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DEVELOPMENT OF LAGOONAL REEFS IN OCEANIC REEF COMPLEXES OF THE SOUTHWESTERN CARIBBEAN: GEOMORPHOLOGY, STRUCTURE AND DISTRIBUTION

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ABSTRACT

Oceanic reef-complexes of the San Andrés and Providencia Archipelago, (Colombia) exhibit semi-enclosed to rather open lagoons allowing almost permanent flushing of waters and a wide spectrum of local wave regimes. Certain areas of the lagoon floor are densely overgrown by reefs. According to the composition and structure of coral communities, four ecological reefs-types were recognized. Geomorphologically these reefs fall into the following categories: knoll reefs, pinnacles, miniatolls, anastomosing reefs, and secondary 'barrier reefs'. In order to determine the distribution and variation of these reef types within the archipelago and within the different lagoons, detailed field observations and mapping supported by aerial photographs were carried out. It was found that both ecological and geomorphological reef types show definite patterns of development and distribution within lagoonal settings mainly in response to hydrodynamic and geomorphological factors.

INTRODUCTION

Geomorphological features common to most oceanic reef complexes of the San Andrés and Providencia Archipelago in the southwestern Caribbean (Colombia) are the presence of wide fore-reef terraces, almost continuous peripheral reefs on the windward side and ill developed reef tracts on the leeward side resulting in lagoons which are open toward the ocean along their leeward margin (Milliman 1969; Geister 1992; Díaz et al. in press; Geister and Díaz in press). These characteristics, together with topographic gradients and a distinct gross geometry, give rise to a wide spectrum of local wave regimes within the lagoons. Wave energy approaches the reef complexes as swell but is modified by the breaking process at the barrier reef crest into secondary waves, being diffracted and refracted around the flanks of the peripheral reef tract. Local wind-generated waves are common everywhere during blowing trade-winds. Patch-reefs and coral carpets cover to some extent the lagoon bottom of these reef complexes, but the composition, spatial arrangement, shape and density of these reefs do certainly not follow a random pattern.

Variations in reef shape are supposed to be primarily controlled by differential growth of the reef building biota in response to bathymetric and hydrologic influences (Maxwell and Swinchatt 1970; Brown and Dunne 1980). It is well known that the distribution of the reef-building biota within reef complexes is largely controlled by environmental factors of physical and biological nature (Sheppard 1982; Geister 1983; Hubbard 1988). Within individual reef systems, differences in wave exposure and light energy may be studied along gradients. Together with antecedent reef topography, they have been found to control development of individual reef types (Geister 1983; Hubbard 1988; Graus and Macintyre 1989). Thus, Caribbean coral reefs exhibit easily recognizable distribution patterns that have been attributed to different responses of the reef-building biota to prevailing wave and light energy conditions and antecedent topography (Adey and Burke 1977; Geister 1977; Wallace and Schafersman 1977, Done 1983).

The Archipelago of San Andrés and Providencia comprises a series of oceanic islands, atolls and coral shoals lined up in a NNE direction and extending over nearly 500 km along the Lower Nicaraguan Rise (Fig. 1). With exception of the reefs surrounding the two permanently inhabited, highstanding islands San Andrés and Providencia (Geister 1973, 1975, 1992; Kocurko 1977; Díaz et al. 1995), other reef complexes of the archipelago have received to date little attention (see Milliman 1969; Díaz et al. in press). The purpose of this paper is to characterize the distribution patterns of both ecological and morphological reef types within the lagoons of four atolls (Albuquerque Cays, Courtown Cays, Roncador Bank and Serrana Bank), and to interprete them in relation to major physical factors. Although one or more sand and shingle cays do exist in each atoll, they are not large enough to warrant permanent human settlement. We may assume on the basis of the available information that the reefs of the four atolls have been subject to the same physical processes over a considerable time span: a) rather strong, predominantely unidirectional trade winds (easterlies or northeasterlies) (Milliman 1969; Díaz et al. 1995), b) heavy, almost unidirectional oceanic swell from the ENE (Geister 1975, 1992), c) moderately strong, unidirectional oceanic currents from the E to NE (Hallock and Elrod 1988), d) relatively low amplitude, semi-diurnal tide regimes (Milliman 1969; Geister 1975), e) sporadic occurrence of tropical storms and hurricanes (Geister 1992), f) gradual subsidence of the volcanic basements and simultaneous capping of the sea mounts by shallow water carbonates in Tertiary to Quaternary times (Geister 1975, 1992), and g) Quaternary sea-level fluctuations with lowstands greatly overprinting the submarine topography (Geister 1975, 1983, 1992; Díaz et al. in press). Hence, one may expect that the primary controls of the structure, morphology and distribution of lagoonal reefs in the four atolls are comparable, and that the differences are caused by topographic and geometric characteristics particular to each atoll.

