ECOLOGY OF SCLERACTINIAN CORALS IN THE DAMPIER ARCHIPELAGO, WESTERN AUSTRALIA

Environmental Protection Authority
Perth, Western Australia
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PREFACE

Very little is known about the ecology of Western Australian coral reefs. Most research to date, has been confined to the high latitude coral reefs of the Houtman Abrolhos Islands. Rapid expansion of industrial development in the northwest of Western Australia and increasing recreational use of Western Australian coral reefs necessitates an understanding of these systems. This will enable the effects of deleterious anthropogenic perturbations on local marine communities to be predicted and minimised, and ensure their long-term conservation.

This report is the first detailed account of tropical coral reef ecology in Western Australia and provides information on selected aspects of the growth, metabolism and reproduction of corals in the Dampier Archipelago. The work was conducted as part of the Dampier Archipelago Marine Study, with the aim of providing information relevant to management of these valuable natural resources.

SUMMARY

Corals and coral reefs are found throughout the Dampier Archipelago and are important components of the local marine ecology. This report describes various aspects of the ecology of the corals and coral reefs of the archipelago and assesses this from a local and geographical perspective.

Annual growth rates of selected species of corals at a site in the Dampier Archipelago during 1982 and 1983, were consistent with the upper range of published values for these species and suggest that conditions on the outer reefs of the archipelago are near optimal for coral growth. On the other hand, 'natural' or baseline conditions for selected environmental parameters at some inshore reefs suggest that, during December to March, corals on inshore reefs may be vulnerable to even small increases in prolonged 'stress'. For example, increases in sediment settling on corals as a result of dredging activities may, depending on the amount and duration, reduce growth rates and/or cause mortality of particular species on these reefs.

The growth of three species of corals in the Dampier Archipelago varied seasonally with maximum rates in summer being approximately twice the minimum rates in winter (June/ July). Between April and November in 1982 and 1983 the temporal variation in growth of three species of coral was significantly correlated with seasonal variation in seawater temperature. During the cyclone season (December and April) variations in growth of *Acropora* spp. were not statistically correlated with environmental factors but, depending on the site, may have been due to mechanical damage by wave action, supra-optimal temperatures, increased reproductive activity and the effects of high sediment deposition rates. Spatial differences in the growth of *Acropora formosa* at three sites were significantly inversely correlated with differences in sediment deposition and was possibly due to the metabolic cost of sediment rejection rather than the effects of reduced light availability.

The high mortality of corals at site 2 appeared to be related to dredging operations that were carried out in the vicinity of this site. Analysis of retrospective growth rates, at an offshore site for the 10 years preceding 1983, suggests that the period between March 1982 and April 1983, when the intensive coral growth studies were conducted at site 1, was within the range of 'average' conditions that prevail in the Dampier Archipelago.

Seasonal and annual estimates of organic productivity and calcification for a reef-flat community in the Dampier Archipelago fall within the range of published values for community metabolism of reef-flats worldwide and support the concept of modality of metabolic performance of coral reefs. Overall the reef at Keast Island was heterotrophic (P/R< 1) and therefore was importing organic carbon.

Coral mass spawning was observed in March 1984 in the Dampier Archipelago, and subsequent studies on these and other coral reefs in Western Australia have shown that many of the coral species that occur on Western Australian reefs participate in this phenomenon. Apart from documenting the timing of mass spawning on many reefs and the modes of reproduction of many of the coral species in Western Australia, these studies also documented the prevailing environmental conditions and identified possible proximal factors that determine the timing of spawning. Before this study, coral mass spawning had only been observed during spring on reefs on the Great Barrier Reef, and the observations of coral mass spawning presented in this report are the first to be recorded in the Indian Ocean. There are many similarities between the coral mass spawnings on the east and west coasts of Australia and, within the breeding season (spring on the Great Barrier Reef and autumn on Western Australian reefs), the time of coral mass spawning on tropical and temperate reefs in Western Australia can now be predicted from lunar and tidal information. Comparisons of environmental parameters such as

annual sea temperature patterns on tropical reefs on the east and west coasts of Australia, and between tropical and temperate reefs in Western Australia, suggest that the breeding season of corals is not determined by exogenous factors but may be the result of an endogenous rhythm. The timing of coral mass spawning on Western Australian coral reefs coincides approximately with the initiation of the Leeuwin Current; a poleward flow of tropical water down the coastline of Western Australia in autumn and winter. This provides a mechanism for the southward dispersal of coral larvae and raises the possibility that regionally separate coral reefs in Western Australia are biologically connected.

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CHAPTER ONE

GENERAL INTRODUCTION

1.1 INTRODUCTION

The past thirty years have seen a marked increase in the amount of research conducted on coral reefs around the world (eg Stoddart and Jahannes, 19787; Barnes, 1983a). Many coral reefs are found along the coastlines of developing nations, where coral reef fish and other animals have been traditionally an important food source for local populations (Salvat, 1981). In addition, many countries such as Malaysia and Indonesia use corals for the production of lime and as building materials (Wood, 1983) and export coral and shells as curios (Wells, 1981). Population increases have placed additional pressures on the resources of reefs and many countries now recognise that coral reefs must be managed effectively if they are to be conserved (see Salvat, 1981; Dahl, 1981).

More recently the value of coral reefs has been recognised increasingly for their potential in the development of tourist industries (see Kelleher and Dutton, 1981), and this has provided an impetus for their conservation. In Australia, the Great Barrier Reef is a major tourist attraction and in the past ten years has become the focus of intensive research (eg Baker *et al.* 1983; Barnes, 1983a) aimed at 'conservation through understanding' so that the many competing uses for the resources of the Great Barrier Reef can be managed effectively. This research has substantially increased the understanding of many key processes of the Great Barrier Reef and of coral reefs in general.

Considerably less is known about the coral reefs of Western Australia, and this is partly related to the lower public awareness of their aesthetic, scientific and economic value and, until recently, their distance from large

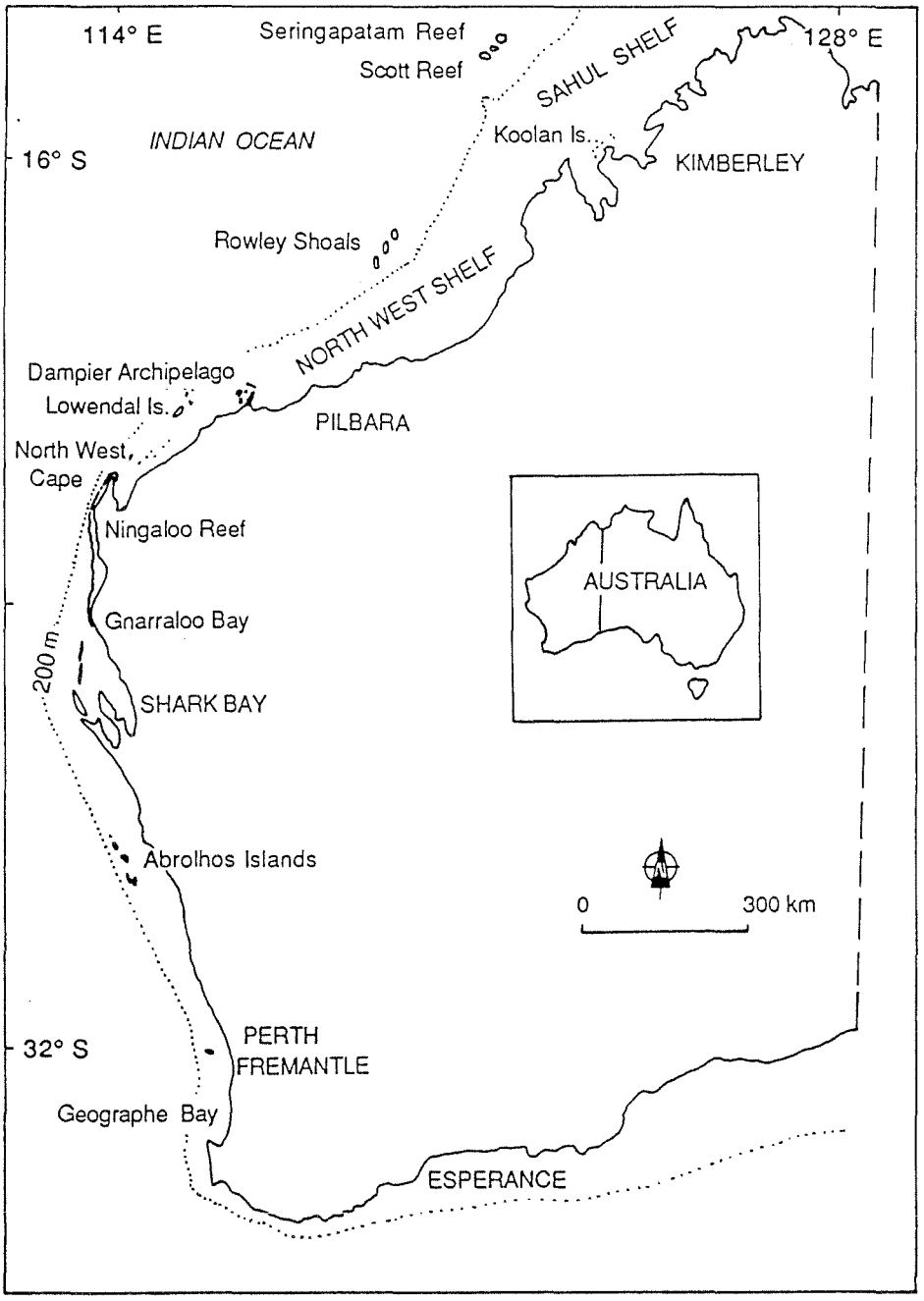


Figure 1.1 Location map of coral reefs in Western Australia.

centres of population. The development of the iron ore industry in the Pilbara in the 1960's and more recent industrial developments such as the North West Shelf Gas Project in the Dampier Archipelago (Fig.1.1) have led to a considerable increase in the population of this region. This has led also to increased recreational usage of local marine resources, as well as to disturbance of local marine communities from industrial activities associated with these developments. Additionally, the rapid expansion in recreational use of other Western Australian coral reefs such as the Rowley Shoals, Ningaloo Reef and the Abrolhos Islands (Fig. 1.1) has increased further the need to understand the processes controlling the ecology of these reefs, so that effective management strategies can be formulated and implemented .

1.2 STUDY APPROACH

Until recently the marine environments of the Dampier Archipelago were largely undescribed, although the archipelago was referred to almost 40 years ago in a regional report by Jutson (1950). Burbidge and Prince (1972) described the flora and fauna of the main islands as well as the planned usage of the Dampier Archipelago prior to the more recent industrial developments. From 1972 to 1974 Wilson and Marsh (1974; 1975) and Wilson *et al.* (1974) studied aspects of the ecology of the crown-of-thorns starfish, *Acanthaster planci*, at Kendrew Island (Fig. 1.2) and in 1978 the Western Australian Museum (1978) conducted surveys of the fish, molluscs, marine plants, corals and associated invertebrate communities. Semeniuk *et al.* (1982) described the marine environments of the Dampier Archipelago and included a detailed description of the main biotic assemblages and Paling (1986) classified a number of reef sites in the archipelago into several broad groups using numerical classificatory techniques based on the

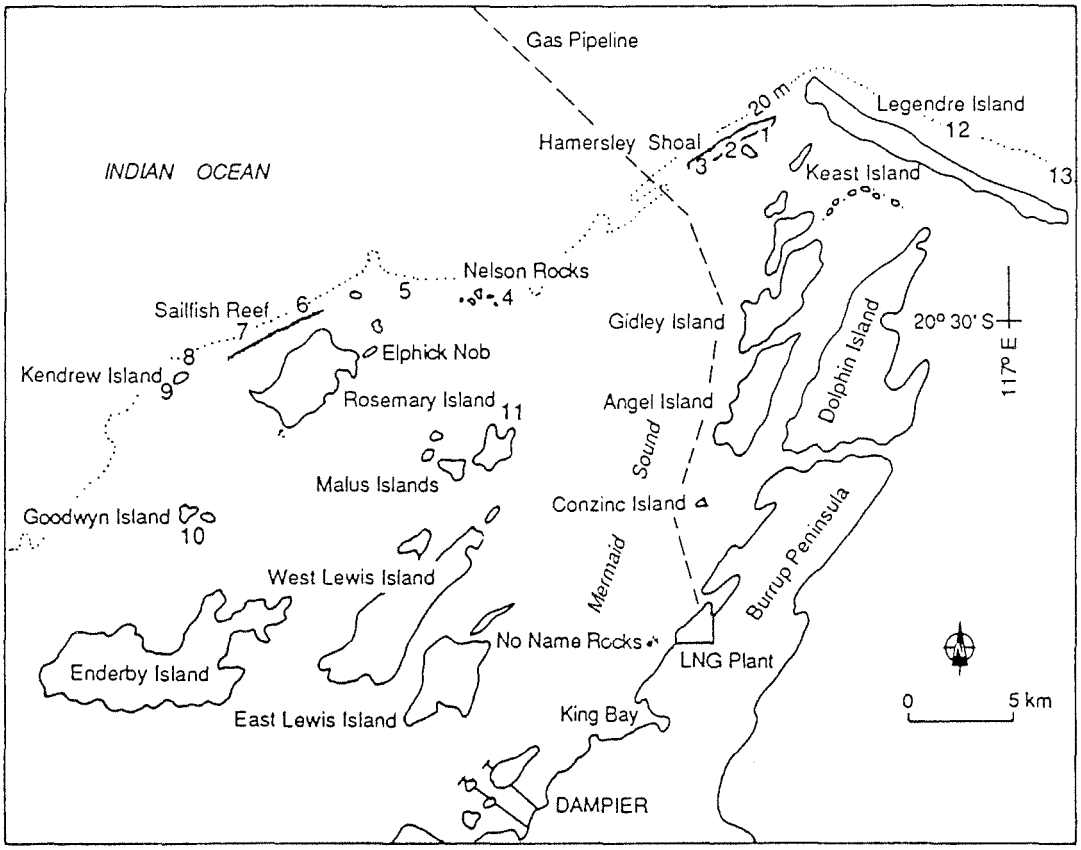


Figure 1.2 Location map of the Dampier Archipelago. Numbers refer to locations of coral transects.

presence and absence of coral species from the data of Marsh (1978).

Although these studies have investigated various aspects of the marine environment of the Dampier Archipelago the ecology of corals and coral reefs in this area remain largely unknown. In addition little is known quantitatively about aspects of the physical environment considered to be important to the growth, reproduction and survival of corals along this coastline. Prior to this work most studies of coral ecology in Western Australia had taken place on temperate reefs of the Houtman Abrolhos Islands (eg Wilson and Marsh, 1979; Crossland, 1981; Smith, 1981; Johannes *et al.* 1983; Crossland *et al.* 1984; Hatcher and Walker, 1984; Stoddart, 1984; Hatcher, 1985). This emphasis was partly due to the expense and logistical problems associated with working on the more remote tropical reefs in Western Australia. This report is therefore an account of the first detailed study of coral ecology conducted on a tropical coral reef ecosystem in Western Australia.

The aim of the work described here is to determine the most important factors controlling the development of reef-building corals in the Dampier Archipelago. The work was viewed as having intrinsic interest, because of its significance to coral reef ecology generally, and as the first of its kind on northwestern Australian coral reefs. It was also viewed as important to management because it would provide information about critical processes which might be affected by man's activities in the area.

The work fell into three parts. Firstly, the environment was reviewed as background to determining possible factors critical to growth and survival of scleractinian corals, particular attention being given to water turbidity and sediment deposition. This was because of the obvious seaward gradients of these factors that exist year round in the Dampier Archipelago and the known effects these factors have on coral growth and survival (eg

Buddemeier and Kinzie, 1976). The physical environments of different reef types were quantified under a range of conditions so that natural fluctuations caused by episodic events such as tropical cyclones, or man-made perturbations such as dredging operations, could be examined in relation to 'normal' conditions. Secondly, the geographical setting was examined to find out if, for example, the corals on selected reefs of the Dampier Archipelago are under extreme conditions for reefs on a worldscale. Growth rates of selected species of corals and rates of community metabolism of 'typical' reefs in the Dampier Archipelago were determined and compared with similar data from other locations to provide a geographical perspective of the corals and coral reefs in the archipelago. Statistical correlations were sought between coral growth and environmental parameters, and were used to infer which factors are likely to be important to the growth and survival of corals in the Dampier Archipelago so that possible effects of future man-made modifications to the natural environment can be determined. Thirdly, the fortuitous discovery of coral mass spawning in March 1984 and subsequent studies in 1985 and 1986 documented, for the first time, the timing and mode of reproduction of many species of coral found in the Dampier Archipelago.

1.3 WORLDWIDE DISTRIBUTION OF CORALS AND CORAL REEFS

Coral reefs are developed most extensively between the tropics and in the central and western sides of the main transequatorial oceans of the world, with the centre of maximum generic diversity in the Indo-West Pacific (Veron, 1985, 1986). Coral reefs are usually confined to waters where temperatures do not fall below 18° C for extended periods (Wells, 1957). Wood (1983) states that '... the most important factors in the formation of these gradients [in coral diversity] are a drop in temperature and the problems of

larval dispersal. There is general agreement that sea water temperatures control reproduction in corals and that different genera have different critical minima for breeding.'. However, as Veron (1985) points out, this effect has yet to be demonstrated. Alternatively he suggests that, below 18° C, the rate of calcification (ie growth) is slowed and corals may require more light to grow. This will reduce the depth limit of corals which may therefore limit their ability to build reefs. Johannes *et al.* (1983), following studies on the high latitude coral reefs at the Abrolhos Islands (Fig. 1.1), suggest that the latitudinal limits of coral reef development may often be determined by competition of macroalgae with corals.

The location of the 18° C isotherm of average winter minimum sea temperature is influenced by global ocean circulation patterns (Veron, 1986). In general, western boundary currents of the world's oceans are strong and poleward, in contrast to eastern boundary currents which are '...slow, broad equatorward meanders, often difficult to detect' (Golding, 1980). Western boundary currents occur in the north-west (Kuroshio Current) and south-west (East Australian Current) Pacific, the north-west Atlantic (Gulf Stream) and the south-west Indian Ocean (Agulhas Current); they extend the 18° C isotherm poleward along the eastern side of the continents of Australasia, the Americas and Africa respectively. In contrast, eastern boundary currents such as the Californian and Peruvian Currents in the north and south Pacific, the Canary and Benguela Currents in the north and south Atlantic are cooler and flow equatorward. These boundary currents form part of the global oceanic recycling systems and are the result of the 'Equatorial Currents' driven westward along the equator by the northeast and southeast trade winds dividing into poleward currents on reaching land. As these currents reach latitudes of 40-50° they are deflected eastward by the west wind drift and on reaching the western side of the continents turn

equatorward as cold currents.

