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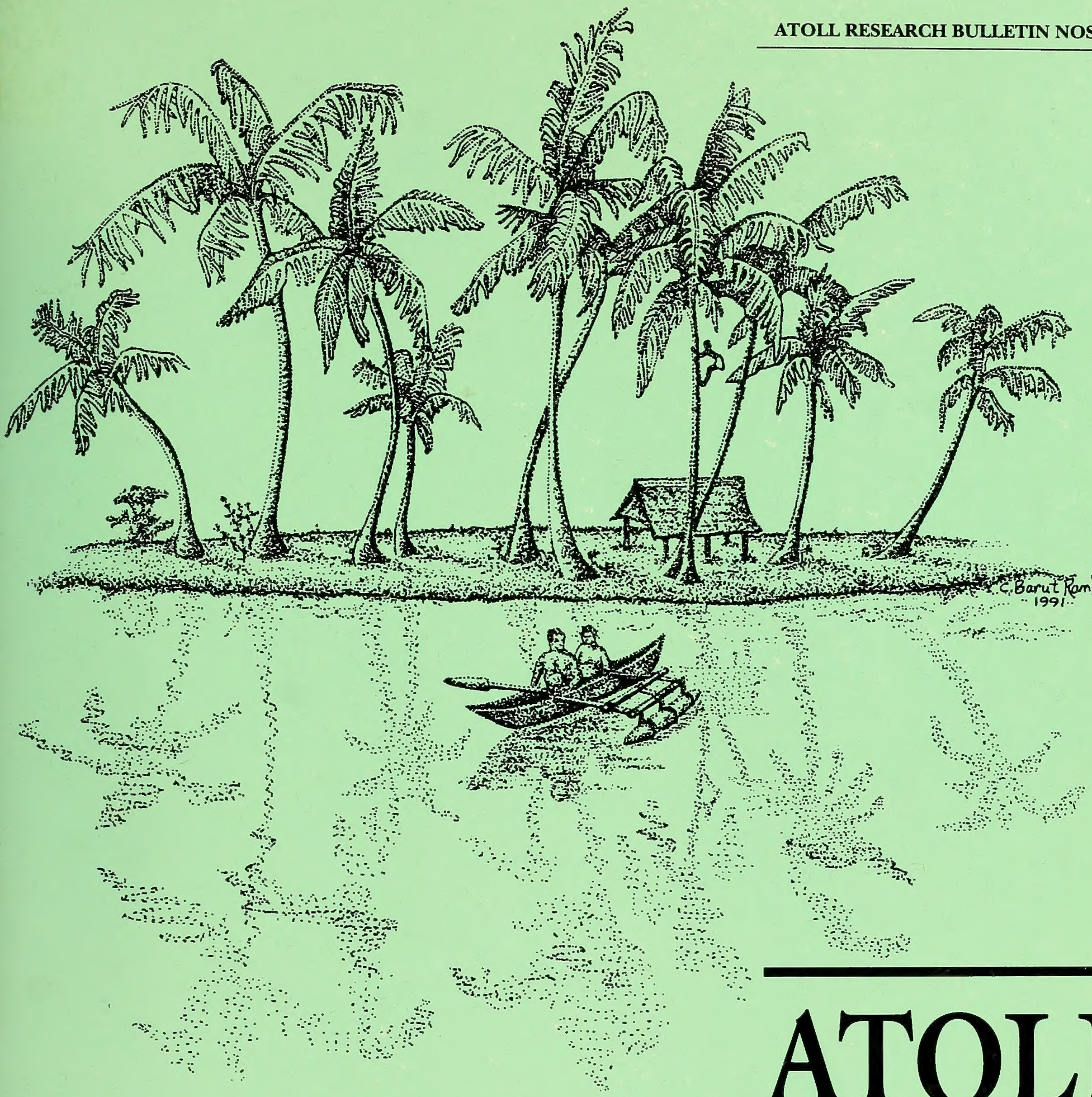

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ECOLOGY AND GEOMORPHOLOGY OF THE COCOS (KEELING) ISLANDS

Issued by

NATIONAL MUSEUM OF NATURAL HISTORY
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WASHINGTON, D.C. U.S.A.
FEBRUARY 1994

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EDITED BY

COLIN D. WOODROFFE

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CHAPTER 1

SCIENTIFIC STUDIES IN THE COCOS (KEELING) ISLANDS: AN INTRODUCTION

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C.D. WOODROFFE AND P.F. BERRY

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96°49'E
96°50'E
11° 49'S
11° 50'S
NORTH KEELING
96°50'E
96°55'E
12°05'S
12°10'S
Horsburgh Is.
Direction Is.
Port Refuge
INDIAN OCEAN
Western Entrance
Turks Reef
Home Is.
Pulu Ampang
Pulu Kembang
Pulu Cepelok
Pulu Wak Banka
Pulu Pandan
Pulu Siput
Pulu Labu
COCOS (KEELING) ISLANDS
West Is.
South Is.
Pulu Kambing
Pulu Maria
South Passage
0
km.
5
96° 50'E
96°55'E

CHAPTER 1

SCIENTIFIC STUDIES IN THE COCOS (KEELING) ISLANDS: AN INTRODUCTION.

BY

C.D. WOODROFFE *

AND

P.F. BERRY **

INTRODUCTION

The Cocos (Keeling) Islands are a particularly isolated group of islands in the eastern Indian Ocean (Fig. 1). They comprise a southern group, the South Keeling Islands (12° 12' S, 96° 54' E), which form a coral atoll with a shallow lagoon fringed by a series of reef islands. A single horseshoe-shaped island (atollon), North Keeling (11° 50' S, 96° 49' E) is located 26 km to the north of the main group. They lie 900 km west of Christmas Island and 1000 km southwest of Java Head.

DISCOVERY AND SETTLEMENT

The group is named after the coconut (*Cocos nucifera*), which grew there in profusion, even before deliberate planting of all of the southern atoll as a part of the Clunies Ross estate, and Captain William Keeling. Keeling is believed to have been the first European to sight the islands in 1609 on his return from Bantam, on behalf of the East India Company, though there is no record of that sighting. The islands are not shown in the 1606 edition of Ortelius *Theatrum Orbis Terrarum*, but do appear in Blaeu's appendix to the third edition produced about 1631. They are recorded with the name *Cocos Eylanden* in a manuscript map drawn by Hessel Gerritsz in 1622, and on Dudley's *Arcano del Mare* (1646) on which it says that they were discovered by the English. On a Dutch chart produced in Amsterdam in 1659 they are called the Cocos Islands; though around this time they were also called the Triangular Islands. The English hydrographer Thornton used the name Kelling Island in his *Oriental Navigation* of 1703. Captain Ekeberg from Sweden visited North Keeling in 1740. There is an account of the islands in van Keulen's *Zeefakkel,* (6th edition, 1753), with a map attributed to the Dutch navigator, Jan de Marre (1729).

In his sailing directory for this region of the Indian Ocean, compiled in 1805, the British hydrographer, James Horsburgh, called them the Cocos-Keeling Islands, and named one of the islands after himself. After settlement the early inhabitants called them the Borneo Coral Reefs after the supply vessel the *Borneo,* owned by John and Joseph Hare and Co, and captained by John Clunies Ross. They were also known as the Keeling-Cocos Islands, and after 1955 they became officially the Cocos (Keeling) Islands.

Despite knowledge of the islands for 200 years or more, it was not until the early nineteenth century that they were settled and an interest was taken in them because they lay

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on a trade route from Europe to the Far East. The first settlement was accidental, Captain Le Cour and the crew of the brig *Mauritius* lived on Direction Island for several weeks after their ship was wrecked on the reef. Captain Driscoll in the *Lonach* went ashore on 24 November 1825, shortly after the men were rescued, and noted the wreck of the *Mauritius*. Shortly thereafter, on 6 December 1825, Captain John Clunies Ross, a Scottish trader sailing the *Borneo* for Alexander Hare's company, made a brief landing on the islands. During his visit he sounded the main channel, cleared an area on Horsburgh and Direction Islands, and planted cereals and vegetables.

In the following year a settlement was established by Alexander Hare, a somewhat discredited trader and associate of Ross, who brought with him a crew of largely Sumatran and Javanese seamen and an entourage of women of various nationalities, on the *Hippomenes*. John Clunies Ross and his family returned on 16 February 1827 (this is the date given by Ackrill 1984; several other authors state that he returned on 27 November 1827, i.e. Hughes 1950; this error appears to have been perpetuated since an account in Gleanings in Science, Anon 1830; the correct dates are given by Gibson-Hill 1952), with the intention of commencing a settlement on the islands. Ross expressed surprise at finding Hare and a large group of people there, although it would seem that he should have known that Hare might already be there, since he had not found him at Cape Town on the outward journey. Relations between Ross and Hare deteriorated; Hare initially lived on Home Island, though with some occupation of West Island, Direction Island, and Horsburgh Island. Ross initially settled on Pulu Gangsa, just to the north of Home Island (presently joined onto Home Island, and the site of the cemetery); but he soon moved his house down to the central part of South Island. Hare, on the other hand, eventually moved from Home Island, to Prison Island, according to poorly substantiated reports because the women of his party were being molested. It appears that he maintained a party of womenfolk, and most of the children, under close supervision in the lower storey of his house. Rear Admiral Sir Edward Owen noted in a letter of 10 July 1830, that Hare engaged in 'unrestricted intercourse with such females of his establishment as he (might) deem worthy of his attentions' . The history of this time is particularly colourful, although it has also been subject to a lot of misrepresentation (Gibson-Hill 1947, Ackrill 1984). In part this results because the only records that survive reflect Ross' view of the circumstances, and his objectives and those of Hare differed. Ross endeavoured to establish a successful settlement, aspiring to a great trading 'entrepot'. Hare, on the other hand, sought obscurity and his behaviour, according to Ross, became increasingly unbalanced and debauched. Initially both claimed ownership of the islands, but in 1831 Hare finally left the atoll, and he died in Batavia in the following year. The Malay workers, who joined with Ross, are the ancestors of many of the Cocos Malays there today, and the Clunies Ross family, who became known as 'Kings of the Cocos', reigned over the islands for more than 150 years (Hughes 1950).

John Clunies Ross died in 1854. He was succeeded by his son John George Clunies Ross until 1871. After his death in 1871 George Clunies-Ross took possession until 1910. John Sydney Clunies-Ross ruled from 1910 to 1944, and John Cecil Clunies-Ross thereafter. The papers of the Clunies-Ross family contain much useful information on the islands. The early papers of John Clunies Ross are particularly valuable for their description of the islands, although some were lost in a fire.

In 1857 the islands were declared a part of the British Dominions by Captain Fremantle who arrived aboard H.M.S. *Juno*, having misread his directions which instructed that he annex Cocos in the Andaman Islands (Gibson-Hill 1947). Responsibility for supervision of the islands was transferred over the years to the Governments of Ceylon (1878), the Straits Settlements (1886), Singapore (1903) and

Ceylon again (1939-1945). In 1886 Queen Victoria granted all of the islands, under certain provisions, to John George Clunies Ross, in perpetuity. They became a Territory of the Commonwealth of Australia in 1955, and in 1978 Australia purchased all of the lands, excepting the family home, from the Clunies Ross family for Aus$ 6.25 million. In 1984 the Malay population voted to become a part of Australia. Initially the Territory was administered by the Commonwealth government, but it is now being transferred to the responsibility of the state government of Western Australia.

Today the islands are inhabited by the descendants of the original (Malay) settlers, though there have been several additional intakes of workers from various parts of Southeast Asia. There are about 400 Malays living in the kampong on Home Island. The Great House of the Clunies Ross family, Oceania House, is also on Home Island, set amongst 5 ha of grounds. Across the lagoon on West Island more than 200 people, associated with various departments of the Australian Government, live alongside the airfield, which was used as an important refueling stop on commercial air routes between Europe and Australia until the advent of larger aircraft in the 1950s allowed Cocos to be by-passed.

NATURAL HISTORY AND SCIENTIFIC DESCRIPTION OF THE ISLANDS

The Cocos (Keeling) Islands have held a special place in the literature on coral atolls because they represent the only atoll that Charles Darwin visited, and they played a central role in his discussion of his theory of coral reef development. The natural history of the islands was, in fact, uncharacteristically well-known by the turn of the century, because of the visits of a number of naturalists in addition to Darwin. It is interesting to note that rather than confirming Darwin's observations and interpretations of the atoll, many of the works of subsequent naturalists lead them into conflict with Darwin's views, and that Cocos was also subject to interpretations completely contrary to Darwin's. Thus, Guppy (Guppy 1889, 1890a, 1890b) subscribed, at least in part to the views of John Murray, who funded his visit. Wood-Jones put forward an entirely alternative view to Darwin's, in his book *Coral and Atolls* (Wood-Jones 1912). However, the strongest criticism of Darwin came from John Clunies Ross himself, who was absent at the time of Darwin's visit. His review of Darwin's book, published posthumously, was a bitter, vitriolic attack on Darwin's ideas (Ross 1855).

Early accounts of the nature of the islands (Anonymous 1830) include a paper on the formation of the islands by Ross (1836), and descriptions from short visits. Owen's description (1831) appears to be based upon observations by Captain Sandilands who visited in February 1830 in the *Comet* (Owen, 1831), and the account in Holman (1840), is based largely on the accounts of Keating who left the atoll in November 1829 after less than a year there with Hare, and those of Captain Mangles. Van der Jagt (1831) visited and mapped the islands in 1829 in the *Blora*.

H.M.S. Beagle called into the Cocos (Keeling) Islands on its way home, in its third year at sea, arriving off the islands on 1 April, and leaving on 12 April 1836 (Darwin 1842, 1845, Fitzroy, 1839). The visit lasted only ten days, and for much of that time Captain Fitzroy and the crew of the *H.M.S. Beagle* were engaged in survey work; this forming the basis of many of the subsequent charts. A more thorough hydrographic survey was undertaken in June and July 1983 by *RAN Moresby*. Darwin's visit has been analysed in detail by Armstrong (1991).

The islands were subsequently visited by Henry Forbes, who arrived at around 17 January 1879, and left on 9 February 1879. Forbes speculated on the origin of the islands, and devoted two chapters (chapters ii and iii) to Cocos in his book on the Eastern Archipelago (Forbes 1879, 1885).

Henry Brougham Guppy visited the Cocos (Keeling) Islands in 1888, his visit being funded by John Murray. Murray had examined a series of rock specimens collected from Christmas Island (Indian Ocean) by Captain Pelham Aldrich who had been there in *H.M.S. Egeria* in 1887, and had found some that were rich in phosphate. He sent Guppy to visit Christmas Island for a further examination. Guppy needed fine weather for a landing on Christmas Island, and took passage on the Clunies Ross vessels as the only way to get there. The weather was apparently not calm enough within the period that Guppy could stay to get to Christmas, and Guppy spent 10 weeks on Cocos waiting, before returning to Europe without getting to Christmas. Gibson-Hill (1947) suggests, however, that during the 5 months that Guppy endeavoured to get to Christmas, George Clunies-Ross' brother managed to visit the island and establish a settlement of a group of Malays in Flying Fish Cove. As a consequence of that settlement, the Clunies-Rosses began with about half of the shares (with John Murray) of the Christmas Island Phosphate Company when that commenced in the 1890s. Guppy meanwhile undertook an extremely detailed account of the Cocos (Keeling) Islands, with extensive observations on the nature and rate of operation of geological processes (Guppy 1889, 1890a, 1890b).

There were other visits and accounts during this time; W.E. Birch, with Rev E.C. Spicer as naturalist, was on Cocos 20-28 August 1885 (Birch 1866). The lone round-the-world sailor Joshua Slocum arrived on 17 July 1897 in the *Spray*, and considered that 'if there is a paradise on this earth it is the Keeling-Cocos' (Slocum 1899).

Wood-Jones was the medical doctor at the Cable Station on Direction Island, and was on Cocos from June 1905 to September 1906. This afforded him ample opportunity to look around the atoll. He revisited Cocos briefly in 1907 as a guest of George Clunies-Ross, and subsequently married one of his daughters. He wrote a book, *Coral and Atolls,* incorporating his observations. However, the book suffered 'in parts from a considerable carelessness, and an over-optimistic acceptance of unconfirmed visual records' (Gibson-Hill 1947 p.159). His view of the mode of formation of the reef differed both from that of Darwin, and that of Murray which received some modification from Guppy.

The detailed observations of Wood-Jones are surpassed only by those of Gibson-Hill. Gibson-Hill was medical officer on Direction Island from 20 December 1940 until 10 November 1941. He made various collections of organisms, some material of which disappeared from the Raffles Museum during the Japanese occupation of Malaya in the World War II. Nevertheless his fascination with Cocos persisted, and Gibson-Hill published a series of notes on the islands, including both his own observations and collections (Gibson-Hill, 1947, 1948, 1949, 1950a, 1950b, 1950c, 1950d, 1950e, 1950f, 1950g), and his reprinting of earlier literature on the atoll (Gibson-Hill 1953).

Since Gibson-Hill's reviews of Cocos natural history, there have been expeditions by the Academy of Natural Sciences of Philadelphia (1963 and 1974) and the Western Australian Museum (Berry 1989), as well as some visits from individual naturalists (e.g. Alfred 1961). Williams has produced an annotated bibliography of the natural history of the islands, which appears in a recent *Atoll Research Bulletin* (Williams 1990). A summary of major collections on Cocos is given in Table 1.

BIOGEOGRAPHICAL RELATIONSHIPS OF THE COCOS (KEELING) ISLANDS BIOTA

The Cocos (Keeling) Islands are not only extremely isolated, but they also lie at the western extension of the Western Pacific marine biogeographic province. For many species Cocos represents their western limit of distribution. The biota is derived, therefore, primarily from that of the tropical Indo-West Pacific; taxa from the western Indian Ocean are poorly represented. The plants contain a large component of drift-dispersed pantropical species, found throughout the Indian and Pacific Oceans, but the major source is western Java (Guppy 1890a). Similarly, in the case of the marine biota, the most likely source of larval recruitment is also the Indonesian and eastern Indian Ocean region.

For all groups covered of marine biota described in subsequent chapters in this volume, significant additions have been made to existing knowledge of taxa occurring at Cocos (Table 1). Total numbers of taxa in the groups discussed in this volume are summarised in Table 2. The level of collecting now undertaken at Cocos means that the terrestrial ecology is relatively well-known, and in the marine groups is such that significant numbers of additional taxa are unlikely to be added. On this basis several generalised conclusions can be drawn regarding the biogeographical relationships of the Cocos (Keeling) Islands.

There is almost no endemism in the Cocos biota. The Buff-banded Rail, *Rallus philippensis andrewsi,* is considered an endemic subspecies, restricted to North Keeling, and the rat on Direction Island, *Rattus rattus keelingensis,* has been accorded subspecies status, and was considered by Wallace (1902) to be an example of rapid divergence; it can be traced back to the *Mauritius* which was wrecked in 1825. The angelfish *Centropyge joculator* is recorded only from Christmas and the Cocos (Keeling) Islands. The Cocos subspecies of *Pandanus tectorius,* which is only localised in occurrence, is also considered endemic (Williams 1990, this volume).

This lack of endemism may reflect the effect of rapidly oscillating sea levels during the late Quaternary, and the pattern of development of coral atolls, whereby the limestone plateau which was exposed at the last glacial maximum perhaps resembling the modern-day Christmas Island, was rapidly flooded during postglacial sea-level rise and all land was submerged in the early Holocene (10,000-8,000 years ago). The present reef islands appear to be no more than 4000 years old (Woodroffe et al. 1990a, 1990b). This implies that all the terrestrial biota must have recolonised the atoll in the last few thousand years. These sea-level fluctuations would also have had substantial implications for shallow-water marine biota, as the nature of the habitats must have altered drastically over that period also.

Some taxa which might be expected are conspicuously absent from Cocos. Guppy (1890a) has drawn attention to the absence of mangroves and *Nypa* palm, despite the arrival of propagules on the shore (The stand of mangroves on the northern end of Horsburgh Island can be attributed to planting by John George Clunies Ross). Some shallow marine taxa usually common on coral reefs are conspicuously absent in apparently suitable habitat (i.e. there are no benthic skates or rays in the lagoon). Marine taxa must either be pelagic as adults or have long-lived larvae or juveniles to reach Cocos.

Christmas Island is the nearest island to Cocos, and there is less similarity than might at first be expected between the biota found at Cocos and that at Christmas (Table 2). Undoubtedly this results from the contrasting physiography of the two islands.

Christmas Island is an uplifted (and apparently still uplifting) limestone island with outcrops of volcanic rocks on it. It reaches a maximum elevation of 361 m, and has probably been above water since the Eocene. It is covered by dense forest, and has only poorly-developed reef fringing its cliffed coastline. There are not the extensive reef flats or shallow lagoonal sandy or muddy areas which are found on Cocos.

In addition to the very different late Quaternary history, and the great contrast in the time available for establishment of terrestrial biota, the Cocos (Keeling) Islands are probably more subject to periodic catastrophic influences on the biota. The atoll has experienced several devastating tropical cyclones, which tend to have an impact all over the restricted land area of Cocos, as well as in shallow parts of the lagoon and reefs. There have been a series of coral and fish kills in the lagoon. Darwin (1842) noted an extensive area of dead coral in the southeastern corner of the lagoon. He speculated initially that this might have been due to slight emergence of the atoll, but then attributed it to the closure of a series of interisland passages through South Island and more resticted circulation in this part of the lagoon. Forbes recorded that in 1876, inky and foul smelling water had spread through the lagoon from the islands on the eastern rim (Forbes 1885). A similiar fish and coral kill has recurred, most noticeably in 1983, but also in intervening years. Its cause is still unclear. Forbes considered that the 1876 event may have been caused as a result of an earth tremor. The 1983 event was correlated with El Niño in an incisive, but unpublished account of it by Blake and Blake, who attributed it to an 'algal bloom' (red tide). An alternative explanation, considered more likely by members of the Western Australian Museum expedition (Berry 1989), is that it was caused by mass coral spawning at a time of poor circulaton as has been described by Simpson et al. (in press) on the Western Australian coast. It is significant that the mortalities at Cocos and Western Australia both occurred in March and this hypothesis for the cause of mass mortality of corals and other organisms in the Cocos lagoon would be further supported if it could be established that coral spawning occurs there in March. A minor episode of fish kill was also observed in 1992 (J. Tranter, pers. comm.). Infestations of *Acanthaster* have been reported from the reefs (Colin 1977), and are reviewed in more detail by Marsh (this volume).

Present diversity and abundance of reef organisms closely associated with living corals may have been reduced by the reduction of coral abundance and diversity on the reef slopes and in the lagoon as a result of these events. In view of the isolation of Cocos and the distance to be covered by propagules, if species are lost from the atoll as a result of such events, they are likely to be slow to recolonise.

Human impact on the Cocos (Keeling) Islands has been most devastating on the South Keeling Islands (the southern atoll), where the vegetation has been almost totally altered to coconut plantation. The birds which once characterised the atoll have all but disappeared, and it is the absence of large numbers of seabirds, which strikes one as the most conspicuous difference between North Keeling and the southern atoll. There have also been impacts on marine organisms which are eaten, *Tridacna gigas*, *Lambis lambis* (gong gong), *Birgus latro* and the palinurid lobsters, though it is to be hoped that management measures prevent the total elimination of any more of these species. At the same time occupation of the atoll has resulted in an influx of new species to the Cocos (Keeling) Islands. These vary from ornamental and food plants, and deliberate animal introductions, such for instance as the Green Jungle Fowl on West Island. Sheep, cattle, alpacas and black rhinoceroses and other animals have been temporarily contained within the Quarantine Station on West Island. Accidental releases, include the rats and the lone King Parrot on West Island. In addition there are numerous insects which have been introduced, and a large number of insect pests (Gibson-Hill 1950f, Holloway 1982).

STUDIES IN THIS VOLUME

The frequent visits of naturalists, and the detailed studies that they undertook, ensured that the Cocos (Keeling) Islands were perhaps the best-known, and certainly the most hotly debated group of reefs in the world, by the end of the nineteenth century. This continued in the first half of the twentieth century. Since the overviews of Gibson-Hill, however, there has been relatively little extension of knowledge about the islands. The terrestrial ecology of the South Keeling Islands has changed markedly since settlement as large areas have had their natural vegetation replaced by coconut plantation (now sadly largely overgrown), and as birds and other food resources have been exploited.

It is now possible to look in greater detail at the geological history of the atoll, and the marine ecology of its reefs and lagoon as the result of the development of several new techniques. Radiometric dating allows a new insight into the age of formation of coral limestones. Subsurface drilling, seismic profiling and dating allow geomorphological insight into those questions which intrigued the early naturalists to study Cocos. In the case of marine ecology, the development of more sophisticated underwater research methods, and particularly the use of SCUBA, has enabled the extension of collections into water depths that were previously only examinable by dredge, or not at all. It is thus in the areas of geological investigations, and in terms of the numbers of marine species on the atoll that the greatest advances in knowledge have been made in recent years.

This volume brings together a series of recent studies on the Cocos (Keeling) Islands. A preliminary examination of the birds of Cocos was undertaken by T. Stokes of the Australian National Parks and Wildlife Service (ANPWS) and others in 1982. Since that time ANPWS has carried out a number of studies of birds, particularly at North Keeling. Vegetation and marine habitats of the atoll have been mapped by D. Williams, who was seconded as Environmental Resource adviser to the Territory of the Cocos (Keeling) Islands in 1986-7. Mapping was undertaken using SPOT satellite imagery, aerial photographs and ground survey on a habitat data sheet, used by Williams and ANPWS staff.

A field survey of the inshore marine fauna and habitats of the Cocos (Keeling) Islands was undertaken 7-28 February 1989 by the Western Australian Museum under the leadership of P. Berry, sponsored by the Australian National Parks and Wildlife Service. During that fieldtrip a total of 37 stations was occupied (some more than once), in order to sample the major marine habitats (Fig. 2), which had been partly described and mapped by D. Williams. The survey of marine fauna involved SCUBA, snorkelling and reef walking, as well as the use of an ichthyocide and a small hand spear in the case of fishes and the photographing of habitats. Specimens have been lodged in the Western Australian Museum. Accounts of the corals, collected and identified by J.E.N. Veron, and of marine molluscs by F. Wells, echinoderms by L. Marsh, fishes by G. Allen and W. Smith-Vaniz, barnacles by D. Jones, and decapod crustaceans by G. Morgan appear in this volume.

Water Resources represent an important aspect of the present settlement of Cocos, and have been studied over the last 6 years by A. Falkland. He describes the climate of Cocos, and the implications for Water Resources in this volume. Drilling undertaken for the water resources study has also provided data for a geomorphological study of the Cocos (Keeling) Islands by C. Woodroffe and R. McLean. Their geological reassessment of Cocos has involved detailed descriptions of reef islands and subsurface stratigraphy and chronology, as well as other studies. The results of seismic profiling are described by

D.E. Searle, lagoon hydrodynamics by P. Kench and lagoonal sediments by S.G. Smithers.

There are some aspects of the ecology and geomorphology of the Cocos (Keeling) Islands which have not been adequately treated in this volume. There is no account of the insect fauna, for instance, nor have the marine algae been studied in any great detail. It is hoped that the studies which are presented here provide a stimulus for continued scientific study and research on the Cocos (Keeling) Islands.

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Table 1. Summary of collections of flora and fauna from the Cocos (Keeling) Islands

Date	Expedition/ Collectors	Group Collected	Publication
1836	*H.M.S. Beagle*	crustacea	Darwin 1845, Chancellor et al. 1988
		fishes	Jenyns 1842
		plants	Henslow 1838
		shells	Marrat 1879
1854-5	A.J. Anderson and G. Clunies-Ross	fishes	Bleeker 1855
1878	H.O. Forbes	corals	Guppy 1889, Ridley 1884, Ridley and Quelch 1985
		plants	Forbes 1885
1905-6	F. Wood-Jones	brachyurans	Wood-Jones 1909
		corals	Vaughan 1918
		echinoderms	Clark 1912
		plants	Wood-Jones 1912
1940-1	C.A. Gibson-Hill	fishes	Marshall 1950
		brachyurans	Tweedie 1950
		stomatopods	Tweedie 1950
		anomura	Forest 1956
		cephalopods	Rees 1950
		echinoderms	Clark 1950
		molluscs	Abbott 1950
		corals	Wells 1950
		birds	Gibson-Hill 1949, 1950e
1963, 1974	Academy of Natural Sciences of Philadelphia	molluscs	Maes 1967
		fishes	Randall 1975, Smith-Vaniz and Randall 1974
1961	A.E. Alfred	birds	Alfred 1961
1985	I.R. Telford	plants	Flora of Australia
1986/7	D.G. Williams	plants	This volume
		marine algae	
1989	Western Australian Museum	coral	Berry 1989,
		echinoderms	This volume
		fishes	
		molluscs	
		barnacles	
		decapod crustaceans	

Table 2. Number of species recorded at Cocos (Keeling) and Christmas Islands.

GROUP	Cocos Is.	Christmas Is.
Reef-building coral	99	85
Decapod crustaceans	198	204
Molluscs	c 610	c 490
Echinoderms	88	90
Fishes	c 550	568
Native birds	38	88
Plants	130	386

Figure 1. The Indian Ocean, showing the location of the Cocos (Keeling) Islands.

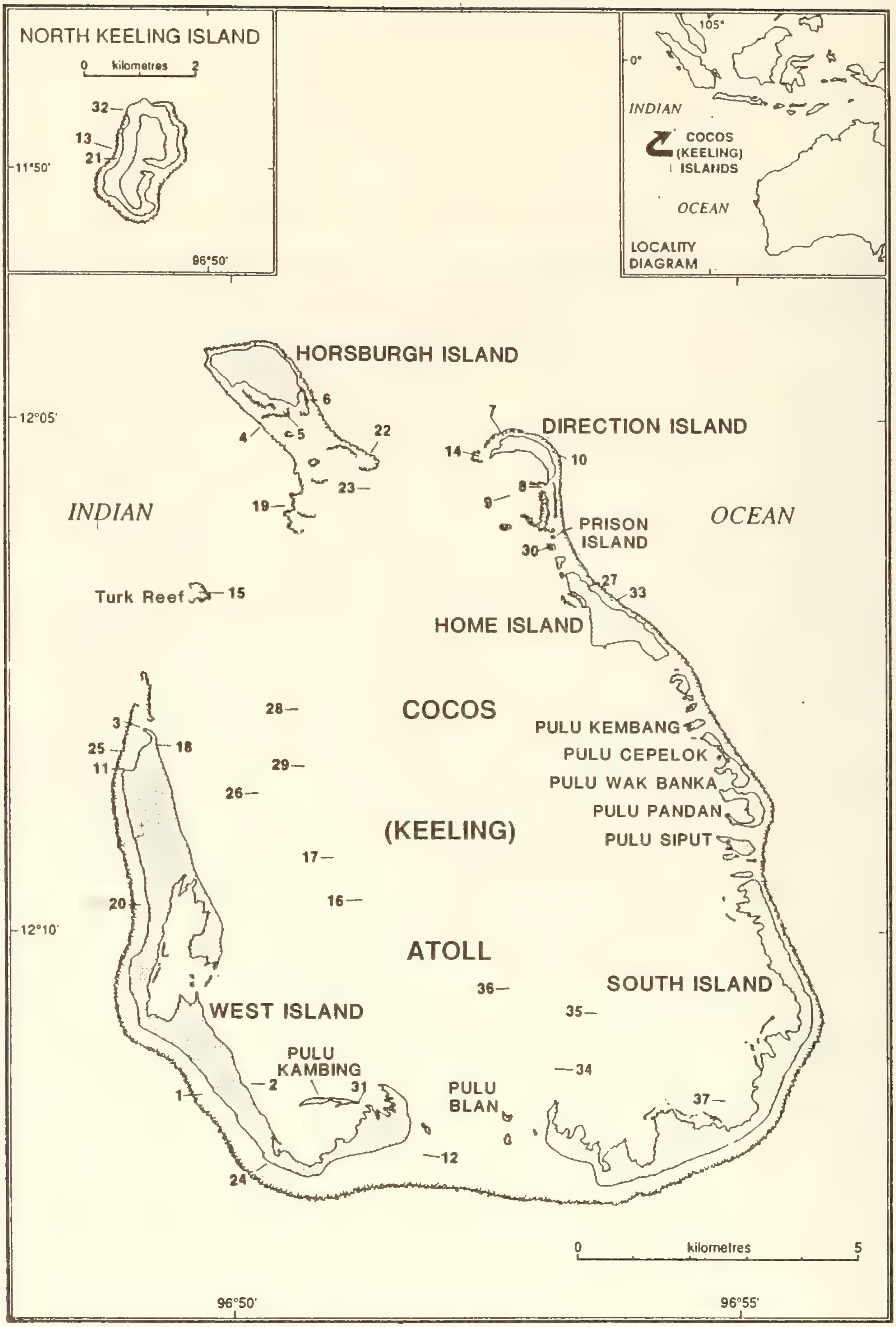

Figure 2. The Cocos (Keeling) Islands, showing stations from which collections were made during the Western Australian Museum expedition in 1989. These stations cover a series of different marine habitats (see Chapter 8, Fig. 1), which can be summarised as: Outer Reef Slope (9 sites: stations 4, 7, 13, 15, 19, 22, 25, 32, and 33), Reef Flat (13 sites: stations 1, 3, 6, 8, 10, 11, 12, 14, 20, 21, 24, 27, and 30) and lagoon (14 sites: stations 2, 9, 16, 17, 18, 23, 26, 28, 29, 31, 34, 35, 36 and 37).

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CHAPTER 2

CLIMATE, HYDROLOGY AND WATER RESOURCES OF THE COCOS (KEELING) ISLANDS

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A.C. FALKLAND

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CHAPTER 2

CLMATE, HYDROLOGY AND WATER RESOURCES OF THE COCOS (KEELING) ISLANDS

BY

A.C. FALKLAND *

CLIMATE AND HYDROLOGY

GENERAL FEATURES

The Cocos (Keeling) Islands are situated in the Humid Tropical zone. For most of the year they are under the influence of South East Trade Winds. Cyclonic conditions are sometimes experienced, particularly between November and March. Rainfall on the island is influenced to some extent by El Niño events.

The main climatic features are:

- annual rainfall varying between about 850 and 3300 mm,
- annual potential evaporation of about 2000 mm,
- relatively uniform temperatures, ranging from about 18°C to 32°C,
- relative humidity varying from about 65% to 84%,
- daily atmospheric pressures ranging from 973 to 1018 hectopascals, and
- mean daily wind speeds varying from 4.7 and 8.1 metres/second with a maximum gust during a cyclone recorded at 48.8 metres/second (176 kilometres/hour).

METEOROLOGICAL DATA

CURRENT NETWORK

A meteorological station (No. 200284, Cocos Island A.M.O.) has been operated continuously on West Island on the eastern side of the airstrip by the Bureau of Meteorology (Australia) since February 1952. It is located at latitude 12°11'S, longitude 96°50'E and at an altitude of 3 metres. At the station, the following meteorological parameters, important to water resources assessment, are measured and recorded:

- air temperature (wet and dry bulb, and dew point),
- atmospheric pressure,
- cloud cover,
- wind speed and direction,
- rainfall, and
- pan evaporation.

Temperature, atmospheric pressure, cloud cover and wind are measured every 3 hours. Daily averages can be derived from eight readings. Daily total wind run is also

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recorded. Rainfall and pan evaporation are measured daily at 9 a.m. Rainfall is also recorded on a pluviograph (continous recorder). In addition to the above surface level measurements, upper air data is collected via regular balloon releases from the station.

Daily rainfall is measured and recorded at two other sites on the South Keeling atoll. The first site is located on a peninsular about 100 metres north of the jetty on Home Island. Data has been recorded at this site by the Cocos (Keeling) Islands Council (formerly Home Island Council) since 28 May 1986. This site is now described as station number 200733 by the Bureau of Meteorology. The second site is located on the eastern side of the administration building at the Quarantine Station on West Island. Data has been recorded at the second site by Quarantine Station personnel since 1 January 1989. Some of the data at both of these sites has not been recorded each day but rather recorded as a total for two or three days. Therefore, these records cannot be used for accurate daily rainfall analyses but they are suitable for monthly rainfall analyses. No meteorological data is recorded on the North Keeling atoll.

PREVIOUS DATA COLLECTION SITES

In 1904 a rainfall station was opened on Direction Island and operated by staff at the cable station. A climatological station was opened "probably soon after, although no files survive to prove this" (Bureau of Meteorology 1978). Other notes in the file entry indicate that this station operated to 1952 when the current station opened on West Island.

There is some anecdotal evidence that the Clunies-Ross family recorded rainfall on Home Island. However, no records were sighted and it is not known whether any of these records were incorporated into the Bureau's records. As the rainfall records extend back to December 1901, it is probable that rainfall was recorded on Home Island from then until the rainfall station on Direction Island was opened in 1904.

Rainfall records under the heading 'Cocos Island Composite' are available from the Bureau of Meteorology for all but 17 months from December 1901 to the present. Months with missing data are November and December 1914, all months of 1915, January 1916, April 1946 and February 1952. An early entry in a Bureau of Meteorology file states that "the records for 1915 were incomplete on account of the instruments being destroyed in November 1914 by German warship 'Emden'. Records were recommenced in November 1915". The missing data in 1946 and 1952 appears to be due to staff and location changes. Overall, the length of record and the small number of missing months (and hence days) of record, have ensured a very good data set for the Cocos (Keeling) Islands.

SELECTED METEOROLOGICAL DATA FROM WEST ISLAND

Graphical and tabular summaries of important meteorological parameters recorded at the West Island meteorological station are presented in this and the next two sections. Summaries of temperature, relative humidity (a derived parameter), atmospheric pressure, cloud cover, wind speed and wind direction are presented in this section. More extensive summaries of rainfall and evaporation are provided below. The data used for these summaries, unless otherwise indicated, are for the period February 1952 to December 1991.

TEMPERATURE

Mean, maximum and minimum daily temperatures are shown in Figure 1 and in Table 1 for each month of the year. The maxima and minima are extreme values derived from all of the 3 hourly data. The mean values were estimated by averaging mean daily maxima and minima.

The mean daily temperature is highest in March (27.5°C) and lowest in July and August (25.8°C). The extreme maximum temperature is 32.4°C recorded in February 1979 and the extreme minimum temperature is 18.3°C recorded in August 1979.

RELATIVE HUMIDITY

Mean, maximum and minimum daily relative humidities are shown in Figure 2 and in Table 2, for each month of the year. These values are derived from 9 a.m. and 3 p.m. readings of wet and dry bulb temperature and atmospheric pressure using standard meteorological methods.

The mean daily relative humidity is highest from April to July (77%) and lowest from September to December (72%). The mean daily maximum relative humidity is 84% recorded in the months of June and July 1960, April and August 1973, and April 1974. The mean daily minimum relative humidity is 65% recorded in November 1956. Extreme maxima and minima were not computed.

ATMOSPHERIC PRESSURE

Mean, maximum and minimum daily atmospheric pressures are shown in Figure 3 and in Table 3, for each month of the year for the period February 1952 to July 1987. The shorter period was used as extreme maxima and minima had not been computed for the full data set. The maxima and minima are extreme values for each month and, as with the mean values, they are derived from the full 3 hourly data set.

The mean daily atmospheric pressure is highest in September (1012.2 hectopascals) and lowest in February (1008.4 hectopascals). The extreme maximum atmospheric pressure is 1018.5 hectopascals recorded during the months of October 1952 and July 1984 and the extreme minimum atmospheric pressure is 970 hectopascals recorded during cyclone 'Doreen' on 21 January 1968.

It is noted that the atmospheric pressures referred to in this section are at the level of the station. The atmospheric pressure at mean sea level is obtained from these readings by adding an amount of less than one hectopascal. Due to this small difference and the low altitude of the islands, the atmospheric pressure at the station can be used as an indicator of atmospheric pressure throughout the islands.

CLOUD COVER

Cloud cover (or cloudiness) is measured in oktas or the number of eigths of the sky filled with cloud. Mean, maximum and minimum daily values for each month of the year are shown in Figure 4 and Table 4. Data are derived from all observations for the period 1952 to 1987.

The mean daily cloud cover varies between 5.0 and 5.3 oktas, from April to July and 4 oktas for the other 8 months. The mean daily maximum cloud cover is 6.8 oktas recorded in November 1973 and the mean daily minimum cloud cover is 3 oktas recorded in December 1987. Extreme maxima and minima were not computed.

WIND SPEED

Mean, maximum and minimum wind speed are shown in Figure 5 and in Table 5, for each month of the year. The mean values are taken from the 3 hourly data set from February 1952 to July 1987. The maxima and minima are extreme instantaneous values for each month for the full period of record (February 1952 to December 1991).

The mean daily wind speed is highest in January (8.1 metres/second) and lowest in February (4.6 metres/second). The mean daily maximum wind speed is highest in August (14.2 metres/second) and the mean daily minimum wind speed is lowest in March (just above zero). The extreme maximum wind speed was recorded at 48.8 metres/second during cyclone 'Doreen' on 21 January 1968. This wind speed is equivalent to 95 knots or about 175 kilometres/hour. The extreme minimum wind speed is zero (calm) which has been recorded on many occasions during all months of the year.

WIND DIRECTION

Figure 6 shows the wind direction resolved as a percentage of time for each month (January to June in left hand graph and July to December in right hand graph). Eight points of the compass are used. The graphs are for average wind directions from 9 a.m. and 3 p.m. readings for the period February 1952 to December 1990. The legends show the percentage of time that calm periods were recorded for each month .

The predominant wind direction is east to south east for all months, showing the influence of the South East Trade Winds on the islands. South easterly winds varied from 37% of the time in February to 60% of the time in November and December. Easterly winds varied from 17% in January to 44% in September. By comparison winds from the north, north east, south west, west and north west occurred for less than 6% of the time in all months and were often 2% or less. Southerly winds were experienced from a low of 2% of the time in September and October up to 17% of the time in January.

OCCURRENCE OF CYCLONES

A cyclone database maintained by the Bureau of Meteorology shows that a number of cyclones have affected the Cocos (Keeling) Islands. Table 6 presents data about cyclones since 1959 which have passed within approximately 100 kilometres of the island. One of the most damaging cyclone appears to have been 'Doreen' which passed directly over the South Keeling atoll. An interesting account of this cyclone is provided in Ryan (undated).

RAINFALL DATA AND ANALYSES

INTRODUCTION

As rainfall is one of the most important determinants of the water resources of the islands, a more detailed analysis of rainfall is presented. This section describes characteristics of the annual, monthly and daily rainfall. In addition to analyses of the temporal distribution of rainfall, comments about the spatial distribution of rainfall on the South Keeling atoll are made.

It is noted that from a water resource viewpoint, rainfall at time scales of days and months are of most significance. For recharge analysis, as part of groundwater studies on atolls such as South Keeling, daily rainfall data has been found to have sufficient time resolution. Monthly rainfall data can be used instead of daily rainfall data with a small loss in accuracy. For rainwater catchment studies, long sequences of daily rainfall data are ideal.

SPATIAL VARIATION OF RAINFALL

At the scale of the Indian Ocean, the variation of rainfall has been reported in Stoddart (1971) and Unesco (1977). Stoddart (1971) reviewed earlier reports and produced updated isohyetal maps for annual, seasonal and monthly rainfall based on coral island stations, primarily those with records longer than 10 years. The mean annual rainfall distribution is shown in slightly modified form in Figure 7.

The isohyetal map of mean annual rainfall shown in Unesco (1977), not shown here, is quite different particularly in the centre of the ocean. In the region of the Cocos (Keeling) Islands, however, the two maps are similar with isohyets approximately horizontal. The reason for the differences is not clear. On the South Keeling atoll, the spatial variation rainfall has been analysed by Falkland (1992a).

ANNUAL RAINFALL

The mean annual rainfall recorded at the West Island meteorological station is 1954 mm for the 40 year period of record from 1953 to 1992. Using the available annual record from 1902 to 1992, the mean annual rainfall is 1982 mm. In the longer data set, the annual rainfalls in 1914, 1915, 1916, 1946 and 1952 are missing giving a total number of 86 years. For the period 1902-1952, during which time the rainfall was recorded primarily on Direction Island, the mean annual rainfall is 2006 mm. Figures 8 and 9 show, respectively, histograms of annual rainfall for the periods 1902 to 1952 and 1953 to 1992.

Using the meteorological station records, the highest annual rainfall on record is 3291 mm which occurred in 1942 (Direction Island) while the lowest is 856 mm in 1991 (West Island). By comparison, the annual rainfall in 1991 on Home Island and at the Quarantine Station were, respectively, 837 and 820 mm.

The difference in the mean annual rainfalls for the two periods 1902-1952 and 1953-1992 is 2.6% of the latter period mean annual rainfall. This is considered a minor difference, given that site differences can easily account for long term rainfall depth differences of 10% or more. This result shows that the total depth of rainfall in the first half of the century (1902-1951), recorded primarily on Direction Island, is similar to that recorded in the second half of the century (1953-1991) on West Island.

The standard deviations of the annual rainfalls for the periods 1902-1992 and 1953-1992 are, respectively, 519 and 594 mm, showing a higher variability in the second half of the century. The coefficient of variation (Cv) of annual rainfall (obtained by dividing the standard deviation by the mean) for the two periods are, respectively, 0.26 and 0.3, again indicating the higher variability of recorded rainfall in the second part of this century on the island. These Cv's of annual rainfall are moderate when compared with other islands, especially low lying coral atolls. Christmas Island (Australia), a raised limestone island, about 900 kilometres north east of the Cocos (Keeling) Islands, has a similar Cv of 0.29. The atolls of Tarawa and Kiritimati (Christmas Island), Republic of Kiribati in the Pacific Ocean have higher Cv's (0.42 and 0.64, respectively). By comparison, Kwajalein atoll in the Marshall Islands Pacific Ocean has a much lower Cv of 0.14 (Falkland et al. 1991). The variation in annual rainfall between the three raingauge sites can be seen in Table 7.

From the data in Table 7, the rainfall for 1987 on Home Island is suspect as it is very low (only 65% of that at the meteorological station) and is inconsistent with the relative rainfall pattern between Home and West Island for the following years. Disregarding the suspect 1987 data for Home Island, there is slightly less rain occurring on Home Island than on West Island. The total rainfall recorded on Home Island from 1988 to 1992 is 5.3% less than at the meteorological station. The data also shows that the rainfall recorded on Home Island and at the Quarantine Station is, respectively, 3.4% less and 5.3% greater than at the meteorological station during the four year period 1989 to 1992.

Overall, the variation of rainfall between the three sites is not greatly significant when it is considered that the recording accuracy of rainfall at any one site is generally not better than about 10%. Although the period of concurrent rainfall records is short and therefore not suitable for making long term predictions, it is reasonable to conclude that the annual rainfall on the South Keeling atoll can be adequately described by the rainfall record at the West Island meteorological station.

MONTHLY RAINFALL

Mean, maximum and minimum monthly rainfalls recorded at the West meteorological station are shown in Figure 10 and in Table 8, for the March 1952 to December 1991. The mean monthly rainfall is highest in April (234 mm) and lowest in October (70 mm). The maximum monthly rainfall is 649 mm recorded in June 1988 and the minimum monthly rainfall is 2.8 mm recorded in September 1986.

A comparison of the monthly rainfalls recorded at the meteorological station and on Home Island for the period 1987 to 1991 is shown in Figure 11. A comparison of the meteorological station and the Quarantine Station monthly rainfalls for the period 1989 to 1991 is shown in Figure 12. A comparison of the cumulative monthly rainfall recorded at the three sites for the period of concurrent records (1989-1991) is shown in Figure 13.

Figures 11 and 13 indicate that the rainfall recorded at the Home Island site is less than that at the meteorological station. The lower rainfall recorded on Home Island may be due to a rain shielding effect of nearby tall vegetation at the raingauge site. Similarly, Figures 12 and 13 show that the rainfall recorded at the Quarantine Station site is slightly greater than that recorded at the meteorological station.

Double mass curves using cumulative monthly rainfall were plotted to check if any changes in the relative rainfall at the Home Island and the Quarantine Station sites had occurred during the periods of concurrent record. Figure 14 is the double mass curve using the rainfall data from the meteorological station and Home Island for the period 1987-1991. The plotted line shows some variation in slope, particularly from the early (1987) data to later data. Figure 15 is the double mass curve using the rainfall at West Island meteorological station and at the Quarantine Station for Home Island for the period 1989-1991. The corresponding Home Island data is also plotted in Figure 15. Very little variation in slope is shown for the Quarantine Station curve, indicating that there has been no major changes in this site or the method of recording since data collection commenced. However, the Home Island data indicates a greater variation. The variations in the Home Island record could be due to a number of reasons including progressive 'shading' of the raingauge from nearby trees, and errors or changes in the method of reading and recording rainfall data.

Regression analyses of monthly rainfalls at Home Island and the Quarantine Station with the meteorological station are summarised in Figures 16 and 17. The analysis using 60 monthly rainfall pairs for Home Island and the meteorological station gave a correlation coefficient (r) of 0.92 which indicates a reasonably good correlation. The value of r for 36 pairs of data from the Quarantine Station and the meteorological station was 0.97 which indicates a very good correlation. The regression equations are shown in Figures 16 and 17, respectively. These could be used to estimate monthly rainfalls at the two sites from the meteorological station monthly rainfall. They should be updated with additional data if they are considered for future use. The Home Island equation should be treated with caution as some of the Home Island data is suspected of being in error.

DAILY RAINFALL

While daily rainfall records are available from the Bureau of Meteorology for the full period of record (1904-1992) from the stations on Direction Island and West Island, only the data from the latter station were obtained for analysis. Daily rainfall has been recorded at the West Island meteorological station from 15 February 1953 to the present.

Daily rainfall has also been recorded on Home island (28 May 1986 to present) and at the Quarantine Station (1 January 1989 to present), as described previously. Daily data from all 3 stations was reviewed to the end of 1992.

The maximum recorded daily rainfall at the West Island meteorological station is 287 mm on 28 August 1956. There have been 54 days when the rain exceeded 100 mm and 6 days when it exceeded 200 mm. The maximum daily rainfall on Home Island, 242 mm, was recorded on 11 November 1989. On the same day the rainfalls recorded at the meteorological station and the Quarantine Station were, respectively, 203 mm and and 220 mm. The maximum daily rainfall at the Quarantine Station was 248 mm, recorded on 4 July 1992. On the same day the rainfalls recorded at the meteorological station was 252 mm. No daily rainfall was recorded at Home island on 4 July 1992 but the three day total to 6 July was only 141 mm.

On a daily basis, the rainfall records show considerable variation between the three rainfall recording sites, as some of the above results show. This is confirmed by general observations that individual storms can affect small areas of the atoll while leaving other areas quite dry. Hence, in the short term the rainfall pattern on Home island or elsewhere on West Island cannot necessarily be deduced from the West Island meteorological station records. Daily variability can also be seen from a number of high rainfall days in 1990 and 1992 when all three rain gauges were operational. The list below shows, in order, the date and the rainfalls at the meteorological station, Home Island and the Quarantine Station:

12 January 1990: 162, 164 and 171 mm,
14 April 1990: 117, 83 and 116 mm,
17 July 1990: 158, 210 and 115 mm,
6 September 1990: 30, 23 and 116 mm,
28 February 1992: 26, 112 and 87 mm,
14 April 1992: 6, 102 and 8 mm, and
4 May 1992: 11, 122 and 29 mm.

The longest period without any rainfall at the meteorological station is a period of 28 days in November 1985. The longest period when the total rainfall was less than 10 mm occurred between November 1985 and January 1986 when only 6.2 mm fell in 69 days. Long dry periods are of particular interest in the study of the island's water resources, as described below.

PLUVIOGRAPH RECORDS

A pluviograph (continuous rainfall recorder) is operated at the West Island meteorological station. These records enable rainfall patterns to be analysed (at time resolution in minutes). Such data are useful to analyse storm events and to construct rainfall intensity-frequency-duration (IFD) curves, for possible use in the design of stormwater facilities (e.g. roof gutters and downpipes). The Bureau of Meteorology has processed IFD information from pluviograph records between 1971 and 1991. This information is not presented here.

EVAPORATION DATA AND ANALYSES

INTRODUCTION

Estimation of actual or catchment evaporation is essential for any water resources study. Evaporation from a catchment includes evaporation from soil, water and other open surfaces such as paved areas and from the leaves of grasses, plants and trees. Evaporation from the stomates of leaves is called transpiration and the combined effects of this process and other evaporation is often described as evapotranspiration. The two processes are basically variations of the one process, namely, the conversion of water from a liquid to a gaseous state and some authors use the term evaporation instead of evapotranspiration. The term evaporation will normally be used instead of evapotranspiration for present purposes.

The estimation of actual evapotranspiration (ET_a) is generally done as a two stage process. Firstly, ET_p is estimated using a method based on meteorological data, such as the Penman (or Combination) formula (Penman 1948, 1956), or from pan evaporation data multiplied by appropriate pan coefficient(s). The Penman equation has generally been found to be a good ET_p estimation method in the humid tropics (Fleming 1987). Estimations using both the pan and Penman methods were made for the study of groundwater resources on the South Keeling atoll (Falkland 1988). Secondly, ET_a is determined using a water balance procedure taking into account the soil and vegetation conditions present on the island.

The estimation of ET_p, using both pan evaporation records and the Penman approach, is described below while the estimation of ET_a is described in a later section on water balance.

PAN EVAPORATION DATA

Daily pan evaporation has been recorded at the West Island meteorological station using a U.S. Class A pan from December 1981 to the present. Mean, maximum and minimum monthly pan evaporation totals are shown in Figure 18 and Table 9, for the period January 1982 to December 1991.

The mean monthly pan evaporation is highest in December (241 mm) and lowest in June (171 mm). The maximum monthly pan evaporation is 273 mm recorded in both December 1983 and December 1985. The minimum monthly pan evaporation is 146 mm recorded in May 1987.

EVAPORATION ESTIMATION (Penman equation)

The following meteorological parameters were available for use in the Penman equation:

- dry bulb temperature,
- wet bulb temperature,
- dew point temperature,
- cloud cover, and
- wind speed.

Using mean monthly values of the parameters above, estimates of monthly ET_p were made using the Penman equation (Penman 1948, 1956) for the period January 1982 to March 1986. This period was the longest period of available concurrent data at the time of investigations (Falkland 1988).

Water balance simulations (Falkland 1988) showed that similar results in terms of groundwater recharge were obtained from monthly data sets using either actual or mean values of ET_p. This shows the relatively constant nature of potential evaporation for a given month from year to year in a humid tropical environment such as the Cocos (Keeling) Islands. In the humid tropics, the net radiation energy term dominates the aerodynamic term in the Penman equation and it has been found that the simplified Priestly-Taylor method can also be used (Chang 1989). In the Priestley-Taylor method ET_p is equated to 1.26 times the energy term from the Penman equation (Priestley and Taylor 1972).

EVAPORATION ESTIMATION (pan method)

Pan evaporation requires multiplication by an appropriate pan coefficient to obtain estimates of ET_p. An initial estimate of the pan coefficient of between 0.7 and 0.75 was obtained by a procedure developed by Doorenbos and Pruitt (1977) using meteorological and specific site parameters.

The pan coefficient was later adjusted to 0.8 after sensitivity analyses were conducted with trial data using water balance simulations. The water balance results in terms of recharge to groundwater using five years of rainfall data (1982 to 1986) were found to be very similar for Penman estimates of ET_a and for pan data using a pan coefficient of 0.8 (Falkland 1988). Results were also similar for simulations using actual and mean monthly pan data.

Figure 19 shows the comparison of mean monthly ET_p estimates using both the Penman and pan methods for the five year period 1982 to 1986. The pan estimates are mean values for each month. The Penman estimates are based on mean monthly values of the relevant meteorological parameters. The mean annual ET_a based on the pan method was 1983 mm compared with the annual ET_a of 2048 mm based on the Penman method. This difference of about 3% is insignificant for practical purposes.

As the results from the two methods are very similar, the pan method using mean monthly data was adopted as ET_p estimates could be more easily computed with this method. Later studies (Falkland 1991, 1992a) used mean monthly pan evaporation data for the period 1982 to 1987. Recently, additional pan data to December 1991 was obtained and the mean monthly estimates of ET_a for the periods 1982-1987 and 1982-1991 were compared. The results are very similar. The mean annual values are in fact only 1 mm different (1986 and 1987 mm for the shorter and longer periods, respectively).

TRANSPIRATION MEASUREMENTS

At the commencement of detailed water resources investigations in 1987, it was realised that coconut trees (*Cocos nucifera*), prolific on most atolls including the Cocos (Keeling) Islands, are a major source of transpiration and, hence, loss from freshwater lenses. Direct measurements of coconut tree transpiration were, therefore, undertaken during the study. Due to time limitations, lysimeter or ventilated chamber methods could not be used. Instead, measurements were undertaken using a heat pulse velocity meter. The meter and its associated electronic data logger measures and records the velocity of an injected heat pulse in the sapwood of a tree by timing movement over a known distance. The technique had been used successfully on other types of trees but never, to the author's knowledge, on coconut trees. The results obtained from the one-week study suggested that transpiration rates per tree varied from about 70 to 130 litres/day (Bartle 1987). The range of values was considered to be the result of diurnal climatic variations.

The values obtained must be considered preliminary owing to a number of simplifying assumptions and the short period of observations. Further study over a longer time period is warranted as part of general scientific research. Based on this limited data, the total transpiration rate due to coconut trees is about 400-750 mm per year per tree in areas with 100% tree cover, where typical tree spacings of about 8 metres prevail. This has implications for water resources management and it may be prudent to selectively clear coconut trees from some freshwater lens areas to maximise the supply of water.

INFLUENCE OF EL NIÑO ON THE CLIMATE

Considerable research has been undertaken into the influence of the El Niño phenomenon (also called the El Niño Southern Oscillation or ENSO) on climatic patterns, particularly in the Pacific Ocean. Effects of strong El Niño events in the Pacific Ocean include significant sea surface temperature changes, ocean current and wind direction reversals, extreme variations in rainfall patterns, higher tides, storm activity in some locations and severe droughts in others.

The influence of the El Niño phenomenon is felt more widely than just the Pacific Ocean. Some research has been conducted into the connections between El Niño events and the weather patterns occurring in the north-eastern Indian Ocean area around Indonesia. Quinn et al. (1978) studied the connections between El Niño events and droughts in Indonesia. Their general conclusion was that droughts in Indonesia, indicated by low rainfall periods on Java, occurred in years when El Niño events were evident. A significant connection between low rainfall years and El Niño events was found for Christmas Island in the Indian Ocean (Falkland 1986).

The influence of El Niño events on the rainfall of the Cocos (Keeling) Islands is outlined in Falkland (1988, 1992a). A graph showing the relationship between the Southern Oscillation Index (an index of the strength of ENSO activity) on an annual basis and annual rainfall (expressed as a percentage of mean annual rainfall) is shown in Figure 20 for the period 1953 to 1991. Negative values of SOI are associated with El Niño activity with the more negative values indicating increased strength. Positive values indicate that El Niño activity is absent.

Figure 20 shows that there is a reasonable correlation between SOI and annual rainfall, with negative annual SOI values corresponding in general with less than average rainfall and vice versa. This trend is not always present, an example being the highly negative SOI during the 1982/83 El Niño when the rainfall was near average. Using linear regression analysis between annual SOI and rainfall data, a correlation coefficient of only 0.58 was obtained, indicating that the correlation is not strong. In certain periods (for example, 1953 to 1960, 1967 to 1981) the correlation is much better as can be seen in Figure 20 (r=0.89 and 0.82, respectively). It can be concluded that there is a reasonable correlation between El Niño activity in the Pacific Ocean and rainfall in the Cocos (Keeling) Islands.

WATER RESOURCES

TYPES

The water resources of the Cocos (Keeling) Islands consist essentially of groundwater and rainwater. Where conditions are favourable, fresh groundwater occurs on coral islands in the form of shallow freshwater lenses. Such lenses are found in some of the larger islands within the Cocos (Keeling) Islands. The groundwater from these lenses has been and is currently used as the major source of freshwater for potable and other uses on Home and West Islands.

Due to the generally porous nature of the soils and underlying geology, there is no significant surface runoff. Runoff only occurs in localised areas where the ground is compacted or paved and only for very short periods after heavy rain. Rainwater collected directly from roofs of buildings is a valuable supplementary source of water.

GROUNDWATER OCCURRENCE

FRESHWATER LENS CHARACTERISTICS

Freshwater lenses occur beneath the surface of some islands. The upper surface of a freshwater lens is the water table and the lower surface is a boundary between freshwater and saline water. The lower boundary is not a sharp interface but rather is in the form of a transition zone. Within the transition zone the water salinity increases from that of freshwater to that of seawater over a number of meters.

A typical cross section through a small coral island showing the main features of a freshwater lens is presented in Figure 21. It must be noted that there is considerable vertical exaggeration in the diagram. In practice, the vertical scale is much smaller compared with the horizontal scale. The transition zone tends to be as thick as or thicker than the freshwater zone on many small coral islands. As shown in the diagram, there is often an asymmetric shape to the lens with the deepest portion displaced towards the lagoon side of the island.

The salinity of the upper surface of a freshwater lens can be obtained by measurements at exposed water surfaces such as wells and pumping galleries. The lower surface can be determined accurately by establishing a recognisable salinity limit for freshwater and drilling through the lens and testing the water at different depths for salinity. It can also be estimated approximately by surface geophysical (electrical resistivity and electromagnetic) techniques.

The salinity limit adopted for freshwater for the Cocos (Keeling) Islands is 600 mg/l chloride ion concentration. This limit is approximately equivalent to an electrical conductivity (specific conductance) reading of 2600 µmhos/cm at the standard temperature of 25°C (Falkland 1988, 1992a).

According to classical 'Ghyben-Herzberg' theory (Badon Ghyben 1889, Herzberg 1901), for every unit height of fresh water occurring above mean sea level there will be about 40 equal units of underlying fresh water below mean sea level. This theory assumes that the two fluids, freshwater and seawater, are immiscible (i.e. that they do not mix). In practice, the two fluids do mix due to mechanical and molecular diffusion and a transition zone forms with salinity gradually increasing from that of freshwater to that of seawater. In practical situations, the 1:40 ratio can be used as a guide to determine the mid-point of the transition zone from the water table elevation above mean sea level. It does not provide a means of determining the base of the freshwater zone and other methods described above are required.

INFLUENCING FACTORS ON FRESHWATER LENSES

The size and salinity distribution of freshwater lenses, particularly the thickness of freshwater and transition zones, are dependent on many factors but the most important are:

- rainfall amount and distribution,
- amount and nature of surface vegetation and the nature and distribution of soils (these factors influence the evapotranspiration),

- size of the island, particularly the width from sea to lagoon,
- permeability and porosity of the coral sediments, and the presence of solution cavities,
- tidal range, and
- methods of extraction and quantity of water extracted by pumping.

For small coral sand islands, an approximate relationship has been derived (Oberdorfer and Buddemeier 1988) between freshwater lens thickness, annual rainfall and island width as follows:

$$H/P = 6.94 \log a - 14.38$$

where

H = lens thickness (depth from water table to sharp interface or mid-point of transition zone in metres),
P = annual rainfall (metres), and
a = island width (metres).

This equation indicates that no permanent freshwater lens can occur regardless of rainfall where the island width is less than about 120 metres. Using the mean annual rainfall (1938 mm measured at the West Island meteorological station) for the Cocos (Keeling) Islands, the minimum island width for a small freshwater lens (say 5 metres thick) to occur is about 280 metres (say 300 metres). Thus, as an approximate guide, it is unlikely that a permanent freshwater lens suitable for groundwater extraction could be found on the South Keeling atoll where the width of the island is less than about 300 metres. It is noted, however, that other factors which are not accounted for in the above relationship, particularly the permeability of the coral sediments and the density of vegetation, have an effect on the occurrence of freshwater lenses. Further comments based on observed data on West Island are given later. The geological influences are considered in more detail below.

GEOLOGICAL INFLUENCES ON FRESHWATER LENSES

The geology of the South Keeling atoll consists of coral sediments, several hundreds of metres thick, overlying a volcanic seamount. From a hydrogeological viewpoint, the geology of most interest is that of the upper part of the atoll where freshwater lenses are found to occur. From a number of recent water investigations on the South Keeling atoll (Falkland 1988, 1991, 1992a, 1992b), freshwater lenses do not exceed 20 metres in thickness. Within this 20 metre zone, two major geological layers are found: a younger (Holocene), upper layer consisting of unconsolidated coral sediments and an older (Pleistocene), deeper layer of coral limestone. While no extensive investigations of surface geology have been undertaken on North Keeling atoll, it is expected that similar geological conditions would prevail there.

Similar to findings on other atolls in the Pacific Ocean, an unconformity was found from drill cores between the relatively low permeability Holocene sediments and underlying higher permeability Pleistocene limestone at depths of less than 20 metres (Falkland 1988). Using the early results and data from additional boreholes on West Island, Home Island, South Island and Horsburgh Island, the unconformity was found at depths varying between about 8 and 17 metres below ground surface (Woodroffe et al. 1991). These depths correspond, respectively, to depths between 7 and 16 metres below mean sea level.

The presence of this unconformity is due to a period of emergence of the island with solution and erosion forming a karst surface. Uranium-series dating of the older limestone indicates that it was formed during the last inter-glacial period about 120,000 years ago (Woodroffe et al. 1991). The upper sediments have been laid down in the Holocene since about 10,000 years ago. Three phases of deposition have been identified in the Holocene (Woodroffe et al. 1990a, this volume). From the start of the Holocene to at least 5000 years ago, sediments accumulated rapidly as sea level rose. A conglomerate platform radio-carbon dated at 3000 to 4000 years ago was then formed during a period of relatively stable sea level. Since then unconsolidated sands and larger sediments have been deposited to form the present reef islands. Dating of *in-situ* corals has shown that the sea level was about 0.5 to 1.5 metres higher about 3000 years ago than today (Woodroffe et al. 1990a, 1990b).

The unconformity described above is very significant to the formation of freshwater lenses. The limestone sediments below this unconformity have relatively high permeabilities and mixing of freshwater and seawater is readily facilitated. In the relatively less permeable upper sediments, mixing is less likely to occur. The unconformity, therefore, is one of the main controlling features to the depth of freshwater lenses.

WATER BALANCE AND RECHARGE ESTIMATION

RECHARGE

The freshwater lenses in the Cocos (Keeling) Islands are recharged naturally from rainfall. Not all rainfall incident on the islands, percolates to groundwater, as much of it is evaporated or transpired. Essentially, natural recharge is the net input from rainfall to groundwater after all evaporative losses have been deducted and soil moisture requirements have been met.

It is important that accurate estimates of recharge be obtained as it is one of the main determinants of the sustainable yield of freshwater lenses. Recharge can be estimated by a number of techniques. One of the most common and useful techniques is a water balance (or water budget) approach where water inputs to, and water outputs from, the surface of the island are quantified. This approach was used in water resources investigations of Home and West Islands (Falkland 1988, 1992a) and South Island (Falkland 1991).

WATER BALANCE EQUATION

Recharge can be described by a water balance equation using a specified reference zone and a specified time interval. The reference zone for a freshwater lens on a coral atoll is that zone extending from above the surface of the island down to the water table. In this zone, the flow of water is essentially vertical. The water balance equation for the upper zone on a coral island, such as those in the Cocos (Keeling) Islands, can be described as:

$$R = P - ET_a + dV$$

where

R = recharge,
P = rainfall,

ET_a = actual evaporation from all surfaces, and
dV = change in storage within the soil moisture zone (it can be a positive or negative change)

As noted earlier, there is no term for surface runoff as this does not occur due to the very high infiltration capacity of the coral soils.

The actual evaporation term (ET_a) includes evaporation from interception storage (for example, the leaves of trees, bushes and grass), from vegetation tapping water from the soil moisture zone and from trees with roots that penetrate to the water table and thus transpire water directly from the freshwater lens.

Computations with this equation were conducted using a daily time interval, as recommended by Chapman (1985). It has been shown that computations using a monthly time step leads to an under-estimation of recharge for the Cocos (Keeling) Islands (Falkland 1988) and on other atolls (for example, Kwajalein: Hunt and Peterson 1980). Daily rainfall data and mean daily evaporation estimates were, therefore, used.

DESCRIPTION OF THE RECHARGE MODEL

A recharge model was developed, and a computer programme (WATBAL) written, to simulate the water balance in the upper zone and derive a monthly time series of recharge. The model is shown in Figure 22 and a brief description follows.

The recharge model allows for interception storage by vegetation. A maximum value for the interception storage (ISMAX) can be defined and it is assumed that this store must be filled before water is made available to the soil moisture storage. Typical values of ISMAX are 1 mm for predominantly grassed catchments and 3 mm for catchments consisting predominantly of trees (particularly coconut trees). The airfield area on West Island is predominantly grassed while South Island and some of the northern parts of West Island consist predominantly of trees. Much of Home Island is intermediate between these two limits. Evaporation is assumed to occur from the interception storage at the potential rate.

The recharge model incorporates a soil moisture zone from which the roots of shallow rooted vegetation (grasses, bushes) and the shallow roots of trees can obtain water. Water requirements of plants tapping water from this zone are assumed to be met before any excess drains to the water table. Maximum (field capacity) and minimum (wilting point) limits are set for the soil moisture in this zone. Above the field capacity, water is assumed to drain to the water table. Below the wilting point, no further evaporation is assumed to occur.

The thickness of the soil moisture zone (SMZ) for the Cocos (Keeling) Islands was estimated as 500 mm based on observations of the soil profile and from studies on other atolls. Field capacity (FC) was assumed to be 0.15 based on observations of local soil type and typical values for this type of soil. Wilting point (WP) was assumed to be 0.05 based on typical values (for example, Linsley and Franzini 1973) for sand-type soils and from studies elsewhere. The operating range of soil moisture is thus assumed to be from 25 mm to 75 mm.

In the model, the amount of evaporation from the SMZ is assumed to be related to the available soil moisture content. At WP, zero losses due to evaporation are assumed to occur from this zone. Maximum or potential evaporation is assumed to occur when the soil moisture zone is at FC. A linear evaporative loss relationship is assumed to apply between the two soil moisture limits. Thus, at a soil moisture content midway between FC and WP, for instance, the evaporation rate is half that of the potential rate.

Water entering the water table is 'gross recharge' to the freshwater lens. A further loss, however, is experienced due to transpiration of trees whose roots penetrate to the water table. 'Net recharge' is that water remaining after this additional loss is subtracted from 'gross recharge'. Observations in dug pits and trenches on Home and West Islands reveal that a considerable number of roots penetrate to the capillary fringe just above the water table which typically occurs at depths of one to two metres below ground level. It is estimated that about 50% of the roots from mature coconut trees penetrate to the water table. Because the movement of the water table is relatively small, even during drought periods, these roots allow transpiration to occur even when the soil moisture store has been depleted. This is the reason that coconut trees are able to survive prolonged drought periods on coral atolls when other shallow rooted vegetation has reached wilting point and possibly died.

Vegetation is assigned a 'crop factor' (Doorenbos and Pruitt 1977) according to its type. Each plant (or crop) type has its evaporative potential compared with that of a 'reference crop'. The reference crop evaporation is equal to the potential evaporation, as derived from an appropriate method. The crop factor is a coefficient which is used to derive an adjusted potential evaporation of other crops from the potential evaporation (or the reference crop evaporation).

The crop factor for most grasses and other shallow rooted vegetation is assumed to be 1.0. The crop factor for coconut trees was taken as 0.8 based on values for similar types of trees listed in Doorenbos and Pruitt (1977). Thus, the potential evaporation rate for coconut trees is taken to be 80% of that for grasses or other shallow rooted vegetation.

The proportions of freshwater lens areas covered by deep rooted vegetation were estimated from coloured aerial photographs taken in April 1987 and from ground inspection. From recent investigations (Falkland 1991, 1992a), the proportions were estimated to be 0.15 for Home Island, 0 for the West Island Airfield and 0.8 for the northern part of West Island and South Island.

RESULTS AND DISCUSSION

Water balance analyses were conducted for freshwater lenses on West, Home and South Islands in a number of studies (Falkland 1988, 1991, 1992a). Series of monthly recharge estimates were obtained in each case, enabling drought sequences to be further analysed for estimation of sustainable yields.

Graphical comparisons of annual recharge and annual rainfall (obtained by summation of monthly values) for the period 1953 to 1991 are provided in Figures 23 and 24 for, respectively, the West Island Airfield Lens and the West Island Northern Lens.

A significant variation in recharge from year to year can be seen from Figures 23 and 24. In some years, recharge is actually negative (i.e. there is a net loss of water from the freshwater lens). Figure 24 shows that 'negative recharge' occurred in the Northern Lens in 1953, 1962, 1977 and 1991 with the most negative value occurring in 1991 (corresponding to the lowest annual rainfall). In general, years of high annual rainfall result in years of high annual recharge and vice versa. However, there is no simple relationship between the two parameters. This is because annual recharge is a function of the pattern of daily rainfall and not simply a function of the annual rainfall total.

For the 39 year period of record (1953-1991), the following mean annual recharge estimates were obtained:

-	West Island Airfield Lens:	950 mm/year (49% of rainfall),
-	Home Island Lens:	855 mm/year (44% of rainfall),
-	West Island Northern Lens:	564 mm/year (29% of rainfall).

The results for South Island are the same as for the Northern Lens as similar parameters were used in the recharge analysis.

Figure 25 compares the annual recharge estimates from three lenses (West Island Airfield and Northern Lenses and the Home Island Lens). There are significant recharge differences between the three lenses, the main cause being differences in the density of the deep rooted vegetation, predominantly coconut trees, above the freshwater lens areas. Figure 26 shows the relationship between mean annual recharge (as a percentage of rainfall) and the percentage tree cover. This graph and the tabulated results above show that recharge can nearly be doubled by reducing the tree cover from 80% (as for the Northern Lens) to zero (as for the Airfield Lens). Due to the significant effect that coconut tree density has on groundwater recharge, one management option for increasing freshwater supplies is to selectively clear vegetation in areas where freshwater lenses occur (see also section on transpiration measurements).

Cumulative annual recharge graphs for the West Island and Home Island lenses are shown in Figure 27. These graphs enable sequences of dry and wet years to be easily seen. For instance the lowest 5 year recharge period occurred from early 1976 to the end of 1981. Another low recharge period of 5 years occurred from early 1961 to the end of 1965.

GROUNDWATER INVESTIGATIONS

In the previous section, a number of freshwater lenses were named (e.g. West Island Airfield Lens, West Island Northern Lens and Home Island Lens). Groundwater investigations over a number of years were conducted to locate and quantify the depth and areal extent of these lenses. This section briefly describes these investigations and details of the freshwater lenses.

PRELIMINARY INVESTIGATIONS

The groundwater resources were first studied by Jacobson (1976a, 1976b). His investigation was limited to Home Island and involved observations of water table elevations and salinities of shallow water obtained from wells. Using this limited information he estimated the thickness of the freshwater lens at 10 to 15 metres and the sustainable yield to be 200 kilolitres per day. He recommended that more detailed investigations were warranted to confirm the preliminary results obtained. Later investigations showed that the actual thickness of the lens was not greater than 6 metres and that the estimated sustainable yield was approximately half of his estimate.

DETAILED INVESTIGATIONS

Detailed investigations of the groundwater resources were undertaken from 1988 to 1992 (Falkland 1988, 1991, 1992a, 1992b). The aims of the groundwater investigations were to determine the location, lateral extent and depth of freshwater lenses and to determine hydrogeological properties necessary for an analysis of long-term sustainable yields from the lenses.

A combined drilling and geophysical programme was used. This combined approach allowed for an accurate determination of the thickness of lenses at selected locations using the drilling programme and for reasonable estimates at intermediate sites using the electrical resistivity method. The drilling programme was relatively slow and costly but yielded accurate data whereas the resistivity programme was relatively quick and inexpensive but had a lower level of accuracy. The latter method, however, provided good estimates of lens thickness after correlation with salinity profiles obtained at borehole sites.

A limited amount of seismic work was conducted at boreholes to gain a better understanding of the subsurface geological properties. Observations of topographic features, measurement of salinity levels at exposed water surfaces (wells, ponds, pumping galleries) and recording of water table movements relative to tidal movements were conducted to provide additional data.

Details of all the investigations are beyond the scope of this report. Some details about the drilling programme are provided, however, as they were the most useful in terms of initial and continuing data about the freshwater lenses.

A total of 29 boreholes were drilled from 1988 to 1992 on West Island (16 holes), Home Island (12 holes) and South Island (1 hole) and equipped with salinity permanent monitoring systems. Details of these holes including year of drilling, reduced level (RL) relative to mean sea level (MSL), depth to water table and depth to the unconformity between Holocene and Pleistocene sediments are shown in Table 10. The location of the boreholes are shown in Figure 28. Drilling logs with further details are contained in Murphy (1988), Falkland (1991), Murphy and Falkland (1992a) and Falkland (1992b).

The permanent salinity monitoring system used in each borehole is shown diagrammatically in Figure 29. Water samples are pumped to the surface from each of the separate tubes by a portable electric pump and tested for electrical conductivity. Using the monitoring data, salinity profiles can be constructed for each borehole at intervals of typically one to three months. By obtaining a set of such salinity profiles, the salinity distribution over time can be viewed for each borehole. This data has yielded valuable information about the response of the freshwater lenses to variations in recharge. Figures 30 and 31 show the variation in the depth to the base of the freshwater zone in a number of West Island (Airfield Lens) and Home Island boreholes together with monthly recharge for the period 1988 to 1991. The antecedent recharge in 1987 is also shown.

The permeability of the coral sediments was measured *in-situ* using falling head tests in some of the boreholes during drilling. The average permeability in the Holocene sediments was about 6 metres per day while the average permeability in the upper part of the Pleistocene sediments was about 30 metres per day. On occasions during drilling below the unconformity, karst zones such as solution channels were intersected where circulation (of water and drilling mud) was lost. In some of these zones, the permeability was estimated to reach 1000 metres per day. The specific yield (or effective porosity) was estimated to be 0.3.

FRESHWATER LENS DETAILS

Using the results of the drilling, geophysical and other investigations, freshwater lenses were located on West, Home and South islands.

On West Island, two permanent freshwater lenses have been identified underlying, respectively, the airfield and the northern part of the island. These have been named, respectively, the Airfield Lens and the Northern Lens. A permanent freshwater lens has been identified on Home Island underlying the inhabited area. In addition, one large and two smaller lenses have been identified on South Island (Falkland 1991). The locations of these lenses are shown in Figure 28.

Approximate areas, maximum freshwater thicknesses, volumes and turnover times of these lenses are shown in Table 11. The areas and volumes vary with time according to antecedent recharge conditions. The areas shown in Table 3 are the maximum values and the volumes are the range of values estimated during the period of record. The turnover times are a measure of the average residence time of water within the freshwater zone and are calculated by dividing the average thickness of the freshwater zone by the mean annual recharge. A cross section through one of the lenses including details of a number of boreholes is shown in Figure 32.

Some of the other islands in the Cocos (Keeling) Islands also have small freshwater lenses. Based on limited on-site tests (Jacobson 1976a, Falkland 1988), a freshwater lens is known to exist on Horsburgh Island but its sustainable yield cannot be assessed without further investigation. Preliminary investigations on North Keeling (Falkland 1988, 1992b) indicate the presence of a very thin freshwater lens at least on part of the island. It is not known whether the lenses on Horsburgh Island and North Keeling are permanent.

A major influence on the thickness of the thicker lenses, particularly the Airfield Lens, is the geological unconformity between upper and lower sediments. As stated earlier, this unconformity is a very significant influence on the formation of freshwater lenses as the sediments below this unconformity have relatively high permeabilities and mixing of freshwater and seawater is readily facilitated. The depths to the unconformity are shown in Table 10. In all but one borehole in the Airfield Lens, the freshwater limit (2600 μmhos/cm) occurs at all times within a zone about 2 to 3 metres below this unconformity. In general, it is evident that the unconformity is providing a limit to the formation of a deeper freshwater lens. When recharge is low, as occurred in 1991, the lens contracted to a position close to or above the unconformity. In dry periods, therefore, the lens becomes limited by recharge at this location while in wetter periods the lens is limited by the geology. It can be concluded that the underlying geology has a strong influence on the freshwater lens at the Airfield. Some of the boreholes in the Northern Lens exhibit similar behaviour while others within that lens and all of the Home Island boreholes show that the freshwater lens is contained wholly within the Holocene sediments.

An interesting observation was made in the most recent investigations (Falkland 1992b). At borehole WI 22 near the southern end of the Northern Lens a reasonably thick freshwater zone of 7 metres was found during drilling in August 1992. The thickness of the lens to the mid-point of the transition zone (25,000 μmhos/cm) was about 11 metres. This result was better than expected as the width of the island at this location is only about 270 metres. Based on the approximate relationship outlined earlier, the minimum width required to support a freshwater lens of this thickness is over 750 metres. This shows that the approximate relationship should be treated with some caution as other factors not accounted for may have a significant bearing on lens thickness. At this borehole the unconformity occurs at almost precisely the same depth as the limit of the freshwater zone, indicating that it is a major influencing factor. Based on thickness and salinity of the freshwater zone at borehole WI 22, it is considered that the lens at this location will not disappear during drought periods. Future monitoring data will be used to establish the validity of this assumption.

FRESHWATER LENS DYNAMICS AND MODELS

Flow through freshwater lenses is complex and is influenced by hydrologic (variable recharge), geologic (variable permeabilities with depth and with distance from one side of island to the other), oceanic (tidal movements) and anthropogenic (water extraction) factors.

Early conceptual models and solution techniques for freshwater lens flow assumed a sharp interface between freshwater and seawater. Observations have shown that this is not the case on atolls and wide transition zones are the norm. Sharp interface models can at best only provide an estimate of the depth to the mid-point of the transition zone, yielding no information about transition zone width. Such models also assumed horizontal flow within the lens with freshwater outflow occurring around the perimeter of the island and did not account for tidal movements.

A more realistic conceptual freshwater lens flow model has evolved (Buddemeier and Holladay 1977, Wheatcraft and Buddemeier 1981, Oberdorfer et al. 1990, Peterson 1991, Underwood et al. 1992) based on detailed observations on atolls. The conceptual model accounts for vertical and horizontal tidal propagation through a dual aquifer system consisting of the upper (Holocene) and lower (Pleistocene) sediments. This conceptual model is supported by observations on a number of atolls in the Pacific (Buddemeier and Holladay 1977, Hunt and Peterson 1980, Wheatcraft and Buddemeier 1981, Anthony et al. 1989) and in the Cocos (Keeling) Islands (Falkland 1988) which have shown that tidal lags and efficiencies at water level monitoring locations within atolls are largely independent of horizontal distance from the shore. Tidal lag and efficiency (or the time difference between, and amplitude ratio of, water table movement to tidal movement) are in fact greatly influenced by the depth of the holes used for water level monitoring. Vertical propagation of tidal signals tends to be dominant in the middle of the island whereas both horizontal and vertical propagation are significant near the edges.

Using the above conceptual model, the numerical solution of freshwater lens flow problems can more realistically be made with models which can account for a two layered hydrogeologic system, flow of variable density water and the mixing of fresh water and seawater. One such computer model, SUTRA, developed by the United States Geological Survey (Voss 1984) has been applied to the study of freshwater lenses and coastal aquifers on a variety of islands. Case studies of atolls and small carbonate islands include Enewetak atoll, Marshall Islands (Oberdorfer and Buddemeier 1988, Oberdorfer et al. 1990), Majuro atoll, Marshall Islands (Griggs and Peterson 1989) and Nauru, a raised atoll, (Ghassemi et al. 1990).

SUSTAINABLE YIELDS

The sustainable (or safe) yield of an aquifer is the rate at which water can be extracted without causing adverse effects. For non-coastal mainland aquifers, the sustainable yield can be approximately equated to the long-term recharge. For freshwater lenses on small islands and some coastal mainland aquifers, such an approximation is not valid as only a small portion of the recharge is available as sustainable yield. Most of the recharge is required to counteract the effects of dispersion between the freshwater layer and underlying saline water.

To avoid adverse effects from extraction (i.e. to avoid an increase in the salinity of extracted water), the overall extraction rate from the lens should not exceed the sustainable yield. An additional requirement is that pumping be distributed over the surface of the lens to avoid local upconing of saline water.

Methods for estimating sustainable yield range from simple empirical approaches to complex numerical models (e.g. SUTRA). Due to time limitations, an empirical approach suggested by Mink (1976) was adopted for the Cocos (Keeling) Islands. Mink suggested that an extraction equal to 25% of the 'flux' or flow through the lens was a good first approximation to the sustainable yield. This is equivalent to 20% of the mean annual recharge based on the simple water balance equation for the freshwater lens outlined below.

The water balance equation within the lens can be expressed simply as:

$$R = Q + X + dV$$

where

R	is the recharge into the lens after all evapotranspiration losses have been taken into account, including transpiration directly from the lens by deep-rooted vegetation,
Q	is the lens 'flux' (outflow at the edge of the lens and mixing with the transition zone at the base of the lens),
X	is the total amount of water pumped from the lens,
dV	is the change to the freshwater volume.

In the long term, dV tends to be negligible and can be removed from the equation. Hence, the equation can be written as:

$$R = Q + X$$

This indicates that the maximum extraction (or sustainable yield) is 20% of mean annual recharge based on the condition that extraction should be less than 25% of flow through the lens. Given that mean recharge in the Cocos (Keeling) Islands is in the order of 25 to 50% of mean rainfall, the allowable extraction (or sustainable yield) is about 5 to 10% of mean rainfall.

In relatively stable lenses, a proportion greater than 20% of the available recharge can be extracted without adverse effects on the lens. In a study of the 'Central Lens' on

Bermuda, for instance, it has been suggested that about 75% of recharge could be extracted (Rowe 1984). This, however, is not considered appropriate for thin lenses, such as the Home Island Lens, at least until further monitoring results provide a more accurate insight into lens dynamics. In fact, because the Home Island Lens is a very thin and fragile lens, there is a strong case for lowering the sustainable yield estimate to slightly less than 20% of recharge. A value of 17% of recharge based on current pumping there (115 kilolitres/day) was adopted as the sustainable yield at least until more extensive salinity monitoring records are obtained and analysed.

Under present vegetation conditions, the sustainable yields of the major lenses are estimated to be (Falkland 1991, 1992a, 1992b):

- West Island Airfield Lens: 520 kilolitres/day,
- West Island Northern Lens: 300 kilolitres/day,
- Home Island Lens: 115 kilolitres/day,
- South Island lenses: 220 kilolitres/day,

If vegetation was substantially cleared from above some of these lens areas, the sustainable yield could be increased. In particular, it is estimated that the yields from the Northern Lens and from the lenses on South Island could be increased, respectively, to 400 and 330 kilolitres/day.

It is noted that the sustainable yields for the Cocos (Keeling) Islands are based on an empirical approach. This approach, based on observations of the effects of pumping and on the results of extensive modelling on other atolls, has been shown to be at least a good approximation. It is noted that a similar 20% of mean annual recharge was used to estimate sustainable yield for the island of Laura on Majuro atoll in the Marshall Islands (Hamlin and Anthony 1987). The effects of pumping at different rates were investigated by Griggs and Peterson (1989) using the SUTRA model. They concluded that the lens was capable of extracting at least 20% and up to 30% of mean annual recharge. At extraction rates of 40% of mean annual recharge, the upconing of seawater below the gallery systems was found to be excessive.

For the freshwater lenses in the Cocos (Keeling) Islands, it is intended that salinity monitoring at the network of monitoring boreholes will continue. Long term records obtained from these boreholes will enable the effects of recharge and extraction on the lenses to be evaluated. Adjustments to the present sustainable yield estimates may then be warranted.

GROUNDWATER DEVELOPMENT

On small coral islands, such as the Cocos (Keeling) Islands, small hand dug wells have been used for extraction of small quantities of water (e.g. at the household level). For larger centralised water supply systems, more extensive systems are required. There are three main alternative systems for larger scale pumping of water from freshwater lenses, as follows:

- borehole systems,
- wells, and
- infiltration galleries.

Boreholes and wells, while possibly suitable in large freshwater lenses, are not considered suitable in the Cocos (Keeling) Islands because they extract from a localised area and can lead to excessive drawdowns. To avoid excessive drawdowns, many boreholes or wells would need to be drilled or dug. The cost of drilling or excavating, pumps and pipework would not be economical for the quantity of water extracted.

Infiltration galleries (or 'skimming wells') are considered to be the best solution as they skim water from the surface of the lens thus minimising drawdown. These types of systems have recently been installed on Home Island and in the West Island Northern Lens. In many cases they have replaced earlier dug well systems with short radial pipes extending from their bases.

Infiltration galleries consist of a horizontal, permeable conduit system laid at or close to mean sea level, enabling water to be easily drawn towards a central pump pit. Figure 33 shows the type of infiltration gallery used on Home Island (Falkland 1988). Salinity data collected before and after the galleries were installed have shown a general reduction in the salinity of the pumped water.

Current water usage from each of the major lenses as a proportion of the estimated sustainable yields are as follows:

- West Island Airfield Lens: 27%
- West Island Northern Lens: 50% (present vegetation), 30% (cleared vegetation),
- Home Island Lens: 100%, and
- South Island lenses: 0%

It can be seen there is ample capacity for expansion of current water usage at the Airfield Lens and no spare capacity on Home Island. The Northern Lens has sufficient spare capacity for some additional use, particularly if some clearing of the existing thick vegetation occurred. South Island remains at present an untapped resource.

OTHER WATER RESOURCES

Roof catchments and relatively small tanks (mainly 4.5 kilolitre capacity) provide supplementary rainwater to Home Island residents. Rainwater is also collected from a limited number of buildings on West Island.

Desalination of seawater or brackish groundwater is a possibility but would be expensive. A detailed analysis of water resources (Falkland 1988) showed that groundwater is the cheapest resource to develop. Using Home Island for a pilot study, it was found that the unit costs (capital plus operating costs) of a desalination plant using the reverse osmosis principle would be about 7 times more expensive than the development of groundwater. Even if groundwater was piped from South Island to Home Island, an option which in the long term may be preferable if the Home Island lens becomes polluted, desalination would be more expensive by a factor of 3. By comparison, rainwater catchment as the sole source of water is the most expensive, being about 10 times more expensive than groundwater development on Home Island.

The most appropriate option from an economic, quality and security viewpoint was the development of groundwater as the primary source of water with rainwater being used as a supplementary source. This option has been implemented.

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Table 1. Temperature (°C): 1952-1991 data.

Month	Daily Mean	Extreme Max.	Extreme Min.
January	27.0	32.1	20.1
February	27.4	32.4	20.1
March	27.5	32.1	19.8
April	27.3	32.2	19.6
May	27.0	31.4	19.4
June	26.3	30.7	20.1
July	25.8	29.9	20.4
August	25.8	29.8	18.3
September	26.0	30.0	19.0
October	26.3	30.6	20.6
November	26.6	31.1	19.3
December	26.8	32.2	21.1

Table 2. Relative humidity (%): 1952-1991 data.

Month	Daily Mean	Mean Daily Max.	Mean Daily Min.
January	74	82	66
February	74	81	66
March	75	81	69
April	77	84	69
May	77	82	70
June	77	84	69
July	77	84	71
August	74	84	69
September	72	81	67
October	72	82	66
November	72	84	65
December	72	82	65

Table 3. Atmospheric pressure (hectopascals): 1952-1987 data.

Month	Daily Mean	Extreme Max.	Extreme Min.
January	1008.8	1015.8	970.0
February	1008.4	1018.1	992.1
March	1008.8	1015.7	987.0
April	1008.8	1015.8	998.2
May	1009.5	1017.7	1000.4
June	1010.3	1017.2	1002.5
July	1011.1	1018.5	1001.0
August	1011.6	1018.5	987.5
September	1012.2	1017.7	1004.8
October	1011.6	1018.5	1001.6
November	1010.8	1017.8	989.4
December	1010.0	1017.6	993.8

Table 4. Cloud cover (oktas): 1952-1987 data.

Month	Daily Mean	Extreme Max.	Extreme Min.
January	5.1	6.0	3.7
February	5.1	6.3	3.0
March	5.1	6.4	4.2
April	5.3	6.3	4.1
May	5.3	6.4	4.4
June	5.2	6.6	4.2
July	5.3	6.2	3.8
August	5.1	6.1	3.9
September	5.1	6.5	3.8
October	5.1	6.4	3.8
November	5.0	6.8	3.8
December	5.1	6.4	3.5

Table 5. Wind speed (metres/sec).

Month	Daily Mean (1952-1987)	Extreme Max. (1952-1991)	Extreme Min. (1952-1991)
January	5.3	48.8	0
February	4.6	34.0	0
March	5.3	28.3	0
April	6.1	29.3	0
May	6.9	27.8	0
June	7.0	30.9	0
July	7.8	24.7	0
August	8.0	36.0	0
September	8.1	24.2	0
October	7.5	24.2	0
November	7.2	40.1	0
December	6.0	27.3	0

Table 6. Cyclones passing over or close to the Cocos (Keeling) Islands, since 1960.

Name and number	Date of passing closest to island	Approx distance away (km)	Min. central pressure when passing closest to island/ min. pressure on island(hecto-pascals)	Max. wind speed on island (km/hour)	Total rainfall (mm)
Unnamed (668)	13/2/61	60	991/992	122	71
Hazel (542)	9/3/64	80	988/991	102	121
Carol (548)	27/12/65	100	997/1002	95	48
Nancy (555)	14/3/66	100	997/1000	91	26
Doreen (566)	21/1/68	20	970/970	176	219
Dianne	6/1/70	80	996/1005	98	124
Paula (591)	27/3/73	20	999/1006	83	25
Annie (682)	25/11/73	40	995/1002	145	71
Deidre (684)	21/12/73	30	995/994	85	72
Denise (455)	23/5/75	30	995/1002	100	28
Daphne (711)	15/1/82	60	995/998	81	66
Annette (696)	5/2/84	30	994/999	81	142
Daryl (699)	11/3/84	80	984/1001	92	253
Ophelia (742)	12/1/86	30	986/1002	93	252
Alison (752)	8/4/86	30	988/1002	106	112
Frederic (784)	30/1/88	40	988/995	111	90
Herbie (783)	19/5/88	50	990/995	87	57
John (767)	25/1/89	10	997/1000	61	106
Leon (769)	17/2/89	90	990/1006	63	27
Pedro (786)	10/11/89	100	982/1001	137	299
Graham (802)	5/12/91	100	925/1004	98	49
Harriet (803)	27/2/92	10	975/982	163	80
Ken	21/12/92	55	990/1001	111	162

Notes:

- data are from the Bureau of Meteorology's cyclone database and other information
- listed are cyclones which passed within 100 km of the islands and had a minimum central pressure less than 1000 hectopascals
- rainfall totals are to the nearest 1 mm over a 2 day period.

Table 7. Annual rainfall (mm) at three raingauge sites on the South Keeling atoll.

Year	West Island (Met Station)	Home Island	West Island (Quarantine)	% variation from West Island
1987	1871	1222	-	
1988	2220	1976	-	
1989	1963	1863	2210	
1990	2271	2145	2410	
1991	856	837	820	
1992	2579	2568	2637	
Total (1987-92)	11760	10611	-	-10.8
Total (1988-92)	9889	9389	-	-5.2
Total (1989-92)	7669	7413	8077	-3.4/+5.3

Table 8. Monthly rainfall (mm): 1952-1991 data.

Month	Monthly Mean	Mean Monthly Max.	Mean Monthly Min.
January	199	561	7
February	161	409	7
March	232	630	39
April	234	551	21
May	194	646	17
June	201	649	7
July	217	643	25
August	201	468	18
September	217	277	3
October	70	512	4
November	94	574	3
December	114	447	5

Table 9. Pan evaporation (mm): 1982-1991 data.

Month	Monthly Mean	Mean Monthly Max.	Mean Monthly Min.
January	220	254	195
February	198	220	170
March	205	226	195
April	189	207	165
May	189	211	146
June	171	186	150
July	186	198	174
August	208	226	171
September	219	249	201
October	229	251	217
November	231	246	222
December	241	273	217

Table 10. Monitoring borehole details.

Lens and Borehole	Year of drilling	RL relative to MSL (m)	Depth of water table (m)	Depth of unconformity (m)
Airfield Lens, West Island				
WI 1	1987	2.16	1.8	12.6
WI 2	1987	2.84	2.6	11.7
WI 6	1987	2.33	1.7	11.8
WI 7	1987	3.11	2.5	12.9
WI 8	1988	1.33	0.9	10.3
WI 9	1988	3.57	3.3	13.4
WI 11	1990	2.93	1.9	12.9
Northern Lens, West Island				
WI 3	1987	1.74	1.5	12.0
WI 4	1987	1.65	1.2	14.9
WI 5	1987	1.85	1.9	14.8
WI 10	1988	1.70	1.2	13.2
WI 12	1990	1.43	1.4	10.5
WI 13	1990	1.18	1.3	15.2
WI 14	1990	1.37	1.5	14.7
WI 15	1990	1.71	1.4	14.6
WI 16	1990	n.a.	1.4	12.3
WI 17	1992	2.56	2.2	12.7
WI 18	1992	2.09	1.6	10.5
WI 19	1992	2.19	1.8	15.4
WI 20	1992	1.81	1.6	12.2
WI 21	1992	1.77	1.4	12.2
WI 22	1992	2.21	2.1	9.3
Home Island				
HI 1	1987	2.05	1.6	>15.5
HI 2	1987	1.26	1.0	10.6
HI 3	1987	1.89	1.6	11.9
HI 4	1987	1.70	1.1	9.6
HI 5	1987	1.65	1.1	>12.2
HI 6	1987	1.59	1.2	17.2
HI 7	1987	1.52	1.0	>15.6
HI 8	1987	1.27	1.0	>12.2
HI 9	1990	1.27	1.1	>15.8
HI 10	1990	1.26	1.0	>16.0
HI 11	1990	1.08	1.5	>16.1
HI 12	1990	1.14	1.7	>15.9
South Island				
SI 1	1990	n.a.	1.4	13.8

n.a. = not available

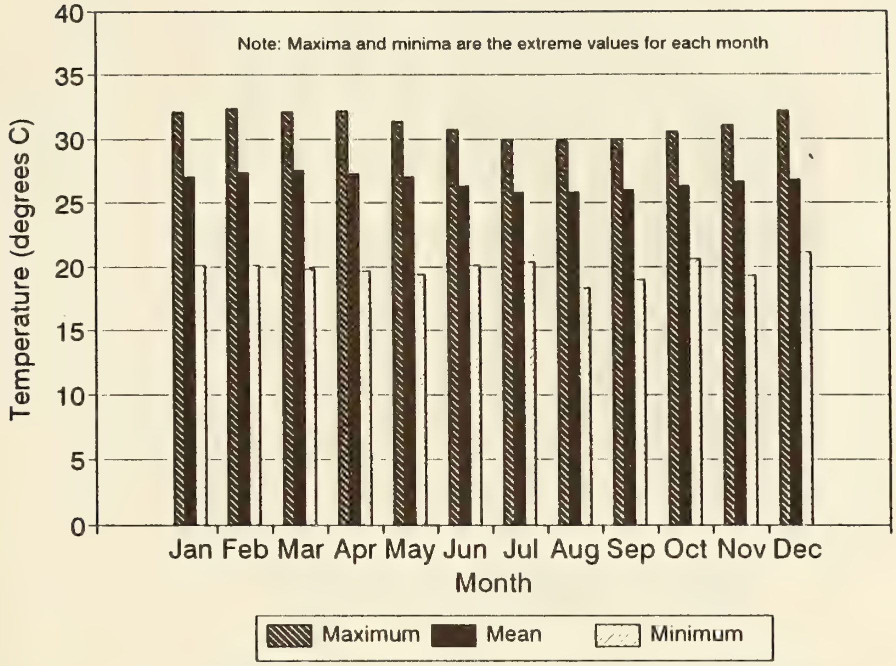


Figure 1. Mean, maximum and minimum daily temperature.

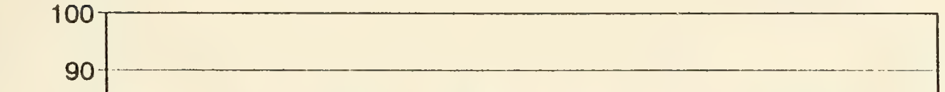


Figure 2. Mean, maximum and minimum relative humidity.

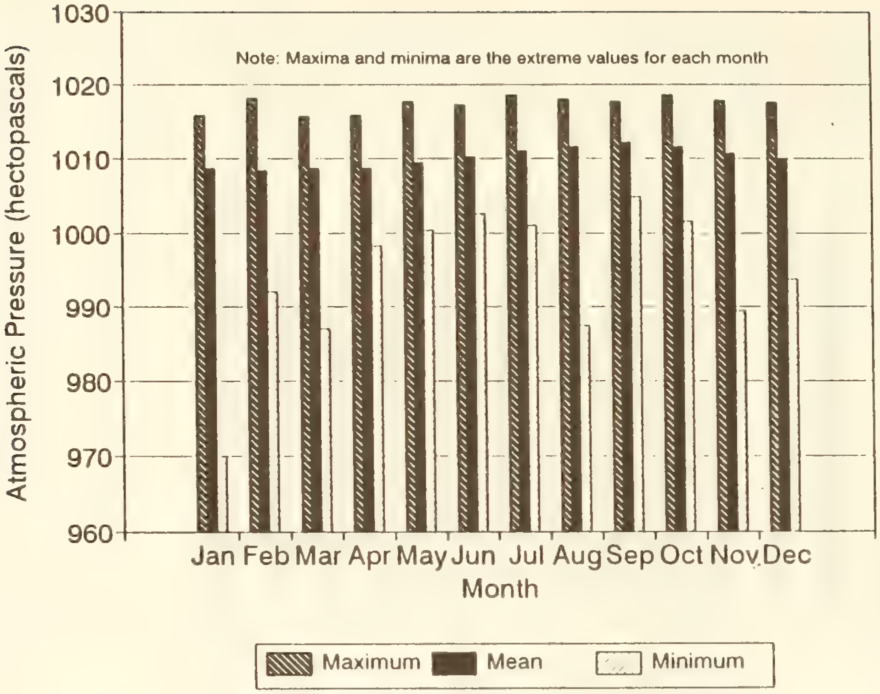


Figure 3. Mean, maximum and minimum atmospheric pressure.

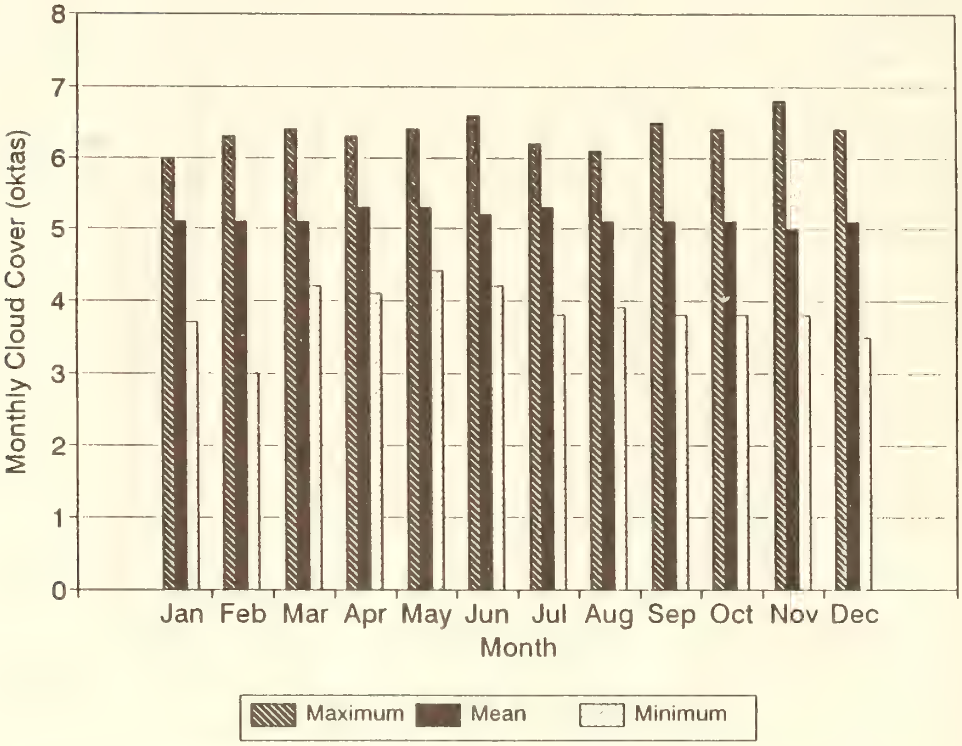


Figure 4. Mean, maximum and minimum cloud cover.

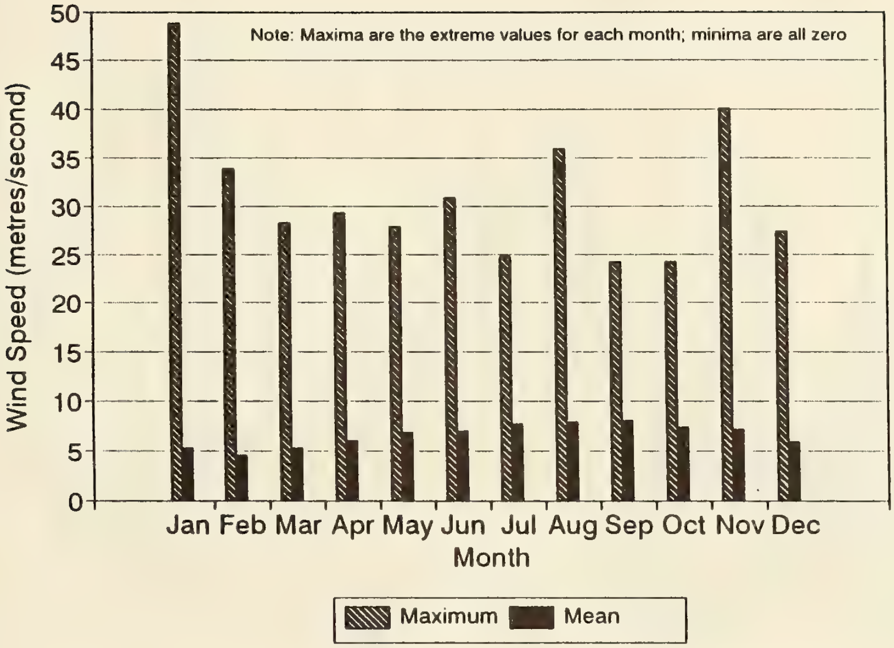


Figure 5. Mean, maximum and minimum wind speed.

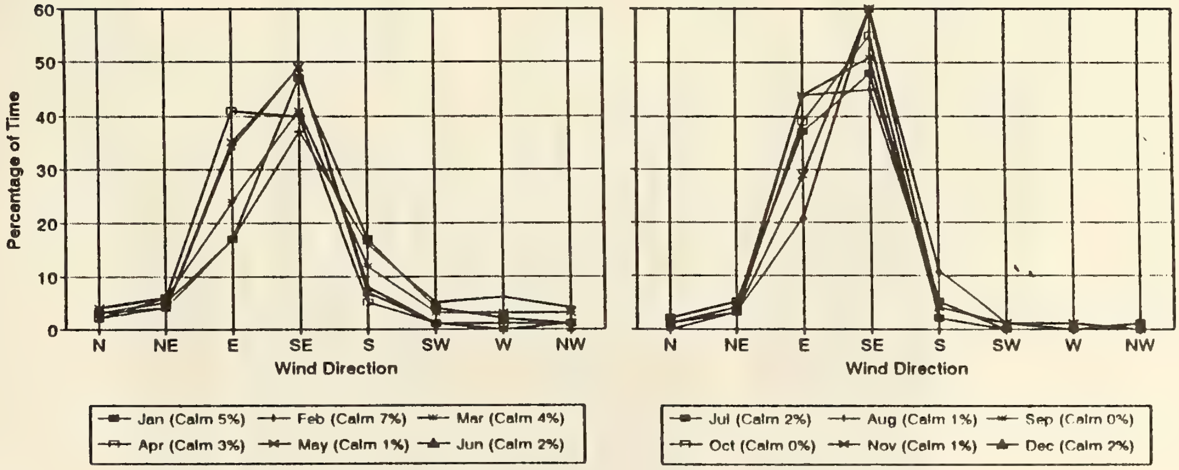


Figure 6. Wind direction.

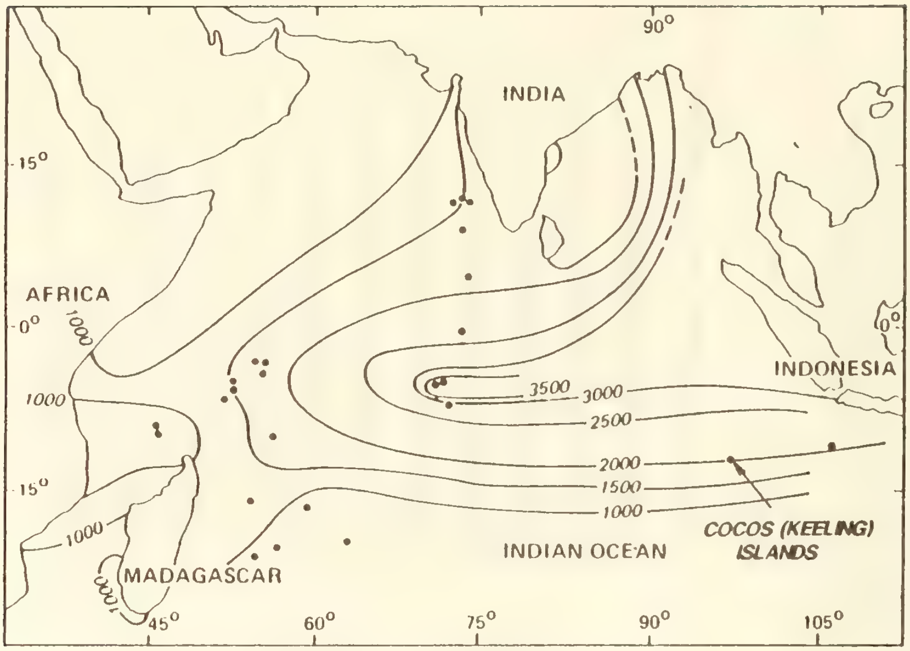


Figure 7. Isohyetal map of mean annual rainfall for the Indian Ocean (modified from Stoddart 1971).

Figure 8. Annual rainfall, 1953-1991 (composite record with some missing data).

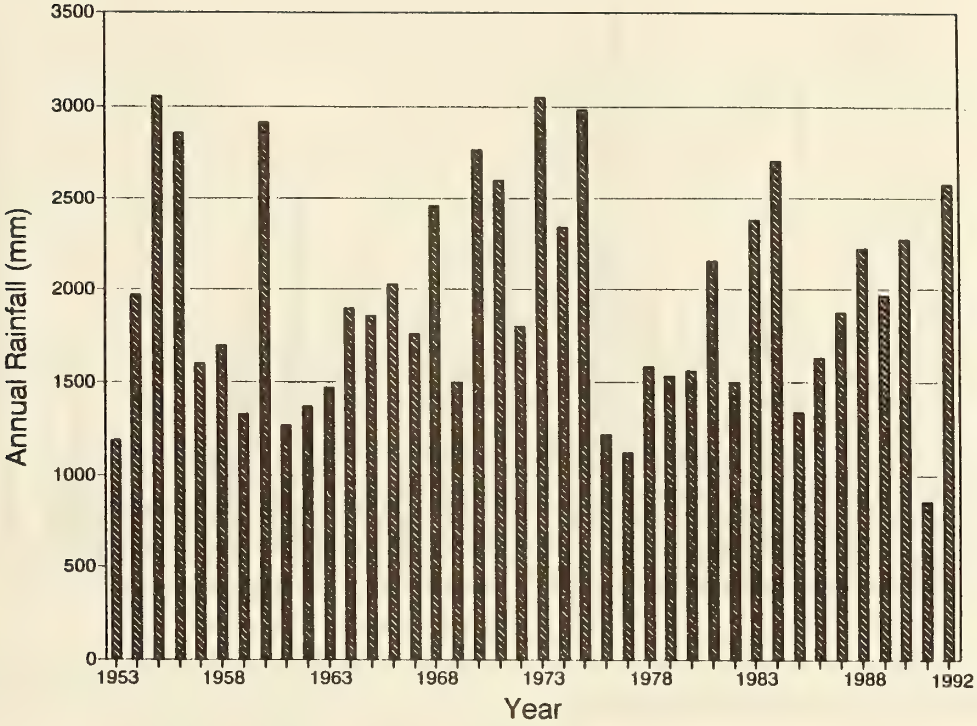


Figure 9. Annual rainfall, 1953-1991 (West Island meteorological station record).

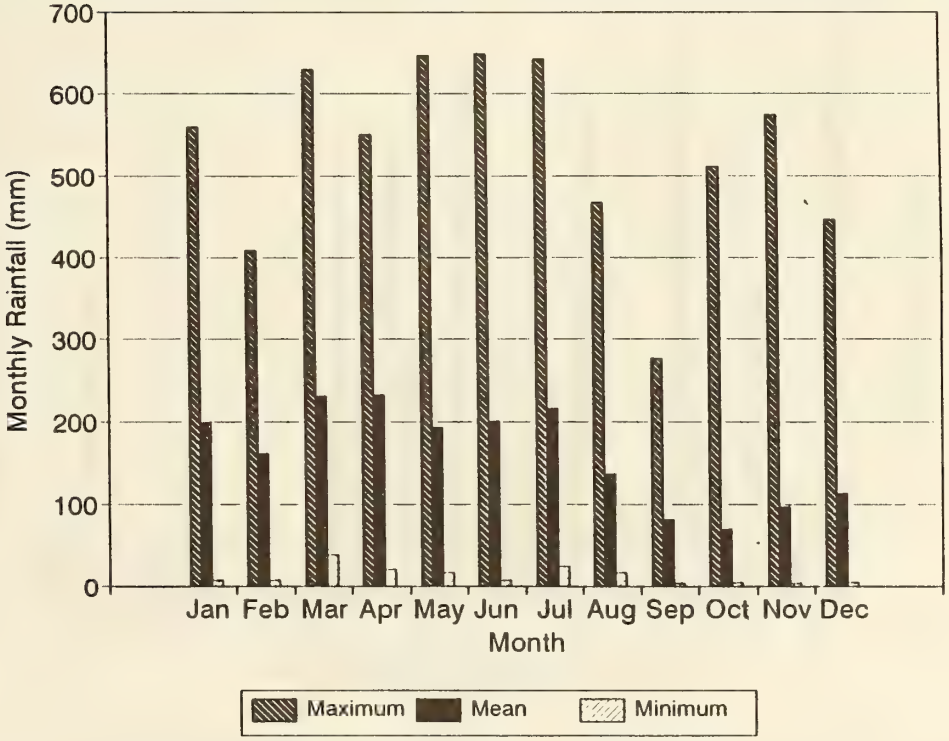


Figure 10. Mean, maximum and minimum monthly rainfall.

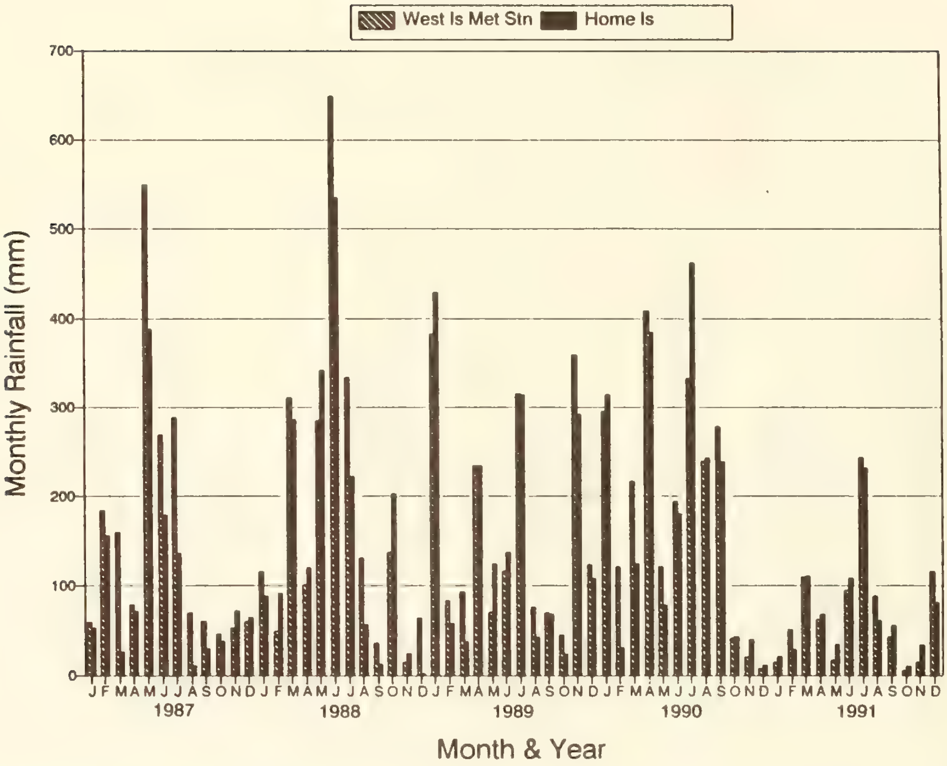


Figure 11. Monthly rainfall at thee meteorological station and Home Island, 1987-1991.

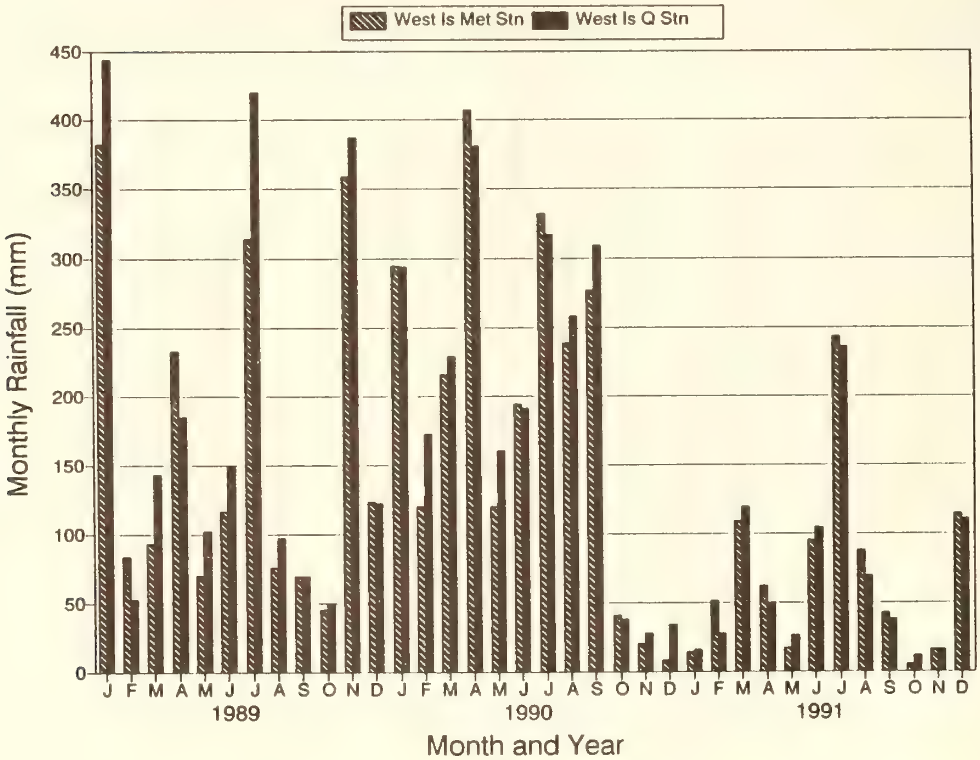


Figure 12. Monthly rainfall at the meteorological and Quarantine stations, 1989-1991.

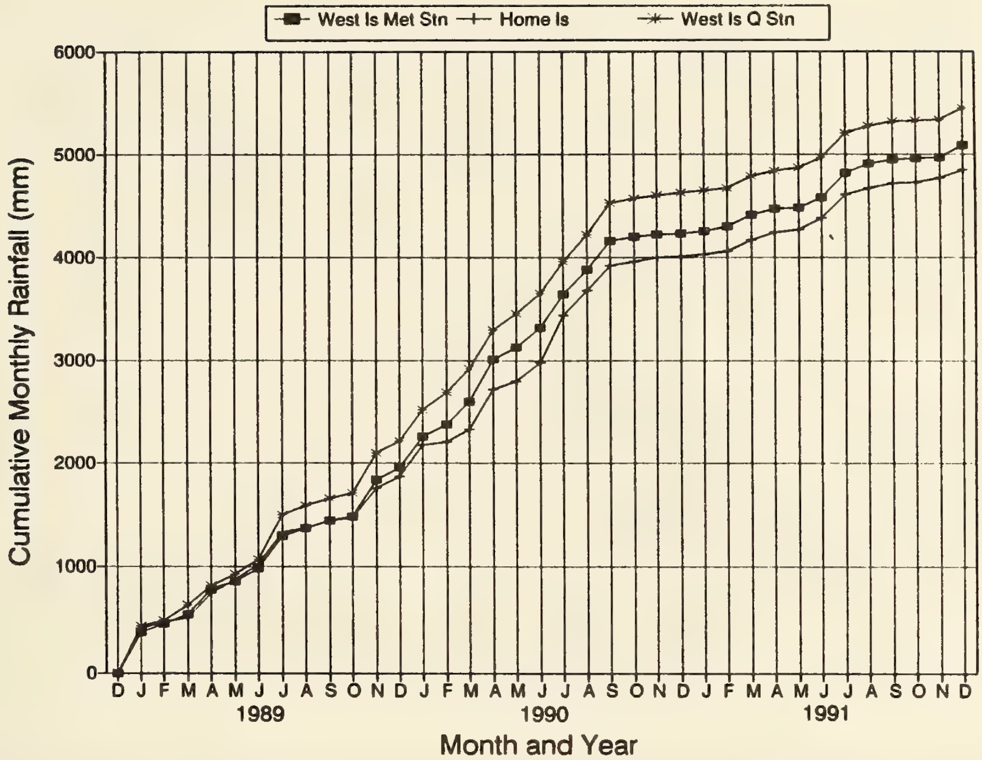


Figure 13. Cumulative monthly rainfall at the meteorological station, Home Island and the Quarantine Station, 1987-1991.

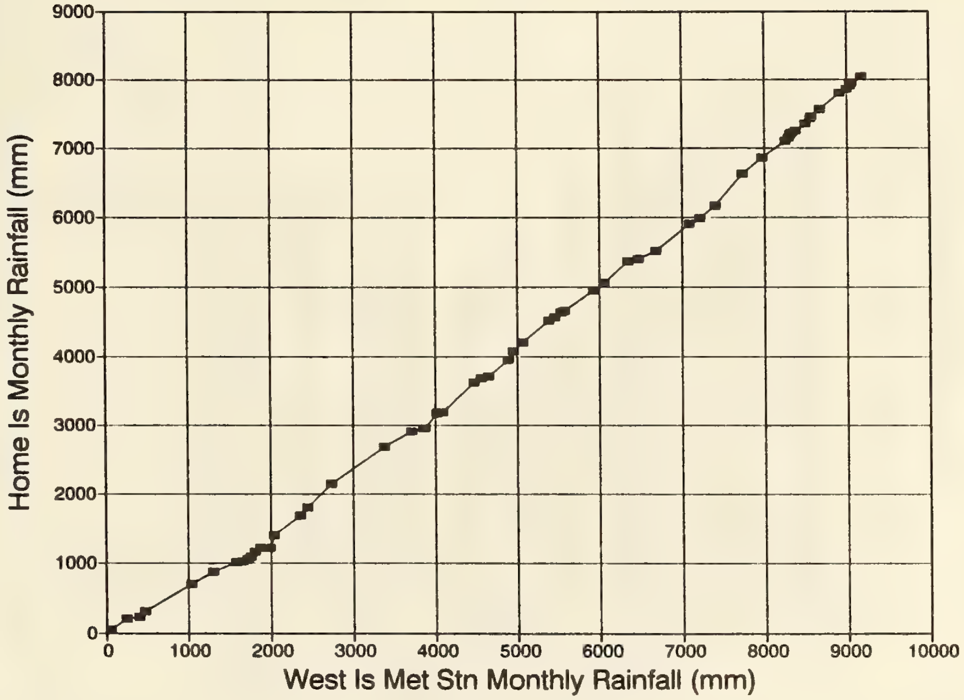


Figure 14. Double mass curve of monthly rainfall for the meteorological station and Home Island, 1987-1991.

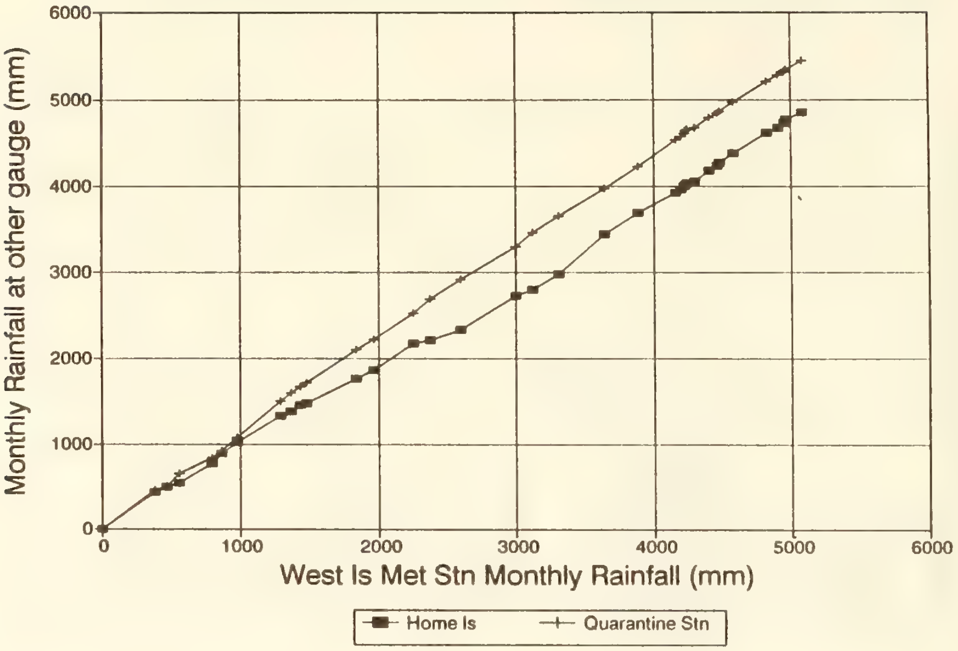


Figure 15. Double mass curve of monthly rainfall for the meteorological station and Home Island and the Quarantine Station, 1989-1991.

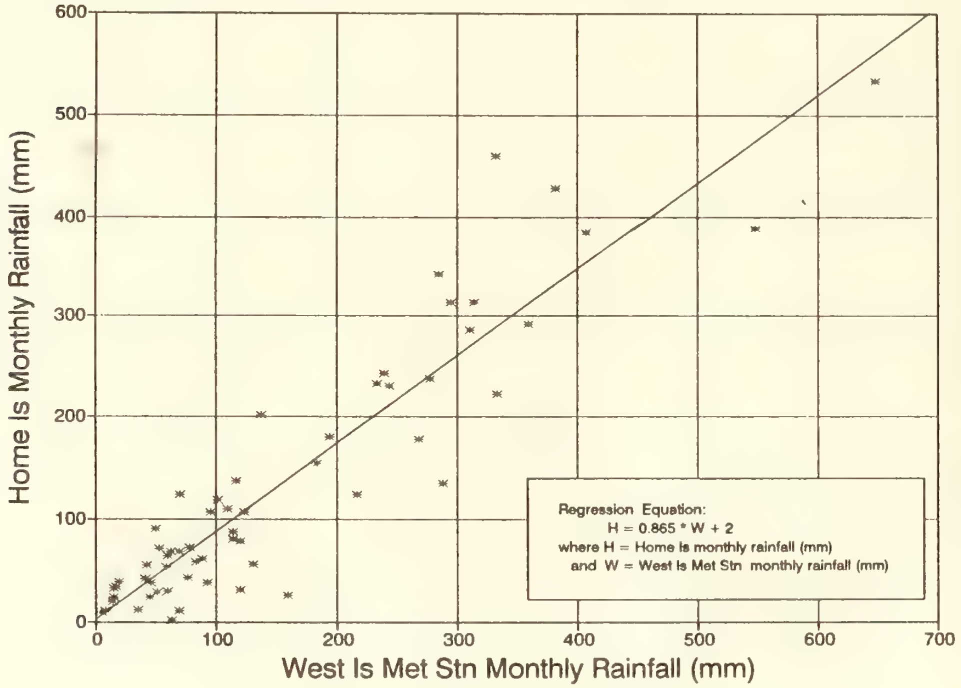


Figure 16. Regression analysis of monthly rainfall at the meteorological station and Home Island, 1987-1991.

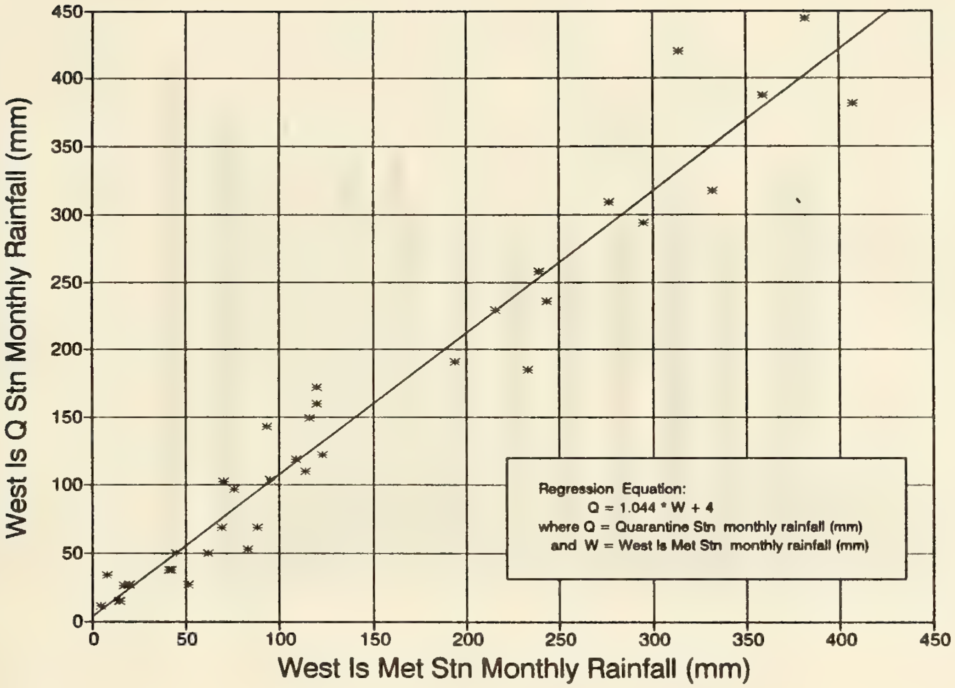


Figure 17. Regression analysis of monthly rainfall at the meteorological station and the Quarantine Station, 1987-1991.

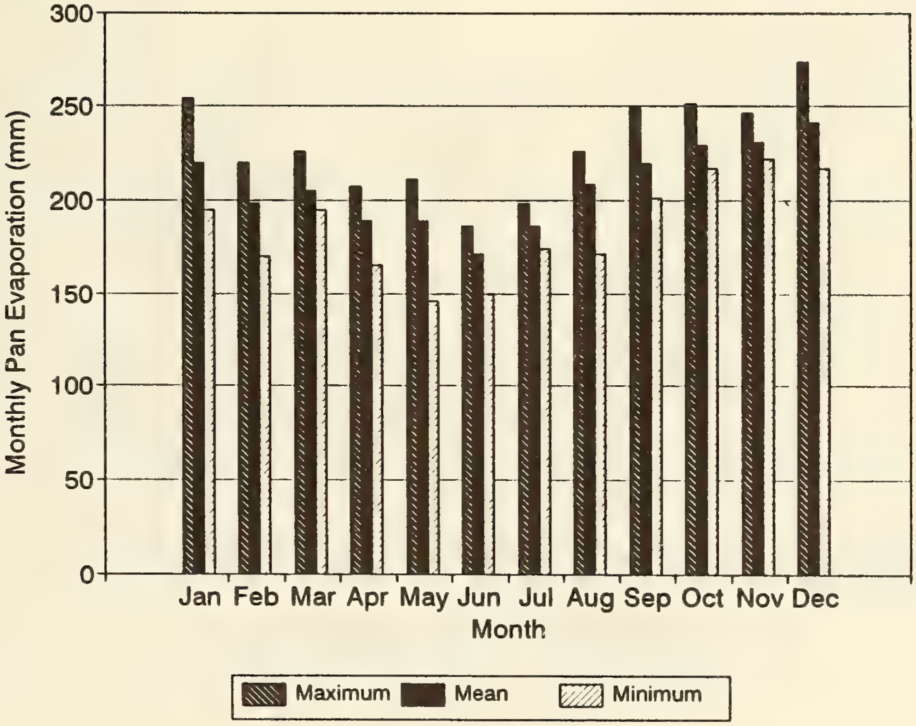


Figure 18. Mean, maximum and minimum pan evaporation.

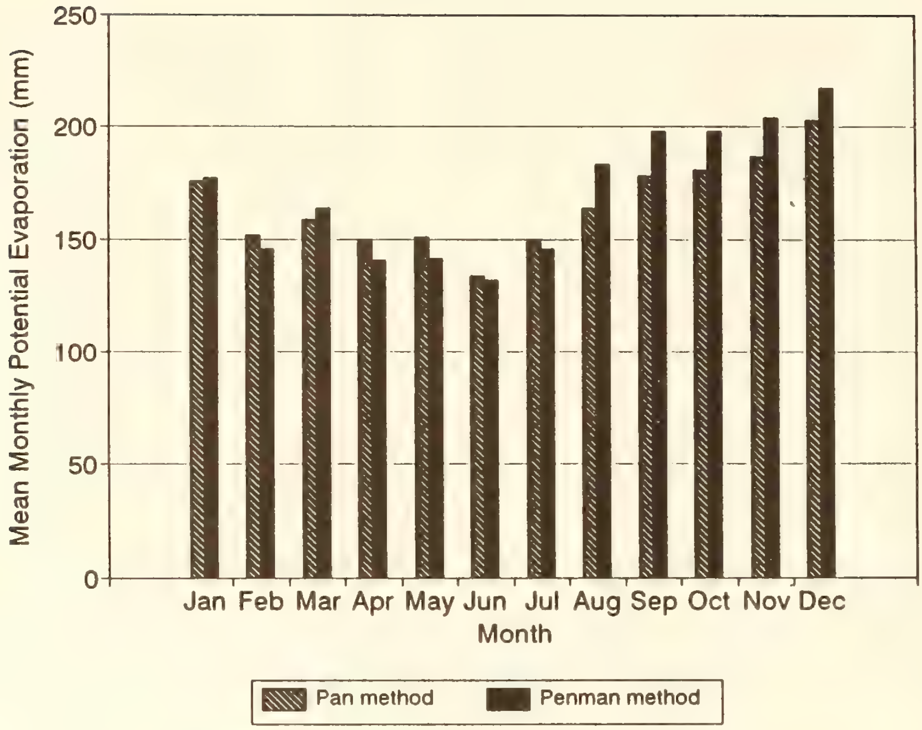


Figure 19. Mean monthly potential evaporation estimates using pan and Penman methods.

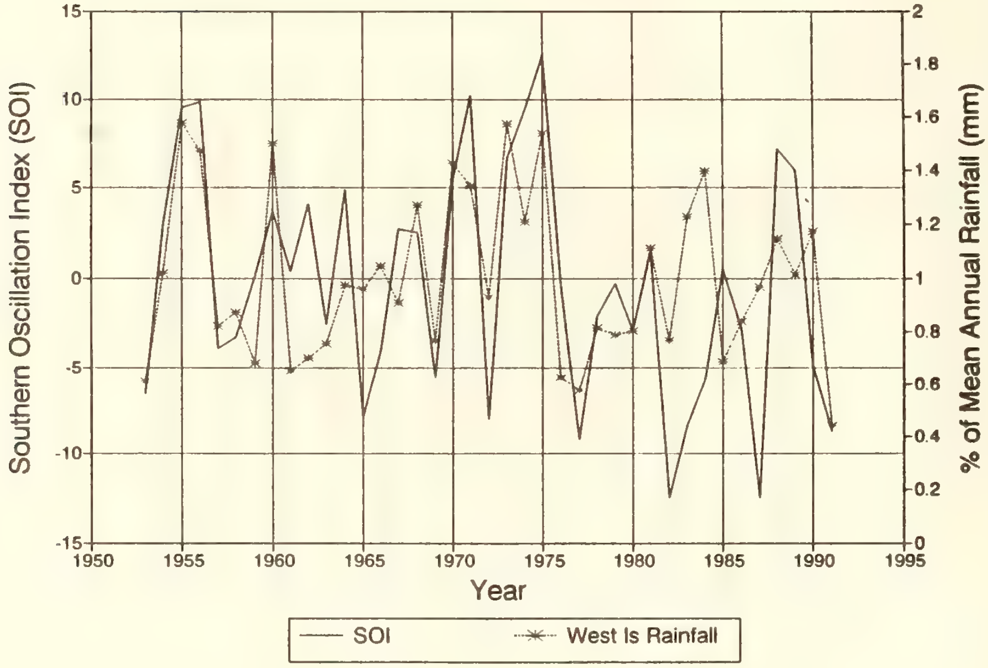


Figure 20. Relation between Southern Oscillation Index and annual rainfall.

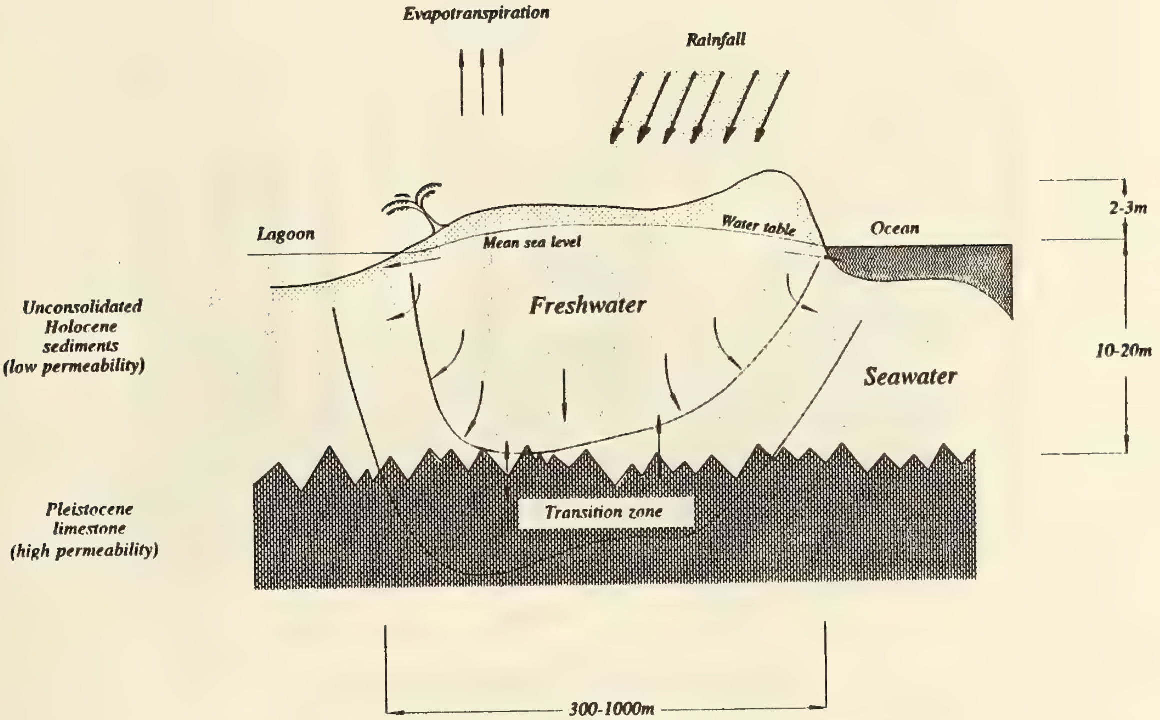


Figure 21. Typical cross-section through a coral island with a freshwater lens.

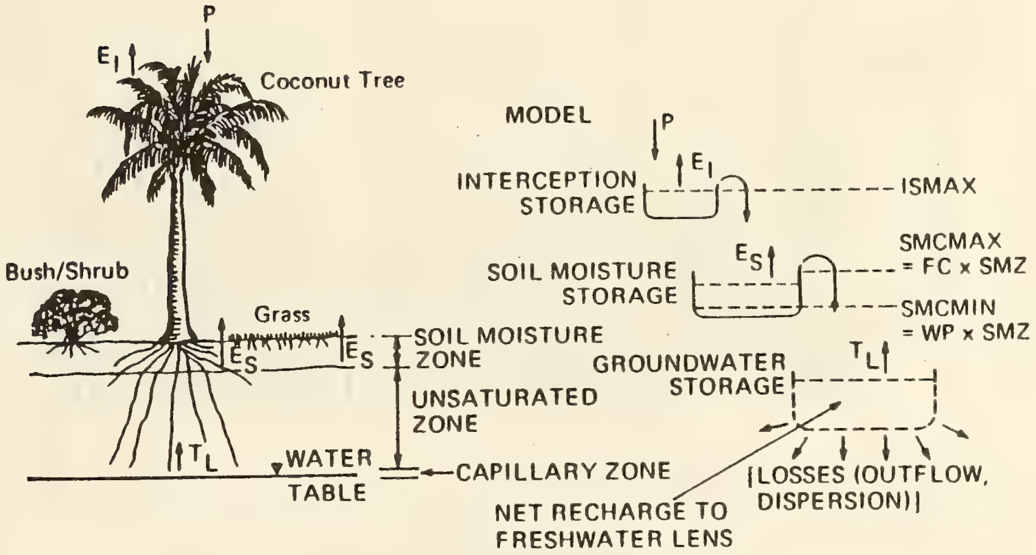


Figure 22. Recharge model.

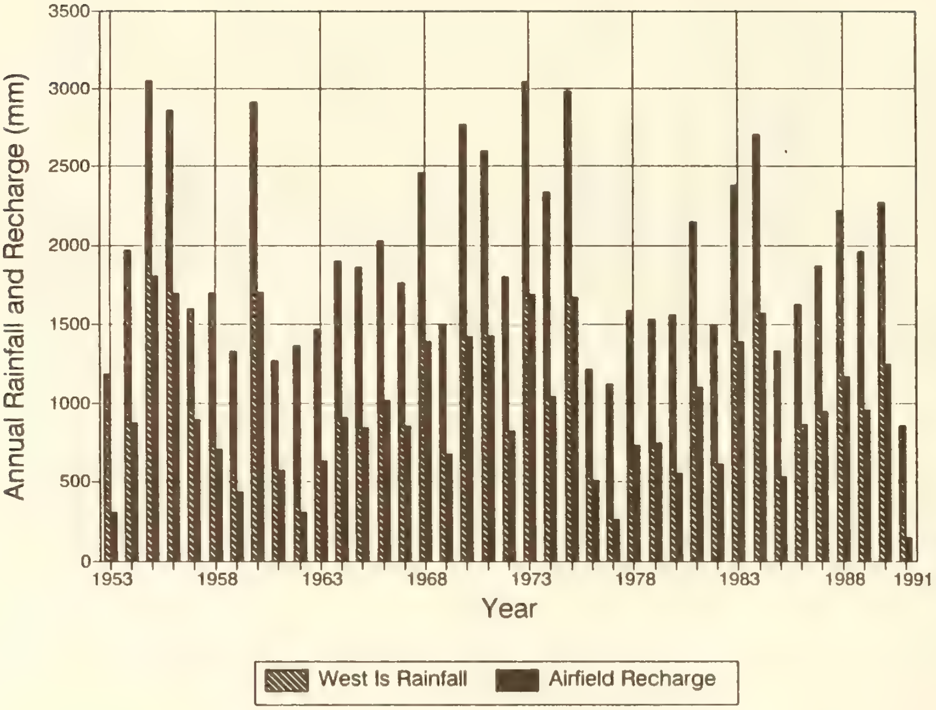


Figure 23. Annual rainfall and recharge, Airfield Lens, 1953-1991.

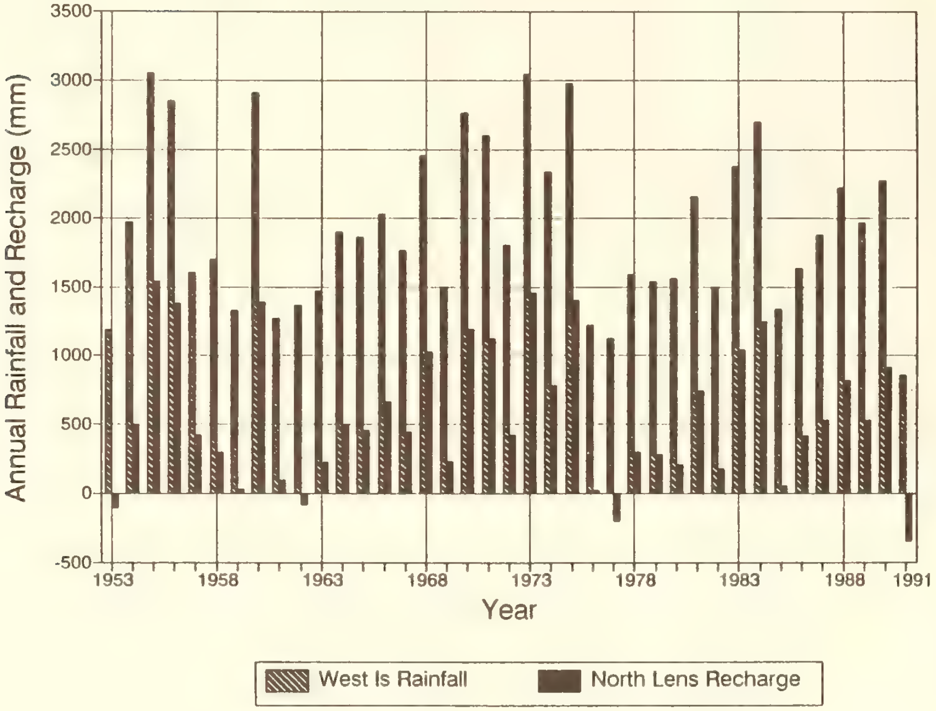


Figure 24. Annual rainfall and recharge, Northern Lens, 1953-1991.

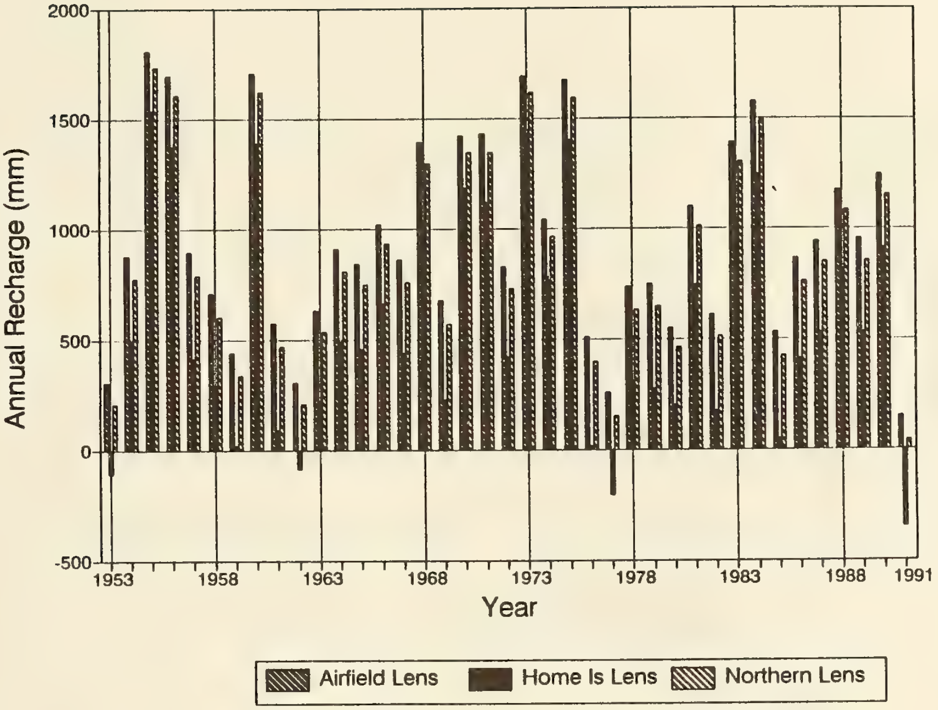


Figure 25. Annual rainfall and recharge, West Island and Home Island Lenses, 1953-1991

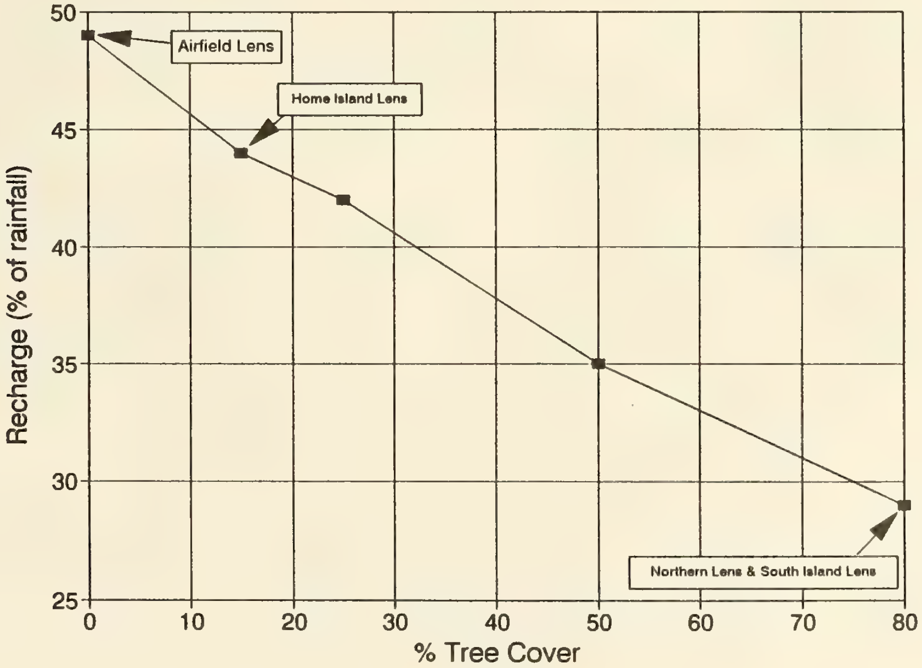


Figure 26. Effects of tree vegetation on mean annual recharge.

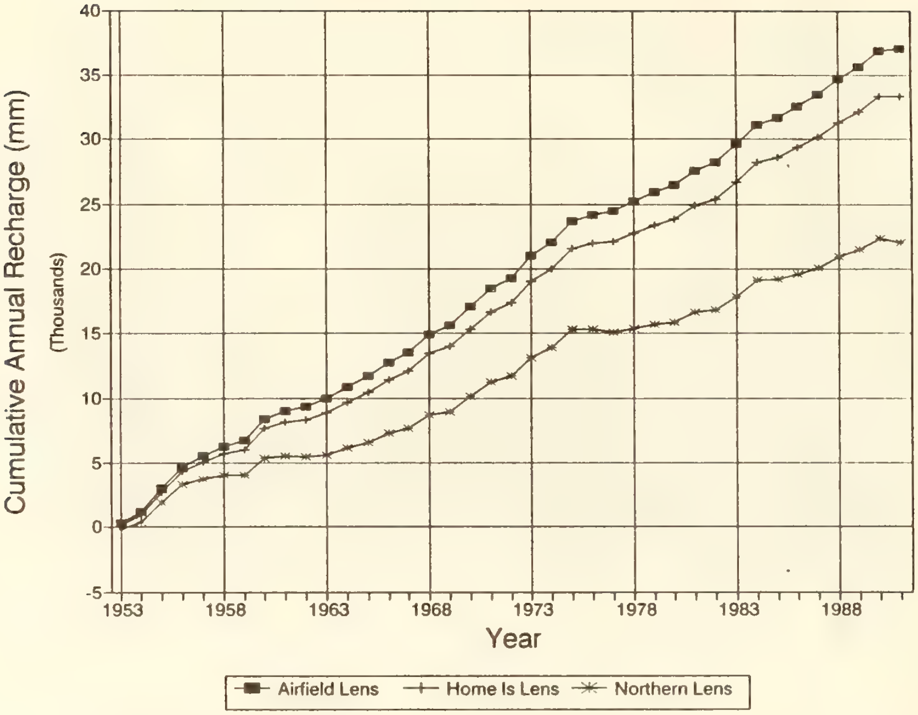


Figure 27. Cummulative annual recharge for West Island and Home Island Lenses, 1953-1991.

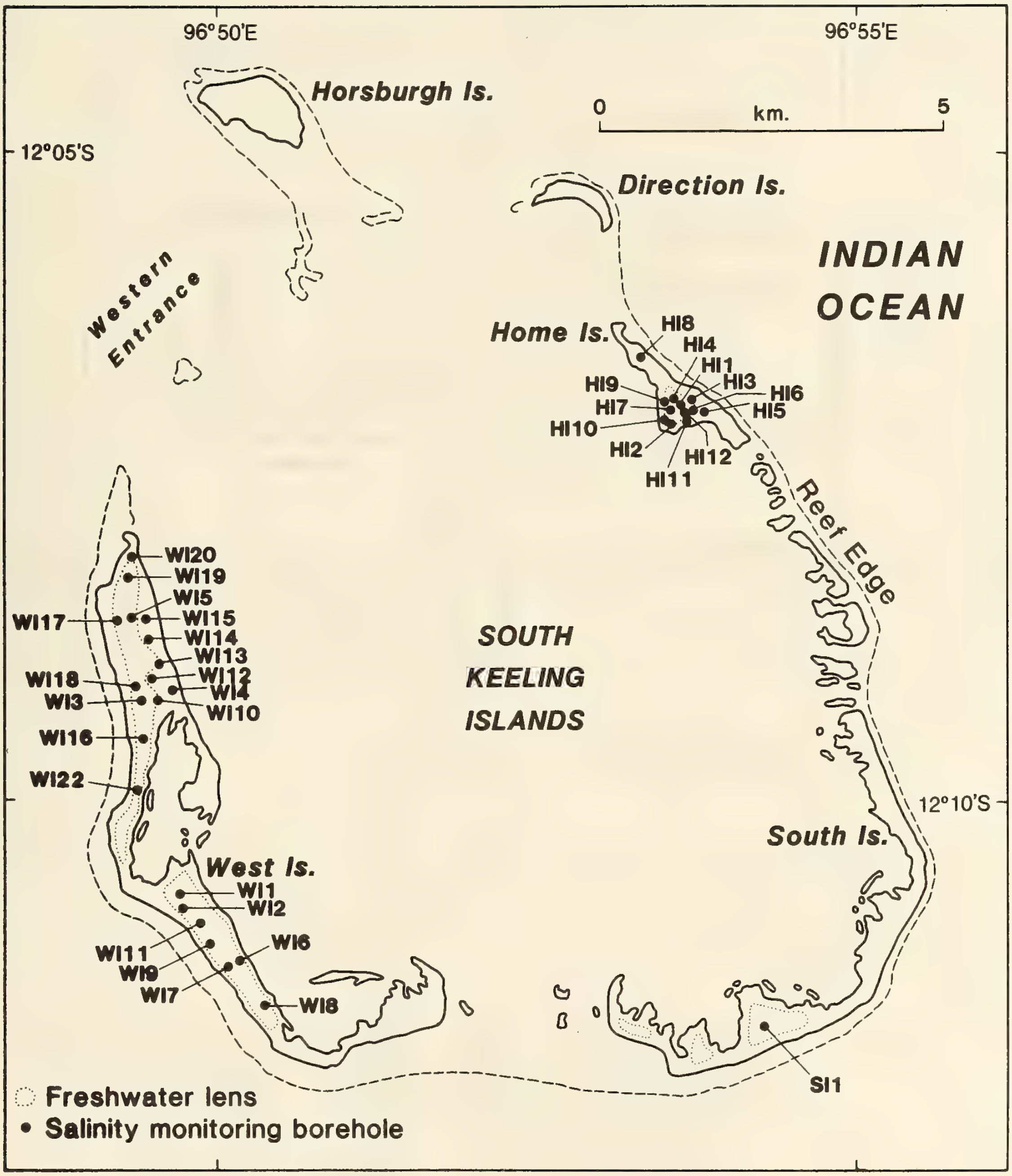


Figure 28. Location of Boreholes and freshwater lenses.

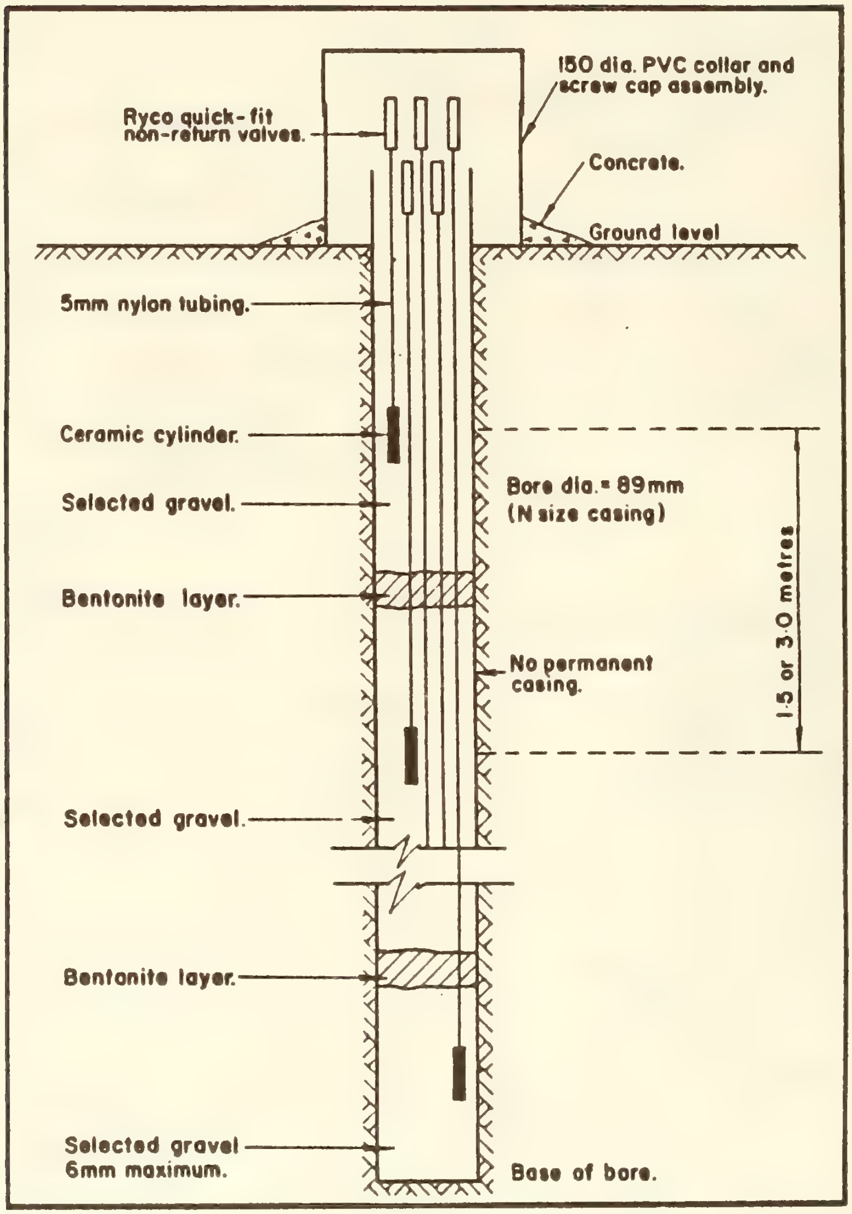


Figure 29. Borehole salinity monitoring system.

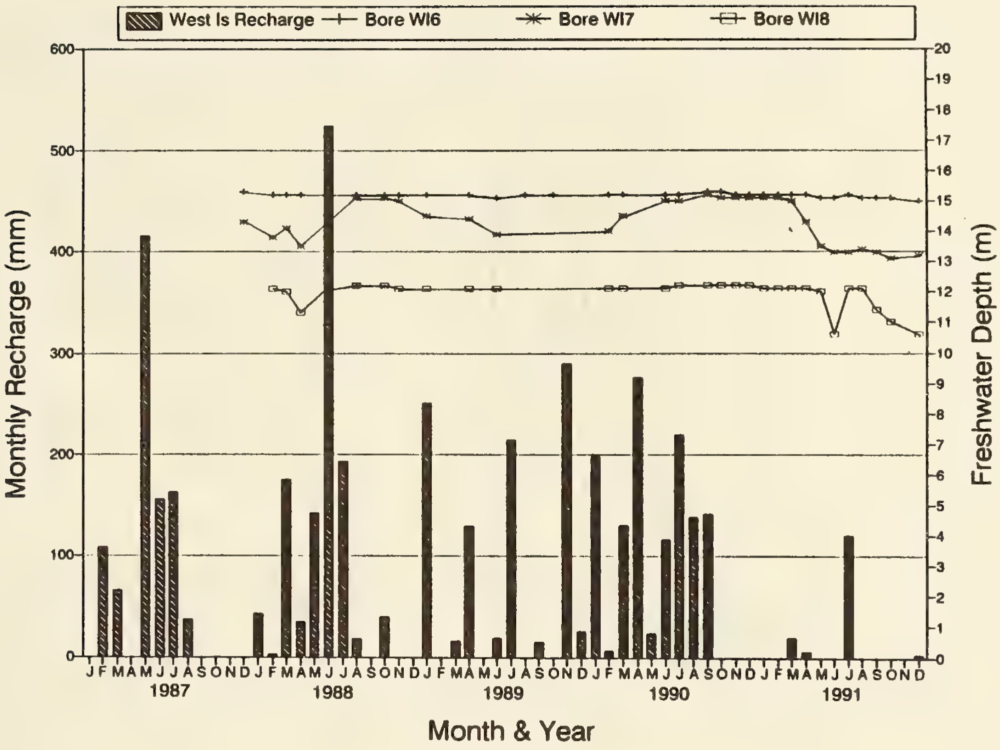


Figure 30. Depth of freshwater zone and recharge for boreholes WI 16, WI 17 and WI 18 on West Island.

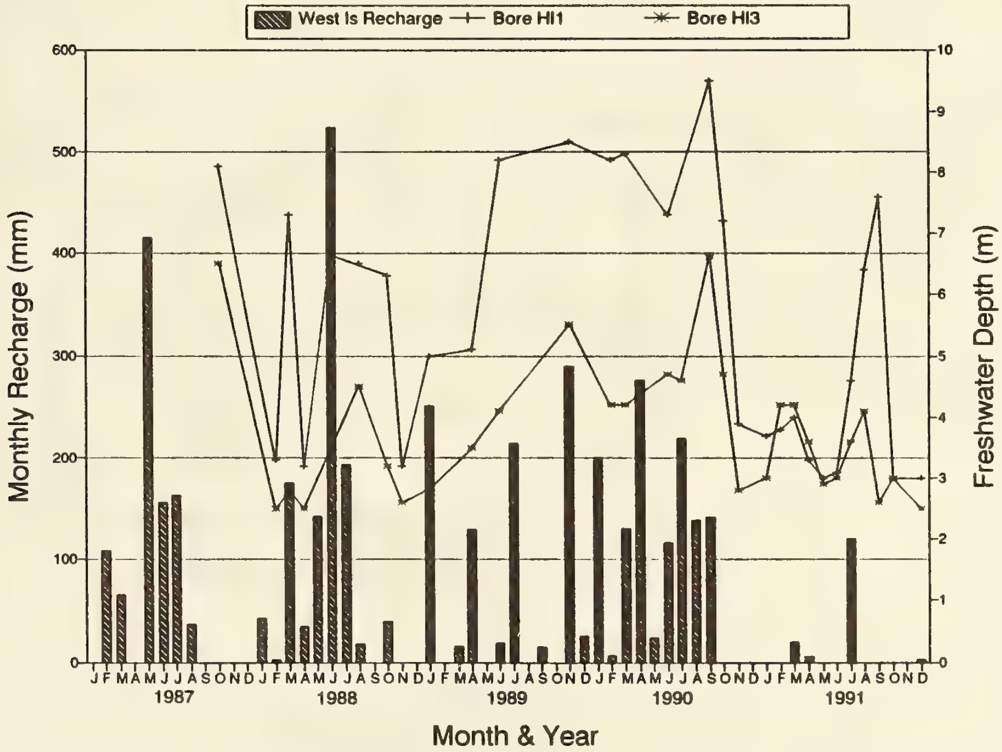
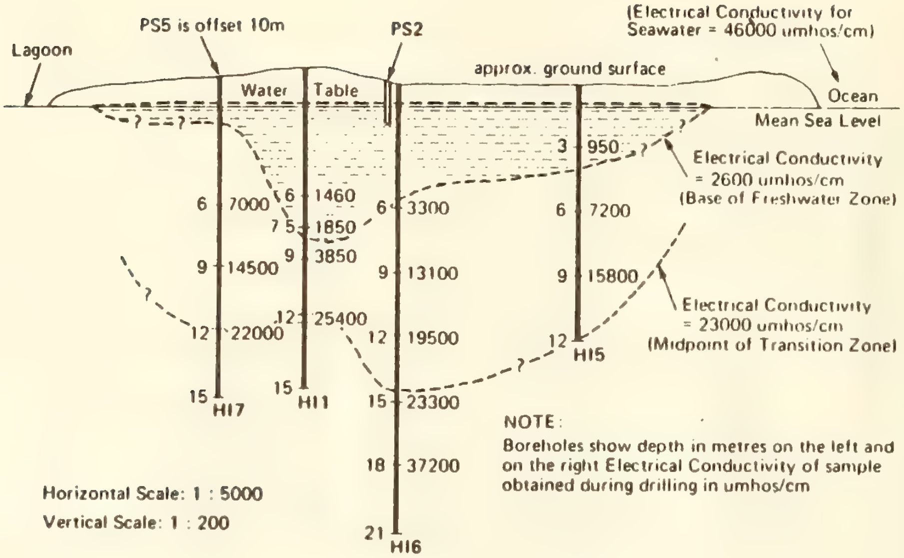


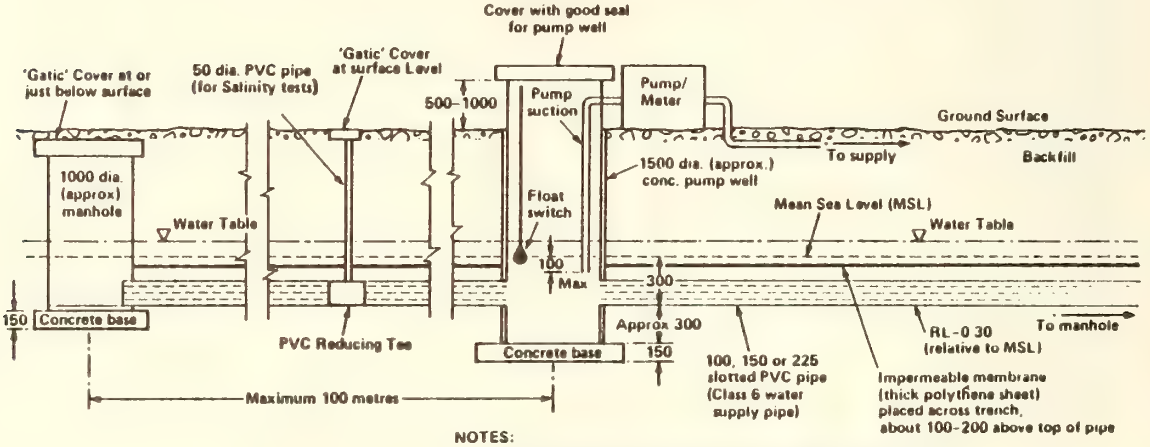
Figure 31. Depth of freshwater zone and recharge for boreholes HI 1 and HI 3 on West Island.



Horizontal Scale: 1 : 5000
Vertical Scale: 1 : 200

NOTE:
Boreholes show depth in metres on the left and on the right Electrical Conductivity of sample obtained during drilling in umhos/cm

Figure 32. Cross-section through Home Island lens showing shape of lens at time of drilling in Oct/Nov 1987.



NOTES:

1. All joints between pipes and pump wells/manholes to be well sealed
2. Float switch level to be as close above base of pump suction as possible (without causing vortex)
3. Optional housing over pump well and pump/meter (not shown)
4. All figures in mm but drawing not to scale

Figure 33. Cross-section through typical Home Island infiltration gallery.

ATOLL RESEARCH BULLETIN

NO. 401

CHAPTER 3

LATE QUATERNARY MORPHOLOGY OF THE COCOS (KEELING) ISLANDS

BY

D.E. SEARLE

ISSUED BY
NATIONAL MUSEUM OF NATURAL HISTORY
SMITHSONIAN INSTITUTION
WASHINGTON, D.C., U.S.A.
FEBRUARY 1994

CHAPTER 3

LATE QUATERNARY MORPHOLOGY OF THE COCOS (KEELING) ISLANDS

BY

D.E. SEARLE *

ABSTRACT

Seismic profiles have been obtained from Cocos lagoon and correlated with radiometric-dated core data. They show that the Last Interglacial atoll had a very similar morphology to the present atoll, and lies 8 to 28 m below sea level. It is overlain by 8 to 18 m of Holocene reefal deposits. Two deeper surfaces, of similar shape to the overlying reef surfaces, are recorded beneath the lagoon. These are tentatively identified as solution unconformities formed during glacial lowstands at oxygen isotope stages 6 and 8. Blue holes in Cocos lagoon are interpreted as solution dolines modified by clastic-controlled growth during submergence and relief enhancement by facies-controlled solution weathering during emergence. The data support the antecedent model of reef development on a subsiding base. However, unlike Purdy's (1974) antecedent karst model, both constructional relief and differential erosion are emphasised. Preservation of thin reef caps indicates that the atoll surface may have been lowered by as much as 18 m during each glacial cycle by subaerial erosion and solution. This allows an improved estimate of 0.02 mm/yr for subsidence of the atoll during the late Quaternary.

INTRODUCTION

Charles Darwin visited the Cocos (Keeling) Islands in 1836 and collected field evidence in support of his subsidence theory of atoll formation. This theory recognises an evolutionary sequence by vertical reef growth from volcanic island fringing reefs, through barrier reefs, to coral atolls driven by gradual subsidence of the volcanic island core. Drilling through Pacific atolls has encountered thick, shallow-water, reef-associated limestone overlying basal basalt; these results have substantiated Darwin's theory. Isostasy and plate tectonics provide explanation for subsidence and co-existence of evolutionary reef phases along linear island chains.

Darwin's field evidence from Cocos consisted of observation of erosion of the shoreline and collapse of coconut palms by undercutting at the shoreline. He inferred subsidence from this geomorphic evidence - an interpretation that has been strongly questioned, for example by Ross (1855).

A cemented coral conglomerate platform underlies many of the Cocos Islands and is exposed along the ocean shoreline. Dating of material from this platform, which has been identified as a former reef flat, indicates that sea level was about 1 m higher than present some 3000 years ago (Woodroffe et al. 1990).

Drilling on the Cocos Islands has intersected the "Thurber" discontinuity, a solution unconformity separating Holocene from Pleistocene reef that, at one site, has been dated at about 120, 000 years B.P. This corresponds to the Last interglacial oxygen

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* Department of Minerals and Energy, P.O. Box 194, Brisbane, Queensland, 4001.

isotope substage 5e (Woodroffe et al. 1991). The discontinuity lies at 6-16 m below sea level (revised depths, see Fig. 1 and Woodroffe et al. this volume). Woodroffe et al. (1991) interpreted the data to imply a subsidence rate of 0.1 mm/yr over the last 120, 000 years.

Thus, the Cocos (Keeling) Islands have been undergoing gradual, long term subsidence. Superimposed on this are millennia scale, glacially-induced eustatic movements in relative sea level and consequent hydro-isostatic adjustments. The most recent relative sea-level change has been a slight fall over the last few thousand years.

This paper is concerned with the structure of the Cocos (Keeling) Atoll during the Late Quaternary, and the influence of antecedent topography on the morphology of the modern atoll.

REGIONAL SETTING

The Cocos (Keeling) Islands, in the eastern Indian Ocean, consist of an atollon - North Keeling Island, and a horseshoe-shaped atoll - South Keeling Islands. The South Keeling atoll lies 40km south of North Keeling and consists of a shallow circular lagoon fringed by a series of reef islands. The islands vary in size from West Island, which is 11km long, to small islands less than a kilometre long (Fig. 1).

The lagoon of South Keeling atoll is 10 km across east to west, and 12 km from north to south. To the south and east, the lagoon connects with the open ocean through inter-island channels that are about 1 m deep. To the north and north west, deep openings occur on either side of Horsburgh Island (see Kench, this volume). Cocos lagoon is shallow to the south, with much of it being exposed at low tide. To the north the lagoon deepens to over 15 m. Much of the central south-eastern part of the lagoon is occupied by steep-sided "blue-holes", some over 15 m deep (Fig. 5). The holes average 100 m across but are generally smaller and more isolated to the south east while towards the centre of the lagoon the holes commonly coalesce. Submerged patch reefs occur in the central lagoon (see Williams, this volume).

METHODOLOGY

A high resolution continuous seismic reflection survey was carried out in the lagoon of the South Keeling Islands. The continuous seismic profiling (CSP) was conducted using a "Uniboom" sound source, triggered every half-second at an energy level of 200 Joules. A single-channel, 8-element hydrophone was used to receive the seismic signal after reflection from the seabed and subsurface. The signal was filtered to remove noise below 500 Hz and displayed as a seismic cross section on a graphic recorder. Seismic profiling was carried out at a speed of 4 knots. Position fixes were obtained every 2 minutes (about every 250 m) using a Trimble GPS unit.

In order to limit the presence of seabed multiples the sound source and hydrophone were deployed from opposite quarters of the vessel. This field technique imposes a geometrical depth scale on the records, and corrections have been applied to depths measured from the seismic records.

RESULTS

A total of 70 km of seismic profile was recorded over the northern and central part of the lagoon, Figure 1. This includes profiles across the blue holes, and profiles approaching Home and West Islands to allow correlation of seismic with drill data. Seismic profiling was not feasible in the very shallow southern part of the lagoon.

Seismic data quality was only fair owing to noise from wind waves in the lagoon generated from the persistent Trade Winds. In the shallow seagrass-covered parts of the lagoon, particularly off Home Island, no seismic signal was received by the hydrophone array. This was due to attenuation of the signal by gas bubbles adhering to the seagrass.

The seismic profiles from Cocos lagoon record subsurface data down to 45-50 milliseconds of reflection time, being limited by the system used and the nature of the sediments encountered. This converts to about 35 m in depth, assuming a conversion velocity of 1500 m/s. This value is close to the seismic velocity of sea water and reef limestone of Holocene age. Older sediments, which may be more compacted and cemented, can have higher velocities. Thickness of older units may be overestimated since a conversion velocity of 1500 m/s has to be used in the absence of measured values.

INTERPRETATION

The seismic profiles record the seabed and subsurface reflectors. The subsurface reflectors are derived from changes in physical properties at geological discontinuities. Experience in reef provinces elsewhere suggests that these discontinuities are commonly solution unconformities formed when reefs were exposed to subaerial processes during glacially-induced, sea-level lowstands (Orme et al. 1978, Searle and Harvey, 1982). Thus reflections from unconformities imply atoll emergence, while the seismic sequences bounded by these reflections are due to reef and lagoonal deposition during interglacials.

Lagoonal bathymetry is one of high relief except for the marginal areas where shallow subtidal flats commonly extend for 2 to 3 km into the lagoon. The deepest water encountered during the seismic survey was in the blue holes. One hole was 18 m deep with a rim barely deep enough to allow passage (0.5 m at high tide). Water to 16 m deep was traversed in the centre of the lagoon and close to the southern tip of Direction Island.

Three subsurface reflectors (referred to as A, B, and C in descending order) are present on the seismic records (Figs. 2 and 3). These reflectors, together with the seabed reflection, form the sequence boundaries of 4 depositional units.

The seismic sequence bounded by reflector A and the seabed varies in thickness from 8 to 18 m. It is thickest towards the southern part of the lagoon where blue holes appear to be infilled (Fig. 3). Unlike seismic data from the Great Barrier Reef Province (see Orme et al. 1978; Searle, 1983; Searle and Flood 1988) little internal structure is apparent in this sequence, and it is not possible to differentiate between reef rock and bioclastic facies.

Reflector A varies in depth from 11.5 m where it rises towards West Island, to 28 m in the centre of the lagoon. The shape of the subsurface defined by reflector A closely matches that of the lagoonal seabed. Both have high relief, except where they rise gently towards the islands; are deepest in the centre of the lagoon; and steepest dips are apparent over the blue holes and their rims. The data have been tested for velocity distortion using published refraction velocities for reefal limestone of Holocene age (Harvey and Hopley 1981). Less than 20% of the relief on reflector A can be accounted for by this effect. Similarities in the morphology of the lagoon and its subsurface as seen on the seismic records are, therefore, real and not attributable to distortion.

A thin sequence separates reflectors A and B. This sequence averages only 1 - 2 m in thickness except off the northern part of West Island where it increases to 5 m (Fig. 2).

Reflector B lies at depths of 16 to 32 m, and generally conforms with the shape of reflector A. It is deepest beneath the centre of the lagoon and shallowest off the northern part of West Island. Here it forms a terrace at -17 m overlying a -20 m terrace defined by reflector C (Figure 2). Beneath the blue holes reflector B lies at a depth of 24 to 26 m, being deeper below the holes and somewhat shallower below their rims.

Sequence B/C, where recognised, is only 1-2 m thick (Figs. 2 and 3).

Reflector C, although commonly lost below the limit of penetration, lies at depths of 18 to 32 m. Reflector C is best developed between the northern part of West Island and the central lagoon where it forms the -20 m terrace that then dips towards the centre of the lagoon (Figure 2). Reflector C is also present at about -22 m off Direction Island, dipping towards the centre of the lagoon.

DISCUSSION

Drilling on the Cocos (Keeling) Islands (Woodroffe et al. 1991; Woodroffe et al. this volume; Falkland, this volume) intersected the "Thurber" discontinuity at depths of 6 to 16 m below mean sea level (Fig. 1). Projection of reflector A from the seismic profiles that come closest to the drillholes on West Island allow correlation with the top of the older limestone at the "Thurber" discontinuity (Figs. 2 and 4). On Cocos this older limestone has been dated as Last Interglacial in age (123 ± 7 ka B.P., Woodroffe et al. 1991). Thus reflector A is interpreted as the weathered surface of the Last Interglacial atoll modified by subaerial exposure prior to the Postglacial transgression, and upon which Holocene reef has developed. Reflector A marks the Holocene/Pleistocene boundary.

Reflectors B and C (Figs. 2 and 3) are interpreted as older solution unconformities formed by subaerial exposure on progressively older atoll surfaces. The sea-level curve of Chappell (1983) shows glacial lowstands reaching minina at 150, 000 and 260, 000 years B.P.; reflectors B and C, respectively, may represent the subaerial surfaces formed during these episodes (oxygen isotope stages 6 and 8) and upon which subsequent reef development took place.

The sequence below reflector C probably consists of reefal deposits dating from the highstand of oxygen isotope stage 9. Seismic sequences B/C and A/B represent reefal limestone deposited during highstand stages 7 and 5e, respectively.

Although reflectors B and C are imperfectly recorded by the seismic system, the shape of the ancestral atoll lagoon (after subaerial weathering) appears to have been preserved during the Late Quaternary through to the present day. Even at the relatively fine scale of blue holes, shape has been preserved, and possibly enhanced (Fig. 3). The most noticeable difference in atoll shape since the formation of surface B has been the progradation of Last Interglacial age reefal sediments over the -17 m terrace off West Island (Fig. 2).

The unconformity defined by reflector A is interpreted as the weathered surface of the Last Interglacial reef. This surface lies 6-16 m below mean sea level beneath the islands (Woodroffe et al. 1991, and this volume), and dips beneath the lagoon to a depth of 28m below mean sea level. Off West Island, where the best subsurface data is available, this Holocene/Pleistocene interface dips at 4 m/km into the lagoon (Fig. 4). Below the blue holes and the submerged patch reefs in the centre of the lagoon surface A is substantially mimiced by the modern reefal surface (Fig. 3). Thus the morphology of the modern atoll is inherited from its antecedent platform, which, in its turn appears to have been inherited from older atoll landforms. In this respect, the data from Cocos support the antecedent karst theory of Purdy (1974).

It appears that atoll landforms maintain and even amplify their antecedent relief. This may be due to either differential accretion during submergence, or to differential erosion during subaerial exposure, or a combination of both processes. Accretion by vertical reef growth during marine transgressions would be more rapid in the shallow photic zone, aided by a process of clastic control whereby coral growth can be retarded by biodetritus deposited in low areas (Goreau and Land 1974).

Subaerial erosion may also amplify relief by facies control of solution weathering (Bloom 1974). Under this process the less permeable lagoonal sand and mud facies would dissolve away faster than the more permeable reef framework and coarse rubble/conglomerate facies. On a smaller scale, facies control accounts for the development of blue holes. Once elevation differences were present in the proto-atoll lagoon the positive features would be exploited by coral colonisation and vertical growth. Then, as now, the lagoon would tend to silt up by progradation of bioclastic sand and mud behind the windward margin. The negative areas between reef patches would gradually infill as an intertidal reef flat developed in the lagoon. Upon emergence the surface would experience facies-controlled differential weathering through internal drainage and solution. This would result in the formation of residual prominences at the site of former patch reefs, and the development of solution dolines in the intervening lagoonal mud and sand facies. Subsequent glacial cycles would emphasise relief by constructional (highstand phases) and solution weathering (lowstand phases) processes forming relatively deep blue holes.

While blue holes are relatively numerous in the Caribbean, few have been reported from the Indo-Pacific region (Purdy 1974). Deep blue holes are not common in the Great Barrier Reef; they occur singly, and partly for that reason are considered as collapsed doline features (Backshall et al. 1979). The blue holes on Cocos, by contrast, dominate the southern central area of the lagoon. They are unlikely to be juxtaposed collapse features, and are considered to be multi-generational solution dolines.

The Holocene pattern of atoll development may be taken as a model for earlier cycles. The difference in thickness between the older Pleistocene reef and associated lagoonal sediments, and Holocene deposits is presumably due to subaerial erosion of the older sediments. It is interesting to speculate on the relationship between reef growth and subaerial erosion, and consider implications of sea level and subsidence for the preservation of the resulting reef cap.

The data from Cocos implies a mean accretion rate of 2 mm/yr, based on an average thickness of Holocene of 16 m deposited since the sea flooded the atoll some 8000 years ago. Reefal accretion could only occur during submergence for, say 10% of each Late Quaternary glacial cycle. This would add 20 m to the reef cap during each interglacial cycle. As sequences A/B and B/C are only 1-2 m thick, 18 m of reef cap must have been eroded during the remaining 90% of time when the atoll was emergent, hence an erosion rate of 0.2 mm/yr is implied.

Data on erosion rates is sparse and values vary greatly. For instance, Trudgill (1976) provides an average value of 0.26 mm/yr from Aldabra Atoll from a range of values that vary with lithology, mineralogy and soil cover. Purdy (1974), quoting Land *et al* (1967), provides values of 0.01-0.04 mm/yr that vary with rainfall. Data for reefal accretion appears less extreme and better established. On Cocos, Holocene accretion estimated from the seismic and core data falls within the range of estimates for other atolls, see, for example, Marshall and Jacobsen (1985).

For the reef cap to be repeatedly accommodated, highstand sea levels must rise, or the atoll must subside. Accepting the latter as the most feasible in the longer term, a subsidence rate of 0.02 mm/yr is implied from the data. This allows for a 2 m increment to the reef cap during each glacial cycle. Subsidence rates for Cocos (Woodroffe et al. 1991) can now be refined to the lower value of 0.02 mm/yr, which is closer to global average oceanic subsidence rates (Ladd et al. 1970, Menard 1986).

CONCLUSIONS

Continuous high resolution seismic data has been obtained from Cocos lagoon. Correlation with radiometric-dated core data from the Cocos islands allows reconstruction of the shape of the Last interglacial atoll.

The Last Interglacial atoll surface, both island and lagoon, has a very similar morphology to the present atoll, and lies 8 to 28 m below sea level. It is overlain by 8 to 18 m of Holocene reefal deposits.

Two deeper surfaces, of similar shape to the overlying reef surfaces, are recorded beneath the lagoon. These are tentatively identified as solution unconformities dating from subaerial exposure of earlier atolls during glacial lowstands at oxygen isotope stages 6 and 8.

A field of partially-infilled blue holes seen in the southern central part of the lagoon is underlaid by antecedent depressions. These are interpreted as solution dolines modified by clastic-controlled growth during submergence and relief enhanced by facies-controlled solution weathering during emergence.

The seismic data, correlated to core data, supports the antecedent model of reef development on a subsiding base. However, unlike Purdy's (1974) antecedent karst model, both constructional relief and differential erosion are envisaged as mechanisms for preserving atoll morphology through late Quaternary time.

The preservation of only thin former reefs indicates that the atoll surface was significantly lowered by subaerial erosion and solution during each glacial cycle. The data allow an improved estimate of 0.02 mm/yr for subsidence of Cocos Atoll during the late Quaternary.

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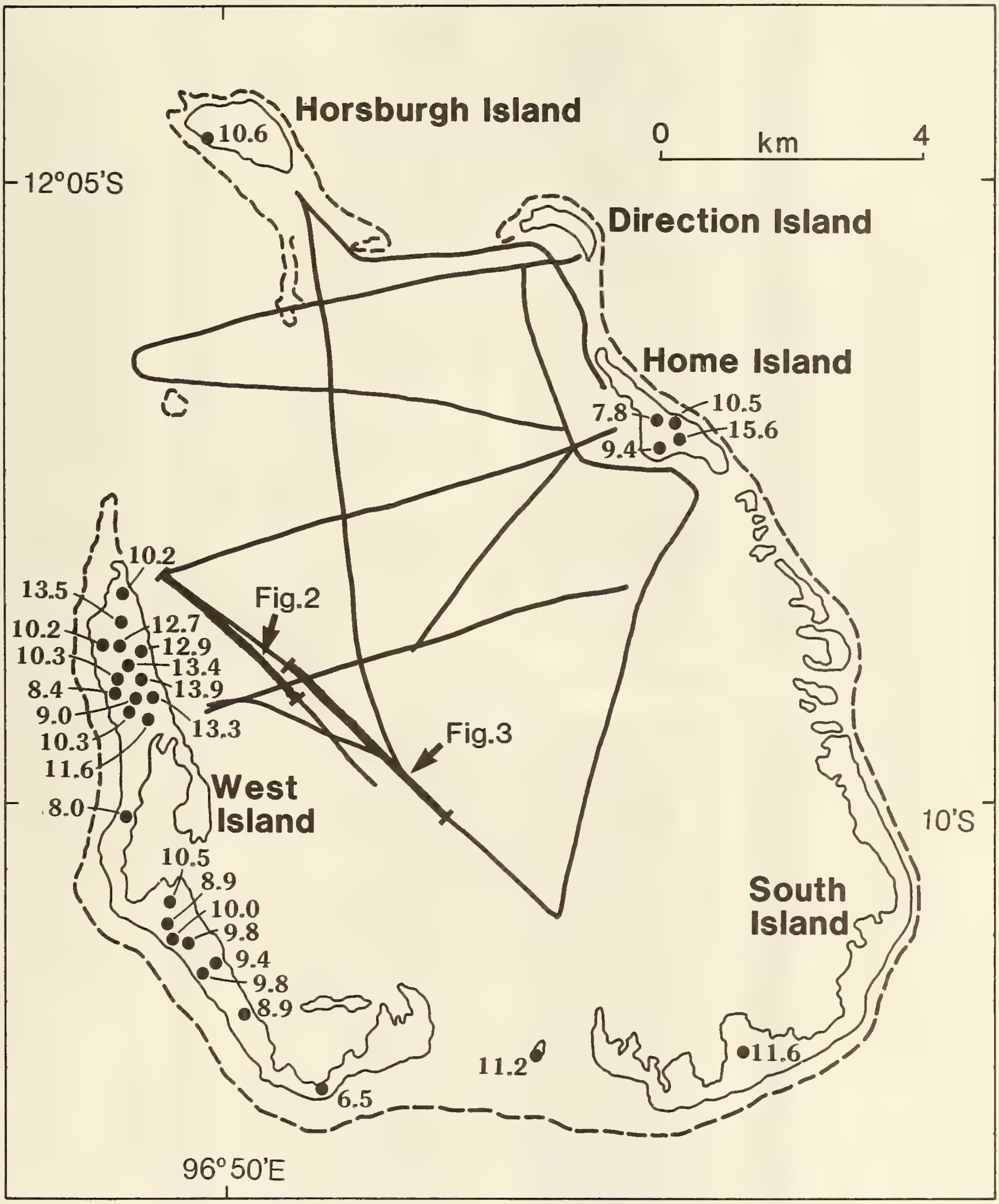

Figure 1. Cocos (Keeling) Atoll, showing the location of seismic tracks, coreholes and depths (below msl) to discontinuity.

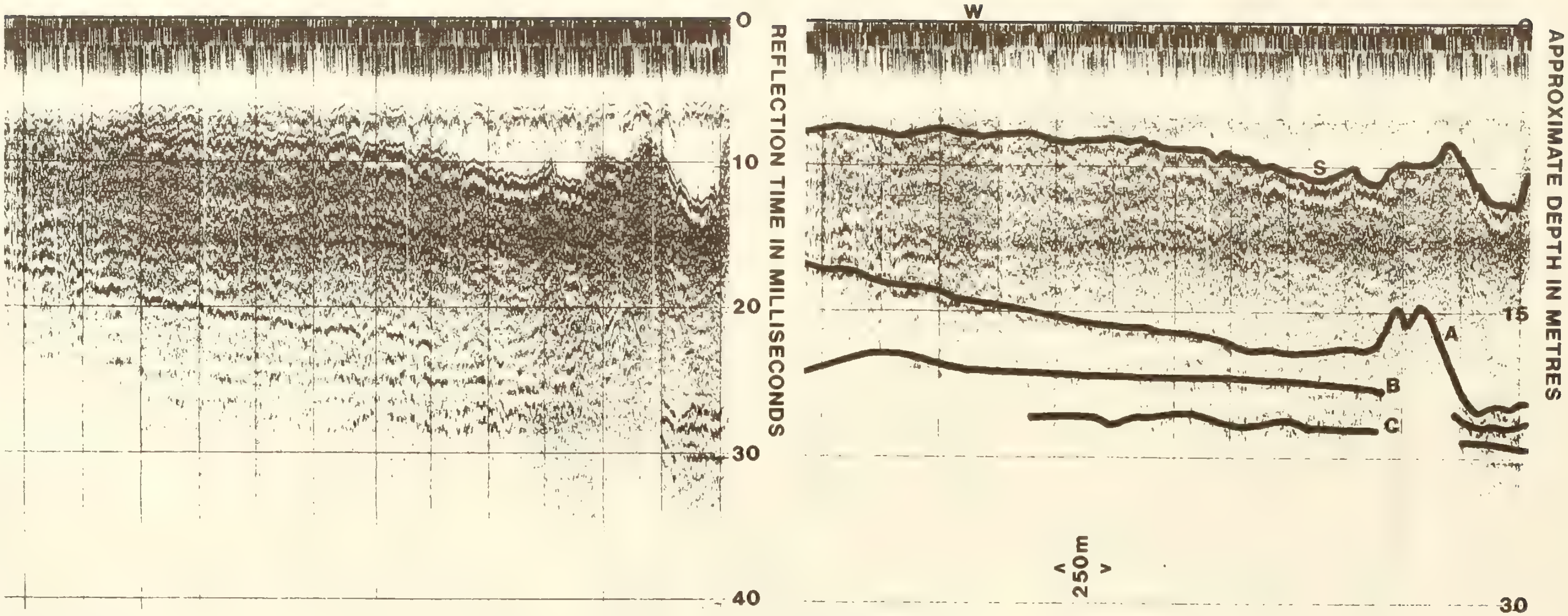

FIGURE 2a

FIGURE 2b

Figure 2. a) CSP record off northern part of West Island. b) Interpreted record. W - water surface, S - seabed, A,B,C - subsurface reflectors. Note Holocene sequence, approximately 10 m thick, overlying the Last Interglacial reef surface (A).

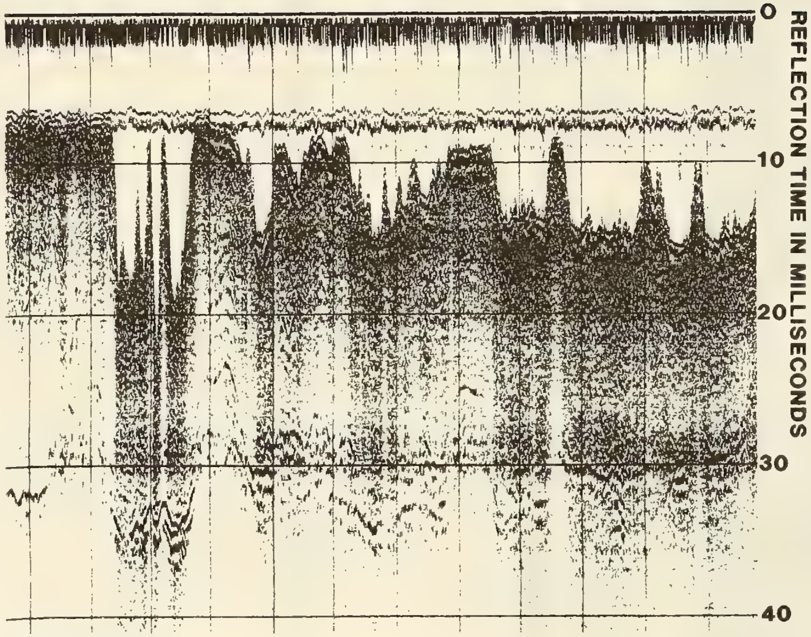

FIGURE 3a

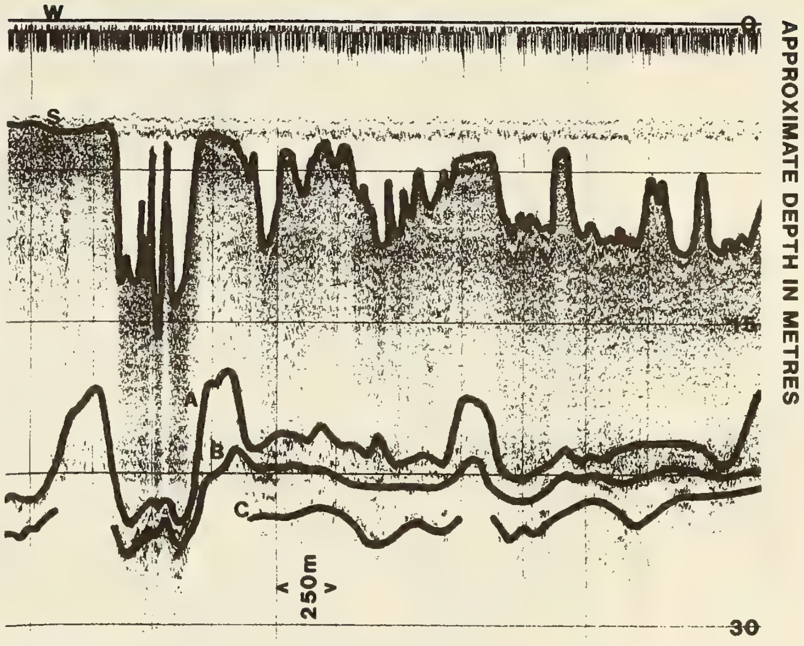

FIGURE 3b

Figure 3. a) CSP record from southern central lagoon, traversing infilled blue hole (LHS), deep blue holes, and patch reefs (RHS). b) Interpreted record. Note general similarity in shape between modern lagoonal surface and antecedent surfaces, and enhanced relief through time.

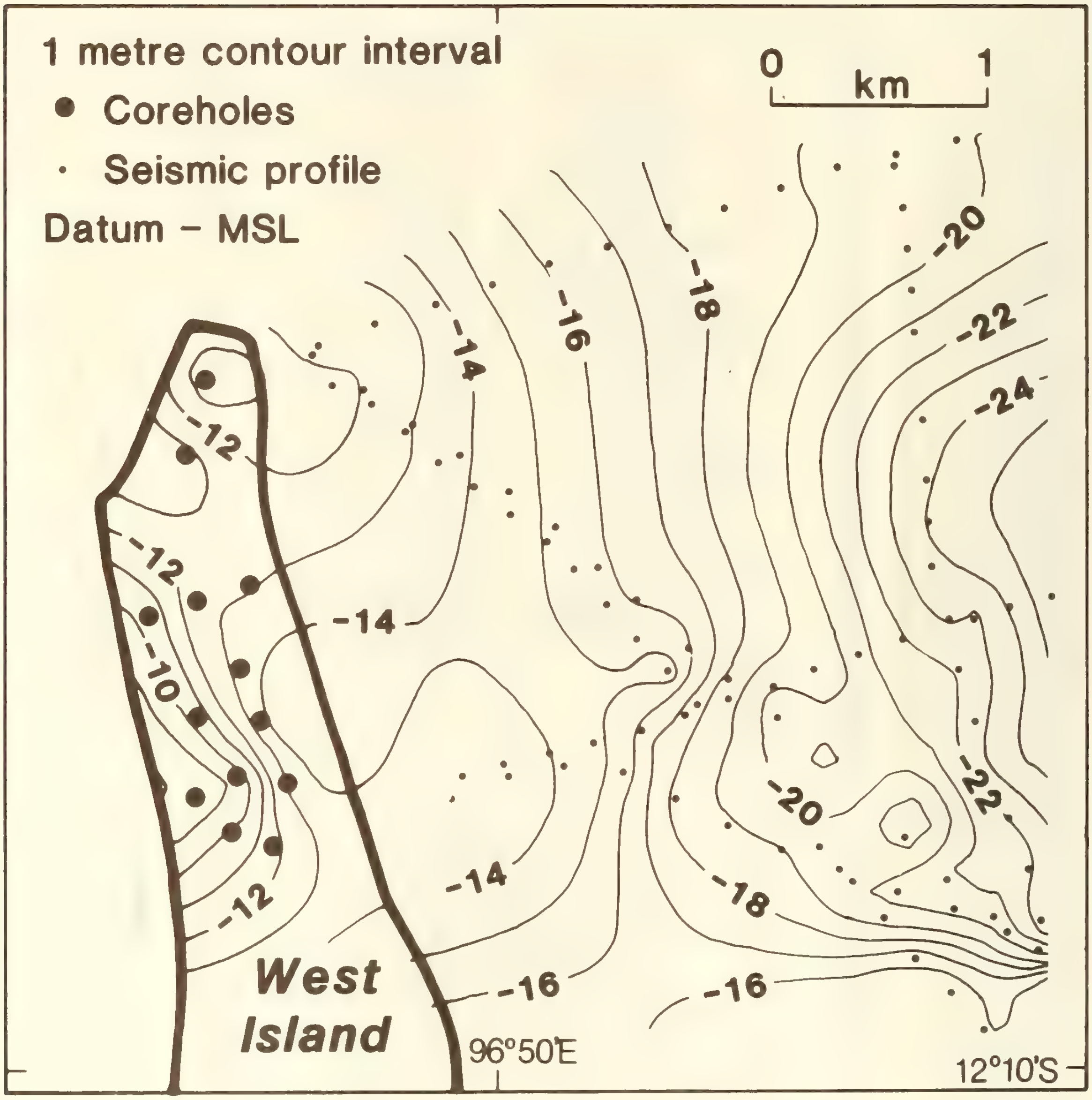

Figure 4. Contour plot of Last Interglacial atoll surface beneath western part of Cocos lagoon, based on seismic and drillhole data.

Figure 5. Oblique aerial photograph, looking east, of southen part of Cocos lagoon showing field of blue holes and atoll rim (between Home and South Islands). The holes are infilled to the south, coalesce in the midfield and pass into submerged patch reefs to the north. The seismic profile shown in Figure 3 passed close to the foreground in this photograph. Foreground width = 1500m.

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CHAPTER 4

GEOMORPHOLOGY OF THE COCOS (KEELING) ISLANDS

BY

C.D. WOODROFFE, R.F. McLEAN AND E. WALLENSKY

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CHAPTER 4

GEOMORPHOLOGY OF THE COCOS (KEELING) ISLANDS

BY

C.D. WOODROFFE *, R.F. McLEAN ** AND E. WALLENSKY ***

INTRODUCTION

Charles Darwin's subsidence theory of coral reef development has gained wide acceptance. The initial idea had occurred to Darwin while he was in South America, and he refined it during his voyage across the Pacific, writing an early draft of a manuscript on Coral Islands, probably between Tahiti and New Zealand (see Stoddart 1962), much of which subsequently appeared in his book on the structure and distribution of coral reefs (Darwin 1842). The Cocos (Keeling) Islands, which Darwin visited in April 1836 during the voyage of *H.M.S. Beagle*, were the only coral atoll on which he ever landed. He sought evidence there in support of the theory of coral reef development, and he left convinced that he had found such support. He wrote enthusiastically to his sister Caroline on 29 April 1836, some days after leaving Cocos, saying "I am very glad we called there, as it has been our only opportunity of seeing one of these wonderful productions of the Coral polypi.- The subject of Coral formation has for the last half year been of particular interest to me. I hope to be able to put some of the facts in a more simple and connected point of view, than that in which they have hitherto been considered".

Lyell (1832) had earlier proposed that atolls, with their characteristic annular reef rims which encircle a central lagoon, consist of a thin veneer of coral growing over the rims of submerged volcanic craters. Darwin considered it improbable that so many volcanic rims would lie within the narrow depth range required for reef growth, and proposed that there "is but one alternative; namely, the prolonged subsidence of the foundations on which atolls were primarily based, together with the upward growth of the reef-constructing corals. On this view every difficulty vanishes; fringing reefs are thus converted into barrier-reefs; and barrier-reefs, when encircling islands, are thus converted into atolls, the instant the last pinnacle of land sinks beneath the surface of the ocean." (Darwin 1842 p109).

Darwin used his observations during his brief visit to Cocos in support of his theory of coral reef development, and wrote a manuscript (termed the Cocos Coral Manuscript by Armstrong 1991) shortly after leaving the islands. Much of the debate for the next 100 years also centred around the Cocos (Keeling) Islands. Thus, although John Murray did not himself visit Cocos, during the voyage of *H.M.S. Challenger,* he funded the visit of Henry Brougham Guppy in 1888 (though his prime interest seems to have been to get Guppy to examine phosphate deposits on Christmas Island). Guppy

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was already critical of Darwin's subsidence theory of reef development, having observed fossil coral reefs elevated above modern sea level in the Solomon Islands, and was sympathetic to the alternative theory put forward by Murray (1889). Murray proposed that atolls were the result of solutional processes concentrated in the lagoon. Guppy (1889) clearly demonstrated that the Cocos lagoon was infilling with sediment, and he described the reef islands in detail. He was on Cocos for 10 weeks and he propounded the view that the reef rim was building out episodically , as Murray had suggested.

Wood-Jones was the doctor on the Cable Station on Direction Island, 1905-1906. He spent a considerable period examining the atoll, and based on his observations wrote a volume entitled *Coral and Atolls*, in which he put forward an alternative view, that the present morphology of the atoll had developed in response to the pattern of sediment production and deposition.

Thus the three views, summarised by Wood-Jones as the Subsidence, Solution, and Sedimentation hypotheses each had a particular connection with Cocos, and had each been tried and accepted by one of its major proponents in these islands. The only other hypothesis deserving serious consideration according to Davis (1928), in a review of the coral reef problem, was the glacial control hypothesis proposed by Daly (1915, 1934).

In this account we present results from a geomorphological reappraisal of the atoll based on a number of visits, and a series of surface and shallow subsurface observations. Our concern is primarily with the development of the surface morphology of the atoll rather than the atoll's structure, a distinction which needs to be made (Stoddart 1973), but which is not always clear in the preceding references. All of the surface features have formed in the mid-late Holocene, over a pre-Holocene surface; there are no surface outcrops of late Pleistocene or older materials anywhere on the atoll. Nevertheless, our interpretations of the surface morphology and Holocene evolution have implications for the structure and longer-term development of the atoll.

REGIONAL SETTING

The Cocos (Keeling) Islands comprise the main atoll of the South Keeling Islands (lat. 12°12'S, long. 96°54'E) and an isolated atollon, North Keeling (lat 11°50'S, long. 96°49'E), 27 km to the north. These are connected by a submerged ridge at a maximum depth of 1000 m. They comprise a single feature rising from an ocean floor depth of about 5000 m (Fig. 1). The age of the ocean floor at this location is not clear, but lies in the range 60-90 million years (Jongsma 1976). In this region the seafloor gets younger to the north, and appears to have been formed from a spreading centre that has been subducted into the Java Trench.

The Cocos (Keeling) Islands lie on the Cocos Rise. To the south, the Umitaka Mary seamount reaches to within 16m of the sea surface. This chain of seamounts, the Vening Meinesz seamounts, can be traced northeastwards towards Christmas Island. They are not, however as regular as linear chains of islands and seamounts seen in the Pacific, and it is uncertain whether they have developed from a single hotspot in the same manner as may Pacific seamounts (Scott and Rotondo 1983).

That Cocos represents a carbonate reefal capping on a volcanic seamount seems extremely likely although the depth to oceanic basalt is unknown. Magnetic surveys show an anomaly, reading 250nT in vertical intensity (Chamberlain 1960, Finlayson

1970). There is also a pronounced gravity anomaly over the island. In addition a basalt and tuff pebble has been dredged from the western end of the Cocos Rise (Bezrukov 1973), further supporting the idea that carbonate overlies a volcanic basement.

The southern atoll consists of a reef rim that surrounds the atoll with two major passages, one to the northwest and one to the northeast. A series of reef islands (described in detail by Woodroffe and McLean, this volume) occur on the horseshoe-shaped reef rim which is continuous from Direction Island to the northern end of West Island. Horsburgh Island is isolated at the north of the lagoon (see Fig. 2). Marine habitats of the atoll are described in detail by Williams (this volume); the reef front, which is relatively barren of living hard corals rises to the reef crest which is algal-veneered with surge channels at intervals of 50-250 m. The reef flat is covered by 1-2 m of water at high tide and part of it dries at low tide. The northern part of the lagoon averages around 15 m deep and is covered with dead coral or sand (see Smithers, this volume). The southern part of the lagoon is shallow, but contains a network of 'blue holes' (see Chapter 3, Fig. 5). Individual holes are 12-20 m deep, but their rims are emergent at low spring tides. Extensive sand flats and sand aprons occur around the margin of the lagoon (see Smithers, and Williams, this volume).

METHODS

Surface sediment characteristics were examined in exposures of lithified sediments, and along surveyed transects. Subsurface investigations were carried out by drilling and by seismic survey. The results of seismic reflection surveys within the Cocos lagoon are described by Searle (this volume). Seismic refraction on the islands was undertaken using a 12-channel Geometrics seismograph.

Drilling was undertaken during several visits. In addition to drilling, aimed specifically at unravelling the geomorphological history of the islands, drillcore logs and in some cases cores drilled as part of a water resources survey (see Falkland, this volume) were also examined. An initial reconnaissance visit was made by Woodroffe in 1986. In 1988 Woodroffe, McLean and Wallensky undertook drilling with a portable, trailer mounted Jacro 105 rotary drill, to depths of up to 9 m on Home Island, West Island and Pulu Wak Banka. In 1990 deeper drilling was undertaken using a Jacro 500, operated by P. Murphy; holes were sunk on Horsburgh, South, West and Pulu Blan Madar Islands. In 1991 seismic reflection surveys were undertaken in the lagoon, and exploratory drillholes were put down to 2.3 m using a hand-held Mindrill on the reef flat to the east and south of West Island. Several vibrocores were taken from the southern and eastern part of the lagoon (Smithers et al., in press), using 75 mm diameter aluminium pipe, vibrated into the lagoon floor with a concrete vibrator. Three long cores of up to 4.2 m length were recovered, together with several shorter ones. Sediment compaction was around 30% in most vibrocores.

Recovery in drillholes varied, but was rarely greater than 70%. Samples of coral and *Tridacna* recovered in the cores were submitted for radiocarbon dating. Samples of coral from the conglomerate platform, or from pits within islands were also submitted for dating. Radiocarbon dating was undertaken principally at the ANU Radiocarbon Dating Laboratory.

Marine carbonate samples usually require an environmental correction for ocean reservoir effect because organisms at their time of death are already somewhat depleted in radiocarbon, as the oceanic reservoir has a substantial circulation time. Marine carbonates therefore have an apparent age at the time of their death. For marine shells from the Australian coast this environmental correction varies, but is generally minus 450 ± 35 years from the conventional radiocarbon age (Gillespie and Polach 1979). On coral atolls there has been some questioning of the estimate of the correction factor, and indeed whether any correction needs to be made. In particular, Pirazzoli has argued that no correction should be necessary for dating of coral samples from within the lagoons of Tuamotu atolls, where there may be limited exchange of waters with open ocean (Pirazzoli et al. 1987). We have examined this in Cocos, taking advantage of earlier coral collections, and by dating samples of corals collected by Wood-Jones in 1906 and Gibson-Hill in 1941 (pre-1950 samples of known age are necessary for such dating as post-1950 samples have elevated radiocarbon levels as a result of radiocarbon released by bomb tests). Results are shown in Table 1, indicating the average correction to be 460 years. The correction is indeed around 450 years, and that is the value that we have used throughout this paper to conform with similar studies elsewhere.

PLEISTOCENE LIMESTONE

Boreholes undertaken as a part of a Water Resources survey of the Cocos (Keeling) Islands (see Falkland, this volume), together with our own drillholes, indicate that a well-lithified, but porous, limestone underlies the poorly consolidated coral shingle and sand deposits of the Cocos reef islands, at depths of around 11-14 m (see Chapter 2, Table 10 and Chapter 3, Fig. 1). This older limestone contains corals, with some travertine deposits in voids, and in at least one drillcore, cemented oolites. Uranium-series disequilibrium dating of a sample of coral at the top of this facies, from 12.6 m depth (10.5 m below MSL) in drillhole WI1 gave an age of 118,000 ± 7000 years B.P. on a bulk sample, but after preparation removing calcite under binocular microscope, the age determined was 123,000 ± 7000 years B.P. (Woodroffe et al. 1991). The age of this limestone suggests it formed during the last interglacial, when the sea was around or slightly higher than present, about 125,000 years ago.

The morphology of the Pleistocene atoll has been revealed in greater detail by seismic reflection profiling across the lagoon, results of which are discussed by Searle (this volume). Woodroffe et al. (1991) argued that the atoll had subsided at a rate of about 0.1 mm/yr based upon subsidence of this surface from above present sea level to 8-11 m below present sea level. The seismic results indicate that the surface actually has a considerable slope on it, becoming much deeper with distance into the lagoon, towards the centre of which it is more than 24 m below present sea level. This morphology seems likely to result from solution during subaerial exposure of the atoll when the sea was low, and Searle (this volume) suggests that the subsidence rate may be only 0.02 mm/yr.

CONGLOMERATE PLATFORM

An important feature of reef islands on Cocos is a platform of coral conglomerate which underlies most of the islands on the atoll rim. The platform was termed 'brecciated coral-rock' by Darwin (1842), 'reef conglomerate' by Guppy (1889), and 'breccia platform' by Wood-Jones (1912).

This near-horizontal conglomerate platform comprises cemented clasts of coral shingle or rubble, found especially along the oceanward shore of many of the islands, but also underlying part of the islands as shown in pits and wells. It occurs up to 0.5 m above MSL, and is thus inundated by the highest tides. Individual coral boulders of *Porites* of up to 2 m in diameter occasionally protrude from the platform, the highest points of which may reach up to 1 m above MSL.

In some places, notably on North Keeling and Horsburgh, and at the southwestern end of West Island, the surface of the conglomerate platform is composed of arcuate, seaward-dipping beds of cemented coral cobbles. These appear to have been interpreted as former reef crests by Guppy (1889), but there is nothing in their composition to substantiate this. Instead, they resemble the foot of the modern beach where there is a rubble component, and we interpret them as beach conglomerate, marking the former position of rubble-strewn beaches.

Guppy (1889) indicated that compositionally the conglomerate platform resembles the modern reef flat. The reef flat is characteristically 1.0-1.5 m lower than the surface of the platform, which is undergoing erosion on its seaward side. The reef flat often forms a hard, relatively smooth surface with encrustation by calcareous algae. This veneer may cover formerly truncated conglomerate platform. On the basis of constituent materials, gross fabric and surface morphology, we have interpreted the conglomerate platform as a fossil emergent reef flat (Woodroffe et al. 1990a, 1990b). Radiocarbon dates on corals from within the conglomerate platform indicate a spread of ages from 4010 ± 85 to 3050 ± 85 years B.P. (Table 2, Fig. 2).

There are a number of sites at which apparently in situ fossil *Porites* microatolls, both massive and branching, have been found within the conglomerate, and which further serve to indicate that sea level was higher than the modern sea level when the conglomerate was formed. These provide a discontinuous record of the pattern of sea-level change over the late Holocene, and are discussed in greater detail below.

Shallow drilling on Home Island and Pulu Wak Banka on the eastern rim of the atoll indicates that the platform is generally better cemented, and consists of coarser clasts nearer to the ocean. Shingle sticks of *Acropora*, often cemented by calcareous algae, form a major component of oceanward drillholes. Similar drilling on the modern reef flat has revealed that that it is also underlain by *Acropora* sticks cemented by calcareous algae. On lagoonward exposures of the platform drilling often encountered sand at 1-2 m depth.

HOLOCENE REEF GROWTH

The stratigraphy and chronology of the Holocene reef rim was examined along a series of transects around the atoll (Fig. 2), with drillholes through islands and the conglomerate platform which surrounds and underlies them, and through the reef flat.

Figure 3 shows a cross-section (transect I) of the southern part of Home Island where observations were obtained from a trench and associated drillhole in the trench floor (CK7). The conglomerate platform was encountered in the floor of the trench at the same elevation that it outcrops on the oceanward side of the island. A radiocarbon date of 5760 ± 95 years B.P. at 310 cm (-2.4 m below MSL) was obtained from the drillhole CK7. The island sediments, which are discussed in more detail in the next chapter, range in age from 1840 ± 125 years B.P. to 1440 ± 80 years B.P.

The age of the conglomerate platform on Home Island is indicated by a radiocarbon date of 3680 ± 105 years B.P. on a coral cemented into the top of the platform at the site of CK1, a drillhole in a sequence (transect II) on the platform at the southern end of this island. The cross-section at this point includes drillhole CK3 which is on the oceanward edge of this platform and is more then 6 m deep. This core contains coral shingle, generally well-cemented with calcareous algae, and at its base is dated 6160 ± 95 years B.P. (see Table 3). The ages above are reversed, but their errors render them statistically indistinguishable. There is apparently a decrease in age as the lagoon is approached with a radiocarbon date of 3490 ± 85 years B.P. at 2.4 m below MSL in the lagoonward core CK2. The platform is less well cemented in this core, and drilling was aborted in sand.

A similar sequence of drillholes was drilled through the conglomerate platform on transect III at the southern end of Pulu Wak Banka. The channel south of this island contains numerous living microatolls. A fossil microatoll was identified within the conglomerate, and this has been radiocarbon dated at 1960 ± 80 years B.P. (Fig. 5), indicating that some material has been added to the conglomerate platform on the margin of the channel in the last 2000 years. A coral within the conglomerate has been dated at 3220 ± 85 years B.P. just near the transect (Fig. 2). The conglomerate platform becomes thinner closer to the lagoon, and drilling in CK6 was aborted in sand. A core into the sand spit extending from the southern end of Pulu Wak Banka into the lagoon, contains coral shingle at about 1 m depth, which has been dated 3170 ± 85 years. It can also be inferred from this date that the lagoon has partially filled since the time of conglomerate platform formation.

Figure 6 indicates the stratigraphy beneath South Island on transect IV, and Figure 7 indicates the stratigraphy beneath Pulu Blan Madar. Both are similar, intercepting the Pleistocene limestone at 13.8 m depth (11.6 m below MSL) and 12.6 m depth (11.2 m below MSL) respectively. The cores recovered shingle or shingle and sand. Coral fragments at 10 m in CK15 dated 6790 ± 80 years B.P. and Tridacna at 6 m in CK14 dated at 6040 ± 80 years B.P.

Figure 8 shows shallow cores into the reef flat on transect VI, south of Pulu Maria. The reef flat appears about 1000 years older close to the oceanward edge, than beneath the island 750 m lagoonward. Radiocarbon dates of 5800 ±70 years B.P. at 2.15 m depth, and 5630 ± 205 years B.P. at 0.6 m depth in CK21 (not statistically significantly different), compare with a date of 4740 ± 85 years B.P. at 2.1 m depth in CK23 (Fig. 8). The conglomerate platform on Pulu Maria contains only relatively fine clasts, and recovery in CK23 was poor, but generally also indicated weakly cemented sand.

Figure 9 shows transect VI across the spits at the eastern end of West Island. Radiocarbon dates on coral shingle, recovered from a series of pits into the sandy spits, demonstrate progressive development of the spits from around 1400 years ago to present (Table 6), with the last spit giving a modern age. CV1 is a vibrocore sunk into the muddy sediments flanking the recent spit and penetrating sand and shingle, and from that vibrocore a date at around 0.9 m (about halfway down the core, allowing for compaction of the core) is 3240 ± 85 years B.P.. This date appears to reflect lagoonal infilling, which must have occurred before the spits began to form. Though hard pan was encountered beneath some spits, this area is not underlain by typical conglomerate platform.

Figure 10 at the southern end of West Island is a combination of several different drillholes undertaken at different times, and amalgamated schematically into a single transect (Transect VIII). Pleistocene limestone was encountered at 6.5 m below MSL. in

CK13, but was not encountered in CK9 which went slightly deeper. CK13, drilled next to a telok (lagoonlet), but through a shingle substrate, encountered mud at 2-4 m depth, similar to that being deposited in the telok, implying that the island sand and shingle have been deposited over the surface of a formerly larger telok (Fig. 10). The sequence of 4 radiocarbon dates from drillholes CK13, CK9 and CK10A show the opposite trend to that generally observed on other transects, in that the older dates (6140 ± 85 years B.P. at 4.4 m in core CK13) are to lagoonward, with younger dates beneath the reef flat (4770 ± 85 years B.P. at 1.5 m in CK10A).

Figure 11 shows transect IX which is at the southern boundary of the Quarantine Station on West Island and crosses the island where it is both especially low and particularly narrow. The most interesting feature of this transect is that there are a number of microatolls, up to 2 m in diameter, which are found along the shore, above the modern limit to coral growth. This together with elevated beachrock at this site provides convincing evidence that the sea has been relatively higher than it is at present. Radiocarbon ages of 2690 ± 85 and 2730 ± 85 years B.P. have been determined on two massive *Porites* microatolls at this site, where they are about 50-60 cm above their modern, living equivalents. In addition a sample of *Porites*, almost certainly a microatoll, was recovered from drillhole CK8 and dated 3190 ± 85 years B.P. at a very similar elevation, indicating that similar, though in this case slightly older microatolls continue beneath the island sediments. The significance of these emergent, in situ corals will be examined below.

Figure 12 shows the stratigraphy of two deep holes drilled on transect X on Horsburgh Island. The Pleistocene substrate was only encountered in the more oceanward drillhole, where it was found at a depth of 13.1 m (10.6 m below MSL). A coral sample from a massive coral colony recovered from almost directly above the Pleistocene/Holocene contact was radiocarbon dated 5540 ± 80 years B.P., while a coral from 4.8 m has been dated 5260 ± 80 years B.P.. These samples are more than 8 m apart and imply a rapid rate of reef accretion in the order of 25-30 mm/yr. CK11 at the lagoonward end of Horsburgh Island was presumably not drilled deep enough to encounter the Pleistocene surface, as subsequent seismic profiling in that part of the lagoon has indicated a reflector, believed to represent the last interglacial surface at depths of more than 20 m. Nevertheless the date of 4610 ± 85 years B.P. on a sample of *Tridacna* at the base of that core, indicates that sedimentation here lagged about 1000 years behind that on the more oceanward side of Horsburgh.

MICROATOLLS AND HOLOCENE SEA LEVEL

The radiocarbon dates from Tables 3, comprising dated samples from transects I-X, have been plotted on an age-depth plot in Figure 13. These ages do not permit the accurate reconstruction of early to mid-Holocene sea-level history on Cocos, because it cannot be established that the corals in the cores are in their position of growth, and even if they were in situ they could have grown in water depths of up to several metres. Samples from the conglomerate platform (Table 2) on the other hand are manifestly not in growth position, and do not indicate the level of the sea at time of deposition. Some corals, however, do record former sea level. Microatolls are flat-topped colonies of coral which have been constrained in their upward growth by subaerial exposure at low spring tides, and have therefore continued to grow only laterally (Scoffin and Stoddart 1978). Their upper surface is related to sea level and the upper surface of fossil microatolls can be used to reconstruct late Holocene sea-level change (Chappell 1982). On the Cocos (Keeling) Islands there are modern, living microatolls, of massive and branching *Porites*, on the reef flat, in interisland passages, and within the lagoon (Woodroffe and McLean 1990). These corals were described by Wood-Jones (1912), though he attributed their form to sedimentation on their upper surface. Detailed survey of modern microatolls around the atoll indicates that they occur in a relatively narrow elevational range (around 0.3 m below MSL), and supports the idea that they are limited by water level (Smithers, unpublished results).

Fossil microatolls, though by no means common, have been identified within the conglomerate platform at several sites on West Island, and on Pulu Pandan and South Island. At the southern end of West Island fossil microatolls of both massive and branching species of *Porites* are found together. Fossil microatolls can also be identified on the reef flat, and at one location in a telok on South Island, where the oldest microatolls so far dated on Cocos have been found (3560 ± 85 years B.P., see Fig. 2). The exact elevation of these remains uncertain, but they appear to be lower than younger specimens on West Island (Table 4). In addition, *Porites* cored in CK8 (CK8.1B/2) almost certainly represents a microatoll dated 3190 ± 85 years B.P. and at a similar elevation to those on the present shoreline (see transect IX, Fig. 11), and so too does that in CK5 (CK5.1B), dated 1960 ± 80 years B.P. and found at around MSL (see transect III, Fig. 5).

The upper surface of these microatolls gives an indication of the elevation of sea level. When compared with the modern elevation of microatolls (around -0.3 m MSL), these corals indicate a trend of gradually falling sea level (Fig. 13), from about 0.9 m above present around 3000 years ago, on the basis of branching microatolls on Pulu Pandan and slightly less if massive microatolls on West Island are considered. A discontinuous record of relative sea-level fall is preserved at the foot of the beach near the Quarantine station on West Island, where a series of microatolls is located (see plot in Fig. 13).

LAGOONAL INFILL

The nature of lagoonal sediments in the South Keeling Islands has been examined by Smithers (this volume), who demonstrates that sediments in the lagoon range from strongly fine skewed gravelly muds (as in the teloks and blue holes) to gravelly sands where sand aprons have encroached upon lagoonal corals. Compositionally they are entirely biogenic, dominated by three factors, coral sediments, molluscan sediments and sediments in which calcareous algal fragments and *Halimeda* plates are an important constituent (Smithers et al., in press).

