

Differential Importance of Biotic and Abiotic  
Factors in Governing Zoanthid Distributions,  
According to Zone on the East Reef  
at Discovery Bay, Jamaica

Rick -

An excellent integration of your  
field and lab results with previous  
published studies and general  
ecological theory. You've come up  
with very plausible explanations  
for your observed distributions  
of the three species.

John

Rick Lathrop '81  
Tropical Marine Ecology  
Winter 1980

## Introduction

Zoanthids, fleshy-polyped colonial cnidarians, are a dominant feature of Discovery Bay reef flats, forming extensive mats. These organisms have been generally overlooked by coral reef researchers. Their taxonomy is in a state of disarray. Little is known of their reproductive biology or growth rates. Zoanthids harbor symbiotic zooxanthellae and meet their energy needs through both autotrophic and heterotrophic means, as do corals.

Three species of zoanthid are found coexisting on the reef flats: Palythoa caribaeorum, Zoanthus sociatus and Zoanthus solandri. Observations reveal that P. caribaeorum is the competitive dominant, capable of extensive overgrowth of both Zoanthus species and a variety of other sessile organisms, including corals. The question is raised on how diversity is maintained on the reef flat. Findings are compared with those of Sebens, a pioneer in zoanthid ecology.

Zoanthids decrease markedly in abundance on the fore reef. Sebens hypothesizes that predation is excluding the two Zoanthus species, while decreasing light limits Palythoa. An alternate hypothesis is proposed in this paper, suggesting

that competition is more important than predation in limiting zoanthids in the fore reef.

### Study site

This study was conducted on the East Back Reef well in near shore. There is a well developed reef crest that slopes quickly from the lagoon. This back edge is composed of rich coral and zoanthid fauna from 1.0-0.4m deep. Next extends the reef flat composed mainly of lithified coral blocks, sandy substrate and rich algal, esp. Pictyota sp. The surge zone is shallower, 0.4-0.6m; here wave surge picks up. The surf zone is a narrow, flat strip with rich algal growth, esp. Acanthophora. Continuous with the surf zone is the living palmata zone. Large ramose colonies dominate this zone. Deeper pools and coral blocks support rich algae and zoanthid mats. Beyond extends the barren zone and then the fore reef itself.

Note: identification of 3 zoanthid species done by using descriptions & photographs in Sebens (1977, 1978)

## Materials & Methods

Mapping of the reef crest was accomplished by line transect. Length covered by the transect line was measured and used to determine percent cover. Initially, a 40m transect was laid perpendicular to the reef crest, extending from the reef flat edge to the surge zone. Later, 20m transects were laid paralleling the reef crest in the reef flat edge, reef flat, surge zone, surf zone and palmata zone. Depth range in each zone was measured.

Data on percent cover in the East Fore Reef, at depths of 20, 40 and 60 feet, was provided by the study group of R. O'Kane, J. Pelton and A. Yoffe.

Observations on growth interactions of the zoanthids were recorded ~~by~~<sup>while</sup> mapping. Zoanthid colony edges were pried up to reveal substrate underneath. Densities of dusky damselfish (*Pomacentrus fuscus*) and fireworm (*Hermodice carunculata*) were also recorded.

Observations were also taken in the lagoon and various depths on the fore reef by means of snorkel and SCUBA.

Lab and field experiments were set up to test for agonistic interactions between corals and zoanthids. Field experiments were performed in both the East Back and Fore Reef, at 50 feet, as there is some evidence that the back reef environment is more stressful on corals (Stoddart, 1969). Thus corals in the back reef may have less energy to expend on defense. Zoanthids and corals were put in direct contact. A variety of aggressively ranked corals, according to Lang (1973), were used. Wire mesh enclosures were used to prevent disturbance by possible predators or curious fish. Observations were taken daily in the lab and twice in eight days in the field. Coral was placed in direct contact with synthetic sponge to assess the effect of direct contact with any soft, pliable substrate.

Lab experiments were performed to assess the three zoanthid species' ability to clear away deposited sediment. Equal amounts of sediment were deposited on equal areas of the three zoanthids. Observations were taken over a two day period.