Boundary currents of the eastern Indian Ocean, that is along the coastline of Western Australia, are the exception to this general pattern. Instead of flowing equatorward, a mass of tropical, low salinity water flows poleward during the austral autumn and winter (March to August), driven by a longshore sea-level gradient (Godfrey and Ridgeway, 1984). This flow was named by Cresswell and Golding (1980) as the Leeuwin Current and is considered to have a major influence on the distribution of scleractinian corals along the coastline of Western Australia (Wilson and Marsh, 1978).

The existence of this current was postulated as early as the end of the last century by Saville-Kent (1897) when attempting to explain the existence of exceptionally diverse, high latitude coral reefs at the Houtman Abrolhos Islands (Fig. 1.1). The recent discovery of coral mass spawning events, during this study, on reefs in Western Australia during autumn (Simpson, 1985b; Chapter 5), approximately coincident with the initiation of the Leeuwin Current, provides additional evidence to support the hypothesis of Saville-Kent. Thus from a biogeographic viewpoint the distribution of marine flora and fauna along the coastline of Western Australia is 'atypical' and, as such, of particular scientific significance and aesthetic appeal.

1.4 DISTRIBUTION OF CORALS AND CORAL REEFS IN WESTERN AUSTRALIA

Well developed coral reefs occur from the northern-most tropical regions of the state (12° S) to the temperate coral reefs at the Abrolhos Islands (28-29° S). These reefs occur at a number of locations along the coastline and continental shelf of Western Australia (Fairbridge,1950) and are shown in Figure 1.1. Isolated atolls such as the Rowley Shoals on the North West Shelf and Seringapatam and Scott Reefs on the Sahul Shelf occur

on the outer continental shelf while patch, fringing and small barrier reefs occur along parts of the mainland and near-shore islands of the Kimberley and Pilbara coasts. The largest fringing coral reef in Australia, the Ningaloo Reef tract, extends from North West Cape to Gnarraloo Bay, a distance of about 280 km (Simpson and Masini, 1986). Furthermore, diverse coral reefs occur at the Houtman's Abrolhos Islands, the most southerly occurrence of extensive coral reef development in the Indian Ocean (Hatcher *et al.* 1987), and reef-building corals are found as far south as Esperance (33° S) on the south coast of Western Australia (Table 1.1).

Table 1.1 Latitudinal decrease in generic diversity of scleractinian corals along the coastline of Western Australia (J E N Veron and L M Marsh, pers. comm; Wilson and Marsh, 1979).

Location	Latitude	Number of genera
Scott Reef	14° S	56
Rowley Shoals	16° S	51
Dampier Archipelago	20° S	57
Ningaloo Reef	22-24° S	53
Shark Bay	25° S	27
Abrolhos Islands	28-29° S	48
Fremantle	32° S	14
Geographe Bay	33° S	7
Esperance	33° S	4

Hatcher *et al.* (1987) state that the variety of reef types found in Western Australia are the result of the interaction of three fundamental factors. Firstly, the geological structure and history of the coastline of Western Australia is characterised by sedimentary forms pierced by igneous intrusions and shaped by a series of marine transgressions. Thus the foundations for reef development during the Holocene are often relict reefs of Pleistocene origin, examples being the Abrolhos Islands and the Dampier

Archipelago. Secondly, climatic conditions became less tropical through the Holocene, resulting in semi-arid deserts throughout much of the land area. Winter rains characterise the southern region from the Abrolhos to Dampier, while a monsoonal weather pattern with a well-defined cyclone season brings summer rains further north. The low terrestrial runoff and sediment input in the central region, has allowed extensive reef development close to the mainland (eg Ningaloo Reef tract). Thirdly the hydrodynamic environment includes unique features of a poleward flowing tropical current along the western shelf edge (the Leeuwin Current) and extremely high amplitude tides in the northern regions; the former resulting in the development of extensive high latitude coral reefs at the Abrolhos Islands and the latter causing turbid conditions and therefore restricting extensive reef development along the northern Pilbara and Kimberley coastlines. Descriptions of the main physical and biological characteristics of some of these reefs are summarised in Hatcher *et al.* (1987).

1.5 REGIONAL SETTING OF THE DAMPIER ARCHIPELAGO

The Dampier Archipelago (Fig. 1.2) is situated on the Pilbara coast, termed Pilbaraland by Jutson (1950) and is a group of islands located on the north-west coast of Australia (Fig. 1.1) between latitude 20° 20' S to 20° 45' S and longitude 116° 20' E to 117° 10' E. The archipelago was first discovered by the English explorer William Dampier in 1699 and subsequently named after him by the Baudin expedition of 1801 (Burbidge and Prince, 1972) and consists of 9 large islands, the largest being Dolphin Island of about 3200 ha, and numerous smaller islands and islets ranging 1-20 km from the mainland. The islands are partly the tops of inundated hills and ridges and comprise about 15% of the surface area of the archipelago and consist of igneous rock of Precambrian age (Semeniuk *et al.* 1982) covered generally by spinifex, *Triodia* spp. Many of the present day coral reefs in the Dampier

Archipelago consist of a living veneer of corals on relic reefs of Pleistocene origin. A concise account of the geology and geomorphology of the Dampier Archipelago can be found in Semeniuk *et al.* (1982).

1.5.1 Climate

The climate of the Pilbara region is tropical and arid (Gentilli, 1972) with a low annual rainfall and high annual evaporation rate (Table 1.2). Winters are mild and summers are hot with temperatures at Dampier during summer sometimes exceeding 47° C (Woodside Petroleum Pty Ltd, 1979).

Table 1.2 Mean monthly climatic data for Dampier from the Western Australian Bureau of Meteorology records for 1975 (from Semeniuk*et al.* 1982).

Parameter	J	F	M	A	M	J	J	A	S	O	N	D
Daily Max Temp (° C)	35.0	37.1	36.0	33.6	29.2	26.3	26.3	26.8	29.7	32.6	34.6	35.3
Daily Min Temp (° C)	26.3	26.4	25.8	22.0	17.8	15.1	14.0	14.9	16.5	19.5	22.1	25.4
Rainfall (mm)	29	57	41	14	70	62	14	10	*	0	2	16
Raindays (No)	4	3	6	1	4	5	4	2	0	0	1	3
Evapor^{n}. (mm)	354	311	325	283	224	198	193	228	291	348	379	384

* between 0.1 and 1.0

Dampier has a recorded average annual rainfal of 315 mm (Woodside Petroleum Pty Ltd, 1979) and is associated with monsoonal activity and tropical low pressure systems (ie cyclones) from the north in summer (December to March) and temperate low pressure systems from the south-west in winter (May to July). Tropical cyclones occur predominantly between December and April, and in the 21 years to 1980 ten cyclones passed

within 150 km of Dampier (Lourensz, 1981). An average of about 3.5 cyclones occur in this area each year (Woodside Petroleum Pty Ltd, 1979). These cyclonic disturbances can generate large waves which can have a destructive influence on the coral communities in the Dampier Archipelago (Marsh, 1978).

The weather pattern of the Dampier Archipelago is moderately predictable, being controlled largely by the seasonal oscillation of the subtropical anticyclonic wind belt. Winds from the west and southwest (monsoons) predominate from September to March and change to the southeast trades from March to August (Hollaway and Nye, 1985). In general westerly winds during summer blow persistently day and night in contrast to the easterly winds in winter which have a pronounced diurnal pattern. These easterly winds increase in speed during the morning to early afternoon before abating and changing to north-westerly sea breezes in the late afternoon to early evening. Periods of variable winds and maximum calms occur during April and August, that is during the changeover of these seasonal wind patterns (Mills and Pitt, 1985).

1.5.2 Oceanography

The Dampier Archipelago lies on the inner part of the north-west shelf. Swell waves from the north, northwest and west impinge on the outer, seaward reefs of the archipelago and are generated by temperate low pressure systems to the south during May to August and intermittently by tropical cyclones during December to April (Woodside Petroleum Pty Ltd, 1979). When cyclones pass to the west of the Dampier Archipelago, swell waves may penetrate into areas of the archipelago, such as the southern end of Mermaid Sound (Fig. 1.2), that are normally protected from long period wave action (Author's personal observation).

Seawater temperature records for the outer (depth 37 m) and inner (depth 11 m) waters of the Dampier Archipelago indicate that the annual range is about 22-30° C and 20-32° C respectively, with minimum temperatures occurring in July/August and maximum temperatures occurring in February/March (Woodside Petroleum Pty Ltd, 1979). Before the present study, the diurnal and seasonal variations in seawater temperature on coral reefs in the archipelago were unknown although diurnal fluctuations in shallow water in bays was known to exceed 5° C (Woodside Petroleum Pty Ltd, 1979). Salinity values of surface waters for nearshore and coastal waters in the Dampier Archipelago indicate that salinity values are close to normal oceanic salinity and that maximum values in summer are in the range of 36-37°/$_{oo}$ (Woodside Petroleum Pty Ltd, 1979).

The Dampier Archipelago is located in the North Western Australian tidal zone where tides are semi-diurnal and macrotidal (Easton, 1970), with a maximum spring tidal amplitude of about 4.9 m (Anon., 1984). Because of this large amplitude, water circulation patterns in the Dampier Archipelago are influenced markedly by tidal action. Before 1982, the circulation of water throughout the archipelago was not well known (Seminiuk *et al.*, 1982) apart from localised areas in Mermaid Sound where water movement was studied in relation to existing or proposed industrial developments (EG&G, 1979; Woodside Petroleum Pty Ltd, 1979). Recently Mills (1985) has developed a hydrodynamic model of water circulation in the Dampier Archipelago and adjacent offshore waters which generates depth-averaged current speeds and directions under variable conditions of tide and wind. Figure 1.3 shows a graphical output from this model and is a computer simulation of spring, ebb tidal currents for the Dampier Archipelago and adjacent offshore waters.

Water clarity in the archipelago varies both temporally and spatially

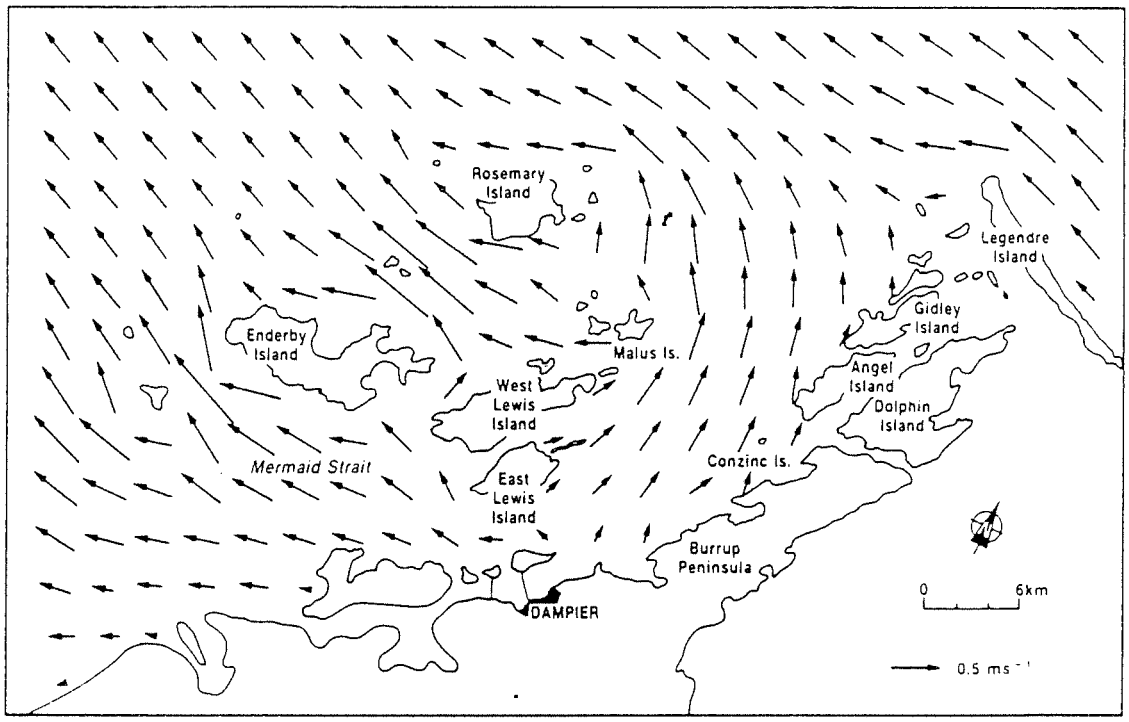


Figure 1.3 Computer simulation of current speeds and directions in the Dampier Archipelago and adjacent offshore waters during a spring, ebb tide (from Mills, 1985).

(Forde, 1985) and is related to biological and physical processes. Blooms of the planktonic blue-green alga, *Trichodesmium erythraeum* (Creagh, 1985), coral mucus and other organic particulate matter all contribute to an increase in turbidity during the December to March period. Fine sediments resuspended by wind waves also reduce water clarity during this period. Forde (1985) has documented the seasonal variation in sediment deposition and light attenuation at a number of sites around Mermaid Sound and found that, in general, sediment deposition and light attenuation in winter (May to August) was less than in summer (December to March).

1.5.3 Coral communities in the Dampier Archipelago

The most conspicuous subtidal communities in the Dampier Archipelago are the corals and associated coral reef communities. Two hundred and nine species of scleractinian corals, from 57 genera, have been recorded in the archipelago (Appendix I), and Marsh (1978) attributes this high diversity of corals to the wide variety of habitats which occur there. At present 16 families of Scleractinia have been recorded,with the families Acroporidae and Faviidae comprising about 56 % of the species recorded so far (Fig. 1.4).

In the Dampier Archipelago corals occur in four main coral habitats: (1) intertidal and subtidal limestone pavement, (2) intertidal and subtidal igneous rock, (3) intertidal and subtidal sand/gravel and (4) subtidal mud. Extensive coral reefs, however, occur mainly on limestone pavement on the seaward periphery of the archipelago as barrier (eg Hamersley Shoal) or fringing (eg north side of Legendre Island) reefs. Small patch and fringing reefs occur on igneous substrata adjacent to islands and rocky outcrops within the archipelago. Coral species composition varies from *Acropora* - dominated reefs such as Hamersley Shoal (Table 6.2) and the fringing reef on

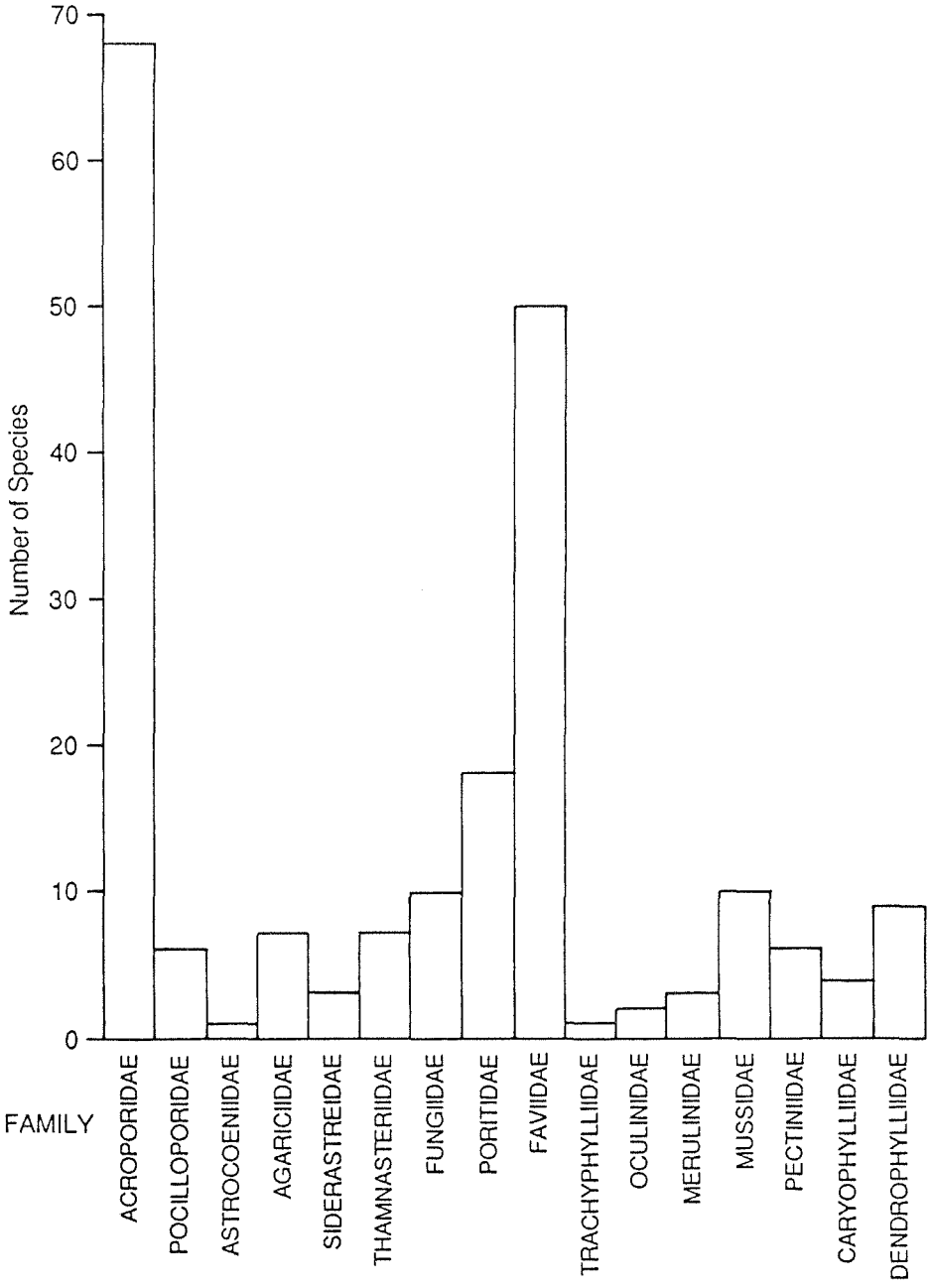


Figure 1.4 Taxonomic distribution of scleractinian corals in the Dampier Archipelago.

the north-west side of Angel Island, to the diverse assemblage of branching and massive coral species found on the north side of Conzinc Island and the more silt tolerant assemblage near King Bay (Fig 1.2; Marsh,1978).

In general live coral cover in the Dampier Archipelago decreases with distance from the open ocean and with depth. Live coral cover on the upper seaward reef slopes during a survey in October 1985 ranged from over 60% (Transect 3.1) on the southern end of Hamersley Shoal to about 2% at Transect 7.1 on Sailfish Reef (Fig. 1.2: Table 1.3). Many of these communities were dominated by tabular acroporiids, especially *Acropora hyacinthus* and, to a lesser extent, the pocilloporids *P. damicornis* and *P. eydouxi*. In depths greater than 6 m below datum, live coral cover on reefs in the western part of the archipelago was generally lower than 10% (mean 7.6%). In contrast, coral cover at similar depths on the eastern reefs of Hamersley Shoal and Legendre Island, was generally above 30 % (mean 44.4%) and ranged from 20% at Transect 1.2 to 73% at Transect 13.2 (Fig. 1.2; Table 1.3).