The lagoon is particularly shallow around much of the southeastern corner, and the surface, which is covered by seagrass, dries out at low tide (Williams, this volume). There is anecdotal evidence that it has filled in rapidly in historical times. Captain John Clunies Ross established his settlement on the middle portion of South Island, where access is now extremely difficult for a boat of any draft at almost any stage of the tide. Rapid infill has been inferred by Forbes (1879, p779). Guppy detected sediment in suspension being carried into the lagoon through the passages, by the predominantly unidirectional currents. He made a series of calculations of sediment transport and sedimentation into the lagoon (Guppy 1889). His estimates were based upon rates of coral growth and sediment production, distributed across the area of the reefs and lagoon that contained coral cover. He calculated that 5000 tons of sediment was carried into the lagoon each year. The majority (5/6) he considered to be deposited in the first 700 m of the lagoon, on the sand aprons. He estimated that these aprons were prograding at a rate of around 1 m/yr (1 yard per year). Vertical sedimentation averaged over the southern part of the lagoon, Guppy estimated to be 1ft/100 years (c. 3mm/yr). Extending these calculations to the northern lagoon, Guppy considered that the lagoon would require a further 4000 years to infill, and that the total time from initiation to complete infill for a lagoon would be about 15-20,000 years.

Wood-Jones, not only realised the importance of this sediment accumulation in the lagoon, but he interpreted sedimentation as the prime control on the formation of the atoll. He compared the atoll as a whole with single colonies of *Porites* microatolls (he termed them an 'atoll reef in miniature', Wood-Jones 1912, p108-109), which he interpreted to be limited in their upward growth by sediment accumulation on their upper surface. Wood-Jones proposed his sedimentation theory of atoll development in opposition to Darwin's subsidence theory, and the solution theory of Murray.

We have examined lagoonal sedimentation in Cocos, based on a series of vibrocores taken in the southern and eastern lagoon. The stratigraphy, sediment grain-size and components, and radiocarbon dating from vibrocores indicate spatial and temporal variations in the nature and rate of sedimentation, controlled primarily by the pattern of sea-level change and the response of the atoll environments, particularly the formation of reef islands on the atoll rim (Smithers et al., in press).

The main contrast is between sand apron sediments, on the one hand, which are composed of skeletal grains typical of a reef flat assemblage, being coarse, clean sands and shingle, with fragments of the algal rhodoliths, *Spongites* sp., and island lee sediments, on the other hand, which are higher in mud content, with occasional coral fragments. The base of vibrocores contains more shingle, and coral, algae and *Halimeda* are generally more common, perhaps reflecting lagoon reefs which have been covered by sand apron and island lee sediments. Sand aprons have encroached episodically into the lagoon and sand appears to have spilled into blue holes as the sedimentation front advanced. It seems highly probable that the sands of the southeastern section of the lagoon have already filled over a patchwork of blue holes, and this may explain the patchy penetration of vibrocores; the shorter ones reaching shingle at much shallower depths than those which penetrated into former sand-filled blue holes.

The sands radiocarbon dated in vibrocores were all younger than 4000 years B.P. (Table 5); the base of CV11 dated 3850 ± 80, while CV1 and CV12 had dates of 3240 ± 85 and 3530 ± 80 years B.P. respectively. These older dates are in those cores closest to islands, and consequently also close to the reef. Cores further into the lagoon had younger dates: CV15 dated 420 ± 65, and CV10 910 ± 80 at its base 2.2 m below the sediment surface, and 130 ± 110 years B.P. in the centre, recording the present progradation of the sand sheets into the area of blue holes.

Radiocarbon dates record the time of death of the coral shingle, and not the time of its deposition. Sediments flooring the lagoon are also likely to be subject to considerable bioturbation. Nevertheless, despite minor age reversals in vibrocores such as in CV2, the dates are generally stratigraphically consistent and indicate the general trend of sedimentation. Vertical accumulation rates are higher in sand aprons than in island lee sediments, being 0.5-1.0 mm/yr in the former, and in the latter, over the last 2000 years, ranging from 0.25-0.5 mm/yr (Smithers et al., in press).

HOLOCENE EVOLUTION OF THE ATOLL

The Holocene atoll has developed over a Pleistocene limestone surface, which has been shown by seismic reflection profiling to be basin shaped probably as a result of solutional weathering during the glacial sea-level low (Searle, this volume). This surface has been flooded by the sea during the postglacial marine transgression. Seismic and drilling results indicate that there is a relatively continuous Pleistocene rim at about 9-10 m below MSL, around the western, southern and eastern sides of the atoll, with a deeper basin to the north, which opened out to the northeast, and perhaps also northwest. When the sea was 12-15 m below present, the Pleistocene rim was still emergent, and lagoonal exchange must have been predominantly through the northern passages. Since that surface has been inundated, as a result of the final stage of the postglacial marine transgression, there has been a phase of rapid vertical reef growth, following the rising sea level, recorded by radiocarbon dates from cores, and shown in Figure 13.

During periods of rising sea level reef growth has adopted one of three strategies, keep-up (where the reef closely tracks the rising sea), catch-up (where reef growth lags behind sea level) and give-up in which there is negligible net reef growth (Neumann and Macintyre 1985). As described above, the coral dates do not indicate the position of the sea, except for during the last 3000 years where there are dated microatolls which have been constrained by water level. Regional sea-level curves indicate a sea-level history in which sea level rose rapidly up until around 6000 years ago when it reached a level close to its present level and has changed by only a metre or so since (Thom and Chappell 1975, McLean et al. 1978, Geyh et al. 1979, Thom and Roy 1985). Vertical reef accretion on Cocos appears to have lagged behind sea level, as also shown on atolls in the Pacific (Marshall and Jacobsen 1985). The three modes of response can be found at different points around an atoll. Reef growth on Cocos has varied from place to place; nowhere does it seem to have kept up with sea level (there are no 6000 year dates at present sea level), but it has lagged behind sea level by different amounts at differing points on the atoll rim.

We identify this period of catch-up reef growth as the first of three phases in the Holocene development of the atoll. The second phase was a period of reef flat consolidation, represented by the conglomerate platform. On the basis of fabric and morphology we attribute the conglomerate platform to formation as a reef flat under conditions of sea level slightly higher than present. That the sea was higher than present is shown most convincingly by the presence of microatolls above the modern limit to coral growth (Table 4). Other data, such as the elevated beachrock (in Fig. 11), and the consistent difference between the conglomerate platform and the modern reef flat, also substantiate that the sea was relatively higher in the mid-Holocene.

Elsewhere similar conglomerate platform has been interpreted as lithified storm-rubble ridges or ramparts similar to those deposited as a result of Tropical Cyclone Bebe on Funafuti in Tuvalu in the Pacific, in front of the elongate reef islands, and subsequently observed to migrate landwards and redistribute over the shoreface (Baines and McLean 1976). We discount this interpretation of the conglomerate platforms on Cocos because of the horizontal nature and width of the platform, and the relatively narrow range of radiocarbon ages from coral clasts. Storm rubble is evidently a component of the platform, with addition of material under non-storm conditions, bound by biological and chemical processes, in a similar way that material is supplied to and incorporated into the interisland reef flat areas on the modern atoll. Reef blocks, as seen in the Pacific storm belt, are relatively rare, though there are blocks of more than 1 m diameter on the reef flat at the southern end of the atoll, one of which has been dated to 610 ± 75 years B.P. (Table 6).

The third phase is a phase of reef island development. The modern reef islands lie primarily on an oceanward outcrop of conglomerate platform, and the appearance of islands in their modern location and form must therefore postdate the formation of the platform. Islands have formed during the last 3000 years when the sea level has been undergoing a relative fall. The age structure of reef islands is still poorly known; some dates are given in Table 6, indicating substantial deposition in the period 1800-1000 years B.P. The issue is examined in greater detail in the next chapter (Woodroffe and McLean, this volume). Progradation of the southern end of West Island in the last 1400 years is apparent from Figure 9.

The three phases that are identified (Fig. 13), have not necessarily been discrete, but some overlap between them is likely. Reefs at the southern end of the atoll appear to have grown fastest, and although they did not keep up with sea level, they lagged only slightly (<1000 years) behind sea level, whereas reefs at Horsburgh appear to have undergone a greater lag before commencing to grow, but to have accreted vertically at a faster rate. Similarly the early stages of island formation appear to have occurred within the final stages of conglomerate platform development, as indicated by beachrock and beach conglomerate outcrops within the platform (i.e. Horsburgh, West Island, and North Keeling). Progression from one phase to another must have been accompanied by substantial changes of energy regime, particularly in the lagoon, which must have been a relatively high energy environment before the reef rim caught up with sea level, and subsequently underwent a further reduction in energy as reef islands were formed around the margin.

DISCUSSION

This three phase model of the Holocene evolution of the atoll incorporates components of each of the earlier theories on the development of atolls. We now examine some of these issues.

The first issue at Cocos is whether the atoll has subsided, and whether it is continuing to subside. As discussed above, the depth of the last interglacial surface is taken by us as an indication of subsidence. The exact elevation of the sea at the peak of the last interglacial is contentious; in some parts of the world it is considered to have been around 5-6 m above present, elsewhere up to 10 m above present. Lambeck and Nakada (1992) indicate that flexural responses of the earth's crust and upper mantle need to be taken into account, and that it need not have been any higher than present. There are many parts of the world where the last interglacial reef is found above present sea level, the nearest being Christmas Island, where coral-bearing reef reaches 12 m above present sea level, but with associated deposits reaching 30m (Woodroffe 1988). We believe that the last interglacial reef on Cocos would have caught up with sea level during the oxygen-isotope 5e sea-level high stand, and we attribute the fact that it is everywhere below present sea level to subsidence. Seismic results indicate that solution is likely to have occurred and deepened the lagoon, but we attribute the fact that contemporaneous limestones are around 12 m above sea level on Christmas Island and 12 m below sea level on Cocos to uplift of the former and subsidence of the latter. Indeed if the atoll were not subsiding, there would be no reason why interglacial limestones should occur in layer-cake fashion beneath the Holocene, as appears to be indicated by seismic profiling (Searle, this volume).

Darwin himself realised that confirmation of his subsidence theory would come from deep drilling of coral atolls. He postulated that such drilling should reveal extensive thicknesses of shallow water limestones, in excess of the present depth range over which corals can grow. The final proof came after World War II with drilling of Enewetak, Mururoa and Midway atolls in the Pacific, in which basalts were encountered beneath the coral limestones at depths down to 1200 m (Ladd et al. 1953, Emery et al. 1954, Lalou et al. 1966). Deep-drilling has not been undertaken on Cocos, and so the depth of the volcanic basement, probably around 400-500 m (Jongsma 1976), is still unknown.

Confirmation of the volcanic basement of open-ocean atolls, and more recently demonstration of the way in which plate tectonics can provide a mechanism (horizontal plate motion), by which subsidence can occur (Scott and Redondo 1983, Grigg and Epp 1989), give strong support to Darwin's theory of atoll origins. Relative and absolute dating of the basement volcanic rocks, and palaeontologic and diagenetic changes within the limestone, indicate that subsidence rates are "imperceptibly slow except in geological perspective" (Stoddart 1973).

While we believe that gradual subsidence is continuing at Cocos, we are unable to accept the local evidence that Darwin invoked to prove his theory. Darwin was shown erosion of the shoreline on West Island, with undercutting of coconuts, which he believed was "tolerably conclusive evidence" of subsidence. His interpretation of this geomorphological evidence has been disputed by several other scientists who have visited the atoll. Most vehement of those disagreeing with Darwin was John Clunies Ross, who was resident on Cocos but, much to his subsequent regret, had been absent on the occasion of Darwin's visit. Evidently concerned at Darwin's suggestion that the islands of which he was in possession were about to disappear beneath the sea, he claimed that a "moderable attentive investigation of the Cocos islets affords ample reasons for believing that they have stood up to the present time above the level of the ocean during hundreds if not thousands of years" (Ross 1855).

Guppy described each of the reef islands but decided that there was evidence for neither recent uplift nor recent subsidence of the atoll (Guppy 1889). On the other hand Forbes, and later Wood-Jones, believed that there was evidence that the sea had been higher with respect to the atoll. Wood-Jones wrote "the undermining of trees and the denudation of shore-lines do not necessarily indicate subsidence, for they are inconstant effects, and an area of land denudation is compensated for by an area of land construction at another part of the island ring" (Wood-Jones 1909 p674). Forbes had similarly argued that the erosion of islands was compensated by the debris being deposited further around the shore, and interpreted elevated fossil shells of clams and oysters on Workhouse Island (south of Direction Island, no longer existing as a distinct island), as an indication of former higher sea levels (Forbes 1879, 1885). The views of Forbes and Wood-Jones for a sea level higher than present revolved around their interpretations of the coral conglomerate that underlies much of the reef islands.

Our data confirm the interpretation of recent emergence (that is a slight fall of sea level relative to the atoll) since the mid-Holocene (Woodroffe et al. 1990a, 1990b). However, although the geomorphological data on the surface morphology of the atoll were misinterpreted by Darwin, the overall atoll structure we do attribute to gradual subsidence as Darwin postulated.

Radiocarbon dates from western, eastern and southern reef flat or oceanward conglomerate platform, imply that the reef near the reef crest lagged only about 1000 years behind sea level. The reef caught up first near the reef margin, and there was more gradual infill to lagoonward; thus on each of these sides we see radiocarbon ages getting younger with distance into the atoll lagoon.

This is contrary to most of the views of other geologists on the atoll. Thus Guppy, following the suggestion of Murray that reefs prograded out over their own talus, considered that there was proof that the reef flat had built out in a series of steps. His view appears to have been based upon description of the reef buttresses off the atoll given him by George Clunies-Ross, and his interpretation of the fossil reef rims as he viewed imbricated, arcuate ridges on North Keeling and Horsburgh Islands. The latter he called parallel lines of old reef margins that protrude above the reef flat, but we have interpreted these as beach deposits, marking instead the former foot of rubble-strewn beaches. Wood-Jones similarly supposed that the breccia (conglomerate platform) was oldest towards the lagoon and youngest toward the ocean (Wood-Jones 1909); whereas our results indicate the reverse trend.

In Figure 14 we summarise the late Quaternary development of the Cocos (Keeling) Islands. Wood-Jones recognised three theories, Subsidence, Solution and Sedimentation (ie. the theories of Darwin, Murray and himself respectively), to which we may add Sea-level (the glacial control theory of Daly).

The surface of the last interglacial at depths of 10-20 m below sea level indicates that the island was not planated as Daly has suggested at the time of sea level low, although our interpretation does emphasise sea-level fluctuations which have been the principal control over the late Quaternary of periods of reef establishment and their demise. We also interpret that it indicates that the atoll is continuing to subside as Darwin envisaged, although at a rate that is imperceptibly slow, even compared with rates of sea-level fluctuation. The form of the lagoon does not result from solution as Murray envisaged, but nevertheless solution does appear to have been important at times of low sea level in accentuating, through karst erosion, the basin-shape of the lagoon as inferred by Purdy (1974) in his antecedent karst hypothesis. Holocene reef morphology mimics this antecedent surface as suggested by Purdy. Finally, the lagoon has been one of the major areas of sediment accumulation, along with reef islands, over the last 3000 years, as envisaged by Wood-Jones, but we interpret this not as the cause of atoll morphology, but more as a response to the evolving morphology.

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Table 1. Radiocarbon dating results on museum specimens of coral, Cocos (Keeling) Islands.

ANU Lab No.	Coral species	Date of collection	Conventional radiocarbon age	Age (pre-1950)	Reservoir correction
6151	*Acropora scherzeriana*	1906 [W-J]	370 ± 60	40	330 ± 60
6152	*Montipora foliosa*	1906 [W-J]	670 ± 60	40	630 ± 60
6153	*Porites nigrescens (=P. cylindrica)*	1906 [W-J]	410 ± 60	40	370 ± 60
7638	*Montipora ramosa*	1941 [G-H]	510 ± 70	10	500 ± 70
7639	*Montipora lobulata*	1941 [G-H]	480 ± 60	10	470 ± 60

Note: W-J = Wood-Jones, G-H = Gibson-Hill.

Table 2. Radiocarbon dating results on conglomerate platform Cocos (Keeling) Islands.

ANU Lab No.	Sample No.	Material	Location	Island	Conventional radiocarbon age	Environmentally corrected age
5411	C4	Coral	from conglomerate in base of well	West Is.	1770 ± 70	1320 ± 80
5412	C5	Coral	from conglomerate platform	West Is.	3890 ± 80	3440 ± 85
5414	C16	Coral, *Porites*	beneath beach conglomerate	North Keeling	3480 ± 80	3030 ± 85
5416	C26	Coral	from conglomerate platform	Direction Is.	3740 ± 80	3290 ± 85
5417	C43	Coral	from conglomerate platform	Pulu Wak Banka	3670 ± 80	3220 ± 85
5418	C48	Coral, *Porites*	cemented to conglomerate platform	North Keeling	4290 ± 80	3840 ± 85
5419	C59	Coral	lower unit of conglomerate platform	Pulu Labu	3950 ± 80	3500 ± 85
5420	C64	Coral	upper unit of conglomerate platform	Pulu Labu	3940 ± 80	3490 ± 85
5421	C65	Coral	from conglomerate platform	Home Is.	4000 ± 80	3550 ± 85
6220	CK1/5	Coral	from conglomerate platform	Home Is.	4130 ± 100	3680 ± 105
6221	C172	Coral	from conglomerate platform	South Is.	3500 ± 80	3050 ± 85
6222	C158	Coral, *Porites*	from conglomerate platform	West Is.	4460 ± 80	4010 ± 85
6224	C154	Coral	from conglomerate on transect IX	West Is.	3550 ± 80	3100 ± 85
7134	C202	Coral, *Pocillopora*	In upper conglomerate	West Is. transect VIII	3690 ± 80	3240 ± 85

Table 3. Radiocarbon dating results from drillholes; Cocos (Keeling) Islands

ANU Lab No.	Sample No.	Material	Location	Island	Elevation (m)[a]	Conventional radiocarbon age	Environmentally corrected age
6223	C153	Coral fragments	from lagoonal infill	Pulu Wak Banka	-1.0	3620 ± 80	3170 ± 85
6227	CK3-5B-4	Coral	Depth 6.2m in core CK3	Home Is.	-6.1	6610 ± 90	6160 ± 95
6641	CK10A.1B	Coral, *Porites*	150cm in core on reef flat	West Is.	-1.9	5220 ± 80	4770 ± 85
6642	CK9.3B	Coral, Faviid	230cm in core on conglomerate	West Is.	-1.7	6000 ± 80	5550 ± 85
6643	CK9.4B	*Tridacna*	380cm in core on conglomerate	West Is.	-3.0	6370 ± 90	5920 ± 95
6644	CK8.1B/2	Coral, *Porites*	140cm in core through beachrock	West Is.	+0.2	3640 ± 80	3190 ± 85
6645	CK7.3B	Coral	310cm in core	Home Is.	-2.4	6210 ± 90	5760 ± 95
6646	CK5.1B	Coral, *Porites*	5cm in core on conglomerate	Pulu Wak Banka	0.0	2410 ± 70	1960 ± 80
6647	CK3.3B	Coral	300cm in core on conglomerate	Home Is.	-3.0	5530 ± 80	5080 ± 85
6648	CK3.2B	Coral	140cm in core on conglomerate	Home Is.	-1.4	5610 ± 80	5160 ± 85
6649	CK2.2B	Coral	In core on conglmerate	Home Is.	-2.4	3940 ± 80	3490 ± 85
7546	CK11/10B	*Tridacna*	1305cm in core	Horsburgh Is.	-11.1	5060 ± 80	4610 ± 85
7547	CK12/3B	Coral fragments	480cm in core	Horsburgh Is.	-2.4	5710 ± 70	5260 ± 80
7548	CK12/12B	Coral Flaviid	1300cm in core	Horsburgh Is.	-10.6	5990 ± 70	5540 ± 80
7549	CK13/5B	Coral	440cm in core	West Is.	-3.0	6590 ± 80	6140 ± 85
7550	CK14/5B	*Tridacna*	600cm in core	South Is.	-2.5	6490 ± 70	6040 ± 80
7551	CK15/6B	Coral fragments	1000cm in core	Pulu Blan Madar	-9.0	7240 ± 70	6790 ± 80
8196	CK21 215	Coral	215cm in core on reef flat	south of West Is.	-2.4	6250 ± 60	5800 ± 70
8198	CK21 60	Coral	60cm in core on reef flat	south of West Is.	-0.8	6080 ± 200	5630 ± 205
8200	WI16/12	Coral	1220cm in core	West Is.	?	41,100 ± 890	
8201	WI16/5	Coral	500cm in core	West Is.	?	6170 ± 70	5720 ± 80
8404	HI12/15	Coral, *Acropora*	1550cm in core	Home Is.	-14.0	7480 ± 110	7030 ± 115
8197	CK17-235	Coral	235cm in core	West Is.	-2.5	6410 ± 70	5960 ± 80
8199	CK23-210	Coral	210cm in core on reef flat	Pulu Maria	-1.7	5190 ± 70	4740 ± 85

Note: [a] metres relative to Mean Sea Level.

Table 4. Radiocarbon dating results on fossil microatolls; Cocos (Keeling) Islands

ANU Lab No.	Sample No.	Material	Location	Island	Elevation (m)[a]	Conventional radiocarbon age	Environmentally corrected age
5415	C18	Microatoll, branching *Porites*	in situ within conglomerate platform	Pulu Pandan	+0.6	3400 ± 80	2950 ± 85
6218	C156	Microatoll, massive *Porites*	in situ adjacent to C155	West Is.	+0.15	3180 ± 80	2730 ± 85
6226	C174	Coral, *Porites*	microatoll in lagoon sediments	South Is.	-0.15	4010 ± 80	3560 ± 85
6228	C155	Microatoll, massive *Porites*	in situ beneath beachrock	West Is.	+0.15	3140 ± 80	2690 ± 85
7135	C 204	Microatoll, massive *Porites*	in situ in conglomerate	West Is.	+0.35	3690 ± 80	3240 ± 85
7136	C 206	Coral, branching *Porites*	in situ in conglomerate	West Is.	+0.35	3710 ± 80	3260 ± 85
7552	μ2	Microatoll, *Porites*	foot of beach	West Is.	-0.2	1500 ± 60	1050 ± 70
7553	μ4	Microatoll, *Porites*	foot of beach	West Is.	+0.1	2990 ± 70	2540 ± 80
7554	μ6	Microatoll, *Porites*	foot of beach	West Is.	+0.15	3470 ± 80	3020 ± 85
8408	μ4	Microatoll, *Porites*	foot of beach	West Is.	+0.1	3160 ± 50	2710 ± 60
8409	μ5	Microatoll, *Porites*	foot of beach	West Is.	+0.07	3430 ± 60	2980 ± 70

Note: [a] metres relative to Mean Sea Level.

Table 5. Radiocarbon dating results from vibrocores; Cocos (Keeling) Islands

ANU Lab No.	Sample No.	Material	Location	Island	Conventional radiocarbon age	Environmentally corrected age
7531	CV2-240	Coral fragments	240cm in vibrocore	Lagoon	2780 ± 100	2330 ± 105
7532	CV2-300	Coral fragments	300cm in vibrocore	Lagoon	3050 ± 90	2600 ± 95
7533	CV2-414	Coral fragments	414cm in vibrocore	Lagoon	2660 ± 130	2210 ± 135
7534	CV3-80	Coral fragments	80cm in vibrocore	Lagoon	1670 ± 110	1220 ± 115
7535	CV3-240	Coral fragments	240cm in vibrocore	Lagoon	2980 ± 70	2530 ± 80
7536	CV10-110	Coral fragments	110cm in vibrocore	Lagoon	580 ±100	130 ± 105
7537	CV10-222	Coral fragments	222cm in vibrocore	Lagoon	1360 ± 80	910 ± 85
7538	CV12-50	Coral fragments	50cm in vibrocore	Lagoon	2520 ± 110	2070 ± 115
7539	CV12-158	Coral fragments	158cm in vibrocore	Lagoon	3980 ± 80	3530 ± 85
7540	CV1-90	Coral fragments	90cm in vibrocore	Lagoon	3690 ± 80	3240 ± 85
7541	CV5-66	Coral fragments	66cm in vibrocore	Lagoon	2490 ± 80	2040 ± 85
7542	CV6-48	Coral fragments	48cm in vibrocore	Lagoon	1850 ± 90	1400 ± 95
7543	CV8-76	Coral fragments	76cm in vibrocore	Lagoon	2970 ± 120	2520 ± 125
7544	CV11-96	Coral fragments	96cm in vibrocore	Lagoon	4300 ± 80	3850 ± 85
7545	CV15-130	Coral fragments	130cm in vibrocore	Lagoon	870 ± 60	420 ± 70
8398	CV3 378	Coral fragments	378cm in vibrocore	Lagoon	3190 ± 50	2740 ± 60
8400	CV3 320	Coral fragments	320cm in vibrocore	Lagoon	3140 ± 60	2690 ± 70
8402	CV2 360	Coral fragments	360cm in vibrocore	Lagoon	3180 ± 50	2730 ± 60

Table 6. Radiocarbon dating results on reef island sediments; Cocos (Keeling) Islands

ANU Lab No.	Sample No.	Material	Location	Island	Conventional radiocarbon age	Environmentally corrected age
5413	C7	Coral	boulder exposed in eroded ridge	North Keeling	2070 ± 70	1620 ± 80
6219	C171	Coral, *Porites*	reef block on reef flat	southern atoll rim	1060 ± 70	610 ± 80
6225	C138	Coral, *Pocillopora*	in bedded sand in wall of trench	Home Is.	1890 ± 70	1440 ± 80
7127	C 72	Coral, *Porites*	In pit	West Is.	1570 ± 80	1120 ± 85
7128	C 104	Bulk sand, foraminifera	In pit, eastern ridge	West Is.	102.6 ± 3.7 %M	MODERN
7129	C 106	Coral, *Pocillopora*	80cm in pit	West Is.	1550 ± 90	1100 ± 95
7130	C 118	Coral, *Acropora*	70cm in pit	West Is.	830 ± 100	380 ± 105
7131	C 133	Coral sand and shingle	in trench	Home Is.	2290 ± 120	1840 ± 125
7132	C 135	Coral sand and shingle	in trench	Home Is.	2020 ± 170	1570 ± 175
7133	C 136	Coral shingle *Porites*	in trench	Home Is.	1950 ± 70	1500 ± 70
7747	C 108	Coral	20-30cm in pit	West Is.	1890 ± 60	1440 ± 60

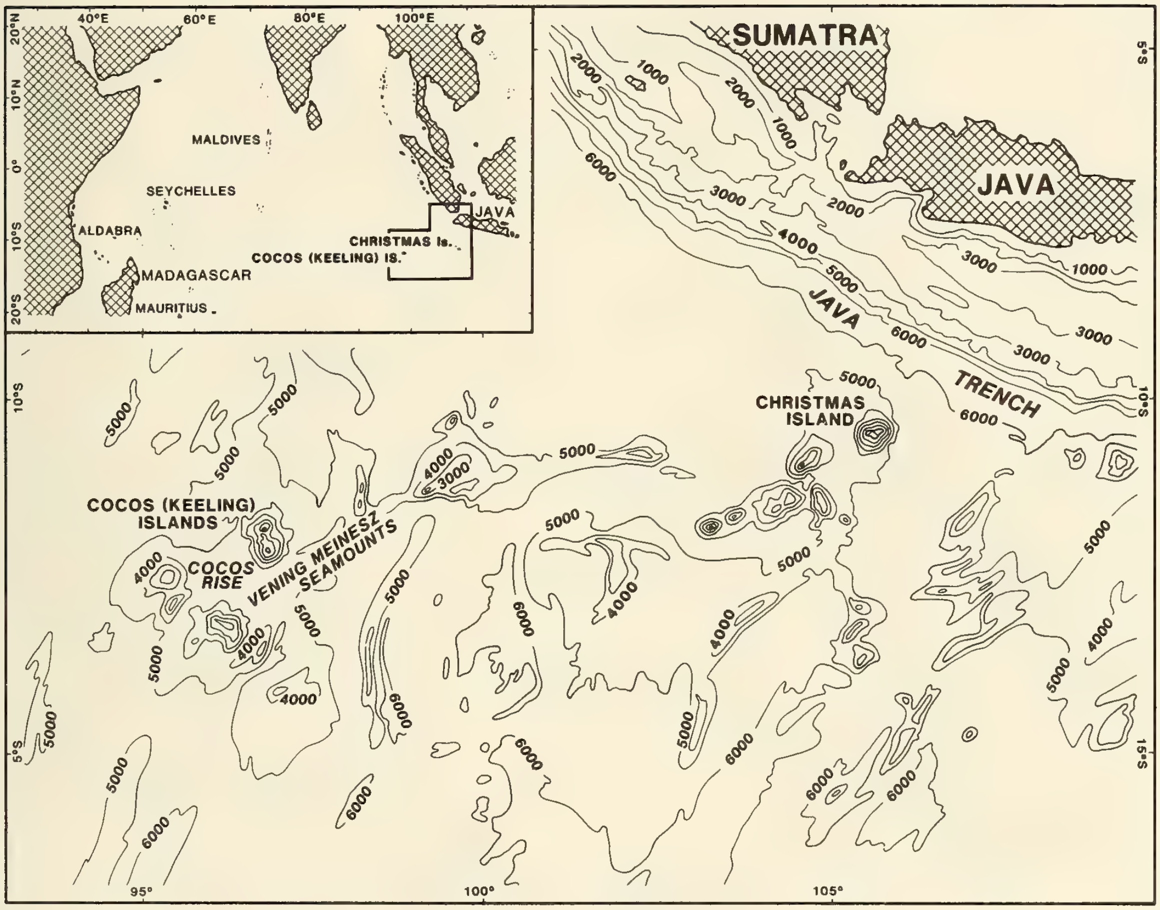

Figure 1. Location of the Cocos (Keeling) Islands and bathymetry (in metres) of the northeastern Indian Ocean.

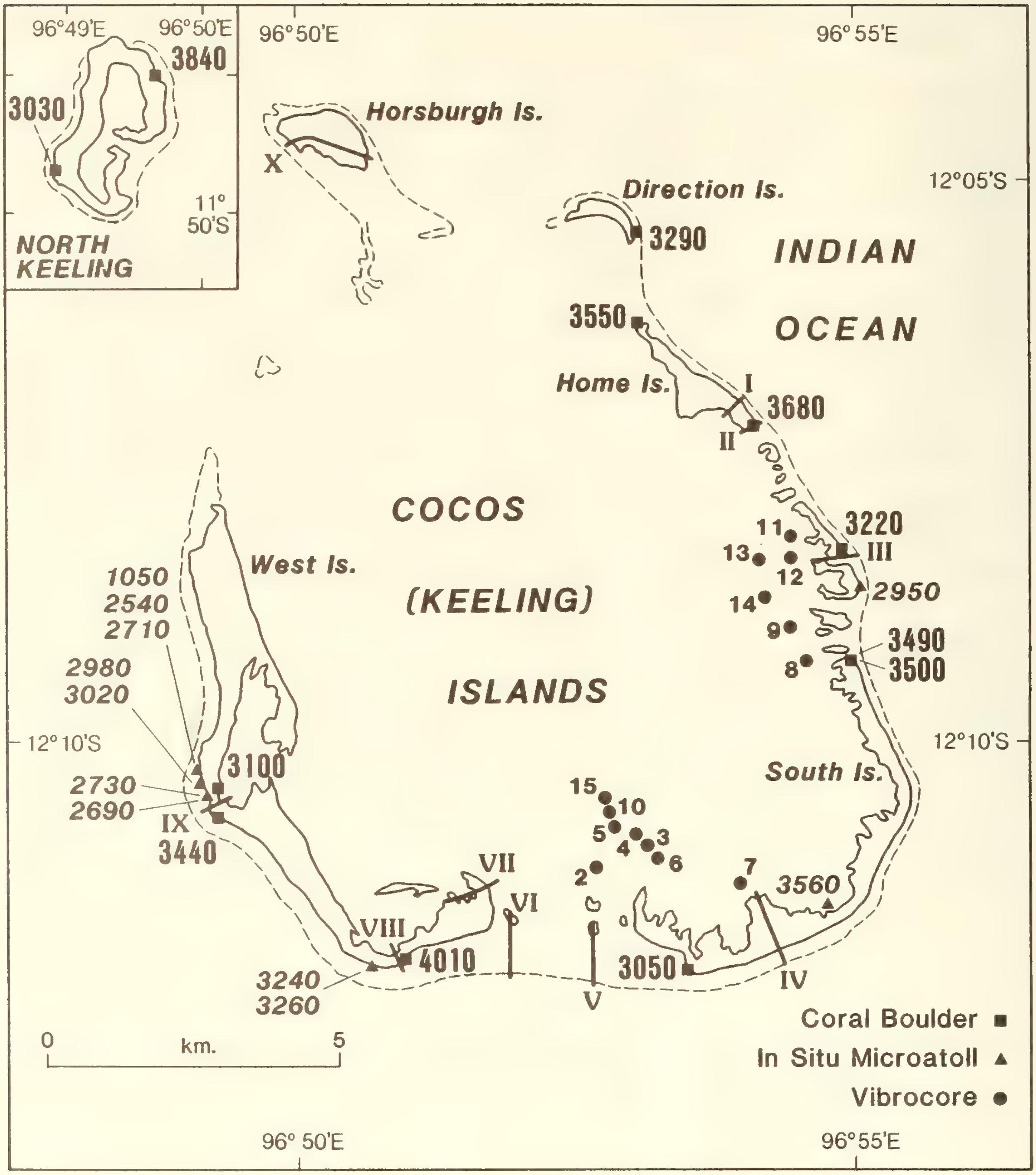

Figure 2. Cocos (Keeling) Islands, showing locations of stratigraphic transects I-X, vibrocores, and radiocarbon dates on coral from conglomerate platform (Table 2) and fossil microatolls (Table 4).

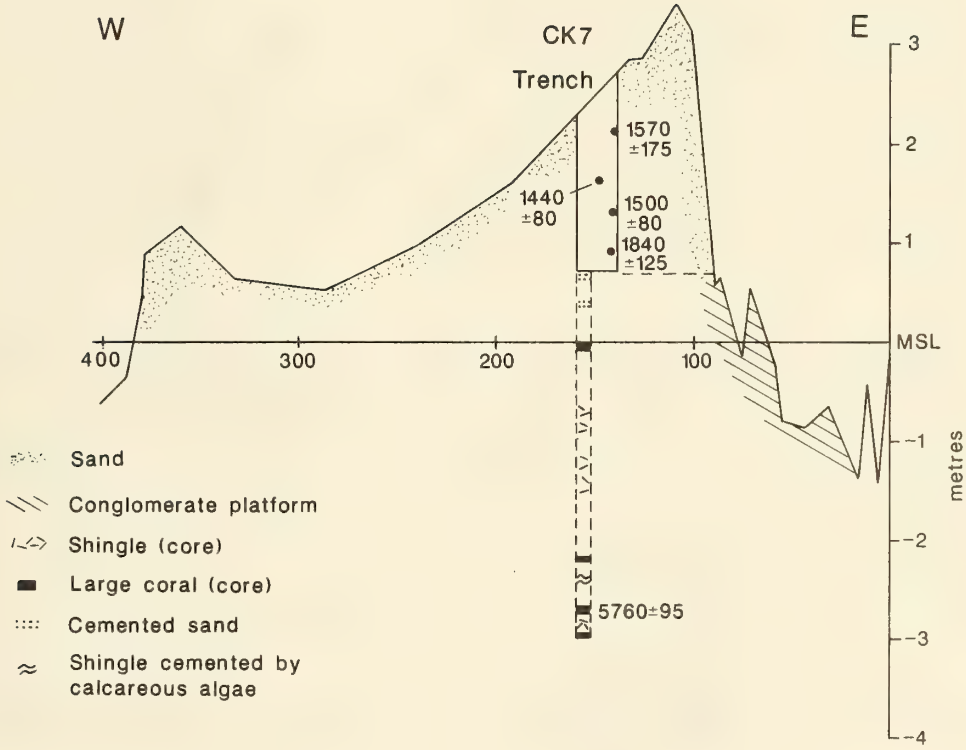

Figure 3. Transect I, Home Island (see Fig. 2 for location): stratigraphy and radiocarbon dates.

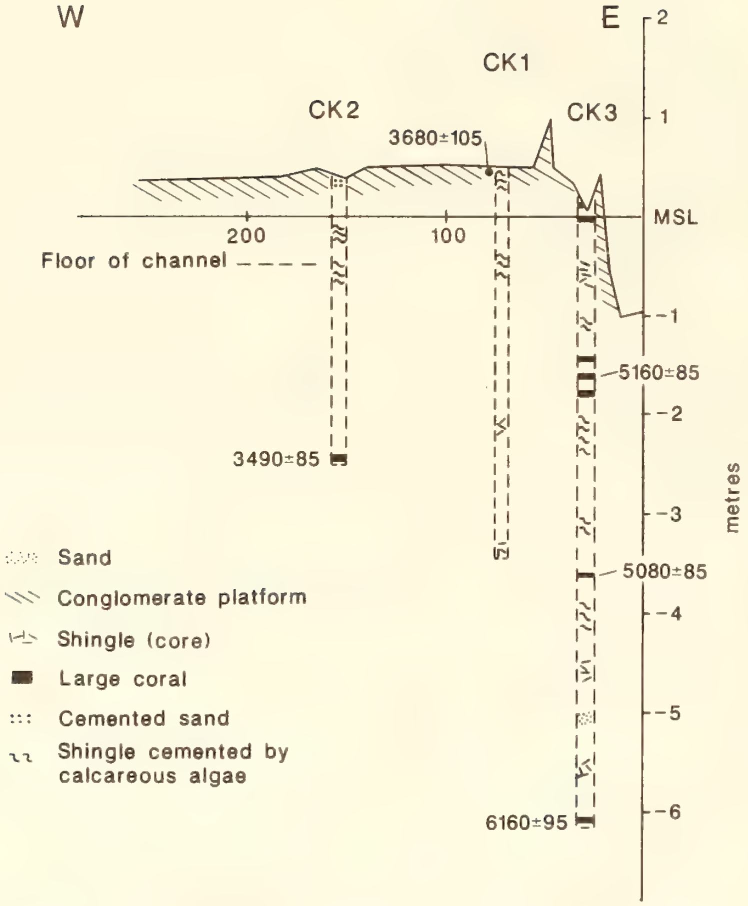

Figure 4. Transect II, Home Island (see Fig. 2 for location): stratigraphy and radiocarbon dates.

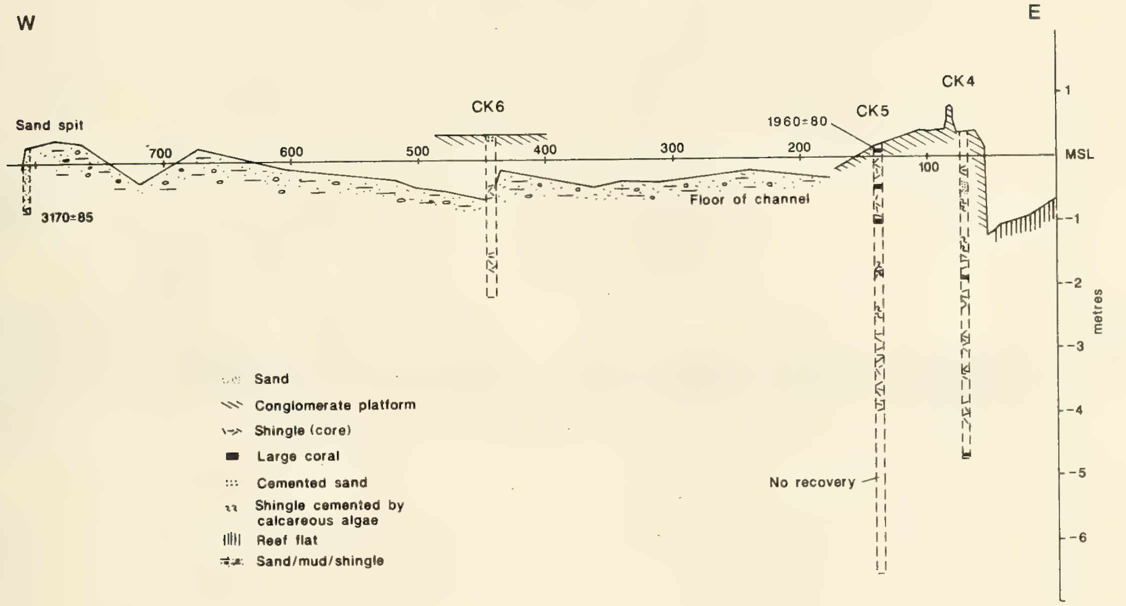

Figure 5. Transect III, Pulu Wak Banka (see Fig. 2 for location): stratigraphy and radiocarbon dates.

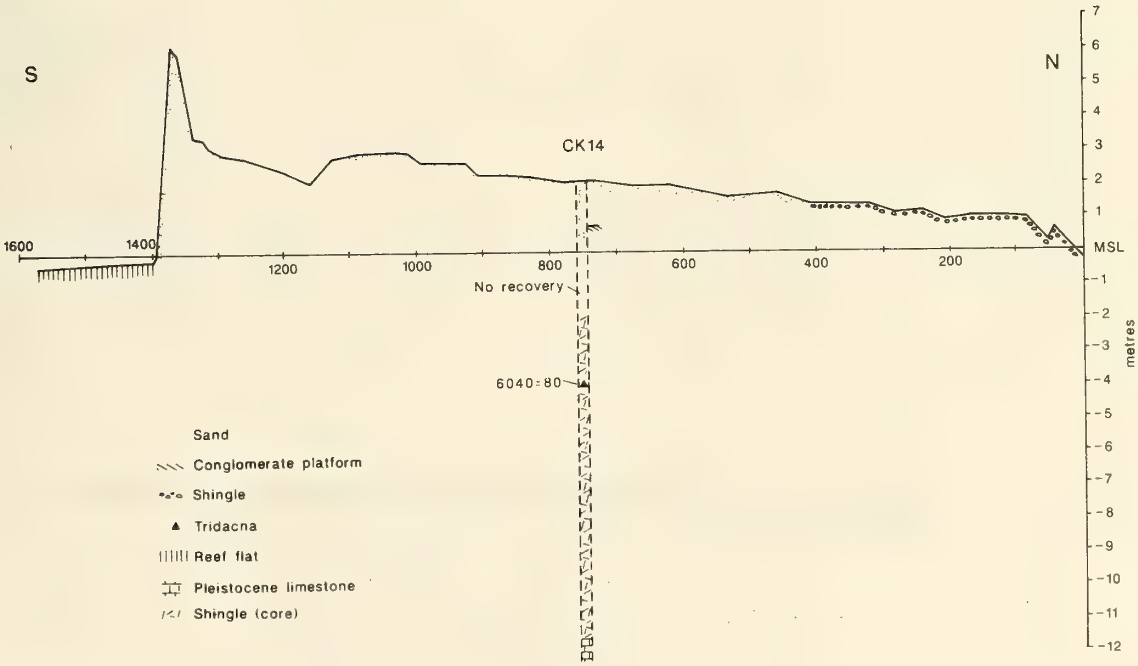

Figure 6. Transect IV, South Island (see Fig. 2 for location): stratigraphy and radiocarbon dates.

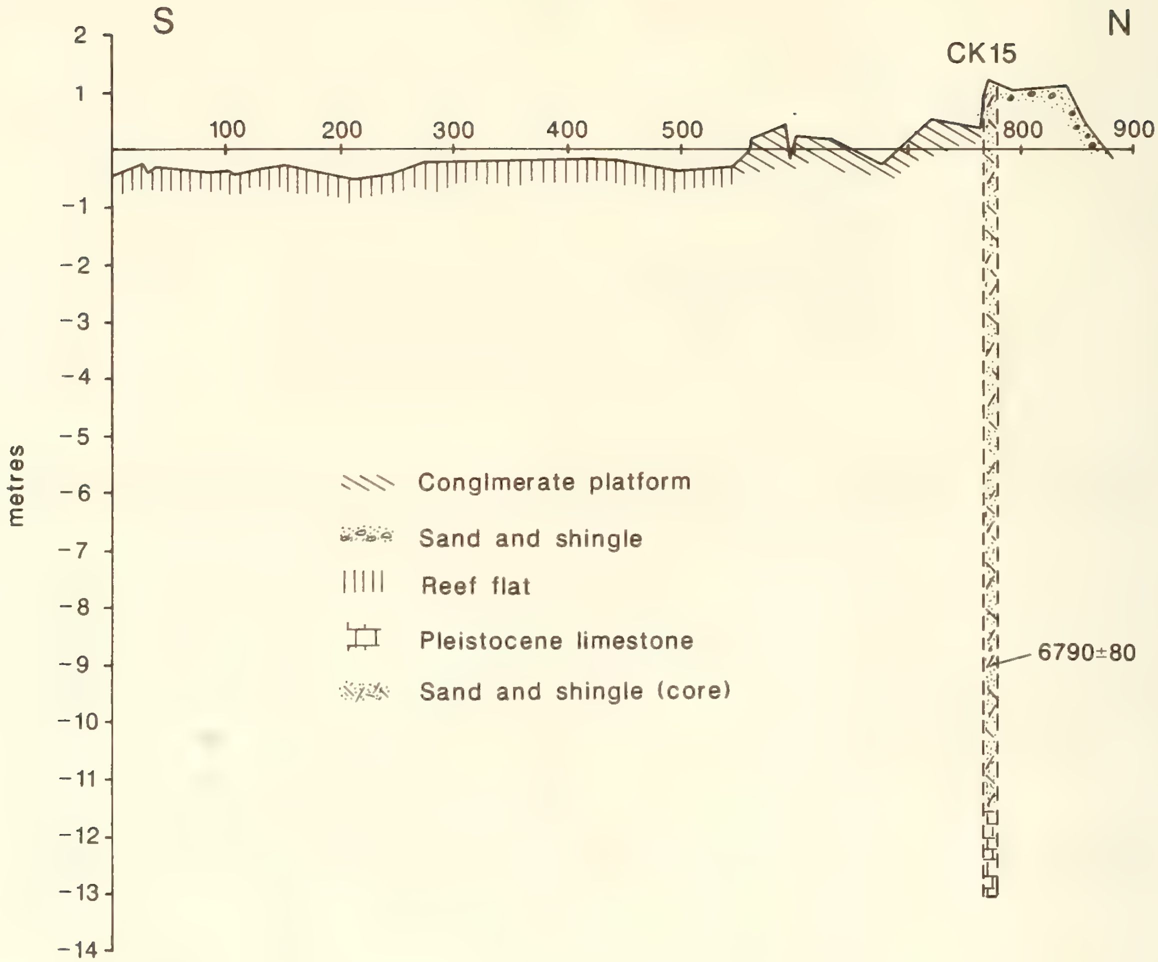

Figure 7. Transect V, Pulu Blan Madar (see Fig. 2 for location): stratigraphy and radiocarbon dates.

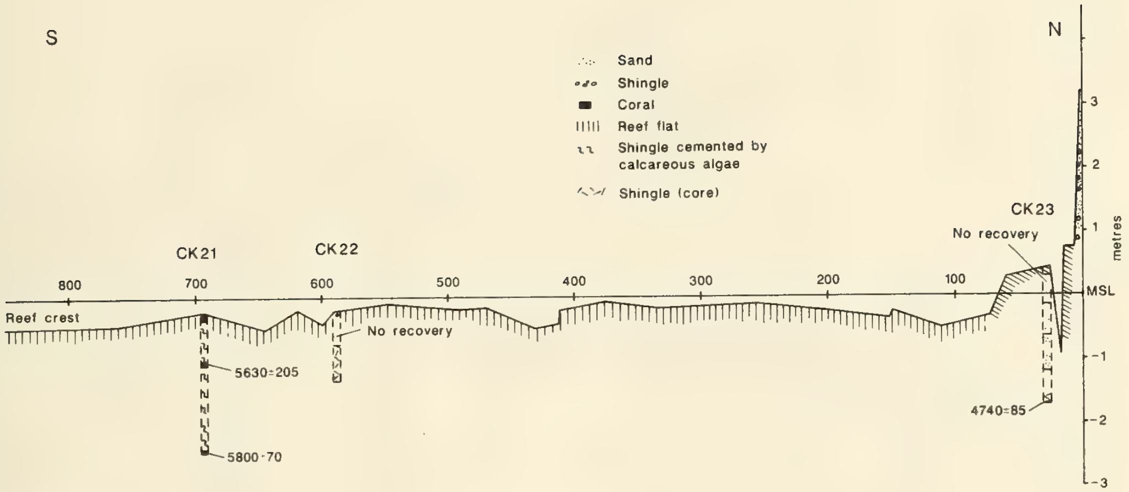

Figure 8. Transect VI, Pulu Maria (see Fig. 2 for location): stratigraphy and radiocarbon dates.

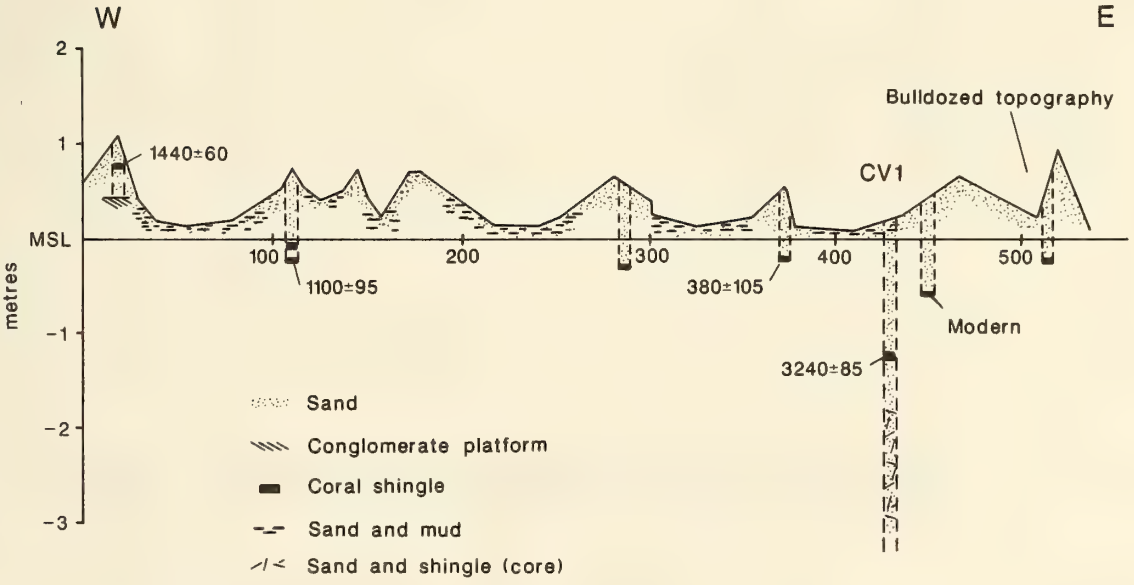

Figure 9. Transect VII, eastern end of West Island (see Fig. 2 for location): stratigraphy and radiocarbon dates.

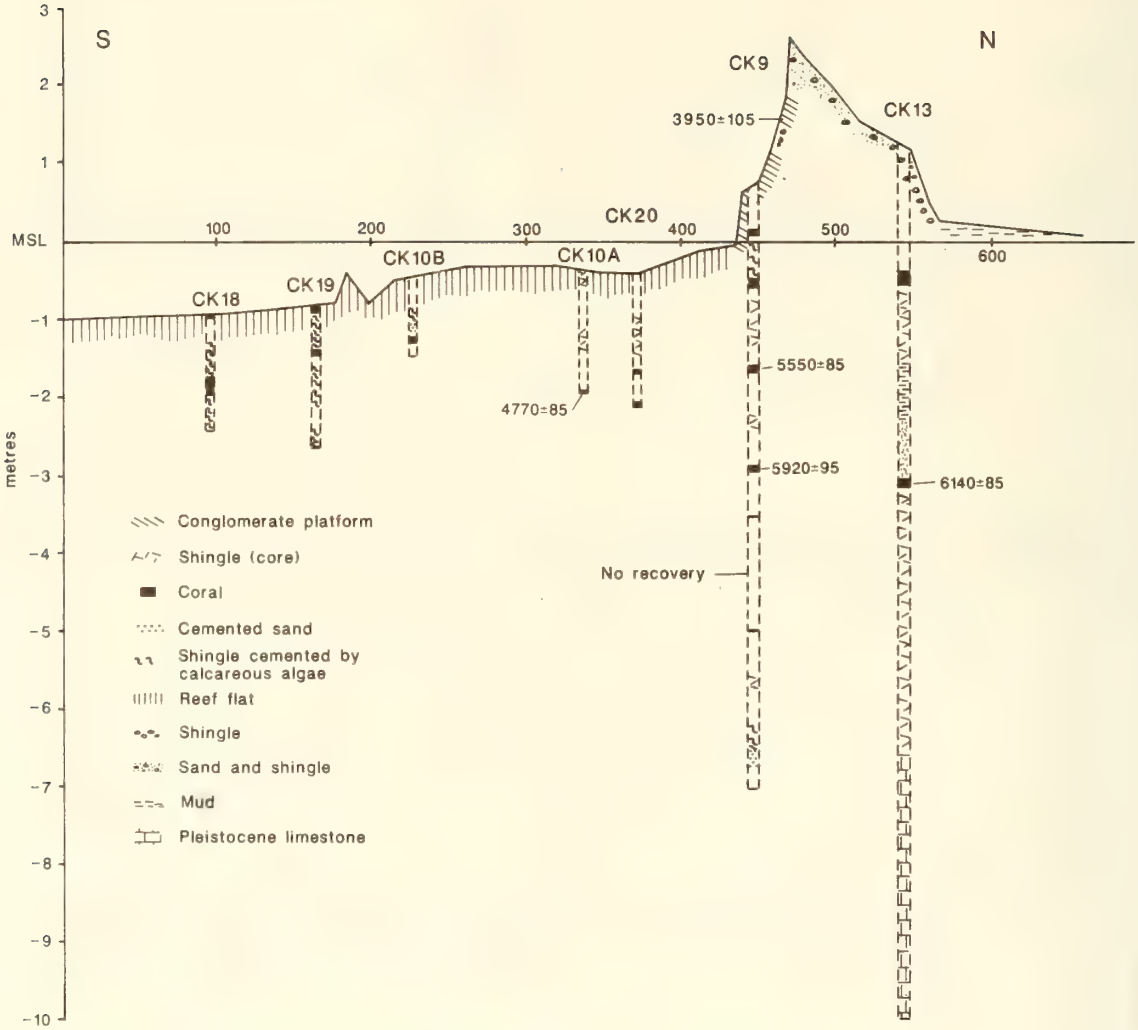

Figure 10. Transect VIII, southern West Island (see Fig. 2 for location): stratigraphy and radiocarbon dates.

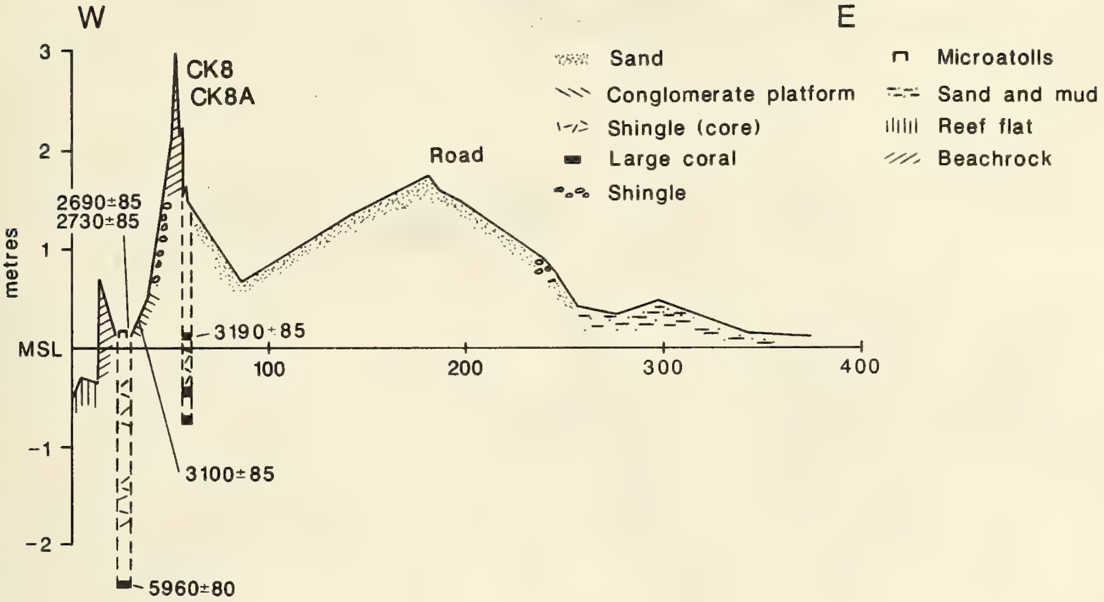

Figure 11. Transect IX, Quarantine station (see Fig. 2 for location): stratigraphy and radiocarbon dates.

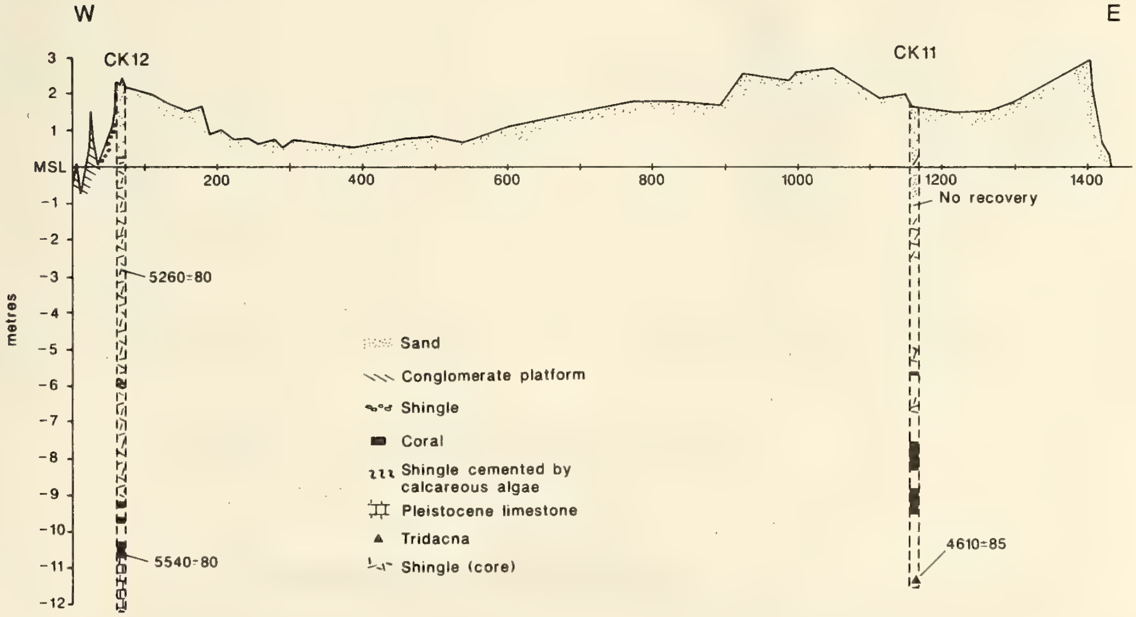

Figure 12. Transect X, Horsburgh Island (see Fig. 2 for location): stratigraphy and radiocarbon dates.

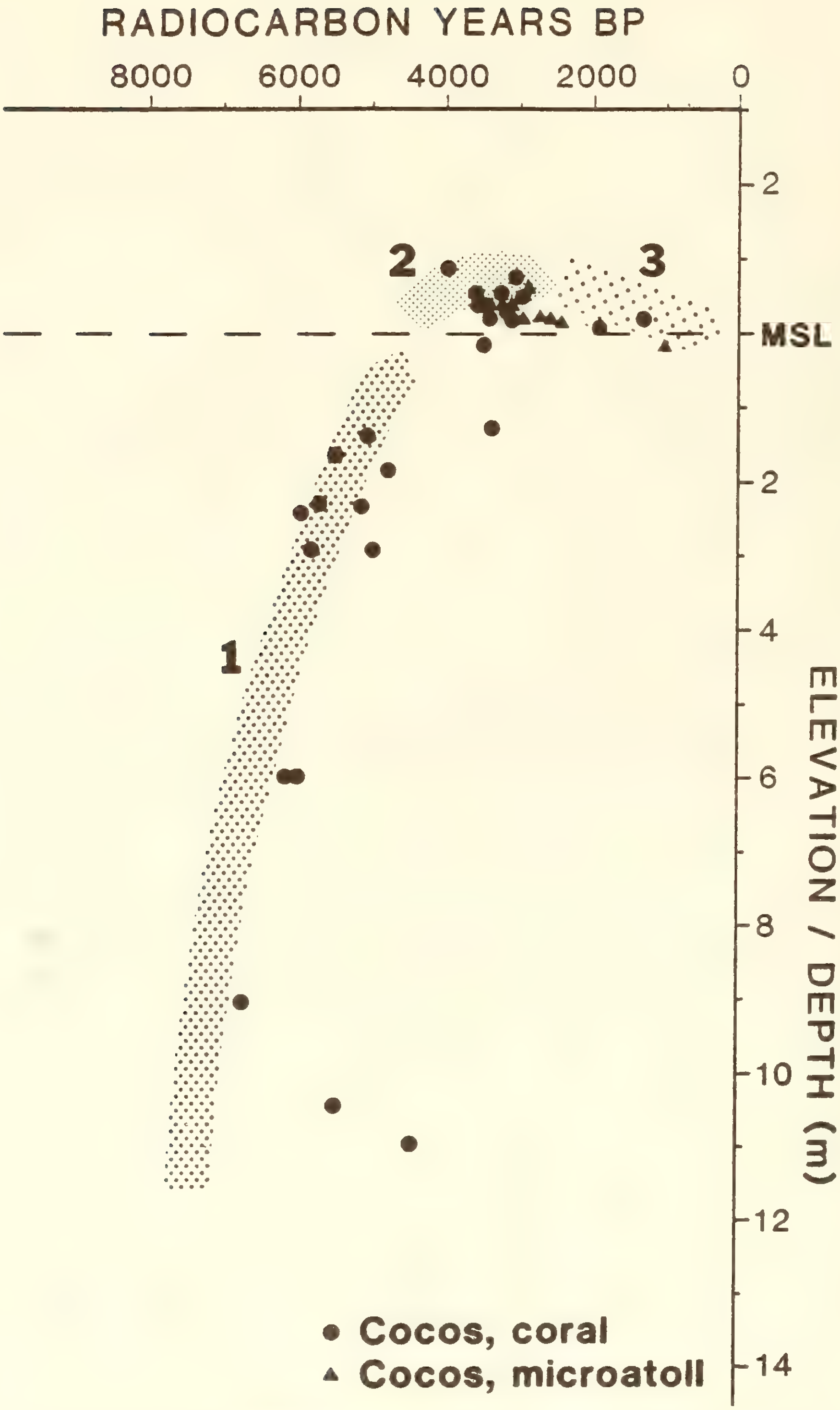

Figure 13. Age-depth plot of radiocarbon dates from Cocos, showing dates from drillholes (Table 3), from conglomerate platform (Table 2) and from fossil microatolls (Table 4). Three phases can be recognised: 1) catch-up reef growth, 2) reef flat consolidation, and 3) reef island formation. See text for details.

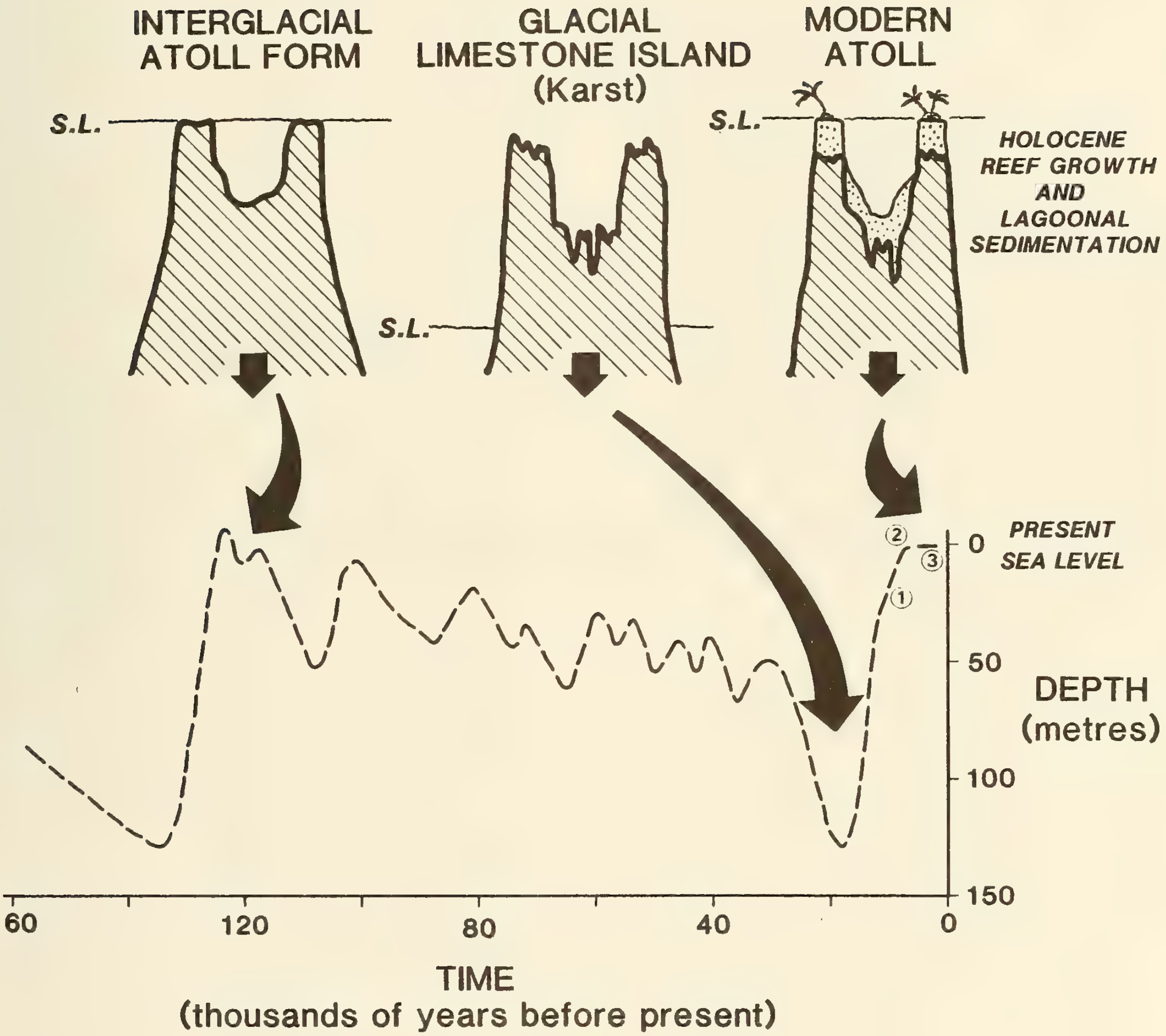

Figure 14. A model of the late Quaternary development of the Cocos (Keeling) Islands. The sea-level curve is derived from Chappell and Shackleton (1986). The atoll is gradually subsiding. The interglacial atoll surface is subject to solutional weathering particularly when the sea is low. During the postglacial marine transgression reefs have re-established over the pre-Holocene surface and the three phases of Holocene atoll development identified in Figure 13 can be recognised.

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CHAPTER 5

REEF ISLANDS OF THE COCOS (KEELING) ISLANDS

BY

C.D. WOODROFFE AND R.F. McLEAN

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CHAPTER 5

REEF ISLANDS OF THE COCOS (KEELING) ISLANDS

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C.D. WOODROFFE *
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INTRODUCTION

Reef islands have developed during the final phase of the Holocene development of the Cocos (Keeling) Islands. The islands are low-lying, and are generally composed of unconsolidated, biogenic sand. In places coral shingle is an important element of the sediments, and in a few localities, as for instance towards the southern end and on the oceanward shore of Pulu Wak Banka, coral rubble, composed of boulders of more than 50 cm diameter, covers the islands seaward margin.

Reef islands often overlie a cemented coral breccia, referred to as conglomerate platform (see previous chapter). Guppy (1889) noted the compositional similarity between this and the material comprising the modern reef flat and reef crest, and as we have demonstrated this platform appears to be an emergent, fossil reef flat dating from the mid-Holocene (Woodroffe et al. 1990a, 1990b). The conglomerate platform underlies many of the islands, although is not found everywhere (Jacobson 1976); it appears to act as an anchor, determining island location. A clinker-like conglomerate, undercut by solution and ringing metallic to the hammer, is found along the lagoonward shore of many islands, and is particularly conspicuous around the perimeter of the lagoonlets or teloks.

In addition to the conglomerate platform there are also cemented deposits of beachrock. Beachrock can be distinguished from conglomerate platform because it is bedded and exhibits a seaward dip (Russell and McIntire 1965, p35); beds are scarped at the landward face, and the deposits are undercut along bedding stratification (Stoddart 1971, p9). In places beachrock overlies conglomerate platform, as on the western shore of Horsburgh Island. In addition there are some isolated cemented deposits which resemble cay sandstone. These are generally less well lithified, and are horizontally bedded; an example occurs on the oceanward shore at the southern end of the airstrip on West Island.

In this section the physical and major vegetation characteristics of individual reef islands are described and mapped. Mapping was undertaken from 1:10,000 colour vertical aerial photographs taken in 1987, supplemented by ground truthing. Elevational information was derived from a series of profiles surveyed across reef islands and related to mean sea level datum. Additional data come from existing surveys and benchmark records.

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The general form of reef islands was summarised diagrammatically by Darwin, who recognised a ledge of conglomerate platform which protruded on the oceanward side of islands, and a ridge, generally sandy, but also of coarser material, which formed the oceanward beach. In common with reef islands on other atolls, Cocos reef islands often show a lower lagoonward beach ridge, in addition to the oceanward beach ridge.

Individual reef islands were described by Guppy (1889). Details of perimeter and island area are given in Table 1; they are examined sequentially below.

REEF ISLANDS

DIRECTION ISLAND

Direction Island (also known as Pulu Tikus, or Rat Island) is a crescent-shaped island. It appears to have been the first island to be inhabited, for it was on Direction Island that the crew, together with the rats, of the *Mauritius* were marooned after their ship was wrecked in 1825. The island was also inhabited for a short period by Alexander Hare and his followers in the same year. It is 1.6 km long and 300 m maximum width, with an area of 0.34 km^2. It is dominated by coconut woodland, but with a band of *Scaevola* scrub along its eastern margin. This island was the site of the Cable Station, with undersea links to Australia, Singapore and South Africa, which came into operation in 1901 and ceased in 1966. In the late 1960s buildings on the island were either translocated to Home and West Island, or bulldozed into the sea along the oceanward margin, and considerable building rubble is conspicuous along the oceanward shore (Fig. 19a).

The eastern portion of the oceanward shore comprises a prominent ledge of conglomerate platform, extending up to 35 m seaward from the beach (Fig. 14). This conglomerate platform is composed particularly of heads of branching *Acropora*. The oceanward beach ridge is composed of coral rubble and shingle along most of the island, and fragments of *Pocillopora* are especially frequent. This coarse substrate overlies sand, and the island can be seen to be composed of sand just over the ridge crest which reaches a height of around 3.0 m along much of the island, but 3.5 m towards the northern end (Fig. 11). The lagoonward shore is dominated by a broad sandy beach. At the northwestern end of Direction Island there are a series of shingle berms marking periodic accretion, in relation to which Guppy proposed that 'as the reef grows seaward the island also gains on the reef flat by a succession of ridges, thrown up during heavy gales, the remains of which are still to be seen in its interior' (Guppy 1889, p463).

Small outcrops of beachrock are found at the northern and southern ends of the lagoonward beach, indicating minor recession of this shoreline at some stage in the past. There is a strong current running through the inter-island channel at the southern end of Direction Island, and called the Rip. Guppy (1889) proposed that such currents served to give the island its crescentic shape.

WORKHOUSE ISLET

There is presently no permanent land at the site of Workhouse Islet, or Pulu Pasir. However, there has been an island of variable size there in the past. A sand bank 150 ft by 100 ft was described by van der Jagt in 1829; Guppy (1889) records that in 1888 it was 6 ft high and dominated by one seaward leaning coconut.

PRISON ISLAND

The island north of Home Island is known as Prison Island; it has been known as Pulu Beras (Rice Island) or Pulu Tuan (Master's island), from the time of Alexander Hare. It is now considerably smaller (88x75 m) than it must have been when Alexander Hare moved his household there in 1827 from Home Island. van der Jagt (1831) recorded that it was 20 ft high in 1829, and Guppy (1889) also states that it was 20 ft high in 1888 and was composed of blown sand. It presently reaches a height of 6.7 m, and so has changed little in overall height in this time, though it is now eroding on all sides (Fig. 19b). It contains a mixture of coconut, *Scaevola* and *Tournefortia*. Bunce (1988) implies that much of this erosion has taken place in the 30 years since Pulu Gangsa has been connected to Home Island.

BUTTON ISLETS

Guppy (1889) records that there were a series of islands, termed the Button Islets, on the 1829 map of van der Jagt, between Prison Island and Pulu Gangsa. The sandy reef islands had already disappeared by 1888, with only conglomerate platform remaining (this platform can be seen in the foreground in Fig. 19b).

HOME ISLAND

Home Island has been a centre of habitation since Alexander Hare chose it for his first permanent settlement in 1826. The burial island, Pulu Gangsa, termed Clunie Island by Guppy (1889), was artificially joined to Home Island by placing coconut logs and concrete-filled drums across the channel in the late 1940s (Bunce 1988). In 1888 the channel between the two had been less than 2 ft deep at low tides (Guppy 1889, p464). The island is also known as Water Island, New Selima or Pulu Selma. It is covered by well-managed coconut woodland, with extensive groves of *Calophyllum*. *Casuarina* was reported as widespread on the island in 1888 by Guppy (1889).

The combined islands have a length of 2.6 km, and reach a maximum width of 800 m (Fig. 2). Their area is 0.95 km^2. Some part of this has been reclaimed from the sea; this is especially true of the landing area north and south of the present jetty, and the part of the village called kampong baru (new village), reclaimed by teams of women earlier this century (Bunce 1988). Oceania House was designed and built by George Clunies-Ross in 1893.

There is considerable survey data available for Home Island. Most of the kampong is 1.20-1.60 m above mean sea level. The island rises generally to an oceanward beach crest that is around 3.30 m (Fig. 11). This beach is covered with coral shingle and coral boulders, but as excavations into the island have shown, these are underlain by sand which is dipping gradually oceanward at 2-6°.

North of the village there is the remnant of a wind-blown dune (see Fig. 11); sand from similar dunes appears to have been removed and used to assist fill in reclaimed areas. The dune presently rises to 5.50 m above mean sea level and contains one of the few remaining stands of *Pandanus*. The sandy lagoonal shore has been extensively modified; sand has been bulldozed, and there is evidence of a series of seawalls along parts of the shore. The village extended along the southern shore, east of Oceania House earlier this century (Gibson-Hill 1950).

On the oceanward shore of Home Island there is a narrow outcrop of conglomerate platform within which branching corals are especially prominent (Fig. 15). Individual *Porites* blocks within the conglomerate platform reach up to 1.0 m mean sea level. The conglomerate platform is overlain by boulder and shingle deposits. It widens into a broader platform at the southern end of the island. Conglomerate also underlies much of the island, as can be seen on the profiles in Figure 11, and from descriptions in Jacobson (1976).

PULU AMPANG KECHIL

Pulu Ampang Kechil is the small island south of Home Island, and forming the northern outlier of the Ampang Islands (Fig. 3). It was called Scaevola Islet by Guppy (1889). It is dominated by *Scaevola*, although with individual coconut and *Tournefortia*. The island is composed of coral shingle, with a sand spit extending to seaward and to lagoonward. It lies on an outcrop of conglomerate platform which contains some particularly large heads of *Porites* coral of over 1 m diameter.

PULU AMPANG

The Ampang Islands, termed Steward's group in van der Jagt's map of 1829, are a group of several small islands on one outcrop of conglomerate platform. The term Pulu Ampang is generally applied to the northernmost of the group, distinguished as Ampang Major by Guppy. This island is horseshoe shaped 625 m long and 275 m wide, with sandy spits extending into the lagoon around the island margins. *Pemphis* grows on these spits and also occurs along a minor bar cutting off the interior lagoonlet. This lagoonlet dries at low tide, and Guppy recounts that J.C. Ross remembers this feature silting up (Guppy 1899, p466). It appears to have changed little from the account given by Guppy over 100 years ago (Fig. 3)

The conglomerate platform is extensive along the oceanward shore of each of the Ampang Islands (see Fig. 19c). It forms a much flatter surface than on Pulu Ampang Kechil, and rises up to heights on individual coral heads within the platform of 0.76 m mean sea level. Much of the conglomerate platform is inundated at high tide, particularly when there is a large swell. The oceanward beach on Pulu Ampang is composed of shingle overlying sand, with individual boulders at the foot of the beach of diameters up to 1 m. The crest of this ridge has a cover of *Scaevola* scrub, which is replaced 10-20 m inland by coconut woodland (Fig. 3).

PULU WA-IDAS

Pulu Wa-idas, called Ampang Minor by Guppy, is separated from Pulu Ampang to the north by a deep pool, which resembles other inter-island passages except that it does not continue through the conglomerate platform as a channel. The conglomerate platform is fissured, and is evidently eroding at this point, and given time it would appear that a channel will form between these two islands. The island is 75 m from north to south, and 320 m from oceanward to lagoonward; it is covered with coconut woodland, with a margin of *Pemphis* along its southern side (shown in Fig. 19c).

PULU BLEKOK

The southernmost of the Ampang islands is Pulu Blekok, called Pulu Bruko by Guppy. In form it is a mirror image of Pulu Wa-idas, with a fringe of *Pemphis* along its northern margin. It is 230 m from oceanward to lagoonward (Fig. 3). The conglomerate platform, although embayed on the oceanward side at this point, does not show the same indications that a channel will form as to the north of Pulu Wa-idas. Indeed Guppy suggested that the vegetation of the two islands was encroaching, and that over time the two islands would unite (Guppy 1889, p466); they have not done so in the 100 years since he observed them. There is a lagoonlet, largely cut off from the lagoon, on the lagoonward side.

PULU KEMBANG

Pulu Kembang, spelt Pulu Kumbang by Guppy, but not described in any detail, sits on its own outcrop of conglomerate platform. The island is 150 m north to south and 390 m from oceanward to lagoonward; it is predominantly sandy, but it has extensive shingle along the margins flanking inter-island channels, and shingle is found at the beach top, where there is a narrow band of *Scaevola*. Much of the island is covered with coconut woodland, though *Pemphis* occurs on the lagoonward most parts of the sandy spits. The sand on the oceanward beach comprises an abundance of foraminifera; it appears to be actively accreting, particularly at the southeastern corner, where *Pemphis* is colonising this sand.

PULU CHEPELOK/PULU WAK BANKA

The island south of Pulu Kembang is a long island which has several names. It was called Armstrong Island on the 1829 map of van der Jagt; Guppy called it Gooseberry Island. On the recent maps its northern part is called Pulu Chepelok (also spelt Pulu Cepelok), while the southern half is named Pulu Wak Banka. The island is 1.15 km long, and up to 400 m wide. It has prominent spits at the northern and southern ends. There are also a couple of similar features extending into the lagoon in the middle of the island, giving the impression that this island may have comprised two or three islands in the past (Guppy 1899, p466).

The island along its oceanward shore is underlain by an extensive conglomerate platform. This contains large boulders in places; there is a large boulder 1.5 m long and 1 m higher than the general conglomerate platform level, reaching an elevation of 1.50 m mean sea level, at the southern end of the island. The nature of the beach sediments on the oceanward shore changes markedly along the island. There are coarse coral rubble deposits, with boulders up to 1 m in diameter, along much of the southern half of the island, reaching up into the *Scaevola* scrub which is dense along the ridge crest (Fig. 20e). On the other hand, where the island is narrowest, the conglomerate platform is no longer present along the oceanward shore, and instead there is a broad sand beach. The ridge crest rises to 3.5 m mean seal level at the southern end of the island, but is only 2.1 m mean seal level where a profile has been surveyed across the island in the centre. On that profile (Fig. 11), it can be seen that the coral shingle overlies sand, and that the conglomerate platform also continues under much of the island. Conglomerate forms a thin crust along the margin of the channel along the southern end of the island.

PULU PANDAN

Pandan Island or Pulu Pandan (also called Misery Island) is the clearest example of a horseshoe shaped island (Fig. 3), called an atollon by Guppy (1889). Despite its name, *Pandanus* is no longer conspicuous element of the island's vegetation. It consists of two distinct sandy spits with a shingle veneer, both covered by coconut woodland with *Pemphis* on the lagoonward extremity (Fig. 16). Maximum width is about 800 m, and the island measures 1.8 km from the end of one spit to the end of the other spit. These spits serve to partially enclose a lagoonlet, with a soft muddy floor and cover of seagrass. The southern spit in particular has recently extended into the lagoon, and there is a further shoal of intertidal sand, with an outpost of *Pemphis* on it which represents a continuation of the island.

On the oceanward shore there is a margin of conglomerate platform extending along the island. For much of its extent this conglomerate comprises an upper unit of shingle-sized clasts cemented into a near horizontal layer (Fig. 19d); this overlies some *in situ* fossil microatolls of branching *Porites* at the eastern end of the surveyed transect. The conglomerate platform surface rises to 1.20 m mean sea level, rather higher than on other islands on the eastern rim of the atoll, suggesting that this shingle conglomerate surface may overlie the more conventional conglomerate platform surface. The transect (Fig. 11) illustrates that the island is composed primarily of sand, rising up to a ridge crest of 4.50 m mean sea level, and does not have the shingle or rubble veneer characteristic of the oceanward shore of islands to the north. Shingle does form low elevation ridges along the lagoonward shore, and there are small outcrops of a clinker-like conglomerate around the margin of the lagoonlet.

PULU SIPUT

Pulu Siput (also called Goat Island) is dominated by coconut woodland, and is 660 m oceanward to lagoonward, and 240 m from north to south (Fig. 3). It has formed on an outcrop of conglomerate platform, and the island is predominantly sandy, with foraminiferal sand accumulating at the northeastern corner of the island. Spits, with a cover of *Pemphis*, but also with occasional *Suriana*, extend into the lagoon.

PULU JAMBATAN

Pulu Jambatan is the name given to the island formed largely of coconut woodland, 340 m long, at the lagoonward end of a long, narrow outcrop of conglomerate platform. There is a much smaller island, less than 50 m long, at the seaward end of this conglomerate platform outcrop, apparently without a name, with a vegetation cover of *Scaevola* with some coconut and *Tournefortia* (Fig. 3). The conglomerate platform between these two islands is smooth, and cover with a veneer of pink algal mat. Seaward of the more oceanward island, the platform is highly irregular, and contains much coarser coral boulders.

PULU LABU

Pulu Labu is the island directly north of South Island, separated from it by a narrow channel (Fig. 3). Most of the island, which is 430 m long, is composed of coconut woodland; there is a broad band of *Scaevola* scrub along the oceanward ridge crest, and on the southeastern corner where sand has recently accumulated, *Pemphis* is established. The form of the island is very similar to that of a series of lagoonward promontories on neighbouring South Island, and it is not unlikely that similar islands to Pulu Labu may have existed in the past, but have now been united with South Island.

SOUTH ISLAND

South Island, also called Pulu Atas (meaning top island in reference to it being upwind), Scott Island and Southeast Island, is the windward island of the atoll. It was chosen as the site for the first settlement by Captain John Clunies Ross in 1827, who dredged a boat channel through the southern lagoon to the centre of the island. The long lagoonal shore is the preferred site for a number of Home Islanders pondoks (weekender shacks), and was also home to a regiment of Kenyan soldiers, the Fifth African Rifles, who were stationed at the southwestern end near the highest point termed 'Gunong', as coastwatchers in World War II.

The island is 9.5 km long, and reaches a maximum width of 1.1 km and is mapped in Figures 5 and 6. Much of the oceanward shore of South Island is formed of a dune (see Fig. 19f). Windblown sand reaches up to 6.3 m on profile I and profile J (Fig. 11). A dune reaches up to 11 m at the 'Gunong' at the southwestern corner of the island. A coral rubble veneer reaches 4.7 m mean sea level on profile H. The vegetation of the dunes is primarily *Scaevola*, though with considerable *Tournefortia*, particularly as isolated shrubs within blowouts along the dune crest. Guppy (1889) recorded that *Pandanus* was found along this dune crest, but it is not a conspicuous element of the vegetation now. While dunes, which are rare on coral atolls, characterise much of the shoreline of South Island, there is also a substantial outcrop of conglomerate. This takes two forms; conglomerate platform occurs in irregular outcrops along much of the eastern part of the island, often rising up to 1.20 m mean seal level. There are also outcrops of conglomerate ramp, a highly worn form of conglomerate platform, which has been bevelled back to a steep ramp-like profile (Fig. 19e). The latter superficially resembles beachrock, which can also be found at sites along the oceanward shore of South Island, but is not imbricated, and on inspection can be seen to have been bevelled to form the dipping outcrop, rather than deposited in dipping stratification. Similar conglomerate ramps are described on Diego Garcia, an atoll in the Chagos group (Stoddart 1971, p18).

The interior of the island is now covered by thick, overgrown coconut woodland which has degenerated from the organised and harvested coconut plantations of the heyday of the Clunies Ross estate. On the oceanward shore and over the narrow necks of the island, there is dense, impenetrable *Scaevola* scrub. Little remains, except isolated stumps of the *Pisonia* and *Cordia* stands which were once widespread on the island. There is a large stand of *Calophyllum* at the southwestern corner of the island (Fig. 5).

The lagoonward shore of South Island is highly irregular. The lagoonal flats are composed of mud or sandy mud, and there are irregular linear shoals, covered by *Pemphis* and inundated at high tide, partially enclosing some of the larger lagoonlets, termed Teloks (Fig. 20c). It is said to have been silting rapidly, which may have lead to the abandonment of the first settlement there; though there can be little doubt that the southern flats of the lagoon must have been shallow even at that time, and access cannot have been easy. The western end of the island has a series of recurved spits; these are not as distinct as those of West Island; nevertheless they were interpreted by Guppy (1889) to indicate that the island had been extending to the west.

Upon first impression this elongate island appears to have been made up from several islands which have been joined together. There are two areas, traversed by profiles H and I respectively, which resemble infilled passages between these former islands. These are covered mainly by *Scaevola* scrub, with few coconuts; those coconuts which do grow there are stunted, and stressed. There is no freshwater lens developed beneath these narrow areas. Soil is absent or poorly developed, and the lagoonward portion of the island is composed of clinker coral shingle. Darwin interpreted these as former channels, and his interpretation was aided by a map that Leisk, the manager in charge of the islands at the time of his visit, told Darwin he had seen. Guppy was rather dismissive of the likelihood that the channels had been infilled as recently as Darwin implied, pointing out that they were closed, and the island one entity even in the map shown in van Keulen's Atlas of 1753 (Guppy 1889, p467). We examine this issue in more detail below.

PULU KLAPA SATU

Pulu Klapa Satu, the island directly west of South Island, is about 125 m long and 75 m wide (Fig. 5). It sits on a long linear exposure of conglomerate platform, which in common with the other islands of the southern passage, is relatively free of large coral clasts, and contains largely sand-sized grains cemented together. In petrography it resembles beachrock, but lacks the stratification which distinguishes the latter.

PULU BLAN AND PULU BLAN MADAR

Pulu Blan and Pulu Blan Madar, also known as Burial Island and East Cay, sit on the same outcrop of fine-grained conglomerate platform. They are composed of sand with some shingle, and carry a vegetation of coconut and *Scaevola*. The oceanward shore of Pulu Blan Madar rises up to a height of 1.20 m mean sea level.

PULU MARIA

Pulu Maraya or Pulu Maria lies on an outcrop of fine-grained conglomerate platform just west of the eastern end of West Island (Fig 8), and is named after one of two European children who disappeared without trace from the island shores in the 1860s. The island is predominantly sandy though with a series of shingle berms on the oceanward shore. It is dominated by coconut woodland, with a fringe of *Scaevola*, replaced with *Pemphis* along the lagoonward flanks.

WEST ISLAND

West Island, also known as Ross Island, or Pulu Panjang (Long Island), is the island upon which the airstrip was built, initially in 1944, but seeing little action in the war, and revamped for use by Qantas in 1951. It was first settled in 1826 by some of

Alexander Hare's followers, probably in the vicinity of Rumah Baru, and has been inhabited discontinuously since. It was home to more than 7000 troops from Britain, Canada, Australia and India in 1944, and has been associated with the airstrip and contains an Australian expatriate population at present.

The island is 12.6 km long and reaches up to just less than 1 km wide at its maximum width. It is mapped in Figures 6, 7 and 8. Most of the 6.2 km^2 was covered by coconut plantation, but much is now covered by buildings, the airstrip, or radio transmitter and receiver aerials. The coconut woodland has ceased to be cleared regularly, and has become largely overgrown, and penetrable with difficulty.

The island comprises three broad sections, connected by narrow sections which may have been former inter-island passages. These lead into the two large lagoonlet areas, Telok Jembu (Fig. 20a) and Telok Kambing (Fig. 20b). Much of the western shore is a sandy beach, with a dune, reaching more than 7 m high, at Beacon Heights, which has been excavated. Groynes have been constructed in front of the settlement to stop northwards movement of sediment, but accumulation within them indicates little net movement. There are extensive outcrops of beachrock, particularly at the southern end of the island, and adjacent to the Quarantine station, at those sites which appear to mark former passages. There is a large area of conglomerate platform at the southwestern end of the island, and isolated outcrops at the westernmost point and to the northwest. The outcrop to the southwest is one of the more elevated outcrops on the atoll rising up to 1.20 m mean sea level, with a further cemented shingle conglomerate up to 1.80 m mean sea level outcropping on the beach behind the conglomerate platform. There are a number of dipping arcuate ridges within this platform, especially at the southwestern corner, resembling the bassett edges recorded on the Great Barrier reef islands (Stoddart et al. 1978).

The easternmost end of the island is characterised by a number of sand spits and ridges, suggesting gradual buildout of the island into the southern passage. Radiocarbon dating of coral shingle from shallow pits in those shown in Figure 9, in the previous chapter, indicates that these spits have been built progressively. The ages are shown on an aerial photograph of the spits in Figure 17.

HORSBURGH ISLAND

Named after James Horsburgh, the British hydrographer, who compiled detailed sailing directions of this part of the Indian Ocean in 1805, Horsburgh Island is also known as Pulu Luar (Outside island). It is 1.7 km long and 0.9 km wide, covering an area of over 1 km^2 (Figs. 9 and 18).

It was almost continuously inhabited from 1826 until after World War II. Initially Alexander Hare put people on the island to grow vegetables and fruit for other islands. This tradition was maintained by the Clunies Ross proprietors, and George Clunies Ross kept deer on the island for hunting. In 1941, gun emplacements were installed on the southern point of the island and manned by Ceylonese troops.

This island sits partly on an outcrop of conglomerate platform. The conglomerate differs from that on other islands; on the eastern shore of Horsburgh it is generally narrow, and often bevelled into a conglomerate ramp. On the western shore there is a broad platform which consists of a series of strata dipping seaward at up to 5°, which resemble beachrock. The platform appears to combine conglomerate platform and beachrock, and suggests that islands here may have formed almost contemporaneously with the development of the emergent reef flat.

Along the southern shore there is a broad sandy beach, in places with outcrops of beachrock which indicate that in the past the shoreline has had a slightly different orientation in this part of the island. The northern shore of the island is particularly exposed and consists of a bevelled conglomerate platform ledge, and boulder deposits over the top. A particularly noteworthy feature of this island is the small lagoonlet which occurs within the interior of the island to the northeast. This feature, blocked of from the sea by a boulder rampart, presently contains brackish water, and a stand of mangrove *Rhizophora apiculata*. Associated with the mangroves are *Cordia* stumps and *Sesuvium*. In his account of Horsburgh in 1888, Guppy (1889) describes the inland lakelet, but does not record mangroves growing there naturally; indeed he makes the point that mangrove propagules are regularly brought to the shores of Cocos, but have not colonised (Guppy, 1890). Guppy indicates that mangroves were planted there by John George Cluines Ross (Guppy 1890, p278). In a photograph of the lakelet, taken in 1941, the mangroves can be still seen (Gibson-Hill, 1950).

Much of the northern part of Horsburgh is composed of shingle or rubble, while the southern part is predominantly sand. Coconut scrub is especially open over the southern part of the island with a sward of grass and the sedge *Fimbristylis*, but forms denser coconut woodland to the north. *Scaevola* scrub is widespread over the island; to the south it is relatively open, but to the north it is dense, and made almost impenetrable by a tangle of *Turnera, Triumfetta, Wedelia, Premna* and the parasitic *Cassytha*.

NORTH KEELING ISLAND

North Keeling Island is named after Captain William Keeling who is believed to have sighted the island in 1609. It was sketched, showing coconuts, by the Swedish captain Ekeberg in 1749 and appears on the chart reproduced by Dalrymple the English hydrographer in 1787. Fitzroy examined and mapped it from *H.M.S. Beagle* in 1836, but made no landing. Unlike the South Keeling Islands, North Keeling has been visited relatively infrequently by naturalists, and therefore does not have the same history of description. It was first described in detail by Guppy (1889) who was there for 6 days in 1888. Wood-Jones (1912) spent a few hours ashore in June 1906, and the most detailed account, especially of the fauna is that of Gibson-Hill (1948, 1950) who visited for 1 day in January and 2 days in early July in 1941.

The island has not been inhabited for any continuous period, and is presently relatively little changed in comparison with the South Keeling Islands. It was visited from Cocos by the Clunies-Ross family, and Home Islanders (up to 40-60) stayed there for up to three months over the November-February period cutting firewood. The Emden beached on the southern shore of North Keeling after being routed by the Sydney in 1914; and the longest period of settlement was probably during the salvage of the Emden October 1915 to January 1916.

The island is 2.0 km long and 1.3 km wide, with a reef crest around all of the island, except the northwestern corner (Fig. 10). Reef island is almost continuous around the perimeter of a shallow lagoon, reaching a maximum width of 320 m and a minimum width of 50 m. There is one major opening into the lagoon on the southeastern corner of the atollon. This is the windward side, and the opening has no channel through the reef, but is a shallow conduit which drains almost totally at lowest tide. The lagoon is shallow, reported as nowhere deeper than 8 feet by Guppy. It's surface sediments are muddy sands, except for two sandy spits which trail in through the entrance. These did not appear on Fitzroy's chart of the island; Guppy added them in his sketch of the island, but shows them scrolled back on themselves. As can be seen in Figure 10 they are presently linear features which extend flanking the channel. Much of the lagoon is covered with sea grass.

The island varies from sand to rubble. On the northern shore there is a broad sandy beach. This continues along the western shore but with varying amounts of shingle. On the profile (Fig. 10) the sandy beach rises up about 4 m above mean sea level. A pit shows some shingle fragments, but indicates that the majority of the substrate is sand. This becomes coarser to the south, where rubble outcrops on the beach, and there is an erosional cliff cut into this rubble. The southern shore of the island is composed of a spectacular steep shingle beach, with a series of berms identifiable. Much of the eastern shore is composed of a series of shingle berms, these are particularly well-developed just south of the channel into the lagoon, but continue to the north as well. Guppy (1889) recorded that pumice from the eruption of Krakatoa had advanced the shore into the lagoon; no evidence of this can be seen today.

There are also outcrops of coral conglomerate. A broad platform of conglomerate extends out over the reef flat at the eastern part of the island, almost closing the channel into the lagoon completely. Along much of the southern and eastern shore the conglomerate outcrops at the foot of the beach but contains a series of parallel rubble ridges, dipping and stratified like beachrock. These appear to be the lines described by Guppy (1889) as old reef margins, and upon which he based his argument that the reef built out by a series of jumps rather than prograding gradually. Similar boulder conglomerates have been described from other reef settings; they closely resemble the adjacent beach in structure and composition and we call them beach conglomerate, believing that they mark the position of former beach lines rather than reef crests (Fig. 20f). At the site of the southern transect (Fig. 10) there are a number of algal terracettes veneering these old beach deposits. Beach conglomerate overlies conglomerate platform in some places (Fig. 10).

The vegetation of the island was conveniently divided into four zones by Gibson-Hill (1950). Much of the island is dominated by *Pisonia* forest (see Williams, this volume, Chapter 6). Coconuts are a conspicuous element of all stands of *Pisonia*, and over much of the island we have chosen to map this as *Pisonia* and coconut woodland. *Tournefortia* is a conspicuous element of the vegetation of the eastern shore, dominating the crest of the shingle or rubble ridges. In some cases *Tournefortia* is monospecific, north of the channel into the lagoon it occurs with *Scaevola* also. Around the margins of the lagoon, *Pemphis* forms a thicket. *Cordia* is also important in this location, and it was to cut this latter species that the Clunies-Ross sent workers. It may have been less important when Gibson-Hill visited because of this history of cutting. Where *Cordia* forms a lagoonal fringe at present it is often fairly even-aged, and much may have grown back since cutting ceased. The final area that Gibson-Hill identified are cleared areas; the grassy and *Sesuvium* covered area to the northwest of the lagoon is the most extensive area of this type.

There has been considerable speculation as to how North Keeling has developed. In particular it seems unusual because the remaining entrance to the lagoon occurs on the most windward side, rather in the shelter that might develop on the leeward. Indeed the island is quite the inverse of the horseshoe shape that Guppy considers the typical style of development on the main atoll. This has lead a number of observers, starting with Fitzroy, to suggest that the island developed from a series of formerly unconnected islands.

REEF ISLAND MORPHOLOGY

The surveyed traverses (Fig. 11 and 12) show three basic cross-island profiles, the simplest of which was first described by Darwin (1842) and illustrated by a woodcut in the chapter on Keeling atoll (this illustration is in fact a section across Whitsunday atoll and not Cocos (Keeling)). Darwin notes that the highest part of the islets is close to the outer beach and that "from the outer beach the surface slopes gently to the shores of the lagoon". Such simple asymmetric profiles are common on West and South Islands and across the centre of the small horseshoe shaped islands on the atoll's eastern side.

The second type of profile is basin shaped, again with a prominent seaward ridge which slopes inland to a central depression before rising to a lower lagoonward ridge. Such profiles are illustrated from Direction Island and the southern end of Home Island (Fig. 11). The third profile type is more complex being composed of a series of subdued ridges and swales between the ocean and lagoonward ridges. This form suggests a more complicated accretionary history.

A characteristic feature of the islands on Cocos is their plan shape, which Guppy (1889) described as semi-crescentric or horseshoe shaped with their convexities to seaward. "The crescentric form is possessed in various degrees by different islands; some of the smaller ones are perfect horse-shoe atollons and enclose a shallow lagoonlet, others again exhibit only a semi-crescentic form, whilst the larger islands have been produced by the union of several islands of this shape." Examples of the first type would include Pulu Ampang, of the second type Direction Island and of the third type South Island.

To Guppy the islands fitted into an evolutionary sequence all stages of which are represented on Cocos "from the islet recently thrown up on the reef to the perfect horse-shoe atollon". Critical in Guppy's interpretation are the lagoonward recurving extremities of the islands which he believed were formed from material brought in by uni-directional currents through the interisland passages and "heaped up in such a manner as to prolong the extremities of each island lagoonward in the form of two horns". In the case of the larger islands a crescentric form results, while for the smaller islands a more perfect horseshoe shape is first attained. After the two horns are stabilised by vegetation, and providing there is an adequate supply of sand, the horns would tend to approach each other and ultimately they would be joined by a bar enclosing a lagoonlet on the island's lagoon side, Guppy called this occluded island form an atollon, and noted that Horsburgh Island "represents the last condition of an atollon, the earlier stages being illustrated by Pandan Island and Pulu Ampang Major".

This view of island evolution differed from that of Darwin who envisaged a difference in formative processes between islands on the windward and leeward sides of the atoll (Darwin 1842). On the windward side, the islands "increase solely by the addition of fragments on their outer side". Thus the gently sloping surface on the western side of the windward island predates the high ridge to seaward, and is lower because waves had further to go from the reef edge and "had less power to throw up fragments". On the leeward islands, Darwin recognised a combination of two processes operating. First, waves from seaward formed the high ocean ridge, and second "little waves of the lagoon, heap up sand and fragments of thinly branched corals on the inner side of the islets on the leeward side of the atoll". As a result "these islets are broader than those to windward, some being even eight hundred yards in width, but the land thus added is very low".

Both Darwin and Guppy, as well as subsequent workers; recognised the association of islands with the conglomerate platform and the fact that the unconsolidated sands and gravels which go to make up the island commonly rest on a solid foundation of conglomerate platform. Indeed Guppy went so far as to suggest that where bare level patches of conglomerate are exposed on the windward side of the atoll these were "the foundation of the islets that have long since swept away" (Guppy 1889, p462).

In our view, the evidence for such an assertion is generally lacking, except in those places where linear or arcuate bands of beachrock or beach conglomerate are firmly cemented onto the conglomerate platform. Examples of such exposures are found along the northwestern side of Horsburgh Island, adjacent to the Quarantine Station on West Island, around the southwestern corners of West and South Island and on North Keeling Island. We believe that these outcrops are residuals from the earliest phase of island building and represent shorelines developed concurrently with the formation of the conglomerate platform at the time of higher sea level. A radiocarbon date of 3030 ± 85 years B.P. from a coral boulder in beach conglomerate to the southwest of North Keeling gives some support to this argument. Landward erosion of these shorelines has subsequently occurred. In some other locations high beachrock or beach conglomerate is found congruent with the present shoreline. In such cases the position of the initial shoreline has been maintained.

While the association of islands and conglomerate platform is the norm, Guppy (1889) also recognised that conglomerate platform is not everywhere present beneath the islands being "absent in those situations where ancient passages have been filled up with sand and reef debris, and also in those places where recent additions have been made to the land surface" (p. 462). Our drilling and field data confirm the validity of this comment, particularly with respect to the "horns" and "bars" of the horseshoe islands and atollons, as well as the extensive area of lagoonward recurving spits at the western end of South Island and eastern end of West Island. Radiocarbon dates recording the development of the last area are shown in Figure 17.

REEF ISLAND FORMATION

Reef islands post-date the conglomerate platform, and it has been demonstrated that the conglomerate platform was deposited 4000-3000 years ago, as shown by the narrow range of radiocarbon ages from within it (Woodroffe et al. 1990a, 1990b, this volume; see chapter 4, Fig. 2). The platform has been interpreted as a former reef flat, deposited under a sea level around 1 m above present, and the islands have formed in the last 3000 years during the time that the sea has fallen to present level.

Some indication of island age has already been given for Home Island (Woodroffe et al. this volume, see last chapter Fig. 3). Samples of coral shingle from a trench through island sediments (shown in Fig. 20d), indicate an age range of 1400-1800 years B.P.

Nevertheless there remains a series of different possible models of island formation, both in terms of oceanward or lagoonward accretion, and in relation to the gradual or episodic nature of deposition of sediment. In order to examine the chronology of island formation in greater detail, three transects of pits were examined on West Island (Fig. 13) and samples of coral shingle submitted for radiocarbon dating.

The radiocarbon dates shown in Figure 13 confirm that the islands contain few sediments greater than 3000 years old. The date of 4280 ± 70 on transect O (T2) came from a depth around mean sea level which would be within conglomerate platform elsewhere. There is no lithified platform at this site, but the date appears to indicate a similar chronology of deposition. Although this transect is across a narrow neck of island flanking a telok (see Fig. 12), termed a barachois in relation to the atoll of Diego Garcia, a date of 3030 ± 70 elsewhere on the transect indicates island formation at an early stage at this site.

Transect P (T1) has been date in some detail. The oldest date 2710 ± 90 years B.P. comes from pit 7 to lagoonward. There is then a progressive decrease in age towards the ocean. Thus contrary to Darwin's expectation, the island appears to have built out towards the ocean even here on the leeward side of the atoll. Dates from pit 3 are stratigraphically consistent and indicate rapid vertical build up. The dominant mode of accretion is horizontal.

A similar trend of older dates to lagoonward, and younger ages to oceanward is seen for transect L (T3), which also ranges from 3000 years B.P. to present. This is particularly significant because this eastern part of West Island has been extending further eastward over the last 1500 years (see Woodroffe et al., this volume, Fig. 9). Radiocarbon ages on individual spits are shown in Figure 17. The main part of this southern section is evidently 3000 years old, like the northern section of West Island.

North Keeling is morphologically distinct from the South Keeling Islands and may have developed differently. It is not unusual in other Pacific and Indian Ocean atoll archipelagoes for the smaller reef platforms to be occupied by one island which is low in the middle, with a lagoon that may or may not be connected to the open ocean. The history of development of these is not known in detail, although there are some radiocarbon dates available from table reefs, or reef-top islands, of this type in Tuvalu (McLean and Hosking 1991).

We have three further radiocarbon dates from North Keeling. A coral from conglomerate on the northeast of the island dated 3840 ± 85 years B.P., similar to but at the older end of the range of dates for conglomerate platform from the South Keeling Islands. An age of 3060 ± 60 years B.P. was derived for coral shingle in a pit in the centre of the island, suggesting little time difference between the formation of the beach at the margin of the reef platform, and the formation of the island. The final date was on a boulder exposed within an erosional scarp in the rubble beach on the southwest of the island, which gave an age of 1620 ± 80 years B.P. Guppy (1889) suggested that the boulders on this beach indicated that it was prograded by coral blocks piled up during a cyclone; this age implies that cyclones may have occurred over the last 1500 years or more. We note that this equates with a phase of island building on other parts of the Cocos (Keeling) Islands.

The radiocarbon ages suggest continual addition to islands over the last 3000 years, but we have insufficient dates to indicate whether this accretion was gradual or whether it occurred in a series of episodes. At this stage we have no dates which allow us to address the morphological issues raised by Guppy. Nevertheless reef islands are geologically young and morphologically dynamic; sediment is continuing to be produced and supplied to islands and the islands are continuing to change through the addition of sediment at some points, but its erosion from elsewhere.

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Table 1. Perimeter and area of the Cocos reef islands

Island	Perimeter (km)	Area (km²)
Horsburgh Island	4.4	1.04
Direction Island	3.4	0.34
Prison Island	0.4	0.02
Home Island	6.7	0.95
Pulu Ampang	1.8	0.06
Pulu Wa-idas	0.7	0.02
Pulu Blekok	1.1	0.03
Pulu Kembang	1.6	0.04
Pulu Wak Banka	2.4	0.22
Pulu Pandan	3.9	0.24
Pulu Siput	2.2	0.10
Pulu Labu	1.3	0.04
South Island	28.5	3.63
Pulu Klapa Satu	0.5	0.02
Pulu Blan Madar	0.7	0.03
Pulu Blan	0.8	0.03
Pulu Maria	0.7	0.01
West Island	38.5	6.23

Table 2. Radiocarbon dating results on reef island sediments, West Island and North Keeling Island.

Beta No.	Sample No.	Island	Depth of sample (cm)	Material	Conventional radiocarbon age
59845	NKI-60	North Keeling	60	Coral shingle	3060 ± 60
59846	WI-T1-P2 95	West Island	95	Coral shingle	570 ± 60
59847	WI-T1 P3 85	West Island	85	Coral Shingle	1990 ± 70
59848	WI-T1 P3 120	West Island	120	Coral Shingle	2010 ± 60
59849	WI-T1 P3 160	West Island	160	Coral Shingle	2110 ± 60
59850	WI-T1 P4 140	West Island	140	Coral Shingle	2130 ± 60
59851	WI-T1 P7 75	West Island	75	Coral Shingle	2710 ± 90
59852	WI-T1 P2 60	West Island	60	Coral Shingle	3030 ± 70
59853	WI-T1 P4 140	West Island	140	Coral Shingle	4280 ± 70
59854	WI-T1 P1 200	West Island	200	Coral Shingle	420 ± 50
59855	WI-T3 P2 70	West Island	70	Coral Shingle	1970 ± 70
59856	WI-T3 P4 55	West Island	55	Coral Shingle	3100 ± 70

Note: Radiocarbon ages determined by Beta Analytic have not been corrected for ∂C^{13} or for environmental reservoir effect. These corrections are of similar magnitude (c 400 years), but cancel each other out. Thus these Beta dates are more-or-less comparable to the environmentally-corrected ages given in the previous chapter.

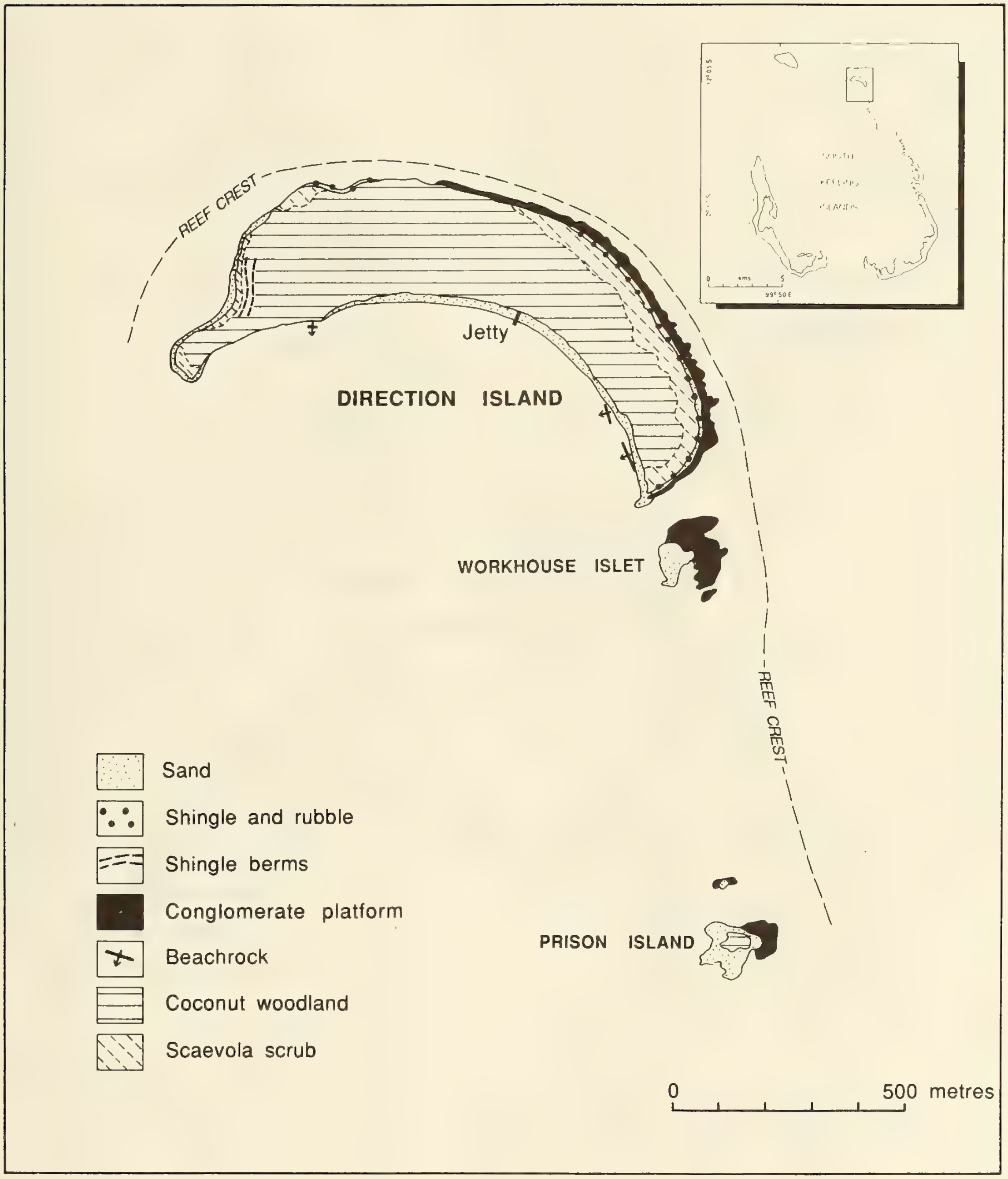

Figure 1. Direction Island, mapped from 1987 aerial photography.

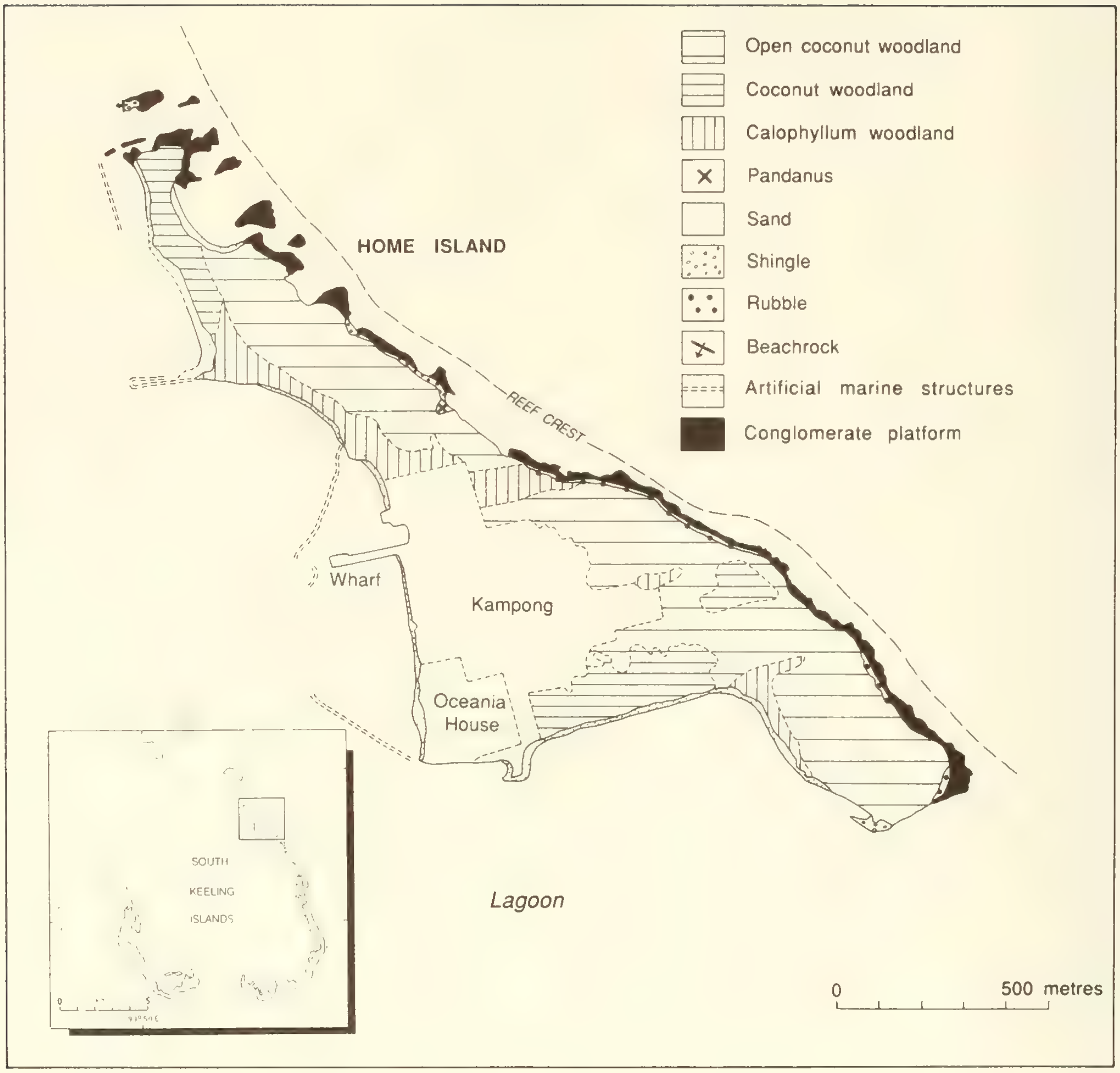

Figure 2. Home Island mapped from 1987 aerial photography.

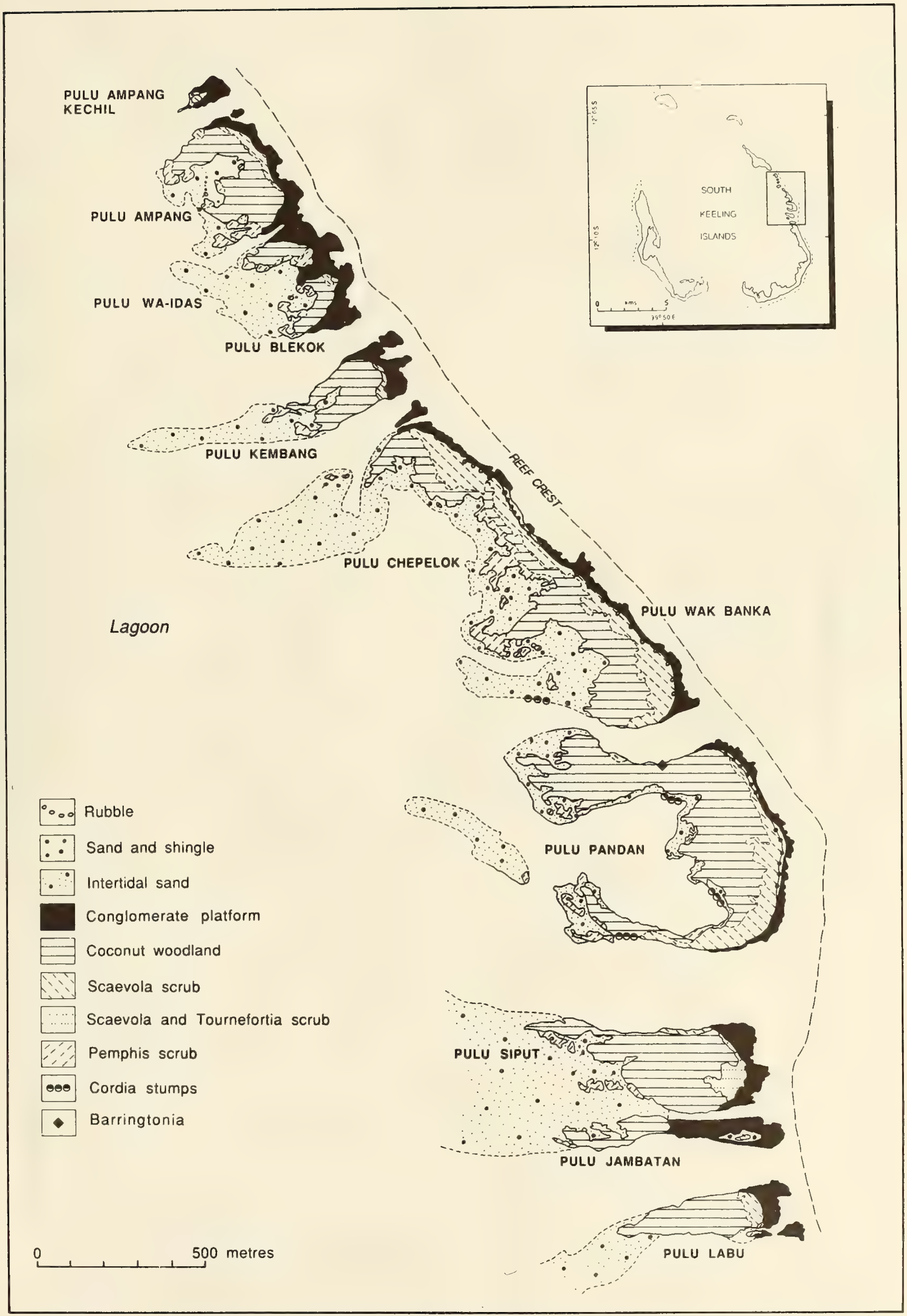

Figure 3. Islands of the eastern rim of the atoll from Pulu Ampang to Pulu Labu, mapped from 1987 aerial photography.

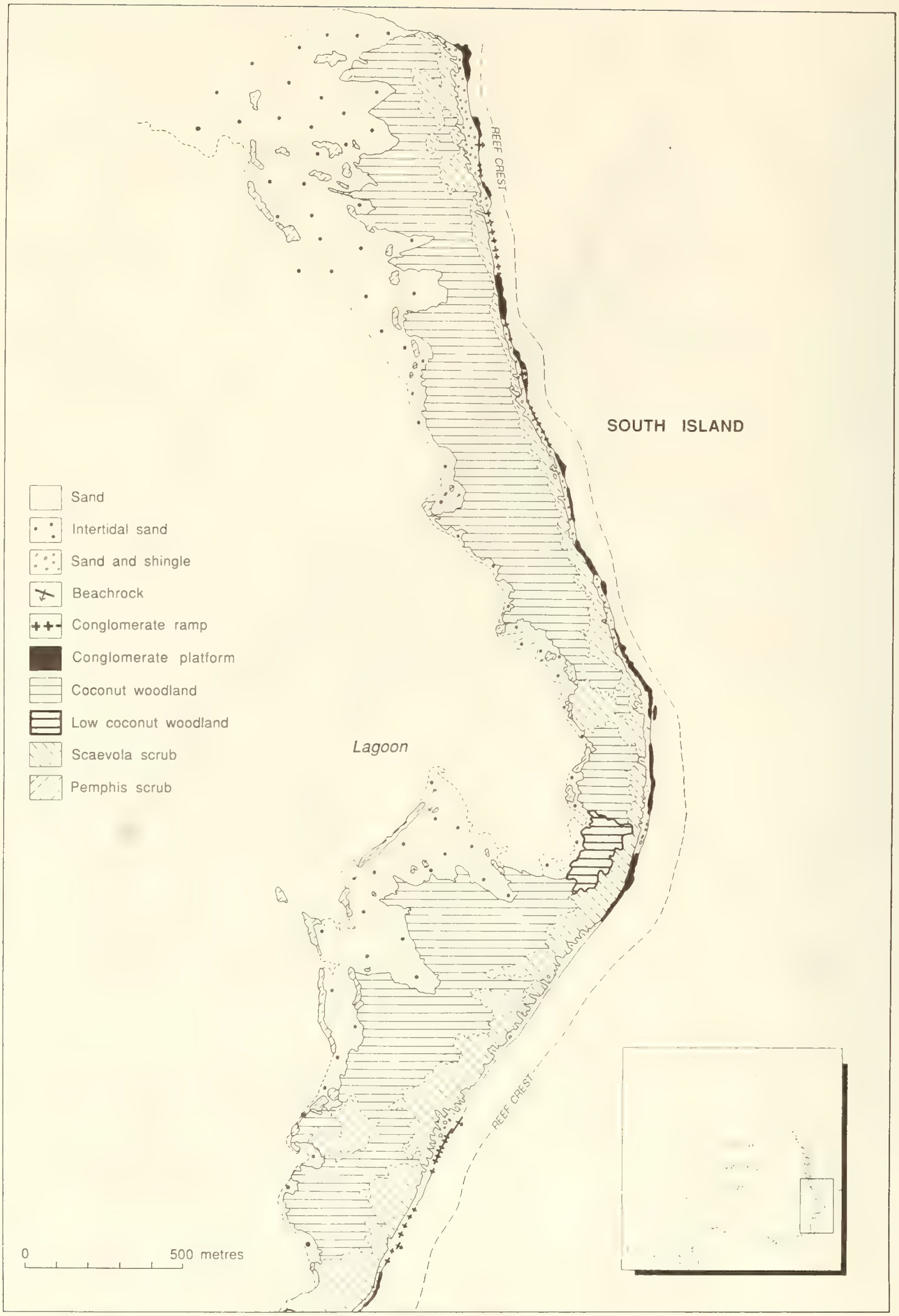

Figure 4. South Island, northern section, mapped from 1987 aerial photography.

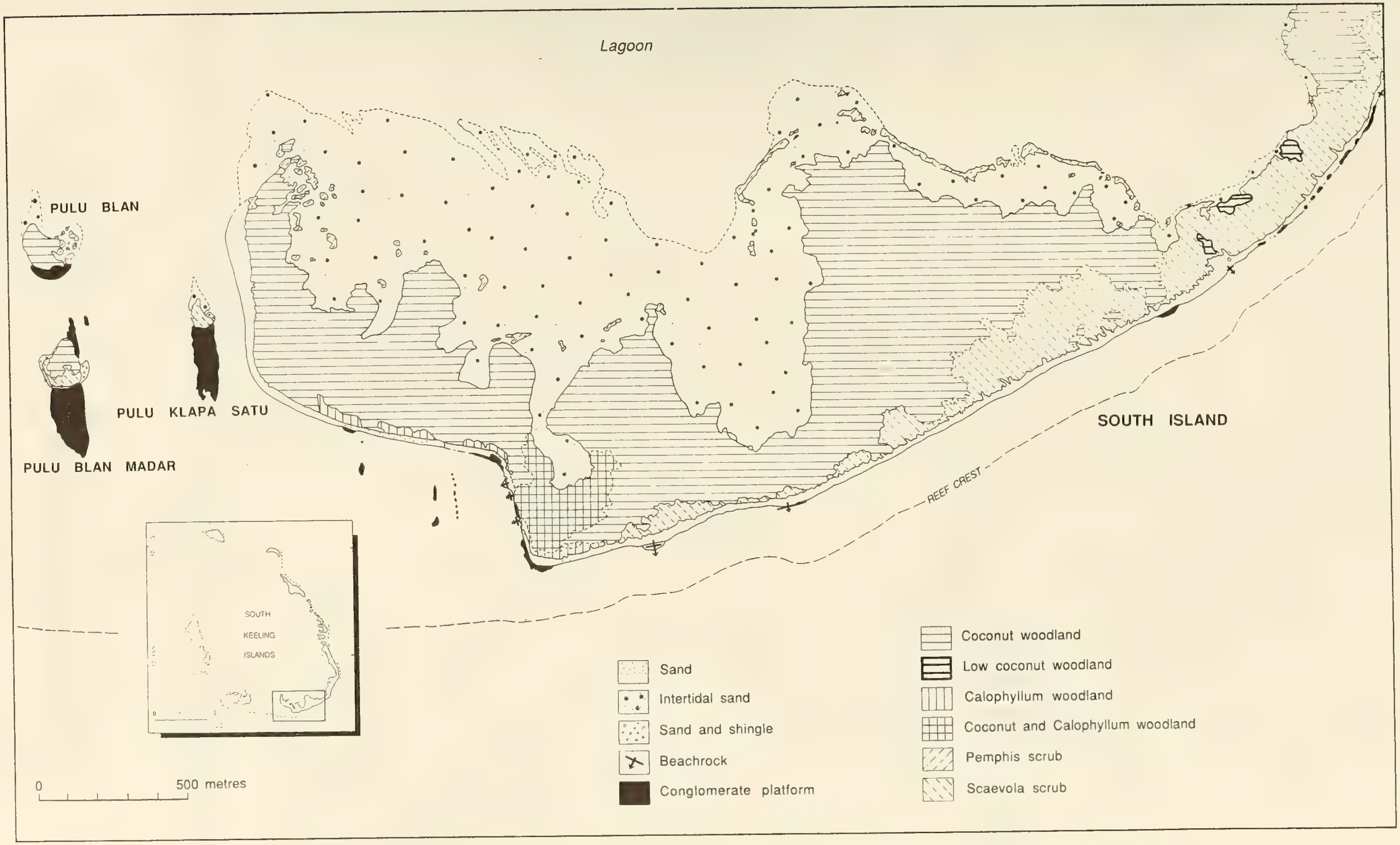

Figure 5. South Island, southern section, mapped from 1987 aerial photography.

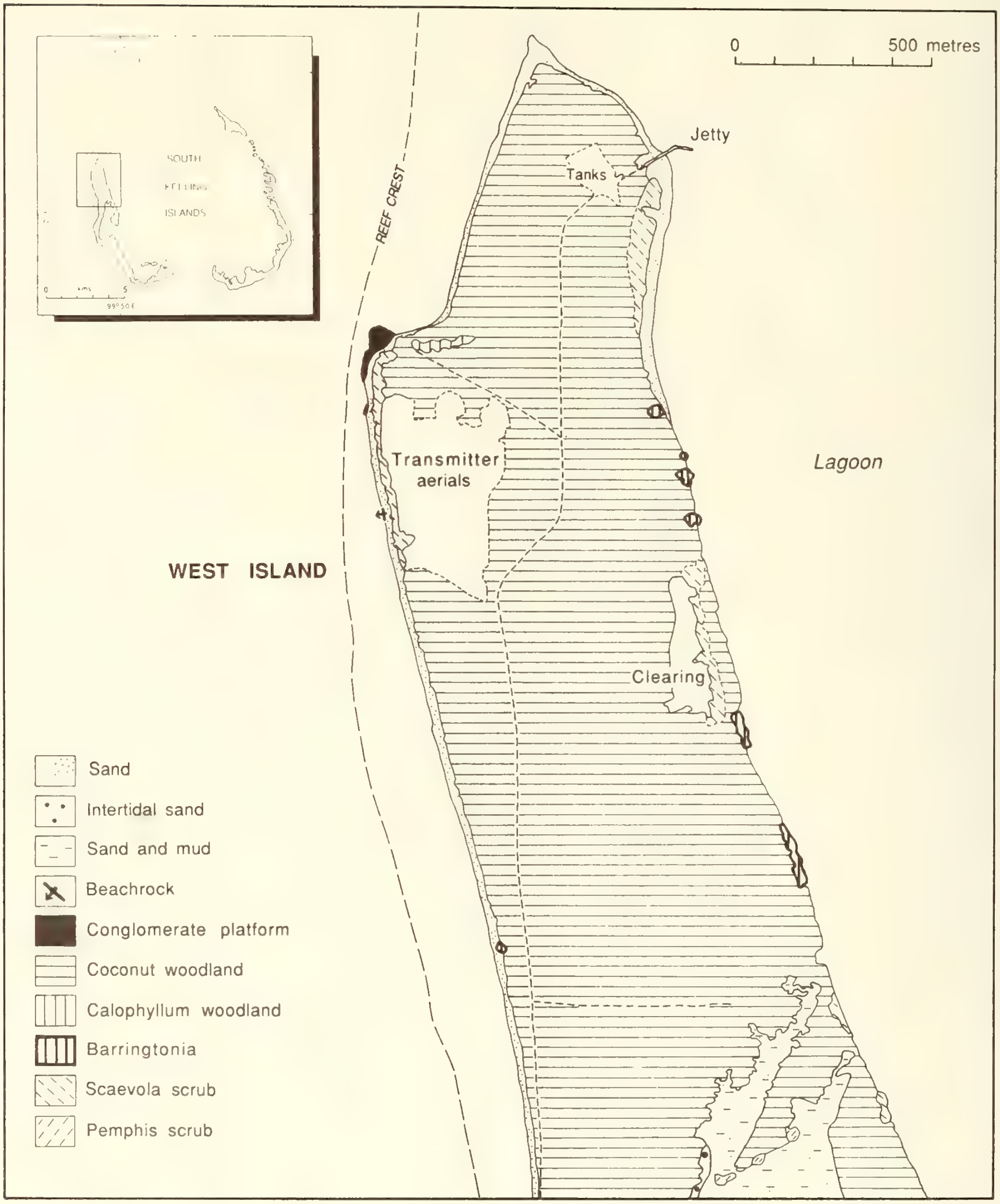

Figure 6. West Island, northern section, mapped from 1987 aerial photography.

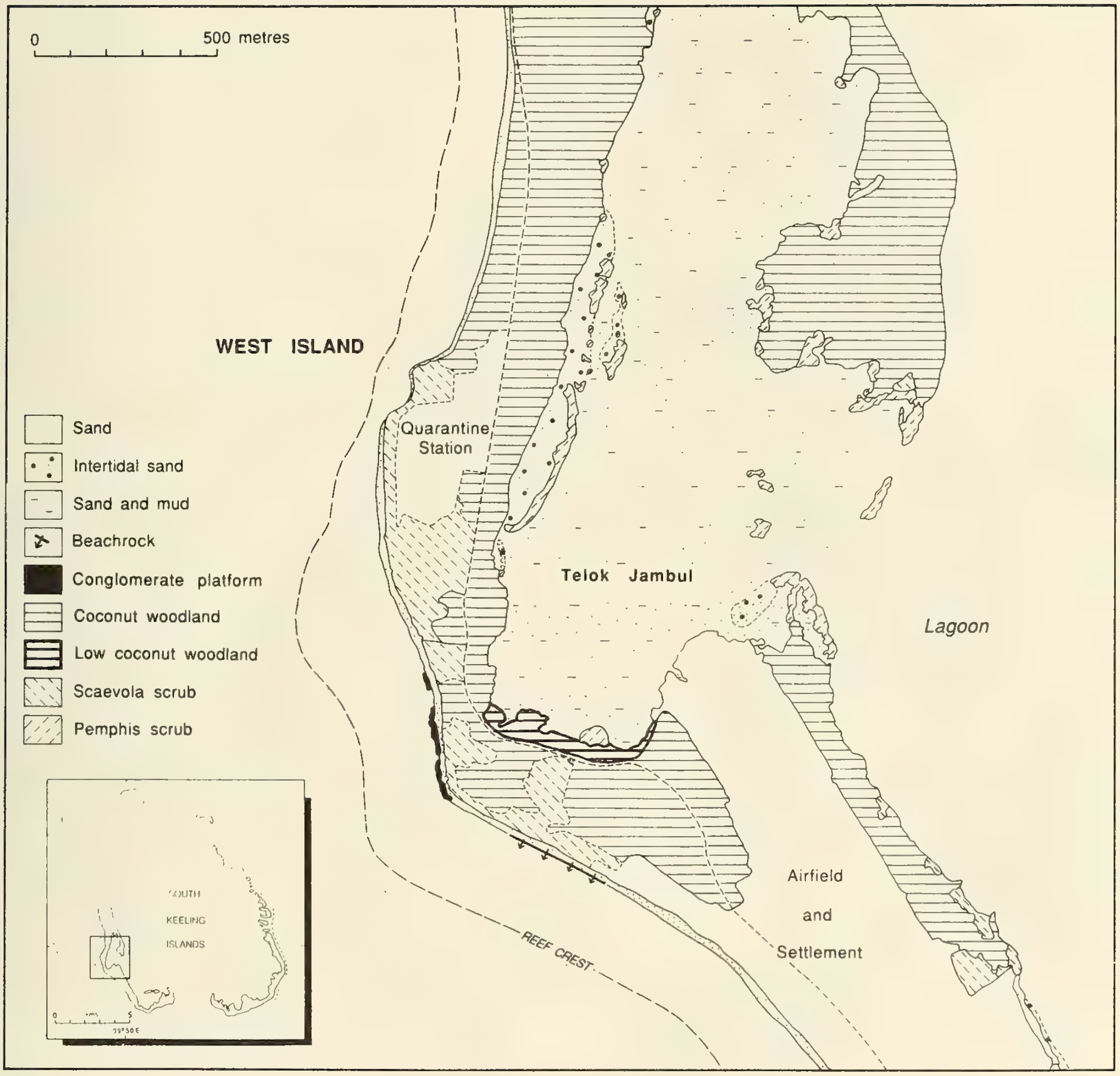

Figure 7. West Island, central section, mapped from 1987 aerial photography.

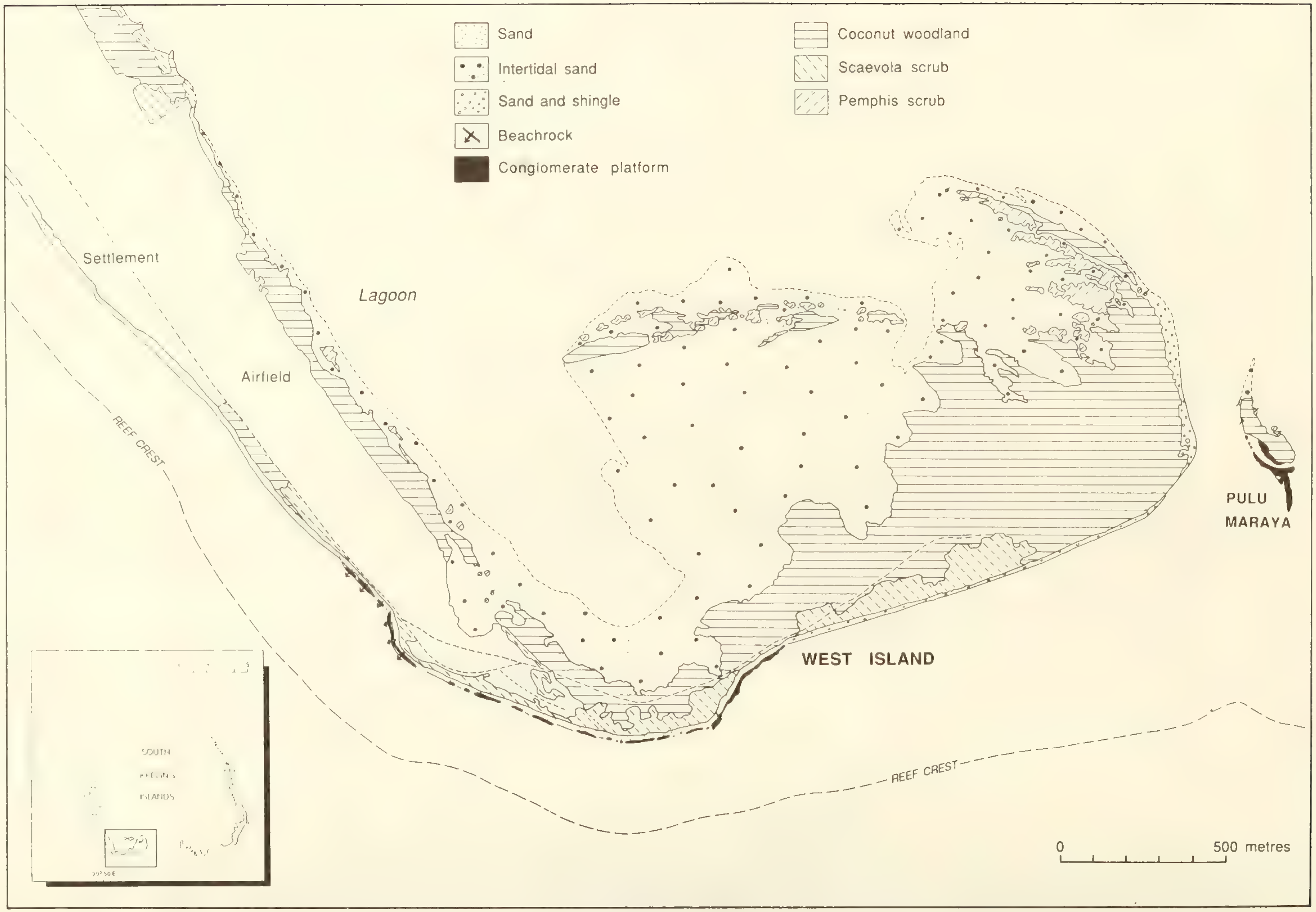

Figure 8. West Island, southern section, mapped from 1987 aerial photography.

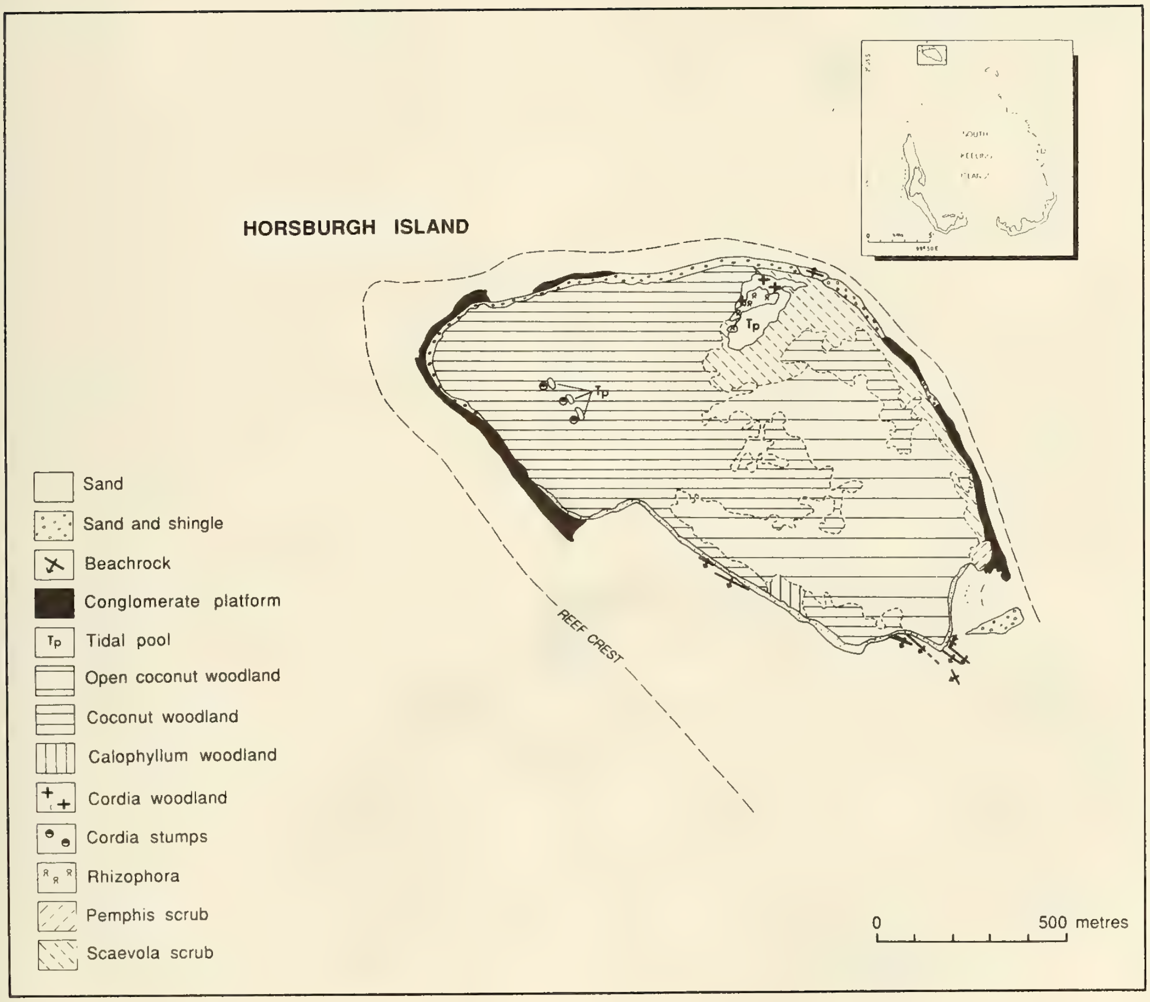

Figure 9. Horsburgh Island, mapped from 1987 aerial photography.

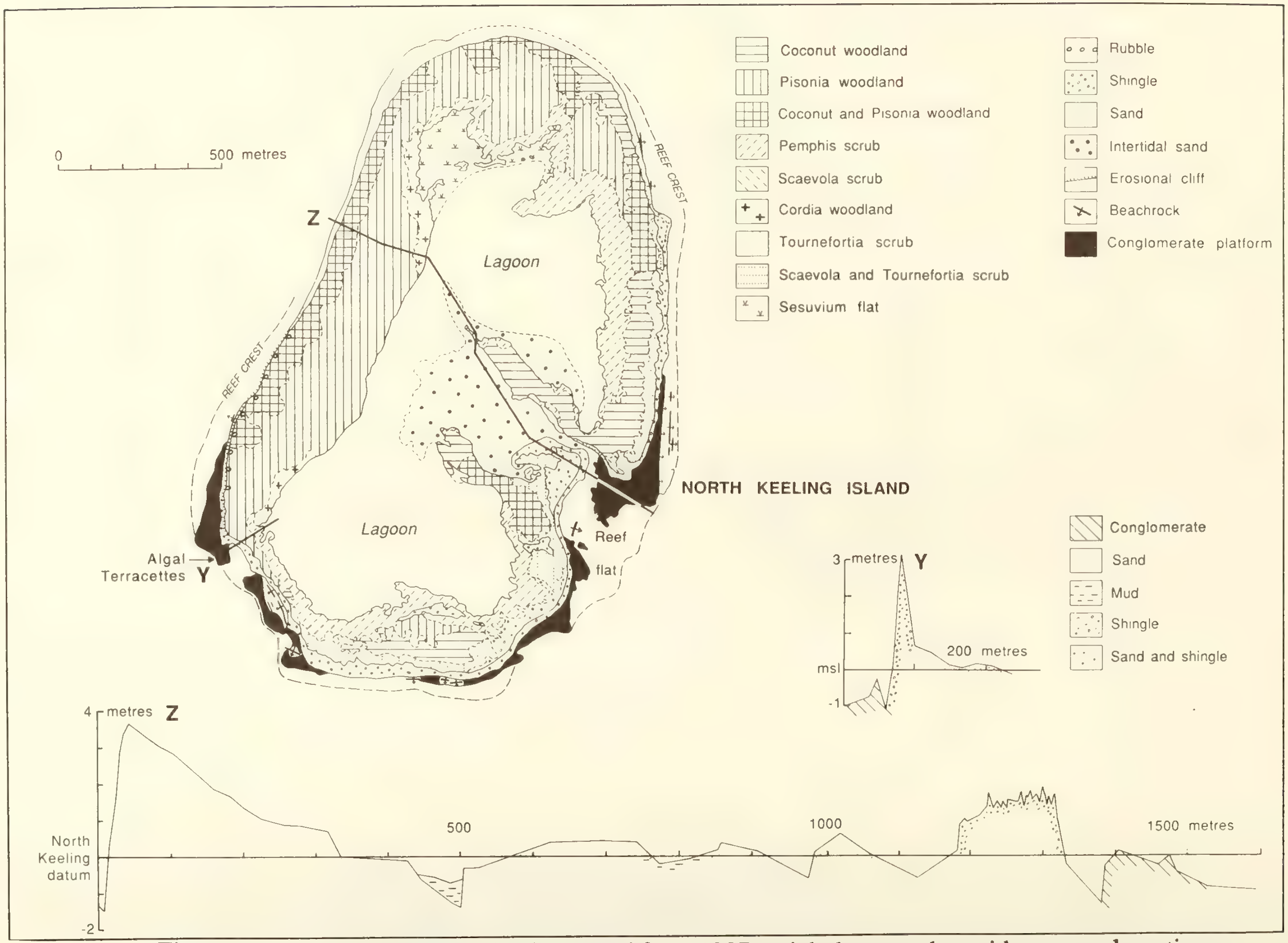

Figure 10. North Keeling Island, mapped from 1987 aerial photography, with surveyed sections.

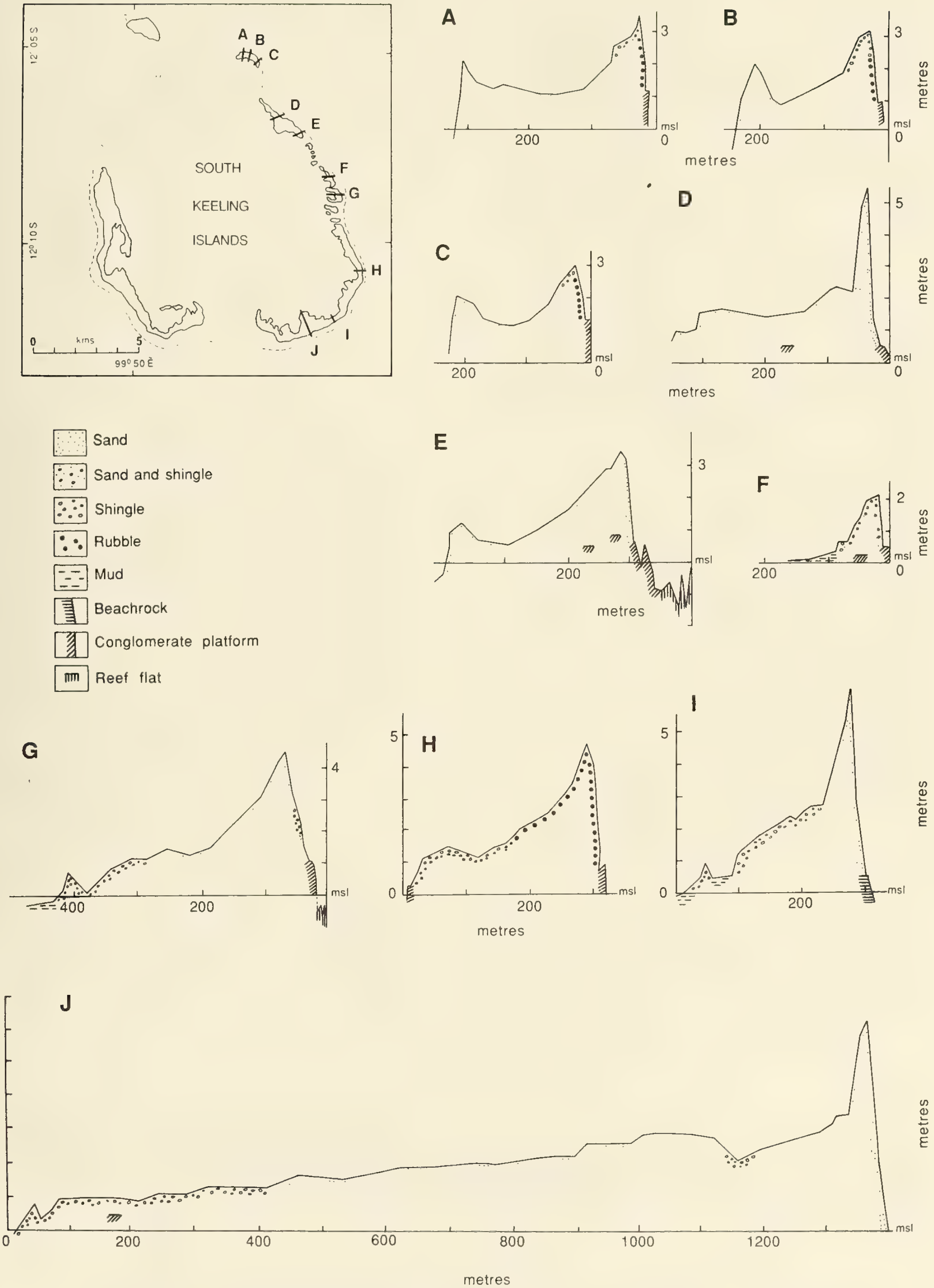

Figure 11. Surveyed sections across islands on the eastern atoll rim.

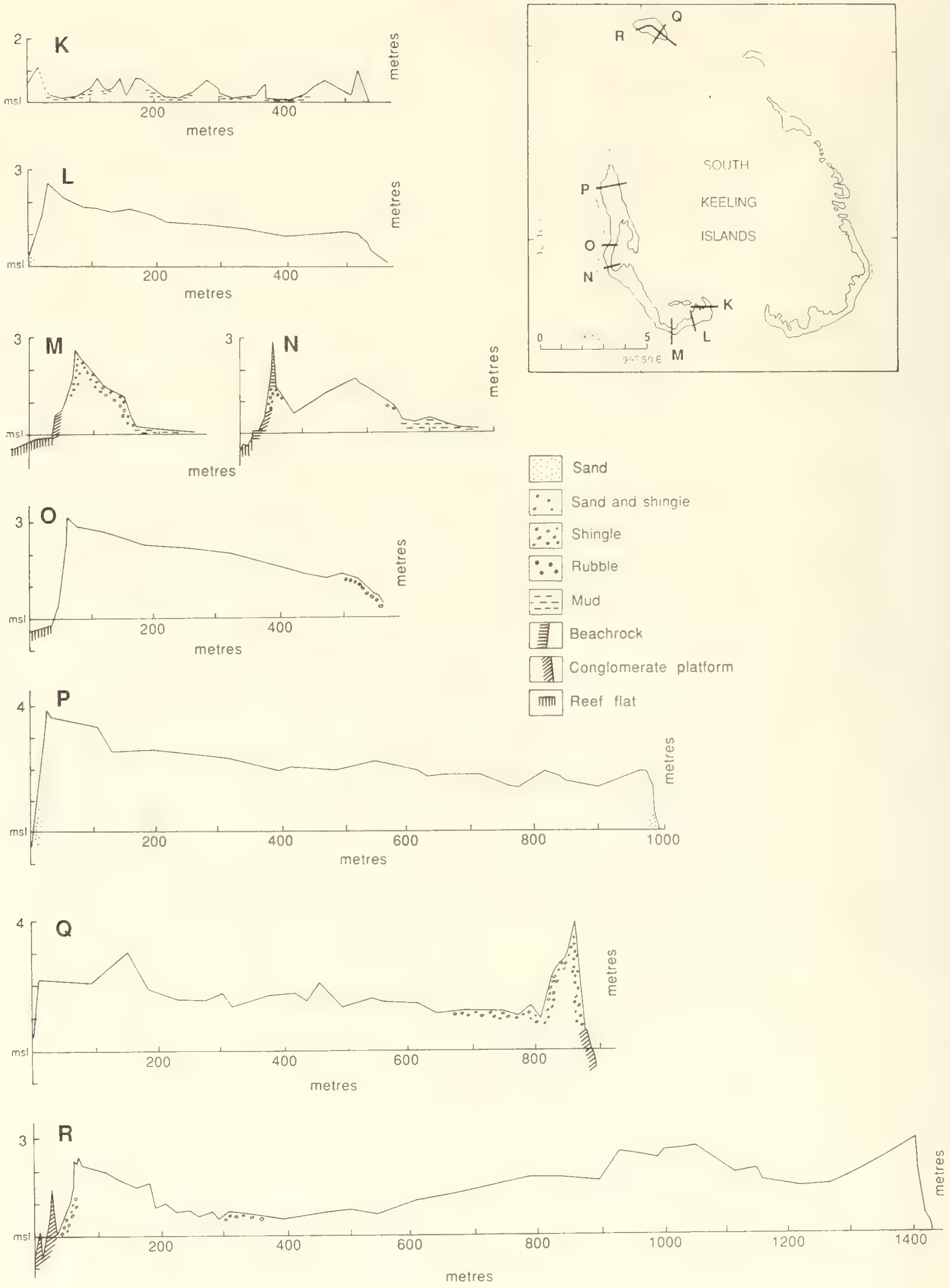

Figure 12. Surveyed sections across West and Horsburgh Islands.

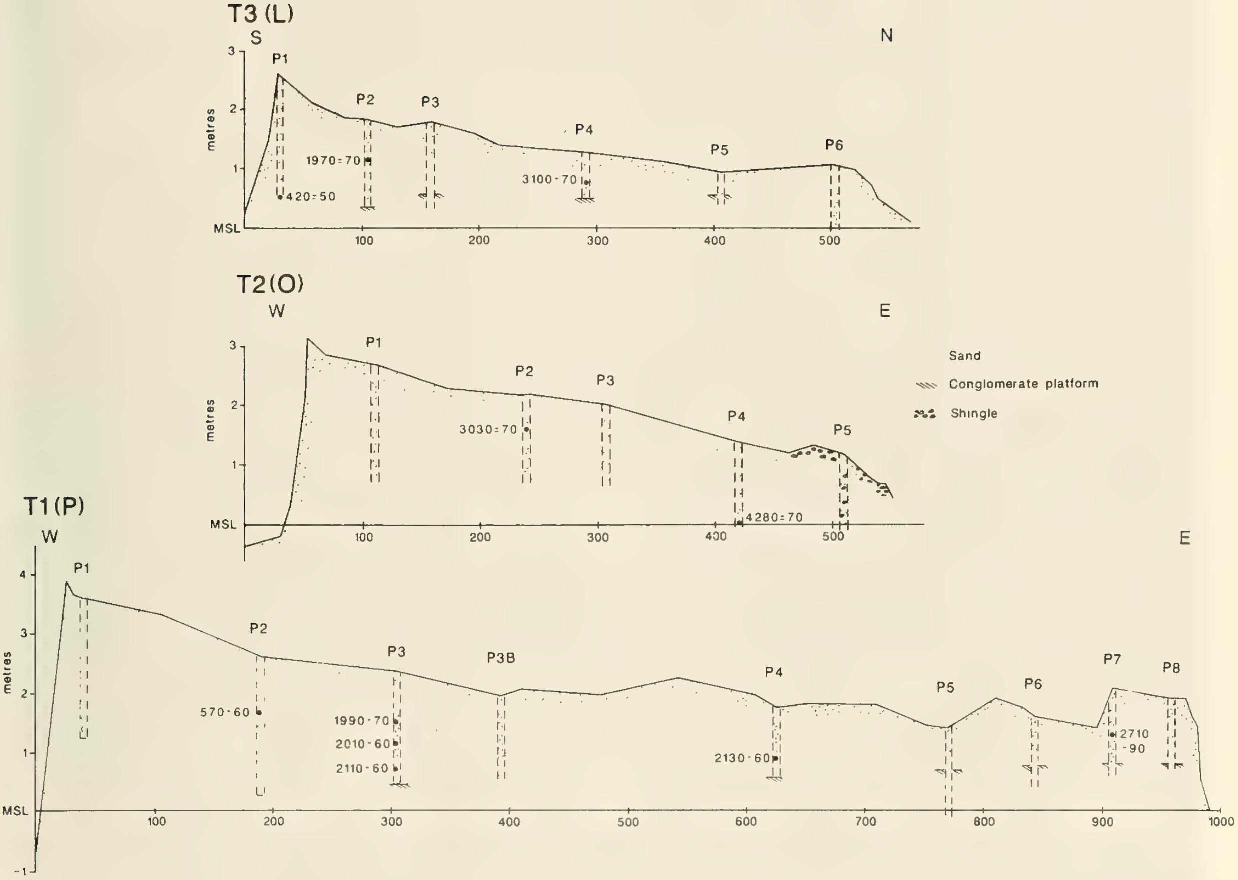

Figure 13. Cross-section and pits from three transects on West Island (see Fig. 12 for locations), showing radiocarbon dates (see Table 2).

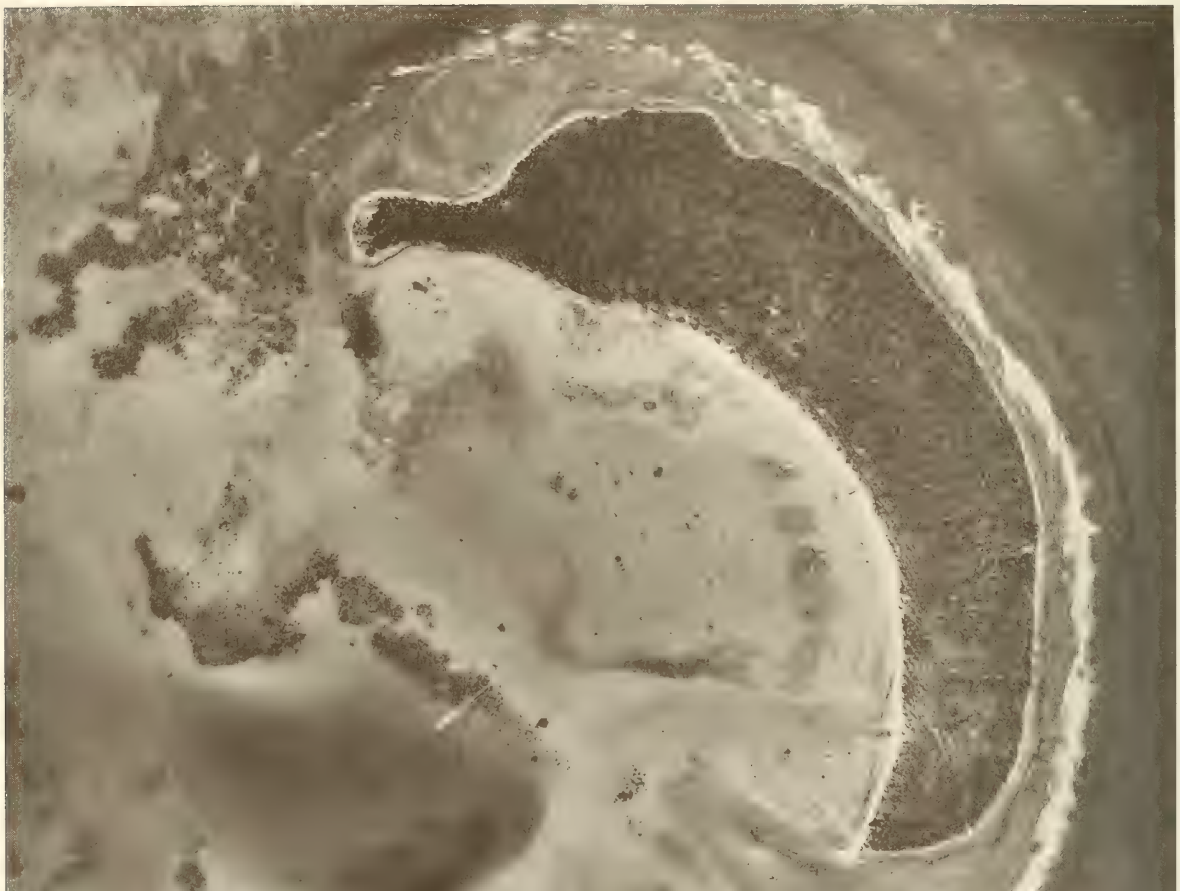

Figure 14. Aerial photograph of Direction Island, 1987 (reproduced by permission of the General Manager, Australian Surveying and Land Information Group, Department of Administrative Services, Canberra).

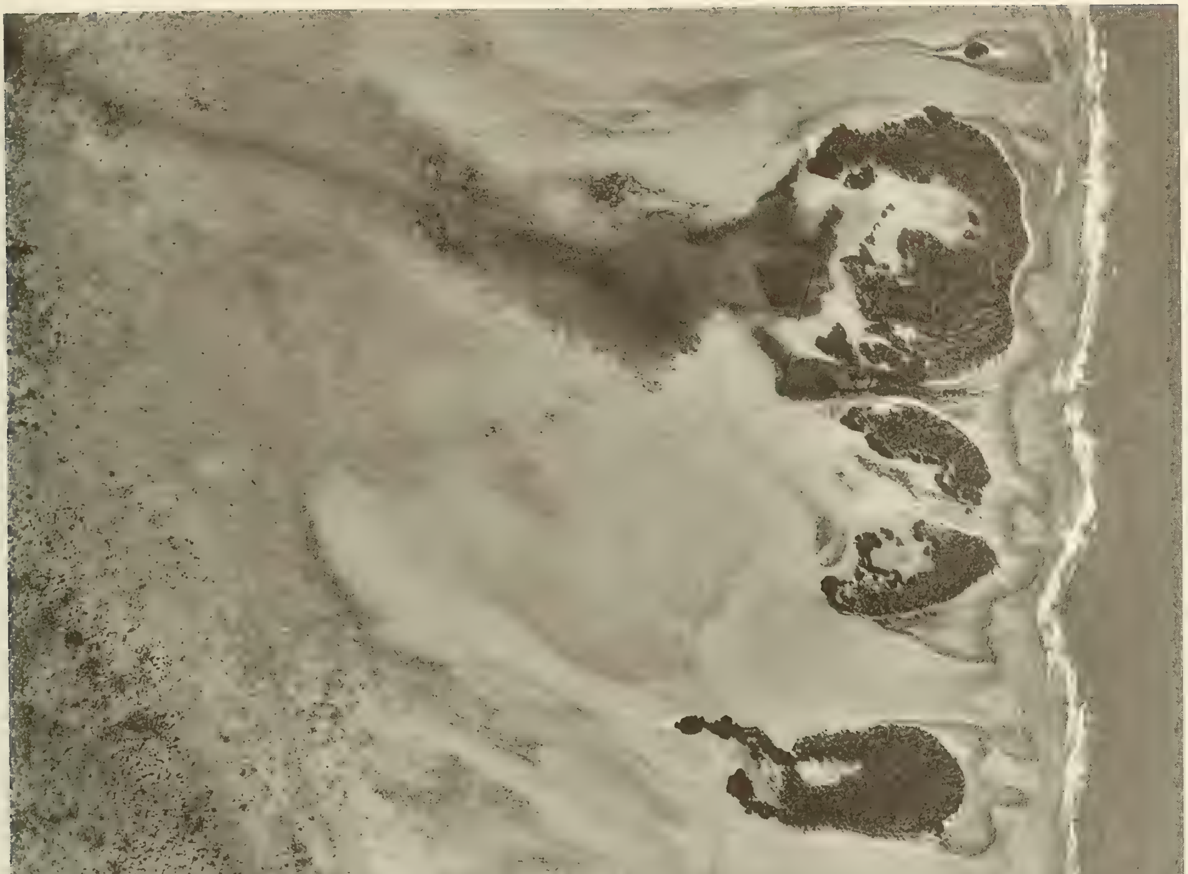

Figure 15. Aerial photograph of Pulu Ampang and neighbouring islands, 1987 (reproduced by permission of the General Manager, Australian Surveying and Land Information Group, Department of Administrative Services, Canberra).

Figure 16. Aerial photograph of Pulu Pandan and neighbouring islands, 1987 (reproduced by permission of the General Manager, Australian Surveying and Land Information Group, Department of Administrative Services, Canberra).

Figure 17. Aerial photograph of eastern end of West Island, 1987. Radiocarbon dates on coral shingle indicate the progressive buildout of the spits (reproduced by permission of the General Manager, Australian Surveying and Land Information Group, Department of Administrative Services, Canberra).

Figure 18. Aerial photograph of Horsburgh Island, 1987 (reproduced by permission of the General Manager, Australian Surveying and Land Information Group, Department of Administrative Services, Canberra).

Figure 19. a: Oceanward shore of Direction Island; rubble is from ruins of Cable Station, b: View looking North from Home Island. Conglomerate platform in middle distance is where Button Islets were, Prison Island is in the middle of the photograph and Direction Island in the distance, c: Conglomerate platform on Ampang Island, d: conglomerate platform on Pulu Pandan; it appears to consist of a shingle conglomerate layer overlying typical conglomerate platform, e: Conglomerate ramp, oceanward shore of South Island, f: Sandy and beach dune on the southern side of South Island.

Figure 20. a: Telok Jambu, West Island viewed from the north, b: Telok Kambing, West Island viewed from the west, c: Sheltered telok on South Island with stand of *Pemphis* on ridge at the mouth of lagoonlet, d: Ocean-dipping bedding revealed in trench on Home Island, e: Rubble-strewn shoreline on Pulu Wak Banka, f: Arcuate ridges, southern North Keeling; these appear to have been termed former reef margins by Guppy, but are reinterpreted as beach conglomerate marking foot of former rubble-strewn beaches.

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CHAPTER 6

VEGETATION AND FLORA OF THE COCOS (KEELING) ISLANDS

BY

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CHAPTER 6

VEGETATION AND FLORA OF THE COCOS (KEELING) ISLANDS

BY

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ABSTRACT

The vegetation and plant species occurring on the 22 vegetated Cocos (Keeling) islands have been classified numerically based on sample plots for the large islands as well as from checklists developed for each island from extensive reconnaissance. The vascular flora of about 130 species comprises approximately 50% native species, but there are no endemic species described. Most of the 69 introduced species are to be found on the larger settled islands and only one of these species has spread to the smaller islands. The relationship between island area and indigenous species richness shows a close fit to a power relationship. The more remote island of North Keeling has a distinct species composition compared to similar-sized islands of the main atoll.

The pre-settlement vegetation has been extensively modified for coconut plantations, except for certain parts of North Keeling, where tall *Pisonia grandis* - *Cocos nucifera* forest occurs with small amounts of *Cordia subcordata* and other species. These forests are fringed on the lagoon shore by *Pemphis acidula* tall shrubland and on the exposed ocean shores by *Argusia argentea* shrubland. Each of these communities support breeding colonies of seabirds. On the main atoll, remnant vegetation occurs most commonly along the strand and in some places appears to be relatively recent. Many species on the Cocos (Keeling) atolls are restricted in their distribution there. In some cases these represent relict distributions, whilst a few could be considered to be pioneer populations.

INTRODUCTION

The Australian external Territory of the Cocos (Keeling) Islands is situated in the north-eastern Indian ocean at 12^{O}S, 96^{O}E, is 2400 km north-west of North West Cape on the Australian mainland and 960 km south-west from Java. The Territory consists of two coral atolls about 25 km apart with a maximum ground elevation of 9 m above mean sea level. The smaller, northern atoll, is known locally and historically as Keeling Island and was inhabited intermittently and on a seasonal basis between *ca.* 1830 and 1929 (Gibson-Hill 1948). The main atoll, which continues to be known by various names and is here referred to as the Cocos atoll, consists of 21 vegetated islands, some of which have been

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inhabited since 1827 and all of which have been extensively cleared for coconut plantations. Keeling Island (North Keeling), on the other hand, has retained more natural vegetation and is still a major seabird rookery for at least six species (Stokes *et al.* 1984).

As the only atolls in the eastern Indian Ocean, and being relatively recently settled, these islands are of considerable scientific interest, but their isolation has prevented intensive scientific study. A series of naturalists have visited, the most notable being Charles Darwin for 11 days in 1836 (Darwin 1845); H.O. Forbes for 22 days in 1879 (Forbes 1879, 1885); H.B. Guppy for 5 months in 1888 (Guppy 1889); F. Wood-Jones for a year in 1905 (Wood-Jones 1912); and C.A. Gibson-Hill for 11 months in 1941 (Gibson-Hill 1950). Gibson-Hill (1948) presented the only systematic account of the vegetation in the form of a description of dominants and a sketch map of the plant communities of Keeling Island. Major plant collections have been made by C. Darwin (Henslow 1838), H.O. Forbes, F. Wood-Jones (1912), H.B Guppy (1889), I. Telford (1985) and the author in 1986-7.

The Cocos (Keeling) Islands lie on an isolated spur of the submarine Ninety-East Ridge and are formed on a volcanic base rising from a depth of 5,000 m, with an unknown thickness of coral over the base (Jongsma 1976). Large solution and/or collapse dolines up to 20 m deep cover the south-eastern bed of the Cocos lagoon and possibly indicate a considerable depth of underlying limestone. Most of the islands are developed from coral sand, shingle and rubble deposits over a breccia platform that is just above mean sea level (Woodroffe *et al.* 1990) and beach rock commonly outcrops on the more exposed sandy shores.

The highest elevations occur on the south and east ocean shores where sand and shingle deposits rise briefly to a maximum of 9 m forming a single elongate coastal dune best developed along the entire length of Pulu Atas as a sand dune and on North Keeling as a shingle ridge. Apart from these dunes, most of the islands are less than 3 m above sea level. The most leeward island of the Cocos atoll (Pulu Luar) displays a more complex geomorphology, being a mature moat island (Stoddart & Steers 1977) with a small saltwater lagoon. Jacobson (1976) studied the freshwater lens on Pulu Selma (Home Island) and concluded that the minimum width of island to sustain an exploitable Ghyben-Herzberg lens was 400 m. However during the present study in April and May 1986, fresh water was observed in wells on islands down to 100 m width (see Falkland 1988). The only naturally occurring surface freshwater is at the seasonal swamp known as Bechet Besar on the north-east shore of Pulu Panjang (West Island). On Pulu Luar (Horsburgh Island) there is a seasonal groundwater swamp identified by a ground layer of *Mariscus javanicus*.

Meteorological records for various periods and locations on the Cocos atoll are available as a composite record from 1902, at least for rainfall. The annual average rainfall for the period 1902-1982 was 1994 mm with a range from 1099 mm to 3288 mm and a median of 1969 mm. Mean monthly rainfall varies from 81 mm in October to 256 mm in April, with the dry season extending from September to December. Temperatures and humidities vary little throughout the year with an absolute annual temperature range from 21°C to 31°C. The wind régime is one of predominantly south-east trades for over 300 days per annum. Wind direction frequency analysis show south-easterly winds dominating from December to March whilst for the rest of the year there is a strong easterly component as well. Cyclone frequency within a five degree cell is about 0.25 in the region. Cyclones have passed near enough to the main atoll to cause damage in 1862, 1876, 1893, 1902, 1909, 1944, 1968, 1973 and 1988.

The purpose of the present survey was to establish the present composition of the flora on an island basis and to analyze the floristic and vegetation patterns of the entire Territory. The delineation of communities, relict stands and rare species distributions will serve as a basis for land use planning, the establishment of conservation priorities and the development of management aims.

METHODS

Circular sample plots of radius 10 m were located on the six largest islands (Keeling, Luar, Tikus, Selma, Atas, Panjang) along transects selected to maximize the detection of vegetation and floristic change along environmental gradients (Gillison & Brewer 1986). The major environmental gradients considered in the layout of the transects were:-

- ocean strand to lagoon strand;
- potential for a freshwater lens; and
- ocean coastline aspect.

Transects were oriented at right angles to the ocean coastline (Fig. 2) and sample plots were positioned on both strandlines (ocean/reef and lagoon) and at 60 m intervals along the transect; unless there was a change in the height or composition of the top stratum, in which case additional plots were selected. In each plot, plant species present were recorded, as well as litter depth, soil surface texture and canopy height and dominants.

All vegetated islands were surveyed (Pulu Pasir supports only occasional sprouting coconuts and was not included). For consistency, the Cocos-Malay names for the islands have been used throughout. Several islands have two Malay names apparently related to their origin from separate islands. In this report, Pulu Selma includes Pulu Gangsa (joined by human intervention) and Pulu Cepelok includes Pulu Wak-Banka, apparently joined by storm deposits before settlement in 1825. During the course of systematic collecting on the islands, the presence of each species on each island was recorded as well as an overall estimate of the species abundance on the island. A six-point ordinal abundance scale from very rare (less than 10 plants sighted) through rare, occasional, frequent, common to abundant was used. A complete set of voucher specimens is deposited at the Australian National Botanic Gardens (CBG) and nomenclature follows the *Flora of Australia* (1993).

The floristic and quantitative data were primarily analyzed using the Pattern Analysis Package (PATN, Belbin 1992) at the C.S.I.R.O. Division of Water and Land Resources. The dissimilarity coefficient used for sites was the Bray-Curtis measure or the Kulczynski coefficient and the two-step procedure (Austin & Belbin 1981) was used for the between-species dissimilarity. Cluster analysis was hierarchical agglomeration using UPGMA fusion with ß set to -0.1 to minimize space distortion (Belbin 1992).

Vegetation patterns were also derived from panchromatic aerial photographs taken in 1976 at a scale of 1:44,400 (R.A.A.F. Film No. 8737) and 1987 colour photography at 1:10,000 (A.S.O. Film SOC760). Interpretation was done using a Zeiss Interpretoscope and transferred to a base map using a Zoom Transfer Scope. Island areas were measured off the R.A.S.C. Series R811 Cocos Island Sheet Special (1:25,000).

RESULTS

THE FLORA

Exclusive of plants found only in cultivation the total vascular species count for these islands is 130 (Appendix 1). Given the variation in sampling intensity by past collectors (Table 1), it is difficult to be certain which species are introduced, except by examination of their biology, biogeography and present-day distribution as well as the historical record. Species found only in heavily disturbed areas and often on one or two large islands only, have usually been regarded as introduced in this analysis, and these account for about 50% of the flora (Table 2). Most of these species are pantropical herbs (Table 2) found on Pulu Panjang and many were probably introduced since the airfield was built on Pulu Panjang in 1944.

The vast majority of the native species are Indo-Pacific strand plants that are predominantly sea-dispersed. There are no endemic species described at this stage, save for the variety *cocosensis* of *Pandanus tectorius* (Appendix 1). Of the 19 vascular species collected by Darwin (Henslow 1838) all but one have been recorded by recent collectors. Most are still common except for *Cordia subcordata, Achryanthes aspera, Neisosperma oppositifolia* and *Laportea aestuans* (Appendix 2).

ISLAND FLORISTICS

INDIGENOUS SPECIES

The relationship between island area and indigenous species richness (Fig. 2) shows a closer fit to a power relationship ($r^2 = 0.87$) than a logarithmic one. When exotic species are included, the power relation is still a good fit ($r^2 = 0.82$), as the larger islands are also the most disturbed and colonized by exotic species.

Cluster analysis for the 22 islands (i.e. including Keeling) based on the species abundance scores shows a clear grouping of islands by size, with Keeling being the most distinct floristically (Table 3, species groups A & E). The strand species form a distinct group (Table 3, species group D) well represented on all but the two smallest islands, Beras and Ampang Kecil, which have areas less than 0.5 ha and support only three of the six common strand species. This strand group comprises *Argusia argentea, Pemphis acidula, Guettarda speciosa, Cocos nucifera, Scaevola taccada* and *Ipomoea macrantha*, all of which have marine dispersal powers.

Some species were found almost exclusively on islands larger than 20 ha, and most of this group were more abundant on Keeling (Table 3, group A). These included the trees *Cordia subcordata, Hernandia nymphaeifolia* and *Pisonia grandis* as well as *Achryanthes aspera, Dicliptera ciliata, Portulaca oleracea, Boerhavia repens, Stenotaphrum micranthum, Lepturus repens* and *Sesuvium portulacustrum.*

Species group B (Table 3) represents those species common on the larger Cocos islands but absent or less abundant on Keeling. Of those species which do occur on Keeling, most are rare there, often recorded from one or two locations only. Species group C consists of three species each found at just a single site on Pulu Panjang. These are *Lepturopetium* sp., *Ximenia americana* and *Enicostema axillare* (Appendix 2).

EXOTIC SPECIES

Only one exotic species, *Turnera ulmifolia*, has spread to all the islands of the Cocos atoll, and it is usually abundant wherever it has established (Table 4). The large but relatively unsettled Pulu Atas has been colonized by six exotic species and five have reached Keeling. Most exotic species are confined to the four large islands that have had or still have intensive settlement. Thirty two of the 63 exotic species occur only on Pulu Panjang and/or Pulu Selma (Table 4, groups C & D, part of A) and nineteen occur on Pulu Panjang only (group C). At the other end of the size scale, the four islands without exotic species (Beras, Blan, Blekok, Jambatan) are all less than 2.5 ha.

VEGETATION PATTERN ON KEELING

Analyses of the transect plot data for Keeling were done with the total set of 26 species recorded in 65 plots along 11 transects. Another 10 species were recorded for North Keeling in reconnaissance. The floristic classification analysis does not exactly correspond with the dominance-based units able to be mapped from aerial photography and ground checking.

Stands of *Pemphis acidula* tall shrubland (2-4 m) and *Cordia subcordata* tall shrubland (3-6 m) occur close to the lagoon shore and are commonly mono-specific (Table 5, site groups 1, 2 & 3), and, where there are finer sediments accumulated, a *Sesuvium portulacustrum* herbland is developed (Table 5, group 1), often lying between or within the two former types (Fig. 3). Site group 4 (Table 5) is characterised by exposed shore halophytes, such as *Portulaca oleracea*, *Lepturus repens* and *Boerhavia repens*, *Cocos* is absent.

Site groups 5 to 8 highlighted floristic sub-units within the closed forest stands characteristically dominated by *Pisonia grandis* and/or *Cocos nucifera* (Table 5, Fig. 3). Group 5 contains the beach halophytes (species group A), group 6 has an understorey of forest mesophytes (species group C), group 7 are stands of pure *Cocos* and *Pisonia*, while group 8 are virtually pure *Pisonia*.

Group 5 mainly represents relatively richer plots (s = 6.7) found within 20 m of the shore which have strand forest dominated by *Cocos* along with halophytic shrubs and herbs which typically occur only near the shoreline. *Pisonia grandis* and *Stenotaphrum micranthum* are constants and the former may be co-dominant on sheltered shores. Some plots in this class fall within areas which are mappable as *Pisonia* shrubland occurring on exposed shores usually behind a beach-fringing *Argusia* shrubland.

Site group 6 (Table 5) corresponds with relatively species-poor areas of forest (mean richness of 3.9) dominated by *Cocos nucifera* and/or *Pisonia grandis*. The associated species include broad-leaved plants such as the climber *Canavalia cathartica*, *Morinda citrifolia*, *Rivina humilis* and *Carica papaya*. Sites in groups 9 & 10 contain species which are uncommon on North Keeling (species groups A & D).

Many species on Keeling have a restricted distribution and most of these are found on the northern peninsula at the entrance to the lagoon or on the north-west lagoon shore and adjacent habitats. The same pattern is evident for the species recorded in transect plots. The richest floristic units, apart from the herblands, are the forest types found near the lagoon entrance and on the northwest side of the island.

VEGETATION CHANGE

A comparison of Fig. 3 with the vegetation map of Keeling Island produced by Gibson-Hill in 1941 (Gibson-Hill 1948) shows geomorphic and vegetational changes evident over the intervening 45 years.

The west-building peninsulas at the lagoon entrances have extended considerably into the lagoon. On the northern peninsula the *Argusia* shrubland mapped by Gibson-Hill is possibly the small area in a similar position mapped in 1986, since it is on a rocky substrate which may have conferred a degree of site stability. The southern arm has a similar clump of *Argusia* that has apparently extended and been flanked by *Cocos* and *Pemphis.* Observations on sand and shingle bars in the lagoon entrance channels show that *Argusia* is the first woody plant to colonize such places in exposed locations and *Pemphis* does the same on more sheltered shores. Both peninsulas show a definite sequence of changing dominance along their strands from *Argusia*, *Pemphis* and *Cocos* on the younger shores to *Cordia* and *Pisonia* on the older ones, reinforcing the interpretation of rapid development of these peninsulas. Being more sheltered, the southern peninsula has developed an area of *Pisonia* forest on its southern end, perhaps largely since 1941.

Another change in the vegetation since 1941 is the loss of the *Argusia* zone along the southwest coastline and possibly on the southeast also. Both locations have 4-5 m high shingle ridges with their seaward faces lying at the repose angle, and show evidence of episodic deposition of shingle into the *Pisonia* zone suggesting storms have removed the *Argusia.*

Gibson-Hill (1948) mapped an area of open grassland on the south-eastern lagoon shoreline which he said was a breeding habitat for shearwaters (*Puffinus* sp.). These birds have not been seen on the island for some years (Stokes *et al.* 1984) and this grassland has now become in parts an open shrubland colonized by *Pemphis*, *Pisonia* and *Argusia* to 3 m high.

VEGETATION OF THE COCOS ATOLL

Cluster analysis of the 106 sample plots on the larger islands (containing 52 species, native and introduced), produced at the ten-group level five major site groups and five further groups represented by a few sites each (Table 6). Floristic definitions of the major site groups emphasise variation in the coconut woodlands and forests in relation to ground layer composition and location relative to the ocean and lagoon. On the most exposed southern and eastern strands of Pulu Atas there are areas of *Argusia - Scaevola* shrubland and patches of *Lepturus - Triumfetta* herbland on the sand and shingle ridge topping the beach.

The minor site groups reflect distinctive relict communities, mainly on Pulu Panjang and Pulu Luar, where strand trees have survived land clearing or colonized recent deposits. Species such as *Calophyllum inophyllum*, *Guettarda speciosa*, *Hibiscus tiliaceus* and *Barringtonia asiatica* characterize these sites and their distribution over the Cocos atoll is very restricted (Fig. 1, Appendix 2). These species occur scattered along the lagoon shores and on the sheltered west shore of Pulu Panjang, mostly as single trees or small clumps. The largest remaining stands of these species are to be found on Pulu Panjang along the northwest shore and adjacent to the swamp at Bechet Besar; along the lagoon shore opposite the northern end of the runway; and on the southern lagoon shore of Pulu Luar (Fig. 1).

Pemphis acidula shrubland forms 2-4 m high shrublands scattered all along the lagoon shore, particularly in areas where sand deposition is occurring (e.g. at Tanjong Klikil at the east end of Pulu Panjang) and also at the lagoonward edge of intertidal sandflats. No other species of plants grow in these offshore strands except for an occasional coconut seedling and epiphytic mosses and lichens.

DISCUSSION

FLORA

Island floras originate from a variety of sources depending on their geographic location and suitability of their habitats for immigrant diaspores. The origins of the Cocos (Keeling) biota have long fascinated biologists, particularly those who have examined their plants and insects (see Guppy 1890, Holloway 1982).

Renvoize (1979) suggested that island structure in terms of elevation and geological substrate are key factors in determining the richness of island floras. In this respect, the Cocos (Keeling) islands bear the greatest similarity to the central Indian Ocean islands (Laccadive, Maldive, Chagos) and to only some of the western Indian Ocean group (Cargados Carajos, Tromelin, Agalega, Amirante group, Alphonse, Gloriosa, Europa and Farquhar group). All these low islands have evolved in isolation from a continent, through the combined forces of vulcanism, subsidence and coral growth, and presently rise less than 10 m above sea level.

The low habitat diversity of these islands leads to a flora characterized by very low endemicity with indigenous taxa of pantropical or Indo-Pacific distribution dominating (Renvoize 1979). Cocos (Keeling) is no exception to this general pattern; it has no endemic flora save for the variety *cocosensis* of *Pandanus tectorius*, and with 61 indigenous species (Table 2), is comparable with the Laccadives (40 indigenous species), the Addu atoll in the Maldives (52 species) and the Chagos group (*ca.* 100 species) (Renvoize 1979). It is also similar in species richness to western Pacific atolls such as Nui (44 species) and Kapingamarangi (50 species) (Woodroffe 1986).

The mechanisms of natural dispersal to oceanic islands include wind, ocean currents, birds and bats. Undoubtedly all of these have contributed to the Cocos flora, (even bats have been occasionally sighted, Marlow 1970), but the only agent for which evidence is certain is that of oceanic drift. Most of the strand species are found as seeds on beaches and there is a further component of the flora that is found only on the drift line (Guppy 1890). The main currents around Cocos (Keeling) are westward and would be expected to derive propagules from northern Australia, Torres Strait and Java. These currents are reinforced for most of the year by the prevailing southeast trade winds.

ISLAND RICHNESS AND COMPOSITION

The power relationship established between indigenous species richness and island area (Fig. 2) is similar to that reported for Nui atoll in the Pacific (Woodroffe 1986) and for the lagoonal islands of Aldabra (Hnatiuk 1979). None of these three species-area relationships support the notion of the small-island effect suggested for Kapingamarangi (Niering 1956, 1963), where very small islands tended to have area-independent species richness.

The six commonest strand species are not always present on the smaller islands and show an increase in frequency of occurrence up to an island size of 10 ha, and are always present above this area (Table 3). If one sets aside these species, i.e. *Argusia argentea*, *Pemphis acidula*, *Guettarda speciosa*, *Cocos nucifera*, *Scaevola taccada* and *Ipomoea macrantha*, then the similarities between the smaller islands are very low. Among the 20 other species, there are only 41 occurrences on the 16 islands smaller than 25 ha. The presence of these species was often correlated with minor and possibly ephemeral habitats; e.g. *Hibiscus tiliaceus* on a small sheltered lagoon-facing shore of Pulu Jambatan where a channel had cut across the prograding western (lagoon) side of the island; *Suriana* on recently formed sandy spits extending lagoonwards on Pulu Siput; and *Mariscus javanicus*, *Fimbristylis cymosa* and *Lepturus repens* where lagoon shorelines distant from inter-island channels had relatively flat shingle embayments at upper tide levels. These observations support the idea that habitat diversity needs to be considered in modelling species richness on islands (Buckley 1982).

Dispersal routes may also contribute to differences between the smaller islands, especially where islands are more likely to receive a high density of propagules. For example, Pulu Labu probably intercepts a higher number of propagules because of its position at the tip of Pulu Atas, where the equatorial current flows northward along Pulu Atas then some sweeps into the lagoon. An exceptionally high abundance of drift seeds was found to occur on the sand dunes at the northern tip of Pulu Atas and in a similar situation on the ocean beach of Pulu Gangsa. This may help to explain the occurrence of *Calophyllum*, *Barringtonia* and *Neisosperma* on the former island and on no other small islands, save for a single *Calophyllum* on Pulu Beras. The latter is also an island which is well situated to receive propagules concentrated by northward transport along the ocean shores of Pulu Selma. However these data are insufficient to suggest such islands have more species for their area, and there are presumably other factors operating, such as stability and age of an island.

Amongst the six larger islands, Pulu Atas has a relatively low richness for its area, possibly related to its more uniform geomorphic structure, rugged ocean coastline and lack of currents flowing along its lagoon shores (although they would have done so in times past before channels closed off).

North Keeling has seven species not found on the main atoll but is also different in composition from the other large islands. Some species (Table 3, group A) are relatively more abundant there, either because of greater areas of suitable habitat on Keeling (e.g. for *Boerhavia repens* and *Portulaca oleracea* in exposed herblands; *Sesuvium portulacustrum* in saltmarshes; *Stenotaphrum micranthum*, *Achryanthes aspera*, *Dicliptera ciliata* in the *Pisonia grandis* rainforest); or due to clearing over the last 160 years (e.g. *Cordia subcordata*, *Hernandia nymphaeifolia* and *Pisonia grandis*). Species group E (Table 3) found only on Keeling may represent in large part the extreme effects of vegetation clearance on the southern atoll. The restricted distribution of *Thespesia populnea* (in a clump of six individuals on Pulu Tikus and in a small mixed stand with *Cordia* on Pulu Luar), probably also represents a relict distribution resulting from extensive cutting in the past, as the bark fibres were once used for netting (Gibson-Hill 1947).

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Table 1. Sampling intensity and the number of native and naturalized (not horticultural) vascular plant species recorded by major collectors and naturalists on the Cocos (Keeling) Islands.

Collector	Year	Period of visit	Islands visited	Number of species
C.R. Darwin	1836	10 days	Cocos atoll	21
H.O. Forbes	1879	22 days	Cocos atoll	38
W.E. Birch	1885	8 days	Cocos atoll	11
H.B. Guppy	1888	10 weeks	Both atolls	53
F. Wood-Jones	1909	15 months	Cocos atoll	46
I.R. Telford	1985	2 weeks	Panjang, Tikus, Atas, Selma, Keeling	93
D.G. Williams	1986/7	9 months	All, including Keeling	130

Table 2. Life forms of the native and naturalized flora.

Origin	Climber	Forb	Graminoid	Seagrass	Shrub	Tree	Total
Native	7	13	11	3	9	18	61
Naturalized	3	29	21	0	10	6	69

Table 3. Two-way classification for **native** species occurring on all islands. Classification based on abundance data standardised by species maximum. The first four letters of the generic name and specific epithet are read vertically. Numerical values represent the abundance scores standardised by species maximum.

```
Island                              Species groups
groups

                 <----A-----> <-----------B-----------> <C> <--D-->       <-E-->

                 |ABPHDSASACPL|CDCCCPTZITEHTCMMMFPSCPVTR|ELX|AIPCSG|V|BN|Q|CEPACL|
                 |COOEIECTCOIE|AORAYHHOPEUIRAEAOIRULAIHH|NEI|RPEOCU|I|AE|U|ARALLA|
                 |AERRCSHEARSP|EDILPYUYORPBISLRRMERENTEI|IPM|GOMCAE|G|RI|E|NYSLEP|
                 |LRTNLURNLDOT|SONOELASMMHIUSAIIBMIRDESZ|CTE|UMPOET|N|RS|E|ATPOOO|
                 |            |                         |   |      | |  | |      |
                 |LRONCPAMISGR|BVAISAIMPCATPFBJCCSMITTPA|AMA|AMANTS|M|AO|H|CVVCGA|
                 |AELYIOSINURE|OISNTMNAEATIRIIAIYEANEROP|XAM|RACUAP|A|SP|Y|AAAOYE|
                 |NPEMLRPCDBAP|NSIOOAVTSTOLOLFVTMRRECIPI|IRE|GCICCE|R|IP|A|TRGBNS|
                 |CERPITERICNE|DCAPLRORCATICILARORIRTFUC|LSR|ERDICC|I|AO|L|HIIBAT|

Keeling          |166666666666|1.......11.....14.3.1....|...|456611|.|..|.|666666|

Luar             |.43.111..311|6626641646163655563....66|...|452662|.|..|.|......|
Panjang          |.1361..1.223|11151166666645455634.1...|666|466664|.|1.|.|......|
Selma            |.11....361..|14451444446634223654666..|...|441662|1|..|.|......|
Atas             |.646.......3|...4.1414..665545.41.....|...|646662|.|.1|.|......|

Tikus            |6.3......3..|1162664146...21666..3..1.|...|122661|.|..|6|......|

Cepelok          |.3........11|.........1....5251.......|...|456665|4|..|.|......|
Pandan           |.........1.3|...............444.......|...|666666|.|..|.|......|

Ampang           |............|..............6...3......|...|456665|6|..|.|......|
Kembang          |............|........1...154...6......|...|415665|.|..|.|......|

Wak-Idas         |............|.............4...3.......|...|356665|.|..|.|......|
Blekok           |............|...............2.........|...|346562|.|..|.|......|
Blan             |...........1|.........................|...|156615|.|..|.|......|
Kambing          |...........1|.........................|...|3456.4|.|..|.|......|
Kelapa Satu      |............|..................1......|...|.5.665|.|..|.|......|
Blan Madar       |............|................1........|...|36.664|.|..|.|......|
Maraya           |.........11.|................3........|...|352664|.|..|.|......|
Siput            |............|.............1.....6.....|...|3.2666|.|..|.|......|
Jambatan         |............|...........1.............|...|4.2665|.|..|.|......|

Labu             |............|...4............4........|...|464665|.|66|.|......|

Beras            |............|...1.....................|...|4..46.|.|..|.|......|
Ampang Kecil     |............|.........................|...|61..6.|.|..|.|......|
```

Table 4. Two-way classification for **exotic** species occurring on all islands. Classification based on abundance data standardised by species maximum. The first four letters of the generic name and specific epithet are read vertically. Numerical values represent the abundance scores standardised by species maximum.

```
Island                          Species groups
groups
              <----------A---------> <-B-> <--------C--------->                <--D--->
              ------------------------------------------------------------------------
              |BTVEEEMACDEEESDSHCSMRP|LCSPR|BBCCCHDCCEIPDAEBSGS|CS|RTT|IS|VS|CBLSSIAZ|
              |OREURUUUEALULPIPEYTAHH|EYCHI|OREHYIEHOMMAEPRRORT|AI|IRU|SE|EO|AREOENEE|
              |EIRPAPNSNCEPEOGEDNACOY|PNOYV|TENLPPSRNIPSSLIARAR|RD|CIR|CS|RL|SYUNNDRP|
              |RDNHGHTTCTUHURIRYOCRES|IOPLI|HYCOEPMYYLESMUOCGSI|IA|IPN|HB|NA|UOCCNIVH|
              |                      |     |                   |  |   |  |  |        |
              |DPCHTPCIEAICRISACDJASM|VADNH|BDCBPLTABSCFBMMBBSA|PA|CTU|MG|CA|EPLOOHLR|
              |IRIIERANCENYUNESOAATPI|IRUOU|LIIAOORCOOYOIUERIPS|AC|ORL|UR|IM|QIELCIAO|
              |FONRNOLUHGDADDTSRCMRAN|RCLDM|ASLRLNIINNLEPTYIC1I|PU|MIM|TA|NE|UNUECRNS|
              |FCETESALIYITEIIUYTAOTI|GUCII|DTIBYGFCACITIIEZO0A|AT|MFI|IN|ER|INCRISAE|
--------------------------------------------------------------------------------------
Keeling       |.....................4|....6|...................|66|.1.|..|..|........|
Atas          |....4.................|61..6|...................|..|.65|..|..|........|
--------------------------------------------------------------------------------------
Luar          |6614.............664.4|...61|...................|..|6.5|66|..|........|
Tikus         |...11661......111.6..6|.....|...................|..|1.6|..|66|.......1|
--------------------------------------------------------------------------------------
Selma         |1164666116666666661664|.....|...................|..|164|..|..|66666666|
Panjang       |6666666666666166611111|66111|6666666666666666666|..|..6|..|..|........|
--------------------------------------------------------------------------------------
Kambing       |......................|..6..|...................|..|..2|..|..|........|
--------------------------------------------------------------------------------------
Ampang Kecil  |......................|.....|...................|..|..1|..|..|........|
--------------------------------------------------------------------------------------
Ampang        |......................|.....|...................|..|..5|..|..|........|
Cepelok       |......................|.....|...................|..|..5|..|..|........|
Pandan        |......................|.....|...................|..|..5|..|..|........|
Siput         |......................|.....|...................|..|..5|..|..|........|
Labu          |......................|.....|...................|..|..5|..|..|........|
Blan Madar    |......................|.....|...................|..|..5|..|..|........|
Maraya        |......................|.....|...................|..|..5|..|..|........|
Wak-Idas      |......................|.....|...................|..|..4|..|..|........|
Kembang       |......................|.....|...................|..|..4|..|..|........|
Kelapa Satu   |......................|.....|...................|..|..4|..|..|........|
--------------------------------------------------------------------------------------
```

Table 5. Two-way classification for all species recorded in transect plots on North Keeling Island. First letter of the site code represents the island name, second and third letters refer to the aspect of the ocean coastline.

```
Site                Species
groups              groups

               <-A-> <---B--->              <----C----> <-D->
--------------------------------------------------------------
              | ASA | ASLGBLP | M | P | PS | CRCPCCDMT | ISP |
              | CIC | RTAUOEO | A | A | EE | AIOIOAIOR | PCR |
              | ADH | GEPEEPR | R | S | MS | NVCSRRCRI | OAE |
              | LAR | UNOTRTT | I | P | PU | AIOODILIP | MEN |
              |     |         |   |   |    |           |     |
              | LAA | AMRSRRO | J | V | AP | CHNGSPCCT | MTS |
              | ACS | RIUPEEL | A | A | CO | AUURUAIIR | AAE |
              | NUP | GCDEPPE | V | G | IR | TMCABPLTI | CCR |
              | CTE | ERECEER | A | I | DT | HIINCAIRF | RCR |
--------------------------------------------------------------
1    KN/0     |     |      *  |   |   | ** |     *     |     |
     KSE/0    |     |         |   |   | ** |           |     |
     KN/1     |     |         |   |   |  * |           |     |
--------------------------------------------------------------
2    KE1/4    |     |         |   |   | *  |           |     |
     KS/7     |     |         |   |   | *  |           |     |
     KSW/2    |     |         |   |   | *  |           |     |
--------------------------------------------------------------
3    KN/2     |     |         |   |   |    |     *     |     |
     KSW/1    |     |         |   |   |    |     *     |     |
--------------------------------------------------------------
4    KN/3     |     |  *   ** |   |   |    |    *  *   |     |
     KW2/6    |     |  *   ** | * |   |    |    **     |     |
     KSE/1    |     |     *** |   |   | ** |    *      |     |
     KSE/2    |     | **  *** |   |   |  * |    *      |     |
     KS/0     |     | **  *** |   |   |    |    *      |     |
     KSE/3    |     |     *** |   | * |  * |           |     |
     KS/6     |     |  *  *** |   |   |  * |           |     |
     KE1/0    |     | **  **  |   |   |    |     *     |     |
--------------------------------------------------------------
5    KE1/1    |     |  *  *** |   |   |    |   **      |     |
     KW1/5    |     |  ** * * |   |   |    |   **      |     |
     KS/1     |     | **  *   |   |   |    |   **      |     |
     KW1/0    |     | **    * |   |   |    |   **      |     |
     KW3/0    |     | *** * * |   |   |    | ****      |     |
     KE2/5    |     | **   ** |   |   | *  |   ***     | *   |
     KNA1/2   |   * | **** *  |   |   |    |   ***     |     |
     KNA2/0   |     | **** *  |   |   |    |   **      |     |
     KNA2/1   |     | ***     |   |   |    |   ***     |     |
     KE2/4    |     |  *      |   |   |    |   ***     | * * |
     KW3/7    |     |  *      |   |   |    | * ***     | **  |
     KNA2/3   |     | *       |   |   |    |   ***     | *   |
--------------------------------------------------------------
6    KN/4     |     |         |   |   |    |   *** *   |     |
     KN/8     |     |  *      |   |   |    |   **  *   |     |
     KW2/3    |     |         |   |   |    | * **  *   |     |
     KN/7     |     |         |   |   |    |   ** **   |     |
     KW3/3    |     |         |   |   |    |   ** *    |     |
     KW3/4    |     |         |   |   |    |  *** ***  |     |
     KE1/3    |     |         |   |   |    |   ***     |     |
     KE2/3    |     |         |   |   |    |   ***     |     |
     KW1/1    |     |         |   |   |    |   ***     |     |
     KW2/5    |   * |         |   |   |    |   ***     |     |
     KW3/1    |     |         |   |   |    |  ****     |     |
     KW2/1    |     |         |   |   |    |  ***      |     |
     KW2/2    |     |         |   |   |    |  ***  *   |     |
     KW3/2    |     |         |   |   |    | ****   *  |     |
     KW3/6    |     |         |   |   |    | * ***  *  |     |
     KW2/4    |     |         |   |   |    | * **    * |     |
     KN/5     |     |  *      |   |   |    |    ** *   |     |
     KS/5     |     |  *      |   |   |    |    **     |     |
     KE1/2    |     |  *      |   |   |    |   **      |     |
     KE2/2    |     |  *      |   |   |    |   **      |     |
     KNA1/1   |     |  *      |   |   |    |   **      |     |
     KNA1/0   |     |  * *    |   |   |  * |   **      |     |
     KW2/0    |     |  **     |   |   |    |  ***      |     |
--------------------------------------------------------------
7    KN/9     |     |         |   |   |    |   **      |     |
     KN/10    |     |         |   |   |    |   **      |     |
     KNA2/2   |     |         |   |   |    |   **      |     |
     KS/2     |     |         |   |   |    |   **      |     |
     KS/3     |     |         |   |   |    |   **      |     |
     KS/4     |     |         |   |   |    |   **      |     |
--------------------------------------------------------------
8    KN/6     |     |  *  *   |   |   |    |    *      |     |
     KW1/4    |     |     *   |   |   |    |    *      |     |
     KW1/2    |     |         |   |   |    |    *      |     |
     KW1/3    |     |         |   |   |    |    *      |     |
--------------------------------------------------------------
9    KE2/0    |     |         |   |   |    |           | **  |
     KE2/1    |     | *       |   |   |    |    *      | *   |
     KSW/0    |     |         |   |   |    |    *      | *   |
--------------------------------------------------------------
10   KW3/5    | *** |         |   |   |    |    *   *  |     |
--------------------------------------------------------------
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Table 6. Two-way classification for all species recorded in transect plots on the Cocos atoll. First letter of the site code represents the island name, second and third letters refer to the aspect of the ocean coastline. Asterisks indicate presence of a species.

