INTERSPECIFIC COMPETITION BETWEEN *PALYTHOA CARIBAEORUM* AND OTHER SESSILE INVERTEBRATES ON ST. CROIX REEFS, U.S. VIRGIN ISLANDS

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ABSTRACT

Palythoa caribaeorum (Duchassaing and Michelotti), an aggressive competitor for space, was observed in the field and tested in the laboratory to determine how interspecific competitive interactions may influence its abundance and distribution in a variety of reef environments. Fore-reef, reef-crest, back-reef, and patch-reef habitats were examined both for abundance patterns and for interspecific competitive battles between *Palythoa* and other sessile reef invertebrates. Variations in the growth rate of *Palythoa* were noted for invertebrates of varying defensive capabilities. Densities of *Palythoa* are affected by variability in environmental conditions. However, growth rates of this zoanthid are not influenced significantly by physical conditions and remain consistently high for all study sites at 2.5-4.0 mm/day. This represents one of the highest known growth rates for an anthozoan. Data also suggest that *Palythoa* can overgrow nearly every other sessile reef invertebrate, placing it at the top of a competitive hierarchy for reef ecosystems.

INTRODUCTION

Competition for space has gained the attention of a wide variety of investigators interested in making long-range predictions about community structure (Dayton 1971, Foster 1972, Lang 1973, Paine 1974, Porter 1974, Osman 1975, Jackson 1977a). In temperate subtidal rock-wall communities there appears to be an unpredictable settlement and overgrowth pattern of encrusting invertebrates probably dependent on both the availability of propagules at any point in time and the rate of lateral growth by each colony (pers. obs.). However, the details of competitive interactions between component species within these communities have not yet been investigated (Karlson 1978, Vance 1979).

In tropical environments, recent work has focused on competitive interactions between scleractinian corals in open reef habitats which apportion space in a hierarchical pecking-order fashion using tentacles, mesenterial filaments and possibly allelochemical mechanisms or by using various growth strategies such as overtopping (Lang 1971, 1973, 1974, Porter 1972, 1974, Connell 1976, Richardson et al. 1979). In contrast, cryptic fauna (living on the undersides of coral plates or in cave environments) may interact in an entirely different fashion, displaying "competitive networks" where no one species is predictably dominant or competitively superior (Jackson 1977a, b, 1979, Jackson and Buss 1975, Buss and Jackson 1979). However, almost no one has reported on how less abundant components of open reef habitats (other than scleractinians) acquire, maintain and defend space on a reef.

Gorgonians, sponges and zoanthids are usually low in abundance, but at times may dominate up to 85% of the cover in some open reef areas, especially in shallow zones (Birkeland and Neudecker 1981, C.S. Rogers, unpubl, pers. obs.). *Palythoa caribaeorum* (Duchassaing and Michelotti) is an especially common zoanthid in certain shallow reef environments on St. Croix (Carpenter and Gladfelter 1979). It appears to acquire and dominate space by killing or directly hindering the growth of its competitors both by physical and chemical means. Physically, it may grow directly over the tissues of nearby corals or other invertebrates, "smothering" them (pers. obs.), but we are aware of no specific work on this interaction. Chemically, *Palythoa* contains a powerful high molecular weight toxin known as palytoxin (Ciereszko and Attaway, 1961, Scheuer 1964, Ciereszko and Karns 1973, Attaway and Ciereszko 1974) which could act as an allelochemical and aid in acquiring space.

Here, we document the abundance and growth rates of *Palythoa* in specific reef environments on St. Croix. We also demonstrate its ability to overgrow nearly every other sessile invertebrate it contacts in the natural environment and report on the competitive interactions it has with these species.

MATERIALS AND METHODS

Competitive interactions of *Palythoa* were examined by field observations and laboratory tests from November, 1980 — April, 1981. In the field *Palythoa* colonies were observed at Buck Island and Tague Bay, St. Croix, U.S. Virgin Islands (17°46'N:64°37'W) in four types of habitats: fore-reef, reef-crest, back-reef and patch-reef environments. Percent cover of *Palythoa* was determined by noting its presence or absence under 100 predetermined points in at least 10 haphazardly placed 1 m^2 quadrats at each site. Three colonies, which were actively overgrowing neighboring organisms, were tagged on each of a fore-reef (at depths of 6.1, 6.4 and 7.6 m), and back-reef area (at depths of 2.9, 3.0 and 3.3 m) and one colony was tagged on a patch-reef at 2.5 m depth. Tagged colonies and the nature of their marginal interactions were observed over periods of approximately 20 days, changes being noted at 3-4 day intervals.

