

## **Black Coral Assemblages from Machalilla National Park (Ecuador)**

Author(s) :Marzia Bo, Antonella Lavorato, Cristina G. Di Camillo, Angelo Polisenò, Andrés Baquero, Giorgio Bavestrello, Yuka Irei, and James Davis Reimer

Source: Pacific Science, 66(1):63-81. 2012.

Published By: University of Hawai'i Press

DOI:

URL: <http://www.bioone.org/doi/full/10.2984/66.1.4>

---

BioOne ([www.bioone.org](http://www.bioone.org)) is a nonprofit, online aggregation of core research in the biological, ecological, and environmental sciences. BioOne provides a sustainable online platform for over 170 journals and books published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Web site, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at [www.bioone.org/page/terms\\_of\\_use](http://www.bioone.org/page/terms_of_use).

Usage of BioOne content is strictly limited to personal, educational, and non-commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

# Black Coral Assemblages from Machalilla National Park (Ecuador)<sup>1</sup>

Marzia Bo,<sup>2,6</sup> Antonella Lavorato,<sup>2</sup> Cristina G. Di Camillo,<sup>2</sup> Angelo Poliseo,<sup>2</sup> Andrés Baquero,<sup>3</sup> Giorgio Bavestrello,<sup>2</sup> Yuka Irei,<sup>4</sup> and James Davis Reimer<sup>4,5</sup>

**Abstract:** Little is known about density and structure of black coral populations of the continental Pacific coasts of Central and South America. Species diversity and ecology of the antipatharian fauna of Machalilla National Park (Province of Manabí, Ecuador) were surveyed using scuba, and two species, *Myriopathes panamensis* and *Antipathes galapagensis*, were identified. New information on the two species and their associated fauna was obtained through both underwater observations and laboratory analyses. Specific associations with stalked barnacles and parasitic zoanths are described. An underwater visual census indicated that the black coral assemblage had a maximal density between depths of 15 and 30 m. *Myriopathes panamensis* commonly occurred below 20 m depth, and *A. galapagensis* was mainly recorded from deeper than 25 m depth. Surveyed sites were characterized by sparse rocks mixed with sandy patches, and occurrence of black corals was mainly related to availability of rocky substrate. With an average density of 0.5 colonies m<sup>-2</sup>, the shallow black coral community of Machalilla National Park is one of the densest in the world. Data from this study represent a clear baseline for monitoring of population dynamics of benthic organisms in an area subjected to periodic El Niño and La Niña events, which may greatly affect composition and abundance of the marine communities.

BLACK CORALS (Anthozoa, Antipatharia) represent a small order of colonial hexacorallians mainly occurring below 100 m depth in both tropical and subtropical regions (Pax et al. 1987). In some areas, however, abundant and diverse communities have been recorded

within 50 m depth (Tazioli et al. 2007), where antipatharians contribute to the three-dimensionality of the coral reefs and host a rich associated fauna.

In South America, the most studied shallow-water populations of black corals (surveyed within the diving depth range) are confined to the Caribbean Sea (Warner 1981, Sánchez 1999), where 16 species have been recorded (Echeverría 2002, Opresko and Sánchez 2005). The most important Caribbean assemblages have been described between depths of 5 and 40 m in Colombia (Opresko and Sánchez 1997, Sánchez et al. 1998, Sánchez 1999), Trinidad and Jamaica (Warner 1981, 2005, Warner and Opresko 2004), Panama (Guzmán and Guevara 1999, Sánchez and Collin 2003), Cayman, Cuba, and Mexico (Castorena and Metaca 1979, Guitart et al. 1997, Padilla and Lara 2003, respectively).

The existing literature concerning the Pacific coasts of Mexico, Panama, Colombia, and Ecuador reports two black coral species, *Myriopathes panamensis* (Verrill, 1869) and *Antipathes galapagensis* Deichmann, 1941 (Verrill 1869, Opresko 1976, Grigg and

<sup>1</sup>Manuscript accepted 1 June 2011.

<sup>2</sup>Dipartimento di Scienze del Mare, Università Politecnica delle Marche, Via Brecce Bianche, 60131 Ancona, Italy.

<sup>3</sup>Fundacion Equilibrio Azul, Quito, Ecuador ([www.equilibrioazul.org](http://www.equilibrioazul.org)).

<sup>4</sup>Molecular Invertebrate Systematics and Ecology Laboratory, Rising Star Program, Trans-disciplinary Organization for Subtropical Island Studies, University of the Ryukyus, 1 Senbaru, Nishihara, Okinawa 903-0213, Japan.

<sup>5</sup>Marine Biodiversity Research Program, Institute of Biogeosciences, Japan Agency for Marine-Earth Science and Technology (JAMSTEC), 2-15 Natsushima, Yokosuka, Kanagawa 237-0061, Japan.

<sup>6</sup>Corresponding author (e-mail: [m.bo@univpm.it](mailto:m.bo@univpm.it)).

Opresko 1977; Martinez and Robinson 1983, Kerstitch 1989, Opresko 2001, 2003, Hickman 2008). Both species are described as occurring only in limited areas: *M. panamensis* in the shallow waters of Panama Bay (9–17 m depth) (Opresko 1976) and Ecuador, mainly the Galápagos archipelago (up to 50 m depth) (Martinez and Robinson 1983, Romero 1997, Hickman 2008), and *A. galapagensis* was originally reported from deep waters (90 m) off the Galápagos (Deichmann 1941, Opresko 2003). The latter species was subsequently reported from the Gulf of California to Ecuador coasts (3–76 m depth) (Kerstitch 1989, Hickman 2008). More recently, Reimer and Fujii (2010) reported this species from the shallow waters (12–35 m) of Costa Rica at Isla del Coco. Black coral surveys in Ecuador have been focused mainly on the Galápagos Islands, where antipatharians were threatened by the commercial harvest for jewelry during the 1970s (Martinez and Robinson 1983, Romero 1997). Despite the known presence of black corals along the continental coasts (provinces of Guayas, Manabí, and Esmeraldas) (Martinez and Robinson 1983, Romero 1997), no specific studies were directed in those areas of Ecuador.

Machalilla National Park is located in the central-western region of the Ecuadorian coast in the province of Manabí, and it consists of more than 500 km<sup>2</sup> of protected lands and coastlines. The area is known to host a high biodiversity of terrestrial fauna and also provides habitat to important marine species (Guzmán and Cortes 1993, Glynn 2001, Cruz et al. 2003).

The main aim of our study was to estimate the species richness and abundance of black coral populations in the national park. Until now, few data have been available regarding the density, structure, and environmental associations of antipatharian assemblages along the continental Pacific coasts of Central and South America. These data are particularly important because they represent a clear baseline for monitoring the population dynamics of benthic organisms in an area subjected to periodic El Niño and La Niña events, which greatly affect the composition and abundance of marine communities (Arriaga 1999, Glynn

2001, Podestà and Glynn 2001). Our second goal was to study the Ecuadorian black coral forest as a center of marine biodiversity, describing, also from the molecular point of view, the benthic species living as epibionts on the coral colonies. Finally, new morphological details were observed and added to the description of the black coral species present in the area.

## MATERIALS AND METHODS

### *Study Area*

The marine protected area included in Machalilla National Park stretches along the coast in front of the town of Machalilla and also includes several islands of volcanic origin, such as Islotes de Salango and Isla de La Plata (Figure 1).

The shallow-water marine biodiversity of Ecuador includes about 2,000 species (Cruz et al. 2003) and is strongly influenced by several geomorphological, climatic, and oceanographic factors (Glynn 2001). As a result of both ocean hydrodynamics and the orographic conditions, the area is characterized by strong seasonal climatic regimes. The Ecuadorian coasts are lashed by the Equatorial Front, a convergence zone where the warm, low-salinity Panama and Niño water masses moving southward meet the cold, high-salinity Humboldt water mass moving northward. The northward shift of the Equatorial Front by a few degrees of latitude during the summer dry season allows the cold Equatorial Deep Current to rise and hit the coast in the region surrounding Machalilla National Park. The strong seasonal sea-surface temperature (SST) variations (15–25°C) and upwelling phenomena, together with periodic El Niño and La Niña events, greatly affect the composition and abundance of marine communities (Arriaga 1999, Glynn 2001, Podestà and Glynn 2001). Corals in particular may undergo mass mortality or adapt to such changes by exhibiting slower growth rates compared with those of other tropical regions (Martinez and Robinson 1983).

In the studied area, small coral gardens composed mainly of antipatharians, sclerac-

