BIOTIC CHANGES IN THE REEF COMPLEX OF SAN ANDRÉS ISLAND
(SOUTHEASTERN CARIBBEAN SEA, COLUMBIA) OCCURRING OVER
NEARLY THREE DECADES

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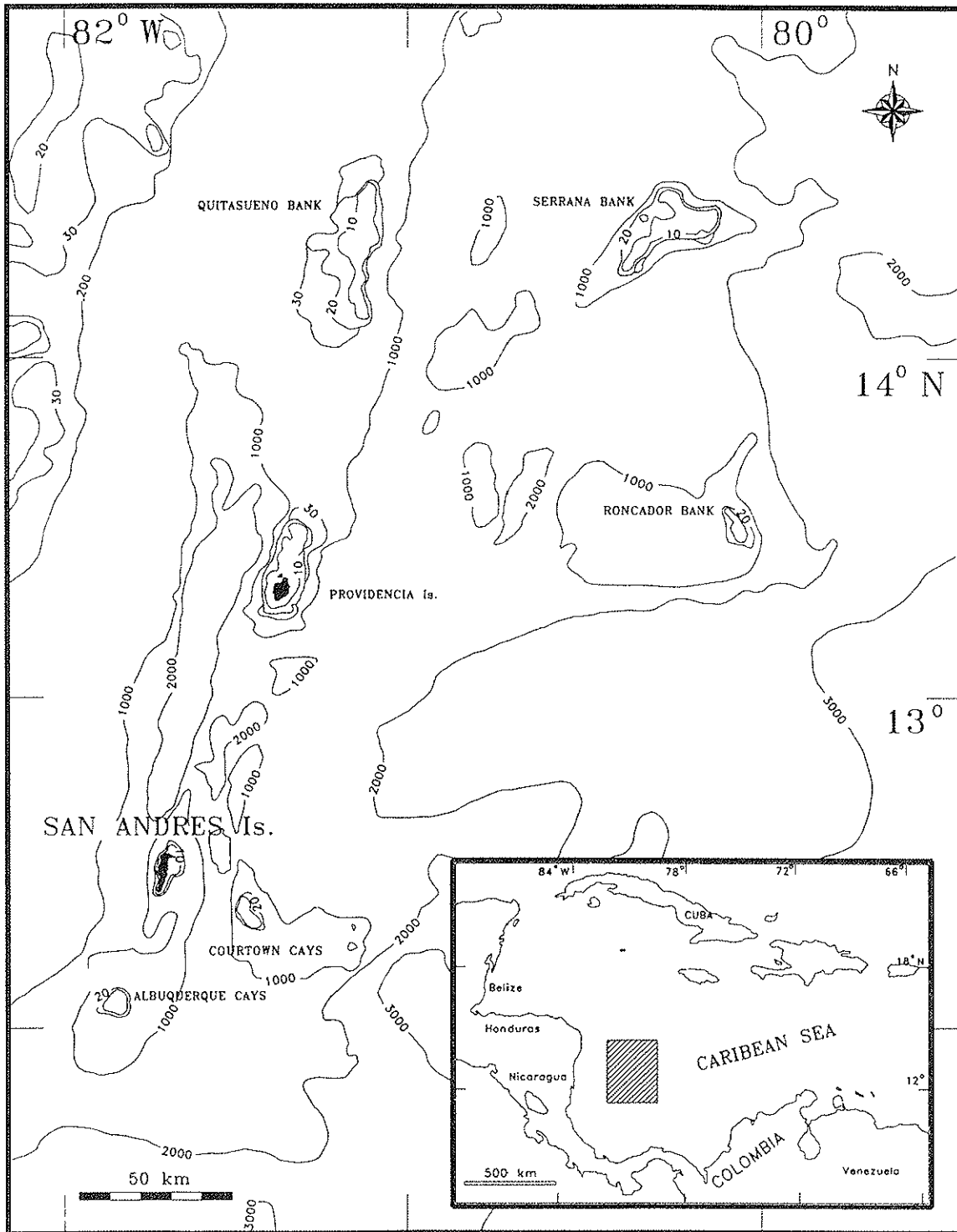S. ZEA, J. GEISTER, J. GARZÓN-FERREIRA AND J.M. DÍAZ

Figure 1. Map of the Southwestern Caribbean with the location of San Andrés Island and other nearby Colombian insular territories. Contour lines are isobaths (in meters).

BIOTIC CHANGES IN THE REEF COMPLEX OF SAN ANDRES ISLAND (SOUTHWESTERN CARIBBEAN SEA, COLOMBIA) OCCURRING OVER NEARLY THREE DECADES

BY

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ABSTRACT

San Andrés Island (SW Caribbean, Colombia), an uplifted oceanic atoll of Miocene origin, consists of a well-developed coral and carbonate bank-barrier reef complex. From a former cotton and coconut economy in 1953, it became a major trade and tourist center currently having a population of more than 50,000 inhabitants in a land area of just 25 km^2 . Human activities directly affecting the marine environment have included dredge and fill operations, shipwrecks and groundings, disposal of urban waste, thermal pollution, over-fishing, construction along the shoreline, and diving, boating and beach-going activities. From qualitative observations carried out from 1968 to 1979, and quali- and quantitative resurveys made in 1992 to 1996, major biotic changes became evident in the upper insular platform (0-25 m in depth). These were: a detectable decline in live coral cover (to an overall mean of 30 % of hard substrata in 1992), extensive recent coral mortality (overall mean in 1992 of 52% of total live + dead coral cover), almost total disappearance of the long-spined urchin *Diadema antillarum* and the sea-fan *Gorgonia ventalina*, proliferation of algae (to about 60-70% cover of the overall reef hard substrata in 1992), and an almost total absence of commercial reef organisms, including both carnivores and herbivores. With exceptions due to localized solid and sewage disposal, coastal construction and ship groundings, coral death followed a spatial pattern of increased values in lagoonal, enclosed environments and lower values in high energy zones and in deep reef areas. The higher coral death in shallow lagoonal areas was interpreted as being directly caused by a greater susceptibility of coral species making up the shallow reef frameworks (i.e., *Acropora*, *Porites*) to hurricane and storm damage and to diseases. Indirectly, it may have been caused by the effect of the prevalent regime in lagoonal areas of higher illumination (allowing greater algal growth after the die-off of *Diadema*), low turbulence and limited water flushing (causing higher susceptibility to bleaching and diseases, and lower rates of natural and artificial lesion regeneration), and by a higher incidence of lethal or chronic effects of anthropogenic activities. San Andrés constitutes a typical example of the widespread phenomenon of over-development and poor planning of small islands. Its growing recreational tourism, which is based mostly on attractive and "healthy" seascapes, will soon be seriously threatened.

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INTRODUCTION

As coral reefs commonly fringe tropical islands and coasts, this resource is increasingly exploited for food through subsistence fisheries by the growing local populations. In addition, coral reefs represent valuable resources of recreational, scenic and cultural importance and thus also become a prime focal point for the local and regional tourist industries. Hence, reef protection and conservation has become an increasingly applied discipline oriented towards the preservation of the economic bases of traditional island communities.

A number of coral reefs throughout the tropical oceans have been investigated during the past decades and alarming signs of degradation have been recorded (see Ginsburg & Glynn, 1994). But the most stirring observation resides in the fact that vast areas of remote reefs have never been studied at all. Thus, an accurate global evaluation of the present world-wide reef decline is not possible, not even within the Caribbean Sea where degradation is especially alarming on a regional scale (see Ginsburg & Glynn, 1994; Hughes, 1994; Shulman & Robertson, 1996).

The Archipelago of San Andrés and Providencia (southwestern Caribbean Sea) comprises a series of islands, atolls and banks, built as oceanic reefs capping steep seamounts, facing an effective windward fetch of about 2000 km which corresponds to the entire width of the Caribbean Sea (see Milliman, 1969; Geister 1973, 1975, 1977, 1992; Díaz et al., 1996; Geister & Díaz, 1996). The surface outcrops of San Andrés, the main island of the archipelago, correspond to a thickness of about 500 m of coral and lagoonal rocks of Miocene age (Geister, 1975). Thus, the geological record of San Andrés alone is proof for the long-term ability of the reef-building community to produce wave-resistant frame-works and to accumulate an extraordinary mass of limestone on top of a subsiding seamount. In spite of major periodic or aperiodic perturbations of the environment that occurred in the geological past (see Copper, 1994), this ability may be under renewed long-term threat in the future as a result of a foreseeable global climate change (see Wilkinson & Buddemeier, 1994). Even worse, however, the short-term survival of the San Andrés reefs is jeopardized, at present, by the acute anthropogenically driven deterioration of the environment. Similar to other Western Atlantic reefs, coral communities around San Andrés show manifest signs of stress and lethal damage. Preliminary observations indicate that these have to be attributed, at least in part, to both heavy over-exploitation of the reef ecosystem by excessive fishing and to an ill-planned tourism development (Díaz et al., 1995). The fate of the already ailing fishing industry and the future tourism industry of San Andrés will depend greatly on a "healthy" condition of its reefs, accessible only for sustainable fishery and recreational activities such as beachgoing and diving.

