ALTERNATIVE COMPETITIVE STRATEGIES IN A PERIODICALLY DISTURBED HABITAT

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ABSTRACT

The outcome of encounters between adjacent, sessile, colonial cnidarians in a shallow, subtidal reef habitat was examined to determine the relative importance of overgrowth and growth inhibition as alternative competitive strategies. It was determined that the gorgonian *Erythropodium caribaeorum* aggressively overgrew other cnidarians at a mean rate of 3.9 cm/yr. Most of the contacts involving the more abundant zoanthid *Zoanthus solanderi*, however, resulted in no apparent growth changes over the 16-month observation period. This absence of growth and skeletal evidence from corals in contact with *Zoanthus* suggest that growth inhibition is responsible for "stand-off" interactions. This non-aggressive competitive strategy appears to be a general feature of colonial organisms which colonize and persist in periodically disturbed habitats. This persistence can result in a depression of local species diversity at intermediate levels of disturbance.

Species abundance patterns within a variety of marine, hard substratum communities are affected by disturbance processes, predation, and competitive interactions (Dayton, 1971; Connell, 1972; Paine, 1974; Menge and Sutherland, 1976). It has been proposed that intermediate levels of disturbance result in higher species diversity than do extremely high or low levels (Paine and Vadas, 1969; Levin and Paine, 1974; Connell, 1978) and that in some communities competitive processes at low levels of disturbance result in succession leading to monopolization of the spatial resource (Levin and Paine, 1974; Porter, 1974). The mechanism whereby a competitive dominant displaces other species in these assemblages of sessile invertebrates usually involves overgrowth in one form or another (Jackson and Buss, 1975; Connell, 1976; Jackson, 1977; Maguire and Porter, 1977; Buss and Jackson, 1979).

Overgrowth, however, is not the only possible result of competitive encounters between these organisms. Such encounters may result in the cessation of growth as observed in bryozoa (Stebbing, 1973a; 1973b), corals (Connell, 1976), and in encrusting hydroids (Karlson, 1978). These "stand-off" interactions among colonial species are probably indicative of a defensive strategy (Connell, 1976; Karlson, 1978) whereby the encrusting organism protects the peripheral bounds of its colony. Possible mechanisms for colony defense may involve the development of specialized spines (Stebbing, 1973a; 1973b), spicules, toxins, or growth inhibitors (Katô et al., 1963; 1967). Competitive mechanisms of sessile organisms have recently been reviewed by Jackson (1977).

Overgrowth can be viewed as a competitive mechanism with which an organism can aggressively acquire additional substratum space at the expense of an inferior competitor. The ability to inhibit being overgrown, on the other hand, represents a nonaggressive mechanism for defending already occupied substratum. These need not be mutually exclusive competitive strategies but they may be selectively advantageous under different environmental conditions. Such habitat characteristics as the rate or intensity of disturbance or predation can affect the availability of bare substratum and the frequency with which competitive encounters occur. When substratum space is in limited supply as in the Jamaican cryptic reef community (Jackson and Buss, 1975; Buss and Jackson, 1979), overgrowth capabil-

ities should be selectively favored. In more disturbed habitats defensive attributes resulting in "stand-off" interactions should be favored (Karlson, 1978). The purpose of this paper is to examine the competitive strategies of some colonial coral reef cnidarians living in a habitat which is periodically disturbed and to provide additional evidence suggesting the importance of growth inhibition as a competitive strategy under these conditions.

METHODS AND RESULTS

The study site is located within the subtidal *Zoanthus* zone (Goreau, 1959) on the east side of Discovery Bay, Jamaica. In the lee of the reef crest is a relatively protected location where several sessile cnidarian species are quite common living on dead, unconsolidated coral substratum. One very common cnidarian here is *Zoanthus solanderi* which is somewhat larger and less well attached to the substratum than is *Zoanthus sociatus,* the common zoanthid on the west side of Discovery Bay (Kinzie, 1970) and at Ocho Rios (Goreau, 1959). Although there are some taxonomic difficulties with this particular genus, the above specific distinction between these two zoanthids does conform with that made by Duerden (1898), Fontaine (1954), and Sebens (1977; 1980). [Note that *Z. sociatus* is synonymous with *Z. flos-marinus* (Pax, 1910).]