## Results & Observations

Percent cover values from the six reef crest transects are tabulated in Table I. Lagoon transect data is not listed as both corals and zoanthids are absent.

### Growth Forms

Palythoa caribaeorum grows in sheetlike colonies, the thickness of which varies from 0.5 to 1.0 cm. There is generally one large central colony surrounded by smaller outlying colonies. The central colony is composed of many arms that have grown together, leaving seams. This general growth pattern was observed to occur across the whole reef transect, from the reef flat down to -60 feet on the fore reef. There was some slight variation in the surf zone, where colonies were very patchy, broken up into many small outliers. Invariably Palythoa caribaeorum is found only growing on hard substrate, either lithified coral rock or the dead bases of coral heads.

Zoonthus solandri has greater variation in growth form. The individual polyps are attached at the base by a filamentous stolon system. The polyps can be tightly

packed forming thick mats or sparsely distributed in small aggregates of several polyps. The mat growth form is generally found on hard substrates, where as the sparse aggregates are found on loose, sandy substrate. Several color morphs are present that are characterized by differently colored oral discs. Z. solandri was observed with dark green, light green, rust and blue colored oral discs.

Zoanthus sociatus has similar growth forms to that of Z. solandri. Its stolon system is more sheetlike than Z. solandri. Sparse aggregates are less common. Oral disc and polyp length are smaller in this species than Z. solandri, whereas the tentacles are longer in Z. sociatus.

### Distribution

Palythoa caribaeorum grows in thick mats on the reef flat edge, in the surge zone, surf zone, palmata zone and fore reef. It was absent in the lagoon and reef flat only. Colony sizes generally were much smaller on the fore reef than on the reef crest.

Zoanthus solandri is found growing in mats in every zone where they are present. These mat formations are found on hard substrates, either lithified coral or dead coral bases. Hard substrate is found in every zone across the reef. Sparse aggregates of Z. solandri are common only on loose, sandy substrates. This type of growth formation and substrate is found commonly only on the reef flat and surge zone. Mat formations in the reef flat ~~where~~ only found under overhanging palmata or on the vertical sides of lithified coral blocks. As in P. caribaeorum, colony size is much smaller and their distribution is much sparser on the fore reef. Interestingly, only the blue color morph is found on the fore reef.

Zoanthus sociatus is restricted to a 20m wide strip composed of the surf zone and living palmata zone. It is found growing both in the deeper pools and on top of flat lithified coral blocks.

Table I.

## Percent Cover on Reef Crest

	Reef Flat Edge	REEF Flat	Surge Zone	Surf Zone	Palmetto Zone	Across REEF Flat
Z. solandieri - mat	18.9	9.6	8.4	6.7	12.7	9.7
Z. solandieri - sparse	0.3	2.0	1.5	1.7	17.3	5.4
Z. sol. overgrown by algae	—	3.3	1.6	—	—	4.3
Z. sol - Thalassia	—	—	3.5	—	—	3.5
Z. sol - Madracis sp.	—	—	10.5	—	—	4.8
Z. sociatus	—	—	—	11.2	17.3	—
Palythoa	15.4	—	7.35	8.6	4.6	1.9
Algae	3.9	41.3	35.0	59.1	15.3	16.8
Sparse algae	—	6.0	—	—	—	4.9
Thalassia	—	—	4.8	—	—	24.6
A. palmata	19.3	1.25	9.5	—	33.3	3.6
P. porites	1.0	—	—	—	—	—
P. asteroides	1.3	2.8	—	—	—	0.4
A. agaricites	0.2	0.7	—	—	—	—
D. strigosa	—	—	—	—	6.6	—
Encr. Gorgonian	0.5	—	1.1	—	—	0.3
Stoichactis	2.1	—	—	—	—	0.3
M. leporus	1.6	—	—	7.5	—	—
Sea whip	1.3	—	—	—	—	—
Sand	—	28.2	2.0	—	—	7.4
Hard Subst	34.9	5.0	13.0	6.9	5.0	8.0

Depth range

0.2-1.0<sub>m</sub>1.3-7<sub>m</sub>3-6<sub>m</sub>3-4<sub>m</sub>4-12<sub>m</sub>



observed caught in this squeeze, their oral discs extended above the Palythoa mat. When edges of Palythoa mats were lifted, remnants of former Zoanthus colonies could be observed.