The purpose of this paper is to document some of the biotic changes observed in the reef complex of San Andrés in the course of the last 28 years (1968-1996), to discuss their distributional patterns around the island, their temporal persistence and probable origin.

STUDY AREA

Location and history

San Andrés (12^0 29'N, 81^0 43'W) is part of an oceanic archipelago comprising two highstanding islands (San Andrés and Providencia) and a number of atolls and coral shoals that line the Lower Nicaraguan Rise for more than 500 km (Fig. 1). The island has a central topographic ridge reaching almost 100 m in height (Fig. 2). It comprises a land area of 25 km^2 and is inhabited by a fast growing population of more than 50,000 (I.E.S.A.P., 1990a) possibly reaching 80,000 today. San Andrés was first settled by English Puritans in 1631 and for almost 200 years it changed hands between Spanish and English rules. Although situated in the southwestern Caribbean Sea far away from the South American mainland and close to the Central American coast, the archipelago has belonged to the Republic of Colombia since 1822 (Parsons, 1964). Its economy developed from early cotton plantations into a coconut monoculture, the latter thriving at the turn of the century, accompanied by subsistence farming and fishing. In the brief time span of about 20 years, starting in 1953, a major tourist and trade center was formed (I.E.S.A.P., 1990b).

In spite of the limitations and the fragility of insular resources (McEachern & Towle, 1974) modern mass tourism was actively developed, which created an unprecedented need for manpower resulting in a sharp increase of the resident population. This demand also fostered investment into the housing and hotel infrastructure. Population pressure and resulting construction activities in turn led to a disorderly urban development, which appears to be one of the principal reasons for the growing environmental problems in the surrounding sea. Hitherto, the anthropogenic deterioration of the environment has been studied in some detail only for the mangroves (Contreras, 1982) and for the coral reefs (Díaz et al., 1995).

Human activities affecting the marine environment

Human activities that have directly affected the local marine environments in the last three decades are the following:

1. Dredge and fill operations carried out at the east coast near the capital of North End from about 1966 to 1970 by the VAM Suramericana S.A. They deepened and widened the harbor, enlarged the wharf, and gained new land for housing the rapidly growing population. These operations destroyed large seagrass flats and nearshore mangrove communities as well as island swamp areas that were filled by sand. Their effect on nearby patch reefs in the eastern lagoon has never been evaluated.
2. Dynamiting of coral shoals near "Entrance" in summer 1970 to permit a free passage to the harbor by vessels of major draught.
3. Ship wrecks and groundings both on the barrier reef and lagoonal reefs.
4. Disposal of urban waste (both sewage and solid) from the leeward coastal cliff directly into the sea.
5. Thermal pollution and pollution by hydrocarbons due to the inadequate cooling system of the local electric power plant destroyed much of the nearshore mangrove

communities along the east coast. The eventual impact on nearshore coral patches and on the seagrass communities has never been studied.

6. Overfishing of both carnivore and herbivore species to meet the needs of a growing resident and tourist population.
7. Construction of hotels along the shoreline or even in the sea along the north coast.
8. Diving, boating and beachgoing activities due to tourism.

Each of these disturbances directly impact only portions of the various marine environments. However, because of the interdependence of the coral reef, mangrove and seagrass ecosystems (Ogden & Gladfelter, 1983), the indirect effects may have been even larger, but not always well understood.

Recent reef complex

The present bank-barrier reef complex on the insular shelf consists of a barrier/fringing reef sheltering a windward lagoon, up to 3 km wide, with patch reefs and minor lagoonal fringing reefs. A 500 m to more than 1000 m wide rocky Fore-Reef Terrace slopes gently (3-8°) from about 8 m in depth to the drop-off of the island slope at around 20 m in depth or more. There is only one short leeward segment of the barrier reef protecting the northern lagoon to the west. Off the western or leeward island coast no structural coral reefs have developed. The insular shelf on this part of the coast is formed by two submarine terraces with marginal escarpments at depths of about 4 m and 20 m. The leeward 20 m terrace represents a continuation of the windward fore-reef terrace which was formed by truncation during a Pleistocene low sea-level stand. It is notable for its dense coral carpets and extensive sediment cover. The Holocene 4 m terrace forms rocky flats showing only very sparse coral cover with exception of its outer margins which are densely overgrown by corals (Fig. 2, 3).

Most reefs show rich coral growth with a clearly discernible zonational pattern (see Geister, 1975, 1977). The breaker zone of the windward barrier crest is dominated by luxuriant growth of the hydrocoral *Millepora* and the colonial zoanthid *Palythoa* with crustose coralline algae (*Porolithon* and others). *Acropora palmata* patches are common in the fore-reef from 4 m down to about 10 m in depth, and in the shallow water behind the reef crest. In localized shoals of particularly heavy surf, true algal ridge formations have developed in the northern part of the insular shelf.

Although no structural reefs grow along the leeward coast, dense coral carpets formed by branching and massive scleractinians with abundant octocorals cover the outer margin of the 20 m terrace between 15 and 20 m in depth. Shoreward from this carpet, between 15 to 8 m deep, there is a zone of varying width characterized by carbonate sand accumulation. The upper island slope below the leeward drop-off at about 20 m is covered by rich coral growth comparable to true fore-reef settings. More detailed descriptions of the geology, geomorphology and marine environment of San Andrés have been published elsewhere (Geister, 1975; Diaz et al., 1995, 1996).

METHODS

Initial observations were carried out between June 1968 and September 1970, in April and May 1973 (Geister, 1973, 1975), in May 1977 and in July 1979 (Geister, unpubl.). These were made almost exclusively by extensive snorkeling accompanied by a dug-out canoe. Almost the whole reef complex was covered in detail by this method from the shore down to the outer edge of the insular shelf. Main observations concerned geomorphology, species composition of reefs and ecological zonation. Observations were noted on board and numerous photographs were taken underwater.

After an interruption of observations for almost 13 years, renewed investigations were undertaken with qualitative and quantitative surveys in May and September 1992 (Garzón-Ferreira & Kielman, 1994; Diaz et al., 1995) followed by a short visit of the reefs in June 1993, a joint resurvey of several original sites in October 1994 and a last visit in 1996.

During the 1992 resurvey, SCUBA was used and observations were made at 48 stations (Fig. 2) each in a relatively homogenous reef zone, visually estimating the percent cover of: (1) major hard bottom components such as live scleractinian and milleporid corals, other invertebrates and algae; (2) live area of dominant coral species relative to total live coral cover; (3) total area of recently dead coral relative to total coral cover (live and dead); (4) dead surface area of each dominant coral species relative to its total cover (live and dead). During these surveys, the presence and the extent of coral diseases or other signs of coral stress, the unusual proliferation or absence of other organisms, and the presence of anthropogenic sources of impact were noted too.

Considerable recent coral death has occurred over the last 2 to 3 decades. For its gross estimation, only those tissue areas which can be expected to be alive in healthy colonies (exposed, non-cryptic sides of coral heads or plates; distal portions of coral branches) were taken into account. Coral skeleton remains not too grossly eroded or collapsed to permit distinction of original colony limits and growth form were also considered for estimation. For gorgonian octocorals, mortality rates were estimated from the percentage of dead skeletal remains relative to the total (live and dead) number of colonies present. The density of this total was also visually estimated. All these estimates can only produce approximate values due to differential colonization of species by epibionts and to different patterns of mortality and subsequent erosion. In addition, it must be taken into account that estimates of live and dead coral cover were each taken by a different observer, though on-board discussions among the diving party, generally, helped to minimize subjective mistakes. More objective observations of coral cover were made from chain transects laid on the sea bottom parallel to the coastline, three in each of 14 stations. The percent cover was calculated from the number of chain links overlying specimens of different taxa and types of substratum relative to the total number of links (600).

The 1994 and 1996 resurveys were carried out by swimming over several of the sites originally surveyed in 1968-73, noting gross changes in species composition and dominance, and the presence and extent of coral death. Coral species-morphs follow Geister (1975); *Montastraea annularis* was at that time not split into its three sibling species under discussion now (see Weil & Knowlton, 1994).

