

Ecological Observations of Some Common Antipatharian Corals in the Marine Park of Bunaken (North Sulawesi, Indonesia)

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Silvia Tazioli, Marzia Bo, Massimo Boyer, Henki Rotinsulu, and Giorgio Bavestrello (2007) Ecological observations of some common antipatharian corals in the Marine Park of Bunaken (North Sulawesi, Indonesia). *Zoological Studies* 46(2): 227-241. The ecology of 16 common antipatharian species, living on shallow reefs in Bunaken National Marine Park (North Sulawesi, Indonesia) is described for the first time. The community structure was evaluated using standard ecological parameters. The vertical distribution and habitats of different species are described. Observations on polyp morphology and feeding behavior made *in situ* are reported, and the most common symbiotic associations are listed. The highly diversified black coral assemblage shows strong site-dependent differences. Generally it is characterized by high values of the H' index (1.5-2.5) indicating high diversity and also high values of equitability (of approximately 1) indicating no real dominance but a functional distribution of species. In general, the abundance of black corals increases with depth. The bathymetric distribution and the preferred habitat of each studied species appear to be the result of interactions among both biological (mainly competition involving stony corals) and abiotic factors (mainly water movement). Due to the numerous symbiotic associations involving black corals (especially with crabs, shrimp, and fish), they must be considered a keystone group in the structure of tropical coral reefs.
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Although black corals are among the most common azooxanthellate corals in tropical reefs, data about their ecology are very scarce. This is mainly due to the paucity of field studies that have focused on this group. One of the few ecological studies dedicated to black coral ecology is that of Grigg (1965) conducted in Hawaii. Other research was devoted to the geographical and bathymetrical distributions or to the population structure of black corals in New Zealand (Grange 1985 1988, Grange and Singleton 1988), St. Paul and Amsterdam Is. (Southern Indian Ocean) (Grasshoff 1988), Hawaii (Grigg 1965 1974), East Malaysia (Oakley 1997), the US Virgin Is. (Olsen and Wood 1979), and the Caribbean Sea (Warner 1981, Sanchez et al. 1998, Sanchez 1999). A few

studies have dealt with the associated fauna (Totton 1923, Warner 1981, Grange 1991, Wirtz and d'Udekem-d'Acoz 2001), reproduction and growth (Oakley 1988, Parker et al. 1997), feeding strategies (Dantan 1921, Lewis 1978, Warner 1981, Pax et al. 1987), competition behavior (Goldberg et al. 1990), and relations with abiotic environmental features like currents (Warner 1981, Genin et al. 1986, Oakley 1997). Other sparse ecological notes are given by different authors in taxonomic or faunistic works, such as ones carried out in the Strait of Gibraltar (Grasshoff 1989), Northeast Atlantic (Grasshoff 1985), Bay of Biscay (Hickson 1907), and Maldives and Laccadive Archipelagos (Cooper 1903 1909).

The aim of the present work was to summa-

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rize many of the ecological observations made during a study of the black coral assemblages in the area of Bunaken Marine Park (North Sulawesi, Indonesia).

The North Sulawesi peninsula, stretching between the Sulawesi Sea (to the northwest) and Maluku Sea (to the southeast), lies in an area known worldwide as a center of marine biodiversity (Sheppard and Wells 1988, Muller 1997, Tomascik et al. 1997, Edinger et al. 1998) due to geographical reasons (because it acts as a link between the Indian and Pacific Oceans), and on account of its complex geological history.

Taxonomic information on several species of antipatharians of the Indonesian Archipelago can be found in 2 detailed monographs (Brook 1889, van Pesch 1914). However neither of these provides a comprehensive evaluation of shallow-water species. Schultze (1896) reports on 7 species collected off the island of Ternate in the northern Moluccas, but no ecological information is provided. Recently, Hoeksema and van Ofwegen (2004) published descriptions and photos of some common shallow-water antipatharian species of the Indo-Malayan region. Information on some species of shallow- and deep-water Indo-Pacific antipatharians can also be found in taxonomic revisions of the families Aphanipathidae, Myriopathidae, Cladopathidae, and Schizopathidae published by Opresko (2001 2002 2003 2004), but a comprehensive taxonomic revision of the shallow-water antipatharians of this region is still needed.

MATERIALS AND METHODS

This study was conducted by scuba diving, both in daytime and at night in July 2004 and Jan. and Sept. 2005 at 8 dive sites off 3 islands in the Marine Park. The dive sites were located at Bajau, Bunaken Timur, Negeri, Likuan 2, Likuan 3, Mapia, Siladen (Onong Resort), and Tanjung Pisok (Fig. 1). These sites are mainly characterized by vertical walls, with the exception of the 2 sites located along the Sulawesi coast. Bajau is characterized by a 10 m vertical cliff, usually lashed by strong currents, which continues on a slight slope (at a 30° inclination), dominated by stony corals and ending at 45 m in depth in a detritic bottom (at a 10° inclination), the homogeneity of which is at times broken up by scattered rocks. Mapia is a sandy slope (at a 30° inclination) with diffuse rocky aggregations, and is characterized by a light current. Bunaken Timur (east coast of Bunaken) is a vertical wall characterized by a slight current. Negeri, Likuan 2, and Likuan 3 (eastern side of the Gulf of Bunaken) are vertical walls characterized by a steep slope (at 80°-90° inclinations) with numerous sparsely distributed crevices, shelves, and vertical canyons, which ends in a detritic bottom at around 50-60 m in depth. Here the current has a variable intensity and unpredictable direction often related to the tides. Siladen (to the southwest of Siladen) is a steep vertical wall often lashed by a very strong current, which may change direction during the day. Tanjung Pisok (Sulawesi

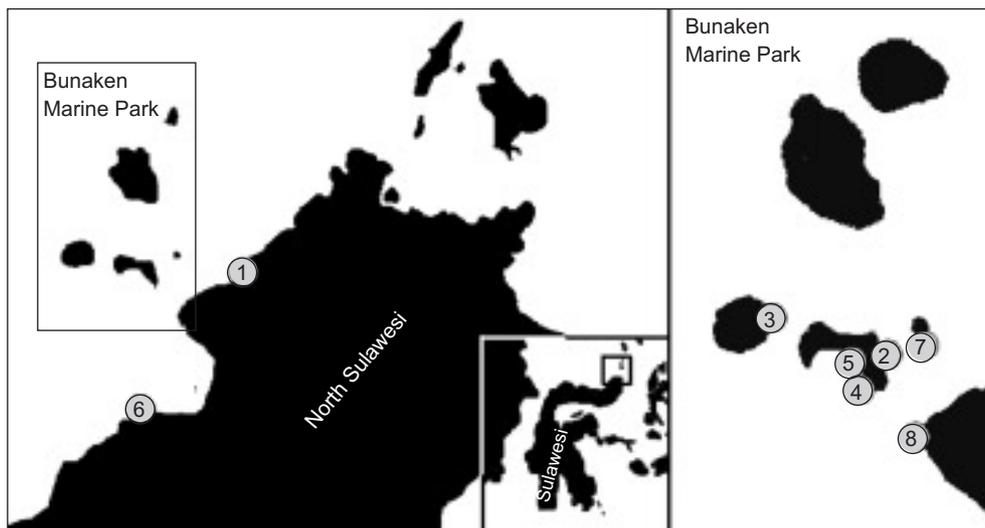


Fig. 1. Map of the study sites in the Marine Park of Bunaken. 1. Bajau; 2. Bunaken Timur; 3. Negeri; 4. Likuan 2; 5. Likuan 3; 6. Mapia; 7. Siladen; 8. Tanjung Pisok.

coast) is a steep vertical wall, which ends in a flat plain at about 45 m in depth, where the current is always strong. At the visited sites, the average temperature during the study period was 27–28 °C from the surface to 30 m in depth.

