

**Changes in Cayo Enrique, La Parguera, Puerto Rico,
From 1936 to 1980 Using Aerial Photoanalysis**

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CHANGES IN CAYO ENRIQUE, LA PARGUERA, PUERTO RICO,
FROM 1936 TO 1980 USING AERIAL PHOTOANALYSIS

By

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SUMARIO

Fotografías aéreas de Cayo Enrique, La Parguera, Puerto Rico, se obtuvieron de los años 1936, 1951, 1963, 1971, 1978, 1979 y 1980. De estas se hicieron ampliaciones a una escala aproximada de 1:4,000 para diferenciar las distintas zonas del arrecife; sin embargo, en esta escala solo las comunidades mayores se pudieron medir con precisión. Los rasgos vistos en las fotos aéreas fueron corroborados por reconocimiento en el campo. Se notaron altas variaciones en las áreas de *Rhizophora mangle* y *Thalassia testudinum* a lo largo de un período de 44 años. La tasa de aumento en estas dos comunidades sugiere que Cayo Enrique se aproxima a una zonación climax dominada primordialmente por especies de plantas.

Cambios detectables en Cayo Enrique, usando una serie cronológica de fotos aéreas, incluye los efectos de los huracanes. Estos efectos consisten de acumulación de coral muerto ("boulder ramparts") en el nano arrecifal y una disminución en el área de mangle vivo. Disturbios periódicos aumentan la diversidad de especies del frontón arrecifal y promueven el establecimiento de comunidades de coral en la laguna y el nano arrecifal.

Se discute el uso de película en blanco y negro, diapositivas a color y película infrarroja de falso color. Información obtenida previamente mediante el uso de fotografías aéreas de arrecifes de coral provee los estudios fundamentales necesarios para evaluar los efectos actuales de interferencia humana y las catástrofes naturales en ecosistemas de arrecifes coralinos.

ABSTRACT

Aerial photographs of Cayo Enrique, La Parguera, Puerto Rico, were obtained for the years 1936, 1951, 1963, 1971, 1978, 1979 and 1980. Enlargements were made to the approximate scale of 1:4000 to differentiate the various reef zones; however, only reef macro-assemblages could be accurately measured at this scale. Features seen in the photographs were substantiated by surface reconnaissance. *Rhizophora mangle* and *Thalassia testudinum* areas, measured with a planimeter, showed the maximum variation of all reef zones for a 43 year period. The rate of increase in these two communities suggests that Cayo Enrique is approaching a climax zonation dominated primarily by plant species.

Detectable changes in Cayo Enrique, using a chronological series of aerial photographs, include the effects of hurricane disturbances. Hurricane effects in Cayo Enrique consist of boulder rampart deposition on the reef flat and an overall reduction of living mangrove area. Periodic disturbances increase the species diversity of shallow fore-reef areas and promote the establishment of coral communities on reef-flat and lagoonal zones.

The use of black and white, color reversal and false-color infra-red films in aerial photoanalysis of coral reefs is discussed. Past aerial coverage of coral reefs provides the baseline data needed to assess present day effects of human interference and natural catastrophes on coral reef communities.

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INTRODUCTION

Coral reefs are among the most biologically productive and taxonomically diverse of ecological communities. They are extremely efficient ecological units which support a large biomass in the relatively barren marine environment (Klim, 1969; Odum & Odum, 1955).

Coral reefs form barriers to waves and currents, protecting coastal areas against erosion. Reefs also modify adjacent sedimentary and depositional patterns creating sandy cays and islands. Coral reef ecosystems, which may comprise over 3,000 species of plants and animals, are increasingly used for recreational purposes and for scientific research.

Coral reefs are absent from the north coast of Puerto Rico. They are common on the eastern and southern sides of the island, reaching their maximum development on the southwestern coast off La Parguera. The study site, Cayo Enrique, is a typical coral reef of La Parguera frequently visited by local fishermen, pleasure boats, and marine scientists.

This study attempts to measure changes in the reef morphology and features of Cayo Enrique over a 44 year period using aerial photo-analysis. This technique has been used before in coral reef studies only to map and differentiate reef zones and for illustrative purposes. A series of vertical panchromatic aerial photographs, dating from 1936 to present, were used to measure various reef macroassemblages such as *Thalassia* beds and mangrove areas.

Detectable changes in the reef morphology and features of Cayo Enrique are correlated to the meteorological record and/or possible human interference. Catastrophic effects of hurricanes are of particular interest in the recent history of Cayo Enrique. Hurricanes David in 1979 and Allen in 1980 caused major coral destruction. Boulder rampart islets were formed on the reef-flat, composed mostly of dead pieces of *Acropora palmata*. Although mangroves and other reef organisms were adversely affected by the hurricane, *Thalassia* beds appeared to be undisturbed.

Human activities in Cayo Enrique appear to have had no detectable effects on the reef environment. Hurricane disturbances of moderate intensity are an important factor in maintaining high species diversity in coral reefs.

The practicality and limitations of aerial photoanalysis in reef studies is discussed. When available, a chronological series of aerial photographs is a useful tool in detecting and measuring trends in coral reefs and provides baseline data by which present and future comparisons can be made.

REVIEW OF LITERATURE

Verrill (1869), one of the earliest workers on West Indian coral reefs, compared the coral fauna of the Atlantic and Pacific coasts off the Isthmus of Darien. Rathbun (1879) described Brazilian corals and coral reefs. Vaughan (1901) was the first investigator to sample and describe Puerto Rican corals.

In Jamaica, Goreau and co-workers did extensive field work on the coral reefs of the north coast of the island. Their exploration of the deeper reef zones revealed active reef framebuilding to a depth of 100 m. Several new coral species were discovered, bringing to 62 the species of scleractinian corals known from Jamaica (Goreau and Wells, 1967).

In Puerto Rico, Almy and Carrion-Torres (1963) studied the coral reefs around the island and reported 38 coral species. Pressick (1970) found 18 scleractinian species in a reef near Icacos Island, on the northeast coast of Puerto Rico. Glynn (1973a, 1973b) described the *Porites* reef-flat biotope of Cayo Laurel in La Parguera. The effects of sedimentation on Puerto Rican reef corals has been discussed by Loya (1976) and Rogers (1977).

Cayo Enrique, besides being one of the largest and best developed reefs of La Parguera, has been studied very little. Wallace *et al.* (1973) described the zonation of Cayo Enrique's fore reef. The effect of burrowing organisms on the reef apron sands of Enrique was described

by Morelock and Mathews (1973) and Mathews (1974). Morelock *et al.* (1977) described the Enrique reef environment and divided it into three different depositional and morphological areas: the reef apron, the reef flat and shoals, and fore reef.

Aerial photography and other remote sensing techniques have been used very little in coral reef studies. As early as 1925, vertical aerial photographs were taken of the Great Barrier Reef in Australia (Hopley, 1977). After the Second World War, many coral reef papers used aerial photography to differentiate reef zones and for illustrative purposes (e.g. Steers, 1945; Teichert and Fairbridge, 1948, 1950).

Kumpf and Randall (1961) used a series of aerial photographs in charting the marine biota around St. John, U.S. Virgin Islands. Kelly and Conrod (1969) made a qualitative analysis of the bottom communities on the Bahama Banks using aerial photography. Guidelines for the use of aerial photography in reef studies are provided by Hopley (1977) and Hopley and Steveninck (1977).

Hurricane effects on coral reefs and shallow-water benthic communities have been documented by many investigators. In a series of papers, Stoddart (1962, 1963, 1974) studied the effects of a severe hurricane that affected reefs in the British Honduras region in 1961. In 1972 a re-survey of these reefs showed that little or no recovery had taken place on reefs subjected to massive damage, whereas complete recovery had occurred on moderately or slightly damaged reefs (Stoddart, 1974).

Other studies on hurricane effects on Caribbean coral reefs and

benthic communities include Thomas *et al.* (1961), Tabb and Jones (1962), Oppenheimer (1963), Vermer (1963), Ball *et al.* (1967), Perkin and Enos (1968), and, in the Pacific Ocean, Flood and Jell (1976), Randall and Eldredge (1977), and Ogg and Koslow (1978).

In Puerto Rico, the effects of Hurricane Edith on La Parguera reefs were documented by Glynn *et al.* (1964). They report minor damage to Cayo Enrique and no coral-shingle islet formation. Glynn (1973, p. 306) reported that extensive areas on the windward and back side of Cayo Laurel were affected after the passage of Hurricane Beulah on September 10, 1967. Twelve years later, Hurricane David (August 25-September 8, 1979) passed 70 to 80 miles south of Puerto Rico on a west-northwesterly course. The effects of this and other hurricanes on Cayo Enrique are documented here by the author (see "Hurricane disturbances, p. 40).

MATERIALS AND METHODS

Aerial Photoanalysis

Vertical panchromatic aerial photographs were analyzed from the years 1936, 1951, 1963, 1971, 1978, 1979 and 1980. The 1936-1971 aerial photographs were obtained from the Photogrammetry Division, Department of Public Works. The 1978 aerial photograph was obtained from Mark Hurd Aerial Surveys Incorporated, San Juan, Puerto Rico. The author photographed the 1979-1980 aerial coverage from a small high-winged airplane. This included vertical and low-altitude oblique panchromatic and color reversal photographs. Kodak Plus-X Pan Professional Film 4147 in 4 X 5 format, and Kodak Kodachrome color reversal and Plus-X Pan Film in 35 mm format were used. A polarizing filter was used with color reversal film to minimize the effects of sun glare.

All photographs were enlarged to the approximate scale of 1:4000. A more exact scale was computed for each photograph using man-made structures, which were measured in the field and compared to their equivalent photographic image measurement using the formula:

$$S = D/P_m$$

where D = the ground measurement and P_m = the photographic image measurement.

The 1979-1980 photographic scale was computed by using:

$$S = F/H$$

where F = the focal length of the camera and H = the flying altitude.