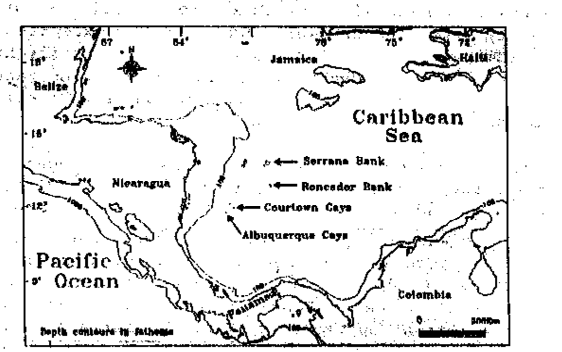

Fig. 1: Map of the southwestern Caribbean showing the location of the four studied atolls.

MATERIAL AND METHODS

This study was part of a much more comprehensive and integrated investigation of the reef complexes of the San Andrés and Providencia Archipelago (cf. Díaz et al. 1995, in press; Sánchez et al. in press).

Reef geometry and patch reef distribution, as well as wave directions and patterns of refraction and diffraction within lagoons were preliminarily determined by photo interpretation on panchromatic total coverage air photography (1971, 1984 and 1990 from the Colombian Geographical Institute). Lagoonal settings corresponding to different wave energy regimes were ordained in five categories (1= very calm to 5= heavy surf) and mapped according to roughness of the sea surface (related to wave height and length) discernible on the photographs. Gross bathymetry of the lagoon floor was deduced from nautical charts [Col-203 (Albuquerque Cays), Col-204 (Courtown Cays), British Admiralty Chart 1334 (Providencia, with Roncador Bank and Serrana Bank)] and published maps (Milliman 1969). Final thematic maps were entered via a digitizing table into a geographic system (GIS-ILWIS) for area measurements and further analysis.

Albuquerque Cays and Courtown Cays were visited in June-May 1994, and Serrana Bank and Roncador Bank one year later. Fourteen to twenty-four, observation stations in every lagoon were chosen in order to include several examples of each reef type recognised in the air photographs (Fig. 2). The reefs corresponding to the stations were mapped using air photographs and underwater control. The zonation and distribution patterns of dominant coral species were recorded. Exact geographical positioning in the field was possible using a GPS instrument. Bottom types, depth, direction and intensity of current (subjectively ranked in one of the following four categories: 1= imperceptible to about 2 m/min; 2= from about 2 to 5 m/min; 3= from about 5 to 8 m/min; and 4= > 8 m/min) and wave regime (verification of preliminarily assigned ranks) were also noted. SCUBA was used for depths beyond 6 m, otherwise skin diving. Complementary depth profiles were recorded with an echosounder (28 khz) along transects across several lagoonal settings.

Morphological and ecological reef classification and terminology vary considerably between authors, but the terms used here to define reef types follow those of Geister (1983).

RESULTS

Fig. 2 illustrates the gross topography and geomorphological features of the four atolls. The area occupied by the lagoons ranges from 6.2 km^2 at Courtown Cays to 237.1 km^2 at Serrana Bank. In the latter atoll, two large and one small lagoonal basins can be distinguished, which are interconnected by shallow-water areas or by more or less wide gaps between shallow reefs. At Albuquerque Cays, the lagoon exhibits two distinct depth levels (9 and 15 m), clearly separated by a meandering ribbon reef. The mean depth of the sand-covered lagoon floor is about the same in all four atolls, about 12 m (slightly less at Courtown), and, with the exception of a few scattered areas at Serrana Bank, which are slightly deeper than 20 m, the depth of the lagoonal basins ranges from 5 to 18 m. However, wide lagoonal areas have literally the same depth in all the atolls.

During the survey periods, the wind direction ranged from NE to E, corresponding approximately to average conditions. Moderately strong water currents (value 3) were observed locally in the lagoons at Albuquerque and at some stations at Serrana close to the passes transecting the peripheral reef where lagoon water exchanges with the open ocean. But generally, currents within the lagoons were weak and mostly wind-driven (to the SW or W), being usually imperceptible at depths greater than 2 m. The net direction of surface drift was ultimately downwind.

The wave regimes observed in the eastern part of the lagoons were mostly the result of wind and the filtering effect of the seaward reef upon oceanic swell. Lagoonal settings protected by long, unbroken, shallow reef crests exhibited very calm waters (values 1-2), whereas those located near the wide passes or discontinuities of the peripheral reef showed rougher surfaces (values 2-3), with refracted and diffracted long waves, the energy of which was not fully attenuated by the seaward reef crest. In the western half of rather wide lagoons relatively high values (3-4) were locally observed, mainly due to relatively high and long wind-driven waves as well as to diffracted oceanic swell introduced around the ends of the peripheral reef. Breakers and moderately heavy surf (values 4-5) within the lagoons were observed only locally around some shallow reefs at Albuquerque and Serrana.