Quantitative data were obtained at each dive site with an adapted belt transect method (Bianchi et al. 2003) counting all the colonies observed during 5 min swims along 5 horizontal transects 2 m wide (including 1 m on each side of the diver) at depths of 45, 35, 25, 15, and 5 m (Fig. 2). Each underwater trail was surveyed by 3 divers swimming parallel at a short distance from each other, and quantitative measurements were based on the mean values obtained from the data of the 3 divers. In total, 40 horizontal transects (each with 3 replicas) were carried out. A similar transect method, but performed in the vertical direction, was used to study the vertical distribution of *Antipathella aperta* (Grange) in New Zealand (Grange 1985).

Using the collected data, we carried out an analysis of biodiversity based on several biological indexes (Danovaro et al. 2004). Species richness (SR, the total number of species observed), abundance (the number of individuals of each species), the Shannon index (H' , calculated as $H' = -\sum p_i \log_2 p_i$, where p_i is n_i/N , n_i is the number of individuals of the i th-species, and N is the total number of individuals), and the evenness index (J' , indicating how the abundances are partitioned across the species) were calculated. Density mea-

surements (colonies/m²) were obtained by estimating a surface area of about 100 m² for each transect, which was calculated considering the width of the belt of observation (2 m) and the length of the transect of about 50 m.

In order to study the gut contents of polyps, portions of colonies of *Cirrhopathes* sp. 1 and *Cirrhopathes* sp. 2 were cut away and directly fixed in 4% formaldehyde underwater during the nighttime. Immediately after the dive, the gut contents of these polyps were analyzed.

The associated epibiontic fauna on the black corals was always photographed *in situ* and, when necessary, collected for identification.

RESULTS

The black coral assemblage

During our survey, we recorded 16 species of black corals belonging to 3 families and 6 genera (Table 1). Some species, like *Cupressopathes* sp., were rare, while others, like *Antipathes* cf. *simplex* (Schultze), were observed inside deep crevices or caves and were difficult to record during the visual censuses. Data on the structures of the assemblages and vertical distributions were obtained for 14 species (Table 1). Detailed descriptions of the undescribed species will be given in separate

Table 1. List of black corals species studied in the Marine Park of Bunaken. Species marked with an asterisk were used in the qualitative analyses

Family	Species
Antipathidae	* <i>Antipathes curvata</i>
	* <i>Antipathes elegans</i>
	<i>Antipathes</i> cf. <i>simplex</i>
	* <i>Antipathes</i> sp.
	* <i>Cirrhopathes spiralis</i>
	* <i>Cirrhopathes contorta</i>
	* <i>Cirrhopathes</i> sp. 1
	* <i>Cirrhopathes</i> sp. 2
	* <i>Cirrhopathes</i> sp. 3
	* <i>Stichopathes</i> sp.
Aphanipathidae	* <i>Rhipidipathes</i> sp.
Myriopathidae	* <i>Myriopathes japonica</i>
	* <i>Myriopathes myriophylla</i>
	* <i>Cupressopathes abies</i>
	* <i>Cupressopathes pumila</i> <i>Cupressopathes</i> sp.

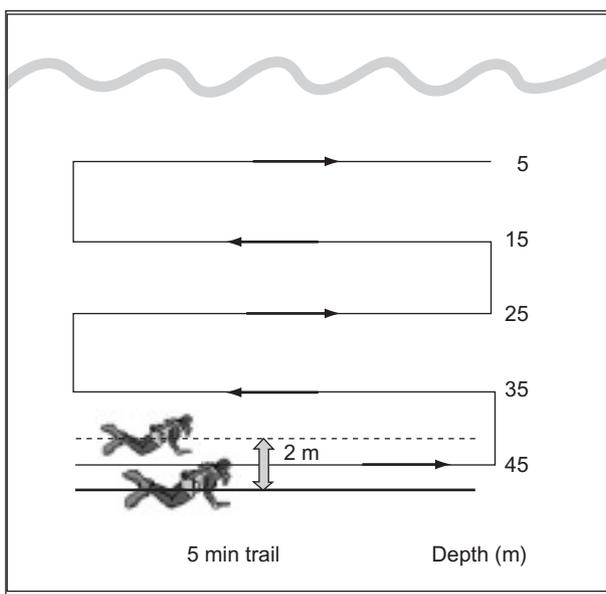


Fig. 2. Scheme of the belt transect method used for sampling.

papers.

These species were identified during the visual census from their gross morphologies (Fig. 3). We took into consideration 5 main categories subdividing the species on the basis of their pattern of ramification: being unbranched, bottlebrush, arborescent, bush, and fan-shaped. *Stichopathes* and *Cirrhopathes* are unbranched, and lack pin-

nules or branches of any order (Fig. 3A-E). The 2 genera differ in the presence of 1 or numerous rows of polyps, respectively (Brook 1889). The various species of *Cirrhopathes* were identified on the basis of shape and the thickness of the axis. Bottlebrush-shaped species (*C. abies* and *C. pumila*) were recognizable because of their cypress-like aspect, characterized by a central axis

