

GORGONIAN COMMUNITIES IN TWO CONTRASTING ENVIRONMENTS ON OCEANIC ATOLLS OF THE SOUTHWESTERN CARIBBEAN

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ABSTRACT

Gorgonian assemblages were surveyed on two oceanic atolls in the southwestern Caribbean Sea (Albuquerque Cays and Courtown Cays, Colombia). Classification analysis showed two well defined assemblages located in two contrasting environments, mid-depth (4 - 11 m) lagoonal patch reefs vs. deeper (10.5 - 20.5 m) leeward and windward fore-reef terraces. Correspondence analysis ordination (COA) yielded a more gradual transition, locating the leeward terrace intermediate between the calm lagoonal patch reefs and the strongly wave-exposed windward fore-reef terrace. Bottom rugosity was significantly correlated to COA scores. Although the counts of gorgonian colonies per station were quite similar in both environments, species number, colony size and cover index values were significantly greater in the fore-reef terraces, suggesting that zones with low relief bottoms exposed to surf and swell represent a more suitable habitat for the development of diverse and structurally more complex gorgonian communities than the calm lagoonal environment. A striking difference between lagoonal and fore-reef terrace assemblages is that each is dominated by closely related species of *Pseudopterogorgia*, suggesting an important role of contrasting environmental conditions in their niche distribution.

In contrast to Pacific atolls, most Caribbean atolls are characterized by the presence of an extensive fore-reef terrace (Milliman, 1973; Díaz et al., 1996a). This mostly gently dipping, calcareous platform constitutes a preferred habitat for dense gorgonian populations (Goldberg, 1973; Lasker and Coffroth, 1983; Jordán, 1989a). Strong wave energy, availability of low relief hard substrata, and other factors favor the settlement and growth of many gorgonian species (Jordán, 1989a). Moreover, gradual variations with depth in light quality, bottom relief and abrasive conditions lead to progressive changes in the composition and structure of gorgonian communities (Yoshioka and Yoshioka, 1989a).

A significant portion of lagoon floor of southwestern Caribbean atolls is overgrown by patch reefs (Milliman, 1969, 1973; Díaz et al., 1996b) also supporting notable gorgonian populations. Contrasting with the windward and leeward fore-reef terraces, the lagoon is a calm environment and patch reefs are greatly variable in shape, relief and size, as well as in the availability of hard substrata and scleractinian dominant species (Díaz et al., 1996b). These two environments are usually sharply separated seawardly by an almost emerging barrier reef and leewardly by a series of detached peripheral reefs. Between-habitat comparisons of gorgonian communities are to date scarce, and quantitative data of gorgonian assemblages in Caribbean oceanic atolls are not yet available. The purpose of this paper is to describe and compare the composition and structure of gorgonian communities in two contrasting environments and to infer which environmental factors are the most important.

