With thanks & best wishes WARN

BULLETIN OF MARINE SCIENCE, 31(1): 147–163, 1981 CORAL REEF PAPER

SPECIES DESCRIPTIONS AND ECOLOGICAL OBSERVATIONS OF BLACK CORALS (ANTIPATHARIA) FROM TRINIDAD

G. F. Warner

ABSTRACT

Eight species of black coral were found off northwest Trinidad, West Indies. *Antipathes thamnea* n. sp. is described and compared with specimens of the closely related species *A. hirta* Gray, 1857 and *A. barbadensis* (Brook), 1889. Two other species, *A. atlantica* Gray, 1857 and *A. gracilis* Gray, 1860, are redescribed and compared.

A sheltered site and one exposed to strong currents were sampled; *A. gracilis* was commoner at the former site and *A. thamnea* at the latter. Most species formed fan-shaped colonies orientated normal to the mainly unidirectional currents. Fans were usually dish-shaped with polyps borne on the convex downcurrent side. Colonies of *A. atlantica* from the exposed site were found to be more densely branched and to have thicker stems than sheltered colonies. Stems from both sites were elliptical in cross section with the long axis of the ellipse at right angles to the fan. Stomachs of polyps of four species were found to contain copepod remains. The occurrence of epizoites was noted; stalked barnacles were common. The results are discussed with relation to the nutritional and mechanical aspects of suspension feeding in currents.

Between north-west Trinidad and Venezuela lies a chain of islands separated by deep (200–300 m) channels of "bocas." These channels comprise the Dragon's Mouth through which a part of the Guyana Current flows north into the Caribbean Sea (Gade, 1961). The current can be swift, particularly when aided by a falling tide, and creates turbulence in the bocas bringing relatively cool water (about 20°C) up close to the surface. The water contains considerable quantities of seston, and light attenuates with depth more rapidly than is normal in the Caribbean. The result is that, within aqualung diving depth, a cool dark environment exists in which a number of relatively deep-water organisms occur. These include ahermatypic corals, deep-water gorgonians, euryalous brittle-stars and black corals. Difficulty was experienced in the identification of three species of black coral which had pinnate branches resembling bottle-brushes. One of these is new to science and is described here under the name of *Antipathes thamnea* new species. The other two are referred to *A. hirta* Gray, 1857 and *A. barbadensis* (Brook), 1889 and these species are redescribed on the basis of the new material. Difficulty was also experienced in distinguishing two fan-shaped species, *A. atlantica* Gray, 1857 and *A. gracilis* Gray, 1860. These two species are contrasted and redescribed.

Little is known of the way of life of black corals (Grigg, 1965; Opresko, 1972) and this area provided a rare opportunity for the direct observation of colonies in the field. Observations were made on distribution, orientation, morphology of colonies under different conditions of water movement, feeding and epizoites.

METHODS

Collections and observations were made by aqualung diving. Twenty hours were spent underwater off the western coast of Huevos and about 4 h at a more sheltered site on the eastern side of Chacachacare Bay just within Point Girod (Fig. 1). Orientations of colonies on the sea bed and current directions were measured with a compass. Current speeds were estimated by timing suspended particles over measured distances. Underwater photographs were taken with a Nikonos underwater camera fitted with extension tubes and electronic flash. Polyps were relaxed with magnesium chloride

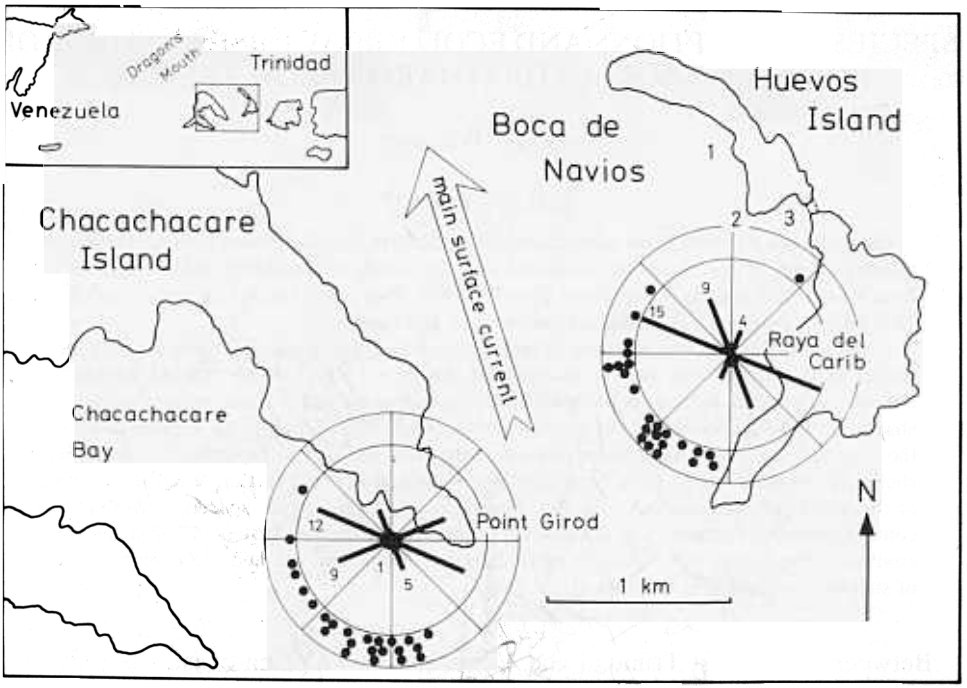


Figure 1. The study area showing orientations of fan-shaped black corals at two sites. Angular orientations of fans are shown in the circular diagrams grouped into four sets, 0–45°, 46–90°, 91–135° and 136–180°, arranged clockwise from North to South. Lengths of radiating lines indicate number of fans in each set; these numbers appear next to their lines. The position towards which the polyp-bearing side of each fan was facing is indicated by a dot in the outer circle (not all polyp-bearing sides were distinguishable). 1, 2 and 3 are sites at which additional observations were made.

and fixed in 5% calciformol. Measurements were made with an eyepiece micrometer from specimens and close-up photographs. Skeletons were prepared by soaking overnight in fresh water, washing with a jet of water and drying. Surface areas of fan-shaped colonies were estimated from traced outlines. Dimensions of stems were measured with an eyepiece micrometer. Small branches for stomach contents examination were collected with a wire cutter and fixed underwater. Polyps were separated from fine branches and squashed on a slide under glycerol. The size of the prey (copepods) was either measured directly—when the prey was intact—or was estimated from the size of an identified fragment, usually the mandible.

Descriptions of Species

Antipathes thamnea new species
Figures 2–4

Syntype Material.—Boca de Navios, N.W. Trinidad, 30 m. Eleven dried specimens and several pieces in calciformol, collected by G. F. Warner. B.M.N.H. registered nos. 1979.6.1.1–6.