A NASA high-altitude infrared color photograph was used to show this film's ability to differentiate shoreline and reef mangrove

vegetation. This photograph was obtained from EROS Data Center, U.S. Geological Survey. Seagrass and mangrove areas were traced from each photograph and measured with a planimeter. A 10 x illuminated hand magnifier was used for detailed observation of the photographs. Different reef features and zones were defined in all aerial photographs according to their tone and their location on the reef (Table 1). The meteorological data was obtained from the Ensenada and Magueyes Island stations of the U.S. National Weather Service.

Field Survey

Cayo Enrique was surveyed by walking on the reef-flat, snorkeling on the back-reef, and SCUBA diving on the fore-reef. Transects were made on the fore-reef using a 10 m long plastic chain placed parallel to depth contours at 2 m intervals. Percentage coral coverage and species diversity were recorded for each transect. Species diversity was measured using the Shannon-Weaver (1949) function:

$$H' = \sum p_i \ln p_i$$

where $p_i = n_i/N$. Evenness was calculated as

$$H'/H'_{\max}$$

where H'_{\max} is the diversity that would exist if all the species pre-sent were distributed equally (Pielou, 1966). Depth was measured using an oil-filled depth gauge. The width of the various reef-flat zones was measured using a 30 m measuring tape and reel. Boulder rampart composition was determined by randomly picking 100 fragments from the eastern and middle boulder ramparts.

Table 1. Criteria used to define reef features and zones of Cayo Enrique using panchromatic photographs.

Feature	Location	Tone
<i>Acropora palmata</i> zone	windward side of reef to 3 m depth	medium to dark gray, contrasting with light substrate
<i>Millepora-Palythoa</i> zone	reef crest	light gray, usually defined by white line of breaking waves
Living and dead <i>Porites</i> and other corals	adja- leeward and cent to reef crest	light gray mixed with sandy areas
<i>Thalassia-Zoanthus</i> zone	most of reef flat areas	medium to dark gray
mangroves	limited to reef flat areas	even medium gray tone, mottled appearance
<i>Thalassia</i> seagrass beds	east and west ends of back reef lagoon	light to medium gray tones
sandy areas	back reef lagoon and slope	white to very light gray tones that vary with depth
small patch reefs	back reef lagoon	dark to very dark spotted pattern over light gray lagoon sands
boulder ramparts	reef flat areas behind reef crest	brilliant white tones with dark edges

The 1979 and 1980 aerial photographs were taken to the field to correlate the features seen in the photographs to the field observations. Color slide film was used to document the effects of Hurricanes David and Allen on the reef.

The Study Site

Cayo Enrique is located 1.5 km south of the village of La Parguera. It is approximately 1.4 km long by 0.4 km at its widest point, and is aligned almost parallel to shore (Fig. 1).

Cayo Enrique was selected for this study because of its relatively large size and the presence of various biotic macroassemblages, such as seagrass beds and mangrove areas. Due to its proximity to land, it also appears in most aerial photographs of the area.

The temperature-salinity characteristics of La Parguera are indicative of a mild hydrographic climate (Glynn, 1973). A continuous surface current flows over the reefs; this and a maximum daily tidal range of only 40 cm prevent marked temperature and salinity differences.

A stable reef-flat and back-reef environment is thus provided. Although heavy mortality of reef-flat organisms related to midday extreme low tidal exposure do occur (Glynn, 1968), their effect on the reef's macro-flora and fauna is negligible when compared to the catastrophic effects of hurricanes.

Cayo Enrique can be classified as an apron reef with a shallow (0.5-3 m deep) area of sand deposition leeward of the reef flat

(Fig. 2). These sediments are medium and coarse-grained sands composed mainly of *Acropora*, *Porites* and *Halimeda* fragments (Morelock *et al.*,

Figure 1. Outline of Puerto Rico with an arrow indicating the location of La Parguera. A detailed map of La Parguera showing the study site, Cayo Enrique, in relation to the coast and other reefs.

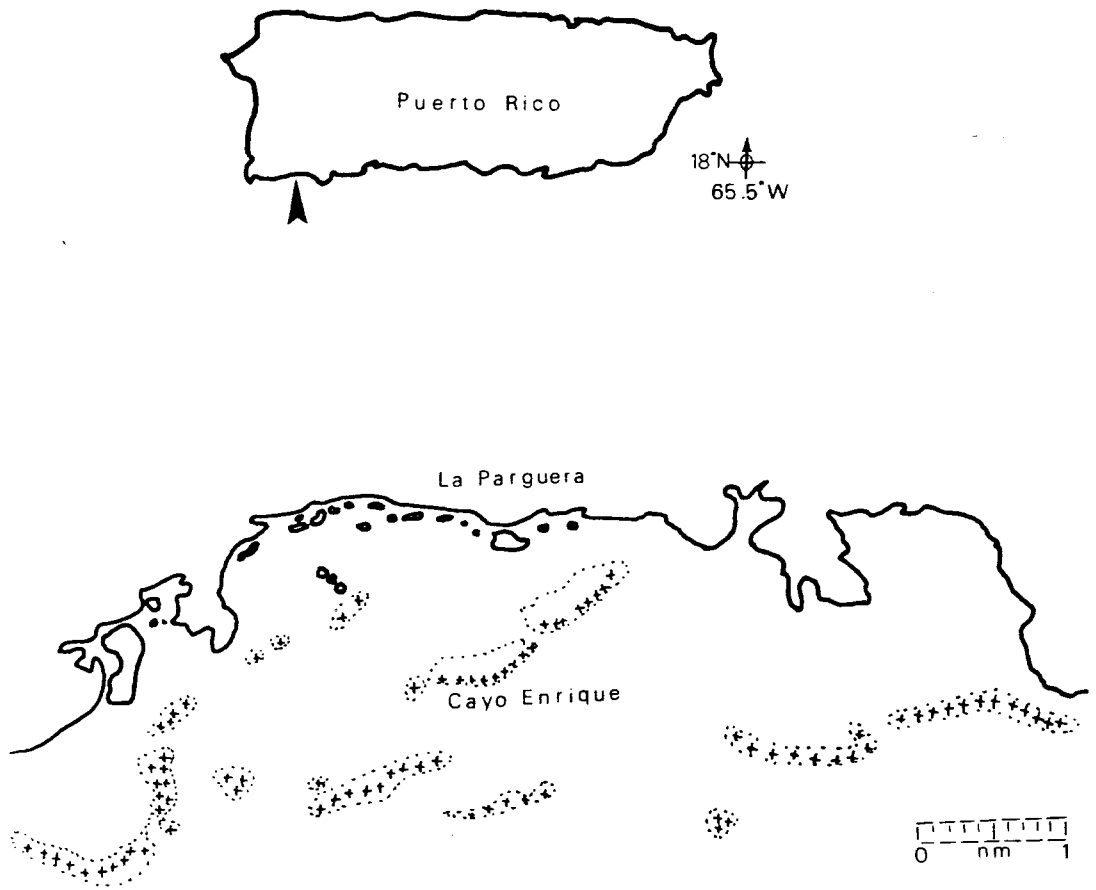
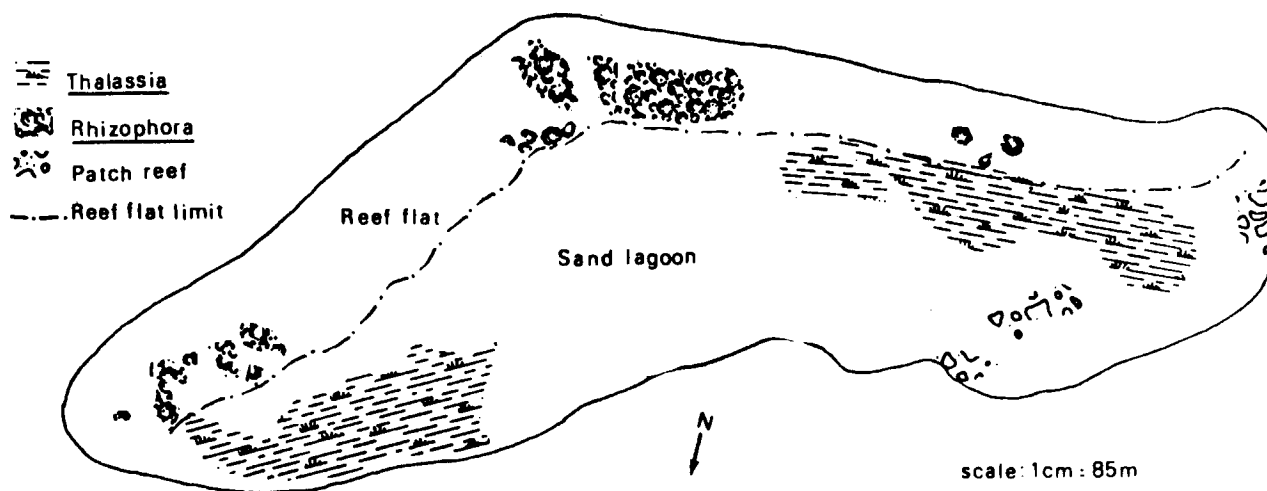


Figure 2. 1978 aerial photograph and diagram of Cayo Enrique showing the various zones and features.



1977). Both seagrass beds and small patch reefs occur in this zone. *Thalassia testudinum* areas are found on both ends of the sandy lagoon and on the reef flat. The seagrass, *Syringodium filiforme*, and the algae, *Dictyota divaricata* and *Spyridia filamentosa*, are usually found associated with *Thalassia*. The sea urchins, *Diadema antillarum*, *Tripneustes ventricosus* and *Lytechinus variegatus*, are common in the sandy lagoon.

The reef flat. is composed mainly of living *Thalassia*, *Zoanthus*, *Porites*, and, occasionally, *Halimeda* clumps. *Rhizophora mangle* occurs in the middle and both ends of the reef flat. A more detailed description of the reef-flat zone, based on aerial photointerpretation, is found on page 17.

