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**EVALUATING CORAL REEF BENTHIC COMMUNITIES IN REMOTE
CARIBBEAN ATOLLS (QUITASUEÑO, SERRANA, AND RONCADOR BANKS)
TO RECOMMEND MARINE-PROTECTED AREAS FOR THE SEAFLOWER
BIOSPHERE RESERVE**

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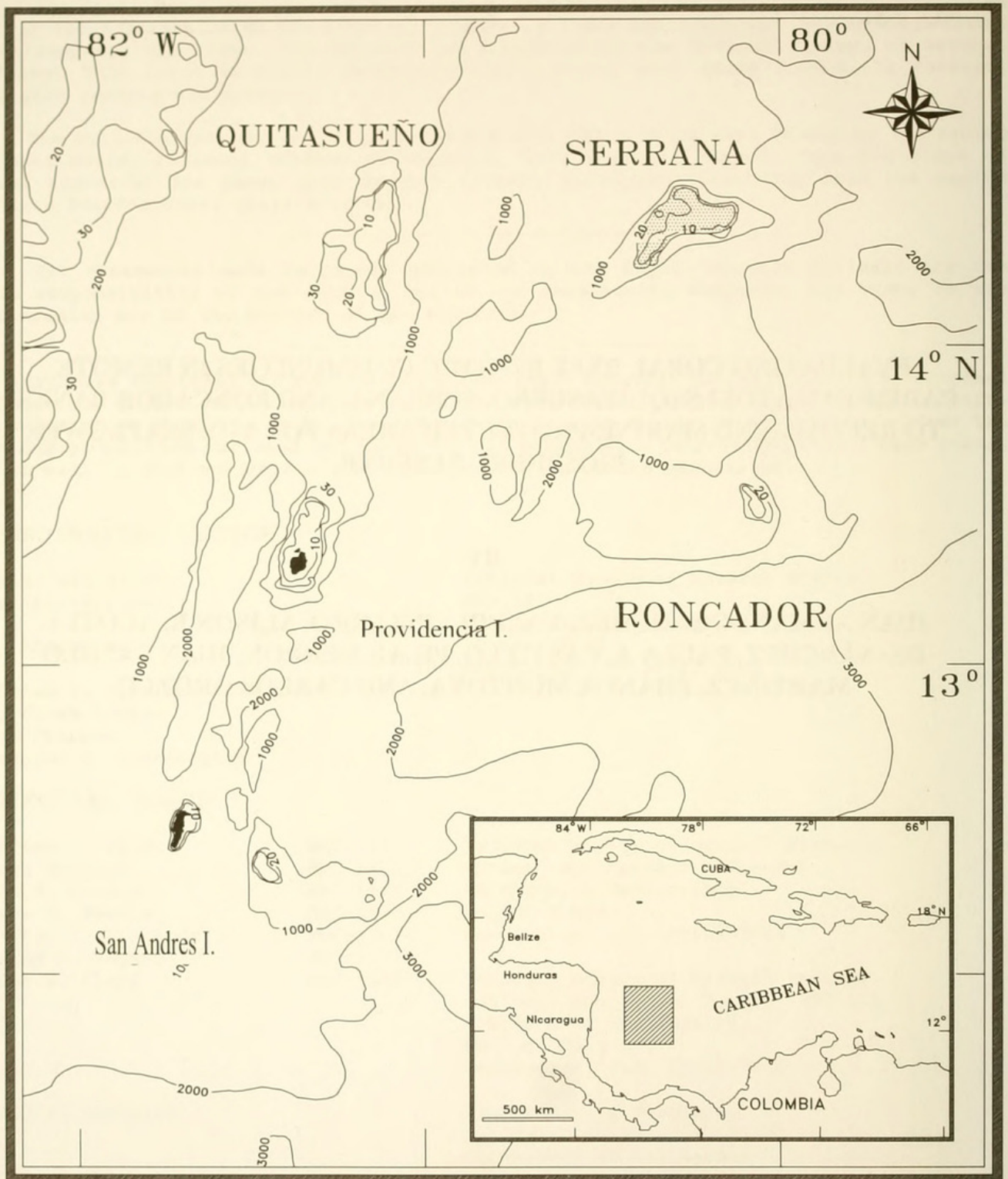


Figure 1. Southwestern Caribbean showing the location of the Northern banks (Colombia).

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ABSTRACT

Three remote oceanic atolls, the Northern Cays (Quitassueño, Serrana, and Roncador Banks, Archipelago of San Andres and Providencia, Colombia) were intensively surveyed during April and May, 2003 through a multilevel quantitative study of the benthic communities (substrate cover: coral-benthos; densities: octocorals and urchins; frequencies: coral diseases). This study is the first approach towards the design of a network of Marine Protected Areas (MPAs) in these Caribbean reefs. We found between 66 and 73 categories of substrates in the benthic communities, including 43-to-46 species of reef-building corals and 38 species of octocorals. Ample ranges of coral cover (2-52 %) and octocoral densities (0-15 col. m⁻²) were observed among stations. The community structure corresponded to shared species-specific environmental preferences, perceptible as minor gradients such as windward-leeward and/or shallow-deep, and to physical/topographical characteristics, which in most habitats were products of the reef-building corals themselves (e.g., '*Montastraea*' or '*Acropora palmata* - *Diploria*' habitats).

Depth was the major structuring force. Species abundance distribution followed the pattern that few species are dominant whereas most of them are rare. Common species were *Montastraea* spp. (reef-building corals), *Pseudopterogorgia bipinnata* (an octocoral) and *Lobophora variegata* (fleshy macroalgae). Sea urchins and coral diseases had a heterogeneous distribution being absent in many stations and frequent in a few. Higher densities of sea urchins (*Diadema antillarum* and *Echinometra viridis*) were encountered in Quitassueño Bank. There were areas of high coral abundance and diversity in the three atolls which can be important for the MPA design. The particular assemblages had mean values of coral cover > 32% (most of them >38%), coral species >16, octocoral densities >0.6 col. m⁻² (usually >2.9 col. m⁻²), and octocoral diversity > 4 (usually >8), which are within the ranges of the best-conserved reefs in the Caribbean. Some areas of special concern were identified that could need special management.

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Difficult management challenges are the high density/diversity areas of endangered and/or rare octocorals (Roncador and Serrana Banks: *Gorgonia* spp. and *P. elisabethae*) as well as heterogeneous shallow patch reefs of endangered corals and highly productive coralline algae (*A. palmata* and *Porolithon pachydermum*) intermingled with *Montastraea* spp. reefs exhibiting disease outbreaks (white plague, bleaching, and dark spots) in Serrana Bank.

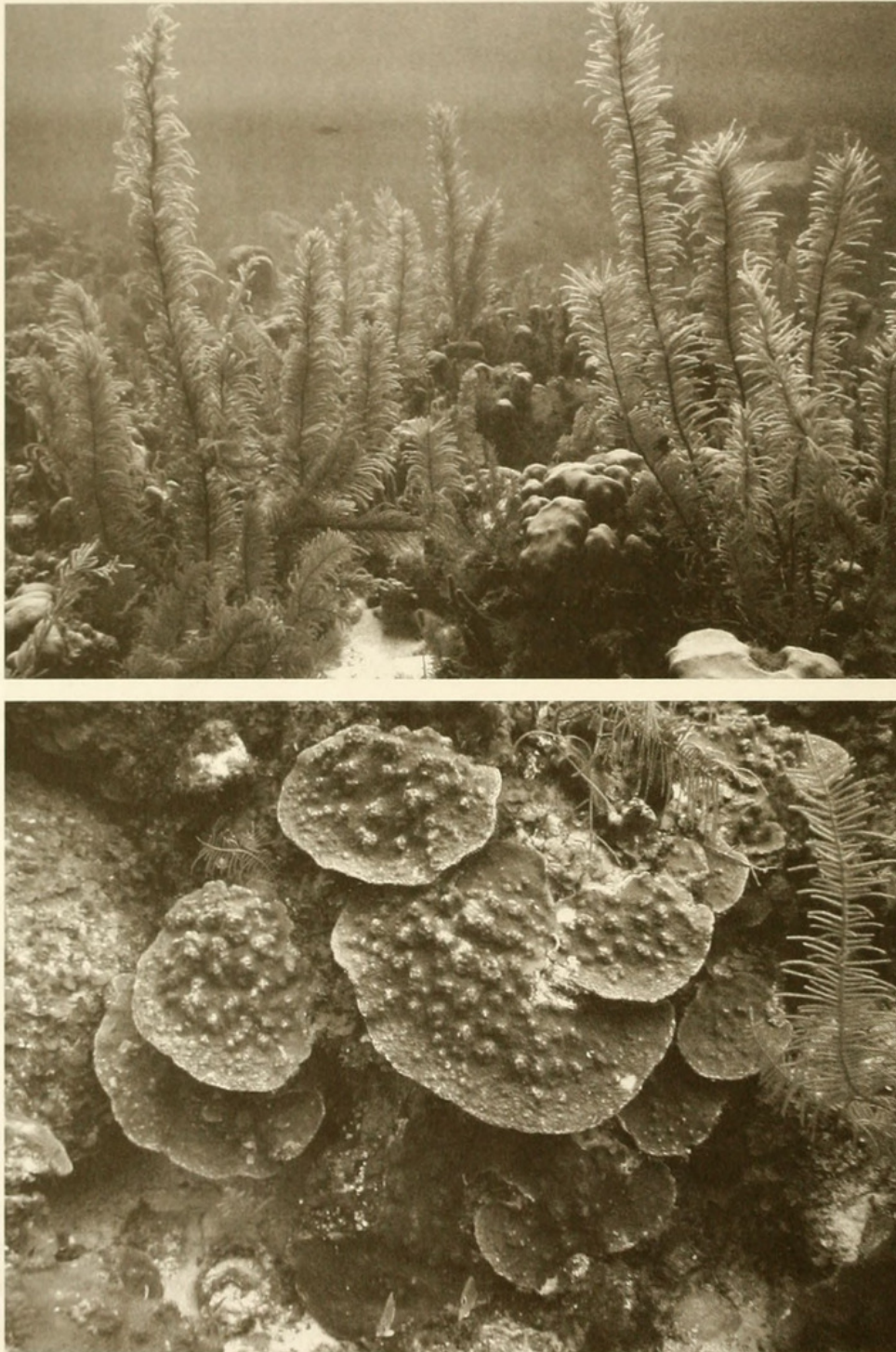


Figure 2. Coral reefs at the *Montastraea* spp. habitat in Roncador Bank, Southwestern Caribbean, Colombia. Upper: Organisms with most of their biomass above the substrate such as gorgonian octocorals (*Pseudopterogorgia* spp.). Below: Organisms covering the reef substrate; dominant coral in the photo is *Montastraea franksi*.

INTRODUCTION

Quitasueño, Serrana and Roncador Banks (Northern Cays) are some of the few true oceanic atolls of the Atlantic surrounded by depths of thousands of meters (Díaz et al., 1996a). The coral-reef banks belong to the Archipelago of San Andrés and Providencia (Colombia) in the southwestern Caribbean (Fig. 1). This area been declared a biosphere reserve by UNESCO (Seaflower Biosphere Reserve) and the local environmental authority (CORALINA) is proceeding with the design of a network of MPAs in the area including the Northern Cays (e.g., Friedlander et al., 2003). However, very little information on the benthic communities of these atolls is available to design a series of MPAs. This study comprises the first detailed and quantitative study of the benthic communities of the coral reefs on Quitasueño, Serrana and Roncador Banks that will contribute to the zoning and design of the MPAs. Ultimately, local authorities will have these recommendations, in addition to parallel studies on fish communities and Queen Conch populations (*Strombus gigas*), to confront with stake-holder needs and finally design a network of MPAs in these banks.

The Archipelago of San Andrés and Old Providence comprises a series of oceanic islands, barrier-reef complexes, atolls and coral shoals on a volcanic basement (Fig. 1) aligned in a north-northeasterly direction over nearly 500 km along the Lower Nicaraguan Rise off the Central American continental shelf (Geister, 1983, 1992; Díaz et al., 1995; Díaz et al., 1996a, 1996b, 2000). Both geomorphological and habitat distribution patterns are similar among these reef complexes mainly due to the strong wave action generated by trade winds. The upper platform of these atolls is surrounded by a rather even 20m-deep terrace. On its windward, fore-reef side it has low relief due to the strong abrasion which allows only sparse growth of encrusting and mound-shaped corals but permits profuse gorgonian development (Sánchez et al., 1997, 1998). This windward, fore-reef terrace gradually slopes upwards emerging on a reef crest which is variably developed as a spur-and-groove system of hydrocorals (*Millepora* spp.), zoanthids and crustose coralline algae (corallinaceae). The crest forms an almost continuous barrier to the waves and fringes the eastern, northern and southern internal margins of the upper platform.

Behind the barrier there is an extensive, sinuous and shallow (1-3 m) sand-and-rubble lagoonal terrace that is connected to the lagoonal basin by an abrupt sandy slope. There is no reef formation behind the crest (e.g., back reef) as in the traditional Caribbean fringing reef (e.g., Jamaica). The mid-depth (12-18 m) lagoonal basin is usually covered by a dense patch-reef network (e.g., Díaz et al., 1996b). These patch reefs are mostly dominated by massive scleractinian corals, especially *Montastraea annularis* and *M. faveolata*. The reefs are irregular in topography with sand patches occurring among the coral heads (e.g., large massive reef-building corals). Bordering the western margin of the lagoon there is a leeward terrace, often times crowned with a discontinuous band of peripheral shallow reefs, inner sand bars and algal ridges that partially enclose the lagoon (e.g., Díaz et al., 1997). The leeward terrace gradually slopes down towards the 20-30m deep break on the outer-slope margin supporting moderate relief reefs with variable live-coral cover (see more details in Milliman, 1969; Díaz et al., 1996a, 2000). The benthic

community structure of these oceanic reef complexes, including Serrana and Roncador, is considerably different than coastal coral reefs (Diaz-Pulido et al. submitted).

The most conspicuous sessile benthic organisms of Caribbean coral reefs are localized at two overlapping layers (Fig. 2). One layer comprises organisms that are covering the substrate, principally scleractinian and milleporinan corals, zoanthids, sponges, and algae, referred to here as the benthic community. The other layer is composed of erect or bushy organisms, present just above the substrate, such as gorgonians, octocorals and black corals, which we refer to as the octocoral community. Typically, these layers have been studied separately and little is known about the joint distribution patterns of the two layers. With a few exceptions (Florida: Goldberg 1973; Wheaton and Jaap, 1989) little is known about the distribution patterns of the benthic and octocoral communities, information which could provide valuable clues on the processes governing the community structure of Caribbean reefs.

Ecological communities or assemblages are composed of individuals of different species that co-occur and potentially interact with one another as determined by past and continuing evolutionary processes (McPeck and Miller, 1996). In the coral-reef benthic community there are several species guilds that coexist over a wide range of environmental conditions. The most conspicuous guilds of benthic sessile organisms show particular morphological adaptations related to precise life-history strategies (Jackson, 1977). Many scleractinian coral species occur over a wide bathymetric range but with similar wave-energy conditions (e.g., Geister, 1977; Graus and Macintyre, 1989). On the other hand, gorgonian octocorals, due to their bushy physiognomy and position in the upper layer, have advantages such as a near absence of competition for space or colonial expansion such as occurs in the coral-reef community. However, they are more affected by drag forces associated with water movement (Jackson, 1977) and thus the octocoral community patterns more closely reflect the influence of wave energy (Kinzie 1973; Alcolado, 1981; Jordán, 1989; Yoshioka and Yoshioka, 1989; Sánchez et al., 1997). This study presents information collected at the same time on both benthic and octocoral communities as two semi-independent sources of community structure information.

The aim of this study was to survey the community/habitat structure and reef condition on Serrana, Roncador and Quitasueño Banks. The specific goals included obtaining quantitative information on: (1) the community of organisms that cover the reef substrate or benthic community; (2) the community of gorgonian octocorals that colonize space above the substrate or octocoral community (a part of the benthic community that is underrepresented using benthic cover methods); (3) the populations of keystone urchin species; (4) the topographical complexity or rugosity of the habitat; and (5) marine diseases affecting reef-building corals.

METHODS

The Northern Cays were intensively surveyed during April 24 to May 11, 2003 on board the M/V Spree and M/N Anglonamar II using enriched air SCUBA techniques

(EANx-Nitrox, O₂ up to 32%). A total of 118 stations were sampled (48 on Quitasueño, 48 on Serrana, and 22 on Roncador). We tried to survey as many habitats as possible, thoroughly covering the reef platform with the guidance of existing habitat maps (Diaz et al. 1996a, 2000). The surveyed habitats included shallow lagoonal sites (e.g., *Acropora-Diploria* or *Montastraea* spp patch reefs and algal mat habitats), leeward terrace sites (e.g., *Montastraea* spp, scattered corals or mixed-coral habitats), and fore-reef terrace sites (e.g., gorgonian octocorals and scattered corals habitat) (see details in results section). The fore-reef terrace, however, was surveyed on Quitasueño Bank. Bad weather prevented access to the habitats on Serrana and Roncador.

The abundance of the organisms covering the reef substrate was estimated as percent cover using the planar point-intercept method (PPI) (Dodge et al., 1982). This method is a modification of the point-intercept method of Loya (1978) in which the points are surveyed within a grid instead of along a line. It has the advantages of both plot and plotless methods as well as typically producing less inter-observer variation than occurs with traditional quadrant methods. Sampling stations consisted of 10 randomly chosen one-square-meter plots out of 50 potential positions along both sides of a 25 m- linear transect. At each position we surveyed the benthic species, genera (for some common algae), functional groups (for particular algae types and sponges), and types of inert substrate on a grid of 64 points. We tried to record 640 points per station, with 500 points being considered the minimum number required to obtain a representative survey of the station. Due to diving safety limits, the number of points varied slightly among stations with a mean of 628 (sd=44, min>500) and no differences detected among the means for the three banks (ANOVA, $P=0.25$, $df=2$, 115). A total of 74,127 points were surveyed at the 118 stations which was equivalent to 7412.7 linear meters of transect with points every 10 cm concentrated within 1158 square meters of grid using 64 points per square meter. Environmental variables recorded at each station were depth and topographic complexity or bottom rugosity. Rugosity, which is an indicator of wave-motion energy and the chronic disturbance effect of waves (Aronson and Precht, 1995), was estimated from the ratio of linear length of a chain that was laid out in a straight line along the bottom following all the vertical relief to its length when stretched out (10 m; e.g., Sánchez et al., 1997).

The transect line was established by a team of three divers surveying fish populations (Dalgreen et al., in prep.) that preceded the benthic team at each station. Each benthic survey was conducted by one of two teams of four observers that alternated dives. Within each team, two divers estimated substrate cover and the other two performed the remaining tasks. One surveyed gorgonian octocorals, urchins, and, if possible, substrate cover. The fourth diver measured bottom rugosity, looked for rare species to estimate more completely coral species diversity (alpha diversity) and examined diseased coral colonies visually identifying the coral species, the disease and estimating the percentage of affected tissue. Gorgonian octocoral density per species was estimated using the same 10 square-meter plots in which all colonies were counted and identified to the species or genus level (e.g., Sanchez, 1999). We counted and identified 4,828 colonies of octocorals at the 118 stations. Sea urchin densities (1,710 counted at the 118 stations), particularly of *Diadema antillarum* and *Echinometra viridis*, were estimated by counting the number

of urchins within 1 m along both sides of the 25 m-long transect (50 m²). All divers were fully trained previously for underwater identifications and data collection.

The species distribution patterns and community structure were analyzed using a variety of multivariable methods. Classification methods identify the similarity of cases (e.g., stations) according to their variable composition (e.g., species). Ordination methods allow the variation from several variables to be concentrated or expressed in a few composite, variance-rich variables to enable the detection of whole-community patterns. Classification and ordination methods can be combined to identify both structure and gradient patterns in the community (Flury & Riedwyl, 1988). Initially the database was organized into species-per-station matrices. For both substrate cover and gorgonian density, stations were classified by normal (Q-mode) cluster analysis using species cover, same as substrate cover, or density data ($\log_{10} [X+1]$ transformed), the Bray-Curtis dissimilarity index, and the Unweighted Pair Group Method (UPGMA) for building dendrograms (Field et al., 1982). Ordination analyses with the same data were obtained by a multivariate eigen-vector procedure, Detrended Correspondence Analysis (DCA) (Ter Brak 1986), which identifies gradients among stations and/or environmental variables. Potential environmental interpretations of the DCA axis values were found through correlation with depth and rugosity (e.g., Sánchez et al., 1997).

Previously, this suite of methods has been applied successfully to similar benthic assessments within the studied Archipelago (Friedlander et al., in press, in prep.). To further understand the relationship between groups or clusters of stations and community variables (e.g., coral cover, octocoral density, urchin density, frequency of coral diseases, etc.) or environmental variables (depth and rugosity), the magnitudes and mean location of these variables were superimposed on DCA 1 vs DCA 2 station ordination plots. Finally, the characteristic species of each successively nested cluster within a dendrogram were determined by recalculating substrate cover or density for each minimal cluster and then accumulating their abundance and successively marking those minimal clusters which contained at least 70% of the species' total abundance (R-mode). Species were then reordered and grouped according to membership within a given cluster or nest of clusters (Kaandorp, 1986; e.g., Sánchez et al., 1998).

RESULTS

Quitasueño Bank

A total of 73 benthic categories among species, genera, and functional groups of sessile organisms were recorded in Quitasueño Bank. There were a total of 46 species of milleporids and scleractinian corals observed qualitatively, 12-to-30 (min-max) coral species recorded quantitatively per station, and a coral cover ranging from 18-to-50%. Overall, analysis of the major functional groups showed that hard corals (Scleractinia and Milleporidae) were the most abundant organisms (18-50% cover), followed by fleshy macroalgae (4-39%), calcareous macroalgae (4-25%), encrusting algae (0.8-10%), and octocoral bases (0-10%), with lesser amounts of filamentous algae and invertebrates

being recorded (Fig. 3). The classification and cluster analyses showed a division of the 48 stations in two minimal groups with less than 40% dissimilarity (I and II), and with two and four major sub-clusters respectively (Figs. 4-5). Station 22 did not cluster with any other station. This station was situated in a typical rubble and algae (*Avrainvillea* spp.) patch in the leeward margin (e.g., Fig. 6 C-D). The most important result from this cluster analysis is that the classification of the stations revealed significant spatial structure on Quitasueño where apparently homogeneous habitats (e.g., habitat map: Fig. 5) had different sub-clusters that correspond to the reef windward-leeward edges (Fig. 5A: clusters D and C). Similarly, some lagoonal-leeward habitats had a spatial differentiation depending on whether they were north or south with respect to the lagoonal basin (Fig. 5A: clusters A and B respectively). Therefore, a characterization of the benthic communities based on the habitat mapping, as observed only with aerial photographs (Diaz et al., 1996, 2000), is not entirely a realistic view of the quantitative benthic community structure. The latter, nevertheless, is not completely disparate with respect to the major habitats (e.g., cluster F: Fig. 5A); these are hypotheses of community structure and for zoning and management purposes the results from the classification analysis and consequent ordination and inverse analyses should be taken in account (see discussion).

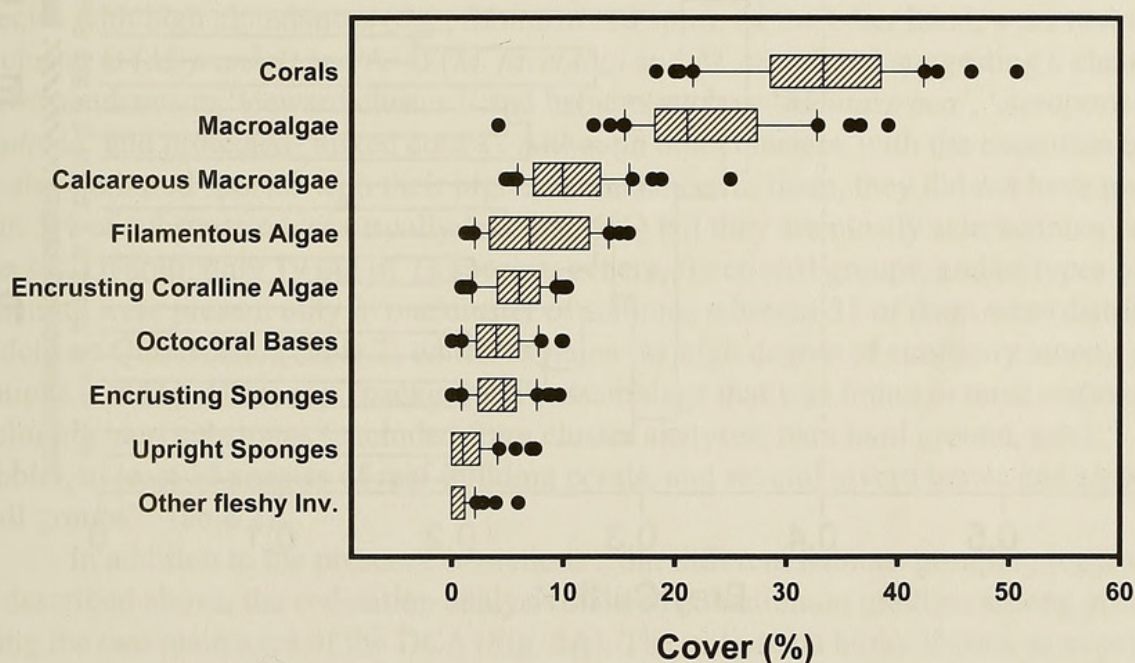


Figure 3. Box plots from the data distribution per station of the major functional benthic groups in the benthic community. The median line is inside the 25th and 75th percentiles with external error bars at the 10th and 90th percentiles. Dots show stations outside the error bars. Quitasueño Bank.

Of the two main station clusters, cluster I is made up of leeward reef stations including sites in the lagoon and on the leeward margin that always had a protected position with respect to the reef crest (Fig. 5: clusters A and B; Fig. 4). As presented in Table 1 and Figures 4-5, sub-cluster A from the 'protected cluster I' is composed of shallow and intermediate depth stations in the lagoon, and sub-cluster B consists of some intermediate depth leeward reefs.