Description.—Colonies mostly 20–40 cm high, but sometimes more than 50 cm, arising from holdfast of several cm². Branching irregular, usually in one plane and up to five orders. Branches pinnate, primary pinnules inclined distally through about 30° and arranged in four longitudinal rows. Pairs of primary pinnules arise alternately from sides of branches with about 2 mm between pairs on the same side. Members of pairs set at about 70° to each other, one member extends on polypar side of colony, the other extends on abpolypar side. Abpolypar pinnules

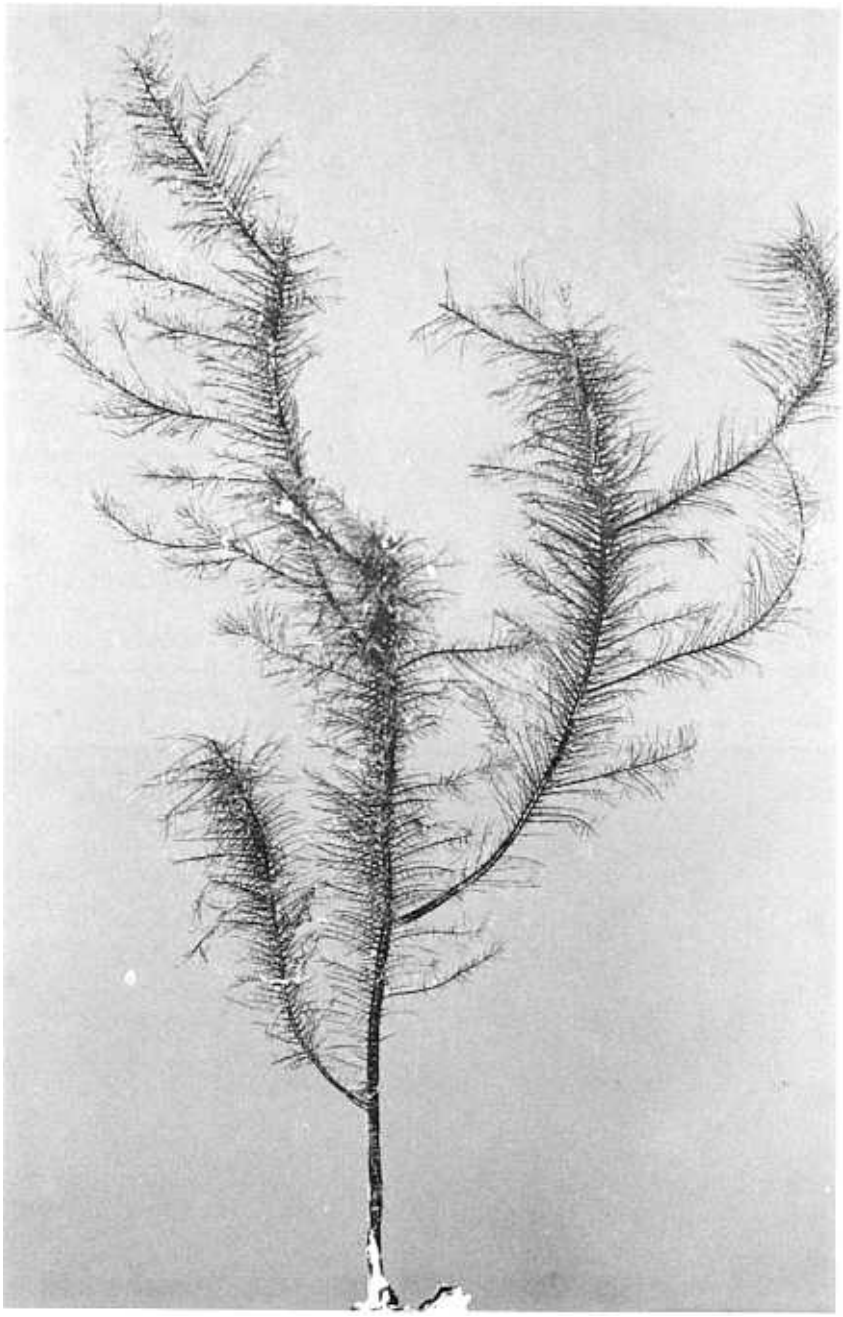


Figure 2. *Antipathes thamnea*: Colony 30 cm tall.

8–25 mm long, polypar pinnules 4–23 mm long. Angle between abpolypar rows about 115° and between polypar rows about 100°. Secondary pinnules usually numerous, 5–10 per 10 mm of primary pinnule, mostly arising from abpolypar side of primaries (Fig. 3). Tertiary pinnules usually borne on inner edges of longer

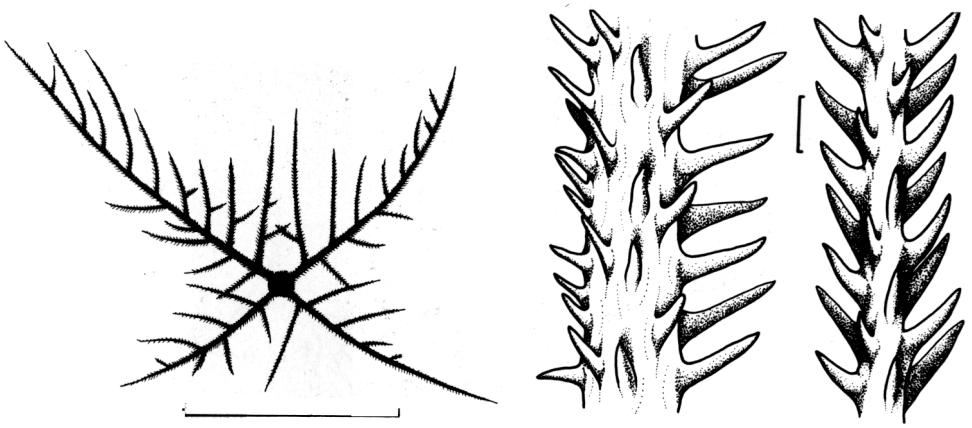


Figure 3. *Antipathes thamnea*: (Left) Section of the axis of a branch showing pinnule arrangement (scale = 1.0 cm); (Center) Spines at the proximal; (Right) Distal ends of a pinnule; polypar spines on the right (scale = 0.1 mm).

secondaries. Occasional specimens show reduced subpinnation with only one or two secondaries at base of abpolypar primaries.

Spines smooth, sub-cylindrical, inclined distally through about 37° and arranged 1–2 spine lengths apart in alternating longitudinal rows: 6–8 rows at tips of pin-

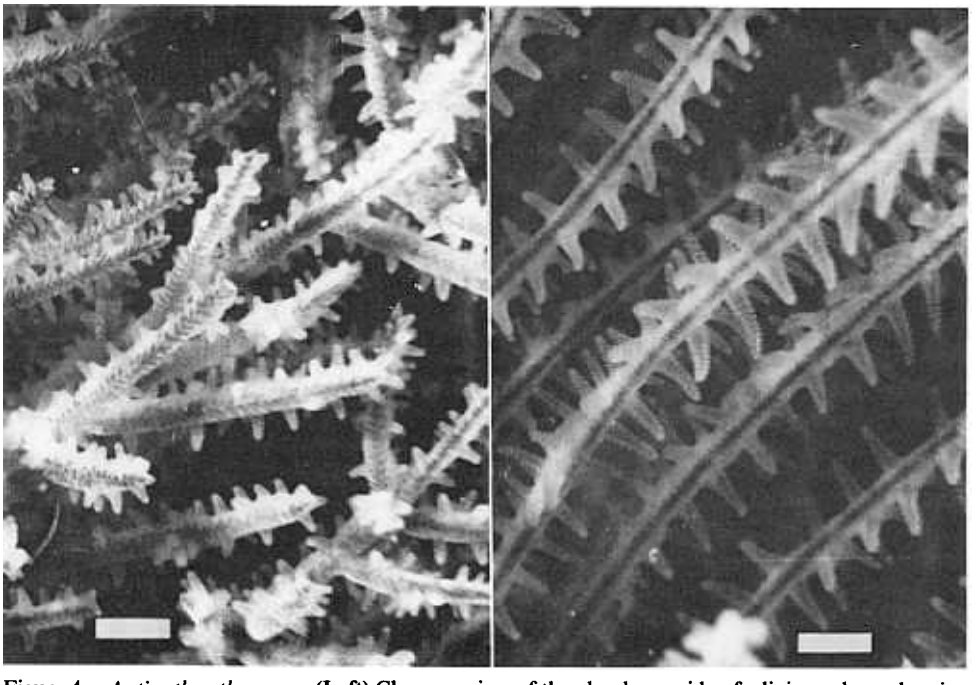


Figure 4. *Antipathes thamnea*: (Left) Close-up view of the abpolypar side of a living colony showing pinnules, tentacles and spines; scale = 1.0 mm.