Palythoa mats were often found in conjunction with Zoanthus colonies on the reef crest.

In a similar manner, Palythoa also overgrows an unidentified encrusting gorgonian and algae. Most red and coralline red algae do not find Palythoa a suitable substrate to colonize. Palythoa mats will surround the calcareous stalks of Halimeda, squeezing them out.

Zoanthus does not form the thick, compact mats of Palythoa and is incapable of the latter's bulldozing style. Its elongated polyps and loose colony structure make it a more suitable substrate for recruitment and colonization by algae and Thalassia. Caulerpa spp., Acanthophora spicifera, Pictyota spp. Halimeda sp. and various coralline red algae were observed overgrowing both Zoanthus species. All these algae species were also observed growing freely on hard substrate with the exception of Caulerpa. Its introduction found only in association with Zoanthus mats.

Table II

## Coral - Zoanthid Interactions

	LAB	EBR	EFR
<i>Mussa angulosa</i>	<u>Mussa</u> - expanded in area of contact. tentacles extended <u>Polythoa</u> - polyps closed. Tissue mucous covered, soft, discol. <u>Z. sol</u> - polyps partially or wholly closed, tissue soft	No discernible difference	—
<i>Meandrina meandrites</i>	<u>Meandrina</u> - tentacles extended <u>Polythoa</u> - mucous, tissue soft + discolored	—	<u>Meandrina</u> - tentacles + mesenteric filaments extended. <u>Zoanthids</u> - polyps closed, withered, tissue soft + discolored
<i>M. cavernosa</i>	<u>Cavernosa</u> - polyps extended in area of contact. <u>Z. sol</u> - polyps closed in area of contact	—	<u>Cavernosa</u> - polyps + mesenteric filaments extended. <u>Z. sol</u> - soft + withered
<i>A. agaricites</i>	<u>agaricites</u> - whitens in area of contact with both zoanthids + synthetic sponge. <u>Zoanthids</u> - healthy	same	same
<i>M. annularis</i>	<u>annularis</u> - whitened in area of contact with zoanthids + synth. sponge. <u>Polythoa</u> - mucous covered, slight softening. <u>Z. sol</u> - polyps closed in area of contact	same	same
<i>P. portis</i>	<u>portis</u> - tentacles extended attached to <u>Z. sol</u> polyp. some bare spots. Mucous in area of contact. <u>Z. sol</u> - polyps partially closed in area of contact. No other discernible diff.	—	—
<i>P. asteroides</i>	<u>asteroides</u> - mucous patches in area of contact, whitened underneath. <u>Zoanthids</u> - healthy	—	—
<i>D. strigosa</i>	—	<u>strigosa</u> - skeleton exposed + flesh soft in area of contact. Mesenteric filaments extended. May have digested itself. <u>Z. sol</u> - withered + dead in area of contact	—

### Zoanthus predator observations

Dusky damselfish, Pomacentrus fuscus, was observed to be very common on the reef flat edge; holding territories adjacent to or including Z. solandri mats. No evidence of predation was discernible. P. fuscus and Abudefduf saxatilis were observed in deeper pools on the reef flat and surge zone. All fish were absent on the surf zone. P. fuscus reappeared in the palmata zone. No quantitative sampling was done.

Fireworms, Hermodice carunculata, were only found in the palmata zone. Here they were found in some abundance. No quantitative sampling was done but in one morning of observation three fireworms were found in area of approximately five square meters. In each case, they were found on Z. sociatus mats.

Results of the lab and field experiments on Coral-Zoanthid interactions are presented in Table II. Agonistic behavior was observed on the part of Mussa angulosa, Meandrina meandrites, Montastrea cavernosa, Porites porites, and Diploria strigosa. In these cases tentacles were extended in areas

of zoanthid contact and in the cases of M. meandrites, M. cavernosa, and D. strigosa mesenterial filaments were extended. In all these cases zoanthids suffered from the corals' defensive mechanisms. M. annularis suffered heavily when in direct contact with zoanthids, its skeleton whitening. This same effect though, was observed when the coral was in direct contact with synthetic sponge. Both Polysiphonia and Zoanthus suffer slightly from M. annularis contact. There is partially closing of polyps, mucous production and softening of tissue. In the cases of A. agaricites, P. pectus and P. asteroides contact, the zoanthids were unaffected, whereas the corals were whitened in area of contact. Again, as in the case of M. annularis, whitening of A. agaricites was brought about by prolonged direct contact with synthetic sponge.