The reef crest is dominated by the hydrocoral, *Millepora complanata*. The zoanthidian, *Palythoa caribbea*, is found near the reef crest encrusting dead corals.

At the eastern end, the fore-reef platform of Cayo Enrique is relatively broad and gradually slopes to a depth of 20 m while be-coming narrower and steeper to the west. This reef lacks spur-and-groove development of the fore-reef but has a well-defined coral zonation. *Acropora palmata* occurs seaward of the reef crest to a depth of 3 m, followed by *Acropora cervicornis* to a depth of 5 m. A zone of massive corals occurs from 5 to 15 m and is composed mainly of *Montastrea*, *Diploria* and *Agaricia*.

The lagoon coral patch-reefs are dominated by the coral, *Montastrea annularis*, in addition to numerous sponges and gorgonians. Other corals present include *Acropora cervicornis*, *Siderastrea siderea*, and *Diploria labyrinthiformis*. Dead coral heads covered with algae are common in this area.

RESULTS

Photointerpretation of reef zones and features

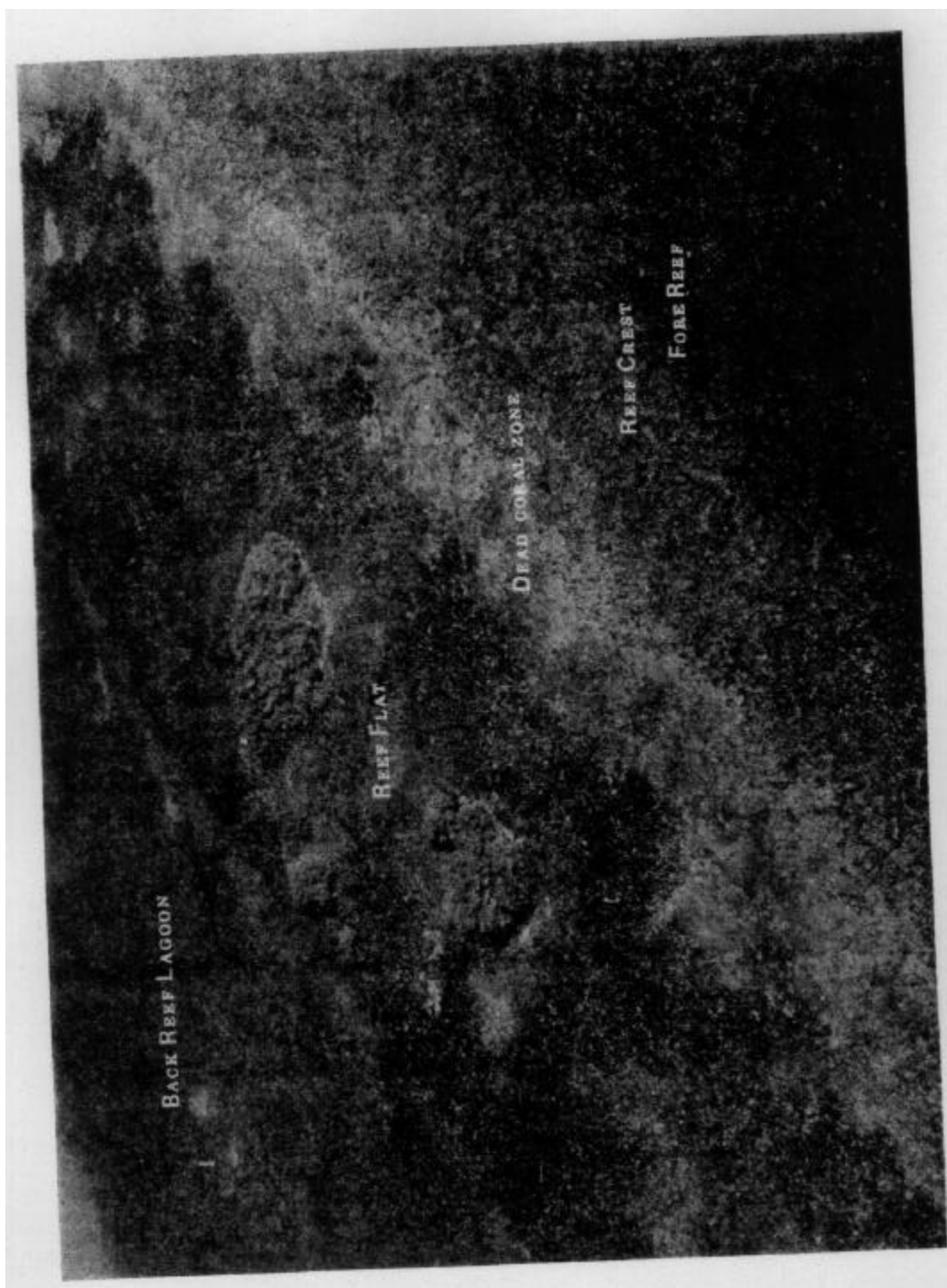
I. Black and white film

Black and white (panchromatic) film was the principal film used in this research. This is the easiest to handle, most economical, and most widely used film in aerial surveys. Reef features and zones are recorded on this film as different tones of gray. Tone and location on the reef was used to differentiate between the various reef features and zones (Table 1). Tones vary from a brilliant white for boulder ramparts to medium and dark gray for mangroves and living coral, respectively. Hopley (1977) stated that dead coral, having a greater light reflectance, appears grayer than living corals in this film.

A vertical panchromatic aerial photograph and diagram of Cayo Enrique was used to show major reef macroassemblages (Fig. 2). This photograph, taken in 1978, can be used in conjunction with the criteria listed in Table 1 to differentiate most reef features.

A low-altitude oblique black and white aerial photograph shows the different reef-flat zones of Cayo Enrique more clearly (Fig. 3). A transect was made across the reef flat on the western part of the reef to interpret the zones seen in the oblique aerial photograph. The reef crest is approximately 8 m wide and is dominated by the hydro-coral, *Millepora complanata*. The zoanthidian, *Palythoa caribbea*, is found here encrusting dead corals. Small colonies of *Porites*

Figure 3. Low-altitude oblique black and white aerial photograph of Cayo Enrique taken in 1980. The different reef-flat zones are discussed in the text.



astreoides, *Montastrea annularis*, *Diploria strigosa*, *Favia fragum*, *Siderastrea siderea* and the urchins, *Tripneustes ventricosus* and *Diadema antillarum*, occur leeward and adjacent to the reef crest. A lead coral zone occurs leeward of the reef crest and is approximately 20 m wide. This sandy dead-coral zone is shown clearly in Figure 3. *Porites* rubble is replaced by living *Porites porites* and *P. astreoides* as one moves farther away from the crest. Some *Halimeda* clumps and sparse *Thalassia* growth occurs near the reef-flat area. The reef flat is dominated by the seagrass, *Thalassia testudinum*, with the zoanthid, *Zoanthus sociatus*, and occasional *Halimeda* clumps. *Rhizophora mangle* occurs only in this area. *Thalassia testudinum* is found on the back-reef lagoon along with *Syringodium filiforme* and the alga *Dictyota divaricata*.

Although only vertical aerial photographs can be used to measure reef areas accurately, low-altitude oblique aerial photographs are useful in differentiating the various reef-flat zones and in depicting relief more clearly.

II. Color film

Contrary to general belief, the introduction of color as a criterion in aerial photointerpretation of coral reef features offers no distinct advantage over black and white film. However, color film is significantly better than panchromatic film in its greater ability to penetrate water (Hopley and Steveninck, 1977). A NASA high-altitude color aerial photograph clearly shows bottom features at a depth of 20 m at the shelf edge off southwestern Puerto Rico. Bottom vegetation is visible to depths of 30 m at the Florida Straits using Ektachrome in 70 mm format color film from an altitude of 60,000 feet (Kelly, 1970).

A vertical aerial color photograph of Cayo Enrique was taken on August 2, 1980 by the author to show the difference between black and white and color film in aerial photointerpretation (Fig. 4). Color and location on the reef were used to differentiate between the various reef features and zones (Table 2). Color classification is after Maertz and Paul (1950). With the exception of rose beige (Maertz and Paul, 1950) for the *Millepora-Palythoa* zone, the names of the color tones or hues are approximations and were established by the author.

III. False color infrared film

Color infrared film has a sensitivity range extending to the near infrared band of the spectrum (700 to 900 nm). Healthy vegetation reflects radiation over most of this band, producing a wider tonal range than regular color photography. In Indo-Pacific coral reefs with large tidal ranges, algal rims and reef-flat organisms such as corals and clams with symbiotic zooxanthellae show infrared reflectance varying from pink to bright red (Hopley and Steveninck, 1977). Seagrasses and marine algae, which also show infrared reflectance, are not re-corded on aerial infrared film unless they are exposed or covered with a few centimeters of water. Water appears either dark blue or black on infrared film, since water readily absorbs near infrared radiation. This provides a useful tool in delineating shoreline and mangrove vegetation

Figure 4. Color aerial photograph of Cayo Enrique taken in 1980.



Table 2. Criteria used to define reef features and zones of Cayo Enrique using color photography. *Color classification after Maertz and Paul (1950).