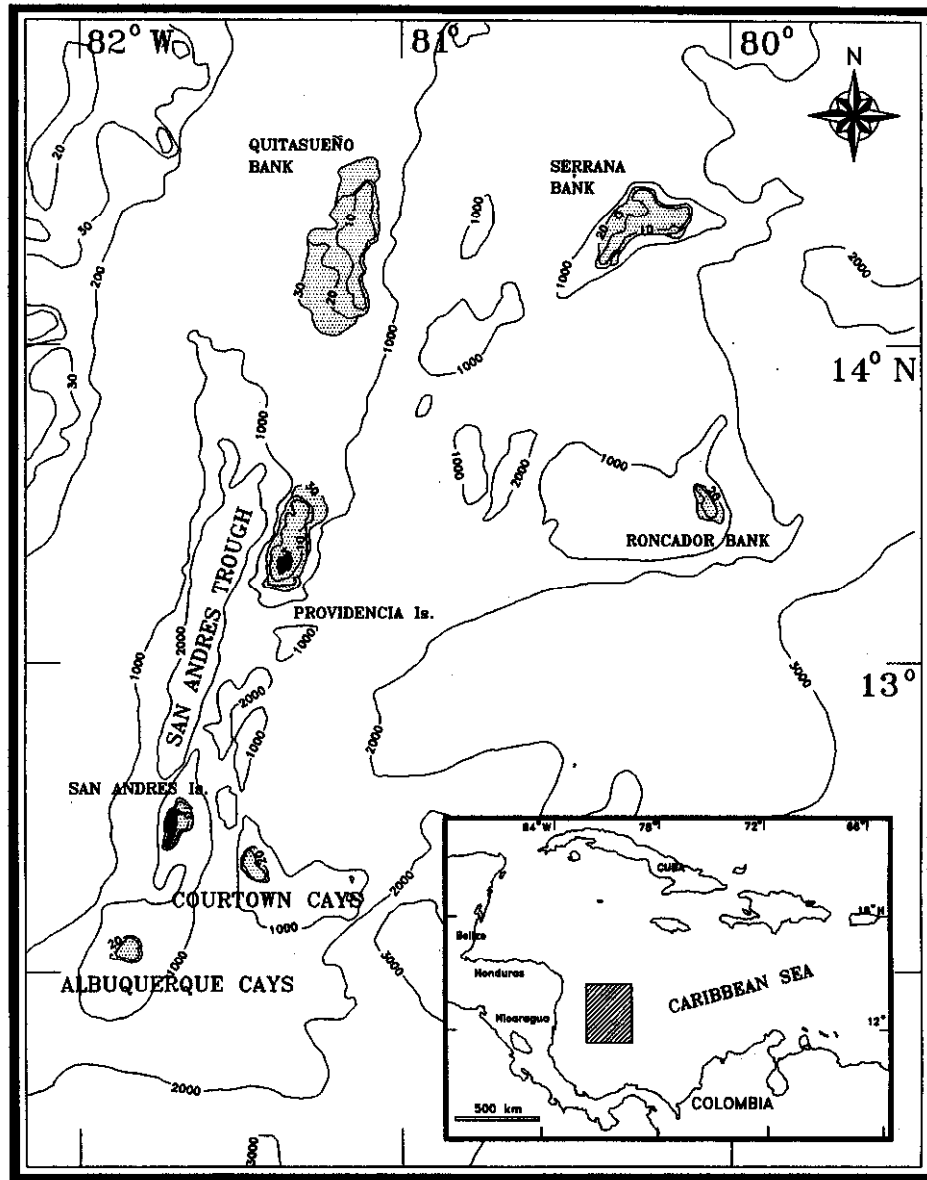


Figure 1. The archipelago of San Andrés and Providencia showing the location of Albuquerque and Courttown cays (depth contours in meters).

MATERIALS AND METHODS

Albuquerque and Courttown are two small, uninhabited oceanic atolls, located in the southwestern Caribbean Sea, belonging to the San Andrés and Providencia archipelago, Colombia (Fig. 1). Comprehensive descriptions of the atolls and their reef structures can be found in Milliman (1969) and Diaz et al., 1996. A strong and almost continuous swell, generated by a NE trade of wind fetch over 2000 km, crosses the windward fore-reef terrace and breaks in the barrier reef; refracted waves

