

**THE EFFECT OF HURRICANE ALLEN
ON THE BELLAIRS FRINGING REEF, BARBADOS**

**Anmarie Janice Mah
Department of Geological Sciences
McGill University, Montreal
May, 1984**

**A thesis submitted to the Faculty of Graduate Studies and
Research in partial fulfillment of the requirements for
the degree of Master of Science.**

© Anmarie J. Mah, 1984

...Thou

For whose path the Atlantic's level powers
Cleave themselves into chasms, while far below
The sea-blooms and the oozy woods which wear
The sapless foliage of the ocean, know
Thy voice, and suddenly grow grey with fear,
And tremble and despoil themselves: O, hear!

from Shelley's "Ode to the West Wind" (1822).

ABSTRACT

On 4 August 1980, Hurricane Allen devastated the northern fringing reef located just offshore from the Bellairs Research Institute of McGill University in Barbados. During the summer and one winter month of 1981, a re-survey of the reef was done using S.C.U.B.A. , and the results compared with a similar survey made in 1974. The point method of line transects was used to record the reef substrates.

The results of the two surveys were compared and statistically tested using a chi-square test(χ^2). As well as determining whether the changes in substrate cover were significant within an individual ellipse, the data for each substrate/species for the entire reef was tested. On a reefal scale, the changes before and after Hurricane Allen were significant for all substrates and species with the exception of Millepora sp. Among the corals, Porites porites has been most affected by the catastrophe : its coverage was reduced by 96% . Madracis mirabilis, another branching coral, decreased by 90% . The other corals (Siderastrea siderea, Porites astreoides, Montastrea annularis, and Agaricia agaricites) were reduced by 75% - 25% . Onshore transport is suggested by the relatively high abundances of Acropora cervicornis (20%) and Madracis mirabilis (30%) in the rubble of the fringing reef (the former only grows seaward of the fringing reef). Offshore

transport is suggested by the relatively poor representation of Porites porites (32%) in the rubble. Shannon-Weaver diversity indices of the corals dropped from 1.61 to 1.26 .

SOMMAIRE

Le 4 août 1980, l'ouragan Allen a dévasté le récif frangeant nord, situé immédiatement au large de l'Institut Bellairs de l'université McGill à la Barbade. L'été et un mois d'hiver en 1981 ont été consacrés à un examen du récif à l'aide de SCUBA. Les résultats ont été comparés à ceux obtenus au cours d'études similaires faites en 1974. Une méthode ponctuelle de cueillette de données le long de parcours linéaires a été utilisée pour déterminer les types de substrats des récifs.

Les résultats des deux observations ont été comparés et évalués statistiquement à l'aide du test khi carré (χ^2). En plus de déterminer si les changements d'aire occupée par diverses espèces coralliennes sont significatifs dans chaque ellipse individuelle, les données relevées pour chaque substrat / espèce ont été évaluées pour l'ensemble du récif. A l'échelle du récif, les changements avant et après l'ouragan Allen se sont avérés significatifs pour tous les substrats et espèces à l'exception de Millepora sp. Parmi les coraux, Porites porites a été le plus affecté par la catastrophe, l'aire qu'il occupait avant l'ouragan ayant été réduit de 96%. L'aire occupée par Madracis mirabilis, un autre corail branchu, a décréu de 90%. L'aire occupée par les autres coraux (Siderastrea siderea, Porites astreoides, Montastrea annularis, et Agaricia agaricites) a décréu de 75% - 25%. Les abondances relativement élevées d'Acropora cervicornis (20%) et Madracis mirabilis

(30%) dans les débris du récif frangeant, alors que l'Acropora cervicornis ne croissent qu'au large de ce récif, indiquent un charriage vers la côte. Par contre, les quantités relativement faibles de Porites porites (32%) suggèrent un transport de débris vers le large. Les indices de diversité de Shannon-Weaver des coraux ont diminué d' 1.61 à 1.26.

TABLE OF CONTENTS

CHAPTER 1	INTRODUCTION.....	1
CHAPTER 2	HURRICANES.....	3
	A) Hurricane season.....	4
	B) Development.....	5
	C) Importance of temperature.....	5
	D) Movement.....	8
	E) Lifetime and speed.....	9
	F) Average frequencies.....	9
	G) Precipitation.....	9
	H) Hurricane Allen.....	11
	1) Impact on Barbados.....	18
	I) Hurricane David.....	19
CHAPTER 3	PHYSICAL PROCESSES AFFECTING REEFS....	22
	A) Normal conditions.....	23
	1) Waves.....	23
	2) Currents.....	24
	B) Storm conditions.....	26
	1) Waves.....	26
	2) Storm surge.....	27
	3) Currents.....	28
	C) The Barbados coast.....	30
	1) Waves.....	30
	2) Currents.....	31
	3) Swells.....	32
	4) Hurricane conditions.....	32
CHAPTER 4	PREVIOUS STUDIES.....	34
	A) Atolls.....	35
	B) Guam.....	37
	C) Belize.....	38
	D) Texas.....	41
	E) South Florida.....	43
	F) Florida-Bahamas region.....	44
	G) Jamaica.....	45
	H) U.S. Virgin Islands.....	47
	I) Miscellaneous effects.....	49
CHAPTER 5	STUDY AREA.....	53
	A) Regional geology.....	54
	B) Study site.....	58
	1) Reef description.....	63

2) Reef Zonation.....	63
-----------------------	----

CHAPTER 6

METHODS.....	67
---------------------	-----------

A) Field methods.....	68
1) Line transects.....	68
2) <u>Diadema antillarum</u> population density.....	71
3) Rubble analysis.....	72
4) <u>Montastrea annularis</u> growth bands.....	72
5) <u>Porites porites</u> breaking points.....	73
B) Methods of data analysis.....	73
1) Pre- and post-hurricane reef coverage.....	74
2) Coral coverage and rank.....	75
3) Diversity indices.....	75
a) Shannon-Weaver's.....	75
b) Simpson's.....	77
4) <u>Diadema antillarum</u> population counts.....	77

CHAPTER 7

RESULTS AND DISCUSSION.....	78
------------------------------------	-----------

A) Changes in the living and non-living substrates.....	79
B) Bioerosion.....	100
C) Analysis of the rubble.....	101
1) Rubble composition.....	101
2) Rubble distribution.....	107
D) Growth and stress in <u>Montastrea annularis</u>	111
E) Coral diversity.....	121
1) The intermediate disturbance hypothesis.....	122
2) Caribbean coral diversity....	129
3) Coral diversity of the study reef.....	130
4) The study reef and the intermediate disturbance hypothesis.....	134
F) Recovery and recolonization....	140
1) Methods of recovery.....	140
2) Recovery time and determining factors.....	141
a) Conditioning period.....	141
b) Grazers.....	141
c) Rubble beds.....	142
d) Colonizing surfaces.....	142
e) Coral community structure.	142

	f) Disturbances.....	143
	g) Pollution levels.....	144
	3) Coral recovery on the Bellairs reef.....	145
	a) Conditioning period.....	149
	b) Grazers.....	149
	c) Rubble beds.....	155
	d) Colonizing surfaces.....	155
	e) Community structure.....	160
	f) Disturbances.....	160
	g) Pollution levels.....	160
CHAPTER 8	GEOLOGICAL RECORD OF HURRICANES.....	163
	A) Holocene storm deposits.....	164
	B) Ancient storm deposits.....	166
	C) Sedimentary record of Hurricane Allen.....	171
CHAPTER 9	CONCLUSIONS.....	173
ACKNOWLEDGEMENTS.....		176
REFERENCES.....		177
APPENDIX.....		192

LIST OF TABLES

<u>Number</u>		<u>Pages</u>
1	Substrate counts per ellipse - pre/post hurricane counts.	80
2	Chi-square test for significance of changes in species counts per ellipse.	93-94
3	Chi-square test for significance of changes in species counts for the entire reef.	95
4	Transect V substrate counts.	97
5	Rubble - counts percentage.	102
6	Rubble - weight percentage.	103
7	Strength of representative skeletal materials.	106
8	Distribution of <u>Porites porites</u> , <u>Madracis mirabilis</u> , and <u>Acropora cervicornis</u> rubble.	108
9	Mean surface temperatures taken from the southern Bellairs reef.	113
10	Coral diversity - Shannon-Weaver diversity indices.	131
11	Coral diversity - Simpson's index.	132
12	T-test on changes in coral diversity (Shannon-Weaver index).	133
13	Percentage loss of coral species.	135
14	Coral ranking - before and after Hurricane Allen.	136
15	<u>Diadema antillarum</u> density.	154
16	Examples of ancient hurricane deposits.	167

LIST OF FIGURES

<u>Number</u>		<u>Pages</u>
1	Principal tracks of tropical cyclones in relation to sea surface temperatures. Isotherms show average sea surface temperature in September for the Northern hemisphere, and in March for the Southern hemisphere (From Palmen & Newton, 1969).	6-7
2	The view from space of Hurricane Allen (courtesy of M. Lawrence).	12-13
3	Satellite photo of Hurricane Allen after passing Barbados.	14-15
4	The path of Hurricane Allen (courtesy of M. Lawrence).	16-17
5	The path of Hurricane David (courtesy of M. Lawrence).	20-21
6	Barbados and the southeastern Caribbean region (Barbados Preliminary Atlas).	55-56
7	Barbados - Location of research area.	59-60
8	The Bellairs fringing reefs.	61-62
9	The ecological zonation on the Bellairs fringing reefs (From Stearn <u>et al.</u> 1977).	64-65
10	Aerial photo of the northern Bellairs fringing reef showing location of the transect lines.	69-70
11-21	Histograms of each substrate type, before and after Hurricane Allen.	
11	Sand	82
12	Rubble	83
13	Rock	84
14	Coralline red algae	85
15	<u>Millepora</u> sp.	86
16	<u>Porites</u> <u>astreoides</u>	87

<u>Number</u>		<u>Pages</u>
17	<u>Porites porites</u>	88
18	<u>Madracis mirabilis</u>	89
19	<u>Montastrea annularis</u>	90
20	<u>Agaricia agaricites</u>	91
21	<u>Siderastrea siderea</u>	92
22	Examples of "stress" bands in <u>Montastrea annularis</u> . Coral A was collected in May 1982, coral B was collected in September 1982.	115-116
23	Normal growth bands in <u>Montastrea annularis</u> . Coral A was collected in May 1982, coral B was collected in September 1982.	117-118
24	Intermediate disturbance hypothesis graph (From Connell 1978).	124-125
25	Intermediate disturbance hypothesis and the Bellairs reef.	137-138
26	<u>Porites porites</u> zone before (1974) Hurricane Allen.	147-148
27	<u>Porites porites</u> zone after (1981) Hurricane Allen.	147-148
28	Newly-colonized <u>Porites porites</u> .	150-151
29	<u>Porites porites</u> colonies at various stages of growth.	150-151
30	Protected <u>Porites porites</u> growth adjacent to sand channel.	152-153
31	Rubble bed, crossed by the transect line	156-157
32	View along a spur of the study reef prior to levelling of <u>Porites porites</u> .	158-159
33	Diversity of surfaces for recolonization on Bellairs reef.	158-159
34	Diverse coral community in 1974.	161-162
35	Hummocky cross-stratification sequence attributed to storm-wave deposition (Dott & Bourgeois 1981).	169

CHAPTER 1

INTRODUCTION

INTRODUCTION

The impact of hurricanes on coral reefs was first studied in the late 1950's (Stephenson et al. 1958). Several studies have followed, with the emphasis on describing the qualitative rather than the quantitative aspects of storm effects.

Recognition that hurricanes have been major forces in determining the nature of the sedimentary record, has given rise to a new form of catastrophism. This "new catastrophism" involves local disturbances rather than world-wide catastrophies. Much of the sedimentary record of the past was affected by intense storm periods of relatively short duration. Ager (1980) suggests that geologic history is composed of "long periods of boredom and brief periods of terror".

The objectives of this study are to determine the qualitative and quantitative changes on the northern Bellairs fringing reef following the passage of Hurricane Allen, and to assess the potential for preservation in the sedimentary record of this "brief period of terror".

CHAPTER 2

HURRICANES

HURRICANES

Hurricane, in the language of the Carib Indians, is huiranvucan or "big wind" (Dunn & Miller, 1964). A hurricane is an intense low-pressure center surrounded by winds greater than 63 knots (73 mph or 33.5 m/s).

Hurricanes originate over all warm tropical oceans in the latitudes between 5° and 30° from the equator. They do not form closer to the equator than approximately 5° N and 5° S, because the Coriolis force at lower latitudes is too small to create the rotational circulation.

Present most of the time over oceans at about 30° latitude, are large high-pressure areas known as the Hawaiian and Bermuda highs in the northern hemisphere. To the north are the prevailing temperate westerlies and to the south are the persistent north-east trade winds. It is within the trade winds that most tropical storms originate.

A) HURRICANE SEASON

The West Indies hurricane season extends from June to November, but most hurricanes occur during the months of August, September, and October, when ocean temperatures are at their peak, and temperature and humidity of the air near the surface are still at their highest. With the start of winter cooling of the air in high latitudes, troughs in the westerlies that serve as external mechanisms for forming hurricanes intrude more frequently

and vigorously into the tropics than during the midsummer (Simpson & Riehl 1981).

B) DEVELOPMENT

Atmospheric vortices, such as hurricanes, frequently develop near the intertropical convergence, a region where the trade winds of the northern and southern hemispheres meet. Low pressure and circular winds are involved in the formation of hurricanes.

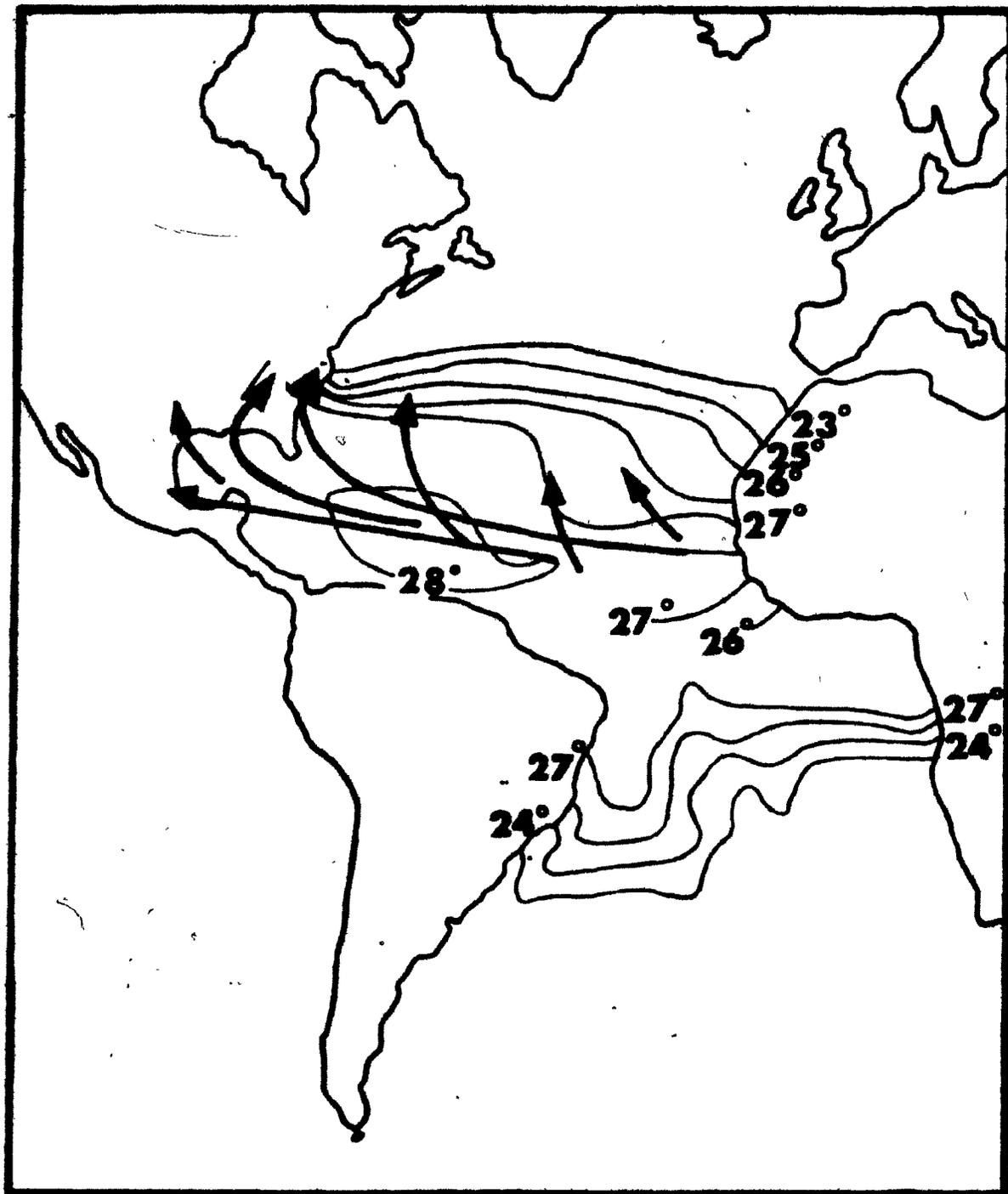
Hurricanes develop as the atmosphere absorbs large quantities of moisture from the ocean. Sunlight falling on the ocean surface adds heat to the water and causes evaporation. The resulting warm, moist air feeds the hurricane as the air is pulled toward the low surface pressure. Within the cloud bands surrounding the eye of the hurricane, the latent heat released by the condensation of vapour to rain (2.4 joules per kilogram) heats the rising air currents, increasing their rate of rise. This process is a major driving force of the hurricane.

C) IMPORTANCE OF TEMPERATURE

Hurricanes rarely develop where ocean surface temperatures are below 26.5° C (Fig. 1). Such high temperatures may be necessary to maintain the vertical circulation in a hurricane.

The sea surface north of 5° N has its highest temperatures from June to November, and these are the

Fig. 1. Principal tracks of tropical cyclones in relation to sea surface temperatures. Isotherms show average sea surface temperature in September for the northern hemisphere and in March for the southern hemisphere (From Palmen & Newton 1969).



months in which hurricanes develop most frequently. There has never been any hurricanes in the South Atlantic Ocean, because the intertropical convergence never lies south of 5° S (Barry & Chorley 1970), and the sea surface temperatures do not reach sufficiently high values (Neiburger et al., 1973).

Hurricanes weaken considerably and may even dissipate when moving over cold ocean currents or water in which the temperatures are below the threshold value of 26.5° C.

Hurricanes dissipate rapidly over landfall. The less humid air and the absence of the warm ocean surface which acts as a heat source drastically decreases the conversion of water vapor to cloud droplets with a reduction in the amount of latent heat to drive the hurricane (Dunn & Miller 1964, Eagleman 1983). Loss of energy by friction over land also slows and dissipates the storm.

D) MOVEMENT

The direction of the surface trade winds, combined with the winds at higher levels, influence the direction of a hurricane. During their early stages in the North Atlantic while the hurricanes are still strongly influenced by the easterly trade winds, they tend to move towards the west or north-west. If they reach north of 30° latitude before dissipating, they are swept by the prevailing upper level westerly winds of the middle latitudes, to the north-east.

E) LIFETIME AND SPEED

The average lifetime of a West Indies hurricane is nine days, although those occurring during August appear to be more durable, lasting for an average of twelve days. The mean speed of travel of a hurricane is only 20 km/h, but a considerable area may be affected within a hurricane's lifetime.

F) AVERAGE FREQUENCIES

Prior to the satellite era, observations of hurricanes over wide expanses of ocean were severely limited. During the past thirty years in the Atlantic region, an average of 9.8 named storms, and 6.0 hurricanes have been recorded per year.

Since 1886, there have been only eight seasons with nine or more hurricanes, which is an average frequency of once every twelve years. During 1980, eleven storms in the Atlantic region were named of which nine attained hurricane status (Lawrence & Pelissier 1981).

G) PRECIPITATION

Most of the rain occurs in the high-wind area close to the center of the hurricane, however at wind speeds above 50 kt (26 m/s or 58 mph), not more than half the falling water may be caught by the typical rain gauge. Many factors affect the rain gauge record: the intensity

and size of the circulation of mass through the hurricane, the hurricane's path with respect to the gauge (whether to the right or the left), the speed at which the hurricane progresses, plus local factors such as buildings, trees, or hills. As a result, a wide range of values of hurricane precipitation have been reported world-wide, from practically nil (despite hurricane-force winds), to as much as a metre of rain.

Since measurement of hurricane precipitation has been inadequate, other methods employing aircraft traverses and numerical computation are now being used. Profiles show that rainfall decreases logarithmically with respect to distance from the center of the storm. An estimate, by computer simulation, of the average amount of rain falling on a rain gauge during a hurricane is 35 cm . Estimates are based on assumptions about the speed of hurricane travel, and assume that passage of a storm takes two days, and that the centre of the hurricane passes directly over the rain gauge (Simpson & Riehl 1981).

H) HURRICANE ALLEN (1 - 11 August, 1980)

Hurricane Allen was the first and most powerful storm of the 1980 Atlantic hurricane season (Fig. 2). A classical Cape Verde hurricane, Allen moved westward off the coast of Africa on 29 July as a disturbance associated with a tropical wave. Allen moved steadily west-northwestward for ten days, guided by a steady steering current and a strong Atlantic subtropical high-pressure ridge (Fig. 3).

Allen was tracked by satellite from the time of its inception on 29 July (Fig. 4). Aircraft reconnaissance missions began on 3 August and continued until landfall in Texas (10 August). Radar fixes were occasionally available as the storm moved within range of the radars along its path.

The storm's motion (direction and speed) was calculated every six hours. It maintained a steady path, but weaved its way among several Caribbean islands, so that the eye always remained over water. The average direction of motion for the ten-day period was toward a heading of 289° with a range of 267° - 308° . The speed of movement ranged from 18 - 22 kt (9.3 m/s - 11.3 m/s) across the Atlantic and eastern Caribbean. Allen began to decelerate on 7 August while centered just south of Cuba, and reached its minimum forward speed of 6 kt (3.1 m/s) late on 9 August, just prior to landfall (Lawrence & Pelissier 1981).

Fig. 2. The view from space of Hurricane Allen.
(courtesy of M. Lawrence).

1800 03AU80 12A-4 00101 19111 WC1



Fig. 3. Hurricane Allen after passing Barbados
(courtesy of M. Lawrence).

1931 04RU80 12A-1 05351 23232 MA14N64U-1

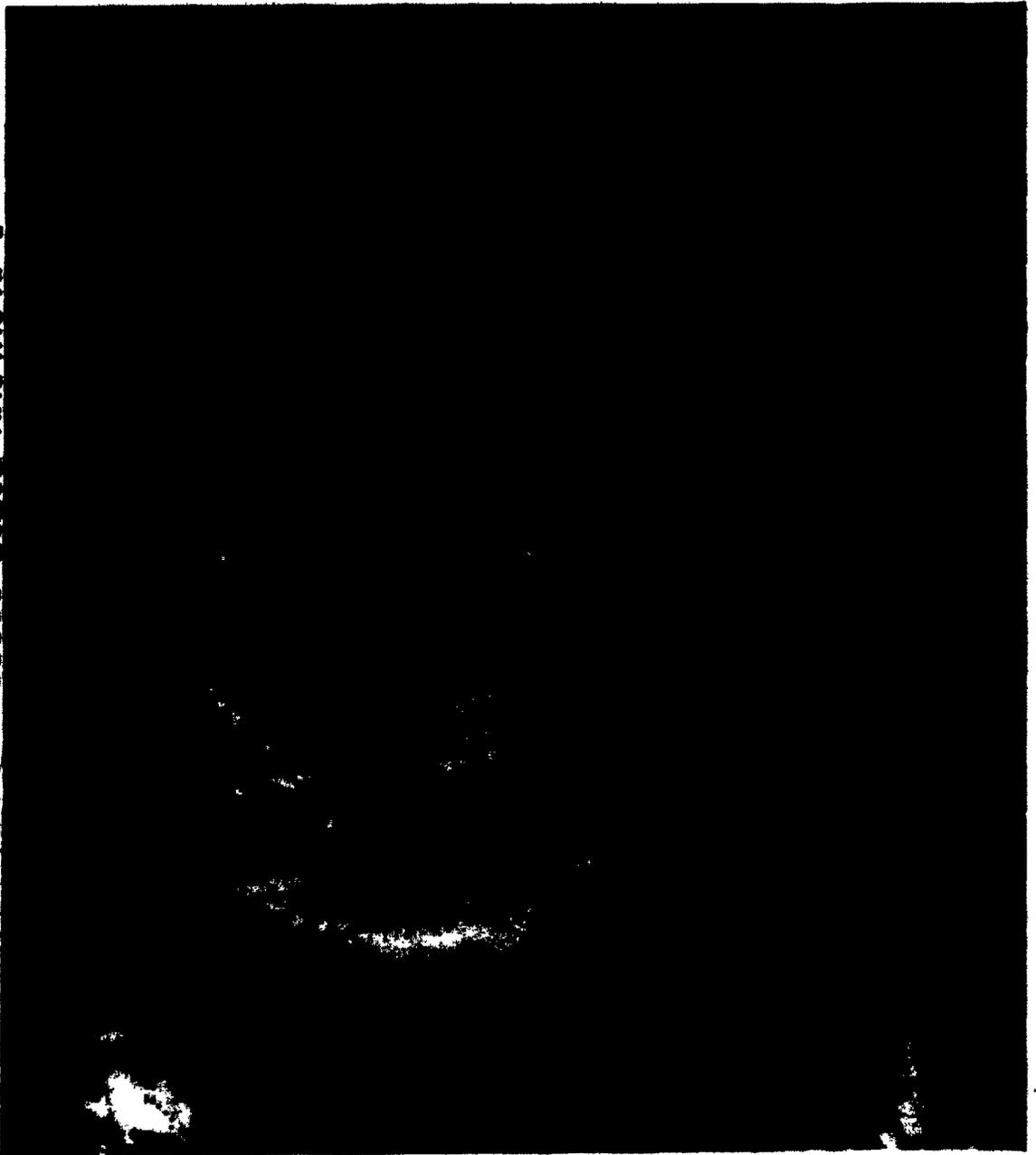
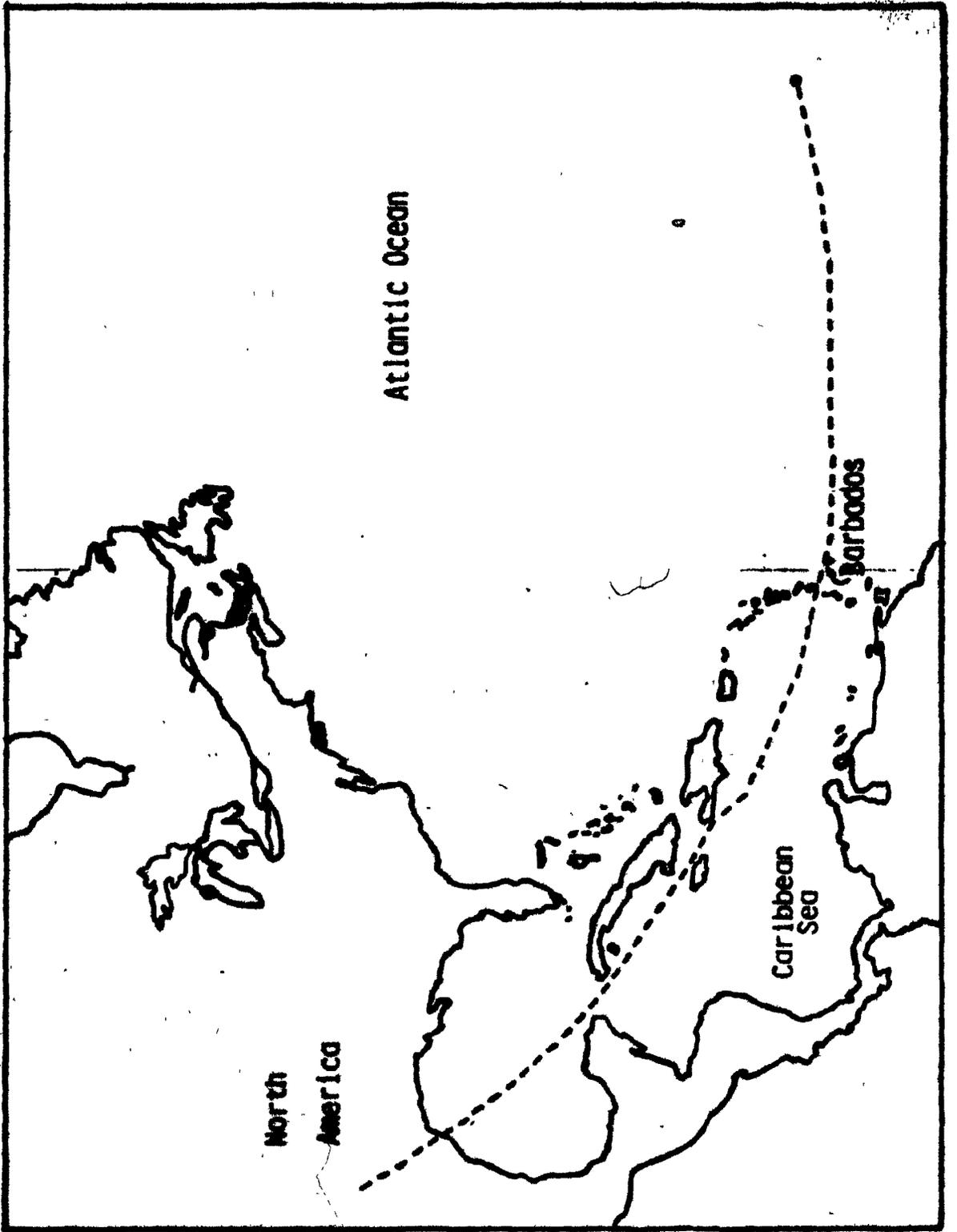


Fig. 4. The path of Hurricane Allen (courtesy of M. Lawrence).



1) Impact on Barbados

The eye of the storm passed just north of Barbados and then just south of St. Lucia early on 4 August. Minimum surface pressure was near 950 mb when the south portion of the eyewall passed very close to extreme northern Barbados at 0000 GMT 4 August.

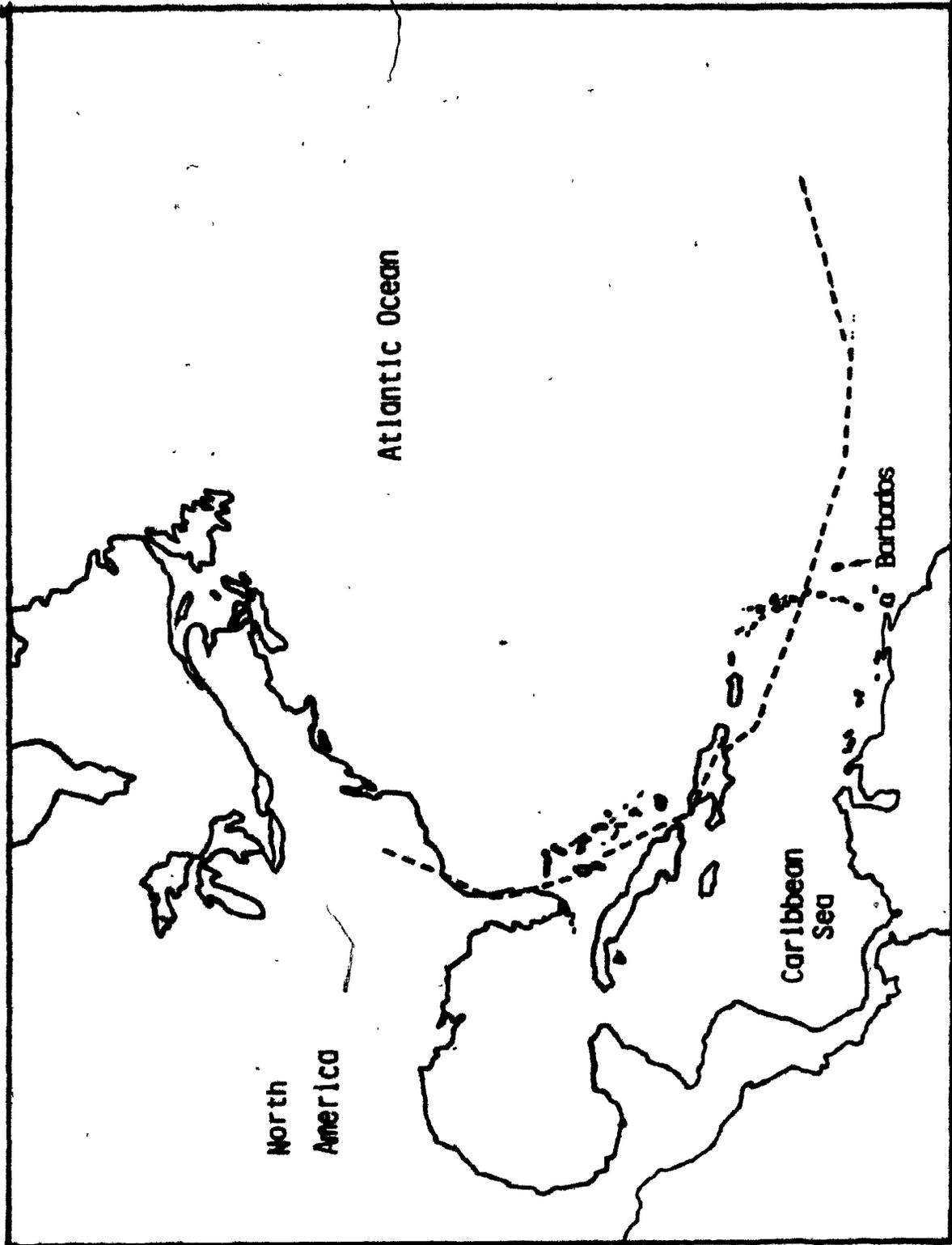
The highest measured wind velocity was only 68 kt (35.0 m/s or 78.3 mph) at the Grantley Adams International Airport on the south coast of the island. Equipment recording wind velocity failed at the Caribbean Meteorological Institute in St. James on the west coast, but rainfall was measured at 10.6 cm. On the north side of the island, no wind measurements were recorded, but a 950 mb hurricane is likely to have winds of 100 kt (51.5 m/s or 115.2 mph) or higher under the eyewall. According to a local newspaper report by A. Brantford of The Nation (August 6, 1980), "Hurricane Allen lashed Barbados with 115 mph winds and torrential rain." Local officials estimated damage at U.S. \$6 million, primarily to agriculture, private housing, and the fishing industry. No deaths were reported.