Figure 5. *Antipathes hirta*: (Right) Close-up view of the abpolypar side of a living colony showing pinnules and tentacles; scale = 1.0 mm.

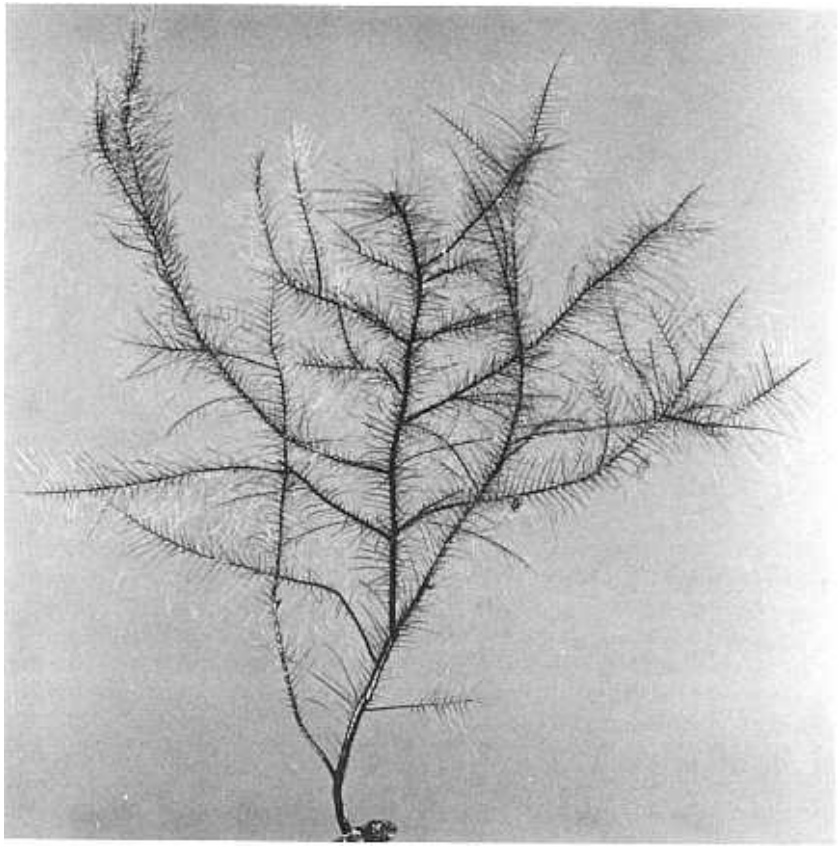


Figure 6. *Antipathes hirta*: Colony 25 cm tall.

nules. Spines 0.05–0.19 mm long (mean = 0.11, n = 50) on abpolypar side of pinnules and 0.09–0.21 mm (mean = 0.17, n = 50) on polypar side. Difference in length between polypar and abpolypar spines diminishes towards tips of pinnules. Spines on major branches often longer and more closely set than on pinnules. Polyps 0.52–0.64 mm long, arranged in rows 10–17 per cm along one side of pinnules (Fig. 4). Tentacles 0.3–0.7 mm in live material and a third to half shorter in relaxed fixed material.

Habitat.—Rocky substrates exposed to strong currents.

Antipathes hirta Gray, 1857 and *Antipathes barbadensis* (Brook), 1889
Figures 5–9

These two species closely resemble *A. thamnea* in morphology, branching and pinnation. Differences arise in details of pinnation and in the size of spines and polyps.

Material.—Boca de Navios, N. W. Trinidad, 30 m. *A. hirta*, four dried specimens and several pieces in calciformol, collected by G. F. Warner. B.M.N.H. registered nos. 1979.6.2.1–4. *A. barbadensis*, two dried specimens and several pieces in calciformol, collected by G. F. Warner. B.M.N.H. registered nos. 1979.6.3.1–3.

Descriptions.—*A. hirta* differs from *A. thamnea* as follows: angle between ab-

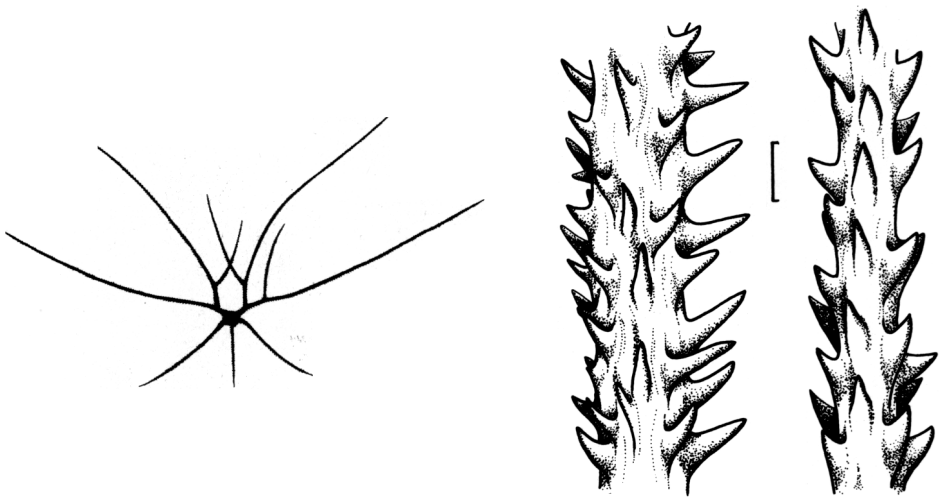


Figure 7. *Antipathes hirta*: (Left) Section of the axis of a branch showing pinnule arrangement; scale = 1.0 cm; (Center) Spines at the Proximal; (Right) Distal ends of a pinnule; polypar spines on the right; scale = 0.1 mm.

polypar primary pinnules 130–180°; a fifth row of primary pinnules arising from polypar sides of branches is frequent in *A. hirta* but rare in *A. thamnea*; secondary and tertiary pinnation sparse but basal abpolypar secondaries often relatively long. Abpolypar spines at bases of pinnules 0.04–0.13 mm long (mean = 0.07, n = 20), polypar spines 0.09–0.17 mm long (mean = 0.11, n = 20). Polyps 10–14 per cm, 0.6–0.8 mm long with tentacles in life 0.6–1.3 mm long (Fig. 4).