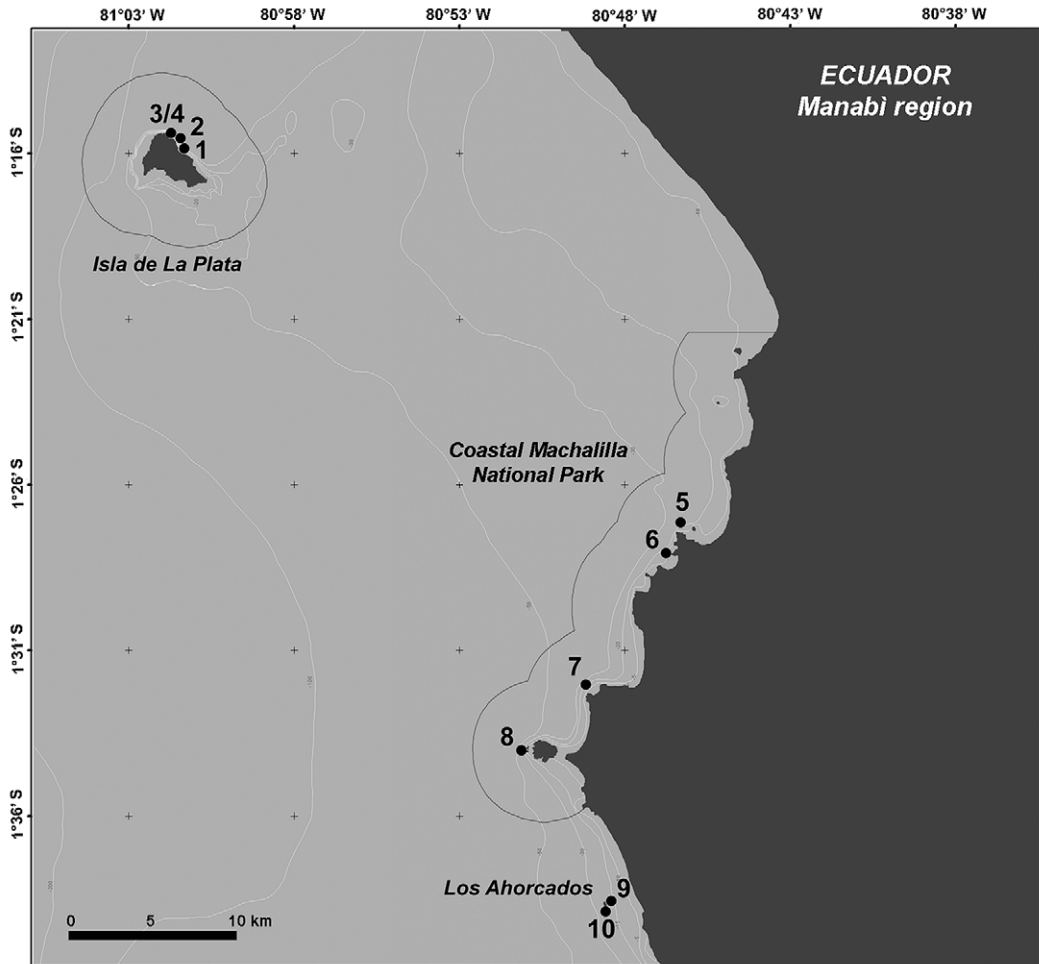


FIGURE 1. Sampling sites. Map of the boundaries of Machalilla National Park and location of sampling sites: 1, Bahía Drake; 2, Punta del Faro; 3, Roca Honda 1; 4, Roca Honda 2; 5, Machalilla; 6, Los Frailes; 7, Punta Mala; 8, Islotes de Salango; 9, Los Ahorcados 1; 10, Los Ahorcados 2.

tinians, and gorgonians generally grow on gently inclined rocky walls or sparse rocks laid on sandy bottoms. The bathymetric extension of these coral assemblages is generally limited to depths shallower than 40 m, below which hard substrate becomes limited because bottoms are mostly sandy.

#### *Sampling Sites*

Black corals were studied between July and October 2009, by scuba dives conducted at 10

sites: four sites located around Isla de la Plata and six situated along the coast of Machalilla National Park (Figure 1).

Isla de la Plata is a small island (about 14 km<sup>2</sup>) 32 km from the continental coast. Four sites were investigated on the eastern side of the island. Bahía Drake is a small bay characterized by very slow currents and a sandy bottom with scattered large rocks between 20 and 25 m depth. Punta del Faro is characterized by a small reef of hard corals between 4 and 8 m depth followed by a rocky slope with

moderate currents that is composed of sparse rocks mixed with sandy patches until a depth of 35 m; below 45 m the bottom turns into a sandy plain. The first 10 m of both Roca Honda 1 and 2 are entirely rocky, and then sand stretches down to 20 m, subsequently followed by large scattered rocks to a depth of 30 m; both of these latter two sites are subjected to strong currents.

The remaining six sites were selected in the area representing the continental part of Machalilla Park, comprising both coastal and insular zones (Figure 1). The northernmost site is Machalilla, located off the coast of the village of Machalilla; the rocky bottom, with moderate currents, is colonized in the first 10 m by a dense meadow of gorgonians (*Muricea* spp.), which mix with black corals up to a depth of 17 m, below which the bottom turns into a wide sandy plain. Los Frailes is situated in front of Los Frailes beach: scattered rocks and sandy patches characterize the bottom down to a depth of 17 m where a sandy plain starts; currents at this site are moderate. The bottom of Punta Mala, with strong currents, is characterized until 22 m by rocks and sandy patches ending with a sandy plain. The bottom of the Islotes de Salango site is characterized by weak currents and contains scattered rocks from 11 to 26 m depth, below which is a gently inclined sandy area. Los Ahorcados 1 and 2 are located, respectively, on the eastern and western sides of the islands of Los Ahorcados. The rocky cliffs, characterized by weak currents, stretch from 3 to 23 m depth, below which they give way to sandy areas occupied by a dense meadow of gorgonians.

#### *Taxonomic Analysis of Black Corals*

The taxonomic identity of black corals and their associated fauna was analyzed using morphological characters and was conducted on 24 black coral colonies. Colonies were photographed underwater, and the height, width, and basal diameter of each colony were measured using a tape and a caliper. Portions of colonies were cut and each sample was then fixed partly in 4% formaldehyde for analyses of polyps, cnidomes, and epibionts; the remaining material was kept dry to study

the patterns of ramification, spines, and epibionts.

The cnidome of each specimen (considered in different portions: mouth, tentacles, and interpolypar coenenchyme) was studied using an optical microscope by squeezing the tissues onto a slide. For scanning electron microscope (SEM) analysis, fragments of branches were washed with distilled water, dehydrated in a graded ethanol series, and dried in a critical point dryer. Finally, they were coated with gold-palladium in an evaporator (Balzer Union) and examined with an SEM (Philips XL20).

#### *Analysis of Epibiotic Zoanthids*

To ascertain the taxonomic identification of the zoanthids observed on the black coral colonies, seven samples were collected and preserved in 70% ethanol for morphological and phylogenetic analyses. Three samples corresponded to a red zoanthid phenotype growing on *Antipathes galapagensis*, one sample corresponded to a cream phenotype growing on *Myriopathes panamensis*, and three samples were of both zoanthid phenotypes growing on the same colonies of *M. panamensis*. In vivo aspect was documented with underwater photographs, and measurements of the living polyps were determined using a caliper. Height, diameter, and number of tentacles were determined using a stereomicroscope.

Phylogenetic analyses were carried out on four zoanthid samples, two red phenotypes (sample numbers DNA1, DNA7) and two cream phenotypes (DNA3, DNA4). DNA extraction was made as in Reimer et al. (2008a) using a blood and tissue extraction kit (Dneasy, Qiagen, Santa Clarita, California) following the manufacturer's protocol. Mitochondrial 16S ribosomal DNA (mt 16S rDNA), cytochrome oxidase subunit I (COI), and the internal transcribed spacer of nuclear ribosomal DNA (ITS-rDNA) were amplified using primers and protocols from previous zoanthid-focused research (Reimer et al. 2004, 2007, Sinniger et al. 2005). Amplified products were visualized by 1.5% agarose gel electrophoresis and sequenced at Macro-Gen Japan (Tokyo, Japan). New zoanthid se-

quences obtained in this study were deposited in GenBank (accession numbers JN582014–JN582023) and compared for similarity with previous zoanthid sequences both by National Center for Biotechnology Information's Basic Local Alignment Search Tool (NCBI BLAST [Altschul et al. 1990]) and by manual visual comparison using the software Se-Al v2.0a11 (University of Edinburgh). Sequences were compared only by similarity, and no further phylogenetic analyses were performed, because the utilization of mt 16S rDNA and COI sequences in tandem (along with ITS-rDNA) has been shown to be generally accurate for barcoding of zoanthids to the species level (Sinniger et al. 2008).

#### *Coral Distribution and Epibiosis*

The bathymetric and geographic distributions (colonies  $m^{-2} \pm SE$  and percentage abundance) of the black corals were studied through visual census using a modified belt transect method (Bianchi et al. 2003), which has previously been employed to investigate antipatharian communities in Indonesia (Tazioli et al. 2007). Visual census was performed by two divers swimming along a linear 50 m horizontal transect (indicated by a line) for each considered depth range, for a maximum of eight ranges, depending on the site (5, 10, 15, 20, 25, 30, 35, 40 m). The divers counted the number of colonies visible in a distinct 1 m wide visual field on each side of the line (for a total investigated surface of 100  $m^2$  at each depth range).

Similarly, to study the level of epibiosis of the zoanthids and to obtain an indicative percentage data of colonized coral colonies, two transects (each 100 m long and 2.5 m wide) were examined by two separate divers at a depth of about 20 m at the Punta Mala site (where both coral species are well represented). The divers counted the total number of coral colonies and noted the presence/absence of zoanthids on each colony. For each colonized colony, the following data were gathered: antipatharian species, zoanthid species, and an estimate of the percentage surface of the antipatharian colony covered by zoanthids (25%, 50%, 75%, 100%).

## RESULTS

### *Species Description*

Of the 24 collected specimens, six belonged to *Antipathes galapagensis* (family Antipathidae) and 18 to *Myriopathes panamensis* (family Myriopathidae).

The morphology of the *Antipathes galapagensis* colonies from Machalilla National Park is in accordance with the descriptions previously reported in literature (Deichmann 1941, Kerstitch 1989, Opresko 2003, 2009, Hickman 2008). Colonies show an arborescent morphology characterized by numerous, dense ramifications ending, in the most peripheral zones of the corallum, with short rigid branchlets inclined upward (Figure 2A–F). Adult colonies may reach large dimensions, as indicated by the underwater measurements of 17 specimens: a height of 10–78 cm, width between 15 and 95 cm, and basal stem diameter between 0.8 and 3.2 cm. Larger colonies have been reported previously, up to 1 m high (Hickman 2008) and 2 m in diameter (Kerstitch 1989). Color of the polyps varies between different tonalities of yellow (Figure 2). Spines on major branches are triangular-conical with a rounded and papillose apex; on pseudopinnules they are more triangular with a pointed, tuberculated tip (Figure 2G–J). Polyps are radial with cylindrical tentacles, irregularly arranged in one line (side by side) on pseudopinnules but sometimes occur on two opposite lines (generally on major branches) (Figure 2K–M). Cnidome consists of basitrich isorhizae (19.0–21.7  $\times$  3.0–4.0  $\mu m$ ) (Figure 2N), microbasic mastigophores (18.6–24.5  $\times$  4.0–5.0  $\mu m$ ) (Figure 2O), and spirocysts (12.0–16.6  $\times$  3.0  $\mu m$ ) (Figure 2P).

