautzenberg, 1900)
				Antillophos sp.
				Nassarius sp.
			Olividae	*Olivella myrmecoon* Dall, 1912
				Olivella sp.
				Olivella watermani McGinty, 1940
			Pseudomelatomidae	*Compsodrillia* sp.
			Terebridae	*Terebra* sp.
			Turridae	*Polystira albida* (G. Perry, 1811)
				Polystira tellea (Dall, 1889)
				Turridae H. Adams and. Adams, 1853 (1838)
[unassigned]			Cerithiopsidae	*Cerithiopsis* sp.

Appendix 1. (Cont.)

Phylum	Class	Order	Family	Species
			Epitoniidae	*Amaea retifera* (Dall, 1889)
				Cirsotrema sp.
				Epitonium candeanum (d'Orbigny, 1842)
				Opalia burryi Clench and R. D. Turner, 1950
				Opaliopsis sp.
			Siliquariidae	*Tenagodus modestus* (Dall, 1881)
			Triphoridae	*Metaxia rugulosa* (C. B. Adams, 1850)
				Triphora melantera Hervier, 1898
			Turritelidae	*Turritella exoleta* (Linnaeus, 1758)
	(Heterobranchia)	Cephalaspidea	Cylichnidae	*Cylichna* sp.
			Haminoeidae	*Atys riiseanus* Mörch, 1875
				Atys sp.
			Rhizoridae	*Volvulella persimilis* (Mörch, 1875)
			Scaphandridae	*Scaphander watsoni* Dall, 1881
			Acteonidae	*Japonactaeon punctostriatus* (C. B. Adams, 1840)
			Architectonicidae	*Adelphotectonica* sp.
				Architectonica nobilis Röding, 1798
			Mathildidae	*Mathilda barbadensis* Dall, 1889
				Mathilda sp.
			Pyramidellidae	*Odostomia* sp.
				Triptychus niveus (Mörch, 1875)
				Turbonilla pusilla (Philippi, 1844)
	Scaphopoda	Dentaliida	Dentaliidae	*Dentalium laqueatum* Verrill, 1885
	Cephalopoda	Sepiida	Sepiolidae	*Semirossia tenera* (Verrill, 1880)
Arthropoda				
Crustacea	Malacostraca	Decapoda	Aethridae	*Osachila antillensis* Rathbun, 1916
			Callianassidae	Callianassidae Dana, 1852
			Goneplacidae	*Chasmocarcinus cylindricus* Rathbun, 1901
			Inachidae	*Anomalothir frontalis* (A. Milne-Edwards, 1879 [in A. Milne-Edwards, 1873-1880])
			Inachoididae	*Stenorhynchus seticornis* (Herbst, 1788)
				Stenorhynchus yangi Goeke, 1989
				Collodes trispinosus Stimpson, 1871
				Pyromaia propinqua Chace, 1940
			Leucosiidae	*Persephona crinita* Rathbun, 1931
			Mithracidae	*Nemausa cornuta* (de Saussure, 1857)
			Paguridae	*Iridopagurus* sp.
			Palicidae	*Palicus sicus* (A. Milne-Edwards, 1880)
	Malacostraca	Decapoda	Plagusiidae	*Euchirograpsus americanus* A. Milne-Edwards, 1880
			Portunidae	*Achelous spinicarpus* Stimpson, 1871
Echinodermata	Crinoidea	Comatulida	Rhizocrinidae	*Democrinus conifer* (A. H. Clark, 1909)
			Antedonidae	*Coccometra nigrolineata* AH Clark, 1918
			Comatulidae	*Comactinia meridionalis* (L. Agassiz, 1865)
				Comissia venustus (AH Clark, 1909)
				Davidaster rubiginosus (Pourtalès, 1869)
			Charitometridae	*Crinometra brevipinna* (Pourtalès, 1868)
			Thalassometridae	*Stylometra spinifera* (Carpenter, 1881)
				Comatulida
		Isocrinida	Isselicrinidae	*Endoxocrinus (Endoxocrinus) parrae* (Gervais in Guérin, 1835)
	Asteroidea	Paxillosida	Astropectinidae	*Plutonaster agassizi agassizi* Verrill, 1880
	Ophiuroidea	Amphilepidida	Amphiuridae	*Amphioplus tumidus* (Lyman, 1878)
				Amphiodia riisei (Lütken, 1859)
			Amphilimnidae	*Amphilimna* sp.