```
Species                                          Site groups
groups

          |LTLLLLLLSSLLPSSPPPPPP|LAAAATPPPSPPPPPPPPAAAPPP|LAAATAAAAAPAAPAPAAAPPAPPAAAAAPAAAAPAA|TTATTAPPPPPTTT|AAAAAAAAP|A|
          |NENNNNNNNNNSNNWWWWNWW|NSSSSNSSSNWWWNWWNNEWWNNN|NSSWESSSNSSSSWSWNNSSEESSNNSEEWNNNNWSS|NNSNNSSSSSWNEE|NESNSSSES|S|
          |////////EE//EEE111W11|/EWWW/EEEE221W1WWW///WWW|/EW//EEEEEEEE2W1EEEEE/EEEEE//1EEEE2EW|//E//EEEEE2///|E/EEEEE/E|E|
          |00462538//792////////|14///5111/////////112///|16/0344314133///2222152221434/2111/2/|0144221111/312|202132222|3|
          |        32  /04347656|0/234 ///101132012   745| /0  ////////458///// /////  0////2/1|  /  /////3    |/ ///// /|/|
          |            1        | 4    132               | 6   12240063   01548 32233   3201 3 |  5  45467     |4 05021 0|1|

ACAL LANC |                     |                        |                                     |    *      *  |         | |
CORD SUBC |                     |                        |                                *    |              |         | |
HERN NYMP |                     | *                      |                                     |  *           |         | |
NEIS OPPO |                     |                        |                                     |  *           |         | |
ARGU ARGE |             *       |     *                  |        *************************    |              |****   **| |
RIVI HUMI |                     |                        |                         * **     ** |              |         | |
LEPT REPE |                     |                  *     |                       *             |              |***      | |

BOHR REPE |                     |                        |                                     |              |  *      |*|
LEPI VIRG |                     |   *                    |                                     |              |         | |

BOTH BLAD |               **    |                        |                                     |              |         | |
VERN CINE |        *      *     |                        |                                     |              |         | |
MACR ATRO |    * *  *           |         *              |                                     |              |         | |
PHYS MINI |   *      *          |                        |                                     |              |         | |
RICI COMM |  **  *              |                        |                                     |    *         |         | |
ISCH MUTI |          **         |                        |                                     |              |         | |

ENIC AXIL |                     |                        |                                     |              |        *| |
PAND TECT |             *       |                        |                                     |              |         | |

CALO INOP |  **      *  **      |             *       *  |*             **                     |              |         | |
CYPE STOL | *** *        *      |     *                  |                                     |   *          |         | |
STAC JAMA |*****        *       |                        |                                     |            * |         | |
IPOM PESC |*           ***      |     *                  |                                     |*  *          |       **|*|
DODO VISC |*     *              |                        |*                                    |              |         | |
TERM CATA |                     |     *                  |*                                    |              |         | |
CASS PILI |* *****              |*********  *** ***  * * |                                     |              |         | |
THUA INVO |*            *       |     *     *******    * |                             *       |              |     *   |*|
PHYL AMAR |  *                  |     * **    **       **|                                     |           ***|         | |
FIMB CYMO |  * *********** ***  |     **** *** ****   *  |                                     |              |         | |
ZOYS MATR |* * *****************|     *********    *  ***|                       *          *  |          *   |       **| |
TRID PROC |    *****    ***     |         *****          |                                     |              |         | |
COCO NUCI |*********************|***  *******************|*************************************|**************| *     * | |
SCAB TACC |** ****   ****  * *  |****************** **  |*   ********* *         *******      |***         **|*********| |
TURN ULMI |                  ***|**** ************    ***|*               **** ********* ******|********* *** |       * | |
MELA BIFL |  **    **     ******|*****   *******       * |            **                  ***  |  *           |         |*|
MORI CITR |   *  *   *** *******|     * *                |*                    ***   *         |***********  *|         | |
CRIN ASIA |                     |        *               |                                     |   *       ***|         | |
MARI JAVA |***                  | *             **       |                        **    *****  |****       ***|         | |
GUET SPEC |**                   |               *    **  |           *         *               |              |         | |
EUPH HIRT | *                   |                        |                                     |            * |         | |

ERAG TENE |                     |  *                     |                                     |          *   |         | |
PASS FOET |                  *  |                       *|                                     |              |         | |
TRIU PROC |                  *  |  **  ***    *    ******|                                     |       **     | ** ** * | |
APLU MUTI |                   * |           *         ***|                                     |              |         | |
EUPH CYAT |                     |           *  *         |                                  *  |          *   |         | |
DESM BIFI |                     |              *         |                                     |              |         | |
IPOM MACR |  *                  |               *      * |                              **     |              |         | |
STEN MICR |                     |                *     * |                             *       |              |         | |
PREM SERR |                     |                  *   * |                                     |              |         | |
SURI MARI |                     |               ***      |                                     |              |         | |

