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YUCATAN PENINSULA, MEXICO

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ABSTRACT

The coastal shelf of the Sian Ka'an Biosphere Reserve was surveyed in order to determine the distribution and composition of coral reefs, and to assess the nature and relative cover of coralline biota along the Reserve shelf, both in reef and non-reef habitats. A census of 11 living morphological attributes (including stony corals, sponges, algae and gorgonians), and 3 non-living ones, was quantitatively estimated by means of line-transects at 30 sampling stations. Well developed coral reef structures, are mostly restricted to shallow _Acropora palmata_ reefs, forming a fringing-barrier reef bordering the shoreline. A relatively high proportion of dead _A. palmata_ was found in these reefs, both in the crest and in the shallow fore reef zone. The cause of _A. palmata_ mortality is unknown. In deeper waters, isolated raised karstic features are colonized by a rich and diverse coral community. However, the majority of the bottom of the shallow shelf consists of hardgrounds with sparse coral cover. Coral community composition and relative degree of development seems to be influenced principally by the magnitude of the submarine topographical relief and depth.

INTRODUCTION

As part of the effort to preserve and protect natural systems threatened by the development of modern society, a large Biosphere Reserve was established in the eastern margin of the Yucatán Peninsula, México, in 1986. The Sian Ka'an Biosphere Reserve encompasses a complex set of environments and communities, ranging from tropical forests, wetlands, estuarine and marine coastal lagoons, to coral reefs. The environment of

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the Sian Ka'an reserve has been studied with a strong emphasis on terrestrial topics (see CIQRO, 1983; Navarro and Robinson, 1990). No similar comprehensive studies of the marine systems in the Sian Ka'an Reserve have been carried out. Long term studies have been restricted to the biology and fishery of spiny lobsters (Lozano-Alvarez, et al., 1991), while other published studies mostly consist of taxonomic lists from the northern part of the reserve or from other nearby, accessible areas (Navarro and Robinson, 1990).

This study was conducted in order to contribute to the understanding of the broad ecological framework of the benthic coastal marine ecosystems in the Sian Ka'an Reserve. Because of the expanse of the reef and coastal system of the Sian Ka'an Reserve, this first work is by necessity a preliminary, general approach.

STUDY AREA

The Sian Ka'an Biosphere Reserve is located on the eastern side of the Yucatán Peninsula, facing the Caribbean Sea (Fig. 1). The Reserve covers an area of approximately 4,500 km^2, of which some 1,200 km^2 correspond to lagoon and marine environments. The marine coastline extends for more than 100 km, and a nearly continuous reef system is found along it.

The Yucatán Peninsula is a large platform formed by extensive carbonate and evaporite deposition, since the lower Cretaceous to the Present (Weidie, 1985). On the eastern margin of the Peninsula are a series of NNE to NE trending ridges and depressions, reflecting the occurrence of the horst and grabben blocks of the Rio Hondo fault zone. The bays of Ascención and Espíritu Santo, the major geomorphological features in the eastern continental margin, are a result of this fault system (Fig. 1). The shelf is covered by carbonate rocks and sediments of Tertiary to Holocene age. In the Sian Ka'an coastal zone, Quaternary sediments predominate from Punta Tupac (section V, Fig. 1) to the north; while older sediments predominate south of Punta Herrero (section VI, Fig. 1; López Ramos, 1973).

The Sian Ka'an Biosphere Reserve has a low relief carbonate coastline of alternating rocky outcrops and sandy beaches, interrupted by the mouths of the two large, shallow bays, and the Boca Paila inlet. The shoreline of the bays and inlets is bordered by a well-developed mangrove forest (Olmsted and Durán, 1990), while the bottoms are predominantly covered by the seagrass Thalassia testudinum. The coastal shelf extends offshore from about 1000m to almost 4000m, gently sloping seaward. At the shelf edge, the shelf abruptly drops to depths in excess of 400m (Fig. 2). The morphology of the shelf is locally modified by erosional terraces and small escarpments. The escarpments are relatively steep (20° to 30°) as compared with the average slope of the shelf (3° to 5°), and they are found in two depth ranges in almost all sections of the shelf. The first escarpment is found at depths of -7 to -10m from sections I to V, and slightly deeper (-9 to -14m) in sections VII to VIII. The second escarpment is found between -33 to -39m in sections IV to VI, and slightly deeper in section VII (-36 to -45m; Fig. 2).

The climate on the Sian Ka'an Reserve is warm and subhumid. Mean air temperature is 25.4 °C, although in the coastal zone air temperature is strongly influenced by predominant winds (pers. obs.). Trade winds predominate from March to September, and colder north winds from November to March. Average rainfall for a fifteen year period (1967-1982) was 1023.3 ± 320.6 mm per year (López-Ornat, 1983). Seventy percent of the yearly rainfall occurs from May to October, with precipitation peaks in June and September.

Hydrological data from both the marine and estuarine-lagoonal environments are scarce, since no systematic survey has been done. The few available data indicate surface salinities in the outer areas of the bays are in the order of 35-36 ppt, and sea surface temperatures range from 31°C in summer, to 23°C in winter (Briones, pers. com.). These values are comparable with those of the Belizean shelf (Purdy et. al., 1975) and with those noted in the northeast end of the Yucatan Peninsula at Puerto Morelos (Merino and Otero, 1991). Run-off and underground seepage may provide enough fresh and brackish water to reach the fringing reefs (particularly at Boca Paila inlet, Section II; Fig. 1). During ebb tide we have observed slightly brownish (mangrove tanins ?) and colder superficial waters flowing through channels in localities III and VI (Fig. 1). Sediment runoff however, is limited due to the karstic nature of the terrestrial substrate and the scarcity of soil on the land. In the case of the banks and barrier reefs that border the two large bays, fresh water influence is perhaps lower due to dilution in the large, predominantly marine, water mass of the bays (pers. obs.).

METHODS

Reef crests and other coastal shallow features were mapped by using LANDSAT color enhanced satellite imagery and low level black and white aerial photography (Fig. 1). The surveyed sections, encompassing the coastline of the reserve (I to VIII, Fig. 1; Table 1) were determined by systematic sampling criteria and to a certain extent by remarkable features of both coast and reef morphology.

Precise geographical positioning of the sections to be sampled (Fig. 1, I to VIII) was obtained by means of satellite navigation system (GPS). The precision of the "fix" was in the order of tens of meters. The same GPS system together with radar bearing checks was utilized to control the registers of the bathymetric profiler on each section. The bathymetric transects were orthogonal to the shoreline, from the edge of the shelf to the shore, and were done in two parts: The first one was made with high resolution echosounders on board the research vessel, from the edge of the shelf to approximately -10m (ship's draft approximately 5m). The second one was made with a portable echosounder, on a small boat following a compass course. Drift and speed of the small boat were tracked by radar from the research vessel.

In each section, a qualitative survey was carried out by means of drift diving at depths of -10m, -20m, -30m and -40m (marked by anchored buoys). Each drift dive extended at least one km north and south from the buoys. A much wider survey of the shallow reef areas was carried out by snorkeling, including important shallow reef structures that were not covered by the diving (Localities A, B and C; Fig. 1). In all qualitative surveys an estimation of the reef structure (dimensions, depth ranges, morphology and setting) was carefully noted on underwater slates and by still photography. The most abundant (relative bottom coverage) species of corals, sponges, gorgonians and macroalgae colonizing all types of substrata were recorded (Jordán, 1990).

The quantitative sampling of the coral communities was designed to provide a global coverage perspective rather than a detailed study of isolated points. The method was based on the estimation of the relative coverage of the sessile coral reef macrobiota as well as substrata apparently devoid of biota. The biota was classified by means of attributes related to biotic substrate control and its relative importance as reef builders (Table 1; see Bradbury et. al., 1986; Reichelt et al., 1986).

For the sampling, we used multiple chain transects (Loya, 1978). At each sampling station five 20m chain transects were randomly laid parallel to the bathymetric profile. This sample size was arbitrarily determined based on previous experiences in a similar environment (Jordán et al., 1981; Jordán, 1989a), because limited ship time, did not allow us to estimate specific sample sizes for the different habitats. The relative importance of each attribute was determined by summing the number of links that covered the biota and non-biotic surfaces under a given transect-chain. The data of the five transects were pooled together to obtain a single value per attribute and per station, and expressed as lineal cm of cover (1 link=3.32cm; Table 2).