Feature	Location	Color Tones	Color classification*		
			plate	row	column
fore-reef zone	windward side of reef to 5 m depth	varies with depth from brown to dark blue	---	---	---
<i>Millepora-Palythoa</i> zone	reef-crest	rose beige	5	10	A
dead coral zone	leeward and adjacent to reef-crest	light beige	---	---	---
<i>Thalassia-Zoanthus</i> zone	most of reef-flat areas	brownish-green tones	14	1	D
mangroves	limited to reef-flat areas	medium to dark green tones	23	12	L
<i>Thalassia</i> seagrass beds	east and west ends of lagoon	olive green tones	24	7	A
sandy areas	back-reef lagoon and slope	light blue	33	1	J
small patch reefs	back-reef lagoon	light brown to dark green tones	---	---	---

A portion of a NASA high-altitude infrared color photograph of La Parguera shows Cayo Enrique's mangrove vegetation effectively outlined (Fig. 5). A uniform red tone (Persian pink, after Maertz and Paul, 1950) indicates a single species, *Rhizophora mangle*, colonizing the reef-flat. Other mangroves such as *Avicennia germinans* and *Laguncularia racemosa* would be recorded as lighter red tones. The back-reef seagrass beds are too deep to reflect near infrared radiation, so they appear medium blue. The sandy lagoon appears light blue, while the surrounding deep water is dark blue. Low-altitude color infrared photographs, taken at low tide, could record sources of infrared reflectance on the reef-flat and crest of Cayo Enrique such as living corals, seagrasses, and algae.

Practicality and limitations of aerial photoanalysis in coral reef studies

Aerial photographs can be vertical, oblique, and high or low altitude. Vertical photographs are used for quantitative work involving measurement of distances, area, and relief. Vertical photographic stereo pairs are used with a stereoscope for accurate measurement of relief. Oblique aerial photographs are helpful in identifying ground features and depict relief more clearly.

In coral reef studies, vertical aerial photographs enable mapping and measuring of reefs and reef zones that can be used in present or future comparisons. Oblique aerial photographs taken at low-altitude show reef-flat features and zones better (Fig. 3). The main advantage of high-altitude aerial photography is the capability of

Figure 5. Infrared color aerial photograph of Cayo Enrique (a portion of a NASA high-altitude infrared color photograph taken in 1974).



covering a large area on a single photographic frame. Kelly and Conrod (1969) described features and anomalous conditions of the bottom biology geology of the Bahama Banks from high-altitude aerial photographs. These features could not be detected from the surface or below. They claimed that "this was either because the features were too large to be resolved from the surface or because the differences in tone were too slight to be seen from the surface or while diving." Geomorphological coral reef features such as spur-and-groove formation are easily detected and mapped. High-altitude aerial and satellite photography has also been used to show the distribution of suspended materials and pollutants in temperate coastal waters (Kelly, 1970). Satellite photography has been used very little in coral reef research. Although it has the advantage of covering very large areas, the scale of these photographs is too small to resolve most coral reef features. Hopley (1977) stated that the greatest value of space imagery of the Great Barrier Reef lies in the fact that it updates and supplements century-old hydrographic charts.

As mentioned previously, the use of color film offers no distinct advantages over black and white film in differentiating coral reef features and zones. Almost all reef features are represented as various brown and green tones. Greater water penetration is, perhaps, the major advantage of color aerial photography.

False-color infrared film is the best film for differentiating shoreline and reef-flat mangrove vegetation. This film records healthy vegetation on a wider tonal range than color film, permitting the identification of different species of mangroves and other emergent

vegetation. Since water readily absorbs near-infrared radiation, sea-grass beds and algae, which show infrared reflectance, are not recorded on this film when covered by as little as a few centimeters of water.

The biggest limitation in the chronological series of aerial photographs used in this study was not the film type (panchromatic) but the photographic scale. Unfortunately the largest scale given (1:4000) was not large enough to resolve individual reef corals or to differentiate between living and dead corals. Therefore, the criteria used here to determine past and future trends in Cayo Enrique is limited to changes in seagrass and mangrove assemblages, and the effects of hurricanes.

Changes in a 44 year period

Detectable changes in Cayo Enrique from 1936 to 1980, using a chronological series of aerial photographs, are limited to biotic macroassemblages and to the effect of hurricanes. These macroassemblages include the back-reef seagrass beds, composed mostly of *Thalassia testudinum*, and the reef-flat mangrove areas, composed of *Rhizophora mangle*.

I. *Thalassia testudinum* areas

Approximately a two-fold increase in lagoonal seagrass areas occurred in Cayo Enrique between 1936 and 1979 (Figs. 6a, 6b and 7). This represents an average increase of 756 m²/yr over a 43 year period. The eastern *Thalassia* bed doubled its area between 1936 and 1951 while, on the western end of the reef, an almost complete disappearance of

Figure 6a. Relative changes in *Thalassia* and mangrove coverage from 1936 to 1963.

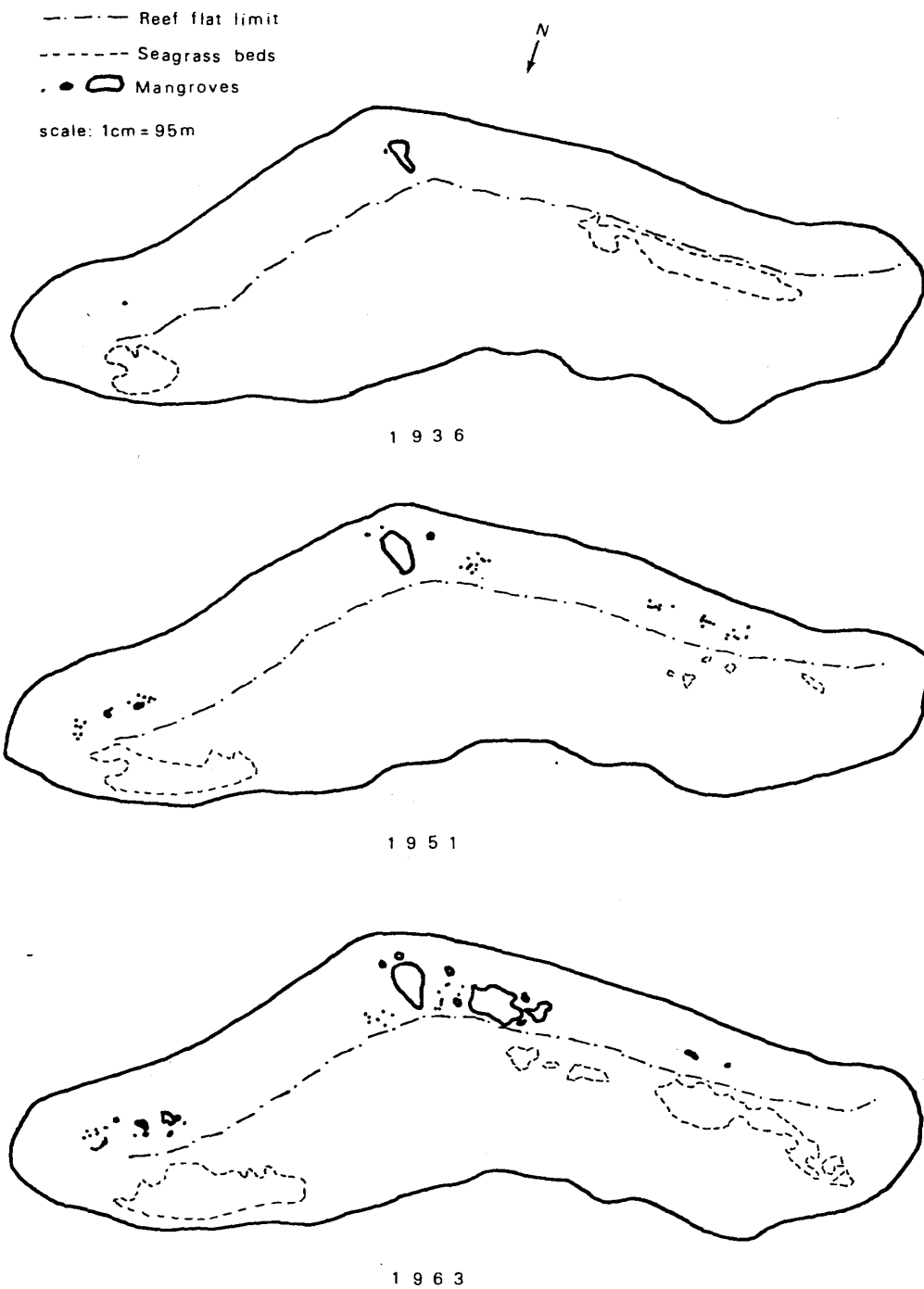


Figure 6b. Relative changes in *Thalassia* and mangrove coverage from 1971 to 1979. Arrows indicate location of boulder ramparts formed by Hurricane David in 1979.