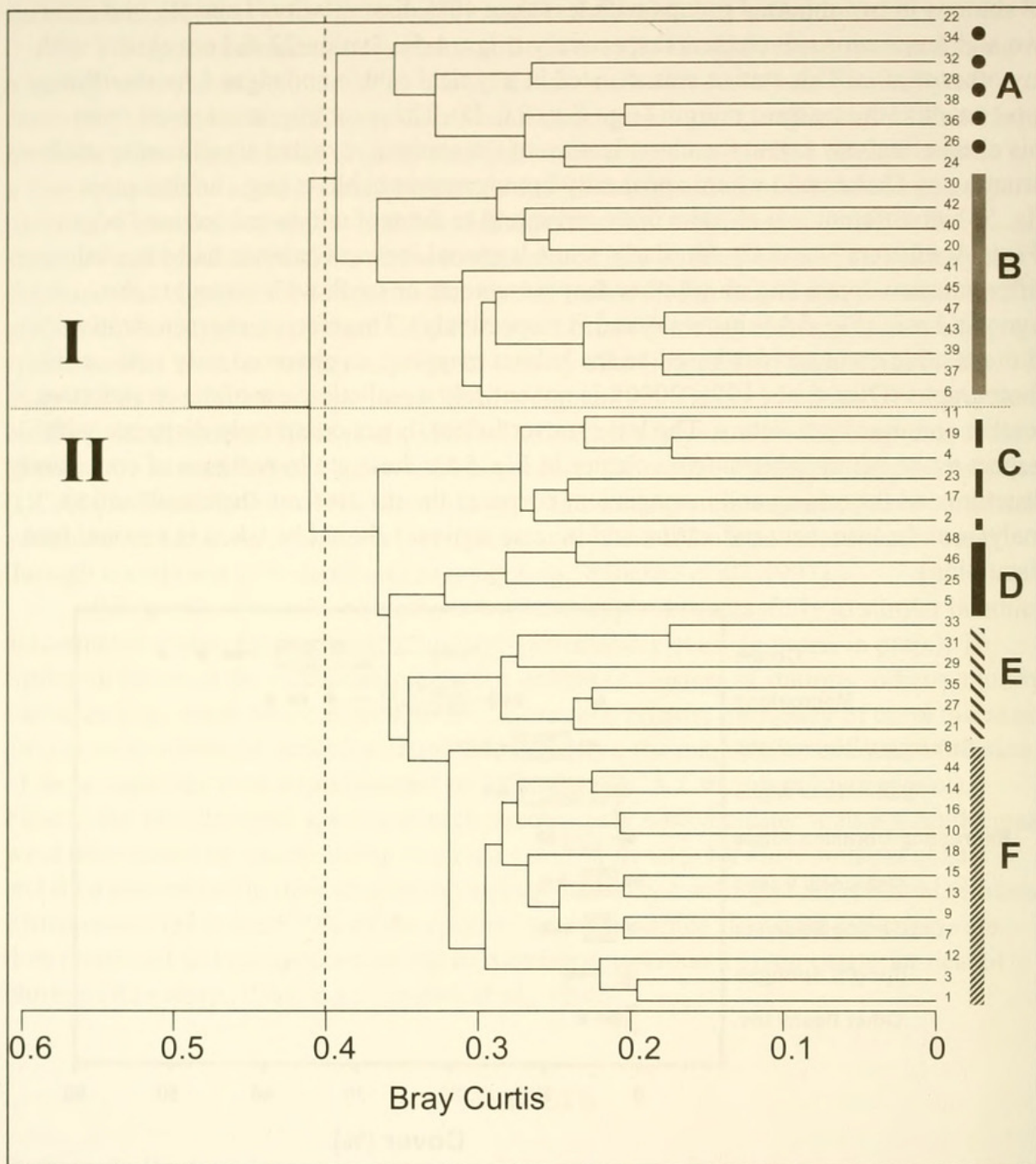


Figure 4. Dissimilarity (Bray-Curtis) dendrogram of the 48 benthic stations on Quitasueño Bank. The dashed line shows the 40% dissimilarity division among groups.

Both sub-clusters A and B had stations placed indiscriminately in three different habitats, '*Acropora - Diploria*', '*Montastraea*', and mixed corals. Cluster II is composed of a mixture of fore-reef and leeward stations that are either windward or well leeward at a greater distance from reef crest compared to cluster I stations. The 'terraces cluster-II' had sub-clusters of stations exclusively from the fore reef and leeward terraces (Fig. 5A [cluster E]; Fig. 4; Fig. 7 A-B) and two sub-clusters (C and D) with stations located

at both north and south ends of the barrier-terrace system (Fig. 5A). Sub-clusters C and F had stations at 'mixed coral' and 'encrusting corals and hard bottom' habitats whereas sub-clusters D and E were on 'mixed coral habitats' (Fig. 5A) which revealed a great deal of sub-habitat divisions in the 'mixed corals' habitats according to the windward, leeward or windward-leeward positioning.

Table 2 presents the community structure according to the cluster analysis discussed above. This analysis presents the species that had their highest peak abundances chosen arbitrarily here as >70 % of the species abundance after totaling all the points of a given species as 100% and then calculating the percentage of each cluster at any given cluster or nest of clusters from Fig. 4. Table 2 represents substrate cover data (totaled by cluster) to visualize the most abundant benthic reef dwellers. Species sharing boxes of peak abundances are expected to group somewhat in an R-mode inverse cluster analysis. For instance, cluster A only had two taxa that had their 70% abundance peak: the algae *Penicillus* spp. and *Turbinaria* spp. (Table 2). *Turbinaria* spp. had high substrate cover (>10%) and was indeed a dominant species in the north lagoonal reefs. Overall, algae with higher abundances (>5% of substrate cover), such as *Dictyota* spp., *Sargassum* spp., filamentous algae, and *Lobophora variegata*, did not have their high distribution peaks in a particular cluster or nest of clusters; they were distributed in most of the groups. Coral species with high abundances (e.g., *Montastraea* spp.), on the other hand, were restricted to cluster B (*M. franksi*) and A+B (*M. faveolata* and *M. annularis*) suggesting a clear correspondence to 'leeward cluster I' and habitats such as 'Montastraea', 'Acropora-Diploria' and protected 'mixed corals'. Although other clusters, with the exception of D, also harbored species with their highest abundances in them, they did not have more than 5% of substrate cover (usually less than 1%) but they are mostly scleractinian coral species. Overall, only 19 out of 73 species, genera, functional groups, and/or types of substrate were present only in one cluster of stations, whereas 31 of them were distributed widely on Quitasueño (Table 2) which explains the high degree of similarity among all stations (~50%). There is a "background" assemblage that was found in most stations including inert substrates (excluded from cluster analyses: bare hard ground, sand, rubble), at least 15 species of reef-building corals, and several invertebrates and algae ("all groups": Table 2).

In addition to the presence of stations from different habitats grouping together as described above, the ordination analysis showed a continuum gradient among groups using the two main axes of the DCA (Fig. 8A). The ordination biplot shows, as expected, maximum separation between fore reef (sub-cluster F) and lagoonal reefs (sub-cluster A) with narrow distances between leeward terrace stations and other lagoonal stations in the middle showing overlap with respect to each of the DCA axes (Fig. 8A). The DCA biplot was used to discern ordination and correspondence patterns. Coral cover and alpha diversity appeared to be uniformly distributed among all clusters (Table 1). Lowest rugosity values appeared to be present in groups C and F from the fore- and windward-leeward-reef terraces (Table 1). The urchin *Diadema antillarum* (0-1 individuals m⁻²) was more abundant on lagoonal and leeward stations (B and E groups: Table 1). *Echinometra viridis* (0-10 individuals m⁻²) was very abundant on the leeward terrace on stations from cluster E (Table 1). Urchins were nearly absent on fore-reef terrace stations. The cover

of sessile invertebrates also had a certain correspondence among stations. Upright and encrusting sponges, octocoral bases and encrusting species such as *Erythropodium caribaeorum* had their higher abundances in the fore-reef and leeward terraces (Table 1). Other fleshy invertebrates, such as tunicates, zoanthids, corallimorpharians, and anemones, were more abundant in leeward reefs (e.g., cluster B: Table 1). Functional groups of algae were distributed haphazardly on the different groups of stations except for calcareous macroalgae which were more abundant on lagoonal stations (cluster I: Table 1).

The most frequent coral diseases and abnormalities encountered during the survey of the three banks were white plague, dark spots, and bleaching. On Quitasueño, white plague was found at over one-half of the survey sites and affected up to three species per site with up to 5% (tissue species⁻¹) of any one species being affected. White plague was much more abundant at two lagoonal stations (Table 1) which were less than 4% of the stations. Dark spots affected corals in a larger number of stations with up to four species per station being affected. Bleaching was also present in most stations but the percentage per species was overall low (Table 1). The highest abundance of these three coral diseases did not correspond at the same stations and no concomitant effects were noted. In each case the diseases affected between 4 and 10% of the tissue species⁻¹; otherwise infection rates were very low. Other diseases such as white and yellow band were also observed with even lower frequencies than white plague.

A total of 38 species or genera of gorgonian octocorals were identified with up to 16 species observed per station. Octocoral densities varied between 0.01 to 12 colonies m⁻². A major difference of the octocoral community was that the minimal clusters, harboring the largest dissimilarity among clusters, had >50% of dissimilarity showing a higher level of structure in terms of species characteristic of each cluster, which is higher than the near 40% observed in the benthic community (Fig. 9). Clusters A and B corresponded to shallow-to-mid-depth stations in the lagoonal basin and leeward margin indiscriminately on 'mixed corals', '*Acropora-Diploria*' and '*Montastraea*' habitats (Figs. 5B, 9). Cluster C was just two shallow fore-reef stations towards the north end of the barrier reef on 'encrusting corals on hard bottom' habitat (Figs. 5 B, 9). Cluster D had stations on two north and south spots at the leeward margin and a few in the south lagoonal basin spanning the same habitat types of clusters A and B but monopolizing most of the south lagoonal stations (Figs. 5B, 9). Clusters E and F had mostly fore-reef stations but cluster F also had a few located on the leeward terrace (Figs. 5B, 9). Station 22 was an outlier of the overall pattern. Table 3 shows the octocoral community structure according to the cluster analysis from Figure 9. As expected, more structuring, i.e. number of species showing a high degree of habitat specificity, of the octocoral community was found than in the benthic community. Cluster B can be characterized by the high abundance of *Plexaura homomalla*, a common gorgonian octocoral from shallow protected reefs (Table 3). Cluster D presented the high-peak abundances of rare and uncommon species such as *Muricea pinnata* and *Eunicea clavigera* (Table 3). Cluster F presented an almost select but inconspicuous, i.e. low density, mixed assemblage of over 10 species: *Eunicea* spp., *Muricea* spp., *Pterogorgia* spp. and *Plexaurella* spp. (Table 3). Clusters D and E presented a close similarity (Fig. 9) and shared the high-peak abundances of the most

dense species of the survey such as *Pseudopterogorgia bipinnata* and *Muriceopsis flavida*, as well as lesser amounts of *Gorgonia mariae* (Table 3). The topological relationships of the dendrogram of Figure 9 for clusters D,E,F,C, and B shared a number of both abundant and habitat generalist species such as the sea candelabra *E. mammosa* and *E. succinea* and the soft octocoral *Briareum asbestinum* (Table 3).

The ordination analysis showed three major groupings, one containing clusters C, D, E, and F (as they are related in the dendrogram from Figure 9 and shared a number of important species) and two corresponding to clusters A and B respectively (Fig. 8B). Except for a few fore-reef stations (cluster F) that had low rugosity (small circles), some leeward places with high octocoral species diversity and cluster A with low octocoral density values, no clear correspondence among the variables could be observed. Because the coral cover was so uniform in Quitasueño Bank as well as the overall rugosity (mean 0.39, sd=0.03), no correspondence was found with the ordination or clustering of the gorgonian community. The cover of encrusting coralline algae, a substrate on which many octocoral recruits settle, was fairly uniform across all stations and no particular correspondence to a particular cluster was detected.

The first DCA axes from the benthic and octocoral communities of Quitasueño, which predominately had information on the variation of the entire species assemblage (i.e., overall patterns or structuring forces as explained in the above analyses), were significantly correlated with both depth and rugosity. Whereas the two variables explained a very low proportion of the benthic variation (multiple $r^2=0.27$; $p<0.001$), depth and rugosity did explain a large proportion of octocoral community variability ($r^2=0.62$; $p<0.001$). Other variables, such as urchin density for both the whole benthic community and octocoral community and coralline algae (for octocoral community only), did not have any significant correlation with the first DCA axis.

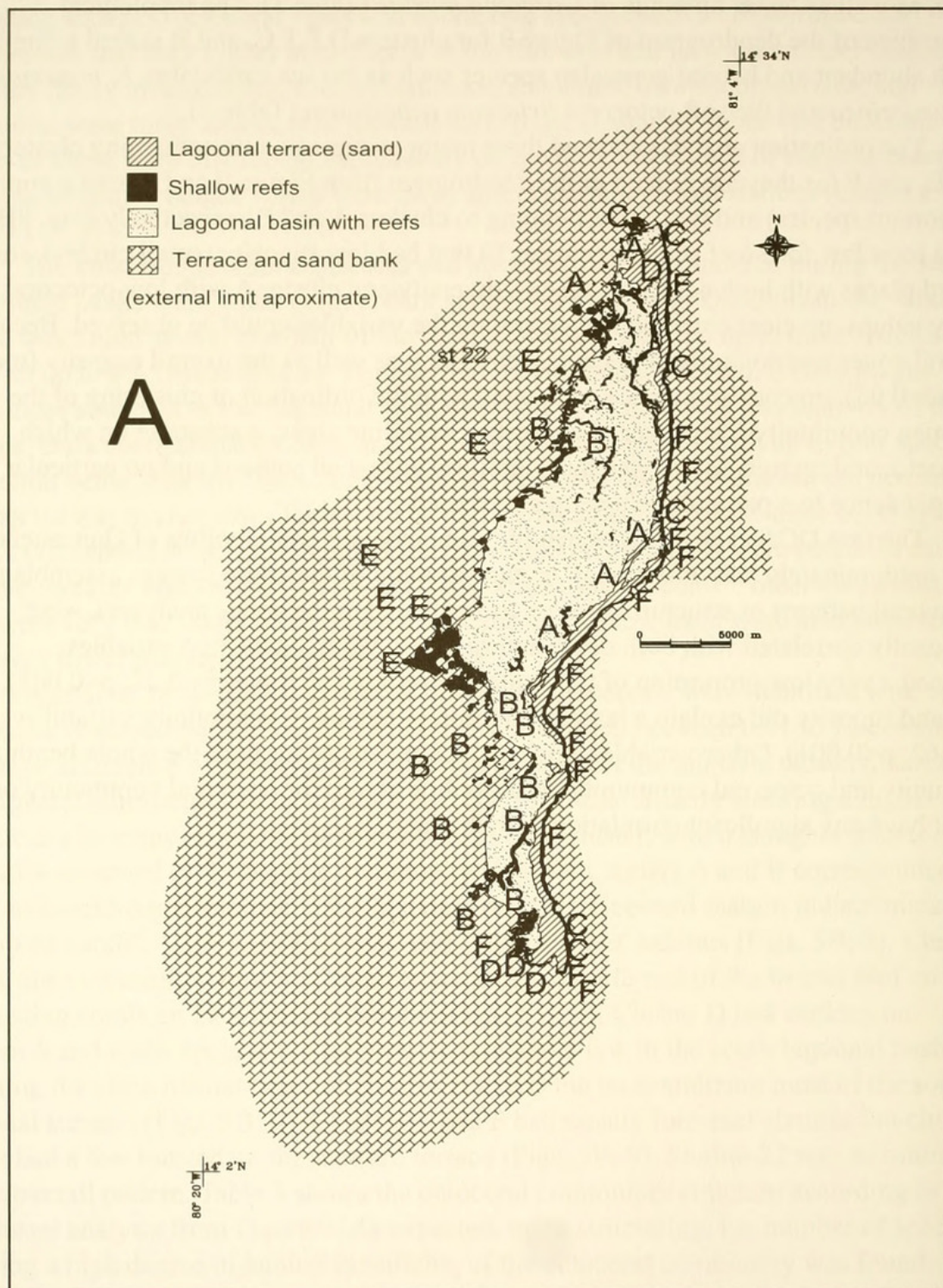


Figure 5 (A). Quitasueño Bank (habitats map: modified from Diaz et al., 2000) with locations of stations. Lagoonal basin presented deep habitats such as *Montastraea* spp. Shallow reefs in the lagoon basin where *Acropora palmata* – *Diploria* and rubble with coralline algae and *Turbinaria* spp. habitats. Terraces presented scattered corals and octocorals in the fore reef and mixed corals, *Montastraea* spp., or algae meadows in the Leeward terrace. Printed scale does not allow seeing more details. A. Distribution of stations according to cluster from Fig. 4. Location of stations approximate.

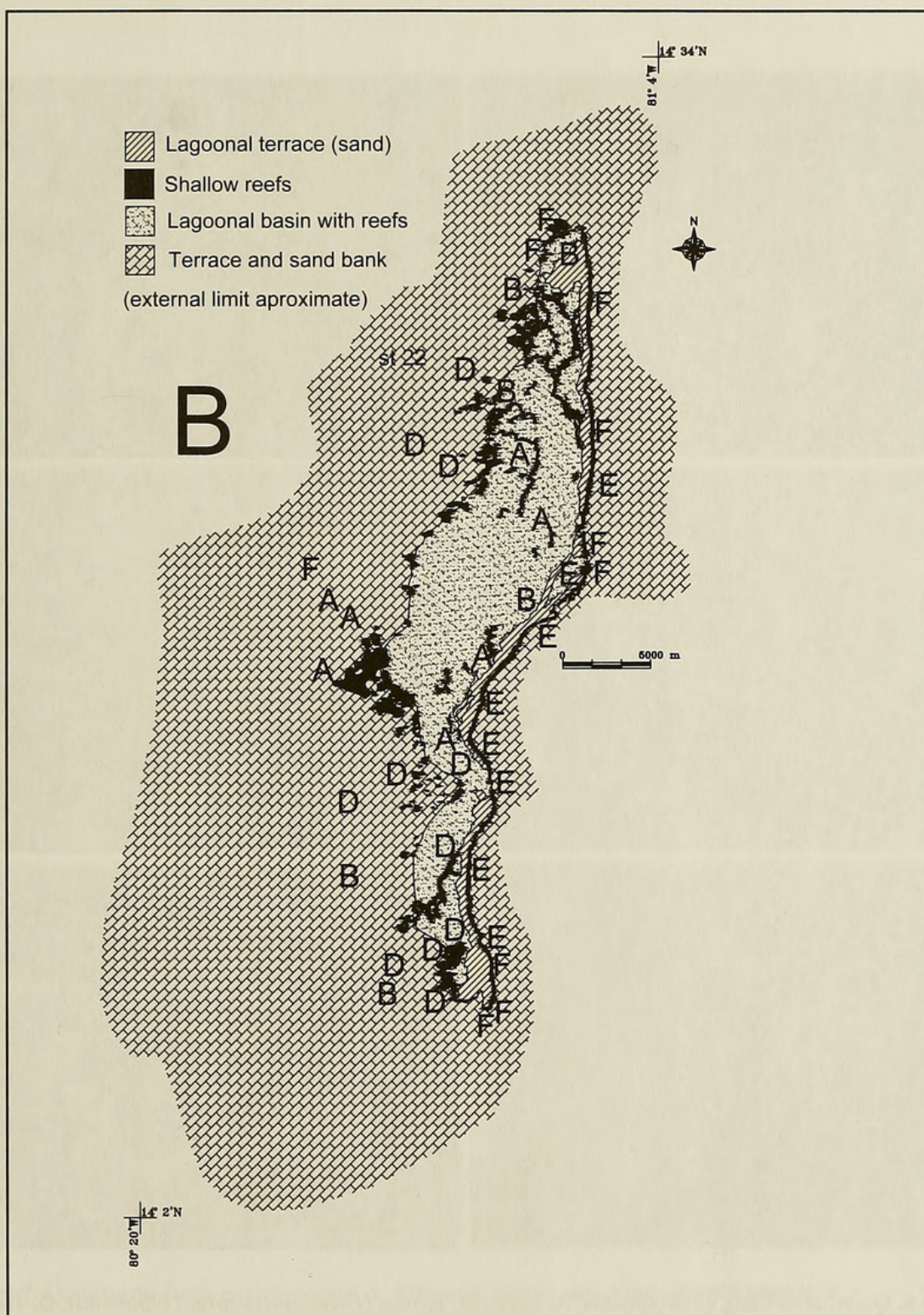


Figure 5 (B). Distribution of stations according to cluster from Fig. 9 (octocoral community).



Figure 6. Quitasueño Bank environments. A. Fore-reef terrace (*Pseudopterogorgia bipinnata*); B. *Turbinaria* spp. on shallow lagoonal reefs; C-D. Fleshy macroalgae, *Avrainvillea* habitat in the leeward margin; E. Urchin *Diadema antillarum* underneath *Montastraea faveolata*; F. *Acropora cervicornis* and *Eunicea fusca* (octocoral) in the leeward margin.

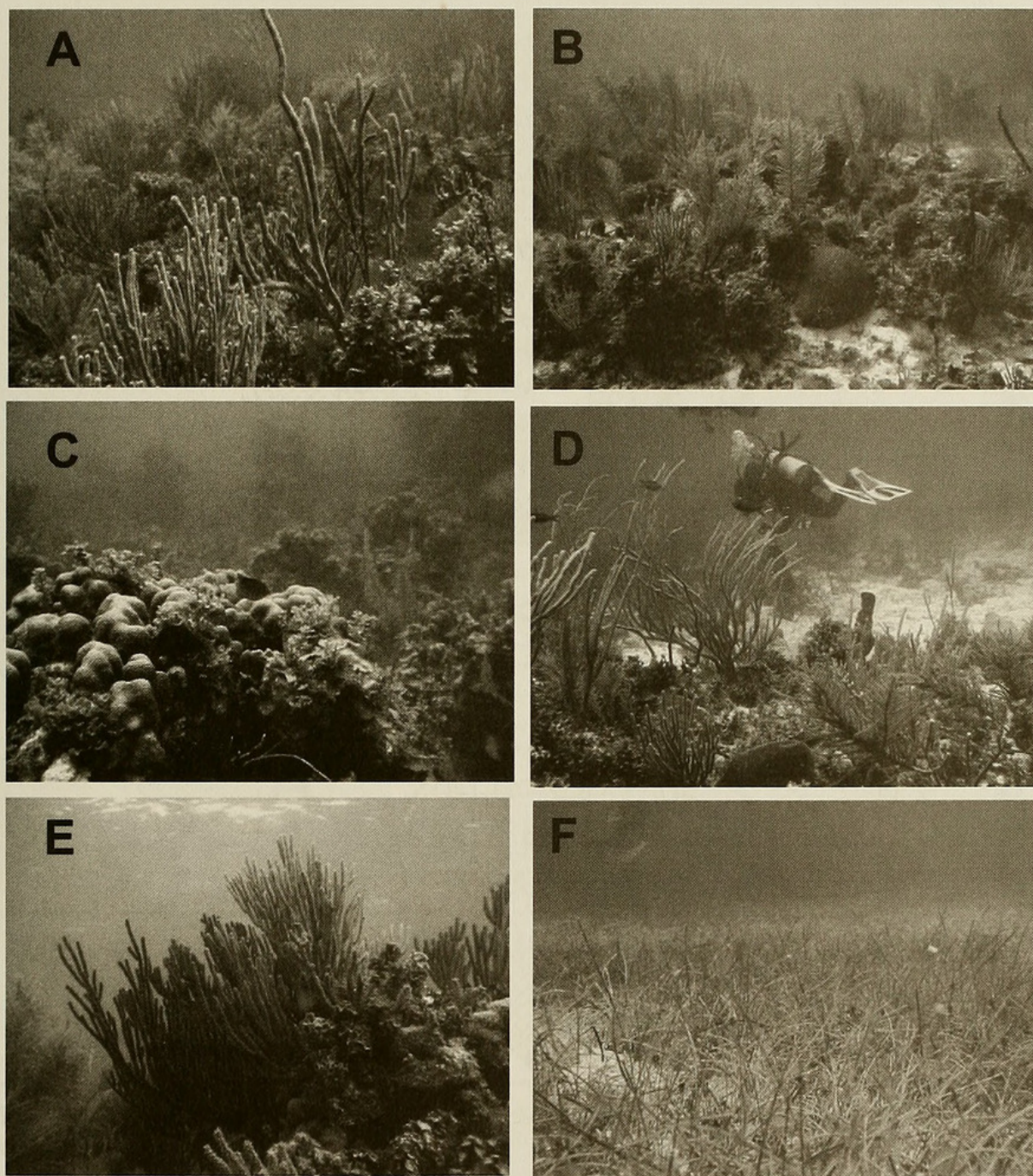


Figure 7. Quitasueño Bank environments. A. Plexaurid octocorals at the leeward terrace; B. *Pseudopterogorgia* spp. on the leeward margin; C. *Montastraea annularis* and fleshy macroalgae in the lagoon; D. Sand canal in the leeward terrace; E. *Plexaura homomalla* and *P. kukenthali* in a shallow patch reef; F. Sea grass in the lagoon basin (*Halodule* and *Syringodium*).