Four sampling stations on each section were quantitatively surveyed: a) Rear Reef-Crest (RR-C, shallow reefs); b) -10m Slope (associated with the first main escarpment); c) -20m Slope (mainly flat hard grounds), and -30m Slope (associated with the main second escarpment). The attribute data were classified by means of cluster analysis (Bradbury et al., 1986), pooling data of sampling stations after logarithmic transformation to eliminate size and abundance effects and to ensure independence of scales (Gower, 1986; Gauch, 1982). The cluster analysis was performed using Euclidean distance as a measure of similarity and average linkage.

RESULTS

I. Reef Morphology

Two main coral reef types can be recognized in the Sian Ka'an Biosphere Reserve: I) **Crest Reefs**. Shallow, mostly emergent reefs, fringing the land margin or forming narrow barriers offshore. II) **Slope Reefs**. Deeper reefs associated with the discontinuous shelf escarpments. Both reef types are strongly influenced by the local coastal and shelf morphology and there was great variability within any particular section. Here, we will describe only the main reef features.

Crest Reefs: A submerged consolidated calcareous crest runs almost continuously, roughly parallel to the coastline at average depths of less than -1 to more than -3m. The consolidated crest, perhaps a former shoreline, is separated from the shore by a shallow lagoon, a few hundred meters wide at most (except in front of the bays). Dense stands of Acropora palmata grow upon this crest forming reefs whose morphology appears to be strongly influenced by the bottom topography. In the majority of the sections, the crest reef structures are better developed lagoonward than seaward (Fig. 3), and there is great variability in the degree of development of the Acropora reefs from one locality to another, mostly as a function of local water depth (Fig. 4).

In sections I, II and V (Fig. 3), the crest reef comprises isolated, elongated coral patches of varying dimensions growing along the submerged crest rarely more than 1.5 to 2m high. The size and relative degree of development of these patches decreases in shallower water. In these localities, A. palmata stands crown the submerged crest and sturdy Millepora complanata colonies may fringe the stands to seaward. In general though, abundant coral growth does not extend much beyond the crest. A relatively poorly developed rear reef community mostly composed of isolated colonies of Montastrea annularis and Agaricia tenuifolia, may extend the patches toward the lagoon. Many other, less abundant, coral species can be found here. The lagoon bottom is sandy and normally covered by Thalassia testudinum seagrass beds. In localities IV and B (Fig. 3), the calcareous pavement is very shallow (less than 1m) and very close to the shore line, sparsely covered by small colonies of M. complanata and A. palmata..

The most developed A. palmata reefs in the Sian Ka'an area are found in sections III and IV. The reef in section III, unlike all others, rises from a relatively deep bottom (2m) and extends seaward to 5m depth from the submerged crest through large, well developed, and irregular spurs (30 to 100m long; 20 to 50m wide at the base; 2 to 3.5m high; Fig. 3). At the time of the survey most of the A. palmata colonies in this formation were dead with few signs that recovery was underway, although encrustation and bioerosion on these colonies was not readily evident. The bottom of the grooves between the spurs, is a flat pavement, covered with a thin layer of sand and colonized by Gorgonia flabellum. A similarly well-developed Acropora reef is found in section VI, and in contrast with the former one A. palmata colonies appear quite healthy. In this reef there are no spurs, starting from a crest crowned with sturdy M. complanata colonies, many large A. palmata colonies form a loose matrix down to -5 to -7m. On the lagoon side, reefs of both sections drop abruptly forming an almost vertical wall of A. palmata, up to 3m high where large colonies of Agaricia tenuifolia and Porites are also abundant. In section VI, large colonies of Montastrea annularis and abundant patches of Acropora cervicornis are found close to this rear wall.

The mouth of Ascencion Bay is framed by a chain of small reef banks, prograding southward from locality A (Fig. 1). The bank reefs are well developed A. palmata formations growing upon a raised platform (-2 to -2.5m). Nicchehabim reef (locality A), has a cuspate shape with the lateral tips deeply curved inside, almost encircling an internal shallow lagoon (Fig. 3). The reef is formed by well developed external belt of partially dead A. palmata, with many large dendritic protrusions extending toward the inner "lagoon". Here, large colonies of M. annularis, Dendrogyra cylindrus, and relatively large patches of Agaricia tenuifolia and Acropora cervicornis predominate. As the banks approach the southern tip of the bay's mouth, the bottom becomes shallower, and they give way to a series of isolated stands, as in section IV.

Espíritu Santo Bay is bordered by a continuous A. palmata barrier, interrupted in only two places by moderately wide channels (Fig. 1). The reefs are similar to those described above, and their degree of development is apparently regulated by the depth of the lagoonal floor, in the sense that the shallower the bottom, both the vertical and horizontal extension of the living reef is smaller. No extensive coverage of reef flats are found here. The bottom is very shallow close to section V and gradually deepens toward the central part of the Bay's mouth (locality C). On the edge of the channels very well developed reefs are found, not unlike those at localities III and VI.

In sections VII and VIII, the submerged crest is absent. Instead a flat calcareous platform, less than 2m deep, extends for several hundred meters offshore (Fig. 3). The seaward part is colonized by gorgonians, mostly Gorgonia flabellum and Plexaura flexuosa, while on the inner part A. palmata stands flourish, together with colonies of A. tenuifolia. In section VIII the seaward section of the platform pavement is deeply pitted, and colonies of Siderastrea siderea roll freely in the bottom of some pits. In the southern end of section VII, at depths of -4 to -8m, a submerged reef is composed of a mixture of large interlocked M. annularis pinnacles, topped in places by large A. palmata colonies and many other coral species. The pinnacles and isolated colonies constitute a rather solid structure, a few hundred meters long.

Fore Reef Slope. Two types of diverse coral communities grow upon well consolidated, raised features associated with small escarpments on the fore reef slope. Plataform reefs are mostly associated with the first escarpment (-7 to -14m), and spur-block reefs are mostly related with a deeper escarpment (-33 to -45m).

Plataform reefs. Coral communities inhabit reefs formed by relatively extensive platforms (more than one hundred meters long) rising from 1 to more than 3m above the mostly denuded basal pavement. This gives the reef the morphology of a raised platform with spur-like extensions on the seaward side, but not on the shoreward margin (Fig. 3).

In section III, a well developed A. palmata reef colonizes the platform (noticeable on the shoreward margin), at depths of -8 to -10m. The reef has irregular spurs, 10 to 12m wide at the base, and often over 3m in height, extending for some 20m to almost 100m meters seaward. As in the shallow crest reefs of section III, most of the A. palmata colonies of the platform reef, were dead. Other coral species, such as A. tenuifolia, M. annularis, P. porites and a few stands of A. cervicornis, are found mostly on the central and back parts of the reef.

In section IV at a depth of -7 to -9m, is another platform reef similar to that described above, however, large colonies of A. tenuifolia dominate on the edge of the spurs and platform. Although many other coral species are present, they are not as abundant; and on the upper part of the platform gorgonians are conspicuous. The platform rises for 2 or 3m on the seaward margin, and in several places erosional notches are found at the base of the spur-like extensions.

At about -17m in section III, a platform reef has irregular spur-like seaward prolongations that are part of the consolidated platform, with a relief of up to 4m above the basal pavement (Fig. 3 and 4). An interesting feature of this platform reef is the presence of inner, fracture-like channels which seem to follow the alignment of the spur-like features. These inner channels are found inside the platform and seldomly reach the edge of the reef platform, they may be former surge channels. The channels are narrow (1 to 1.5m), shallow (-1 to -2m) and of variable longitude, the bottom is more or less flat and mostly covered with sand. The walls of these channels are vertical and in places the channels are blocked by _M. annularis_ colonies growing from the bottom, or are covered by colonies of the same species. The coral community of this platform reef is rich, dominated by massive and encrusting corals, colonizing the upper parts of the platform edges.

Spur-block Reefs. These reefs are mostly found at a depth of approximately 30m, associated with the main second escarpment (Fig. 4). They consist of a nearly parallel series of irregular and mostly discontinuous raised blocks and elongate domes, running at orthogonal angles to the general trend of the shoreline alternating with sandy grooves. The overall impression is that of a set of independent, eroded spurs (Fig. 3).