In the laboratory, the ability of *Palythoa* to overgrow other invertebrates was tested by placing 17 potential competitors (mostly scleractinian corals) approximately 3 mm from the margin of an intact *Palythoa* colony in running seawater tables. Regular observations were made over a 14-day period. The non-contact margins of the potential competitors acted as controls.

RESULTS

Palythoa was most abundant in the shallow reef-crest and back-reef habitats at Buck Island. Table 1 gives the percent cover as taken from the 1 m^2 quadrat point counts in the habitats studied. Individual percent cover estimates were as high as 83% for some areas on the reef-crest and 68% in the back-reef zone, but the variability was high in all regions. Colonies occur both as large sheets (sometimes over 1.5 m across) often with hummocked areas of growth in the central regions, and as numerous isolated small colonies which could have been formed by the deterioration of a larger parent colony or by the recent settlement of propagules. Although no *Palythoa* were recorded in the point counts for the fore-reef region of Buck Island (Table 1), several colonies were noted as deep as 10 m.

Invertebrates which were found being overgrown by *Palythoa* are listed in Table 2. Most of these observations were made almost exclusively in the shallow reef-crest or back-reef regions of Buck Island. Marginal interactions between *Palythoa* and other species can be separated into three major types: lateral aggression, overtopping and point settlement (Fig. 1). Each has different implications as to the types of interactions taking place between *Palythoa* and the competitor. With lateral aggression and no physical contact with live tissue of the subordinate (Fig. 1A), there exists a margin of dead tissue in front of the advancing *Palythoa* colony and it is assumed that some form of allelochemical interaction is likely occurring. However, it is also possible that the *Palythoa* colony had previously advanced, "smothering" the coral polyps, then retracted, leaving a margin of bare space before advancing again. In Fig. 1B (lateral aggression with physical contact at the interface) the interaction may involve some tentacular action on the part of *Palythoa* or an actual "smothering" of the subordinate species. With overtopping and no physical contact (Fig. 1C), subordinates with zooxanthellae would be shaded out of existence; it is likely that heterotrophic feeding would be severely impeded in

Table 1. Average percent cover of *Palythoa* at Tague Bay and Buck Island, St. Croix, n = number of quadrats sampled.

	Average % Cover ± S.E.	Range of % Cover	n	Depth (m)
TAGUE BAY:				
Fore-reef	0.8 ± 1.0	0 — 3	10	to 10
Back-reef	0.0	0	10	1 — 5
Patch-reef	0.3 ± 0.5	0 — 1	10	1 — 3
BUCK ISLAND:				
Fore-reef	0	0	10	to 12
Reef-crest	36.1 ± 26.4	6 — 83	16	≤ 1
Back-reef	10.2 ± 16.6	0 — 68	22	1 — 3
Patch-reef	0	0	10	2 — 5

Table 2. Subordinate species which *Palythoa* can overgrow.

SCLERACTINIAN CORALS:	HYDROZOAN CORALS:
Acropora cervicornis	*Millepora alcicornis*
Acropora palmata	*Millepora complanata*
Acropora prolifera	*Millepora squarrosa*
Agaricia agaricites	
Dichocoenia stokesii	
Diploria clivosa	ZOANTHIDS:
Diploria labyrinthiformis	
Diploria strigosa	*Zoanthus solanderi*
Eusmilia fastigiata	
Favia fragum	PORIFERA:
Isopyllia sinuosa	
Meandrina meandrites	
Montastrea annularis	*Haliclona* sp.
Montastrea cavernosa	several other unidentified sponges
Mycetophyllia aliciae	
Mycetophyllia ferox	
Porites astreoides	GORGONACEA:
Porites furcata	
Porites porites	*Pseudopterogorgia* sp.
Siderastrea radians	*Plexaurella* sp.
Siderastrea siderea	
Stephanocoenia michelini	

this case as well. No allelochemical or tentacular effects need be invoked here. In Fig. 1D (overtopping with physical contact) "smothering" would again prevail, eventually killing the subordinate. Here, only a rapid growth rate would be necessary to overtake the other species. Fig. 1E shows the settlement of *Palythoa* directly onto a living organism, with subsequent spreading by any of the mechanisms described above.

