

Ecological Studies of Black Coral in Hawaii¹RICHARD W. GRIGG²

THE BLACK CORALS (Order Antipatharia) are found in all oceans. However, the great majority of the 150 species have been collected with dredges below the limits of human observation (see Table 1). It is therefore not surprising that very little ecological work has been done within this group. The anatomy and taxonomy have been reviewed by Brook, 1889, Cooper, 1907-1909, and Van Pesch, 1914.

In 1958 off Lahaina, Maui, Jack Ackerman and Larry Windley, using SCUBA equipment, accidentally discovered a vast "bed" of black coral in 50 m of water. Previous to this find, the black coral *Antipathes grandis* Verrill had rarely been observed in Hawaii. Only occasionally had divers found stunted colonies in shallow caves where surge was not excessive.

At least three species of black coral are represented in the Hawaiian Islands, all limited to deeper water generally beyond 30 m. Only one species has been recorded in the literature, *A. grandis*, and since it is the most common form, it was selected for this study (Fig. 1).

The purpose of this research was to study and delineate the ecological factors which limit the distribution of this animal to deeper water.

METHODS AND MATERIALS

Plan of Work

A series of stations was selected, some with and some without colonies of actively growing *A. grandis* (Fig. 2). Over a period of six months, hydrographic data were collected: light penetration, current, turbidity, surge, oxygen concentration, salinity, temperature, and depth. In addition, the texture and type of substrate were analyzed and population counts were made. By so doing, a comparison between stations could

readily be made and the factors limiting distribution could be outlined.

Branches of the living colonies were transplanted to various habitats, where regular observations could be made to determine if the animal was alive, dying, or dead. These transplants were put in places where it was hoped the effects of environmental extremes could be discovered. For example, the headland off Moku Manu Islands, Oahu, was selected because here wave action and surge reach a maximum, while turbidity, oxygen concentration, salinity, and temperature are relatively constant. On the other hand, the muddy bottom of Kaneohe Bay, Oahu, was also used, for it is extremely turbid, with no excessive fluctuations in salinity, oxygen concentration, temperature, and surge. Thus, it was attempted to measure one factor while keeping the other factors relatively stable, thereby using the environment as a natural laboratory. Experiments in the laboratory were impractical because of the problem involved with handling the animal.

Collection of Data

LIGHT: Light measurements were carried out with a flat plate irradiance meter which was calibrated with a footcandle meter. Two photoelectric cells were first connected to a galvanometer which was adjusted to a zero reading

TABLE 1

THE BATHYMETRIC DISTRIBUTION OF 66 SPECIES OF ANTIPATHARIA COLLECTED BY THE CHALLENGER EXPEDITION DURING THE YEARS 1872-1876 (BROOK, 1889)

ZONE	METERS	NUMBER OF SPECIES
1	0-18	6
2	18-183	25
3	183-914	26
4	914-1,829	2
5	1,829-3,658	3
6	3,658-5,486	4

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FIG. 1. Large colony of *A. grandis*, at 58 meters, off Lahaina, Maui (Station 9). It is approximately $3\frac{1}{2}$ meters across and 2 meters high. Photo by Ron Church.

while the two cells were exposed to full sunlight. Then one cell was lowered to the bottom and the difference in electrical potential was measured with the galvanometer. This value can be converted to percent surface light or to $\text{gm cal. cm}^{-2} (24 \text{ hr})^{-1}$, and plotted against depth (Fig. 6).

These measurements were taken at an hour when the sun was at maximum altitude on days when turbidity was at a minimum. Thus it was attempted to measure the maximum penetration of light for a particular depth.

TURBIDITY: Samples of water were collected from various stations and analyzed with a Tyndall meter so that turbidity values could be compared. Since only relative values were required, it was not necessary to calibrate the Tyndall meter.

OXYGEN CONCENTRATION: Dissolved oxygen was measured by the Modified Winkler Method (Hydrographic Office Pub. No. 607).

SALINITY: The Knudsen Method was employed to measure chlorinity, which is easily converted to salinity by the formula: $\text{Salinity} = 0.03 + (1.805 \times \text{chlorinity})$ (Hydrographic Office Pub. No. 607).

TEMPERATURE: Temperature as a function of depth was recorded by using a bathythermograph. Data were also collected with a simple 110° Celsius thermometer carried to the bottom by a diver. Temperature increase due to hydrostatic pressure was assumed to be negligible and thus was not taken into account.

SUBSTRATE: Portions of the substrate were chiseled with an axe and sledge hammer and

carried to the surface by a diver. The substrate was examined for special features such as texture and chemical composition (e.g., CaCO_3 or basalt). It was possible to draw bottom profiles of the substrate *in situ*, using a grease pencil and plastic slate.

CURRENTS: Currents were measured in three ways. Data off Sandy Beach, Oahu, and Kaena Point, Oahu, were collected with the aid of the research vessel "Neptune I." In these cases, surface currents were measured by tracking the movement of drifting current crosses.

The Carruthers' Current Cone (Carruthers, 1957) was used when sampling was carried out in an 18-foot skiff. It operates on a waer-resistance principle, much like a flag fluttering in the wind. Attached to a stationary line, the cone is lifted by the current at an angle proportional to the intensity of flow. At this point a dissolving cube of sugar triggers the device so that a reading is obtained. Observations of this instrument during use showed that the angle of the cone at any one instant was highly variable, subject to the oscillatory movements of surge

and swell. Hence, under very rough conditions this instrument is not accurate.

The third, and simplest, method of measuring current (and the most accurate) was timing the horizontal drift of suspended particles over a known distance. Currents less than 0.5 knots were referred to as slight, from 0.5 to 1.5 as moderate, and over 1.5 knots as heavy.

SURGE: Surge is herein defined as a back-and-forth movement of water over short distances which is generally caused by long waves (swell). It is dependent upon the amplitude and the wavelength of the swell. The period of oscillation usually varies between 6 and 16 seconds. The movement of water particles in waves with short wavelengths is nearly circular at the surface. The radii of these circles decrease exponentially with depth and are imperceptible at a depth which equals the wavelength (Sverdrup, Johnson, and Fleming, 1940). In waves with longer wavelengths, the movement of water particles follows a more elliptical orbit.