Pinnation in *A. barbadensis* is less regular than in *A. thamnea* and *A. hirta*. Primary pinnules are up to 45 mm long in 4–5 rows, subpinnation sparse (Fig. 9). Spines inclined distally through about 45°, 0.5–1.5 spine-lengths apart in a row; polypar and abpolypar spines on pinnules 0.12–0.23 mm long (mean = 0.18, n = 40). Polyps 10–14 per cm, 0.5–0.7 mm long, relaxed fixed tentacles 0.2–0.6 mm long.

Remarks.—The present description of *A. hirta* fits with that given by Opresko (1972) except that he described more subpinnation and gave tentacle length as 0.2 mm; these tentacles were probably strongly contracted. For *A. barbadensis* the present description is similar to that of Brook (1889) for *Aphanipathes barbadensis* except that Brook's specimens lacked polyps. However, Brook (and Opresko, personal communication) described *A. barbadensis* as unbranched whereas my specimens merely show a lower frequency of branching than is shown by *A. thamnea* and *A. hirta*. Following Opresko's (1972) redefinition of *Aphanipathes* it seems correct to transfer this species to *Antipathes*.

The above descriptions unambiguously distinguish *A. thamnea, A. hirta* and *A. barbadensis* on the basis of extent of subpinnation, spine length and polyp size.

Antipathes atlantica Gray, 1857 and *Antipathes gracilis* Gray, 1860
Figures 10–13

These two species form flabellate colonies up to about 0.3 m^2 in area with some anastomosis between branches. Brook (1889) pointed out the shortcomings of

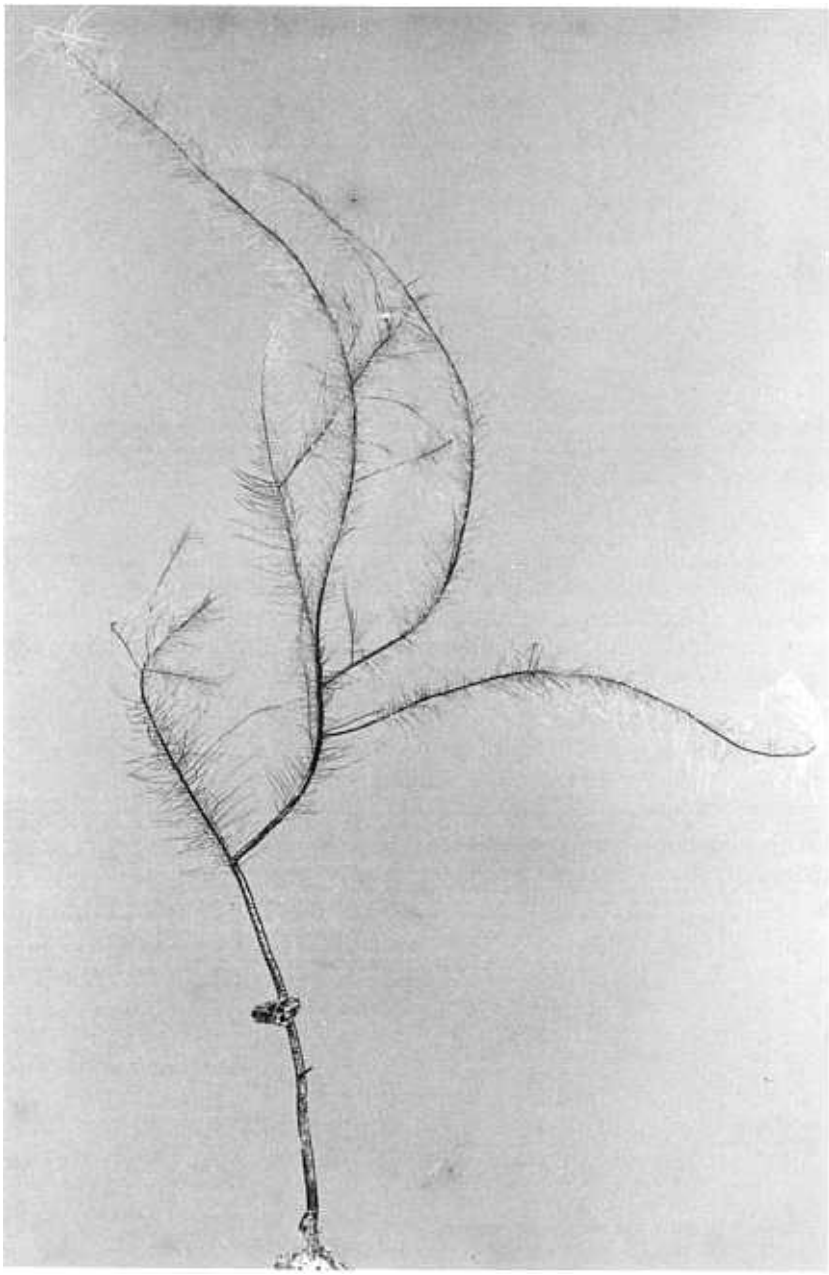


Figure 8. *Antipathes barbadensis*: Colony 61 cm tall.

Gray's (1857; 1860) descriptions, particularly of *A. gracilis*, and the lack of evident type specimens, but nevertheless redescribed the two species on the basis of dried material in the British Museum (Natural History) which he believed represented Gray's type material. These descriptions are not helpful in separating the two species. On colony morphology *A. atlantica* was described as more

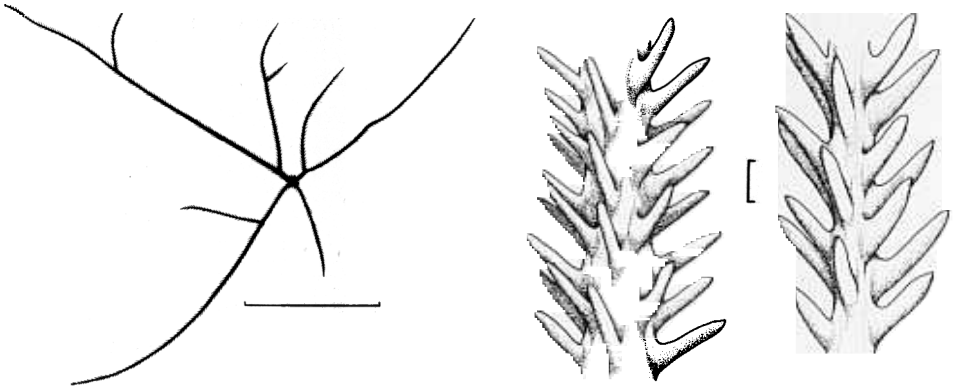


Figure 9. *Antipathes barbadensis*: (Left) Section of the axis of a branch showing pinnule arrangement; scale = 1.0 cm; (Center) Spines at the proximal; (Right) Distal ends of a pinnule; polypar spines on the right; scale = 0.1 mm.

delicate and less bushy than *A. gracilis* and the spines on the branches were described as being arranged respectively in "steep sinistrorse spirals" and "dextrorse spirals which are not nearly as steep" (as in *A. atlantica*). Delicacy and bushiness are influenced by the environment (see below) and spine arrangement was regarded as an unreliable taxonomic character by Opresko (1972).

Material.—Boca de Navios, N. W. Trinidad, 30 m. *A. atlantica,* 37 dried specimens and several pieces in calciformol. *A. gracilis,* 14 dried speicmens and several pieces in calciformol. Discovery Bay, Jamaica, 30 m, *A. atlantica,* two dried specimens.