Similarly, the morphology of the specimens assigned to *Myriopathes panamensis* is generally in accordance with what has previously been reported in literature (Verrill 1869, Brook 1889, Opresko 1976, 2001, Hickman 2008). The examined colonies show a flabellate, ramified, and pinnulated morphology (Figure 3A–F). They reach notable dimensions, with heights between 22 and 150 cm, widths between 28 and 340 cm, and basal diameters between 0.8 and 5.9 cm. Colonies

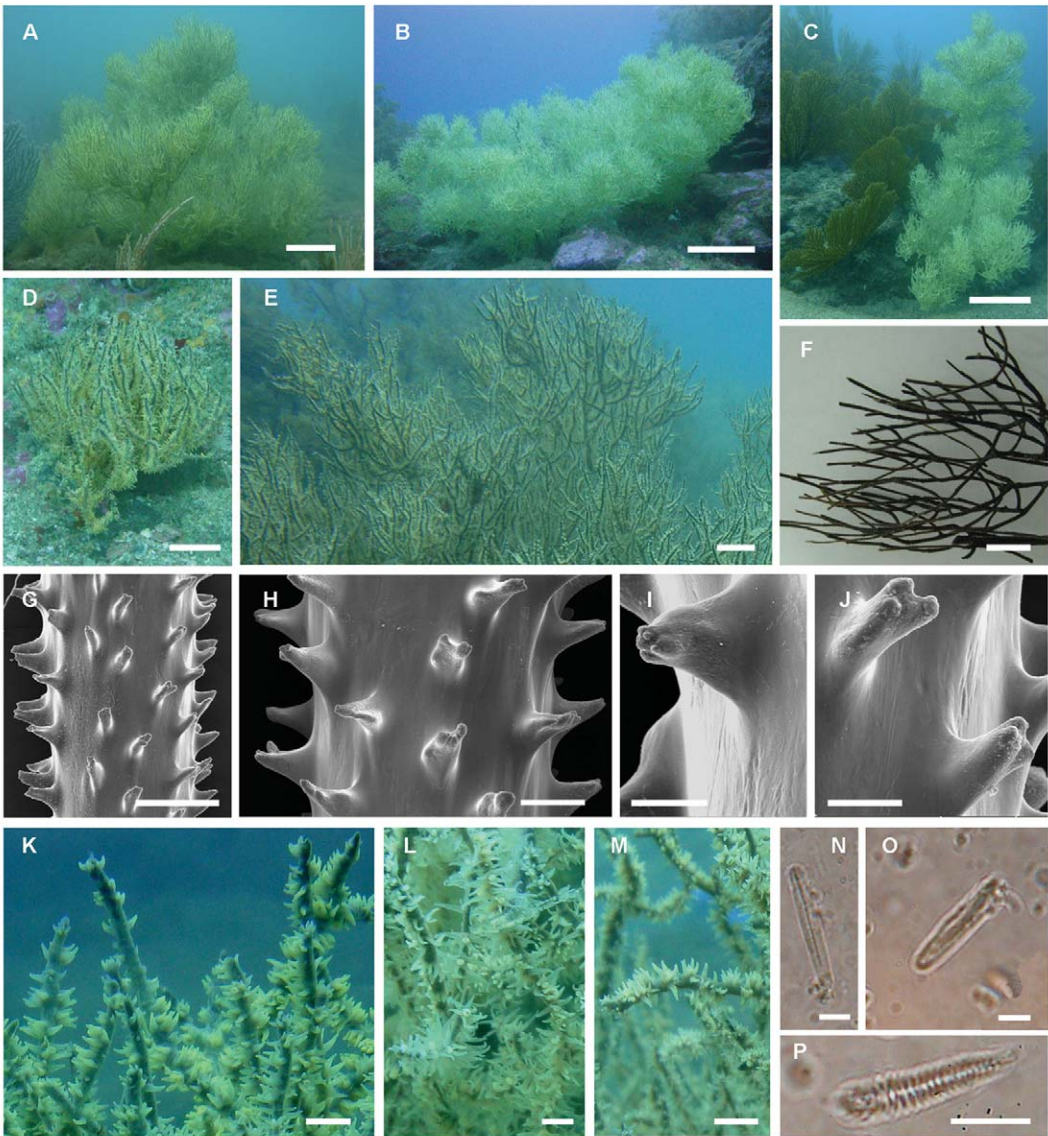


FIGURE 2. *Antipathes galapagensis*. A–C, Underwater photographs of *A. galapagensis* colonies; D, juvenile colony; E–F, pattern of pinnulation of the colonies; G–J, arrangement of the triangular, tuberculated spines on ramifications and close-up views of the spines' ornamentation; K–L, in vivo pictures of expanded polyps showing irregular arrangement of zooids on both one and two opposite rows; M, polyps with sagittal expanded tentacles; N–P, cnidome composed of three typologies: isorhiza (N), mastigophore (O), spirocyst (P). Scale bars: A–C, 20 cm; D, E, 5 cm; F, 1 cm; G, 0.5 mm; H, 0.2 mm; I, J, 0.1 mm; K–M, 2 mm; N–P, 5  $\mu$ m.

tend to grow in width, getting thicker because of the successive overlapping of ramified fans, which arise from a short basal stem (Figure 3A–B). Colonies show a great variability of

colors: the most common type is brown (dark or light), but there are also orange, pink, green, or gray phenotypes (Figure 3A–C). Spines on branches are cylindrical, pointed,

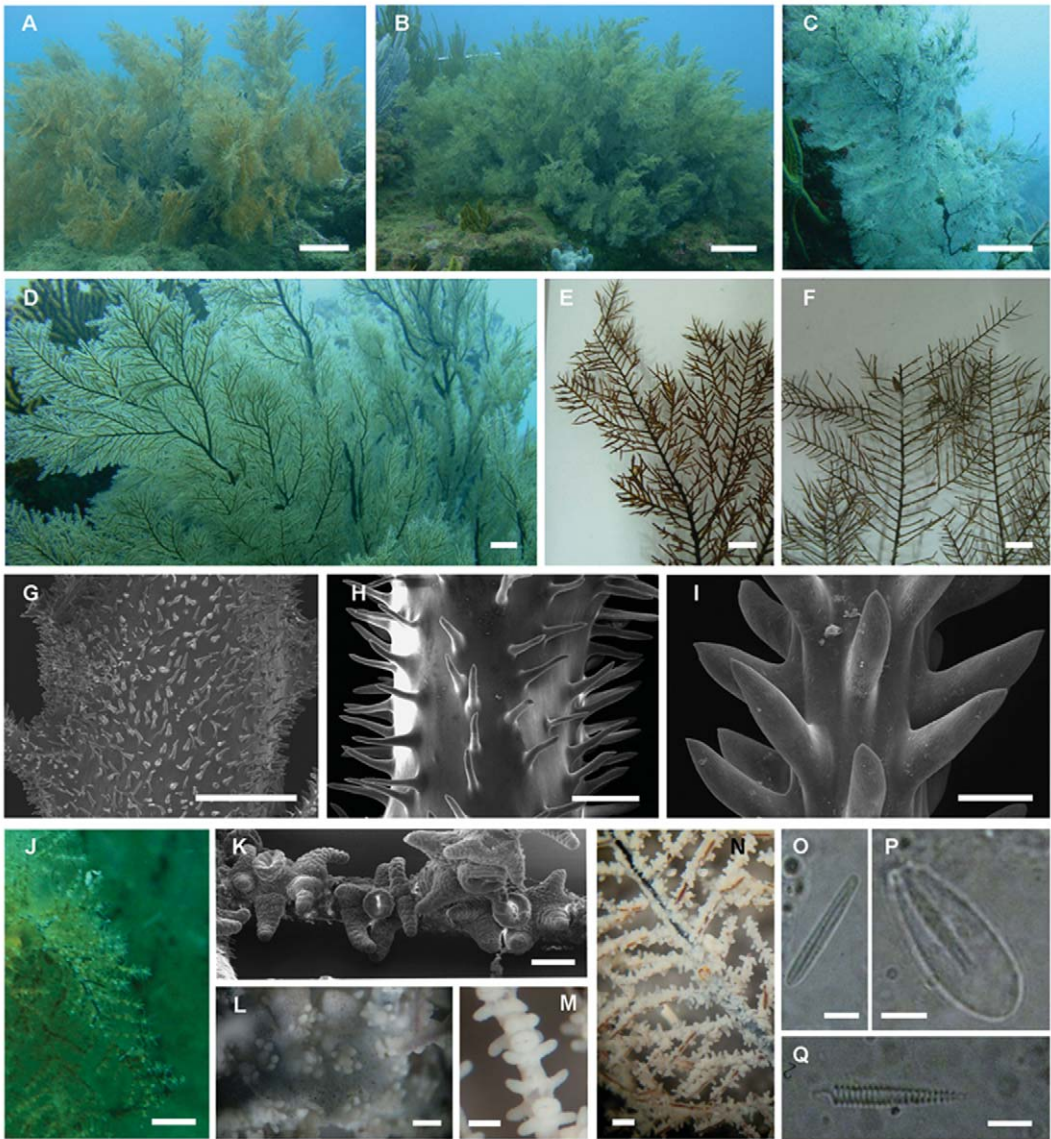


FIGURE 3. *Myriopathes panamensis*. A–B, Underwater photographs of *Myriopathes panamensis* colonies; C, underwater photograph of gray, single-fan variation of a *M. panamensis* colony; D, pattern of ramification; E–F, different patterns of pinnulation, with pinnules respectively more or less densely arranged; G–H, arrangement of cylindrical spines on major ramifications; I, arrangement of horn-shaped spines of a pinnule; J, in vivo picture of expanded polyps; K, polyps with elevated oral cones and sagittal tentacles inserted at a lower level; L, radial polyps irregularly distributed on a branch; M–N, transversally elongated polyps arranged in one row on pinnules. Cnidome composed of three typologies: isorhiza (O), mastigophore (P), spirocyst (Q). Scale bars: A–C, 20 cm; D–F, 1 cm; J, 5 mm; G, L, N, 1 mm; K, M, 500  $\mu$ m; H, 200  $\mu$ m; I, 100  $\mu$ m; O–Q, 5  $\mu$ m.



with a narrow base and a slightly papillose distal surface (Figure 3G–H). On the major branches, spines are distributed irregularly. Spines on pinnules present a typical horn-shaped morphology (not laterally compressed), with a convex proximal side (Figure 3I). Polyps are elongated in the transversal direction with cylindrical tentacles (Figure 3J–N). They are arranged in one row on the same side of the colony, but on the stem and principal branches, zooids, smaller or incomplete, are arranged irregularly (Figure 3L–N). The cnidome of this species is made up of basitrich isorhizae ( $17.6\text{--}23.0 \times 3.0\text{--}3.5 \mu\text{m}$ ) (Figure 3O), microbasic mastigophores ( $16.6\text{--}20.9 \times 6.0\text{--}7.0 \mu\text{m}$ ) (Figure 3P), and spirocysts ( $12.0\text{--}18.0 \times 3.0 \mu\text{m}$ ) (Figure 3Q).