Cartography was based on maps published by Geister (1973), as well as on the following aerial photographs obtained from the "Instituto Geográfico Agustín Codazzi" (IGAC) at Bogotá: flights C-2123 (1984), C-2420 (1990) and C-2422 (1990). In addition, the British Admiralty Chart 1511 surveyed in 1834 was used as well as the nautical chart of the Colombian Navy COL-201 published in 1972.

RESULTS

Coral decline
Although percentages of live and dead coral cover were not recorded in 1968-73, field records and underwater photographs show clearly that the coral formations around San Andrés were in healthy condition at that time except for local damage recorded in the NE and N lagoons (see below) (Geister, 1975). During the 1992, 1994 and 1996 resurveys it became certain that live coral cover diminished considerably during the last 28 years due to intensive and widespread coral mortality in the reefs.

Present live coral cover
Visual estimates of live coral cover made in 1992 at 47 stations (50 data points) ranged from 0 % to 60 % of hard substrata with a mean of 26 % (Table 1). This indicates that on an average less than one third of the hard substrata of the San Andrés shelf is presently covered by live corals. Quantitative data obtained from chain transects at 14 stations gave similar values of mean live coral cover of the hard substrata (30 %, Table 1). Values of live coral cover equal to or surpassing 40% were found in the southern portion of the leeward 20 m terrace (Station 39), and at scattered stations in the windward barrier reef, at the outer edge of the fore-reef terrace and in parts of the lagoon (stations 8, 10 and 20) (Table 1, Fig. 3). As there are no quantitative data from previous years, we cannot directly estimate the decline in coral cover. Nevertheless, other evidence, such as photographs of sites revisited again and the omnipresence of great amounts of recently dead coral colonies are indicative of such a decline.

In 1992, low coral cover was observed in areas of the leeward terraces in the neighborhood of the raw sewage outlet and solid waste disposal area (Horn Landing, Station 44-45, airport runway, Stations 46-48), when compared to similar stations of the same facies in the SE sector of the island. However, coral species composition and relative cover did not vary much on average between the stations in the NW and SE, suggesting that the above pollution did not cause a noticeable coral species replacement.

Recently dead coral

High levels of recent coral mortality were recorded at San Andrés in 1992. Visual estimates of the proportion of dead coral at 47 stations showed an overall mean of 52%, ranging from 10 to 99% (Table 1). More than half of the stations had mortality values higher than 50%. The highest levels (>80%) were found in the lagoon, on the patch reefs dominated by one or two species of branching or foliose corals (*Acropora, Porites, Millepora*), while the lowest mortality values were estimated in the spur and groove system of the barrier reef where the dominant species was *Millepora complanata* (Table 1, Fig. 4). When comparing these visual estimations to those obtained from chain transects (Table 1), it is noticeable that some are similar (Stations 8, 25 and 28), but the majority show a difference of 20% or more in the chain estimations. This is probably due to a closer and more detailed exploration of the reef substrata during the chain samplings, incorporating dead lateral portions of coral heads which were not easily seen in the visual estimations made when swimming at the surface, 1-2 or more meters above the substratum.

Coral species affected

During the 1992 San Andrés survey it was found that 19 coral species were affected by recent mortality (Table 2). Fourteen of these reached per-station mortality levels of 50% and more. *Acropora cervicornis* and *A. palmata, Agaricia agaricites, Eusmilia fastigiata, Millepora complanata, Montastraea annularis, Porites furcata* and *Siderastrea* showed mortality levels of 50% and more. These eight species had also the highest values of overall mean mortality (>25%) and relative frequency of mortality (stations with mortality over stations found) (>55%), with exception of *A. agaricites* and *P. furcata* which showed frequency values of only 24 and 41% respectively. On the other hand, *Diploria strigosa* and *D. labyrinthiformis* also had high mortality frequencies (58-60%). Only four species reached mean mortality levels of more than 50%: *A. cervicornis, A. palmata, E. fastigiata* and *Colpophyllia natans*. The most common coral was *A. cervicornis* which formed thickets in 1968-1970 at several sites within the lagoonal area (Geister, 1975)(Fig. 5a); these thickets were partly necrose, covered by filamentous algae and occupied by pomacentrid fish in 1977 (Fig. 5b). By 1979 this condition worsened considerably, so that more than half of these thickets were dead (Fig. 5c). During the 1992 to 1994 re-surveys, no living specimens of *Acropora cervicornis* (only dead fragments) of this species were seen at this site (Fig. 5d). Only a few small and isolated colonies of *A. cervicornis* were observed alive in deeper reefs (10-20 m). So it is possible to assert that less than 1% of the populations of this species survive at present.

Two of the most important species in shallow reef frameworks at San Andrés, *A. palmata* and *M. complanata*, showed very high mortalities in the lagoon and in the back of the barrier reef, as compared to the deeper inner fore-reef terrace (6 to 8 m) in front of the windward barrier where mortality levels were much lower (Table 1). Mortality of *A. palmata* was especially impressive in the shallow patch reefs of the northern lagoonal basin that were once dominated by flourishing stands of this species (see Geister, 1975: pl. 4 b+c). In 1993-6 the *A. palmata* in these reefs were mostly in their once-living positions, but were completely dead with the exception of a few younger colonies; only in

one single flourishing coral patch, about 10 m in diameter, *A. palmata* seemed to be in vigorous expansion.

Another important branching species, *Porites furcata,* which dominated many of the shallow, protected reefs of the eastern lagoon shelf in 1970, was found almost totally dead in several of those patches adjacent to urban areas in 1992 (Table 1). However, some patches were already dead by 1970, and a few others retained healthy populations by 1992 (Fig. 6) and still by 1996.

Increase in algal cover and algal biomass

In 1968-70 the algal cover in the San Andrés reefs was very low as compared to the present values. Though no counts were made at that time, it can be shown by underwater photographs of sites resurveyed in 1994 that the reef became heavily overgrown by different species of macroalgae, even at sites where formerly no presence of algae was noticeable.

Frondose algae were prolific at many sites in 1992, 1994 and 1996, especially in areas protected from direct wave energy where they partially covered live coral colonies. Brown algae (Dictyotaceae, *Lobophora variegata* and *Stypopodium zonale*) were especially abundant, followed by the green calcareous algae *Halimeda* spp. (Figure 7). The proliferation of *Halimeda* in certain localized reef areas was quite impressive. Due to the fast growth rate of their thalli (see Hudson, 1995), these algae were able to outgrow and to overgrow both massive (*Montastraea*) and branching (*Acropora*) coral tissues which were ultimately killed, probably by overshadowing and suffocation. The coral tissue under the recently encroaching *Halimeda* was pale to white due to expulsion of zooxanthellae but was still alive, whereas it was already absent on the flanks which were overgrown earlier. The parts of a colony still emergent from the algal cover retained their original color and had a healthy appearance. In 1992 to 1996 the brown alga *Dictyota* and related species formed almost coherent carpets on the dead hard substratum of most reefs. These were practically devoid of algae in 1968-70.

The per-station algal cover in Table 1 indicate that algae, including crustose, turf and frondose forms by 1992 were a dominant group within the coral reef biota of San Andrés: In 85% of the stations, algae covered more than 50% of the hard substrata, whereas in the remaining stations they reached values ranging from 35 to 50%. Only in a few stations did live coral cover on hard substrata exceeded that of algae. In 10 stations algae had cover values greater than 80%, reaching up to 95%. With the exception of stations located on the shallow leeward 4m terrace, such high values corresponded to sites of considerable recent coral mortality. On an average, algal cover was near 70% (25-26% of frondose algae) in 1992. With a few exceptions algal cover values obtained from chain transects were similar to those estimated visually, the latter ranging from 29 to 90%, with an overall mean of 62% (Table 1).

Mortality of gorgonian octocorals

During the earliest surveys, the sea fan *Gorgonia ventalina* was a conspicuous and frequent species of San Andrés reef environments that were moderately exposed to swell and waves. It was observed commonly in shallow waters down to about 20 m in depth (Geister, 1975) and was especially conspicuous in shallow seaward fore-reef settings such as the barrier fore-reef slope between 3 and 8 m and the inner and middle fore-reef terraces between 8 and 15 m. In these areas, often largely devoid of scleractinians, the sea fans together with sea whips (plexaurids) formed lush "octocoral gardens" on hard bottom. *Gorgonia* was equally abundant in lagoonal patch reefs (see Geister, 1975: Pls. 3 and 4). However, in 1992, 1994 and 1996 there were very few live colonies of sea fans remaining, mostly young specimens. But numerous dead axial skeletons were seen, still attached to the substratum. Also partly dead colonies were conspicuous. The dead skeletons were overgrown by algae. Per-site mortality was estimated in 1992 to be from 60 to 100%, with a mean of 91.4% (Table 2). In addition, low mortality levels of several species of other gorgonians was detected. These were found in the dense octocoral stands on the leeward 4 m terrace (Stations 41, 43, 46 and 47) where 5% of the upright branches were observed dead at the northernmost station (Station 41) and 20% at the southernmost station (Station 47).