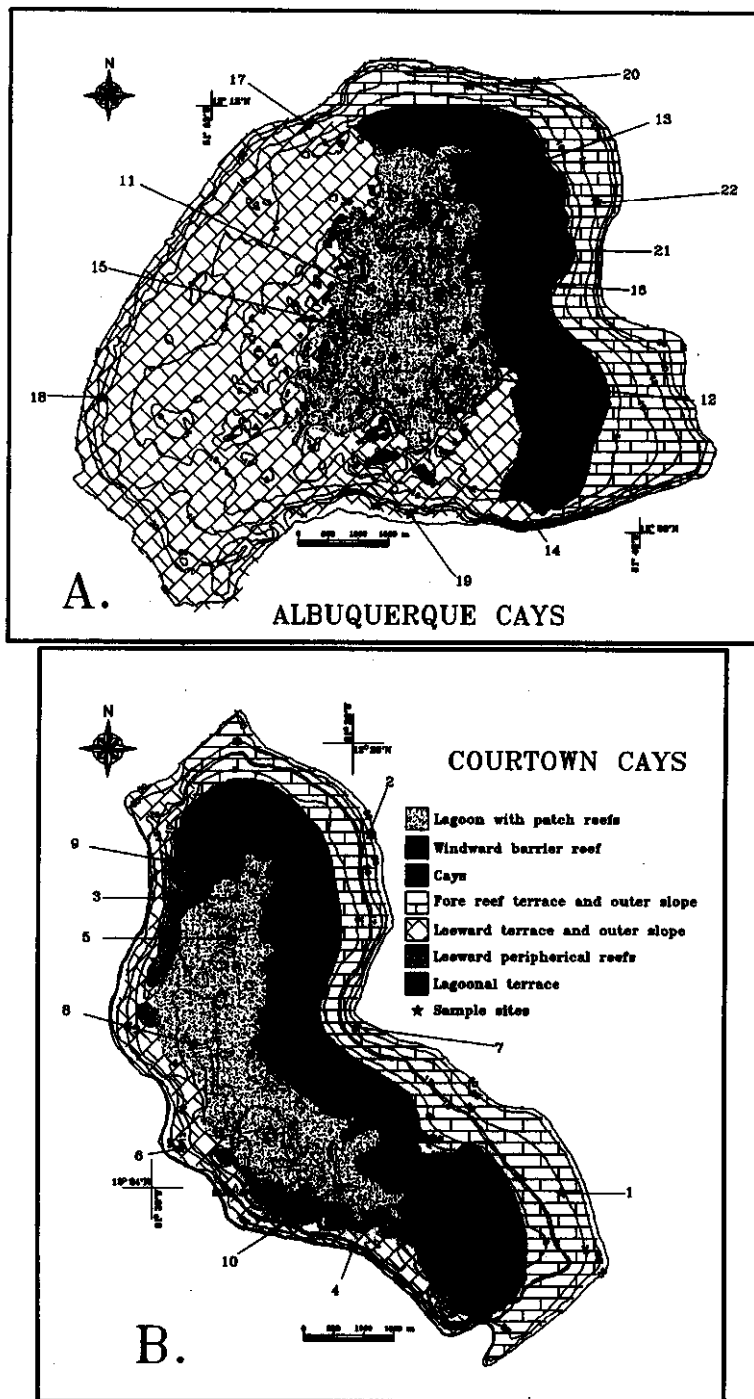


Figure 2. Geomorphologic-bathymetric maps of Albuquerque (a) and Courtown (b) atolls showing the location of the sampling stations (depth contours in meters).

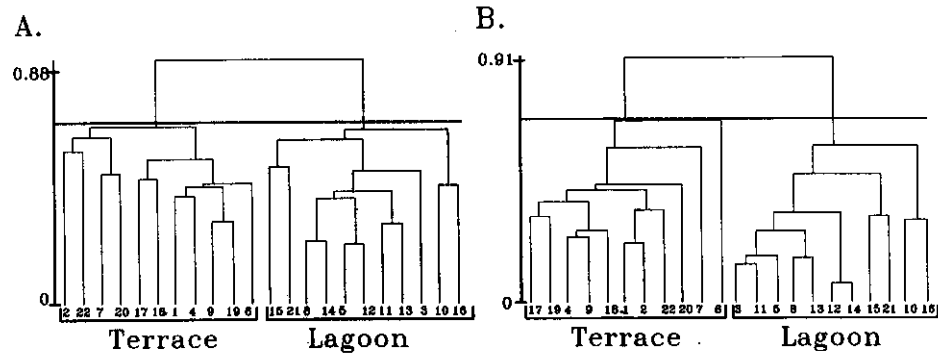


Figure 3. Normal (Q-mode) cluster analysis dendrograms of the 22 stations applying the Bray-Curtis dissimilarity index to cover index (Cophenetic Correlation Coefficient-C.C. = 0.9564) (A); and number of colonies (C.C. = 0.8969) (B).

also break in the NW and SW peripheral reefs. Occasional weather systems generate waves from other directions also exposing the leeward terrace and the peripheral reefs to strong turbulence (Hallock and Elrod, 1988). Barrier and peripheral reefs protect the lagoonal environment from becoming too turbulent. Lagoonal patch reefs are mostly dominated by large massive scleractinians, especially *Montastraea annularis* and *M. faveolata*, forming an irregular topography with deep holes between the coral heads. Instead, the windward terrace is a calcareous nearly even, and low-relief surface sparsely overgrown by crustose and small bushy algae and scattered crustose mound-shaped corals as well. The leeward terrace with moderate relief shows much of the coral dead and overgrown by fleshy algae; however, coral cover can increase with depth towards slope edge (Díaz et al., 1996a).

In May-June 1994, a total of 22 sample stations were surveyed on the windward and leeward fore-reef terraces and lagoonal patch reefs of both atolls (Fig. 2). Species abundance was determined employing the line intercept method, according to the modifications introduced by Jordán (1989a) to the traditional chain transect procedure (cf. Porter, 1972). On each station, three 10-m long metallic chains (for a total of 30 m) were extended over the bottom following its irregularities and relief. Cumulative species diversity curves obtained in an earlier survey employing this method proved that representative samples are attainable with less than 20-m transects (Sánchez and Ramírez, 1994). Colonies whose area of projection against the bottom intercepted the chain were counted, examined and identified. By means of a 1-m long graduated rod, their height, and upper-view maximal and minimal diameter were measured. Their abundance in terms of size per colony was estimated applying the "cover index" for branching organisms (Müller-Dombois and Ellenberg, 1974; Jordán and Nugent, 1978). Other erect sessile organisms occupying the same layer in the water column and exhibiting similar physiognomic features, such as some sponges, as well as dead gorgonians overgrown by the encrusting hydrocoral *Millepora alcicornis*, and filamentous algae (i.e., Ceramiaceae or Cyanobacteria), were also considered. Rugosity, an index that indicates bottom relief, was estimated from the ratio of the chain length to the projected length (Rugosity = 10 m of chain / real length). Stations were ranked by their prevailing surf and swell conditions using photointerpretation of the wave refraction patterns (total panchromatic coverage air photographs: 1971 and 1984 by the Colombian Geographical Institute-IGAC) and in situ observation on each site.