When waves begin to "feel" the bottom, the movement of water particles close to the sub-

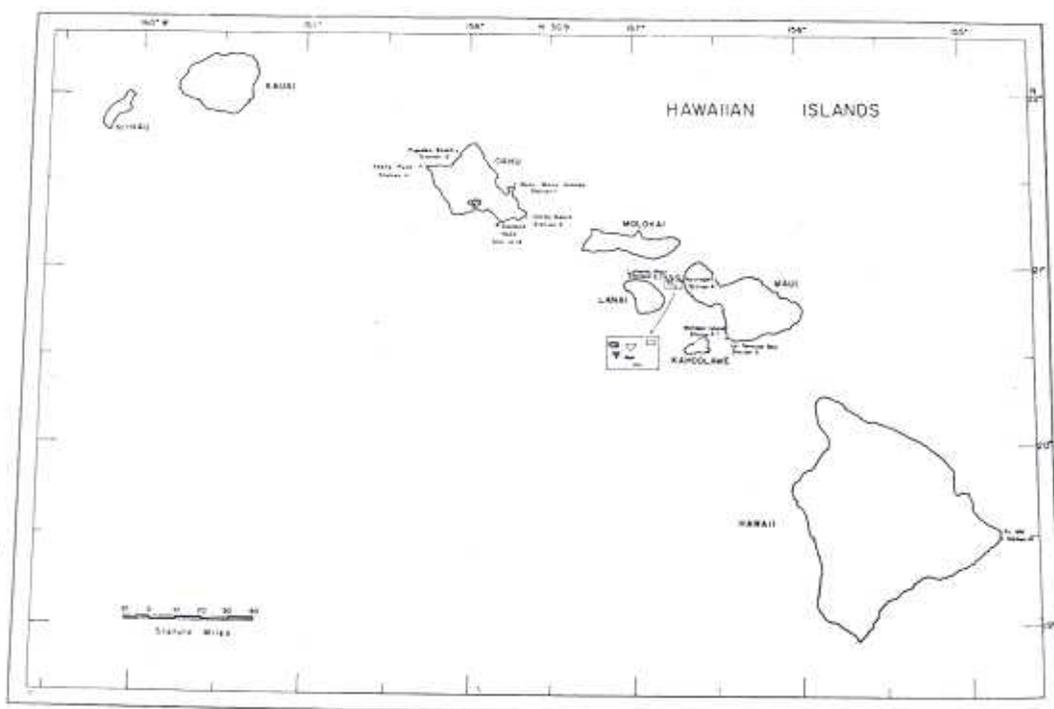


FIG. 2. The position of selected stations in the Hawaiian Islands.

strate will take the form of a flat ellipse so that the water is practically oscillating back and forth in a horizontal plane. This type of surge was found to be of particular importance in this research.

Currents are often superimposed upon surge. For example, if the current is running in the same direction as the swell, it will reinforce surge in one direction and inhibit it in another. If the current is strong enough, the latter direction can be nullified altogether so that motion is uni-directional, speeding up and slowing down depending upon whether current and surge are in or out of phase.

Surge was estimated by watching suspended particles in the water. A back-and-forth movement of water with a horizontal displacement of less than 1 foot was considered slight, of 1-3 feet moderate, and more than 3 feet heavy.

DEPTH: Depth was recorded in two ways. A fathometer or continuous depth recorder was used to outline bottom profiles, and a depth gage worn by a diver made *in situ* measurements possible.

TRANSPLANTS: Transplanting fixtures had to be made so that broken branches of black coral could be anchored firmly to the bottom. Cement blocks were made with a pipe placed in the center (Fig. 3). A hole near the end of the pipe was threaded so that a bolt could be tightened down on an inserted branch. Metal contact caused the animal to die within 1 cm of the bolt but did not appear to affect the remainder of the branch. The fixtures weighed between 10 and 15 pounds.

In another experiment, a half-inch line was anchored to a projecting piece of fossil coral on the bottom at 43 meters. The end of the line was buoyed up with three metallic floats which at no time were visible from the surface (Fig. 4). Branches of *A. grandis* were tied to this line using a ring-stand clamp and string at 12, 18, 24, and 30 meters.

POPULATION DENSITY: Counts of the number of colonies on the bottom were made, using a 10-meter marked line placed on the substrate so that the area could be estimated. Correlation of the population density with the inclination and configuration of the bottom was attempted.

EPIFLORA AND EPIFAUNA: Collection of associated organisms was made both at the bottom and on the surface after the colony had been brought up (Fig. 5).

FEEDING: Observations on the feeding habits and on the type of food ingested were carried out. In addition a plankton tow was made at 50 meters to determine roughly the type of food present in the natural environment.

DISCUSSION AND RESULTS

Light

Since colonies of *A. grandis* are found only in deeper waters, where the amount of light is considerably reduced, it seems probable that strong light intensity is important as a limiting factor. Indeed, when colonies of black coral are found in shallow water, their bases are always situated in dimly lit areas such as overhangs and caves. Pérès (1949) has found a similar condition in the underwater "grottos" off Marseilles, where certain deeper sea species were found at much higher levels in submarine caves.

The shallowest depth at which the author has observed *A. grandis* was at 7 meters off Hanauma Bay, where a colony about 30 cm high, was found growing from the ceiling of a very dimly lit cave. Off east Lanai and Hana, Maui, small stunted colonies, which frequently anastomose, are fairly common in caves at about 20 meters. The Kekaha coast of Kauai (off Port Allen) has extensive areas at 30 meters where colonies up to 2 meters high have been taken. It is interesting to note that in all of these regions the water is at times quite turbid because of run-off during heavy rains. Off Lahaina, Maui, where the shallowest colonies are generally found at approximately 40 meters, the water is extremely clear the year round. This area is 5 miles offshore and thus is not contaminated by run-off water. Light penetration, of course, is affected by depth as well as by the amount of suspended material in the water (Poole, 1938).