Descriptions.—Living *A. atlantica* from Trinidad were gelatinous grey sometimes tinged with pink but from Jamaica were greenish. Branching irregular, alternately pinnate, mostly in one plane and to 8–9 orders in larger colonies (Fig. 10). Branch-



Figure 10. *Antipathes atlantica*: (Left) Colony 41 cm tall.

Figure 11. *Antipathes gracilis*: (Right) Colony 40 cm tall.

Table 1. Dimensions of polyps of two black coral species from Trinidad taken from underwater photographs (Figs. 12, 13); all lengths in mm; tentacle length in relaxed fixed material is a third to a half shorter

	Antipathes gracilis	*Antipathes atlantica*
	$\bar{x}$	
Tentacle length	44	80
Polyp length	27	49
No. polyps per cm branch	24	37

ing often sympodial and main branches frequently deliquescent. Anastomosis common and often forming a reticulum. Spines on fine branches in about eight alternating longitudinal rows, 0.03–0.07 mm long and 3–5 spine lengths apart in a row, Polyps of Trinidad specimens, see Table 1; polyps of Jamaican specimens similar but tentacles up to 3.0 mm long.

Living *A. gracilis* were bright orange-red. Branching irregular, alternately pinnate, mostly in one plane and to 8–9 orders in larger colonies (Fig. 11). Branching usually monopodial and main branches generally excurrent. Anastomosis fairly frequent but not forming a reticulum except at base of larger colonies. Spines identical to *A. atlantica*. Polyps, see Table 1.

Remarks.—Color and slight differences in polyp size can aid identification of live and preserved material but identification of dried material depends upon arbitrary differences in branching pattern. In *A. gracilis* the main branches are generally relatively thick and straight and are recognizable as primary supports right out to the distal margin of the colony (excurrent). In *A. atlantica,* however, the main branches are less easy to distinguish and their supporting function may not persist to the distal edge, being taken over by a subsidiary branch or by the reticulum (deliquescent). These differences sound distinct but in practice are not so because branching frequency, which affects apparent branching pattern, is strongly influenced by the environment (see below). Thus in my collections there are two colonies of each species (judged by color in life) which could not have been identified by branching pattern alone.

Ecological Observations

The Environment: Topography and Currents

The islands of Huevos and Chacachacare (Fig. 1) are rocky and steep and this topography continues underwater to at least 50 m deep. Currents off the western coast of Huevos at 20–40 m were very variable. Speeds of 10–15 cm sec^{-1} were frequent but the range was from almost zero to currents so strong that diving was impossible. Current direction was mostly southward but reversals to a northward flow were sometimes observed and might last from 5 to more than 30 min. Direction along the bottom was influenced by topography; the current followed the contours of the slope unless this became irregular in which case eddies were often observed. These long-shore currents appear to be part of a counter-current system induced by the main northward flow in the Boca de Navios (Fig. 1).

Currents at 20–40 m at the site in Chacachacare Bay were never too strong for diving. Current speed was usually 5–10 cm sec^{-1} and direction was generally towards the south-east, out of the mouth of the bay. This direction, however, was often masked by the tendency of the current to follow the contours of the slope in and out of a series of small bays along the inside of Point Girod (Fig. 1).

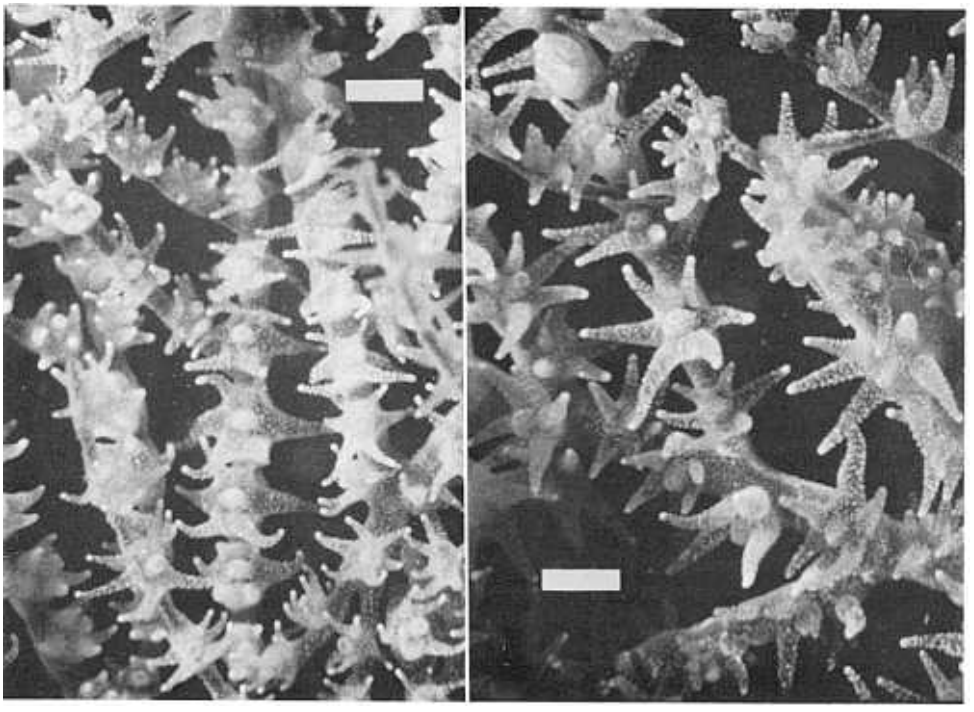


Figure 12. *Antipathes atlantica*: (Left) Close-up view of the polypar side of a living colony; scale = 1.0 mm.

Figure 13. *Antipathes gracilis*: (Right) Close-up view of the polypar side of a living colony; scale = 1.0 mm.

RESULTS

Occurrence and Distribution.—Eight species of antipatharian were collected in the area. These were *Cirripathes lütkeni* Brook, *Antipathes pennacea* Pallas, *A. furcata* Gray, *A. gracilis, A. atlantica, A. hirta, A. barbadensis* and *A. thamnea* new species. All species were attached firmly to rocks by a holdfast of skeletal material which spread over several cm^2 in an irregular disc.

To investigate the distribution and morphology of these species with relation to current strength, collections were made off Point Girod just inside Chacachacare Bay (sheltered) and off Raya del Carib (exposed). All colonies, except those of *C. lütkeni,* which were seen during a 20-min dive at each site, were collected.

Table 2. Numbers of specimens collected on two 20-min dives at two sites

	Raya del Carib (exposed)	Point Girod (sheltered)
A. atlantica		
A. gracilis		
A. furcata	1	
A. thamnea	10	
A. hirta		2
A. barbadensis		2