Mortality of the long-spined sea urchin *Diadema antillarum*

This urchin was formerly very abundant in the San Andrés reef complex as witnessed during visits between 1968 and 1979, being especially frequent in the shallow back-reef areas, such as the hard bottom of the boat channel of the seaward fringing reef south of Sound Bay and in the marginal areas of lagoonal patch reefs. *Diadema* was also ubiquitous among the coral communities along the 4 m terrace and the adjacent coastal cliff of the leeward coast.

In 1973 and 1975, *Diadema* clusters of up to 10 specimens and more were commonly noted on sandy bottoms of the shallow lagoonal terrance between East Reef and in the nearshore seagrass flats near Dry Shoal and Long Shoal. Here *Diadema* was especially conspicuous and easily recognizable as dark patches in shallow water. This aspect had changed radically when the reefs were revisited in 1992, i.e., 9 years after the Caribbean-wide 1983-84 die-off of the *Diadema* population (Lessios et al., 1984). Unfortunately, there are no recorded observations that might document the timing and impact of this event on the San Andrés reefs (Geister, 1992).

By 1992, only a few isolated specimens of *Diadema* were observed in the *A. palmata-Diploria-Millepora* zone of shallow reefs in the northern lagoon. *Diadema* also occurred rarely in occasional clusters of 3-4 specimens on coral patches behind the barrier reef. In June 1993, this situation was basically unchanged, but by October 1994 and October 1996, it seemed to have improved somewhat. But the *Diadema* population did nowhere attain the levels present before the die-off. Occasional *Diadema* were spotted in most reef habitats of the barrier, fringing and patch reefs. No *Diadema* clusters were seen in pure lagoonal sand areas and in seagrass habitats as observed before the die-

off. The sea urchin was also still very rare in 1994 within the shallow coral associations of the leeward coast.

Reduction in populations of commercial organisms

We did not carry out population censuses of commercially important reef organisms at San Andrés. However, it was noted during the 1992 and 1994 surveys that certain of these species decreased in number to such an extent since the 1968-70 survey that today their exploitation is no longer economic or had to be abandoned because of the quasi-absence of the target species.

The queen conch *Strombus gigas* has been a popular food resource on the island and provides a number of typical island dishes. Traditionaly it was taken from San Andrés and also brought in numbers from the neighboring atolls of Courtown Cays and Albuquerque Cays. In 1968-70, the queen conch was still picked up regularly in the lagoon of San Andrés by spearfishermen . There were also a few natives who made their living by collecting conchs free-diving from small dug-out canoes in the northern lagoon. The catch was sold to the local population, and generally, a half-day's collecting trip was sufficient for a fisherman's subsistence. Therefore, it was most surprising that during the 1992-1996 surveys not a single living specimen even of a juvenile *Strombus gigas* was seen either in the northern or eastern lagoons, in spite of several days spent in the water by four experienced reef scientists.

Once, the spiny lobster *Panulirus* argus. was commonly collected by local spearfishermen, though already by 1968-70 it was less abundant than in the nearby atolls and in the reefs around Providencia Island. In 1992, 1994 and 1996 specimens were rarely observed, all of them of minor size. High demand by the local hotel industry resulting in overfishing is certainly one of the main reasons that lead to the decline of this valuable resource.

Large commercial fishes like snappers (*Lutjanus* spp.), groupers (*Mycteroperca* spp., *Epinephelus* spp.), grunts (*Haemulon* spp.), queen triggerfish (*Balistes vetula*), hogfish (*Lachnolaimus maximus*) and the great barracuda (*Sphyraena barracuda*) are rare to almost absent in San Andrés reefs. In 1968-70, all these species were caught by subsistence fishery and by spear-fishermen who also sold to the local hotels. By in 1970 a considerable amount of fish had to be imported from the Courtown Cays, Albuquerque Cays, and from Providencia to satisfy the needs of the local tourist industry. With increasing fishing pressure, the stocks in high-quality fish diminished drastically in the San Andrés reefs and also in those of the nearby cays. Hence, in recent years formerly despised non-traditional, lower-quality fishes, such as parrotfishes (*Scarus* spp., *Sparisoma* spp.), angelfishes (*Pomacanthidae*) and surgeonfishes (*Acanthurus* spp.), became also a major target for the local fishery. Since local reef fish became more and more scarce in the last 20 years, it has been noted in 1994 that more fish supplied to local restaurants are hemipelagic species such as the bonito (*Euthynnus alletteratus*), which are caught on off-shore banks over deeper water. Also deeper water species such as the silk snapper (*Lutjanus vivanus*) are caught on offshore banks. This species is commonly sold

nowadays in local restaurants to clients as "red snapper" or "pargo rojo" (*Lutjanus jocu*) because the more favored species is practically absent from the local reefs.

Reef sharks (*Carcharhinus* spp.) were common in the 1968-70 period in the San Andrés barrier reef and especially frequent in the wave-swept Blowing Rocks area where they could be observed in packs of 4 to more than 10 individuals (Geister, 1975). During visits to the Blowing Rocks in 1993, 1994 and 1996 not a single shark was sighted. Shark meat is not used for human consumption by the population of San Andrés except for occasional production of shark liver oil. Occasional catches of sharks are sold to immigrants from the Colombian coast. The reasons for the quasi-absence of sharks are far from clear. In recent years the Blowing Rocks area - renowned for frequent shark encounters - as well as the barrier reef, were frequented more and more by divers and underwater photographers, which by their presence may have scared the sharks away. Also the main prey of reef sharks - large and medium-sized fishes - became rare in the shallow reef mainly due to overfishing by speargun.

Solid waste in the reefs
A wide marine area along the NW coast at the SW end of the airport runaway is largely littered by garbage which was discharged from trucks until the end of the eighties. It accumulated mainly on the 20 m terrace. Glass bottles, cans and other trash occupy many of the interspaces between coral heads on this deep terrace and many items have been incorporated into the reef framework. Up to 10 items per square meter were found at Station 45. On the shallow 4m terrace there was less dense but more diverse trash, also including wrecked vehicles, cardboard, ropes, nylon lines, cloth etc. In 1992, trash also occurred farther south. Some garbage was also found on the lagoonal terrace and in the lagoonal basin north of the island.

In recent years, this type of waste disposal has been abandoned and garbage is stored, burned and partly recycled on land. It may be expected that much of the garbage remaining in the sea will be overgrown by reef builders in the near future or covered by sediment. It is uncertain if any toxic substances impregnate sediment and skeletons, thus entering the food chain via grazing organisms.

Physical damage to the reef
Ship wrecks and groundings
Shipwrecks and groundings are a major problem to the San Andrés reefs. In 1994 and 1996 four major shipwrecks were visible alone in the barrier reef. Shipwrecks are especially destructive because corals and entire reef spurs are not only smashed during the stranding, but ship hulls tend to move shoreward subsequently bumping the sea floor with the rise and fall of waves and tides thus leaving a broad trail of death and destruction behind. This may reach from the higher fore-reef to the reef crest area. With time, wrecks tend to disintegrate during heavy storms, each piece being moved separately on the ground by the breaking waves. As a result, shattered ship planks, masts and motors commonly create a sphere of destruction where coral life is totally annihilated. Corrosion and abrasion of the iron stains the sediment, which is deposited in the lee of the wrecks.

In 1994, reef damage by wrecks was especially conspicuous at East Reef and Half-a-Reef, where entire thickets of *Acropora palmata* were fragmented and where *Millepora* reef spurs were entirely ripped off. At Half-a-Reef, several shipwrecks ocurred since 1970, the last being the "Anancy" from Kingston. The most beautiful spurs photographed in 1970 and figured in Geister (1975: pl.5-d) and Geister (1983: pl.27-2) were entirely destroyed by the pounding effect of these wrecks.

The effects of ship groundings that did not result in abandonement were observed in the ship channel that leads from Entrance to San Andrés Harbor. Here entering ships produce occasionally large cuts on the crests of shallow patch reefs. On the other hand tourist boat traffic inside the lagoon is presently so heavy that it poses a significant source of damage to local shallow reefs. Broken colonies of *P. furcata* in the very shallow fringing reefs may also have been caused by the effect of trampling tourists or storm waves. Several characteristic scars in the shallow seagrass beds along the northern shore, easily visible from air, were definitively produced by boat propellers.