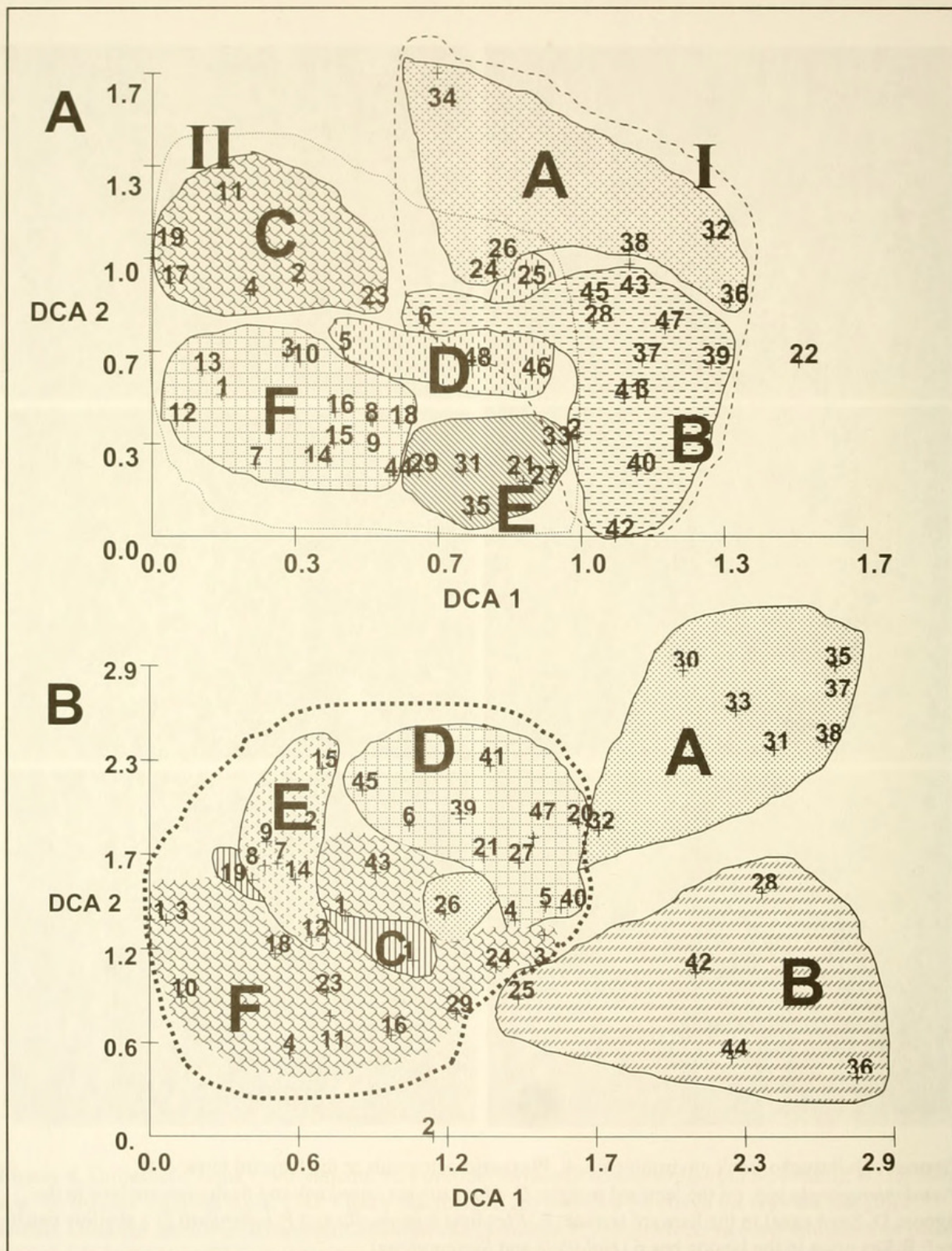


Figure 8. Quitasueño benthic DCA biplots and community structure according to the groups from the cluster analysis of Figures 4 (A. benthic community) and 9 (B. gorgonian community).

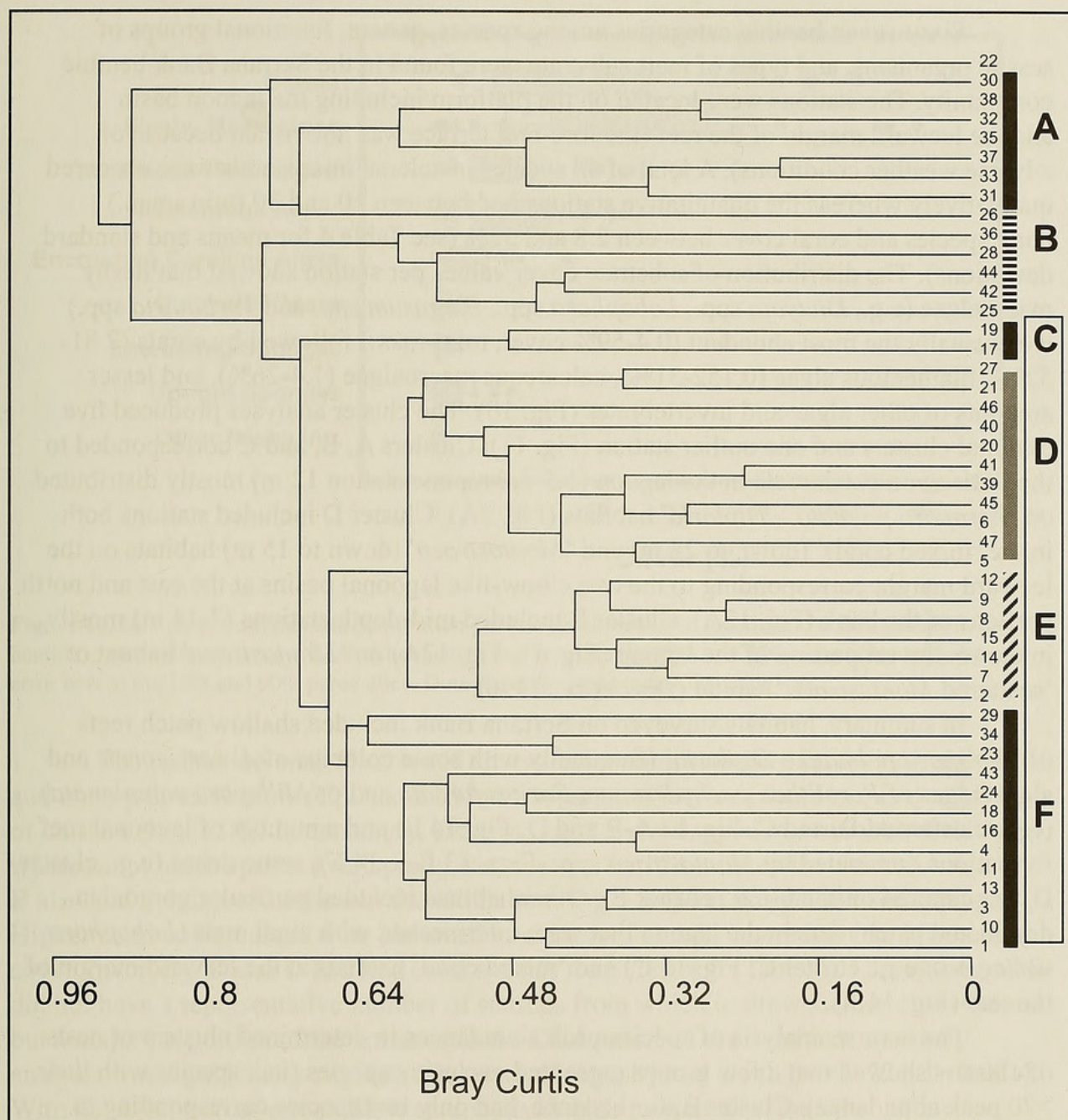


Figure 9. Dissimilarity (Bray-Curtis) dendrogram of the 47 stations Quitasueño Bank with presence of octocorals.

Serana Bank

Sixty-seven benthic categories among species, genera, functional groups of sessile organisms, and types of inert substrate were found in the Serrana Bank benthic community. The stations were located on the platform including the lagoon basin and the leeward margin of the reef (the fore-reef terrace was not visited because of adverse weather conditions). A total of 48 species of scleractinian corals were observed qualitatively whereas the quantitative stations had between 10 and 30 (min.-max.) coral species and coral cover between 2.8 and 52% (see Table 4 for means and standard deviations). The distribution of substrate cover values per station showed that fleshy macroalgae (e.g., *Dictyota* spp., *Lobophora* spp., *Sargasum* spp. and *Turbinaria* spp.) were usually the most abundant (0.4-59% cover, min.-max.) followed by corals (2.81-52%), filamentous algae (0.152-31%), calcareous macroalgae (1.4-26%), and lesser amounts of other algae and invertebrates (Fig. 10). The cluster analyses produced five minimal clusters and one outlier station (Fig. 11). Clusters A, B, and C corresponded to the stations on patch reefs in the lagoon (1.5-3.0 m, one station 12 m) mostly distributed on '*Acropora palmata* – *Diploria*' habitats (Fig. 3A). Cluster D included stations both in the 'mixed corals' (down to 24 m) and '*Montastraea*' (down to 15 m) habitats on the leeward margin corresponding to the two elbow-like lagoonal basins at the east and north portions of the bank (Fig. 12A). Cluster E included mid-depth stations (7-14 m) mostly in the southwest portion of the lagoon (Fig. 11, Fig. 12A) on '*Montastraea*' habitat or 'scattered *Montastraea*' habitat (Diaz et al., 1996).

In summary, habitats surveyed on Serrana Bank included shallow patch reefs of '*Acropora palmata* – *Diploria*' (frequently with some colonies of *A. cervicornis* and algal ridges of *Porolithon pachydermum*, *Porites furcata* and/or *Millepora complanata*) (e.g., clusters A, B, and C: Fig. 13 A-B and D; Fig. 14 E) and a number of lagoonal reef formations dominated by *Montastraea* spp. (Figs. 13 E-F, 14 F), some dense (e.g., cluster D) or scattered on sand (e.g., cluster E). Other habitats included particular gorgonian-dominated patch reefs in the lagoon that were intermeshed with algal mats (*Lobophora variegata*) (e.g., cluster C: Fig. 13 C) and 'mixed coral' habitats at the leeward margin of the reef (Fig. 14 A).

The inverse analysis of species peak abundances in determined clusters or nests of clusters showed that a few groups presented exclusive species (i.e., species with their >70 peak abundance). Cluster B, for instance, had only two species corresponding to uncommon scleractinian corals (*Agaricia fragilis* and *Mycetophyllia aliciae*: Table 5). Cluster C had peak abundances of two important reef-building corals, *Montastraea faveolata* (>10 % of substrate cover) and *Acropora cervicornis*, whereas Cluster D had 14 species including 10 reef-building corals including *A. palmata* and *Millepora complanata*, two fast-growing corals, and >6% cover values of cyanophyta algae (Table 5: Fig. 14 D). Most other benthic species were distributed within the combined clusters C and D or C-D-E (Table 5). Clusters C and D shared the highest abundance of two important habitat- and reef-building corals, *M. annularis* and *M. franksi* (Table 5). The most abundant species in all the groups were algae species such as *Halimeda* spp., *Lobophora variegata*, *Sargasum* spp., *Dictyota* spp., encrusting coralline algae, and filamentous algae (Table 5).

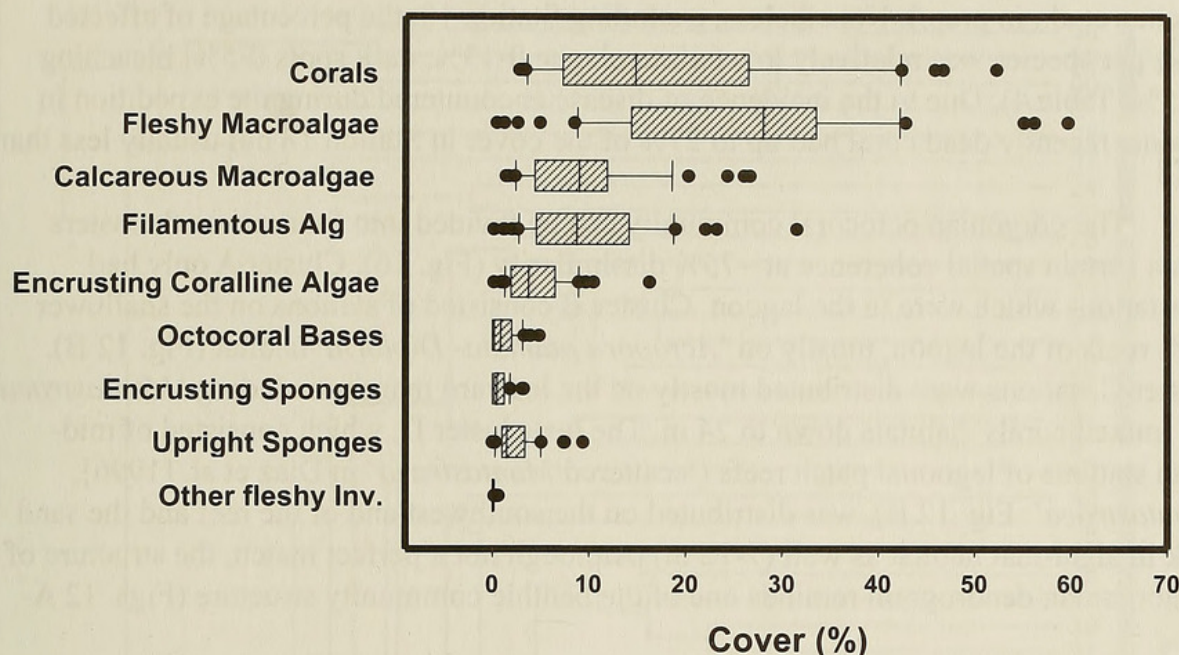


Figure 10. Box plots from the data distribution per station of the major functional benthic groups in the benthic community of Serrana Bank. The median line is inside the 25th and 75th percentiles with external error bars at the 10th and 90th percentiles. Dots show stations outside the error bars.

The ordination analysis showed an overlap among stations of clusters A and B and among three clusters (C, D, and E) but a separation between these two major groups of clusters (Fig. 15A). Interestingly, clusters D and E overlapped in a number of stations whereas not much spatial overlapping was noted (Fig. 12A). Likewise clusters A and B also had overlap of stations in the ordination (Fig. 15A) but no spatial overlapping. Higher coral cover values were observed in clusters C and D, whereas E had low coral cover. Inversely, C and D had less coral species than cluster E (Table 4). Clusters A and B did not have a representative number of stations from which to draw similar observations, but a major proportion of the variance in the DCA axis 1 of the benthic community analysis was significantly explained in terms of rugosity and depth ($r^2 = 0.724$, $P < 0.001$). With the exception of one shallow station, most urchins were distributed at a few stations from clusters C and E (Table 4). It is important to notice that urchin densities at the sampled environments of Serrana Bank were overall low (*D. antillarum* 0-0.76 individuals m^{-2} , *E. viridis* 0-0.56 ind. m^{-2}). In general, most invertebrate species also had their higher abundances on the deeper stations of cluster E where sponges and octocoral bases had very similar distributions (Table 4). Algae functional groups were also more abundant towards deeper clusters with their major abundances on the border between clusters D and E (Table 4).

Coral diseases were particularly noticeable on Serrana Bank. Minor white plague outbreak areas were observed throughout the Serrana Bank on lagoonal coral habitats deeper than 7 m where the disease was primarily observed. However, on Station 18 (14°

27° 53.24" N and 80° 14' 22.27" W; 12 m depth) mass coral mortality was observed in the northern portion of the bank on some shallow *Montastraea* patch reefs (see details in: Sanchez et al., in prep.). Nonetheless, excluding Station 18, the percentage of affected tissue per species was relatively low (white plague 0-13%; dark spots 0-5%; bleaching 0-2.5%: Table 4). Due to the incidence of disease encountered during the expedition in Serrana, recently dead coral had up to 27% of the cover in Station 18 but usually less than 4%.

The gorgonian octocoral community can be divided into four minimal clusters with a certain spatial coherence at ~75% dissimilarity (Fig. 16). Cluster A only had two stations which were in the lagoon. Cluster B consisted of stations on the shallower patch reefs of the lagoon, mostly on '*Acropora palmata*-*Diploria*' habitat (Fig. 12 B). Cluster C stations were distributed mostly on the leeward margin including '*Montastraea*' and 'mixed corals' habitats down to 24 m. The last cluster D, which consisted of mid-depth stations of lagoonal patch reefs ('scattered *Montastraea*' in Diaz et al. [1996]; '*Montastraea*': Fig. 12 B), was distributed on the southwest end of the reef and the sand bank in algal-mat habitat as well (7-12 m). Although not a perfect match, the structure of the gorgonian dendrogram reminds one of the benthic community structure (Figs. 12 A-B).

Octocoral community cluster A had the peak abundances of *Gorgonia mariae* and *Eunicea* sp. (*E. colombiana* n. sp.: Sánchez, submitted) which were absent in the rest of the stations (Table 6: please note that fore-reef terrace habitats were not sampled). The most abundant species on Serrana Bank had their peak abundances in cluster C, *Pseudopterogorgia bipinnata*, with densities of up to three colonies m⁻² (Table 6). Cluster C also had the peak abundances of *P. elisabethae*, a species of commercial importance elsewhere in the Caribbean, and *Briareum polyanthes*, an encrusting soft coral. Cluster D had peak abundances of 19 species with particular high densities of *Pseudoplexaura* spp. (Table 6), and with colonies reaching over 2 m in height (Fig. 13 C). This highly diverse cluster D corresponded to the 'scattered *Montastraea*' habitat from Diaz et al. (1996) which is a combination of rubble, sand, hard ground and scattered corals that seemed the most suitable habitat for complex octocoral assemblages in the leeward and lagoonal habitats of Serrana Bank.

The ordination analysis for the octocoral community exhibited an interesting continuum gradient along the DCA axis 1 (clusters C, D, and B in that order: Fig. 15B). The gradient seems to be correlated to depth with the highest density of species occurring at the deeper sites (14-24 m). Depth explained a large proportion of the variation in the DCA axis 1 (multiple $r^2 = 0.563$; $P < 0.001$). A correspondence of high octocoral density with high coral cover was noticed (Table 4) which also was significant in a bivariate scheme ($r^2 = 0.357$, $P < 0.001$). Cluster A was largely separated from B-C-D (composed of only two stations, not shown in Fig. 15B). Stations 33 and 35 comprised outliers.

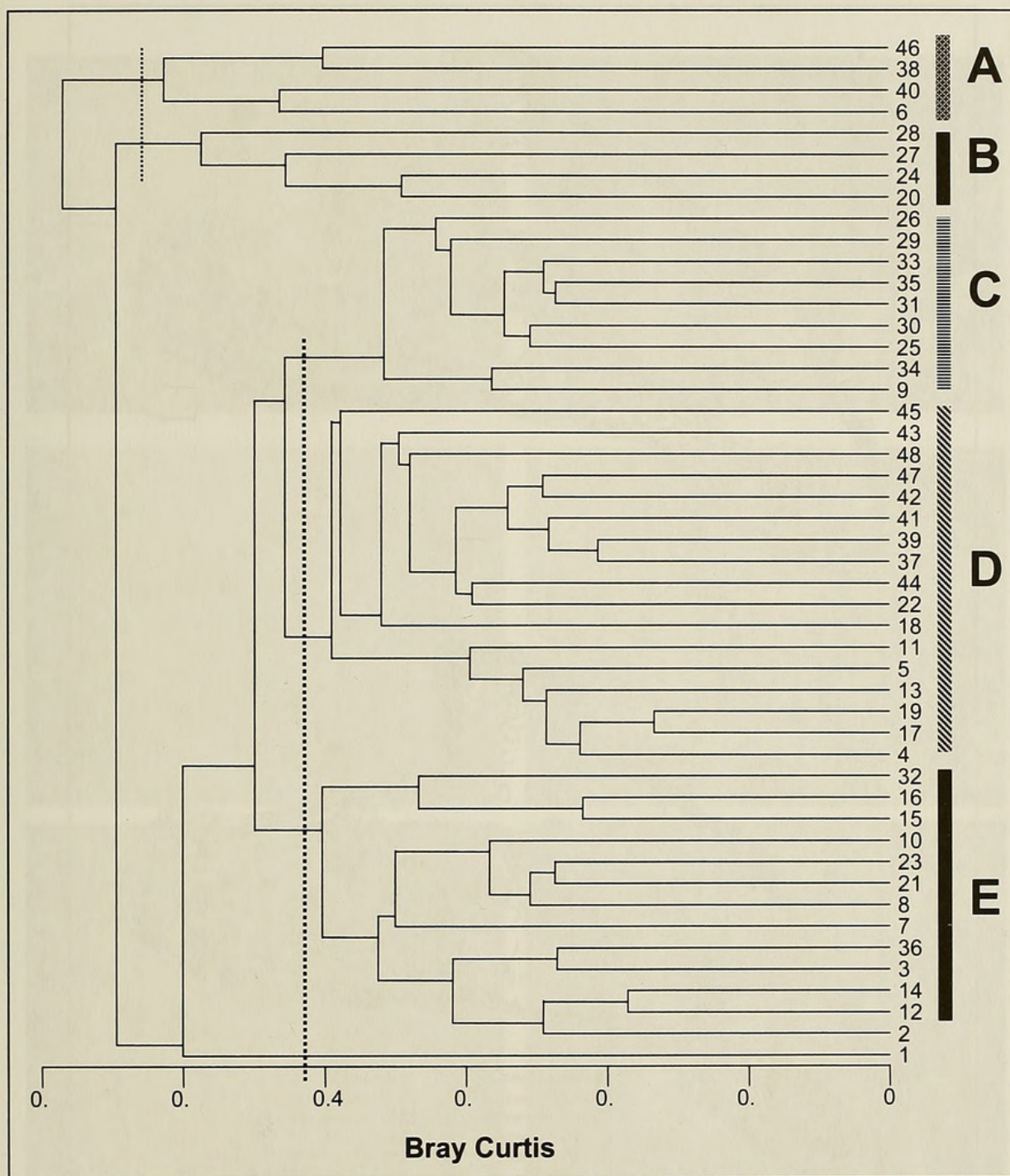


Figure 11. Dissimilarity (Bray-Curtis) dendrogram of the 48 from the benthic stations on Serrana Bank. The dashed line shows dissimilarity division among chosen groups.

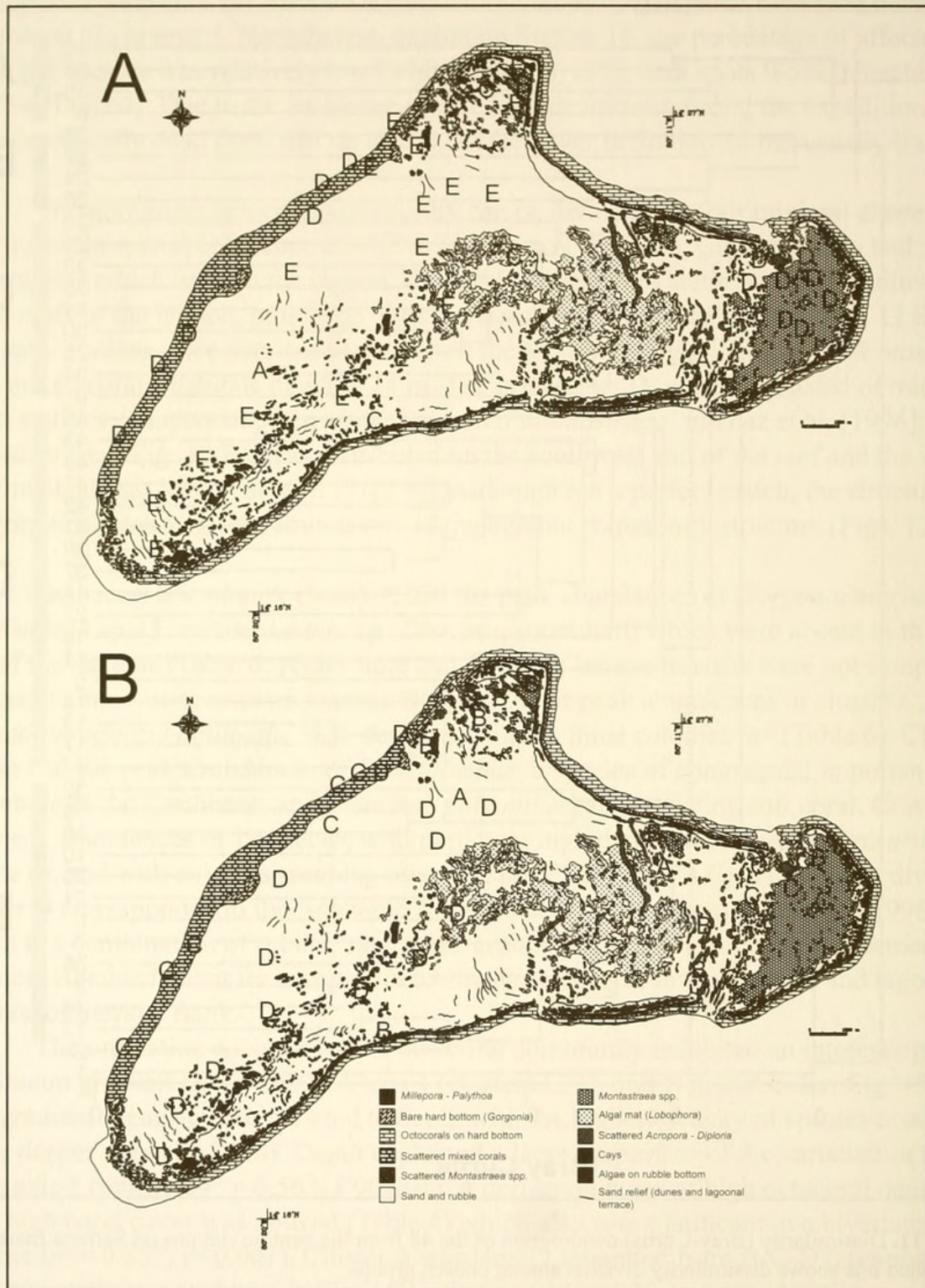


Figure 12. Serrana Bank habitats (modified from Diaz et al., 1996) with locations of stations (approximate). A. Distribution of stations according to cluster from Fig. 11. B. Distribution of stations according to cluster from Fig. 15.