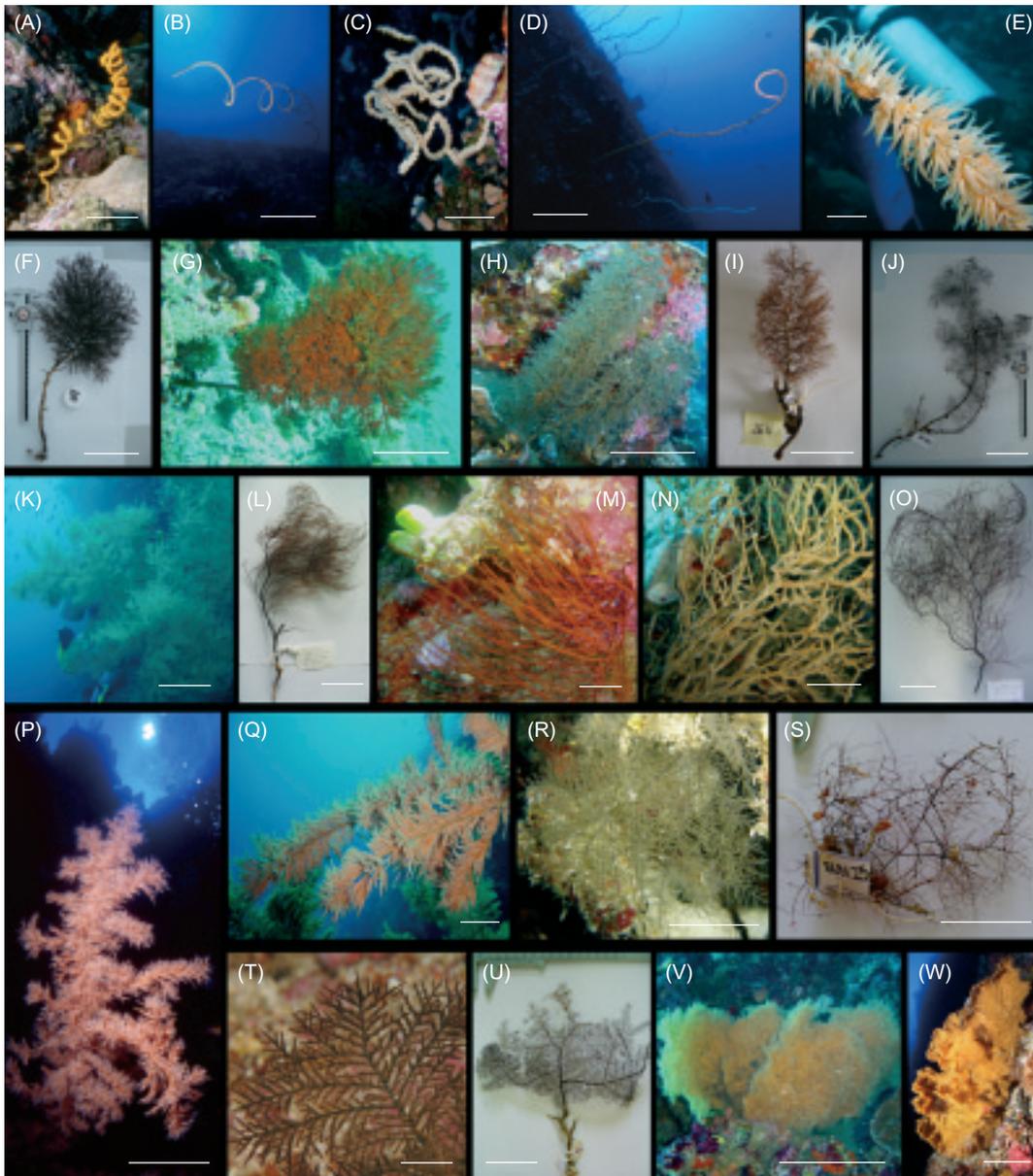


Fig. 3. Morphology of the colonies. (A, B) Unbranched spiral shape of *Cirrhopathes spiralis* and *Cirrhopathes* sp. 1; (C) unbranched crooked specimen of *Cirrhopathes contorta*; (D) meadow of unbranched straight coral of *Cirrhopathes* sp. 2 and *Stichopathes* sp.; (E) unbranched straight coral of *Cirrhopathes* sp. 3; (F, G) bottlebrush colonies of *Cupressopathes abies*; (H, I) bottlebrush colonies of *Cupressopathes pumila*; (J) bottlebrush colony of *Cupressopathes* sp.; (K, L) arborescent colonies of *Antipathes* sp.; (M) arborescent colony of *Antipathes elegans*; (N, O) arborescent colonies of *Antipathes curvata*; (P, Q) arborescent colonies of *Myriopathes japonica*; (R, S) bushy colonies resembling *Antipathes* cf. *simplex*; (T, U) fan-shaped colonies of *Myriopathes myriophylla*; (V, W) fan-shaped colonies of *Rhipidipathes* sp. Scale bars: E, 0.5 cm; T, 1 cm; C, L, R, S, 5 cm; A, F, G, H, I, J, M, N, O, Q, U, 10 cm; W, 25 cm; D, K, P, V, 50 cm; B, 100 cm.

surrounded by numerous rows of pinnules (Fig. 3F-I). *Cupressopathes* sp. is characterized by a branched axis (Fig. 3J). The arborescent species *A. elegans*, *A. curvata*, *Antipathes* sp., and *M. japonica* show a distinct tree-like shape, with a major axis giving rise to several secondary branches; they were easily identified on the basis of the pattern of ramification (Fig. 3K-Q). The bushy *A. cf. simplex* is characterized by a small, net-like corallum showing many anastomoses between its ramifications (Fig. 3R, S). The fan-shaped species (*M. myriophylla* and *Rhipidipathes* sp.) possess a planar or multi-planar flabellate corallum and were identified on the basis of the pattern of ramification and anastomoses (Fig. 3T-W).

From qualitative and quantitative points of view, strong differences among the studied sites were recorded (Fig. 4). At Negeri, the species richness (8-10 species) and the number of specimens (about 20 per transect) were almost constant at all sampled depths. The H' index was about 1.5-2.5, and the high value of equitability (J') indicated that there were no dominant species at any depth. At other stations (Siladen, Bunaken Timur, and Likuan 2), both the species richness (5-12) and the number of specimens (5-50) increased with depth. In all these sites, the H' index ranged from about 1.5 to 2.5, and the high values of J' indicated that there were no dominant species. At Bajau, both the number of specimens and the species richness were very low and decreased with depth. This was due to the presence of a vertical cliff from the surface to 10 m in depth where colonies were abundant. The cliff ended on a slope completely covered by a dense population of the stony coral *Euphyllia ancora* to a depth of 40 m, below which the bottom was detritic.

A peculiar situation was also noted at Tanjung Pisok where the values of equitability were very low, particularly from 15 to 35 m. In this zone, the black coral assemblage was completely dominated by *Stichopathes* sp., which occurred in very high densities.

Vertical distribution

Considering the presence or absence of each species at all of the studied sites, it was possible to recognize differences in their patterns of vertical distribution on the coral reefs of the Bunaken area (Fig. 5). Some species, such as *Antipathes* sp. and *Cirrhopathes spiralis*, were abundant at all studied depths, although with a slight increase with depth. Another group of species, represented pri-

marily by *Myriopathes japonica*, *Cirrhopathes* sp. 1, and *Antipathes elegans*, was also present across the entire studied bathymetric range, but these species showed clear increases in abundance with depth. Finally, the 2 species of *Cupressopathes* and *Rhipidipathes* sp. were almost exclusively found below 30 m in depth, towards the base of the cliffs. The only species with an opposite strategy in its spatial distribution was *Cirrhopathes contorta*, which reached its highest densities at 5 m in depth. In deeper sites, the species was still present but at decreasing densities.

Habitat

Underwater observations indicated that for each studied species or group of species, a peculiar habitat could be identified (Fig. 6). *Cirrhopathes contorta* was typically found associated with stony corals where it grew out of crevices between coral colonies. For other species, the trend in density followed an inverse relationship between the abundance of black corals and stony corals. Particularly, both the unbranched forms (*Cirrhopathes* and *Stichopathes*) and the bottlebrush forms (*Cupressopathes*) lived in exposed habitats where strong currents flow from varying directions. The most common situation on the reefs of the Bunaken Marine Park is one in which on the same cliff, the intensity and direction of the current change several times during the day.

The arborescent colonies of *Antipathes* sp., *A. curvata*, *A. elegans*, and *Myriopathes japonica* and the flabellate colonies of *M. myriophylla* and *Rhipidipathes* sp. escaped competition with stony corals by being more abundant with increasing depth, as the abundance of scleractinian corals decreased with depth. On the other hand, these species were never present on exposed cliffs, but instead generally lived in vertical canyons where they avoided direct exposure to currents. Moreover, in the canyons, the water movement generally followed alternating periods of ascending and descending flow, and the large arborescent planar colonies grew perpendicularly to these movements.

A peculiar case was that of a large population of *Stichopathes* sp. that was found at the sampling site of Tanjung Pisok where the current was always extremely strong and more constant in direction.