Although the greater part of the lagoon floor in the four atolls is covered by loose carbonate sediments, countless patch reefs are present in all the atolls (Fig 3). According to morphology, the following reef types were recognized: knoll reefs, miniatolls, pinnacles, ribbon reefs, anastomosing reefs and inner (secondary) 'barrier' reefs. However, not each type was encountered in every atoll: Pinnacles occurred scarcely only at Courtown in the poorly defined transition zone between the lagoonal basin and the southernmost flank of the peripheral reef. Miniatolls were seen only at Albuquerque and Serrana. At three of the four atolls secondary, discontinuous 'barrier' reefs are vaguely recognizable behind the continuous seaward reef tract. But these are located on the rear reef flat and not within the lagoonal basins, except at Serrana, where rather long 'inner barrier reefs' divide the lagoon into three parts. By contrast, knoll and astomosing reefs cover rather wide areas of the lagoon floors in the four atolls.

Patch reefs were classified according to the dominant coral species of the reef crest area. As a result, the following

Table 1: Physiographic (area, depth) and hydrographic (degree of current strength and wave exposure) characteristics of the lagoonal basins, and absolute and relative surface areas occupied by patch reefsin general and by the various morphological and ecological reef types in the four atolls: AL = Albuquerque Cays, CO = Courtown Cays, RO = Roncador Bank, SE = Serrana Bank; ecological reef types: M= *Millepora*, Ap-D= *A. palmata*-*Diploria*, Ac= *A. cervicornis*, Msp: *Montastraea* spp.

	Basin area (km^2)	Depth range (m)	Mean depth (m)	Dominant depth (m)	Current strength (range)	Wave exposure (range)	Absolute and relative (to basin area) areas occupied by reefs (km^2, %)	Morphological reef types and their absolute and relative surface areas (to total reef area) (km^2, %)	Ecological reef types and their absolute and relative surface areas (to total reef area) (km^2, %)
AL	9.6	0-17	12	9	1-3	1-4	2.23 (23.2)	Miniatoll: 0.31 (13.9) Knoll: 1.22 (54.7) Ribbon: 0.12 (5.4) Anastomosing: 0.5 (26)	D-Ap: 0.18 (8) Msp: 2.05 (92)
CO	6.1	1-15	10	9	1-2	1-3	1.74 (28.5)	Pinnacle: 0.003 (0.2) Knoll: 1.15 (66) Anastomosing: 0.59 (34)	M: 0.003 (0.2) D-Ap: 0.04 (2.3) Msp: 1.44 (82.5) Ac: 0.26 (15)
RO	17.4	0-18	12	10	1-2	1-4	5.74 (32.9)	Knoll: 2.54 (44.1) Anastomosing: 3.21 (55.9)	D-Ap: 0.15 (2.6) Ac: 0.059 (1.2) Msp: 5.52 (96.2)
SE	196.7 38.7 1.7	1-12 0-23 0-11	12	10	1-3	1-5	14.3 (6)	Miniatoll: 0.04 (0.3) Knoll: 4.87 (34) Anastomosing: 7.3 (51) "Inner barrier": 2.1 (14.7)	D-Ap: 2.83 (19.8) Ac: 0.12 (0.84) Msp: 11.35 (79.4)