Storm waves

Occasional storms may cause heavy damage to the reef framework, especially to branching scleractinians (Geister, 1992: 44-46). Fragmentation of colonies is especially apparent after hurricane passage and the most conspicuous impact is on *Acropora cervicornis*. Extensive rubble of dead fragmented *A. cervicornis* colonies was found all over the western end of Little Reef in 1968. The colonies had not recovered until 1994. Their destruction may have occurred during the passage of hurricane Hattie in 1961. Storm damage inflicted to *A. cervicornis* thickets at Half-a-Reef in about 1972 (Geister, 1975, Plate 6a-b) was still present in 1994. The *A. palmata* thickets from this same site were still flourishing in 1973, but in 1992 they were all fragmented and dead, probably smashed by waves of hurricane Joan which passed near San Andrés in 1988 (Geister, 1992). In 1992 and 1994 large coral colonies of the more robust *Diploria strigosa* and *Acropora palmata* also were seen overturned though still alive in parts of the northern lagoon and on the 4 m terrace of the west coast. There, piles of dead detached coral heads were also seen at the base of the shallow submarine cliff that connects the 4 m terrace to the inner margin of the 20 m terrace. Along the west coast, in places formerly rich in coral growth, many skeletons were broken and rocky surfaces polished due to abrasion by coral shingle. These sights were rather uncommon in 1968 to 1979 and must be attributed to physical drag and abrasion by hurricane "Joan".

DISCUSSION

Spatial patterns of coral death vs. causes

Considerable changes in the environment have been observed during the time lapse under consideration. Most dramatic is the high mortality of corals, the substantial decrease of commercial organisms, the almost total absence of the herbivore *Diadema antillarum*, and the proliferation of algae. Hughes (1994) identified a chain of causal agents on Jamaican coral reefs, ranging from overfishing, to the proliferation of *Diadema* due to

lower predation and competition for algal resources, to extensive hurricane damage, to the demise of *Diadema* and the subsequent frondose algal bloom, which, together with further damage from coral bleaching, led to widespread coral mortality and recruitment inhibition, decreasing coral cover from 50% in the late 1970s to less than 5% today. Eutrophication has been pointed out as another agent causing algal bloom at Jamaica (Lapointe et al., 1997, Goreau et al., 1997).The same chain of events can be more or less traced at San Andrés and many other Caribbean reefs, with local or regional variations depending on factors such as occurrence of hurricanes, extent of overfishing, occurrence of widespread coral diseases, and induced anthropogenic damage from nautical activities, sewage discharge and excessive sedimentation, among others (cf. Ginsburg, 1994).

From the results presented herein, a spatial pattern emerges of greater coral death in lagoonal settings, and of lower coral death in high-energy zones (i.e., the barrier reef) and in the deep terraces and outer slope.

The high coral death in shallow, protected areas seems related directly to the susceptibility of the then dominant species to hurricane and storm damage and to diseases, and indirectly to the prevalent regime of high illumination, low turbulence, limited water flushing, and higher incidence of anthropogenic activities. It appears that part of the destruction of *A. cervicornis* and *A. palmata* in the lagoon was due to storm damage, but the epidemic white band disease which occurred in the Caribbean on Acroporid corals in the early 1980s (Peters, 1984), may have also been responsible. In contrast to the virtually total disappearance of *A. cervicornis* in shallow reefs of San Andrés, in other areas like Florida, Jamaica, Curaçao and Santa Marta (Colombia), where there were also mass mortalities of this species, there remained small populations that apparently are in the process of recovery (Bak & Criens, 1981; Jaap et al., 1988; Knowlton et al., 1990 ; pers. obs.). This may indicate either that recolonization by larval immigration has not taken place due to the geographical isolation of San Andrés, or that the conditions for the re-establishment of this species are not yet appropriate.

As in Jamaica (cf. Hughes, 1994), in the overfished reefs of San Andrés, *Diadema* lived in high densities in shallow, well illuminated and relatively calm reef areas. Its disappearance in San Andrés around 1983 (cf. Lessios et al., 1984) also resulted in widespread frondose algal growth, and probably had a major role in additional coral death and recruitment inhibition from shading and smothering (cf. Sammarco, 1980; Liddell & Ohlhorst, 1988; Carpenter, 1990a; 1990b). Further algal increases could have been fueled locally by nutrients from sewage discharges and groundwater seepage (cf. Walker & Ormond, 1982; Cuet et al., 1988), and by the more recent overfishing of reef herbivores.

On the other hand, in the enclosed lagoonal areas of San Andrés, water flushing is restricted, causing high thermal stress during El Niño warming events or during calms associated to intense insolation, which may have produced coral bleaching and widespread tissue mortality (see Geister, 1992; Williams & Bunkley-Williams, 1990). Also, depending on the length of the warm period, lower rates of (natural or artificial) lesion regeneration and increased tissue mortality (Meesters & Bak, 1993), may have occurred. Apparently,

susceptibility to coral diseases such as black band disease may have also increased in these warm periods (Rützler et al., 1983). Furthermore, the increased sedimentation rates and turbidity from anthropogenic activities may have made corals more susceptible to diseases (Peters, 1984), and may have retarded the regeneration of tissue lesions (Meesters et al., 1992), which probably increased in proportion as a result of the heavy boat traffic and diving activities.

The high energy, shallow spur and groove zone of the barrier reef at San Andrés was (Geister, 1977) and still is dominated by hydrocorals, zoanthids and crustose coralline algae. This lack of an apparently significant change in comparison to other reef zones could have several explanations. During heavy surge, damage occurring on the small *Millepora* branches could be quickly restored by fast growth and by reattachment after breakage (Denny et al., 1985). Thus, even though contemporaneous coral death rates may be high, instantaneous measurements yield low proportions of dead tissues. In general, probably owing to a combination of strong turbulence and high density of herbivorous fishes (cf. Lewis & Wainwright, 1985; Steneck & Dethier, 1994; Díaz-Pulido & Díaz, in press) frondose algae at the San Andrés barrier reef tend to be restricted to crevices and grow in between and beneath coral branches. The excessive algal growth apparently was not as high as other reef zones after the *Diadema* die-off presumably because this species was already scarce in this habitat. Perhaps the overfishing of carnivores has also increased herbivorous fish populations, although these may have been recently overfished as well. In addition, high energy zones are continuously flushed, even during periods of calms, making temperature increases and their associated effects on coral tissues moderate at most during warming events (Geister, 1992). This could explain the lower degree of mortality found in the *A. palmata* stands on the barrier reef outer base than in those of the lagoon (see Peters, 1984).

With localized exceptions, several sites of the leeward 20 m terrace and outer fore-reef terrace edge, and the outer slope show, when compared to shallow lagoonal areas, lower coral mortality levels. Since there are less herbivores in deep reef areas, which allow for a higher frondose algal cover, the *Diadema* demise apparently did not trigger further algal blooms due to low light levels (cf. Lewis & Wainwright, 1985; Morrison, 1988; Díaz-Pulido & Díaz, in press). The greater depths also imply lower turbulence during storms, and prevent heating-up and the associated stress during calms. Hurricanes (cf. Woodley et al., 1981), and mass bleaching events (cf. Williams & Bunkley-Williams, 1990; Shulman & Robertson, 1996, but see Lang et al., 1988) have had their greater impact in Caribbean shallow reef areas in comparison to deeper ones. Localized damage to deep areas of San Andrés was associated with local garbage and sewage discharges.

Algal proliferation
The mean values of frondose algal cover at San Andrés are fairly high when compared to those published from Barbados (0%), Curacao (0%), Santa Marta (Colombia)(0%), Jamaica (0.7 - 2.8%) and Venezuela (12.8%) (see Liddell & Ohlhorst, 1988). However, the last values were recorded before 1982, i.e., before the die-off of *Diadema* occurred. Records after the demise of *Diadema* measured in Alacran Reef,

Mexico, amounted to 45.6% algal cover (Liddell & Ohlhorst, 1988). Fleshy algal cover on the reefs of the San Blas Archipelago rose from about 2% in 1983 to nearly 28% in 1990 (Shulman & Robertson, 1996). Recent estimates in some reefs of Santa Marta, subjected to high downward fluxes of sediments and raw sewage outflows, showed values of algal cover of 40-50% (see Zea, 1993, 1994). These estimates are as high as those measured in 1992 in some areas of San Andrés.

Gorgonian mortality

The mass mortality of *Gorgonia* in San Andrés was probably related to similar events which occurred in other areas of the southern Caribbean during the 1980s, whose origin is attributed to a highly specific pathogen (Guzmán & Cortés, 1984; Garzón-Ferreira & Zea, 1992). A less intense *Gorgonia* mortality event was recorded again during 1995 throughout most of the Caribbean (Nagelkerken et al., in press), and a putative pathogen was isolated and identified as a fungus of the genus *Aspergillus,* a typical soil inhabitant (Smith et al., 1996). Noteworthy, sea fan mortalities do not seem to have affected populations of Serrana Bank, belonging also to the archipelago and located about 240 km NE from San Andrés (Fig. 1)(Díaz et al., 1996).