Comparison of results of lab with field experiments show some variation. In the cases of M. meandrites and M. cavernosa, the extrusion of mesenterial filaments was only observed in the field. Whereas in the case of M. angulosa, extension of tentacles was only observed in the laboratory. In the cases of A. agaricites and M. annularis, similar results were obtained in

both field and lab.

### Sedimentation Experiments

Zoanthus solandri and Z. sociatus reacted quickly to the effects of sedimentation. As the sediment pushed the polyps down. Within minutes the polyps were trying to regain their vertical position, pushing away the sediment. Once righted, they expanded their oral discs well above the sediment. In both cases, half the colony was extended above the sediment within an hour. Ten hours later, the whole colony was above the sediment.

Palythoa caribaeorum did not fare as well. Not until 10 hours later were any polyps free of sediment, and then only a few. These polyps pushed away the sediment and did not expand above it. Two days later several more polyps were free of sediment but the majority of the colony remained buried.

## Discussion

Niche theory states that all organisms live within the bounds of certain environmental limitations - the potential niche. This full potential range is rarely fully utilized, rather the organism is restricted by some factor, i.e. competition or predation (Connell 1975). The potential niche of zoanthid is determined by numerous physical factors: light, sedimentation, emersion.

Autotrophic contribution of symbiotic zooxanthellae to the energy needs of zoanthids is very important (Sebens, 1977). Light attenuates rapidly, even in the clear waters of tropical coral reefs. Photosynthetic efficiency ~~is~~ varies asymptotically with light intensity. Once a certain light intensity is reached, the photosynthetic system becomes saturated and efficiency plateaus. Conversely, photosynthetic efficiency drops away rapidly below that plateau value. This has been found to be the case in corals, below a certain depth light intensity is too low and corals dropout (Glynn, 1976). A similar phenomena would be expected in the case of zoanthids. Growth rate of

zoanthids would also be expected to decrease with depth. Sibens (1978) made some initial observations that this may be the case with Palythoa caribaeorum. Palythoa is found with regular frequency down to at least 60 feet (personal observation) and probably extends further. Zoanthus solandri is found with regular frequency down to 130 feet, (personal communication, Roddy Warnock). This represents a wide range of potential habitat.

Sedimentation may also represent a restrictive physical factor. My results on sedimentation agree with Koehl's (1977) study. Palythoa caribaeorum is the least able to tolerate sedimentation. This may ~~exclude~~ Palythoa from the reef flat where turbidity and loose sediment cover is highest, restricting<sup>ing</sup> to areas of sufficient water flow to reduce sedimentation. Zoanthus solandri is best able to handle sedimentation because its taller polyps extend up higher. Z. sociatus is capable of handling of sedimentation but only Z. solandri is found on the reef flat.

I observed no clear zonation of zoanthids with depth. According to Sibens (1978),

Z. solandri is found highest on the reef crest as it is most resistant to emersion. Sebens conducted his study on a Panama coral reef with a high exposed algal ridge, a formation that is absent on these windward Jamaican reefs.

Other factors are important in zoanthid distribution that I will call "semi-biological" factors, notably zooplankton prey abundance and dissolved nutrient concentrations.

Zoanthids also depend on heterotrophic means of nutrition. Palythoa caribaeorum and Zoanthus solandri have been found to ingest live zooplankton prey. But content analysis reveals little intake of zooplankton by Zoanthus sociatus (Sebens 1977).