BARR ASIA |                     |                     *  |                                     |              |   *     | |
CAES BOND |                     |                     *  |                                     |              |         | |
HIBI TILI |                     |                     *  |**                                   |              |         | |
```

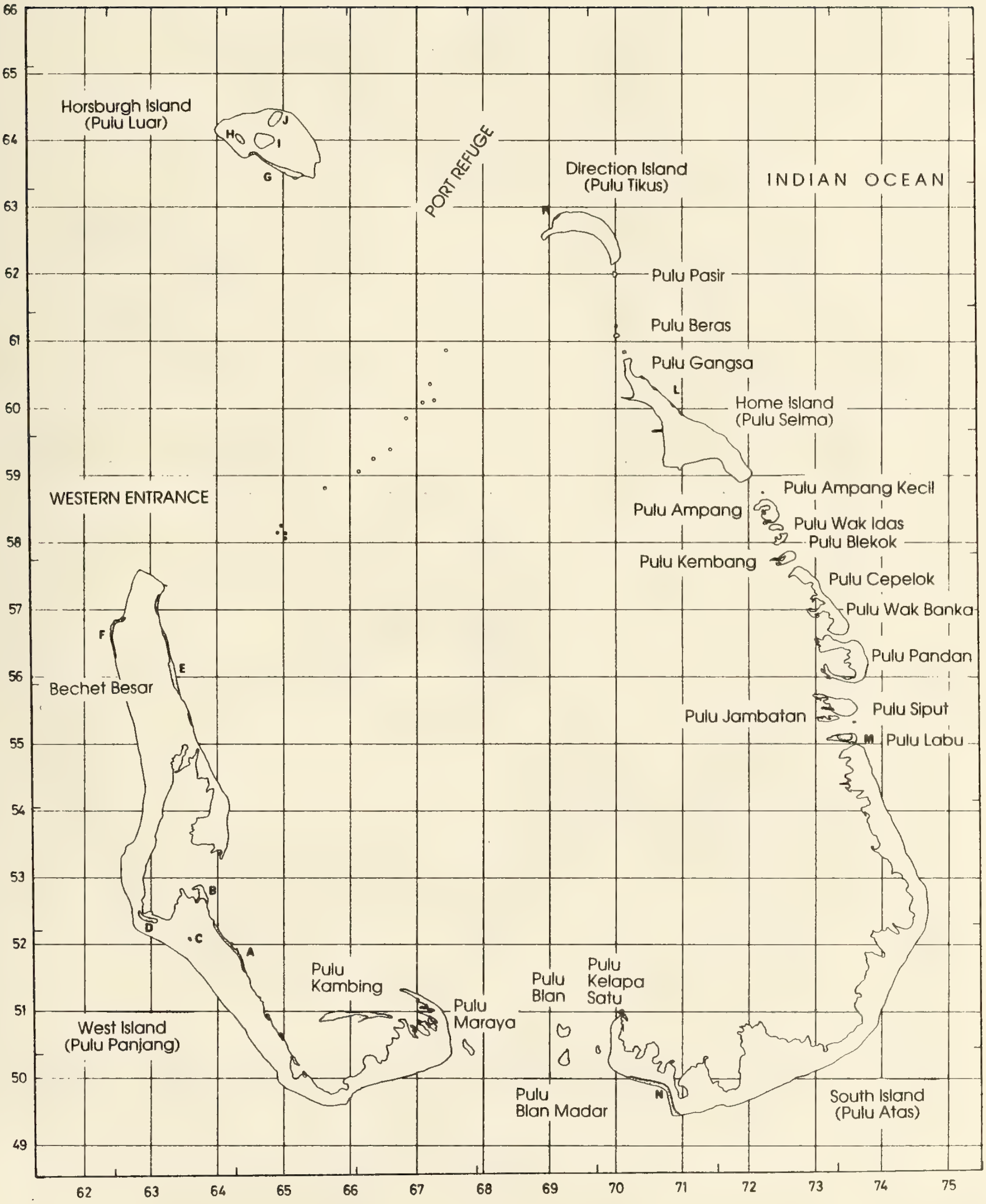

Figure 1. Location map showing island names, localities mentioned in the text and remnant vegetation patches on the Cocos atoll. Refer to Appendix 3 for a description of the remnant vegetation units. Gridlines represent 1000 m grid of the Australian Map Grid, Universal Transverse Mercator Projection. Map base derived from R.A.S.C. Series R811 Sheet Special Cocos Island 1979.

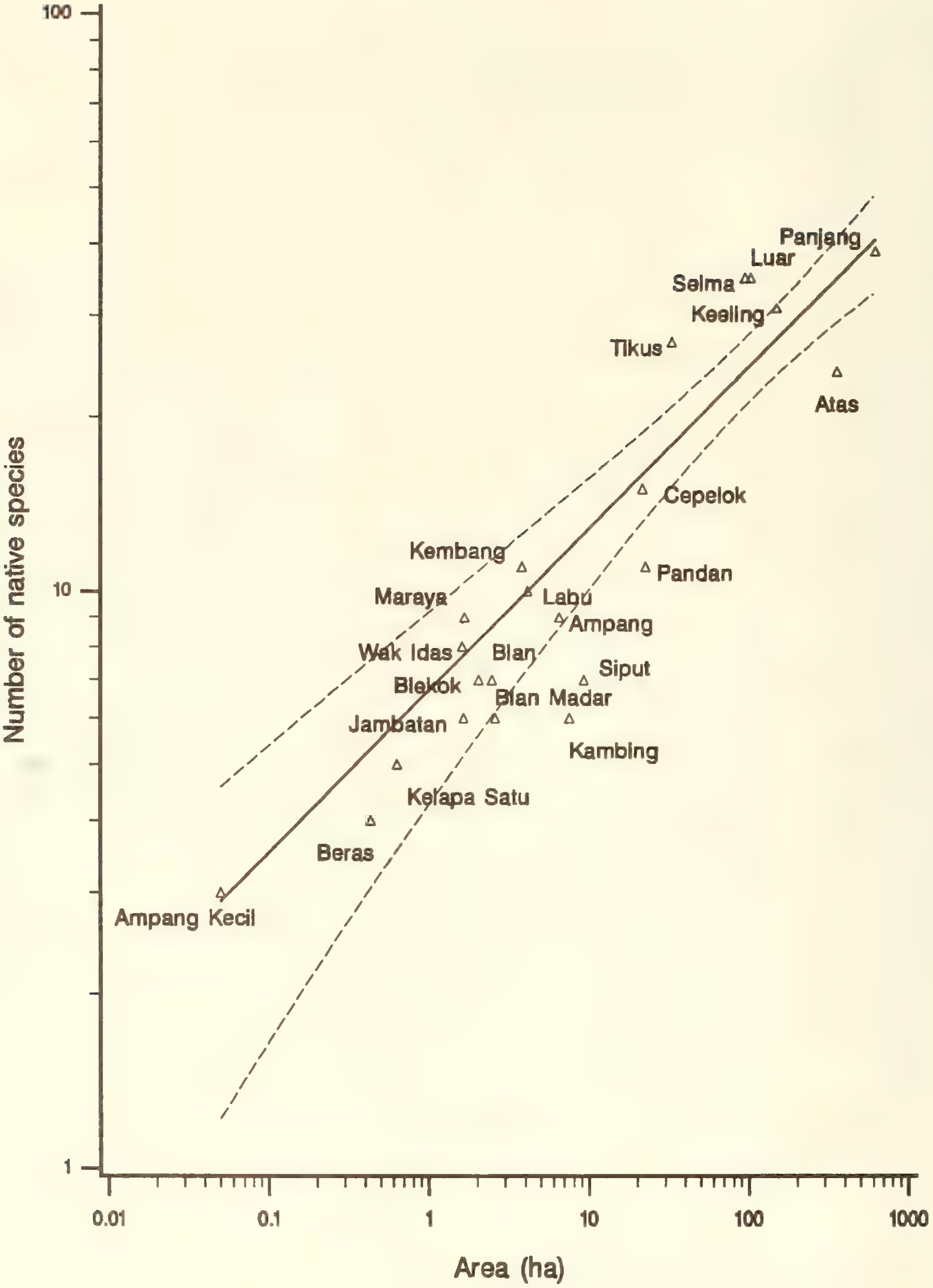

Figure 2. Species-area relationship for indigenous plant species richness for the 21 vegetated islands of the Cocos atoll and the island of North Keeling, showing approximate 95% confidence limits. Non-linear regression fitted to obtain the equation $s = 6.73a^{0.28}$.

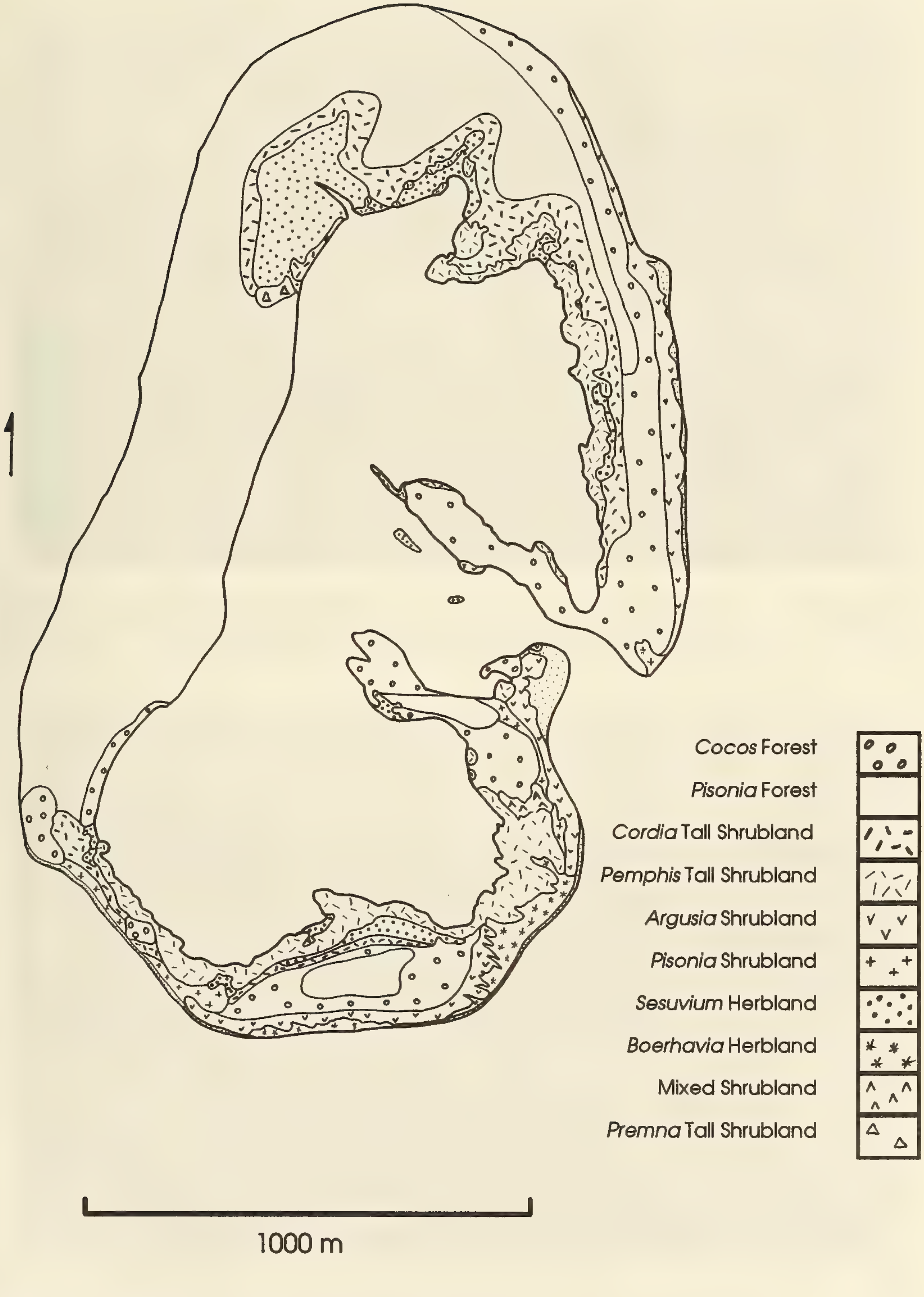

Figure 3. Vegetation map of North Keeling Island.

Figure 4. Pulu Beras, one of the smallest vegetated islands, with a cover of *Cocos nucifera*, *Argusia argentea* and *Scaevola taccada*.

Figure 5. *Boerhavia repens* herbland grading into wind-sheared *Argusia argentea* shrubland on the south-east coast of North Keeling island. This is the breeding habitat for the Brown Booby.

Figure 6. *Sesuvium* herbland adjoining *Pemphis* shrubland with *Cocos -Pisonia* forest in the background, on North Keeling island.

Figure 7. *Rhizophora apiculata* grove on Pulu Luar lagoon. *Sesuvium* herbland on coral shingle in the foreground.

Appendix 1. Vascular plant species list for the Cocos (Keeling) Islands. Asterisk indicates introduced species.

Family	Generic Name	Specific Epithet	Authority	Var./ Subsp.	Common Name	Local Name
ACANTHACEAE	Dicliptera	ciliata	Decne.			
AIZOACEAE	Sesuvium	portulacustrum	(L.) L.		Sea Purslane	
AMARANTHACEAE	Achryanthes	aspera	L.	var villosior (Henslow) D.Porter	Chaff Flower	
	* Aerva	lanata	(L.) Schult.			
APOCYNACEAE	Neisosperma	oppositifolia	(Lam.) Fosb. & Sachet			Kayu Laki
ASTERACEAE	* Austroeupatorium	inulifolium	(Humb.,Bonpl. et Kunth)King et H.Robinson		Stinkweed	
	* Conyza	bonariensis	(L.) Cronquist		Fleabane	
	* Eleutheranthera	ruderalis	(Sw.) Sch. Bip.			
	* Emilia	sonchifolia	(L.) DC.			
	Melanthera	biflora	(L.) Wild.		Beach Sunflower	
	* Sonchus	oleraceus	L.		Milk Thistle	
	* Synedrella	nodiflora	(L.) Gaertn.			
	* Tridax	procumbens	L.			
	* Vernonia	cinerea	(L.) Less.	var. cinerea		
	* Vernonia	cinerea	(L.) Less.	var lanata J.T. Koster		
BORAGINACEAE	Argusia	argentea	(L.f.) Heine		Octopus Bush	Kayu Sireh
	Cordia	subcordata	Lam.		Sea Trumpet	Geron-ggang
BRASSICACEAE	* Lepidium	virginicum	L.			
CAESALPINIACEAE	Caesalpinia	bonduc	(L.) Roxb.		Nicker Nut	Kelenchi
	* Senna	occidentalis	(L.) Link			
CAMPANULACEAE	* Hippobroma	longiflora	(L.) G.Don			
CAPPARACEAE	Cleome	gynandra	L.			
CARICACEAE	* Carica	papaya	L.		Pawpaw	Katis
CASUARINACEAE	Casuarina	equisetifolia	L.	subsp. equisitifolia	Coastal Sheoak	Cemara
CLUSIACEAE	Calophyllum	inophyllum	L.		Alexandrian Laurel	Nyampl-ong
COMBRETACEAE	Terminalia	catappa	L.		Sea Almond	Ketapang
CONVOLVULACEAE	Ipomoea	macrantha	Roem. & Schult.		Moon Flower	
CONVOLVULACEAE	Ipomoea	pes-caprae	(L.) R.Br.	subsp. brasiliensis (L.) Ooststr.	Goat's-foot Convolvulus	Kangkong Meryap
CRASSULACEAE	* Bryophyllum	pinnatum	(Lam.) Oken			
EUPHORBIACEAE	Acalypha	indica	L.			
	Acalypha	lanceolata	Willd.			
	* Breynia	disticha	J.R.Forst. & G.Forst.			
	Euphorbia	atoto	G. Forst.			
	* Euphorbia	cyathophora	Murray		Dwarf Poinsettia	
	* Euphorbia	hirta	L.			

EUPHORBIACEAE	*	Euphorbia	prostrata	Aiton			
		Phyllanthus	amarus	Schumach & Thonn.			
	*	Ricinus	communis	L.		Castor Oil Plant	Pokok Jaru Jarak
	*	Sauropus	androgynus	(L.) Merr.			Keretu
FABACEAE	*	Alysicarpus	vaginalis	(L.) DC.			
		Canavalia	cathartica	Thouars. in A.N. Desvaux		Sea Bean	
	*	Crotalaria	retusa	L.	var. retusa		
	*	Desmodium	triflorum	(L.) DC.			
		Erythrina	variegata	L.		Coral Tree	Kayu Dedap
	*	Indigofera	hirsuta	L.			
	*	Macroptilium	atropurpureum	(DC.) Urb.		Siratro	
	*	Sesbania	cannabina	(Retz.) Poir.	var. cannabina		
	*	Sesbania	grandiflora	(L.) Poir.			Turi
		Vigna	marina	(Burm.) Merr.			
FLACOURTIACEAE	*	Muntingia	calabura	L.			Buah Cheri
GENTIANACEAE		Enicostema	axillare	(Lam.) A. Raynal	subsp. littorale (Blume) A.Raynal		
GOODENIACEAE		Scaevola	taccada	(Gaertn.)Roxb.		Sea Lettuce	Kayu Kankong
HERNANDIACEAE		Hernandia	nymphaeifolia	(C.Presl) Kubitzki		Sea Hearse	Kayu Jambu Hutan
LAURACEAE		Cassytha	filiformis	L.		Devil's Twine	
LECYTHIDACEAE		Barringtonia	asiatica	(L.) Kurz.		Box Fruit	Kayu Besagi
LYTHRACEAE		Pemphis	acidula	J.R.Forst. & G.Forst.			Kayu Keriting
MALVACEAE		Hibiscus	tiliaceus	L.	subsp. tiliaceus	Cotton Tree	Pokok Waru
	*	Sida	acuta	Burm. f.			
		Thespesia	populnea	(L.) Sol. ex Correa		Portia Tree	Waru Hutan
MIMOSACEAE	*	Leucaena	leucocephala	(Lam.) de Wit		Leucaena	Peteh
MYRTACEAE	*	Eugenia	sp.				Jambu Ayer
	*	Psidium	guajava	L.		Guava	Jambu Biji
NYCTAGINACEAE	*	Boerhavia	albiflora	Fosberg			
	*	Boerhavia	diffusa	L.			
		Boerhavia	repens	L.			
		Pisonia	grandis	R.Br.		Pisonia	Ampol
OLACACEAE		Ximenia	americana	L.		Yellow Plum	Rukam
PASSIFLORACEAE	*	Passiflora	foetida	L.	var hispida (DC. ex Triana & Planch.) Killip	Stinking Passionflower	
PHYTOLACCACEAE	*	Rivina	humilis	L.		Coral Berry	
PORTULACACEAE		Portulaca	oleracea	L.		Pigweed	
RHIZOPHORACEAE		Rhizophora	apiculata	Blume		Spider Mangrove	

RUBIACEAE		Guettarda	speciosa	L.			Kembang Melati Hutan
		Morinda	citrifolia	L.		Cheesefruit	Mengkudu
	*	Oldenlandia	corymbosa	L.			
	*	Spermacoce	assurgens	Ruiz & Pav.			
RUTACEAE	*	Triphasia	trifolia	(Burm.f.) P.Wilson			Buah Kengkit
SAPINDACEAE		Allophylus	cobbe	(L.) Blume			
		Dodonaea	viscosa	Jacq.	subsp. viscosa	Hopbush	
SCROPHULARIACEAE	*	Scoparia	dulcis	L.			
	*	Striga	angustifolia	(D.Don) Saldanha			
SOLANACEAE	*	Physalis	minima	L.			Chepelok
	*	Solanum	americanum	Mill.		Blackberry Nightshade	
SURIANACEAE		Suriana	maritima	L.			
TILIACEAE		Triumfetta	repens	(Blume) Merr. & Rolfe		Bingil Burr	
TURNERACEAE	*	Turnera	ulmifolia	L.			
URTICACEAE		Laportea	aestuans	(L.) Chew.			
VERBENACEAE	*	Clerodendrum	indicum	(L.) Kuntze			
		Clerodendrum	inerme	(L.) Gaertn.		Sorcerer's Flower	
	*	Phyla	nodiflora	(L.) Greene			
		Premna	serratifolia	L.			
	*	Stachytarpheta	jamaicensis	(L.) J.Vahl		Blue Snakeweed	
		Vitex	trifolia	L.			
ARECACEAE		Cocos	nucifera	L.		Coconut	Kelapa
COMMELINACEAE	*	Rhoeo	spathacea	(Sw.) Stearn			
CYMODOCEACEAE		Syringodium	isoetifolium	(Asch.) Dandy		sea grass	
		Thalassodendron	ciliatum	(Forssk.) Hartog		sea grass	
CYPERACEAE		Cyperus	stolonifer	L.		Nut Grass	
		Fimbristylis	cymosa	R.Br.			
		Mariscus	javanicus	(Houtt.) Merr.& F.P.Metcalfe			
	*	Pycreus	polystachyos	(Rottb.) P.Beauv.			
		Queenslandiella	hyalina	(Vahl) F.Ballard			
HYDROCHARITACEAE		Thalassia	hemprichii	(Ehrenb.) Asch.		sea grass	
LILIACEAE		Crinum	asiaticum	L.		Crinum Lily	
	*	Zephyranthes	rosea	(Spreng.) Lindl.			
PANDANACEAE		Pandanus	tectorius	Park.	var. cocosensis B.C.Stone	Screw Palm	Pandan
POACEAE	*	Apluda	mutica	L.			
	*	Bothriochloa	bladhii	(Retz.) S.T.Blake			
	*	Brachiaria	brizantha	(Hochst.ex A.Rich.)Stapf			
	*	Cenchrus	ciliaris	L.			
	*	Cenchrus	echinatus	L.		Sand Burr	
	*	Chloris	barbata	Sw.			

POACEAE	*	Chrysopogon	acicularis	(Retz.) Trin.		
	*	Cynodon	arcuatus	J.Presl. & C.Presl.		
	*	Cynodon	dactylon	(L.) Pers.		Couch
	*	Dactyloctenium	aegyptium	(L.) Willd.		
	*	Desmostachya	bipinnata	(L.) Stapf		
	*	Digitaria	setigera	Roth		
	*	Eleusine	indica	(L.) Gaertn.		Crowsfoot Grass
	*	Eragrostis	tenella	(L.) P.Beauv. ex Roem. & Schult.		
	*	Eriochloa	meyeriana	(Nees) Pilg.		
	*	Imperata	cylindrica	(L.) P.Beauv.	var. major	Bladey Grass
	*	Ischaemum	muticum	L.		
		Lepturopetium	sp. aff. marshallense			
		Lepturus	repens	(G.Forst.) R.Br.		Stalky Grass
	*	Panicum	repens	L.		
		Paspalum	vaginatum	Sw.		
	*	Sporobolus	fertilis	(Steud.) Clayton		Sand Couch
		Stenotaphrum	micranthum	(Desv.) C.E.Hubb.		Beach Buffalo Grass
		Thuarea	involuta	(G.Forst.) R.Br.ex Roem. & Schult.		Bird's-beak Grass
		Zoysia	matrella	(L.) Merr.	subsp. matrella	
	*	Unidentified	sp.			

Appendix 2. Notes on plant species of restricted distribution on the Cocos (Keeling) Islands, along with collection numbers held at CBG.

Achryanthes aspera: Common on Keeling and found elsewhere only near some senescent *Pisonia* trees around the small lagoon on Pulu Luar. [D.G. Williams 45,52,211]

Barringtonia asiatica: A solitary tree of great stature occurs on Pulu Panjang with numerous supressed-advance seedlings underneath the canopy. The only other *Barringtonia* seen were a few saplings in the recent strand forest along the lagoon shore 150 m south of the northeast point of Pulu Panjang. [D.G. Williams 110]

Casuarina equisetifolia: Planted indiviuals are found in and near the settlements on Pulu Panjang and Pulu Selma and one large tree is on the lagoon shore north of the kampong. Guppy (1890) reported that the plant was introduced and spreading from island to island but no evidence was found for the latter. No seedlings were seen. [D.G. Williams 155]

Cordia subcordata: Now occurs on the Cocos atoll only as large senescent individuals along the lagoon shore. No young plants were seen, although germination was common on North Keeling lagoon shore in April. [D.G. Williams 20,54]

Enicostema axillare: Known only from two adjacent locations on southern Pulu Panjang, where it occurs amongst *Zoysia matrella* and *Ipomoea pes-caprae* in open coconut woodlands. It occurs from the ocean beach up to 100 m inland. Although flowering freely, these populations appear to be extending largely by rhizome extension, to judge by their compact, circular distribution. [D.G. Williams 79]

Erythrina variegata: A small but healthy grove of trees found at the north end of Keeling in *Pisonia* forest [D.G. Williams 53]. Likewise *Allophylus cobbe* [D.G. Williams 44,48] and *Cleome gynandra* [D.G. Williams 36] were found only in this area, the latter at the upper limit of the saltmarsh.

Laportea aestuans: Previously collected here only by Darwin on the Cocos atoll in 1836. Since collected only on the beach top along the western shore of North Keeling island. [D.G. Williams 154]

Lepturopetium sp.: A western Pacific genus of putative hybrid origin (Fosberg and Sachet 1982), found here only at the southern end of the runway on Pulu Panjang, growing on low-lying land occasionally inundated by rain or heavy seas. [D.G. Williams 267]

Neisosperma oppositifolia: Found occuring as a stand only on Pulu Labu, where there are twenty or so mature trees forming abundant fruits. A solitary specimen without fruit was found on Pulu Atas and two apparently planted trees occur in the Pulu Panjang settlement. [D.G. Williams 25,145,175]

Pandanus tectorius var. *cocosensis*: The only stands are on Pulu Selma where some of the clumps on high dunes have died out recently, possibly due to firing. A single clump on Pulu Panjang at the entrance to Telok Jambu appears to be all male, and therefore probably a single genet representing a solitary establishment event. [D.G. Williams 103]

Pisonia grandis: A few small clumps remain on the Cocos atoll of what must have been the dominant tree on the larger, higher islands before settlement. [D.G. Williams 21,43]

Rhizophora apiculata: Occurs around the saline swamp on Pulu Luar and produces numerous seedlings there. One established seedling was found on the southern point of Pulu Selma but had disappeared a year later. Guppy (1890) stated that the populations were derived from beach drift planted on Pulu Luar by J. G. Clunies-Ross about 1850-60. [D.G. Williams 171]

Suriana maritima: Occurs, in any abundance, only on recent sand deposits. Said by Guppy (1890) to have first colonized the atoll in about 1850, when it appeared on the ocean side of Pulu Cepelok, although it was not found there in this survey. [D.G. Williams 176]

Ximenia americana: Found only as a few plants on the lagoon shore of Pulu Panjang. [D.G. Williams 183]

Appendix 3. Remnant native vegetation of the Cocos atoll referred to map units indicated by letters on Fig. 1. The map does not show the following types of native vegetation:-

- *Pemphis acidula* and *Suriana maritima* shrublands on sheltered shores;
- *Scaevola taccada* and *Argusia argentea* shrublands along exposed coastlines;
- solitary individuals or small clumps of native species.

Pulu Panjang (West Island)

A Major area of strand forest with single large *Barringtonia asiatica*, several *Cordia subcordata*, *Calophyllum inophyllum*, *Hibiscus tiliaceus*, *Hernandia nymphaeifolia*, and *Morinda citrifolia.*

B Strand vegetation of *Pemphis acidula* with the only stand of *Pandanus tectorius* on West Island (burnt in October 1987) and some *Hibiscus tiliaceus* and *Hernandia nymphaeifolia.*

C A small clump of mature *Pisonia grandis.*

D Scattered individuals of *Hernandia nymphaeifolia* occur in this area, most of which is cleared for the aerial field.

E Strand lined with patches of large *Calophyllum inophyllum* and freshwater swamp lined with *Hibiscus tiliaceus. Suriana maritima*, *Guettarda speciosa* and *Pemphis acidula* occur locally.

F *Guettarda speciosa* and *Scaevola taccada* scrub along the strand opposite the aerial field and merging northward with tall *Guettarda speciosa* and *Calophyllum inophyllum* strand forest which extends inland, indicating a former shoreline.

Pulu Luar (Horsburgh Island)

G Well developed strand forest of *Calophyllum inophyllum*, *Terminalia catappa*, *Dodonaea viscosa*, *Hibiscus tiliaceus*, *Premna serratifolia*, *Guettarda speciosa.*

H Stand of *Thespesia populnea* and *Cordia subcordata* trees growing along a saltwater seep.

I Disturbed forest of *Morinda citrifolia*, *Premna serratifolia*, *Guettarda speciosa*, *Terminalia catappa.* Associated with a seasonally water-logged swamp dominated by *Mariscus javanicus.*

J Saltwater swamp with fringing *Cordia subcordata*, *Rhizophora apiculata* and a few *Pisonia grandis. Achryanthes aspera* and *Sesuvium portulacustrum* also occur.

Pulu Tikus (Direction Island)

K A small clump of *Thespesia populnea* occurs here amongst *Scaevola taccada* at the top of a rubble beach.

Pulu Selma (Home Island)

L Scattered clumps of *Pandanus tectorius* occur on the coastal dune; some burnt in 1987. *Guettarda speciosa* and *Premna serratifolia* are also present.

Pulu Labu

M The interior of this island has several large *Barringtonia asiatica* and a number of small and large *Neisosperma oppositifolia.*

Pulu Atas (South Island)

N Strand forest ranging from exposed to sheltered with *Calophyllum inophyllum* mainly, but also *Hibiscus tiliaceus*, *Guettarda speciosa*, and *Premna serratifolia.*

ATOLL RESEARCH BULLETIN

NO. 405

CHAPTER 7

AN UPDATE ON BIRDS OF THE COCOS (KEELING) ISLANDS

BY

T. STOKES

ISSUED BY
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CHAPTER 7

AN UPDATE ON BIRDS OF THE COCOS (KEELING) ISLANDS

BY

T. STOKES *

INTRODUCTION

The birds of the Cocos (Keeling) Islands were reviewed by Stokes et.al. (1984) and this paper summarises that paper and provides additional species records. It also provides an update of conservation comments provided in that paper.

Forty-four species of bird (6 introduced) have been recorded from the Cocos (Keeling) Islands (Appendix). The following species notes are additional to those recorded by Stokes et. al. (1984).

SPECIES

Herald Petrel *Pterodroma arminjoniana*. A few were recorded on two occasions at North Keeling Island in April and June 1986 on the ground and in the air, suggesting nesting (Stokes and Goh 1987).

Christmas Frigatebird *Fregata andrewsi*. An adult female was recorded on 21 March 1986 at North Keeling Island (Stokes and Goh 1987).

Glossy Ibis *Plegadis falcinellus*. Four were recorded by a party of touring bird-watchers at the airstrip on 8-9 May 1990 (Richard Jordan and Peter Goh pers. comm.).

Greater Flamingo *Phoenicopterus ruber*. A vagrant was recorded on North Keeling Island from April-June 1988 (Marchant and Higgins 1990).

Australian Kestrel *Falco cenchroides* . A pair were recorded over several weeks at the West Island airport in May-June 1990 (P. Stevenson, pers. comm.). They are common on Christmas Island and may have originated from there.

Buff-banded Rail *Rallus philippensis andrewsi*. An endemic endangered subspecies, formerly widespread on the main atoll and now virtually restricted to North Keeling Island where it is common (Stokes et. al. 1984). However occasional birds are still seen on the main atoll and the latest was a carcass, probably cat killed, found in 1991 at the West Island settlement (P. Stevenson, pers. comm.).

Bridled Tern *Sterna anaethetus*. A specimen was collected on North Keeling Island by Gibson-Hill (1948) and there was a local report that it nested there. It has not been recorded since.

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CONSERVATION

When Charles Darwin visited the Cocos (Keeling) Islands in April 1836, the "immense number" of marine birds recorded in 1828-29 on the main atoll (cited Gibson-Hill 1949) were probably still present though somewhat diminished. He refers to trees on the island where he first landed on the main atoll, as being occupied by many nests of gannets (sic), frigatebirds and terns, and to a smell in the air which led him to call it a "sea rookery" (Darwin 1979). From his diary it would appear that the forest of the main atoll was by then well on the way to be being transformed into the monoculture coconut plantation that it was by 1885 when most main atoll birds had been eliminated (Forbes 1885). The reason for the decline in main atoll birds was almost certainly due to habitat change, intense hunting by people and predation by cats and rats . Today there are still very few birds on the main atoll.

However birds remain in large numbers on North Keeling Island due to its isolation, the difficulty of landing, and access restrictions placed by the former Clunies-Ross clan rulers up to the mid 1970s. In the late 1970s and early 1980s, the lifting of access restrictions and the acquisition of more efficient boats and weapons by the Cocos-Malay people greatly increased the frequency and efficiency of bird-hunting on North Keeling Island. In the early 1980s the Australian Government became aware of concern on the islands and elsewhere that the number of seabirds being taken was not sustainable. I was despatched in January 1982 by the Australian National Parks and Wildlife Service (ANPWS) to investigate the situation and urgent control of hunting was recommended (Stokes et. al. 1984).

In March 1986, the ANPWS Conservator on Christmas Island, about 900 km east of Cocos, was required also to provide conservation advice to the Cocos (Keeling) Islands Administrator. As incumbent at the time, I or my assistant (Peter Goh) flew to the Islands every 4-6 weeks to discuss conservation matters on the Islands and to survey North Keeling Island seabirds. By July 1986 agreement had been reached with the Cocos-Malay people :

- to introduce a moratorium on seabird hunting on North Keeling Island pending seabird survey results,
- to restrict any future seabird hunting to red-footed boobies,
- to permit while the North Keeling moratorium was in place, certain numbers of red-footed boobies to be taken on Horsburgh Island on the main atoll (where small numbers come to roost in certain weather conditions at certain times of the year),
- that hunters would try to avoid killing adult birds, and on
- a series of administrative arrangements to regulate seabird hunting.

The conclusion of the 1986 seabird hunting agreement brought considerable praise to the Cocos-Malay community from the Australian and international community. ANPWS created a permanent Conservator position on the Cocos (Keeling) Islands in December 1986. The moratorium on hunting at North Keeling Island eventually extended to December 1988 by which time surveys had revealed that about 34 000 pairs of red-footed boobies nested annually on the Island. Although hunting was prohibited on North Keeling between 1986-88 many illegal hunting trips probably occurred and one person was prosecuted. Hundreds and possibly thousands of red-footed boobies are believed to have been taken in the period. A cyclone in January 1989 caused considerable damage to the North Keeling Island vegetation and post-cyclone surveys suggested that more than 40% of red-footed booby chicks raised in the previous breeding season , and 1300 (or

1.9%) of breeding adults were killed (ANPWS 1989). In the subsequent breeding season there was a 60% reduction in the number of red-footed booby nests on North Keeling Island compared to the number at the peak of the best previous season in 1987 (ANPWS 1990). Although seabird poaching was reported to have declined in the 1989/90 with the purchase of a new patrol vessel, no seabird population surveys occurred in 1990 or 1991 due to lack of suitable transport (ANPWS 1990, J. Tranter pers. comm.). Monthly surveys recommenced in the second half of 1992. A clear picture of the red-footed population status will not emerge until late 1993. However it appears that a cyclone in February 1992 caused sufficient damage to significantly reduce breeding success in the year (J. Tranter pers. comm.). The level of seabird poaching is reported to have been very high in 1990 and 1991 (J Tranter pers. comm.). This was exarcerbated by a lack of adequate patrol vessels. However a new vessel was acquired in late 1992.

An action plan to assist the recovery of the endangered rail population has been proposed by Garnett (1992). It includes enhanced access by management staff to North Keeling Island, a research program on the Island, declaration of the Island as a reserve, rat and cat control on main atoll islands and, if necessary, the re-introduction of rails to predator-free islands as conditions become suitable. Education to assist conservation is also proposed. Restrictions to ensure that North Keeling Island remains cat and rat free should also be considered.

Since the mid-1980s ANPWS has developed a limited conservation education program in the Islands. This is being enhanced (J. Tranter pers. comm.) and should be accompanied by the declaration of North Keeling Island as a Nature Reserve, as recommended by Stokes et. al. in 1984. Seabird populations have low natural recruitment, and usually only inhabit and survive on islands free of predators. Although there may be a case for arguing that seabird hunting on the Cocos (Keeling) Islands is a legitimate part of the traditional Cocos-Malay culture, it should only continue if the take is sustainable and hunting is restricted to red-footed boobies on the main atoll under tight and enforcable controls. There will remain justifiable cause for conservation concern about seabird status in the Islands until this occurs. For this reason the International Council for Bird Preservation (ICBP) and other conservation agencies should continue to monitor the situation and seek rectification where necessary.

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LIST OF BIRDS RECORDED FROM THE COCOS (KEELING) ISLANDS

KEY TO SYMBOLS

* = introduced,
r = resident,
m = migratory,
v = vagrant,
e = no longer occurs on the Islands ,
b = breeding,
? = unknown status.

Herald Petrel *Pterodroma arminjoniana*	(?)
Wedge-tailed Shearwater *Puffinus pacificus*	(mb)
Red-footed Booby *Sula sula*	(rb)
Masked Booby *Sula dactylatra*	(rb)
Brown Booby *Sula leucogaster*	(rb)
Christmas Frigatebird *Fregata andrewsi*	(v)
Great Frigatebird *Fregata minor*	(rb)
Least Frigatebird *Fregata ariel*	(rb)
Red-tailed Tropicbird *Phaethon rubricauda*	(rb)
White-tailed Tropicbird *Phaethon lepturus*	(rb)
White-faced Heron *Ardea novaehollandiae*	(r - possibly breeding)
Cattle Egret *Ardeola ibis*	(v)
Eastern Reef Egret *Egretta sacra*	(rb)
Rufous Night Heron *Nycticorax caledonicus*	(rb)
Glossy Ibis *Plegadis falcinellus*	(v)
Greater Flamingo *Phoenicopterus ruber*	(v)
Unidentified hawk	(v)
Marsh Harrier *Circus aeruginosus*	(v)
Australian Kestrel *Falco cenchroides*	(v)
Feral Chicken *Gallus gallus*	(rb)
Guinea Fowl *Numida meleagris*	(*rb)
Buff-banded Rail *Rallus philippensis andrewsi*	(rb-endemic subspecies)
Lesser Golden Plover *Pluvialis dominica*	(m)
Ruddy Turnstone *Arenaria interpres*	(m)
Little Curlew *Numenius minutus*	(m)
Common Sanfdpiper *Tringa hypoleucos*	(m)
Greenshank *Tringa nebularia*	(m)
Pin-tailed Snipe *Gallinago stenura*	(m)
Sanderling *Calidris alba*	(m)
Oriental Pratincole *Glareola maldivarum*	(m)
White-winged Tern *Chliudonias leucoptera*	(m)
Sooty Tern *Sterna fuscata*	(rb)
Bridled Tern *Sterna anaethetus*	(v b - specimen record of Gibson-Hill 1948, overlooked by Stokes et. al. 1984)
Common Noddy *Anous stolidus*	(rb)

White Tern *Gygis alba*	(rb)
Christmas Island Imperial-Pigeon *Ducula whartoni*	(*e)
Unidentified dove	(v)
Unidentified nightjar	(v)
Unidentified swift	(m)
Barn Swallow *Hirundo rustica*	(rmb)
Unidentified wagtail	(v)
Christmas Island Thrush *Turdus poliocephalus erythropleurus*	(*e)
Christmas Island Whiteye *Zosterops natalis*	(*rb-restricted to Horsburgh and possibly West Islands)
Java Sparrow *Padda oryzivora*	(*e)

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CHAPTER 8

MARINE HABITATS OF THE COCOS (KEELING) ISLANDS

BY

D.G. WILLIAMS

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CHAPTER 8

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BY

D.G. WILLIAMS *

ABSTRACT

The marine environments of the main atoll of the Cocos (Keeling) Islands have been mapped at a field compilation scale of 1:25,000 scale using 1976 and 1987 aerial photography and field survey. Twenty two habitat units were recognized and mapped, with greater differentiation possible in the lagoon because of easier access and shallower depth. Qualitative descriptions of the habitats were made based on surface and SCUBA observations in the field.

INTRODUCTION

The Cocos (Keeling) Islands, located in the north-east Indian Ocean, comprise a main atoll (96° E; 12° S) called here the Cocos atoll and consisting of 25 vegetated coral cays, and a northern atoll 27 km away, called North Keeling Island, which is now a single island atoll. The nearest other land mass is Christmas Island, 900 km to the northeast and Java, 1200 km to the north. The islands were discovered (apparently not previously inhabited) in the early 17th century but were not settled until 1826 (Bunce 1988).

Various naturalists have visited the islands, including Charles Darwin on H.M.S. *Beagle* in 1836 (see Armstrong 1991), just 10 years after settlement. Of the hundreds of atolls seen by Darwin during the voyage, this was the only atoll which he explored on foot. The experience was significant in the development of his coral reef theory (Woodroffe *et al.* 1990). Faunal studies of the corals, echinoderms, molluscs, crustacea and fishes were made by Gibson-Hill in the 1940's but, save for one survey by Maes (1967) on molluscs and Colin (1977) on fishes, there were no modern studies of the marine environments and organisms prior to those contained in the present volume (Williams 1990).

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Despite the various studies mentioned, no consistent overview of the marine habitats was able to be achieved until aerial photographic coverage was available. In this context, and that of an increasing need to better manage the atoll's marine living resources, the objective of this study was to describe and delineate the distribution of the major marine habitat types for both the lagoon, reef flat and outer reef slopes of the Cocos atoll. Difficulty of access prevented sub-tidal survey on North Keeling.

METHODS

A preliminary photo-interpretation was done on panchromatic 1976 Royal Australian Air Force 1:44,400 complete coverage photography and this was used as a basis for field sampling. Location of sample sites attempted to include several examples of each of the photo-pattern units defined on the basis of tone, texture, bathymetry and location. The exact placement of field sites was able to be done with an accuracy of 100 m in most cases by reference to the photographs in the field. Over 50 sites were observed using SCUBA for depths over about 8 m and on snorkel or walking for shallower areas and observations recorded on a data sheet.

Initially, fifteen different lagoon photo-patterns were described using the panchromatic photography. Further detail of the reef flats and of the outer reef was obtained from colour photographic coverage of the land areas only (1987 Australian Survey Office 1:10,000). These included the location of the "drop-off", (i.e. the top of a Pleistocene cliff at 18 m depth), the presence of sand chutes and deposits on the outer reef slope, spurs and grooves, reef crest surge channels, aligned coral flats, seagrass beds, conglomerate platform (Woodroffe *et al.* 1990) and beach rock deposits (Russell & McIntire 1965).

Some further refinement of the map units was done from a classified SPOT image taken in May 1987. This imagery enabled more consistent delineation of some of the shallow water habitats but did not provide as much detail in the deeper lagoon and outer reef slope zones. Seagrass beds of two species in the deeper lagoon were not detected on the classified image, although no specific training was attempted.

A description of each of the final mapping units is given below with cross referencing to map units (Table 1) and grid references on Fig. 1. The descriptions include habitat structure and dominant organisms as observed in the field, with other comments on structure or function within and between habitats. Reef classification and terminology varies considerably between authors and, where possible, the terms used here follow those of Hopley (1982). The marine areas of atolls and other reefs are commonly divided into three major zones. These are the seaward reef front which lies outside the line of breaking waves, the reef flat, which extends from the breakers to the shore or into the lagoon, and the lagoon itself. Each of these major units are further subdivided and described in the following scheme.

RESULTS

REEF FRONT

The reef front (unit A) on Cocos is marked by a major slope change, usually at 15-18 m depth, and below this the slope is greater than 45 degrees to depths over 50 m. Above the abyssal slope there is a gentle terrace of about 50 m to 2 km width, rising gradually to the reef crest at approximately the mean low water mark. On aspects more exposed to the south-east trades, the terrace has a well-developed spur and groove (buttress) morphology, which in several locations on the west side appears almost to form a secondary reef front due to very large buttresses located beyond the reef crest. The buttress systems are most pronounced on the southern reef.

The reef terrace is the habitat of most abundant and diverse coral growth. In places the terrace has up to 60% cover, mainly of soft corals, whereas elsewhere there are sand deposits or very sparsely covered rock or sand slopes. Much of the wide terrace opposite the West Island settlement (grid reference 6251), for example, has a sparse coral cover on a hard basement, whereas the terrace further north (6256) is well covered in coral from the reef crest to the outer terrace.

Because of the water depth over the terrace there were few mappable features. These were:- the break of slope at *ca.* 18 m, the presence and orientation of buttresses (spurs and grooves) and the presence of large sand deposits on the terrace. Terrace sand deposits are most abundant on the leeward side of the atoll. Opposite the northern half of West Island they form shore-parallel dunes at around 10 m depth (6257), usually lying between a buttress system and the coral-covered lower end of the terrace. Around Horsburgh Island sand is abundant and often covers much of the terrace and flows into deeper water via sand chutes (6561).

THE REEF FLATS

This component of the reef is also very varied and grades into the lagoon habitat in the channels between islands. The following units or features of the reef flat have been mapped:-

- position of the coralgal crest and its surge channels;
- sand and coral flats;
- seagrass beds (*Thalassia hemprichii*);
- aligned coral flats.

Components of the flats which were not able to be mapped were boulder zones and algal flats. The former are especially well developed on parts of the southern inter-island reef flat where the combination of southeast wind and southwest swell produce the highest wave energy conditions. This is also reflected in the greater development of buttress systems and surge channels along the southern reef front.

The structure of the coralgal crest also varies in relation to aspect. On the eastern and northern sides of the atoll it is poorly developed and very close (< 50 m) to the shore. Along the southern crest, calcareous red algae dominate and often form a honeycomb-like matrix that is exposed only during calm weather low tides. Along the western reef opposite West Island, the crest is dominated by seasonally varying stands of brown algae (mainly *Turbinaria* sp.), or a turf of red algae growing on smooth rock or algal-encrusted pavements. The crest exposed at the lowest tides is usually less than 10 m wide and rises 30-50 cm above the adjacent reef flat.

The reef crest has well-developed surge channels every 50-250 m, particularly along high-energy shores opposite islands. Associated with these channels are pockets of deeper water on the reef flat, these being possibly important in the movement of larger animals onto the reef flat, e.g. turtles, parrotfish and crayfish.

The reef flats opposite islands (unit B) are generally zoned landward from the crest with a sparse coral zone, then an algal zone (usually brown algae), then a sand or rock zone and in places an inshore seagrass bed on trapped sediment. However, much variation exists and these zones are not always present nor clearly defined.

Beds dominated by the seagrass *Thalassia hemprichii* (unit E) are developed on the inshore reef flat where sand has accumulated to about 5 cm or more depth and this usually occurs within 20 m of sandy beaches. In a few places sand has been trapped by exposed beach rock formations and this has enabled seagrass beds to develop.

The coral zone of the reef flats (unit C) is well developed in only two localities — at the northern end of West Island (6257) and the south-western side of Horsburgh Island (6563). In both locations there are reef flats dominated by hard branching corals and this may be attributable to both sites being of moderately low wave energy as well as experiencing a constant flow of fresh oceanic water that is relatively less turbid.

The aligned coral zone (unit D) is developed only on inter-island reef flats and usually extends from the crest into the lagoon to a point opposite the lagoon shores of the adjacent islands. The aligned corals are mostly hard massive species orientated parallel with the current. This is a faunally rich area dominated by clams, echinoderms and holothurians. At the lagoon end of the aligned coral zone and where the water is deeper than a metre, there is sometimes a well-developed area of outcrops composed of massive hard corals, surrounded by sand sheets.

Beach rock deposits are common around the seaward beaches of Cocos (Keeling) and when exposed they provide a protective rampart to the coastline, which they often parallel. In some places they diverge from the shore and so indicate recent changes in shoreline position.

THE LAGOON

Moderately large by Pacific standards, the Cocos lagoon is distinctive for the high proportion of its area covered by what appear to be fields of collapse and/or solution dolines, commonly known as "blue holes" (units K, L & M). These depressions vary in their size, shape and depth of their surrounding patch reefs. Other major habitats mapped are the prograding sand sheets (unit F), opposite to and fed by the aligned coral zone; seagrass beds dominated mainly by *Thalassia hemprichii* (unit H) and with smaller areas of *Syringodium isoetifolium* (unit U) and *Thalassodendron ciliatum* (unit T); intertidal sand and mud flats (unit G); sand flats and shoals; coral flats and patch reefs.

The continuous supply of sand from the outer and inner reef flat produces extensive sediment fans (unit F, Fig. 2), which are size proportional to the area of reef flat supplying them and the energy level of the coastline. The largest prograding sand sheets are the ones opposite the southern pass (between West and South Islands) and another fed by passes either side of Pulu Siput in the east. These deposits slope gently down into the lagoon and slowly engulf lagoon patch reefs and blue holes. Their margin with the aligned coral zone is not always distinct and it may be that the coral zone is extending slowly lagoonward across the sand sheet in places.

In their most active places the sand sheets appear almost devoid of surface life other than algal crusts, but in more stable locations there is a sparse covering of *Thalassia hemprichii*, *Halimeda* (a sand-producing alga), *Padina* and *Hydroclathrus* (both brown algae). Areas of high bioturbation due to sea cucumbers and worms are also common. The spider shell, *Lambis lambis,* is locally abundant.

Thalassia hemprichii dominates the seagrass beds (unit H, Fig. 3) developed from the Low Water Mark to depths of about one metre, close inshore to all the islands except Direction and Horsburgh. There is some variation in the structure of the beds with water depth and distance from the shore. Closer inshore, *Thalassia* is dominant but forms a discontinuous cover due to wave effects. Shallow intertidal areas are dominated by the seagrass and algae such as *Gracilaria* and *Acanthophora*, whilst subtidal areas have more coral and algal cover. In several places these seagrass beds (unit I, Fig. 3) show obvious lineation, and this represents overgrowth among the remnants of a prior aligned coral zone in places where a channel between islands has been closed off by storm activity. These sites are off South Island (7351, 7353) and West Island.

The most conspicuous fauna of the inshore seagrass bed is the Portunid crab, *Thalamita crenata*, which makes shallow burrows, as does the much less common mud crab, *Scylla serrata*. The crabs appear to feed on burrowing bivalves and winkles, and numerous small fish shelter in the extensive crab burrow systems.

Syringodium isoetifolium (units U, V) is a more restricted seagrass growing at depths from 1-6 m on sand in relatively clear water, mainly at the northern end of Home and West Island and in the bay of Direction Island (6962). It grows with *Thalassia* and various green algae including *Caulerpa* spp. in the former shallow sites, but is almost mono-specific dominant at Direction Island in 2-6 m of water.

Thalassodendron ciliatum, a large, robust seagrass, grows attached to rubble and rock. There is one large bed (unit T) of this species in the central northern lagoon in 8 m of water on sandy rubble, and smaller patches of this species possibly occur on the outer reef south-east of Horsburgh Island. The species grows in the lagoon in large circular clumps, some of which appear to be showing central die-off and hence taking on an annular shape. Small hard coral outcrops occur within some of these beds.

All three seagrasses appear to be grazed by green turtles, which are regularly seen along the northeast shore of West Island and in Direction Island bay. None were seen near the *Thalassodendron* bed but it did show signs of grazing by large animals — possibly turtles.

Shoreward of the *Thalassia* beds along the southern and eastern sides of the lagoon there are extensive intertidal sand and mud flats (unit G, Fig. 3). These are often demarcated from the seagrass by a sandbank which is usually colonized by a line of the shrub *Pemphis acidula*, which thereby stabilizes the bank and forms a mangrove-like vegetation. It is rather surprising that no mangroves have colonized these flats since such habitats are generally occupied by them on other reefs around the world. The finer sediments tend to accumulate in the more sheltered inlets of the lagoon side of the islands and generally where current and wave action is minimal. These form the major habitat for the fiddler crab *Uca chlorophthalmus* and *Macrophthalmus verreauxi*, which occur here in high numbers.

Major subtidal sand flats (unit Q) which are not directly associated with passes between islands occur northeast of West Island and south of Horsburgh Island. These locations are where sand is accumulated on the leeward lagoon margin and where it may eventually be carried to the outer reef. At West Island the sand flat has a highly mobile offshore sand bank (unit R) and there is major sand accretion onshore. The sand flat south of Horsburgh Island lies in a westerly current flow and is connected to the outer reef slope by a major sand chute which continues across the reef terrace.

Much of the central lagoon is a mosaic of "blue holes" of varying sizes and shapes and depth of surrounding patch reefs. Smaller, more discrete holes (unit K) occur towards the shallows and these ones are, in some cases, being filled by prograding sand sheets. Around the fringe of each depression there is a band of staghorn coral rubble which extends down the sides of the hole for about 2-5 m before passing into a sand slope going to as deep as 20 m. The water in the smaller holes is usually fairly turbid and the bottom is composed of sand and finer sediments.

In a few places large clumps of the foliose hard coral, *Echinopora*, were dominant on the edges of holes. These seemed to be more common in the small patch reefs developed in the middle of large holes (units L, M, Fig. 2) where turbidity was low. Away from the fringes of holes the coral cover is usually sparse and consists of the branching *Acropora* and outcrops of massive corals such as *Porites*. Bivalve molluscs and holothurians are often abundant and there is, in places, a high degree of bioturbation, perhaps associated with areas of finer sediments. At least two species of mushroom corals also occur around these patch reefs.

Although several different blue hole morphologies have been mapped, sampling has not been sufficiently intense to determine whether there are significant biological differences. The main difference evident on photography is between small, iso-diametric holes which cover 10-30% of the area, through to the holes in deeper water which are large, irregular and occupy more than 80% of the area. These sub-units tend to be separated by east-west lines of shallow water (of unit J), these perhaps representing former beachlines.

The deeper central lagoon opposite Home Island appears to show a broad pattern of reticulate reefs (unit N) but without deep blue holes. Much of the bottom cover is very thick staghorn rubble, tightly interlaced and bonded by overgrowth of algae, particularly a *Padina* sp. There are occasional sandy patches, as well as large mostly dead outcrops of *Porites* spp.

North of the previously described habitat is an extensive area (unit O) composed of mainly dead outcrops of massive corals with intervening sand patches. There are large areas of included sand flat on the eastern side and generally very small amounts of hard coral regrowth.

Well-developed coral flats lie between West Island and Horsburgh Island and, since there is no reef crest here, these lagoon flats at a depth of around 8 m merge into the outer reef terrace.

Between the seagrass beds on the east and west sides of the lagoon and the deeper habitats of the central lagoon, there is a large and variable shallow-water habitat (unit J) with various mixtures of sand, algal and coral cover. The sandy substrate, which appears to be rather thin, is often strewn with fine coral and shell fragments and there may be a sparse cover of *Thalassia* and/or *Caulerpa* spp. Patches of very dense *Halimeda* cover occur and these are often overgrowing small coral boulders. A small black sea cucumber is very abundant here. Large skeins of the net-like alga *Hydroclathrus* drift along and accumulate on obstructions. Colonies of *Porites* occur, some forming microatolls of considerable size.

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Table 1. Marine Habitats of the Cocos (Keeling) Islands Main Atoll and their corresponding map units.

Habitat System	*Habitat Unit*	*Map Unit*
OUTER REEF	**Coral Terrace** • stipple areas indicate sand deposits • hatching indicates the approximate length, width and direction of major buttresses • outer solid line indicates lower depth limit of the outer terrace	A
REEF FLAT	**Coral and Algal Flat** • includes areas of platform rock, beach rock and beaches • reef crest (coralgal rim) shown as a dashed line • surge channels shown as an arrowhead	B
	Coral Flat - branched hard corals dominant	C
	Aligned Coral Flat - small massive corals dominant	D
	Seagrass Flat (*Thalassia hemprichii*)	E
LAGOON	**Prograding Sand Sheet**	F
	Intertidal Sand and Silt Flat • lines of *Pemphis acidula* on offshore sandbanks shown stippled	G
	Seagrass Sand and Silt Flat (*Thalassia hemprichii*)	H
	Seagrass Flat - on prior aligned coral flat (*Thalassia hemprichii*)	I
	Coral and Algal Flat with sparse *Thalassia hemprichii*	J
	Blue Hole Mosaic 1 - small scattered isodiametric depressions	K
	Blue Hole Mosaic 2 - large, irregular depressions, prominent shallow coral rims	L
	Blue Hole Mosaic 3 - large, irregular depressions, deep rims	M
	Algal-covered Staghorn Rubble with occasional sandy patches	N
	Massive Coral Outcrops with sandy patches	O
	Emergent Reef (Turk's Reef)	P
	Sandy Lagoon Floor with occasional Coral Outcrops	Q
	Sand Shoal	R
	Sandy Lagoon Floor with scattered Coral Outcrop and Seagrass Beds (*Thalassodendron ciliatum*)	S
	Seagrass Bed (dense *Thalassodendron ciliatum*) and occasional coral outcrops	T
	Seagrass Bed (*Syringodium isoetifolium*) and occasional coral outcrops	U
	Mixed Seagrass & Algal Bed (*Syringodium isoetifolium, Thalassia hemprichii, Halimeda* spp., *Caulerpa* spp.)	V

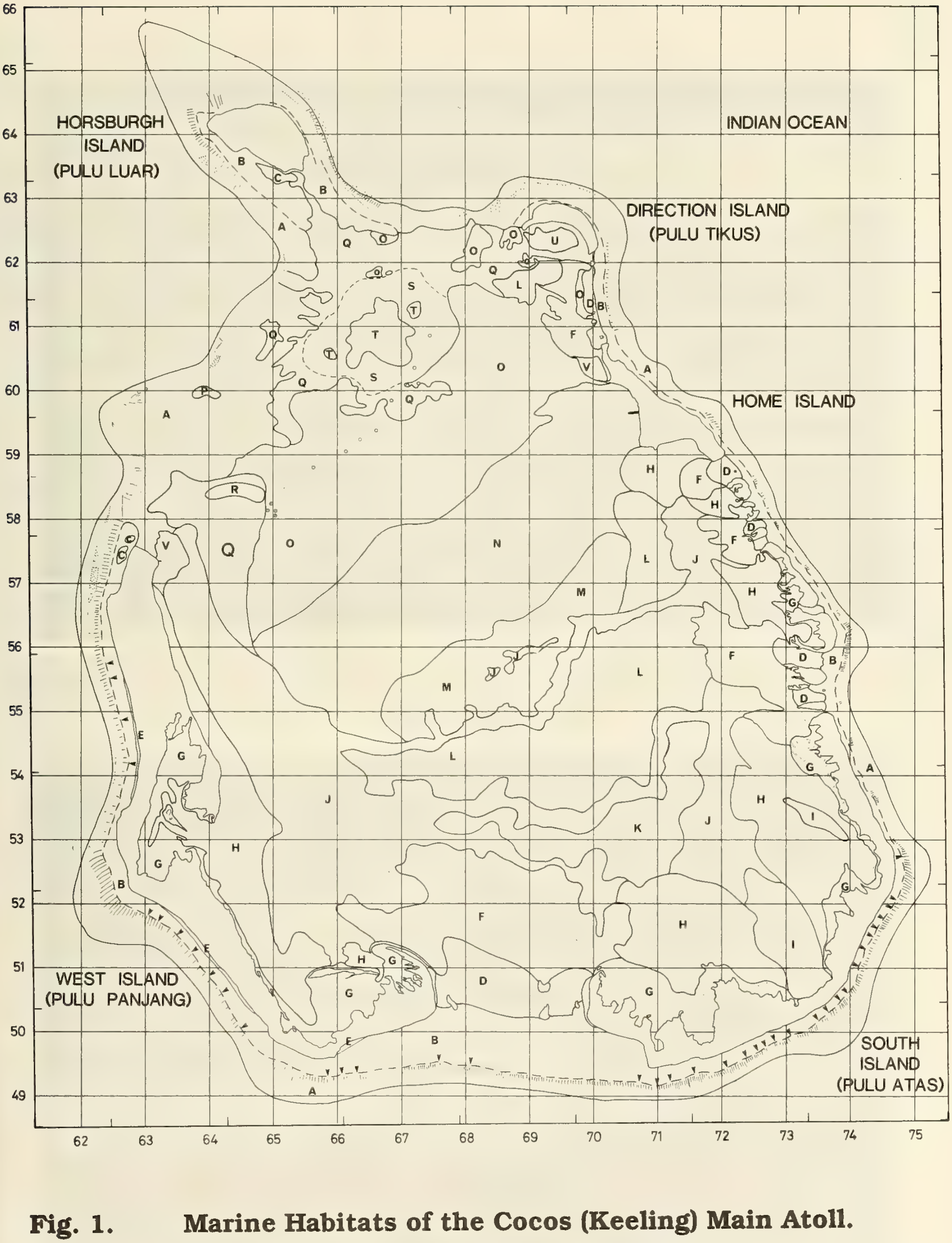

Fig. 1. **Marine Habitats of the Cocos (Keeling) Main Atoll.**

Numbered grid lines are 1000 m intervals of the Universal Transverse Mercator Grid, Zone 47. Habitats mapped from field survey by D.G. Williams in 1986/7, using R.A.A.F. 1976 panchromatic (1:44,400) and A.S.O. 1987 colour (1:10,000) aerial photography. Map field compiled at 1:25,000 on base derived from R.A.S.C. Series R811 Sheet Special Cocos Island 1979.

Figure 2. Aerial oblique view over the southern lagoon, looking east towards the northern end of Pulu Atas, showing blue holes (unit L), coral algal flat (unit J), seagrass flats (Unit H) and pograding sand sheet (Unit F).

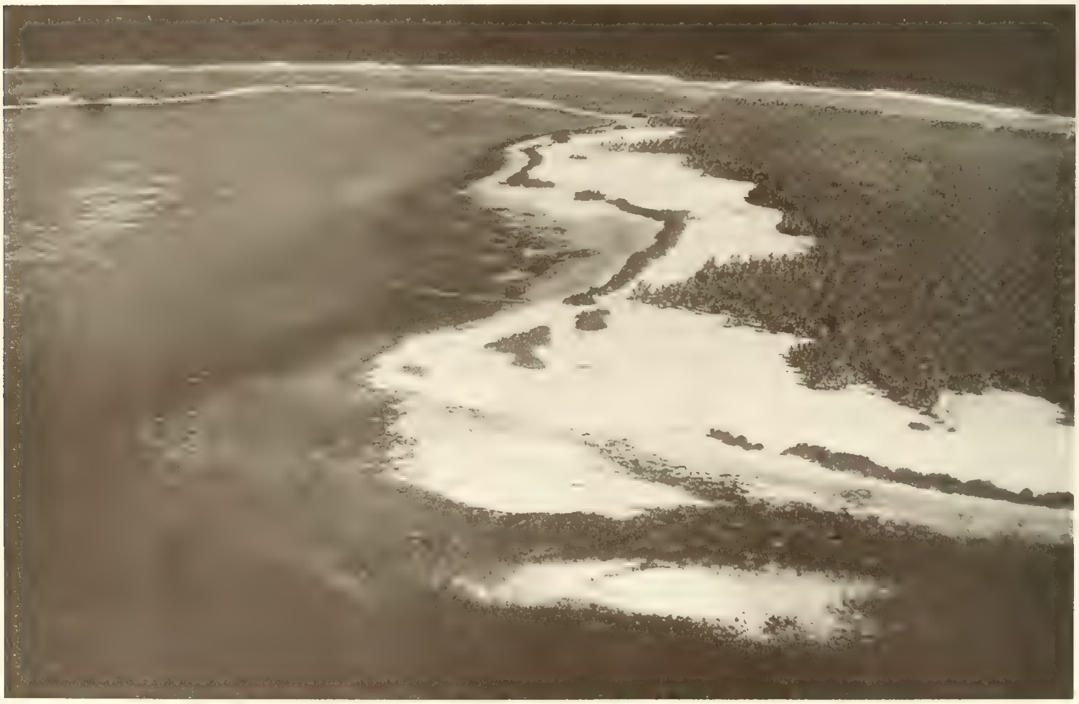

Figure 3. Aerial oblique view of the southern lagoon, looking east across Pulu Atas, showing seagrass beds (Unit H) and lines of *Pemphis acidula* at the edge of sand and silt flats.

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CHAPTER 9

SEDIMENT FACIES OF THE COCOS (KEELING) ISLANDS LAGOON

BY

S.G. SMITHERS

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CHAPTER 9

SEDIMENT FACIES OF THE COCOS (KEELING) ISLANDS LAGOON

BY

S.G. SMITHERS *

ABSTRACT

Surficial sediments from the Cocos (Keeling) Islands lagoon were classified according to texture and composition using factor analysis. Six main textural facies: i) slightly gravelly coarse sands, ii) slightly gravelly medium sands, iii) gravelly sands, iv) sandy gravels, v) gravelly muds, vi) slightly gravelly fine sands; and three main compositional facies (i) coral-type sediments, ii) molluscan mud sediments, iii) coralline algae/*Halimeda* type sediments were identified, accounting for over 90% of sediment variation in the lagoon. These facies can be related to the provenance of constituent components and lagoonal hydrodynamics.

INTRODUCTION

The main atoll of the Cocos (Keeling) Islands (96°48'-56'E; 12°04'S) consists of a horse-shoe shaped reef rim, on which 26 reef islands lie, surrounding a central lagoon of approximately 190 km^2. The lagoon can be divided into two broad provinces, the deeper (8-15 m) northern basin and the shallower southern flats (0-3 m) (Fig.1). Blue holes exceeding 20m depth occur in several parts of the lagoon, but are most obvious across the shallower southern flats. A more detailed description of lagoonal marine habitats is provided by Williams (this volume), and they are mapped in Figure. 2. At the north of the atoll, deep and wide passages either side of Horsburgh Island connect the lagoon to the open ocean. Other exchange between the lagoon and ocean is restricted to 11 shallow reef flat passages situated on the eastern and southern atoll rim. Currents through these reef passages are predominantly unidirectional into the lagoon, probably driven by the persistent southeast trade winds which prevail for most of the year, and wave set-up generated by the swells which continually break over the windward reef crest. The hydrodynamics of this atoll have been examined recently by Kench (this volume).

Lagoonal infilling by sediments produced on the reef rim is generally accepted as the dominant constructional process on atolls after the reef rim has reached a stable sea level (Marshall and Davies 1982, Frith 1983, Tudhope 1989). Upward growth of the reef rim has been limited by sea level for more than 2000 years on the Cocos (Keeling) Islands (Woodroffe et al. 1990a, 1990b, this volume), and historical accounts (Darwin 1842, Guppy 1889) indicate that much of the southern part of the lagoon has been rapidly infilled. During his visit in 1836 Darwin sailed to the south of the lagoon through channels dredged through living coral. Sand sheets or seagrass meadows which are often exposed at low tides now cover these areas. Vibrocore data were used to establish the nature and chronology of longer term (mid-late Holocene) accretion in several parts of the lagoon (Smithers et al. in press).

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Sediments infilling atoll lagoons consist almost entirely of skeletal carbonate secreted by reef organisms, and facies development within atoll lagoons is governed by interaction between the supply and physical properties of the source material and the various processes which degrade, redistribute and stabilize sediments (Maxwell et al. 1964, Milliman 1974). Biogenic carbonates may consist of either rigid reef framework or unconsolidated detrital material, and may be produced and deposited *in situ* (autochthonous) or produced outside the lagoon and transported in before deposition (allochthonous). The relative contributions of allochthonous and autochthonous sediments usually varies around a lagoon, and can be determined from the texture and provenance of contributory components (Swinchatt 1965, Orme 1973). Reconciling the habitat zone of the source organism with the location of the depositional zone, and the determination of textural gradients between sediment sources and sinks, allows hydrodynamic, sediment transport, and facies development processes to be inferred.

There have been few studies of the lagoonal sediments of Indian Ocean atolls and the lagoon of the Cocos (Keeling) Islands differs in several ways from other atolls where sedimentation has been examined. Firstly, the sediment producing biota of the Cocos (Keeling) Islands appear to differ from other atolls, possibly due to its extreme isolation. Secondly, the size, bathymetry and hydrodynamics of this lagoon differ from other atolls where carbonate sedimentation has been investigated. Early studies chiefly examined sediments from the relatively large and deep Pacific atolls with lagoons which deepen towards the centre (e.g. Kapingamarangi - McKee et al. 1959, Bikini, Rongelap, Enewetok - Emery et al. 1954). Smaller atoll lagoons with complex bathymetry have more recently received some attention (Mataiva, Takapoto - Adjas et al. 1990, Henderson Reef - Chevillon and Clavier 1990, Mataiva - Desalle et al. 1985), but once again are concentrated in the Pacific. This paper reports on an examination of the surficial lagoonal sediments of the Cocos (Keeling) Islands, a moderately sized Indian Ocean atoll with a complex lagoonal bathymetry. The primary aims were to: (1) determine the textural and compositional characteristics of lagoon surface sediments; (2) identify and map textural and compositional facies; and (3) relate facies distribution to specific biotic/physiographic environments.

METHODS AND MATERIALS

The lagoon floor was examined on a series of boat and snorkel transverses. A total of 167 sediment samples were collected from the lagoon bed (Fig. 3), using a sampling strategy based on environments determined from aerial photographs and SPOT satellite imagery. Not surprisingly, the lagoonal environments delineated in this way are very similar to the marine habitat units established by Williams (this volume). Samples were collected by scooping unconsolidated sediments into plastic bags except in depths that exceeded 8m when a weighted steel dredge was used.

Seventy-six sediment samples were analysed granulometrically using the techniques of Folk (1974), making sure that several samples from each lagoonal environment were examined. Where necessary the mud fraction was first separated by wet sieving; these samples were washed with 200 ml of distilled water and approximately 1ml of 10% Calgon for each gram of estimated mud content. The mixture was left to stand overnight then mechanically stirred for 3 minutes and washed through a 4ø sieve. Sediments larger than 4ø were dried, weighed and between 50-70grams transferred to a nest of sieves ranging from -2ø to 4ø, with a 0.5ø interval. The sieves were mechanically shaken for 15 minutes and the fraction retained on each sieve (and the pan) weighed.

Mean grain size, sorting and skewness were determined using the graphic methods of Folk and Ward (1957).

The skeletal compositions of 50 sediment samples were examined. Representative subsamples were taken from sieve fractions greater that 3.5ø and grains were identified and point-counted using a binocular microscope. Approximately 100 grains were identified for each sieve fraction. Fifteen component categories were recognized: (i) coral shingle and grit; ii) *Halimeda* fragments; iii) coralline algae (principally *Spongites* rhodolith fragments); iv) *Homotrema*; v) gastropod fragments; vi) pelecypod fragments; vii) unknown molluscan fragments; viii) *Marginopora*; ix) *Amphistegina*; x) other foraminiferans; xi) echinoids; xii) annelids; xiii) alcyonarian spicules; xiv) crustacean fragments; and xv) indeterminate or unrecognisable grains. Component representation in the total sample was expressed as a weight percentage of the total sample. Granulometric and compositional data were analysed using Q-mode factor analysis (Klovan 1966, 1975, Gabrie and Montaggioni 1982, Montaggioni et al. 1986) in order to classify sediments according to their compositional and textural characteristics (Smithers 1990).

RESULTS

SEDIMENT TEXTURE

The textural characteristics of seventy-six sediment samples from the Cocos (Keeling) Islands lagoon are presented in Table 1 and descriptive statistics for each of the lagoonal environments provided in Table 2. These results indicate that the Cocos (Keeling) Islands lagoon is dominated by poorly sorted, slightly gravelly (<10%) fine to coarse sands. Several general trends in sediment texture can be identified. Mean grain size is greatest in the interisland channels and is lowest in the seagrass meadows and intertidal sand and mud flat areas. Gravel abundance appears closely related to coral outcrop proximity, the highest mean values occuring in the interisland channels where autochthonous gravels are deposited with allochthonous gravels transported from the reef flats, and in the blue hole mosaic where gravels derived from patch reefs are common. Occasional high gravel values in samples collected elsewhere in the lagoon can largely be attributed to the deposition of autochthonous carbonates. Mud content peaks at around 45% in the seagrass meadows but generally comprises 0-2% of most sediment samples. Sorting is typically poor, but improves in the exposed sandy areas in the north of the lagoon. Skewness values range from strongly fine skewed to strongly coarse skewed, and in different areas may reflect either *in situ* sediment production or else the selective removal of certain grain sizes by incident currents. The significance of variation in the textural traits of lagoon sediments will be addressed in the discussion.

Six factors were extracted from the data matrix of 14 variables (weight % of sediment in each sieve fraction) and 76 observations (sediment samples) using a Q-mode factor analysis which can account for 91.7% of the data variance. Communality values are high for all samples indicating that a good description of all samples is given by these factors. Sediment samples were classified according to the factor axis each was most heavily loaded upon; samples belonging to each class are listed in Table 3. The grain size distributions of samples with the highest loading on each factor axis are presented in Figure 4 and the average textural statistics of sediments assigned to each factor are given in Table 4.

Descriptions of the textural sediment types classified on each factor axis are provided below and their distribution is shown in Figure 5:

Factor One - Slightly Gravelly Coarse Sands. These sediments account for over one third of the samples and are chiefly composed of coarse sands with a minor gravel component (Fig. 4a and Tables 1 and 2). The grain size distribution is characterised by a primary mode in the 0ø-0.5ø range and the mean grain size is around 0.5ø. Muds usually form less than 1% of these sediments. Sorting and skewness are variable; ranging from moderately well to poorly sorted and from strongly fine to strongly coarse skewed. Slightly gravelly coarse sands occur throughout the lagoon, but appear to be most concentrated in the exposed areas of the deeper northern part of the lagoon and around the interisland channels.

Factor Two - Slightly Gravelly Medium Sands. These sediments are very similar to those defined by factor one, however the sand fraction is finer with the principle mode being between 1.5ø-2ø (Fig. 4b). Sediments represented by this factor range from moderately well to poorly sorted and show a tendency to be coarse skewed. These sediments cover much of the lagoon floor, being patchily interspersed with the slightly gravelly coarse sands in the north of the lagoon and covering large areas north of the southern passage.

Factor Three - Sandy Gravels. High gravel content is the definitive trait of these sediments, with the grain size distributions peaking in the >-2ø interval (Fig. 4c). They are typically finely or very finely skewed and range from poorly to moderately sorted. A second, smaller modal peak may occur in the sand sized range. Sandy gravel patches are sporadically distributed within the lagoon, with three distinct patches located in the centre of the lagoon and another occuring south of Horsburgh Island. Smaller pockets of sandy gravel are located just north of both Pulu Maria and the seagrass meadows behind South Island.

Factor Four - Gravelly Sands. These sediments are composed principally of sands, but also have a moderate gravel content (Fig. 4d). Grain size distributions are often bimodal, reflecting the poor sorting and variable skewness of most of these sediments. Gravelly sands are also patchily distributed over the lagoon, with a distinct band located lagoonward of the islands on the eastern rim. Several smaller patches occur towards the lagoon centre.

Factor Five - Gravelly Muds. Abundant fine sands and muds characterize these sediments, although gravels are also moderately well represented (Fig. 4e). Sorting, therefore, is typically poor and most grain size distributions coarsely skewed. Gravelly muds occur in the lee of the windward islands and in the shallow embayments locally known as Teloks.

Factor Six - Slightly Gravelly Fine Sands. Fine sands in the 2.5ø-3.0ø range dominate these sediments. The fine sands may grade into muds in some samples and they are usually coarse skewed and poorly to moderately sorted (Fig. 4f). Patches of slightly gravelly fine sands are found throughout the lagoon, however they are more common in the north central areas.

SEDIMENT COMPOSITION

The skeletal compositions of 50 samples collected from the Cocos (Keeling) Islands lagoon are listed in Table 5 and the average composition of sediments deposited in each lagoonal environment presented in Table 6. It is evident from this table that the abundance of skeletal constituents may vary markedly between different lagoonal environments. Furthermore, relatively large standard deviation values suggest that sediment composition may also vary markedly within lagoonal environments.

Nevertheless, several general statements can be made about the composition of sediments deposited within this lagoon. Coral debris clearly dominates most samples (range: 81.46% in sample 12 to 11.05% in sample 58), comprising the major identifiable component in all lagoon environments (see Table 6). *Halimeda* and coralline algae also contribute significantly to many samples (*Halimeda* >15% of samples 24, 29, 45, 48, 49, 58, 124, 171; coralline algae >15% of samples 6, 34, 58, 66, 125, 164, 165, and vibrocore cv15), particularly those collected where hard coral substrates exist, such as the blue hole mosaic and the interisland channels. Coralline algae may either encrust other constituents or consist of rhodolith debris, the later being spherical coralline algae colonies which are particularly abundant in the high energy interisland channels. The *Acropora* shingle which is widespread over the central lagoon floor is also heavily encrusted with coralline algae and represents a potential source of this material. *Homotrema* is a minor contributor to lagoonal sediments (range: 2.48% in sample 24 to 0% in many samples) but appears most abundant close to high energy, hard substrate environments. Gastropod detritus comprises around 5% of the sediment in most lagoonal environments, rising to an average of over 10% in the intertidal sand and mud flat areas, and accounting for more than 10% of some samples from the seagrass meadows (117, 122). Pelecypods comprise less than 5% of most samples, but contribute 9.8% and 9.35% of samples 108 and 38 respectively. *Marginopora* tests make up 0-4% of most samples with no clear pattern to their distribution being immediately apparent. *Amphistegina* is a widespread but locally significant component, being most prolific on the reefs south of Horsburgh Island and in the sandy lagoon floor region in the north of the lagoon. Annelida, alcyonarian spicules, crustacean debris and echiniod spines are generally present in small quantities. Crustacean detritus can, however, occasionally be quite high in areas where living crustaceans are plentiful (i.e. sample 39 from Telok Jambu - 7.85%). Alcyonarian spicules represent only a small proportion of most sediments (range: 6% in sample 50 to 0% in many) but appear most abundant in samples just lagoonward of the reef rim. Indeterminate sediments include sediments <3.5ø and those not readily recognisable because of corrosion. As outlined in the textural results, the abundance of fine sediments is greatest in the seagrass meadows and intertidal sand and mud flat areas. The -0.5ø fraction of a sheltered seagrass meadow, interisland channel, interisland channel/ sand apron and central lagoon sample is presented in Figure 10a-d.

Three factors were extracted from the data matrix covering 15 component variables and 50 sediment samples. All samples except 153 have high communality values, suggesting that a good description of most samples is given by these factors. The lower value for sample 153 probably reflects the exceptionally high representation of *Amphistegina* in this sample, this being more than five times greater than in the sample with the next highest representation. Samples were classified according to the axis upon which they were most heavily loaded except where samples had similar loadings on more than one axis. Loadings were considered similar if the absolute difference between loadings on different axes was less than a third of the larger loading value, and where this occurred samples were deemed to be hybrids. Samples belonging to each class defined by the factor analysis are listed in Table 7 and pie charts showing the composition of the sample most heavily loaded on each factor axis are presented in Figure 6. These and the average compositional facies statistics are presented in Table 8.

Descriptions of the compositional sediment types discriminated by the factor analysis are provided below and their distribution is presented in Figure 7.

Factor One: Coral-Type Sediments. Coral-type sediments are chiefly characterised by the compositional dominance of the sample by coral debris. More than 60% of samples collected from the Cocos (Keeling) Islands lagoon are classified as coral-type sediments, conforming with the preponderance of coral evident in the raw compositional data. Skeletal material derived from organisms commonly associated with hard coral substrates (i.e. *Homotrema, Amphistegina,* annelids and alcyonarian spicules) also reach their highest representation in this facies. Most of the lagoon bed is covered by sediments most adequately described as coral-type, the main exceptions being the areas in the lee of the windward islands.

Factor Two: Molluscan Mud Sediments. A large indeterminate component is characteristic of these sediments and they contain a noticeably smaller quantity of recognisable coral debris than the coral-type sediments depicted by factor one. Gastropod debris is also found in these sediments in moderate amounts, reaching its highest representation in this facies. Crustacean debris is also significantly more abundant in these sediments than in any of the other facies, and *Marginopora* is most prolific in these sediments. Molluscan mud sediments are predominately restricted to the shallow protected parts of the lagoon, however there are outlying patches in the north and central lagoon.

Factor Three Coralline Algae/Halimeda Type Sediments. These sediments are essentially differentiated because they contain a relatively high proportion of coralline algae and *Halimeda* and a relatively low proportion of coral debris. Abundant rhodolith debris determines that sediments deposited in the lee of Pulu Maria and Pulu Siput are most heavily weighted on this factor, whilst *Halimeda* debris is responsible for sediments on the edge of the seagrass meadows in the lee of South Island being loaded on the third factor axis.

DISCUSSION

The nature and distribution of sedimentary facies in the Cocos (Keeling) Islands lagoon essentially reflects the interaction of wave and current energy on skeletal sediments derived from a range of organisms growing in different lagoon environments. The reef islands and a discontinous reef rim control the distribution of wave and current energy within the lagoon; directly controlling the entry and distribution of allochthonous sediment, indirectly controlling the distribution of autochthonous sediments by influencing biotic zonation, and controlling the redistribution of sediments within the lagoon. Three main features characterise the sedimentary facies of the Cocos (Keeling) Islands lagoon, these being: 1) the domination of the lagoon by coral derived sediments; 2) sediment sorting in areas of relatively high hydrodynamic energy and the deposition of predominantly poorly sorted sands and gravels in the centre of the lagoon; and 3) the concentration of mud deposits in the lee of the windward islands, almost exclusively in the seagrass and intertidal sand and mud flat environments.

The predominance of coral derived sediments and subsequent coverage of most of the lagoon by the coral-type compositional facies is a striking feature of the Cocos (Keeling) Islands lagoon (Fig. 7), which is even more remarkable considering the dearth of living coral presently on this atoll. Compared to other carbonate lagoons coral components comprise an inordinate proportion of the sediments deposited in this lagoon (Fig. 8). Several possible reasons exist for the high representation of coral sediments in this lagoon, including its relatively small size and shallow nature. Milliman (1974) suggested that because the ratio of lagoonal area to reef rim becomes smaller as atoll size declines smaller lagoons are more likely to receive a higher proportion of reef flat sediments, including a substantial proportion of coral material. Alternatively, because much of the Cocos (Keeling) Islands lagoon is less than 10 m deep, a depth range dominated by corals in many reef environments (Emery et al. 1954 Stoddart 1969, Milliman 1974), it is perhaps not surprising that coral sediments are abundant here. Indeed, coral outcrops are common throughout most of the Cocos (Keeling) Islands lagoon, imparting a reefal character on most lagoonal sediments. Moreover, lack of net bathymetric relief has restricted the habitat potential of this lagoon and many components and facies derived from organisms normally found in deeper water are poorly represented here (e.g. the deep water *Halimeda* facies reported from deeper lagoons like Suwarrow (Tudhope et al. 1985), Kapingamarangi (McKee et al. 1959) and Enewetok (Emery et al. 1954)).

The geomorphic history of the atoll may provide another explanation for the abundance of coral derived sediments in this lagoon. Woodroffe et al (1990a, 1990b, this volume) have established that approximately 3000 years ago sea level on this atoll was close to 1m higher than present, and that at this time a sea-level limited reef flat encircled much of the lagoon. Sea-level has subsequently fallen to its present level and most of this higher reef flat has been substantially eroded, remnants existing as the contemporary conglomerate platform. Clearly the erosion of this fossil reef flat comprises a potentially significant source of coral sediments which may have been transported around the atoll under different physiographic conditions as the atoll has developed. Prior to the consolidation of the larger islands (particularly South Island), for example, coral sediments were presumably transported into the lagoon through more numerous interisland channels and could potentially achieve a more widespread coverage of the lagoon.

Although coral-type sediments veneer most of the lagoon (Fig. 7), specific areas are covered by sediments which are more or less coral-type than others (i.e. are more or less heavily loaded on the first factor axis due to variations in the abundance of coral and other components), and textural parameters delineate two distinct source zones, the reef rim and the lagoon. Deposits formed by allochthonous material transported from the reef rim are typically most strongly defined as coral-type sediments and those composed of autochthonous material produced within the lagoon less so, reflecting a change from a strongly reefal component assemblage (i.e. coral, coralline algae, *Homotrema,* alcyonarian spicules, *Amphistegina*) to a moderately lagoonal one (reefal components less well represented, fine indeterminate sediments more abundant) (Table 6).

The sandy lagoon floor region is exposed to high levels of wave and current action due to the discontinuous nature of the reef rim at the north of the atoll and the textural traits of sediments deposited there reflect this position. Extensively rippled coarse sands which are near symmetrically skewed and well sorted dominate this area, interupted sporadically by localised seagrass patches and small coral bommies. Sediments deposited here are texturally mature; reflecting the relatively high levels of wave and current energy affecting this area and the rarity of locally generated gravels. Speculation of a peripheral reef source for these sediments is supported by high *Homotrema, Amphistegina* and alcyonarian spicule content; these components normally originating from high energy reef zones and confering a strong coral-type classification on these sediments. Ripple orientation suggests that most of this material is transported from the northeast reef rim. Unlike in much of the southern part of the lagoon these sediments remain submerged at all tidal stages and are continually affected by waves and currents, enhancing their sorting potential. Similarly well sorted and rippled sands are described from the Alacran Reef Complex, Mexico (Kornicker and Boyd 1962) and the lagoon of Enewetok atoll (Wardlaw et al. 1991) and are thought to have developed under similar environmental conditions.

Interisland channels link the high energy and highly productive outer reef flats to the lagoon along the eastern and southern atoll margin and act as a conduit for hydrodynamic energy and sediments entering the lagoon. Waves and currents forced over the windward reefs are concentrated through these channels developing relatively high levels of hydrodynamic energy which dissipates into the lagoon. The composition and texture of sediments deposited through these channels is distinctly reefal, consisting of sands and gravels derived from organisms typically located on high energy reefs such as coral, coralline algae, alcyonarian spicules, *Homotrema* and *Amphistegina*. Not suprisingly these sediments are unequivocally coral-type in composition. The relatively high levels of hydrodynamic energy which affect these channels is reflected by the mean grain size (0.02ø: the largest in the lagoon), and by the deficiency of fine sediments which are continually winnowed and transported into the lagoon. Despite the winnowing of fine sediments interisland channel deposits are generally poorly sorted and texturally immature, reflecting the heterogeneity of contributing organisms and the continual addition of variably degraded 'in-train' clasts. Three samples from the Southern Passage illustrate the coarse nature, in-train addition and textural immaturity of sediments deposited in the interisland channels, these samples (23, 24, 58) located in close proximity to each other and classified respectively as a slightly gravelly coarse sand, a sandy gravel and a gravelly sand.

Coral-type sediments dominate the slightly gravelly medium sands which extend from the interisland channels over the sand aprons and through much of the lagoon centre (Figs. 4 and 6). Despite the continuity of these facies beyond the sand apron fringe (Fig. 2), however, textural gradients in samples collected from the sand aprons and changes in minor component abundance suggest that sediments deposited over sand aprons are allochthonous whilst those deposited beyond these features are autochthonous. The evolution of analogous textural attributes in skeletal carbonate deposits due to either hydrodynamic sorting or skeletal architecture is a principal shortcoming of carbonate texture as an environmental discriminator (Stoddart 1969, Montaggioni et al. 1986) and is well demonstrated here. The redeeming usefulness of textural gradients for environmental interpretation is, however, also confirmed.

Extending into the lagoon over the sand aprons a marked decline in gravel content (24.89% to 7.94%) and an increase in the proportion of sands (74.92% to 90.97%) and muds (0.18% to 1.08%) occurs, conforming elegantly with models of lagoonal sedimentation which predict a systematic decline in mean grain size with distance from the reef rim (Frith 1983, Chevillon and Clavier 1988). Size-sorting is characteristic of backreef sand aprons on other reefs where hydrodynamic energy levels abate into the lagoon and are paralleled by a decline in mean grain size (Macintyre et al. 1987). Size-sorting generally becomes evident from around the mid-range of sand aprons extending into the Cocos (Keeling) Islands lagoon; sediments deposited at this distance from the interisland channels sufficiently removed from locally generated sediment sources to attain some degree of textural maturity. Textural gradients and composition indicate that the sand aprons predominantly comprise allochthonous sediments shed from the reef rim. Similar backreef sand deposits are described in the Pacific (Marshall and Jacobson 1985, Scoffin and Tudhope 1985, Tudhope 1989), where medium grade coral sands also dominate the lagoonward fringe. The penetration of allochthonous sand aprons in the Cocos (Keeling) Islands lagoon is similar to that reported from other reefs (Scoffin and Tudhope 1985), however at this atoll they are spatially restricted to where interisland channels link the outer reef flat to the lagoon and concentric backreef facies belts do not develop.

The systematic decline of mean grain size ceases at the lagoonward margin of the sand aprons essentially marking the limit of allochthonous slightly gravelly medium sand penetration into the lagoon. Grain component data (Table 6) support the assertion that allochthonous sediments (greater than mud-sized) penetrate the lagoon only as far as the sand apron margins, sediments deposited over the lagoonward parts of the sand aprons being generally rounded whilst those deposited beyond sand apron fringes are predominantly angular and autochthonous. The range of the coralline algae/*Halimeda* facies which extend from the interisland channels immediately east of West Island and north of South Island further supports this speculation, and demonstrates the utility of skeletal carbonates derived from habitat specific organisms as biogenic tracers of sediment transport. These facies are chiefly comprised of rhodolith debris originating from these channels which can be traced, and is size-sorted, towards the lagoonward sand apron fringe. Kench (pers. comm) has suggested that the flood tidal wave entering the lagoon from the north opposes currents flowing through the Southern Passage around the lagoonward sand apron fringe, possibly impeding the transport of allochthonous sediments beyond this point. Immediately beyond the lagoonward sand apron margins the textural trends imposed by hydrodynamic sorting are corrupted by the addition of autochthonous gravels and sands and the skeletal architecture of contributing organisms becomes the principal determinant of facies texture. The lagoonal limit of allochthonous sediments may be obscured, however, when they prograde over gravel bearing reefs such as those fringing the blue holes behind the eastern reef islands. Here a band of gravelly sands has developed when transported and sorted allochthonous sands mix with and are texturally overwhelmed by gravels derived from the lagoonal patch reefs.

The irregular mosaic of textural facies covering the central part of the lagoon suggests that sedimentation is chiefly governed by the locally abrupt bathymetric (and environmental) change imposed by the blue holes and the sporadic occurrence of patch reefs and lag gravel deposits. Formed as autochthonous material is deposited *in situ*, the textural characteristics of these facies are dependant on the grain sizes yielded as contributing organisms degrade, and the extent to which hydrodynamic conditions modify these deposits. Sediments through the centre of the lagoon are characteristically poorly sorted and coherent textural gradients are lacking, indicating the absence of significant hydrodynamic modification. Low mud values suggest, however, that fines may be winnowed from exposed deposits. The prevalence of coral debris through the centre of the lagoon is convincingly demonstrated by the distribution of the coral-type compositional facies, and the mosaic of textural facies which occurs through the same region can largely be ascribed to the variable representation of epilithic gravels derived from lagoonal patch reefs. The irregular bathymetry around the blue holes further ensures an erratic distribution for textural facies in this part of the lagoon via its control of patch reef distribution. Essentially these sediments are composed of medium to coarse coral sands supplemented with varying amounts of epilithic coral gravels to form various grades of gravelly sand and sandy gravel facies. The distribution of compositional facies other than coral-type is related to the occurrence of the definitive organisms, the presence of which may also impart distinctive textural properties. Isolated molluscan mud and coralline algae/*Halimeda* facies in the central part of the lagoon, for example, occur where the representation of their definitive components is high, and where largely intact and gravel sized mollusc shells and *Halimeda* segments respectively induce local coarsening of facies texture. Though coral detritus undoubtedly dominates most sediments through this area of the lagoon, the extent to which it does so and the representation of minor components varies considerably both within and between lagoonal environments (Tables 5 and 6), largely reflecting the diffuse and weakly zoned distribution of contributing organisms and the *in situ* deposition of derived sediments. Despite local variations in the representation of minor components, however, the overwhelming dominance of coral debris and the relative constancy of the component assemblage through the lagoon centre, which can be attributed to the lack of strong environmental and hydrodynamic gradients, has determined that except for at the extreme environments in this lagoon distinctive correlations between lagoonal environment and compositional/textural facies are difficult to define. Widespread facies-environment coincidence has been demonstrated in many carbonate emvironments (Ginsburg 1956, Swinchatt 1965, Boscence et al. 1985), however similarly poor correlations between facies distribution and lagoonal environment are reported from other lagoons where environmental/hydrodynamic condtions remain constant over most of their area (Colby and Boardman 1989).

The distribution of fine sediments within the Cocos (Keeling) Islands lagoon exhibits the strongest and most consistent textural/compositional facies and lagoonal environment correlation. In contrast to other lagoons where muds winnowed from the high energy peripheral zones accumulate in the lagoon centre (McKee et al. 1959, Roy and Smith 1971), significant mud deposits in the Cocos (Keeling) Islands lagoon are confined to the sheltered depositional environments in the lee of the windward islands. The concentration of mud facies behind windward reef islands is also described from the Tarawa atoll and Chesterfield Islands lagoons where reef islands effectively isolate the lagoon in their lee from erosional waves and currents. In the Cocos (Keeling) Islands lagoon muds are almost exclusively deposited in the seagrass meadow and intertidal sand and mud flat environments in the lee of South Island and in the West Island teloks (Figs. 2 and 4), with a marked concurrence of environment and facies boundaries. In addition to the sheltered position, the current reducing affects of benthic flora may enhance fine sediment deposition over the seagrass meadows (Ginsburg and Lowenstam 1958, Swinchatt 1965, Scoffin 1970), and intertidal periods of subaerial exposure may aid the accumulation of fine sediments in the intertidal sand and mud flat areas. Adjas et al. (1990) have demonstrated that most carbonate muds deposited in atoll lagoons are biogenic rather than chemogenic, and it is likely that the muds deposited in the Cocos (Keeling) Islands lagoon are produced by the attrition of larger skeletal carbonates (due to biological and physical action). Although some of these fine sediments are no doubt produced *in situ* it is likely that fines winnowed from elsewhere in the lagoon and transported to these sites comprise a significant proportion of these muds. In these low energy settings 'currents of delivery' rather than 'currents of removal' (Orme 1973) principally govern facies texture. The muds are deposited with autochthonous gravels and sands derived from indigenous molluscan, and to a lesser extent crustacean and coral gravels to form the gravelly mud/molluscan mud facies depicted in Figures. 3, 4, 5 and 6. Abundant molluscan and crustacean faunas presently inhabit the areas of the lagoon where muds are deposited and generate significant quantities of gravel sized sediment, however coral gravels in these deposits usually consist of lag material deposited under different physiographic conditions (i.e. prior to being isolated from the reef rim by the reef islands) or else brought to the surface by bioturbation. The skeletal remains of organisms indigenous to the seagrass meadows and intertidal sand and mud flats are particularly well represented in the recognisable fraction of these sediments (e.g. crustaceans, gastropods, *Halimeda, Marginipora*), and are normally deposited reasonably intact. The fragile tests of the epibiontic foraminiferan *Marginopora,* for example, remain relatively undamaged in these deposits but are usually fragmented in sediments deposited elsewhere. Furthermore, minor components derived from high energy reef areas (e.g. *Homotrema, Amphistegina,* alcyonarian spicules) are poorly represented.

Muds are only nominally present outside of these areas, isolated deposits of finer sediment elsewhere in the lagoon essentially developing due to local modification of the hydrodynamic regime by seagrass beds, patch reefs and bathymetric change. Isolated patches of slightly gravelly fine sand amongst the generally coarse sediments of the high energy sandy lagoon environment can be directly attributed to patches of the seagrass *Thalassodendron,* the blades of which reduce current velocity and induce the deposition of finer sediment which is then stabilised by the root system (Scoffin 1970). The association of molluscs (and molluscan debris) and seagrass evident in the *Thalassia* seagrass meadows behind South Island is also apparent in the isolated *Thalassodendron* patches, and sediments over these patches are compositionally classified as molluscan mud sediments. Muds also settle from suspension and accumulate at the base of many of the blue holes where low energy levels predominate, and pockets of muddier sediment are often deposited around patch reefs which impede current flow. These sediments are also often compositionally classified as molluscan muds, however it is the domination of fine indeterminate/mud sediments in these areas which confers this classification. The deposition of muds adjacent to patch reefs due to their modification of lagoonal currents has similarly been reported by Frith (1983) and Delasalle et al. (1985) and muds are reported to accumulate at the bottom of lagoonal 'pools' in Fanning Lagoon (Roy and Smith 1971). The concentration of fine sediments in sheltered areas behind the windward islands and their general absence elsewhere suggests that ambient lagoonal currents are sufficient to entrain and transport most fines out of the lagoon. The burrowing shrimps which inhabit areas of the lagoon bedded by sand may aid this process by resuspending sediments ejected from their burrows into the water column (Tudhope and Scoffin 1984, Scoffin and Tudhope 1985, Tudhope 1989). A sizable sediment shute extending seawards between Turk's reef and Horsburgh Island physically records the transport of sediment out of this lagoon, although the character of these sediments is not known. The purging of sands and muds outside of reef systems has, however, been well documented (Neumann and Land 1975, Roberts and Suhayda 1983, Frith 1983).

It is interesting to note that the sediments deposited in this lagoon do not appear to conform with the Sorby principle (Folk and Robles 1964) which predicts the generation of size specific grain size populations controlled by the skeletal architecture of the contributing organisms (Fig. 9). Non-conformance with the Sorby principle is not uncommon however, with several authors reporting no apparent size specificity in sediments derived from different constituent organisms (Clack and Mountjoy 1977, Flood and Scoffin 1978, Gabrie and Montaggioni 1982). The ubiquity of coral sediments at all grain sizes is apparent in Figure 9, and may possibly distort the recognition of distinctive component-specific grain size populations simply by dominating grain counts.

CONCLUSION

The lagoonal sediments of the Cocos (Keeling) Islands are principally composed of gravels and sands derived from corals with minor components such as mollusc, *Halimeda* and rhodolith debris becoming locally important. Coral-type sediments overwhelmingly dominate the lagoon, reflecting the lack of significant populations of carbonate producing organisms other than coral on this atoll. Textural and compositional trends indicate that allochthonous sediments are deposited in this lagoon only as far as the sand aprons and sandy lagoon floor environments, beyond which sediments are almost entirely autochthonous. Allochthonous coral-type sediments can be identified by the inclusion of significant quantities minor components which are of distinctly high energy reef origin and by size-sorting along established hydrodynamic gradients. The irregular distribution patttern of textural facies in the centre of the lagoon reflects the deposition of epilithic gravels and sands produced as sporadically distributed patch reefs and lag material degrades *in situ* .

The concurrent distribution of the gravelly mud textural facies, the molluscan mud compositional facies and the seagrass meadow and intertidal sand and mud flat environments is remarkable, and largely reflects the extent to which depositional conditions in these facies/environments are differentiated from the rest of the lagoon. Depositional conditions in these areas are characterised by low hydrodynamic energy levels, either as a function of position relative to the high energy interisland channels and/or as a function of the current reducing action of benthic flora. Fine sands and muds, which may be both allochthonous and autochthonous are deposited in these zones with a coarse gravel component derived from the remains of indigenous organisms such as gastropods and crustaceans

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Table 1. Sedimentological data and statistics for 76 sediment samples from the Cocos (Keeling) Islands lagoon. Key to abbreviations as for Table 2.

Sample	Grainsize Weight %														Mean	Sorting	Skewness	%Gravel	%Sand	%Mud	Environment
	-2	-1.5	-1	-0.5	0	0.5	1	1.5	2	2.5	3	3.5	4	>4.0							
11	18.5	7.5	8	26.8	9.9	18.9	7.5	1.7	0.6	0.2	0.1	0.1	0	0	-0.81	1.09 (PS)	'-0.08 (NS)	34.01	65.98	0	I
12	15.1	8.9	10.4	20.2	18.3	17.7	7.4	1	0.2	0.7	0	0	0	0	-0.75	1.04 (PS)	'-0.14 (CS)	34.41	65.59	0	I
22	0.9	0.9	3.1	9	21.1	5.8	18.4	17	12.8	6.5	3.1	1.1	0.3	0.2	0.70	1.09 (PS)	'-0.04 (NS)	4.84	94.99	0.16	I
23	4.4	4.6	10.6	21.6	6.5	15.1	11	10.8	8.3	6.5	0.4	0.1	0	0	0.12	1.28 (PS)	0.03 (NS)	19.68	80.31	0	I
24	3.6	4.1	6.5	12.4	14.7	17.2	13.4	12	8.2	5.4	2.2	0.3	0.1	0.1	0.28	1.23 (PS)	0.01 (NS)	14.21	85.73	0.05	I
58	29.3	3.6	6.1	9.8	2.8	6.3	6.8	7.6	9.2	7.2	5.7	3.2	1.1	1.4	-0.10	1.94 (PS)	0.17 (FS)	38.92	59.62	1.44	I
152	53.7	6.8	6.8	6.5	1.7	4.4	5.1	6.2	5.2	2.3	0.8	0.3	0.1	0.1	-1.16	1.47 (PS)	0.81 (SFS)	67.27	32.59	0.12	I
153	1.5	0.1	0.1	1	1.1	31.8	17.7	26	14.5	4.6	1.2	0.2	0.1	0	0.92	0.69 (MS)	0.09 (NS)	1.74	98.25	0	I
157	20	5.7	6.9	9.1	2.9	6.8	6.1	7.9	13.3	13.8	6.3	0.8	0.4	0	0.17	1.84 (PS)	'-0.13 (CS)	32.51	67.48	0	I
167	0.3	0.4	0.7	5.8	6.7	53.2	24.9	6.3	1.4	0.2	0.1	0.1	0	0	0.40	0.5 (WS)	0.08 (NS)	1.32	98.67	0	I
1	0.3	0.4	1.5	13.2	6.2	15.6	17.3	16.4	17.7	10.9	0.4	0	0	0	0.76	1.06 (PS)	'-0.12 (CS)	2.2	97.8	0	II
32	0	0.8	2.4	9.8	4.6	11.8	14.4	16.4	19.9	13.6	5	0.9	0.3	0.1	1.05	1.12 (PS)	'-0.18 (CS)	3.25	96.59	0.14	II
34	4.9	3.1	2.5	7.2	6.8	10.3	18.6	21	15.6	6.2	2.3	0.5	0.2	0.9	0.70	1.26 (PS)	'-0.49 (SCS)	9.66	89.46	0.88	II
35	3	1.5	1.6	13.8	4.6	11.2	11.7	14.4	18.3	11.8	5.7	1.4	0.4	0.6	0.87	1.33 (PS)	'-0.21 (CS)	6.12	93.32	0.55	II
38	13.6	0.4	2.9	8.2	2.8	6.9	8.2	11.5	14.9	15.6	9.3	33.5	1.2	0.9	0.86	1.73 (PS)	'-0.35 (SCS)	17.01	82.06	0.91	II
114	1.1	0.6	2.9	12	4.2	9	12.7	14.9	17.9	14.3	6.8	1.9	0.7	1	1.01	1.29 (PS)	'-0.20 (CS)	4.57	94.44	0.98	II
141	0.1	1.5	1.9	5.8	10.1	21.7	16	11.5	10.3	11.9	8.2	0.8	0.1	0.1	0.94	1.15 (PS)	0.15 (FS)	3.49	96.39	0.1	II
164	1.3	1.9	2.6	19	5.8	10.6	8.9	8.6	9.4	9.4	8.7	6.4	3.5	3.8	1.00	1.66 (PS)	0.09 (NS)	5.88	90.36	3.75	II
165	8.1	5.2	6	17	4.1	7.6	7.1	8.8	11.5	9.6	7.4	3.8	1.4	2.5	0.60	177 (PS)	'-0.03 (NS)	19.24	78.3	2.45	II
2	4.6	4.3	5	7.9	4.1	8.2	9.6	11	14.6	13.4	8.7	3.6	2.3	2.7	1.00	1.69(PS)	'-0.22 (CS)	13.97	83.32	0.27	III
3	7.5	3.6	3.7	5.6	2.6	8.1	11.6	13.3	16.2	12.6	8.1	3.7	1.7	1.7	0.95	1.67(PS)	'-0.28 (CS)	14.83	83.45	1.7	III
5	17.5	9.4	9.4	15.1	4	6.8	5.9	6	7	6.1	5	3.4	2.8	1.5	-0.12	1.94 (PS)	0.34 (SFS)	36.3	62.15	1.53	III
30	4.6	4.6	9.9	18.4	8.8	9.2	9.3	10	7.4	7.3	2.8	3.5	2.2	1.9	0.40	1.59 (PS)	0.44 (SFS)	19.11	79.89	1.9	III
84	0.6	0.7	0.9	2.6	1.4	4.8	7	11.8	21	22.5	17.8	5.7	1.6	1.5	1.87	1.06 (PS)	'-0.22 (CS)	2.3	96.18	1.51	III
89	9.2	2	3.3	9.4	3.5	3.5	5.9	7.8	11.2	18.3	12	9.1	4.9	0	1.20	1.78 (PS)	'-0.60 (SCS)	13.76	81.01	5.23	III
117	4.9	3.1	2.5	7.2	6.8	10.3	18.6	21	15.6	6.1	2.3	0.5	0.2	0.9	0.70	1.26 (PS)	'-0.49 (SCS)	15.66	41.02	43.32	III
120	10.3	4.7	6.5	7.6	1.8	3.7	4	4.2	4.4	3.7	2.5	1.3	0.5	44.8	1.76	2.45 (VPS)	'-0.35 (SCS)	21.46	33.75	44.78	III
122	8.3	2.2	2.5	2.7	0.8	1.7	2.3	4	5.9	5.8	7.7	6.8	4.1	45.1	2.47	2.18 (VPS)	'-0.66 (SCS)	13.02	41.9	45.07	III
142	0.1	0.1	0.3	1.9	1.2	3.6	3.9	4.5	6.4	8.6	14.8	21.3	14.8	18.4	2.90	1.27 (PS)	'-0.32 (SCS)	0.51	81.09	18.38	III
147	0	0.1	0.1	0.5	0.4	1.4	2.5	4.1	5.8	11.5	33.1	30.7	9.3	0.7	2.77	0.75 (MS)	'-0.27 (CS)	0.14	99.18	0.67	III
149	0.9	0.6	1.3	17.4	27.8	11.2	26.2	8.9	2.4	2.4	0.9	0	0	0	0.15	0.79 (MS)	0.16 (FS)	2.78	97.21	0	III
6	6.1	3.4	3.4	15.7	5.6	10.6	17	12.9	10.7	8.5	4.2	1.2	0.5	0.2	0.56	1.43 (PS)	'-0.13 (CS)	12.91	86.92	0.16	IV
8	7.7	6.1	7.6	22.7	5.9	10.7	8.6	8.8	9.8	6.9	3.6	1.1	0.3	0.3	0.15	1.50 (PS)	0.11 (FS)	21.31	78.42	0.26	IV
10	26.6	6.9	18.3	22.9	4.5	7.3	4.8	5.3	2.5	0.7	0.2	0	0	0	-0.97	1.20 (PS)	0.18 (NS)	51.67	48.32	0	IV
29	5.5	3.4	5.3	18.4	5.9	10.3	8.3	7.7	9.7	9.4	8	3	2.6	2.5	0.71	1.71 (PS)	0.09 (NS)	14.26	83.2	2.53	IV
48	5.9	1.8	2	7.5	9.6	10	12	13.4	12.1	12.1	9.3	3.1	0.8	0.5	0.95	1.15 (PS)	'-0.16 (CS)	9.71	89.82	0.45	IV
163	6.5	4	5.1	8.3	2.4	5.6	6.5	10.6	16.7	16.3	10.9	0.1	5.4	1.6	1.10	1.77 (PS)	'-0.33 (SCS)	15.61	82.82	1.56	IV
169	2.7	2.44	5.4	18.4	5.1	9.8	8.6	9	10.4	8.8	9.8	5.8	2.1	1.7	0.90	1.63 (PS)	0.03 (NS)	10.55	87.79	1.65	IV

Table 1. continued

170	2.8	3.5	6.1	12.8	3.8	8	8.6	9.5	11.2	11.8	8.8	6.6	4	2.6	1.10	1.74 (PS)	'-0.11 (CS)	12.36	85.04	2.58	IV
9	0	2.4	3.2	4.6	3.9	9.8	12.3	14.5	17.9	15.8	11.8	3.2	0.5	0.1	1.35	1.21 (PS)	'-0.21 (CS)	5.62	94.26	0.11	V
50	1.2	3.7	5.7	9.9	5.3	17.7	20.3	17.1	14	4	0.7	0.1	0	0	0.51	1.11 (PS)	'-0.21 (CS)	10.59	89.4	0	V
60	0	0.1	0.1	7.1	0.6	1.8	2.5	4.2	7.6	11.9	21.9	21.1	12.7	8.4	2.66	1.30 (PS)	'-0.33 (SCS)	0.24	91.38	8.37	V
124	13.2	25.8	25.5	15.4	3.1	3.5	2.5	2.8	3.8	1.9	0.9	0.9	0.3	0.3	-1.03	1.16 (PS)	0.44 (SFS)	64.46	35.22	0.31	V
125	27.1	21.7	8.8	1.9	4.7	4.3	4.7	4.8	7.2	5.3	5.6	2.3	1.5	0.2	-0.49	1.85 (PS)	0.72 (SFS)	57.15	41.91	0.94	V
128	11.2	15.1	13.8	3.4	3.2	4.5	9.9	10.3	12.2	5.8	4.9	3.3	2.5	0.4	0.17	1.78 (PS)	0.17 (FS)	39.01	58.46	2.53	V
130	1.3	0.1	0.6	1.7	2.7	5.6	10.4	15	15	14.6	14.5	9.6	5	4	1.92	1.24 (PS)	'-0.03 (NS)	1.91	94.1	3.97	V
171	3.2	4.8	8.6	15.7	4.4	9.4	9.1	10	12.5	10.3	6.9	0	3.8	1.3	0.70	1.64 (PS)	0.00 (NS)	16.64	82.12	1.23	V
21	1.7	1.7	2.7	15.3	7.8	16.2	18	13.5	6.9	5.5	4.4	2.3	1.9	2.3	0.66	1.36 (PS)	0.11 (FS)	6.07	91.65	2.26	VI
39	7.8	2.2	3.3	7.6	17.9	5.2	3	2.1	5	4.4	6.1	7.3	10.9	17.2	1.44	2.19 (VPS)	'-0.12 (CS)	13.3	69.47	17.23	VI
161	8	3.2	1.1	6.7	5.7	10.3	11.8	10	6	3.2	3.1	2.3	1.5	27.2	1.47	2.14 (VPS)	'-0.05 (NS)	12.35	60.44	27.21	VI
15	1.1	0.5	0.5	3.9	4.7	32.4	31.9	11.2	4.3	2.8	3.9	2.1	0.3	0.2	0.69	0.83 (MS)	0.23 (FS)	2.13	97.71	0.16	VII
16	2.6	1.8	1.9	8.3	5.5	28	18.2	5.9	4.4	3.8	5.5	8.3	3.7	2	0.99	1.55 (PS)	0.32 (SFS)	6.33	91.7	1.96	VII
57	0	0.2	1.2	7.9	2.3	4.2	4.8	6	8.9	12	17.8	21.3	10.7	2.7	2.18	1.43 (PS)	'-0.47 (SCS)	1.35	95.96	2.67	VII
65	0	0.1	0.1	0.3	0.8	11.3	18.7	19	18.1	14.9	11.5	4.4	0.7	0.4	1.55	0.92 (MS)	0.08 (NS)	0.11	99.49	0.39	VII
66	52.8	17	13.2	0	8.5	1.9	2.8	3.8	0	0	0	0	0	0	-1.60	0.96 (MS)	0.98 (SFS)	81.57	18.43	0	VII
70	0	0	0.1	4.1	5.1	17.1	16	14.4	13.7	12.5	9.5	4.4	1.7	1.4	1.34	1.15 (PS)	0.09 (NS)	0.07	98.51	1.4	VII
79	1.4	2.6	4.4	13.5	4.8	11.4	10.9	12	14.6	11.6	7	3	1.1	1.7	0.90	1.46 (PS)	'-0.11 (CS)	8.41	89.88	1.7	VIII
132	22.7	0.2	0.2	0.8	1.2	5.1	8.5	11.9	15.1	15	13.1	5.2	0.8	0.3	0.65	2.03 (VPS)	'-0.46 (SCS)	23.11	76.54	0.33	VIII
134	3.4	1.9	5.6	8.2	13	15	15.4	13.3	10	7.6	4.5	1.2	0.3	0.4	0.60	1.29 (PS)	'-0.01 (NS)	10.99	88.62	0.37	VIII
136	0	1.8	2.4	7.3	6.3	8	14	9.7	5.5	1.3	0.6	39	2.3	1.9	0.68	1.33 (PS)	0.65 (SFS)	8.02	89.11	2.88	VIII
145	7.4	5.9	6.1	11.7	15.2	13.9	8.3	9.5	14.2	6.6	1.1	0.1	0	0	0.19	1.41 (PS)	0.00 (NS)	19.39	80.55	0.04	VIII
148	3.7	1.9	3.5	13.4	7.2	19.7	18.5	14.6	10.7	4.6	1.9	0.2	0	0	0.45	1.16 (PS)	'-0.11 (CS)	9.13	90.84	0.01	VIII
150	1.8	1.8	2.6	11.8	5.9	18.8	16.8	12	11.4	11.9	5	0.2	0	0	0.73	1.23 (PS)	'-0.02 (NS)	6.21	93.78	0	VIII
156	0	0	0.1	5.7	5.5	20.5	22.8	14.7	8.2	5.7	7.1	6.7	2.5	0.3	1.18	1.20 (PS)	0.30 (SFS)	0.14	99.58	0.27	VIII
13	2.8	3	4.2	19.8	13.1	33.1	12.1	4.1	3.6	2.5	1.2	0.4	0.1	0.1	0.03	0.95 (MS)	'-0.06 (NS)	9.92	90	0.07	IX
14	5.4	2.4	2.5	9.5	21	28.8	12.7	3.4	2.7	4.2	5.2	1.6	0.4	0.2	0.24	1.21 (PS)	0.10 (FS)	10.29	89.5	0.2	IX
45	0.6	0	0.4	3.4	2.8	10.6	16.5	23.1	26.6	13.7	2	0.1	0	0.1	1.25	0.82 (MS)	'-0.20 (CS)	1.07	98.85	0.06	IX
46	0	0	0.2	3.9	1.5	1.8	0	6.5	19.2	25.6	22.3	13.1	5.9	2.8	2.41	0.82 (MS)	0.04 (NS)	0.23	96.92	2.84	IX
49	2.9	2.9	3	8	2.6	4.7	6.4	6.7	13.5	20.3	19	7.7	1.4	0.9	1.42	1.60 (PS)	'-0.47 (SCS)	8.85	90.25	0.89	IX
104	2.2	1.6	1.7	6.3	2.5	5.8	6.8	7.8	10.3	9.7	14.2	18.3	8.7	4.1	1.94	1.59 (PS)	'-0.32 (SCS)	5.53	90.39	4.06	IX
143	0	0	0	0.1	0.3	1.7	7.7	25.4	45.1	18.4	1.14	0	0	0	1.63	0.50 (MWS	'-0.13 (CS)	0.06	99.93	0	IX
144	0.7	1.2	2.2	13.2	8.2	23	21.9	17.3	8.9	2.6	0.7	0.1	0	0	0.46	0.92 (MS)	'-0.08 (NS)	4.14	95.85	0	IX
146	0.1	0.1	0.1	1.7	1.9	10.3	21.4	24.8	13	13.7	10.6	1.9	0.2	0	1.40	0.89 (MS)	0.15 (FS)	0.27	99.69	0.03	IX
151	5.4	7.4	11.1	15.3	3.2	10.1	18	21	1.4	0.2	6.7	0	0	0	0.11	1.38 (PS)	'-0.16 (CS)	23.95	76.04	0	IX
154	1.1	1.6	3.9	12.8	4.6	13.7	19.6	25	14.6	2.6	0.4	0.1	0	0	0.58	1.02 (PS)	'-0.30 (SCS)	6.61	93.38	0	IX
155	0	0	0.1	0.1	0.1	0.8	2	5.6	14.2	36.9	38.3	1.8	0	0	2.31	0.54 (MS)	'-0.25 (CS)	0.1	99.89	0	IX

Table 2. Summary of textural statistics for each lagoonal environment: (n) denotes number of samples per environment.

	Lagoonal Environment								
	I	II	III	IV	V	VI	VII	VIII	IX
(n)	(10)	(9)	(12)	(8)	(8)	(3)	(6)	(8)	(12)
Mean (ø)	0.02 (0.68) Coarse Sand	0.87 (0.15) Coarse Sand	1.34 (1.02) Medium Sand	0.56 (0.70) Coarse Sand	0.72 (1.22) Coarse Sand	1.46 (0.02) Medium Sand	0.83 (1.20) Coarse Sand	0.74 (0.24) Coarse Sand	1.05 (0.89) Medium Sand
Sorting (ø)	1.28 (0.45) PS	1.37 (0.27) PS	1.54 (0.53) PS	1.52 (0.24) PS	1.41 (0.30) PS	2.17 (0.04) VPS	1.23 (0.26) PS	1.39 (0.30) PS	1.00 (0.34) MS
Skewness	0.08 (0.28) NS	-0.15 (0.20) CS	-0.21 (0.35) CS	-0.04 (0.17) NS	0.05 (0.39) NS	-0.09 (0.05) NS	0.23 (0.67) FS	0.03 (0.35) NS	-0.10 (0.15) NS
Gravel %	24.89 (20.71)	7.94 (6.19)	12.82 (10.46)	18.55 (13.86)	24.45 (25.59)	12.81 (0.68)	2.03 (2.68)	10.98 (6.14)	6.90 (7.93)
Sand %	74.92 (20.83)	90.97 (6.78)	73.35 (23.10)	80.29 (13.38)	73.36 (24.47)	65 (6.40)	96.63 (3.26)	88.13 (5.96)	92.58 (7.79)
Mud %	0.18 (0.45)	1.08 (1.24)	13.70 (19.16)	1.15 (1.07)	2.18 (2.84)	22.19 (7.03)	1.33 (0.94)	0.88 (1.16)	0.61 (1.35)

Key

Sorting		**Skewness**	
PS	Poorly Sorted	NS	Near Symmetrical
VPS	Very Poorly Sorted	CS	Coarse Skewed
MS	Moderately Sorted	SCS	Strongly Coarse Skewed
WS	Well Sorted	FS	Fine Skewed
MWS	Moderately Well Sorted	SFS	Strongly Fine Skewed

Environment

I	Interisland Reef Flats	VI	Intertidal Sand and Mud Flats
II	Sand Aprons	VII	Algal Covered Acropora Rubble
III	Seagrass Meadows	VIII	Massive Corals Interspersed with Sandy Patches
IV	Variable Coral and Algal Flat	IX	Sandy Lagoon Floor
V	Blue Hole Mosaic		

Table 3. Sediment sample textural classification based on factor analysis. Bold numbers represent samples with the highest loading on each factor axis.

Sediment Classification	Samples
Factor One	1, 6, 12, 13, 14, **15**, 16, 21, 24, 34, 50, 70, 134, 136, 141, 144, 148, 149, 150, 151, 153, 154, 156, 167.
Factor Two	2, 3, 9, 32, 35, 38, 45, 46, 48, 49, 84, 89, 114, 128, 130, **143**, 155, 163.
Factor Three	5, 10, 58, 66, 125, **152**.
Factor Four	**8**, 23, 29, 30, 164, 165, 169, 170, 171.
Factor Five	39, **117**, 120, 122, 161.
Factor Six	57, 60, 104, 142, **147**.
Variable Mixtures	11, 65, 79, 124, 126, 132, 145, 146, 157.

Table 4. Textural characteristics of sediment types discriminated by factor analysis. Abbreviations as per Table 2. Standard deviations in parentheses.

Factor	1	2	3	4	5	6
(n)	25	19	6	9	5	5
Var. %	37.7	23.4	12.3	6.8	5.8	5.3
Cum. Var.%	37.7	61.1	73.4	80.2	86	91.3
Mean (ø)	0.55 (0.44)	1.31 (0.55)	-0.74 (0.60)	0.63 (0.35)	1.82 (0.42)	2.49 (0.41)
Sorting (ø)	1.11 (0.24)	1.26 (0.45)	1.56 (0.42)	1.61 (0.15)	2.27 (0.14)	2.72 (0.32)
Skewness	0.03 (0.23)	-0.14 (0.23)	0.53 (0.35)	0.07 (0.15)	-0.34 (0.26)	-0.33 (0.54)
Gravel %	8.02 (7.89)	8.32 (9.51)	55.48 (17.20)	15.45 (5.10)	15.16 (3.74)	1.55 (2.27)
Sand %	91.51 (7.82)	90.29 (10.12)	43.84 (16.62)	82.83 (4.21)	49.32 (14.97)	91.60 (6.86)
Mud %	0.46 (0.84)	1.25 (1.46)	0.67 (0.72)	1.82 (1.19)	35.52 (12.66)	6.83 (7.05)

Table 5. Skeletal composition of 50 sediment samples from the Cocos (Keeling) Islands lagoon.

Sample	3	6	9	10	12	24	29	30	32	34	38	39	45	48	49	50	56
Coral	58.13	44.53	58.51	61.32	81.46	44.92	39.95	40.91	75.60	55.64	66.32	24.50	27.58	50.86	27.58	62.67	59.67
Halimeda	0.66	4.11	9.57	20.71	1.75	27.42	19.82	13.66	5.71	11.33	2.13	3.22	18.80	18.56	18.80	12.55	4.58
Coralline Algae	14.37	29.93	15.20	5.06	1.26	6.31	9.37	2.31	11.36	15.54	6.89	0.00	2.97	12.25	2.97	1.90	0.00
Homotrema	0.00	0.00	0.00	0.00	0.20	2.48	0.00	0.00	0.57	0.81	0.60	0.00	0.00	0.00	0.00	0.71	0.00
Gastropods	3.94	6.82	2.58	6.70	8.50	1.82	9.45	7.08	1.91	2.39	1.08	11.80	5.47	6.14	5.57	3.41	7.88
Pelecypods	0.54	2.33	2.00	1.40	0.12	1.18	0.78	0.17	1.38	1.83	9.35	0.00	0.79	0.65	0.79	0.40	2.66
Unknown Molluscs	0.99	6.59	3.86	2.55	1.61	3.82	5.19	4.88	0.49	0.94	4.02	6.54	2.12	4.73	2.12	3.65	3.78
Marginopora	0.40	1.31	0.97	0.33	0.00	3.75	1.92	2.64	1.40	3.06	1.36	3.25	3.14	1.45	3.14	0.00	3.01
Amphistegina	1.48	0.38	0.00	0.00	1.65	2.58	0.00	0.00	0.93	1.13	0.43	0.00	0.06	0.27	0.06	0.92	0.00
Unknown Foraminiferans	2.61	2.89	0.62	0.30	0.00	0.56	1.41	1.18	2.38	3.46	2.35	2.45	5.02	1.49	5.02	0.39	2.15
Annelida	1.39	0.00	0.00	0.42	0.20	2.77	0.00	0.00	0.00	0.00	0.00	0.00	0.04	0.00	0.04	0.07	0.00
Alcyonarian Spicules	1.09	0.54	0.73	0.00	1.95	0.28	0.64	0.58	0.95	1.43	0.91	0.00	0.69	0.37	0.69	6.00	0.00
Crustaceans	0.27	0.00	0.50	1.06	0.98	0.00	1.63	1.55	0.43	0.58	0.11	7.85	2.33	0.13	2.33	0.09	1.67
Echinoids	0.00	0.57	0.31	0.15	0.43	0.00	0.00	0.00	0.00	0.61	0.00	0.00	0.00	0.00	0.00	1.35	0.00
Indeterminable	14.13	0.00	5.14	0.00	0.10	2.12	9.84	25.05	1.26	1.24	5.51	40.41	30.99	4.30	30.99	0.12	14.61
Environment	III	III	IV	IV	I	I	V	III	II	II	II	VI	VIII	V	V	IV	VIII

Sample	57	58	60	65	66	77	79	84	89	104	108	114	117	120	122	124	125
Coral	44.27	11.05	39.05	55.68	80.77	63.62	51.22	68.61	52.48	77.34	31.01	50.07	14.88	51.65	3.55	57.06	56.97
Halimeda	13.87	16.41	5.08	13.89	0.00	4.18	9.85	6.58	2.32	1.05	14.76	5.69	6.94	12.14	3.79	17.95	6.00
Coralline Algae	3.53	44.95	0.11	1.98	19.23	0.00	1.98	0.41	1.25	0.00	12.71	8.29	0.00	1.50	0.00	7.77	18.80
Homotrema	0.00	0.53	0.82	0.28	0.00	0.00	0.12	0.00	0.00	0.91	0.00	0.92	0.00	0.00	0.00	0.03	2.43
Gastropods	6.80	7.14	0.64	6.47	0.00	3.57	8.99	3.49	6.83	3.81	5.93	6.57	12.53	18.69	14.21	8.56	2.78
Pelecypods	3.58	0.83	4.14	2.11	0.00	0.00	4.30	0.90	0.00	2.78	9.80	2.61	3.20	6.30	3.69	4.31	1.86
Unknown Molluscs	4.31	5.87	0.93	2.22	0.00	2.67	3.71	2.30	0.81	3.08	3.70	1.41	2.10	3.24	1.58	1.33	1.32
Marginopora	1.35	2.98	0.66	2.37	0.00	1.76	8.42	1.17	4.00	0.98	1.19	9.70	3.68	0.24	0.19	0.00	3.50
Amphistegina	0.00	0.61	0.03	0.00	0.00	0.00	0.69	0.26	0.00	7.51	0.08	1.29	0.00	0.16	0.12	0.00	1.21
Unknown Foraminiferans	0.96	0.00	2.27	3.00	0.00	2.63	1.32	4.03	4.74	1.15	2.23	0.00	1.53	0.22	4.65	0.04	0.00
Annelida	0.00	0.00	0.00	0.06	0.00	0.00	0.00	0.19	1.93	0.00	0.07	0.21	0.00	0.04	0.31	0.12	2.76
Alcyonarian Spicules	0.49	0.67	0.00	0.40	0.00	0.46	0.00	2.07	0.00	1.98	0.25	1.19	0.00	0.11	0.00	0.08	0.00
Crustaceans	0.95	0.97	0.43	0.17	0.00	0.00	3.40	0.67	3.05	0.00	1.84	3.90	2.83	1.02	2.99	0.24	0.00
Echinoids	0.11	0.00	0.04	0.27	0.00	0.00	0.80	0.52	0.83	0.00	0.09	2.83	0.00	0.17	0.00	0.92	0.62
Indeterminable	19.77	8.00	44.99	14.10	0.00	21.11	5.21	8.29	21.75	0.49	16.36	5.33	52.30	3.90	64.66	1.57	1.74
Environment	VII	I	IV	VII	VII	VII	VIII	III	III	IX	V	II	III	III	V	IV	IV

Table 5. continued

Sample	130	132	136	138	143	144	147	153	156	157	161	163	164	165	171	CV15
Coral	54.31	77.25	63.91	64.75	66.63	69.46	36.25	54.72	66.80	74.67	30.27	49.73	34.21	46.79	48.86	34.26
Halimeda	8.31	5.95	2.41	8.09	11.27	8.55	6.72	12.11	6.58	7.07	8.79	14.02	10.69	12.15	24.68	6.58
Coralline Algae	3.15	4.17	0.67	2.02	10.89	3.30	0.15	1.56	2.76	0.65	12.47	12.87	23.81	21.89	7.48	17.04
Homotrema	0.75	0.24	0.00	1.45	0.37	0.00	0.57	1.72	0.12	1.16	0.00	2.05	0.11	0.08	0.00	0.72
Gastropods	8.82	1.88	1.77	4.24	0.06	1.35	1.57	11.86	1.74	3.78	8.75	5.28	6.09	3.66	4.80	4.19
Pelecypods	1.21	0.73	4.27	0.55	0.63	2.76	0.79	0.02	1.14	0.59	0.37	2.81	1.30	0.11	1.38	11.77
Unknown Molluscs	2.83	2.43	3.16	5.65	3.05	2.08	5.40	3.46	2.48	5.03	1.67	4.51	6.49	3.85	4.66	7.46
Marginopora	4.68	0.15	6.19	1.27	0.13	2.22	1.35	0.58	0.40	1.27	3.19	0.23	0.00	0.21	0.91	8.91
Amphistegina	0.00	0.13	1.49	2.48	2.20	3.83	0.19	33.87	0.40	1.50	0.00	0.00	0.00	0.00	0.00	0.00
Unknown Foraminiferans	2.45	1.50	1.92	0.00	1.45	0.00	7.02	0.64	0.47	1.70	0.00	0.00	2.66	0.08	0.00	0.00
Annelida	0.00	0.01	0.00	0.86	0.00	0.00	0.00	0.01	0.00	0.00	0.00	0.08	0.30	0.09	0.34	0.00
Alcyonarian Spicules	0.00	0.37	0.00	0.00	1.75	1.16	0.69	2.63	3.24	1.26	0.00	0.00	0.97	0.47	0.00	1.09
Crustaceans	0.00	0.06	1.51	1.73	0.00	1.89	1.18	0.00	0.09	0.06	5.95	0.22	0.15	2.32	1.46	3.76
Echinoids	0.59	0.00	0.00	1.13	1.47	3.40	0.10	0.32	0.13	0.15	0.00	1.20	0.28	0.76	0.43	0.72
Indeterminable	12.90	6.28	12.72	5.79	0.05	0.00	38.04	0.26	9.45	0.88	28.56	7.44	13.71	7.31	5.06	2.79
Environment	IV	VIII	VIII	IX	IX	IX	III	IX	VII	IX	VI	V	III	II	IV	V

Table 6. Summary of the proportion of skeletal components in samples from each depositional environment (Mean [S.D.]).

	Lagoonal Environment.								
	I	II	III	IV	V	VI	VII	VIII	IX
(n)	3	5	9	7	8	2	4	6	5
Coral (%)	45.8 [35.1]	58.1 [10.7]	44.7 [15.7]	33.7 [15.9]	55.4 [8.2]	27.4 [4.1]	61.1 [15.3]	63.0 [9.1]	65.4 [12.9]
Halimeda (%)	15.2 [12.9]	7.4 [4.3]	7.1 [4.4]	13.7 [6.3]	13.2 [7.2]	6.0 [3.9]	8.0 [7.0]	5.9 [2.5]	7.5 [3.9]
Coralline Algae (%)	17.5 [23.9]	12.7 [6.1]	8.2 [11.6]	9.6 [6.0]	7.5 [6.5]	6.2 [8.8]	6.2 [8.8]	4.1 [7.5]	3.0 [4.5]
Homotrema (%)	1.1 [1.2]	0.6 [0.3]	0.1 [0.2]	0.4 [0.8]	0.6 [0.8]	0	0.1 [0.1]	0.5 [1.0]	1.1 [0.4]
Gastropods (%)	5.8 [3.5]	3.1 [2.2]	7.5 [5.3]	7.3 [3.4]	4.8 [3.0]	10.3 [2.2]	4.2 [3.2]	4.2 [3.3]	4.3 [3.4]
Pelecypods (%)	0.7 [0.5]	3.0 [3.6]	1.7 [2.0]	4.3 [4.6]	2.1 [1.4]	0.2 [0.3]	1.4 [1.8]	2.5 [1.5]	0.9 [1.1]
Unknown Molluscs (%)	3.7 [2.1]	2.1 [1.7]	3.6 [2.3]	4.3 [2.0]	2.7 [1.4]	4.1 [3.4]	2.3 [1.8]	2.8 [0.9]	3.9 [1.3]
Marginopora (%)	2.2 [2.0]	3.1 [3.8]	1.6 [1.5]	2.4 [3.0]	1.4 [1.7]	3.2 [0.1]	1.4 [1.0]	3.6 [3.2]	0.8 [0.5]
Amphistegina (%)	1.6 [1.0]	0.8 [0.5]	0.3 [0.5]	0.1 [0.1]	0.3 [0.5]	0	0	0.7 [0.6]	8.2 [11.0]
Other Foraminiferans (%)	0.2 [0.3]	1.6 [1.5]	3.0 [2.1]	2.1 [2.0]	0.8 [1.0]	1.2 [1.7]	0.9 [1.2]	1.2 [0.8]	1.0 [0.7]
Annelida (%)	1.0 [1.6]	0.1 [0.1]	0.4 [0.7]	0.1 [0.1]	0.5 [0.9]	0	0	0.5 [1.1]	0.2 [0.1]
Alcyonarian Spicules	1.0 [0.8]	1.0 [0.4]	0.7 [0.7]	0.4 [0.4]	0.9 [2.2]	0	0.3 [0.2]	0.6 [1.4]	1.4 [0.9]
Crustaceans (%)	0.7 [0.6]	1.5 [1.6]	1.2 [1.1]	1.8 [1.4]	0.5 [0.5]	6.9 [1.3]	0.3 [0.5]	1.1 [1.4]	0.4 [0.8]
Echinoids (%)	0.1 [0.3]	0.8 [1.2]	0.3 [0.3]	0.3 [0.5]	0.6 [0.5]	0	0.1 [0.1]	0.3 [0.4]	0.6 [0.7]
Indeterminate (%)	3.4 [4.1]	4.1 [2.8]	19.7 [16.8]	19.5 [22.2]	9.0 [15.3]	34.4 [8.4]	13.8 [9.7]	8.4 [4.9]	1.5 [2.4]
Grain Presentation	Angular/fresh.	Variable, some show evidence of rounding.	Variable, some organic stained, others fresh and appearing unaffected.	Variable, some fresh and angular, others worn and corroded.	As for IV.	As for IV.	As for IV.	Angular/fresh near reefs, rounded with distance.	Macroscopic sediments angular, some with corroded surfaces.

Table 7. Component classification based on factor analysis. Bold numbers represent samples with the highest loadings on the three factor axes.

Sediment Classification	Samples
Factor One:	3, 9, 10, **12**, 24, 29, 32, 34, 38, 48, 50, 56, 65, 66, 77, 79, 84, 89, 104, 114, 120, 124, 125, 130, 132, 136, 138, 143, 144, 153, 156, 157, 163, 171, cv15.
Factor Two:	39, 45, 49, 60, 147, 161, 117, **122**.
Factor Three:	**58**, 164.
Hybrid: Factors One and Two	30, 57.
Hybrid: Factors One and Three	6, 165.
Hybrid: Factors Two and Three	108.

Table 8. Component facies statistics. Bold values denote representative component types.

Factor	1	2	3	Hybrid	Hybrid	Hybrid
Var. %	69.9	20.6	9.5			
Cum. Var. %	69.9	90.5	100			
Sediment-type (samples)	*Coral -type*	*Molluscan Muds*	*Coralline Algae/ Halimeda Type*	*Coral-Molluscan Mud Hybrid.*	*Coral-Coralline Algae/ Halimeda Hybrid*	*Molluscan Mud-Coralline Algae/ Halimeda Hybrid*
Coral	**59.9** **(11.5)**	27.21 (11.97)	29.84 (11.97)	**42.59** **(2.38)**	**45.72** **(1.68)**	31.01
Halimeda	9.38 (6.86)	9.54 (6.08)	**10.38** **(6.16)**	13.76 (0.15)	**8.14** **(5.71)**	**14.76**
Coralline Algae	6.47 (6.02)	2.33 (4.02)	**32.84** **(10.96)**	2.92 (0.87)	**25.94** **(5.65)**	**12.71**
Homotrema	0.52 (0.71)	0.16 (0.32)	0.21 (0.28)	0	0.04 (0.06)	0
Gastropods	4.97 (3.70)	**7.51** **(4.77)**	0.67 (0.57)	**6.94** **((0.20)**	5.25 (2.73)	**5.93**
Pelecypods	2.15 (2.57)	**1.55** **(1.65)**	1.48 (0.77)	**1.88** **(2.41)**	1.22 (1.57)	**9.80**
Unknown Molluscs	2.97 (1.62)	**3.04** **(2.0)**	6.30 (0.38)	**4.60** **(0.40)**	5.23 (1.93)	**3.70**
Marginopora	2.19 (2.60)	2.36 (1.28)	1.43 (1.49)	2.0 (0.91)	0.76 (0.78)	1.19
Amphistegina	1.71 (4.70)	0.05 (0.07)	0.33 (0.31)	0	0.19 (0.27)	0.08
Unknown Foraminiferans.	1.19 (1.28)	3.24 (2.29)	1.84 (1.60)	1.07 (0.16)	1.48 (1.97)	2.23
Annelida	0.33 (0.74)	0.04 (0.1)	0.1 (0.17)	0	0.04 (0.06)	0.07
Alcyonarians	0.92 (1.26)	0.3 (0.35)	0.72 (0.22)	0.54 (0.06)	0.5 (0.5)	0.25
Crustaceans	0.88 (1.14)	3.05 (2.37)	0.37 (0.52)	1.25 (0.42)	1.16 (1.64)	1.84
Echinoids	0.55 (0.78)	0.02 (0.03)	0.28 (0.29)	0.06 (0.08)	0.67 (0.13)	0.09
Indeterminate	5.88 (6.02)	**39.62** **(12.83)**	7.20 (6.84)	**22.41** **(3.74)**	3.66 (5.18)	**16.36**

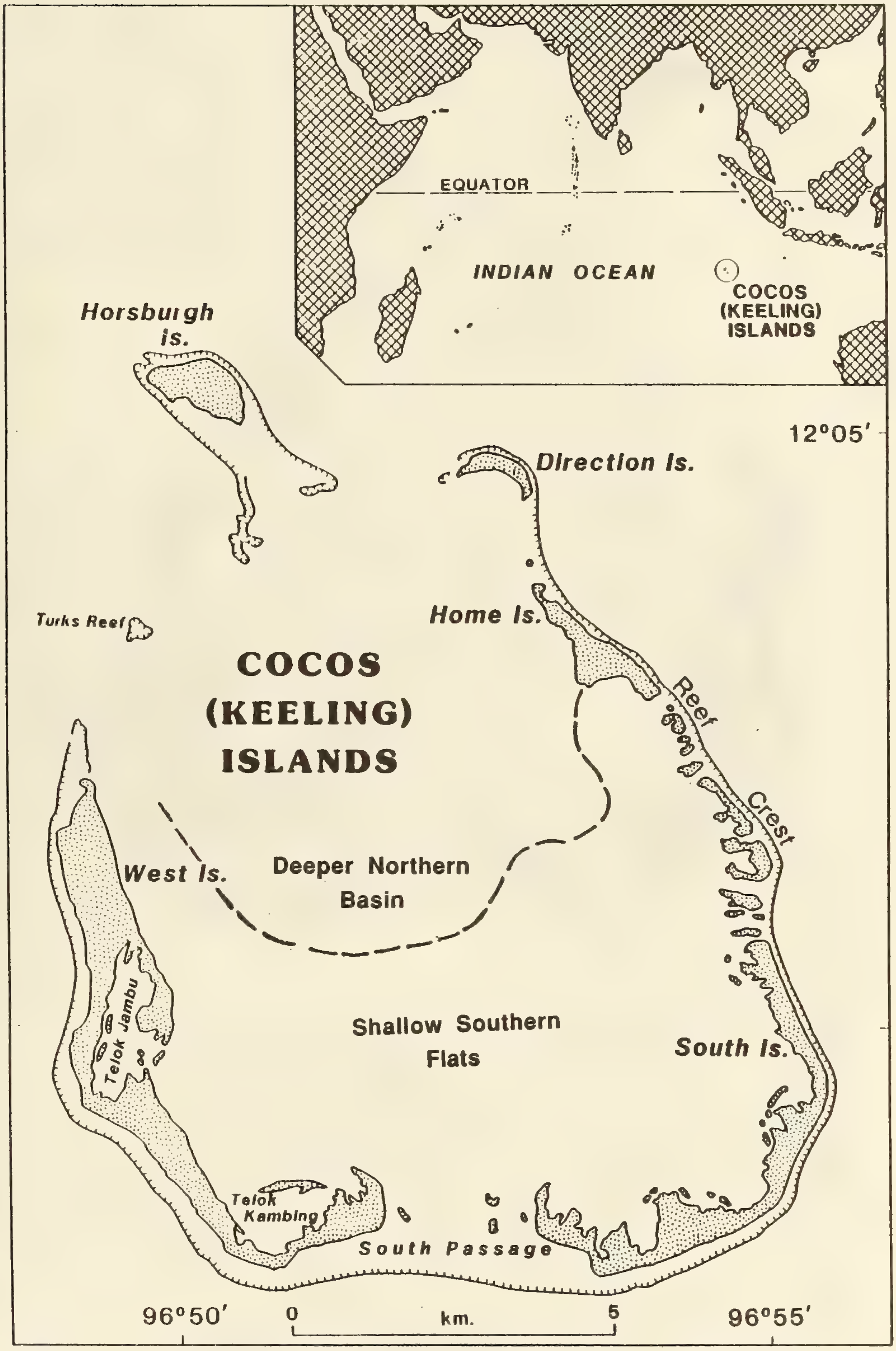

Figure 1. Location map of the Cocos (Keeling) Islands, showing bathymetric precincts.

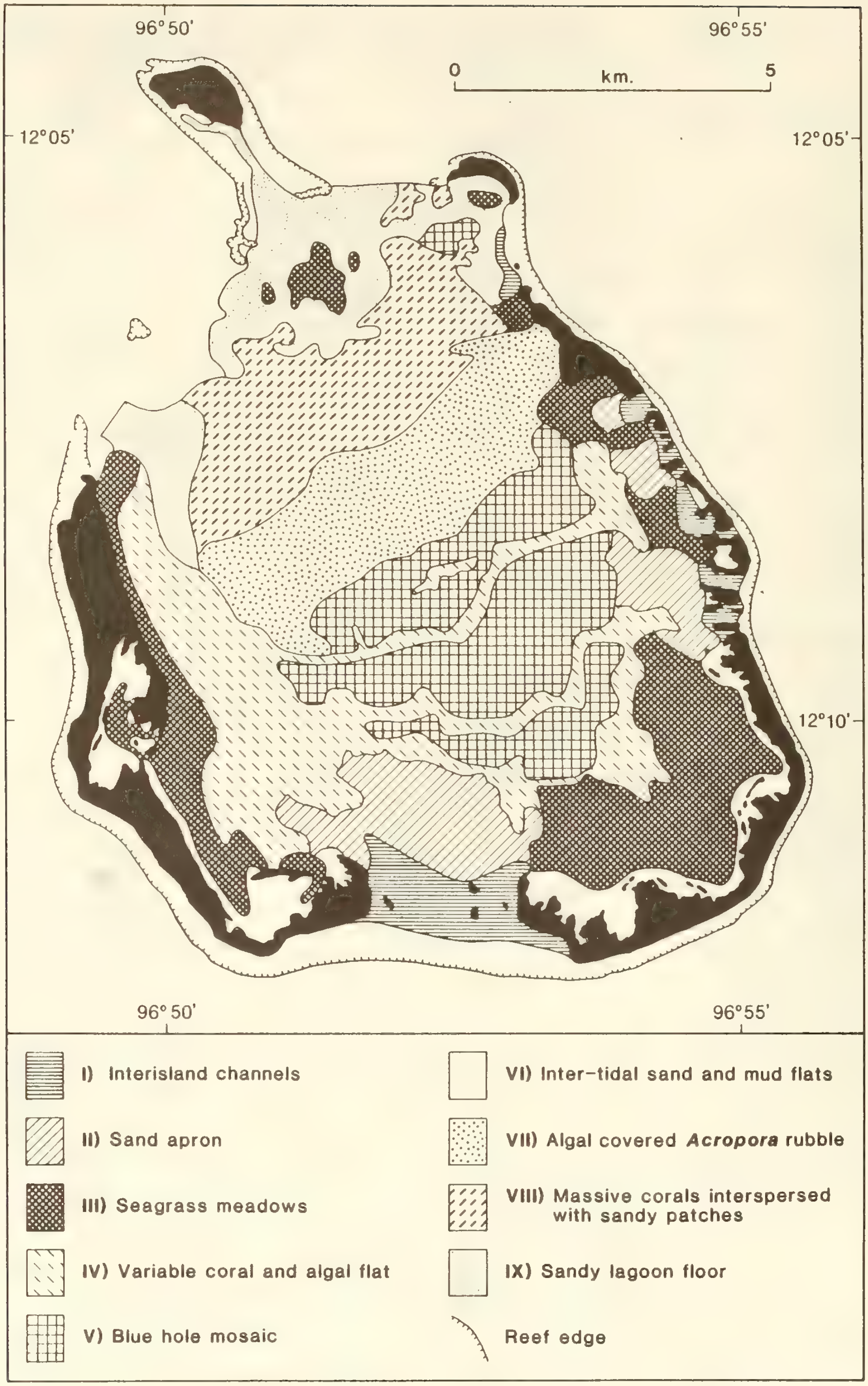

Figure 2. Lagoonal environments of the Cocos (Keeling) Islands.

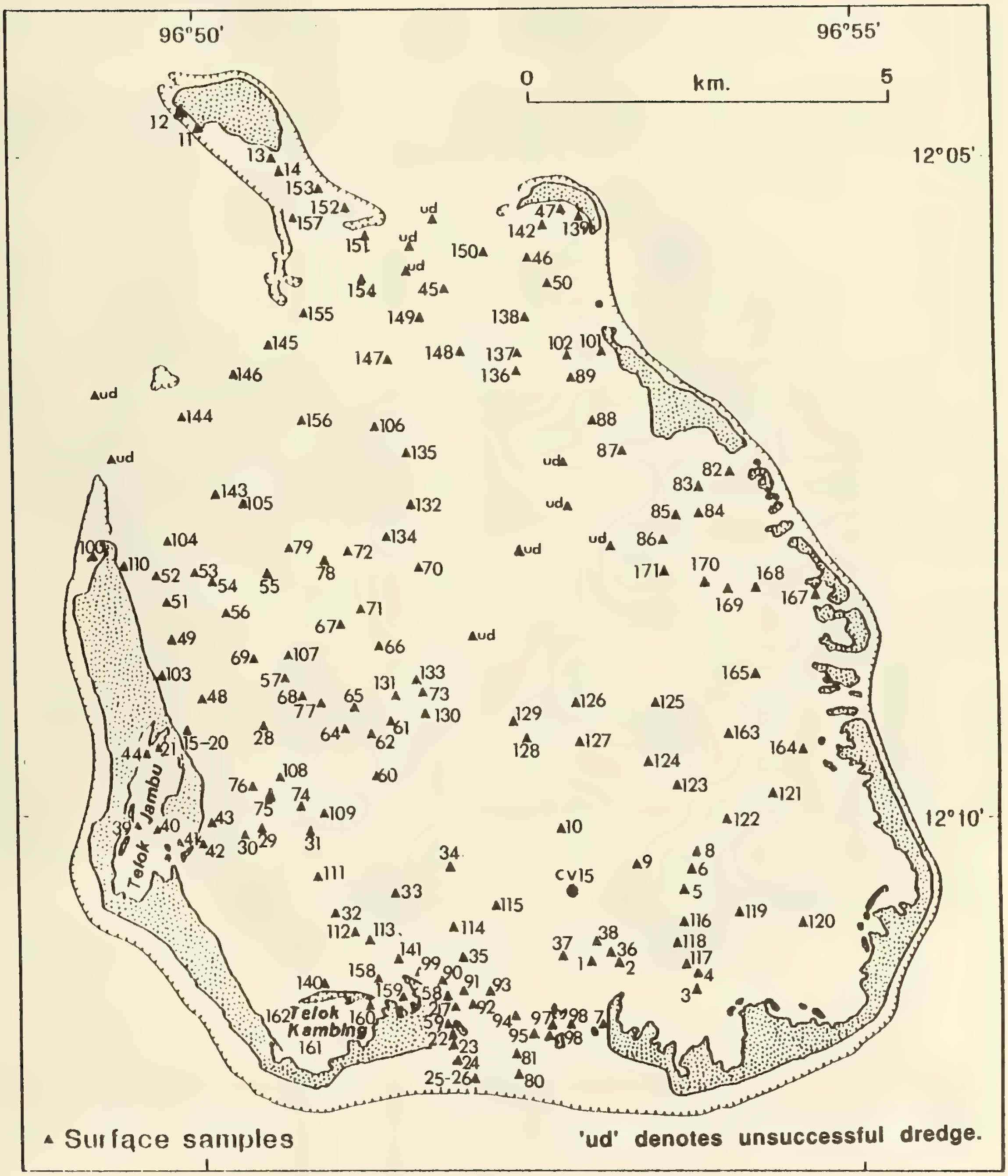

Figure 3. Sediment sample locations.

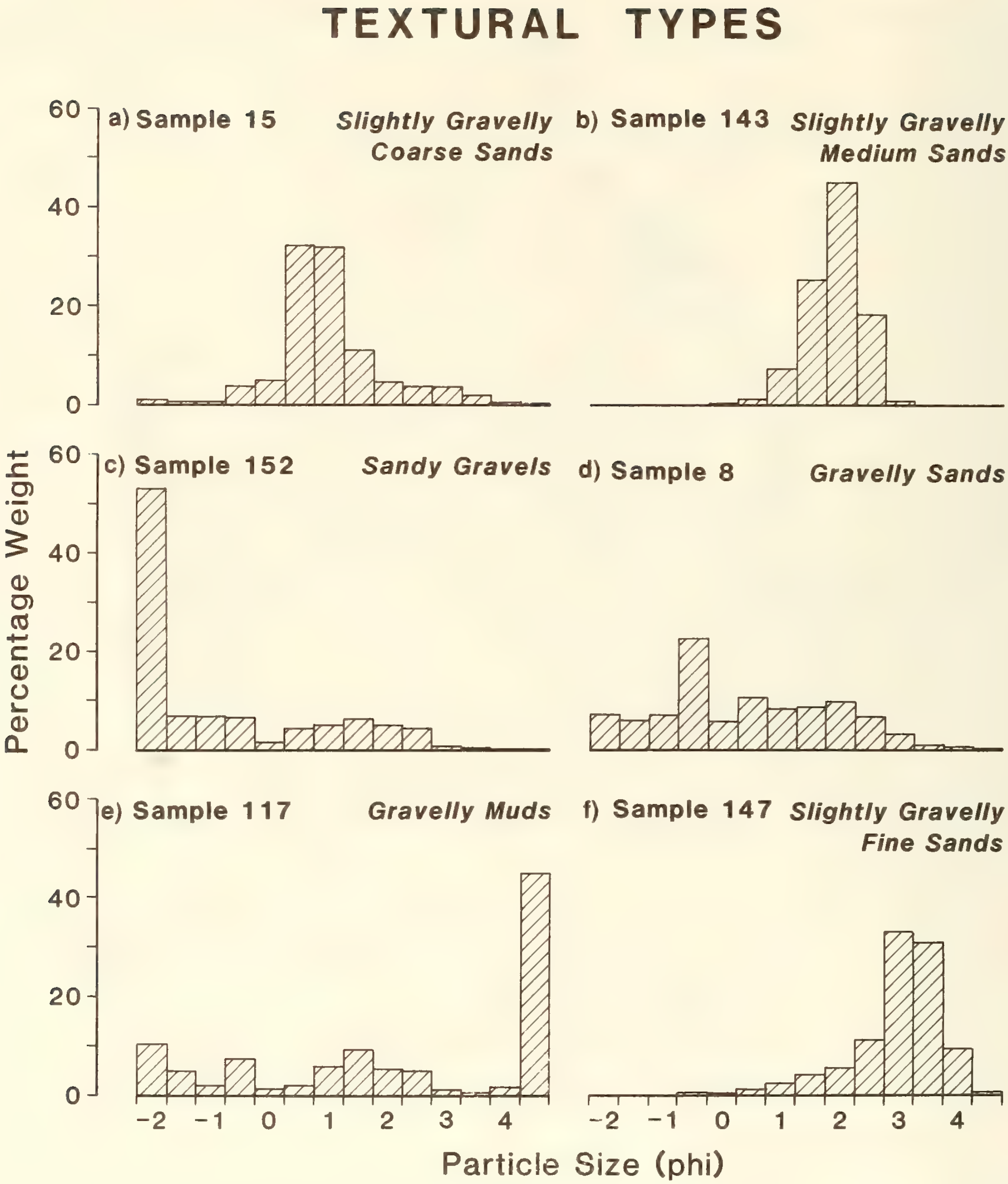

Figure 4. Grain size histograms of samples with the highest loadings on a) factor 1; b) factor 2; c) factor 3; d) factor 4; e) factor 5; f) factor 6.

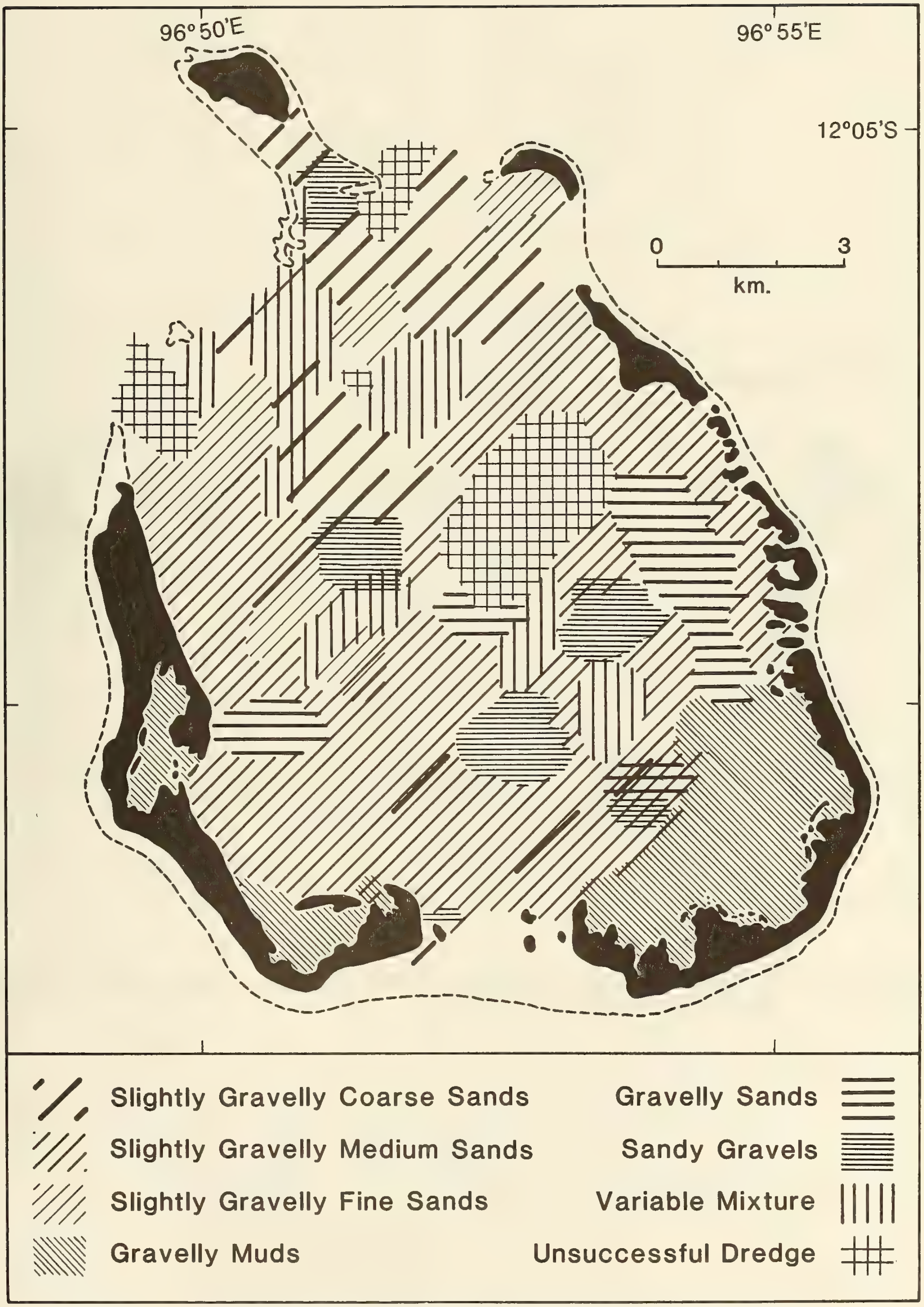

Figure 5. Textural facies distribution, Cocos (Keeling) Islands lagoon.

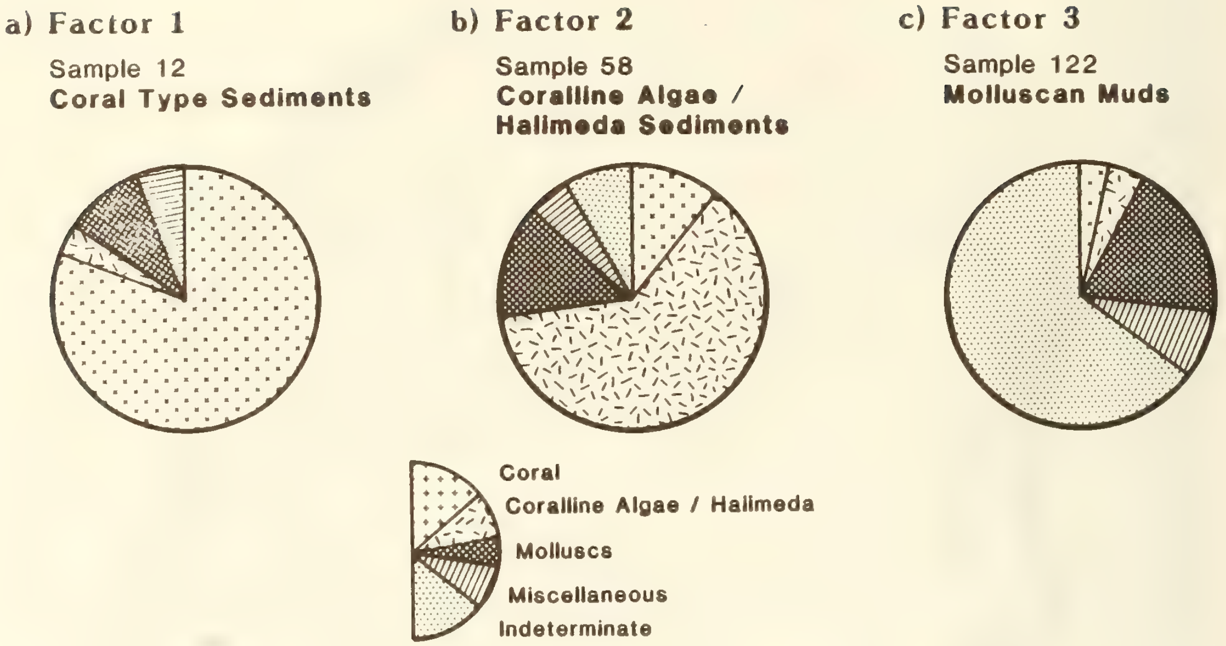

Figure 6. Pie charts showing sediment composition of samples with the highest loadings on a) factor 1; b) factor 2; c) factor 3.

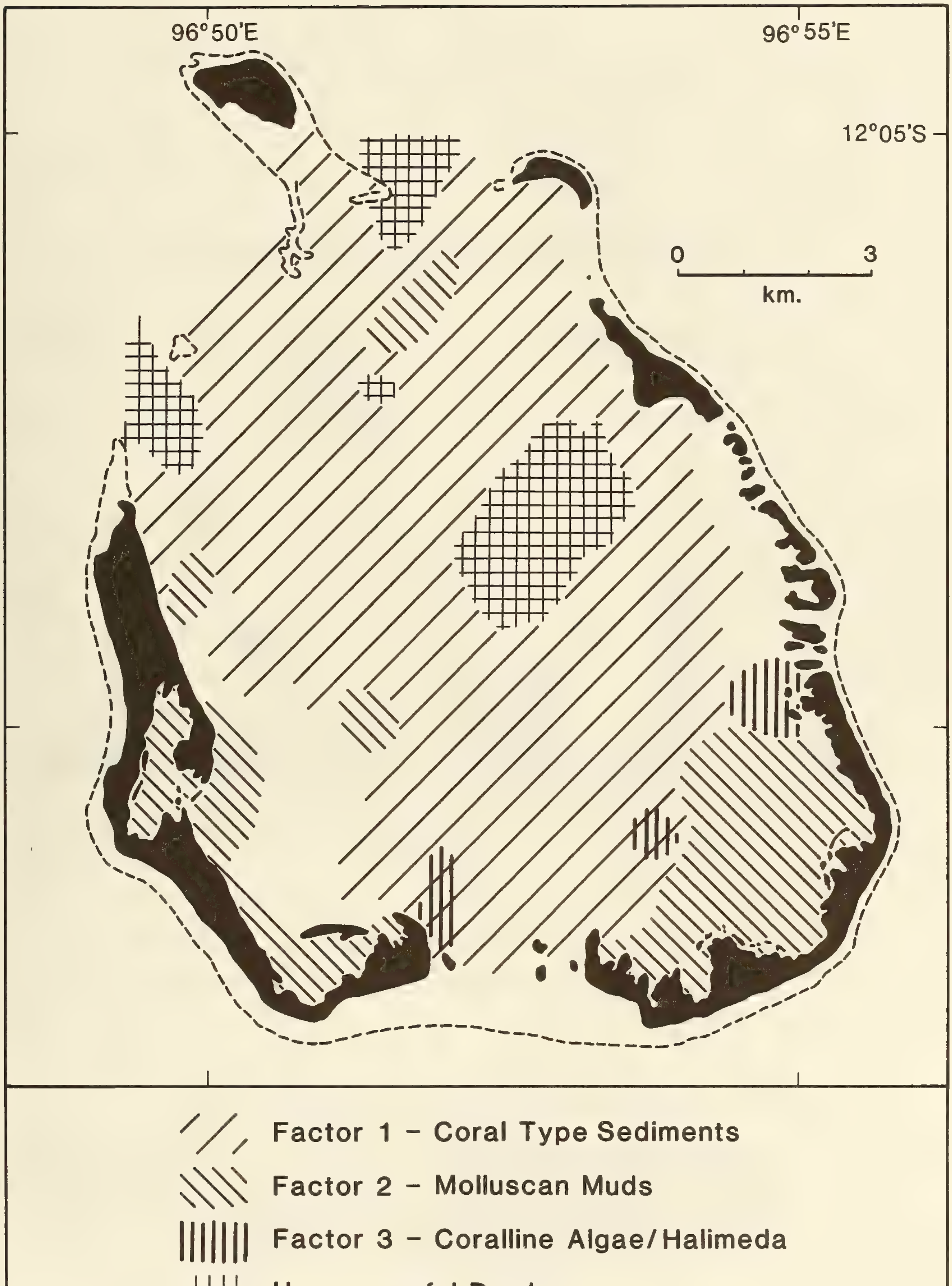

Figure 7. Compositional facies distribution, Cocos (Keeling) Islands lagoon.

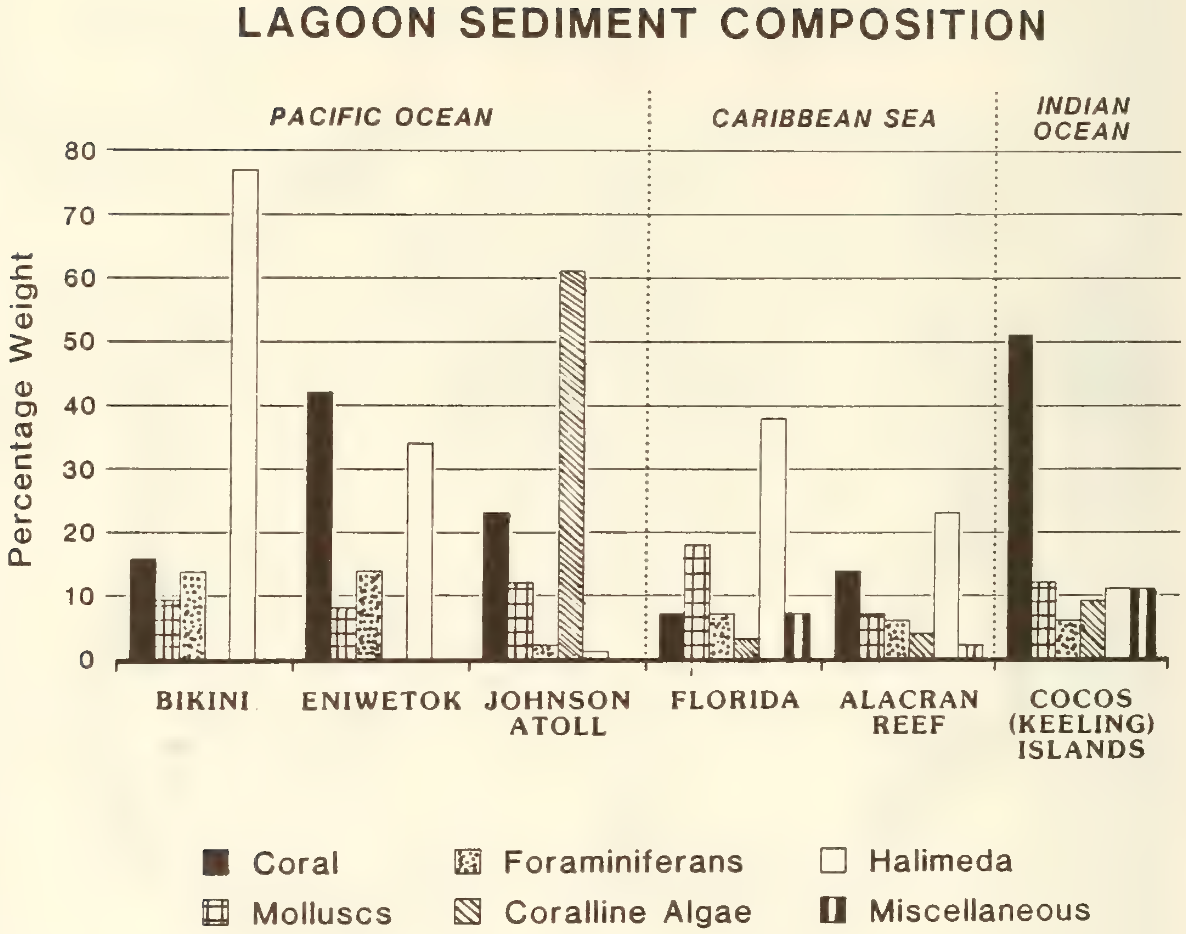

Figure 8. Histogram comparing of skeletal composition of the Cocos (Keeling) Islands lagoon to other carbonate lagoons. Data for other lagoons from: Bikini - Emery et al. 1954, Enewetok - Emery et al. 1954, Johnson Atoll - Emery 1962, Florida - Ginsburg 1956, Alacran Reef - Hoskin 1966.

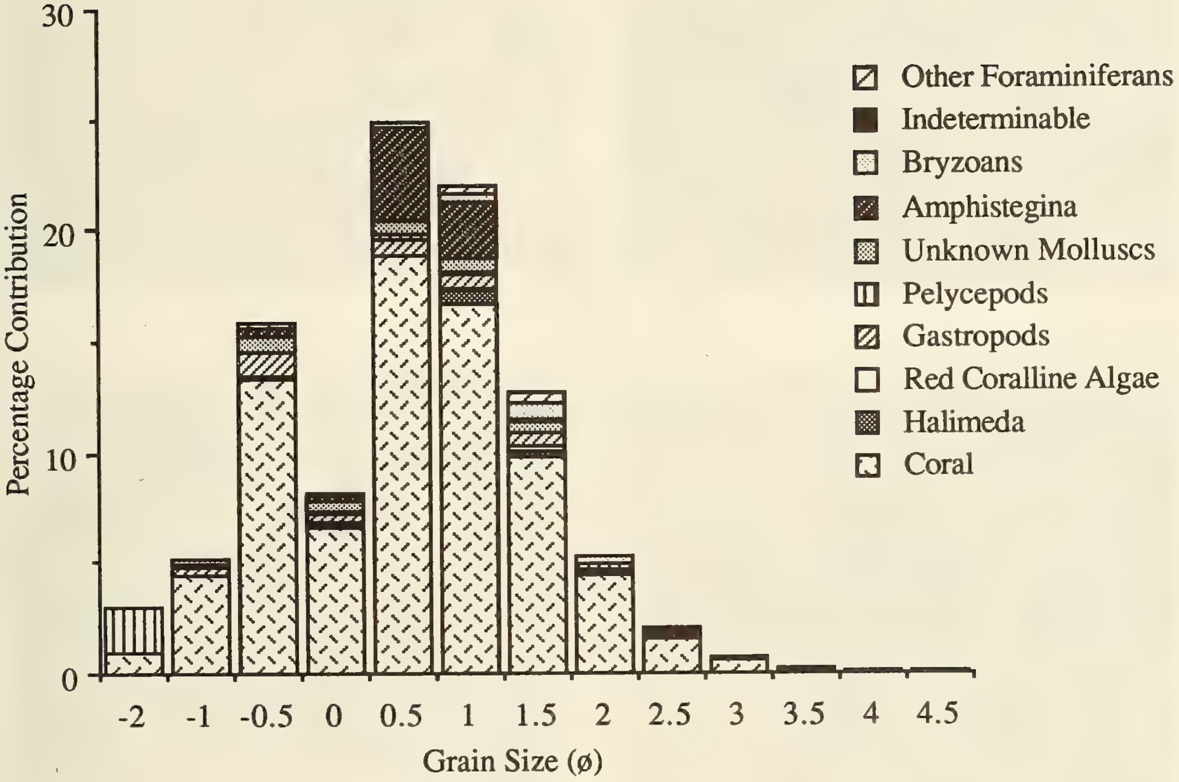

Figure 9. Histogram showing grain size distribution of sample 104 and the size distribution of skeletal components.

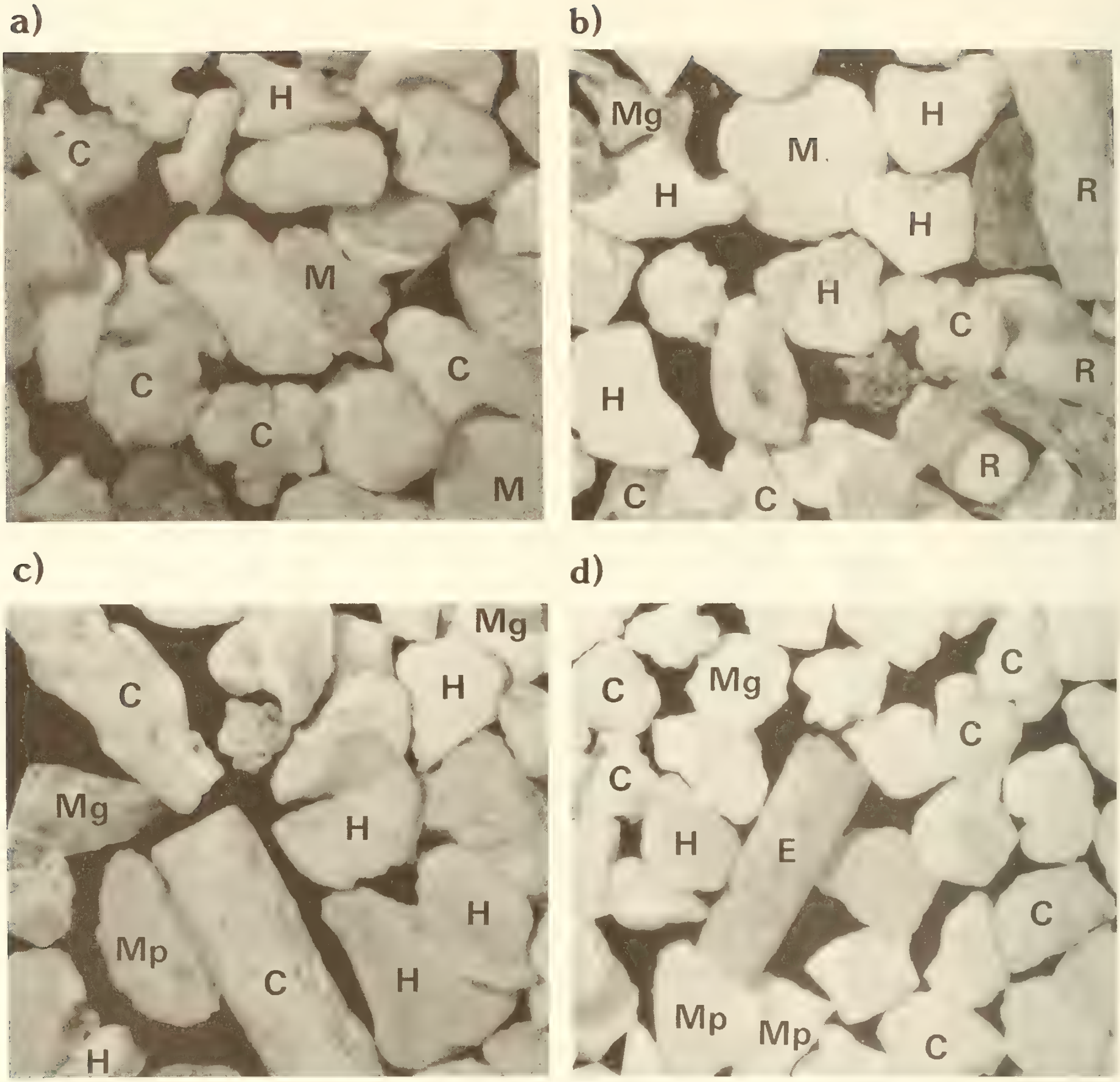

Figure 10. -0.5ø fraction of sediments from various parts of the Cocos (Keeling) Islands lagoon. (a) Sample 24 from the interisland channel. Note the dominance of coral components. Mixed rounded and angular sediments indicative of texturally immature deposit. (b) Sample 58, collected from the lagoonward margin of the interisland channel. Samples predominantly rounded, reflecting the high levels of hydrodynamic energy through this zone. Note rhodolith debris. (c) Sample 120, collected from the seagrass meadow behind South Island. Note the abundance of molluscan material and *Halimeda* flakes. Angular fragments common. (d) Sample 70 collected from the centre of the lagoon. Note the dominance of coral which is variably rounded and encrusted with coralline algae. *Halimeda* flakes, mollusc debris, echinoid spines also apparent. Key: C - coral; E - echinoid; H - *Halimeda*; M - *Marginopora*; Mg - gastropod; Mp - pelecypod; R - rhodolith.

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CHAPTER 10

HYDRODYNAMIC OBSERVATIONS OF THE COCOS (KEELING) ISLANDS LAGOON

BY

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CHAPTER 10

HYDRODYNAMIC OBSERVATIONS OF THE COCOS (KEELING) ISLANDS LAGOON

BY

P. KENCH *

INTRODUCTION

Atoll lagoon hydrodynamic studies to date have primarily focused on the mass flux of water and nutrients through lagoon systems and identified the principle driving mechanisms of lagoon circulation and flushing (von Arx 1948, 1954, Gallagher et al. 1971, Stroup and Meyers 1974, Smith and Jokiel 1978, Atkinson et al. 1981, Gilmour and Colman 1990).

In general, lagoon circulation has been found to respond to three driving mechanisms: wind-driven set-up on the windward ocean reef; wind stress on the lagoon surface, and tides (Atkinson et al. 1981, Andrews and Pickard 1990). Wind has been identified as the the primary driving mechanism of lagoon circulation in deeper lagoon systems (e.g. Bikini Atoll - 60m deep, von Arx 1954, Enewetak Atoll- 50 m deep, Atkinson 1981). Wind is not, however, thought to play a large role in the exchange of water between lagoon and ocean. In shallow lagoons such as that of Fanning Atoll (5 m) tidal forces are found to dominate both lagoon circulation and lagoon-ocean water exchange (Stroup and Meyers 1974).

The degree to which a lagoon is dominated by wind or tidal forces is found to depend on the lagoon depth and the degree of connection between the lagoon and open ocean (Wiens 1962, Stroup and Meyers 1974). The speed of lagoon-ocean exchange is also reliant upon the 'openness' of the lagoon with the ocean.

The majority of atoll hydrodynamic studies have been performed in the Pacific Ocean within deeper lagoons (50-60 m, Enewetak, Bikini lagoons) with the exception of the shallow Fanning Atoll lagoon (5m). There has been little research on the hydrodynamic processes within Indian Ocean atolls, except for research on the tidal characteristics of several atolls in the Western Indian Ocean (Farrow and Brander 1971, Pugh 1979, Pugh and Rayner 1981).

This paper describes results from the examination of the hydrodynamic processes of the lagoon of the Cocos (Keeling) Islands, in the eastern Indian Ocean (Fig. 1). It has three aims: first, to describe the tidal regime of the Cocos atoll lagoon; second, to examine the water currents and circulation within the lagoon and connections between the lagoon and ocean; and third, to establish the flushing characteristics of the atoll.

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FIELD LOCATION

The main lagoon of the Cocos (Keeling) Islands is enclosed by 26 islands and has a surface area of 190 km^2. The lagoon can be divided into two distinct morphological zones: a deep (8-12 m) northern portion and a large shallow (0-3 m) southern region (Fig. 1). A network of deep blue holes exists in this shallow region with depths in excess of 20m. The lagoon opens to the northwest and northeast either side of Horsburgh Island where passes are deep (12-14 m) and wide (2-5 km). Eleven shallow passages (<2 m) connect the ocean and reef to the lagoon on the eastern and southern sides of the atoll.

The atoll is dominated by the southeast trade winds which prevail for most of the year. The islands also lie within the equatorial (westward flowing) ocean current (Neumann 1968), which reaches a maximum velocity of more than 1 knot (Tchernia 1980). In the northern hemisphere winter, movement of the Inter Tropical Convergence Zone (ITCZ) south of the equator produces variable winds and the Equatorial Counter Current (eastward flowing) may develop. The degree to which the Cocos (Keeling) Islands are affected by this counter current is dependent upon the extent of southward migration of the ITCZ (Neumann 1968).

The closest amphidromic point to the Cocos (Keeling) Islands is situated off the southwest coast of Australia (Platzman 1984, for the M_2 tide). The anti-clockwise rotation of the tidal wave around this point and the location of the Cocos (Keeling) Islands, suggest the tidal wave sets from the east-northeast.

METHODS

A field measurement program was undertaken from November 1991 to January 1992. Tidal observations have been taken on Cocos, by the Australian CSIRO Oceanography Division since 1963, from a permanent tide gauge on Home Island jetty (Fig. 1). For the duration of the field measurement period a temporary pressure tide gauge was deployed in the south of the atoll (Fig. 1) to identify any changes in tidal characteristics between the northern (deep) and southern (shallow) regions of the lagoon. This gauge operated successfully for 20 days before being fouled by marine algae. The permanent tide gauge was inoperative during the period of measurement by the temporary gauge. This limits direct comparison of observed elevation and time data. A harmonic analysis (Foreman 1979a) of water level observations from November 17 to December 6 (temporary gauge), and from March to April 1988 (permanent tide gauge) has been made to resolve the major tidal constituents at each location (ease of access to permanent tide gauge data being the primary factor deciding the period analysed).

Current speeds and directions were obtained using five bidirectional electromagnetic current metres. These metres were deployed for 16 day periods in 7 shallow passages and 5 sites within the lagoon (Fig. 1). Current metres were mounted 0.4 m above the bed in the passages and 0.5 m above the bed in the lagoon. Additional, shorter records (1-2 day) were obtained from the deeper passages to the northwest and northeastern sections of the lagoon, and from one station in the middle of the lagoon (Fig. 1). For these experiments 3 current metres were deployed vertically, at depths of 2 m below the surface, mid-depth and 1m above the bed. Current records, in all sampling periods, were 1 minute averages of current velocity taken at 10 minute intervals.

Current time series have been harmonically analysed to resolve the major tidal current constituents (Foreman 1979b). Constituents resolved for each time series were used to predict the tidal currents for the period analysed. Predicted currents were then subtracted from the observed current data to identify those components of the current record not attributed to tidal forces. These currents are termed 'residual currents'.

Velocity profiling using an impellor current metre was undertaken during neap and spring tidal conditions in all shallow passages. Velocity measurements at stations across each channel were corrected to 20 minute intervals and the cross-sectional area of each channel identified for each time increment. Cross-sectional area discharge relationships were then derived for each shallow passage.

Tidal prism - the volume of water entering and leaving the lagoon during a tidal cycle -was calculated for a 1m and 0.4m spring and neap tide respectively. Bathymetric charts (1983) provided lagoon depths relative to 0.7m below Mean Sea Level, corresponding to zero on the Home Island tide gauge. The surface area of the lagoon at low and high tide was estimated through planimetric analysis. The change in depth (1m-spring; 0.4m-neap) was then applied to the respective low and high tide surface areas to calculate the volume of the lagoon. Differences between high and low tide lagoon volumes provide estimates of tidal prisms for the neap and spring tides. With an estimation of total lagoon tidal prism, the contribution of shallow passage water flux to lagoon flushing is identified, and the ocean lagoon exchange time calculated.

RESULTS

Tides

Harmonic analysis of the tidal records identify the semi-diurnal constituents of greatest importance (Table 1) with the M_2 and S_2 constituents having amplitudes of 29 and 14 cm in the north of the lagoon and 25 and 5.6 cm in the south of the lagoon. These amplitudes also display a marked attenuation from north to south within the lagoon. The K_1 constituent has an amplitude of 12.19 cm and 10.28 cm for the north and southern parts of the atoll respectively (Table 1).

The southern lagoon tides lag those of the northern lagoon (Table 1). This lag is evident in the tidal records with observed high tides lagging those in the north by 15-55 minutes dependent on the tidal range and regime (spring or neap tides). Shallow water tides (M_4) are much larger in the shallow southern region of the atoll than the deeper northern lagoon.

The form of the tides as identified by the amplitude ratio [$F = (K_1 + O_1)/(S_2 + M_2)$] is 0.44. This describes the tides as mixed mainly semi-diurnal. These tides characteristically have large inequalities in range and time between the highs and lows each day (Pond and Pickard, 1983). Mean spring tidal ranges using the equation $S = 2(M_2 + S_2)$ are 87 cm and 61.2 cm for the north and south of the atoll. These amplitudes display a marked attenuation of the tide from north to south. The analysis also identifies a 6.02 cm (north) and 7.21 cm (south) increase in Mean Sea Level between neap and spring tide conditions (Msf constituent, Table 1).

Current Circulation

Progressive vector plots of current information are shown in Figures 2-5 for forty-eight hour periods during neap and spring tides. Distance between the 6.5 hour increments allow comparison of the relative velocity and/or duration of tidal flow to be made between stations.

Lagoon

In all areas of the lagoon, except for the western shoreline, currents appear to be tidally modulated during both neap and spring tides (Figs. 2 and 3). The western shoreline of the lagoon exhibits a unidirectional northwestward flow throughout the rising and falling of the tide.

In the eastern part of the lagoon the net flow westward, during neap tides (Fig. 2), is indicative of the longer duration or faster velocity of the westward flowing ebb currents. This pattern changes during spring tidal conditions to a net movement to the northwest (Fig. 3). The southeastward rising tide current is however more prominent during spring tides and penetrates the lagoon to within 1 km of the lagoon shoreline of the eastern islands.

In the southeast of the lagoon net current movement is toward the southwest (neap tides) and west (spring tides). Westward drift is reduced during spring tidal conditions due to the greater oscillation of rising and falling tide currents in the southeast and northwestward directions (Fig. 3).

Current patterns in the southwest lagoon are similar for both the neap and spring tidal conditions. There is a net movement northwestward throughout the 48 hour period displayed. It is evident that rising tide currents penetrate south to within 1 km of the southern passage.

Tidal elevation plays an important role in the magnitude and time period of current reversal in the east and southeast sections of the lagoon. Comparisons of the neap and spring tidal currents identify a greater net movement of water during neap tidal conditions as shown by the distance between starting and finishing points of each 48 hour period. Net flow direction in the east and southeastern sectors of the lagoon rotate 45° toward north during spring tide conditions. This highlights the increased importance of the south/north tidal flow on current direction during spring tides.

Current measurements taken at the deep northeastern passage (Fig. 2) convey a tidally modulated reversal in direction between the ocean and lagoon. This is accompanied by a net movement to the west. Measurements taken in the northwest passage, however, display a unidirectional flow to the southwest. This movement is hard to interpret. There appears to be no marked reversal of current direction with the oscillation of the tide and the direction seems to suggest water is leaving the lagoon. These currents are weak (5-10 cm/s)when compared to those of the northeastern passage. Measurements taken at mid-depth and 1m above the sea bed display similar current patterns to those shown by the surface current record in the deeper passages. Currents in the mid-lagoon are weak (0-7 cm/s) and appear to oscillate with the rising and falling tide (Fig. 2).

Shallow Passages

The shallow passages display a unidirectional flow from ocean-side reef to lagoon during neap tide conditions (Fig. 4). During spring tides the southern passages maintain the unidirectional flow (Fig. 5), while the eastern passages display a reversal in flow direction around low tide (Fig. 5). Due to the intertidal nature of the eastern passages at spring low tide the current record is broken causing distortion to the observed pattern. It is however clear that currents do travel from lagoon to ocean for part of the spring tidal cycle in the eastern passages.

Tidally Driven Currents

As tidal currents vary in speed their direction rotates, usually with a semi-diurnal period dominating (Pond and Pickard 1983). The figure traced out by the tip of a vector representing the tidal current will be an ellipse. Tidal current constituents are presented in Table 2 as properties of tidal current ellipses for the M_2 and K_1 constituents. Figure 6 presents the physical appearance of the M_2 tidal ellipses within the lagoon and shallow passages.

Lagoon currents are dominated by the M_2 tidal constituent (Table 2, Fig. 6) which is strongest in the southwest section of the lagoon at 16.95 cm/s. This constituent is also strong in the eastern side of the atoll at 11.36 cm/s. While the K_1 currents are the second strongest, they are much weaker than the M_2 currents ranging between 0.77cm/s and 4.84cm/s. M_3 and M_4 constituents (not listed) are the next strongest but are generally less than 1 cm/s. The narrow M_2 current ellipses in the east and southwestern sections of the lagoon (Fig. 6) reveal the strong oscillatory nature of tidal currents in these zones which are enhanced by the shallow passage flow. The small and wide ellipse of the southeastern lagoon portrays the weaker currents experienced in this zone. The shallow nature of this area and the curvature of South Island may contribute to the observed weak currents and direction of net flow to the west.

The M_2 currents in the southeast section of the lagoon have a phase lead over the eastern and southwestern areas of the lagoon. The K1 constituent, however, shows a phase lead of 5^o in the east of the lagoon followed by the southwestern section of the lagoon, with the southeastern portion lagging the east by 13^o. This lag may reflect the location of the current metre in the wide shallow western section of the lagoon causing shoaling of the tide. This is supported by the shallow water constituent (M4) having its largest magnitude in this zone (2.2 cm/s).

As with the lagoon currents, the shallow passage tidal currents are dominated by the M_2 tide which is strongest in the southern passages at 7.6 cm/s. The K_1 constituent is of secondary strength within the passages (Table 2).

Residual currents are those components of the observed currents that cannot be explained through gravitational tidal forces. They are produced by wind stress, wind waves and or internal waves (i.e. temperature or pressure gradients). Analysis of lagoon currents identifies a mean of 15.6% of observed currents that are produced by these 'other' forces (Table 2 and Figs. 7a and 7b). Within the lagoon residual currents have their greatest magnitude in the southeast lagoon where 17.2% of the northing component and 27% of the easting component not driven by tidal forces (Table 2). Residual currents account for up to 52% of the observed shallow passage currents. This explains the small semi-major axes lengths of the M_2 ellipses within the passages (Fig. 6), with residual currents being twice as strong as the M_2 tidal current. The orthogonal with the greatest residual strength coincides with the orientation of the passage, i.e. in the southern passages the residual current is greatest for the north-south component of velocity (Table 2 and Fig. 7c).

Figures 7a, b and c show the observed and residual current data for locations within the southeast and southwest regions of the lagoon and the southern passage. Apart from the first four days of observations within the southeast section of the lagoon the residual easting component currents flow to the west (Fig. 7a). It is suggested that residual currents in this section of the lagoon are driven by the southeast trade winds. The strength of the residual current would, therefore, depend on wind strength. Residual currents in the southwest section of the lagoon (Fig. 7b) appear to fluctuate with tidal elevation. The magnitude of these currents is small. The large node in the southern passage residual current (Fig. 7c), coincides with tropical cyclone activity that influenced the island from December 5-8, 1991. The marked velocity increase, may have been the result of increased wave action and tidal elevation at the reef crest together with increased wind speeds. Correlation of wind strength and direction, and current direction, is required to identify the driving mechanisms of the residual currents.

Shallow Passage Water Flux, Tidal Prisms and Lagoon Exchange

Lagoon tidal prisms calculated for a 1m (spring) and 0.4m (neap) tide are presented in Table 3. The spring tidal prisms for each shallow passage are shown in Figure 8 and cumulative spring and neap prisms for the shallow passages are presented in Table 3. A relationship is found between the cross-sectional area of each passage and the tidal prism, with larger passages transmitting greater volumes of water from ocean to lagoon (Fig. 8).

On the rising spring tide the shallow passages contribute 10% to the tidal prism. The deeper passages to the north and northeast therefore must transmit 90% of the rising spring tide prism. During the falling tide shallow passages still transmit water from the ocean to the lagoon (approximately 50% of the flood tide contribution). Over a full tidal cycle, therefore, the shallow passages contribute 14% of the total spring tidal prism. Invoking a neap tidal range of 0.4 m the rising tide prism is much smaller than the spring tide prism (Table 3). The shallow passages contribute 16.9% to the neap rising tide prism. Over an entire tidal cycle the contribution of the shallow passages to the prism is proportionately much greater than it is for spring tides (22%).

In calculating the flushing time of the lagoon several assumptions have been made. First, the volume of water that enters the lagoon during the rising tide equals that leaving the lagoon during the falling tide. Water entering the lagoon through the shallow passages during the falling tide, will however, be retained within the lagoon. The semi-diurnal nature of the tidal regime would also result in more water being retained in the lagoon if the low tide did not equal the original tide level. Second, the falling tide prism expels water that resided in the lagoon at low tide. With these assumptions it requires a minimum of 2.36 days (spring tide) and 5.54 days (neap tide) for the lagoon to exchange its volume with the ocean.

DISCUSSION

It is evident that the Cocos (Keeling) Islands lagoon experiences mixed semi-diurnal tides with a marked diurnal inequality (Table 1). The spring tidal range in the north of the lagoon of 0.82 m, although higher than most central Pacific atolls, falls within the lower range of Indian Ocean tidal ranges (Farrow and Brander 1971) and is considerably less than the 2.74m experienced at Aldabra atoll. A phase lag is identified within the lagoon; with the tide in the south of the atoll lagging the north. This phase lag is also manifested in the tidal current properties for the K_1 currents (Table 2). Southern passage M_2 currents lag those of the eastern passages by 111°. This evidence supports the tidal lag relationship, suggesting that the tide sets from the east-northeast and travels south through the lagoon.

Attenuation of tide heights was observed from north to south within the lagoon but due to the short length of data in the south of the atoll (20 days) it is not appropriate to place great significance on these differences. The broad, shallow nature of the southeastern section of the lagoon is responsible for the significant shallow water effects (M_4 constituent) in this region. Shallow water effects were identified by Pugh and Rayner (1981) in Salomon atoll, which they attributed to the more enclosed nature of the lagoon.

Pugh and Rayner (1981) highlighted the importance of an atoll's tidal characteristics in contributing to the ecological behaviour of reef systems. Farrow and Brander (1971) established that the timing of extreme low water at Aldabra Atoll was synchronous with maximum solar radiation. This was thought to maximise stress on many organisms on the reef. Within the Cocos lagoon the maximum exposure of reef flats occurred at midnight with the second, higher low-tide of the day occurring around midday. Reef organisms were, therefore, not stressed by solar radiation during the most extreme low tide levels.

Lagoon currents and circulation are driven by the tidal regime (Table 2, Figs 2 and 3), with rising tide currents penetrating south into the lagoon within 1km of the eastern and southern passages. The component of observed currents not attributable to tidal forces, may be driven by the influence of wind and lagoon generated waves, or internal salinity differences within the lagoon. These currents are small within the lagoon (mean 15%), during the observation period, and have not been further investigated. It is suggested however, that the southeast trade winds would play a major role in driving these currents.

The unidirectional ocean to lagoon flow that occurs in the shallow passages, for all but spring low tides in the east of the atoll, can be explained through the interaction of tidal height and wave action, with the height of the reef crest. As the tide rises above the reef crest, waves incident at the reef break, reform (Gourlay 1990), travel over the reef and through the passage. These translatory currents comprise the bulk of the current accounted for by the residuals (Table 2). As the waves travel across the reef-flat, friction (induced by the reef flat morphology) slows the wave induced currents. This produces a build up of water at the reef crest which forms a hydraulic gradient from the reef crest to lagoon (Tait 1972). The movement of waves across the reef is still possible on the falling tide until the water height falls below that of the reef crest. The reversal in current direction in the eastern passages, around spring low tide, results from the interaction between tidal height at the reef crest and the height of the lagoonward sand bodies. As shown in Figure 9 the maximum height of the lagoonward sand body is greater than the reef crest. As the spring low tide falls below the level of the reef crest, water is ponded inside the sand apron with no connection to the deeper lagoon. A surface water gradient forms from lagoon to ocean producing a slow reefward flow. The magnitude of this reversing flow is small.

That tidal currents were observed within 1km of shallow passages, indicate that shallow passage currents have negligible effect in driving circulation beyond 1km of the passage exit. They may, however, be important in retarding and deflecting lagoon currents.

During the rising tide there is an opposition of currents entering the lagoon through shallow passages and the tidal currents penetrating the lagoon from the north-northwest toward the lee of the islands. The angle of opposition of these currents on the eastern side of the lagoon would indicate there is a deflection of rising tide water to the southeast. Net flow westward is the result of longer duration ebb flow which is reinforced by the continued flux of water through the shallow passages. Water behind South Island flows southward on the rising tide and west-southwest on the falling tide, as if of a semi-circular nature, driven by the shallow bathymetry and closed lagoon shoreline in this region (Figs. 2 and 3). Flow in the southwest is predominantly in the north-south direction with net movement northward. This net flow direction is thought result from the increased volume of water entering via the south passage and that volume of the lagoon prism that flows from the eastern side of the lagoon. The build up of water in the west of the lagoon is evacuated by the unidirectional northward flow along the western shoreline. Water may also be built up along this shoreline due to the southeast trade winds forcing surface water northwest. As the trade winds drop there may be a small flow of water toward the east to equalise this pressure gradient.

The northeastern passage experiences strong current reversals with tidal stage, whilst the northwestern passage exhibits a unidirectional and slow movement exiting the lagoon. The increased influx of water entering through the shallow passages for the duration of the tidal cycle must increase the length and or velocity of currents exiting the lagoon on the falling tide through these large passages. It is proposed that as the tidal wave sets from the east-northeast, the northeast passage is the major conduit for tidal inflow, while the northwest passage is dominated by net flow out of the lagoon (Fig. 2).

A general circulation model of the lagoon, therefore, has water entering and flowing down the eastern and central sections of the lagoon, on the rising tide; being deflected west inside South Island and flowing north up the central and western sides of the lagoon, and exiting the northwest pass during the falling tide (Fig. 10). The northeast pass also evacuates water from the lagoon on the falling tide. Results from vector plots (Figs. 2-5) identify a net flow within the lagoon which mirrors that of the falling (Fig. 10b) except for the northeast passage experiencing a westward flow. Tidal oscillation is superimposed on this net flow. There are two possible mechanisms of this net northwestward flow. First, the prevailing southeast wind may produce a small surface current, as seen in the southeast lagoon residual current (Fig. 7a). If this mechanism is important, ocean-lagoon exchange time will decrease during stronger wind conditions. Second, due to the ebb prism being greater than the flood prism, because of the continuous shallow passage input, the falling tide is of longer duration, producing a net movement in the vector plots toward the deep northwest passage. The unidirectional ocean to lagoon flux of water through the passages also retards the rising currents penetrating the lagoon from the north. Continued influx of water at slack tide and the falling tide may create a pressure head from the south and east toward the northwest and may also accelerate flow toward the northwest deep passage.

That circulation in the Cocos (Keeling) Islands lagoon is driven by tidal forces is consistent with other shallow lagoon studies in Pacific atolls (e.g. Stroup and Meyers 1974). While tidal forces dominate ocean-lagoon water exchange, the wave induced water flux through the shallow passages plays an important role in this exchange, especially during neap tides where shallow passage flux can represent 22% of the entire prism. Shallow passage water flux is also identified as a primary mechanism of lagoon-ocean water exchange by Atkinson et al. (1981) in Enewetak Atoll.

The flushing time of the lagoon is estimated at a minimum of 2.36 days and a maximum of 5.4 days for spring and neap tides. This time period is comparable with lagoons of similar size and depth including Aldabra atoll (Pugh and Rayner 1981) and Britomart lagoon, Great Barrier Reef (Wolanski and Pickard 1983). Fanning and Canton Atoll lagoons which have similar dimensions to the Cocos lagoon (15 km wide, 6 m deep) have far greater flushing time scales (50-95 days, Canton and <300 days Fanning) due primarily to the enclosed nature of the lagoon with few connections to the ocean.

CONCLUSION

The Cocos (Keeling) Islands are influenced by mixed mainly semi-diurnal tides. Tides in the shallow south of the lagoon and currents in south passage, lag those of the deeper northern lagoon and eastern passages.

The Cocos (Keeling) Islands lagoon circulation is tidally driven with strong tidal currents penetrating the lagoon from the northeastern passage to within 1km of the shallow passages. The tidal range has a significant impact on net flow direction in the east and southeastern sections of the lagoon. Shallow tidal constituents are important in the shallow southeastern section of the lagoon that is bordered by South island.

A general circulation model has been derived in which water entering the northeastern passage travels down the eastern shoreline of the lagoon, is deflected westward, and flows northwestward exiting through the northwest deep passage.

The role of wind was found to be small in driving lagoon circulation. Wind stress may contribute to the residual currents which produce a northwestward flow. However, these currents were weak within the lagoon.

Shallow passages experience unidirectional ocean to lagoon flow throughout neap tides and during spring tides in the south of the atoll. This unidirectional flow contributes to the net movement of lagoon water toward the northwest throughout the tidal cycle. Eastern passages display a reversal in current direction around spring low tides due to the interaction of tidal height at the reef crest and height of the sand apron lagoonward of the passage. Exposure of the sand apron crest produces a temporary reversed hydraulic gradient and current flow.

Shallow passage currents are dominated by translatory wave motion across the reef flat. Tidal currents contribute less than 50% to observed passage currents. The influence of shallow passage hydrodynamics on lagoon circulation is negligible. Shallow passage currents penetrate up to 1km lagoonward of the passage exit. These currents deflect water entering the deep lagoon to the southeast in the eastern side of the lagoon. Unidirectional passage flow increases the ebb prism and ebb tide current velocities.

Shallow passages were found to be important mechanisms for the exchange of water between ocean and lagoon with up to 15% (springtides) and 22% (neap tides) of total water entering the lagoon over a tidal cycle being transmitted through the shallow passages.

Flushing times of the Cocos lagoon were found to vary between 5.4 and 2.3 days for neap and spring tidal conditions respectively. These results were consistent with atoll lagoons of similar dimension and high degree of connection with the ocean.

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Table 1: Harmonic analysis of lagoon tides, centimetres and degrees in relation to Greenwhich. Major tidal constituents at the permanent Home Island tide gauge and temporary location in South Passage. Symbols indicate tidal properties of amplitude (a) and phase (g). Due to the short length of record from the temporary tide gauge (20 days) the N_2 constituent was unable to be resolved.

Constituents	Frequency (hours)	Home a (cm)	Island g(deg)	South a(cm)	Passage g(deg)
MSF	354.37	6.02	60.16	7.21	237.33
O_1	25.82	7.82	236.50	8.23	256.37
K_1	23.93	12.19	259.44	10.29	282.27
N_2	12.65	10.92	118.03	——	——
M^2	12.42	29.39	140.84	25.02	149.35
S_2	12.00	14.26	186.36	5.58	186.48
M_4	6.21	0.21	205.31	3.92	244.04

Table 2: Tidal current constituents at M2 (12.42 hrs) and K1 (23.93 hrs) frequencies. The symbols indicate current ellipse properties of semi–major axis length (a), semi–minor axis length (b), phase (g) and orientation (θ) measured anticlockwise from east. Residual, percentages of the orthogonal components of velocity (northing – n and easting – e) indicate the percentage of observed currents not able to be accounted for by tidal forces.

			M_2				K_1		Residuals	
Mooring	a (cm/s)	b (cm/s)	g (deg)	θ (deg)	a (cm/s)	b (cm/s)	g (deg)	θ (deg)	n (%)	e (%)
E Lagoon	11.36	0.56	219.36	146.98	2.61	0.17	325.44	142.01	13.8	5.0
SE Lagoon	7.03	3.68	216.32	117.84	2.49	0.99	338.25	140.17	17.2	27.0
SW Lagoon	16.95	1.03	219.09	105.81	5.56	0.03	330.13	111.03	12.1	19.1
South Pass	7.60	2.11	337.79	263.88	4.13	0.80	235.32	82.21	46.4	29.9
East Pass	5.15	1.13	226.33	29.47	2.19	0.18	181.89	210.49	38.96	52.8

Table 3: Lagoon volumes and tidal prism calculations for the Cocos (Keeling) Islands Lagoon. Low–High = low to high tide shallow passage flux.

	Lagoon (M^3 High Tide	Volume x 10^6) Low Tide	Tidal Prism (M^3 x 10^6)	Shallow Flux Low–High	Passage (M^3 x 10^6) High–Low	Total (M^3 x 10^6)
SprinTides	612.5	505.5	107	10.5	5.1	15.6
Neap Tides	571.9	524.5	47	8.0	3.6	11.6

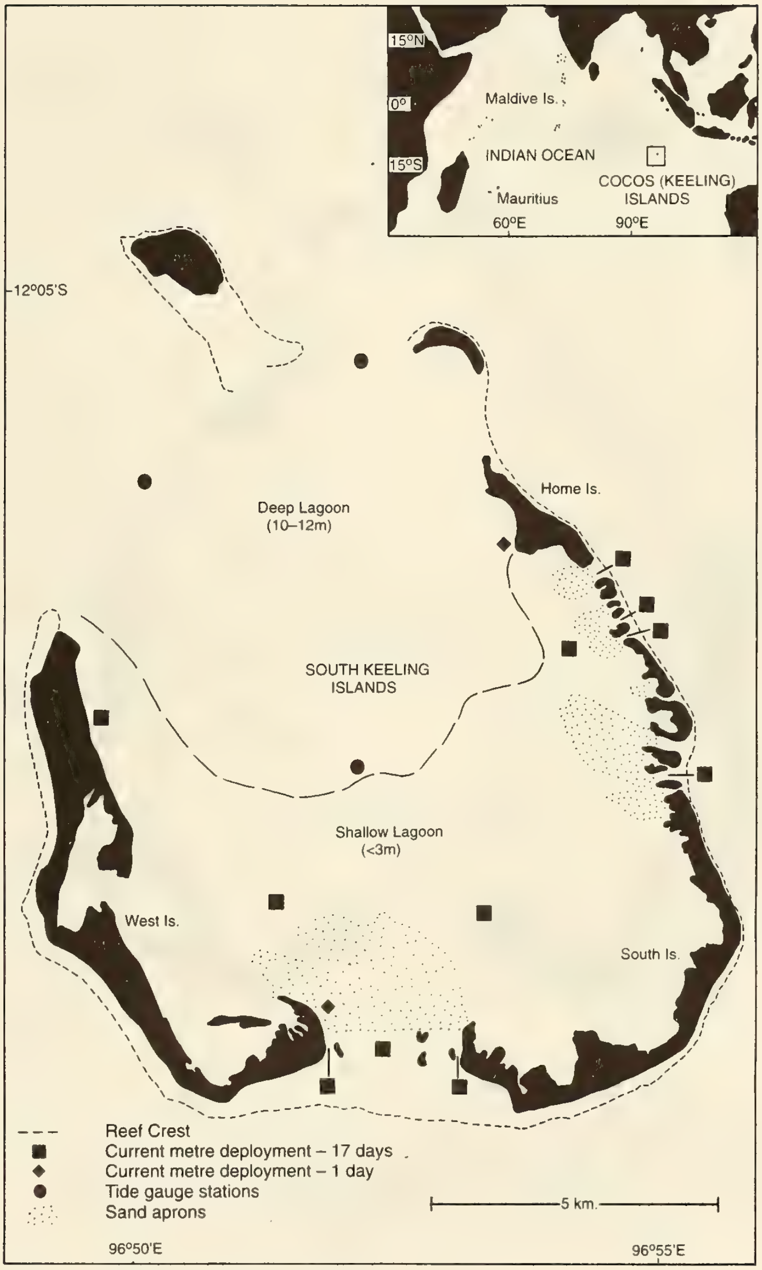


Figure 1. Field and Instrument location

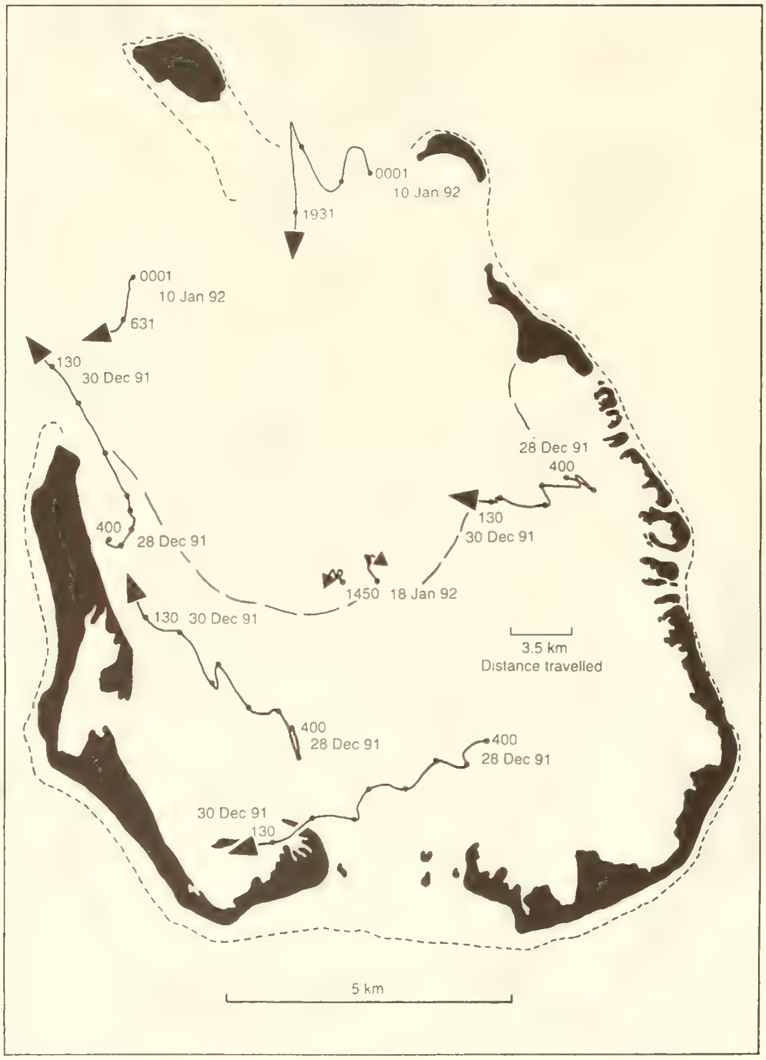


Figure 2. Lagoon progressive vector plots, neap tide. The four shallow lagoon locations show a 48 hour period starting 28/12/91 at 4am (low tide). The northwest passage is a 12 hour record and the northeast and mid lagoon locations are 24 hour records of current speed and direction.

Figure 3. Lagoon progressive vector plots, spring tide. Each location displays a 48 hour period beginning 19/12/91 at 830am (low tide).

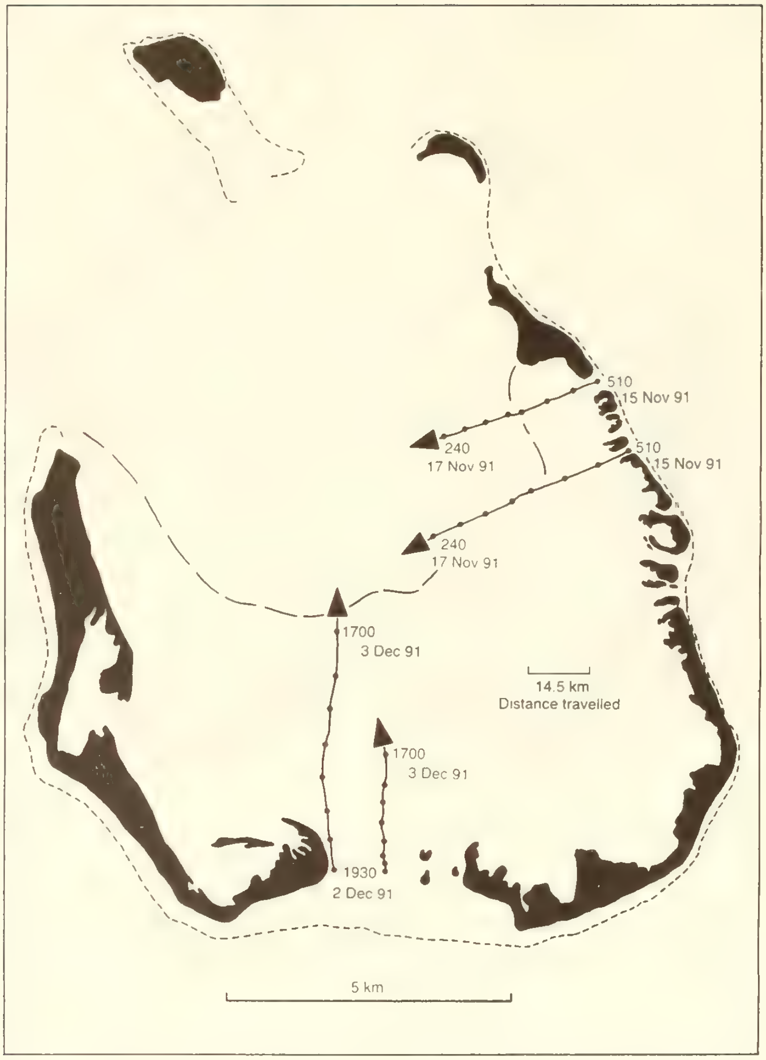


Figure 4. Shallow passage progressive vector plots, neap tide. 48 hour periods starting at low tide on the 15/11/91 at 510am in the eastern passages and 1/12/91 at 730pm in the southern passages.

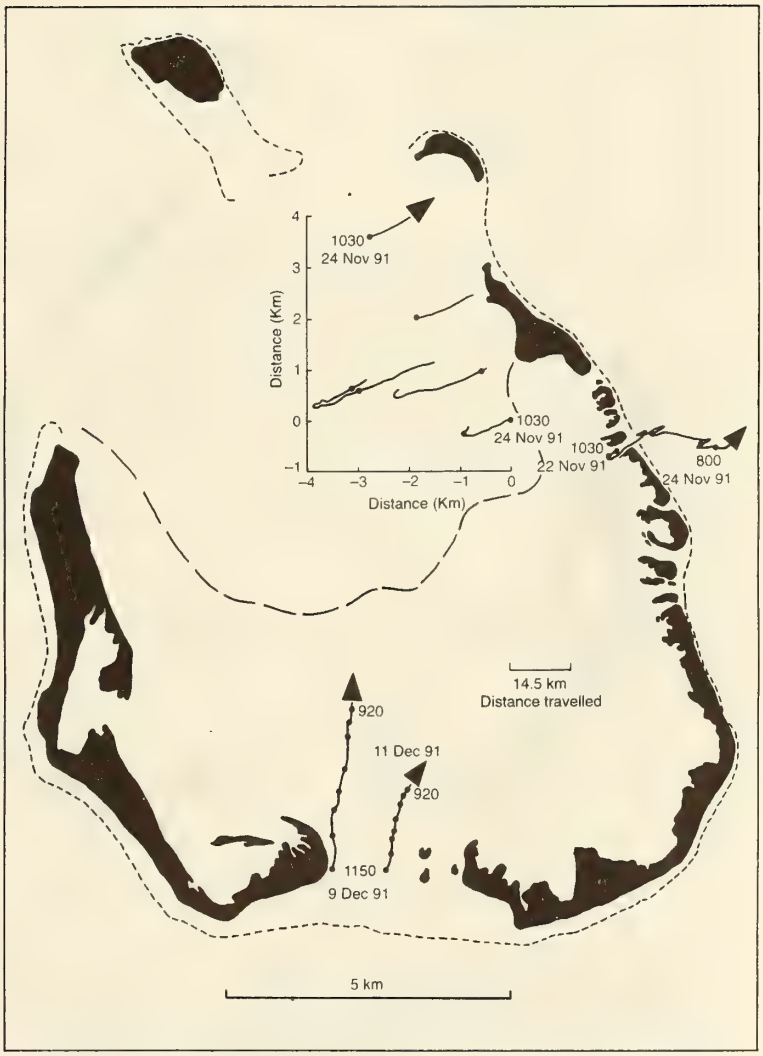


Figure 5. Shallow passage progressive vector plots, spring tide. 48 hour periods starting at low tide on the 22/11/91 at 1030am in the eastern passages and 9/12/91 at 1150am in the southern passages.

Figure 6. M2 tidal current ellipses for the shallow lagoon and passages. All display anti–clockwise rotation.

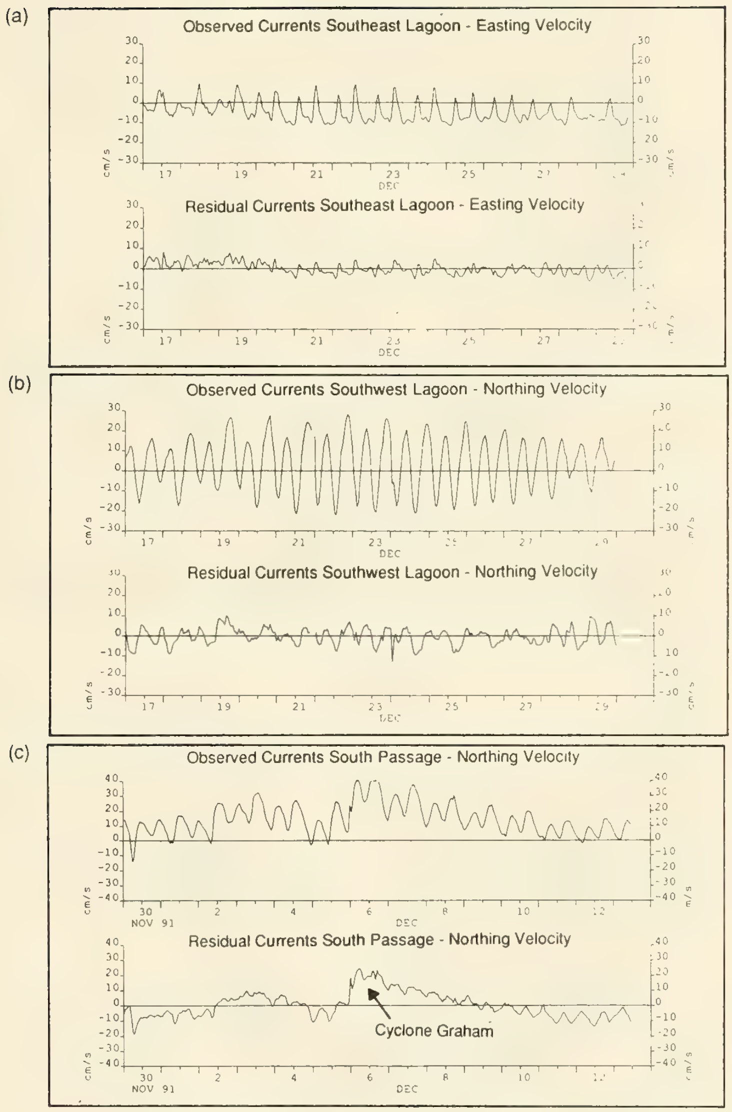


Figure 7. Observed and residual current information for selected sites. Residuals are derived by subtracting tidal current components from the observed current record. (a) Southeastern lagoon Showing the easting component of velocity. Negative values indicate flow to the west. (b) South west lagoon, showing the northing component of velocity. Negative values indicate flow to the south. (c) Southern passage, northing component of velocity.

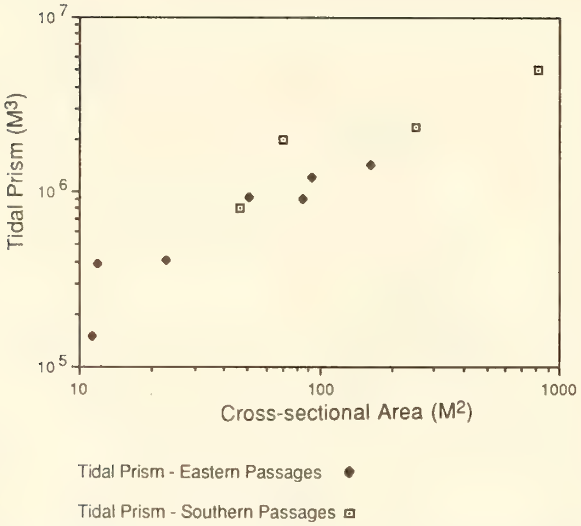


Figure 8. Spring tidal prism vs cross–sectional area (at MSL) relationship for the shallow passages.

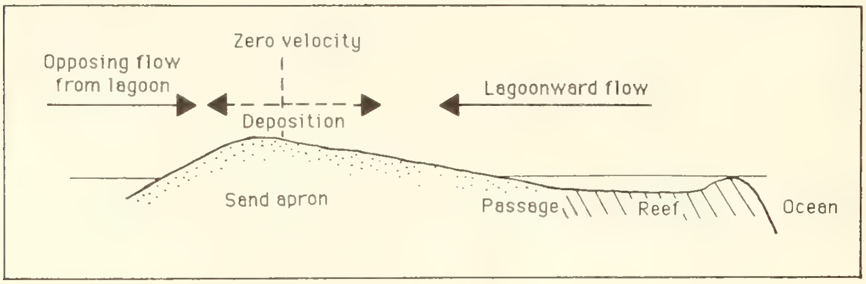
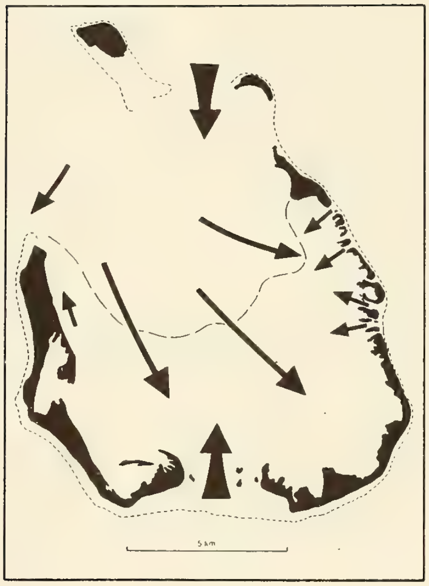


Figure 9. Relative height of sand apron and reef crest, eastern side of the atoll. The opposition of currents entering the lagoon via the deep passes and shallow passages is also shown.

(A) Rising tide



(B) Falling tide

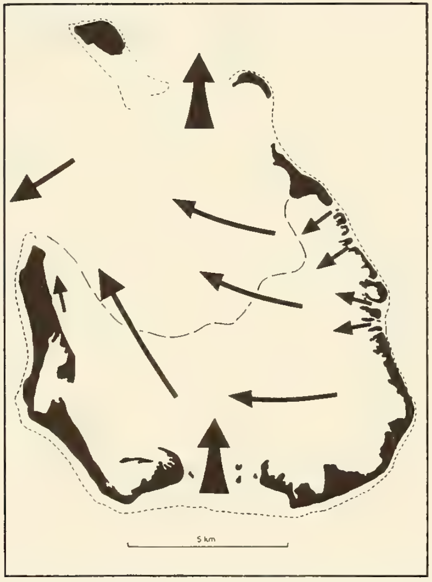


Figure 10. General circulation of the Cocos (Keeling) Islands lagoon on the rising (A) and falling (B) tide.

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CHAPTER 11

HERMATYPIC CORALS OF THE COCOS (KEELING) ISLANDS: A SUMMARY

BY

J.E.N. VERON

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CHAPTER 11

HERMATYPIC CORALS OF COCOS (KEELING) ISLAND: A SUMMARY

BY

J.E.N. VERON *

ABSTRACT

Ninety nine species of reef corals are recorded from Cocos (Keeling) Atoll. Of these, all but twelve are known from Western Australia. Nine species are not recorded elsewhere in the eastern Indian Ocean and two (one being taxonomically doubtful) are possibly endemic.

This account is a summary only of *Re-examination of the reef corals of Cocos (Keeling) Atoll* (Veron 1990a)

SYSTEMATIC ACCOUNT

FAMILY Astrocoeniidae Koby

Genus *Stylocoeniella* Yabe and Sugiyama

Stylocoeniella guentheri (Bassett-Smith)

Records: Wells (1950), Veron (1990a)

Notes: Found on most reef slopes. Inconspicuous. Usually dark green, encrusting to submassive. Septa strongly alternate. Primary septa do not reach the boss-like columella.

Stylocoeniella armata (Ehrenberg)

Records: Veron (1990a)

Notes: Rare, inconspicuous. Septa clearly alternate. Primary septa reach the columella which is thin, style-like.

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Stylocoeniella cocosensis Veron 1990

Record: Veron (1990b)

Notes: Corallites are irregularly exsert. Septa are in two sub-equal cycles, fine. Columellae are very small. Coenosteum spinules very fine. Each corallite has a prominent style.

FAMILY Pocilloporidae Gray

Pocillopora is abundant in almost all coral communities, *Seriatopora* is usually uncommon. The other genera, notably *Stylopora,* have not been recorded.

Genus *Pocillopora* Lamarck

Pocillopora damicornis (Linnaeus)

Records: Ridley and Quelch (1885) (as *P. brevicornis*), Vaughan (1918), Wells (1950), Veron (1990a)

Notes: Uncommon but found in a wide range of environments. Usually pink in colour. Indistinguishable from mainland Australian colonies.

Pocillopora verrucosa (Ellis and Solander)

Records: Vaughan (1918), Wells (1950), Veron (1990a)

Notes: Common on most upper reef slopes. Yellow or pinkish in colour. Indistinguishable from mainland Australian colonies.

Pocillopora meandrina Dana

Records: Vaughan (1918), Wells (1950), (both as *P. elegans* Dana), Veron (1990a)

Notes: Common on most upper reef slopes. Distinguished from *P. verrucosa* by having smaller verrucae and as described by Veron and Pichon (1982).

Pocillopora woodjonesi Vaughan

Records: Vaughan (1918) with the Cocos (Keeling) Islands as type locality, Wells (1950), Veron (1990a)

Notes: Uncommon. Difficult to distinguish from *P. eydouxi*. Colonies identified as *P. woodjonesi* in situ did not have the species specific skeletal characters described by Vaughan (1918) and Wells (1950) and used by the present author. The `taxonomic status of this species requires further study.

Pocillopora eydouxi Edwards and Haime

Records: Vaughan (1918), Veron (1990a)

Notes: Common in most coral communities. Indistinguishable from mainland Australian colonies.

Genus *Seriatopora* Lamarck

Seriatopora hystrix Dana

Records: Vaughan (1918), Wells (1950) (both as *S. angulata* Klunzinger), Veron (1990a)

Notes: The few colonies observed during the present study were small and isolated. Indistinguishable from mainland Australian colonies.

Family Acroporidae Verrill

Genus *Montipora* de Blainville

Montipora monasteriata (Forskal)

Records: Veron (1990a)

Notes: Common in a wide range of environments. Indistinguishable from mainland Australian colonies.

Montipola tuberculosa (Lamarck)

Records: Veron (1990a)

Notes: Common. Indistinguishable from mainland Australian colonies.

Montipora lobulata Bernard

Records: Wells (1950), Veron (1990a)

Notes: Has not been recorded elsewhere in Australia.

Montipora mollis Bernard

Records: Veron (1990a)

Notes: Probably uncommon. Indistinguishable from mainland Australian colonies.

Montipora peltiformis Bernard

Records: Veron (1990a)

Notes: Common on some reef slopes.

Montipora capricornis Veron

Records: Veron (1990a)

Notes: Uncommon except in the atoll lagoon where this species is an early coloniser of denuded areas.

Montipora spumosa (Lamarck)

Records: Vaughan (1918) and Wells (1950)

Notes: Possibly now extinct at Cocos (Keeling).

Montipora danae (Edwards and Haime)

Records: Veron (1990a)

Notes: Uncommon. Indistinguishable from mainland Australian colonies.

Montipora angulata (Lamarck)

Records: Vaughan (1918) (as M. *cocosensis* Vaughan, with Cocos (Keeling) Island as type locality), Veron (1990a)

Notes: Uncommon. Found only on reef flat or sub-tidal sand flats with *M. digitata*. Thick branches becoming columnar, with conspicuous open corallites.

Montipora digitata (Dana)

Records: Ridley and Quelch (1886) (as *M. laevis* Quelch), Wells (1950) (as *M. laevis* Quelch *M. ramosa* Bernard and *M. rubra* Quoy and Gaimard), Veron (1990a)

Notes: Forms extensive monospecific stands on intertidal sand flats. Intermixed with *Montipora* sp. Indistinguishable from mainland Australian colonies.

Montipora sp.

Records: Veron (1990a)

Notes: A sub-arborescent species similar to *M. digitata*, primarily distinguished by high reticulum ridges between corallites and flattened branch tips with few corallites.

The present specimens do not belong to any previously recorded or described species known to the author.

Montipora efflorescens Bernard

Records: Veron (1990a)

Notes: Indistinguishable from mainland Australian colonies.

Montipora grisea Bernard

Records: Veron (1990a)

Notes: Indistinguishable from mainland Australian colonies.

Montipora informis Bernard

Records: Vaughan (1918), Veron (1990a)

Notes: Rare. Indistinguishable from mainland Australian colonies.

Montipora foliosa (Pallas)

Records: Vaughan (1918), Wells (1950), Veron (1990a)

Notes: Uncommon.Indistinguishable from mainland Australian colonies.

Montipora aequituberculata Bernard

Records: Veron (1990a)

Notes: Common on some outer slopes. Usually dark grey or brown. Indistinguishable from mainland Australian colonies.

Genus *Anacropora* Ridley

Anacropora forbesi Ridley, 1884

Records: Ridley (1884), with Cocos (Keeling) Atoll as type locality

Notes: Many now be extinct at Cocos (Keeling).

Genus *Acropora* Oken

One of the most distinctive characters of Cocos (Keeling) Island corals is the low diversity and, usually, the low abundance of *Acropora*. The only extensive stands of living

Acropora are on reef flats. Very extensive stands of dead arborescent species, mainly *pulchra* and *formosa,* occur in the lagoon and extensive dead tabular colonies, no longer identifiable, occur at North Keeling Island.

Acropora palifera (Lamarck)

Records: Vaughan (1918), Veron (1990a)

Notes: Seldom common. Both reef slope and lagoon colonies are similar in growth form and corallite structures and represent only a small part of the variation described by Veron and Wallace (1984).

Acropom ocellata (Klunzinger)

Records: Vaughan (1918), Wells (1950), Veron (1990a)

Notes: Uncommon. This species belongs with the *A. humilis* group, with a growth form similar to *A. humilis* (Dana). Axial corallites are similar in size and shape to those of *A.monticulosa* (Bruggemann). Radial corallites are large, round, irregular, some immersed, others large and elongated, becoming incipient axials. Living colonies are pale brown with white branch tips.

Acropora robusta (Dana)

Records: Wells (1950) (as *A. pinguis,* described as a new species from Cocos (Keeling) Atoll), Veron (1990a)

Notes: Very rare.

Acropora danai (Edwards and Haime)

Records: Wells (1950) (as *A. irregularis,* described as a new species from Cocos (Keeling) Atoll), Veron (1990a)

Notes: Rare. Growth form is the same as mainland Australian colonies. Corallites near branch tips may become relatively elongate.

Acropora sp. 1

Records: Vaughan (1918), Wells (1950) (as *A. pharaonis* Edwards and Haime), Veron (1990a)

Notes: Sometimes common in shallow water. Colonies are arborescent, forming thickets in shallow water where some branches may be fused. Branches are mostly straight and tapered. Radial corallites are of two sizes, the larger arranged in rows. They are similar in structure to those of A. *valenciennesi.*

Acropora formosa (Dana)

Records: Wells (1950), Veron (1990a)

Notes: Uncommon except on some reef flats. Reef flat colonies have short branches with proliferous sub-branches. No colonies with long undivided branches were seen. Mostly yellowish in colour.

Acropora microphthalma (Verrill)

Records: Veron (1990a)

Notes: Common on reef flats and some reef slopes. Indistinguishable from mainland Australian colonies.

Acropora exquisita Nemenzo

Records: Possibly Wells (1950) (as *A. irregularis* (Brook), Veron (1990a)

Notes: Uncommon. Indistinguishable from more robust colonies from mainland Australian North-west shelf reefs. Pale colours.

Acropora aspera (Dana)

Records: Vaughan (1918) (possibly as *A. spicifera*), Wells (1950) (as *A. hebes*), Veron (1990a)

Notes: Mostly uncommon and only found on reef flats. Reddish-brown in colour. Indistinguishable from mainland Australian colonies.

Acropora pulchra (Brook)

Records: Vaughan (1918), Veron (1990a)

Notes: Formerly very abundant throughout much of the southern lagoon, forming very extensive stands often over 20 m across. Now common on some reef flats and also found on some reef slopes. Indistinguishable from mainland Australian colonies.

Acropora cytherea (Dana)

Records: Veron (1990a)

Notes: Uncommon. The largest colonies observed were < 1 m diameter. Indistinguishable from mainland Australian colonies.

Acropora paniculata Verrill

Records: Veron (1990a)

Notes: Rare. It appears that this is a distinct geographic sub-species of *A. paniculata,* but as the latter is know in the Indian Ocean from only a single specimen (from Ashmore Reef, Veron and Marsh, 1988), no definite conclusion is possible.

Acropora hyacinthus (Dana)

Records: Veron (1990a)

Notes: Rare. Only stunted reef flat colonies were found.

Acropora latistella (Brook)

Records: Veron (1990a)

Notes: Rare, found only on reef flats. This species was not found as large tabular colonies. Branchlets are thinner than usual for shallow-water mainland Australian colonies.

Acropora nana (Studer)

Records: Wells (1950), Veron (1990a)

Notes: Found only on outer reef flats and upper slopes. Colonies are relatively small, otherwise indistinguishable from mainland Australian colonies.

Acropora subulata (Dana)

Records: Veron (1990a)

Notes: Rare. Nothing is known of environment-related growth form variation.

Acropora valida (Dana)

Records: Vaughan (1918) and Wells (1950) (as *A. variabilis* (Klunzinger)), Veron (1990a)

Notes: Rare, Gibson-Hill records this species from several reef flat localities (Wells 1950). Corallites are smaller and have thinner walls than usual for the species, but nothing is known of environment-related variation. Coralla from Cocos (Keeling) illustrated by Vaughan (1918, pl. 80) have the characters of the species more clearly developed. Gibson-Hill (and this author) records the colour as "dirty-white, with faint lavender-blue tips" (Wells 1950).

Acropora sp. 2

Records: Veron (1990a)

Notes: Rare. Colonies are irregularly arborescent. Corallites are very irregular, some being *valida*-like and strongly oppressed. The species was not sufficiently abundant for detailed study and nothing is known of environment-related skeletal variation.

Acropora schmitti Wells

Records: Wells (1950), described as a new species from Cocos (Keeling) Atoll, Veron (1990a)

Notes: Not found during the present study. Gibson-Hill notes, "This coral, which is rather similar to [*A. valida*] in both colour and form, occurs in shallow pools on the middle section of the barrier, and on part of its seaward edge. It is not very plentiful, but it seems to be most numerous at the back of Pulo Tikus, where [five] specimens were taken" (Wells 1950). Wells (1950) notes that "the distinctive character of this species is the extraordinary thickness of the outer lip of the radial corallites, which gives them the appearance of hemispherical bowls attached to the branch by one side or by a very short thick handle".

Genus *Astreopora* de Blainville

Astreopora myriophthalma (Lamarck)

Records: Vaughan (1918), Wells (1950), Veron (1990a)

Notes: Common in a wide range of environments. Indistinguishable from mainland Australian colonies. Colours vary from dark purple to cream and pale pink.

Astreopora gracilis (Bernard)

Records: Veron (1990a)

Notes: Usually uncommon. Indistinguishable from mainland Australian colonies. Colours are cream and pale pinkish-purple.

Family Poritidae Gray

Goniopora and *Alveopora* have not been recorded from Cocos (Keeling) Atoll.

Genus *Porites* Link

Porites solida (Forskal)

Records: Vaughan (1918) and Wells (1950), Veron (1990a)

Notes: Uncommon. Two specimens studied were indistinguishable from mainland Australian coralla.

Porites lobata Dana

Records: Veron (1990a)

Notes: Indistinguishable from mainland Australian colonies.

Porites australiensis Vaughan

Records: Veron (1990a)

Notes: Corallites have a very distinct wall formed by lateral fusion of denticles.

Porites somaliensis Gravier

Records: ?Guppy (1889) (as *P. clavaria*), Vaughan (1918), Veron (1990a)

Notes: The most abundant massive *Porites* on some reet flats. Colonies from shallow water usually have a knobbly growth form. Corallites are closest to *P. stephensoni* but the present species appears to be distinct from any mainland Australian species. The triplet is sometimes fused and columellae are laterally compressed in the line of the directive septa forming a conspicuous line.

Porites cf. *evermanni* Vaughan

Records: Veron (1990a)

Notes: Rare, but very distinctive. Indistinguishable from specimens of this species recorded from Australia, the Philippines (Veron and Hodgson 1989) and elsewhere.

Porites cylindrica Dana

Records: Guppy (1889) (as *P. palmata*), Ridley and Quelch (1885) (as *P. levis Dana*), Vanghan (1918) (as *P. nigrescens*), Wells (1950) (as *P. nigrescens* and *P. gibsonhilli*). Cocos (Keeling) atoll is the type locality of *P. gibsonhilli* Wells. *Porites cocosensis* Wells, described from two specimens from Cocos (Keeling) Atoll, may also be a synonym of *P. cylindrica*

Notes: The most common species of intertidal reef flats and forms extensive stands on some upper reef slopes. Indistinguishable from mainland Australian coralla.

Porites lichen Dana

Records: Vaughan (1918)

Notes: Indistinguishable from mainland Australian coralla.

Porites rus (Forskal)

Records: Veron (1990a)

Notes: Common. Forms extensive flat plates with short, irregular columns and branches. Usually fawn or brown.

Porites sp.

Records: Veron (1990a)

Notes: Forms plates and irregular branches and columns. Corallites are essentially similar to those of *P. rus* and *P. latistellata* Quelch, but are smaller than both. The species appears to be undescribed. Usually brightly coloured: green, blue or yellow.

Family Siderastreidae Vaughan and Wells

Pseudosiderastrea and *Coscinaraea* have not heen recorded from Cocos (Keeling).

Genus *Psammocora* Dana

Psammocora digitata Edwards and Haime

Records: Wells (1950) (as *P. togianensis* Umbgrove)

Psammocora superficialis Gardiner

Records: Vaughan (1918) (as *Psammocora* sp.), Veron (1990a)

Notes: Uncommon. Indistinguishable from mainland Australian colonoies. Colonies are encrusting and may be over 1 m diameter. These large colonies have relatively coarse skeletal characters. Colour is very uniform within colonies, mostly battleship grey, rarely bright green.

Psammocora profundacella Gardiner

Records: Vaughan (1918) and Wells (1950) (as *P. haimeana*), Veron (1990a)

Notes: Very common in a wide range of environments. Indistinguishable from mainland Australian colonies. It may form coralliths. Usually pale pink or green, but may be dark green. Sometimes with blue centres. Gibson-Hill, referring to reef-flat colonies, notes that "it is a pearl-grey colour" (Wells 1950)

Family Agriciidae Gray

Genus *Pavona* Lamarck

Pavona cactus (Forskal)

Records: Wells (1950), Veron (1990a)

Notes: Common only in small isolated patches. Indistinguishable from mainland Australian colonies

Pavona frondifera Lamarck

Records: Veron (1990a)

Notes: Common only in small isolated patches intermixed with *P. cactus*. Colonies are partly encrusting and have small, irregular, upright fronds. Dark greenish-brown with pale fronds.

Pavona decussata (Dana)

Records: Vaughan (as *P. danai* (Edwards and Haime), Wells (1950), Veron (1990a)

Notes: Known from two reef flat colonies only. Coralla are colllposed of highly anastomosed plates, a growth form common on reef flats. Skeletal detail is indistinguishable from mainland Australian coralla.

Pavona explanulata (Lamarck)

Records: Veron (1990a)

Notes: Usually uncommon but conspciuous. Colonies are massive or columnar. Pale or dark brown in colour. Plate-like colonies common in Australia, were seldom seen.

Pavona minuta Wells

Records: Veron (1990a)

Notes: Common on some exposed reef sites. Colonies are massive or columnar, rarely encrusting. All colonies observed were < 0.5 m. Grey in colour.

Pavona varians Verrill

Records: Vaughan (1918), Veron (1990a)

Notes: Very common in a wide range of reef slope environments. Forms large encrusting plates under overhangs. Very dark colours except in niches exposed to strong sunlight.

Pavona venosa (Ehrenberg)

Records: Veron (1990a)

Notes: Septa are very coarse making the single specimen found very distinctive.

Pavona maldivensis (Gardiner)

Records: Vaughan (1918), Veron (1990a)

Notes: Rare. Indistinguishable from mainland Australian colonies.

Pavona sp.

Records: Veron (1990a)

Notes: Rare. Colonies are flat unifacial plates. Corallites are very small similar to those of *P. bipartita* Nemenzo, but with smaller calice centres and tendency to become subplocoid.

Genus *Leptoseris* Edwards and Haime

Leptoseris papyracea (Dana)

Records: Veron (1990a)

Notes: Forms an extensive carpet of some hundreds of square metres at one lagoonal site. Indistinguishable from fine, highly compact mainland Australian colonies. Pale pinkish-brown in colour.

Leptoseris explanata Yabe and Sugiyama

Records: Veron (1990a)

Notes: Rare. The single specimen studied is indistinguishable from mainland Australian colonies.

Leptoseris mycetoseroides Wells

Records: Veron (1990a)

Notes: Rare. Indistinguishable from mainland Australian colonies.

Genus *Gardineroseris* Scheer and Pillai

Gardineroseris planulata (Dana)

Records: Veron (1990a)

Notes: Uncommon although found in a wide variety of habitats. Colonies flat or dome-shaped, up to 1 m high, pale brown in colour. Indistinguishable from mainland Australian colonies.

Genus *Pachyseris* Edwards and Haime

Pachyseris speciosa (Dana)

Records: Veron (1990a)

Notes: Forms very extensive monospecific stands south of 'Boat Passsage'. Indistinguishable from mainland Australian colonies.

FAMILY Fungiidae Dana

Genus *Fungia* Larnarck

Fungia fungites (Linnaeus)

Records: Wells (1950), Veron (1990a)

Notes: Uncommon. Indistinguishable from mainland Australian coralla.

Fungia concinna Verrill

Records: Veron (1990a)

Notes: This is the only record of the species. The single specimen collected is indistinguishable from mainland Australian coralla.

Fungia granulosa Klunzinger

Records: Veron (1990a)

Notes: This is the only record of the species. Indistinguishable from mainland Australian coralla.

Fungia scutaria Verrill

Records: Vaughan (1918), Wells (1950), Veron (1990a)

Notes: Common on reef slopes. Indistinguishable from mainland Australian coralla except for colour. Usually cream with blue or white tentacular lobes, occasionally pink.

Genus *Herpolitha* Eschscholtz

Herpolitha limax Houttuyn

Records: Vaughan (1918) (as *H. crassa* Dana), Wells (1950), Veron (1990a)

Notes: Seen, but not examined by the author.

Genus *Sandalolitha* Quelch

Sandalolitha robusta (Quelch)

Records: Veron (1990a)

Notes: Usually rare. Colonies are up to 0.5 m diameter, flattened. Small colonies are oval, larger ones are contorted according to irregularities in the substrate. The flattened irregular appearance combined with wide corallum margins free of centres, suggests a different species from that found in Australia is involved. There are, however, no skeletal details which reliably distinguish Cocos (Keeling) coralla from those of Australia. *Sandalolitha dentata* Quelch may be a distinct species with the growth form of the present species, but this has yet to be established.

FAMILY Pectiniidae Vaughan and Wells

This family is represented only by *Oxpora lacera*

Genus *Oxypora* Saville-Kent

Oxypora lacera (Verrill)

Records: Veron (1990a)

Notes: Rare. Indistinguishable from mainland Australian colonies.

FAMILY Mussidae Ortmann

This family is represented only by *Lobophyllia hemprichii*

Genus *Lobophyllia* de Blainville

Lobophyllia hemprichii (Ehrenberg)

Records: Veron (1990a)

Notes: Usually uncommon but very conspicuous. Indistinguishable from mainland Australian colonies and shows the full range of the species except that very large colonies were not found. Often brick red in colour.

FAMILY Merulinidae Verrill

This family is represented only by *Hydnophora microconos.*

Genus *Hyndophora* Fischer de Waldheim

Wells (1950) lists *H. exesa* (Pallas) as recorded from Cocos (Keeling) by Vaughan (1918). This appears to be a mistake.

Hydnophora microconos (Lamarck)

Records: Vaughan (1918), Veron (1990a)

Notes: Uncommon but occurs in a wide range of habitats. Indistinguishable from mainland Australian colonies.

FAMILY Faviidae Gregory

Genus *Favia* Oken

Favia stelligera (Dana)

Records: Vaughan (1918), Wells (1950), Veron (1990a)

Notes: Common in most communities with moderate diversity. Indistinguishable from mainland Australian colonies.

Favia pallida (Dana)

Records: Vaughan (1918) (as *F. speciosa*), Veron (1990a)

Notes: Colonies are small submassive to encrusting. They are mostly mottled dark colours.

Favia matthaii Vaughan

Records: Veron (1990a)

Notes: Uncommon. Corallites are smaller than those of eastern mainland Australian colonies but similar in size to those from equatorial localities. Skeletal detail is similar throughout this range.

Genus *Barabattoia* Yabe and Sugiyama

Barabattoia amicorum (Edwards and Haime)

Records: Veron (1990a)

Notes: Rare. Indistinguishable from mainland Australian colonies. All specimens observed were dark brown in colour.

Genus *Favites* Link

Favites abdita (Ellis and Solander)

Records: Vaughan (1918), Veron (1990a)

Notes: Usually uncommon. Colonies are small, usually encrusting. Corallites of colonies in high energy environments may have greatly thickened walls.

Favites pentagona (Esper)

Records: Vaughan (1918) (as *F. melicerum* Ehrenberg), Veron (1990a)

Notes: Common. Coralla have most of the range of corallite characters described by Veron et al. (1977) except that all have exsert irregular septa and no ecomorphs associated with very strong wave action were found. The size of corallites overlaps with those of eastern mainland Australian colonies, but most are slightly smaller.

Genus *Leptoria* Edwards and Haime

Leptoria phrygia (Ellis and Solander)

Records: Vaughan (1918), Wells (1950), Veron (1990a)

Notes: Usually uncommon. Always a uniform dark grey. Indistinguishable from mainland Australian colonies.

Genus *Montastrea* de Blainville

Montastrea curta (Dana)

Records: Veron (1990a)

Notes: Usually uncommon. Colonies are small, encrusting, pale coloured. Corallites are small (most <6mm diameter with calices <3mm) and are uniform in size. This identification is tentative only because the species is very variable and lacks conservative character and also because no colonies were found on reef flats where it would be expected to be most abundant.

Genus *Plesiastrea* Edwards and Haime

Plesiastrea versipora Edwards and Haime

Records: Vaughan (1918), Veron (1990a)

Notes: Rare. Colonies are pale cream, submassive to encrusting. Skeletal structure is indistinguishable from mainland Australian colonies.

Genus *Leptastrea* Edwards and Haime

Leptastrea transversa Klunzinger

Records: Veron (1990a)

Notes: Uncommon. The characters of the species are better defined than in most mainland Australian coralla. Corallites are of relatively uniform size, with well-defined walls.

Leptastrea pruinosa Crossland

Records: Veron (1990a)

Notes: Uncommon. Indistinguishable from mainland Australian colonies. Usually brightly coloured.

Leptastrea bottae (Edwards and Haime)

Records: Vaughan (1918), Wells (1950), Veron (1990a)

Notes: Common over a wide range of environments. Colonies are submassive or encrusting. Corallites are relatively uniform in size, circular, with well defined walls. Septa are thin, with little ornamentation. Colonies from exposed environments are mostly creamy coloured with very dark calices.

Genus *Cyphastrea* Edwards and Haime

Cyphastrea serailia (Forskal)

Records: Wells' (1950) record of *C. chalcidicum* (Forskal) appears to be this species. Veron (1990a)

Notes: Common in a wide range of environments. Indistinguishable from mainland Australian colonies.

Cyphastrea microphthalma (Lamarck)

Records: Vaughan (1918), Veron (1990a)

Notes: Common. Indistinguishable from mainland Australian colonies.

Cyphastrea agassizi (Vaughan)

Records: Veron (1990a)

Notes: Uncommon. Colonies are encrusting with widely spaced, exsert, corallites. Colonies are nearly uniform white in colour. May form coralliths.

Genus *Echinopora* Lamarck

Echinopora lamellosa (Esper)

Records: Ridley and Quelch (1885), Vaughan (1918), Wells (1950), Veron (1990a)

Notes: Only three small colonies were observed *in situ*. Indistinguishable from mainland Australian colonies.

FAMILY Dendrophylliidae Gray

Genus *Turbinaria* Oken

Turbinaria reniformis Bernard

Records: Veron (1990a)

Notes: Usually rare but forms very extensive monospecific stands at 2-20 m depth north of 'Boat Passage'. Indistinguishable from mainland Australian colonies and has the same yellow polyps as Great Barrier Reef colonies. Polyps were extended during the day.

BIOGEOGRAPHIC AFFINITIES

Many common and widespread Indo-Pacific taxa have not been recorded from Cocos (Keeling) and are almost certainly absent. There are no Oculinidae or Caryophylliidae. The Pectiniidae, Mussidae and hermatypic Dendrophylliidae are represented by only one species each. There are no recorded *Stylophora, Goniopora, Alveopora, Coscinaraea, Cycloseris, Polyphyllia, Lithophyllon, Podabacia, Goniastrea, Platygyra* and many minor east Indian Ocean genera.

Of the genera that are present, only *Sandalolitha* does not have a distribution range crossing the Indian Ocean (Veron 1986).

At species level, the isolation of the atoll from Australia is reflected in:

(a) the number of species which are known from western Australia but are absent from the atoll: (223 species or 70 % of the western mainland Australian total of 318 species).

(b) the number of species which are present but have not been recorded from anywhere in Australia (12 species: *Stylocoeniella cocosensis*, *Montipora lobulata*, *Montipora* sp., *Acropora ocellata*, *Acropora* sp. 1, *Acropora* sp. 2, *Acropora schmitti*, *Porites somaliensis*, *Porites* sp., *Pavona Frondifera*, *Pavona* sp., *Cyphastrea agassizi*), and

(c) the substantial proportion of species (perhaps 30 %) which are present but show points of difference from their western mainland Australian counterparts (e.g. differences in colour, habitat preferences as well as skeletal and growth form differences).

It may be noted that of the 12 species not recorded from Australia ('b' above), 3 have been recorded from the Philippines (Veron and Hodgson 1989). The remaining 9 have not been previously recorded from any eastern Indian Ocean locality, but only *Stylocoeniella* sp. (a doubtful species), *Porites* sp. and *Pavona* sp. have not been previously recorded anywhere. Although it is possible that the latter are endemic, the corals of Indonesia are poorly known and they, along with most or all Cocos (Keeling) species, may well occur in Indonesia.

The principal difference between the corals of Cocos (Keeling) and Christmas Islands, is in the much greater number of species of *Montipora* at Cocos (Keeling) and the greater genetic richness of Christmas Island. The latter however, is a high island with a very restricted range of habitats, especially sheltered ones. The presence or absence of corals is therefore likely to be as much a function of habitat diversity as geographic isolation or relative dispersal ability. The only general observation of this data made here is that there is no clear evidence that Christmas Island has acted as a 'stepping stone' for the dispersal of corals to Cocos (Keeling).

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CHAPTER 12

MARINE MOLLUSCS OF THE COCOS (KEELING) ISLANDS

BY

F.E. WELLS

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CHAPTER 12

MARINE MOLLUSCS OF THE COCOS (KEELING) ISLANDS

BY

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INTRODUCTION

Compared to other localities in the eastern Indian Ocean, the molluscs of the Cocos (Keeling) Islands were relatively well known prior to the Western Australian Museum survey in February 1989. Two short papers on the molluscs of the atolls were presented by Marratt (1879) and Rees (1950). A much more extensive list was prepared by Abbott (1950). Mrs. R.E.M. Ostheimer and Mrs. V.O. Maes spent the first two months of 1963 on Cocos collecting for the Academy of Natural Sciences of Philadelphia, as part of the International Indian Ocean Expedition. Maes (1967) presented a complete list of the species collected, and included records of species recorded by Marratt (1879) or Abbott (1950) that she did not collect on the islands. A total of 504 species were recorded, 379 of which were identified to species.

With their longer time on the atoll Maes and Ostheimer naturally collected more species than the Western Australian Musuem expedition, but their collections were primarily restricted to relatively shallow water as they did not scuba-dive. They did however do some dredging in the lagoon. The Museum team collected in many of the same localities as Maes and Ostheimer, but also dived in a number of areas. Because of this many of the species which live in deeper water that were recorded by only a few specimens by Maes (1967) were shown to in fact be common.

The following list shows all of the mollusc species known from Cocos (Keeling). Station numbers are those of the Western Australian Museum expedition (see Chapter 2). Indications of abundance are given in four categories: abundant, common, uncommon and rare. These are subjective and not quantitative. The abundance categories are based partly on the number of stations at which a species was collected, but also on the number of specimens collected and whether or not the specimens were collected alive or as a broken dead shell. Thus it is possible for a bivalve species collected at two stations as single dead valves to be rare while another species collected at one station may be listed as common because several live animals were collected. Despite these limitations use of the four categories can provide an idea of the relative abundances of the different species. In a number of cases species recorded by previous papers were not collected by the Western Australian Museum team; these are included in the species list and are annotated. In some cases Maes (1967) recorded a species whose name has subsequently been changed or provided a photograph that we consider represents a different species. To avoid confusion by people not familiar with molluscs in comparing the two species lists I have annotated our identification of the species with the name used by Maes. Several pelagic molluscs recorded by Maes have been deleted as they occur in the water column and not on the bottom. Maes recorded species in a number of families that were identified only to generic level. To avoid the possibility of duplication, these have been excluded from the list where the Western Australian Museum team found species recorded in the family that were not

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found by Maes. In a survey such as this where molluscs of all groups have been collected species identifications should be regarded with caution. The list however does provide a good basic knowledge of the molluscs which live on the Cocos (Keeling) Islands.

The following list shows that 610 species of molluscs are known from the Cocos (Keeling) Islands. There are 496 gastropods, 109 bivalves, 1 chiton, and 4 cephalopods. No monoplacophorans, aplacophorans or scaphopods are known from the islands. The fauna is diverse, and compares favourably with the total number of species known from nearby areas that have been studied: 543 from the Maldives (Robertson, unpublished list cited by Maes), 490 from Christmas Island (Wells and Slack-Smith, 1987), and 581 from atolls off the coast of northwestern Australia (Wells, 1987).

Maes (1967) was intrigued by the zoogeographical relationships of the 379 mollusc species she was able to identify to species: 82% were widespread Indo-Pacific forms, 15% were Pacific species and only 3% had Indian Ocean affinities. She thus concluded that while Cocos (Keeling) is in the Indian Ocean, the islands have a greater faunal affinity with the western Pacific than with the remainder of the Indian Ocean. However since her paper was published the Western Australian Museum has had a number of expeditions to the coral atolls off the northwest coast of Western Australia and also to Christmas Island, some 900 km northeast of Cocos (Keeling), the molluscs of which are reported in a series of papers and reports (Wells 1986; 1987; Wells and Slack-Smith 1987). Comparison of these recent data with Cocos (Keeling) will provide a better idea of the zoogeographic relationships of the atoll.

Many of the species at Cocos and in the other areas are either not identified to species or are identified only provisionally. For these reasons Wells (1986) selected 20 families of prosobranch gastropods for a detailed examination of the zoogeographic relationships of the molluscs of the atolls off northwestern Australia. The families were selected because the individual species are generally large and well known taxonomically, and they are well represented in museum collections. The same 20 families are examined here. For the Cocos material 248 species of the total of 584, or 42%, of all species collected belong to the 20 families. Thus they can be considered as representative of molluscs as a whole. An index of overlap (Krebs 1978) was calculated for all combinations of Cocos (Keeling), Christmas Islands and atolls off the northwestern Australian coast. The index varies from 0 where there is no overlap to 1 where the overlap is total. Values obtained were:

Cocos-Christmas	0.52
Cocos-Northwestern Australian atolls	0.57
Christmas-Northwestern Australia	0.52