Decrease of reef fish stock

Evidently, over-fishing is the prime reason for the dwindling stocks of reef fishes on the island. But it must be noted, however, that all the major environmental changes observed in the reefs during the past two decades had an impact on these biotopes that provide food and shelter to specialized reef fish species. It should also be noted that the large-scale destruction of the coastal mangrove communities and part of the seagrass flats by measures aimed to develop the island deprived many reef fishes of their preferred nursery and feeding grounds (Heald & Odum, 1970; Ogden, 1980). As a consequence, juvenile reef fishes may have been subjected to increased predation pressure, thus having less chance to grow to a reproductive age.

CONCLUDING REMARKS

As we have shown, remarkable biotic changes have occurred in the reef complex of San Andrés during the last two decades. Some changes, especially those involving coral decline, appear to be mainly related to the macroregional, well-documented, increasing degradation processes of reefs in the wider Caribbean (see Ginsburg, 1994; Hughes, 1994) caused, apparently, by both natural and human induced regional and global changes (chronic diseases of corals and other reef organisms, coral bleaching, increase in algal cover due to release of grazing pressure and to overall nutrient enrichment). However, increasing and poorly planned human activities on the island are directly or indirectly responsible for many of the recorded biotic changes.

For example, over-exploitation of commercial organisms causes reduction in populations of some fishes and invertebrates, leading to disarrangement of trophodynamic processes which are yet not well understood, but whose effects may become evident, such

as the increase in cover of fleshy algae. Because of the lack of an adequate sewage system, the increase of nutrient availability in sea water also stimulates algal blooms and reduces coral cover on reefs.

San Andrés serves as a good example of the phenomenon of over-development and poor planning on small islands. It developed from a small nucleus of fishermen and coconut planters to a major tourist resort and commercial center in the brief space of 25 years, during which the sharply increasing population and numbers of tourists and associated large investment to meet infrastructure requirements led to disorderly land development and serious urban problems. The growing recreational tourism at San Andrés is greatly based on attractive seascapes and a "healthy" marine environment. However, as has been shown, the consequences of unplanned development and largely unrestrained over-fishing can also be clearly traced in the marine environment. Since, direct uses of the reef complex depend for their sustainability upon the ability of reef environments to provide opportunities in the form of harvestable resources or of quality sites for non-extractive activities (cf. Kenchington, 1988), it seems clear that if the processes causing man-induced degradation of the marine environment continue, the major economic income-producing activity of San Andrés will soon be seriously threatened.

ACKNOWLEDGMENTS

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Table 1. Distribution of live coral (relative to hard substrata) , recently dead coral (relative to total coral cover, live+dead) and algal cover (percent frondose algae in parenthesis) at San Andrés, estimated from visual surveys (visual) and chain transect surveys (trans.) carried out in 1992. (+) = present, but cover<5%; (-) = no data.

Reef zone/ station	Live coral (%)		Recently dead coral (%)		Algae (%)	
	visual	trans.	visual	trans.	visual	trans.
Barrier, back reef						
3	35	-	60	-	65(10)	-
17	22	-	70	-	72(11)	-
29	43	-	90	-	50(+)	-
34	20	-	70	-	78(17)	-
Barrier, fore-reef slope (spur and groove)						
2	22	-	40	-	74(11)	-
6	35	46	10	32	35(5)	29(4)
18	40	45	20	40	45(13)	42(19)
23	40	-	20	-	30(5)	-
30	30	-	10	-	55(+)	-
35	30	16	20	43	40(5)	72(24)
37	25	-	30	-	75(15)	-
Windward inner fore-reef terrace						
5	26	-	30	-	60(10)	-
31	53	-	50	-	42(+)	-
Windward middle fore-reef terrace						
4	22	-	30	-	72(6)	-
24	20	-	40	-	60(20)	-
Windward outer fore-reef terrace (edge-slope)						
19	17	-	70	-	75(75)	-
25	15	26	60	53	80(30)	61(22)
32	50	-	50	-	55(19)	-
36	25	23	30	54	70(40)	73(21)

Table 1 (continued from previous page)

Reef zone/ station	Live coral (%)		Recently dead coral (%)		Algae (%)	
	visual	trans.	visual	trans.	visual	trans.
Lagoonal *A. palmata-Diploria-Millepora* reefs						
7	30	-	80	-	70(5)	-
9	30	-	70	-	70(15)	-
11(flat)	30	-	-	-	70(50)	-
11(crest)	28	-	60	-	72(33)	-
12	33	-	60	-	67(39)	-
13(flat)	35	-	-	-	65(35)	-
13(crest)	33	-	60	3[*]	67(45)	54(9)
27	21	9	70	5[*]	79(5)	90(38)
33	5	-	90	-	95(5)	-
28	21	29	50	44	79(21)	66(12)
Lagoonal *Montastraea-Siderastrea* deep reefs and shallow reef bases						
8	50	38	60	61	50(25)	57(47)
21(base)	22	-	50	-	78(22)	-
22(flat)	-	-	90	-	-	
22(base)	38	21	30	52	62(-)	69(41)
26	7	-	60	-	86(29)	-
10	40	-	70	-	60(40)	-
Leeward 4 m terrace						
38	20	16	30	53	80(10)	78(8)
41	12	-	35	-	88(14)	-
43	10	-	30	-	90(45)	-
44	5	-	60	-	90(50)	-
46	5	-	50	-	95(-)	-
47	15	-	30	-	80(-)	-
Leeward 20m terrace						
39	56	41	35	57	44(38)	51(39)
40	25	-	-	-	-(-)	-
42	38	-	45	-	56(56)	-
45	29	14	60	84	58(58)	80(62)
48	21	-	60	-	79(79)	-
Mean	26	30	52	44	68(25)	62(26)

* Data not comparable with visual estimation

Table 2. Species-specific coral mortality levels at San Andrés in 1992. Range and mean of per-station proportion of dead coral (percent of dead relative to live + dead coral), and percent frequency of mortality (number of stations with dead tissues/number of total stations where the species was found).