Each spur-block can be formed by several smaller blocks with roughly the same orientation. In contrast with the platform reefs, the sides of the blocks descend at a shallow angle toward the basal pavement. Dimensions of these structures are highly variable from one section to the other. In sections VI and VII the width of the blocks varies between 8 and 12m. They rise for 1 to 2m above the sea floor and are separated by narrow grooves 1 to 2m wide. In sections IV and V the blocks range in length from less than 10m to more than 40m, rise to more than 3m high, and the grooves vary from 3 to 5m wide. The community that colonizes the deep spur-blocks is different from that found on the shallow platform reefs. Consisting of a rich assemblage of gorgonians, sponges, sea whips, and macroalgae. Scleractinians are poorly represented, mostly by encrusting forms of _Agaricia agaricites_, and small colonies of _A. fragilis_, _Mycetophyllia_ spp., and _Scolymia lacera_.

In sections VII, the shallowest spur-block reefs are found at a depth of 9m. The blocks rise up 2 or 3m high, and are 8 to 12m wide, with gently sloping sides and narrow grooves of 1 to 3m width. An abundant coral community grows on top, including some large colonies of _A. palmata_ and _M. annularis_ (Fig. 4).

Non-Reefed substrata. In sections IV and VII, the surface of the escarpment is deeply pitted with a relatively sparse community of small gorgonians and sponges. Most of the substrate is covered by the brown alga *Lobophora variegata*. On the bottom of sections I and II, no escarpments were detected in the -20 to -30m range (Fig. 4). The bottom is covered by a layer of sand and colonized by calcareous macroalgae of the genera *Avrainvillia*, *Udotea*, *Rhipocephallus*, and *Penicillus*.

Below -40m the bottom is covered by small, rounded coral patch reefs, 1 to 2.5m in diameter and rising to 1 to 1.5m above the pavement (sections IV to VIII). In some of these sections a mixture of flat hard grounds and poorly developed spur-block reefs are found (sections IV and VII; Fig. 4).

II. Coral Community

The quantitative sampling of benthic macrobiota covered the principal biotic environments in the exposed Sian Ka'an shelf, to depths of 30m. Most of the sampled space corresponded to denuded hard grounds, sand and rubble with no apparent macrobiota (68%), with a relatively low percentage of biotic cover (17%). Dead coral, mostly in growth position, accounted for the remaining 5% (Table 2). Non-living attributes were excluded from the analysis to produce a cluster classification based solely on biotic components.

The resulting dendrogram (Fig. 5) suggests two main groups: I) A High-Cover cluster, corresponding mostly to the crest and platform reef stations, with a relatively high average percent biotic cover (33%; Fig. 6). II) A Low-Cover cluster, mostly composed of slope stations with a relatively low average percent biotic cover (11%; Fig. 6). These two main groups are further divided in sub-clusters, which reflect different secondary patterns. The High-Cover cluster is composed of two main sub-groups: The RR-C group, mainly formed by rear reef-crest stations (six out of eight), and the P-R group mostly composed by platform reefs. The Low-Cover cluster is divided into three sub-groups: The N-C group is composed of stations with sandy substrates and without scleractinians (Table 2); The MIDDLE group corresponds mostly to stations at -10m and -20m levels, where prominent reef features are scarce (Fig. 4). The DEEP group, mostly contains the -30m stations and spur-block communities. Although there are some discrepancies in the classification (for example -10m stations in the DEEP cluster, or reef crest stations in the P-R cluster), the resulting grouping seems coherent with the observed distribution patterns of the coral communities.

Presumably the differences in reef morphology and physiography determine different environments along the shelf, and thus the dendrogram reflects the structural changes of the coral community from one environment to another. Thus, the main patterns indicate that there are two main community types: a) A shallow water community colonizing raised features (platform reef communities are included in here), strongly dominated by scleractinian corals in both sub-clusters (RR-C and P-R) of the High-cover group. The other three main biotic attributes follow a similar relative abundance pattern in both sub-clusters (Fig. 7). b) A deeper water community colonizing raised features, or a shallow environment without raised features, corresponding to the Low-cover group stations. Here scleractinian corals are the least important component and the community is dominated by gorgonians. In this Low-cover group secondary relative abundance patterns are different for each subcluster (Fig. 7). Variability within the main attributes is considerable as indicated by the large standard deviations (Fig. 7), in both High and Low cover groups. These relatively large values reflect both a high level of patchiness and the substantial variability in reef morphology even on similar reef types. A practical consideration emerging from these results is that censuses at a small spatial scales may provide quite different results from site to site.

Scleractinians. The scleractinian coral community of the High-cover group shows a different structure in the two sub-clusters (Fig. 8). In terms of mean linear coverage, in the shallower RR-C group the dominance of A. palmata is evidently high (mean=1744cm; CV=74%), in comparison to the other main coral attributes: encrusting corals (mean=193cm; CV=101%), and massive corals (mean= 90cm; CV=97%). In contrast, in the P-R cluster, dominance among the main coral attributes is low: encrusting corals (mean=495cm; CV=74%); M. annularis (mean=455cm;CV=103%); A. palmata (mean=407cm; CV=88%). In this High-cover group, the proportion of dead coral is high in terms of average percentage (up to 20%), resulting mostly from the A. palmata reefs, that have a large proportion of dead corals (Fig. 6).

A. palmata is by far the most abundant coral attribute in the shallow reefs. Other branching corals such as A. cervicornis or Porites spp. tend to be scarce in all clusters and seem to be the least important coral component in all sampled reefs. In contrast, leafy corals such as A. tenuifolia are important in both High-cover clusters. Massive M. annularis and other massive coral species as Diploria clivosa, D. strigosa and Colpophyllia natans, and encrusting corals (mostly forms of Agaricia agaricites) are more abundant in well-developed reef structures, and are rather scarce on hard ground (Table 3).

Gorgonians. In general, gorgonians are important throughout the study area, including the shallow water communities. Their proportion is similar in both High-cover clusters: RR-C (mean=

207cm; CV=138%); P-R (mean=169cm; CV=88%), but more variable in the RR-C cluster (Fig. 7). In the Low-cover cluster gorgonians are relatively more abundant: N-C (mean=373cm; CV=70%); MIDD (mean=228cm; CV=103%); DEEP (mean=168cm; CV=89%). However, the relative importance of gorgonians with respect to the other main biotic attributes is probably underestimated because the chain method is not efficient in recording small gorgonian colonies (Jordán, 1989).

The gorgonian zonation patterns are similar to those found on the NE shelf of the Yucatán peninsula, where gorgonians are a very conspicuous component of the community (Jordán, 1989a; 1990). Gorgonian communities in shallow areas are dominated by *Gorgonia flabellum*, *Plexaura flexuosa* and *Eunicea tournefortii* in exposed areas, and by *G. flabellum*, *Pseudopterogorgia americana*, and *Plexaura homomalla* in protected or rear reef areas, where species richness is much higher. On the slope, the same species that dominate on exposed shallow environments are found, and again species richness increases as moderate depths are reached. On the deeper -30m level (Spur-block reefs) *Pseudopterogorgia elizabethae*, *Plexaurella dichotoma* and *Muricea muricata* are usually dominant. Non-zooxanthellate species are found occasionally on deeper locations including isolated colonies of *Iciligorgia schrammi*, and less commonly colonies of *Elisella barbadensis* and *Nicella sp.* in heavily shaded areas (Table 3). In many areas, hydroids are abundant either forming dense stands (*Gynangium longicauda*) or as isolated colonies (mainly species of *Sertularella*).

Sponges. Sponges show relatively similar proportions in both the High-cover group (RR-C: mean= 98cm; CV=79%; P-R: mean= 67cm; CV=132%), and in the Low-cover groups: (N-C: mean=105cm; CV=118%; MIDD: mean=141cm; CV=113%; DEEP: mean=140cm; CV=100%), as observed in Fig. 7. As with the other attributes the variability of the sponge community is relatively high.

Sponges in the High-cover cluster are mostly encrusting species (RR-C=98%; P-R=85%) of mainly boring sponges growing upon dead coral heads or hard ground patches, primarily *Anthosigmella* sp. and *Cliona* spp. In contrast in the Low-cover cluster, erect sponges are more important (N-C= 87%; MIDD= 63%; DEEP= 49%), especially at the -10m and -20m levels. Apparently, the erect sponge composition of a given site is influenced by changes in substrate type. On flat, hard ground, massive vase sponges, mainly of the genera *Xestospongia* and *Ircinia*, are abundant. In a more rugose substrate a multi-species sponge assemblage is found, mostly vase and tubular sponges of the genera *Agelus*, *Verongia* and *Haliclona*. In areas where gorgonians dominate, the sponges *Haliclona hogarthi* and *Iotrochota virotulata* typically grow amongst the gorgonian fronds.