These observations suggest that *A. grandis* will settle in water shallower than 40 meters, but only in areas where the light penetration is periodically reduced by the presence of turbid water or by topographical features of the bottom which cut off direct rays of sunlight.

The adult colonies, however, do grow toward the source of light. This fact is especially obvious in caves or under overhangs where in semi-darkness the major branching is always in the direction of the light (Fig. 6).

In addition, adult colonies have been transplanted in calm water as shallow as 1.5 meters

off Coconut Island, Oahu, where they have survived for over 90 days. The light intensity at this point approaches 60%³ of the surface light. On the other hand, the shallowest colonies of *A. grandis* in the natural habitat do not appear

³ Approximately $475 \text{ gm cal cm}^{-2} 24 \text{ hr}^{-1}$.

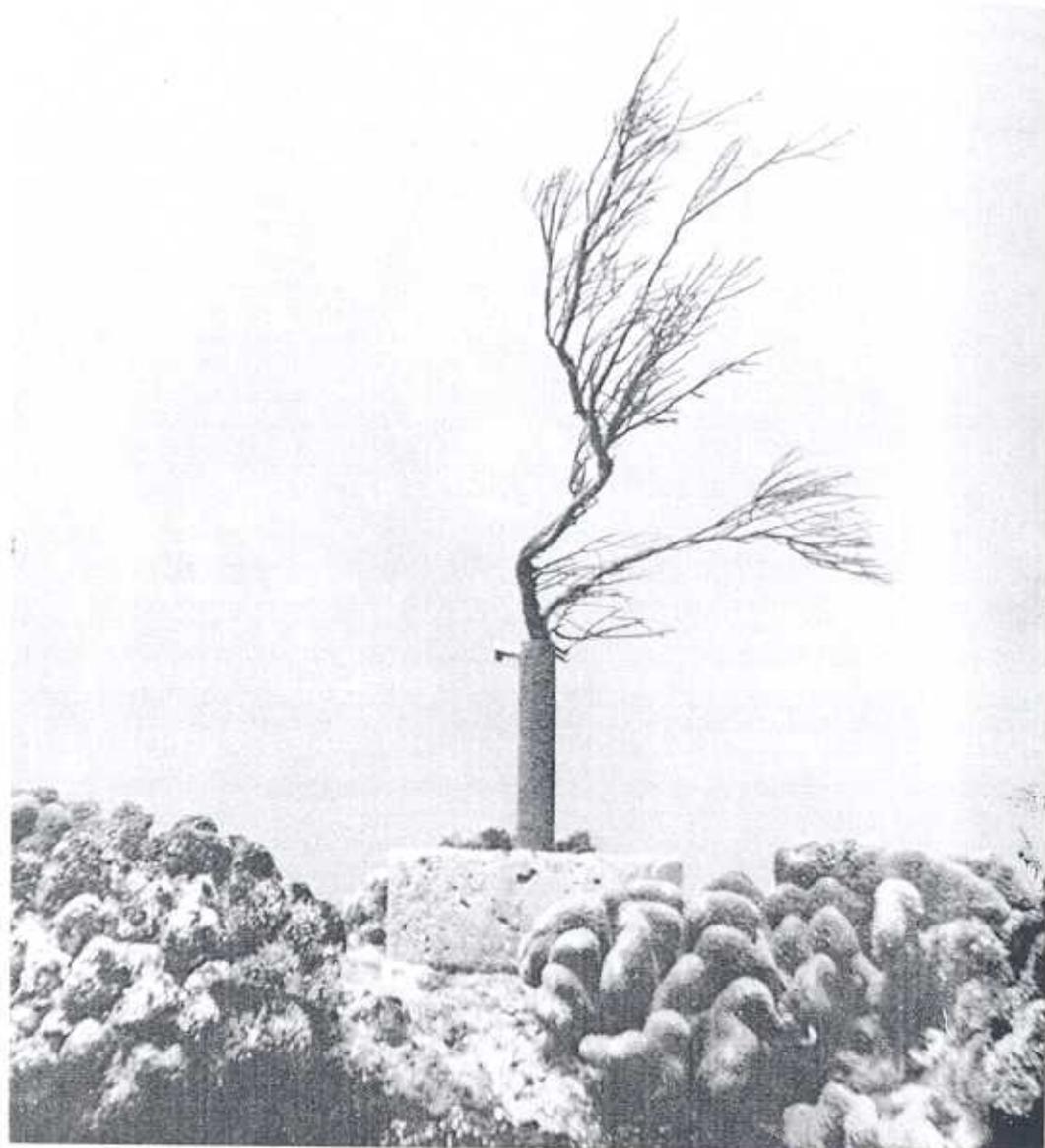


FIG. 3. A living branch of *A. grandis* taken from 43 meters, transplanted in 12 meters of water off Moku Manu Islands, Oahu.

above the 25%⁴ level. This value would approximate 35 meters of depth, in the clearest water off the Hawaiian Islands (Fig. 7). Thus, if strong light intensity is a limiting factor, it must be operational only on the larval stage. The larvae, of course, could be limited to deeper water because of other ecological factors.

Nevertheless, in corals that have no photophilous algal symbionts light is not essential; and in fact where these corals live within the photic zone they shun direct illumination, living in caves, or on undersurfaces of projecting rocks (Wells, 1957).

Microscopic examination of the tissues of *A. grandis* has not revealed the presence of any zooxanthellae. The planulae, however, have not been observed, and therefore it cannot be said for certain that the larval stage is also free of dinoflagellate symbionts.

Dendrophyllia,⁵ a deeper water coral that has extended its vertical range into shallow water, has no zooxanthellae and shows no positive reaction to light. Moreover, the planulae settle in darkness, while those of reef builders do not (Edmondson, 1929). Edmondson found that *Dendrophyllia*, like other planulae observed, exhibits a positive phototaxis when first expelled. This response, however, is only temporary, and within a few days the organism moves toward the darker portion of the bottom and either settles or dies. The author suspects that in the case of *A. grandis* larvae a similar mechanism takes place, thereby limiting these animals to the deeper and darker recesses of the reef. This hypothesis is supported by observations in sites shallower than 40 meters, where colonies are found only when the basal attachment is situated in a dimly lit area, such as a cave or an overhang. Beyond 40 meters the population density slowly increases with depth, and at 75 meters the colonies no longer aggregate in shaded areas. Below 75 meters very little observation has been done; only several glimpses by the author have been made in drop-off areas where the population appears to become increasingly dense.

