# COMPETITIVE STRATEGIES BETWEEN *PALYTHOA CARIBAEORUM* AND *ZOANTHUS SOCIATUS* (CNIDARIA: ANTHOZOA) AT A REEF FLAT ENVIRONMENT IN VENEZUELA

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## ABSTRACT

The competitive interactions and recolonization processes of two Caribbean zoanthids, *Palythoa caribaeorum* and *Zoanthus sociatus*, were studied in the field. Their competitive abilities (i.e., overgrowth capacity or growth inhibition) were evaluated by means of periodical observations of naturally occurring contact margins in 64-cm² non-disturbed areas. Recolonization and growth rates were assessed through experimental removal (64-cm² clearings) of different proportions of the zoanthid's initial cover of both species. Interactions were observed during 8 months, whereas a 10-month period was allowed for recolonization. Results showed that contact margins between both species remained unchanged along time, suggesting that stand-off or growth inhibition was the main strategy used. For the removal experiments, the initial proportion cleared for each species within the experimental patches was important for the final cover achieved. For *P. caribaeorum*, the greater the initial cover removed, the greater the final cover achieved. This tendency was not as evident for *Z. sociatus*. Growth rates were highly variable, ranging from $0.08 \pm 0.20$ to $0.12 \pm 0.06$ cm²·cm border⁻¹·month⁻¹ for *P. caribaeorum*, and from $0.05 \pm 0.15$ to $0.14 \pm 0.51$ cm²·cm border⁻¹·month⁻¹ for *Z. sociatus*. In general, we found a reduction of the growth rates through time, and *P. caribaeorum* exhibits a faster initial growth rate. Because the kind of disturbance applied in this study (cover removal) did not favor *Z. sociatus*, considered as a weaker competitor compared to *P. caribaeorum*, another compensatory mechanism that allows the coexistence of these species in this reef platform must exist. Several alternatives are proposed. The importance attributed to disturbances as a mechanism that explains the coexistence of species was not evident in our study, providing the disturbance intensity (patch size and proportion of initial cover removed) did not exceed that tested.

Researchers have been studying the effects of disturbances in marine ecosystems over the last 2 decades. Species diversity maintenance has been the main role attributed to disturbance processes. It is assumed that in hierarchical competitive interactions (Lang and Chornesky, 1990), as in those where different species show different longevity, the disturbances maintain patch diversity through two possible mechanisms: compensatory mortality and the presence of intermediate disturbances (reviewed by Sousa, 1984).

The disturbance mediated hypothesis of species coexistence assumes a hierarchical transitive pattern in the competitive abilities of the species, where results are consistent and symmetrical: one species always gains the encounter (Connell, 1978; Sousa, 1984; Connell and Keough, 1985). However, sessile subtidal assemblages are rarely completely hierarchical (Buss and Jackson, 1979; Kay and Keough, 1981; Bak et al., 1982; Dai, 1990), because the competitive abilities between species are similar, and the result is rather stochastic (Sousa, 1984; Connell and Keough, 1985). Furthermore, there are profound doubts about the strictly symmetrical competition in nature (Lang and Chornesky, 1990).

Karlson (1980) speculates that the local dominance of some colonial invertebrates and perennial plants can be achieved at intermediate levels of disturbance through vegetative colonization (growth) over disturbed areas and the subsequent defense of them. The competitively dominant species may delay the substratum monopolization as a result of this "preemptive" competitive strategy (Karlson, 1980), decreasing the rate of community succession (Connell and Slatyer, 1977).

An alternative explanation (Karlson, 1983) is that intermediate level of distur-
bances create bare substratum and significantly reduce the abundance (through
compensatory mortality) of competitive superior species [e.g., the encrusting oc-
tocoral *Erythropodium* (Karlson, 1980) or the zoanthid *Palythoa caribaeorum* in
the present study], allowing species, as the cnidarian *Zoanthus sociatus,* to persist
as a quantitatively dominant (i.e., abundant) species in the same reef environ-
ments.

It has been postulated that competitive networks strongly influence marine hard
bottom community structure and diversity (Jackson and Buss, 1975; Buss and
Jackson, 1979; Jackson, 1979; Karlson and Jackson, 1981). Species in these en-
vironments may gain substratum through at least three known mechanisms (re-
viewed by Connell and Keough, 1985): a) the invasion of newly open patches
(primary space); b) overgrowth of neighbors; and c) invasion of dead surfaces of
organisms (secondary space).

Overgrowth is not the unique result of interactions, but also "stand-off" or
growth inhibition between species may occur, as has been observed in bryozoans,
corals (Lang, 1973), encrusting hydrozoans (Karlson, 1978); zoanthids (Karlson,
1980) and epifaunal communities (Kay and Keough, 1981; Russ, 1982). Such
interactions may indicate defensive strategies, through which a colonial species
protects its boundaries (Karlson, 1980).

