

Morphological plasticity in the reef zoanthid *Palythoa caribaeorum* as an adaptive strategy

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We compared morphology of *Palythoa caribaeorum* (number of polyps, area, diameter and height) occupying three sites located at different distances from a harbor area and with different environmental conditions, such as sedimentation. Seasonality was also considered by comparing morphology during the wet and dry seasons. GLM analyses showed significant main and first-order interaction effects between sites and seasons for each of the four morphological variables measured. Only at the site directly in front of the harbor area there was no seasonal variation. At the other two sites, no significant differences were found when the average pairwise distance of each morphological character was compared between seasons for each site. This indicates that these characters vary in a similar way and suggests growth conditions intrinsic to the species. Environmental homogeneity at the harbor area seems to promote homogeneous morphometry, which indicates different biological strategies and suggests that this species adapts to distinct environments.

Introduction

The vastness of oceans, with their different currents, topography, environmental gradients, historical events and human activities, provides opportunities for biological divergence (Palumbi 1994). The sea is not a homogeneous habitat. This is especially true for benthic species whose dispersal abilities are often restricted to certain parts of their life cycle. Indeed, opportunities

for reproductive isolation may be higher than previously thought for these organisms (Soong *et al.* 1999). Morphological stasis within species complexes might reflect constraints from external morphology, recent common ancestry and/or the decoupling of physiological and ecological divergence from morphological change (Knowlton 1993).

Intraspecific morphological variation in corals is familiar to those who have attempted to

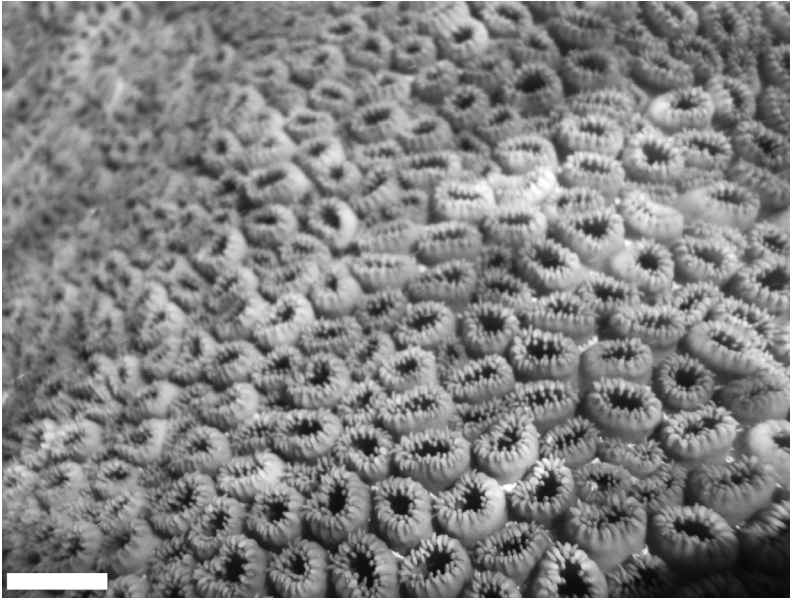


Fig. 1. Detail of a colony of *Palythoa caribaeorum*. Scale bar = 8 mm.

identify them (Amaral 1994, Todd *et al.* 2001). As with plants, such variety can be attributed to genetic differentiation, phenotypic plasticity, or a combination of both, and often appears to be environmentally correlated (Foster 1979). Researchers have identified distinct plastic responses in some corals, but due to the heterogeneous nature of the reef environment they have been unable to attribute their findings to any one physical variable (Miller 1994, Bruno & Edmunds 1997).

Zoanths have high morphological plasticity, which leads to taxonomic problems in this group (Reimer *et al.* 2006a). Molecular studies have confirmed the morphological plasticity of some species (e.g., intraspecific variation in oral disk color and diameter, number of tentacles and polyp length in *Zoanthus sansibaricus*) (Reimer *et al.* 2004), while allowing the refinement of previously described species and the identification of new ones (Reimer *et al.* 2006b).