Algae. Algal cover is relatively constant in proportion among the different clusters in both cover groups. Mean values are less variable in the High-cover group (RR-C: mean=184cm; CV=105%; P-R: mean=120cm; CV=98%), than in the Low-cover groups: (N-C: mean=243cm; CV=83%; MIDD: mean=23cm; CV=228%; DEEP: mean=119cm; CV=112%), as observed in Fig. 7. Fleshy macroalgae are more abundant in the deeper stations (N-C= 85%; MIDD= 76%; DEEP= 62%), than in the shallower ones (RR-C=13%; P-R=23%), where turf algae become more important. However, this may be a biased estimate because loosely integrated filamentous algae that do not form turfs, were included into the hard ground attribute. In the N-C cluster where the highest macroalgae abundance is found the substrate is mostly covered by sand. Here, the dominant species are calcareous green algae of the genera Udotea, Penicillus and Rhipocephallus. In other areas the macroalgae set comprises a multi-species mixture of brown and green algae species. The most abundant are Lobophora variegata and species of Stypopodium and Dictyota, and also species of Halimeda and Caulerpa. In many areas of hard grounds the brown algae Sargassum spp. and Turbinaria turbinata are extremely abundant.

DISCUSSION

Perhaps the most striking characteristic of the reef system of the Sian Ka'an Biosphere Reserve is the paucity of reef growth upon the shelf compared to other Caribbean localities such as the Belizean reefs a hundred km south (Rützler and Macintyre, 1982). In fact, well-developed shelf reefs are found a few tens of kilometers south of the Sian Ka'an area, both along the continental margin (Jordán, in press) and on insular shelves (Jordán and Martín, 1988). On the other hand, poorly-developed reefs on the shelf are the dominant feature along the Yucatán eastern margin, north of the Sian Ka'an Reserve (Jordán et al., 1989a; Jordán, 1989b). Although a few, well-developed reefs of limited extension can be found on several localities, both on the northern eastern Yucatán shelf (Jordán, 1989b) and in the central part of the eastern shelf (this work), it appears that a characteristic of the gently sloping shelf of the eastern Yucatán is the scarcity of well-developed reefs. This observation coincides with that of Stoddart (1976) and others, and seems to be the case as well for the Honduras and Nicaraguan shelves.

The presence of well-developed coral communities in the Sian Ka'an shelf seems to be linked to the relatively few, raised topographic features, such as terraces and scarpments. The shelf physiography suggests that there was both karst erosion and bevelling during low sea level stands as has been found in many other shelves in the Caribbean region (Logan, 1969).

This idea is further strengthened by our finding of erosional notches at the base of the spur-like extensions of the platform reefs in section IV. Therefore, we speculate that the raised features upon which the crest and platform reefs are developed may be remnants of pre-Holocene calcareous platforms, or consolidated shorelines, karstified by rainfall and percolating water. The shape of these structures, mostly those of the small sized platform (and internal, dead end channels), and spur-block reefs, would thus result from subaerial processes and not from reef building (Purdy, 1974). However, coral growth upon them will maintain and perhaps enhance the old structures, as observed in the spurs of platform reefs, or over the spur-block reefs.

Well-developed A. palmata reefs growing upon a submerged consolidated crest are found on the NE margin of the Yucatán peninsula (Jordán et al., 1981). Most likely, their development in the Sian Ka'an area, as in the northern region, is influenced by topography, water depth and wave action (Geister, 1977). A striking example of this situation may be found in the rich development of the crest reefs near gaps and channels in front of the Espíritu Santo and Ascención Bays. The submerged crest together with the coral reef growth upon it, effectively isolates the bays from the oceanic regime and constitute a barrier to free water movement between the bays and the open sea. Thus, relatively strong currents are found in the tidal channels and gaps, in spite of the low tide range within the region (Kjerve, 1982). The relatively intense tidal flux together with the greater depths in the gaps may enhance the growth of the coral reef builders. Since most of the gaps and channels are at least a few hundred meters wide (see locality A), wave refraction could intensify the water movement over the reefs, further stimulating the growth of A. palmata colonies (Geister, 1977).

The coral communities growing upon the raised features on the shelf (platform reefs, spur-block reefs and the pinnacle reefs at section VII), are considerable more developed in species richness and relative abundances, than those over the reefless hard bottoms. These well-developed, but isolated, coral communities indicate that the environmental setting is suitable for the growth of reef biota in the shelf, in spite of the extensive un-reefed areas, and also that raised topographical features are an important factor in the eventual success of these communities. Jordán (1989b) has observed that well-developed reef communities in the northern continental shelf of the Yucatán, are also dependent on bottom relief; as well as those on the eastern Cozumel island (see also Boyd et. al., 1963; on coralline microatolls in the seaward margin of Cozumel Island).

The scarcity of well developed coral communities on the hardgrounds of the shelf according to Jordán et al., (1981) and Jordán (1989b), is possibly related to the low slope of the shelf and wave action. According to this hypothesis, the gentle slope contributes to a stressful environment for corals by a more or less continuous accumulation of unconsolidated sediments over the hardgrounds. This sediments are also continuously re-suspended and re-deposited by wave action, thus affecting individual corals in different ways. This ecological condition may reduce the coral growth rates (Hubbard and Pockock, 1972; Cortés and Risk, 1985), generate lethal conditions (Rogers, 1983) and diminish the surface available for larvae settlement (Babcock and Davies, 1991) of key reef-building coral species. Under this stress coral colonies may also be handicapped to successfully cope with competitors and predators (Loya, 1976; Cortés and Risk, 1985). Isolated colonies able of attaining larger sizes and thus "escape" from the stressful bottom environment (Connell, 1975; Jackson, 1982) on the exposed and almost featureless shelf, still have a high probability of being broken and detached by high energy waves from storms and hurricanes (Jordán, 1989b). This situation is partially the result of weak colonies due to extensive internal bioerosion of the corallum (pers. obs.; Hutchings, 1986). In contrast, on crests, platforms and spur-blocks, survival and success of coral colonies is more likely, because these features moderate the effects of wave action.

Another possible source of stress for these coral communities is that of occasional up-wellings, that result from the Yucatán current running northward along the eastern continental slope. Whenever an upwelling occur there is a possibility of colder and nutrient-rich waters spreading over the shelf. Such waters could stress or kill scleractinian corals, and temporarily contribute the ecological success of macroalgae, further stressing scleractinians and other slow growers. The relatively large proportion of brown macroalgae colonizing the deep spur-block systems, suggests that this is another possibility.

Other events of biological nature, triggered or not by physical forcing, such as Diadema mass mortalities (Lessios et al., 1984), unrecorded widespread bleachings (Glynn, 1993) or unrecorded widespread diseases such as white and black band disease (Antonius, 1985; Edmunds, 1991), may also have played in the past and present times, an important role in shaping this reef system. The complexity of biological and physico-biological interactions in the reef community are further confounded by the lack of appropriate historical records. For example, the cause of the relatively large mortality of A. palmata colonies in the more developed Acropora reefs of the Sian Ka'an is unknown, and at the time of the survey (summer of 1987) there were few signs of recovery. This however, is not a unique situation. Several reports in the Caribbean region have shown that large areas of previously healthy Acropora reefs have suffered widespread mortality for largely unknown reasons (Davies, 1982; Dustan and Halas, 1987; Jordán, 1992).

Finally, a Biosphere Reserve is designed as a series of zones ranging from controlled utilization to total conservation. Both the coast line and shelf of Sian Ka'an fall under the controlled utilization category. At the moment, fishery activities are the only intense activity and this is carried out mostly by trapping in the seagrass areas (Lozano-Alvarez et al., 1991). However, with the enormous expansion of tourism in the Mexican Caribbean, the coastal areas may soon be affected by "non-damaging" recreational activities. Thus, we strongly advise that total conservation zones should also be implemented in the marine environment of the Reserve. Based on the findings of this study, Punta Allen (section III), the Nicchehabim and nearby bank reefs (locality A), and Punta Herrero (section VI), should be the first areas where total conservation should be implemented.

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Scleractinia		
	1	A. palmata
	2	M. annularis
	3	Massive
	4	Branching
	5	Encrusting
	6	Leaffy
Sponges		
	7	Encrusting
	8	Erect
Octocorallia		
	9	Gorgonians
Algae		
	10	Turf algae
	11	Macroalgae
Other		
	12	Dead coral
Non–biotic		
	13	Sand/rubble
	14	Hard ground

TABLE 1. Structural Attributes utilized on the quantitative sampling.