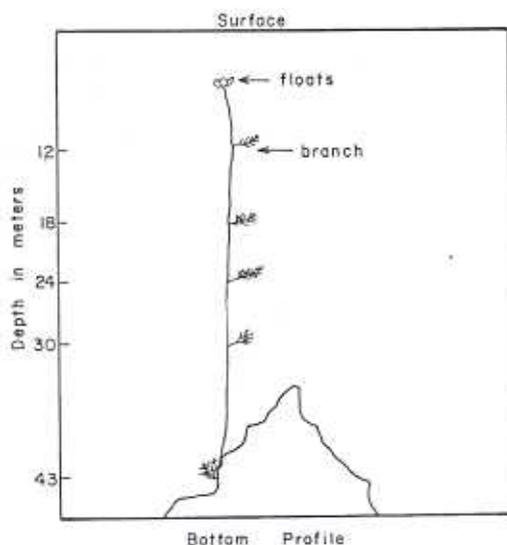


FIG. 4. A line was anchored to the bottom at 43 meters, while the other end was buoyed up by three sub-surface floats. Branches of *A. grandis* were tied at the indicated levels along this line.

Transplants and Surge

Colonies of *A. grandis* require a firm substrate so that water movements, current and surge, do not dislodge them. Once dislodged, the colonies are eroded along the bottom and eventually die because of tissue abrasion. Hence, for these studies, it was necessary to improvise anchoring fixtures such that branches could be transplanted from their normal habitat into shallow water (Fig. 3).

Extreme magnitudes of surge were measured at various depths on days when excessively large waves were present. On February 22, 1963, for example, the sea surface was very calm but at the same time a 15-foot swell predominated from the north. In an area with a bottom depth of 40 meters, at slack current, the horizontal movement due to surge at the bottom was 1.5 feet, 3 feet at 20 meters, 6 feet at 10 meters, and 8 feet at the surface. On this day, it was observed that a current of 0.25 knots was superimposed upon the surge at 40 meters, causing water movement to be uni-directional, speeding up and slowing down depending upon whether the current and surge were in or out of phase.

A control was set up by cutting a branch,

⁴ Approximately 200 gm cal cm⁻² 24 hr⁻¹.

⁵ *Dendrophyllia* is said to be incorrectly identified in Hawaii and should be placed within the genus *Tubastrea* (Wainwright, personal communication).



FIG. 5. Large colonies of *A. grandis* must be tied to the anchor line and later hauled to the surface.

bringing it to the surface, and then taking it back to the original site where it was re-anchored to the bottom.

Table 2 summarizes the results of all transplanted branches, including those tied to a buoyed line (transplants 11, 12, 13, and 14). The surge at each station is also included.

The viability of transplanted colonies was determined by observing the polyp condition. Contracted tentacles indicated a less than ideal environment, while mucus formation or denuded portions of the coenosarc indicated that the animal was dying.

The data compiled in Table 2 show that transplanted colonies (numbers 1-7) are able to survive in the calm waters of Kaneohe Bay, Oahu, in quite shallow water for long periods of time. Here the light penetration is very strong, and on clear days approaches 60% of the surface light. Branches transplanted in 12 to 18 meters of water, 50 yards off the wave-beaten head-

land of Moku Manu, did not fare as well, even though the light penetration (40% of the surface light) was less than that in Kaneohe Bay. The lack of marked variation in other chemical and physical factors suggests that surge was the prime factor influencing the survival of these transplanted branches.

The manner in which the animal died also implicates surge and, to a lesser degree, light intensity. Transplants 1, 2, 3, 4, 11, 16, and 18 all illustrate this phenomenon. After approximately one week the coenosarc covering the skeleton of these branches was completely intact, except for a narrow band along the upper surfaces where it was entirely removed. The animal tissues that cover the upper portions of the black skeleton were exposed to turbulent down-eddies accompanying heavy seas. At the same time, the light intensity was strongest upon these surfaces. Hence, an interaction of surge and light intensity acting as limiting factors may be quite possible.

The fact remains, however, that branches did survive in calm water as shallow as 1.2 meters. Hence, surge appears to be the prime factor limiting the viability of adult colonies.

The fact that the tissue was denuded from the skeleton illustrated the abrasive effects of surge. The author believes that suspended particulate material was largely the cause of this abrasion, rather than the frictional drag of the water itself. This view is supported by the fact

that *A. grandis* is able to withstand currents as high as 3 knots in the Auau Channel between Maui and Lanai, where the water is remarkably free of suspended material.

Figures 8 and 9 picture two branches of *A. grandis*, at 12 and 24 meters respectively, which had been secured above the bottom on a buoyed line (Fig. 4), 200 yards off Moku Manu Islands for a period of 90 days. After two weeks about 50% of the branch at 12 meters was alive, while