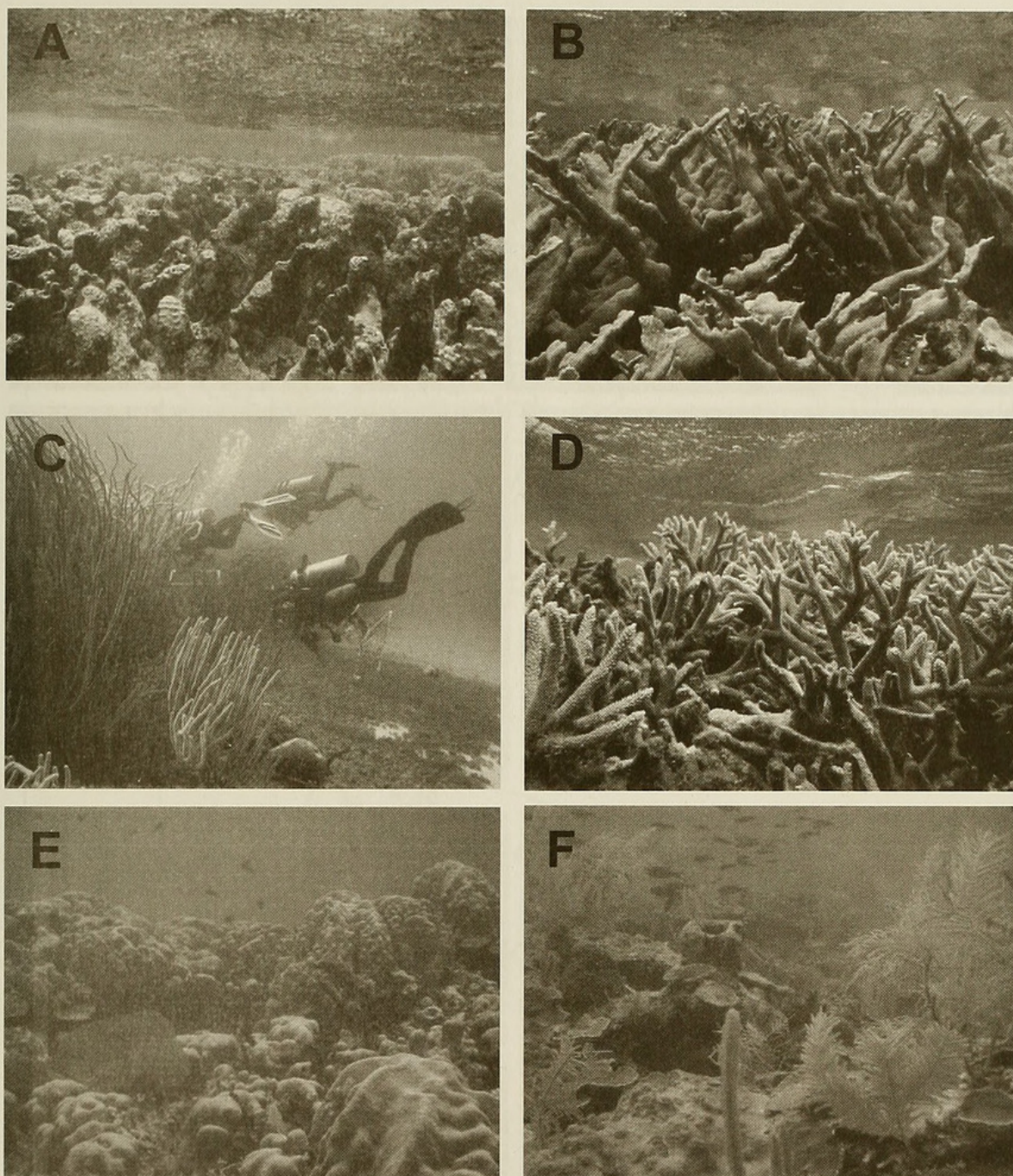


Figure 13. Serrana Bank environments. A. *Porolithon pachydermum* ridge on dead *Acropora palmata*; B. *A. palmata*; C. *Pseudoplexaura* spp. in the lagoon; D. *A. cervicornis*, E. *Montastraea* spp. patch reefs; F. deep leeward margin (*Pseudopterogorgia bipinnata*).

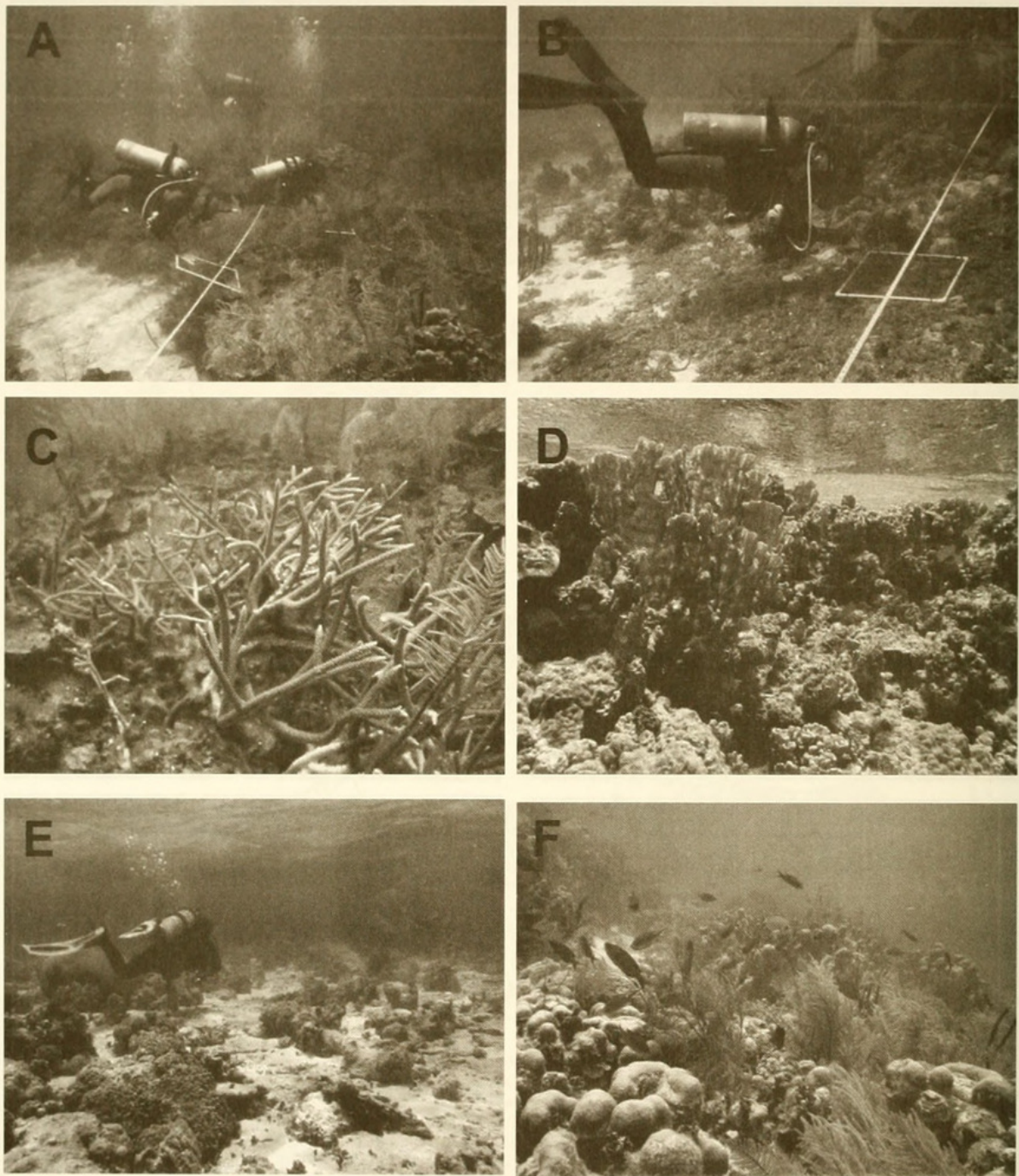


Figure 14. Serrana Bank environments. A. Leeward terrace; B. lagoon basin with *Lobophora variegata* mat; C. *Acropora cervicornis* on the leeward terrace; D. *Millepora complanata* on top of *A. palmata* reef; E. shallow lagoonal patch reefs; F. *Montastraea annularis* in the lagoon and gorgonians (*Pseudopterogorgia bipinnata*).

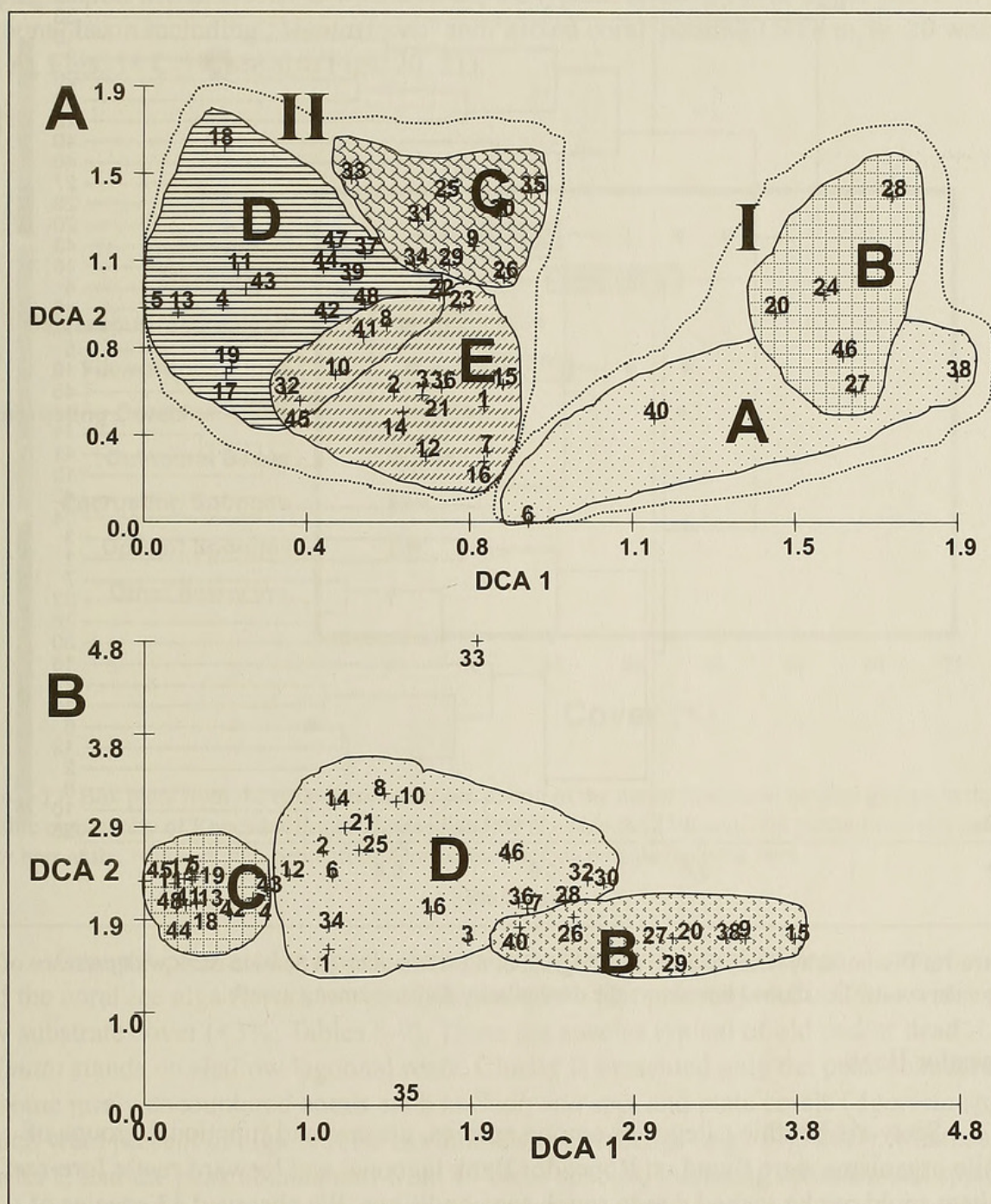


Figure 15. Serrana Bank DCA biplots and community structure according to the groups from the cluster analysis of Figures 11 (A. benthic community) and 16 (B. octocorals, cluster A not shown).

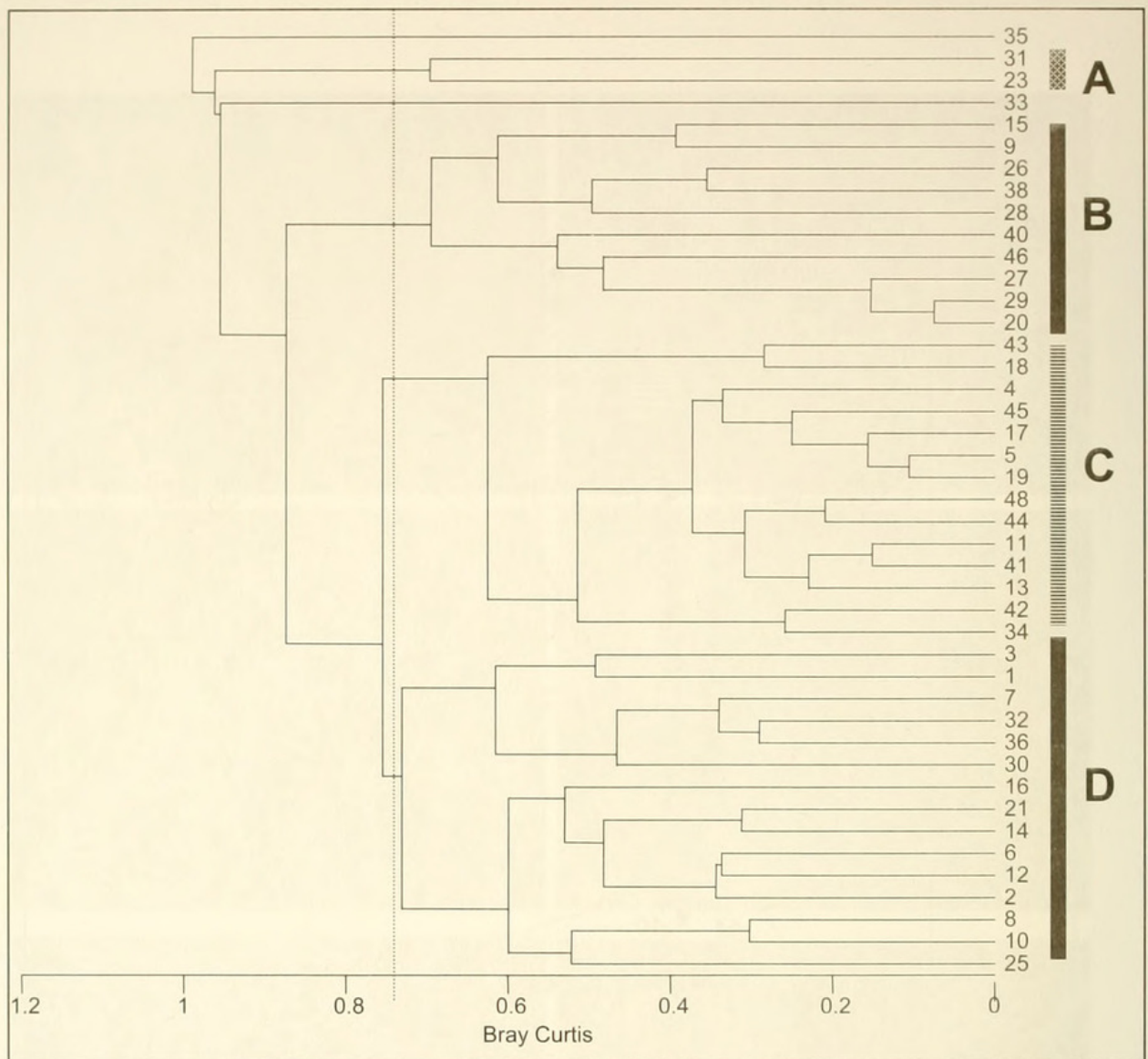


Figure 16. Dissimilarity (Bray-Curtis) dendrogram of the 47 stations on Serrana Bank with presence of gorgonian corals. The dashed line shows the dissimilarity division among groups.

Roncador Bank

Sixty-six benthic categories among species, genera, and functional groups of sessile organisms were found on Roncador Bank lagoonal and leeward reefs; fore-reef habitats could not be visited due to rough sea conditions. We observed 43 species of reef-building corals, 12-29 (min.-max.) species recorded per station, and coral cover from 3.5 to 41%. Overall, fleshy macroalgae were the most abundant sessile reef dweller on the sampled stations (10-59%) followed by hard corals (3.5-41%), filamentous algae (2.5-36%), calcareous macroalgae (1.4-18%), and lesser amounts of other sessile benthic organisms (Fig. 17: Table 7). The benthic community cluster analysis revealed three minimal groups with less than 40% dissimilarity (Fig. 18). Cluster A only had two stations corresponding to shallow (1.8-3 m) lagoonal reefs, probably on small not-mapped '*Acropora palmata*-*Diploria*' habitats intermingled with '*Montastraea*' (Fig.

19A). Cluster B was a clear group of stations on a deep leeward terrace corresponding to the 'mixed coral' habitat (22-28 m) (cluster B: Figs. 18-19A). Most of the stations were grouped within cluster C with mid-depths typical of the leeward upper platform or lagoonal basin including '*Montastraea*' and 'mixed coral' habitats (6-16 m, st. 20 with 1.2 m, Figs. 18 C-19, see also Figs. 20, 21).

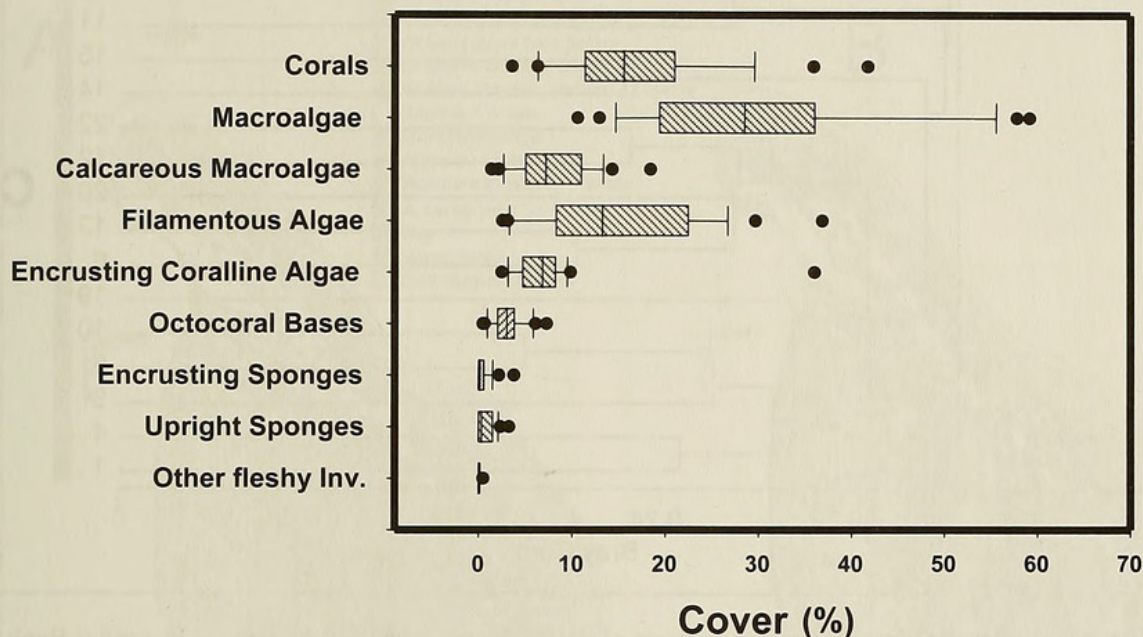


Figure 17. Box plots from the data distribution per station of the major functional benthic groups in the benthic community of Roncador Bank. The median line is inside the 25th and 75th percentiles with external error bars at the 10th and 90th percentiles. Dots show stations outside the error bars.

Group A presented the peak abundances of the hydrocoral *Millepora complanata* and the coralline alga *Porolithon pachydermun*, two fast growing reef builders with low substrate cover (<3%; Tables 8-9). These are species typical of old and/or dead *A. palmata* stands on shallow lagoonal reefs. Cluster B presented only the peak abundances of some rarely encountered corals such as *Scolymia* spp. and plate corals (*Agaricia* spp.), which were present in high relief areas and under overhangs (e.g., Fig. 20D), whereas cluster C had the peak abundances from 17 coral species, including *Montastraea* spp., *Diploria* spp., and many other sessile organisms typical of a complex and mixed-species zone (Tables 8-9; Figs. 20, 21). As observed in the other banks, the dominant organisms covering the substrate were algae such as *Halimeda* spp., filamentous and encrusting coralline algae (Table 7).

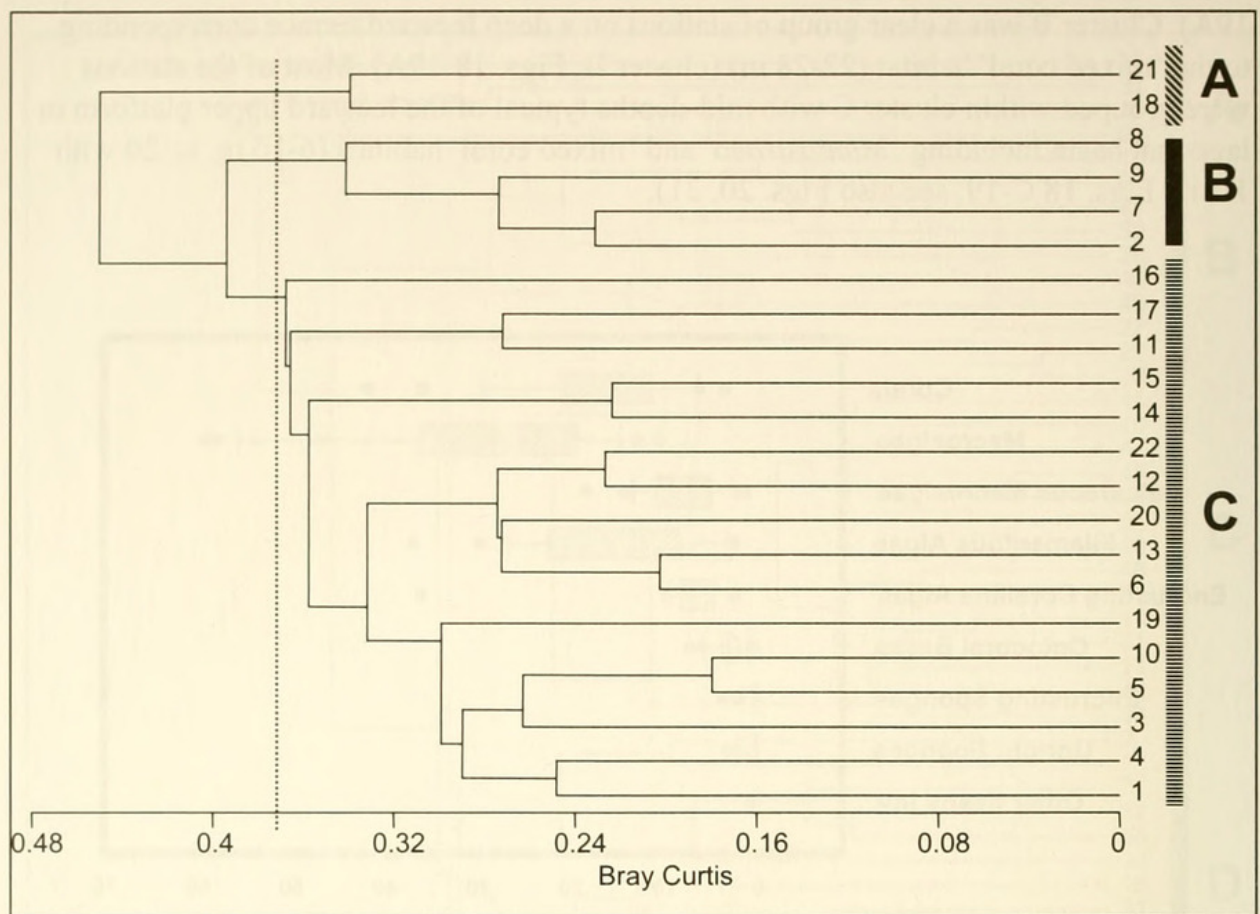


Figure 18. Dissimilarity (Bray-Curtis) dendrogram of the 22 from the benthic stations on Roncador Bank. The dashed line shows dissimilarity division among groups.

The studied habitats on Roncador Bank (please note that fore-reef habitats were not sampled) had two particularities: high bottom rugosity as well as the highest abundance of octocorals among the three banks (Figs. 20 and 21). The ordination analysis presented a fairly discrete distribution of the clusters, with clusters B and C very close to each other in the DCA axes 1 and 2 biplot (Fig. 22A), which is a similar result as the cluster analysis (Fig. 18). Coral cover appeared to correspond with high rugosity (Table 7) and was somewhat statistically correlated ($r^2=0.244$, $P<0.05$). Depth, on the other hand, explained a significant proportion of the DCA axis 1 variation ($r^2 = 0.41$, $P<0.01$). Urchins had low abundances in Roncador Bank with the presence of only a few individuals in lagoonal habitats (*D. antillarum* 0-0.12 ind. m⁻²; *E. viridis* 0-0.56 ind. m⁻²; Table 7). Sponges were particularly abundant on the deeper stations of cluster B and octocoral bases on cluster C (Table 7). Higher abundances of fleshy, filamentous, and calcareous algae were encountered on the lagoonal stations of cluster C which also presented overall low values of coralline algae (Table 7). Coral diseases were also present on Roncador Bank in relatively low proportions in the affected species (e.g., white plague 0-5% average affected tissue per species; dark spots 0-10%; bleaching 0-5%), which were usually less than four affected species per station (Table 7).

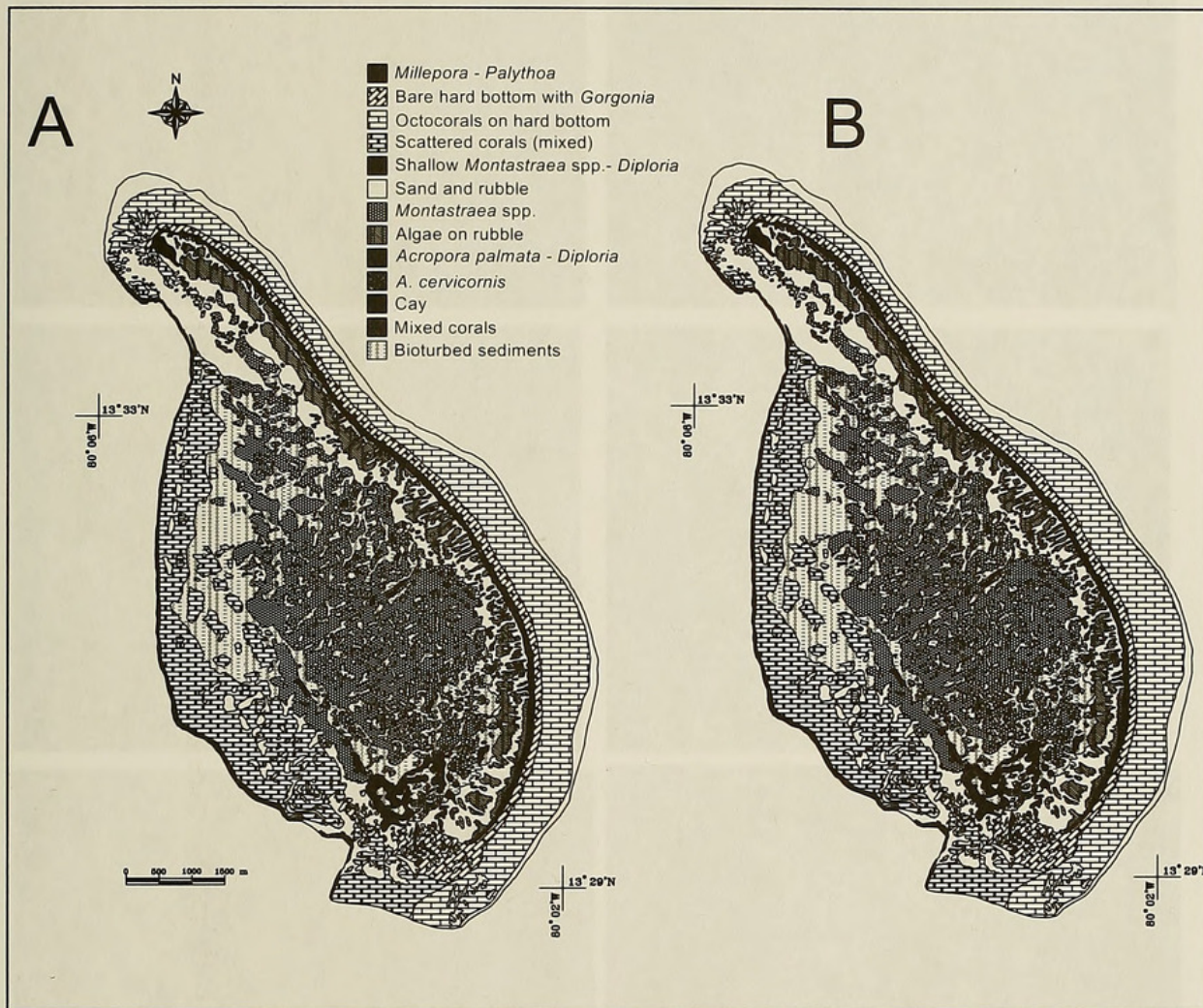


Figure 19. Roncador Bank habitats map (modified from Diaz et al., 1996) with locations of stations. A. Distribution of stations according to cluster from Fig. 18; B. Distribution of stations according to cluster from Fig. 23.