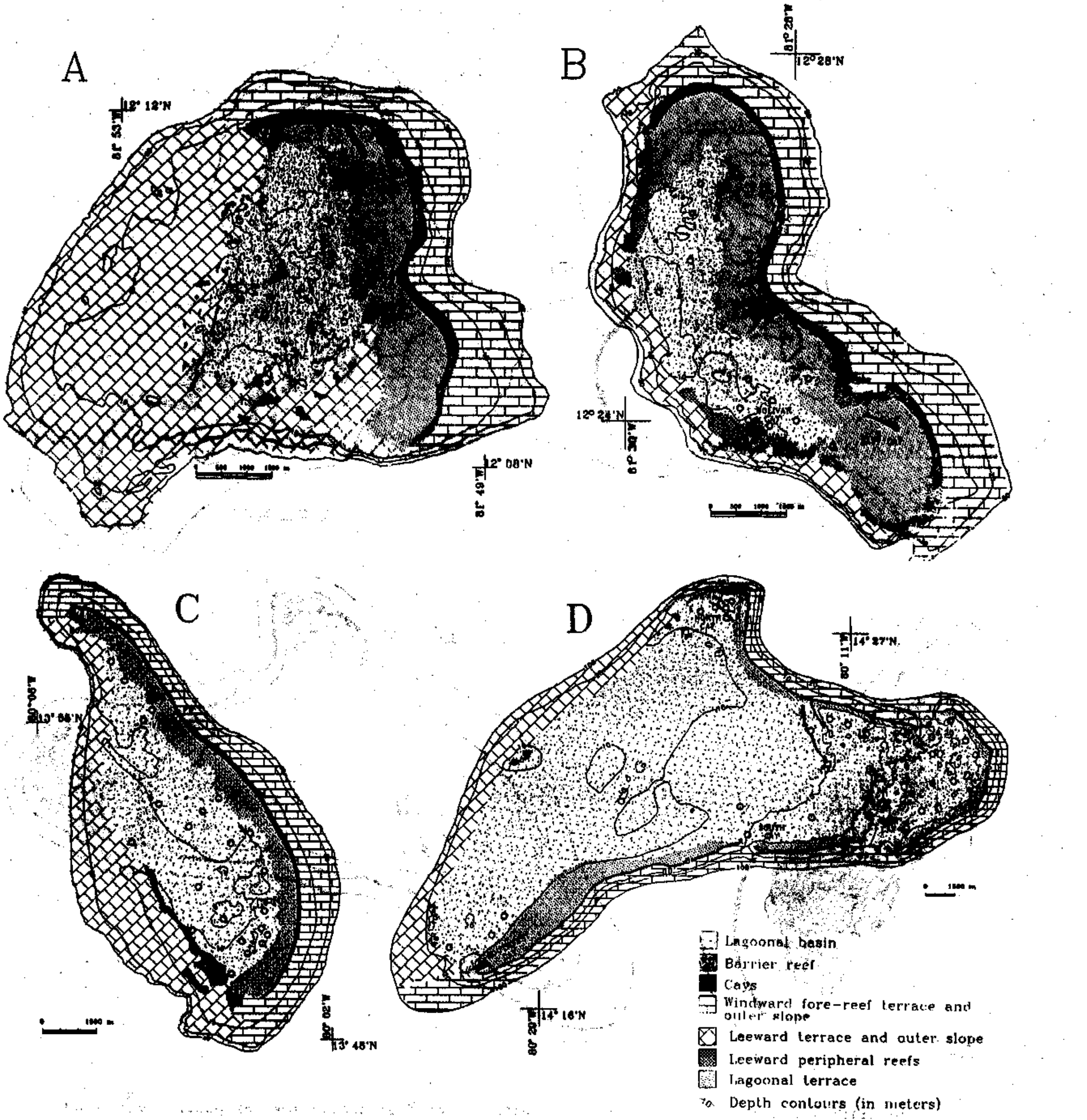

Fig. 2: Bathymetry and geomorphological characteristics of the four atolls; A) Albuquerque Cays; B) Courtown Cays; C) Roncador Bank; D) Serrana Bank; small circles indicate the position of observation sites.

ecological reef types were distiguished:

1) *Millepora* (M): pinnacles only
2) *Diploria-Acropora palmata* (D-Ap): Miniatolls, inner barrier-reefs, and almost emerging knoll and anastomosing reefs.
3) *Acropora cervicornis* (Ac): inner barriers, knoll reefs and anastomosing reefs.
4) *Montastraea* spp. (*M. annularis, franksi* and *faveolata*: Msp): knoll reefs, ribbon reefs and anastomosing reefs.

The morphological and hydrological characteristics of the lagoonal basins, and the absolute and relative areas occupied in the four atolls by the various reef types are summarized in Table 1.

The most important reef-building corals within the lagoons of the four atolls belong to the *Montastraea annularis* complex (*M. annularis, faveolata* and *franksi*, see Weil and Knowlton 1994). Together they grow over about 90% of the surface area covered by scleractinians in all reefs below 4 m water depth. The three species usually occur together, but one of them is always dominant. *M. annularis* (sensu stricto) is by far the most common species at shallow depths, dominating widely the crest area of almost emerging reefs in quiet-water environments, such as those found in the SW sector of the lagoon at Roncador Bank. *M. faveolata* is the dominant species on all reefs below 4 m water depth, being the main frame-builder of all knoll, ribbon and anastomosing reefs. On the contrary, *M. franksi* was never dominant, although it becomes a frequent species on deeper reefs. On rather diffuse, shallow reefs of the Msp-type a central lagoon-like area was usually observed, in which scattered living thickets of *A. cervicornis* colonize the sand-covered substrate of coral rock. Collapsed stands of this species