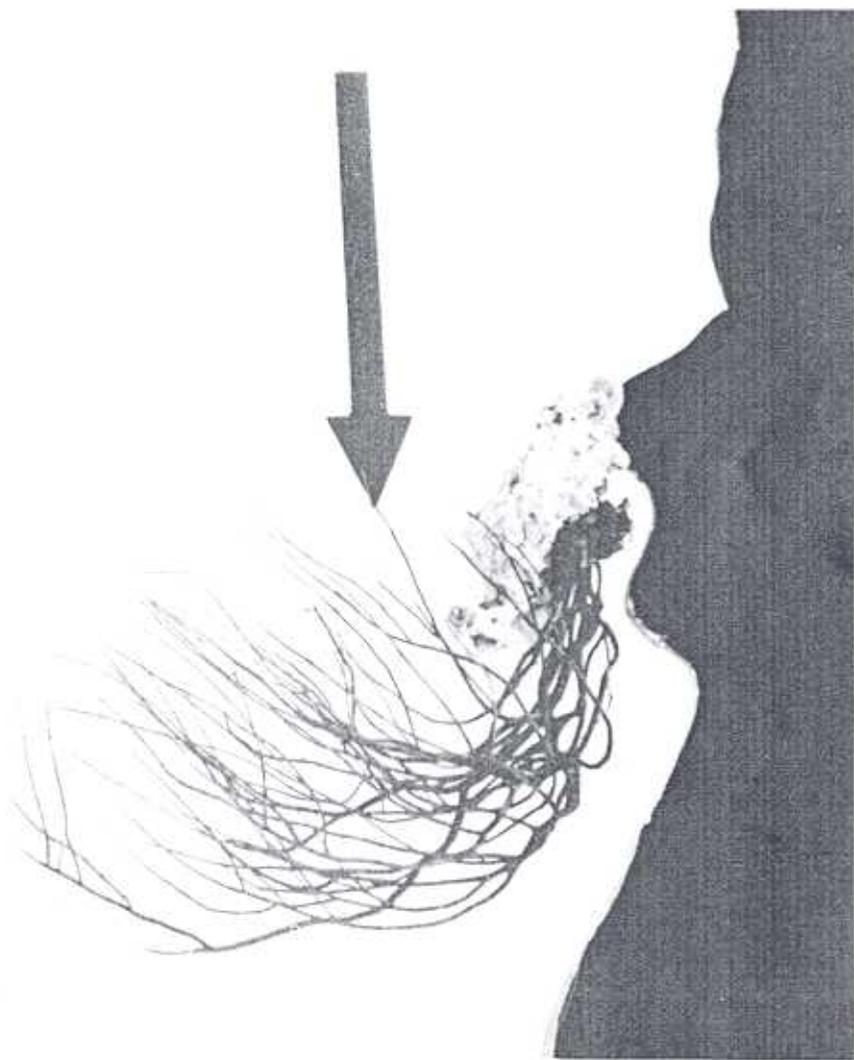


FIG. 6. This schematic photograph simulates the *in situ* orientation to light of a young colony of *A. grandis*, originally collected in 25 meters of water off Kawaihoa, Oahu. Notice the positive photo-tropism (toward arrow), whereas the site of implantation indicates that the larva is negatively phototaxic. $\frac{1}{3} \times$.

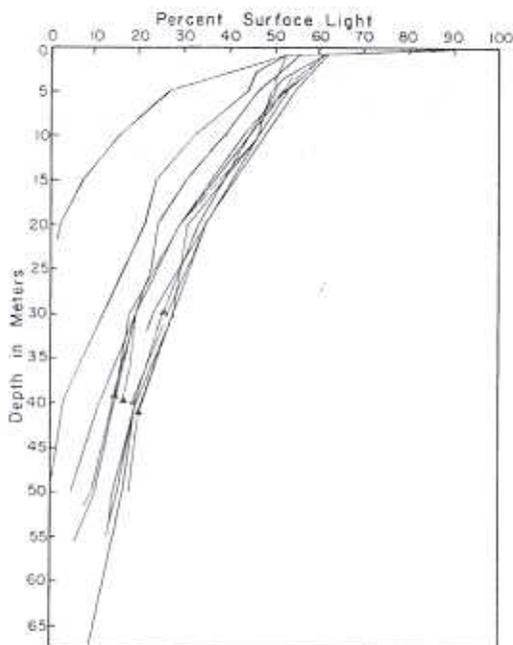


FIG. 7. Percent surface light is plotted against depth. The triangles represent the position of the first colonies of *A. grandis* (shallowest) observed in areas where a shallow bottom rapidly dropped off into deep water.

the entire branch at 24 meters was healthy. After 90 days only 5% of the former branch was alive, while the latter was still completely healthy. The living tissue on the branch in shallow water had been removed by the action of the surge and the denuded skeleton was overgrown with filamentous green algae.

During the 90-day period surge reached excessive magnitudes on three occasions, twice during wind storms with gusts over 70 miles per hour, and once during a 2-day period of 15-foot ground swells. Very turbid water accompanied these extreme conditions.

Transplant 18, which had been fixed on the bottom in 18 meters of water, was 80% alive after the same 90-day period. Along the bottom, of course, there is more particulate material suspended in the water, hence tissue abrasion would be considerably greater than in the case of the branches tied to a buoyed line where the branches were above the bottom.

These results indicate that the limiting effect

of surge is operational to a depth of approximately 20 to 24 meters. Below this level surge will very rarely reach limiting magnitudes. The only specimens of *A. grandis* found in water shallower than 24 meters during this research were in relatively protected areas, where surge was not excessive.

Turbidity

A. grandis is normally found in extremely clear water. Transplanted colonies, however, survived well under varied turbidity conditions. In Kaneohe Bay, for example, where fluctuations of turbidity were quite pronounced, transplanted branches survived for 6 months, after which the experiments were terminated. It does not appear, then, that turbidity per se limits the growth of this animal. If a heavy current or surge, however, is coincidental with very turbid conditions, then the suspended particulate material may become limiting by abrading the tissues of the black coral.

Oxygen, Salinity, and Temperature

In contrast to inshore areas and surface waters, where fluctuations in oxygen concentration, salinity, and temperature are quite common, the deeper off-shore waters are relatively stable with respect to these factors. At all stations during the period from December through May, the maximum differences in oxygen concentration, salinity, and temperature between the surface and the bottom (60 meters) were only on the order of 2 ml oxygen/liter, 1‰ salinity, and 2° Celsius, respectively. The magnitude of these differences is very small, and hence it is not likely that any of these factors is operative in limiting *A. grandis* to its exclusive habitat in deep water.