Figure 1.5 shows the change in coral diversity along an approximately inshore to offshore gradient. Relatively low diversity and high abundance of live corals occur on the offshore reefs and are probably due to the constant high wave energy and low sediment deposition that prevents other species competing successfully against more robust, faster growing species such as *Acropora hyacinthus*. In contrast the low diversity and abundance on the inshore reefs are probably related to the intolerance of many species of corals to the higher rates of sediment deposition that were found during this study to occur on some inshore reefs . The high diversity of corals found in the mid-shore region of Mermaid Sound probably reflects the intermediate environment found between these two extremes and appears to support the 'intermediate disturbance' hypothesis as proposed by Connell (1978), highest

Table 1.3. Percent live coral cover and dominant community type on selected reefs in the Dampier Archipelago in October 1985. Live coral was estimated as the proportion of live coral intersecting a 100 m transect (after Loya, 1978). Transects (Fig. 1.2) were located on the upper (x.1; mean depth 2.8 m) and middle (x.2; mean depth 7.3 m) seaward reef slopes (except 10, 11) and parallel to the reef crest. Depths are below chart datum.

Transect number	Maximum Depth (m)	Percent Live Coral	DominantCommunity Type
1.1	3.6	2.94	macroalgae/algal turf/coral
1.2	8.1	20.45	coral/algal turf
2.1	3.6	58.00	coral
2.2	5.5	37.01	coral
3.1	1.5	63.94	coral
3.2	7.2	37.76	coral
4.1	4.1	23.93	coral
4.2	6.5	7.50	coral/algal turf
5.1	2.7	15.39	soft coral/coral
5.2	6.9	1.62	soft coral
6.1	3.1	5.87	coral/algal turf/zooanthids
6.2	7.8	2.83	soft coral
7.1	2.6	2.07	coral/algal turf/zooanthids
7.2	6.4	6.35	coral/soft coral/algal turf
8.1	3.8	27.86	coral
8.2	8.5	25.61	coral/soft coral
9.1	0.6	30.10	coral
9.2	6.2	1.80	algal turf/soft coral
10.1	0.5	17.65	coral/algal turf
11.1	0.8	80.90	coral
12.2	9.4	54.22	coral
13.2	8.0	72.63	coral

diversity being maintained in areas of the Dampier Archipelago which are subject to large seasonal changes in sediment deposition and periodic, intermediate disturbance by cyclonic waves.

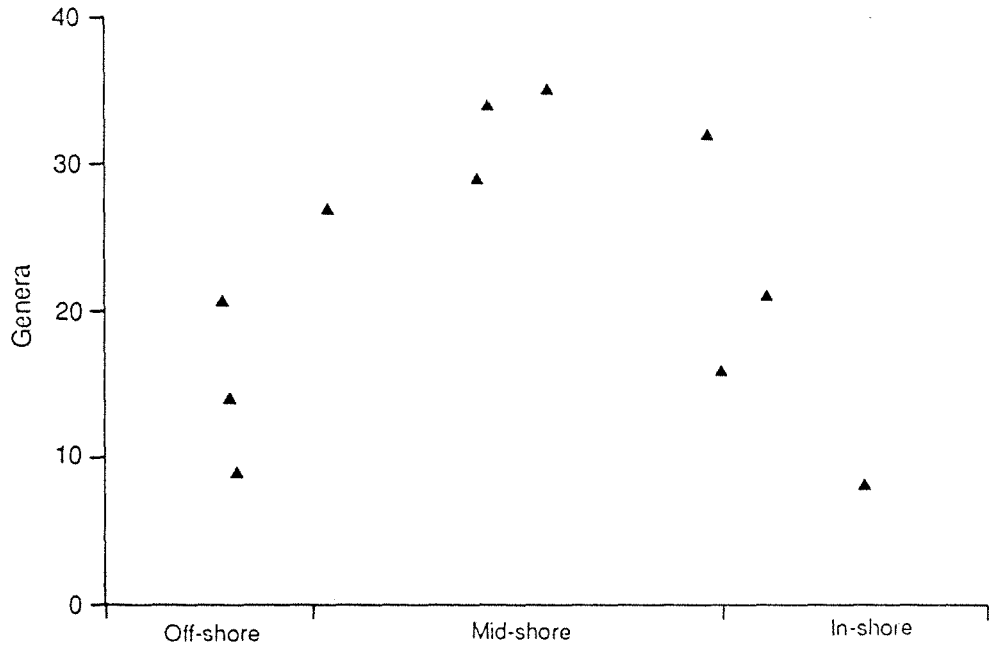


Figure 1.5 Variation in generic diversity of scleractinian corals along an offshore-inshore gradient in the Dampier Archipelago.
Data from transects recorded by Marsh (1978). Transects located in bays and channels are not included.

CHAPTER TWO

TEMPORAL AND SPATIAL VARIATION IN THE PHYSICAL ENVIRONMENT

2.1 INTRODUCTION

The growth and survival of corals is influenced by many factors including salinity, temperature, light, nutrients, dissolved gases, sediment deposition and water movement (see Buddemeier and Kinzie, 1976; Gladfelter, 1985). In relatively shallow, coastal marine ecosystems there are often considerable spatial and temporal (daily, 'seasonal' or intra-year and inter-year) variations in these factors. Because these variations are not necessarily in phase, coral growth may be limited by different factors at different times.

This chapter describes temporal and spatial variation in selected aspects of the physical environment at three sites (1, 2 and 3; Fig.2.1) on inshore and offshore coral reefs in the Dampier Archipelago. These sites were chosen along an inshore to offshore turbidity gradient that exists throughout the year. In addition to providing an environmental framework for subsequent chapters, the data have been used to characterise conditions on different reefs in the archipelago so that approximate baseline conditions for some reef types could be described. The factors chosen for investigation at these three sites were seawater temperature, salinity, water clarity and sediment deposition. Photosynthetic Photon Flux Density (PPFD) was calculated by a computer program (Appendix VI) and meteorologic and oceanographic data were obtained from Dampier Salt Pty. Ltd. and Woodside Petroleum Pty. Ltd., respectively.

The effects of natural episodic events (eg cyclones) and man-made

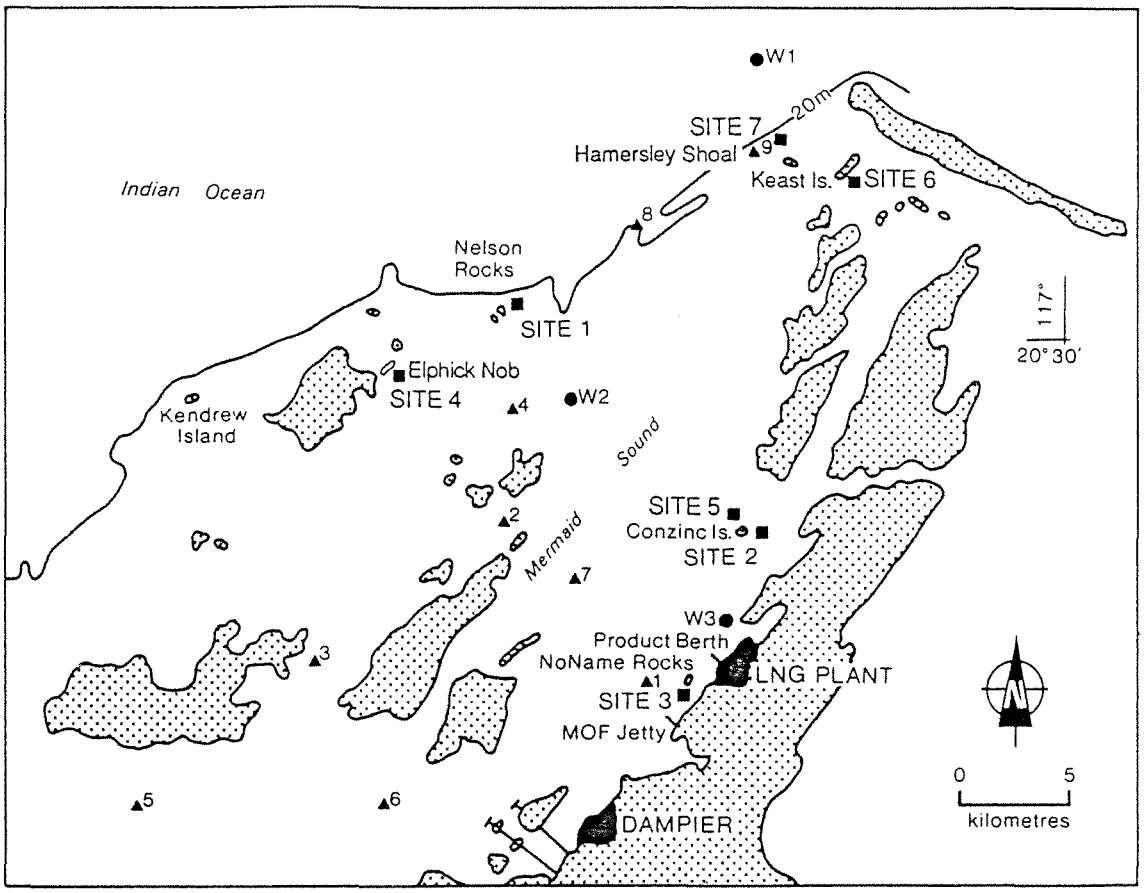


Figure 2.1 Study sites and instrument mooring locations in the Dampier Archipelago. (■) study sites, (▲) current meters, (●) waverider buoys.

perturbations (eg dredging and dumping activities) on the physical environment are also considered in relation to the 'natural' background conditions to provide a perspective from which to view future man-made changes to the waters of the Dampier Archipelago. In addition comparisons with other coral reef systems are considered to provide a geographic perspective.

2.2 MATERIALS AND METHODS

2.2.1 Study sites

The study sites and the instrument mooring sites are shown in Figure 2.1. Site 1 is in a shallow depression about 4 m below mean low water spring datum (hereafter referred to as datum) on the reef flat of the fringing reef at Nelson Rocks. This site is characterised by clear water and low sediment deposition rates and is exposed to moderate long period wave action. The coral community at this site is dominated by tabular acropores, especially *Acropora hyacinthus*, and the pocillopore *Pocillopora damicornis*. Site 2 (about 1.5 - 2 m below datum) is located on a small patch reef (<1 ha) of relatively large (for the Dampier Archipelago), monospecific stands of arborescent *Acropora* species on the sheltered south eastern side of Conzinc Island. This site is characterised by turbid water, especially in summer, and is protected from swell. Site 3 (about 1.5 - 2 m below datum), on the eastern side of the No Name Rocks, is similar to site 2 although this site is less protected from cyclonic wave activity and, as shown below, the water is generally turbid all year round. Arborescent *Acropora* and massive species (*Porites* sp., *Goniopora* sp., and *Platygyra* sp.) are common at this site.

It was presumed that there would be a major hydrographic difference between the offshore site (1) and the two inshore sites (2,3), because of the

proximity of the open ocean at site 1 and the coarser sediment, with a higher calcium carbonate and lower clay content at that site.

2.2.2 Environmental data

Temperature

Seawater temperature (± 0.05° C) was measured at the surface (depth ~0.1 m) and 0.1 m above the sea-bed using a salinity-temperature meter (Yeo-Kal Model 602) calibrated with a high precision mercury thermometer (± 0.01° C). Maximum and minimum thermometers (± 0.2° C) were installed at sites 1, 2 and 3 from June 1982 to April 1983. In addition, seawater temperatures (± 0.05° C) were recorded at 5 minute sampling intervals by current meters (Neil Brown Instrument Systems, Inc., Mass. U.S.A.) deployed from September 1981 to November 1983 at different depths and locations throughout the Dampier Archipelago (Fig. 2.1). Temporal trends in seawater temperature were determined from daily noon values recorded by these instruments (Mills *et al.*,1986). Spatial and vertical differences between the study sites and the current meter mooring locations were determined from temperature survey data collected every 6 weeks on neap tides at 37 stations throughout the Dampier Archipelago as part of a concurrent oceanographic programme (D. A. Mills, unpublished data). Mean seawater temperature, at each site, was the average of the adjusted daily noon temperatures for each sampling period.

Salinity

Salinity (± 0.05°/$_{oo}$) was measured at the surface (depth ~0.1 m) and 0.1 m above the seabed using a salinity-temperature meter (Yeo-Kal, Model 602). The probe was immersed for 15 minutes in 0.1 M HCl before use each day and at least 1 sample of seawater per day was collected for calibration of the

salinity-temperature meter against a salinity sample measured on an inductive salinometer. Instrument drift, if used as above, is less than $0.1^{o}/_{oo}$ per day (D. A. Mills, pers. comm.). Mean salinity was the average value of salinities recorded during field trips at the beginning and end of each sampling period.

Sediment deposition

Sediment deposition rates were estimated using an array of 8 sediment traps moored on a taut wire mooring (Fig. 2.2), 0.5 m above the seabed. Each trap consisted of a 0.3 m length of 50 mm diameter plastic pipe with a piece welded onto one end. Traps were deployed and retrieved (after capping) by divers at the beginning and end of each field trip. Longer term deployments (ie between field trips) were undertaken only between April and November to avoid the excessive fouling of traps observed during December to March (see Fig. 2.7). Deployments within and between field trips were of about 8 ($x = 7.9$, $sd = 1.7$, $n = 26$) and 37 ($x = 37.4$, $sd = 7.6$, $n = 15$) days duration respectively.

In the laboratory each trap was allowed to stand for a minimum of 3 hours before decanting 90% of the seawater. The sediment was then washed into a 600 ml beaker with distilled water, made up to approximately 550 ml and allowed to stand for 3 hours before 90% of this water was decanted off. The remaining water (about 60 ml) was decanted after a further 3 hour period, and the residue washed into a labelled 140 ml vial with distilled water. Two ml of 10% formalin were added to each vial.

The sediment from each vial was washed into a preweighed crucible with distilled water and dried to a constant weight at ~120° C to obtain total dry weight. In order to partially fractionate the sediment an empirical method was adopted. Each crucible was heated to ~600° C for 1.5 hours, reweighed to determine the organic fraction, reheated to ~1000° C for 1.5

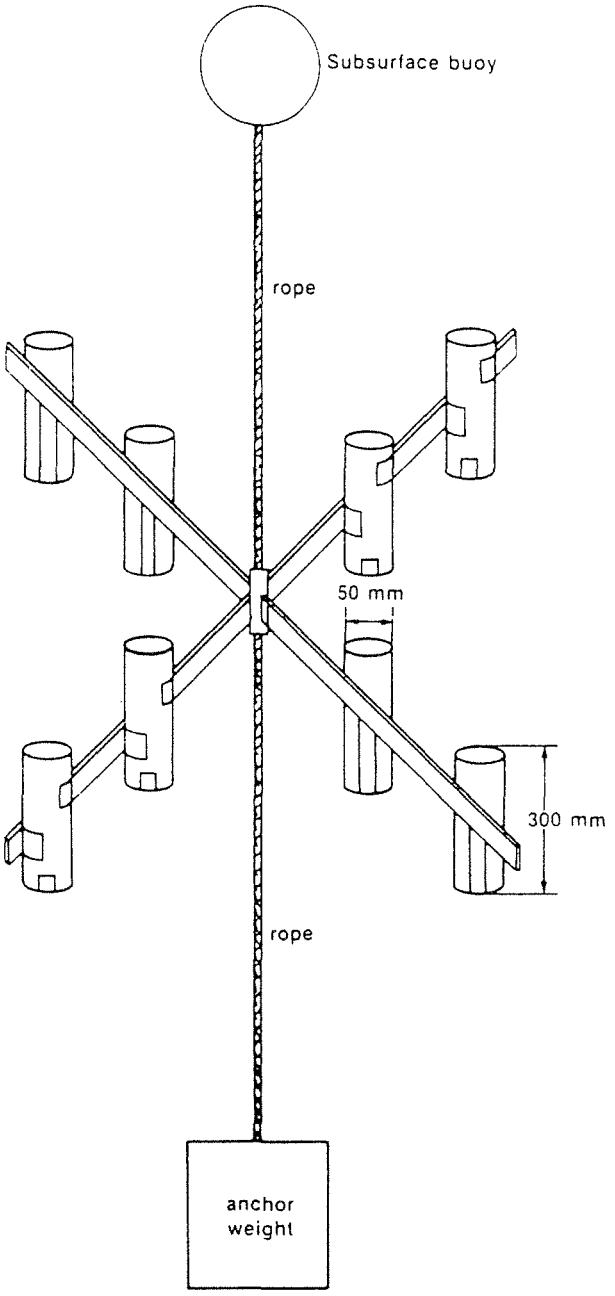


Figure 2.2 Diagram of sediment trap and mooring configuration used in this study (Forde, 1985).

hours and reweighed to determine the carbonate fraction (after a CaO correction was applied). The refractory fraction (ie inorganic, non-carbonate fraction) is determined by subtraction. S V Smith (pers. comm.) has suggested that this method may introduce errors (eg by overestimating the organic fraction) due to premature loss of $CaCO_3$ at the 600° C stage. Before weighing each crucible was cooled in a desiccator and weighed to ± 0.001g on a digital balance (Sartorius 1265 MP). Five replicates per deployment were analysed. In this study 'sediment deposition rate' refers to the rate of deposition of the refractory fraction unless otherwise stated. Sediment deposition rates were calculated using a computer program (Appendix III) and means were the average of two short term deployments within field trips at the beginning and end of a sampling period or the mean of a long term deployment between field trips.

Global Radiation

Global radiation data for Dampier from September 1, 1981 to January 31, 1984 were obtained from Dampier Salt Pty. Ltd. Measurements were made with a Rimco Integrating Pyranometer and represent daily integrated values for incoming global radiation at the earth's surface at Dampier in units of mW. H. cm^{-2}. Mean values for each sampling period were the average of the daily values.

Cloud cover

Cloud data (type and cover) at Dampier, from September 1, 1981 to January 31, 1984 were obtained from Dampier Salt Pty. Ltd. Observations were made daily (0600, 0900, 1200 and 1500 hrs) and recorded in octal format. Mean cloud cover for each sampling period was the average of the daily values. Daily mean cloud cover was an average of the maximum

observations for each recording and thus estimates mean cloud cover during daylight without considering the type of cloud.

Hours of daylight

Calculations for hours of daylight follow the equations given in Pascoe (1984). For a given location with latitude, ø (south negative), the solar declination, 'a' is given by: $\text{Sin } a = -0.398 \text{ Cos } (2\pi\, {}^{d}n/_{365})$ (approx) where d_n is the Julian day number and January 1 is day 0.

The half day length W_S (in radians) is given by: $\text{Cos } W_S = -\text{Tan } ø . \tan a$

The hours of daylight (DL) can then be calculated by: $DL = 24\, W_S/\pi$.

Mean hours of daylight for each sampling period was calculated for Dampier (20^{o} 30' S).