Palythoa caribaeorum (Duchassaing and Michelotti 1860) is a colonial zoanthid that inhabits extensive areas of Brazilian intertidal beachrocks and is commonly known as *baba-de-boi* (ox spit) (Soares *et al.* 2006) (Fig. 1). Polyps are embedded in a thick, mat-like coenenchyme containing debris and parts of reef elements that offer support. Zooids have wide,

flattened oral disks and diversely-shaped tentacles that surround its outer margin (Pérez *et al.* 2005). Suchanek and Green (1981) reported high growth rates ($2.5\text{--}4.0\text{ mm day}^{-1}$) for *P. caribaeorum*, making it one of the fastest-growing anthozoans. Data also suggest that this zoanthid can overgrow nearly every other sessile reef invertebrate, which places it at the top of a competitive hierarchy in reef ecosystems (Suchanek & Green 1981, Pérez *et al.* 2005).

This study focuses on *P. caribaeorum* and analyzes the extent to which this species' morphology is sensitive to human activity and seasonal variation on two different beachrocks off the coast of the Brazilian state of Pernambuco. The study involved colonies occupying three sites at different distances from a harbor area and with distinct environmental conditions, such as sedimentation. Seasonality was also considered by comparing the wet season (70%–75% of the annual precipitation) with the dry season. We assumed that, if this species is indeed highly plastic as suggested by Reimer *et al.* (2004, 2006b), morphological variation should occur in response to different human impacts and environmental conditions found at the sites studied. Thus, the following hypotheses were tested: (1) there are differences in the average (a) number, (b) area, (c) diameter, and (d) height of *P. cari-*

baeorum polyps in the studied sites during the wet (rainy) and dry seasons; (2) polyp morphometry differs between the three sites studied, and (3) the population of *P. caribaeorum* in front of the harbor (which is under direct impact of port activity) has an annual morphometry pattern that is different from those of the populations of the two other sites.

Material and methods

Study site

The study area is located off the coast of the state of Pernambuco, Brazil (Fig. 2) and is characterized by extensive linear beachrock formations along the seaboard. The width, length and thickness of these formations vary and most of them become exposed during low tide. Climate is warm-humid, pseudo-tropical (Köppen As'), with a mean annual temperature of 24 °C and 1500–2000 mm yearly rainfall that is concentrated between March and August (Silva *et al.* 2004). There are two distinct seasons: wet (W) between April and June (autumn–winter rainfall constituting 70%–75% of the total annual precipitation), and dry (D) between January and March. Predominant winds come from the southeast (Medeiros *et al.* 1999).

The reefs of Suape Bay and Gamela Beach were compared because the former is a highly impacted site due to harbor activity. Landfilling, dredging and construction had the most obvious impacts on the area's geomorphology, hydrodynamics and plankton (Silva *et al.* 2004). In the Suape area, the original Atlantic rainforest has been largely replaced by sugarcane monoculture. Before the port was built, four rivers (the Massangana, Tatuoca, Ipojuca and Merepe) drained into Suape Bay — an estuary partly isolated from the ocean by an extensive sandstone reef line approximately 3500 m long and 80 m wide (Fig. 2b). Today only the Massangana and Tatuoca rivers continue to drain into the bay. The Ipojuca and Merepe rivers had their connection with Suape Bay interrupted by intensive embankment constructed for the Suape Industrial Port Complex (Neumann *et al.* 1998) (Fig. 2b). Overall, more than 600 ha of man-