#### *Associated Fauna*

Dead portions of all coral colonies were frequently encrusted by algae, ascidians, sponges, barnacles, and bryozoans, and occasionally bivalves were found hanging on the branches of the colonies with their shells covered by the coral skeleton. The most representative organisms recorded as epibionts on the living portions of the corals were stalked barnacles (Figure 4) and zoanthids (Figure 5).

*Myriopathes panamensis* hosted numerous barnacles belonging to the genus *Oxynapsis*, commonly described in association with antipatharian colonies by previous authors (Totton 1923, Tazioli et al. 2007, Molodtsova and Poltarukha 2008) (Figure 4A). Individuals were 0.7 cm long, with a 0.4 cm long capitulum and a 0.3 cm long peduncle. They grew mainly on stems and major branches of the colonies with an average density of  $2.3 \pm 0.3$  specimens  $\text{cm}^{-1}$  (range between one and five individuals  $\text{cm}^{-1}$ ) (Figure 4B). Juvenile barnacles were occasionally observed, near the adult specimens (Figure 4C). These epibionts anchored on the coral skeleton, which covered them with a thin sheet bearing spines and coenenchyme, from which polyps emerged (Figure 4D–F). The coral spines covering the barnacles showed a different morphology with respect to the typical one. They were small (0.05 mm high), tuberculated, and

densely arranged near the aperture of the capitulum, where cirri emerged (Figure 4G–H). On the remaining part of the valves, spines were more sparsely and irregularly distributed (Figure 4I). The peduncle of the barnacle, finely corrugated, was covered by long (0.13 mm), tuberculated, densely packed spines (Figure 4J–K). The peduncle emerged from a flared opening of the tubular sheath formed on the axis of the coral branch (Figure 4J). At times this cover caused adjacent ramifications to coalesce.

The phylogenetic and morphological analyses identified two species of parasitic zoanthids: *Antipathozoanthus* cf. *bickmani* Reimer & Fujii, 2010, and *Terrazoanthus onoi* Reimer & Fujii, 2010 (Figure 5). Specimens of *A.* cf. *bickmani* had small white-yellow polyps, uniformly arranged along the ramifications (4–6 polyps  $\text{cm}^{-1}$ ), 1.5–3 mm high from the coenenchyme, with an oral disk 1.5–2.5 mm in diameter, and 27–28 white tentacles (1.8–2.5 mm long when expanded) emerging from a light yellow column entrapping sand inclusions (Figure 5A–B). The large, crowded, bright red to red-brown polyps of *T. onoi* (3–4 polyps  $\text{cm}^{-1}$ ) were 1.5–7 mm high from the coenenchyme, with an oral disk 1.5–4 mm in diameter, and 32–33 red tentacles (2–3.5 mm long when expanded) emerging from a light brown column with densely packed sand inclusions (Figure 5C–D). The polyps of both species were often covered by a thin red film of algae (Figure 5B, D).

Acquired novel DNA sequences ( $n = 2$  each) of mt 16S rDNA, COI, and ITS-rDNA for the red-phenotype zoanthids all matched 100% with previously reported sequences for *Terrazoanthus onoi* from the Galápagos Islands (Reimer et al. 2008b, Reimer and Fujii 2010). mt 16S rDNA and COI sequences ( $n = 2$  each) for the cream phenotypes matched 100% with previously reported specimens of *Antipathozoanthus* from the Galápagos (*A. bickmani* [Reimer et al. 2008b, Reimer and Fujii 2010]) and Cape Verde (*A. macaronensis*). Polymerase chain reactions (PCR) for ITS-rDNA sequences for these specimens were unsuccessful despite repeated attempts.

During the visual census, 117 black coral colonies were counted, 44 of which hosted

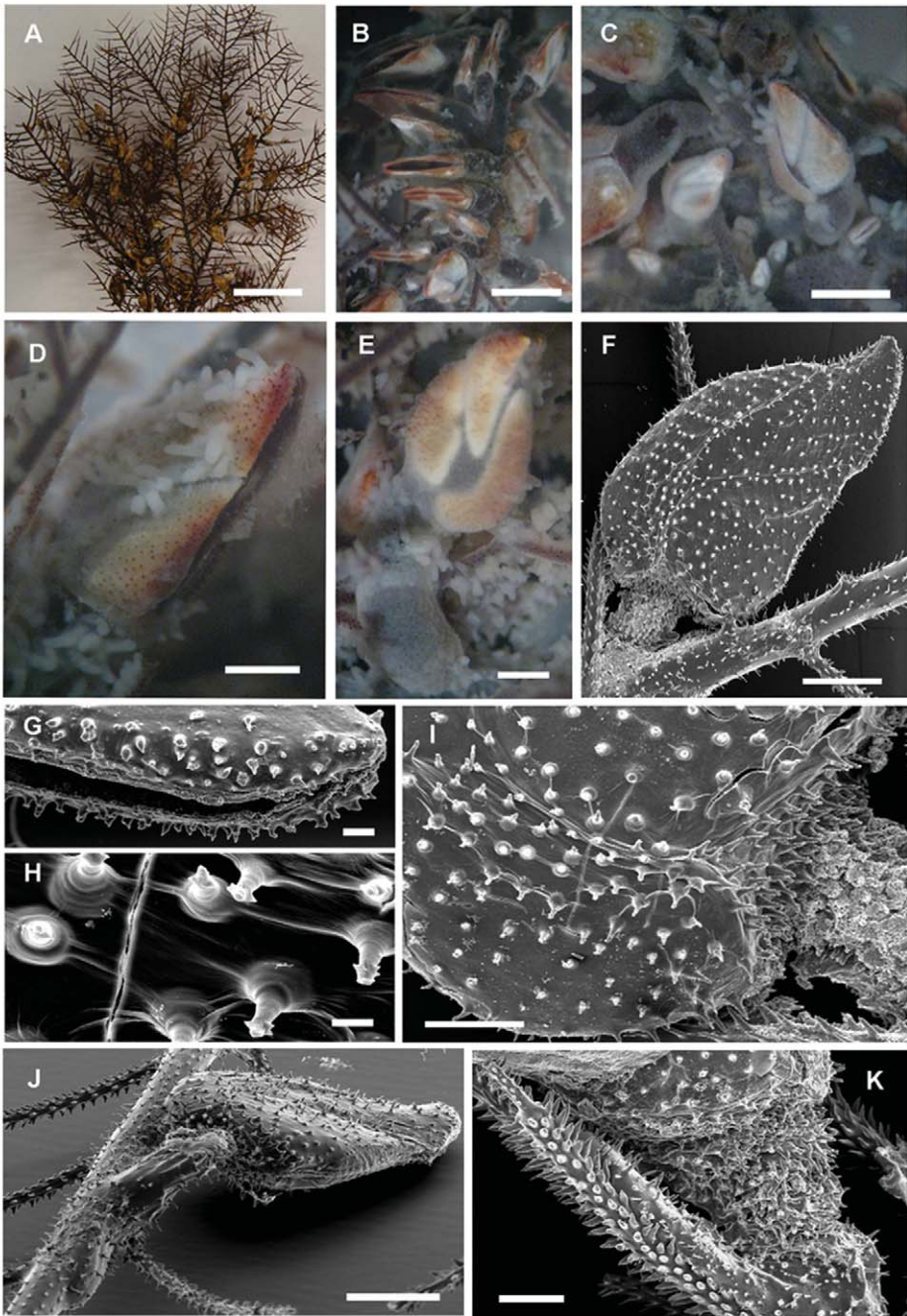


FIGURE 4. Associated stalked barnacles. *A*, Dry sample of *Myriopathes panamensis* with densely crowded associated barnacles; *B*, arrangement of stalked barnacles on a ramification; *C*, juveniles on the coral; *D*, black coral polyps on the cirriped's valves; *E*, barnacle anchored on the coral ramification; *F*, SEM image of the coral skeletal tissue covering the stalked barnacle; *G*, spines along the aperture of the barnacle; *H*, *I*, tuberculated spines on the capitulum surface; *J*, skeletal gall near the anchoring area of the barnacle; *K*, spines on the peduncle. Scale bars: *A*, 2 cm; *B*, *C*, 0.5 cm; *D*–*F*, *J*, 1 mm; *I*, *K*, 500  $\mu$ m; *G*, 100  $\mu$ m; *H*, 50  $\mu$ m.