All forms of these marginal interactions were found in the field and some species showed several different types of interactions with *Palythoa* with different colonies. Interaction type IA was relatively common, especially with scleractinian corals such as *Diploria*, *Siderastrea* and *Agaricia* with a consistent dead tissue margin of approximately 5 mm. *Siderastrea*, in particular, showed an obvious 5-10 mm dark stained zone just ahead of the *Palythoa* front. One peculiarity of this interaction is that sediment often accumulated in the marginal area. In other cases, another zoanthid *(Zoanthus solanderi)* would completely fill the gap between an advancing *Palythoa* colony and the living tissue of an adjacent scleractinian coral. Overtopping with no physical contact (1C) was even more common, occurring with nearly all species of scleractinian subordinates observed, usually with about a 5 mm overlap. Types 1B and 1D were often difficult to distinguish in the field, but on some occasions up to 20 mm of relatively healthy tissue was found under an advancing *Palythoa* colony, indicating the advantage of an extremely rapid growth rate (1D). This physical interference was evident in the interactions of *Palythoa* with sponges, gorgonians, *Millepora* spp. and other zoanthids, particularly *Zoanthus solanderi*. Small isolated *Palythoa* colonies were noted in the central region of only very few healthy coral colonies (1E) and we cannot be certain that they were able to settle directly onto live tissue. They may have settled on the site of an injury and only later grew over healthy tissue.

Field colonies showed relatively comparable growth rates for *Palythoa* at all three study sites. For Tague Bay fore-reef, the average increase in colony size over a 20-day period was 62.0 mm, yielding an average growth rate ± standard error of 3.1 ± 0.4 mm/day. On the back-reef and patch-reef sites, the average growth rates were 2.8 ± 1.0 ± mm/day and 3.5 mm/day respectively (range=2.5-4.0 mm/day). This figure (4.0 mm/day) represents the fastest known growth rate of any anthozoan. Even some of the fastest growing scleractinian corals such as *Acropora palmata* only reach a maximum of approximately 99 mm/yr (=0.27 mm/day) (Gladfelter et al. 1978).

Overgrowth rates of *Palythoa* onto staged competitors in the running seawater tables showed a wide range of results from 0.0 mm/day for a sponge and *Meandrina* to 1.4 mm/day for *Agaricia* (Fig. 2). These rates are considerably slower than those for colonies in situ and perhaps the stress of removing colonies from the field or keeping them in an artificial environment altered the growth potential of *Palythoa*.