All three overlaps are relatively low, probably due to our rather limited knowledge of the fauna of the three areas. However the overlaps are similar among the three areas. Most of the species recorded were found at two or three of the areas. Maes (1967) commented upon several species as not occurring in Western Australia; all were found on the surveys of offshore coral reefs. Based on the increased data now available it appears that the molluscs of Cocos (Keeling) have very close faunal affinities with those of Christmas Island and the offshore areas of Western Australia. Many of the species that Maes considered to be western Pacific are in fact found throughout the three areas of the eastern Indian Ocean and should be considered to be Indo-Pacific species. Perhaps if there is a specific Indian Ocean mollusc fauna it occurs primarily in the western Indian Ocean and only a few species reach as far east as Cocos (Keeling), or in the case of species such as *Drupa lobata* even as far as the west coast of Western Australia.

Neither Maes (1967) nor the Western Australian Museum survey recorded the largest of the giant clam species, *Tridacna gigas*, as living on Cocos (Keeling). However large numbers of long dead shells line the shoreline of Home Island. This suggests that *T. gigas* occurred on the atoll when it was first inhabited but became locally extinct as it was collected by Cocos Malays for food.

The spider shell *Lambis lambis* occurs in large numbers in shallow water in the southern part of the lagoon at Cocos. It is easily collected and is regarded as a delicacy by the Cocos Malays. The same species is also collected for food in many other areas of the Indo-Pacific but a thorough literature search failed to find a single study of the fishery biology of any species of *Lambis*. Being a relatively large species that occurs in shallow water *L. lambis* could be easily fished out, and become locally extinct as did *T. gigas*. If there is to be effective management of the marine environment of the Cocos (Keeling) Islands a study of the population biology of *Lambis lambis* is urgently needed.

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I would like to personally thank the people and organisations acknowledged at the beginning of this report for their help to the Museum team, and would also like to thank the other team members for help in the field and provision of specimens. In addition to his technical work for the entire group, C.W. Bryce collected numerous mollusc species and photographed most of the opisthobranchs alive. G.M. Hansen and G.W. Buick identified most of the specimens during my absence on other museum projects, and C.W. Bryce identified many of the opisthobranchs; their contribution is significant and very much appreciated.

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LIST OF MOLLUSCS

CLASS POLYPLACOPHORA

ACANTHOCHITONIDAE	
Acanthochitona sp.	Maes

CLASS GASTROPODA

SCISSURELLIDAE	
sp.	Maes
FISSURELLIDAE	
Emarginula sp.	Maes
TROCHIDAE	
Ethalia striolata (A. Adams, 1853)	Maes
Euchelus foveolatus (A. Adams, 1851)	Maes
Euchelus cf. *instrictus* (Gould, 1851)	Maes
Monilea cf. *nucleus* (Philippi, 1849)	9, 13, 23, Rare
Trochus maculatus Linnaeus,1758	1, 2, 6, 9, 10, 12, 14, 15, 16, 17, 23, 25, 26, 27, 29, 36, Abundant.
STOMATIIDAE	
Broderipia rosea (Broderip, 1834)	Maes
Stomatella impertussa (Burrow, 1815)	Maes
Stomatia phymotis Helbling, 1779	Maes
Stomatia cf. *rubra* (Lamarck, 1822)	Maes
Synaptocochlea sp.	Maes
TURBINIDAE	
Astralium calcar (Linnaeus, 1758)	32, Uncommon
Astraea helicina (Gmelin, 1791)	6, 9, 10, 12, 15, Uncommon
Leptothyra solida Preston, 1908	Maes
Parviturbo parvissima (Hedley, 1899)	Maes
Turbo lajonkairii Deshayes, 1839	1, 5, 7, 10, 11, 12, 14, 15, 23, 27, 30, 32, Abundant
Turbo petholatus Linnaeus, 1758	2, 16, 17, 23, Uncommon
PHASIANELLIDAE	
Hiloa variabilis (Pease, 1860)	Maes
NERITIDAE	
Nerita albicilla Linnaeus. 1758	2, 6, 10, 12, 27, 30, Common
Nerita costata Gmelin, 1791	Maes
Nerita maxima Gmelin, 1791	Maes
Nerita plicata Linnaeus, 1758	1,2, 6, 10, 12, 21, 30, Abundant

Nerita polita Linnaeus, 1758	27, Common
Nerita undata Linnaeus, 1758	2, Common
Nerita sp.	2, Uncommon
Smaragdia rangiana (Recluz, 1841)	Maes
Smaragdia souverbiana (Montrouier, 1865)	Maes
PHENACOLEPIDAE	
Phenacolepas cf. *senta* Hedley, 1899	Maes
Phenacolepas sp.	Maes
NERITOPSIDAE	
Neritopsis radula (Linnaeus, 1758)	13, 23, Rare
LITTORINIDAE	
Littoraria coccinea (Gmelin, 1791)	Abbott
Littoraria glabrata (Philippi, 1846)	Maes
Littoraria scabra (Linnaeus, 1758)	2, Uncommon
Littoraria undulata (Gray, 1839)	2, 12, 21, Common
Nodilittorina pyramidalis (Quoy and Gaimard, 1833)	Maes
Tectarius granularis (Gray, 1839)	Maes
VITRINELLIDAE	
Teinostoma sp.	Maes
Vitrinella sp.	Maes
TRUNCATELLIDAE	
Truncatella guerinii A. and J. Villa, 1841	Maes
RISSOIDAE	
Haurakia isolata Laseron, 1956	Maes
Pyramidelloides cf. *miranda* (A. Adams, 1861)	Maes
Rissoina ambigua Gould, 1851	Maes
Rissoina balteata Pease, 1870	Maes
Rissoina ephamilla Watson, 1886	Maes
Rissoina exasperata Souverbie, 1866	Maes
Rissoina polytropa Hedley, 1899	Maes
Rissoina cf.*tenuistriata* Pease, 1867	Maes
Rissoina triticea Pease, 1862	Maes
Rissoina turricula Pease, 1860	Maes
Rissoina sp.	Maes
Zebina semiplicata (Pease, 1862)	Maes
Zebina tridentata Michaud, 1860	Maes
ASSIMINEIDAE	
Assiminea sp.	Maes
OMALOGYRIDAE	
Omalogyra sp.	Maes
RISSOELLIDAE	
3 undetermined species	Maes

ARCHITECTONICIDAE	
Heliacus sp.	13, 23, Rare
Philippia radiata (Röding, 1798)	22, Rare
VERMETIDAE	
Dendropoma maxima (Sowerby, 1825)	5, 6, 7, 10, 12, 19, 36 Abundant
CAECIDAE	
Caecum sp.	Maes
PLANAXIDAE	
Planaxis lineatus (DaCosta, 1776)	Maes
MODULIDAE	
Modulus tectum (Gmelin, 1791)	Maes
CERITHIIDAE	
Bittum sp.	9, 16, 23, 29, Common
Cerithium atromarginatum Dautzenberg and Bouge, 1933	10, 12, 13, 27, Uncommon
Cerithium columna Sowerby, 1831	1, 6, 7, 13, 23, 27, 32, Abundant
Cerithium echinatum Lamarck, 1822	5, 7, 9, 13, 15, 19, 22, 23, 25, 32, Abundant
Cerithium egenum Gould, 1849	13, 27, Rare
Cerithium cf. *ianthinum* Gould, 1851	13, Rare
Cerithium nesioticum Pilsbry and Vanetta, 1905	13, 19, 22, 32, Common
Cerithium nodulosum (Bruguière, 1792)	1, 2, 5, 9, 11, 12, 17, 29, 35, Common
Cerithium piperitum Sowerby, 1855	Maes
Cerithium purpurascens Sowerby, 1855	Maes
Cerithium rarimaculatum Sowerby, 1855	7, 13, 22, 25, 32, Common
Cerithium rostratum Sowerby, 1855	9, 13, 23, Uncommon
Cerithium trailli (Sowerby, 1855)	16, 26, 29, Uncommon
Diala albugo (Watson, 1886)	Maes
Gourmya gourmyii (Crosse, 1861)	19, Rare
Obtortio diplax (Watson, 1886)	Maes
Rhinoclavis asper (Linnaeus, 1758)	12, 22, Uncommon
Rhinoclavis diadema Houbrick, 1978	5, 6, 7, 9, 12, 13, 15, 19, 22, 23, Adundant
Rhinoclavis fasciatus (Bruguière, 1792)	9, 14, 15, 17, 19, 22, 32, Abundant
(referred to *R. procera* (Kiener, 1841) by Maes)	
Rhinoclavis sinensis (Gmelin, 1791)	1, 5, 6, 9, 10, 27, Common
Rhinoclavis vertagus (Linnaeus, 1767)	2, 9, 12, 17, 27, 29 36 Common
Clypeomorus bifasciata (Sowerby, 1855)	2, 7, 21, 27, 35, 36, Adundant
CERITHIOPSIDAE	
Cerithiopsis four unidentified species	Maes

TRIPHORIDAE	
Triphora alveolata Adams and Reeve, 1850	Maes
Triphora concors Hinds, 1843	Maes
Triphora rubra Hinds, 1843	Maes
Triphora ustulata Hervier, 1897	Maes
Triphora verrucosa Adams and Reeve, 1850	Maes
Triphora violacea Quoy and Gaimard, 1834	Maes
Triphora sp.	Maes
Viriola cancellata (Hinds, 1843)	Maes
Viriola intergranosa (Hervier, 1897)	Maes
Viriola interfilata (Gould, 1861)	Maes
EPITONIIDAE	
Epitonium alata (Sowerby, 1844)	Maes
Epitonium martinii (Wood, 1828)	Maes
Epitonium "muricatum" Risso (of Kiener, 1838-39)	Maes
Epitonium cf. *symmetrica* (Pease, 1867)	Maes
Nodiscala? attenuata (Pease, 1860)	Maes
Epitonium 3 unidentified species	Maes
EULIMIDAE	
Balcis cumingi (A. Adams, 1854)	Maes, 13 Rare
Balcis 4 additional species	Maes
Sp. 1	10, Rare
STILIFERIDAE	
?Stilifer dubia Sowerby, 1878	Abbott
FOSSARIDAE	
Couthouyia stoliczkanus Nevill, 1871	Maes
VANIKORIDAE	
Vanikoro cancellata (Lamarck, 1822)	25, Rare
Vanikoro distans (Recluz, 1843)	25, Rare
HIPPONICIDAE	
Sabia concia (Schumacher, 1817)	12, 23, 27, Common
CALYPTRAEIDAE	
Cheilea equestris (Linnaeus, 1758)	12, 23, Uncommon
Cheilea hipponiciformis (Reeve, 1858)	Maes
STROMBIDAE	
Lambis chiragra (Linnaeus, 1758)	1, 7, 12, Uncommon
Lambis lambis (Linnaeus, 1758)	9, 12, 35, 36, Adundant
Lambis truncata (Humphrey, 1786)	23, Rare
Strombus aurisdianae Linnaeus, 1758	Maes
Strombus gibberulus Linnaeus, 1758	5, 9, 12, 15, 27, 29, Common
Strombus lentiginosus Linnaeus, 1758	5, 23, Rare
Strombus luhuanus Linnaeus, 1758	9A, 23, Uncommon
Strombus microurceus (Kira, 1959)	9A, Uncommon]

Strombus mutabilis Swainson, 1821	1, 5, 9, 12, 27, Common
NATICIDAE	
Eunaticina papilla (Gmelin, 1791)	19, Rare
Natica fasciata (Röding, 1798)	17, Rare
Natica gualtieriana (Recluz, 1844)	2, 27, 35, Common
Natica lemniscata Philippi, 1852	Maes
Natica lineozona Jousseaume, 1874	Maes
Natica marochiensis Gmelin, 1791	Maes
Natica orientalis Gmelin, 1791	Maes
Natica robillardi Sowerby, 1893	9, 29, Rare
Polinices mammilla (Linnaeus, 1758)	Maes
Polinices melanostomus (Gmelin, 1791)	7, Rare
Polinices simiae (Deshayes, 1838)	Maes
Polinices tumidus (Swainson, 1840)	5, 6, 9, 10, 12, 13, 15, 23, Adundant
LAMELLARIIDAE	
Lamellaria sp.	Maes
ERATOIDAE	
Proterato sulcifera (Gray, 1832)	Maes
Trivia insecta (Mighels, 1845)	Maes
Trivia oryza (Lamarck, 1810)	Maes
Trivia pellucidula (Reeve, 1846)	Maes
Trivia producta (Gaskoin, 1836)	Maes
OVULIDAE	
Calpurneus lacteus (Lamarck, 1810)	13, Rare
Calpurneus verrucosus (Linnaeus, 1758)	Maes
Ovula ovum (Linnaeus, 1753)	Maes
Pseudocypraea adamsoni (Gray, 1832)	Maes
CYPRAEIDAE	
Cypraea annulus Linnaeus, 1758	1, 6, 10, 27, Common
Cypraea arabica Linnaeus, 1758	12, 27, Uncommon
Cypraea boivinii Kiener, 1843	Maes
Cypraea caputserpentis Linnaeus, 1758	1, 11, 12, 27, Common
Cypraea carneola Linnaeus, 1758	13, Uncommon
Cypraea caurica Linnaeus, 1758	Maes
Cypraea chinensis Gmelin, 1791	Maes
Cypraea coloba Melvill, 1888	9A, Rare
Cypraea depressa Gray, 1824	1, 10, 12, 27, Common
Cypraea erosa Linnaeus, 1758	5, 12, 27, Uncommon
Cypraea fimbriata Gmelin, 1791	13, 19, Rare
Cypraea globulus Linnaeus, 1758	3, 13, Rare
Cypraea helvola Linnaeus, 1758	1, 12, 13, 23, Uncommon
Cypraea hirundo Linnaeus, 1758	1, 19, Uncommon
Cypraea histrio Gmelin, 1791	1, 6, 7, 12, 21, 23, Common
Cypraea isabella Linnaeus, 1758	9, 12, 13, 25, 32, Common

Cypraea labrolineata Gaskoin, 1849	7, 13, 15, 19, 22, 23, Common
Cypraea lynx Linnaeus, 1758	3, 7, Uncommon
Cypraea mauritiana Linnaeus, 1758	27, Rare
Cypraea microdon Gray, 1828	Maes
Cypraea moneta Linnaeus, 1758	1, 2, 5, 6, 9, 10, 12, 16, 17, 26, 27, 29, 35, 36, Adundant
Cypraea nucleus Linnaeus, 1758	Maes
Cypraea poraria Linnaeus, 1758	27, 32, Uncommon
Cypraea punctata Linnaeus, 1771	13, Uncommon
Cypraea stolida Linnaeus, 1758	32, Uncommon
Cypraea talpa (Linnaeus, 1758)	13, 15, Rare
Cypraea teres Gmelin, 1791	13, 25, 32, Rare
Cypraea testudinaria Linnaeus, 1758	Maes
Cypraea tigris Linnaeus, 1758	12, 18, 22, 36, Rare
Cypraea vitellus Linnaeus, 1758	36, Uncommon

TONNIDAE

Malea pomum (Linnaeus, 1758)	12, Rare
Tonna canaliculata (Linnaeus, 1758)	36, Rare
Tonna perdix (Linnaeus, 1758)	12, 27, 30, Rare

CASSIDAE

Casmaria erinaceus (Linnaeus, 1758)	Maes
Cypraecassis rufa (Linnaeus, 1758)	Maes

CYMATIIDAE

Charonia tritonis (Linnaeus, 1758)	12, 21, Rare
Cymatium aquatile (Reeve, 1844)	16, Rare
Cymatium lotorium (Linnaeus, 1758)	Maes
Cymatium nicobaricum (Röding, 1798)	2, 6, 9, 10, 15, 16, 17, 27, 29, 35, 36
Cymatium pileare (Linnaeus, 1758)	Maes
Cymatium pyrum (Linnaeus, 1758)	13, 23, Uncommon
Cymatium rubeculum (Linnaeus, 1758)	9, 32, Uncommon
Cymatium vespaceum (Lamarck, 1822)	Maes
Distorsio anus Linnaeus, 1758	6, Rare
Gutturnium muricinum (Gmelin, 1791)	1, 9, 29, 36, Uncommon
Septa gemmata (Reeve, 1844)	1, 10, 17, 18, 27, 29, Common
Gelagna succincta (Linnaeus, 1771)	13, Rare
Linatella clandestina (Lamarck, 1816)	Abbott

BURSIDAE

Bursa bufonia (Gmelin, 1791)	1, 10, 12, 27, Common
Bursa cruentata (Sowerby, 1841)	13, 23, 32, Common
Bursa granularis (Röding, 1798)	1, 5, 6, 9, 10, 12, 27, 32, Common
Bursa lamarcki (Deshayes, 1853)	19, Rare
Bursa rhodostoma (Sowerby, 1835)	9, 23, Uncommon
Bursa tuberosissima (Reeve, 1844)	25, Rare
Tutufa rubeta (Linnaeus, 1758)	23, Rare

COLUBRARIIDAE

Colubraria nitidula (Sowerby, 1833)	15, Rare
Colubraria muricata (Lightfoot, 1786)	7, 9, Uncommon

MURICIDAE

Aspella anceps (Lamarck, 1822)	Maes
Chicoreus saulii (Sowerby, 1841)	7, 6, 9, 13, 15, 19, 21, 22, 23,32, Abundant
(listed as *Murex torrefactus* Sowerby, 1841 by Maes)	
Murex ramosus Linnaeus, 1758	Abbott
Naquetia triquetra (Born, 1778)	23, Rare

THAIDIDAE

Cronia crassulnata (Hedley, 1915)	27, Rare
Drupa clathrata (Lamarck, 1816)	Maes
Drupa grossularia Röding, 1798	Maes
Drupa lobata (Blainville, 1832)	23, Uncommon
Drupa morum (Röding, 1798)	1, 5, 6, 10, 11, 12, 27, Common
Drupa pophyrostoma (Reeve, 1846)	6, Rare
Drupa ricinus (Linnaeus, 1758)	1, 6, 12, 15, 27, 30, Common
Drupa rubusidaeus Röding, 1798	13, 15, 23, 32, Common
Drupella chaidea (Duclos, 1832)	Maes
Drupella cornus (Röding, 1798)	10, 13, 16, 29, 30, 36, Common
Drupella ochrostoma (Blainville, 1832)	Maes
Maculotriton digitalis (Reeve, 1844)	13, 27, Uncommon
Maculotriton sculptilis (Reeve, 1846)	Maes
Maculotriton serriale (Deshayes, 1834)	6, 10, 13, 27, 30, Common
Morula anaxeres (Kiener, 1845)	6, Rare
Morula biconica (Blainville, 1832)	Maes
Morula fiscella (Gmelin, 1791)	27, Rare
Morula fusconigra (Dunker, 1871)	Maes
Morula granulata (Duclos, 1832)	6, 10, 12, 27, 30, Common
Morula margariticola (Broderip, 1832)	1, 6, 12, 13, 27, 29, 32, 36, Common
Morula marginatra (Blainville, 1832)	Maes
Morula nodicostata (Pease, 1868)	13, 30, Common
Morula spinosa (H. and A. Adams. 1835)	1, 7, 13, 19, 25, 32, Common
Morula uva (Röding, 1798)	1, 5, 6, 9, 10, 12, 13, 19, 22, 23, 27, 30, 32, Abundant
Nassa serta (Bruguière, 1789)	Maes
Purpura persica (Linnaeus, 1758)	Maes
Thais aculeata (Deshayes, 1844)	5, 6, 10, 19, 27, Uncommon
Thais armigera (Link, 1807)	1, 10, 12, 27, Uncommon
Thais hippocastanum (Linnaeus, 1758)	Maes

CORALLIOPHILIDAE

Coralliophila deformis (Lamarck, 1822)	Maes

Coralliophila erosa (Röding, 1798)	13, 36, Uncommon
Coralliophila robillardi (Lienard, 1870)	13,30, Uncommon
Coralliophila violacea (Kiener, 1836)	5, 7, 9, 12, 13, 15, 19, 22, 23, 26, 32, Abundant
Quoyula madreporarum (Sowerby, 1832)	7, 10, 13, 23, 32, Common
Rapa rapa (Gmelin, 1791)	7, 13, 25, 32, Common

COLUMBELLIDAE

Aesopus cumingi (Reeve, 1859)	Maes
Mitrella marquesa (Gaskoin, 1851)	Maes
Pyrene obtusa (Sowerby, 1832)	5, 7, 13, 23, 32, Common
Pyrene turturina (Lamarck, 1822)	5, 7, 9, 10, 12, 13, 19, 22, 23, 29, Common
Pyrene varians (Sowerby, 1832)	9, 13, 32, Uncommon
Zafra sinensis (Sowerby, 1894)	Maes

BUCCINIDAE

Cantharus cf. *fragaria* (Reeve, 1846)	7, 13, 19, 23, Common
Cantharus fumosus (Dilwyn, 1817)	9, 17, Uncommon
Cantharus iostomus (Gray, 1834)	19, 22, 29, Uncommon
Cantharus pulcher (Reeve, 1846)	7, 19, 32, Uncommon
Cantharus undosus (Linnaeus, 1758)	1, 5, 6, 10, 27, Common
Engina incarnata (Deshayes in Laborde and Linant, 1834)	7, Rare
Engina lauta (Reeve, 1846)	Maes
Engina lineata (Reeve, 1846)	13, 27, Uncommon
Engina melanozona Tomlin, 1928	Maes
Engina mendicaria (Linnaeus, 1758)	27, Uncommon
Engina parva Pease, 1867	13, Rare
Engina zonalis (Lamarck, 1812)	6, 27, Uncommon
Nassaria pusilla (Röding, 1798)	32, Rare
Pisania fasciculata (Reeve, 1846)	Maes
Pisania marmorata (Reeve, 1846)	Maes
Pisania truncata (Hinds, 1844)	Maes

NASSARIIDAE

Nassarius gaudiosus (Hinds, 1844)	1, 7, Rare
Nassarius graniferus (Kiener, 1834)	5, 7, 9, 13, 15, 19, 22, 32, Abundant
Nassarius margaritiferus (Dunker, 1847)	6, 12, 27, Uncommon
Nassarius oneratus (Deshayes, 1863)	23, Common
Nassarius papillosus (Linnaeus, 17 58)	5, 13, Uncommon

FASCIOLARIIDAE

Latirus nodatus (Gmelin, 1791)	10, Rare
Latirus polygonus (Gmelin, 1791)	5, 10, 16, 17, 19, 26, 27, 30, 32, Common
Latirus turritus (Gmelin, 1790)	32, Rare
Latirus sp.	13, 29, 32, Common
Peristernia fragaria (Wood, 1828)	Maes
Peristernia nassatula (Lamarck, 1822)	1, 6, 7, 13, 15, 19, 23, 27, Common
Peristernia ustulata (Reeve, 1847)	27, Rare

OLIVIDAE	
Oliva annulata (Gmelin, 1791)	7, 13, 15, 19, 22, 23, 32, Common
Oliva caerulea (Röding, 1798)	6, 13, 19, 25, Common
Oliva episcopalis Lamarck, 1811	Maes
Oliva panniculata Duclos, 1835	13, Rare
MARGI NELLIDAE	
Marginella neville Jousseaume, 1875	Maes
MITRIDAE	
Cancilla carnicolor (Reeve, 1844)	7, Rare
Cancilla filaris (Linnaeus, 1771)	Maes
Imbricaria conovula (Quoy and Gaimard, 1833)	7, 9, 12, 13, 15, 32, Common
Imbricaria olivaeformis (Swainson, 1821)	15, 19, 22, Common
Imbricaria punctata (Swainson, 1821)	22, Rare
Imbricaria vanikorensis (Quoy and Gaimard, 1833)	Maes
Imbricaria virgo (Broderip, 1836)	Maes
Mitra acuminata Swainson, 1824	5, Rare
Mitra ambigua Swainson, 1832	Maes
Mitra columbelliformis Kiener, 1838	12, Rare
Mitra contracta Swainson, 1820	13, Rare
Mitra decurtata Reeve, 1844	6, 10, 27, Uncommon
Mitra eremitarum Röding, 1798	9, Rare
Mitra fraga Quoy and Gaimard, 1833	13, 29, Rare
Mitra imperialis Röding, 1798	Maes
Mitra litterata Lamarck, 1811	6, 27, Common
Mitra mitra (Linnaeus, 1758)	Maes
Mitra paupercula (Linnaeus, 1758)	6, 10, 27, Uncommon
Mitra oleacea (Reeve, 1844)	1, Rare
Mitra rosacea Reeve, 1845	19, Rare
Mitra scutulata (Gmelin, 1791)	27, Rare
Mitra stictica (Link, 1807)	1, Rare
Mitra ticaonica Reeve, 1844	13, Rare
Mitra turgida Reeve, 1845	Maes
Neocancilla papilio (Link, 1807)	19, Rare
Pusia areolata (Reeve, 1844)	Maes
Pusia cancellarioides (Anton, 1839)	Maes
Scabricola fusca (Swainson, 1824)	23, Rare
Scabricola fissurata (Lamarck, 1811)	5, 9, 15, 19, 22, 23, Common
Scabricola granatina Lamarck, 1811	Maes
Scabricola scabricula (Linnaeus, 1758)	Maes
Subcancilla annulata (Reeve, 1844)	19, Rare
COSTELLARIIDAE	
Vexillum armigera (Reeve, 1845)	Maes
Vexillum cadaverosum (Reeve, 1844)	5, 9, 19, 22, Uncommon
Vexillum cancellarioides (Anton, 1838)	32, Rare
Vexillum cf. *corallina* (Reeve, 1845)	7, Rare

Vexillum crocatum (Lamarck, 1811)	7, Rare
Vexillum mutabile (Reeve, 1845)	Maes
Vexillum pardalis (Kuster, 1841)	13, Rare
Vexillum speciosum (Reeve, 1844)	15, 25, 32, Uncommon
Vexillum tuberosa (Reeve, 1845)	13, 22, 23, Uncommon
Vexillum turrigerum (Reeve, 1845)	9, 19, Uncommon
Vexillum unifascialis (Lamarck, 1811)	9, Rare
Vexillum zelotypum (Reeve, 1845)	7, 22, 23, Uncommon

VASIDAE

Vasum turbinellum (Linnaeus, 1758)	1, 5, 7, 10, 11, 14, 15, 19, 22, 23, 25, 27, Abundant

HARPIDAE

Harpa amouretta Röding, 1798	Maes

TURRIDAE

Carinapex sp.	Maes
Clavus laeta (Röding, 1798)	7, 13, 15, 22, 23, Common
Clavus lamberti (Montrouzier, 1860)	7, 23, 32, Uncommon
Clavus sp.	13, Rare
Crassispira sp.	13, Rare
Daphnella atractoides Hervier, 1897	Maes
Daphnella cf. *boholensis* (Reeve, 1843)	Maes
Daphnella delicata (Reeve, 1846)	Maes
Daphnella sp.	13, Rare
Etrema scalarina (Deshayes, 1863)	Maes
Eucithara souverbii (Tryon, 1884)	Maes
Eucithara stromboides (Reeve, 1846)	Maes
Hemidaphne reeveana (Deshayes, 1863)	Maes
Hemidaphne rissoides (Reeve, 1843)	Maes
Iredalea pygmaea (Dunker, 1860)	Maes
Iredalea sp.	15, Rare
Lienardia sp.	Maes
Macteola cf. *thiasotes* (Melvill and Standen, 1897)	Maes
Mitromorpha atramentosa (Reeve, 1849)	5, Rare
Mitromorpha lachryma (Reeve, 1845)	Maes
Mitromorpha stepheni (Melvill and Standen, 1897)	Maes
Philbertia barnardi (Brazier, 1876)	Maes
Philbertia pustulosa (DeFolin, 1867)	Maes
Philbertia granicostata (Reeve, 1846)	Maes
Philbertia tincta (Reeve, 1846)	Maes
Philbertia sp.	27, Rare
Turridrupa cincta (Lamarck, 1822)	Maes
Turridrupa sp.	32, Rare
Turris spectabilis (Reeve, 1843)	Maes
Xenoturris cingulifera (Lamarck, 1822)	13, 19, 22, Uncommon
Xenoturris kingae Powell, 1964	15, 22, 23, Uncommon

CONIDAE

Conus arenatus Hwass in Bruguière, 1792	1, 9, 19, 22, 23, Common
Conus aulicus Linnaeus, 1758	Maes

Conus betulinus Linnaeus, 1758	Maes
Conus capitaneus Linnaeus, 1758	9, 22, 32, Common
Conus catus Hwass in Bruguière, 1792	1, 12, 27, Uncommon
Conus chaldeus (Röding, 1798)	1, 6, 10, Common
Conus coronatus Gmelin, 1791	1, 6, 10, 27, Common
Conus distans Hwass in Bruguière, 1792	7, 10, 23, 27, Common
Conus eburneus Hwass in Bruguière, 1792	9, 15, Uncommon
Conus ebraeus Linnaeus, 1758	1, 6, 10, 12, 27 Abundant
Conus flavidus Lamarck, 1810	1, 7, 10, 23, Common
Conus frigidus Reeve, 1848	Maes
Conus hevassi A. Adam, 1853	Maes
Conus imperialis Linnaeus, 1758	1, 7, 10,13,14, 19, Common
Conus leopardus Röding, 1798	9, Uncommon
Conus litoglyphus Hwass in Bruguière, 1792	7, 22, Uncommon
Conus litteratus Linnaeus, 1758	7, 9, 23, 30, Uncommon
Conus lividus Hwass in Bruguière, 1792	1, 5, 6, 7, 10, 12, 13, 27, Adundant
Conus marmoreus Linnaeus, 1758	23, Uncommon
Conus miles Linnaeus, 1758	5, 9, 15, 19, 22, 23, 25, 27, 32, Abundant
Conus miliaris Hwass in Bruguière, 1792	1, 6, 12, 13, 15, 23, 27, 32, Abundant
Conus moreleti Crosse, 1858	7, 13, Uncommon
Conus musicus Hwass in Bruguière, 1792	5, 7, 13, 15, 19, 22, 23, 25, Uncommon
Conus obscurus Sowerby, 1833	5, 22, 23, 32, Common
Conus pertusus Hwass in Bruguière, 1792	13, Rare
Conus pulicarius Hwass in Bruguière, 1792	5, 7, 9, 9A, 12, 13, 15, 19, 23, 27, Abundant
Conus quercinus Solander, 1786	9, 12, Uncommon
Conus rattus Hwass in Bruguière, 1792	5, 6, 7, 13, 27, Common
Conus sponsalis Hwass in Bruguière, 1792	1, 6, 9, 10, 12, 15, 19, 22, 23, 30, Abundant
Conus straitellus Link, 1807	13, 22, Uncommon
Conus striatus Linnaeus, 1758	7, Rare
Conus tenuistriatus Sowerby, 1857	13, Rare
Conus tessulatus Born, 1780	19, 22, Uncommon
Conus textile Linnaeus, 1758	Maes
Conus tulipa Linnaeus, 1758	Maes
Conus vexillum Gmelin, 1791	9, 32, Uncommon
Conus virgo Linnaeus, 1758	9, Rare
Conus vitulinus Hwass in Bruguière, 1792	Maes
Conus zonatus Hwass in Bruguière, 1792	Maes
TEREBRIDAE	
Hastula penicillata (Hinds, 1844)	9, 13, Uncommon
Terebra affinis Gray, 1834	5, 7, 9, 13, 15, 22, 23, Common
Terebra areolata Link, 1807	Maes
Terebra argus Hinds, 1844	9, 13, Uncommon
Terebra babylonia Lamarck, 1822	13, 15, 32, Uncommon
Terebra casta Hinds, 1844	Maes

Terebra cerithina Lamarck, 1822	Maes
Terebra chlorata Lamarck, 1822	5, 15, Uncommon
Terebra columellarisaris Hinds, 1844	15, 19, Uncommon
Terebra cerithina Lamarck, 1822	5, Rare
Terebra crenulata (Linnaeus, 1758)	5, 12, 13, 23, 32, Common
Terebra dimidiata (Linnaeus, 1758)	5, 6, 12, 13, 19, Common
Terebra felina (Dillwyn, 1817)	7, 9, 12, 22, 29, Common
Terebra funiculata Hinds, 1844	9, 15, 32, Uncommon
Terebra guttata Burch, 1965	19, Rare
Terebra hectica (Linnaeus, 1758)	Abbott
Terebra laevigata Gray, 1834	Maes
Terebra lanceata (Linnaeus, 1767)	9, 13, 15, 19, Uncommon
Terebra maculata (Linnaeus, 1758)	5, 9, 12, 15, 19, 22, 32, Common
Terebra nebulosa (Sowerby, 1825)	7, 15, 19, 22, Uncommon
Terebra pertussa (Born, 1778)	15, Rare
Terebra subulata (Linnaeus, 1767)	9, 12, 15, 19, 23, Uncommon
Terebra solida (Gmelin, 1791)	19, Rare
Terebra undulata Gray, 1834	15, 19, Uncommon
Terenolla pygmaea (Hinds, 1844)	7, 13, 23, Rare

SUBCLASS OPISTHOBRANCHIA

PYRAMIDELLIDAE

Odostomia peasei Dautzenberg and Bouge, 1933	Maes
Odostomia 6 species	Maes
Otopleura mitralis (A. Adams, 1854)	Maes
Pyramidella acus (Gmelin, 1791)	12, 13, 17, 23, Common
Pyramidella dolabrata (Linnaeus, 1758) (Listed as *P. terebellum* (Müller, 1774) by Maes	9, Rare
Pyramidella sulcata (A. Adams, 1854)	9, Uncommon
Turbonilla 2 species	Maes

ACTEONIDAE

Pupa sulcata (Gmelin, 1791) (Listed as *Pupa glabra* (Reeve, 1842) by Maes)	9, 17, 23, 29, 35 Uncommon
Pupa nitidula (Lamarck, 1816)	Maes

BULLINIDAE

Bullina sp.	Maes

HYDATINIDAE

Hydatina amplustre (Linnaeus, 1758)	Maes
Hydatina physis (Linnaeus, 1758)	Maes
Micromelo guamensis (Quoy and Gaimard, 1825)	Maes

BULLIDAE

Bulla vernicosa Gould, 1859	9, 12, 17, 19, 27, 30, Uncommon

ATYIDAE	
Atys cylindricus (Helbling, 1779)	9, 17, Uncommon
Haminoea cymbalum (Quoy and Gaimard, 1835)	7, 10, Uncommon
Phanerophthalmus cylindricus (Pease, 1861)	12, Rare
GASTROPTERIDAE	
Gastropteron sp.	13, Rare
SCAPHANDRIDAE	
Cylichna sp.	Maes
AGLAJIDAE	
Philinopsis gardineri (Eliot, 1903)	5, 23,Rare
APLYSIIDAE	
Aplysia dactylomela Rang, 1828	Maes
Dolabella auricularia (Solander, 1786)	1, 12, Rare
Dolabrifera dolabrifera (Rang, 1828)	1, 3, 12, 24, Rare
PLEUROBRANCHIDAE	
Bertheliina citrina (Rüppell and Leuchkart, 1828)	12, 27, Rare
Pleurobranchus cf. *forskali* Rüppell and Leuckart, 1828	
UMBRACULIDAE	
Umbraculum sinicum (Gmelin, 1791)	Maes
ELYSIIDAE	
Elysia sp.	1, 18, Common
PLAKOBRANCHIDAE	
Placobranchus ocellatus van Hasselt, 1824	1, 5, 12, 27, 35, Common
CYLINDROBULLIDAE	
Ascobulla sp.	18, Common
OXYNOEIDAE	
Lobiger sp.	Maes
Oxynoe delicatula (G. and H. Nevill, 1869)	Maes
VOLVATELLIDAE	
Volvatella cincta (G. and H. Nevill, 1869)	Maes
Volvatella sp.	Maes
JULIIDAE	
Julia borbonica (Deshayes, 1863)	Maes
HEXABRANCHIDAE	
Hexabranchus sanguineus (Rüppell and Leuckart, 1828)	5, 12, Rare
AEGIRIDAE	
Notodoris minor Eliot, 1904	1, 29, Uncommon

Notodoris citrina Bergh, 1875	1, Rare
DORIDIDAE	
Halgerda tessellata (Bergh, 1880)	13, Rare
Jorunna funebris (Kelaart, 1858)	12, Rare
Platydoris cruenta (Quoy and Gaimard, 1832)	1, Uncommon
Platydoris scabra (Cuvier, 1804)	13, Uncommon
Dorid sp.	24, Rare
DENDRODORIDIDAE	
Dendrodoris nigra (Stimpson, 1855)	1, 10, Uncommon
CHROMODORIDIDAE	
Chromodoris elisabethina Bergh, 1877	4, 15, Rare
PHYLLIDIIDAE	
Phyllidia coelistis Bergh, 1905	23, Uncommon
Phyllidia elegans Bergh, 1869	13, Uncommon
Phyllidia cf. *pustulosa* Cuvier, 1804	12, Common
Phyllidia sp. 1	12, 15, 26, Common
Phyllidia sp. 2	4, 25, Uncommon
Phyllidia sp. 3	13, 15, Uncommon
TETHYDIDAE	
cf. *Melibe* sp.	1, Rare
SUBCLASS PULMONATA	
SIPHONARIIDAE	
Siphonaria atra (Quoy and Gaimard, 1833)	Maes
Siphonaria cf. *normalis* Gould, 1848	28, Common
ELLOBIIDAE	
Auricula sp.	2, Uncommon
Melampus castaneus (Muhlfeld, 1818)	1, 7, Common
Melampus flavus (Gmelin, 1791)	2, 7, 21, Common
Melampus fasciatus (Deshayes, 1830)	Maes
Pythia sp.	Maes

CLASS BIVALVIA

LIMOPSIDAE	
Cosa sp.	Maes
ARCIDAE	
Arca plicata (Dillwyn, 1817)	7, 13, Rare
Arca ventricosa Lamarck, 1819	12, Uncommon
Barbatia decussata (Sowerby, 1833)	Maes
Barbatia tenella Reeve, 1844	22, Rare
Barbatia velata (Sowerby, 1843)	7, 12, 22, 23, Uncommon

MYTILIDAE	
Lithophaga nasuta (Philippi, 1846)	Maes
Lithophaga teres (Philippi, 1846)	16, Common
Modiolus phillipinarum Hanley, 1843 (listed as *Modiolus modulaides* by Maes)	1, 2, 22, 27, Uncommon
Modiolus sp.	12, 25, 35, Uncommon
PINNIDAE	
Atrina vexillum (Born, 1778)	Maes
Pinna muricata Linnaeus, 1758	12, 36, Uncommon
Streptopinna saccata (Linnaeus, 1758)	13, 19, 22, Uncommon
PTERIIDAE	
Electroma alacorvi (Dillwyn, 1817)	Maes
Pinctada margaritifera (Linnaeus, 1758)	23, Rare
Pteria penguin (Röding, 1798)	Maes
Pteria sp.	27, Rare
ISOGNOMONIDAE	
Isognomon ephippium (Linnaeus, 1758)	Maes
Isognomon isognomum (Linnaeus, 1758)	9, Rare
Isognomon legumen (Gmelin, 1791)	Maes
Isognomon perna (Linnaeus, 1767)	6, 7, 10, 13, Uncommon
PECTINIDAE	
Chlamys coruscans (Hinds, 1844)	Maes
Chlamys irregularis (Sowerby, 1842)	7, 15, 22, 23, 32, Common
Chlamys lentiginosus (Reeve, 1853)	23, 25, Common
Chlamys squamosus (Gmelin, 1791)	Maes
Chlamys sp.	13, Rare
Decatopecten radula (Linnaeus, 1758)	9, 29, 36, Uncommon
Pecten pyxidatus Born, 1778	Maes
Semipallium tigris (Lamarck, 1819)	26, Rare
PLICATULIDAE	
Plicatula chinensis Mörch, 1853	Maes
SPONDYLIDAE	
Spondylus lamarckii Chenu, 1845	6, 9, 29, Uncommon
Spondylus nicobaricus Schreibers, 1793	13, 16, 17, 19, Uncommon
Spondylus sanguineus Dunker, 1852	13, Common
LIMIDAE	
Lima cf. *annulata* Lamarck, 1819	6, 13, 15, 26 29 Uncommon
Lima fragilis (Gmelin, 1791)	9, 12, 36, Uncommon
Limaria orientalis (Adams and Reeve, 1850)	7, 16, 19, 26, 30, 32, Common
OSTREIDAE	
Ostrea sp.	16, 27, 28, 30, Common

GRYPHAEIDAE	
Hyotissa hyotis (Linnaeus, 1758)	9, Uncommon
CHAMIDAE	
Chama aspersa Reeve, 1846	Maes
Chama imbricata Broderip, 1834	Maes
Chama cf. *iostoma* Conrad, 1837	6, 12, 15, 29, Uncommon
Chama lazarus Linnaeus, 1758	6, 26, 28, 29, Uncommon
Chama sp.	1, 9, 10, 16, Common
LUCINIDAE	
Anodontia edentula (Linnaeus, 1758)	15, 31, Uncommon
Anodontia pila (Reeve, 1850)	21, 23, 30, Uncommon
Cavatidens sp.	Maes
Ctena sp.	36, Rare
Codakia divergens (Philippi, 1850)	Maes
Codakia punctata (Linnaeus, 1758)	5, 9, 10, 12, 19, 32, 35, 36, Common
Glycodonta sp.	15, 19, Rare
Wallucina gordoni E. A. Smith	17, 30, Rare
ERYCINIDAE	
Barrimysia incerta (Deshayes, 1863)	Maes
Erycinacea sp.	Maes
Fronsella cf. *fugitaniana* (Yokoyama, 1927)	Maes
Hitia ovalis Dall, Bartsch and Rehder, 1938	Maes
Besobornia pacifica (Hedley, 1899)	Maes
GALEOMMATIDAE	
Scintillona sp.	5, Rare
CARDITIDAE	
Cardita variegata (Bruguière, 1792)	5, 7, 13, 15, 16, Common
DIPLODONTIDAE	
Diplodonta sp.	Maes
SPORTELLIDAE	
cf. *Anisodonta* sp.	Maes
CARDIIDAE	
Acrosterigma alternatum (Sowerby, 1841)	29, 36, Uncommon
Acrosterlgma orbita (Broderip and Sowerby, 1833)	6, 7, 13, 15, 22, 23, 25, Common
Corculum cardissa (Linnaeus, 1758)	Maes
Fragum fragum (Linnaeus, 1758)	2, 5, 9, 12, 35, 36
Fragum unedo (Linnaeus, 1758)	17, Rare
TRIDACNIDAE	
Tridacna derasa (Röding, 1798)	Maes
Tridacna gigas (Linnaeus, 1758)	6 dead valves

Tridacna maxima (Röding, 1798)	1, 5, 6, 7, 10, 12, 19, 36, Common
TELLINIDAE	
Arcopagia palatum Iredale, 1929	Maes
Cadella semitorta (Sowerby, 1867)	Maes
Arcopagia scobinata (Linnaeus, 1758)	5, 9, 12, 13, 15, 19, 22, 23, 29, 35, Common
Macoma obliquilineata (Conrad, 1837)	29, Rare
Quadrans gargadia (Linnaeus, 1758)	15, Rare
Tellina chariessa Salisbury, 1934	Maes
Tellina clathrata (Deshayes, 1835)	9, 30, 36, Common
Tellina crassiplicata (Sowerby, 1869)	Maes
Tellina crucigera Lamarck, 1818	23, Rare
Tellina dispar (Conrad, 1837)	2, 9, 17, 36, Uncommon
Tellina linguafelis Linnaeus, 1758	26, Rare
Tellina obliquaria (Deshayes, 1854)	Maes
Tellina palatum (Iredale, 1929)	2, Common
Tellina perna Splenger, 1798	12, 35, Rare
Tellina pinguis (Hanley, 1845)	Maes
Tellina pulcherrima (Sowerby, 1867)	Maes
Tellina robusta (Hanley, 1844)	9, 13, 36, Uncommon
Tellina tenuilirata (Sowerby, 1867)	Maes
Tellina tongana (Quoy and Gaimard, 1835)	30, 32, Rare
Tellina sp.	17, Rare
PSAMMOBIIDAE	
Asaphis violaceans (Förskal, 1775)	35, Rare
Gari sp.	17, Rare
SEMELIDAE	
Semele crenulata (Sowerby, 1853)	17, 29, Rare
Thyella cf. *lamellosa* H. Adams, 1873	Maes
TRAPEZIIDAE	
Trapezium oblongum (Linnaeus, 1758)	35, Rare
VENERIDAE	
Katelysia cf. *striata* (Gmelin, 1791)	Maes
Lioconcha castrensis (Linnaeus, 1758)	29, Rare
Lioconcha hebraea (Lamarck, 1818)	6, 9, 17, 22, 23, 26, 36, Common
Periglypta chemnitzii (Hanley, 1844)	9, Rare
Periglypta clathrata (Deshayes, 1853)	Maes
Periglypta crispata (Deshayes, 1859)	29, Rare
Periglypta puerpera (Linnaeus, 1771)	9, Rare
Pitar cf. *affinis* (Gmelin, 1791)	22, Uncommon
Pitar prora (Conrad, 1837)	9, 17, 29, 35, Uncommon
Protothaca marica (Linnaeus, 1758)	Maes
Tapes cf. *literatus* (Linnaeus, 1758)	9, 26, 29, Rare
Ventricolaria toreuma (Gould, 1846)	25, Rare

CORBULIDAE	
Corbula ustulata Reeve, 1844	Maes
Corbula sp.	Maes
GASTROCHAENIDAE	
Gastrochaena cuneiformis (Splengler, 1783)	Maes

CLASS CEPHALOPODA

NAUTILIDAE	
Nautilus pompilius Linnaeus, 1758	5, Rare
LOLIGINIDAE	
Sepioteuthis lessoniana Lesson, 1830	Rees
OCTOPODIDAE	
Octopus cyanea Gray, 1849	1, 12, Common
SEPIIDAE	
Sepia latimanus Quoy and Gaimard, 1832	9, Rare

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CHAPTER 13

ECHINODERMS OF THE COCOS (KEELING) ISLANDS

BY

L.M. MARSH

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CHAPTER 13

ECHINODERMS OF THE COCOS (KEELING) ISLANDS

BY

L.M. MARSH *

INTRODUCTION

The first extensive collection of echinoderms of the Cocos (Keeling) Islands was made by C.A. Gibson-Hill who was Resident Medical Officer at the Cable Station on Direction Island (Pulu Tikus) between December 1940 and November 1941. Prior to this Gibson-Hill was Resident Medical Officer at Christmas Island from September 1938 to December 1940, where he also made extensive natural history collections. His specimens and field notes were deposited in the Raffles Museum, Singapore in 1941. One of Gibson-Hill's aims was to be able to compare the fauna of the Cocos (Keeling) Islands with that of Christmas Island. His other aim was to document the terrestrial and reef fauna of the Cocos (Keeling) Islands as it stood at that time.

Unfortunately some of his notes and collections were lost during the wartime occupation of Singapore. Among the marine invertebrates the specimens and field notes of soft corals and anemones and most holothurians were lost but a copy of the field catalogue of the holothurians remained (Gibson-Hill 1950a, b).

A.H. Clark (1950) described Gibson-Hill's echinoderm collection and included his very useful field notes. Clark notes that specimens of the family Linckiidae (Ophidiasteridae) were sent to Dr H. Engel of Amsterdam who was preparing a monograph on this family for the Siboga expedition reports. Unfortunately neither the 'Linckiidae' of the Siboga Expedition nor those of Cocos (Keeling) were published.

The present collection numbers 82 species collected from 13 reef flat sites, nine outer slope sites and 13 lagoon sites (Chapter 1, Fig. 2). It consists of 2 species of Crinoidea, 15 Asteroidea, 17 Ophiuroidea, 14 Echinoidea and 34 Holothurioidea listed at the end of this report. Most are widespread Indo-West Pacific species but there are several westward extensions of range from Indonesia or Christmas Island and one south-eastward extension from Sri Lanka. When added to the species recorded by Clark (1950) the total known echinoderm fauna is now 89 species (4 crinoids, 17 asteroids, 17 ophiuroids, 17 echinoids and 34 holothurians).

Crinoidea

Clark (1950) noted that crinoids were rare on the accessible portions (reef platforms) of the Cocos (Keeling) Islands. From the present survey I can confirm this and note that they are also rare on the outer slopes. Crinoids were only collected at four sites, three on the outer slopes and one in the northern part of the lagoon. Only two species were represented, one of which was also recorded by A.H. Clark (1950). Colin (1977) notes that in five weeks of collecting (fishes) in 1974 only a single small crinoid was found.

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The crinoid fauna is even more depauperate than that of Christmas Island where eight species were recorded (Marsh 1988). This compares with 38 species found at Ashmore Reef (Marsh et al. in press) and 17 at the Rowley Shoals and Scott Reef (Marsh 1986) off north-western Australia and five from the isolated Western Indian Ocean atoll of Aldabra (Sloan et al. 1979). Clark and Taylor (1971) did not record any crinoids from Diego Garcia in the central Indian Ocean.

Coral reef crinoids have a short larval life (Mortensen 1938) and few species are widely distributed in the Pacific and Indian Oceans. The species found at the Cocos (Keeling) Islands are among those whose distribution extends from the Red Sea or Western Indian Ocean to the western Pacific Ocean, apart from *Stephanometra spinipinna* (recorded by A.H. Clark), which is known only from Indonesia and northern Australia.

Asteroidea

Clark (1950) recorded only four species of starfishes from Gibson-Hill's collection but these did not include any members of the family Ophidiasteridae (Linckiidae), the family generally best represented on coral reefs. Gibson-Hill collected 141 specimens of this family, which were sent to Engel in Amsterdam who was currently working on a collection of the same family from Indonesia. Unfortunately Engel did not complete either project. I had been told that the Cocos specimens were still at the Natural History Museum in Amsterdam but on a recent visit there the collection could not be found. Neither is it in the University Museum collection in Singapore (formerly the Raffles Museum Collection). There is therefore no historical record of Ophidiasterids from the Cocos (Keeling) Islands.

The present collection contains 15 species of Asteroidea and a further two were recorded by Clark (1950). This is the same number as that recorded from the Rowley Shoals (Marsh 1986), however only 11 species are in common. If the Rowley Shoals, Scott Reef and Ashmore Reef are taken together, 15 species are in common with Cocos, the same number as are in common between Cocos and Indonesia; however, Ashmore Reef has a much richer fauna (28 species) including four Oreasterids, generally regarded as ‘continental’ species. Cocos has more asteroid species (17) than Christmas Island (13) with only eight species in common, probably due in part to the more extensive reef flats at Cocos. When compared with the isolated atoll of Aldabra, in the Western Indian Ocean only seven of Aldabra's 19 species are in common with the Cocos Islands. A single species, *Culcita schmideliana*, is recorded from Diego Garcia, in the central Indian Ocean (Clark and Taylor 1971).

As at Christmas Island and Aldabra the small *Linckia multifora*, which reproduces asexually by autotomy, is the most common asteroid and is found in all habitats at Cocos (Keeling), from the outer slopes (6 sites) and reef flats (6 sites), where it is usually small, to the lagoon where exceptionally large individuals (for the species) were found at site 35.

Most other species were found at only two or three sites but *Ophidiaster granifer* was unexpectedly found on the outer slope, on reef flats and in the lagoon. This species is usually confined to reef flats.

Nardoa tuberculata, usually found in the open on reef flats, was only found in lagoon holes on coral rubble.

Several species were only found at one site and it is possible that other uncommon species may be found in areas not sampled in this survey.

Acanthaster planci (crown-of-thorns starfish) was found on the outer slope, on a reef flat and in the lagoon but was only seen at three sites. In a lagoon hole, south of Direction Island about 20 individuals were observed but the greatest number (> 50) were seen on the outer slope of Turk Reef (stn 15) at 10-45 m, where there was very little coral. The following records indicate that large populations of *A. planci* have been present more than once in the past. Clark (1950) quoted from Gibson-Hill's field notes stating that "*A. planci* is very conspicuous on the atoll but not very common. It occurs among coral rocks near the low tide level over the centre and outer portions of the barrier. It is most plentiful on the north and east coasts of the atoll". In 1971 a former resident of Cocos (Keeling) reported to the Western Australian Museum that the reef off Ujong Tanjong, at the north end of West Island, which had been a flourishing coral reef in 1963 was, by the end of 1969, considerably damaged by *A. planci* predation and there was a very large population of young specimens from about 100 to 320 mm in diameter. She did not find any near Pulu Beras where Gibson-Hill had collected them in 1941. There is no record of any observations on the outer slopes during this period. Ms Anne Waldron, who collected echinoderms on the reef flats at a number of localities around West Island in January 1972, did not find any *A. planci*, but noted that residents of West Island said they were present but not in large numbers. During the course of an ichthyological survey of the Cocos reefs in 1974 Colin (1977) found extensive areas of dead coral on the outer slopes to a depth of 45 m which he attributed to *Acanthaster* predation. Large *A. planci* were abundant at depths of 15-30 m on the outer slopes, at a density of about 1 per 200-400 m^2 but few small individuals were seen. He also noted 'islands' of living coral on some of the buttresses of the outer slope while adjacent areas were dead. It seems likely therefore that recurring high levels of *Acanthaster* predation are responsible for the low level of coral cover on the outer reef slopes.

Of great interest was the finding of several specimens of *Tegulaster ceylanicus*, on the outer slope of the Home Island reef. This species was previously known only from Sri Lanka and the Lakshadweep Islands, although a congener has been collected on the Great Barrier Reef, Queensland. The two species differ slightly but, as both are described from single specimens it is not possible to determine whether they are variations of the one species.

The collections made on the Cocos (Keeling) reefs have extended the known distribution of several species: *Celerina heffernani* for which the only previous Indian Ocean locality was Christmas Island (Western Australian Museum coll.); it is also known from Indonesia (Guille and Jangoux 1978) and the Western Pacific. Similarly, the range of *Neoferdina cumingi*, is extended westward from Christmas Island; published records are from the Central Pacific to Christmas Island (Jangoux 1973). *Ophidiaster granifer* has not previously been recorded from the Indian Ocean although there is a specimen in the Western Australian Museum collection from Madagascar; previous records are from the western Pacific to Indonesia. *Nardoa tuberculata* is a common species on reef flats in Indonesia and northern Australia but the only previous record from the Indian Ocean is Andrews (1900) record from Christmas Island. However, this species was not found there by the Western Australian Museum in 1987 and its occurrence may be sporadic.

Ophiuroidea

Clark (1950) recorded only eight species of Ophiuroids, most of these being large species common on the reef flats. The present collection numbers 17 species (including all the species recorded by Clark) a low number compared with Christmas Island (33) (Marsh 1988), the Rowley Shoals (28), Scott Reef (38) (Marsh 1986), Ashmore Reef (42) (Marsh et al. in press), Aldabra (39) (Sloan et al. 1979) and Diego Garcia (10) (Clark and Taylor 1971).

The low number of species may to some extent reflect less collecting effort on the outer slopes than at Christmas Island. However, extensive sampling of lagoon and reef flat habitats including sand sifting, examination of weed mats and breaking up rocky substrate yielded very few small species. Large ophiocomids were common and in some cases abundant under boulders on the reef flats. *Ophiocoma scolopendrina* and *Ophiomastix annulosa* were the most abundant, often with 4-5 of the latter under almost every boulder. *O. scolopendrina* was found under boulders but also occupied crevices in the reef from which it extended 3-4 arms which turn upside down to sweep the surface scum on the incoming tide. *Ophiocoma brevipes* was moderately common among seagrasses on sandy areas of the reef flats while *O. erinaceus* was found under boulders on the mid and outer reef flats. *O. anaglyptica* was found on the mid and outer reef flats, exposed to surf.

The only new record for the Indian Ocean is *Ophiarachnella similis* whose range is extended westward from Indonesia. Fifteen of the 17 species are in common with Christmas Island and all occur off north-western Australia and Indonesia. Eleven are in common with Aldabra and six with Diego Garcia.

Echinoidea

A.H. Clark (1950) recorded 15 species of echinoid of which we failed to find three, but added another two making a total of 17 species now known from the Cocos (Keeling) Islands. The species are all widespread throughout the Indo-West Pacific including north-western Australia. Twelve species are in common with Christmas Island which apparently lacks all but one of the sand-dwelling Brissids and the Clypeasterid but has several species on surf-swept rocky shores, not found at Cocos, giving it a total of 18 species. In comparison with north-western Australian reefs there are more species than at the Rowley Shoals, where 14 are recorded although 22 have been found on the Rowley Shoals and Scott Reef combined and 23 on Ashmore Reef. Fourteen of the species are in common with Aldabra which has a total of 31 species (Sloan et al. 1979) and eight of Diego Garcia's nine species are in common with Cocos (Keeling).

The brissids and clypeasterid were found only in the South Passage area and no live specimens were taken apart from one freshly predated specimen of *Metalia spatagus*. Extensive observation of the sand flats at the south end of the lagoon failed to find any others. Clark (1950) reports that Gibson-Hill found brissids near passages on the eastern side of the atoll but we were unable to examine this area.

Despite the extensive die-off of lagoon fauna in 1983 (see Woodroffe and Berry, this volume) we found *Parasalenia gratiosa* to be abundant under dead coral slabs in lagoon holes in the same habitat as that described by Gibson-Hill (1950). This was the only habitat in which this species was found.

Holothurioidea

As noted in the introduction, Gibson-Hill's collection of holothurians from the Cocos (Keeling) Islands was destroyed during World War II in Singapore.

The present collection is thus the only record of holothurians from the islands. The Cocos (Keeling) Islands have a fairly rich fauna of holothurians, including most of the species used for trepang (Bêche-de-mer). Thirty four species were collected compared with 16 at Christmas Island, 28 at Scott Reef/Rowley Shoals (Marsh 1986), 47 at Ashmore Reef (Marsh et al. in press) and 35 species at Aldabra (Sloan et al. 1979).

Although the extensive sand flats in the lagoon might be regarded as suitable habitat for holothurians, the majority (30 species) were found either on reef flats or in sandy areas adjacent to reef flats, as at South Passage. Only four species were found on the outer slopes. Ten species were found at lagoon sites but only one of these (*Synaptula recta*) was not found in other habitats.

All but three of the holothurians are species widespread in the Indo-West Pacific, the exceptions are *Holothuria* (*Acanthotrapeza*) *coluber*, *H.* (*Metriatyla*) *aculeata* and *Chiridota rigida* the range of which is extended westward from Indonesia and north-western Australia to the Cocos (Keeling) Islands.

The zonation of common reef flat species near the settlement on West Island is shown in Figure 1.

Trepang (Bêche-de-mer species)

Species of a large size with a thick body wall are the only ones suitable for processing for food. At the Cocos (Keeling) Islands seven species of commercial value have been found. No estimates of population size could be made in the time available but indications are given of the sites where the commercial species were most common.

The most valuable species are the teat fish, *Holothuria* (*Microthele*) *nobilis*, and other species of the subgenus. *H.* (*Microthele*) spp. are nowhere common but individuals were seen or collected at five reef flat and two lagoon sites (List of echinoderms). *Thelenota ananas* (prickly red fish) is another large, valuable species but this was only found at one outer slope site. Other commercial species, their value depending to some extent on size, are two species of *Actinopyga* (*A. echinites* and *A. mauritiana*), both common to abundant on reef flats particularly at West Island; another commercial species *A. miliaris* may occur at Cocos but was not found during the survey. Several less valuable commercial species were also found: *Bohadschia marmorata* (chalky fish), *Holothuria* (*Metriatyla*) *scabra* (sand fish) and *H.* (*Halodeima*) *atra*. *B. marmorata* and *H. scabra* were found on the lagoon side of South Passage near Pulu Maria where the former was moderately common. *B. marmorata* was also seen in the lagoon south of Direction Island. *H. atra* is the most widespread of any species at Cocos and was common in all habitats but it is of very little commercial value unless individuals are of a very large size; it is a highly toxic species. *Bohadschia argus* (leopard or tiger fish), although of fairly large size, and common on some of the sandy reef flats has a very low commercial value partly because of the toxic cuvierian tubules ejected when the animal is touched. None of the other species listed is believed to have any commercial value. Little is known of growth rates of commercial species and any attempt at exploitation of the populations should be carefully monitored and certain areas reserved from exploitation. Quantitative population studies need to be made of the potentially commercial species before any fishing takes place and on-going studies of recruitment and growth should be initiated.

It should be noted that all the commercial species have water soluble toxins in the body wall and can only be eaten after correct preparation.

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LIST OF ECHINODERMS

KEY TO SYMBOLS:

C = A.H. Clark, 1950 (C) species by another name
\+ = Spec. from various sources in Western Australian Museum
eg 6 = Western Australian Museum 1989 station numbers
V = Visual records
* = New records
\# = Extension of distribution

	Echinodermata	Previous Records		Collection Station
	Crinoidea			
	COMASTERIDAE			
*	*Comaster multifidus* (Müller, 1841)	-	-	15,19
	MARIAMETRIDAE			
	Stephanometra indica (Smith, 1876)	C	-	-
	S. spicata (Carpenter, 1881)	C	-	13,23
	S. spinipinna (Hartlaub, 1890)	C	-	-
	Asteroidea			
	OREASTERIDAE			
	Culcita schmideliana (Retzius, 1805)	(C)	-	7,12
	OPHIDIASTERIDAE			
#*	*Celerina heffernani* (Livingstone, 1931)	-	-	7,25
*	*Cistina columbiae* Gray, 1840	-	-	25
*	*Dactylosaster cylindricus* (Lamarck, 1816)	-	-	11,12,24
*	*Fromia milleporella* (Lamarck, 1816)	-	-	13,32
*	*Linckia guildingi* Gray, 1840	-	-	4,19
*	*L. laevigata* (Linnaeus, 1758)	-	-	12,30V
*	*L. multifora* (Lamarck, 1816)	-	-	3,4,6,7,10,12,13,14, 15,19,30,32,35
#*	*Nardoa tuberculata* Gray, 1840	-	-	29,36
*	*N. galatheae* (Lütken, 1864)	-	-	7,9,19,23
#*	*Neoferdina cumingi* (Gray, 1840)	-	-	13,22
#*	*Ophidiaster granifer* (Lütken, 1872)	-	-	4,6,26,27,29,30
*	*O. cribrarius* Lütken, 1872	-	-	8

MITHRODIIDAE				
	Mithrodia clavigera (Lamarck, 1816)	C	-	-
ASTERINIDAE				
#*	*Tegulaster ceylanicus* (Döderlein, 1889)	-	-	33
ACANTHASTERIDAE				
	Acanthaster planci (Linnaeus, 1758)	C	-	8,9V,15V
ECHINASTERIDAE				
	Echinaster luzonicus (Gray, 1840)	C	-	-
Ophiuroidea				
AMPHIURIDAE				
*	*Amphipholis squamata* (Delle Chiaje, 1829)	-	-	24,35,37
OPHIACTIDAE				
*	*Ophiactis savignyi* (Müller and Troschel, 1842)	-	-	9,12,20,28,32,35
OPHIOTRICHIDAE				
	Macrophiothrix longipeda (Lamarck, 1816)	C	-	1,12,13,14,24,32
OPHIOCOMIDAE				
	Ophiarthrum elegans Peters, 1851	C	-	13
*	*Ophiocoma anaglyptica* Ely, 1944	-	+	1,12,14,24,27,30
*	*O. brevipes Peters*, 1851	-	+	1,5,10,14,24,27,30
	O. dentata Müller and Troschel, 1842	C	+	1,10,12,13,14,20, 24,27
	O. erinaceus Müller and Troschel, 1842	C	-	1,6,8,9,12,13V,20, 24,27,30,32
	O. pica Müller and Troschel, 1842	C	-	13,14,27,32
*	*O. pusilla* (Brock, 1888)	-	-	32
	O. scolopendrina (Lamarck, 1816)	C	+	1,6,10,12,20,24,27
*	*O. schoenleini* Müller and Troschel, 1842	-	-	9
*	*Ophiocomella sexradia* (Duncan, 1887)	-	+	3,20,24,35
	Ophiomastix annulosa (Lamarck, 1816)	C	-	1,3V,12,20,24,27,30
OPHIONEREIDIDAE				
*	*Ophionereis porrecta* Lyman, 1860	-	-	9
OPHIODERMATIDAE				
#*	*Ophiarachnella similis* (Koehler, 1905)	-	-	32
	Ophiopeza spinosa (Ljungman, 1867)	C	-	14
Echinoidea				
CIDARIDAE				
	Eucidaris metularia (Lamarck, 1816)	C	+	7,12,25,32

DIADEMATIDAE				
	Diadema savignyi Michelin, 1845	C	-	1,12,30V
	Echinothrix calamaris (Pallas, 1774)	C	-	30
	E. diadema (Linnaeus, 1758)	C	-	1,12,24V,27V,30V
TEMNOPLEURIDAE				
	Mespilia globulus (Linnaeus, 1758)	C	-	16,29
TOXOPNEUSTIDAE				
	Toxopneustes pileolus (Lamarck, 1816)	C	-	-
	Tripneustes gratilla (Linnaeus, 1758)	C	-	1,3V,9,12V,30
PARASALENIIDAE				
	Parasalenia gratiosa A. Agassiz, 1863	C	-	16,17V,36
ECHINOMETRIDAE				
	Echinometra mathaei (de Blainville, 1825)	C	-	1,12,24
*	*Echinostrephus molaris* (de Blainville, 1825)	-	-	27
	Heterocentrotus mammillatus (Linnaeus, 1758)	C	+	4, 12, 19
ECHINONEIDAE				
	Echinoneus cyclostomus Leske, 1778	C	-	-
CLYPEASTERIDAE				
	Clypeaster reticulatus (Linnaeus, 1758)	C	-	12
BRISSIDAE				
*	*Brissus latecarinatus* (Leske, 1778)	-	-	12,16
	Metalia dicrana H.L. Clark, 1917	C	-	12
	M. spatagus (Linnaeus, 1758)	C	-	12
	M. sternalis (Lamarck, 1816)	C	-	-
Holothurioidea				
HOLOTHURIIDAE				
*	*Actinopyga echinites* (Jaeger, 1833)	-	-	1,3V,12,24V,27V,30V
*	*A. mauritiana* (Quoy and Gaimard, 1833)	-	+	1,3V,5V,10V,12V,20V,24,27V,30V
*	*Bohadschia argus* Jaeger, 1833	-	+	5V,8V,12,30V
*	*B. graeffei* (Semper, 1868)	-	-	19
*	*B. marmorata* Jaeger, 1833	-	-	9V,12
*	*Labidodemas semperianum* Selenka, 1867	-	-	12
#*	*Holothuria (Acanthotrapeza) coluber* Semper 1868	-	-	9V,12
*	*H. (Cystipus) rigida* (Selenka, 1867)	-	-	1
*	*H. (Halodeima) atra* Jaeger, 1833	-	+	1,2,3V,5V,6V, 9V, 12V, 16, 18V, 19, 20V, 24V, 27V, 30V, 34V,36V,37V
*	*H. (H.) edulis* Lesson, 1830	-	-	9,16,19,30
*	*H. (Lessonothuria) lineata* Ludwig, 1875	-	-	3,12

*	*H.* (*L.*) *pardalis* Selenka, 1867	-	-	1,30
*	*H.* (*Mertensiothuria*) *leucospilota* (Brandt, 1835)	-	-	10,12
*	*H.* (*Metriatyla*) *scabra* Jaeger, 1833	-	-	12
#*	*H.* (*M.*) *aculeata* Semper, 1868	-	-	12
*	*H.* (*Microthele*) *nobilis* (Selenka, 1867)	-	-	1,12,24,27,36V
	H. (*M.*) *sp.*	-	-	12,14,23
*	*H.* (*Platyperona*) *difficilis* Semper, 1868	-	-	1,24,27
*	*H.* (*Semperothuria*) *cinerascens* (Brandt, 1835)	-	+	1, 20, 24, 27
*	*H.* (*Stauropora*) *pervicax* Selenka, 1867	-	-	3
*	*H.* (*Thymiosycia*) *hilla* Lesson, 1830	-	+	8,12,23,30V
*	*H.* (*T.*) *impatiens* (Forskål, 1775)	-	+	8,9,12
STICHOPODIDAE				
*	*Stichopus chloronotus* Brandt, 1835	-	+	1,3V,5V,6V,9, 12, 27V, 30V,34V,36V
*	*S. horrens* Selenka, 1867	-	+	12V,16
*	*S. variegatus* Semper, 1868	-	-	5
*	*Thelenota ananas* (Jaeger, 1833)	-	-	19
PHYLLOPHORIDAE				
*	*Afrocucumis africana* (Semper, 1868)	-	-	1,3,6,14,24,27
SYNAPTIDAE				
*	*Euapta godeffroyi* (Semper, 1868)	-	-	1
*	*Opheodesoma grisea* (Semper, 1868)	-	-	12
*	*Synapta maculata* (Chamisso and Eysenhardt 1821)	-	-	5,12V
*	*Synaptula recta* (Semper, 1868)	-	-	35,37
CHIRIDOTIDAE				
#*	*Chiridota rigida* Semper, 1868	-	-	1,12
*	*Polycheira rufescens* (Brandt, 1835)	-	-	10

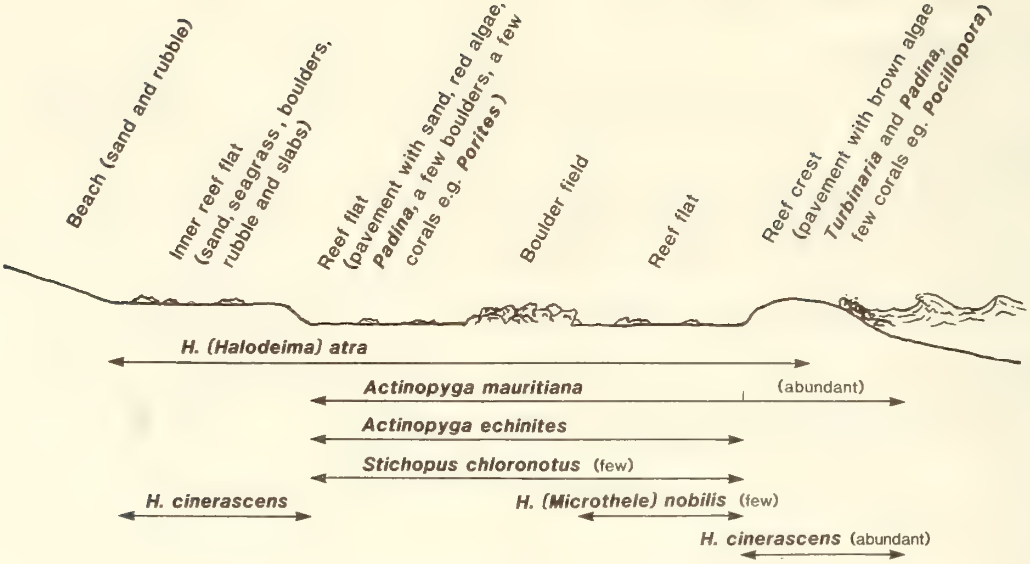

Figure 1. Zonation of holothurians on reef flat near settlement, West Island.

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CHAPTER 14

FISHES OF THE COCOS (KEELING) ISLANDS

BY

G.R. ALLEN AND W.F. SMITH-VANIZ

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CHAPTER 14

FISHES OF THE COCOS (KEELING) ISLANDS

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AND

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ABSTRACT

Extensive fish collections were obtained at the Cocos (Keeling) Islands by the Academy of Natural Sciences of Philadelphia in 1973 and the Western Australian Museum in 1989. The combined collections document the occurrence of 533 species. For many Indo-west Pacific fishes (about 85 species), Cocos represents their westernmost limit of distribution. The faunal composition is typical of Indo-West Pacific coral reefs. Only 5 percent of the ichthyofauna consists of exclusively Indian Ocean species. The largest families are as follows (number of species in parentheses): Labridae (54), Gobiidae (51), Pomacentridae (38), Apogonidae (30), Serranidae (30), Acanthuridae (25), Muraenidae (24), Chaetodontidae (23), Blenniidae (21), Scaridae (20), and Holocentridae (20). Collectively these 11 families comprise 63 percent of the fauna. Little or no endemism is present.

INTRODUCTION

The first fishes collected at the Cocos (Keeling) Islands were taken by the crew of the Beagle and subsequently reported by Jenyns (1842), who listed 10 species. Numerous fish records were recorded in a series of papers by Pieter Bleeker (1854-1859) that were published in *Natuurkundig Tijdschrift voor Nederlandsch Indie*. Fish specimens were sent to Bleeker from the Cocos Islands by A. J. Anderson and G. Clunies-Ross. The Cocos fauna was summarised by Bleeker (1859) as consisting of approximately 104 species. Most of the fishes reported by Bleeker were eventually deposited in the Rijksmuseum in Leiden.

The only other major ichthyological collection from Cocos was made by C. A. Gibson-Hill, who visited the islands from January to November 1941. The fishes from this expedition were reported by Marshall (1950) and included 119 new records, thus raising the total species known from the island group to approximately 220. The Gibson-Hill collections are presently housed at the British Museum (Natural History).

In 1973 an expedition from the Academy of Natural Sciences of Philadelphia (ANSP) collected marine organisms at Cocos (Keeling) during February and March. Team members, including ichthyologists Patrick L. Colin and William Smith-Vaniz, collected fishes at 68 stations. A variety of collection methods were employed: rotenone

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(35 stations), explosives (17), quinaldine (14), angling (1), and spearing (31), usually as a supplemental means of collection. This effort resulted in a large fish collection containing 6,780 specimens in 1,443 lots. Approximately 425 species were obtained.

A team of biologists from the Western Australian Museum and Australian Institute of Marine Sciences conducted a faunal survey at Cocos (Keeling) during February 1989. Fishes were collected mainly with rotenone (24 stations), supplemented by spear and dipnets (1 station each). These efforts yielded a total of 1,814 specimens, including 465 lots and approximately 245 species. In addition, underwater observations were conducted in which the name of each species seen was written on a waterproof sheet. These "spot" identifications were based on the senior author's extensive experience in the Indo-Pacific region. Only fishes whose identity was absolutely certain were recorded. This method provided an additional 203 records, thus a total of 448 species was noted. The combined ANSP-Western Australian Museum collections (and observations) include a total of 533 species.

Many of the species reported by Bleeker (1859) and Marshall (1950) are junior synonyms or were based on misidentifications. It is beyond the scope of the present study to determine the current status of most of the species they listed. However, we estimate that only about 20 of their species represent additions not seen during the 1973 and 1989 visits. Therefore, the total known fish fauna of Cocos (Keeling) is approximately 550 species. The following species listed by Marshall (1950) almost certainly represent additions to the Cocos ichthyofauna: Albulidae - *Albula vulpes* (Linnaeus); Exocoetidae - *Cheilopogon atrisignis* (Jenkins) and *C. cyanopterus* (Valenciennes); Syngnathidae - *Hippocampus trimaculatus* Leach; Ostraciidae - *Lactoria cornuta* (Linnaeus).

Some authors have questioned the providence of material Bleeker reported as originating from Cocos (Keeling), including several new species he described from there. Dawson (1982) cited the type locality of *Micrognathus andersonii* (Bleeker) as "Novaselma, Kokos [Cocos] Is. [Indonesia]," and stated (p. 677) that Marshall's (1950) listing of the species (as *M. brevirostris*) from Cocos-Keeling is based on a "misidentification of the type-locality..." We do not agree with Dawson's assertion that Bleeker's material did not originate from Cocos-Keeling. In the introduction of his first paper Bleeker (1854a) gave the correct coordinates for "Kokos-eilanden" and referred to J. C. Ross. (These islands were originally settled in 1827 by a Scottish sea captain named John Clunies-Ross.) In a later paper Bleeker (1858) thanked both Dr A. J. Anderson "geneesheer" [= physician] and J.G.C. Ross "tegeneewoordigen beheerder" [= present-day administrator] of Cocos Island.

Through the kindness of Dr. Tyson Roberts we received a copy of a letter signed by A. J. Anderson (original deposited in the RMNH archives), with the heading "Cocos - July -1860," and addressed to Dr. Bleeker, concerning specimens of "trepang fish" [= Carapidae] that had been sent to Batavia. In the same letter Anderson asked to have Bleeker's European address (Bleeker returned to the Netherlands in September 1860) "in the event of my attaining other interesting specimens." No additional correspondence in the RMNH Bleeker files apparently exists concerning Cocos Is. (T. Roberts, *in lit.*). Presumably much of Bleeker's correspondence while he was in Batavia did not survive. In the absence of any evidence to the contrary, we conclude that all Bleeker's material stated to have come from "Kokos-eilanden" refers to Cocos-Keeling. Although we did not duplicate Bleeker's Cocos record of *Micrognathus andersonii*, it is a broadly distributed Indo-Pacific species and we have no reason to doubt its occurrence there.

SPECIES COMPOSITION AND ZOOGEOGRAPHY

The ichthyofauna of Cocos (Keeling) consists primarily of species that are associated with coral reefs. The largest families are summarised in Table 1. The eleven most speciose groups (Labridae, Gobiidae, Pomacentridae, Apogonidae, Serranidae, Acanthuridae, Muraenidae, Chaetodontidae, Blenniidae, Scaridae and Holocentridae) account for 63 percent of the total fauna. These families are typically abundant throughout the tropical Indo-Pacific region. Most of these 11 families contain fishes that are diurnally active which either dwell on or near the reef surface, or forage on plankton a short distance above it. Exceptions are the nocturnal apogonids and holocentrids, and the crevice-dwelling morays (muraenidae).

The fish fauna is similar to that of Christmas Island, the nearest land mass, lying about 850 km to the northeast. Allen and Steene (1987) recorded 575 species from Christmas, of which about 350 species also occur at the Cocos group. The approximately 175 species that are present at Cocos, but lacking at Christmas are primarily inhabitants of the lagoon, a habitat that does not occur at Christmas Island. It is more difficult to explain the occurrence of approximately 210 species of Christmas fishes that are apparently absent from Cocos (Keeling). Two of the most notable disparities are shown by the Serranidae and Blenniidae in which 25 and 14 species, respectively, and 7 genera in each family were found only at Christmas. Perhaps this anomaly can be at least partly be explained by the greater isolation of Cocos (Christmas Island is only about 290 km from Java).

Compared to other oceanic atolls the Cocos Group appears to have a relatively impoverished fish fauna. For example Randall and Randall (1988) and Winterbottom et al. (1989) recorded approximately 800 and 700 species, respectively, for the Marshall Islands in the central Pacific and Chagos Archipelago (incorporating several atolls) in the western Indian Ocean. There are probably several reasons for the diminished Cocos fauna including (1) its small physical size; (2) relative isolation and lack of surrounding "island stepping-stones;" and (3) lesser collecting activity. In addition, the extensive coral die-back at Cocos (Colin, 1977) may be responsible for the exclusion of some species.

Although we believe the ichthyofauna of Cocos has been reasonably well sampled (except for epipelagic fishes), we certainly did not collect all of the species of shorefishes that occur there. That the fauna may not be as well sampled as we would like to believe is suggested by the fact that a number of shallow-water, cryptic species were taken at only one of our combined 59 rotenone stations. Scorpaenids are cryptic bottom dwellers (except *Pterois* spp.) yet, inexplicably, only 2 of 16 species we report from Cocos were collected or observed by both museum expeditions.

A zoogeographic analysis of the Cocos fauna is presented in Table 2. The majority of fishes have distributions that cover relatively wide areas in the Indo-Pacific region. There is a much greater affinity to the Western Pacific than to the Indian Ocean region. Indeed, only about 5.1 percent of the species are Indian Ocean forms. There is no endemism in the Cocos fish fauna, although one anglefish, *Centropyge joculator*, is known only from Cocos and Christmas Island and an undescribed goby of the genus *Trimma* may have the same distribution. The Indian Ocean coasts of Java and Sumatra are poorly sampled, however, and it is likely that one or both species will be found there eventually. *Scorpaenoides keelingensis* Marshall which, as the name suggests, Marshall (1950) believed to be endemic to the Cocos group is almost certainly a junior synonym of *Scorpaenoides kelloggi* (Jenkins) (W. N. Eschmeyer, pers. comm.). Nearly all of the reef fishes found at Cocos are characterised by a pelagic larval stage of up to several weeks duration. Hence, the widespread nature of the individual species distributions.

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CHECKLIST OF COCOS (KEELING) FISHES

The following list includes fishes that were either collected or observed during the 1973 and 1989 surveys. Asterisk or numbers preceding species names indicate the following distributional data: * = also known from Christmas Island; 1 = widespread Indo-Pacific or Indo-west Pacific; 2 = West Pacific species that reach their western distributional limit at Cocos (Keeling); 3 = Indian Ocean species (may include western extremity of west Pacific); 4 = Circumtropical or cosmopolitan; 5 = uncertain extralimital distribution; Square brackets appearing after each species citation indicate that specimens are deposited at the Academy of Natural Sciences, Philadelphia [P], the Western Australian Museum [W], or were observed only [O].

Sphyrnidae - Hammerhead sharks

4 **Sphyrna lewini* (Grffith and Smith, 1834)	[O]

Carcharhinidae - Requiem sharks

1 **Carcharhinus amblyrhynchos* (Bleeker, 1856)	[P]
1 **C. melanopterus* (Quoy and Gaimard, 1824)	[O]
4 **Galeocerdo cuvier* (Peron and LeSueur, 1822)	[O]
1 **Triaenodon obesus* (Rüppell, 1837)	[O]

Mobulidae - Manta rays

4 **Manta birostris* (Donndorff, 1798)	[O]

Moringuidae - Worm eels

1 *Moringua ferruginea* Bliss, 1883	[W]
1 **M. javanica* (Kaup, 1856)	[W]
1 **M. microchir* Bleeker, 1853	[P,W]

Chlopsidae - False morays

3 **Kaupichthys* n. sp. [K. Tighe, pers. comm., 1993]	[P,W]

Muraenidae - Moray eels

2 *Anarchias cantonensis* (Schultz, 1943)	[P]
1 **A. seychellensis* Smith, 1962	[P,W]
1 **Echidna nebulosa* (Ahl, 1789)	[P]
1 **E. polyzona* (Richardson, 1844)	[P]
2 **Enchelycore bayeri* (Schultz, 1953)	[W]
1 **E. pardalis* (Temminck and Schlegel, 1842)	[P,W]
2 **Enchelynassa canina* (Quoy and Gaimard, 1824)	[P]
1 **Gymnothorax enigmaticus* McCosker and Randall, 1982	[W]
1 **G. buroensis* (Bleeker, 1857)	[P]
1 *G. fimbriatus* (Bennett, 1831)	[P,W]
1 **G. flavimarginatus* (Rüppell, 1830)	[P,W]
1 **G. javanicus* (Bleeker, 1859)	[O]
1 **G. margaritophorus* Bleeker, 1865	[P,W]
1 **G. melatremus* Schultz, 1953	[P]
1 *G. monochrous* Bleeker, 1864	[P]
1 **G. monostigma* (Regan, 1909)	[P]
1 **G. rueppelliae* (McClelland, 1845)	[P,W]
1 *G. undulatus* (Lacepède, 1803)	[P,W]
1 **G. zonipectus* Seale, 1906	[P,W]

1	**Siderea picta* (Ahl, 1789)	[P,W]
1	**S. thrysoidea* (Richardson, 1845)	[P,W]
1	**Uropterygius concolor* (Rüppell, 1838)	[W]
1	**U. marmoratus* (Lacepède, 1803)	[W]
1	**U. xanthopterus* Bleeker, 1859	[P,W]

Ophichthidae - Snake eels

2	*Callechelys catostomus* (Bloch and Schneider, 1801)	[W]
1	**Leiuranus semicinctus* (Lay and Bennett, 1839)	[P,W]
2	*Muraenichthys brevis* Günther, 1876	[P]
1	**M. laticaudata* (Ogilby, 1897)	[W]
1	*M. macropterus* Bleeker, 1857	[W]
2	*Schultzidia johnstonensis* (Schultz and Woods, 1949)	[W]

Congidae - Conger eels

1	**Conger cinereus* Rüppell, 1830	[W]
3	*Gorgasia maculata* Klausewitz and Eibl-Eibesfeldt, 1959	[P,W]
1	**Heteroconger hassi* (Klausewitz and Eibl-Eibesfeldt, 1959)	[P,W]

Clupeidae - Herrings

1	*Sardinella melanura* (Cuvier, 1829)	[P]
1	*Spratelloides delicatulus* (Bennett, 1831)	[P,W]

Synodontidae - Lizardfishes

1	**Saurida gracilis* (Quoy and Gaimard, 1824)	[P,W]
1	**Synodus englemani* Schultz, 1953	[P]

Chanidae - Milkfishes

1	*Chanos chanos* (Forsskål, 1775)	[O]

Ophidiidae - Cusk-eels

1	**Brotula multibarbata* Temminck and Schlegel, 1846	[P,W]

Bythitidae - Viviparous brotulas

1	**Brosmophyciops pautzkei* Schultz, 1960	[P,W]
5	**Ogilbia* sp.	[P,W]

Antennariidae - Anglerfishes

1	**Antennarius coccineus* (Lesson, 1831)	[P,W]
1	*A. dorehensis* Bleeker, 1859	[P,W]

Notocheiridae [=Isonidae] - Surf spites

3	*Iso natalensis* Regan, 1919	[P]

Hemirhamphidae - Halfbeaks

1	*Hyporhamphus affinis* (Günther, 1866)	[P,W]
1	*H. dussumieri* (Valenciennes, 1847)	[P]
2	*Zenarchopterus dispar* (Valenciennes, 1847)	[W]

Belonidae - Needlefishes

1	*Platybelone argalus platyura* (Bennett, 1831)	[W]
1	**Tylosurus crocodilus* (Peron and LeSueur, 1821)	[P]

Holocentridae - Squirrelfishes

1	*Myripristis adusta* Bleeker, 1853	[P,W]
1	**M. berndti* Jordan and Evermann, 1903	[W]
1	*M. chryseres* Jordan and Evermann, 1903	[P]
1	**M. kuntee* Cuvier, 1831	[W]
1	**M. murdjan* (Forsskål, 1775)	[P]
1	**M. parvidens* Cuvier, 1829	[P]
1	*M. pralinia* Cuvier, 1829	[W]
1	**M. vittata* Valenciennes, 1831	[W]
1	*M. violaceus* Bleeker, 1851	[O]
1	*Neoniphon argenteus* (Valenciennes, 1831)	[P,W]
1	*N. opercularis* (Valenciennes, 1831)	[O]
1	*N. sammara* (Forsskål, 1775)	[P,W]
1	**Plectrypops lima* (Valenciennes, 1831)	[P,W]
1	**Sargocentron diadema* (Lacepède, 1801)	[P,W]
3	**S. lepros* (Allen and Cross, 1983)	[W]
1	**S. microstoma* (Günther, 1859)	[W]
1	**S. caudimaculatum* (Rüppell, 1838)	[W]
1	**S. punctatissimum* (Cuvier, 1829)	[P]
1	**S. tiere* (Cuvier, 1829)	[P]
1	*S. spiniferum* (Forsskål, 1775)	[P]

Aulostomidae - Trumpetfishes

1	**Aulostromus chinensis* (Linnaeus, 1766)	[P]

Fistulariidae - Cornetfishes

1	**Fistularia commersonii* Rüppell, 1838	[O]

Syngnathidae - Pipefishes

1	**Choeroichthys sculptus* (Günther, 1870)	[P,W]
1	*Corythoichthys flavofasciatus* (Rüppell, 1838)	[P,W]
1	**Cosmocampus banneri* (Herald and Randall, 1972)	[W]
1	**Doryrhamphus excisus excisus* Kaup, 1856	[P,W]
2	**Micrognathus brevirostris pygmaeus* Fritzsche, 1981	[W]
1	*Phoxocampus belcheri* (Kaup, 1856)	[W]

Scorpaenidae - Scorpionfishes

1	*Parascorpaena mossambica* (Peters, 1855)	[P]
1	**Pterois antennata* (Bloch, 1787)	[W]
1	**P. radiata* Cuvier, 1829	[P,W]
2	**P. volitans* (Linnaeus, 1758)	[W]
	[We follow Schultz (1986) in recognizing *Pterois miles* Bennett as an Indian Ocean species distinct from the Pacific *P. volitans*.]	
1	**Scorpaenodes albaiensis* (Evermann and Seale, 1907)	[P]
1	**S. guamensis* (Quoy and Gaimard, 1824)	[P]
1	**S. hirsutus* (Smith, 1957)	[P,W]
1	*S. kelloggi* (Jenkins, 1903)	[P]
1	*S. littoralis* (Tanaka, 1917)	[P]
1	*S. minor* (Smith, 1958)	[P]
1	**S. parvipinnis* (Garrett, 1863)	[P]
1	**Scorpaenopsis diabolus* (Cuvier, 1829)	[O]
1	**Sebastapistes cyanostigma* (Bleeker, 1856)	[P]
1	**S. strongia* (Cuvier, 1829)	[P,W]

5 *Sebastapistes* sp. [P]
1 **Synanceia verrucosa* Bloch and Schneider, 1801 [P]

Platycephalidae - Flatheads
1 **Thysanophrys otaitensis* (Cuvier, 1829) [P]

Caracanthidae - Orbicular velvetfishes
2 **Caracanthus maculatus* (Gray, 1831) [P]
1 **C. unipinna* (Gray, 1831) [P]

Serranidae - Sea basses
[We follow Baldwin and Johnson (1993) in including the Grammistidae and Pseudogrammidae in this family.]
1 **Anyperodon leucogrammicus* (Valenciennes, 1828) [P]
1 **Cephalopholis argus* Bloch and Schneider, 1801 [P,W]
1 **C. leopardus* (Lacepède, 1801) [P,W]
1 **C. polleni* (Bleeker, 1868) [P]
1 **C. spiloparaea* (Valenciennes, 1828) [P,W]
1 **C. urodeta* (Valenciennes, 1828) [P,W]
[Randall (1991 p.70) noted that this species consists of two allopatric color forms, the western Indian Ocean *C. nigripinnis* (Valenciennes) and the nominal Pacific form; he regarded them as conspecific because Christmas Is. specimens have somewhat intermediate color patterns. The color pattern of Cocos specimens agrees well with the Pacific form.]
3 *Epinephelus faveatus* (valenciennes, 1828) [W]
1 *E. fuscoguttatus* (Forsskål, 1775) [O]
1 **E. hexagonatus* (Bloch and Schneider, 1801) [W]
2 *E. maculatus* Bloch, 1790 [O]
1 **E. merra* Bloch, 1793 [P,W]
1 *E. macrospilus* (Bleeker, 1855) [P]
[Randall (1991 p.187) noted that this species consists of two allopatric color forms, the western Indian Ocean *E. cylindricus* Günther said to differ from the Pacific and eastern Indian Ocean *E. macrospilos* by larger and more closely spaced spots. Because only spot size appeared to distinguish the two forms they were considered to be conspecific.]
1 *E. microdon* (Bleeker, 1856) [P]
1 **E. spilotoceps* Schultz, 1953 [P,W]
1 **E. tauvina* (Forsskål, 1775) [P,W]
1 **Gracila albomarginata* (Fowler and Bean, 1930) [P]
1 **Grammistes sexlineatus* (Thunberg, 1792) [P,W]
5 **Luzonichthys* sp. [O]
2 **Plectranthias nanus* Randall, 1980 [P,W]
1 *Plectropomus areolatus* Rüppell, 1828 [P]
2 *P. leopardus* (Lacepède, 1802) [P]
2 *P. maculatus* (Bloch, 1790) [P]
1 *Pseudanthias cooperi* (Regan, 1902) [P,W]
3 **P. evansi* Smith, 1954 [P,W]
2 **P. smithvanizi* (Randall and Lubbock, 1981) [P,W]
5 *Pseudanthias* sp. [P]
[Winterbottom et al. (1989) give color photographs (plates IVE,F) of this species, which they report as *Anthias* sp. from the Chagos Archipelago.]
2 *Pseudogramma bilinearis* (Schultz, 1943) [P]
1 **P. polyacantha* (Bleeker, 1856) [P,W]

2	**Suttonia lineata* Gosline, 1960	[W]
1	**Variola louti* (Forsskål, 1775)	[P]

Pseudochromidae - Dottybacks

1	*Pseudoplesiops* n. sp.	[P,W]
2	*P. multisquamatus* Allen, 1987	[P]

Plesiopidae - Longfins

1	**Plesiops coeruleolineatus* Rüppell, 1835	[P,W]
2	**P. corallicola* Bleeker, 1853	[P,W]

Kuhliidae - Flagtails

1	**Kuhlia mugil* (Bloch and Schneider, 1801)	[P,W]

Priacanthidae - Bigeyes

1	**Heteropriacanthus cruentatus* (Lacepède, 1801)	[P,W]

Apogonidae - Cardinalfishes

1	**Apogon angustatus* (Smith and Radcliffe, 1911)	[P,W]
2	*A. bandanensis* Bleeker, 1854	[P,W]
1	*A. crassiceps* Garman, 1903	[P,W]
1	*A. cyanosoma* Bleeker, 1853	[P,W]
2	*A. dispar* Fraser and Randall, 1976	[P]
1	**A. evermanni* Jordan and Snyder, 1904	[P]
1	*A. exostigma* (Jordan and Starks, 1906)	[P,W]
1	*A. guamensis* Valenciennes, 1832	[P,W]
1	**A. kallopterus* Bleeker, 1856	[P,W]
1	*A. leptacanthus* Bleeker, 1856	[P]
2	*A. melas* Bleeker, 1848	[W]
2	**A. novemfasciatus* Cuvier, 1828	[P,W]
1	**A. taeniophorus* Regan, 1908	[P,W]
1	**A. taeniopterus* (Bennett, 1835)	[P]
1	**Apogonichthys ocellatus* (Weber, 1913)	[P,W]
1	*A. perdix* Bleeker, 1854	[P]
1	**Cercamia eremia* (Allen, 1987)	[P,W]
1	*Cheilodipterus lineatus* Cuvier, 1828	[W]
2	**C. macrodon* (Lacepède, 1802)	[P,W]
1	**C. quinquelineatus* Cuvier, 1828	[P,W]
1	**Fowleria aurita* (Valenciennes, 1831)	[P,W]
1	*F. isostigma* (Jordan and Seale, 1906)	[P]
1	*F. variegata* (Valenciennes, 1832)	[W]
2	*Gymnapogon urospilotus* Lachner, 1953	[P]
1	*Neamia octospina* Smith and Radcliffe, 1912	[P]
1	*Pseudamia gelatinosa* Smith, 1955	[P,W]
2	**Pseudamiops gracilicauda* (Lachner, 1953)	[P,W]
1	*Rhabdamia gracilis* (Bleeker, 1856)	[O]
2	*Siphamia majimae* Matsubara and Iwai, 1959	[P,W]
2	*Sphaeramia nematoptera* (Bleeker, 1856)	[P]

Malacanthidae - Tilefishes

1	**Malacanthus brevirostris* Guichenot, 1848	[P]
1	**M. latovittatus* (Lacepède, 1801)	[P]

Carangidae - Trevallies
1 *_Carangoides ferdau_ (Forsskål, 1775) [P]
1 *_C. orthogrammus_ (Jordan and Gilbert, 1882) [P]
1 *_Caranx ignobilis_ (Forsskål, 1775) [O]
4 *_C. lugubris_ Poey, 1860 [P]
1 *_C. melampygus_ Cuvier, 1833 [P]
1 *_C. sexfasciatus_ Quoy and Gaimard, 1825 [P]
4 *_Decapterus macarellus_ (Cuvier, 1833) [P]
4 *_Elagatis bipinnulatus_ (Quoy and Gaimard, 1825) [P]
1 *_Scomberoides lysan_ (Forsskål, 1775) [P]
1 *_Trachinotus bailloni_ (Lacepède, 1801) [P]
1 _T. blochii_ (Lacepède, 1801) [P]

Lutjanidae - Snappers
1 *_Aphareus furca_ (Lacepède, 1802) [P]
1 *_Aprion virescens_ Valenciennes, 1830 [O]
1 *_Lutjanus bohar_ (Forsskål, 1775) [P]
1 *_L. fulvus_ (Bloch and Schneider, 1801) [P,W]
1 *_L. gibbus_ (Forsskål, 1775) [P]
1 *_L. kasmira_ (Forsskål, 1775) [P]
1 _L. monostigma_ (Cuvier, 1828) [P,W]
1 *_Macolor niger_ (Forsskål, 1775) [P]

Caesionidae - Fusiliers
1 *_Caesio teres_ Seale, 1906 [P]
1 _C. xanthonota_ Bleeker, 1853 [P]
1 *_Pterocaesio lativattata_ Carpenter, 1987 [P]
1 *_P. tile_ (Cuvier, 1830) [P,W]

Haemulidae - Sweetlips
2 _Plectorhinchus chaetodontoides_ Lacepède, 1800 [P,W]

Lethrinidae - Emperors
1 *_Gnathodentex aurolineatus_ (Lacepède, 1802) [P,W]
1 _Gymnocranius grandoculis_ (Valenciennes, 1830) [O]
2 _Lethrinus atkinsoni_ Seale, 1909 [P]
1 _L. harak_ (Forsskål, 1775) [P,W]
1 _L. hypselopterus_ Bleeker, 1873 [P]
1 _L. lentjan_ (Lacepède, 1802) [P]
1 _L. microdon_ Valenciennes, 1830 [W]
1 _L. obsoletus_ (Forsskål, 1775) [P,W]
1 _L. xanthochilus_ Klunzinger, 1870 [W]
1 *_Monotaxis grandoculis_ (Forsskål, 1775) [P]

Nemipteridae - Threadfin breams
2 _Scolopsis lineatus_ (Quoy and Gaimard, 1824) [P,W]

Gerreidae - Mojarras
1 _Gerres acinaces_ Bleeker, 1854 [W]

Mullidae - Goatfishes
1 *_Mulloides flavolineatus_ (Lacepède, 1801) [P,W]
1 *_M. vanicolensis_ (Valenciennes, 1831) [P]

1 *Parupeneus barberinus* (Lacepède, 1801)	[P,W]
1 **P. bifasciatus* (Lacepède, 1801)	[P,W]
1 **P. cyclostomus* (Lacepède, 1801)	[P]
1 **P. macronemus* (Lacepède, 1801)	[O]
2 **P. multifasciatus* (Quoy and Gaimard, 1824)	[P,W]
1 **P. pleurostigma* (Bennett, 1831)	[P,W]
Kyphosidae - Rudderfishes	
1 **Kyphosus cinerascens* (Forsskål, 1775)	[P]
1 *K. vaigiensis* (Quoy and Gaimard, 1825)	[O]
Pempheridae - Sweepers	
1 **Pempheris oualensis* Cuvier, 1831	[P,W]
Ephippidae - Batfishes	
1 **Platax orbicularis* (Forsskål, 1775)	[O]
1 **P. teira* (Forsskål, 1775)	[P]
Chaetodontidae - Butterflyfishes	
1 **Chaetodon auriga* (Forsskål, 1775)	[P,W]
1 *C. bennetti* Cuvier, 1831	[P]
1 **C. citrinellus* Cuvier, 1831	[P,W]
1 *C. ephippium* Cuvier, 1831	[P,W]
3 **C. guttatissimus* Bennett, 1831	[P]
1 **C. kleinii* Bloch, 1790	[P]
1 **C. lineolatus* Cuvier, 1830	[P]
1 **C. lunula* (Lacepède, 1803)	[P,W]
3 **C. madagaskariensis* Ahl, 1923	[P]
1 **C. melannotus* Bloch and Schneider, 1801	[P]
1 **C. meyeri* Bloch and Schneider, 1801	[P]
3 **C. mitratus* Günther, 1860	[P,W]
1 **C. ornatissimus* Cuvier, 1831	[P]
1 **C. semeion* Bleeker, 1855	[P]
1 **C. trifascialis* Quoy and Gaimard, 1824	[P]
1 **C. trifasciatus* Park, 1797	[P,W]
2 *C. ulietensis* Cuvier, 1831	[P,W]
1 **C. unimaculatus* Bloch, 1787	[P]
1 **C. vagabundus* Linnaeus, 1758	[P,W]
1 **Forcipiger flavissimus* Jordan and McGregor, 1898	[P,W]
2 **Hemitaurichthys polylepis* (Bleeker, 1857)	[P]
1 *Heniochus chrysostomus* Cuvier, 1831	[P]
1 **H. monoceros* Cuvier, 1831	[P]
Pomacanthidae - Angelfishes	
1 **Apolemichthys trimaculatus* (Lacepède, 1831)	[P]
2 *Centropyge colini* Smith-Vaniz and Randall, 1974	[P]
1 **C. flavissimus* (Cuvier, 1831)	[P,W]
3 **C. joculator* Smith-Vaniz and Randall, 1974	[P,W]
2 *C. multifasciatus* (Smith and Radcliffe, 1911)	[P]
2 *Genicanthus bellus* Randall, 1975	[P,W]
1 **Pomacanthus imperator* (Bloch, 1787)	[P]
Pomacentridae - Damselfishes	

1	**Abudefduf notatus* (Day, 1869)	[P]
1	**A. septemfasciatus* (Cuvier, 1830)	[O]
1	**A. sordidus* (Forsskål, 1775)	[P]
1	**A. vaigiensis* (Quoy and Gaimard, 1825)	[O]
2	**Amblyglyphidodon aureus* (Cuvier, 1830)	[P]
2	*A. curacao* (Bloch, 1787)	[P]
1	**Amphiprion clarkii* (Bennett, 1830)	[P]
2	**A. perideraion* Bleeker, 1855	[P]
2	**Chromis alpha* Randall, 1988	[P]
2	**C. amboinensis* (Bleeker, 1873)	[P,W]
2	**C. atripes* Fowler and Bean, 1928	[W]
2	**C. caudalis* Randall, 1988	[O]
2	**C. delta* Randall, 1988	[O]
3	**C. dimidiata* (Klunzinger, 1871)	[O]
1	**C. elerae* Fowler and Bean, 1928	[P]
1	**C. lepidolepis* Bleeker, 1877	[P,W]
2	**C. margaritifer* Fowler, 1946	[P,W]
3	**C. nigrura* Smith, 1960	[P,W]
3	**C. opercularis* (Günther, 1867)	[P,W]
1	**C. ternatensis* (Bleeker, 1856)	[P,W]
1	*C. viridis* (Cuvier, 1830)	[P,W]
2	**C. xanthura* (Bleeker, 1854)	[P]
1	*Chrysiptera biocellata* (Quoy and Gaimard, 1824)	[P,W]
1	**C. glauca* (Cuvier, 1830)	[P,W]
1	*Dascyllus aruanus* (Linnaeus, 1758)	[P,W]
2	**D. reticulatus* (Richardson, 1846)	[P]
1	**D. trimaculatus* (Rüppell, 1828)	[P]
1	**Plectroglyphidodon dickii* (Liénard, 1839)	[P,W]
1	**P. imparipennis* (Vallant and Sauvage, 1875)	[P,W]
1	**P. johnstonianus* Fowler and Ball, 1924	[P]
1	**P. lacrymatus* (Quoy and Gaimard, 1825)	[P,W]
1	**P. leucozonus* (Bleeker, 1859)	[P,W]
1	**P. phoenixensis* (Schultz, 1943)	[P]
1	*Pomacentrus pavo* (Bloch, 1787)	[P,W]
1	**Stegastes albifasciatus* (Schlegel and Müller, 1839)	[P,W]
1	**S. fasciolatus* (Ogilby, 1889)	[P,W]
1	*S. lividus* (Bloch and Schneider, 1801)	[P,W]
1	*S. nigricans* (Lacepède, 1802)	[P,W]

Cirrhitidae - Hawkfishes

1	**Amblycirrhitus bimacula* (Jenkins, 1903)	[P,W]
2	*Cirrhitichthys aprinus* (Cuvier, 1829)	[P]
1	**C. oxycephalus* (Bleeker, 1855)	[P]
1	**Cirrhitus pinnulatus* (Schneider, 1801)	[P]
1	**Oxycirrhites typus* Bleeker, 1857	[P]
1	**Paracirrhites arcatus* (Cuvier, 1829)	[P]
1	**P. forsteri* (Schneider, 1801)	[P,W]
2	**P. hemistictus* (Günther, 1874)	[P]

Mugilidae - Mullets

1	**Crenimugil crenilabis* (Forsskål, 1775)	[P,W]
1	*Liza vaigiensis* (Quoy and Gaimard, 1824)	[W]

Sphyraenidae - Barracudas

4	*_Sphyraena barracuda_ (Walbaum, 1792)	[P,W]
1	*_S. flavicauda_ Rüppell, 1838	[P]

Polynemidae - Threadfins

1	_Polydactylus sexfilis_ (Valenciennes, 1831)	[P]

Labridae - Wrasses

1	*_Anampses caeruleopunctatus_ Rüppell, 1829	[P]
1	*_A. meleagrides_ Valenciennes, 1840	[P]
1	*_A. twistii_ Bleeker, 1856	[P]
1	*_Bodianus anthioides_ (Bennett, 1830)	[P,W]
1	*_B. axillaris_ (Bennett, 1831)	[P]
1	*_B. diana_ (Lacepède, 1801)	[P]
1	_Cheilinus bimaculatus_ Valenciennes, 1840	[O]
1	_C. chlorurus_ (Bloch, 1791)	[P,W]
1	_C. fasciatus_ (Bloch, 1791)	[P]
1	*_C. trilobatus_ Lacepède, 1801	[P]
1	*_C. undulatus_ Rüppell, 1835	[P,W]
2	*_C. unifasciatus_ Streets, 1877	[O]
1	*_Cheilio inermis_ (Forsskål, 1775)	[P]
1	*_Cirrhilabrus exquisitus_ Smith, 1957	[P]
2	_Cirrhilabrus rubrimarginatus_ Randall, 1992	[P]
1	*_Coris aygula_ Lacepède,1801	[P]
2	*_C. dorsomacula_ Fowler, 1908	[W]
1	*_C. gaimard_ (Quoy and Gaimard, 1824)	[P,W]
1	_Cymolutes praetextatus_ (Quoy and Gaimard, 1834)	[P,W]
1	*_Epibulus insidiator_ (Pallas, 1770)	[P,W]
2	*_Gomphosus varius_ Lacepède, 1801	[P,W]
2	_Halichoeres chloropterus_ (Bloch, 1791)	[P]
1	_H. hortulanus_ (Lacepède, 1801)	[P]
1	*_H. marginatus_ Rüppell, 1835	[P,W]
2	*_H. melasmapomus_ Randall, 1980	[P]
2	*_H. ornatissimus_ (Garrett, 1863)	[P,W]
1	*_H. scapularis_ (Bennett, 1831)	[O]
2	*_H. trimaculatus_ (Quoy and Gaimard, 1834)	[P,W]
1	*_Hemigymnus fasciatus_ (Bloch, 1792)	[P]
1	*_H. melapterus_ (Bloch, 1791)	[P]
1	*_Hologymnosus doliatus_ (Lacepède, 1801)	[P]
1	*_Labroides bicolor_ Fowler and Bean, 1928	[P]
1	*_L. dimidiatus_ (Valenciennes, 1839)	[P,W]
2	*_L. pectoralis_ Randall and Springer, 1975	[P]
1	*_Labropsis xanthonota_ Randall, 1981	[P]
2	_Macropharyngodon meleagris_ (Valenciennes, 1839)	[P,W]
1	_Novaculichthys macrolepidotus_ (Bloch, 1791)	[W]
1	*_N. taeniourus_ (Lacepède, 1801)	[P,W]
1	*_Pseudocheilinus hexataenia_ (Bleeker, 1857)	[P,W]
1	*_P. octotaenia_ Jenkins, 1900	[P,W]
2	_Pseudocoris aurantifasciatus_ Fourmanoir, 1971	[P]
1	*_Pseudodax moluccanus_ (Valenciennes, 1839)	[P]
2	*_Stethojulis bandanensis_ (Bleeker, 1851)	[P,W]
1	*_S. strigiventer_ (Bennett, 1832)	[P,W]
1	*_Thalassoma amblycephalum_ (Bleeker, 1856)	[P,W]

1 **T.* *hardwickei* (Bennett, 1828) [P,W]
1 **T.* *jansenii* (Bleeker, 1856) [W]
1 **T.* *lunare* (Linnaeus, 1758) [P]
1 **T.* *lutescens* (Lay and Bennett, 1839) [P,W]
1 **T.* *purpureum* (Forsskål, 1775) [P,W]
1 **T.* *quinquevittatum* (Lay and Bennett, 1839) [P,W]
1 **T.* *trilobatum* (Lacepède, 1801) [P]
2 *Xyrichtys aneitensis* (Günther, 1862) [P]
1 **X.* *pavo* Valenciennes, 1840 [P]

Scaridae - Parrotfishes
1 **Bolbometopon muricatum* (Valenciennes, 1840) [O]
1 *Calotomus carolinus* (valenciennes, 1840) [P]
1 *C. spinidens* (Quoy and Gaimard, 1824) [P]
2 *Hipposcarus longiceps* (Valenciennes, 1840) [P]
1 *Leptoscarus vaigiensis* (Quoy and Gaimard, 1824) [P]
2 *Scarus atropectoralis* Schultz, 1958 [P]
3 *S. enneacanthus* Lacepède, 1802 [P,W]
2 **S.* *forsteni* (Bleeker, 1861) [O]
1 **S.* *frenatus* Lacepède, 1802 [P]
1 **S.* *ghobban* Forsskål, 1775 [P]
1 *S. globiceps* Valenciennes, 1840 [P]
1 **S.* *niger* Forsskål, 1775 [O]
2 **S.* *oviceps* Valenciennes, 1840 [P,W]
1 **S.* *prasiognathos* Valenciennes, 1840 [P]
1 **S.* *psittacus* Forsskål, 1775 [P]
1 **S.* *rubroviolaceus* Bleeker, 1847 [O]
2 **S.* *schlegeli* (Bleeker, 1861) [P]
1 **S.* *sordidus* Forsskål, 1775 [P,W]
3 *S. strongylocephalus* Bleeker, 1854 [P]
[This species, restricted to the Indian Ocean and Indonesia, has frequently been misidentified as *S. gibbus* Rüppell, a closely related Red Sea endemic.]
3 *S. viridifuratus* (Smith, 1956) [P]

Pinguipedidae - Sandperches
1 **Parapercis clathrata* Ogilby, 1911 [P,W]
1 *P. hexophthalma* (Cuvier, 1829) [P,W]
1 **P.* *schauinslandi* (Steindachner, 1900) [P]

Creediidae - Sandburrowers
2 **Chalixodytes tauensis* Schultz, 1943 [P,W]
3 *Limnichthys nitidus* Smith, 1958 [P]

Tripterygiidae - Triplefins
3 **Enneapterygius elegans* (Peters, 1876) [P]
5 **Enneapterygius tutuilae* Jordan & Seale, 1906 [W]
5 **Enneapterygius* sp. 1 [W]
2 *Helcogramma capidata* Rosenblatt, 1960 [P]

Blenniidae - Blennies
1 *Aspidontus dussumieri* (Valenciennes, 1836) [P]
1 **A.* *taeniatus* Quoy and Gaimard, 1834 [P]
1 **Cirripectes castaneus* (Valenciennes, 1836) [P,W]

3 _C. gilberti_ Williams, 1988 [P]
1 *_C. polyzona_ (Bleeker, 1868) [P]
1 _C. quagga_ (Fowler and Ball, 1924) [P]
1 *_Escenius bicolor_ (Day, 1888) [P,W]
1 *_E. midas_ Starck, 1969 [P]
2 *_Entomacrodus caudofasciatus_ (Regan, 1909) [P]
1 *_E. epalzeocheilus_ (Bleeker, 1859) [W]
1 _E. striatus_ (Quoy and Gaimard, 1836) [P,W]
1 *_Exallias brevis_ (Kner, 1868) [P]
1 _Glyptoparus delicatulus_ Smith, 1959 [P]
2 *_Istiblennius chrysospilos_ (Bleeker, 1857) [P]
1 *_I. edentulus_ (Schneider, 1801) [P]
1 *_I. lineatus_ (Valenciennes, 1836) [W]
1 *_I. periophthalmus_ (Valenciennes, 1836) [P,W]
1 _Petroscirtes xestus_ Jordan and Seale, 1906 [P,W]
1 *_Plagiotremus rhinorhynchos_ (Bleeker, 1852) [P,W]
1 *_P. tapeinosoma_ (Bleeker, 1857) [P]
1 _Stanulus seychellensis_ Smith, 1959 [P]

Callionymidae - Dragonets
1 _Diplogrammus goramensis_ (Bleeker, 1858) [P]

Gobiidae - Gobies
2 _Amblygobius decussatus_ (Bleeker, 1855) [P]
2 _A. phalaena_ (Valenciennes, 1837) [P]
3 _A. semicinctus_ (Bennett, 1833) [W]
3 _A. tekomaji_ (Smith, 1959) [W]
1 _Asterropteryx semipunctatus_ Rüppell, 1830 [P,W]
1 *_Bathygobius cocosensis_ (Bleeker, 1854) [P,W]
1 *_B. cyclopterus_ (Valenciennes, 1837) [P]
1 _Bryaninops ridens_ Smith, 1959 [P]
1 _Cabillus tongarevae_ (Fowler, 1927) [P]
1 _Callogobius maculipinnis_ (Fowler, 1918) [W]
1 *_C. sclateri_ (Steindachneri, 1880) [W]
5 _Callogobius_ sp. [P,W]
1 _Discordipinna griessingeri_ Hoese and Fourmanoir, 1978 [P]
2 _Eviota lachdeberei_ ? Giltay, 1933 [W]
2 _E. latifasciata_ ? Jewett and Lachner, 1983 [W]
1 _E. melasma_ Lachner and Karanella, 1980 [P,W]
1 _E. prasina_ (Klunzinger, 1871) [W]
5 *_Eviota_ sp. 1 [W]
5 *_Eviota_ sp. 2 [W]
5 *_Eviota_ sp. 3 [W]
5 _Eviota_ sp. 4 [W]
1 _Exyrias belissimus_ (Smith, 1959) [P,W]
1 _Fusigobius duospilus_ Hoese and Reader, 1985 [W]
1 _F. neophytus_ (Günther, 1877) [P,W]
5 *_Fusigobius_ sp. [P,W]
1 _Gnatholepis anjerensis_ (Bleeker, 1850) [P,W]
3 _G. caurensis_ (Bleeker, 1853) [P,W]
5 _Gnatholepis_ sp. [W]
2 *_Gobiodon okinawe_ Sawada, Arai, and Abe, 1973 [P]
1 *_G. rivulatus_ (Rüppell, 1830) [P]

5 *Oplopomops* sp. [P,W]
1 *Oplopomus oplopomus* (Valenciennes, 1837) [P]
1 *Palutrus pruinosus* (Jordan and Seale, 1906) [P,W]
1 *Paragobiodon echinocephalus* (Rüppell, 1830) [P]
1 **Priolepis cincta* (Regan, 1908) [P]
1 *P. inhaca* (Smith, 1949) [P]
1 **P. semidoliatus* (Valenciennes, 1837) [P,W]
2 *Psilogobius prolatus* Watson and Lachner, 1985 [P]
1 *Sueviota lachneri* Winterbottom and Hoese, 1988 [W]
1 **Trimma emeryi* Winterbottom, 1985 [P,W]
1 *T. hoesei* Winterbottom, 1984 [W]
1 *T. macrophthalma* (Tomiyama, 1936) [P,W]
1 **T. taylori* Lobel, 1979 [P]
1 *T. undisquamis* (Gosline, 1959) [W]
3 *T. winchi* Winterbottom, 1984 [P]
3 **Trimma* sp. [P,W]
2 **Trimmaton sagma* Winterbottom, 1989 [P]
1 **Valenciennea helsdingenii* (Bleeker, 1858) [P]
1 **V. sexguttata* (Valenciennes, 1837) [P]
1 **V. strigata* (Broussonet, 1872) [P]
1 *Vanderhorstia ornatissima* Smith, 1959 [P,W]

Xenisthmidae - Sandfishes
3 *Xenisthmus africanus* Smith, 1958 [P,W]
2 *X. clara* (Jordan and Seale, 1906) [P,W]

Microdesmidae - Hovergobies
[We follow Randall and Hoese (1985) in including *Nemateleotris* and *Ptereleotris* in this family.]
1 **Gunnelichthys monostigma* Smith, 1958 [W]
1 **Nemateleotris decora* Randall and Allen, 1973 [P]
1 **N. magnifica* Fowler, 1938 [P]
1 **Ptereleotris evides* (Jordan and Hubbs, 1925) [P]
1 **P. heteroptera* (Bleeker, 1855) [P]
1 **P. microlepis* (Bleeker, 1856) [P,W]
1 **P. zebra* (Fowler, 1938) [P]

Kraemeridae - Sand darts
1 *Kraemeria samoensis* Steindachner, 1906 [P]

Acanthuridae - Surgeonfishes
1 **Acanthurus blochii* Valenciennes, 1835 [O]
2 **A. guttatus* Bloch and Schneider, 1801 [O]
2 **A. leucosternon* Bennett, 1832 [P]
1 **A. lineatus* (Linnaeus, 1758) [O]
2 **A. maculiceps* (Ahl, 1923) [O]
1 **A. mata* (Cuvier, 1829) [P]
2 **A. nigricans* (Linnaeus, 1758) [P,W]
1 **A. nigricauda* Duncker and Mohr, 1929 [O]
1 **A. nigrofuscus* (Forsskål, 1775) [W]
1 *A. nigroris* Valenciennes, 1835 [P]
2 **A. olivaceus* Bloch and Schneider, 1801 [P]
1 **A. pyroferus* Kittlitz, 1834 [O]

1 *_A. thompsoni_ (Fowler, 1923) [P]
1 *_A. triostegus_ (Linnaeus, 1758) [P]
1 *_A. xanthopterus_ Valenciennes, 1835 [O]
1 *_Ctenochaetus striatus_ (Quoy and Gaimard, 1825) [P,W]
1 *_C. strigosus_ (Bennett, 1828) [P,W]
1 *_Naso brevirostris_ (Valenciennes, 1835) [P]
1 *_N. hexacanthus_ (Bleeker, 1855) [P]
1 *_N. lituratus_ (Bloch and Schneider, 1801) [P,W]
1 *_N. unicornis_ (Forsskål, 1775) [P,W]
1 *_N. vlaminghi_ (Valenciennes, 1835) [P]
1 *_Paracanthurus hepatus_ (Linnaeus, 1766) [P]
3 _Zebrasoma desjardinii_ (Bennett, 1835) [P]
[Most recent authors have recognized this Indian Ocean surgeonfish as a subspecies of the Pacific Z. _veliferum._ We follow Burgess (1973) in recognizing them both as distinct species, and note that in contrast to Cocos, Christmas Is. fish have the typical _veliferum_ coloration.]
1 *_Z. scopas_ (Cuvier, 1829) [P,W]

Zanclidae - Moorish Idols
1 *_Zanclus cornutus_ (Linnaeus, 1758) [P]

Siganidae - Rabbitfishes
1 _Siganus argenteus_ (Quoy and Gaimard, 1825) [P]
2 _S. puellus_ Schlegel, 1852 [P]
2 _S. punctatus_ (Bloch and Schneider, 1801) [P]
3 _S. stellatus_ Forsskål, 1775 [O]

Scombridae - Tunas
4 *_Acanthocybium solandri_ (Cuvier, 1831) [O]
1 *_Gymnosarda unicolor_ (Rüppell, 1836) [O]
4 *_Thunnus albacares_ (Bonnaterre, 1788) [O]

Bothidae - Flounders
1 *_Bothus mancus_ (Bonnaterre, 1782) [P,W]
1 *_B. pantherinus_ (Rüppell, 1830) [W]

Soleidae - Soles
5 *_Aseraggodes_ sp. 1 [P]
5 _Aseraggodes_ sp. 2 [P]

Balistidae - Triggerfishes
1 *_Balistapus undulatus_ (Park, 1797) [P]
1 *_Balistoides viridescens_ (Bloch and Schneider, 1801) [O]
1 *_Melichthys indicus_ Randall and Klausewitz, 1973 [P]
4 *_M. niger_ (Bloch, 1786) [P]
1 *_M. vidua_ (Solander, 1844) [P]
1 *_Odonus niger_ (Rüppell, 1837) [P]
1 _Pseudobalistes flavimarginatus_ (Rüppell, 1829) [P,W]
1 _Rhinecanthus aculeatus_ (Linnaeus, 1758) [P,W]
1 *_R. rectangulus_ (Bloch and Schneider, 1801) [P]
1 *_Sufflamen bursa_ (Bloch and Schneider, 1801) [P]
1 *_S. chrysopterus_ (Bloch and Schneider, 1801) [P]
1 _S. fraenatus_ (Latreille, 1804) [P]

1 **Xanthichthys auromarginatus* (Bennett, 1831)	[P]
1 **X. caeruleolineatus* Randall, Matsuura and Zama, 1978	[O]
Monacanthidae - Leatherjackets	
4 **Aluterus scriptus* (Osbeck, 1765)	[P]
1 **Cantherines dumerilii* (Hollard, 1854)	[P]
1 **C. pardalis* (Rüppell, 1837)	[O]
1 **Pervagor aspricaudus* (Hollard, 1854)	[P,W]
Ostraciontidae - Boxfishes	
1 **Ostracion cubicus* Linnaeus, 1758	[P,W]
Tetraodontidae - Puffers	
1 **Arothron hispidus* (Linnaeus, 1758)	[P,W]
1 **A. nigropunctatus* (Bloch and Schneider, 1801)	[P]
1 **Canthigaster amboinensis* (Bleeker, 1865)	[P]
1 **C. bennettii* (Bleeker, 1854)	[P]
1 **C. janthinoptera* (Bleeker, 1855)	[P,W]
1 **C. valentini* (Bleeker, 1853)	[P]
Diodontidae - Porcupinefishes	
4 **Diodon hystrix* Linnaeus, 1758	[P]

Table 1. Comparison of total ichthyofauna[1] and selected families of fishes occuring at Cocos-Keeling (CK) or Christmas Island (CI); numbers in parentheses are percent of total fauna; data for Christmas Island based on slightly updated version of checklist given in Allen and Steene (1987).

Family	number of species CK (%)	number of species CI (%)	shared spp.	CK only	CI only
Labridae	54 (10.2)	61 (10.8)	43	11	16
Gobiidae	51 (9.6)	36 (6.4)	18	33	18
Pomacentridae	38 (7.2)	44 (7.8)	31	7	11
Apogonidae	30 (5.7)	22 (3.9)	12	20	10
Serranidae	30 (5.7)	44 (7.8)	19	11	25
Acanthuridae	25 (4.7)	26 (4.6)	24	1	2
Muraenidae	24 (4.5)	34 (6.0)	20	4	14
Chaetodontidae	23 (4.3)	27 (4.8)	19	4	8
Blenniidae	21 (4.0)	28 (5.0)	14	7	14
Scaridae	20 (3.8)	15 (2.7)	11	9	6
Holocentridae	20 (3.8)	15 (2.7)	12	8	3
Scorpaenidae	16 (3.0)	19 (3.4)	11	5	8
Balistidae	14 (2.6)	12 (2.1)	11	3	1
Carangidae	11 (2.1)	13 (2.3)	10	1	2
Lethrinidae	10 (1.9)	2 (0.0)	2	8	0
Lutjanidae	8 (1.5)	15 (2.7)	7	1	8
Cirrihitidae	8 (1.5)	7 (1.2)	7	1	0
Mullidae	8 (1.5)	7 (1.2)	7	1	0
Pomacanthidae	7 (1.3)	12 (2.1)	4	3	8
Microdesmidae	7 (1.3)	7 (1.2)	7	0	0
Tetradontidae	6 (1.1)	9 (1.6)	6	0	3
Ophichthidae	6 (1.1)	7 (1.2)	2	4	5
Syngnathidae	6 (1.1)	7 (1.2)	4	2	3
Total fauna[1]	530	563	351	176	212

[1] The following families of epipelagic fishes were unsampled or undersampled at Cocos (Keeling) Island, and to make the above faunal comparisons more meaningful, species of these families are not included in the total fauna counts (percentages were also calculated using the adjusted totals): Rhincodontidae, Exocoetidae, Coryphaenidae, Gempylidae, Scombridae and Istiophoridae.

Table 2. Zoogeographic analysis of the Cocos (Keeling) fish fauna.

Distribution	No. species	percent of total fauna
Widespread Indo-Pacific or Indo-west Pacific	388	72.8
West Pacific & Cocos Is.	85	15.9
Indian Ocean	31	5.8
Circumtropical	12	2.3
Uncertain	17	3.2
total	533	100.0
Also known from Christmas Is.	354	66.4

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CHAPTER 15

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CHAPTER 15

BARNACLES (CIRRIPEDIA, THORACICA) OF THE COCOS (KEELING) ISLANDS

BY

D.S. JONES *

INTRODUCTION

The barnacle fauna of the Cocos (Keeling) Islands has not been documented prior to the present report. Previous reports on the crustaceans of these islands have listed Brachyura, Anomura, Caridea, Stomatopoda and Paguridae (Calman 1909, Wood-Jones 1909, Gibson-Hill 1947, 1948, Tweedie 1950, Forest 1956).

The present collection of barnacles was made by sampling a wide variety of habitats throughout the atoll. Sampling stations included all reef flat zones and a range of lagoonal habitats and outer reef slopes (see Chapter 1, Fig. 2, List of barnacles). Specimens were collected by walking on shores and reef flats during low tide, snorkelling and SCUBA diving.

A total of 13 species of barnacles in 11 genera are now recorded from the Cocos (Keeling) Islands. Nine of these species were collected at one locality only. Although the number of barnacles is small, this collection is of considerable interest since nothing is known of the barnacles of these islands, and knowledge of the barnacle fauna of coral atolls in the Indian Ocean in general is scanty. Eleven species were collected during the Western Australian Musum Cocos (Keeling) Island expedition of February, 1989. Two additional species from these islands (*Capitulum mitella, Megabalanus ajax*) are housed in the crustacean collection of the Western Australian Museum and are included in the species list. The species list given below must be considered provisional and further detailed collecting may well reveal additional species, particularly from sub-tidal areas.

DISCUSSION

The barnacle fauna of the Cocos (Keeling) Islands is composed of widespread Indo-West Pacific species (8) and species exhibiting cosmopolitan distributions (5).

Of the cosmopolitan barnacles, *L. anatifera* and *L. anserifera* are pelagic in habitat and attach to floating objects. Freshly beached specimens were collected on reef platforms and beaches, attached to bamboo, wood, etc. However, large numbers of the abundant terrestrial hermit crab *Coenobita perlatus* Milne Edwards were observed actively predating these barnacles. Consequently strandings of pelagic barnacles may be more numerous, and more pelagic species may be represented than are presently recorded, but ensuing rapid predation (by terrestrial hermit crabs in particular) makes the collection of all but recently stranded specimens unlikely.

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* Western Australian Museum, Francis Street, Perth, Western Australia, 6000.

The cosmopolitan pedunculate barnacle *O. lowei* occurs on the gills of decapod crustaceans and was obtained from the gills of the rock lobster *Panulirus penicillatus* Oliver at the Cocos Islands. The cosmopolitan fouling species, *M. tintinnabulum*, occurred on mooring buoys in the main lagoon. This species may have been introduced via shipping since it was not found elsewhere in island waters and the species is a well-known fouler of ship hulls. *T. divisa* has a circumtropical insular and occasional mainland distribution. This species was first described from material collected on the west coast of Sumatra and the Java Sea. At Cocos (Keeling) the species was rare, only a few specimens being collected from deep, narrow crevices in beachrock.

The Indo-West Pacific species *T. wireni* was the only sessile species collected at more than one locality. It was collected subtidally from a variety of hard substrata (mooring buoys, carapace of *P. penicillatus*, shell of *Trochus maculatus* Linnaeus) as well as from a sponge collected in beach drift. *L. nicobarica* bores into limestone substrates in the Indo-West Pacific region. The species was rare at the Cocos (Keeling) Islands, boring into the upper areas of coral and limestone boulders on intertidal and seaward reef flats. The Indo-West Pacific species *C. mitella* occurs in crevices in mid-tidal areas under conditions of semi to full wave exposure. *T. fissum* occurs on the mouthparts of decapod crustaceans in the Indo-West Pacific region, and was collected from the third maxillipeds of *P. pencillatus*. Two balanomorphs, *E. hembeli* and *M. ajax*, both very large, robust species, are known from the Indo-West Pacific region although both are extremely rare. *E. hembeli* occurs on high intertidal rocks and shores and at the Cocos (Keeling) Islands a solitary individual was collected from high up on the limestone boulder on an ocean reef flat. *M. ajax* occurs mainly in the subtidal on corals. The low live coral cover at Cocos is reflected in the very low number of coral barnacles collected. Although numerous samples of live and dead coral were examined, only one sample harboured coral barnacles - viz. *S. dentatum* on the coral *Favia stelligera* (Dana). The genus *Acasta* occurs in sponges and has many Indo-West Pacific representatives. Parietal plates of *Acasta* sp. were obtained from a sponge found in beach drift at the Cocos (Keeling) Islands.

Barnacles are relatively rare and inconspicuous intertidal organisms at Cocos (Keeling) and their paucity in the overall marine invertebrate community is notable. The total of 13 species is small and may reflect inadequate sampling procedures. It may, however, be a true representation, since coral reefs are known to be unfavourable habitats for cirripedes (Darwin 1854, Borradaile 1903). The lack of development of barnacle populations on coral reefs has been documented in the tropical West Pacific (Newman 1960), the Tokara Islands, Japan (Utinomi 1954) and Heron Island, Australia (Endean et al. 1956). The scouring action of waves by rolling light coral limestone fragments and boulders is restrictive or adverse to barnacle settlement, especially in intertidal areas, where settlement would be restricted to crevices and underhangs. Newly settled and juvenile barnacles are indirectly predated on by herbivorous fish, which rasp limestone and coral reefs for micro-algae. Consequently barnacles may be restricted to higher intertidal areas or to boring into limestone substrata. Other known predators in the marine environment are molluscs (e.g. whelks) and sublittoral echinoderms (e.g. *Diadema*). These factors may all contribute to the general lack of intertidal barnacles at the Cocos (Keeling) Islands. In intertidal areas barnacles occur rarely and very sparsely, in interstices in or between and under rocks (e.g. *C. mitella, T. divisa*) or high on rocks which are only covered during high tides (*E. hembeli*). Burrowing forms occur in limestone and coral boulders (*L. nicobarica*) or live coral (*S. dentatum*). Some *T. divisa* individuals collected at Cocos (Keeling) exhibited gastropod bore holes in parietal plates.

On fouling buoys in the main lagoon a small fouling community (e.g. sponges, ascidians, barnacles) is developing and many large specimens of the fouler *M. tintinnabulum* were collected here as well as individuals of *T. wireni*. The presence and abundance of *M. tintinnabulum* and *T. wireni* at this site compared to the paucity of barnacle species elsewhere may be associated with a lack of coral. This, combined with a lack of shelter from piscivorous fish, may result in an absence of reef fish (e.g. Scaridae) and hence the predation pressure on newly settled barnacles and juveniles may be correspondingly reduced. The origin of the Cocos specimens of *M. tintinnabulum* is unknown. However, the presence of this species may be of some concern since it is a noted fouling species overseas.

The thoracic cirripede fauna of the Indian Ocean is relatively well-known, with upwards of 280 species estimated to occur there (Stubbings 1936, Nilsson-Cantell 1938, Daniel 1972). The nearest localities to the Cocos (Keeling) Islands are Christmas Island, 900 km to the east and Java Head, 1000 km to the north-east. Only two cirripede species are recorded from Christmas Island (Nilsson-Cantell 1934 Daniel 1972), but the Western Australian Museum crustacean collection holds an additional five species making a total of seven. Java is part of Indo-Malay faunistic province, an area rich in both number of species and in the geographical distribution of cirripedes. At least 246 species are recorded from this area (Hoek 1907, 1913, Broch 1931, Nilsson-Cantell 1934). Compared to the nearest mainland shores (Sumatra, Java) which exhibit rich barnacle faunas in both the intertidal and the sub littoral (Nilsson-Cantell 1921), the fauna of the Cocos (Keeling) Islands must be considered depauperate.

The number of cirripedes recorded from the Cocos (Keeling) Islands is larger than that at present recorded from other isolated Indian Ocean atolls (e.g. Diego Garcia, Chagos) but less than that presently known from larger atoll groups (e.g. Maldives and Laccadives). Table 1 compares the numbers of barnacle species recorded from islands and atolls in the Indian Ocean, and the species in common with the Cocos (Keeling) Islands. However, meaningful comparisons with other atolls and islands are difficult to make since the collecting effort at these localities is not known.

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LIST OF BARNACLES

x = specimens without precise locality data

ORDER THORACICA	**Collection Station**
Suborder Lepadomorpha	
Family Scalpellidae Pilsbry, 1916	
Subfamily Lithotryinae Gruvel, 1905	
Lithotrya nicobarica Reinhardt, 1850	1, 32
Subfamily Pollicipinae Gruvel, 1905	
Captitulum mitella (Linnaeus, 1767)	x
Family Lepadidae Burmeister, 1834 ("Fam. Lepadea")	
Lepas anatifera Linnaeus, 1767	24, 27, 30
Lepas anserifera Linnaeus, 1767	27, 30, 32
Family Poecilasmatidae Annandale, 1910	
Temnaspsis fissum Darwin, 1851	10
Octolasmis lowei (Darwin, 1851)	20
Suborder Balanomorpha	
Family Chthamalidae Darwin, 1854	
Subfamily Euraphiinae Newman & Ross, 1976	
Euraphia hembeli Conrad, 1837	1
Family Tetraclitidae Gruvel, 1903	
Subfamily Tetraclitinae Gruvel, 1903	
Tetraclita divisa Nilsson-Cantell, 1921	10
Tesseropora wireni Nilsson-Cantell, 1921	1, 2, 6, 20 ,28
Family Archaeobalanidae Newman & Ross, 1976	
Acasta sp.	1
Family Pyrgomatidae Gray, 1825	
Savignium dentatum (Darwin, 1854)	31
Family Balanidae Leach, 1817	
Megabalanus ajax (Darwin, 1854)	x
Megabalanus tintinnabulum (Linnaeus, 1758)	28

Table 1 : A comparison of the numbers of thoracic cirripede species recorded from Indian Ocean atolls (A) and islands, and the species in common with the Cocos (Keeling) Islands.

Locality		**Total Species**	**Spp. in common with Cocos (Keeling)**	**References**
Christmas I.		7	4	Nilsson-Cantell 1934; Daniel 1972; WA Museum Collection
Diego Garcia	(A)	3	3	Smith 1971
Chagos	(A)	6	3	Gruvel 1909
Andamans & Nicobars		17	2	Gruvel 1909; Daniel 1972
Sri Lanka		31	3	Annandale 1906; Daniel 1972
Maldives & Laccadives	(A)	25	2	Borradaile, 1903; Annandale 1906; Daniel 1972
Seychelles		9	2	Gruvel 1909; Taylor 1968
Providence I.		2	0	Gruvel 1909

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DECAPOD CRUSTACEANS OF THE COCOS (KEELING) ISLANDS

BY

G.J. MORGAN *

INTRODUCTION

Prior to the present study, the crustacean fauna of the Cocos (Keeling) Islands had been collected intensively only once, by C.A. Gibson-Hill in the years 1940-41. The Brachyura and Stomatopoda of his material were taxonomically reviewed by Tweedie (1950) and the hermit crabs by Forest (1956). Gibson- Hill's collection represents almost exclusively intertidal and terrestrial faunas. In the present survey, SCUBA was employed extensively to augment the poorly known subtidal faunas. Xanthoid crabs (families Xanthidae, Trapeziidae, Pilumnidae, Menippidae) and marine hermit crabs (families Diogenidae and Paguridae) are dominant decapod components of tropical rocky and coral reef ecosystems and were collected preferentially. Conversely, some taxa (e.g. caridean shrimps) are poorly represented in the present collection.

Specimens were sampled by reef walking in the intertidal and by SCUBA or snorkelling in the subtidal habitats. A total of 198 species of Decapoda is recorded of which 78 are new records for the Cocos (Keeling) Islands (see list of species). Station localities are listed by number (see Chapter 1, Fig.2) and some additional sites sampled are recorded by name. Station 9 (Direction Island) has been divided for this list into 9(a): blue hole south of Direction I. and 9(b): sand shallows between island and blue hole. In order to compile as complete a record of decapod crustaceans as possible, the list includes species recorded by the previous workers noted above. The species names are those currently used in the scientific literature and not necessarily the names cited by historical workers. The historical collections have not been examined and hence the accuracy of early identifications cannot be ascertained.

DISCUSSION

The most diverse decapod taxa of the Cocos (Keeling) Islands are the xanthoid and paguroid crabs with 77 and 48 species recorded respectively. Both taxa are particularly evident in subtidal and intertidal reef habitats, although the abundance of xanthoids was found to be somewhat lower than expected on the 1989 sampling expedition.

The islands can be divided broadly into several major habitat types with a convenient dichotomy between lagoon and outer oceanic environments.

In the lagoon, only a few species of hermit crab notably *Clibanarius longitarsus* and *Calcinus laevimanus* are present in the sheltered shallow intertidal areas of fine mud sediment. Hermits appear to be absent from the very extensive soft grey sediment flats in North and South Lagoons of West Island, but these flats support high numbers of

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* Western Australian Museum, Francis Street, Perth, Western Australia, 6000.

Macrophthalmus verreauxi and *Uca chlorophthalmus*. The latter produces a distinct pattern of hexagonal territories in some upshore areas. The portunid *Thalamita crenata* is common in the shallows of the lagoon. Tweedie (1950) identified *T. spinimana* as the species plentiful in the shallow sandy, slightly weedy water of the lagoon' (Gibson-Hill, in Tweedie 1950) but in 1989 the common portunid in this habitat was *T. crenata*. It is possible that Tweedie's identification was spurious but he has recorded *T. crenata* from the 'outer edge of the atoll'. The large edible mud or mangrove crab *Scylla serrata* occasionally is caught by locals in the very sheltered areas of the lagoon but is rarely seen and presumably occurs in very low numbers. Ghost crabs, *Ocypode ceratophthalma* and *O. cordimana*, forage across the lagoon flats from their upshore burrows and are also numerous on the oceanic beaches. *O. ceratophthalma* occurs in its two colour morphs, with the olive green form far outnumbering the cream and brown morph. The terrestrial crab *Cardisoma carnifex* also feeds on exposed flats of the lagoon at low tide.

The continual natural process of sedimentary infilling of the lagoon, together with the occurrence of the above crabs in very high numbers, indicate that the populations of soft sediment crustaceans are relatively secure for the foreseeable future. In deeper areas of the lagoon and near the major channels allowing entry of oceanic water, hard and soft corals are present to a variable extent.

The 1983 El Niño effect resulted in very extensive coral death and over much of the lagoon only small colonies of live hard corals have re-established. As many species of crustaceans are either symbiotic with live corals or prefer the live coral habitat, loss of corals is reflected in crustacean occurrences. Where live coral, especially *Pocillopora* spp., is present, the crustacean assemblage resembles that discussed for outside reef coral habitats. The dead coral rubble supports a lower diversity of hermit crabs with the diogenid *Calcinus latens* and several small species of pagurids dominant in numbers. Portunids and xanthoids are also present but often difficult to collect in the deep layer of coral fragments. Sandy areas and beds of the seagrass *Thalassia* and the alga *Caulerpa* support *Calcinus latens* and *C. laevimanus* in relatively low populations and several pagurids in high numbers, especially *Micropagurus vexatus*. Sandy areas are also habitat for several portunid species and *Calappa hepatica*.

If further live coral dieback were to occur in the lagoon, the symbiotic faunal communities would be placed at considerable risk. Presumably there has been, and would continue to be, replacement of coral crustacean communities by rubble and sand-living species.

The oceanic reefs of the Cocos (Keeling) Islands have also experienced major reduction of the live coral habitat. Percentage cover of live hard corals is low and many of the outside reefs are dominated by bare, wave scoured dead coral or coral rubble. The shallow subtidal and intertidal reef habitats are home to a variety of hermit crabs with *Calcinus minutus*, *C. latens*, C. sp. 1 (an undescribed species), *Dardanus crassimanus* and *D. lagopodes* common. The large *Dardanus* species, *D. megistos, D. guttatus, D. gemmatus* and *D. deformis* occur on shallow reef flats and adjacent sandy environments. A variety of xanthoids especially *Pilodius areolatus*, are fairly numerous under the coral and coral rubble. Where live branching coral is present, especially *Pocillopora*, symbiotic species of xanthoids (e.g. *Trapezia* and *Cymo*), and alpheids (e.g. *Alpheus lottini*), occur. Under coral slabs, particularly in the subtidal, several species of pagurid are common with the bright lilac *Pylopaguropsis magnimanus* especially obvious. As was recorded for Christmas Island (Morgan, unpublished), pagurids can be quite diverse and common in tropical reef habitats and their taxonomy requires considerable attention. Interestingly, the populations and diversity of porcellanids (porcelain crabs) were low at Cocos (Keeling).

There seemed no obvious explanation for this apart from the possible effects of a paucity of live coral.

Intertidal rock and rock-sand platforms support quite high populations of hermit crabs with *Calcinus laevimanus* most widespread and *C. latens* and *Clibanarius humilis* common in areas. High on the platforms, in very warm pools flushed only by spring tides, the only hermit crab is *Calcinus seurati*. Xanthoids are also characteristic of rocky platforms, especially species of *Leptodius*. Grapsids are usually the most conspicuous crabs on intertidal hard substrata, with *Grapsus tenuicrustatus* and *G. intermedius* the largest species on Cocos (Keeling). Three species of *Pachygrapsus* occur in a range of intertidal habitats, usually on or under rock or coral slabs.

Prior to this study, two species of rock lobster, *Panulirus penicillatus* and *P. versicolor* were recorded from the Cocos (Keeling) Islands (George 1968). The presence of a third species, *P. ornatus*, commonly referred to on the islands as the `leopard cray', was confirmed during the 1989 study. All three species are very widespread in the Indo-West Pacific area. *Panulirus* species have extended larval stages of several months with the planktonic phyllosoma capable of drifting great distances on ocean currents before settlement as the puerulus. It is probable that rock lobster stocks at Cocos (Keeling) are dependent upon larvae originating considerable distances from the islands and hence fishing overexploitation of the local breeding population is unlikely to severely effect settlement. It is certainly possible, however, that heavy fishing might deplete the population of table-size lobsters. Some form of monitoring of fishing effort would provide information on distribution of the species and their present abundance.

The Cocos (Keeling) Islands do not support the numbers or diversity of true terrestrial crabs so obvious on Christmas Island (Indian Ocean). The gecarcinid *Cardisoma carnifex* is very common on West Island, with apparently lower populations elsewhere. No specimens of *C. rotundum* recorded by Tweedie (1950) (as *C. frontalis*), were collected on the 1989 expedition. The grapsids *Geograpsus crinipes* and *G. grayi* co-occur on the islands, in lower numbers than *Cardisoma*. The presence of the Christmas Island `red crab', *Gecarcoidea natalis*, was confirmed on North Keeling Island, but the species occurs in only small numbers. Tweedie (1950) stated that its occurrence was due to introduction with soil from Christmas Island to Direction Island and thence by larvae to other islands in the Cocos. This argument is convincing, given the small population of *G. natalis* on Cocos (Keeling) and the great distance (900 km) to Christmas Island, the only other habitat of the species.

Only one species of the terrestrial hermit crab family Coenobitidae had been recorded previously from Cocos (Keeling), namely *Coenobita perlatus* (Forest 1956). It is odd that the two additional species collected in this study, *C. rugosus* and *C. brevimanus*, were not represented in Gibson-Hill's collection as the former in particular is not uncommon. The coconut or robber crab, *Birgus latro*, was not found during the 1989 expedition, despite searches for it, but is reported by local people to occur on at least West and North Keeling Islands, the latter occurrence being confirmed by the ANPWS ranger, Mr Paul Stephenson (pers. comm.). In addition, a specimen of *B. latro* is on display in the local museum on Home Island, reportedly collected on Cocos (Keeling). Charles Darwin (1845) noted that *B. latro* was common at the time of his visit in 1836 and it might be suggested that the presently very low population of the species is due to overexploitation by the islands' local inhabitants. Protection of the existing specimens will be necessary to ensure their continued survival on Cocos (Keeling).

There are no naturally occurring bodies of freshwater on the islands, although a brackish lake (Bechet Besar) is present towards the north end of West Island. Freshwater must be accessed by sinking wells into subterranean reserves. It is scarcely surprising therefore that no freshwater crustacea were collected, unlike Christmas Island. *Cardisoma carnifex* was observed to concentrate at temporary rainwater pools and several specimens were seen in a shallow well, totally immersed in freshwater.

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LIST OF DECAPOD CRUSTACEA

KEY TO SYMBOLS

+ New record for Cocos (Keeling) Islands

* Not collected during this survey

$ Not collected but occurrence confirmed

Numbers = sampling station (see Chapter 1, Fig.2)

STENOPODIDEA

STENOPODIDAE

+	*Stenopus hispidus* (Olivier, 1811)	1

CARIDEA

ALPHEIDAE

+	*Alpheus lottini* Guérin, 1829	12
+	*Alpheus macrodactylus* Ortmann, 1890	1
+	*Alpheus strenuus strenuus* Dana, 1852	1,12
+	*Alpheus* sp.	1
+	*Synalpheus stimpsoni* (De Man, 1888)	19

PALINURA

PALINURIDAE

	Panulirus penicillatus (Olivier, 1791)	1,10,20
$	*Panulirus versicolor* (Latreille, 1804)	
+$	*Panulirus ornatus* (Fabricius, 1798)	

ANOMURA

DIOGENIDAE

+	*Aniculus retipes* Lewinsohn, 1982	4,19,32
	Aniculus ursus (Olivier, 1811)	1,11
+	*Aniculus* sp.	1
+	*Calcinus argus* Wooster, 1984	4
	Calcinus elegans (H. Milne Edwards, 1836)	1,6,11,12,18,30
	Calcinus gaimardii (H. Milne Edwards, 1848)	1,6,9(a),11,25
+	*Calcinus guamensis* Wooster, 1984	11
	Calcinus laevimanus (Randall, 1839)	2,6,10,12,30,34

	Calcinus latens (Randall, 1839)	1,6,8,9(a),9(b),12, 17, 18,22,23,30,34, 36
+	*Calcinus minutus* Buitendijk, 1937	4,6,7,13,15,19,25,32
+	*Calcinus pulcher* Forest, 1958	4,9(a),15,32
+	*Calcinus seurati* Forest, 1951	10,30
+	*Calcinus* sp. *1*	4,7,13,15,19,22,25, 32
+	*Calcinus* sp. *3*	4
+	*Calcinus* sp. *4*	4,6,15,25
+	*Calcinus* sp. *5*	15
+	*Calcinus* sp. *6*	25
	Clibanarius corallinus (H. Milne Edwards, 1848)	6,10,12,30
*	*Clibanarius eurysternus* Hilgendorf, 1878	
+	*Clibanarius humilis* Dana, 1852	2,30
+	*Clibanarius laevimanus* Buitendijk, 1937	2
+	*Clibanarius longitarsus* (De Haan, 1849)	2
*	*?Clibanarius merguiensis* De Man, 1888	
*	*Clibanarius striolatus* Dana, 1852	
+	*Dardanus crassimanus* (H. Milne Edwards, 1848)	1,4,8,15,19,23,32
	Dardanus deformis (H. Milne Edwards, 1836)	12
	Dardanus gemmatus (H. Milne Edwards, 1848)	1,24
	Dardanus guttatus (Olivier, 1811)	1,6,8,11,30
	Dardanus lagopodes (Forskål, 1775)	7,8,12,13,15,19,32
	Dardanus megistos (Herbst, 1804)	6,9(b),11,12,17,18, 19,34
	Dardanus scutellatus (H. Milne Edwards, 1848)	6,9(b),12,17,34
+	*Diogenes* sp.	9(b),19,22
+	*Paguristes* sp.	4,6,25,32
+	*Trizopagurus strigatus* (Herbst, 1804)	7,22
PAGURIDAE		
+	*Micropagurus vexatus* Haig and Ball, 1988	4,7,9(a),13,15,19,22, 23,25,26,32
+	*Nematopagurus* cf. *muricatus* (Henderson, 1896)	22
+	*Pagurixus anceps* (Forest, 1954)	1,6,12,30
*	*Pagurixus tweediei* (Forest, 1956)	
+	*Pagurixus* sp.	1,7,13,19,22,25,32
+	*Pylopaguropsis magnimanus* (Henderson, 1896)	4,7,13,25,32
+	*Pagurid* sp. *1*	1,6
+	*Pagurid* sp. 2	9(a),15,16,26,36
+	*Pagurid* sp. *3*	1,16,17,18,26
+	*Pagurid* sp. *6*	22
COENOBITIDAE		
$	*Birgus latro* (Linnaeus, 1767)	North Keeling
+	*Coenobita brevimanus* Dana, 1852	21
	Coenobita perlatus H. Milne Edwards, 1837	1,2,6,10,21
+	*Coenobita rugosus* H. Milne Edwards, 1837	2,6,10,13,21
PORCELLANIDAE		
+	*Petrolisthes asiaticus* (Leach, 1820)	6

+	*Petrolisthes carinipes* (Heller, 1861)	1
	GALATHEIDAE	
+	*Galathea* sp.	1,19,23

BRACHYURA

	Dromiacea	
	DYNOMENIDAE	
*	*Dynomene hispida* Desmarest, 1825	
+	*Dynomene* cf. *pilumnoides* Alcock, 1899	4,32
*	*Dynomene praedator* A. Milne Edwards, 1879	
+	*Dynomene* sp.	4,25,32
	Oxystomata	
	CALAPPIDAE	
	Calappa hepatica (Linnaeus, 1758)	9(b),19
	Oxyrhyncha	
	MAJIDAE	
	EPIALTINAE	
+	*Huenia grandidierii* A. Milne Edwards, 1865	20
	Menaethius monoceros (Latreille, 1825	1,20,24
	Perinia tumida Dana, 1852	1,24
+	*Simocarcinus obtusirostris* (Miers, 1879)	18
	MAJINAE	
	Cyclax suborbicularis (Stimpson, 1907)	1
+	*Schizophrys aspera* (H. Milne Edwards, 1834)	1,32
	MITHRACINAE	
+	*Micippa thalia* (Herbst, 1803)	11
	PARTHENOPIDAE	
	AETHRINAE	
	Actaeomorpha erosa Miers, 1878	20
	EUMEDONINAE	
*	*Eumedonus pentagonus* (A. Milne Edwards, 1879)	
	PARTHENOPINAE	
*	*Daldorfia horrida* (Linnaeus, 1758)	
	Cancridea	
	ATELECYCLIDAE	
*	*Kraussia integra* (De Haan, 1835)	
+	*Kraussia* cf. *nitida* Stimpson, 1858	23
*	*Kraussia rugulosa* (Krauss, 1843)	
	Brachyrhyncha	
	PORTUNIDAE	
	CATOPTRINAE	
*	*Carupa tenuipes* Dana, 1851	

PORTUNINAE

+	*Charybdis erythrodactyla* (Lamarck, 1818)	12
*	*Charybdis obtusifrons* Leene, 1936	
	Portunus granulatus (H. Milne Edwards, 1834)	1
+$	*Scylla serrata* (Forskål, 1775)	
	Thalamita admete (Herbst, 1803)	1,6,9(a),12,17,18,36
+	*Thalamita chaptali* (Audouin and Savigny, 1825)	36
	Thalamita crenata H. Milne Edwards, 1834	2
+	*Thalamita dakini* Montgomery, 1931	18,24
+	*Thalamita demani* Nobili, 1905	4
*	*Thalamita integra* Dana, 1852	
*	*Thalamita picta* Stimpson, 1858	
*	*Thalamita spinimana* Dana, 1852	
+	*Thalamitoides quadridens* A. Milne Edwards, 1869	20,25,32
	Thalamitoides tridens A. Milne Edwards, 1869	9(a),16,36

XANTHIDAE

POLYDECTINAE

	Lybia tessellata (Latreille, 1812)	27
*	*Polydectus cupulifer* (Latreille, 1812)	

CYMOINAE

	Cymo andreossyi (Audouin, 1826)	12,27
*	*Cymo quadrilobatus* Miers, 1884	

LIOMERINAE

*	*Liomera bella* (Dana, 1852)	
*	*Liomera caelata* (Odhner, 1925)	
*	*Liomera laevis* (A. Milne Edwards, 1873)	
+	*Liomera monticulosa* (A. Milne Edwards, 1873)	4
*	*Liomera pallida* (Borradaile, 1900)	
+	*Liomera rugata* (H. Milne Edwards, 1834)	6
*	*Liomera stimpsoni* (A. Milne Edwards, 1865)	
	Liomera tristis (Dana, 1852)	1,23
+	*Liomera venosa* (H. Milne Edwards, 1834)	32
+	*Liomera* sp.	25

EUXANTHINAE

*	*Euxanthus exsculptus* (Herbst, 1790)	
+	*Paramedaeus simplex* (A. Milne Edwards, 1873)	13,19

ACTAEINAE

*	*Actaeodes consobrinus* (A. Milne Edwards, 1873)	
+	*Actaeodes tomentosus* (H. Milne Edwards, 1834)	6,27
+	*Gaillardiellus orientalis* (Odhner, 1925)	12,20,27
*	*Gaillardiellus superciliaris* (Odhner, 1925)	
*	*Paractaea rufopunctata* (H. Milne Edwards, 1834)	
	Psaumis cavipes (Dana, 1852)	6,12,18
*	*Pseudoliomera granosimana* (A. Milne Edwards, 1865)	
	Pseudoliomera speciosa (Dana, 1852)	25

	ZOSIMINAE	
*	*Atergatopsis signatus* (Adams and White, 1848)	
	Lophozozymus dodone (Herbst, 1801)	1,17,34
	Lophozozymus pulchellus A. Milne Edwards, 1867	1
*	*Platypodia cristata* (A. Milne Edwards, 1865)	
*	*Platypodia granulosa* (Ruppell, 1830)	
+	*Platypodia* cf. *pseudogranulosa* Serene, 1984	4,32
*	*Zozymodes pumilus* (Jacquinot and Lucas, 1852)	
	Zosimus aeneus (Linnaeus, 1758)	1
	XANTHINAE	
*	*Lachnopodus gibsonhilli* (Tweedie, 1950)	
*	*Lachnopodus subacutus* (Stimpson, 1858)	
*	*Lachnopodus tahitensis* De Man, 1889	
+	*Leptodius exaratus* (H. Milne Edwards, 1834)	6,30
*	*Leptodius gracilis* (Dana, 1852)	
	Leptodius nudipes (Dana, 1852)	30
	Leptodius sanguineus (H. Milne Edwards, 1834)	6,10,12,27
	Lioxanthodes alcocki Calman, 1909	24
	Macromedaeus nudipes (A. Milne Edwards, 1867)	18
	Neoxanthias impressus (Lamarck, 1818)	1,11
	ETISINAE	
+	*Etisus bifrontalis* (Edmondson, 1935)	18
+	*Etisus demani* Odhner, 1925	1
	Etisus dentatus (Herbst, 1785)	1
+	*Etisus frontalis* Dana, 1852	17,18,20
*	*Etisus laevimanus* Randall, 1840	
+	*Paraetisus* sp.	13
	CHLORODIINAE	
	Chlorodiella barbata (Borradaile, 1900)	9(a),17,36
+	*Chlorodiella cytherea* (Dana, 1852)	1,27
*	*Chlorodiella laevissima* (Dana, 1852)	
+	*Phymodius granulosus* (De Man, 1888)	1
	Phymodius monticulosus (Dana, 1852)	17,36
	Phymodius ungulatus (H. Milne Edwards, 1834)	6
	Pilodius areolatus (H. Milne Edwards, 1834)	1,6,12,18,20, 23,27
*	*Pilodius pubescens* Dana, 1852	
	Pilodius scabriculus Dana, 1852	1,6,12
+	*Tweedieia odhneri* (Gordon, 1934)	6,7,22,32
TRAPEZIIDAE		
	TRAPEZIINAE	
	Tetralia glaberrima (Herbst, 1790)	16,27
*	*Trapezia areolata* Dana, 1852	
	Trapezia cymodoce (Herbst, 1799)	1,4,7,13,24,25, 27,32
*	*Trapezia digitalis* Latreille, 1825	
	Trapezia ferruginea Latreille, 1825	7,32
	Trapezia guttata Ruppell, 1830	25,36
	Trapezia rufopunctata (Herbst, 1799)	7,22

+	*Trapezia septata* Dana, 1852	7,12,22,27
	DOMECIINAE	
	Domecia hispida Eydoux and Souleyet, 1842	9(a),27
	CARPILIIDAE	
*	*Carpilius convexus* (Forskål, 1775)	
*	*Carpilius maculatus* (Linnaeus, 1758)	
	MENIPPIDAE	
	OZIINAE	
	Lydia annulipes (H. Milne Edwards, 1834)	2
*	*Ozius tuberculosus* H. Milne Edwards, 1834	
	ERIPHIINAE	
*	*Eriphia scabricula* Dana, 1852	
	Eriphia sebana (Shaw and Nodder, 1803)	6
	DACRYOPILUMNINAE	
	Dacryopilumnus rathbunae Balss, 1932	Loc. unrecorded
	PILUMNIDAE	
+	*Pilumnus minutus* (De Haan, 1835)	27
	INCERTAE SEDIS	
	Daira perlata (Herbst, 1790)	1,8,11,24,27,32
	Pseudozius caystrus (Adams and White, 1848)	6,30
	PALICIDAE	
+	*Crossotonotus brevimanus* (Ward, 1933)	19
	OCYPODIDAE	
	OCYPODINAE	
	Ocypode ceratophthalma (Pallas, 1772)	1,2,6,10, West Island
	Ocypode cordimana Desmarest, 1825	1, West Island
	Uca chlorophthalmus (H. Milne Edwards, 1837)	2
	MACROPHTHALMINAE	
	Macrophthalmus verreauxi H. Milne Edwards, 1848	2
	GRAPSIDAE	
	GRAPSINAE	
	Geograpsus crinipes (Dana, 1851)	1, 21
	Geograpsus grayi (H. Milne Edwards, 1853)	2, 21
	Grapsus intermedius De Man, 1887	2, 6, 30
	Grapsus tenuicrustatus (Herbst, 1783)	2,6,27,buoys(lagoon)
	Metopograpsus thukuhar (Owen, 1839)	2
+	*Pachygrapsus minutus* A. Milne Edwards, 1873	1,12,30
	Pachygrapsus cf. *planifrons* De Man, 1888	6,12
	Pachygrapsus plicatus (H. Milne Edwards, 1837)	12
	SESARMINAE	
+	*Cyclograpsus integer* H. Milne Edwards, 1837	2,6

	Sesarma (*Parasesarma*) *sigillata* Tweedie, 1950	2
	Sesarma (*Parasesarma*) *lenzii* De Man, 1895	2
+	*Sesarma* (*Chiromantes*) sp.	2
	PLAGUSIINAE	
	Percnon abbreviatum (Dana, 1851)	12
*	*Percnon affine* (H. Milne Edwards, 1853)	
+	*Percnon guinotae* Crosnier, 1965	1,7
	Percnon planissimum (Herbst, 1804)	12,27
	Plagusia depressa tuberculata Lamarck, 1818	Buoys (lagoon)
	VARUNINAE	
+	*Pseudograpsus albus* Stimpson, 1858	6
	Thalassograpsus harpax (Hilgendorf, 1892)	10
GECARCINIDAE		
	Cardisoma carnifex (Herbst, 1794)	2, West Island
*	*Cardisoma rotundum* (Quoy and Gaimard, 1824)	
	Gecarcoidea natalis (Pocock, 1888)	21
CRYPTOCHIRIDAE		
+	*Hapalocarcinus marsupialis* Stimpson, 1859	4

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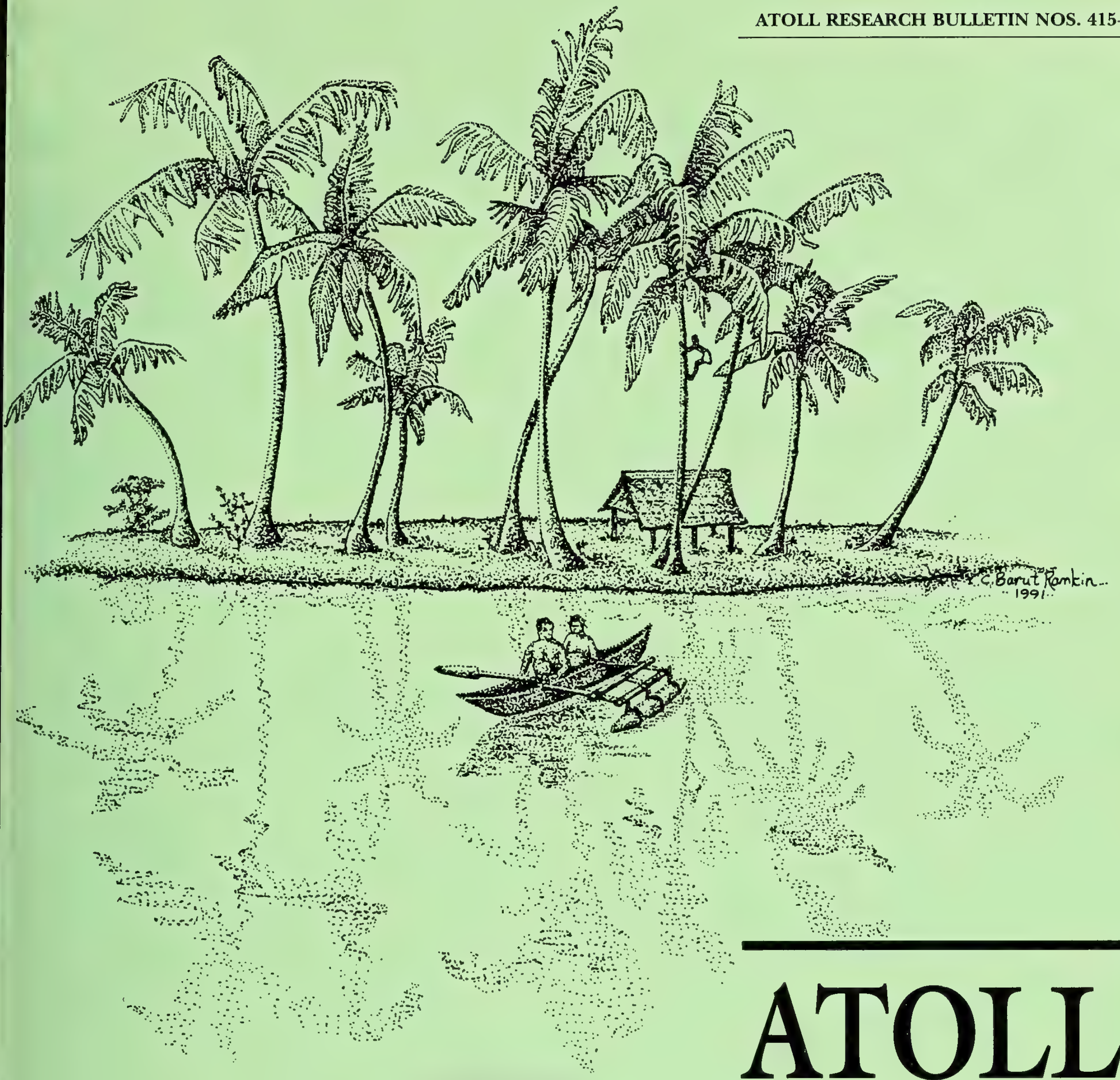

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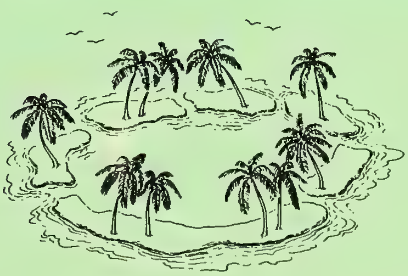

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NO. 415. TIKEHAU
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BY A. INTES AND B. CAILLART

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Articles submitted for publication in the Atoll Research Bulletin should be original papers in a format similar to that found in recent issues of the Bulletin. First drafts of manuscripts should be typewritten double spaced and can be sent to any of the editors. After the manuscript has been reviewed and accepted, the author will be provided with a page format with which to prepare a single-spaced camera-ready copy of the manuscript.

Cape of Three Points, Ghana, Gulf of Guinea
November 1990

ANDRÉ GUILCHER
(1913 - 1993)

ANDRÉ GUILCHER 1913-1993

For over 40 years, André Guilcher was an eminent coastal geomorphologist and marine geographer. He was born in Brest, France, received his PhD from the Sorbonne in 1948, taught in several French universities and retired from the Universitiy of Brest, with which he was affililiated, in 1981. He served on many national and international editorial boards and scientific committees, received numerous awards and honors and had been proposed for the last Darwin Award.

He started work on coral reefs in the early 1950s, taking part in the first *Calypso* expedition in the Red Sea. The discovery of reefs was one of immense excitement for Guilcher, and permanently marked his future research work. Subsequent field expeditions took him to Madagascar, Mayotte, New Caledonia, French Polynesia, the Solomon Islands, Kiribati, Vanuatu, Lord Howe Island, Florida, Sinai, the West Indies, Brazil, Kenya and elseware. The results of his work were published in over fifty books and articles. One of his later works was *Coral Reef Geomorphology* (Wiley, 1988), the first global synthesis of the morphology and typology of reefs, and a thorough review of the evolution of modern regional variations in reef structure and development. This book was also significant in introducing into the international literature important examples of reef geomorphology found in areas that are seldom visited by English-speaking workers.

Guilcher assisted and influenced many people in the course of his long academic career and was a model for many of his students. His scientific and leadership skills and his integrity earned the respect of all his colleagues. These and his many friends will greatly miss him.

Paolo A. Pirazzoli

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FOREWORD

In 1982, ORSTOM, a french institution for the development of cooperation in scientific research (Institut Francais de Recherche Scientifique pour le Développement en Coopération) launched the program "ATOLL" in French Polynesia under the dynamic leadership of André INTES, who built up the program while going on with his own research on pearl oyster.

The launch of this program took place in a historical context of scientific research and of institutional specialisms. Research on coral ecosystem in French Polynesia had started to develop at the end of the nineteen-sixties and the beginning of the seventies (Research on the atolls of the south-east of Tuamotu was carried out in liaison with the Direction des Centres d'Expérimentations Nucléaires and the implementation on Moorea in the Society Islands, of the antenne Museum EPHE Research Center). In 1974, research started under the auspices of the MAB program (Man and Biosphere) of UNESCO, an interdisciplinary program for ecology and the rational use of insular ecosystems. The objectives of that program were, even at that time (20 years ago), to specify the exact, natural and social sciences, which were the necessary basis for the rational use and conservation of island ecosystems. The two islands of Moorea and Takapoto were selected. A large number of natural, social and medical research organisations from both mainland France and the French Territories participated in the work. A great many reports (1, 2, 3, 4) were produced on these two ecosystems whose coral reefs are among the most studied and documented in the world.

With the program "ATOLL", ORSTOM started in 1982 its study of the Polynesian coral reef ecosystem. The choice of Takapoto Atoll was made by the legislature of the Territory in 1973 when the pearl industry was developing, and at the request of scientists. For scientific reasons the latter had asked for the selection of a closed atoll which had no pass : there is less complexity in studying such a lagoon thus giving the best approach to the scientific work. The choice of Tikehau by ORSTOM for the siting of a field station and the development of programs was due to the fact that it was necessary to select an open atoll with a pass to go further in the study of (1) a small scale fishery and (2) the assessment of the exchanges between the lagoon and the ocean. It is in this context that research was developed on Tikehau between 1982 and 1987, research by scientists from ORSTOM and by other organisations working in collaboration with them, and research which has proved to be very beneficial. This station is still in existence with an on-going program, "CYEL" (Energy and Matter Cycles in Atoll Lagoons) having followed on from "ATOLL".

In a document edited by ORSTOM, André INTES and his collaborators (5) have already described in minute detail their activities on Tikehau during this five years period. It has now become necessary to condense this information into synopses which are to be published in English. Such is the objective of the three aticles which follow. The first (by A. INTES and B. CAILLART) describes the nature and human environment of the atoll, detailing its characteristics. This contribution is well suitable for publication in Atoll Research Bulletin, now the most important reference for useful descriptions of atolls all over the world. The second article by C.J. CHARPY-ROUBAUD and L. CHARPY deals with matter and energy budgets for Tikehau's coral reefs. This subject is very topical: what about nutrient enrichment for coral reef lagoons and atolls? what about autotrophy and eutrophication due to human activity? The third one by B. CAILLART, M.L. HARMELIN-VIVIEN, R. GALZIN and E. MORIZE presents all the available information on the fish fauna of the atoll lagoon and outer slope, including the communities and yields. Such an account is necessary when looking at the managment of fishing, recruitment, and the movement, or not, of populations between islands.

Bernard SALVAT

Moorea and Perpignan, march 1993.

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All the work done on the field would not have been possible without the kind hospitality and active cooperation of the population of TIKEHAU. It is a great pleasure for the editors to dedicate this volume to the people of this atoll.

Many scientists from different institutions contributed to the program "ATOLL" in a friendly collaboration. They came mainly from Centre National de la Recherche Scientifique (CNRS), Ecole Pratique des Hautes Etudes (EPHE), Museum National d'Histoire Naturelle de Paris (MNHN), Institut Francais de Recherche pour l'Exploitation de la Mer (IFREMER), Service Mixte de Contrôle Biologique (SMCB), but also from the ORSTOM center of Nouméa (New Caledonia). Most of them became our friends.

The preparation of the report involved few people who gave unrestricted thought and time to bring this collective work into publication.

We wish to extend our thanks to all of them, listed below, regardless of the nature of their contribution. Some of them may have been overlooked, and we apologize for these unfortunate oversights.

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Eric MORIZE

PART I. ENVIRONMENT AND BIOTA OF THE TIKEHAU ATOLL (TUAMOTU ARCHIPELAGO, FRENCH POLYNESIA)

BY

A. INTES AND B. CAILLART

THE REGIONAL BACKGROUND

The islands of French Polynesia are scattered throughout a considerable oceanic area located on the eastern boundary of the Indo-Pacific Province. This area stretches from 134°28' W (*Temoe* Island) to 154°40' W longitude (*Scilly* Island), and from 7°50' S (*Motu one* Island) to 27°36' S latitude (*Rapa* Island). Out of the 118 islands constituting French Polynesia, 35 are high volcanic islands and 83 are low-relief islands or atolls. Altogether, the territory of French Polynesia represents an area of 4000 km^2 of dry land, 12,000 km^2 of lagoonal water and a huge Exclusive Economic Zone (EEZ) covering 5,500,000 km^2 of oceanic water (Gabrie and Salvat, 1985).

French Polynesia is divided into five archipelagos all oriented parallel to a northwest-southeast axis (Fig. 1). These are the **Society archipelago**, the **Tuamotu archipelago**, the **Austral archipelago**, the **Marquesas archipelago** and the **Gambier archipelago**.

The **Tuamotu archipelago** stretches over a distance of 1800 km. Its 76 atolls cover a total area of 13,500 km^2 of which 600 km^2 are dry land.

GEOLOGY OF THE TUAMOTU ARCHIPELAGO

As figured by Montaggioni (1985), the Tuamotu atolls cap the top of cone-like volcanoes which rise steeply from the floor of a huge ridge forming wide shelves ranging in depth from 1,500 to 3,000 m. Geomorphological and geochronological evidences support the fact that the formation of the Tuamotu chain is much older than that of other neighboring islands of French Polynesia. The foundations of extinct volcanoes appear to have been simultaneously, and not sequentially, active for at least the Northwestern Tuamotu chain. The existence of a massive submerged ridge and the lack of high volcanic islands are in accordance with average ages found out by the Deep Sea Drilling Project (summarized by Clague, 1981 and Schlanger, 1981) : reef debris of the early to late Eocene (50-51 mybp) have been sampled in two holes drilled on the northeastern flank of the Tuamotu archipelago and on the ridge itself. The occurrence of these fossils leads to the conclusion that vulcanism would have stopped between late Cretaceous and early Eocene for at least the northwestern part of the Tuamotu chain. The large number and the close-spacing pattern of the Tuamotu atolls are indicative of their origin in shallow waters close to the East Pacific ridge.

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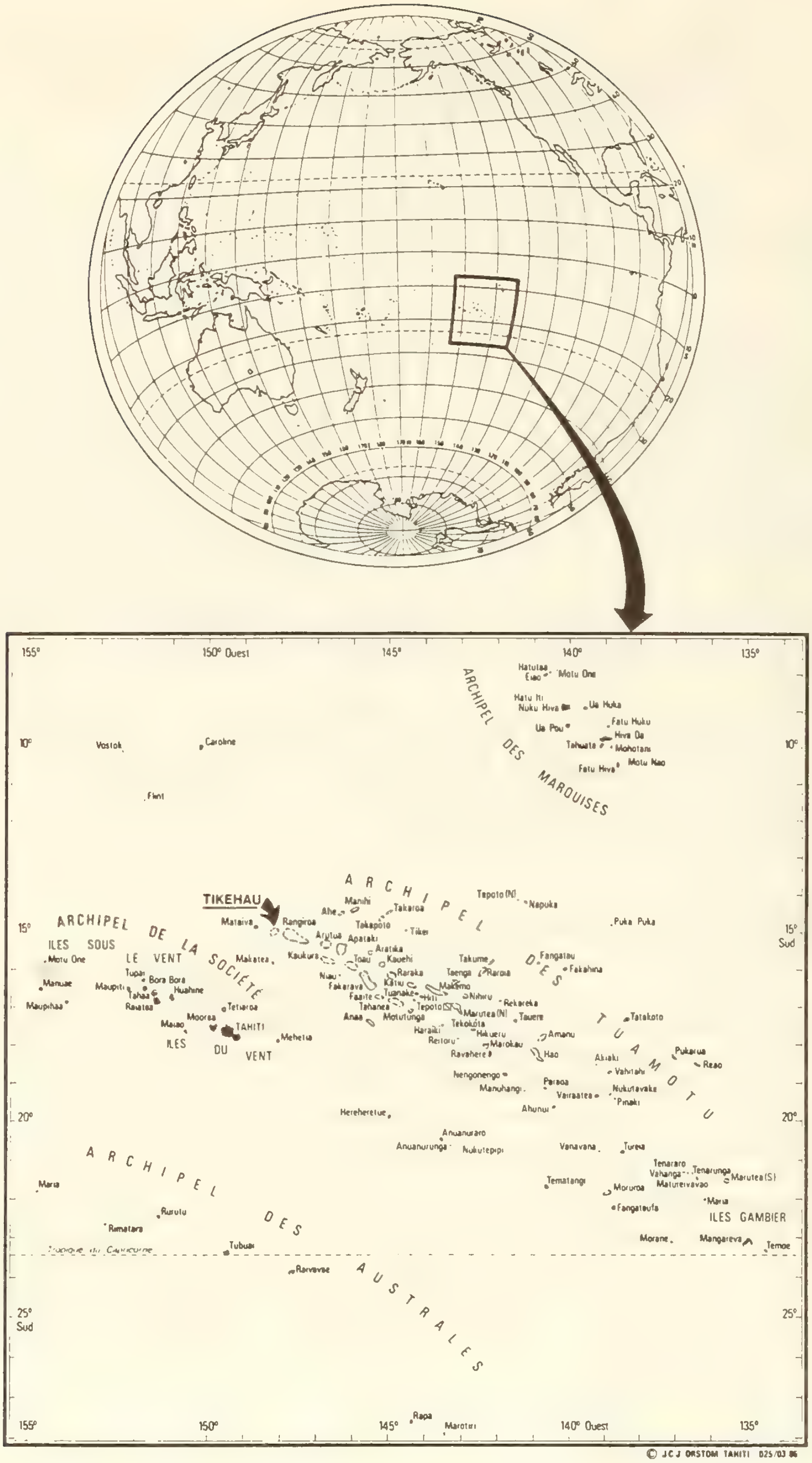

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Fig. 1 : Map of French Polynesia and location of the Tikehau atoll, Tuamotu.

In the northwestern Tuamotu, several atolls (including Tikehau), located in the vicinity of recently active volcanoes (Tahiti, Moorea, Mehetia), have been lifted up. Lambeck (1981) pointed out that the tectonic uplift of these atolls was a result of the loading effects of the nearby Tahiti volcanic complex. The magnitude of uplift was a few ten meters with respect to present sea level, without considering the unusual case of Makatea which, located near the center of the load, has its highest point 133 m above present sea-level. Since age dating of the oldest volcano (Moorea) is around 1.5 mybp, the tectonic uplift of atolls is thought to have been initiated in early Pleistocene.

At Tikehau, the magnitude of uplift can be related to the present day elevation of the numerous old reef remnants (locally termed *Feo*) that stand on the atoll rim (Plate 1). *Feo* are highly recrystallized and dolomitized old reef remnants, that witness a long period of subaerial weathering. Although there is insufficient evidence to accurately date the *Feo*, a comparison with analogous structures on Makatea confirms their emergence in the early Pleistocene (Pirazzoli and Montaggioni, 1985). On the southern shores of Tikehau, *Feo* can be as high as 12 m above present sea-level. Many other lower *Feo* are located on the eastern and western reef flats.

Studies from Holocene fluctuations in sea level can be useful in interpreting individual reef histories. In Tikehau as well as in most of the islands of French Polynesia, cemented coral reef conglomerates, often found around islands and alongshore shallow channels, and notches, undercutting *Feo* near their bases are evidences to support a higher-than-present relative sea level between 5200 and 1200 ybp. This higher sea level may have been 0.9 m greater than the present sea level. In this region, the lowering of the sea level near to its present datum is thought to be a very recent phenomenon which has occurred not earlier than around 1200 ybp.

GENERAL OCEANOGRAPHY OF THE TUAMOTU ARCHIPELAGO

Current and oceanic water characteristics

Tikehau, as all the northwestern parts of the Tuamotu archipelago, resides in the South Equatorial Current. The current has a general westward drift between 40 to 50 cm s^{-1} down to 200 m depth, steady throughout the year. The southern boundary of the current moves northward during the southern hemisphere summer and shifts back toward the south in winter. Currents near the atolls may vary in both speed and direction due to the dynamic topography and rather permanent eddies probably exist, though their occurrence has never been demonstrated in French Polynesia.

In the south of the northwestern part of the Tuamotu archipelago, variations in the current directions are considerable and may influence to some extent oceanographic patterns around Tikehau. Rougerie and Chabanne (1983) pointed out that during the summer, the current in the vicinity of Tahiti may be an extension of the South Equatorial Countercurrent which originates in the Solomon Sea and has a general eastward-southeastward drift. The salinity is low (34.8 ‰) reflecting the annual net rainfall in the South Pacific Convergence Zone (SPCZ) which occurs along a Solomon-Samoa-Tahiti line at this time of year. During winter, the SPCZ shifts northward and the trade winds strengthen somewhat over the Tahiti region. The current flows westward carrying high salinity water (36.4 ‰) drawn from the Central Pacific barren zone where evaporation exceeds precipitation by 50 cm per year (Rougerie, 1981).

Surface water temperature varies seasonally in a spread of 25.5°C to 29°C and reaches an average value of 28°C. The main thermocline is weak and is located between 400 and 600 m in depth with a temperature of 10°C at 400 m. By 1000 m, the temperature drops to 3°C.

Chemical data for ocean water (summarized in Table 1) show that the ocean surrounding the Tuamotu archipelago is nutrient-poor and is actually one of the poorest oceans in the world. For example, the average copepod surface population living in that oligotrophic environment is of 20 individuals m^{-3} near the surface while it is between 50 and 80 between New-Caledonia and Tonga, greater than 100 in the south of the Coral Sea, reaches 300 at the equator and exceeds 1000 to the south of Galapagos Islands.

Table 1 : Average chemical data for ocean water (0 to 100 m in depth) in the Tahiti zone. (DOM : Dissolved Organic Matter, chl a : Chlorophylle a, PProd : Primary Production, * : data measured during winter of southern hemisphere, ** : data measured in summer). Adapted from Rougerie and Wauthy (1985).

	Temp	Sal	PO4P	NO3N	SiO3	DOM	chl *a*	PProd
	(°C)	(‰)	(mmoles m^{-3})				mg m^{-3}	gCm^{-2}g^{-1}
Ocean	25.5* 29.0**	36.4* 34.8**	0.25	0.10	1.0	0.5	0.1	30

Waves and Tides

Waves in the Tuamotu archipelago are mostly from the east, a consequence of persistent trade winds. Waves are generally between 1 and 3 m high, breaking at a 6 to 9 s period. Swells from distant storms can reach the Tuamotu and create a different situation in which shores exposed to the swell (which can be either windward or leeward) are heavily pummeled, whereas the waves produced by the wind in the immediate area may be small. Northern hemisphere storms that occur in the Alaskan gulf during summer of the southern hemisphere generate waves from north-northwest which are generally about 4 m high and break at a period between 10 and 18 s on Polynesian shores. In winter, southern hemisphere storms generated in the lower southern latitudes may send associated waves to the Tuamotu zone. These 7 to 10 s period waves can exceed 3 m high and reach the southeast shores of the islands. Several cyclones and near-cyclones have passed by or over the Northwestern Tuamotu in 1982 and 1983. These storms have produced waves greater than 10 m high from various directions related to the storm track.

The tides at Tikehau are usually in good agreement with the French Navy (SHOM)* tide table established for Tahiti. However, ocean tide records at Tikehau show differences in timing. The time-lag between the tide at Tikehau and the tide at Tahiti is approximately 72 hours. The amplitude of spring tides is only 15 cm in the vicinity of Tikehau whilst neap tide amplitude is almost zero. Spring tides occur three days before the new moon and the full moon.

WEATHER AND CLIMATE

The Tuamotu archipelago lies in the tropical oceanic climate area. It has a distinct wet-dry annual cycle. The wet and hot season occurs from November through April and the dry and cold season from May to October. Since all of the islands are low and of a small area, they do not alter weather conditions by their presence. Data presented hereafter were provided by the National Meteorological Station of Rangiroa, except when otherwise mentioned as no weather records are available at Tikehau. Weather conditions have been recorded continuously from 1972 onward by this station.

Air Temperature

Average air temperature on a monthly basis for the 1972-1985 period ranges from 25.5 °C in August to 27.5 °C in March. There is little variation in these quantities through the year. Extreme temperatures have been recorded but provide little additional information since they rarely occur. The absolute minimum value recorded was 18 °C and the maximum 32 °C.

Wind

A summary of surface wind data is shown in Fig. 2. Tikehau is within the trade wind belt with a nearly consistent easterly wind. During much of the year, the wind blows from northeast to southeast 70 % or more of the time (*i.e.* 250 days/year). From June to September average wind speed increases slightly but rarely exceeds 6 of the Beaufort scale.

The occurrence of wind from west around to north is very low. The maximum frequency is in November, December and January when the South Pacific Convergence Zone is closest on the average and subsequently, disturbances most common.

Tropical storms and cyclones strike Tikehau infrequently, mostly during the wet season. An average of four cyclones per century is likely to occur in this area.

Precipitation, evaporation

The rainfall distribution throughout the year is shown in Fig. 3. The annual average rainfall of 1780 mm is not distributed uniformly throughout the year as about 65 % comes during the wet season. The maximum monthly average value is 229 mm in January and the minimum 75 mm in August. The variability of rainfall is high from year to year and data presented should be considered only as a general trend.

Evaporation reaches an average of 1800 mm a year and balances precipitation, as measured by the National Meteorological Station of Mururoa. Maximum evaporation takes place in December, January and February (179 mm, 193 mm and 188 mm), minimum values in June, July and August (109 mm, 109 mm and 124 mm).

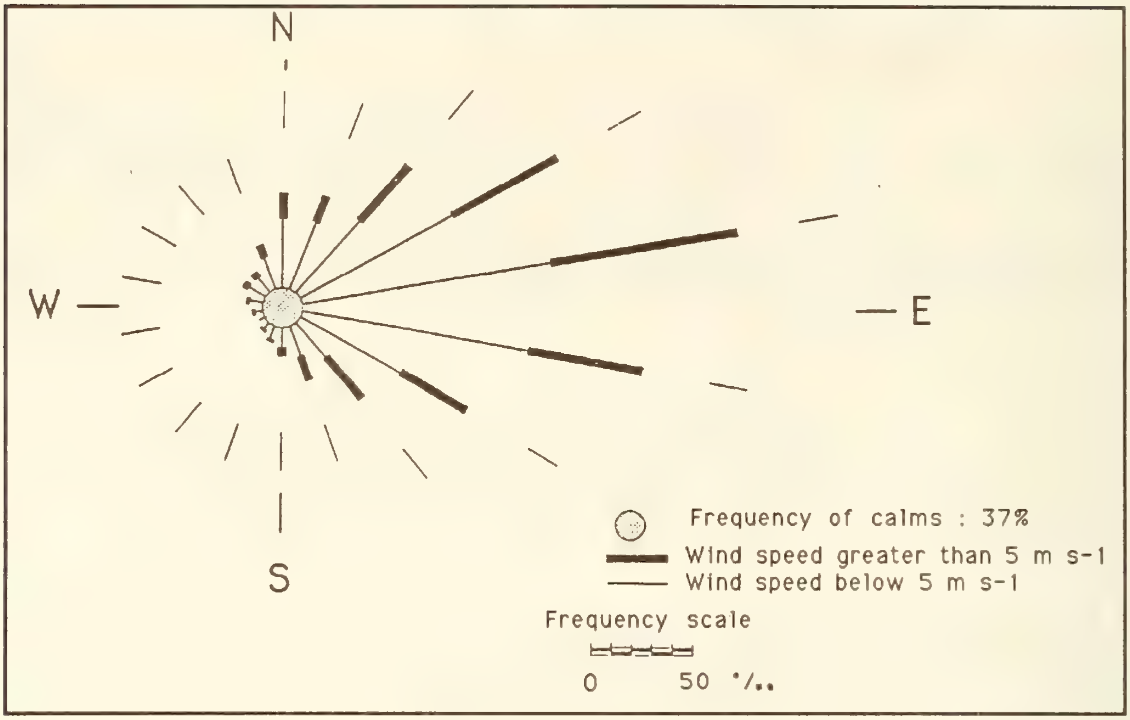

Fig. 2 : The yearly mean of surface wind data recorded at Rangiroa (Rangiroa is located 30 km to the east of Tikehau). Data provided by Meteorologie Nationale, Tahiti-Faaa.

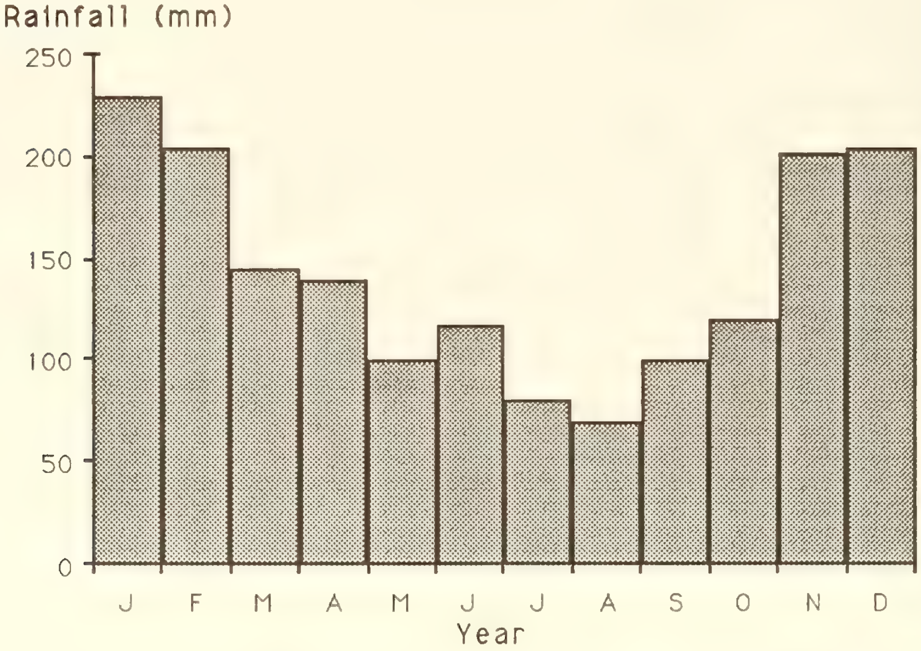

Fig. 3 : Average rainfall amounts for each month recorded at Rangiroa (Rangiroa is located 30 km to the east of Tikehau). Data provided by National Meteorological station of Tahiti-Faaa.

LOCATION AND SIZE OF TIKEHAU ATOLL

Atolls can be described as more or less continuous coral reefs (corals or other calcium carbonate producing organisms) which surround a deeper lagoon and drop steeply to oceanic depth on the seaward margin. All islands are typically low with soil derived primarily from reef rubble and sand.

Although almost identical in their general shape, atolls of the Tuamotu archipelago are different by the characteristics of their lagoon and the number of passes on which depends the amount of water circulation. As shown in Table 2, a few atolls have one or two passes and are termed **open atolls**, most have no pass and are termed **closed atolls**, four atolls have a dry lagoon, filled up by reef detritic and are termed **filled atolls**, one island, Makatea, has been uplifted by tectonic movements probably linked with the formation of Tahiti and is termed a **raised atoll**. Lastly, Portland is a **submerged atoll** .

Table 2 : Classification of the atolls of the Tuamotu archipelago based on the geomorphological characteristics of their lagoon.

Atoll group	Example
Open atolls with more than one pass	**Rangiroa** **Fakarava** **Toau**
Open atolls with one pass	**Tikehau** **Mataiva** **Arutua**
Closed atolls	**Takapoto** **Hikueru** **Reao**
Filled atolls	**Akiaki** **Nukutavake** **Tikei**
Raised atoll	**Makatea**
Submerged atoll	**Portland**

Tikehau has a large somewhat elliptically shaped lagoon, numerous shallow channels cutting the reef flat especially on the windward side, one pass between the lagoon and ocean, and narrow shelves dropping steeply into deep sea on all sides. A succession of small islands, locally termed *Motu*, constitute the dry land.

Tikehau is located in the northwestern Tuamotu archipelago with its center at 15°00'S and 148°10'W (Fig. 1). It is approximately 300 km from Tahiti to the south, 30 km from Rangiroa to the east and 20 km from Mataiva to the west. By French Polynesia standards, Tikehau is a relatively large elliptical atoll, about 20 km by 28 km in size, covering a total area of about 420 km^2 . Among the 76 islands of the Tuamotu archipelago, Tikehau is the 11th largest. It is exceeded, among others, by Rangiroa (1640 km^2), Fakarava (1220 km^2) or Makemo (910 km^2), the three largest islands. Small atolls are generally a pattern of the Tuamotu since 45 out of the 77 islands cover less than 100 km^2 (Mataiva : 50 km^2 , Taiaro : 14 km^2 , Tikei : 4 km^2).

THE TERRESTRIAL ENVIRONMENT

Since few scientists conducted research in the terrestrial environment with respect to the marine environment of the Tikehau atoll, little is known about this part of the ecosystem. This section contains a review of what is known about atoll soils and associated vegetation, reports on the terrestrial fauna (birds and other vertebrates), and finally provides an overview of Tikehau human population evolution over the last century. Information is drawn from Jamet (1985) for soils, Florence (1985) for vegetation, Poulsen *et al.* (1985) for avifauna, and Sodter (1985) for human demography.

SOILS AND VEGETATION

Tikehau soils exclusively originate from the alteration of a mother rock made up of reef forming or reef living organisms. The micro-splitting of particles mostly through chemical processes leads to the formation of clay or carbonated silt in which the percentage can reach 40 % in sandy soils. Carbonates accumulate above the upper zone of the groundwater lens forming a calcareous crust. Organic matter is usually mixed with fine materials in a topsoil horizon fairly thick but it can also accumulate superficially in marshy depressions. Following these alteration processes, Tikehau atoll soils fall into four types :

- Rough mineral soils formed of accumulations of unaltered recent sediment.
- Weakly developed soils made up of coarse materials with low content of organic matter, found mostly on the oceanic shoreline of the island.
- Magnesium-calcite soils with a dark, developed A horizon more or less thick and with variable organic matter content. This kind of soils covers the majority of the islands at Tikehau.
- Marsh soils very rich in organic matter, located in island floor depressions (Plate 2).

Unlike high island soils, atoll soils almost lack silica, aluminium and iron. The mineralogy is almost exclusively calcium carbonate (80 to 95% of calcite and aragonite) which fine soluble particles represent 3 to 5 % in rough soils, more than 20 % in humus horizon, and exceed 30 % in marshes. Magnesium carbonate represents less than 1 %. Potassium and phosphorus content are generally less than 0.05 % in subsoils but fecal matter of birds and vegetation remains locally contribute to a ten fold increase in K and P concentrations of topsoils. Sodium concentration is lower (0.5 %) than expected in this kind of ecosystem.

The fertility of atoll soils is almost entirely dependant on the content of organic matter. Accounting for less than 2 or 3 % in rough soils, organic matter can reach 15 % in humus horizons and much more in marshy areas. Organic matter not only carries out the normal role of soil organic matter in storing and recycling nutrients, but it is also the major moisture storage component in the soils, since coral sands and rocks have an extremely limited moisture storage capacity. This is all important in atolls where evaporation exceeds precipitation eight months of the year. Organic matter lowers pH which ranges between 8 and 9 in subsoils. The pH is almost neutral in topsoils, leading to a better nutrient assimilation.

Atoll soils have considerable influence on the composition of vegetation. There is a marked gradient from the beach toward the center of the island.

- Unaltered rough sediment soils are constantly rearranged and do not enable settlement of durable vegetation.

- Weakly developed soils constituted by coarse materials oceanward and fine sands lagoonward have a low organic matter content in the first 10 or 20 cm, forming patches or stretches. Two types of vegetation settled there :

Vegetation of the oceanic side of the island is a low and open assemblage of *Guettarda speciosa, Scaevola sericea* and *Tournefortia argentea.* Behind the beach, the assemblage gets richer with *Euphorbia atoto, Timonius polygamus* and *Pandanus tectorius.* On cemented coral substrata, *Pemphis acidula* forms bushes and on sand patches, *Suriana maritima* and *Lepturus repens* develop.

Vegetation of the lagoon side of the island is still well represented eastward the atoll whereas it was cleared by coconut plantations in other places. Bush assemblage is dominated by *Suriana maritima* and *Scaevola sericea,* but *Guettarda speciosa* and *Tournefortia argentea* occur sporadically. The herbaceous stratum is varied with *Triumfetta procumbens* and *Lepturus repens* dominating.

Magnesium calcite soils (found in the center of the island) cover the area of the forest. Although coconut plantation cleared much of the original vegetation, two facies can be distinguished :

- On weakly developed soils, *Pandanus tectorius* dominates the tree stratum along with *Tournefortia* and *Guettarda.* Among the bush, *Scaevola sericea, Pipturus argenteus* and *Timonius polygamus* were recorded. Herbaceous vegetation is rare : *Psilotum nudum, Cassytha filiformis* and *Nesogenes euphrasioides* were recorded nonetheless.

- On sandy soils, the original forest of *Pisonia grandis* has almost disappeared whereas *Guettardia speciosa* still occurs. Bushes are made up of *Pipturus argenteus, Morindia citrifolia* or *Euphorbia atoto.* The herbaceous stratum is varied with *Achyranthes velutina, Laportea ruderalis, Digitaria stenotaphrodes, Boerhavia tetrandra.*

Coconut plantations

Sand and gravel soils which are the most favourable for coconut agriculture have been planted mostly during the last century. The western coast has coarse substratum only allowing coconut trees to be planted on the lagoon side of the islands. From place to place, components of the original vegetation are encountered such as *Guettarda speciosa, Pisonia grandis* or *Pandanus tectorius* for trees, *Euphorbia atoto* or *Morinda citrifolia* for the bush, *Lepturus repens, Boerhavia tetrandra* and *Triumfetta procumbens* on the ground.

Feo vegetation

Feo are located north of the island supporting the main village and surrounded by coconut plantations. Being as high as 7 meters, they present a compact substratum with a low moisture storage capacity, and tiny soils in small caves. Tree stratum is composed of *Pandanus tectorius* and *Thespesia populnea.* Bush is made up of *Pipturus argenteus, Euphorbia atoto* and rarely *Capparis cordifolia.* On the ground, *Lepturus repens* and *Triumfetta procumbens* were recorded but also ferns such as *Asplenium nidus, Nephrolepis biserrata* or *Phymatosorus grossus.*

In a hydromorphic depression, vegetation is a Cyperaceous assemblage. *Cladium jamaicense* is so overwhelmingly dominating that the assemblage is almost monospecific, reaching 3 m high. On the edges of the marsh, *Mariscus pennatus* and *Eleocharis geniculata* are found.

THE TERRESTRIAL FAUNA

Avifauna

Sedentary terrestrial species widespread in all atolls are Tuamotu warbler *(Acrocephalus atypha)* of which 150 pairs were counted at Tikehau, at least 10 pairs of green pigeon *(Ptilinotus coralensis)*, between 150 and 200 individuals of pacific reef heron *(Egretta sacra)*. Tuamotu loriket *(Vini peruviana)* resides in a few atolls of western Tuamotu and breeds on Tikehau on western islands. About 20 pairs were counted. Sooty crake *(Porzana tabuensis)* was observed in the marshy area of the island supporting the village. New Zealand cuckoo *(Eudynamis taitensis)* is the only migrant species exclusively terrestrial sighted in autumn (May).

Shorebirds : especially present in winter of southern hemisphere, the most readily observable species are lesser golden-plover *(Pluvialis dominica)*, bristle-thighed curlew *(Numenius tahitiensis)*, wandering tattler *(Heteroscelus incanus)*. Less abundant though regular visitors of Tikehau, ruddy turnstone *(Arenaria interpres)*, sanderling *(Calidris alba)* and pectoral sandpiper *Calidris melanotos* account.

Seabirds : Red-footed booby *(Sula sula)* forms some small nesting colonies in trees *(Pisonia grandis)*. Brown booby *(Sula leucogaster)* and frigatebirds (*Fregata ariel* and great frigatebird *Fregata minor)* regularly occur but no breeding evidences were recorded. Terns are well represented with gray-backed tern *(Sterna lunata)* of which a 20 pairs nesting colony was sighted, sooty tern *(Sterna fuscata)* which seems only vagrant, great crested tern *(Sterna bergii)* of which about 50 pairs nest on the atoll, blue tern *(Procelsterna coerulea)* of which a few pairs are supposed to nest at Tikehau, the very common brown noddy *(Anous stolidus)* of which 1500 nests were censused in small trees (*Pemphis, Tournefortia)*, 800 nests of black noddy (*Anous tenuirostris*) in trees (*Pisonia, Guettarda)*, and lastly a nesting population of 3000 individuals of white tern *(Gygis alba)*.

Other seabirds as petrel *(Pterodroma rostrata)* and skua *(Stercorarius pomarinus)* sometimes approach Tikehau.

Other vertebrates

Except marine green turtle *(Chelonia mydas)*, reptiles reported to occur at Tikehau are lizards azure-tailed skink (*Lygosoma cyanurum*) which occurs in sunny forest floor, and house gecko (*Hemidactylus frenatus*). Among mammals, rodents are best represented with polynesian rat (*Rattus exulans*) and Norway rat (*Rattus norvegicus*). Some domestic cats returned to the wild were seen wandering in coconut plantations and marshes.

PEOPLE OF TIKEHAU, PAST AND PRESENT

Tikehau could have been one of the atolls discovered by Turnbull in February 1803 when he was sailing from Tahiti to Hawaii, but neither positions nor name were given. In 1816, Otto von Kotzebue, Russian master of the "Rurick" first identified the atoll of Tikehau and gave it the name of one of his shipmates : "Krusenstern". In May 1848, the atoll was once again described by a trader, Lucett. Given the poor knowledge of the danger of the island, none of those first discoverers attempted to land and as a result, nothing is known about the population during this period. However, archeological remains of the past (*marae*) attest that Tikehau was inhabited at the time of the Christ. In all probability, age dating of the sites would push the date for settlement of Tikehau further back in time.

The first information on the total number of inhabitants was given in 1862. Ten persons were counted but this total is probably unrealistic because the census method did not take into account the frequent seasonal movements of the population around the island.

In 1902, an official census made by French Authorities gives a total of 156 inhabitants for both Tikehau and Mataiva. The following census in 1911 gives a total of 95 inhabitants on Tikehau and 58 on Mataiva. Until the end of World War II, no information on Tikehau and Mataiva population is available. In 1946, 376 persons had been registered on both Mataiva and Tikehau.

From 1950 to 1983

From 1950 on, census at regular intervals allow to follow population variations. Census reliability depends however on how the important mobility of the population is taken into account. Census methods sometime tend to overestimate the population by counting a single person twice (in 1956 for instance).

As illustrated by information displayed in Table 3, the level of the population of Tikehau in 1983 is slightly the same as in 1951 though the total population of French Polynesia doubled meanwhile. Trends in population variation are difficult to analyse without precise individual information on place of birth and location of main home.

Table 3 : Variations of Tikehau, Mataiva, both Tikehau and Mataiva, and French Polynesia populations between 1946 and 1983. All census were made by French Authorities. Results of 1956 census are to be interpreted very cautiously since census method tends to over-estimate the actual population by counting some single person twice.

	1946	1951	1956	1962	1967	1971	1977	1983
Tikehau	- -	259	349	275	287	246	266	279
Mataiva	- -	126	241	162	138	147	178	183
Both	376	385	590	437	425	393	444	462
French Polynesia	55,424	62,678	76,327	84,551	98,378	119,168	137,382	166,753

The Population in 1983

A typical feature of the population of Tikehau , like of the population of French Polynesia, is the high proportion of young people : 28.7 % of the population is less than 10 years old and 52.7 % less than 20. The worker age class is very low, especially between 30 and 39 which represents only 5 % of the population.

The high migratory rate of the population, the main source of difficulties to accurately measure the population, is confirmed by the proportion of Tikehau inhabitants (21 %) having spent more than six months in a row in another district of French Polynesia. For 91 % of the people having moved, the island of Tahiti is the main destination, and 70 % of the 91 % go to Papeete.

The working population is composed by 90 persons, 76 men and 14 women. Among the 76 men, 50 put up with copra production, 14 are fishermen, 9 are artisans, 2 are employed by the government and 1 is administrative officer. Among women, 8 are administrative officers, 3 are shopkeepers and 3 are artisans ; 3 men and 33 women have declared to be looking for a job.

Conclusion

The main characteristics of Tikehau population are :

- High proportions of young people under 20 years old and, as a consequence, low proportions of people in the worker age class.
- High migratory rate.
- Men professional activities primarily oriented toward agriculture, especially copra production. Women professional activity is low but high employment request exists.

THE MARINE ENVIRONMENT

PHYSIOGRAPHY OF THE MARINE AREA

Definition of reef units

In order to classify reef units of the atoll, Faure and Laboute (1984) described three main types of reef units as follows :

- **Compartments** defined on a physiographic basis
- **Zones** assessed on a morphological basis
- Zones divided into **biota** according to bionomic field data

The three compartments are the **outer slope**, the **reef flat**, and the **lagoon formations**. A fourth virtual compartment termed **morphological discontinuities** grouping pass and shallow channels is also studied. Fig. 4 lists the different units classically found around an atoll.

BIOTA		ZONES		COMPARTMENTS
Lower part	>60-70 m	Deep slope	25-75 m	OUTER SLOPE
Middle part	35-60 m			
Upper part	25-35 m			
Lower part	15-25 m	outer terrace	10-25 m	
Upper part	0-15 m			
Fore reef platform	4-10 m	Fore reef area	0-10 m	
Spur and groove zone	0-4 m			
Algal ridge		outer reef flat		REEF FLAT
Submerged reef flat				
Inner flat		inner reef flat		
Inner slope		inner slope		LAGOON STRUCTURES
Down slope reef patches				
Coral patches		Low depth coral patches		
Upper zone	0-2 m	Pinnacles		
Middle zone	2- 6 m			
Lower zone	6-15 m			
Pass		Pass and Hoa		MORPHOLOGICAL DISCONTINUITIES
Gutter (or Hoa)				

Fig. 4 : Inventory and repartition of the different atoll units (from Faure and Laboute, 1984).

The outer slope

The outer slope is the seaward part of an atoll which drops more or less steeply to oceanic depth. In Tikehau, the outer slope is divided into three zones :

- The **fore reef area** located between 0 and 10 m depth. This zone itself is subdivided into the **spur and groove** zone (0-4 m) and the **fore reef platform** (4-10 m). The spur and groove system is a succession of reef fingers projecting seaward where the waves break, oriented perpendicular to the reef front. Spurs are relatively flat on top. Their width ranges from 8 to 12 m with a low slope gradient of 2 to 4°. Grooves are shallow (1 to 3 m) and relatively narrow (2 to 3 m). The walls of the grooves are sub-vertical and their bases are floored with cobbles and dead coral boulders, precluding the development of any significant sessile benthic life (Plate 4). Just seaward of the spur and groove, the bottom flattens somewhat with the fore reef platform.

- The **outer terrace** begins at a depth of 10 m with a distinct change from a gentle slope of a few degrees to an angle of approximatively 45 °. It presents an irregular surface with small periodic shallow grooves oriented parallel to the slope direction, well distinguished from the spur and groove formations described above. This structure could be considered as an old spur and groove system (Chevalier, 1973).

- The **deep slope** (or drop off) begins below 25 m at an angle often greater than 45°. According to coral community distribution, the slope can be separated into three biota : the upper part (25-35 m), the middle (35-65 m) and the lower part from 70 m downwards.

The reef flat

The **outer reef flat** begins seaward by the **algal ridge** and ends lagoonward by the emerged conglomerate or the island. On leeward reef, the algal ridge is low (20 cm above low tide level) and has a width of 10 m while on windward shelves, the algal ridge is larger (30-40 m) and higher (40 cm above low tide level). Numerous deep grooves (1-3 m) extend across the windward algal ridge. Just inshore of this formation, a slight depression of the reef flat can occur, especially on the windward sides of the atoll. To this follows an emerged hardened conglomerate which can be considered as the remains of a past algal ridge. As shown in Fig. 5, the outer reef flat morphology varies considerably in different area, particularly between the windward and the leeward sides. Its width ranges from 150 to 180 m as measured on West-Southwest transects to 20 to 40 m on eastern shores. It consists of an area of rock pavement derived from an old conglomerate submerged under 10 to 50 cm of water with a rough bottom, pitted by small erosional pools. The floor is covered by a thin sedimental detritic layer that get thicker toward the beach.

The **inner reef flat** begins just lagoonward of the motu or the emerged conglomerate, and ends where the bottom starts to slope into the lagoon. The width of the inner reef flat varies considerably around the atoll rim. On windward shores, the inner lagoon margin flat is protected from trade winds by the outer reef flat, the motu and its associated vegetation. The inner reef flat is therefore somewhat dead and resembles a slight sandy slope. A different situation exists on the lagoon border in the lee of the atoll. Because of exposure to trade wind across the fetch of the lagoon, these areas are well-formed reef flats composed of an old conglomerate covered by a thin sedimental layer that gets thicker lagoonward.

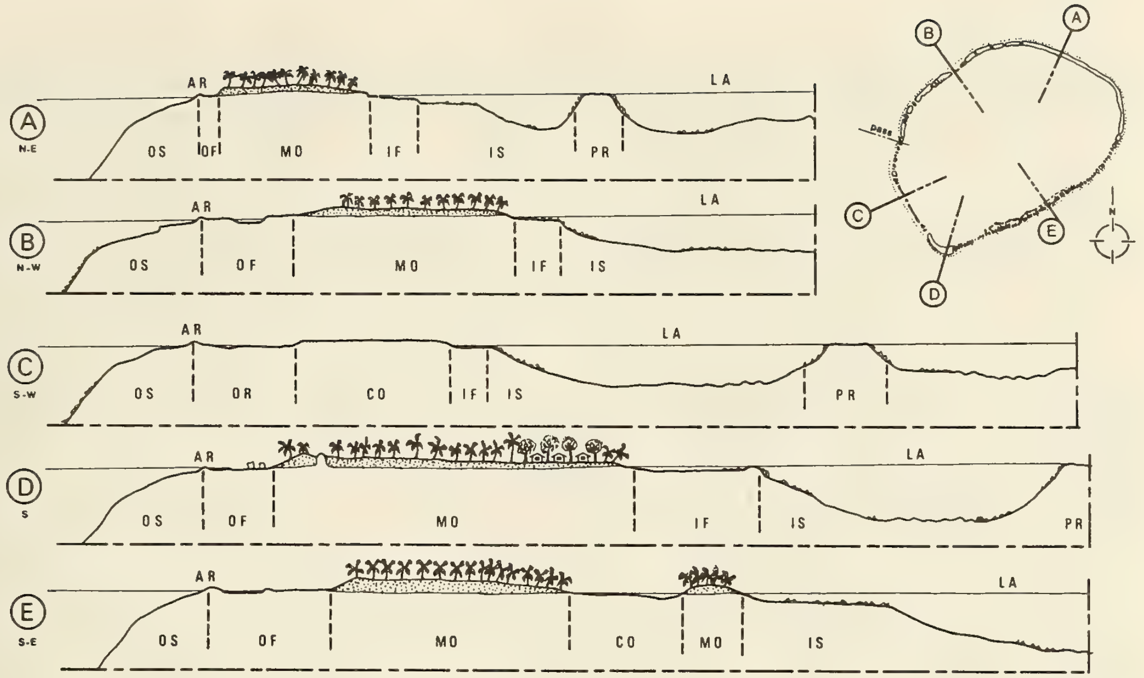

Fig. 5 : Cross atoll rim sections at various locations of the Tikehau atoll (OS : outer slope; AR : algal ridge; OF : outer reef flat; MO : island; CO : conglomerate IF : inner reef flat; IS : inner slope; LA : lagoon; PR : pinnacle reef) - from Harmelin-Vivien (1985).

Lagoon structures

Immediately after the inner reef flat, the **lagoon inner slope** is a relatively steep sediment and rubble slope which extends to depth of 2-6 m. When the slope begins to flatten out, numerous coral patches protrude from the sediment bottom. Where the water flow across the reef is unimpeded by islands, these coral colonies can be numerous and healthy. The lagoon floor is essentially flat with a low slope gradient. The bottom is primarily a fine sandy bottom. This is studied in more detail in a subsequent chapter of this volume.

Many coral **pinnacles** are scattered all over the lagoon. Up to 300 pinnacles visible from the surface (locally called *Karena*) have been counted. They are quite unevenly spaced throughout the lagoon since half of them can be found in the southwest part. Pinnacle reefs vary greatly in size, ranging from a few tens of meters to over 200 m in diameter for the largest.

The shape of the pinnacles can be roughly related to their size : the smaller the pinnacle reef's diameter, the steeper its slope. On small pinnacles, much of the slope is nearly vertical. The largest pinnacles are somewhat flat on top and an emergent one can support bushes or small trees. However, they still slope to the lagoon floor at an angle of at least 20°. Pinnacle reef shapes also vary considerably between the windward and the leeward sides. The windward side usually presents a steep subvertical slope whereas the leeward side of the pinnacle gently slopes to a detrital zone. Coral community zonation is rather regular among pinnacle reefs, and three biota may be recognized : the upper (0-2 m), middle (2-6 m) and lower zones (6 m downward).

Morphological discontinuities

Passes can be defined as major deep channels between the ocean and the lagoon. In Tikehau, the only pass, called *Tuheiava,* is located at the western part of the atoll. Localisation of the pass on the leeward side of atolls appears to be a general trend of the Tuamotu archipelago. Minimal depth of the pass is about 4 m and is sufficient for a small boat to traverse. The bottom, of bare eroded flagstone, slopes steeply seaward and gradually deepens lagoonward until it merges with the lagoon floor. Current direction in its vicinity reverses, depending on the tide and on the height of water in the lagoon. When tidal currents run against the trade winds, steep standing waves can occur in the pass, hampering sailing and fishing activities. When sea-level is high in the lagoon, the current is mostly unidirectionnal out of the lagoon. This occurs frequently when storm associated waves break on windward reef and drive large quantities of water into the lagoon. On an annual basis, the net flow through the pass is an outflow. Main features of water circulation at Tikehau are studied out in details in a subsequent chapter of this volume.

Hoa, also termed rips or gutters, are shallow channels which cut the reef flat superficially. They draw their flow from the shallow reef flat and channelize the flow of water into the lagoon between the motu (Plate 5). In Tikehau, their width ranges from a few tens of meters to 500 m. When currents can freely flow through *hoa* across the atoll rim, *hoa* are termed **open** or **functional *hoa***. On the contrary, when currents do not flow or flow only when a storm occurs because the channel is obstructed by boulders on the outer flat and/or is closed by littoral sand shoals or rubble accumulations lagoonward, *hoa* are termed **closed** or **non functional *hoa***. The shape of these channels is subject to major changes owing to sedimentation and high erosion. *Hoa* are shallow on the outer reef flat (10 to 20 cm) but deepen towards the lagoon (1-3 m). On their lagoonward end where current flow slows down, *hoa* usually have shallow sand shoals. *Hoa* have sandy bottoms sculptured by current fluxes with more or less patch reefs. The amount of patch reefs are directly related to the intensity of water circulation through them.

Up to 150 *hoa* have been counted around the atoll rim. More than 100 are concentrated on the southeast coast and are mostly open channels. The current flow through them is almost unidirectional, from ocean into the lagoon, depending on water level in the lagoon. The 50 other *hoa* are principally located on the northwest coast. A few of them are functional.

Hoa, as well as the pass, are the major source of water movements between the ocean and lagoon.

BATHYMETRY OF THE LAGOON

Knowledge of the bathymetry of the lagoon is basic data for all marine research carried out on the lagoon. There is no detailed marine chart of the lagoon available and an attempt to map the Tikehau lagoon bottom from the satellite LANDSAT proved to be unsuccessful. The main cause was the high and uneven turbidity of the water in the lagoon which prevented LANDSAT from mapping the bottom efficiently. The bathymetry of the lagoon of Tikehau was mapped using field measurements (Lenhardt, 1987). A *SIMRAD EY-M* echo-sounder (frequency 70 khz, range 0-60m) was used on board a motor boat and depth continually recorded on eight transects across the lagoon. The boat was steaming at a regular speed of 3.2 knots on the magnetic North-South axis (declination : 13 °). Results obtained have been cross-checked with results from five other transects. To discretize the continuous series of data, one depth measure was taken every 80 m and raw data smoothed to eliminate numerous local minor unevenness of the bottom.

Pass morphology was studied by recording depth on three transects, one through and two across the pass.

Bathymetric map

Smoothed depths recorded on transects were contoured to map the bathymetry of Tikehau (Fig. 6). The greatest depth recorded was 38 m in the central northeastern part of the lagoon. The main lagoon basin appears to be a relatively flat area with gentle slopes.

Depth histogram

The histogram presented on Fig. 7 shows that the general shape of the lagoon is that of a basin with steep walls. Depths between 0 and 15 m represent only 7 % of the total surface of the lagoon S (S = 420 10^6 square meters).

Other geometric data

The mean depth P as well as the total volume V of the lagoon is of great interest for other studies. Mean depth is calculated by computing the mean depth of each transect with mean length and width of each transect. The result is an average depth of P = 25 m. The total volume of the lagoon is calculated by multiplying the total surface of the lagoon by its mean depth. The result is V = 10^{10} cubic meters. The confidence interval of those data is about 5% which meets the requirement for precision of other research.

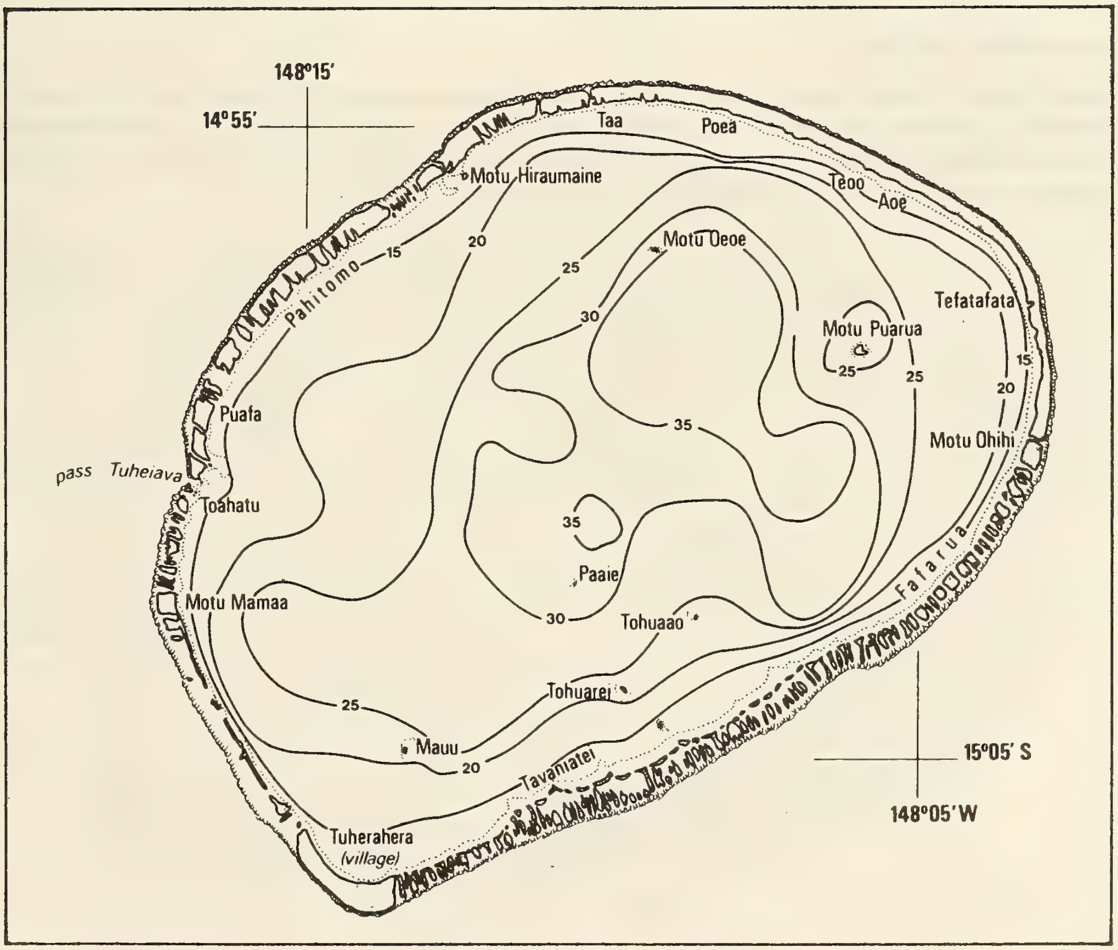

Fig. 6 : Contoured depths (in m) in the lagoon of Tikehau.

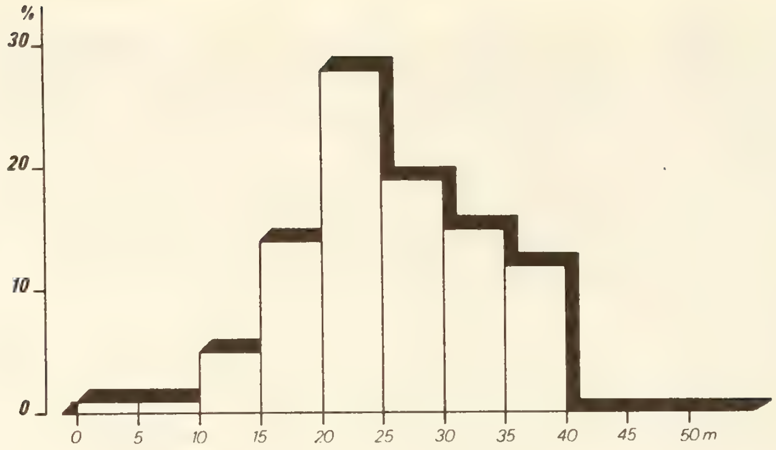

Fig. 7 : Average Tikehau lagoon surface per 5 m depth intervals expressed as a percentage of total lagoon surface.

Characteristic of the pass

Fig. 8 shows the bathymetric map of the pass, transects to record the depth and the smoothed shape of the bottom. The minimal depth recorded in the pass is 4 m. For further modelisation of the flow through this channel and water circulation in the lagoon, the mean section of the pass is estimated at 1000 square meters and average length at 600 m.

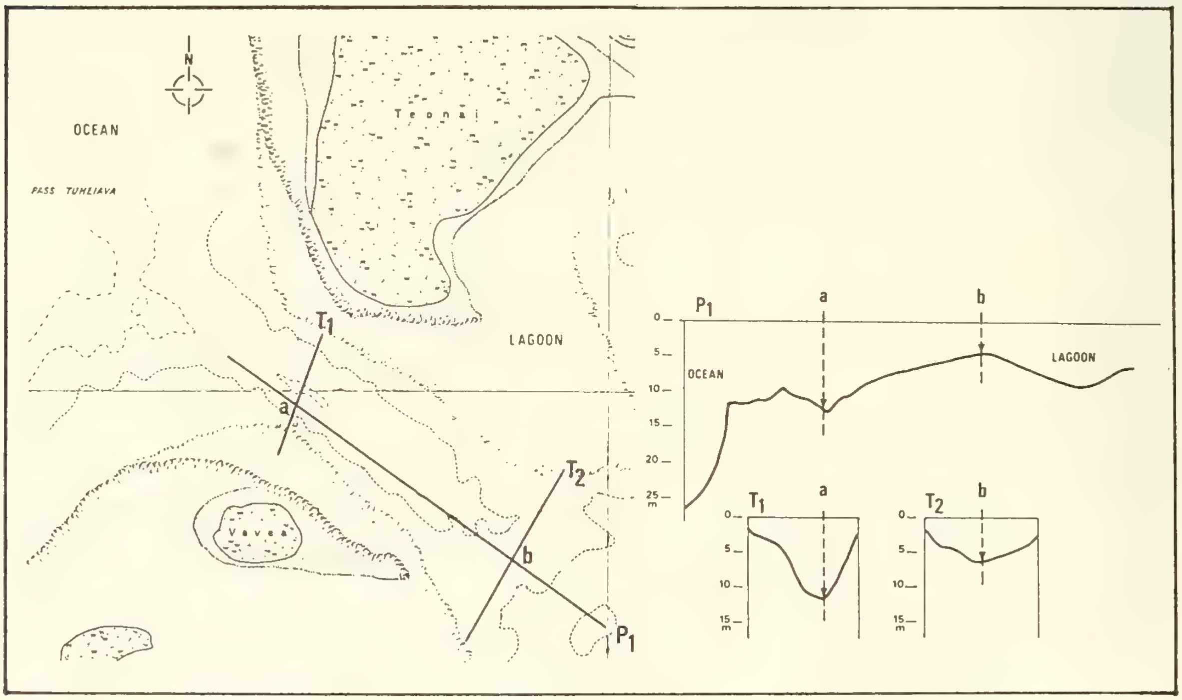

Fig. 8 : Bottom profile of Tikehau atoll pass.

NATURE AND DISTRIBUTION OF LAGOON SEDIMENTS

The bottom sediments of the Tikehau lagoon were characterized by Intes and Arnaudin (1987). Fifty four samples of bottom sediment were taken in various location of the lagoon and subsequently sorted and analyzed in the laboratory.

Findings were that the sediments are all calcareous organic sands. They consist of the following chief components : *Halimeda* segment sand, Foraminifera (family *Miliolidae)* test sand, mollusc shell sand and miscellaneous debris.

Halimeda segment sand is the first common material. It is present in almost all samples and predominates in most of them, especially in samples taken in the western part of the lagoon. As shown on Fig. 9, *Halimeda* segment distribution follows an horizontal west-east gradient and a vertical gradient since its abundance decreases steadily below a 20 m depth. Foraminifera test is the second most common material. Large stretches of foram sand occur on shallow bottoms less than 10 m deep along the southern and southeastern lagoon margin. Moreover, a large foram sand patch extends in the northern central part of the lagoon between a depth of 20 and 35 m. Mollusc shell sand and gravel are never abundant and never dominate the sediment composition.

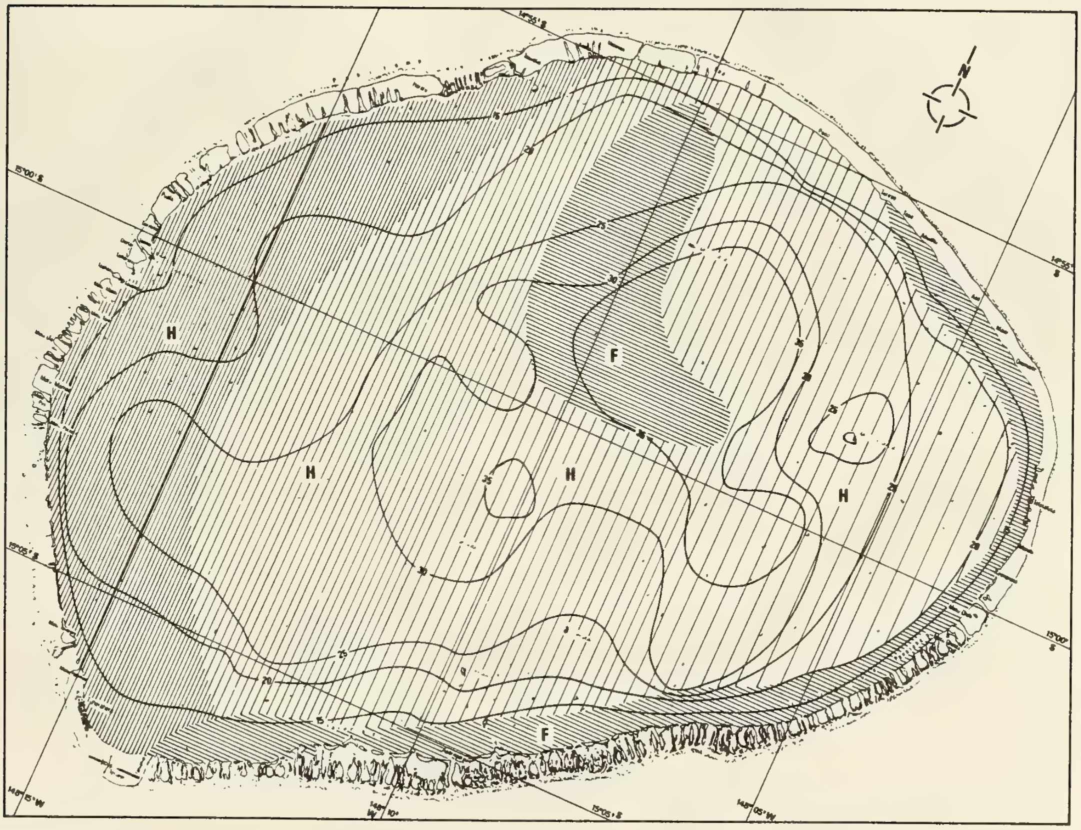

Fig. 9 : Contoured bottom sediment data of Tikehau lagoon characterized by their chief components (H : *Halimeda* sands, F : Foraminifera sands).

The mean size of the sand taken in every sample was estimated by sieving in order to classify the sediment into three size classes : very fine sand (STF - less than 0.25 mm), fine sand (SF - between 0.25 and 0.50 mm) and medium sand (SM - greater than 0.50 mm). Sediment smaller than 0.04 mm was not studied. Contoured data (Fig 10) show that lagoon sediments are mostly fine sand, found in a wide range of depths. However, a large stretch of very fine sand was found in the central northern part of the lagoon between 15 and 30 m, and on an irregular discontinuous strip located 20 to 30 m leeward the eastern and southern reef at depth between 9 and 30 m. Some small medium sand patches are scattered along the lagoon margin down to a 10-15 m depth and a large stretch occurs across the deep central basin of the lagoon.

Most of the materials of the sand sample taken proved to be quite heterogeneous with a large size range and a symmetric distribution, except for foram medium sands that are homogeneous. Sands easily driven by currents are logically found in area of important water transport (*i.e.* lagoonward *hoa*, in the vicinity of the pass) and unexpectedly at a 34 m depth in the center of the lagoon which is an area thought to be calm.

Fig. 10 : Contoured bottom sediment data of Tikehau lagoon characterized by mean sand size (STF : very fine sand, SF ; fine sand; SM medium sand; see text for definition of size-classes).

BIOLOGICAL COMMUNITIES OF THE OUTER SLOPE

This chapter, as well as the following ones, does not attempt to provide a comprehensive description of the fauna in Tikehau but descriptive information about marine habitat. Determination of many coral and sponge species is still underway and furthermore, fauna description is limited to the first 90 m in depth. Depths below are unpractical for sustained SCUBA diving operations and should be sampled remotly. The information presented hereafter has been drawn from publications of Faure and Laboute (1984) for coral species census and distribution, Peyrot-Clausade (1984) for cryptofauna distribution and unpublished data of Intes for zoobenthos of sediments. Fish fauna distribution will be studied in a subsequent chapter of this volume.

The fore reef area

In the **spur and groove zone** (0-4 m), corals are largely dominated by calcareous algae which become increasingly dominant as exposure to trade wind increases. Total coral coverage rate ranges from 5 to 25 %. Spur and groove have on them coral adapted to withstand this high energy environment. The top of the spur and the parts of the wall of the grooves are colonized by small branching *Pocillopora* (*P. verrucosa, P. meandrina, P. damicornis*) ; small massive *Favia rotumana, F. stelligera, Montastrea curta, Pavona clavus* ; encrusting forms of *Montipora caliculata, Acropora robusta, Millepora platyphylla* and *Acropora abrotanoides*.

Algae are the major component of this substrate. The main species are green algae *Halimeda opuntia, H. discoidea, Caulerpa pickerengii, C. seuratii, Neomeris van bosse, Microdyction* and the red algae *Dasya* to some extent.

Sessile cryptofauna is abundant, sheltering among coral branches or small grooves in the rock. The highest richness is reached on overhangs and in small caves as noticed on the south southeast coast (Sponges, Hydroids *Solanderia,* Bryozoans, Stylasterids, Dendrophiliids, Didemnid and Polyclinid Ascidians). An important motile cryptofauna occurs in this zone. Polychaetes and Crustaceans dominate and borers (mainly Sipunculids) are rare.

On the **fore reef platform** (4-10 m), the amount of coral coverage increases (60-80%) as well as its diversity. The most conspicuous coral species are short bunches of *Acropora humilis, A. digitifera, A. variabilis, Astreopora myriophtalma,* the first noticed Fungid (*Fungia fungites* and *F. scutaria*), and all the coral species cited above. On the northwest shelves where the platform is wide, the fore reef platform is also highly colonized by algae of the genus *Microdyction, Halimeda* and *Caulerpa.*

Cryptic community biomass decreases slightly, still dominated by Polychaetes and Crustaceans.

The outer terrace

Between 10 and 15 m depth, grooves floored with rubbles alternate with coral ridges. Communities are made up of *Favia stelligera, Pocillipora eydouxi, Astreopora myriophtalma, Acropora abrotanoides, Platygyra daedalea, Porites lobata, Favia rotumana, Millepora platyphylla.* Coral coverage rate is about 60 %. From 15 m to 25 m, *Porites lobata* progressively dominate followed in, order of abundance, by *Pocillipora eydouxi, Favia stelligera, F. rotumana, Astreopora myriophtalma, Acanthastrea echinata, Pavona varians, Herpolitha limax* and *Acropora sp.*.

Calcareous algae *Porolithon* and *Peyssonnelia* along with soft algae colonize the outer terrace bottom to depth of 25 m. On the windward coast, algae coverage can be important to some extent.

Sessile fauna, except for some sponges as *Astroclera sp.*, shelter among coral patches and is rather scarce. Echinoderms, Molluscs and Crustaceans are abundant but remain hidden during daytime. The only occurrence of the invertebrate coral predator, the crown-of-thorn starfish *Acanthaster planci*, was recorded in this zone. Its population level seems to be very low and no evidence of an extensive coral predation was found.

Motile cryptofauna is dominated by Polychaetes and Crustaceans. Its biomass is low and is reduced by half between 10 and 20 m in depth.

The deep slope

The living coral coverage rate of the deep slope is high ranging from 50 to 100 %. At these depths, the amount of light energy reaching the bottom decreases steadily, inducing a colonization of the bottom by coral species fitted to dim recess conditions. The plate-like *Pachyseris speciosa* is thus the major component of the coral fauna, so much that this zone is termed the "*Pachyseris speciosa* area". In the **upper zone** (25-35 m), most of the dominant species of the previous zone (*Porites lobata, Pocillipora eydouxi, Favia stelligera* and *Acropora sp.*) are progressively replaced by species more shade-tolerant as *Gardinoseris planulata, Lobophyllia sp., Coscinarea sp.* and small colonies of *Pachyseris speciosa* are located in the shade of large vasiform coral species. The live coral coverage rate is above 50 %. In the **middle zone** (35 to 60-70 m), *Pachyseris speciosa* sharply predominates colonies of *Porites lobata, Pavona varians, Leptoseris incrustans, Gardineroseris planulata* and *Echinophyllia aspera*. In the **lower zone** (from 60-70 m downwards), numerous colonies of *Leptoseris* (*Leptoseris hawaiensis, L. scabra, Leptoseris sp.*) and *Echinophyllia* (*E. aspera, E. echinata*) appear among well-developed colonies of *Pachyseris speciosa* with a nearly flat upper surface well adapted for best capturing sunlight. *Stylaster* and especially the red coral *Stylaster sanguineus* are common species below 60 m but they are already found from 40 m downward in places well protected from light (*i.e.* : on overhangs, in small caves or in the shade of larger species). No SCUBA diving investigations were made below 85 m but given the transparency of the water, it has been observed that the *Pachyseris-Leptoseris* population is still developing with the same energy below a depth of 90 m.

Algae zonation is not restricted to the upper strata of the slope. When a dead coral leaves a living site, the vacated space can be reoccupied by *Caulerpa urvilliana* (to depths of 65 m), *Caulerpa seuratii* (15-70 m), *Caulerpa bikinensis* (to depths of 75 m and probably below), *Microdyction sp.*, (1-65 m) or an unidentified species of *Halimeda*.

The black sponge *Astroclera sp.* remains the most conspicuous species among the 25 observed sponge species. It reaches its maximum density at a depth of 40 m but is still abundant in small colonies at 70 m. The paucity of other sessile invertebrates like Gorgonians, Anthipatharians or large Hydroids is noteworthy. Unlike many Indo-Pacific coral reefs, this is a common feature of outer slope of atoll in the Tuamotu archipelago.

BIOLOGICAL COMMUNITIES OF THE REEF FLAT

In all aspects, the reef flat is quite variable. Various authors have described this zone at Tikehau, usually in combination with a description of cross-reef flat transects on several parts of the atoll rim.

The algal ridge