Substrate

A. grandis requires a firm substrate on which to grow. The type and texture of the substrate is also important in limiting the distribution of this animal. Cary (1914), in his studies on the ecology of gorgonians, observed that distribution was related to the texture of the substratum. He found that, in every case, a one-year-old

TABLE 2
RESULTS OF TRANSPLANTS

Place	200yd off Moku Manu Islands, Oahu				50yd off Moku Manu Islands, Oahu					Control	
Surge	MODERATE to HEAVY		SLIGHT		MODERATE TO OCCASIONALLY HEAVY					Slight	
Depth	12 meters	18 meters	24 meters	30 meters	12 meters	12 meters	15 meters	18 meters	18 meters	43 meters	
DAYS	1	100% alive	100% alive	100% alive	100% alive	100% alive	100% alive	100% alive	100% alive	100% alive	100% alive
	3										
	5										
	7										
TIME IN	14	50% alive	70% alive	100% alive	100% alive	50% alive		70% alive	100% alive	100% alive	100% alive
	21	* During this period two Kona Storms swept this area with winds up to 73 M.P.H.									
	28	50% alive	gone	100% alive	100% alive	20% alive		70% alive	80% alive	100% alive	
	42	10% alive									
	50							50% alive		gone	100% alive
	90	5% alive		100% alive	gone				80% alive		100% alive
	120	Dead									
	Number	11	12	13	14	15	16	17	18	19	20

TABLE 2 (Cont.)

Place	Off Coconut Island Reef, Oahu					Off La Perouse Bay, Maui					
Surge	MODERATE			SLIGHT		SLIGHT			MODERATE		
Depth	.6 meters	.6 meters	.6 meters	9 meters	1.2 meters	1.8 meters	4 meters	1.2 meters	1.8 meters	4 meters	
DAYS	1	100% alive	100% alive	50% alive	50% alive	100% alive	100% alive	100% alive	100% alive	100% alive	100% alive
	3	100% alive	100% alive								
	5			10% alive	30% alive						
	7			Dead	10% alive				100% alive	100% alive	90% alive
TIME IN	14										
	21	Dead	Dead		10% alive	100% alive	100% alive				
	28				10% alive						
	42										
	50					100% alive		100% alive			
	90						100% alive	95% alive			
	120							95% alive			
	Number	1	2	3	4	5	6	7	8	9	10

specimen had its base in a depression: "Thus the presence of small depressions or cracks where it was least likely for other more rapidly growing organisms to obtain a foothold seemed a prerequisite for fixation."

With *A. grandis* there is similar evidence that a texture preference does exist (Fig. 10). The basaltic ledges, for example, that are found off Molokini at depths in excess of 40 meters, are exceptionally smooth and do not support many colonies. However, where there are depressions, cracks, or other rugged features along these steep facades, one always finds a vigorous growth of black coral.

The type of substrate is also of considerable importance. Few colonies were found growing directly on a basaltic base. On the lava flows off La Perouse Bay, Maui (dated 1770 ± 20 years) and off Kapoho, Hawaii (dated 1926), where several dives were made to 60 meters, not one colony of *A. grandis* was found. Off Molokini, where colonies did attach to a basaltic substrate, there was invariably a thin encrustation of CaCO_3 . This condition was not apparent unless the colonies were chipped off and brought to the surface, where they were carefully examined.

The most favorable substrate is a fossil coral reef, defined as a CaCO_3 conglomerate of madre-



FIG. 8. This branch of *A. grandis* was tied to a vertical line at 12 meters and remained there for 90 days. The animal tissue was completely removed by the abrasive effects of surge, after which the black skeleton was overgrown with filamentous green algae.

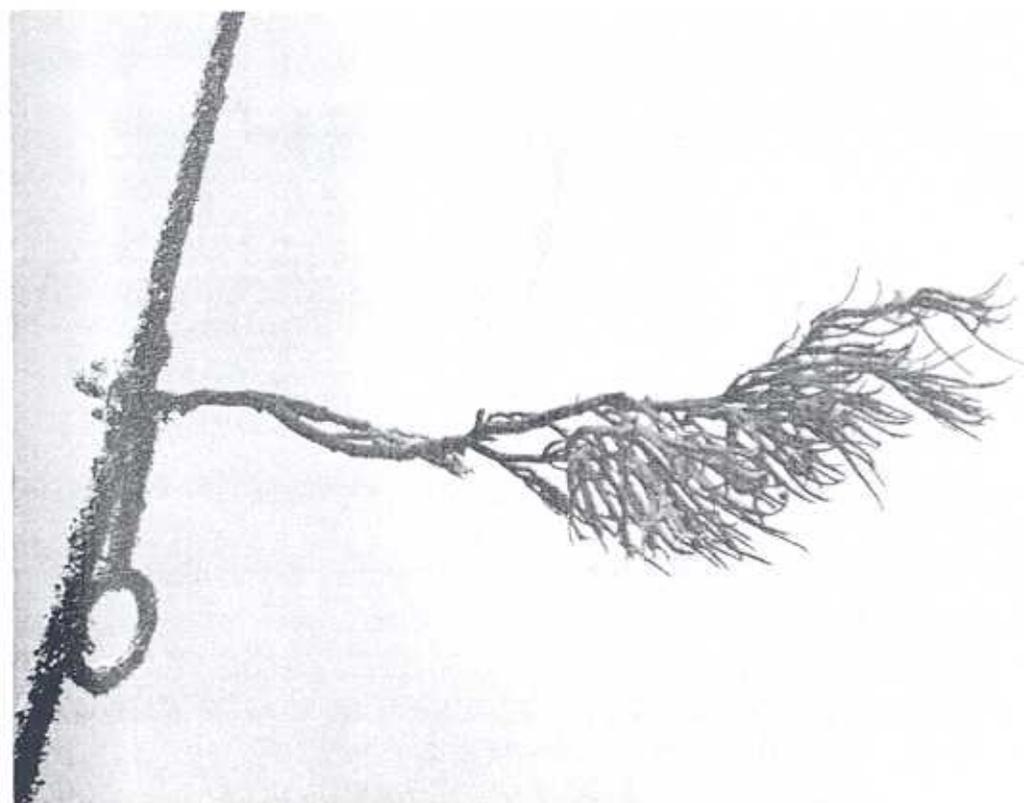


FIG. 9. Tied to a vertical line at 24 meters, this branch of *A. grandis* was quite healthy after 90 days. (Compare with Figure 8, a branch at 12 meters, also fixed to the line for the same 90-day period.)

porian coral cemented massively by coralline algae, Bryozoa, and other calcium-depositing organisms. In Figure 11 the population density is shown in five different areas having a calcium carbonate substrate. The population density off Molokini (a basaltic substrate) ranged between 0.0 and 0.2 colonies/square meter, considerably less than that of a calcium carbonate substrate of equivalent depth and inclination.