Vertical attenuation coefficient

Light intensity (Q) profiles were measured at 0.5 (0-2 m depth) - 1.0 m (>2 m) intervals with a Li-Cor Integrating Quantum Sensor (LI-192S) and a Li-Cor Underwater Quantum meter (LI-188B). The sensor is cosine corrected and measures photosynthetic photon flux density (PPFD) from 300-700 nm in units of micro - mole per square meter per second (μmol m^{-2} s^{-1}). The attenuation of PPFD can be approximately described by the equation: $Q = Q_0 . 10^{-Ez}$ where E is the vertical attenuation coefficient (m^{-1}) and Q and Q_0 are the downward quantum irradiances in the photosynthetic waveband at z meters, and just below the surface, respectively (Kirk, 1977). Values of E are reported as positive values, in this study following the convention of Kirk (1977) and thus the higher the value of the attenuation coefficient the more turbid the water. Mean attenuation coefficients for each sampling period were calculated as the area under the curve of best fit for the raw data for each site. The photic zone (ie the distance from the surface to the depth

which corresponds to 1 % of surface light) was calculated from the formula:

$$\text{Depth (1\%)} = 2.00 / \text{light attenuation coefficient}$$

Photosynthetic photon flux density (PPFD)

A computer program (Appendix VI) using the measured mean vertical attenuation coefficients, mean global radiation, mean cloud cover, Campbell-Stokes mean hours of sunlight, mean hours of daylight and mean depth (ie mean sea level) was used to calculate mean PPFD for each sampling period at sites 1,2 and 3. The ratio of Photosynthetically Active Radiation (P A R) to global radiation was adjusted from 0.45 for relatively clear (cloudless) skies to 0.54 for cloudy skies 100% cover) (Blackburn, 1983). Albedo (% reflected at the water surface) was specified at 0.065 of P.A.R. (Li-Cor, Inc) and the Immersion Effect Factor was 0.02 (Li-Cor, Inc). Conversion of radiometric units to photon units is : 1Watt $m^{-2} \approx 4.6$ µmol m^{-2} s^{-1} (Li-Cor, Inc).

Light loggers (Mcilwraith Instrumentation Pty., Ltd., Tas.) recording 15 minute integrated values of PPFD, 0.7 m above the seabed, were deployed at Nelson Rocks (site 1) and Conzinc Island (site 2) from 3 - 15 November, 1983.

Wind

Wind speed and direction were recorded by an anemometer on Conzinc Island (Fig.2.1) as part of a physical oceanographic programme (Mills and Pitt, 1985). Mean wind speed for each sediment trap deployment period and sampling period was determined with a planimeter (Summagraphics Corp, U.S.A.) as the area under the curve of the graphical output.

Waves

The graphical output of wave data (significant wave height, significant

wave period, average zero crossing period and period of peak spectral ordinate) for three stations (W_1, W_2, W_3; Fig. 2.1) was obtained from Woodside Offshore Petroleum Pty. Ltd. Wave data recorded at W_3, for the period from January 1, 1982 to December 31, 1983, was used to estimate wave parameters at site 3. Wave parameters at site 1 were estimated from data recorded at W_1 (January 1 to December 31, 1982) and W_2 (January 1, 1983 to December 31,1983). Maximum significant wave height was determined for each sampling period and mean significant wave height, for each sampling period and sediment trap deployment period, was determined as the area under the curve of the graphical output of the wave data. Mean energy density (E) for each sampling period was calculated as: $E = (p.g.H_s^2)/_8$ where p is the density of seawater (kg m^{-3}), g is the acceleration due to gravity and H_s is the mean significant wave height. E has units of J m^{-2} and is an index of relative wave energy (US Army Coastal Engineering Research Centre, 1975).

2.2.3 Statistical treatment

Data were collected during field trips at approximately six-weekly intervals between February 1982 and April 1983 (at sites 1, 2 and 3) and after this at site 1, at 5-, 11-, 11- weekly intervals until November 1983. Mean values for each parameter were calculated for the intervening 'sampling' or 'growth' periods and are used in the statistical analyses to facilitate direct comparisons with mean coral growth rates (Chapter Four). To determine whether gross spatial and temporal differences existed in the measured environmental variables the study period was divided into two 'seasons': 'winter' (April 1 - August 31) and 'summer' (September 1 - March 31). Data from March 1982 and March/April 1983 were not complete (due to cyclone damage) and have been omitted from the spatial analyses leaving 4 sampling

periods per 'season', from April 1, 1982 to March 2, 1983. Data for site 1 in both years have been used in the analysis of temporal differences giving 6 sampling periods per 'season, from April 1, 1982 to November 15, 1983. The date of the median day for each sampling period is used to determine the 'season'.

'Replicate' measurements for temperature, salinity, global radiation, cloud cover, PPFD, H_s, and E are the mean values for each sampling period occurring in 'summer' and 'winter'. 'Replicates' for sediment deposition rates and wind speed are the mean values for simultaneous deployments, at the 3 sites, during each 'season'. 'Replicates' for vertical attenuation coefficients are the values recorded within each season.

Model 1, one-way and two-way ANOVA (Snedecor & Cochran, 1978) were performed to determine whether sample population variances differed significantly between sites and within seasons and between sites and seasons respectively. Parametric (Student's t-test, Paired t-test; Snedecor & Cochran, 1978) and the non-parametric analogues of these tests (Mann-Whitney U-test, Wilcoxon two-sample test) were then performed on all the data to determine whether pairs of sample means were significantly different. The parametric test statistic is given here if results of the parametric and non-parametric tests are in agreement. In the case of disagreement the non-parametric test statistic is given on the assumption that the discrepancy between the tests is due to the criteria applying to parametric tests (eg normal distribution, homogeneous variances) not being met.

2.3 RESULTS

2.3.1 Seawater Temperature

Daily noon seawater temperatures are shown in (Fig. 2.3). Maxima of 31.3° C occurred in February, and minima of 18.4° C in July of 1983. Periods of high and relatively constant temperatures occurred from December to April in both years, with sharp declines in May and June. In 1981, seawater temperatures declined sharply from 27.8° C on November 4 to 23.5° C on December 1 and then increased to 30.2° C 23 days later. In contrast, the spring rise in sea temperatures took place at a relatively constant rate in 1982 and 1983.

Spatial variation

Mean seawater temperature showed similar trends at all 3 study sites, with mean maxima in February/March and mean minima around July of each year (Fig. 2.4). Mean seawater temperatures at site 1, on the outer fringing reef, were lower in summer and higher in winter (by about 1° C) than at the two inshore locations (sites 2,3). Mean temperatures at site 2 were always within 0.2° C of site 3. High mean temperatures (>27° C) were maintained from late October 1982 to mid - April 1983, with sharp declines occurring in April to June of each year. The statistics in Table 2.1 indicate that a significant difference in mean temperature exists between 'seasons' but not between sites.

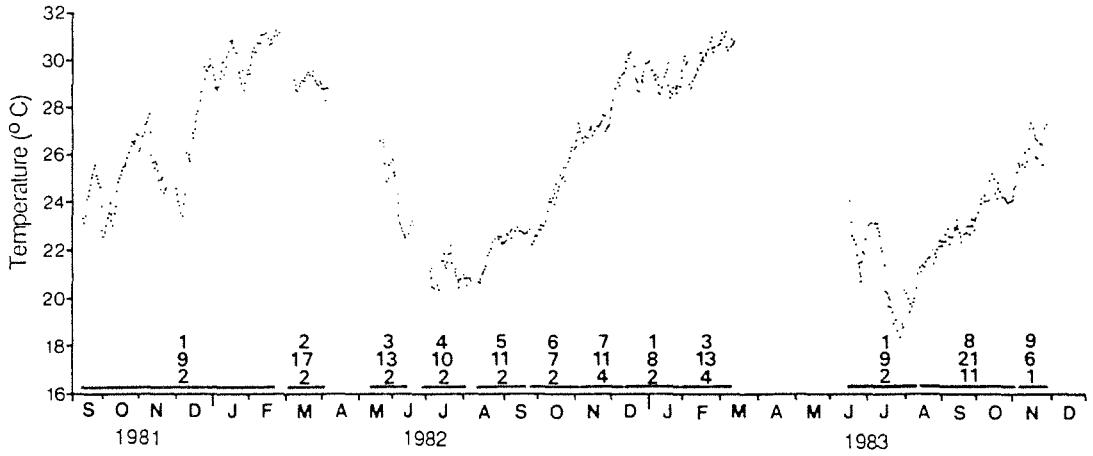


Figure 2.3 Daily noon seawater temperatures from different locations and depths in the Dampier Archipelago from current meter records (Mills *et al.*, 1986).
Numbers are: (top) current meter mooring locations from Figure 2.1, (middle) depth below datum, (bottom) sensor height above the seabed. Solid lines show deployment periods.

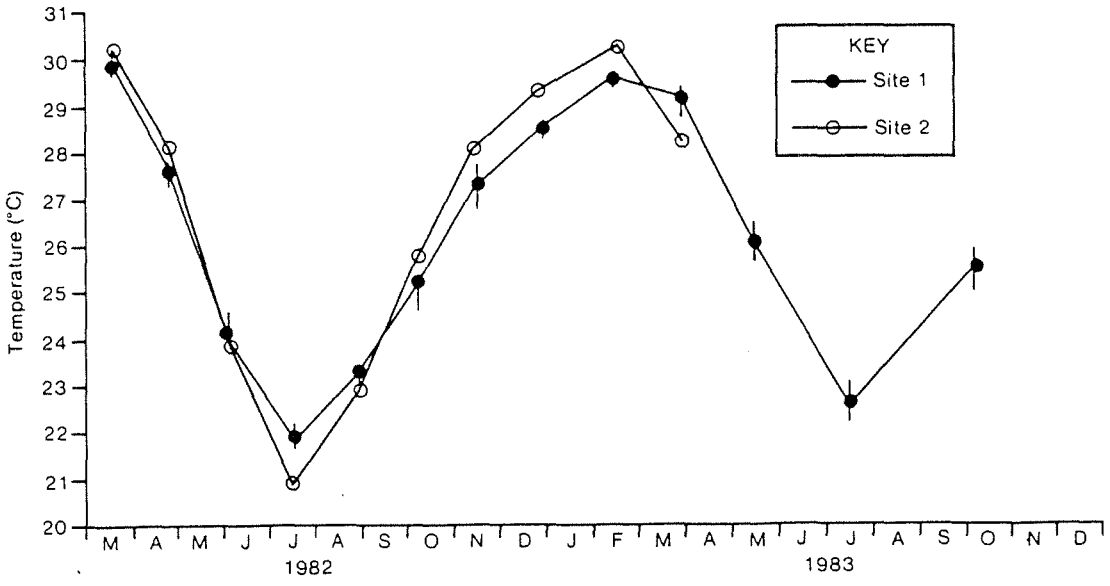


Figure 2.4 Seasonal variation in mean seawater temperatures at sites 1 and 2.
Error bars are 95%confidence intervals. Mean temperatures at site 3 were within 0.2° C of site 2.

Table 2.1 Summary of ANOVA for mean temperatures at sites 1, 2 and 3 during 'summer' and 'winter'

Source of variation	DF	SS	MS	F	P
Seasons	1	103.75	103.75	17.23	0.0006*
Sites	2	0.14	0.07	0.01	0.9888
Seasons x sites	2	1.51	0.75	0.13	0.8832
Residual	18	108.38	6.02		
Total	23				

* significant at the 0.05 probability level

Temporal variation at site 1

Mean seawater temperature at site 1 (Fig. 2.4) during 'summer' (x = 27.6, sd = 1.9, n = 6) was significantly higher (t = 2.751, df = 11) than during 'winter' (x = 24.3, sd = 2.2, n = 6). Mean minimum temperature was higher in July 1983 (22.6^{o} C) due to a longer measurement period than in the previous year (21.9^{o} C).

Diurnal variation

Diurnal variations in seawater temperature in the deeper (>10 m), well-flushed waters of the Dampier Archipelago are generally about 1-2^{o} C (Mills *et al.* 1986) but are more pronounced (2^{o} - 4^{o} C) over shallower reefs (<3 m) with a variation of over 4^{o} C being recorded over a period of 14 hours at Keast Island during March 1985 (Fig. 5.6a).

Maximum and minimum temperatures

Ambient seawater temperatures and maxima and minima recorded during the previous period (about 40 days) from July 1982 to April 1983 are shown for the 3 study sites (Fig. 2.5). The temperature range during this

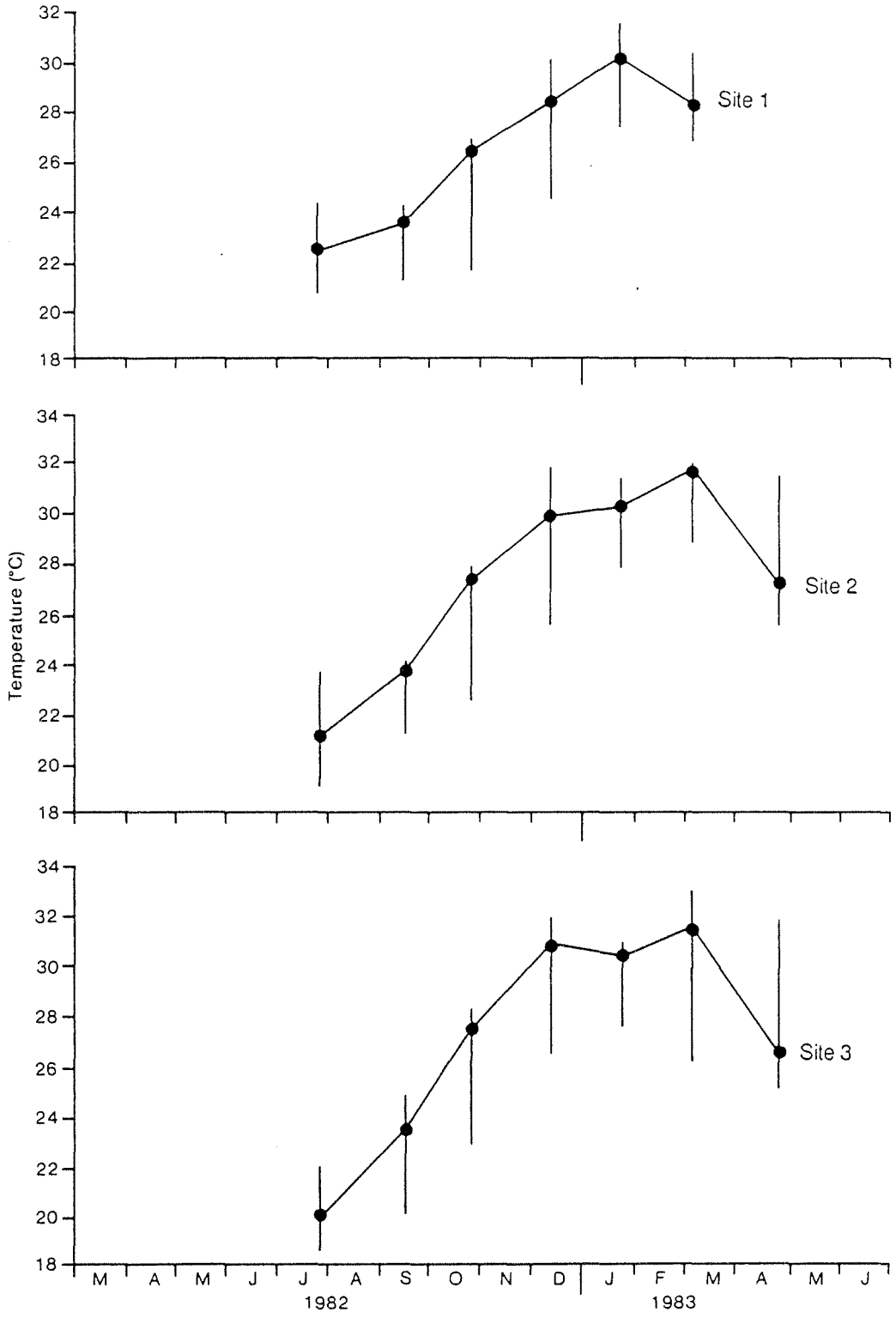


Figure 2.5 Instantaneous seawater temperatures and range (vertical bars) for the previous period recorded by maximum and minimum thermometers at sites 1, 2 and 3.

period increased with the distance of each site from the open ocean, with ranges at sites 1, 2 and 3 of 10.7° C (20.6 - 31.3° C), 12.6° C (19.2 - 31.8° C) and 14.0° C (18.7 - 32.7° C) respectively. Temperature depressions in January, 1983 following a cyclonic event (T.C. Jane: 7 - 9 January, 1983) are evident in the records from site 2 and site 3. On an intertidal reef near Keast Island, seawater temperatures extremes of 18.0° C and 33.3° C were recorded on July 10, 1984 and April 4, 1986 respectively.

3.2.2 Salinity

Spatial variation

The range of seawater salinities measured at the three study sites during 1982 and 1983 was 35.4 -37.1°/$_{oo}$ with a smaller range at the offshore site (site1; 35.4 - 36.1°/$_{oo}$) than at either site 2 (site 35.8 - 37.1°/$_{oo}$) or site 3 (35.8 - 36.8°/$_{oo}$). Mean salinities at all three sites showed similar seasonal variation, with minima occurring in July/August and maxima during November to February (Fig. 2.6). The differences in mean salinities at sites 2 and 3 were generally less than 0.3°/$_{oo}$, whereas salinities at these sites were about 0.4°/$_{oo}$ higher in winter and 0.9°/$_{oo}$ higher in summer, in comparison with site 1. Significant differences in mean salinities existed between sites and between seasons (Table 2.2).