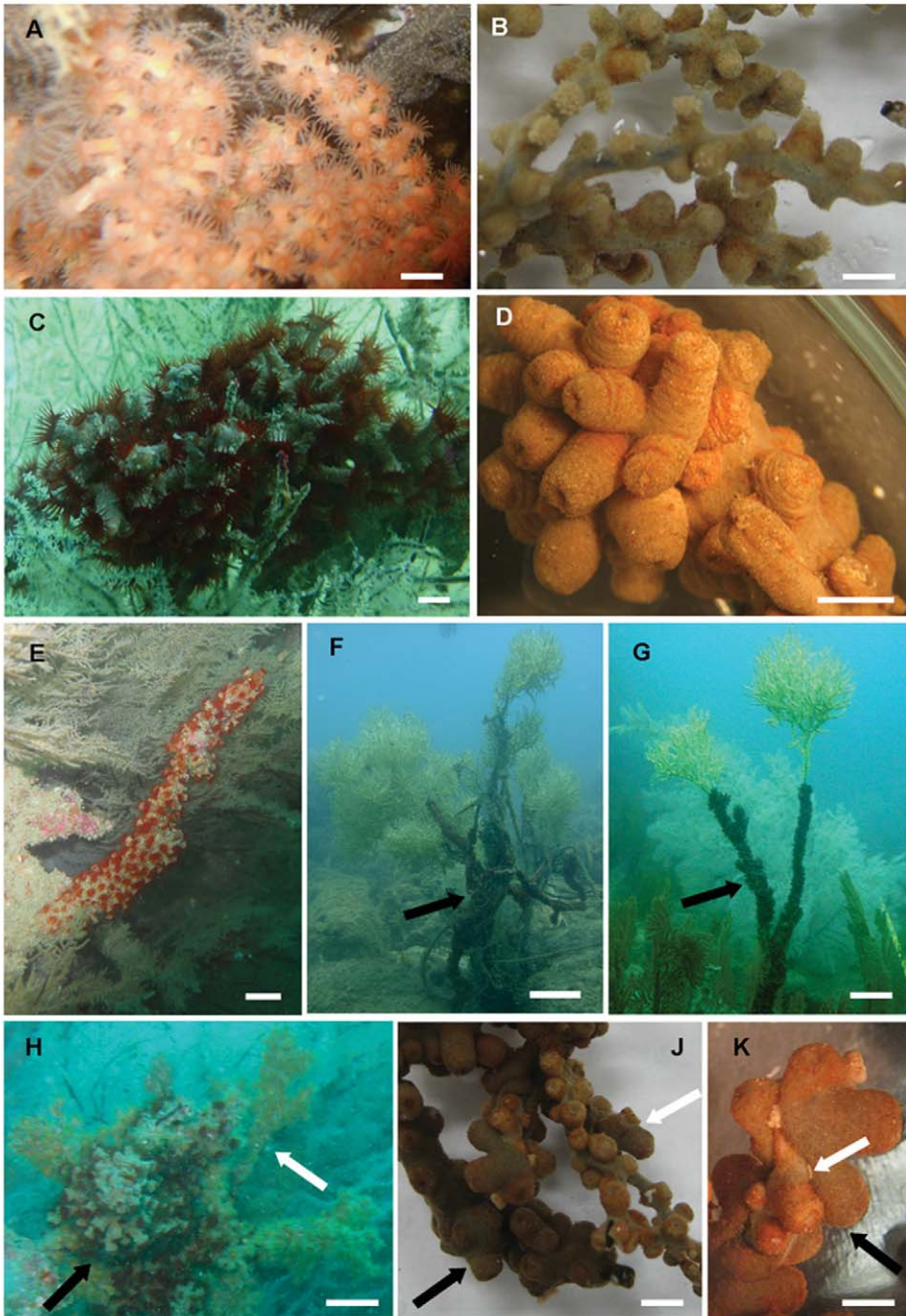


FIGURE 5. Associated zoanthids. *A*, Underwater photograph of *Antipathozoanthus* cf. *bickmani* on the pinnules of *Myriopathes panamensis*; *B*, close-up view of the polyps of *A.* cf. *bickmani*; *C*, underwater photograph of *Terrazoanthus onoi* on the pseudopinnules of *Antipathes galapagensis*; *D*, close-up view of the polyps of *T. onoi*; *E*, *T. onoi* completely covering a lateral branch of *M. panamensis*; *F*, *T. onoi* covering the stem and major branches of *A. galapagensis*; *G*, free distal pseudopinnules of an *A. galapagensis* colony with parasitic *T. onoi*; *H*, colony of *M. panamensis* covered by both zoanthid species: *T. onoi* on the major branches and *A.* cf. *bickmani* on the lateral branches and pinnules; *J–K*, comixture of the two zoanthid species along a branchlet of *M. panamensis*. Black arrow, *T. onoi*; white arrow, *A.* cf. *bickmani*. Scale bars: *F–G*, 10 cm; *E*, 2 cm; *H*, 1 cm; *A–D*, *J–K*, 5 mm.

parasites (38% of the total colonies). Of the two black coral species, *M. panamensis* was most affected (51% of the counted colonies) (Figure 5E), while *A. galapagensis* was less colonized (30% of the counted colonies) (Figure 5F–G). The majority of the colonized colonies were covered for up to 50% of their surface (34% and 39% of colonized colonies, respectively, for 25% and 50% coverage of the colony) (Figure 5E); 20% of the colonized colonies were covered for up to 75% of their surface (Figure 5F), and only a small proportion (7%) was completely covered. At all sites, most covered colonies lacked numerous thinner ramifications, with the zoanthids crowding the stem and major branches, and only apical portions of pseudopinnules were parasite-free (Figure 5G).

Generally only one species of zoanthid was recorded on each black coral colony, but a few *M. panamensis* specimens hosted both zoanthid species (Figure 5H–K). In these cases, zoanthids clearly occupied different regions

of the colony, with *T. onoi* on the stem and major branches and *A. cf. bickmani* on the thinner branchlets and pinnules (Figure 5J–K). Occasionally the two zoanthid species were observed mixed in the areas of contact (Figure 5K). The observed colonies of *A. galapagensis* hosted only the red polyps of *T. onoi*. This species was also occasionally seen on various gorgonian species (Muriceidae) present in the area.

#### Black Corals Distribution

A total of 4,294 colonies was counted along the 20 transects (two for each site). The average density of the black corals in the Machalilla area was  $0.5 \pm 0.05$  colonies  $m^{-2}$ . The highest values were recorded for insular sites in the area of Isla de la Plata (Punta del Faro and Bahia Drake, with average densities of  $0.9 \pm 0.1$  colonies  $m^{-2}$  and  $1.0 \pm 0.5$  colonies  $m^{-2}$ , respectively) and at Islotes de Salango ( $0.9 \pm 0.3$  colonies  $m^{-2}$ ) (Figure 6). The

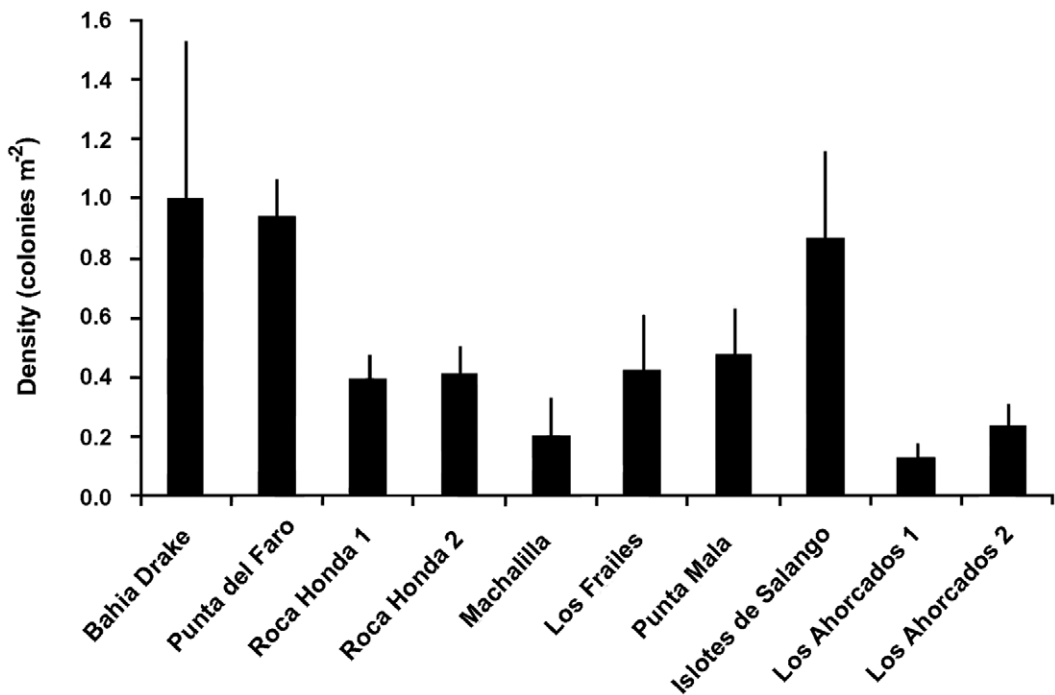


FIGURE 6. Total average density (colonies  $m^{-2} \pm SE$ ) in the 10 explored sites of Machalilla National Park.

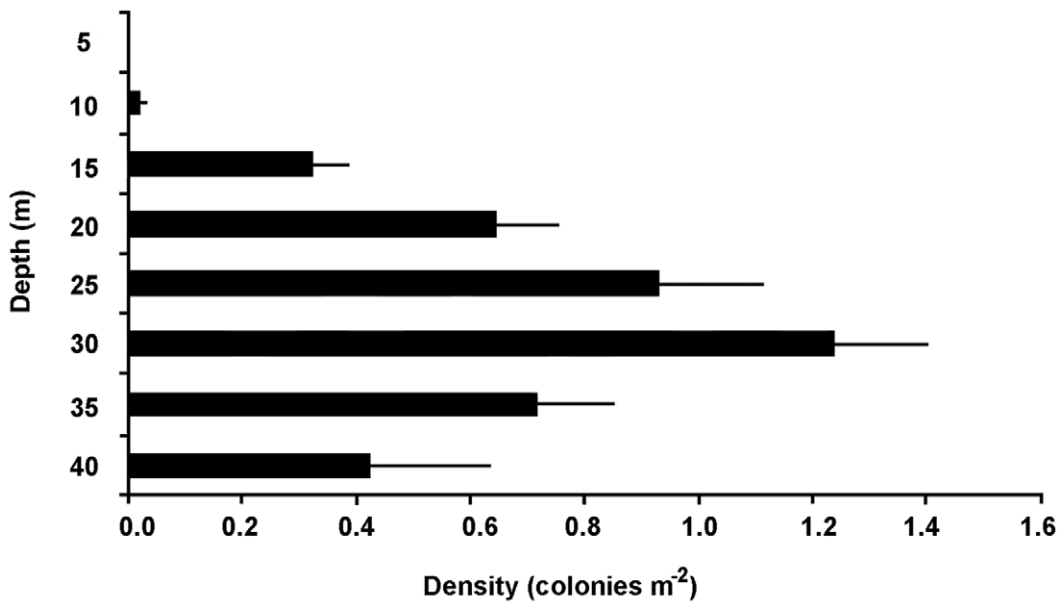


FIGURE 7. Bathymetric distribution of the total average density (colonies  $m^{-2} \pm SE$ ) of black corals in Machalilla National Park.

localities showing lower abundances were the coastal site of Machalilla ( $0.2 \pm 0.1$  colonies  $m^{-2}$ ) and the insular sites close to the coast: Los Ahorcados 1 with an average density of  $0.1 \pm 0.04$  colonies  $m^{-2}$ , and Los Ahorcados 2 ( $0.2 \pm 0.07$  colonies  $m^{-2}$ ).