In this study, these competitive abilities (overgrowth capacity or growth inhi-
bition) and reinvasion, of two Caribbean zoanthids (*Palythoa caribaeorum* and
*Zoanthus sociatus*), were assessed in two ways: a) in unmanipulative observation
of natural interactions and, b) through clearing of the substratum between the two
species. The study was designed to test the following hypotheses: 1) If the growth
inhibition is an "advantageous" strategy as has been postulated for organisms in
periodically disturbed areas, it is expected to be a common outcome in natural
encounters between both species; 2) If *Z. sociatus* is not a superior competitor
compared to *P. caribaeorum* in terms of overgrowth, but exhibits equal abundance
in the study area, it would be expected to gain substratum by faster invasion of
newly open space, at least in small disturbed patches.

## METHODS

*Study Site.*—This study was done on a reef platform located in Isla Raton (10°29'15"N, 68°58'5"W),
a coralline key at Quizandal (Puerto Cabello, Venezuela), near the "Centro de Estudios Oceanológi-
cos" of the Universidad Simón Bolívar (Fig. 1).

This platform has a maximum depth of 1 m and extends about 20 m from the key shore to the
fore-reef zone. The mean surface temperature of the water, measured at noon, was 29.08 ± 2.01 and
ranged between 32°C (August 1990) and 26.9°C (February 1991).

The platform is covered by a patchy distribution of zoanthid species (*Palythoa caribaeorum, P.
mammillosa, P. grandis, Zoanthus sociatus* and *Z. solanderi*), macroalgae (mostly *Caulerpa racemosa,
Laurencia* spp., *Halimeda opuntia, Dictyota* sp.) and hexacorals (*Montastrea annularis, Porites as-
treoides, Diploria strigosa*). The more abundant organisms are *P. caribaeorum* (mean cover 36.33 ±
3.93%), *Z. sociatus* (19.81 ± 2.22%) and the macroalgae (33.91 ± 4.94%) that altogether cover
between 83% and 95% of the platform. The species cover varies significantly along the platform: from
the littoral to the fore-reef, *Z. sociatus* and the macroalgae decrease in cover as *P. caribaeorum*
increases. The covers for the main species remained unchanged during the study period (January 1990
to January 1991).

The platform is exposed to natural disturbances which create patches within the community, caused
by fragments of corals, woods, debris (physical impact), predation, or air exposure.

In Venezuela, *P. caribaeorum* and *Z. sociatus* have been reported at the "Parque Nacional Mor-
rocoy," where Weil (1980) defines a *P. caribaeorum* (reported as *P. mammillosa*) zone between 0.20
and 1.80 m depth at three reef sites. *Z. sociatus* and other isolated cnidarian colonies were also present.
*Palythoa* and *Zoanthus* are widely distributed along reef areas and rocky shores in Venezuelan coasts
(C. Bastidas and D. Bone, pers. obs.).

*Species Description.*—It has been suggested that *P. mammillosa* and *P. caribaeorum* are synonymous
(Sebens, 1982). As zoanthid taxonomy is so scarce, we included a brief description of the *Palythoa*
species we used in these experiments. In the study site two different forms of growth of the encrusting
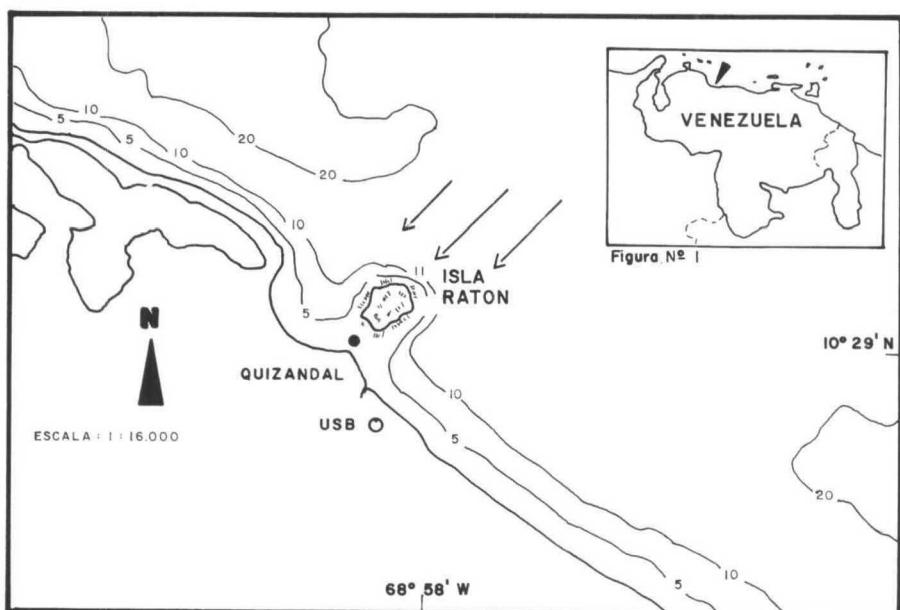
Figure 1.  Map showing the general and detailed location of study site at Isla Ratón (Carabobo State, Venezuela). The platform of study is at the northeastern part of the island. The arrows indicate prevailing wind direction.