The restriction of Z. sociatus to the narrow strip of the surf and palmata zones may have an explanation. Sebens found Z. sociatus situated in a unidirectional current downstream from the algal ridge. Z. sociatus may depend heavily on its zooxanthellae to fuel its energy needs and thus rely on the presence of dissolved organic nutrients. It has been shown that a dense algal zone harboring blue green algae epiphytes and herbivores

It doesn't follow that zooplankton is dependent upon zooxanthellae! 500m!

release dissolved nutrients in high concentrations. (Siebens 1978). The surf and palmata zone of the East Fore Reef supports a rich algal community. Furthermore the barren zone, which supports a dense population of herbivores, notably Diadema antillarum, is in a unidirectional current upstream. Thus Z. sociatus may be restricted to the surf and palmata zone where dissolved nutrients are in high enough concentrations to sustain growth.

The effect of zooplankton abundance on the distribution of zooanthids is unknown. Glynn (1976) has shown that pelagic zooplankton carried by currents across a reef flat are removed by predators, chiefly corals. In terms of the relative abundances of pelagic zooplankton and demersal plankton in various locations on the East Fore Reef I have no data, and care not to speculate.

I have reviewed most of the factors affecting the potential distribution of zooanthids. I will now look at some of the other factors affecting the zooanthids' realized niches.

Zoanthids are indeed the dominant organism on the reef crest. Enough so that Goreau (1959) called the reef flat, the zoanthus zone.

Analysis of percent cover values shows that Z. solandri is most abundant from the reef flat edge to the surge zone, where it is somewhat displaced by Z. sociatus in the surf and palmata zones. On the reef flat edge and surge zone P. caribaeorum and Z. solandri grow together. In the surf and palmata zone, all three species coexist.

Observations show that P. caribaeorum is the dominant spatial competitor. It is overgrowing and excluding the two Zoanthus species along with other sessile benthic organisms. Why hasn't P. caribaeorum colonized all available space? What factors are maintaining diversity on the reef crest?

A variety of theories have been proposed to explain the maintenance of diversity in marine systems. Competitive networks have been proposed by Jackson (1975), where there is no supreme competitive dominant.

Keystone predator theory states that the dominant competitor is preferentially preyed upon and thus suppressed, allowing room for competitive inferiors. Physical disturbance

may differentially affect populations, with a higher mortality rate of coral dominant competitors (Doughton 1971). Disturbance leads to microscale successional events, creating "patchiness" (Levin and Paine 1974).

Clearly the zoanthid community does not represent a competitive network, P. coribaeorum is a competitive dominant. Predation on P. coribaeorum is rare as it contains potent toxins (Sebens 1978). Evidence points strongly to disturbance as the key factor maintaining diversity. P. coribaeorum appears to be more susceptible to a variety of disturbances than the two zoanthid species.

Abnormally low tides occur periodically on coral reefs throughout the world, causing mass mortalities of corals and other reef organisms (Glynn 1976, Fishelson 1970). Sebens has also found this to occur on the reefs in Panama. Desiccation studies show that P. coribaeorum is the least resistant to desiccation. Prolonged exposure during an abnormally low tide can lead to mass mortalities of P. coribaeorum colonies. The frequency of abnormal low tides is not known for Jamaican north shore reefs but in all probability does occur.

Storms are capable of widdling great damage to a reef. Colonies of coral can be uprooted and carried. Large amounts of sediment can be removed or deposited (Stoddart 1969). My personal observations agree with those made by Sebens on the relative fragility of P. caribaeorum. It is easily bruised, leading to damage and possibly infection. This infection can consume the entire colony, causing death and rot. Seben (1978) thought that storm damage could pay a heavy toll on P. caribaeorum. Storm deposited sediments would also negatively affect P. caribaeorum to a greater degree than the other two zoanthid speals, as shown earlier.

Thus disturbance helps to keep P. caribaeorum in check. After a disturbance, there is vegetative regrowth of all three zoanthid species. Higher survival rates by the two Zoanthus species would give them the jump on space colonization but once established P. caribaeorum is as relentless as the tortoise.

The next question to be approached is if zoanthids can survive and prosper in this harsh environment, why don't they prosper in the more benign environment

of the fore reef. Physical processes determine community structure on the reef crest, whereas in the more benign environment of the fore reef biological processes dominate (Glynn 1976). Predation, competition, bioturbation and mutualism become the overriding factors determining community structure.