REAR REEF-CREST

	I	II	III	IV	V	VI	VII	VIII
	a	a	a	a	a	a	a	a
A. palmata	287	0	1816	213	1517	3840	1363	717
M. annul.	187	0	0	0	0	0	50	127
C. massive	33	0	173	17	213	40	97	0
C. branch.	37	0	230	7	0	33	0	0
C. encrust.	57	0	400	20	40	433	13	250
C. leaffy	333	0	460	360	93	633	1113	150
S. encrust.	0	80	77	333	337	310	17	87
S. erect	20	0	17	0	0	0	0	0
Gorgonians	110	400	133	3	180	50	97	777
Turf algae	307	217	403	23	410	137	70	897
Macroalgae	113	143	130	117	0	17	0	3
Dead coral	737	0	5036	440	193	2026	350	117
Sand/rubble	2016	1300	0	430	0	13	0	0
Hard ground	5763	7859	1123	8036	7016	2466	6829	6876

FORE SLOPE (-10m)

	I	II	III	IV	V	VI	VIII
	b	b	b	b	b	b	b
A. palmata	20	0	903	380	23	0	0
M. annul.	153	0	203	273	227	0	0
C. massive	30	247	267	53	213	67	30
C. branch.	13	100	90	83	80	0	173
C. encrust.	10	33	943	433	283	0	103
C. leaffy	0	0	523	1157	30	0	0
S. encrust.	253	37	333	27	90	60	313
S. erect	83	107	0	3	90	87	30
Gorgonians	40	677	390	67	280	70	300
Turf algae	267	0	0	0	20	0	0
Macroalgae	43	177	87	273	3	0	0
Dead coral	17	70	4606	247	17	0	7
Sand/rubble	570	373	150	0	63	0	57
Hard ground	8499	8179	1503	7003	8579	9716	8986

FORE SLOPE (-20m)

	I	II	III	IV	V	VI	VII	VIII
	c	c	c	c	c	c	c	c
A. palmata	0	0	57	0	0	0	0	0
M. annul.	99	0	1157	0	7	13	0	83
C. massive	71	0	623	100	23	0	70	63
C. branch.	0	0	770	7	17	0	3	0
C. encrust.	0	0	547	13	233	20	10	0
C. leaffy	20	0	537	0	0	0	0	7
S. encrust.	137	0	97	53	130	70	63	63
S. erect	183	400	53	80	343	300	297	93
Gorgonians	37	100	110	183	10	30	327	87
Turf algae	323	0	10	0	0	0	110	0
Macroalgae	243	397	170	0	20	7	13	423
Dead coral	7	0	1830	0	0	7	0	23
Sand/rubble	1067	7799	243	0	243	90	607	877
Hard ground	7813	1303	3796	9562	8972	9462	8499	8279

FORE SLOPE (-30m)

	I	II	IV	V	VI	VII	VIII
	d	d	d	d	d	d	d
A. palmata	0	0	0	0	0	0	0
M. annul.	31	0	113	200	13	180	117
C. massive	77	0	133	60	53	283	110
C. branch.	3	0	23	150	0	20	13
C. encrust.	35	0	220	300	13	373	77
C. leaffy	0	0	23	3	23	0	0
S. encrust.	13	0	183	320	70	277	3
S. erect	87	150	263	80	320	77	110
Gorgonians	20	620	223	500	150	247	93
Turf algae	247	0	10	0	17	0	17
Macroalgae	97	700	290	33	137	33	187
Dead coral	0	0	13	0	110	7	7
Sand/rubble	177	7629	583	427	200	27	3236
Hard ground	9212	900	7919	7926	8892	8476	6029

Table 2. Attributes sustrate coverage in linear cm per station. The number in the code above each data set indicates the corresponding section and the letter the depth level of the station.

SPECIES	RR-C	P-R	SB-R	H.G.
Gorgonians				
Briareum asbestinum	C	C	R	R
Erythropodium caribaeorum	A	R	X	X
Gorgonia flabellum	A	A	R	C
G. mariae	X	R	C	R
Pseudopterogorgia americana	C	C	C	R
P. bipinnata	X	R	R	R
P. acerosa	R	C	C	R
P. rigida	X	R	C	X
P. kallos	C	R	X	X
Pterogorgia anceps	R	R	C	R
P. guadalupensis	X	C	C	R
P. citrina	C	A	C	X
Lophogorgia sanguinolenta	C	R	X	X
Ellisella barbadensis	X	X	R	R
Nicella sp.	X	X	R	X
Iciligorgia schrammi	X	X	R	X
Plexaura homomalla	C	R	X	X
P. flexuosa	A	A	A	R
Pseudoplexaura porosa	R	R	C	R
P. flagellosa	R	R	R	X
Plexaurella dichotoma	R	C	C	X
P. nutans	X	R	R	X
P. grisea	X	R	R	X
Eunicea mammosa	C	A	A	R
E. succinea	R	C	C	X
E. calyculata	X	X	C	R
E. tournefortii	C	C	R	X
E. laciniata	X	R	R	X
E. fusca	R	R	C	X
E. laxispica	R	C	R	X
Muricea atlantica	X	C	C	R
M. muricata	X	C	R	X
M. elongata	X	R	X	X
Muriceopsis flavida	C	A	C	R
Hydrocorals				
Millepora complanata	A	R	R	X
M. alcicornis	R	C	C	R

Scleractinians

Stephanocoenia michelini	X	R	C	C
Oculina diffusa	R	R	X	X
Madracis decactis	X	C	C	R
Acropora palmata	A	C	X	R
A. cervicornis	R	R	X	X
Agaricia agaricites	C	A	A	R
A. humilis	C	C	R	X
A. fragilis	X	R	R	X
A. lamarcki	X	X	R	X
Leptoseris cucullata	R	C	C	X
Siderastrea siderea	R	C	C	X
S. radians	X	C	C	R
Porites porites	C	C	R	X
P. furcata	R	C	R	X
P. divaricata	R	R	X	X
P. astreoides	C	C	R	X
Favia fragum	A	R	X	X
Diploria clivosa	C	A	C	R
D. strigosa	R	C	C	R
D. labyrinthiformis	X	R	R	X
Manicina aereolata	C	X	X	X
Colpophyllia natans	R	C	R	X
Solenastrea bournoni	X	R	R	X
Montastrea annularis	C	A	R	R
M. cavernosa	R	C	C	R
Meandrina meandrites	R	R	C	C
Dichocoenia stokessi	R	R	R	X
Dendrogyra cilindrus	R	R	R	X
Mussa angulosa	R	C	C	X
Scolymia lacera	X	C	C	R
Isophyllia sinuosa	C	C	R	X
Isophyllastrea rigida	C	C	R	X
Mycetophyllia lamarckiana	X	R	R	X
M. aliciae	X	X	R	X
M. ferox	X	X	R	X
Eusmilia fastigiata	R	C	R	X

Table 3. Commonly found gorgonian, hydrocoral and scleractinian species of the coral reef environment on the Sian Ka'an Biosphere Reserve. **RR-C:** Rear reef-Reef crest; **P-R:** Platform-reefs; **SB-R:** Spur Block reefs; **H.G.:** Hardgrounds. **A:** Abundant; **C:** Common; **R:** Rare; **X:** Not found.