During October 1976, twenty-four 0.25 m^2 quadrats were located along four transect lines set up within an area (~42 m^2) dominated by *Zoanthus solanderi.* Photographic sampling followed by planimetry on each quadrat print was used to determine the relative abundances of the sessile epifauna. These data clearly document the prevalence of *Zoanthus* (Table 1) within these local areas.

Larger scale relative abundance estimates were determined in January 1980 along a 40-m transect at a depth of 1.5–3.5 m. At 10-m intervals along this transect a set of approximately 1,000 randomly placed drops of a weighted line (a modified random point method) was used to estimate percent cover within 3 m of each interval mark. Pooled data from these five sets appear in Table 1. The two most abundant cnidarians are *Zoanthus solanderi* and *Stoichactis helianthus.*

To contrast overgrowth and "stand-off" interactions as alternative competitive strategies among east back reef cnidarians, encounters with well-defined contact zones were selected and marked using small, coded plexiglass labels beginning in October 1976. These encounters involved several colonial species which were only capable of overgrowing adjacent competitors at the contact zone, being overgrown, or in maintaining a stable "stand-off." Contacts involving mobile actinians and corallimorpharians had originally been included, but were subsequently eliminated because their contact zones were not well-defined. Virtually all such contacts resulted in movement of these cnidarians away from the contact zones making it impossible to distinguish aggressive *versus* non-aggressive interactions.

By February 1978, 87 encounters had been systematically photographed at least five times during the previous 12–16 months. Evaluation of growth changes in successive photographs of each encounter resulted in the determination of relative competitive abilities. Encounters for each species were scored in one of four categories: those resulting in overgrowth could have been won or lost; there may have been no apparent growth changes during the observation period (estimated minimum detectable growth = 2 mm/yr); or storm damage, predation, or some other unspecified cause may have disturbed the initial encounter situation. Of these 87 encounters, 42.5% resulted in overgrowth, 35.6% in no apparent growth changes, and 21.8% had been disturbed (Table 2).

Based purely on the relative overgrowth capabilities of these cnidarians, it is evident that the encrusting gorgonian *Erythropodium* is an aggressive competitive dominant in this species assemblage. *Erythropodium* overgrew both zoanthids, *Zoanthus* (X8) and *Palythoa* (X3), and the corals *Porites astreoides* (X5), *P. porites* (X1), *Agaricia* (X8), *Siderastrea* (X1), and *Acropora* (X1). These represent 73.0% of all the encounters which resulted in overgrowth and 75.0% of the 36 undisturbed, *Erythropodium* encounters (Table 2). The average rate at which *Erythropodium* overgrew these other cnidarians was 3.9 cm/yr (range = 0.9–9.1 cm/yr). *Palythoa* was the second most aggressive cnidarian overgrowing *Zoanthus* (X2), *P. astreoides* (X2), and *Agaricia* (X4) as well as *Millepora* (X1) at an average rate of 1.3 cm/yr (range = 0.3–3.5 cm/yr). However, overgrowth occurred in only 48% of the 25 undisturbed contacts involving *Palythoa.*

In only one case was *Zoanthus solanderi* observed to overgrow another cnidarian, this being *Montastrea annularis* which was overgrown at a rate of 3.1 cm/yr. Most of the undisturbed *Zoanthus* encounters (60.7%) resulted in no apparent growth changes and these represent 54.8% of all the encounters resulting in no changes (Table 2). This suggests that *Zoanthus* growth is inhibited by contact with other sessile cnidarians. It is also apparent that the growth of both members of encounters involving *Zoanthus* is inhibited. Close inspection of the skeleton of *Millepora, Agaricia, Porites,* and *Acropora* reveals a characteristic concavity at that portion of the edge of these corals which had been

Table 1.   Mean percent cover and rank abundance estimates from quadrat and random point sampling