| Species	Proportion (%)		Frequenc
	Range	Mean	
Acropora cervicornis	0 -100	75.0	75
A. palmata	0 - 95	59.2	89
Agaricia agaricites	0 - 80	6.8	24
Colpophyllia natans	30 - 70	52.9	100
Dendrogyra cylindrus	0 - 30	8.0	40
Dichocoenia stokesi	0 - 70	13.8	50
Diploria clivosa	0 - 30	5.2	23
D. labyrinthiformis	0 - 40	17.1	60
D. strigosa	0 - 60	16.4	58
Eusmilia fastigiata	0 - 80	52.5	75
Isophyllastrea rigida	0 - ?	?	11
Meandrina meandrites	0 - 40	8.8	25
Millepora complanata	0 - 90	31.3	70
Montastrea annularis	0 - 90	37.5	81
M. cavernosa	0 - 70	22.3	73
Porites furcata	0 -100	25.9	41
P. porites	0 - 70	21.5	48
Siderastrea siderea	0 - 80	31.7	74
Stephanocoenia	0 - 50	16.7	29
Gorgonia sp.	60 -100	91.4	100
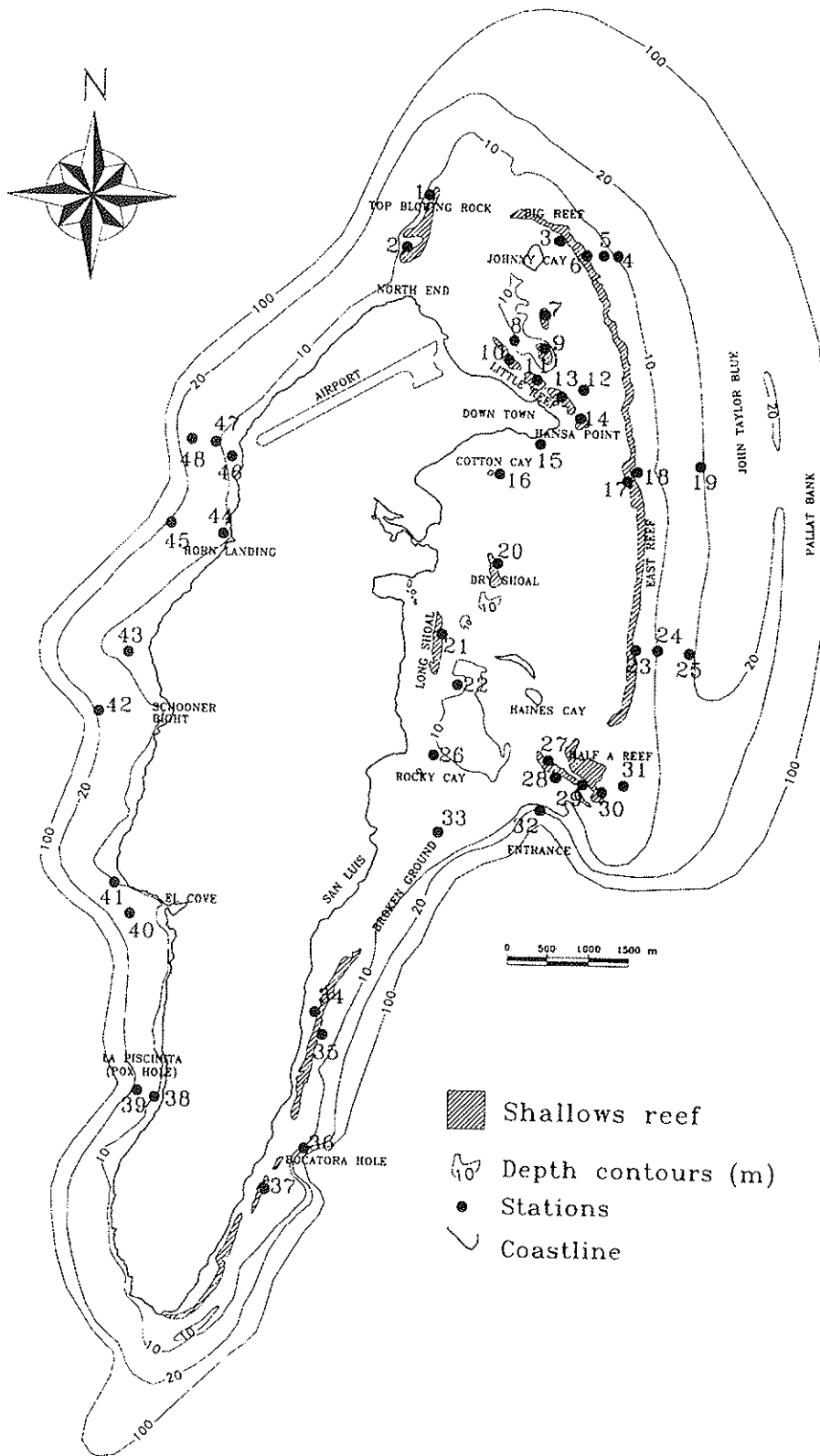
Figure 2. Topographic features of the insular shelf of San Andrés and location of stations where quantitative data on coral and algal cover were obtained in 1992.
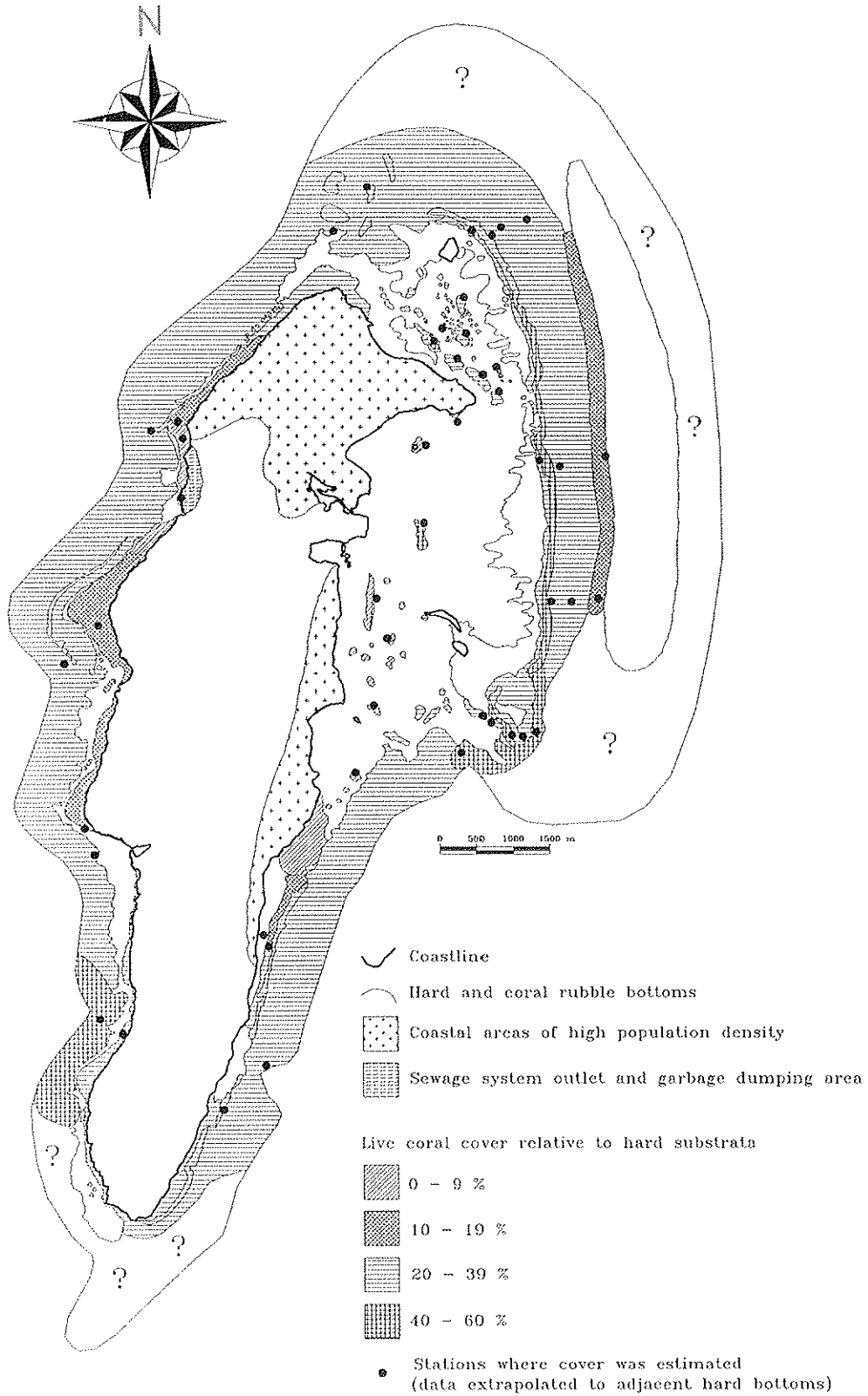
Coastline

Hard and coral rubble bottoms

Coastal areas of high population density

Sewage system outlet and garbage dumping area

Live coral cover relative to hard substrata

0 - 9 %

10 - 19 %

20 - 39 %

40 - 60 %

Stations where cover was estimated
(data extrapolated to adjacent hard bottoms)

Figure 3. Distribution of live coral cover (relative to hard substrata) at San Andrés.