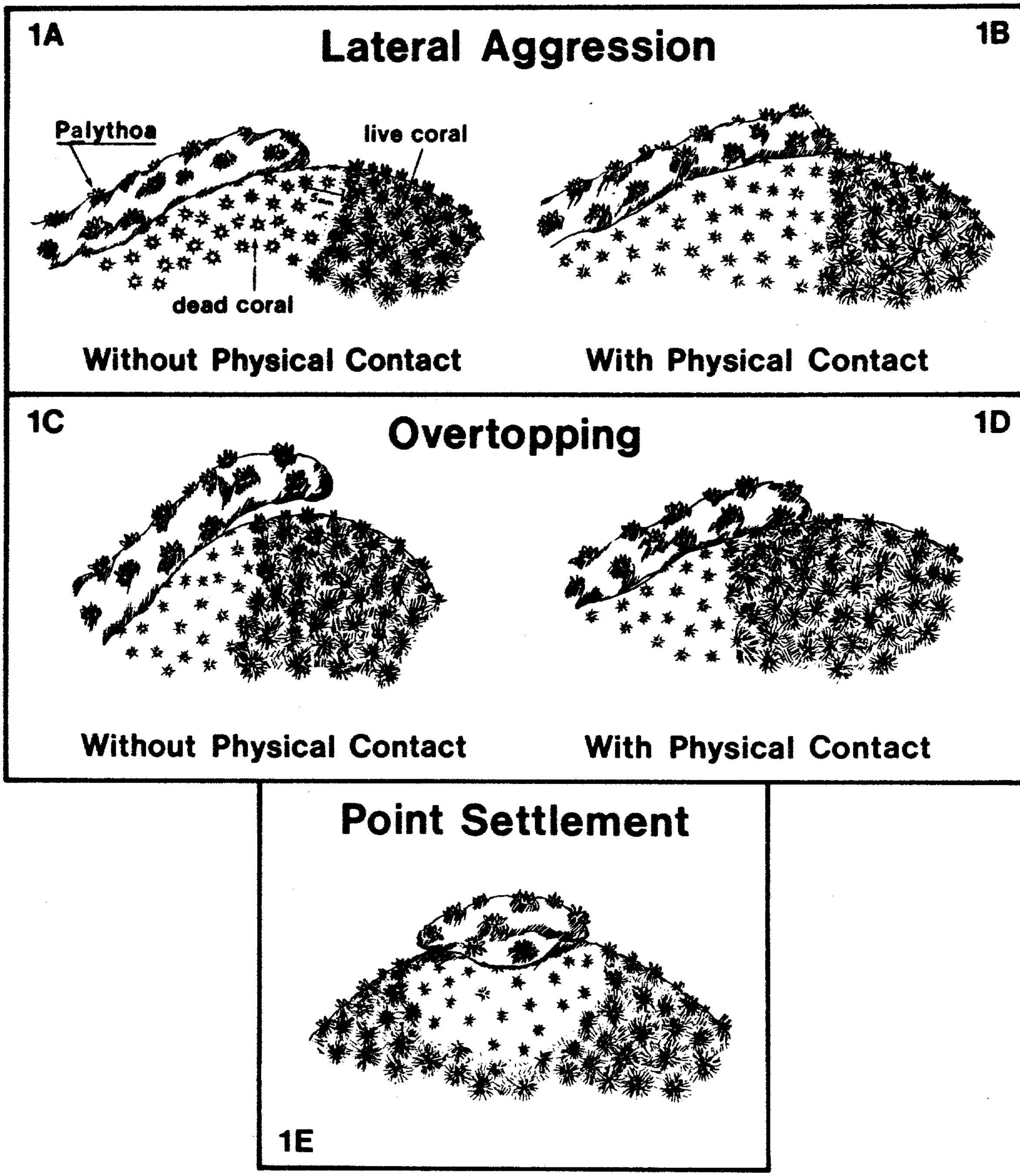

Figure 1. Types of overgrowth interactions be Palythoa over subordinate species. Coral depicted in diagrams is *Montastrea annularis.*

DISCUSSION

The average abundance of *Palythoa* at Buck Island reaches 36.1% on the reef-crest and 10.2% on the back-reef areas with virtually none being found on deep fore-reef regions. However, with a potential marginal growth rate of 4 mm/day, and its ability to overgrow nearly every other colonial invertebrate it