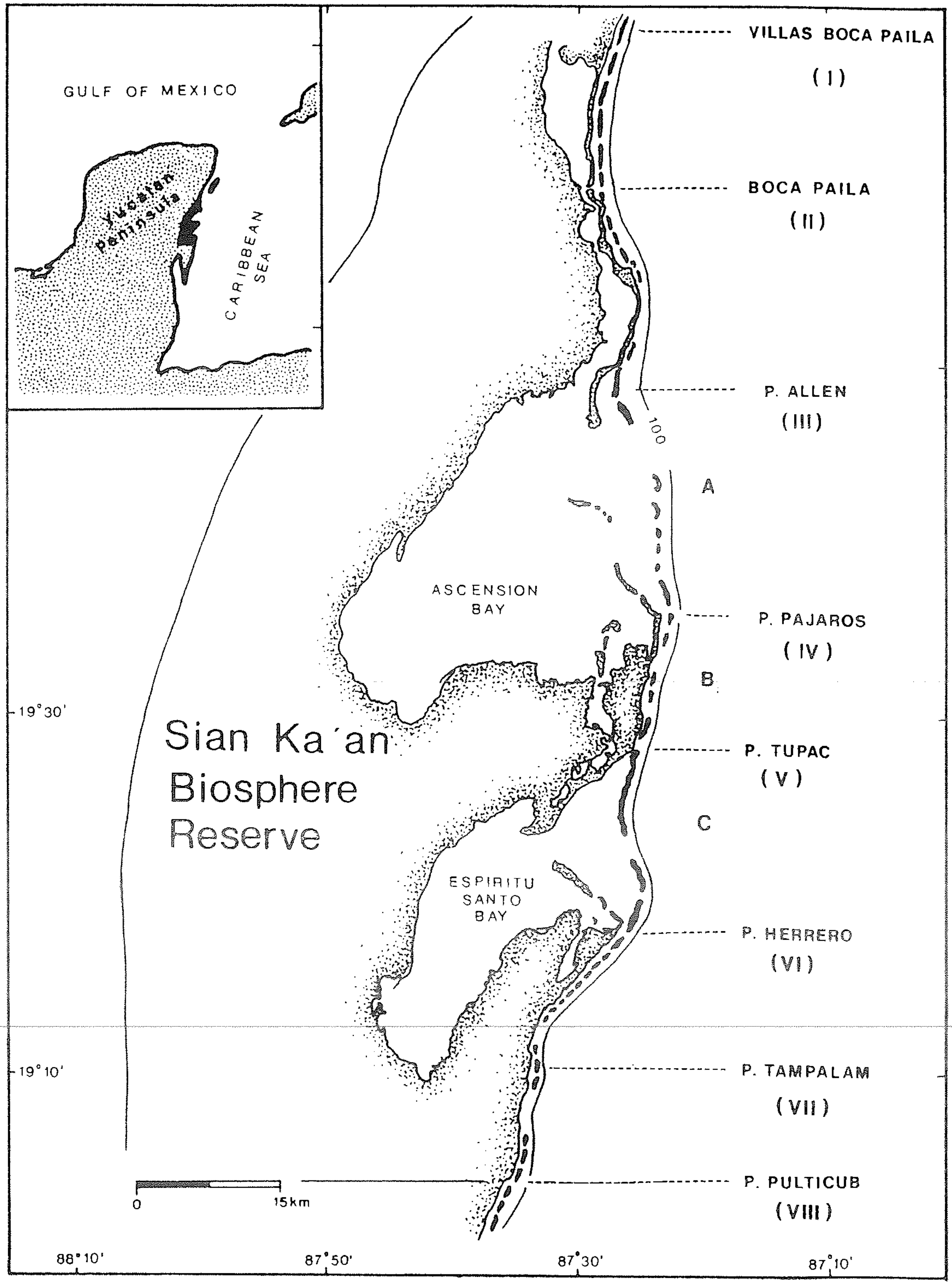

Figure 1. Map showing the geographical position of the Sian Ka'an Biosphere Reserve and location of the sampling sections. Roman numerals below correspond to code numbers.

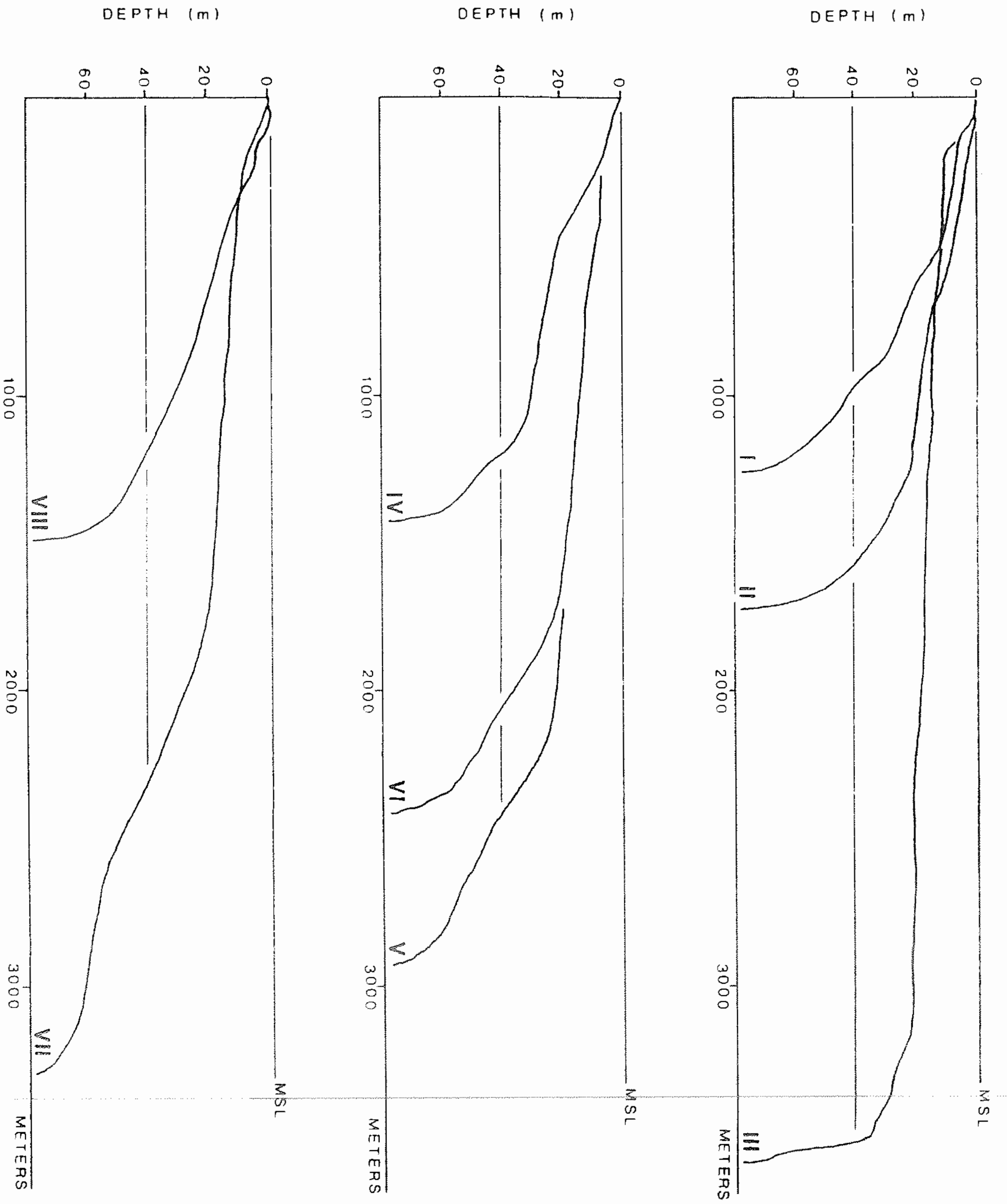

Figure 2. Bathymetric profiles for each section. The horizontal line at the -40m level marks the deeper limit of underwater observations.