Along these lines, in highly unpredictable stressful environments such as the reef crest, predation is reduced. Prey species can find refuge. This is how Sebens (1978) explained that Zoanthus were restricted to the reef crest. His predation experiments showed that there was significant removal in the fore reef areas. The main Zoanthus predators are dusky damselfish (Pomacentrus fuscus) and fireworms (Hermodice carunculata). He observed that these predators were excluded from the reef crest on his study site.

My personal observations conflict with those of Sebens, suggesting the situation is different on Jamaican reefs. The reef crest does not appear to provide a significant refuge from predators. Pomacentrus fuscus were observed in high numbers concurrently with high cover by

zoanthids. OTT and Lewis (1972) found highest densities of Hermodice carunculata in the shallow waters of the near fore reef and reef crest. Personal observations, as well as those of DBML researchers (Roddy Warnock, personal communication) show that Hermodice carunculata densities are highest on the reef crest. I see no evidence of over-grazing or that the potential predators are having any great effect on zoanthid species distributions.

Perhaps, then competition is the key factor determining zoanthid distributions. I am mainly concerning myself with P. coribaeorum and Z. solandri. Z. sociatus appears to be restricted to the reef crest for nutritional reasons. Spoboden and Sanders (1969) state that organisms adapted to life in a stressful, unpredictable environment must be generalized and have a broad tolerance range. Even then these tolerances are exceeded, as seen in the case of disturbance effects on zoanthids. In a more benign, predictable environment organisms are capable of greater specializations. Jackson ( ) states that there is a tradeoff between the advantage of a

species in occupying marginal, stressful environments and maintenance of superior competitive ability for space in physically less stressful subtidal environments. Many organisms find refuge in the intertidal zone, or in this case the reefcrest, from superior space competitors.

Zoanthids share similar resource requirements with corals, notably light, zooplankton prey and possibly dissolved nutrients. These resources are not competed for directly but rather indirectly. Space on which to live is the most limiting resource and competed for most intensely (Jackson 1977, Connell 1973). Interference competition strategies are numerous and diverse. It can take the indirect form of a colony overshadowing another, cutting off light and water flow (Connell 1973). More direct forms of interference have been observed. Corals have been found to digest other corals by extrusion of mesenterial filaments (Lang 1973). Sponges have been found to produce allelopathic chemicals (Jackson 1975). I have shown that corals, the chief space occupiers on the fore reef, are capable

of digestion of zoanthids by extrusion of their mesenterial filaments. Zoanthids come out losers when placed in direct contact with corals, except with corals of lowest digestive ranking, in this case Posteroide and A. agaricites. Corals of a variety of digestive ranking were capable of defensive actions. Zoanthids were observed in the field growing on dead coral bases and extending upwards, sometimes slightly overgrowing live coral. This was ~~observed~~ more commonly observed on the back reef. On the fore reef, generally only standoffs were observed. Those corals that were overgrown have a low digestive ranking: A. agaricites, Posteroide, Madracis mirabilis.