Although most gorgonian species could be easily identified in situ, voucher fragments of some colonies were sampled and fixed in 70% alcohol for external and sclerite analysis following Bayer (1961). Reference specimens were deposited in the collection of INVEMAR at Santa Marta, Colombia.

Table 1. Number of colonies and cover index of 34 species in terraces (Windward fore-reef terrace and Leeward terrace) and lagoonal habitats [all species are gorgonaceans except encrusting filamentous algae (A), encrusting milleporid hydrocorals (HC) and erect sponges (S)]. Data are mean (Min.-Max.) of each cluster of figure 4 calculated from per-station (30 m transect) values. (-) = absent.

Species/habitat	Terraces				Lagoon	
	Windward FRT		Leeward T		N.C.	C.I.
	N.C.	C.I.	N.C.	C.I.		
Terrace assemblage						
<i>Pseudopterogorgia acerosa</i>	1.2 (0-3)	450.2 (0-2251)	-	-	-	-
<i>Pterogorgia citrina</i>	3.2 (0-7)	1.8 (0-9)	-	-	-	-
<i>Eunicea tourneforti</i>	0.2 (0-1)	19.6 (0-98)	-	-	-	-
<i>Plexaurella grisea</i>	0.2 (0-1)	19.2 (0-96)	-	-	-	-
<i>P. fusifera</i>	0.2 (0-1)	12.6 (0-63)	-	-	-	-
<i>Eunicea</i> sp. 2	0.18 (0-1)	2.27 (0-25)	-	-	-	-
<i>Gorgonia ventalina</i>	0.2 (0-1)	1.6 (0-8)	-	-	-	-
<i>Pterogorgia anceps</i>	0.2 (0-1)	13.6 (0-68)	-	-	-	-
<i>Aplysina fulva</i> (S)	0.4 (0-2)	1 (0-5)	-	-	-	-
<i>Pseudopterogorgia kallos</i> *	13 (5-13)	105.8 (81-529)	20* (2-34)	442.7* (152-745)	-	-
<i>P. rigida</i>	0.8 (0-2)	259.8 (0-1299)	0.2 (0-1)	12 (0-72)	-	-
<i>P. elizabethae</i>	0.2 (0-1)	0.6 (0-3)	0.7 (0-3)	99 (0-572)	-	-
<i>E. knigthi</i>	0.6 (0-3)	0.2 (0-1)	0.2 (0-1)	0.2 (0-1)	-	-
<i>Eunicea</i> sp. 1	0.2 (0-1)	0.0	0.2 (0-1)	4.2 (0-25)	-	-
<i>Eunicea</i> sp. 3	-	-	0.2 (0-1)	49.5 (0-297)	-	-
<i>Pseudopterogorgia hystrix</i>	-	-	0.2 (0-1)	47.5 (0-285)	-	-
<i>P. americana</i>	6.6 (4-12)	1023.6 (0-5118)	4.3 (1-8)	353.5 (7-2121)	0.18 (0-2)	51.2 (0-564)
<i>Briareum polyanthes</i>	0.2 (0-1)	22.6 (0-113)	0.2 (0-1)	0.8 (0-5)	0.36 (0-1)	0.1 (0-09)
<i>Plexaurella dichotoma</i>	0.4 (0-1)	6.4 (0-32)	0.2 (0-1)	0.2 (0-1)	0.09 (0-1)	2.63 (0-29)
<i>Muriceopsis flavida</i>	1.4 (0-4)	42 (0-210)	1.7 (0-5)	41.7 (0-246)	1.6 (0-6)	5.18 (0-52)

* could be included several unidentified *Pseudopterogorgia bipinnata* complex species.

Table 1. Continued.