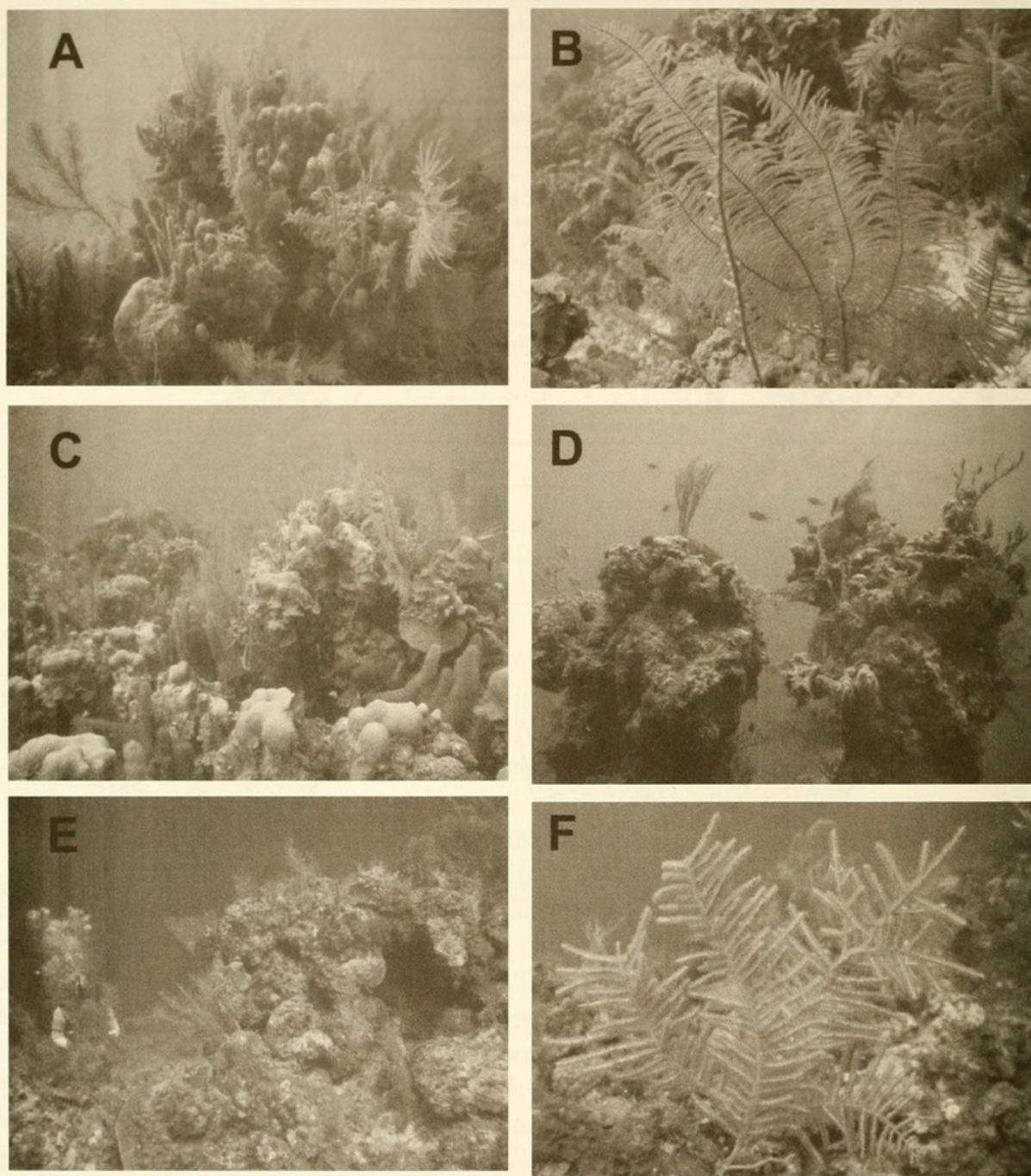


Figure 20. Roncador Bank environments. A. High relief lagoonal patch-reef; B. Leeward margin (*Pseudopterogorgia bipinnata*); C. Lagoonal reef (*Briareum asbestinum*); D. Old pinnacle-like coral head in the lagoon; E. Leeward drop-off; F. *P. elisabethae* in the leeward margin.

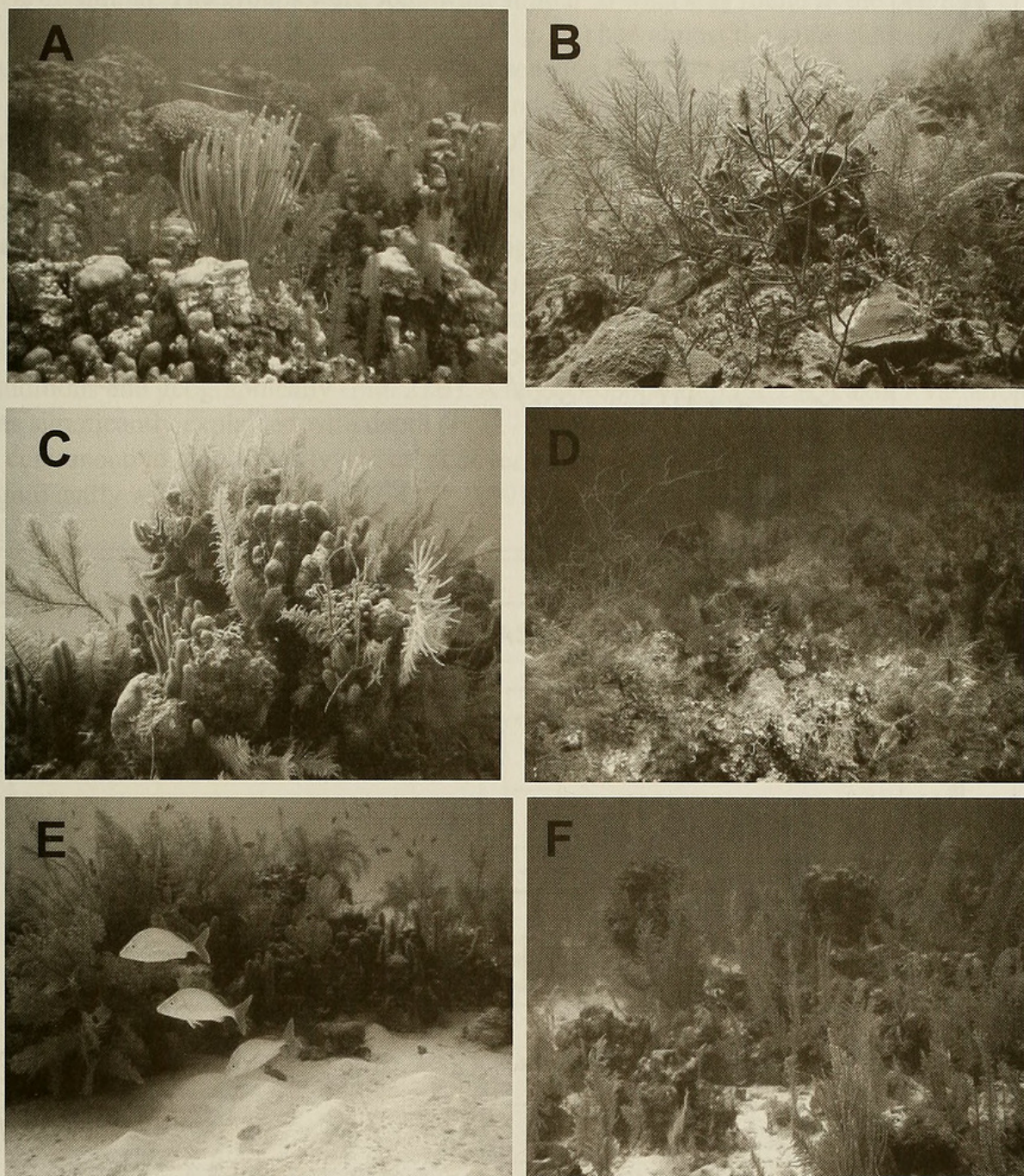


Figure 21. Roncador Bank environments. A. Lagoonal patch-reef; B. Leeward terrace; C. High relief lagoonal reef; D. Leeward terrace; E. Patch reef on sand channel; F. Gorgonians in the leeward margin (*Pseudopterogorgia* spp.).

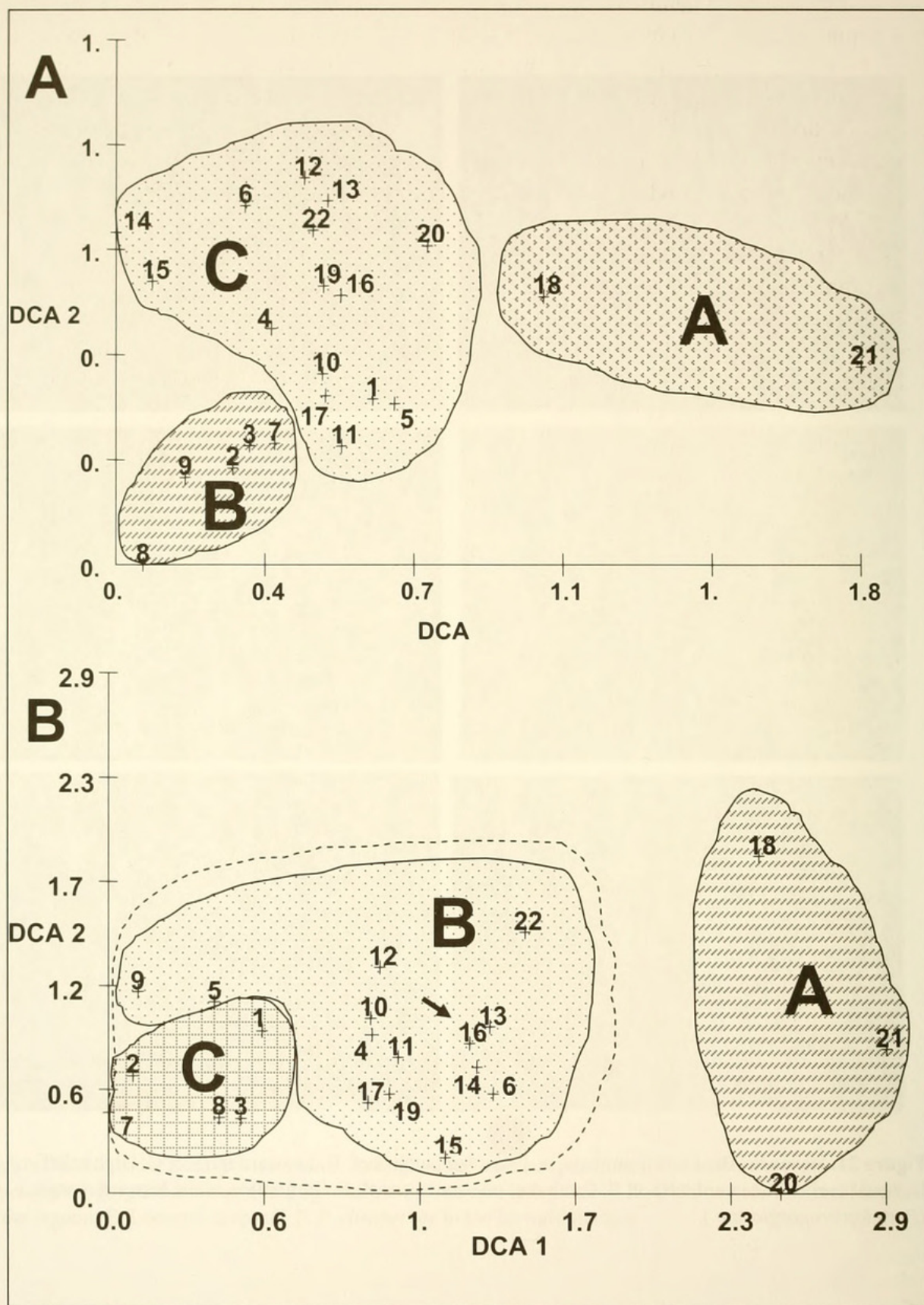


Figure 22. Roncador Bank benthic DCA biplots and community structure according to the groups from the cluster analyses of Figs. 18 and 23.

The octocoral community was also structured in three major minimal clusters of stations with less than 60% of dissimilarity (Fig. 23). Cluster B and C were nearly 50% dissimilar. The groups were somewhat similar to what was found in the benthic community. For instance, clusters B and C (Fig. 23) had almost the same stations as clusters C and B, respectively, in Figure 18 (see also Fig. 19A-B). Eight species such as *Plexaura homomalla*, *Plexaurella grisea* and *Eunicea laxispica* had their peak abundances in cluster A which corresponds to shallow lagoonal patch reefs (Table 9; Fig. 21A). Cluster B had an assemblage of 14 octocoral species corroborating again the 'mixed coral' nature of those stations in the leeward upper platform and some lagoonal reefs (Table 9). Cluster B also included the high peak abundances of the densest species in the sample habitats such as *Briareum asbestinum* and *Pseudopterogorgia bipinnata* (>1 colony m^{-2} ; Table 9; Fig. 21B). The ordination analysis also showed a gradation between clusters B and C, which are composed of stations that overlap in environmental conditions and geographically (Fig. 22B). A large proportion of the DCA axis 1 variation was significantly explained with depth ($r^2=0.762$; $P<0.001$). Octocoral density seemed to correspond to high rugosity and coral cover values (Table 7) but only correlated significantly with the latter ($r^2=0.230$; $P<0.001$).

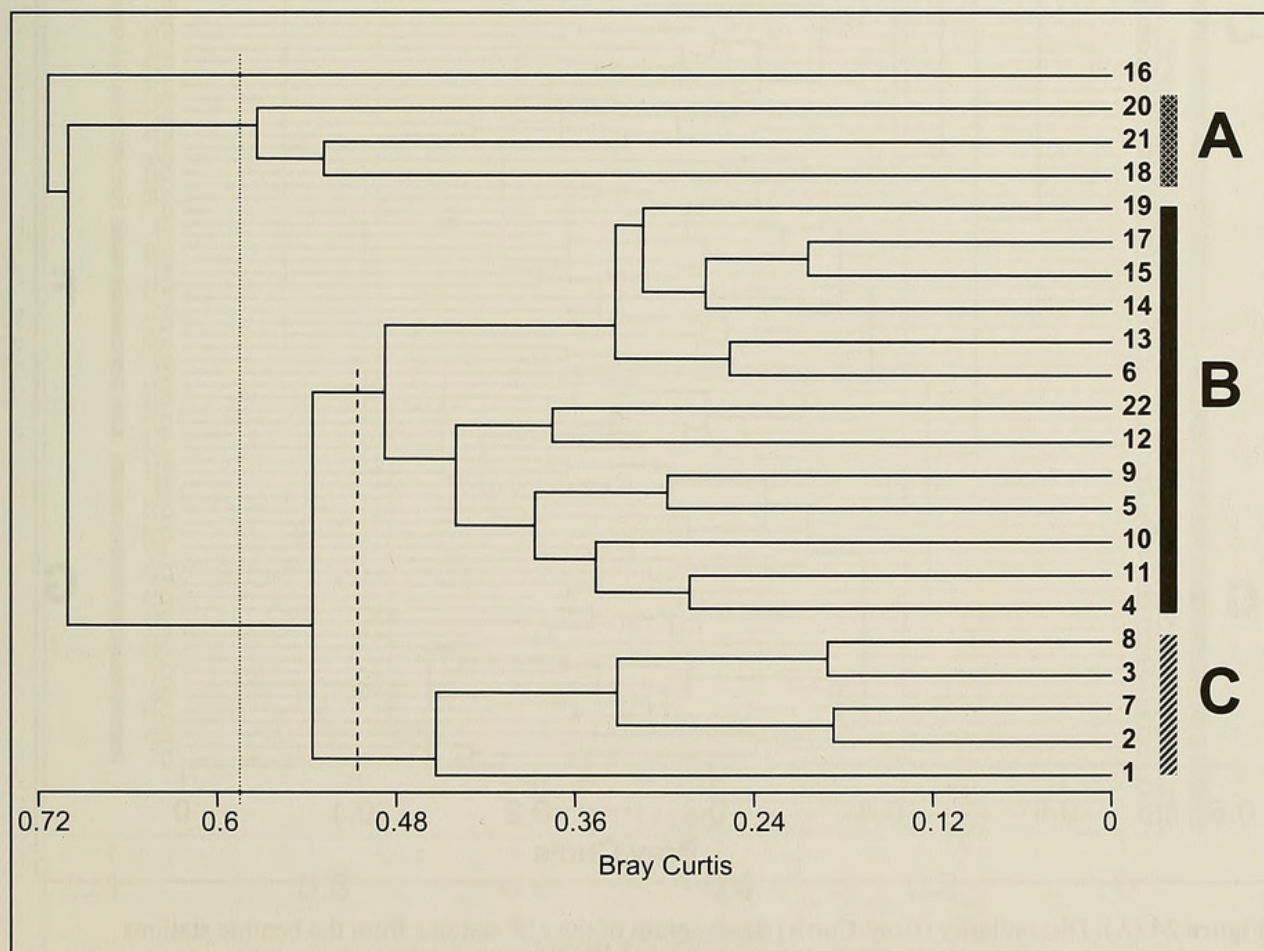


Figure 23. Dissimilarity (Bray-Curtis) dendrogram of the 22 stations on Roncador Bank with presence of gorgonian corals. The dashed line shows the dissimilarity division among groups.

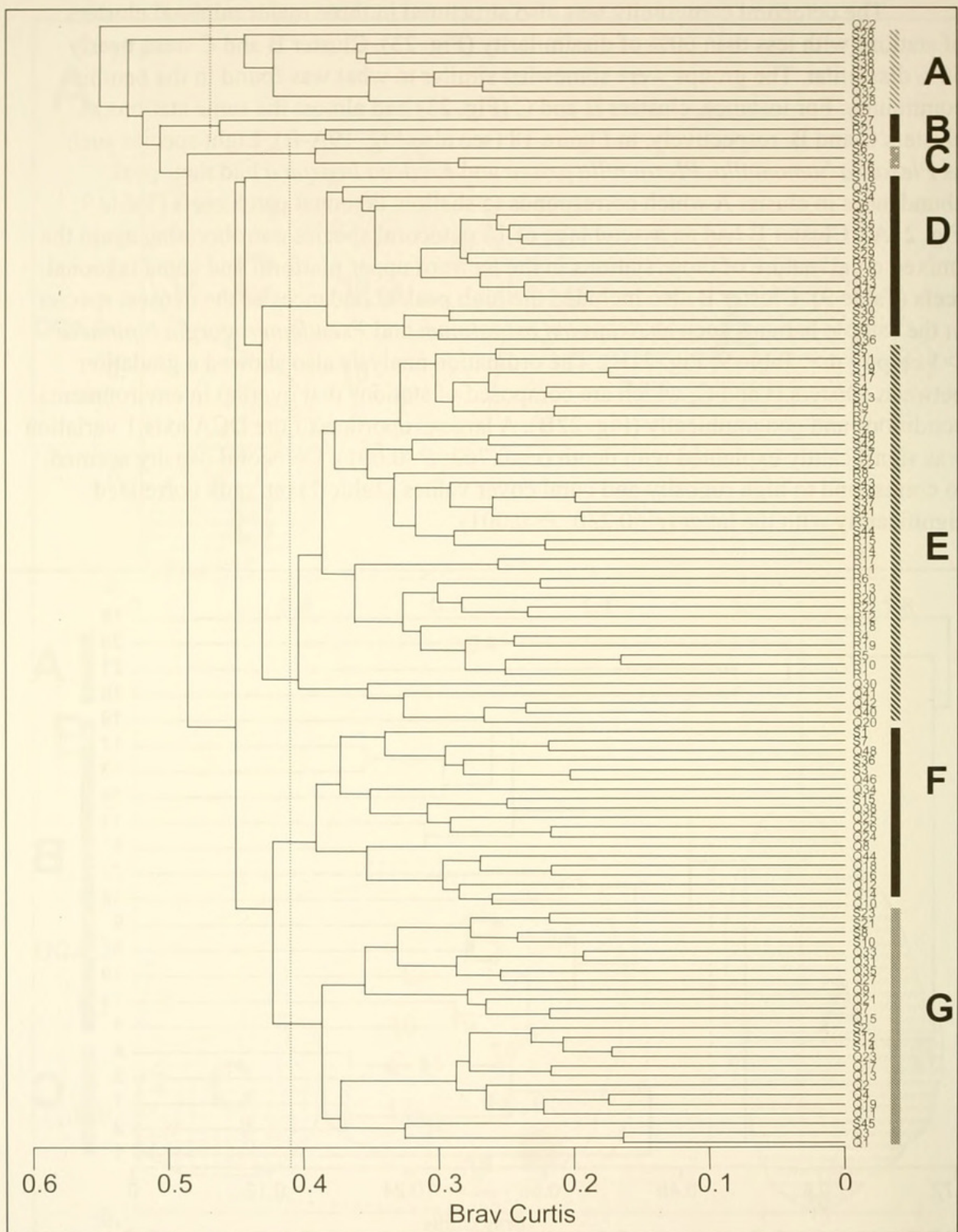


Figure 24 (A). Dissimilarity (Bray-Curtis) dendrogram of the 118 stations from the benthic stations including the three banks (Q. Quitasueño, S. Serrana, and R. Roncador). The dashed line shows dissimilarity division among groups.



Figure 24 (B). Dissimilarity (Bray-Curtis) dendrogram of the 118 stations on the three banks (octocoral data). The dashed line shows dissimilarity division among groups.

Northern Cays

Analyzing the 118 stations of the three banks as one whole community, it was found that there is some structure in terms of major reef (e.g., Serrana, Quitasueño and Roncador Banks) at both benthic (substrate cover) and octocoral assemblages (colonies density) (Figs. 24A-B). A larger number of minimal clusters was found using the same dissimilarity criterion than the analysis of each particular bank ($<40\%$; Fig. 24A) which was expected given that there are many more stations and a much wider geographic range. In the benthic community, most of Roncador stations grouped almost exclusively with Serrana Bank stations but Quitasueño Bank grouped with only a few Serrana stations distributed in every cluster except C (Fig. 24A). A similar pattern was found using the data from the octocoral community (Fig. 24B). The results may be affected by an artifact because we sampled neither the fore-reef terraces on Serrana and Roncador Banks nor the leeward slope margin of Quitasueño Bank. Nonetheless, Roncador and Serrana Banks were similar since a large number of their stations grouped together.

DISCUSSION

The results presented here show once again the great complexity in the organization and structure of coral-reef communities. In spite of this, overall patterns were identified, which explained some aspects of the benthic community organization affecting the three studied Caribbean atolls (Northern cays: Quitasueño, Serrana, and Roncador Banks). Differences and particularities of each coral bank with respect to the others were also distinguished. Our results comprise the most recent survey (April, 2003) in these extensive coral reef areas and some historical differences were noted when comparing with studies from the previous decades. Nonetheless, several high coral- and octocoral-diversity/abundance areas were also recognized which provides flexibility and basis for the design and management of a network of MPAs in the Northern banks.

Patterns in the Northern Cays Benthic Communities

The Northern Cays had between 66 and 73 types of substrates as part of the benthic communities including 43-to-46 species of reef-building corals and 38 species of octocorals. Large ranges of coral cover (2-52%) and octocoral densities (0-15 col. m⁻²) were observed among stations. Octocoral diversity could certainly have been higher since we did not collect specimens and some species could not be differentiated visually to the species level *in situ*, such as most *Pseudoplexaura* spp. (3) and some of the *Eunicea* (3) and *Muricea* (2) species. The octocoral fauna seems to be similar to what is found in the nearby Providencia island barrier-reef complex which comprises 44 species, the highest in the Western Caribbean (Sánchez et al., 1998). The coral diversity is similar to that of any other well-developed Caribbean reef (e.g., Cairns, 1982) or Colombian coast reef (e.g., Sánchez, 1995). High coral-octocoral diversity and abundance were located on wave-protected and mid-depth environments in leeward zones. As suggested by Bak and

Povel (1988, 1989), coral diversity and abundance are arranged (min.-max.) according to prevailing environmental conditions from 'exposed' to 'sheltered' sites. Leeward terraces, including part of the 'mixed coral' habitat, in the Northern Cays represent a suitable environment for both coral and octocoral growth exhibiting almost all coral-octocoral species within a small reef portion which has also been called the 'edge effect' (Porter, 1972; Liddell and Ohlhorst, 1987). Long-term evidence shows that the deeper environments remain as the most constant habitat as opposed to the potentially disturbed shallower reef portions (Bak and Nieuwland, 1995) which in turn allows high coral and octocoral diversity in the 'mixed coral' habitat.