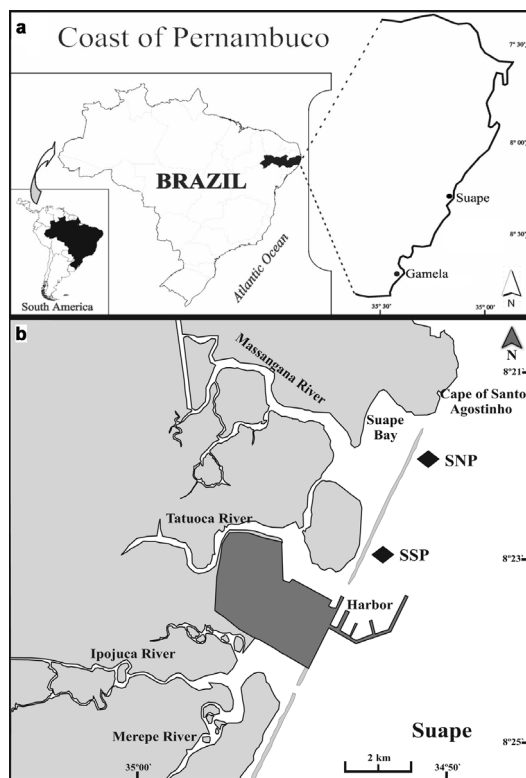


Fig. 2 (a) Suape and Gamela Beaches on the Pernambuco coast, Brazil; (b) Suape Bay sample sites. SNP = Suape North Point; SSP = Suape South Point.

grove forest have been destroyed to build port infrastructure (Silva *et al.* 2004).

We selected three sites located along the reef line of two beaches, Suape and Gamela. The southern reef limit (SSP = Suape South Point) is directly in front of the port complex and is influenced by the Tatuoca river estuary (Fig. 2b). This reef area has the highest heavy metal concentration (Mn, Pb, Zn, Cr, Ni) in the state of Pernambuco — a consequence of the harbor's high industrial activity, intensified by continuous dredging (Chagas *et al.* 2004). For this reason, SSP has deeper and more turbulent surrounding waters. The northern limit of the same reef (SNP = Suape North Point) is closer to Suape Bay and to the coastal town of Cabo de Santo Agostinho (Fig. 2b). The third site, Gamela Beach (GAM) (Fig. 2a), is a part of an Environmental Protected Area (Guadalupe) with little human presence. The beachrock is approximately 450 m long and 250 m wide.

Palythoa caribaeorum populations are distributed throughout reef tops in independent patches of different sizes, and are exposed during low tide, yet protected from wave action.

Sampling strategy

During low tide, five colonies (all larger than 2500 cm²) from each sampling site (SNP, SSP and GAM) were randomly chosen. Sampling areas were delimited using 10 × 10 cm PVC squares; samples were collected with the aid of a spatula and fixed *in situ* in 4% formalin. To ensure that different colonies were collected, chosen colonies had to be at least 2 m apart and have no contact around the edges. Samples were collected once per season (wet = May/June 2006 and dry = November/December 2006). To avoid any possible intracolony variation in polyp morphology confounding the results (Veron 1995), two 100 cm² samples were collected from each colony (one at the most central area and another at the seaward-facing area), which totaled 60 samples.

The number of polyps was estimated by counting them from 100 cm² (area of the sampling square). Individual *P. caribaeorum* polyps were measured to examine small-scale morphological variations. The diameter and height of 45 polyps were measured from each sample — approximately 2700 polyps were measured overall. The maximum and minimum diameters of each polyp were also measured, and their average and area (ellipse area) were estimated. Voucher specimens were deposited in the Anthozoan Research Group Collection at the Biodiversity Laboratory of the Federal University of Pernambuco (GPA 550, GPA 551, GPA 552).

Statistical analyses

In order to test our hypotheses that there are differences in the average (a) number, (b) area, (c) diameter, and (d) height of *P. caribaeorum* polyps in the study sites during the wet and dry seasons, we used a generalized linear model, GLM (3 × 2 two-way factorial ANOVA between groups, followed by Tukey's HSD post-hoc comparisons). This model was applied to evaluate the

extent to which the sites (GAM, SNP and SSP), periods (wet and dry) or higher-order interaction terms (sites × seasons) predict the mean of each of the four dependent factors (number of polyps, area, diameter and height). After running the models, we performed a residual analysis (raw residual normality and leverage). The assumption was that all models were consistent as in each of them the residuals showed approximately normal distributions; no outliers were found and there were no correlations between averages and variances (McCullagh & Nelder 1989).