Species/habitat	Terraces				Lagoon	
	Windward FRT		Leeward T		N.C.	C.I.
	N.C.	C.I.	N.C.	C.I.		
Lagoon assemblage						
<i>Eunicea mammosa</i>	0.2 (0-1)	0.4 (0-2)	-	-	0.18 (0-2)	2.27 (0-25)
<i>Aplysina cauliformis</i> (S)	0.6 (0-1)	0.2 (0-1)	0.2 (0-1)	0.2 (0-1)	0.27 (0-2)	8.6 (0-62)
<i>Plexaura flexuosa</i>	0.2 (0-1)	1.6 (0-8)	0.7 (0-2)	1.7 (0-6)	1 (0-4)	52.8 (0-279)
<i>E. succinea</i>	1 (0-4)	0.8 (0-4)	0.5 (0-2)	0.5 (0-2)	0.81 (0-2)	1.18 (0-5)
<i>Millepora</i> sp. (HC)	1.2 (0-3)	16.6 (0-63)	0.7 (0-3)	4.7 (0-17)	2.81 (0-6)	41.2 (0-97)
<i>Pseudoplexaura</i> spp.	0.2 (0-1)	2.8 (0-14)	0.3 (0-1)	2.7 (0-13)	0.09 (0-1)	0.45 (0-5)
<i>Pseudopterogorgia bipinnata</i>	-	-	0.4 (0-2)	1.2 (0-6)	19.72 (5-38)	263.7 (25-525)
<i>Briareum asbestinum</i>	-	-	1.3 (0-2)	12.7 (0-61)	3.36 (1-8)	22.5 (0-81)
<i>E. fusca</i>	-	-	0.5 (0-4)	1.5 (0-9)	0.18 (0-1)	3.54 (0-25)
<i>Pseudoplexaura porosa</i>	-	-	-	-	0.18 (0-1)	18.54 (0-200)
<i>Plexaura homomalla</i>	-	-	-	-	0.36 (0-20)	3.81 (0-26)
<i>Plexaura</i> sp.	-	-	-	-	0.36 (0-4)	3.18 (0-35)
<i>Pseudoplexaura crucis</i>	-	-	-	-	0.81 (0-8)	34.18 (0-299)
<i>Filamentous algae</i> (A)	-	-	-	-	0.09 (0-1)	1.54 (0-17)
<i>Callyspongia vaginalis</i> (S)	-	-	-	-	0.09 (0-1)	2.27 (0-25)

To discriminate gorgonian assemblages, stations were grouped according to per species number of colonies and cover index using normal (Q-mode) cluster analysis applying the Unweighted Pair Group Method (UPGMA) to the Bray-Curtis dissimilarity index (Field et al., 1982). Correspondence Analysis scores (COA, also called reciprocal averaging; Ludwig and Reynolds, 1988) of per station biotic composition were related to some environmental and community parameters through simple linear regression. COA is a procedure with a double-transformation (i.e., by species and stations) of community data, which has already demonstrated its usefulness in the assessment of gorgonian assemblages (Yoshioka and Yoshioka, 1989a).

RESULTS

A total of 716 colonies belonging to 35 species were sampled during the survey. Number of colonies fluctuated between 10 and 49 per station, whereas species number varied between 3 to 15 per station.