*Palythoa* were observed: one which exhibits small clumps, larger polyps that do not touch each other when extended, and the other that forms extensive mats, but had smaller polyps. We chose the second species (or morphotype), because it was more abundant in the platform and its contact margins were clearly distinguishable.

*Methodology.*—The competitive interactions between *Palythoa caribaeorum* (from here on *Palythoa*) and *Zoanthus sociatus* (from here on *Zoanthus*) and their ability to gain space were studied under two conditions: an unmanipulative follow-up of contact margins and a manipulative experiment.

The platform was arbitrarily divided in two sections, east and west, to observe if interaction processes were the same throughout the platform. This subdivision was considered as a factor in the analysis due to previous observations that suggested possible current baffling effects on the west side of the platform. Experimental patches were randomly selected along the platform, inside an area of about 1,200 m². The patch size chosen for sampling was a square of 64 cm², based on short assays of the reinvasion rates of the species and on the growth rates reported. In the same platform, Bastidas (1991) found that naturally formed patches of 63 cm² account for 7.7% of the patches of this size or greater present in the platform. This indicates that the clearing done in this study was within the range of naturally occurring patches due to disturbances. A patch was defined as a denuded space where the substratum was exposed and/or covered by minute algae filaments or encrusting algae, which indicate the patch was recently formed.

The patch (which includes the contact margin) was marked with two diagonal nails, which were used as references for measuring the coverage of each colony monthly by planimetry. The coverage was quantified using color slides, taken with a Nikonos III (35 mm) and a close-up lens (fixed distance at 25 cm) in disturbance experiments. For the non-disturbance experiments, black and white photographs printed on paper were used.

*Experimental Design.*—Two types of experiments were established: 1) Non-disturbance experiment, where contact margins between *Palythoa* and *Zoanthus* remained unmanipulated and were followed through time.

The objective was to observe the progress and variation of the margin between both species to determine if overgrowth or stand-off occured, as alternative competitive strategies for space. Colonies were observed at permanent plots (N = 28). The total area covered by *Palythoa* was quantified monthly for 8 months (from July 1990 to February 1991). This information was sufficient to know how the contact margins changed between both species (*Palythoa* was easier to quantify in the photographs than *Zoanthus*).

Table 1.  ANOVA results (with repeated measures) for the *Palythoa caribaeorum* cover in unmanipulated experiments. The factors are: A) Side of platform (two levels: E and W); B) Orientation (two levels: N–S and E–W), and the Time of the observations (8 months). N = 11, n.s. = not significant.

| Source of variation | Degrees of freedom | Mean square values | F-value | p-value |
|---|---|---|---|---|
| A) Between replicates | | | | |
| Side of platform | 1 | 866.54 | 3.17 | n.s. |
| Replicates within groups | 9 | 272.99 | | |
| Within replicates | | | | |
| Time | 7 | 36.74 | 1.70 | n.s. |
| Side × Time | 7 | 34.59 | 1.60 | n.s. |
| Time × Replicates within groups | 56 | 21.61 | | |
| B) Between replicates | | | | |
| Orientation | 1 | 236.52 | 0.69 | n.s. |
| Replicates within groups | 9 | 343.00 | | |
| Within replicates | | | | |
| Time | 7 | 36.74 | 1.52 | n.s. |
| Orientation × Time | 7 | 11.02 | 0.46 | n.s. |
| Time × Replicates within groups | 42 | 24.17 | | |

Initially the contact margins were chosen so that each colony covered approximately 50% of the experimental patch. Two different orientations of the contact margin were considered: E-W and N-S. The orientation was included to determine the effect (if any) of current direction and the growth by either of the two species. The current was normal to the interaction margins oriented N-S, but it was parallel to the ones oriented E-W.

2) Disturbance experiments, where clearings were made in adjacent areas and including the contact margins between *Palythoa* and *Zoanthus* colonies.

The objectives were to measure the reinvasion abilities of both species, and to determine their growth rates in denuded patches. It must be noted that we did not differentiate between reinvasion and recolonization. We assumed that the reoccupation of cleared patches was mainly through reinvasion due to growth of adjacent colony borders, however, recolonization could have occurred, either by larvae or by small fragments. After the initial parameters were recorded (cover of each species and mapping of the original contact margin), an area of 64 cm² was removed, using pincers and spatula, following three treatments: 2.a) Clearing of equal proportions of each species around the contact margin (50% *Palythoa* and 50% *Zoanthus*), which will be denoted as P2 (N = 10). 2.b) Clearing of unequal proportions for only one of the species along the contact margin: 2.b.1) Clearing of 100% *Palythoa,* denoted as P1 (N = 10), 2.b.2) Clearing of 100% *Zoanthus,* denoted as P3 (N = 10).

It must be noted that cleared areas were approximate, since it is very difficult to obtain a straight line between the colonies and some of the polyps of the other species were damaged. This part lasted 10 months, between April 1990 and January 1991.