*Antipathes galapagensis* was the species with the highest density ( $3.3 \pm 0.4$  colonies  $m^{-2}$ , with a maximum of 185 colonies in a single transect), and *Myriopathes panamensis* had a density of  $1.5 \pm 0.4$  colonies  $m^{-2}$ , with a maximum of 138 colonies in a single transect. Consistent with this, 62% of the total investigated colonies belong to *A. galapagensis* and 38% to *M. panamensis*.

The total average density distribution of antipatharians at different depths in Machalilla National Park showed a progressive increase from 5 to 30 m depth range ( $1.2 \pm 0.2$  colonies  $m^{-2}$ ) when the substrate was generally rocky (Figure 7).

The bathymetric trend of the black coral density varied as a function of the availability of rocky substrate, but similar patterns between sites were observed. In the area of Isla de La Plata different distributions were ob-

served (Figure 8A–D): at Bahia Drake the community was dominated by *A. galapagensis* (maximum average density of  $3.3 \pm 0.4$  colonies  $m^{-2}$  at 25 m depth) and *M. panamensis* was almost absent (Figure 8A). At Punta del Faro (Figure 8B) both species were present, with *M. panamensis* more common in shallow transects ( $1.5 \pm 0.4$  colonies  $m^{-2}$  at 20 m depth) and *A. galapagensis* more common in deep waters ( $1.8 \pm 0.07$  colonies  $m^{-2}$  at 40 m depth). Both sites of Roca Honda (Figure 8C–D) showed similar results.

In the coastal area of the park, the distribution pattern described for Isla de La Plata, characterized by a higher abundance of *A. galapagensis* and by a preference of this species for the deeper regions, was repeated for all sites (Figure 8E–J).

The height and width ratio of the studied specimens gives some indications about the growth strategy of these species. *Myriopathes panamensis* has a typical flabellate colony with maximum expansion in width (average ratio height/width = 0.6). There was no evident difference with respect to the collection site; however, considering width, the colonies of

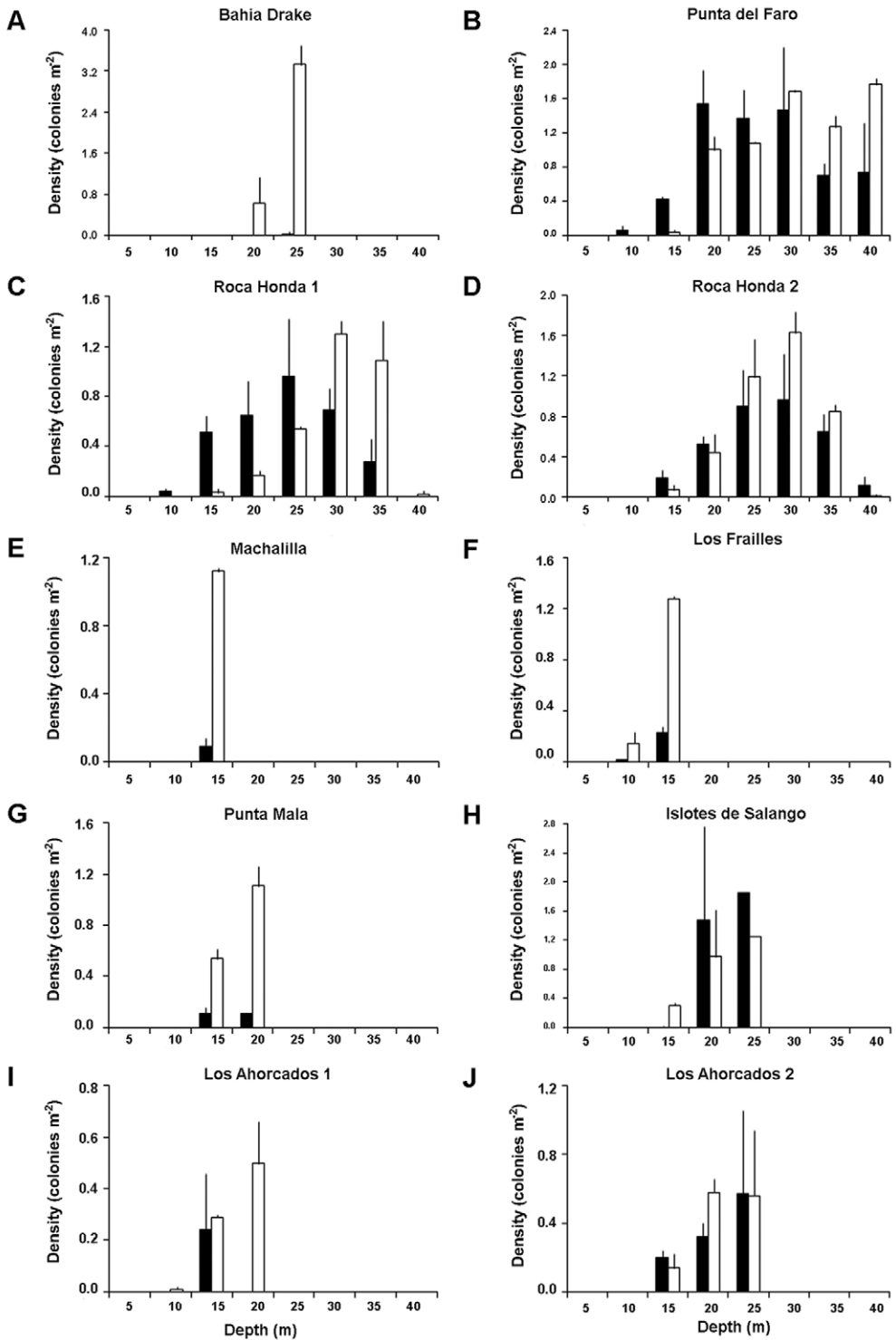


FIGURE 8. Bathymetric distribution of the species' average densities (colonies m<sup>-2</sup> ± SE) in the explored sites: *A*, Bahia Drake; *B*, Punta del Faro; *C*, Roca Honda 1; *D*, Roca Honda 2; *E*, Machalilla; *F*, Los Frailes; *G*, Punta Mala; *H*, Islotes de Salango; *I*, Los Ahorcados 1; *J*, Los Ahorcados 2. *Myriopathes panamensis*, black; *Antipathes galapagensis*, white.

Los Frailes, Punta Mala, Machalilla, and Punta Faro (characterized by stronger currents) were larger. As for *A. galapagensis*, the height-to-width ratio was 0.8, indicating that the colonies tend to have a more arborescent morphology, with no evident difference in width and height. *Antipathes galapagensis* colonies were also larger at sites with stronger currents (Machalilla and Los Frailes).

#### DISCUSSION

This work characterized the taxonomy and ecology of the black coral fauna found in Machalilla National Park (Ecuador), considered a high biodiversity area of the Ecuadorian coast (Cruz et al. 2003). The species described in this study had previously been recorded from Ecuador (mainly the Galápagos Islands), but we have added a description of morphological details of living colonies, as well as new information on their distribution and associated fauna, which seems typical of the continental assemblages.

Antipatharians hold an important ecological role in benthic communities, in particular due to their branched morphology, which can host a rich, sometimes species-specific, associated fauna (Totton 1923, Wirtz and d'Udekem-d'Acoz 2001, Love et al. 2007, Tazioli et al. 2007). For example, for the Ecuadorian black corals, Kerstitch (1989) reported some mimic vagile fauna living on the branches of *A. galapagensis*, such as the shrimp *Periclimenes infraspinis* (Rathbun, 1902) and the fish *Oxyrrhites typus* (Bleeker, 1857). The recorded stalked barnacles of the genus *Oxynopsis*, epibionts of *Myriopathes panamensis*, exploit the net of branches as a settling space. This genus is described as exclusively associated with antipatharians, with 14 species found on 11 black coral genera (Molodtsova and Poltarukha 2008). Our study confirms that these organisms prefer densely reticulated colonies (Molodtsova and Poltarukha 2008) like those of *M. panamensis*, where the filtering efficiency is higher.

The morphological modifications of the black coral's spines growing on the stalked barnacles have already been documented in the literature (Molodtsova and Poltarukha

2008). In our study, the barnacle's settling induced a skeletal reaction resulting in an outgrowth of skeletal tissue with modified spines. The different morphology of the spines on the carbonatic plates of the barnacle may depend on some kind of chemical reaction caused by the crustaceans (Molodtsova and Poltarukha 2008); however, explanations concerning the settling, growth, and spine modification of these organisms are still lacking.

Parasitic zoanthids are known to occur on black corals, such as those of the recently described genus *Antipathozoanthus* (family Parazoanthidae) (Sinniger et al. 2009), which is currently limited to species associated with antipatharians, including *A. macaronesicus* (Ocaña & Brito, 2003) living on *Tanacetipathes cavernicola* Opresko, 2001. The parasitic zoanthids recorded on Ecuadorian black corals belong to two species, *Antipathozoanthus* cf. *bickmani* and *Terrazoanthus onoi*, and were first described from the Galápagos Islands (Reimer and Fujii 2010).