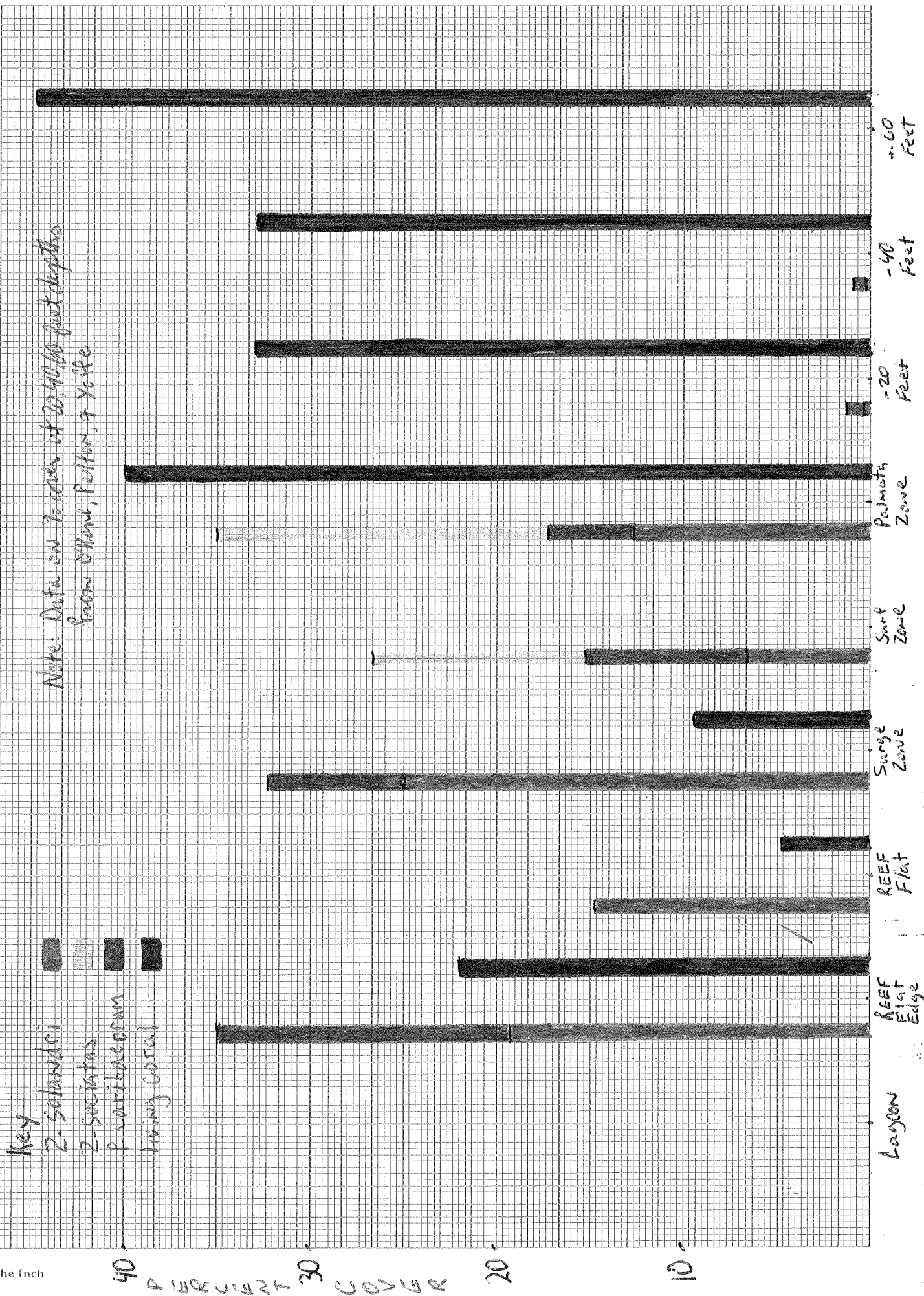
Thus corals have the ability to defend their space and gain new space in interactions with zoanthids. There appears to be <sup>an</sup> inverse relation between zoanthid cover<sup>n</sup> and coral cover (Fig. I). Not as much available free space is open to zoanthids in the fore reef. Zoanthids are restricted to small patches on dead coral bases.

There expansion upward is restricted by most coral's defensive capabilities of their mesenterial filaments. Furthermore what open hard substrate that is open is contested for by other benthic marine

invertebrates that have interference strategies of their own, i.e. allelopathy of sponges, nematocysts of sea anemones. Zoanthids appear to have no interference strategy other than overgrowth. This strategy appears to be insufficient, making zoanthids inferior space competitors in the competitively intense fore reef environment. I think this partly explains why zoanthids are relatively scarce in the fore reef. Especially in the case of P. caribaeorum, competition and not predation is excluding zoanthids. Thus zoanthids prosper only on the reef crest where they find refuge from spatial competition.

Though I'm offering spatial competition as a major limiting factor on zoanthid growth in the fore reef, I'm not discounting the importance of decreasing photosynthetic efficiency with depth. Sebens (1978) had some indication that growth rate of P. caribaeorum decreased with depth. More work needs to be done to characterize the effects of depth on photosynthetic efficiency and growth rate before we can fully determine the effect of depth on distribution of zoanthids.

Figure  
Percent Cover of Zonithids in Relation to Living Coral Cover



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### Errata

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