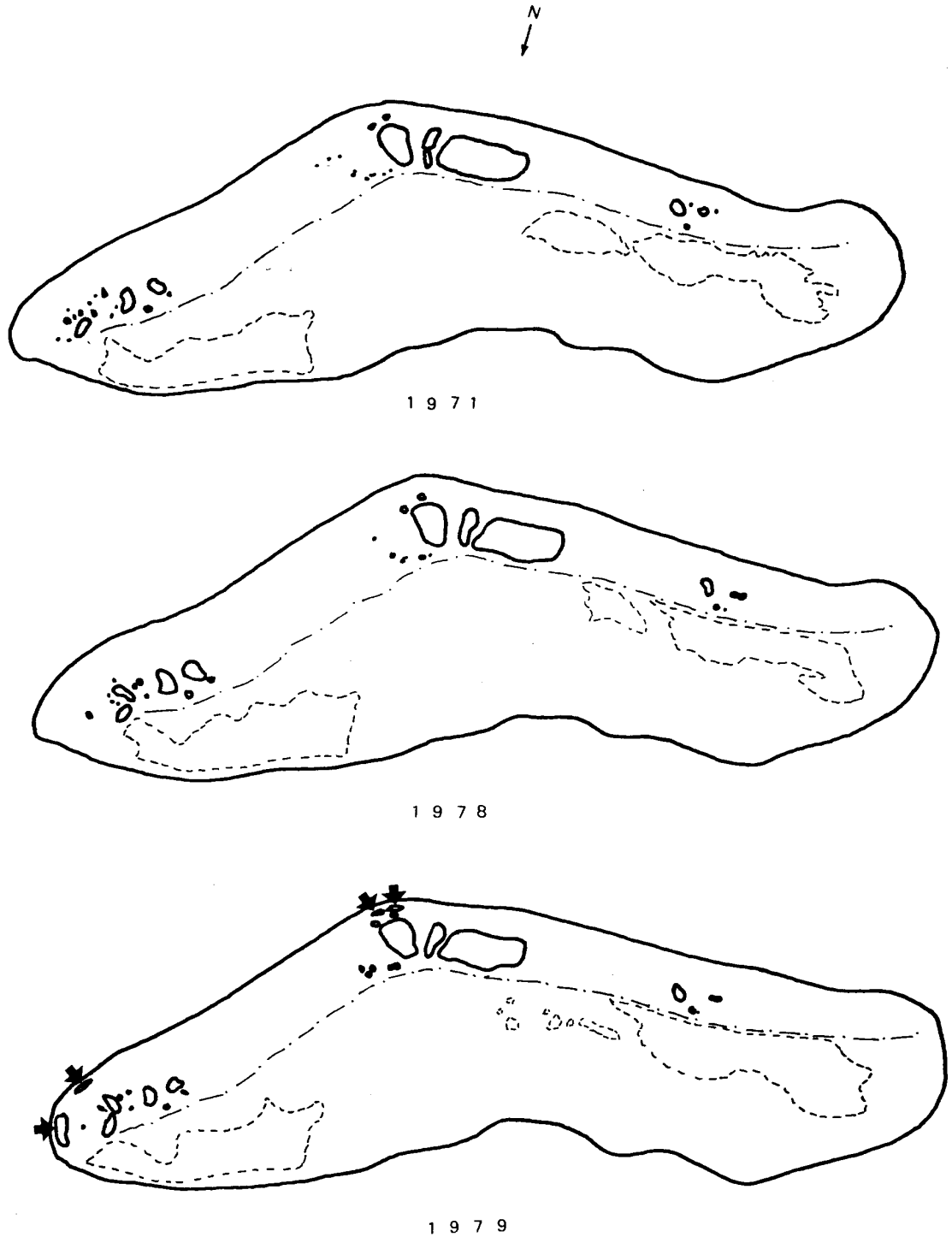
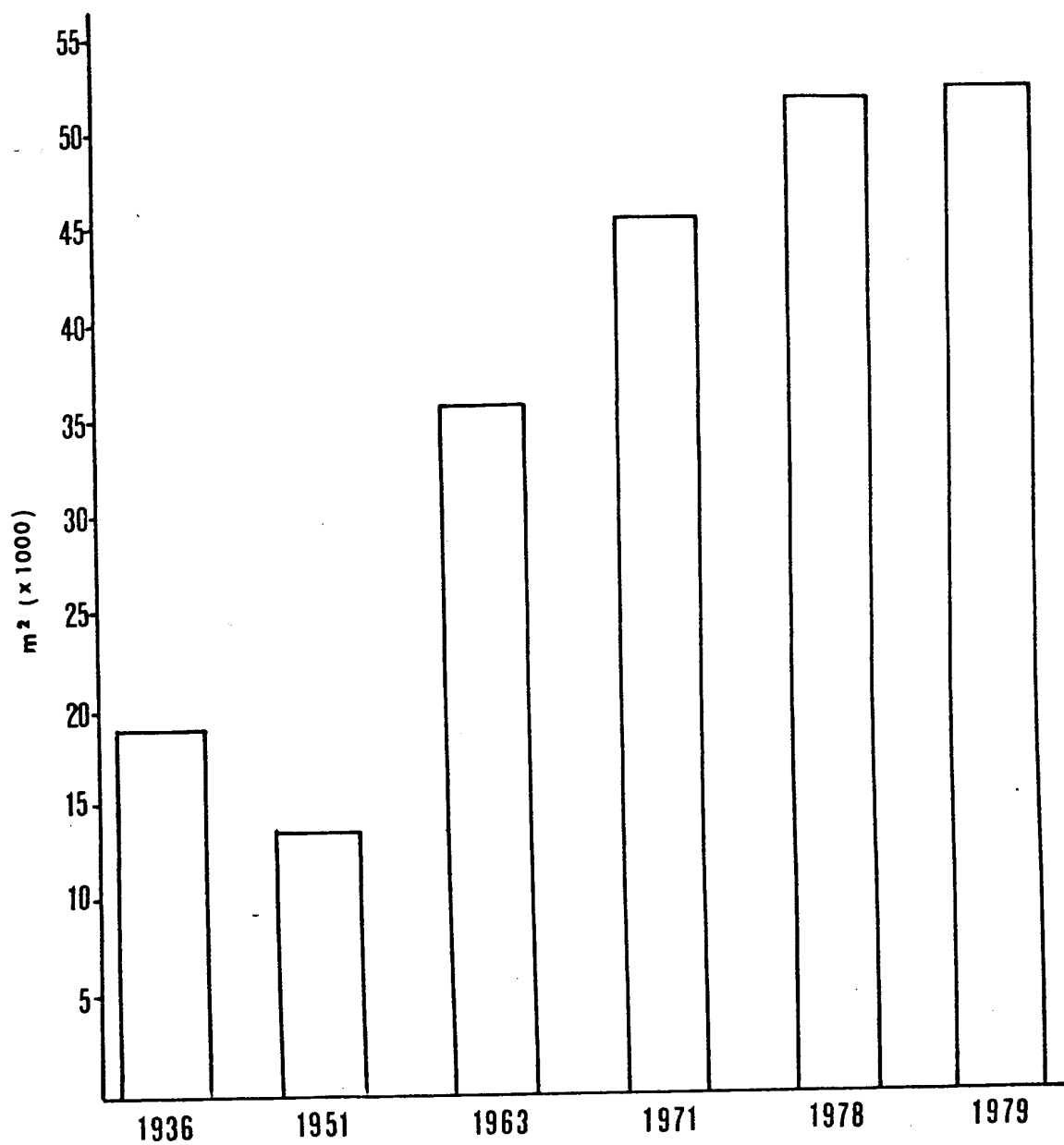


Figure 7. Area measurements of *Thalassia* beds in Cayo Enrique.



Thalassia occurred during the same time period. Since the meteorological record shows no major hurricane affecting the area during those years, an alternate mechanism for such a widespread destruction is yet to be found. One possibility is overgrazing by reef fishes and echinoids that underwent a population explosion. In Florida, Camp *et al.* (1973) observed massive destruction of seagrass beds by the urchin, *Lythechinus variegatus*. Areas of hundreds of square meters were heavily grazed by these urchins. The urchin, *Diadema antillarum*, has also been observed grazing heavily on seagrasses (Vicente, personal communication).

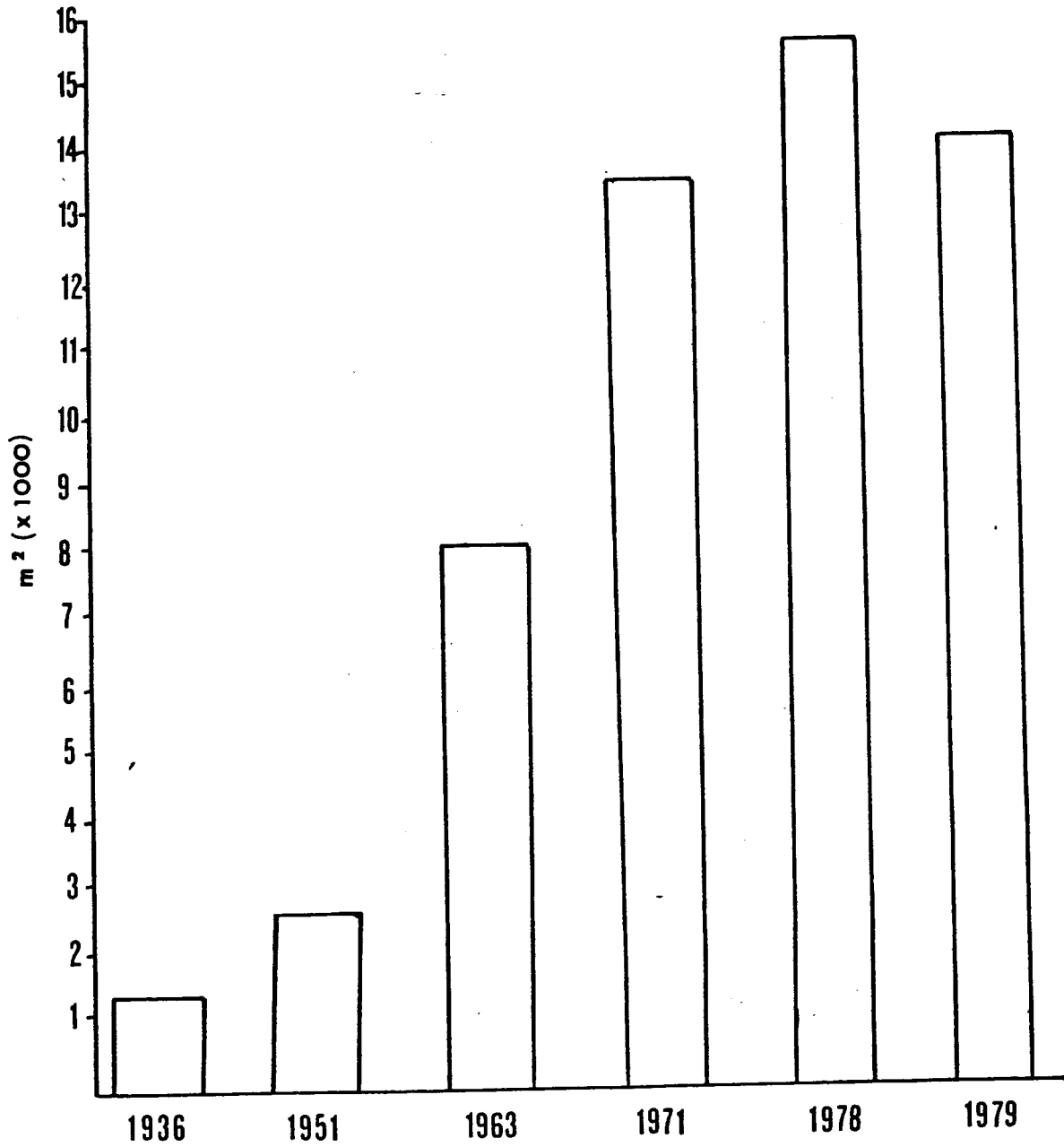
No reduction in *Thalassia* coverage resulted from the passage of Hurricane David in 1979. Hurricane effects on *Thalassia* beds and man-grove areas are discussed under "Hurricane disturbances" on page 40.

