

Proceedings, Third International Coral Reef Symposium
Rosenstiel School of Marine and Atmospheric Science
University of Miami
Miami, Florida 33149, U.S.A.
May 1977

WATER FLOW AND THE MORPHOLOGY OF ZOANTHID COLONIES

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ABSTRACT

I conducted a comparative study of two species of zoanthids to elucidate types of polyp and inter-polyp gross morphologies that are well suited to different water flow regimes. The large polyps of Palythoa variabilis colonies are connected to each other only by stolons at their bases, whereas the small polyps of Palythoa caribaeorum share column walls. Although P. variabilis often occurred in areas of less rapid flow than P. caribaeorum, the tall, separate polyps of a P. variabilis colony tended to stick out of the slowly moving water near the substratum more than did the polyps of an even-surfaced P. caribaeorum colony. The low degree of interpolyp connection of P. variabilis rendered these zoanthids much more deformable than P. caribaeorum. P. variabilis had longer tentacles and caught more prey per polyp than P. caribaeorum. P. variabilis, which often occurred in sandy areas, appeared to shed sediment more readily in slowly moving water than did P. caribaeorum. Thus, the structure of P. variabilis can compensate for the lack of external transport by flowing water, whereas the structure of P. caribaeorum can minimize the mechanical effects of flowing water. I would expect to find large, long-tentacled polyps with a low degree of interpolyp attachment in microhabitats of a coral reef that are characterized by low flow velocities and to find short-tentacled, small polyps (or closely-connected polyps that are functionally small) in microhabitats characterized by rapid flow.

KEY WORDS: Zoanthids, Flow, Biomechanics, Polyps, Morphology, Palythoa, Feeding, Sediment-Clearing, Colonies, Reefs.

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Introduction

Moving water transports food and essential substances to sessile marine organisms and carries wastes and sediment away from them. If a sessile organism is to benefit from the transport of materials by moving water, the organism must be able to withstand the mechanical forces (drag) imposed on it by that flow. Thus, sessile organisms that encounter rapidly flowing water tend to have features which minimize the mechanical effects of flow, whereas sessile organisms that are not subjected to flow tend to have features which compensate for the lack of external transport by moving water (1).

One of the most striking features of a coral reef is the great diversity of structure of the sessile cnidarians composing and living on the reef. The gross morphologies of colonial sessile cnidarians differ on several levels of organization: a) the structure of individual polyps, b) the morphological association of polyps to each other, and c) the over-all shapes of entire colonies. The relationships to water flow of various colony shapes have been considered for a number of sessile cnidarians (reviewed in (1)). My purpose in conducting the present study was to elucidate types of polyp and interpolyp gross morphologies that are well suited to different flow regimes. The flat colonies of zoanthids are a simple system in which these two levels of organization can be studied without the complications of intricate three-dimensional colony geometries. I conducted a comparative study relating the gross morphologies of two zoanthid species (*Palythoa variabilis* (Verrill) and *Palythoa caribaeorum* Duchassaing and Michelotti) to their mechanical behavior, their feeding, their sediment-clearing abilities, and their distribution in different water flow regimes.

Materials and Methods

My studies of *P. caribaeorum* and *P. variabilis* were conducted at a Caribbean coral reef exposed to wave action (Galeta, Panama) and at a protected rocky shore (São Sebastião, Brazil). I surveyed the distributions of both species at these two sites during low tides and SCUBA dives. I measured water velocities at different times during the tidal cycle in August, 1976, to characterize the flow habitats of each *Palythoa* species under non-storm conditions. By using two simple mechanical flow meters affixed 15 cm apart on a rod, I measured simultaneously water currents at the surfaces of zoanthid colonies and 15 cm above them ("mainstream"). Each flow meter consisted of a flexible rubber pointer attached at one end to a glass plate; the

distance that the free end of the pointer moved over a mm grid was proportional to the speed of the water pushing the pointer (standard error, SE = 10%). I held the flow meters so that the plates were parallel to a colony's surface and the pointers normal to the predominant flow direction. Measurements of mainstream velocities were also obtained by timing with a stopwatch particles in the water moving from one marked point to another. I released with a syringe small volumes of sea water marked with rhodamine B upstream from zoanthid colonies so that I could observe the patterns of water flow over the surfaces of the polyps in the field.