The small bush-like colonies of *A. cf. simplex* were recorded hidden in crevices and gorges of the reef where their dense branches trapped detri-

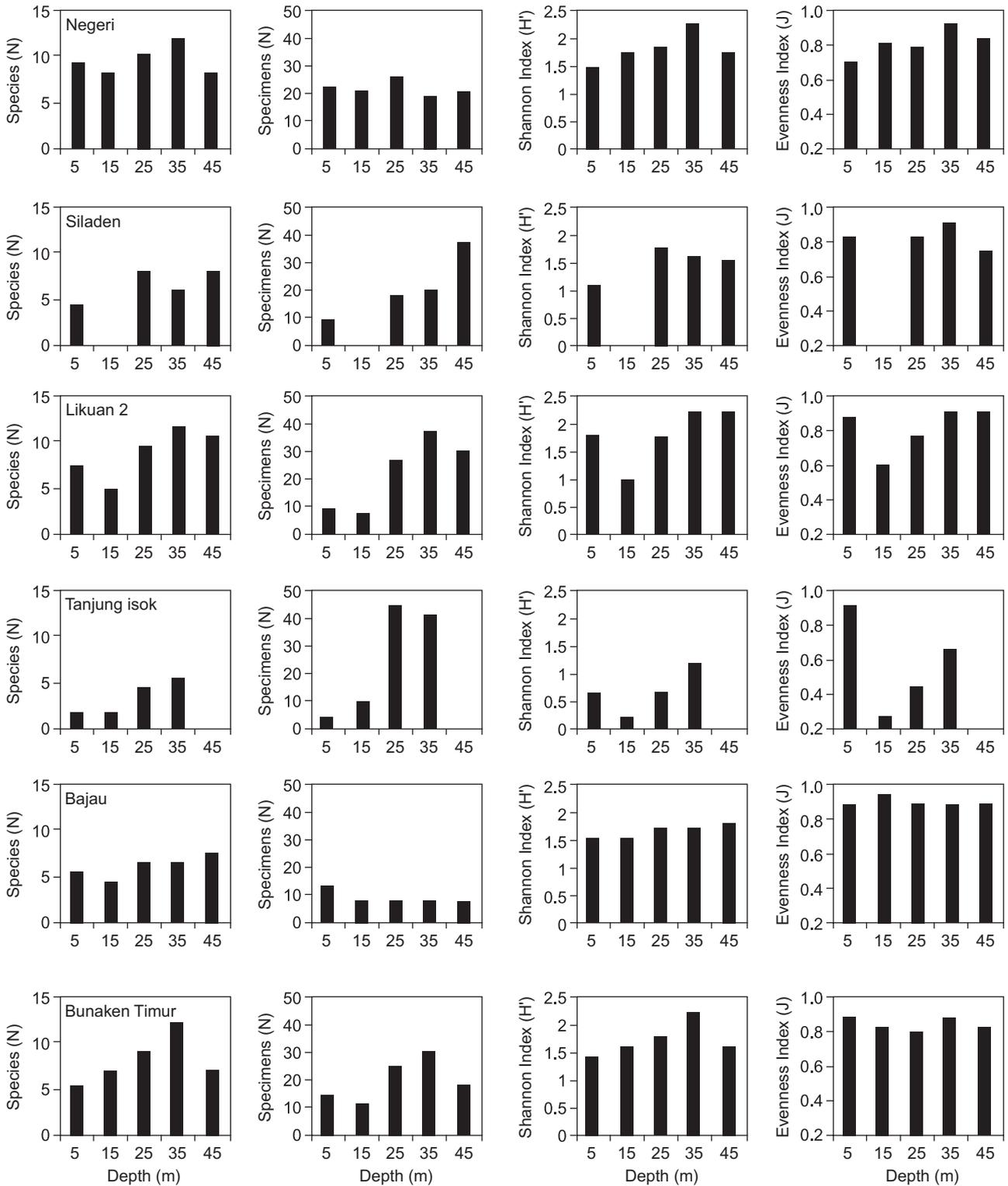


Fig. 4. Graphics showing species richness (number of species), abundance (number of specimens), Shannon index (H'), and evenness index (J') for each study site.

tus and fragments of other organisms rolling down along the wall.

Morphology of living polyps

Information about the appearance of live black coral polyps is generally lacking in the literature. This fact presents a problem in characterizing species, because in many cases, living zooids greatly differ from fixed ones in terms of color, shape, and dimensions of the tentacles.

The use of underwater photography in studying species with large polyps (*Cirripathes* spp. and *Stichopathes* sp.) allowed us to obtain many details about their live shape.

In several species, the aspect of the polyps varied according to circadian rhythms. Zooids of *Cirripathes spiralis* (Fig. 7A, B), *C. contorta*, *Cirripathes* sp. 1, *Cirripathes* sp. 2, and *Stichopathes* sp. (Fig. 7C, D) were contracted during the day while completely expanded during the

night starting at sunset. In *Cirripathes* sp. 3 (Fig. 7E, F), the crowded arrangement and large size of the polyps (1.7 mm in medium transverse diameter and 3.2 mm in medium length of the sagittal tentacles) together with the small diameter of the axis did not allow the zooids to completely contract; thus the tentacles were only slightly reduced in size, and the coenenchyme was never clearly visible. With regard to other species, the polyps were often too small for an appropriate *in situ* distinction between an expanded and a contracted status. Nevertheless, macro photos indicate that polyps of *Antipathes* (Fig. 7G-I) and *Rhipidipathes* sp. (Fig. 7J) were usually completely expanded both during the day and at night.

The living polyps of most species had tentacles reaching a length which usually exceeded the value measured in the preserved condition (up to 2 or 3 times the width of the polyp, according to Lewis 1978). For example, in *Cirripathes* sp. 3 (Fig. 7E, F, L), the preserved sagittal tentacles had

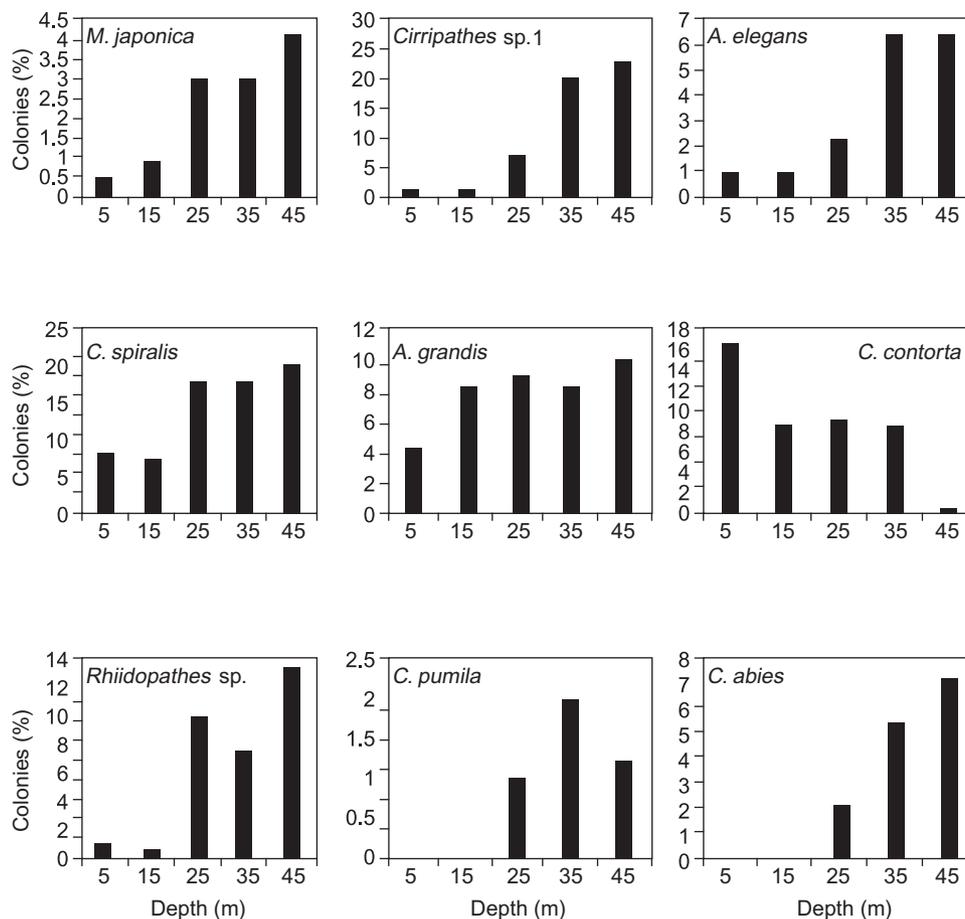


Fig. 5. Graphics showing the percentage abundances of some common species of the entire antipatharian community at each depth for all study sites.

