

## CHANGES IN GORGONIAN MORPHOLOGY ALONG A DEPTH GRADIENT AT ISLA ALCATRAZ, SAN ESTEBAN NATIONAL PARK, VENEZUELA

*Mauricio Rodríguez-Lanetty, Luis Miguel Marquez and Freddy Losada*

Gorgonian growth form represents a trade-off between selective forces related at least to feeding (Leversee, 1976; Sebens, 1984; Sponaugle and LaBarbera, 1991; Patterson, 1991a; b), gas exchange (Patterson and Sebens, 1989), resistance to dislodgment caused by wave action and current (Wainwright and Dillon, 1969; Rees, 1972; Mosquera, 1991; Weinbauer and Velimirov, 1995; Lin and Dai, 1996) and light capture (West et al. 1993). Several authors, however, have suggested that hydrodynamic regime within coral reefs is one of the most important factor determining gorgonian morphology (Wainwright and Dillon, 1969; Grigg, 1972; Velimirov, 1976; Muzik and Wainwright, 1977; Jordan and Nugent, 1978; Weinbauer and Velimirov, 1995). Under wave-generated bidirectional current or high unidirectional current, gorgonians and other soft corals tend to grow fan-form and typically oriented perpendicularly to the current (Theodor and Denyzot, 1965; Wainwright and Dillon, 1969; Koehl, 1982). This growth form seems to minimize the axial rod torsion and colony detachment (Theodor and Denyzot, 1965; Lin and Dai, 1996), and on the other hand, to maximize the food capture as well (Leversee, 1976, Patterson, 1991a). Alternatively, gorgonians grow arborescently tree-form under low-impact hydrodynamic regimes (Grigg, 1972). Thus, according to Sebens (1987), the change in gorgonian morphology along the depth gradient mirrors the change in hydrodynamic regime. Along depth gradients, in which the hydrodynamic stress decreases from wave-exposed shores toward deeper areas, shallow colonies should tend to be fan-form whereas deep ones should be tree-form. Here we set out to test a widely cited concept that gorgonian morphology seems to be a direct reflection of hydrodynamic regime on a coral reef. Our observational data suggests that the effect of hydrodynamic regime on gorgonian morphology is species-specific.

### METHODS

Our study site was a fringing coral reef located in a coralline key on the coast of Venezuela (Fig. 1A, 10°30'38"N, 67°58'18"W). Within 42 3 × 2 m quadrats, we measured the longest and shortest diameter of the planar projection of each colony from the five most abundant species of gorgonians in the locality. From a previous survey, these species were determined to be *Eunicea fusca*, *Plexaura flexuosa*, *Plexaura homomalla*, *Pseudopterogorgia americana* and *Pseudopterogorgia acerosa* (Marquez et al., 1997). We placed the quadrats randomly in relation to the shoreline but at fixed depths: six quadrats at every 2 m depth intervals, between 6 m and 19 m depth. To quantify colony morphology we used the coefficient between the longest (LD) and shortest diameter (SD) (Jordan and Nugent, 1978). When LD/SD > 2, colonies were considered fan-form and they were considered tree-form when LD/SD < 2. We compared the frequencies of forms within each depth interval using binomial tests (Conover, 1980), and used correlations (Sokal and Rohlf, 1995) to determine the association between morphology and depth.

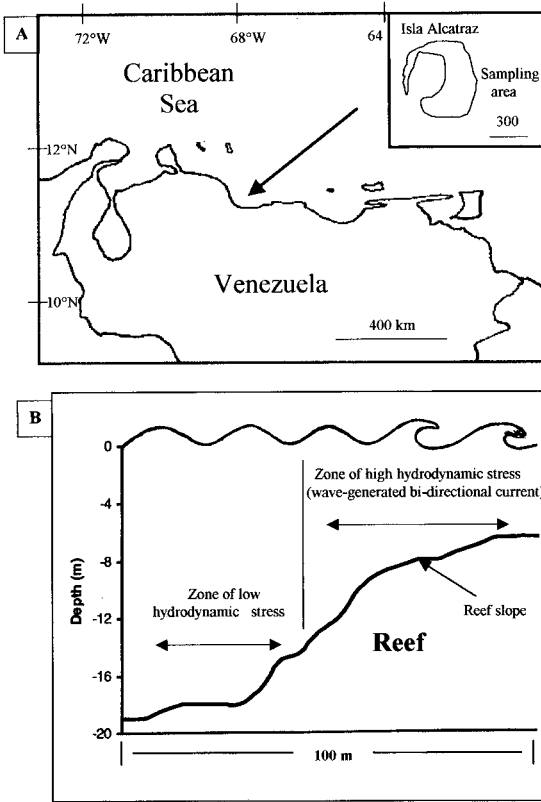


Figure 1. (A) Geographical map indicating the sampling site on the south part of the Caribbean Sea. (B) Reef profile of the study site showing the hydrodynamic features from different depth zones.

RESULTS AND DISCUSSION

Only two out of five species showed the morphology pattern predicted on the basis of hydrodynamic change along the depth gradient (Fig. 2A–B). In *E. fusca* and *P. flexuosa*, fan-form colonies were more abundant than tree-form ones in the shallow depth intervals (6 to 13 m intervals pooled, Binomial test  $P < 0.05$ ). In these species there is a decrease in the relative frequency of fan-form colonies and consequently an increase in tree-form colonies along the depth gradient (Pearson, *E. fusca*  $r = 0.97$ ,  $P = 0.0012$ ; *P. flexuosa*  $r = 0.95$ ,  $P = 0.0013$ ). The depth (~13 m) in which the switch of form proportion was observed also coincides with the part of the reef with the highest slope recorded (see Table 1). We also found out remarkable changes in the zonation and community structure from the same depth, and correlated also this to the slope topography of the studied reef (Marquez et al., 1997). It might be that considerable changes in the intensity of water movement associated to this change of slope are playing a key role determining two different sections or zones of depth in terms of hydrodynamic conditions (see Fig. 1B).