The topographical features of the bottom strikingly influence the distribution of *A. grandis* within the zone of observation (75 meters). A sloping substrate, the presence of overhangs, caves, ledges, and drop-offs, all significantly increase the population density. This tendency is illustrated in Figure 11, which shows a high population density in such areas. Below 75 meters this tendency is not so apparent. As was pointed out earlier, the aggregation of *A. grandis* in dimly lit areas is probably a result of a negative

phototaxis of the planulae. A vertical substrate, of course, is relatively free of silt and detrital material which might otherwise inhibit planulae fixation.

In summary, then, the most favorable substrate consists of a rough-textured CaCO_3 material with many shaded areas resulting from an irregular bottom profile.

Current

Food and oxygen come to the sedentary corals by way of water eddies and currents. Such water movements also carry away metabolic wastes.

Hickson (1932) found that a flow of water in one direction over a rocky bottom seems to favor the growth of gorgonian corals. Wells (1957) also pointed out that a current aids the growth of corals: "In still water, accumulation of sedi-



FIG. 10. At 55 meters off Molokini, a 2-meter colony growing on the edge of a jutting ridge of basalt. Notice the barren ledge in the background, which is not supporting a single colony of *A. grandis*.

ment inhibits coral growth, in heavy currents there is too much abrasion by small fragments of coral and rock; coral planulae do not settle or remain attached where currents are strong,

hence moderate currents promote most vigorous growth."

Tide tables (U. S. Coast and Geodetic Survey, 1961) indicate that mixed tides predominate in

Hawaiian waters, with generally one major peak and another lower peak during a lunar day. Tidal elevations vary little from location to location around the islands, and the maximum elevation is only about 3 feet above mean lower low water.

Measurements made during this study illustrate several interesting features of the current. First of all, the surface current and bottom current do not necessarily coincide. They may, in fact, be in opposition during certain tidal moments and wind conditions. The surface currents, of course, are affected by the wind, whereas bottom currents are mainly influenced by tidal conditions and bottom topography.

It was found that the surface currents were swifter than those close to the bottom. This was especially true in areas where the bottom topography was extremely irregular.

Second, along coastal borders and in channel areas, it is known that tidal currents assume the form of a long ellipse (Neumann, 1960). In all cases, except at Kaena Point, Oahu, the currents followed this general pattern, being multi-directional depending upon the tide. It is quite likely that, for this reason, the colonies of *A. grandis* do not orient themselves in one direction with respect to the current.

Off Kaena Point, however, where currents very commonly exceed 2 knots and are in general unidirectional, a definite orientation of the fern type black coral (Genus *Antipathella*) in a fashion perpendicular to the current has been observed. It is significant that specimens of *A. grandis* are absent or extremely rare in this environment. Kaena Point is subject to heavy wave activity in winter months, during which the water is very turbid. This fact, coupled with the intense current, could well be producing an extreme abrasive effect which has been found to be limiting to *A. grandis* (as with the abrasive effects of surge on transplanted colonies off Moku Manu Islands). Evidently the fern type is more tolerant of these conditions.

Third, the current measurements in this study, in all cases except at Kaena Point, ranged between 0 and 2 knots. In shallow water close to shore the currents during any 24-hour cycle re-

main at zero for very short periods, during which time the tide peaks and the current changes direction. Offshore currents are rotary and at no time are completely slack.

Colonies of *A. grandis* do well under these conditions and in fact can tolerate regular currents as high as 2 knots. In those locations where a dense population of *A. grandis* is found (Stations 3, 7, 8, 9), it is significant that the water is free of suspended abrasive particles. For this reason, it is postulated that excessive currents (over 2 knots) may only become inhibiting to the growth of *A. grandis* when the water mass contains a high amount of abrasional fragments such as sand or other particulate inorganic material.

Finally, transplanted colonies in Kaneohe Bay survived very well in areas off Coconut Island where currents rarely exceed 0.5 knot (Avery, Cox, and Laevastu, 1963). These colonies were observed to feed and actually to grow through asexual reproductive processes. It is not known whether sexual reproduction is possible under these conditions, but even if it were the planulae would probably not be able to find a suitable site for fixation.

On the basis of the evidence, then, it does not seem that strong currents are necessary to support the growth of this animal. And since average currents are generally in excess of 0.5 knot in almost all exposed offshore localities in Hawaii, it does not appear that lack of current restricts the growth of *A. grandis*. On the other hand, currents higher than 0.5 knot are necessary to sweep the bottom clean of accumulated sediments. The inclination of the bottom is important, of course, in this respect also. Since colonies of *A. grandis* are found only in cleanly swept areas, it is reasonable to assume that the planulae cannot settle on a substrate covered with an accumulation of sediment.

In summary, then, the most favorable range of average current approximates values between 0.5 and 2 knots. The presence of inorganic particulate material magnifies the abrasive effect of current and therefore lessens the range under which the animal can survive.