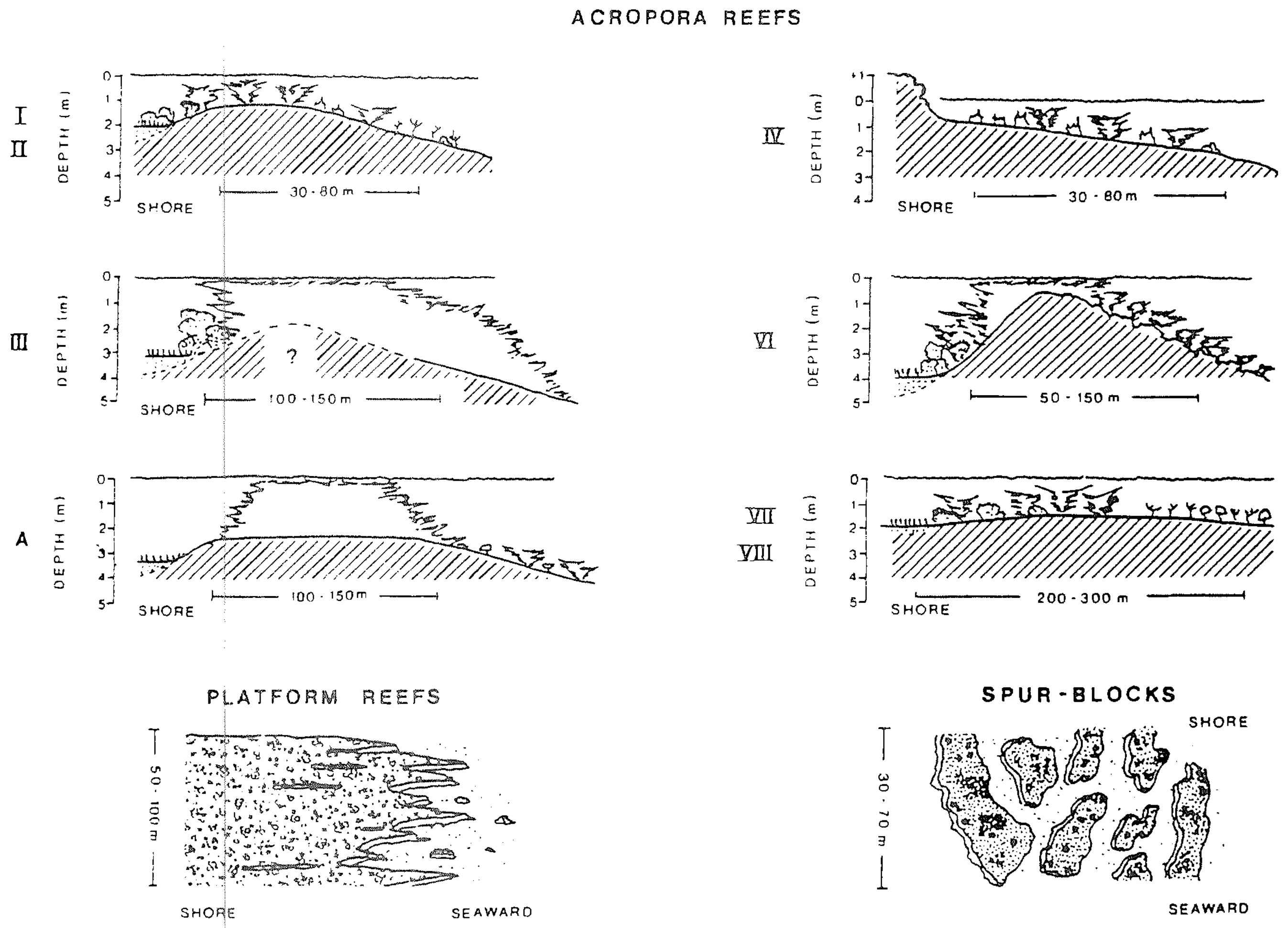

Figure 3. Sketches of the main reef types found in the study area. Dimensions are approximate and represent averages of several sets of measurements.

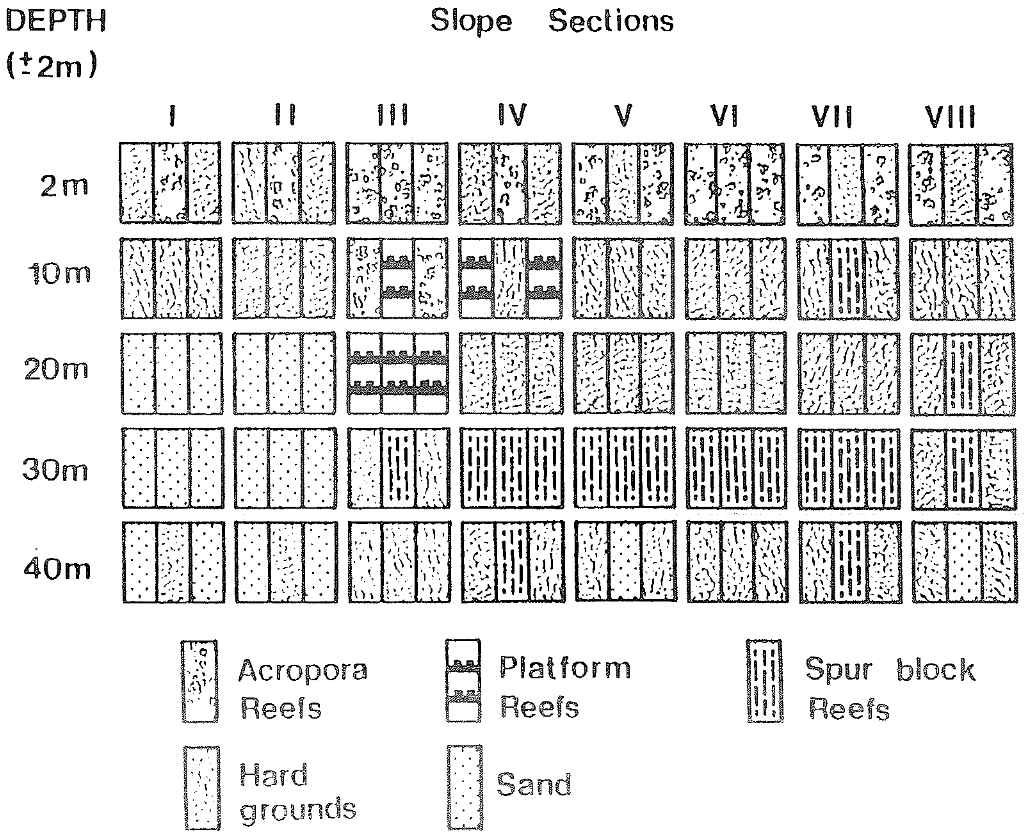

Figure 4. Main reef and substrata distribution on the shelf of Sian Ka'an.

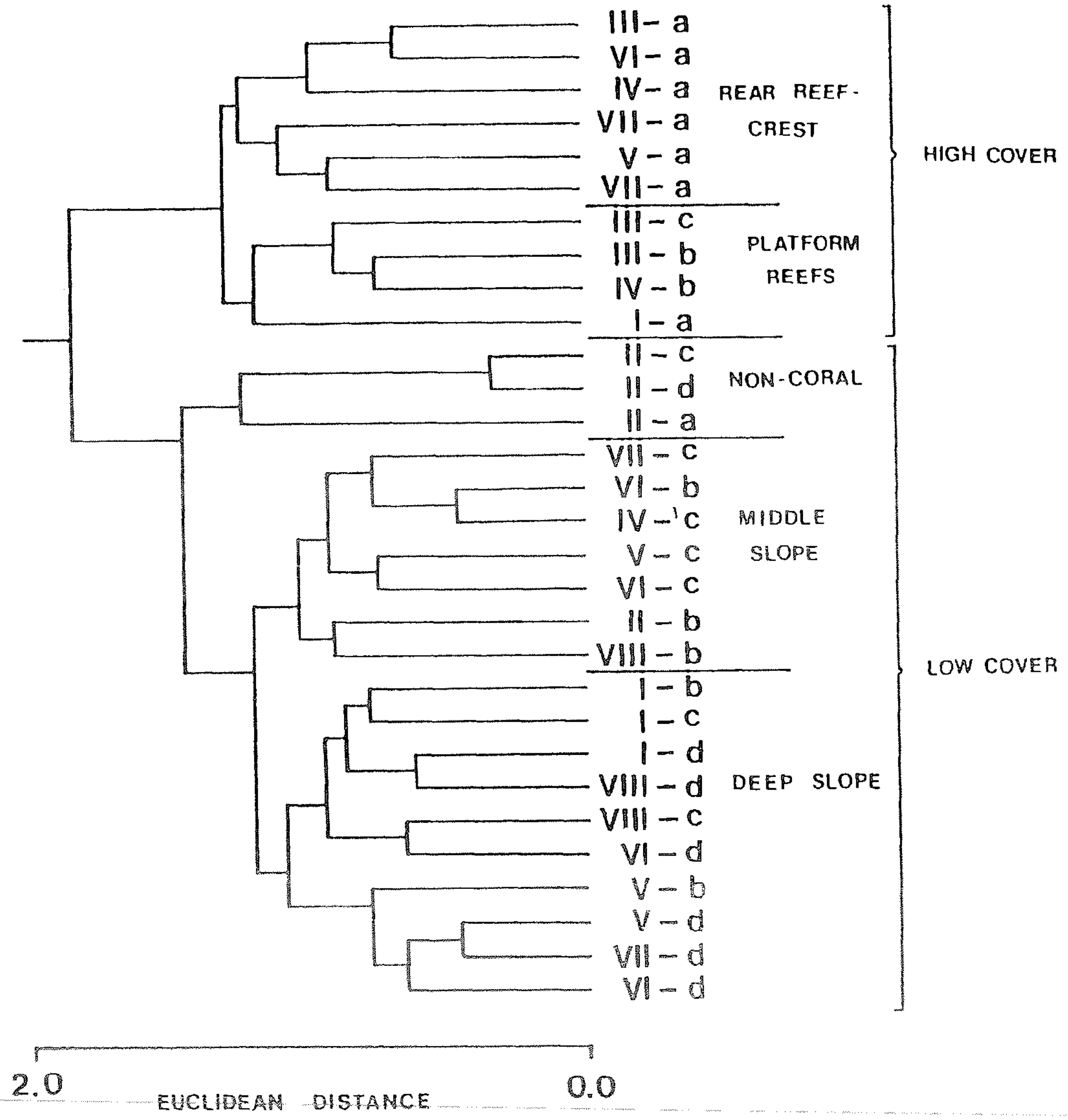

Figure 5. Dendrogram of cover attributes (excluding hard ground and sand). Cluster analysis of log-transformed cover data with average linkage.