Table 2.2 Summary of ANOVA for mean salinities at sites 1, 2 and 3 during 'summer' and 'winter'

Source of variation	DF	SS	MS	F	P
Season	1	1.55	1.55	26.36	0.0001*
Sites	2	1.92	0.96	16.32	0.0001*
seasons x sites	2	0.14	0.07	1.16	0.3352
Residual	18	1.06	0.06		
Total	23				

*significant at the 0.05 probability level

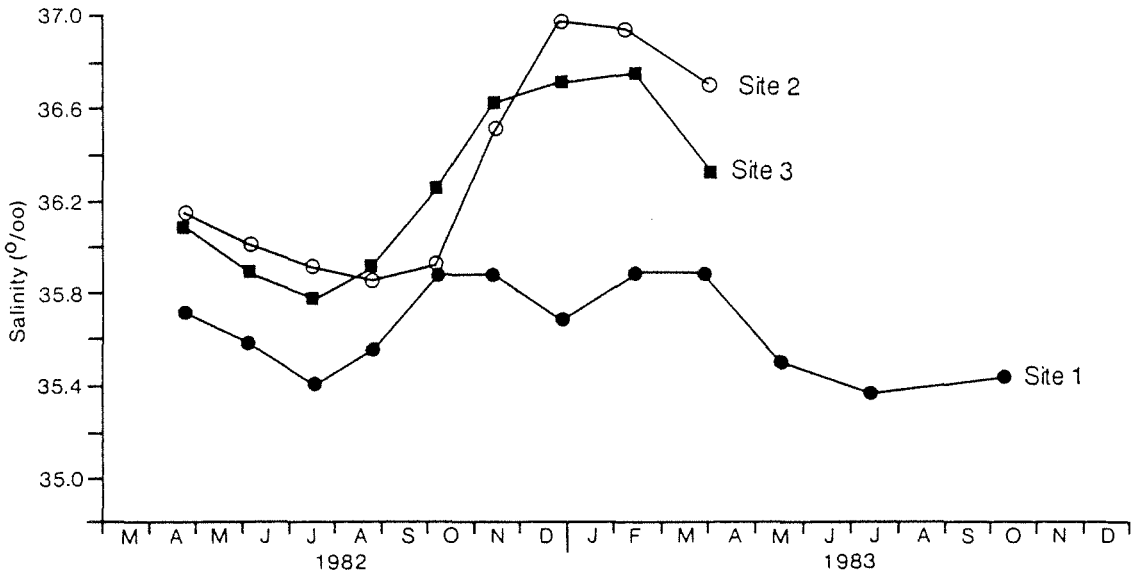


Figure 2.6 Seasonal variation in mean salinity at sites 1, 2 and 3.

During 'winter' the mean salinity at site 1 was significantly lower than at site 2 ($t = -4.5978$, $df = 7$) and site 3 ($t = -6.103$, $df = 7$). Sites 2 and 3 were not significantly different. During 'summer' the mean salinity at site 1 was significantly lower than site 2 ($t = -3.049$, $df = 7$) and site 3 ($t = -6.103$, $df = 7$). Sites 2 and 3 were not significantly different.

Temporal variation at site 1

Mean salinities at site 1 (Fig. 2.6) varied by less than $0.5^{o}/_{oo}$ throughout the study period with salinities being only slightly elevated above ocean values (about $35.0^{o}/_{oo}$). During 'winter' mean salinities at site 1 were significantly lower ($t = -2.724$, $df = 11$) than during 'summer'.

2.3.3 Sediment deposition

The sediment collected in traps was analysed to determine the organic, carbonate and refractory (ie the remaining) fractions and results are tabulated in Appendix II. The mean deposition rate of the refractory fraction is a more spatially comparable index of the medium-term (about 40 days) sediment depositional environment between the three sites, and is used in preference to the total amount trapped which, at site 1, occasionally included large fragments (up to 5 mm) of coral rubble resuspended by short periods (1-2 days) of intense swell activity. This possibly accounts for a lower correlation between the total and refractory fraction deposition rates at site 1 ($r=0.896$, $n=14$) than at site 3 ($r=0.992$, $n=15$). Attention was also directed to the refractory fraction because this component of the suspended sediment was considered more likely to have an influence on coral growth.

Due to the excessive fouling of sediment traps in summer (December to March) by filamentous algae (Fig. 2.7), sediment deposition rates were

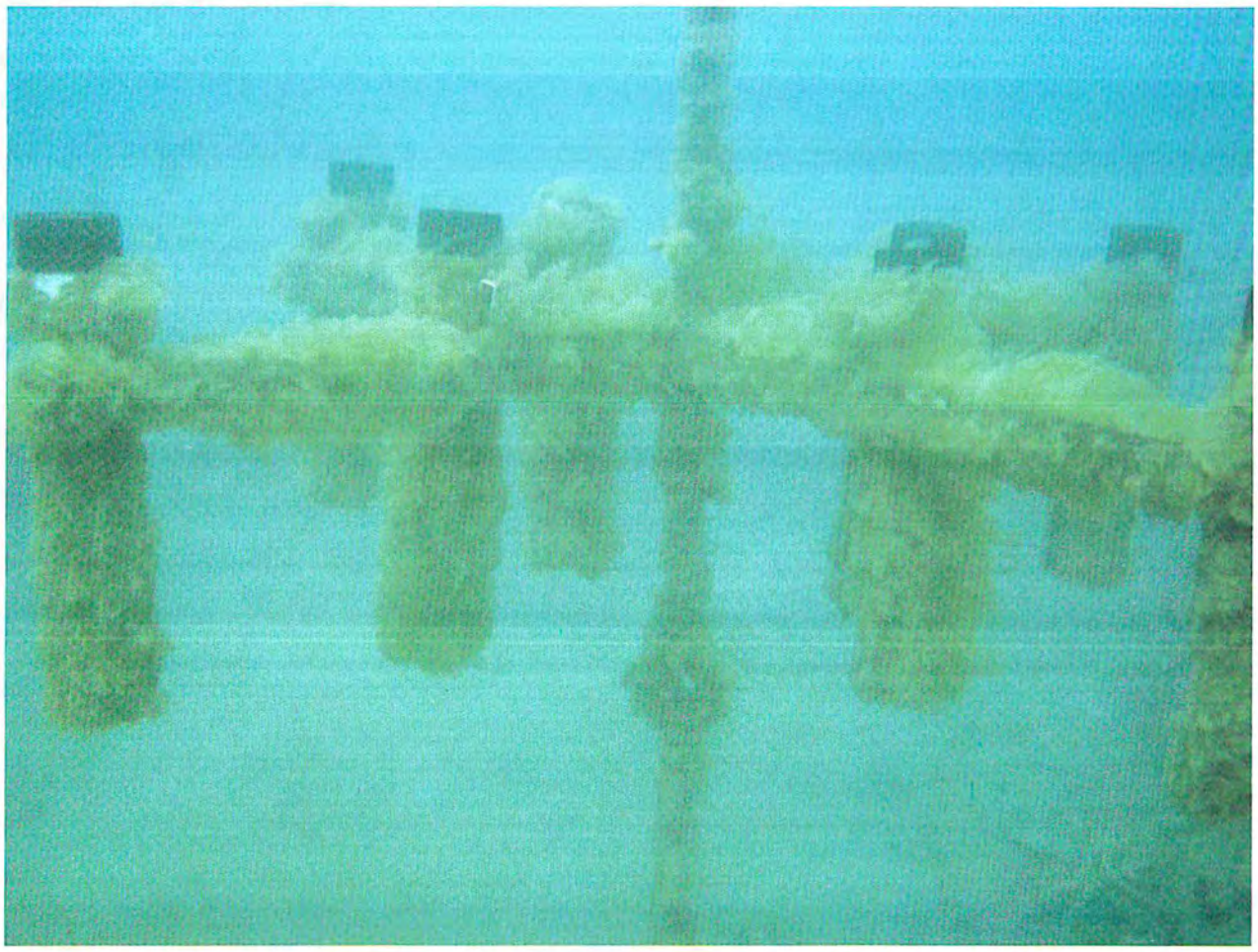


Figure 2.7 Photograph of filamentous algae fouling a sediment trap after 35 days at site 2 from January 26 to March 2, 1983.

estimated by averaging the mean rates of two short-term deployments. There was no significant difference (t_p = 0.0816, $p>0.05$, n=9) between sediment deposition rates estimated during the non-summer months from the average of two short-term deployments and one long-term deployment suggesting that during summer under 'normal' (ie non-cyclonic) conditions, two short term (~8 day) deployments at the beginning and end of a period provide a representative estimate of the sediment deposition environment for the intervening period.

Spatial variation

The mean sediment deposition rates of the refractory fraction at the three study sites, periods of cyclonic wave activity and major dredging operations in the vicinity of sites 2 and 3 are shown in Figure 2.8. Sediment deposition rates at the offshore site (1) were generally lower and displayed less seasonal variation than the two inshore sites (2, 3). Mean sediment deposition rates during 'winter' were approximately 80%, 20% and 50% of the mean 'summer' rate at sites 1 (14 g m^{-2} d^{-1}), 2 (110 g m^{-2} d^{-1}) and 3 (50 g m^{-2} d^{-1}) respectively. Before November 1, 1982 mean sediment deposition rates at site 3 were significantly correlated with site 1 ($r=0.82$, $p<0.05$) and site 2 ($r=0.88$, $p<0.05$). After this date mean sediment deposition rates at site 3 were significantly correlated with site 1 ($r=0.94$, $p<0.02$) but not with site 2 ($r=0.32$, $p>0.05$). High (>110 g m^{-2} d^{-1}) and constant rates of sediment deposition were recorded at site 2 during the dredging operations. From September 1982 to April 1983 the difference in sediment deposition rates between sites 1 and 3 remained relatively constant (about 38 g m^{-2} d^{-1}) including when a cyclone (T.C. Lena) occurred during a long period deployment at both sites in March/April 1983 . The statistics in Table 2.3 indicate that a significant difference in mean sediment deposition rates

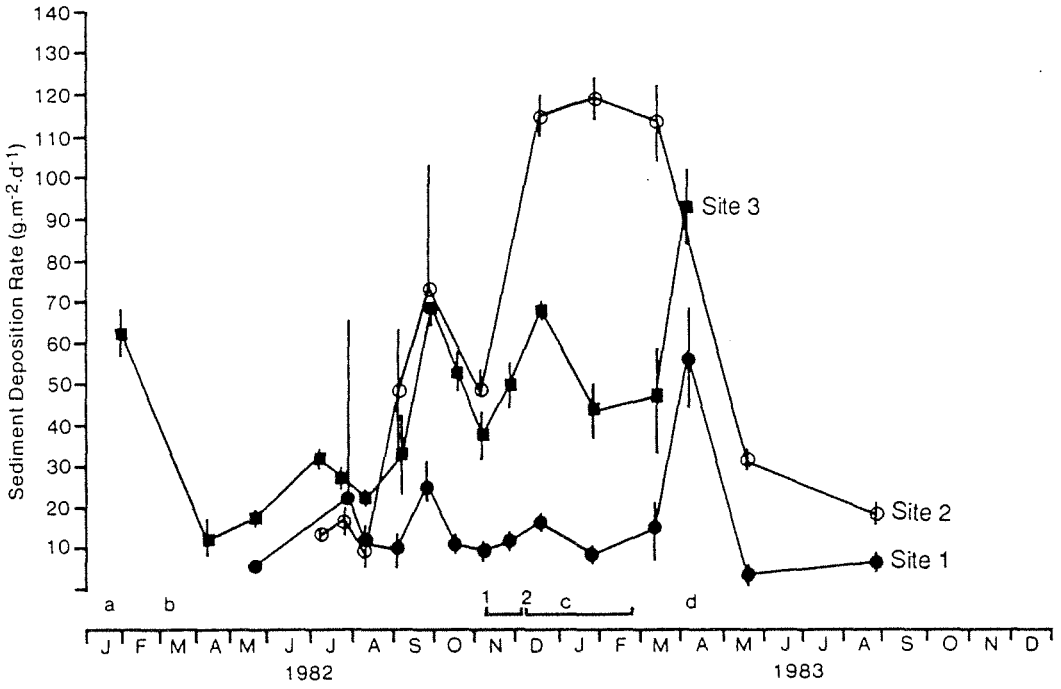


Figure 2.8 Seasonal variation in sediment deposition rate of the refractory fraction at sites 1, 2 and 3.
Error bars are 95 % confidence intervals. Periods of dredging activity are shown: (1) November 1-27, 1982 at MOF jetty ; (2) December 1, 1982 to February 21, 1983 at Product Berth. Occurrence of tropical cyclones is shown (a) T.C. Bruno, January 16-21, 1982; (b) T.C. Ian, March 5-6, 1982; (c) T.C. Jane, January 7-9, 1983; (d) T.C. Lena, April 7-8, 1983.

existed between sites and between seasons. The interaction (sites x seasons) was also significant.

Table 2.3 Summary of ANOVA for simultaneous mean sediment deposition rates of the refractory fraction at sites 1, 2 and 3 during 'summer' and 'winter'

Source of variation	DF	SS	MS	F	P
Seasons	1	5857.2	5857.2	17.19	0.0006*
Site	2	11222.3	5611.6	16.46	0.0001*
Seasons x Sites	2	4598.6	2292.3	6.75	0.0065*
Residual	1	86134.9	340.8		
Total	23				

* significant at the 0.05 probability

A spatial comparison of sediment deposition rates within each 'season' indicates that there was no significant difference between the three sites during 'winter' (Table 2.4) but that a significant difference between the sites existed during 'summer' (Table 2.5).

Table 2.4 Summary of ANOVA for simultaneous sediment deposition rates of the refractory fraction at sites 1, 2 and 3 during 'winter'.

Source of variation	DF	SS	MS	F	P
Between	2	247.7	123.9	0.7445	0.5142
Within	6	998.2	166.4		
Total	8	1245.9			

Table 2.5 Summary of ANOVA for simultaneous sediment deposition rates of the refractory fraction at sites 1, 2 and 3 during 'summer'.

Source of variation	DF	SS	MS	F	P
Between	2	15574.2	7787.0	18.19	0.0002*
Within	12	5136.7	428.1		
Total	14	20710.9			

*significant at the 0.05 probability level

During 'summer' the mean sediment deposition rate at site 1 (x = 14.84, sd= 7.06, n = 5) was significantly lower than site 2 (x = 93.74, sd = 32.04, n = 5; t = -5.378, df = 9) and site 3 (x = 52.46, sd = 14.42, n = 5, t = -5.238, df=9). In addition, site 2 was significantly greater than site 3 (t = 2.627, df=9).

Temporal variation at site 1

Sediment deposition rates at site 1 were low and constant throughout the study period with 80% of deployments having mean sediment deposition rates of less than 20 g m^{-2} d^{-1} (Fig. 2.8). Mean sediment deposition rate during April 1983, when a cyclone occurred (T.C. Lena), was approximately 10x greater than during May 1983. Mean sediment deposition rates at site 1 during 'winter' (x = 9.75, sd = 6.64, n = 6) were not significantly different than during 'summer' (x = 19.10, sd = 16.04, n = 8). Statistical tests on log-transformed data (variances equal) were in agreement with the results of the same tests on the untransformed (variances unequal) data .

Composition of sediment trap material

The percentage of organic, carbonate and refractory material are shown in Appendix II. In general the sediment trapped at sites 2 and 3 had similar compositions with mean fractions for all deployments of approximately 15% organic, 35% carbonate and 50% refractory material. In contrast, site1 had 19% organic, 50% carbonate and 31% refractory material. During a 48 day period in March/April 1983 site 1 had a mean total sediment deposition rate of 326.5 g $m^{-2}d^{-1}$ and consisted of 8.4% organic, 74.3% carbonate and 17.3% refractory material. The large carbonate fraction was due to several large pieces of coral rubble that were probably resuspended by large waves (>3 m at W_2, Fig. 2.12b) that occurred during this period as a result of Tropical Cyclone Lena. At site 3, during the same period, the total mean sediment deposition rate over 40 days was 211.2 g $m^{-2}d^{-1}$ and consisted of 13.3% organic, 42.0% carbonate and 44.7% refractory material. Further details of the composition of trapped sediments can be found in Appendix II.

Composition of bottom sediments at sites 1, 2 and 3

The surface 50 mm of sediment from cores taken at site 3 consisted of 92.3 % calcium carbonate, 2.2% organic and 3.9% refractory material. Granulametric analysis showed that these sediments were 66.0% sand, 11.8% silt and 22.2% clay. At site 2, cores consisted of 6.1% organic, 87.3% calcium carbonate and 6.6% refractory material with 99.8% sand and 0.2% clay. Cores were not taken at site 1 due to the predominance of coral rubble.

2.3.4 Cloud cover

Cloud cover was highly variable throughout the study period with a minimum mean percentage cloud cover of 13% in August 1982 and a

maximum of 46% in March/April 1983. In 1982, maximum cloud cover had a bimodal distribution with peak values occurring in January and July. Low cloud cover (<20%) occurred during August to October 1982, and from May to October in 1983 (Fig. 2.9a). Mean cloud cover in 'winter' (x = 24.8%, sd = 9.1, n = 6) was not significantly different to mean cloud cover during 'summer' (x = 30.0%, sd = 12.3, n = 6).

2.3.5 Global radiation

Mean global radiation varied throughout the study period from a minimum mean value of 434 mW H cm^{-2} in June 1982 to a maximum mean value of 720 mW H cm^{-2} in January 1983 (Fig. 2.9b). Mean global radiation during the three sampling periods from November 1982 to February 1983 were not significantly different. The minimum mean global radiation in 1983 (535 mW H cm^{-2}) was higher than in 1982 (434 mW H cm^{-2}) and was due to a longer measurement period (75 days in 1983; 35 days in 1982) and lower cloud cover (33% in 1982 and 18% in 1983). Mean global radiation during 'winter' (x = 529, sd = 65, n = 6) was significantly lower (t = -4.704, df = 11) than during 'summer' (x=683, sd=45, n=6).

2.3.6 Hours of daylight

Mean hours of daylight for the sampling periods throughout the study period ranged from 10.8h in June/July 1982 to 13.1h in December/January 1983 (Fig. 2.9c).