1) HURRICANE DAVID (25 August - 7 September, 1979)

Hurricane David originated as a depression approximately 2400 km east of the Lesser Antilles on 25 August 1979, and intensified to its maximum strength just south of Puerto Rico. Hurricane David passed far to the north-northwest of Barbados on 28 August 1979 (Fig. 5), and data recorded at Grantley International Airport indicated maximum sustained wind speeds were 29 mph (12.96 m/s), with peak gusts of 40 mph (17.88 m/s) (Hebert 1980). The highest measured wind velocity was only approximately half the 78.3 mph (35.0 m/s) winds which accompanied Hurricane Allen one year later and were also measured at the airport. Rainfall recorded on the day of Hurricane David on the west coast Husbands station of the Caribbean Meteorological Institute was 1.68 cm, an insignificant rainfall when compared to the 10.6 cm which fell on the day of Hurricane Allen.

Barbados did not receive the full force of Hurricane David, but the seas were disturbed from the usual calm state. Damage to the coral reefs following Hurricane David was not investigated by the researchers present at the Bellairs Research Institute at that time. Therefore the re-survey done in 1981, records the damage caused by Hurricane Allen and may represent a minor amount of damage from Hurricane David.

Fig. 5. The path of Hurricane David (From Hebert 1980).



Atlantic Ocean

North
America

Caribbean
Sea

Barbados

CHAPTER 3

PHYSICAL PROCESSES AFFECTING REEFS

A) NORMAL CONDITIONS

1) Waves

Waves which have travelled great distances across the ocean, are greatly modified by reef morphology before they reach the shoreline.

As the wave enters shallow water (water of depth less than $1/25$ of the wave length), wave orbits are modified from circles to ellipses and become progressively more elongate near the bottom. The water particles adjacent to the bottom have only horizontal movement, shifting landward under the passing crest, and seaward under the passing trough. The frictional drag causes a loss of energy and wave speed is decreased. Although wave speed diminishes shoreward, the wave period remains constant, therefore wave length decreases and the wave crests become more closely spaced.

As waves move into shallower water, the wave height begins to increase sharply until the wave breaks. A height increase of more than 50 % may occur.

Waves are refracted by irregular coastlines and shallow bottom topography. Water depth under a single wave crest is different from point to point and the reduction of wave speed does not take place evenly. As a result the wave becomes curved or refracted.

Orthogonals are imaginary lines perpendicular to the wave crest. Over reefs where the orthogonals converge, wave energy is crowded into a narrower zone and

concentrated. The waves increase greatly in height and large breakers are produced. In bays, where orthogonals diverge, the original unit of wave energy is spread more thinly along a greater length of wave crest, causing the wave to be attenuated, and to lose height despite the normal tendency of shoaling waves to increase in height. As a result, on bay shores, waves break with little force.

2) Currents

As the incoming waves approach the shoreline, the waves break and momentum forces are released as the wave energy is dissipated (Collins 1976). These forces are then available to drive longshore currents and rip currents. Wave energy is released as heat, sound, and stirring up of the sediments (Beer 1983).

Rip currents and associated longshore currents comprise the nearshore cell circulation system. A longshore current forms when waves approach a straight shoreline obliquely. The current flows parallel to the coastline close to shore, but its velocity rapidly decreases beyond the breaker zone. Rip currents flow directly seaward at nearly right angles to the shoreline. They are fed by a system of longshore currents which increase in velocity approximately half-way between two adjacent rip currents (Beer 1983). To compensate for the water moving seaward with the rip currents, there is a slow mass transport of water moving shoreward through the breaker zone between the rip currents.

Marsh et al. (1982) describe water circulation on two Guam reef flats. Wave-driven water crosses the margin roughly perpendicular to the shoreline. It then gradually changes direction until it is flowing as a longshore current in a moat adjacent to the shoreline. After flowing in the longshore current for distances of up to 1500 m , the water moves seaward in a more dispersed pattern and exits the reef flat through major cuts or grooves in the reef margin. Current speeds under non-existent to moderate surf conditions range from 0.0 - 0.6 m/s on the windward side, and up to 0.6 m/s, although usually less than 0.2 m/s , on the leeward side. These results agree with other studies, where measured values range from 0.0 - 0.5 m/s (Maragos 1978).

B) STORM CONDITIONS

1) Waves

Three important differences between the generation of wind waves under hurricane conditions and the generation of normal wind waves are:

- a) winds within a hurricane are not constant in speed
- b) the direction of winds within a hurricane is circular. Normal winds are generated by winds blowing in one direction
- c) the hurricane moves over waves generated at various angles to the path of the storm. The resulting pyramidal waves are formed by two wave trains approaching at a wide angle to each other (Bretschneider 1959).

Waves, in addition to being modified by reef morphology, also rework the nearshore sediments and modify the topography. Ocean waves remove energy from the wind, store it as potential and kinetic energies, and transmit it towards the shorelines. The wave energy is dissipated near shore in a relatively narrow zone. A fringing reef, if present, receives the brunt of the wave forces, and as a result offers considerable protection to the shoreline.

Shorelines which are not protected by reefs, or coastlines exposed to storm or hurricane conditions, may be severely eroded. Hurricane - driven waves can scour out 10 - 15 m of beach within a few hours. A severe hurricane of 5 - 6 hours duration can completely wash away sand dunes 3 - 6 m high and 33 m thick at the base (Dunn &

Miller 1964).

2) Storm Surge

Storm surge which oftens accompanies a hurricane, is a rapid, local elevation of sea level due to a combination of the wind driving the water against the land and a drop in atmospheric pressure. Many factors affect the height of the surge :

- 1) the central pressure
- 2) the radius of maximum winds
- 3) the speed of the approach to a coast
- 4) the angle the hurricane track makes with the coastline
- 5) convergence of wind-driven currents at sea
- 6) the shape and slope of the continental shelf
- 7) the shape of the coastline
- 8) the stage of the tide
- 9) short-period waves, breakers, and swells

(Dunn 1964, Simpson & Rieh 1981).

Hurricane Eloise (1975) made landfall over the Florida panhandle. The rise in sea level above the mean was 4.9 m . The area affected was to the right of the hurricane's path where the highest storm surge is generated. The configuration of the coast, the relatively steep offshore profile, and the fast forward motion of the storm contributed to the high sea level. The storm crossed a steep segment of the continental shelf in the northern Gulf of Mexico where water depths average less

than 3 m nearshore and drop rapidly to depths of more than 15 m in less than 1 km (Simpson & Riehl 1981). The storm approached the Florida coast at nearly 40 km/h and had estimated (equipment failed) wind velocities in excess of 210 km/h (Morton 1976). Wave energy and currents moved large masses of rubble. Sand removed from the beach was transported alongshore and offshore.

3) Currents

In the northern hemisphere, the winds are fastest on the right-hand side of the moving hurricane, therefore the greatest rise of water in coastal areas occurs when the angle between the coast and the hurricane path is less than 90° on the right-hand side. Under these conditions, water is trapped between the shore and the hurricane, and fast bottom currents can be produced (Murray 1970).

Murray (1970) studied bottom currents off the Florida panhandle during the passage of Hurricane Camille (1969). During the storm, bottom current speeds ranged up to 1.6 m/s and their direction rotated from alongshore parallel to the wind, to seaward against the wind.

Off the island of St. Croix, U.S. Virgin Islands, the sediment transport rates in the shore zone in Cane Bay were between 0.2 and $1.2 \times 10^5 \text{ m}^3/\text{yr}$ during fair weather, and $1.0 \times 10^6 \text{ m}^3/\text{yr}$ or greater during storms (Hubbard et al. 1982). Turbulent suspension by breaking waves, and mass transport by unidirectional longshore currents are responsible for almost all sediment transport (Hubbard et

al., 1982).

In St. Croix, on the outer shelf which begins at the seaward base of the reef, strong wave-generated currents move large amounts of carbonate material offshore, primarily during storms. Sediment transport rates of 14 - 151 kg/m yr during fair weather, are considerably less than the rates of 146 - 247 kg/m yr measured during storms.

The large differences in transport rates are explained by Hubbard et al. (1982) as a function of two processes. First, oscillatory wave motion is much more effective in suspending bottom sediments during storms. Second, at a point when the waves can no longer sustain the hydraulic head resulting from water being piled up against the shore by storm waves, water flows seaward along the bottom at velocities estimated at 0.5 - 0.8 m/s. This latter process is considered to be the major mechanism for offshore sediment transport during storms.

C) THE BARBADOS COAST

The wave conditions around the island of Barbados are primarily influenced by the trade winds which blow from the east. Disturbances to the normal conditions are caused by the passage of easterly waves, hurricanes, tropical storms, and localized squalls and thunderstorms. Hurricanes and tropical storms cause the major disturbances to the wind regime (Deane 1974).

The leeward or west coast is protected from the prevailing waves generated by the trade winds, but is susceptible to damage caused by hurricanes in the summer, and swells during the winter.

1) Waves

Waves generated by the trade winds arrive on the west coast from the north and south ends of the island. The annual shore wave energy is of the order of 1 - 2.5 magnitudes greater on the north, east, and south-east coasts than on the leeward west coast (Hernandez-Avila & Roberts 1974).

Observations of wave direction, height, and period for nine of the twelve months from April 1969 to March 1970, were conducted in deep water off the west coast of Barbados (Bird et al. 1979). The recurrence of waves from the north and the south was observed to be approximately the same (Bird et al. 1979), although in an earlier study (Richards & Bird 1970) the prevailing direction of wave approach during a two-year period (1967 - 1969) was

determined to be from the south-west. The high energy period was primarily in the winter when the waves were from the north.

The outer bank reef, meanders along the west coast at an average distance of 400 m offshore, and rises to within 9 - 10 m of the surface in some places. This bank refracts the incoming waves (Richards & Bird 1970), causing the direction of wave travel to change with decreasing depth of water so that the crests are parallel to the depth contours (Beer 1983).

2) Currents

As waves shoal and break across the fringing reefs, a surf zone is created in which piling of water occurs to produce the longshore drift (Wong 1971). The longshore drift diverges from the mid points of the coral-fringed headlands to meet a much weaker and variable flow from the bayheads. They combine to form an oblique seaward flow at the edge of the reefs where the water depth changes abruptly. This is an example of nearshore cell circulation. Towards high tide the pattern is clearer than at low tide and seaward drift speeds of up to 0.3 m/s are recorded at the reef edges. During storm conditions, the drift becomes more complex with greater fluctuations in direction and speeds which may exceed 0.5 m/s (Bird et al. 1979).

3) Swells

Swells are surface gravity waves with a period of about ten seconds (Beer 1983). They are slow, rolling waves, but close to shore are observed as breakers. In Barbados, swells are most common in the winter, and are the result of mid-latitude disturbances in the North Atlantic. The effect of the swells on the west coast of Barbados is dependent on their direction of origin. Swells arriving from the north-east strike the north-east coast with relatively little refraction, and the west coast is sheltered from their effects. Swells arriving from the north spread southward along both the east and west coasts of Barbados, but are considerably refracted in developing surf along the shore (Donn & McGuinness 1959).

4) Hurricane Conditions

The majority of Caribbean storm tracks pass well north of Barbados, but occasionally storms of hurricane magnitude pass over, or close to, the island. In the first two centuries of historical records (1651-1850), eleven hurricanes passed near the island of which three were devastating.

Prior to Hurricanes David and Allen in 1979 and 1980 respectively, the only hurricanes recorded in the past century were in 1898 and 1955 (Skeete 1963). The predominant winds of the 1955 hurricane came from the north-east and south-east and coincided with low tide. The storm passed quickly and there was no storm surge.

The historical records of Barbados and the other Caribbean islands, indicate that the passage of a slow-moving fully developed hurricane over the north end of Barbados, comparable to Hurricane Allen, may produce surges of at least 2 metres and possibly 4 metres above mean levels on the west and south-west coasts, with breaking waves considerably higher (Bird et al. 1979).

CHAPTER 4

PREVIOUS STUDIES

PREVIOUS STUDIES

Storm effects have been studied by comparing pre- and post-hurricane conditions since the late 1950's, but only within recent years have the comparisons been quantitative, in addition to descriptive. The earlier studies in Jaluit and Funafuti Atoll, Guam, Belize, Texas, Florida, and the Bahamas were largely qualitative descriptions. Later work in Jamaica and the U.S. Virgin Islands contained quantitative comparisons.

A) ATOLLS

The changes produced by hurricanes on atolls have been documented on Jaluit Atoll in the Marshall Islands (Blumenstock et al. 1961) and on Funafuti Atoll (Maragos et al. 1973, Baines & McLean 1976).

The initial effects produced by tropical storms at these locations include the creation or extension of rubble bars, deposition of thick sheets of coral gravel, and scouring of channels. On Funafuti Atoll (8°S, 179°E) after the passage of Hurricane Bebe (October 1972), a rampart was formed along the southeastern seaward reef flat of the atoll. The rampart had the following dimensions: length 18 km, mean height above reef flat 3.5 m, and width 37 m. Much of the debris originated from a submarine reef terrace situated in water depths of 10 - 20 m. The mean diameter of the rampart components was 9 -

10 cm ; the largest storm block had a diameter of 7 m. Most of the fragments were poorly sorted pre-storm coral rubble and shingle. Five percent of the total mass was derived from the skeletons of recently living corals such as Acropora, Pocillopora, and Pavona (Maragos et al. 1973).

On the shallow reefs (water depth 2 - 10 m), the reef framework remained intact, although the reef biota was virtually destroyed. The survivors, (a few colonies of Pocillopora, Acropora, and Porites, some echinoids, and small patches of coralline red algae) were found in recessed areas where there had been protection from the destructive surge and scour.

Jaluit Atoll, hit by Typhoon Ophelia in 1958, was surveyed shortly thereafter (Blumenstock, 1958) and resurveyed in 1960 by Blumenstock et al.(1961). Funafuti Atoll was re-examined by Baines & McLean in 1973 and 1975, or one and three years after the 1972 passage of Hurricane Bebe. The findings were similar at both locations. The primary change seen after the initial post-typhoon survey was the landward movement of the rubble bars or rampart. Maragos et al. (1973) and Baines & McLean (1976) speculated that the rampart would eventually connect with the existing island, and add to the atoll's land area. The gravel sheets and scour channels were also expected to be permanent features.

The most notable effect of hurricanes on atolls is the formation of ramparts or ridges resulting from the

transport of rubble from offshore reefs at depths of 10 - 20 m, to the shallow reef flat.

B) GUAM

A typhoon is likely to pass over Guam every seven years (Randall & Eldredge 1977). The effects of the most recent typhoon, Typhoon Pamela (1976) were recorded by Randall & Eldredge (1977), and Ogg & Koslow (1978).

The breaking of waves which normally occurs at the fore-reef edge of the reef-flat platform is shifted seaward into deeper water during tropical storms. Typhoon Pamela produced on the reef-flat platform, new deposits of freshly broken coral transported from the reef margin and reef front zones, a minor redistribution of unconsolidated deposits, and fragmentation of branching and foliaceous growth forms (Randall & Eldredge 1977). Typhoon-induced distribution of fragments on sandy substrates promoted colonization of these unstable substrates. The few corals which were overturned, had been poorly attached to the substrate.

In the reef margin zone, the surge channels and buttresses were effective in dissipating wave energy. The effects of the typhoon were minimal : breaking of branches of ramose corals, toppling of isolated corals, and scouring and abrasion of the outer ends of the surge channels.

Most damage was found in the deeper forereef slope

zones, because the biota in this region are the least adapted to high wave regimes. To a depth of 20 m coral branches were fragmented, large coral colonies were toppled, and branches from stout colonies were snapped. Much of the damage was caused by large colonies breaking off from the substrate and rolling around.

Ogg & Koslow (1978) described considerable beach erosion and deposition, and storm effects to the Guam reefs. The patchy nature of the damage suggests that it was caused by the movement of rubble and tree limbs. Within a few days of Typhoon Pamela, on the east coast where the most damage had occurred, a bright green mat of early colonizing algae (Bryopsis, Enteromorpha) appeared. The green algae were succeeded by red algae and within 18 months the red algae had been largely replaced by newly recruited corals.

Both studies concluded that because Guam is located within a storm track and is therefore regularly exposed to typhoons, the reefs are adapted to withstand the storm waves and suffer only minimal damage.

C) BELIZE

Hurricane Hattie, one of the most severe hurricanes of 1961, passed over the Belize reefs on October 30 - 31. The area which includes three atolls, numerous cays, coastal lagoons, and a 130-mile long barrier reef, had been studied by Stoddart from 1959 - 1961, prior to the

hurricane (Stoddart 1962). The reefs were re-surveyed following Hurricane Hattie, in 1962, 1965, and 1972.

A 1962 resurvey of the barrier reef which was approximately 8.1 km north of the storm centre, determined that 75 - 80% of the corals had been destroyed. The corals most heavily damaged included Acropora cervicornis, A. palmata, Porites porites, P. furcata, Cladocera arbuscula, Manicina areolata, Siderastrea radians, Eusmilia fastigiata, Favia fragum, Isophyllastrea rigida, Mycetophyllia lamarckana and Agaricia agaricites. Roughly 100% of Acropora cervicornis and 80% of A. palmata were killed. Montastrea annularis had the highest survival rate (50%), but corals with similar growth forms such as Diploria labyrinthiformis, D. strigosa, D. clivosa, Siderastrea siderea, Solenastrea bournoni, and Porites astreoides, also had better survival rates than the more fragile branching corals. Survival of the massive, slower-growing species and destruction of fragile, rapidly-growing corals also occurred at Low Isles, Great Barrier Reef, with the passage of a cyclone (Stephenson et al. 1958), and in Puerto Rico, with Hurricane Edith (Glynn et al. 1965).

The re-survey of 1965 (Stoddart 1969, 1971) indicated that very little recolonization had occurred. In a region extending at least 24 km north and 19 km south of the storm track, the only corals found alive (Montastrea annularis, Siderastrea sp., Diploria sp., and Acropora palmata) were those which had survived the hurricane.

Recolonization was limited to sparsely scattered Acropora palmata, Millepora, and minor non-frame building corals : Agaricia sp., Manicina areolata, Porites astreoides, Eusmilia fastigiata, and Mycetophyllia lamarckana. Acropora cervicornis was still rare or absent. The rubble and dead coral heads were covered with Padina, Halimeda and other algae. Sponges and gorgonians were recovering more rapidly than the corals.

By 1972 additional recovery had taken place, but despite the fact that 10 years had passed since the hurricane there were still wide areas devoid of living coral. Pieces of massive corals were scattered over the reef surface and fields of finger-sized Porites and Acropora debris remained where they had been felled. Acropora cervicornis was more widespread than in 1965 but still relatively scarce. In contrast to the other corals, Acropora palmata was making a good recovery and many new colonies ranging in height from a few centimetres to one metre were growing on coral skeletons (Stoddart 1974).

The major effects of hurricanes on the Belize reefs are : 1) removal of live corals over several kilometres of reef, 2) selective destruction of fast-growing branching species over a more extensive area, 3) interruption of active reef growth for an undetermined period of time, and 4) generation of large amounts of coarse sediments which accumulate on the reef flats and in the sediment aprons at

the foot of reef slopes.

Stoddart observed that recovery of reefs which have suffered massive damage takes more than 10 years, although reefs which have only been subjected to moderate damage will recover in less than a decade.

D) TEXAS

The area around central Padre Island, Texas, was hit by an intense hurricane, Carla, in September 1961, and a much weaker hurricane, Cindy, in September 1963. Hayes (1967) observed the affected area for a two and a half year period beginning in September 1961 and ending in May 1964.

Hurricane Carla was described by the New Orleans Hurricane Centre (U.S. Weather Bureau), as one of the largest, most intense, and most destructive hurricanes ever to strike the U.S. Gulf Coast. Rock fragments, macro-invertebrates, and coral blocks were transported from depths of 15 - 24 m and thrown onto the beach. Following the passage of the storm, density currents spread a layer of sand over a previously homogeneous mud bottom in depths of 14 - 18 m, and deposited a turbidite further out on the shelf.

A hurricane beach ridge was formed on the barrier island complex. Coarse shells and sand, were deposited as hurricane beach deposits. Other storm effects included deposition and burial of Sargassum spp. seaweed and cutting back of foredunes by 30.5 m. As many as four of

the environmental assemblages described by Parker (1960) in his study of the ecology and distributional patterns of marine macro-invertebrates of the northern Gulf of Mexico, were mixed together in hurricane beach sediments.

Hurricane Cindy, with maximum winds of only 128 km/h was a weak hurricane. Its major effect was the deposition of a swash bar over the contact between the Hurricane Carla beach and the forebeach zone. In April 1964, less than a year after Hurricane Cindy, no evidence of the swash bar remained.

Hayes (1967) concluded from his study of the effects of Hurricane Carla and Cindy that hurricanes cause much mixing of faunal assemblages, are important sediment movers, and disrupt normal sedimentary processes. Mild-storm sediments are not as common in the rock record as those formed during major storms or during normal conditions. Hayes also noted the similarity between quantum theory and energy expenditure in nearshore marine environments. Quantum theory accounts for the stability of the atom on the premise that in radiation the energy of electrons is discharged not continuously but intermittently in discrete amounts or quanta. Energy in nearshore sedimentary environments seems to be expended in a similar manner i.e. within short time intervals that are separated by long periods of relative calm.

E) SOUTH FLORIDA

Hurricane Donna crossed south Florida September 9 - 10, 1960 and was comparable in severity to the "Labor Day Storm" of 1935, previously the strongest of Florida's recorded hurricanes.

Post-Donna conditions were examined by Ball et al. (1967). Pre-Donna conditions were determined from photographs, cores, maps, and bottom markers made available by the Shell Development Company to the investigators.

On the seaward reefs of the Florida reef tract, massive head corals were the most storm-resistant. Coral colonies which had branches leaning away from the incoming waves suffered less damage than those colonies with branches oriented in other directions. Boulder pavements were formed from freshly broken coral rubble. Rubble and sand were transported shoreward.

The patch reefs located in the inner portions of the reef tract were less affected than the outside reefs, although there was much variability in the degree of damage. The predominance of massive coral forms and the relatively protected position of the reefs were factors probably responsible for the sparse damage to the patch reefs. The variation in damage may have been due to different distances of the patch reefs from the protection of a seaward reef, and to different water depths over the patch reefs.

In Florida Bay, deposition of sand over mudbanks took place in the tidal passes between the Keys. The lagoons and linear mudbanks suffered some erosion, but the general topography remained unchanged. Extensive layers of mud and marine grass were deposited in supratidal environments. A small island, Sandy Key, was breached by storm currents, and a cross-bedded spillover lobe of skeletal sand 213 m long, 91 m wide and 2 m thick formed.

F) FLORIDA - BAHAMAS REGION

Five years after the passage of Hurricane Donna over the Florida Keys, Hurricane Betsy swept by with comparable intensity over the same area.

On the reef tract, Hurricane Betsy acted upon a biota whose less resistant elements had been removed by Hurricane Donna. However damage attributed to Hurricane Betsy included uprooted and overturned Acropora palmata, fragmentation and redistribution of A. cervicornis, and truncation of Millepora complanata. Little damage to head corals was observed (Perkins & Enos, 1968). Even less damage was observed on the patch reefs. A few coral heads were overturned and sea fans uprooted.

Hurricane Donna produced more rubble than Hurricane Betsy and caused large-scale movement of sand. The extensive supratidal sedimentation which occurred during Hurricane Donna was almost nonexistent during Hurricane Betsy. Paucity of loose sediment and meagre recolonization of corals limited the amount of material

available for rubble and redistribution. Perkins & Enos (1968) suggested that locally, sediments deposited by Hurricane Donna would be recorded in the sedimentary record, but little evidence of Hurricane Betsy would remain.

6) JAMAICA

In addition to Barbados, Jamaica was also severely affected by Hurricane Allen. Winds were approximately 110 km/h at Discovery Bay on the north coast of Jamaica. The effects on the nearby reefs were described by Woodley (1980) and Woodley et al. (1981).

The dominant coral in the shallow (0 - 5 m) reef zone, Acropora palmata, was devastated. Damage was caused by violently-moving water, rolling corals, suspended fragments, and scouring sand. Hurricane effects were visible to a depth of 50 metres, but dissipation of wave impact depended on, in addition to depth, aspects of the local reef profile such as slope and shelf width. Damage decreased with increased depth in all corals. The densities of Diadema antillarum in shallow areas were more sharply reduced than in deeper areas. At a depth of 5 metres, the number of D. antillarum per metre squared was reduced from 9.3 to 0.1, at 8 metres from 13.3 to 6.1, and at 10 metres the density dropped from 6.3 to 3.8 D. antillarum/m².

The amount and type of damage to sessile organisms

was dependent on their shapes, sizes, and mechanical properties. Damage to gorgonians, corals, and sponges was caused by the abrasion, burial, and tearing or fracture of tissue and skeleton. The subsequent mortality of the organisms ranged from partial in cases where damage was minimal, to complete mortality where damage was extensive.

The relationship between coral growth forms and susceptibility to damage was illustrated. At a depth of 6 metres, planar living areas of branching Acropora sp. were reduced by up to 99%, colonies of foliaceous and encrusting Agaricia agaricites were reduced by 23%, and massive Montastrea annularis by only 9%. At a depth of 14 metres, Acropora cervicornis was reduced to 40% of its 1977 coverage, almost all colonies had broken away from the substrate, and maximum transport of live fragments was 6 metres. Only 2% of encrusting colonies of Agaricia agaricites had become detached (Woodley et al., 1981).

Survival of Acropora sp. fragments was very poor. Only 4 of 254 A. cervicornis fragments tagged nine days after the hurricane were alive five months later. Of fifty-four fragments of A. palmata tagged at depths of 2, 4, and 6 metres within four weeks of the hurricane, only 28% were alive after sixteen weeks. The survivors had had significantly larger areas of live tissue than those that died.

Large amounts of substratum were exposed by abrasion, erosion, fracture, and death, and were suitable for recolonization. At a depth of 16 metres, a 100-m² plot

assessed in 1976 as 13% bare or covered with filamentous algae, was re-assessed as 37.5% bare six weeks after Hurricane Allen. Woodley et al. (1981) believe that the almost total mortality of the slowly sexually recruiting Acropora cervicornis which is a good space competitor under usual wave conditions found at Discovery Bay should favor the growth and recruitment of the hardier, longer-lived Montastrea annularis and more fecund Agaricia agaricites which survived the storm. Areas exposed to strong wave forces may therefore become dominated by massive and encrusting or foliaceous corals.

H) U.S. VIRGIN ISLANDS

Hurricanes David (1979), Frederic (1979), and Allen (1980) passed close to the U.S. Virgin Islands. Of the three hurricanes, David, accompanied by heavy swells caused the most damage in this area.

Rogers et al. (1982) examining the effects in St. Croix of Hurricanes David and Frederic, found much of the dominant shallow water reef coral, Acropora palmata, overturned, and segments of A. cervicornis, Millepora complanata, and Dendrogyra cylindrus toppled or scattered over the reef. On the north coast, damage was heavy but patchy. Pre-hurricane data were available for the south shore forereefs of Robin Bay. The structural complexity of the reefs was determined by the following procedure: A diver stretched a 10-m line just above the reef bottom of

each transect, then extended a chain below this line following the contours of the reef. The ratio of the number of metres of chain to the number of metres of line gives an index of reef topography or structural complexity. By comparing this index before and after the hurricane, the change in structural complexity was evaluated. The structural complexity of the Robin Bay reef decreased uniformly indicating the uniformity of destruction at that site.

The survey was done approximately one month after the hurricanes, and the percentage of live A. palmata was the same as before the hurricanes because the broken branches were still alive.

On the north coast, the mean number of broken A. palmata branches per metre squared decreased with depth. Eight labeled A. palmata fragments were examined thirteen months after the storms for invertebrate colonizers. A total of 61 taxa were found from the following groups: foraminifera, sponges, polychaetes, tunicates, bryozoans, and some hydroids, corals, and other cnidaria. Of the settled scleractinian colonies, 84% were Agaricia spp., 12% Porites spp., and 4% Favia spp.

Hurricane David resulted in a decrease in the amount of live coral and an increase in the amount of rubble on the reefs of St. Thomas and St. Croix (Rogers et al. 1983). No significant changes were recorded in the mean percent cover of the most abundant coral species, total number of coral species within transects, diversity

indices or evenness. Rogers et al. (1983) conclude from the results that coral mortality was not species specific.

1) MISCELLANEOUS EFFECTS

In addition to the papers cited above which deal solely with hurricane effects, several studies refer briefly to the topic.

Bak & Luckhurst (1980) working in Curaçao, found more spatial change in quadrats at 10 and 20 metre depths, than in deeper quadrats at 30 and 40 metres. This difference they attributed partially to the influence of storms. Mortality of large coral colonies was highest in the shallower zones where physical and biological disturbances were more pronounced. Mortality was lower in more constant environments (i.e. deeper water), although in Puerto Rico Luckhurst observed extensive damage to beds of Acropora cervicornis at a depth of 21 metres following the passage of Hurricane David.

After the flood rains and extensive fresh water runoff of Hurricane Flora, Goreau (1964) observed bleaching of Scleractinia, Millepora, Zoanthidea, and Actiniaria. He concluded that the bleaching under these circumstances was due to contact with low-salinity surface water, although this phenomena had also been observed under natural, non-stressed conditions at depths below 30 metres by Goreau. Jaap (1979) observed discoloured colonies of Millepora complanata, Acropora palmata,

Montastrea annularis, and Palythoa spp. on the reef flats at Middle Sambo Reef, Florida Keys. He believed that the expulsion of the endosymbiotic algae, Gymnodinium microadriaticum, resulting in the discolouration or bleaching, was caused by thermal stress.

I have also observed examples of Dendrogyra cylindrus in a bleached, but otherwise healthy state, off the west coast of Barbados in approximately 9.2 m of water. On two subsequent dives, approximately two weeks apart, some of the bleached coral colonies had regained their normal color, some were mottled, and others had become bleached.

A similar situation termed "polyp bail-out" occurs on the Great Barrier Reef. The partial or total spotting of colonies and the actual dissociation of polyps was observed in the coral Seriatopora hystrix Dana. (Sammarco 1982c) suggested that polyp bail-out is an escape response to some unknown environmental stress and a form of asexual reproduction.

The direction of hurricanes on the western tidal flats of Andros Island are known from the presence of hurricane "trails" (Bourrouilh-Le, 1982). The hurricane "trails" have an elongated and elliptic shape ranging from 200 - 300 m wide, and 1 - 5 km long. They are an accumulation of thick layers of aragonitic mud more or less dolomitized, alternating with stromatolitic crusts, pisoid layers, intraclast layers, or stromatolitic thin laminations with mangrove leaves.

Gulf Coast cores show that major hurricanes produced extensive shell layers in lagoonal environments, and graded beds on the inner continental shelf (Mummedal 1982). These diagnostic units, and dating by radioisotopic methods of the core sediments are extending our knowledge of hurricane chronology.

A study of the population dynamics of the reef fish, the redlip blenny, Ophioblennius atlanticus, on the Bellairs and nearby fringing reefs (Labelle, 1982) included the period when Hurricane Allen hit the island of Barbados.

Many species of inshore fish still behaved abnormally a week after the hurricane. Territorial fish were re-establishing their territorial boundaries or acquiring the territories of fish lost in the hurricane. Many fish had severe cuts on their bodies or were empaled with sea urchin spines. Unusually large numbers of moray eels and other predators were observed.

The redlip blennies population was abnormally small in the early part of 1981. The actual mechanism by which the population was drastically reduced is not known, although there are several possibilities :

- 1) the pool of larvae available for recruitment was washed away
- 2) damage to the reef resulted in loss of shelters
- 3) "sandblasting" caused elimination of the food supply (coralline red algae and other algae).

The redlip blenny population was able to withstand the high levels of mortality and regained its original abundance after a few months.

CHAPTER 5

STUDY AREA

STUDY AREA

This study was conducted from the south-eastern Caribbean island of Barbados which is located at latitude 13° N , and longitude 59° 30 ' W. Barbados is approximately 161 km east of the chain of islands comprising the Lesser Antilles, and 322 km northeast of Trinidad (Fig. 6).