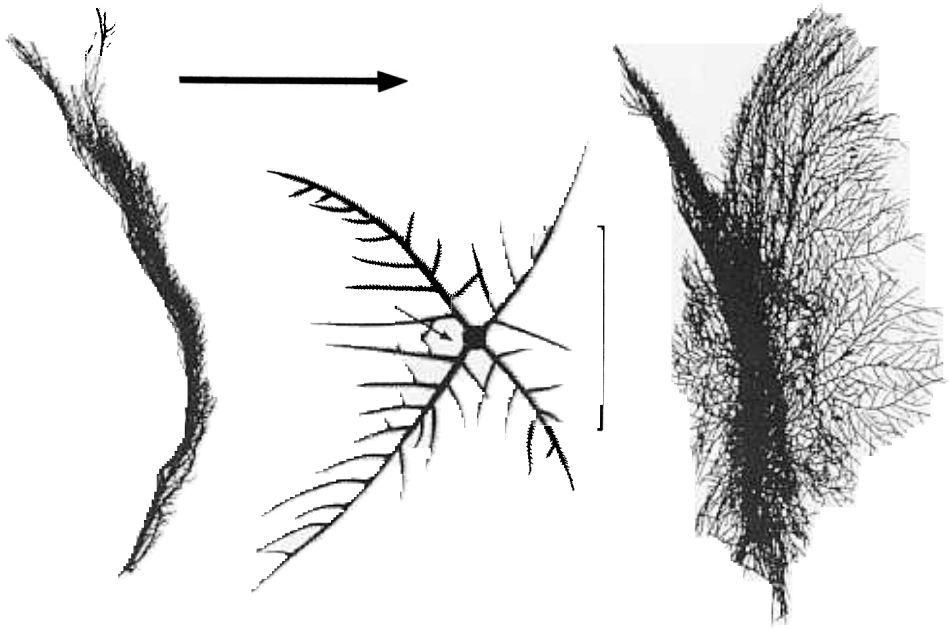


Figure 14. Skeleton form and current direction. (Left) Side view of a 15 cm high piece of an *A. atlantica* colony showing the bushy nature of the convex leeward side. (Center) View along the axis of a branch of an *A. thamnea* colony showing pinnule arrangement; scale = 10 mm. Large arrow indicates normal current direction, small arrow indicates position of a common epizoic polychaete worm. (Right) Oblique side view of an *A. atlantica* colony 19 cm high by 21 cm wide orientated to face in opposite directions.

The numbers of each species are shown in Table 2. *A. pennacea* is rare in this area and was not seen during these dives. The results suggest that *A. gracilis* is commoner in sheltered areas and *A. thamnea* is more frequent in areas exposed to stronger currents. *A. atlantica* is common in both environments. Notes made on other dives support these conclusions.

Orientation and Current Direction.—Most colonies of all species (except *C. lütkeni* which is unbranched) adopt a fan-like growth form. These fans, except in *A. furcata,* were usually dish-shaped with a concave abpolypar side and a convex polypar side (Figs. 4, 5, 12, 13, 14, 18). One hundred observations of colony orientation and, where possible, polyp position were made at sites marked in Figure 1.

At sites 1, 2 and 3 the sea bed was irregular and current direction very variable. Colonies were often seen orientated normal to local currents but consistent orientation over a wide area was not found. Inside Point Girod and off Raya del Carib the current pattern was less complex and orientation was more consistent. At Point Girod 27 measurements comprising 20 *A. atlantica,* 3 *A. gracilis,* 2 *A. furcata* and 2 *A. thamnea* were taken; off Raya del Carib 28 measurements comprising 9 *A. atlantica,* 16 *A. thamnea,* 2 *A. furcata* and 1 *A. gracilis* were taken. The results are shown in Figure 1. Off Raya del Carib most fans were orientated normal to the southward current and inside Point Girod orientation was normal to the longshore currents as they followed the contours of the slope

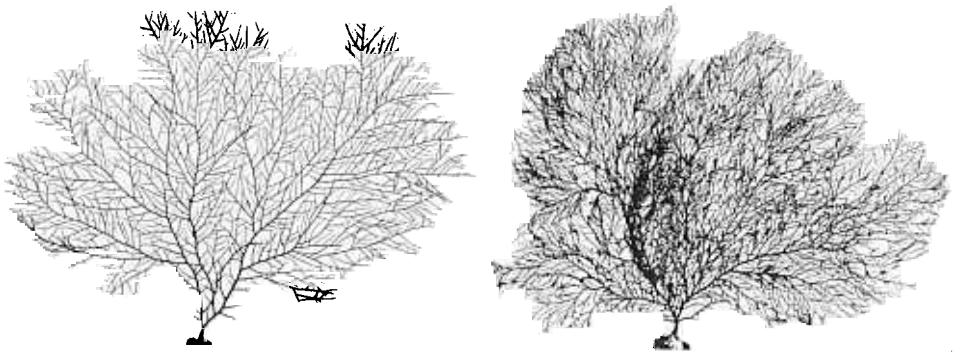


Figure 15. Colonies of *A. atlantica*. (Left) 19 cm high from a sheltered site. (Right) 21 cm high from an exposed site.

out of the small bays and towards the headland. The convex polypar sides of fans almost always faced downcurrent. Observations on other occasions supported these findings.

Smaller-scale features of colonies which relate to current direction were also observed. In *A. atlantica*, and to a lesser extent in *A. gracilis*, the convex leeward side has a bushy appearance in comparison with the concave windward side which appears rather smooth (Fig. 14). This results from the fact that most of the numerous short fine branches which arise from the major branches do so at an angle to leeward of the plane of the colony of about 20°. The tips of these fine branches bend further to leeward and so project downcurrent. In contrast, the concave windward sides of *A. thamnea* and *A. hirta* colonies are more bushy than the leeward sides. This is because abpolypar pinnation is more extensive than polypar pinnation (Figs. 3, 7). The arrangement with relation to current is shown in Figure 14.

Bushy colonies without clear orientation were sometimes found in areas that appeared to lack a prevailing current: turbulent areas in the lee of large rocks, or shallower sites (10–15 m) where water movement produced by waves on the surface was at right angles to the longshore current. Antipatharians were not common in shallow water but occasionally *A. atlantica* was found in this environment. One specimen of *A. atlantica* collected off Raya del Carib from an area apparently between two opposing eddies showed unusual orientation (Fig. 14). This colony arose from a single base to form two dish-shaped fans joined polypar side to polypar side allowing it to face simultaneously in opposite directions.

Colony Morphology and Current Speed.—Table 2 shows that the only species which was plentiful at both sheltered and exposed sites was *A. atlantica*. A comparison of the skeletons of these specimens was made to investigate the effects of exposure to different current speeds. The following measurements were taken from each specimen: area of fan, number of branches arising along a 10-cm length of branch in the distal parts of the colony (mean of five measurements, referred to as the branching index), and the diameter of the stem just above the holdfast at right angles to the fan (*a*) and parallel to the fan (*b*). Stems were roughly elliptical in cross-section and *a* was almost always the major axis. Diameters were used to calculate cross-sectional area and the ratio *a*/*b* which measures ellipticity at right angles to the fan (1 = a circular stem). A summary of the results is given in Table 3. The main findings were that colonies from Raya del

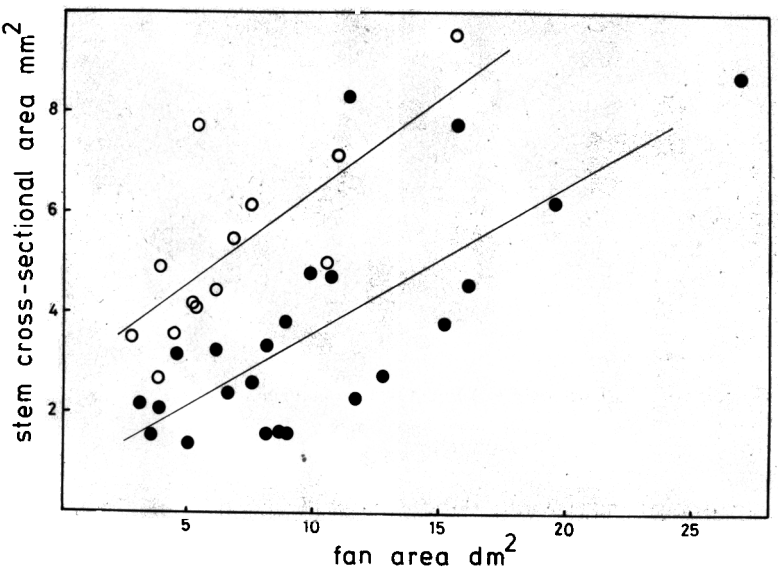


Figure 16. The relationship between fan area and stem cross-sectional area in colonies of *A. atlantica* from a sheltered site (closed circles) and an exposed site (open circles). Lines, fitted by least squares method, are significantly different ($P < 0.001$).