II, *Rhizophora mangle* areas

Mangrove areas increased 15 fold between 1936 and 1978 (Figs. 6a, 6b and 8). This represents an average increase in area of 338 m²/yr for a 42 year period. An approximate decrease in mangrove area of 1,560 m² occurred in 1979 due to the catastrophic effects of Hurricane David.

Levine (personal communication) reported an increase in mangrove area of 1,960 m²/yr for Joyuda Lagoon on the west coast of Puerto Rico. While this rate is more than five times the average rate of mangrove increase for Cayo Enrique, the difference is easily explained when one considers the two environments: a calm, nutrient-rich, protected lagoon compared to an exposed, high-energy reef environment.

Figure 8. Area measurements of mangroves in Cayo Enrique



Not all *Rhizophora* seedlings arrived on Cayo Enrique by natural means. In 1939-1940, a government sponsored, mangrove propagation program was carried out in most reefs of La Parguera. An estimate of 1,000 to 2,000 *Rhizophora* seedlings were planted on the reef-flat of Cayo Enrique.

The only information on Cayo Enrique before 1936 is in "United States Coast Pilot, 1929." On page 92, it states that "There is a good-sized clump of mangroves on the middle of its south side, and a small clump at its northeast end." These are the same mangroves that appear in the 1936 aerial photograph of Cayo Enrique. This could indicate that the rate of natural colonization by mangroves on other parts of the reef is very slow. The substantial increase in mangrove colonies appearing in the 1951 aerial photograph of Cayo Enrique could have resulted exclusively from artificial seedling propagation by man.

III. Hurricane disturbances

Catastrophic effects of tropical storms in both Atlantic and Pacific ocean coral reefs have been documented by numerous investigators during the last 20 years. In Puerto Rico, the effects of Hurricane Edith on La Parguera reefs were documented by Glynn *et al.* (1964). The outer reefs, which received the full impact of storm waves, suffered the greatest damage. This included more than half to complete destruction of *Acropora* and *Porites furcata* and the formation of coral shingle islets. Although coral destruction on the outer reefs was extensive, Cayo Enrique and other inner reefs suffered *Acropora* destruction to an extent of 10 to 50 per cent. "Only the *Porites* at the western end of Cayo Enrique showed signs of destruction" (Glynn *et al.*, 1964, p. 342). Coral-shingle islet formation was not reported for Cayo Enrique.

Sixteen years later, Hurricane David passed 70 to 80 miles south of Puerto Rico on a west-northwesterly course. On the afternoon of August 30, David was at its closest point to La Parguera, with a central pressure of 924 mb and maximum winds of 150 knots. Early in the afternoon, waves were seen breaking on a submerged patch-reef five meters deep, located

seaward of La Gata and Caracoles reefs. By late afternoon, wind speed had reached approximately 50 knots and waves were breaking at the shelf edge, 11.3 km south of La Parguera, at a depth of 20 meters. During that night and the following day it rained sporadically, and strong wave action was still observed on the reefs. Precipitation recorded at the Magueyes Island station after Hurricane David was 19.19in. This accounts for 95% of the total rain for the month of August.

The maximum tide recorded at Magueyes Island station during David was 1.89 m (6.21 ft.) on August 31 at 0300. The mean high water (MHW) value for the month of August was 1.31 m (4.31 ft.). This storm caused a maximum water level that was 0.58 m (1.9 ft.) higher than the MHW for that month.

The outer reefs (Laurel, Media Luna, and Turrumote) received the full impact of the storm waves. As in Hurricane Edith (Glynn *et al.*, 1964), these reefs were affected the most. Broken corals were deposited on reef flats forming shingle and boulder ramparts. A survey of Cayo Enrique after Hurricane David showed the following effects:

(1) Recently dead corals formed boulder ramparts at the eastern and southern windward sides of the reef-flat (Fig. 9a,b); (2) numerous dead invertebrates, mostly echinoderms and mollusks, were present on the reef-flat; and (3) *Thalassia* and *Syringodium* blades were piled up against the mangroves and boulder ramparts. These higher plants probably broke free from the outer reefs due to wave action and floated downcurrent, accumulating on Cayo Enrique (Fig. 10).

Four 5 m phototransects made on the fore-reef of Cayo Enrique before and after the hurricane showed a significant ($P = 0.001$) difference in *Acropora* coverage, while no significant difference was observed in the massive coral zone (Ramirez, personal communication).

On page 50, the effects of hurricanes on the fore-reef species diversity of Cayo Enrique are

discussed. In a study on storm effects in British Honduras reefs, Stoddart (1962) observed that coral species most affected were *Acropora palmata*, *A. cervicornis*, *Porites porites*, and other fragile species. Massive hemispherical colonies of *Montastrea annularis* survived in greater numbers while *Diploria*, *Solenastrea*, *Siderastrea*, and *Porites astreoides* survived in fewer numbers.

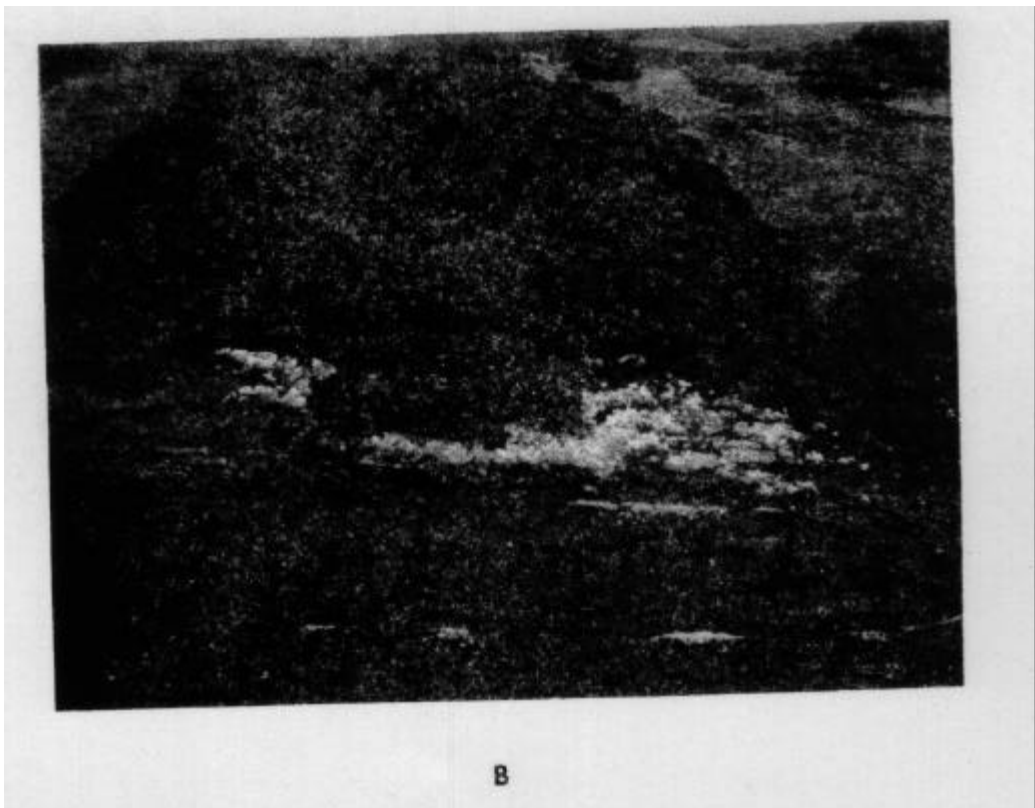
When the boulder rampart constituents of Cayo Enrique were examined quantitatively, the results closely reflected the effects observed on the fore reef. Boulder ramparts were sampled by randomly picking 100 fragments from the eastern and middle ramparts and recording the coral genera and other components (Fig. 11). *Acropora* fragments were the major component, followed by *Millepora* blades and *Porites* fragments. Minor components were mollusks (mostly *Citarium*

Figure 9. Oblique low-altitude aerial photographs of Cayo Enrique showing boulder rampart formations on the reef flat.

- (A) Boulder rampart at the eastern end of the reef, and
- (B) boulder rampart at the south windward side of the reef.