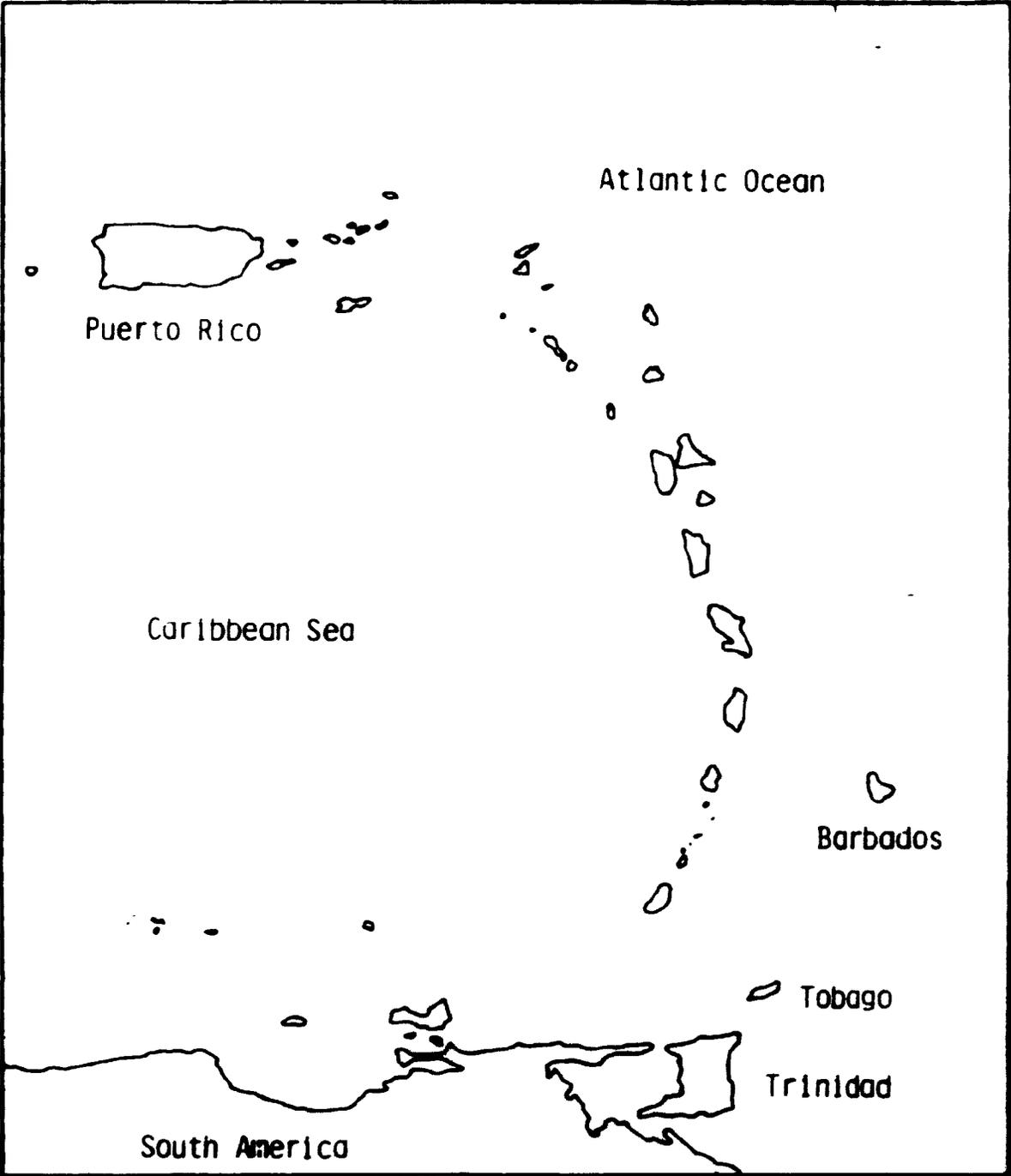
The island of Barbados is the only emergent portion of the Barbados ridge which curves northeast from the broad Venezuelan shelf to Barbados and then extends northwest until it terminates northeast of Guadeloupe (Officer et al. 1959). Barbados is bounded by steep sea-floor slopes that to the east grade into an abyssal plain of the Atlantic Basin at a depth of 4,575 m , and to the west, descend 2,562 m into the Tobago Trough (U.S. Navy Hydrographic Office 1964).

A) REGIONAL GEOLOGY

Barbados lies west of a subduction zone whose trench has been filled by the deltaic sediments of the Orinoco River system. The intensely deformed early Cenozoic sediments of the east side of the island are part of an accretionary prism, and the Tobago Trough between Barbados and the Lesser Antilles volcanic arc represents a fore-arc basin (James et al. 1977).

Barbados occurs at the structural high, the thickest and probably oldest part of the accretionary prism.

Fig. 6. Barbados and the southeastern Caribbean region
(From Barbados Preliminary Atlas).



and probably oldest part of the accretionary prism. Geophysical studies indicate that the prism is composed of deformed sedimentary rocks that attain a structural thickness of at least 20 km near the forearc basin boundary and wedge out to the east over a distance of 300 km (Westbrook 1975).

Barbados may be considered to be composed primarily of three layers (Speed 1979, 1981, Speed & Larue 1982):

- 1) an upper layer of autochthonous Pleistocene reefs (Mesollella et al. 1970) that cover all but approximately 50 km of the island's 430 km .
- 2) an intermediate zone of one or more nappes of early Eocene - middle Miocene pelagic rocks, which are thought to be allochthonous forearc basin deposits.
- 3) a basal complex of deformed layered rocks of probable accretionary origin.

The extensive accretionary prism of the Lesser Antilles forearc is underthrust by the relatively west-moving Atlantic lithosphere. This activity was responsible for the gradual tectonic uplift of Barbados and the intense deformation of the early Cenozoic sediments. Throughout the Pleistocene, the relatively slow uplift of the island continued while fringing reefs developed during eustatic high stands of sea level (Mesollella et al. 1969, 1970). The Pleistocene reefs form the noticeably terraced topography of Barbados. In 1891, Jukes-Brown and Harrison, correctly identified the terraces as fossil coral reefs. It had earlier been

thought that the terraces had been formed by wave-cutting. Absolute dating of the reefs indicates that the age of the reefs increases with increasing elevation and distance inland. The terraces have been dated at 60,000 B.P. (James et al. 1971), 82,000 , 105,000 and 125,000 B.P. A higher elevation series formed between 170,000 and 230,000 B.P. (Mesolella et al. 1969). In addition, work by Bender et al. (1972) indicates that some reef tracts may be more than 700,000 years old.

B) STUDY SITE

Research was based at the Bellairs Research Institute of McGill University. The institute is located just north of Hometown on the west or leeward coast of the island of Barbados (Fig. 7).

The west coast is dotted with fringing reefs which extend most commonly from the headlands. In front of the research institute are two fringing reefs : the northern and southern Bellairs fringing reefs (Fig. 8). The reefs are growing on a gently sloping shelf which extends from the beach into water of 10 m depth at approximately 300 m from shore. Beyond the shelf, the sea floor gradually deepens to form a narrow trough with a depth of 20 m. A bank reef lies seaward of this trough. Situated between the seaward edge of the shelf and the bank reef are several depressions of a maximum depth of 34 m , which are thought to represent sinkholes which formed when sea level

Fig. 7. Barbados - location of research area.

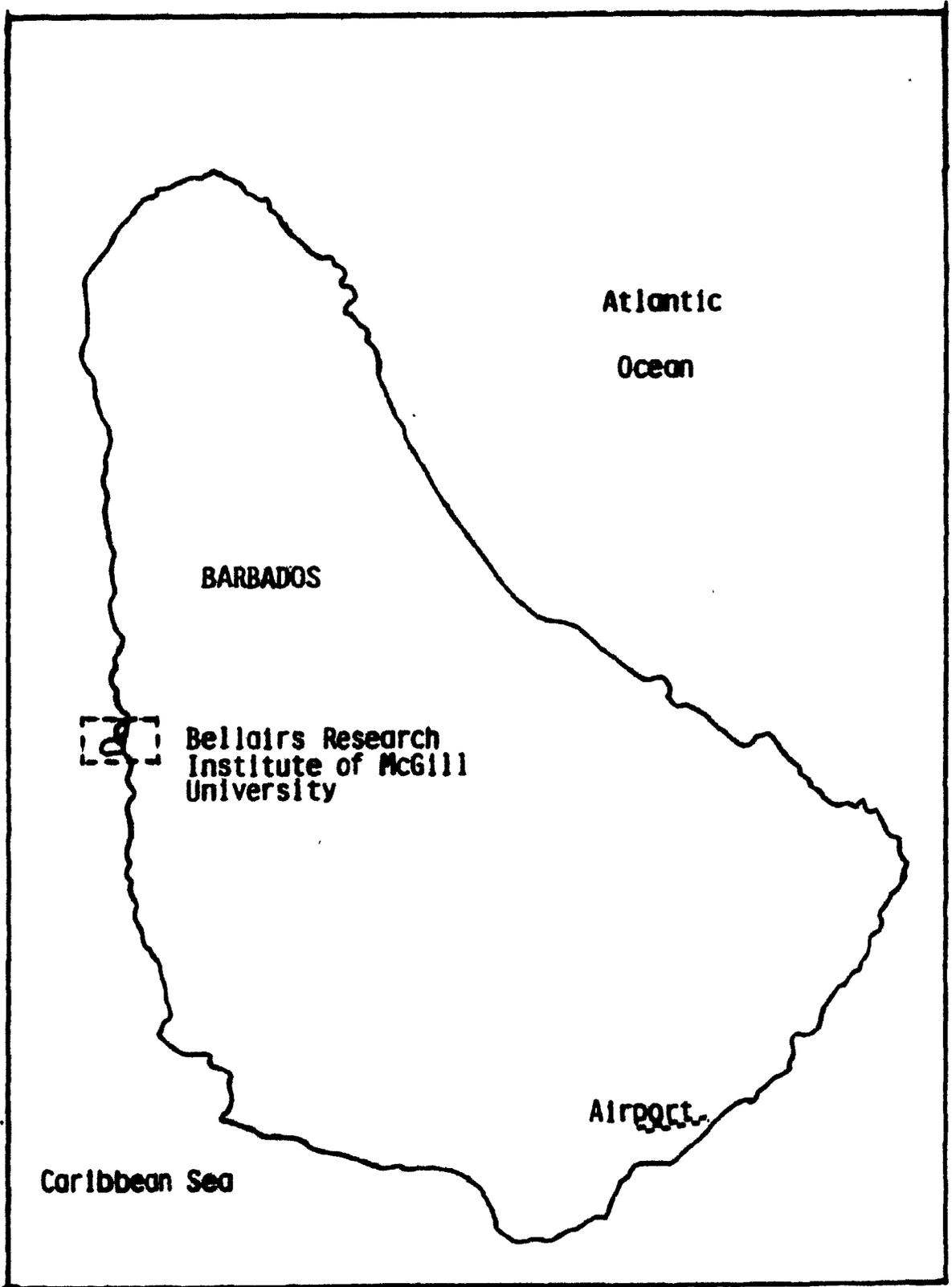


Fig. 8. The Bellairs fringing reefs.



was lower. The depressions are currently being investigated (T. Ortiz, in prep.).

1) Reef Description

The northern Bellairs fringing reef is approximately 200 m x 150 m. Water depth ranges from an inshore depth of one metre to the fore-reef depth of seven metres, but portions of the inshore reef crest may emerge during spring low tides. The mixed semi-diurnal tides have a mean range of 0.7 m and a diurnal range of 1.10 m (Lewis 1960).

2) Reef Zonation

The Bellairs fringing reefs have been described and zoned by Lewis (1960) and Stearn et al. (1977). The terms used in the latter paper are adopted in the description that follows (Fig. 9).

The swash zone, comparable to Lewis' reef flat zone, is the innermost region of the reef. Its width is 20 - 30 m and its depth at low tide ranges from 0 - 1 m. Since the waves commonly break in this zone, the substrate is composed primarily of mobile sand and dead coral rock.

The crest zone (Lewis' Diploria - Palythoa zone) extends approximately 40 m from the swash zone. An irregular surface, composed of coralline algae-encrusted coral skeletons is the predominant substrate and is at an average depth of one metre. There are few corals (small numbers of Porites porites and Porites astreoides) but Favia fragum attains its highest representation within

Fig. 9. Ecological zonation on the Bellairs fringing reefs (From Stearn et al. 1977).

Key to ecological zones :

- a. Swash
- b. Crest
- c. Coalesced spurs
- d. Spurs and grooves
- e. Porites porites
- f. sand
- g. rubble
- h. Madracis mirabilis
- i. Acropora cervicornis
- j. pillar coral
- k. Bank reef
- l. Platy coral



this zone.

The coalesced spur zone or reef crest zone of Lewis, is a region of diverse corals (Porites porites, Porites astreoides, Agaricia agaricites, Montastrea annularis, Montastrea cavernosa, Siderastrea siderea, Favia fragum, Millepora squarrosa, Millepora complanata, and Madracis mirabilis) at a depth of 1 - 2 m. Irregular sand areas at depths of 2 m occur between the coral-covered coalesced spurs. Corals represent approximately 50 % of the hard substrate with coralline red algae and coral skeletons making up the remainder.

The spur and groove zone (seaward slope, Lewis 1960) is the zone where Porites porites is most prominent. Other corals that are well-represented are Porites astreoides, Montastrea annularis, Montastrea cavernosa, Agaricia agaricites, Madracis mirabilis, Millepora complanata, and Millepora squarosa. This region represents the seaward face of the fringing reefs.

In addition to these zones, Stearn et al. (1977) described a Porites porites bank zone which was found only on the southern side of the southern Bellairs fringing reef in approximately 3 metres of water and is not present in the study area.

This zonation may still be applied to the northern Bellairs fringing reef although in the survey following the passage of Hurricane Allen, the diversity of the corals and particularly the abundance of Porites porites has been drastically reduced.

CHAPTER 6

METHODS

METHODS

Stearn et al. (1977) surveyed the northern Bellairs fringing reef in 1974, in order to determine the carbonate budget of the reef. This survey allowed a comparison to be made of the state of the reef, before and after, Hurricane Allen.

A) FIELD METHODS

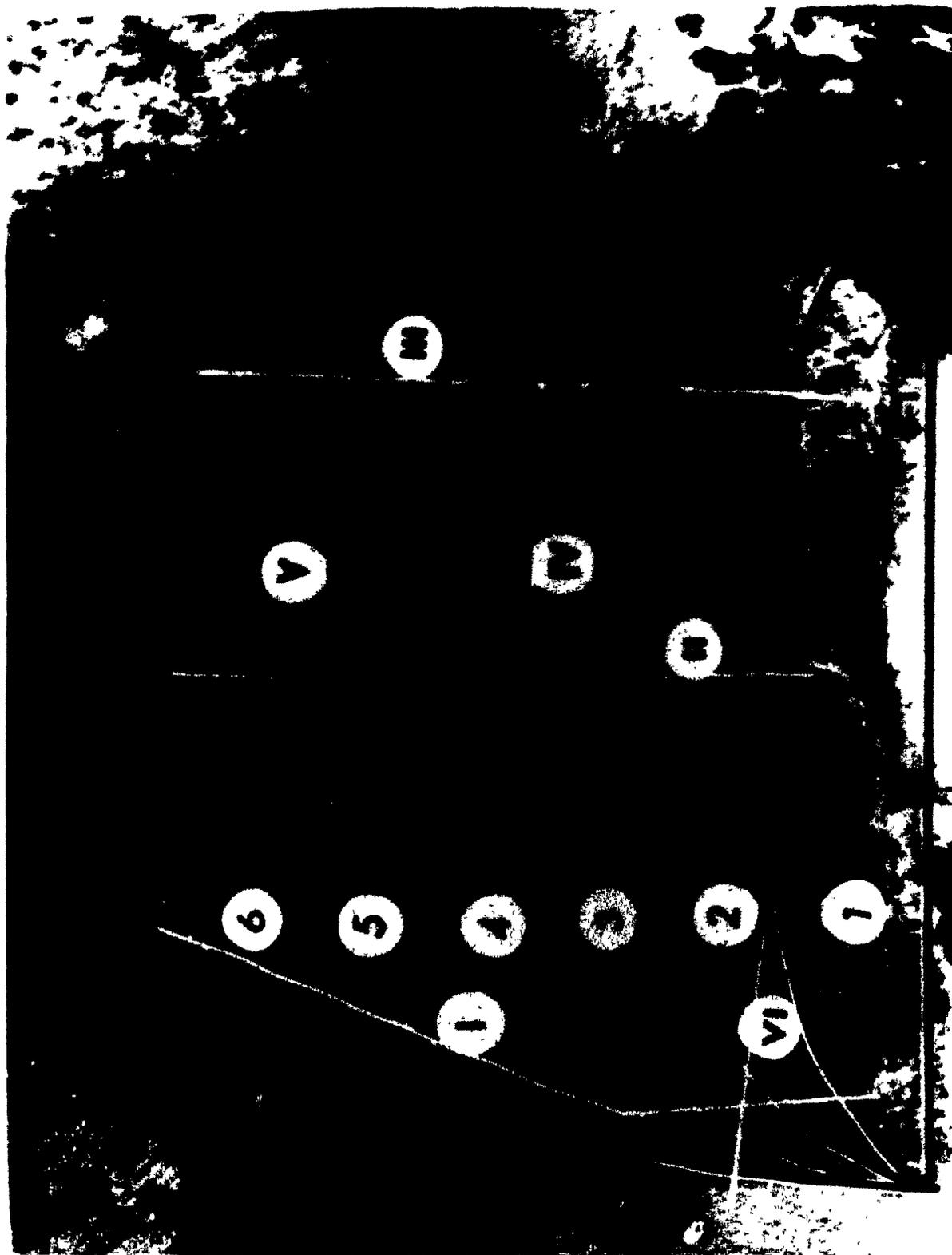
SCUBA (Self Contained Underwater Breathing Apparatus) was used to carry out the field work.

1) Line Transects

Six line transects were laid out on the northern Bellairs fringing reef to correspond as closely as possible to those surveyed in 1974 (Fig. 10). The location of these transects was determined from close examination of an air photo showing the transects on the reef in 1974, characteristic reef morphology and compass bearings. The three longest transects, passing through the northern, central, and southern portions of the reef, extended from near-shore to the seaward lobes. The other transects, each cut perpendicularly through one of the longer transects, and were therefore roughly parallel to shore.

A rope, marked at one-metre intervals, was stretched along the contours of the reef. Nails, painted bright orange for easier visibility, were hammered into the reef

Fig. 10. Aerial photo of the northern Bellairs
fringing reef, showing location of
transect lines and ellipses.



at the points corresponding to the metre marks on the rope.

The data were recorded by swimming over the transect line with a half-metre rod in hand. This rod, marked at 10 cm intervals, was placed at each nail, along the transect line. The substrate type directly adjacent to each mark was then recorded for the initial 50 cm of each metre ; that is, five readings were taken in each metre interval. The types of substrate encountered included : rock, rubble, sand, coralline red algae (CRA), Porites astreoides, Porites porites, Millepora sp., Siderastrea siderea, Montastrea annularis, Montastrea cavernosa, Agaricia agaricites, Madracis mirabilis, Favia fragum, and Palythoa mammillosa. The methods used for the line transects were a duplication of those used by Scoffin and Martindale, and described in Stearn et al.(1977).

Water depth was measured by stretching a calibrated line from the water's surface, straight down to the relevant substrate. The line was attached to a diver's flag - inner tube float at the sea surface.

Underwater photographs were taken using a Nikonos II camera and an Oceanic or Sekonic underwater light meter.

2) Diadema antillarum Population Density

To estimate the number of Diadema antillarum on the reef, a continuous recording method was used. The diver swam over the transect line. A one-metre rod, was carried in one hand, with half a metre extending on each side of

the transect line. Each time a D. antillarum was found beneath the rod, it was registered in a plastic digital counter held in the other hand. Population density was expressed as the number of individuals per square metre of reef surface, calculated from the known length of the transect line and the total number of individuals counted.

3) Rubble Analysis

30 samples of rubble were randomly collected, usually from an area adjacent to a transect line. Rubble was scooped up and deposited in a labeled plastic bag.

In the lab, each bag of rubble was emptied into a labeled glass dish and left to soak in a 10% solution of household bleach for approximately 24 hours. After the sample was rinsed with fresh water, it was placed in an oven until drying was completed.

After the samples were cooled, they were sorted into the various constituents composing the rubble i.e. P. porites, A. cervicornis, etc. The number of fragments, size range, and degree of alteration, were recorded for each sample before they were placed in a plastic bag, weighed, and labeled.

4) Montastrea annularis Growth Bands

Heads of M. annularis were collected from the reef, rinsed, and then bleached in a 10% solution of household bleach.

A diamond - bladed saw in the Department of Geological Sciences at McGill University, was used to

slice the coral heads, along the growth axis, into slabs 0.5 - 0.7 cm thick. These slabs were then x-rayed with a Picker Industrial Minishot II instrument and Kodak Industrex AA2 film. Exposure time was 7.5 seconds at 40 - 50 kilovolts.

5) Porites porites Breaking Points

An approximate measure of the force required to break a branch of P. porites was determined by using a simple spring balance. The model used was a Mariner fish weighing scale with a maximum capacity of 7.25 kg .

The hook was replaced with a fine, looped cord. The loop was placed around a branch of P. porites and a pulling force was applied. At the moment of branch breakage, the force (weight) was recorded. These measurements were done underwater in-situ, and in the laboratory.

B) METHODS OF DATA ANALYSIS

Substrate data collected along the six transect lines were compared to the raw data of the 1974 survey. T. Scoffin graciously supplied the 1974 data. For purposes of statistical analysis, he divided the reef into six equal-area ellipses whose boundaries approximated the zonation of the reef (Fig. 10). The boundaries of these ellipses were not clearly defined in the transect counts supplied by Scoffin, but divisions in the data made it

possible to redefine the boundaries of the ellipses on the re-surveyed transects. The total numbers of substrate counts within each ellipse of the re-survey closely approximates those of the original survey.

1) Pre- and Post-Hurricane Reef Coverage

The chi-square test was chosen to test the significance of the reef changes because the test determines whether or not the difference between two proportions is significant (Simpson et al. 1960). The most commonly used significance level is 0.05. There is only one degree of freedom in a 2 x 2 contingency table. The contingency table is set up as follows:

	<u>Substrate type</u>	
	<u>Present</u>	<u>Absent</u>
Pre-hurricane survey	a	b
Post-hurricane survey	c	d
Totals	a + c	b + d
N_1	= a + b	
N_2	= c + d	
N	= a + b + c + d	

The formula used to determine the value of chi-square is :

$$\chi^2 = \frac{N(ad - bc) - N/2)^2}{(a + b)(c + d)(a + c)(b + d)}$$

The null hypothesis is that there is no difference in the reef before and after the hurricanes. A value of chi-square will be greater than 3.84 for five per cent of the trials, and will exceed 6.63 for one per cent of the trials. As 0.05 is the level of significance adopted here,

if a value of chi-square greater than or equal to 3.84 is calculated, then the null hypothesis is rejected and the reef is considered significantly changed.

2) Coral Coverage and Rank

The change in coverage of each species was derived by the following formula, using Porites porites as an example:

$$100\% - \frac{\text{no. of P. p. counts (post-hurr.)} \times 100\%}{\text{no. of P. p. counts (pre-hurr.)}}$$

To determine if the species had changed in terms of coverage rank, the total number of counts per species were divided by the total number of all coral counts. This was done for both pre- and post-hurricane coral counts. The coral ranking obtained indicated whether the dominant species prior to the hurricane had persisted, or had been replaced by a new or new dominant species.

3) Diversity Indices

The Shannon & Weaver, and Simpson coral diversity values of the six equal-area ellipses of the study reef were compared before and after the hurricane.

a) Shannon & Weaver's Diversity Index - The point method of line transects is based on the expectation: the total number of coral points / total number of transect points = coral coverage (Dodge et al. 1982). The relative frequency or coverage of a species is determined by dividing the total number of points covering the species of interest,

by the total number of all coral points. Shannon & Weaver's (1948) index of diversity may be calculated from the relative abundance (H'n) or from the relative living coverage (H'c). H'c is used when data is collected by the point method of line transects.

$$H'c = - \sum_{i=1}^k p_i \log_e p_i$$

where p_i is the living coverage proportion of the i th species in the sample. The correlation between H'c (living coverage) and H'n (number of colonies) is highly significant ($r = 0.95$), so either measurement may be used for comparative studies of coral species diversity in different areas or at different times (Loya 1972).

A t-test (Hutcheson 1970) was used to test the significance of the decreases in diversity values. The formula to find t is :

$$t = \frac{H_1 - H_2}{S_H - S_H}$$

where $S_{H_1} - H_2 = \sqrt{S^2_{H_1} + S^2_{H_2}}$

The variance of H may be approximated by

$$S^2_H = \frac{\sum f_i \log^2 f_i - (\sum f_i \log f_i)^2/n}{n^2}$$

where n = sample size and f_i = number of observations in category i . The degrees of freedom is approximated by

$$V = \frac{(S^2_{H_1} + S^2_{H_2})^2}{\frac{(S^2_{H_1})^2}{n_1} + \frac{(S^2_{H_2})^2}{n_2}}$$

b) Simpson's Index - To compare Simpson's index to Shannon & Weaver's index, Simpson's index was modified by Loya (1972) to the following form:

$$D_c = 1 - \sum_{i=1}^s p_i^2$$

D_c measures the probability that two specimens picked at random from a sample belong to different species. $D_c = 0$ (as does H') if only one species is found in the sample. Simpson's index, D_c , measures how equally or unequally coverage is distributed among the species. It may be considered a measure of the degree of dominance in a sample. The less numerically equal the species are, the less diverse is the sample and the greater the degree of dominance.

4) Diadema antillarum Population Counts

To determine the significance of the difference of the Diadema antillarum population counts in 1974 and 1981, a t-test was used :

$$t = \frac{\bar{x}_1 - \bar{x}_2 \sqrt{N_1 N_2 / N_1 N_2}}{\frac{(N_1 - 1)S_1^2 + (N_2 - 1)S_2^2}{N_1 + N_2 - 2}}$$

where degrees of freedom = $N_1 + N_2 - 2$.

CHAPTER 7

RESULTS AND DISCUSSION

A) CHANGES IN THE LIVING AND NON-LIVING SUBSTRATE

The 1981 re-survey of the transects originally done in 1974, on the northern Bellairs fringing reef, produced data for a quantitative comparison of the reef before and after the hurricanes (Table 1). Abiotic and biotic coverage on the reef had obviously changed (Figs. 11 - 21), but chi-square tests were applied to the data to determine the degree of significance of the changes.

Each species or substrate type was tested individually per ellipse (Table 2), and for the reef overall (Table 3) using a chi-square test. For the reef in general, rock, coralline red algae, sand, rubble, Porites porites, Porites astreoides, Siderastrea siderea, Montastrea annularis, Favia fragum, Agaricia agaricites, and Madracis mirabilis had significant levels of change. Only Millepora sp. ($P = 0.074$) did not change significantly.

The hydrozoan, Millepora sp., had a high rate of survival because the morphologies of the species growing on the fringing reef are wave-adapted. Millepora squarrosa's box-like structure is highly wave-resistant, and Millepora complanata's bladed skeleton is sturdy and easily sheds sediments. In addition, Millepora complanata tends to orient itself to best withstand strong wave action (Stearn & Riding 1973). The coverage of Montastrea cavernosa was unchanged. In both the original and the re-survey, only five counts of Montastrea cavernosa were

TABLE 1 . SUBSTRATE COUNTS PER ELLIPSE - PRE / POST HURRICANE COUNTS.

SUBSTRATE	ELLIPSE (PRE/POST COUNTS)					
	I	II	III	IV	V	VI
Rock	18/16	64/114	54/123	59/107	65/194	41/73
C.R.A.	19/21	208/156	175/182	106/111	134/101	55/41
Rubble	1/1	37/49	33/47	30/51	67/63	20/19
P. astreoides	1/2	28/13	29/6	36/5	48/13	19/8
F. fragum	-	5/1	2/0	1/0	1/0	-
Millepora sp.	-	8/9	8/5	7/3	21/12	6/4
Sand	-	14/31	57/30	44/108	66/169	40/123
S. siderea	-	1/1	8/1	7/0	24/7	16/5
P. porites	-	18/4	26/2	56/0	101/3	44/2
M. annularis	-	2/1	17/15	15/0	21/13	29/10
A. agaricites	-	10/18	19/24	28/12	40/25	24/12
M. cavernosa	-	1/3	0/2	4/0	-	-
M. mirabilis	-	1/0	3/0	6/0	16/3	3/0

FIG. 11 - 21. Histograms of each substrate (counts per ellipse) before and after  Hurricane Allen.