In general, species assemblages within each community structure (e.g., benthic or only octocorals) corresponded to shared species-specific environmental preferences, perceived as minor gradients such as windward-leeward and/or shallow-deep, and, of course, to physical/topographical characteristics which in most habitats were the product of the reef-building corals themselves (e.g., '*Montastraea*' or '*Acropora palmata-Diploria*' habitats). Species-abundance distribution followed the pattern found everywhere in natural communities: few species are highly abundant as compared to most of the species which are rare (see review in Marrugan and Henderson, 2003) which has been called the "inherent rarity" property of ecological communities (e.g., Maina and Howe, 2000). Highly abundant species in the benthic community, i.e., from the three banks and most habitats, were *Montastraea* spp. (reef-building corals), *Pseudopterogorgia bipinnata* (octocoral), and *Lobophora variegata* (fleshy macroalgae). These species are also highly abundant in the southern cays and Providencia Island (Sanchez et al., 1997, 1998; Friedlander et al., in press) and seem to be particular features of the Archipelago region. Other algae can also be considered highly abundant functional groups, which comprised a generalized "background assemblage" that was present in most stations; however, it is expected that a few species, that were treated here at the generic or functional level, are more abundant within each functional group. Nonetheless, since highly abundant species are also known to have a larger geographical distribution than rare species (e.g., Brown, 1995), local abundance of rare species also should be considered important in terms of conservation priorities. Locally abundant species in terms of a particular bank and/or habitat will also be discussed below.

The community structure always separated shallow vs. deeper habitats and exposed from protected environments usually exhibited a continuum which was better explained in terms of depth as the major structuring force in the Northern cays. Certain unpredictable patchiness, though, was found in some shallow habitats. For instance, the north vs. south habitats in Quitasueño Bank presented certain structure independently of the habitat type. This could be due to the heterogeneous effects of past physical disturbances such as hurricanes (e.g., 1987 Joan) and the seasonal effect of the 'Northerns', winds that are potential chronic disturbance events at the Archipelago of San Andres and Providencia (Geister, 1992) and which can irregularly affect leeward portions of the reef. Studies on gorgonians have elucidated that their communities could be distributed along an environmental continuum due to topographic relief and wave-exposure (e.g., Yoshioka and Yoshioka, 1989). This pattern has been found in the gorgonian community of the Southern Cays, where the most contrasting habitats (lagoon

and fore-reef terrace) have a gradual change with the leeward terrace as intermediate in terms of species composition and structure (Sanchez, et al., 1997). Octocoral axes have a determined content of elastic fibers and carbonate depending upon the turbulence regime that each species withstands (Lewis et al., 1992) which explains specificity in contrasting environments. The mix of assemblages seems to occur thanks to the plasticity of some species such as *Pseudopterogorgia bipinnata*, a super abundant species, distributed from 1-to-45 m and with a wide range of wave-exposure as well (Sánchez, in prep.). A reef-building coral example can be observed with species such as the *Montastraea annularis* complex, *M. annularis*, *M. faveolata* and *M. franksi*, where some are found shallower whereas some sustain more sediment exposure (e.g., Van Veghel, 1994). It is important to notice that *Montastraea* spp. provide a high topographic complexity with elevated rugosity and multiple refuges for vagile invertebrates and fish. Consequently, *Montastraea*-dominated reefs in the Northern Cays should be considered among the conservation priorities.

The community-structure patterns found here have also been observed in other ecological communities from the northern banks and the islands of San Andres and Providencia. Similar ordination and classification patterns, as presented here, were observed at the algae community level of Serrana, Roncador and the Southern Cays (Diaz-Pulido and Diaz, 1997). In communities such as reef fish of Serrana and Roncador Banks there were greater differences among reef habitats than among banks and contrasting habitats such as fore-reef terrace and lagoon were not significantly different (Mejia and Garzon-Ferreira, 2000). Likewise, Dahlgren et al. (in prep., this report), in a parallel study including the three banks surveyed here, found an evident fish-community structure among the habitats and also among the banks exhibiting a higher heterogeneity compared to the benthic community structure presented here. Dahlgren et al. (in prep., this report) discuss in detail the likely causes for such heterogeneity in the fish community, which could be of anthropogenic origin. Sponges show even greater heterogeneity among the banks of the archipelago (Roncador, Serrana and Albuquerque), probably due to disparate founder populations and the differential effect of physical disturbance (Zea, 2001). Nonetheless, Zea (2001) noted that the sponge density in the archipelago was lower than in continental areas, possibly due to lower suspended matter in these oceanic banks. We also found low sponge abundance in the northern banks.

Current State of the Benthic Communities

Overall, coral cover in Quitasueño Bank was the highest among the three studied atolls with a mean of 32.9 % (min.-max.: 18.3- 50.7%) versus 19.2 % (2.8-52.3%) in Serrana and 16.9 % (3.5- 41.7) in Roncador Banks. However, it is important to note that the fore-reef terrace habitats were not visited at Serrana and Roncador banks. A survey on the fore-reef terrace by Diaz-Pulido et al. (submitted) of the latter banks revealed a mean coral cover of 19.7 (7.4 SD) which is certainly low compared to 32.9% mean coral cover (cluster F: 18-50% min.-max., Table 1) found at Quitasueño Bank in this study. Coral cover values in other leeward areas of the reef during 1995 had values of 19.4 % (10.4 SD) on the leeward terrace, 37.4% (6.5 SD) in the mid-depth lagoon (< 8m), and 46%

(14.5 SD) in the shallow '*Montastraea*' habitat (Diaz-Pulido et al., submitted), which are values within the range of what was found in Serrana and Roncador Banks during 2003 in this study (Tables 4 and 7). For instance, the leeward terrace of Serrana Bank (e.g., Table 4, Fig. 12A: cluster D) had 11.6 % (5.3 SD) of coral cover, in the analogous habitat in Roncador Bank there was 16.3 % (2.1 SD) (e.g., Table 7, cluster B). Fairly high coral covers were also found in the mid-depth (7-9 m) lagoon sites of Roncador (mean 41.9%, Table 7, Fig. 18A: cluster C). Nonetheless, the same habitat at Serrana Bank had lower coral cover (mean 21.3%; 10.4 SD; Table 4; Fig. 12A: cluster D) than Roncador Bank and the data from 1995 suggest certain reduction in the coral cover at the Serrana Bank lagoon.

Shallow habitats had a more heterogeneous structure among the banks and, since the exact location of the Diaz-Pulido et al. (submitted) stations as well as ours could not be matched exactly due to GPS incompatibilities, accurate comparisons between the two studies could not be made. It was clear that, overall, Quitasueño Bank exhibited the highest coral cover values throughout shallow habitats and Roncador had the highest coral cover in a particular habitat, whereas Serrana Bank presented a reduction in coral cover in the lagoon. It is important to note that the edge of the leeward terrace, where most of the stations were placed at Serrana and Roncador Banks, was not surveyed at Quitasueño Bank. It is unknown if there is such a habitat or if there is a different type of environment. Indeed, one of the stations at the leeward most region of the bank (st 22 Quitasueño) was situated in an atypical rubble and algae (*Avrainvillea* spp.) environment patch in the leeward margin (e.g., Fig. 6 C-D), which also had an atypical fish community (Dahlgren et al. in prep.). Due to time constraints and the enormous size of Quitasueño Bank, a limited number of stations were surveyed and more exploration should be done on the leeward most areas of the bank to depict both geomorphology and benthic communities.

Decline in coral cover and the effects of mass mortalities have been noted in nearby areas of the archipelago (San Andres Island: Zea et al., 1998; Providencia Island: Sanchez et al., 1998). Besides, during 1988 hurricane 'Joan' had affected this area and *Acropora* species have declined abruptly in the coral reefs of San Andres (Zea et al., 1998). Particularly, the urchin mortality associated with the Caribbean-wide die-off in 1983-84 provoked algae blooms with the further loss of coral cover in many areas due to competition and suffocation by algae (e.g., Hughes et al., 1987; Hughes, 1989, 1994; Coyer et al., 1993). An important part of the benthic community in the Northern Cays was indeed dominated by highly opportunistic algae such as *Lobophora variegata* and *Dictyota* spp. These turnovers in the dominant algae species could provoke changes in the normal algae community structure of coral reefs (Steneck and Dethier, 1994) and, indeed, more coral reef-benign types of algae (e.g., coralline, calcareous, and filamentous) were affected and reduced in abundance, which was particularly notable in Serrana and Roncador (fleshy-algae dominated) compared to Quitasueño (coral dominated). It is worth noting that the highest, though very localized and heterogeneous, sea urchin densities were observed in Quitasueño Bank, which suggests a link for a coral-dominated benthic community. In any case, fleshy fish-unpalatable (e.g., *Lobophora* and *Dictyota*) algae were the dominant functional algal group in the three banks.

Besides the multiple aspects enhancing macroalgae dominance in the Northern Cays at present, it is possible to speculate on the degradation of their coral reefs due to coral diseases. The latter was particularly noticeable in the lagoonal habitats of Serrana Bank towards the semi-enclosed lagoonal basins from the north and east elbow-like ends. White-plague (e.g., Dustan, 1977; Dustan & Halas, 1987; Richardson et al., 1998), bleaching, and dark spots (Gil-Agudelo & Garzon-Ferreira, 2001) were observed on several habitats throughout the banks. These diseases have been observed in these areas of Colombian reefs since the mid 1990s (see review in Garzon-Ferreira et al., 2001 and references therein). Effects from white plague were particularly serious in a localized but extensive area of Serrana Bank (Sánchez et al, submitted).

Coral diseases and bleaching have been observed for over two decades in the area of the archipelago and still coral reefs exhibit some high coral cover habitats as signs of resilience in the system (e.g., Providencia: Friedlander et al., in press; San Andres: Friedlander et al., in prep.). The answer to this interesting behavior can be found in coral reefs that have been under a steady state of stressors (e.g., hot temperatures, sediments, nutrients, etc.), which exhibit mean coral cover >40% (e.g., Imelda Bank, Cartagena: Sánchez, 1999; Bocas del Toro, Panama: Guzman and Guevara, 1999). Another substantial amount of evidence comes from the concept of “adaptive” bleaching hypothesis (Buddemeier and Fautin, 1993) and zooxanthellae (coral symbiotic microscopic dinoflagellate algae) specificity and “naïve” reefs (see reviews in Rowan, 1997; Baker, 2003). Corals acclimatize (= “adapt”) to changing ocean conditions by changing their symbionts for more resistant species (=clades) of zooxanthellae (clade D: Baker, 2003). Coral reefs from regions that have not been affected by bleaching are considered “naïve” reefs, which in turn can acclimatize and prevent further bleaching. As a hypothesis, remote and oceanic reefs, such as the Northern Cays, are increasingly affected by global change (e.g., global warming) and their coral populations have started to acclimatize which was noticed by the heterogeneous distribution of bleaching throughout the habitats. Nonetheless, it is unknown if the pattern of bleaching as acclimatization appears as heterogeneous as we saw it or if it is a massive event. Further studies on this, including zooxanthellae genotyping, should address this question and the Northern Cays provide an interesting situation for that. It is still unknown if the observed diseases (e.g., white plague and dark spots) could be due to similar complex interactions, but in this case, within the coral microbial flora. In summary, the evaluation of the current state of the Northern Cays coral reefs is optimistic when observing different states of conservation among habitats with a noticeable degree of decline in some semi-enclosed lagoonal reefs in Serrana Bank. Described below are those highly conserved habitats as well as habitats that deserve further observation.

Areas of Special Ecological Interest: Concluding Remarks

Besides the overall patterns of community structure, it is important to highlight areas with high coral abundance and diversity, which in turn will contribute to the planning and zoning of a network of MPAs in the Northern Cays. In addition, some areas of special concern were also identified that could need special management and/or further

monitoring. The areas of high coral abundance and diversity had mean values of coral cover $> 32\%$ (most of them $> 38\%$), coral species > 16 , octocoral densities $> 0.6 \text{ col. m}^{-2}$ (usually $> 2.9 \text{ col. m}^{-2}$), and octocoral diversity > 4 (usually > 8) (Table 10), which are within the ranges of the best conserved coral reefs on the Colombian coast (e.g., Imelda Bank, Colombia: Sánchez, 1999) and southern Caribbean (Bocas del Toro, Panama: Guzman & Guevara, 1999). In the Caribbean Sea, areas with coral cover $> 32\%$ are considered of high coral abundance (e.g., Edmunds, 2002). Therefore, these identified areas in the Northern Cays, exceeding coral cover $> 32\%$, are among the most conserved in Colombia and the Caribbean Sea but in need of protection. Unfortunately, not all the habitats fall in this category but probably more than half of the coral areas in the Northern Cays do. Apparently, these habitats have endured the coral reef decline of the last two decades. In addition, since most of the coral reef areas of the Northern Cays belong to Quitasueño (1320 km^2 vs. 321 km^2 [Serrana Bank] and 50 km^2 [Roncador Bank]: Diaz et al., 2000) and it was the bank with the highest coral abundance and diversity areas, it is recommended that a good portion of the MPAs' network covers this bank (e.g., Fig. 25 A).

The highest gorgonian density ever found in the Colombian Caribbean with up to 22 colonies m^{-2} (compare to Sánchez, 1999; Sánchez et al., 1997; 1998), as well as the highest mean coral cover found in the Northern Cays (41.9%), was observed in the '*Montastraea*' habitats in the lagoon and leeward margin of Roncador Bank. The habitats of high coral abundance and diversity were distributed in the three atolls, but Quitasueño Bank had the largest extent and number of stations in these areas (Table 10; Fig. 25). Overall the areas with high coral/octocoral abundance and diversity were always distributed on '*Montastraea*' and/or 'mixed corals' (one case included '*Acropora palmata* – *Diploria*') and with the exception of the Quitasueño fore-reef terrace, all of them were distributed in the lagoonal basin or the leeward terrace. In terms of choosing ecologically important habitats (i.e., those with high abundance of habitat-forming organisms plus high diversity) the zones described in Table 10 and Figure 25 comprise the best options within the surveyed habitats of the Northern Cays.

Areas of especial interest or concern included those habitats that harbor particular species, or group of species, that are somewhat endangered or are considered rare nowadays in the Caribbean. For instance, sea fans *Gorgonia ventalina* and *G. flabellum* have undergone mass mortalities and in other regions of the archipelago they are very scarce (Southern Cays: Sánchez et al., 1997; San Andres island: Zea et al., 1998; Providencia island: Sanchez et al., 1998). The fore-reef terraces from Serrana and Roncador particularly harbored among the most dense and abundant sea-fan zones, just as observed in 1995 (Diaz et al., 1996a; Sánchez, unpublished). Together with Bushnell shoal off the Colombian coast (Diaz et al., 1996c), Roncador and Serrana comprise some of the few places that were not affected by the sea fan mortality that occurred in the 1980s (Smith et al., 1996; Nagelkargen et al., 1997). The fore-reef terrace habitat in these two banks is largely inaccessible due to high seas and rough conditions which was the reason we could not survey such habitats during this study. Nonetheless, it is a habitat of importance due to the luxuriant sea fan populations observed during 1995, which could be a natural reservoir of this species for the Archipelago of San Andres and Providencia

and the southwestern Caribbean as well. A further exploration of this habitat is necessary.

Gorgonian octocorals, which are distributed worldwide, have been for many years harvested as precious and semiprecious jewels (e.g., red coral in the Mediterranean, gold and pink coral in Hawaii, Grigg, 1994; sea fans and sea candelabrams in the Caribbean, pers. obs., etc.). In the nearby islands of San Andres and Providencia as elsewhere in the Caribbean (e.g., Bahamas, Mexico, Puerto Rico, Belize, Panama, Trinidad and Tobago, pers. obs. J. A. Sanchez and A. R. Acosta-de-Sanchez), native handicrafts ("artesanias") containing gorgonian octocoral axes are commonly encountered. It is unknown what the effects of this type of extraction is on the populations of gorgonian octocorals, but in some regions of mainland Colombia, such as Isla Grande, Rosario Islands (pers. obs. J. A. Sanchez), octocorals are locally extinct due to past extractive activities whereas protected nearby islands harbor luxuriant communities (e.g., isla Tesoro: Sánchez, 1995). The success of a network of marine reserves is found in the conservation of the integrity of the ecosystem (e.g., McClanahan and Arthur, 2001). Therefore, octocoral rich habitats should also be considered among the areas of high coral abundance and diversity. Nonetheless, there are also some important reasons to consider some octocoral-rich areas special. For instance, Caribbean gorgonian octocorals (sea fans, feathers, candelabrams, etc.) also harbor a great diversity of secondary metabolites in their soft tissues, which have been demonstrated to have a strong anti-inflammatory, anti-carcinogenic, and anti-tumor activity in the laboratory (see review in Rodriguez, 1995). Gorgonians are the dominant component of the underwater landscape in southwestern Caribbean atolls (Sánchez et al., 1997). Some Caribbean gorgonians, such as *Pseudopterogorgia elisabethae*, have been harvested for the extraction of anti-inflammatory metabolites by the cosmetic industry (e.g., Mayer et al., 1998), which has brought along economic benefits for local communities in the Bahamas. Some areas of Roncador and Serrana banks (Table 10, Fig. 25 B-C) distributed on the leeward margin, in the drop-off edge particularly, presented a high abundance of this species (up to 2.4 col. m⁻²), which could be a potential zone for the study or exploitation of this species. Nevertheless, a proper survey of the populations is necessary to access the potential risk of that kind of extractive activity.

The largest concentration of reefs in the Northern Cays is the reticulate network of *Montastraea* spp. patch reefs on the north and east elbow-like lagoonal basins of Serrana Bank (Diaz et al., 1997). Although there were over 10 species of reef-building corals with their highest peak abundances in this area, the distribution of coral cover was highly heterogeneous (Table 10; Fig. 25 B). The community seemed the same as in the leeward margin (Fig. 12 A, cluster D) with dominance of algae (cyanophyceae, filamentous, and *Lobophora variegata*), which we could speculate as the aftermath of recurrent disease and/or bleaching outbreaks. This scenario was observed in some of the stations that presented acute white plague disease outbreak despite *Montastraea* spp. have shown high resilience and regeneration rates in other Caribbean reefs (e.g., Sánchez et al., 2004). The dominant reef-building coral in most stations was *Montastraea franksi*. Surprisingly, the shallow habitats or "flats" of some of these patch reefs exhibited very healthy small aggregations of *Acropora palmata* (sometimes together with *A. cervicornis* and *Porites furcata*), particularly towards the west lagoonal basin. This kind of habitat harbors a rich fish community (Lerman, 1999; see also Dahlgren et al., this report). It is

worth noting than the *A. palmata* ridges were observed in isolation of each other, 100-200 m apart in the closest cases, and usually small ($< 100 \text{ m}^2$) including depths ranging from 10-to-20 m in the sandy areas between the patches. It is known that the main spatial propagation strategy of Caribbean acroporids is fragmentation (e.g., Lerman, 2000) which in turn generates clonal dominance. This has been considered as a weakness of Caribbean reefs where just a few species and a few genotypes dominate extensive reef areas, which make them vulnerable due to poor genetic diversity. Susceptible genotypes, to disease for instance, could perish resulting in a population collapse. In Serrana Bank we are most likely have the scenario where multiple genotypes of *A. palmata* co-occur due to the heterogeneous distribution of shallow patch-reef flats in the lagoonal basin. Hypothetically, higher genetic diversity could be found in this patch reef as compared to fringing coastal reefs. In addition, dead skeletons of *A. palmata* were observed colonized by *Porolithon pachydermum* and its symbiotic chiton *Choneplax lata*, which comprise one of the fastest reef-building systems known (Littler et al., 1995). In brief, both the vulnerability to disease of the deep parts and the ecological importance of the heterogeneous shallow *Acropora* habitats made the reticulate patch-reef network of Serrana an area of special concern deserving of further detailed studies and complex management.

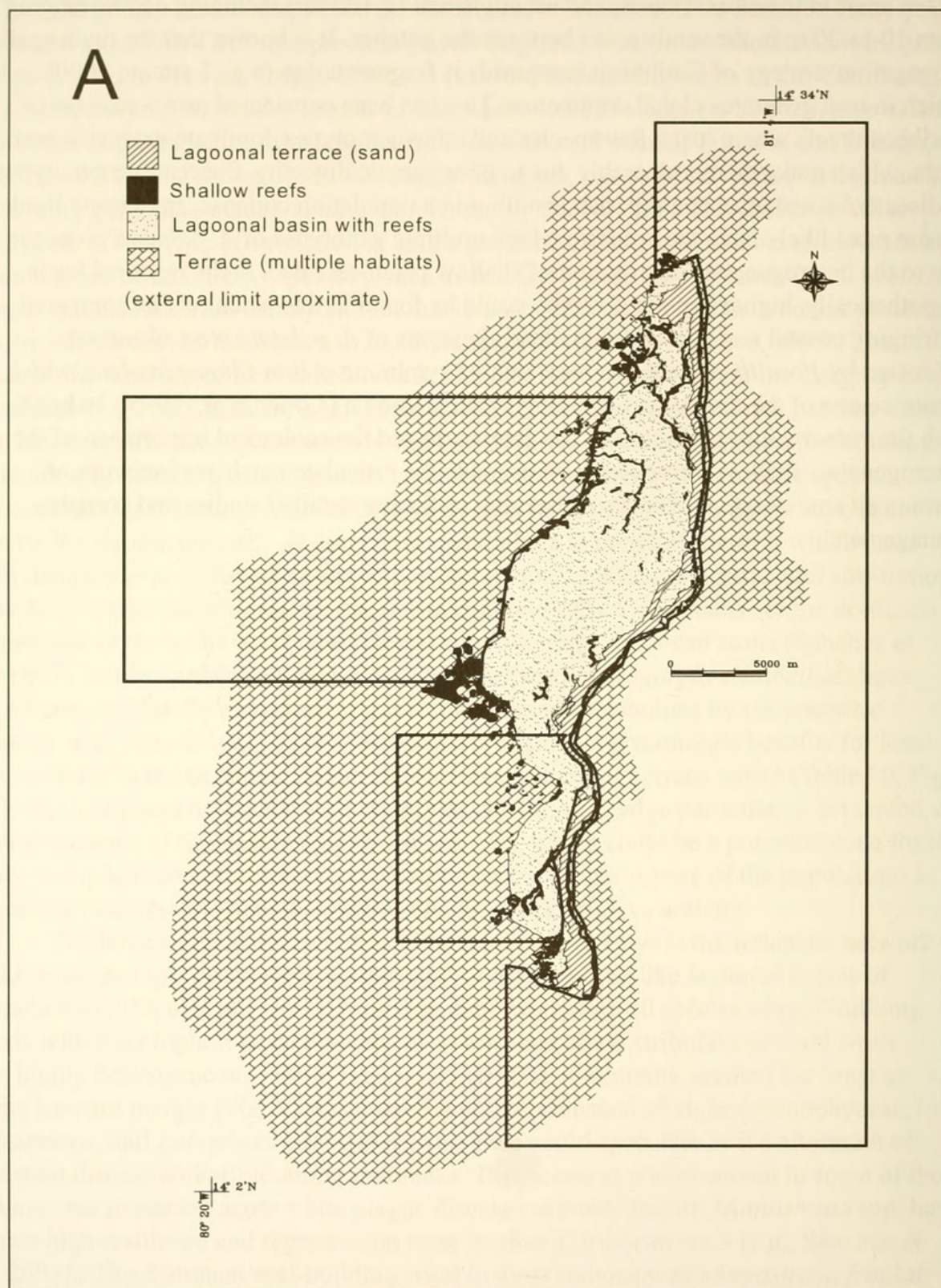


Figure 25 (A). Areas of particular interest. A. high coral and abundance and diversity areas in Quitasueño Bank (see details in Table 10).

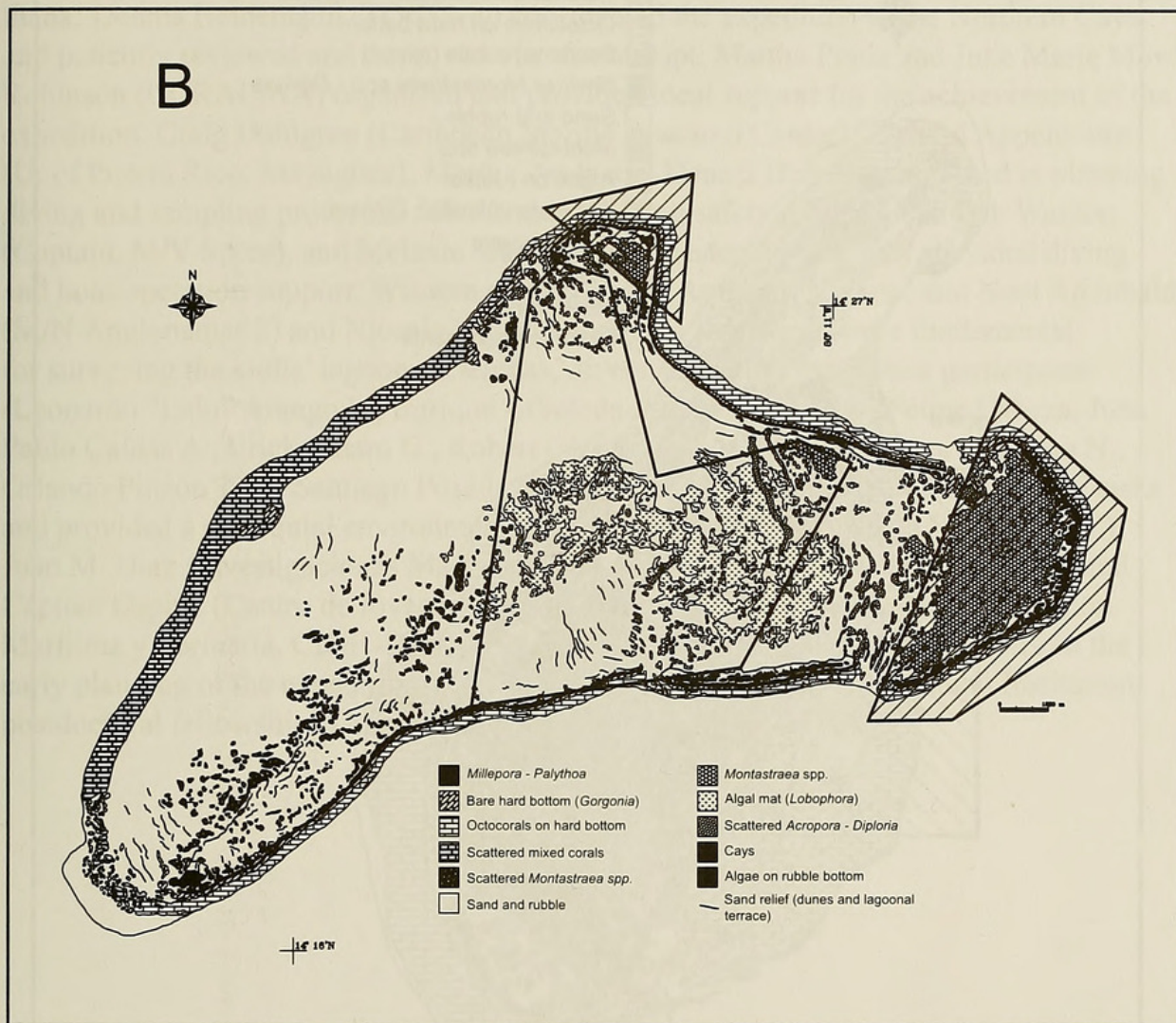


Figure 25 (B). Areas of particular interest. B. high coral and abundance and diversity areas in Serrana Bank (open polygon) and areas of particular concern (hatched polygons) (see details in Table 10). 'Bare hard bottom *Gorgonia*' habitat is also an area of particular concern.