an average length of 3.2 mm, whereas the expanded size was 4.2 mm; in *Stichopathes* sp. (Fig. 7D) they measured 1.0 mm when preserved and 1.6 mm when expanded; and in *Cirrhopathes* sp. 1 (Fig. 7K) they measured 1.5-2.0 mm when preserved and 2.6 mm when expanded.

The tentacle shape was conical in the observed species of *Cirrhopathes*, *Stichopathes*, and *Antipathes* (Fig. 7B, D, F-H, K-M), and cylindrical, with a rounded tip in *Rhipidipathes* (Fig. 7J).

The oral cone, especially during the nighttime, was much elevated and extended, assuming a trumpet-like shape as previously observed by Lewis (1978). The margin of the mouth when open was thin and stretched showing 2 distinct colors between the external (epidermal) and internal (gastrodermal) sides. For example in the pink *Cirrhopathes* sp. 3, the external margin was salmon-colored, while the internal margin was orange (Fig. 7L). During the daytime, we observed specimens of *Stichopathes* and *Cirrhopathes* with their mouths completely open, assuming a circular shape with the lips outstretched (Fig. 7C, N).

When expanded, the mouths of feeding polyps were never covered by tentacles, which projected out in distinct directions. Generally, in *Cirrhopathes* the 4 lateral tentacles were distinctly inserted at a higher level than the sagittals, and all of the tentacles were directed upwards. The lateral tentacles were always grouped together around the mouth (Fig. 7B, F, K, L). In contrast, in *Antipathes* and *Stichopathes*, the sagittal tentacles were directed downwards, while they were directed laterally in *Rhipidipathes* (Fig. 7 G-J, M). Moreover in *Antipathes* and especially in *Rhipidipathes*, all of the tentacles were usually inserted at approximately the same level, and were much further separated than in *Cirrhopathes*. The laterals were far from the mouth, and the sagittal ones were arranged as 2: 2: 2 (3 parallel pairs). In both situations, the tips of the tentacles, especially those of the sagittal ones, were often observed to be twisted in different directions (Fig. 7F, L). Considering that in these colonies the arrangement of polyps is uniserial, the general appearance of the tentacles was very peculiar. Especially

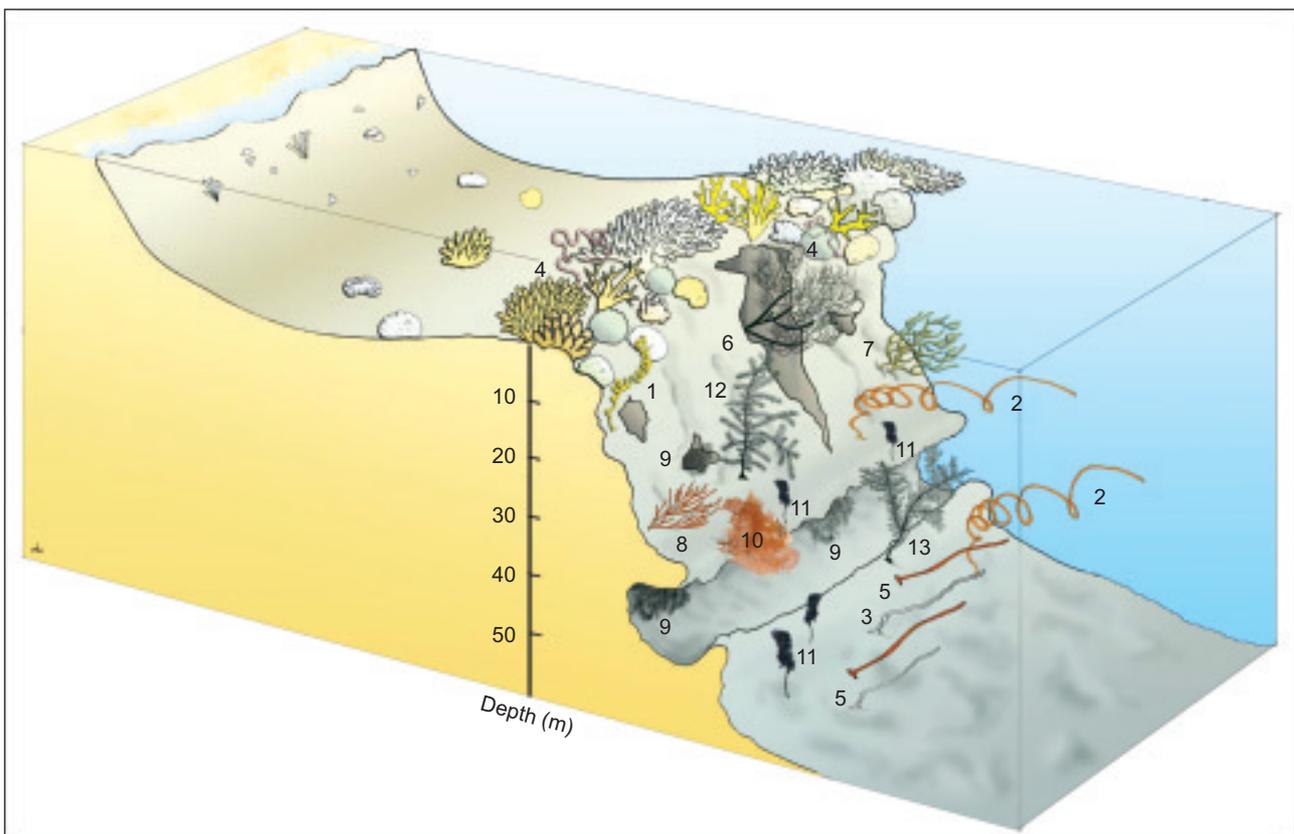


Fig. 6. Black coral zonation in the Bunaken Marine Park. (1) *Cirrhopathes spiralis*; (2) *Cirrhopathes* sp. 1; (3) *Cirrhopathes* sp. 2; (4) *Cirrhopathes contorta*; (5) *Stichopathes* sp.; (6) *Antipathes* sp.; (7) *Antipathes curvata*; (8) *Antipathes elegans*; (9) *Antipathes* cf. *simplex*; (10) *Rhipidipathes* sp.; (11) *Cupressopathes* spp.; (12) *Myriopathes japonica*; (13) *Myriopathes myriophylla*.