sand

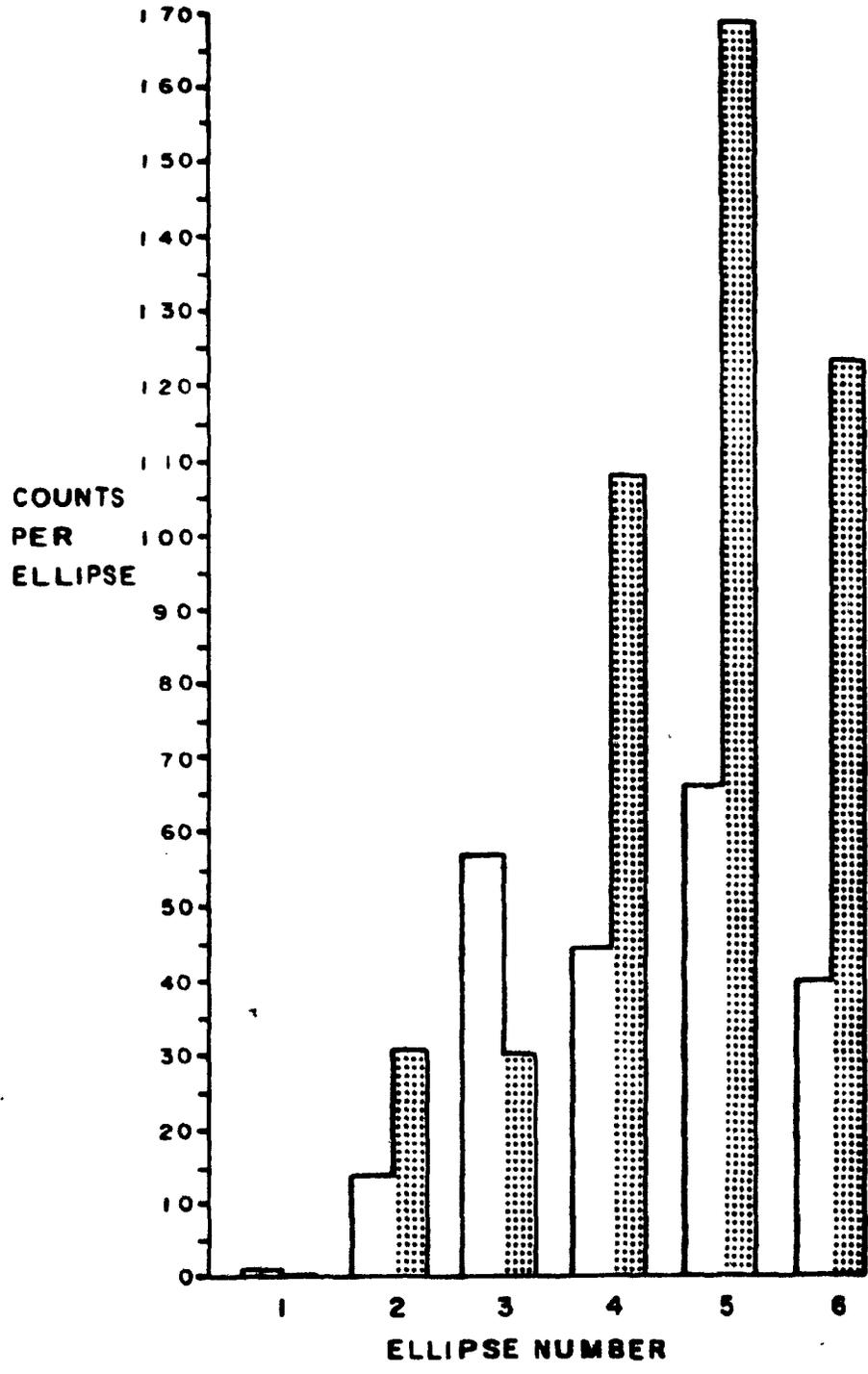


Fig. 11

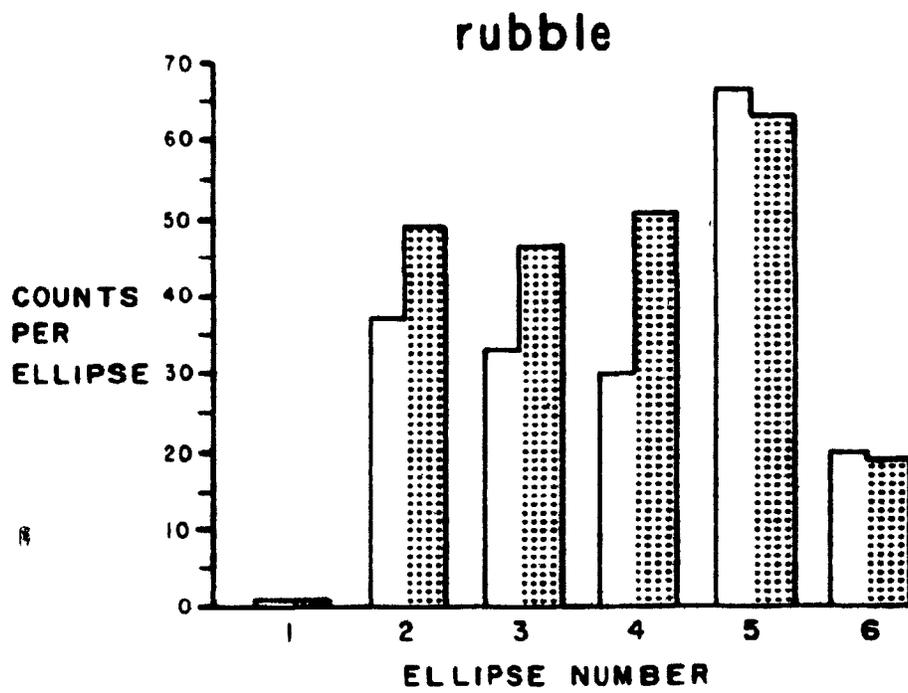


Fig. 12

rock

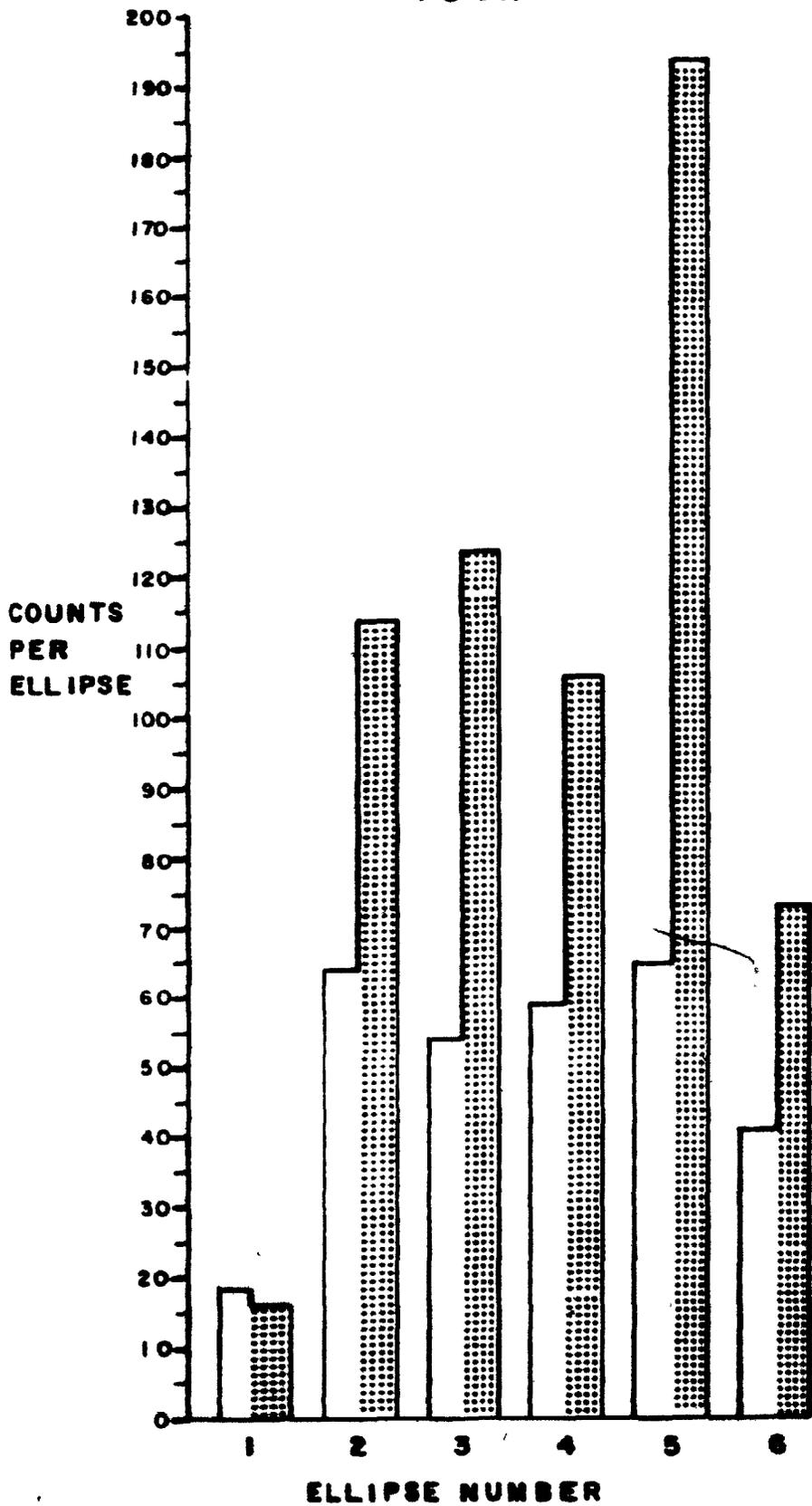


Fig. 13

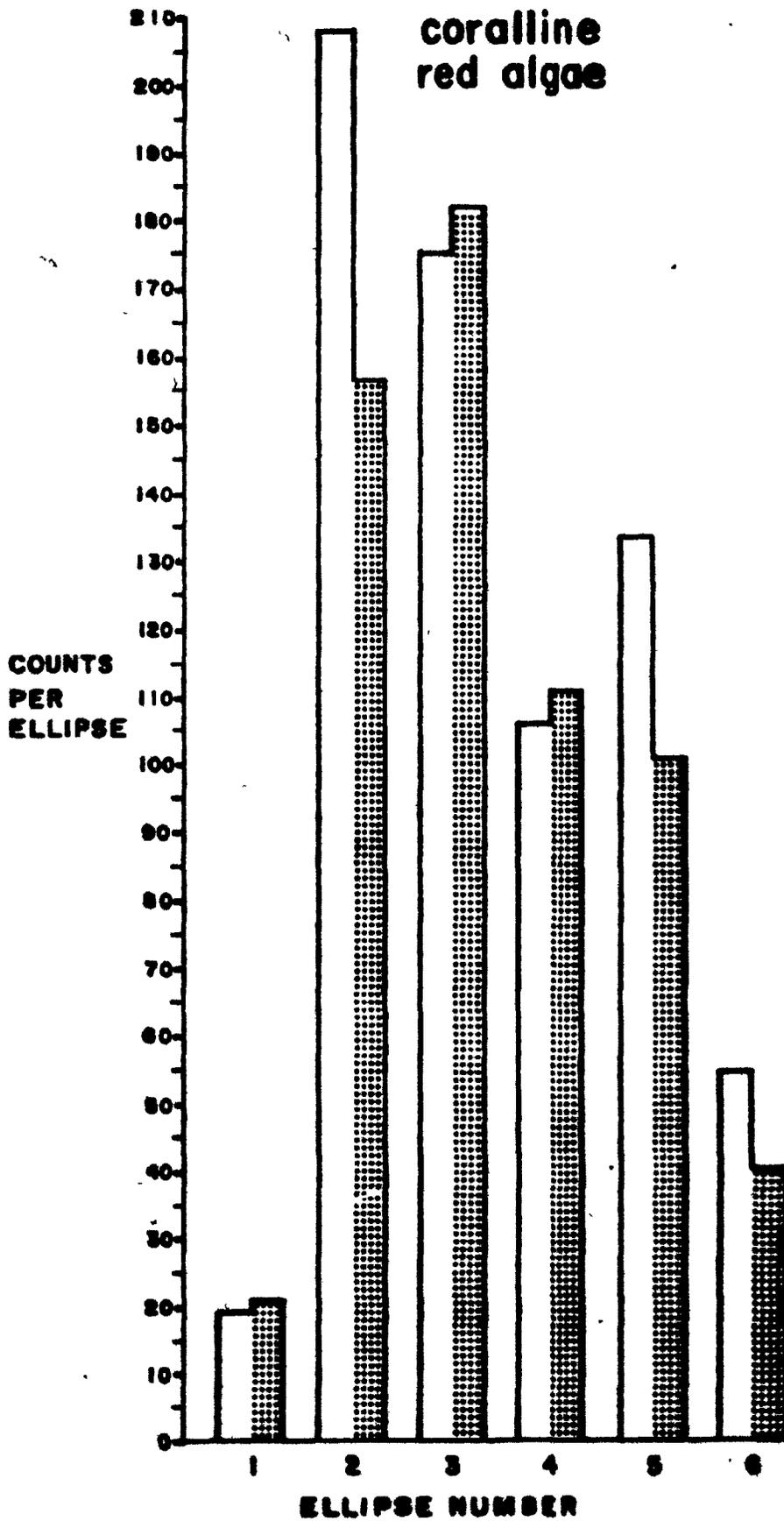


Fig. 14

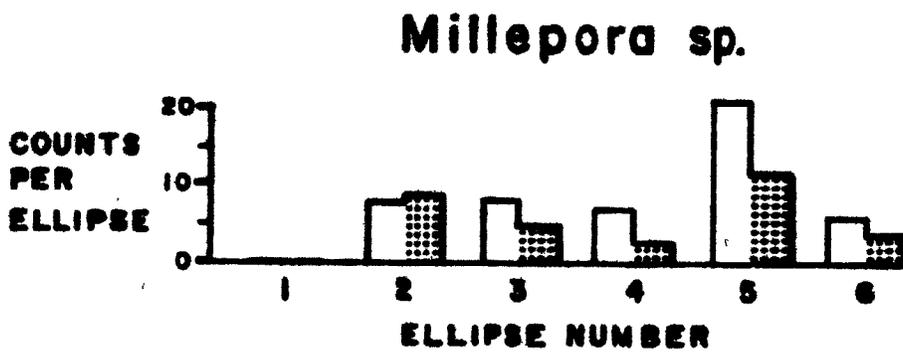


Fig. 15

P. astreoides

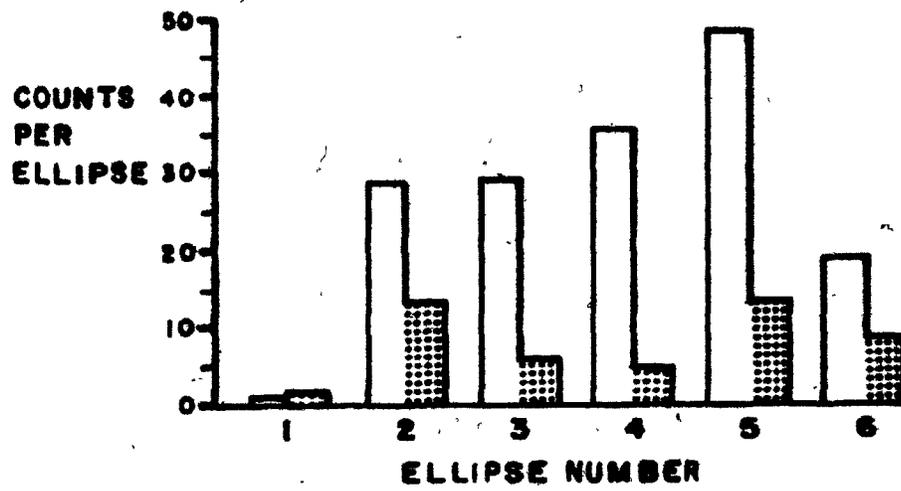


Fig. 16

P. porites

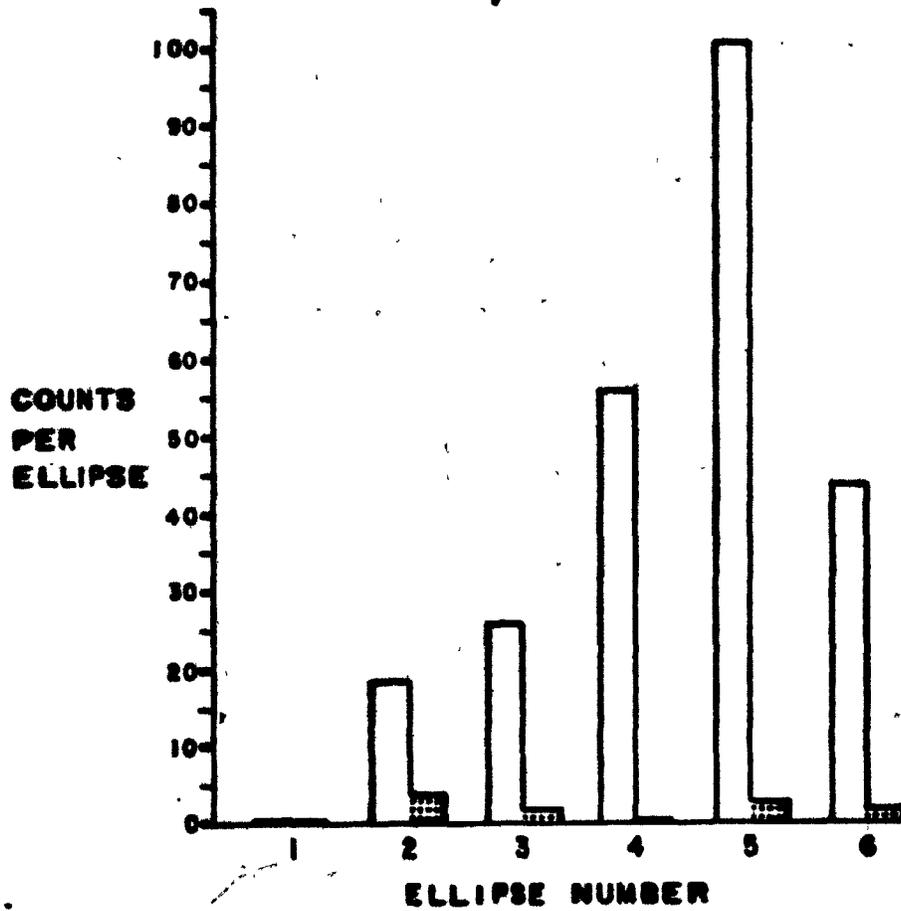


Fig. 17

M. mirabilis

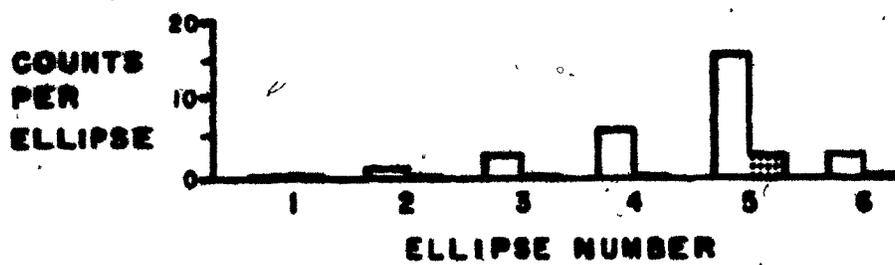


Fig. 18

M. annularis

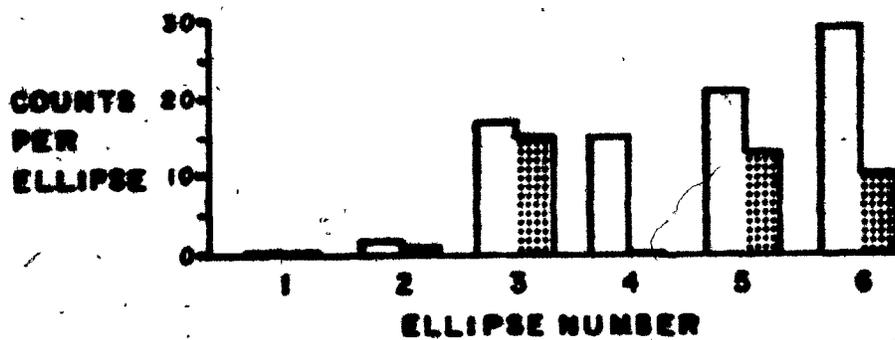


Fig. 19

A. agaricites

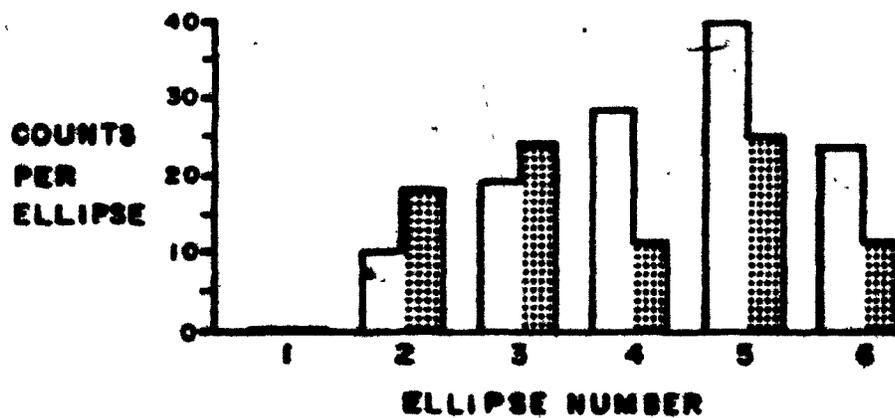


Fig. 20

S. siderea

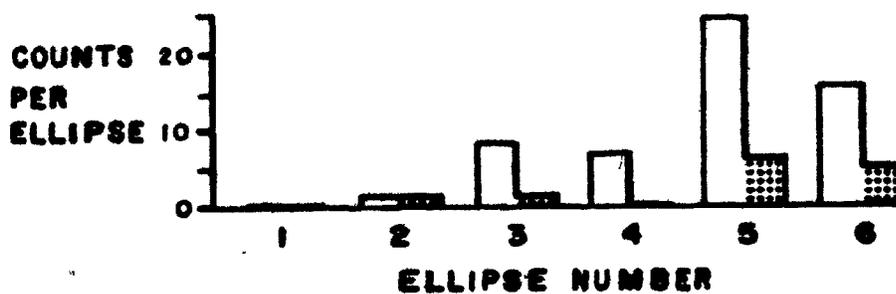


Fig. 21

TABLE 2 . CHI-SQUARE TEST FOR SIGNIFICANCE OF CHANGES
IN SPECIES COUNTS PER ELLIPSE,

<u>ELLIPSE</u>	<u>SPECIES</u>	<u>x²</u>	<u>DIFFERENCE</u>
I	rock	0.051	not sig.
II	rock	17.349	sig.
III	rock	31.647	sig.
IV	rock	16.802	sig.
V	rock	80.812	sig.
VI	rock	10.432	sig.
I	C.R.A.	0.050	not sig.
II	C.R.A.	13.111	sig.
III	C.R.A.	0.059	not sig.
IV	C.R.A.	0.101	not sig.
V	C.R.A.	5.345	sig.
VI	C.R.A.	2.100	not sig.
I	rubble	0.513	not sig.
II	rubble	1.576	not sig.
III	rubble	2.133	not sig.
IV	rubble	5.496	sig.
V	rubble	0.072	not sig.
VI	rubble	0.000	not sig.
I	P. astreoides	0.000	not sig.
II	P. astreoides	5.039	sig.
III	P. astreoides	14.729	sig.
IV	P. astreoides	23.140	sig.
V	P. astreoides	19.900	sig.
VI	P. astreoides	3.880	sig.
I	F. fragum	-	-
II	F. fragum	1.511	not sig.
III	F. fragum	0.515	not sig.
IV	F. fragum	0.000	not sig.
V	F. fragum	0.000	not sig.
VI	F. fragum	-	-
I	Millepora sp.	-	-
II	Millepora sp.	0.000	not sig.
III	Millepora sp.	0.341	not sig.
IV	Millepora sp.	0.911	not sig.
V	Millepora sp.	1.980	not sig.
VI	Millepora sp.	0.102	not sig.

I	sand	0.000	not sig.
II	sand	6.028	sig.
III	sand	9.040	sig.
IV	sand	32.256	sig.
V	sand	55.186	sig.
VI	sand	56.852	sig.
I	S. siderea	-	-
II	S. siderea	0.501	not sig.
III	S. siderea	4.126	sig.
IV	S. siderea	5.188	sig.
V	S. siderea	8.449	sig.
VI	S. siderea	4.936	sig.
I	P. porites	-	-
II	P. porites	7.899	sig.
III	P. porites	19.854	sig.
IV	P. porites	58.095	sig.
V	P. porites	98.826	sig.
VI	P. porites	39.611	sig.
I	M. annularis	-	-
II	M. annularis	0.000	not sig.
III	M. annularis	0.048	not sig.
IV	M. annularis	13.317	sig.
V	M. annularis	1.471	not sig.
VI	M. annularis	8.891	sig.
I	A. agaricites	-	-
II	A. agaricites	1.813	not sig.
III	A. agaricites	0.335	not sig.
IV	A. agaricites	5.922	sig.
V	A. agaricites	3.163	not sig.
VI	A. agaricites	3.578	not sig.
I	M. cavernosa	-	-
II	M. cavernosa	0.251	not sig.
III	M. cavernosa	0.487	not sig.
IV	M. cavernosa	2.261	not sig.
V	M. cavernosa	-	-
VI	M. cavernosa	-	-
I	M. mirabilis	-	-
II	M. mirabilis	0.000	not sig.
III	M. mirabilis	1.366	not sig.
IV	M. mirabilis	4.198	sig.
V	M. mirabilis	7.680	sig.
VI	M. mirabilis	1.340	not sig.

TABLE 3. CHI-SQUARE TEST FOR SIGNIFICANCE OF CHANGES
IN SPECIES COUNTS FOR THE ENTIRE REEF

<u>SPECIES</u>	χ^2	<u>DIFFERENCE</u>
rock	143.765	sig.
C.R.A	7.992	sig.
rubble	4.346	sig.
P. astreoides	64.748	sig.
F. fragum	4.927	sig.
Millepora sp.	3.182	not sig.
sand	97.745	sig.
S. siderea	24.503	sig.
P. porites	225.907	sig.
M. annularis	16.303	sig.
A. agaricites	4.241	sig.
M. cavernosa	0.098	not sig.
M. mirabilis	19.734	sig.

recorded.

Transect V was surveyed in the summer of 1981 and then re-surveyed a year later in 1982. The counts were very similar (Table 4). The differences were not significant, except for those of coralline red algae which increased in coverage ($\chi^2 = 9.70$, $P = 0.002$). The increase may have been due to the colonization of rock by coralline red algae, or due to the difficulty of distinguishing coral rock from coralline red algae which may also be white in colour.

It is difficult to assess how much of the changes between the original and the re-survey substrate counts are due to different researchers. I would estimate that "operator error" is minimal, since recordings made during the re-survey were compared with those obtained by a diving assistant, and the results matched.

The changes of the living and non-living substrate types were overwhelmingly significant on a reefal scale , but less significant when examined ellipse-by-ellipse. Ellipse 4 included the most affected portion of the reef where nine of thirteen substrate types had changed significantly. The breaking of the storm waves in ellipse 4 (T. Tomascik, personal communication) instead of closer to shore as is the norm, caused major damage. Ellipse 1, located closest to shore, was the least changed due to its constant exposure to turbulent water.

The coverage of non-living substrates (rock, rubble and sand) was greater in the re-survey than in the

TABLE 4 . TRANSECT V SUBSTRATE COUNTS

<u>SUBSTRATE TYPE</u>	<u>SUMMER 1981</u>	<u>SUMMER 1982</u>	<u>x²</u>	<u>DIFFERENCE</u>
rock	72	58	1.860	not sig.
coralline algae	20	44	9.703	sig.
rubble	16	14	0.036	not sig.
P. astreoides	1	2	0.000	not sig.
F. fragum	0	0	-	-
Millepora sp.	3	0	1.343	not sig.
sand	94	88	0.237	not sig.
S. siderea	5	6	0.00	not sig.
P. porites	0	1	0.00	not sig.
M. annularis	0	0	-	-
A. agaricites	3	3	-	-
M. cavernosa	0	0	-	-
M. mirabilis	2	0	0.502	not sig.

original survey. This increase in coverage was at the expense of the living components of the substrate such as corals, Millepora sp., and coralline red algae. Sand and rock more than doubled : sand increased from 221 to 461 counts, and rock increased from 301 to 627 counts. Rubble increased from 188 counts to 230 counts.

Dead coral was classified as rock or rubble. Rubble was any piece of loose, dead coral. Dead portions of a coral within a live colony were considered rock. The increased coverage of rock was due to the death of corals and scouring.

The greater sand coverage resulted from the deposition of sand in topographically low areas of the reef during the storm. Another possible explanation for the increased amount of sand is a higher production of sand following the hurricane due to the greater availability of rubble, and increased abundance of Diadema antillarum. Folk & Robles (1964) suggested that initially, massive corals break down into large boulders, and branching corals break down into sticks. Coral skeletons further disintegrate due to abrasion, into medium to fine-grained sand with a mean grain size of approximately 2 phi (0.25 mm). Chave (1960, 1964) reported that the breakdown by abrasion of Acropora cervicornis produced very fine (< 63 μ m) grains. Abrasion of Porites porites and Madracis mirabilis from the Bellairs reef also produced silt-sized particles (Hunter 1977). Diadema antillarum and parrotfish (Gygi 1969)

however, can account for the coral sediments on the reef since they produce grains of 2 - 2.5 phi (0.25 - 0.177 mm) and 1 - 3 phi (0.50 - 0.125mm), respectively.

B) BIOEROSION

Bioerosion is a common process on coral reefs. Sponges, sipunculid worms, polychaete worms, bivalves, arthropods, echinoids (sea urchins), and fish (parrotfish) are the principal agents of bioerosion.

Bioerosion weakens the bases of massive corals making them more susceptible to detachment from the substrate during storms. The branching corals tend to be bored along the central axes of branches, which significantly weakens their structure.

The massive corals of the fringing reef are less affected by sponge borers than the deeper water bank reef corals because the former calcify more rapidly and they lack an exposed base which sponges can penetrate. Coral breakoff on the fringing reef results primarily from storm wave impact.

Evidence obtained during dives made after a winter storm period (December 1975) suggested to MacGeachy (1978) that sponge boring greatly increased the susceptibility of P. porites branches to breakage. He observed newly broken branches in and around the P. porites zone on the southern Bellairs reef. The breakages commonly occurred at the sites of sponge chambers. He believed that most of the damage was caused by blocks of coral rubble which were thrown onto, and tossed about the P. porites beds by the storm waves.

C) ANALYSIS OF THE RUBBLE

The composition and distribution of the rubble on the northern Bellairs fringing reef was examined. The distribution of coral species in the rubble was compared to the distribution of living counterparts growing on the reef.

1) Rubble Composition

The rubble is composed of Porites porites, Acropora cervicornis, Madracis mirabilis, coralline red algae, Agaricia agaricites, Favia fragum, Siderastrea radians, Montastrea annularis, Millepora sp., Stylaster roseus, mollusc fragments, echinoderm fragments, and pieces that are impossible to identify due to erosion or encrustation of the surfaces. Some of the specimens appeared relatively fresh with unaltered corallites, while other specimens were highly bored or encrusted. The percentage of each component in the rubble was determined in two ways: 1) according to its proportion of the total number of pieces of rubble (count percentage), and 2) according to its proportion of the total weight (weight percentage). Only three corals, Porites porites, Acropora cervicornis, and Madracis mirabilis were present in significant quantities in the rubble (Table 5 and Table 6). The mean percentages of all the other identified components collectively represent 9.5% of components, and 8.3% of rubble weight.

TABLE 5 . RUBBLE - COUNTS PERCENTAGE

<u>RUBBLE TYPE</u>	<u>MEAN %</u>	<u>STANDARD DEVIATION</u>
A. cervicornis	20	13
A. palmata	0.01	0.06
P. porites	32	22
coralline algae	3	4
M. mirabilis	30	17
A. agaricites	2	2
F. fragum	1	1
S. radians	0.3	1
M. annularis	1	1
Millepora sp.	0.04	0.2
S. roseus	0.06	0.2
mollusc fragments	2	2
echinoderm fragments	0.1	0.3
unknown	10	9

TABLE 6 . RUBBLE - WEIGHT PERCENTAGE

<u>RUBBLE TYPE</u>	<u>MEAN %</u>	<u>STANDARD DEVIATION</u>
A. cervicornis	32	19
A. palmata	0.04	0.2
P. porites	40	20
coralline algae	2	4
M. mirabilis	13	12
A. agaricites	3	3
F. fragum	1	1
S. radians	0.8	3
M. annularis	0.8	1
Millepora sp.	0.3	1
S. roseus	0.02	0.06
mollusc fragments	0.4	0.5
echinoderm fragments	0	0
unknown	7	6

The three principal constituents of the rubble, Porites porites, Acropora cervicornis, and Madracis mirabilis, share a similar branching morphology which was highly susceptible to breakage. Porites porites formed 32% of the number of rubble fragments, and 40% of the rubble weight. Acropora cervicornis comprised 20% of the number of rubble fragments, and 32% of the rubble weight. Madracis mirabilis represented 30% of the number of rubble fragments, and 13% of the rubble weight. The small size of Madracis mirabilis branches (average diameter of 0.8 cm), accounts for its relatively low representation by weight. Fragments of Madracis mirabilis were smaller and lighter than the heavier, thicker-branched (1.3 cm average diameter) Acropora cervicornis and Porites porites. Fresh branches of Acropora cervicornis are also more dense (less pore space) than Porites porites, and Madracis mirabilis, although boring altered the densities of the fragments.

The force required to break a branch of Porites porites was determined in-situ and in the laboratory. The value obtained in-situ was 5.9 kg (standard deviation 0.9 kg). In the lab, the force required was 5.5 kg (standard deviation 0.6 kg). Freshness of the Porites porites was not critical as indicated by the similarity of the in-situ values and the values recorded in the lab. Chamberlain (1978) determined that the greater the amount of viscoelastic organic matter present in the material being

tested, the greater the strength and the greater the difference in testing fresh materials and materials which have dried out. Corals, when compared to molluscs, echinoids, and vertebrate bones, have little organic material and are among the weaker skeletal materials (Table 7).

The breaking points of ten Acropora palmata colonies were determined in-situ at Grand Cayman Island by Hernandez-Avila et al. (1977). Twenty-three to thirty-five kilograms of force were required to break branches with a mean diameter of 13 cm . Breakage always occurred in bored areas of the stem.

At present, there are no live colonies of Acropora palmata growing on the northern Bellairs fringing reef, although there remains a massive dead colony in growth position. There is strong evidence that the west coast fringing reefs are built on a foundation of Acropora palmata. On the west coast, close to Bridgetown, a harbour channel was cut through the reef. The walls of the channel are a cross-section of the reef. The reef foundation is composed of Acropora palmata and boulder corals. Although living Acropora palmata is rare on Barbados reefs today, and non-existent on the northern Bellairs reef, observation of the harbour reef foundations suggest that Acropora palmata was once a common reef coral. Core hole information from a Caribbean fringing reef in Panama indicated to Macintyre & Glynn (1976) that Acropora palmata was the dominant reef frame-builder from

Table 7. Strength of representative skeletal materials in meganewtons per square metre. Volume % organics = % organic material by volume contained in material. Porosity = pore volume / total volume of material. Data for coral strength and porosity from Chamberlain (1978). Data on molluscs and echinoids from Mainwright et al. (1976).

		<u>STRENGTH</u>	<u>VOL.% ORGANICS</u>	<u>POROSITY</u>
CORALS		12-81	.02-.2	.3
MOLLUSCS	Gastropods	110-270		
	<u>Nautilus</u>	174	5	0
	<u>Pelecypods</u>	88-250		
ECHINOIDS		48-96	1	.5

approximately 7,000 years B.P. until 3,000 - 2,000 years B.P.

2) Rubble Distribution

The three main components of the rubble, Acropora cervicornis, Porites porites, and Madracis mirabilis were not randomly distributed over the reef. The greatest proportion of Acropora cervicornis rubble was in the northern portion of the reef, Porites porites rubble was concentrated in the south to mid-south sections of the reef, and Madracis mirabilis rubble was concentrated in the northern to central portions of the reef (Table 8).

Acropora cervicornis does not grow on the northern Bellairs fringing reef, but does grow in an area seaward of the reef, at depths of 16 - 20 metres (Fig. 9). Therefore all the Acropora cervicornis rubble present on the reef was transported shoreward.

The greater proportion of Madracis mirabilis rubble in the northern and central sections of the reef relative to the rest of the reef, corresponds with the pre-hurricane living coverage. An estimated 180 m² of the total reef area of 18,360 m² was live Madracis mirabilis in 1974. In the re-survey approximately 26 m² are live Madracis mirabilis, and 583 m² are Madracis mirabilis rubble. Fragmented branches have likely been transported by the storm currents onto the reef from the M. mirabilis zone which is located between the fringing reef and the A.

TABLE 8. DISTRIBUTION OF Porites porites, Madracis mirabilis, and Acropora cervicornis rubble.

<u>COUNT %</u>	<u>PERCENTAGES OF REEF SECTIONS</u>				
<u>CORAL SPECIES</u>	NORTH	NORTH-MID	MID	MID-SOUTH	SOUTH
P. porites	28%	23%	22%	43%	48%
M. mirabilis	39%	33%	34%	22%	17%
A. cervicornis	20%	29%	20%	16%	9%

<u>% RUBBLE WEIGHT</u>					
<u>CORAL SPECIES</u>	NORTH	NORTH-MID	MID	MID-SOUTH	SOUTH
P. porites	36%	32%	35%	46%	54%
M. mirabilis	10%	13%	17%	14%	6%
A. cervicornis	43%	43%	33%	20%	21%

cervicornis zone (Fig. 9).