			Ophiothamnidae	*Histampica duplicata* (Lyman, 1875)
			Ophionereididae	*Ophioplax ljungmani* Lyman, 1875
			Ophiotrichidae	*Ophiothrix (Acanthophiothrix) suensoni* Lütken, 1856
			Amphilepidida Incertae Sedis	*Ophiothyreus goesi* Ljungman, 1872
		Ophiacanthida	Ophiacanthidae	*Ophiacantha* sp.
				Ophiomitrella laevipellis (Lyman, 1883)
			Ophiotomidae	*Ophiotreta valenciennesi* (Lyman, 1879)
				Ophiopristis hirsuta (Lyman, 1875)
			Ophiodermatidae	*Ophioderma appressum* (Say, 1825)
			Ophiacanthida Incertae Sedis	*Ophiopaepale goesiana* Ljungman, 1872
		Ophiurida	Ophiuridae	*Ophiura acervata* (Lyman, 1869)
		Ophiurida	Ophiosphalmidae	*Ophiomusa acufera* (Lyman, 1875)
				Ophiomusa testudo (Lyman, 1875)
				Ophiomusa valida (Ljungman, 1872)
		Euryalida	Gorgonocephalidae	*Asteroporpa (Asteroporpa) annulata* Örsted and Lütken in Lütken, 1856
				Astrocnida isidis (Duchassaing, 1850)
		Ophioscolecida	Ophioscolecidae	*Ophiosyzygus disacanthus* H. L. Clark, 1911
				Ophiuroidea Gray, 1840
	Echinoidea	Arbacioida	Arbaciidae	*Coelopleurus floridanus* A. Agassiz, 1872
		Cidaroida	Cidaridae	*Stylocidaris lineata* Mortensen, 1910
		Clypeasteroida	Clypeasteridae	*Clypeaster euclastus* H. L. Clark, 1941
	Echinoidea	Clypeasteroida	Clypeasteridae	*Clypeaster lamprus* H. L. Clark, 1914
		Spatangoida	Paleopneustidae	*Paleopneustes cristatus* A. Agassiz, 1873
				Paleopneustes tholoformis Chesher, 1968
		Spatangoida	Prenasteridae	*Agassizia excentrica* A. Agassiz, 1869
	Holothuroidea	Holothuriida	Holothuriidae	*Holothuria (Cystipus) occidentalis* Ludwig, 1875
Chordata	Actinopterygii	Batrachoidiformes	Batrachoididae	*Thalassophryne maculosa* Günther, 1861
		Gadiformes	Bregmacerotidae	*Bregmaceros atlanticus* Goode and Bean, 1886
			Moridae	*Physiculus fulvus* Bean, 1884
		Gasterosteiformes	Fistulariidae	*Fistularia petimba* Lacepède, 1803
		Lophiiformes	Lophiidae	*Lophiodes reticulatus* Caruso and Suttkus, 1979
			Ogcocephalidae	*Zalieutes mcgintyi* (Fowler, 1952)
		Perciformes	Acropomatidae	*Synagrops bellus* (Goode and Bean, 1896)
			Carangidae	*Caranx hippos* (Linnaeus, 1766)
				Carangidae Rafinesque, 1815
			Chaetodontidae	**Prognathodes guyanensis* (Durand, 1960)
			Gobiidae	*Bollmannia* sp.
			Grammatidae	*Lipogramma evides* Robins and Colin, 1979
			Labridae	*Decodon puellaris* (Poey, 1860)
			Priacanthidae	*Pristigenys alta* (Gill, 1862)
			Serranidae	*Epinephelus* sp.
				Serranus phoebe Poey, 1851
				Serranus atrobranchus (Cuvier, 1829)
				Pronotogrammus martinicensis (Guichenot, 1868)
			Uranoscopidae	*Kathetostoma cubana* Barbour, 1941
		Pleuronectiformes	Paralichthyidae	*Ancylopsetta cycloidea* Tyler, 1959
				Citharichthys cornutus (Günther, 1880)
			Cynoglossidae	*Symphurus piger* (Goode and Bean, 1886)
		Scorpaeniformes	Triglidae	*Bellator brachychir* (Regan, 1914)
				Prionotus beanii Goode, 1896
			Scorpaenidae	*Neomerinthe beanorum* (Evermann and Marsh, 1900)
				Pontinus nematophthalmus (Günther, 1860)
				Pterois volitans (Linnaeus, 1758)
				Scorpaena agassizii Goode and Bean, 1896
		Tetraodontiformes	Tetraodontidae	*Sphoeroides* sp.
		Zeiformes	Caproidae	*Antigonia capros* Lowe, 1843
			Caproidae	*Antigonia combatia* Berry and Rathjen, 1959