Fig. 7. Living polyp morphology. (A) Daytime contracted polyps of a *Cirripathes spiralis*, in which tentacles are completely hiding in the mouths; (B) nighttime expanded polyps of *Cirripathes spiralis*, in which all tentacles are projecting upwards; (C) contracted polyps of *Stichopathes* sp. with 2 wide-open mouths; (D) row of expanded polyps on 1 side showing the trumpet-like oral cones in a *Stichopathes* sp.; (E) partially contracted polyps of *Cirripathes* sp. 3; (F) perfectly extended polyps of *Cirripathes* sp. 3; (G-I) extended tentacles of *Antipathes curvata*, in which the sagittal ones are directed downwards as in other *Antipathes* species; (J) small polyps of *Rhipidipathes* sp. with a parallel arrangement of the tentacles; (K) long extended tentacles of *Cirripathes* sp. 1; (L) close view of a *Cirripathes* sp. 3 polyp with a dichromatic mouth and moving tentacle tips; (M) back view of the cross arrangement of tentacles in *Stichopathes* sp.; (N) wide-open mouth of *Cirripathes* sp.; (O) polychaete trapped by a *Cirripathes* sp. polyp. Scale bars: A, B, C, D, G, H, I, K, M, N, L, 1 mm; E, 3 mm; F, O, 2 mm; J, 0.5 mm. Scale bars: A, B, C, D, G, H, I, K, M, N, L, 1 mm; E, 3 mm; F, O, 2 mm; J, 0.5 mm.

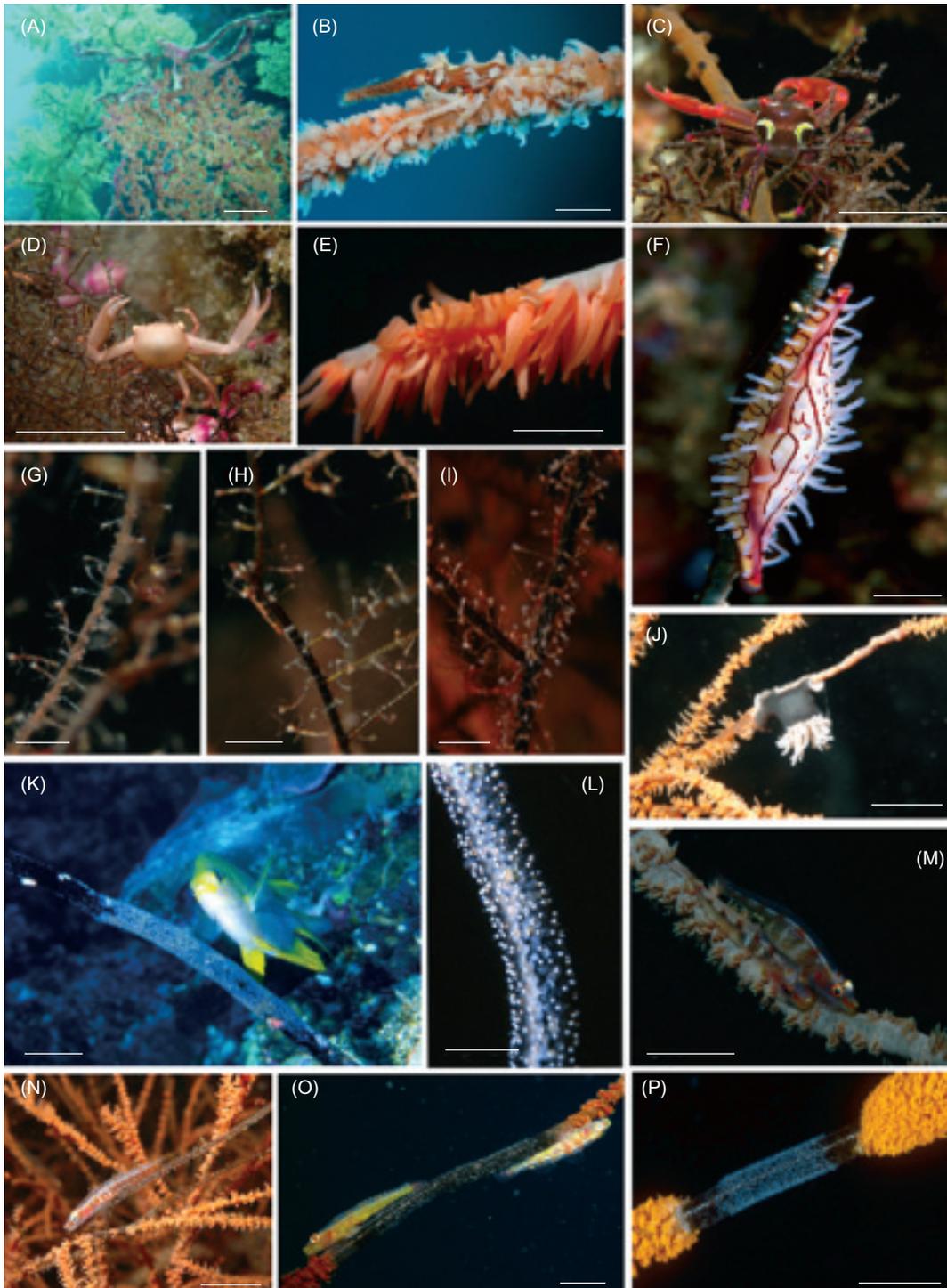


Fig. 8. Epibionts. (A) Colony of *Myriopathes* sp. partially covered by *Zoanthus* sp.; (B) a majid, *Xenocarcinus tuberculatus*, using the polyps of *Cirrhipathes* spp. for camouflage; (C) a xanthid, *Quadrella maculosa*, living on *Cupressopathes abies*; (D) a xanthid, *Quadrella* sp., on an *Antipathes* sp. colony; (E) perfect mimicry of the pink shrimp, *Pontonides unciger*, between polyps of *Cirrhipathes* sp. 3; (F) parasitic ovulid, *Phenacovolva weaveri*, on an antipatharian colony; (G, H, I) different stages of predation of caprellids on *Antipathes* sp.; (J) solitary parasitic black anemone, *Nemanthus* sp., on a colony of *Antipathes* sp.; (K) male *Amblyglyphidodon aureus* (Pomacentridae) guarding its eggs laid on *Cirrhipathes* sp., on which the base of the axis had been peeled bare; (L) a nest of *Amblyglyphidodon aureus* with eyed eggs; (M) a couple of gobiids, *Bryaninops yongei*, on *Cirrhipathes* sp. exhibiting courtship behavior; (N) *Bryaninops tigris* with eggs on a branch of *Antipathes* sp.; (O) a couple of *Bryaninops yongei* with eggs on the axis of *Cirrhipathes* sp. 1; (P) a nest of *Bryaninops yongei* with visible evidence of polyp accumulation at the extremities of the bare peeled axis. Scale bars: A, 5 cm; B, C, D, F, J, K, L, M, N, O, P, 1 cm; E, G, H, I, 0.5 cm.

in *Stichopathes* and in some *Antipathes*, from a lateral view, the tentacles were in the shape of a cross as previously observed by Warner (1981): 2 pairs directed upwards and 2 tentacles directed downwards (Fig. 7M). In this way, 1 side of the axis (Fig. 7D) was characterized by 1 line of mouths, while the other side was completely free of polyps (Fig. 7M).