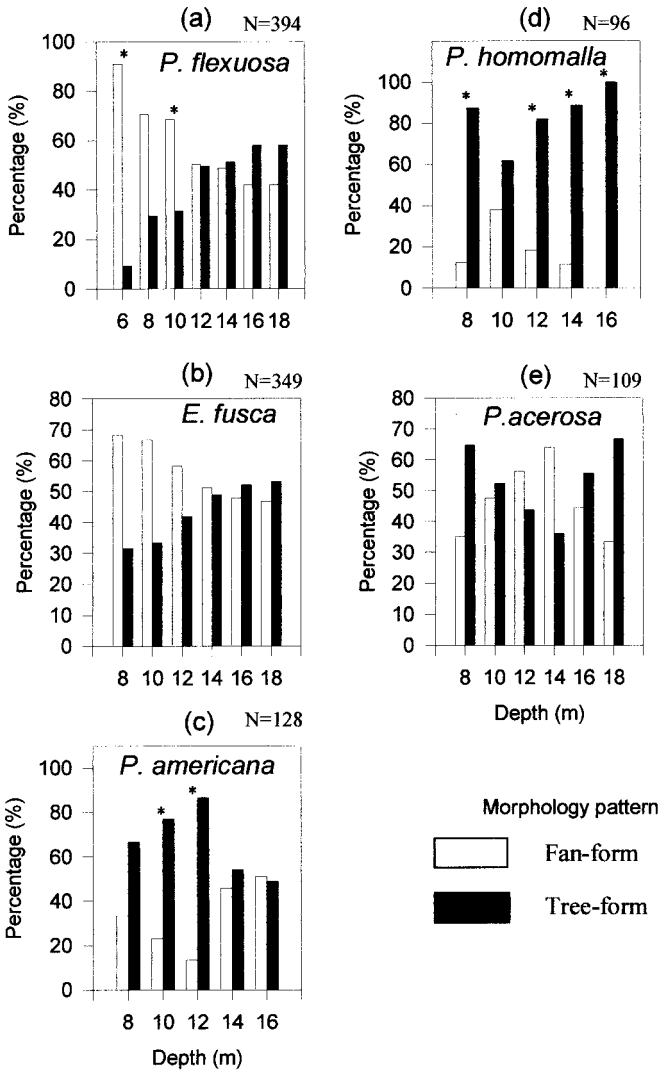


Figure 2. Distribution of colony morphology for five common gorgonian species along a depth gradient. Note: the asterisk (\*) above the bars indicates significant differences between forms at each depth, and N, the sample size.

The proportion of tree-form colonies of *P. homomalla* was higher than fan ones along the entire depth gradient (Binomial Test,  $P < 0.05$ ; see Fig. 2D). Similarly, the proportion of tree-form colonies of *P. americana* was higher than fan-form but only at depths shallower than 14 m depth (Binomial test,  $P < 0.05$ ; see Fig. 2C). In deeper waters, the proportion of both morphologies for *P. americana* is the same (Binomial test,  $P > 0.05$ ). *P. acerosa* did not show statistically significant pattern in colony shape with depth (Binomial test,  $P > 0.05$ ; see Fig. 2E), although proportion of tree-form colonies appears to increase at the ends of the depth gradient. Contrary to our results, other authors have

Table 1. Reef slope average at different depths within the study site.

Depth (m)	Slope (°)	Depth (m)	Slope (°)
6–7	4.5	13–15	12.5
7–9	5.5	15–17	10.0
9–12	7.0	17–18	4.5
12–13	15.0	18–19	3.0

reported a greater proportion of fan-form colonies of *P. homomalla* from shallow reef areas (e.g., Jordan and Nugent, 1978; Mosquera, 1991). We propose that this difference might be due to greater wave energy in their study sites.

The greater structural flexibility of *Pseudopterogorgia* species may explain why their morphologies are not as affected by the hydrodynamic regime. However, the main selective force over coral polymorphism may not be the hydrodynamic environment but related to resource-based or trophic selective pressures (Willis et al., 1997). In fact, experimental data suggested that the water drag force might not be the main selective pressure on *Pseudopterogorgia* flexibility, but feeding efficiency (Sponaugle and LaBarbera, 1991). Moreover, ambient light levels may also have an important role defining gorgonian morphology, since most of these organisms depend physiologically in some extent on their autotrophic endosymbiotic micro-algae (dinoflagellates) (Sorokin, 1991). Currently, there is no information on the photo-physiological performance of these soft corals along depth gradients, however, changes in colony form (e.g., arborescent form) that increase the light capture efficiency in low-light depths would benefit certainly the performance of these soft corals in deep waters. Further experimental and genetic studies are needed to determine the nature of polymorphism in reef soft corals. Our results call to attention the risk involved in generalizing ecological processes from observations on single species.

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ADDRESSES: CORRESPONDING AUTHOR: (M.R.-L.) *Centre for Marine Studies, University of Queensland, St. Lucia QLD 4068, Australia. Fax 61-7-33654755. E-mail: <rodrigm@science.oregonstate.edu>*. (L.M.M.) *Department of Biochemistry, James Cook University, Townsville, Australia.* (F.L.) *Departamento de Biología de Organismos, Universidad Simón Bolívar, Caracas, Venezuela.*