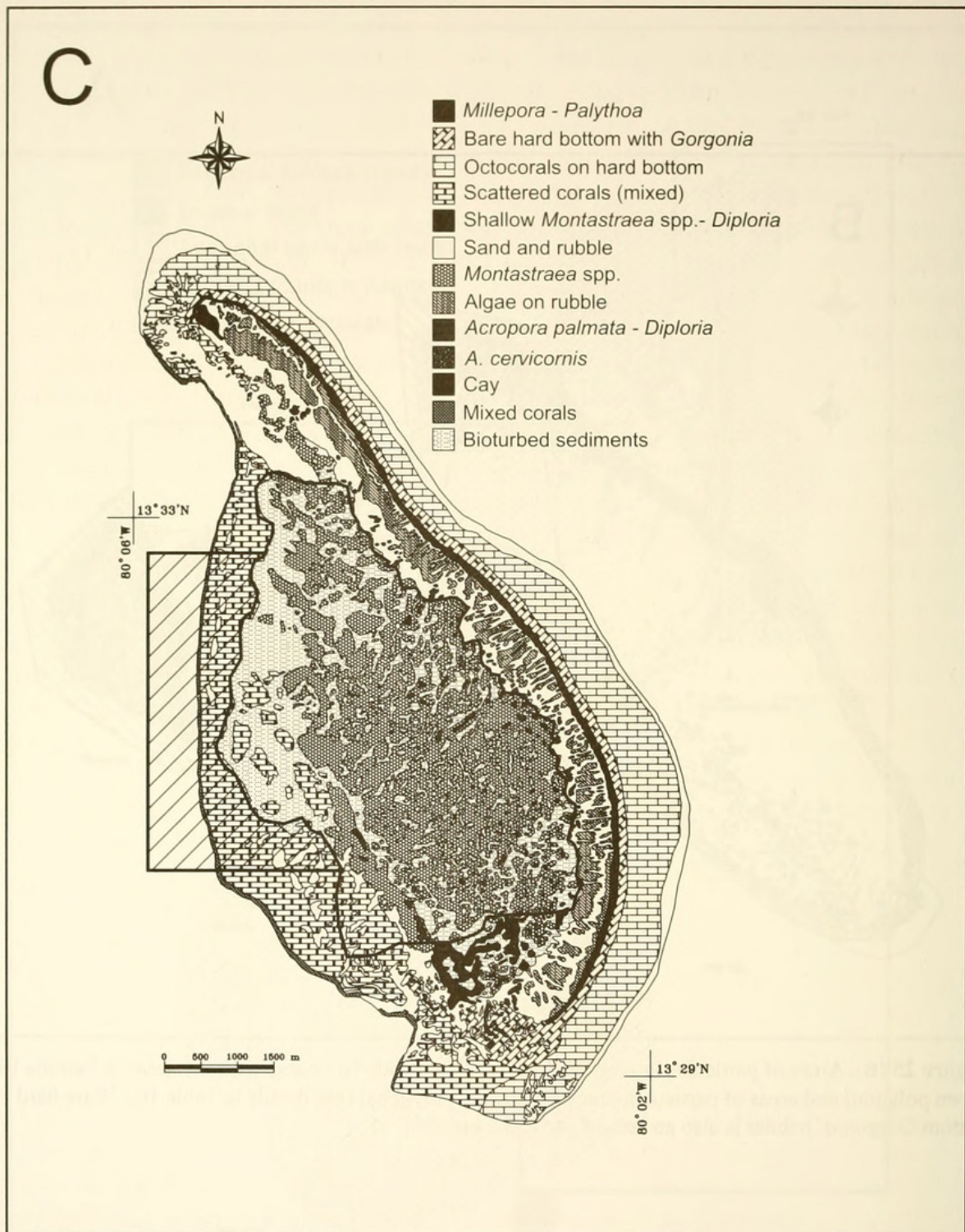


Figure 25 (C). Areas of particular interest. C. high coral and abundance and diversity areas in Roncador Bank (open polygon) and areas of particular concern (hatched polygon) (see details in Table 10). 'Bare hard bottom with *Gorgonia*' habitat is also an area of particular concern.

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Table 1. Mean values (X) and standard deviations (sd) for different variables of the benthic communities at Quitasueño bank according to the classification of Figure 4.

| Cluster | A | | B | | C | | D | | E | | F | |
|---|--------|-------|--------|-------|--------|-------|--------|--------|--------|-------|--------|-------|
| | X | sd | X | sd | X | sd | X | sd | X | sd | X | sd |
| Rugosity index | 0.370 | 0.198 | 0.610 | 0.169 | 0.122 | 0.084 | 0.461 | 0.036 | 0.507 | 0.135 | 0.267 | 0.121 |
| Depth (m) | 6.267 | 4.407 | 10.109 | 5.855 | 16.401 | 2.339 | 14.700 | 7.596 | 12.136 | 3.768 | 19.240 | 4.948 |
| Coral species | 18.571 | 3.155 | 20.364 | 4.105 | 16.500 | 3.271 | 19.750 | 2.630 | 23.667 | 4.274 | 22.538 | 3.230 |
| Octocoral species | 6.000 | 4.967 | 8.727 | 2.412 | 9.333 | 1.751 | 11.250 | 1.708 | 11.833 | 3.545 | 10.692 | 2.810 |
| SUBSTRATE COVER (%) | | | | | | | | | | | | |
| Coral cover | 26.859 | 5.361 | 35.666 | 5.365 | 22.263 | 4.121 | 36.277 | 10.201 | 39.678 | 5.486 | 35.664 | 4.423 |
| Encrusting algae | 4.951 | 2.762 | 5.979 | 1.902 | 7.812 | 1.739 | 4.712 | 2.955 | 8.882 | 0.997 | 4.775 | 2.470 |
| Calcareous macro algae | 15.695 | 4.923 | 11.953 | 3.501 | 10.197 | 1.856 | 8.757 | 3.645 | 9.793 | 2.019 | 7.302 | 2.246 |
| Fleshy macro algae | 26.849 | 7.883 | 19.290 | 3.566 | 32.674 | 4.820 | 19.237 | 6.451 | 15.298 | 5.930 | 22.877 | 4.152 |
| Filamentous algae | 3.633 | 1.883 | 8.900 | 5.406 | 13.930 | 1.175 | 4.065 | 2.850 | 9.070 | 2.077 | 5.938 | 3.443 |
| Other fleshy invertebrates | 0.523 | 0.921 | 1.148 | 1.384 | - | - | 1.156 | 0.833 | 0.636 | 0.774 | 0.215 | 0.424 |
| Encrusting sponges | 0.590 | 1.011 | 1.190 | 1.290 | 0.831 | 1.250 | 0.216 | 0.431 | 4.095 | 2.528 | 2.229 | 1.528 |
| Erect Sponges | 3.542 | 2.121 | 1.988 | 1.434 | 4.203 | 1.744 | 4.731 | 2.630 | 3.039 | 1.209 | 6.915 | 1.651 |
| Octocoral bases | 1.767 | 2.365 | 3.644 | 1.994 | 2.781 | 1.691 | 5.542 | 2.900 | 4.350 | 3.503 | 6.287 | 1.972 |
| Bare hard ground | 7.605 | 0.878 | 2.701 | 2.788 | 0.293 | 0.455 | 4.019 | 2.975 | 1.620 | 0.458 | 4.696 | 3.742 |
| Rubble | 2.900 | 0.753 | 1.376 | 1.681 | - | - | 2.245 | 2.417 | 0.269 | 0.421 | 0.535 | 0.776 |
| Sand | 5.087 | 1.510 | 6.164 | 2.896 | 5.016 | 2.458 | 9.042 | 1.315 | 3.270 | 2.235 | 2.565 | 2.224 |
| DENSITIES | | | | | | | | | | | | |
| Octocorals (colonies m ⁻²) | 2.186 | 4.536 | 2.955 | 1.664 | 2.500 | 0.772 | 4.050 | 0.676 | 4.450 | 4.333 | 4.431 | 2.184 |
| Diadema antillarum (individuals m ⁻²) | 0.143 | 0.361 | 0.124 | 0.159 | - | - | 0.005 | 0.010 | 0.127 | 0.192 | 0.003 | 0.008 |
| Echinometra viridis (ind. m ⁻²) | 0.029 | 0.046 | 0.304 | 0.369 | - | - | - | - | 3.617 | 3.948 | 0.002 | 0.006 |
| CORAL DISEASES | | | | | | | | | | | | |
| White Plague-WP (No. affected spp.) | 0.857 | 0.900 | 1.000 | 0.775 | 0.667 | 0.516 | 0.250 | 0.500 | 1.333 | 1.211 | 0.385 | 0.650 |
| WP-average of percentage affected tissue | 1.002 | 1.825 | 1.136 | 1.518 | 0.667 | 0.516 | 0.003 | 0.005 | 0.778 | 0.655 | 0.232 | 0.438 |
| Dark Spots-DS (No. affected spp.) | 0.857 | 1.069 | 1.273 | 1.009 | 1.333 | 1.366 | 1.500 | 0.577 | 2.167 | 1.329 | 1.385 | 0.506 |
| DS-average of percentage affected tissue | 0.147 | 0.376 | 2.017 | 2.870 | 1.000 | 0.843 | 1.754 | 1.751 | 2.972 | 1.714 | 0.852 | 0.981 |
| Bleaching (No. affected spp.) | 0.571 | 0.787 | 1.000 | 0.632 | 1.000 | 1.095 | 0.750 | 0.957 | 1.667 | 0.816 | 0.923 | 1.188 |
| BL-average of percentage affected tissue | 0.146 | 0.377 | 1.910 | 2.844 | 0.667 | 0.516 | 0.503 | 0.998 | 1.333 | 0.516 | 0.425 | 0.639 |

Table 2. Benthic community assemblages (data as coral cover per group letter). Boxes mark all the species characteristic of each successively nested cluster according to Figure 6 (R-mode analysis including the 70% relative abundance of each species in determinate cluster[s]). Quitasueño Bank. Shaded cells represent values >5% of coral cover.

| SPP | A | B | C | D | E | F | s22 |
|--|-------|-------|-------|-------|-------|-------|-------|
| Cluster A | | | | | | | |
| Penicillus spp. | 0.45 | 0.03 | - | 0.04 | - | - | - |
| Turbinaria spp. | 12.12 | 0.49 | 0.67 | 5.05 | 0.10 | 0.13 | - |
| B | | | | | | | |
| Dyctiosoma sanctitomae | - | 0.03 | - | - | - | - | - |
| Isophyllia sinuosa | - | 0.01 | - | - | - | - | - |
| Hydroids | - | 0.01 | - | - | - | - | - |
| Caulerpa spp. | - | 0.14 | - | - | 0.03 | - | 0.16 |
| Montastraea franksi | - | 1.67 | 0.03 | 0.66 | 0.68 | 0.08 | - |
| A+B | | | | | | | |
| Diploria clivosa | 0.07 | 0.11 | 0.03 | - | - | 0.01 | - |
| Agaricia humilis | 0.02 | 0.04 | - | - | - | 0.01 | - |
| Montastraea faveolata | 2.72 | 6.35 | 0.03 | 5.50 | 0.31 | 0.75 | - |
| Montastraea annularis | 4.17 | 7.22 | 0.06 | 0.66 | 3.09 | 0.70 | - |
| Favia fragum | 0.14 | 0.11 | - | - | - | 0.01 | - |
| Diploria labyrinthiformis | 0.50 | 0.28 | - | - | 0.18 | 0.14 | - |
| Ventricaria spp. | 0.02 | 0.03 | - | - | - | - | 0.16 |
| C | | | | | | | |
| Anadyomene spp. | 0.05 | - | 0.39 | - | - | - | - |
| Padina spp. | - | 0.08 | 0.56 | - | - | 0.01 | - |
| E | | | | | | | |
| Mycetophyllia aliciae | - | - | - | - | 0.10 | - | - |
| F | | | | | | | |
| Agaricia lamarcki | - | - | - | - | - | 0.03 | - |
| Mycetophyllia sp. | - | - | - | - | - | 0.01 | - |
| Palythoa spp. | - | - | - | - | - | 0.01 | - |
| Porolithon pachydermum | - | - | - | - | - | 0.06 | - |
| Agaricia spp. (plate-like) | - | 0.01 | - | - | - | 0.09 | - |
| Madracis decactis | - | - | - | - | 0.03 | 0.08 | - |
| Leptoseris cucullata | - | 0.04 | - | - | 0.03 | 0.23 | - |
| E+F | | | | | | | |
| Montastraea cavernosa | - | - | 0.22 | - | 1.07 | 1.18 | - |
| Colpophyllia natans | - | 0.20 | - | - | 0.44 | 0.44 | - |
| Mycetophyllia ferox | - | - | - | - | 0.10 | 0.04 | - |
| Stephanocoenia intersepta + Solenastrea hyades | 0.09 | 0.03 | 0.06 | - | 1.40 | 0.19 | 0.16 |
| E+F+D | | | | | | | |
| Millepora alcornis | 0.09 | 0.08 | 0.70 | 0.49 | 0.55 | 0.91 | 0.16 |
| Acropora cervicornis | - | 0.06 | - | 0.08 | 0.10 | 0.09 | - |
| E+F+D+C | | | | | | | |
| Wrangellia spp. | - | - | 0.03 | - | - | 0.03 | - |
| Meandrina meandrites | - | - | 0.14 | 0.04 | 0.05 | 0.10 | - |
| Neomeris spp. | 0.05 | - | 0.08 | - | - | 0.06 | - |
| Styopodium zonale | 0.79 | 0.03 | 5.28 | 0.66 | - | 3.10 | - |
| Erect sponges | 1.22 | 0.59 | 2.18 | 1.52 | 1.07 | 3.54 | 4.82 |
| Siderastrea siderea | 0.93 | 0.60 | 1.93 | 2.01 | 2.39 | 2.62 | 0.93 |
| Octocoral bases | 0.97 | 1.00 | 0.98 | 1.35 | 2.37 | 2.39 | 0.62 |
| Encrusting sponges | 0.11 | 0.25 | 0.48 | 0.16 | 1.51 | 0.79 | 3.11 |
| Dictyota spp. | 11.33 | 4.60 | 28.45 | 16.63 | 7.33 | 11.44 | 2.49 |
| Other Algae | 0.02 | 0.01 | 0.11 | 0.04 | - | 0.03 | - |
| Laurencia spp. | - | 0.21 | 0.92 | - | - | 0.10 | - |
| Anadyomene spp. | 0.05 | - | 0.39 | - | - | - | - |
| St. 22 | | | | | | | |
| Dictyoteris spp. | - | - | - | - | - | - | 3.89 |
| Avranvillea spp. | 0.02 | - | 0.03 | - | 0.03 | - | 14.77 |
| All groups | | | | | | | |
| Dichocoenia stokesi | - | - | - | 0.08 | 0.05 | 0.09 | 0.78 |
| Diploria strigosa | 0.79 | 0.03 | 0.11 | 0.41 | 0.13 | 0.80 | - |
| Ricordea florida | - | 0.03 | - | 0.12 | 0.03 | - | - |
| Sargassum spp. | 7.61 | 10.39 | 8.64 | 8.54 | 16.31 | 10.99 | - |
| Rhiphocephallus spp. | 0.07 | 0.07 | 0.17 | 0.12 | - | 0.06 | - |
| Scolymia spp. | - | 0.04 | 0.03 | - | 0.10 | - | - |
| Manicina aerolata | - | 0.03 | 0.03 | - | - | 0.03 | - |
| Filamentous algae | 4.76 | 10.29 | 13.08 | 5.25 | 10.30 | 4.88 | 1.71 |
| BARE HARD GROUD | 15.88 | 3.34 | 0.25 | 5.01 | 0.75 | 16.17 | 14.15 |
| Isophyllastrea rigida | - | 0.04 | - | - | - | 0.05 | - |
| Cyanophyceae | 0.27 | 2.70 | 4.58 | - | 0.96 | 0.93 | 0.93 |
| Lobophora variegata | 5.78 | 20.83 | 12.02 | 3.28 | 15.50 | 17.34 | 25.04 |
| Porites astreoides | 0.43 | 1.25 | 0.17 | 1.03 | 0.91 | 0.89 | 0.16 |

Table 2. continued.

| | 9.40 | 10.81 | 7.24 | 25.04 | 3.59 | 6.36 | 8.55 |
|---------------------------|------|-------|------|-------|------|------|------|
| SAND | | | | | | | |
| Halimeda spp. | 4.67 | 4.15 | 2.91 | 1.68 | 7.57 | 2.40 | 5.91 |
| Eusmilia fastigiata | - | 0.13 | 0.03 | 0.04 | 0.13 | 0.04 | - |
| Agaricia agaricites | 3.29 | 3.11 | 0.73 | 3.69 | 2.81 | 2.36 | - |
| Porites furcata | 0.32 | 0.31 | - | 0.21 | 0.21 | 0.32 | - |
| Scolymia wellsi | - | 0.03 | - | - | - | 0.03 | - |
| Mussa angulosa | - | 0.01 | 0.03 | - | - | - | - |
| Udotea spp. | 1.00 | 0.14 | 0.03 | 1.15 | 0.44 | 0.05 | 0.16 |
| Mycetophyllia lamarckiana | - | 0.07 | - | - | - | 0.06 | 0.16 |
| Agaricia fragilis | 0.02 | 0.04 | - | - | 0.08 | - | - |
| Porites porites | 0.32 | 0.85 | 0.03 | 1.15 | 0.29 | 0.18 | - |
| RUBBLE | 3.44 | 1.84 | - | 5.13 | 0.08 | 0.49 | - |
| Sea Anemones | 0.11 | 0.13 | - | 0.08 | 0.08 | 0.04 | - |
| Galaxaura spp. | 0.09 | 0.18 | 0.17 | 0.08 | 0.03 | - | - |
| Tunicates | 0.07 | 0.03 | - | 0.04 | 0.16 | - | 2.33 |
| Amphiroa spp. | 1.02 | 0.35 | 0.17 | - | 0.13 | 0.18 | 1.09 |
| Agaricia humilis | 0.02 | 0.04 | - | - | - | 0.01 | - |
| Jannia spp. | 1.52 | 0.60 | 0.50 | 0.04 | 0.16 | 0.16 | 6.38 |
| Porites divaricata | 0.02 | 0.28 | - | - | 0.13 | - | 0.78 |

Table 3. Octocoral community assemblages (colonies m^{-2} per group letter). Boxes mark the species characteristic of each successively nested cluster as in Figure 14 (R-mode analysis, 70% relative abundance of each species in determinate cluster[s]). Quitasueño bank. Shaded cells represent values >0.2 colonies m^{-2} (>2 colonies every $10 m^{-2}$).

| SPP | A | B | C | D | E | F | St22 |
|-----------------------------|-------|-------|-------|-------|-------|-------|-------|
| Cluster B | | | | | | | |
| Briareum polyanthes | - | 0.060 | - | - | - | - | - |
| Eunicea laxispica | - | 0.080 | - | 0.009 | - | - | - |
| Plexaura homomalla | - | 0.920 | - | 0.127 | - | 0.023 | - |
| D | | | | | | | |
| Muricea pinnata | - | - | - | 0.009 | - | - | - |
| Eunicea clavigera | - | - | - | 0.073 | - | 0.023 | - |
| F | | | | | | | |
| Plexaurella spp. | - | - | - | - | - | 0.015 | - |
| Muricea spp. | - | - | - | - | - | 0.008 | - |
| Pseudopterogorgia acerosa | - | - | - | - | - | 0.069 | - |
| Pterogorgia anceps | - | - | - | - | - | 0.008 | - |
| Plexaura kuna | - | - | - | - | - | 0.008 | - |
| Eunicea tourneforti | - | - | - | 0.009 | 0.071 | 0.146 | - |
| Pterogorgia citrina | - | 0.040 | 0.150 | - | 0.029 | 0.162 | - |
| Eunicea fusca | - | - | - | 0.045 | 0.043 | 0.185 | - |
| Muricea atlantica | - | - | - | 0.009 | - | 0.023 | - |
| Muricea muricata | - | - | - | 0.018 | - | 0.038 | - |
| D+E | | | | | | | |
| Pseudopterogorgia bipinnata | 0.025 | - | 0.150 | 1.882 | 3.057 | 0.077 | - |
| Gorgonia mariae | - | - | - | 0.082 | 0.186 | 0.031 | - |
| Muriceopsis flavida | - | - | - | 0.527 | 0.529 | 0.231 | - |
| Eunicea colombiana* | - | - | 0.100 | 0.118 | 0.029 | 0.031 | - |
| D+E+F | | | | | | | |
| Plexaurella fusifera | - | - | - | 0.018 | 0.086 | 0.054 | - |
| Eunicea tayrona* | - | - | - | 0.036 | 0.186 | 0.077 | - |
| Pseudopterogorgia americana | 0.013 | 0.060 | 0.250 | 0.027 | 0.500 | 0.554 | 0.100 |
| Muricea elongata | - | 0.020 | 0.050 | 0.045 | 0.014 | 0.046 | - |
| Plexaura flexuosa | 0.013 | 0.180 | - | 0.055 | 0.086 | 0.231 | - |
| Pseudoplexaura spp. | - | 0.280 | 0.250 | 0.264 | 0.129 | 0.231 | - |
| Eunicea pallida | - | 0.020 | - | 0.009 | - | 0.015 | - |
| Gorgonia ventalina | 0.050 | 0.080 | 0.200 | 0.036 | 0.186 | 0.138 | - |
| Plexaurella nutans | - | 0.040 | - | 0.018 | 0.029 | 0.008 | - |
| Plexaura kukenthalii | 0.013 | 0.460 | 0.050 | 0.236 | 0.014 | 0.246 | - |
| Plexaurella grisea | 0.013 | 0.520 | 0.200 | 0.445 | 0.043 | 0.146 | - |
| D+E+F+C | | | | | | | |
| Eunicea calyculata | - | - | 0.100 | 0.009 | 0.014 | - | - |
| Eunicea laciniata | 0.013 | - | 0.100 | 0.009 | - | 0.015 | - |
| D+E+F+C+B | | | | | | | |
| Eunicea mammosa | - | 0.240 | - | 0.127 | 0.043 | 0.062 | - |
| Eunicea asperula | - | 0.040 | - | 0.009 | - | 0.023 | - |
| Briareum asbestinum | 0.338 | 0.380 | - | 0.627 | - | 0.100 | - |
| Plexaurella dichotoma | - | 0.120 | - | 0.018 | 0.029 | 0.023 | 0.200 |
| Eunicea succinea | 0.050 | 0.840 | - | 0.109 | 0.100 | 0.015 | - |
| Pseudoplexaura crucis | 0.038 | 0.120 | - | - | - | 0.031 | - |

* Sánchez (submitted).