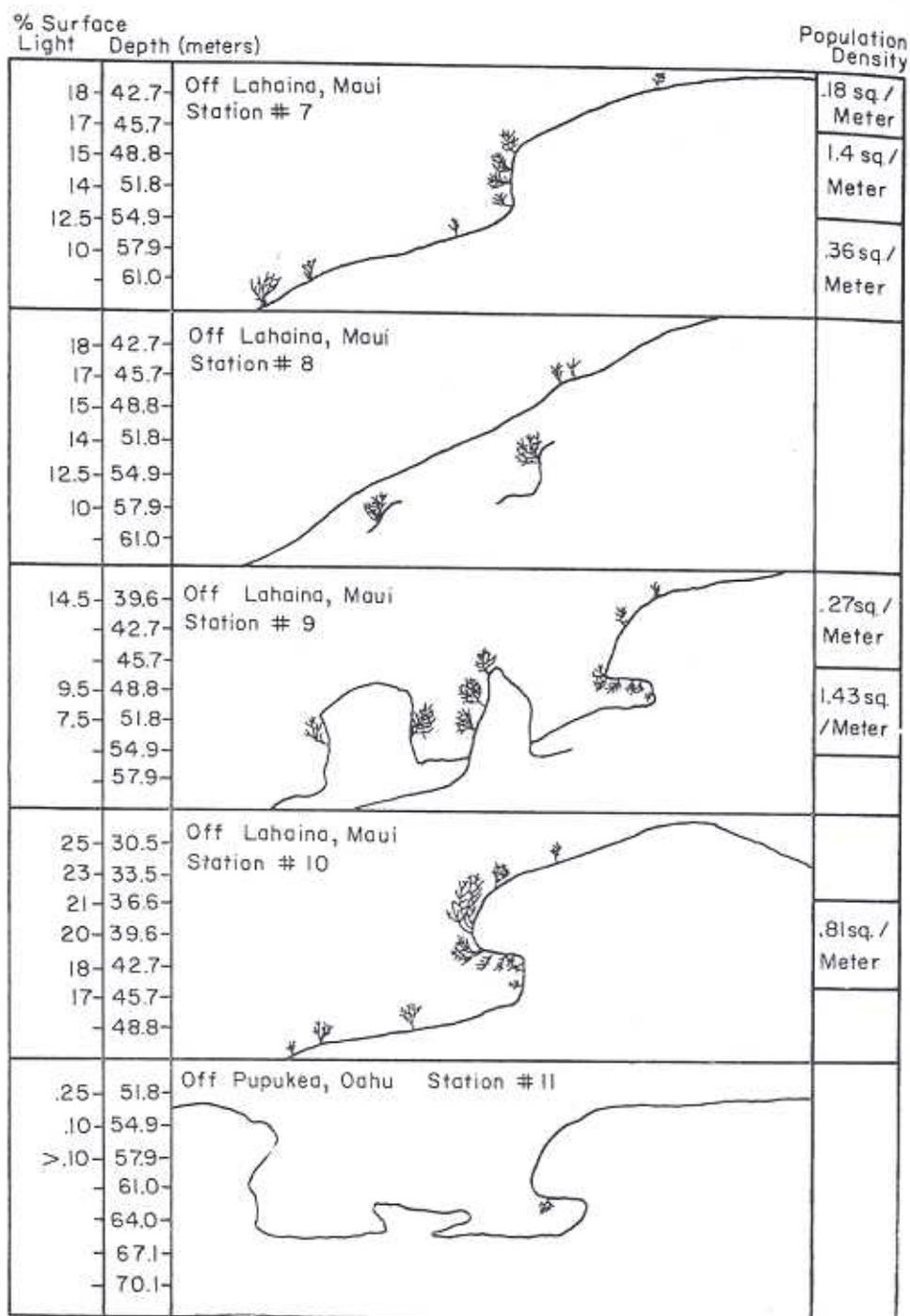


FIG. 11. Bottom profiles of several stations are shown with the depth, light intensity, and the population density indicated.

Feeding

Edmondson (1929) working on the inshore reef at Waikiki, and Motoda (1939) working in Iwayama Bay, Palau, found a considerable variation in plankton density from day to day. Gardner (1931) found, on the other hand, a small fluctuation in plankton density in his work on atolls in the Pacific.

Wells (1957) states that the food requirements of madreporian corals are low. If this condition holds for the antipatharian corals, then plankton density may not be a limiting factor. This statement is not based on a quantitative study, and is purely speculative.

Plankton-rich water from Kaneohe Bay was introduced into a finger bowl in which living branches of *A. grandis* were observed through a binocular microscope. Ingested plankton, under these conditions, included amphipods, copepods, and chaetognaths (*Sagitta*).

A plankton tow off Moku Manu Islands in 45 meters of water revealed a large amount of detritus, many amphipods, copepods, and foraminifera and, in lesser amounts, radiolaria, dinoflagellates, and ostracods. No chaetognaths were found, hence *Sagitta* may not be a natural food.

Unlike most stony corals, the polyps of *A. grandis* have been observed to be expanded during the day; therefore feeding probably is not restricted to certain hours.

SUMMARY AND CONCLUSIONS

Ecological factors which limit the distribution of *A. grandis* were studied in an attempt to understand the biology of this species. Research methods are described and ecological and biological information is presented.

The results indicate that:

1. Adult colonies can withstand light intensities up to 60% of the surface incident light.
2. Adults can tolerate ranges in depth (and consequently in pressure) from 1 to 146 meters, indicating that pressure is not likely to be a limiting factor, at least within the littoral zone.
3. Oxygen concentration, salinity, and temperature are relatively stable in the natural environment, and do not appear to be of limiting importance.
4. Adult colonies are limited by the abrasive

effects of surge and cannot tolerate this factor in waters shallower than 24 meters where surge is heavy. In protected areas, however, colonies may survive in very shallow water.

5. Since colonies are commonly found only below 35 meters in most areas in Hawaii, it is postulated that the larval stage reacts negatively to strong light intensities. The lack of marked variations in other environmental gradients supports this view. Evidently the larvae will not settle or survive unless the light penetration is less than 25% of the surface light. In the clearest water around Hawaii this value would correspond to about 35 meters in depth. Only in turbid water or in shaded areas are colonies found any shallower.

6. There is evidence that a CaCO_3 substrate is more favorable than a basaltic substrate for the growth of *A. grandis*. Also, a rough or uneven substrate will support a larger population than will a smooth substrate. And, finally, within the zone of observation (0 to 75 meters), a vertical and undercut substrate is able to support a denser population than is an otherwise equivalent horizontal substrate. This last phenomenon may be due to the fact that less light is present in such environments.

7. The most favorable range of current for the growth of *A. grandis* is between 0.5 and 2 knots. Presence of suspended sand particles or other particulate material intensifies the abrasive effects of the current, and therefore reduces the range under which the coral can grow.

8. Only animal material was observed to be ingested.

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