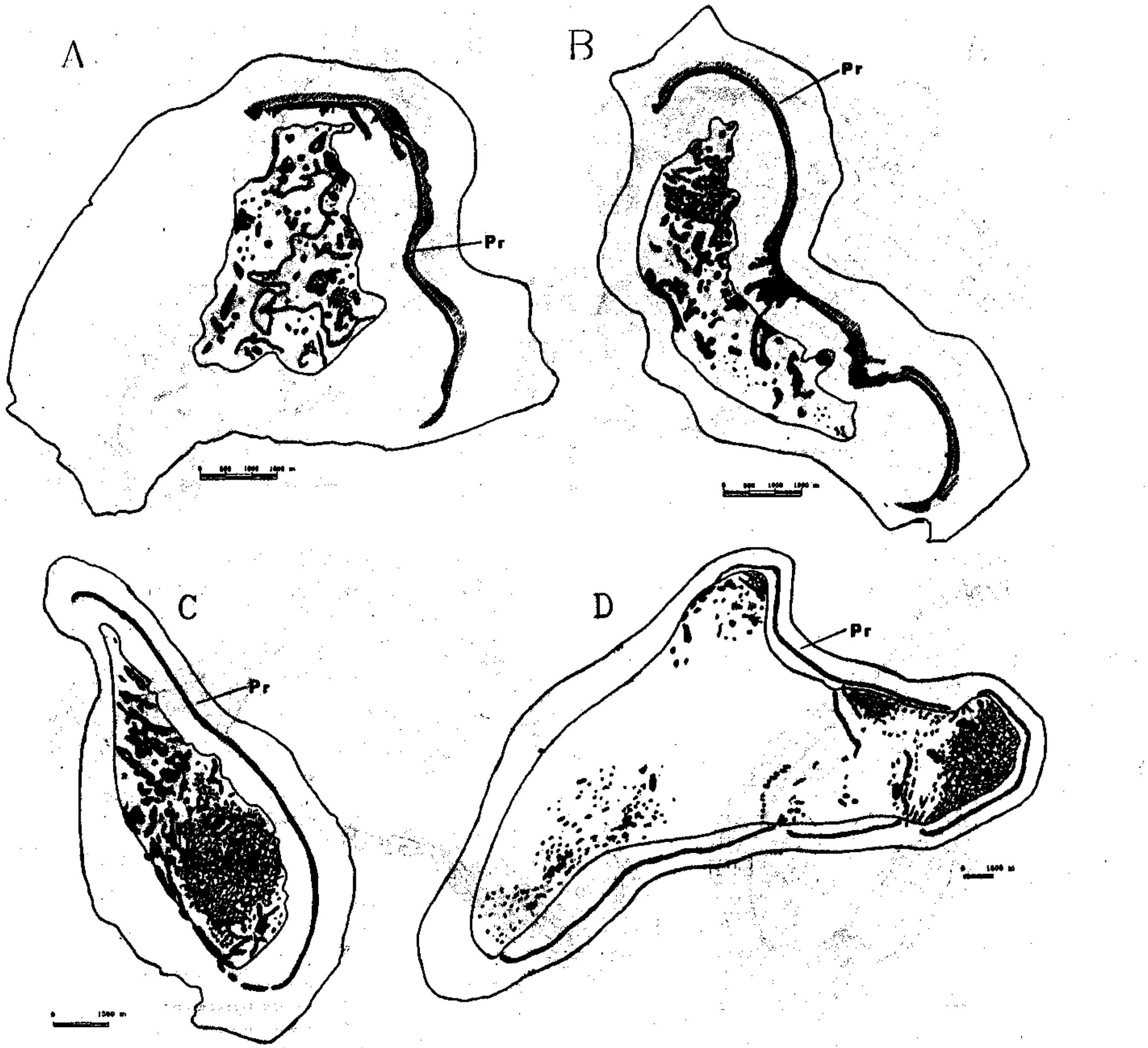

Fig. 3: Distribution and geometry of lagoonal reefs in the four atolls (b= peripheral reef tract).

and large amounts of coral debris were commonly observed within and around reef knolls. Extensive knoll reefs of the Msp-type with irregular outline were generally found in the leeward, usually deeper half of the lagoons. They exhibited mostly a scattered, patchy distribution of the coral colonies. It is clear from aerial photographs that the preferential orientations of knoll reefs are consistent with the input directions of prevailing current and wave energy.

A remarkable percentage (Table 1) of the coral framework develop as ribbon and anastomosing reefs (the latter may be regarded as complex ribbon reefs). Dense, intricate networks of meandering interconnected reefs, chiefly of the Msp-type, are preferentially concentrated in extreme calm-water lagoonal settings. Thus, anastomosing reefs cover more or less extensive areas on the western, less turbulent halfs of the lagoons. A dense meshwork of reefs occupies virtually the entire floor of the two minor, almost closed lagoonal basins at Serrana (Fig. 4) and nearly 70 % of the area in the southern half of the lagoon at Roncador. Most anastomosing reefs develop in intermediate depths (8-14 m). They are low, rising no more than 4-5 m above the adjacent sea bottom (i.e. up to about 4 m below sea level), and attain 8 to 20 m in width. They are largely dominated by *M. faveolata* and *M. annularis*, but some become almost emergent and form even a breaker zone with *A. palmata*. The bottom of the cell-shaped spaces surrounded by reticulate coral ribbons is covered by highly bioturbated carbonate sediments and exhibit usually different depth levels even between neighbouring ''cells'' (Fig. 4). The general outline, width and entanglement of the anastomosing reefs seem to follow a definite pattern in certain lagoonal settings, but in others they are quite incidental.