*Effects of the Distance to the ShoreLine on the Interactions between* P. caribaeorum *and* Z. sociatus.— Due to the existence of a clear zonation of both species on the platform (Bastidas, 1991), we wanted to determine a posteriori whether or not there was an effect of this differential abundance on the space reinvasion results (disturbance experiment). *Zoanthus* is more abundant in the shallow back-reef zone (nearest to the shore), whereas *Palythoa* dominates (in terms of abundance) the shallow zone near to the fore-reef. Although the ultimate factor that causes such zonation remains unknown, different tolerance to desiccation between both species has been observed (Karlson, 1983; Sebens, 1985). This zonation pattern found on the study site is consistent with that reported by Sebens (1982) in Panama.

It was expected that the most abundant species of each zone "wins" in the reinvasion of the cleared patch. Thus, Zonation (*Zoanthus*-abundant and *Palythoa*-abundant Zone) was added to the analysis as a factor. This would indicate an effect (if any) of the spatial location of the patch within the platform.

From the total available replicates we chose those located at the end limits of their spatial distribution (N = 20). Thus, we used a repeated measures ANOVA that had two crossed factors—Zonation and Initial Proportion—and Time as the repeated measure.

The results indicated no significant effect of the distance to the shore (zonation) on the final cover achieved for each species within the patch, neither for *Palythoa* (F = 1.25, P = 0.27, d.f. = 17) nor for *Zoanthus* (F = 0.31, P = 0.59, d.f. = 17). The effects of other factors on reinvasion of cleared patches remained the same as in the other analyses.

Table 2. ANOVA results (repeated measures) for the cover (cm²) of *Palythoa caribaeorum* (P) and *Zoanthus sociatus* (Z) in disturbance experiments (n.s. = not significant; * = P < 0.05; ** = P < 0.01; *** = P < 0.001)

| Source of variation | Degrees of freedom P and Z | Mean square values | | F-value | |
|---|---|---|---|---|---|
| | | P | Z | P | Z |
| Between replicates | | | | | |
| Side of platform | 1 | 175.23 | 822.55 | 2.59 n.s. | 14.98*** |
| Initial proportion | 2 | 4732.81 | 792.93 | 69.99*** | 14.44*** |
| Side × Initial proportion | 2 | 56.38 | 139.85 | 0.83 n.s. | 2.55 n.s. |
| Within replicates | | | | | |
| Time | 7 | 408.27 | 551.43 | 6.04*** | 10.04*** |
| Side × Time | 7 | 3.94 | 76.15 | 0.06 n.s. | 1.39 n.s. |
| Initial proportion × Time | 14 | 88.08 | 93.23 | 1.30 n.s. | 1.70 ns. |
| Side × Proportion × Time | 14 | 11.23 | 73.50 | 0.17 n.s. | 1.34 n.s. |
| Time × Replicates within groups | 128 | 67.62 | 54.92 | | |

*Data Analysis.*—Both experiments had two crossed factors: Side of the Platform and Orientation of the contact margin, for the non-disturbance experiments; and Side of the Platform and Initial Proportion of each species, for the disturbance experiments. A third factor, Time, was considered as a repeated measure for both experiments.

An ANOVA with repeated measures was used for these analyses following the procedure described by Winner (1962). Residual analyses were performed to verify the ANOVA assumptions, and when departure from these was observed, the necessary transformation was made. Only the growth rates required a square root transformation.

## RESULTS

*Non-disturbance Experiments.*—The overall live cover of *Palythoa* remained unchanged on both sides of the platform (E and W) for the 8-month period, as well as for both orientations of the contact margin, (E-W, N-S) (F = 3.17 and 0.69 respectively, *P* > 0.05, Table 1). However, *Palythoa* partial cover changed during this time, gaining or losing substrate. The decrease in cover of *Palythoa* was mainly due to mortality caused by invasion of macroalgae (*Caulerpa racemosa* and *Halimeda opuntia*), which occurred in 12 of the 28 replicates. From these 12 replicates affected by algae, 7 showed an important decrease (between 100 and 73%) of the initial cover of *Palythoa.*

Thus it may be considered that the contact margin between both species remained unchanged along time, suggesting that stand-off or inhibition of growth was the main strategy for both species.

*Disturbance Experiments.*—COVER OF SPECIES. Cover for both species changed significantly through time for all three proportions (Table 2). It can be considered that both species showed an effective recolonization or reinvasion capability to grow over the cleared areas.