The algal ridge is mostly built by calcareous algae of genus *Porolithon* and *Chevaliericrusta* along with *Pocockiella variegata* and algal turf made of *Caulerpa, Halimeda, Microdyction* and *Liagora*.

Coral coverage rate is low, less than 2 % on windward reef and less than 10 % on leeward shelf. Coral colonies generally flourish on the wall of the grooves which are emergent only when low spring tide occurs. Coral species are short, small and blunt ecomorphs fit to withstand the high-energy environment generated by wave action. The main components of this community are : *Pocillipora damicornis, Porites lobata, Pocillipora verrucosa, Montipora caliculata, Acropora humilis, A. digitifera* and *Millepora platyphylla.*

Three echinoderms, *Heterocentus mammillatus, Colobocentrotus pedifer, Actinopyga mauritania* and lesser number of juvenile sea-urchins sheltered in holes with *Echinometra sp.,* are often abundant. Among molluscs, the most seaward species is *Platella flexuosa* followed lagoonward by *Drupa ricinus, D. morum, Turbo setosus, Morula uva* and two species of Vermetid.

The algal ridge structure provides numerous small cavities which afford protection from the wave surge (and predation) to motile cryptofauna. Its biomass is high and mostly consists of Polychaetes and Crustaceans. Sessile cryptofauna has a high species richness index but since its living space is restricted by the availability of cavities always submerged, the total biomass is low.

The outer reef flat

The coral community of the outer reef flat is extremely poor with only two species censused, *Pocillipora damicornis* and *Porites lobata,* covering less than 1 % of the area. Algae are scarce.

Among the most conspicuous molluscs, *Drupa grossularia, Conus sponsalis, C. ebraeus, Erosaria moneta, Cerithium alveolus,* young *Tridacna maxima* and *Chama imbricata* are frequently encountered.

The conglomerate has evidence of extensive rock boring by numerous Lithophagids (up to 50 individuals m^{-2}). Various sessile invertebrates shelter under blocks and in cavities but their abundance is quite low. Motile cryptofauna is scarce and of low biomass, dominated by Polychaetes and Molluscs.

The inner reef flat

Algae are the main components of the innermost part of the reef flat. The primarily fine sandy bottom is colonized by *Halimeda opuntia, Caulerpa serrulata* and *C. urvillana.* Many sand mounds of the mud shrimp *Callichirus armatus* are scattered all over this area, attesting an important burrowing activity.

Lagoonward the inner reef flat and down to a 2 m depth, the coral community consists of *Pocillipora damicornis, Acropora digitifera, A. abrotanoides, A. corymbosa, A. humilis, Favia stelligera, Montastrea curta, Platygyra daedalea.* Live coral fauna covers about 25 % of the substrate.

Algae coverage is high over blocks and sites left by dead coral colonies. Species identified are Dictyotales, *Halimeda sp., Mycrodyction sp., Pocockiella sp.* and a thick algal turf. A great abundance of *Cerithium alveolus* and *Erosaria moneta* is remarkable.

Shapes and extensions of dead coral colonies provide a lot of space for a motile cryptofauna settlement. As a consequence, its biomass is high, dominated by motile and boring Molluscs and Sipunculids which account for more than 30 % of the total cryptofauna biomass. Main species of Ascidians are from the families of Didemnidae and Polycitoridae.

BIOLOGICAL COMMUNITIES OF THE LAGOON

The lagoon slope

The important sedimental layer of the **inner slope** hampers somewhat the development of coral communities. Live coral coverage rate is less than 10 % and consists of *Pocillipora sp.* mostly settled in the shallowest part of the slope, followed downward by massive and encrusting forms of *Porites lobata, Leptastrea purpurea, Pavona varians, Platygyra daedalea, Montipora verilli* and *Fungia sp.*.

Algae are generally scarce. *Microdyction* have colonized hard substrate on the windward side of the atoll. On the west coast, not far from the pass, an algal flat community dominated by *Caulerpa sp.* extends on the slope with some *Halimeda sp.* found where the slope flattens out and merges with the lagoon bottom.

Invertebrates occur sporadically in this barren area.

Between 6 and 12 m depth, the lagoon margin has areas of abundant patch reefs. Particularly in places exposed to an abundant water circulation but protected from sediment overwash, lagoon margin patch reefs have well developed coral communities which can be either multispecific coral heads of *Pseudocolumastrea pollicata, Platygyra daedalea, Leptastrea purpurea, Pavona varians, P. minuta, Stylocoeniella sp., Astreopora sp., Fungia ssp., Porites lutea, Stylophora pistillata, Montipora verrucosa, M. verrilli* or paucispecific bunches of *Acropora formosa* and *Acropora vaughani*.

A few sessile bivalves grow on the sides of the patch reefs. The most frequently encountered species are *Arca ventricosa, Pinctada maculata* and rarely the pearl oyster *Pinctada margaritifera*. In addition to some echinoids hidden in shelters provided by coral patches, beche-de-mer *Halodeima atra, Thelenota ananas* and several species of synaptid commonly feed in this area.

The lagoon bottom

The nature of lagoon bottom substrate has not been studied in detail but obviously, soft sediment substrata overwhelmingly dominate hard coral substratum. The lagoon floor can be characterized as large stretches of sand with occasional patch reefs. Wide areas of soft bottom are covered with a thin algal mat of brown Cyanophycae. Other Cyanophycae are visible on the sediment as large red balls. Species of *Halimeda* (principally *H. opuntia*) and *Caulerpa* (*C. serrulata, C. urvilliana*) can build up large algal flat areas. *Caulerpa sp.* grows via rhyzomes, spreading out over the bottom in easily distinguishable patterns. Sea grass beds of the marine phanerogame *Halophila ovalis* reach high density in some places.

Little is known on the fauna buried in, or on, sediments. Epifauna is composed mostly of sponges (*Echinodictyon, Axinella*) scattered over sediment surface. From place to place, some bivalves of the genus *Pinna* raise from the sediment. Holothurian *Halodeima atra* concentrates in great numbers, up to 10 individuals per square meter in the shallowest sandy areas. Polychaetes and Molluscs alternatively dominate the endofauna. Sedentary Polychaetes are well represented mostly by the families of Spionidae (*Prionospio sp., Aonides oxycephala*), Maldanidae (*Axiothella sp.*), Capitellidae (*Dasybranchus* and *Notomastus*) and Terebellidae. A few errant species live in the sediments ; they belong to the families of Glyceridae, Eunicidae and Nephtyidae. Molluscs are essentially little bivalves like Tellinidae but some carnivorous gastropods exist (Naticidae, Strombidae). Among Echinoderms, only a few ophiuroids may be encountered. Very motile crustaceans as Portunid crabs may bury in sediments. Lancelets are locally abundant, especially in coarse sands. Small conical mounds disrupting the sediment surface are evidences of the presence of mud-shrimps. Their density is quite high, approximately 15 mounds per ten square meters. Mounds can be as large as 50 cm diameter on bottom of deep zones.

Stretches of hard bottom are found down to a 20 m depth. They are often restricted to areas of a few square meters but around the largest pinnacle reefs, they can cover areas of hundreds of square meters. Coral communities are made up of either multispecific patches of *Porites lobata, Psammocora sp., Montipora sp. Astreopora sp.,* or paucispecific bunches of *Acropora spp.*. Macroalgae, particularly species of *Halimeda*, are often found among the corals.

Pinnacle reefs

The pinnacle reefs of Tikehau cover only a few percent of the lagoon bottom area but concentrate a great biological diversity, harbouring a wealth of various organisms. The **upper zone** (0-2 m) can be emergent at low tide. The center of the largest pinnacle reefs is rugged with sediment and rubble, colonized by algae *Halimeda, Pocockiella, Caulerpa, Padina* and *Lobophora*. On the windward side, very large colonies (6 to 8 meters) of *Porites lutea* and *Millepora platyphylla* grow along with a few *Pocillipora meandrina* and *Acropora abrotanoides*. The leeward side supports branched colonies dominated by *Acropora variabilis, A. hyacinthus, A. hemprichi* and *Montipora spp.*.

The motile cryptofauna of the upper zone is rich and dominated by Molluscs. Borers are rare.

The bottom of the **middle zone** (2-6 m) is largely a rocky substrate with shelves on which considerable quantities of sediment and rubble are retained, promoting the development of *Halimeda* and *Caulerpa* algal flat. Some coral heads of *Montipora verrucosa, Astreopora sp., Psammocora sp., Porites lobata, Platygyra daedalea* and *Pavona varians* intersperse among sediment stretches.

Cryptofauna abundance decreases somewhat, being still dominated by Molluscs. Boring invertebrates, mostly Molluscs and Sipunculids, represent almost 40 % of the total biomass. The important sediment deposition in this zone precludes the development of any significant sessile fauna.

The **lower zone** (6-15 m) of the pinnacle reef is covered by coral patches of *Montipora verrucosa, Stylocoenilla sp., Platygyra daedalea* and branched forms of *Acropora formosa, Stylophora pistillata* and *Favia favus*. Below 15 m, coral colonies vanish under the sediment.

BIOLOGICAL COMMUNITIES OF MORPHOLOGICAL DISCONTINUITIES

The pass

Numerous live coral ridges oriented parallel to the pass axis are scattered over the bottom of the pass. These colonies are characterized by an outstanding development of *Pocillipora* (*P. meandrina, P. verrucosa, P. eydouxi, P. damicornis*) measuring up to 3 m. Live coral coverage rate is about 80 % and reaches 100 % alongshore. Small colonies of *Leptastrea purpurea, Montipora sp. Fungia fungites, F. scutaria* and *Millepora platyphylla* are found protected from current on the flagstone between ridges.

Algae and invertebrates are rare in the pass owing to extremely rough current conditions. Some sponges (*Aurora sp.*), beche-de-mer (*Thelenota ananas*) or Asterids settled there nonetheless.

Hoa

The seaward bare bottom of *hoa* is colonized by a great number of *Cerithium alveolus* and often bored by numerous lithophagid. The top of many dead coral blocks is covered with the black Cyanophyceae *Hassalia byssoides*. Pink sands rich in Cyanophyceae and bacteria have accumulated alongside the edge of the channel. Coral patches of *Porites lobata, Leptastrea purpurea, Porites cf andrewsi* and *Platygyra daedalea* appear lagoonward, downcurrent of the reef where sediment overwash is weaker. Echinoid species (*Echinometra,* *Echinothrix, Diadema)* are concentrated in some numbers around these coral heads. Some bivalves *Tridacna* grow on top of them.

The motile cryptofauna dominated by Crustacean and Polychaetes is poor due to the paucity of suitable substrates.

OCEANOGRAPHY OF THE TIKEHAU LAGOON

The understanding of lagoonal water circulation is of primary interest for all biological and chemical studies carried out in the lagoon. Current data were recorded by four current meters set in the *hoa* of the windward reef, of the southwestern reef, of the northwestern reef, and in the pass. A tide gauge continually recorded water height in the lagoon. Modeling of the lagoon circulation was furthermore attempted.

Pass currents

The pass current is reversing. Its speed and timing are in phase with the tide. Data from Lenhardt (1991) show that the current speed usually ranges from 0 to 120 cm s^{-1}, increasing from 0 to maximum speed in about 3 hours and then decreasing to slack water in another 3 hours. The period of slack water in the pass is only a few minutes. When water level is high in the lagoon, the pass has a nearly continuous outflow. The current speed may exceed 3 m s^{-1} under these frequent conditions and can last from 3 to 10 days.

The volume of transport of the pass current varies between neap and spring tide and more importantly with water height figures in the lagoon. Data available did not enable us to estimate the outflow through the pass but the average inflowing water transport was estimated to be 400 m^3 s^{-1} over a tidal cycle. It was furthermore estimated that the net transport volume of the pass is approximatively zero over a tidal cycle under normal lagoon water level conditions.

Hoa currents

Hoa currents or cross-reef currents involve a shallow flow over the reef margins. *Hoa* draw their flow from the outer reef flat and channelize the water off the reef into the lagoon between islands. *Hoa* currents are a result of breaking waves over the algal ridge on the windward reef. They vary in response to surf height and therefore to regional oceanographic patterns. Lenhardt (1991) pointed out that *Hoa* currents do not reverse direction at Tikehau, they always flow from ocean to lagoon even when water level is high in the lagoon.

Cross-reef currents do not flow in any well developed pattern as summarized in Table 4. The average current speed is low, generally less than 30 cm s^{-1}. It ranges from 0 to 120 cm s^{-1} when high surf occurs. Current speed also varies seasonally, it is highest in *hoa* of the northwestern coast in summer of southern hemisphere while it is maximum in *hoa* of southeastern and southwestern reefs in winter. Table 4 shows that volume transport across the windward reef (southeast shore) accounts for more than 60 % of cross-reef water input whereas southwestern water transport accounts for 31 % and northwestern reef for 9 %. Average inflow per unit length of open coast (hereafter expressed lineic flow rate in m^3 s^{-1}/m or m^2 s^{-1}) is an useful data. Its variations over the year are summarized in Fig. 11. Bases for calculation are : length of South-East coast 23 km; length of South-West coast 11 km; length of North-West coast 11 km.

Table 4 : Estimates of monthly inflowing current speed and associated water transport in hoa and pass of the Tikehau atoll. Sse : current speed in southeastern channels, Ssw : current speed in southwestern channels, Snw : current speed in northwestern channels, Tse, Tsw and Tnw : relevant water volume transport. Rt : residence time. Bases for calculation : equivalent section of southeastern reef front : 5000 m^2 ,southwestern reef : 2600 m^2 , northwestern reef : 80 m^2 . Total inflow is the sum of inflow through pass and hoa.

Month	Cross-reef current and transport						Pass inflow	Total inflow	Rt
	Sse cm s^{-1}	Tse $m^3 s^{-1}$	Ssw cm s^{-1}	Tsw $m^3 s^{-1}$	Snw cm s^{-1}	Tnw $m^3 s^{-1}$	$m^3 s^{-1}$	$m^3 s^{-1}$	days
January	5.5	270	2.5	65	18	15	260	600	
February	3.0	140	3	75	21	18	180	400	230
March			4	100	17	14	150		
April			7.5	200	28	18	250		
May	15	800	10.5	280	9	7	100	1200	
June	20	1000	6	160	13	11	70	1200	105
July	11	550	7.5	190	3	2	100	900	

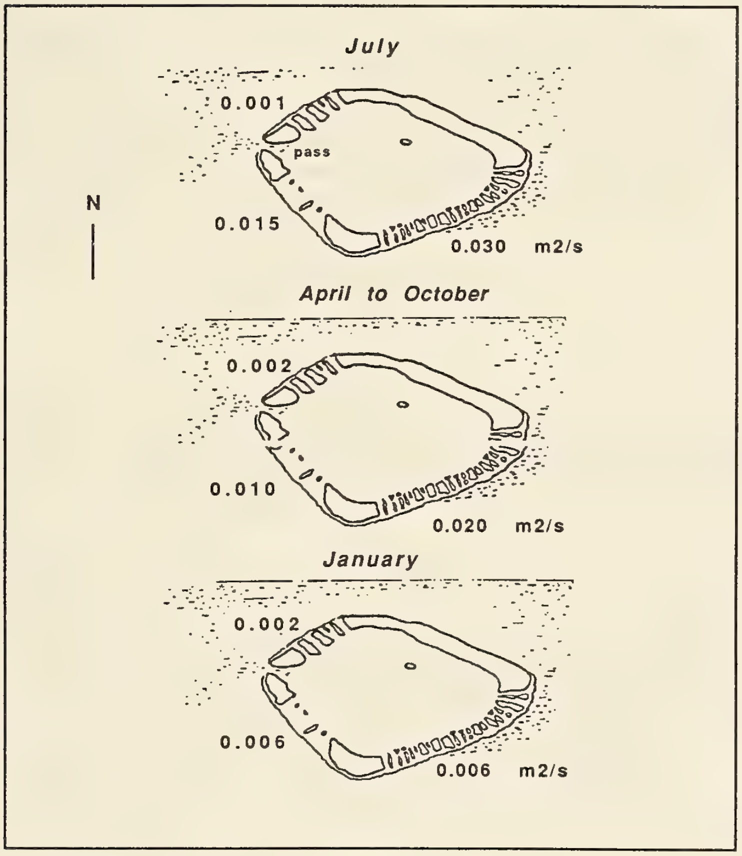

Fig 11 : Variations of lineic flow rate through *hoa* of Tikehau over the year.

Lagoon currents

Suspended acoustic drifter releases at a 4 m depth, in various points of the lagoon, show that the surface current in the lagoon is primarily wind-driven. The general surface drift is downwind (or roughly westerly) at a speed of approximately 1 % of the wind speed. Lagoon currents in the vicinity of pass and *hoa* is strongly altered by local current conditions. Current patterns were found to vary with depth. Current in the deep layers of the lagoon is upwind and flows at about one half of the surface current speed.

Water budget and residence times

Because the cross-reef currents never reverse, the volume transport over the reef through *hoa* represent a net input of water into the lagoon. Water furthermore flows into the lagoon from the pass. The water can flow out of the lagoon only from the pass. As the quantity of water entering the lagoon and the quantity of water exiting out of the lagoon must be balanced, the net inflow must exit as outflow out of the pass. Thus, water transport in the pass is indicative of water budget figures in the lagoon. The volume transport Q ($m^3\ s^{-1}$) flushing in the pass was found to be a simple function of the difference in m between height of lagoon (h) and ocean (z) according to :

$$Q = \varepsilon\, 3000 \sqrt{|h-z|}$$

ε being -1 if water flows out of the lagoon, +1 if water flows in.

The average residence time of water in the lagoon can be estimated by dividing the lagoon volume (*i.e.* 10. $10^9\ m^3$) by the net rate of water input presented in Table 4. Under these very simple assumptions, the calculation yields a residence time of 230 days in summer and 105 days in winter, the yearly average value being 170 days. Because the water entering the southeastern lagoon must transit the entire lagoon before exiting through the pass and because it probably undergoes mixing by the wind-driven circulation, during that transit, the residence time of this part of the inflow will be longer. Conversely, water inflowing through northwestern channels will be expected to have a residence time shorter than the average. The residence times estimated at Tikehau can be compared to those estimated in the lagoon of a high island (Moorea, 6.5 hours) and in the lagoon of a closed atoll (Takapoto, between 4 and 5 years).

Circulation model

Lagoon circulation can be explained as a response to three sources of energy : the tide, the surf on the ocean reef and the wind. Lenhardt (unpublished data) proposed a bi-dimensional finite difference model using vertically integred Navier-Stockes equations to model the response of lagoon circulation to these three sources of energy taken separately then altogether.

Fig. 12a shows the residual tide-induced circulation in the lagoon. Tidal currents influence the flow of water only in the immediate area of the pass. Current speed is greater than 1 cm s^{-1} only within 4 km of the pass. Elsewhere in the lagoon, tidal current speed is very low (a few mm s^{-1}) and can hardly be measured. The tide generates a conspicuous clockwise local eddy south to the pass and a weak counter clockwise eddy north of the pass.

Fig. 12b shows the circulation induced by the surf on the windward reef. The oceanic water spreads into the lagoon, moving downwind toward the pass. Currents are significant only in the southern part of the lagoon with speed of about 1 cm s^{-1}. The northern part of the lagoon appears to be poorly affected by this circulation with modeled current speed less than 0.5 cm s^{-1}.

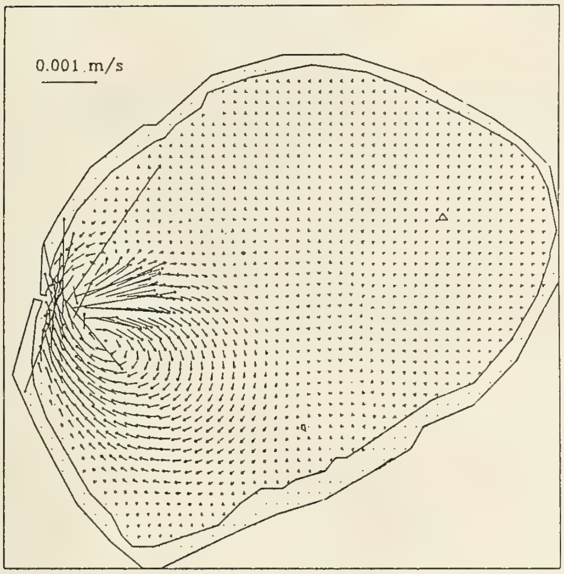

Fig 12a : Lagoon residual circulation generated by the tide at Tikehau (amplitude 10 cm ; arrows : current vectors).

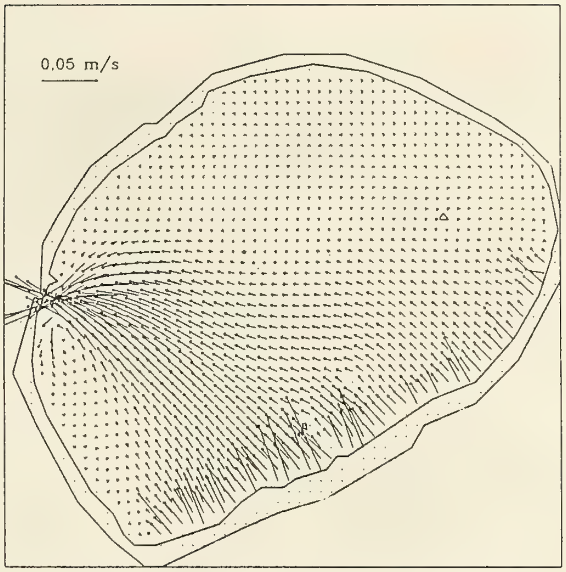

Fig 12b : Lagoon circulation generated by surf on the windward reef of Tikehau (lineic flowing current : 0,3 m3 s^{-1}/m).

Fig. 12c shows the circulation generated by a constant, unidirectionnal easterly windstress of 10 m s^{-1} (about 20 knots). Closed and impermeable boundaries were set to the atoll rim in order to avoid effects of water inflow for modelisation purposes. As measured by drogue releases, current speeds are strongly related to wind speeds (*e.g.* current speed is 1 to 2 % of the wind speed). In shallow part of the lagoon, the wind creates a downwind drift and an upwind drift in the deepest area. The wind-driven circulation induces two large conspicuous counter-rotating bodies of water, a counter clockwise northern eddy and another clockwise southern eddy.

Fig.12d shows the connection the effects of the three sources of energy, the tide, the surf and the wind. Given the low current speed of the tide-induced circulation, the connection of the three sources is actually the sum of the wind and surf-driven circulation. Fig. 12d shows a general downwind drift toward the pass in the southern lagoon and a weak water circulation in the northern lagoon.

The relevance of the model is somehow limited by the fact that it is bi-dimensionnal. The model gives only an average of the current speed and direction over the whole water layer and cannot take into account changes in current with depth. In all probability, and as confirmed by acoustic drogue releases and current speed records at various depths, the pattern of circulation in the lagoon must be a general downwind surface drift oriented toward the pass, balanced by an upwind low-depth drift. Moreover, the lagoon rim is closed neither to the pass nor windward. Large quantities of water are introduced along the windward edge and flushed out of the pass, and considerably modify wind-driven current patterns in the lagoon. Further circulation models should therefore be developed in three dimensions though information supplied by the bi-dimensional model meets biological research requirements.

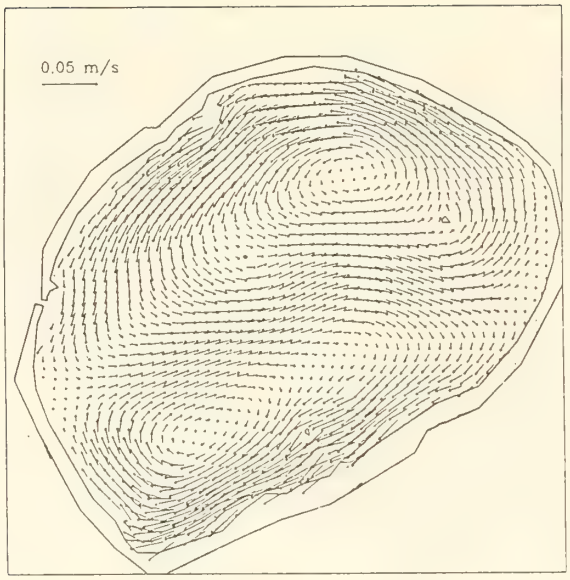

Fig 12c : Lagoon circulation generated by a constant 10 m s^{-1} easterly wind at Tikehau.

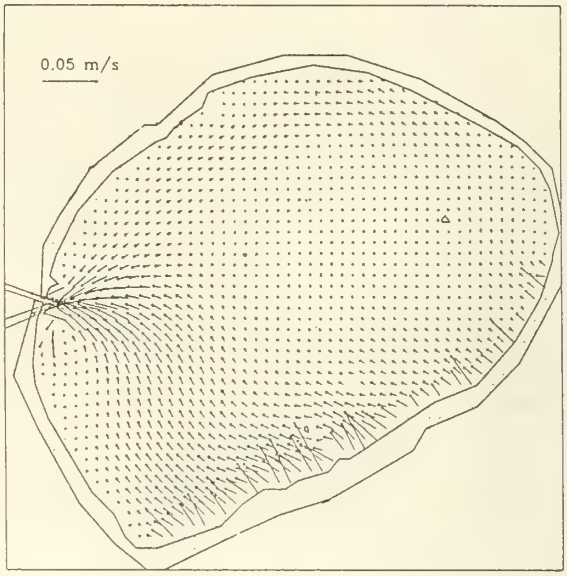

Fig. 12d : Lagoon circulation generated by the connection of the three sources of energy (tide : 10 cm, surf : 0,3 m3 s-1/m and wind : 4 m s-1) at Tikehau.

AN EXAMPLE OF MAJOR DISTURBANCE : CYCLONES

About four cyclones per century are likely to occur in the Tuamotu archipelago but during the hot season 1982-1983, no less than four cyclones (Orama, Reva, Veena and William) and a tropical storm (Lisa) ravaged French Polynesia, causing severe damages to human installations, vegetation and coral reef ecosystems. This meteorological phenomenon of an outstanding frequency and intensity induced waves measuring more than 10 meters, a sea-level rising of 3 meters above predicted tidal levels, and a wind blowing in excess of 160 km per hour with gusting to over 200 km per hour. In particular, the cyclone Veena occurred in the vicinity of Tikehau between the 6th and 13th of April 1983. SCUBA Dive surveys carried out on the same transects before and after that disaster allow to assess the magnitude of damage caused to coral communities, and to explain destruction mechanisms. Two years later, SCUBA Dive surveys carried out on the same transects showed that time of recovery is very long. It will take at least five decades to have the coral communities in the state observed prior 1983.

Damage assessment

Damaged area (*SD*) is assessed by multiplying the length of destroyed reef (*L*) by 200 m (this value is the average length *l* of the outer slope between the depth of 0 and 90 m where hermatypic corals live). L is an estimation based on field observations made during 22 SCUBA Dive surveys around the atoll rim. In Tikehau, an area of 13 million square meters is estimated to have been damaged. This represents 80 % of the outer slope (Laboute, 1985). The area located windward of the atoll (from the north around to the south-west through the east) has been destroyed to a magnitude exceeding 90 %. Areas located north-north-west and west have been damaged to a magnitude varying between 30 and 80 %. The western side of the atoll remained intact.

Destruction mechanisms

Based on the outer slope morphology, three types of destruction mechanism were figured by Laboute (1985) and Harmelin-Vivien and Laboute (1986) following field observations. These theoretical processes are subject to variations with local details of the slope.

The reef flat is narrow, the fore reef area above a depth of 15 m and the slope very steep (> 45°) as on the western coast of the atoll. Between 0 and 15 m, plate-like and branching madreporic species are abundant. They are of the genus of *Pocillipora, Acropora, Montipora, Astreopora, Favia* and *Pavona*. All those species are fragile and have been uprooted then reduced to rubble by the strength of the swell. The remains have contributed to destroy more resistant species by recurrent impacts and abrasion. Most of the remains have been thrown up on the reef flat.

At 12-15 m on the fore reef area, massive and heavy madreporic species like *Porites lobata* and *Montipora* prevail. As above, those species have been uprooted by the swell but since they were growing near or on high-angle substrates, remains rolled down the steep slopes weeping deeper colonies often more fragile, such as the plate-like *Pachyseris speciosa*, the dominant species below 40 m. Destructive effects of this underwater avalanche increased with depth as shown in Fig. 13. It is likely that coral blocks accumulated at some level between 300 and 500 m where the slope begins to flatten out, contributing to the formation of a detrital cone surrounding the atoll (Harmelin-Vivien and Laboute, 1986).

So far, this avalanche phenomenon has never been described elsewhere. All previous hurricane effect descriptions were done for islands without this typical steep outer slope and as a result, cyclone damages were thought to be limited to the upper level of the ecosystem.

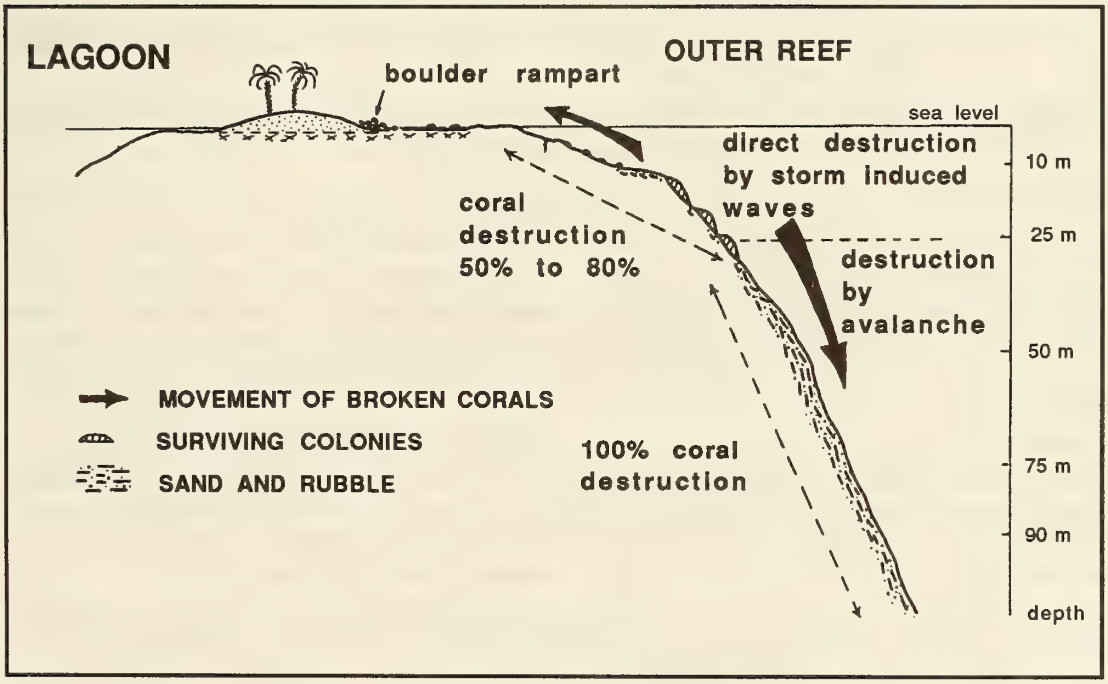

Fig. 13 : Cross section of the west coast of Tikehau with explanatory hypothesis of deep coral destruction : direct coral destruction by storm-induced waves occured between the surface and 20 to 22 m depth. Most remains of broken coral rolled down the slope breaking fragile deeper colonies (after Harmelin-Vivien and Laboute, 1986).

The reef flat is large with a low slope gradient, the fore reef area deeper (25 m) and the outer slope less steep (< 45 °) as on the northern coast of the atoll. Coral colonies have been broken down to 15 m. Part of their remains were thrown up on the reef flat, the other part remaining on the same area. Many coral skeleton were covered by algae (genus *Microdyction* and calcareous algae). Massive species between 15 and 25 m have been uprooted too but given the distance to the steep slope, no avalanche occurred and therefore deeper colonies remained undamaged.

The reef flat is equally large or narrow but there is a depression or a very low-angled zone just before the fore reef area. Madreporic species located above a depth of 15 m have been destroyed following the previous process, but part of their remains have been trapped in that depression, preventing an avalanche. Thus, *Porites lobata* and *Pachyseris speciosa* colonies of deeper zones have been preserved.

Whatever the shape of the deep slope is a shallow fore reef coral community (composed of small colonies well adapted to withstand high energy level environment) suffered less than deeper reef communities. Coral destruction, estimated at 50 %, resulted primarily from abrasions by dislodged material, rolling remains and scouring sand.

Destruction mechanism in the pass and in the vicinity is of a particular nature. The Tikehau pass, located at the west of the atoll, was colonized by numerous species of the genus *Pocillopora* (*P. meandrina, P. verrucosa, P. eydouxi* and *P. damicornis*). The live coral covering rate was high, reaching 80 % to 100 % alongside the edge of the pass, between 2 and 8 meters. Those colonies remained intact as observed during SCUBA Dive surveys carried out six months after the cyclone Veena. More than one year later, all species were dead and skeleton still in place. This can be explained by the following observations : after the cyclone, the sea-level in the lagoon was high and currents constantly flowed out of the lagoon. Water was loaded with a considerable amount of suspended particulate matter and was, as a result, very turbid. Sedimentation was very important in the vicinity of the pass and therefore the amount of light energy reaching the bottom decreased dramatically and subsequently, corals died.

In all cases, most of the coral associated fauna (sessile fauna and fish) disappeared owing to a high mortality rate and to a lack of food and shelter.

Recovery processes

Coral resettlement became visible only one year after the cyclone in an area restricted to the upper 15 m as pointed out by Laboute (1985). In May 1984 *Pocillipora* (measuring between 2 and 4 cm) were dominating followed by encrusting forms of *Favia stelligera, Acropora* (size range : 2-7 cm), *Millepora platyphylla* and to some extent, small colonies of *Pavona minuta* and *Favia rotumana*. In the ravaged areas, no new madreporic colonies were seen below 15-20 m.

In February-March of 1985, an important madreporic and algae resettlement could be seen on the West coast of the atoll between 3 and 15 m. Species inventoried were : *Pocillipora* - obviously the most numerous - (size range : 1-20 cm), *Montipora caliculata, Montipora verrili, Astreopora myriophtalma* (size range : 10-30 cm), *Favia stelligera* (size range : 2-12 cm), algae *Halimeda taenicola, Mycrodyction and Caulerpa urvilliana*.

In June of 1985, algae and madreporic species were still resettling on the outer slope especially between 3 and 15 m. Species were : *Pocillipora* (size range : 4-23 cm), two or three species of *Acropora* (4-20 cm), *Favia rotumana* (4-15 cm), *Porites lobata* (2-11 cm), *Pavona minuta* (5-9 cm), *Millepora platyphylla* (15-50 cm). Algae *Halimeda taenicola, Microdyction* and *Caulerpa urvilliana* were as abundant as before the cyclone. In the area partly damaged and below a depth of 15 m, madreporic resettlement seemed to be faster owing to the presence of some sparse colonies which survived the cyclone. For instance :

At 20 m *Acropora robusta* was 60 cm large but still very encrusting except on its edge, *Favia stelligera* numerous in some place (size range : 10-40 cm), sparse *Porites lobata* (6-17 cm).

At 30 m, numerous *Fungia fungites* (size range : 8-10 cm), *Millepora platyphylla* as large as 1 m but still thin and encrusting.

At 40 m, *Astreopora myriophtalma* measuring between 8 and 35 cm, sparse 17 cm *Porites lobata* very thin which had settled on previous base of same species.

At 50 m, rare *Fungia sp.* of 3 cm and *Pachyseris speciosa* (size range : 4-7 cm).

The impact of cyclones on fish fauna has been studied in detail and the results are presented in a later number of this issue.

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Plate 1 : Uplifted reefs, locally known as "FEO", are distributed along the northern coast of the atoll. Some of them, basaly notched, may be seen on the outer reef flat. (Photo Intes)

Plate 2 : The marshy depression is covered with the cyperaceous assemblage dominated by *Cladium jamaicense*. (Photo Intes)

Plate 3 : Local popular game of javelin throwing. (Photo Intes)

Plate 4 : The spur and groove zone (eastern coast, 4 m). (Photo Laboute)

Plate 5 : The ocean water flows into the lagoon through shallow channels called "Hoa". (Photo Intes)

Plate 6 : A large *Acropora* colony overturned by the wave action induced by the hurricane "Veena" in April 1983 (eastern outer slope, 8 m). (Photo Laboute)

Plate 7 : The avalanche effect may destroy 100% of the corals of the outer slope (eastern outer slope, 22 m). (Photo Laboute)

Plate 8 : Recolonisation of the fore reef platform two years after hurricane "Veena" (eastern coast, 8 m). (Photo Laboute)

PART II. NUTRIENTS, PARTICULATE ORGANIC MATTER, AND PLANKTONIC AND BENTHIC PRODUCTION OF THE TIKEHAU ATOLL (TUAMOTU ARCHIPELAGO, FRENCH POLYNESIA)

BY

C.J. CHARPY-ROUBAUD AND L. CHARPY

NUTRIENTS IN OCEANIC AND LAGOONAL WATERS

Matter and energy budgets for coral reefs, their components, and the world around them can, do, and must balance in a theorical context (Smith and Kinsey, 1988). In this paper, we will try to establish nitrogen, phosphorus and silica budgets between ocean and lagoon waters of Tikehau atoll in the purpose to learn more about the functioning of coral reef lagoons. Nutrient concentrations (dissolved components and particulate organic matter) were measured in the lagoon and in the surrounding oceanic surface waters between 1983 and 1987.

DISSOLVED COMPONENTS

Ocean waters

Five oceanic stations shown on Fig. 1 have been sampled to a 500 m depth. At the most remote ocean station, OS7 (considered as representative of oceanic conditions), the upper 50 m surface layer displayed the characteristic temperature (29.5 °C) and the salinity (35.5 ‰) of oceanic waters. Below this superficial layer (120 to 150 m) a temperature of 25 °C and a maximum salinity of 36.2 ‰ were recorded. Nutrient profiles were typical of offshore oceanic waters, with a very low nutrient concentration down to 200 m depth. As summarized in Fig. 1, nutrient concentrations increased to 15 mmol NO_3 m^{-3} and 2.5 mmol PO_4 m^{-3} at 500 m.

The nitrite concentration displayed a maximum at 175 m (0.1 mmol m^{-3}). Nutrient concentrations in the upper 200 m proved to be higher at the stations located in the immediate vicinity of the atoll.

The atoll therefore seems to disturb the standard vertical profiles of nutrient observed at station OS7, which in turn, results in an enrichment of nitrogen and phosphorus in the euphotic layer. The enrichment is probably due to a turbulent vertical mixing caused by the atoll mass effect, *i.e.* by internal waves (so, Andrews and Gentien , 1982, consider upwelling to be a source of nutrients for the Great Reef ecosystem) and also, perhaps, by an up surge of deep waters from the atoll coral base as hypothesized by Rougerie and Wauthy (1986).

ORSTOM-Tahiti, BP 529, Papeete, French Polynesia

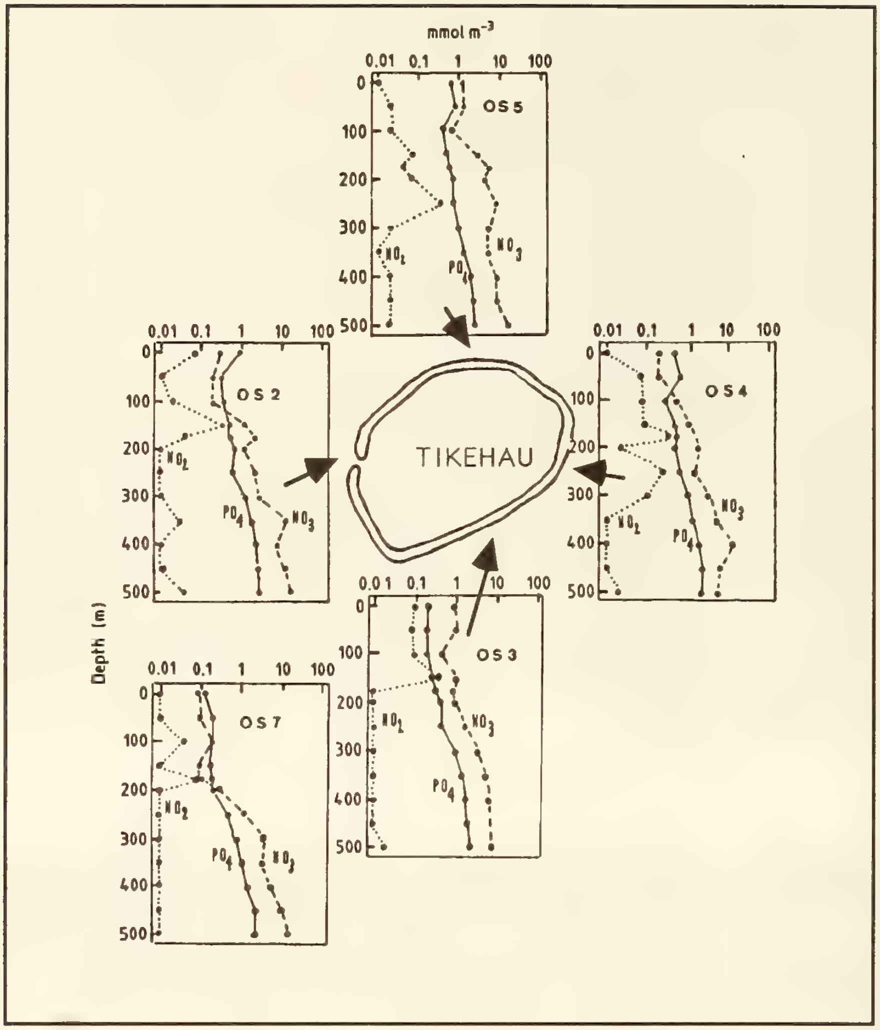

Fig. 1 : Inorganic nutrient concentration profile (mmol m^{-3}) at oceanic stations near the Tikehau Atoll (from Charpy-Roubaud *et al.*, 1990).

Table 1 : Summary of concentrations (mmol m^{-3}) of nutrients, dissolved organic phosphorus (DOP), and dissolved organic nitrogen (DON) in the lagoon of Tikehau (s : standard deviation, (n) : number of samples) (from Charpy-Roubaud *et al.*, 1990).

Variable	Range	Mean	s	(n)
NH_4	0.14 - 9.11	2.10	1.95	(96)
NO_2	0.01 - 0.18	0.02	0.03	(180)
NO_3	0.01 - 0.83	0.08	0.12	(184)
DON	0.40 - 8.20	1.80	2.39	(93)
PO_4	0.01 - 0.89	0.16	0.13	(232)
DOP	0.01 - 1.47	0.39	0.24	(142)
SiO_2	0.07 - 1.72	0.83	0.42	(130)

Lagoonal waters

The average nutrient concentrations listed in Table 1 were not unusual, being of the same order of magnitude as the standing stock nutrient concentrations in coral-reef waters as reviewed by Crossland (1983).

Nutrient concentrations vary considerably with time. NH_4, PO_4 and SiO_2 concentrations were twice as high in 1985 as in other years. The average monthly NO_3 count lays close to the detection limit (between 0.01 and 0.1 mmol m^{-3}), except in February (0.24 ± 0.06 mmol m^{-3}) and August (0.14 ± 0.05 mmol m^{-3}). The monthly average value of PO_4 varies in a spread of 0.1 to 0.2 mmol, except in January (0.4 ± 0.1 mmol). Concentrations of nutrients were found to be homogeneous throughout the lagoon.

PARTICULATE ORGANIC MATTER (POM)

Charpy (1985) emphasized that the particulate organic matter (POM) content of the water column appears to be a good indicator of lagoon productivity. Measurements of deposition rates of organic material are very important. Nutrient requirements for lagoonal production may be met partially through recycling autochthonous material in sediments. One of the principal factors which governs the rate of nutrient regeneration from sediments is the amount of organic matter incorporated into these sediments from the overlying waters (Koop and Larkum, 1987).

POM in oceanic waters

Table 2 : Cruises between 1983 and 1985 in oceanic waters near Tikehau Atoll.

date	July 1983	November 1983	March 1984	November 1985
Name	TIK3	TIK5	TATI	TATU
Stations	OS2, OS5	OS2, OS3, OS4, OS5	OS2, OS3, OS4, OS5	OS2
Depths (m)	0, 25, 50, 100, 150, 200	0, 25, 50, 75, 100, 125, 150, 175, 200, 250	0, 50, 100, 125, 150, 175, 200	0, 25, 50, 75, 100, 125, 150, 200
Parameters	Chl a, Phaeo a	Chl a, Phaeo a, ATP	Chl a, Phaeo a, ATP, POP	Chl a, Phaeo a, ATP, POP, POC, PON

ATP concentrations are greatest in the upper 100 m of ocean waters ranging from 0.05 to 0.12 mg m^{-3}. No significant differences among sampling stations were detected.

Chlorophyll profiles displayed in Fig. 2 show a deep maxima between 100 and 200 m depth. Concentrations recorded in March 1984 reached 0.24 mg m^{-3} at these depths whereas surface concentrations were five time smaller (0.05 mg m^{-3}).

Particulate organic phosphorus, carbon and nitrogen (respectively POP, POC and PON) profiles are shown on Fig. 3. Concentrations generally decrease with depth. The high concentration values that were observed in surface waters in March 1984 were probably due to abundant detritus export from the reef flat and thus overestimated.

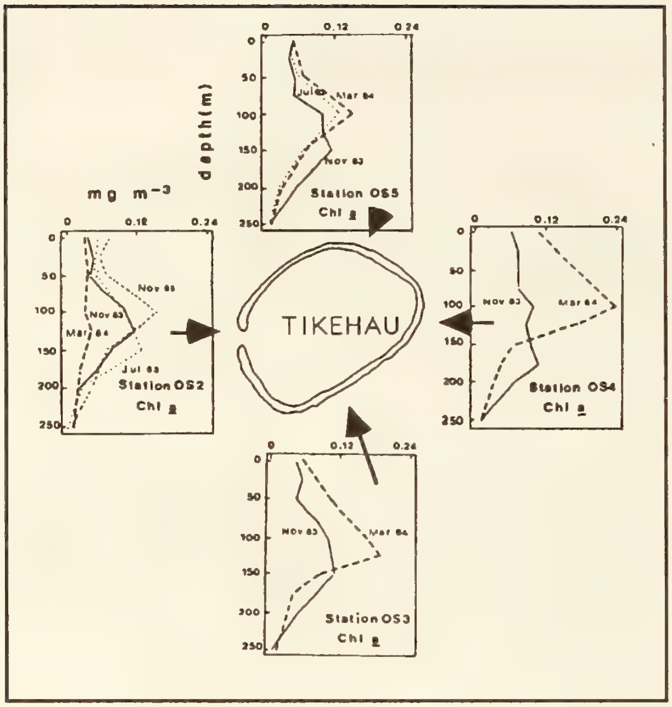

Fig. 2 : Chlorophyll a (chl a) concentration profiles (mg m^{-3}) at oceanic stations near Tikehau .

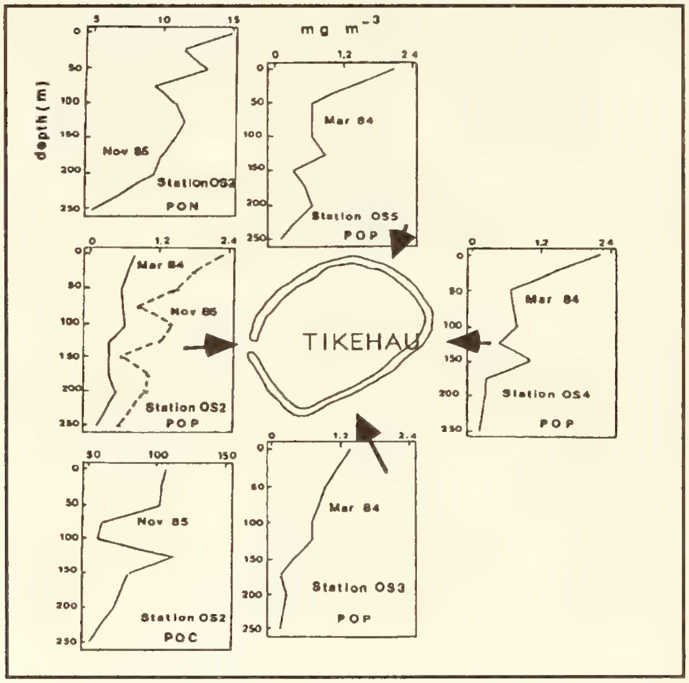

Fig.3 : Particulate organic phosphorus, carbon and nitrogen (POP, POC and PON) concentration profiles (mg m^{-3}) at oceanic stations near Tikehau (from Charpy and Charpy-Roubaud, 1991).

POM in the lagoon and oceanward the pass.

Average POC, PON, POP, ATP and pigments concentrations in samples taken between 1983 and 1987 in the lagoon (all stations and depths included) are presented in Fig. 4. The level of POM concentration observed at OS1 is correlated with the level of POM concentration observed in lagoonal waters. This is more evident for POC ($r = 0.94$, $p = 0.0005$) and PON ($r = 0.86$, $p = 0.006$) but is also true for chl a ($r = 0.59$) and POP ($r = 0.50$). Therefore, the POM water content of OS1 was influenced by the lagoonal discharge. Quasim and Sankaranaryanan (1970) observed a similar feature : POC concentration in surface oceanic waters at 2 km from the Karawatti atoll (Laccadives) was 3 times higher than POC concentration 12 km seawards. We can estimate the average POC and PON concentrations in oceanic waters when the lagoonal discharge is zero by the intercepts of the regression lines : POC concentration at OS1 versus POC concentration in the lagoon (58 ± 26 mg C m^{-3}), and PON concentrations at OS1 versus PON concentration in the lagoon (6 ± 3 mg N m^{-3}). The POP concentration in oceanic waters can be calculated from the POP average concentration measured in the upper 100 m (0.7 ± 0.3 mg P m $^{-3}$)

Table 3 : Average concentrations of POM in the lagoon of Tikehau and oceanward the pass.

	Chl a mg m^{-3}	Phaeo a mg m^{-3}	ATP mg m^{-3}	POC mmol m^{-3}	PON mmol m^{-3}	POP mmol m^{-3}	C/N at : at
Ocean							
Mean	0.06	0.03	0.02	52	6	0.7	8.7
SE	0.004	0.003	0.004	3	0.5	0.1	0.4
(n)	58	58	13	31	31	41	31
Lagoon							
Mean	0.18	0.07	0.11	192	21	2.7	9.1
SE	0.003	0.002	0.005	5	1	0.1	0.2
(n)	409	409	162	290	289	224	289

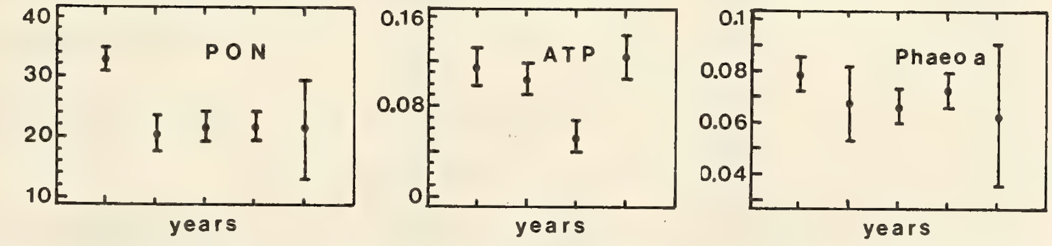

Fig 4 : Mean (± SE) POC, PON, POP, ATP and pigment concentrations in the lagoon of the Tikehau atoll as function of year (expressed in mg m^{-3}).

Concentrations are found to vary with depth in response to a resuspension of detritus that accumulates in deep waters. On the average, POC concentrations recorded near the lagoon floor were 37% higher than those measured in surface water, whereas PON were 27% greater, 31% for POP, 32% for Chla, 43% for phaeo a and 1% for ATP. The average POM concentrations in the lagoon may be strongly influenced by climatological events such as storms or hurricanes. The average POC concentration in the lagoon was unusually high in July 1983 (466 mg m^{-3}) after cyclones that occured at Tikehau in early 1983.

POM size and composition

Size repartition of the POM is summarized in Table 4. On the average, 50% of the POM is made up of suspended particles smaller than 5 µm but this percentage can vary considerably : *i.e.* : 72 to 90% of the POM was in the 0.7-3 µm size class in April 1986. This discrepancy is probably due to the use of Nucleopore filters instead of Millipore filters. New results at different times have shown that 80 % of the POM pass through a Nucleopore 3 µm. Therefore, the average POM passing through 5 µm is probably much higher than 50 %.

Table 4 : Means (± SE) of POM passing through a 5 µm (1984 and 1985) or 3µm (1986) pore filter as a percentage of total POM at the Faufaa station, south of the Tikehau lagoon. Standard error of samples taken at same dates are given (from Charpy and Charpy-Roubaud, 1991).

Date	Chl a (%)	Phaeo a (%)	ATP (%)	POC (%)	PON (%)	POP (%)
23 Nov 1984	-		47 ± 2	35 ± 0	24 ± 1	75 ± 19
24 Nov 1984	66 ± 5	-	48 ± 26	61 ± 7	57 ± 3	88
2 Apr 1985	57 ± 25	-	-	43 ± 14	55 ± 23	27 ± 7
9 Apr 1985	32 ± 6	40 ± 35	68 ± 11	33 ± 11	46 ± 16	47 ± 20
12 Jul 1985	57	29 ± 17	30	35	32	29
13 Aug 1985	25 ± 4	34	20 ± 5	-	-	24 ± 12
7 Apr 1986	92 ± 5	74 ± 3	75 ± 24	81 ± 1	77 ± 13	99 ± 2
Average ± SE	50 ± 6	45 ± 8	46 ± 6	50 ± 6	54 ± 5	49 ± 6

Phytoplankton account for 35% of the living carbon with a strong dominance of cyanobacteria while heteroflagellates and ciliates account for 6% of the living carbon (fig.5) (Blanchot *et al.*, 1989).

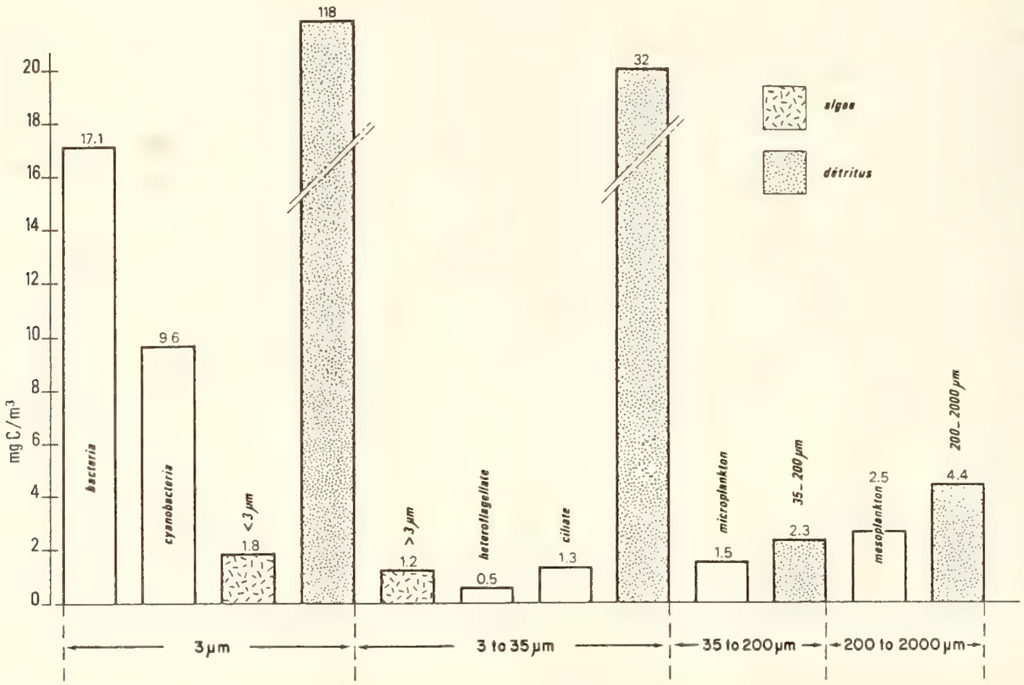

Fig. 5 : Size distribution of organic seston weight (mg C m^{-3}) for different size-classes of seston (<3 µm, 3 to 35 µm, 35 to 200 µm, 200 to 2000 µm) in the Tikehau lagoon. Data for living C of 35 to 200 µm and 200 to 2000 µm size class were calculated using ATPx125 (from Blanchot *et al.*, 1989).

Sedimentation of Particles

Sedimentation rates as well as settling velocities of POM were studied by setting a sediment trap far enough from the bottom (5 m) to collect only materials sinking from surface layer. Results listed in Table 5 show that the sedimentation rate of POC and PON (*i.e.* : 350 and 36 mg m^{-2} d^{-1}) are close to the values given by Taguchi (1982) in Hawaii. Sedimentation rates at Tikehau are however four times lower than the values for organic deposition in the lagoon of One Tree Island (Australia) given by Koop and Larkum (1987) and are also 2.4 times lower than the POC deposition rate found by Chardy and Clavier (1989) in New Caledonia.

The mean sedimentation rate of total pigments (*i.e.* : 0.23 mg m^{-2} d^{-1}) is four times lower than sedimentation rate given by Taguchi (1982) in Hawaii and four times lower than Chl a deposition rate calculated from Chardy and Clavier (1989) in New Caledonia.

The average POC:PON:POP ratio on a mass basis in trapped material was 117:12:1 while the ratio in suspended material estimated during trapping experiment was 68:7:1. The loss of phosphorus in trapped particles indicates that organic matter was dead and that a non-negligible part of POM is mineralized in the water column. This was latter confirmed by ATP measurements in trapped materials which were all zero.

Table 5 : Mean (16 data) trapping rate (TR ; mg m^{-2} d^{-1}), settling velocities (SV ; m d^{-1}) and C:N:P ratio (w/w) of trapped material measured at Faufaa station, south of the Tikehau lagoon.
In brackets, coefficient of variation (%)

Chl a		Phaeo a		POP		POC		PON		C:N:P
TR	VS	TR	VS	TR	VS	TR	VS	TR	VS	
0.11	0.6	0.12	1.4	3.2	1.7	350	2.6	36	2.2	117:12:1
(66)	*(72)*	*(67)*	*(74)*	*(78)*	*(25)*	*(94)*	*(116)*	*(97)*	*(104)*	

Origin of lagoonal POM

Findings of Charpy and Charpy-Roubaud (1990b) indicate that the detritus pool (84% of POC) originates in lagoonal primary production whereas detritus reef flat export toward the lagoon is insignificant. The phytoplankton production ingested and then excreted as fecal pellets by zooplankton cannot alone explain the levels of POC sedimentation rate. Export of POM from lagoon pinnacle reefs may thus be the other major POC source.

NUTRIENT BUDGET

Fluxes between lagoon and ocean can be estimated by :

Flux (mmol m^{-2} d^{-1}) = F \f(Cl-Co,Ls)

Where F is the annual average flow through the pass and the reef-flat spillways (6 10^8 m^{-3} d^{-1} in Lenhardt, 1991), Ls is lagoon surface (4.2 10^8 m^2) and Cl and Co are concentration of total nitrogen (ΣN), total phosporus (ΣP) or silicate in the lagoon - Cl -and ocean - Co - ($\Sigma N = NO_2+NO_3+NH_4+DON+PON$ and $\Sigma P = PO_4+DOP+POP$ where DON and DOP are dissolved organic nitrogen and phosphorus concentrations). Average concentrations in the lagoon and ocean are recapitulated in Table 6.

If we compare this data with the water composition at Christmas Island given by Smith *et al.* (1984), we observe that Tikehau surrounding waters present similar ΣP concentration but lower ΣN and silicon concentrations. Inside the lagoon, nutrient concentrations are quite similar exept for the silicon which was 3.5 times higher in Christmas Island.

Table 6 : Average concentrations ± 95% confidence intervals (mmol m^{-3}) of total nitrogen (ΣN), total phosphorus (ΣP) and silicate in oceanic (Co) and lagoonal waters (Cl) (from Charpy-Roubaud *et al.*, 1990).

Nutrient	Ocean waters	Lagoon waters
NH_4	0.80	1.90
NO_2	0.04	0.02
NO_3	0.30	0.09
DON	2.30	4.60
PON	0.40	1.40
ΣN	3.80 ± 1.30	8.01 ± 0.90
PO_4	0.38	0.16
DOP	0.26	0.39
POP	0.02	0.10
ΣP	**0.66 ± 0.12**	**0.65 ± 0.06**
SIO2	1.00± 0.20	0.80± 0.40

Nitrogen budget

During their crossing over the reef-flat and their residence in the lagoon, oceanic waters become impoverished in NO_2 and NO_3 and enriched in NH_4 and organic nitrogen. The total nitrogen concentration in the lagoon is roughly twice as great than in the ocean (*i.e.* : 8.0 mmol N m^{-3} *vs* 3.8 mmol N m^{-3} in ocean). Therefore, according to the flux equation, the nitrogen concentration of oceanic water increases at a rate of 0.6 mmol N m^{-2} d^{-1} during its residence time in the lagoon.

Increase in the nitrogen content of water flowing above the reef-flat is attributed to gaseous nitrogen fixation mostly by cyanobacteria of which a great variety occur on limestone substrata of coral reefs. At Tikehau, large quantities of cyanobacteria (*i.e.* : 150,000 cells ml^{-1}) were recorded in the lagoon water column by Blanchot *et al.* (1989). Charpy-Roubaud *et al.* (1989) have estimated that their productivity, added to that of benthic cyanophycean communities, is 0.69 g C m^{-2} d^{-1}. This carbon production would require nitrogen assimilation of approximately 3.6 mmol N m^{-2} d^{-1}, part of which could originate from dissolved molecular nitrogen.

Phosphorus budget

Mineral phosphorus (PO_4) water content decreases and organic phosphorus (DOP+POP) content increases during crossing of oceanic waters over the reef edge and during the residence time in the lagoon. Depletions of reactive phosphorus below oceanic levels were also observed by Smith (1984) and Smith and Jokiel (1975) in Christmas Island and Canton Atoll lagoons, both located in the Pacific. The total phosphorus concentration in the lagoon (ΣP = 0.65 mmol P m^{-3}) is of the same order of magnitude than phosphorus in the surrounding oceanic waters (ΣP = 0.66 mmol P m^{-3}). The phosphorus budget therefore appears to be well balanced.

The pattern of production emerging from all the foregoing discussion is that the high primary production over the reef and in the lagoon results from an input of nitrate and phosphate from enriched oceanic waters, from a great gaseous nitrogen fixation by cyanobacteria and from the mineralization of organic compounds in the lagoon.

NUTRIENTS IN SEDIMENTS OF THE LAGOON : FIRST RESULTS

Nutrient mineralization may occur in the water column (excretion and bacterial metabolism), at the sediment-water interface (hereafter expressed SWI) or within the sediments. The importance of recycling of autochtonous material at SWI and within sediments was estimated by measuring nutrient fluxes at the sediment-water interface. Two different approaches were used in order to assess these fluxes. These were : 1) direct measurement which uses a benthic chambers technique described by Hall (1984), carrying out the experiments in oxic (supply with oxygen) and anoxic (asphyxiation) dark conditions and 2) calculations through measurements of chemical gradients close to SWI, in peeper, following method previously described by Hesslein (1976). The results presented here have to be considered as preliminar.

Nutrients in sediment were studied at four sampling stations shown in Fig. 6.

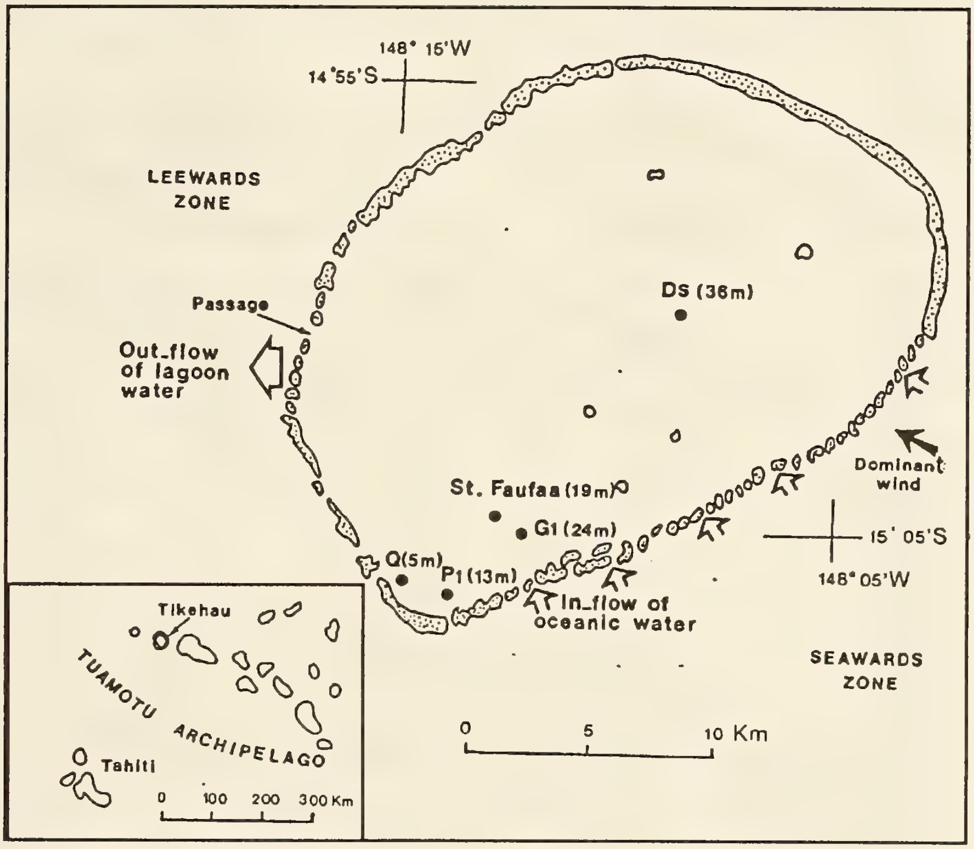

Fig. 6 : Location of sediment flux sampling stations (e.g. : Ds, G1, Q, P1 and Station Faufaa).

Dark benthic chambers were used at stations Q and P1 because of the shallowness of these sites. In order to compare fluxes measured in oxic and anoxic conditions, the only analytical results taken into account are those obtained after oxygen depletion was achieved in the non-O_2 supplied chamber (hereafter termed asphyxiated chamber). Fluxes (F in μmol m^{-2} d^{-1}) can be estimated from the slope dC/dt of a plot of concentrations versus time multiplied by the ratio of supernatant-water volume V to chamber area S (V = 0.025 m^3; S = 0.11m^2). The formula is :

F = \f(dC,dt) x \f(V,S)

The *in situ* peeper sampling method was used at three stations (DS, G2 and P1 see Fig. 6)

Benthic chambers

Variations of the chemical composition of water enclosed in the benthic chambers *vs* time is shown on Fig. 7. NO_3 and NO_2 concentrations do not appear because they were below the detection limit (<1 mmol m^{-3}).

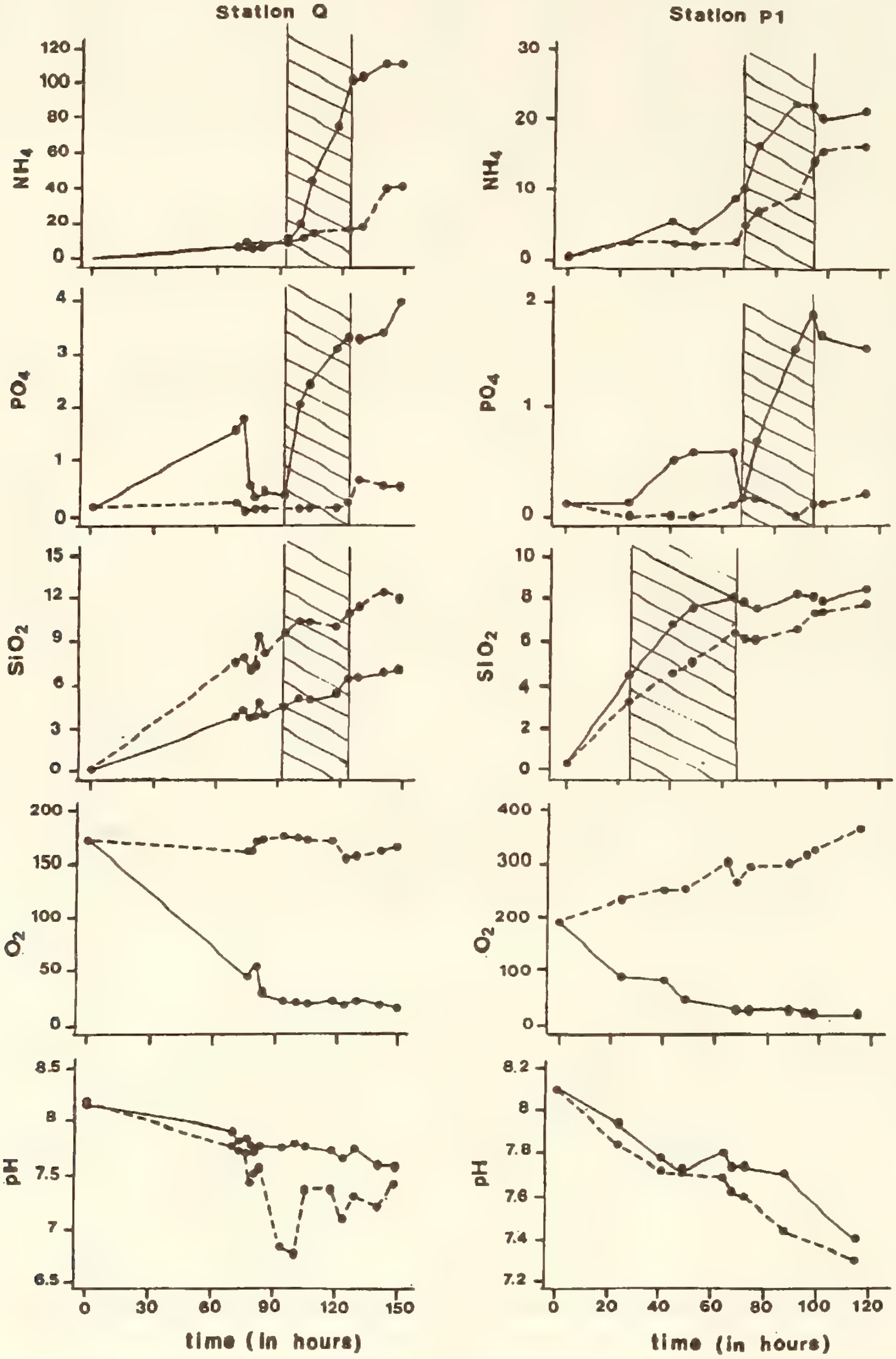

Fig. 7 : Evolution of inorganic nutrients (mmol m^{-3}), dissolved O_2 (mmol m^{-3}) and pH of overlying water inside asphyxiated and oxygenated dark benthic chambers at station Q and P1. Nutrient fluxes are calculated in the shaded area.

Station Q : In the asphyxiated chamber, O_2 concentration decreases with time and was less than 30 mmol m^{-3} after 90 hours of incubation while nutrient concentrations sharply increased. In the oxygenated chamber, a slight increase in concentration was observed for NH_4 and SiO_2 , but the PO_4 concentration remained nearly constant at a very low level. The concentration plateau that was observed after 125 hours was most likely due to a steady state occuring between enclosed and interstitial waters. Therefore fluxes are calculated between 90 and 120.25 hours, figured by the shaded area on Fig. 7.

Station P1 : Oxygen depletion in asphyxiated chambers occured after 69 hours. The same trends were observed for PO_4 and NH_4 like at station Q in both chambers. Silica concentrations exhibit a plateau after 65 hours of incubation. NH_4 and PO_4 fluxes were therefore calculated between 68.75 and 95.25 hours while the SiO_2 flux was calculated between 24 and 64.5 hours.

The foregoing drives to notice that an increase in NH_4 and PO_4 occurs in asphyxiated chambers at both sites. When oxygen concentration is preserved, a slight increase occurs in NH_4 while PO_4 remains constant at a very low level. Dissolved silica exhibit similar patterns at both sites and do not seem to be related to oxic/anoxic conditions. Calculations of nutrient fluxes are summarized in Table 7.

Table 7 : Dissolved nutrient concentration increases (dC in µmol m^{-3}) during dt = 30.25 hours at station Q and dt = 26.5 hours at station P1 and fluxes (F in µmol m^{-2} d^{-1}) from the sediments of the Tikehau lagoon. asph. = asphyxiated chamber; oxy. = oxygenated chamber.

		NH_4		PO_4		N/P		SiO_2	
Station	param.	asph.	oxy.	asph.	oxy.	asph.	oxy.	asph.	oxy.
Q	dC	92.7	6.6	2.9	0.21			1.8	1.5
	dt	30.25	30.25	30.25	30.25			30.25	30.25
	F	**16.71**	**1.18**	**521**	**38**	**32**	**31**	**329**	**274**
P1	dC	12.2	9.2	1.7	0.0			4.7	3.1
	dt	26.5	26.5	26.5	26.5			40.5	40.5
	F	**2.25**	**1.89**	**356**	**0**	**7**		**630**	**411**

As a general trend, fluxes of nutrients are higher in anoxic than in oxic conditions. This is more obvious for PO_4, of which fluxes were close to 0 when oxygen was present but when the oxygen level was less than 0.30 mmol m^{-3}, they reach between 356 and 521 µmol m^{-2} d^{-1} . These differences can be interpreted as the result of biological and/or chemical processes. The biological process can be summarized as follows : the onset of anoxia allows some micro-organisms to metabolize organic material in the upper part of the sediment column (*i.e.* : increase in NH_4 flux may be due to amnonifier metabolism). Anoxia can possibly kill aerobic micro-organisms at SWI which in natural conditions have a dark uptake of N and P without any silica requirement. The chemical process can be that in oxic conditions, scavenging of P onto $FeOOH_2$ is commonly observed in marine sediments. Therefore, fluxes measured in asphyxiated chambers probably overestimate actual fluxes while those obtained when oxygen is present can estimate a nutrient availability for lagoonal primary producers.

Pore water

Pore-water profiles of nutrients display significant concentration gradient with depth as shown in Fig. 8. These gradients are maximum within the first top centimeters and correlated with the decrease in pH. Pore-water nutrient concentrations increase with depth, being greater at deep sampling stations. H_2S appears to be below the SWI, at about 1 cm depth at station DS and 5 cm at P1 and G2.

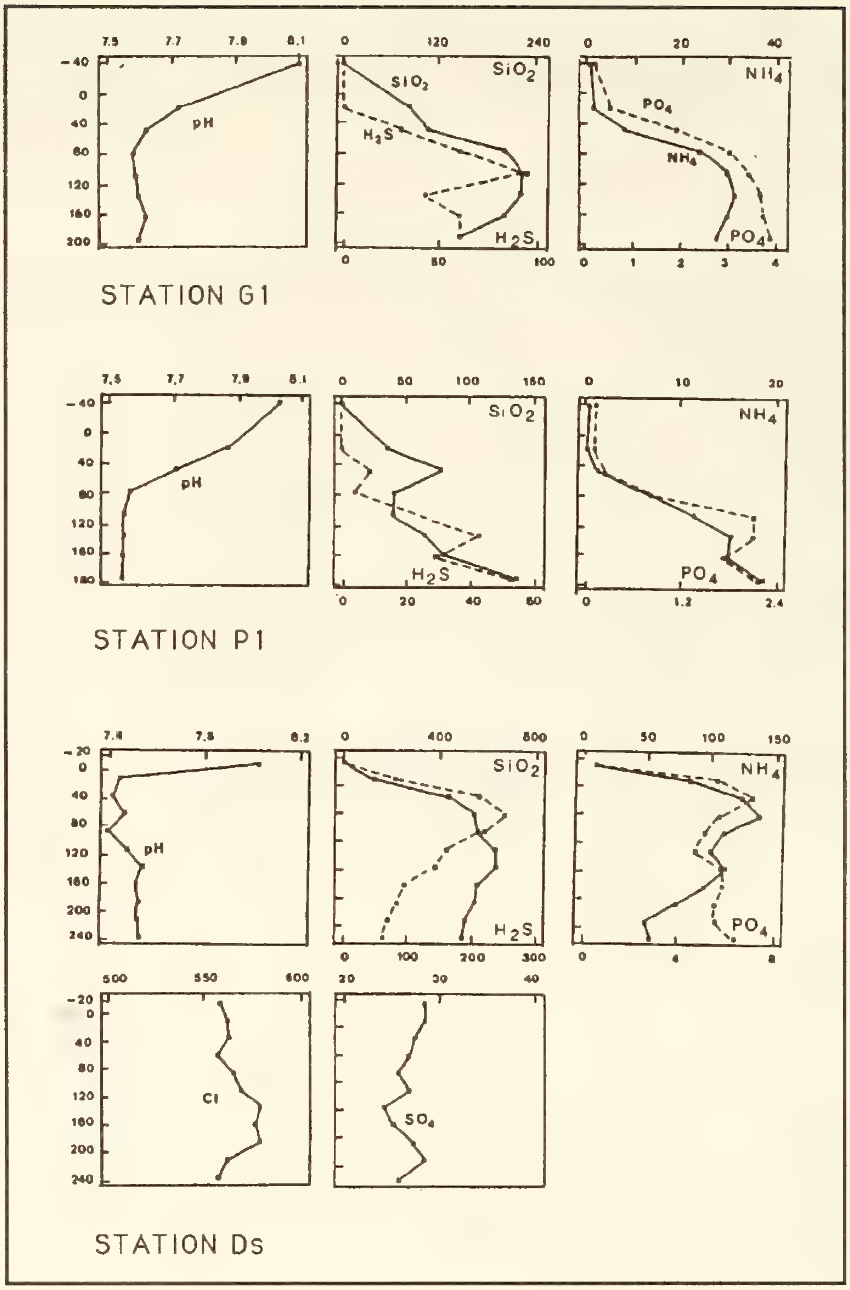

Fig. 8 : Variations of pH, inorganic nutrients (µmol m^{-3}), hydrogen sulphide (µmol m^{-3}), chloride (mmol m^{-3}) and sulphate (µmol m^{-3}) in sediment pore-waters at various stations (G1, P1 and Ds) in Tikehau lagoon .

The acidification of pore water downward in the sediment core, reflects the increase in total dissolved CO_2 related to mineralization processes. At the top of the sedimentary column, dissolved O_2 is the main electron acceptor. Oxygen is replaced downward by sulfate and H_2S appears in profiles owing to sulfate reduction. Deeper, there is a decrease in H_2S concentrations which is probably linked to a chemical control by FeS precipitation.

Positive gradient of concentrations close to SWI allow diffusion of nutrients from medium pore water to overlying sea water. PO_4 concentrations are lower than NH_4 concentrations (*i.e.* : 7 mmol m^{-3} PO_4 against 137 mmol m^{-3} NH_4). However, phosphate has been shown to strongly adsorb on calcium carbonate. This has been used to explain why calcium carbonate-rich sediments contain low concentrations of dissolved phosphate in their pore waters (Krom and Berner, 1980).

The calculation of fluxes (F in µmol m^{-2} d^{-1}) using pore water data can be calculated after Fick 1st law. The equation can be written :

F = Ø x Ds x \f(dC,dz)

where Ø is the interconnected porosity estimated at 0.70 ± 0.01, Ds is the *in situ* diffusion coefficient in m^2 d^{-1} where tortuosity is taken into account, dC/dz is concentration gradient in µmol m^{-4} when z tends toward zero. Results are presented in Table 8. They show that for each nutrient, flux increases with lagoon depth.

Table 8 : Average ± SE of dissolved nutrient fluxes calculated with pore-water gradient concentrations (µmol m^{-2} d^{-1}).

Station	NH_4	PO_4	SiO_2
Ds	493 ± 192	13 ± 5	466 ± 164
G1	11 ± 5	0.5 ± 0.3	164 ± 68
P1	0	0	68 ± 27

Comparisons between calculated fluxes with pore water data and observed fluxes in benthic chamber

Observed fluxes for ammonium in oxygenated and asphyxiated chambers are much greater than fluxes calculated using pore water data (which are close to 0). Observed fluxes for PO_4 are higher in asphyxiated chambers. Observed fluxes for Si are 6 to 9 times higher than calculated fluxes. Therefore, diffusion processes through SWI are unable to explain NH_4, PO_4 and Si fluxes observed in an asphyxiated chamber, but can explain the light PO_4 flux and 17% of Si flux measured in oxygenated chamber. The enhancement of transport across the interface may be due to bioturbation of sediment located in the upper part of sedimental layer. Nutrients coming into benthic chambers are then uptaken following different rates depending on oxygen conditions and on the elements considered ; P is probably uptaken more quickly than N and Si. So in this kind of environment, it seems more realistic to define a dispersion coefficient rather than a diffusion one. For dissolved silica, the dispersion coefficient is $5.7\ 10^{-5}$ cm^2 s^{-1}, about 10 times greater than difusion coefficient Ds (*i.e.* : Ds = $6.5\ 10^{-6}$ cm^2 s^{-1}). Therefore, nutrient fluxes measured in oxygenated chamber are assumed representative of real fluxes.

LAGOON PRIMARY PRODUCTION

PHYTOPLANKTON PRODUCTION

Phytoplankton of coral-reef ecosystems have often been considered as a low primary producer since the overwhelming majority of coral-reef studies were carried out in shallow ecosystems. In atoll lagoons, the reef area *vs* the total area (reef and lagoon) ratio is low. Lagoonal plankton may thus be a major contributor to total primary productivity of the ecosystem as a whole.

Carbon production

Table 9 gives an account of the average of mean carbon assimilation rates (hereafter expressed AC) by depth intervals measured through an estimation of ^{14}C and ^{32}P assimilation rates. The average AC is clearly related to depth, being higher in the surface layer than at other depths. No photoinhibition at high light intensity occur.

Table 9 : Average carbon assimilation rate (AC ; mg C m^{-3} h^{-1}) and assimilation number (AN ; mg C mg^{-1} Chl-a h^{-1}) in relation with depth (n = number of samples) (from Charpy-Roubaud *et al.*, 1989).

Depth (m)	n	AC	AN
0 - 2	52	3.92 ± 1.02	21.1 ± 7.5
2 - 5	22	2.27 ± 0.67	13.0 ± 5.1
5 - 10	42	2.68 ± 1.33	13.5 ± 4.9
10 - 15	21	2.00 ± 0.72	11.2 ± 5.6
15 - 20	7	1.17 ± 1.15	4.7 ± 3.5
20 - 24	2	0.54	4.2

Phytoplankton production integrated up to 15 m depth drops during May, June and August. This decrease is correlated with light energy reduction that occurs in winter of the southern hemisphere. Phytoplankton biomass is low (*e.g.* : 0.18 ± 0.01 mg Chl-a m^{-3}) but this is typical of coral reef ecosystems. Biomass is greater in May, June and July while conversely, production rates are lowest. Concentrations in the lagoon are approximately three times greater than those found in surface oceanic waters.

Daily phytoplankton production estimated for each bathymetric intervals reaches an average of 0.44 g C m^{-2} d^{-1} for the entire lagoon, equivalent to 0.012 g P m^{-2} d^{-1}. This value is high compared to the low phytoplankton biomass measured. The representative assimilation number estimated from the average hourly production (*i.e.* : 44 mg C m^{-2} h^{-1}) and the average chlorophyll integrated over 25 m (4.86 mg m^{-2}) is 9.8 mg C mg Chl a^{-1} h^{-1}, a value characteristic of small-sized plankton. The assimilation number is conspicuously high in the surface layer (*i.e.* : 21 mg C Chl-a h^{-1}). Approximately 1.4% of daily production is lost by sedimentation of organisms while the exit of particles out of the lagoon represents a loss of 0.2%.

Phytoplankton biomass and composition

Charpy (1985) and Blanchot *et al.* (1989) had previously shown that a great part of lagoon phytoplankton is made up of cells smaller than 5 µm with cyanobacteria dominating. Cyanobacteria can contribute to up to 75% of the carbon production of plankton primary producers. Table 10 allows comparison between phytoplankton production of waters pre-filtered on Nucleopore 5µm and of waters unfiltered. The percentage of total production due to phytoplankton of a size smaller than 5µm varies in a spread of 13 to 90% with average at 38 ± 10%, whereas the percentage of 0-5 µm chlorophyllian organisms is 61 ± 12% on the average in unfiltered waters. It appears that the smallest cells are being differentially ruptured to a greater extent than large cells, leading to an underestimation of carbon uptake (but not chlorophyll content) by the smallest cells.

Table 10 : Phytoplankton Carbon assimilation (mg m^{-2} h^{-1}) in samples filtered on 5µm (AC<5µ) and without filtrations (ACt); AN = assimilation number (mg Chl a^{-1} h^{-1}); %AC = AC<5µx100/ACt; %Chl = percent of chlorophyll passing through 5 µm filter (from Charpy-Roubaud *et al.*, 1989).

Date	St.	Depth	ACt	AC<5µ	%AC	ANt	AN<5µ	%Chl
24 Jul 83	2	0	4.9	2.3	47	13.3	7.3	86
		5	2.8	2.3	82	7.4	6.4	95
		10	3.2	1.8	56	9.0	4.9	99
26 Jul 83	9	0	4.0	2.6	65	14.7	14.0	68
		5	3.1	2.8	90	10.0	12.4	73
		10	3.7	2.0	53	11.8	8.6	74
23 Nov 83	6	0	5.6	2.5	44	18.7	12.4	67
24 Nov 84	6	0	2.6	1.5	58	11.7	8.3	81
		2	2.5	1.3	51	12.4	7.2	90
		10	3.6	1.5	42	17.2	8.3	86
		15	2.5	1.1	44	13.2	6.1	95
27 Jan 85	6	0	2.2	0.4	18	10.0	3.9	47
12 Jul 85	6	0	4.5	0.6	14	15.4	3.8	54
13 Aug 85	6	0	2.1	0.3	14	10.2	4.9	30
		2	1.4	0.2	14	5.5	4.5	17
		4	1.5	0.3	20	7.9	5.7	28
		6	1.4	0.2	15	8.2	4.5	26
		8	1.1	0.2	18	7.0	4.1	31
		10	0.9	0.2	28	4.7	5.7	18
		15	0.7	0.1	18	3.3	2.6	18
14 Aug 85	6	0	1.2	0.3	25	5.5	3.1	44

Relationship between phytoplankton production and light energy

Phytoplankton production is significantly correlated with light energy. Phytoplankton production (PP in mg C $m^{-3}\ h^{-1}$) can be estimated from the equation :

$$PP = 1.29\ Eh^{0.39}$$

where Eh is incidental light energy in E $m^{-2}\ h^{-1}$.

MICROPHYTOBENTHIC PRODUCTION

Carbon production

Primary production was estimated by O_2 budget, measured within clear and dark plexiglass domes. In order to assess the influence of light energy on net oxygen production, measurements of O_2 budgets were carried out continuously at various depths. Net O_2 production and light energy were positively correlated (r=0.7, n=91) and thus, daily production (DBP) was estimated by equation :

$$DBP\ (mg\ O_2\ m^{-2}\ d^{-1}) = P_{t\text{-}to} \times \backslash f(Ej\ ,Et\text{-}to)$$

where $P_{t\text{-}to}$ = net production in mg O_2 m^{-2} during incubation period t-to

Ej = Daily incidental light energy in E $m^{-2}\ d^{-1}$

$E_{t\text{-}to}$ = Incidental light energy in E $m^{-2}\ d^{-1}$ during incubation period t-to

The mean hourly respiration rate measured in dark domes was 31 ± 7 mg O_2 m^{-2} with a respiratory and photosynthetic coefficient chosen as being equal to 1 for latter conversion in carbon production. By averaging production by depth intervals, the overall lagoon microphytobenthos production was found to be equal to 0.25 gC $m^{-2}\ d^{-1}$. This value is of the same order of magnitude as production values for tropical marine sediments reviewed by Charpy-Roubaud (1988).

Benthic carbon production (BP) can thus be related to incidental light energy (Eh in E $m^{-2}\ h^{-1}$) by the equation :

$$BP\ (mg\ C\ m^{-2}\ h^{-1}) = 28.78\ Eh^{0.45}$$

Biomass

Microphytobenthic biomass was measured in 185 samples taken at different stations and at different time of the year. There are considerable variations among sampling stations. The average total chlorophyll biomass is 19.7 ± 1.4 mg m^{-2} whereas the average active chlorophyll is 9.6 ± 1.4 mg m^{-2}. The mean hourly assimilation number estimated from the latter biomass is of 2.6 mg C mg chlorophyll^{-1} h^{-1}. Biomass is significantly higher in the 0-3 m depth interval than in deeper intervals.

COMPARISON BETWEEN PHYTOPLANKTON AND MICROPHYTOBENTHIC PRIMARY PRODUCTION

Fig. 9 shows phytoplankton, microphytobenthic and total primary production by a 5 m depth interval. Total primary production is slightly the same whatever the depth interval is. Phytobenthic production is greater than phytoplankton production within the first 10 meters, being 25 times higher in the 0-5 m depth interval. From 20 m downward, phytoplankton is the major contributor to total primary productivity of the whole ecosytem. On the average, phytoplankton primary production is 1.8 times greater than phytobenthic production.

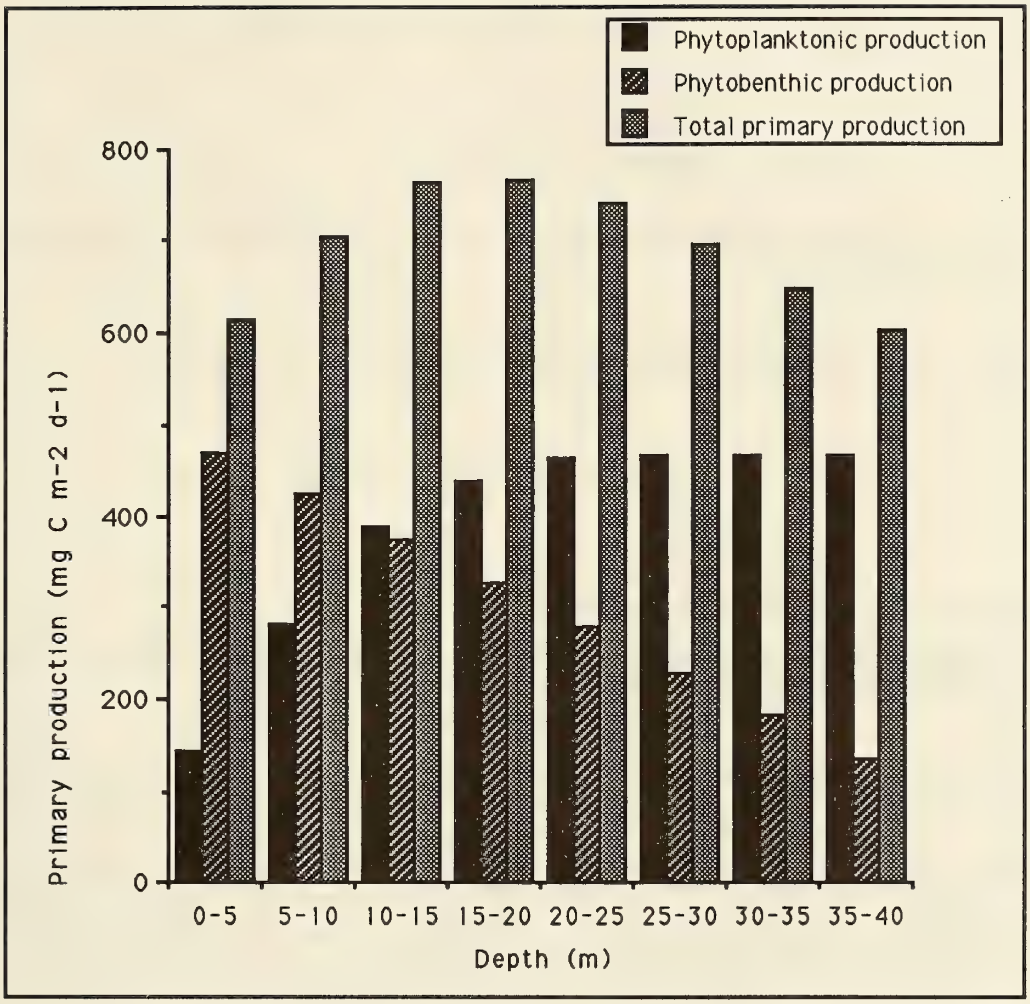

Fig. 9 : Benthic, planktonic and total primary productions in the Tikehau lagoon by a 5 m depth interval (from Charpy-Roubaud, 1988).

RELATIONSHIP BETWEEN LIGHT AND PRIMARY PRODUCTION IN THE LAGOON.

Light energy

Percentages of light energy measured at surface decreases with depth d (m) according to the equation :

$$\% \text{ of incident energy} = e^{(4.45 - 0.06d)}$$

It was measured that 17% of surface light energy reached 25 m (average depth of the lagoon).

Phytobenthos and phytoplankton production

According to the foregoing sections, phytoplankton production (PP) can be related to incidental light energy (Eh) with a standard error of 0.6 mg C m^{-3} h^{-1} by the equation :

$$PP = 1.29\ Eh^{0.39} \qquad (1)$$

Phytoplankton production per unit volume can then be converted into production per unit area according to the equation :

$$PPd = \int_0^d PPz\,dz \qquad (2)$$

where PPd (mg C m^{-2} h^{-1}) = production at depth d per unit area, PPz (mg C m^{-3} h^{-1}) = production at depth z per unit volume.

Using equation (1) and (2), phytoplankton production is related to light by the equation :

$$PPd = \int_0^d e^{0.254}\ [e^{(4.45-0.06z)}E_{hs}\ /100\ ]^{0.39}$$

where Ehs (E m^{-2} h^{-1}) is light energy at the surface.

Similary, the relationship between phytobenthos production at depth d (BPd in mg C m^{-2} h^{-1}) and light energy Ehs at surface level can be written :

$$BPd = 28.78\ (e^{(4.45-0.06d)}\backslash F(Ehs,100))^{\,0.454} \qquad (3)$$

Predicted plankton and benthic production were calculated at depths between 0 and 36 m (*i.e.* : maximum depth of the lagoon) for different Ehs values observed in natural conditions (1 - 8 E m^{-2} h^{-1}). Results presented in Fig. 10 indicate that phytobenthos production exceeds phytoplankton production in the upper 18 m. The total primary production (PT) is relatively constant with depth and depend primarily on light energy reaching the surface. Therefore, an average PT can be obtained for each Ehs value and subsequently, a linear relation linking PT and Ehs, *i.e.* :

$$PT = 6.5\ Ehs + 31.5$$

Therefore, daily total production PTd can be calculated assuming a sun time of 10 hours a day by the equation :

$$PTd\ (mg\ C\ m^{-2}\ d^{-1}) = 6.5\ Eds\ (E\ m^{-2}\ d^{-1}) + 315 \qquad (4)$$

The PTd value for Eds = 0 is 315 mg C m^{-2} d^{-1}; may be interpreted as the respiration in the water column and sediments. Daily light energy data obtained in 1986 can be converted into daily primary production using equation (4). Monthly averages of PTd are plotted in Fig. 11. Over the entire year, the surface lagoon received a total of 15,550 E m^{-2} of which water column and sediments produced a total of 216,709 mg C m^{-2}, equivalent to a daily average of 0.59 mg C m^{-2} d^{-1}, not very different of the value of 0.69 mg C m^{-2} d^{-1} estimated through field experiments.

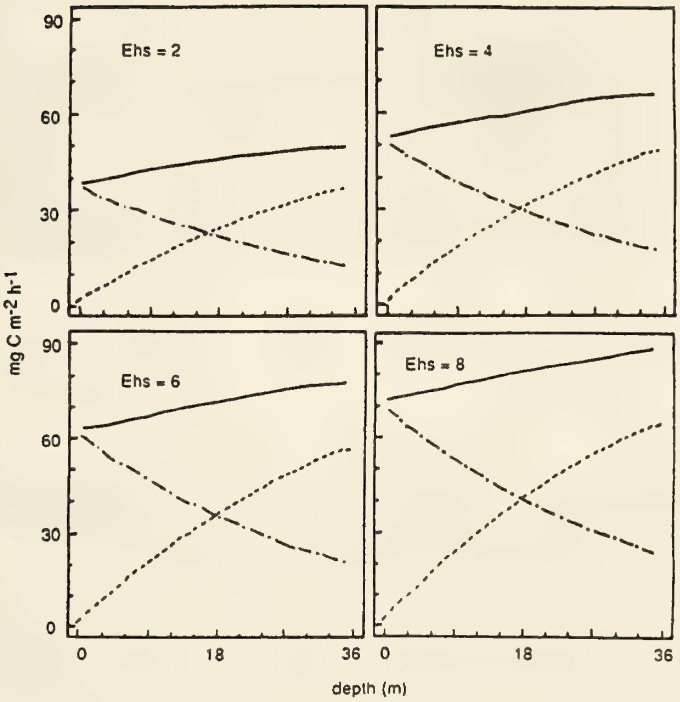

Fig. 10 : Predicted phytoplankton production (dashed line), phytobenthic production (dotted line) and total production for different surface light energy levels (Ehs : E m^{-2} h^{-1}) in Tikehau lagoon from Charpy and Charpy-Roubaud (1990a).

The photosynthetic efficiency of lagoonal communities can be summarized as follows :

- One mg of Chl a allows an hourly growth production of 4.2 mg carbon
- One Einstein reaching lagoon surface allows the growth production of 14 mg of organic carbon in the water column and sediments.

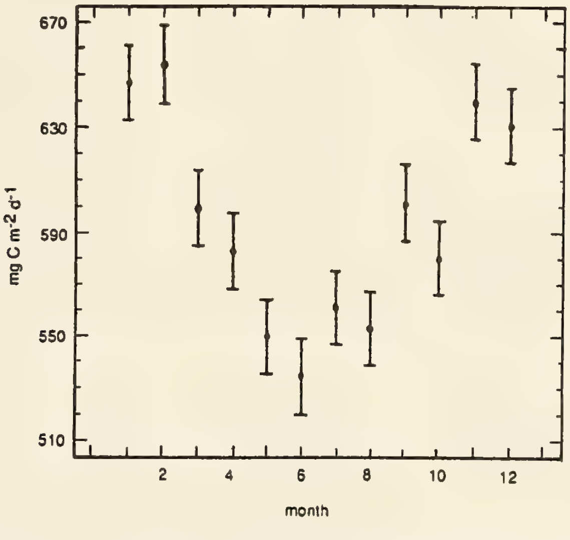

Fig. 11 : Monthly averages and confidence intervals (p=95%) of predicted total primary production (plankton and benthos) in 1986 in Tikehau lagoon (from Charpy and Charpy-Roubaud, 1990a).

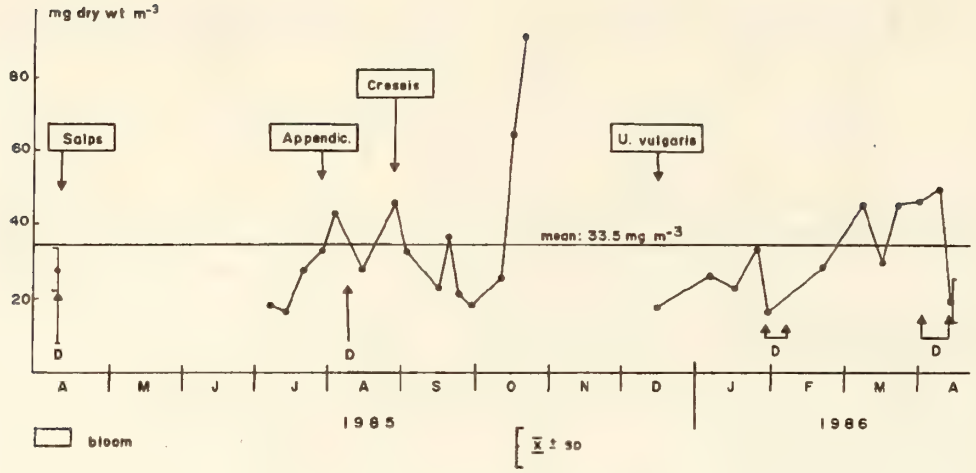

Fig. 12 : Variations in mesozooplankton dry weight from April 1985 to April 1986 in the Tikehau lagoon. Blooms of *Thalia democratica* (Salps), appendicularians (Appendic.), the pteropod *Creseis chierchiae* and the copepod *Undinula vulgaris* are shown. D : large amount of detritus (from Le Borgne *et al.*, 1989).

Table 11 : Relative contributions (%) of the main taxa to total zooplankton biomass in Tikehau lagoon. Percent contributions of non-living organisms (detritus) to total dry weight is also shown (from Blanchot and Moll, 1986 and Blanchot *et al.*, 1989).

[a]: Three samples of mesozooplankton were measured in April 1986 (from Le Borgne *et al.*, 1989).

Date	Size class	Taxon	% total biomass	% detritus
April 1985	Microzooplankton 35-200 µm	nauplii	39.2	70
		copepods	30.6	
		bivalve larvae	19.8	
		polychaete larvae	10.4	
	Mesozooplankton 500-2000 µm	copepods	68.4	14
		chaetognaths	19.3	
		salpids	8.8	
	Macrozooplankton >2000 µm	salpids	63.2	
		copepods	22.8	
		chaetognaths	1.8	
April 1986	Mesozooplankton 200-2000 µm	copepods	73.8	3,10,49[a]
		larvaceans	5.0	
		brachyuran larvae	8.7	
		chaetognaths	5.6	

ZOOPLANKTON BIOMASS AND METABOLISM

The fate of the abundant particulate organic matter in the Tikehau lagoon and the level of efficiency of utilization by consumers are two aspects which are of primary importance to an understanding of the functioning of the lagoon pelagic food-web. Once sunk to the bottom, is seston consumed mostly by pelagic animals in the water column or by benthic ones ? Do they give rise to a significant predator biomass or is the efficiency of energy transfer between food and consumers low ? In order to provide answers to these questions, zooplankton have been studied at Tikehau during two 10 d periods in April 1985 and April 1986, and additionally by weekly samples taken in between.

ZOOPLANKTON BIOMASS

Fraction 3 to 35 µm (nanozooplankton)

An average number of 71 ± 14 heteroflagellates ml^{-1} and 7 ciliates ml^{-1} were found in samples taken in April 1986 in the lagoon. The mean individual volumes were of 542 ± 96 μm^3 for heteroflagellates and of 14 246 ± 7 427 μm^3 for cilates. In order to assess the relative biomass of these taxa, mean individual volumes were converted into carbon using a conversion factor chosen equal to 0.08 pg C μm^{-3} according to Sherr *et al.* (1984). The average biomass of heteroflagellates is approximately 3.1 ± 0.7 mg C m^{-3} while ciliate biomass is 7.6 ± mg C m^{-3}. These values are of the same order of magnitude as those found by Hirota and Szyper (1976) in Hawaii though the method used does not make any difference between dead and live plankters.

Fraction 35 - 200 µm (microzooplankton)

Microzooplankton consists of 43% of organisms smaller than 100 µm of which 73% are protozoans (tintinnids *Rhabdonella* sp., *Codonellopsis* sp. and *Epiplocyclis* sp. accounting for 64% ; naked ciliates for 5%). Foraminifers and radiolarians are poorly represented (less than 1%). Metazoans account for only 27%. The second most abundant taxon smaller than 100 µm consists of naupliar copepods (18%) and the third of meroplankton bivalve larvae (8%). Out of organisms larger than 100 µm, protozoans account for 33% of total numbers of which 23% are tintinnids. Metazoans are noticeably dominant, accounting for 67% of the total. Copepod nauplii are the most abundant organisms (41%). Bivalve larvae do not exceed 7% of total numbers.

By using a C/ATP ratio of 125, live microzooplankton biomass can be estimated at 1.52 mgC m^{-3}. Together with nanozooplankton, biomass of heteroprophs smaller than 200 µm reaches a value of 3.3 mg C m^{-3}.

Fraction 200 - 2000 µm (mesozooplankton)

Variations in mesozooplankton dry weight were monitored as regularly as possible in the lagoon and displayed a measurement of two maxima in October 1985 (65 and 93 mg dry wt m^{-3}). Zooplankton at Tikehau are characterized by periodic blooms of copepods, larvae, pteropods and salpe. As shown in Fig. 12, the annual mean value is 33.5 mg m^{-3}, which is six times greater than the oceanic plankton concentrations measured in the vicinity of the pass (*i.e.* : 5.4 mg m^{-3}). Relative contributions of various size classes and taxa to zooplancton biomass are displayed in table 11.

Table 12 : Live biomass and detritus in terms of C, N, P estimated from the percentage of detritus in seston and from particulate organic carbon values in the Tikehau lagoon. - a : ATP x 125 b : POC - (ATP x 125)

Size class (µm)	year	Live			Dead		
		C	N	P	C	N	P
35-200	1985	0.36	0.07	0.03	0.84	0.16	0.06
	1986	1.02	0.19	0.08	2.37	0.45	0.18
	1986	1.5a			2.30b		
200-2000	1985	5.22	0.98	0.39	0.85	0.16	0.06
	1986	2.80	0.53	0.21	0.74	0.14	0.06
	1986	2.5a			4.4b		
> 2000	1985	3.23	0.61	0.24	0	0	0
	1986	0			0		

Table 13 : Metabolic atomic ratios and contribution of inorganic excretion to total excretion (%) in the Tikehau lagoon. $O:O_2$ respired; NH_4, Nt, PO_4, Pt : ammonia, total nitrogen, phosphate and total phosphorus excreted. nd : no data (from Le Borgne *et al.*, 1989).

Date	Size class/species	$O:NH_4$	O:Nt	$O:PO_4$	O:Pt	$NH_4:PO_4$	Nt:Pt	NH_4:Nt	PO_4:Pt
April 1985	Microzooplankton	7.2	6.9	144	104	12.1	11.1	85.4	74.4
	Mesozooplankton	10.8	10.8	119	92	11.4	8.6	100.0	76.5
	Undinula vulgaris	18.4	13.2	132	100	7.9	7.9	48.2	43.1
	Thalia democratica	15.5	8.1	103	56	7.4	6.9	58.3	54.3
April 1986	Microzooplankton	nd	7.7	124	96	nd	12.5	nd	77.5
	Mesozooplankton	nd	7.1	144	110	nd	8.4	nd	76.3

Table 14 : Zooplankton. Net growth efficiencies (K_2) in terms of nitrogen and phosphorus for total populations and sorted species or taxa, calculated from N : P ratios of particles (a_1), zooplankton excretion (a_2), and body constituents (a_3). Number of replicates in (brackets) (from Le Borgne *et al.*, 1989).

Date	Size class/species	a_1	a_2	a_3	$K_{2,N}$	$K_{2,P}$
1985	Mesozooplankton (9-10 April)	13.9 (25)	8.6 (4)	15.0 (2)	0.894	0.828
	Undinula vulgaris	13.9 (25)	7.9 (2)	25.7 (2)	0.623	0.337
	Thalia democratica	13.9 (25)	6.9 (12)	20.4 (2)	0.761	0.519
1986	Mesozooplankton (7-9 Apr.)	18.2 (4)	10.8 (2)	26.0 (1)	0.695	0.487
	(10-12 Apr.)	16.3 (4)	10.8 (2)	26.0 (1)	0.695	0.487
	(13-16 Apr.)	13.9 (4)	9.2 (2)	20.5 (1)	0613	0.416
	mean	16.1	8.4	23.3	0.748	0.517
	Mixed copepods	16.1 (12)	8.4	37.6 (1)	0.616	0.264
	Microzooplankton	16.1 (12)	12.5 (6)	16.7 (5)	0.889	0.857

Zooplankton biomass in terms of C, N, P

By removing detritus of samples and by calculating their relative contribution to seston dry weight, live zooplankton biomass can be estimated. Detritus dry weight represents 70% of 5-200 µm particles, between 1% and 21% of 200-2000 µm particles, and 0% of particles larger than 2000 µm. Contributions of carbon, nitrogen and phosphorus to dry weight of detritus and zooplankton taken separately were estimated by Le Borgne *et al.* (1989) enabling them to calculate biomass as shown in Table 12.

METABOLISM

Zooplankton respiration and excretion were measured in three organism size-classes and in species, *Undinula vulgaris* and *Thalia democratica,* which are abundant in the lagoon. Results of metabolic atomic ratios and contribution of inorganic excretion to total excretion are summarized in Table 13. Growth efficiency for the total population and sorted taxa are displayed in Table 14 and assimilation efficiencies of copepods are listed in Table 15. As a general pattern, efficiencies estimated for microzooplankton are greater than for mesozooplankton. Excreted nitrogen and phosphorus are mostly inorganic. They meet 32% and 18% of phytoplankton nitrogen and phosphorus requirements.

Production was then estimated. All P/B ratios presented in Table 16 are greater than 34% which is equivalent to a three day turnover time of the biomass. The turnover rate is shorter for mixed zooplankton, close to one day and even shorter for the salp *Thalia democratica* due to, in all probability, asexual reproduction, high water temperature (29.5 °C) and abundances of food as emphasized by Le Borgne and Moll (1986). On the average, P/B ratios for zooplankton are 5.7 times lower than P/B ratios estimated for phytoplankton.

The nitrogen and phosphorus assimilation rates in Table 17 are the sum of production and total excretion rates. Ingestion is calculated from assimilation and its relevant effficiency.

Table 15 : Assimilation efficiencies (*D*) of C, N, P and their ratios ($a_4=D_N:D_p$ $a'_4=D_C:D_N$). Calculations made by the method of Conover (1966) using organic carbon, nitrogen and phosphorus percentages of dry weight in feces and food. nd : no data (from Le Borgne *et al.*, 1989).

Date	Species	Faeces			Food			D (%)			a_4	a'_4
		C	N	P	C	N	P	C	N	P		
1985	*Undinula vulgaris*	0.40	0.10	0.048	2.36	0.25	0.081	83.6	60.1	38.3	1.57	1.39
1986	Small copepods	0.59	0.17	0.025	15.4	1.86	0.258	96.8	91.0	90.2	1.01	1.06
		0.62	0.09		5.37	0.85	0.139	89.0	89.5	nd	nd	0.99

Table 16 : Production rates in terms of C, N, P (µg mg^{-1} dry wt d^{-1}) and daily P:B ratios at Station 6. Body C, N and P, as percentages of dry weight, allows the conversion of rates into P:B (from Le Borgne *et al.*, 1989).

Date	Sizeclass /species	Production rates			Body constituents			P:B
		C	N	P	C	N	P	(%)
April 1985	Mesozooplankton	164	44.65	3.565	20.7	4.12	0.37	102.0
	Undinula vulgaris	108	29.97	2.604	31.4	8.73	0.76	34.3
	Thalia democratica	190	42.88	5.859	1.91	0.43	0.0725	816.0
April 1986	Mesozooplankton	331	73.64	7.061	38.4	8.50	0.81	86.4
	Mixed copepods	147	39.80	2.346	27.1	7.31	0.43	54.4

Table 17 : Zooplankton. Assimilation and ingestion rates (µg C, N or P mg^{-1} dry wt d^{-1}) in the Tikehau lagoon (from Le Borgne *et al.*, 1989).

Date	Size class/species	Assimilation			Ingestion		
		C	N	P	C	N	P
April 1985	Mesozooplankton	656	71.7	10.57	785	102	15.1
	Undinula vulgaris	515	48.3	7.75	616	80	20.2
	Thalia democratica		56.4	11.28	617	81	16.1
April 1986	Mesozooplankton	724	98.4	13.54	804	109	15.0
	mixed copepods	473	64.6	4.67	526	72	5.2

TROPHIC STRUCTURE AND PRODUCTIVITY OF THE ECOSYSTEM

With all data estimated in the foregoing sections of this chapter, biomass and fluxes of matter in plankton and in benthos can be assessed. In order to enable comparisons between benthic and planktonic ecosystems, standing stocks are in mg C m^{-2} and fluxes in mg C m^{-2} d^{-1}. The trophic web is illustrated in Fig. 13.

We did not measure directly the biomass of bacteria, but we think that we can obtain an order of magnitude by the difference between liv C estimated from ATP and the other biomasses measured or estimated. Therefore, free bacteria biomass (BB) may be calculated with the equation:

$$BB = \text{liv } C_{(< 5\ \mu m)} - \text{phy } C_{(< 5\ \mu m)}$$

with: liv $C_{(< 5\ \mu m)}$ = percentage of $ATP_{(< 5\ \mu m)}$ x ATP x 250

phy $C_{(< 5\ \mu m)}$ = percentage of chl $a_{(< 5\ \mu m)}$ x chl a x (C/chl-a ratio).

The average value C/chl a = 50 (Charpy and Charpy-Roubaud, 1990 b) lies within the range reported by Takahashi *et al.* (1985) for picoplankton and is very close to the ratio of 46 found by Laws *et al.* (1987) for oligotrophic Pacific waters. Therefore :

$$BB = (0.46 \times O.11 \times 250) - (0.5 \times 0.18 \times 50) = 8.2 \text{ mg C m}^{-3}$$

The liv $C_{(5 - 35\ \mu m)}$ is made up of heterotrophs and phytoplankton (4.5 mg C m^{-3}). It can be calculated using $ATP_{(5 - 35\ \mu m)}$ data : 0.54 x 0.11 x 250 = 14.9 mg C m^{-3}. The carbon content of heterotrophs in the size range from 5 to 35 µm was therefore equal to : 14.9 - 4.5 = 10.4 mg C m^{-3}. The biomass of ciliates and heteroflagellates was equal to 1.8 mg C m^{-3} (Table 3), and the difference (= 8.6 mg C m^{-3}) was certainly due to bacteria adsorbed onto the detritus (Charpy, 1985).

The total biomass of bacteria was therefore equal to : free bacteria + adsorbed bacteria = 16.8 mg C m^{-3}. Such a biomass is commonly observed in waters over reefs ; Sorokin (1974) summarizes data for biomasses of bacteria which range from 11 to 170 mg C m^{-3}. More recently, Moriarty *et al.* (1985) reviewed the productivity and trophic role of bacteria on coral reefs. They give biomass values ranging from 19 to 150 mg C m^{-3}. Linley and Koop (1986) observed in the coral reef lagoon of One Tree Island (Great Barrier Reef) a biomass of heterotrophic bacteria ranging from 1.2 to 16.2 mg C m^{-3}, and Hopkinson *et al.* (1987) observed a bacterial biomass of 2 mg C m^{-3} in the water column of Davies Reef (Australia). In Tikehau, in April 1986, the biomass of bacteria was estimated at 17.1 mg C m^{-3} by Blanchot *et al.* (1989). The observed ratio free bacteria / adsorbed bacteria = 2 is consistent with the ratios given by Moriarty (1979) and Moriarty *et al.* (1985) in coral reef areas.

The estimated bacterial biomass was 2 times higher than the phytoplanktonic C in the Tikehau lagoon. Dominance of bacterial biomass was also observed in the oligotrophic waters of the Sargasso Sea by Fuhrman *et al.* (1989); the interpretation of these authors was that bacteria consume sigificant amounts of carbon probably released from phytoplankton directly or via herbivores.

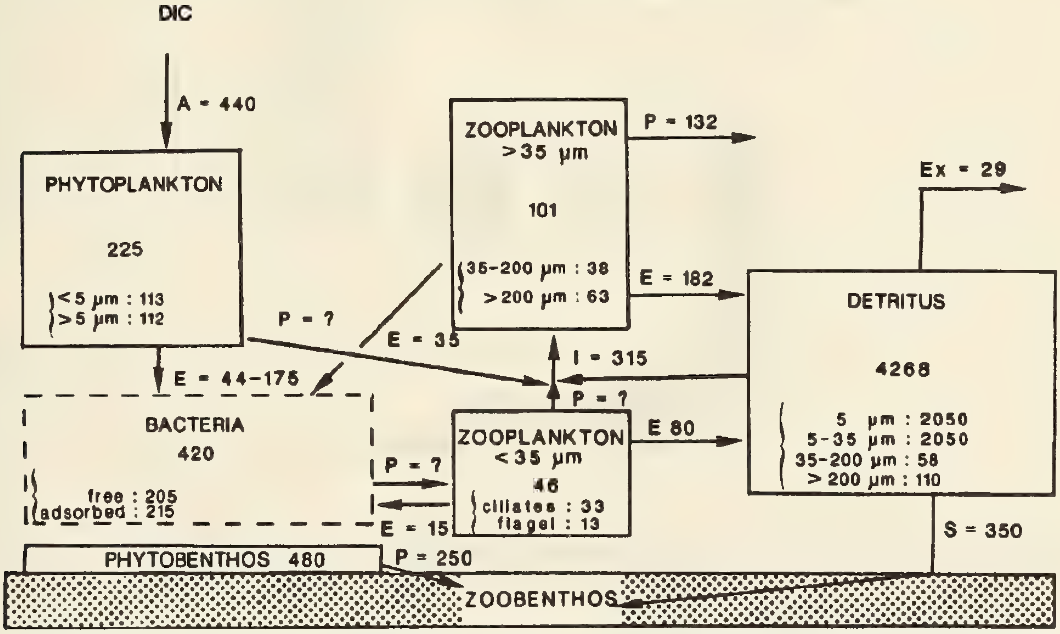

Fig. 13 : Trophic structure and productivity of the Tikehau lagoon communities. Standing stocks (mg C m^{-2}) are in boxes , and fluxes (mg C m^{-2} d^{-1}) are represented by arrows. A = assimilation, E = excretion, Ex = export, I = ingestion, P = production, S = sedimentation, DIC = dissolved inorganic carbon (from Charpy and Charpy-Roubaud, 1990b).

Detritus, smaller than 35 µm, represent the most important particulate organic carbon pool in the lagoon. They originate from lagoonal primary production (Charpy and Charpy-Roubaud, 1990b) and their sedimentation onto the bottom exceeds benthic primary production. Plankton bacteria biomass is of same order of magnitude as microphytobenthos biomass and is equal to twice the phytoplankton biomass. Pelagic bacteria dominance can be interpreted by a microbial loop returning energy released as dissolved organic matter by phytoplankton and zooplankton, but also energy released as mucus from lagoon coral communities.

ZOOBENTHOS BIOMASS IN SEDIMENTS : FIRST RESULTS

A survey of 20 random stations was realised in the lagoon by A. Intes to provide a first assessment of the macro-zoobenthos of the soft bottoms. These unpublished data have to be considered as preliminary results.

Taxonomic structure - results (Fig. 14)

In terms of abundance, the Molluscs and the Polychaetes dominate the endofauna with a mean density of 11.3 and 10.4 ind m^{-2} respectively. The crustaceans count for less than 2 ind m^{-2} and the Echinoderms as well as the lancelets less than 1 ind m^{-2}. The abundance of the Crustaceans is probably under estimated as only large apparent Invertebrates were counted and no digging operations were carried out. Large Invertebrates burrowing in the sediment are not taken into account and their biomass remains unknown. However, the average density of the big burrowing species can be estimated to stand around 0.3 ind m^{-2} as revealed by hole density.

Regarding the epifauna, the Sponges clearly dominate with around 0.5 colony m^{-2}. The other organisms are generally scarce except in some very localised areas harbouring high densities of holothuroid (*Halodeima atra*).

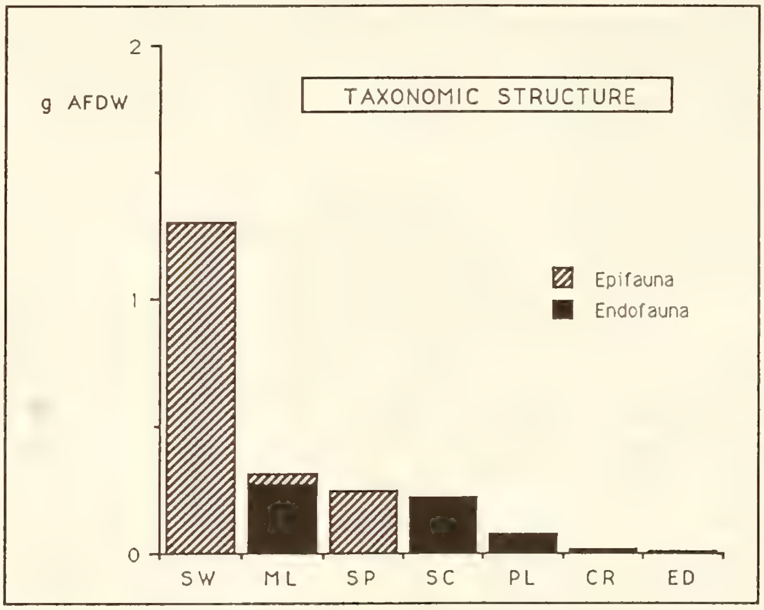

Fig. 14 : Taxonomic structure of zoobenthos biomass in sediment (SW : Sea weeds ; ML : Molluscs ; SP : Sponges ; SC : Sipunculids ; PL : Polychaetes ; CR : Crustaceans ; ED : Echinoderms) expressed in Ash Free Dry Weight (AFDW).

In terms of biomass, the global structure is not very different : the Molluscs remain at first rank with 36% of the animal organic matter (AOM), followed by the Sponges with 27% of AOM. The third class includes the Sipunculids, but also all the fauna living in the dead shells and in all probability some micromolluscs. This represents about 25% of AOM. The other groups stand far behind in importance : the Polychaetes are mainly small animals and contribute for only 9% to AOM. The crustaceans are essentially little species such as Tanaidacae or Mysidacae. Some crabs (mostly Portunids) are rarely collected in the endofauna and the contribution of the group to the biomass is poor : 2% of AOM. Once again, this is under estimated by the lack of information on the big burrowing forms. The Echinoderms are very few represented on the soft bottoms (Ophiuroids) with only 1% of AOM.

Considering the total living biomass, the primary producers largely dominate with about 60% of the total organic matter.

They are sea weeds such as *Halimeda* or *Caulerpa* belonging to several species, but they may also be Phanerogams *Halophila ovalis*. (the sole species encountered in this lagoon).

Trophic structure - results (Fig. 15)

The deposit feeders are considered as a unique group. No distinction between the surface deposit feeders and the burrowing deposit feeders is made. They are slightly the best represented with 46% of AOM, but it must be emphasized that they belong to the endofauna (except the Holothuroid *Halodeima atra*).

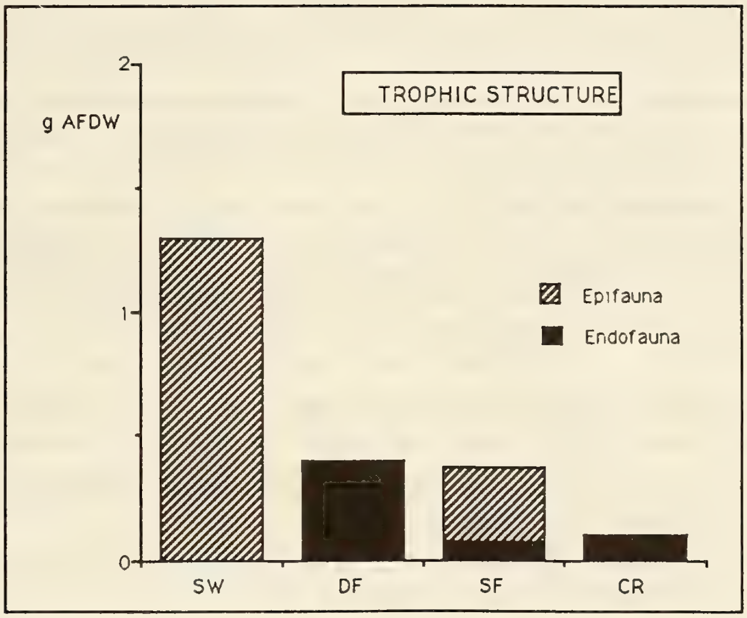

Fig. 15 : Trophic structure of zoobenthos in sediments (SW : Sea weeds ; DF : Deposit-feeders ; SF : Suspension -feeders ; CR : Carnivorous).

The suspension feeders stand in the same order of magnitude with 42% of AOM. Most of them belong to the same epifauna as Sponges do, but also some molluscs such as the bivalves *Pinna* are found.

The carnivores are the least represented with only 12% of AOM. They are collected in the epifauna (Molluscs as *Strombus spp.* or *Nassarius spp.*) as well as in the endofauna (some Crustaceans and Polychaeta).

The deposit feeders are under estimated because the mud shrimps, or the Cardiidae for example, are not taken in account by the sampling method.

Discussion :

A first biocenotic survey carried out by Faure and Laboute (1984) concluded from the study of the coral species distribution that the whole lagoon belongs to a sole community inside which the species distribution depends on geomorphological or physical factors. The study of the fish community by Morize *et al.* (1990) leads to the same finding : there is only one fish community in the lagoon, but its observed structures (which varies in space and biomass) are greatly heterogenous without any evident explicative factor. The spatial heterogeneity of the benthic biomasses cannot be explained by the classic factors such as sediment characteristics, bathymetry, and distance to the rim.

Two hypothesis can be advanced nevertheless :

1 -The mapping of the biomasses matches the mapping of the bidimensional modelisation of the water circulation under the influence of the trade winds (see fig.12 of the first chapter). If the model can be considered as relevant, the vortex generated by the wind will be a facilitating factor for the organic matter sedimentation and consequently, would allow the development of the greatest amount of benthic biomass of bottom invertebrates.

2 - The sample distance from a lagoon reef construction may be the best explicative factor. These reefs, considered as a source of organic matter via the detritus released, may govern the bottom invertebrates distribution. This hypothesis will be tested in the forthcoming research program "Cyel".

As only the soft bottoms were investigated in this quantitative survey, no cnidarians were collected : the free living scleractinia as *Heteropsammia, Cycloseris,* or *Trachyphyllia* do not exist in French Polynesia. Apart from this, the general structure is close to the structure observed in the New Caledonia lagoon by Chardy and Clavier (1989). The three main groups in terms of biomass are the same, respectively the macrophytes, the sponges and the molluscs. The crustaceans and especially the echinoderms are relatively less represented in the Tikehau lagoon than in New Caledonia. Few species of crabs and quite no pagurids, no urchins, no asterids were collected in or on the sediment.

The biomass of the macrophytes is higher than the total animal biomass, but its trophic role in the bottom network cannot be appraised as few invertebrates seem to feed on them. Among the animals, the suspension feeders stand to the same order of magnitude of biomass than the deposit feeders in the Tikehau lagoon. Chardy and Clavier (1989), in New Caledonia, observed a suspensivores biomass about twice the one of the deposit feeders. The lack of soft bottom free living scleractinians may partly explain this fact.

The general trends of the trophic network described on the soft bottoms of the Tikehau lagoon may be summarised as :

A highly simplified fauna in which most of the zoological groups are represented, but with a little number of species (about 80 taxa).

The trophic network is basically highly dominated by the macrophytes production, but their consumers do not belong to the invertebrates fauna.

Among the animals, the suspension feeding guild is mainly represented on the sediment surface by the sponges, but also by some molluscs or polychaetes living in the sediment.

The deposit feeding guild is better represented among the zoological groups, where the molluscs and shell living organisms dominate in weight.

The two main guilds are quite equally represented at least on the soft bottoms. A first attempt to explain this may be the weakness of the currents in the lagoon, allowing a near vertical sedimentation on which only filter feeding organisms (*i.e.* actively pumping the sea water) may feed in sufficient quantity before bottom accumulation. This hypothesis mark a basic difference with the bottom network of New Caledonia, where the water circulation allows a higher contribution of the suspension guild to the benthic network.

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PART III. REEF FISH COMMUNITIES AND FISHERY YIELDS OF TIKEHAU ATOLL (TUAMOTU ARCHIPELAGO, FRENCH POLYNESIA)

BY

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INTRODUCTION

Fish communities in the lagoon of the Tikehau atoll were studied by only a few researchers. Harmelin-Vivien (1984) studied the distribution of the main herbivorous families (Scaridae and Acanthuridae) in the lagoon and on the outer slope to 30 m in depth. The total fish community of the outer slope was studied by Galzin (1985, 1987) at 12 m in depth. These studies were carried out in the southwestern part of the atoll. Spatial organization of coral associated fish community was studied throughout the lagoon by Morize *et al.* (1990). Most of the other studies undertaken at Tikehau involved the artisanal fishery (Morize, 1984, 1985 ; Caillart and Morize, 1986, 1988) and the biology of some target species to the exploited stock (Caillart et *al.*, 1986; Caillart, 1988; Morize et Caillart, 1987). It seems worthwhile to present in this special issue of ARB, all the available information on the fish fauna of Tikehau. Furthermore, this overview allows us to compare our results with others in the Indopacific region.

FISH COMMUNITIES OF TIKEHAU ATOLL

METHODS

To study the fish communities of Tikehau, two complementary methods were used : visual census and rotenone poisoning.

Many synthesis (GBRMPA, 1978; Barans and Bortone, 1983; Harmelin-Vivien *et al.*, 1985) describe the method for estimating *in situ* fish communities and populations using visual censuses. These methods, widely used on coral reefs, enable scientists to study fish communities without perturbation. In the Tikehau atoll, visual censuses were carried out by SCUBA diving on 50 m length and 5 m width transects. The transects on the outer slope and the inner reef flat were parallel to the reef. Around the pinnacles, the sampling line was curved around them. In each transect, abundance inside three caregories of size (small - medium - large) were recordered for all species encountered (St. John *et al.*, 1990).

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Fish hidden in reef shelters and in sediment were caught with ichtyotoxic rotenone. Individual fish were measured to the nearest millimeter (standard and total length), weighted to the nearest gram and preserved in a 10% neutral formalin. Length-weight relationships were subsequently computed for all species caught, providing that the sample size was large enough.

The two methods were used to study fish communities in the lagoon, but only visual censuses were used on the outer slope.

FISH COMMUNITIES OF THE OUTER SLOPE

Fish communities of the outer slope are strongly influenced by environmental factors : primary substratum types, slope gradient, level of wind exposure, and magnitude of the 1983 cyclonic damages on coral assemblages. Several surveys of the outer slope fish fauna were carried out on the southwestern outer slope of the atoll (Fig. 1). For the damages induced by the cyclones and the description of the outer slope, see the previous chapter on the environment by Intes and Caillart.

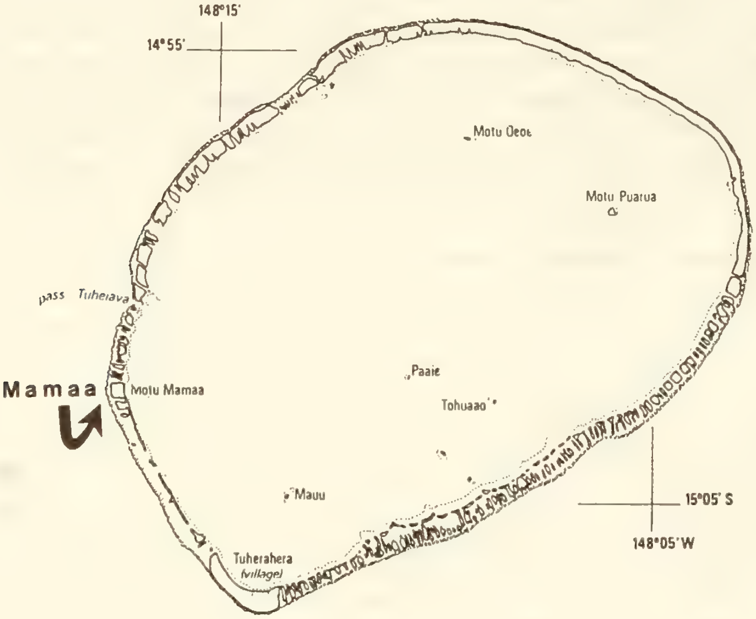


Fig. 1 : Location (*Mamaa*-arrow) of fish community sampling station on the outer slope of the Tikehau atoll .

The fore reef area (0-10 m)

The spur and groove zone is an area of very high fish abundance. In particular surgeonfish *Acanthurus achilles, A. nigroris, A. guttatus, A. lineatus* and parrotfish *Scarus sordidus* , *Scarus sp.* are typical features of this zone. Small coral dependant fish found are Cirrhitidae, small Serranidae (*Cephalopholis urodelus*), Chaetodontidae (*Chaetodon quadrimaculatus*) Pomacanthidae (*Centropyge sp.*), Labridae (*Thalassoma fuscum*), numerous Balistidae (*B. viridescens, B. undulatus* and *Melichthys niger* and *M. vidua* in mid-water). The shark *Carcharhinus melanopterus* and a great variety of Carangidae are also frequentely encountered in this productive and well oxygenated area.

On the fore reef platform (4-10 m), benthic fish fauna (*e.g.* : Gobiidae, Chaetodontidae, Acanthuridae, Serranidae, Labridae) can be distinguished from zooplankton-feeding mid-water fish fauna (*e.g.* : *Anthias* spp., Pomacentridae, nocturnal Holocentridae and *Naso spp.*), and upper-water fish fauna (Balistidae, sharks, tunas and Sphyraenidae).

The outer terrace (10-25 m)

The fish fauna of this zone present a great diversity (more than 100 species), and an abundance of fishes. The most conspicuous families are Holocentridae (genus *Holocentrus, Sargocentron, Myripristis*) numerous around coral patches, Lutjanidae (*Lutjanus bohar, L. gibbus, L. kasmira*) forming schools of several hundred individuals, Acanthuridae (*Ctenochaetus striatus, C. strigosus, Zebrasoma scopas, Acanthurus glaucopareius, A. nubilus* and schools of *Naso spp.*), Serranidae (genus *Variola, Gracila* and the common grouper *Epinephelus microdon*), Chaetodontidae and some Scaridae (*Scarus gibbus, S. niger, Cetoscarus bicolor*).

The deep outer slope (from 25 m)

Abundance and diversity of fish fauna decrease somewhat but a new, more characterized, species assemblage occurs with depth. Holocentridae and Scaridae are less important while the abundance of large Serranidae, some Labridae (genus *Bodianus, Cirrhilabrus*), Zanclidae and *Heniochus* noticeably increase. Among Chaetodontidae still present, species of the genus *Hemithaurichtys* appear. Among the Acanthurid censused are, *Acanthurus bleekeri, A. pyroferus, A. xanthopterus* and large schools of *Naso hexacanthus* and *Naso vlamingii.* Lutjanidae, with large *Lutjanus bohar,* are numerous as well. The abundance of parrotfish decreases rapidly below 30 m.

Fish assemblage was not studied below 40 m on the outer slope of the Tikehau atoll.

Temporal variations of fish communities

Numerous authors working on coral reef ecosytems, and Bell and Galzin (1984) and Galzin *et al.* (1990) in French Polynesia, emphasized that a strong relationship exists between the live coral coverage rate and fish repartition. As shown in Table 1, dramatic changes occured in live coral coverage rate on transect under investigations in five years, inducing a renewal of fish assemblages. Most of these dramatic changes were induced by six cyclones which ravaged french Polynesia during the hot season 1982-83 (Harmelin-Vivien and Laboute, 1986).

Table 1 : Live coral coverage rate of the southwestern outer slope of the Tikehau atoll before, immediatly after and five years after cyclones.

Depth	1982 Before the cyclones (Faure et Laboute, 1984)	1983 After the cyclones (Harmelin-Vivien et Laboute, 1986)	1987 (Galzin et Harmelin-Vivien, unp data)
3 m	5 to 25 %	<5 %	-
5 m	40 to 60 %	20 to 25 %	56 to 62 %
10 m	40 to 60 %	20 to 25 %	42 %
20 m	40 to 60 %	15 %	22 to 24 %
30 m	40 to 60 %	15 %	16 to 24 %

Data displayed in Table 2 permit the assessment of fish fauna temporal variations. Between 1983 and 1987, total number of species on the fore reef area increased from 46 to 56 due to a conspicuous resettlement of Serranidae, Pomacentridae and Labridae. On all other biota of the outer slope, the total number of species decreased between 1983 and 1987. Most of the Scaridae, Acanthuridae and Balistidae left the 10 m depth area whereas most of Holocentridae, Lutjanidae and Mullidae usually encountered around 20 m in depth, moved away. Fish densities at 20 m depth decreased dramatically between 1983 and 1987 (*i.e.* : from 3.4 ind m^{-2} in 1983 to 2.6 ind m^{-2} in 1987 on the average).

Table 2 : Main characteristics of the ichtyological fauna on the outer slope of Tikehau at different depths before, just after, and five years after cyclones of late 1982 - early 1983. Nhs : Number of herbivorous species, Dih : Number of individuals of herbivorous species . 100 m^{-2}.,Nst : Total number of species, Dsi : Number of all individuals . 100 m^{-2}. (– : no data).

Depth (m)	1982 Before cyclones				1983 After cyclones				1987			
	Nhs	Dih	Nst	Dsi	Nhs	Dih	Nst	Dsi	Nhs	Dih	Nst	Dsi
5	15	159	–	–	17	213	46	–	19	143	56	–
10	20	188	–	–	21	78	40	337	12	55	69	260
20	21	199	–	–	19	174	78	–	25	152	67	–
30	19	140	–	–	17	101	58	–	22	152	–	–

Herbivorous species were studied in more detail. Data listed in Table 2 and 3 show that for herbivorous fishes the mean number of individuals is relatively constant at 5, 20 and 30 m depths between 1982 and 1987. As previously noticed, the only anomality is found at a 10 m depth where the number of herbivorous species on the outer slope undergo a veritable decrease : 1.7 ind. m^{-2} in 1982, 1.4 ind. m^{-2} in 1983 and 1.2 ind m^{-2} in 1987.

After the cyclones, fish fauna decreased considerably. A great number of cryptic species died with associated corals, another part remained unsheltered and suffered subsequently from higher predation by piscivorous species like *Epinephelus microdon* that became more abundant after the cyclones. Another part of fish fauna escaped toward undamaged reef areas. A re-arrangement of fish fauna was noticed on the outer slope ; a greater number of species were counted in shallow areas.

COMPARISON WITH FISH COMMUNITIES OF OTHER OUTER SLOPES

Galzin (1985) has compared fish communities in the outer slopes of 2 high islands (Moorea, Mehetia) and 3 atolls (Tikehau, Takapoto and Mataiva) of French Polynesia. Qualitative and quantitative studies show that fish communities found at a 12 m depth on atoll outer slopes are different than those found on high island outer slopes (Moorea, Fig. 2).

Out of the 189 species censused in ten sampling stations, 8 (4%) are found exclusively at Tikehau. These are : *Elagatis bipinnulata, Lethrinus elongatus, Lethrinus xanthochilus, Chromis margaritifer, Bodianus loxozonus, Cetoscarus bicolor* and *Scarus niger*. Pomacentrid *Chromis xanthura* is unexpectedly absent from Mataiva and Tikehau outer slopes whereas it is present at the 8 other sampling stations.

Differences in coral coverage can also be a major factor since outer slope sampled at Tikehau and Mataiva have been damaged by cyclones to a greater extent than the southwestern outer slope of Takapoto (Galzin, 1987 ; Harmelin-Vivien and Laboute, 1986). The current state of knowledge does not enable to isolate the major factors influencing fish repartition on atoll outer slopes in French Polynesia.

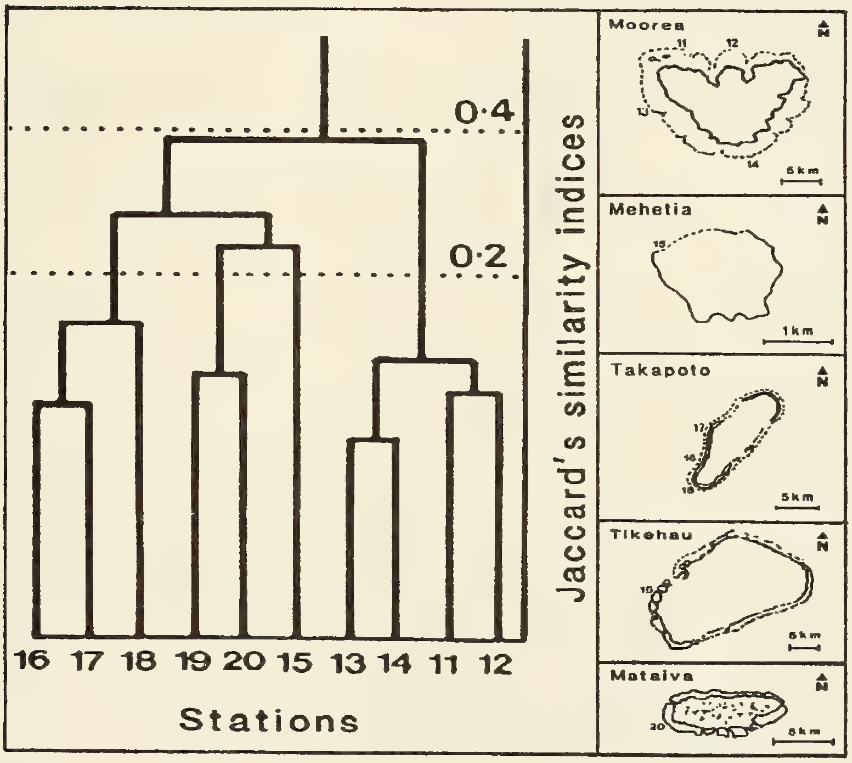


Fig. 2 : Location of sampling stations on each of the five islands and dendrogram derived from similarity matrices. Numbers refer to the 10 sampling sites distributed among the five islands (from Galzin, 1987).

Table 3 : Temporal variability for two families of herbivorous fish (Scaridae and Acanthuridae) on the outer slope of the Tikehau atoll. (number of individuals . 1000 m^{-2})).

	1982				1983				1987			
	-5	-10	-20	-30	-5	-10	-20	-30	-5	-10	-20	-30
SCARIDAE												
Cetoscarus bicolor		7	3	4		2	6	2			2	
Hipposcarus longiceps		1	4			2			11	2		
Scarus altipinnis	5	12	6	7	3	5	4		1		4	1
Scarus forsteri												1
Scarus frenatus	5	9	11		14	2	5	4	1		5	2
Scarus frontalis		8	2		5	1		4				
Scarus ghobban	5	10	4			2	1	4	2	3	4	3
Scarus gibbus	8	13	30	16		1	10	12	3	1	4	
Scarus globiceps					1				4		1	
Scarus niger			1	8	3			16			3	2
Scarus oviceps							1					
Scarus psittacus					2				6		1	
Scarus rubroviolaceus		1			2		1					
Scarus schlegeli		1				9					2	6
Scarus sordidus	27	15	21	17	77	7	50	18	14	9	13	48
Scarus juv.	15	26	6			10						
Number of species	**6**	**11**	**10**	**5**	**8**	**10**	**8**	**7**	**8**	**4**	**10**	**7**
Number of individuals	**65**	**103**	**88**	**52**	**107**	**41**	**78**	**60**	**42**	**15**	**39**	**63**
ACANTHURIDAE												
Acanthurus achilles	24	8			51				10			
Acanthurus bleekeri				3								
Acanthurus glaucopareius	21	26	111	5	35	2	36	4	6		17	3
Acanthurus guttatus	13				13				4			
Acanthurus nigricauda				1		2	2	4			24	13
Acanthurus nigroris	108	85			145	74			170	75		
Acanthurus nubilus				9			4	14			4	2
Acanthurus olivaceus						11				9	7	8
Acanthurus pyroferus			2	24			46	40			19	37
Acanthurus thompsoni			34	27							3	30
Acanthurus triostegus	2				6	3			86			
Acanthurus xanthopterus			14	60								
Ctenochaetus striatus	90	149	14	16	153	15	72	12	5	14	50	48
Ctenochaetus strigosus	60	63	164	104		2	148	74	2	2	75	50
Naso brevirostris			10	7			7	14			12	5
Naso hexacanthus												8
Naso lituratus	7	13	52	15	12	34	24	6	20	8	23	46
Naso vlamingii				1				6			3	6
Zebrasoma rostratum	8	4	1	6	8	7	1		10	3	13	2
Zebrasoma scopas		17	6	21		3	15	18	1	7	79	59
Zebrasoma veliferum		2	2			1	3		1		8	1
Acanthurus juv.					2					5	4	
Number of species	**9**	**9**	**11**	**14**	**9**	**11**	**11**	**10**	**11**	**8**	**15**	**15**
Number of individuals	**333**	**367**	**410**	**299**	**425**	**154**	**358**	**192**	**315**	**123**	**341**	**318**

FISH COMMUNITIES ASSOCIATED WITH CORAL FORMATIONS

In the lagoon of Tikehau, three main types of biotopes can be distinguished : coral reef formations, sediments and mid-water. Coral reef formations are composed by the inner reef flat, pinnacles and coral patches. They are scattered all over the lagoon but are more numerous in the front of channels (Harmelin-Vivien, 1985). In the southern and western part of the lagoon, the inner reef flat that edges the atoll rim lagoonward does not extend deeper than 5-6 m. Live corals extend down to 15 m depth on pinnacle slopes. Pinnacles are more abundant in the western part of the lagoon, especially between the village and the pass.

Fish abundance on Takapoto's outer slope (4 to 5 ind . m^{-2}) appears to be greater than that on the outer slopes of Tikehau and Mataiva (3 to 4 ind . m^{-2}) (Table 4). However, the difference is not statistically significant. This difference can be explained either by geomorphological considerations (presence/absence of a pass) or by variations in longitudinal position.

Table 4 : Comparative quantitative data for the coral reef fish community at 12 m depth of the outer-slope of 5 islands in French Polynesia. NI : Number of individuals . 100 m^{-2}, NS : Number of species . 100 m^{-2}.

		NI		NS	
	stations	NI	Mean (s.d.)	NI	Mean (s.d.)
	11	575		44	
	12	428		32	
MOOREA	13	220	400	27	35
	14	378	(146)	37	(7)
	16	487		46	
TAKAPOTO	17	435	442	41	45
	18	404	(42)	47	(3)
MEHETIA	15	516		46	
TIKEHAU	19	337	418	43	45
MATAIVA	20	400	(91)	47	(2)

Only the fish community associated with coral formations was studied in detail (Harmelin-Vivien, 1984; Morize *et al.*, 1990). The total fish fauna of the lagoon is obviously richer because soft-bottom and mid-water fish communities were under-sampled (St. John *et al.*, 1990). Lagoon fish communities are divided as follows : 1) fish species remaining in the lagoon during their entire life span after recruitment to the reef, 2) fish species that, at least at one time of their life, live on the outer slope or in ocean water, 3) and species living on the outer slope but that migrate toward the lagoon for reproduction. Species with different life cycles gather especially near the pass.

Structure of the coral associated fish fauna in Tikehau lagoon.

A total of 164 fish species, belonging to 34 families were censused around the coral formations in the Tikehau lagoon : 99 species were observed by visual census and 108 species were caught by rotenone poisoning (Appendix 1). The most diversified families are Labridae (21 spp.), Acanthuridae (20 spp.), Scaridae (14 spp.), Serranidae and Chaetodontidae (7 spp.). All species recorded only by visual census live in mid-water. These species belong to families of Carcharinidae, Fistularidae, Echeneidae, Carangidae, Lutjanidae, Lethrinidae and Zanclidae.

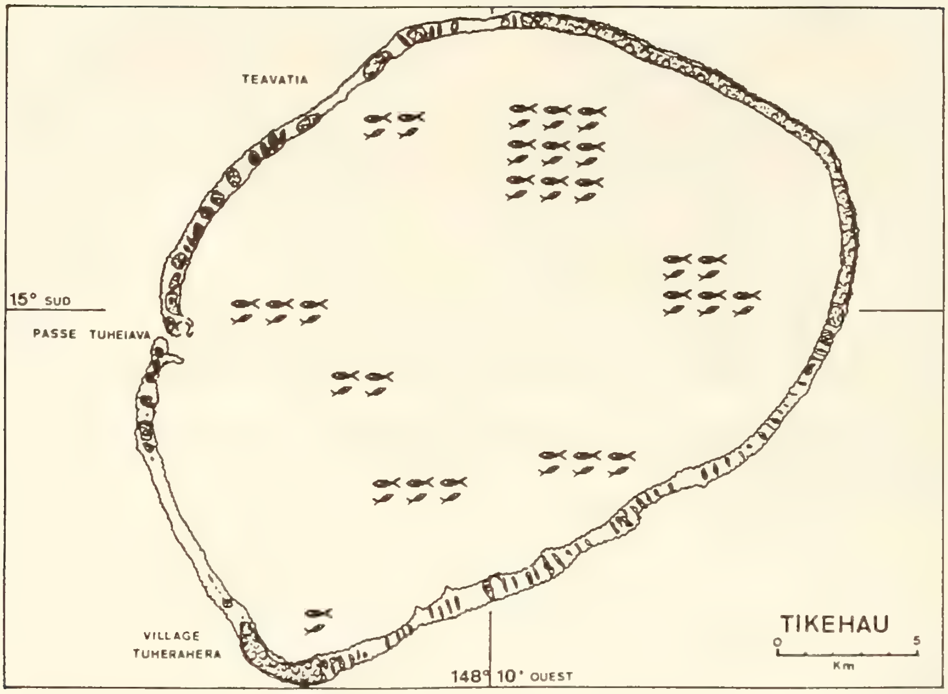


Fig. 3 : Mean fish densities at different sampling stations in the Tikehau lagoon (2 fish : 100 ind . 100 m-2) (Morize *et al.*, 1990).

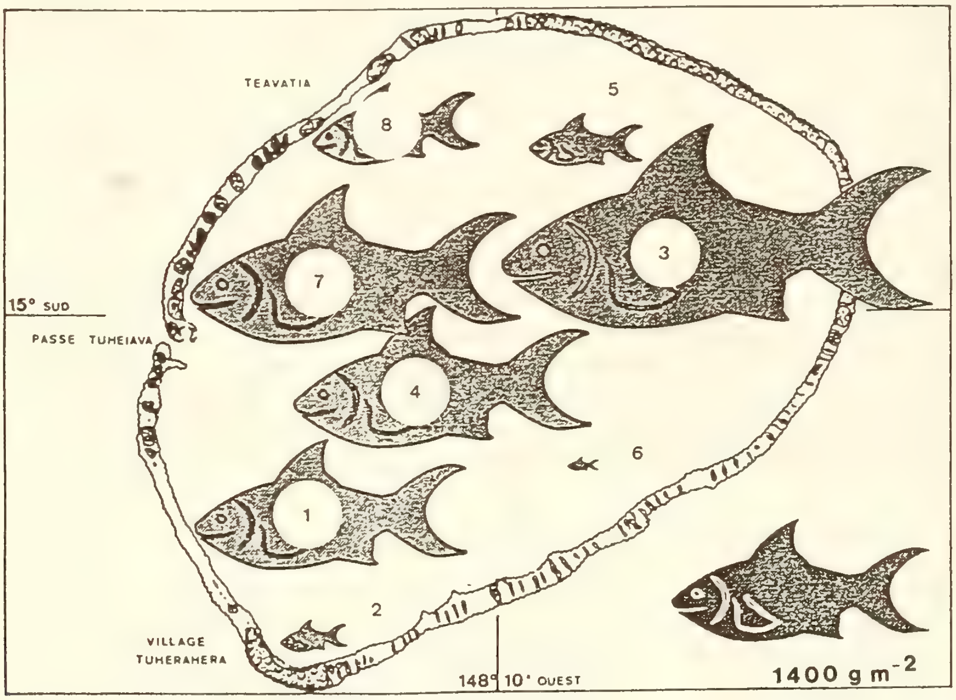


Fig. 4 : Mean fish biomass at different sampling stations (numbers) in the Tikehau Lagoon (modified from Morize *et al.*, 1990).

On the other hand, species recorded only by rotenone poisoning, are cryptic species or live buried in sediments (Congridae, Ophichthidae, Ophidiidae, Scorpaenidae, Blenniidae and Bothidae). Only a part of the fish fauna of coral formations can be recorded by each method (60% by visual census and 67% by rotenone poisoning). Only 30 % of all species are recorded by both methods.

The composition of fish species is relatively homogeneous throughout the whole lagoon. Down to a depth of 15 m, the distribution of species does not show any gradient over the whole lagoon (Morize *et al.*, 1990). The same fish community is found around coral reef patches of the lagoon of Tikehau. On a biomass basis, this community is made up of about 70% of carnivorous species, 14% of omnivorous species and 17% of herbivorous species (Table 5). However the trophic structure of the community observed is different according to the method of sampling. Samples obtained by rotenone poisoning allow to have a better estimation of the abundance of nocturnal plankton feeders, nocturnal carnivores and omnivores. On the other hand, diurnal plankton feeders, sessile invertebrates feeders and herbivorous species are better sampled with visual censuses.

Table 5 : Comparison of trophic structure of fish community in the Tikehau lagoon related to the two assessment methods (expressed as percentage of total number of species).

		Total community	Visual counts	rotenone poisoning
Total number of species		161	97	108
% piscivorous		9.4	8.3	10.2
% other carnivorous	nocturnal	18.7	11.5	20.4
	diurnal	20,6	20,8	22,2
% planktivorous	nocturnal	8.8	4.2	12.0
	diurnal	3.1	5.2	1.9
% sessile invertebrate browsers		9.4	14.6	9.3
% omnivorous		13.7	8.3	18.5
% herbivorous		16.3	27.1	5.5

Spatial distribution of fishes in the Tikehau lagoon

Geographical distribution

The small-scale spatial heterogeneity of fish community in the lagoon is considerable. However the distribution of this community follows a steady pattern all around the pinnacles. On the windward area of the pinnacles, species richness, density, and biomass of fish are always higher (between 1.5 to 4 times) than on leeward ones (Morize *et al.*, 1990).

In spite of a relatively homogeneous distribution of fish in the whole lagoon, densities, biomass and length frequencies of fish of this community present a heterogeneous spatial distribution.

Densities : Depending on the sites, average fish density around pinnacles of the Tikehau lagoon vary from 102 to 1274 fishes per 100 m^2. The highest mean densities are located windward of the atoll (in the northeastern part of the lagoon, Fig. 3).

Biomass : The biomass of the 31 most abundant species varies from 0.8 to 34.4 kg . 100 m^{-2} and display a considerable spatial heterogeneity. The spatial variations of biomass seem to depend in part upon the localisation of studied sites from the reef flat, the village and the pass (Morize *et al.*, 1990). The most important average biomass is recorded near the center of the lagoon and at the pass of the atoll (Fig. 4).

Table 6 : Mean demographic structure of fish populations around coral pinnacles in the Tikehau lagoon (D : mean density of individuals 100 m^{-2} ; % : percentage of each total population size class).

		Juveniles		Adults		Olds	
Station	location	D	%	D	%	D	%
1	S W	12.4	8.0	82.9	53.6	59.3	38.4
2	S W	6.0	12.9	27.2	58.5	13.3	28.6
4	W	20.7	18.4	49.1	43.6	42.8	38.0
7	W	7.9	5.2	103.9	68.9	39.0	25.9
3	E	26.1	10.7	159.0	65.3	58.3	24.0
5	NNE	31.6	6.7	293.9	62.3	146.5	31.0
6	SE	20.5	13.0	93.3	59.2	43.8	27.8
8	N N W	19.8	14.0	76.9	54.6	41.4	29.4

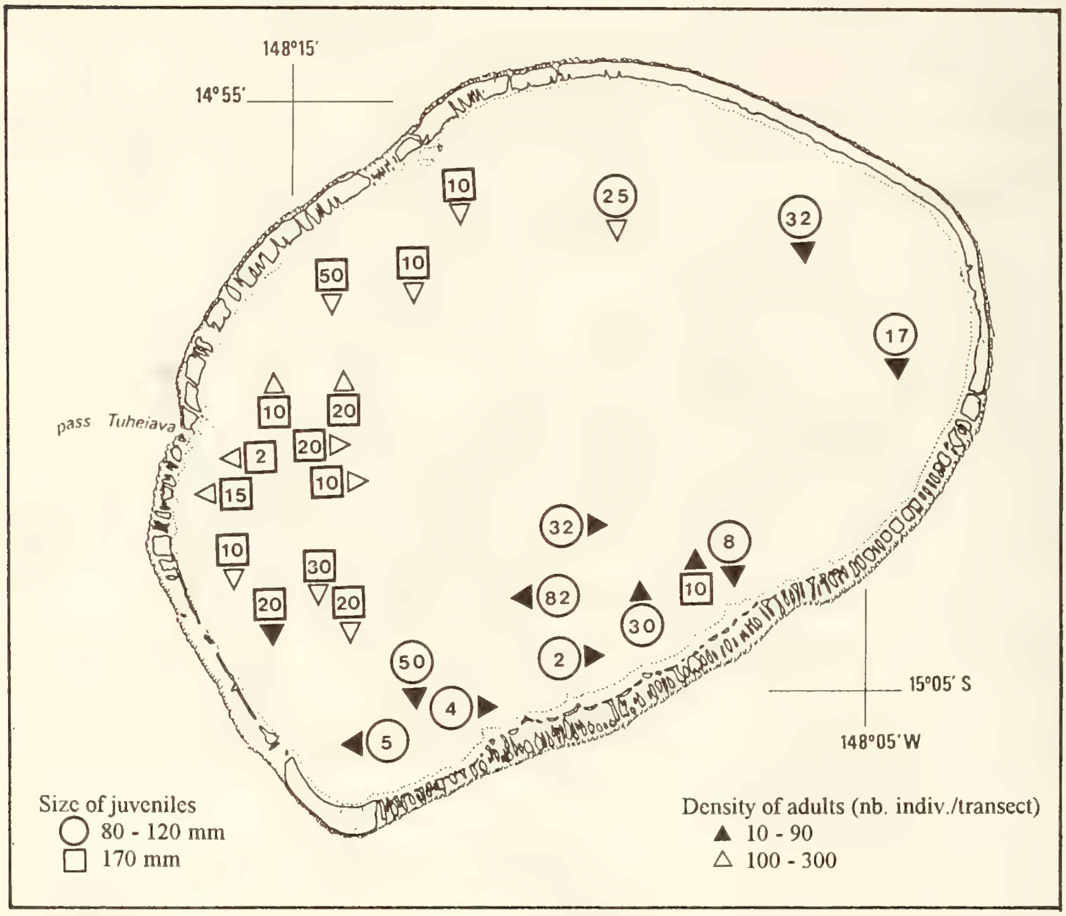


Fig. 5 : Size-class repartition of *Naso brevirostris* in the Tikehau Lagoon. (number : number of juveniles recorded per transect).

Age structure : Generally, middle sized fish are the most numerous and represent from 44 up to 70% of the total number of fish (Table 6). The number of the largest fish varies between one fourth and one third of the total population, while juveniles are less numerous (5 to 8%). The low abundance of juveniles may be due to the fact that they are not easily seen by divers or that they recruit somewhere else to other biotopes. Furthermore, the length frequency distribution throughout the lagoon is not homogeneous. Juveniles are more numerous in northern and eastern parts of the lagoon. These areas receive oceanic water passing over the reef flat through hoa which are particularly numerous. The distribution of length frequencies of *Naso brevirostris* is a good example that shows differences in juvenile and in adult fish distribution (Fig. 5). All small juveniles (80-120 mm) were observed in the eastern part of the lagoon while larger juveniles (170 mm) were seen mostly in the western part (Caillart, 1988). Conversely, the density of adult fishes in the western part, and particularly near the pass, is four time higher than in the eastern part.

Distribution with depth

Specific composition : The species richness of the fish community in the lagoon is greater between 3 and 5 meters depth : 87 species were recorded at these depths by visual censuses. From 10 to 15 m, the community is poorer (only 65 species censused) but is not qualitatively different. Only one species, Gobiidae *Amblygobius phalaena*, appears to be a characteristic species of this deeper zone. Inversely, some Mullidae (*Mulloides spp., Parupaeneus porphyreus*), Pomacanthidae, some Labridae (*Gomphosus varius, Thalassoma amblycephalum*), Scaridae (*Scarus globiceps*) and Acanthuridae (*Acanthurus nigroris, Zebrasoma veliferum*) were not inventoried deeper than 5 m.

Density and biomass : For the whole community, there is no significant difference in mean fish density and biomass between 5 m and 15 m in the Tikehau lagoon (Table 7). However, most species or families are not uniformly distributed with depth : Scaridae and Acanthuridae densities are greater on the inner reef flat and on the top of pinnacles, and decrease with depth (Harmelin-Vivien, 1984). Similarly, Labridae are more numerous near the surface than at 15 m. Conversely, the density of Lutjanidae, Gobiidae and some Pomacentridae, like *Pomacentrus pavo*, are higher at 15 m (Morize *et al.*, 1990).

Table 7 : Mean density and mean biomass of reef fishes estimated from visual census according to depth (number of replicates n=8).

	Density Nd indiv. 100 m^{-2}		Biomass g 100 m^{-2}	
	- 5 m	- 15 m	- 5 m	-15 m
mean	413.5	318.0	11465.6	10236.0
SD	365.5	195.0	10236.0	10109.6

Age structures : The average density of larger fishes on the whole fish community is more important between a depth of 3 to 5 m (Fig. 6). It decreases with depth and on reef flats (Harmelin-vivien, 1984 ; Morize *et al.*, 1990). The average density of juvenile fish is in turn more important at 15 m deep than at 5 m.

Meanwhile, distribution of length classes with depth differs among families. The highest densities of juveniles of Scaridae and Acanthuridae were observed in shallow waters (0-2 m) (Table 8). Conversely, juveniles of Lutjanidae, Labridae and Pomacentridae are more numerous between 10 and 15 m depth.

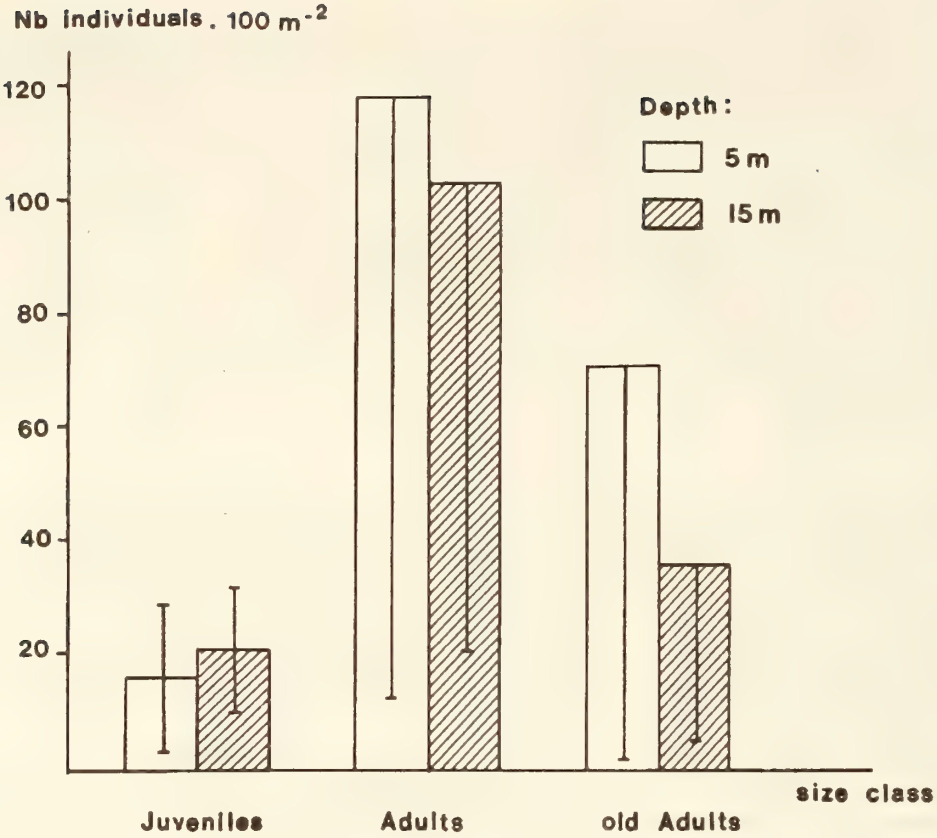


Fig. 6 : Mean demographic structure of fish community at two depths (5 and 15 m) around pinnacle reefs of Tikehau lagoon.

Table 8 : Mean density of juvenile parrotfishes (Scaridae) and juvenile surgeonfishes (Acanthuridae) with depth in Tikehau lagoon (number of individuals . 100 m^{-2}).

		0-2 m	3-5 m	10-15 m
Scaridae	mean	12.3	9.6	7.2
	SD	5.4	8.3	5.6
Acanthuridae	mean	2.9	0.4	0.2
	SD	1.5	0.9	0.2

Comparison with other Tuamotu atolls

The fish communities of atoll lagoons were studied by different authors with a different sampling design in five other Tuamotu atolls, Takapoto, Scilly, Mataiva, Fangataufa and Mururoa (Table 9). Each of these lagoonal communities differs somehow from the other, either by its specific composition or by its average density and biomass, whereas the outer reef slopes look much alike (Galzin, 1987).

Table 9 : Comparison of lagoon fish communities associated with coral formations of six Tuamotu atolls : total number of species and mean density of individuals.

Atoll	Number of fish species	Depth (m)	Density (nb indiv 100 m-2)		reference
			mean	range	
Takapoto	170	0-20	-	-	1
Scilly	180	0-30	-	-	2
Tikehau	161	3-5	414	102-1274	3
		10-15	318	104-612	3
Mataiva	157	0-3	50	3-125	4
Fangataufa	128	0.3	164	54-275	5
Mururoa	230	12	188	56-531	6

References :

1 . Bagnis, Galzin and Bennett, 1979 (28 sites in lagoon, 16 in hoa)

2 . Galzin, Bagnis and Bennett, 1983 (2 transects in lagoon, 2 transects in hoa, 4 transects on outer reef flat).

3 . Morize, Galzin, Harmelin-Vivien and Arnaudin, 1990 (8 sites in lagoon, 4 transects on inner reef flat).

4 . Galzin, Bell and Lefèvre, 1990 (8 sites in lagoon surveyed 4 times in 8 years).

5 . Galzin, unpublished data (7 sites in lagoon).

6 . Galzin, unpublished data (10 sites in lagoon, 6 sites on inner reef slope)

The observed species richness is low in the Fangataufa lagoon (128 spp.), an atoll without a natural pass. It is in turn very high in the Mururoa lagoon (230 spp.), an atoll widely opened to oceanic waters. The number of species recorded in the four other atolls are closely related in spite of differences in morphological structures : Tikehau and Mataiva have a pass whereas Takapoto and Scilly do not.

The mean fish density is very low in the lagoon of Mataiva (Table 9) ; this phenomenon can be explained by a distrophic crisis that seems to affect this atoll (Galzin *et al.*, 1990). On the other hand the mean density of fish is higher in the Tikehau lagoon, in spite of a considerable exploitation of fish stock. At a 12 m depth, the density of fish is lower at Mururoa than at Tikehau. However, the average length of fish is much larger at Mururoa where there is no fishery. The average biomass of fish is probably the same in these two lagoons.

Conclusion

Only one fish community is observed around coral formations (pinnacles) in the lagoon of Tikehau. The mean fish density and biomass do not vary with depth, although the species richness is lower at 15 m deep than between 3 and 5 m. The highest fish densities, characterized by a great proportion of juveniles, are generally found in the northern and eastern parts of the lagoon. Mean biomass per unit area is generally the highest in the southern and particularly the western part of the lagoon, near the pass, characterized by a great proportion of large-sized fishes. The depth *vs* age structure of population relationship varies according to families or species. Juvenile densities are higher in shallow water for some families (Scaridae, Acanthuridae) or in deeper water for other families (Lutjanidae, Labridae, Pomacentridae).

Lagoon - outer slope comparison

Fish community of the outer slope of the Tikehau atoll is more diversified than the lagoonal fish community (Appendix 1). Indeed, twice as many species of fish were recorded on the outer slope as in the lagoon by visual censuses. Around Moorea island, Galzin (1987) recorded also a greater fish species richness on the outer slope than in the lagoon and on reef flats.

Among families, some fish species are more numerous on the outer slope than in the lagoon of Tikehau and vice versa. Serranidae, Cirrhitidae, Carangidae, Lutjanidae, Chaetodontidae and Balistidae species are more numerous on the outer slope (31 spp.) than in the lagoon (24 spp.) (Harmelin-Vivien, 1984). However, the mean Acanthuridae density is higher on the outer slope, whereas Scaridae density is higher in the lagoon (Table 3). Other families, like Lethrinidae and Mullidae are more diversified and their populations are much more abundant in the lagoon as compared to the outer slope.

The distribution of length class, and sex ratio may be also different into or out of the lagoon for a same species or a same family. The most juvenile Scaridae were observed in the lagoon. Immature males and females are more abundant in the lagoon, whereas ripe males are much more numerous on the outer slope (Harmelin-Vivien, 1984).

Fish communities of the outer slope and of the lagoon of the Tikehau atoll are different not only by their species richness and population density, but differ also by their age and trophic structures.

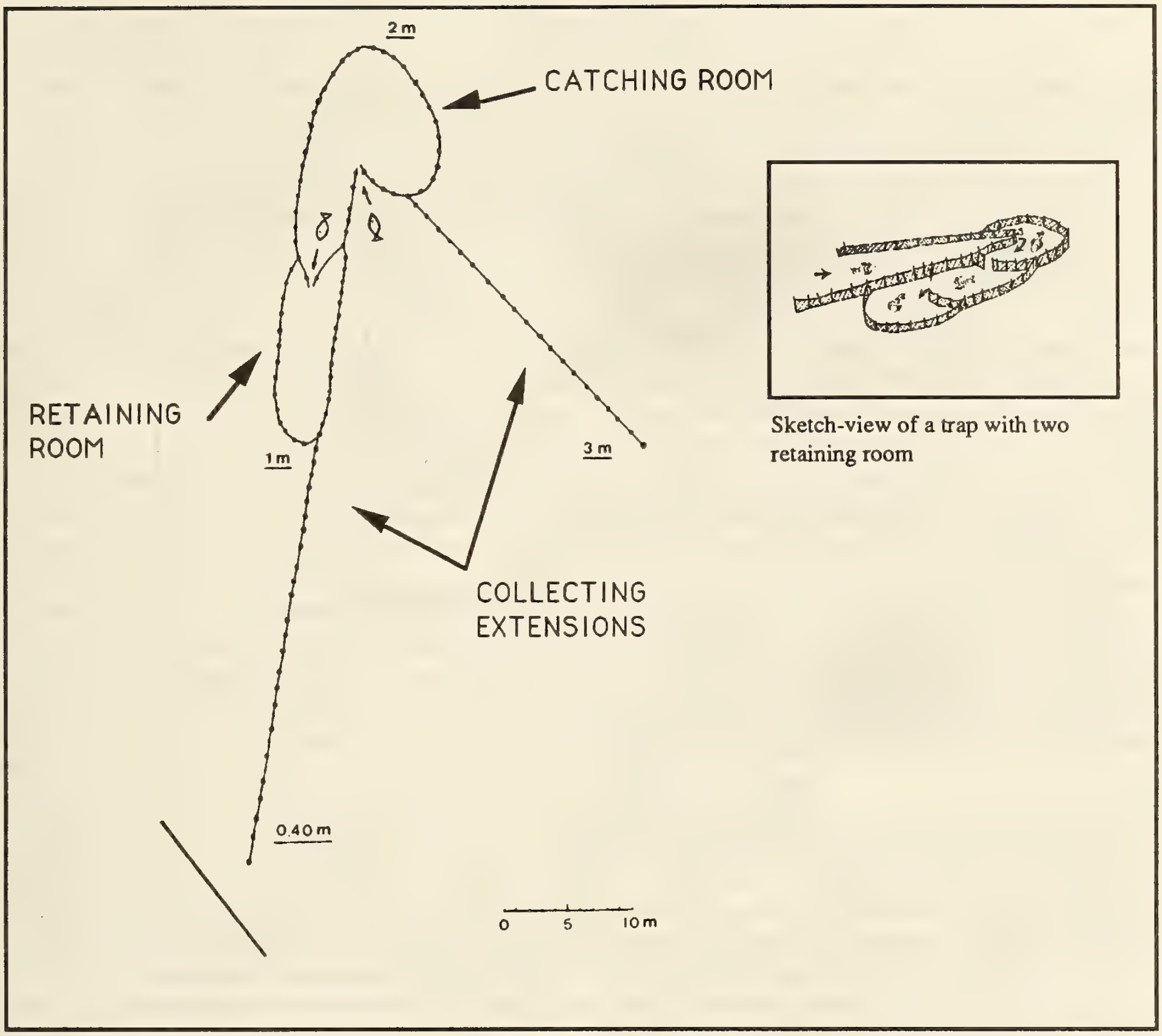
THE EXPLOITED LAGOON RESOURCE : THE FISHERY OF TIKEHAU

The fishery of Tikehau is of artisanal nature, in which fish are sought for commercial and subsistence purpose. It is based principally upon the use of a relatively simple gear : bottom-fixed fish traps. Additionally, an important proportion of fish is occasionally taken with hook and line or spear gun. The fishery of Tikehau was thoroughly studied for four years. Numerous data on the fishery yields and on the biology and behavior of the target species have been gathered in order to assess the reef fish stock for management purposes.

THE FISHERY OF TIKEHAU

The fishing gear

Traditionally, fish traps were built in shallow waters using rocks or coral boulders. Blanchet *et al.* (1985) pointed out that yields were low but satisfactory sufficient to meet the needs of the low-level human population. In the middle of the century, intensive phosphate mining on the neighboring island of Makatea created and kept a high sustained demand of fish to feed the population of workers (about 3,000 in 1962). As a result, the subsistence fishery of Tikehau developed into a commercial fishery by setting traps in more productive areas (in the vicinity of the pass), using modern building materials (wire net, iron stakes) as well as traditionnal wooden stakes. After the close-down of the mining site in 1966, fish trading logically reoriented toward the Tahiti fish market.



Sketch-view of a trap with two retaining room

Fig 7 : Diagram of a typical Tikehau fish trap (actually fish-trap n°2, see text for more details). As shown in the framed sketch-view, there can be two retaining rooms. Dotted line : wire-net, underlined number : depth at which the part of the trap is set.

The general shape of a Tikehau fish trap is presented on Fig. 7. A fish - or a school of fish - coming across the large collecting extensions of wire net (locally termed *Rauroa*) are naturally driven toward the catching room (locally called *Aua)* in which they enter through a narrow opening. At least every day, trapped fish are herded off the trap by fishermen banging on the water surface and driven into a first retaining room (*Tipua*) where they can be held alive for a couple of weeks until they are sold. The fish are landed when the small trading vessel, able to load between 12 and 15 metric tons of catches, arrives at Tikehau (usually once a week), and subsequently shipped to Tahiti.

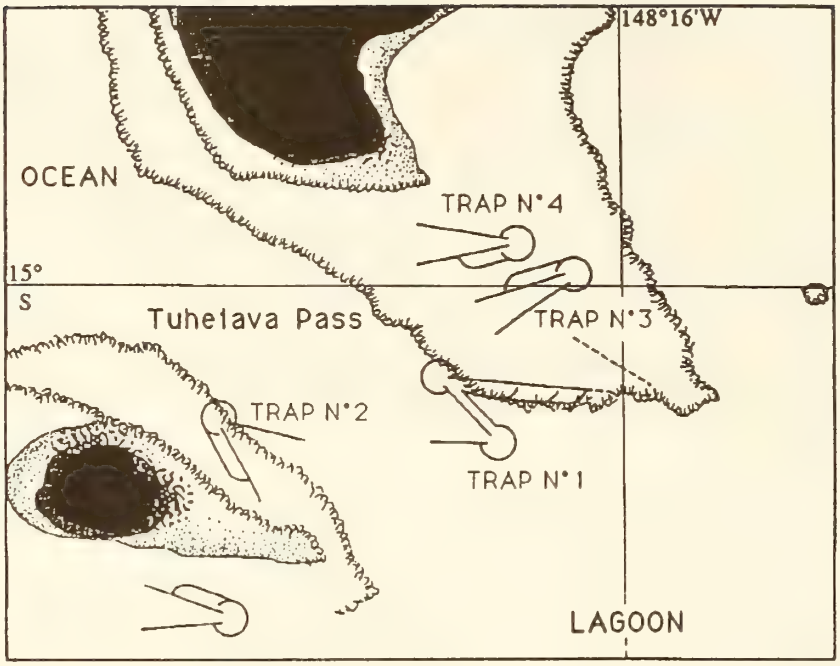


Fig. 8 : Location of fish traps in the pass of Tikehau. Trap n°1 and n°2 located close to the middle of the pass are far more efficient than the two others located lagoonward on the reef flat. Although the origin of a great part of the catches has not been accurately determined, data available indicate that trap n°1 and n°2 yield at least 78 % of the total catches.

The main fishery of Tikehau uses four fish traps, all located in or around the vicinity of the pass. Two traps (trap #1 and #2) are set quite in the middle of the pass by up to a 5 m depth (Fig. 8), and the two others traps (#3 and #4) are located lagoonward on the northern shore of the pass in shallower water (1 to 2 m). When fish is thought to be abundant in the pass and if current speed allows underwater work, a net is set across the pass between trap #1 and trap #2 and a "scare line" driving technique is used to increase catches.

Handlines and spear-guns are used mostly for a subsistence purpose. The use of these kind of gears can however significantly contribute to commercial catches when there are huge concentrations of groupers or emperors in the pass making these species readily available in large quantities. Fishermen retain a portion of their catch for their own use and sell the remainder to the trader.

Fishery yield

In Tikehau, statistical sampling of the catches was done by a local agent who noted down on a log sheet the species composition of the catch, weights sold on a species basis and the number of fish traps that provided the catch. Various information relevant to fishing such as current strength in the pass and weather were also recorded (Morize, 1984). Data were recorded from 1983 to 1987. As fishing activities are maximal by the end of the year and lower by July - August, a fishing year was defined to run from 1st of July to 30th June. Thus, the study of the fishery of Tikehau was carried out upon four fishing years : 83-84, 84-85, 85-86 and 86-87.

Morize (1984) pointed out that fishing effort is somewhat difficult to appraise but since the shape, the number and the location of the traps have not been modified during the study, the fishing effort can be assessed as the number of days with a fully efficient presence of the traps on the fishing grounds. As the level of fishing effort can be estimated to have been constant, variations of catch per unit effort (c.p.u.e.) correspond with variations of catch.

Table 10 gives an inventory list of species caught in Tikehau fish traps (comprehensive studies available in Morize, 1985 ; Caillart and Morize, 1986). Almost fifty species are likely to be trapped, covering a complete trophic spectrum of species ranging from piscivorous to herbivorous species. Although the selectivity of the gear appears to be poor, no more than fourteen species significantly contribute to the catch by accounting for about 85 % of the total landing. These fish include lutjanid *Lutjanus gibbus* and *Lutjanus fulvus,* lethrinid *Lethrinus miniatus,* carangid *Caranx melampygus, Decapterus macarellus* and *Selar crumenophthalmus,* serranid *Epinephelus microdon,* acanthurid *Naso brevirostris* and *Acanthurus xanthopterus,* mullid *Upeneus vittatus* and *Mulloides spp.,* albulid *Albula vulpes,* sphyraenid *Sphyraena forsteri,* and lastly holocentrid *Myripristis spp.*

Table 11 shows that total harvests obtained through trap fishing range from 144 metric tons to 207 metric tons a year with an average value of 165 metric tons. *Lethrinus miniatus* is the principal component of the catches with an average landing of 32 metric tons per year. It is followed by *Lutjanus gibbus, Caranx melampygus* and *Selar crumenophthalmus* representing a yearly average catch of respectively 17, 16 and 14 metric tons. These species can be dubbed target species though fishing activity is not specifically oriented toward them. Landings of the other species are less abundant ranging from 2 to 10 tons a year on the average.

Local consumption of fish is difficult to appraise since every inhabitant of the atoll meets his needs himself. Morize (1984) had estimated that about 150 kg of fish per year and per person are likely to be consumed. Given the total population of Tikehau, an additional 40 metric tons of fish would be landed every year for subsistence. Species readily available to various simple gear (handline, spear) such as groupers, surgeonfish or parrotfish are probably the principal components of this secondary fishery.

Temporal variations of the catch

Although total landings are somewhat homogeneous from year to year (average value of 165 metric tons), with a slight upward trend (Table 11), the relative species abundance in the catches varies considerably. In 1985-86, about 14 tons of *Lethrinus miniatus* have been fished whereas more than 50 tons were caught the next year with the same fishing effort applied to the stock. At the same time, *Epinephelus microdon* yield changed from 5 to about 50 tons and that of *Naso brevirostris* dropped from 19 to 2 tons. These variations are extremes but in general, only a handful of minor species are equally harvested from year to year. For most of the target species, yield can double or conversely, be reduced by half from year to year without any predictive signs. However, the great number of species available to the traps tend to buffer large fluctuations in total catches by changes in recruited population levels of individual species.

Table 10: Check-list of species (italic) caught in Tikehau fish traps with indicative figures of their diet (P : piscivorous, I : invertebrate feeders, H : herbivorous) and indications on their relative abundance in the catches (* : low, erratic catches generally less than 1 % of the total catches; ** : medium abundance, species often fished but representing less than 5 % of the annual total catches ; *** : high abundance, species regularly catched accounting for more than 5 % of the total).

Family	Species	Diet	Harvest
Holocentrid	*Sargocentron spiniferum*	I	*
	Myripristis sp.	I	**
Sphyraenid	*Sphyraena forsteri*	P	**
Siganid	*Siganus argenteus*	H	*
Serranid	*Epinephelus merra*	P,I	*
	Epinephelus microdon	P,I	***
Priacanthid	*Priacanthus cruentatus*	I	*
Carangid	*Alectis indicus*	P	*
	Carangoides orthogrammus	P	*
	Caranx ignobilis	P	*
	Caranx lugubris	P	*
	Caranx melampygus	P	***
	Caranx sp.	P	*
	Decapterus macarellus	P	**
	Elagatis bipinnulata	P	*
	Scomberoides lysan	P	*
	Selar crumenophthalmus	P	***
Lutjanid	*Lutjanus fulvus*	P,I	***
	Lutjanus gibbus	P,I	***
Mullid	*Mulloides flavolineatus*	I	***
	Mulloides vanicolensis	I	***
	Parupeneus barberinus	I	*
	Upeneus vittatus	I	**
Mugillid	*Mugil cephalus*	I	*
	Liza vaigiensis	I	*
Chanid	*Chanos chanos*	I	*
Lethrinid	*Lethrinus mahsena*	P,I	*
	Lethrinus miniatus	P,I	***
	Monotaxis grandoculis	I	**
Chaetodontid	*Chaetodon auriga*	I,H	**
Albulid	*Albula vulpes*	I	**
Kyphosid	*Kyphosus cinerascens*	H	*
Scarid	*Scarus gibbus*	H	*
	Scarus sp.	H	*
Acanthurid	*Acanthurus xanthopterus*	H	**
	Ctenochaetus striatus	H	*
	Naso brevirostris	I,H	***
	Naso lituratus	I,H	*
	Naso unicornis	I,H	*
	Naso vlamingii	I,H	*
Balistid	*Balistoides viridescens*	I	*

Table 11 : Yearly total weight landed (kg) of the fourteen main species caught by Tikehau fish traps and yearly total (kg) including all species. Mean year calculated by averaging data of the four year.

	83-84	84-85	85-86	86-87	Mean
Lethrinus miniatus	34,812	29,923	13,961	50,983	32,419
Lutjanus gibbus	8,152	11,371	24,374	24,354	17,062
Caranx melampygus	24,357	21,332	10,213	11,214	16779
Selar crumenophthalmus	8,337	14,201	17,133	16,063	13,933
Epinephelus microdon	180	810	5,183	48,902	13,786
Lutjanus fulvus	11,226	15,962	13,050	7,694	11,983
Naso brevirostris	3,036	15,299	19,374	2,293	10,000
Mulloides sp.	9,593	8,506	11,066	5,359	8,631
Albula vulpes	12,292	7,889	6,391	5,099	7,918
Upeneus vittatus	9,454	882	6,206	1,085	4,406
Sphyraena forsteri	2,835	2,835	5,085	2,954	3,427
Acanthurus xanthopterus	2,085	6,229	307	1,661	2,270
Myripristis sp.	2,475	1,559	2,931	1,851	2,204
Decapterus pinnulatus	m.d.	1,424	3,580	1,582	2,195
Other species	15,484	15,974	16,152	26,348	18,489
total	**144,318**	**154,236**	**155,006**	**207,442**	**165,250**

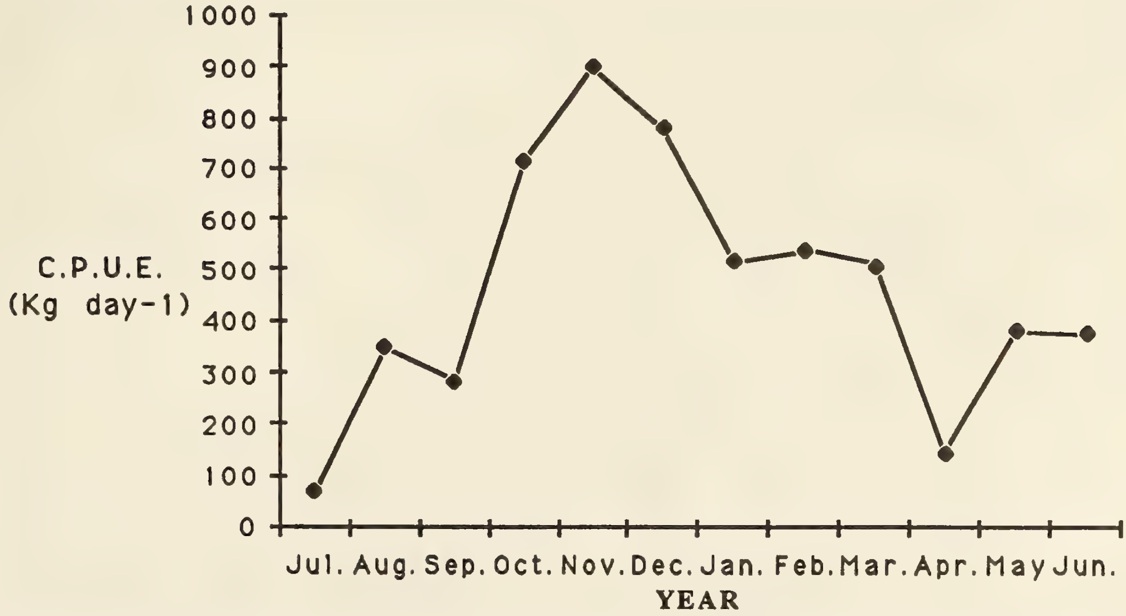


Fig.9 : Temporal variations of Catch per Unit Effort (C.P.U.E.) over an average year in the fishery of Tikehau.

Fig. 9 shows fairly wide fluctuations in the overall monthly catch per unit effort through an average year. Yield ranges from 68 kg per day in July to 898 kg per day in November. The highest productivity of the fishery occurs from October through January and the lowest from April through August. Individual yields of the overwhelming majority of the target species follow these variations but maximal c.p.u.e. of a few species are reached at a different time of the year. Noteworthy is the example of *Epinephelus microdon* in which the presence on the fishing ground peaks in April. Behind these strong seasonal fluctuations, c.p.u.e.s have a clear relationship depending on the time of the lunar month. Yields of the target species noticeably increase the week prior to the new moon and drop around the full moon.

Obviously, yields of the target species are strongly related to seasonal spawning aggregations in the vicinity of the pass. Biological sampling of landed fish carried out every month of the study confirmed that all fish trapped are adult fish, most of them having ripe gonads. Such spawning movements in other tropical areas are also well documented in numerous published observations reviewed by Johannes (1978). Thus temporal variations of c.p.u.e.s of the fishery of Tikehau would have a strong relationship with the time of the breeding period of the major components of the catches as emphasized by Caillart and Morize (1988).

BIOLOGY AND ECOLOGY OF TARGET SPECIES

The biology of the main species caught by fish traps in Tikehau has been studied. The overwhelming majority of the fish sampled was collected in the fishery landing. Additionally, some fish were collected by experimental fishing in the lagoon or on the outer slope using a handline or spear gun. The biological study presented hereafter is restricted to the seven major species : lethrinid *Lethrinus miniatus*, carangid *Caranx melampygus*, serranid *Epinephelus microdon*, lutjanids *Lutjanus gibbus* and *Lutjanus fulvus* and acanthurids *Acanthurus xanthopterus* and *Naso brevirostris*.

Reproduction

Reproductive patterns of the target species were followed throughout the year on a monthly basis. For all samples taken, gonosomatic indices (GSI) were calculated for individual males and/or females as GSI = 100xgonad wt/fish wt.

Fig. 10 summarizes the observations gathered on the time of spawning of the target species. At Tikehau, fish typically have extended breeding seasons with more or less conspicuous seasonal peaks in breeding activity. For *Lethrinus miniatus*, spawning is virtually confined from September to December with most spawning through September. The snappers *Lutjanus fulvus* and *Lutjanus gibbus* appear to spawn between October and June with two seasonal peaks that occur in November and in March. The average GSI remain however at significant levels all year round suggesting that some individual spawning may occur at an odd time. The data for *Caranx melampygus* indicates that spawning occurs throughout the year with slight peaks in July, October and February. Lastly, spawning of *Epinephelus microdon* and *Naso brevirostris* is virtually confined to a short period of three months. The records for *Epinephelus microdon* show a maximum in the period between March and May with the greatest proportion of ripe fish found in April. The surgeonfish *Naso brevirostris* spawns between December and February with most spawning in December. For this last species, the time of spawning was confirmed by two additional methods : maturity stages assigned to female fish using a five stage scale and a study of frequency distributions of egg size within ovaries over the year (Caillart, 1988). Patterns in fecundity of *Naso brevirostris* were drawn from this last meaningful method. A female would spawn about 160,000 eggs, on the average, within a breeding season. Batch fecundity averaged over the complete breeding season, about 221 eggs g^{-1} body weight, indicated that each female *N. brevirostris* must release its eggs in about three times, providing that discrete spawning occurs (Caillart, 1988).

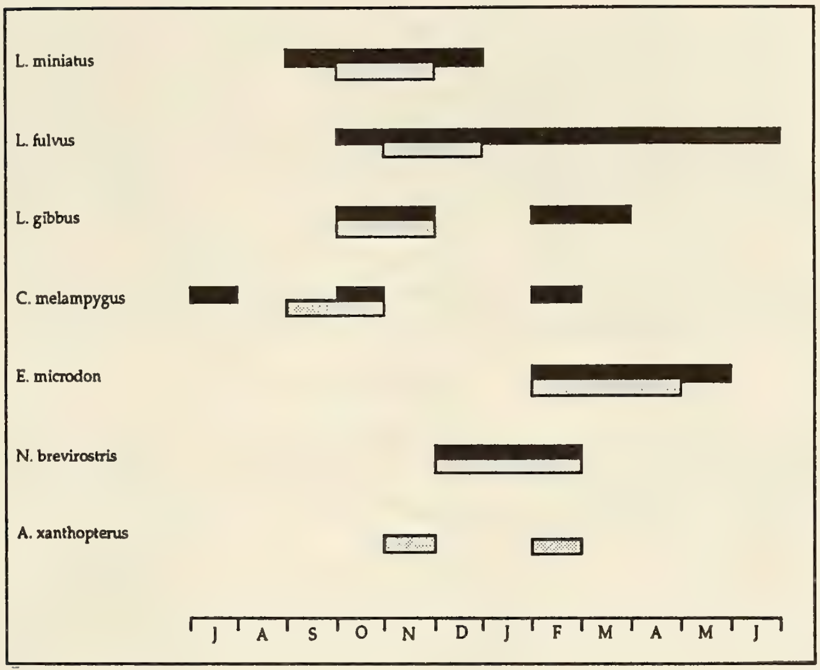


Fig. 10 : Summary of information on time of spawning of the target species of the fishery of Tikehau drawn from GSI variation study, and relationship with time of maximum catch per unit effort (cpue) over an average year (dark bars : breeding season, dotted bars : cpue). No data available to determine the breeding season of *A. xanthopterus* .

For most species, occasional individual spawning is likely to happen in all months, but maximum activity takes place in the earlier months of the year. However, the sole study of GSI variations only gives general trends and is probably insufficient to accurately provide estimates of the occurrence of breeding seasons in the tropics.

Table 12 : Fork-length at first reproduction (mm) of the target species of the fishery of Tikehau obtained from length-frequency data of the catches in fish traps. (* : length-frequency data inadequate to calculate length for both sexes ; ** : relevant data available only for females).

Species	Male	Female
Lethrinus miniatus	410	370
Lutjanus gibbus	220	210
Caranx melampygus	270	250
Epinephelus microdon	m.d.	310 **
Lutjanus fulvus	200	200
Acanthurus xanthopterus	320 *	320 *
Naso brevirostris	260	220

Length at first reproduction was determined under the assumption that the relationship between fishery yields and spawning activity does exist. The first group in the length-frequency distributions of the catch is assumed to actually represent the earlier migrating spawner group (*i.e.* : fish newly recruited to the fishery). Therefore length at first reproduction was calculated as the length in which summed length-frequency reaches 50 % of the total number of fish in the first cohort (Table 12).

Growth

Information on the age and growth of fishes is a central element in fishery management analysis. Common biological characteristics of fishes of Tikehau such as a missing seasonal growth and an extended breeding season throughout the year, have made growth rate determination difficult. Basically, three approaches to the determination of age and growth of the target species were attempted. These were 1) modal progression analysis in a time series of length-frequency histograms ; 2) tag-recapture study and 3) the aging of individuals on the basis of regular periodic (daily) markers in otoliths.

The growth rate of fishes has been described by the Von Bertalanffy Growth formula (hereafter expressed VBGF) because it fits most of the data obtained on fish growth and it can be readily incorporated into models of stock assessment. The VBGF expression is :

$$L(t) = L_\infty (1 - \exp(-k(t-t_0))$$

where $L(t)$ is the length at time t, L_∞ is the asymptotic length, k the rate at which the fish approaches the asymptotic length and t_0 the origin of the growth curve. All length measurements presented herein are fork lengths in mm unless stated otherwise.

Table 13 : VBGF growth parameter estimations for the main species caught in the fishery of Tikehau. L_∞ is given in mm, k and t_0 on a year basis. (σ : standard deviation of relevant parameter when available, Meth : method used ; 1 : modal progression analysis of length-frequency histograms, 2 : tag-recapture study and 3 : otolith microstructure examination).

	L_∞	σ_{L_∞}	k	σ_k	t_0	σ_{t0}	Meth
Lethrinus miniatus	560	110	0.42	0.32	-0.49	1.09	1
Lutjanus gibbus	360	70	0.60	0.26	-0.59	0.83	1
Lutjanus fulvus	280	—	0.89	—	-0.05	—	3
Caranx melampygus	610	367	0.20	0.30	-1.80	1.50	1
Epinephelus microdon	610	—	0.35	—	—	—	2
Epinephelus microdon	690	301	0.31	0.03	0.22	0.08	1
Acanthurus xanthopterus	490	—	0.30	—	-0.00	—	1
Naso brevirostris (male)	380	—	0.33	—	-0.39	—	1
Naso brevirostris (female)	350	—	0.26	—	-0.80	—	1

Length-frequency histograms were examined. A random length sample of the main target species was taken serially, whenever possible. For species in which spawning season is confined to a short period (*Lethrinus miniatus, Lutjanus gibbus, Epinephelus microdon* and *Naso brevirostris*), analysis was carried out under the assumption that cohorts are separated by a time interval of one year. The VBGF parameter estimations presented in Table 13 probably lack robustness but figures generated correspond to some extent to growth parameters reviewed by Munro and Williams (1985) and can be considered as reliable. Several limitations arise on the results presented on *Caranx melampygus* and *Acanthurus xanthopterus* because breeding seasons tend to be prolonged over several months and as a result, age classes are not readily separable from one another. In that case, mode discrimination involves a large part of subjectivity.

A tag-recapture study was undertaken on grouper *Epinephelus microdon* (Morize and Caillart, 1987). Between 1984 and 1987, over one thousand tags were released all over the lagoon. Most recoveries occurred within one month of tagging and very close to the point of release but there is a tendency for at least a part of the population to seasonally migrate toward the pass since a few fish tagged in various locations of the lagoon were recaptured in the vicinity of the pass during the breeding season (*i.e.* : April). For growth rate estimation purposes, all tagged fish were measured upon release and fishermen were asked to provide information on the length of fish recaptured. Out of the thousand tags released, only 47 tags recovered met this basic requirement. Data were fitted to the VBGF using the method of Fabens. The VBGF parameter estimations are presented in Table 13.

Otoliths are structures that are commonly used to age tropical fishes (Panella, 1971). The relatively new finding that many fish deposit otolith growth increments with a daily periodicity appeared to offer a method of assessing age and growth with greater accuracy than was previously possible through other classical methods. Otolith microstructures of the target species of the fishery of Tikehau were examined (Caillart *et al.*, 1986 ; Caillart, 1988) for *Lethrinus miniatus, Lutjanus gibbus, Caranx melampygus* and *Naso brevirostris*. Ages determinated through increment counts appeared to be obviously underestimated although the actual age-increment discrepancy has not been measured. Tetracycline injected into adult *Epinephelus microdon* reared for more than one year was used to verify the periodicity of increment deposition (Caillart and Morize, 1989). For this species held in captivity, one ring was laid down every two days on an average. If this result applies to *Epinephelus microdon* in their natural environment, aging fishes under the assumption that otolith increments are daily, would have lead to underestimate the actual age by a factor of two.

In spite of all the limitations raised by the foregoing discussion, growth parameters of *Lutjanus fulvus* were calculated by fitting the VBGF to the results of otolith increment counts because either the length-frequency histograms method or the tag-recapture operation failed to give results (Table 13).

Table 14 : Length (in mm) at age (in year) of the target species of the fishery of Tikehau during the exploited phase (data backcalculated with VBGF growth parameters presented in table 13). (*) : Data backcalculated with the tag-recapture VBGF, (**) : Data backcalculated with the modal progression analysis VBGF.

Age	*L.*	*L.*	*L.*	*C.*	*E.*		*A.*	*N.*	
	miniatus	*gibbus*	*fulvus*	*melampygus*	*microdon*		*xanthopterus*	*brevirostris*	
					(*)	(**)		male	female
1		221		262					
1.5		257	210	295	249				
2	363	284	235	325	307	293			
2.5	400	304	251	352	356	350		234	
3	431			376	397	399		256	220
3.5	455				431	440		275	236
4	475				460	476	342	291	250
4.5	491				484		363	304	262
5	504				504		381	316	273
5.5	515						396	326	282
6							409		
6.5							420		
7							430		
7.5							438		

Lengths at age back calculated from the VBGF growth parameters are presented in Table 14. Only the portion of the growth curve covering the range of data used to establish the predictive equation was taken into account. Since this range of data corresponds with the exploited phase of the fishes, Table 14 gives insight into the duration of the phase. Certain patterns emerge pertaining to the main species and can be summarized as follows : the duration of the exploited phase is generally short ranging from three years (*Naso brevirostris, Caranx melampygus*) to four years (*Lethrinus miniatus, Epinephelus microdon* and *Acanthurus xanthopterus*). In the case of lutjanids, the vulnerability to fishing gear appears to last two years. Data furthermore suggest that fishes are fully recruited to the fishery at an average age of three years for acanthurids, and two years for the others. It is most likely that fishes disappear from the fishing ground due to a dramatic mortality rate since experimental fishing carried out in various locations of the lagoon and off the reef yielded a very few fish beyond the maximal size recorded in the catches. *Caranx melampygus* is however an exception. The adult population of this species shifts later in its life-cycle toward the pelagic environment of the outer slope, out of the reach of fishing gears.

Length-weight relationships

The relation of weight (W in g) to the fork length (Lf in mm) was calculated for the seven target species. The parameters a and b of the formula :

$$W = aL^b$$

are listed in Table 15 (Morize, unpublished data). For all species under investigation, samples of a few hundred fish taken in the catches were used to derive the regression equations. Correlation coefficients r obtained ranged from 0.95 to 0.99.

ASSESSMENT OF THE FISHERY OF TIKEHAU

The problem of stock assessment in the fishery of Tikehau mostly relates to the fact that it is based upon at least fourteen species in which none of them is overwhelmingly dominant. Given the set of data obtained on the fishery (catch statistics, common biological parameters of individual species), two techniques are available for appraising potential harvests. Firstly, assessment can be based upon a comparison with known harvests per unit area taken by fisheries of a similar environment. Secondly, analytical models requiring reliable estimates of either biological or fishery parameters can be used in order to model the response of the stock to exploitation.

Table 15 : Length-weight relationship for the main species caught in Tikehau fish-traps (a and b, parameters of the equation $W=aL^b$ where W = weight in g, L = fork length in mm).

	a ($.10^{-5}$)	b
Lethrinus miniatus	3.4	2.8
Lutjanus gibbus	2.1	3.0
Lutjanus fulvus	11.0	2.8
Caranx melampygus	6.4	2.8
Epinephelus microdon	0.5	3.2
Acanthurus xanthopterus	9.3	2.8
Naso brevirostris	3.8	2.8

Yield per unit area

On the average, 200 metric tons of finfishes per year are caught in the main fishery of Tikehau. Additionally, 40 metric tons are taken for subsistence and another 40 tons are fished by occasional fishermen for commercial purposes (Morize, 1984 ; Morize, 1985). That is, the fishery of Tikehau produces an average of 280 tons per year (table 16). The area covered by the lagoon of the Tikehau atoll is about 420 km^2 and the annual harvest per unit area of 0.7 tons . km^{-2}. Marshall (1980) pointed out that a finfish harvest of 3 to 5 tons . km^{-2} may be upheld as a generalization for the potential fishery yields of coral reefs and adjacent shallow water environments. Although records presented in Table 16 fall far below the suggested potential, data are somewhat homogeneous, ranging from 0.6 tons . km^{-2} in the fishery of Ontong Java to 1.3 tons . km^{-2} in the fishery of Mataiva with the noticeable exception of Rangiroa where fishery harvests reach only 0.2 tons . km^{-2}. However a limitation arises to permit the comparison of the different harvests per unit area recorded.

Table 16 : Harvests per unit area for a selection of exploited coral atolls (for the Tuamotu coral atolls, groups included in catch statistics are only finfishes. For Kapingamarangi and Ontong Java, composition of the catches is unknown),

	Total catch (metric tons)	Lagoon area (square kilometers)	Harvest per unit area (Tons/km^2)	Ref.
Kapingamarangi (Caroline islands)	280	400	0.7	1
Ontong Java (Solomon islands)	122	79	0.6	2
Rangiroa (Tuamotu)	350	1600	0.2	3
Kaukura (Tuamotu)	500	500	1.0	3
Mataiva (Tuamotu)	63	50	1.3	3
Tikehau (Tuamotu)	280	420	0.7	4

Reference

1- Stevenson and Marshall (1974) ; 2 - Munro and Williams (1985)

3 - Galzin *et al.* (1989) ; 4 - Caillart (1988)

As a reef fishery is generally a patchwork of coral reef patches (which are highly productive) and sandy bottoms (which is not that productive) ; the yield per unit area can very much depend upon the area and the percentage of area that is actually covered by hard coral substrate. Some fishery records like these of Rangiroa cover a large area, only part of which is actually covered by coral, whereas other records of fish yield apply to very small areas like Mataiva or Ontong Java where a hard substrate coverage is much greater. Moreover the potential fish yield from a given area cannot be inferred from sole catch records without even a rough reference to the fishing effort. In Rangiroa and Mataiva, the level of exploitation applied to the stock is low with regard to fishing effort in Tikehau or Kaukura.

Information on yield assessment and management in the fishery of Tikehau can be drawn from the comparison with the neighboring atoll of Kaukura. These two atolls have a comparable surface and morphology. In Tikehau, the fishery is based on bottom fixed fish traps all located in the vicinity of the pass. Yield relies on the behavior of species most prone to migrate for spawning. These fish are primarily carnivorous species as indicated by the specific composition of the catches. In Kaukura, bottom fixed fish traps are set not only in the vicinity of the pass but also all around the atoll rim, on the shallow inner reef flat.

Species caught are for a great percentage non territorial herbivorous species which wander to seek for food (Stein, *in* Galzin *et al.*, 1989). So, higher yields in Tikehau could probably be achieved by setting traps in various locations of the lagoon which in turn would probably exploit the food chain more efficiently. The total harvest of the Tikehau fishery could also be increased by diversifying the fishing gears, and setting classical bottom free fish traps around the numerous coral knolls scattered in the lagoon. Although we believe that it would be quite impossible to reach the potential yield suggested by Marshall (1980) (*i.e.* : 3 to 5 tons . km^{-2}), it would be at least possible to attain a harvest of 1 ton . km^{-2} recorded at Kaukura. This would result in a substantial increase of the catch of about 140 tons.

If this simple but nevertheless useful approach can be used to set a likely estimate of the potential fish yield of Tikehau, it is obvious that more thorough evaluations must be undertaken in order to focus management issues not only on optimum yield but also on preferred species.

Analytical assessment models

Analytical assessment models have been widely used in temperate water fisheries but they have been applied to coral reef fisheries in a limited number of cases. If these models cannot take into account the numerous and intricate relationships between all the components of the multi-species fishery, they are nevertheless of great value in giving an insight into the state of the fishery. There were two means used to provide estimates of the status of the fishery of Tikehau. One mean was a length converted catch-curve analysis (*in* Ricker, 1980). The other mean was to use yield per recruit estimates in a length structured model in which fishing mortality vector (F) is obtained from a length cohort analysis (Jones, 1974).

No adequate data sets on Tikehau fish stocks exist for an accurate determination of natural mortality (M). This parameter was estimated by two empirical formulas (Hoenig, 1984 and Pauly, 1980) that provided rough estimates of the value of M (Table 17). The real value of M is expected to lie in between these two estimates.

The specific exploitation rate E is given by :

$$E = \frac{F}{F+M}$$

where F is the fishing mortality. E estimated through length-converted catch curve analysis is found greater than 0.5 for *Lutjanus gibbus, L. fulvus, Caranx melampygus* and *Epinephelus microdon*, and less than 0.5 for *Lethrinus miniatus, Acanthurus xanthopterus* and *Naso brevirostris*. Gulland (1973) pointed out that a value of 0.5 of the exploitation rate can be roughly set as a limit below which a fish stock is lightly exploited and over which over-fishing may occur.

Table 17 : A range of values of natural mortality M (yr^{-1}) chosen for Tikehau target species. Mmin is given by Hoenig (1984) empirical formula, Mmax by Pauly (1980) equation.

Species	M min	M max
Lethrinus miniatus	0.43	0.66
Lutjanus gibbus	0.57	0.96
Lutjanus fulvus	0.46	0.88
Caranx melampygus	0.43	0.72
Epinephelus microdon	0.61	0.88
Acanthurus xanthopterus	0.43	0.72
Naso brevirostris	0.60	0.80

Yield per recruit model results listed in Table 18 are strongly related to the estimate of M chosen and have considerable different responses to F variations with respect to the species under investigation. For *Lethrinus miniatus, Acanthurus xanthopterus* and *Naso brevirostris,* a substantial increase of yield per recruit (more than 10% on the average) can be achieved if the fishing mortality vector is 50% or 100% higher. The snapper *Lutjanus gibbus* and *L. fulvus* yield per recruit estimates appears to be poorly increased (5% on the average) when fishing mortality vector increases. Lastly, yield per recruit estimates of *Epinephelus microdon* and *Caranx melampygus* do not significantly increase and can even decrease if an attempt to increase F is made.

Table 18 : Range of yield per recruit variations of the target species of Tikehau fishery (in % of present yield per recruit) in response to variations of fishing effort (µF : Fishing mortality coefficient, lowest value of yield per recruit correspond to the highest natural mortality figure).

Species	µF = 0.5	µF = 1	µF = 1.5	µF = 2
Lethrinus miniatus	-30 / -20	0	+20 / +8	+27 / +10
Lutjanus gibbus	-30 / -15	0	+12 / +3	+20 / +3
Lutjanus fulvus	-25 / -12	0	+10 / +2	+15 / +2
Caranx melampygus	-25 / -8	0	+10 / 0	+20 / -1
Epinephelus microdon	-15 / -6	0	+6 / -1	+8 / -2
Acanthurus xanthopterus	-40 / -30	0	+20 / +10	+40 / +20
Naso brevirostris		0	+19 / +26	+32 / +20

According to the foregoing results, the Tikehau fishery appears to be well fitted to carnivorous fish stock exploitation. The evidence from these analytical models suggests that Tikehau fish stocks are being fished at or near the Maximum Sustainable Yield (MSY). No major change in the direction of the present trap fishing strategy (increases or decreases in effort) is justifiable, although yield per recruit of certain species (emperors, surgeonfishes and snappers to a lesser extent) could be improved by a moderate increase of fishing effort. And it is unlikely that the grouper and jack fisheries could tolerate a heavy effort increase.

Higher harvests of carnivorous species could probably be achieved by using more selective fishing gears. For instance, the abundant stock of *Lethrinus miniatus* could provide substantial additional catches if handlines were more heavily used when the fish are abundant in the pass and hence, readily available. It has been mentioned that the herbivorous fish stock at Tikehau is very lightly exploited. The principal management issue would probably be to orient fishing pressure toward this part of the resource by setting traps on shallow areas all around the atoll rim where availability of herbivorous species is greater.

CONCLUSION

A total of 276 species belonging to 47 families have been recorded on the Tikehau atoll (Appendix 1). The real number of species is obviously under-estimated since rotenone poisonning was not used in all sites, and only one transect was regularly studied on the outer slope. The number of species censused in the lagoon was 167, 39 in the pass and 180 on the outer slope.

Only 17 species (6.2% of the total richness species) were encountered in the three environments : *Sargocentron spiniferum, Epinephelus merra, Epinephelus microdon, Caranx melampygus, Lutjanus gibbus, Lutjanus fulvus, Lethrinus miniatus, Monotaxis grandoculis, Mulloides vanicolensis, Chaetodon auriga, Scarus gibbus, Acanthurus xanthopterus, Ctenochaetus striatus, Naso lituratus, Naso unicornis, Naso vlamingii* and *Balistoides viridescens.* An unusual paucity of Carcharhinidae, Synodontidae, Apogonidae, Mugilidae, Sphyraenidae, Caesionidae and Tetraodontidae was noted while fish of the families of Holocentridae, Serranidae, Carangidae, Lutjanidae, Lethrinidae, Mullidae, Chaetodontidae, Pomacanthidae, Pomacentridae, Labridae, Scaridae, Acanthuridae and Balistidae were abundant.

A key question in fishery management is the correspondence between adult stock size and the number of each new cohort reaching the mean size of capture by the fishing gear. Recruitment to the fishery is preceded by a pre-recruit phase from birth to recruitment to the ecosystem and followed by a post recruit phase consisting of a pre-exploited phase. No study of larval recruitment was carried out at Tikehau though the knowledge of this part of the life-cycle is critical for understanding the dynamics of reef fish populations. Recruitment processes in coral reef fishes are however well documented (reviews in Munro and Williams, 1985 ; Richards and Lindeman, 1987) and much of the findings can apply to Tikehau.

Most reef fishes spawn externally in the water column above hard bottom structures. Off-shore larval dispersal is thought to be an evolutionary response to intense predation pressure in the adult habitat (Johannes, 1978). Fish community studies at Tikehau suggest that, adult fishes of various species gather off or in the pass to release their offspring in oceanic water. Larvae or fertilized eggs subsequently undergo oceanic advection and diffusion and juveniles enter the lagoon through shallow channels of the eastern coast. Most coral reef fishes characteristically present a two part life-cycle ; a pelagic larval phase during which extensive dispersal is possible and a relatively site-attached phase during in which movements are somewhat restricted. According to relevant data presented by Brothers *et al.* (1983), the duration of the pelagic stage of the main families exploited in Tikehau is estimated to range from about one month (Lethrinidae, Lutjanidae) to over three months in the case of *Naso sp.* (Acanthuridae). Absolute survivalship during planktonic life stages is a function of highly complex interactions among predation, oceanographic processes, growth and food availability. Mortality rates through this phase are subject to tremendous variations which considerably affect the availability of recruits to the atoll fish community. Although of a lesser order of magnitude, additional losses in subsequent post-settlement life due to innapropriate habitat and predation can in turn impact the number of recruit to the fishery. Variations in recruitment can also contribute to significant shifts in species composition within the exploited stock as it does occur in Tikehau.

Knowledge on the extent of fish population exchange between islands through the pelagic phase is of particular importance to effectively manage a fishery. The management strategy will vary greatly depending on the extent to which recruitment to the atoll is derived from within the fished population or is spawned outside the system. Due to the close-spacing pattern of the atoll of the Tuamotu archipelago, it might be expected that the stocks of species having a long pelagic larval stage occurring in a given atoll may be recruited from parent stocks living in areas further upstream. If the exploited stock of Tikehau is recruited largely from atolls located upstream like Rangiroa and Arutua, regulations for the conservation of the spawning stock will be ineffective and will be of benefit only to islands lying downstream (Mataiva). We have yet insufficient information to determine any general patterns, but there is an urgent need for further studies aiming to determine the potential limits of stock exchanges between atolls and the unit stock of a given species.

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Appendix 1 : Check-list of the fishes of Tikehau atoll (L : lagoon, P : pass, O : ocean)

CARCHARHINIDAE			
Carcharhinus melanopterus (Quoy et Gaimard, 1824)	L		
ALBULIDAE			
Albula vulpes (Linné, 1758)		P	
CHANIDAE			
Chanos chanos (Forsskäl, 1775)		P	
MURAENIDAE			
Echidna polyzona (Richardson, 1844)	L		
Gymnothorax buroensis (Bleeker, 1857)	L		
Gymnothorax fimbriatus (Bennett, 1831)	L		
Gymnothorax javanicus (Bleeker, 1859)	L		O
Gymnothorax margaritophorus Bleeker, 1864	L		
Gymnothorax zonipectis Seale, 1906	L		
*Gymnothorax sp.*3	L		
Gymnothorax sp. 16	L		
Gymnothorax sp. 18	L		
Uropterygius xanthopterus Bleeker, 1859	L		
CONGRIDAE			
Conger cinereus Rüppell, 1828	L		
OPHICHTHIDAE			
Leiuranus semicinctus (Lay and Bennet, 1839)	L		
Muraenichthys macropterus Bleeker, 1857	L		
ATHERINIDAE			
Atherinidae sp.	L		
SYNODONTIDAE			
Saurida gracilis (Quoy et Gaimard, 1824)	L		
Synodus variegatus (Lacepède, 1803)	L		
ANTENNARIIDAE			
Antennarius sp. (juv.)	L		
OPHIDIIDAE			
Brotula multibarbata Temminck and Schlegel, 1846	L		
HEMIRAMPHIDAE			
Hyporhamphus acutus (Günther, 1871)			O
HOLOCENTRIDAE			
Myripristis kuntee Valenciennes, 1831	L		O
Myripristis murdjan Forsskäl, 1775	L		O
Myripristis pralinia Cuvier, 1829			O
Myripristis violacea Bleeker, 1851	L		
Myripristis sp.	L	P	O
Neoniphon argenteus (Valenciennes, 1831)	L		
Neoniphon opercularis (Valenciennes, 1831)	L		O
Neoniphon sammara (Forsskäl, 1775)	L		O
Sargocentron caudimaculatum (Rüppell, 1838)			O
Sargocentron diadema (Lacepède, 1802)	L		
Sargocentron microstoma (Günther, 1859)	L		O
Sargocentron spiniferum (Forsskäl, 1775)	L	P	O
AULOSTOMIDAE			
Aulostomus chinensis (Linné, 1766)			O
FISTULARIIDAE			
Fistularia commersonii (Rüppell, 1838)	L		O
SYNGNATHIDAE			
Corythoichthys flavofasciatus Rüppel, 1838	L		
SCORPAENIDAE			
Scorpaenodes parvipinnis (Garrett, 1863)	L		
SERRANIDAE			
Anthias lori Randall and Lubbock, 1976			O
Anthias olivaceus Randall and Mc Cosker, 1892			O
Anthias pascalus (Jordan and Tanaka, 1927)			O
Anthias squamipinnis Peters, 1855			O
Cephalopholis argus (Bloch and Schneider, 1801)	L		O
Cephalopholis urodelus (Bloch and Schneider, 1801)			O
Epinephelus fasciatus (Forsskäl, 1775)			O
Epinephelus hexagonatus (Bloch and Schneider, 1801)	L		O
Epinephelus merra Bloch, 1793	L	P	O
Epinephelus microdon (Bleeker, 1856)	L	P	O
Epinephelus socialis (Günther, 1873)			O
Epinephelus sp.			O

Appendix 1 (cont'd)

Gracila albomarginata (Fowler and Bean, 1930)			O
Grammistes sexlineatus (Thunberg, 1792)	L		
Pseudogramma bilinearis (Schultz, 1943)	L		
Pseudogramma polyacantha (Bleeker, 1856)	L		
Variola louti (Forsskäl, 1775)			O
KUHLIIDAE			
Kuhlia marginata (Cuvier, 1829)	L		
PRIACANTHIDAE			
Priacanthus cruentatus (Lacepède, 1801)		P	O
CIRRHITIDAE			
Paracirrhites arcatus (Cuvier, 1829)			O
Paracirrhites forsteri (Bloch and Schneider, 1801)			O
Paracirrhites hemistictus (Günther, 1874)			O
APOGONIDAE			
Apogon angustatus (Smith and Radcliffe, 1911)	L		
Apogon coccineus Rüppell, 1838	L		
Apogon fraenatus Valenciennes, 1832	L		
Apogonichthys ocellatus (Weber, 1913)	L		
Cheilodipterus quinquelineatus Cuvier, 1828	L		
Fowleria aurita (Valenciennes, 1831)	L		
Fowleria marmorata (Alleyne and Macleay, 1876)	L		
Ostorhynchus savayensis (Günther, 1871)	L		
Pristiapogon snyderi Smith, 1961	L		
Pseudamia gelatinosa Smith, 1955	L		
MUGILIDAE			
Liza vaigiensis (Quoy et Gaimard, 1825)		P	
Mugil cephalus (Linné, 1758)		P	
SPHYRAENIDAE			
Sphyraena forsteri Cuvier, 1829		P	
ECHENEIDIDAE			
Echeneis naucrates Linné, 1758	L		
CARANGIDAE			
Alectis indicus (Rüppel, 1830)		P	
Carangoides orthogrammus (Jordan and Gilbert, 1881)	L	P	
Caranx ignobilis (Forsskäl, 1775)		P	O
Caranx lugubris Poey, 1860			O
Caranx melampygus (Cuvier, 1833)	L	P	O
Caranx sp.		P	
Decapterus macarellus (Valenciennes, 1833)		P	
Elagatis bipinnulata (Quoy et Gaimard, 1825)	L		O
Scomberoides lysan (Forsskäl, 1775)			
Selar crumenophthalmus (Bloch, 1793)			
LUTJANIDAE			
Aphareus furca (Lacepède, 1801)			O
Aprion virescens Valenciennes, 1830			O
Lutjanus bohar (Forsskäl, 1775)			O
Lutjanus fulvus (Bloch and Schneider, 1801)	L	P	O
Lutjanus gibbus (Forsskäl, 1775)	L	P	O
Lutjanus kasmira (Forsskäl, 1775)			O
Lutjanus monostigmus (Cuvier, 1828)	L		O
LETHRINIDAE			
Gnathodentex aureolineatus (Lacepède, 1802)	L		O
Lethrinus elongatus Valenciennes, 1830			O
Lethrinus mahsena (Forsskäl, 1775)		P	
Lethrinus miniatus Smith, 1959	L	P	O
Lethrinus variegatus Ehrenberg, 1830		P	
Lethrinus xanthochilus Klunzinger, 1870			O
Monotaxis grandoculis (Forsskäl, 1775)	L	P	O
MULLIDAE			
Mulloides flavolineatus (Lacepède, 1801)	L	P	
Mulloides vanicolensis (Valenciennes, 1831)	L	P	O
Parupeneus barberinus (Lacepède, 1801)	L	P	
Parupeneus bifasciatus (Lacepède, 1801)	L		O
Parupeneus ciliatus (Lacepède, 1801)			O
Parupeneus multifasciatus (Quoy et Gaimard, 1825)	L		O
Parupeneus porphyreus (Jenkins, 1900)	L		O
Upeneus vittatus (Forskäll, 1775)		P	

Appendix 1 (cont'd)

PEMPHERIDAE			
Pempheris oualensis Cuvier, 1831			O
KYPHOSIDAE			
Kyphosus cinerascens (Forsskäl, 1775)		P	
CHAETODONTIDAE			
Chaetodon auriga Forsskäl, 1775	L	P	O
Chaetodon bennetti Cuvier, 1831			O
Chaetodon citrinellus Cuvier, 1831	L		
Chaetodon ephippium Cuvier, 1831	L		O
Chaetodon lunula (Lacepède, 1802)	L		O
Chaetodon ornatissimus Cuvier, 1831			O
Chaetodon pelewensis Kner, 1868			O
Chaetodon quadrimaculatus Gray, 1831			O
Chaetodon reticulatus Cuvier, 1831			O
Chaetodon trifasciatus Mungo Park, 1797	L		O
Chaetodon ulietensis Cuvier, 1831	L		O
Chaetodon unimaculatus Bloch, 1787			O
Forcipiger flavissimus Jordan and Mc Gregor, 1898			O
Forcipiger longirostris (Broussonet, 1782)			O
Hemitaurichthys polylepis (Bleeker, 1857)			O
Hemitaurichthys zoster (Bennett, 1831)			O
Heniochus acuminatus (Linné, 1758)			O
Heniochus chrysostomus Cuvier, 1831			O
Heniochus monoceros Cuvier, 1831	L		O
POMACANTHIDAE			
Centropyge flavissimus (Cuvier, 1831)	L		O
Centropyge loriculus (Günther, 1874)			O
Pomacanthus imperator (Bloch, 1787)			O
Pygoplites diacanthus (Boddaert, 1772)	L		O
POMACENTRIDAE			
Abudefduf sexfasciatus (Lacepède, 1801)	L		
Abudefduf sordidus (Forsskäl, 1775)	L		
Amphiprion chrysopterus Cuvier, 1830			O
Chromis iomelas Jordan and Seale, 1906			O
Chromis margaritifer Fowler, 1946			O
Chromis vanderbilti (Fowler, 1941)			O
Chromis viridis (Cuvier, 1830)	L		
Chromis xanthura (Bleeker, 1854)			O
Chrysiptera glauca (Cuvier, 1830)	L		
Chrysiptera leucopoma (Lesson, 1830)	L		
Dascyllus aruanus (Linné, 1758)	L		
Dascyllus flavicaudus Randall et Allen, 1977			O
Dascyllus trimaculatus (Rüppell, 1828)			O
Plectroglyphidodon dickii (Liénard, 1839)			O
Plectroglyphidodon johnstonianus Fowler and Ball, 1924			O
Pomacentrus fuscidorsalis Allen and Randall, 1974			O
Pomacentrus pavo (Bloch, 1787)	L		
Stegastes albofasciatus (Schlegel and Müller, 1839-44)	L		
Stegastes aureus (Fowler, 1927)			O
Stegastes nigricans (Lacepède, 1803)	L		
LABRIDAE			
Anampses caeruleopunctatus Rüppel, 1828			O
Bodianus axillaris (Bennett, 1831)			O
Bodianus loxozonus (Snyder, 1908)			O
Cheilinus chlorourus (Bloch, 1791)	L		O
Cheilinus trilobatus (Lacepède, 1801)	L		O
Cheilinus undulatus Rüppel, 1835	L		O
Cirrhilabrus exquisitus Smith, 1957	L		
Cirrhilabrus scottorum Randall and Pyle, 1856			O
Coris aygula Lacepède, 1801			O
Coris gaimard (Quoy et Gaimard, 1824)	L		O
Cymolutes praetextatus (Quoy et Gaimard, 1824)	L		
Epibulus insidiator (Pallas, 1770)	L		
Gomphosus varius Lacepède, 1801	L		O
Halichoeres hortulanus (Lacepède, 1801)	L		O

Appendix 1 (cont'd)

Halichoeres melasmapomus Randall, 1980			O
Halichoeres trimaculatus (Quoy et Gaimard, 1834)	L		O
Hemigymnus fasciatus (Bloch, 1792)			O
Labridae sp. (juv.)	L		
Labridae sp. 8 (juv.)	L		
Labroides bicolor Fowler and Bean, 1928			O
Labroides dimidiatus (Valenciennes, 1839)	L		O
Novaculichthys taeniourus (Lacepède, 1801)	L		O
Pseudocheilinus hexataenia (Bleeker, 1857)			O
Pseudocheilinus octotaenia Jenkins, 1900	L		O
Stethojulis bandanensis (Bleeker, 1851)	L		O
Stethojulis strigiventer Bennett, 1832	L		
Thalassoma amblycephalum (Bleeker, 1856)	L		O
Thalassoma hardwicke (Bennett, 1830)	L		
Thalassoma purpureum (Forsskäl, 1775)			O
Thalassoma quinquevittatum (Lay and Bennett, 1839)	L		O
Thalassoma trilobatum (Lacepède, 1801)			O
Wetmorella ocellata Schultz and Marshall, 1954	L		
SCARIDAE			
Calotomus carolinus (Valenciennes, 1839)			O
Cetoscarus bicolor (Rüppell, 1829)	L		O
Hipposcarus harid (Forsskäl, 1775)		P	
Hipposcarus longiceps (Valenciennes, 1839)	L		O
Leptoscarus vaigiensis (Quoy et Gaimard, 1824)			O
Scarus altipinnis Steindachner, 1879	L		O
Scarus brevifilis (Günther, 1909)			O
Scarus festivus , Valenciennes, 1840			O
Scarus forsteri (Bleeker, 1861)	L		O
Scarus frenatus Lacepède, 1802	L		O
Scarus frontalis Valenciennes, 1839			O
Scarus ghobban Forsskäl, 1775	L		O
Scarus gibbus Rüppell, 1828	L	P	O
Scarus globiceps Valenciennes, 1840	L		O
Scarus niger Forsskäl, 1775	L		O
Scarus oviceps Valenciennes, 1839	L		O
Scarus psittacus Forsskäl, 1775	L		O
Scarus rubroviolaceus Bleeker, 1849	L		O
Scarus schlegeli Bleeker, 1861	L		O
Scarus sordidus Forsskäl, 1775	L		O
Scarus sp. rayé (juv.)	L		O
Scarus sp. gris (juv.)	L		O
Scarus sp. marron (juv.)	L		O
Scarus sp. parc		P	
Scarus sp. vert (juv.)			O
BLENNIIDAE			
Enchelyurus ater (Günther, 1877)	L		
Istiblennius periophthalmus (Valenciennes, 1836)	L		
Plagiotremus tapeinosoma (Bleeker, 1857)	L		
CALLIONYMIDAE			
Callionymus simplicicornis Valenciennes, 1837	L		
GOBIIDAE			
Amblygobius phalaena (Valenciennes, 1837)	L		
Asterropteryx ensiferus (Bleeker, 1874)	L		
Asterropteryx semipunctatus (Rüppell, 1830)	L		
Callogobius sclateri (Steindachner, 1880)	L		
Eviota afelei Jordan and Seale, 1906	L		
Eviota sp.	L		
Fusigobius neophytus (Günther, 1877)			O
Gnatholepis cauerensis (Bleeker, 1853)	L		
Gobiidae sp. 5	L		
Nemateleotris magnifica Fowler, 1938			O
Ptereleotris evides (Jordan and Hubbs, 1925)	L		
Quisquilius eugenius (Valenciennes, 1836)	L		
ISTIOPHORIDAE			
Istiophorus platypterus (Shaw and Nodder, 1792)			O
ZANCLIDAE			
Zanclus cornutus (Linné, 1758)	L		O

Appendix 1 (cont'd)

ACANTHURIDAE			
Acanthurus achilles Shaw, 1803	L		O
Acanthurus bleekeri Günther, 1861			O
Acanthurus glaucopareius Cuvier, 1829	L		O
Acanthurus guttatus Bloch and Schneider, 1801	L		O
Acanthurus leucopareius (Jenkins, 1903)			O
Acanthurus lineatus (Linné, 1758)	L		O
Acanthurus mata (Cuvier, 1829)	L		O
Acanthurus nigricauda Duncker and Mohr, 1929	L		O
Acanthurus nigrofuscus (Forsskål, 1775)	L		O
Acanthurus nigroris (Valenciennes, 1835)	L		O
Acanthurus nubilus (Fowler and Bean, 1929)			O
Acanthurus olivaceus Bloch and Schneider, 1801			O
Acanthurus pyroferus Kittlitz, 1834			O
Acanthurus thompsoni (Fowler, 1923)			O
Acanthurus triostegus (Linné, 1758)	L		O
Acanthurus xanthopterus (Valenciennes, 1835)	L	P	O
Acanthurus sp. (Juv.) jaune	L		O
Ctenochaetus striatus (Quoy et Gaimard, 1825)	L	P	O
Ctenochaetus strigosus (Bennett, 1828)			O
Naso annulatus (Quoy et Gaimard, 1825)	L		O
Naso brachycentron (Quoy et Gaimard, 1825)			O
Naso brevirostris (Valenciennes, 1835)	L	P	O
Naso hexacanthus (Bleeker, 1855)	L		O
Naso lituratus (Bloch and Schneider, 1801)	L	P	O
Naso unicornis (Forsskål, 1775)	L	P	O
Naso vlamingii (Valenciennes, 1835)	L	P	O
Zebrasoma rostratum (Günther, 1873)			O
Zebrasoma scopas (Cuvier, 1829)	L		O
Zebrasoma veliferum (Bloch, 1795)	L		O
SIGANIDAE			
Siganus argenteus (Quoy et Gaimard, 1825)		P	O
BOTHIDAE			
Bothus mancus (Broussonet, 1782)	L		
BALISTIDAE			
Balistapus undulatus (Mungo Park, 1797)	L		O
Balistoides viridescens (Bloch and Schneider, 1801)	L	P	O
Melichthys niger (Bloch, 1786)			O
Melichthys vidua (Solander, 1844)			O
Odonus niger (Rüppell, 1837)			O
Rhinecanthus aculeatus (Linné, 1758)	L		O
Rhinecanthus rectangulus (Bloch and Schneider, 1801)	L		O
Sufflamen bursa (Bloch and Schneider, 1801)			O
Sufflamen fraenatus (Latreille, 1804)			O
Xanthichthys caeruleolineatus (Randall, Matsuura, Zama, 1978)			O
MONACANTHIDAE			
Aluterus scriptus (Osbeck, 1765)			O
Amanses scopas (Cuvier, 1829)			O
Cantherhines dumerilii (Hollard, 1854)			O
OSTRACIIDAE			
Ostracion cubicus Linné, 1758	L		
Ostracion meleagris Shaw, 1796	L		O
TETRAODONTIDAE			
Arothron hispidus (Linné, 1758)	L		
Canthigaster bennetti (Bleeker, 1854)	L		
Canthigaster solandri (Richardson, 1844)	L		
Canthigaster valentini (Bleeker, 1853)	L		

Plate 1 : Most of the fish traps are located around Tuheiava pass. (Photo Morize)

Plate 2 : The fishes held in the traps are collected about once a week. (Photo Intes)

Plate 3 : The fish are tighed by about 3 kg bundles before loading on the transport ship. (Photo Intes)

Plate 4 : A "goelette" weekly brings the fishes caught in Tikehau to the Papeete market. (Photo Morize)

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COLONIZATION OF FISH LARVAE IN LAGOONS OF RANGIROA (TUAMOTU ARCHIPELAGO) AND MOOREA (SOCIETY ARCHIPELAGO)

BY

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ABSTRACT

The colonization of the lagoon by coral reef fish larvae was compared between two islands of French Polynesia, the atoll of Rangiroa and the high volcanic island of Moorea. In both cases the larval flux coming into the lagoon followed a daily cycle. Larvae were mainly caught at dusk and during the night, and on both islands the colonization was higher during moonless than moonlit periods. The larval flux did not appear to be dependent on the waterflow in the lagoons. A comparison of larval abundance and taxonomic lists indicates that Scarids and Labrids were dominant in Rangiroa while Gobiidae was the major family on Moorea. This difference could be in part related to the different sampling periods, but other environmental and biological factors could also be important.

INTRODUCTION

Most reef fishes have a pelagic larval phase, ending with the colonization of the reef (Leis, 1991). This recruitment of fish larvae on coral reefs is now studied in detail since it has been assumed that events occuring during this period determine the characteristics of reef-fish stocks (Sale, 1980; Richards and Lindeman, 1987; Doherty and Williams, 1988). Although some studies emphasized the importance of the processes during the settlement of fish larvae among coral reefs (Sweatman, 1985, 1988; Victor, 1986), this phenomenon is not clearly understood. For fifteen years, scientists have studied mechanisms of this return to the parental habitat. These studies have been limited mainly to continental reefs (e. g.: reefs of Central America), or patch reefs along continental platforms (e.g.: Great Barrier Reef of Australia) with very little data available on recruitment of reef fish species in oceanic islands and in atolls. This is a first attempt to compare some features of fish colonization of the lagoons of two geomorphologically different islands located in French Polynesia.

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Although the data were not obtained simultaneously in both islands, it is still useful to compare these two sets of data. It is also worth considering whether or not the observed differences are due to the location, the geomorphological features of the islands, or the time lag between sample collecting on the two islands.

MATERIAL AND METHODS

STUDY AREA

Rangiroa Atoll (figure 1) is one of the largest atolls in the world and the most important of the Tuamotu Archipelago (Ricard, 1985). It is 70 km long, 30 km wide and the peripheral rim is 225 km long. One third of the rim is above the sea surface and consists of small cays separated by channels. The rim flat is generally wider in the northern than in the southern part (800 m vs 500 m). The lagoon is biologically very rich compared to the other atolls of Tuamotu and is one of the most important reef fisheries centers of this Archipelago. The maximum estimated depth is 35 m and a lot of pinnacles are evenly distributed on its surface. Two passes, 450 to 550 m wide and 14 to 35 m deep are located in the North coast and lagoon waters are flushed out through these passes during ebb tides (35 cm to 60 cm tide range). Oceanic waters flow into the lagoon through channels over the atoll rim and the two passes during flood tides and also when trade winds blow. The fish larvae were collected in a channel, midway between the two passes.

Moorea Island (figure 1) is located 25 km north-west of Tahiti (Galzin and Pointier, 1985). This volcanic island has a triangular shape with a 61 km coastline and a relief of 1200 m. The island is surrounded by a barrier reef, which encloses a lagoon, 800 to 1600 m wide. The reef is intersected by several passes. Two bays are located on the northern part of the island. The lagoon is generally shallow (1 to 5 m), but deeper near the passes. The oceanic water enters the lagoon by waves breaking over the outer reef crest, and return to the ocean through the passes. The very weak tides on Moorea (average range 15 cm) do not reverse the current in the passes. Sampling was carried out on the outer reef crest, 600 m away from the pass.

METHODS

Samples were collected off the northern coasts of both islands. Fish larvae were collected with an anchored net that filtered the waterflow coming into the lagoon. The net with rectangular mouth (1 x 0.25 m) was of mesh size 0.5 mm. A General Oceanics flowmeter was fixed in the mouth of the net.

On Rangiroa Atoll, the net filtered the water coming from the seaward reef flat to the lagoon. It was located 500 m from the outer reef front. The channel was made of gravel in a shallow area (0.5 m).

On Moorea Island, the fish larvae were collected on the outer reef crest. The net was fixed on the reef substrate and filtered the water coming over the crest with the breaking waves. Thus, the water flow was not constant but it was estimated over the time period of each sample (10 minutes).

The time lag between two samples was 1h or 2h. Two diel cycles were made in February 1989 on Rangiroa. At Moorea, two diel cycles were made in April 1989 and a third one was made in October 1989. At Rangiroa, the first cycle was 3 days before the new moon and the second was around the first quarter. The diel cycles were made during same lunar phases on Moorea.

The collected larvae were then fixed with 5% formalin seawater and identified under a dissecting microscope at the lowest taxonomic level following the recommendations of Leis and Rennis (1983) and Leis and Trnski (1989). This correspond to a family-level identification for all the larvae but the Gobioids. In several cases, genus-level identification was accomplished. Most of the larvae caught were in the postflexion stage or in metamorphosis and were identified. Abundances of unidentifiable preflexion larvae and juveniles were very low and were simply pooled into preflexion and juveniles types. Results are expressed in larval abundance per sample which represents the larval flux, i. e. the number of larvae for 1m of reef section and for 10 minutes (Dufour, 1993).

RESULTS

DIEL CYCLES

The diel cycles from Rangiroa (figure 2) represent changes in larval composition over a two night period. Although the samples do not cover 24 hours, they take into account the two consecutive daily changes at dusk and dawn. Our data clearly indicate that fish larvae were present only at night and during twilight. Because the waterflow may influence the larval flux, the volume filtered by the net was also presented. The Kendall coefficient correlation rank calculated with Statview software (Abacus Concepts, Inc, Berkeley, 1992) was significant for the comparison between the two larval fluxes of the two cycles and also between the two water flows (Table I). But it was positive between the larval fluxes (+0.524) while it was negative between the water flows (-0.486). This result indicates that the change of the larval flux was somewhat similar during the two sampling periods. But the water flow was negatively correlated between the two cycles. The Kendall coefficient correlation rank calculated between the water flow and the larval flux for the two diel cycles made on Rangiroa was very small and not significant (table II). However, the second cycle shows a strong decrease of the water flow in the middle of the night and this decrease was also observed for the larval abundance. These results indicate that there was no clear link between water flow and larval flux, except for low water flow, which could hinden larval colonization in the lagoon.

The diel cycles made on Moorea also show that most fish larvae were taken at night and dusk (figure 2). The Kendall 's tau calculated between the larval flux and the water flow (Table II) was not significant. The absence of significant correlation in the four studied cycles confirms that larval flux did not seem to be quantitatively dependent of the water flow.

The study of larval flux on the two islands reveals that the larval flux on Rangiroa reached 3 times the value of 500 larvae per sample, which was obtained only once on Moorea, despite a larger sampling effort. On both islands these larval peaks occured in the early evening. A second peak was found just before dawn on the second cycle on Rangiroa. The water flow during these larval peaks on Rangiroa was not very high and similar to that found during larval peaks of Moorea. As a result, these high peaks of larval colonization on Rangiroa and Moorea do not appear to be created by variation in water flow over the reef of these islands. The comparison of the average larval flux recorded on the two islands at different times indicates that this flux appears to be more significant on Rangiroa than on Moorea (Table III). It was obvious that a high larval flux from these islands was never recorded during full moon. However, during moonlight periods of the first lunar quarter, the larval abundance on Rangiroa was higher than the abundance on Moorea.

TAXONOMIC ANALYSIS OF THE SAMPLES

The number of larvae and the number of larval types were different between the two islands (Table IV). The total number of larvae from Rangiroa was almost half the number of those collected from Moorea during eleven months, although the number of samples was higher. Based on the two studied periods, the average larval flux on Rangiroa reached three times the average larval flux on Moorea. The number of larval types on Moorea was 56 for the three cycles. The number of larval types on Rangiroa during only two nights was 43. Several larval types from Moorea were not found on Rangiroa, while only one larval type from Rangiroa was missing from Moorea. Some of these types were represented by more than 50 larvae. The comparison between Rangiroa and all the samples of Moorea indicates that the number of types was twice as less as that found in all the samples of Moorea despite the fact that the number of samples collected was eight times higher and the sample period was much longer in Moorea. Therefore, the number of larval types caught in two nights on Rangiroa was significantly higher that those caught off Moorea.

The list of the larval types and their abundance is presented for both Rangiroa and Moorea (Fig. 3). The pie diagrams show the percentages of the main larval types for each island. The abundance of the larvae from Moorea is presented for all the 358 samples made between March 1989 and November 1989 (grey bars) and for the three diel cycles previously studied (black bars). The most abundant larval type on Rangiroa was the Scaridae forming 52% of the total catch. The two most abundant larval types on Moorea were Gobiidae (Gobiidae type 1 and Gobiidae type 56). The abundance of Gobioid types on Moorea represents 63% of the total catch. Scaridae were the second most abundant family on Moorea but they represented half the number of Scaridae collected from Rangiroa. On Rangiroa Gobioid types were the second most important group but their number were far below those of the Scaridae. The other significant larval types were found in similar numbers on both islands although periods of sampling were different. This was the case for the Labridae, the Callionymidae and the Schindleriidae. It is apparent that the number of larvae of these families would have been much higher on Rangiroa if the extent of sampling was similar to that carried out off Moorea. The Apogonidae type 2 were more abundant on Rangiroa but the total number of Apogonidae from both areas was not very different. Juvenile fishes were caught in both islands in relatively high number. Different families were gathered in this type (Mullidae, Holocentridae...). It is interesting to note that these juveniles were collected at dusk despite the fact that daylight was supposed to assist in a higher avoidance of the net. The Gobiidae type 8 was only collected at Rangiroa.

DISCUSSION

The daily patterns of the reef colonization by reef fish larvae have been demonstrated only recently on coral reefs (Dufour, 1991, 1993). The fish larvae that enter the lagoon were caught only at night and dusk. Their abundance was also found to be higher during moonless periods. This pattern has been confirmed by samples over a two years period. The data from Rangiroa in this study confirm this finding. Each cycle made at Rangiroa demonstrated that fish larvae were abundant during the moonless nights in the channel of the atoll. The larval abundance could reflect higher larval activity above the reef at night (Hobson et Chess, 1978). However, the fixed nets could not catch larvae that do not move into the lagoon. Hobson and Chess (1978, 1986) have demonstrated that planktonic organisms drifted at night over the reef of Enewetak atoll to enter the lagoon. Their appearence over the reef was related to a vertical migration at night, followed by a passive drift in a current flow induced by breaking waves. However, colonization by fish larvae at Rangiroa and at Moorea was only accomplished by individuals ready to settle. The larval flux observations do not include preflexion larvae because these larvae were scarce in samples, although they could have drifted more easily than postflexion larvae. It is known that postflexion larvae are able to swim (Blaxter, 1986; Webb and Weihs, 1986). Moreover, reef fish larvae can avoid the reef area until they are competent for metamorphosis (Kingsford and Choat, 1989). These phenomena imply other mechanisms of colonization in addition to passive drift. The larval flux in the lagoon could thus be viewed as an active process made nightly by competent fish larvae. Night activity correllated to the darker phases of the moon cycle has also been demonstrated for other planktonic organisms over reefs (Aldredge and King, 1980, Tranter and al., 1981). These authors found that this moonless activity was an adaptative advantage against predation. In a similar way, the colonization of fish larvae occurs at night when predation is lower (Hobson, 1973, 1975). Therefore, larval colonization of the lagoons at night could be viewed as an adaptative process against predation, as predation plays a major role during the recruitment of reef fishes (Shulman and Ogden, 1987, Victor, 1986, Hixton, 1991). Both the geomorphology of the reef and hydrodynamic characteristics of the waters flushing into the lagoons appear to have no significant control on larval colonization.

The difference of the abundance of fish larvae between the two islands can be explained by the difference of the sampling periods. Although it has not been established that fish larvae were more abundant in French Polynesia during February than during