I made a variety of morphological and mechanical measurements (summarized in Table 1) on both species. The forces (to the nearest 0.01 N) required to push individual polyps laterally a distance of 1 mm at their free ends was measured with a Scherr-Tumico dynamometer. I made such force measurements on polyps in intact colonies and on the same polyps after I had dissected away their neighbors.

The diel cycles of zoanthid expansion and feeding were studied in collaboration with K. Sebens, who has described our procedures (2). We also observed the feeding behavior of zoanthids in situ and in a flow tank.

I observed the sediment-clearing behavior of zoanthid colonies in situ and of colonies I had transplanted 24 hours earlier to areas of different flow. After releasing 20 cc of sediment (sand collected where the zoanthids occurred) 10 cm above each colony, I photographed each colony at intervals timed with a stopwatch. The percentage of colony map area covered by sediment was estimated for each photograph (3.5"x5") by tracing the picture onto graph paper (20 divisions/inch) and counting the squares over sediment and over clean polyp surface.

Results and Discussion

Gross Morphology

A *P. caribaeorum* colony is a solid mat of polyps attached to each other laterally, whereas a *P. variabilis* colony is a loose cluster of polyps that are attached to each other only by stolons at their bases. Various dimensions of polyps and colonies of each species are summarized in Table 1.

The oral disks of expanded *P. variabilis* (Fig. 1,a) are about twice as wide as those of expanded *P. caribaeorum* (Fig. 1,c). The tentacles of *P. variabilis* are longer and more widely spaced than those of *P. caribaeorum*.

Table 1. Dimensions and Stiffnesses of Zoanthids

	mean for <i>P. caribaeorum</i>	mean for <i>P. variabilis</i>	significantly different?	measured with:
mid-colony polyp height	17 mm	21 mm	yes $F(1,112) = 6.90, 0.01 < P < 0.025$	mm ruler (distance applicator stick inserted in polyp)
expanded oral disk diameter	6 mm	14 mm	yes $F(1,132) = 360.67, P < 0.001$	vernier calipers (on photograph)
lower column diameter	3 mm	6 mm	yes $F(1,18) = 64.10, P < 0.001$	vernier calipers
polyp column wall thickness	0.50 mm (shared wall of 2 polyps)	0.56 mm (wall of single polyp)	no $F(1,46) = 1.31, 0.25 < P < 0.5$	vernier calipers
colony area	$1.6 \times 10^3 \text{ cm}^2$	$1.4 \times 10^2 \text{ cm}^2$	yes $F(1,58) = 2.54, 0.01 < P < 0.025$	cm ruler (length x width)
tentacle length	2.4 mm	7.2 mm	yes $F(1,86) = 568.63, P < 0.001$	vernier calipers (on photograph)
mid-tentacle diameter	0.5 mm	1.0 mm	yes $F(1,140) = 87.32, P < 0.001$	vernier calipers (on photograph)
mid-tentacle horizontal spacing within a row	0.4 mm	2.5 mm	yes $F(1,64) = 234.55, P < 0.001$	vernier calipers (on photograph)
vertical distance between tentacle tips	2.0 mm	10.3 mm	yes $F(1,40) = 453.00, P < 0.001$	vernier calipers (on photograph)
force to deflect polyp laterally 1 mm in intact colony	5.44 N	0.08 N	yes $F(1,18) = 223.50, P < 0.001$	dynamometer
effective EI	$1 \times 10^5 \text{ N}\cdot\text{m}^2$	$1 \times 10^4 \text{ N}\cdot\text{m}^2$	yes $F(1,18) = 10.38, 0.005 < P < 0.01$	
<u>effective EI</u> EI	22	2	yes $F(1,18) = 101.08, P < 0.001$	