Carib, exposed to strong currents, were more densely branched and had thicker stems than those from the sheltered Point Girod site (Fig. 15, 16).

Stems from Raya del Carib showed slightly more ellipticity at right angles to the fan than did those from Point Girod but the difference was not significant.

Lack of sufficient material prevented detailed studies on the morphology with relation to current of the other fan-shaped black corals. There was evidence, however, of increased branching in *A. gracilis* in exposed environments and elliptical stems, like those of *A. atlantica,* were noted in all fan-shaped species. In addition, ellipticity was frequently observed in main branches of colonies. Stem and branch cross-sections were usually not perfect ellipses: they tended to be parallel sided with semi-circular ends.

Feeding.—Undisturbed leeward polyps of all species were observed to dispose their six tentacles in a characteristic pattern. The middle or sagittal pair of tentacles is generally the longest and these were extended laterally and aborally, across and somewhat into the current. The proximal and distal pairs were ex-

Table 3. Measurements of specimens of *A. atlantica* from sites differing in current strength (SD = standard deviation)

	Raya del Carib (exposed)	Point Girod (sheltered)
Range of fan areas, cm²		
Range of stem areas, mm²		
Mean branching index (SD)		
Mean stem ellipticity, *a/b* (SD)		
Number in sample		

* Significantly different, $P < 0.001$.

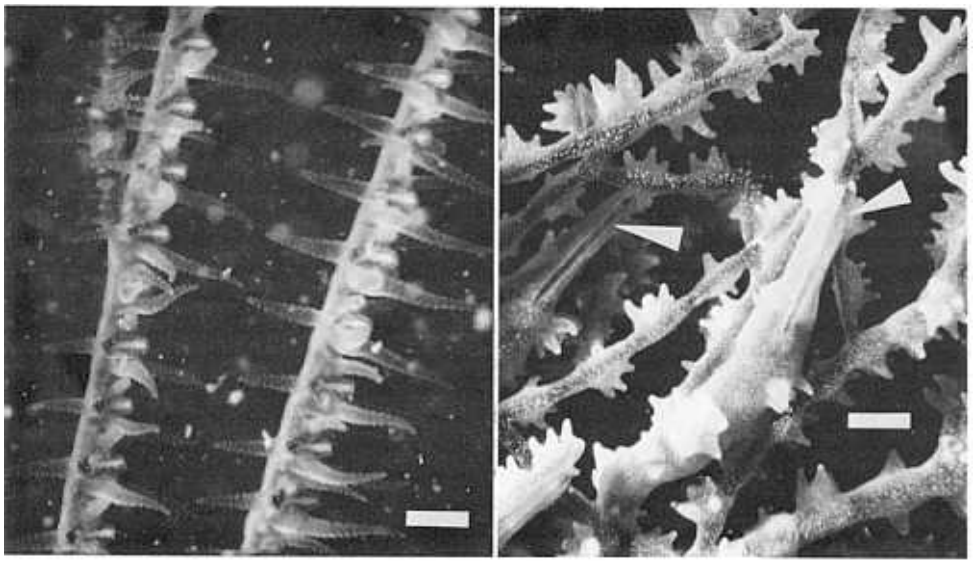


Figure 17. *A. furcata*: (Left) Side view of polyps with tentacles extended. Oral cones are to the right of each branch, current from left to right. Scale = 1.0 mm.

Figure 18. *A. atlantica*: (Right) Abpolypar side of living colony; arrows indicate stalked barnacles facing the current. Scale = 10 mm.

tended obliquely downcurrent. This posture is shown clearly in Figures 5 and 17, the tentacles forming four rows down the length of each branch.

Parts of colonies were collected for later examination of stomach contents. The contents of 25 polyps of *A. atlantica*, *A. gracilis*, *A. furcata* and 25 pairs of polyps of *A. thamnea* were examined. Whole copepods and pieces of copepod were the only items found sufficiently often and in sufficient bulk to be considered important as food (Table 4). Phytoplankton and detritus were hardly ever present.

Epizoites.—Most colonies supported epizoites. The commonest were stalked barnacles; several can be seen in Figure 18 and the fan on the right in Figure 15 bears 285 barnacles. Stalked barnacles were always orientated so that the cirri, when extended, formed a dish-shaped net facing to windward—tiny dishes within the main dish of the antipatharian colony. In all barnacles that were examined closely it was observed that antipatharian tissue had grown over the stalk and valves (Fig. 18). Another common epizoite, an errant polychaete, was found on almost every colony of *A. thamnea* and sometimes on *A. hirta*. This worm lived in a tube-shaped cage formed by the pinnules of the black coral: it lay along the

Table 4. Stomach contents of the polyps of four species

	Number polyps examined	Polyp length (mm)	Live tentacle length (mm)	Preparations containing copepods	Copepods body length (mm)
A. furcata	25			12	0.72–1.18
A. gracilis	25			9	0.76–0.87
A. atlantica	25			6	0.94–1.47
A. thamnea	25 pairs			8	0.80–1.70

windward side of the axis of a branch enclosed by rows of primary, secondary and tertiary pinnules (Fig. 14). Other epizoites included anemones, sponges, bryozoans, serpulid polychaetes, acorn barnacles, oysters, vermetid gastropods and crinoids.

Discussion

Orientation.—Orientation normal to current direction in fan-shaped suspension feeding organisms has often been described (Warner, 1977). Leversee (1976) showed that it was an efficient orientation for food capture and Wainwright and Dillon (1969) demonstrated its hydrodynamic stability in wave-induced oscillation. Dish-shaped filter-feeding structures with the concave side facing the current have also been observed. Dish-shapes occur in gorgonians (Theodor, 1963; Grigg, 1972; Warner, 1977; Muzik and Wainwright, 1977), in some echinoderms (Macurda and Meyer, 1974; Meyer and Lane, 1976) and on a smaller scale in such animals as barnacles, porcelain crabs and black fly larvae (*Simulium*). Simple experiments with models (Warner, 1977) suggested that a dish-shaped filtering structure with concave side to the current traps more of the available particles than a flat structure of the same surface area. Thus dish-shapes are probably nutritional adaptations to unidirectional flow.

The leeward location of polyps also has precedents in the literature (Wainwright et al., 1976; Svoboda, 1976; Muzik and Wainwright, 1977; Warner, 1977). A likely advantage is that food particles may be more easily captured in turbulent eddies to leeward than in parts of colonies exposed to direct current flow (Wainwright et al., 1976; Leversee, 1976; Warner, 1977). Branches of many species of black coral appear to bear polyps on one side only (Opresko, 1972) and it is tempting to suggest that this indicates a general adaptation to life in unidirectional currents. Black corals are mainly deep-water organisms, not usually affected by wave action (Grigg, 1965), and perhaps the presence of unidirectional ocean currents is a frequent feature of their main habitats.