April, the summer season was considered to be the recruitment season in other coral reef areas (Williams, 1983, Victor, 1987). Thus, the lower abundance in samples from Moorea could be explained by variations related to seasonal recruitment. The difference in abundance and diversity of fishes during colonization between these two islands could also be related to the size of the lagoon. The quotient of reef periphery to surface of the lagoon is also much lower for Rangiroa than for Moorea. This is because the lagoon of Moorea encloses the volcanic island and does not cover all the surface delimited by the outer reef like an atoll. On Moorea, the quotient of the lagoon surface to the reef length is around 0.86 km^{-1} (60 km/70 km^2), on Rangiroa it is 0.11 km^{-1} (230 km/2100 km^2), but the sand cays over one third of the reef lower this coefficient to 0.074. This last value is more than 10 times smaller than on Moorea. If we could assume that the density of the larval flux per unit of lagoon surface over the crest was related to this coefficient, the number of fish colonizing the lagoon should be proportionally higher. This assumption could explain the higher rate of colonization for Rangiroa. This hypothesis cannot be verified, however, because the larval flux over all the reef rim has not been determined.

The difference between the major larval types from the two islands could also be explained by other hypothesis. The composition and diversity of adult fishes in both lagoons was probably not the same. It is possible that the number of fish species in the lagoons of atoll is related to the surface area of these atolls (Galzin et al., 1994). Scaridae and Labridae are among the most abundant fishes in atoll lagoons (Bouchon-Navarro, 1983, Morize et al., 1990), while Pomacentridae and Acanthuridae are more abundant in Moorea lagoon (Galzin, 1987). Although we have no information about their density in Rangiroa atoll, the higher abundance of Scaridae larvae on Rangiroa was not surprising. But this higher abundance could be related to the low number of samples collected in Rangiroa, and the period when they were collected. It is possible, however, that the pattern of settlement of fish larvae on reefs could be relatively unpredictable and chaotic and peaks of larvae have be described as randomly distributed at different time scales (Doherty and Williams, 1988). Another explanation could be the reproduction period of Scaridae, which could occur earlier. Larvae of Scaridae, however, were caught on Moorea until the end of June and Scaridae and Labridae were also the most abundant families in samples made in May and June 1988 on Moorea.

CONCLUSIONS

The study of the larval flux over the reef on Rangiroa and Moorea was useful to the understanding of some aspects of the settlement processes of fish larvae in lagoons. This study has confirmed some trends in the diel and lunar cycles of reef colonization by fish larvae. The difference of larval abundance between samples on both islands can be related to the time lag between the sampling periods of each island. The sizes of the two lagoons could also play a role in this difference. It was more difficult to understand the taxonomic difference. It could be explained by the difference in size of the two lagoons, or by the period of fish reproduction or even by the density of the different families, but few data were available to confirm these hypotheses.

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Table I: Values of the Kendall coefficient correlation rank for the larval flux and the water flow between the two diel cycles from Rangiroa (n.s: not significant at 5%, s: significant at 5%).

Rangiroa	Kendall coefficient
Comparison of the larval fluxes	0.524 s
Comparison of the Water flows	-0.486 s

Table II: Values of the Kendall coefficient correlation rank between the water flow and the larval flux (n.s: not significant at 5%).

	Rangiroa 1	Rangiroa 2	Moorea 1	Moorea 2	Moorea 3
Kendall coefficient	0.206 n.s	-0.176 n.s	-0.109 n.s	-0.036 n.s	0.345 n.s

Tableau III : Average values of the water flow and the larval flux for the cycles from Rangiroa (R) and Moorea (M), standard deviation are in brackets.

sampling dates	water flow : -m^3·sample^{-1}	abundance : larves.sample^{-1}
R 03.02	109.9 (54.01)	72.4 (118.4)
R 10.02	71.41 (47.53)	122.5 (156.4)
M 05.04	41.3 (6.47)	74.5 (130)
M 12.04	48.6 (12.1)	8.45 (8.47)
M 23.10	35.9 (11.1)	38.1 (25.9)

Tableau IV : Abundance of larvae and larval types from Rangiroa and Moorea

	Rangiroa	Moorea (3 cycles)	Moorea (all samples)
number of samples	44	34	358
number of larvae	4165	1369	10050
larvae / sample	94.66	40.26	28.1
number of types	43	56	71

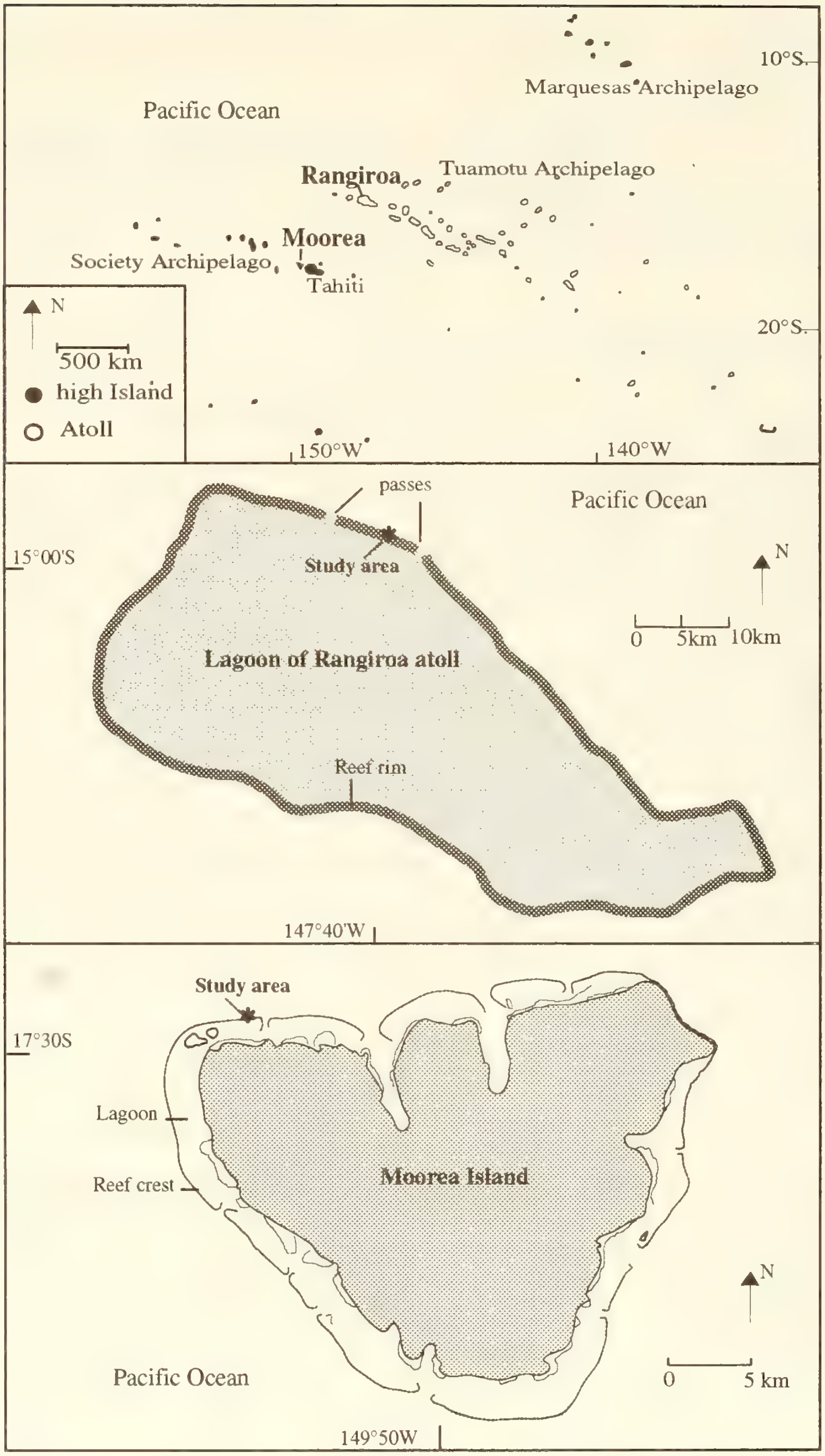

Figure 1. French Polynesia (above) with the atoll of Rangiroa, Tuamotu archipelago (middle), and the high Island of Moorea, Society archipelago (below).

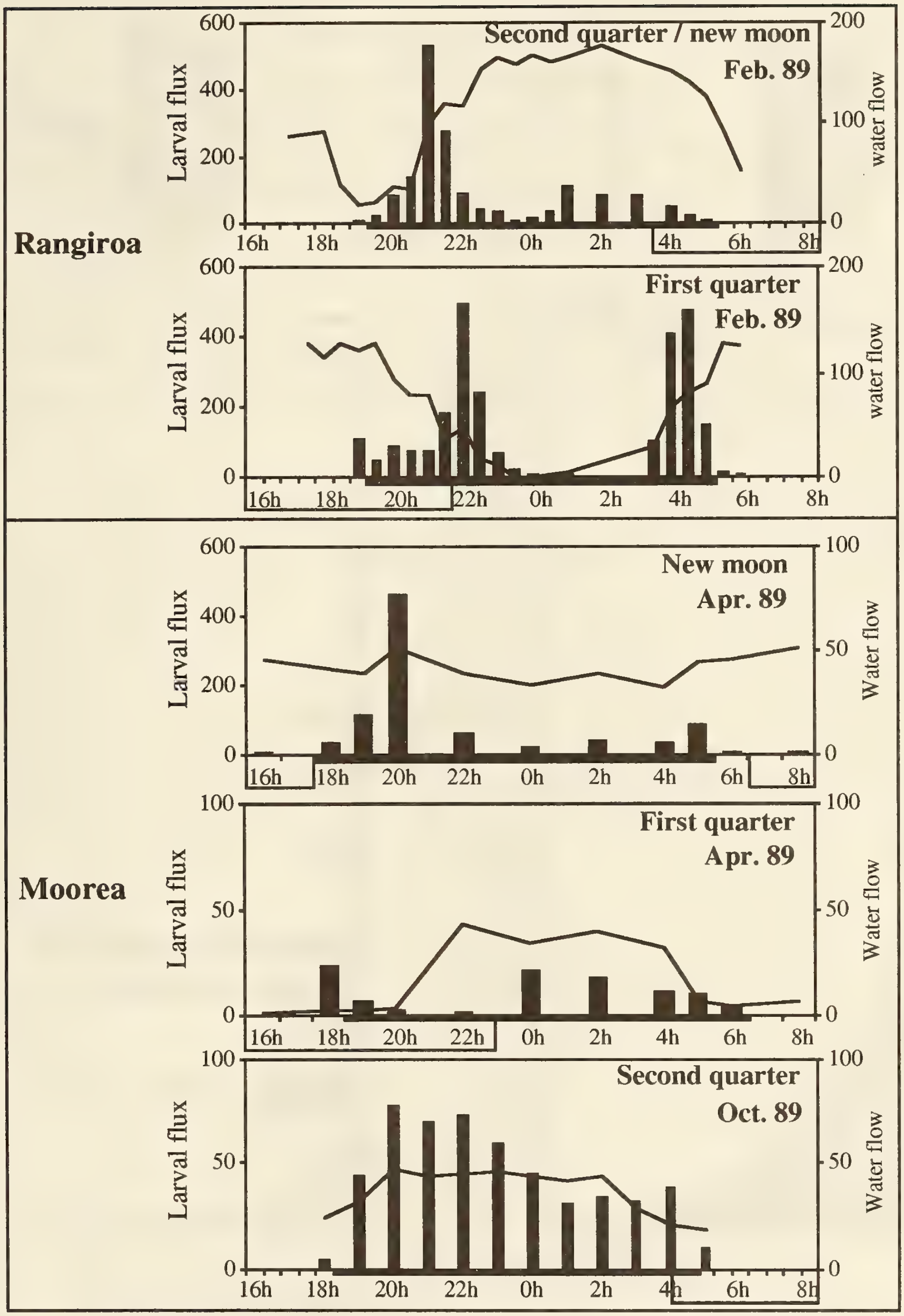

Figure 2. Evolution of the larval flux expressed in number of larvae. sample^{-1} (bars) and the water flow in m^{-3}. sample^{-1} (line) during nycthemeral cycles made on Rangiroa and on Moorea. The black thickness on the categories axis represents the night hours, the white frame on the same axis represents moonlit hours.

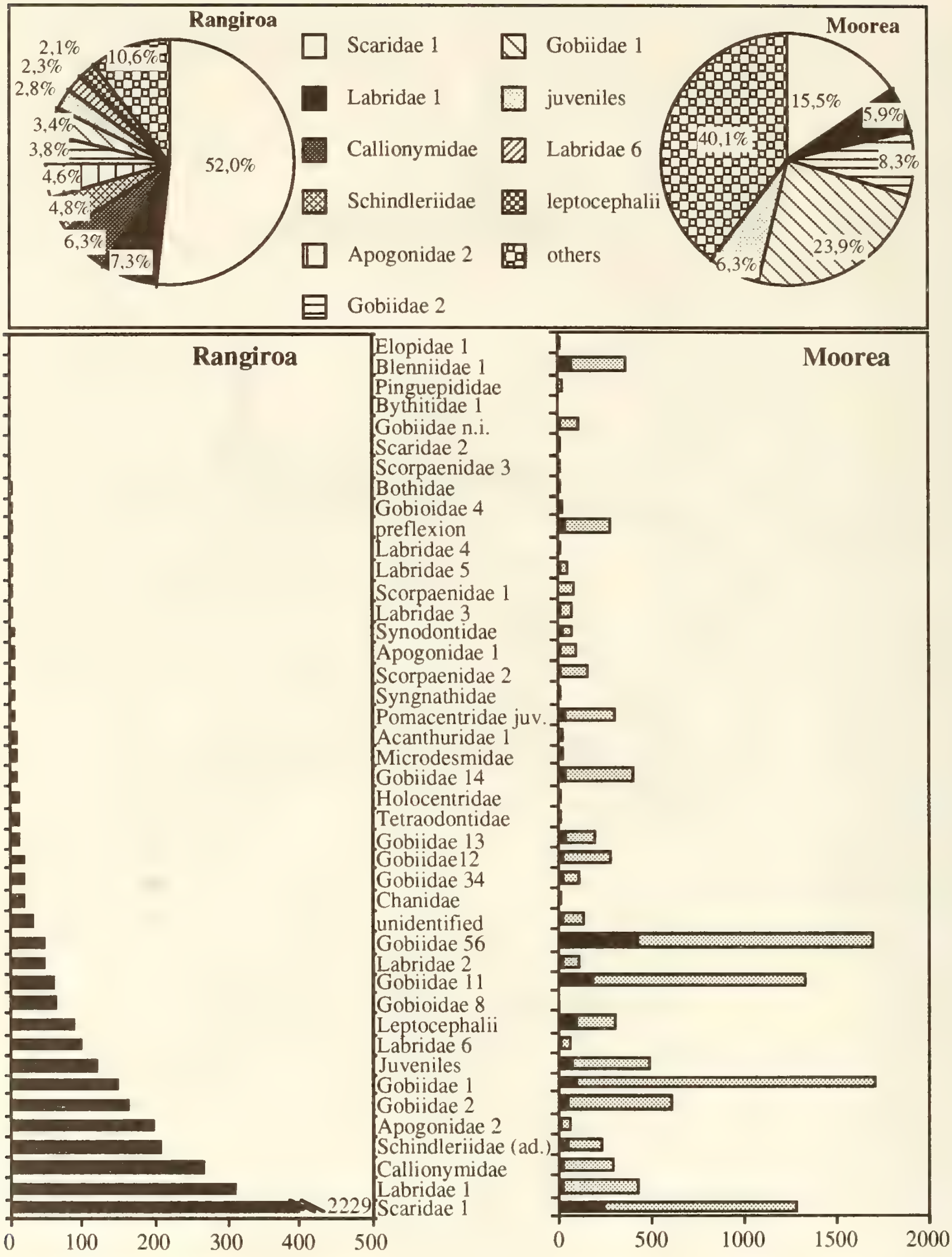

Figure 3. Percentage of the main larval types collected on Moorea and Rangiroa (above) and diagram of larval abundance (below) for all the samples from Rangiroa and for the three cycles of Moorea (black) and all the samples from Moorea (grey). n.i.: not identified to lower taxonomic level; juv.: juvenile; ad.: adulte fishes are also included in this neotenic family.

ATOLL RESEARCH BULLETIN

NO. 417

CAVES AND SPELEOGENESIS OF MANGAIA, COOK ISLANDS

BY

JOANNA C. ELLISON

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CAVES AND SPELEOGENESIS OF MANGAIA, COOK ISLANDS

BY

JOANNA C. ELLISON

ABSTRACT

Ten caves in the makatea limestone of Mangaia, Cook Islands were explored and mapped, totalling over 3.7 km of passage. Of these, there was an apparent grouping by elevation that corresponds with previously described sea-level terraces in the makatea. Four caves have major level sections 10-20 m above sea-level, corresponding with a 14.5 m Pleistocene terrace. The high dimensions of these caves indicate downcutting during slow uplift, or multiple reoccupations by highstands of Pleistocene sea-levels. One major cave has level passage 20-30 m above sea-level, corresponding with a 26-27.5 m terrace. Three caves have level passage 40 m above sea-level, corresponding with a 34-39 m terrace. Active conduit caves are developed at the present sea-level, but are closed with heavy clay deposits from recent soil erosion.

INTRODUCTION

Mangaia is the second largest and most southerly of the Cook Islands (21°54'S, 157°58'W), with a land area of 52 km^2 (Fig. 1). The island is divided into two concentric geological zones. The inner zone is a subdued basaltic volcanic cone rising to 168 m, flattened at the summit possibly by marine erosion prior to its uplift (Wood, 1967), dating between 17-19 m yr BP (before present) (Dalrymple et al., 1975). The outer zone is a complete raised limestone rim or makatea, 0.7 to 2 km wide, up to 70 m in height, with erosional topography of steep terraces on the outer edge, and cliffs on the inner edge (Stoddart et al., 1985).

Yonekura et al. (1988) showed from the identification of planktonic foraminifera in makatea limestone that these are up to 17 m years old, indicating that coral reefs developed shortly after the volcanic island formed. While the major part of the limestone is Tertiary, Pleistocene deposits occur on the seaward margins to an elevation of 14.5 m (Stoddart et al., 1985). Emergence occurred in late Tertiary to Quaternary times, during which there were two periods of stability in relative sea-level to cut marine terraces at 26-27.5 m and 18-20 m (Stoddart et al., 1985).

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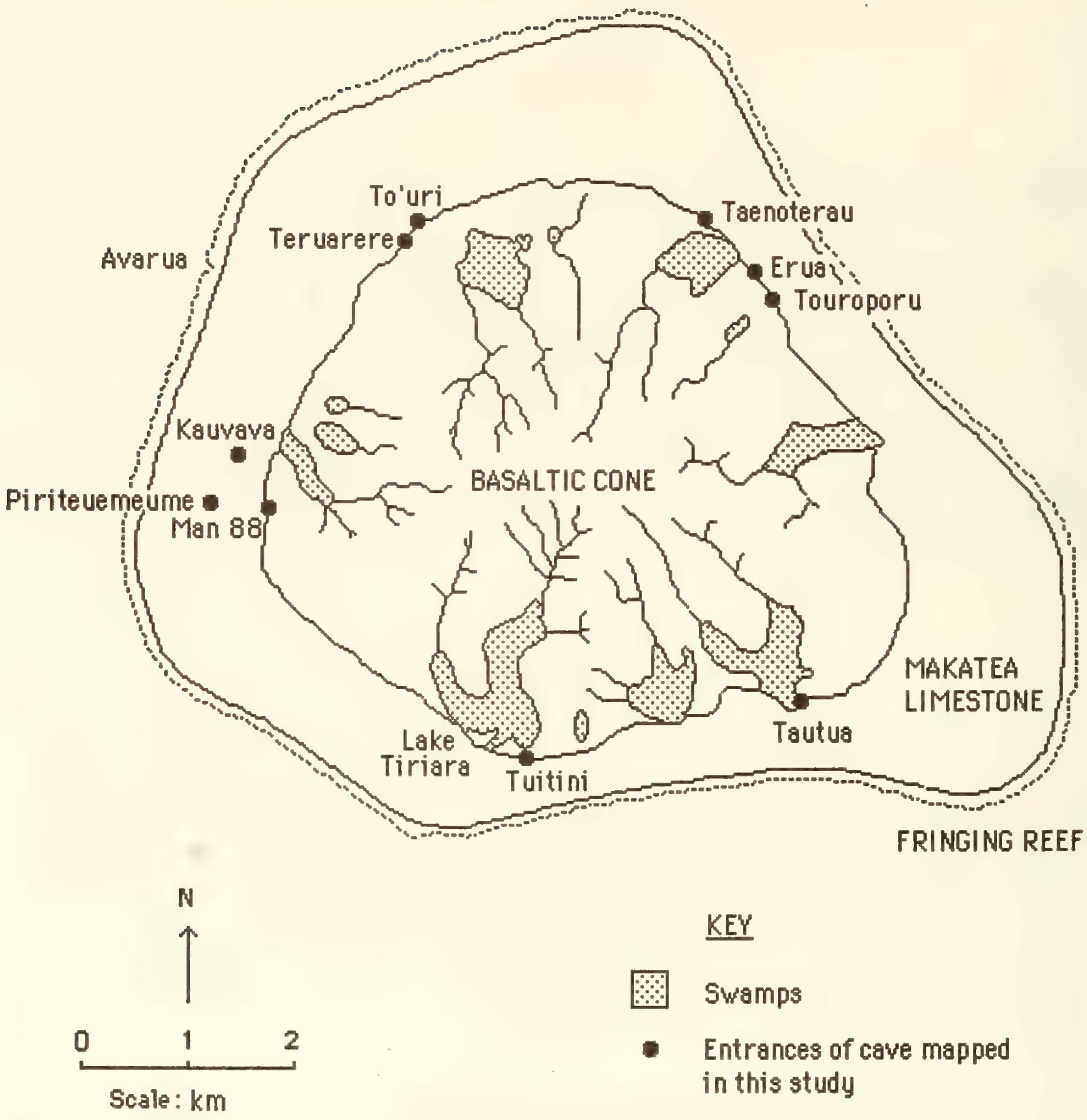


Figure 1. Map of Mangaia, showing geology and locations of entrances to caves in this study

Mangaia receives a mean annual rainfall of 1967 mm, with range in the period 1914-1984 of 1024 to 2983 mm (Thompson, 1986). There is a pronounced wet season from November to April, and dry season from May to October. Drainage is radial, with deeply incised first and second order streams off the central cone feeding lowland taro swamps collected against the inner makatea cliff. Water from the swamps sinks beneath the makatea limestone in radially draining cave systems. Stoddart et al. (1985) showed that stream water entering the makatea limestone is aggressive, supporting the interpretation that the cliffs of the inner makatea are erosional remnants from a former complete cover of limestone to equivalent elevations on the volcanic slopes (Stoddart and Spencer, 1987, Figure 4).

The purpose of this study is to investigate how these events are expressed in the speleogenesis of Mangaia. Many cave entrances can be seen in the makatea cliffs, and the topographic map of Mangaia shows 65 sink holes on the top of the makatea, which considering that the map was made from air photographs of a heavily forested area must under-estimate total numbers. The sinkholes are strongly clustered to indicate traces of cave systems. A few are used for burials or settlement and hence are of archaeological interest. As commented by Gill (1894), "the numerous and extensive caves that honeycomb the makatea were formerly used as habitations, cemeteries, places of refuge, and stores. Scores of them are filled with dessicated human bodies".

While very little work has been done on the cave systems of makatea islands, but the following principles on cave evolution are suggested from the surface geomorphological work.

1. As cave development is most active at the water table, those that are presently under active development can be found at the vadose conduits where streams enter the makatea. These decline slightly along their course, similar to a stream.

2. Caves above these levels are fossil conduits, with a positive relationship between elevation and age, resultant from uplift of Mangaia and general decline in sea-levels from the Tertiary to the Quaternary (Haq et al., 1987).

3. Fossil conduit caves should decline slightly from the influent entrance at the inner edge of the makatea to the coast, at an elevation that is slightly above the sea-level position at the time of development. On low limestone islands, such caves can be used as an indicator of former sea-level (Mylroie and Carew, 1988).

4. Higher elevation caves should therefore show features of older caves, with collapse, flowstone infill and large speleothem formations. Lower elevation caves should show features of younger caves, with more even walls and floor, and smaller formations.

5. A conduit cave could cut into its floor during uplift of the makatea, developing a deeply rifted cave. Such caves could indicate a period of slow uplift, while rapid uplift would result in abandonment of the former conduit and development of a new cave at a lower level.

METHODS

In July 1991 ten caves were explored and surveyed, to the British Cave Research Association Grade 5b standard, using a Suunto compass and clinometer, and 50 m fibreglass tape. This standard requires a station- to-station survey, with passage details recorded at the time (Ellis, 1976). Cave maps produced are shown in plan view, so it must be remembered that passages are not shown at their actual length unless they are horizontal. A profile view is also shown of the cave passage. No vertical techniques were possible in this study, and climbing risks not taken owing to lack of back-up support.

Where possible, surface survey was continued to a known elevation to give the altitude of the cave as indicated on the maps, otherwise it was estimated from contours on the topographic map.

DESCRIPTIONS OF THE CAVES

Tuitini cave, Veitatei (Figure 2)

Tuitini is the largest cave explored in this study, with two entrances about 100 m to the east of Lake Tiriara. It would have been the conduit cave for the Veitatei drainage basin, which is the largest on Mangaia, when relative sea-level was 20 m higher. Survey was continued to the water level of the lake to establish the altitude. The main passage is large, with few formations, while the upper passages to the south and east are well decorated with formations. There are four burials in the cave, permission to explore should be sought from the chief in Kaumata village (Oneroa).

The main passage indicates downcutting, with heights of 20 to 25 m, while the upper passages have low ceilings of 10 m or less. There are sections in the main passage with collapse, it is necessary to climb around or over large boulders. At the end of the surveyed section the main passage continues at the base of a 7 m pitch, at which point the cave is around 30 m high.

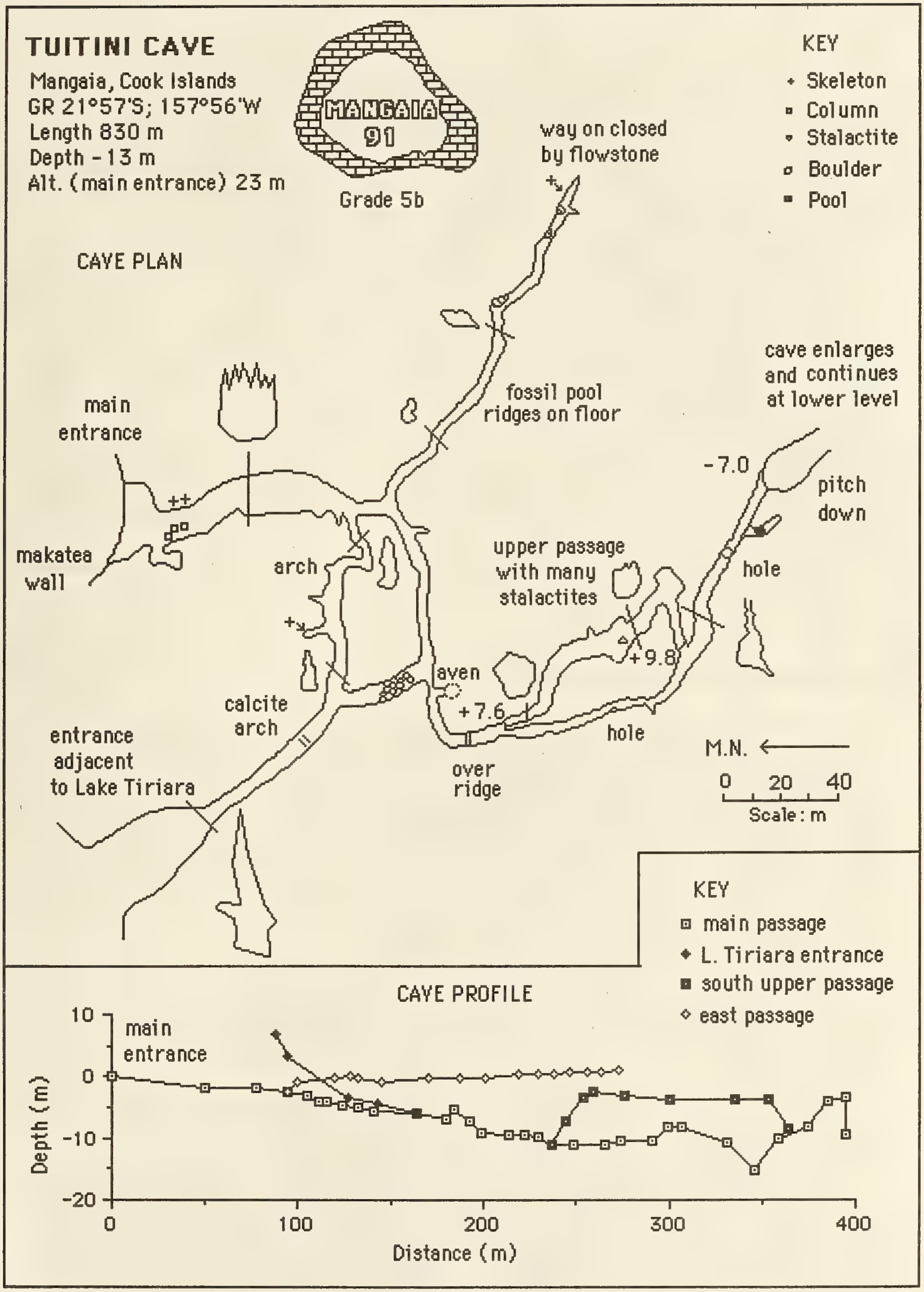

TUITINI CAVE
Mangaia, Cook Islands
GR 21°57'S; 157°56'W
Length 830 m
Depth - 13 m
Alt. (main entrance) 23 m
MANGAIA 91
Grade 5b
KEY
Skeleton
Column
Stalactite
Boulder
Pool
CAVE PLAN
way on closed by flowstone
fossil pool ridges on floor
cave enlarges and continues at lower level
main entrance
makatea wall
arch
-7.0
pitch down
upper passage with many stalactites
hole
+9.8
aven
+7.6
hole
calcite arch
entrance adjacent to Lake Tiriara
over ridge
M.N.
0
20
40
Scale: m
KEY
main passage
L. Tiriara entrance
south upper passage
east passage
CAVE PROFILE
main entrance
10
0
-10
-20
Depth (m)
0
100
200
300
400
Distance (m)

Figure 2.

To'uri cave, Tava'enga (Figure 3)

The entrance to To'uri is where the depression to the west of Tava'enga swamp meets the makatea wall. A stream leads to the cave entrance, which is approached by a steep climb down over boulders and ferns into a large overhang. The cave is partially an active streamway, with heavy wet red clay deposits throughout. A bank of red clay at the entrance has been incised by headward erosion of the stream to create a 2 to 3 m profile.

The small stream follows the left hand side of the cave for 60 m, then sinks into a hole. In the stream water are small black fish.

To'uri cave indicates recent stream flow that has downcut through older clay deposits, leaving exposed mud sections along sections of the passage wall. The cave is large in passage dimensions relative to others in Mangaia, the roof a wide vertical fissure visible to 20-30 m, the passage 3-10 m wide. There are occasional rocks fallen down, and occasional large stalagmite or flowstone formations. Stalactites are the more common.

After 490 m of passage there is a clay bank 2.5 m down to flowing water, which heads out through a tight passage to the north. The water tasted salty and waves could be heard. Opposite, up a clay climb, the cave continues to the west. This was not explored.

Elevations for Tou'ri and Teruarere caves are based on the salt water being at sea-level.

Teruarere cave, Tava'enga (Figure 4)

This is the second largest cave explored in this study, located 40 m above the entrance to To'uri Cave, along the makatea wall to the SW.

The cave is accessed from the top of the makatea. The entrance rift trends east- west, and there is a 10 m climb down to the cave entrance 50 m back from the makatea edge, assisted by roots. A large *Hernandia moerehroutiana* tree grows out of entrance. Where the rift reaches the makatea edge one can look down on entrance to To'uri cave, some 100 m to the left. Strong winds come through the cleft. The cave entrance leads away from makatea edge, under the entrance climb.

Cave is simple fossil streamway, 10-30 m high, 1-10 m wide, dry. It contains at least 7 skeletons lying on the floor near the cave wall, surrounded by stones. This is a burial cave, in the charge of Tuara George of Oneroa village, from whom permission to explore the cave should be obtained.

Cave has been studied by the ornothilogist D. Steadman, showing from fossil bird bones that early Polynesian settlement caused extinction of many species (Steadman, 1985, 1986).

The rift opens above to four daylight avens in the first 200 m of the cave. Formations are mainly calcite cascades, curtains and flowstones, with vandalism of whatever possible. The floor is hard red mud, with occasional patches of rubble. Lower in the cave, calcite flows cover the floor, and there are places where ridges on the floor indicate fossil pools. Towards the end of the main passage of the cave, there are a couple of climbs down, then a

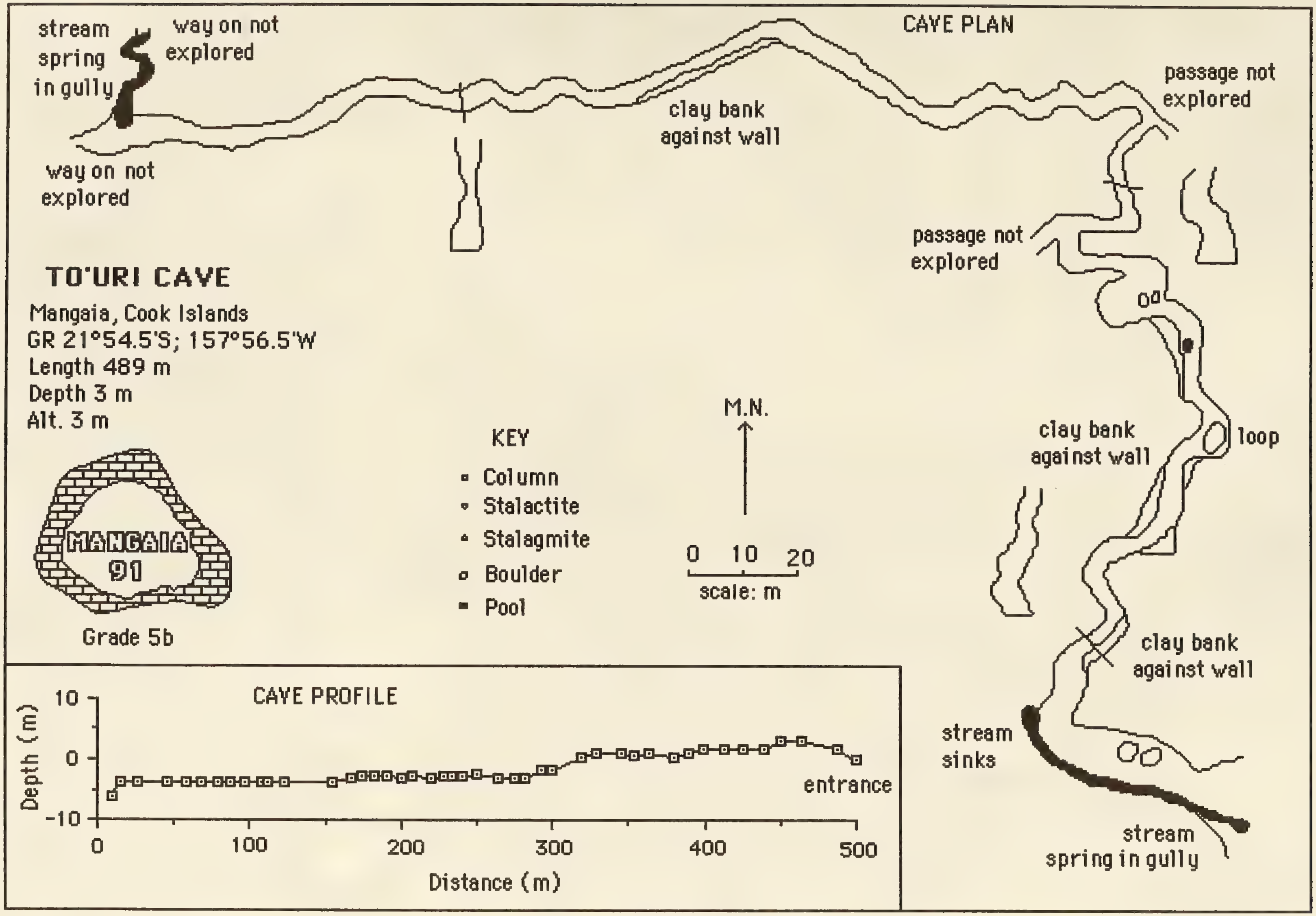

CAVE PLAN
stream
spring
in gully
way on not
explored
way on not
explored
clay bank
against wall
passage not
explored
passage not
explored
clay bank
against wall
loop
clay bank
against wall
stream
sinks
stream
spring in gully
TO'URI CAVE
Mangaia, Cook Islands
GR 21°54.5'S; 157°56.5'W
Length 489 m
Depth 3 m
Alt. 3 m
MANGAIA
91
Grade 5b
KEY
▫ Column
▿ Stalactite
▵ Stalagmite
▱ Boulder
▪ Pool
M.N.
0
10
20
scale: m
CAVE PROFILE
Depth (m)
10
0
-10
0
100
200
300
400
500
Distance (m)
entrance

Figure 3.

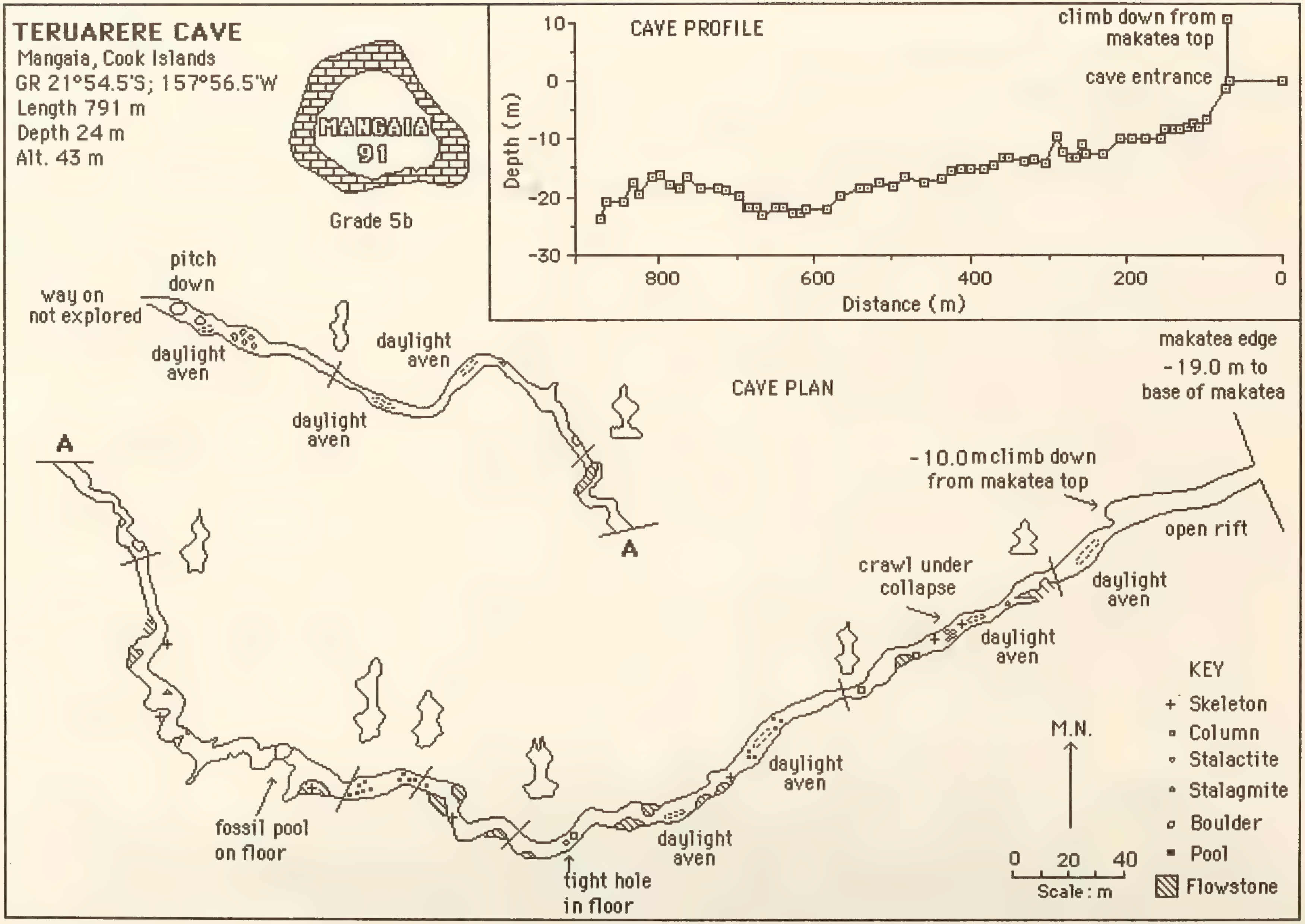

TERUARERE CAVE
Mangaia, Cook Islands
GR 21°54.5'S; 157°56.5'W
Length 791 m
Depth 24 m
Alt. 43 m
MANGAIA
91
Grade 5b
CAVE PROFILE
Depth (m)
10
0
-10
-20
-30
800
600
400
200
0
Distance (m)
climb down from makatea top
cave entrance
CAVE PLAN
way on not explored
pitch down
daylight aven
daylight aven
daylight aven
A
A
makatea edge
-19.0 m to base of makatea
-10.0 m climb down from makatea top
open rift
crawl under collapse
daylight aven
daylight aven
daylight aven
daylight aven
fossil pool on floor
tight hole in floor
M.N.
0 20 40
Scale : m
KEY
+ Skeleton
Column
Stalactite
Stalagmite
Boulder
Pool
Flowstone

Figure 4.

pitch down that was not explored. Some daylight comes through high above the pitch. The upper passage continues, but is a tricky climb past the pitch, this was not explored.

Touropuru cave, Ivirua (Figure 5)

This is the third largest cave explored in this study. The entrance is 10 m up the makatea wall adjacent to the small Kirikiri swamp, between the larger Karanga and Ivirua taro swamps. Adjacent to the entrance to the south was a large cave shelter used for habitation, which has unfortunately recently collapsed.

This cave is the burial cave of the Totongaiti tribe, with 22 skeletons in the main cave and 9 in a small cave above the lower entrance. Permission to explore this cave must be obtained from a member of the tribe in Ivirua village, such as Ma'ara Ora, Director of Forestry. Just inside the entrance is a side passage to the right, 39 m long to a window 10 m up the makatea wall. The passage is narrow and lined by 19 skeletons in open coffins, mostly of planks (post-contact), but some canoes (pre-contact).

The main passage is a fossil vadose stream passage, generally 1-2 m wide and 3 m high, but sections which widen to some 6 m, and sections where the rift above is visible to some 15 m. After 350 m the passage forks, the left passage closing up with flowstone after 150 m, the right fork leading to the base of a doline entrance in Ivirua village, that has a 22.5 m pitch that can be climbed (GR 21° 54' 45" S, 157° 54' 15" W). The main passage has been closed in by flowstone deposits and some collapse, causing the route to go up and down, but from the entrance to the fork over a distance of 350 m there is no elevation change. There are three more skeletons at the start of the main passage, then no more. Formations are mainly curtains and flowstones, though there are some large stalagmites and columns and more smaller stalactites. There is less vandalism of formations in the final left branch. After the fork, both passages climb some 4 m. There are some small passages off the main route, some of which may have unexplored sections.

Erua Cave, Karanga (Figure 6)

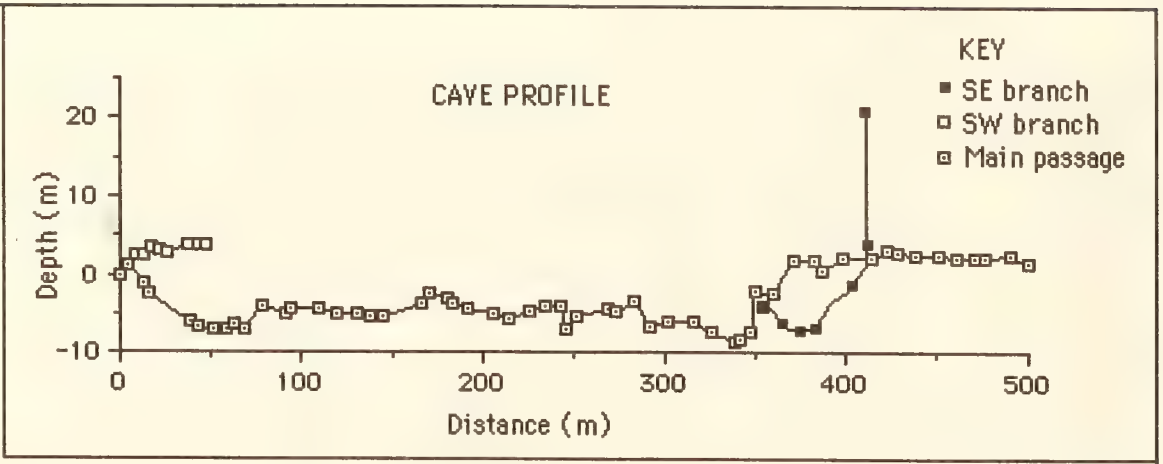
The cave entrance is located some 200 m to the south of the Karanga swamp conduit entrance, just north of where the path from Karanga village descends the makatea to the Karanga swamp. The cave entrance is conspicuous, 14 m above the base of the makatea, a rift 20 m tall, and a strong through breeze can be felt. The passage of this cave is wide and high, with few formations and a mud floor with frequent cobble-sized angular rocks. It was used as a refuge during prehistoric wars, and several human structures and midden deposits can be seen, but no burials. Like Tautua cave, which was also used as a war refuge, Erua has light inside the cave, from an aven. There is a debris slope from material which has fallen through the aven, including some animal skeletons. The few formations are large

TOUROPOROU CAVE

Mangaia, Cook Islands
GR 21°54.7'S; 157°54.5'W
Length 587 m
Depth (main passage) +4.2 m
Alt. (west entrance) 16 m

MANGAIA 91

Grade 5b



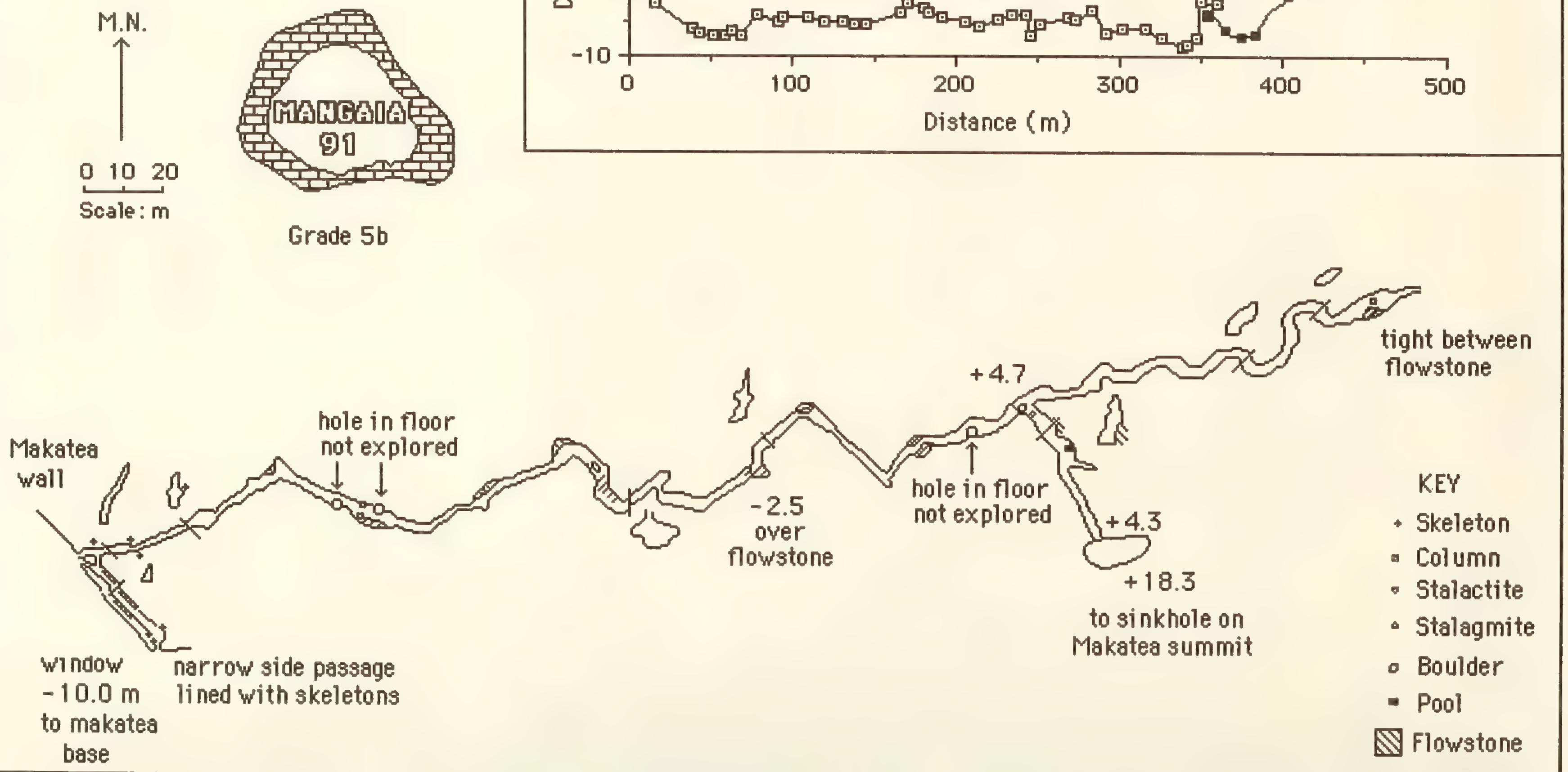


Figure 5.

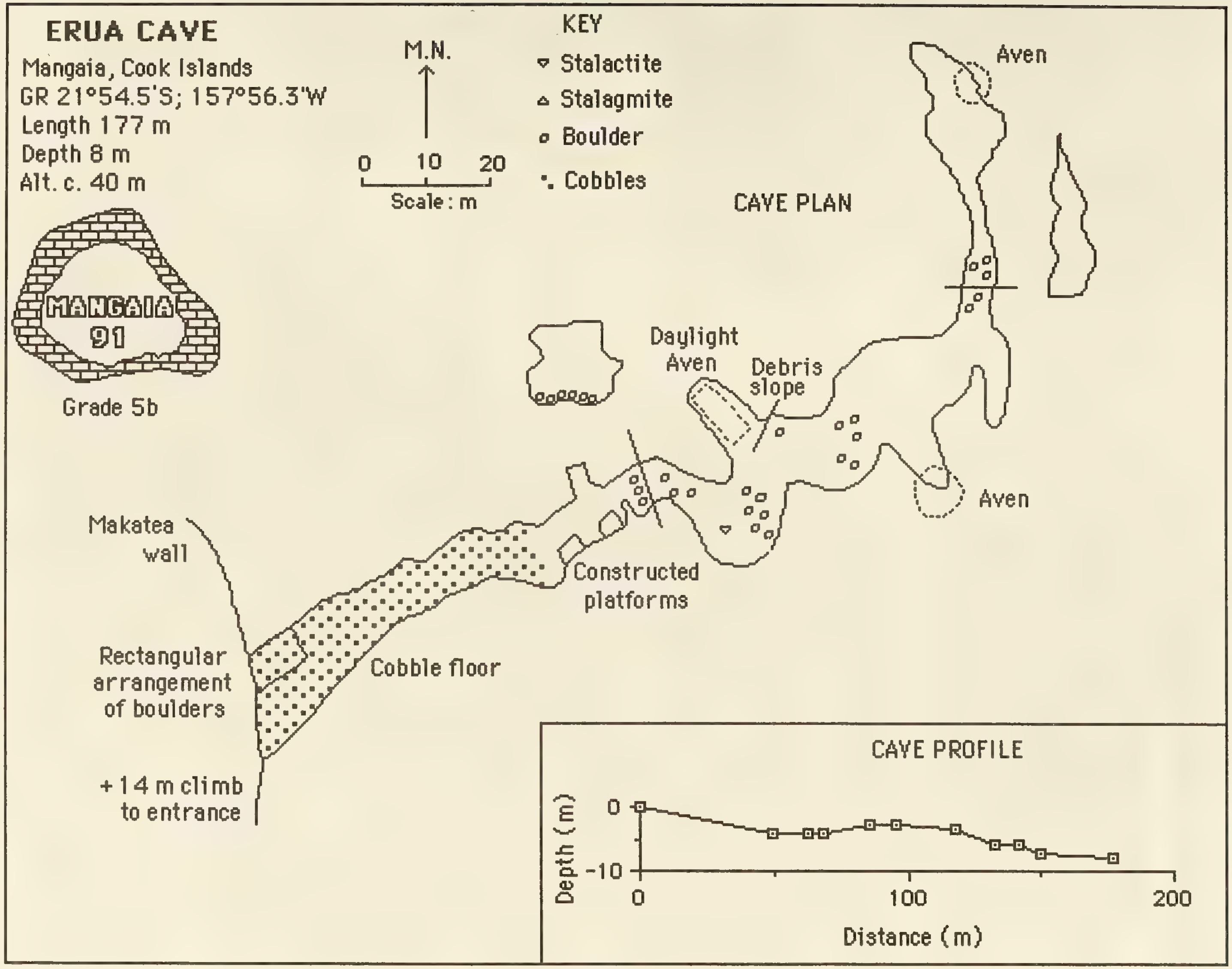

ERUA CAVE
Mangaia, Cook Islands
GR 21°54.5'S; 157°56.3'W
Length 177 m
Depth 8 m
Alt. c. 40 m
MANGAIA
91
Grade 5b
M.N.
0
10
20
Scale : m
KEY
▽ Stalactite
△ Stalagmite
○ Boulder
⁚ Cobbles
CAVE PLAN
Aven
Daylight Aven
Debris slope
Aven
Makatea wall
Constructed platforms
Rectangular arrangement of boulders
Cobble floor
+ 14 m climb to entrance
CAVE PROFILE
Depth (m)
0
-10
0
100
200
Distance (m)

Figure 6.

stalactites and stalagmites, and there are two avens which could extend the cave.

Taenoterau Cave, Karanga (Figure 7)

The cave entrance is located to the north of the Karanga swamp conduit entrance, 20 m above the level of the swamp. Behind the large rock at the entrance are trenches where a Japanese archaeological group dug in 1990. The lighted entrance is some 25 m tall, but falls to 5-10 m as the cave begins. Flowstone formations have blocked the passage twice in the first 20 m, so one has to climb over. The formations are all large, stalactites, stalagmites and dripstones, and crystalline flowstone walls.

Tautua cave, Tamarua (Figure 8)

At the makatea wall where the East Tamarua swamp collects there is a large cavern, over 30 m high and 100 m across (Plate 1). The floor is covered by large boulders from collapse, and there are old, vertical stalactites on the ceiling, indicating that the cavern has been exposed by makatea retreat. The stream from the swamp enters the cavern and through a conduit cave that is 15 to 20 m wide, mostly 1 to 2 m high, with extensive wet clay deposits.

Above the conduit is the entrance to Tautua cave, up an 11 m climb. At the entrance the cave is 15 to 20 m high, and this height continues along the right branch just inside the entrance. This does not extend far, and has two connections with the lower streamway.

On the left branch are habitation sites clustered around a window out of the makatea wall. The cave is well known from oral traditions as the primary refuge of the Tonga'iti tribe in times of war (Gill 1894, Buck 1934). Permission to explore the cave should be obtained from a member of that tribe, such as Noka Tumarama of Tamarua village. There are stone faced platforms, a *marae* (worship place), a tupe disk pitch (for playing a bowling-type game), and midden deposits. The site was analysed by P. Kirch and other archaeologists from University of California at Berkeley in 1989, and mapped by theodolite in 1991.

The site was a retreat in times of war as it is easily defended. The lower entrance is a vertical climb, and defenders could bombard invaders with rocks. Past the archaeological site is a T junction, where the left branch leads up to a high makatea entrance, used as an escape route or otherwise blocked with stones. The right branch leads down to the main part of the cave, which was mapped here until a pitch down was reached.

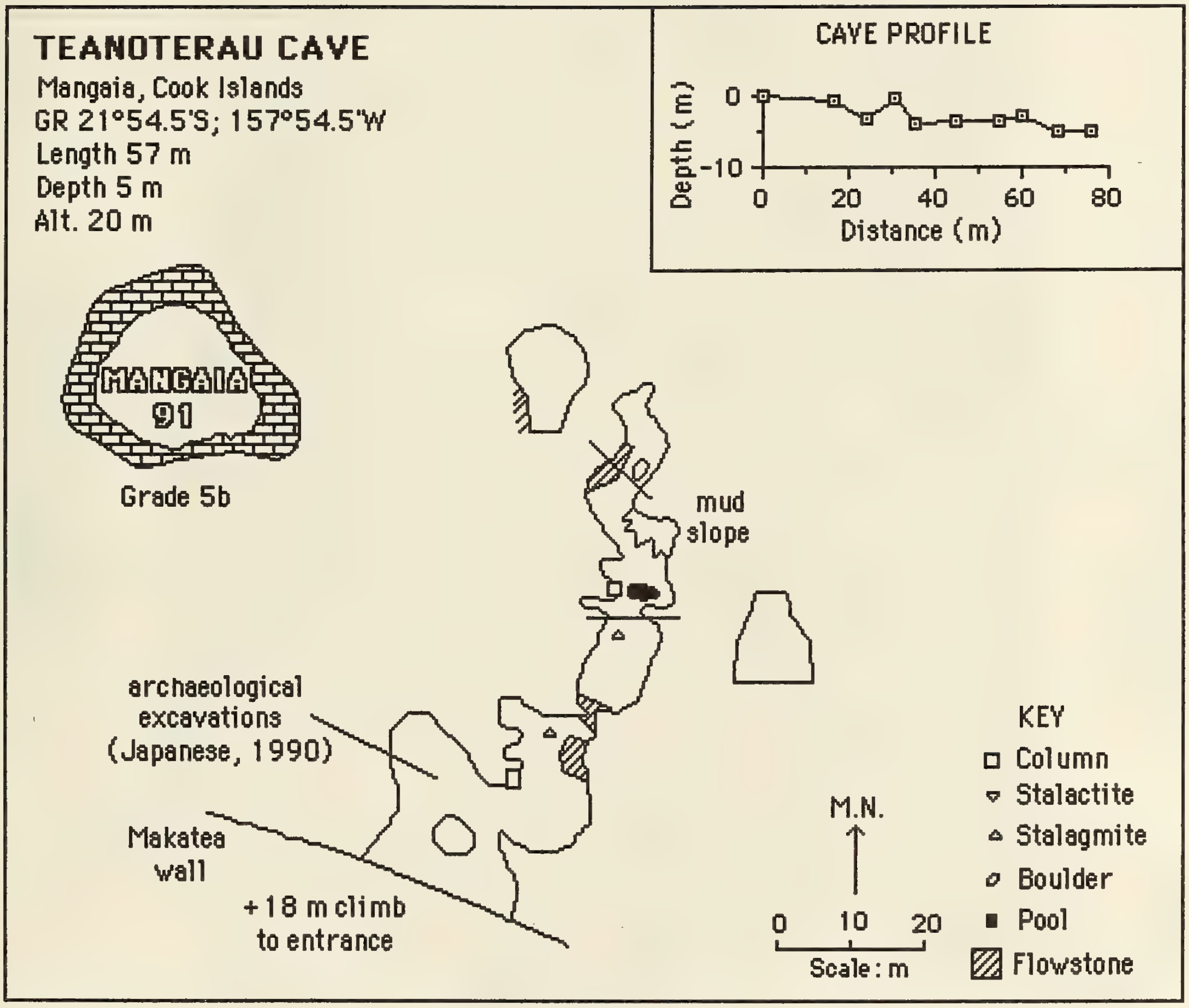

TEANOTERAU CAVE
Mangaia, Cook Islands
GR 21°54.5'S; 157°54.5'W
Length 57 m
Depth 5 m
Alt. 20 m
MANGAIA 91
Grade 5b
CAVE PROFILE
Depth (m)
0
-10
0
20
40
60
80
Distance (m)
mud slope
archaeological excavations (Japanese, 1990)
Makatea wall
+18 m climb to entrance
M.N.
0
10
20
Scale: m
KEY
□ Column
▽ Stalactite
△ Stalagmite
○ Boulder
■ Pool
▨ Flowstone

Figure 7.

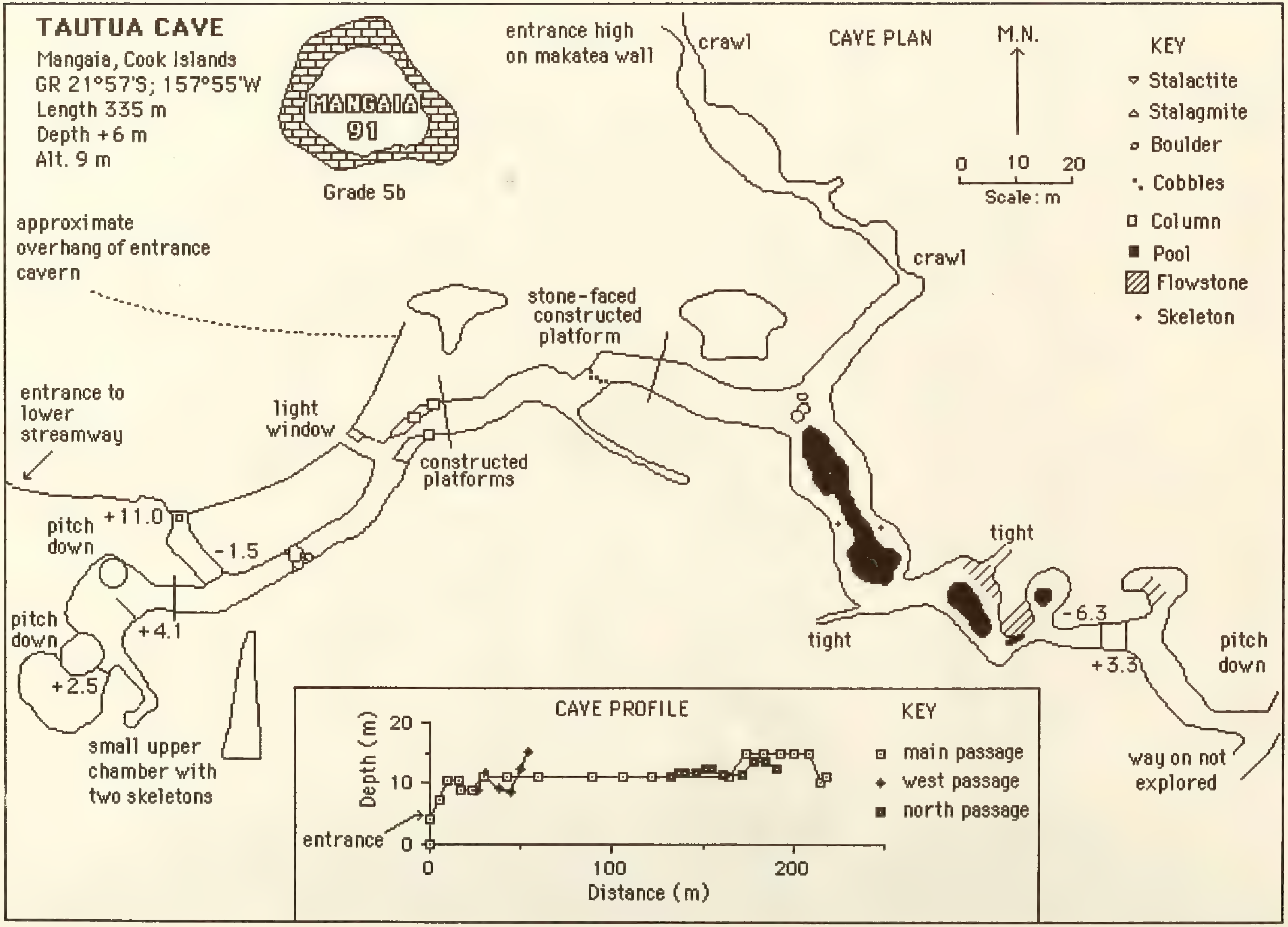

TAUTUA CAVE
Mangaia, Cook Islands
GR 21°57'S; 157°55'W
Length 335 m
Depth +6 m
Alt. 9 m
MANGAIA
91
Grade 5b
entrance high on makatea wall
crawl
CAVE PLAN
M.N.
0 10 20
Scale : m
KEY
Stalactite
Stalagmite
Boulder
Cobbles
Column
Pool
Flowstone
Skeleton
approximate overhang of entrance cavern
crawl
stone-faced constructed platform
entrance to lower streamway
light window
constructed platforms
pitch down
+11.0
-1.5
pitch down
+4.1
+2.5
small upper chamber with two skeletons
tight
tight
-6.3
+3.3
pitch down
way on not explored
CAVE PROFILE
Depth (m)
20
10
0
entrance
0
100
200
Distance (m)
KEY
main passage
west passage
north passage

Figure 8.

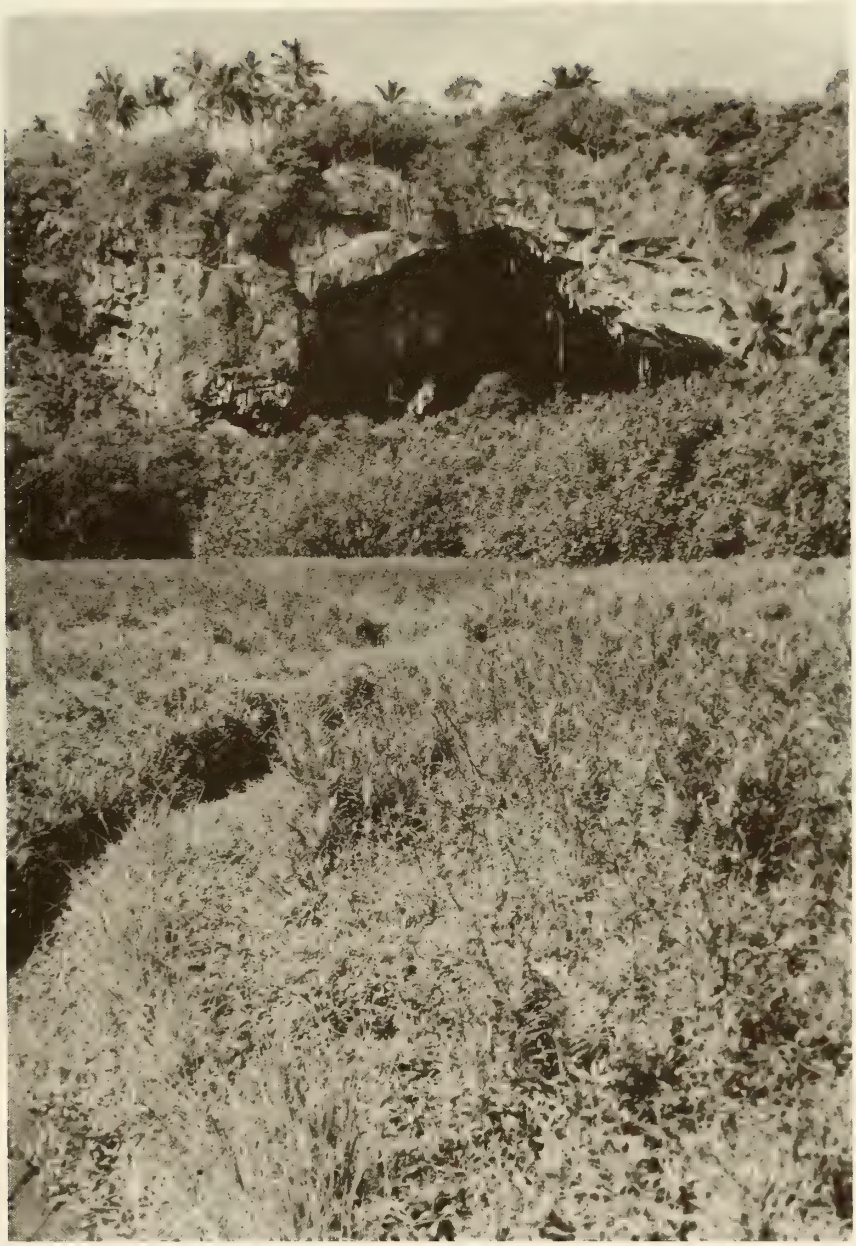


Plate 1. Entrance cavern by Tautua cave, East Tamarua swamp

Other Active Conduit Caves

Ivirua Conduit Cave

GR 21° 55' 30" S, 157° 54' 00" W. Where the Ivirua swamp drains through the makatea is a cave entrance similar to Tautua cave in the East Tamarua swamp. Above the stream is a large overhang some 25 m high, with old stalactites. The stream has red clay banks, and in pools there are many freshwater prawns (*Macrobranchium lar*). The conduit cave is wide and low, with few and small formations, and heavy red clay deposits, similar to East Tamarua. Neither of these active streamway caves were explored far because of problems of sinking in the wet clay. A small raft is recommended, as this could be dangerous.

To the north of the streamway, there is a cave entrance up a 10 m climb, resembling the position of Tautua cave in Tamarua. The cave was not explored.

Lake Tiriara Conduit

GR 21° 57' 00" S, 157° 56' 15" W. Lake Tiriara in Veitatei, adjacent to Tuitini cave, drains through a large cave entrance (Plate 2). These dimensions continue for some 50 m, with 2 m depth of water, then the cave narrows and the roof meets the water level. Figure 2 shows that the main passage of Tuitini cave trends towards the Lake Tiriara conduit, and it is possible that they connect in the lower unexplored section of Tuitini cave.

On the makatea summit directly above where the Lake Tiriara conduit enters the cliff, c. 10 m back from the cliff face, there is an arch some 15 m high, and a pitch cave entrance in the south wall of the arch. The topographic map shows a number of clustered cave entrances on the makatea summit above the Tuitini and Lake Tiriara conduit cave systems.

Kauvava cave, Temakatea (Figure 9)

Kauvava and Piriteumeume caves both have doline entrances, rather than makatea wall former streamway entrances. As they are of the highest elevation of caves explored, they could have been formed before erosion developed the makatea wall.

The southern entrance to this cave is the large doline to the N of Temakatea village. Permission to explore the cave should be requested from Papa Tua, who lives to the east of the cave entrance. At the base of the doline is a 6 m climb down at the entrance, which is filled with boulders and other debris. The entrance passage has rounded walls, indicating meandering stream activity, but is presently dry. The cave is mostly a tall rift, visible to 20 m. Some 60 m into the cave the passage descends and narrows, indicating a sink which is now infilled by deposits of clay. This is the lowest part of the cave between the two avens.

Towards the northern aven flowstone has closed the passage, but there is a tight climb up the rift over this. The aven is 23 m high, the opening is behind the Mormon church in Temakatea village. Below the aven the cave

Plate 2. Conduit cave entrance in Lake Tiriara, Veitatei.

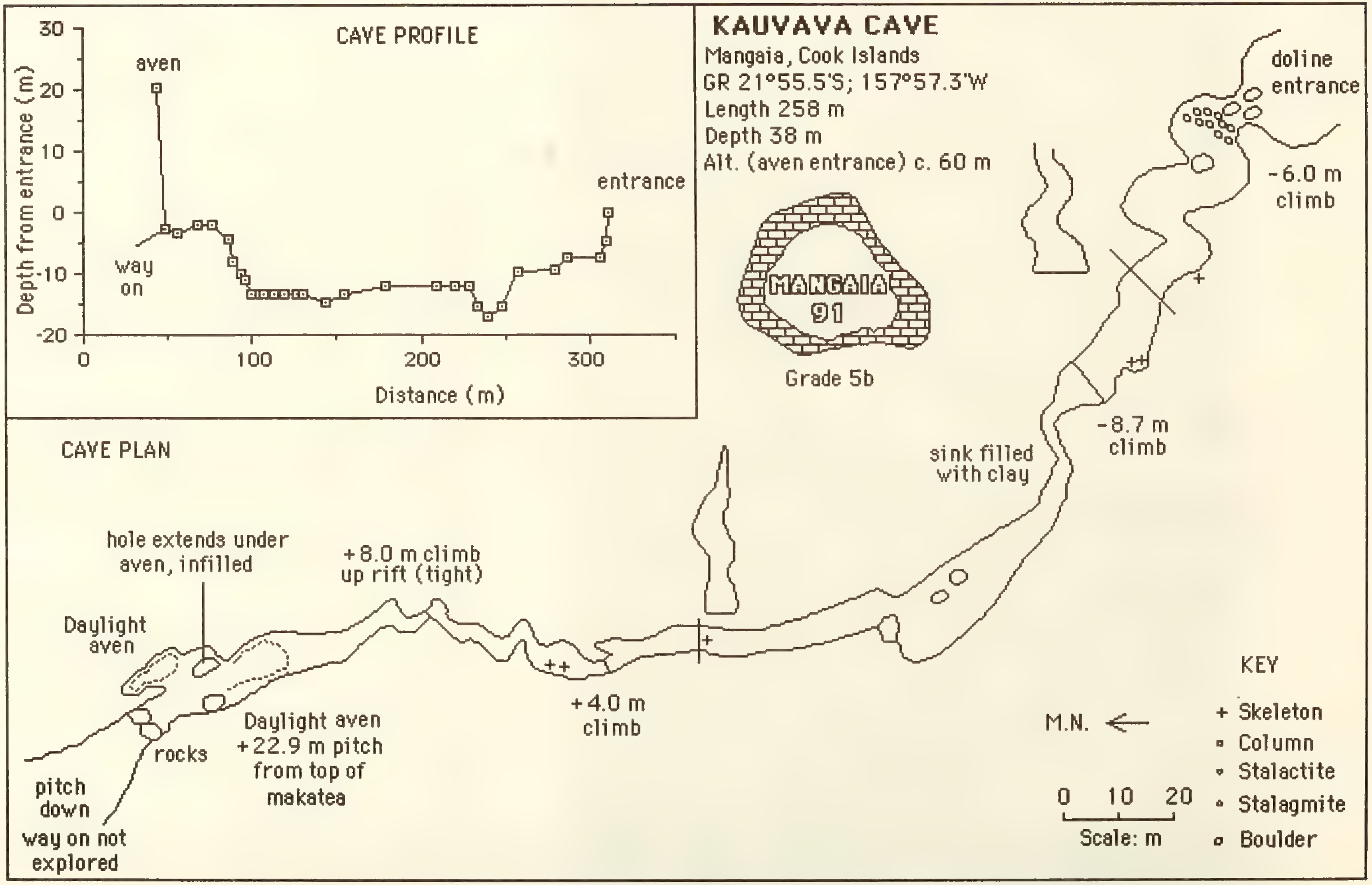

KAUVAVA CAVE
Mangaia, Cook Islands
GR 21°55.5'S; 157°57.3'W
Length 258 m
Depth 38 m
Alt. (aven entrance) c. 60 m
MANGAIA 91
Grade 5b
CAVE PROFILE
Depth from entrance (m)
30
20
10
0
-10
-20
0
100
200
300
Distance (m)
aven
way on
entrance
CAVE PLAN
doline entrance
-6.0 m climb
-8.7 m climb
sink filled with clay
+4.0 m climb
+8.0 m climb up rift (tight)
hole extends under aven, infilled
Daylight aven
Daylight aven +22.9 m pitch from top of makatea
rocks
pitch down
way on not explored
M.N.
0
10
20
Scale: m
KEY
+ Skeleton
Column
Stalactite
Stalagmite
Boulder

Figure 9.

continues to the north, but this is down a pitch so could not be explored in this study.

Pirituemeume cave, Temakatea (Figure 10)

The makatea summit is characterised by deep (5-10 m) dissection, with "karst streets" that follow the joints (Stoddart, et al., 1985). The entrance to Piriteumeume cave is a small doline in a karst corridor to the south of the inland road from Temakatea village, opposite the quarry. There are old (dry) flowstone walls at the entrance, and a strong draft.

The cave is relatively old, indicated by its elevation, collapse features and large formations. It links three dolines, and has a low daylight aven towards the northern end. The height varies from 4 to 15 m, and the floor is irregular and filled with collapsed boulders. The flowstone walls are dry and rough, indicating that they are no longer under formation. The southern section of the cave has a cavern with large stalactites and dripstones, while the northern section has several large columns.

Man 88 cave, Keia (Figure 11)

No name could be found for this cave, so it is described by the archaeological site number of P. Kirch, who excavated both in the cave and below its entrance in 1991. The entrance is 8 m from the makatea base, a large lighted cavern adjacent to a pool of water further inside the cave, with signs of occupation. The cave does not extend far, and seems to have been closed by calcite deposits.

SPELEOGENESIS

The ten caves described include the major caves of Mangaia, but many more remain to be explored. However, there is an apparent grouping of these caves according to elevation of major sections, as shown in Table 1.

The lowest caves are the present conduits, such as To'uri cave, and the East Tamarua conduit below Tautua cave, as well as the Lake Tiriara and Ivirua conduit caves described. These contain an active streamway, few formations, and heavy clay deposits resulting from soil erosion off the volcanic cone. The elevations are close to sea-level, and they resurge at the coast as seen at Avarua landing, or on the reef flat as at Tamarua.

Tuitini, Touropouru, Tautua and Taenoterau caves all have major level sections between 10 and 20 m above sea-level. This suggests that they were conduit drainage caves corresponding with the 14.5 m elevation of Pleistocene

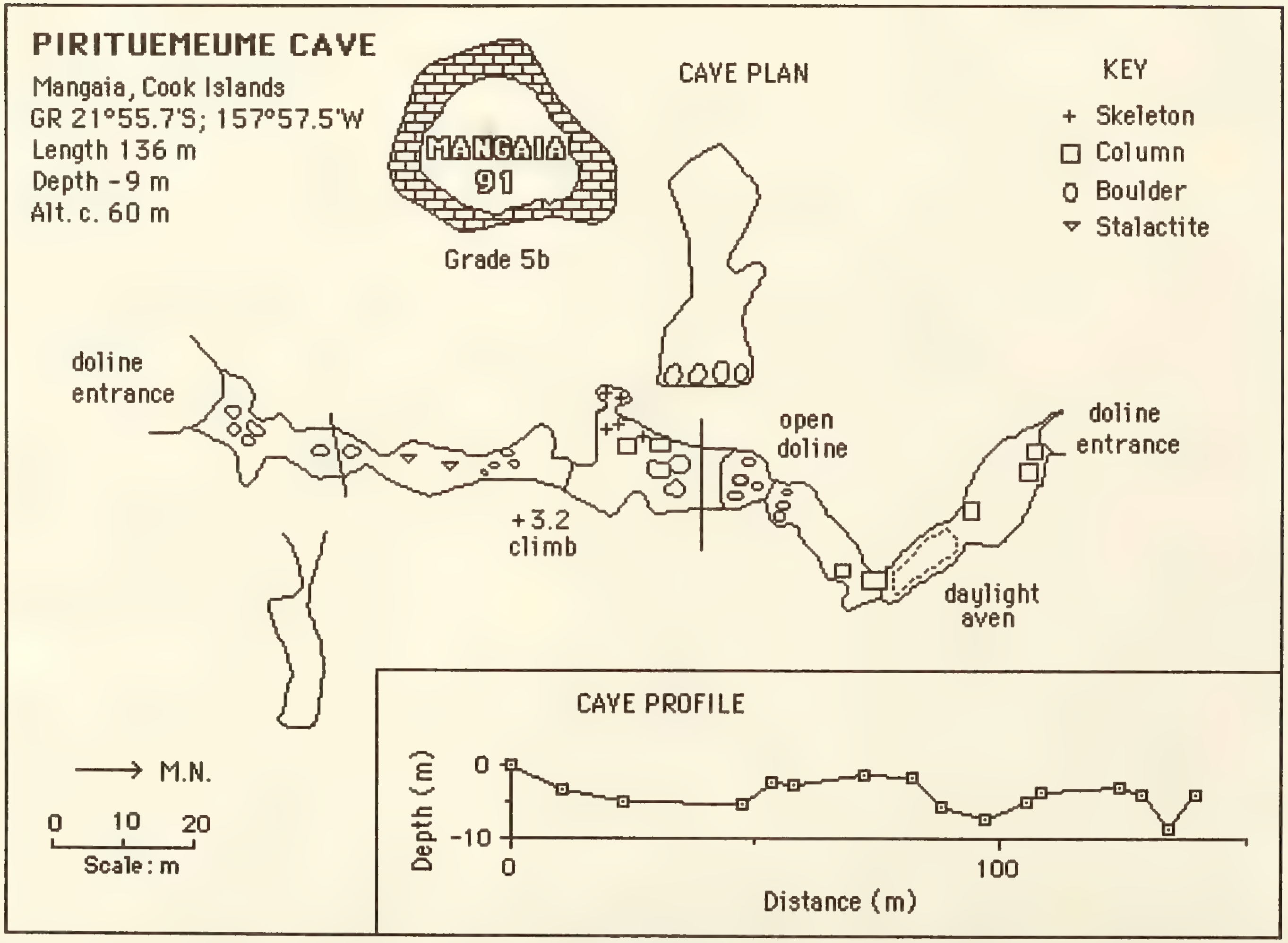

PIRITUEMEUME CAVE
Mangaia, Cook Islands
GR 21°55.7'S; 157°57.5'W
Length 136 m
Depth -9 m
Alt. c. 60 m
MANGAIA
91
Grade 5b
CAVE PLAN
KEY
+ Skeleton
□ Column
o Boulder
▿ Stalactite
doline
entrance
open
doline
doline
entrance
+3.2
climb
daylight
aven
→ M.N.
0
10
20
Scale: m
CAVE PROFILE
Depth (m)
0
-10
0
100
Distance (m)

Figure 10.

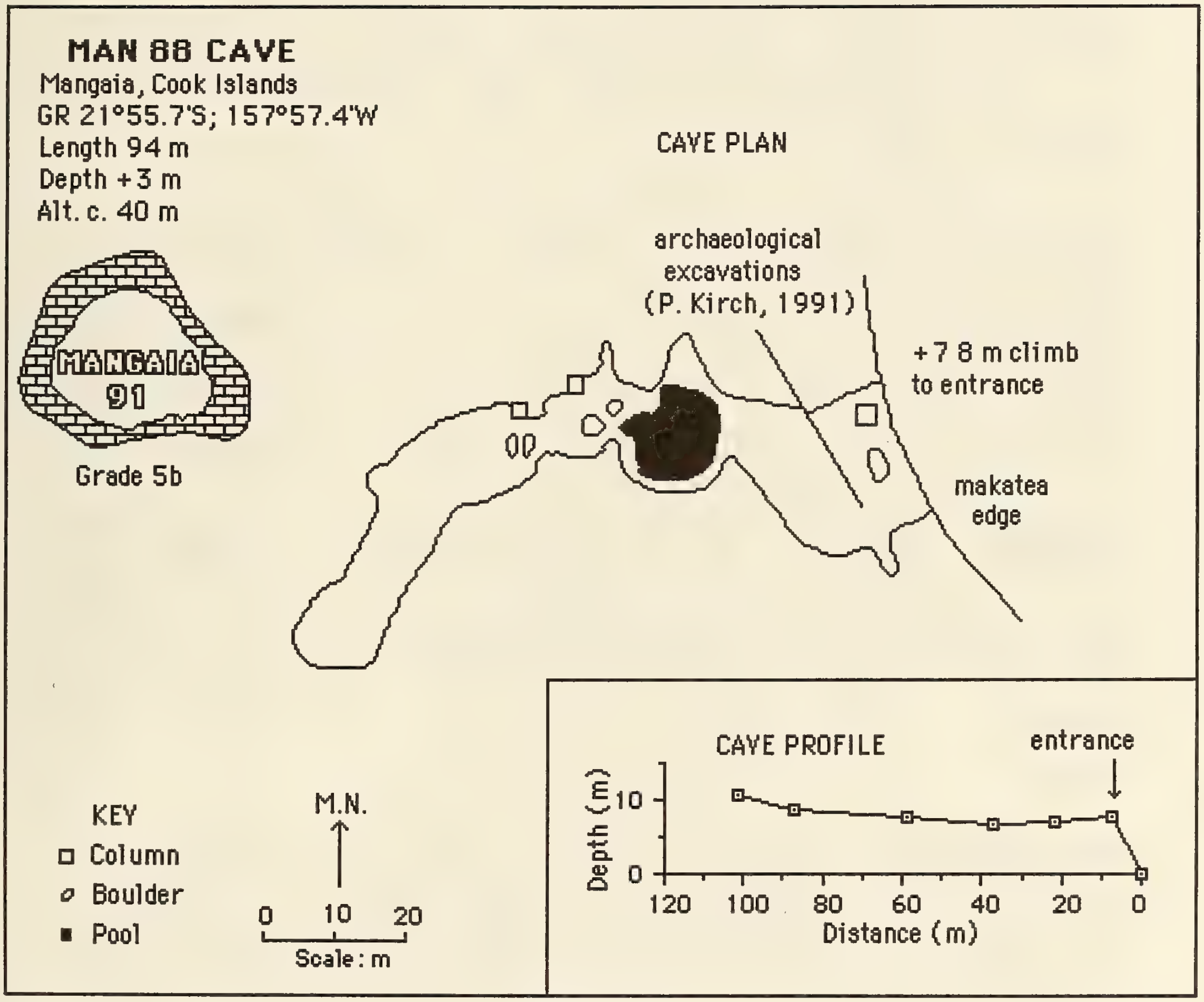

MAN 88 CAVE
Mangaia, Cook Islands
GR 21°55.7'S; 157°57.4'W
Length 94 m
Depth +3 m
Alt. c. 40 m
MANGAIA
91
Grade 5b
CAVE PLAN
archaeological
excavations
(P. Kirch, 1991)
+ 7 8 m climb
to entrance
makatea
edge
KEY
□ Column
▱ Boulder
■ Pool
M.N.
0
10
20
Scale : m
CAVE PROFILE
entrance
Depth (m)
10
0
120
100
80
60
40
20
0
Distance (m)

Figure 11.

Table 1. Dimensions and elevations of Mangaia caves (m)

Cave	Length explored	Altitude of entrance	Depth	Elevation of level sections	Height of rift
To'uri	489	3	-3	1	20-30
Tuitini	830	23	-13	10 & 20	20-25
Touropouru	587	16	+4	10 & 18	15
Tautua	335	9	+6	15 & 19	10-20
Taenoterau	57	20	-5	17	5-10
Teruarere	791	43	-24	20 & 30	10-30
Erua	177	c. 40	-8	c. 40	20
Kauvava	358	c. 60	-38	c. 40	20+
Man 88	94	c. 40	+3	c. 40	10-15
Piriteumeume	136	c. 60	-9	c. 55	4-15

limestones, probably formed at the same time as a relative sea-level 20 m higher than present (Woodroffe et al., 1991). Reef groove-and-spurs formed at this time are now 2 to 11 m above sea-level (Stoddart et. al, 1985). Thus it is indicated from three corresponding features that sea-level was in this position for considerable time.

Teruarere cave is a major feature of Mangaia, a minimum of 791 m of continuous level passage ranks with the spectacular find of Ana Maui by the Tonga '87 caving expedition on 'Eua (the cave named after the Tongan demi-god) (Lowe, 1988). It declines from 30 to 20 m above sea-level, a simple fossil streamway, corresponding with the 26-27.5 terrace described by Stoddart et al. (1985). The terrace is deeply dissected, and was believed to represent a very old sea-level feature. Similarly, Teruarere cave has a number of high daylight avens, indicating long-term dissolution and collapse. The pitch at the end of the surveyed section indicates that one of these cut down to a deeper level after uplift of the main passage.

Erua, Kauvava and Man 88 caves all occur at about 40 m above sea-level, and could correspond with the 34-39 m terrace identified by Schofield (1967), Wood and Hay (1970), and Ward et al., (1971), and shown by several profiles of Stoddart et al., (1985). However, this feature is so old that they must have eroded dowm from their formative elevation. While Erua and Man 88 caves are closed by calcite deposits, the pitch beneath the 23 m aven at the northern end of Kauvava cave indicates that flow through here allowed the cave to cut down to a deeper level after uplift.

The highest elevation cave in this study is Piriteumeume, which has all the features of an old cave, with large formations, collapse and irregularity, and dryness. During development of the cave the dolines would have drained a higher surface, and the karst corridors leading to the entrance would also have been caves. The makatea surface has many such small relic caves to be found in the karst corridors, though the caver will probably get lost finding them!

CONCLUSIONS

Cave systems are a relatively neglected aspect of study of raised limestone islands, possibly owing to the specialised techniques of survey, and potential dangers. This study shows that they can make a contribution to the knowledge of limestone geomorphology and changes in relative sea-level .

Features of the caves explored indicate the validity of the principles of makatea cave development outlined in the introduction.

It is apparent that caves of lower elevation are of larger dimensions than those higher. This could be because parts of the higher caves have been lost with time, but as well as length the lower caves have higher rifts or vadose slots. This could result from slower rates of island uplift that allowed the streams to downcut their caves, or it could indicate the sea-level changes of the Pleistocene that have caused multiple reoccupations of these caves.

ACKNOWLEDGEMENTS

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ATOLL RESEARCH BULLETIN

NO. 418

SHALLOW-WATER SCLERACTINIAN CORALS FROM KERMADEC ISLANDS

BY

VLADIMIR N. KOSMYNIN

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AUGUST 1994

SHALLOW-WATER SCLERACTINIAN CORALS FROM KERMADEC ISLANDS

BY

VLADIMIR N. KOSMYNIN

INTRODUCTION

Shallow-water scleractinian corals were collected in the Kermadecs (South-West Pacific) in April-May of 1990 during the 18th cruise of the USSR Academy of Sciences' R/V "Akademik Alexandr Nesmeyanov", which sailed from Vladivostok to the Western Pacific. The objective of this expedition was to study the influence of volcanic gas and hydrothermal activity on sublittoral communities. Dredging operations were performed on the slopes of Kermadecs: underwater observations were made near Curtis Island and corals were collected at several points near Raoul Island and nearby islets using SCUBA (fig. 1).

Despite numerous previous visits to the Kermadec Islands by research vessels, very little information has been reported on the scleractinian fauna. The presence of corals in bottom communities in this area was mentioned by Nelson and Adams (1984) and coral communities were noted when Shiel et al. (1986) described the sublittoral zonation, but neither publication provided a list of species. The last publication dealt directly with corals from the Kermadec Islands was that of Vaughan (1917). This paper was based on the material collected early this century by R.W.B.Oliver, former director of the New Zealand National Museum of Natural History, who described the Kermadecs in several publications. Material from this collection are deposited in the Museum of New Zealand (MNZ) in Wellington and at National Museum of Natural History (NMNH) in Washington. Some additional Kermadec corals collected and kept in the New Zealand National Museum were identified by D.F.Squires. Soviet expeditions also worked there, but their results are not yet published.

A SHORT DESCRIPTION OF SITES OF CORAL COLLECTING

Near Raoul Island two sublittoral areas were studied: one north of Blue Lake and another in the southern part of Denham Bay. Meyers and Napier Islets were also studied and corals were collected (Figure 1).

North of Blue Lake at the depth of 10-15 m the foreshore is characterized by a gently sloping floor. The floor shows an alternation of areas covered by ripple sands with separate boulders and patches of boulder pavement, among which some boulders that are 1-2 m high. Unlike the barren ripple sands, bottom communities on large boulders are rich and include fleshy algae as well as calcareous geniculated *Corallina* on upper surfaces and incrusting *Lithothamnium* under overhangings, and many sea urchins that include at least two species. Corals are abundant there and are mostly encrusting forms of *Hydnophora*, *Goniastrea* and *Montastrea* 50-60 mm in size on top surfaces of boulders, and *Dendrophyllia* under overhangings (Tabl. 1). Life is less diverse on the

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surface of boulder pavement in comparison to that found on large boulders probably because of sand abrasion.

The foreshore in the southern part of Denham Bay is considerably different from that described above. It is steeper and at a distance of 50-70 m from the shoreline the depth is 15-20 m. The slope is composed of large basalt blocks, each several cubic meters. They are arranged on the slope either in dense groups or scattered individuals. Coarse-grained sand and gravel are accumulated between boulders.

These boulders support rich flora and fauna on their tops, whereas at the base, where light is weaker and sand-gravel erosion is stronger, the boulders are poorly inhabited. Along with macrophytes, these rich communities contain a considerable number of corals, primarily colonies of *Turbinaria bifrons*, which form large flat coralla up to 1.5 m in diameter. There are also abundant encrusting colonies of *Goniastrea australiensis* with a corallum size up to 20 cm, and smaller coralla of *Montipora*, *Leptoseris* and Cyphastrea. These corals cover no more than 10-20% of the surface even at the top of boulders. The maximum number of corals appears to occur at depths of 13-15 m and decrease rapidly up the slope, probably because of the increasing abrasive effect of the resuspended sediments.

The richest coral communities were discovered on the western side of the Meyers islets opposite a channel separating them. Here at depth of 22-24m there is a terrace that looks like a wave cut platform. It may be in fact a submerged coast-line. On the surface of the terrace there are thin lenses of coarse-grained sand and gravel, as well as individual colonies of *Turbinaria radicalis* with coralla up to 0.5m in diameter. Rocks of different height occur on the surface of the terrace, some of them reach a depth of 10-12 m, while others extend up to almost the surface. The rocks contain very rich communities in which corals play an important role sometimes covering up to 25% of the surface. Life forms of corals are mainly encrusting such as *Goniastrea*, *Leptoseris* and *Montipora*, or massive or columnar such as *Hydnophora exesa*. Branching forms are represented by sparse small colonies of *Pocillopora damicornis*, which inhabit the tops of boulders. *Turbinaria radicalis* and *Turbinaria bifrons* form the largest colonies and are more noticeable than other corals. *Hydnophora exesa* form the second largest colonies, with coralla up to 40 cm in diameter.

On vertical cliffs there are frequent *Dendrophyllia* sp. together with gorgonian corals. The latter grow abundantly at a depth of more than 25 m, and up the slope on more gently sloping areas there are abundant alcyonarian corals. In the communities at the depths of less than 25 m other sedentary animals are numerous along with the corals, including sponges, tunicates, hydroids, sea lilies, sea urchins and the notorious sea-star *Acanthaster planci*. Similar communities were noted also near Napier island.

The Kermadec Islands are also characterised by abundant deep water scleractinian corals at the depth of 375-1000 m. In particular, a large quantity of fragments of *Goniocorella dumosa* (Alcock,1902) were dredged from the depth of 1000 m by trawl at 30°28'0"S 178°37'2"W, as well as corals such as *Madrepora vitiae* Squires & Keyes,1967 and *Flabellum gracile* (Studer,1877).

DISCUSSION

The deep water scleractinian corals mentioned above are related to the fauna from New Zealand, whereas the shallow water Kermadec corals are linked with the Tonga and Fiji Islands to the north and the Norfolk Islands on the west. There is a certain affinity of the latter with the Great Barrier Reef of Australia through the Norfolk and Lord Howe Islands but the diversity is considerably lower. Further studies will undoubtedly increase the list of corals for the Kermadec Islands. Some fossil corals were also noted by Vaughan (1917): *Leptoria phrygia* (Ellis & Solander,1786; USNM 93896), *Alveopora* sp. (USNM 93898), *Acropora* sp.(sample I failed to find in USNM) and *Cynarina* *lacrymalis* (Milne Edwards & Haime,1848) (USNM 93899), which may quite possibly be alive on Kermadecs.

The low diversity of reef-building coral species off the Kermadecs is probably due to several reasons. I tend to agree with Schiel et al.(1986) that it is not a result of competition for space with other organisms, in particular algae. Among the main factors are the relative isolation of the islands, their young age and recent activity of volcanic processes as well as wave erosion (abrasion). The development of coral reefs near Raoul Island is limited not only by low water temperatures but more by relief and coastal geomorphic processes. Quick wave erosion of volcanic shores and mobility of floor substrates limit the possibilities for establishment of reef building corals. The coral fauna adjacent to Raoul Island small islets is richer than the coral fauna of Raoul Island itself. The precipitous rocky foreshores of small islets almost lack sediments. For corals it is more suitable to settle and grow there than on the relativly gentle slopes of Raoul Island where the mobile coarse bottom sediments limit coral growth.

The water temperatures near the Raoul Island are not optimal for reef corals but does not fall to the lethal winter limit of 15°C for the majority of hermatypic corals. The summer temperatures, which are about 24°C, is close to normal for coral reproduction.

The establishment/recruitment of new species of corals on Kermadec Islands is quite possible. It can happen not only by the distribution of planula by but also by rafting, for example, by fragments of pumice-stone carried by currents from northern volcanic islands. The discovery of fossil colony fragments of such species as *Acropora* and *Alveopora* (Vaughan,1917) indicate that some species could have established in this area but the conditions are not favorable for survival of new populations. In particular, their survival is considerably limited by abrasion and mobility of sediment material, and by volcanic activity.

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Table 1. The list of shallow water scleractinian corals from Kermadec Islands.

Species name	North coast Raoul	Denham Bay	Napier Islet	Meyers Islets
Hydnophora exesa (Pallas,1766)	1-10-4,5,6,7,9		2-22-1,2,6,11,13	4-5(15)-7,8
Goniastrea favulus (Dana,1848)*				
Goniastrea australiensis (Milne Edwards & Haime,1857)	1-10-4,7,17, 18,19,23	3-14-4,8,11, 13,14,17,18	2-22-3,15	4-5(15)-1,2,15,19
Leptoseris mycetoseroides Wells,1954		3-14-7,15,16,24		
Leptoseris hawaiiensis Vaughan,1907		3-14-4	2-22-10,12	4-5(15)-10
Cyphastrea serailia (Forskal,1775)		3-14-5,6,9,12	2-22-3	4-5(15)-13
Montastrea curta (Dana,1846)	1-10-3,8		2-22-4,9	4-5(15)-3
Montipora cf. *millepora* Crossland,1952		3-14-22	2-22-8	4-5(15)-12
Montipora cf. *spumosa* (Lamarck,1816)**				
Pocillopora damicornis (Linnaeus,1758)				4-5-30,31,32
Plesiastrea versipora (Lamarck,1816)**				
Turbinaria radicalis Bernard,1896	1-10-22	3-14-20		4-5(15)-4,5,6,17
Turbinaria bifrons Bruggemann,1877		3-14-10	2-22-5	4-5(15)-14
Dendrophyllia sp.	1-10-24	3-14-1	2-22-14	4-5(15)-16

* according to Shiel et al.,1986.

** according to Vaughan,1917. Comments to some of these species see in text.

1-10-3 - Paleontological Museum of Moscow recent scleractinian corals collection number. First number is the site of collecting (the same as on the chart, fig.1); second number is depth of collecting (if 5(15) - it means range 5-15 meters); third is number of sample from this site. Dublicates of these spesimens with the same indexation were transmitted to MNZ in Wellington.

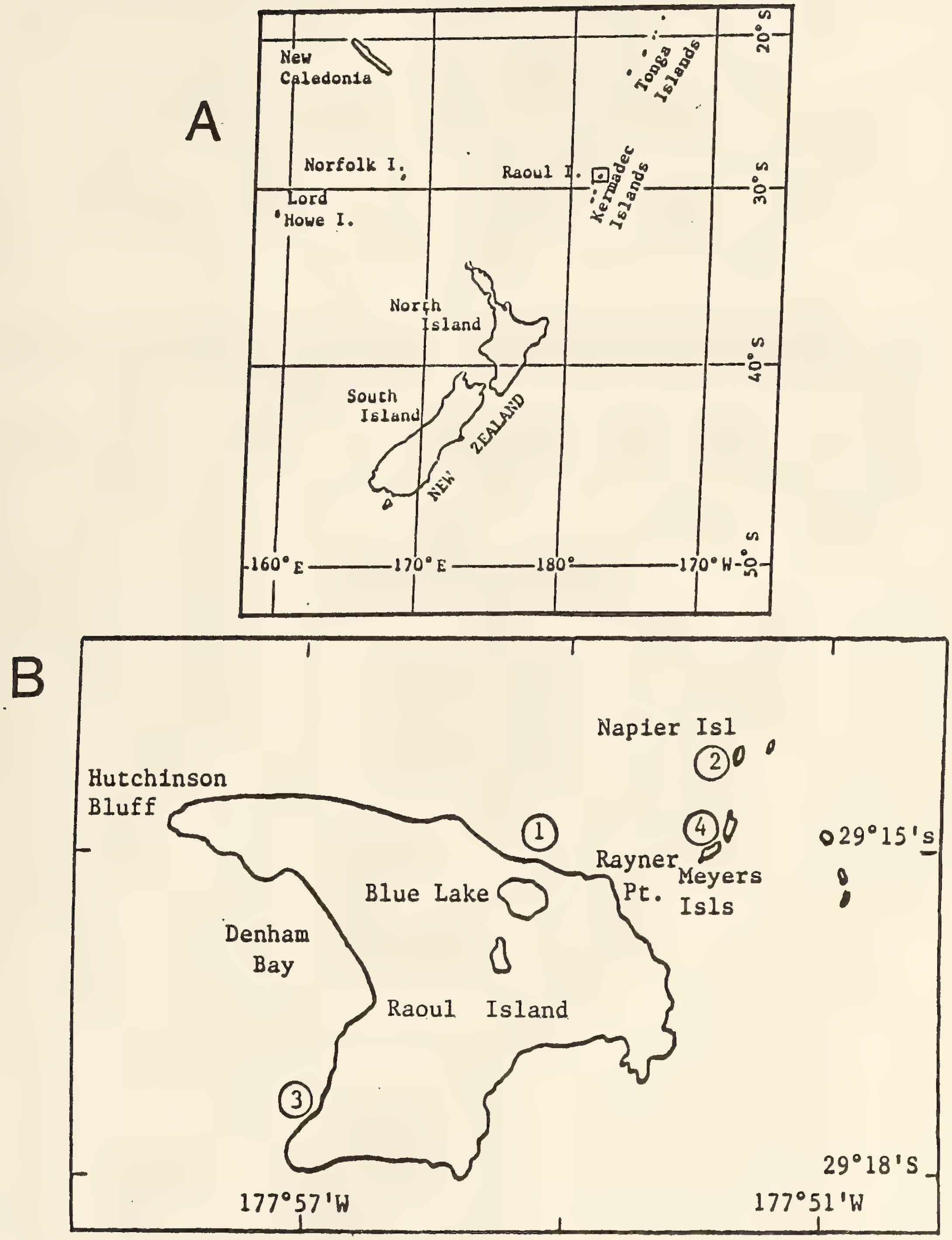

Figure 1.
A. The location of the Kermadec Islands, north of New Zealand.
B. Enlarged map of Raoul Island in the Kermadecs showing smaller islets, with sites of coral collecting (1 - 4).

ATOLL RESEARCH BULLETIN

NO. 419

DESCRIPTION OF REEFS AND CORALS FOR THE 1988 PROTECTED AREA SURVEY OF THE NORTHERN MARSHALL ISLANDS

BY

JAMES E. MARAGOS

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DESCRIPTION OF REEFS AND CORALS FOR THE 1988 PROTECTED AREA SURVEY OF THE NORTHERN MARSHALL ISLANDS

BY

JAMES E. MARAGOS

Abstract

The Republic of the Marshall Islands requested a natural and cultural biodiversity survey of 6 northern atolls (Bok-ak, Pikaar, Tōke, Wōtto, Roñdik, Ādkup) and one reef island (Jemo̧) which was accomplished over 17 days in September 1988. This report covers the results of the survey of the reefs and corals during the expedition. Ninety-five marine sites were snorkeled and the shorelines of all island were surveyed during the expedition. A total of 168 species and 55 genera and subgenera of stony corals were reported including several new species and one new genus recorded (Polyphyllia) for the Marshalls.

Bok-ak Atoll, the northernmost atoll, supports large giant clam populations, a completely native flora, and the largest seabird populations in the Marshalls. Pikaar Atoll also supports large giant clam populations and the largest sea turtle nesting populations in the Marshalls. Both Bok-ak and Pikaar are isolated from other atolls and have shallow lagoons elevated slightly above sea level due to their geomorphological configuration. Tōke Atoll is located about 10 km from inhabited Utrōk Atoll, and supports healthy coral reef habitats and giant clams. Jemo̧ Island supports large seabird populations and is the second most important sea turtle nesting site in the Marshalls. Boat access to Jemo̧, Pikaar and Bok-ak is hazardous due to wave exposure or strong currents. Roñdik Atoll supports healthy coral reefs, blue coral habitats, pink foraminiferan sand beaches, and large coconut crab populations. Ādkup supports abundant seabird populations, sea turtle nesting populations, and healthy coral reefs. Inhabited Wōtto also supports healthy coral, coconut crab, sea turtle and giant clam habitats and has beautiful beach, reef and lagoon habitats.

On the basis of the surveys, Bok-ak, Pikaar and Jemo̧ are recommended for designation as limited entry ecological preserves. Tōke is recommended as a national park accessible to both tourists and residents. Limited sport diving and beach-going is also suitable for Roñdik and Ādkup. Assistance should be provided to the people of Wōtto Atoll to fulfill their desire for small scale adventure tourism.

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I. INTRODUCTION

Oceania represents one of the last frontiers for the assessment of biological diversity, especially for shallow water marine ecosystems. Coral reefs are among the most widely distributed ecosystems on the face of the earth, and within Micronesia they dominate in terms of area. They also provide critical physical and ecological support to most other ecosystems including those of low coral islands. Because of remote access, geographic isolation, and the physical limitations of underwater surveying techniques, most marine areas in Micronesia remain unstudied. Yet assessment of the ecological and biological importance of reef areas for conservation, subsistence, recreation, visitor and commercial uses must require on-site surveys to some extent. With many thousands of reefs and islands yet to be evaluated, new techniques must be employed to allow a rapid but technically adequate evaluation of reef sites. Existing regional evaluations (IUCN, 1989; 1988; Dahl, 1980) provided valuable information on many areas with respect to park and reserve potential, but the emphasis has been placed on terrestrial (island) ecosystems which are easier to visit and survey. The Marshall Islands study of September 1988 offered a unique opportunity to accomplish a marine oriented regional survey of reefs using a non-conventional rapid field assessment technique relying on a combination of field observations, teamwork, aerial photographs, underwater photographs, available maps, and interviews with knowledgeable islanders.

The study is primarily based on the results of a three week expedition to six atolls and one table reef in the northern Marshalls during September 1988. The areas surveyed were the atolls of Bok-ak, (Taongi, Bokak, Pokak), Pikaar (Bikar), Tōke (Taka), Ādkup (Erikub), Rōn̄dik (Rongerik), and Wōtto (Wotho) and the table reef of Jemo̧ (Table 1, Fig. 1). The name spellings used above reflect the most current official RMI linguistical determinations. Those in parentheses above reflect spellings commonly used in the past.

The field expedition concentrated on evaluating the following categories of resources with respect to potential justification and interest in protected area designation; names in parentheses refer to the expedition team members responsible for collecting information about the resources:

* island vegetation (Derral Herbst),
* seabird nesting, resting and feeding (James Juvik),
* other terrestrial animals (James Juvik, Peter Thomas),
* turtle nesting and feeding habits (John Naughton, James Maragos, Peter Thomas),
* nearshore reef fishes (John Naughton, R. Virgil Alfred and Paul Maddison),
* giant clams and other edible shellfish (John Naughton, R. Virgil Alfred, James Maragos),
* coral and reef features (James Maragos),
* pelagic fisheries and marine mammals (Paul Maddison, R. Virgil Alfred, and John Naughton),

- cultural historical and archaeological resources (Charles Streck Jr.), and
- tourism, park and reserve feasibility (Peter Thomas)

The present report describes the results of the surveys of reefs and corals with emphasis on ecology and related oceanographic and geological characteristics. It is meant to serve as a technical supplement to the report prepared by Thomas et al (1989), a summary of all survey results.

Table 1. Physiographic data on the atolls and table reef visited during the September 1988 expedition to the northern Marshall Islands.

NAME	TOTAL ISLAND AREA (km^2)	NO. OF ISLANDS	LAGOON AREA (km^2)	LATITUDE (N)	LONGITUDE (E)	DIMENSIONS (km^2) (L X W)	POPULATION (1989)
Ādkup	0.91	14	231.32	9°08’	170°02’	27 X 24	0
Bok-ak	3.77	11	78.38	14°43’	168°57’	18 X 8	0
Jemo̧	0.18	1	0	10°06’	169°30’	8 X 2	0
Pikaar	0.49	6	37.57	12°15’	170°07’	12 X 7	0
Roñdik	2.11	17	144.59	11°21’	167°26’	18 X 18	0
Tōke	0.57	5	93.52	11°07’	169°46’	14.5 X 14.5	0
Wōtto	4.16	13	95.34	10°06’	165°59’	18 X 14.5	103

II. MATERIALS AND METHODS

Limited field time required that maps, aerial photographs, underwater photographs, and other sources of valuable information be consulted before the design and execution of field observations. For one, the time available to cover such a large number of reef areas was too short to warrant quantitative sampling surveys. Field work concentrated on collecting qualitative information on several subjects for a broad number of sites. During the 17 days of the expedition (7-24 September 1988), four days were spent in transit between atolls leaving 13 days field time on station at the study sites, or an average of about two days per atoll. Three days were spent on Bok-ak allowing 20 marine sites there to be surveyed. Elsewhere 12-13 sites were surveyed at the remaining atolls and table reef. Only one day was spent at Jemo̧ due to the small size of the reef and lack of safe overnight anchorage. Field time at Ron̄dik was cut short due to a medical emergency. Thus the western half of Ron̄dik could not be investigated. A total of 95 marine sites were surveyed at the seven areas during the September 1988 expedition. Additional observations were also made on land, along sandy beaches (especially for evidence of turtle nesting) and during small boat travel.

Most observations were made underwater using snorkeling equipment. SCUBA diving was not possible. Notes and reef profiles were recorded in situ on waterproof paper attached to clipboards, (See Appendix A). Underwater photographs of each site were obtained using Nikonos cameras. Most coral species and all coral genera were identified in situ by visual observation. A few specimens were collected to clarify or confirm species identification. Major reference books on the taxonomy of reef corals were brought on the expedition and include Veron (1986), Veron and Wallace (1984), Veron and Pichon (1976, 1979, 1982), Veron et al (1977), Randall (1984), and Wells (1954). At the end of each day's field work, these reference guides were consulted to finalize species assignments and to compile lists of corals for each station. Master coral lists for the expedition and for each atoll were compiled (Tables 2 and 3).

Corals

Relative abundance of each coral species was visually estimated in the field and assigned to one of the five following abundance categories:

D = dominant
A = abundant
C = common
O = occasional
R = rare

Definitions of each of these categories are provided in Appendix B. Previous coral records from the region include 35 species reported in Wells (1954) based upon collections and observations at Bok-ak and Ron̄dik (Table 4). There are no published records of corals from the five other reefs visited in 1988. Thus, most compiled species constitute new atoll records. Other important coral surveys in the Marshalls were reviewed and include Wells (1951), Hiatt (1951), Titgen et al (1988), Devaney and Lang (1987), Maragos and Lamberts (1989), Lamberts and Maragos (1989), Scanland (1977), and Maragos, in preparation.

Reef Geomorphology

Previous geological studies of the Marshalls were consulted, including Wells (1954), Fosberg (1988), MacNeil (1969), Fosberg et al (1956), Tracey et al (1948), Nugent (1946), MacNeil (1954), Ladd et all (1953), and Emory (1948). A few of these included descriptions of the atolls visited in September 1988. Observations on reef features concentrated on confirming earlier evaluations, identifying trends or changes, and describing features not previously reported (particularly underwater features).

Map Sources

The U.S. Army Mapping Service (AMS) compiled topographic maps at a scale of 1:25,000 for all of the seven visited areas, except Wōtto whose maps were compiled at a scale of 1:50,000. The AMS maps were based upon limited ground truthing and aerial photo-interpretation of low altitude black and white imagery flown by the U.S. Army in 1944. Later the Defense Mapping Agency reviewed, updated, and corrected many of the AMS maps and published navigation charts of all atolls at a smaller scale. A listing of all maps of the seven areas within the DMA and AMS catalogues is found in Appendix C.

Aerial Photographs

Copies of 1944 black and white Army aerial photographs were available for inspection at the Bernice P. Bishop Museum Map Collection, Honolulu. In addition, the U.S. Department of Energy sponsored complete coverage of 15 northern Marshall atolls and collection of color aerial photographs at a scale of 1:30,000. A few additional photographs were flown at a scale of 1:8,000 for the northern Marshall Atolls in 1978 (E G & G, 1978). Unfortunately, Bok-ak was not surveyed. The 1978 photographs include outstanding detail of all islands and most reef areas to depths of 15m or more. The 1978 photographs allowed photo interpretation and comparison to the earlier 1944 photographs and maps to determine the extent of geomorphological changes to reefs and islands for five of the seven visited areas (all except Bok-ak and Ādkup). Appendix D provides a listing of the 1944 and 1978 aerial photographs reported for the seven visited reef areas.

Marine Protected Area Evaluative Criteria

A number of criteria were used during evaluation of the marine sites surveyed during the 1988 expedition (Table 5). These criteria were not assigned ranks or numerical weights so that each site could be "quantitatively" evaluated. Such approaches are highly subjective, and given the lack of quantitative data collected during field surveys, quantitative comparisons are not justified. However, the gross number of positive criteria identified for each site gave a good approximation of the value it serves a candidate protected area. Most importantly, the criteria provide a useful checklist from which to identify truly significant or substantial resource values and attributes.

Ship Itinerary

Figure 1 consists of a map of the northern Marshalls which shows the atolls visited during the 1988 field expedition. The RMI government kindly made available their fisheries patrol vessel Ionmeto I to provide transportation and lodging during the expedition. With a top speed of 22 knots and modern navigation equipment, use of the ship reduced travel time and increased survey time at each of the target study areas. The maximum distance between Majuro (Mājro) (port of departure) and the most outlying atoll (Bok-ak) was nearly 500 miles. The 17 day expedition covered approximately 2,000 miles, including two unscheduled (medical and supply) stops at Kuwajleen (Kwajalein) Atoll.

Digitizing of Maps

Original maps were prepared by CORIAL for presentation in this report. The maps were digitized using Intergraph ® MGE and MapInfo ® software. Maps of all atolls are being digitized as part of a geographic information system now being developed for the Marshall Islands termed the Marshall Atoll Resource Information System (MARIS).

Table 2. Check list of corals observed in the Northern Marshall Islands, September 1988.

P = Pikaar Atoll, B = Bok-ak Atoll, T = Tōke Atoll, J = Jemo̧ Island, W = Wōtto Atoll, R = Roñdik Atoll, and A = Ādkup Atoll. Letters in parenthesis are additional records reported in Wells (1954) at the same atolls.

Stony Corals (Scleractinia, calcified octocorals, calcified hydroids)

FAMILY ACROPORIDAE

Acropora abrotanoides (Lamarck) - P, B
A. aculeus (Dana) - P, B
A. acuminata Verrill - P, B, T, W, (R)
A. austera (Dana) - B, W, A
A. cerealis (Dana) - P, B
A. cytherea (Dana) - T, J, W, R, A
A. danai (Edwards and Haime) - B, (R)
A. digitifera (Dana) - P, B, T, J, W
A. diversa (Brook) - P
A. echinata (Dana) - (R)
A. formosa (Dana) - P, B, T, W, R, A
A. florida (Dana) - W, R, A
A. gemmifera (Brook) - P, B, W, A
A. grandis (Brook) - W
A. granulosa (Bernard) - B, W
A. glauca (Brook) - B, T, W
A. horrida (Dana) - W
A. humilis (Dana) - P, B, T, W, R, A
A. hyacinthus (Dana) - P, T, W
A. irregularis (Brook) - P, B, T, W
A. loripes - (R)
A. lovelli Veron and Wallace - P, B, W, A
A. microphthalma Verrill - B
A. millepora (Ehrenberg) - W
A. nasuta (Dana) - P, B, T, W, R, A
A. robusta (Dana) - A
A. nobilis (Dana) - B, W
A. polystoma (Brook) - P, B, T, W
A. selago (Studer) - P, B, T, W
A. striata - (R)
A. surculosa (Dana) - P, B, T, W, R, A
A. syringodes (Brook) - W
A. squarrosa (Ehrenberg) - P
A. tenuis (Dana) - B
A. vaughani Wells - P, B, T, W
A. yongei Veron and Wallace - P, B, W
A. spp (6) - P, R, A
Acropora (Isopora) palifera (Lamarck) - P, B, J, R, A
A. (I) brueggemanni (Brook) - P
A. (I) cuneata (Dana) - W, R
Anacropora forbesi Ridley - B
Astreopora explanata Veron - B, T, R, A
A. gracilis Bernard - P, B, T, J, W, A
A. listeri Bernard - B, T, R

A. myriophthalma (Lamarck) - P, B, T, J, W, R, A
A. sp. (1) - T, R, A
Montipora aequituberculata Bernard - P, B, J, W, R, A
M. caliculata (Dana) - B
M. foliosa (Pallas) - P, B, T, J
M. foveolata (Dana) - P, B, T, J, W, R, A
M. hoffmeisteri Wells - P, B, T, W, R
M. informis (Bernard) - T, W, R
M. marshallensis Wells - P, B
M. monasteriata (Forskål) - P
M. tuberculosa (Lamarck) - P, B, T, J, R, A
M. venosa (Ehrenberg) - B, T, W
M. verrucosa (Lamarck) - P, B, T, W, R, A
M. spp (3) - B, T, R, A

FAMILY ASTROCOENIIDAE

Stylocoeniella armata (Ehrenberg) - P, B, T

FAMILY POCILLOPORIDAE

Pocillopora damicornis (Linnaeus) - P, B, W, R, A
P. brevicornis Lamarck - B
P. eydouxi Edwards and Haime - P, B, R
P. meandrina Dana - P, B, T, J, W, R, A
P. verrucosa (Ellis and Solander) - P, B, T, J, W, R, A
Seriatopora hystrix Dana - P, B, T, W, R, A
S. angulata Klunzinger - P, B, T, W, R, A
Stylophora pistillata (Esper) - P, B, T, W, R, A

FAMILY PORITIDAE

Goniopora lobata Edward & Haime - B, A
G. columna Dana - T, W
Porites australiensis Vaughan - P, B, T, J, R, A
P. cylindrica Dana - P, B, T, W, R, A
P. lichen Dana - P, B, T, J, W, R, A
P. lobata Dana - P, B, T, J, W, R, A
P. lutea Edwards & Haime - P, B, T, W, R, A
P. murrayensis Vaughan - P, B, W
P. solida (Forskål) - P
P. superfusa Gardiner - B, R
P. vaughani Wells - T, W, A
P. spp (2) - R
Porites (Synaraea) rus (Forskål) - T, W

FAMILY SIDERASTREIDAE

Coscinaraea columna (Dana) - P, T, W, R, A
Psammocora haimeana Edwards & Haime - T
P. nierstraszi Van der Horst - B
P. profundacella Gardiner - P, B, T, A

FAMILY AGARICIIDAE

Pavona clavus (Dana) - P, B, T
P. minuta Wells - P, B, J, W, R, A
P. varians Verrill - P, B, T, W, R, A
P. venosa Ehrenberg - P
P. maldivensis (Gardiner) - B, T
Leptoseris mycetoseroides Wells - P, B, T, A

FAMILY FUNGIIDAE

Fungia fungites (Linnaeus) - P, B, W, A
F. (Danafungia) valida Verrill - P, B, T, W, A
F. (D) horrida Dana - A
F. (Pleuractis) paumotensis Stutchhbury - T, W, R, A
F. (P) scutaria Lamarck - P, B, T, R, A
F. (Verrillofungia) concinna Verrill - P, W, R
F. (V) repanda Dana - B, W, R, A
Cycloseris sp - W
Halomitra pileus (Linnaeus) - W
Herpolitha limax (Houttyun) - P, B, T, W, A
Polyphyllia talpina Lamarck - W
Sandalolitha robusta (Quelch) - T, W

FAMILY MUSSIDAE

Acanthastrea echinata (Dana) - P
Lobophyllia hemprichii (Ehrenberg) - P, B, T
L. hataii Yabe, Sugiyama and Eguchi - P
L. corymbosa (Forskål) - B, T, R
Symphyllia radians Edwards & Haime - P, B, W, R, A
S. recta (Dana) - P, B, J, (R)

FAMILY MERULINIDAE

Hydnophora microconos (Lamarck) - P, B, J, A
Scapophyllia cylindrica Edwards & Haime - P, B, T, W, R, A

FAMILY FAVIIDAE

Favia spp (2) - P, T, J, W, R, A
F. matthaii Vaughan - P, B, T, W, R, A
F. pallida (Dana) - P, B, T, W, R, A
F. rotundata (Veron, Pichon, & Best) - P, T
F. speciosa (Dana) - P, B, T, W, R, A
F. stelligera (Dana) - P, B, T, W, A
Favites flexuosa (Dana) - P, B, T, W, R
F. halicora (Ehrenberg) - P, B, T, R
F. spp (2) - P, B, J, W, R
Goniastrea edwardsi Chevalier - P, B, T, W
G. pectinata (Ehrenberg) - P, B, T, R
G. retiformis (Lamarck) - P, B, T, W, R, A

Leptoria phrygia (Ellis & Solander) - P, B, W
Plesiastrea versipora (Lamarck) - R
Oulophyllia crispa (Lamarck) - B, T, W, R
Platygyra daedalea (Ellis & Solander) - P, B, T, J, W, R, A
P. pini Chevalier - B, W
P. sinensis (Edwards & Haime) - B
P. lamellina (Ehrenberg) - B
P. sp (1) - A
Leptastrea purpurea (Dana) - P, B, T, J, W, R, A
L. transversa (Klunzinger) - P, R, A
L. sp (1) - P, T
Cyphastrea serailea (Forskål) - P, R
C. microphthalma (Lamarck) - P, B, T, W, R, A
Echinopora lamellosa (Esper) - P, B, T, R, A
E. sp (1) - R, A
Montastrea curta (Dana) - P, B, T, W, R, A
M. valenciennesii (Edwards & Haime) - (R)

FAMILY PECTINIIDAE

Pectinia lactuca (Pallas) - P

FAMILY DENDROPHYLLIDAE

Turbinaria frondens (Dana) - P
T. stellulata Lamarck - P, B, T, W, R, A
T. sp (1) - R, J

FAMILY CARYOPHYLLIDAE

Euphyllia glabrescens Chamisso & Eysenhardt - A, (R)

FAMILY TUBIPORIDAE

Tubipora musica (Linnaeus) - B, W, R, A

FAMILY HELIOPORIDAE

Heliopora coerulea (Pallas) - P, B, T, J, W, R, A

FAMILY STYLASTERIDAE

Stylaster sp (1) - B, A
Distichopora violacea (Pallas) - P

FAMILY MILLEPORIDAE

Millepora platyphylla Hemprich & Ehrenberg - B, T, J, W, R, A
M. exaesa (Forskål) - B, T, W, R, A
M. dichotoma (Forskål) - P, B, R, A

SOFT CORALS

Sinularia sp (1) - P, B, T, J, W, R, A
Sarcophytum sp (1) - P, B, T, W, A
Xenia sp (1) - P, W
colonial clownfish anemones - A
Palythoa sp (1) - R
unidentified alcyonacean - A

TOTALS genera and (subgenera): 50 + 5 = 55
species: 164 (1988 surveys) + 4 (from Wells, 1954) = 168

Table 3. Relative diversity and distribution of major stony coral genera (and subgenera) and species observed in shallow water at seven northern Marshall atolls in Sep 1988.

NAME OF GENUS (OR) SUBGENUS	NUMBER OF SPECIES AT EACH ATOLL							
	BOK-AK ATOLL	PIKAAR ATOLL	TŌKE ATOLL	JEMO̧ ISLAND	WŌTTO ATOLL	RŌNDIK ATOLL	ĀDKUP ATOLL	TOTALS
Acropora	22	21	17	10	26	11	12	40
(Isopora)	1	2	1	1	2	2	1	3
Anacropora	1							1
Astreopora	4	2	5	2	2	4	4	5
Montipora	8	8	8	4	6	7	6	15
Stylocoeniella	1	1	1					1
Pocillopora	5	4	2	2	3	4	3	5
Seriatopora	2	2	2		2	2	2	2
Stylophora	1	1	1		1	1	1	1
Goniopora	1		1		1		1	2
Porites	7	7	6	3	7	7	7	11
(Synaraea)			1		1			1
Coscinaraea		1	1		1	1	1	1
Psammocora	1		2				1	3
Pavona	3	4	3	1	2	2	2	5
Leptoseris	1	1	1	?			1	1
Fungia	1	1	1		1		1	1
(Danafungia)	1	1	1		1		2	2
(Pleuractis)	1	1	2		1	2	2	2
(Verrillofungia)	1		1		2	2	1	2
Cycloseris					1			1
Halomitra					1			1
Herpolitha	1	1	1		1		1	1
Polyphyllia					1			1
Sandalolitha			1		1			1
Acanthastrea		1						1
Lobophyllia	2	2	2			1		3
Symphyllia	2	2	?	1	1	1	1	2
Hydnophora	1	1	?	1			1	1
Scapophyllia	1	1	1		1	1	1	1
Favia	4	5	5	3	4	4	5	7
Favites	2	3	2	1	3	3	1	4
Goniastrea	2	3	3	?	2	2	1	3
Leptoria	1	1	?		1			1
Plesiastrea						1		1
Oulophyllia	1		1		1	1		1
Platygyra	3	3	1	1	3	1	2	4
Leptastrea	1	3	2	1	1	2	2	3
Cyphastrea	1	1	1		1	2	1	2
Echinopora	1	1	1			2	2	2
Montastrea	1	1	1		1	1	1	1
Heliopora	1	1	1	1	1	1	1	1
Millepora	3	2	2	1	2	3	3	3
Pectinia		1						1
Tubipora	1				1	1	1	1
Turbinaria	1	2	1	1	1	2	1	3
Stylaster	1		?		?		1	1
Distichopora		1	?		?			1
Euphyllia							1	1
TOTALS: GENERA	38	35	35	16	36	29	35	
&								
SPECIES PER ATOLL	93	93	93	33	88	74	75	158

TABLE 4. Previous coral records from the atolls studied during the September 1988 expedition to the Northern Marshall Islands. Compiled from Wells (1954). R = Roñdik, B = Bok-ak

PREFERRED NAME	NAMES OF SAME SPECIES (NOW JUNIOR SYNONYMS) LISTED IN WELLS (1954)	LOCATION
Stylophora pistillata	*Stylophora mordax*	R, B
Seriatopora hystrix		R, B
Pocillopora damicornis		R
P. verrucosa	*Pocillopora elegans*	R, B
P. eydouxi		R
Acropora acuminata		R
A. cytherea	*Acropora corymbosa*	R
A. (*I.*) *cuneata*		R
A. nasuta	*A. cymbicyathus*	R
A. echinata		R
A. humilis		R
A. (*I.*) *palifera*		R
A. danai	*A. rotumana*	R
A. loripes	*A. squarrosa*	R
A. striata		R
Astreopora myriophthalma		R, B
Fungia (*P*) *scutaria*		R, B
Porites cylindrica	*Porites andrewsi*	R
P. lichen		R
P. lobata		R
Favia pallida		R
F. speciosa		B
Montastrea valenciennesii	*Favites valenciennesii*	R
Favites flexuosa	*Favites virens*	R
Goniastrea retiformis		R
Platygyra daedalea	*Platygyra rustica*	R
Leptoria phrygia	*Leptoria gracilis*	B
Hydnophora microconus		B
Echinopora lamellosa		B
Lobophyllia hemprichii	*Lobophyllia costata*	B
Symphyllia recta	*Symphyllia nobilis*	R, B
Euphyllia glabrescens		R
Tubipora musica		R
Heliopora coerulea		R
Millepora platyphylla		R

TOTALS 21 GENERA AND 35 SPECIES, 30 SPECIES OF WHICH WERE REPORTED FROM RON̄DIK AND 11 SPECIES OF WHICH WERE REPORTED FROM BOK-AK

Table 5. Criteria for evaluating candidate reef areas as marine protected areas and parks in the RMI.

1. high diversity of stony corals
2. high abundance of stony corals
3. high bathymetric relief for reef habitat
4. high abundance of reef fish
5. high diversity of reef fish
6. high abundance of giant clams
7. high diversity of giant clams
8. presence of *Tridacna gigas* (the rarest & largest giant clam)
9. high abundance of large sand dwelling mollusks
10. high abundance of top shell and other reef dwelling mollusks
11. black coral and other precious corals
12. aesthetic stony corals (e.g. Stylasteridae)
13. aesthetic soft corals (e.g. Alcyonaria)
14. high abundance of sharks, skates, rays
15. absence of crown-of-thorns starfish infestations
16. absence of pollution or human damage
17. swimming or feeding sea turtles
18. resting sea turtles
19. nesting habitat for sea turtles
20. large populations of coconut crabs
21. coral and algal encrusted ship & plane wrecks
22. flourishing lagoon reef pinnacles
23. well developed patch reef system
24. overhanging ribbon reef formations
25. lagoon or ocean reef fingers and extensions
26. deep lagoon reef holes or sublagoons
27. unusual reef geomorphological features
    a. perched lagoons
    b. blue coral moats
    c. coral-algae dams
    d. restricted meandering passes
    e. ocean reef pinnacles
28. wide reef flat with micro atoll zone
29. wide reef flat with coral moats
30. wide reef flat with room and pillar formations
31. wide reef flats with productive algal turf zones
32. seagrass beds or meadows
33. mangrove associations
34. tidal lagunas and inlets
35. complex emergent reef rock formations
36. marine mammal aggregation sites
37. sea snakes and crocodiles
38. back reef coral heads & blue coral zones
39. unique marine species or new records for the region (RMI)
40. safe ocean reef slope snorkeling sites
41. safe atoll reef pass snorkeling sites
42. accessible spur-and-groove formations
43. narrow reef isthmuses and indentations
44. sites of historic or cultural significance

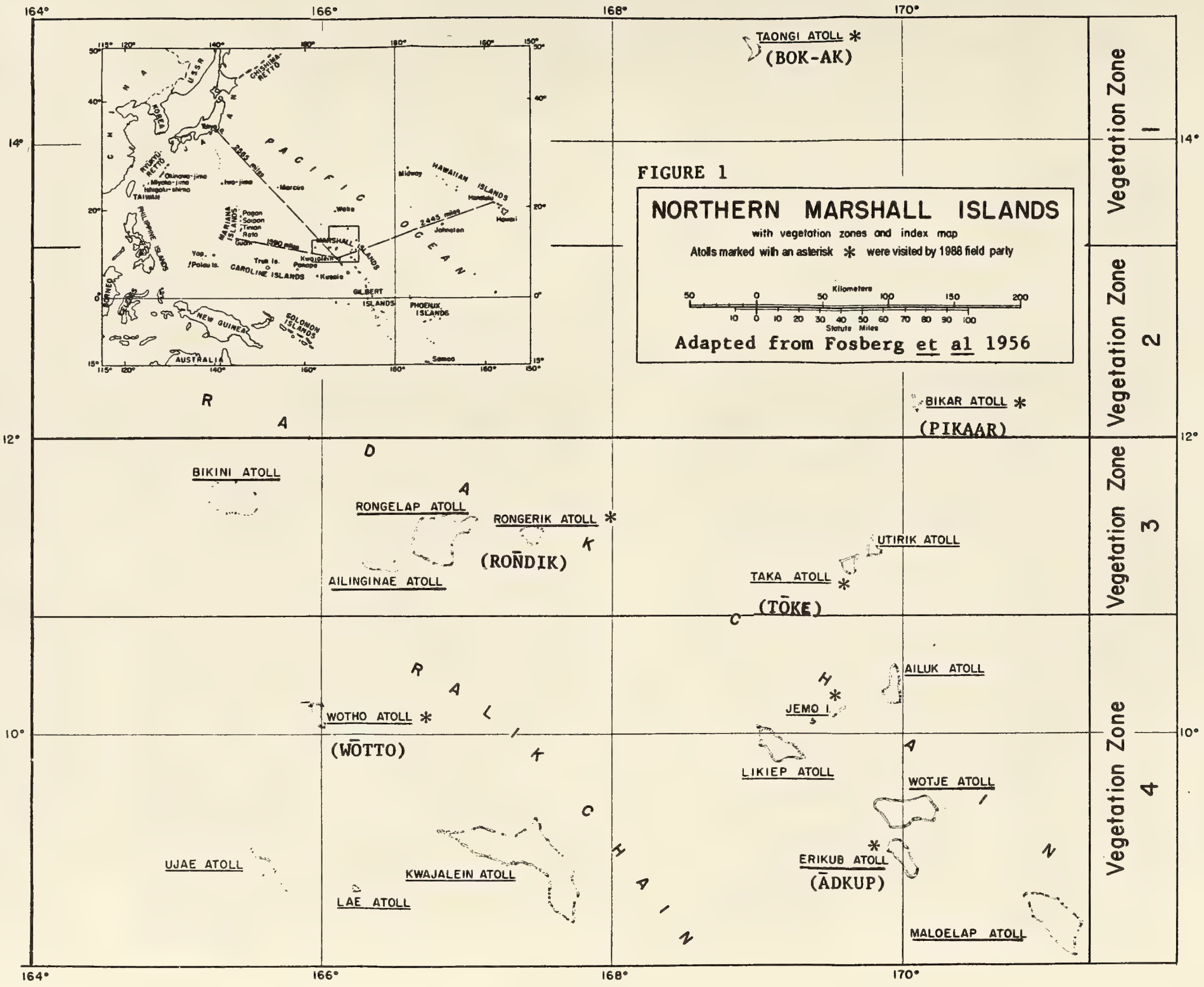


FIGURE 1

NORTHERN MARSHALL ISLANDS

with vegetation zones and index map

Atolls marked with an asterisk * were visited by 1988 field party

Adapted from Fosberg *et al* 1956

III. RESULTS

General descriptions of the reef and island systems of the seven areas are found in Fosberg (1988) and Fosberg et al (1956). Maps and additional geological information are reported in MacNeil (1969). The six atolls (Bok-ak, Pikaar, Wōtto, Tōke, Roñdik, and Ādkup) are generally small compared to the average size of atolls in the rest of the Marshalls, in terms of island land area and lagoon area (Table 1). The island of Jemo̧ is also smaller than the average size of islands on the other four table reefs in the Marshalls (Mejit, Kili, Lib, Jabat). All areas visited are not permanently inhabited except Wōtto. Jemo̧, Tōke, and Ādkup are occupied for brief periods during seasonal harvesting of fish, turtles and their eggs, coconut crabs, or other resources. The other areas (Roñdik, Pikaar, and Bok-ak) appear to be visited less frequently based upon our 1988 field observations. A combination of factors discourages permanent occupation of the uninhabited areas, including limited fresh water supplies and rainfall, poor soil conditions for cultivation, remoteness from nearby population centers, difficult or hazardous boat access to main islands, and perhaps greater vulnerability of the small islands to exposure from storm waves and surges. General physiographic data on the seven areas are summarized in Table 1. Reef profiles of most stations are found in Figures A-1 to 14 in Appendix A, and maps of many reefs and islands constitute Figures 2 through 37 in the text.

Climate and Oceanography

The ocean in the region of the northern Marshalls is between 4,500 and 5,400m deep (Fosberg et al, 1956). The northern Marshalls are semi arid and experience less than average annual rainfall compared to atolls and islands more to the south. The two northernmost atolls, Bok-ak and Pikaar are the driest Marshall atolls, (excluding Enen Kio (Wake) which is under U.S. jurisdiction, drier still, and further to the north). Of the six atolls and one island surveyed in September 1988, Ādkup, which is situated in the central Marshalls, is the wettest of the group. The dryness limits groundwater and vegetation development, and Fosberg et al (1956) divides the Marshalls into several vegetative zones (see Figure 1). The northern atolls are exposed to stronger tradewinds and associated wave action. Although tropical storms and typhoons tend to spawn in lower latitudes further to the west, sometimes the storms gain intensity, move into the Marshalls, usually from the south, and cause extensive damage to shorelines, islands and some reefs. Even infrequent storms can modify the distribution of islands on atoll reefs with long lasting effects, as reported for Arno Atoll (Wells, 1951). The typhoon frequency in the Northern Marshalls is of the order of 50 to 100 yrs, and the visible results of typhoons, especially on atoll islands are the record of at least a thousand years or more (MacNeil, 1969).

The major tropical current system in the northern Marshalls is a large westward flowing current between latitudes 10 and 20 degrees, north termed the North Pacific Equatorial Current (NPEC). This current mostly affects deep ocean circulation patterns off shore. Nearshore effects of the NPEC are masked by much stronger but localized currents caused by the tides, winds, and wave action.

JEMO REEF (Figures 2-4, and A-8)

Jemo̧ is the only reef of the seven visited that is classified as a table reef and is one of only 5 table reefs (compared to 29 atolls) located in the Marshall Islands. A table reef consists of an isolated flat topped coral reef which reaches the sea surface but which lacks a lagoon (MacNeil, 1969). These reefs tend to be small, sometimes linear, and are exposed to wave action due to the lack of sheltered lagoon reefs. The table reef supporting Jemo̧ Island is 8 km long, slightly arcuate, and is situated along a SW to NE axis (Figure 2). Jemo̧ Island is egg shaped and about one-third mile long.

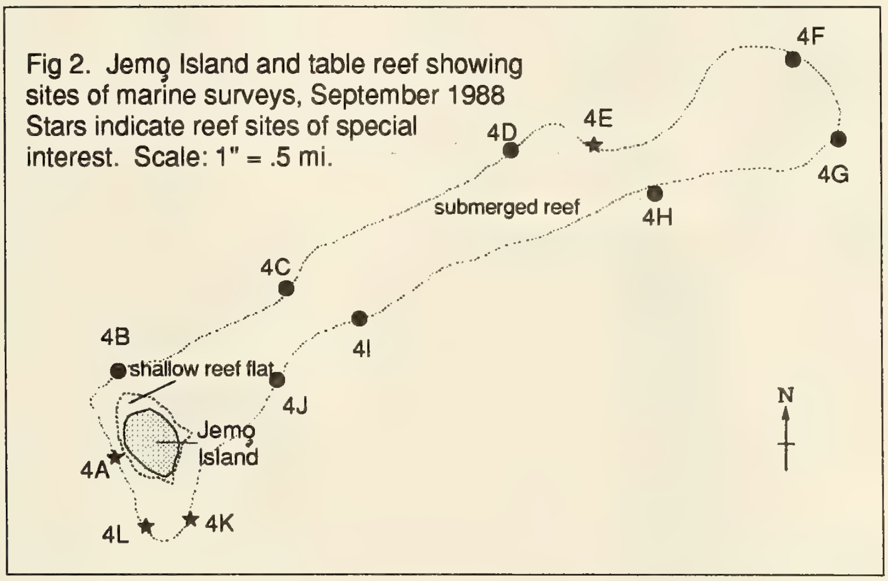


Fig 2. Jemo̧ Island and table reef showing sites of marine surveys, September 1988 Stars indicate reef sites of special interest. Scale: 1" = .5 mi.

Exposure of the reefs and island to heavy waves and storms from virtually any direction has controlled and shaped reef development at Jemo̧. Underwater observations, published charts, and color aerial photographs all document that the flanks of the table reef drop off near precipitously to great depths within a kilometer of the reef crest. Shallow reef flats emerge at low tide only at the southwest end upon which rests the single island of Jemo̧ (Figures 2-4). Elsewhere, an extensive system of sand covered surge channels (see Figures 3, 4) traverse the reef crest in a north-south axis and at depths of 2-4m. At the NE end, which receives the most exposure from trade-wind waves, the reef resembles a rounded knob in which the surge channels give way to well developed spur-and-groove formations. Elsewhere the outer margin of the reef crest consists of flat pavement-like and heavily scoured ramps descending at a moderate angle from a depth of 2-3m to a drop off at a depth of about 6-8m. Below the drop off, the reefs are steep vertical walls sometimes overhanging (Figure A-8, sites 4B, 4L, 4E, 4J, and 4D).

Perhaps due to the long NW facing axis of the reef oriented away from the prevailing NE tradewinds, typical spur and groove formations are lacking along the reef margin except at the NE end. These features, along with the prominent series of sand bottomed surge channels across the reef crest, are clearly displayed in the 1978 color aerial photographs of the island and reef at Jemo̧ taken at scales of 1:30,000 and 1:8,000.

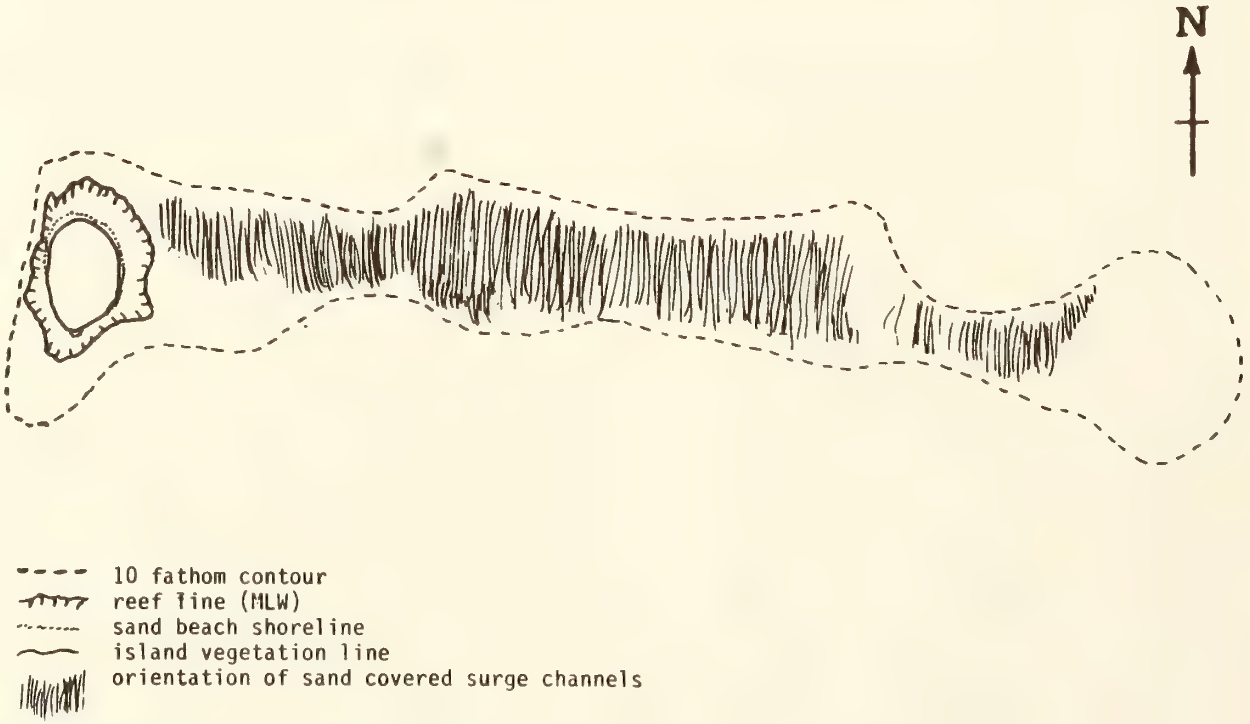


Figure 3. Jemo Island and table reef showing distribution of shallow reefs and surge channels on the reef crest. Map drawn from 1978 color aerial photographs. Scale 1:30,000.

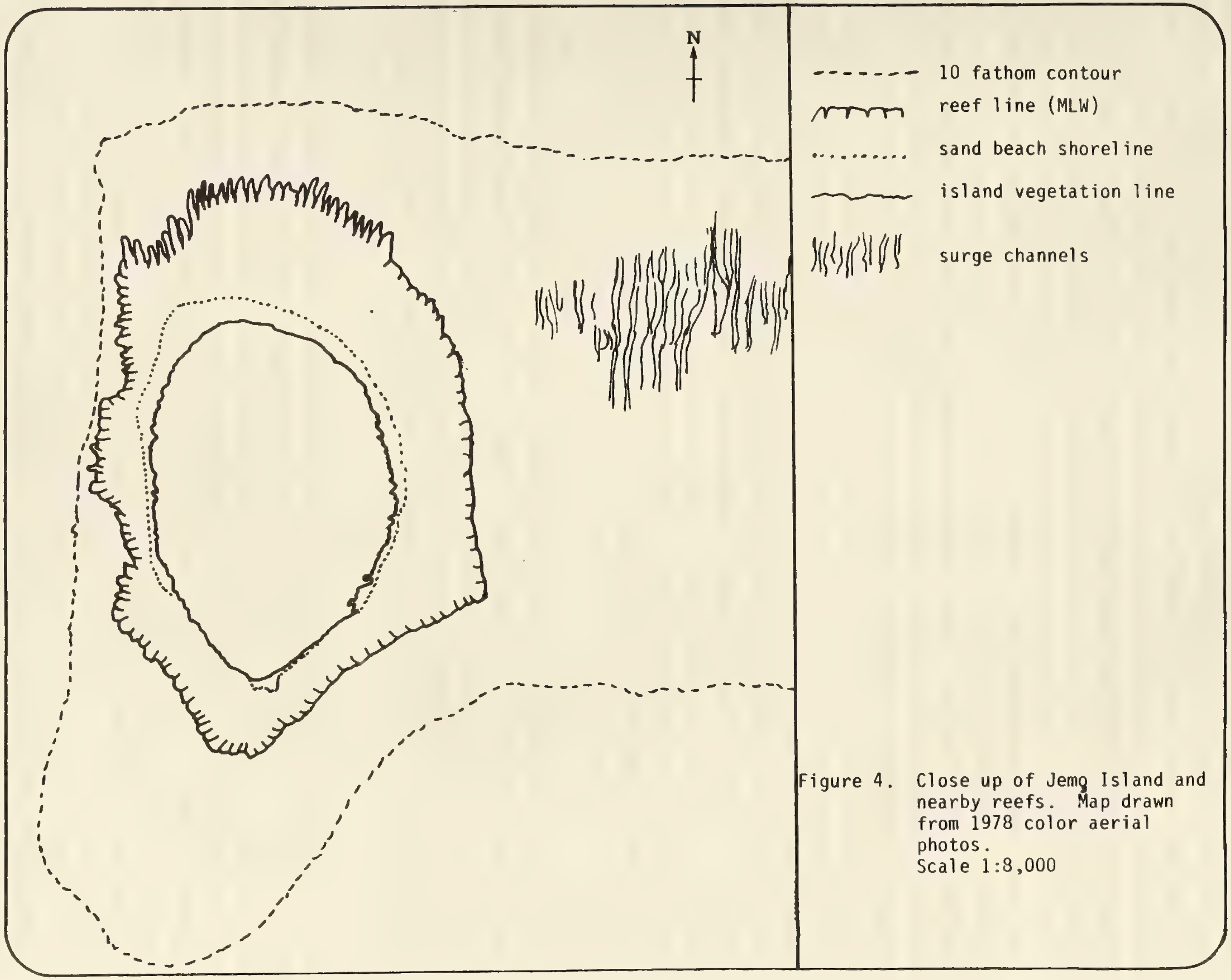


Figure 4. Close up of Jemo Island and nearby reefs. Map drawn from 1978 color aerial photos.
Scale 1:8,000

There are no major accumulations of loose boulders strewn on the reef crest. Small boulder beaches occur along the south and southeast facing shorelines of Jemo̧ Island. The reef margins off the elongate SE facing reef axis appear to be depositional in character, with sand, gravel and other sedimentary materials apparently carried through the surge channels over the crest of the reef from the other (NW) side. Thick accumulations of sediments were observed at the base of canyons between steeply sloping massive rounded reef buttresses along the SE reef margin. In contrast, the NW reef margin lacked any loose sediment, and coral formations consisted of robust, low profile colonies. The bare reef pavement ramps appeared heavily scoured. Ailuk Atoll affords Jemo reef some protection from northeast swells, Likiep, provides protection from the southwest, and Wotje and Ādkup provide protection from the southeast, leaving the northwest face of Jemo̧ reef the most exposed to heavy seas. Movement of reef materials appears to be from a northwest to southeast direction, with the northwest face of the reef potentially more exposed to damage from wave energy.

Another unusual feature of Jemo̧ reef is the truncated sheer face of the southwest end of the reef adjacent to the island. This wall drops vertically from depths of 6m to 50m or more with some major overhangs (Figure A-8). The margin of the reef is nearly perfectly straight along a northwest to southeast axis (see Figs. 3 & 4) as if a giant knife had sliced away the reef mass further to the southwest. I can think of no explanation for this unusual geomorphic feature, except that a previously existing extension of this reef to the SE may have fractured and slumped down towards greater depths, leaving a vertical face on the remaining reef.

Since none of the other table reefs in the Marshalls have been described in much detail, it is impossible to compare Jemo̧'s features to them. It is possible that Jemo̧'s table reef might be the peripheral remnant of a once larger atoll, the rest of which has been displaced by faulting below the depths required for active upward reef growth. Clearly Jemo̧'s reefs are unusual with features not having been previously reported in the scientific literature.

Despite the abundance of hard reef surfaces and transparent well illuminated waters, coral abundance and diversity were low. Coverage on the pavement terraces was low and nearly absent from the walls of the sand channels. Highest coral development occurred in a NW facing reef indentation near the NE end of Jemo̧ reef. This indentation apparently affords the reef slopes some protection from heavy wave action, allowing luxuriant, three-dimensional coral development. Typical vertical profiles of all reef sites sketched in the field are presented in Appendix A (Figure A-8 covers Jemo).

The absence of a more extensive and shallow reef flat and the presence of the surge channels on the reef crest is curious. Perhaps the reef is too narrow or wave action too severe to facilitate shallower reef flat development. Wave action was observed to be approaching Jemo̧ from all directions, although heaviest from the north during our visit. The bulbous NE terminus of the reef was the zone of maximum wave action.

Landing on Jemo̧ Island is extremely hazardous as noted in Fosberg et al (1956), Fosberg (1988), and as experienced first-hand in 1988. The transition from deep to shallow water is abrupt off the SW end (the only safe "access" point to the island) and the spur and groove formations and unpredictable wave action renders boat navigation dangerous. During our landing, the shaft of the outboard motor struck the reef and broke off, causing our skiff to swamp. The lack of safe anchorage and access must have contributed historically to the lack of permanent habitation on Jemo̧. During heavy surf it would be impossible to land at the island from any direction.

Rare Marine Species at Jemo̧

Evidence of sea turtle nesting activity was high along Jemo̧ Island's sandy beaches and the level of evidence (53 pairs of turtle tracks) was second only to Pikaar's. Signs of recent harvesting of green turtle was evident, and one nest with fresh eggs was discovered. Although uninhabited, Jemo̧ lies close to inhabited Wotje, Likiep, and Ailuk atolls. According to Fosberg (1988), Jemo̧ was in pre-European times a turtle sanctuary, and only infrequent visits were permitted; turtles and eggs were taken in limited numbers under close supervision by priests (Jack Tobin, pers comm. to Ray Fosberg). Although not rare species, numerous sharks also inhabit the reef waters off Jemo̧.

Jemo̧'s Corals

Jemo̧'s coral fauna is noticeably depauperate with only 33 species and 16 genera reported after surveying 12 separate sites. These numbers compare to 74-93 species and 29-35 genera reported from atolls subject to the same sampling intensity (Table 2) during the 1988 survey. The most common Jemo̧ species were ramose stony corals (Acropora (I) palifera, Pocillopora verrucosa, P. meandrina), robust firecorals (Millepora platyphylla), encrusting colonies (Montipora spp) massive brain corals (Platygyra daedalea, Favia spp, Hydnophora microconos) other reef corals (Symphyllia radians, Astreopora spp, Turbinaria sp, Porites spp, the soft coral Sinularia, and the blue coral (Heliopora coerulea). Maximum coral abundance and diversity occurred at depths between 7-10m and especially where reef indentations afforded corals some protection from heavy wave exposure. Free living forms such as the mushroom corals (Fungia and related genera) were not reported. Coral coverage appeared lower along the southeast facing slopes probably due to substrate instability of disturbance from moving sediment.

ATOLL GEOMORPHOLOGY AND OCEANOGRAPHY

Atolls are annular (perimeter) reefs enclosing lagoons which usually contain passes through the reefs, islets on the reef, and lagoon reef formations (MacNeil, 1969). The six remaining areas surveyed in 1988 are atolls with perimeter reefs affording protection and surrounding semi-enclosed lagoons. At least five or more small to moderate sized islets are situated on the shallow reef flats along the perimeter reefs of each atoll. All six atolls include at least one natural deep passage through the perimeter reefs, allowing sub-tidal exchange between ocean and lagoon waters. There are more islands and fewer passes on the windward side than on the leeward side. The perimeter reefs of atolls in the Marshalls are usually between 1,000 and 2,000 feet wide, with windward reefs usually slightly higher in elevation. The six atolls can be divided into two major geomorphological groups with gradients between one another along a north-south axis:

1) Small Northern Atolls. These have shallow lagoons with maximum depths of 13m or less, a very narrow single passage along the west side, and elevated (perched) water levels in the lagoon during low tide. This category includes Bok-ak and Pikaar. Tōke Atoll is intermediate between the two groups. Wake (traditional Marshallese name Enen Kio) is located further to the north of the Republic of the Marshalls, is under U.S. military jurisdiction and is more closely allied to this group. The climate is dry and prevailing trade winds are heavy. In addition, the semi-enclosed nature of the lagoons of Ebon and Namorik (Namdik) Atolls and the two semi-enclosed sublagoons of Arno Atoll, all in the southern Marshalls, show some functional resemblances to the first group.

2) Central Atolls. These have deeper, more open lagoons with maximum water depths of 49m or more, larger, deeper or more numerous passages, and lagoon tidal fluctuations more closely corresponding to those of the adjacent ocean areas. Included in this category are Roñdik, Wōtto, and Ādkup. These three atolls more closely resemble most of the other atolls in the Marshalls.

Due to Wake's proximity to Bok-ak and Pikaar, all three may have undergone a similar geological evolution. Wake has no natural passage through its reef, and the maximum depth of its lagoon is only 4m. Wake represents one extreme in the gradient between the two groups of atolls in terms of small pass development, shallowness of lagoon, and small lagoon area. At the other extreme would be the more typical atolls of the Marshalls charactered by larger and more numerous passages and lagoons, well developed perimeter reefs and islands, and passages generally concentrated along the south and west rims (Wiens, 1963).

Tōke Atoll, intermediate between the two extremes, most closely resembles nearby Utrōk Atoll, with comparable angular shape, size, moderate depth of the lagoon, and small size and position of the single deep western passage.

The Perched Lagoons of Bok-ak and Pikaar:

The raised perimeter reefs and the single narrow western passage off both Bok-ak and Pikaar atolls restrict tidal exchange between the lagoon and ocean (Fosberg et al, 1956). More water is pumped into the lagoon by wave action along the eastern (windward) reefs than exits from the lagoon through the pass and over the reefs at low tide along the western (leeward) side. This factor causes average lagoon water levels to be higher compared to those on the ocean side. Since water levels in the lagoon never get as low as the low tide levels outside the lagoon, perimeter reefs may have continued to grow upward in response to the constant washing from higher lagoon water levels.

The raised nature of the peripheral reefs, especially along the leeward rim prevents tidal exchange over the reefs except at moderate to high tide, further increasing the accumulation of water pumped in the lagoon from the windward side wave action relative to that which exits the lagoon. Coupled with the limited drainage of lagoon waters out of the narrow pass of each atoll, the "low" tide water levels in the lagoon were observed to be two - three feet higher than corresponding levels on the ocean side. Lagoon tidal amplitude is very small and is nearly completely out of phase with ocean side tidal fluctuations. During low tides on the ocean side, lagoon waters were observed to stream out of the pass, dropping up to three feet and resembling white water "rapids" over a distance of about 100m.

As a consequence, the leeward perimeter reefs of both Bok-ak and Pikaar atolls serve as natural dams and spillways, ponding lagoon waters and dampening outside tidal fluctuations. Only during the few hours of high tide do all perimeter and lagoon reef flats completely submerge, allowing free exchange of lagoon and ocean waters over the reef. At the time of highest tide (on the ocean tide) current flow out the channel reverses direction, running into the lagoon for an hour or so. Perhaps in response to less water level fluctuations in the lagoon, living corals and coralline algae grow to higher elevations, displaying prominent overhanging reef wall formations.

In contrast, the central group of atolls (Ādkup, Wōtto, and Ron̄dik) display localized oceanographic conditions more typical of the rest of the Marshalls. Wave action along windward reefs pumps water over the perimeter reefs into the lagoon during virtually all stages of the tide. Water also enters the lagoon during flooding tides through all passes and over most shallow perimeter reefs. During ebb tide, water flow out of the passes, and ebb flow over leeward reefs is likely to be strong (but not specifically observed during the 1988 study). Lagoon and ocean tidal fluctuations appear more closely synchronized and show similar amplitudes. Wave action inside the lagoons is moderately high due to the more open configuration and larger size of the lagoons for the central atolls compared to those of the small northern atolls.

BOK-AK ATOLL (Figures 5-9; A-1 through A-3)

Aelon-in Bok-ak (also called Taongi, Bokaak, or Pokak Atoll) is the Republic's most isolated atoll with the nearest reefs and islands located 150 NM to the southeast at Pikaar Atoll and 300 NM to the north at Wake Atoll (Enen kio). Also an unnamed bank at a depth of seven fathoms lies 100 NM south of Bok-ak (MacNeil, 1969). Bok-ak is unusual from several respects, not the least of which is the elevated configuration of its living lagoon reefs. The atoll is crescent shaped (Figure 5), curving to the west with reef horns extending off the northern and southern tips of the atoll reef, and is about 11 miles long from reef tip to reef tip. The 1988 team was able to spend three field days at Bok-ak allowing 20 marine sites, including five leeward ocean reef sites to be surveyed (Figure 5).

Fig 5. Bok-ak (Taongi) Atoll showing sites of marine surveys September 1988. Stars indicate reef sites of special interest. Scale: 1" = 1.970 mi.

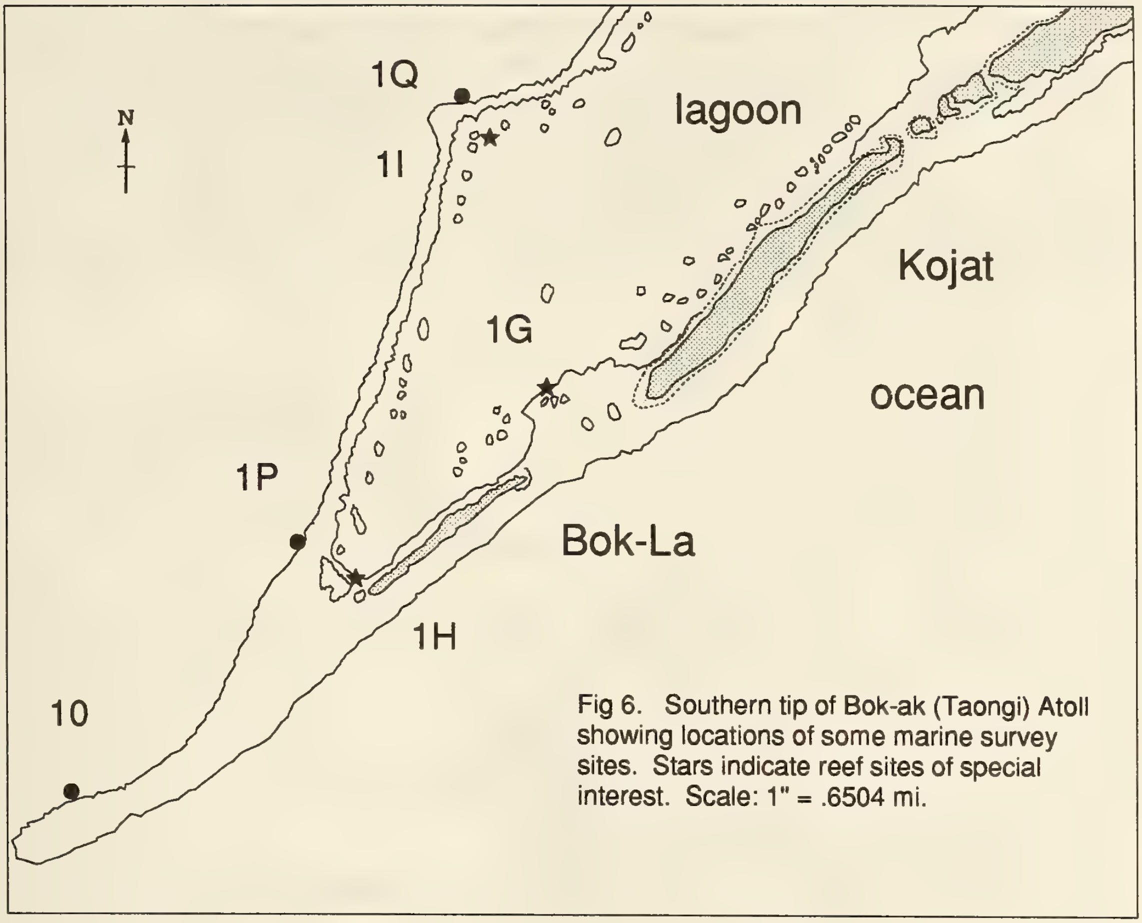


Fig 6. Southern tip of Bok-ak (Taongi) Atoll showing locations of some marine survey sites. Stars indicate reef sites of special interest. Scale: 1" = .6504 mi.

A near continuous string of islands (Figures 6, 7) extends along the SE windward reefs. The NE windward reef and the entire western (leeward) reef lacks islands. Island land area totals 1.45 square miles (3.8 km^2) for Bok-ak, the second most of any of the seven areas surveyed in 1988 after Wōtto. There is no fresh water at Bok-ak and even wells dug in the center of large islands are quite salty (Fosberg et al, 1956).

Bok-ak lies far enough north for tropical storms originating in the central Marshalls to have gained full typhoon intensity, and the atoll's islands and reefs display extensive evidence of typhoon effects (MacNeil, 1969). Boulder ramparts, beaches, and concentrations of strewn boulders are thought to have been formed during intense storms and are most concentrated on the east and SE ocean facing sides of islands at Bok-ak Atoll (MacNeil, 1969; Fosberg, 1988).

Many patch reefs throughout the lagoon are elongated into ribbon reefs with vertical or overhanging walls. The lagoon averages seven fathoms (13m) in depth with the greatest recorded depths being eight fathoms (15m), mostly in the western lagoon. The tops of many lagoon patch and ribbon reefs are awash at low tide with overhangs of profusely growing corals just below the surface. The tops of the shallowest reefs are smooth pavements of living crustose coralline algae. Over a full tidal cycle, lagoon water levels were observed to fluctuate less than one foot. At high tide all reefs and corals are flooded to depths of a few inches or more. Water levels in the lagoon never dropped below mean tide level. Sand deposits covered the floor of the lagoon while most elevated surfaces were covered with live coral. Lagoon coral communities were very healthy with only a few dead corals observed. Giant clam populations in the lagoon were huge, including the species Tridacna maxima, T. squamosa, and Hippopus hippopus. Despite an intensive search neither live or dead remains of the largest species Tridacna gigas were reported. Neither were sea turtles observed at Bok-ak. Sharks were numerous, especially black tips inside the lagoon and grey and white tip reef sharks outside the lagoon.

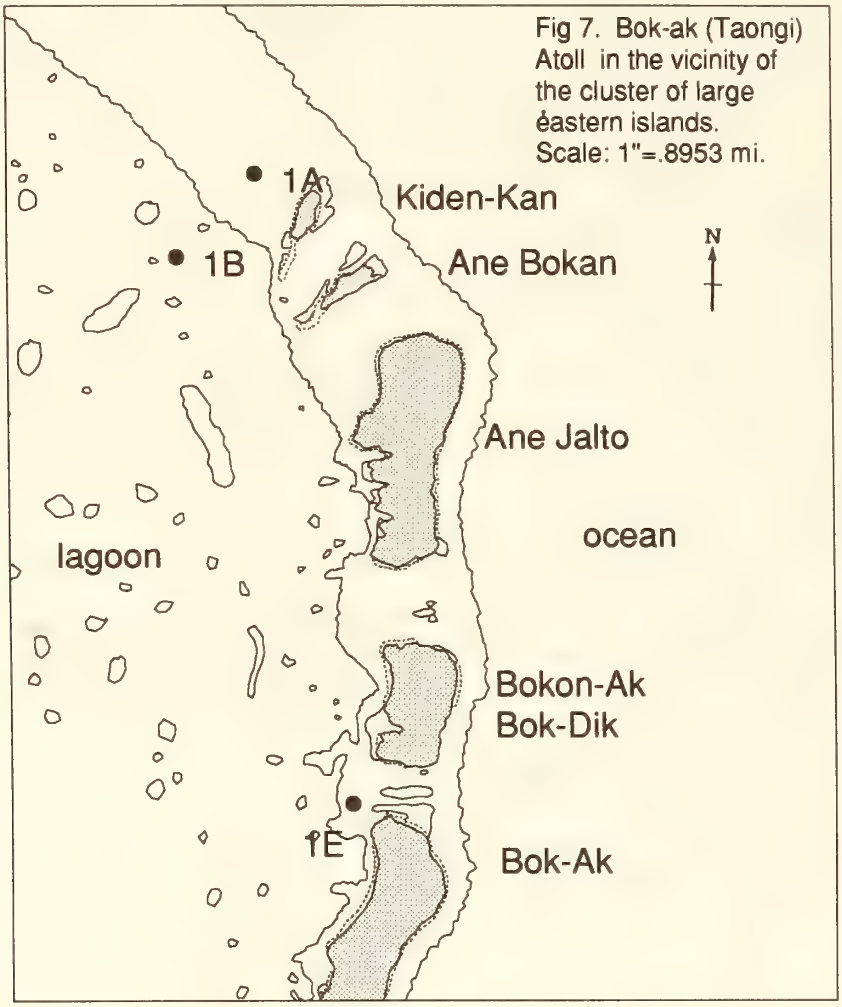


Fig 7. Bok-ak (Taongi) Atoll in the vicinity of the cluster of large eastern islands. Scale: 1"=.8953 mi.

Eastern (windward) perimeter reefs at Bok-ak are different in shape compared to those of larger more open atolls to the south in the Marshalls. Observations at an elevation of about 8m, from the deck of a recently wrecked Japanese longliner fishing vessel on the windward reef (site 1-C), revealed that spur and groove formations are well developed and typical. However, the coralline algal ridge was a wide irregular feature, rather than a more typical elevated ridge measuring only a few meters in width (see also Fosberg, 1988). The reef crest was generally flat but elevated 2 or more feet above mean low water. The back lagoon edge of the reef abruptly drops as a pronounced step 1-2m in depth. Elsewhere in the Marshalls back reef slopes towards the lagoon are generally more gentle. Lagoonward water flow over the reef was also not as swift as reported for many windward reef flats in the Marshalls. The higher observed lagoon water levels may prevent more rapid "downhill" movement of waters from the ocean side.

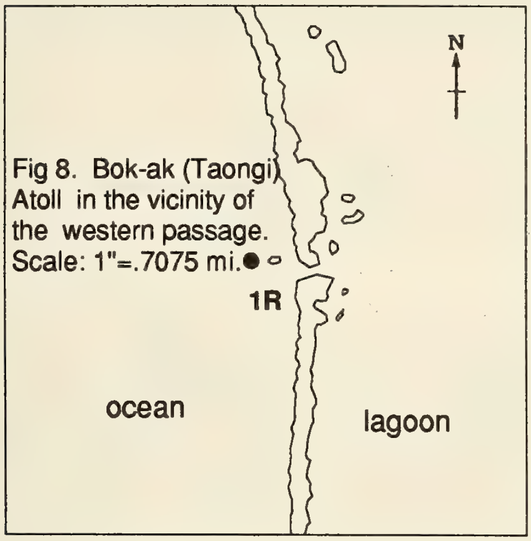


Fig 8. Bok-ak (Taongi) Atoll in the vicinity of the western passage. Scale: 1"=.7075 mi.

Leeward perimeter reefs were unusually narrow, averaging less than 100m in width (Figures 8, 9). Except for a small coralline algal ridge-like feature at the crest of the reef near its lagoon margin (see Fosberg, 1956; et al, 1988), the upper reef surface is smooth and covered with living crustose coralline algae and slopes down two to three feet from the lagoon side to the ocean side. This tiny ridge, up to 10-15 cm in height, is also reported on windward facing edges of patch reefs in the lagoon and along the lagoon shores of some islets. The living reef flat serves as a coral-algal dam and spillway, holding back higher lagoon water levels except for excess water trickling downslope to the ocean margin. Even at low tide (outside), water was seen constantly spilling over the dam and down the spillway to the ocean, with flow presumably maintained by the constant wave action pumping water into the lagoon from the windward side.

The ocean face of the leeward reefs resembled the steep slopes, reentrant/canyons, high coral cover, and diversity typically reported for such environments elsewhere in the Marshalls. Water currents were strong and turbulent off the leeward side of the southern reef extension or horn (site 1-O). Loose sediment and sand were absent from the shallow ocean reef slopes. Seven of the 20 sites surveyed at the atoll displayed exceptional or unique coral reef features (Figs. 5, 6, 9, A-1, A-2, and A-3).

One unusual feature was an ocean patch reef (site 1-S) separated from the main ocean reef slope by a deep chasm. Other exceptional sites included a windward reef flat (site 1C), lagoon patch and ribbon reefs (sites 1K, 1N, 1I, 1G and 1H).

Corals of Bok-ak Atoll

Bok-ak was one of three atolls where the most species of corals were observed during the expedition. Ninety-three species belonging to 38 genera and subgenera were reported at Bok-ak based upon surveys at the 20 field sites, including five ocean sites.

In contrast, 93 species were reported at both Tōke and Pikaar after surveys at only 13 sites which included no ocean sites at Tōke and only two ocean sites at Pikaar. Thus, despite the high number of coral species reported at Bok-ak, Tōke and Pikaar would appear to support high numbers of species, based upon equivalent sampling intensity. The condition of the coral communities of Bok-ak was healthy and flourishing at all observed lagoon and ocean reef sites. Thus a lower number of coral species does not appear to be related to environmental stress.

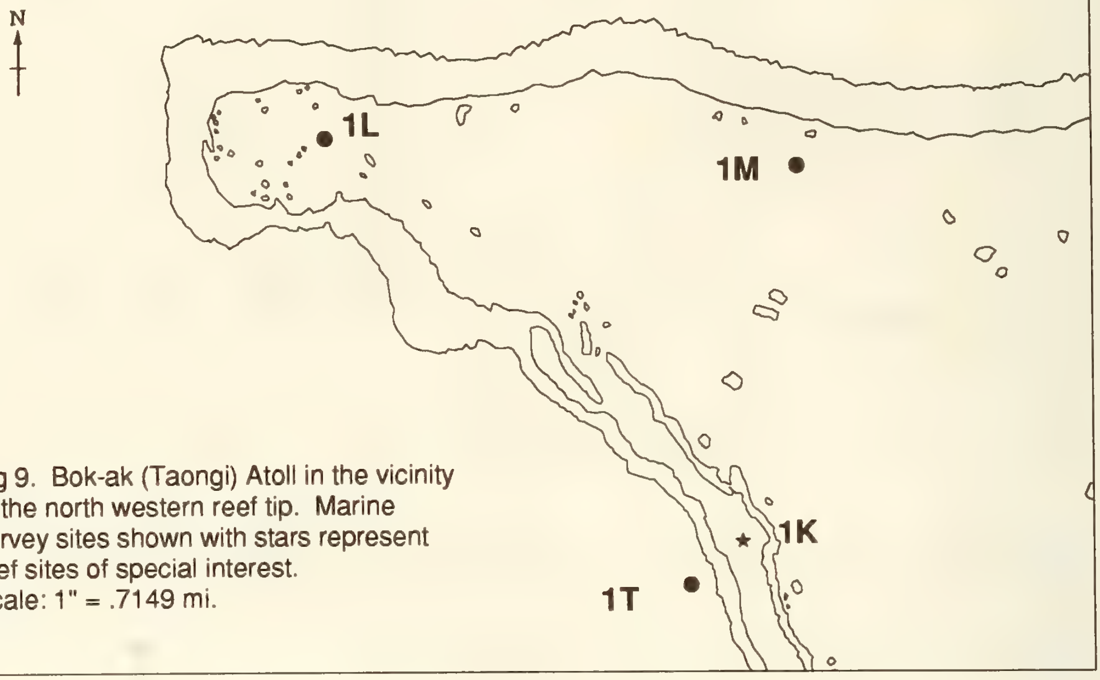


Fig 9. Bok-ak (Taongi) Atoll in the vicinity of the north western reef tip. Marine survey sites shown with stars represent reef sites of special interest.
Scale: 1" = .7149 mi.

Because of the elevated nature of the lagoon coral communities, they may be more isolated from ocean reefs due to restricted tidal exchange. Furthermore, the remote position of Bok-ak from its nearest reef neighbors may reduce the number of coral species which can successfully migrate and establish at Bok-ak. Over prolonged periods this might be reflected in fewer total species of coral that are established at Bok-ak.

Several reef genera which are common elsewhere in the Marshalls were absent from Bok-ak: Porites (Synaraea), Coscinaraea and Distichopora. Some genera were conspicuously more abundant at Bok-ak including Platygyra and to a lesser extent Anacropora. These observations lend further support to the hypothesis of geographic isolation of Bok-ak from nearby atolls.

However, coral communities at Bok-ak achieve an unprecedented level of abundance and development. Lagoon habitats were complex three dimensional coral dominated environments, with many overhangs, mounds, walls and elevated ledges. The protected shallow lagoon environment appears to promote optimal coral growth due to abundant light, transparent waters, lack of suspended sediment and only minor wave action.

Along windward perimeter reefs, the stepped back reef margins included many abundant corals: Acropora (I) palifera, other Acropora spp, Porites lobata, Cyphastrea microphthalma, Goniastrea spp, Pavona minuta, Seriatopora aculeata, Heliopora coerulea, Stylophora pistillata, encrusting Montipora spp, Pocillopora spp, Favia spp, Leptastrea purpurea, Platygyra spp, Millepora spp, and Astreopora spp.

On the slopes of lagoon pinnacles, the following corals were common: Porites cylindrica (fingercoral), Astreopora gracilis, Goniastrea pectinata, Favia pallida, Stylophora pistillata, Porites spp, Fungia fungites, Lobophyllia hemprichii, Montipora spp, Pocillopora spp, and Acropora spp, especially staghorn corals, and others.

On leeward ocean reef slopes and margins, the following corals achieved prominence: Millepora spp, Acropora digitifera, A. palifera, Porites superfusa, Montipora tuberculosa, Stylophora pistillata, Ecinopora lamellosa, Goniastrea retiformis, Favia stelligera, Turbinaria stellulata, Symphyllia spp, Favia spp, other Acropora spp (tables), Porites spp, and Cyphastrea microphthalma. Many other species were common, and the leeward ocean reef slopes displayed the highest reef coral abundance and diversity observed of any habitat at Bok-ak.

Rare Species at Bok-ak Atoll

The smaller giant clam species which were abundant in Bok-ak lagoon are considered rare species. However, there was no evidence of the rarest and largest giant clam species nor of sea turtles or coconut crabs. Bok-ak, along with Pikaar and Jemo̧ was regarded as a bird and turtle reserve by the Marshallese prior to the era of European influence (Jack Tobin pers. comm. to Ray Fosberg, in Fosberg 1988), and in the early 1960's Bok-ak was designated as a reserve by the then District Administrator of the Marshalls.

PIKAAR ATOLL (Figures 10-15, A-4 to A-5)

Aelon-in Pikaar (also called Bikar Atoll) is the Republic's second most isolated atoll with the nearest reefs and islands being Utrōk and Tōke Atolls some 80 NM (146 km) to the south and Bok-ak Atoll some 150 NM (247 km) to the north. An unnamed bank with a depth of seven fathoms lies about 50 NM (91 km) north of Pikaar Atoll. Pikaar most closely resembled Bok-ak in geomorphology but has much less land area. In fact, with only 0.19 square miles (0.49 km^2) of land, Pikaar has the least amount of land of any atoll in the Marshall Islands, and only the table reef at Jemo has less island area. Storm generated boulder ramparts and concentrations of strewn boulders occur only along the northwest shoreline of Jeliklik Island and along the lagoon face of northwestern

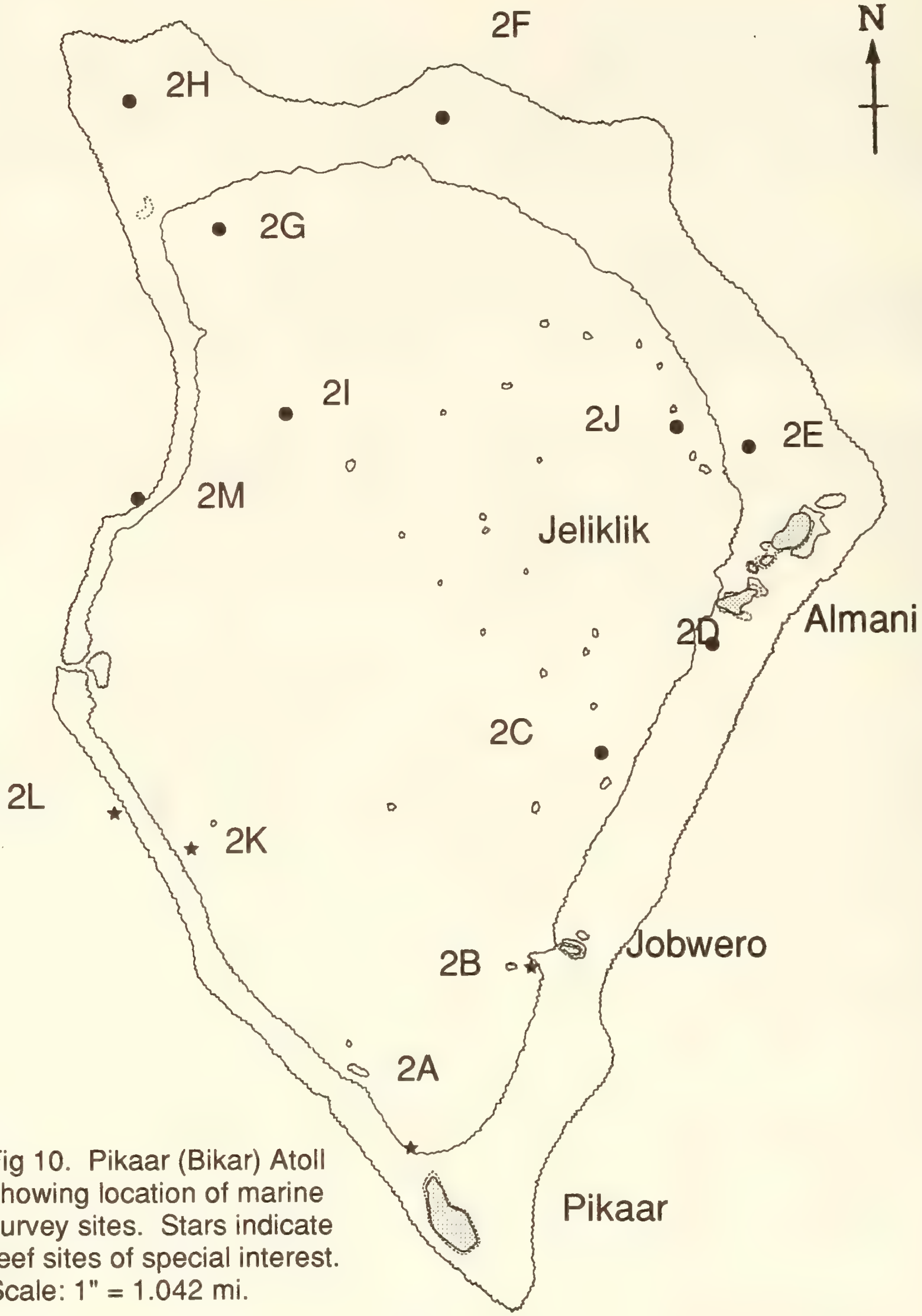


Fig 10. Pikaar (Bikar) Atoll showing location of marine survey sites. Stars indicate reef sites of special interest. Scale: 1" = 1.042 mi.

perimeter reef flats (MacNeil 1969). Although no wells have been dug, the small size of the largest islands and dryer climate argue against potable groundwater at Pikaar Atoll (Figure 10).

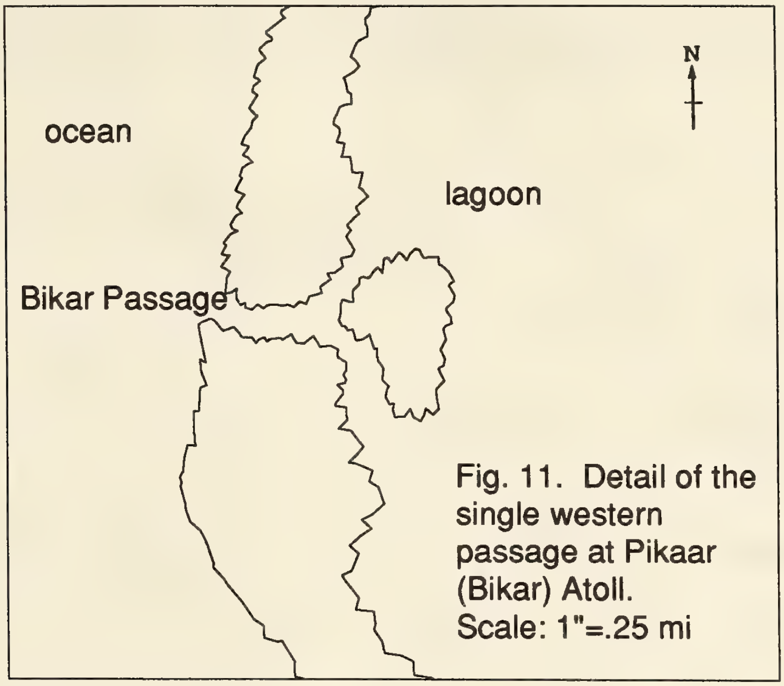


Fig. 11. Detail of the single western passage at Pikaar (Bikar) Atoll.
Scale: 1"=.25 mi

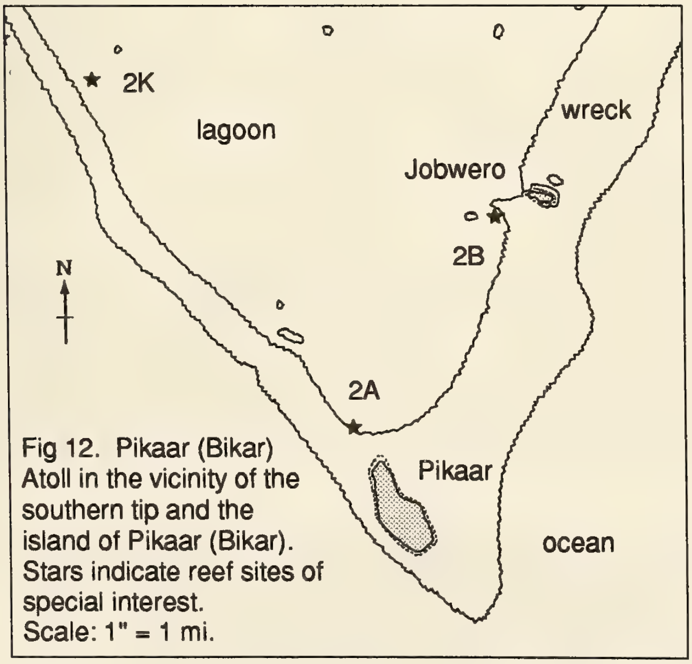


Fig 12. Pikaar (Bikar) Atoll in the vicinity of the southern tip and the island of Pikaar (Bikar). Stars indicate reef sites of special interest.
Scale: 1" = 1 mi.

The top of Pikaar's reef formations are living and elevated some two to three feet above mean low water. Its one single pass (Fig. 11) is narrow and forked to the lagoon side along the western rim of the atoll. Small boat navigation through the pass at low tide is extremely hazardous, and many reef sharks patrol its waters. Pikaar Atoll's largest island is Pikaar Island, resting on the widest section of the perimeter reef at the southern tip of the atoll (Figure 12). Remaining islands are very small or are only sand cays (Figures 13-14). Pikaar's lagoon is deeper than Bokak's, varying in depth between five and 13 fathoms (9-24m). The lagoon near the southern tip and western pass region is shallower, averaging eight fathoms (15m), but most of the lagoon floor is situated at depths between 10-11 fathoms (18-20m). As with the reefs of Bok-ak, the tops of the shallowest reefs are smooth pavements of living crustose coralline algae. Ribbon reefs fill the lagoon with the walls dominated by live coral and with pronounced overhangs near the tops of the reefs. Sand deposits cover the floor of the lagoon.

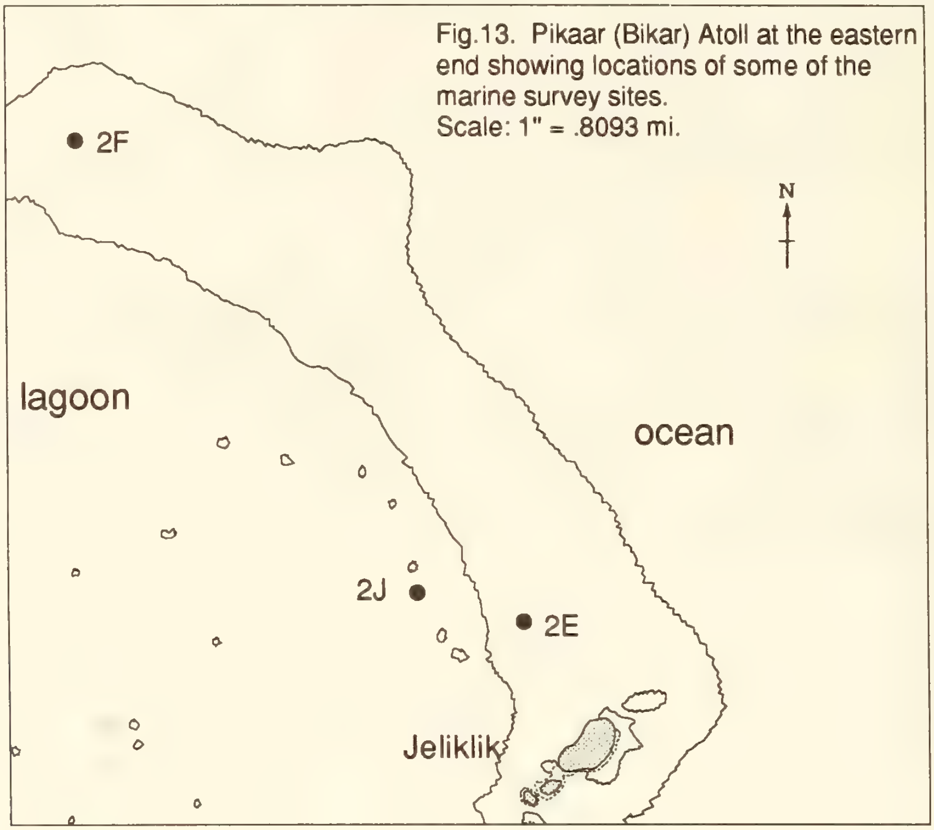


Fig.13. Pikaar (Bikar) Atoll at the eastern end showing locations of some of the marine survey sites.
Scale: 1" = .8093 mi.

Tidal characteristics at Pikaar appear to be very similar to those of Bok-ak although there was less time in the field (1-1/2 days) to observe them. At low tide, the tops of lagoon reefs are awash but rest some two to three feet higher than the margin along the ocean side of the reef at mean low water. Over a full tidal cycle lagoon water levels were observed to fluctuate less than one foot. At high tide all living reefs and corals are flooded to depths of one foot or more. Water levels in the lagoon never dropped below mean tide level.

Huge populations of giant clams (especially Tridacna maxima, T. squamosa, and Hippopus hippopus) were found throughout the lagoon, resembling those of Bok-ak. Swimming green sea turtles were observed both inside and outside the lagoon, and evidence of recent sea turtle nesting activity was evident along the sand beaches of most islands, especially Pikaar.

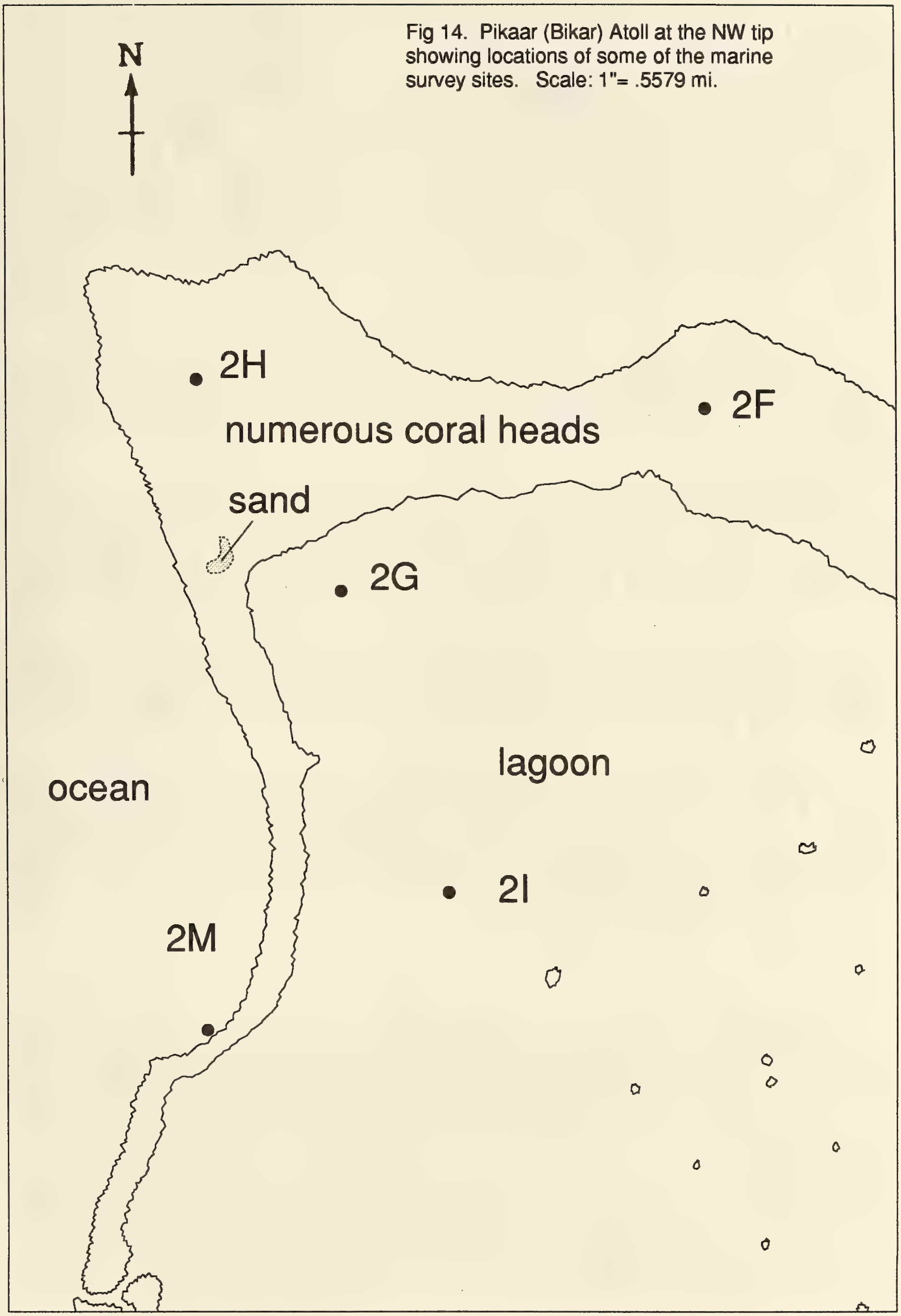


Fig 14. Pikaar (Bikar) Atoll at the NW tip showing locations of some of the marine survey sites. Scale: 1"= .5579 mi.

The windward, eastern facing perimeter reefs of Pikaar resembled those of Bok-ak in terms of form and coral species composition. The back lagoon edge of the reef flat drops down as a pronounced step one or more meters in depth. This feature shows up well in the color aerial photographs, and the stepped or double reef feature is also marked on available maps and charts. The fact that the stepped reefs were reported only from the reefs of Bok-ak and Pikaar suggests that higher average lagoon water levels may have something to do with the formation of the steps. Stepped reefs occur also along the southwest and northwest lagoon faces at perimeter reefs at Pikaar atoll. Compared to those of Bok-ak Atoll, leeward (western) perimeter reefs at Pikaar Atoll are generally wider. Only the NW section to the north of the pass region shows narrow perimeter reefs.

The perched lagoon water levels are maintained by wave action pumping water into the lagoon at a rate faster than can drain out the deep western pass at low tide. The water circulation dynamics in Pikaar's lagoon appear very similar to those of Bok-ak lagoon.

Several coral and reef habitats (sites 2A, 2B, 2C) at Pikaar displayed exceptional or unique characteristics (Figs. 10, 11, A-4, and A-5). Site 2A is a deep reef flat moat to the west of the main island (Pikaar). Site 2B is a back reef environment on the windward side, and site 2L is an ocean reef slope along the leeward side of the atoll.

Comparison between 1944-based maps/aerial photographs and 1978 color aerial photographs indicate that sandy beach habitat around Pikaar Island has increased substantially during the 34 year period (Figure 15). Hence, suitable nesting habitat for sea turtles may have increased during the interval.

Fosberg (1988) reports that Pikaar showed signs of extensive change from a typhoon between 1945 and 1952 including possible loss of some of the small islets. During our visit in 1988 there was extensive damage to the Pisonia forest on Pikaar and near total destruction of it on Jobwero and Almani islands from high winds, possibly during a recent tropical storm or typhoon.

Corals of Pikaar

Ninety-three species of corals belonging to 35 genera and subgenera were reported from the surveys of Pikaar which encompassed 13 marine sites. Of interest was the presence of the purple fan coral Distichopora on ocean reef environments at Pikaar. This species was absent from Bok-ak although a related coral, Stylaster, was common. Stylaster was absent from Pikaar, suggesting that these two different species are filling the same niches in their respective atolls, occupying similar habitats. The presence of Pectinia in Pikaar's lagoon is only the second record of this coral from the Marshall Islands. Other corals present at Pikaar but absent from nearby Bok-ak include Coscinaraea and Acanthastrea. Curiously the common corals Oulophyllia and Goniopora were absent at Pikaar although present at Bok-ak. Other "missing" corals from Pikaar

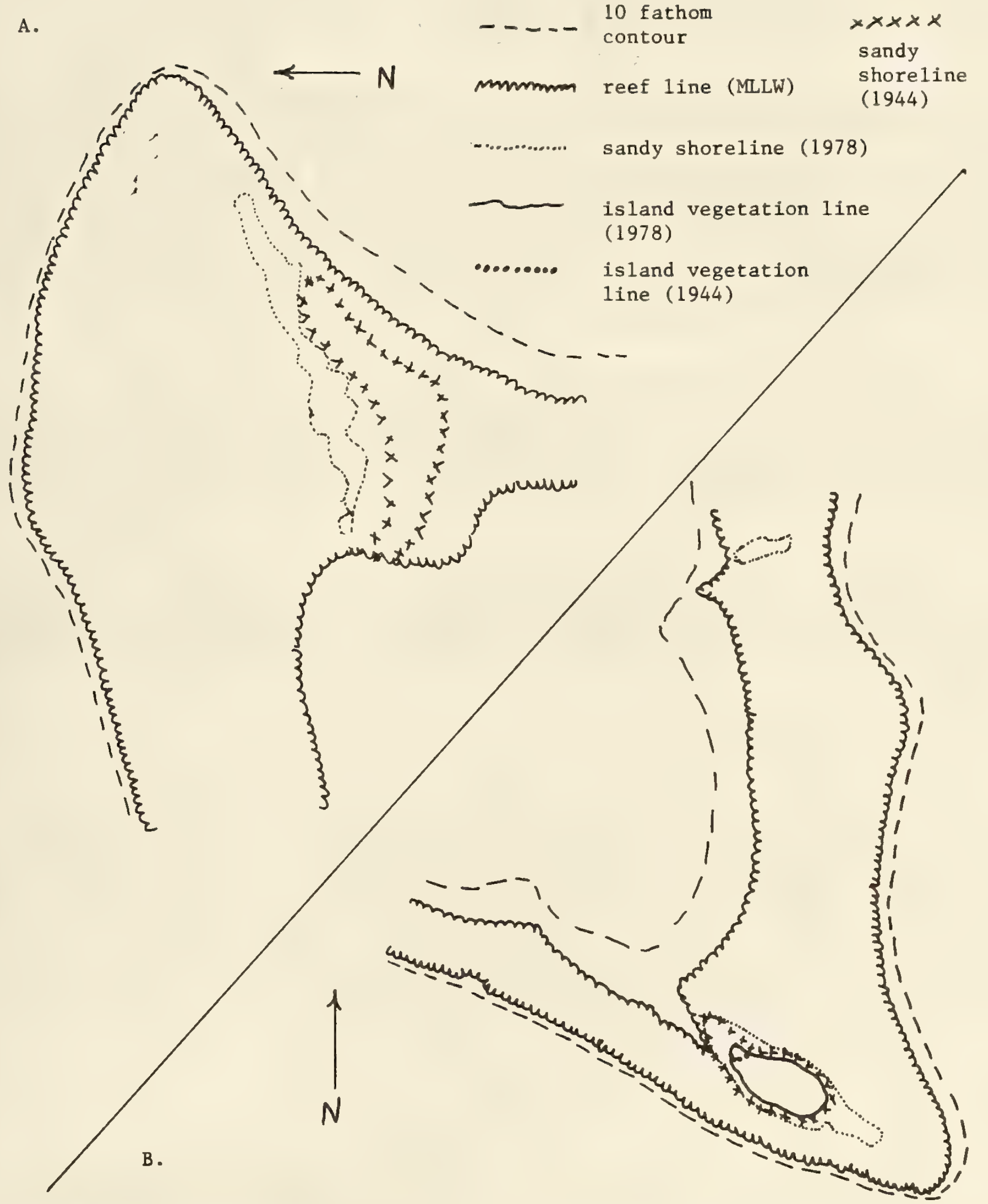


FIGURE 15. Shoreline changes between 1944 and 1978 at selected locations in the Northern Marshall Islands. A. sand cay at northeast corner of Tōke Atoll. B. Pikaar Island, southern Pikaar Atoll. Comparisons based upon U.S. Army 1944 black and white aerial photographs and E. G. & G. 1978 color aerial photographs. Scale: 1:30,000.

which are normally common reef components include Psammocora, Porites (Synaraea), Cycloseris, and Halomitra. It seems plausible that some of these and other widespread genera would have been reported from surveys conducted at more sites and in deeper water, especially along ocean facing reef slopes.

Common and abundant corals on reef flats and moat environments included the fire corals Millepora spp, the blue coral Heliopora coerulea, the corals Favia stelligera, Pocillopora spp, Pavona spp, Porites spp, Goniastrea retiformis, other Favia spp, Montipora spp, Cyphastrea spp, Astreopora spp, Leptastrea spp, Acropora spp, Seriatopora angulata, Stylophora pistillata, the soft corals Sinularia sp and Xenia sp, the free living corals Herpolitha limax and Fungia spp, the brain corals Montastrea curta and Platygyra sp, and the explanate corals Turbinaria spp and Echinopora sp.

Common and abundant corals on pinnacles and ribbon reefs included: the fingercoral Porites cylindrica, the corals Stylophora pistillata, Favia stelligera, Cyphastrea microphthalma, Acropora spp, Herpolitha limax, Millepora platyphylla, Scapophyllia cylindrica, Favites halicora, other Favia spp, Fungia spp, and Seriatopora angulata.

Common and abundant corals along ocean facing reef slopes along the leeward side of Pikaar include Pocillopora spp, Millepora spp, Acropora spp, Porites spp, Goniastrea spp, Favia spp, Montipora spp, Platygyra sp, Lobophyllia spp, Symphyllia spp, and Favites spp.

Rare Species at Pikaar

Pikaar is the most important sea turtle nesting area in the Marshall Islands. Over 264 sets of turtle nesting tracks were observed at the atoll around the perimeter of Pikaar (176), Jobwero (74), and Almani (14) islands. One set of fresh tracks was probably those of a hawksbill sea turtle while remaining tracks were of green sea turtles. One pair of green sea turtles were observed to be mating in waters offshore from Pikaar Atoll (see Thomas, 1989). Since pre-European times, the Marshallese have considered Pikaar to be a turtle and bird sanctuary (Fosberg 1988).

TŌKE ATOLL (Figures 16-21, A-6, and A-7)

At its closest point Aelon-in Tōke (also called Taka Atoll) lies only 7.3 km southwest of Utrōk (Utirik) Atoll. However, due to the position of Tōke's single deep pass along the western atoll rim, it takes about 46 km by boat to travel from the largest island of Utrōk Atoll to the largest island of Tōke Atoll (Tōke). Both atolls are roughly triangular in shape. Although Tōke has a larger lagoon area than Utrōk (94 km^2 vs. 57 km^2), the land area of Tōke is comparatively quite limited (0.57 km^2 vs 2.4 km^2). In fact, Tōke ranks only ahead of Pikaar with respect to land area for atolls in the Marshall Islands. Tōke's land area consists of five islands of which only Tōke and Allook are large enough to support permanent vegetation. One centrally located well dug at Tōke Island yielded non-potable groundwater (chlorides 440-840 ppm). Two other peripherally

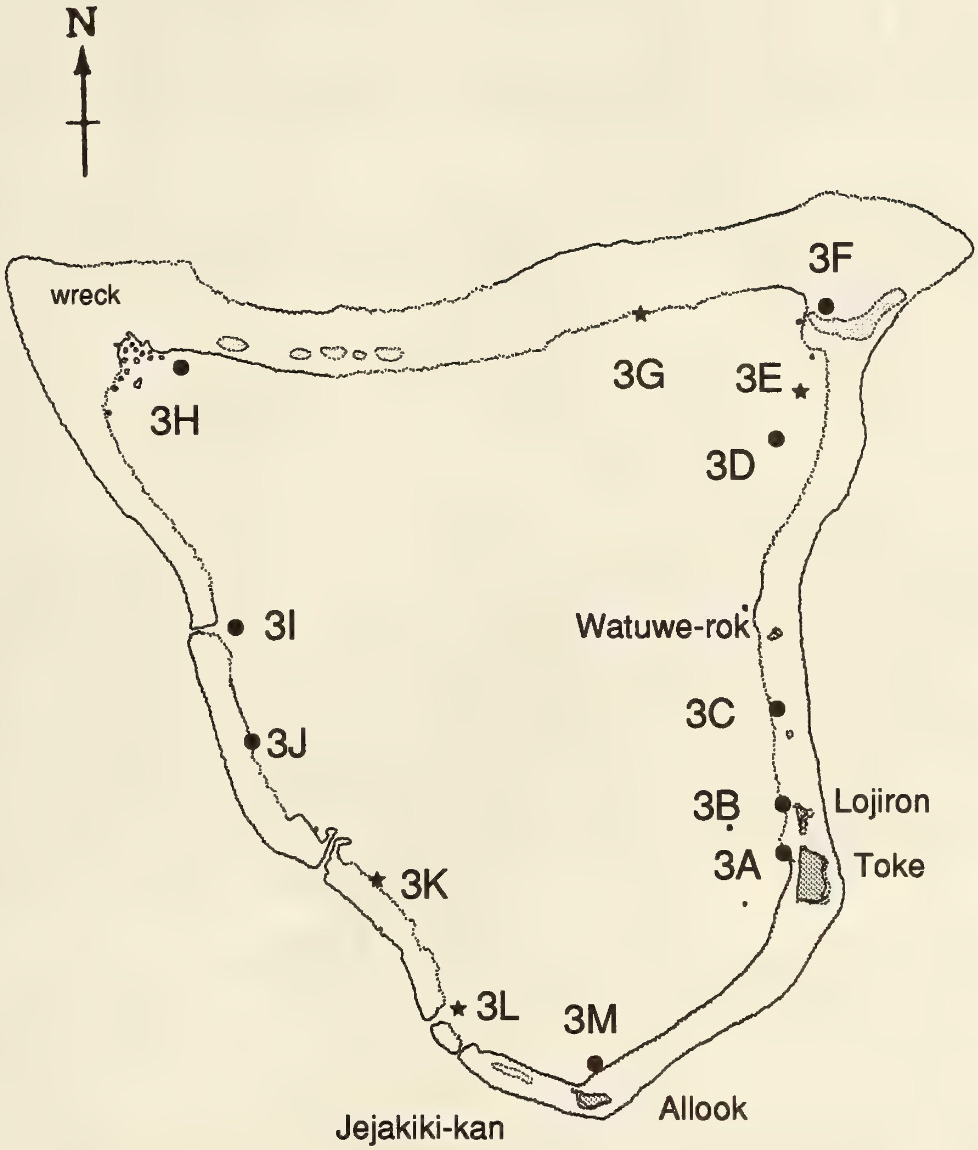


Fig 16. Toke (Taka) Atoll showing locations of marine survey sites. Stars represent reef sites of special interest. Scale: 1" = 1.970 mi.

located wells yielded very salty non-potable water (Fosberg et al 1956). Although Tōke's pass is deep and narrow, boat passage is not hazardous. Tōke's windward reefs are also afforded some protection from the upwind position of Utrōk Atoll. Storm generated boulder beaches are not well developed along Tōke Atoll's island shorelines. They are best developed along the eastern face of the southernmost island Watuwe-rok and the western (lagoon) faces of Tōke and Lojiron islands along the eastern perimeter (MacNeil, 1969). Fosberg (1988) also describes the effects of a typhoon which passed over Tōke in 1951.

Unlike the lagoons of Bok-ak and Pikaar, Tōke's lagoon is deeper (maximum reported depth of 28 fathoms or 51m) and with many soundings between 18-22 fathoms or 33-40m (Figures 16-18).

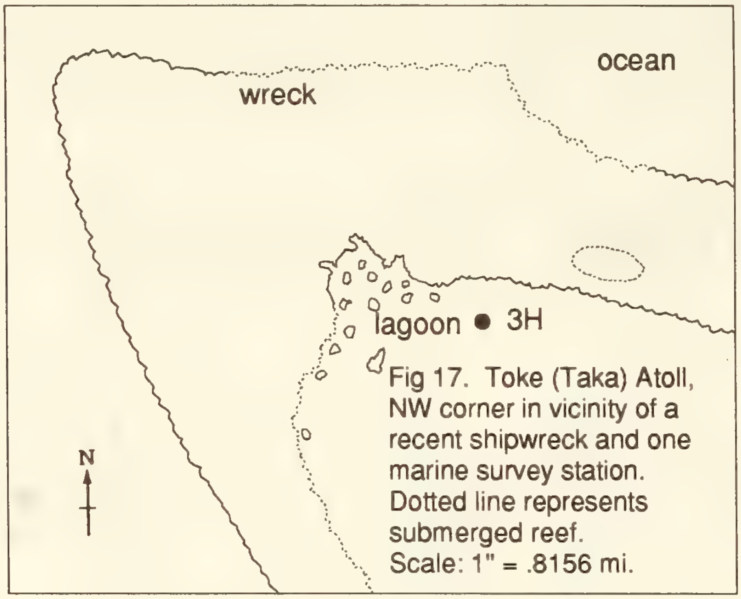


Fig 17. Toke (Taka) Atoll, NW corner in vicinity of a recent shipwreck and one marine survey station. Dotted line represents submerged reef. Scale: 1" = .8156 mi.

Tōke's lagoon has fewer pinnacles and patch reefs (less than 50 total) all of circular shape and generally concentrated in the southern half of the lagoon and near the deep western passage (Figures 16-18). Despite Utrōk's smaller size, its lagoon contains over twice as many patch and pinnacle reefs. These factors help to explain why Tōke is not permanently inhabited. Land, water, and lagoon reef resources are larger and more conveniently located on Utrōk. Fishermen from inhabited Utrōk Atoll occasionally visit Tōke to fish and to harvest shellfish and sea turtles. The land owners and managers of Tōke reside at Utrōk, but the expedition was not able to visit Utrōk because the limited field time was cut short due to an unscheduled stop at Aelon-in Kuwajleen (Kwajalein Atoll) for provisions.

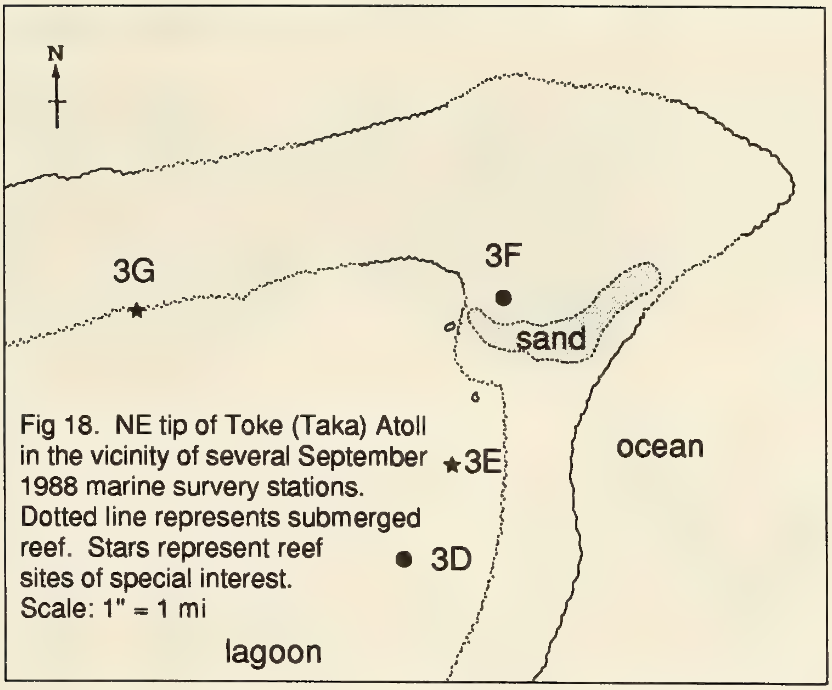


Fig 18. NE tip of Toke (Taka) Atoll in the vicinity of several September 1988 marine survery stations. Dotted line represents submerged reef. Stars represent reef sites of special interest. Scale: 1" = 1 mi

The lagoon margins of Tōke's perimeter reefs are not elevated above mean low water as is the case at Pikaar and Bok-ak atolls. Furthermore, lagoon tidal fluctuations are more closely in phase and amplitude with those on the ocean side. At the most, water levels in the lagoon at low tide were only a few inches higher than outside low tide levels. Thus, Tōke's lagoon does not have the perched or elevated lagoon reefs and water levels characterizing the other two atolls, and exchange of waters between the lagoon and ocean is more pronounced. Besides the deep passage near Tōke island with a depth of 12 fathoms (22m) and a width of over 100m (Figures 19-20), Tōke Atoll also has several other shallower passages through the western reef, three of which were visited during the 1988 surveys (sites 3I, 3J, and 3L).

Four of the 13 marine sites surveyed at Tōke displayed unique or exceptional reef characteristics. All were situated along the lagoon margins of perimeter reefs, two near the passes (sites 3K and 3L) and two in the northeast corner of the lagoon (sites 3G and 3E) where reef pinnacle and patch reef formations are slowly being buried under accumulating sand deposits washing over the reef flats from windward directions (N & E). The team was unable to visit any ocean reef slope sites at Tōke due to safety and time limitations. Observations from the ship indicate that live corals dominate the slopes of ocean facing reefs and that sharks were numerous.

One of the largest sand cays visited during the expedition occurred at the northeast corner (Figure 18) of Tōke Atoll (site 3F). Comparison between Army maps based upon 1944 aerial photographs and 1978 color aerial photographs reveal the shape and position of the sand cay has changed drastically. During the 34-year interval, the deposit elongated and shifted 200m to the north. Our sea level observations in 1988 could not determine whether additional changes had occurred since 1978. The instability of the deposit and low elevation may explain the lack of vegetation on the sand cay.

Corals of Tōke Atoll

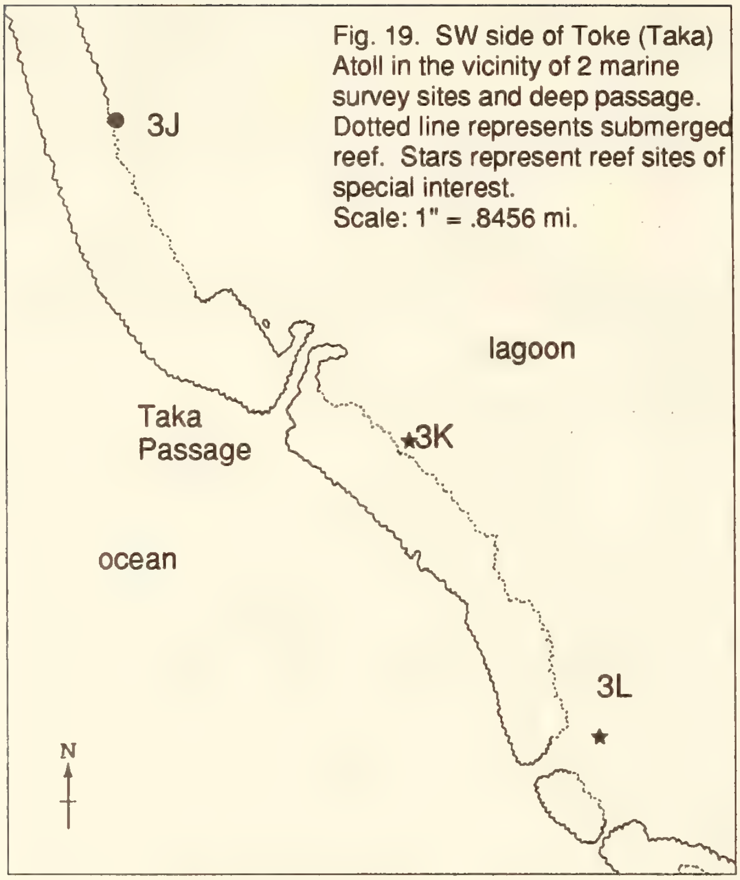


Fig. 19. SW side of Toke (Taka) Atoll in the vicinity of 2 marine survey sites and deep passage. Dotted line represents submerged reef. Stars represent reef sites of special interest.
Scale: 1" = .8456 mi.

Ninety-three species of corals belonging to 35 genera and subgenera were reported collectively from the 13 marine sites at Tōke Atoll. Of interest was the presence of <u>Porites</u> (<u>Synaraea</u>) and <u>Sandalolitha</u> which were absent from both Pikaar and Bok-ak. The reported absence of several common reef genera from Tōke may be attributed to the lack of observations along ocean facing reef slopes where different and more diverse coral assemblages are expected. As a result, the species diversity of corals at Tōke might be higher than observed at Pikaar and Bok-ak. The number of species reported per site was also relatively high at Tōke, and coral communities were well developed and diverse.

In back reef environments along windward (eastern) reefs, the following corals were abundant or common: <u>Acropora</u> spp, <u>Cyphastrea microphthalma</u>, <u>Pavona varians</u>, <u>Montastrea curta</u>, <u>Tubipora musica</u>, <u>Favia</u> spp, <u>Platygyra daedalea</u>, <u>Fungia</u> spp, <u>Astreopora</u> spp, <u>Montipora</u> spp, <u>Favites abdita</u>, <u>Pocillopora verrucosa</u>, <u>Sinularia</u> sp, <u>Porites</u> spp, <u>Millepora</u> spp, <u>Echinopora lamellosa</u>, <u>Turbinaria stellulata</u>, <u>Goniastrea</u> spp, <u>Heliopora coerulea</u>, <u>Stylophora pistillata</u>, <u>Psammocora profundacella</u>, and <u>Leptastrea purpurea</u>.

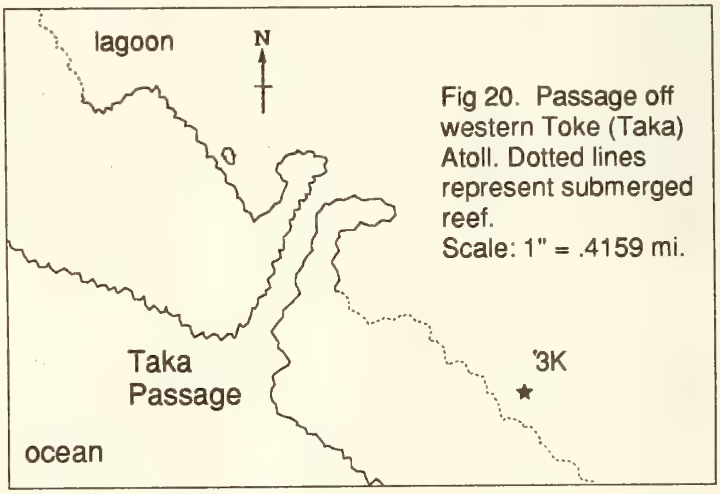


Fig 20. Passage off western Toke (Taka) Atoll. Dotted lines represent submerged reef.
Scale: 1" = .4159 mi.

Further offshore on shallow pinnacles and on the slopes of larger patch reefs the following corals were common or abundant: Porites spp (both fingercoral and massive forms), Pocillopora spp, Acropora spp, Montipora spp, Fungia spp, Goniopora lobata, Astreopora spp, Pavona spp, Tubipora musica, Coscinaraea columna, Oulophyllia crispa, Leptastrea purpurea, Seriatopora spp, Lobophyllia hemprichii, Millepora platyphylla, Stylophora pistillata, Stylocoeniella armata, Goniastrea spp, Cyphastrea microphthalma, Favia spp, Porites (Synaraea) rus, Montastrea curta, Psammocora profundacella, Echinopora lamellosa, Herpolitha limax, Leptoseris mycetoseroides, Heliopora coerulea, Scapophyllia cylindrica, Turbinaria stellulata and Favites russelli.

Rare Marine Species

Evidence of green sea turtle nesting activity was observed along the shorelines of Tōke Island (16 sets of tracks), Lojiron Island (4 sets of tracks), and Allook Island (4 sets of tracks) (Figure 21). Of the seven areas visited Tōke Atoll ranks fourth behind Pikaar, Jemo̦, and Ādkup with respect to the level of sea turtle nesting evidence. The only sighting of a Hawksbill sea turtle during the expedition was off the NE sand cay at Tōke (site 3F). It was observed to be feeding and swimming at a depth of 2-3m off the bottom.

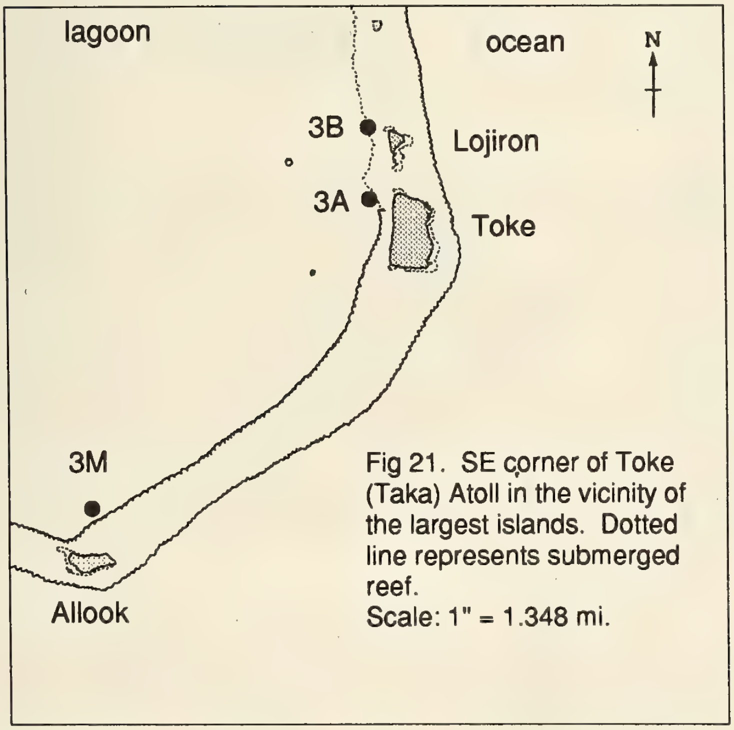


Fig 21. SE corner of Toke (Taka) Atoll in the vicinity of the largest islands. Dotted line represents submerged reef.
Scale: 1" = 1.348 mi.

Tōke Atoll was the first in which live specimens of the rare giant clam, Tridacna gigas were observed, primarily in shallow lagoon environments near islands or back reefs. However, there were many more dead shells of the species observed on the reefs (only 5 of 24 were alive). Live individuals of the smaller species were present but in smaller numbers than reported for Pikaar and Bok-ak. It was reported by islanders from Mājro (Majuro) and Wōtto that overseas fishermen illegally poach live individuals of T. gigas to obtain the abductor muscles which fetch high prices in Asian markets. Evidence obtained during our surveys suggest that uninhabited Tōke Atoll may be an inviting target for illegal poaching of the rare giant clam Tridacna gigas. Interviews with the residents of Utrōk might shed additional light on the extent of traditional harvesting and illegal poaching of giant clams at Tōke Atoll.

WŌTTO ATOLL (Figures 22-25, A-9, and A-10)

Originally, uninhabited Ailinginae Atoll was to be visited during the expedition. However, the failure to obtain approval to visit the atoll, and a subsequent invitation extended by the leaders of Wōtto Atoll, led the expedition to visit Wōtto instead of Ailinginae on 18-19 September 1988. Aelon-in Wōtto (also referred to as Wotho Atoll) is the only inhabited atoll surveyed during the 1988 expedition, and is only one of two atolls visited within the Ralik (western or "sunset") chain of the Marshalls. Wōtto is relatively small in terms of lagoon area and is located within the dryer belt of the RMI. However, land area is greater (4.2 km^2), the most of any of the seven areas visited during the 1988 expedition (Figures 22-23). Of the 22 inhabited atolls in the Marshalls though, Wōtto ranks only ahead of Utrōk (Utirik) and Namdik (Namorik) in terms of land area.

Its population is about 100, the smallest of any inhabited atoll, and ranks ahead of only Jabat and Lib which are inhabited table reefs. Of the 18 islands at Wōtto, only the largest (Wōtto) is occupied (Figure 24). The atoll, including its islands, reefs, and village setting, is very scenic, relatively undisturbed, and harbors considerable natural and cultural diversity. Apparently, large land areas were never cleared and planted to coconuts (Fosberg et al, 1956). The nearest atolls to Wōtto are Kuwajleen (Kwajalein) to the southeast; Ujae to the south; Bikini to the north; and Ailinginae, Roñlap (Rongelap), and Roñdik (Rongerik) to the northeast. Due to the clustering of several large atolls in the vicinity of Wōtto, only the atoll's southwest quadrant is considered vulnerable or exposed to heavy open ocean seas.

Wōtto Atoll is roughly triangular in shape with the widest reefs and the largest islands situated at the apexes. Wōtto Island, the atoll's largest, is at the NE tip of the atoll. The longest axis is the southwest facing side of the atoll, some 20 km between Majur-wor Island at the NW tip and Kapen Island (Figure 25) at the south. Most of the SW facing axis consists of several wide but shallow passages between smaller clusters of shallow reefs. The main navigational passage occurs just north of Pik-en Island near the northwest end of the axis. The three islets along the SW axis, Pik-en, Anbwil-en, and Ane-aidik are very small. The rest of Wōtto Atolls perimeter reefs along the N and E facing axes are shallow and contain numerous islands and cays. The largest sand dune reported by MacNeil (1969) in the northern Marshalls occurred along the lagoon side of Ane-aidik Island, Wōtto Atoll.

The three largest islands also display large boulder beaches and concentrations of strewn boulders most likely tossed up on the reefs during storms. The boulder beaches face seaward to the north on the two large northern islands (Majur-wor and Wōtto) and face seaward to the south off the southern islands of Kapen and Ane-jaito. A small boulder beach also occurs on the north side of Kapen Island.

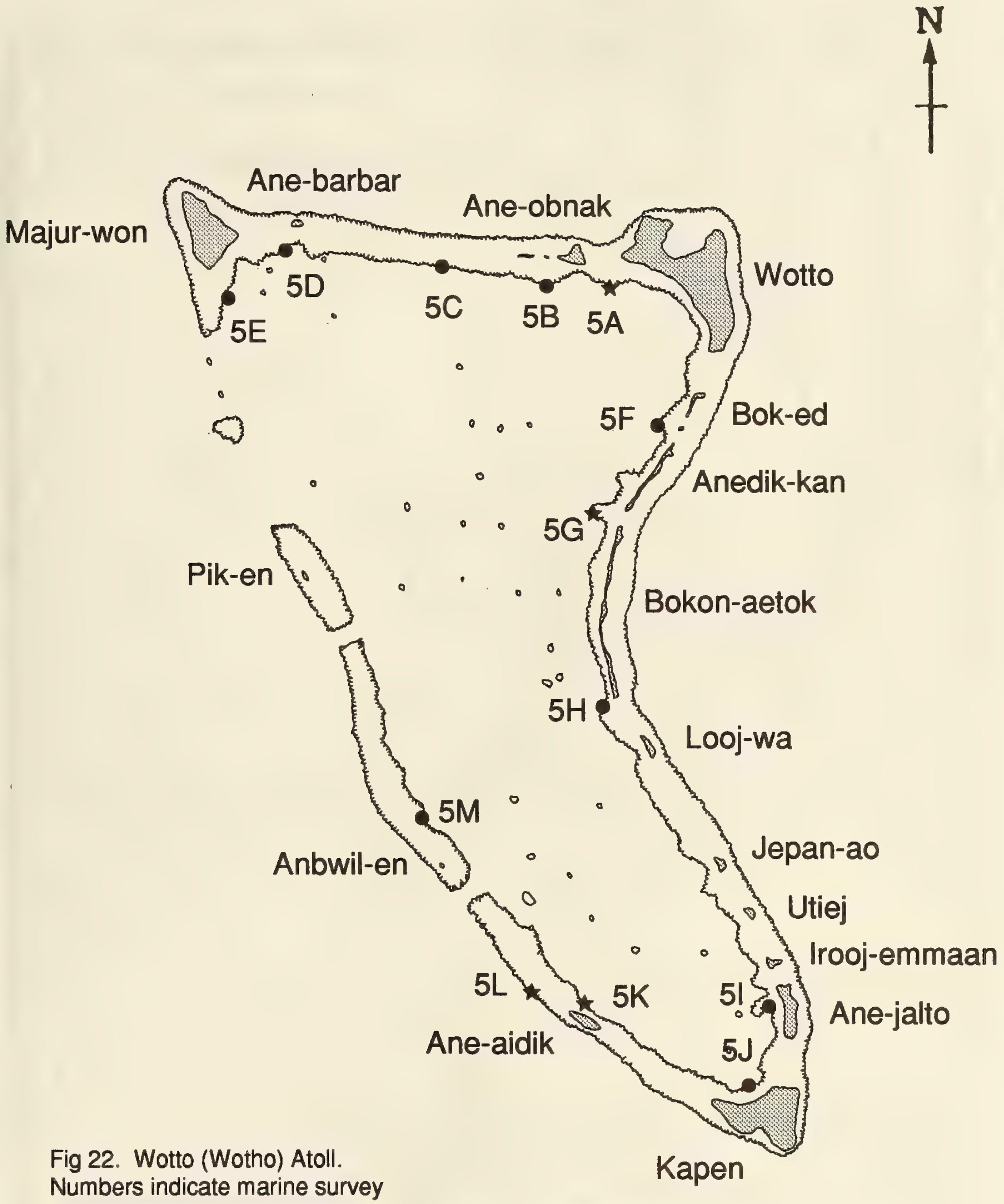
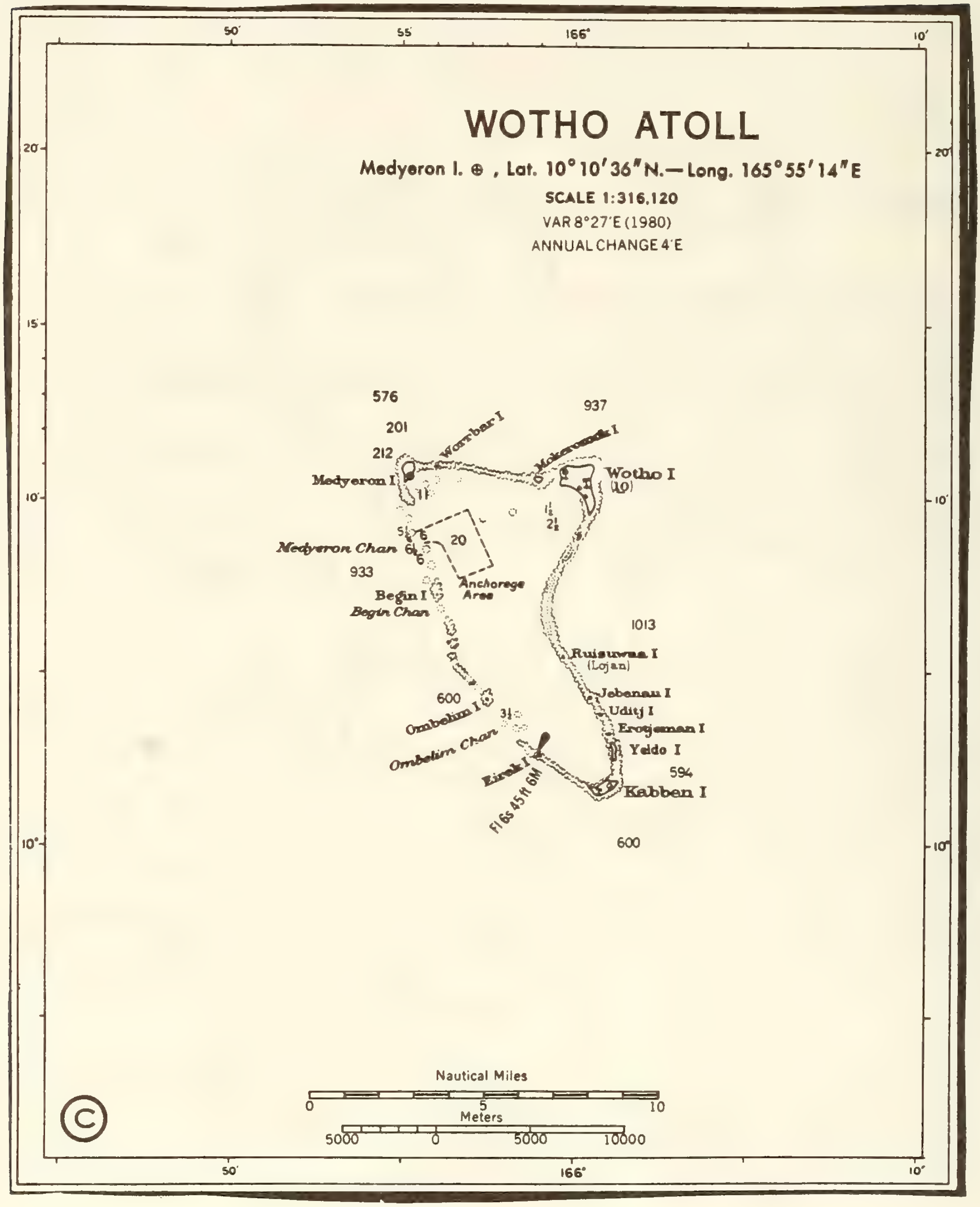


Fig 22. Wotto (Wotho) Atoll.
Numbers indicate marine survey
sites. Stars show reef sites
of special interest.
Scale: 1" = 2.058 mi.

Figure 23 . Defense Mapping Agency Chart of Wotto (Wotho) Atoll. Scale 1:316,120. Soundings in fathoms.



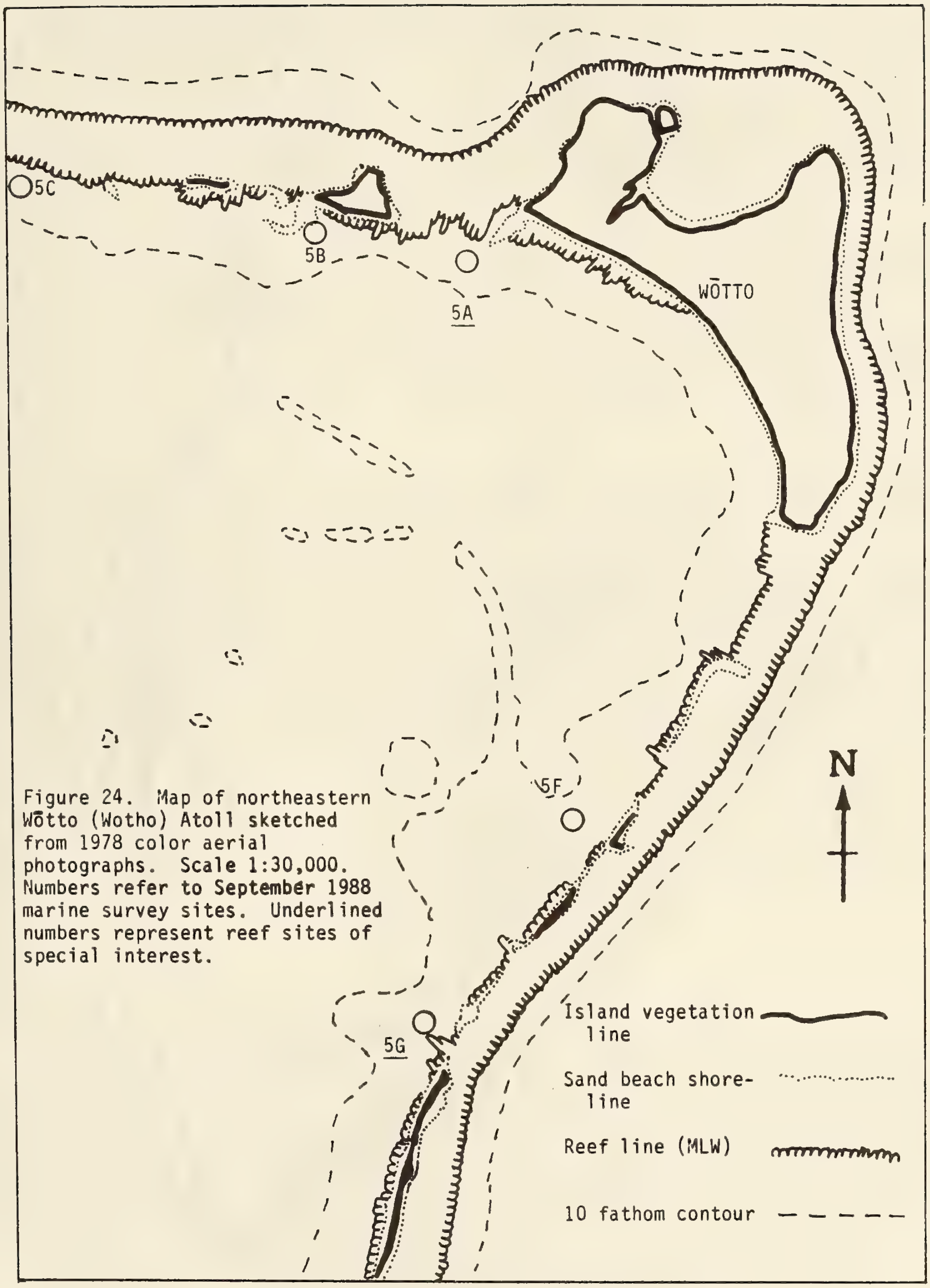


Figure 24. Map of northeastern W̄otto (Wotho) Atoll sketched from 1978 color aerial photographs. Scale 1:30,000. Numbers refer to September 1988 marine survey sites. Underlined numbers represent reef sites of special interest.

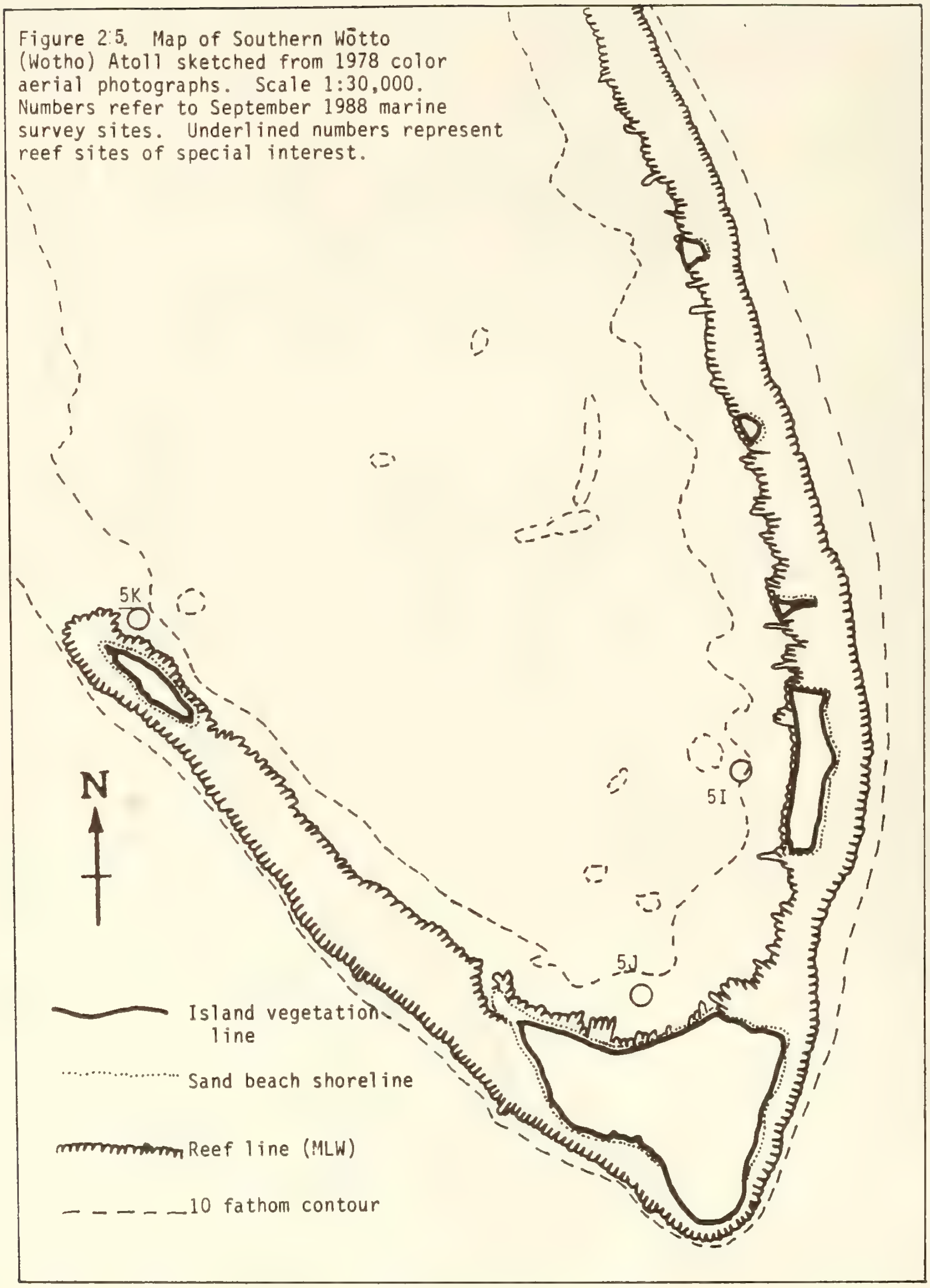


Figure 2.5. Map of Southern Wōtto (Wotho) Atoll sketched from 1978 color aerial photographs. Scale 1:30,000. Numbers refer to September 1988 marine survey sites. Underlined numbers represent reef sites of special interest.

Patch reefs are not numerous in Wōtto's lagoon and consist of three small clusters. One cluster off Kapen island in the south lagoon includes five reefs. A second cluster of seven reefs occurs in the south central lagoon east of Anbwil-en Island. The third and largest cluster of 10 reefs in the north central lagoon occurs east of Pik-en Island. Our limited time at Wōtto did not permit field visits to patch reefs in the deeper lagoon.

There is very little easily available information about the depths and bathymetry of Wōtto's lagoon. The only published soundings (Figure 22-23) show depths of at least 20 fathoms (37m) in the lagoon anchorage east of the main navigation channel which shows a depth of 6 to 6-1/2 fathoms (11-12m). The channel south of Anbwil-en Island shows a depth of 3-1/2 fathoms (6.4m). Some lagoon areas closest to Wōtto Island may be shallow, with published depths of 1-1/2 to 2-1/2 fathoms(3-4.6m). Inspection of 1978 color aerial photographs of Wōtto indicate that most of the lagoon appears deep and in excess of 10 fathoms (18m) and probably close to 20 fathoms (37m) or more. Thirteen field sites were visited at Wōtto, all along perimeter reefs (Figure 22). Only site 5L was on the ocean side of the reef.

Limited time did not permit more than cursory observations of water current and circulation patterns at Wōtto Atoll. During late afternoon fieldwork on 19 September 1988 on the shallow pass area between Ane-aidik and Anbwil-en islands (site 5L), a strong 2 kt current coinciding with rising tide was flowing north through the channel and into the lagoon. The depth of the top of reef varied from 2-3m. Wōtto's lagoon appears to be well flushed, based upon an analysis of the configuration of Wōtto's reefs and the presence of wave action along the ocean sides of the north and eastern reefs. The wave action continually pumps fresh ocean waters into the lagoon from the windward (NE) sides during essentially all stages of the tide. This cooler water probably sinks to the bottom of the lagoon displacing less dense water which exits the lagoon over the western reef during ebbing tides. As noted during our limited field observations flood tide currents are strong and ebb tide currents are expected to be strong if not stronger. Although the western passes are shallow, their great width enhances the exchange of lagoon and ocean waters during tidal fluctuations.

Corals of Wōtto

A total of 88 species belonging to 36 genera and subgenera were reported from Wōtto based upon surveys at 13 sites. However, time was very limited at several stations where observations were hampered by low light conditions during a cloudy late afternoon. In general, coral communities were diverse and in good health. Genera reported at Wōtto which were not observed elsewhere during the expedition were Cycloseris, Halomitra, and Polyphyllia, all being free living mushroom corals. The last (Polyphyllia) is a new generic record from the Marshall Islands. A few common coral genera should have been reported but were not and include: Psammocora, Lobophyllia, Hydnophora, and Echinopora. More extensive surveys on ocean facing reefs might have yielded some of these genera as well as others.

Four of the 13 stations surveyed displayed unique or exceptional characteristics worthy of some mention. Three of these were lagoon reef slope habitats (sites 5A, 5G, and 5K) and all supported live individuals of the rare giant clam Tridacna gigas. Three of the sites (except 5G) had high live coral coverage of 60% or more. The single ocean facing reef slope site surveyed showed spectacular relief and well developed coral communities (site 5C), but numerous sharks and strong currents hampered the collection of additional information. The slope was characterized by a series of large coral canyons with flat scoured floors.

Abundant and common corals on the ocean reef slope site were Millepora platyphylla, corymbose and table coral species of Acropora, Pocillopora spp, Turbinaria stellulata, Porites lobata, Montipora spp, Stylohora pistillata, Platygyra pini, Favia spp, Favites spp, Pavona minuta, Acropora palifera and Pavona spp.

Corals on a deep pinnacle along the western perimeter reef (site 5M) included Acropora spp, Millepora spp, Stylophora pistillata, Pavona minuta, Pocillopora meandrina and Montipora aequituberculata.

Abundant and common corals along the sheltered lagoon slopes (sites 5A-5K) of perimeter reefs included: Seriatopora hystrix, Acropora (many species), Astreopora spp, Stylophora pistillata, Millepora exaesa, Fungia spp, Porites spp, Montipora spp, Oulophyllia crispa, Goniastrea retiformis, Pavona spp, Pocillopora spp, Scapophyllia cylindrica, Acropora palifera, the blue coral Heliopora coerulea, Favia spp, Platygyra spp, Porites (Synaraea) rus, Coscinaraea columna, Herpolitha limax, and Cyphastrea sp.

Rare Marine Species

Giant clams of several species were reported from Wōtto including the most living specimens (15) of the largest and rarest species, Tridacna gigas. Some individuals were very large, and Wōtto was the only area where living specimens approached the numbers of dead shells of the largest species (15 vs. 16). Interviews with the islanders revealed the Taiwanese fishermen visited Wōtto "about six or eight years ago" to seek permission to harvest T. gigas. After it was granted, the fishermen proceeded to harvest many clams but taking only the abductor muscle and leaving the dead shells and remaining tissue "to rot in the sun." This experience seemed to have shocked the islanders and made them more conscious of the need to protect remaining giant clams. No doubt the presence of the islanders discourages further harvesting. Despite recording the highest number of living Tridacna gigas at Wōtto Atoll, it is important to note that the ratio of dead to live clams is still relatively high despite a hiatus on harvesting the species over a period of six to eight years. This fact points to the vulnerability of such a population to overexploitation, even from occasional or one-time harvests (Thomas 1989).

The smaller giant clam species are preferred by the islanders for consumption; for one, they are easier to collect and shuck. Although all common species of giant clams were observed on Wōtto's reefs, the smaller species seemed less numerous than reported at Pikaar, Bok-ak, and perhaps Tōke.

Green turtles nest at Wōtto but only in low numbers. The most pairs of tracks (4) were spotted on the beaches of Pik-en, (Figure 22), with two pairs of tracks observed at Long Island (Bokon-aetok) and two pairs at Kapen Island (Figure 25). During the night of 18 September 1988, the ship's crew captured a female Green sea turtle after it had laid its eggs on Long Island, and gave it to the villagers. The Wōtto islanders harvest the turtles only infrequently for special or ceremonial occasions, usually during the summer months off the beaches of uninhabited islands. The villagers seem very conscious of the vulnerability of the nesting turtle population and limit their harvesting practices accordingly (Thomas, 1989).

Coconut crabs are heavily harvested by the islanders, primarily at Kapen Island, and approximately 500 crabs per year are captured and consumed locally. The average size of the crabs during our visit was about 0.5 kg, somewhat smaller than those observed at Roñdik. Harvesting pressure on coconut crabs at Wōtto could be higher except that a fuel shortage during most of 1988 prevented small boat travel and access to outer islands including Kapen.

ROÑDIK ATOLL (Figures 26-30, A-11 and A-12)

Aelon-in Roñdik (previously referred to as Rongerik Atoll) is moderately sized and is located just east of Roñlap (Rongelap) and Ailinginae, northeast of Wōtto, north of Kuwajleen (Kwajalein), west of Tōke and Utrōk, and northwest of Jemo̧ and Likiep. It is generally afforded some protection from storms and large waves by the positions of these atolls. However, Roñdik is exposed to open sea conditions from the north. Roñdik is roughly circular in outline, has the second largest lagoon area (145 km^2) and the third largest land area (0.81 sq. mil) of the six atolls and one table reef visited in September 1988. All but one (Bok) of its 17 islands are located along the eastern perimeter of the atoll (Figure 26).

Roñdik's lagoon is very open with major gaps in the perimeter reefs along the northwest and west sectors. The navigation chart of Roñdik shows several major navigable passes: Jeteptep and an unnamed passage to the north, Bok Passage to the west, and Enewetak Pass (Āne-wetak) to the south (Figures 27-28). Bok Passage is over three miles wide, and together with the lack of islands and shallow reefs along the west rim, renders the lagoon and lagoon shorelines of islands facing to the southwest exposed to heavy wave action.

Fig 26. Rondik (Rongerik) Atoll showing locations of marine survey sites. Stars represent reef sites of special interest. Scale: 1" = 2.335 mi.

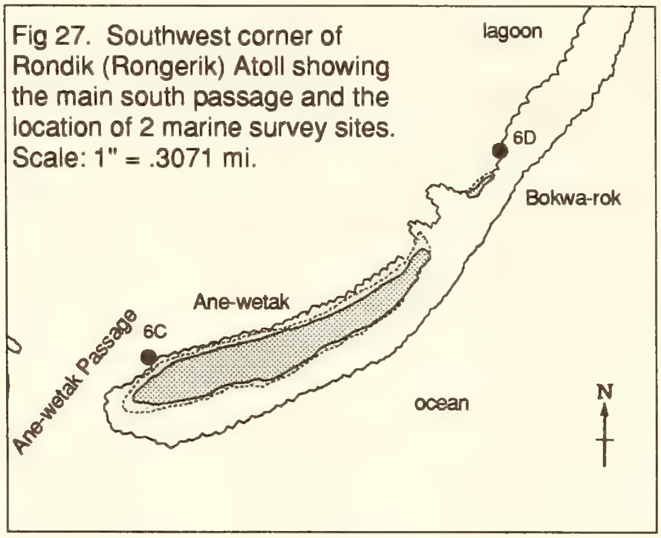


Fig 27. Southwest corner of Rondik (Rongerik) Atoll showing the main south passage and the location of 2 marine survey sites. Scale: 1" = .3071 mi.

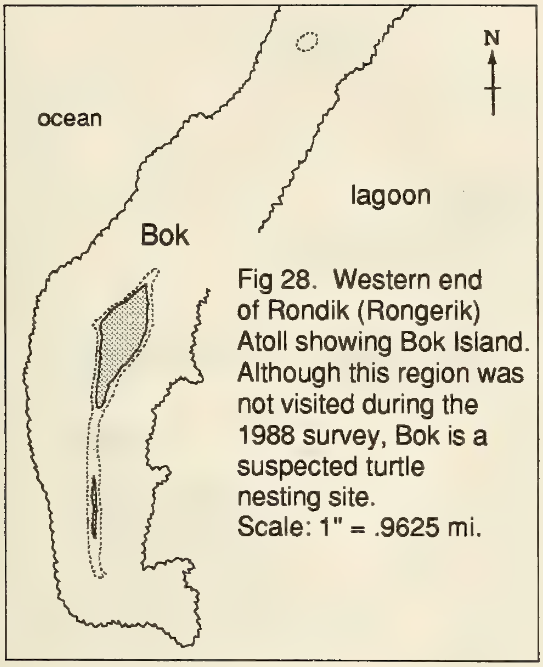


Fig 28. Western end of Rondik (Rongerik) Atoll showing Bok Island. Although this region was not visited during the 1988 survey, Bok is a suspected turtle nesting site.
Scale: 1" = .9625 mi.

It is interesting to note that the shorelines of several islands and sand cays along the northeast rim of the atoll have undergone considerable change between 1944 and 1978 comparing earlier and later sets of aerial photographs. The island of Roñdik shows minor accretion of the beach and vegetation along the SW facing lagoon shoreline. However, the W tip of Roñdik, the lagoon shorelines of two large islands (Patpat and Pikonaden), and several sand cays between the islands have undergone beach erosion and some receding of the vegetation line, especially along W and SW facing shorelines. Perhaps large waves or storms traversing the lagoon from the exposed W and SW directions were responsible for these shoreline modifications. Elsewhere on the atoll, beach and vegetation lines along the shorelines of islands have remained unchanged. The lagoon side of Āne-wetak Island has an unusually high sand dune (Fosberg, et al, 1956). According to Fosberg (1988) the island was also much disturbed by construction of a radio station involving bulldozing a strip across the center and a road along the length of the seaward coast prior to 1956 (Figure 28).

Roñdik's lagoon is fairly deep (maximum reported sounding of 28 fathoms or 51m) with many pinnacles and patch reefs which breach the sea surface. Most shallow lagoon reefs are patch reefs, circular or eliptical in shape and located in the eastern and central lagoon. Primarily deeper lagoon pinnacles are found in the western lagoon and are not as numerous or spatially dense. No soundings or bathymetric data are presented for the north and southwest extremities of the lagoon.

The survey of Roñdik was cut short due to a sudden medical emergency and the need to transport a sick seaman to the nearest hospital on Epja (Ebeye) island at Kuwajleen (Kwajalein) Atoll. As a consequence, the western half of the atoll was not surveyed including Bok (Bock) island and the extensive reef and lagoon areas to the NW and SW of it. Small boat travel in the open lagoon was more turbulent the further away from the upwind (NE) reefs, and most of the 12 marine survey sites were within the lagoon shelter of the NE perimeter reef between Āne-wetak (Eniwetak) and Jeteptep islands.

Six of the 12 marine survey sites demonstrated unique or exceptional natural characteristics worthy of mention (sites 6F, 6G, 6I, 6J, 6K, and 6A) and of possible conservation importance (Figure 30). Site 6A was a shallow downwind lagoon reef

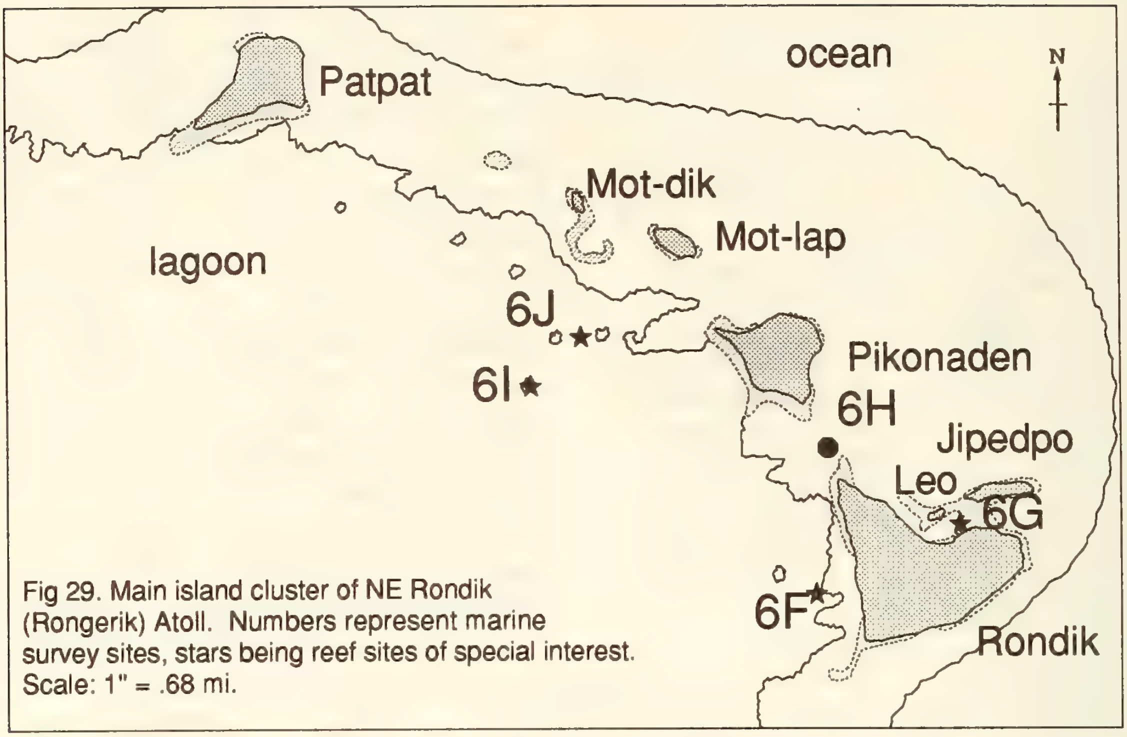


Fig 29. Main island cluster of NE Rondik (Rongerik) Atoll. Numbers represent marine survey sites, stars being reef sites of special interest. Scale: 1" = .68 mi.

complex with table corals and gigantic spectacular colonies of the yellow foliaceous coral Turbinaria. Site 6F was a shallow lagoon reef adjacent to Roñdik island with exceptional coral diversity. Also one live but six dead Tridacna gigas giant clams were reported there. Site 6G was a spectacular deep reef flat moat environment on the windward side of Roñdik dominated by extensive platforms and microatolls of the blue coral Heliopora coerulea. The high development of blue coral was unique and is probably maintained by wave-generated water currents which constantly flush clean ocean water through the moat system. Site 6I was the only deeper lagoon pinnacle reef surveyed and contained very high coral abundance (over 90% live coral coverage) and diversity of reef fishes. Sharks, however, were numerous and aggressive, preventing more detailed listing of corals. Sites 6J and 6K were shallow lagoon pinnacle habitats near the NE perimeter reef with fairly high coral coverage and very high coral diversity. The blue coral back reef zone of site 6K was exceptional, and underwater visibility and relief were also excellent.

The expansive pink sand beaches of the NE islands of Roñdik atoll are also worthy of mention. The beaches are formed primarily of the remains of pink foraminiferal tests. Although foraminiferal sand beaches are commonly observed in the Marshalls, their extensive development and coloration at Roñdik added substantially to the natural beauty and aesthetics of the atoll's island ecosystems.

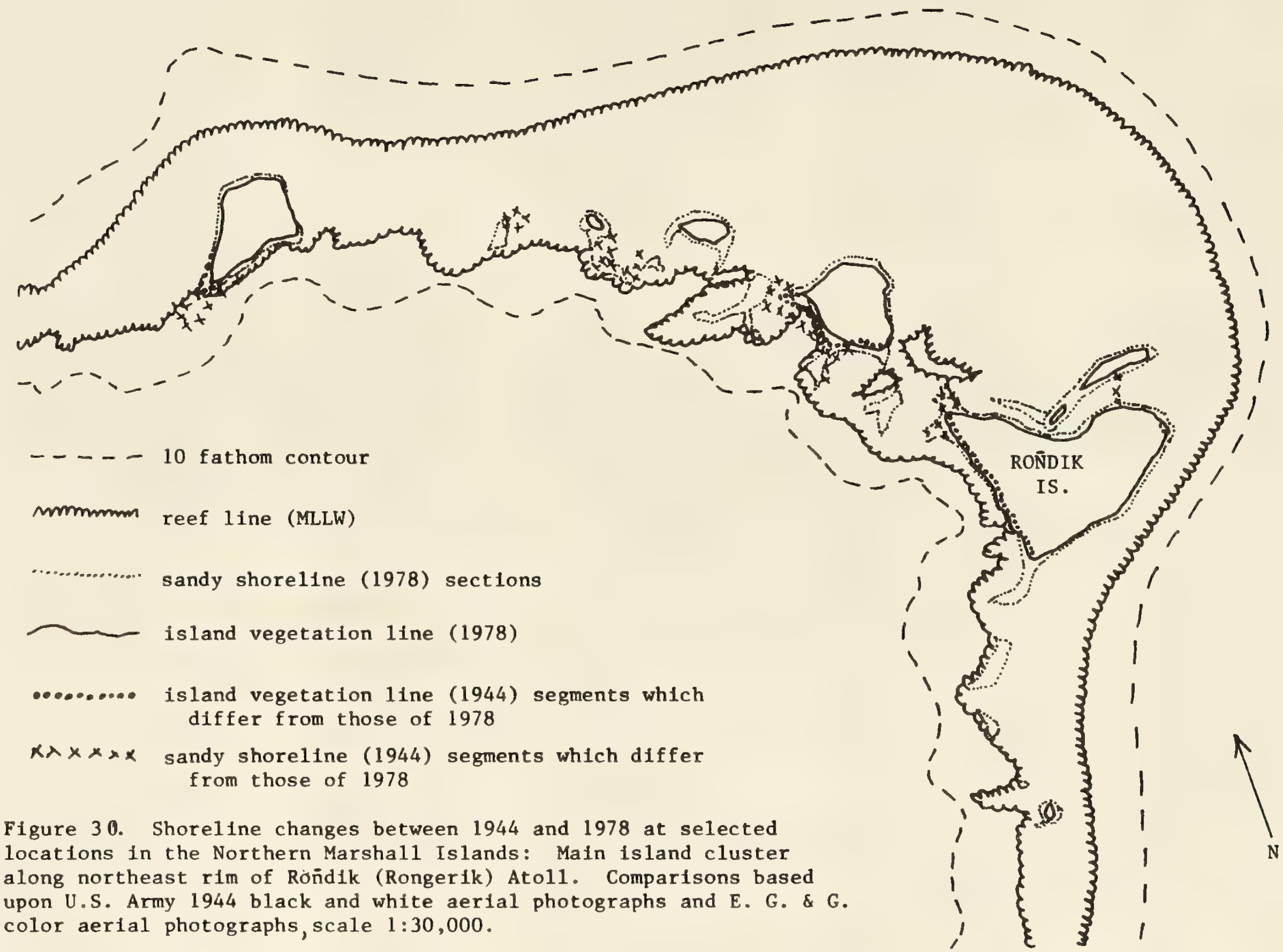


Figure 30. Shoreline changes between 1944 and 1978 at selected locations in the Northern Marshall Islands: Main island cluster along northeast rim of Ron̄dik (Rongerik) Atoll. Comparisons based upon U.S. Army 1944 black and white aerial photographs and E. G. & G. color aerial photographs, scale 1:30,000.

Rare Marine Species

Evidence of substantial recent sea turtle nesting was observed along the lagoon beaches of Āne-wetak (Eniwetak) island. A total of 33 pairs of tracks were observed along Āne-wetak and one additional pair was observed on Kaarooka island.

A school of large bottlenose dolphins was seen swimming outside the reef on the ocean side. Although bottlenose dolphins are common throughout the tropical Pacific, marine mammals were observed only on this occasion during the 1988 expedition. There is no obvious explanation for this curious lack of sightings of marine mammals elsewhere during the northern Marshalls expedition.

The several smaller species and the rare larger species of giant clams were present at Rōndik but not common. Only four live individuals compared to 16 dead shells of Tridacna gigas were observed on the reefs, suggesting heavy collection during the recent past. Except during a brief period in 1946-1948, when Rōndik was inhabited by the displaced Bikinians, there are no other known periods of occupation of Rōndik during the recent historical past. Hence the high mortality of giant clams may be best explained as the consequence of unauthorized (and unobserved) poaching.

The largest concentration of coconut crabs observed during the expedition was reported from Rōndik islet. Other large islands at Rōndik Atoll may also harbor large coconut crab populations, but only Rōndik and Āne-wetak islands are said to be planted in coconuts (Fosberg et al, 1956). Not only were the crabs very numerous, but many individuals were large, exceeding two to three kg in weight. In a few hours time, several of the ships crew were able to collect over 100 crabs without much effort, all of which were 0.5 kg or more in weight.

The large population of coconut crabs at Rōndik is best explained by infrequent harvesting pressure by islanders (since Rōndik is uninhabited), and the abundance of coconut trees. Coconuts are the preferred food of the crabs. Although coconut crab is a favorite delicacy of the Marshallese and other Pacific islanders, crab populations at Rōndik atoll may be contaminated with radionuclides.

In 1954, the U.S. accomplished BRAVO, the atmospheric testing of a large thermonuclear device (H-Bomb) at Bikini Atoll, some 230 km west of Rōndik. Due to unanticipated adverse (westerly) wind conditions and higher than expected energy yields from the detonation, radioactive fallout from the BRAVO blast penetrated the upper atmosphere and drifted east. Fallout from BRAVO was observed to contaminate Bikini, Rōnlap (Rongelap) and Utrōk (Utirik) Atolls and may have contaminated other nearby atolls, some of which are uninhabited. Rōndik lies on a direct line between the contaminated atolls of Utrōk and Rōnlap, and thus it is likely to have been contaminated by fallout from BRAVO. Radiological studies at Āne-wetak (Eniwetak) and Bikini Atolls reveal that the radionuclides cesium-137 and strontium-90 are taken up and concentrated in the tissues of coconut trees and nuts. The consumption of contaminated coconuts was probably the most likely pathway explaining how returning Bikinians received excessive dosage of these radionuclides during their aborted resettlement during the 1970's (see BARC, 1985; 1986; USACE, 1986). Coconut crabs can also become contaminated by eating contaminated nuts, and in turn humans can become exposed to the radionuclides by consuming effected coconut crabs or nuts. Although there has not been radiological surveys of the trees and crabs of Roñdik Atoll, the consumption of these foods poses a potentially serious health risk, especially since the coconut crab population is very large and since the crabs are a favored delicacy, in great demand.

Comparison of 1944 and 1978 shoreline configurations for NE Roñdik Atoll did not reveal significant changes (Figure 30).

Corals of Roñdik

Only 74 species belonging to 29 genera and subgenera of corals were reported from Roñdik Atoll based upon the results of visits to 12 marine survey sites. These numbers reflect lower levels and diversity of sampling at Roñdik compared to the other atolls. Only one lagoon pinnacle and no ocean reef sites were surveyed, and survey time at the most northerly sites were shortened due to the need to leave Roñdik earlier than planned due to a medical emergency. The entire western lagoon of the atoll was also left unsurveyed.

Many common coral species were not observed at Roñdik, including Stylocoeniella, Porites (Synaraea), Psammocora, Hydnophora and Leptoria. Most of these would be expected on ocean reef slopes if they could have been examined. Underrepresented during the survey were several genera and species of common free living mushroom corals. Of interest was the recording of Plesiastrea versipora at Roñdik, the only atoll where this coral was reported during the 1988 study.

Abundant and common corals on lagoon pinnacle reef environments included: Acropora spp (table and staghorn coral), Pavona spp, Stylophora pistillata, Montastrea curta, Pocillopora spp, Cyphastrea spp, Astreopora spp, Montipora spp, the blue coral Heliopora coerulea, Porites spp, the leafy yellow coral Turbinaria, the fire corals Millepora spp, Fungia spp, and Seriatopora hystrix.

Abundant and common corals along the windward (NE) lagoon perimeter reef slopes included: Heliopora coerulea, Acropora spp, Goniastrea retiformis, Fungia scutaria, Astreopora spp, Pavona minuta, Stylophora pistillata, the conspicuous table coral Acropora cytherea, Porites spp, Montipora spp, Leptastrea spp, Millepora spp, Montastrea curta, Favia spp, Pavona minuta, Turbinaria stellulata, Platygyra daedalea, Pocillopora spp, Goniastrea retiformis, Favites spp, the fingercoral Porites cylindrica, Seriatopora spp, the soft coral Sinularia sp, Cyphastrea spp, and the organ pipe coral Tubipora musica.

Abundant and common corals within blue coral dominated reef moat and back reef flat environments included: Heliopora coerulea, Stylophora pistillata, Seriatopora hystrix,

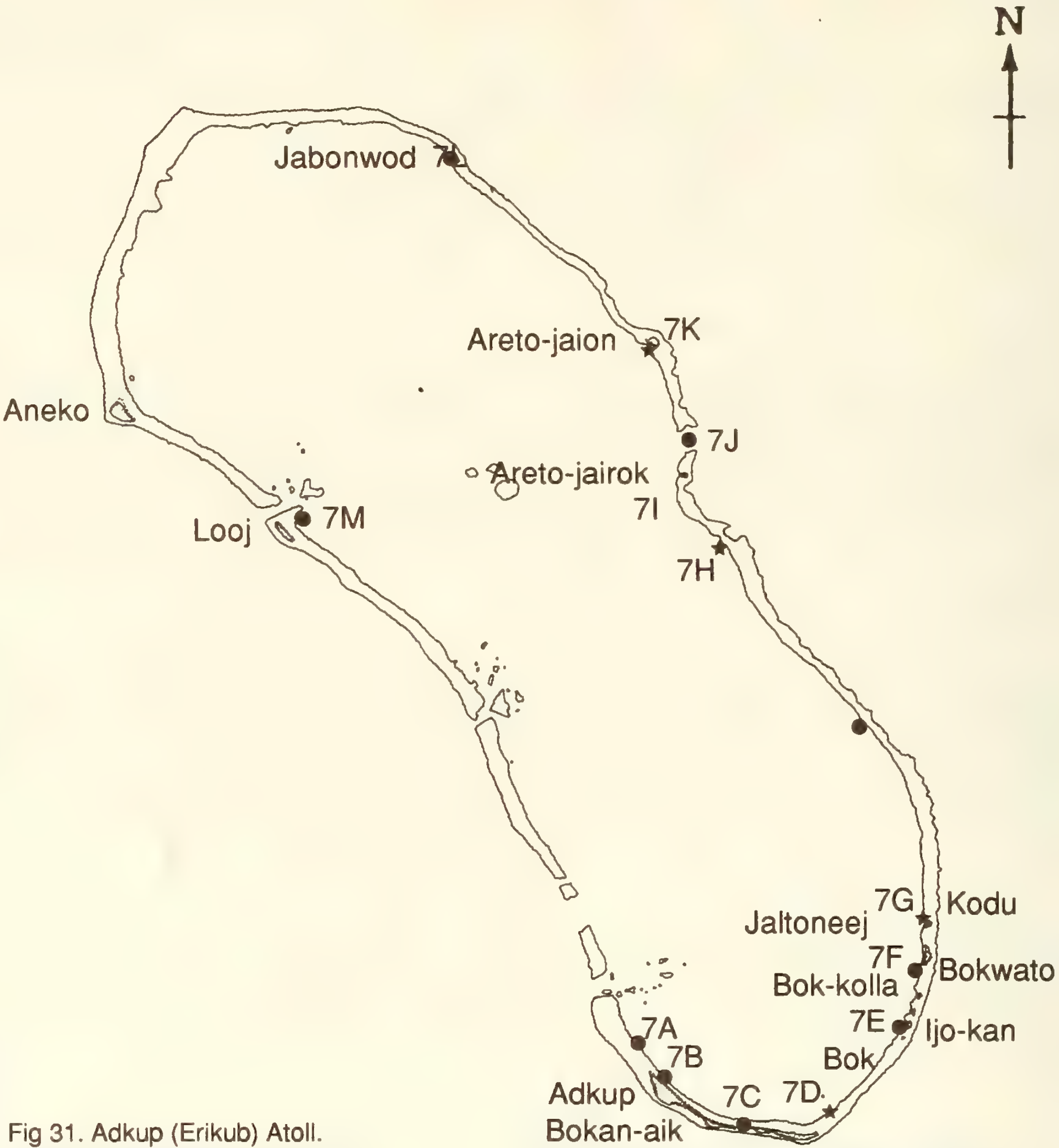


Fig 31. Adkup (Erikub) Atoll. Numbers indicate marine survey sites with stars showing reef sites of special interest. Map created by CORIAL using MARIS. Scale: 1"= 3.146 mi.

Pocillopora damicornis, Acropora palifera, Porites spp, and Leptastrea purpurea. Giant clams were abundant in these environments and along the slopes of perimeter reefs, but most were dead and some stacked in piles - clear evidence of unauthorized poaching. Nurse sharks (a harmless species) were also numerous.

ĀDKUP ATOLL (Figures 31-37; A-13, and A-14)

Aelon-in Ādkup (also referred to as Erikub Atoll) has the form of an ellipse with its long axis (about 27 km long) facing NE and SW (Figure 31). It is the largest and most southerly of the atolls visited during the 1988 expedition. In comparison to the rest of the Marshall Islands, Ādkup is centrally located and of intermediate size in terms of lagoon surface area (232 km^2), ranking 15th of 28 atolls. In terms of land area (1.53 km^2) however, Ādkup ranks much lower, 25th, and even the table reef of Mejit has more island area. Due to its lower latitude, Ādkup probably experiences a greater average annual rainfall rate than the other six areas visited in 1988, and its islets are densely forested.

Ādkup is clustered among several other atolls including Wotje just five NM to the north, Maloelap and Aur to the southeast, and Likiep to the northwest. Perhaps due to limited land and water area, Ādkup is not permanently inhabited. However, residents of nearly Wotje regularly visit Ādkup to gather copra, fish, and other food. At the time of our visit on 22-23 September 1988, there was evidence of a very recent visit to the main island (Ādkup) of the atoll probably to harvest sea turtles, fish, and crabs. Due to its central location, Ādkup is sheltered by other nearby atolls from heavy exposure to storms, surges, and waves, except those approaching from the south.

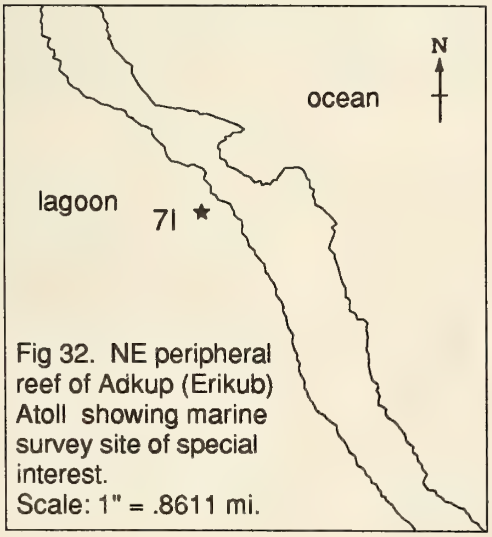


Fig 32. NE peripheral reef of Adkup (Erikub) Atoll showing marine survey site of special interest.
Scale: 1" = .8611 mi.

There are no recent available navigation charts of the atoll, and the 1978 aerial photography of the northern Marshalls did not include Ādkup. Eventually, after considerable searching, a complete set of the U.S. Army Map Service topographic series maps of Ādkup was obtained and analyzed (Figures 32-37).

Ādkup's lagoon and reefs show some unusual features. Lagoon patch reefs and pinnacles are rare, given the large size of the lagoon. Three clusters of patch reefs, each of less than 20 reefs occur opposite three of the atoll's six passes (for example Figures 31, 36). Elsewhere in the lagoon there are only a few isolated patch reefs (only seven could be counted from the AMS maps) and reef pinnacles were only slightly more abundant (for example see Figures 31-34, 36). Unfortunately, time did not permit the team to visit patch or pinnacle reefs in the deeper lagoon. A limited number of soundings have been taken in Ādkup's lagoon, especially near the passes, and reveal that the lagoon is deep. At least one lagoon area in the vicinity of the west central lagoon shows depths of 30 fathoms (55m) or more.

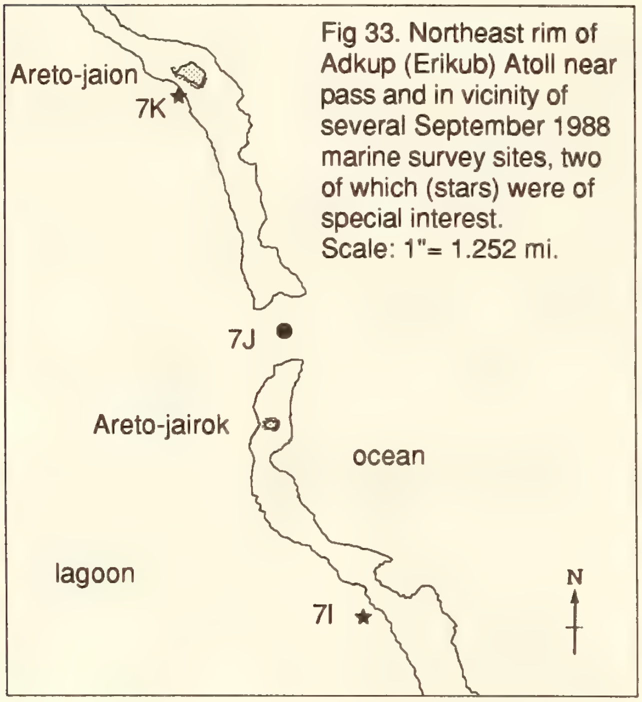


Fig 33. Northeast rim of Adkup (Erikub) Atoll near pass and in vicinity of several September 1988 marine survey sites, two of which (stars) were of special interest.
Scale: 1"= 1.252 mi.

Six deep passes cut through Ādkup's perimeter reefs (see Figures 31, 33, 34, and 36) and all are considered navigable. One pass to the north of Areto-jairok Island is on the windward (eastern) side of the atoll (site 7J; Figure 33) and is the only windward pass present at any of the six atolls surveyed during the 1988 expedition. The AMS map lists the depth of this pass at 3-3/4 fathoms (7m) and a width of about 60 m, but based upon my snorkeling observations, the minimum depth of this pass may be less (about 4m). The other passes are deeper. For example, the northwestern pass near Looj Island is 12 to 23 fathoms (22-42m) deep, and the southwest pass closest to Ādkup Island is 18-20 fathoms (33-37m) deep. Two additional deep passes are located just north of this latter pass.

The rest of the passes are generally spaced out and are probably effective in keeping all portions of the lagoon well flushed from tidal fluctuations and currents. The northeast orientation of the atoll's long reef axis maximizes the constant pumping of fresh ocean water into the lagoon from wave action along the windward ocean reef slopes. The lagoon gave the impression of a well mixed open system.

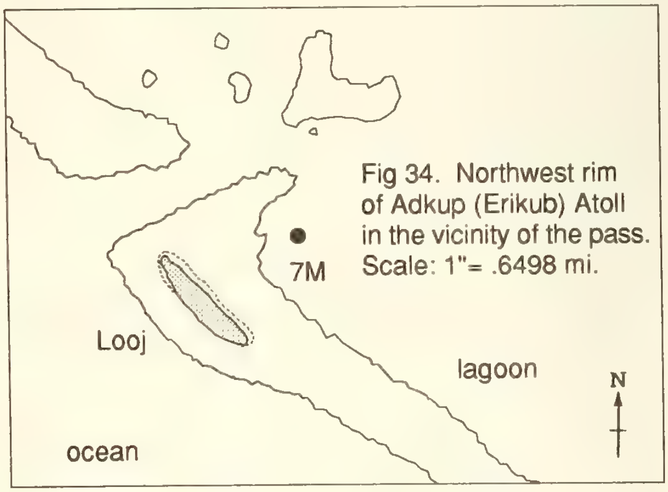


Fig 34. Northwest rim of Adkup (Erikub) Atoll in the vicinity of the pass.
Scale: 1"= .6498 mi.

Fourteen islands occur at Ādkup Atoll, but most are concentrated at the southern end where most of the land area is also situated (Figures 36, 37). To the north of this island cluster are found only three islands along the windward reef, and two islands along the leeward reef throughout the rest of the atoll.

Rare Marine Species

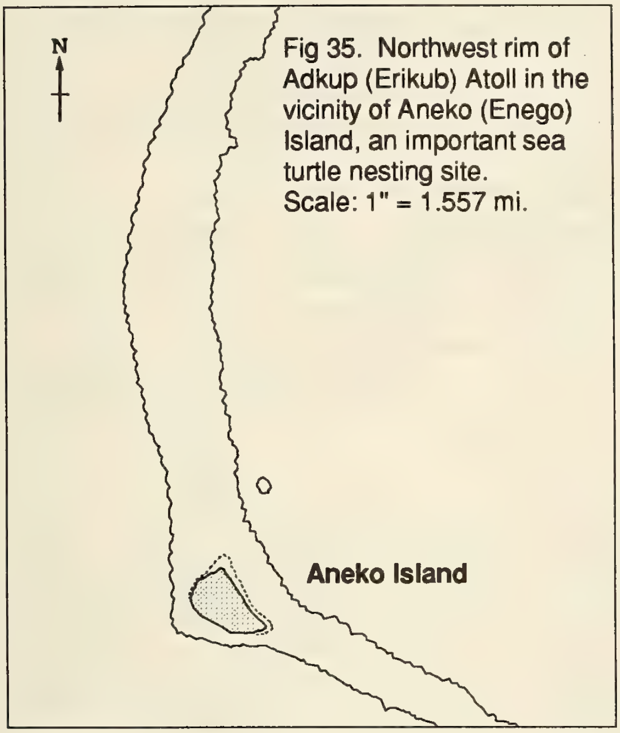


Fig 35. Northwest rim of Adkup (Erikub) Atoll in the vicinity of Aneko (Enego) Island, an important sea turtle nesting site. Scale: 1" = 1.557 mi.

There was extensive evidence of recent sea turtle nesting activity on the beaches of several islands. Twenty-three pairs of sea turtle tracks were reported from Āneko Island (Figure 35), a large island near the northwest end of the atoll. Fewer pairs of tracks were recorded on the other islets: Ādkup (13 pairs), Ijo-kan (6), Areto-jairok (3), and Looj (4). The collective totals for Ādkup atoll rank it third behind Pikaar and Jemo with respect to the level of sea turtle nesting activity recorded during the 1988 expedition. However, the nesting turtles and their eggs appear to be subject to heavy harvesting pressure. Recent human footprints were found along all beaches where turtle tracks were reported. Numerous nest marker sticks, temporary camps, and the remains of sea turtles and their eggs were also conspicuous. Most likely the turtle harvesting is accomplished by residents of Wotje, but we were not able to visit Wotje and query its islanders.

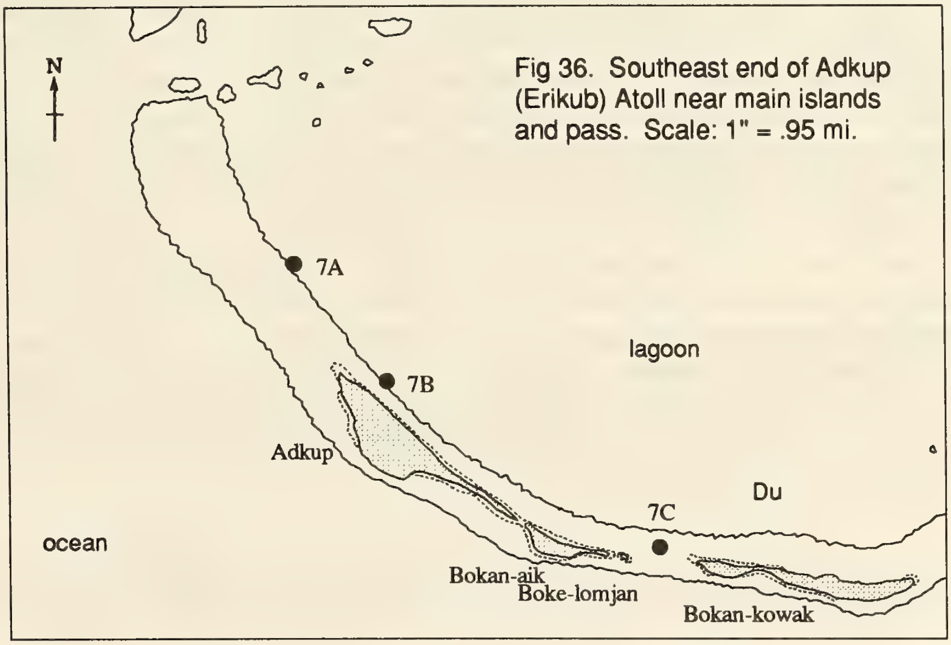


Fig 36. Southeast end of Adkup (Erikub) Atoll near main islands and pass. Scale: 1" = .95 mi.

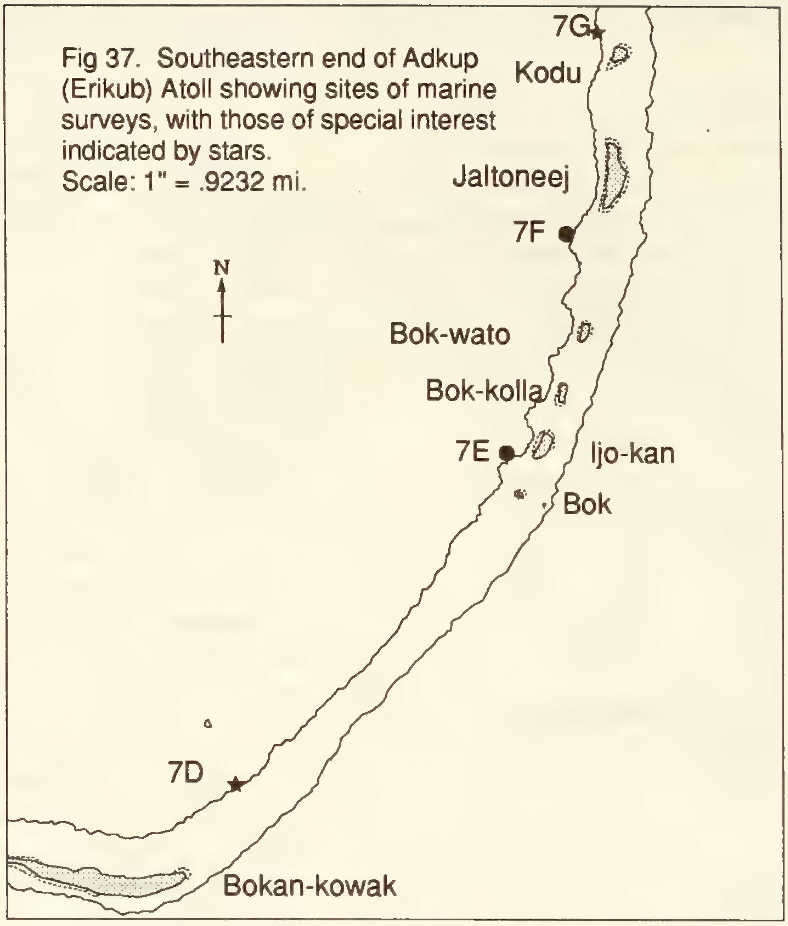


Fig 37. Southeastern end of Adkup (Erikub) Atoll showing sites of marine surveys, with those of special interest indicated by stars.
Scale: 1" = .9232 mi.

Interviews with the crew and Marshallese from Majuro indicate that Ādkup Island is famous for its large coconut crab population. Indeed crabs were reported during the survey, but most all were small. Only one crab approached the large (2 kg) size of the many large crabs observed at Roñdik Island (Roñdik Atoll). The crabs were similar in size as those observed at Kapen Island (Wōtto Atoll), but were not nearly as numerous. We conclude that the Ādkup crabs are also subject to intense harvesting pressure.

Giant clams of all four species were observed on the lagoon reefs of Ādkup but only *Tridacna maxima* and *Hippopus hippopus* were common. There were many more dead shells than live clams, and only one live individual of *Tridacna gigas* was reported. The lagoon slopes of the eastern perimeter reefs were unusually steep. These habitats may be suboptimal for the giant clam *T. gigas* at Ādkup due to substrate instability. It is also possible that the giant clam populations at Ādkup are subjected to heavy harvesting pressure from islanders at nearby atolls.

Of the 13 marine sites surveyed at Ādkup Atoll, four (7D, 7G, 7I, and 7K) were considered unique or exceptional with respect to natural characteristics. All of the sites were lagoon facing sides of perimeter back reefs and reef slopes along the windward side. All displayed complex three-dimensional coral communities on steep reef slopes characterized by moderate to high fish abundance and high coral cover and diversity. Live giant clams were present at all four sites and live coral coverage was 40% or more. At site 7D underwater visibility on the lagoon slope (low tide) was 45 m. The slope at site 7I consisted of a patch reef half buried by a sand talus where wave action and strong currents constantly transport sand lagoonward and down the slope. Site 7K included nurse sharks and several rarer corals among the 30+ species recorded.

The windward pass area (site 7J) was also of interest. At the time of my surveys (morning of 23 September 1988) a strong flood tide of two to three kts was entering the channel. The floor of the channel consisted of a hard reef pavement at a depth of 4m which gradually deepened to 15m and transitioned to a sand bottom in a lagoonward direction. The sides of the channel supported exceptional live coral development and abundant reef fish populations.

Corals of Ādkup

A total of 75 species belonging to 35 genera and subgenera were reported from Ādkup Atoll based upon observations at the 13 marine sites. The lower totals compared to some of the other atolls reflect the lack of observations on ocean reef slopes, lagoon pinnacles and other reef habitats expected to harbor additional species. One species reported from Ādkup at site 7E, Euphyllia glabrescens was not observed elsewhere during the 1988 expedition and is a rare coral elsewhere in the Marshalls. Several common genera or subgenera were not reported at Ādkup, including Stylocoeniella, Porites (Synaraea), several mushroom corals, Lobophyllia, Leptoria and others (Table 2). Some of these would be expected to be seen after more intensive surveys.

Abundant and common species along Ādkup's back reef flats and shallow lagoon reef slopes along windward perimeter reefs include: fingercoral (Porites cylindrica) Acropora spp (tables), Stylophora pistillata, Favia spp, Montipora spp, Pavona spp, other Porites spp, Acropora palifera, the soft corals Sinularia and Sarcophyton spp, Millepora spp, Pocillopora spp, Astreopora myriophthalma, Echinopora lamellosa, Cyphastrea microphthalma, Montastrea curta, Heliopora coerulea, Platygyra daedalea, Fungia spp, Turbinaria stellulata, Seriatopora spp, Favites halicora, Scapophyllia cylindrica, Goniastrea spp, and Leptastrea purpurea.

Abundant and common coral species along the windward facing lagoon reefs on the western perimeter of the atoll include: staghorn and table coral species of Acropora, Pavona minuta, Millepora platyphylla, Favia stelligera, Pocillopora spp, and Montipora spp.

CORALS: COMBINED SPECIES LIST

Prior to the 1988 surveys, coral records for the seven areas were extremely limited, a combined 35 species from Bok-ak and Rōn̄dik (Wells, 1954) (Table 3). All but four of these species were subsequently reported in 1988, and a total of 168 species belonging to 55 genera and subgenera have now been recorded for the seven areas. Several of the species and one genus (Polyphyllia) are new records for the Marshall Islands. Despite limited deep water and ocean reef sampling, the 168 species is a sizable total comparable to the faunas of Bikini, Āne-wetak (Enewetak), and Arno Atolls (Wells 1951, 1954; Maragos, 1989; Devaney and Lang, 1986), where much more extensive surveys and sampling for corals was accomplished. The species totals for the individual atolls surveyed in 1988 are lower than reported from each of Bikini, Arno, and Āne-wetak Atolls due to the 1988 sampling limitations.

IV. DISCUSSION

An excellent overview of the feasibility, justification and procedures to establish a system of protected areas in the Marshall Islands is found in Thomas (1989) and covers terrestrial, cultural, and marine factors. The present report concentrates on marine resources, and assesses the consequences of establishing marine parks and reserves (Table 5). The feasibility of other resource uses at the seven studied areas is also assessed since atolls and islands that the RMI does not establish as preserves or parks may be earmarked for other forms of development (Table 6).

Most of the Republic's natural resources are marine resources, and the seven studied areas represent a major proportion of the undisturbed reef systems in the country. Although none of the study atolls is large, the RMI is home to the world's largest atolls. More atolls are found in the RMI (28) compared to any other country except the Federated States of Micronesia (42) and French Polynesia. But unlike the FSM and French Polynesia, the RMI is comprised of only atolls, table reefs, and low coral islands. As such, the land resources are small and lack rich and abundant soil and groundwater resources. Hence the RMI must look to marine and coastal environments for future economic development. The RMI is also faced with rapid population growth and the need to reduce balance of trade deficits and unemployment. Self reliance is the central theme for the Republic's future development goals.

Fully a quarter of the RMI's atolls are uninhabited (including Ailinginae which was not studied), and at least one or two others have been temporarily evacuated (Ron̄lap and Bikini due to concerns over contamination from nuclear testing). Thus the RMI perceives most of these uninhabited areas as major resource development opportunities. The RMI government also recognizes and supports the traditional use of several of these atolls as wildlife reserves or "pantry" reserves, and specifically requested the study team to evaluate the uninhabited areas (and inhabited Wōtto) as possible parks and reserves. Those areas which are not established as protected areas are theoretically open for subsistence activities, resort development, small scale (nature based) tourism, agriculture, mariculture, urbanization or settlement, and industry. However, the inaccessibility, geographic isolation, small land areas, limited fresh water, and vulnerability to typhoons and other natural hazards render most of the areas unfavorable for intensive development (see Table 6).

Marine Reserves

At least portions of all seven areas visited harbor marine resources and sites worthy of marine reserve and preserve status. The entire reef ecosystems (along with the islands) of Bok-ak Atoll, Rikaar Atoll, and Jemo Island warrant reserve status, a designation which would be entirely consistent with the traditional and cultural uses of these reefs as practiced by the Marshallese for many centuries. All three areas are acknowledged reserves for either nesting seabirds, nesting sea turtles, or both. All three have unique coral reef features and habitats which have been little studied scientifically.

RESOURCES USES	biological diversity	biological productivity	other natural resources	cultural importance	aesthetics	non-polluted/pristine	accessibility	water supply	protection from natural hazards	docks	airfields	power	sewage disposal	public safety	climate	land and soils	CANDIDATE ATOLLS AND REEFS
Preserves & reserves	●	O	●	●	O	●	·	·	·	·	·	·	·	·	·	·	Bok-ak, Pikaar, Jemo̧ and portions of other atolls
Parks & recreation areas	●	O	●	●	●	●	O	O	O	O	O	·	O	●	·	·	Tōke, Wōtto, portions of Ron̄dik and Ādkup
Subsistence gathering & fishing	●	●	O	O	·	●	●	·	O	·	·	·	·	●	O	O	Ādkup, Tōke & Wōtto. Ron̄dik (marine resources only)
Aquaculture/mariculture	·	●	O	·	·	●	●	O	O	●	●	O	O	●	O	·	Wōtto, and possibly Tōk^{e}a, Ron̄dik and Ādkup
Agriculture	·	●	O	·	·	O	●	●	●	●	O	·	●	●	●	●	Possibly Wōtto
Commercial fishing	O	●	O	·	·	O	O	·	·	●	●	O	·	·	·	·	Possibly Wōtto and territorial waters at other reefs
Small scale tourism	●	·	●	●	●	O	●	●	●	O	●	●	●	●	O	O	Wōtto
Resorts	●	·	●	O	●	O	●	●	●	●	●	●	●	●	O	●	None
Permanent settlements	·	·	·	·	·	O	●	●	●	●	●	●	●	●	O	●	None
Industrial development	·	·	●	·	·	·	O	●	●	●	O	●	O	●	·	●	None

● - very important O - moderately important · - unimportant

Table 6. Relationship between various types of resource uses for Northern Marshalls reefs and atolls and the required criteria for their feasibility

The lagoons of Bok-ak and Pikaar also support huge populations of several of the smaller species of giant clams which is perhaps the most important reason to establish them as marine reserves. The lagoons also support exceptional populations of reef corals and reef fishes and the whole ecosystems are in pristine condition. The designation of any area for reserve or protected status will require the cooperation of persons with traditional rights to these areas.

At a smaller scale there are unique or exceptional coral reef habitats at the other atolls (Wōtto, Ādkup, Roñdik, and Tōke) that also merit marine reserve designation due to the abundance, diversity or unique features of coral reef populations and reef features. For example, the pink sand beaches and high dune systems, blue coral moats and flourishing lagoon pinnacles at Roñdik deserve special recognition as do other lagoon reef formations at the other atolls.

Marine Parks and Recreational Areas

Several of the atolls offer major advantages with few disadvantages to support marine park designation. The variety, accessibility, safety, and pristine condition of lagoon reefs (and perhaps ocean reefs as well) at Wōtto and Tōke support the entire atolls being designated as National Marine Parks. Portions of Ādkup and Roñdik also contain diverse and accessible reef habitats to support at least Regional Marine Park status. These parks would serve both the residents of the RMI and visitors and would be oriented to provide recreation and educational opportunities. Visiting tourists to these parks could provide the fees to support park management, jobs, travel, and educational opportunities for Marshallese residents, including school students.

Of the four areas, Wōtto has the most potential to serve as a national park, because of an onsite residential population interested in pursuing marine park and nature based tourism. Wōtto also contains food and water supplies, and its airstrip allows the atoll to be serviced by weekly commuter flights from Mājro or Kuwajleen (Kwajalein) Atolls. The large population of American defense workers at Kwajalein may find the opportunity to visit Wōtto an attractive prospect. Many other people from the urban settings of Mājro and Kuwajleen may also be interested in experiencing the natural and cultural resources of Wōtto.

The atolls of Tōke, Ādkup, and Roñdik are somewhat less accessible to serve park visitors. The nearest airstrip and inhabited population from Tōke is at Utrōk atoll, and the Utrōk islanders need to be queried as to their interest in park designation for Tōke. Likewise, Ādkup and Roñdik are close by other atolls (Wojte and Roñlap) where airstrips are present. Wotje is inhabited while Roñlap has been temporarily evacuated. On a long range basis, park designation and development is theoretically possible for these areas, as well as for Ailinginae (which was not visited) which is also near Roñlap (see Figure 1). Park development at Pikaar, Bok-ak, and Jemo̧ is not feasible due to hazardous access, remoteness, vulnerability to large waves and typhoons, and lack of potable water. Heavy visitation to these areas could also disturb wildlife resources (especially sea turtles, sea birds, and possibly clam populations). Any form of physical development at these atolls would compromise the value of a reserve, and could disrupt reef and island ecosystems. As with any other proposed use, park designation of these areas will require the cooperation of persons with traditional rights to these areas.

Subsistence Activities

Very limited harvest of sea turtles and seabirds for ceremonial purposes has been traditionally practiced at Bok-ak, Pikaar, and Jemo̧. Such visits, if continued to be limited to one or two per year, do not pose a danger to the vulnerable wildlife at these sites and would be in keeping with long established cultural practices. However, harvesting of larger numbers of wildlife for purely subsistence purposes would be disruptive to bird, turtle and clam populations, and may endanger their status as the most important populations in the RMI.

The remaining four areas are suitable for traditional level subsistence activities and would be compatible with park reserve designations if planned properly. For example, marine resources and sites at Wōtto used for subsistence activities could be identified and sustained for such uses, and visitor or recreation sites would be best located at separate sites.

There should be controls established over the taking of rare marine species (sea turtles, their eggs, and giant clams) from Ron̄dik and Ādkup Atolls to ensure that important breeding populations are not depleted or threatened. One way to accomplish this is first to establish critical habitat areas as reserves.

Radiological Contamination

Consumption of coconuts or coconut crabs from Ron̄dik Atoll may pose as health hazards to islanders. In addition, subsistence use of terrestrial resources from Ailinginae, if any, should likewise be discouraged until radiological surveys document that consumption of these resources will not pose a hazard to public health. It is possible but highly unlikely that consumption of marine resources from these two atolls as well as from Tōke would pose a health problem.

Resident coconuts, breadfruit, pandanus, and coconut crabs from Ron̄dik Atoll may be contaminated with the radionuclides cesium-137 and strontium-90. These radionuclides were generated during the BRAVO hydrogen bomb test at Bikini in 1954 and carried with the nuclear fallout from the blast. Although Bikini is located over 125 NM west of Ron̄dik (and 100 NM west of Ailinginae and Ron̄lap), fallout from BRAVO was reported to have been carried into upper atmospheric winds and to the east, where some of it eventually rained down on Ron̄lap and Utrōk Atolls, which were inhabited at the time. The fallout also probably rained down on other nearby atolls, but since they were uninhabited, evidence of fallout must be derived from analysis of plants and soils. Ron̄dik falls within a straight axis between Ron̄lap (25 NM to the west) and Utrōk (140

NM to the east) (see Figure 1). Thus it is highly likely that Roñdik, and perhaps Ailinginae were contaminated with the fallout.

Studies at Bikini and Āne-wetak Atolls after the nuclear testing period reveal that coconut trees (especially the living nuts) and other crops take up and bioaccumulate cesium-137 and strontium-90 in their tissues. The concentrated radiation levels in the coconuts posed a much greater health risk than radiation in the soils, because resettled Bikinians subsisted regularly off locally grown but contaminated coconuts between 1969-1978. Excessive whole body dose counts of the Bikinians in 1978 measured by Brookhaven National Laboratory prompted the evacuation of the Bikinians from their home atoll on short notice in 1978.

Coconut crabs as well as humans subsist on coconuts, and the crabs can also bioaccumulate Ce-137 and Sr-90 in their tissues by foraging off contaminated nuts, as studies by Lawrence Livermore National Laboratory at Āne-wetak Atoll have demonstrated (BARC, 1984; 1985; 1986). The radionuclides could then be passed up the food chain to man if he eats contaminated coconut crabs. Unlike the small crab populations at Bikini and Āne-wetak, Roñdik supports huge coconut crab populations. This raises the possibility of a greater public health hazard since there may be many more potentially contaminated crabs at Roñdik. Regular consumption of coconuts, breadfruit and other crops at Roñdik is more likely and could also pose a risk.

Tōke and Ailinginae Atolls were also within the fallout zone. Although Tōke's edible vegetation and coconut crab populations are very small, the extent of Ailinginae's is not known since the team was unable to visit the latter atoll. Thus radiological surveys may be warranted for Roñdik as well as Tōke and Ailinginae to document the extent of radiation hazard from ingesting food crops and coconut crabs. Roñlap, and Utrōk are presently being monitored for radiation by Lawrence Livermore National Laboratory.

Mariculture

The shallow protected lagoons and broad reef flats and shelves within the Northern Marshalls offer ideal locations for certain forms of mariculture development. Several marine species with mariculture potential were observed during the expedition including: giant clams (Tridacna, Hippopus), topshell (Trochus), black-lipped pearl oysters (Pinctada), milkfish (Chanos), mullet (Mugil) and reef groupers (Epinephelus). Mariculture would be more feasible within atoll reefs and lagoons accessible by air and sea transportation and near population centers. Mariculture thus would be feasible at Wōtto, with its airstrip, protected anchorage, resident population and proximity to urban Kuwajleen. Tōke is somewhat less feasible since the nearest airstrip and residential population is at Utrōk. Similarly, Ādkup is removed from Wotje, the nearest population and airstrip. Mariculture would more likely be developed at the populated atolls (Utrōk and Wotje) rather than at their uninhabited neighbors (Tōke and Ādkup). Roñdik is less feasible for mariculture due to the lack of inhabited atolls nearby, although Roñlap, which is serviced by an airstrip and protected anchorage was only recently evacuated and may be eventually resettled (Rongelap Reassessment Project, 1989).

The remaining reef and atolls (Bok-ak, Pikaar, and Jemo̧) are not feasible due to remoteness, lack of safe access, lack of safe anchorages, and relatively inhospitable living conditions. Extensive mariculture development at Pikaar and Bok-ak might also conflict with other values and uses such as protected reserves or preserves. The large giant clam populations in the lagoons of Pikaar and Bok-ak may eventually serve as important brood stock and a source of giant clam seed, if the smaller giant clam species become severely depleted in the RMI. For this reason, the giant clam populations at the two atolls should be maintained as reserves indefinitely.

Agriculture

Although the focus of this report is on marine resources, a few comments on the feasibility of agriculture at the seven studied areas can be offered. Due to lack of water and good soil, agriculture at Pikaar, Tōke and Bok-ak is not feasible. Although Jemo Island has thicker soil and more abundant water, agriculture is also difficult due to hazardous access and limited land and settlement options. Ron̄dik Atoll should not be considered feasible for agriculture unless radiological surveys and analyses project it to be safe. Subsistence level agriculture is already practiced on inhabited Wōtto, including some copra harvest. Likewise, Ādkup is subject to limited copra harvest, but is small land areas limit greater agricultural development.

Commercial Fishing

Commercial fishing activity by resident Marshallese would be feasible at inhabited Wōtto, which has accessible ocean fishing grounds. Fishing vessels from Wotje, Utrōk, and Ron̄lap could also fish the coastal waters of Ādkup, Tōke, or Ron̄dik, especially for game fish and tunas. Controlled commercial fishing in the lagoons of uninhabited atolls is also possible unless it competes with the subsistence needs of the nearby inhabited atolls which own or traditionally control lagoon fishing grounds. Commercial fishing is less feasible at Pikaar and Bok-ak atolls due to remoteness. Fishing in the lagoons would be further discouraged by numerous reefs and hazardous access through the single narrow meandering passes. Permanent occupation of the atolls to promote commercial fishing would be extremely disruptive to rare marine species, reef life and nesting seabirds. Controlled commercial fishing for tunas and other migratory species along the ocean sides (territorial waters) of all atolls is feasible but should be limited to Marshallese and monitored to avoid poaching of turtles, giant clams, and other rare species within or near designated marine reserves.

Small Scale Tourism

Small scale tourism in this report means small lodges or beach cabanas, limited to about 20 rooms which take advantage of the natural features, scenic beauty, and cultural resources within the vicinity of the tourism facilities (e.g. nature based tourism). This style and level of tourism at Wōtto is very feasible given the interests of the islanders to pursue it and the host of natural amenities and attributes. Reliable sources of water and food appear feasible to obtain and the major infrastructure requirements would include the accommodations, power generation (for lights and refrigeration, ceiling fans, etc.), catchment water storage, and waste disposal. Wōtto is already serviced by weekly commuter air service and has a protected anchorage. Thomas et al (1989) provides a detailed account of the feasibility of small scale tourism at Wōtto Atoll. Many existing marine resources and features could be incorporated into a tourism operation. Visitor destination attractions include flourishing coral communities at safe and accessible lagoon areas. Corals, fish, giant clams and other reef life could be observed via diving and snorkeling. Mariculture and fishing activity at the atoll could provide fresh fish and shellfish to feed visitors. Beaches and other coastal sites at islands away from the existing village could also be visited. Interpretive and educational displays regarding marine life could be established. Swimming, gamefishing, diving, some boating, and sailing activities could also be included. The focus of small scale tourism at Wōtto should be nature based, with considerable emphasis on marine resources.

Tōke Atoll also has many attributes to support tourism visitation, but accommodations for tourists would be best placed on Utrōk, subject to the views, approvals and guidance of the Utrōk people. The survey team could not find the time to visit the Utrōk islanders and obtain their views on tourism. The water and land resources at Tōke are too limited to support development of self-contained permanent tourism accommodations. Tōke would best serve as a day visitor area or for limited overnight "rustic" camping. Access to the atoll would be gained by boat from Utrōk. Land resources at Tōke are too limited to justify an airstrip, and dredging and filling to construct a reef runway could have major adverse impacts on marine resources.

Similar limitations on tourism development apply at Roñdik and Ādkup atolls. Although land resources are more abundant, the lack of permanent residents would require infrastructure development for accommodations, power, water supply and transportation. Airfields would most likely be required to attract tourists to the atolls, and reef runways would be needed. Tourism development would be expensive and would need to be well planned to avoid serious socioeconomic and environmental impacts. Most importantly, tourism development, if any, would require the approval and support of the traditional land managers, owners, and users of both atolls.

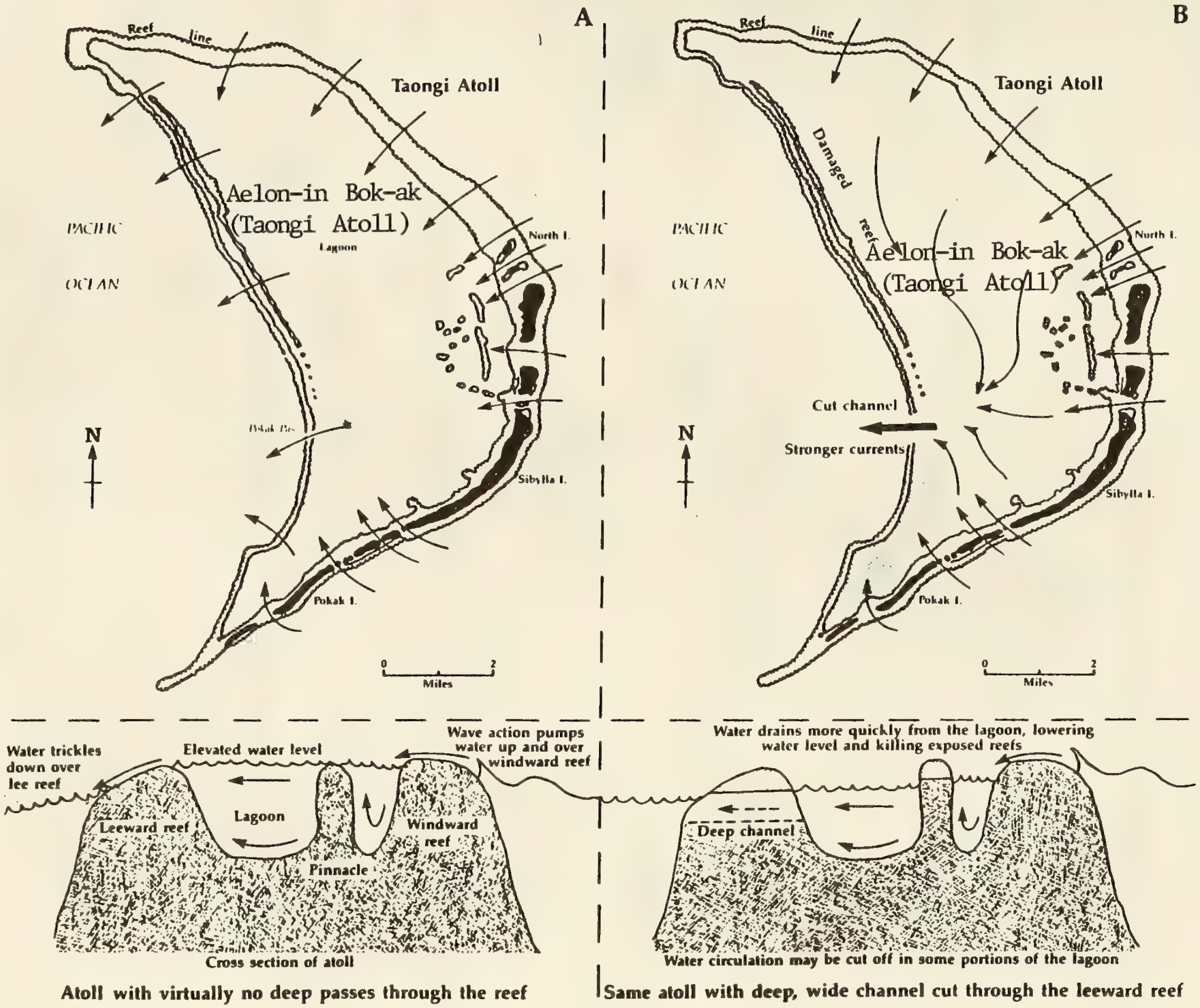
Tourism development is not feasible at Jemo, Pikaar and Bok-ak due to remoteness, hazardous accessibility, lack of reliable fresh water, lack of a permanent work force, and the significant expected economic costs and environmental impacts. Of the three areas, only Bok-ak has sufficient land for an airstrip, but substantial bird nesting on the islands poses serious constraints. Disruption of nesting activity and collisions between birds and airplanes are highly likely in nesting areas and contrary to the designation of the atoll as a wildlife refuge. Safe boat access to either Bok-ak or Pikaar would require major dredging and other coastal construction activity in the vicinity of the existing passes. Additional lagoon reefs may also need to be dredged or knocked down to provide safe access across the lagoons to the destination islands. The clearing of safe navigation channels could have major adverse effects on coral reefs and giant clam populations, and may also disturb some sea turtle nesting. Major widening or enlarging of the passes could also lower lagoon water levels, exposing and killing many shallow reef flats, disrupting lagoon circulation, and possibly degrading coral reef and giant clam habitat (see Figure 38). For these reasons permanent occupation or settlement of Pikaar and Bok-ak for tourism and other purposes (e.g. resettlement, industrial, development) would pose serious threats to the natural resources of most value at the atolls and should be strongly discouraged.

Variations in the depths of living reef flats: revisiting some widely held assumptions

It is generally thought that living reef flats on coral atolls and barrier reefs can grow no higher than mean low water due to the requirement of the reef building organisms (e.g. corals, coralline algae), to be regularly immersed in sea water for survival. As growing coral reefs reach the sea surface, further upward growth is inhibited while lateral growth lagoonward and seaward can continue (see Figure 39). Over time and with stable sea level, cessation of upward growth and continued lateral reef expansion would result in the formation of wide reef flats. Their widespread occurrence is indisputable evidence on the limitation of marine organisms to grow above a level of regular exposure to sea water.

One widely observed exception to the "mean low tide rule" is the presence of elevated living coralline algal ridges along the margins of many windward reef flats of many atolls, especially those of the RMI (Tracey et al, 1948. Wells, 1954; 1957a, b). The fact that these ridges occur only along windward reef flats suggests a relationship between the ridges and the wave action generated by the tradewinds. The most widely supported hypothesis is that the constant wave action generates wave wash or splash that constantly bathes the ridges, and keeping the reef building marine organisms (primarily crustose coralline algae and some reef corals) alive. This wave wash can regularly immerse surfaces up to two or three feet above mean low water during low tide conditions on the ocean side of the reefs which explains why ridges at this elevation remain alive. Wave wash passing over the ridge then moves downhill toward the lagoon and mixes with lagoon waters, eventually exiting through the passes or over the tops of reefs along leeward sides.

Another less widely known exception to the "mean low tide rule" became evident after the visits to Bok-ak and Pikaar Atolls. Here, not only were windward algal ridges found to be alive and growing above mean low water, but so were many other lagoon reefs. The elevated living nature of some lagoon reefs were reported by Fosberg et al (1956) and Fosberg (1988) at Pikaar and Bok-ak. These authors and the 1988 field team also observed the elevated lagoon water levels at "low tide" at these atolls. Similar elevated lagoon and leeward reef flats were also reported by Wells (1951) at Arno Atoll's northern sublagoon (Namdik), later corroborated by Maragos and Lamberts (1989). I also



Atoll with virtually no deep passes through the reef

Same atoll with deep, wide channel cut through the leeward reef

Fig. 38. Possible adverse effects of cutting channels through semi-enclosed atoll lagoons. Some atolls (such as Bok-ak, which is pictured, and Pikaar) have elevated lagoon water levels because of wave action pumping water over windward reefs and the lack of large, deep channels to drain the excess water. The reefs grow above normal ocean sea level because of constant water flow and in response to higher lagoon water level. Cutting a deep channel through such an atoll reef would cause waters to drain more quickly, lowering lagoon water level and killing emergent reefs.

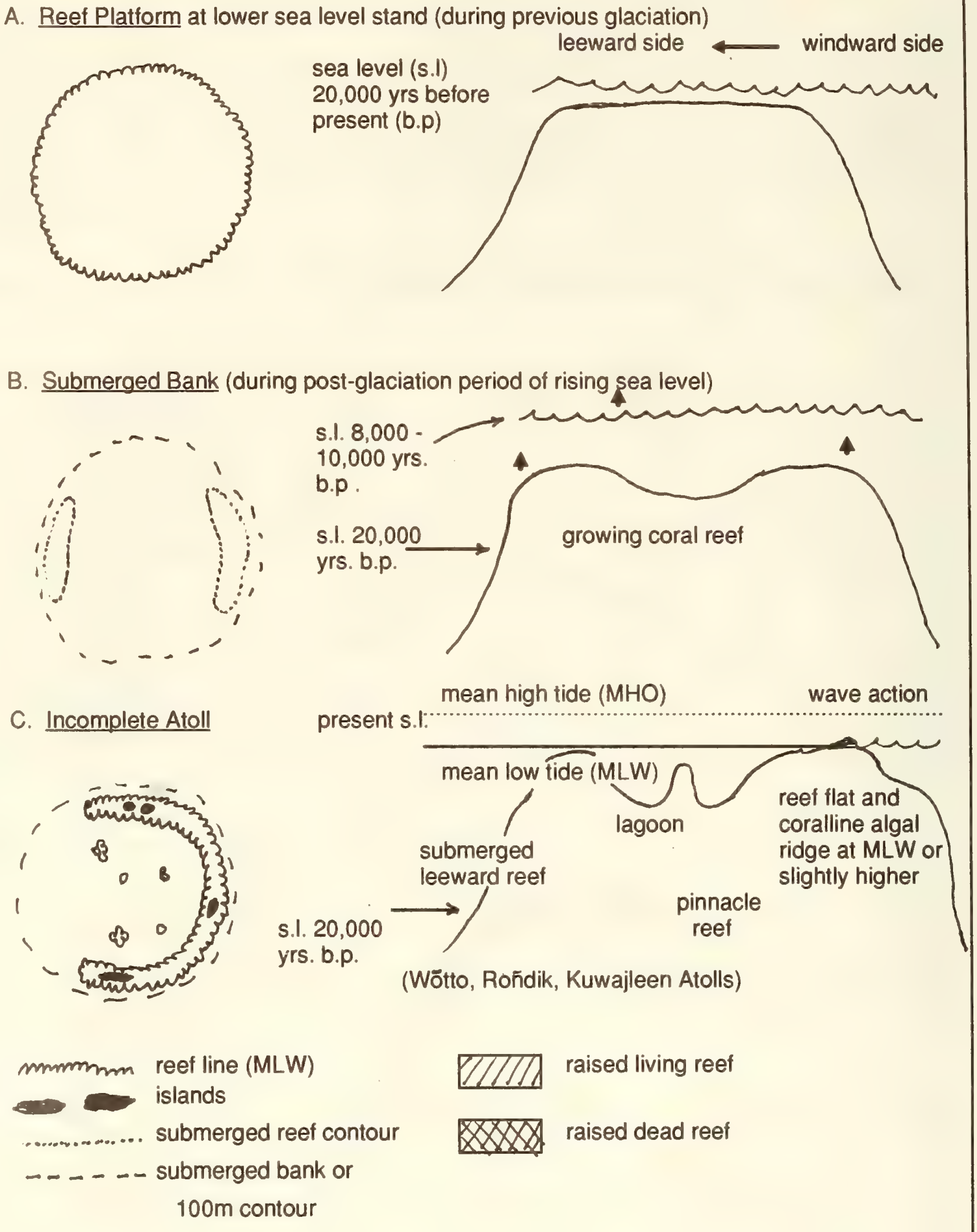
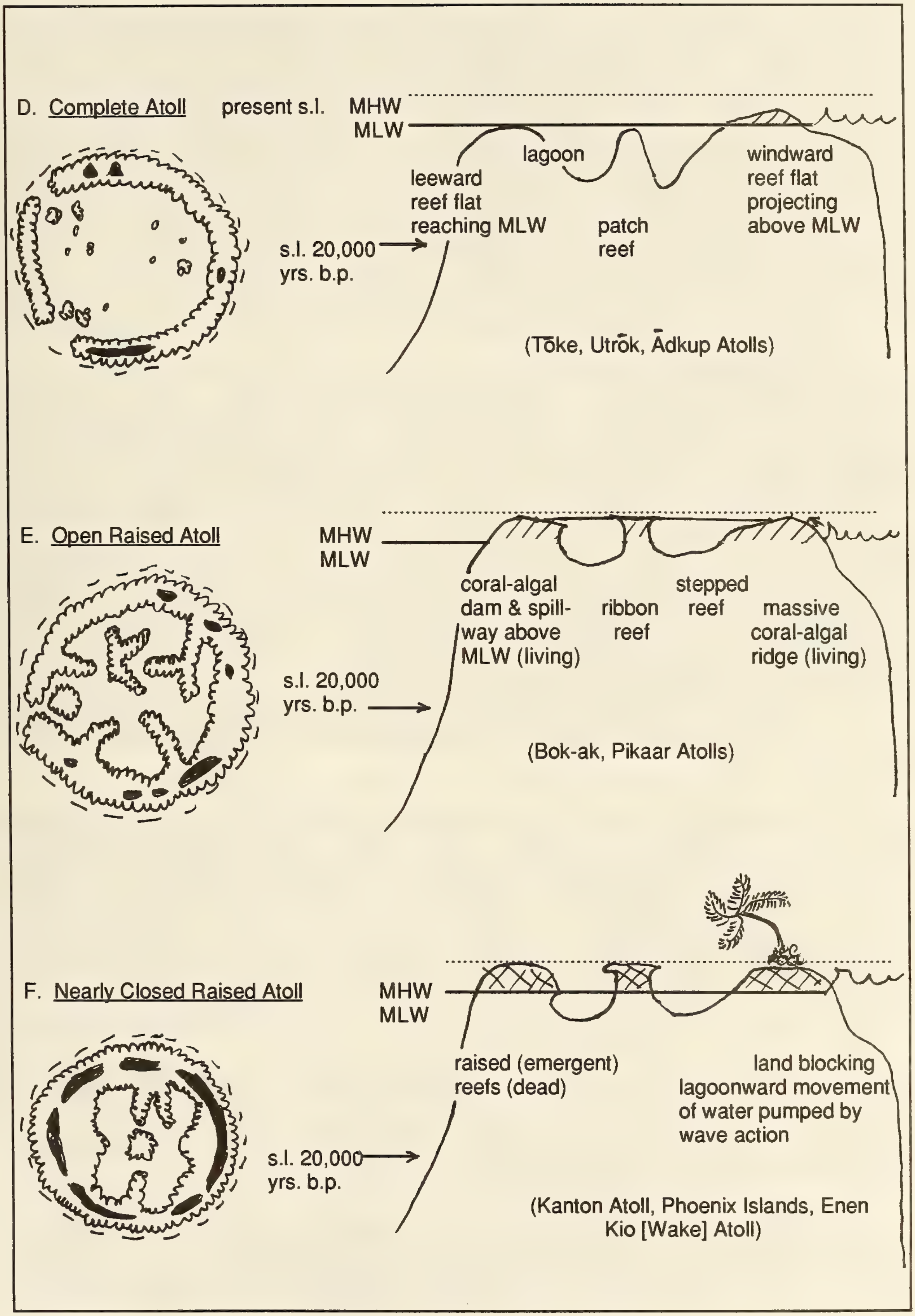


Figure 39. Progressive development of reef flat features on atolls.


D. Complete Atoll
present s.l.
MHW
MLW
lagoon
leeward
reef flat
reaching MLW
patch
reef
windward
reef flat
projecting
above MLW
s.l. 20,000
yrs. b.p.
(Tōke, Utrōk, Ādkup Atolls)
E. Open Raised Atoll
MHW
MLW
coral-algal
dam & spill-
way above
MLW (living)
ribbon
reef
stepped
reef
massive
coral-algal
ridge (living)
s.l. 20,000
yrs. b.p.
(Bok-ak, Pikaar Atolls)
F. Nearly Closed Raised Atoll
MHW
MLW
raised (emergent)
reefs (dead)
land blocking
lagoonward movement
of water pumped by
wave action
s.l. 20,000
yrs. b.p.
(Kanton Atoll, Phoenix Islands, Enen
Kio [Wake] Atoll)

observed elevated lagoon and leeward reefs at Namdik (Namorik) Atoll in 1971, and former residents of nearby Ebon Atoll also noted the elevated nature of perimeter reefs (pers. comm. to J. Maragos by N. Neimon). All five of these atoll lagoons have two things in common: 1) exposure of windward reef flats to prevailing wave action generated by the trade winds, and 2) restricted passages or no passages through the reef. These two factors are interrelated in explaining the presence of elevated living lagoon and leeward reefs (Figure 39). Progressive development of reef flat features on atolls explain how contemporary reefs in the northern Marshalls can grow above low tide level without the need for a higher "Holocene" sea stand. Stage A. Antecedent reef platform at the end of the previous ice age. Stage B. Subsequent melting of the glaciers causes sea level to rise, drowning the reef platform and renewing upward coral reef growth. Stage C. Upward reef growth eventually reaches sea level (mean low tide) on the windward side. Coralline algal ridges projecting above mean low tide may develop in response to constant wave action. Stage D. All perimeter (annular) reefs grow upward to mean low tide level except where passes cut through the reef. Coralline algal ridges and windward reef flats continue to broaden. Stage E. Eventually the passes close off to the extent that water pumped into the lagoon by constant windward wave action is greater than can exit the passes at low tide, causing average lagoon water levels to rise. Remaining (leeward) perimeter reefs, now constantly submerged, begin to grow upward, forming coral-algal dams, spillways, and perched lagoon reefs. Stage F. Storms naturally cast sand and rubble on top of windward reefs, forming cays, ramparts or islands, or man builds causeways along windward reefs to connect islands. In either case they block the pumping of seawater into the lagoon by wave action. As a result, water levels in the lagoon drop, permanently exposing raised reefs which dry out and die, leaving intact "fossil" raised reefs. The cutting or enlarging of passes through perimeter reefs can have the same effect by draining lagoon waters more quickly and lowering average water levels (see Figure 38).

The restricted passages result in more water entering the lagoon over windward reefs than can exit through passes at low tide. In response to the restricted discharges, average lagoon water levels increase with the excess water spilling over leeward reef flats as well as through the passes. If the passes begin to close off, restrictions increase, causing lagoon water levels to rise further. Higher water levels in the lagoon, especially during low tide, result in more and more water spilling over the leeward reef flats until the latter are constantly immersed even at low tide. Prolonged immersion may in turn ultimately cause leeward reef flats to grow upward, since the reef organisms are no longer limited by exposure at low tide (see Figure 39). Eventually, perimeter reefs along leeward sides of the atoll grow upward. Supplementing the coralline algal ridges along windward reef margins are smaller coralline algal ridges and coral-algal dams and spillways along leeward reefs. Lagoon reefs also grow upward in response to the progressively higher lagoon water levels.

Maximum upward reef growth depends upon the magnitude of prevailing wave action and the extent of open reef flats along the windward side of the atoll. Some of the kinetic energy of wave action is converted into potential energy by pumping water up on higher reef flats. Wave action can constantly pump ocean waters into the lagoon over the ridge and reef flats. If lagoonward water movement is blocked by the presence of islands or rubble ramparts created during tropical storms, lagoon water levels could drop. Man's intervention, either by building causeways along windward reefs (which blocks wave pumping of water into the lagoon), or by enlarging passes through leeward reefs (which drains water more quickly from the lagoon), can also lower average lagoon water levels. The lowered water levels could then result in the emergence and death of exposed reefs, which may have occurred at Kanton Atoll, where a near continuous causeway was built around the perimeter reefs of the atoll, and where recently exposed reefs were observed (Jokiel and Maragos, 1978; Smith and Jokiel, 1978). The hypothetical evolution of atoll reef flats based upon the above scenario is depicted in Figure 39.

Geologists often rely the elevation of previously intact fossil reef flats to estimate the extent and age of relative sea level stands in various parts of the world. Two implicit assumptions in many of these studies is that all or most modern living reef flats grow no higher than mean low water elevation, and that intact previously living reef flats found emerged on present day reefs must have formed when relative sea level was higher. Based upon the 1988 observations at Bok-ak and Pikaar, supplemented by the observations at other atolls (Arno and Namdik), the first, and perhaps both of these assumptions may be incorrect. First, in the case of Bok-ak, Pikaar, Arno, Namdik, and perhaps other atolls, many present day living reef flats occur above low tide level due to factors other than a higher sea level stand. More importantly, some of these same reefs may become reexposed due to natural factors, such as islands, cays, and rubble ramparts forming on the windward sides of atolls with elevated leeward and lagoon reef flats, thereby blocking lagoonward movement of water pumped by wave action.

As a consequence, the hypothesis of a higher Holocene sea level stand some 4,000-6,000 years ago that is based upon the evidence of higher stands of recent reefs less than one meter above present sea level may need to be reexamined. The complex interaction of prevailing wave action, restricted passages through reefs, open windward reef flats, the frequency of storms, and other factors can alternatively explain the upward growth of living reefs above normal low tide levels and their subsequent reemergence. Reliance on evidence from prehistoric reef stands in support of hypotheses on previous sea level stands must involve an examination of the geomorphology, oceanography, and geological history of the reefs in question.

Rapid Marine Field Assessment Procedures