Coastline

Hard and coral rubble bottoms

Coastal areas of high population density

Sewage system outlet and garbage dumping area

Proportion of recently dead coral

> 80 %

50 – 70 %

30 – 40 %

5 – 20 %

Stations where mortality was estimated
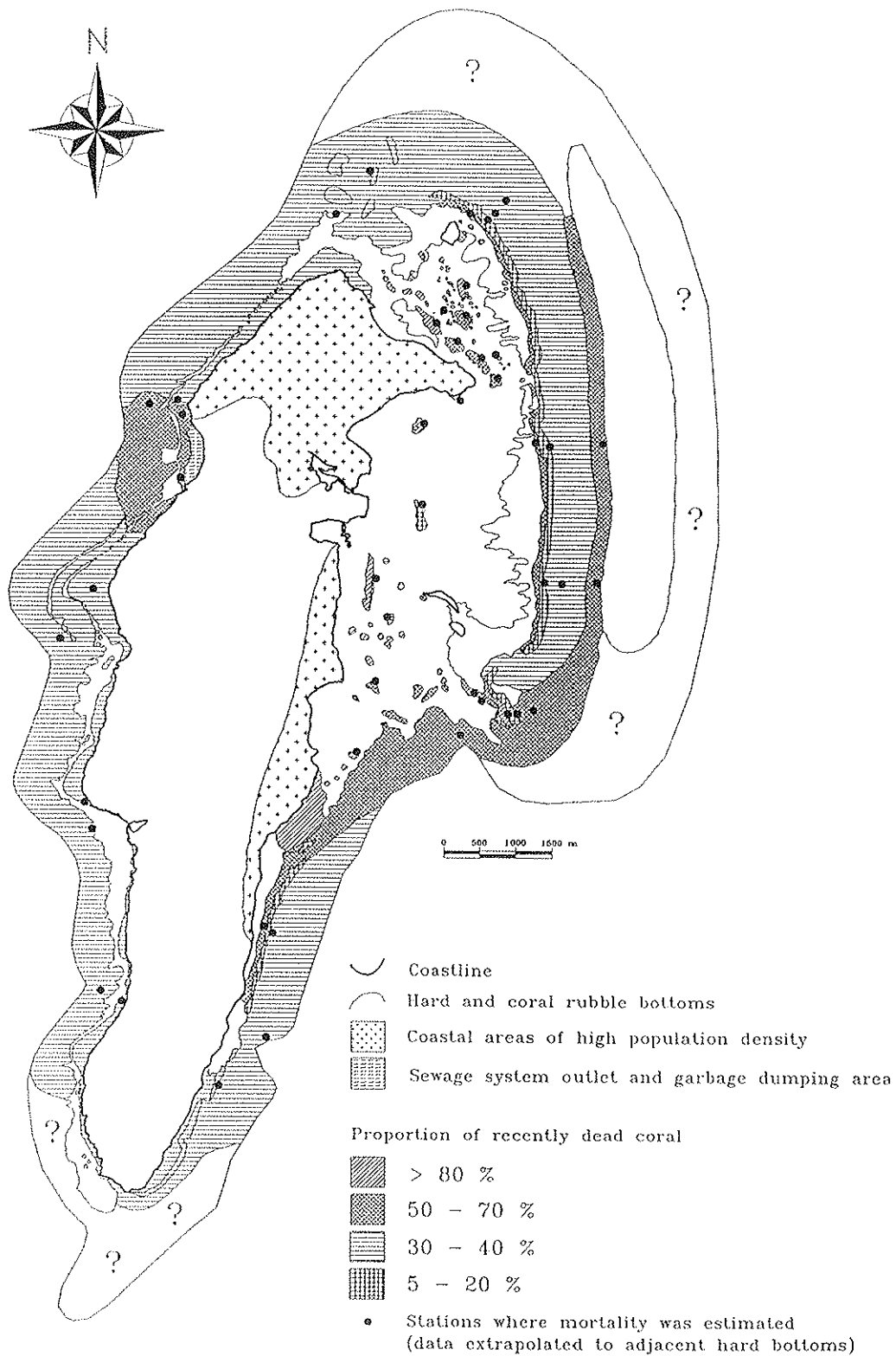(data extrapolated to adjacent hard bottoms)

Figure 4. Distribution of the proportion of recently dead coral (relative to total, live+dead, coral).

Figure 5 (continued on the next page). *Acropora cervicornis* stands in the northern lagoonal basin of San Andrés, 1-2 m in depth. **(a)** 1970, live, healthy thickets. **(b)** 1977, partly necrose and covered by filamentous algae.
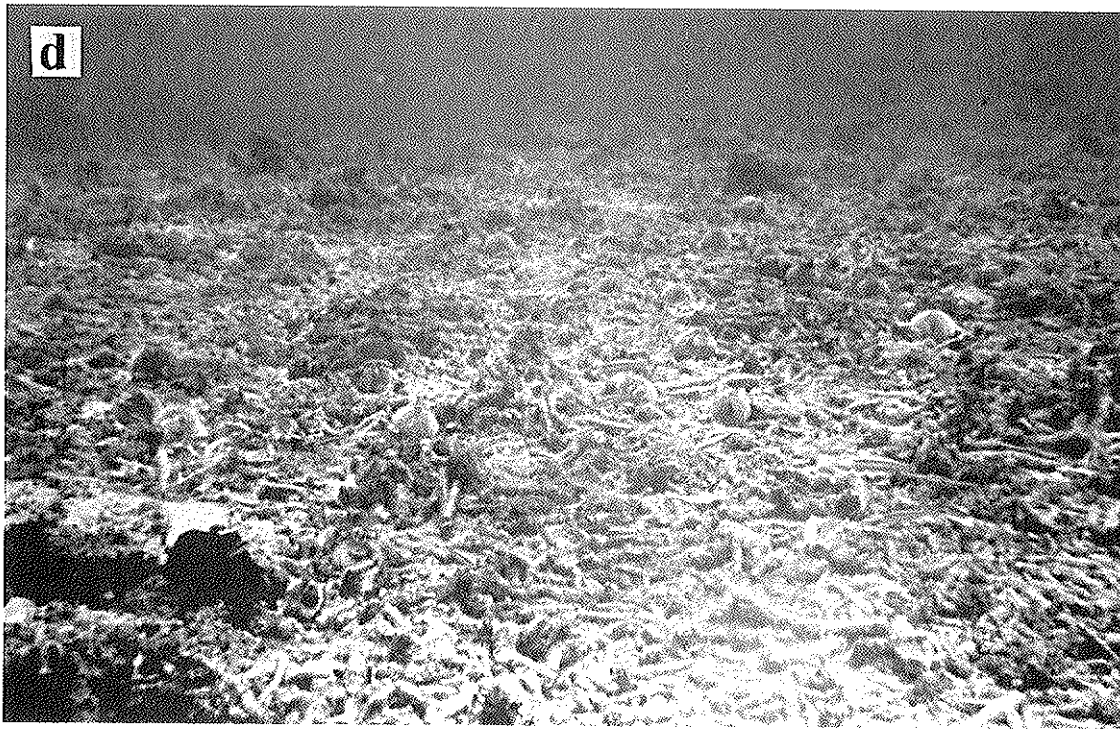
Figure 5 (continued from the previous page). **(c)**. 1979, more than 80% of coral tissues dead. **(d)** 1992, 100% mortality and collapse of skeletons.
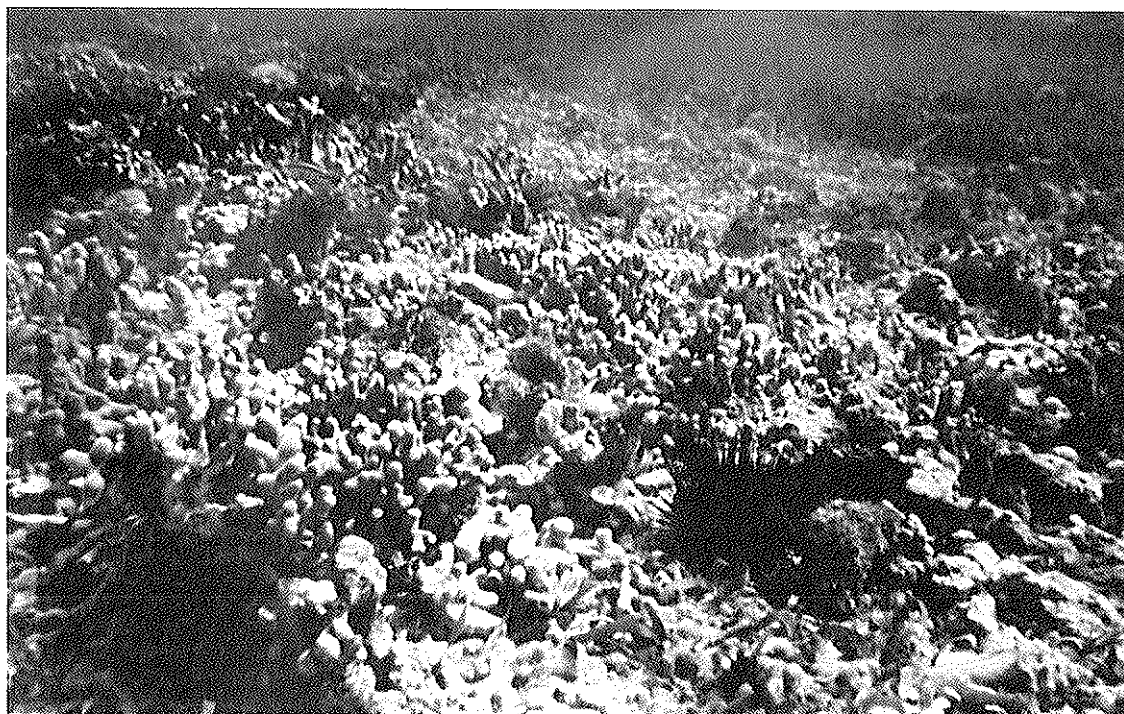
Figure 6. Shallow reef at Cotton Cay with live *Porites furcata* and the long-spined urchin *Diadema antillarum*, 0.5 m in depth, 1992.

Figure 7. Coral patch in the northern lagoonal basin of San Andres, 1-3 m, 1992. The carpets of the finger coral *Porites porites* are densely covered by brown algae (Dictyotaceae)