The reef crests rising almost to near low tide or even breaking the surface (''inner barrier reefs'', miniatolls and limited portions of some knoll and anastomosing reefs) consist generally of an upper (or central) core of *Acropora palmata* and *Diploria strigosa* surrounded by *Montastraea annularis* and *M. faveolata*. Living remnant colonies of *A. cervicornis* are mostly concentrated to the windward margins of these reefs moderately exposed to waves (values 2-4) where they form a diffuse belt between the D-Ap and Msp-zones. Patch reefs exhibiting such well-zoned slopes develop mostly

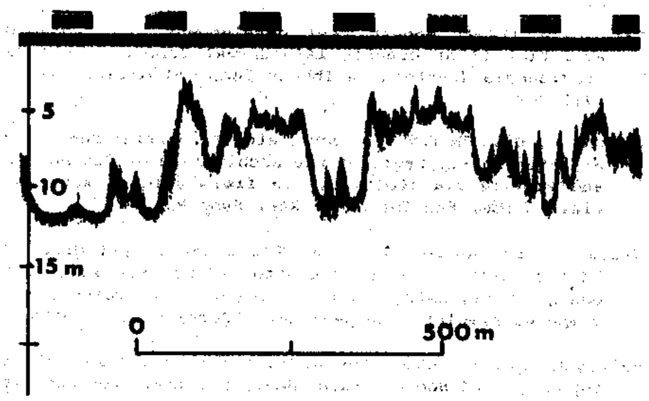

Fig. 4: Echo-sounder profile accross a central portion of the eastern lagoonal basin at Serrana Bank showing a highly irregular bottom trace corresponding to the dense network of anastomosing reefs.

isolated from other reefs and preferably in the peripheral zones of the lagoons, where they are not protected by other high reliefs from the incoming waves. In rather wave-exposed areas, these reefs form usually a conspicuous breaker zone. Colonies of *A. palmata* aligned in the direction of prevailing currents and waves were commonly found in the seaward edge of some shallow patches at Albuquerque, Roncador and Serrana.

Elongated coral shoals form usually ridge-like structures which trend preferentially in nearly a right angle to the prevailing wave direction thus forming 'inner barrier reefs'. At Serrana, some of these structures extend almost continuously for more than 2 km and divide the lagoonal area into two major and one minor basins. Coral growth in the crest area is dominated by living and dead colonies of *A. palmata* aligned toward the incoming waves. Patches of *A. cervicornis* (mostly dead), *Porites astreoides* and *Diploria spp.* are common on the higher flanks. *Montastraea* spp. and isolated colonies of *Siderastrea siderea* and *Dendrogyra cylindrus* were observed on deeper crests and slopes.

DISCUSSION

Patch reefs in the lagoons of the four atolls studied occur in a wide range of scales, shapes and species compositions (from extremely small sized pinnacles of *Millepora* to kilometers long ribbon reefs). Despite noticeable differences in size and geometry between the four atolls, the aereal distribution of both ecological and morphological reef types in their respective lagoons reveal a consistent pattern. This pattern becomes apparent when comparing both common and diverging geomorphological and hydrological characteristics of the reefs. As a result, it appears that the mutual relationship between wave energy and bottom depth constitutes the primary control upon the structure and morphology of reefs. At San Andrés and Providencia (Geister 1975, 1992), as well as in other Caribbean reef-complexes (e.g. Adey and Burke 1977; Rützler and Macintyre 1982; Graus and Mcintyre 1989), the ecological classification of patch reefs according to the predominant coral fauna of the reef crest reflects well their degree of exposure to prevailing waves. Although Hubbard (1974), based on calibrated current experiments, designated *M. annularis* as a species which should settle on more exposed areas in sheltered environments, Geister (1977, 1982) describes this species as dominant in quiet-water patch reefs of wave-protected settings. The latter has more recently been confirmed by observations on the Nicaraguan Shelf (Roberts and Murray 1983; Geister 1992). The scleractinian composition of most lagoonal reef structures in the four studied atolls is highly biased toward the *Montastraea annularis* species-complex, suggesting the predominance of wave-protected environments. With exception of '*Porites* reefs' (although '*Porites* zones' were locally found) and 'Melobesiae reefs' (the latter well represented at Courtown Cays by algal ridge-like structures of *Porolithon* sp. on a detached row of leeward, wave-exposed peripheral reefs outside the lagoonal basin, see Diaz et al. in press), all the main reef framework associations (or wave zones) in the Caribbean Sea recognized by Geister (1977) were encountered in the lagoons. Although the primary physical requisites for the development of *P. porites* reefs (Geister 1977, 1983) seem to occur at some lagoonal settings (i.e. very shallow, rather wave-protected zones), they are entirely absent. As suggested by Wallace and Schafersman (1977), *Porites*-assemblages may represent early colonizing stages in coral-population successions in Caribbean patch reefs. On the other hand, according to Littler at al. (1989), the zonal patterns of *Porites* spp. in Caribbean reefs seem to be strongly associated with the feeding intensity of parrotfishes and herbivory rather than with physical factors. At present, no accurate explanation for the lack of *Porites*-dominated reefs in the four atolls can be given that would be based on topographic and hydrologic characteristics alone.