Some morphologic and ecologic differences were observed for the zoanthids with respect to their original descriptions. The morphometric analysis of our cream phenotype did not completely match with what has previously been reported for *A. bickmani*. Moreover, *A. galapagensis* has been considered to be the specific host of *A. bickmani* (Hickman 2008, Reimer et al. 2008b, Sinniger et al. 2009, Reimer and Fujii 2010), but in the study reported here *A. cf. bickmani* was always found associated with *M. panamensis*. Thus, due to morphological differences in tentacle number, plus preference for a different substrate, the identity of the cream phenotype specimens as truly *A. bickmani* or instead a closely related but different species remains unknown. Furthermore, both *A. bickmani* from the Galápagos and *A. macaronesicus* from the Atlantic have identical mt 16S rDNA and COI sequences, suggesting that DNA barcoding using these DNA markers may not always be accurate for *Antipathozoanthus* spp.

Both black coral species were instead covered by *T. onoi*, a zoanthid known to occur from the Gulf of California to the Galápagos (3–76 m depth) but described as usually settling on abiotic substrates (Kerstitch 1989,

Hickman 2008, Reimer and Fujii 2010) and, occasionally, encrusting gorgonian stalks (Kerstitch 1989). In our study area, however, it was never recorded on abiotic substrate, although we did not specifically search in areas without antipatharians. However, all three DNA markers, including the faster-evolving ITS-rDNA marker, as well as morphological data for red-phenotype zoanths fit with *T. onoi*, and thus we are confident that red-phenotype specimens in this study belong to this species.

The parasitic association between zoanths and black corals was the most common symbiotic relationship in the study area and apparently greatly affects the survival of antipatharians. A large proportion of antipatharian colonies hosted zoanths (38%), and approximately 7% were completely covered by their polyps. It seems that there was a slight preference for *M. panamensis* for both zoanthid species, but *A. galapagensis* was more often completely covered. The thick pseudopinnules of *A. galapagensis* may enhance the expansion of the large polyps of *T. onoi* up to the most peripheral region of the colony.

The epibiosis of *T. onoi* on black corals generally starts from the stem of the colony and progressively covers the branches until the complete death of the coral. The colonies with the skeleton greatly covered by *T. onoi* showed a more simple ramification pattern due to the breakdown of small branches where the large zoanthid polyps were not able to expand. *Antipathozoanthus* cf. *hickmani*, perhaps because of its smaller polyps, is more adapted to expand on the smaller branches and pinnules of *M. panamensis*. A similar differentiation in the growth strategy by two zoanths on a host has recently been described in Indonesia for two *Hydrozoanthus* species growing on the hydroid *Dentitheca habereri* (Stechow, 1909) (Di Camillo et al. 2010), suggesting that polyp size may be a constraining factor for zoanthid expansion.

Due to their rigid arborescent structure black corals are prone to epibiosis from encrusting filter feeders. In Hawai'i more than 80% of the large bushy colonies of *Antipathes griggi* Opresko, 2009, and *A. grandis* Verrill, 1928, were described as affected by the epibi-

osis of the alien octocoral *Carijoa riisei* (Duchassaing & Michelotti, 1860) (Kahng and Grigg 2005). The parasitic overgrowth was reported to start on patches of bare skeleton and then extended to the entire surface of the corals, causing their death. Similarly to zoanths, the epibiosis of *C. riisei* also started on the basal major branches and stems, expanding toward the distal ends of the colonies. In contrast to what is reported here, the octocoral did not cause the breakdown of thinner ramifications but continued to grow rapidly along all pinnules as a thin sheet, such that it completely covered the corals, which kept their original branching pattern unchanged (Kahng and Grigg 2005). Finally, because of the similar corallum morphology, no different overgrowth patterns were observed between the two Hawaiian black coral species (Kahng and Grigg 2005).

Our visual census revealed that black corals, together with gorgonians, are among the most important three-dimensional structuring organisms of the Ecuadorian reefs. The dominant species was *A. galapagensis*, with 62% of the total counted colonies distributed along the entire depth range with a peak of abundance toward the maximum surveyed depths (25–35 m). Also at the Galápagos Islands this species is mainly distributed at major depths (Kerstitch 1989, Hickman 2008). On the contrary, *M. panamensis* is more distributed between 15 and 25 m depth. These data partially corroborate previous observations conducted on vertical rocky faces at the Galápagos, where the greatest density of black coral species is at 15 m depth (Martinez and Robinson 1983). On the basis of the growth rates indicated in that latter study, the observed coral colonies of *Machalilla* (with special reference to *M. panamensis*), showing a basal diameter of 0.8–6.0 mm, are between 3 and 14 yr old.

The observed site-related differences in black coral abundances strongly depend on the topography of the bottom. Particularly, differences were observed between insular sites and coastal sites, with the former being characterized by higher densities. With the exception of Bahia Drake, insular sites present a more extended rocky slope, whereas coastal



sites are characterized by rocky masses up to 15–20 m depth with wide sandy patches. It therefore seems that the availability of rocky substrate is the most important abiotic factor limiting the settling of black corals in this area.

At some sites (Machalilla, Los Ahorcados, Punta Mala, Islotes de Salango) the first 10 m are dominated by fan-shaped gorgonians, which progressively give way to black corals in the deeper depth ranges. Fan-shaped gorgonians occur again on the deep sandy plains, where antipatharians cannot settle. A similar octocoral-antipatharian distribution has been recorded at some Colombian reefs, where zooxanthellate gorgonians, better adapted to tidal action, inhabited shallow areas, and azooxanthellate species shared the deeper ranges with antipatharians (sciophilous and adapted to steeper slopes) (Sánchez et al. 1998, Sánchez 1999).

The studied antipatharian community shows an average total density of  $0.5 \pm 0.05$  colonies  $m^{-2}$ , higher than what has been reported in literature for different areas: 0.25 colonies  $m^{-2}$  for Indonesian reefs (Tazioli et al. 2007), up to 0.2 colonies  $m^{-2}$  for a Hawaiian community (Grigg 1965), and 0.25 colonies  $m^{-2}$  for an *Antipathella fiordensis* (Grange, 1990) meadow in the New Zealand fjords (Grange 1985). Density data reported from a Colombian community including both octocorals and antipatharian corals was 3.2 colonies  $m^{-2}$ , but black corals contributed only a minor part of that value (Sánchez et al. 1998). Now, only a Mediterranean meadow of *Antipathella subpinnata* (Ellis & Solander, 1786) has been found to have a higher density (1.4 colonies  $m^{-2}$ ) (Bo et al. 2009).

Despite the high abundance of black corals, the species richness of the Ecuadorian shallow-water community is low and consists of only two species (Martinez and Robinson 1983). This low coral diversity is probably due to the oceanographic features of the area characterized by a complex hydrographic system creating strong seasonal variations in water temperature and salinity (Glynn 2001). This, together with the periodic El Niño and La Niña events, induces stress in benthic organisms that reduces the marine biodiversity of the area.

Moreover, on an oceanic scale, it is possible to identify a decreasing biodiversity gradient of shallow-water black coral fauna from the Indonesian “hot spot” (several dozen species [Schultze 1896, Brook 1889, Cooper 1909, Silberfeld 1909, van Pesch 1914, Tazioli et al. 2007]), to Hawai‘i (seven species [Grigg and Opresko 1977, Grigg 2001, Fenner 2005]), to the Ecuadorian coast (two species).

Black corals have been intensively collected in Ecuador from the 1980s and have completely disappeared at several sites (Martinez and Robinson 1983, Romero 1997). Currently collection is strongly reduced, because of both overexploitation of the resource stock and likely also due to management within the marine protected areas, such as the Galápagos Islands and Machalilla National Park. The data presented here may represent a benchmark for future studies focused on the coral reef management in Machalilla Park and to aid in developing recovery plans for black coral populations.

#### ACKNOWLEDGMENTS

We thank the Ecuadorian Ministry for Environment, the Province of Manabí, the National Park of Machalilla, and Universidad Estatal Peninsula Santa Elena (UUPSE) for their help and support during the period of this study.

#### Literature Cited

- Altschul, S. F., W. Gish, W. Miller, E. W. Myers, and D. J. Lipman. 1990. Basic local alignment search tool. *J. Mol. Biol.* 215:403–410.
- Arriaga, L. 1999. Informe sobre el evento La Niña en la pesca. Programa de Pesca VECEP/Instituto Nacional de Pesca, Guayaquil, Ecuador.
- Bianchi, C. N., R. Pronzato, R. Cattaneo-Vietti, L. Benedetti Cecchi, C. Morri, M. Pansini, R. Chemello, M. Milazzo, S. Fraschetti, A. Terlizzi, A. Peirano, E. Salvati, F. Benzoni, B. Calcinai, C. Cerrano, and G. Bavestrello. 2003. I fondi duri. Pages 199–232 in M. C. Gambi and M. Dappiano, eds. *Manuale di metodologie di campio-*