The distribution of Porites porites rubble corresponds with its pre-hurricane live coverage. Porites porites coverage had been greatest along transects I and II in the southern and central portions of the reef respectively. The sharp decrease in Porites porites coverage following the hurricane is not fully accounted for in the rubble. Roughly 2,203 m² were live Porites porites in the original survey. The post-hurricane survey indicated that only 94 m² are covered by live Porites porites, and 777 m² are covered by Porites porites rubble. A small fraction of rubble may have broken down into sand-sized fragments, but most of the Porites porites rubble was probably transported off the reef by seaward currents and deposited in the deeper water rubble zone (Fig. 9). This zone is primarily composed of Acropora cervicornis rubble and may have been the source of some of the older, more altered pieces of rubble found on the fringing reef after Hurricane Allen.

The water circulation pattern during Hurricane Allen is indicated by the movement of the rubble. Wave-generated currents from the north-west passed through the Acropora cervicornis and Madracis mirabilis zones. Rubble and freshly broken fragments of Acropora cervicornis and Madracis mirabilis were carried onto the fringing reef and deposited predominantly on the northern and north-central sections of the reef. A longshore current flowed parallel to shore gradually dropping in velocity. Offshore or rip

currents flowed over the southern portion of the reef and through the grooves and sand channels, and are presumed to have carried away much of the newly-created Porites porites rubble.

D) GROWTH AND "STRESS" BANDS IN *Montastrea annularis*

Early studies of coral banding (Ma 1933), led to the conclusion that a pair of high and low density bands are produced annually (Knutson et al. 1972). Periods of no-growth are not recorded, therefore only a minimum age for the coral head can be determined by counting the growth band couplets. Stresses such as cold and possibly hurricanes which affected the coral during its growth may be recorded as wide, high density bands.

Deposition of the high and low density bands is affected by several factors : light, sediments, wind, water temperature, reproduction, and nutrient availability. Many researchers favor light as the principal factor (Buddemeier 1974, Buddemeier et al. 1974, Bak 1974, Baker & Weber 1975, Dodge & Vaisnys 1975, Dodge et al. 1977, Dodge 1978, Stearn et al. 1977, and Wellington & Glynn 1983). Other studies suggest the importance of temperature as a factor (Weber & White 1974, 1977, and Glynn & Wellington 1980). Highsmith (1979) found both light and temperature to be critical for band formation. He concluded that high density bands are formed during low light levels when water temperatures are above 28.5° C and below 23.7° C. Low density bands are formed during high light levels and at water temperatures between 23.7° C and 28.5° C. Nutrient availability, in association with upwelling is considered a factor (Glynn 1977) although it may reflect dependence on water

temperature. Buddemeier & Kinzie (1975), and Highsmith (1979) noted that high density bands are formed at times of sexual reproduction. The possibility that internal mechanisms regulate coral banding may explain the differences in banding of neighbouring corals.

In the Florida Straits, Montastrea annularis deposits high density bands from July to September (Hudson et al. 1976). Pavona sp. in Panama produces its high density bands from July to December (Wellington & Glynn 1983). Stearn et al. (1977) suggest that in Barbados, the relatively sharp decrease in ambient light in early autumn (September - November) stimulates production of high density bands in Montastrea annularis. Surface water temperatures are also above 28.5° C during these months (Table 9).

In response to stress, Montastrea annularis may accrete thick, high density bands which are wider than the normal high density bands of late summer - early fall. "Stress bands" in Montastrea annularis have been reported by Hudson et al. (1976) in response to unusually cold conditions in Florida, and as a result of relocating corals further inshore (Hudson 1981). Hudson et al. (1976) did not however, find in the coral skeletons any trace of the many hurricanes which had passed over the Florida Keys.

Thermal stress was the factor affecting the Montastrea annularis described in Hudson's papers (Hudson et al. 1976, Hudson 1981). Stress on the corals during

TABLE 9 . MEAN SURFACE TEMPERATURES TAKEN FROM THE SOUTHERN BELLAIRS FRINGING REEF (from T. Tomascik, personal communication.)

<u>MONTH & YEAR</u>	<u>MEAN TEMPERATURE (°C)</u>
September 1981	29.21
October 1981	29.17
November 1981	29.07
December 1981	28.08
January 1982	27.30
February 1982	26.40
March 1982	26.60
April 1982	27.20
May 1982	27.80
June 1982	27.60
July 1982	27.70
August 1982	28.50

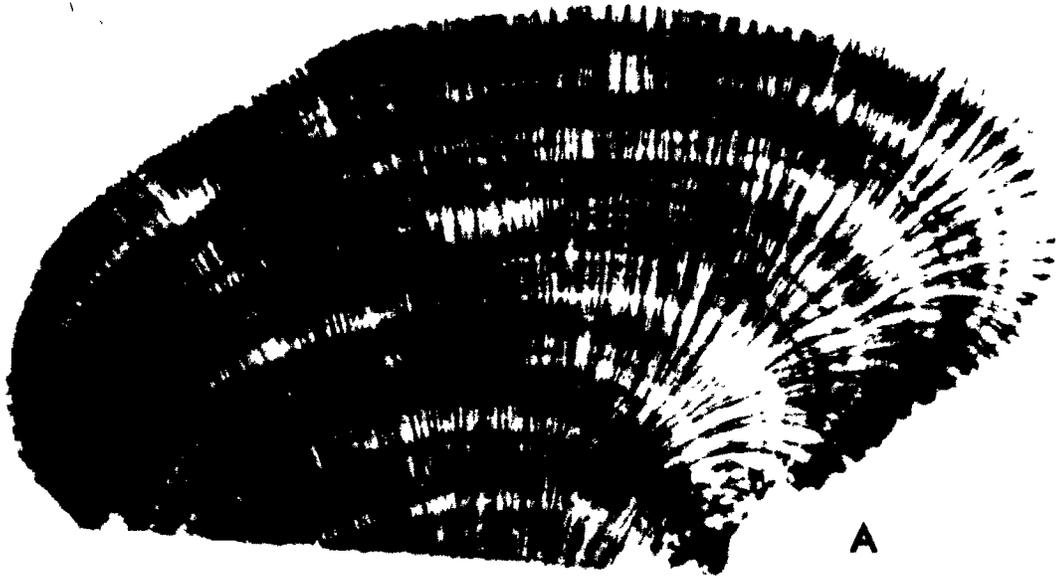
\bar{x} = 27.89°C
s = 0.95

the hurricane in Barbados was likely caused by decreases in light due to increased cloudiness, and increased water turbidity. The high winds accompanying the disturbance may have affected the corals by causing : (1) high resuspension of sediments, (2) high water motion around coral tissue thereby affecting food capture (Hubbard 1974), or (3) reduced light levels through turbidity effects (Upchurch 1970).

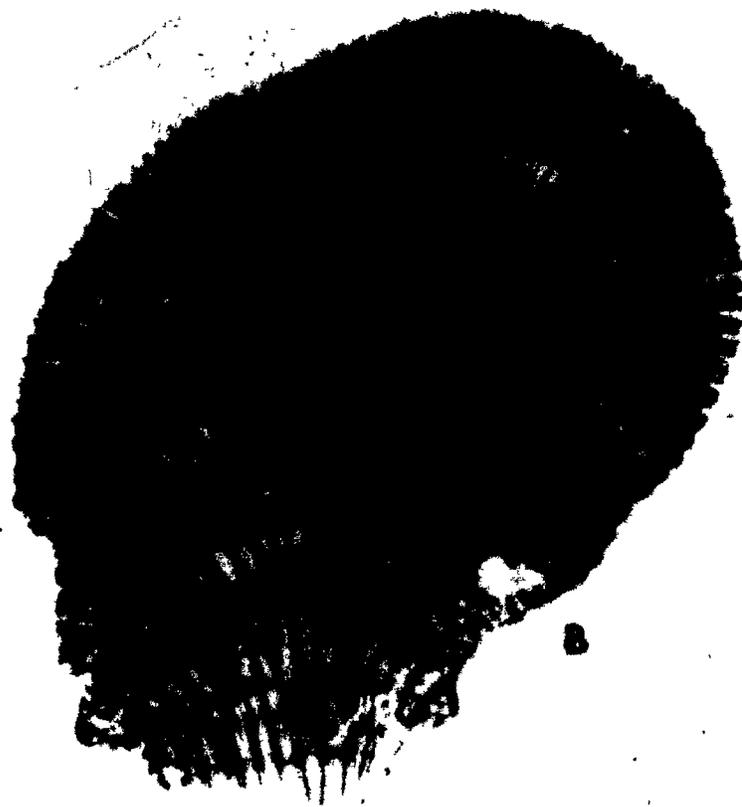
Thirty-one heads of Montastrea annularis were collected from the Bellairs northern fringing reef in 1982 and 1981 to determine if Hurricane Allen had affected the growth patterns. Although in some of the examples of Montastrea annularis there was some evidence of stress banding or unusual growth patterns in the year of the hurricane (Fig. 22), no conclusive "stress bands" were consistently found, and most coral heads displayed regular banding (Fig.23). Under normal conditions, heads of Montastrea annularis growing side-by-side will not have the same growth rate, therefore each coral head may respond to stress in a unique manner. Montastrea annularis heads collected in the summer of 1983 from other Barbados west coast fringing reefs also showed possible "stress bands" (T. Tomascik, personal communication), but again not conclusively. The "stress bands" shown in Hudson's et al.'s (1976) paper were not remarkably distinct.

If coral "stress" bands were deposited during the

Fig. 22. Examples of "stress" bands in Montastrea annularis. Coral "A" was collected in May 1982, coral "B" was collected in September 1982.



A



B

Fig. 23. Normal growth bands in Montastrea annularis.
Coral "A" was collected in May 1982, and
coral "B" was collected in September 1982.



A



B

passage of the hurricane in Barbados, they may have been masked by the onset of the normal accretion of high density bands. In Florida, the "stress" bands caused by unusually cold winter temperatures (Hudson et al. 1976) were deposited during the period of low density band deposition therefore any high density deposition at that time would be sharply defined. Whether or not "stress" bands are recorded, may be dependent on when the stress occurs relative to the high-low density band depositional cycle.

There is too much variation in band thicknesses to state with absolute certainty that a "stress band" is present in the Barbados corals. Coral growth rates are highly variable, but measurements may be recorded and a mean value for growth rate calculated.

Growth rates of Montastrea annularis in the Caribbean and Florida range from 5 mm/yr (Vaughan 1915, direct measurements) to 12 mm/yr (Lewis et al. 1968). Stearn et al. (1977) obtained an average growth rate of 11.1 mm/yr for Montastrea annularis in Barbados. Thirty-one heads of Montastrea annularis collected from the study reef in the summer of 1982, and some samples collected in 1981, had a mean growth rate of 6.3 mm/yr \pm 2.0 mm. The value of 6.3 mm/yr was obtained by counting every distinct dense band in each of the thirty-one coral heads. This procedure differed from the one used by Stearn et al. (1977). The method as described by Stearn (personal communication), involved counting only the very sharply-defined dense

bands and rejecting coral heads which contained equivocal banding. These conditions eliminated all but eighteen of the thirty-one coral heads. The growth rate obtained from these eighteen corals was 8.31 mm/yr. The use of different methods and freedom in interpretation may partially account for the wide range of growth rates found in the literature.

E) CORAL DIVERSITY

Tropical ecosystems are complex and highly diverse, and have long been considered to be inherently stable. The equilibrium hypothesis assumes that the species composition of communities is usually in a state of equilibrium and following a disturbance it returns to that state. High diversity is then maintained without continual changes in species composition. This viewpoint was recently challenged (May 1973, Connell 1978) with the nonequilibrium hypothesis.

The nonequilibrium group of hypotheses is based on the assumptions that the species composition of communities is seldom in a state of equilibrium, and that high diversity is maintained only when the species composition is continually changing (Connell 1978). There exists three hypotheses associated with the nonequilibrium school of thought : the intermediate disturbance hypothesis, the equal chance hypothesis, and the gradual change hypothesis. According to the intermediate disturbance hypothesis, diversity is higher when disturbances are intermediate in terms of frequency and intensity. The equal chance hypothesis suggests that species have equal abilities to colonize, exclude potential competitors, and resist environmental fluctuations. The local diversity therefore depends only on the number of species available in the geographical area and the local population density. The equal chance

hypothesis can be rejected because corals are not equal in their resistance to physical extremes, nor are they equally adept colonizers. Boulder corals such as Siderastrea siderea and Montastrea annularis are better suited to withstand extreme wave activity than Porites porites and Madracis mirabilis. Corals are not equally adept colonizers. Corals which can reproduce by fragmentation have a greater chance of survival, than corals which rely totally on planulae for recolonization. The gradual change hypothesis assumes that gradual environmental changes which alter the ranking of competitive abilities, occur at a rate high enough so that competitive elimination is rarely, or never attained. Very little support exists for this hypothesis.

1) The Intermediate Disturbance Hypothesis

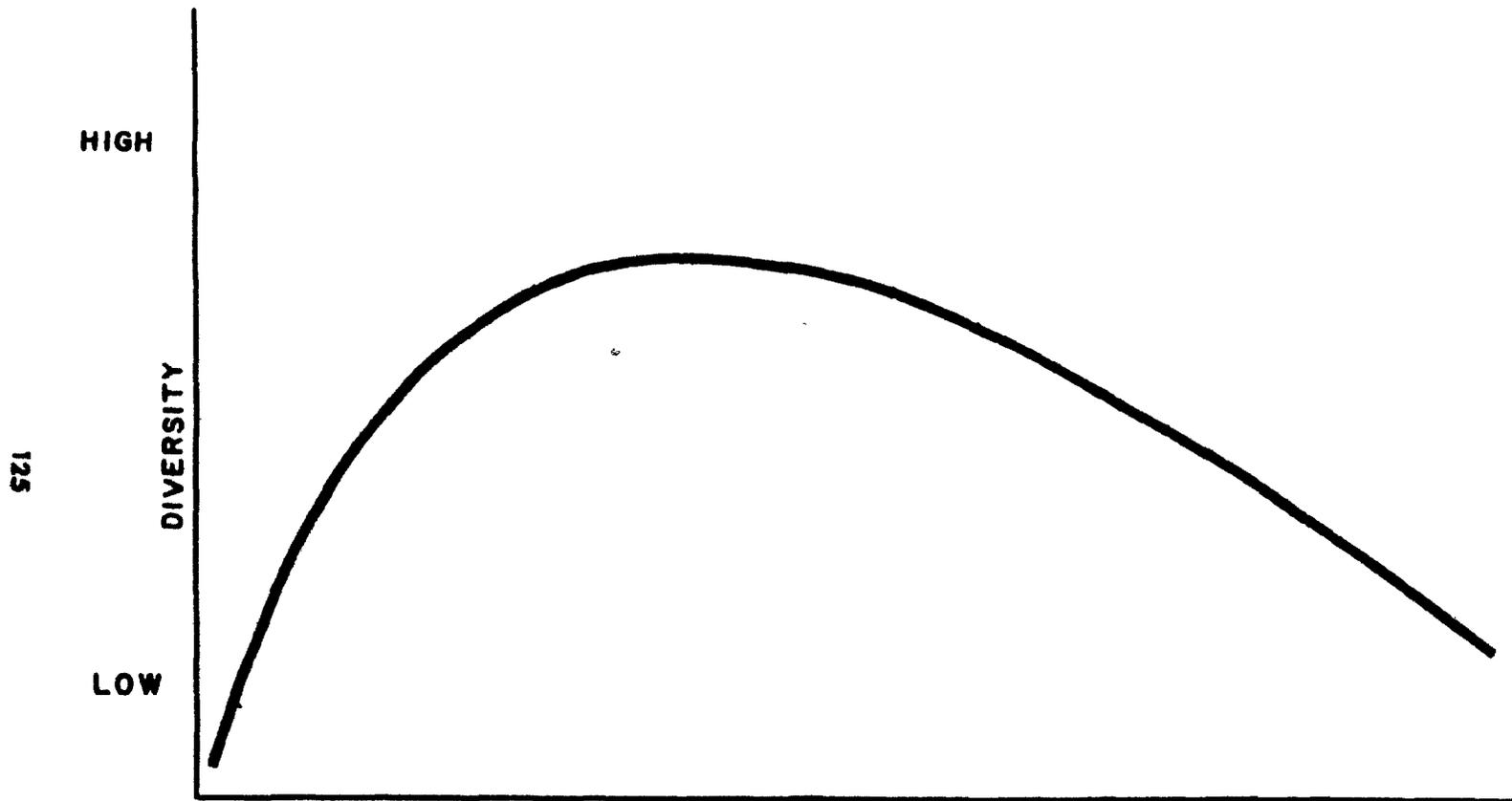
This nonequilibrium hypothesis has been applied to the tropical rain forests of Africa, tropical America, and south-east Asia, and the coral reefs of Heron Island, Australia (Connell 1978). On a coral reef, following a catastrophic disturbance such as a severe hurricane and its accompanying powerful waves, larvae of a few species will soon arrive at the newly modified substrate. Diversity is low since only the species that are producing larvae and are within dispersal range will be able to colonize. As time progresses diversity will increase since more species will have had the opportunity to colonize the substrate. If another disturbance does not

occur while the reef is still at its maximum diversity level, diversity will gradually decrease because the most efficient competitors will dominate the other coral species (Fig. 24). The highest diversity levels are maintained where disturbances are intermediate in frequency and intensity, and where the reef community is kept as far from competitive exclusion (reduction or exclusion of some species) as possible, while allowing the greatest number of species to recover from the disturbance (Huston 1979).

A disturbance may be either physical or biological in nature. Physical disturbances which could affect reef corals include hurricanes (cyclones, typhoons), storms, swells, extremely cold or warm water temperatures, unusually low tidal levels, changes in light intensities, salinity extremes, sedimentation, volcanic activity, nuclear blasting, or pollution. Biological disturbances which can affect a coral's growth include : (1) predation by fish, echinoderms (especially sea urchins and the starfish, Acanthaster planci), and other invertebrates, and (2) competitive interaction among corals, or involving corals and other reef organisms. Biological disturbances are not the subject of this discussion therefore they will not be discussed further.

Studies of the effects of physical disturbances such as lava flows, storms, extremely low tides, and hurricanes have been conducted on coral reefs. Recolonization of coral communities on submerged lava flows in Hawaii offers

Fig. 24. Intermediate disturbance hypothesis graph (From Connell 1978).



DISTURBANCES FREQUENT-----▶ **INFREQUENT**
SOON AFTER A DISTURBANCE-----▶ **LONG AFTER**
DISTURBANCE LARGE-----▶ **SMALL**

support for the intermediate disturbance hypothesis. Grigg & Maragos (1974) reported that diversity increases during succession, but reaches a peak value before climax conditions are attained. The decline in diversity as climax is approached is believed to be due to interspecific competition for space. Disturbances in the form of exposure to sea and swell, can interrupt and set back the process of competitive exclusion. At the exposed lava flow sites, coral cover is low and diversity relatively high. The species are relatively evenly distributed since there is little competition for space. At the leeward sites, where succession is less likely to be interrupted, coral cover is high, diversity is low, and competition is intense.

Dollar (1982) analyzed the "immediate" effects of intermediate and severe storm disturbances on fringing reefs off the west coast of Hawaii. Fourteen days after a 1974 disturbance intermediate in terms of frequency and intensity, Dollar found that species cover diversity was overall significantly higher over the reef. Diversity increased in zones that had been previously dominated by a single species, and decreased in zones of previously equitable distribution. A re-survey, thirty days after a severe 1980 disturbance indicated that the entire reef had been reset at an early, low diversity, successional stage. The number of coral species did not significantly decrease as a result of either disturbance.

Extremely low tides in the Gulf of Eilat, Red Sea,

act as a diversifying force, by preventing competitive exclusion on the reef flats (Loya 1976):

Rogers et al. (1982) found that hurricanes could increase or decrease coral diversity. If only moderate destruction took place, diversity could be increased by elimination of the dominant branching corals thereby increasing the amount of light reaching the slower-growing head corals. Diversity could decrease as a result of elimination of coral species, or initiation of new colonies from fragments of the already dominant species.

Rosen (1981) is critical of the intermediate disturbance hypothesis on two points. First, cyclones are the main agent of disturbance cited but much of the tropics and zooxanthellate coral belt lies outside the influence of the two global cyclone belts. This point does not invalidate the intermediate disturbance hypothesis. As shown by several studies, factors other than cyclones may produce disturbances. Extremely low tides (Loya 1976), surge and swell (Grigg & Maragos 1974), herbivores (Paine 1966), Acanthaster planci (Porter 1972, Glynn 1973), and Diadema antillarum or sea urchins as a group (Sammarco 1982a, 1982b) are capable of creating intermediate disturbances. Rosen's second objection is that some areas of high diversity on a coral reef lie in deeper water and would therefore be less susceptible to cyclonic disturbance than the shallower, often lower diversity reef environments. This point has some merit

although the effects of Hurricane Allen were visible down to a depth of 50 m off Discovery Bay, Jamaica (Woodley et al., 1981). In addition, steep slopes located in deep water are susceptible to another disturbance, slumping (Loya 1972).

2) Caribbean Coral Diversity

The pre-hurricane coral diversity, of the Bellairs northern fringing reef, measured as H'c (relative living coverage) is equal to 1.61. This is comparable to the diversity of other Caribbean fringing reefs, but low compared to the bank reef in Barbados (Ott, 1975) or Pacific reefs (Bull 1982, Dana 1979, Pichon & Morrissey, 1981). Shannon-Weaver diversity values for the latter two locales average from 2.0 to 3.0. Coral diversity on reefs has been assessed in many studies, but actual values of diversity indices were rarely reported. In Bermuda, diversity values were obtained for three shallow water reefs (reef tops at depths of 3 - 5 m). Data was gathered by the point method of line transects (similar to the method used in this study). The values of H'c obtained were 1.55, 1.71, and 1.04 (Dodge et al. 1982).

In the U.S. Virgin Islands, the passage of Hurricane David (August 1979) was responsible for a decrease in the amount of live coral, and an increase in the amount of coral rubble. Hurricane David did not, however, significantly change diversity values (H'). Because the hurricane did not preferentially destroy the dominant species, its effect on diversity was inconsistent. Pre / post hurricane H' values for four sites in the U.S. Virgin Islands were 1.52/1.63, 1.55/1.39, 1.87/1.77, and 1.79/1.81 (Rogers et al. 1983). An increase in coral diversity would have resulted if the dominant corals had been most severely damaged. Only the first site was a

windward fringing reef (4 m deep), the other three sites were also windward, but located on submerged barrier reefs at depths of 5 - 6 m .

3) Coral Diversity of the Study Reef

In Barbados, diversity on the Bellairs northern fringing reef dropped following the passage of Hurricane Allen ($H'c = 1.26$). In each ellipse there was a marked decrease in diversity following the hurricane (Table 10 and Table 11). The sharpest decline was in ellipse 4, where the breaking of the storm waves had caused especially severe damage in that region (T. Tomascik, personal communication). The changes in Shannon-Weaver diversity indices before and after the hurricanes were significant in ellipses 3 - 6 inclusive (Table 12, $P < 0.05$). Species number was unchanged with eight coral species recorded in both the original and the re-survey. Coral coverage was greatly reduced. The post-hurricane (1981) coral count was 211 compared to a the pre-hurricane count of 713 corals ; this is equivalent to a 70% loss of coral coverage.

Coral mortality was species-specific, or at least morphology-specific. Branching corals such as Porites porites and Madracis mirabilis suffered the greatest reduction in coverage on the reef (96 % and 90 % reduction respectively). The encrusting corals (Agaricia agaricites, Porites astreoides) and boulder corals (Siderastrea siderea, Montastrea annularis, Montastrea

TABLE 10 . CORAL DIVERSITY - SHANNON-WEAVER DIVERSITY INDICES (H') BEFORE (1974) AND AFTER (1981) HURRICANE ALLEN

<u>ELLIPSE</u>	<u>1</u>	<u>2</u>	<u>3</u>	<u>4</u>	<u>5</u>	<u>6</u>
Before	0.00	1.50	1.68	1.64	1.61	1.62
After	0.00	1.42	1.30	0.61	1.53	1.48

TABLE 11. CORAL DIVERSITY - SIMPSON'S INDEX OF DIVERSITY BEFORE (1974) AND AFTER (1981) HURRICANE ALLEN.

<u>ELLIPSE</u>	<u>1</u>	<u>2</u>	<u>3</u>	<u>4</u>	<u>5</u>	<u>6</u>
Before	0.00	0.72	0.79	0.76	0.76	0.78
After	0.00	0.69	0.66	0.42	0.75	0.75

TABLE 12 . t-TEST ON CHANGES IN CORAL DIVERSITY
(SHANNON-WEAVER INDEX, H'_c).

<u>ELLIPSE</u>	<u>t VALUE</u>	<u>DEGREES OF FREEDOM</u>	<u>DIFFERENCE</u>
1	-	-	-
2	1.07	87	not significant
3	6.86	75	significant
4	20.20	33	significant
5	2.03	104	significant
6	3.80	63	significant

cavernosa) were not as severely damaged (Table 13).

Coral rank and relative coverage of each species changed following Hurricane Allen. Porites porites slipped from its pre-hurricane dominant position to a post-hurricane fifth out of eight positions. Coverage of Porites porites before the hurricane represented 34% of the corals, but its post-hurricane coverage was reduced to only 5% of the corals (Table 14). Overall, the branching corals decreased in dominance while boulder and encrusting corals remained relatively unchanged, or increased their proportion in the coral community.

4) The Study Reef and the Intermediate Disturbance Hypothesis

In the pre-hurricane survey, coral diversity was relatively high ($H'c = 1.61$) despite the dominance of Porites porites. If the Bellairs northern fringing reef was following the theoretical undisturbed succession, in 1974 it was likely at, or approaching the climax stage of competitive exclusion (Fig. 25). However due to Hurricane Janet in 1955 and other previous hurricanes, the pattern of diversity on the Bellairs reef was probably closer to the peak diversity of the hypothetical disturbed model. The passage of Hurricane Allen reset the successional process back to an early, almost pioneer stage with low coral diversity ($H'c = 1.26$). If left undisturbed, the diversity of the reef will continue to increase until it reaches its maximum level. If there are no disturbances during the recovery time of the northern Bellairs reef,

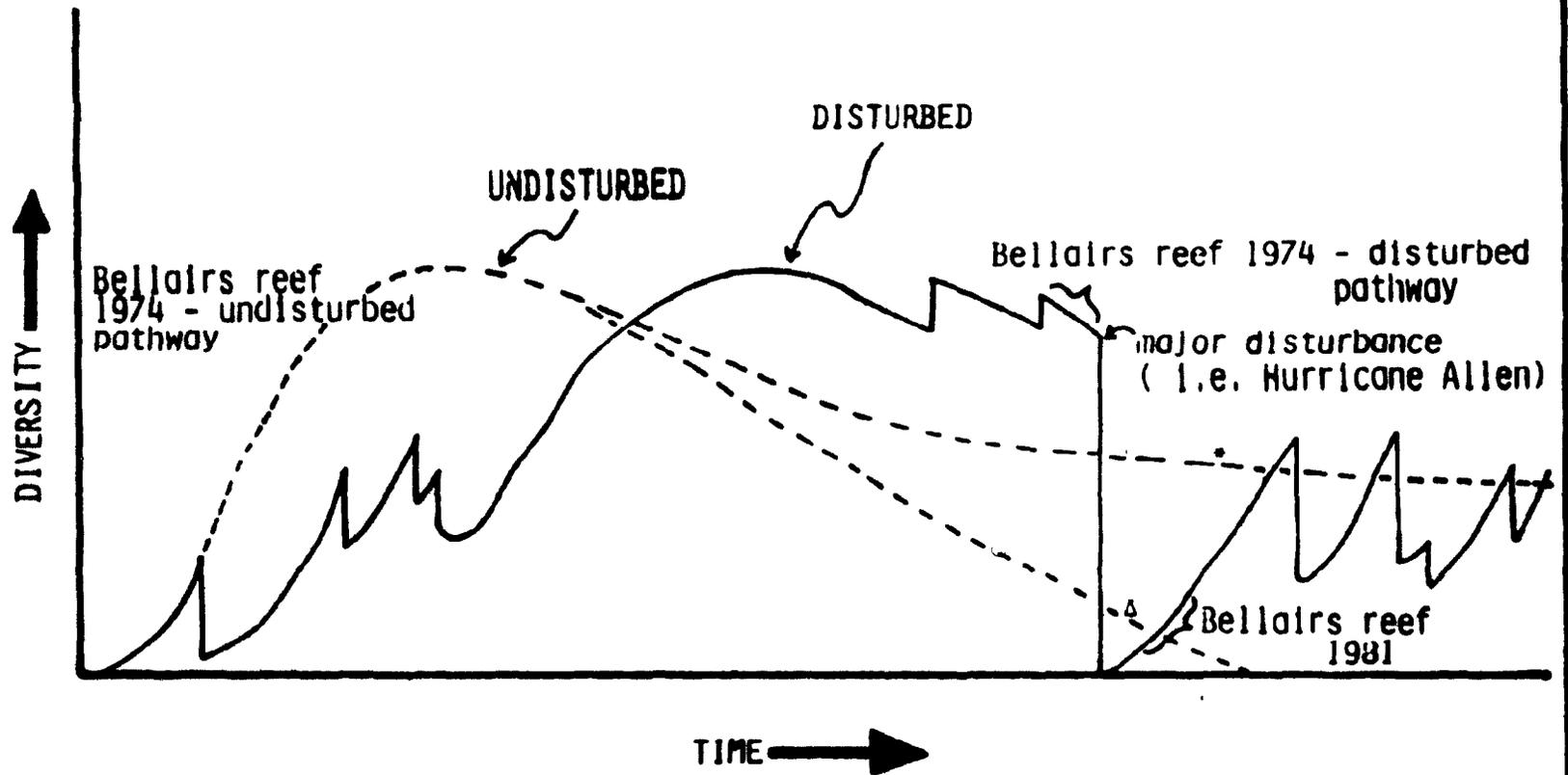
TABLE 13 . PERCENTAGE LOSS OF CORAL SPECIES

<u>CORAL SPECIES</u>	<u>PRE-HURRICANE COUNTS</u>	<u>POST-HURRICANE COUNTS</u>	<u>% LOST</u>
A. agaricites	122	91	25%
F. fragum	9	1	89%
M. mirabilis	29	3	90%
M. annularis	85	39	54%
M. cavernosa	5	5	0%
P. astreoides	162	47	71%
P. porites	245	11	96%
S. siderea	56	14	75%

TABLE 14 . CORAL RANKING - BEFORE AND AFTER HURRICANE ALLEN

	<u>PRE-HURRICANE</u>		<u>POST-HURRICANE</u>	
	<u>RANK</u>	<u>% OF CORALS</u>	<u>RANK</u>	<u>% OF CORALS</u>
A. agaricites	3	17%	1	43%
F. fragum	7	1%	8	0.5%
M. micabilis	6	4%	7	1%
M. annularis	4	12%	3	18%
M. cavernosa	8	1%	6	2%
P. astreoides	2	23%	2	22%
P. porites	1	34%	5	5%
S. siderea	5	8%	4	7%

Fig. 25. Intermediate disturbance hypothesis and the
Bellairs fringing reef.



• typical reefs

--- undisturbed succession

△ competitive exclusion

— disturbed succession (After Grigg 1983)

diversity may eventually decline as the more successful competitors dominate (competitive exclusion), as suggested by the undisturbed pathway (Fig. 25). If the reef is again affected by a severe disturbance (the disturbance model), the coral diversity would be reduced to a low, early-successional level. An intermediate disturbance would lower the diversity to a level where high diversity could be regained after a relatively short period of time and would delay or prevent competitive exclusion. Unlike the Pocillopora reefs in Panama, none of the coral species on the Bellairs reefs are overwhelmingly dominant, therefore a moderate disturbance which preferentially destroys the dominant species would not increase the diversity. The intensity of the hurricane would have to be greater than that of Hurricane Allen to affect species number.

Recolonization of the reef by Agaricia agaricites and the quickly-growing Porites porites suggests that the reef is beginning its recovery and will continue to the climax stage unless interrupted by a hurricane, or by some other factor or disturbance which affects coral recovery.

F) RECOVERY and RECOLONIZATION

Coral recovery, as defined by Pearson (1981), is "the restoration following a disturbance of a coral assemblage to a degree comparable to its original state".

1) Methods of Recovery

Recovery of corals may be attained by asexual regeneration or sexual reproduction. Regeneration involves the regrowth of partially damaged colonies or growth of new colonies from fragments. Fragmentation was an important means of recovery of Acropora cervicornis in the Florida Keys following the passage of Hurricanes Donna and Betsy (Shinn 1976). Survival of Acropora palmata fragments in a storm's aftermath were observed in Florida (Ball et al. 1967, Perkins & Enos 1968), Puerto Rico (Glynn et al. 1965), and Belize (Highsmith et al. 1980) where 46% of A. palmata fragments (average length 37.6 cm) survived following the passage of Hurricane Gerta.

In Belize, small coral fragments (less than 40 cm) were more numerous than large ones which may be indicative of the pre-hurricane coral size distribution and/or reflect a greater susceptibility of small branches or corals to breakage. Fragment size and percent survival are directly related. Fragments larger than 40 cm had 50% survival, while 80% of fragments larger than 75 cm survived (Highsmith et al. 1980).

Deposition of sexually-produced planulae on newly

available substrate (coral recolonization), is especially important where coral mortality was extensive or total in an area. An unusually severe shemal (cold front with strong northerly winds) caused widespread mortality of Acropora along the Qatar Peninsula in the Persian Gulf. Recolonization was achieved by the arrival and survival of planulae from the nearest reefs, 61 km away (Shinn 1976).