A

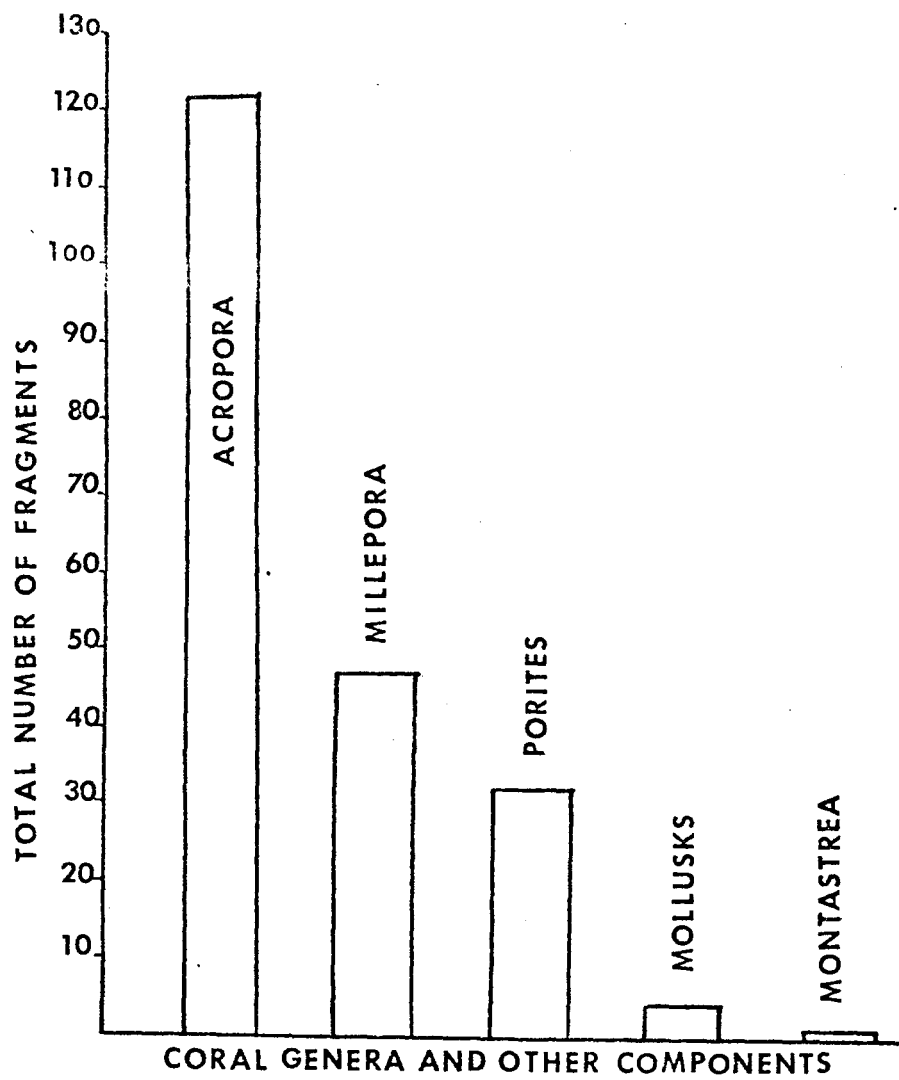


B

Figure 10. Accumulation of *Thalassia* and *Syringodium* blades on Cayo Enrique after Hurricane David.



Figure 11. Histogram of constituents of the boulder ramparts of Cayo Enrique.



pica) and fragments of *Montastrea*.

An approximate decrease of 1,560 m² in living *Rhizophora mangle* area (see Fig. 8) occurred due to the catastrophic effects of Hurricane David. While some mangroves were completely uprooted, most of the damage was caused by hurricane winds and sea-spray scalding of the leaves with subsequent defoliation (Almodovar, personal communication). Mechanical damage of *Rhizophora* prop-roots resulted from abrasion and piling-up of coral boulders against them. Mangrove defoliation also occurred in exposed localities after the passage of Hurricane Edith (Glynn *et al.*, 1964). Wadsworth and Englerth (1959) reported breakage and uprooting of *Laguncularia racemosa* trees on the southeastern coast of Puerto Rico after Hurricane Betsy. Craighead and Gilbert (1962) reported widespread destruction of mangroves in southern Florida after Hurricane Donna. In addition to defoliation, they claimed that mechanical damage, root damage, and oxygen deficiency resulted in mangrove mortalities of 25-75% over large areas, reaching up to 90% locally. Stoddart (1971) observed that mangroves that were completely defoliated in the British Honduras cays after Hurricane Hattie suffered permanent damage. He claimed that dead mangroves, in the absence of fires, can remain in place for years or even decades.

No reduction in *Thalassia* coverage resulted from the passage of Hurricane David. This agrees with the Thomas *et al.* (1961) report of light damage to the *Thalassia* beds of Biscayne Bay after Hurricane Donna. Oppenheimer (1963) stated that, after Hurricane Carla, not only did the grass flats remain intact

but they appeared more healthy than at any time during the previous three years. He suggested that wave motion apparently removed old and unattached grasses and algae, leaving clean grass flats. While this is true for effects of minor to moderate disturbances on protected seagrass beds, the effects of major disturbances on exposed seagrass beds could be catastrophic.

Several weeks after Hurricane David, there was a bloom of the alga, *Trichosolen duchassaingii*, on the reef-flat of Cayo Enrique and on other reefs of La Parguera. This alga is an opportunistic species that covers newly available substrates (Matta, personal communication).

A re-survey of Cayo Enrique was done on August 4, 1980, almost one year after Hurricane David. On the fore-reef zones, massive and hemispherical corals were alive and looked healthy, while the mixed coral zone was mostly reduced to *Acropora cervicornis* rubble. Several dead colonies in growing position were covered with algae. The *A. palmata* zone was predominantly covered by fragmented *in situ* colonies of the same species. Regeneration was evident, as some *A. palmata* colonies showed a low-relief healthy growth. This probably resulted from fragments of *A. palmata* that survived the hurricane and remained *in situ*. Highsmith *et al.* (1980) reported 39% survivorship of coral fragments and detached colonies after Hurricane Greta in Belize. High survivorship, plus fast calcification rates in *Acropora*, promotes rapid reef recovery.

Numerous mangrove seedlings were starting to grow near the mangroves and on the boulder ramparts. It was evident that just one year after Hurricane David corals and mangroves were starting to colonize the reef again.

On August 5, 1980, Hurricane Allen, one of the severest storms of the

century, passed approximately 200 miles south of La Parguera with maximum winds of 148 knots near its center. Although the total rainfall recorded on Magueyes Island Station was only 0.04 m on the day of the storm, strong wave action affected the reefs. The following day a survey of Cayo Enrique showed the following effects: (1) the boulder rampart on the middle part of the reef was moved leeward and piled-up against the mangroves. A new boulder rampart was deposited to windward near the reef-crest. This was composed mostly of old dead coral fragments (resulting from Hurricane David) which were transported by wave action from the fore-reef; (2) mangrove seedlings growing on the boulder ramparts were destroyed by abrasion and burial, while seedlings that were established near the mangroves to leeward survived the hurricane; and (3) on the eastern reef-flat area there were uprooted, small, mangrove trees, dead sea fans and gorgonians, and other dead invertebrates.

Unfortunately, the 1980 aerial photograph of Cayo Enrique (Fig. 4) could not be used to measure the seagrass and mangrove areas after Hurricane Allen because the photograph is slightly oblique. As mentioned before, only vertical aerial photographs can be used to measure reef areas accurately.

In the recent history of Cayo Enrique, two hurricanes (David, 1979 and Allen, 1980) were responsible for considerable damage to various reef features and zones. These hurricane-generated changes were detectable in the aerial photographs of those years. Other hurricanes have also affected the reefs of La Parguera since 1936 (e.g. Hurricane Edith in 1963), but none have caused as much damage to Cayo Enrique as Hurricanes David and

Allen. Hurricane David also caused extensive damage to *Acropora cervicornis* colonies at a depth of 20 m at the shelf edge off La Parguera (Boulon, 1981). Hurricane David was undoubtedly the largest storm to affect La Parguera reefs during the last four decades.

Hurricanes Betsy (1956), Edith (1963), Beulah (1967), David (1979), and Allen (1980) have been reported in the literature or in this study as hurricanes affecting La Parguera reefs. Glynn (1973, p. 110) reports damage to many areas of Laurel reef due to Hurricane Beulah (September 10, 1967). The tracts of these hurricanes and their minimum distances from the south coast of Puerto Rico (see Appendix, p. 69) have been used to establish the distance of 60 nautical miles as the minimum distance from shore for hurricanes to have any effects on the reefs of La Parguera. This arbitrary distance of 60 nautical miles is an approximation, since not only is the distance from shore important, but also the magnitude of the storm and the speed of translocation. Hurricane Allen (1980) was of such great magnitude that, even at a distance of 180 nautical miles it did considerable damage to the reefs of La Parguera. A total of 17 hurricanes have potentially affected Cayo Enrique and the other reefs of La Parguera over the last 100 years. This represents an average of 1.7 hurricanes of minor to moderate intensity per decade. Using this rationale, it can be expected that the reefs of La Parguera will suffer the effects of cyclonic disturbances on the average of one to two per decade.

Major hurricanes affecting Puerto Rico are very rare. Hurricanes San Ciriaco of 1899 and San Felipe of 1928 are known to have caused widespread destruction to the island. San Felipe (1928) is claimed to have been the worst

hurricane affecting the southwestern coast of Puerto Rico (Cote, personal communication). After these two hurricanes David (1979) is perhaps the worst hurricane affecting the La Parguera area in the last 100 years. This suggests that the frequency of major hurricanes affecting the reefs of La Parguera is between two and three per century.

IV. Human interference

In the central reef-flat area of Cayo Enrique there is a patch of dry land within the mangroves where a single tree of *Avicennia germinans* is living along with nearly a dozen damaged *Laguncularia racemosa* trees. Both species lack many branches and leaves and there is evidence that they were cut for firewood or other purposes. Because there are few leaves and branches remaining, and because they are nearly covered by dense *Rhizophora* foliage, *Avicennia* and *Laguncularia* do not appear in the aerial color infrared photograph of Cayo Enrique. The colonization and establishment of these mangroves in Cayo Enrique appears to be limited by man's activities and not by natural factors.

Cayo Enrique is frequently visited by pleasure boats and yachts that stay up to 3-4 days at anchor in the calm sandy lagoon. No detrimental effects on the reef have been observed that can be related to boating activities. Boats tend to avoid *Thalassia* beds in favor of sandy areas that provide a better holding ground for anchoring. Destruction of *Thalassia* caused by boat propellers in shallow bays has been reported by Phillips (1960). This was not observed in Cayo Enrique, probably due to the deeper distribution of *Thalassia* there.