The initial proportion cleared for each colony within the experimental patch was important for the final cover achieved for both species (Table 2: F = 69.9 for *Palythoa* and F = 14.4 for *Zoanthus, P* < 0.001). A posterior SNK test performed to check all pairwise comparison of means for *Palythoa*'s final cover at each proportion showed that its final cover under P1 treatment was higher (in average) than in P2, and those in turn were higher than the one under P3 (Table 3, *P* < 0.05). This means that the greater the initial cover cleared, the greater the final cover achieved for *Palythoa.*

This tendency was not as evident for *Zoanthus.* The final cover under P1 was

Table 3. Average cover (cm²) for both species within each initial proportion and platform side in disturbance experiments: P1 = 100%P – 0%Z, P2 = 50%P – 50%Z, P3 = 0%P – 100%Z. Test SNK for mean comparisons (n.s. = not significant, * = P < 0.05)

|  | Palythoa caribaeorum | | | Zoanthus sociatus | | |
|---|---|---|---|---|---|---|
|  | P1 | P2 | P3 | P1 | P2 | P3 |
| **East** | | | | | | |
| N | 40 | 16 | 32 | 40 | 16 | 32 |
| X ± SD | 23.66 ± 12.77 | 11.71 ± 6.0 | 7.18 ± 5.62 | 10.26 ± 6.59 | 18.28 ± 10.37 | 19.84 ± 13.01 |
| **West** | | | | | | |
| N | 40 | 32 | 32 | 32 | 24 | 32 |
| X ± SD | 25.56 ± 9.08 | 15.98 ± 9.37 | 7.26 ± 4.48 | 11.74 ± 7.72 | 9.37 ± 5.43 | 13.73 ± 9.40 |

Palythoa caribaeorum:

|  | P3 | P2 | P1 |
|---|---|---|---|
| P3 |  | — | * |
| P2 |  | — | * |

Zoanthus sociatus:

|  | P1 | P2 | P3 |
|---|---|---|---|
| P1 |  | — | * | * |
| P2 |  | — | — | n.s. |

Table 4. Species recover ratio (Final Area/Initial Area) in disturbance experiments, for each initial cover of the species within the experimental patch. Mann-Whitney's Test for the recovery differences between species (n.s. = not significant; *** = $p < 0.001$).

| Species | | Initial cover of each species within the patch | | |
| --- | --- | --- | --- | --- |
| | | 0% | 50% | 100% |
| *Palythoa* | N | 8 | 6 | 8 |
| | X ± SD | 3.84 ± 2.27 | 0.67 ± 0.47 | 0.63 ± 0.02 |
| | Range | 0.4–7.2 | 0–1.29 | 0.37–0.9 |
| *Zoanthus* | X ± SD | 4.31 ± 2.78 | 0.68 ± 0.46 | 0.20 ± 0.12 |
| | Range | 1.78–9.0 | 0.05–1.42 | 0.05–0.37 |
| Mann-Whitney | | n.s. | n.s. | *** |

significantly less than under P2 and P3 (Table 3, $P < 0.05$), with no differences between these two.

These results suggest that the initial proportions affected by the clearings are important for the gaining of space (substrate), as expected. In other words, the gaining of space is in direct relation to the length of the border available for growth, at least for *Palythoa*.

The side of the platform (E vs. W) did not have a significant influence on *Palythoa*'s final cover whereas it was important for *Zoanthus* (Table 2). A review of the sums of squares' homogeneity of the replicates within the groups (for repeated measures, following Winner 1962), revealed that variation was rather high on the West side. Therefore only the data collected on the East side were used for the subsequent pairwise comparisons of cover.

REINVASION OF SPACE. Table 4 shows the Final/Initial Area ratios for each species under each treatment, that represent the proportion of the initial area removed that each species recovered during the experiment. When the initial area was equal for each species (50% or P2), both species recovered an average area of 68% (the ratio is 0.68 ± 0.46 for *Zoanthus* and 0.67 ± 0.47 for *Palythoa*). When the initial area was unequal, the ratio of both species behaved similarly: a) when the initial cover cleared was high (near 100% for each species within the patch), neither of the species recovered it completely. Under this condition *Palythoa* recovered an average of 63% (corresponding ratio of 0.63 ± 0.02) of its initial cover, whereas *Zoanthus* recovered only 20% (corresponding ratio of 0.20 ± 0.12) of it. This difference between the species was significant (Table 4, Mann-Whitney test, $P < 0.001$). b) when the initial cover cleared was very low (a mean cover of 4.0% for *Palythoa* under P3, and 5.3% for *Zoanthus* under P1), both species recovered, in average, more space than they originally had. *Palythoa* recovered, in average, 431%, while *Zoanthus* recovered 384%. In this case the species recovered their space and gained some additional substrate, and the difference between species was not significant.

GROWTH RATES. Absolute growth rates for both species were highly variable, ranging from 0.08 ± 0.20 to 0.12 ± 0.06 $cm^2 \cdot cm$ $border^{-1} \cdot month^{-1}$ for *Palythoa* and from 0.05 ± 0.15 to 0.14 ± 0.51 $cm^2 \cdot cm$ $border^{-1} \cdot month^{-1}$ for *Zoanthus* (Table 5).