2) Recovery Time and Determining Factors

Coral recovery time is variable. The recovery time can range from a minimum of one year to as much as fifty years. The time required for recovery is dependent on several factors : conditioning period, grazers, rubble beds, available colonizing surfaces, community structure of the corals, exposure to wave stress and other disturbances, and the degree of pollution on the reef.

a) Conditioning Period - The conditioning period refers to the time required for the establishment of those algal communities (i.e. crustose coralline algae) which form favorable surfaces for larval settlement, survival and growth (Bak 1976). Pearson (1981) estimates that at least one year is required for the surface to be conditioned.

b) Grazers - Grazing may be either beneficial or detrimental to coral recovery. Fish and echinoids can aid coral recolonization by cropping fleshy frondose and filamentous algae, thereby freeing space for crustose coralline algae and corals (Dart

1972). Although acanthurids and schools of Scarus croicensis avoided grazing on recently settled corals as small as 3 mm (Birkeland 1977), other species of parrotfish and echinoids have been observed to feed on larger corals (Glynn 1973, Randall 1974, Bak & van Eys 1975, Frydl 1977, Neudecker 1977, Glynn et al. 1978).

c) Rubble Beds - Extensive rubble lawns, because of their instability as a substrate, hinder coral recovery (Stephenson et al. 1958, Goreau 1959, Stoddart 1969, 1974).

d) Colonizing Surfaces - Diversity of colonizing surfaces is important. The availability of crevices, vertical faces, undersurfaces, and ridges enhance coral recovery (Lewis 1974a, Schuhmacher 1974, 1977, and Birkeland 1977). On the Bellairs reef, P. porites grows on horizontal substrates, with some colonies in slightly sheltered locations. Agaricia agaricites however was observed on a variety of substrate orientations.

e) Coral Community Structure - The time required for reef recovery is dependent on whether rapid-growth branching corals or slow-growth massive corals are growing on the reef. This factor can be illustrated by comparison of the recovery time of two reefs. Shinn (1976) observed that the Florida Keys reefs recovered from Hurricane Donna (1960) in less than five years, and required two years to recover from Hurricane Betsy (1965). Stoddart (1974) estimated recovery time for Belize reefs is thirty years.

One of the major reasons for the discrepancy in recovery times is the difference in coral communities at the two locations. The Florida Key reefs were predominantly Acropora cervicornis, while the Belize reefs were a mixed assemblage of corals including Acropora palmata, Acropora cervicornis, and massive corals such as Diploria sp., Montastrea sp., and Siderastrea sp. (Stoddart 1963). The Florida reefs recovered rapidly because they were largely composed of Acropora cervicornis which can reproduce by fragmentation and has a rapid growth rate, whereas in Belize, recovery was delayed by the slow growth rates of the massive corals. Reproduction by fragmentation of Montastrea annularis (Jones 1977), Acropora palmata (Bak & Engel 1979, Highsmith *et al.* 1980) and Acropora cervicornis (Gilmore & Hall 1976, Shinn 1976, and Tunnicliffe 1978, 1980) may speed up recovery.

f) Disturbances - Grigg & Maragos (1974) concluded that recolonization of corals on Hawaiian lava flows is dependent on exposure to sea and swell. Recovery time in exposed areas is estimated to be 20 years, and 50 years on sheltered lava flows. Exposed areas are at a lower level of ecological succession than sheltered sites, so recovery time is less.

The frequency of hurricanes will also affect recovery time. Shinn's (1976) estimate of recovery time of the Florida Keys reefs corresponded to the estimated interval between hurricanes in that area, once every six years (Ball, Shinn & Stockman 1967). Stoddart's (1974) estimated

period of recovery in Belize, also agreed with the average hurricane frequency, once every thirty years. The reefs in Guam only suffer minor damage during the frequent typhoons. Randall & Eldredge (1977), and Ogg & Koslow (1978) suggest that the minimal damage and rapid rate of recovery of the reefs is a function of hurricane frequency. Woodhead (Appendix E, in Walsh et al. 1971) on the basis of good coral coverage before the 1967 cyclone at Heron Island, Australia, and the knowledge that the previous major cyclone happened twenty years earlier, determined that complete recovery of corals occurred in twenty years or less.

g) Pollution Levels - Three years after a catastrophic low tide on the Gulf of Eilat Red Sea reef flats, the recovery of a non-polluted control reef and a polluted reef were at distinctly different levels (Loya 1976). The control reef had more coral colonies and species than before the low tides, although Loya estimated that 5 - 6 years would be required for full coral coverage to return. The polluted reef, exposed to chronic oil and mineral pollution, had undergone significantly less recovery in terms of species numbers, percentage coral, and numbers of colonies of the more common species. Both reefs had had a similar proportion of surviving corals (10-20%) following the catastrophic low tides, but recolonizing corals were twenty-three times more abundant on the unpolluted reef. Loya (1975) reasoned that the poor recolonization on the

polluted reef resulted because the pollution damaged the reproductive system of the corals, decreased the viability of the coral larvae, or interfered with the settling of coral planulae by changing some physical properties of the reef flat. Loya (1975,1976), Weiss & Goddard (1977), and Mergner (1981) suggest that although reefs are capable of recovering from natural disturbances, man-made disturbances may have an irreversible effect.

3) Coral Recovery on the Bellairs Reef

Recolonization of Porites porites and Agaricia agaricites are promoting the recovery of the Bellairs northern fringing reef.

Agaricia agaricites was the dominant coral (43% of the corals) in the re-survey, one year following the passage of Hurricane Allen. Its coverage loss was the least (25%) which may partially explain its new dominant position among the corals. Many of the Agaricia colonies encountered along the transect line were small in size (mean length 4.01 cm, mean width 2.95 cm, n = 37). Agaricia agaricites has a diameter growth rate of 2.45 cm/yr (Bak 1976). The dimensions of the colonies encountered were randomly measured in the summer of 1982 after it became apparent that many of the colonies were small in size, and indicative of recolonization.

Although the hurricanes destroyed some of the Agaricia colonies, it may have acted beneficially as a

means of reproduction through fragmentation. The splitting of colonies and settlement of larvae are means by which Agaricia spp. colonizes a substrate. Decay in one part of a colony may lead to the splitting of the colony into several fragments (Lewis 1974). At Bellairs, Agaricia may have been fragmented under pressure from storm waves, or due to bombardment by loose reefal material.

Early observations that Agaricia has a tendency to grow in shaded habitats (Lewis 1974), is partially supported by this study since 44% of the Agaricia colonies were recorded on a vertical substrate.

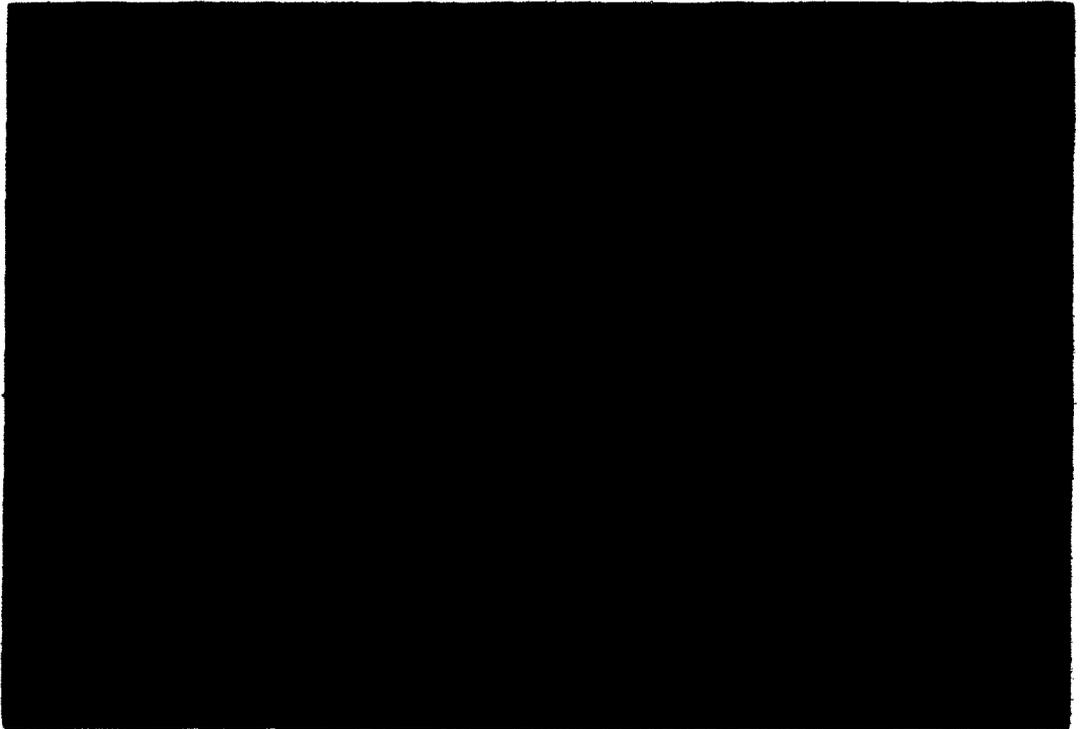
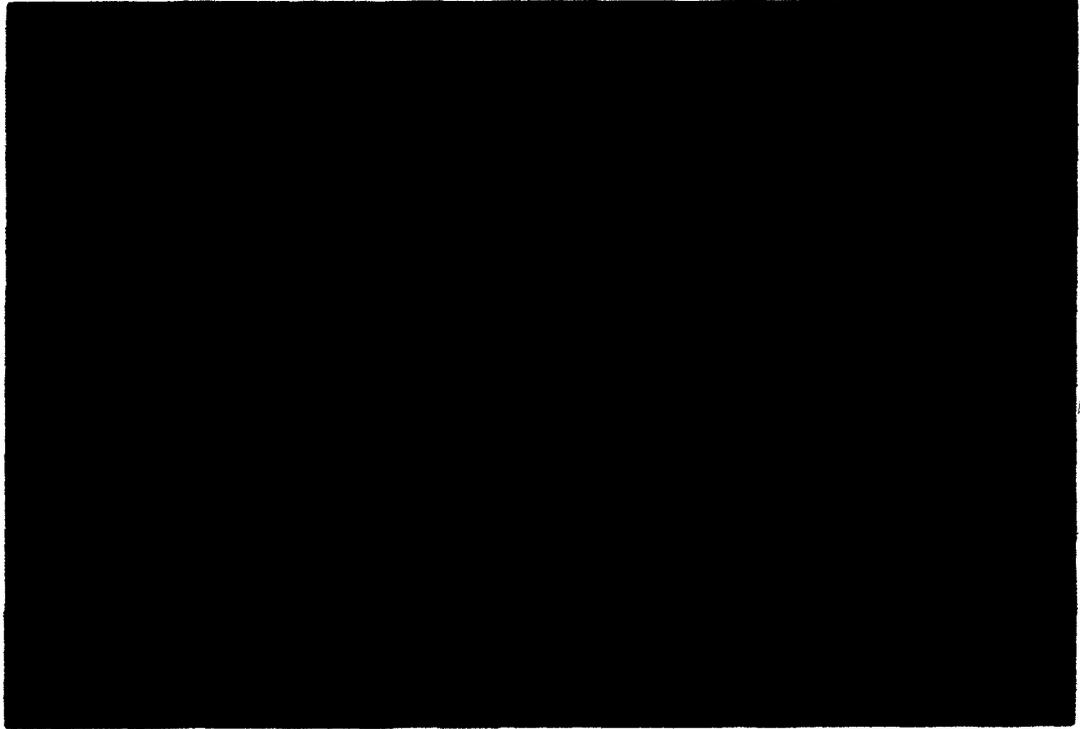
The Porites porites colonies now on the reef constitute only 4% (Table 13) of their pre-hurricane coverage. Photographs taken in the Porites porites zone of the southern Bellairs reef in 1974 and 1982, show the extent of the Porites porites destruction (Fig. 26 and Fig. 27). Similar damage was recorded on the study reef.

Most of the Porites porites colonies now on the northern Bellairs reef, originated after the hurricane. One hundred and seventy-three branches of thirty-three colonies were measured. The mean length of the branches was 4.9 cm (standard deviation 0.7 cm). Since Porites porites grows at a rate of 3.6 cm/yr in Barbados as reported by Lewis et al. (1968), and the measurements were done two years after the hurricane, the branches of Porites porites 4.9 cm long represent, on average,



Fig. 26. Porites porites zone before (1974)
Hurricane Allen.

Fig. 27. Porites porites zone after (1981)*
Hurricane Allen.



colonies that are less than 2 years old, and therefore most have grown after the hurricane (Figs. 28, 29. and 30).

The following factors are relevant to the recovery of the Bellairs reef :

a) Conditioning Period - The time required for conditioning of the substrate was probably minimal (i.e less than a year), because algal and coralline algal communities were well-established in most areas of the reef.

b) Grazers - The density of Diadema antillarum increased following the hurricanes (Table 15). Post-hurricane density was $24.6 \text{ Diadema antillarum} / \text{m}^2 \pm 6.4$ compared to a pre-hurricane density of $17.3 \text{ Diadema antillarum} / \text{m}^2 \pm 6.4$ (Hawkins 1979). The difference in means is significant, ($t = 17.44, P < 0.001$). Identical methods were used for data collection. A reduction in the numbers, due to over-fishing, of Queen Triggerfish may be partly responsible for the increased density of Diadema.

Such an increase in density would likely restrict filamentous algal growth, freeing more substrate for coral colonization. The importance of Diadema antillarum in cropping and maintaining the filamentous algae population at a minimum was recently proven by the widespread mortality of Diadema antillarum in the Caribbean. In October 1983, D. antillarum were washed up onto the Barbados beaches in large numbers. Dr. J. B. Lewis, in

Fig. 28. Newly-colonized Porites porites colony
on the study reef.

Fig. 29. Porites porites colonies at various
stages of growth on the northern
Bellairs fringing reef.

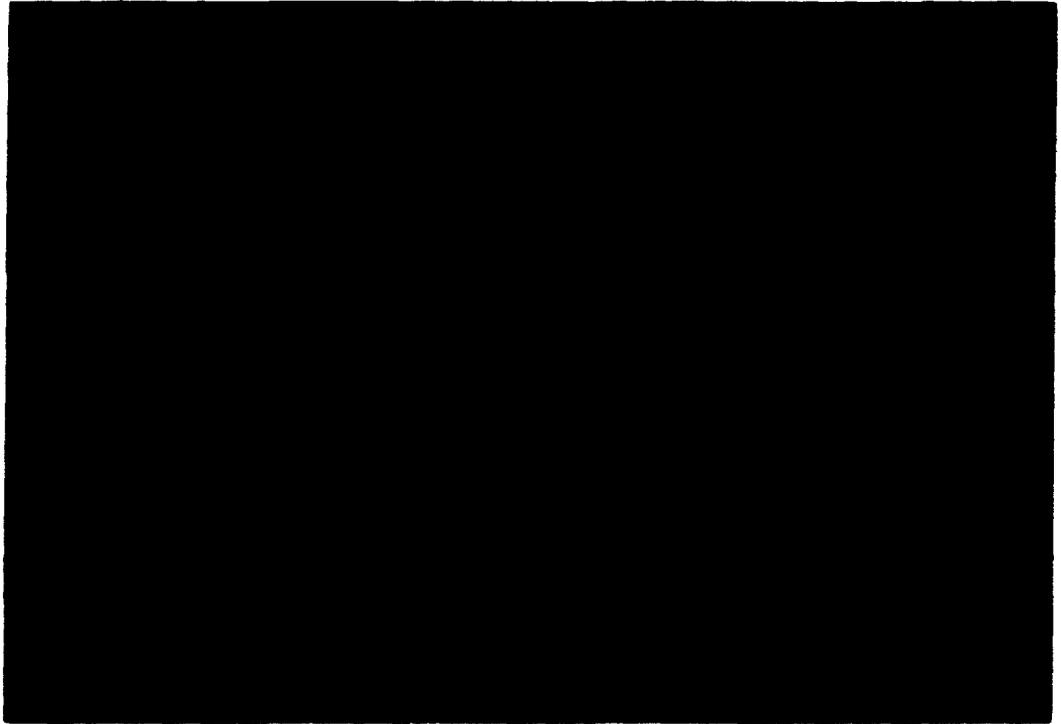




Fig. 30. Protected Porites porites growth adjacent
to sand channel.

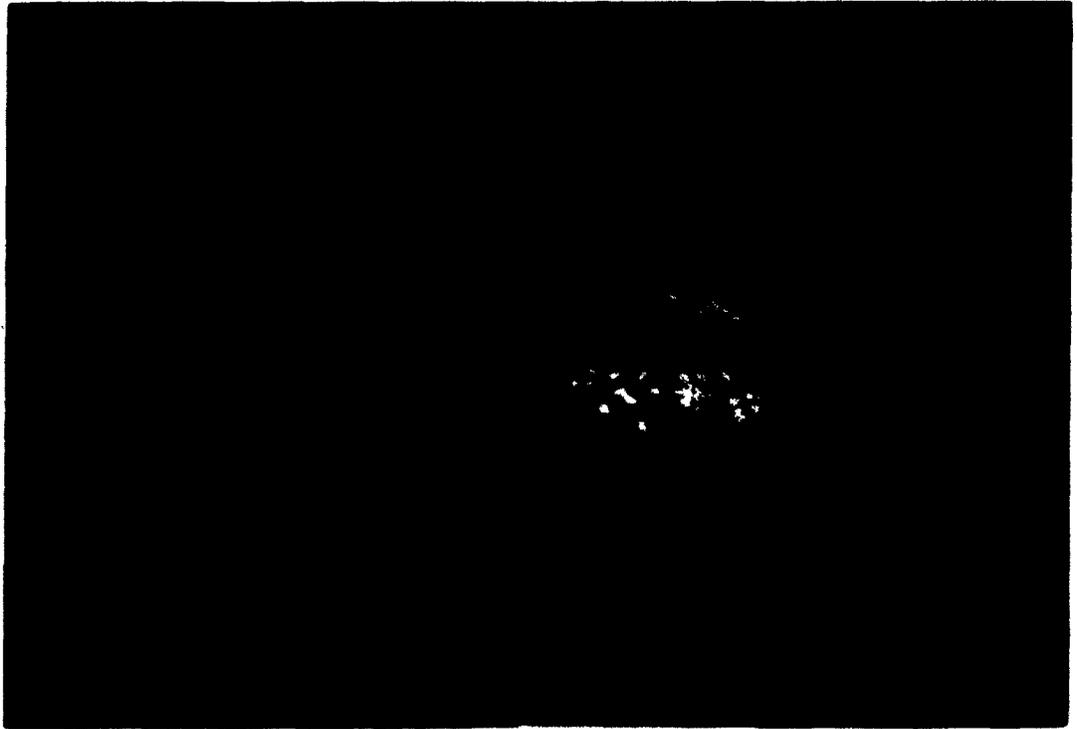


TABLE 15 . Diadema antillarum DENSITY

<u>TRANSECT NUMBER</u>	<u>NUMBER OF <u>Diadema</u>/m²</u>	<u>DATE RECORDED</u>
I	24.3	Dec. 27, 1981
II	22.3	Jan. 1, 1982
III	38.2	Sept. 28, 1982
IV	18.2	Sept. 28, 1982
V	20.9	Jan. 1, 1982
V	20.8	Sept. 17, 1982
VI	23.6	Sept. 27, 1982

Average density of D. antillarum = 24.6 / m² +6.4

December 1983, estimated the Diadema antillarum population at 0.3 - 0.4 Diadema antillarum / m² . The Bellairs reef is now covered with filamentous algae except in small areas where aggregations of Diadema antillarum are present. The cause of the mortality throughout the Caribbean is unknown. Preliminary studies of the phenomenon have begun in Barbados and a study of its effect on coral recolonization will begin this summer.

c) Rubble Beds - Rubble beds have probably not slowed coral recovery on the Bellairs Reef. Large patches of rubble accumulate in topographic lows such as the sandy groove areas (Fig. 31). In this type of environment, the rubble is a more suitable substrate than the surrounding sand. Rubble which accumulates on the reef tops and sides is cemented by sponges and coralline algae, and forms a stable substrate.

d) Colonizing Surfaces - Except for the levelling of Porites porites (Fig. 32), reef morphology has remained essentially unchanged. Crevices, vertical faces, under-surfaces, and ridges are abundant therefore availability of colonizing surfaces is not a limiting factor on the study reef (Fig. 33).

e) Community Structure - The Bellairs northern fringing reef is composed of a diverse coral community including massive, branching and encrusting growth forms of corals (Fig. 34). Recovery of the reef will likely require 20 - 25 years due to the presence of slow-growth corals which only reproduce sexually.

Fig. 31. Rubble bed, crossed by transect line.

9

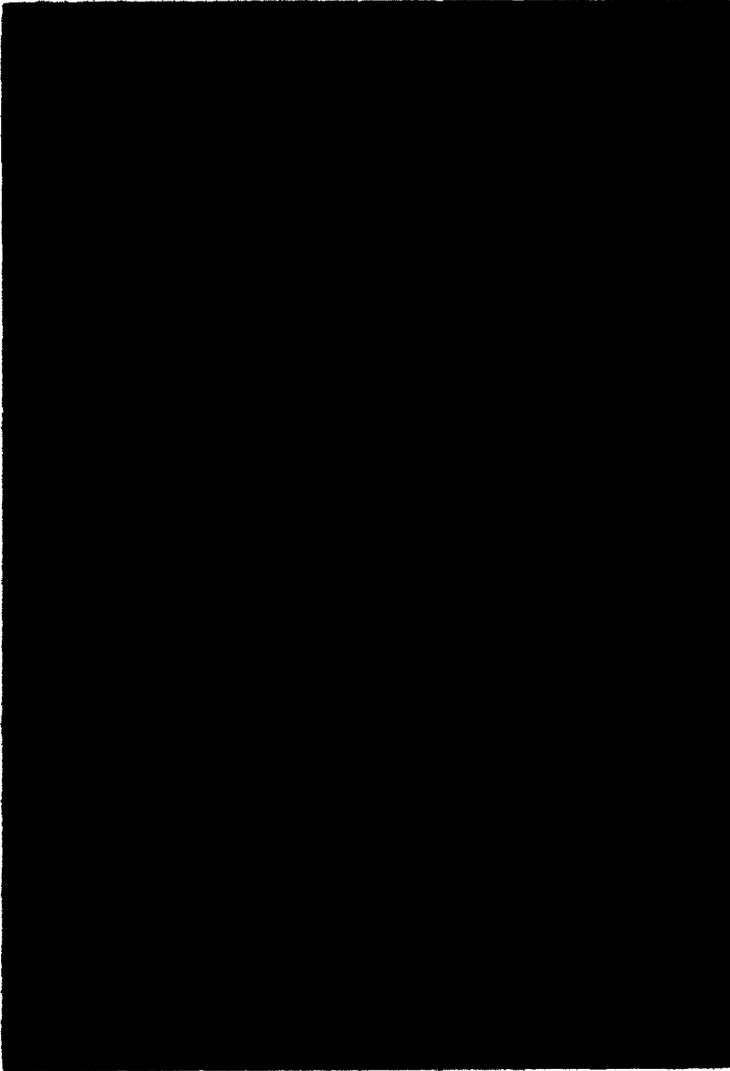


Fig. 32. View along a spur of the study reef prior to levelling of Porites porites.

Fig. 33. Diversity of surfaces for recolonization on northern Bellairs fringing reef.



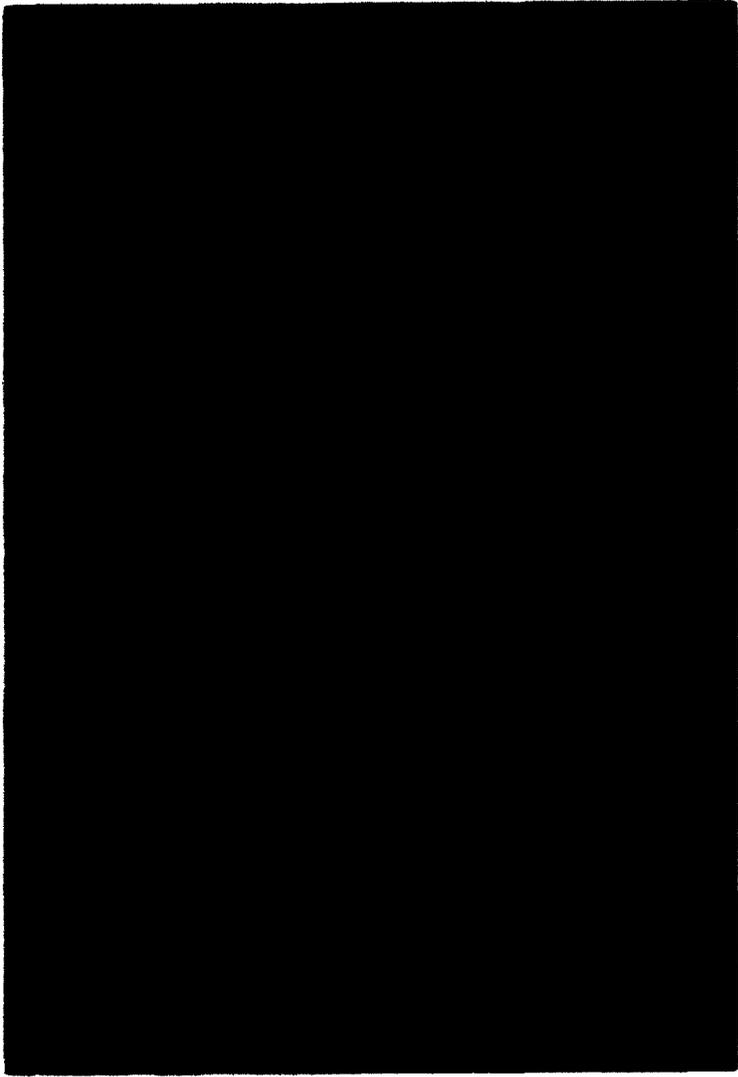
f) Disturbances - The average interval between hurricanes in Barbados in this century is 20 - 25 years, but another hurricane could affect recovery at any time. Other disturbances such as the widespread mortality of Diadema antillarum may delay recovery.

g) Pollution Levels - Increasing levels of pollution in the waters around Barbados may adversely affect coral recovery. If pollution from urban and agricultural sources reaches critical levels, then full recovery of the reef could be retarded or prevented altogether. Pollution effects on Barbados reefs are under investigation (T. Tomascik, in progress).

Of all the factors which could affect coral recovery on the Bellairs reef, the most significant are the density of grazers (Diadema antillarum), the diversity of the coral community, disturbances (biological and physical), and pollution levels.

Fig. 34. Diverse coral community on the northern
Bellairs reef in 1974.

C



CHAPTER 8

GEOLOGICAL RECORD OF HURRICANES

GEOLOGICAL RECORD OF HURRICANES

A) HOLOCENE STORM DEPOSITS

Recently more storm deposits are being recognized in the sedimentary record, but many Holocene hurricane deposits, especially those of reefs and carbonate sedimentation areas do not have much potential for preservation in the rocks.

Various types of storm deposits have been reported following hurricanes. On the Great Barrier Reef, Cyclone David (January 1976) caused the movement of sediments greater than -1 phi (2 mm) to the outer reef top, and the removal of sediments less than 3 phi (0.125 mm). The latter group of sediments were redeposited in the inner reef areas (Flood & Jell 1977).

Hurricane Donna passed over the Florida Keys in September 1960. Five years later the same area was affected by Hurricane Betsy. The major effect of Hurricane Donna was extensive supratidal sedimentation. Boulder-sized rubble, resulting from storm-breakage of corals, was transported to the leeward sides of the reefs. Cross-bedded spillover lobes were formed by the storm currents. The scale of the cross-bed sets (0.5 - 1.5 m thick) is comparable to the examples found in ancient marine sand sequences (Ball et al. 1966). Muddy sediment mounds were not eroded by the storm waves or currents, suggesting that ancient mud mounds were storm resistant.

Hurricane Betsy's effect was the erosion and recycling of sediments in the subtidal environment and non-deposition in the supratidal environment (Perkins & Enos 1968). Perkins & Enos suggested that the sediments deposited by Hurricane Donna would be recorded in the sedimentary record, but little or no evidence of Hurricane Betsy would be recorded.

Graded sediments, in large bays adjacent to the coast of S.W. Florida, were deposited when hurricanes passed over the area. The vertical sequence includes a basal shell lag, with fragments one or more centimetres in length, overlain by quartz sand. The sand-sized quartz grains were only observed following major storms (Perlmutter 1978, 1979), and were not observed during normal conditions or winter storms. The quartz sand fines upward to sandy-silt and silt. These finer grains were deposited during waning post-storm stages (Perlmutter 1978, 1979).

Graded sediment sequences, 6 cm thick, deposited off the central Texas coast in 1961 by Hurricane Carla were observed by Hayes (1967). Twenty years later, J. McGowen (oral communication to R.H. Dott, Jr., 1981), found that the graded layers had been so thoroughly bioturbated, that they were no longer recognizable.

Three factors determine the preservation of hurricane effects in the sedimentary record: 1) the volume of the deposits (which is a reflection of process intensity), 2) the frequency of the events, and 3) the degree of

modification of the deposits by biological activity, winnowing, and removal by scour (Dott 1983). Supratidal sedimentation is preserved in the sedimentary record because once the sediments are deposited above the mean high tide level, they are not susceptible to marine reworking. Few organisms can withstand the exposure and fluctuating salinity in the supratidal environment, therefore there is minimal destruction of primary sedimentary features (Shinn, 1983). Sediments deposited within the intertidal zone and above normal wave base, have the smallest probability of preservation, as they are exposed to constant reworking by wave action and by burrowing organisms. Sedimentary structures formed during storms below wave base may be preserved if they are not heavily bioturbated.

In the Pleistocene reef complex of Barbados, layers of Acropora palmata are interbedded in the Acropora cervicornis zone. James et al. (1977) suggest this may be due to pruning of the seaward Acropora palmata zone by hurricanes, followed by deposition leeward in the Acropora cervicornis zone.

B) ANCIENT STORM DEPOSITS

Many sedimentary structures and lithologic features in the sedimentary record are attributed to hurricanes (Table 16) and storms. These structures and features include : truncated erosional surfaces, intraformational

TABLE 16. EXAMPLES OF ANCIENT HURRICANE DEPOSITS (from Marsaglia & Klein 1983)

AGE	EXAMPLE	REFERENCE
Ordovician	Ellis Bay Fm. Anticosti Is. Canada	Dixon (1970)
	Reedsville Fm. Appalachians U.S.A	Thompson (1972)
	New Market Ls. MD, U.S.A	Matter (1967)
	Juniata & Sequatchie Fms. Appalachians U.S.A.	Thompson (1970)
	Martinsburg Fm. VA, U.S.A.	Kreisa (1979, 1981)
	Eden Shale IN, KY, OH, U.S.A.	Anstey & Fowler (1969)
	Cincinnati Series OH, U.S.A.	Kreisa <u>et al.</u> (1981)
Silurian	Rochester Fm. Ont., Canada	Thusu (1972)
	Keefer Quartzite PA, U.S.A	Goldring & Bridges (1973)
Devonian	Baggy Fm. England, U.K.	Goldring & Bridges (1973)
	Pilton Fm. England, U.K.	Goldring & Bridges (1973)
	Eiffelian Germany	Goldring & Bridges (1973)
	Arisaig Grp. N.S., Canada	Cant (1980)
Mississippian	Visean Morocco	Kelling & Mullin (1975)
Jurassic	Upper Jurassic Morocco	Ager (1974)

conglomerates and intraclasts, bioturbation structures (the nature and periodicity of the structures indicating fair-weather regimes between storm events), hummocky cross-stratification, shell lags, mixed faunas, parallel laminae, and graded bedding (Kreisa 1981). The well-described storm deposits are primarily in clastic rocks.

A storm or hurricane origin for hummocky cross-stratification has recently been suggested (Duke 1982, Harms et al. 1975). The structure is characterized by sets of beds with an erosional lower contact of low relief, laminae above the erosional base which parallel it, and systematic thickening and thinning of laminae within each set of beds (Harms et al. 1975). Hummocky cross-stratification has been attributed to storm-generated oscillatory and three-dimensional vortex wave action (Dott & Bourgeois 1982, Walker 1982, Harms et al. 1982). This bedform has been observed during flume experiments (Carstens et al. 1969, Harms et al. 1982), but has not been observed to form in sands of Holocene subtidal regimes (Marsaglia & Klein 1983).

Dott & Bourgeois (1982) described a hummocky sequence from the Eocene Coaledo Formation of Oregon. The sharp base of the storm sequence is overlain by hummocky-stratified sand that grades upward into parallel-bedded sand. Above this lies a micro cross-laminated zone capped by a mudstone which may be burrowed (Fig. 35).