Since seasonal differences were found for most of the response variables analyzed at sites GAM and SNP, we also performed parametric and non-parametric comparisons (one-way ANOVA for diameter and area and the Kruskal-Wallis test for number of polyps, respectively) for the pairwise average distance of each variable between the two periods (wet and dry) in each of the sites (GAM and SNP). This analysis aimed to verify if these two sites varied in a similar way and to reveal a possible seasonal growth pattern for *P. caribaeorum*.

After checking for normality and homogeneity of variance (Lilliefors test), the Kruskal-Wallis test was applied to analyze the effect of harbor proximity on the annual mean of each dependent factor (excluding number of polyps) by comparing the two sampling sites in Suape.

All analyses were carried out using Statistica software ver. 7.0 (StatSoft, Tulsa OK). The significance level used for all tests was set at $\alpha = 0.05$.

Results

In the wet and dry seasons, a total of 855 of 12 258 polyps from Gamela (GAM), 810 of 12 552 polyps from Suape North Point (SNP) and 855 of 10 746 polyps from Suape South Point (SSP) were measured.

The variables measured (number of polyps, area and diameter) followed different trends according to the area. The number of polyps showed important seasonal differences at SNP and GAM: there was a higher number of polyps during the wet season than in the dry season (39.54% and 28.4%, respectively); whereas at

SSP, the number of polyps did not show much seasonal difference (0.87% increase) (Table 1). Polyp size (area and diameter) followed the same pattern as that for polyp number, with higher values during the dry season and a greater increase in polyp area (20% at GAM and 20.15% at SNP) when compared with diameter (8.07% at GAM and 12% at SNP). Overall polyp size exhibited great homogeneity at SSP throughout the year, with minimal increase during the wet season (3.04% for polyp area and 0.24% for diameter) (Table 1).

During the wet season, polyp height was uniform at all three sites (Table 1) — variation was only 8.25% between the highest and lowest values. Conversely, polyp height increased considerably during the dry season at the three sites sampled (Table 1); however, this increase was greater at GAM and SSP (32% and 27%, respectively) than at SNP (12%).

According to the GLM analysis, there was a significant first-order interaction for each of the four dependent variables (number of polyps, area, diameter and height) among sites and seasons. We also found significant differences for each of the main effects (Table 2 and Fig 3). Tukey's HSD post-hoc test showed that SSP was the only site with no significant seasonal variation in number of polyps ($p = 0.999$), their area

($p = 0.827$) and diameter ($p = 0.999$) (Fig. 3). Polyp height presented the same overall pattern at the three sampling sites and was significantly higher during the dry season (Tukey's HSD post-hoc test: GAM $p < 0.001$, SSP $p < 0.001$, SNP $p < 0.001$) (Fig. 3). Average polyp size (area, diameter and height) was significantly greater at SSP than at SNP (Table 3).

Palythoa caribaeorum polyps were less numerous and had greater area, diameter and height at GAM and SNP during the dry season (Fig. 3). This difference between the dry and wet periods shows the same seasonal pattern within the two sites. Additionally, neither site showed statistically significant differences when the pairwise average distance of each morphological character was compared between the two seasons.

Discussion

Overall, the most disturbed site (SSP) lacked seasonal patterns regarding morphological parameters, while the other two sites displayed similar patterns. The morphometric analysis of *P. caribaeorum* populations from the two Suape sites and Gamela indicated a considerable overlap between the populations of Suape North

Table 1. *Palythoa caribaeorum* characters measured. Data are presented as means \pm SD.