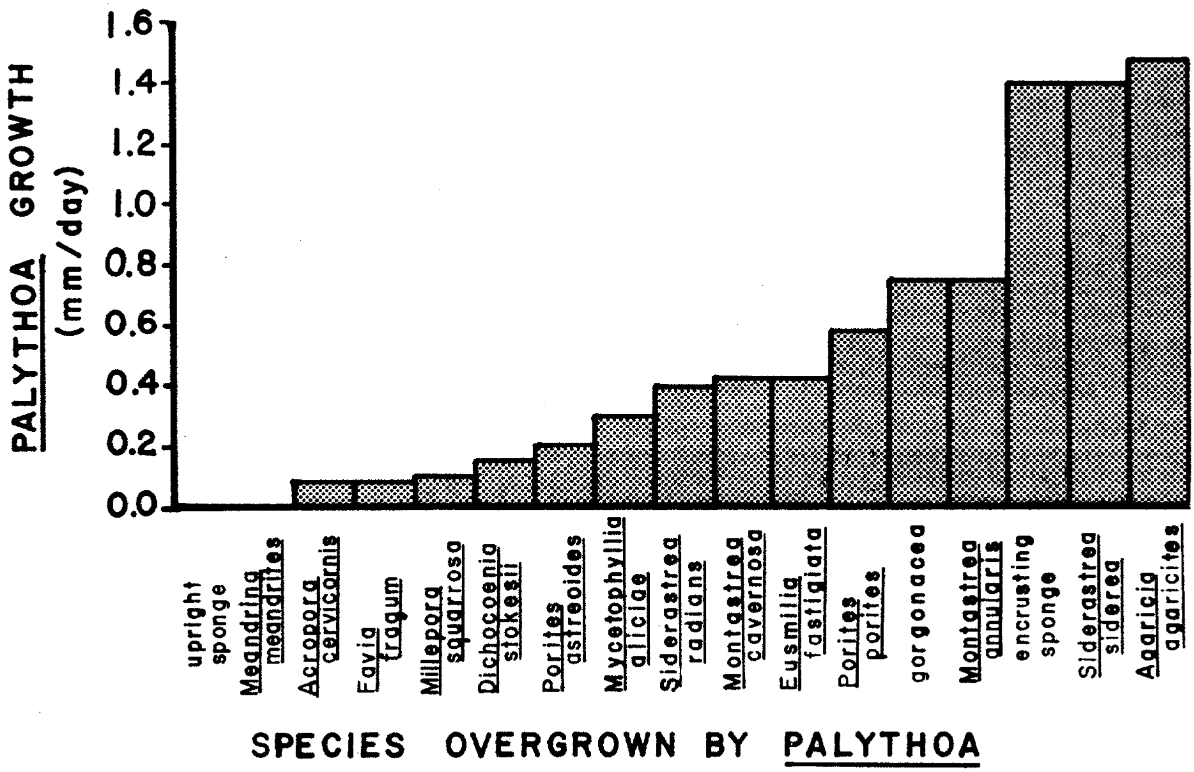

Figure 2. Average rate of *Palythoa* growth over various species during staged interactions (for 14 day trials) in running seawater tables.

encounters, it seems clear that in a relatively short time, *Palythoa* should be able to cover even more area on the reef than it does. Only two other species are known to have the ability to overgrow *Palythoa*: an encrusting gorgonian *Erythropodium caribaeorum* (Duchassaing and Michelotti) reported by Karlson (1980) in Jamaica and an encrusting colonial tunicate *Trididemnum solidum* (Birkeland et al. 1981 in Panama).

What, then, limits the growth and/or abundance of *Palythoa?* First, the genus *Palythoa* is characterized by having encrustations in the body wall, discouraging predation. Secondly, the presence of palytoxin (Ciereszko and Karns 1973) may act in the same fashion but may also be involved in the acquisition of space. Although the morphology and biochemistry of *Palythoa* is a deterrent, predation does occur. We have observed the fireworm *Hermodice carunculata* (Pallas) feeding on *Palythoa* on two occasions. Both of our records were in the early afternoon, in concurrence with the timing of observations by Ott and Lewis (1972) who reported *Hermodice* feeding abundantly on a different species, *Palythoa mammillosa* (Lamouroux), from 1500 h until sunset. Only one other report (Sebens, in prep) reports *Hermodice* feeding on *P. caribaeorum* (in Panama). *Palythoa* abundance may therefore be partially controlled by *Hermodice* predation although we feel this is probably not a major limiting factor.

Palythoa depends both on heterotrophic and autotrophic nutrition and demonstrates diel behavioral changes associated with polyp expansion and contraction (Sebens 1977, Suchanek and McFarland, in prep.). Because its distribution is so skewed toward the shallow reef zones, it may be much more dependent on autotrophy than heterotrophy, or it may be eliminated from deeper zones by predators, although we know of no such published reports. Studies are now in progress (by Suchanek) monitoring *Palythoa* colony expansion or contraction on a seasonal basis in order to assess long-term changes in competitive abilities and eventual coral community structure in shallow open reef habitats.

Staged competitive battles in the laboratory showed that corals appear to have different inherent abilities to resist being overgrown by *Palythoa* (Fig. 2). Lang's (1973) scleractinian competitive hierarchy was based on coral-coral interactions. Of the 11 coral species tested against *Palythoa* which coincide with Lang's ranking list, 7 also suggest a possible trend in their relative abilities to resist overgrowth by the zoanthid. *Meandrina meandrites, Acropora cervicornis, Mycetophyllia aliciae, Montastrea cavernosa* and *Eusmilia fastigiata*, corals which effectively defend space against many other subordinate corals, also were most effective at resisting overgrowth by *Palythoa*. *Siderastrea siderea* and *Agaricia agaricites*, corals very low on Lang's scleractinian ranking list, showed the least ability to resist *Palythoa*. However, four species showed contradictory results: *Porites astreoides, Siderastrea radians, Porites porites* and *Montastrea annularis*. It is possible that artificial laboratory conditions may have altered results from what might be found under natural conditions. These very preliminary results suggest the possibility that a common mechanism exists for scleractinian corals to resist not only other scleractinians, but other invertebrates, in general.

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