Morphology and Current Speed.—Studies on the form of the gorgonian *Eunicella* from sheltered and exposed environments have shown that exposure, in this case to wave action, reduces branching frequency and increases the thickness of branches (Velimirov, 1976). These adaptations presumably minimize drag and increase the strength of the branches. In *A. atlantica* the increase in branching with exposure to stronger currents is likely to increase drag. A possible explanation is that, for each hydrodynamic regime, a balance exists between axial growth and growth by branching, this balance acting to keep the current speeds to which the colonies are exposed within limits. Axial growth might be favored in a weak current allowing rapid increase in fan area and extension into mainstream currents; in stronger currents branching growth might be favored, slowing down the rate of increase in fan area and avoiding, for a time, exposure to mainstream currents. On this model, assuming equal growth rates, one would predict that colonies from the sheltered site would be younger than colonies of the same fan area from the exposed site. An alternative possibility is that the greater branching in exposed colonies serves, by increasing drag, to slow down the current flowing past the polyps. A relatively slow current through the tentacles may be important in feeding. In both cases one might expect thicker stems in exposed colonies: on the first hypothesis their thickness would be due to greater age, and on the second, it would be an adaptation to resist greater drag.

The elliptical stem cross-section with the long axis of the ellipse at right angles to the fan—parallel to the water flow in the environment—resists bending forces

normal to the fan better than would a circular cross-section of the same area (Wainwright et al., 1976). This adaptation has been recorded in some gorgonians (Muzik and Wainwright, 1977) but the opposite adaptation—the long axis of the ellipse parallel to the fan—occurs in other gorgonians where it serves to facilitate bending in environments subject to wave action (Wainwright and Koehl, 1976). In the black corals the adaptation helps colonies to stand upright in currents, no doubt so that they can continue to filter the water for food. The ellipticity observed in main branches of colonies should reduce bending in the distal parts of fans but, as pointed out by Wainwright and Koehl (1976), it also streamlines the branches.

In the gorgonian *Eunicella* more polyps per cm branch were found in colonies from an exposed site (Velimirov, 1976); this may be a result of the greater branch thickness in exposed colonies. In *A. atlantica* the polyps usually occur in a single row along one side of a branch and no differences were observed either in size of polyps or in the number of polyps per cm between sheltered and exposed colonies. Owing to the greater branching index of exposed colonies, however, there were many more polyps per cm^2 of fan surface in specimens from the exposed site than from the sheltered site.

Feeding.—Lewis (1978) studied the feeding of various antipatharians in the laboratory and reported trapping by nematocysts of animal plankton and ingestion of fine particles embedded in a mucus net. My observations of stomach contents suggest that off Trinidad the former method is probably the most important. A surprising result is that the largest copepod was caught by *A. thamnea,* the species with the smallest polyps (Table 4). It is possible that neighboring polyps cooperate to secure such large prey.

Using the dimensions of tentacles and prey it was calculated, following Rubenstein and Koehl (1977), that in all four species of black coral direct interception was the most important way in which the food encountered the feeding surfaces. Mobile particle deposition is another possibility considering the live nature of the food. However, consideration of the size of the copepods and the dense branching of the corals suggests that colonies probably make quite efficient sieves. To avoid being sieved a copepod would have to fold its antennae and dive through a space between polyps; it would then be caught in the zone of turbulence and the polyps would be given a second chance of catching it—I have observed particles swirling in turbulent eddies amongst leeward polyps.

Acknowledgments

I am grateful to Dr. D. M. Opresko for helpful identifications and correspondence and to Dr. P. F. S. Cornelius for his criticism of the taxonomic part of the manuscript. I also thank Dr. D. Ramsaroop and Mr. I. Younglao for considerable help in the field.

Literature Cited

Brook, G. 1889. Report on the Antipatharia. Challenger Reports, Zoology 32. vi + 222 pp.

Gade, H. G. 1961. On some oceanographic observations in the southeastern Caribbean Sea and the adjacent Atlantic Ocean with special reference to the influence of the Orinoco River. Bol. Inst. Oceanogr. Univ. Oriente 1: 287–342.

Gray, J. E. 1857. Synopsis of the families and genera of axiferous zoophytes or barked corals. Proc. Zool. Soc. Lond. 25: 278–294.

———. 1860. Notice of new corals from Madeira. Ann. Mag. Nat. Hist. Ser. 3, 6: 311.

Grigg, R. W. 1965. Ecological studies on black coral in Hawaii. Pacif. Sci. 19: 244–260.

———. 1972. Orientation and growth form of sea fans. Limnol. Oceanogr. 17: 185–192.

Leversee, G. 1976. Flow and feeding in fan-shaped colonies of the octocoral, *Leptogorgia virgulata.* Biol. Bull. 151: 344–356.

Lewis, J. B. 1978. Feeding mechanisms in black corals (Antipatharia). J. Zool. Lond. 186: 393–396.
Macurda, D. B., and D. L. Meyer. 1974. Feeding posture of modern stalked crinoids. Nature Lond. 247: 394–396.
Meyer, D. L., and N. G. Lane. 1976. The feeding behaviour of some paleozoic crinoids and recent basketstars. J. Paleont. 50: 472–480.
Muzik, K., and S. Wainwright. 1977. Morphology and habitat of five Fijian sea fans. Bull. Mar. Sci. 27: 308–337.
Opresko, D. M. 1972. Redescriptions and reevaluations of the antipatharians described by L. F. De Pourtalès. Bull. Mar. Sci. 22: 950–1017.
Rubenstein, D. I., and M. A. R. Koehl. 1977. The mechanisms of filter feeding: some theoretical considerations. Am. Natur. 111: 981–994.
Svoboda, A. 1976. The orientation of *Aglaophenia* fans to current in laboratory conditions (Hydrozoa, Coelenterata). Pages 41–48 *in* G. O. Mackie, ed. Coelenterate ecology and behavior. Plenum, New York.
Theodor, J. 1963. Contribution à l'étude des gorgones. 3. Vie Milieu 14: 815–818.
Velimirov, B. 1976. Variations in growth forms of *Eunicella cavolinii* Koch (Octocorallia) related to intensity of water movement. J. Exp. Mar. Biol. Ecol. 21: 109–117.
Wainwright, S. A., W. D. Biggs, J. D. Curry, and J. M. Gosline. 1976. Mechanical design in organisms. Arnold, London. 423 pp.
Wainwright, S. A., and J. R. Dillon. 1969. On the orientation of sea fans (genus *Gorgonia*). Biol. Bull. Mar. Biol. Lab. Woods Hole 136: 130–139.
Wainwright, S. A., and M. A. R. Koehl. 1976. The nature of flow and the reaction of benthic cnidaria to it. Pages 5–21 *in* G. O. Mackie, ed. Coelenterate ecology and behavior. Plenum, New York.
Warner, G. F. 1977. On the shapes of passive suspension feeders. Pages 567–576 *in* B. F. Keegan, P. O'Ceidigh and P. J. S. Boaden, eds. Biology of benthic organisms. Pergamon, Oxford and New York.

DATE ACCEPTED: May 19, 1980.

ADDRESS: *Department of Zoology, The University, Whiteknights, Reading, RG6 2AJ U.K.*