Site and character	Wet	Dry
Gamela (GAM)		
Polyp		
number (per 100 cm ²)	756.66 \pm 124.79	541.8 \pm 93.31
area (mm ²)	12.70 \pm 4.74	15.11 \pm 5.30
diameter (mm)	3.99 \pm 0.74	4.34 \pm 0.76
height (mm)	12.72 \pm 4.00	16.18 \pm 3.50
Suape South Point (SSP)		
Polyp		
number (per 100 cm ²)	567.90 \pm 141.98	563.00 \pm 84.38
area (mm ²)	14.15 \pm 6.56	13.72 \pm 4.64
diameter (mm)	4.17 \pm 0.96	4.16 \pm 0.7
height (mm)	12.32 \pm 4.86	16.80 \pm 6.24
Suape North Point (SNP)		
Polyp		
number (per 100 cm ²)	893.625 \pm 194.14	540.30 \pm 119.64
area (mm ²)	10.23 \pm 4.96	12.81 \pm 3.60
diameter (mm)	3.54 \pm 0.85	4.02 \pm 0.57
height (mm)	11.67 \pm 3.27	13.30 \pm 4.24

Point and Gamela. Variables such as number of polyps, area, diameter and height showed the same seasonal pattern in both of these reefs, whereas Suape South Point's population did not follow such a pattern (Fig. 3). In Suape North Point and Gamela, *P. caribaeorum* had larger and fewer polyps in the dry season when compared with the wet season, which indicates strong seasonality at both sites. Moreover, when differences in the magnitude of each characteristic for each season were compared between the two sites, no significant differences were found. This indicates that — other than having a similar seasonal pattern (fewer and bigger polyps during the dry season) — variation in the characteristics studied were also similar; i.e., this species seems to follow an intrinsic biological growth pattern as seen at Gamela and SNP, yet not observed at SSP due to an unidentified factor extrinsic to the species' biology. Harbor activities (e.g., dredging

and industrial waste) seem to have an impact on Suape South Point and to modify the ecological parameters that affect its populations' biology (Silva et al. 2004).

According to Bohlen et al. (1979), dredging and canal construction are significant sources of suspended sediments and associated pollutants, and such physical modifications result in habitat destruction and hydrological disturbances. Continuous impact throughout the year may be the reason why most characters analyzed showed no seasonal variation at Suape South Point (Fig. 3 and Table 1). In fact, harbor areas around the world show great homogeneity throughout the year (Ruiz et al. 1997), which might be explained by the continuous and uniform impact suffered. Homogeneity involves great environmental stability in order to balance seasonal variations. This may justify the different morphological patterns observed for

Table 2. GLM model results of each of the four dependent variables (number of polyps, area, diameter and height) of *Palythoa caribaeorum*.

Models	SS	df	MS	F	p
Number of polyps					
Full model	936522.9	5	187304.6	11.23	< 0.001
Intercept	23060121	1	23060121	1382.517	< 0.001
Sites	211914	2	105957	6.352	0.003
Season	507452	1	507452	30.423	< 0.001
Sites × season	283700	2	141850	8.504	< 0.001
Error	833990	50	16680	—	—
Area					
Full model	5500.57	5	1879.98	94.08	< 0.001
Intercept	430895.0	1	430895.0	16809.89	< 0.001
Sites	3135.6	2	1567.8	61.16	< 0.001
Season	1450.6	1	1450.6	56.59	< 0.001
Sites × season	1199.2	2	599.6	23.39	< 0.001
Error	64442.4	2514	25.6	—	—
Diameter					
Full model	143.30	5	28.66	48.25	< 0.001
Intercept	40837.33	1	40837.33	68753.08	< 0.001
Sites	79.42	2	39.71	66.86	< 0.001
Season	45.8	1	45.8	77.1	< 0.001
Sites × season	27.69	2	13.84	23.31	< 0.001
Error	1493.24	2514	0.59	—	—
Height					
Full model	9399.90	5	1879.98	94.05	< 0.001
Intercept	479024.1	1	479024.1	23963.68	< 0.001
Sites	2234.3	2	1117.2	55.89	< 0.001
Season	6372.7	1	6372.7	318.8	< 0.001
Sites × season	859.3	2	429.7	21.49	< 0.001
Error	50253.8	2514	20.0	—	—