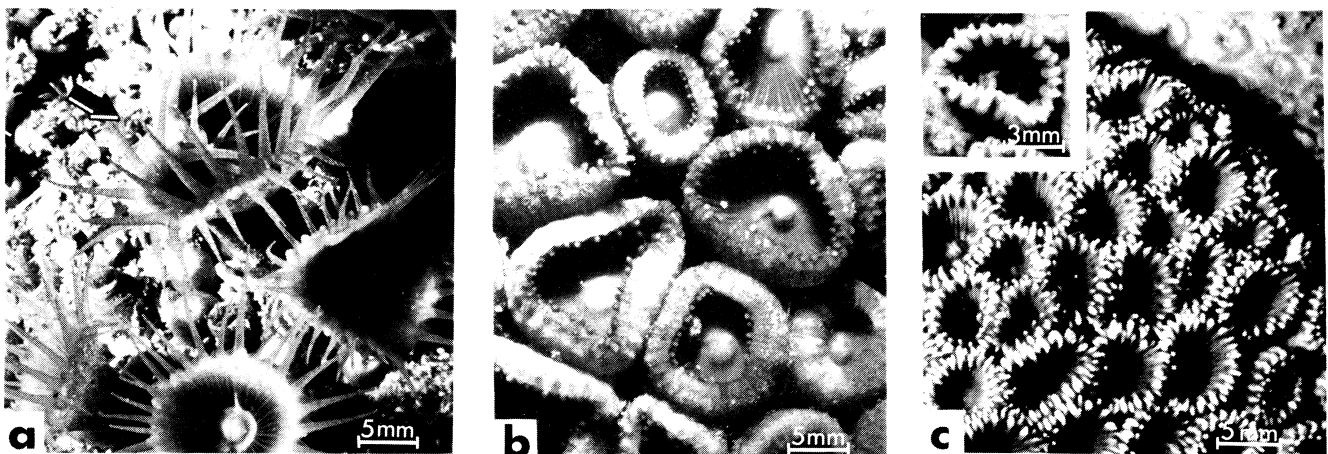


Fig. 1. Photographs of: a. Expanded *P. variabilis* at night (arrow indicates a polyp feeding) (photograph by K. Sebens); b. Cup-shaped *P. variabilis* during the day; c. Expanded *P. caribaeorum* (note edge of retracted colony in upper right); polyp in insert is feeding.

Polyps in *P. variabilis* colonies tend to be taller than those in *P. caribaeorum* colonies. The surface of a *P. caribaeorum* colony is very regular and presents no abrupt edges to flowing water. The variance of polyp heights in a *P. variabilis* colony is much greater than in a *P. caribaeorum* colony; wider polyps tend to be taller in a *P. variabilis* colony, thus the colony surface is irregular. The polyps in the edges of *P. variabilis* colonies facing predominant flow directions tend to be shorter and those on edges bordering sand tend to be taller than polyps in the centers of the colonies (Fig. 2).

Distribution

São Sebastião. The distributions of both *Palythoa* species along a transect are diagrammed in Fig. 3. Both species were found on cobble and boulders, but 33% of the *P. variabilis* colonies along the transect were on cobble surrounded by sand, whereas only 2% of the *P. caribaeorum* were on cobble in sand. At other protected sites where the substratum consisted entirely of cobble in sand, only *P. variabilis* were found, and at rocky, current-swept sites only the vast carpets of *P. caribaeorum* were found. The lower limit of *P. caribaeorum* varied in depth but always occurred where the substratum type changed abruptly from rock to sand.

Galeta. *P. variabilis* were most commonly found on sandy coral rock in shallow water on the reef flat, whereas *P. caribaeorum* occurred on coral rock further seaward in the surf zone and on the fore-reef. A few *P. variabilis* colonies were found in depressions in the surf zone. A quantitative description of zoanthid distributions on the Galeta reef is in preparation (Sebens).