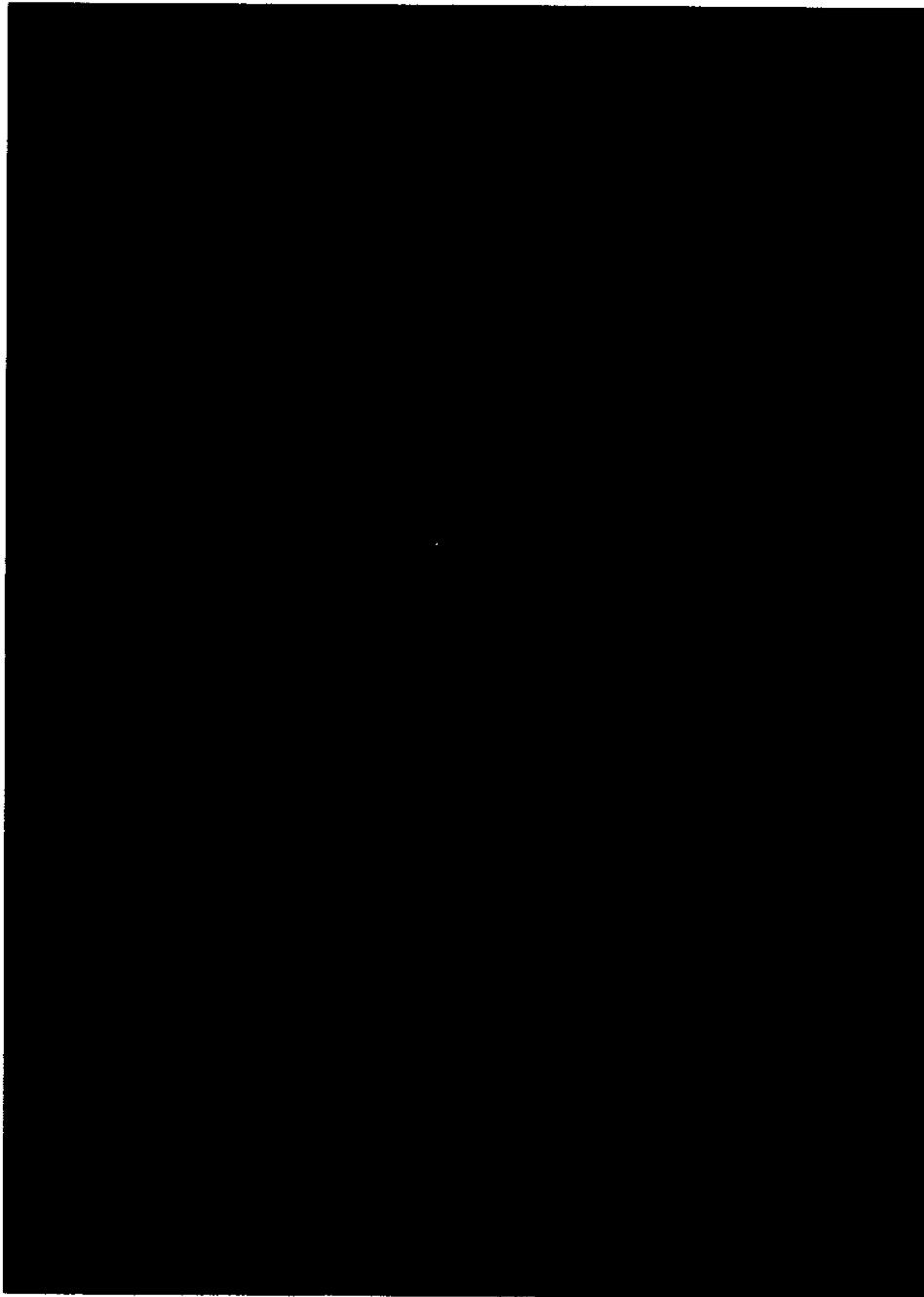


Figure 4. Photographs of *Pseudopterogorgia bipinnata* (upper) in the lagoon (7 m; 40 cm in height) and *P. kallos* (below) in the fore-reef terrace (20 m; 35 cm in height) at Albuquerque atoll.

Table 2. Mean (Min-Max.), per station number of species and colonies, cover index, bottom, rugosity, depth and diversity index (H') in terrace and lagoonal environments.

Items\Cluster	Terraces (b)	Lagoon (a)
Number of stations	11	11
N. species	7.3 (3-15)	6.1 (4-11)
N. colonies	32.4 (15-45)	32.7 (10-49)
Cover index****	1504.8 (585-4991)	527.2 (84-928)
Rugosity****	1.26 (1.11-1.38)	1.42 (1.14-1.61)
Depth****	17.4 (10.5-20.5)	7.4 (4-11)
H' (N. colonies)	1.513 (0.699-2.362)	1.221 (0.59-2.019)
H' (Cover index)	1.046 (0.625-1.519)	0.997 (0.564-1.672)

**** Items with significant differences ($0.01 < P < 0.02$, Mann-Whitney test)

The classification analysis showed two detached clusters which respectively correspond to the stations located on the fore-reef terraces and on lagoons across both atolls (Fig. 3). From a total of 34 species, 29 were found in stations located on the terraces, and 15 (52%) were exclusive to them. Twenty species showed a 90% value of cover index of its colonies on the fore-reef terrace stations. The most common were two species of *Pseudopterogorgia* (*P. kallos* and *P. americana*) and *Pterogorgia citrina* (Table 1). Of the remaining species, 11 were uncommon (i.e., recorded only in one station). On the other hand, 19 species were recorded in lagoonal patch reefs, of which 6 species (32%) were exclusive. Five were uncommon. Lagoonal patch reef assemblages were widely dominated by *Pseudopterogorgia bipinnata*, followed by *Briareum asbestinum*, *Eunicea mammosa*, *E. succinea*, *E. fusca*, *Pseudoplexaura porosa*, and *Millepora* sp., the latter primarily encrusting axes of *P. bipinnata*. *Muriceopsis flavida*, *Plexaura flexuosa* and *P. crucis*, as well as the sponge *Aplysina cauliformis*, exhibited similar abundances in both the terrace and the lagoon, but their cover index was larger in either one of the environments (Table 1). With exception of *Eunicea mammosa*, all other species occurring both in the lagoon and the windward fore-reef terrace were also present in the leeward terrace. On the other hand, dominant species in the lagoon yielded lower abundances in the leeward terrace, whereas in this latter environment *Pseudopterogorgia kallos* and *P. americana* attained their greatest abundances (Table 1).

Table 2 compares the values of some biotic and physical attributes between the two main cluster groups. Despite the fact that mean number of colonies and species per station were not significantly different between groups, cover index values were higher on the terrace. Likewise, the diversity values, measured with the traditional Shannon-Weaver index, were not very different between both environments, although the mean values, particularly those obtained by applying the index to number of colonies, were indeed somewhat higher on the terrace. Significant differences between the two groups were found in regard to cover index, bottom rugosity and depth.