The Moosebar and Gates formations (Cretaceous) of northeastern British Columbia contain hummocky

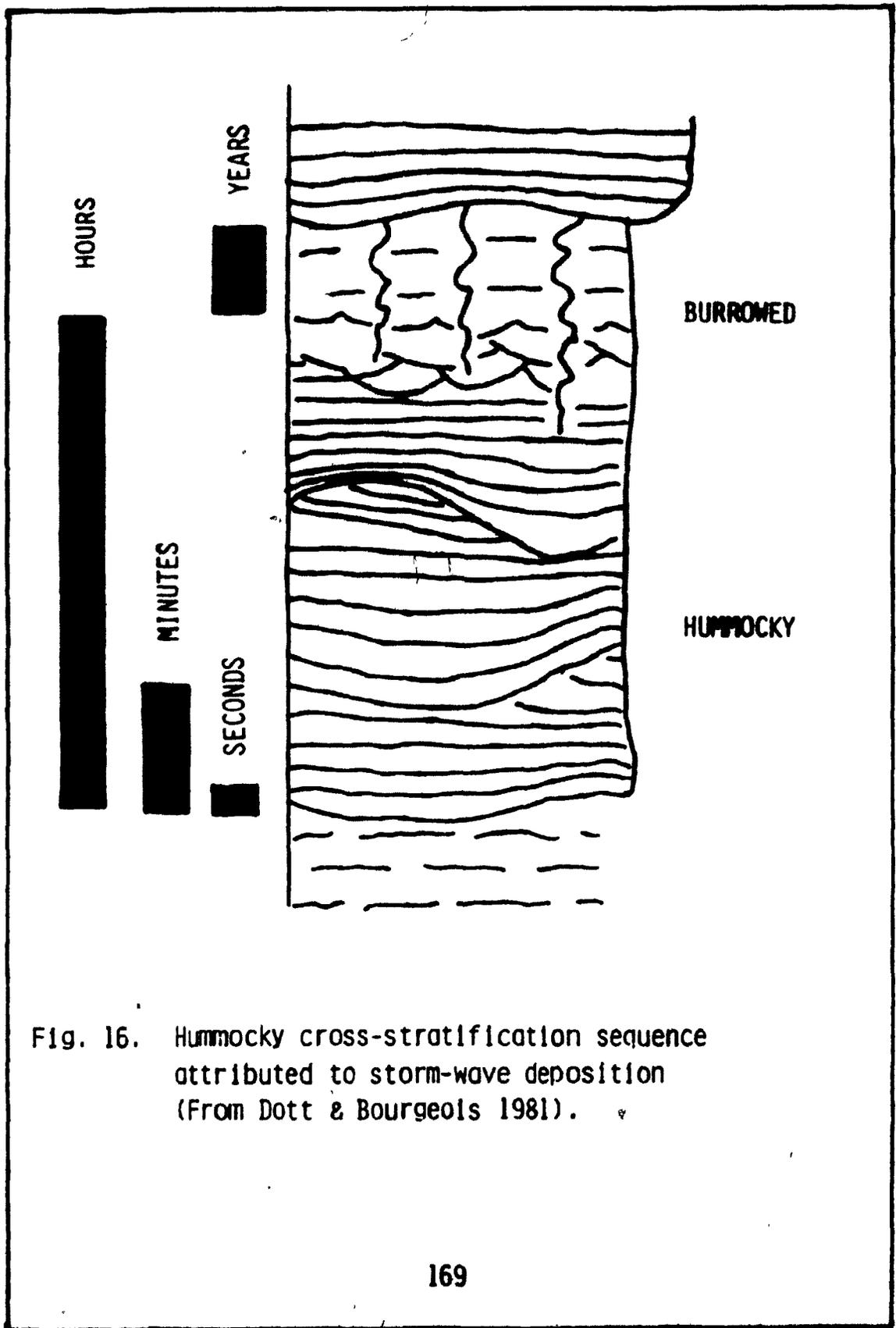


Fig. 16. Hummocky cross-stratification sequence attributed to storm-wave deposition (From Dott & Bourgeois 1981).

stratification (Leckie & Walker 1982). The overall progradational coarsening-upward trend is postulated to be due to a shoaling history of a storm-dominated shelf sequence into a coastal and non-marine sequence. Other sequences containing storm-produced hummocky cross-stratification include the Fernie-Kootenay transition (Hamblin & Walker 1979), the Martinsburg Formation (Kreisa 1981), and the Campito Formation (Mount 1982).

Cambrian conglomerates in Wisconsin are evidence of storm activity. Layers containing rounded boulders of red quartzite up to 1.5 m in diameter, are interlayered with cross-bedded marine sandstones. The sources of these boulders were quartzite islands in the Late Cambrian Sea. Rounding and distribution of the boulders was attributed to storm waves of estimated heights of 6 - 8 m (Dott 1974). The typical Cambrian sediments in Wisconsin are marine, cross-bedded, medium-grained sandstones. Dott believes these sandstones were deposited during storms, because he estimated that a current velocity of approximately 100 cm/s was required for formation of the bedform. Dott postulated this velocity was twice the velocity of normal currents, and was attained only during storms. The upper layers of the sandstone are heavily bioturbated. The tops of the burrowed sequences are sharply truncated, indicating the episodic nature of sand transport and deposition. Dott (1974) suggests that submarine dunes were active only during storms, and during the longer fair-weather intervals the organisms

extensively burrowed the sediments. The time required for deposition of the various layers within a sequence, ranges from a few seconds to several years (Fig. 28).

Vertical sequences of storm deposits may be fining-upwards as in the Martinsburg Formation (Kreisa 1981), or coarsening-upwards as in the Moosebar and Gates formations (Leckie & Walker 1982).

Alternating fossil-rich layers and unfossiliferous layers indicate episodic deposition which may be storm-produced. An example is found in the Lower Emsian La Vid shales of N.W. Spain (Stel 1975). The shales are unfossiliferous, except for the presence of some microplankton (Cramer 1964). Stel (1975) suggests that hurricanes altered the water circulation in the depositional area, and conditions changed from anaerobic to aerobic. A pioneer fauna established itself on rubble brought in by the storms. Eventually abiotic conditions returned and shales were again deposited.

C) SEDIMENTARY RECORD OF HURRICANE ALLEN

Storms and hurricanes appear to have been important agents in the deposition of sedimentary rocks, but the impact of Hurricane Allen on the northern Bellairs fringing reef may not be indelibly recorded. Rubble deposited on the reef will either be broken down into sand and silt-sized particles, or will be cemented to form a part of the reef structure. Sand and sedimentary

structures which formed immediately after the hurricane have been reworked, therefore neither cross-laminations, nor graded bedding will be preserved for the sedimentary record. No significant supratidal sedimentation occurred. Storm deposits in the deeper water seaward of the fringing reef may be preserved, if not greatly affected by bioturbation.

CHAPTER 9

CONCLUSIONS

CONCLUSIONS

Hurricane Allen's major effects on the northern Bellairs fringing reef include : 1) a severe reduction in the coverage of branching corals, especially Porites porites, 2) a decrease in coral diversity, and 3) on-reef transport of Acropora cervicornis and Madracis mirabilis rubble, and off-reef transport of Porites porites rubble. An overall increase in non-living substrate coverage (sand, rock, and rubble) was at the expense of the living substrate coverage (primarily the corals). The corals, Millepora sp., and coralline red algae collectively represented 67% of the reef coverage in the original survey. By the time of the re-survey, the non-living substrates had decreased to 38% of the reef coverage.

Recovery of the corals is indicated by the new colonies of Porites porites and Agaricia agaricites. The time required for recovery cannot be predicted due to the multitude of factors involved.

The effects of Hurricane Allen will probably not be preserved in the sedimentary record except perhaps in deeper-water deposits. Hurricane deposits on the fringing reef are subjected to bioturbation and reworking by the waves during normal conditions and during occasional winter storms.

Further work suggested by this study includes : 1) a complete study similar to the one done by Stearn et al.

(1977) to estimate the present calcium carbonate budget and 2) a re-survey along the 6 transect lines every 5 years to monitor the progress of the recovery of the reef. The changes in diversity values of the northern Bellairs fringing reef through time, could then be plotted.

ACKNOWLEDGEMENTS

I wish to express my deepest gratitude to Dr. Colin W. Stearn for his encouragement, support, and guidance throughout this study. Comments made during the writing of this thesis were invaluable.

I am also grateful to Dr. Ron Doig for his assistance with the statistics, to Dr. Eric W. Mountjoy for his critical review of the manuscript, and to Mr. Richard Yates for his advice and help with the diagrams and photographs. Thanks are extended to the former director of the Bellairs Research Institute of McGill University, Dr. Finn Sander, for his kindness and hospitality during the duration of my field work in Barbados.

A special thanks to Tom Tomascik for providing diving assistance, and for sharing his knowledge of the Bellairs Research Institute, Barbados, and its coral reefs.

Financial assistance was provided by Dr. Colin W. Stearn through Natural Science and Engineering Research Council grants, and through a McGill Summer Research Fellowship to the author for 1982.

REFERENCES

- Ager, D.V., 1974. Storm deposits in the Jurassic of the Moroccan High Atlas. *Paleogeography, paleo-climatology, and paleocology* 15: 83-93.
- Ager, D.V., 1980. *The Nature of the Stratigraphic Record* (2nd ed.). John Wiley and Sons, New York. 122 p.
- Anstey, R.L., and Fowler, M., 1969. Lithostratigraphy and depositional environment of the Eden Shale (Ordovician) in the Tri-state area of Indiana, Kentucky, and Ohio. *Journal of Geology* 77: 668-682.
- Baines, G.B., and McLean, R.F., 1976. Sequential studies of hurricane deposit evolution at Funafuti Atoll. *Marine Geology* 21: M1-M8.
- Bak, R.P.M., 1974. Available light and other factors influencing growth of stony corals through the year in Curacao. *Proceedings of the Second International Coral Reef Symposium* 2: 229-233.
- Bak, R.P.M., 1976. The growth of coral colonies and the importance of crustose coralline algae and burrowing sponges in relation with carbonate accumulation. *Netherlands Journal of Sea Research* 10:285-337.
- Bak, R.P.M., and Engel, M.S., 1979. Distribution, abundance and survival of juvenile hermatypic corals (*Scleractinia*) and the importance of life history strategies in the parent coral community. *Marine Biology* 54: 341-352.
- Bak, R.P.M., Luckhurst, B.E., 1980. Constancy and change in coral reef habitats along depth gradients at Curacao. *Oecologia* 47: 145-155.
- Bak, R.P.M., and vanEys, G., 1975. Predation of the sea urchin *Diadema antillarum* Philippi on living coral. *Oecologia* 20:111-115.
- Baker, P.A., and Weber, J.N., 1975. Coral growth rate: variation with depth. *Earth and Planetary Science Letters* 27: 57-61.
- Ball, M.M., Shinn, E.A., and Stockman, K.W., 1967. The geological effects of hurricane Donna in south Florida. *Journal of Geology* 75: 583-597.

- Barry, R.G., and Chorley, R.J., 1970. Atmosphere, weather and climate. Holt, Rinehart & Winston. New York. 82 p.
- Beer, T., 1983. Environmental Oceanography. An introduction to the behavior of coastal waters. Pergamon Press. Oxford. 262 p.
- Bender, M.L., Taylor, F.T., and Matthews, R.K., 1972. Helium-uranium dating of corals from Middle Pleistocene Barbados reef tracts. Quaternary Research 3: 142-146.
- Bird, J.B., Richards, A., and Wong, P.P., 1979. Coastal sub-systems of Western Barbados, West Indies. Geography Annales 61A (3-4): 221-236.
- Birkeland, C., 1977. The importance of rate of biomass accumulation in early successional stages of benthic communities to the survival of coral recruits. Proceedings of the Third International Coral Reef Symposium 1: 15-21. University of Miami.
- Blumenstock, D.I., 1958. Typhoon effects at Jaluit Atoll in the Marshall Islands. Nature 182: 1267-1269.
- Blumenstock, D.I., Fosberg, F.R., Johnson, C.G., 1961. The re-survey of the typhoon effects on Jaluit Atoll in the Marshall Islands. Nature 189: 618-620.
- Bourrouilh-Le, J.F.G., 1982. Hurricane trails: supratidal mud bodies on the tidal flats of western Andros, Bahamas. Stromatolite Newsletter 9: 17-18.
- Bretschneider, C.L., Asce, A.M., 1959. Hurricane design-wave practices. Transactions of the American Society of Civil Engineers 124(2965): 39-62.
- Buddemeier, R.W., 1974. Environmental controls over annual and lunar monthly cycles in hermatypic coral calcification. Proceedings of the Second International Coral Reef Symposium 2: 259-267.
- Buddemeier, R.W., and Kinzie, R.A., III., 1975. The chronometric reliability of contemporary corals. In: Rosenberg, G.D., and Runcorn, S.K., (eds.). Growth rhythms and the history of the earth's rotation, John Wiley and Sons, London. p. 135-147.
- Buddemeier, R.W., Maragos, J.E., and Knutson, P.W., 1974. Radiographic studies of reef coral exoskeletons: rates and patterns of coral growth. Journal of Experimental Marine Biology and Ecology 14: 179-

199.

- Bull, G.D., 1982. Scleractinian coral communities of two inshore high island fringing reefs at Magnetic Island, North Queensland. *Marine Ecology Progress Series* 7: 267-272.
- Carstens, M.R., Neilson, F.M., and Altinbilek, H.D., 1969. Bed forms generated in the laboratory under an oscillatory flow: analytical and experimental study. U.S. Coastal Engineering Research Center Technical Memoir 29. 39 p.
- Chamberlain, J.A., Jr., 1978. Mechanical properties of coral skeleton: compressive strength and its adaptive significance. *Paleobiology* 4: 419-435.
- Chave, K.E., 1960. Carbonate skeletons to limestone: problems. *New York Academy of Science Transactions*, Series 2, 23:14-24.
- Chave, K.E., 1964. Skeletal durability and preservation. In: Imbrie, J., and Newell, N., (eds.). *Approaches to Paleo-ecology*. John Wiley & Sons, New York. p. 377-387.
- Collins, J.I., 1976. Wave modelling and hydrodynamics. *Society of Economic Paleontologists and Mineralogists Special Publication* 24: 54-68.
- Connell, J.H., 1978. Diversity in tropical rain forests and coral reefs. *Science* 199: 1302-1310.
- Cramer, F.H., 1964. Microplankton from three Paleozoic formations in the province of Leon (NW-Spain). *Leidse Geologische Mededelingen* 30: 155-361.
- Daña, T.F., 1979. Species-numbers relationships in an assemblage of reef-building corals: McLean Island, Phoenix Islands. *Atoll Research Bulletin* 228: 1-27 and appendix.
- Dart, J.K.G., 1972. Echinoids, algal lawn, and coral colonization. *Nature* 239: 50-51.
- Deane, C., 1974. Wave climate in the eastern Caribbean. *Proceedings of the International Symposium on Ocean Wave Measurement and Analysis*. Vol. 1: 214-232.
- Dixon, O.A., 1970. Nautiloids and current ripples as paleo-current indicators in Upper Ordovician limestones, Anticosti Island, Canada. *Journal of Sedimentary Petrology* 40: 682-687.

- Dodge, R.E., 1978. The natural growth records of reef building corals. PhD thesis. Yale University. New Haven. 237 p.
- Dodge, R.E., Logan, A., and Antonius, A., 1982. Quantitative reef assessment studies in Bermuda : a comparison of methods and preliminary results. *Bulletin of Marine Sciences* 32(3): 745-760.
- Dodge, R.E., and Vaisnys, J.R., 1975. Hermatypic coral growth banding as environmental recorder. *Nature* 258: 706-708.
- Dodge, R.E., and Vaisnys, J.R., 1977. Coral populations and growth patterns: responses to sedimentation and turbidity associated with dredging. *Journal of Marine Research* 35(4): 715-730.
- Dollar, S.J., 1982. Wave stress and coral community structure in Hawaii. *Coral Reefs* 1: 71-81.
- Donn, W.L., and McGuinness, W.T., 1959. Barbados storm swell. *Journal of Geophysical Research* 64: 2341-2349.
- Dott, R.H., Jr., 1974. Cambrian tropical storm waves in Wisconsin. *Geology* 2: 243-246.
- Dott, R.H., Jr., 1983. Episodic sedimentation - How normal is average? How rare is rare? Does it matter? *Journal of Sedimentary Petrology* 53: 5-23.
- Dott, R.H., and Bourgeois, J., 1981. Sedimentary rocks hummocky cross-stratification. In: McGraw Hill Yearbook of Science and Technology. p. 349-351.
- Dott, R.H., and Bourgeois, J., 1982. Hummocky stratification: significance of its variable bedding sequences. *Geological Society of America Bulletin* 93: 663-680.
- Duke, W.L., 1982. Hummocky cross-stratification, tropical hurricanes, and intense winter storms. *Geological Society of America Abstract* 14(7): 478.
- Dunn, G.E., and Miller, B.I., 1964. Atlantic Hurricanes. Louisiana State University Press. 377 p.
- Eagleman, J.R., 1983. Severe and Unusual Weather. Van Nostrand Reinhold Co., New York. 372 p.
- Flood, P.G., and Jell, J.S., 1977. The effect of cyclone "David" (January 1976) on the sediment

- distribution pattern on Heron Reef, Great Barrier Reef, Australia. Proceedings of the Third International Coral Reef Symposium 2: 119-125.
- Folk, R.L., and Robles, R., 1964. Carbonate sands of Isla Perez, Alacran Reef complex, Yucatan. Journal of Geology 72: 255-292.
- Frydl, P., 1977. The geological effect of grazing by parrotfish (Scaridae) on a Barbados coral reef. Msc.thesis. McGill University, Montreal. 136 p.
- Gilmore, M.D., and Hall, B.R., 1976. Life history, growth habits, and constructional roles of Acropora cervicornis in the patch reef environment. Journal of Sedimentary Petrology 46: 519-522.
- Glynn, P.W., 1973. Acanthaster : effect on coral reef growth in Panama. Science 180: 504- 506.
- Glynn, P.W., 1977. Coral growth in upwelling and non-upwelling areas of the Pacific coast of Panama. Journal of Marine Research 35: 567-585.
- Glynn, P.W., Almodovar, L.R., and Gonzalez, J.G., 1965. Effects of hurricane Edith on marine life in La Parguera, Puerto Rico. Caribbean Journal of Science 4: 335-345.
- Glynn, P.W., and Wellington, G.M., 1980. An ecological study of corals and coral reefs in the Galapagos Archipelago. Smithsonian Contribution to Zoology (in Prep).
- Glynn, P.W., Wellington, G.M., Birkeland, C., 1978. Coral reef growth in the Galapagos: limitation by sea urchins. Science 203: 47-49.
- Goldring, R., and Bridges, P.H., 1973. Sublittoral sheet sandstones. Journal of Sedimentary Petrology 43: 736- 747.
- Goreau, T.F., 1959. The ecology of Jamaican coral reefs. I. Species composition and zonation. Ecology 40: 67-90.
- Goreau, T.F., 1964. Mass expulsion of zooxanthellae from Jamaican reef communities after Hurricane Flora. Science 145: 383-386
- Grigg, R.W., 1983. Community structure, succession and development of coral reefs in Hawaii. Marine Ecology, Progress Series 11: 1-14.

- Grigg, R.W., and Maragos, J.E., 1974. Recolonization of hermatypic corals on submerged lava flows in Hawaii. *Ecology* 55: 387-395.
- Gygi, R.A., 1969. An estimate of the erosional effect of *Sparisoma viride* (Bonnaterre), the green parrotfish, on some Bermuda reefs. In: Ginsburg, R.N., and Garret, P., (eds.), Seminar on Organism-Sediment Interrelationships. Bermuda Biological Station Special Publication 2: 137-143.
- Hamblin, A.P., and Walker, R.G., 1979. Storm-dominated shallow marine deposits: the Fernie - Kootenay (Jurassic) transition, southern Rocky Mountains. *Canadian Journal of Earth Sciences* 16: 1673-1690.
- Harms, J.C., Southard, J.B., Spearing, D.R., and Walker, R.G., 1975. Depositional environments as interpreted from primary sedimentary structures and stratification sequences. *Society of Economic Paleontologists and Mineralogists Short Course Notes* 2. 161 p.
- Harms, J.C., Southard, J.B., Spearing, D.R., and Walker, R.G., 1982. Structures and sequences in clastic rocks. *Society of Economic Paleontologists and Mineralogists Short Course Notes* 9. 249 p.
- Hayes, M.O., 1967. Hurricanes as geological agents, South Texas coast. *American Association of Petroleum Geologists Bulletin* 51(6): 937-958.
- Hebert, P.J., 1980. A "normal" year for hurricanes. *Weatherwise* 33: 26-30.
- Hernandez-Avila, M.L., and Roberts, H.H., 1974. Form-process on island coasts Louisiana State University, Coastal Studies Institute Technical Report 166. 76 p.
- Hernandez-Avila, M.L., Roberts, H.H., and Rouse, L.J., 1977. Hurricane-generated waves and coastal boulder rampart formation. *Proceedings of the Third International Coral Reef Symposium* 2:71-78.
- Hightsmith, R.C., 1979. Coral growth rates and environmental control of density banding. *Journal of Experimental Marine Biology and Ecology* 37: 105-125.
- Hightsmith, R.C., Riggs, A.C., and D'Antonio, C.M., 1980. Survival of hurricane-generated coral fragments and a disturbance model of reef calcification / growth rates. *Oecologia* 46: 322-329.
- Hubbard, D.K., Sadd, J.L., and Roberts, H.H., 1982. The role of physical processes in controlling sediment transport patterns on the insular shelf of St.

Croix, US Virgin Islands. Proceedings of the Fourth International Coral Reef Symposium 1: 399-404.

- Hudson, J.H., 1981. Response of Montastrea annularis to environmental change in the Florida Keys. Proceedings of the Fourth International Coral Reef Symposium 2: 233-240.
- Hudson, J.H., 1981. Growth rates in Montastrea annularis: a record of environmental change in Key Largo coral reef marine sanctuary, Florida. Bulletin of Marine Science 31(2): 444-459.
- Hudson, J.H., Shinn, E.A., Halley, R.B., and Lidz, B., 1976. Sclerochronology: a tool for interpreting past environments. Geology 4: 361-364.
- Hunter, I.G., 1977. Carbonate sediments of the Bellairs fringing reef, Barbados, West Indies. MSc. thesis. McGill University. 83 p.
- Hustons, M., 1979. A general hypothesis of species diversity. American Naturalist 113: 81-101.
- Hutcheson, K., 1970. A test for comparing diversities based on the Shannon formula. Journal of Theoretical Biology 29: 151-154.
- Jaap, W.C., 1979. Observations on zooxanthellae expulsion at Middle Sambo reef, Florida Keys. Bulletin of Marine Science 29 (3): 414-422.
- James, N.P., Mountjoy, E.W., and Omura, A., 1971. An early Wisconsin reef terrace at Barbados, West Indies, and its climatic implications. Geological Society of America Bulletin 82: 2011-2018.
- James, N.P., Stearn, C.W., and Harrison, R.S., 1977. Field Guidebook to Modern and Pleistocene Reef Carbonates, Barbados, West Indies. Third International Coral Reef Symposium. University of Miami, Florida. 30 p.
- Jones, J.A., 1977. Morphology and development of south-eastern Florida patch reefs. Proceedings of the Third International Coral Reef Symposium 2: 231-235.
- Kelling, G.V., and Mullin, P.R., 1975. Graded limestones and limestone quartzite couplets: possible storm deposits from the Moroccan Carboniferous. Sedimentary Geology 13: 161-190.
- Knutson, D.W., Buddemeier, R.W., and Smith, S.V., 1972. Coral

chronometers : seasonal growth bands in reef corals. *Science* 177:270-272.

Kreisa, R.D., 1979. Storm-generated sedimentary structures in the upper Martinsburg Formation (Upper Ordovician) in southwest Virginia. *Geological Society of America Abstracts with Programs* 11: 185-186.

Kreisa, R.D., 1981. Storm-generated sedimentary structures in subtidal marine facies with examples from the Middle and Upper Ordovician of south-western Virginia. *Journal of Sedimentary Petrology* 51: 823-848.

Kreisa, R.D., Dorobek, S.L., Accorti, P.J., and Ginger, E.P., 1981. Recognition of storm-generated deposits in the Cincinnati Series, Ohio. *Geological Society of America Abstracts with Programs* 13: 285.

Labelle, M., 1982. Some aspects of the population dynamics of the redlip blenny, *Ophioblennius atlanticus* (Teleostei : Blenniidae). MSc. thesis, University of Alberta. 186 p.

Lawrence, M.B., and Pelissier, J.M., 1981. Atlantic hurricane season of 1980. *Monthly Weather Review* 109(7): 1567-1582.

Leckie, D.A., and Walker, R.G., 1982. Storm- and tide-dominated shorelines in Cretaceous Moosebar-Lower Gates Interval - outcrop equivalents of deep basin gas traps in western Canada. *American Association of Petroleum Geologists Bulletin* 66: 138-157.

Lewis, J.B., 1960. The coral reefs and coral communities Barbados, West Indies. *Canadian Journal of Zoology* 38: 1133-1145.

Lewis, J.B., 1974a. The settlement behavior of planula larva of the hermatypic coral *Favia fragum* (Esper). *Journal of Experimental Marine Biology and Ecology* 15: 165-172.

Lewis, J.B., 1974b. Settlement and growth factors influencing the contagious distribution of some Atlantic reef corals. *Proceedings of the Second International Coral Reef Symposium* 2: 201-206.

Lewis, J.B., Axelsen, F., Goodbody, I., Page, C., and Chislett, G., 1968. Comparative growth rates of some reef corals in the Caribbean. *Marine Sciences Manuscript Report* 10. 26 p.

- Loya, Y., 1972. Community structure and species diversity of hermatypic corals at Eilat, Red Sea. *Marine Biology* 13: 100-123.
- Loya, Y., 1975. Possible effects of water pollution on the community structure of Red Sea corals. *Marine Biology* 29: 177-185.
- Loya, Y., 1976. Recolonization of Red Sea corals affected by natural catastrophes and man-made perturbations. *Ecology* 57: 278-289.
- Ma, T.Y.H., 1933. On the seasonal change of growth in some Paleozoic corals. *Proceedings of the Imperial Academy (Tokyo)* 9: 407-408.
- MacGeachy, J.K., 1978. Geological significance of boring sponges on Barbados reefs. PhD thesis, McGill University, Montreal.
- Macintyre, I.G., and Glynn, P.W., 1976. Evolution of modern Caribbean fringing reef, Galeta Point, Panama. *American Association of Petroleum Geologists Bulletin* 60: 1054-1072.
- Maragos, J.E., Baines, G.B.K., and Beveridge, P.J., 1973. Tropical cyclone Bebe creates a new land formation on Funafuti Atoll. *Science* 181: 1161-1164.
- Marsaglia, K.M., and Klein, G.D., 1983. The paleogeography of Paleozoic and Mesozoic storm depositional systems. *Journal of Geology* 91: 117-142.
- Marsh, J.A., Ross, R.M., and Zolan, W.J., 1982. Water circulation on two Guam reef flats. *Proceedings of the Fourth International Coral Reef Symposium* 1: 353-358.
- Matter, A., 1967. Tidal flat deposits in the Ordovician of western Maryland. *Journal of Sedimentary Petrology* 37: 601-609.
- May, R.M., 1973. *Stability and complexity in model ecosystems*. Princeton University Press, Princeton. 265 p.
- Mergner, H., 1981. Man-made influences on and natural changes in the settlement of the Aquaba Reefs (Red Sea). *Proceedings of the Fourth International Coral Reef Symposium* 1: 193-207.

- Mesolella, K.J., Matthews, R.K., Broecker, W.S., and Thurber, d.l., 1969. The astronomical theory of climatic change : Barbados data. *Journal of Geology* 77: 250-274.
- Mesolella, K.J., Sealy, H.A., and Matthews, R.K., 1970. Facies geometries within Pleistocene reefs of Barbados, West Indies. *American Association of Petroleum Geologists Bulletin* 54: 1899-1917.
- Morton, R.A., 1976. Effect of Hurricane Eloise on beach and coastal structures, Florida panhandle. *Geology* 16: 277-280.
- Mount, J.F., 1982. Storm-surge ebb origin of hummocky cross-stratified units of the Andrews Mountain Member, Campito Formation (Lower Cambrian), White - Inyo Mountains, Eastern California. *Journal of Sedimentary Petrology* 52(3):941-958.
- Murray, S.P., 1970. Bottom currents near the coast during hurricane Camille. *Journal of Geophysical Research* 75: 4579-4582.
- Neiburger, M., Levin, Z., and Rodriguez, L., 1973. Experimental evaluation of collection and coalescence efficiencies of cloud drops. *Journal of Atmospheric Science* 30: 944-946.
- Neudecker, S., 1977. Transplant experiments to test the effects of fish grazing on coral distribution. *Proceedings of the Third International Coral Reef Symposium* 1: 317-323.
- Nummedal, D., 1982. Geological effects of Gulf Coast hurricanes. *Geological Society of America Abstracts with Programs* 14(7):578.
- Officer, C.B., Ewing, J.I., Hennion, J.F., Harkrider, D.G., and Miller, D.E., 1959. Geophysical investigations in the eastern Caribbean : summary of 1955 and 1956 cruises. In: Ahrens, L.H. et al. *Physics and Chemistry of the Earth*. Pergamon Press, New York. p.17-109.
- Ogg, J.G., and Koslow, J.A., 1978. The impact of typhoon Pamela (1976) on Guams's coral reefs and beaches. *Pacific Science* 32(2): 105-118.
- Ott, B., 1975. Community patterns on a submerged barrier reef at Barbados, West Indies. *Internationale Revue gesamten Hydrobiologie systematische beihefte* 60: 719-736.

- Paine, R.T., 1966. Food web complexity and species diversity. *American Naturalist* 11: 65-75.
- Parker, R.H., 1960. Ecology and distributional patterns of marine macro-invertebrates, northern Gulf of Mexico. In: Shepard, F.P., Phleger, F.B., and van Andel, T.J.H., (eds.), *Recent Sediments, northwest Gulf of Mexico*. American Association of Petroleum Geologists. p. 302-344.
- Pearson, R.G., 1981. Recovery and recolonization of coral reefs. *Marine Ecology Progress Series* 4: 105-122.
- Perkins, R.D., and Enos, P., 1968. Hurricane Betsy in the Florida-Bahamas area - geological effects and comparison with hurricane Donna. *Journal of Geology* 76: 710-717.
- Perlmutter, M.A., 1978. Storm-produced layering in the bays, lagoons, and channels of southwest Florida. *Geological Society of America Abstracts with Programs* 10: 470.
- Perlmutter, M.A., 1979. Recognition of storm-produced layering in the Ten Thousand Islands region of south-west Florida. *GSA Abstracts* 11: 493-494.
- Pichon, M., and Morrissey, J., 1981. Benthic zonation and community structure on South Island Reef, Lizard Island (Great Barrier Reef). *Bulletin of Marine Science* 31: 581-593.
- Porter, J.W., 1972. Predation by *Acanthaster* and its effects on coral species diversity. *American Naturalist* 106: 487-492.
- Randall, J.E., 1974. The effect of fishes on coral reefs. *Proceedings of the Second International Coral Reef Symposium* 1: 159-166.
- Randall, R.H., and Eldredge, L.G., 1977. Effects of typhoon Pamela on the coral reefs of Guam. *Proceedings of the Third International Coral Reef Symposium* 2: 525-531.
- Richards, A., and Bird, J.B., 1970. Beach studies on the west coast of Barbados 1967-1969. McGill University, Department of Geography Report, 83 p.
- Rogers, C.S., Gilnack, M., and Fitz, H.C., III., 1983. Monitoring of coral reefs with linear transects: a study of storm damage. *Journal of Experimental Marine Biology and Ecology* 66: 285-

300.

- Rogers, C.S., Suchanek, T.H., and Pecora, F.A., 1982. Effects of hurricanes David and Frederic (1979) on shallow Acropora palmata reef communities: a St. Croix, U.S. Virgin Islands. *Bulletin of Marine Science* 32(2): 532-548.
- Rosen, B.R., 1981. The tropical high diversity enigma - the corals' - eye view. From Forey, P.L., (ed.), *Chance, change and challenge. The evolving biosphere.* British Museum (Natural History), and Cambridge University Press. p. 103-129.
- Sammarco, P.W., 1982a. Echinoid grazing as a structuring force in coral communities : whole reef manipulations. *Journal of Experimental Marine Biology and Ecology* 61: 31-55.
- Sammarco, P.W., 1982b. Effects of grazing by Diadema antillarum Philippi (Echinodermata : Echinoidea) on algal diversity and community structure. *Journal of Experimental Marine Biology and Ecology* 65: 83-105.
- Sammarco, P.W., 1982c. Polyp bail-out : an escape response to environmental stress and a new means of reproduction in corals. *Marine Ecology Progress Series* 10:57-65.
- Schuhmacher, H., 1974. On the conditions accompanying the first settlement of corals on artificial reefs with special reference to the influence of grazing sea urchins (Eilat, Red Sea). *Proceedings of the Second International Coral Reef Symposium* 1: 257-267.
- Schuhmacher, H., 1977. Initial phases in reef development, studied at artificial reef types off Eilat (Red Sea). *Helgolander wissenschaftliche Meeresuntersuchungen* 30: 400-411.
- Shannon, C.E., and Weaver, W., 1948. *The Mathematical Theory of Communication.* University of Illinois Press, Urbana. 117 p.
- Shinn, E.A., 1983. Tidal flat environment. In: Scholle, P.A., Bebout, D.G., and Moore, C.H., (eds.), *Carbonate Depositional Environments.* American Association of Petroleum Geologists. p. 171-210.
- Shinn, E.A., 1976. Coral reef recovery in Florida and the Persian Gulf. *Environmental Geology* 1: 241-254.