Water Flow

Water velocities close to the substratum are lower than mainstream, therefore sessile organisms generally are exposed to slower water flow than are tall organisms occurring in the same area (1). I therefore expected that the tall, separate polyps of *P. variabilis* colonies would encounter more rapid flow than would the polyps in mat-like *P. caribaeorum* colonies when mainstream velocities over the two species were the same. At the Sao Sebastiao site, both species were exposed to bidirectional flow associated with the passage of gentle waves. I found that mainstream velocities were generally 0.3 to 0.5 m·s⁻¹. The mean ratio of water velocity at a colony surface to mainstream velocity for *P. variabilis* ($\bar{x} = 0.8$) was significantly greater than for *P. caribaeorum* ($\bar{x} = 0.6$) ($F_{(1,64)} = 16.83, P < 0.001$).

The mainstream velocities I measured over *P. caribaeorum* and *P. variabilis* on the Galeta reef are summarized in Table 2. *P. caribaeorum* in the surf zone were subjected to the surge and backwash of breaking waves. *P. variabilis* on

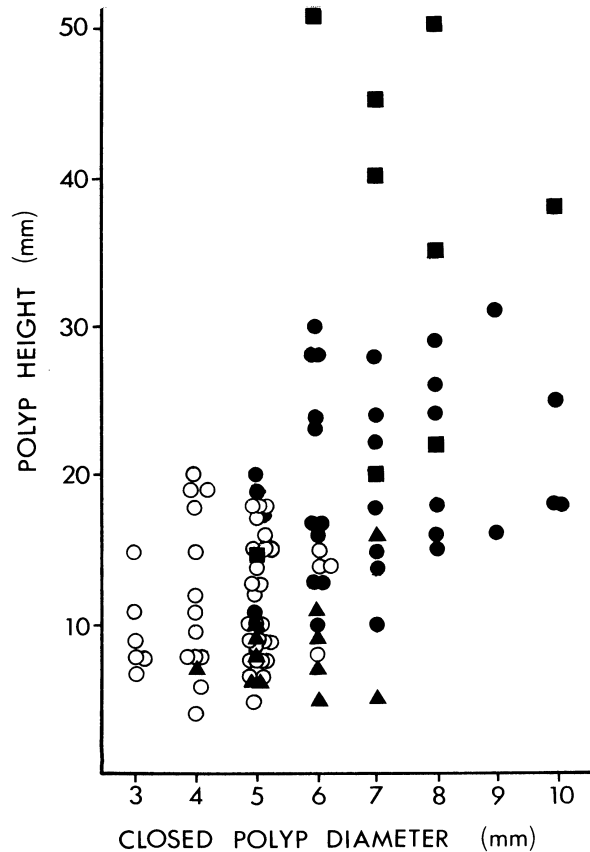


Fig. 2. Heights and diameters (oral ends of retracted polyps) of *P. caribaeorum* polyps (O) (5 colonies), and of *P. variabilis* polyps on colony edges bordering sand (■), on colony edges facing into currents (▲), and in the centers of colonies (●) (4 colonies).

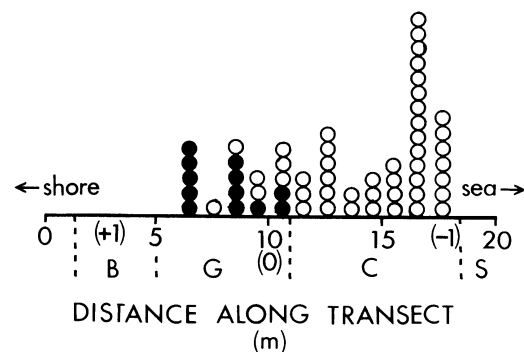


Fig. 3. Distribution of *Palythoa* along a transect run normal to the shore at São Sebastião. Letters between dashed lines indicate zones: B = barnacle zone; G = *Gigartina-Amphiroa* (algae) zone; C = *P. caribaeorum* zone. Numbers in parentheses indicate elevation relative to mean low spring tidal level (mean spring tidal range = 1.2 m). The elevations of *P. caribaeorum* ranged from -1.0 to +0.6 because they grew up boulders in the C zone. O = one *P. caribaeorum* colony; ● = one *P. variabilis* colony.