- namento e studio del benthos marino mediterraneo. *Biologia Marina Mediterranea*. Erredi, Genoa, Italy.
- Bo, M., G. Bavestrello, S. Canese, M. Giusti, E. Salvati, M. Angiolillo, and S. Greco. 2009. Characteristics of a black coral meadow in the twilight zone of the central Mediterranean Sea. *Mar. Ecol. Prog. Ser.* 397:53–61.
- Brook, G. 1889. Report on the Antipatharia. *Rep. Sci. Results Voyage Challenger* 32:5–222.
- Castorena, V., and M. Metaca. 1979. El coral negro, una riqueza en peligro. *Tec. Pesq.* 141:22–27.
- Cooper, C. F. 1909. Antipatharia. Reports of the Percy Sladen Trust Expedition to the Indian Ocean. *Trans. Linn. Soc. Lond.* 12:301–323.
- Cruz, M., N. Gabor, E. Mora, R. Jiménez, and J. Mair. 2003. The known and unknown about marine biodiversity in Ecuador (continental and insular). *Gayana* 67:232–260.
- Deichmann, E. 1941. Coelenterates collected on the presidential cruise of 1938. *Smithson. Misc. Coll.* 99:1–18.
- Di Camillo, C., M. Bo, S. Puce, and G. Bavestrello. 2010. Association between *Dentitheca habereri* (Cnidaria: Hydrozoa) and two zoanthids. *Ital. J. Zool.* 77:81–91.
- Echeverria, C. A. 2002. Black corals (Cnidaria: Anthozoa: Antipatharia): First records and a new species from the Brazilian coast. *Rev. Biol. Trop.* 50:1067–1077.
- Fenner, D. 2005. Corals of Hawai'i: A field guide to the hard, black, and soft corals of Hawai'i and the Northwest Hawaiian Islands, including Midway. Mutual Publishing, Honolulu.
- Glynn, P. W. 2001. Coral communities and coral reefs of Ecuador. Page 24 in J. Cortés, ed. *Latin American coral reefs*. Elsevier Science B.V., Amsterdam.
- Grange, K. R. 1985. Distribution, standing crop, population structure, and growth rates of black coral in the southern fiords of New Zealand. *N. Z. J. Mar. Freshwater. Res.* 19:467–475.
- Grigg, R. W. 1965. Ecological studies of black coral in Hawaii. *Pac. Sci.* 19:244–260.
- . 2001. Black coral: History of a sustainable fishery in Hawai'i. *Pac. Sci.* 55:291–299.
- Grigg, R. W., and D. M. Opresko. 1977. Order Antipatharia: Black corals. Pages 242–261 in D. V. Devaney and L. G. Eldredge, eds. *Reef and shore fauna of Hawaii*. Section I: Protozoa through Ctenophora. Bishop Museum Press, Honolulu, Hawai'i.
- Guitart, B., E. Gonzalez, and M. García. 1997. Evaluation of the black coral populations in the Cuban west. *Congreso de Ciencias del Mar, Cuba* 4:74.
- Guzmán, H. M., and J. Cortéz. 1993. Arrecifes corallines del Pacifico oriental tropical: Revision y perspectivas. *Rev. Biol. Trop.* 41:535–557.
- Guzmán, H. M., and C. A. Guevara. 1999. Arrecifes coralinos de Bocas del Toro, Panamá: III. Distribución, estructura, diversidad y estado de conservación de los arrecifes de las islas Pastores, Cristóbal, Popa y Cayo Agua. *Rev. Biol. Trop.* 47:659–676.
- Hickman, C. P., Jr. 2008. A field guide to corals and other radiates of Galápagos. Sugar Spring Press, Lexington.
- Kahng, S. E., and R. W. Grigg. 2005. Impact of an alien octocoral (*Carijoa riisei*) on black corals in Hawaii. *Coral Reefs* 24:556–562.
- Kerstitch, A. 1989. Sea of Cortez marine invertebrates: A guide for the Pacific coast, Mexico to Ecuador. Sea Challengers, Monterey, California.
- Love, M. S., M. M. Yoklavich, B. A. Black, and A. H. Andrews. 2007. Age of black coral (*Antipathes dendrobristos*) colonies, with notes on associated invertebrate species. *Bull. Mar. Sci.* 80:391–400.
- Martinez, P., and E. Robinson. 1983. Investigación sobre la explotación del coral negro (*Antipathes panamensis*) en las islas Galapagos, Ecuador. Instituto Nacional de Pesca (INP). *Bol. Cient. Tec.* 6:107–123.
- Molodtsova, T., and O. Poltarukha. 2008. Cuticular spines of *Oxynaspis* spp. (Pedunculata: Cirripedia): An inheritance from antipatharian host. *Proc. 4th Deepsea Coral Symp., Wellington, New Zealand*.

- Opresko, D. M. 1976. Redescription of *Antipathes panamensis* Verrill (Coelenterata, Antipatharia). *Pac. Sci.* 30:235–240.
- . 2001. New species of antipatharians (Cnidaria: Anthozoa) from Madeira with the establishment of a new genus. *Proc. Biol. Soc. Wash.* 114:349–358.
- . 2003. Redescription of *Antipathes dichotoma* Pallas, 1766. *Zool. Meded. (Leiden)* 77:481–493.
- . 2009. A new name for the Hawaiian antipatharian coral formerly known as *Antipathes dichotoma* (Cnidaria: Anthozoa: Antipatharia). *Pac. Sci.* 63:277–291.
- Opresko, D. M., and J. A. Sánchez. 1997. A new species of antipatharian coral (Cnidaria: Anthozoa) from the Caribbean coast of Colombia. *Caribb. J. Sci.* 33:75–81.
- . 2005. Caribbean shallow-water black corals (Cnidaria: Anthozoa: Antipatharia). *Caribb. J. Sci.* 41:492–507.
- Padilla, C., and M. Lara. 2003. Banco Chinchorro: The last shelter for black coral in the Mexican Caribbean. *Bull. Mar. Sci.* 73:197–202.
- Pax, F., M. van-Praët, and D. Doumenc. 1987. Ordre des Antipathaires. *Traite de Zoologie. Anatomie, Systematique, Biologie.* Pages 189–210 in D. Doumenc, ed. *Cnidaires Anthozoaires.* Masson, Paris.
- Podestà, G. P., and P. W. Glynn. 2001. The 1997–98 El Niño event in Panama and Galápagos: An update of thermal stress indices relative to coral bleaching. *Bull. Mar. Sci.* 69:43–59.
- Reimer, J. D., and T. Fujii. 2010. Four new species and one new genus of zoanthids (Cnidaria, Hexacorallia) from the Galápagos Islands. *ZooKeys* 42:1–36.
- Reimer, J. D., S. Hirano, Y. Fujiwara, F. Sinniger, and T. Maruyama. 2007. Morphological and molecular characterization of *Abyssanthus nankaiensis*, a new family, new genus and new species of deep-sea zoanthid (Anthozoa: Hexacorallia: Zoantharia) from a Northwest Pacific methane cold seep. *Invertebr. Syst.* 21:255–262.
- Reimer, J. D., M. Nonaka, F. Sinniger, and F. Iwase. 2008a. Morphological and molecular characterization of a new genus and new species of parazoanthid (Anthozoa: Hexacorallia: Zoantharia) associated with Japanese red coral (*Paracorallium japonicum*) in southern Japan. *Coral Reefs* 27:935–949.
- Reimer, J. D., S. Ono, Y. Fujiwara, K. Takishita, and J. Tsukahara. 2004. Reconsidering *Zoanthus* spp. diversity: Molecular evidence of conspecificity within four previously presumed species. *Zool. Sci.* 21:517–525.
- Reimer, J. D., F. Sinniger, and C. P. Hickman Jr. 2008b. Zoanthid diversity (Anthozoa: Hexacorallia) in the Galapagos Islands: A molecular examination. *Coral Reefs* 27:641–654.
- Romero, X. M. 1997. Ecuador's vanishing black corals. *Aquaticus: J. Shedd Aquarium* 26:21–25.
- Sánchez, J. A. 1999. Black coral–octocoral distribution patterns on Imelda Bank, a deep-water reef, Colombia, Caribbean Sea. *Bull. Mar. Sci.* 65:215–225.
- Sánchez, J. A., and R. Collin. 2003. Common octocorals and black corals of Boca del Toro, Panama. Boca Research Station, Smithsonian Tropical Research Institute, Unit 0948, APO AA34002, USA.
- Sánchez, J. A., S. Zea, and J. M. Díaz. 1998. Patterns of octocoral and black coral distribution in the oceanic barrier reef-complex of Providencia Island, southwestern Caribbean. *Caribb. J. Sci.* 34:250–264.
- Schultze, L. S. 1896. Beitrag zur Systematik der Antipatharien. *Abh. Senckenb. Naturforsch. Ges.* 23:1–40.
- Silberfeld, E. 1909. Japanische Antipatharien. *Abh. Math.-Phys. Klasse K. Bayer. Akad. Wiss. I.* 7:30.
- Sinniger, F., J. I. Montoya-Burgos, P. Chevallon, and J. Pawlowski. 2005. Phylogeny of the order Zoantharia (Anthozoa, Hexacorallia) based on the mitochondrial ribosomal genes. *Mar. Biol. (Berl.)* 147:1121–1128.
- Sinniger, F., J. D. Reimer, and J. Pawlowski. 2008. Potential of DNA sequences to identify zoanthids (Cnidaria: Zoantharia). *Zool. Sci.* 25:1253–1260.
- . 2009. The Parazoanthidae DNA taxonomy: Description of two new genera. *Mar. Biodivers.* 40:57–70.

- Tazioli, S., M. Bo, M. Boyer, H. Rotinsulu, and G. Bavestrello. 2007. Ecology of some common antipatharians from the Marine Park of Bunaken (North Sulawesi, Indonesia). *Zool. Stud.* 46:227–241.
- Totton, A. K. 1923. Coelenterata. Part III. Antipatharia (and their cirripede commensals). *Nat. Hist. Rep. Br. Antarct. Exped.* 5:97–120.
- van Pesch, A. J. 1914. The Antipatharia of the Siboga Expedition. *Siboga Exped. Monogr.* 17:1–258.
- Verrill, A. E. 1869. Review of the corals and polyps of the west coast of America. *Trans. Conn. Acad. Arts Sci.* 1:377–570.
- Warner, G. F. 1981. Species descriptions and ecological observations of black corals (Antipatharia) from Trinidad. *Bull. Mar. Sci.* 31:147–163.
- . 2005. The occurrence of black corals in Jamaican reef environments, with special reference to *Stichopathes lutkeni* (Antipatharia: Antipathidae). *Rev. Biol. Trop.* 53:61–66.
- Warner, G. F., and M. Opresko. 2004. A new black coral (Anthozoa: Antipatharia) from a reef wall environment in Jamaica. *Bull. Mar. Sci.* 74:169–174.
- Wirtz, P., and C. d'Udekem-d'Acoz. 2001. Decapoda from Antipatharia, Gorgonaria and Bivalvia at the Cape Verde Islands. *Helgol. Mar. Res.* 55:112–115.