While diving at night, we documented for the 1st time directly in the field the feeding activity of large zooids of *Cirrhopathes*. Qualitative observations of the gut contents indicated that the most common prey of these species were large planktonic organisms such as large copepods, polychaetes, amphipods, ostracods, and chaetognaths. When a polyp interacted with a prey, its tentacles began to move and to hold the animal firmly. Then the tentacles bent, directing the prey into the mouth where it was quickly engulfed (Fig. 7O). When the prey was a long polychaete, 2 or 3 polyps might have been involved in the capture.

Epibionts

In the Bunaken area, antipatharians appeared to be a very favorable environment for an abundant and diversified associated fauna, which we summarize by functional group.

1. Filter feeders. Crinoidea and Ophiuroidea were occasionally observed hanging onto the terminal branches of *Antipathes* spp. or onto the terminal part of the axis of *Cirrhopathes* spp. Bivalves like *Pteria* spp. could settle on the bare parts of the skeleton and reached a considerable size (over 10 cm in height) in wide colonies of *Antipathes* sp. In a typical assemblage including *Zoanthus* sp. (Fig. 8A), several species of hydroids and colonial ascidians were commonly found covering dead colonies.

2. Commensal decapods. Many different species of Decapoda were observed in association with antipatharians, where they find shelter and food. Among crabs, *Xenocarcinus tuberculatus* (family Majidae) was usually found firmly attached to *Cirrhopathes* spp., with its long legs, collecting coral polyps and growing them on its carapace for camouflage (Fig. 8B). *Quadrella* spp. (like *Q. maculosa*, of the family Xanthidae) live in pairs hiding among the thick branches of different antipatharians, in particular *C. abies* and, less frequently, *Antipathes* spp. (Fig. 8C, D). Apart from these almost obligate commensal associations, other crabs, like the majid, *Naxiodes taurus*, were observed, especially at night, walking on large

colonies of *Antipathes* or *Rhipidipathes*.

Among shrimp, *Pontonides unciger* and *Dasycaris zanzibarica* (Pontoninae) lived in obligate association with *Cirrhopathes* spp. (Fig. 8E). The saw blade shrimp *Tozeuma armatum* (family Hippolitidae) lived on *Antipathes* spp. These 3 species showed a convergent color pattern, with opaque vertical bands on a transparent background, mimicking the shape and color of the coral polyps. The tone was variable, but always matching the host. The pontonid shrimp, *Periclimenes psamathe*, was an occasional commensal of antipatharians.

Even if uncommon in the Bunaken area, several specimens of *Chirostylus dolichopus* (Anomura: Chirostylidae) were found to always be associated with large *Rhipidipathes* colonies.

3. Parasitic invertebrates. These included the ovulid, *Phenacovolva weaveri* (Fig. 8F), which grazes on the coenenchyme of *Cirrhopathes* and *Antipathes* spp. Ovulids did not seem to cause irreversible damage, allowing tissue regeneration. Their camouflage is noteworthy, based on the mantle of the gastropod, mimicking the color and shape of the coral polyps with their dorsal papillae (Schiaparelli et al. 2005).

We occasionally observed colonies of *Antipathes* sp. covered by thousands of caprellids feeding on the living tissue, which led to the death of the entire colony (Fig. 8G-I). At times, solitary or grouped anemones of the genus *Nemanthus* (Fig. 8J) were seen attached to branches of *Antipathes* sp. colonies.

4. Fishes. Fish-antipatharian associations have manifold aspects, as described recently for Hawaiian black coral assemblages (Boland 2005). Many fish find shelter close to larger colonies of *Antipathes* or *Rhipidipathes*, including aggregations of juvenile planktivorous Pomacentridae (such as *Amblyglyphidodon* spp.), diurnal aggregations of nocturnal planktivorous species of *Apogon*, aggregations of *Centriscus scutatus*, juvenile *Macolor macularis*, and fish predators like *Aulostomus chinensis* and *Oxycirrhites typus*. Individuals of all these species swim among the black coral branches, except for *O. typus*, which lay on the main branches waiting for prey.

Chaetodon bennetti (Chaetodontidae) was the only fish species we observed feeding on antipatharian tissue. *Amblyglyphidodon aureus* (Pomacentridae) laid its eggs at the base of large colonies of *Antipathes* spp. or *Cirrhopathes* spp. The male prepared the nest, probably biting and peeling off the living tissue, thus exposing the bare

skeleton. Females were attracted to lay eggs on the black coral skeleton. The male guarded the nest by showing aggressive behavior toward potential predators (Fig. 8K, L).

At least 2 species of Gobiidae lived in obligate association with antipatharians: *Bryaninops yongei* on *Cirrhopathes* spp. (Fig. 8M, O, P) and *Bryaninops tigris* on *Antipathes* spp. (Fig. 8N). Specimens of both species nested on an antipatharian host. The nesting behavior of *B. yongei* is known in great detail: a 3-cm-long band, located 15-25 cm from the tip of the black coral colony is cleaned of living tissue. Eggs are laid directly on the skeleton. *Bryaninops yongei* individuals live in pairs, and sex reversal from female to male probably occurs (Myers 1991). In the Bunaken area, gobies were observed to bite the coenenchyme, pulling at it on both sides, causing the polyps to accumulate at the extremities of the bare space created in the middle (Fig. 8P). *Bryaninops tigris* probably has the same nesting style. It was significant that only gobies nesting on antipatharians prepared the nest in this way; similar species (e.g., *Bryaninops amplus*) that lived on gorgonians simply laid eggs attached to the coenenchyme. The absence of sclerites in black coral tissues probably makes peeling the tissue easier.

DISCUSSION

The shallow-water antipatharian community of Bunaken Marine Park shows high species diversity, which was expected for this area, considering observations of other taxa, like sponges, hydroids, scleractinian corals, and fishes (Tomascik et al. 1997). Our data confirm the significance of the Indo-Malayan area as an important world hotspot of biodiversity (Roberts et al. 2002).

The 16 species considered in our study represent just a portion of the total antipatharian fauna classified for systematic purposes. This work only lays the groundwork for further ecological considerations. In this study, the richest assemblage of black corals ever studied at scuba depths is described on the basis of several standard ecological indexes, such as species richness (SR), Shannon index (H'), and evenness index (J'). We recorded strong site-dependent differences (Fig. 4), but the most common situation, related to steep vertical walls, was characterized by a high values of the H' index (of about 1.5-2.5) indicating high diversity and high values of equitability (of approxi-

mately 1) indicating no real dominance, but a functional distribution of species. At these sites, the diversity of black corals and the number of specimens increased with depth, reaching maximums at 35-45 m. A similar trend of increasing abundance and species diversity of black corals with depth was also observed in the Caribbean (Sanchez et al. 1998, Sanchez 1999). The high diversity of these sites can also be explained by the steep slope of the substratum since it is known that black coral settlement is more likely to occur on inclined and shaded calcareous substrata (Grigg 1965, Oakley 1988), at times on the shady undersides and in crevices of foliaceous and sub-massive stony corals (Sanchez 1999). Exceptions to this general pattern occurred at some dive sites (Fig. 1) like Negeri, where a constant high number of species was recorded at all depths and at Bajau where the trend was reversed with antipatharians growing only on the shallow wall and not on the deeper slope where stony corals were dominant and outcompeted the antipatharians. At Tanjung Pisok, the equitability index was very low due to a wide meadow of *Stichopathes* sp. that completely dominated the seascape at depths of around 40 m. Other work indicated that *Stichopathes* specimens are usually the most abundant black corals in deeper parts of the reef slope, with densities of 1.5-7.32 colonies/ m² (Sanchez et al. 1998, Sanchez 1999). In spite of their high species diversity, the density of black corals in the Bunaken area was notably low, i.e., never reaching 0.5 colonies/m².