We obtained negative growth rates or decrease in cover that indicated losses, due to algae invasion, or detachment of fragments. Fission has been reported for other colonial cnidarians including zoanthids (Karlson, 1991). Excluding negative growth rates and replacing them by zero we obtained the colony growth potential

Table 5. Species growth rate (cm²·cm margin⁻¹·month⁻¹) for each initial proportion of species. The growth rates (X ± SD) for the seven periods of time and for both sides assessed were pooled. The absolute growth rates include the negative partial growths and the potential growth excludes them. N = number of observations.

| N | P1 (100%P—0%Z) 56 (=8 × 7) | | P2 (50%P—50%Z) 42 (=6 × 7) | | P3 (0%P—100%Z) 56 (=8 × 7) | |
|---|---|---|---|---|---|---|
| | *Palythoa* | *Zoanthus* | *Palythoa* | *Zoanthus* | *Palythoa* | *Zoanthus* |
| Absolute growth | 0.12 ± 0.06 | 0.14 ± 0.51 | 0.10 ± 0.13 | 0.13 ± 0.11 | 0.08 ± 0.20 | 0.05 ± 0.15 |
| Potential growth | 0.12 ± 0.17 | 0.37 ± 0.49 | 0.26 ± 0.28 | 0.16 ± 0.20 | 0.19 ± 0.28 | 0.15 ± 0.20 |

(sensu Brazeau and Lasker, 1992), that is higher than absolute growth rates, as expected (Table 5). Using the potential growth rates, the ANOVA results (not shown in table) indicate that Time had a significant influence on both species (*Palythoa*: F = 5.03, d.f. = 7, $P < 0.001$; *Zoanthus*: F = 2.81, d.f. = 7, $P < 0.05$). Thus, the growth was not constant throughout the experiment (Fig. 2).

The growth rates grouped for other factors and expressed by time periods (Fig. 2) are slightly higher than those expressed by proportions (and grouped by time, Table 5).

*Palythoa* showed high growth rates in two periods: at 69 days (June), and at 234 days of the experiment (November). There were fewer differences between *Zoanthus* growth rates through time: only at the latest period the growth rate was the lowest. *Palythoa* and *Zoanthus* differ in their growth rates specially at 234 days of experiment (November) probably due to macroalgae invasion, which seems to affect more the *Zoanthus* cover. Both species showed a minimum growth rate in the latest sampling period that corresponded to January and indeed with the temperature drop at the end of the year (Fig. 2). In general, there is a reduction in the growth rates through time, and an increasing variability in the replicates, probably due to stochastic processes between the patches.

## DISCUSSION

Growth inhibition as well as stand-off interactions have been postulated by Karlson (1978), as usual defensive strategies in competition for space. They have
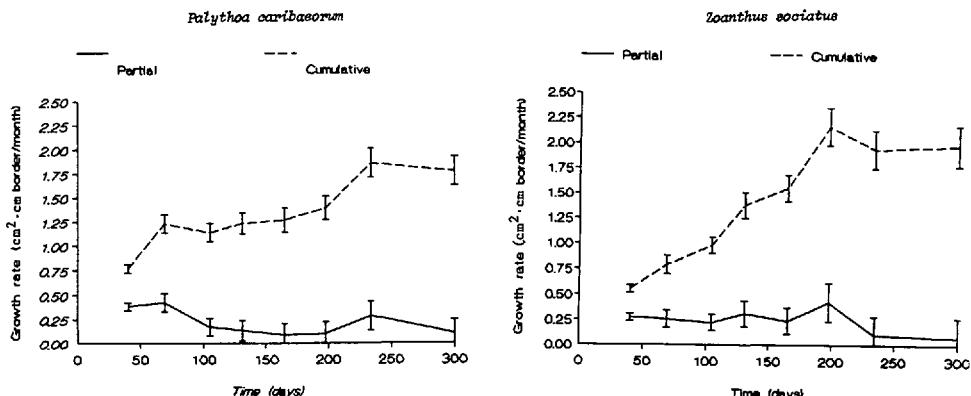


Figure 2. Cumulative (dashed line) and partial (solid line) growth rates for *Palythoa caribaeorum* and for *Zoanthus sociatus* in disturbance experiments. Error bars represent standard error of the mean for each time period. The growth rate data for each side of the platform, as well as for each initial proportion treatment, were combined at each time period. The negative growth rates were excluded.

also been reported as important strategies in hard bottom marine communities, for example: for corals of the same species placed experimentally in contact (Lang, 1973); for the colonial hydrozoan *Hydractinia* from sessile epifaunal communities (Karlson, 1978); for the 54.8% of the total interactions observed between *Zoanthus solanderi* and other organisms (Karlson, 1980); for 41% of the interactions observed between pairs of species of a temperate fouling community (Sebens, 1985); for the aggregation of clonal fragments of *Z. solanderi* (Karlson, 1988b); and for the algae *Laurencia* in Panama (Kilar and McLachlan, 1989).

In our study, growth inhibition or stand-off predominated in the natural interactions (undisturbed contact margin) between *Palythoa* and *Zoanthus,* at least for an 8-month period. The platform side and the orientation of the margin with respect to the current did not influence this result.