- Simpson, R.H., and Riehl, H., 1981. The Hurricane and its Impact. Louisiana State University Press. Baton Rouge. 398 p.
- Simpson, G.G., Roe, A., and Lewontin, R.C., 1960. Quantitative Zoology. Harcourt, Brace & Company, New York. 440 p.
- Skeete, C.C., 1963. A description of the weather of the island of Barbados, West Indies. Unpublished MS., Woods Hole Oceanographic Institute, May 1963. 284 p.
- Speed, R.C., 1979. New views on the geology of Barbados : Fourth Latin American Geological Congress, Trinidad, 1979. Transactions (in press).
- Speed, R.C., 1981. Geology of Barbados : implications for an accretionary origin. Oceanologica Acta, Actes 26th Congres International de Geologie, Paris, 1980. p. 259-265.
- Speed, R.C., and Larue, D.K., 1982. Barbados : architecture and implications for accretion. Journal of Geophysical Research 87: 3633-3643.
- Stearn, C.W., and Riding, R., 1973. Forms of the hydrozoan Millepora on a Recent coral reef. Lethaia 6: 187-200.
- Stearn, C.W., Scoffin, T.P., and Martindale, W., 1977. Calcium carbonate budget of a fringing reef on the west coast of Barbados. Bulletin of Marine Science 27(3): 479-510.
- Stel, J.H., 1975. The influence of hurricanes upon the quiet depositional conditions in the lower Emsian La Vid shales of Colle (NW Spain). Leidse Geologische Mededelingen 49(3): 475-486.
- Stephenson, W., Endean, R., and Bennet, I., 1958. An ecological survey of the marine fauna of Low Isles, Queensland. Australian Journal of Marine and Freshwater Research 9: 261-318.
- Stoddart, D.R., 1962. Catastrophic storm effects on the British Honduras reefs and cays. Nature 193: 512-515.
- Stoddart, D.R., 1963. Effects of Hurricane Hattie on the British Honduras reefs and cays, October 30-31, 1961. Atoll Research Bulletin 95: 1-42.

- Stoddart, D.R., 1969. Post-hurricane changes on the British Honduras reefs and cays: re-survey 1965. Atoll Research Bulletin 131: 1-31.
- Stoddart, D.R., 1971. Coral reefs and islands and catastrophic storms. In: Steers, J.A., (ed.), Applied Coastal Geomorphology. Macmillan, London. p. 155-197.
- Stoddart, D.R., 1974. Post-hurricane changes on the British Honduras reefs: re-survey of 1972. Proceedings of the Second International Coral Reef Symposium 2: 473-483.
- Thompson, A.M., 1970. Tidal-flat deposition and early dolomitization in Upper Ordovician rocks of the southern Appalachian valley and ridge. Journal of Sedimentary Petrology 40: 1271-1286.
- Thompson, A.M., 1972. Shallow-water turbidites in Ordovician flysch, central Appalachian Mountains, USA. XXIV International Geologic Congress Proceedings, Section 6: 89-99.
- Thusu, B., 1972. Depositional environments in the Rochester Formation (Middle Silurian) in southern Ontario. Journal of Sedimentary Petrology 42: 930-934.
- Tunncliffe, V., 1978. The role of boring sponges in coral fracture. In: Levi, C., Boury-Esnault, N., (eds.), Biologie des Spongiaires. Centre National de la Recherche Scientifique, Paris. p. 309-315.
- Tunncliffe, V., 1980. Biological and physical processes affecting the survival of a stony coral, Acropora cervicornis. PhD. thesis, Yale University, New Haven.
- Upchurch, S., 1970. Sedimentation on the Bermuda platform. U.S. Lake Survey Research Report 2-2. 192 p.
- U.S. Navy Hydrographic Office, 1964. Bathymetric map of the Caribbean.
- Walker, R.G., 1982. Some limiting conditions on the formation of Hummocky Cross stratification. XI International Association of Sedimentological Congress Abstracts : 104.
- Walsh, R.J., Harris, C.L., Harvey, J.M., Maxwell, W.G.H., Thomson, J.M., Tranter, D.J., 1971. Report of the committee on the problem of the crown-of-thorns

starfish. Council of Scientific and Industrial Research, Melbourne.

- Weber, J.N., and White, E.W., 1974. Activation energy for skeletal aragonite deposited by the hermatypic coral Platygyra spp. *Marine Biology* 26: 353-359.
- Weber, J.N., and White, E.W., 1977. Caribbean reef corals Montastrea annularis and Montastrea cavernosa - long-term growth data as determined by skeletal x-radiography. In: Frost, S.H., Weiss, M.P., Saunders, J.B., (eds.), *Reefs and Related Carbonates - Ecology and Sedimentology*. American Association of Petroleum Geologists Studies in Geology 5: 171-179.
- Weiss, M.P., and Goddard, D.A., 1977. Man's impact on coastal reefs - an example from Venezuela. In: Frost, S.H., Weiss, M.P., and Saunders, J.B., (eds.), *Reefs and Related Carbonates - Ecology and Sedimentology*. American Association of Petroleum Geologists Studies in Geology 4: 111-124.
- Wellington, G.M., and Glynn, P.W., 1983. Environmental influences on skeletal banding in eastern Pacific (Panama) corals. *Coral Reefs* 1: 215-222.
- Westbrook, G.K., 1975. The structure of the crust and upper mantle in the region of Barbados and the Lesser Antilles. *Geophysical Journal* 43: 1-42.
- Wong, P.P., 1971. Beach changes and sand movement in low energy environments, West Coast, Barbados. Bellairs Research Institute, Barbados, and Department of Geography, McGill University, Montreal. 108 p.
- Woodley, J.D., 1980. Hurricane Allen destroys Jamaican coral reefs. *Nature* 287: 387.
- Woodley, J.D., Chornesky, E.A., Clifford, P.A., Jackson, J.B.C., Kaufman, L.S., Knowlton, N., Lang, J.C., Pearson, M.P., Porter, J.W., Rooney, M.C., Rylaarsdam, K.W., Tunnicliffe, V.J., Wahle, C.M., Wulff, J.L., Curtis, A.S.G., Dallmeyer, M.D., Jupp, B.P., Koehl, M.A.R., Neigel, J., and Sides, E.M., 1981. Hurricane Allen's impact on Jamaican coral reefs. *Science* 214: 749-755.

APPENDIX

KEY TO ABBREVIATIONS USED IN RAW DATA

A.a. = *Agaricia agaricites*

CRA = coralline red algae

F.f. = *Favia fragum*

M.a. = *Montastrea annularis*

M.c. = *Montastrea cavernosa*

M.m. = *Madracis mirabilis*

M.s. = *Millepora squarosa*

P.a. = *Porites astreoides*

P.p. = *Porites porites*

S.s. = *Siderastrea siderea*

* = boundary between ellipses

APPENDIX

RAW DATA FOR RE-SURVEYED TRANSECT LINES

<u>DISTANCE (m) FROM</u> <u>START OF TRANSECT 1</u>	<u>m+0.1</u>	<u>m+0.2</u>	<u>m+0.3</u>	<u>m+0.4</u>	<u>m+0.5</u>
0	rock	rock	rock	rock	rock
1	rock	rock	rock	rock	rock
2	rock	rock	rock	rock	rock
3	rock	rock	rock	rock	rock
4	rock	rubble	rubble	rubble	rubble
5	rock	rock	rock	rock	rock
6	rock	rubble	rock	rock	rock
7	rock	rock	rock	rock	rock
8	CRA	CRA	CRA	CRA	CRA
9	CRA	CRA	CRA	CRA	CRA
10	P.a.	F.f.	CRA	CRA	CRA
11	rock	rock	rock	rock	rock
12	rock	rock	rock	rock	rock
13	rock	rock	rock	rock	rock
14	rock	rock	rock	rock	P.a.
15	rubble	rubble	rubble	rubble	rubble
16	rock	rock	rock	rock	rock
17	* rubble	rock	P.a.	P.a.	CRA
18	CRA	CRA	CRA	rock	rock
19	rock	rock	rock	rock	rock
20	rock	rock	rock	rock	rock
21	* rubble	rubble	rock	rubble	rubble
22	rubble	rock	rock	rubble	rubble

<u>DISTANCE (m) FROM</u>	<u>m+0.1</u>	<u>m+0.2</u>	<u>m+0.3</u>	<u>m+0.4</u>	<u>m+0.5</u>
<u>START OF TRANSECT I</u>					
23	rubble	rubble	rubble	rubble	rubble
24	CRA	rock	CRA	rock	rock
25	sand	rock	rock	rock	sand
26	rock	rubble	rubble	CRA	CRA
27	CRA	CRA	CRA	CRA	CRA
28	rock	CRA	sand	sand	CRA
29	P.a.	CRA	CRA	P.a.	P.a.
30	CRA	CRA	rubble	M.s.	CRA
31	CRA	CRA	CRA	rubble	rubble
32	P.a.	rubble	rubble	P.a.	P.a.
33	sand	sand	sand	sand	sand
34	sand	rubble	rubble	rubble	rubble
35	A.a.	P.p.	M.s.	P.a.	* A.a.
36	A.a.	CRA	A.a.	CRA	CRA
37	A.a.	CRA	CRA	CRA	CRA
38	rubble	rubble	A.a.	rock	P.a.
39	A.a.	rubble	rubble	rubble	rubble
40	rock	A.a.	A.a.	M.s.	CRA
41	rubble	rubble	rock	rock	rock
42	P.a.	rock	A.a.	M.a.	CRA
43	CRA	M.a.	A.a.	CRA	CRA
44	CRA	P.p.	CRA	CRA	CRA
45	* rubble	rubble	rock	rubble	rock
46	rubble	sand	rubble	rubble	rock
47	rock	rock	rock	rock	rubble
48	sand	sand	sand	sand	sand

<u>DISTANCE (m) FROM</u> <u>START OF TRANSECT I</u>	<u>m+0.1</u>	<u>m+0.2</u>	<u>m+0.3</u>	<u>m+0.4</u>	<u>m+0.5</u>
49	sand	sand	sand	sand	sand
50	rubble	sand	rubble	rubble	rubble
51	rubble	sand	sand	sand	sand
52	sand	sand	sand	sand	sand
53	sand	sand	rubble	rubble	rubble
54	CRA	A.a.	rock	P.a.	A.a.
55	rubble	rubble	rubble*	rubble	rubble
56	CRA	A.a.	A.a.	A.a.	CRA
57	CRA	A.a.	CRA	A.a.	CRA
58	CRA	CRA	CRA	A.a.	CRA
59	CRA	A.a.	CRA	rock	CRA
60	A.a.	CRA	P.a.	A.a.	rock
61	A.a.	CRA	A.a.	CRA	M.s.
62	P.p.	CRA	rock	P.a.	A.a.
63	M.s.	P.a.	P.a.	rock	rock
64	CRA	P.a.	P.a.	P.p.	P.p.
65	A.a.	P.a.	rock	A.a.	CRA
66	M.a.	CRA	M.s.	M.a.	M.a.
67	CRA	CRA	CRA	CRA	CRA
68	rubble	rock	CRA	P.a.	P.a.
69	rubble	rubble	rubble	rock	rubble
70	rock	rock	rubble	rubble	rubble
71	rubble	rubble	CRA	rock	rock
72	rubble	rubble	rubble	rubble	rubble
73	rubble	rubble	rubble	sand	sand

<u>DISTANCE (m) FROM</u> <u>START OF TRANSECT I</u>	<u>m+0.1</u>	<u>m+0.2</u>	<u>m+0.3</u>	<u>m+0.4</u>	<u>m+0.5</u>
74	rubble	rubble	rubble	sand	rubble
75	M.a.	CRA	CRA	rock	rubble
76	rock	sand	rubble	rock	rock
77	rock	rubble	rubble	rubble	CRA
78	CRA	M.a.	M.a.	M.a.	M.a.
79	M.a.	rubble	rubble	rubble	rubble
80	CRA	rock	CRA	CRA	CRA
81	CRA	A.a.	A.a.	rubble	A.a.
82	CRA	CRA	rock	rock	rubble
83	rubble	rock	rock	rubble	rock
84	rock	rock	rock	rubble	rock
85	sand	sand	sand	sand	sand
86	rock	sand	sand	sand	sand
87	rock	rock	CRA	CRA	CRA
88	CRA	rock	P.a.	S.s.	S.s.
89	CRA	A.a.	rock	rock	CRA
90	CRA	CRA	CRA	A.a.	CRA
91	CRA	rock	rock	sand	rubble
92	rock	sand	sand	sand *	sand
93	sand	sand	sand	sand	sand
94	sand	sand	sand	sand	sand
95	sand	sand	sand	sand	sand
96	sand	sand	sand	sand	sand
97	sand	sand	sand	sand	sand
98	rock	CRA	CRA	A.a.	A.a.
99	CRA	rock	rock	rock	sand

<u>DISTANCE (m) FROM START OF TRANSECT I</u>	<u>m+0.1</u>	<u>m+0.2</u>	<u>m+0.3</u>	<u>m+0.4</u>	<u>m+0.5</u>
100	sand	sand	sand	sand	A.a.
101	rock	CRA	rock	CRA	A.a.
102	S.s.	S.s.	S.s.	S.s.	S.s.
103	sand	sand	sand	sand	sand
104	sand	sand	sand	sand	sand
105	sand	sand	sand	sand	sand
106	sand	sand	sand	sand	sand
107	sand	sand	sand	sand	sand
108	sand	sand	sand	sand	sand
109	sand	sand	sand	sand	sand
110	sand	sand	sand	sand	sand
111	A.a.	CRA	A.a.	CRA	rock
112	rock	rock	rock	rock	rock
113	sand	sand	sand	sand	sand
114	sand	sand	sand	sand	sand
115	sand	sand	CRA	CRA	CRA
116	rock	rock	rock	rubble	rubble
117	P.a.	A.a.	CRA	rock	P.a.
118	rock	rock	M.a.	M.a.	rock
119	rock	M.a.	M.a.	M.a.	M.a.
120	M.s.	P.a.	P.a.	P.a.	P.a.
121	CRA	A.a.	rock	rock	rock
122	CRA	CRA	CRA	rock	rock
123	rock	rock	CRA	CRA	CRA
124	A.a.	M.s.	P.p.	P.p.	A.a.

<u>DISTANCE (m) FROM</u>	<u>m+0.1</u>	<u>m+0.2</u>	<u>m+0.3</u>	<u>m+0.4</u>	<u>m+0.5</u>
<u>START OF TRANSECT I</u>					
125	rubble	rubble	rubble	rubble	rubble
126	rock	A.a.	rock	rock	rock *

TRANSECT II

<u>DISTANCE (m) FROM</u>	<u>m+0.1</u>	<u>m+0.2</u>	<u>m+0.3</u>	<u>m+0.4</u>	<u>m+0.5</u>	
<u>START OF TRANSECT II</u>						
0	*	CRA	CRA	CRA	CRA	CRA
1		CRA	CRA	CRA	CRA	CRA
2	*	CRA	A. a.	rock	CRA	CRA
3		CRA	rock	rock	CRA	CRA
4		CRA	P. a.	A. a.	A. a.	rock
5		rubble	rubble	rubble	rubble	rubble
6		rubble	rubble	rubble	rock	rock
7		rock	rock	rock	rock	CRA
8		CRA	CRA	CRA	CRA	CRA
9		A. a.	CRA	CRA	rock	CRA
10		CRA	CRA	CRA	CRA	rock
11		CRA	CRA	CRA	CRA	A. a.
12		CRA	P. p.	CRA	rock	CRA
13		M. s.	A. a.	rock	CRA	CRA
14		CRA	rock	CRA	CRA	rock
15		rock	rock	rock	CRA	rock
16		CRA	CRA	rubble	rubble	rubble
17		rubble	rubble	rubble	rubble	rubble
18		rock	rock	sand	rock	rock
19		rock	rock	sand	rock	rock
20		CRA	CRA	CRA	CRA	CRA
21		CRA	M. a.	CRA	M. s.	rubble
22		CRA	CRA	rock	A. a.	CRA
23		CRA	rock	P. p.	A. a.	M. s.

<u>DISTANCE (m) FROM</u> <u>START OF TRANSECT II</u>	<u>m+0.1</u>	<u>m+0.2</u>	<u>m+0.3</u>	<u>m+0.4</u>	<u>m+0.5</u>
24	M.s.	rock	rock	CRA	CRA
25	rock	A.a.	rock	rock	A.a.
26	P.a.	CRA	rock	CRA	rock
27	rock	rock	CRA	rock	rock
28	rock	P.a.	P.a.	CRA	* CRA
29	rock	rock	CRA	rock	rock
30	CRA	CRA	rock	M.s.	CRA
31	rubble	rubble	rubble	rubble	rubble
32	rock	CRA	rock	rock	rock
33	rubble	rubble	rubble	rubble	rubble
34	rock	rubble	rubble	rubble	rubble
35	rubble	rubble	rubble	rubble	rubble
36	CRA	rock	rock	rock	CRA
37	A.a.	CRA	CRA	CRA	CRA
38	sand	sand	rock	A.a.	rock
39	CRA	CRA	rock	rock	rock
40	rubble	rubble	rubble	rubble	rubble
41	rock	rock	M.s.	CRA	CRA
42	rock	sand	CRA	CRA	CRA
43	CRA	CRA	rock	CRA	CRA
44	CRA	CRA	rock	CRA	rock
45	CRA	rock	rock	CRA	CRA
46	CRA	CRA	CRA	rock	rock
47	M.a.	M.a.	M.a.	M.a.	M.a.
48	M.a.	M.a.	M.a.	M.a.	M.a.
49	M.a.	M.a.	CRA	CRA	CRA

<u>DISTANCE (m) FROM</u> <u>START OF TRANSECT II</u>	<u>m+0.1</u>	<u>m+0.2</u>	<u>m+0.3</u>	<u>m+0.4</u>	<u>m+0.5</u>
50	CRA	rock	rock	rock	CRA
51	rock	rock	rock	rock	rock
52	sand	* sand	sand	rubble	sand
53	sand	sand	rock	rock	rock
54	rock	rubble	M.s.	CRA	rock
55	CRA	CRA	rock	rock	CRA
56	CRA	sand	rock	rock	rock
57	sand	rubble	rubble	sand	sand
58	sand	sand	sand	sand	sand
59	rock	rock	rock	rock	rock
60	sand	sand	sand	sand	rock
61	CRA	CRA	rock	rock	rock
62	CRA	CRA	rock	rock	rock
63	rock	CRA	rock	rubble	rubble
64	rock	P.a.	CRA	CRA	CRA
65	CRA	A.a.	rock	rock	A.a.
66	CRA	rock	rock	rock	rock
67	sand	sand	sand	sand	sand
68	sand	sand	sand	sand	sand
69	CRA	rock	rock	* rock	rock
70	rock	CRA	CRA	rock	rock
71	rubble	rubble	rubble	rubble	sand
72	rock	rock	rock	rock	rock
73	N.a.	N.a.	M.a.	CRA	rock
74	rock	rock	M.s.	CRA	rock
75	rock	rock	CRA	N.m.	rock

<u>DISTANCE (m) FROM</u> <u>START OF TRANSECT I I</u>	<u>m+0.1</u>	<u>m+0.2</u>	<u>m+0.3</u>	<u>m+0.4</u>	<u>m+0.5</u>
76	CRA	CRA	CRA	CRA	rock
77	P. a.	rock	rock	rock	CRA
78	rock	rock	rock	rock	rock
79	CRA	CRA	rock	rock	rock
80	rock	rock	rock	rock	rock
81	sand	rock	rock	rock	rock
82	rock	rock	sand	sand	sand
83	P. a.	rock	rock	CRA	rock
84	rock	rock	M. a.	CRA	A. a.
85	rock	rubble	rubble	rubble	rubble
86	rock	rock	rock	rock	rock
87	rock	rock	CRA	CRA	rock
88	CRA	rock	rock	CRA	rock
89	rock	rock	rock	rock	rock
90	rock	rock	rock	rock	rock
91	M. s.	M. s.	rock	rock	CRA
92	rock	CRA	rock	rock *	rock
93	rubble	CRA	rubble	CRA	rock
94	rock	CRA	rock	rock	rock
95	CRA	CRA	CRA	CRA	CRA
96	CRA	rock	rock	rock	rock
97	CRA	CRA	CRA	CRA	rock *

TRANSECT III

<u>DISTANCE (m) FROM</u>	<u>m+0.1</u>	<u>m+0.2</u>	<u>m+0.3</u>	<u>m+0.4</u>	<u>m+0.5</u>
<u>START OF TRANSECT III</u>					
0	* CRA	CRA	rock	CRA	CRA
1	CRA	rock	rock	CRA	CRA
2	* CRA	rock	CRA	rock	rock
3	CRA	rock	CRA	CRA	rock
4	M. s.	CRA	rock	rock	CRA
5	CRA	rock	CRA	rock	rock
6	rock	rock	rock	rock	rock
7	rock	CRA	rock	rock	rock
8	CRA	CRA	CRA	CRA	CRA
9	CRA	CRA	CRA	CRA	CRA
10	CRA	CRA	rock	rock	rock
11	CRA	CRA	CRA	CRA	CRA
12	CRA	CRA	A. a.	CRA	CRA
13	CRA	CRA	CRA	rock	rock
14	CRA	rock	CRA	CRA	CRA
15	CRA	rock	rock	CRA	CRA
16	CRA	CRA	CRA	CRA	CRA
17	rock	CRA	rock	rock	rock
18	sand	sand	sand	rock	rock
19	sand	sand	sand	sand	sand
20	rubble	rock	rock	rock	sand
21	rubble	rubble	CRA	CRA	rock
22	CRA	CRA	sand	sand	rock
23	rock	rock	rock	rock	rock
24	rock	rock	rock *	rock	rock

<u>DISTANCE (m) FROM</u> <u>START OF TRANSECT III</u>	<u>m+0.1</u>	<u>m+0.2</u>	<u>m+0.3</u>	<u>m+0.4</u>	<u>m+0.5</u>
25	rock	rock	rock	rubble	rock
26	rubble	rubble	sand	sand	sand
27	rock	CRA	CRA	CRA	CRA
28	rock	CRA	CRA	rock	CRA
29	CRA	CRA	CRA	CRA	CRA
30	CRA	CRA	A. a.	CRA	rock
31	rock	rock	CRA	CRA	CRA
32	CRA	CRA	CRA	CRA	CRA
33	CRA	P. a.	CRA	CRA	CRA
34	CRA	CRA	CRA	CRA	CRA
35	CRA	CRA	rock	CRA	CRA
36	A. a.	CRA	CRA	CRA	rock
37	CRA	CRA	CRA	rock	CRA
38	CRA	rock	P. a.	rock	rock
39	CRA	CRA	CRA	CRA	CRA
40	CRA	CRA	CRA	CRA	CRA
41	rock	rock	rock	rock	rock
42	rock	rock	sand	sand	sand
43	A. a.	A. a.	M. s.	rubble	sand
44	CRA	A. a.	CRA	rubble	rubble
45	rubble	rubble	rubble	sand	sand
46	sand	rock	sand	sand	rock
47	CRA	CRA	CRA	CRA	A. a.
48	rock	rock	rubble	rock	rock
49	rock	rock	rock	rock	rock
50	rock	S. s.	A. a. *	CRA	A. a.

<u>DISTANCE (m) FROM</u>	<u>m+0.1</u>	<u>m+0.2</u>	<u>m+0.3</u>	<u>m+0.4</u>	<u>m+0.5</u>
<u>START OF TRANSECT</u>	<u>III</u>				
51	M.s.	CRA	CRA	CRA	ROCK
52	rock	rock	rock	P.a.	rubble
53	sand	sand	sand	sand	sand
54	sand	sand	sand	sand	sand.
55	rock	rock	rock	rock	rock
56	CRA	CRA	CRA	CRA	CRA
57	rock	CRA	CRA	CRA	CRA
58	rock	P.a.	CRA	CRA	CRA
59	sand	sand	rock	sand	sand
60	sand	sand	sand	sand	sand
61	sand	sand	sand	sand	sand
62	sand	sand	sand	sand	sand
63	CRA	rock	CRA	CRA	rock
64	CRA	CRA	CRA	CRA	CRA
65	CRA	CRA	CRA	A.a.	CRA
66	CRA	CRA	CRA	CRA	CRA
67	CRA	CRA	CRA	CRA	CRA
68	CRA	CRA	CRA	CRA	CRA
69	CRA	CRA	CRA	CRA	CRA
70	* CRA	CRA	CRA	CRA	CRA
71	CRA	CRA	CRA	CRA	M.s.
72	CRA	CRA	CRA	A.a.	CRA
73	sand	sand	sand	rock	rock
74	sand	sand	sand	sand	sand
75	sand	sand	sand	rock	rock
76	sand	sand	sand	sand	sand

<u>DISTANCE (m) FROM</u> <u>START OF TRANSECT III</u>	<u>m+0.1</u>	<u>m+0.2</u>	<u>m+0.3</u>	<u>m+0.4</u>	<u>m+0.5</u>
77	sand	sand	sand	sand	sand
78	sand	sand	sand	sand	sand
79	sand	sand	sand	sand	sand
80	sand	sand	sand	sand	sand
81	sand	sand	sand	sand	sand
82	sand	sand	sand	sand	sand
83	* sand	sand	sand	sand	sand
84	sand	sand	sand	sand	sand
85	sand	sand	sand	sand	sand
86	sand	sand	sand	sand	sand
87	sand	sand	sand	sand	sand
88	sand	sand	sand	sand	sand
89	sand	sand	sand	sand	sand
90	sand	sand	sand	sand	sand
91	rock	rock	CRA	rock	P. a.
92	M. a.	M. a.	M. a.	M. s.	rock
93	rock	M. a.	CRA	CRA	M. s.
94	rock	CRA	rock	CRA	rock
95	rock	rock	rock	rock	rock
96	CRA	rubble	rubble	rubble	rubble
97	rubble	rubble	rubble	rubble	rubble
98	rock	rock	rock	rock	rock
99	CRA	CRA	CRA	rock	rubble *

TRANSECT IV

<u>DISTANCE (m) FROM</u> <u>START OF TRANSECT IV</u>	<u>m+0.1</u>	<u>m+0.2</u>	<u>m+0.3</u>	<u>m+0.4</u>	<u>m+0.5</u>
0	* sand	sand	rock	rock	rock
1	rubble	rubble	rock	sand	sand
2	CRA	rock	rock	CRA	CRA
3	rock	CRA	CRA	rock	rock
4	rock	rock	rock	rock	rock
5	sand	rubble	rubble	rubble	rubble
6	sand	sand	rubble	sand	sand
7	rock	rubble	rubble	rock	rock
8	rock	rock	rubble	CRA	CRA
9	rubble	rubble	rubble	rubble	rubble
10	rubble	sand	sand	rubble	sand
11	CRA	rock	rock	rock	rock
12	CRA	sponge	sponge	CRA	CRA
13	rock	sand	rubble	sand	rock
14	rubble	sand	rubble	rubble	sand
15	sand	sand	rock	rock	rock
16	CRA	CRA	CRA	rubble	rock
17	CRA	rubble	A. a.	rubble	CRA
18	CRA	CRA	A. a.	CRA	CRA
19	CRA	CRA	CRA	CRA	CRA
20	CRA	CRA	CRA	CRA	CRA
21	CRA	CRA	P. a.	CRA	CRA
22	CRA	CRA	A. a.	CRA	CRA
23	CRA	CRA	CRA	rock	A. a.
24	CRA	CRA	rock	A. a.	CRA

<u>DISTANCE (m) FROM</u>	<u>m+0.1</u>	<u>m+0.2</u>	<u>m+0.3</u>	<u>m+0.4</u>	<u>m+0.5</u>
<u>START OF TRANSECT IV</u>					
25	A. a.	M. s	rock	rock	rock
26	sand *	sand	sand	sand	sand
27	sand	sand	sand	sand	sand
28	CRA	CRA	CRA	rock	CRA
29	CRA	rock	rock	rock	rock
30	CRA	CRA	CRA	CRA	M. s.
31	CRA	CRA	P. a.	CRA	CRA
32	CRA	CRA	CRA	CRA	rock
33	M. c.	M. c.	CRA	CRA	rock
34	rock	rock	rock	CRA	sand
35	rock	rock	rubble	rock	sand
36	CRA	CRA	CRA	CRA	CRA
37	CRA	CRA	CRA	CRA	CRA
38	CRA	rock	rock	A. a.	CRA
39	CRA	CRA	rock	rock	CRA
40	CRA	CRA	CRA	CRA	CRA
41	CRA	CRA	CRA	CRA	CRA
42	* rock	CRA	CRA	CRA	CRA
43	sand	sand	rubble	A. a.	CRA
44	CRA	CRA	CRA	CRA	CRA
45	rock	rock	rock	rock	rock
46	CRA	rock	CRA	CRA	CRA
47	CRA	CRA	CRA	CRA	CRA
48	CRA	CRA	CRA	rock	CRA
49	rock	rock	rock	rock	rock

TRANSECT V

<u>DISTANCE (m) FROM</u> <u>START OF TRANSECT V</u>	<u>m+0.1</u>	<u>m+0.2</u>	<u>m+0.3</u>	<u>m+0.4</u>	<u>m+0.5</u>
0	rock	rock	rubble	rubble*	rock
1	rubble	rock	rock	rock	CRA
2	rock	M.m.	rock	rock	rock
3	rock	rock	rock	rock	rock
4	rock	rock	rock	rock	rock
5	rubble	rock	M.m.	rock	P.a.
6	rubble	CRA	CRA	CRA	CRA
7	rock	rock	rock	rock	rock
8	S.s.	S.s.	S.s.	S.s.	S.s.
9	sand	sand	sand	sand	sand
10	rock	rock	sand	sand	sand
11	rock	sand	sand	sand	sand
12	rock	rock	rock	sand	sand
13	rubble	rock	rubble	rubble	rubble
14	A.a.	A.a.	A.a.	M.s.	M.s.
15	rock	rubble	sand	sand	sand
16	rubble	rock	rock	rubble	rock
17	rock	rock	rock	CRA	rock
18	rock	rock	rock	M.s.	rock
19	CRA	CRA	CRA	CRA	CRA
20	rubble	rubble	rubble	sand	sand
21	rock	sand	sand	sand	sand
22	sand	sand	rock	rock	rock
23	rock	rock	rock	sand	sand

<u>DISTANCE (m) FROM</u> <u>START OF TRANSECT V</u>	<u>m+0.1</u>	<u>m+0.2</u>	<u>m+0.3</u>	<u>m+0.4</u>	<u>m+0.5</u>
24	rock	rock	rock	CRA	CRA
25	rock	rock	sand	sand	sand
26	sand	sand	sand	rock	sand
27	sand	sand	sand	sand	sand
28	sand	sand	sand	sand	sand
29	sand	sand	sand	sand	rock
30	rubble	rock	CRA	rock	CRA
31	rock	rock	CRA	CRA	CRA
32	rubble	rubble	rock	CRA	CRA
33	sand	sand	sand	sand	sand
34	sand	sand	sand	sand	sand
35	sand	rock	sand	sand	sand
36	sand	sand	sand	rock	sand
37	rock	sand	sand	sand	sand
38	sand	sand	sand	sand	sand
39	rock	sand	sand	sand	sand
40	sand	sand	sand	sand	sand
41	sand	sand	sand	sand	sand
42	sand	sand	sand	sand	sand
43	rock	rock	rock	rock	rock

TRANSECT VI

<u>DISTANCE (m) FROM START OF TRANSECT VI</u>	<u>m+0.1</u>	<u>m+0.2</u>	<u>m+0.3</u>	<u>m+0.4</u>	<u>m+0.5</u>
0	* rock	CRA	rock	rock	F.f.
1	rock	rock	CRA	CRA	rock
2	CRA	CRA	CRA	CRA	CRA
3	rock	rubble	rubble	rubble	rock
4	rock	rock	A.a.	M.s.	A.a.
5	CRA	CRA	CRA	CRA	CRA
6	CRA	CRA	CRA	CRA	CRA
7	CRA	CRA	M.c.	M.c.	M.c.
8	rubble	rubble	rubble	rubble	rubble
9	CRA	CRA	CRA	A.a.	CRA
10	A.a.	P.p.	P.a.	CRA	CRA
11	S.s.	CRA	CRA	CRA	CRA
12	sand	sand	sand	sand	sand
13	rock	rock	CRA	A.a.	M.s.
14	CRA	P.a.	A.a.	CRA	CRA
15	rock	rock	rock	sand	* rock
16	rubble	rubble	rock	rubble	rock
17	CRA	CRA	CRA	CRA	CRA
18	CRA	P.a.	CRA	CRA	CRA
19	rock	rock	rock	rock	rock
20	CRA	rock	rock	A.a.	A.a.
21	rubble	sand	CRA	rock	rock
22	CRA	CRA	CRA	M.a.	CRA
23	sand	rubble	CRA	rock	rock
24	rock	rock	A.a.	rock	CRA

<u>DISTANCE (m) FROM</u>	<u>m+0.1</u>	<u>m+0.2</u>	<u>m+0.3</u>	<u>m+0.4</u>	<u>m+0.5</u>
<u>START OF TRANSECT VI</u>					
25	CRA	rock	rock	CRA	A.a.
26	rock	CRA	CRA	rock	CRA
27	rock	P.p.	CRA	rock	rock
28	CRA	rock	rock	rock *	rock
29	CRA	rock	rock	rock	CRA
30	rock	rock	sand	sand	rock
31	sand	sand	sand	rock	rock
32	rock	rock	rock	rock	rock
33	rock	rock	rock	rock	rubble
34	sand	sand	rubble	sand	sand
35	* sand	sand	sand	sand	sand
36	sand	sand	rock	rock	rock
37	rock	rock	rock	rock	rock
38	M.s.	M.s.	rock	rock	A.a.
39	* rock	rock	A.a.	rock	CRA
40	rock	rock	rock	rock	P.a.
41	rock	rock	rock	rock	rock*