In Table 3, stations were sorted in descending order of their bottom rugosity index. With some exceptions, the stations of the windward fore-reef terrace and the lagoonal patch reefs were ranked respectively in the lower and upper extremes of rugosity, while the leeward terrace stations were intermediate, in inverse relationship with the prevailing surf and swell conditions. High COA axis II values corresponded to lagoonal stations with low to medium swell and rugged bottom and vice versa for windward fore-reef

Table 3. Stations (ST.) sorted in descending order of bottom rugosity index (RUG.), data on surf and swell (S.: L=Low; M= Moderate; H= High), geomorphological zone (G.; L= Lagoon, LT= Leeward terrace; WT= Windward fore-reef terrace) and COA II value.

RUG.	ST.	S.	G.	COA II
1.11	22	H	WT	0.058
1.14	1	H	WT	-0.752
1.14	14	M-L	L	0.018
1.15	7	H	WT	0.116
1.19	18	M	LT	0.039
1.22	2	H	WT	1.487
1.28	4	M-H	LT	-0.472
1.32	20	H	WT	-0.431
1.34	19	M-H	LT	-0.242
1.35	6	M-H	LT	0.185
1.36	9	M	LT	0.356
1.36	13	L	L	1.525
1.37	17	M	LT	-0.009
1.38	16	M	L	-0.512
1.38	21	L	L	-0.046
1.41	11	L	L	-0.538
1.42	15	M-L	L	-0.985
1.43	8	L	L	1.200
1.46	5	M-L	L	1.866
1.47	12	M	L	-0.177
1.56	3	L	L	3.637
1.61	10	M-L	L	2.727

terrace. The influence of bottom relief upon the community structure was evident from the significant regression (t: $P < 0.015$, residuals normally distributed, Kolmogorov-Smirnov test: $DN = 0.12$, $P = 0.91$.) of this factor with COA-axis II; an $r^2 = 26\%$ of total COA-II variation was explained by the rugosity index.

Noticeable was the relative frequent occurrence in the lagoon (data not shown) of the encrusting form of *M. alvicornis* overgrowing the axis of some live gorgonian species, particularly *P. bipinnata*.

A distinguishing feature of the gorgonian assemblages in both environments was the occurrence in each of them of a closely related species of *Pseudopterogorgia* (Fig. 4). *Pseudopterogorgia kallos* was the dominant species on the terrace and almost not a single colony of it was recorded in lagoonal patch reefs. On the contrary, whereas *P. bipinnata* dominated largely in the lagoon, it was moderately common in the leeward terrace (Table 1).

DISCUSSION

Differences in gorgonian species composition and a greater overall cover index on the fore-reef terrace in comparison to the lagoon, appear to be related to the differences in turbulence, substratum inclination and sedimentation. A greater cover index at the ter-

ances, which has been shown to be a good indicator of biomass (Jordán and Nugent, 1978), suggests that this environment allows a greater colony development. Octocoral communities of tall and strongly built colonies on habitats exposed to strong surf and currents have been amply documented (Wainwright and Dillon, 1969; Rees, 1972; Birkeland, 1973; among others). In general, the arborescent and flexible physiognomy of octocorals, which counters drag with deflection (Vogel, 1983) and distances the colony from close-to-the-bottom abrasive forces and interactions (Jackson, 1977), allows them to colonize successfully turbulent environments. The composition of their axial core varies in the content of elastic fibers and carbonates to produce a rigidity tuned to the turbulence regime that each species may withstand (Jeyasuria and Lewis, 1987; Esford and Lewis, 1990; Lewis et al., 1992). This shows a species-specific dependence of the hydrodynamic regime that is hence reflected in the distinctive composition and the marked exclusiveness of species on the fore-reef assemblage when compared to the lagoonal one.

Interestingly, throughout a gradient of turbulence correlated to depth from the breaker zone of the barrier and peripheral reefs to the edge of the fore-reef terraces at Courtown and Albuquerque, the greater development of gorgonian assemblages occurs at the deeper areas (10 - 25 m). Indeed, on the shallower (< 10 m) areas of the windward fore-reef terrace the flat substratum is virtually devoid of sessile animals (Díaz et al., 1996b); also, on the very shallow (< 4 m) leeward and peripheral reefs, the octocoral fauna is remarkably poor, excepting a few patches of *Plexaura-Pseudoplexaura* species (Díaz et al., 1996b). This contrast with other reef complexes of the southwestern Caribbean such as Roncador and Serrana Banks, whose barrier reef crests and shallow fore-reef terraces harbor dense populations of the sea-fan *Gorgonia ventalina*, and of *P. flexuosa* and *Pterogorgia citrina* (unpublished data). The absence of *Gorgonia* at Albuquerque and Courtown seems to have been caused by the same agent that produced its massive die-off in the southern Caribbean (Garzón-Ferreira and Zea, 1992), which also occurred at nearby San Andrés (Díaz et al., 1995). The virtual absence of other gorgonians in shallow turbulent areas could have been caused by storm waves. Albuquerque and Courtown were along the path of four hurricanes this century. The last one was "Joan" in 1988, whose eye passed south of San Andrés, closer to Albuquerque, producing still visible damage in their reefs (Geister, 1992; Díaz et al., 1996b). Although hurricane effect on gorgonian communities could be unpredictable (Yoshioka and Yoshioka, 1987), it is probable that shallow and exposed sites of these atolls suffered greater damage from storms than deeper or sheltered areas such as the lagoon and fore-reef terraces.