Table 4. Mean values (X) and standard deviations (sd) for different variables of the benthic communities at Serrana bank according to the classification of Figure 11.

| Cluster | A | | B | | C | | D | | E | |
|--|--------|--------|--------|--------|--------|--------|--------|--------|--------|--------|
| | X | sd | X | sd | X | sd | X | sd | X | sd |
| Rugosity index | 0.230 | 0.132 | 0.643 | 0.318 | 0.672 | 0.187 | 0.516 | 0.211 | 0.306 | 0.184 |
| Depth (m) | 5.839 | 4.379 | 4.875 | 5.318 | 8.226 | 1.088 | 15.681 | 6.234 | 10.497 | 2.032 |
| Coral species | 7.500 | 4.722 | 3.000 | 2.160 | 4.778 | 1.856 | 4.882 | 3.059 | 11.818 | 4.119 |
| Octocoral species | 14.000 | 2.608 | 13.750 | 0.957 | 17.556 | 3.046 | 21.235 | 5.142 | 17.545 | 4.034 |
| SUBSTRATE COVER (%) | | | | | | | | | | |
| Coral cover | 6.844 | 4.551 | 14.394 | 5.779 | 38.931 | 12.137 | 21.321 | 10.461 | 8.873 | 7.075 |
| Encrusting algae | 2.801 | 2.170 | 7.149 | 6.452 | 3.932 | 1.694 | 4.750 | 3.400 | 4.317 | 2.494 |
| Calcareous macro algae | 6.826 | 4.207 | 8.565 | 2.853 | 12.974 | 7.660 | 12.413 | 5.706 | 4.234 | 2.676 |
| Fleshy macro algae | 17.098 | 17.838 | 23.781 | 15.679 | 18.561 | 6.734 | 22.901 | 11.208 | 39.926 | 12.587 |
| Filamentous algae | 2.913 | 2.093 | 14.568 | 6.444 | 9.708 | 5.051 | 12.157 | 7.270 | 9.813 | 6.514 |
| Other fleshy invertebrates | 0.026 | 0.063 | - | - | 0.101 | 0.167 | 0.113 | 0.206 | 0.028 | 0.063 |
| Encrusting sponges | 0.363 | 0.635 | 0.752 | 0.670 | 0.881 | 0.617 | 1.260 | 1.142 | 0.399 | 0.255 |
| Erect Sponges | 2.026 | 1.850 | 0.765 | 1.032 | 1.387 | 0.635 | 2.713 | 2.728 | 3.576 | 1.698 |
| Octocoral bases | 1.661 | 1.229 | 0.199 | 0.300 | 0.376 | 0.477 | 1.324 | 1.315 | 1.530 | 1.318 |
| Bare hard ground | 6.316 | 8.127 | 7.758 | 9.029 | 4.662 | 6.352 | 4.143 | 5.082 | 4.858 | 8.107 |
| Rubble | 12.741 | 13.282 | 8.836 | 9.952 | 1.141 | 2.331 | 2.970 | 6.074 | 2.083 | 4.187 |
| Sand | 40.386 | 28.154 | 13.233 | 7.402 | 7.347 | 5.792 | 13.935 | 12.136 | 20.361 | 12.940 |
| Recently dead coral | - | - | - | - | 0.801 | 1.423 | 1.639 | 6.556 | - | - |
| DENSITIES | | | | | | | | | | |
| Octocorals (colonies m⁻²) | 1.783 | 1.566 | 0.150 | 0.191 | 0.656 | 0.606 | 3.500 | 3.659 | 2.209 | 1.424 |
| Diadema antillarum (individuals m⁻²) | - | - | 0.205 | 0.371 | 0.042 | 0.045 | 0.008 | 0.014 | 0.004 | 0.008 |
| Echinometra viridis (ind. m⁻²) | - | - | 0.085 | 0.114 | 0.236 | 0.308 | 0.015 | 0.030 | - | - |
| CORAL DISEASES | | | | | | | | | | |
| White Plague-WP (No. affected spp.) | 0.333 | 0.516 | 0.500 | 0.577 | 2.556 | 2.128 | 3.118 | 3.160 | 0.182 | 0.405 |
| WP-average of percentage affected tissue | 0.333 | 0.516 | 0.500 | 0.577 | 2.556 | 2.128 | 3.118 | 3.160 | 0.182 | 0.405 |
| Dark Spots-DS (No. affected spp.) | 0.500 | 0.837 | - | - | 0.778 | 0.972 | 0.765 | 1.091 | 2.000 | 1.342 |
| DS-average of percentage affected tissue | 0.333 | 0.516 | - | - | 0.391 | 0.781 | 0.903 | 1.484 | 1.510 | 1.112 |
| Bleaching (No. affected spp.) | 0.333 | 0.516 | 0.500 | 0.577 | 0.222 | 0.441 | 0.588 | 0.939 | 0.455 | 0.688 |
| BL-average of percentage affected tissue | 0.003 | 0.005 | 0.253 | 0.498 | 0.002 | 0.004 | 0.461 | 0.807 | 0.185 | 0.602 |

Table 5. Benthic community assemblages (data as coral cover per group letter). Boxes mark all the species characteristic of each successively nested cluster according to Figure 18 (R-mode analysis including the 70% relative abundance of each species in determinate cluster[s]). Serrana bank. Shaded cells represent values >5% of coral cover.

| SPP | A | B | C | D | E | St 1 |
|----------------------------|------|-------|-------|-------|-------|-------|
| B | | | | | | |
| Agaricia fragilis | - | 0.04 | - | - | - | - |
| Mycetophyllia aliciae | - | 0.04 | - | - | - | - |
| C | | | | | | |
| Acropora cecicornis | - | - | 0.16 | - | - | - |
| Montastraea faveolata | 0.16 | 0.20 | 10.12 | 0.72 | 0.95 | 2.27 |
| D | | | | | | |
| Galaxaura spp. | - | - | - | 0.02 | - | - |
| Isophyllastraea rigida | - | - | - | 0.02 | - | - |
| Mussa angulosa | - | - | - | 0.02 | - | - |
| Mycetophyllia ferox | - | - | - | 0.01 | - | - |
| Solenastrea bournoni | - | - | - | 0.01 | - | - |
| Avranvillea spp. | - | - | - | 0.07 | 0.01 | - |
| Acropora palmata | 0.18 | - | - | 0.38 | - | - |
| Agaricia spp. (plate-like) | - | - | - | 0.10 | 0.03 | - |
| Eusmilia fastigiata | - | - | 0.02 | 0.09 | 0.01 | - |
| Manicina aerolata | - | - | - | 0.05 | 0.01 | - |
| Mycetophyllia lamarckiana | - | 0.08 | - | 0.12 | - | 0.15 |
| Recently dead coral | - | - | 0.79 | 1.68 | - | - |
| Cyanophyceae | 0.23 | 2.26 | 0.95 | 6.35 | 0.83 | 0.15 |
| Scolymia spp. | - | - | - | 0.03 | - | 0.15 |
| Millepora complanata | 0.21 | - | - | 0.21 | - | - |
| E | | | | | | |
| Laurencia spp. | - | - | - | - | 0.03 | - |
| C+D | | | | | | |
| Anadyomene spp. | - | - | 0.05 | 0.04 | - | - |
| Penicillus spp. | 0.18 | 0.04 | 0.79 | 1.13 | - | - |
| Agaricia lamarcki | - | 0.08 | 0.14 | 0.23 | 0.01 | - |
| Colpophyllia natans | - | 0.16 | 0.84 | 1.07 | 0.03 | 1.52 |
| Caulerpa spp. | - | - | 0.09 | 0.04 | 0.01 | - |
| Jania spp. | - | 0.40 | 1.03 | 0.27 | 0.01 | 0.15 |
| Tunicates | - | - | 0.09 | 0.02 | 0.01 | - |
| Porites furcata | 0.29 | 0.12 | 1.17 | 0.25 | 0.04 | - |
| Montastraea franksi | 0.03 | 5.81 | 2.76 | 7.01 | 0.36 | - |
| Montastraea annularis | 0.70 | 2.30 | 15.96 | 1.86 | 2.99 | - |
| Encrusting Sponges | 0.36 | 0.48 | 0.88 | 1.32 | 0.40 | - |
| Amphiroa spp. | - | 0.44 | 0.59 | 0.12 | 0.07 | - |
| Rhipocephallus spp. | 0.10 | 0.12 | 0.07 | 0.23 | 0.04 | - |
| Porites porites | 0.26 | 0.69 | 2.22 | 0.47 | 0.40 | 1.36 |
| Agaricia agaricites | 0.52 | 1.94 | 2.09 | 3.00 | 1.12 | 2.73 |
| Porolithon pachydermun | 0.08 | 0.12 | 0.07 | 0.11 | - | - |
| Agaricia humilis | - | 0.04 | 0.02 | 0.04 | - | 0.15 |
| Halimeda spp. | 6.36 | 7.95 | 10.13 | 10.16 | 3.70 | 2.27 |
| C+D+E+st. 1 | | | | | | |
| Leptoseris cucullata | - | - | 0.05 | 0.05 | 0.01 | 0.45 |
| Ricordea florida | - | - | - | 0.02 | 0.01 | - |
| Other macroalgae | - | - | 0.03 | 0.03 | 0.04 | - |
| Styopodium zonale | - | - | - | 0.11 | 0.12 | - |
| Stephanocoenia intersepta | - | - | - | - | - | - |
| + Solenastrea hyades | - | - | 0.07 | - | 0.01 | 0.15 |
| Montastraea cavernosa | - | 0.08 | 0.09 | 0.18 | 0.24 | - |
| Diploria labyrinthiformis | 0.03 | 0.48 | 0.79 | 0.14 | 0.47 | 1.52 |
| Upright Sponges | 2.02 | 0.97 | 1.38 | 2.71 | 3.54 | 0.91 |
| Filamentous algae | 2.67 | 9.04 | 8.70 | 6.61 | 8.89 | 5.76 |
| Lobophora variegata | 5.58 | 13.80 | 8.74 | 15.84 | 13.86 | 0.30 |
| Sargassum spp. | 3.89 | 3.15 | 3.53 | 2.10 | 12.22 | - |
| Dictyota spp. | 6.41 | 4.84 | 5.57 | 2.92 | 12.31 | 31.52 |
| Encrusting corallinaceae | 2.73 | 5.28 | 3.88 | 4.97 | 4.29 | 4.85 |
| Udotea spp. | 0.18 | 0.40 | 0.29 | 0.28 | 0.35 | 0.15 |
| Millepora alcicornis | 0.39 | 0.12 | 0.09 | 0.36 | 0.40 | 0.30 |
| Favia fragum | 0.05 | 0.12 | 0.03 | 0.12 | 0.01 | 0.15 |
| Siderastrea siderea | 1.12 | 0.65 | 0.72 | 0.51 | 1.24 | 2.42 |
| Octocoral bases | 1.66 | 0.85 | 0.38 | 1.15 | 1.54 | 4.85 |
| Dichocoenia stokesi | 0.08 | - | - | 0.03 | 0.04 | 0.45 |
| Bare Hard ground | 6.33 | 7.91 | 4.79 | 4.15 | 4.94 | 22.58 |

Table 5. continued.

C+D+E+st. 1+B

| | | | | | | |
|---------------------------|--------------|-------------|-------------|--------------|--------------|-------------|
| Erythropodium caribaeorum | - | 0.16 | - | 0.04 | - | - |
| Turbinaria spp. | 1.22 | 8.47 | 0.52 | 0.29 | 1.28 | - |
| Siderastraea radians | 0.05 | 0.08 | - | 0.01 | 0.07 | 0.15 |
| Porites astreoides | 1.64 | 1.82 | 0.78 | 1.55 | 0.24 | 1.36 |
| Diploria strigosa | 0.70 | 1.17 | 0.02 | 0.41 | 0.13 | 0.91 |
| Sand | 40.32 | 8.39 | 7.25 | 15.01 | 20.48 | 8.48 |

All groups

| | | | | | | |
|--------------------|--------------|-------------|------|------|------|------|
| Porites divaricata | 0.23 | 0.16 | - | 0.10 | 0.01 | - |
| Rubble | 12.77 | 8.75 | 1.19 | 3.03 | 2.12 | 1.82 |
| Madracis decactis | 0.10 | - | - | 0.04 | - | - |
| Anemones | 0.03 | - | 0.02 | - | - | - |
| Diploria clivosa | 0.13 | - | 0.09 | - | - | - |

Table 6. Octocoral community assemblages (data as colonies m^{-2} per group letter). Boxes mark all the species characteristic of each successively nested cluster according to Figure 28 (R-mode analysis including the 70% relative abundance of each species in determinate cluster[s]). Serrana bank. Shaded cells represent values >0.2 colonies m^{-2} (>2 colonies every $10 m^{-2}$).

| SPP | A | B | C | D | E | F |
|-------------------------------|-------|--------------|--------------|--------------|-------|-------|
| A | | | | | | |
| Eunicea colombiana* | 0.050 | - | - | - | - | - |
| Gorgonia mariae | 0.100 | - | - | - | - | - |
| C | | | | | | |
| Pseudopterogorgia bipinnata | - | - | 3.179 | 0.173 | - | - |
| Pseudopterogorgia elisabethae | - | - | 0.271 | 0.027 | - | - |
| Briareum polyanthes | - | - | 0.043 | 0.013 | - | - |
| D | | | | | | |
| Eunicea asperula | - | - | - | 0.020 | - | - |
| Eunicea calyculata | - | - | - | 0.007 | - | - |
| Eunicea clavigera | - | - | - | 0.007 | - | - |
| Eunicea fusca | - | - | - | 0.073 | - | - |
| Eunicea mammosa | - | - | - | 0.033 | - | - |
| Eunicea pallida | - | - | - | 0.007 | - | - |
| Eunicea succinea | - | - | - | 0.047 | - | - |
| Eunicea tayrona* | - | - | - | 0.013 | - | - |
| Eunicea tourneforti | - | - | - | 0.013 | - | - |
| Muricea atlantica | - | - | - | 0.020 | - | - |
| Plexaurella fusifera | - | - | - | 0.020 | - | - |
| Plexaurella grisea | - | - | 0.007 | 0.193 | - | - |
| Pseudoplexaura spp. | - | 0.040 | - | 0.413 | - | - |
| Plexaura flexuosa | - | 0.010 | - | 0.120 | 0.100 | - |
| Plexaura kukenthali | 0.050 | 0.020 | - | 0.173 | - | - |
| Plexaurella nutans | - | - | 0.007 | 0.053 | - | - |
| Muricea muricata | - | 0.010 | - | 0.033 | - | - |
| Plexaurella dichotoma | - | - | - | 0.033 | - | 0.100 |
| Eunicea laciniata | - | - | 0.007 | 0.027 | - | - |
| C+D | | | | | | |
| Pseudopterogorgia americana | 0.050 | 0.010 | 0.193 | 0.387 | - | - |
| Briareum asbestinum | - | 0.060 | 0.393 | 0.620 | - | - |
| Muriceopsis flavida | - | 0.030 | 0.114 | 0.047 | - | - |
| C+D+B | | | | | | |
| Plexaura homomalla | - | 0.120 | - | 0.047 | - | - |
| Gorgonia ventalina | - | 0.320 | 0.036 | 0.060 | - | - |
| Outliers | | | | | | |
| Muricea spp. | - | - | - | 0.007 | 0.100 | - |
| Plexaura kuna | 0.100 | 0.010 | - | - | - | - |

* from Sánchez (submitted).

Table 7. Mean values (X) and standard deviations (sd) for different variables of the benthic communities at Roncador Bank according to the classification of Figure 17.

| CLUSTERS | A | | B | | C | |
|---|--------|--------|--------|--------|--------|--------|
| | X | sd | X | sd | X | sd |
| Rugosity index | 0.584 | 0.379 | 0.664 | 0.096 | 0.729 | 0.339 |
| Depth (m) | 2.437 | 0.862 | 24.754 | 3.734 | 11.748 | 4.037 |
| Coral species | 16.000 | 4.243 | 24.250 | 2.986 | 22.313 | 4.527 |
| Octocoral species | 11.500 | 2.121 | 7.000 | 1.826 | 10.875 | 4.884 |
| SUBSTRATE COVER (%) | | | | | | |
| Coral cover | 8.714 | 3.345 | 15.615 | 2.330 | 18.260 | 10.424 |
| Encrusting algae | 20.360 | 22.164 | 7.231 | 2.868 | 6.148 | 2.157 |
| Calcareous macro algae | 10.460 | 0.876 | 6.930 | 1.438 | 7.976 | 4.985 |
| Fleshy macro algae | 24.251 | 6.685 | 31.276 | 19.301 | 30.612 | 14.151 |
| Filamentous algae | 19.053 | 6.053 | 17.918 | 11.966 | 13.829 | 8.891 |
| Other fleshy invertebrates | - | - | 0.039 | 0.077 | 0.078 | 0.127 |
| Encrusting sponges | 1.976 | 2.593 | 1.089 | 0.855 | 0.224 | 0.301 |
| Erect Sponges | - | - | 1.756 | 1.160 | 0.598 | 0.790 |
| Octocoral bases | 3.610 | 3.533 | 1.788 | 0.802 | 3.496 | 1.728 |
| Bare hard ground | 0.071 | 0.100 | 3.663 | 2.781 | 2.020 | 2.827 |
| Rubble | 0.071 | 0.100 | 0.859 | 1.335 | 1.389 | 1.827 |
| Sand | 11.435 | 16.171 | 11.835 | 12.894 | 15.369 | 12.527 |
| DENSITIES | | | | | | |
| Octocorals (colonies m ⁻²) | 4.550 | 2.475 | 5.725 | 2.980 | 11.256 | 4.930 |
| Diadema antillarum (individuals m ⁻²) | 0.020 | 0.028 | 0.005 | 0.010 | 0.030 | 0.048 |
| Echinometra viridis (ind. m ⁻²) | - | - | 0.005 | 0.010 | 0.028 | 0.055 |
| CORAL DISEASES | | | | | | |
| White Plague-WP (No. affected spp.) | 1.000 | - | 0.250 | 0.500 | 0.438 | 0.512 |
| WP-average of percentage affected tissue | 1.000 | - | 0.003 | 0.005 | 0.689 | 1.447 |
| Dark Spots-DS (No. affected spp.) | 1.000 | - | 0.500 | 0.577 | 0.938 | 1.340 |
| DS-average of percentage affected tissue | 15.000 | 7.071 | 1.000 | 1.155 | 1.261 | 2.561 |
| Bleaching (No. affected spp.) | 1.000 | - | 1.000 | 0.816 | 0.500 | 0.730 |
| BL-average of percentage affected tissue | 0.505 | 0.700 | 0.503 | 0.574 | 0.502 | 1.316 |

Table 8. Benthic community assemblages (data as coral cover per group letter). Boxes mark all the species characteristic of each successively nested cluster according to Figure 32 (R-mode analysis including the 70% relative abundance of each species in determinate cluster[s]). Roncador Bank. Shaded cells represent values >5% of coral cover.

| SPP | A | B | C |
|-----------------------------|-------|-------|-------|
| A | | | |
| Laurencia spp. | 1.50 | - | - |
| Millepora complanata | 1.05 | - | - |
| Porolithon pachydermun | 2.47 | - | - |
| B | | | |
| Agaricia fragilis | - | 0.04 | - |
| Scolymia cubensis | - | 0.04 | - |
| Scolymia wellsii | - | 0.12 | - |
| Tunicates | - | 0.04 | - |
| Agaricia spp. (plate-like) | - | 0.23 | 0.02 |
| C | | | |
| Agaricia humilis | - | - | 0.01 |
| Anemones | - | - | 0.02 |
| Caulerpa spp. | - | - | 0.03 |
| Diploria clivosa | - | - | 0.07 |
| Isophyllastrea rigida | - | - | 0.01 |
| Manicina aerolata | - | - | 0.04 |
| Mycetophyllia ferox | - | - | 0.07 |
| Meandrina meandrites | - | - | 0.01 |
| Other macroalgae | - | - | 0.02 |
| Porites divaricata | - | - | 0.01 |
| Ricordea florida | - | - | 0.05 |
| Styopodium zonale | - | - | 0.03 |
| Wrangelia spp. | - | - | 0.01 |
| Zoanthids | - | - | 0.01 |
| Diploria labyrinthiformis | 0.07 | - | 0.39 |
| Montastraea annularis | 2.10 | 0.04 | 7.23 |
| Amphiroa spp. | 0.07 | 0.04 | 0.45 |
| Porites porites | 0.37 | - | 1.04 |
| Diploria strigosa | - | 0.12 | 0.60 |
| Porites furcata | 0.15 | - | 0.33 |
| Riphocephallus spp. | - | 0.04 | 0.12 |
| Colpophyllia natans | - | 0.27 | 0.83 |
| Penicillus spp. | 0.22 | 0.23 | 0.77 |
| Siderastrea siderea | - | 0.39 | 0.77 |
| Sargassum spp. | 0.30 | 0.39 | 0.98 |
| Porites astreoides | 0.90 | 0.43 | 1.53 |
| Rubble | 0.07 | 0.86 | 1.32 |
| Jania spp. | 0.37 | 0.04 | 0.30 |
| Octocoral bases | 3.75 | 1.79 | 3.47 |
| Sand | 12.07 | 11.79 | 15.16 |
| Scolymia spp. | - | 0.04 | 0.03 |
| Agaricia lamarcki | 0.07 | - | 0.03 |
| Dictyota spp. | 21.74 | 1.01 | 9.42 |
| Lobophora variegata | 0.97 | 29.93 | 20.38 |
| Galaxaura spp. | 0.15 | - | 0.05 |
| Millepora alcicornis | 0.22 | 0.66 | 0.47 |
| Montastraea faveolata | - | 1.28 | 0.77 |
| B+C | | | |
| Dichocoenia stokesi | - | 0.04 | 0.02 |
| Upright Sponges | - | 1.75 | 0.61 |
| Montastraea cavernosa | - | 0.39 | 0.12 |
| Mycetophyllia lamarckiana | - | 0.43 | 0.12 |
| Avranvillea spp. | - | 0.04 | 0.01 |
| Eusmilia fastigiata | - | 0.19 | 0.05 |
| Mycetophyllia aliciae | - | 0.04 | 0.01 |
| Montastraea franksi | - | 9.46 | 2.24 |
| Leptoseris cucullata | - | 0.12 | 0.02 |
| Madracis decactis | - | 0.23 | 0.04 |
| Stephanocoenia intersepta + | - | 0.12 | 0.02 |
| Solenastrea hyades | - | 0.12 | 0.02 |
| Bare Hard ground | 0.07 | 3.66 | 2.07 |

Table 8. continued.

| | | | |
|--------------------------|--------------|--------------|-------------|
| All Groups | | | |
| Udotea spp. | 0.22 | 0.51 | 0.37 |
| Cyanophyceae | 3.22 | 7.51 | 3.77 |
| Filamentous algae | 15.59 | 10.35 | 9.87 |
| Halimeda spp. | 9.45 | 6.07 | 6.01 |
| Favia fragum | 0.07 | 0.12 | 0.03 |
| Encrusting corallinaceae | 17.02 | 7.24 | 6.12 |
| Agaricia agaricites | 3.82 | 0.82 | 1.38 |
| Encrusting Sponges | 1.87 | 1.09 | 0.23 |

Table 9. Octocoral community assemblages (data as colonies m^{-2} per group letter). Boxes mark all the species characteristic of each successively nested cluster according to Figure 41 (R-mode analysis including the 70% relative abundance of each species in determinate cluster[s]). Roncador bank. Shaded cells represent values >0.2 colonies m^{-2} (>2 colonies every $10 m^{-2}$).

| SPP | A | B | C | St.16 |
|-------------------------------|--------------|--------------|--------------|--------------|
| A | | | | |
| Eunicea succinea | 0.033 | - | - | - |
| Eunicea tourneforti | 0.033 | - | - | - |
| Muricea elongata | 0.100 | - | - | - |
| Muricea spp. | 0.033 | - | - | - |
| Plexaura homomalla | 0.200 | - | - | - |
| Eunicea tayrona* | 0.133 | - | 0.020 | - |
| Plexaurella grisea | 0.967 | 0.062 | 0.020 | - |
| Eunicea laxispica | 0.400 | 0.031 | - | - |
| B | | | | |
| Eunicea asperula | - | 0.015 | - | - |
| Eunicea clavigera | - | 0.008 | - | - |
| Eunicea fusca | - | 0.608 | - | - |
| Eunicea knighti | - | 0.038 | - | - |
| Eunicea pallida | - | 0.008 | - | - |
| Muricea atlantica | - | 0.015 | - | - |
| Muricea laxa | - | 0.015 | - | - |
| Plexaura kuna | - | 0.008 | - | - |
| Pseudoplexaura spp. | - | 0.008 | - | - |
| Muriceopsis flavida | - | 0.108 | 0.020 | - |
| Briareum polyanthes | 0.067 | 0.185 | - | 0.100 |
| Briareum asbestinum | 0.767 | 1.854 | 0.100 | 0.400 |
| Pseudopterogorgia bipinnata | 1.967 | 8.331 | 5.020 | 0.100 |
| Eunicea colombiana* | - | 0.023 | 0.020 | - |
| C | | | | |
| Pseudopterogorgia elisabethae | - | 0.100 | 0.900 | - |
| B+C | | | | |
| Plexaurella dichotoma | - | 0.015 | 0.040 | - |
| Plexaurella nutans | - | 0.031 | 0.060 | - |
| Pseudopterogorgia americana | - | 0.400 | 0.700 | - |
| Plexaurella fusifera | - | 0.015 | 0.020 | - |
| Eunicea laciniata | 0.033 | 0.023 | 0.020 | - |
| B+C+A | | | | |
| Muricea muricata | 0.033 | 0.008 | 0.020 | - |
| Plexaura flexuosa | 0.067 | 0.023 | 0.020 | - |
| Gorgonia mariae | 0.033 | 0.015 | - | - |
| Gorgonia ventalina | 0.533 | 0.154 | - | - |
| Eunicea mammosa | 0.200 | 0.038 | - | - |
| Plexaura kukenthalii | 0.367 | 0.054 | 0.040 | - |

* from Sánchez (submitted).

Table 10. Areas of especial ecological interest (benthic communities) in the Northern Cays; mean values (min-max).

| Location | Important feature | Habitat distribution | Coral spp. | Coral cover (%) | Octocoral spp. | Octocoral density col. m ⁻² |
|---|--|---|------------------|---------------------|----------------|--|
| High coral abundance and diversity areas | | | | | | |
| Roncador bank: Fig. 19 A; cluster C; Fig. 24C | Mixed corals and highest gorgonian densities and coral cover. Dominant spp.: <i>Pseudopterogorgia bippinata</i> & <i>Montastraea annularis</i> | ' <i>Montastraea</i> ' | 22 (12-29) | 41.9 (23.2-52.3) | 10 (3-22) | 11.2 (0.6-22.4) |
| Serrana bank Fig. 12 A; Clt. C.; Fig. 24 B | <i>M. faveolata</i> and scattered <i>Acropora cervicornis</i> populations. | ' <i>Acropora palmata</i> - <i>Diploria</i> ' ' <i>Montastraea</i> ' | 17 (13-22) | 38.9 (14.6-52.3) | 4 (3-8) | 0.65 (0.1-1.6) |
| Quitasueño Bank Fig. 5A: clt. F; Fig. 24A | Extensive mixed coral area at exposed Fore-reef terrace. (naturally protected) | 'mixed corals' | 22 (17-28) | 32.9 (18.3-50.7) | 10 (6-16) | 4.4 (2.2-9.7) |
| Quitasueño Bank Fig. 5A: clt. B; Fig. 24A | South lagoonal-leeward terrace patch reefs (<i>Montastraea</i> spp.) | ' <i>Montastraea</i> ' 'mixed corals' | 20 (12-27) | 35.6 (25.3-42.9) | 8 (4-12) | 2.9 (0.3-5.6) |
| Quitasueño Bank Fig. 5A: clt. E; Fig. 24A | Extensive leeward mixed coral areas. | 'mixed corals' | 23 (18-30) | 39 (33.3-46.6) | 11 (7-15) | 4.45 (0.4-10.6) |
| Areas of particular concern (Fig. 24 B-C) | | | | | | |
| Roncador & Serrana banks fore-reef terrace (Fig. 24 B-C) | High densities of endangered sea fan species <i>Gorgonia ventalina</i> and <i>G. flabellum</i> . | 'Octocorals and mixed corals' high relief spur & groove | 19.7* ±7.4 SD | ~13* | ~14** | 5.8** (2.6-9) |
| Roncador bank: Fig. 19 A: clt. B (see also Serrana bank; Fig. 12 B, clt. C) | Mixed corals and high densities of a commercially important octocorals: <i>P. elisabethae</i> | 'Mixed coral' | 24 (20-27) | 15 (13.2-18.1) | 7 (5-9) | 5.7 (2.3-9.5) |
| Serrana bank*** Fig. 12 A; Clt. D. | <i>Montastraea</i> spp. patch reefs, shallow area with <i>A. palmata</i> and coralline algae. | <i>Acropora palmata</i> - <i>Diploria</i> ' ' <i>Montastraea</i> ' | 21 (12-30) | 21.3 (7.1-41.8) | 4 (1-14) | 3.5 (0-13.9) |

* From Diaz-Pulido et al. (submitted); ** From Sánchez J.A. (unpublished, 1995)

*** Heterogeneous area showing both degradation in deeper parts and active *A. palmata* reefs in the shallow parts.

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