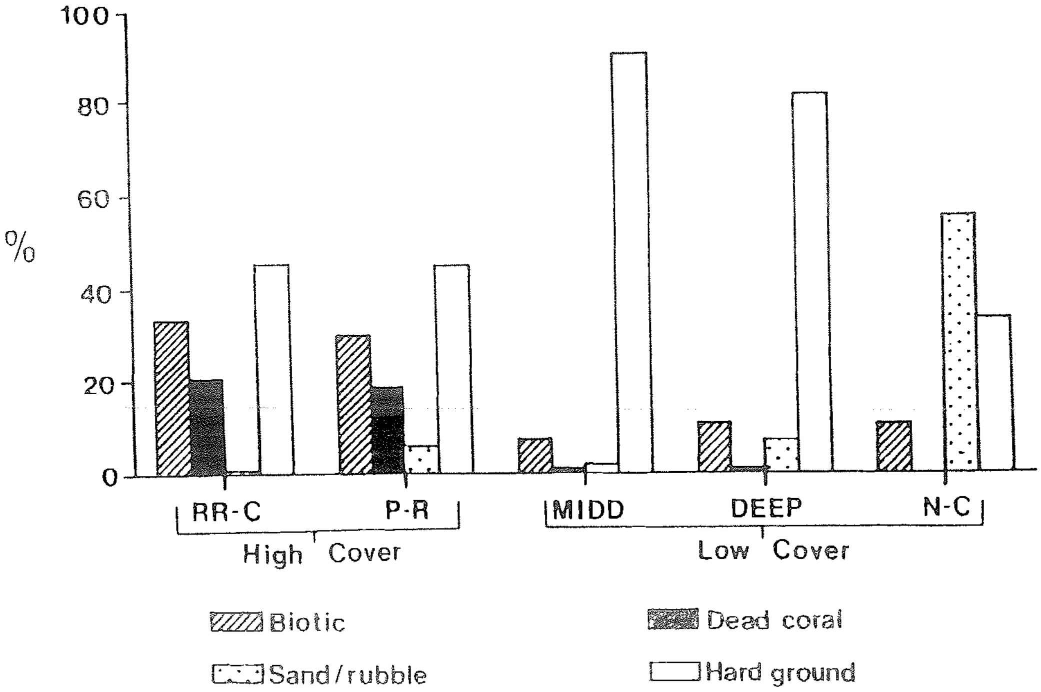

Figure 6. Percentage of cover for biota, dead coral, hard ground and sand, for each of the clusters suggested by the dendrogram in Fig. 5.

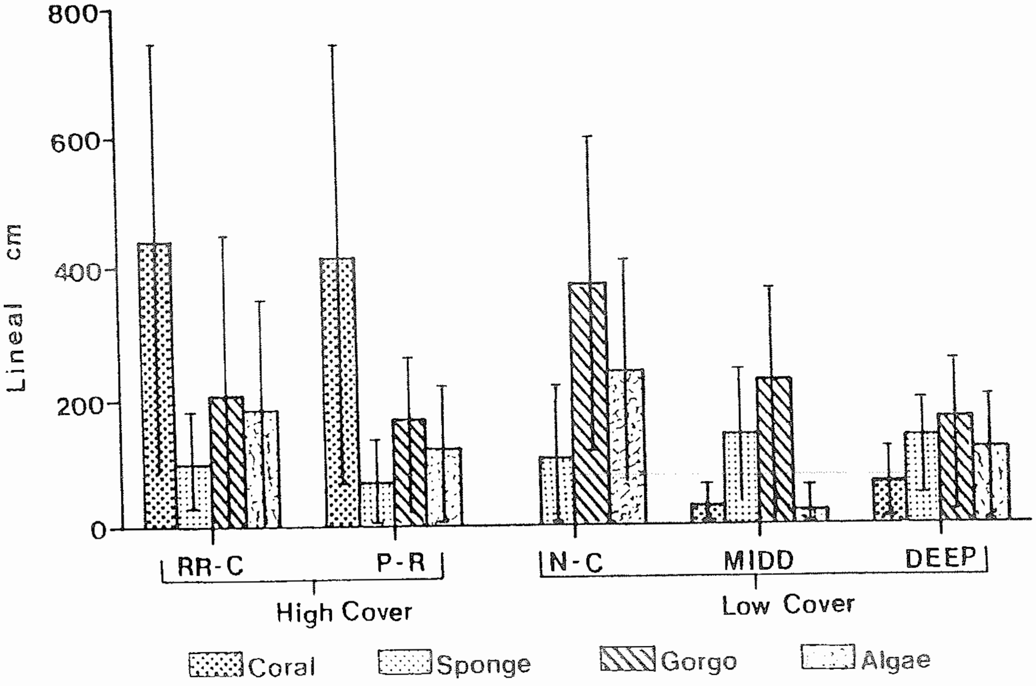

Figure 7. Mean lineal cover of the main biotic attributes, for each of the clusters suggested by the dendrogram in Fig. 5. The vertical line indicates one standard deviation.

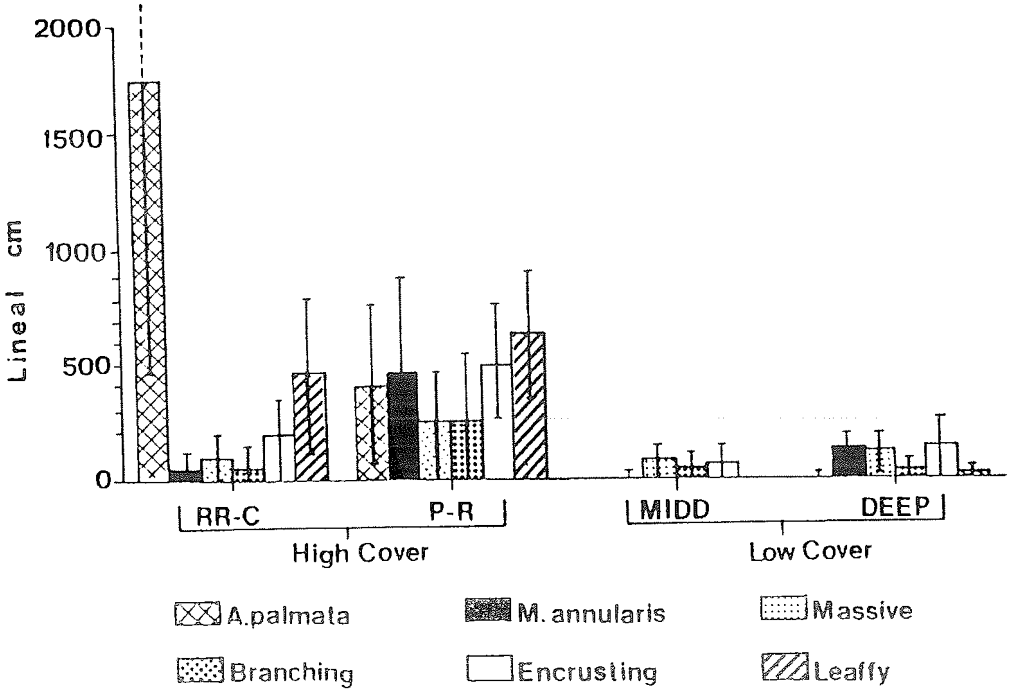

Figure 8. Mean lineal cover of the coral attributes for each of the clusters suggested by the dendrogram in Fig. 5. The vertical line indicates one standard deviation.