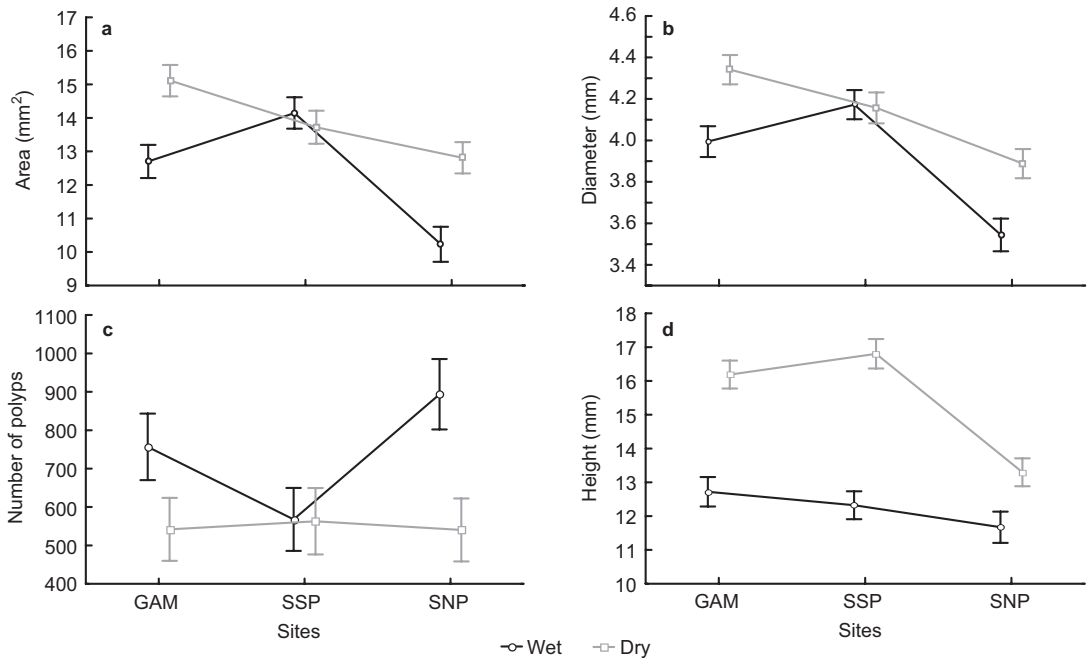


Fig. 3. Comparison of four morphological characters of *Palythoa caribaeorum* between sites and seasons. (a) Area of polyps, (b) diameter of polyps, (c) number of polyps (per 100 cm²), and (d) height. GAM = Gamela, SSP = Suape South Point and SNP = Suape North Point. Data are presented as means \pm SE.

P. caribaeorum at Suape South Point. As such, this may be the reason why the northern limit of the same reef (only 3.0 km apart) is ecologically more similar to Gamela Beach, 40 km away. The environmental homogeneity of the harbor is reflected by the homogeneous polyp morphometry found in Suape South Point, which perhaps indicates a different biological strategy (e.g., growth and reproduction). According to Devassy and Goes (1988), any environmental disturbance produces changes in an organism's growth variables, which frequently leads to community reorganization. Future experiments involving colony transplantation would be worth considering.