Local fishermen frequently walk on the reef-flat in search of octopus and

other edible mollusks. Although these activities could potentially destroy fragile corals such as *Porites furcata* and other reef organisms, its real effect is yet to be determined.

Oil pollution, in the form of tar balls, was observed on the boulder ramparts during the last two years. This could represent, if it continues and increases over the years, a major source of pollution and an unnecessary stress upon the reef environment.

In just a decade, human and industrial wastes caused the death of fringing and patch reefs off the coast of Venezuela (Weiss and Goddard, 1977). The main causes of pollution there were particulate and soluble organic wastes that entered the water by dumping, drainage, and sewage. The Parguera area is beginning to suffer problems similar to the ones reported from Venezuela. Numerous "casetas" (wooden houses on stilts) are built along the coast among the mangroves. These are the main source of nutrients that enter the water by the dumping of sewage and household detergents. As a result of this, the coastal *Thalassia* beds are mostly covered by floccules of the blue-green algae *Microcoleus lyngbyaceus*, an indicator of organic pollution. The concentration of the coliform bacteria in these waters has been found to be up to 200 bacteria/ml (Imam, personal communication). According to the EPA Water Quality Criteria (1974), this value is 100 times the maximum acceptable limit for water contact sports. Destruction of *Thalassia* by boat propellers is common along the shallow, coastal seagrass beds.

Sediment resuspension by boat traffic creates high levels of turbidity that decreases the amount of light required by *Thalassia* for photosynthesis. Turbidity is

highest during weekends when boat traffic reaches its maximum. These effects are restricted to the nearshore coastal area of La Parguera due to the prevailing winds and currents.

Cayo Enrique and the outer reefs, located upcurrent and windward of the pollution source, appear not to be affected by these factors. However, some recreational activities, if unregulated, can potentially damage the reef community. These include overfishing, shell and coral collecting, cutting of mangroves, and dumping of sewage and garbage by visiting pleasure boats. As this reef, and the other reefs of La Parguera, become more accessible to a larger number of persons, the effects of human interference will influence, to a greater extent, the future health of the reef.

Theoretical aspects and future trends

The main ecological concept considered here is whether Cayo Enrique can be considered a high-diversity community and how this diversity is maintained. The concept of reefs as highly diverse communities evolved mostly from studies of the rich coral assemblages of fore-reef areas. Theories explaining the existence of high local diversity in coral reefs and tropical rain forests are discussed by Connell (1978).

Before Hurricane David, the diversity, as measured by Shannon and Weaver (1949) on the fore-reef of Cayo Enrique, was .18 for the *Acropora palmata* zone and .51 for the mixed zone, with an evenness of .12 and .32 respectively (Goenaga and Cintron, 1979). These low diversity and evenness values indicate high dominance by *A. palmata* and, in the mixed zone, by *A. cervicornis*. A slightly

higher diversity and evenness value in the mixed zone indicates the presence of other corals not found in the previous zone. Goenaga and Cintron (1979) also report *Agaricia agaricites*, *Montastrea annularis*, and *Diploria* sp. in the mixed coral zone.

A year and a half after Hurricane David, along with the cumulative effects of Hurricane Allen, a re-survey was done on the same fore-reef zones of Cayo Enrique. Species diversity in the *A. palmata* zone increased to 1.33 since the stress, while the value for the mixed coral zone was .79. Evenness values were .96 and .46 respectively. The *A. palmata* zone increased its diversity substantially from .18 to 1.33. The evenness value for this zone (.96) indicates high evenness, or least dominance by any species. While the diversity for the mixed zone increased slightly to .79, the evenness remained low (.46), indicating moderate to high dominance. In this case, the massive coral *Montastrea annularis*, representing 79% of the living coral cover, was the dominant species.

The results discussed here were obtained using 10 m transects made parallel to depth contours at two and four meters depth on the middle fore-reef zone of Cayo Enrique. These results are thus preliminary and suggest only that hurricane disturbances are capable of increasing the diversity of shallow fore-reef areas.

Qualitative observations on the mixed zone of Cayo Turrumote made two years after Hurricane David leads to similar conclusions. This zone is deeper (10 m) and was exposed to heavier wave action than Cayo Enrique during the hurricanes. A total of 13 species of juvenile Scleractinian corals were found in an area that was dominated by *A. cervicornis* before Hurricane David. The larvae of

these corals settled on the newly available substrate composed of dead *A. cervicornis* branches increasing the species richness and, undoubtedly, its diversity.

Moderate hurricane disturbances can increase the species diversity of a reef by interrupting the competitive process that leads to dominance by one or few species and by providing new substrata (a major limiting factor) for the settlement of new coral recruits. Major disturbances can drastically prolong the recovery process. Recovery periods for coral reefs can range from a few years to several decades, depending on the magnitude of the storm and the distance from its center. Ten years after Hurricane Hattie, Stoddart (1974) found little or no recovery on reefs subjected to massive damage, while complete recovery had taken place in little or moderately damaged reefs. He suggests that "there is a threshold of damage beyond which storm effects are likely to be prolonged." Recovery in severely damaged reefs will largely depend upon recruitment by larvae from a distant source, while, on moderately damaged reefs, a high survivorship of coral fragments may explain the rapid recovery of reefs (Highsmith *et al.*, 1980). They propose a model in which periodically disturbed reefs will have the highest long-term calcification and growth rates.

Periodic hurricane disturbances of moderate intensity are important factors in maintaining high species diversity in fore-reef areas. In the reef-flat and back-reef areas, moderate disturbances have fewer effects in the community structure and species diversity than in fore-reef areas.

The rate by which seagrasses are covering lagoon areas, and the extent of mangrove colonization on the reef flat, may indicate that Cayo Enrique is

approaching a climax zonation dominated primarily by plant species. The reef-flat and lagoon areas are becoming dominated by two species, *Rhizophora mangle* and *Thalassia testudinum*. On a large scale, this represents a low diversity equilibrium condition for the reef in general. However, when viewed on a small scale, both mangrove and seagrass communities increase the species diversity of the reef by stabilizing the seabed and increasing the surface area available for marine organisms to live. This biotic substrate extension supports diverse epiphytic algal, fish, and invertebrate assemblages by providing either food, substrate, shelter, or a combination of these. Dominance by *Rhizophora* and *Thalassia*, and whether this dominance increases or decreases the total diversity of the reef, is largely a problem of scale.

During Hurricane David, coral boulders were transported to the reef-flat and lagoon areas, where they provided new substrate for other corals to settle. An actual example of this occurred after Hurricane Beulah when the reef flat in Cayo Laurel was extended laterally 0.5 m (Glynn, 1973, p. 306). He proposes that leeward expansion of the reef flat could be a result of deposits becoming stabilized and providing substrate for new coral growth. Davies (1977) goes one step further, proposing that under the present hydraulic regime, reefs in the Great Barrier Reef are growing backwards (i.e. on their lee sides). He claims that windward reef extension is unlikely and that spur and groove formations, originally described as of constructional origin (Goreau, 1959; Shinn, 1963), could represent the original front of an eroding reef.

The future of Cayo Enrique, based on observed trends in the past 44 years, and if unaffected by man, will largely depend on the occurrence and frequency of

physical disturbances. Hurricanes have been the main agents of change for the reef zones and features of Cayo Enrique. Although major hurricanes can be catastrophic and prolong the recovery process, they are rare--on the order of 2-3 per century. Moderate hurricane disturbances are more common and actually benefit the reef in many ways. They increase the species diversity of the fore-reef, and, to a lesser extent, of the reef-flat and back-reef lagoon areas. The rate at which mangroves and seagrasses are colonizing available substrate may lead to a climax zonation until a major disturbance interrupts this process. Long term transport of coral colonies to leeward shores by hurricane waves provides the necessary substrate for-the establishment of "patch reefs" or coral communities. This, and the slow but definite expansion of the reef flat, indicates that Cayo Enrique could also be growing backwards.

CONCLUSIONS

Two major communities of Cayo Enrique, the reef-flat *Rhizophora mangle* and the lagoonal *Thalassia testudinum* areas, showed the maximum variations of all reef zones over the last 44 years as was determined by a chronological series of aerial photographs. The rate of increase of these biotic macroassemblages suggests that Cayo Enrique is approaching a climax zonation dominated primarily by plant species. Hurricane disturbances of moderate intensity are an important factor in maintaining high species diversity in fore-reef areas, and, to a lesser extent, in reef-flat and lagoonal areas. Moderate disturbances also affect the reef by depositing dead corals on the reef-flat, forming boulder ramparts that can become colonized by mangroves. Hurricanes also adversely affect mangrove areas, but appear not to affect lagoonal seagrass beds significantly. A new transport of corals to leeward by hurricane waves enhances the expansion of the reef flat and the establishment of coral communities on the back-reef lagoon.

Human activities in Cayo Enrique appear to have no significant effects on the reef environment. Whether this can also be said in future years will depend on whatever measures are taken today to protect this reef, as well as the other reefs of La Parguera, from future adverse direct and indirect effects of man.

The use of aerial photoanalysis in coral reef studies provides a mechanism by means of which reefs can be studied over a long time period. Black and white film is the easiest and most widely used film in aerial surveys. Color film offers no significant advantages over black and white film except for greater water penetration. False-color infrared film is best for differentiating shoreline and reef-flat mangrove vegetation. Its major disadvantage is that water readily absorbs near-infrared radiation, preventing submerged vegetation from being recorded on this film. High-altitude aerial and satellite photography of coral reefs have the advantage of covering large areas in a single

photographic frame at the expense of not effectively resolving individual reef features and zones. I propose a combination of high-altitude and low-altitude photography of coral reefs to maximize the amount of information obtained from this remote sensing technique.

When available, a chronological series of aerial photographs is a useful tool in detecting and measuring trends in coral reefs and provides baseline data by which present and future comparisons can be made.

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Appendix. A list of hurricanes, with their tracks, that have been reported in the literature or in this study as hurricanes affecting La Parguera reefs.