The bathymetric distributions and habitat preferences of the studied species appear to be the result of interactions among biotic and abiotic factors. In terms of biotic factors, competition for space with stony corals in the shallow portion of the reef is the most probable reason that the antipatharians showed a trend of increasing abundance and diversity with depth, as observed on Caribbean reefs by Sanchez et al. (1998) and Sanchez (1999). On densely colonized surface areas of the reefs in the Bunaken Marine Park, black corals were usually scarce, being incapable of competing with the massive incrusting hard corals with extensive coverage which characterize these reefs. The only way an antipatharian can compete at these depths is to settle in crevices among the stony corals, and in fact, only the unbranched *C. contorta*, which occupies a minimum amount of substrate surface and is able to adapt its corallum shape to the available space, coexists with scleractinian corals (Fig. 6).

It is also possible that at greater depth, the conditions of light and water movement are optimal for several species of black corals. Sanchez et al. (1998) and Sanchez (1999) listed light attenuation, substratum inclination (shading), suspended food, flow regimes, wave exposure, and historical events as major factors explaining the distribution of black corals. In the Bunaken area, the current (in terms of intensity and direction) is the major abiotic factor determining the distribution of different species.

According to their plastic morphology, antipatharians must compromise between prey supply (enhanced by water movements) and frictional stresses (which increase in accordance with water speed) which the skeleton of the colony must face (Vogel 1981). In the Bunaken area, we recorded different forms of colonies adapted to a wide range of hydrodynamic conditions (Fig. 6). On cliffs exposed to the highest levels of water movement, we mainly recorded unbranched colonies that exploit the quick currents to obtain a suitable food supply, while the shape of their corallum minimizes frictional stresses caused by the moving water. These species solve the problem of growth by increasing their length such that they reach several meters, and at the same time, they also escape competition from other plankton feeders of the lower levels. In areas where the current direction is variable, there are forms with polyps all around the axis (*Cirripathes* spp.). In places characterized by unidirectional currents, we found polyp forms with a uniserial disposition (*Stichopathes* spp.). Observations made in the meadow of *Stichopathes* (Fig. 3D) revealed that the polyps of all of the colonies showed the same orientation. According to Warner (1981), they offer the free side to the current, so as to expose just the expanded sagittal tentacles, which turn towards the mouth, placed on the leeward side of the axis, when a prey is caught. Bottlebrush forms (*Cupressopathes* spp.) represent a compromise between the highly branched colony development and minimal frictional stresses. Ramifications arising all around the axis allow these animals to capture prey from all directions. The large arborescent and fan-shaped forms (*Antipathes* spp., *Rhipidipathes* sp., *Myriopathes myriophylla*, and *M. japonica*) with densely branched and pinnulated colonies are at the other extreme of the morphological range of black corals: they have a highly efficient filtering apparatus but their skeleton is not able to withstand very high frictional stresses. For this reason on the cliffs of the Bunaken area, we found bigger colonies of these species in protected

sites or in shallow places like vertical canyons and their borders.

It is possible to hypothesize that the presence of circadian rhythms in the expansion/contraction of polyps, as previously observed by Lewis (1978), is also related to the level of exposure to strong currents. Species living in areas of strong currents (*Cirripathes* spp. and *Stichopathes* spp.) have polyps that were contracted during the day and expanded during the night. Maintaining large, expanded polyps with long tentacles under conditions of strong water movement is energetically very expensive. It is probable that during the day, when plankton is scarce, the polyps contract to save energy, while during the night, when prey capture is highly productive due to the increasing concentration of macroplankton, polyps are expanded. In contrast, species living in areas of low water movement (*Antipathes* spp. and *Rhipidipathes* spp.) are able to keep their polyps expanded during both the day and night with a negligible increase in energy costs.

The shape of living polyps is probably also related to lifestyle: in unbranched black corals, the large polyps bend their tentacles upward, forming a basket-like structure around the mouth, while in flabellate colonies, all tentacles extend out laterally, increasing the net effect produced by the branching pattern. The basket shape seems to be more suitable for the capture of large isolated prey, whereas the net strategy optimizes the filtering of small suspended particles.

Warner (1977) described antipatharians as passive suspension feeders. But laboratory experiments performed on *Antipathes grandis* indicate that animals of this species are able to capture zooplanktonic prey like amphipods, copepods, and chaetognaths with the help of ciliary currents (Grigg 1965). Field observations made by Warner (1981) indicate that direct interception is the most important way in which food can be trapped on the feeding surfaces, and that the major free-living prey are copepods. Our observations confirmed this last interpretation: the large polyps of *Cirripathes* are able to capture any kind of macroplanktonic prey up to about 1-2 mm, but large polychaetes exceeding 1 cm in length were also taken. Lewis (1978) describes the use of a mucous-ciliary feeding strategy for fine suspended particulate matter in aquarium-reared specimens of *Cirripathes lütkeni* (Brook), *Plumapathes penancea* (Pallas), and *Antipathes* sp., as well as the occurrence of clusters of nematocysts on the tentacles and less commonly in the mesenterial fila-

ments in order to catch larger prey. However, we have never observed mucus traps ourselves; the ones expelled in Lewis' experiments (1978) were possibly due to stressed rearing conditions. Goldberg and Taylor (1989) indicated 3 trophic strategies in *Antipathella aperta* (Grange): predation, suspension feeding performed by mucous nets in part due to discharged spirocyst microfibrils, and filter feeding performed with an interconnected pharyngeal surface set for unicellular and particulate food material. The wide open mouths that we sometimes observed in *Stichopathes* and *Cirripathes* polyps during the daytime (Fig. 7C, N) can possibly be attributed to the egestion of undigested portions of prey engulfed during the night.

The highly diversified epibiotic fauna on black corals probably finds shelter due to the 3-dimensional arborescent shape of the colonies. Generally, the diversity of the epibiotic community is related to colony shape. On unbranched colonies, there was usually only 1 type of epibiont, often a couple of crabs or shrimp, while on flabellate colonies, we found a wider range of species. Some of these symbioses are already known in the literature: for example the association with errant or serpulid polychaetes, commensal cirripedes (often overgrown by the polypar coenenchyme and spiny branched sclerenchyme), anemones, sponges, bryozoans, oysters, vermetid gastropods, and crinoids (Totton 1923, Warner 1981). Less commonly known are more-specific associations with decapod crustaceans (Wirtz and d'Udekem-d'Acoz 2001), as well as mutualistic relationships with ophiuroids (Grange 1991).

We observed for the first time the death of a black coral involving caprellid amphipods (Fig. 8G-I). It was not clear if the mortality was directly due to the crustacean predation on normal colonies or if they exploited diseased colonies under stressed conditions that were unable to resist the caprellid predation.

It is known that the variety and complexity of biotic relationships, in particular coevolved ones, are directly related to the level of biodiversity of an ecosystem, but it is important to note that these relationships may be considered not only as the result but also as the source of increasing levels of biodiversity. This is particularly evident in coral reefs, one of the most diverse habitats in the world that arises from the symbiotic association of benthic organisms and zooxanthellae (Cerrano et al. 2006). Due to the high number of symbiotic relationships involving black corals, they must be considered a keystone group in the structuring of tropi-

cal coral reefs and have to be studied and preserved as a reservoir of endangered life histories.

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