Furthermore, well developed *A. cervicornis* reefs are nowadays virtually inexistent. However, the large amounts of debris of *A. cervicornis* observed in lagoonal settings of the four atolls suggest that this species was common until recently. Earlier observations in these atolls by Milliman (1969) support the obove statement. Recent accounts noted the virtual disappearance of this species from the nearby San Andrés reef complex (Diaz et al. 1995) and from elsewhere in the Caribbean (Hughes 1993; Garzón-Ferreira and Kielman 1993) within the last two decades. Thus, variations in the relative surface cover of the reef types on the four atolls are primarily the consequence of different wave regimes related with bathymetry, even though complex biotic interactions and long-term physical perturbances exert important controls as well. Nevertheless, the observed tendencies in spatial arrangement of the above ecological reef types within the lagoons may be represented in a simplified schema that considers only the basic physiographic and hydrologic features shared by the four atolls (Fig. 5A).

A gradation of morphological reef-types across the main physical gradients is not clear at all, and thus an evolutionary sequence of reef development in the studied atolls is as yet difficult to achieve. However, as have been shown above the best represented morphological reef types (knoll reefs, anastomosing reefs and 'inner barrier reefs') exhibit definite spatial arrangements, and they seem to be related to the key physiographic and hydrologic features as well (Fig. 5B). Furthermore, the elongation of some knoll reefs in a preferential direction indicates the importance of the intensity and direction of currents and wave exposure as primary controls of reef morphology. Brown and Dunne (1980) have shown that even under relatively low but constant current velocities and moderate wave exposure these factors appear to be responsible for a marked orientation and elongation of patch reefs. It has been suggested as well (Roberts and Murray 1983) that wave input and refracted pathways of waves play also an important role upon preferential reef orientation.

It appears that the entire reef configuration in the lagoons today has developed in Holocene times, and these reefs have probably grown up from a base-level at around the present maximum depth found in the lagoons (about 25 m). Topographic features inherited from the Pleistocene landscape cannot be unmistakably inferred from the present lagoon topography but it is likely that at least some of the patch reefs formed already on top of a Pleistocene patch reef, as has been shown for Florida (Shinn et al. 1977) and Belize (Halley et al. 1977). Thus, if any, no karst controls for patch reef development seem evident. Furthermore, considering that the time lapse since the submergence has been geologically short, only a limited amount of reef accretion could have taken place (Geister 1983). This becomes apparent because only few lagoonal reefs rise today to near low tide level.

At Serrana, the prevailing NE-SW orientation of the 'inner barrier reefs' across the eastern part of the lagoon, and the alignment in about the same direction of two wide and rather deep passes through the peripheral reef in this area,

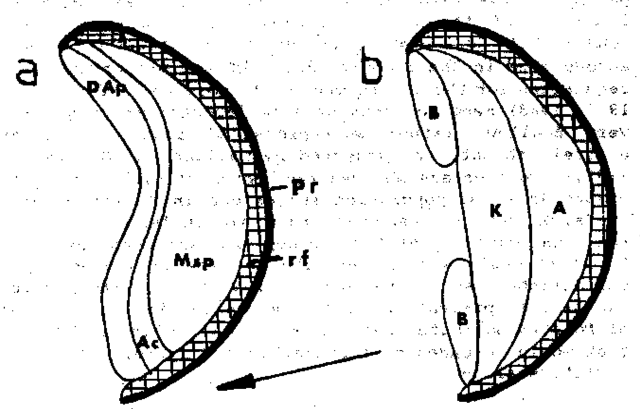

Fig. 5: Generalized distribution patterns of ecological (a) and morphological (b) reef types within the lagoonal basin of an idealized southwestern Caribbean atoll; Msp=*Montastraea* spp., Ac=*Acropora cervicornis*, DAp=*Diploria-Acropora palmata*, A=anastomosing reefs, K=knoll reefs, B='inner barrier reefs', Pr=peripheral reef tract, rf=rear reef flat; arrow indicates the direction of prevailing swell and wind

suggest a possible tectonic control of these features. Most coral banks, atolls and island reef complexes of the Archipelago of San Andrés and Providencia trend NE-SW as does the SE margin of the upper Nicaraguan Rise. In addition, several of these carbonate platforms are aligned in the same direction (Geister, 1992).