A possible explanation for the increased diameter and height of polyps found during the dry season might be related to the reproductive stage. Although *Palythoa caribaeorum*'s reproductive cycle has not yet been studied for the Pernambuco coast, Ryland (1997) showed that polyp size (diameter and height) can affect this species' fecundity. Boscolo and Silveira (2005) studied its reproductive biology in the São Sebastião Channel (state of São Paulo, Brazil) and recorded continuous egg release; sperm

release, however, was recorded only during half of the year studied. Karlson (1981) observed that differences in fecundity are inversely proportional to polyp size in *Zoanthus pulchellus*. Nevertheless, although Boscolo and Silveira (2005) recorded that the polyps of *Z. pulchellus* were only half the size of those of *Protospalythoa variabilis*, the percentage of fertile polyps was very similar for both species (81% and 83%, respectively). The variation in frequency of zoanthids' fertile polyps may depend on local abiotic factors (Ryland & Babcock 1991). The different environmental conditions in the sites studied (the two Suape sites and Gamela) may

Table 3. Overall means (\pm SE) of characters measured on *Palythoa caribaeorum* in Suape South Point (SSP) and Suape North Point (SNP).

Character	SSP	SNP	<i>p</i> <
Polyp			
area (mm ²)	13.95 \pm 5.73	11.66 \pm 4.45	0.05
diameter (mm)	4.17 \pm 0.84	3.81 \pm 0.75	0.05
height (mm)	14.01 \pm 5.97	12.17 \pm 3.95	0.05

have affected *P. caribaeorum*'s biology. Thus, an explanation for the seasonal morphological differences recorded for Pernambuco populations could relate to the distinct stages of the reproductive cycle, perhaps following the same pattern reported by Boscolo and Silveira (2005).

For corals, differences in morphology have been linked to respiration (Lasker 1981, Telesnicki & Goldberg 1995), depth and light (Bosscher & Meesters 1992, Beltran-Torres & Carricart-Gavinet 1993), hydraulic energy (Vosberg 1977, Chappell 1980) and sediment (Hubbard & Pocock 1972, Dodge 1982). Many studies indicated that large polyps may contribute to active sediment rejection (Stafford-Smith & Ormond 1992, Stafford-Smith 1993). Todd *et al.* (2001) morphometrically compared different populations of the hard coral *Favia speciosa* in Singapore, and established a possible relationship between polyp size and sedimentation rates for the studied area. Three sites were studied and the largest polyps and highest sedimentation rates were recorded jointly, possibly indicating some relationship between them. In our case, continuous dredging from the harbor near Suape South Point leads to increased water turbidity due to sediment resuspension (Silva *et al.* 2004).

The fact that the largest average size of *P. caribaeorum* polyps were found in the Suape South Point population could be an ecological strategy to prevent suffocation and death due to sediment accumulation. Another possibility is enhanced polyp growth as a response to turbidity, yet related to feeding habits; as turbidity increases, plankton may become more available and thus result in more prey, which would allow for increased growth. *Palythoa* polyps could then rely more on plankton capture and less on zooxanthellae, as the latter is affected by turbidity. In fact, the efficiency of *Palythoa* as a plankton feeder has already been reported (Sebens 1977, Fabricius & Metzner 2004).

Genotypes with a phenotypic advantage in local environments may be actively selected for (specialization), species might have plastic phenotypes that respond to prevalent conditions, or both of the above may work together. However, it is clear that the role of genotype *versus* environmental interactions varies according to species (Willis 1985, Ayre & Willis 1988,

Weil 1993). Alternatively, the distribution in morphological parameters could simply be due to random processes that affect genotypes in small populations (genetic drift). Nevertheless, if there is a causal relationship between sediment (or other unknown factors) and polyp size, the underlying question of how a large polyp may be of benefit is the same whether specialization or phenotypic plasticity is in effect (Todd *et al.* 2001).

Results obtained here make the environmental effects on the studied characteristics of *P. caribaeorum* seem obvious. This agrees with the idea of plasticity suggested by Reimer *et al.* (2004, 2006b). However, it is difficult to determine which environmental parameter is at play; according to Miller (1994) when studying corals, some species showed different phenotypic responses to distinct reef environments. However, the heterogeneous nature of these ecosystems makes it impossible to attribute such responses to a single physical variable.

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