Table 2. Mean Maximum Shoreward* Velocities ($m \cdot s^{-1}$) Over P. caribaeorum (P.c.) and P. variabilis (P.v.) at Galeta

	P.c.	P.v.	significantly different?
low tide	1.9	0.3	$F_{(1,20)} = 35.15$ $P < 0.001$ yes
incoming tide	2.2	0.4	$F_{(1,9)} = 18.19$ $0.001 P < 0.005$ yes
high tide	1.7	0.4	$F_{(1,10)} = 23.10$ $P < 0.001$ yes
outgoing tide	0.8	0.5	$F_{(1,11)} = 0.72$ $0.25 < P < 0.5$ no

*Shoreward flow was generally faster (often by a factor of 1.5 to 2) than seaward flow.

the reef flat were subjected to the overwash of broken waves. Flow velocities in the surf zone were significantly faster than those on the reef flat throughout most of the tidal cycle. I could detect no difference between flow velocities at the surfaces of P. variabilis colonies on the reef flat and the mainstream velocities over them, but I found velocities at the surfaces of P. caribaeorum to be lower than mainstream (mean ratio of colony surface velocity to mainstream velocity = 0.6, standard deviation, SD = 0.1, n = 16). Nonetheless, the mean of velocities I measured at P. caribaeorum colony surfaces ($\bar{x} = 1.1 m \cdot s^{-1}$) were significantly higher than the mean of velocities at P. variabilis colony surfaces ($\bar{x} = 0.3 m \cdot s^{-1}$) ($F_{(1,20)} = 14.86$, $P < 0.001$).

Mechanical Behavior

Polyp and interpolyp structure affect the mechanical responses of P. caribaeorum and P. variabilis to imposed loads such as drag forces. A polyp subjected to a drag force can be considered as a cantilevered beam supporting a load (Fig. 4). The linear deflection (δ) of the oral end of such a polyp is approximately

$$\delta = \frac{F(L)^3}{EI} \quad (1)$$

where F is the drag force, L is the height of the

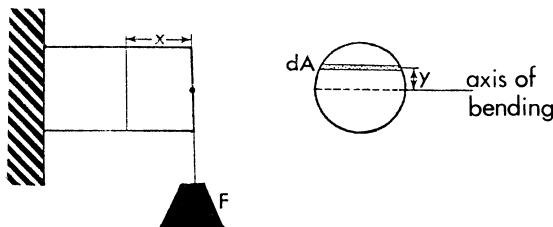


Fig. 4. Diagram of a cantilever supporting a load (F). The cross-section of the beam at distance x from its free end is diagrammed next to the beam.

polyp, E is the elastic modulus (rigidity) of the material composing the polyp's body wall, and I is the second moment of area of a cross-section of the polyp. The second moment of area, a measure of the distribution of material around the axis of bending of the loaded polyp, is given by

$$I = \int y^2 dA \quad (2)$$

where dA is a unit of area at distance y from the axis of bending. Note that the deflection of a polyp for a given load is inversely proportional to the product of E and I; EI is known as the "flexural stiffness" of a beam. Because I is roughly proportional to the radius of a polyp raised to the fourth power, the flexural stiffness of a polyp is considerably higher in wide regions of the body than in narrow regions. Note also that a slight increase in the height of a polyp produces a very large increase in the deflection of that polyp for a given load.

The force required to deflect laterally the oral disk of a P. caribaeorum polyp in an intact colony is nearly two orders of magnitude greater than the force required to deflect the same distance a P. variabilis polyp in an intact colony (Table 1). This striking difference in mechanical behavior could be due to a difference in the rigidity of the materials composing P. caribaeorum and P. variabilis, and/or to a difference in their shapes.