From personal observations in the study site and from the literature (Karlson, 1980; Suchanek and Green, 1981) it has been suspected that *Palythoa* can overgrow *Zoanthus.* Before drawing conclusions regarding overgrowth, we must consider the scale of time of this study. It may be necessary to extend observations over a longer period of time than the one used here (10 months) to clearly detect if overgrowth between these species occurs. In this study, some minor changes may have occurred due to overgrowth, with no net significant effect on the overall cover of each species within the patch. The process of alternative gaining and losing substratum (repeated reversals) was reported by Chornesky (1989), who followed the results of interspecific competition for space in corals at small scales (mm). Similar observations were reported by Ayling (1983) for temperate sponges, and by Wethey and Walters (1986) for the colonial ascidian *Botryllus* during a 40-day period of observation. These studies highlight the importance of the duration of the observations, because short experiments could lead to erroneous conclusions on which species gained or lost space (Chornesky, 1989). Moreover, short field experiments that address interactions between species that began at unknown time in the past for each patch could lead to final winners or losers, when we are really witnessing a snap-shot of the processes.

We believe it is possible that repeated reversals also occur between zoanthid species competing for space, but this needs further research. Such repeated reversals could lead to a type of stand-off interaction but through an active mechanism of aggression (Chornesky, 1989). Again the type of mechanism involved could correspond to one or another depending on the scale of observation.

Macroalgae represent an important group of organisms to be considered within the frame of competitive interactions at our study site. Algae distribution along the platform was similar to the *Zoanthus* distribution. Also we observed a higher proportion of *Zoanthus*-macroalgae interactions (specially with *Caulerpa* sp., *Halimeda* sp. and *Laurencia* sp.) (Bastidas, 1991). Nevertheless, macroalgae seem to adversely affect the polyps of *Palythoa* more severely than *Zoanthus* due to shading effects. *Palythoa* polyps bleach within less than 2 months and the shaded portion of the colony could die (C. Bastidas, pers. obs.). In shaded portions, the polyps of *Zoanthus* are elongated, but neither the colony seemed dead nor the polyps bleached, after 10 months. The shading effect on *Zoanthus* was studied by Karlson (1983), who reported that initially, the polyps increased in height and oral diameter, but decreased in density.

The algae invasion over the experimental patch prevented us from using the full-strength of our treatment replicates (they were excluded), because it could interfere with the competitive processes between the zoanthids. However, it could be experimentally addressed as an important mechanism that could lead to tem-

poral variability in the environment and promote coexistence (Karlson and Hurd, 1994).

*Disturbance Experiments.*—This experiment allowed us to determine that both zoanthids species are able to recolonize an artificially cleared area (64 cm²) within a 10-month period.

The initial proportion removed from the colonies affected the reinvasion of each species. We found a direct relationship between this factor and the final cover of *Palythoa*'s colonies: the greater the initial proportion cleared (or the length of the border) of the colony, the greater its final cover (or recovery) of the space cleared, as expected. However, it is unknown if there is any other factor (rather than the perimeter length) affecting these results (e.g., chemical "track"). This tendency was not as clear for *Zoanthus,* i.e., the maximum recovery was not achieved in the 100% removal treatment (P3).

The capacity to recover the area initially occupied by the colony was the same for both species, except when initial areas removed were close to 100%. This is consistent with the results of growth rates, because when the colonies occupied almost all the area cleared, *Palythoa* (under P1) had its greatest growth rate, whereas *Zoanthus* (under P3) had its lowest.

The growth rates were highly variable among proportions, especially for *Zoanthus*. Thus, we could not find significant relationships between the growth rates and the main factors considered in the analyses. Other factors that could influence this parameter were not considered in this study, such as the whole size of the colony, the spatial heterogeneity and the macroalgae interactions. The great variability between patches at the end of the study may resemble that of the communities. Thus, the coexistence of the zoanthid species could be seen as a result of the high variable outcome in the interaction processes between them.

The growth rates exhibited opposite tendencies (not significant) within both species under the different initial proportions: *Palythoa* had the highest growth rate when it had the largest initial perimeter, whereas the opposite was true for *Zoanthus*. However, more information about the biology of both species is needed to adequately interpret these results, such as the size classes of each colony. The colony size is difficult to determine, as colonies of *Zoanthus* may be composed of fragments of 1.7 to 4.5 polyps·fragment⁻¹, which are formed by losses of the stoloniferous connections (Karlson, 1980). Considering this and the fact that many cnidarians show a growth rate inversely related to colony size (Hughes and Jackson, 1980), the tendencies for *Zoanthus* growth rates could be explained as follows: if the size dependent growth hypothesis is true for this species (Karlson, 1988a), we are witnessing an assemblage of small colonies that has a maximum growth potential.