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REFERENCES

Adey WH, Burke RB (1977) Holocene bioherms (algal ridges and bank-barrier reefs) of the eastern Caribbean. Geol Soc Amer Bull 87:95-109

Brown BE, Dunne RP (1980) Environmental controls of patch-reef growth and development. Mar Biol 51:381-388

Díaz JM, Garzón-Ferreira J, Zea S (1995) Los arrecifes coralinos de la Isla de San Andrés, Colombia: estado actual y perspectivas para su conservación. Acad Col Cienc Exac Fis Nat, Col Jorge Alvarez Lleras 7:1-150

Díaz JM, Sánchez JA, Zea S, Grazón-Ferreira J (in press) Morphology and marine habitats of two southwestern Caribbean atolls. Atoll Res Bull

Done TJ (1983) Coral zonation: its nature and significance. In: Barnes DJ (ed) Perspectives on coral reefs. Brian Clouston Publ, pp 107-147

Garzón-Ferreira J, Kielman M (1993) Extensive mortality of corals in the Colombian Caribbean during the last two decades. Proc Coll Global Aspects Coral Reefs, Miami:247-253

Geister J (1975) Riffbau und geologische Entwicklungsgeschichte der Insel San Andrés (westliches Karibisches Meer, Kolumbien). Stutt Beitr Naturk (Geol, Paläont) 15:1-203

Geister J (1977) The influence of wave exposure on the ecological zonation of Caribbean coral reefs. Proc 3th Int Coral Reef Symp Miami 1:23-29

Geister J (1983) Holozäne westindische Korallenriffe: Geomorphologie, Ökologie und Facies. Facies 9:173-284

Geister J (1992) Modern reef development and Cenozoic evolution of an oceanic island/reef complex: Isla de Providencia (western Caribbean Sea, Colombia). Facies 27:1-70

Geister J, Díaz JM (1996) Oceanic atolls, barrier reefs and elevated fossil reefs of the archipelago of San Andrés and Providencia (Colombia); a field guide. Excursion Field Guide, 8th Int Coral Reef Symp Panama

Graus RR, Macintyre IG (1989) The zonation patterns of Caribbean coral reefs as controlled by wave and light energy imput, bathymetric setting and reef morphology: computed simulation experiments. Coral Reefs 8:9-18

Halley R, Shinn EA, Hudson JH, Lidz B (1977) Recent and relict topography of Boo Bee Patch Reef, Florida. Proc 3th Int Coral Reef Symp Miami 2:29-35

Hallock P, Elrod JA (1988) Oceanic chlorophyll around carbonate platforms in the western Caribbean; observations from CZCS data. Proc 6th Int Coral Reef Symp Australia 1:103-113

Hubbard DK (1988) Controls of modern and fossil reef development: common ground for biological and geological research. Proc 6th Int Coral Reef Symp 1:243-252

Hughes TP (1993) Coral reef degradation: a long-term study of human and natural impacts. Proc Coll Global Aspects Coral Reefs Miami:208-213

Kocurko MJ (1977) Preliminary survey of modern marine environments of San Andrés Island, Colombia. Tulane Stud Geol Paleont 13(3):111-134

Littler MM, Taylor PR, Littler DS (1989) Complex interactions in the control of coral zonation on a Caribbean reef flat. Oecologia 80:331-340

Maxwell WGH, Swinchatt JP (1970) Great Barrier Reef: regional variation in a terrigenous-carbonate province. Geol Soc Amer Bull 81:691-724

Milliman JD (1969) Four southwestern Caribbean atolls: Courtown Cays, Albuquerque cays, Roncador Bank and Serrana Bank. Atoll Res Bull 129:1-26

Roberts HH, Murray SP (1983) Controls on reef development and the terrigenous-carbonate interface on a shallow shelf, Nicaragua (Central America). Coral Reefs 2:71-80

Rützler K, Macintyre IG (1982) The habitat distribution and community structure of the barrier reef complex at Carrie Bow cay, Belize. In: Rützler K, Macintyre IG (eds) The Atlantic barrier reef ecosystem at carrie Bow Cay, Belize, I. Structure and communities. Smith Contrib Mar Sci 12:9-45

Sánchez JA, Díaz JM, Zea S (in press) Gorgonian communities in two contrasting environments on oceanic atolls of the Southwestern Caribbean. Bull Mar Sci

Sheppard CRC (1982) Coral populations on reef slopes and their major controls. Mar Ecol Prog Ser 7:83-115

Shinn EA, Hudson JH, Halley RB, Lidz B (1977) Topographical control and accumulation rate of some Holocene coral reefs; South Florida and Dry Tortugas. Proc 3th Int Coral Reef Symp Miami 2: 1-7

Wallace RJ, Schafersman SD (1977) Patch-reef ecology and sedimentology of Glovers Reef Atoll, Belize. In: Reefs and related carbonates-ecology and sedimentology. Amer Ass Petrol Geol, Studies in Geology 4:37-52

Weil E, Knowlton N (1994) A multi-character analysis of the Caribbean coral *Montastraea annularis* (Ellis & Solander, 1786) and its two sibling species, *M. faveolata* (Ellis & Solander, 1786) and *M. frankai* (Gregory, 1895). Bull Mar Sci 55(1):151-175