Elastic Modulus (E). By assuming isolated polyps to be hollow cylindrical cantilevers, I calculated from measured forces to deflect such polyps rough estimates of the E's of their body walls. The E's of body walls from both species estimated in this way are on the order of $10^6 N \cdot m^{-2}$ and are not significantly different from each other ($F_{(1,18)} = 1.44$, $0.1 < P < 0.25$). This observation is consistent with the observation by Sebens (pers. com.) that the spicule contents of both Palythoa species are about the same. The spicule-reinforced walls of these zoanths are an order of magnitude stiffer than the spiculeless body walls of sea anemones (3). If the materials composing the polyps of both species are of similar rigidity, then the observed difference in their resistance to deflection must be due to their respective shapes.

Flexural Stiffness (EI). A polyp that is a member of a colony may be supported against deflection by its neighboring polyps. Therefore, the "effective EI" of a polyp in a colony should be greater than its actual EI when isolated. I estimated effective EI's using measured forces to deflect polyps in intact colonies of both species. The effective EI's of P. caribaeorum polyps connected to each other are twenty times greater than their actual EI's when isolated, whereas the effective EI's of the more loosely attached P. variabilis polyps are only two times higher than their actual EI's (Table 1).

Although P. caribaeorum polyps have body walls that are no thicker than (Table 1) and that

are composed of material no more rigid than those of *P. variabilis* polyps, the former are much stiffer than the latter. Tight interpolyp attachment may be a cheap way to increase the stiffness of polyps in a colony.

Shapes of Solitary and Colonial Polyps.

Solitary polyps exposed to high flow velocities tend to be short, thereby minimizing drag forces and deflection due to drag. The stresses (force per cross-sectional area) produced in a polyp's column wall when loaded by a drag force are greatest near the base of the body if the polyp is of uniform cross-sectional dimensions. Polyps are more resistant to bending where their I's are highest; solitary polyps on hard substrata tend to have higher I's near their bases and at their oral disks (3), which must be held open if the polyps are to feed. The almost-solitary polyps at the leading edges of *P. variabilis* colonies are short and are wide at their bases like solitary polyps. In contrast, *P. variabilis* mid-colony polyps (which are no doubt supported by the sand in which they are often partially buried) and *P. caribaeorum* polyps are tall and are narrowest at their bases. The amount of structural material that must be invested in the reinforcement of lower columns of polyps that are supported by their neighbors or by surrounding sediment appears to be minimized.

Feeding

Large-polyped corals with extended tentacles capture more food than small-polyped and short-tentacled corals (4,5). I thus expected that *P. variabilis* might be more effective at catching food than *P. caribaeorum*. We observed that both *Palythoa* species tended to expand at night and to retract during the day (2). Expanded *P. variabilis* captured particles with their long tentacles (Fig. 1,a). *P. variabilis* during the day (Fig. 1,b) and expanded *P. caribaeorum* (Fig. 1,c) were cup-shaped and collected particles by eddy-feeding as diagrammed in Fig. 5. During the day when both species were cup-shaped, they took roughly the same number of prey per polyp. However, at night when *P. variabilis* extended their tentacles, these zoanthids took six times as many prey per polyp as did *P. caribaeorum*. The short-tentacled *Zoanthus solanderi* and *Z. sociatus* also caught fewer prey than did *P. variabilis* (2). It seems that long-tentacled polyps can gather more prey than can cup-shaped, short-tentacled polyps. The mean sizes of prey taken by the two *Palythoa* species are not significantly different (2); however, it appears that *P. variabilis* can handle larger prey than can *P. caribaeorum* (Fig. 6,a). The observation that the size-frequency distributions of *P. variabilis* gut contents in the day and in the night were not different (Fig. 6,b) indicates that switching from eddy-feeding to long-tentacle feeding does not necessarily expand the size range of prey caught.