Order and Species	% (quadrats)	Rank	% (random points)	Rank
Actiniaria				
Condylactis gigantea	.1	9	.3	16
Heteractis lucida	1.5	4	1.4	9
Lebrunia coralligens	<.05	11.5	0	—
Stoichactis helianthus	0	—	16.9	1
Zoanthidea				
Palythoa caribaeorum	.5	7	2.1	6
Zoanthus sociatus	0	—	1.5	8
Zoanthus solanderi	66.5	1	13.2	2
Scleractinia				
Acropora cervicornis	0	—	.3	16
Acropora prolifera	0	—	<.05	20
Acropora palmata	0	—	10.2	3
Agaricia agaricites	.6	6	2.0	7
Colpophyllia natans	0	—	.2	18.5
Diploria labyrinthiformis	0	—	.1	19
Diploria strigosa	0	—	.3	16
Montastrea annularis	.1	9	.7	12
Porites astreoides	3.1	3	3.7	5
Porites porites	3.2	2	7.6	4
Siderastrea siderea	0	—	.4	14
Gorgonacea				
Erythropodium caribaeorum	0	—	1.2	10
Corallimorpharia				
Recordia florida	.8	5	1.1	11
Rhodactis sanctithomae	<.05	11.5	0	—
Hydrocorallina				
Millepora alcicornis	.1	9	.6	13
Millepora complanata	0	—	.2	18.5
Miscellaneous Algae	5.8		10.9	
Other	1.7		2.3	
Bare Substratum	15.8		22.9	

Table 2.   Summary of encounter data

Species	Overgrowth		No Apparent Change	Disturbed	Total
	Won	Lost			
Erythropodium caribaeorum	27 (8)	0	9 (1)	8 (2)	44
Zoanthus solanderi	1	10	17	7	35
Palythoa caribaeorum	9 (2)	3	13 (4)	7 (3)	32
Agaricia agaricites	0	12	9 (3)	9 (1)	30
Porites astreoides	0	7	11 (6)	7 (1)	25
Siderastrea siderea	0	1	2 (2)	0	3
Porites porites	0	1	1 (1)	0	2
Millepora complanata	0	1	0	0	1
Montastrea annularis	0	1 (1)	0	0	1
Acropora palmata	0	1	0	0	1
TOTAL	37 × 2		31 × 2	19 × 2	87 × 2

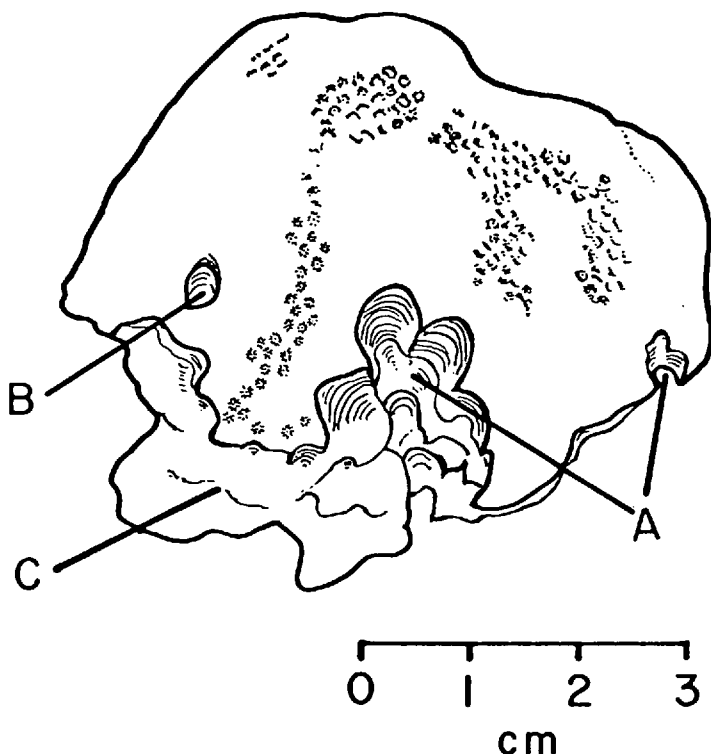( ) indicates number of encounters with *Zoanthus*.

Figure 1.   Schematic diagram of a small *Porites astreoides* colony with grooves (A) and a ring (B) formed by contact with *Zoanthus solanderi* polyps. The largest groove in the dead coral skeleton (C) of this specimen is 2.8 cm deep.

in contact with the soft-bodied *Zoanthus* polyps (Fig. 1). Successive layers of coral skeleton maintain this configuration forming grooves (Fig. 1A) in the shape of *Zoanthus* polyps. In some cases, the growing lateral edge of the coral has continued to grow around these polyps thus forming rings and isolating them. Such rings in *Millepora* have been observed to continue growth tangentially along the polyps forming collars. On the other hand, rings formed by *P. astreoides* continue to grow concentrically resulting in the reduction of zoanthid polyp diameter (Fig. 1B). I have observed these isolated polyps within a few centimeters of the colony edge but not within the older, central portion of *P. astreoides* colonies. This suggests that the coral eventually eliminates these polyps. The time required for this process to occur, however, must be quite long since linear (presumably uninhibited) growth rate estimates for *P. astreoides* are reported to be 3.0–3.5 mm/yr (Gladfelter et al., 1978).