Although the main factor conditioning the settlement of gorgonians is the availability of hard substrata (Kinzie, 1973), it has been shown that the irregularity of the bottom, from the scale of a few centimeters to a few meters, can strongly control community composition; vertical to overhanging substrata usually hold a few gorgonian species, while flat to inclined substrata favor their lush growth (Yoshioka and Yoshioka, 1989b). However, excessive sedimentation may hinder octocoral recruitment (Gotelli, 1988) and growth (Yoshioka and Yoshioka, 1989b). Thus, the mid to low relief of the fore reef terraces, with a greater sediment resuspension and transport due to turbulence, allow for a greater diversity and cover than on the lagoon environment. Indeed, the detrimental abrasive effect of sediment resuspension on terrace scleractinian corals (Jordán, 1989b), evident at Albuquerque and Courtown (Díaz et al., 1996b) seems not to strongly affect gorgonians, whose basal holdfasts are apparently resistant. In contrast, the greater bottom relief, calm waters and greater sedimentation of the lagoon implies a lower gorgonian colony development,

and condition gorgonian species composition. Indeed, the greater incidence of overgrowing of gorgonians by *Millepora* found in the lagoon, is in agreement with the findings of Wahle (1983, 1985) of a greater degree of colony overgrowth, injuries and a lower degree of regeneration in wave-protected, rear-reef habitats. On the other hand, the greater availability of cracks, crevices and overhanging substrata augments the possibility of attachment and directed growth to the light by thinly branched species such as *P. bipinnata*; this species has a long-lived larva lacking zooxanthellae (Kinzie, 1974), a feature that allows it to settle on darker areas free of sediments. Its susceptibility to *Millepora* overgrowth seems to be counterbalanced by constantly high recruitment rates, as evidenced from its size-frequency distribution at several southwestern Caribbean atolls (unpubl. data).

Some species are able to thrive in an ample range of environmental conditions, due in part to a plastic morphology (i.e., degree of branching, thickness of branches, West et al., 1993; Weinbauer and Velimirov, 1995, among others) or to their ability to capture food at various depth or flow regimes (Lasker et al., 1983; Dan and Lin, 1993). This may explain why the lagoon assemblage shares several species with the terrace assemblage, especially those species occurring also on the leeward terrace; the latter habitat has a relatively lower incidence of surge and a slightly stronger relief in relation to the fore-reef terrace, allowing for the presence of species adapted to the moderate conditions in between the extremes represented by the fore-reef terrace and the lagoon. Indeed, those species occurring on both the windward fore-reef terrace and the lagoon are always also present on the leeward terrace, which suggests them to be generalists.

Pseudopterogorgia is one of the most conspicuous genus of gorgonians on shallow reefs in the Tropical Western Atlantic (Bayer, 1961), and species of this yielded the greatest abundances in both Albuquerque and Courtown atolls. This genus usually exhibits high rates of recruitment and juvenile survival, and some species, such as *Pseudopterogorgia americana* and *P. kallos*, are characteristically members of shallow, wave-exposed, fore-reef assemblages in the Caribbean (Lasker and Coffroth, 1983; Jordán, 1989a, among others). In contrast, *P. bipinnata* prefers somewhat deeper and calmer zones (Goldberg, 1973; Kinzie, 1973). Whether this two closely-related forms are definitively different species is a matter of discussion.

In conclusion, the distribution and abundance of coral reef associated gorgonians at Courtown, Albuquerque and elsewhere, is related to the conditions which occur along an environmental continuum from high turbulence and low topographic relief, to low turbulence and high topographic relief (Yoshioka and Yoshioka, 1989a). The windward fore-reef terrace and the lagoon are near these two extremes, with the leeward terrace somewhere in between but closer to the high turbulence side. Other approximations with yet other benthic variables have also shown patterns of distributions of reef organisms associated to conditions between exposed and protected zones, and in relation to bottom relief and light attenuation (i.e., depth) (Graus et al., 1984; Graus and Macintyre, 1989; Bak and Povel, 1989).

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