Sediment Clearing

The time course of removal of the sediment that landed on *P. variabilis* and *P. caribaeorum* colonies under different flow conditions are presented in Fig. 7. The initial rapid removal of sediment by zoanthids in moderate currents (O in Fig. 7) was due to protrusion and expansion of polyps through the sediment; the slower clearance that followed was due to the dumping of sediment off the oral disks. The rapid disappearance of sediment from zoanthids in the surge zone (♦ in Fig. 7) occurred when waves passed over retracted polyps. Although in areas of rapid flow the smooth surfaces of retracted *P. caribaeorum* colonies were

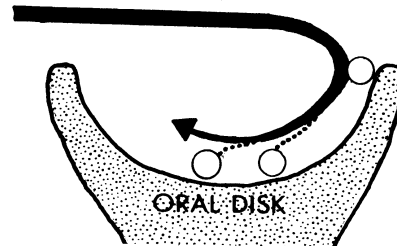


Fig. 5. Dye streams (arrow) revealed that eddies of slowly moving water formed over cup-shaped oral disks. Some particles (circles) in the water were intercepted by the short tentacles at the rims of the oral disks and other particles appeared to settle out of the slowly moving water over the oral disks. In faster currents it appeared that more particles were captured by direct interception and fewer by gravitational sedimentation, as would be predicted by filtration theory (6). Thus, there is actually a continuum of particle capture modes of these zoanthids from eddy-feeding to capture of particles by short and by long tentacles.

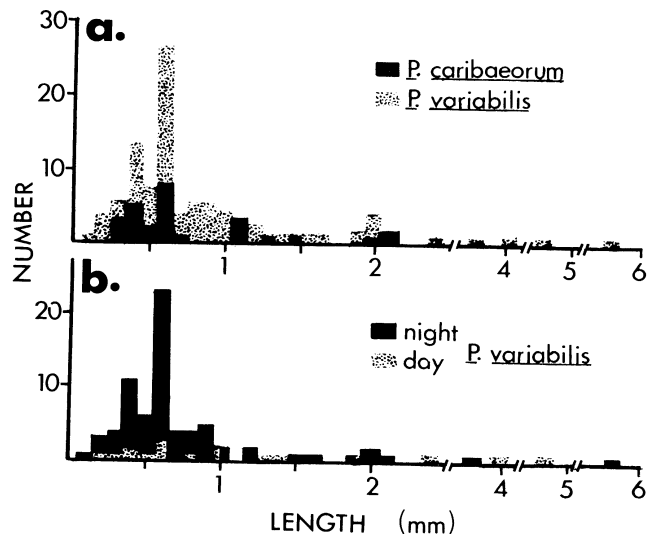


Fig. 6. Size-frequency distributions of items in guts of: a. *P. caribaeorum* and *P. variabilis* (750 polyps of each species); b. *P. variabilis*, day (500 polyps) and night (250 polyps). Data from São Sebastião and Galeta are pooled.

rapidly swept clear of sediment, it appeared that in slowly moving water the large, separate polyps of *P. variabilis* were able to protrude through the sediment more readily than were the polyps of mat-like *P. caribaeorum*.

Conclusions

The large polyps of *Palythoa variabilis* colonies are connected to each other by stolons at their bases, whereas the small polyps of *Palythoa caribaeorum* share column walls. Although *P. variabilis* often occurred in areas of less rapid flow than *P. caribaeorum*, the tall, separate polyps of a *P. variabilis* colony tended to stick out of the slowly moving water near the substratum more than did the polyps of an even-surfaced *P. caribaeorum* colony. The low degree of interpolyp connection of *P. variabilis* rendered these zoanthids much more deformable than *P. caribaeorum*. *P. variabilis* had longer tentacles and caught more prey than *P. caribaeorum*. *P. variabilis*, which often occurred in sandy areas, appeared to shed sediment more readily in slowly moving water than did *P. caribaeorum*. Thus, the structure of *P. variabilis* can compensate for the lack of external transport by flowing water, whereas the structure of *P. caribaeorum* can minimize the mechanical effects of flowing water.