DISCUSSION

Although *Zoanthus solanderi* is the most abundant, sessile, permanently attached epifaunal organism occurring on the east back reef (Table 1), it is clearly not a competitive dominant in terms of overgrowth ability (Table 2). Almost all contacts involving *Zoanthus* resulted in its being overgrown (e.g., by *Erythropodium*) or in no apparent growth changes (Table 2). This absence of growth and the skeletal evidence from corals such as *P. astreoides* (Fig. 1) indicate that growth inhibition is a common feature of encounters involving these encrusting organisms. Such growth inhibition can result in "stand-off" interactions or in greatly reduced rates of overgrowth.

Overgrowth is the usual means by which encrusting colonial organisms compete for substratum space (Jackson, 1977). Growth inhibition, on the other hand, is

less commonly encountered, but it does appear to represent a viable competitive strategy in at least some habitats. Connell (1976) noted several "stand-off" interactions (45.1% of 82 encounters) between corals in a shallow reef habitat at Heron Island. This habitat is subjected to physical disruption during storms; hurricanes, of course, represent the most severe disturbance (Connell, 1976; 1978). This is also true of the *Zoanthus* zone where 35.6% of 87 encounters resulted in "stand-offs" (Table 2). Buss and Jackson (1979), however, reported that encounters resulting in the apparent cessation of growth were quite rare in the Jamaican cryptic reef community where predation and disturbance rates are very low (Jackson and Buss, 1975; Buss and Jackson, 1979). The availability of little "free" space in this latter situation should greatly favor organisms with superior overgrowth capabilities.

The occurrence of growth inhibition among interacting corals and zoanthids living in disturbed reef habitats may be a general phenomenon. Similar inhibitive abilities have been reported for some temperate situations involving: the subtidal success of *Hydractinia echinata* in the presence of disturbance created by the predaceous echinoid *Arbacia punctulata* (Karlson, 1978), the dominance of broomsedge *Andropogon virginicus* as a persistent intermediate successional stage in old-fields (Rice, 1972), and the association of perennials such as *Solidago rigida* with badger mound disturbances (Platt, 1975; Platt and Weis, 1977). Furthermore, the recolonization of disturbed habitats in all of these examples involves vegetative growth as well as that by sexually produced propagules. Newell and Tramer (1978) point out the immediate reproductive strategy of *Solidago* spp. involving both sexual and asexual reproduction and the dominance of these perennials in 10-year old-fields, an intermediate successional stage.

The prevalence of *Zoanthus* at the seaward edge of the rear zone (Goreau, 1959; Kinzie, 1970) also represents an intermediate successional stage. In the absence of physical disturbance or predation, corals, gorgonians and other zoanthids will eventually displace *Zoanthus*. The *Zoanthus* zone is susceptible to severe storm damage, but it is also partially protected by the reef crest from wave activity and water turbulence. This zone "abruptly gives way to a narrow zone which is populated almost exclusively by huge tree-like colonies of *Acropora palmata* that take the full force of the surf" (Goreau, 1959). The bottom in this seaward zone "is in many places littered with broken, dead, and overturned colonies of *A. palmata*" (Goreau, 1959) and it is this dead coral which is transported leeward during storms and provides the bulk of the unconsolidated substratum in the *Zoanthus* zone.

An interesting result of the predominance of *Zoanthus, Hydractinia* (Karlson, 1978), *Andropogon,* and *Solidago* at intermediate levels of disturbance involves their effect on local species diversity patterns. Recently Connell (1978) has proposed that the high species diversity characteristic of coral reefs and tropical rainforests is due to intermediate levels of a variety of disturbance phenomena. The above examples indicate that there are both temperate and tropical situations in which intermediate levels of disturbance result in the opposite pattern, a depression at least in local species diversity [e.g., *Andropogon* (Bazzaz, 1975), *Solidago* (Tramer, 1975)]. These examples suggest that intermediate levels of disturbance tend to favor adaptations resulting in growth inhibition and vegetative capabilities for recolonization of periodically disturbed habitats.

ACKNOWLEDGMENTS

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