2.3.7 Vertical attenuation coefficient

Spatial variation

Vertical light attenuation coefficients show similar seasonal trends at all three sites with higher water clarity (lower attenuation coefficient)

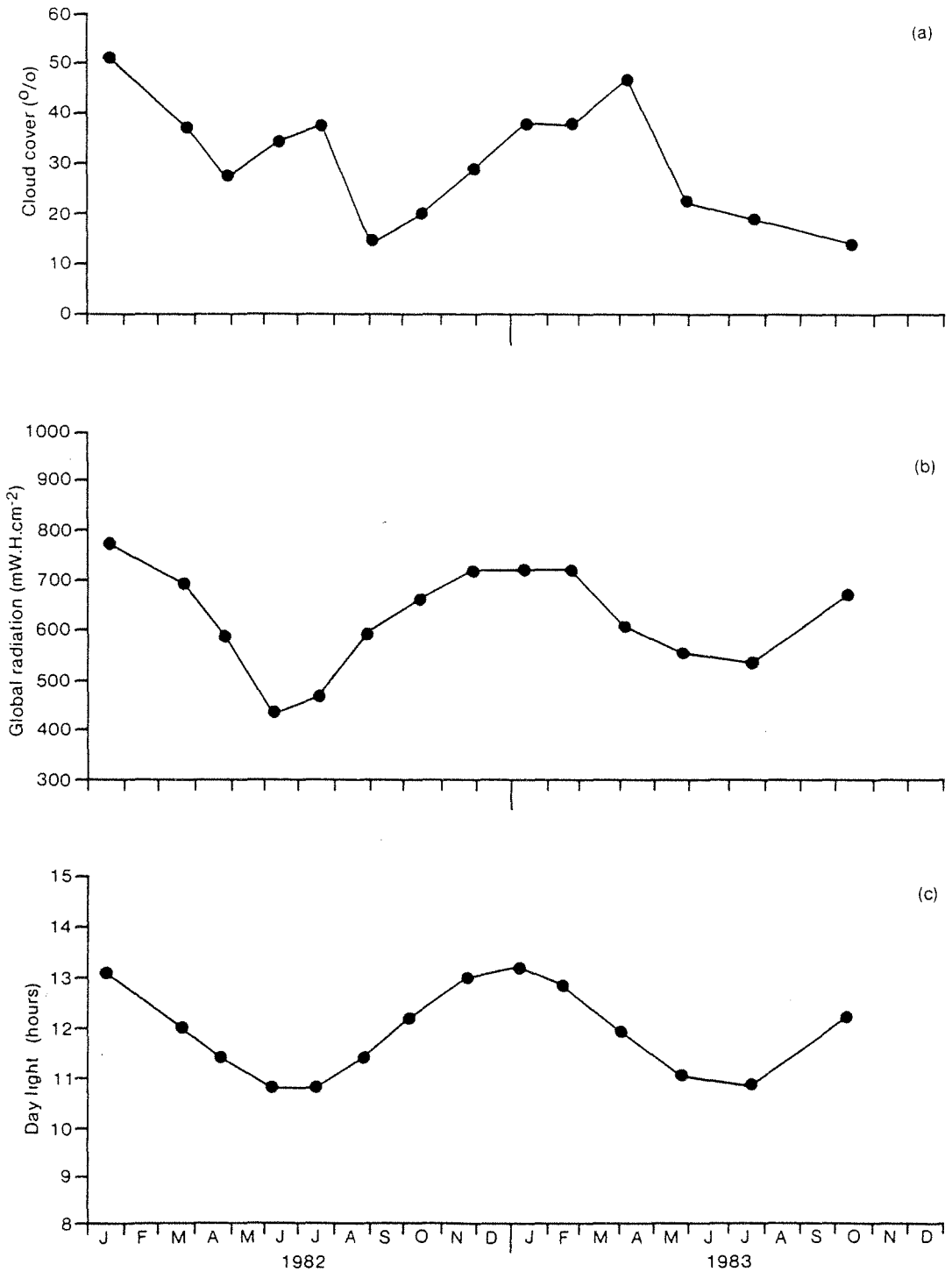


Figure 2.9 Seasonal variation in (a) mean cloud cover (b) mean global radiation and (c) mean daylight hours at Dampier.

occurring during 'winter' (Figs. 2.10 a, b, c). Water clarity at sites 2 and 3 were similar throughout the study period with vertical attenuation coefficients ranging from 0.10-0.24 m^{-1} and 0.09-0.24 m^{-1} respectively. At site 1, vertical attenuation coefficients ranged from 0.05-0.15 m^{-1}. Water clarity decreased sharply at sites 2 and 3 during November / December 1982, coinciding with dredging activities at the MOF jetty and Product Berth (Fig. 2.1). Similarly, water clarity increased sharply at these two sites when dredging concluded on February 21, 1983. The statistics in Table 2.6 indicate that significant differences in water clarity exist beween sites and seasons.

Table 2.6 Summary of ANOVA for light attenuation coefficients at sites 1, 2 and 3 during 'summer' and 'winter'.

Source of Variation	DF	SS	MS	F	P
Sites	1	0.02	0.02	24.28	0.0000*
Seasons	2	0.00	0.02	22.30	0.0000*
Seasons x Sites	2	0.00	0.00	2.47	0.0933
Residual	57	0.06	0.00		
Total	62				

* significant at the 0.05 probability level

During 'summer' the mean vertical attenuation coefficient at site 1 (x = 0.10, sd = 0.02, n = 13) was significantly lower than site 2 (x = 0.16, sd = 0.04, n = 16; t = -4.487, df= 28) and site 3 (x = 0.18, sd = 0.04, n = 15; t = -6.764, df = 27). Sites 2 and 3 were not significantly different.

During 'winter' site 1 (x = 0.08, sd = 0.01, n = 9) was significantly lower than site 3 (x = 0.11, sd = 0.03, n = 5; t = -2.875, df = 13) and site 2 (x=0.12,

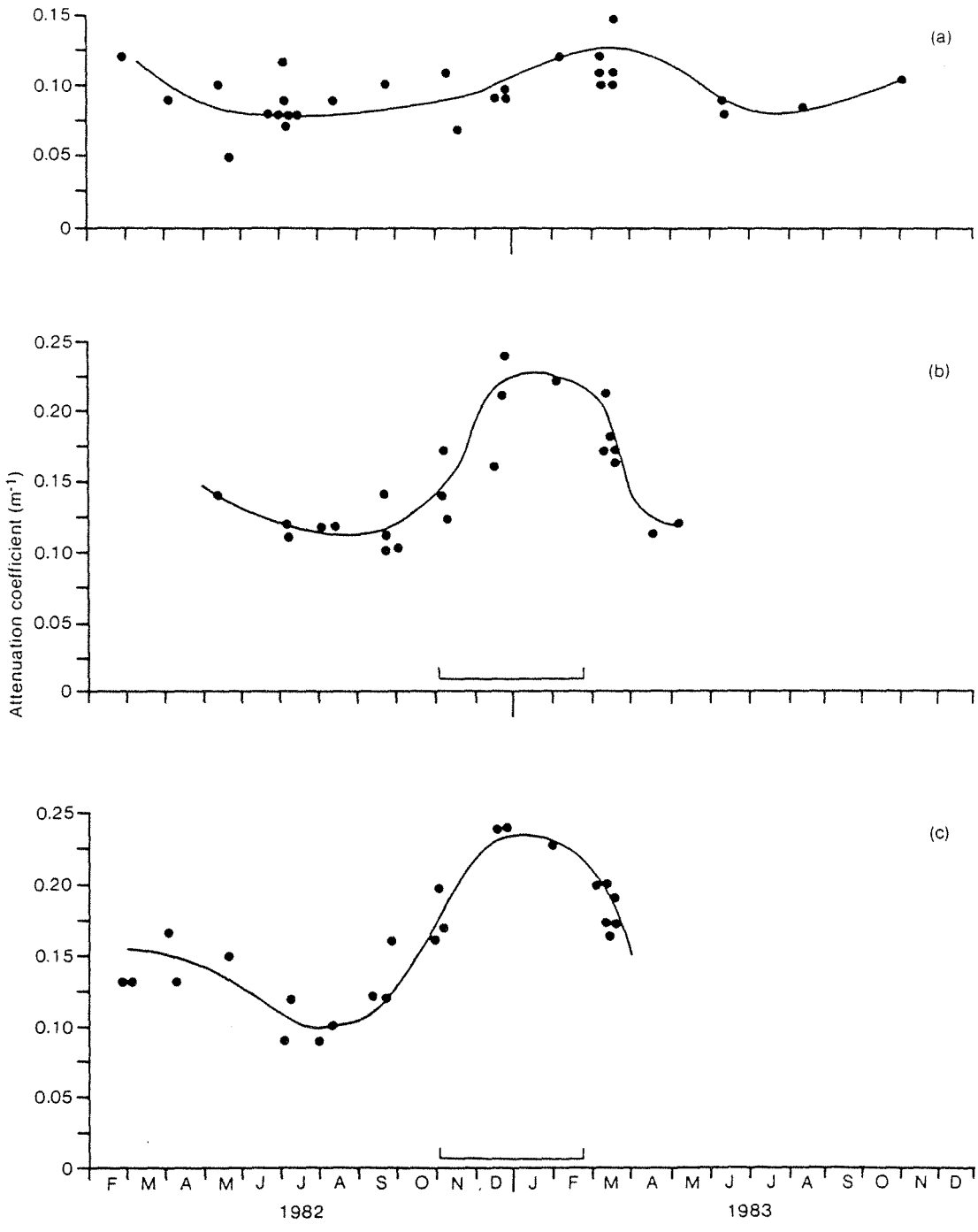


Figure 2.10 Seasonal variation in vertical light attenuation coefficients at site 1 (a) site 2 (b) and site 3 (c). Solid lines show period of dredging activity.

sd=0.01, n=5; t=-5.719, df=13). Sites 2 and 3 were not significantly different.

Temporal variation at site 1

At site 1 mean light attenuation during 'winter' (x = 0.08, sd = 0.014, n = 13) was significantly lower (t = -2.239, df = 27) than during 'summer' (x = 0.10, sd = 0.019, n = 15).

2.3.8 Computed mean photosynthetic photon flux density (PPFD)

Spatial variation

PPFD at the three sites showed a bimodal distribution with low values occurring during June 1982 and in January/February 1983. High values occurred in March/April 1982 and in the August to November period of 1982. PPFD at sites 2 and 3 were generally lower and displayed greater seasonal variation than at site 1. Similar PPFD values occurred at all sites in the June to September period of 1982 (Fig. 2.11). Significant differences existed in PPFD between sites and seasons (Table 2.7).

Table 2.7 Summary of ANOVA for PPFD at sites 1, 2 and 3 during 'summer' and 'winter'.

Source of variation	DF	SS	MS	F	P
Seasons	1	21840.7	21840.7	7.19	0.0152*
Sites	2	24690.3	12345.2	4.07	0.0390*
Seasons x Sites	2	5174.3	2587.2	0.85	0.4430
Residual	18	54625.5	3036.2		
Total	23				

*significant at 0.05 probability level

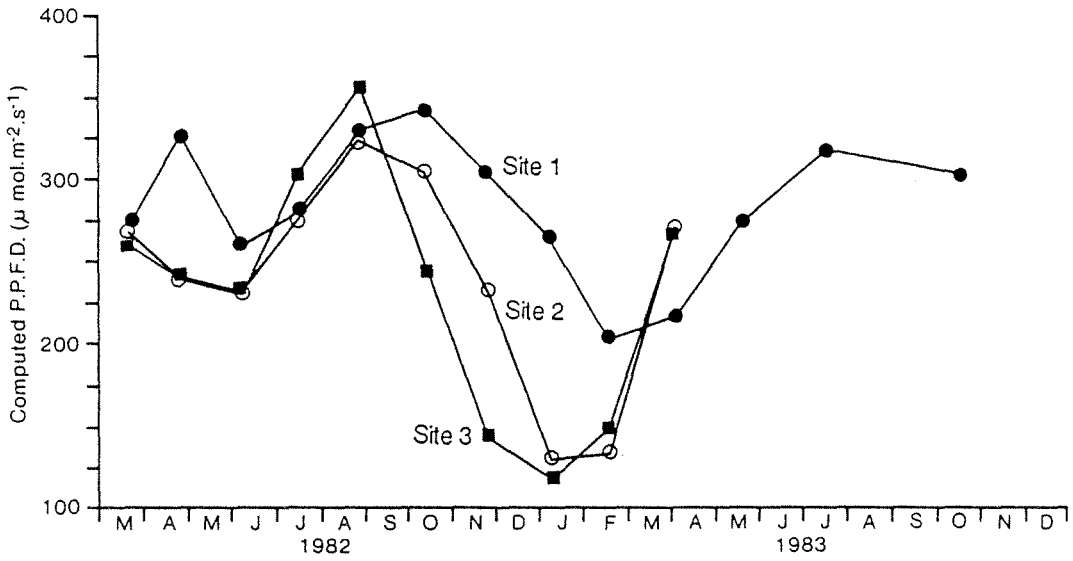


Figure 2.11 Seasonal variation in computed mean photosynthetic photon flux density at sites 1, 2 and 3.

During 'winter' PPFD was not significantly different between the three sites. During 'summer' PPFD at site 1 ($x = 277$, $sd = 60$, $n = 4$) was significantly higher ($t = 2.658$, $df = 7$) than at site 3 ($x = 165$, $sd = 59$, $n = 4$) but not significantly different to site 2 ($x = 201$, $sd = 29$, $n = 6$).

Temporal variation at site 1

At site 1, maximum PPFD occurred in late spring (October) with minima in winter (June) and in late summer (February/March). PPFD during 'winter' ($x = 297$, $sd = 29$, $n = 6$) was not significantly different than during 'summer' ($x = 271.3$, $sd = 54$, $n = 6$).

2.3.9 Wind

During 1982 and 1983, winds in the Dampier Archipelago generally blew from the east during May to July and from the west during September to February. Periods of relative calm, when winds were light and omnidirectional, occurred during the changeover periods in March/April and in August. Additionally, easterly winds in winter were strong during the day and abated at night in contrast to the westerly winds in summer, which generally blew persistently day and night (Mills and Pitt, 1985). Mean wind speed ($m\ s^{-1}$) during 'winter' ($x = 4.3$, $sd = 0.9$, $n = 7$) was significantly lower ($t = -4.966$, $df = 13$) than mean wind speed during 'summer' ($x = 6.7$, $sd = 1.1$, $n = 7$).

2.3.10 Waves

Wave energy at the offshore and inshore sites

The outer reefs in the Dampier Archipelago are affected by long period wave action generated from temperate low pressure systems during winter and from tropical low pressure systems (ie cyclones) in summer.

Swell waves come from the west in winter and from west to north in summer depending on whether cyclones cross the coast to the north or south of the archipelago . Under cyclonic conditions swell waves can penetrate into Mermaid Sound as far south as Dampier. In general, however, while the outer peripheral reefs of the archipelago are affected by constant swell action the inner regions of Mermaid Sound are more commonly affected by wind waves. Wave energy during 1982 and 1983 at the offshore site (W_1) have a bimodal distribution with peak mean wave energies of about 1100 J m^{-2} occurring in January and July, and associated with tropical and temperate low pressure systems respectively. These maxima were approximately 6x and 18x higher respectively, than wave energy at the inshore site (W_3) during the same periods (Fig. 2.12a). Mean wave energy at the offshore site was about 15x higher during 'winter' and about 4x higher during 'summer' than mean wave energy at the inshore site. Significant differences in mean wave energy existed between the offshore and inshore sites (Table 2.8).

Table 2.8 Summary of ANOVA for wave energy at the offshore and inshore sites during 'summer' and 'winter'.

Source of variation	DF	MS	SS	F	P
Seasons	1	81652.1	81652.1	1.90	0.1933
Sites	1	917285.1	917285.1	21.34	0.0006*
Seasons x Sites	1	152295.1	152295.1	3.54	0.0843
Residual	12	515898.2	42991.5		
Total	15				

* significant at the 0.05 probability level

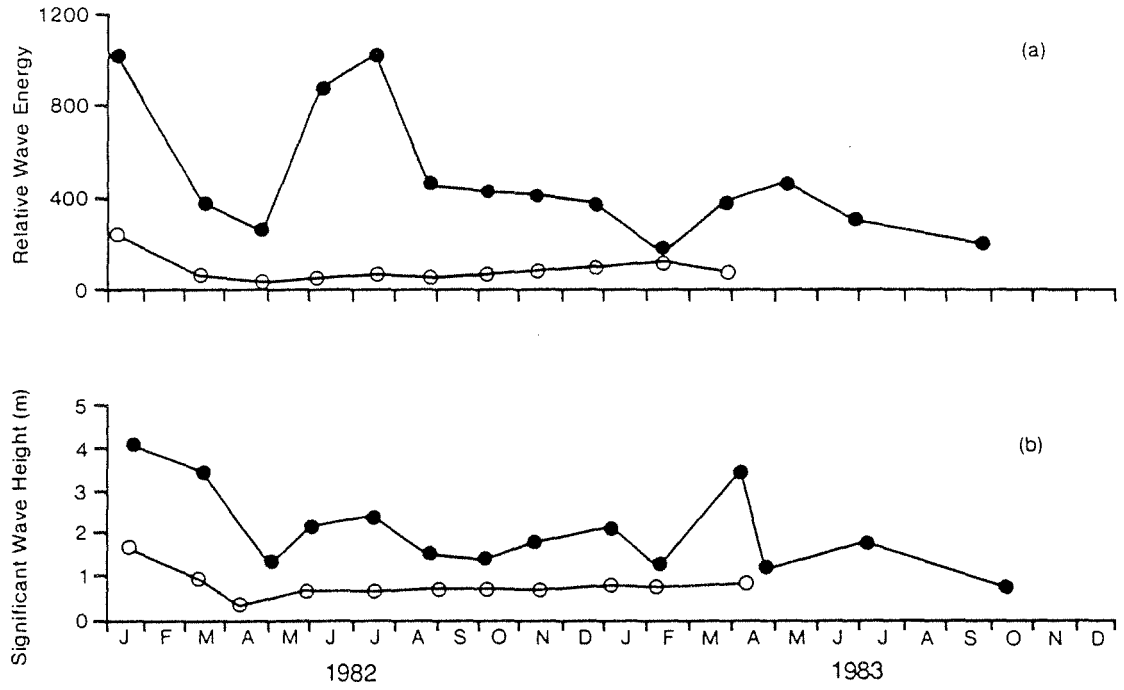


Figure 2.12 Seasonal variation in (a) relative mean wave energy and (b) maximum significant wave height at the offshore (●) and inshore (○) sites in the Dampier Archipelago.

Temporal variation in wave energy at the offshore site

Wave energy at the offshore site showed a bimodal distribution with periods of high energy occurring in January of 1982 and in June and July of 1982 (Fig. 2.12a). Periods of low wave energy occurred during March to May of 1982 and from September 1982 to October 1983. Mean wave energy for the offshore site during 'winter' (x = 621, sd = 344, n = 6) was about 2x the mean during 'summer' (x = 363, sd = 134, n = 6) although these mean values were not significantly different.

Maximum significant wave height at the offshore and inshore sites

Maximum significant wave heights (H_s) during the study period at the inshore site off Withnell Bay (W_3) was lower and less variable than at the offshore site near Legendre Island (W_1) (Fig. 2.12b). Significant wave height exceeded 1 m at Withnell Bay during a cyclone in January 1982. Peak significant wave heights at the offshore site were recorded during swell activity generated by cyclones (between December to April) although the maximum significant wave height in May (2.29 m) and July (2.52 m) 1982 was higher than during January 1983 (2.12 m) when a cyclone occurred (T.C. Jane). The statistics in Table 2.9 indicate that significant differences in maximum significant wave height existed between the offshore and inshore sites.

Table 2.9 Summary of ANOVA for maximum significant wave height at the offshore and inshore sites during 'summer' and 'winter'.

Source of variation	DF	MS	SS	F	P
Seasons	1	0.05	0.05	0.35	0.5637
sites	1	4.28	4.28	31.21	0.0001*
Seasons x Sites	1	0.31	0.312	2.24	0.1600
Residual	12	1.65	0.14		
Total	15				

* significant at the 0.05 probability level

Temporal variation in H_S at the offshore site

Mean maximum significant wave heights at the offshore site during 'summer' (x=1.74, sd=0.92, n=6) and winter' (x = 1.77, sd = 0.53, n = 6) were not significantly different.

2.3.11 Correlation of environmental parameters

Correlation coefficients (r) between the mean values of environmental parameters for each sampling period at site 1 between April 1, 1982 and November 15, 1983 (n = 12) are summarised in Table 2.10. Although a significant correlation does not necessarily imply causality, possible causal relationships and cross correlations between variables are identified and discussed below.

Table 2.10 Correlation coefficient matrix for environmental parameters at site 1. (1, mean temperature; 2, mean salinity; 3, mean PPFD; 4, mean global radiation; 5, mean daylight hours; 6, mean maximum significant wave height; 7, mean wave energy; 8, mean cloud cover).