From these results we conclude that small-scale (64 cm²) one-time disturbances that mainly affect *Palythoa* at the margin of contact with *Zoanthus* would confer reinvasion advantage to *Palythoa.* However, under the same treatment, there is no evidence to suggest that the kind of small-scale disturbances used in this study confer any advantage to *Zoanthus* for the reinvasion of cleared space. In other words, if Karlson's hypothesis is true [i.e., intermediate disturbance levels will favor the presence of *Zoanthus* (Karlson, 1983)], then the magnitude of our disturbance may not be regarded as intermediate. However, unless these interactions can be assessed under different degrees of disturbances, neither the Karlson hypothesis can be discarded, nor the kind of disturbance applied in this study may be considered as intermediate. Efforts have been made to review and unify the discussion about patch dynamics and the perturbation processes within marine
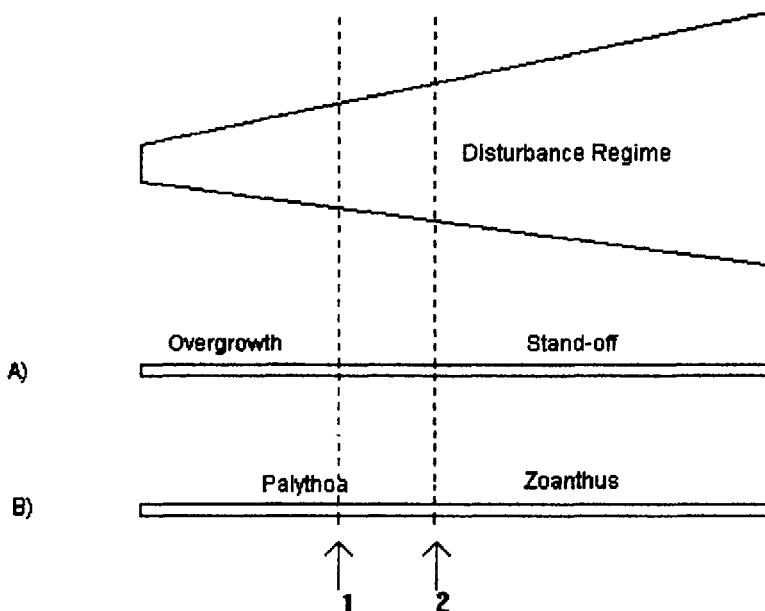
Figure 3. Hypothetical scheme of competitive interactions between *Palythoa caribaeorum* and *Zoanthus sociatus* in relation to general models for disturbances. The A) bar represents the strategies for non-disturbed margins of contact between species (hypothesis derived by multiple authors: Buss and Jackson, 1979; Karlson, 1978, 1980). The B) bar represents the dominance of the species of zoanthids in disturbed margins (derived from Karlson's hypothesis). If these hypotheses were true, we could speculate about the disturbance regime, as proposed by Menge and Sutherland (1987): (1) Should represent the "type" of experimental disturbance used in this study, and (2) the natural disturbance that occurs in the study platform, as results from the abundances of each species.

hard bottom communities, but it is yet very difficult to establish the intensity scale of disturbances to make the results comparable (Sousa, 1984; Pickett and White, 1985; Petraitis et al., 1989). That is the case for the present study and the "intermediate levels of disturbance" in the hypothesis postulated by Karlson (1983).

Only a small portion of the colony was monitored in the present study (64 cm$^2$), and the outcome of the competitive interactions of the colony as a whole is unknown. However cover of both species is constant in the platform, at least over 4 years (Bastidas, unpubl. data). Since *Palythoa* will gain space under certain encounter conditions, we must consider another "compensatory" mechanism (such as predation, desiccation resistance, macroalgae resistance or other disturbance intensities), which allows the coexistence of these species.

Our results, as well as those of previous studies, suggest that although *Zoanthus* is not a dominant species (in terms of overgrowth capabilities) it acquires space in shallow flat reefs platforms in the Caribbean, together with *Palythoa*. In this study, the clearing and subsequent reinvasion of a small space between both species are not the factors that confer advantage to *Zoanthus* over *Palythoa*. However, *Palythoa* is not as highly competitive as it seems from previous studies (Suchanek and Green, 1981), since in an 8-month period, this species did not significantly overgrow *Zoanthus* in the non-disturbed interactions' margins. It could be useful to study the effects of different degrees of disturbances (clearing areas) as well as the spatial pattern of the whole colony on the competitive interactions between both species, for further conclusions.

It is difficult to avoid thinking about the fitness of different strategies under

different disturbance scales for coral reef communities (Karlson, 1978; Buss and Jackson, 1979; Karlson, 1980). We can see overgrowth and stand-off as alternative competitive strategies for *undisturbed margins* under a general disturbance gradient from low to high respectively (Fig. 3). On the other hand, the outcome of reinvasion in *disturbed margins* between competitors could depend also on a disturbance gradient, where *Palythoa* gains more space in less disturbed areas (size of patch in this study), whereas *Zoanthus* could gain for an undetermined degree of disturbance. At the end of this gradient there is no advantage for any of the competitors. If the adequate group of hypotheses were formulated and disproved, the disturbance regime of our study site could be "evaluated" through the competitive status of these species.

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