The results of the 17 day visit to 95 marine sites and other numerous shoreline sites at seven atolls and reefs in the northern Marshall Islands demonstrate that qualitative data gathering procedures can be very useful in describing marine areas. Preliminary assessment of biological and ecological diversity can be accomplished without the need for transect and quadrant surveys if the purposes and goals of such studies are clearly identified in advance. With the primary emphasis of the 1988 expedition on evaluation of natural diversity and feasibility for park and protected area development, it was possible to collect valuable information on species, habitats, bathymetry, geomorphology, and oceanography, relying primarily on shallow water snorkeling observations. Coupled with the availability of aerial photographs, and previous map sources, field work was designed to sample a greater variety of habitats than would have been otherwise possible. Although the literature was scant and the opportunity to interview knowledgeable informants limited (since all but one of the sites were uninhabited), good maps and aerial photographs can be consulted to improve the efficiency of field work. Modern satellite imagery from the French Satellite SPOT now has resolution (10m) which can supplement photo interpretation of maps, especially where conventional aerial photographs are not available.

Collectively these data acquisition strategies may become increasingly important in evaluating the multitude of marine resources and habitats in the South Pacific. With many thousands of reefs and islands, and hundreds of atolls, many of which are remote, innovation will be required to allow rapid evaluation of particularly valuable areas. As population levels and development pressures increase, more and more natural marine areas will become vulnerable to exploitation and degradation. A systematic inventory and evaluation of candidate marine protected and park areas throughout the tropical Pacific will become an even more important goal of proponents of both conservation and development.

V. SUMMARY

Six atolls: Bok-ak (Taongi), Pikaar (Bikar), Tōke (Taka), Wōtto (Wotho), Ron̄dik (Rongerik), and Ādkup (Erikub) and one table reef (Jemo̧) were surveyed during a 17-day expedition in September 1988 to the Northern Marshall Islands to describe coral communities and reef formations as part of a larger natural diversity survey. Only observations using snorkeling gear, underwater writing slates and underwater cameras were possible during the approximately 2-day visit to each atoll. A total of 95 sites were surveyed, ranging from 12 to 20 sites per atoll. Additional observations were made during boat travel and walks along shorelines of islands. Over 160 species of reef corals belonging to 55 genera and sub genera were reported from the seven areas, including several species and one genus as new records from the Marshall Islands. The abundance and distribution of corals varied from one atoll to the next and may reflect geographic isolation from adjacent reefs, limitations on habitat diversity (in the case of Jemo), and limitations on larval recruitment (in the case of Bok-ak and Pikaar). Several of the coral communities and habitats were unique or have not been previously described. Many sites displayed exceptional coral development, and sites of special interest were identified on maps and are highlighted in the report. The reef geomorphology of the seven areas is also described and each belongs to one of three distinct physiographic categories:

i) small semi-enclosed atolls (Bok-ak, Pikaar, Tōke)
ii) larger open atolls (Wōtto, Ron̄dik, Ādkup)
iii) exposed table reef (Jemo̧)

Lagoon and adjacent perimeter reef formations at Bok-ak and Pikaar are elevated two or more feet above mean low tide level. These elevated reefs are living and perhaps growing, and are maintained by a combination of water being pumped into the lagoon from wave action on the windward sides, and the inability of the narrow passes to drain water from the lagoon at an equivalent rate during low tides. Unique features at both atolls associated with the elevated reefs include overhanging ribbon reefs, coral-algal dams, spillways and steep water level gradients in each atoll pass during low tide. Navigation through the passes during low tide is treacherous due to the narrow and meandering configuration of the passes, and the turbulent water flow caused by a two to three foot drop from the higher lagoon water levels over a short distance. Huge undisturbed giant clam populations (*Hippopus* sp. and *Tridacna* spp, but not the largest species, *T. gigas*) occur extensively in the lagoons of both Bok-ak and Pikaar. The author has never observed such high giant clam densities elsewhere in the central west Pacific. Furthermore, extensive sea turtle nesting and swimming activity was reported at Pikaar.

Tōke Atoll is more properly intermediate in form between the semi enclosed atoll and open lagoon atoll groups. Like Bok-ak and Pikaar, Tōke atoll has a single narrow pass on the western side. Unlike the other two atolls, Tōke's lagoon is deep and lacks the ribbon reef formations. Lagoon patch and pinnacle reefs are more circular in form, and lagoon reefs are not elevated above mean low tide levels as noted for Bok-ak and Pikaar. Giant clam populations at Tōke are smaller but include live specimens of the rare largest species, Tridacna gigas. The only sighting of a hawksbill sea turtle during the expedition occurred in northeast Tōke lagoon. Although uninhabited, Tōke is near Utrōk (Utirik) Atoll. The owners of Tōke Atoll reside at Utrōk, and Utrōk fishermen occasionally visit Tōke to harvest fish and shellfish. Small boat navigation through the channel and landing small boats at islands along the lagoon shorelines are relatively safe. Several important reef areas of special interest due to good coral development and diversity were observed at Tōke Atoll.

Jemo is one of only five table reefs in the Marshalls and the only one which was visited. Due to the lack of a lagoon, and heavy exposure to ocean waves and swells from virtually any direction, Jemo's reefs have unusual geomorphology and limited coral development. Only the southwestern end of the reef is shallow enough to form a reef flat exposed at low tide, upon which Jemo Island is situated. Elsewhere, Jemo's reef crest does not emerge at mean low tide and is dominated by a curious but extensive network of sand covered surge channels oriented in a north-south axis

The outer reef margins consist of scoured sloping pavements with limited coral growth. Coral species diversity is low, less than half of that of the other areas surveyed, and is probably controlled by exposure to heavy waves and limitations in habitat diversity and abundance. The very steep, deeper reef slopes showed higher coral diversity. The best coral development occurred within a semi-protected reef indentation on the north side. Jemo's beaches support the second largest sea turtle nesting population observed in the Marshalls (only Pikaar's population is reported to be larger). Jemo island itself is relatively inaccessible due to hazardous reef conditions, lack of protection from waves, and the lack of a safe approach to the island except during calm seas. The numerous sharks and large swells would also discourage snorkeling and diving interest at Jemo.

Wōtto, Roñdik, and Ādkup are the largest of the atolls visited during the September 1988 expedition, but are relatively modest in size compared to many other atolls in the Marshalls. All three have large passes, deep open lagoons, and a diverse set of lagoon and ocean reef habitats. Wōtto and Roñdik in particular have unique and aesthetically interesting coral and beach habitats, including pink sand beaches. A blue coral reef moat occurs at Roñdik, and diverse and flourishing coral and clam habitats occur at Wōtto. Boat passage through channels and lagoon access to islands are safe. The inhabitants of Wōtto have expressed strong interest in promoting tourism at their atoll and prior to our expedition, requested financial and technical assistance to develop a tourism facility.

From the standpoint of uniqueness of reef forms, Bok-ak, Pikaar, and Jemo all warrant special recognition and research interest. The huge giant clam populations at Bok-ak and Pikaar, and the large sea turtle nesting populations at Pikaar and Jemo also argue for marine and island reserve designations. When coupled with the extraordinary seabird nesting populations at Bok-ak and lesser but important bird populations at Pikaar and Jemo, all three areas should be established as part of a system of national ecological reserves (Thomas et al 1989). Such designation will require the cooperation of persons with traditional rights to these areas. All three of these areas are unsafe with respect to boat access and landing, which reinforces their preferred status as limited entry reserves. In particular, the clam and turtle populations would be vulnerable to over exploitation, and access to the three areas should be strictly controlled in any case.

Proposals to enlarge or widen the reef passes at Bok-ak and Pikaar to promote safe boat access would result in major and perhaps catastrophic impact to lagoon reefs. Aside from direct destruction of reefs, low tide water levels in the lagoons would probably drop, exposing and killing the living tops of elevated reefs throughout the atolls' lagoons. Circulation in the lagoons would also change and possibly harm resident giant clam populations.

Tōke and Wōtto Atolls seem well suited as possible national marine parks open to both tourism and resident recreational use. Residents could manage and monitor the areas as marine parks, perhaps as part of small scale tourism development. Access and landing at both atolls is relatively safe, accessible snorkeling areas exist, and diversity and development of coral reef environments is high. Although residents expressed strong interest in tourism and marine park development at Wōtto, it was not possible to query the Utrōk islanders on their views for similar development at Tōke. Nature based tourism and park use would benefit the natural and cultural resources in both areas if properly planned and managed.

Ādkup and Roñdik atolls likewise have many attributes supporting marine park designation. Ādkup, although uninhabited, is heavily utilized as a traditional harvest ("pantry") area by visiting fishermen and islanders from nearby Wotje Atoll. Any future designation of portions of Ādkup for marine park and sanctuary status should reflect the coordination with and the views of the traditional resource users and owners. Although specific areas of both Ādkup and Roñdik are suitable candidates for marine parks or reserves, there is less justification to designate the entire atolls as reserves or parks.

Western Roñdik Atoll could not be surveyed, but Bok (Bock) island is suspected as an important sea turtle nesting area due to its extensive white sand beaches. Follow-up observations could confirm the importance of the island for turtle nesting. Roñdik Atoll's pink sand beaches, blue coral moat, and luxuriant lagoon coral formations would be of great recreational interest to both visitors and residents.

The large populations of coconut crabs at Roñdik may eventually be heavily harvested since coconut crab is a favorite islander delicacy. However, Roñdik was exposed to fallout from the "BRAVO" atmospheric thermonuclear detonation at nearby Bikini Atoll in 1954. Fallout from the blast contaminated Bikini and the atolls of Roñlap (Rongelap) and Utrōk. Given the close proximity of Roñdik to these other atolls, a radiological survey of the atoll is warranted to determine possible health hazard from ingestion of crabmeat and coconuts. Coconuts are known to concentrate the radionuclides cesium-137 and strontium-90 in their tissues, based upon sampling of coconut trees at both Bikini and Āne-wetak (Enewetak) Atolls conducted by Lawrence Livermore

Laboratories. Since coconut is the preferred food of the crabs, radiological contamination of coconut crabs is a definite possibility. Consumption of Ron̄dik coconut crabs should therefore be discouraged until radiological tests have determined the crabs are safe to eat.

VI. ACKNOWLEDGEMENTS

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A number of officials in the Republic of the Marshall Islands provided critical support for the project: we thank Peter Oliver, Special Assistant to the Chief Secretary; Oscar De Brum, Chief Secretary; the late Stephen Muller, Director of the RMI Marine Resources Authority; Larry Muller, Captain of the patrol vessel Ionmeto I, and the vessel crew; Gerald Knight, Director of the Alele Museum; Alfred Capelle, RMI Resource Protection Officer; Abacca Anjain, Acting Secretary of Interior and Outer Island Affairs; and the atoll owners and land managers (alab) for granting access to their island and reefs. We thank the project leader, Dr. Lawrence Hamilton, Research Associate, EAPI for administrative support, and the late Dr. F. Raymond Fosberg of the Smithsonian Institution for sharing his extensive experience and advice on the Marshall Islands. Finally, I extend my appreciation to the other members of the expedition who assisted on the marine surveys, especially Peter Thomas, Virgil Alfred, Paul Maddison, and John Naughton; and to Linda Mizuguchi, Karen Tomoyasu, Chris Cabacungan, Jan Eber, Jody Oyama, Jennifer Gorospe, Mary Hayano, Gidget Tsui, and Karin Z. Meier for word processing and/or editing support. I thank Jim Laurel of Aspect Software Engineering Inc. and Karin Z. Meier of CORIAL for digitizing the maps, and preparing most of the map figures for this report. Finally, I thank Mr. Alfred Capelle for providing the correct spellings of place names used in the text and added to the maps.

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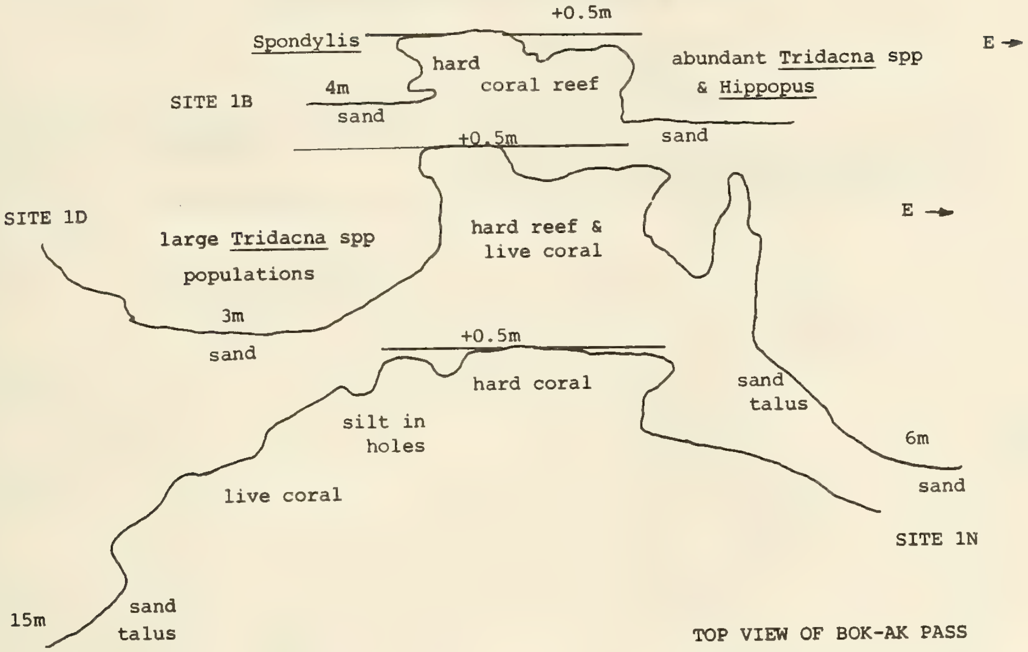
Appendix A.

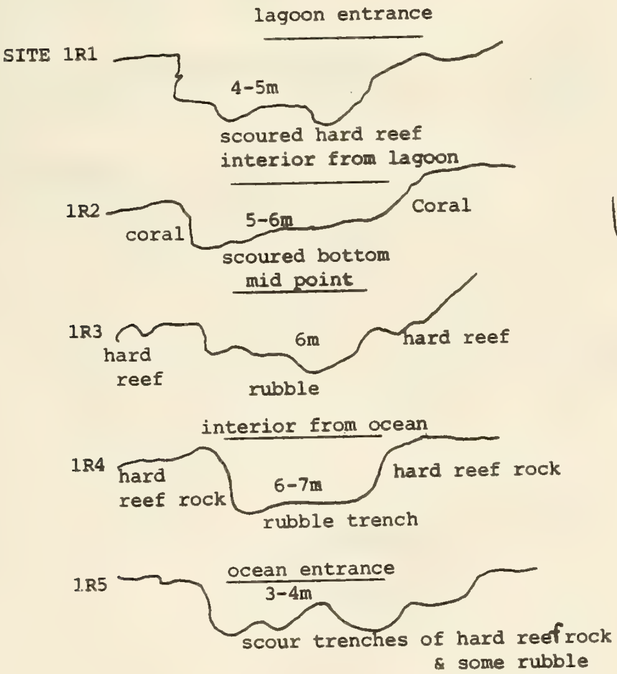
Fig. A-1

BOK - AK Atoll

REEF PROFILES: LAGOON AND PASS REEFS



TOP VIEW OF BOK-AK PASS



CROSS SECTIONS OF BOK-AK PASS

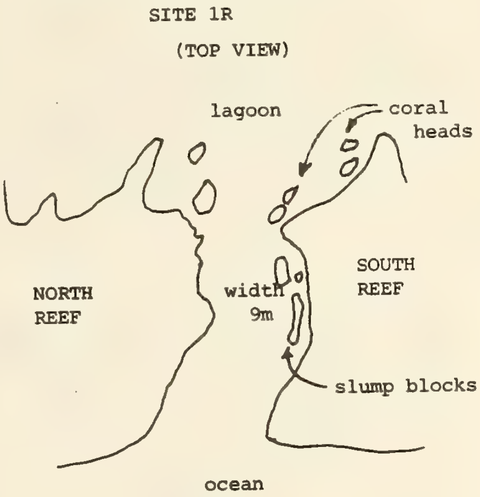


FIG A-2

BOK - AK Atoll

REEF PROFILES: EASTERN PERIMETER REEFS

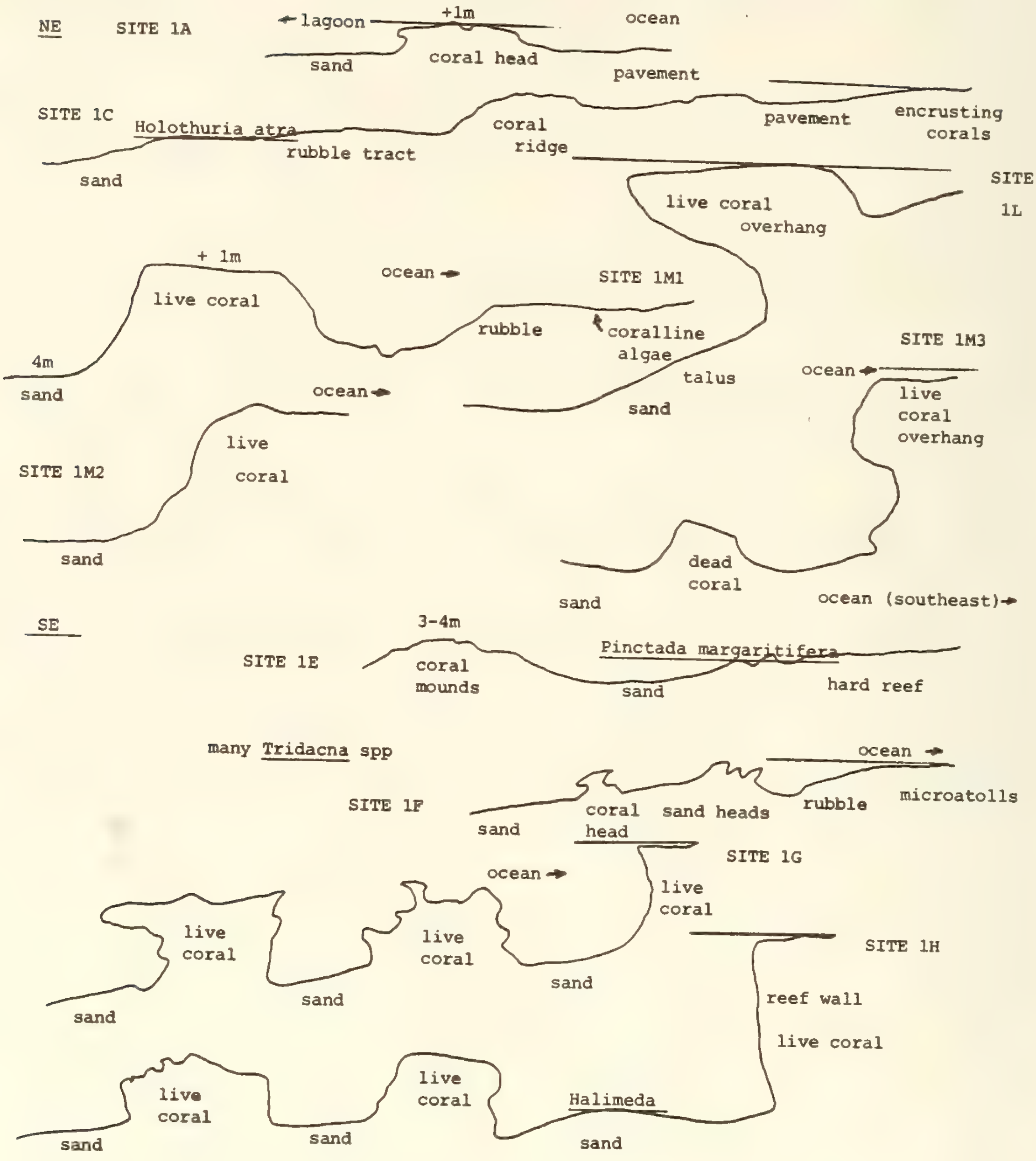


FIG. A-3
BOK - AK Atoll REEF PROFILES: WESTERN PERIMETER REEFS

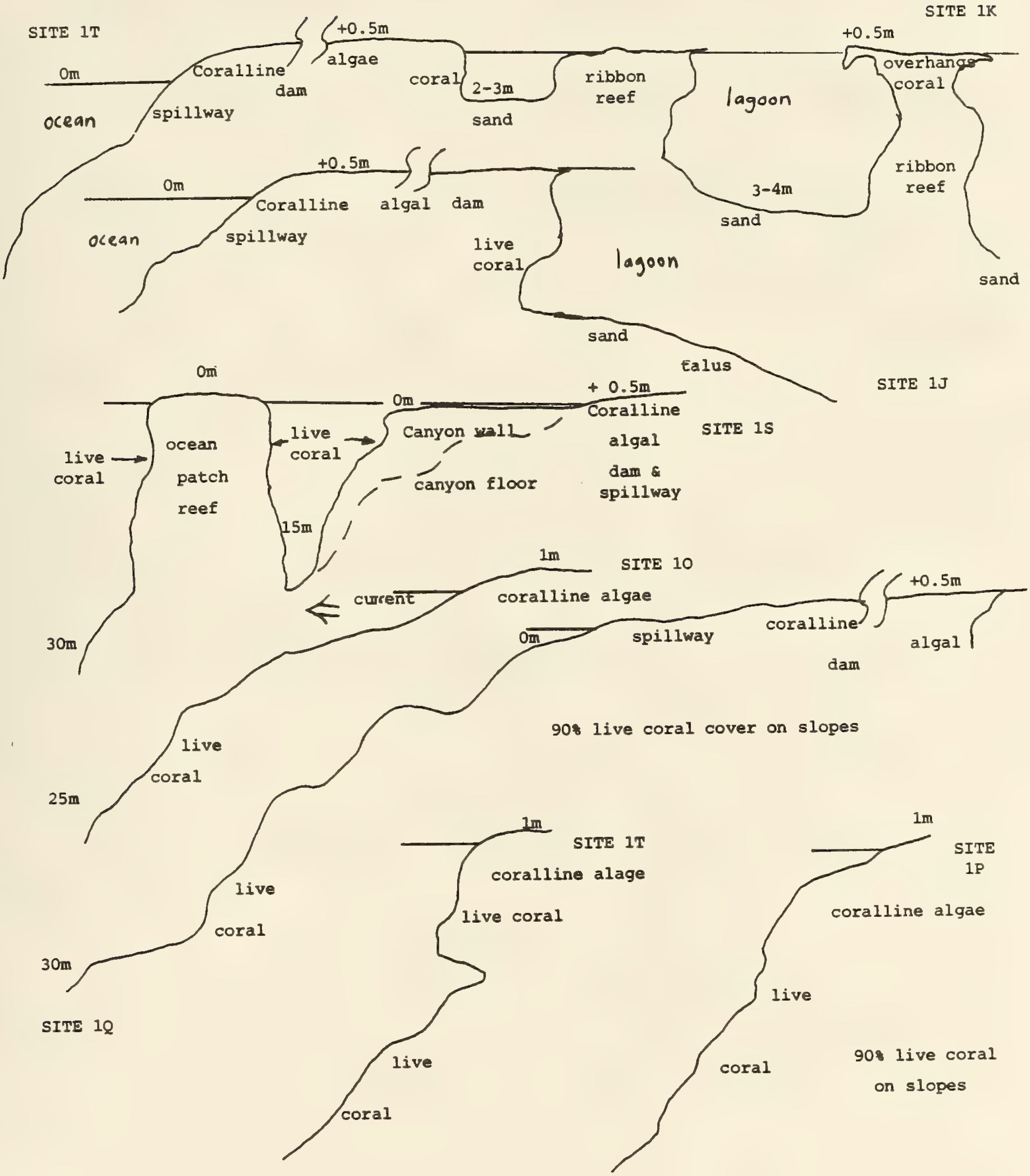


FIG. A-4

PIKAAR ATOLL REEF PROFILES: PERIMETER REEFS

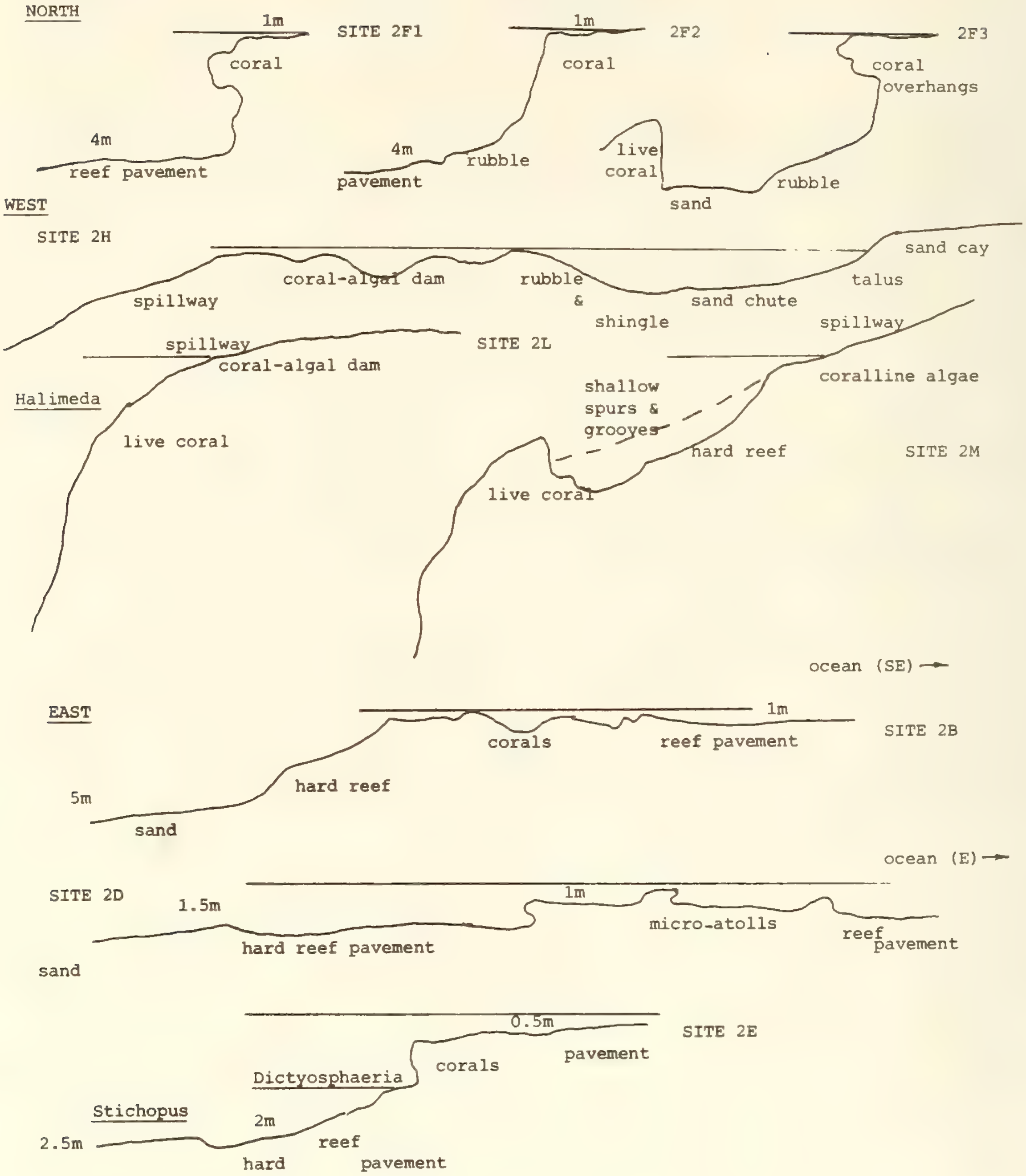


FIG. A-5

PIKAAR ATOLL REEF PROFILES: LAGOON REEFS & PERIMETER REEF

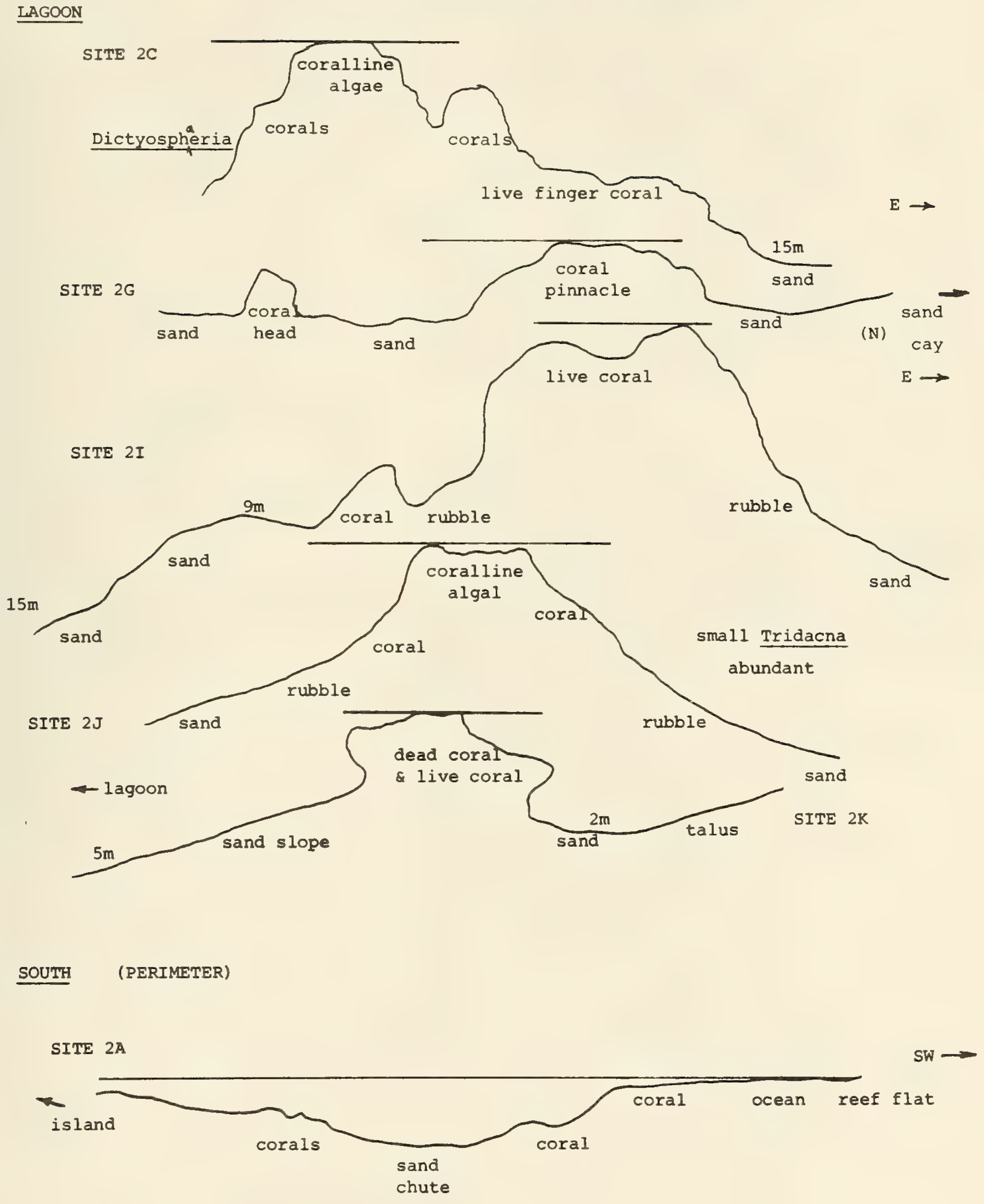


FIG. A-6
TŌKE ATOLL

REEF PROFILES: PERIMETER REEFS

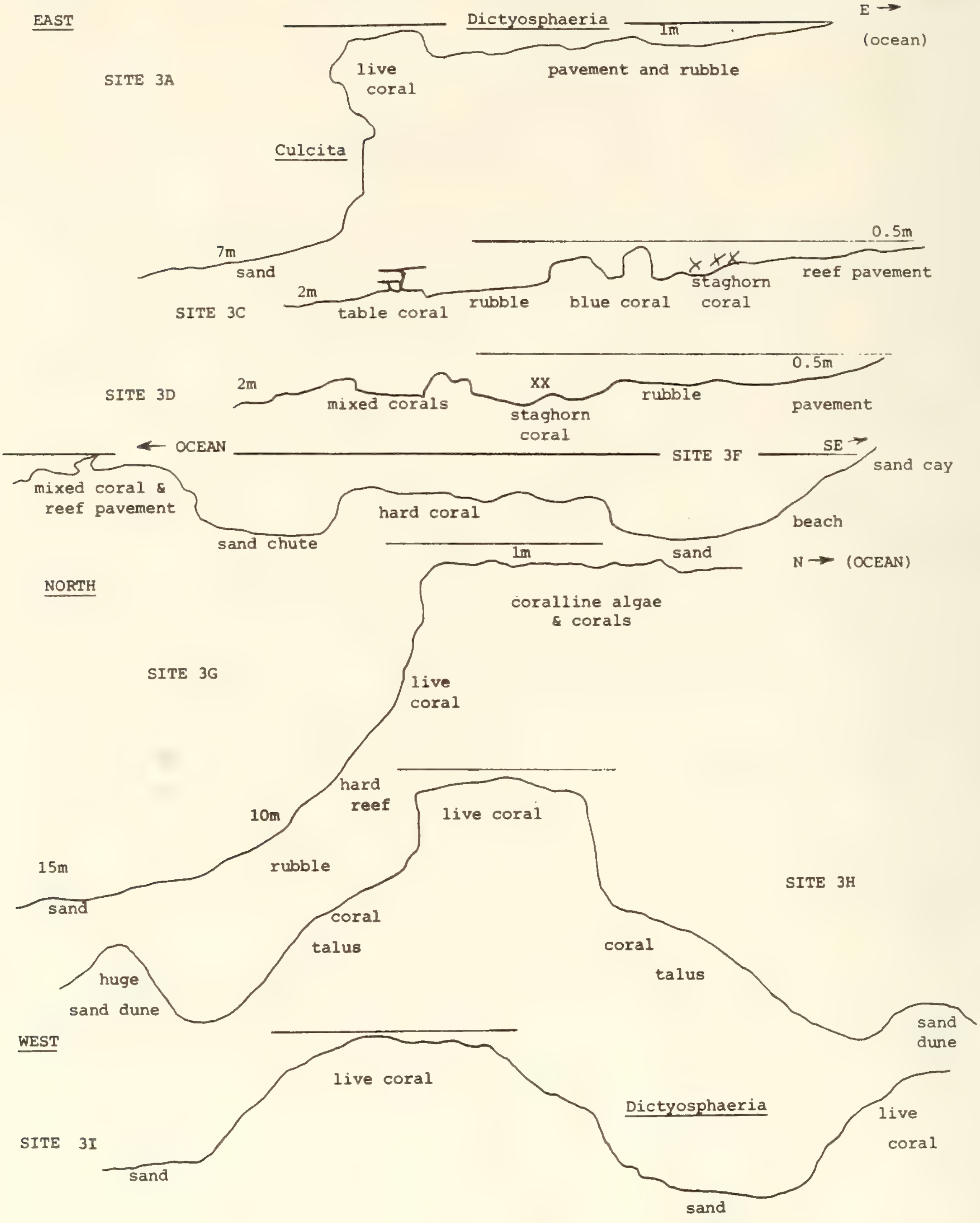


FIG. A-7
TŌKE ATOLL

REEF PROFILES: WESTERN PERIMETER AND LAGOON REEFS

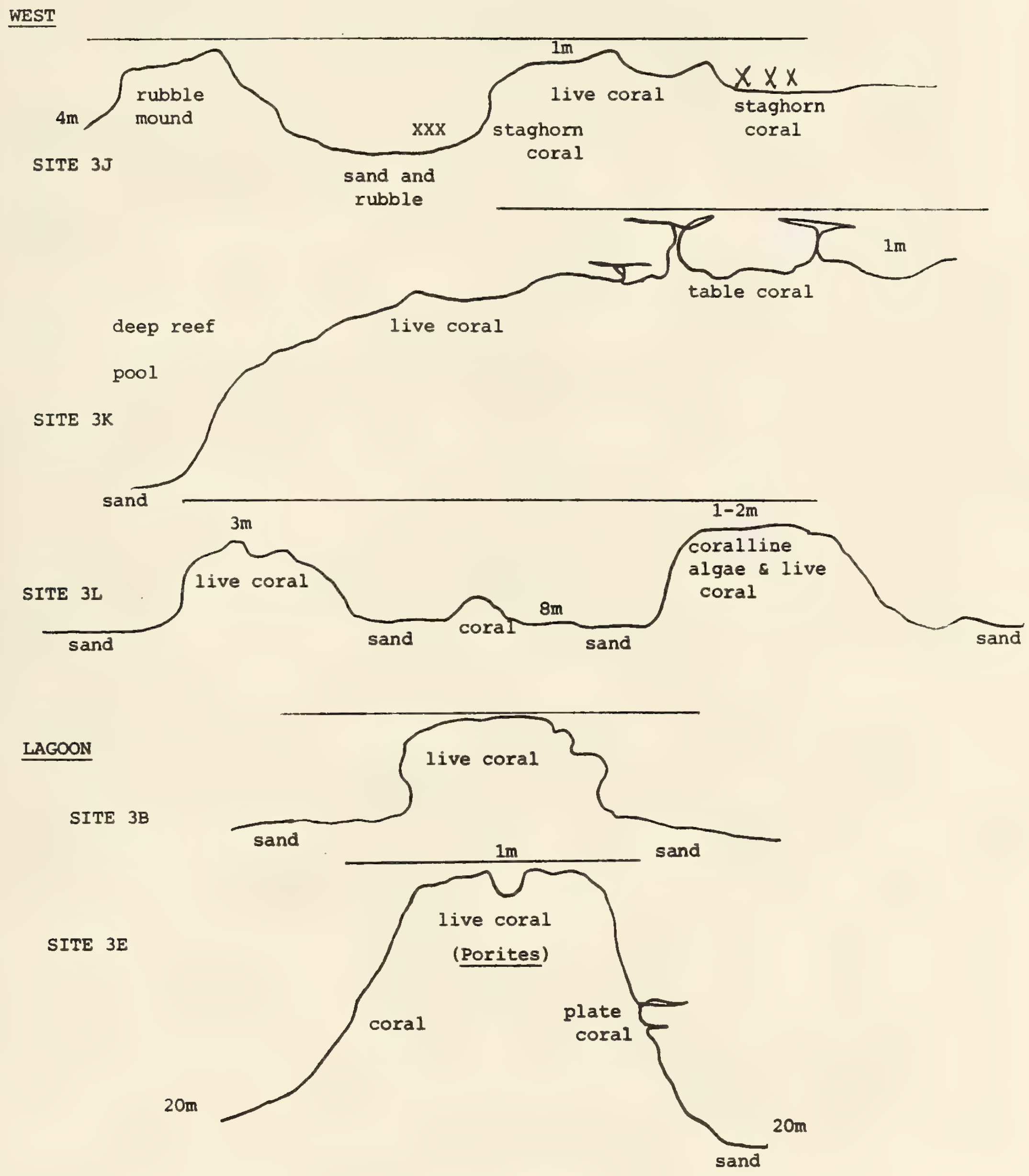


FIG. A-8

JEMO

REEF PROFILES: OCEAN SLOPES

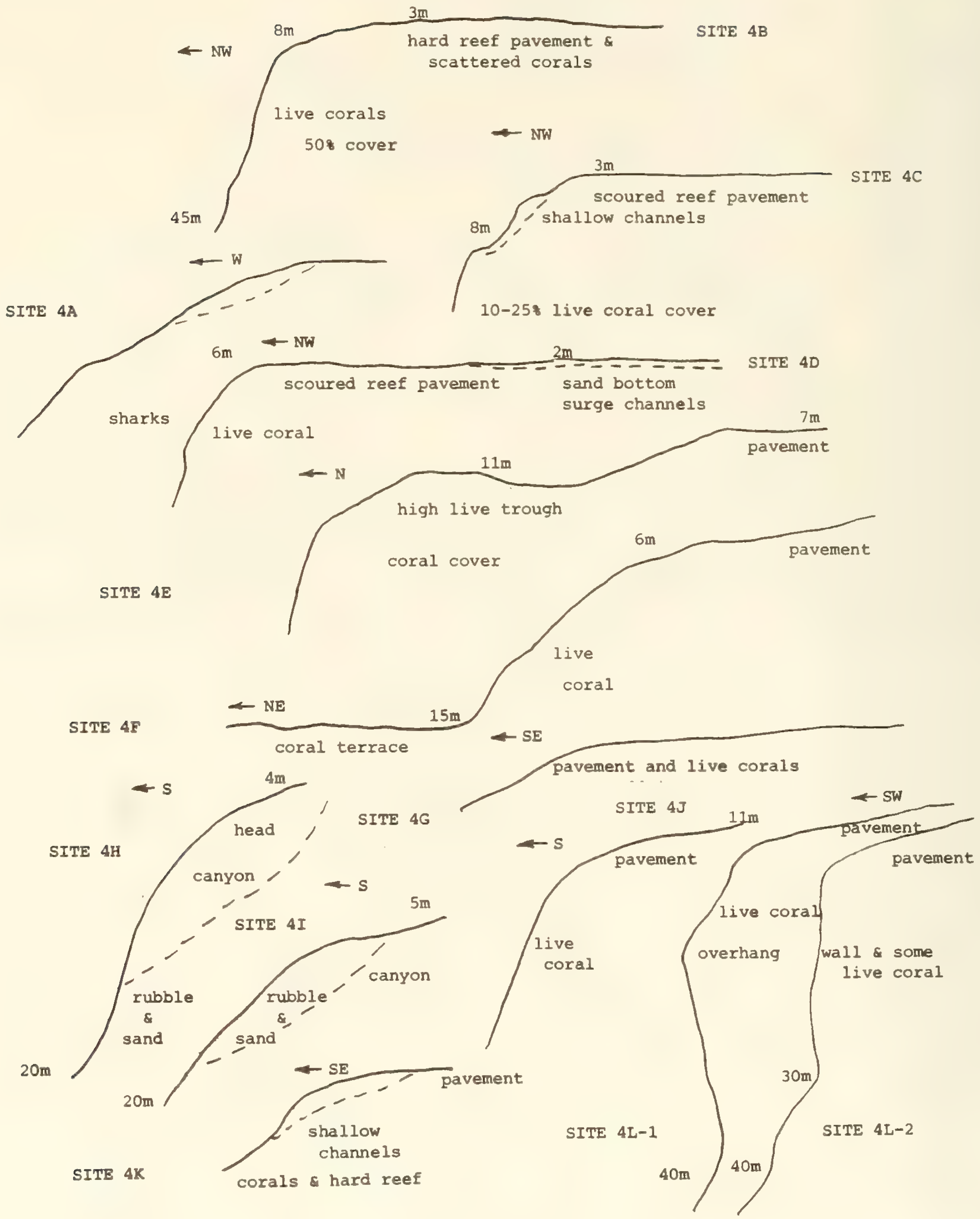


FIG. A-9

WŌTTO ATOLL
REEFS

NORTH

REEF PROFILES: NORTH AND EASTERN PERIMETER

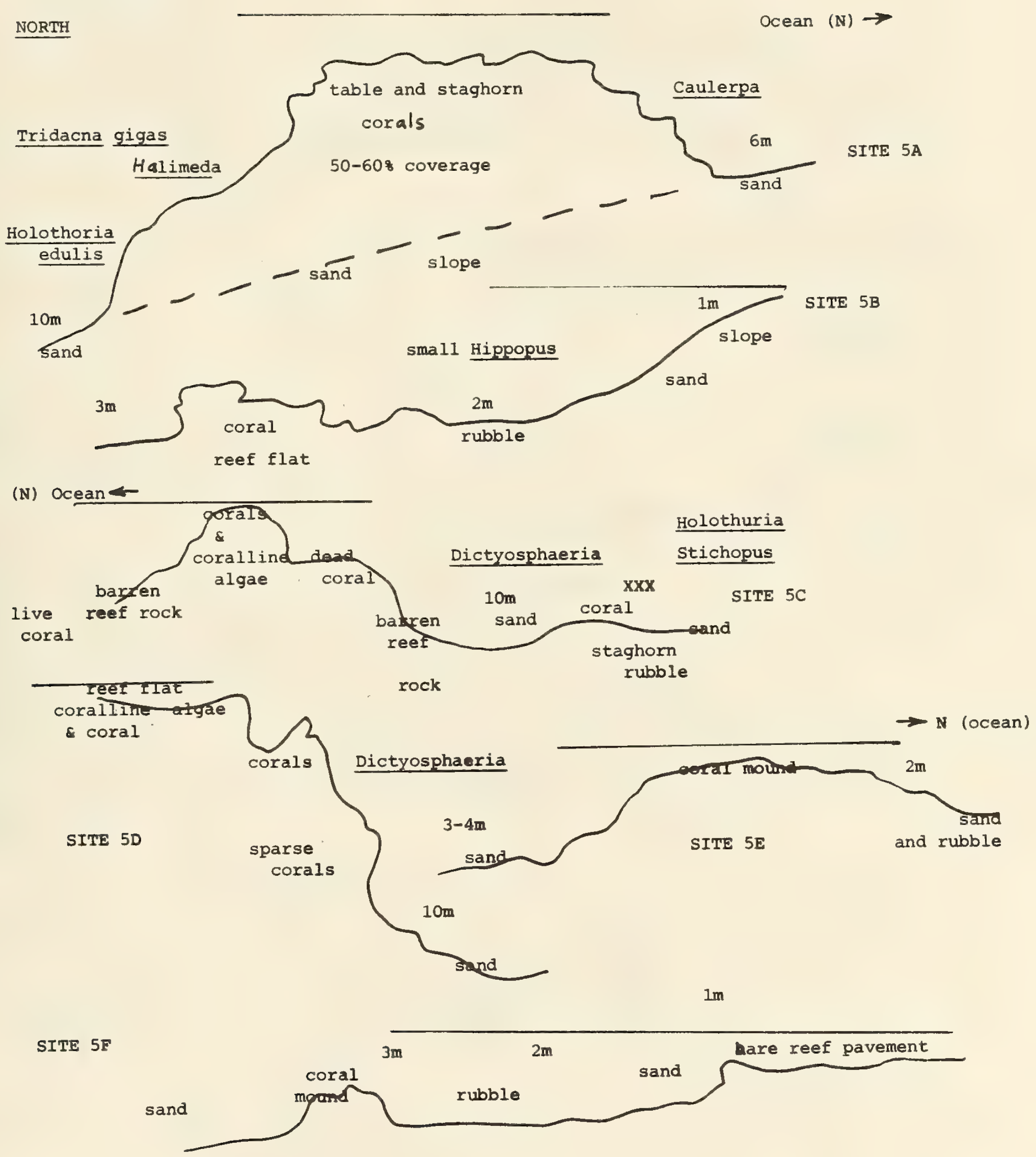


FIG. A-10

WŌTTO ATOLL REEF PROFILES: EASTERN AND SOUTHERN PERIMETER REEFS

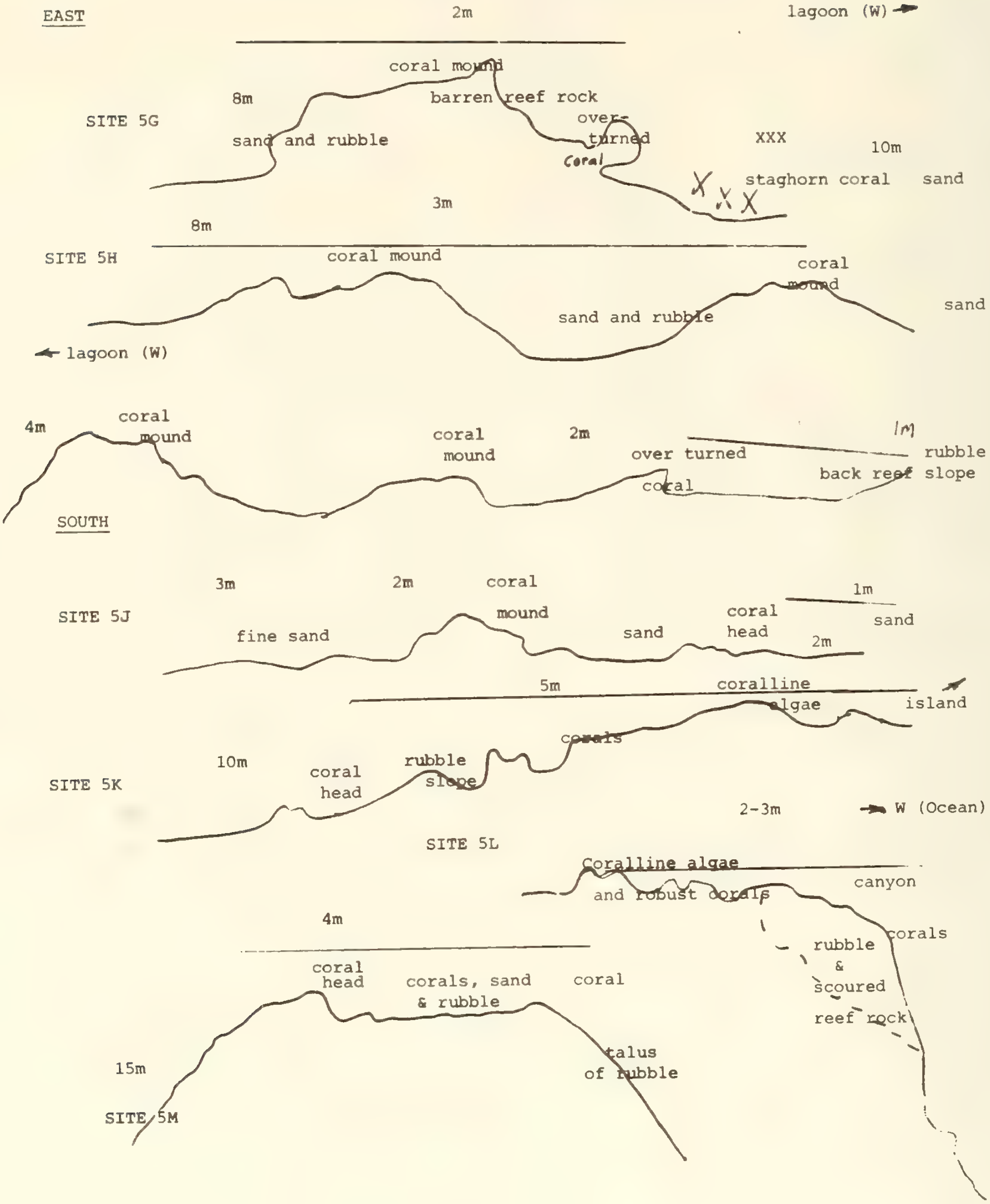


FIG. A-11

RON̄DIK ATOLL REEF PROFILES: SOUTHEAST PERIMETER REEFS

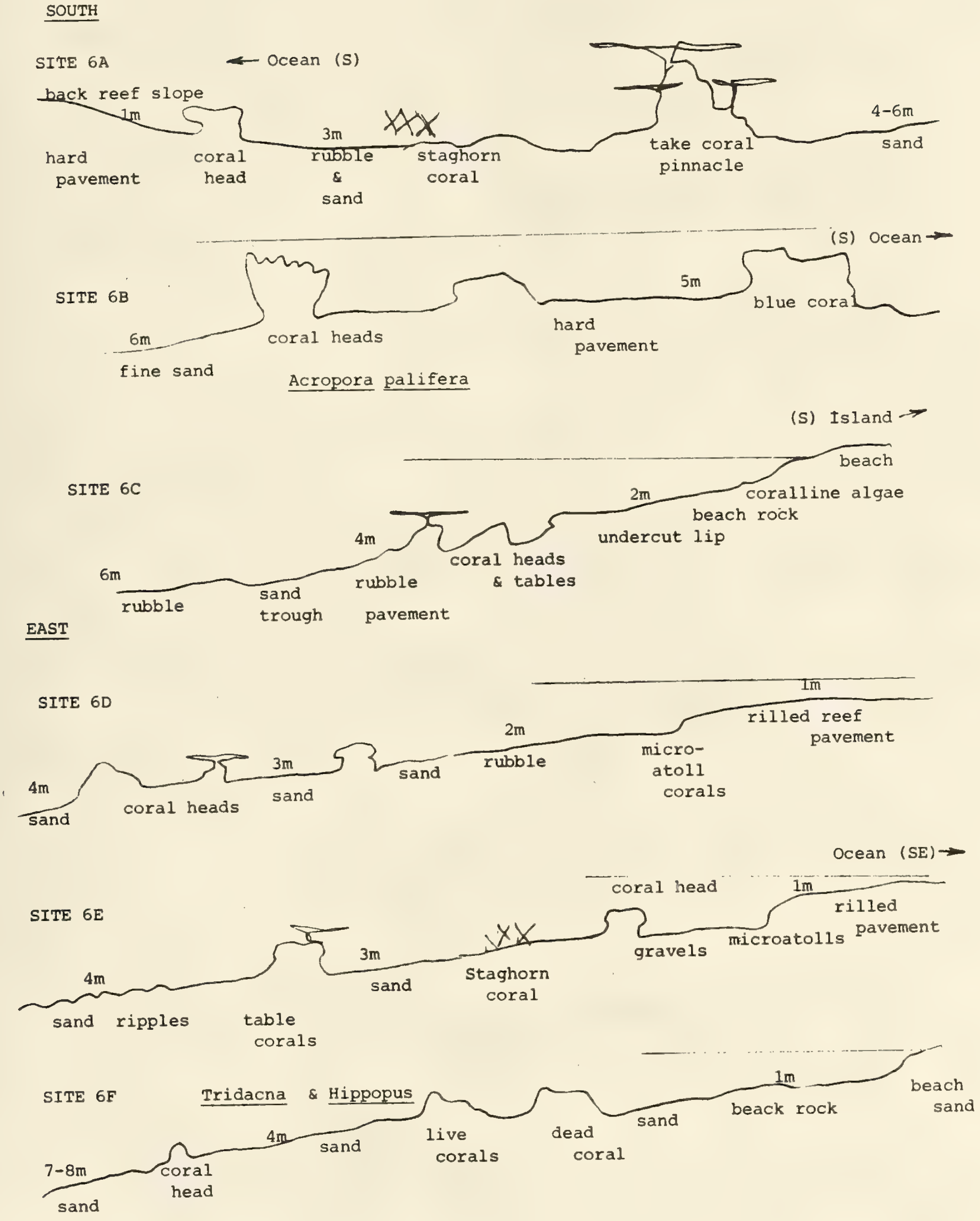


FIG. A-12

RON̄DIK ATOLL REEF PROFILES: NORTHEAST PERIMETER AND LAGOON REEFS

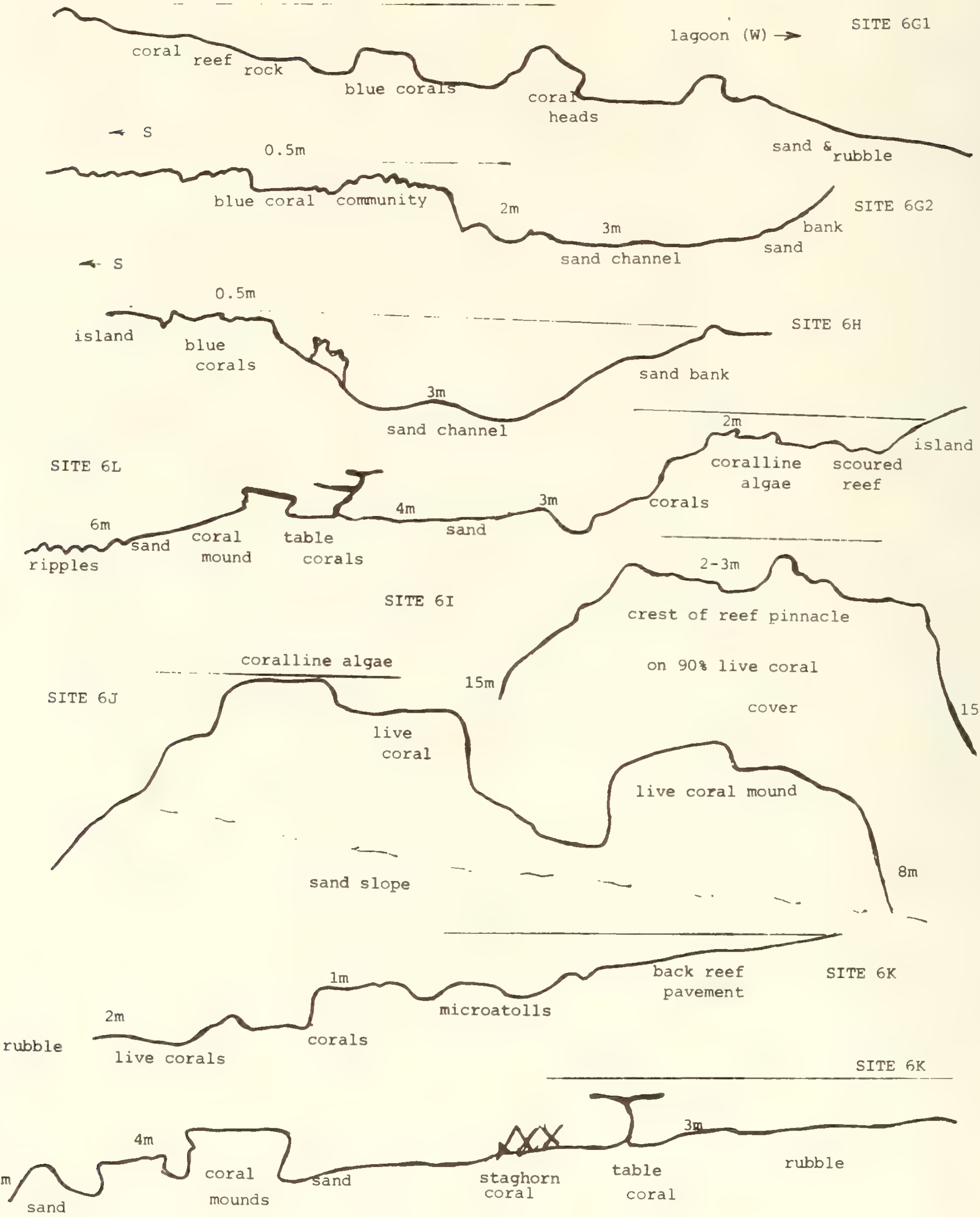


FIG. A-13

ĀDKUP ATOLL REEF PROFILES: SOUTHERN PERIMETER REEFS

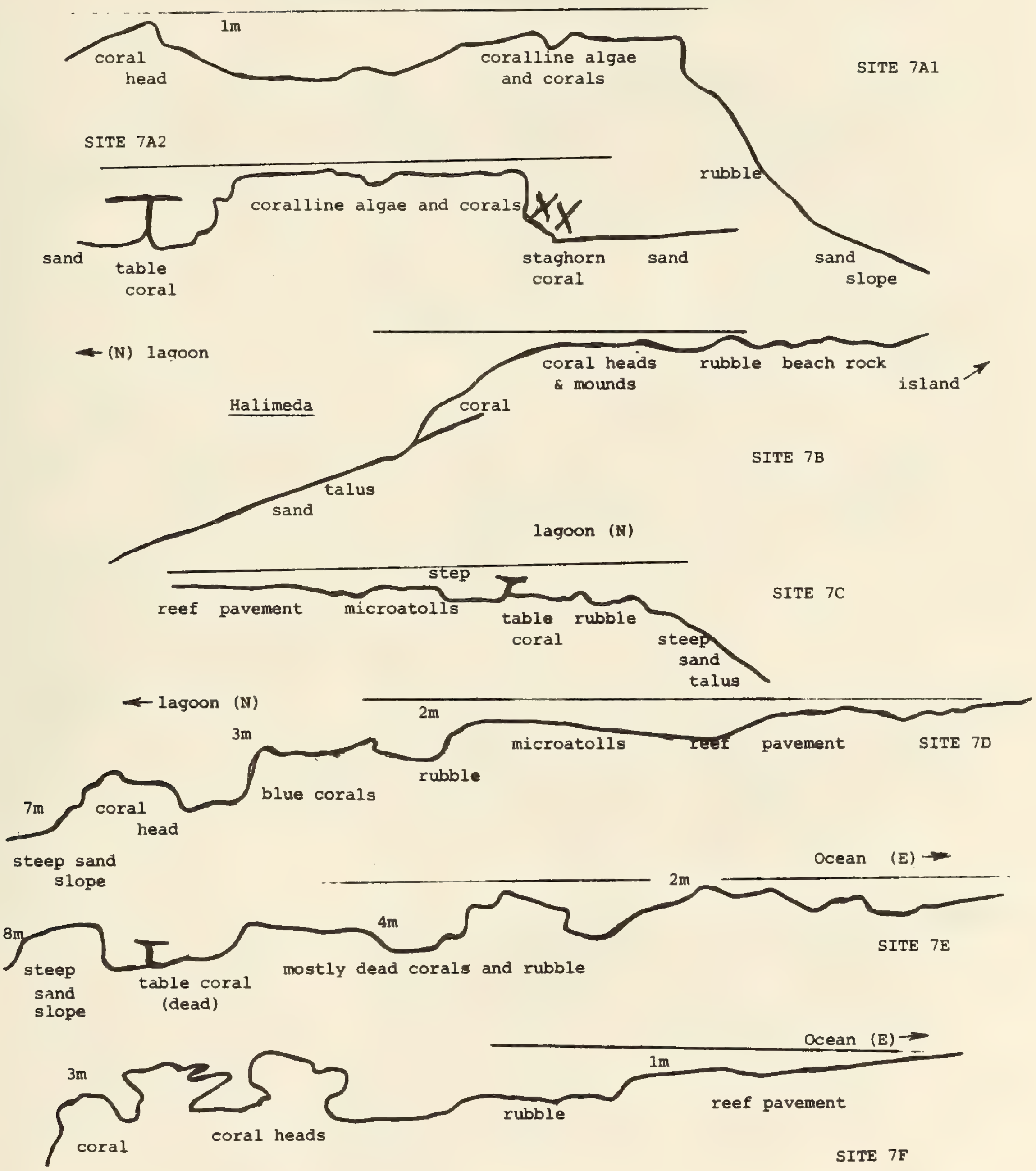
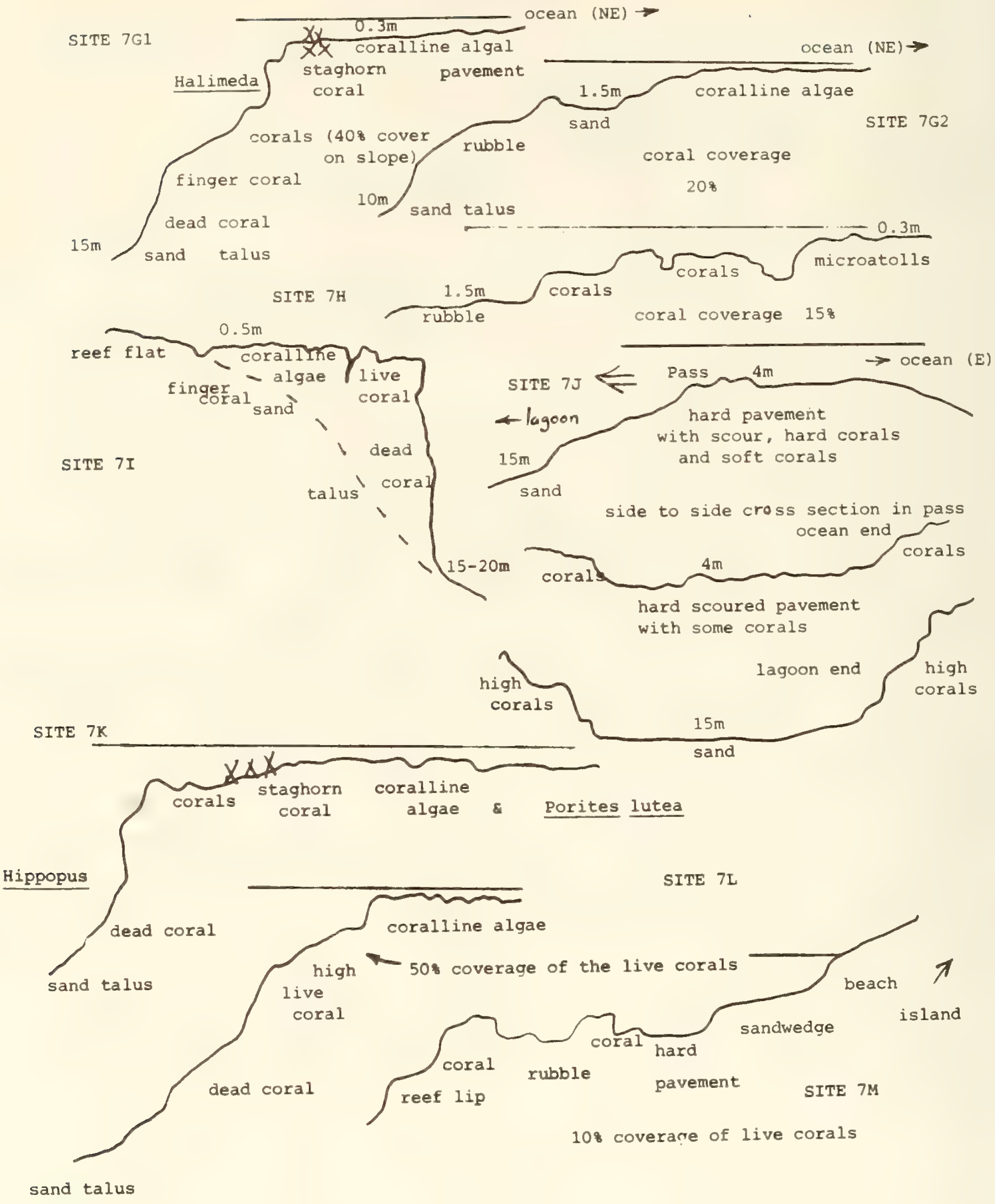


FIG. A-14

ĀDKUP ATOLL REEF PROFILES: NORTHERN PERIMETER REEFS



Appendix B.

Definitions for relative abundance terms used in the field for corals

SYMBOL	TERM	DEFINITION (WITHIN A ZONE OR HABITAT TYPE ON THE REEF)	DEFINITION (FOR THE REEF SITE AS A WHOLE)
D	dominant	the coral constitutes a majority in abundance or coverage (50% or more of total)	the coral contributes substantial abundance or coverage (25% or more of total) or is conspicuous in all zones
A	abundant	the coral contributes substantial abundance or coverage, or is very numerous	coral is conspicuous in most zones or is dominant within a single zone
C	common	coral present as several or more individuals or as a few larger colonies	coral conspicuous in only one or a few zones or locally substantial in a single zone
O	occasional	uncommon, present only as a few individuals, or present as a single conspicuous individual	present more than once but not substantially within a single zone
R	rare	reported only once as a single individual	reported only once from the reef

Appendix C.

Map sources for selected northern Marshall atolls.
AMS = Army Map Service Series W861 (all at scale 1:25,000, except Wōtto which has a scale of 1:50,000).
DMA = Defense Mapping Agency charts (various scales).

ĀDKUP (ERIKUB)
AMS - 8249 I SW, II NW, SW, III NE; IV NE, SE
DMA - none

BOK-AK (TAONGI)
AMS - 8066 III NE, SE; IV SE
DMA - 81626A (1:50, 190)

JEMO̧
AMS - 8152 III SW
DMA - none

PIKAAR (BIKAR)
AMS - 8258 IV NW, SW
DMA - 81626B, C (1:10,110; 1:50,200)

RON̄DIK (RONGERIK)
AMS - 7755 IV NE, NW, SE, SW
DMA - 81557A (1:50,000)

TŌKE (Taka)
AMS - 8155 III NE, NW, SE, SW
DMA - 81616A (1:10,000; 1:50,310)

WŌTTO (WOTHO)
AMS - 7352 II (1:50,000)
DMA - 81030C (1:316,120)

ALINGINAE
AMS - 7455 II NW, SE, SW; III SE
DMA - 81557B (1:72,500)

Appendix D.

Index of aerial photographs consulted during the study from 1978 color (EG&G) and 1944-1945 black-and-white U.S. War Dept. (VD3) sources, the latter at the Bernice P. Bishop Museum Map and aerial photo collections, Honolulu.

RON̄DIK (RONGERIK) ATOLL

EG&G Roll 8, perf 2234: frames 59-60, 62, 70-79, 82-90, 93-95, 101-110 (35 negatives, scale 1:30,000; 16 Aug 1978)

VDB - oblique aerial photos only

TŌKE (TAKA) ATOLL

EG&G Roll 7, perf 2205: frames 22-23, 102-106, 110-123, perf 2185: frames 208-216 (38 negatives, scale 1:30,000; 11 Aug 1978)

VDB - p. 40316-36 frames 1-14; VD3-AP47A figures 1-41; and VD3 - AP47B photomosaic (55 negatives, scale unknown; 5 March 1944)

PIKAAR (BIKAR) ATOLL

EG&G Roll 12, perf 2305: frames 9-94, 98-103, 121, 123, 125, 137-139 (16 negatives, scale 1:30,000; 8 Aug 1978)

VD3 - oblique aerial photos only

WŌTTO (WOTHO) ATOLL

EG&G Roll 10, perf 2259: frames 4, 6, 8, 10, 54, 56-59, 108-109, 116-118, 134-138, 153-157, (24 negatives, scale 1:30,000; 18 Aug 1978)

VD3 - AP41B frames 1-39 (39 negatives, unknown scale; 29 Feb 1944)

JEMO̧

EG&G Roll 1, perf 2096: frames 33, 35, 36 (3 negatives, scale 1:30,000; 29 July 1978), Roll 2, perf 2122: frame 150 (1 negative, scale 1:8,000; 5 Aug 1978)

VD3 - oblique aerial photos only

ĀDKUP (ERIKUB) ATOLL

VD3 - AP16A frames 1-8 and VD3-AP16B frames 1-2 (10 negatives, unknown scale; 4 Feb 1944)

BOK-AK (TAONGI, POKAK) ATOLL

VD3-12, frames 1-10 (10 negatives, unknown scale; 28 Mar 1945)

ATOLL RESEARCH BULLETIN

NO. 420

QUATERNARY OOLITES IN THE INDIAN OCEAN

BY

C.J.R. BRAITHWAITE

ISSUED BY
NATIONAL MUSEUM OF NATURAL HISTORY
SMITHSONIAN INSTITUTION
WASHINGTON, D.C., U.S.A.
AUGUST 1994

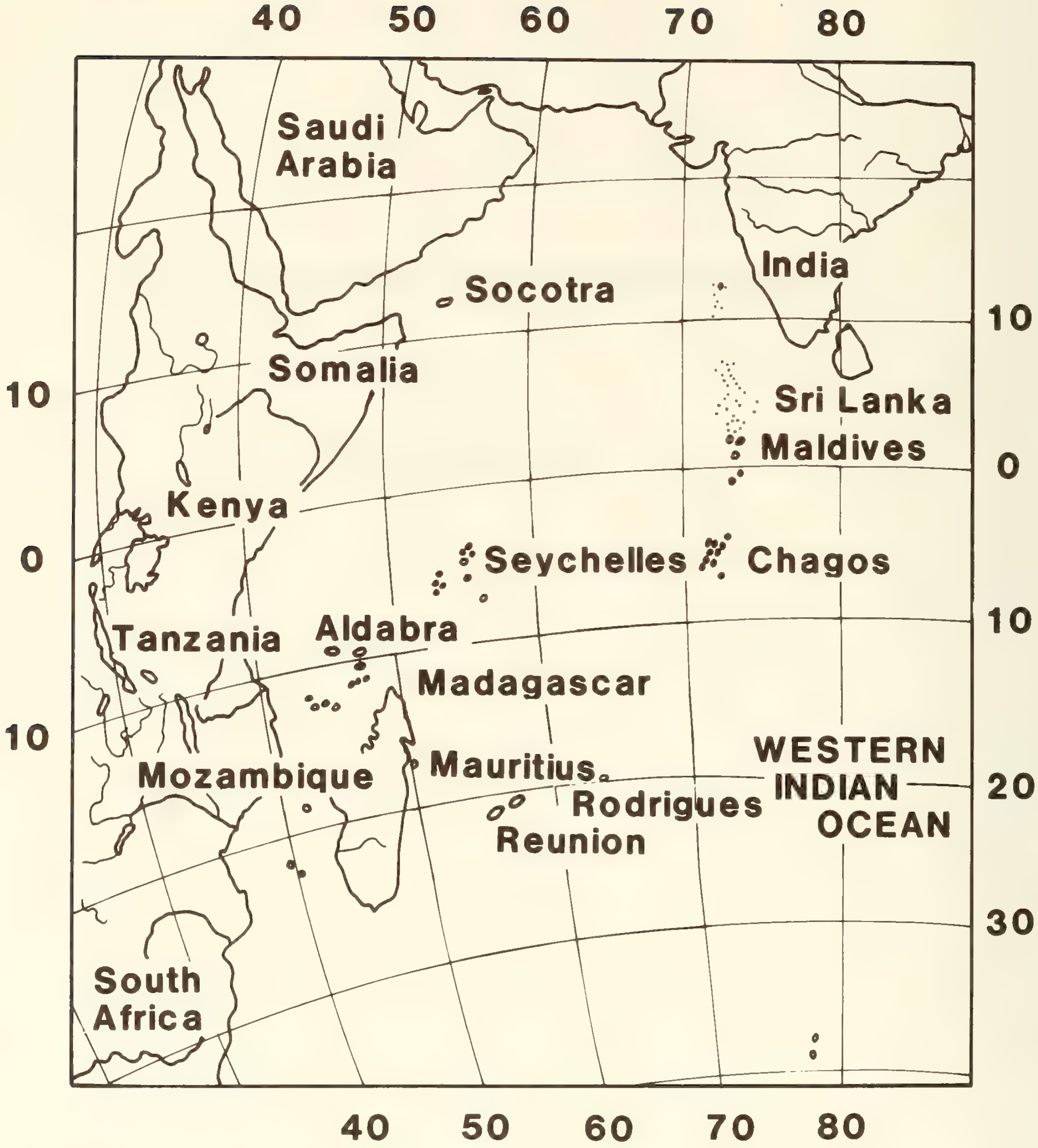


Fig. 1 General map of the Indian Ocean indicating positions of the principal locations referred to in the text.

QUATERNARY OOLITES IN THE INDIAN OCEAN

BY

C. J. R. BRAITHWAITE

ABSTRACT

Aeolian calcarenites from Rodrigues in the Western Indian Ocean include oolites. No recent oolites are recorded in the Indian Ocean and there is only one other Pleistocene record. The calcarenites are compared with deposits in the Seychelles, East Africa, India, and South Africa which consist of marine-derived bioclasts. In general they indicate critical water depths over generating shelves and thus particular stages in sea-level change. They are characteristic of both early phases of cooling and later stages of warming events. There seems to be no explanation for the restricted distribution of oolites in the Indian Ocean.

INTRODUCTION

Aeolianites are widespread in the Pleistocene deposits of the Western Indian Ocean. Those on Rodrigues are unusual in that those on the east coast consist of oolites with a relatively small bioclastic component. With the exception of deposits in Kathianar in India, described by Chapman (1900) and Evans (1900), these are the only oolitic deposits known from the Pleistocene or Holocene of the Western Indian Ocean.

FIELD DESCRIPTION

Rodrigues lies about 650 km east of Mauritius, Lat. 19° 42' S, Long. 63° 25' E (Fig. 1). It is approximately 18.3 km long and 6.3 km wide, consisting predominantly of young undersaturated basalts erupted between 1.5 and 1.5 million years ago (McDougall *et al.* 1965). The south-eastern and south-western margins of the island are blanketed by a discontinuous cover of cross-bedded calcarenites (Fig. 2). These were known a hundred years ago when they were described by Balfour (1879) and Slater (1879) who visited the island during the Transit of Venus expedition to make observations on the general geology. Their reports describe caves in these limestones in which the bones of the Solitaire and other flightless birds were found.

Although Rodrigues has a surface area of only about 120 km^2 the platform on which it rests is at least 1650 km^2. The island surface slopes gently outwards to about 100 m depth before plunging into deeper water. The island is bordered on its south-western coast by a fringing reef 4-8 km from the shore and Admiralty Charts show that the lagoon area within this is generally very shallow (McDougall *et al.* 1965). However, the shallow platform beneath extends a considerable distance both to the west and the east and, as will be shown, probably played a significant part in the formation of the calcarenites.

Most of the calcarenites are bioclastic and were originally marine, but those in

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south-eastern localities (Pointe Coton, Trou d'Argent) are clean-washed oolites. In both south-eastern and south-western areas grains are well rounded and well sorted within individual laminae. Cliff sections show well-defined high-angle cross bedding in sets of up to 10 m, forming cosets locally of more than 20 m thickness (Figs. 3 and 4). Cross-laminae dip at angles up to 30-35° and set-bounding surfaces generally dip a few degrees in a seawards, (generally southerly) direction. In some areas the upper margins of dunes are full of casts of branching root systems which imply colonization by substantial trees. There are, however, no distinctive *terra rossa* or palaeosol deposits and plants must have grown in unconsolidated sand before and perhaps during cementation.

The thickness of the calcarenites is quite variable. In western localities they blanket a gently undulating ramp, while in the east they occupy an erosional bench cut into the underlying basalts. Significantly, in both areas basal surfaces appear to extend below present sea-level. McDougall *et al.* (1965) recorded these limestones as occurring at more than 60 m above present sea-level, while Snell and Tams (1920) claimed that they extend up to 500 ft (165 m). Present observations suggest that the lower figure is more realistic. The thickest sequences are found in the south-west of the island in the area of Caverne Patate where cave systems penetrate at least 30 m of limestone. Montaggioni (1973) suggested that typical thicknesses are 15-20 m).

McDougall *et al.* (1965) thought that the depositional morphology of the calcarenites had been obscured by recent erosion. In fact, low dune ridges can be seen in south-western areas and air photographs reveal a spectacular series of parallel dune crests facing north and north-east and having a wave length of from tens to hundreds of metres. These extend for several kilometres from the present shoreline (Fig. 5). Groups of steep foreset laminae are visible on air photographs and can be traced across outcrops. Interdune areas are less conspicuous and are characterized in limited outcrops by low angle lamination and shallow troughs.

PETROGRAPHY

The oolites have a mean diameter of about 300µm (medium sand), many nuclei are dark micritic peloids while others are bioclasts. Cortical layers have the tangential structure typical of recent aragonitic ooids and may be more than 100µm thick (Fig. 6). Bioclast calcarenites consist predominantly of foraminifera, including *Marginopora* and *Heterostegina*, together with echinoderm plates, calcareous algal fragments (cf. *Goniolithon* and *Halimeda*), mollusc shell and coral fragments. In the samples examined grains have a mean size of 400-800µm. The marked contrast in grain typebetween oolitic and bioclastic rocks are paralleled by differences in mineralogy and diagenetic history. The bioclastic limestones include both aragonite and calcite (identified by X-ray diffraction) but have only a sparse fine-grained blocky calcite cement. This is restricted to patches where it forms meniscus bridges between grains and occasional pendant drops, suggesting deposition in the vadose zone, although it lacks the fibrous or prismatic textures typical of such environments. By contrast, in oolites, the ooliths themselves consist of aragonite and they are commonly embedded in a coarse blocky calcite cement which may completely fill pores and locally extends inwards from grain surfaces as a neomorphic replacement of the original tangential structure.

INTERPRETATION

The distinctive high-angle lamination which characterizes the calcarenite deposits on Rodrigues, and the occurrence of calcarenites over such a range of altitude, seems to confirm an aeolian origin. Submarine sand-waves might be of similar size but would generally be expected to have lower angle cross-bedding and are unlikely to have accumulated over such a slope. They would, moreover, have had to be related to a sea-level more than 60 m higher than at present. Deposition of these rocks must have occurred at a time when sea-level stood **lower** than at present, perhaps by about 10 m. However, the sediments were of marine origin and reflect generation in shelf environments. Thus, sea-level must have been high enough to maintain a permanent water cover over a sufficiently large area. The large area of gently-sloping surface beneath present reefs would have ensured that a suitable shelf was present over a range of sealevels, although not during the glacial maximum. Grains generated within the shelf were swept onshore by storm waves and accumulated as beach and, ultimately, dune deposits, the latter probably migrating several kilometres from the shoreline. Correlation with a lower sea-level implies a general correlation with a cooler climate.

THE AGE OF THE DEPOSITS

Two different calcarenite types are present on Rodrigues and since lithological variations are paralleled by diagenetic differences the rocks are likely to be of at least two different ages. Montaggioni (1970) referred to **three** separate dune assemblies in the eastern area but these have not been identified here. The calcarenites have not been precisely dated but it is clear that they are not Recent. The active phase of accretion was followed by a passive phase of colonization by trees, and the whole assemblage has been dissected by a mature karst system which, judging from the included fauna, is at least late Pleistocene (see again Slater, 1879). However, the ages inferred for these deposits have been determined by reference to associated limestones. Montaggioni (1970) regarded them as of the same age as calcarenites on Mauritius. In this interpretation they should equate with high sealevel stand dates of ^{230}Th/^{234}U ages of 120 ±15-20 ka obtained by Battistini (1976) for Pleistocene limestones on Mauritius, which were compared in turn with dates of 160 ±40 ka and 110 ±40 ka given by Veeh (1966) and of 114 ±6-7 ka and 104 ±4-6 ka given by Elbez (1976). However, none of these ages was obtained from calcarenites and, for reasons of environment, it is unlikely that the aeolian calcarenites on Rodrigues were contemporary with the marine deposits from which the dates were obtained. There are no observations of rocks overlying the Rodrigues calcarenites and this contrasts with the relative positions of aeolianites in Kenya (Braithwaite, 1984) and on Aldabra (Braithwaite *et al.*, 1973) which are probably substantially older (see below).

OTHER INDO-PACIFIC DEPOSITS

Within the western Indian Ocean aeolianites (calcarenites with characteristics similar to those described) have been identified in a number of areas. In northern Madagascar Battistini (1976) recorded dune-bedded carbonate rocks low in the Pleistocene. These overlie his Recif I but appear to be older than Recif II, dated at 160 ±10-15 ka. This dune assemblage is said to be more than 200 m thick but only about 15 m are shown on the published synthetic section extending for 25 km in the south. It is considerably thinner on the north and east coasts. Like the deposits on Rodrigues the top is marked by non-deposition, in this case resulting in a dissected erosion surface and what are described as "decalcified pockets".

In East Africa, calcarenites with high angle cross-bedding and consisting of marine-derived grains are exposed on the northern coast of Kenya, south of Malindi, and in the extreme south, near Shimoni and Wasini Island (Braithwaite, 1984). In both of these areas the deposits are believed to extend **below** present sea-level but are stratigraphically **above** coral-bearing marine limestones which were apparently the source of material dated by Battistini (1976) as 240 ±40-70 ka. They are overlain by younger limestones which have been described by Crame (1980, 1981) and which appear similar to the youngest coral-bearing limestones on Aldabra. Aldabra has a small area of calcarenites with high angle cross-bedding exposed on the south coast (Braithwaite *et al.,* 1973). These are overlain by two marine limestones, the youngest of which has been dated by Thomson and Walton (1972) as forming between 118-136 ±9 ka. It is this which is equivalent to the younger coral limestone in Kenya. These calcarenites, in which grains are entirely of marine bioclasts, formed when Aldabra was a shallow marine platform with only small sand cays accumulating along what is now the southern coast and in a relatively large area to the north-east.

The aeolian calcarenites of southern India have already been referred to (Chapman, 1900, and Evans, 1900). Knox (1977) described other calcareous aeolian dune deposits of supposed middle to late Pleistocene age from Saldanha Bay in South Africa. These average 30 m in thickness but are reported by Visser and Schoch (1973) to be as much as 88 m locally. Once more they consist predominantly of marine bioclasts.

DISCUSSION

The descriptions given reinforce the view that aeolian deposits are a common, even characteristic, feature of Pleistocene limestone successions in the Indian Ocean. They are of a variety of ages but have commonly (although not exclusively) formed in areas which do not have present day dunes. It might be argued that winds were stronger in the past and that the absence of present-day dunes is a reflection of the inadequacy of present day winds. However, this is unlikely, Bagnold (1941) and Wolman and Miller (1960) have indicated that in dune formation the net transport of sands is controlled more by prevailing winds above threshold velocity than by extreme wind events. In almost all of the Indian Ocean examples the sands were of medium to fine grade and therefore do not reflect excessive wind speeds. Elsewhere, in Bermuda (Mackenzie 1964), aeolianites show palaeowind vectors which are essentially the same as present directions while in the Turks and Caicos islands (Lloyd *et al.* 1987) palaeocurrents in both Pleistocene and recent aeolianites (which include oolites) can be related to south-easterly Trade Winds.

The presence of oolites remains enigmatic. Their formation, and that of the bioclasts, was probably critically dependent on water depths over the generating shelves. If sealevel is too high shelves are deeply flooded and unlikely to reach the necessary saturation conditions. If it is too low shelves are restricted (or dry) and again fail to generate sediment. Thus it seems that the oolites and the aeolianites generally are characteristic of early stages of cooling and later stages of warming events when sealevel was only marginally below its present position. Why they were not more widespread in the Indian Ocean, where there are several extensive shallow banks, is not known. Marine-deposited oolites may be present but if they are it is likely that all lie beneath present-day shelves.

ACKNOWLEDGEMENTS

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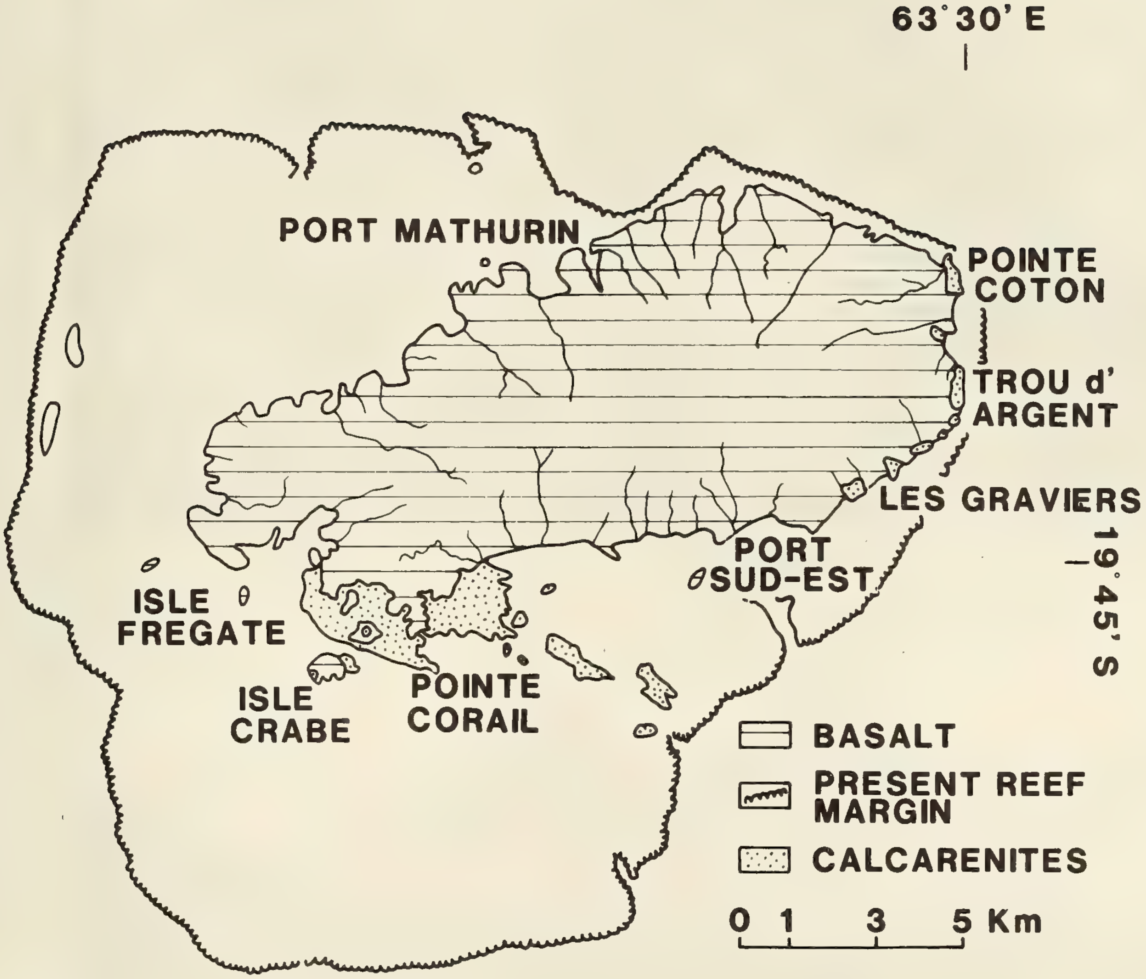

Fig. 2 General map of Rodrigues showing distribution of main areas of calcarenites. Based on air photographs and Montaggioni (1973).

Fig. 3 High angle dips in cross-laminae of calcarenites. Sante François, Rodrigues. Metre rule gives scale.

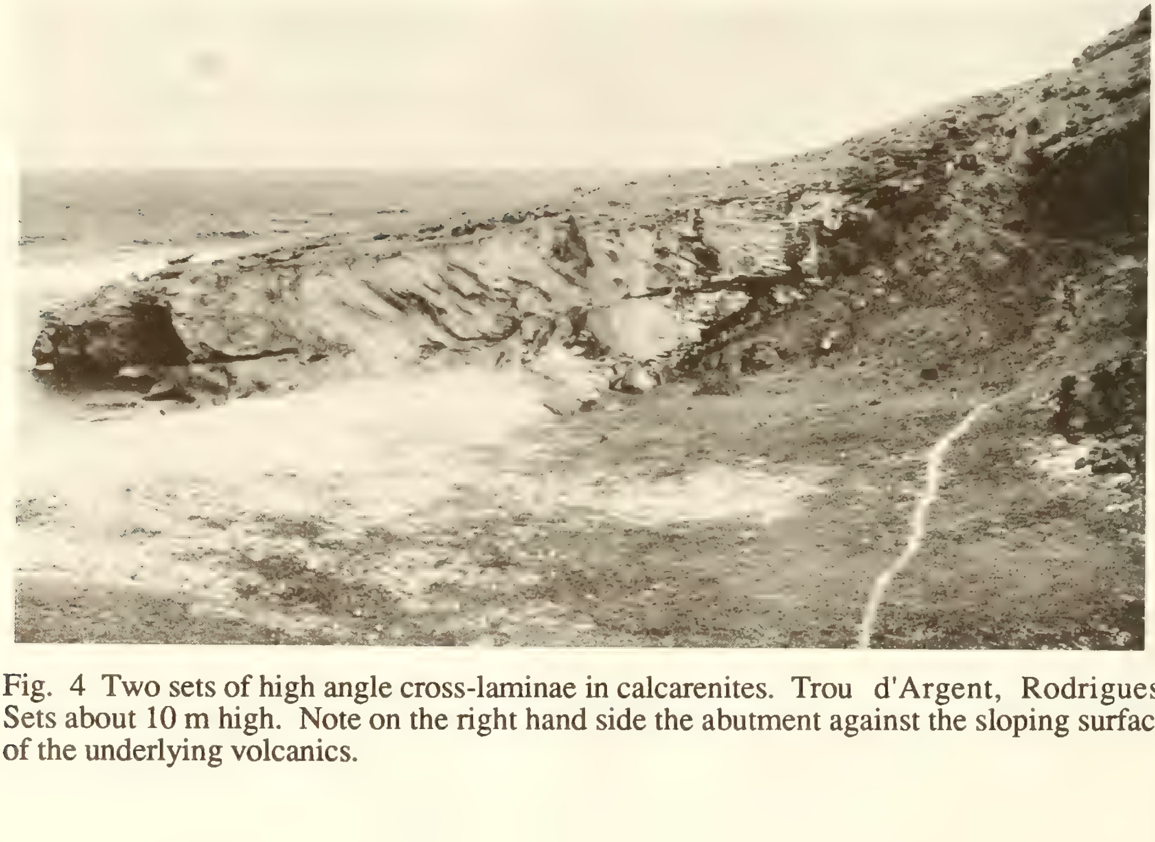

Fig. 4 Two sets of high angle cross-laminae in calcarenites. Trou d'Argent, Rodrigues. Sets about 10 m high. Note on the right hand side the abutment against the sloping surface of the underlying volcanics.

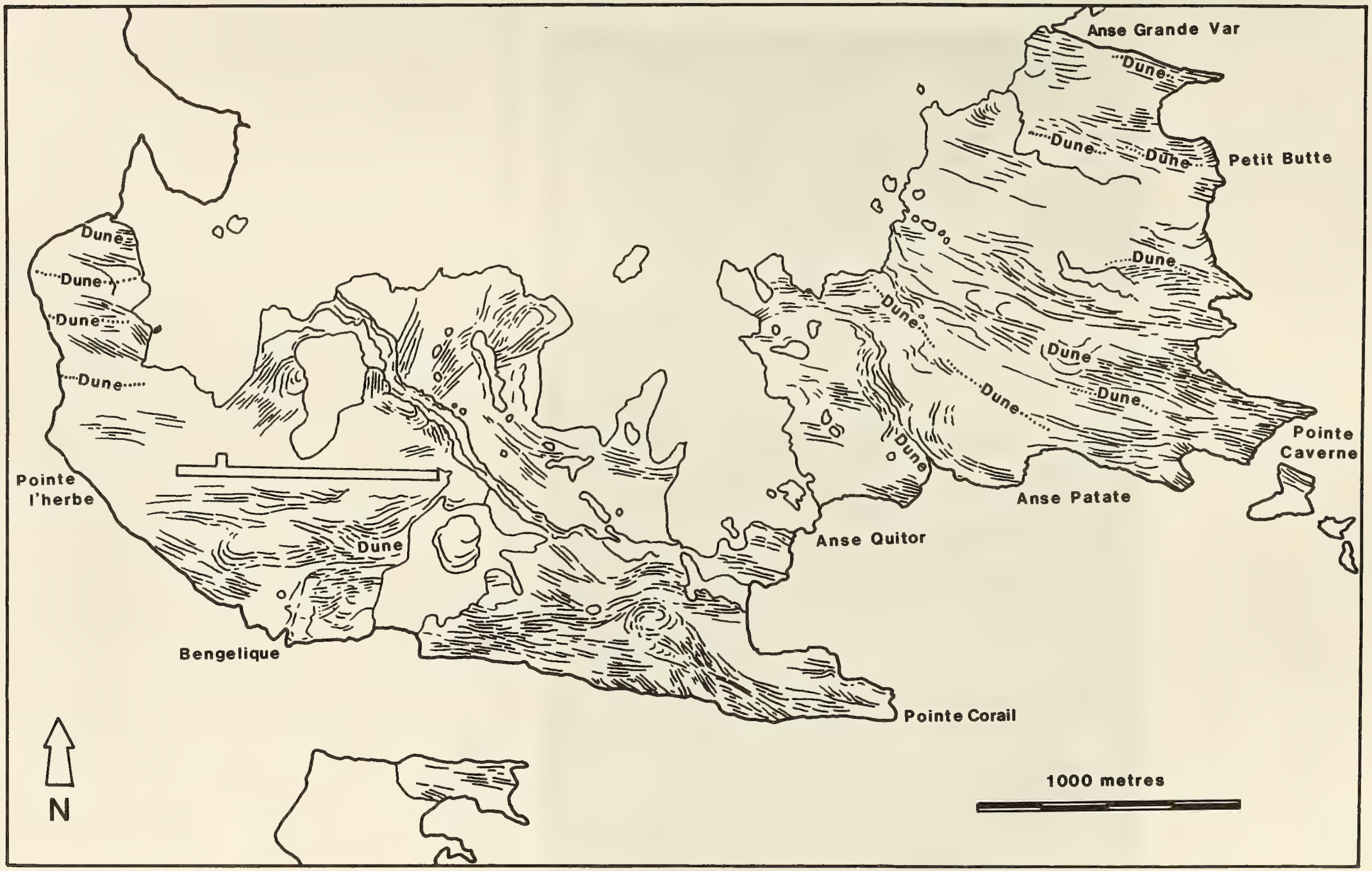

Fig. 5 Air photograph interpretation of the south-eastern coast of Rodrigues showing the extent of calcarenite outcrops, their boundary with the underlying basalts, structural lines which are principally cross-bedding laminae, and the location of major fossil dunes.

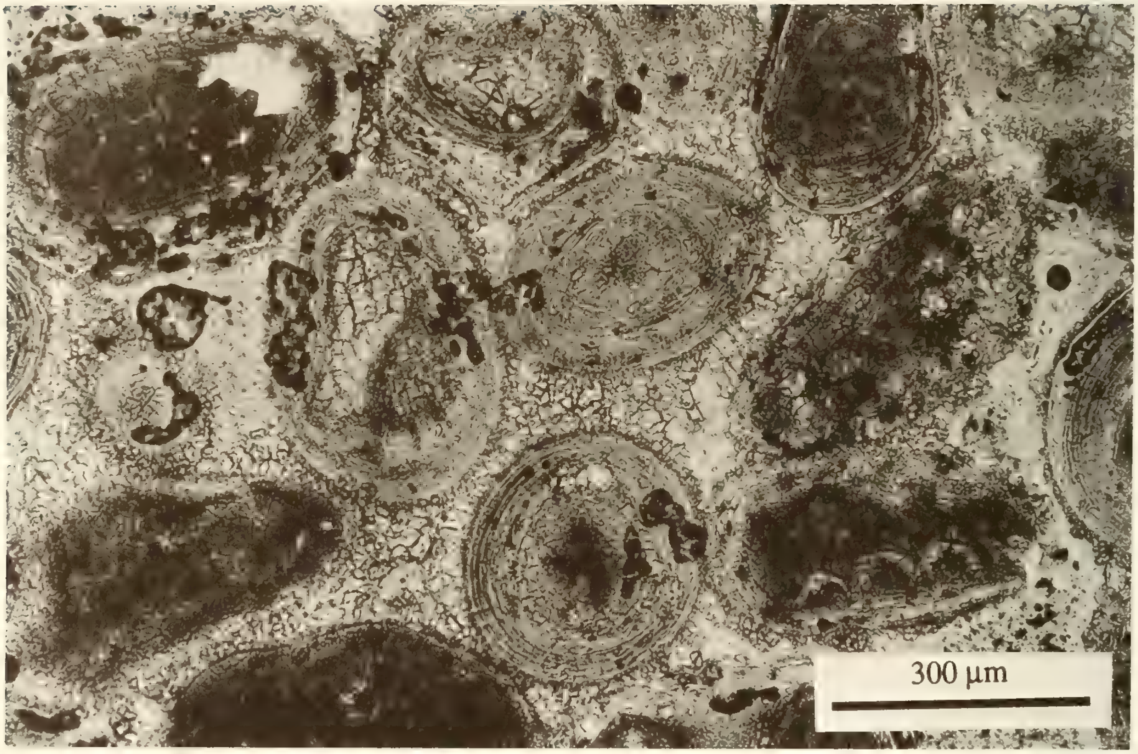

Fig. 6 Thin section showing tangential structure of aragonitic ooliths. Note that ooliths are about 300µm in diameter.

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NO. 421

LARGE-SCALE, LONG-TERM MONITORING OF CARIBBEAN CORAL REEFS: SIMPLE, QUICK, INEXPENSIVE TECHNIQUES

BY

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BY

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ABSTRACT

With coral cover and diversity declining on many coral reefs, a clearer understanding of large-scale reef dynamics is imperative. This paper presents a sampling program designed to quantify the sessile biotas of Caribbean reefs on large spatiotemporal scales. For each reef sampled, data are gathered along replicate, 25-m transects located within the habitat of interest. Herbivore impact is estimated by fish and echinoid censuses along the transects. High-resolution videotapes are used to estimate the percent cover of corals, algae, and other substratum occupants, and to estimate coral diversity. Finally, topographic complexity is measured along the transects. In at least some reef habitats, this index of three-dimensional structure provides a measure of the total disturbance regime, with flatter areas having been subjected to more intense, more frequent, and/or more recent sources of coral mortality. The techniques and statistical analyses described in this paper are simple, quick and inexpensive. Repeated sampling on multiple reefs will enable the investigator to detect changes in community structure and to test hypotheses of the causes of those changes.

INTRODUCTION

Coral reefs are complex, diverse, productive tropical ecosystems in which multiple physical and biological processes covary in space and time (Huston 1985). Discerning the contributions of those processes to the community structure of reefs has been and will continue to be extremely difficult. The question of the appropriate scales at which to search for pattern and process is fundamental to unraveling these multiple causal connections (Jackson 1991, 1992; Karlson and Hurd 1993). Are ecological parameters such as coral cover and diversity determined primarily by small-scale processes, such as the local level of herbivore activity (Sammarco 1980; Lewis 1986), or are larger-scale, regional disturbances more important? Such questions are becoming increasingly

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germane as we confront the possibility that human interference is altering coral reef ecosystems (e.g., Brown 1987).

Over the past two decades, the "health" of many coral reefs worldwide has deteriorated, as measured by indicators such as the diversity and abundance of reef-building corals (Rogers 1985; Dustan and Halas 1987; Hatcher et al. 1989; Grigg and Dollar 1990; Porter and Meier 1992; Ginsburg 1994). Hurricanes (Woodley et al. 1981; Rogers et al. 1982, 1991; Edmunds and Witman 1991; Hubbard et al. 1991; Bythell et al. 1993), coral bleaching (Oliver 1985; Brown and Suharsono 1990; Williams and Bunkley-Williams 1990; Glynn 1993), coral diseases (Gladfelter 1982; Rützler et al. 1983; Edmunds 1991), mortality of the sea urchin *Diadema antillarum* (Lessios et al. 1984; Levitan 1988; Lessios 1988; Carpenter 1990) and outbreaks of the seastar *Acanthaster planci* (Moran 1986; Endean and Cameron 1991) may all be involved. At present, it is unknown whether any or all of these problems are due to recent human activities, or whether they are part of natural, long-term trends or cycles (Brown 1987; Richards and Bohnsack 1990).

In addition, reefs are directly affected by human activities, particularly fishing, sedimentation, eutrophication and pollution (Brown 1987, 1988; Hatcher et al. 1989; Rogers 1990; Richmond 1993; Sebens 1994). These stresses reduce coral survivorship and growth and may promote macroalgal growth. Furthermore, marine pollution may increase the susceptibility of corals to disease (Brown 1988; Peters 1993).

Reef dynamics are governed by multiple causes operating on multiple scales (Grigg and Dollar 1990). For example, the recent decline in coral cover and increase in macroalgal cover on the well-studied reef at Discovery Bay, Jamaica appears to have resulted from a variety of interacting processes: Hurricane Allen (1980), which opened substratum for colonization; feeding by corallivorous snails, which increased the mortality of hurricane-fragmented corals; the *Diadema* dieoff, which reduced herbivory drastically; and a history of overfishing by humans, which had previously removed herbivorous reef fishes (Hughes et al. 1987; Knowlton et al. 1990; Hughes 1994). Likewise, the catastrophic effects of the 1982-83 El Niño event on eastern Pacific coral reefs were due to the interaction of physical changes and a variety of biological processes (Glynn 1990).

One of the greatest challenges to ecology is determining the relative importance of numerous causes to ecosystem structure and function (Quinn and Dunham 1983). Yet, even choosing the correct range of scales on which to understand coral reef dynamics seems a forbidding task. It is becoming increasingly clear that quadrat-scale observations (square meters or smaller) have less explanatory power than larger-scale observations (Jackson 1991). Those larger scales range from the landscape within a reef (hundreds of m^2 to hectares), to the area encompassing multiple reefs within a locality (hundreds of km^2), to an entire region such as the Caribbean.

The need for large-scale and long-term (>5 yr) monitoring programs for coral reefs has been emphasized over the past few years (Rogers 1988, 1990; Ogden and Wicklund 1988; D'Elia et al. 1991; Jackson 1991; Ray and Grassle 1991; Smith and Buddemeier 1992; Bythell et al. 1993; Glynn 1993; Hughes 1994), although less attention has been given to the hypotheses that should be driving the research (Hughes 1992). Few such studies have been undertaken, in part because hypotheses are so difficult to formulate and test (Hughes 1992). Such hypotheses might, for example, include an inverse relationship between the degree of disturbance and coral cover; the intermediate disturbance hypothesis (Connell 1978; Rogers 1993), which postulates that coral diversity should be highest at intermediate frequencies and intensities of disturbance; and complex relationships between herbivory, nutrients, coral and algal cover, and diversity (Littler et al. 1991; Knowlton 1992; Hughes 1994). However, with so many possible causes of community change, and with the ecological implications of each putative cause unknown, highly variable and/or controversial, it is hard to know which variables to monitor in order to test hypotheses adequately.

This paper outlines procedures for comparing coral reef community structure and disturbance regimes across space and through time, with a view toward eventually testing hypotheses such as those listed above. The methods were developed during continuing studies of four western Atlantic coral reefs: Carrie Bow Cay, on the Belizean Barrier Reef; Discovery Bay, Jamaica; and Conch and Carysfort Reefs, off Key Largo, Florida. Since funding for monitoring programs is difficult to obtain and since field time is usually limited, our goal was to create an accurate, relatively inexpensive, "rapid assessment" sampling program for Caribbean coral reefs, with sufficient statistical power to detect biologically meaningful differences. Video transects are used to describe the sessile biota, and fish and echinoid censuses provide estimates of the intensity of herbivory. Since the importance of each type of reef disturbance has not been conclusively demonstrated, we advocate combining them in a single disturbance index, topographic complexity. Topographic complexity reflects the total disturbance regime in at least some reef habitats, integrated on a time scale of years.

METHODS

1. Sampling Design

Any study that compares reefs must be standardized with respect to habitat. The design described here is for a common Caribbean fore-reef habitat: the spur-and-groove habitat of windward-facing reefs at 12-15 m depth. Ten 25-m long transects are sampled at each site. The transects are placed along the central axes of replicate, haphazardly chosen spurs. Sandy areas and the edges of the spurs are avoided. In the present study, each transect was placed on a different spur, except at Discovery Bay. A number of spurs at Discovery Bay were >25 m wide; 2 transects, spaced >10 m apart, were surveyed on some of those wide spurs. It is important to choose sites that will accommodate at least 25-30 transects, so that the transects sampled during different visits to a site will not be identical.

The use of band transects is dictated in this particular application by the elongate shape of the spurs, and in general by the desire to encompass as great an area as possible in each sample. The 25-m transect length was chosen to be as great as possible while still restricted to a narrow depth and habitat range on the spurs. A 25-m transect, when extended over a 3-m depth range, requires spurs that slope at angles of no more than 7°.

For each transect, scuba divers unreel a 25-m fiberglass surveyor's tape, laying it taught along the center of the spur. The tape is left undisturbed for 3-5 min, at which point the divers commence surveys of the mobile fauna.

2. Fish and Echinoid Censuses

Coral reef researchers have yet to agree on a single, reliable method for quantifying the activity of herbivores (Steneck 1983). The simplest measure is the abundance of herbivores, which correlates with their impact among habitats within reefs (Hay and Goertemiller 1983; Lewis and Wainwright 1985). Therefore, before the fish are disturbed further, a visual census is conducted along each transect. A diver swims along the tape at a standard slow speed, recording the number of parrotfish (Labridae, formerly Scaridae) and surgeonfish (Acanthuridae) within a visually-estimated 2 m on either side. The fishes are classified as small (≤ 10 cm Standard Length), medium (10-25 cm), or large (>25 cm). The small transect width minimizes the underestimate of true fish population density inherent in the transect method (Sale and Sharp 1983). Divers then carefully explore the 100 m^2 area, recording the number and species identities of damselfish (Pomacentridae), as well as censusing *Diadema* and other regular echinoid species. The echinoids can be extracted from their shelters and measured (test diameter) with calipers. Size distributions of echinoid species can then be used to estimate their impacts on algal assemblages (Levitan 1988). It should be noted that daytime censuses underestimate echinoid densities; more accurate estimates can be obtained by censusing at night (e.g., Carpenter 1981, 1986).

An alternative approach is to examine the *process* of herbivory by counting the number of bites that parrotfish and surgeonfish take per unit time from small areas of algal turf (Steneck 1983). This technique is more time-consuming than counting fish. A more serious concern is that some habitats on some reefs are currently so overgrown with fleshy macroalgae that finding even a square meter of algal turf would be problematic. For example, at Discovery Bay in 1992 macroalgal cover was >90 %, coral cover was <3 %, and the cover of algal turfs, crustose coralline algae, and bare space combined was <6 % at 15 m depth (as assessed by the video technique described below; Table 1, p. 11). Large differences in the availability of algal turfs could lead to differences in fish foraging behavior, independent of fish abundance. It is important to recognize that both the abundance and bite frequency methods yield short-term "snapshots" of herbivory, which may not adequately reflect longer-term variability.

3. Percent Cover and Scleractinian Diversity

Photography provides the only practical means of sampling large areas underwater, given the time constraints of scuba diving. Littler (1980) discussed the advantages of photography over recording data *in situ*. High-resolution video technology makes the approach all the more attractive because videotaping is easier and less time-consuming than still photography. While still photographs provide better resolution than videotapes, the resolution of videotapes is adequate for work of the type described here. Videotapes enable the investigator to cover a far greater area per unit sampling effort. In addition, video exposures are automatic, continuous and do not require developing.

In this method, a diver swims slowly along the transect, videotaping a 40-cm wide swath of reef from a height of approximately 40 cm, using a high-resolution (Hi-8) video camera in an underwater housing, fitted with a wide-angle lens. A 15-cm gray plastic bar is attached to a rod that projects forward from the video housing. The bar, which is held at the level of the substratum during taping, provides scale in the videotaped images and also ensures that the camera is held a constant distance from the bottom.

Individual video frames are displayed on a high-resolution monitor in the laboratory. A clear plastic sheet with 10 random dots is laid over the monitor screen, and the sessile organisms underlying the dots are recorded (Sebens and Johnson 1991; see **Sample Sizes**, p. 8, for number of dots per frame). The videotape is then advanced to a new, non-overlapping position. Each 25-m transect yields 50 video "quadrats", for a total of 500 points per transect. The point count data are used to calculate percent cover and the Shannon-Wiener diversity index, *H'*, for each transect. Since this and similar sampling methods tend to be biased against the inclusion of rare species, presence-absence data are also gathered for coral species by viewing the entire videotape of each transect (Chiappone and Sullivan 1991).

By holding the camera perpendicular to the substratum, swimming slowly along the transect, and using a pair of video lights (50 or 100 watts each), it is possible to produce clear stop-action images. Corals, sponges, and some gorgonians and macroalgae can be identified to species, down to a diameter of approximately 5 cm. A drawback of this method is the difficulty of distinguishing fine algal turfs, crustose coralline algae and bare space from the tapes; these are lumped into a single category, which can be resolved by closeup, still photography if desired.

Ecologists have devoted a great deal of effort to developing and comparing methods for quantifying coral reef community structure, with variable results (e.g., Loya 1978; Dodge et al. 1982; Ohlhorst et al. 1988; Chiappone and Sullivan 1991; Porter and Meier 1992). Porter and Meier (1992) examined some of the biases introduced to surface area estimates by photographic and video techniques. Such errors include non-orthographic projection, in which coral heads that stick up above the surrounding substratum are closer to the camera lens and therefore artificially enlarged, and parallax. These problems are difficult to correct (Porter and Meier 1992).

Whorff and Griffing (1992) found that point counts from video frames overestimated the percent cover of intertidal barnacles and bivalves, compared to computer image-processing of the video frames. More dots per frame yielded better percent cover estimates. On the other hand, Foster et al. (1991) concluded that point counts from photographs underestimated cover in multilayered, temperate subtidal assemblages, compared to point counts done in the field. The point count method is not as accurate as planimetry of the individual colonies in each frame or fully-automated image processing. However, planimetry is so time-consuming as to be impractical. Image processing is also difficult at present because subtle color and pattern differences must be detected; most corals and algae are quite similar in color, and reasonably-priced, hand-held video lights provide limited color saturation. The point count method is capable of detecting significant among-site differences in percent coral cover and diversity (see **Sample Sizes**, p. 8). Video has its problems and biases like other techniques, but it remains a simple, cost-effective comparative method.

Another concern is the seasonality of macroalgal growth (Carpenter 1981; Hughes et al. 1987). Seasonal changes within a site could change estimates of coral cover, as more or less living coral is obscured by the algae (J. C. Lang, personal communication). The constraints of time, logistics and funding do not always permit the investigator to standardize sampling by season, and the error in coral cover estimates caused by seasonal variations in algal growth are unknown. In the present study, Carrie Bow Cay was sampled in the late spring, Discovery Bay in the winter, and Conch and Carysfort Reefs in the fall of 1992. If algal growth is maximal in the summer and algal destruction by storms is maximal in the winter, then, all other things being equal, macroalgal cover, and the error in coral cover estimates due to macroalgal cover, should have been greatest in Florida (after the summer's algal growth), intermediate at Carrie Bow Cay (before the summer's growth), and least at Discovery Bay (during the stormy season). In fact, macroalgal cover was highest at Discovery Bay, intermediate at Conch Reef and Carrie Bow Cay, and lowest at Carysfort Reef (Table 1, p. 11). In this study, differences in macroalgal cover among sites apparently outweighed any error in coral cover estimates associated with seasonal differences.

The species diversity of scleractinian corals is evaluated as species richness, S, and as the Shannon-Wiener index, H'. S is measured for each site as the asymptote of the rarefaction curve (cumulative species numbers plotted against number of transects videotaped). Species richness is not calculated for each transect since reefs with lower coral cover are expected to have lower S per transect simply because fewer colonies are sampled (Magurran 1988). The Shannon-Wiener index is calculated for each transect as $H'=-\Sigma(p_i[\ln p_i])$, where p_i is the proportion of the ith species in the sample. Vast size differences among coral colonies and colony fragmentation and fusion obscure the meaning of H' calculated from numbers of "individuals". Unless the investigator is prepared to establish the genetic identity of all ramets, we recommend H' indices based on areal coverage for a general characterization of reef communities.

4. An Integrated Measure of Disturbance

Historical records of disturbance do not exist for most coral reefs. Even where such records are available, there is no obvious way to sum the different disturbances to reflect the total disturbance regime; one cannot simply score three disturbance points for a hurricane and two for a bleaching event. We present topographic complexity as a technique for measuring disturbance, along with its rationale and sources of error, so that the individual investigator can decide whether or not it will be useful.

Topographic complexity is measured by carefully conforming a 5-m length of fine brass chain to the substratum adjacent to the central part of each transect tape. The chain is conformed to the finest topographic features that the 17-mm links permit; it is carefully inserted into small cavities and into the spaces within thickets of foliose and branching corals. The 5-m chain length was chosen so that the procedure could be completed in a reasonable length of time (10-15 min); the chain must be carefully straightened before it is conformed to the substratum. A complexity index, C, is calculated as $C=1-d/l$, where d is the horizontal distance covered by the conformed chain (measured against the transect tape) and l is its length when fully extended (e.g., Risk 1972; Rogers et al. 1982; Aronson and Harms 1985; Hubbard et al. 1990; Connell and Jones 1991).

Disturbances that lead to the partial or complete mortality of coral colonies decrease this topographic complexity. Hurricanes decrease complexity directly by toppling branching and head corals (e.g., Rogers et al. 1982; Kaufman 1983), although this is not true in all reef habitats (Rogers et al. 1991; see below). In addition, once dead coral skeletons are exposed by a disturbance of any sort, they are colonized by bioeroders, including bivalves, sponges, sipunculans, polychaetes and echinoids, which break down the reef framework (Hutchings 1986). Disturbances that cause partial to complete mortality of coral colonies, provide fresh substratum for bioeroders, and in fact lead to increased bioerosion rates include hurricanes (Moran and Reaka-Kudla 1991), El Niño-induced coral bleaching (Glynn 1990) and damselfish territoriality (Kaufman 1977), although damselfish can have a negative effect on bioerosion by excluding echinoids from their territories (Eakin 1988; Glynn 1990). Naturally and artificially high levels of nutrients on reefs also increase bioerosion rates (Highsmith 1980; Tomascik and Sander 1987; Hallock 1988). Overfishing off the coast of Kenya increased bioerosion and decreased topographic complexity as well, by releasing burrowing echinoids from predation (McClanahan and Shafir 1990). Furthermore, coralline algae, which are important in cementing the reef framework (and thus important in maintaining topographic complexity), are suppressed by macroalgae, which are promoted by nutrient input and the removal of herbivores (Littler and Littler 1985; Lewis 1986; Carpenter 1990). Coral growth, by contrast, generally increases topographic complexity at the scale under consideration (Dahl 1976). To a first approximation *in certain situations*, the topographic complexity index should be inversely related to total disturbance, with lower values indicating flatter terrain and suggesting more frequent, more recent and/or more intense disturbance.

No measure of disturbance is free of bias, including topographic complexity. One source of error is that coral mortality does not lead to the immediate loss of structure because bioerosion takes time. In addition to this time lag, the relationship between coral mortality and physical complexity is not always direct. Some coral species can survive breakage in storms and even reproduce asexually as a result (*Acropora* spp.: Highsmith et al. 1980; Tunnicliffe 1981); low complexity accompanied by high coral cover is a possible consequence. Conversely, bioerosion following partial or complete mortality of massive coral heads could initially increase complexity rather than decrease it.

While these problems introduce error to estimates of disturbance, that error should be minimal in the spur-and-groove down to 15 m depth. Throughout Florida and the Caribbean, those habitats are now or were formerly (before disturbance) dominated by branching or other delicate coral species, including *Acropora cervicornis* (Belize, Jamaica, the Florida Keys and many other localities), branching *Porites* spp. (some reefs in St. Croix, U. S. Virgin Islands), and *Agaricia tenuifolia* (Belize). For all of these corals, complexity in their habitats should decline rapidly following mortality. Topographic complexity would not be as useful an indicator of disturbance in certain other reef habitats, such as shallow-water hardground areas, which are characterized by isolated head corals on limestone pavements. Similarly, deep-reef areas dominated by corals with a plating morphology could have high coral cover but low topographic complexity.

Another potential complication in separating disturbance and herbivory effects is an observed positive correlation of fish abundance and topographic complexity. Herbivorous (and other) fish avoid low-relief areas, including those which have been disturbed (Hay and Goertemiller 1983; Kaufman 1983). Areas with fewer herbivores may experience increased algal cover, decreased coral cover, and increased bioerosion, leading to even flatter topography (reviewed in Hutchings 1986). This feedback loop does not appear to be a problem in the reefs studied (see **Sample Sizes**).

SAMPLE SIZES

The techniques outlined above are intended for testing hypotheses on large scales, ranging from a landscape scale (among spurs in the spur-and-groove habitat within reefs), to a subregional scale (among reefs within an area such as the Florida Keys), to a regional scale (among reefs throughout the Caribbean). In order to determine the appropriate sample sizes for statistical comparisons among reefs, preliminary surveys were conducted during 1992-93 in the spur-and-groove habitats of the four sites mentioned in the **Introduction**. Ten transects were completed at each site, and an additional 10 transects were videotaped only (see comments below on species richness). Two investigators can sample a site in 3-4 days, assuming 2-3 "full" transects per dive and 2 dives per day. Where funding and equipment are available, the use of nitrox diving techniques increases bottom time substantially, increasing the number of transects that can be completed per dive.

Percent cover and *H'* are estimated by point counts from each of 10 video transects per site. Fifty non-overlapping, video frame "quadrats" cover most of the length of the transect videotape. The question is how many random dots to use per video frame. For each of the 50 frames in each of the 10 Carrie Bow Cay and 10 Discovery Bay transects that were analyzed, the substratum occupants under 25 random dots were recorded, in groups of 5 dots. The means and standard deviations of percent cover of hard corals and *H'* for scleractinians remained virtually unchanged when the number of dots used was ≥ 10 (Figs. 1, 2). Therefore, an appropriate sampling protocol is 50 video frame "quadrats" per transect and 10 random dots per video frame. Each 500-dot data set constitutes a single sample, requiring 2-3 hours for trained personnel to extract from the videotaped transect. Because each video transect is a single sample, increasing the number of random dots per frame yields no advantage in terms of statistical power.

The only parameter for which more than 10 video transects per reef are required is species richness, *S*. Plots of cumulative *S* for Conch Reef and Discovery Bay reach their asymptotes after 9 and 15 transects, respectively, and the curves for Carysfort Reef and Carrie Bow Cay both asymptote after 13 transects (Fig. 3). The difference in sample sizes required to estimate *H'* and *S* is due to rare species, which add little to the coral cover from which *H'* is calculated. We recommend 20 transects to estimate species richness for a site.

The percent cover and topographic complexity data were arcsine-transformed and the fish census data logarithmically transformed, so that they conformed to the assumptions of parametric statistics (Sokal and Rohlf 1981). The square root transformation, often recommended for data in the form of counts (Sokal and Rohlf 1981), was not used on the census data. This transformation assumes that the data in question are Poisson distributed, but count data are not necessarily so distributed. Transformation of the *H'* data was unnecessary because *H'* is normally distributed (Magurran 1988) and the data collected in this study were homoscedastic. (See Clarke and Green [1988] for a detailed discussion of data transformations.)

A one-way analysis of variance (ANOVA) on the arcsine-transformed percent coral cover data showed significant among-site differences ($p<0.0005$; Table 1). Tukey HSD multiple comparisons revealed the following differences between sites, listed in order of increasing cover (<, significantly less than; =, not significantly different from at $\alpha=0.05$):

Discovery Bay < Conch Reef < Carrie Bow Cay = Carysfort Reef.

The ANOVA results were used to estimate the minimum detectable difference, δ, in transformed percent cover at a significance level of $\alpha=0.05$ with a power of $1-\beta=0.90$ (Zar 1984; Clarke and Green 1988). For an ANOVA comparing 4 sites, $\delta=0.13$. This calculated δ was then used to estimate the range of the minimum detectable difference in actual (untransformed) percent cover by the following procedure:

1. adding δ to the (transformed) lowest mean, back-transforming that value to actual percent cover, and taking the difference between the back-transformed value and

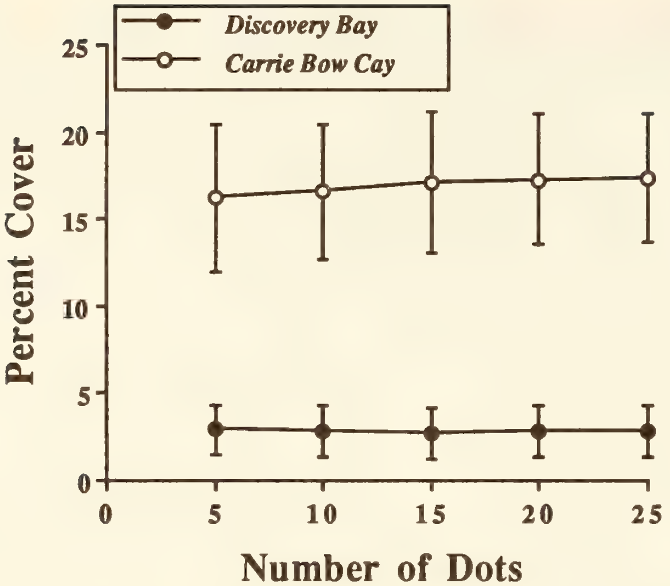

Fig. 1. Percent cover of hard corals as a function of the number of random dots used per video frame in transects from Discovery Bay, Jamaica and Carrie Bow Cay, Belize. Fifty frames were analyzed in each of 10 transects for each site. Error bars represent standard deviations.

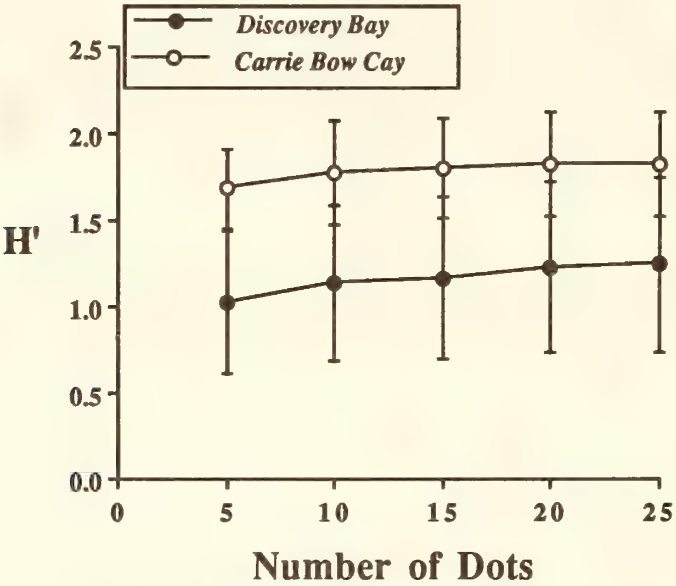

Figure 2. Shannon-Wiener diversity of Scleractinia, *H'*, as a function of the number of random dots per video frame in transects from Discovery Bay and Carrie Bow Cay. Sample sizes as in Fig. 1. Error bars represent standard deviations.

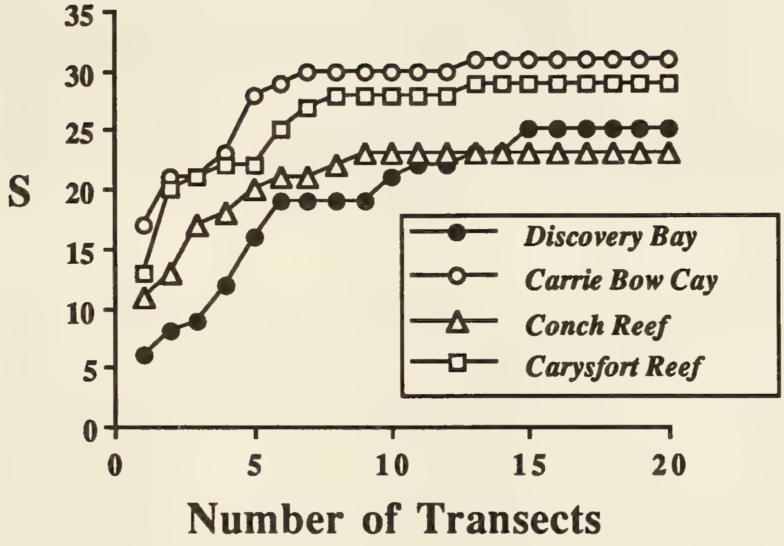

Figure 3. Cumulative species richness curves for scleractinian corals in video transects from the four sites surveyed.

Table 1. Means ± standard deviations of parameters measured in 1992 at four coral reef sites.

	Field Site			
Parameter	Discovery Bay	Carrie Bow Cay	Conch Reef	Carysfort Reef
A. Percent Cover				
Hard corals	2.8±1.5	16.7±3.8	6.4±4.0	21.2±7.7
Macroalgae	91.2±4.3	63.2±6.9	65.7±8.8	40.9±12.0
B. Scleractinian Diversity				
H'	1.22±0.28	1.81±0.29	1.04±0.55	1.21±0.58
C. Integrated Disturbance Index				
C	0.184±0.078	0.403±0.089	0.194±0.077	0.335±0.106
D. Fish Abundance (number/transect)				
Parrotfish	31.5±10.0	24.6±7.4	17.0±8.3	34.2±15.8
Damselfish	7.5±4.5	38.5±7.9	58.5±14.2	18.5±7.8

the observed (untransformed) lowest mean, and

2. subtracting δ from the (transformed) highest mean, back-transforming that value to actual percent cover, and taking the difference between the observed (untransformed) highest mean and the back-transformed value.

The minimum detectable difference ranged from 5.2 % where coral cover is minimal (a few percent cover) to 9.8 % at high values of coral cover (approximately 20 % cover; Table 1). In fact, *a posteriori* comparisons after ANOVA on the arcsine-transformed percent cover data detected a significant difference between the sites with the two lowest means, Discovery Bay and Conch Reef, which differed by only 3.6 % cover (Table 1). If the study were expanded to include surveys of 10 sites instead of just 4, the minimum detectable difference would range from 6.3 to 11.1 % cover.

A one-way ANOVA on the *H'* data also revealed significant differences among sites ($p<0.005$), which are listed in the same format as for percent coral cover:

Conch Reef = Carysfort Reef = Discovery Bay < Carrie Bow Cay.

A power analysis gave $\delta=0.81$ for an ANOVA comparing 4 sites and $\delta=0.93$ for an ANOVA comparing 10 sites, at $\alpha=0.05$ and $1-\beta=0.90$. *A posteriori* comparisons detected a significant difference between the sites with the two highest means, Carrie Bow Cay and Discovery Bay, which actually differed in mean *H'* by only 0.57. The video method thus provides a statistically powerful tool for detecting differences in coral cover and diversity among sites.

The estimates of percent cover and *H'* for Discovery Bay were compared to estimates obtained independently at the same time (during the winter of 1992) by the linear point-intercept (LPI) method (Ohlhorst et al. 1988). A 10-m surveyor's tape was positioned randomly at 15 m depth, and the sessile organisms underlying the tape were recorded every 10 cm, for a total of 100 points per transect. The LPI method gave a higher estimate of coral cover (mean 4.4±0.9 SD, based on 5 transects) than the video transects (Table 1), but the two estimates were not significantly different by Student's *t*-test ($t_s=2.207$, df=13, $0.05<p<0.10$). In contrast, the LPI method underestimated *H'* (mean 0.72±0.18 SD) compared to the video transects ($t_s=3.577$, df=13, $p<0.005$). The significant difference in species diversity obtained by the two methods is largely an artifact of the number of points used to calculate *H'*. Since coral cover was so low at Discovery Bay, the *H'* value calculated for each 100-point LPI transect was based on a maximum of only 5 points overlying coral. With 5 times as many points per sample, undersampling corals was not a problem in the video transects (Fig. 2).

Hughes (1994) employed line-intercept transects to document reef dynamics at Discovery Bay at 10 m depth. Using a 10-m surveyor's tape, he recorded the lengths of tape overlying different species. His value for coral cover in 1993, approximately 3 %, agrees with the mean reported for 15 m depth in Table 1. In addition, Hughes (1994) monitored permanent photoquadrats at a site near Discovery Bay. In 1993, he obtained values of coral and macroalgal cover at 15-20 m depth that are nearly identical to those listed in Table 1 for Discovery Bay.

Analysis of the topographic complexity data showed that the chain method is capable of detecting significant differences among sites (ANOVA, $p<0.0005$):

Discovery Bay = Conch Reef < Carysfort Reef = Carrie Bow Cay.

Interestingly, the four sites display the same qualitative differences in topographic complexity that they do in coral cover. Jackson (1991) used coral cover as a proxy for disturbance, with higher coral cover indicating a lower level of disturbance. Our suggested measure of disturbance, topographic complexity, agrees with Jackson's (1991) for the reefs studied. We prefer the complexity index, because it avoids the circularity of using Jackson's (1991) method to test for a causal relationship between disturbance and coral cover.

The log-transformed abundance of damselfish differed from site to site (ANOVA, $p<0.0005$):

Discovery Bay < Carysfort Reef < Carrie Bow Cay = Conch Reef.

Apart from damselfish, which actually promote algal growth, parrotfish were by far the most abundant herbivorous fishes in the spur-and-groove habitat (Lewis and Wainwright 1985); 82-98 % of the herbivores were parrotfish in censuses at the four sites. Surgeonfish and echinoids were virtually absent, and they were ignored in this analysis. Among-site differences were also detected in log-transformed parrotfish abundance (ANOVA, $p<0.0005$):

Conch Reef < Carrie Bow Cay = Discovery Bay = Carysfort Reef.

Multiplying parrotfish abundance in the three size classes by average length to calculate "biomass" did not alter these patterns. As suggested in the section on fish and echinoid censuses, parrotfish and surgeonfish abundance can be highly variable, and counts of these mobile herbivores should be interpreted with caution.

For long-term studies of particular reefs, our protocol has distinct advantages over the traditional approach of permanent transects or quadrats. The marine environment is highly variable, and independent sampling during each site visit (factorial, with time as a factor; Green 1979) encompasses more of that variation than a permanent transect approach (repeated measures). While it is true that independent sampling makes it more difficult to detect significant effects, conclusions are not bound to the particular histories of individual organisms and the particular areas of reef framework on which they live. An independent/factorial approach thus gives investigators increased scientific confidence in the signals detected, but less statistical power to detect those signals, than a permanent/repeated measures approach. Furthermore, since the independent sampling approach avoids the expensive and time-consuming procedures involved in permanently marking study areas, it is more practical for reef monitoring in developing countries.

CONCLUSION

The methods outlined in this paper were developed to combine logistical ease, low cost and statistical power. The point-count data extracted from the videotapes can be taken beyond univariate statistical treatments to more sophisticated, multivariate ordinations and tests. Differences in species composition among reefs can then be considered in light of differences in geomorphology and oceanography as well as differences in disturbance regime.

Coral reefs have been central to the development of ecological theory (Connell 1978), yet we still need basic information on their dynamics (Jackson 1991; Ginsburg 1994). As reef ecosystems become increasingly threatened, commitment to large-scale management is growing in the United States and abroad. However, effective management policy cannot be created without an understanding of reef dynamics and the effects of disturbance. The methods described in this paper can provide the necessary information. Large-scale and long-term data collected now will be of particular value if and when conditions change (e.g., recovery of *Diadema* populations, future hurricanes).

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ATOLL RESEARCH BULLETIN

NO. 422

CHANGES IN THE COASTAL FISH COMMUNITIES FOLLOWING HURRICANE HUGO IN GUADELOPE ISLAND (FRENCH WEST INDIES)

BY

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CHANGES IN THE COASTAL FISH COMMUNITIES FOLLOWING HURRICANE HUGO IN GUADELOUPE ISLAND (FRENCH WEST INDIES)

BY

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ABSTRACT

Hurricane Hugo swept the island of Guadeloupe (French West Indies) on 16 and 17 September 1989. Sustained winds were of 140 knots and gusts exceeded 160 knots. This hurricane was one of the most devastating of the century for the Lesser Antilles.

The mangroves were completely defoliated and anoxic conditions of the water induced considerable fish mortality. Consequently, the fish community was modified in terms of species composition, structure and biomass. Four months later, the fish assemblages of the mangroves returned to conditions previous to the hurricane in species composition and community structure.

The impact on the marine phanerogams was more destructive on the *Syringodium filiforme* seagrass beds than on those of *Thalassia testudinum*. In this ecosystem, the effect of the hurricane was minor on the fish community. Changes in the fish community occurred four months later in the seagrass beds and were apparently induced by a delayed mortality of the *Thalassia testudinum*.

In the coral reef environment, the impact of the hurricane surge on the coral community mainly affected the branched coral species located between the surface and 15 m deep. The fish assemblages were not modified concerning their species composition. However, the proportion of juveniles in the community drastically dropped after the hurricane. Four months later, the proportion of juvenile fishes was still reduced.

The overall effects of hurricane Hugo on the coastal fish communities of the island of Guadeloupe were minor considering the magnitude of the hurricane.

I. INTRODUCTION

In the Lesser Antilles, hurricanes are considered one of the major factors controlling the coastal marine ecosystems. In the island of Guadeloupe, these are represented by mangrove, seagrass beds and coral reefs.

Hurricane Hugo reached Guadeloupe in the night of 16 September 1989, travelled the length of the island until the following morning, with the 37 Km-diameter eye passing over

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the Grande Terre (Fig. 1). The atmospheric pressure dropped to 941,5 millibars and the wind was recorded at 140 knots with squalls exceeding 160 knots. In some areas, rainfall reached 300 mm in one day. Such a rainfall rate has a probability of occurence lower than 1 per 50 years (Anon., 1990).

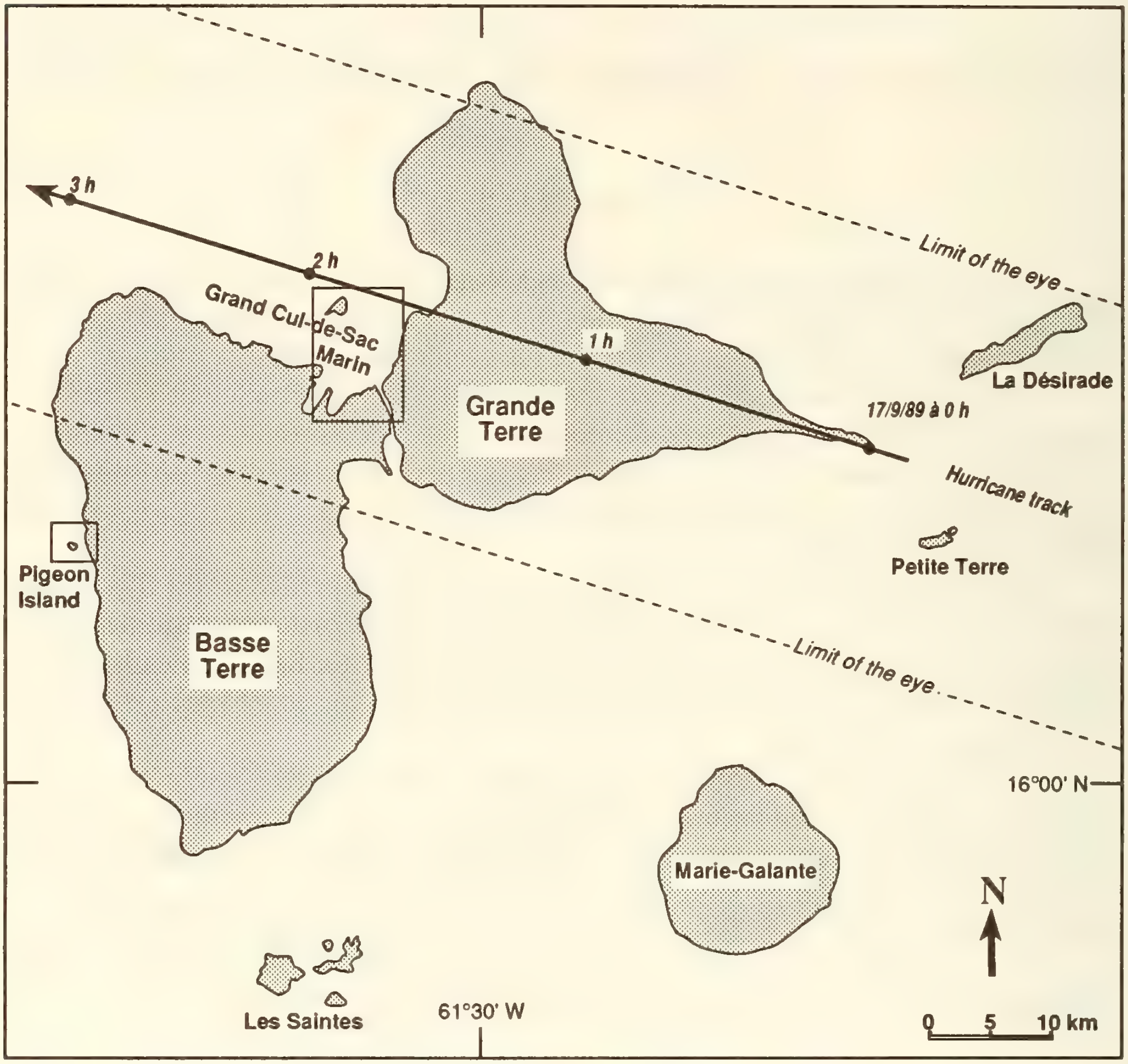

Figure 1 : Guadeloupe Island. Track of the hurricane. Location of the study areas.

Only few observations were available concerning the effects of the hurricane on the sea conditions.The theoretical calculation of the storm tide predicted a 3 m rise of the mean sea level (Anon., 1990). Our examination of the high-water marks after the storm indicated that the tide did not exceed 1,5 m. Offshore, the predicted amplitude of the swell was 5 m (Anon., 1990). On the shore, the structure of the waves is normally variable and depends on the morphology of the sea bottom and the incidence of surge along the coast. Unfortunately, no observations were made during the hurricane. However, the amplitude of the waves observed for similar hurricanes in the Caribbean area varied between 10 and 12 m (Stoddart, 1974 ; Woodley *et al.*, 1981 ; Kjerfve et Dinnel, 1983).

The general impact of Hurricane Hugo on the different coastal communities of the island of Guadeloupe was previously reported by Bouchon *et al.* (1991). The present work summarizes the observations made on the changes in the fish communities during the months preceding and following the hurricane.

II. STUDY AREAS AND METHODS

Observations were made in the Grand Cul-de-Sac Marin bay, for the fish in the mangrove and the seagrass beds. The coral reef fish community was studied near Pigeon Island, on the west coast of Guadeloupe (Fig. 1). These areas were chosen because previous data were available for them and provided a basis for comparison.

After the hurricane, the first observations were made on 24 September, 1989 at Pigeon Island and on 25 September in Grand Cul-de-Sac Marin.

The fish communities were studied with different sampling techniques because of the varied habitat. In the mangrove, where the water was turbid, fishes were sampled with a special fishing net called "capéchade". This device consisted of a fence net (45 m long and 2 m high), placed perpendicular to the mangrove front and three hoop-nets that trap the fishes. From the mouth to the extremity of the hoop-nets, the mesh-size decreased from 13.8 mm to 6 mm (Fig. 2). The sampling station was located in the "Manche à Eau", a mangrove lagoon (Fig. 3) and important nursery zone for the fishes in Guadeloupe (Louis et Guyard, 1982). In the seagrass beds, fishes were collected with a seine net, 50 m long and 2 m high, used to encircle the sampling area. Two stations were chosen in Grand Cul-de-Sac Marin : one at Lambis Point and the other at Christophe Islet (Fig. 3).

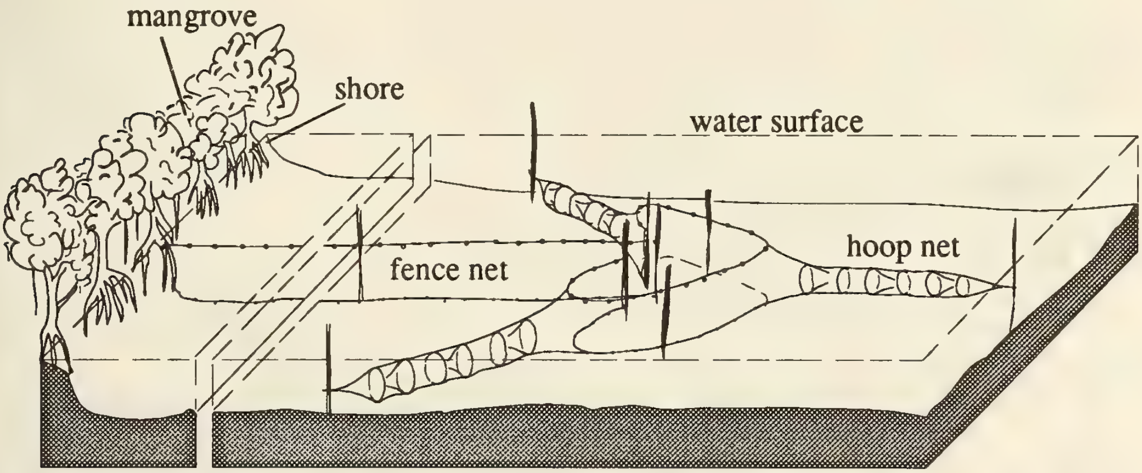

Figure 2 : A "capéchade" : the fishing device used in the mangrove.

The sampling area for the coral reef fish community was located near Pigeon Island at 15 m deep (Fig. 1). The fishes were counted, by SCUBA diving, inside a quadrat of 300 m^2 (150 m long, 2 m wide) defined by transect lines on the bottom. The water column investigated was about 3m high. Each fish censused was assigned one of three size-classes (juvenile, medium-size, big-size) based on the size range of each species (Bouchon-Navaro and Harmelin-Vivien, 1981).

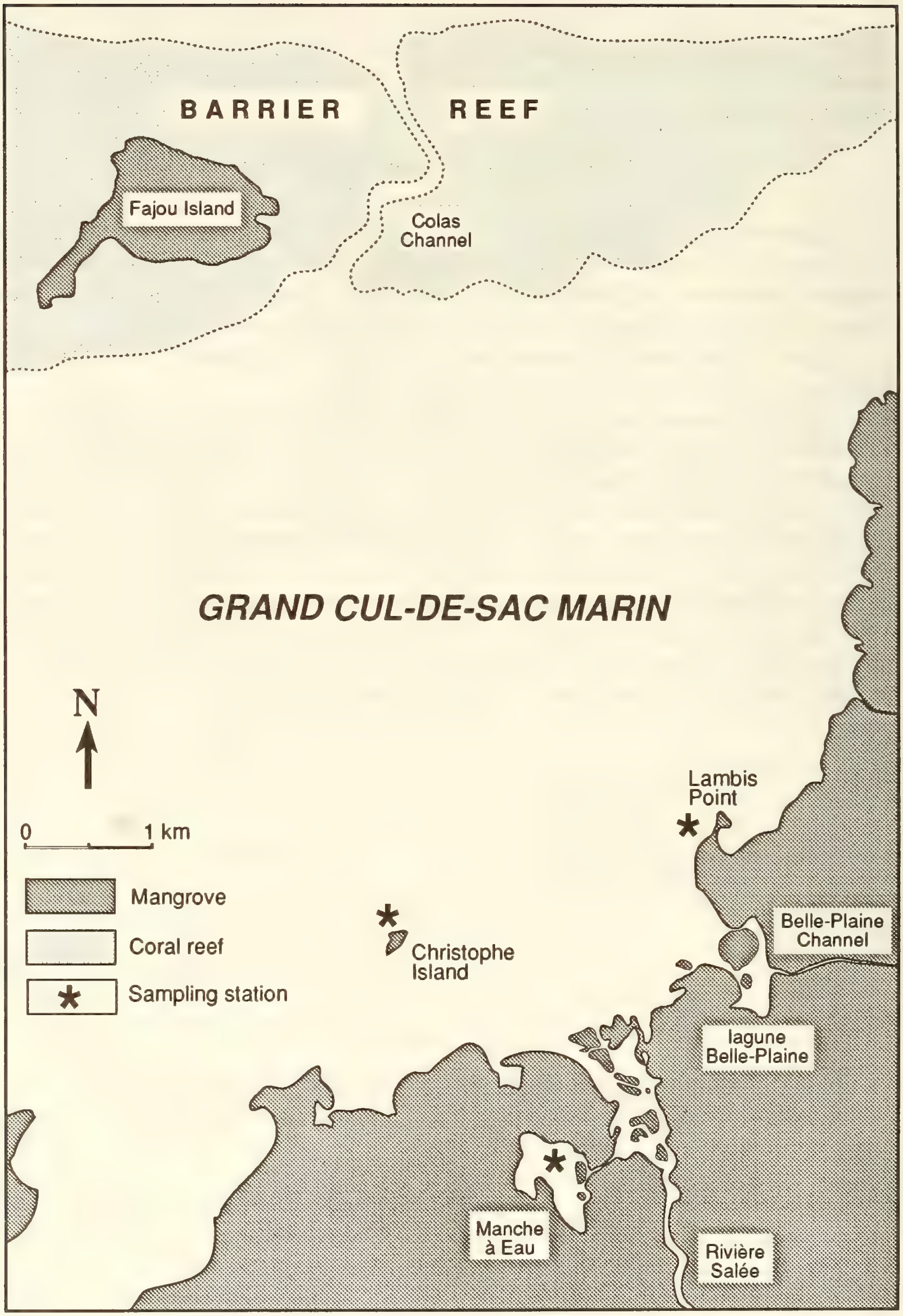

Figure 3 : Location of the sampling stations in Grand Cul-de-Sac Marin Bay.

From the data, several biological indices were computed such as species richness, species diversity (H') calculated according to Shannon and Weaver (1948), and evenness index (E) of Pielou (1969) that gives an indication on the community structure. E fluctuates between 0 (only one species in the community) and 1 (all the species of the community have the same importance). These indices were calculated using biomass values for the mangrove and seagrass fishes and the number of individuals for the reef fishes.

Data did not fit a gaussian distribution, even when using current transformation techniques (Log, square root, hyperbolic...). Three non parametric statistical tests were used to analyse the data : the Wilcoxon signed-ranks test, the Spearman rank correlation and the Friedman two-way analysis of variance by ranks (Siegel, 1956). Results are given with their exact probability of occurence. We considered that the results of the tests were statistically significant when probabilities were ≤ 0.05.

III. RESULTS

A. Mangrove areas

The hurricane was accompanied by a storm tide which was followed by a rise in sea level of at least one meter. The mud from the bottom in shallow waters was stirred up by the waves. Considerable amounts of freshwater runoff flushed the mangroves. These phenomena induced a drop in salinity (to 7‰) and quite anoxic conditions ($0.2\ mg.O_2.l^{-1}$) that lasted several days (Bouchon *et al.*, 1991).

After the hurricane, numerous dead fishes were floating at the surface of the water in the mangrove. Some fishes were observed dead on the substrate between the mangrove roots and up to 20 m inshore. The dead fish species were the following : *Gerres cinereus, Eucinostomus gula, Eugerres brasilianus, Bairdiella ronchus, Lutjanus apodus, Haemulon bonariense, Mugil curema, Sphyraena barracuda, Chaetodipterus faber, Archosargus rhomboidalis, Diodon holacanthus* and *Sphoeroides testudineus.*

Fish surveys were conducted from 24th September 1989 (one week after the hurricane) and the data could be compared to data acquired previously at the same station. In the Manche-à-Eau lagoon, the results were compared to data from June 1989 (3 months before the hurricane) and additional samples made in January 1990 (4 months after the hurricane) and in March 1990 (6 months later) (Annex I).

The Friedman two-way analysis of variance by ranks was used to compare the fish biomass among the four samples. A global statistical significant difference was found between the samples ($X_r^2 = 11.709$; $p = 0.0084$).

The Wilcoxon signed-ranks test was used to compare the samples pairwise (Tab. 1). The results show that the fish community observed before the hurricane (June 1989) was different from the one observed after the hurricane (September 1989). Surveys conducted in January and March 1990 were also different from the September 1989 sample. But in January and March 1990, 4 and 6 months after the hurricane, fish biomass returned to the previous situation of June 1989.

A drop in fish biomass was observed just after the hurricane. In January 1990, fish biomass had returned to the pre-hurricane values. Decreases in the number of species and number of individuals, as well as the diversity indices, were also noticed one week after the hurricane.

The fish community observed in the mangrove lagoon during the study period comprised 32 species. A Spearman rank- correlation coefficient calculated with the pre and post-hurricane data showed a significant inverse correlation between the quantitative fish dominances ($Z = -2.817$, $p = 0.048$). Before the hurricane, the dominant species in biomass were : *Sphoeroides testudineus, Bairdiella ronchus, Archosargus rhomboidalis, Eucinostomus argenteus* and *Eucinostomus gula*. These species usually correspond to the fishes permanently residing in the mangrove (Louis and Guyard, 1982). After the hurricane, these species were no longer present in the surveys, except for A. *rhomboidalis* (three individuals collected). Moreover, gobiid fishes which were not commonly sampled in the mangrove (chiefly *Gobionellus oceanicus*) were dominant in the community.

Thus, significant changes in the fish community were observed just after the hurricane in the mangrove : 4 and 6 months later, the community had returned to its previous situation.

Table 1 : Results of the Wilcoxon tests concerning the fishes of Manche-à-Eau lagoon
(Z = values of the Wilcoxon test ; p = probability of realization of Ho ; * = significant values).

	June 89	September 89	January 90	March 90
June 89		Z = -2.354	Z = -0.457	Z = -0.943
September 89	p = 0.019 *		Z = -2.623	Z = -2.650
January 90	p = 0.648	p = 0.009 *		Z = -1.628
March 90	p = 0.346	p = 0.008 *	p = 0.104	

B. Seagrass beds

In seagrass areas, a total of 50 fish species were collected in October 1988 (one year before the hurricane), in October 1989 (10 days after), in January 1990 (4 months after) and in March 1990 (6 months after the hurricane) (Annex II).

At Christophe Islet, the Friedman analysis of variance revealed a significant difference between the fish biomass in the four samples ($X_r^2 = 17.891$; $p = 0.0013$).

The Wilcoxon test was used to test the difference between the samples pairwise (Tab. 2). Only samples collected in January 1990 appeared significantly different from those of October 1989 and March 1990. No significant difference was found in biomass between the samples collected in October 1988 and the 3 samples collected after the hurricane. Thus, there was no change in fish biomass immediately after the hurricane.

Table 2 : Results of the Wilcoxon tests on the fish community of Christophe Islet (Z = values of Wilcoxon test ; p = probability of realization of Ho ; * = significant values).

	October 1988	October 1989	January 1990	March 1990
October 1988		Z = - 1.589	Z = - 1.663	Z = 0.368
October 1989	p = 0.1120		Z = - 4.086	Z = - 1.305
January 1990	p = 0.0964	p = 0.0001 *		Z = - 3.346
March 1990	p = 0.7132	p = 0.1919	p = 0.0008 *	

At Lambis Point, the Friedman test also revealed a significant difference between the samples ($X_r^2 = 13.05$; $p = 0.011$). The Wilcoxon test showed a significant difference only between the samples of October 1988 and January 1990, and between those of January 1990 and March 1990 (Tab. 3). As for the previous station, there was no change in fish biomass just after the hurricane.

Conversely, a comparison of the Spearman rank correlation coefficients (r_s) indicated that the fish community structure differed significantly before and after the hurricane in both stations ($r_s = -1.086$, $p = 0.277$ at Christophe Islet and $r_s = 0.311$, $p = 0.756$ at Lambis Point). These differences are partly due to the appearance in the samples of schooling transient fishes (*Anchoa lyolepis*, *Diapterus rhombeus*). Their suppression from the analysis increased the values of the correlation coefficients.

Table 3 : Results of the Wilcoxon tests on the fish community of Lambis Point. (Z = values of Wilcoxon test ; p = probability of realization of Ho ; * = significant values).

	October 1988	October 1989	January 1990	March 1990
October 1988		Z = - 0.886	Z = - 2.739	Z = 0.444
October 1989	p = 0.3754		Z = - 1.305	Z = - 0.243
January 1990	p = 0.0062 *	p = 0.1919		Z = - 2.341
March 1990	p = 0.6567	p = 0.8078	p = 0.0192 *	

C. The coral reef areas

Pigeon island, a volcanic formation, is devoid of true coral reefs, but its steep slopes support the most flourishing hermatypic coral community of Guadeloupe. Concerning the fish communities, the results presented hereafter cover a 9 month period from April 1989 to January 1990. During this period, 12 censuses were made respectively before and after the hurricane. These censuses were separated by a 12-day interval. A total of 89 fish species were observed (Annex III).

The Wilcoxon signed-rank test was used to compare the biological parameters obtained from the data collected before and after the hurricane, i. e., species richness, the total density of fishes; the number of juveniles; the number of medium-size fishes; the number of big-size fishes; the number of species possessing juveniles; the Shannon-Weaver diversity and the evenness index (Tab. 4).

A significant difference was found for the total density of fishes, the number of juveniles, H' and the Pielou evenness. The other parameters such as the species richness, the number of big and medium-size fishes were not significantly different before and after the hurricane. Since there were no significant changes in the amount of medium and large fishes, only the juveniles were responsible for the observed changes in total abundance.

Table 4 : Results of the Wilcoxon test concerning the fish community of Pigeon Island (Z = values of the Wilcoxon test ; p = probability of realization of Ho ; * = significant values).

	Z	Probability
Species richness	- 0.3	0.7525
Total density per 300 m^2	- 3.0	0.0047 *
Number of juveniles	- 3.0	0.0022 *
Number of medium size individuals	- 0.2	0.8753
Number of big size individuals	- 1.0	0.2892
Number of species with juveniles	- 1.0	0.5733
Shannon index	- 3.0	0.0060 *
Pielou evenness	- 3.0	0.0037 *

Moreover, a Spearman ranks correlation coefficient was computed between the profiles of fish abundances before and after the hurricane. The correlation was highly significant showing that there were no noticeable changes in the species composition or their dominance ranks within the community.

Figure 4 shows the change in numbers of juveniles for the 24 samples distributed before and after the hurricane. An important drop in the abundance of juveniles can be observed just after the hurricane. The density observed remained low even four months after the hurricane and these conditions would probably persist until the next period of recruitment that occurs in summer.

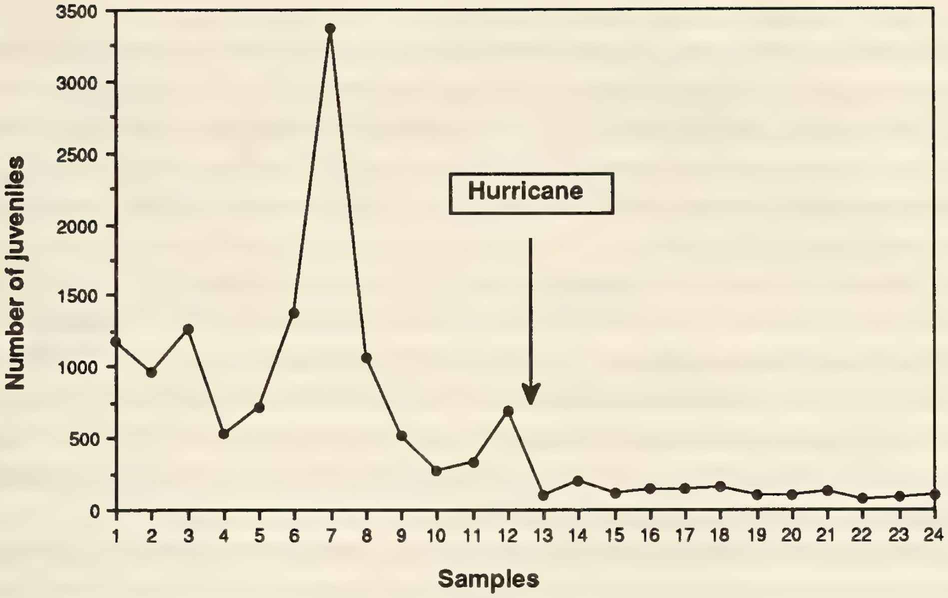

Figure 4 : Change in number of juvenile fishes before and after the hurricane.

IV. DISCUSSION AND CONCLUSION

The effects of severe storms or hurricanes on the fish communities have been documented from many parts of the world. For the Atlantic region, reports can be found for Florida (Robins, 1957 ; Breder, 1962 ; Springer and McErlean, 1962 ; Tabb and Jones, 1962 ; Beecher, 1973 ; Bortone, 1976), Jamaica (Woodley *et al.*, 1981 ; Kaufman, 1983 ; Williams, 1984), Puerto Rico (Glynn *et al.*, 1964) and Texas (Hubbs, 1962. For the Indo-Pacific region, observations have been reported for Hawaii (Walsh, 1983), the Great Barrier Reef of Australia (Lassig, 1983), the Fiji Islands (Cooper, 1966), Japan (Araga and Tanase, 1966 ; Tribble *et al.*, 1982) and Reunion Island (Letourneur, 1991). However, as pointed out by Walsh (1983), the effects of catastrophic storms on fish communities is still unclear. Some authors reported a high fish mortality after a hurricane, while others observed noticeable changes in the fish communities. Some did not observe any significant alterations in the community due to the storm.

Among the authors who did not find noticeable changes in the fish communities after a hurricane are Springer and McErlean (1962) and Bortone (1976) in Florida. Springer and McErlean (1962) noticed that reef fish populations were not much disturbed after a hurricane although reef formations were destroyed. However, their observations occurred one month after the hurricane. Bortone (1976) concluded that no major changes occurred in the fish community as a result of Hurricane Eloise. He related this to the location of the study area (well oxygenated waters and not directly affected by the surge) and to the possible presence of protective shelters for the fishes.

Robins (1957) was the first to report on the effects of a severe storm on fishes. He observed numerous dead specimens washed onshore after a severe storm in Florida. In the same region, Hurricane Donna also caused a high fish mortality (Tabb and Jones, 1962). After Hurricane Edith at Puerto Rico, Glynn *et al.* (1964) reported dead fishes floating near the coast. Cooper (1966) presented a dismal picture of the reefs of Fiji Islands after the hurricane of February 1965 ; dead fishes were floating on the water and thousands were washed up on the beach. High fish mortality was also recorded in Japan after typhoons (Araga and Tanase, 1966 ; Tribble *et al.*, 1982). Araga and Tanase (1966) made quantitative observations on the stranded fishes and noticed that about 84 % of the species and 98 % of the individuals were inshore inhabitants. In general, the fish communities from the shallow coastal waters are mostly affected.

In the mangrove areas of Grand-Cul-de-Sac Marin, the trees were completely defiolated after the hurricane. However, the loss of wood biomass was variable according to the area. In the part of the mangrove areas dominated by the red mangrove, the estimation of the loss of biomass fluctuated between 25 and 75 % (Bouchon *et al.*, 1991). Fish mortality mainly occured in the mangrove areas where the fishes were exposed to low salinity, high levels of suspended sediments and oxygen depletion. The post-hurricane fish community was significantly different to the pre-hurricane community.

The impact of Hurricane Hugo on the seagrass beds was varied. The *Thalassia testudinum* beds, even those situated in shallow waters, were only slightly affected by the direct impact of the cyclonic surge. On the contrary, the *Syringodium filiforme* beds were much more affected. A large amount of *S. filiforme* leaves and roots were washed onshore. In the months following the hurricane, a delayed mortality of the *T. testudinum* meadows was observed in the Grand Cul-de-Sac Marin. In some places, *T. testudinum* was progressively replaced by *S. filiforme* (Bouchon *et al.*, 1991). In the seagrass beds, the observed changes in the fish community were more complex. They only appeared a few months after the hurricane. This may be related to the delayed mortality of *Thalassia testudinum*.

In the coral reef environment the observed changes were less important than would be expected from the strength of the hurricane. For the benthic community, the damage due to the cyclonic surge mostly affected branching species of corals, such as *Millepora alcicornis* (especially in shallow waters), *Madracis mirabilis*, *Acropora cervicornis*, *Porites porites* and *Eusmilia fastigiata*. These colonies, broken and tossed by the waves, smashed the other benthic organisms. Massive corals withstood the hurricane better than branching corals. The soft benthic organisms, such as sponges and gorgonians were greatly damaged especially in shallow waters (Bouchon *et al.*, 1991). During the weeks following the hurricane, a "bleaching" phenomenon affected many coral colonies. This bleaching consisted in the loss of their symbiotic unicellular algae (zooxanthellae). This is generally linked to a state of stress of the animals. Most of these corals finally died. Three months after the hurricane, the bleaching phenomenon progressively disappeared. Before the hurricane a dense algal community, dominated by species belonging to the genus *Dictyota*, were present at Pigeon Island. These algae were washed ashore by the storm waves. A few weeks after, an outbreak of a red algae belonging to the genus *Liagora* occurred. Three months after, the *Liagora* population disappeared and the *Dictyota* resettled (Bouchon *et al.*, 1991).

In the study area, Hurricane Hugo mainly affected the juvenile fishes. Their density on the study reef drastically decreased the week following the hurricane. The same observations were made by Lassig (1983) on the Great Barrier Reef of Australia who noted that "the cyclone had little effects on adults but caused high juvenile mortality and re-distribution of sub-adult individuals". Beecher (1973) also reported a high mortality of juveniles of a Pomacentrid fish, *Pomacentrus (=Stegastes) variabilis*, after Hurricane Agnes in Florida.

In Guadeloupe, no specific changes in reef fish behavior were noticed after the hurricane. This is contrary to what had been described in Jamaica after Hurricane Allen (Woodley *et al.*, 1981 ; Kaufman, 1983) where cryptic species were observed in the open waters and planktivorous species swam near the bottom. The territorial fishes such as *Stegastes planifrons* became more aggressive and schools of parrotfish were reduced in size. In Hawaii, Walsh (1983) reported that fishes from the reef flats moved down to the deeper zones.

During the weeks following the hurricane in Guadeloupe, some acanthurid species (*Acanthurus bahianus* and *A. coeruleus*) were observed browsing the algae belonging to the genus *Liagora* that abnormally proliferated in the coral community. Nevertheless, examination of the survey results showed that the density of herbivorous fishes in the study areas did not increase significantly after the hurricane. This is contrary to what had been noticed in Martinique following the proliferation of *Sargassum* (Bouchon *et al.,* 1988). In Jamaica, Williams (1984) and Kaufman (1983) had reported an increase in the number of *Stegastes planifrons*, an herbivorous species, after Hurricane Allen.

The consequences of a hurricane on fish communities depend on various factors: the violence of the phenomenon ; the geographical location of the study areas ; the reef topography ; the depth location of the observations ; and above all, the magnitude of the damage on the reef associated benthic communities. In the island of Guadeloupe, the immediate impact of Hurricane Hugo was important for the fish communities situated in the mangrove. However, in this habitat, the fish community is well adapted to variations in environmental factors and apparently recovered within a few months. The changes which occurred in the seagrass beds reflect a long term decay of this habitat. As for the reef fishes, the drastic drop of juveniles may have an influence in the structuring of the fish community in the long term.

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Annex I : Numbers (N), biomass (W) and diversity indices for the fish samples collected with the specific hoop-net.

FAMILIES	**SPECIES**	June 89		Sept. 89		Jan. 90		March 90	
		N	W (g)	N	W (g)	N	W(g)	N	W (g)
MEGALOPIDAE	*Megalops atlantica*			8	8198				
ENGRAULIDAE	*Anchoa lyolepis*	31	180.2			4759	6900.1	662	1847.6
	Anchovia clupeoides					2	11		
CLUPEIDAE	*Harengula clupeola*					2301	6127.4	309	1828
	Harengula humeralis	2	17.7			2	12.2	3	11.9
	Opisthonema oglinum	1	38.7					3	105.9
MURAENIDAE	*Gymnothorax funebris*	4	9740						
BELONIDAE	*Tylosurus acus*					1	133.7		
HEMIRAMPHIDAE	*Hyporhamphus unifasciatus*					38	305.5		
CICHLIDAE	*Sarotherodon mossambica*			1	140.3				
MUGILIDAE	*Mugil curema*							2	0.9
SPHYRAENIDAE	*Sphyraena barracuda*	4	636			4	183.6	7	558.5
CENTROPOMIDAE	*Centropomus undecimalis*	5	210.3	3	1.4				
	Centropomus ensiferus					2	30		
CARANGIDAE	*Caranx latus*	6	83.3			2	152	9	317.5
	Oligoplites saurus					6	45.1	6	60.6
	Chloroscombrus chrysurus	1	46.4						
LUTJANIDAE	*Lutjanus apodus*					1	917		
POMADASYIDAE	*Haemulon bonariense*	1	57.9					2	91
SPARIDAE	*Archosargus rhomboidalis*	49	9350.1	3	656.5	25	3646.8	154	23022.3
SCIAENIDAE	*Bairdiella ronchus*	233	16037.3			202	4858.9	270	5629.1
GERREIDAE	*Diapterus rhombeus*	162	4120.1			967	4433.1	1220	7955.4
	Eucinostomus argenteus			1	3	164	344.3	592	2157.9
	Eucinostomus gula	119	2077.8			312	1484.3	444	2934.4
	Eugerres brasilianus	12	1368.1			1	10.7	4	43.3
	Gerres cinereus			6	10.2	24	150.1	162	1110.1
EPHIPIDAE	*Chaetodipterus faber*							1	128.5
BOTHIDAE	*Citharichthys spilopterus*							1	22.9
GOBIDAE	*Bathygobius soporator*			13	27.1				
	Gobionellus oceanicus			119	672			1	24.8
	Gobionellus sp			6	26.1				
TETRODONTIDAE	*Sphoeroides testudineus*	245	24017.3			7	193.1	15	680.8
Total		875	67981.2	160	9734.6	8820	29938.9	3867	48531.4
Species richness	32 species		15		9		19		20
Shannon Index			2.48		0.89		2.91		2.57
Pielou Index			0.63		0.28		0.69		0.58

Annex II (continued) : Numbers (N), biomass (W) and diversity indices for the fish samples collected with a seine net in the seagrass beds of Grand Cul-de-Sac Marin Bay.

FAMILY	SPECIES	LAMBIS POINT							
		Oct. 88		Oct. 89		Jan. 90		March 90	
		N	W (g)	N	W (g)	N	W(g)	N	W (g)
ALBULIDAE	*Albula vulpes*								
CLUPEIDAE	*Harengula clupeola*								
ENGRAULIDAE	*Anchoa cf lyolepis*			81	922.2	98	309.1	6	27.1
SYNGNATHIDAE	*Cosmocampus elucens*					2	1.9		
	Syngnathus sp							3	6.1
HOLOCENTRIDAE	*Holocentrus rufus*								
SPHYRAENIDAE	*Sphyraena barracuda*					3	105.4		
SERRANIDAE	*Hypoplectrus puella*	1	9.7	5	28.1	2	17.5		
	Serranus flaviventris	6	32.3	2	6.3	6	17.3	10	37.3
CARANGIDAE	*Caranx latus*								
	Oligoplites saurus					1	8.3		
	Selene vomer								
LUTJANIDAE	*Lutjanus analis*								
	Lutjanus apodus	5	31.3	2	12.1	8	106.1	1	15
	Lutjanus griseus	1	3.2						
	Lutjanus synagris			4	24.5	1	63		
	Ocyurus chrysurus	138	633.7	90	287.5	183	975.6	153	396
POMADASYIDAE	*Haemulon aurolineatum*								
	Haemulon bonariense								
	Haemulon chrysargyreum	1	12.3	3	43				
	Haemulon flavolineatum					11	60.6	7	14.2
	Haemulon plumieri			2	23.8	6	85.3	7	42.4
	Haemulon sciurus			2	2.6	2	7.6	9	57.3
SPARIDAE	*Archosargus rhomboidalis*	2	10.5	1	9	6	193.3	12	83.9
	Calamus sp							1	2.6
SCIAENIDAE	*Bairdiella ronchus*								
GERREIDAE	*Diapterus rhombeus*			9	390.5				
	Eucinostomus argenteus	1	1.5			11	60.4		
	Eucinostomus gula	18	85.5	34	151.7	22	157.3	2	20.4
	Gerres cinereus					19	152.2	3	12.8
BOTHIDAE	*Citharichthys spilopterus*								
SOLEIDAE	*Achirus lineatus*							2	0.3
	Pseudupeneus maculatus							1	23.8
SCORPAENIDAE	*Scorpaena grandicornis*	1	4.2						
CHAETODONTIDAE	*Chaetodon capistratus*	32	88.2	2	7.1	1	3.1		
LABRIDAE	*Lachnolaimus maximus*					1	0.8		
SCARIDAE	*Sparisoma chrysopterum*	2	0.4	4	15.1			4	3.1
	Sparisoma radians								
GOBIDAE	*Gobidae sp.1*								
	Gobidae sp. 2								
	Gobidae sp.3								
	Gobionellus oceanicus								
ACANTHURIDAE	*Acanthurus bahianus*								
	Acanthurus chirurgus								
MONACANTHIDAE	*Monacanthus ciliatus*	1	3.3						
TETRODONTIDAE	*Sphoeroides nephelus*	1	1.4	1	8.4				
	Sphoeroides greeleyi								
	Sphoeroides spengleri	4	43.2	1	13.9	5	42.5	2	1.6
	Sphoeroides testudineus					1	6	1	5.2
DIODONTIDAE	*Diodon holacanthus*	1	85	2	528.6	2	249.3	1	293.8
Total		215	1045.7	245	2474.4	391	2622.6	225	1042.9
Species richness	50 species		16		17		21		18
Shannon Index			2.14		2.58		3.18		2.7
Pielou Index			0.54		0.63		0.72		0.65

Annex II : Numbers (N), biomass (W) and diversity indices for the fish samples collected with a seine net in the seagrass beds of Grand Cul-de-Sac Marin Bay.

FAMILY	SPECIES	CHRISTOPHE ISLET							
		Oct. 88		Oct. 89		Jan. 90		March 90	
		N	W (g)	N	W (g)	N	W(g)	N	W (g)
ALBULIDAE	*Albula vulpes*					1	5.8	1	20.3
CLUPEIDAE	*Harengula clupeola*					27	81		
ENGRAULIDAE	*Anchoa cf lyolepis*			8	13.9	347	995.3	360	550.5
SYNGNATHIDAE	*Cosmocampus elucens*								
	Syngnathus sp								
HOLOCENTRIDAE	*Holocentrus rufus*	1	43.6						
SPHYRAENIDAE	*Sphyraena barracuda*	2	143.5	6	8.9	4	134.5		
SERRANIDAE	*Hypoplectrus puella*	1	2.8			8	77	2	14.7
	Serranus flaviventris	10	42.7	3	3.8	17	51.6	4	13.1
CARANGIDAE	*Caranx latus*			1	2	1	6		
	Oligoplites saurus								
	Selene vomer			5	11.9			1	5
LUTJANIDAE	*Lutjanus analis*	1	21.9						
	Lutjanus apodus	3	13			1	24.1		
	Lutjanus griseus								
	Lutjanus synagris			75	55	43	278.2	12	88.5
	Ocyurus chrysurus	152	595.2	9	69.3	115	583.8	5	18.1
POMADASYIDAE	*Haemulon aurolineatum*					4	4.5		
	Haemulon bonariense	1	8.8	1	5.1			2	10.1
	Haemulon chrysargyreum	2	17.6						
	Haemulon flavolineatum					13	18.2	2	5.2
	Haemulon plumieri					14	114.1		
	Haemulon sciurus								
SPARIDAE	*Archosargus rhomboidalis*	2	81.7	1	31.8	2	45.5		
	Calamus sp								
SCIAENIDAE	*Bairdiella ronchus*					3	16.9		
GERREIDAE	*Diapterus rhombeus*			128	945.3	398	1173.6	99	344.9
	Eucinostomus argenteus			12	23.5			31	135.4
	Eucinostomus gula	70	293.7	258	358.6	200	609.9	103	472
	Gerres cinereus					2	8.6	8	63.4
BOTHIDAE	*Citharichthys spilopterus*			1	15.7	9	23.7	4	19.1
SOLEIDAE	*Achirus lineatus*					20	355.7	11	4
	Pseudupeneus maculatus							1	14.3
SCORPAENIDAE	*Scorpaena grandicornis*								
CHAETODONTIDAE	*Chaetodon capistratus*	7	14.6			1	6.6		
LABRIDAE	*Lachnolaimus maximus*	1	49						
SCARIDAE	*Sparisoma chrysopterum*	1	58.3						
	Sparisoma radians					5	51.6		
GOBIDAE	*Gobidae sp.1*			17	5.7				
	Gobidae sp. 2							2	0.4
	Gobidae sp.3			4	0.9			1	0.1
	Gobionellus oceanicus					5	1.5		
ACANTHURIDAE	*Acanthurus bahianus*	1	17.2			1	2.9		
	Acanthurus chirurgus	1	8.4			1	1.2		
MONACANTHIDAE	*Monacanthus ciliatus*								
TETRODONTIDAE	*Sphoeroides nephelus*							1	0.2
	Sphoeroides greeleyi	1	4.3			2	0.9		
	Sphoeroides spengleri	1	12	1	0.6	1	0.5		
	Sphoeroides testudineus			1	0.5	2	9	1	1
DIODONTIDAE	*Diodon holacanthus*	2	139			4	987.9		
Total		260	1567.3	531	1552.5	1251	5670.1	651	1780.3
Species richness	50 species		19		17		29		20
Shannon Index			2.98		1.83		3.29		2.66
Pielou Index			0.7		0.45		0.68		0.61

Annex III : Number of indivuals per species observed before (1 to 12) and after (13 to 24) the hurricane at Pigeon island.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24
Lycodontis moringa	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Muraena miliaris	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Synodus intermedius	0	0	1	2	3	0	1	0	0	1	2	1	0	0	0	1	0	2	1	0	1	2	0	0
Neoniphon marianus	1	0	3	2	1	1	1	1	4	4	0	0	1	2	2	10	5	7	6	4	2	2	1	0
Holocentrus rufus	2	4	2	4	3	3	2	3	5	0	2	0	7	4	6	4	5	4	6	3	6	3	0	1
Myripristis jacobus	16	18	17	18	17	35	33	27	54	22	13	15	36	22	26	48	44	25	16	13	22	14	14	14
Aulostomus maculatus	4	5	2	3	2	1	5	4	2	5	3	4	6	11	4	5	4	6	9	5	4	4	3	5
Fistularia tabacaria	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Scorpaena plumieri	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Cephalopholis cruentatus	3	6	2	1	7	3	5	6	2	4	4	5	4	5	6	5	9	14	6	1	6	1	1	4
Cephalopholis fulva	0	0	1	1	3	1	1	1	1	1	1	4	0	3	4	7	3	4	3	3	3	1	1	0
Epinephelus adscensionis	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Hypoplectrus chlorurus	0	0	0	0	0	1	1	1	0	0	1	0	0	0	0	0	0	1	1	0	0	0	0	0
Hypoplectrus cf guttavarius	2	3	1	0	0	3	1	0	0	3	2	0	1	0	1	1	1	2	1	2	0	1	3	2
Hypoplectrus nigricans	0	0	0	0	0	1	0	0	0	0	1	0	1	0	0	0	0	1	0	0	0	0	1	1
Hypoplectrus puella	3	7	6	7	9	7	8	11	4	4	6	6	4	9	9	4	6	6	8	8	5	7	4	3
Hypoplectrus sp. 1	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Mycteroperca interstitialis	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Paranthias furcifer	23	0	0	0	0	0	5	0	1	1	0	4	1	0	1	2	0	0	0	0	0	0	0	0
Serranus tabacarius	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Serranus tigrinus	3	2	2	7	7	6	5	5	6	3	7	2	5	4	6	5	4	7	4	7	5	2	5	3
Heteropriacanthus cruentatus	1	0	0	1	0	0	0	1	2	0	0	1	0	0	0	0	0	1	0	1	1	0	2	0
Carangoides ruber	1	0	1	0	0	2	0	0	3	2	0	1	1	0	1	1	0	0	0	1	0	0	0	0
Caranx latus	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Selar crumenophthalmus	8	0	0	0	0	0	40	0	240	40	0	0	275	4	0	20	0	0	0	0	0	0	0	0
Inermia vittata	0	20	20	0	0	0	40	0	115	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Lutjanus apodus	0	1	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	1	0	2	0	0
Lutjanus jocu	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0
Lutjanus mahogoni	0	1	2	2	0	0	0	1	0	0	3	1	0	0	0	0	0	0	0	0	0	0	0	0

Annex III (Continued) : Number of indivuals per species observed before (1 to 12) and after (13 to 24) the hurricane at Pigeon island.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24
Ocyurus chrysurus	4	2	7	3	1	3	0	1	4	5	5	8	9	3	5	29	10	3	10	9	10	5	9	11
Anisotremus virginicus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0
Haemulon carbonarium	0	1	0	0	1	0	0	1	0	1	1	0	0	0	1	2	0	0	0	1	1	1	3	1
Haemulon chrysargyreum	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0
Haemulon flavolineatum	3	2	2	1	2	0	0	3	1	1	2	4	1	1	2	2	1	2	2	2	2	0	3	3
Haemulon plumieri	0	0	1	0	1	0	0	0	0	2	1	0	0	0	1	2	0	0	1	0	0	0	1	6
Haemulon sciurus	1	0	1	2	1	1	0	0	1	0	1	0	1	1	0	0	0	1	2	0	1	0	0	0
Calamus bajonado	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	1	0	1
Calamus calamus	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	2	0	0	0	0	1	0	0	1
Equetus punctatus	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Mulloides martinicus	5	5	3	3	6	5	28	12	13	13	8	21	8	6	12	0	14	8	2	0	0	2	0	1
Pseudupeneus maculatus	0	1	0	1	1	1	1	0	0	1	1	1	2	2	1	1	0	2	1	1	1	2	0	0
Kyphosus sectatrix	0	0	1	0	1	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0
Chaetodon aculeatus	1	1	1	1	2	4	2	3	2	1	2	4	4	1	3	0	4	1	1	2	2	1	1	1
Chaetodon capistratus	16	9	21	9	15	7	10	13	4	1	6	9	14	9	21	13	12	14	13	7	7	8	11	15
Chaetodon striatus	0	2	0	0	0	0	1	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0
Holacanthus tricolor	2	0	0	0	1	0	2	0	0	1	0	0	0	0	1	0	0	0	0	0	1	0	3	1
Pomacanthus paru	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	2	0	0	1	0	0	0
Abudefduf saxatilis	1	1	5	6	0	1	1	2	2	1	2	1	1	3	2	3	0	2	3	0	1	3	1	0
Chromis cyanea	791	446	190	282	250	304	287	139	136	134	168	217	76	87	88	160	112	112	77	126	90	60	96	72
Chromis multilineata	115	78	528	68	79	120	616	87	134	40	60	310	100	139	83	203	40	230	239	117	40	120	81	123
Microspathodon chrysurus	2	1	1	1	0	0	0	0	1	2	0	1	0	0	1	1	1	2	0	1	2	0	0	3
Stegastes partitus	124	136	86	162	218	298	153	216	59	154	226	158	96	140	200	186	208	206	86	142	134	154	116	118
Stegastes planifrons	27	28	25	34	28	25	22	23	23	34	36	27	21	24	30	28	36	37	36	27	27	24	25	25
Amblycirrhitus pinos	0	0	0	0	1	0	1	0	1	0	0	0	0	1	2	0	0	0	0	1	1	1	0	0
Sphyraena barracuda	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Bodianus rufus	0	0	0	4	3	0	3	9	2	0	0	1	1	0	1	1	1	1	1	2	0	0	1	2
Clepticus parrae	496	381	3015	159	95	615	3159	648	212	48	155	590	434	14	12	409	40	0	1579	40	1	20	20	8
Halichoeres garnoti	25	21	18	23	15	19	12	13	19	18	21	16	5	20	20	23	24	21	12	14	20	20	16	17

Annex III (continued) : Number of indivuals per species observed before (1 to 12) and after (13 to 24) the hurricane at Pigeon island.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24
Halichoeres radiatus	0	0	0	1	0	0	0	0	0	1	1	0	1	0	1	0	0	1	0	1	0	0	1	0
Lachnolaimus maximus	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Thalassoma bifasciatum	68	48	83	153	141	288	224	197	158	128	115	138	48	82	39	55	58	70	67	45	83	30	39	48
Scarus guacamaia	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Scarus iserti	0	1	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	1	1
Scarus taeniopterus	11	30	42	46	38	57	45	38	18	27	19	8	35	22	19	23	9	20	22	18	21	18	15	7
Scarus vetula	1	2	1	0	3	0	0	3	0	1	2	2	0	0	1	1	2	1	1	1	0	0	0	0
Sparisoma aurofrenatum	10	17	24	18	20	20	27	23	9	16	19	16	9	19	16	17	21	24	15	8	16	9	9	12
Sparisoma chrysopterum	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0
Sparisoma rubripinne	0	3	0	1	5	2	0	3	2	4	1	0	0	2	2	1	1	1	1	0	5	0	1	0
Sparisoma viride	5	5	5	2	5	8	8	2	2	4	11	8	4	11	11	8	5	11	4	6	11	7	5	4
Sparisoma atomarium	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Coryphopterus personatus	0	0	0	82	80	100	375	895	235	505	315	495	60	80	140	60	24	48	36	40	28	20	0	0
Acanthurus bahianus	2	1	4	1	3	3	0	0	1	1	2	0	2	1	1	2	40	2	40	2	1	2	1	1
Acanthurus chirurgus	0	0	0	0	0	0	0	0	0	0	0	20	0	0	0	0	75	0	75	0	0	0	0	0
Acanthurus coeruleus	0	0	3	2	1	1	1	0	1	5	3	9	3	3	2	6	78	4	79	4	4	2	2	3
Scomberomorus regalis	0	0	92	0	2	0	0	13	1	0	1	0	0	0	0	1	0	1	0	0	0	0	0	0
Bothus lunatus	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cantherhines macrocerus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	1	0
Cantherhines pullus	6	2	1	0	2	2	1	0	1	2	2	1	3	2	2	0	1	0	2	0	0	0	0	1
Melichthys niger	0	0	0	0	0	0	0	0	0	3	0	0	0	0	1	0	0	1	2	0	0	0	0	0
Acanthostracion polygonius	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Lactophrys bicaudalis	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Lactophrys triqueter	3	1	0	2	1	1	1	0	0	3	0	0	0	3	1	3	2	1	2	2	2	0	0	0
Canthigaster rostrata	0	2	3	2	1	2	5	1	1	5	0	2	1	2	4	6	3	1	4	1	3	4	0	1
Cyclichthys antennatus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Diodon holacanthus	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Juvéniles sp1	0	115	20	20	200	20	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

ATOLL RESEARCH BULLETIN

NO. 423

THE SIAN KA'AN BIOSPHERE RESERVE CORAL REEF SYSTEM,

YUCATAN PENINSULA, MEXICO

BY

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MARTÍN SÁNCHEZ-SEGURA, AND ALEJANDRO GONZALEZ DE LA PARRA

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ABSTRACT

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

INTRODUCTION

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

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

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

STUDY AREA

The Sian Ka'an Biosphere Reserve is located on the eastern side of the Yucatán Peninsula, facing the Caribbean Sea (Fig. 1). The Reserve covers an area of approximately 4,500 km², of which some 1,200 km² correspond to lagoon and marine environments. The marine coastline extends for more than 100 km, and a nearly continuous reef system is found along it.

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

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

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

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

METHODS

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

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

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

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

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

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

RESULTS

I. Reef Morphology

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

II. Coral Community

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

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

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

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

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

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

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

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

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

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

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

DISCUSSION

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

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

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

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

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

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

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

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

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

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

TABLE 1. Structural Attributes utilized on the quantitative sampling.

REAR REEF-CREST

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

FORE SLOPE (-10m)

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

FORE SLOPE (-20m)

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

FORE SLOPE (-30m)

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

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

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

Scleractinians

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

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

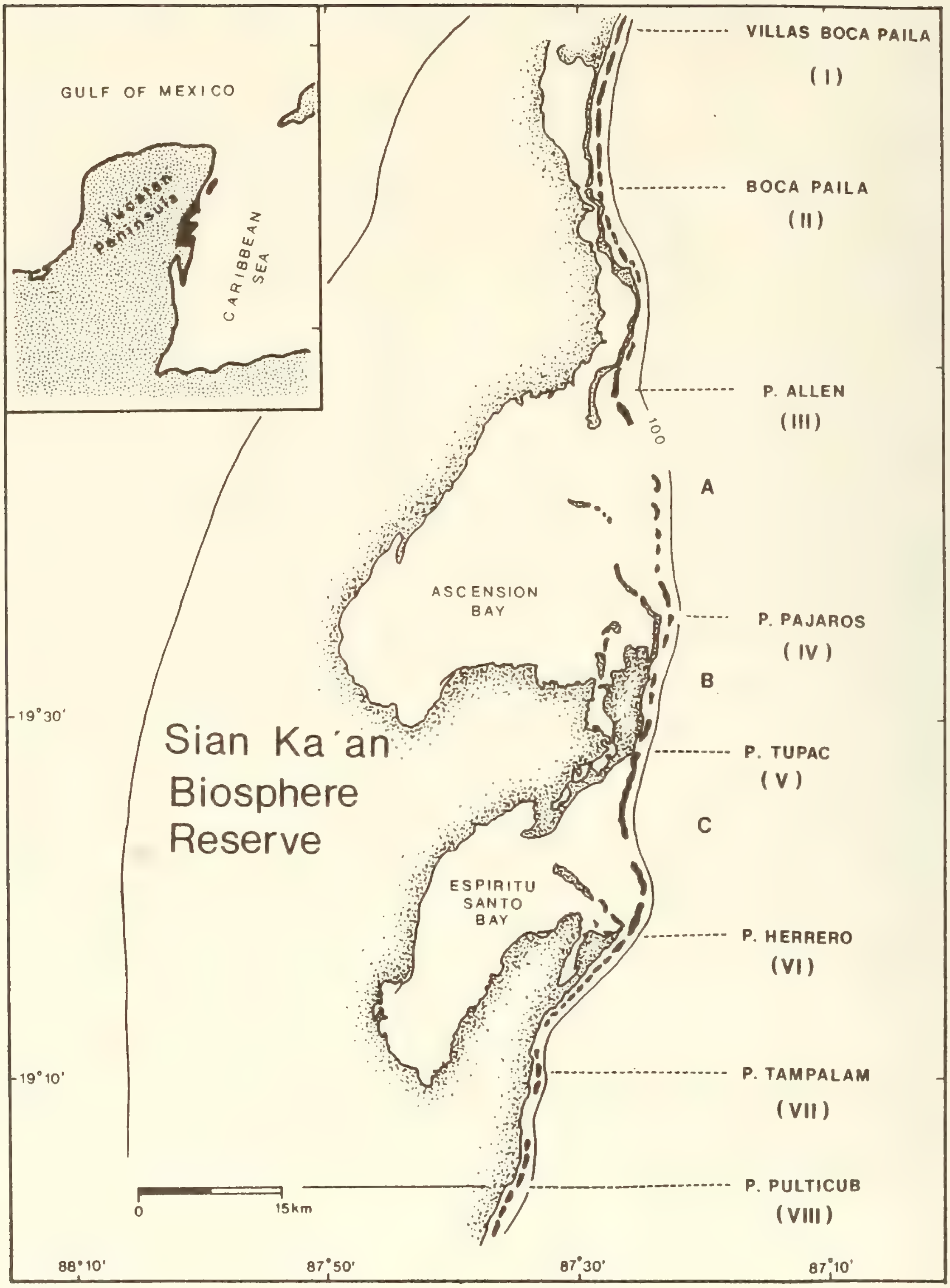

Figure 1. Map showing the geographical position of the Sian Ka'an Biosphere Reserve and location of the sampling sections. Roman numerals below correspond to code numbers.

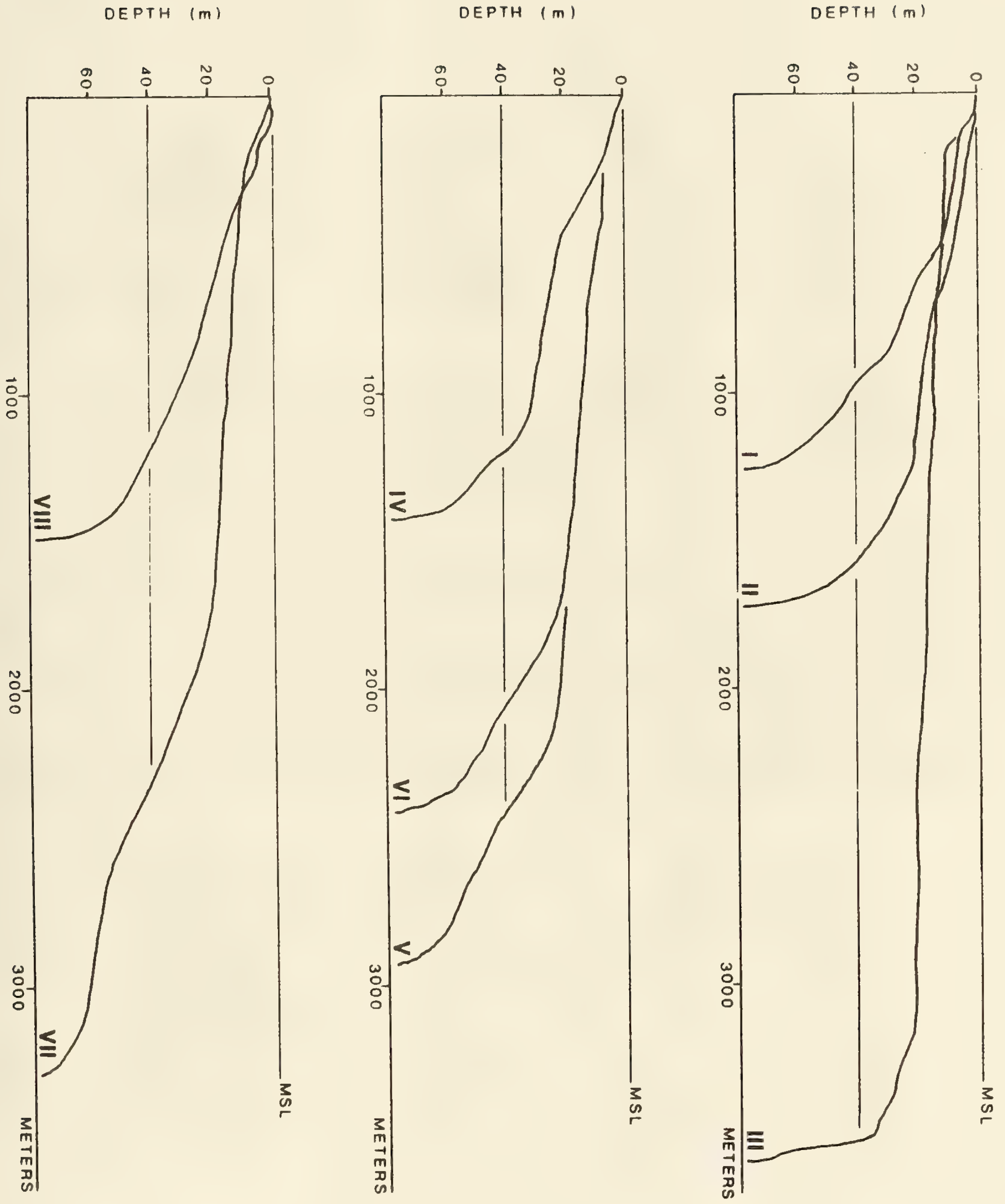

Figure 2. Bathymetric profiles for each section. The horizontal line at the -40m level marks the deeper limit of underwater observations.

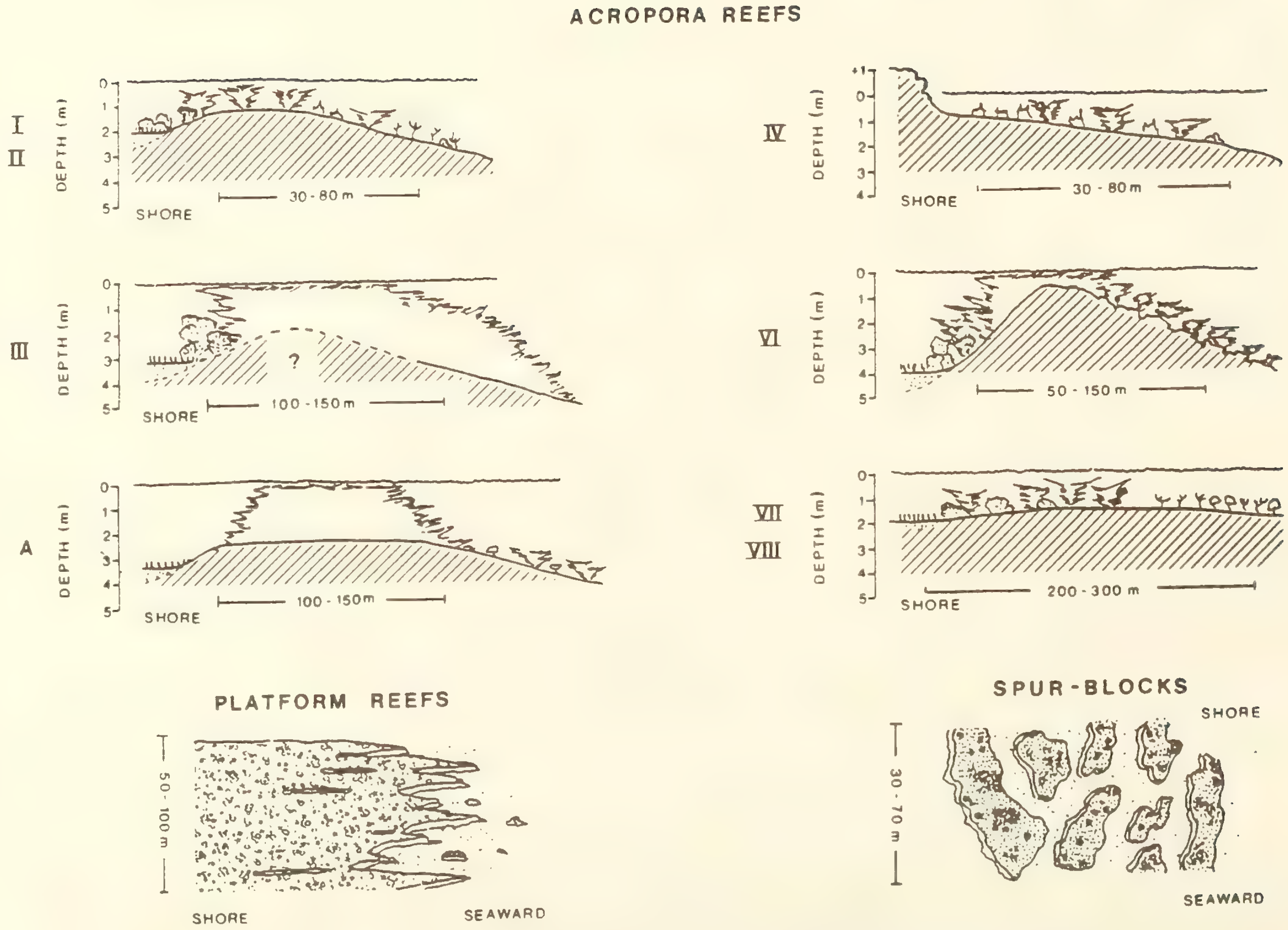

Figure 3. Sketches of the main reef types found in the study area. Dimensions are approximate and represent averages of several sets of measurements.

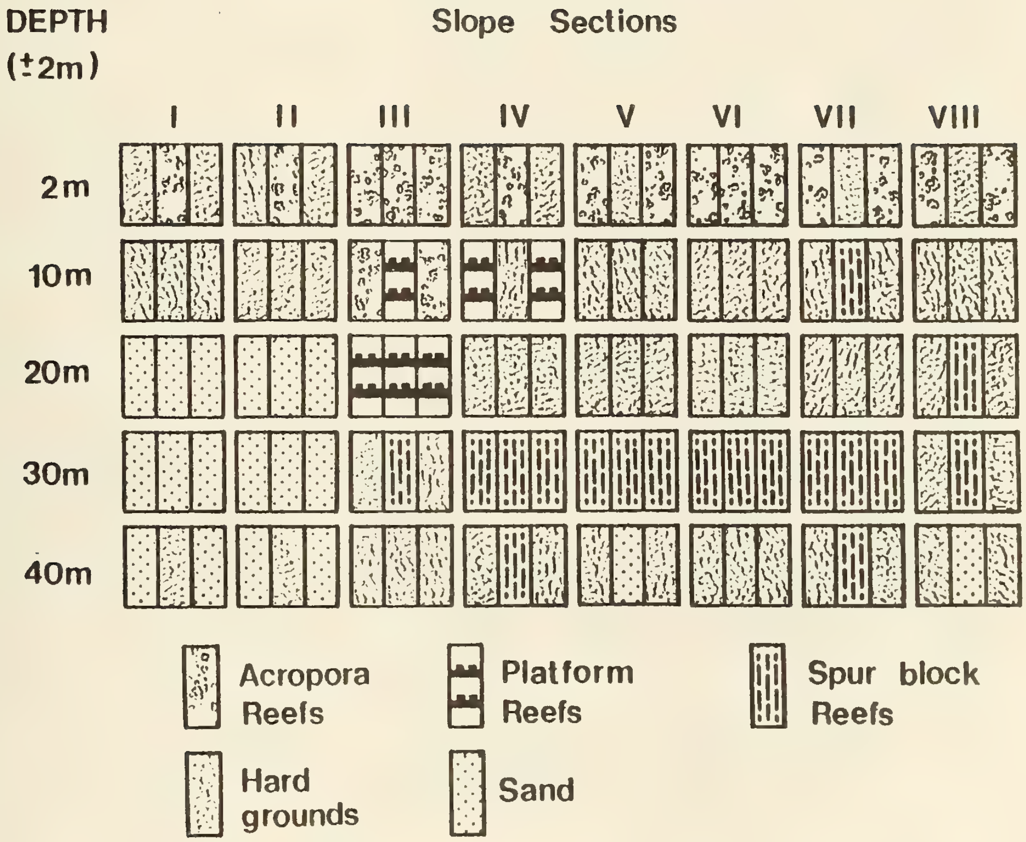

Figure 4. Main reef and substrata distribution on the shelf of Sian Ka'an.

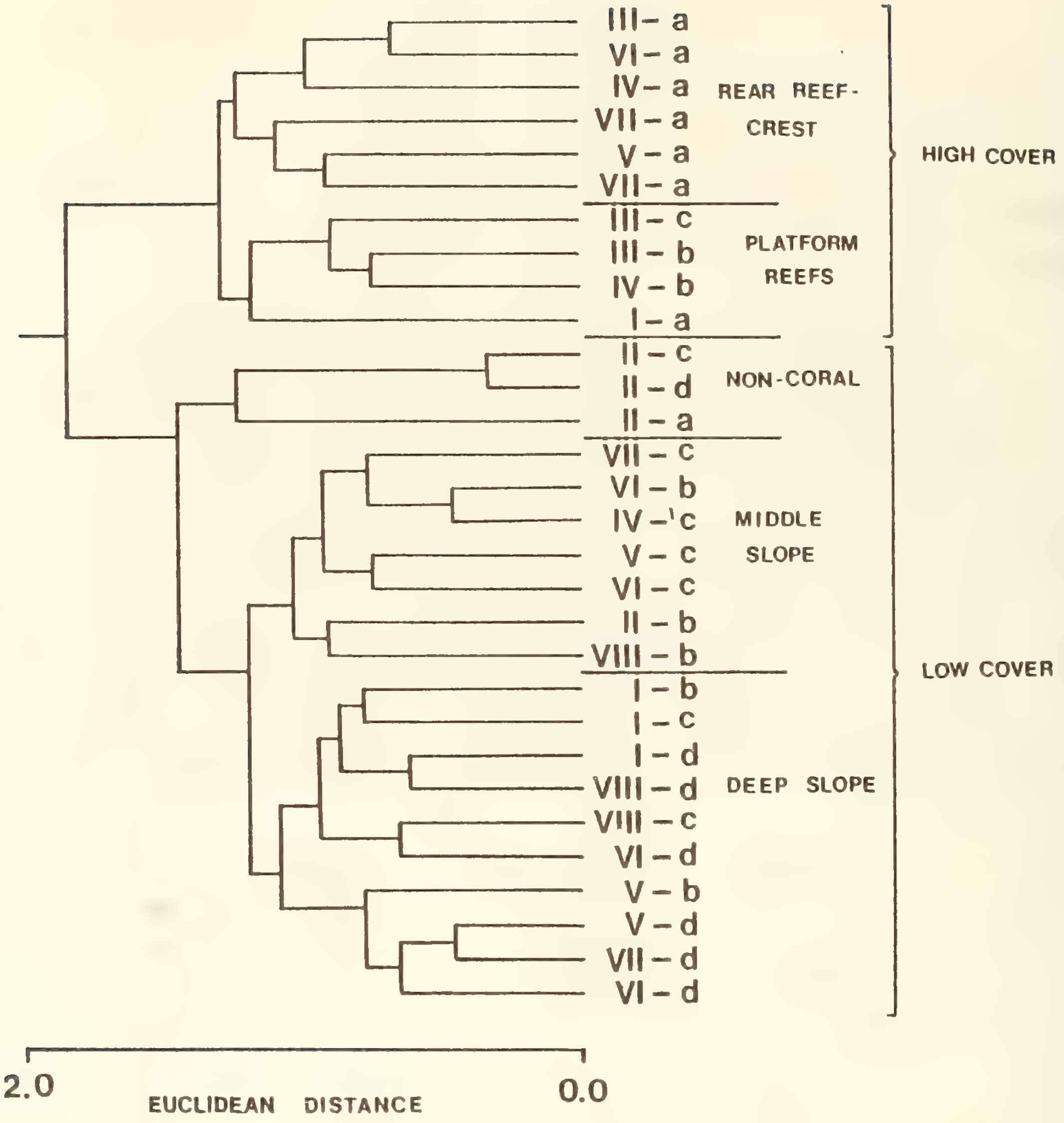

Figure 5. Dendrogram of cover attributes (excluding hard ground and sand). Cluster analysis of log-transformed cover data with average linkage.

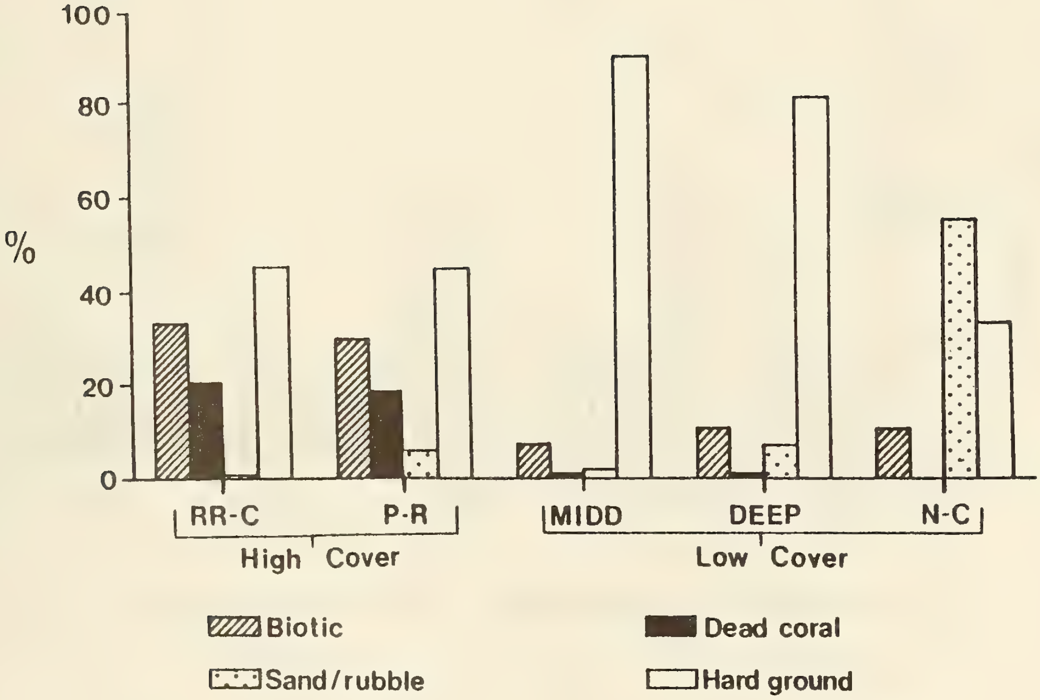

Figure 6. Percentage of cover for biota, dead coral, hard ground and sand, for each of the clusters suggested by the dendrogram in Fig. 5.

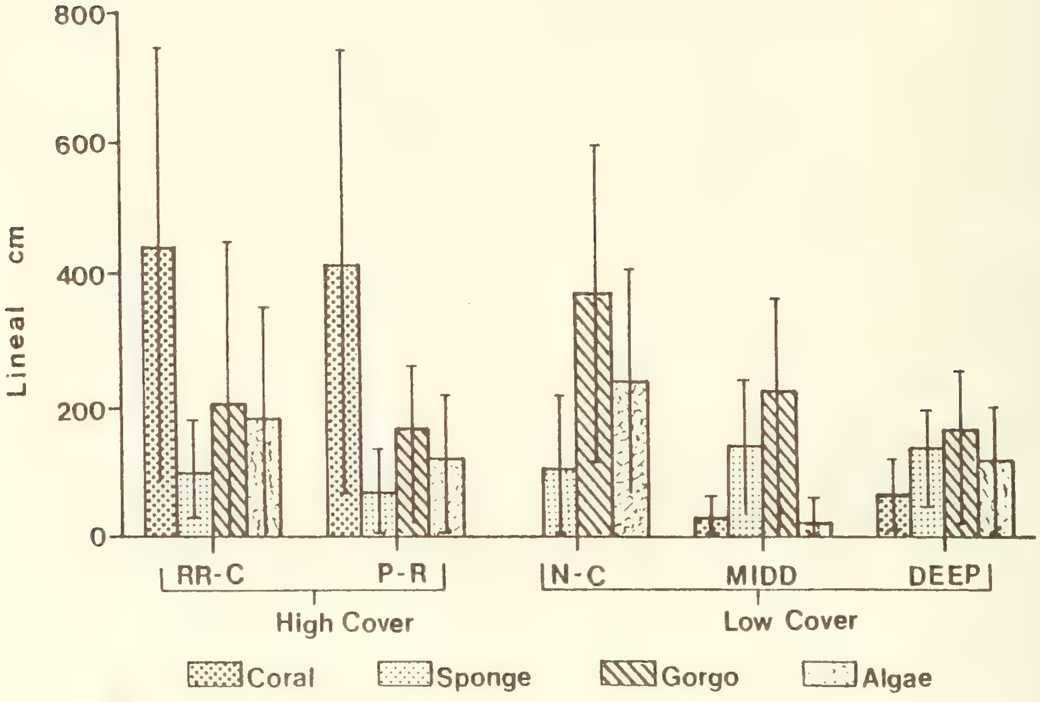

Figure 7. Mean lineal cover of the main biotic attributes, for each of the clusters suggested by the dendrogram in Fig. 5. The vertical line indicates one standard deviation.

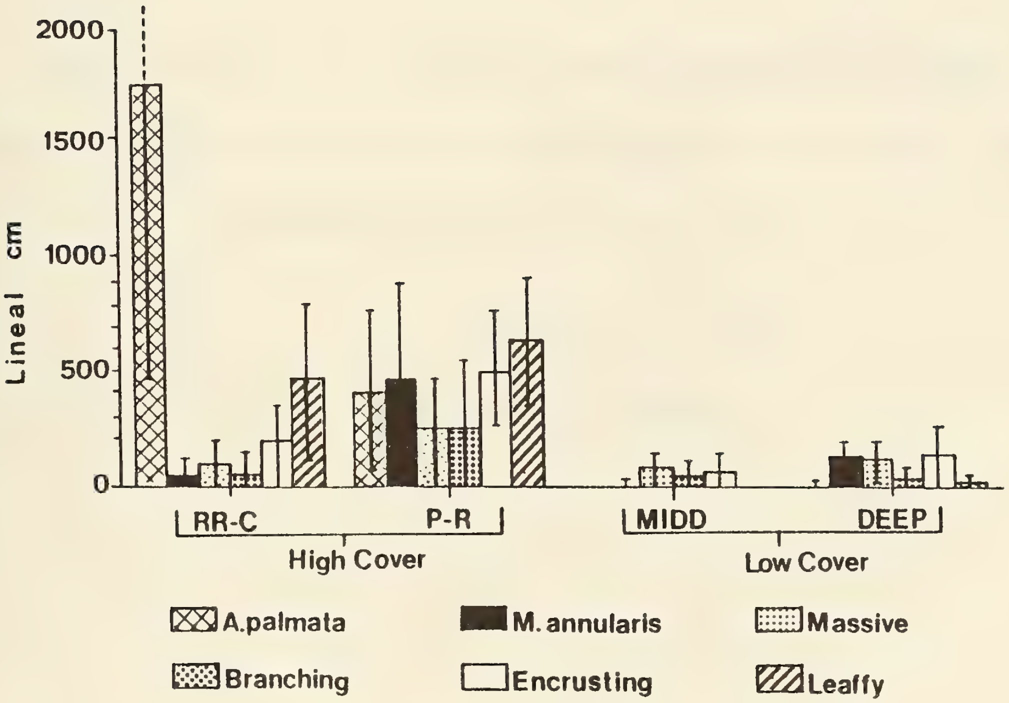

Figure 8. Mean lineal cover of the coral attributes for each of the clusters suggested by the dendrogram in Fig. 5. The vertical line indicates one standard deviation.

ATOLL RESEARCH BULLETIN

NO. 424

A PRELIMINARY EVALUATION OF THE COMERCIAL SPONGE RESOURCES OF BELIZE WITH REFERENCE TO THE LOCATION OF THE TURNEFFE ISLANDS SPONGE FARM

BY

J.M. STEVELY AND D.E. SWEAT

ISSUED BY
NATIONAL MUSEUM OF NATURAL HISTORY
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WASHINGTON, D.C., U.S.A.
AUGUST 1994

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SUMMARY OF FINDINGS

Our discovery of concrete disks used for planting sponge cuttings confirms the location of the Turneffe Island sponge farm activities as described by Smith (1941). It is hoped that this information will be useful to the Government of Belize in identifying potentially historic or unique marine resources.

We here also report the occurrence of the velvet sponge, Hippospongia gossypina, at Turneffe Islands. The occurrence of the velvet sponge is particularity worthy of note since a devastating commercial sponge mortality in 1938-39 drastically reduced velvet sponge abundance throughout a portion of its geographic distribution. We observed that the attachment substrate of the Turneffe Islands velvet sponge, mangrove peat, was different than that reported for sheepswool sponge, Hippospongia lachne, and different than the attachment substrate previously reported for velvet sponge.

The quality of the Turneffe Islands velvet sponge is such that it is commercially marketable, but would be less valuable than the sheepswool sponge. The velvet sponge is sufficiently abundant at one location to support commercial fishing activity. However, our survey work was not adequate to establish whether the abundance of velvet sponges was sufficiently extensive to support a sustainable sponge fishery. The lack of more extensive data on abundance and the historical accounts indicating the effects of past sponge disease and fishing pressure on velvet sponge distribution warrant a conservative approach to managing velvet sponges as a commercial fishery resource. Additional survey work will be required to more fully understand the commercial sponge resources of Belize.

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INTRODUCTION

The usefulness of commercial sponges is based on their soft, compressible nature and their ability to absorb and hold water. Sponges from the genera Spongia and Hippospongia have been used for personal bathing and household cleaning for thousands of years. The taking of sponges for commercial purposes was first practiced in the Mediterranean Sea and the sponge fishery was often noted in early Greek literature (Moore, 1951). More recently, commercial sponges have been used in manufacturing pottery and ceramics, and in a variety of applications in surgery, painting, polishing, printing, horse grooming, and professional cleaning services. Synthetic sponges have replaced natural sponges for many of these uses because they are cheaper and more readily available. Today, natural sponges are principally used for bathing (Josupeit, 1991) and the application of cosmetics by people in westernized communities because these people prefer a natural product (Wilkinson, unpub. mans.). Although synthetic sponges are less expensive, they cannot equal the softness and absorbency of natural sponges, and, importantly, natural sponges can be more easily and thoroughly cleaned due to the truly porous nature of the sponge skeleton.

Until the 1840's the world's sponge supply was derived solely from the waters of the Mediterranean. However, the discovery of quality commercial sponges in the Bahamas and Florida Keys led to the rapid development of sponge fisheries in Caribbean and Gulf of Mexico waters. During the early part of the 20th century (1900 - 1940's) the commercial sponge fishery was the most economically important fishery in Florida, U.S.A. (Stevely, et al., 1978). Cuba produced 440,000 lb (198,000 kg) of sponges, the Bahamas 670,000 (302,000 kg), while U.S. production totaled 610,000 lb (275,000 kg) (Moore, 1951). The large-scale attempts to culture sponges in the Bahamas (Storr, 1964), Belize (Smith, 1939) and Florida (Moore, 1910a; Shubow, 1969) further attest to the importance of sponges as a fishery resource during this period.

A sponge disease swept through the Caribbean and Gulf of Mexico in 1938-39 and dramatically reduced commercial sponge abundance. The decline in supply caused by the disease and the outbreak of World War II, which curtailed production in the Mediterranean, resulted in dramatically higher prices. Although production in Florida declined precipitously in the 1940's, rapidly escalating prices were sufficient to increase fishing effort and actually increase the total value of the fishery. The result was increased fishing effort at a time when fishing effort probably should have been curtailed to allow the commercial sponge populations to recover (Storr, 1964). The Florida commercial sponge grounds were depleted to the point of causing the virtual economic extinction of the fishery and many years were required for commercial sponges to increase to abundances that approached those found before the sponge disease epidemic. The effects of the sponge blight were similar throughout the Caribbean. The cause of the disease has been confused somewhat by the presence of bacteria including symbionts, that live in close association with sponge tissue (Lauckner, 1980).

Although the Caribbean sponge disease and introduction of synthetic sponges in the post World War II era has resulted in reducing the world sponge trade to a fraction of its former importance, a significant sponge trade still exists. Prior to WW II (1927-1936), world sponge production annually averaged 1,346.1 MT, and in more recent times (l977-l986) it has annually averaged 222.1 MT (Josupeit, l991). The world's supply of bath sponges comes from the lesser-developed countries of the Mediterranean and Caribbean: Tunisia (48%), Greece (17%) and Cuba (26%) are the principal suppliers. Countries importing the largest volume of natural sponges are France (37%), USA (26%), Japan (l0%), and Italy (9%) (Josupeit, 1991). In terms of the quantity landed by weight, most fishery managers would consider the world sponge fishery to be insignificant. However, it must be noted that the highest grade of commercial sponge can command a price of over U.S. $50.00/lb ($110.00/kg) in the export market.

Currently, market demand for natural sponges is such that the opportunity exists for expanded production from the Caribbean and Gulf of Mexico. A decline in commercial sponge abundance caused by disease (Gaino and Pronzato), l989), and pollution and overfishing (Verdenal and Verdenal, l986) has significantly reduced the supply of Mediterranean sponges. Reduced supply has resulted in higher commercial sponge prices and focused attention on increasing sponge production on other areas of the world. For example, Josupeit (l991) reported that, in France, the reduced sponge supply, as well as a general trend for increased use of natural products, resulted in retail sponge prices doubling and even trebling. During l988, Florida sponge prices more than doubled and fishing effort and production significantly increased (Stevely, pers. obs.). Although Florida sponge prices have stabilized below the peak prices of l988, they are still substantially higher than pre-l988 prices.

Increased market demand and the consequent higher prices for Caribbean sponges has resulted in a need to carefully assess sponge fishery potential and fishery management needs throughout the region. The objectives of this project were to (1) evaluate the fishery potential for harvesting commercial sponges in the marine waters of Belize, (2) provide the Belizean Fisheries Unit with information pertinent to management of a commercial sponge fishery, and, (3) establish the location of the historic Turneffe Islands commercial sponge farm before its location was lost to posterity in general, and to the fisheries heritage of Belize in particular. Project funding was provided by the Smithsonian Institution's Caribbean Coral Reef Ecosystem Program (CCRE Contribution No. 402).

METHODS AND MATERIALS

Field surveys to determine the distributions and abundance of commerical sponges were conducted from l4 May to 30 May, l989. These surveys were performed using dive mask, snorkel and fins. To cover large areas, a diver was towed by boat for 30 to 90 minutes. Three locations were surveyed (Figure 1): Carrie Bow Cay, Ambergris Cay, and Turneffe Islands. The maximum and minimum diameters of commercial sponges were measured with a pair of large calipers. Field notes on duration of tow and habitat type were recorded. Plans to collect commercial sponge abundance within quantifiable transect lines had to be aborted due to inclement weather and contractual problems with a local fishing guide.

Surveys at Carrie Bow Cay, capitalizing on the Smithsonian Institute facilities there, were conducted to field-test survey procedures, and collect information on the distribution of commercial sponges in the vicinity of the barrier reef and associated

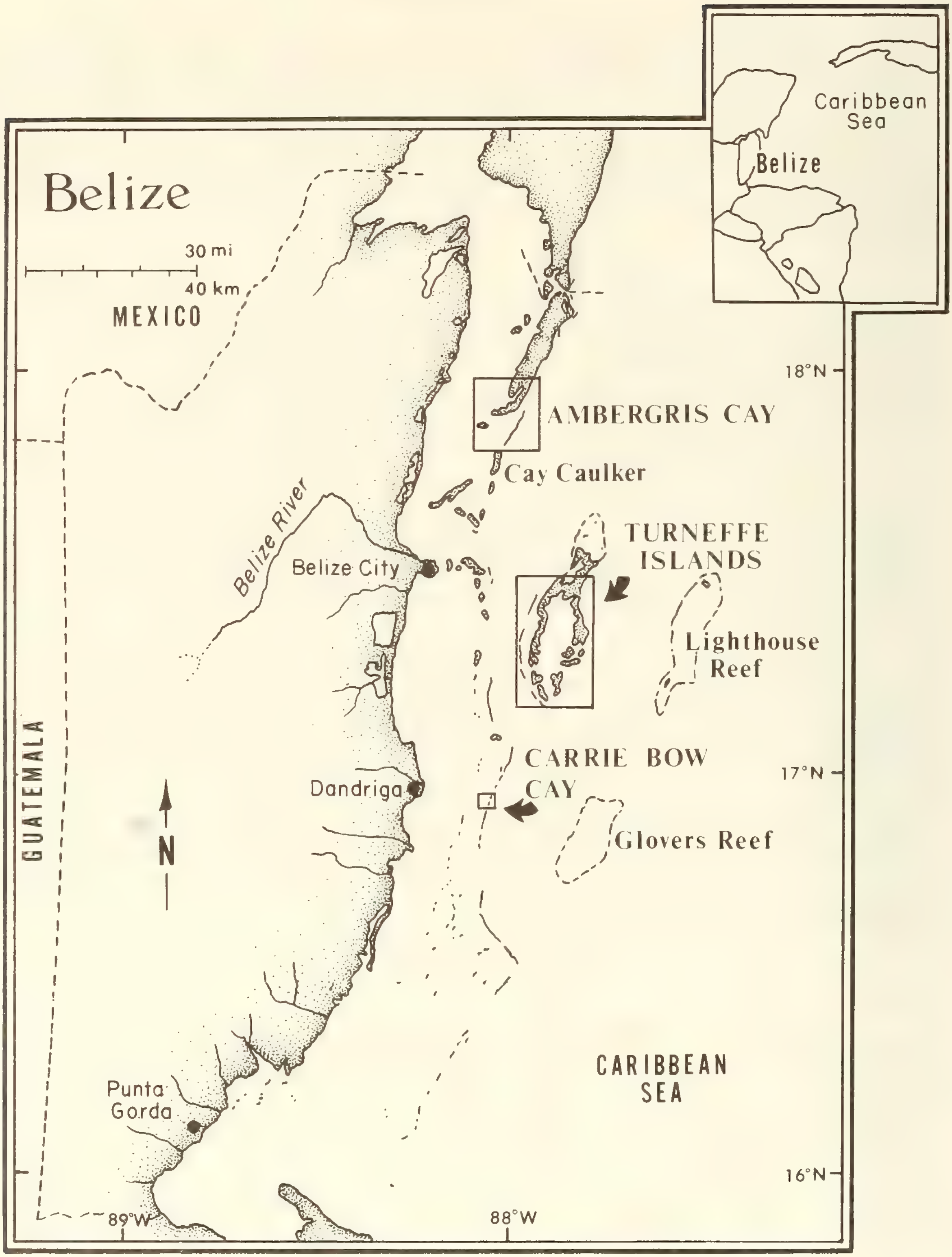

Figure 1. Location of commercial sponge survey sites (Carrie Bow Cay, Ambergris Cay, and Turneffe Islands).

habitats. Ambergris Cay was chosen as a survey site because anecdotal observations suggested that commercial sponges could be found there and because a fishery cooperative was located at San Pedro. Turneffe Island was selected as a survey area because it was the reputed site of a large scale sponge farm in the 1930's and interviews with fishermen indicated that Turneffe Islands was the most likely area where commercial sponges could be found. To assist with the Turneffe Islands field work, the services of two fishermen were contracted, one of which was old enough to have personal knowledge of the sponge farm location. Fisheries Unit personnel, commercial fishermen and fishing guides were interviewed to obtain information prior to conducting the field work in each area.

RESULTS

A total of 19 locations were surveyed by either towing a diver or by having the boat follow 2 divers. These surveys represent a total of 24 hours of underwater observations.

Distribution and Abundance of Commercial Sponges

Carrie Bow Cay

No commercial sponges of the genera Spongia and Hippospongia were found. Habitats surveyed included: seagrass beds surrounding Twin Cayes (occasional loggerhead sponges, Spheciospongia vesparium, were seen), seagrass beds west of South Water Cay, Barrier Reef sand/rubble zone, and Barrier Reef habitat accessible by snorkeling from South Water Cay through South Water Cut (Figure 2). Strong winds precluded surveying exposed areas, and, by necessity, surveys had to be conducted in nearby protected locations. The inability to travel appreciable distances limited the thoroughness of the survey. In general, the Carrie Bow Cay vicinity did not appear to be a productive area for commercial sponges. However, one of the authors (Stevely) has observed the presence of the reef sponge (Spongia obliqua) in patch reef areas located between the mainland and barrier reef during field work on a different project. The reef sponge is generally not considered to be of sufficient quality to support commercial harvest.

Ambergris Cay

No commercial sponges were found. Based on conversations with local fishing guides, five potential sponge habitat areas in the vicinity of Ambergris Cay were surveyed. These included: north of San Pedro, south of San Pedro, offshore of Laguna de Boca Ciega, seagrass beds near Congrejo Cay, and Cayo Romero (Figure 3). Survey sites north of San Pedro, south of San Pedro, and offshore of Laguna de Boca Ciega were "hard bottom" habitats with numerous "loggerhead" sponges (Spheciospongia vesparium), and represented habitat in which commercial sponges are sometimes found in Florida.

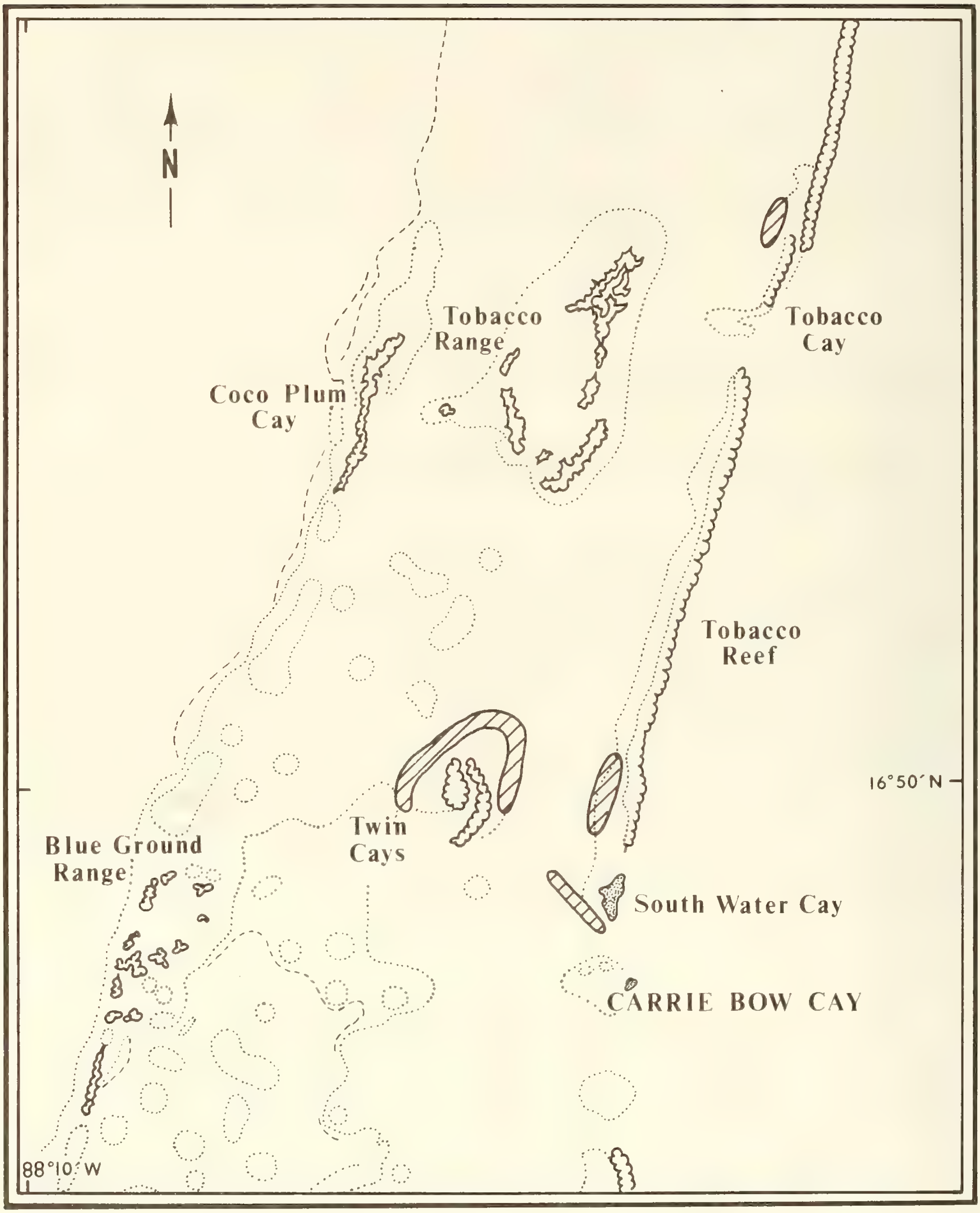

Figure 2. Carrie Bow Cay commercial sponge survey sites.

Key: ▨ = survey site

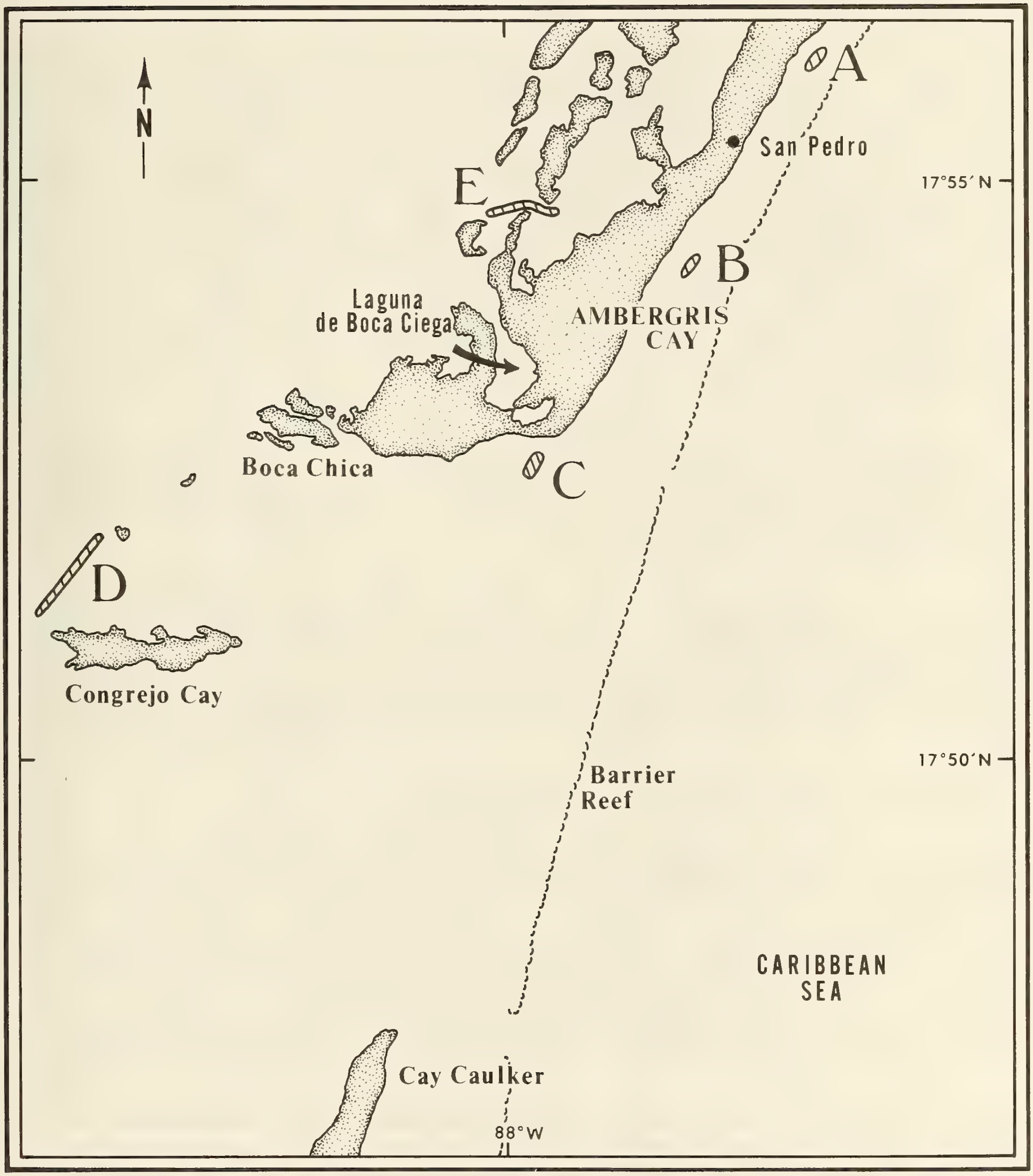

Figure 3. Ambergris Cay survey sites. A - north of San Pedro, B - south of San Pedro, C - offshore of Laguna de Boca Ciega, D - seagrass beds near Congrejo Cay, E - Cayo Romero.

Key: ⊘ = survey site

Turneffe Island

A total of 9 areas within the Turneffe Islands lagoon were surveyed, but velvet sponges, Hippospongia gossypina, were found only in one location, the "Crooked Creek" area (Figure 4). Velvet sponges were abundant in water 3-6 ft (1-2 m) deep, 400-500 ft (400-500 m) north of the Crooked Creek entrance into the Turneffe Islands lagoon (a tidal cut between mangrove islands). Ircinia sp. and Spheciospongia vesparium, were also present at this location. Additional field observations made on October 19, 1991, as part of a different survey project, documented the presence of velvet sponges in other areas within the Turneffe Island lagoon. These areas included: the eastern shoreline of Soldier Bight and shallow waters near mangrove islands and mangrove shoreline in the vicinity of the western opening of Grand Bogue Creek into the main lagoonal area. The October 19th, 1991 observations did not include measuring the sponges or recording quantifiable data on whether the sponges were attached to the substrate.

Data on maximum and minimum sponge diameter and type of attachment to the substrate was recorded for a total of 15 velvet sponges (Table 1). The velvet sponges were growing on a mangrove/seagrass peat substrate. A considerable percentage of these sponges had broken free from their attachment to the substrate, with only 53% found growing attached to the substrate.

A species of Spongia, probably a variety of sponge that would commonly be referred to as "yellow sponge" in the commercial trade (Spongia barbara, sensu de Laubenfels and Storr, 1958), was found in patch reef habitat to the west of Douglas Cay (outside the lagoon environment). This sponge did not appear to have significant value for commercial trade. Unfortunately, the collected specimens were lost in the process of having the specimens shipped.

Evaluation of Commercial Sponge Fishery Potential

A commercially valuable grade of velvet sponge (Hippospongia gossypina) was found at Turneffe Islands (Figure 5). After evaluating a sample of 13 Turneffe Island sponges, tarpon Springs, Florida sponge buyers indicated that they would pay US $2.00-3.00 per sponge. The velvet sponge quality was such that it would be considered to be somewhat inferior to the sheepswool sponge (Hippospongia lachne), but would have a market value greater than that of other commercial sponge varieties. Velvet sponges tear more easily than sheepswool sponges, partially because of the characteristic presence of large pseudoscula or vents on the upper surface (Moore, 1910b).

Based on our experience with sponge fisheries in Florida and the Bahamas, we estimate that the value and quantity of sponges at Turneffe Islands were sufficient to support sponge fishing activities. Field observations indicated that it would not be unreasonable for a 2-man fishing team to produce in excess of 100 sponges per day. For example, we collected 15 sponges in 1 hour, and this included time taken to measure each sponge and record data. However, there are several important factors and limitations which must be considered before the fishery potential can be properly evaluated. These are considered in detail in the following discussion section.

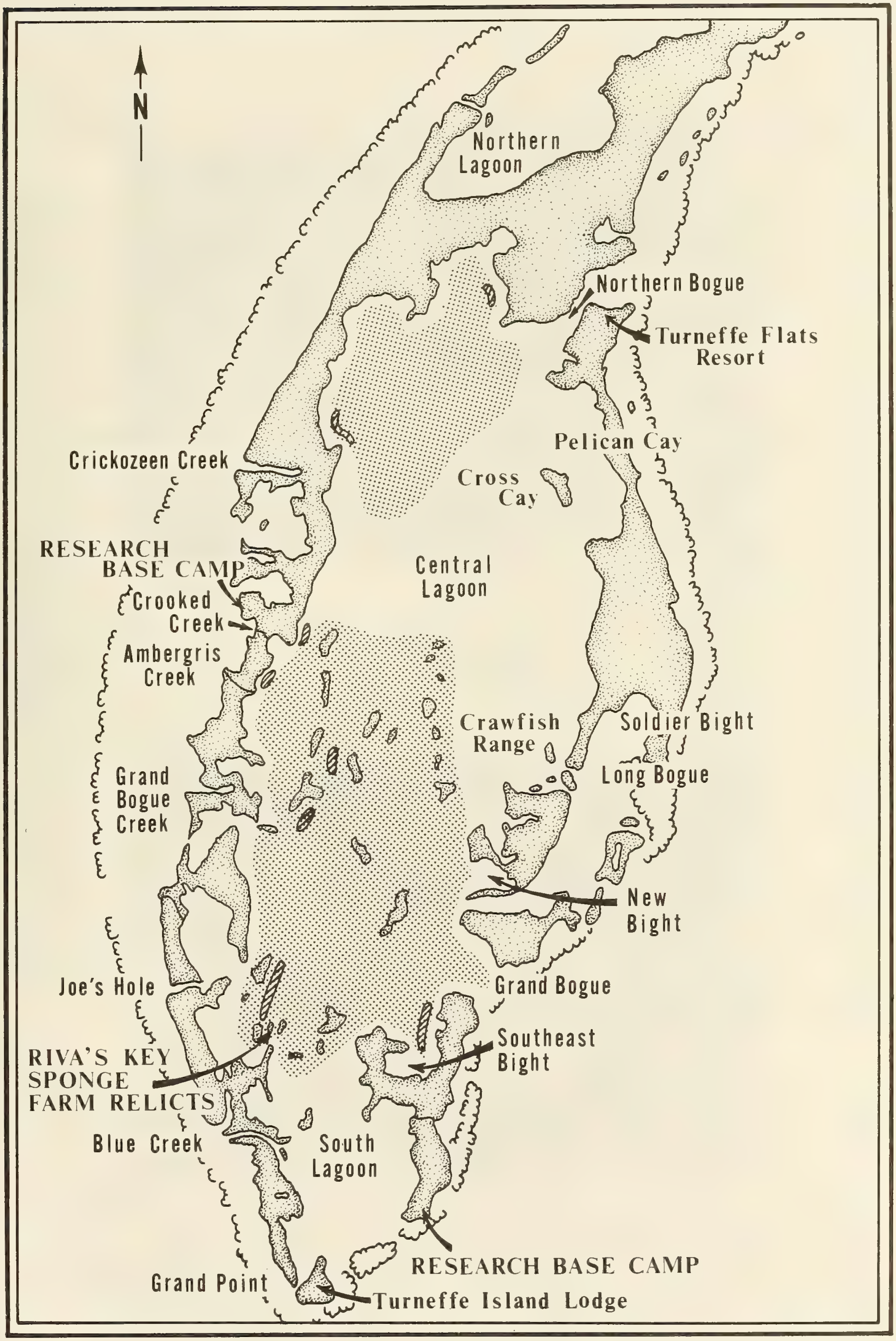

Figure 4. Turneffe Islands survey sites and approximate location of the sponge farming area (stipled area).

Table 1. Maximum and minimum sponge diameters and category of attachment to the substrate for 15 velvet sponges (*Hippospongia gossypina*) collected at Turneffe Islands, Belize, May 24, 1989.

Maximum Diameter in (cm)	Minimum Diameter in (cm)	Attachment to Substrate
10.8 (27)	9.6 (24)	Attached
11.2 (28)	10.8 (27)	Unattached
10.8 (27)	8.8 (22)	Attached
11.2 (28)	11.2 (28)	Unattached
7.2 (18)	6.8 (17)	Attached
12.8 (32)	12.4 (31)	Attached
13.2 (33)	12.4 (31)	Unattached
13.6 (34)	13.2 (33)	Unattached
12.8 (32)	12.0 (30)	Unattached
12.0 (30)	11.6 (29)	Attached
15.6 (39)	10.0 (25)	Unattached
10.0 (25)	8.8 (22)	Unattached
8.0 (20)	6.4 (16)	Attached
6.8 (17)	6.8 (17)	Attached
3.6 (9)	3.6 (9)	Attached
Mean Diameter Maximum 10.6 (27)	Minimum 9.6 (24)	Percent Attached 53%

Location of the commercial sponge farm

Information provided by local fishermen (Mr. Joseph Garbutt, Mr. Carl Carbal) indicated the approximate location of sponge planting areas in the Turneffe Islands lagoon (Figure 4). The approximate location of the sponge planting area in the southern portion of the lagoon was verified by finding the concrete disks used to "plant" sponges (Figure 6) on the western side of Riva's Cay, approximately 200 m south of the northern tip of the island (Figure 4). The disks found along the mangrove shorline and in the water immediately adjacent to the shoreline. This site marked the location where sponge farm workers docked a live-aboard boat. No navigation charts that located Rivas Cay could be found. However, the approximate location, as determined by triangulation on the open water is shown in Figure 4. Smith (1941) did not describe the precise location of the sponge farm but his figure showing the

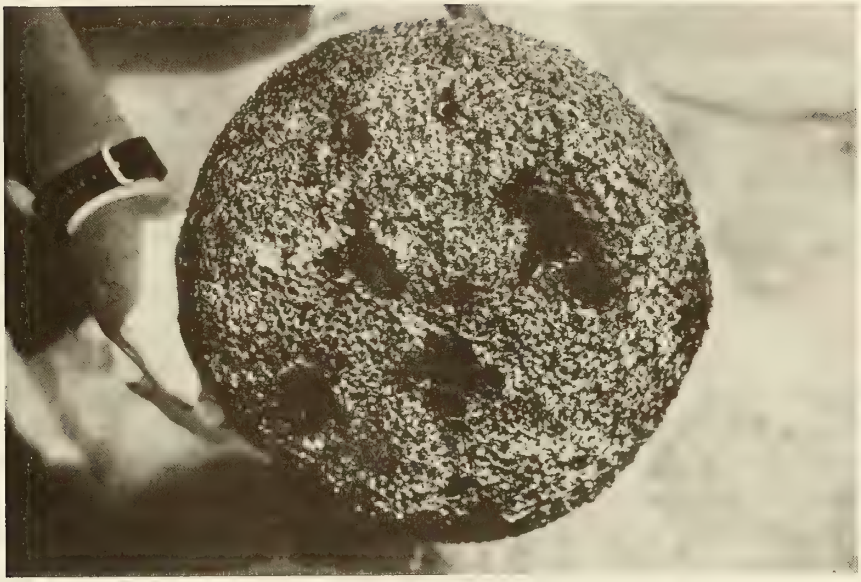

Figure 5. Live velvet sponge (Hippospongia gossypina) removed from water. Note pseudoscula described by Moore, 1910b.

Figure 6. Concrete disks used to "plant" sponge cuttings at the Turneffe Islands sponge farm.

progression of sponge disease throughout the large planting areas is consistent with our location of the sponge planting areas.

The area where sponges were planted was extensively surveyed, but no concrete disks were found. Wood stakes were found which the local guide (Joseph Garbutt) claimed were marking the sponge planting area. These wood stakes were obviously much older than stakes used to mark lobster traps (they were covered with an extensive growth of fire coral). Although all of Mr. Garbutt's comments during the expedition proved to be accurate, the verification of these stakes as artifacts from the sponge farm was impossible.

DISCUSSION

Inclement weather (sustained 25-30 mph winds) and failure of a local guide to provide contracted services (a new Turneffe Islands expedition team had to be organized) reduced opportunities to conduct more extensive surveys. These factors prevented the collection of quantitative data on sponge density and population structure. However, two significant goals were realized: useful ecological and fishery information was collected on the velvet sponge, Hippospongia gossypina, in the marine waters of Belize and the location of the Turneffe Islands sponge farm was documented. These observations increase the information available for understanding and managing the marine biological and fishery resources of Belize.

Distribution and Abundance of Commercial Sponges

Within the Turneffe Island lagoon (the only location where commercially valuable sponges were found), velvet sponge were found growing on a mangrove peat substrate. Although the mangrove peat provides a substrate for sponge attachment (Figure 7), it crumbles easily and is sufficiently soft to allow the establishment of the seagrass Thallassia testudinum. Our observations indicate that, although this substrate is adequate for the attachment of sponges, many of the sponges eventually break loose (Table 1). Sponges that break loose from the substrate but continue to survive and grow are commonly called "rollers" in the commercial trade (Figure 8). The percentage of rollers was much higher than the percentage observed in the Florida commercial sponge harvest (Stevely, pers. obs). The occurrence of commercial sponge growing on a non-rock substrate was a new observation for us. In our extensive field observations in both the Gulf of Mexico and the Bahamas, we have found commercial sponge species (Hippospongia and Spongia growing either attached to rock outcroppings or to any suitable hard surface (coral/rock fragments, gorgonians, etc). De Laubenfels (l948) reported that sheepswool and velvet sponge were common on these substrates, often in precisely the same localities.

Although the previously noted additional field observations taken on October l9, l99l were extremely cursory, they did confirm the observation that the velvet sponge was found growing on mangrove peat/seagrass substrate. Also, there was a general impression that the percentage of "roller" sponges varied considerably from site to site. In some areas it seemed that most sponges were found growing attached to the substrate. In the Soldier Bight area it appeared as if almost all the velvet sponges were rollers and that they had accumulated along the eastern shoreline as a result of

Figure 7. Live velvet sponge (Hippospongia gossypina) removed from water to show growth habit of attachment to mangrove peat substrate.

Figure 8. Live velvet sponge (Hippospongia gossypina) removed from water to show growth habit of "roller sponge". Former point of attachment to substrate is now covered by ectosome.

tidal and/or wind driven currents. However, these observations need to be verified by more detailed field work.

Smith (1941), in describing the Turneffe Islands lagoon sediments, stated that "the floor of the lagoon consists of calcarious mud, with admixed shell and coral sand predominate near the eastern entrances, and with organic matter formed from the detritus of eel-grass and mangrove roots present in varying degree throughout the lagoon". Mangrove/seagrass peat substrate was observed in several areas in the Crooked Creek and Chickozeen vicinity. The depth of the mangrove peat appeared to be considerable. On one occasion crevices were seen in the mangrove peat which extended 6-8 ft (2-2.5 m) in depth. Observations made while snorkeling Crooked Creek (a channel between mangrove islands carved boy tidal currents) indicate the depth of the mangrove peat deposits extended to at least 30 ft (10 m). These observations suggest that the Turneffe Islands represent an atoll formation consisting of mangrove peat and suggest that mangrove peat formation has kept pace with seamount subsidence/and or sea level rise.

Prior to the 1938-39 sponge mortality, the velvet sponge was known for its commercial value and was considered to be the most valuable commercial sponge after the sheepswool sponge (Moore, 1910b). Although it was considered to be less compressible, absorbent, and durable compared to the sheepswool sponge, velvet sponges from some area (e.g., the Bahamas) were regarded as almost equivalent in quality to the sheepswool sponge.

Moore (1910b) reported the velvet sponges were found in the straits of Florida, the Caribbean Sea, and the Bahamas. De Laubenfels and Storr (1958) stated that velvet sponges had been common around Florida and the west Indies. In Florida, velvet sponge was harvested from the fishing grounds between Key West and Cape Florida (Moore, 1910b) in living coral areas at depths of 3-25 ft (1-8 m) (Storr, 1964). Florida sponge fishermen produced 8,000 lb (3,600 m) of velvet sponge in 1899 (Moore, 1910b). Although velvet sponges were sufficiently abundant to sometimes be reported in Florida commercial sponge landings, they were the least abundant of the commercial sponges (Smith, 1898). The best quality of velvet sponge was regarded to be from the Bahamas (Moore, 1910b), and at one time it was the principal commercial sponge of the Bahamas (de Laubenfels and Storr, 1958). Moore (1910b) noted some commercial sponge production from the British Honduras, including velvet sponge. Moore also reported that sheepswool, velvet and grass sponges (Spongia sp.) were found along the entire coast of British Honduras, in the shallow waters about the numerous islands, rocks, and banks, and that many commercial sponge varieties grow "attached to staghorn corals and gorogonians". No mention was made of either sponges at Turneffe Islands or velvet sponges found growing attached to mangrove peat substrate. Cresswell (1935) mentioned an effort by commercial sponge fishermen in 1895 to explore the waters of British Honduras and reported that velvet sponge was the most common sponge harvested.

After the devastating sponge mortality, the velvet sponge was thought to be essentially extinct in areas that had been known to produce commercial quantities, although many years later a few were reported from Cuba (de Laubenfels and Storr, 1958; Storr 1964). An extensive survey of the Florida sponge grounds in 1947 and 1948 was conducted to evaluate the condition of the sponge grounds following the effects of the sponge disease and overfishing during the early 1940's. The resulting fishery report did not report the occurrence of any velvet sponge (Dawson and Smith, 1953). However, later taxonomic study of the sponges collected during the survey reported a velvet sponge specimen collected from a station in the northern Gulf of Mexico (de Laubenfels, 1953). Storr (1964) stated that the velvet sponge had not been reported in the Bahamas since the disease. In 1975 a report on the Bahamian sponge fishery indicated that the fishery was based on the harvest of sheepswool and grass sponge and contained no reference to velvet sponge (Thompson, unpubls. mans.). Wiedenmayer (1977) surveyed the shallow-water sponges of the western Bahamas and reported eighty-two sponge species, including 3 commercial species of the genus Spongia but no velvet sponge (his study was not intended as a survey of commercial varieties). Repeated communication with Florida sponge fishermen and sponge buyers has failed to indicate even the rare occurrence of the velvet sponge. The effects of disease and overfishing were apparently sufficiently severe to drastically reduce velvet sponge abundance throughout a major portion of its geographic range. In view of the long-term change in distribution and abundance of the velvet sponge and a lack of knowledge of its current distribution, the apparently healthy population at Turneffe Islands is worthy of note to fishery managers and scientists.

The Turneffe Island's velvet sponge population may represent a relatively small genetically isolated population. Storr (1964) indicated that the sheepswool sponge (Hippospongia lachne) larval state is short-lived (1-2 days) and does not have strong swimming capabilities. The Turneffe Islands atoll is separated from other shallow water habitats by waters at least 250 fathoms in depth. Prevailing surface current patterns (Hartshorn et al., 1984: Figure 9, this report) support the idea that larval recruitment (i.e., genetic exchange) may be limited between Turneffe Islands and other shallow water Caribbean sponge populations. If the prevailing surface currents depicted in Figure 9 accurately indicate a likely transport mechanism for velvet sponge larvae, then the larvae would have to traverse open Caribbean Sea waters in a relatively short time.

The ability of the velvet sponge to grow attached to a mangrove peat substrate, and possibly the ability to utilize a food source enriched with detrital particles may help to explain to future investigators subtle differences and commonalities in the ecological niches occupied by commercial sponge species. Although speculative, field observations may suggest that seagrass/mangrove derived detrital particles may contribute to velvet sponge nutrition. On windy days, waves and currents agitated the shallow water where the velvet sponges were found, and, in effect, produced a suspension of detrital material consisting of decaying seagrass leaves and eroding mangrove peat. The detrital suspension was sufficient to noticeably reduce water clarity in mangrove peat areas exposed to windy conditions. Sponges are efficient filter feeders, evidently capable of filtering bacteria size food particles. It is possible that fine detrital particles in the water column could either directly or indirectly, by promoting bacterial growth or elevating the level of dissolved organic, contribute to nutritional intake. Lauckner (1980) reviewed data that suggest the presence of symbiotic bacteria associated with several sponge genera, including Spongia and Hippospongia, which possibly could assist the sponge in utilizing dissolved organic substances.

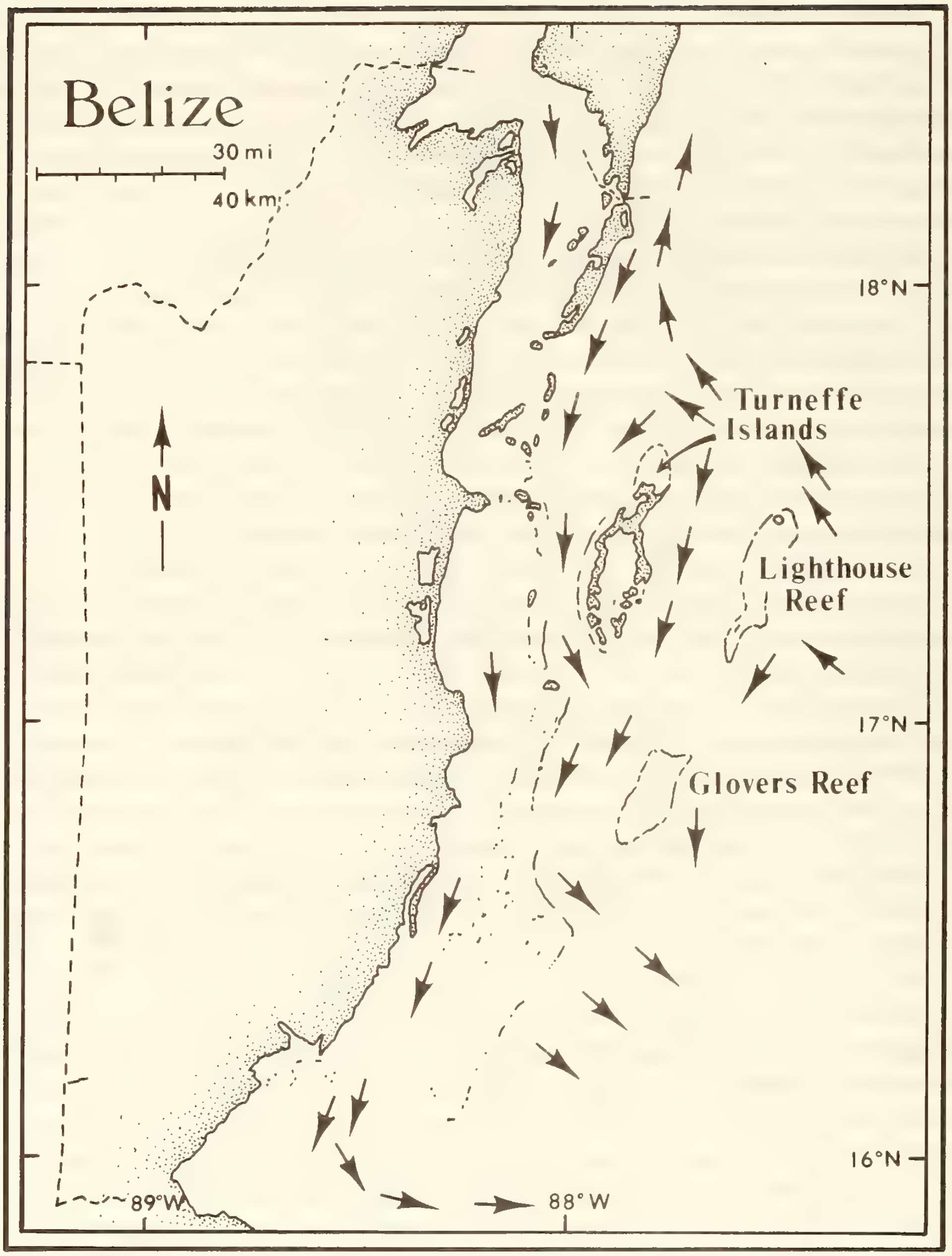

Figure 9. Prevailing surface currents for waters of Belize (adapted from Hartshorn et al., 1984).

Evaluation of Commercial Sponge Fishery Potential

Although a commercially valuable grade of velvet sponge was found to occur at a density capable of supporting fishery activities, several important factors must be considered before the fishery potential can be properly evaluated. Most importantly, the extent of sponge producing areas within the Turneffe Islands lagoon must be assessed more thoroughly. Although the additional field work conducted on October 19, 1991 found more areas that supported velvet sponge growth, the areas were limited in size and might be easily depleted by continuous intensive fishing effort. The comments by Moore (1910b) indicating the presence of several varieties of commercial sponges from the coast of British Honduras suggest that additional surveys are required to more fully define the commercial sponge resources of Belize.

The unique substrate to which the Turneffe Islands sponges are attached may not be conductive to allowing long-term harvest. Sponge fisheries in Florida and the Bahamas are supported by harvesting sponges that grow attached principally to carbonate rock outcroppings. Field observations in the Bahamas (Stevely, pers. obs.) and experimental work in the Florida Keys (Stevely and Sweat, 1985) indicate that when sponges are either cut or torn from such substrate, a significant quantity of sponge tissue sometimes remains attached to the substrate. This tissue is capable of regenerating to produce another viable sponge. In Florida, survival of harvested sponges ranged from 30% for sponges torn free using a sponge hook to 70% for sponges cut free with a knife. In Turneffe Islands, where sponges are anchored only to mangrove peat, it is likely that all the sponge tissue would be taken when the sponges were harvested by either hooking or cutting and that no attached sponge tissue would remain for regeneration. The same would be true for harvested roller sponges.

The large size of the Turneffe Islands velvet sponges (Table 1) may suggest that the legal size for sheepswool sponge required by either Florida (5 in, 12.5 cm, minimum diameter) or Bahamian law (7 in, 17.5 cm, minimum diameter) would provide little protection for the resource if sponge harvesting was economically feasible. Only one of the 15 sponges measured (Table 1) would have been protected by a law requiring a minimum harvest size of 5 in (12.5 cm). However, may more sponges from several areas should be measured before fishery management regulations are suggested. Also, consideration must be given to managing a regularly harvested resource compared to harvesting a virgin stock. A conservative approach that insures adequate protection of the resource should be taken in managing Turneffe Islands sponge fishery development until more complete information is available. Establishing an enforceable minimum legal size of 8-9 in (20-22.5 cm) exemplifies such a conservative approach.

Conservative management of the Turneffe Islands sponge fishery requires protection of reproductive stocks. Historically, research on reproduction in commercial sponges has focused on the more valuable sheepswool sponge, and essentially no information on velvet sponge biology is available. The sheepswool sponge attains reproductive maturity at a size of from 3 in (7.5 cm) in the Florida Keys to 5.5 in (14 cm) in the northernmost Florida west coast sponge grounds; reproductive maturity is attained at a smaller size in the warmer portions of its geographic range (Storr, 1964). Assuming a similar trend in the size of maturation in the velvet sponge it is reasonable to assume that a minimum size of 8 or 9 inches (20-22.5 cm) in Belizean waters would protect sponges capable of a significant contribution to larval production.

The physical remoteness of Turneffe Islands presents transportation problems for sponge fishermen. Most likely, it would be necessary to store sponges accumulated for several weeks before transport to the mainland. Fortunately, cured and dried sponges do not require refrigeration and could be collected over weeks or months while intermittently pursuing other fishing activities. Storage of cleaned sponges would require some shelter to prevent rotting and long-term exposure to the sun. Cleaned sponges are also lightweight and can be easily transported by small boats.

Proper cleaning of sponges is hard work, but it is critical for receiving top price; improperly or incompletely cleaned sponge are either worthless or are worth only a fraction of their true value. In addition to time allotted for sponge harvesting, the sponge fishermen must commit an equal proportion of effort to cleaning, storing, and transporting the catch.

Conversations with fishery cooperative manager indicated some lack of interest in exporting sponges for two reasons: they were unfamiliar with the current value of commercial sponge in the export market and they did not know whether sponges were sufficiently abundant to support fishery development. The fishery cooperatives are the obvious focal points for collecting and exporting sponges. Belizean fishery cooperatives routinely ship seafood to Florida. Sponges are a highly valuable commodity (e.g., US $20.00-50.00/lb; $44.00-110.00/kg), and reasonable shipping costs (e.g. US $l.00-2.00/lb; $2.00-4.00/kg) would not be prohibitively expensive. Thus, sponge exports may significantly increase the cash flow and profitability of fishery cooperatives. For example, a 5,000 lb (2250 kg) annual shipment could easily result in an annual cash flow of $l00,000 based on an estimated minimum price of US $20.00/lb ($44.00/kg) for velvet sponge. If a reliable supply of quality velvet sponges was established, it is reasonable to expect that the price paid for sponge to further increase.

Location of the Commercial Sponge Farm

A significant amount of historical information exists for sponge culture work in the Florida Keys, Bahamas, and Pacific Ocean (Stevely et. al., l978). However, only sparse notes in the literature, referring principally to the occurrence of sponge disease and briefly describing sponge farm operations and location are available for the Turneffe Islands sponge farm (Smith, 1941). Smith (l941) stated, "Cultivation consists of cutting the sponge into small pieces, attaching these to stone or cement disks and allowing them to grow to market size on areas of the lagoon bottom most favorable to fast and healthy development". In the Bahamas, a length of palmetto string made from splitting a palmetto palm leaf was used to tie the cut sponge pieces to the concrete disk (Storr, l964). One of the sponge disks found during our investigation still had a piece of aluminum wire attached through the small hole in the disk, suggesting that aluminum wire was at least sometimes used to attach sponge cuttings at Turneffe Islands. Aluminum wire also was used in sponge farming attempts in the Florida Keys (Stevely, et. al., l978). The Turneffe Islands concrete sponge planting disks (Figure 6) were similar in appearance to those used in both the Bahamas (Storr, 1964; Figure 9) and Florida Keys (Stevely et al., 1978, Figure 15).

Smith (1941) stated that the farm was run by concessionaires (Messers. R.E. Foote and H.T. Grant) licensed by the British Honduras Government. At the time of the sponge disease mortality, approximately 700,000 sponges were under cultivation (225,000 sheepswool sponges, and 475,000 velvet sponges). Mortality of the densely planted sponge cuttings (in some places one per square meter) was estimated to be 95%.

Some of the geographical advantages of attempting sponge farming in the Turneffe Islands lagoon are readily apparent. The lagoon contains extensive shallow areas 3-12 ft (1-4 m) deep that are reasonably protected by mangrove islands. Sheltered and relatively clear waters would permit sponge farm operations to proceed in all but the most severe weather conditions. The remoteness of the Turneffe Islands would probably assist in enforcing security of the farm. Difficulty with protecting sponge plantings from theft has been a major problem for sponge farming attempts in many areas (Stevely et al, 1978). However, Turneffe Islands sponge farm workers living in the immediate vicinity of the farm could serve as security guards in the area. Potential thieves interested in stealing sponges from the farm would have to establish a camp for harvesting, cleaning, and storing a sufficient number of sponges to justify transport back to mainland. In general, it would be difficult for a potential sponge poacher to escape notice in these remote surroundings populated principally with sponge farm workers.

Finally, the abundance of "wild" sponge stock in the lagoon may have played a key role in the decision to attempt sponge farming. The natural sponge populations may have been insufficient to support a fishery harvesting hundreds-of-thousands of sponges, but capable of producing tens-of-thousands of "seed" sponges for propagation.

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ATOLL RESEARCH BULLETIN

NO. 425

SPATIAL AND TEMPORAL VARIATIONS IN GRAZING PRESSURE BY HERBIVOROUS FISHES: TOBACCO REEF, BELIZE

BY

PETER N. REINTHAL AND IAN G. MACINTYRE

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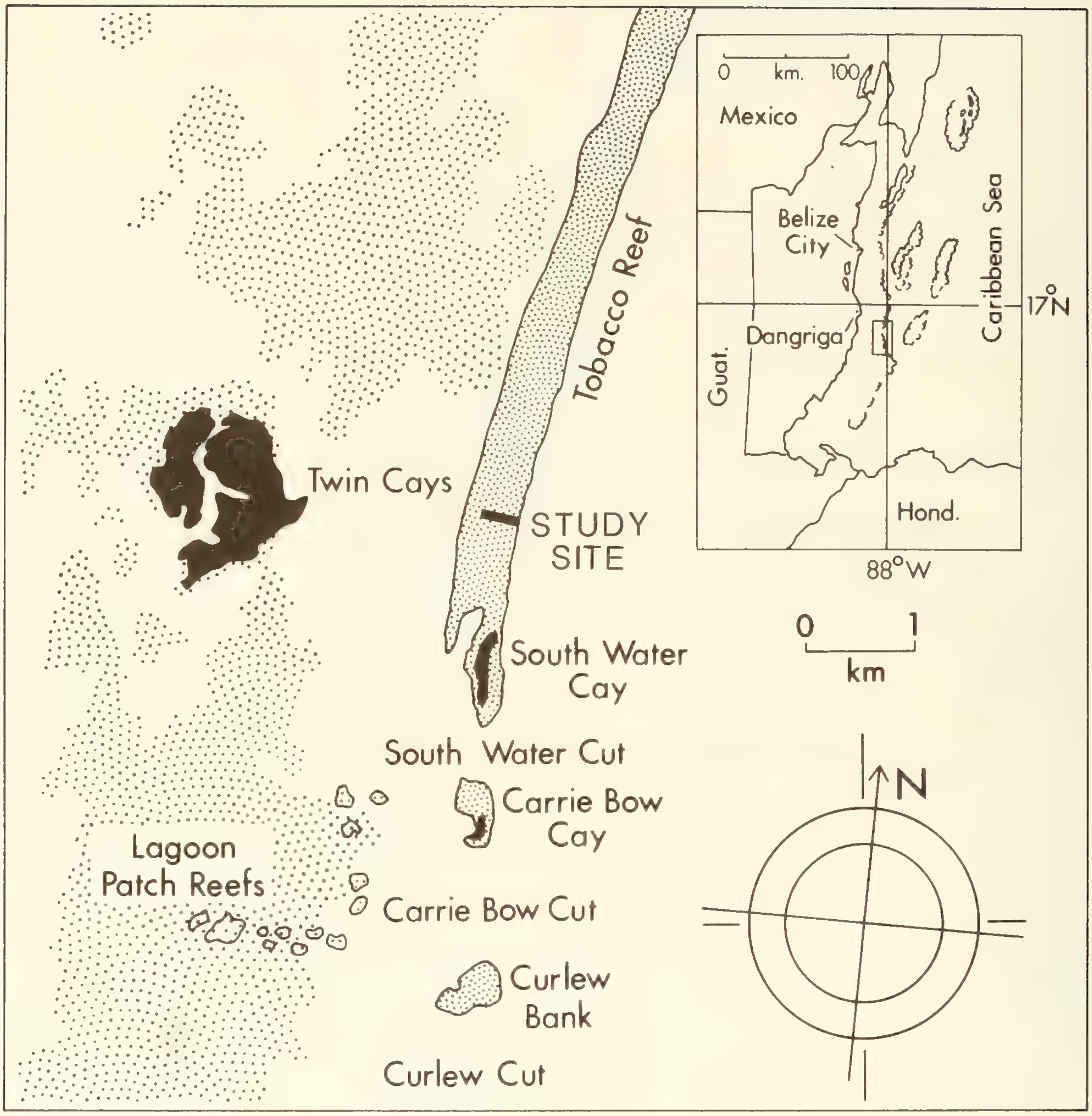

FIGURE 1 - Index map showing location of study transect on Tobacco Reef.

SPATIAL AND TEMPORAL VARIATIONS IN GRAZING PRESSURE BY HERBIVOROUS FISHES: TOBACCO REEF, BELIZE

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ABSTRACT

Fish herbivory appears to play an important role in the pattern of macrophyte zones running parallel to the crest of the Belizean barrier reef. The experimental relocation's of reef macrophytes seaward of the reef in 1984 and 1989 revealed that algal species with herbivore-resistant strategies are predominant in the zones of strongest herbivory near the reef crest, whereas those highly susceptible to fish grazing occur well lagoonward of the reef crest. The foraging ranges of herbivorous fish are thought to depend in large part on their proximity to suitable shelter. These trends in herbivore activity were observed in both 1984 and 1989, although the grazing pressure was uniformly less for all algal species studied in 1989. These findings may be related to seasonal (May 1984 versus March 1989) or annual variations in grazing pressure, or to a general decrease in grazing pressure over the five-year study period.

INTRODUCTION

The patterns of abundance and distribution of coral reef macrophytes are well known to be influenced by grazing activities of herbivorous fishes (Stephenson and Searles 1960, Randall 1961, 1965, John and Pope 1973, Wanders 1977, Hay 1981a, b, Hay *et al.* 1983, Hay 1984, Lewis 1986, Horn 1989, Choat 1991, Hay 1991) and urchins (Ogden *et al.* 1973, Sammarco *et al.* 1974, Sammarco 1980, Lawerence and Sammarco 1982, Hay 1981a, b, 1984). However, only recently have studies been conducted on spatial variation in herbivore activity patterns and the effects of spatial patterns of herbivory on macrophyte distributions (Hay *et al.* 1983, Lewis 1986, Macintyre *et al.*. 1987, Morrison 1988; Hay 1991). Spatial heterogeneity in grazing intensity has been found to contribute to regional diversity among and within tropical reef habitats (e.g. Lewis 1986) and fishes appear to play a major role in structuring shallow water macrophyte communities (e.g. Morrison 1988).

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FIGURE 2 - Aerial view of Tobacco Reef looking south towards South Water and Carrie Bow Cays. Note location of study transect and biogeological zones on sediment apron. (1. Coralline-Coral-*Dictyota* pavement; 2. *Turbinaria*-*Sargassum* rubble; 3. *Laurencia*-*Acanthophora* sand and gravel; 4. Bare sand; 5. *Thalassia* sand.) Emergent reef crest and deep fore-reef on left.

In this study we used transplanted samples of various reef macrophytes as a bioassay for an assessment of fish grazing in the backreef habitat. The grazing activity was then compared to observed patterns of macrophyte zonation and evaluated to determine relative grazing pressures on various macrophytes as a function of distance from the reef crest. Varying selective pressures from fish herbivory and substrate requirements appear to be important factors in determining the distribution and zonation patterns of reef macrophytes (Macintyre *et al.* 1987).

Preliminary results found in 1984 (Macintyre *et al.* 1987) prompted us to repeat similar experiments in 1989 when we were able to replicate the treatments at three separate locations (versus one location in 1984) and provide a caged control treatment at one of the locations. This approach allowed us to look at spatial variation in grazing as both a function of distance from the reef crest and variation along the reef crest. The results raise a number of interesting questions concerning spatial and temporal variation in fish grazing activity in the back reef habitat.

MATERIALS AND METHODS

This study was conducted during May 1984 and March 1989 in the backreef habitat at Tobacco Reef, north of the Smithsonian Institution's field station at Carrie Bow Cay, Belize, Central America (16°48' N, 88°05' W; Fig. 1). The topography, geology and zonation of the region and the floristic and fish distribution patterns are described in detail elsewhere (Rutzler and Macintyre 1982, Norris and Bucher 1982, Lewis and Wainwright 1985, Macintyre *et al.* 1987). A primary study site representative of the reef was identified on the sediment apron of Tobacco Reef approximately 1 km north of South Water Cay (Fig. 1). Three sites that were separated approximately 100 m (north, middle and south) were used as replicate localities.

We transplanted samples of eight reef macrophytes to 0 m., 40 m., 90 m. and 150 m. from the reef crest to determine fish grazing activity as a function of distance from the reef crest. The distances were related to the observed patterns of macrophyte zonation and five distinct biogeological zones (Fig. 2): (1) 0 m: coralline-coral-*Dictyota* pavement, (2) 40 m: *Turbinaria-Sargassum* rubble, (3) 90 m: *Laurencia-Acanthophora* sand and gravel, (4) 150 m: bare sand and (5) *Thalassia* sand. These zonation patterns and various abiotic factors affecting macrophyte distribution are discussed elsewhere (Macintyre *et al.* 1987).

The eight macrophytes used in the grazing assay were *Turbinaria turbinata, Sargassum polyceratium, Thalassia testudinum, Padina jamaicensis, Acanthophora spicifera, Laurencia papillosa, Laurencia intricata* and *Dictyota* sp. The *T. testudinum* blades and other species were free of epiphytes as were all macrophytes. These macrophytes were chosen because they are common and abundant members of the backreef community and show variation in distribution patterns. A mixed assay allowed us to determine grazing intensity with respect to the variety of herbivore groups observed to be active in this area. For example, previous studies (Lewis 1985) have shown that *T. turbinata, S. polyceratium, T. testudinum* and *P. jamaicensis* are preferred and primarily consumed by parrotfish (*Sparisoma* and *Scarus* spp.). In contrast the red algal species, *A. spicifera, L. papillosa* and *L. intricata,* are preferred and primarily consumed by acanthurid species (*Acanthurus bahianus, A. coeruleus* and *A. chirugus*) (Lewis 1985). Another herbivore, *Diadema antillarum,* was not considered in this study because it had undergone a massive die-off throughout the Caribbean (Lessios *et al.* 1983) and was never common on this back-reef sediment apron of Tobacco Reef. Moreover, fish are considered to be the grazers of prominent

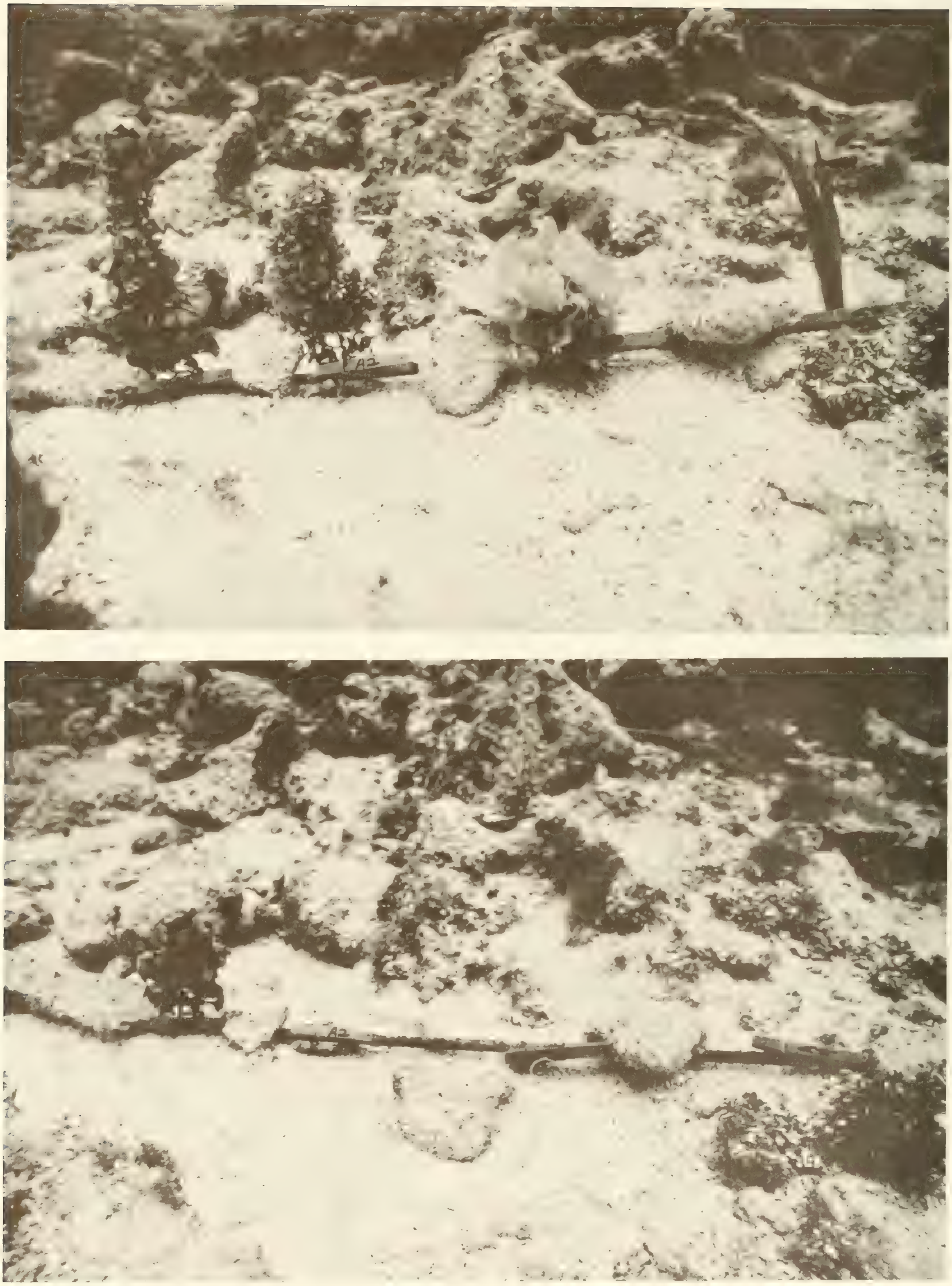

FIGURE 3 - Before and after photographs of test set of four macrophytes (left to right: Turbinaria turbinata, Sargassum polyceratium, Padina jamaicensis, and Thalassia testudinum) at reef crest site.

importance on many tropical reefs (Hay 1984, Lewis 1986, Morrison 1988). No other organisms were found grazing on any of the assays.

The pattern of herbivore pressure as a function of distance from the reef crest was measured by placing complete spin dried and weighed sets of the assay in the back reef at distances of 0, 40, 90 and 150 m behind the reef crest. Samples of each of the macrophyte species were held in wooden clothespins attached to metal rods (Fig. 3). All trials were run for 8 h from 0830 to 1630 h at each experimental grazing site. The samples were then spin dried and reweighed. In 1984, four trials were conducted at each distance at one location each on different days. The amount of macrophyte used in the assays was consistent with the size of macrophytes observed in the study area. In all trials a small piece of the macrophyte remained in the clothespins where it was inaccessible to herbivores. The remaining macrophytes, grazing scars and field observations indicated that macrophytes were not lost by wave action.

In 1989 the trials were replicated on different days three times at each of three locations approximately 100 m apart for all four distances from the reef crest. The middle site was approximately at the same location as that used in 1984. At the northern most locality, 1 m^3 cages constructed from 1/4" wire mesh were placed at each distance from the reef crest. Grazing assays with the eight macrophytes were placed in the cages as controls for the amount of macrophyte lost due to wave action when fish grazers are excluded. Special care was taken to avoid placing macrophyte assays near the guarded territories of damselfish.

Fish counts were made in 1984 along a series of four replicated visual line transect censuses (50 m x 2 m) between 0800 and 1600 h at each experimental grazing site. All parrotfish (*Scarus* and *Sparisoma* spp.) and surgeonfish (*Acanthuridae*) were counted to determine distribution patterns and densities. The methodology applied here is similar to that used by Lewis and Wainwright (1985) in their study of distributions of herbivores among reef habitats.

RESULTS

1984 Experiments

In 1984, a distinct fish-grazing pattern emerges from the data on percent weight loss for the macrophyte species used in this study. Average percent weight loss generally decreases with distance from the reef crest for seven of the macrophytes studied (the exception being *Dictyota* sp.) and shows highly significant weight-loss differences with respect to distance from the reef crest (ANOVA, $P < 0.005$ in all cases) (Table 1).

For all macrophytes except *Dictyota divaricata*, grazing pressure was homogeneously heavy in 1984 at 0 and 40 m from the reef crest as indicated by Duncan multiple range tests (Table 1): the average percent weight loss at 0 and 40 m are included in the same homogeneous subset whose highest and lowest means do not differ by more than the shortest significant (.05 level) range for a subset of that size. For two macrophyte species, *Padina jamaicensis* and *Thalassia testudinum*, the homogeneity of heavy grazing pressure extends to 90 m. These two macrophyte species are highly preferred by parrotfish in field feeding trials (Lewis 1985, Lewis and Reinthal in prep.). *Turbinaria turbinata* and *Sargassum polyceratium*, also preferred by parrotfish, appear to be subject to the same heavy grazing pressure at 0 and 40 m, but little or moderate grazing pressure at 90 and 150 m.

The situation was similar for the macrophytes preferred by surgeonfish (Acanthuridae) (Lewis 1985, Lewis and Reinthal, in prep.). The grazing pressure on *Acanthophora spicifera* and *Laurencia papillosa* is homogeneously heavy at 0 and 40 m, moderate at 90 m, and light at 150 m as indicated by the homogeneous subsets in the Duncan's Multiple range test (Table 1). Heavy grazing pressure is also observed at 0 and 40 m for *L. intricata* but grazing is homogeneously moderate to weak at 90-150 m.

In the case of *Dictyota divaricata* sp., grazing pressure was homogeneously light and no significant differences were found between average weight loss at various distances (ANOVA, P = 0.68) (Table 1). The Duncan's Multiple range test included all distances in the same homogeneous subset. The weight loss in this case is thought to be due primarily to experimental error caused by the removal of small fragments through wave action and this was the only macrophyte that proved difficult to retain as one piece in a clothespin.

Distribution patterns identified for herbivorous fish (Table 2) coincide with grazing patterns identified here. Fish densities were highest at 0 and 40 m, the areas with the greatest grazing pressure. Even though most of the fish observed at 90 m were juvenile *Acanthurus bahianus*, the sighting of a large heterospecific school of adult herbivorous fish outside the transect area (approximately 60 *A. bahianus*, 10 *A. chirugus*, 4 *A. coeruleus* and 13 *Sparisoma chrysopterum*) indicates these fish do extend their foraging to 90 m. Many heterospecific schools were also observed at 0 and 40 m. No schools were sighted at 150 m and only 1 individual was counted in the transects.

1989 Experiments

There were no significant differences between the three replicate locations for all eight macrophytes nor were there any significant distance*location interaction effects (ANOVA $p > .05$ in all cases). Thus, the three locations were grouped together for purposes of analyses.

The caged treatment showed no significant distance effects for macrophyte loss due to wave action (ANOVA $p > .05$ in all cases) and all distances were included in the same homogeneous subset (Table 1).

For the experimental assays, a similar pattern of spatial variation in grazing intensity emerges with respect to distance from the reef crest as that found in 1984 (Table 1) but grazing pressure was uniformly weaker. At all distances, for all macrophyte species, the percent weight loss was less in 1989 than that found in 1984 (ANOVA; $p<.01$). For six of the eight macrophytes there was a significant difference between the distances (ANOVA; $p < .0005$; Table 1). Only *Turbinaria turbinata* and *Dictyota* sp. showed no significant differences between distances.

The grazing intensity observed in 1989 appears to be uniformly less than that found for all macrophytes in 1984. The Duncan's multiple range tests for 1989 show the same grazing pattern but a fairly consistent shift in the grazing pressure toward the reef crest and in no cases was grazing pressure heavier nor further extended than that found in 1984 (Table 1).

DISCUSSION

Spatial Patterns of Herbivory

The data presented here show distinct spatial grazing patterns on the macrophyte species under study. For all macrophyte species, except *Dictyota divaricata*, the grazing pressure in 1984 is heavy at 0 and 40 m from the reef crest, moderate to light at 90 m and absent at 150 m. The same general results were found in 1989 but the grazing pressure was uniformly less. These results are associated with zonation patterns and biogeologic zones observed for this backreef habitat and the distribution of biological assemblages appears to be controlled mainly by a combination of grazing pressure of herbivorous fish, which is a function of distance from the reef crest, and both physical factors and hydrodynamic conditions which are discussed elsewhere (Macintyre *et al.* 1987). Thus, while spatial heterogeneity in herbivore grazing represents a biotically generated mechanism contributing to high regional diversity among reef habitats (Lewis 1986, Hay 1981a, 1985; Morrison 1988), the patterns of zonation and habitat diversity within the Tobacco Reef backreef appear to be under a similar mechanistic control.

Dictyota spp. in general, probably because they contain noxious chemical compounds (Gerwick 1981, Norris and Fenical 1982), are notably avoided by herbivorous fish (Montgomery 1980, Hay 1981a, Littler *et al.* 1983). Surgeonfish were occasionally observed taking single bites of *D. divaricata* but would not continue to feed or graze with the same intensity as they did on *Laurencia papillosa* or *Acanthophora spicifera.*

The grazing pressure may be determining the zonation pattern through either direct effects or an indirect effect by inhibiting an efficient competitor. Lewis (1986) directly compared grazed backreef versus ungrazed backreef and found that *Sargassium*, *Padina* and *Turbinaria* did increase significantly in the absence of fish herbivory and outcompeted corals and other slow-growing benthic species. Hay (1981a, b) and Hay *et al.* (1983) showed that algal species characteristic of the deep sand plains and intertidal reef flats may be restricted from the reef slope by herbivory, and suggested that these species would represent potentially dominant competitors on the reef slope in the absence of herbivory. The same may be true for the Tobacco Reef backreef habitat.

Macroalgae species found at the greatest distances from the reef crest and found in low-herbivory habitats were found to be the macrophytes most highly susceptible to grazing by herbivorous fishes. Other studies have indicated that many algal species characteristic of habitats with high grazing intensities are resistant to herbivorous fish grazing and, conversely, algae in habitats with low grazing intensity are susceptible to herbivory (Hay 1981b, 1984, Littler *et al.* 1983, Lewis 1985, 1986). For example, the coralline-coral-*Dictyota* zone (Macintyre *et al.* 1987) is the zone in which we measured the highest levels of herbivory. The dominant biota have well-documented herbivore defense strategies (Norris and Fennical 1982, Paul and Hay 1986).

Fish grazing intensity has been found to decrease with depth on forereefs and exhibits an inverse relationship to algal abundance (Morrison 1988). The decreasing herbivory is thought to be the result of diminishing trophic carrying capacity and increased risk of predation (Hay and Goertemiller 1983, Steneck 1983, Lewis 1986). The latter may well apply to the habitat studied here but the argument concerning trophic carrying capacity is not applicable in the shallow back-reef.

Proximity to suitable shelter has long been recognized as a critical factor in determining herbivore foraging ranges on patch reefs in tropical seagrass beds (Randall 1965), on deep sand plains adjoining reef slopes (Earle 1972, Hay 1981a, b) and in the backreef areas remote from the reef crest (Lewis 1986, Lewis and Wainwright 1985). Although we have no experimental evidence to explain why herbivorous fish do not graze further from the reef crest, they may be constrained by predatory piscivorous fishes (Ogden *et al.* 1973) and birds. Barracuda (Sphyraenidae), jacks (Carangidae) and snapper (Lutjanidae) were often seen swimming in the study area. This might also explain why only heterospecific schools of fishes, not solitary adult individuals, were seen at the 90 m site. Heterospecific schooling is considered to provide predator avoidance advantages to participants (see Morse 1977 for review).

All three study areas for 1989 showed the same pattern of herbivory and no significant differences were found between the different locations for all macrophytes. Thus, while the data clearly indicates that herbivore pressure varies perpendicular to the reef crest, it is also consistent along the reef at any one distance from the crest.

Temporal Patterns of Herbivory

In 1989, the grazing pressure for all macrophytes was homogeneously less than the grazing pressure found in 1984. These differences could represent seasonal fluctuations in herbivory pressure or resource availability (May versus March) or longer term patterns of variation (1984 versus 1989). The seasonal patterns could be the result of differences in productivity or resource availability to the herbivorous fish. Unfortunately, seasonal variation in grazing pressure or herbivore diets has been largely ignored and warrants further research. There may also be seasonal differences in fish movement patterns or community composition that may influence herbivory patterns.

Alternatively the long term effects could be the result of the *Diadema* die-off (Lessios *et al.* 1983) such that there is less competition for resources among herbivores. Morrison (1988) demonstrated that fish grazing intensity tripled after the Diadema die-off. Thus the increased herbivore pressure in 1984 could be the fish responding to the lack of a competition and a new equilibrium is established by 1989. An alternative explanation could be that in 1984, the macrophytes had not yet responded to the overall decrease in grazing and the fish were showing the same grazing pattern had *Diadema* been present. By 1989 the fish were no longer required to venture as far into the backreef to graze on macrophytes since they were no longer competing with *Diadema.*

Fish grazing intensity has also been found to vary between reefs because of heavy fishing pressure (Hay 1984). Thus the decrease in grazing pressure from 1984 to 1989 could also be the result of a decrease in the fish populations through an increase in fishing pressure.

CONCLUSION

From these data we may conclude that herbivorous fish have a strong impact on the distribution patterns of various reef macrophytes and this impact is a function of the distance from the reef crest. The data also indicate that there is temporal variation in herbivory patterns. While grazing pressure did not vary at three locations along the reef crest, it appears effective in preventing the establishment of many macrophytes within 90 m of the reef crest in the backreef habitat. The herbivory patterns found here are consistent with the macrophyte distribution patterns and suggests that fish grazers are of primary importance in controlling these distributional patterns. These patterns are, in turn, directly correlated with the distance from the reef crest.

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Table 1. Results of macroalgal transplant experiments: mean percentage macrophyte weight loss (± standard deviation) after exposure to or caging from herbivores at varying distances from the reef crest in the Tobacco Reef backreef habitat for 8-h trials. Four replicate trials were conducted at one location at each distance in 1984 (N=4) and three replicate trials were conducted at each of three locations in 1989 with no differences found between locations (N=9). 1989 Cage are the results from three replicate trials placed in fish exclusion cages at one location (N=3). Groupings between distances are based on Duncan's multiple range test.

<table>
<tr><th>SPECIES</th><th colspan="4">MEAN PERCENT WEIGHT LOSS (± S.D.)</th><th colspan="2">ANOVA</th></tr>
<tr><th></th><th>0 m</th><th>40 m</th><th>90 m</th><th>150 m</th><th>F</th><th>P</th></tr>
<tr><td colspan="7">*Thalassia testudinum*</td></tr>
<tr><td>1984</td><td>83.4 (6.2)</td><td>76.4 (10.7)</td><td>78.7 (6.5)</td><td>11.7 (23.3)</td><td>24.98</td><td><.0001</td></tr>
<tr><td></td><td colspan="3">|--------------------------------------|</td><td>|----------|</td><td></td><td></td></tr>
<tr><td>1989</td><td>77.3 (6.7)</td><td>36.9 (40.0)</td><td>0.0 (0.0)</td><td>0.0 (0.0)</td><td>30.39</td><td><.0001</td></tr>
<tr><td></td><td>|----------|</td><td>|----------|</td><td colspan="2">|-----------------------|</td><td></td><td></td></tr>
<tr><td>1989
Cage</td><td>0.0 (0.0)</td><td>2.3 (3.3)</td><td>0.0 (0.0)</td><td>0.0 (0.0)</td><td>1.00</td><td><.4411</td></tr>
<tr><td></td><td colspan="4">|--|</td><td></td><td></td></tr>
<tr><td colspan="7">*Padina jamaicensis*</td></tr>
<tr><td>1984</td><td>93.8 (3.0)</td><td>91.5 (5.1)</td><td>87.8 (9.8)</td><td>11.8 (6.8)</td><td>142.2</td><td><.0001</td></tr>
<tr><td></td><td colspan="3">|--------------------------------------|</td><td>|----------|</td><td></td><td></td></tr>
<tr><td>1989</td><td>81.3 (29.3)</td><td>42.4 (33.4)</td><td>6.4 (6.4)</td><td>11.0 (6.8)</td><td>21.17</td><td><.0001</td></tr>
<tr><td></td><td>|----------|</td><td>|----------|</td><td colspan="2">|-----------------------|</td><td></td><td></td></tr>
<tr><td>1989
Cage</td><td>10.3 (5.6)</td><td>15.0 (6.4)</td><td>14.0 (4.5)</td><td>11.3 (8.4)</td><td>0.23</td><td><.8707</td></tr>
<tr><td></td><td colspan="4">|--|</td><td></td><td></td></tr>
<tr><td colspan="7">*Turbinaria turbinata*</td></tr>
<tr><td>1984</td><td>86.4 (25.3)</td><td>61.1 (44.3)</td><td>8.9 (3.5)</td><td>7.1 (5.5)</td><td>9.37</td><td><.0018</td></tr>
<tr><td></td><td colspan="2">|-----------------------|</td><td colspan="2">|-----------------------|</td><td></td><td></td></tr>
<tr><td>1989</td><td>21.8 (28.5)</td><td>6.9 (4.5)</td><td>5.4 (5.0)</td><td>3.8 (2.0)</td><td>2.26</td><td><.1031</td></tr>
<tr><td></td><td colspan="3">|--------------------------------------|</td><td></td><td></td><td></td></tr>
<tr><td></td><td></td><td colspan="3">|--------------------------------------|</td><td></td><td></td></tr>
<tr><td>1989
Cage</td><td>4.3 (0.9)</td><td>5.7 (1.7)</td><td>4.7 (2.9)</td><td>4.0 (0.0)</td><td>0.35</td><td><.7934</td></tr>
<tr><td></td><td colspan="4">|--|</td><td></td><td></td></tr>
<tr><td colspan="7">*Sargassum polyceratium*</td></tr>
<tr><td>1984</td><td>97.3 (2.0)</td><td>61.2 (42.2)</td><td>31.2 (36.1)</td><td>10.0 (4.3)</td><td>7.40</td><td><.0046</td></tr>
<tr><td></td><td colspan="2">|-----------------------|</td><td colspan="2">|-----------------------|</td><td></td><td></td></tr>
<tr><td></td><td></td><td colspan="2">|-----------------------|</td><td></td><td></td><td></td></tr>
<tr><td>1989</td><td>48.7 (36.0)</td><td>9.4 (5.4)</td><td>5.8 (3.6)</td><td>7.4 (4.2)</td><td>9.32</td><td><.0002</td></tr>
<tr><td></td><td>|----------|</td><td colspan="3">|--------------------------------------|</td><td></td><td></td></tr>
<tr><td>1989
Cage</td><td>4.7 (3.3)</td><td>10.7 (4.6)</td><td>8.0 (6.2)</td><td>6.3 (3.1)</td><td>0.65</td><td><.6023</td></tr>
<tr><td></td><td colspan="4">|--|</td><td></td><td></td></tr>
</table>

Table 1 (cont.).

<table>
<tr><th rowspan="2">SPECIES</th><th colspan="4">MEAN PERCENT WEIGHT LOSS (± S.D.)</th><th colspan="2">ANOVA</th></tr>
<tr><th>0 m</th><th>40 m</th><th>90 m</th><th>150 m</th><th>F</th><th>P</th></tr>
<tr><td colspan="7"><i>Acanthophora spicifera</i></td></tr>
<tr><td>1984</td><td>93.3 (2.8)</td><td>89.1 (11.7)</td><td>71.2 (11.6)</td><td>4.0 (6.1)</td><td>87.14</td><td><.0001</td></tr>
<tr><td></td><td colspan="2">|------------------------------|</td><td>|------------|</td><td>|----------|</td><td></td><td></td></tr>
<tr><td>1989</td><td>74.8 (26.7)</td><td>73.1 (19.8)</td><td>18.6 (16.5)</td><td>5.3 (6.4)</td><td>31.22</td><td><.0001</td></tr>
<tr><td></td><td colspan="2">|------------------------------|</td><td colspan="2">|----------------------------|</td><td></td><td></td></tr>
<tr><td>1989</td><td>3.3 (1.2)</td><td>19.3 (12.5)</td><td>2.7 (2.0)</td><td>5.3 (3.9)</td><td>2.79</td><td><.1090</td></tr>
<tr><td>Cage</td><td>|----------|</td><td>|------------|</td><td>|---------|</td><td>|---------|</td><td></td><td></td></tr>
<tr><td colspan="7"><i>Laurencia intricata</i></td></tr>
<tr><td>1984</td><td>73.6 (19.7)</td><td>77.9 (18.5)</td><td>39.8 (19.4)</td><td>13.7 (8.7)</td><td>12.35</td><td><.0006</td></tr>
<tr><td></td><td colspan="2">|------------------------------|</td><td colspan="2">|----------------------------|</td><td></td><td></td></tr>
<tr><td>1989</td><td>42.1 (16.5)</td><td>28.0 (17.7)</td><td>15.1 (13.3)</td><td>10.1 (4.6)</td><td>8.13</td><td><.0005</td></tr>
<tr><td></td><td colspan="2">|------------------------------|</td><td colspan="2">|----------------------------|</td><td></td><td></td></tr>
<tr><td></td><td></td><td colspan="2">|-----------------------------|</td><td></td><td></td><td></td></tr>
<tr><td>1989</td><td>19.7 (7.0)</td><td>16.3 (5.3)</td><td>18.0 (5.0)</td><td>21.3 (6.9)</td><td>0.25</td><td><.8621</td></tr>
<tr><td>Cage</td><td colspan="4">|---|</td><td></td><td></td></tr>
<tr><td colspan="7"><i>Laurencia papillosa</i></td></tr>
<tr><td>1984</td><td>93.4 (3.1)</td><td>95.1 (3.7)</td><td>51.4 (27.9)</td><td>10.9 (6.9)</td><td>30.20</td><td><.0001</td></tr>
<tr><td></td><td colspan="2">|----------------------------|</td><td>|------------|</td><td>|-----------|</td><td></td><td></td></tr>
<tr><td>1989</td><td>82.7 (15.9)</td><td>77.8 (17.4)</td><td>8.6 (7.9)</td><td>4.3 (5.6)</td><td>85.65</td><td><.0001</td></tr>
<tr><td></td><td colspan="2">|------------------------------|</td><td colspan="2">|---------------------------|</td><td></td><td></td></tr>
<tr><td>1989</td><td>13.0 (8.5)</td><td>20.0 (10.2)</td><td>8.3 (4.1)</td><td>8.0 (7.8)</td><td>0.98</td><td><.4477</td></tr>
<tr><td>Cage</td><td colspan="4">|---|</td><td></td><td></td></tr>
<tr><td colspan="7"><i>Dictyota sp.</i></td></tr>
<tr><td>1984</td><td>28.5 (11.7)</td><td>27.3 (6.5)</td><td>21.0 (11.3)</td><td>27.4 (7.5)</td><td>0.52</td><td><.6778</td></tr>
<tr><td></td><td colspan="4">|---|</td><td></td><td></td></tr>
<tr><td>1989</td><td>17.4 (7.3)</td><td>17.4 (9.1)</td><td>15.1 (6.8)</td><td>14.6 (9.4)</td><td>0.28</td><td><.8371</td></tr>
<tr><td></td><td colspan="4">|---|</td><td></td><td></td></tr>
<tr><td>1989</td><td>29.0 (10.7)</td><td>29.7 (9.3)</td><td>29.0 (9.4)</td><td>29.7 (10.9)</td><td>0.00</td><td><.9998</td></tr>
<tr><td>Cage</td><td colspan="4">|---|</td><td></td><td></td></tr>
</table>

Table 2. Mean fish counts (densities per 100 m^2, N=4) along line transects (50 x 2 m) at the four distances (m) from the reef crest (herbivory test sites) (from Macintyre *et al.* 1987). The Acanthuridae juveniles (Juv) and adults (Ad) were both counted and the species represented are Bah. = *A. bahianus,* Coe. = *A. coeruleus* and Chi. = *A. chirugus.* All Scaridae individuals were included in counts and species represented are Ise. = *S. iserti,* Chr. = *S. chrysopterum,* Rub. = *S. rubripinne,* Vir. = *S. viride* and Rad. = *S. radians*

	ACANTHURIDAE						SCARIDAE				
Dist.	Bah.		Coe.		Chi.		Ise.	Chr.	Rub.	Vir.	Rad.
(m)	Juv	Ad	Juv	Ad	Juv	Ad					
150	0	0	0	0	0	0	0.25	0	0	0	0
90	16	0	0	0	0	0	0.50	0	0	0	2.75
40	23	4.5	0	2.5	1.3	1.3	5.00	0.50	0	0	0.25
0	14	1.5	0.5	2.5	0	0.8	10.5	1.25	1.0	3.5	0

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NEWS AND COMMENTS

F. RAYMOND FOSBERG (1908-1993)

A CELEBRATION

On May 19 1994, just a day before what would have been Ray Fosberg's 86th birthday we held a celebration in his honor in the Learning Center of the National Museum of Natural History. Approximately 60 people participated in this commemoration of Ray's life achievements, including several members of his family.

The activities began with Warren Wagner, Chairman of the Department of Botany, who welcomed everybody to this celebration of Francis Raymond Fosberg's life and introduced the Guest Speaker David R. Stoddart from the University of California at Berkeley. Along with a general biographical review of both Ray Fosberg and David Stoddart, Warren, in a lighter vein, mentioned Ray's comment in a letter to Dr. William Stearn of the British Museum, that despite the poor quality of David's initial plant collection, David, unlike "most geographers" was capable of learning how to collect botanical specimens.

Warren Wagner introduces the Guest Speaker. (photo by Bill Boykins)

In reviewing Ray Fosberg's career, David Stoddart made particular mention of the early stage of development of the Coral Atoll Program and the initiation of the Atoll Research Bulletin. He also talked about Ray's wide range of interests in natural history, which extended well beyond his specialty in floristic and taxonomic studies. In addition, he described Ray's profound influence on his own career, starting with those first lessons in plant collecting. Finally he discussed Ray's strong commitment to conservation, highlighted with the successful preservation of Aldabra, in the western Indian Ocean -- an island that was scheduled to be converted into a military base in the mid-1960s. David worked very closely with Ray on this crusade.

David Stoddart gives the Guest Speaker's address. (photo by Bill Boykins)

Ian Macintyre followed with a report on the current status of one of Ray's major legacies -- the Atoll Research Bulletin. He indicated that there has been a considerable increase in the editorial board in the hope of attracting manuscripts from a wider variety of disciplines. The new members include Steve Cairns (Invertebrate Zoology), Brian Kensley (Invertebrate Zoology), Wayne Mathis (Entomology), Victor Springer (Vertebrate Zoology), Warren Wagner (Botany), and Roger Clapp (National Biological Survey). Ian also mentioned that three Special Issues of the Bulletin are in press, including a Fosberg Commemorative Issue along with issues on Caroline Atoll and the Cocos (Keeling) Islands. With another regular issue in preparation, he suggested that Ray would be rather pleased with our progress.

Ian Macintyre reports on the status of the Atoll Research Bulletin. (photo by Bill Boykins)

The last speaker was Dan Nicolson, who read a few letters that he had recently received from some of Ray's former colleagues. He then went on to cite statistics on Ray's work that he had assembled for the Fosberg Commemorative Issue. At least 51 plants were named for Ray and each year for about 60 years

Dan Nicolson cites statistics on Ray Fosberg's work. (photo by Bill Boykins)

Ray named about 20 new taxa, with a total of about 1,000. His publication record was even more impressive, with an average of about 10 papers a year, resulting in 625 papers to date with still more to come. Most spectacular of his achievements was his average yearly collection of 1,000 plants, with a total of 66,369.

After thanking the many people who had worked on Ray's backlog and assisted with the organization of this event, Dan asked the audience if anybody wanted to make a statement. At least 6 people responded, including Frank Whitmore, who hired Ray to work in the US Geological Survey to work on the Pacific Geologic Mapping Program; Elbert Little, who was one of the Cinchona Mission collectors who Ray lead during the Second World War; and Lee Talbot, who talked about Ray's contribution to conservation.

A member of the audience, Frank Whitmore comments on his past association with Ray Fosberg. (photo by Bill Boykins)

After about an hour of talking, all of which was recorded by the Smithsonian Institution Archives staff, the participants socialized over a light serving of food and drinks. It was at this time that Ray's family mentioned that they had just spent the morning driving out to the Blue Ridge Mountains where they scattered Ray's ashes in places where he used to love visiting with them.

ATOLL RESEARCH BULLETIN

NOS. 415–425

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