Speculations

Large polyps with a low degree of interpolyp attachment appear to be well suited for clearing sediment and for escaping from the slowly moving boundary layer water near the substratum. Small polyps with a high degree of interpolyp attachment are well suited to rapidly flowing water because their structure minimizes both drag forces

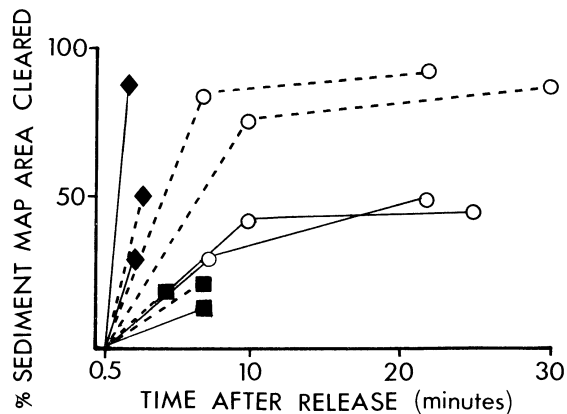


Fig. 7. Graphs of percent of the map area of sediment that landed on a colony (30 s after sediment release) cleared by *P. caribaeorum* (solid lines) and by *P. variabilis* (dashed lines) at various times after sediment release. Diamonds (◆) indicate colonies in surge ($1.5 - 2.0 \text{ m}\cdot\text{s}^{-1}$), circles (○) indicate those in moderate flow ($0.3 - 0.5 \text{ m}\cdot\text{s}^{-1}$), and squares (■) indicate those in still water.

and the deflection resulting from those forces. Although long-tentacled polyps can gather more prey than short-tentacled polyps, the feeding advantage of long tentacles (high L, low I) would be diminished in rapidly flowing water where they are likely to be blown over. I would expect, therefore, to find large, long-tentacled polyps with a low degree of interpolyp attachment in microhabitats of a coral reef that are characterized by low flow velocities and to find short-tentacled small polyps (or closely-connected polyps that are functionally short) in microhabitats characterized by high flow velocities.

If the external skeletons of colonial sessile cnidarians are considered as the terrain on which their polyps sit, the following general pattern of flow microhabitats on a coral reef can be postulated. Although flow velocities decrease as water moves into branched coral colonies (7), polyps on the tops and sides of the branching and plating corals characteristic of shallow, turbulent waters (8) no doubt encounter faster flow than do polyps on the massive corals of the understory (4) and of deeper, calmer water (8). The relative velocity of water over polyps on flexible skeletons can be lower than the relative velocity over polyps on rigid skeletons exposed to the same mainstream current (9). Polyps in holes and crevices encounter slow or no water movement. In protected areas polyps on branching canopy corals are less subjected to sedimentation than polyps on understory corals. The polyps on canopy corals tend to be smaller than the polyps on understory corals and some sea whips and fans (4). The largest polyps on a reef, sea anemones, are found on the substratum (short, aggregating forms) and in holes and crevices (large, solitary forms) (10). The tall branching and plating skeletal geometries of corals that maximize light-gathering for photosynthesis (4) probably also tend to position polyps in high flow velocities. The large, long-tentacled polyp morphologies that maximize food-gathering (2,4,5) also tend to minimize burial of polyps by sediment and to maximize drag forces on and mechanical deformation of polyps (3). Therefore, it is not surprising that the distribution on a coral reef of polyp types that I predict on the basis of mechanical considerations is the same as that predicted by Porter (4) on the basis of trophic considerations.

Acknowledgments

This study was supported by a Cocos Foundation Training Grant in Morphology to the author and by a National Science Foundation Grant (#DES 75-14378) to R. T. Paine. I offer special thanks to K. P. Sebens for collaboration in part of this study and for many helpful discussions. I am grateful to J. Lunetta for the use of facilities at the Instituto da Biologia Marinha of the University of São Paulo, and to I. Rubinoff for the use of facilities at the Galeta Laboratory of the Smithsonian Tropical Research Institute. I thank J. Peterson for his extensive help and ad-

vice, and A.M.M.B. deAlmeida, G. Hendler, and J. Stames for their assistance.

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