VAR								
1	1.0000							
2	0.7462	1.0000						
3	-0.5412	-0.2620	1.0000					
4	0.6907	0.6087	-0.0651	1.0000				
5	0.7086	0.6829	-0.2017	0.9430	1.0000			
6	-0.0676	-0.0818	-0.4248	-0.4867	-0.3424	1.0000		
7	-0.5836	-0.3144	-0.0127	-0.7418	-0.5305	0.4963	1.0000	
8	0.4896	0.4206	-0.7890	-0.0212	0.2017	0.7246	0.2792	1.0000
	1	2	3	4	5	6	7	8

If $r \geq 0.576$ then r is significant at the 0.05 probability level.

2.4 DISCUSSION

2.4.1 Seawater temperatures

Seawater temperatures during 1982-1983 had a recorded range of 14.1° C (at site 3) with a minimum of 18.6° C in July 1982 and a maximum of 32.6° C in March 1983. A range of 15.3° C recorded on an intertidal reef at Keast Island is probably close to the extremes of the temperature range in shallow, well-flushed areas of the Dampier Archipelago. Proximity to the open ocean modifies the seasonal temperature extremes on seaward, peripheral reefs resulting in a smaller annual temperature range than at more inshore reefs.

The advection of cooler ocean water into Mermaid Sound during cyclones can lower seawater temperatures markedly, and this was observed during January 1983 at sites 2 and 3 when temperatures decreased as a result of tropical cyclone Jane which occurred on January 7-9, 1983 (Fig. 2.5). Similarly, seawater temperatures, recorded by current meters deployed near site 3, dropped by 2° C on January 8, 1983 (Mills *et al.* 1986).

As expected the annual pattern of seawater temperatures in the Dampier Archipelago is correlated significantly with global radiation (Table 2. 10). However, if corresponding means for seawater temperature and global radiation are offset by one sampling period (eg mean temperature of period 8 to mean global radiation of period 7) the correlation increases from r= 0.691 to r=0.966, suggesting that the phase lag between incoming radiation and a change in seawater temperature is in the order of about 40 days.

During February and March in 1982 and 1983 bleaching (loss of zooxanthellae) occurred in some scleractinian coral species (*Acropora* spp. at all sites, *Platygyra* spp. at site 3). In March 1984 isolated incidences of bleaching were observed in many arborescent *Acropora* spp. In all cases seawater temperature exceeded 31° C. Conversely, partially bleached colonies (*Platygyra* spp. at site 3; *Acropora* spp. at site 2) were observed during July 1982 and 1984, respectively, when seawater temperatures were approximately 19° C. By September, in both years, these colonies had regained zooxanthellae and appeared healthy. Additionally, the presence of bleached coral colonies in the Dampier Archipelago was recorded by Marsh (1978) during a survey of corals in July 1978.

The expulsion of zooxanthellae or 'bleaching' can be triggered by stress (Goreau, 1964; Bak,1978), and bleaching has been often associated with elevated sea temperatures (Shinn, 1966; Jokiel and Coles, 1974, 1977; Coles,

1975; Lasker *et al.* 1984; Glynn, 1983, 1984, 1985; Japp, 1985). Oliver (1985) hypothesised that a synergistic effect between high light and high temperatures may cause this stress and Harriot (1985) and Fisk & Done (1985) suggested the possibility that UV light was implicated in bleaching events on the Great Barrier Reef. Many studies have shown that the optimum seawater temperature for coral growth of many species is between 25-30° C (Vaughan and Wells, 1943; Shinn, 1966; Glynn and Stewart, 1973; Jokiel and Coles, 1977; Highsmith, 1979). Gladfelter (1984) suggests that the optimum range for staghorn *Acropora* spp. is 26-29° C and agrees with the findings reported later in this thesis where maximum growth rates of the staghorn coral *Acropora formosa* in the Dampier Archipelago occurred at temperatures of 27-28° C. In contrast, Yap and Gomez (1981) attributed reduced growth of *Acropora pulchra* in the Philippines to the effect of supra-optimal (> 30° C) sea temperatures and Shinn (1966) attributed a decrease in the linear extension of *Acropora cervicornis* to seawater temperatures falling below 26° C. Wells (1957) states that '... no significant reefs occur where temperatures during the year fall below about 18° C except for very short periods' and, in the Persian Gulf, Kinsman (1964) found flourishing reefs that had a seasonal range of 16 - 40° C. In the Dampier Archipelago seawater temperatures can exceed 30° C for extended periods. For example, between December 17, 1981 and February 21, 1982, seawater temperatures near site 3 were over 30° C on 59 days (or about 87% of the time) and occasionally exceeded 32° C. Most studies indicate that bleaching occurs at temperatures of about 30° C or greater (eg Shinn, 1966; Jokiel and Coles, 1974, 1977; Coles, 1975; Lasker *et al.* 1984; Glynn, 1985; Oliver, 1985) and the presence of bleached corals in the Dampier Archipelago during summer and winter indicate that some species are under stress. Other marine invertebrates including the crown-of-thorns starfish *Acanthaster planci*,

have been observed showing signs of stress during periods of high seawater temperatures in the Dampier Archipelago (L M Marsh, pers. comm).

2.4.2 Salinity

Seawater salinity in the Dampier Archipelago rarely exceeds $2^{o}/_{oo}$ above average tropical ocean values of about $35^{o}/_{oo}$ (Kinsman, 1964) and the seasonal variation is correlated significantly with global radiation (Table 2.10). This suggests that the higher salinities that occur throughout the summer at all sites were due to higher evaporation rates (Table 1.1) in summer and that the differences in salinity between site 1 and sites 2 and 3 were due to the closer proximity of lower salinity ocean water to site 1 and the longer residence time of seawater in the inner waters (sites 2 and 3) of the archipelago . The low annual rainfall in this region, about 300 mm (Table 1.1) is unlikely to have any significant effect on the salinity of seawater in the Dampier Archipelago. The salinities reported here are well within the range of salinities on reefs where corals flourish and are close to the optimum range of 34-36 $^{o}/_{oo}$ (Kinsman, 1964).

2.4.3 Sediment deposition

Sediment deposition at sites 2 and 3 showed a marked seasonal variation, with maxima at both sites occurring during summer. In contrast, sediment deposition rates at site 1 were relatively constant. Before November 1, 1982 mean sediment deposition rates at site 3 were significantly correlated with sites 1 ($r=0.82$, $p<0.05$) and 2 ($r=0.88$, $p<0.05$) for simultaneous deployments. Between November 1982 and March 1983 site 3 was significantly correlated with site 1 ($r=0.94$, $p<0.05$) but not with site 2 ($r=0.32$, $p>0.05$). In addition, sediment deposition rates at site 2, before November 1, were similar to site 3 but between November 1982 and March

1983 sediment deposition rates at site 2 were approximately twice those at site 3 over simultaneous periods. The presence of a significant correlation in sediment deposition rates between sites 2 and 3 before November 1, 1982 and the absence of significant correlation after that date, suggest that the causal factor(s) relating to sediment deposition at one or both of these sites had altered.

The high levels at site 2 coincided with the commencement of dredging and dumping activities in the vicinity of the MOF jetty and the Product Berth (Fig. 2.1). From November 1-27, 1982 140 000 m^{-3} of dredge spoil was dumped into Mermaid Sound about 1.5 km from the MOF jetty. A further 400 000 m^{-3} of dredge spoil was dumped in the upper area of No Name Creek between December 1, 1982 and February 21, 1983. In December 1982 and February and March 1983, sediment plumes, originating from No Name Creek near site 3, were observed to extend to Conzinc Island, a distance of about 8 km. The significant correlation before and after November 1 and the constant difference in sediment deposition rates (about 38 g $m^{-2}d^{-1}$) between sites 1 and 3 during September 1982 to April 1983, suggest that the rate of sediment deposition at site 3 was not greatly affected by the dredging activities. Field observations of the spoil plume support this conclusion. It is assumed that site 1 was not affected due to the distance (over 15 km) and location, in relation to water circulation patterns, of this site to the dredging and dumping acctivities (see Fig. 1.3). These data and observations suggest that the high levels of sediment deposition at site 2 were the result of the dredging and dumping activities.

Correlation coefficients (r) between total and refractory sediment deposition rate and wind and wave parameters at site 3, between February 21, 1982 and December 6, 1982 (n = 11) are summarised in Table 2.11.

Table 2.11 Correlation coefficient (r) matrix between sediment deposition rates and wind and wave parameters at site 3 for each deployment period.

1, mean total sediment deposition rate; 2, mean refractory sediment deposition rate; 3, mean wind speed; 4, mean wave energy.

Var				
1	1.0000			
2	0.9917	1.0000		
3	0.7513	0.7809	1.0000	
4	0.8069	0.7937	0.7985	1.0000
	1	2	3	4

If $r \geq 0.602$ the r is significant at 0.05 probability level.

Significant correlations exist between mean sediment deposition rate (total and refractory fractions) and mean wind speed and wave energy. In addition, mean wind speed is significantly correlated with mean wave energy. This latter correlation suggests that the waves at site 3 were locally generated wind waves and not swell. This conclusion is supported by the generally low period of peak spectral ordinate (<10 s) at this site (Steedman and Associates, 1983) and field observations over a three year period during which swell was only observed in the vicinity of site 3 during cyclonic activity. This suggests that the sediment deposition rates at site 3 were related to wind speed through the resuspension of sediments by wind waves.

During the winter months winds were generally from the east and had a lower mean wind speed than during summer due to a pronounced diurnal land/sea breeze pattern (Mills and Pitt, 1985). Thus lower mean wind speed

and small fetch (at sites 2 and 3) during 'winter' probably resulted in lower sediment resuspension by wind waves at these inshore sites and probably account for the relatively low sediment deposition rates recorded at sites 2 and 3 during this period. Conversely, in summer, the higher mean wind speed of the more persistent westerly winds and longer fetch resulted in higher sediment deposition rates at site 3. At site 2, the effects of the dredging activities were superimposed on the higher 'summer' 'background' rates resulting in very high rates of sediment deposition at this site during November, 1982 to March, 1983.

For the offshore site (1) correlation coefficients between total and refractory sediment deposition rates and wind and wave parameters between May 8, 1982 and August 27, 1983 (n = 12) are summarised in Table 2.12.

Table 2.12 Correlation coefficient matrix between sediment deposition rates and wind and wave parameters at site 1 for each deployment period.

1, mean total sediment deposition rate; 2, mean refractory sediment deposition rate; 3, mean wind speed; 4, max. significant wave height; 5, mean wave energy.

Var					
1	1.0000				
2	0.8963	1.0000			
3	0.2276	0.2129	1.0000		
4	0.6647	0.5958	-0.0055	1.0000	
5	0.6890	0.6814	-0.0526	0.6682	1.0000
	1	2	3	4	5

If $r \geq 0.576$ then r is significant at the 0.05 probability level.

At site 1 significant correlations exist between total and refractory sediment deposition rate and maximum significant wave height and mean wave energy. In addition, significant correlations exist between maximum wave height and mean wave energy. The absence of a significant correlation between mean wind speed and mean wave energy suggest that the waves were not generated locally, but were long period waves (swell); the rate of sediment deposition at site 1 was related directly to the size and duration of these swell waves. For example, during a 48 day sampling period in March/April 1983 mean total sediment deposition rate was 326.5 g $m^{-2}d^{-1}$. Mean wind speed and maximum significant wave height for this period were 5.9 ms^{-1} and 3.4 m, respectively. In contrast, during a 35 day period from November 1 1982, a mean total sediment deposition rate of 35.2 g $m^{-2}d^{-1}$ was recorded when mean wind speed was slightly lower at 5.7 m s^{-1} and maximum wave height was markedly lower at 1.5 m. Furthermore the mean wave energy during these two periods was similar, suggesting that a high proportion of the sediment trapped during the March/April 1983 period occurred as a result of two days of high wave activity that was generated from tropical cyclone Lena.

The lack of seasonal differences in sediment deposition at site 1 was a result of the bimodal distribution of the offshore wave parameters (Fig. 2.12). This was due to large, infrequent swells generated in summer from tropical cyclones and to the lower, more persistent winter swells generated from temperate low pressure systems further south.

During 'winter' mean sediment deposition rates (refractory fraction) at the 3 sites were not significantly different, and ranged from about 10 g $m^{-2}d^{-1}$ at the offshore site (1) to about 22 g $m^{-2}d^{-1}$ at sites 2 and 3. These levels appear to approximate 'natural' levels of sediment deposition at these sites

during winter. During 'summer' mean sediment deposition rates at all 3 sites were significantly different with site 2 > site3 > site 1. At sites 1 and 3, during non-cyclonic conditions in 'summer', mean sediment deposition rates were, respectively, 14 g $m^{-2}d^{-1}$ and 52 g $m^{-2}d^{-1}$, which, again appear to approximate 'natural' levels of sediment deposition on the outer and inner reefs respectively, of the archipelago. At site 2, the mean sediment deposition rate during the same period was 94 g $m^{-2}d^{-1}$, presumably representing artifically-elevated levels of sediment deposition at this site during the 'summer' of 1982/1983. The rates of sediment deposition at this site for 3 sampling periods during the dredging operations were 115 g $m^{-2}d^{-1}$, 119 g $m^{-2}d^{-1}$ and 114 g $m^{-2}d^{-1}$. These levels are higher than the sediment deposition rates that were measured at sites 1 (56 g $m^{-2}d^{-1}$) and 3 (94 g $m^{-2}d^{-1}$) during March/April 1983 when a cyclone (T. C. Lena) occurred. These data suggest that sediment deposition rates over a similar time scale (ie 3 months) and magnitude as the rates measured at site 2 during the dredging operations are unlikely to occur naturally at the inshore reefs and even less likely to occur naturally at the offshore reefs in the Dampier Archipelago. Field observations support the assumption that although extremely high levels of sediment resuspension occur in the Dampier Archipelago during cyclonic conditions, a high proportion of this sediment settles within a few days of the wind and waves abating.

It has long been known qualitatively that high levels of sedimentation are detrimental to coral growth and survival, and is a major control on reef growth (Wood-Jones, 1910). On reefs in the Panama sedimentation ranged from 32-59 g $m^{-2}d^{-1}$ (Glynn, 1977) and in Jamaica, Dodge *et al.* (1974) and Aller and Dodge (1974) found the growth of *Montastrea annularis* was inversely related to sediment resuspension rates ranging from 110 to 47 g $m^{-2}d^{-1}$. Clear water reefs with a high cover of live corals in Puerto Rico (Loya,

1976) and in New Guinea (Kojis and Quinn, 1984) had average sedimentation rates of about 30 g $m^{-2}d^{-1}$ and 10 g $m^{-2}d^{-1}$ respectively, while turbid reefs with a lower cover of live corals had average sedimentation rates of about 150 g $m^{-2}d^{-1}$ with maximum rates of 190 g $m^{-2}d^{-1}$ in Puerto Rico and 240 g $m^{-2}d^{-1}$ in New Guinea. Kojis and Quinn (1984) also found the fecundity of *Acropora palifera* was inversely related to the rate of sedimentation. Charuchinda and Hylleberg (1984) found that mean sedimentation rates on a fringing reef in Thailand ranged from 204 g $m^{-2}d^{-1}$ in June to November (maximum 250 g $m^{-2}d^{-1}$) to 110 g $m^{-2}d^{-1}$ in December to April and coincided approximately with minimum and maximum growth rates of *Acropora formosa* respectively. These data suggest that the average total sedimentation rates on clear water coral reefs with a high cover of corals is less than 50 g $m^{-2}d^{-1}$ and that where average sedimentation rate exceeds 100 g $m^{-2}d^{-1}$, reductions in growth rates, fecundity and live coral cover may occur. In the Dampier Archipelago mean total sediment deposition rate on the offshore reef at site 1 was 58 g $m^{-2}d^{-1}$ (including 1 sampling period of 326 g $m^{-2}d^{-1}$) and 100 g $m^{-2}d^{-1}$ at site 3 suggesting that the inshore corals may be vulnerable to small increases in suspended sediment load. Mean total sediment deposition at site 2 during the dredging operations was about 262 g $m^{-2}d^{-1}$ and coincided with a decrease in the linear extension of *Acropora formosa* at this site. Twelve months after the dredging activities ceased most of the corals at this site, including colonies estimated to be over 10 years old, were dead.

2.4.4 Vertical attenuation coefficients

The attenuation of light in the water column is due to absorption by water molecules, phytoplankton, inorganic particulate matter such as clay or silt and also to reflection and scattering by particulate matter. Light can

also be absorbed by dissolved organic molecules commonly called 'yellow colouring matter', 'gilvin' or 'gelbstoff' (see Kirk, 1977).

Forde (1985) measured light attenuation coefficients at 23 sites throughout Mermaid Sound on six occasions from April 1982 to March 1983 and analysed spatial and temporal patterns in water clarity. In general water clarity was higher during winter than summer with a gradient all year round from inshore (low water clarity) to offshore (high water clarity). He also found a significant linear relationship between total and organic suspended matter and light attenuation coefficients measured in March but not in December 1983. The lack of a significant relationship in December was due probably to the patchy distribution of blooms of the planktonic blue-green alga *Trichodesmium erythraeum* that occurred at the time. The intercept value (ie when total suspended material ~0) for the relationship in March was ~0.05 which is within the range (0.04-0.05)of the lowest light attenuation coefficients measured by Forde (1985) for the adjacent offshore waters of the Dampier Archipelago in winter. This range corresponds to a photic zone of 40 - 50 m and is probably close to the maximum light penetration for the nearshore and adjacent offshore waters in this area..

In this study water clarity was significantly lower during 'summer' at all sites and was due to higher biological productivity, including widespread 'blooms' of the tropical, planktonic blue-green alga *Trichodesmium erythraeum* (Creagh,1985), and increased turbidity due to local resuspension of sediment by wind waves. Throughout the study period, water clarity was significantly higher at the offshore site (1) than at the two inshore sites (2 and 3) and was due to higher rates of resuspension of fine material at sites 2 and 3 and the dredging operations that occurred in the vicinity of sites 2 and 3 from November 1982 to February 1983.

Light attenuation coefficients provide a useful means to quantify

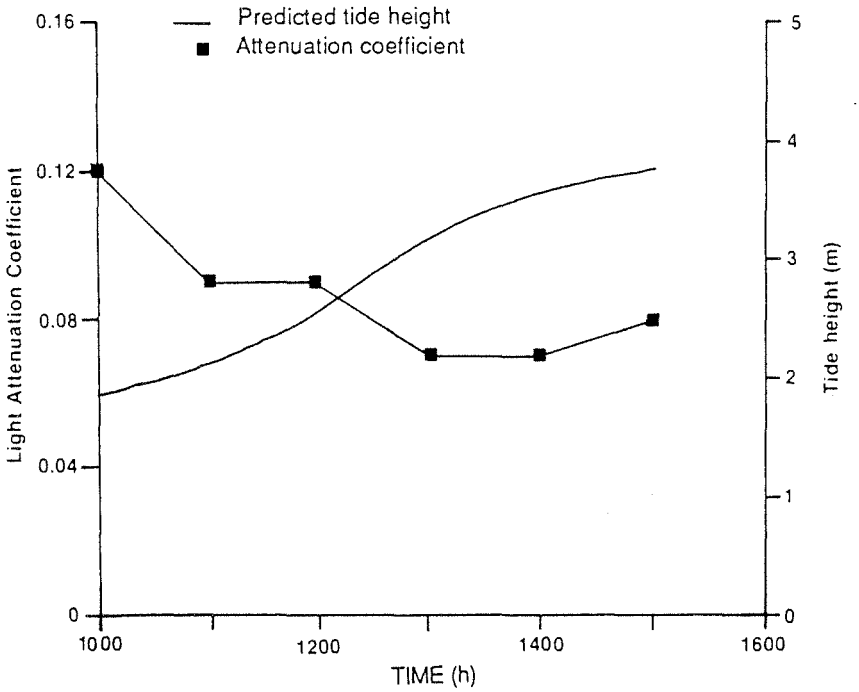


Figure 2.13 Variation in light attenuation coefficient during a flood tide on June 28, 1982 at site 1.

water clarity and the depth of the photic zone. However, the relatively low density of data in Figure 2.10 and the large amount of scatter indicate that these data should be regarded as an approximation of spatial and temporal trends in light penetration at these sites. In the Dampier Archipelago this short term variability is due to a number of factors. Turbidity patterns in the vicinity of sites 2 and 3 can vary considerably over a day and within a few kilometres. Sediments in the vicinity of these sites are extremely fine, with a high percentage of clay and silt (see 2.3.3) which are easily resuspended by wind waves; several hours of strong winds can cause marked changes in water clarity in this area. In addition strong currents are generated in the channels between islands by spring tides and can cause large turbidity plumes over extensive areas. At the offshore site (1) water clarity is influenced by turbid water from Mermaid Sound on ebb tides and by clear oceanic water on flood tides and probably accounts for much of the short term variability at this site (Fig. 2.13).

2.4.5 Photosynthetic Photon Flux Density (PPFD)

Tropical reef-building corals contain large concentrations of the endosymbiotic dinoflagellate *Gymnodinium microadriaticum* and algal photosynthesis contributes significantly to coral metabolism (Muscatine and Cernichiari, 1969; Smith *et al.* 1969; Muscatine et al.1972; Muscatine, 1980) and calcification (Goreau, 1959; Goreau and Goreau, 1959; Vandermeulen *et al.* 1972; Chalker and Taylor, 1975). Chalker and Dunlap (1983) found that photoadaptation of many *Acropora* spp. over depths of 1 to 38 m resulted in relatively constant diel photosynthetic rates on clear days. These depths corresponded to 83% and 5.8% of transmitted surface light respectively.

In the Dampier Archipelago, mean computed PPFD was not

significantly different between the sites apart from sites 1 and 3 in 'summer'. In addition the computed mean PPFD during 'summer' and 'winter' at site 1 were not significantly different. This low spatial and temporal variation in PPFD is attributable to several factors. In summer, higher global radiation and cloud cover and lower water clarity at site 1 contribute to the absence of significant seasonal variation. A combination of deeper and clearer water at the offshore site (site 1) in comparison to the shallower, more turbid inshore sites (2 and 3) contributes to the low spatial variability. The minimum mean value of computed PPFD during daylight was 118 μmol m^{-2} s^{-1} (~10% of mean irradiance on a cloudless day in December in the Dampier Archipelago) suggesting that even during the dredging activities in the vicinity of sites 2 and 3, light was not significantly limiting coral growth during this study (Chalker and Dunlap,1983).

The accuracy of computed PPFD depend partly on the estimation of mean light attenuation coefficients for each sampling period which, as mentioned in the previous section, at best only approximate the light penetration at these sites. To verify the results of the light simulation program light data loggers were deployed over two 12 day periods in August and November 1983 at sites 1 and 2. Although instrument malfunction at site 2 during August precluded 'winter' comparisons, the measured PPFD at sites 1 and 2 between November 3-15, 1983 were compared (Fig. 2.14).. Mean values during daylight hours at sites 1 (mean depth 5.5 m) and 2 (mean depth 3.5) were 420 μmol m^{-2} s^{-1} and 400 μmol m^{-2} s^{-1} respectively, and were not significantly different. Mean computed PPFD at site 1 between August 18 and November 15, 1983 was 303 μmol m^{-2} s^{-1} (Fig. 2.11) and was calculated at a mean depth of 6.2 m. The greater depth and longer time period (ie lower mean global radiation) used to calculate computed PPFD probably account in part for the difference between computed and measured PPFD at site 1

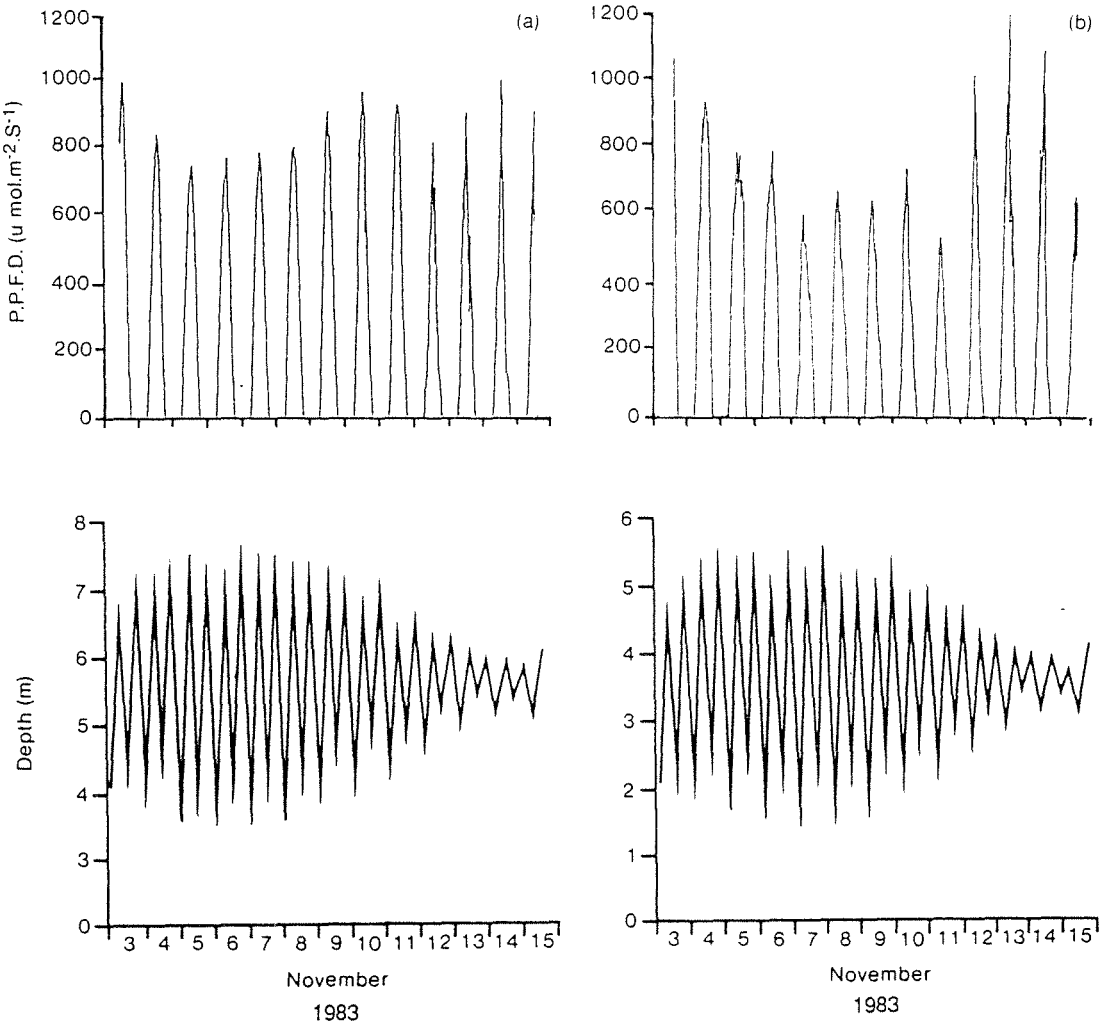


Figure 2.14 Variation in photosynthetic photon flux density and depth to sensor height at (a) site 1 and (b) site 2 between November 3-15,1983.
PPFD values were recorded continuously and each datum was integrated over 15 minutes. The light sensor was ~0.7 m above the seabed.

during this period. With this consideration in mind these results are in sufficient agreement to support the assumption that computed PPFD provide a reasonable estimate of actual PPFD and suggest that the above spatial comparisons are valid.

2.4.6 Tropical cyclones

Catastrophic coral mortality can be caused by tropical storms or 'cyclones' on reefs, especially reefs dominated by branching corals, which are more fragile than massive forms (eg Stoddart, 1963; Stephenson *et al.* 1958; Glynn *et al.* 1965; Laboute, 1985). Destruction is mostly mechanical through the action of waves although the mass expulsion of zooxanthellae from corals after a storm in Jamaica was presumed to have resulted from physiological stress (Goreau, 1964).

In the Dampier Archipelago tropical cyclones occur regularly from December to April and 10 cyclones have passed within 150 km of Dampier in the 21 years to 1980 since records have been kept (Lourensz, 1981). The most severe cyclone to affect the coral reefs in the Dampier Archipelago in recent years was Tropical Cyclone Trixie which passed the Dampier Archipelago on February 19, 1975 with recorded wind gusts of 190 km h^{-1}. Two massive colonies of *Platygyra sinensis* , about 1 m in diameter and alive on the reef flat of Kendew Island (Fig.1.2) in 1974, were found on the beach in 1978 (L. M. Marsh, pers. comm.). Extensive damage to other reefs in the Dampier Archipelago were also observed during 1978 and thought to be associated with T C Trixie (L M Marsh, 1978). During this study damage to experimental corals by waves associated with cyclones occurred in January and March 1982 and in January and April of 1983. However, damage to the reefs in general was not extensive.

CHAPTER THREE

CORAL GROWTH METHODS AND EVALUATION OF EXPERIMENTAL MANIPULATION

3.1 INTRODUCTION

Skeletal accretion or growth of scleractinian corals has been investigated by numerous methods, including long-term observation, radiometric analysis of skeletal banding, vital staining with sodium alizarin sulphonate and radiotracer techniques (see Buddemeier & Kinzie, 1976). Diurnal and seasonal variations in branch elongation rate have been measured by time-lapse photography (Barnes & Crossland, 1980) and Shinn (1966) and Charuchinda and Hylleberg (1984) used rubber bands and pieces of wire respectively on branches of arborescent *Acropora* spp. as a reference point for measuring branch extension rates. Many of these methods require extensive sample manipulation and consequently, possible modification of 'normal' growth rates.

There is general agreement that shock or injury may retard calcification, although little documentation of this effect exists; Wood-Jones (1907) suggested that localised injuries may activate a more rapid 'repair-growth' response. Thus the growth of coral may be possibly retarded or promoted depending on the degree of sample manipulation. The extent and duration of any such alteration in growth rate is unpredictable and becomes increasingly important as the time scale of the experiment is reduced.

Many coral growth experiments are concerned with the effects of particular factors such as temperature and light on growth (eg Buddemeier & Kinzie, 1976; Gladfelter, 1985) and providing each experimental treatment is consistent, 'relative' coral growth rates can be used to assess these effects.

Although the use of 'relative' growth rates precludes the necessity to examine the effects of sample manipulation, it prevents the estimation of 'absolute' growth rates that more readily facilitate the determination of quantitative relationships between coral growth and environmental factors. In addition, if temporal comparisons between the growth of a species are made, some knowledge of the effects of sample manipulation (eg the application of tags at the beginning of an experiment) is necessary to avoid incorrect interpretations. Furthermore comparisons between different geographical locations are more meaningful if 'absolute', rather than 'relative', coral growth rates are estimated.

In this study, 'real time' growth of branching corals has been measured *in situ* by staining and tagging to provide a reference point from which subsequent growth can be measured, or by measuring increases in the projected area of colonies by calibrated photography. In contrast, growth rates of massive corals have been estimated retrospectively from skeletal density bands identified by X- radiography. 'Real time' methods involve varying degrees of sample manipulation; to assess the effects of this manipulation a series of experiments were undertaken. The results of these experiments are considered within the context of medium term (30 to 80 days) growth periods used in this study, and the conclusions drawn from these data refer only to this time scale. Possible effects of sample manipulation on coral growth over a time scale of hours to days would be lost in the high inherent variability of coral growth when measured over a time scale of weeks or months. However, the purpose of these experiments described in this chapter was to identify and quantify possible systematic effects on coral growth relevant to this study.

In this thesis a 'colony' is defined as a collection of coral polyps and coensarc which share a common skeleton. However in species that

reproduce both sexually and asexually different colonies of the same species may or may not be different genotypes. In areas of the Dampier Archipelago, such as site 1 (Fig. 2.1), where reproduction of fragile species like *Acropora formosa* probably occurs both asexually (by fragmentation) and sexually, so-called discrete colonies of this species may consist of multiple clones of a few genotypes (asexual reproduction dominant), many colonies or 'individuals' of different genotypes (sexual reproduction dominant) or more probably somewhere in between.

Thus investigating the inter-colony variation in the growth of this species may be an estimate of the variation of growth between clones, genotypes or a combination of the two. Although the distinction between colonies and individuals is important for genetical studies of corals (see Stoddart, 1984) it is of less concern here as the use of multiple colonies in growth studies is an attempt to provide a reproducible estimate of mean growth for a particular species. This is based on the assumption that different colonies, whether clones or individuals, may have different rates of growth and the use of mutiple colonies will minimise this variation if the data is pooled.

Definitions and units of coral growth used in this study are summarised in Table 3.1.

Table 3.1 Definitions and units of coral growth used in this study

Growth	
Acropora formosa	a measured increase in linear extension of the axial corallite of peripheral apical branches (mm).
Acropora hyacinthus	(circular colonies) a computed increase in radial extension (mm) from measured increases in projected area (mm^2).
Acropora hyacinthus	(irregular colonies) a measured maximum increase in radial extension (mm).
Pocillopora damicornis	a measured maximum increase in length of peripheral apical branches (mm).
Platygyra daedalea	A measured annual growth along the axis of maximum vertical growth (mm).
Growth rate	a standardised measure of growth (mm per 30 days).

3.2 MATERIALS AND METHODS

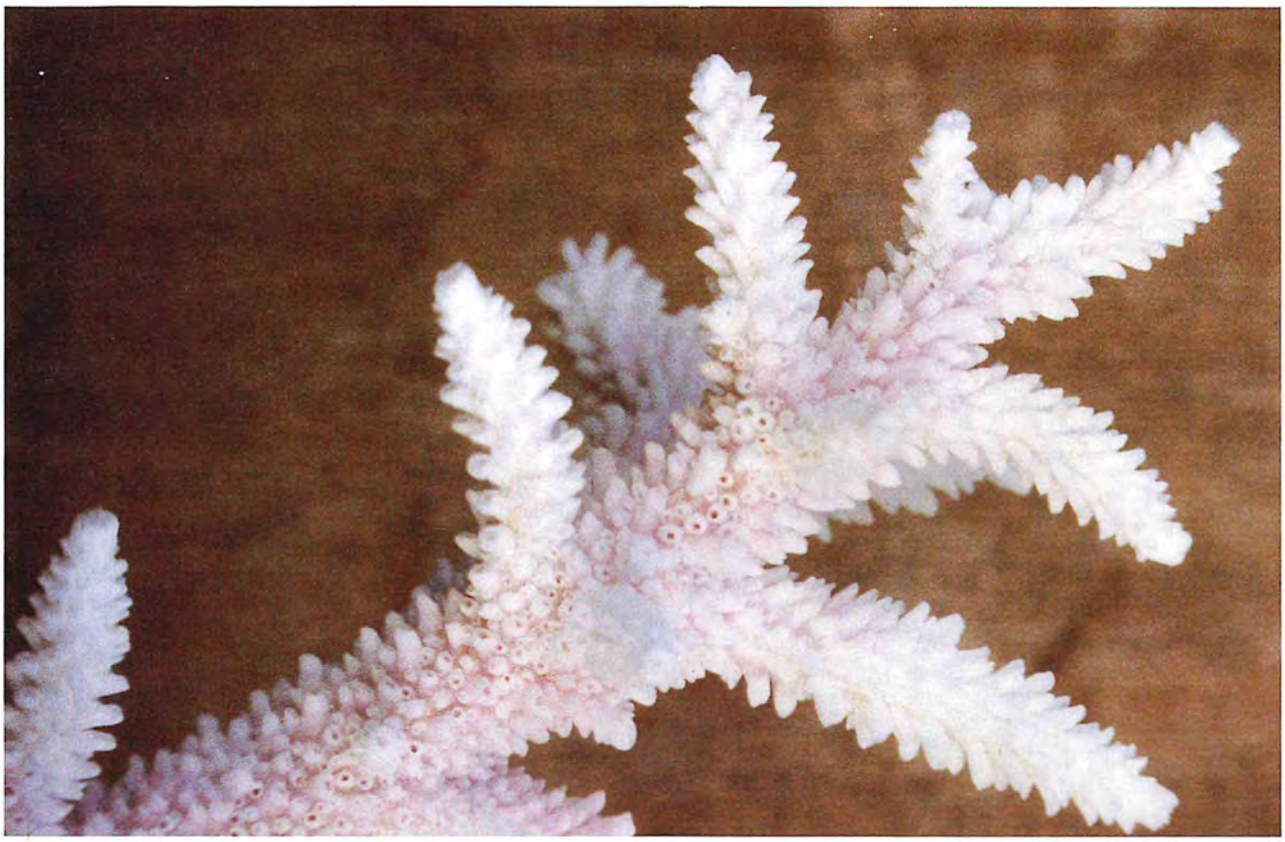
3.2.1 Coral Growth

Staining with Alizarin Red S

Coral branch linear extension rates were estimated by marking living colonies with the vital stain sodium alizarin sulphonate [$C_6H_4COC_6H(OH_2(SO_3Na))CO$] which is incorporated into the skeleton of the coral and from which subsequent growth of the branch is measured (Barnes, 1970, 1972; Lamberts, 1974; Fig.3.1). Coral colonies were isolated *in situ* from the surrounding seawater in large, clear plastic bags or in plastic-covered stainless steel domes (0.9 m diameter, 0.7 m high). After injection of the stain to a final concentration of about 10 mg l^{-1}, colonies were exposed to the stain for 3 - 6 hours. A strip of yellow 'Day Glo' with the colony identification number and date of staining, was attached to the base of each colony.

Peripheral, apical branches (Fig. 3.2) possessing zooxanthellae-free

a



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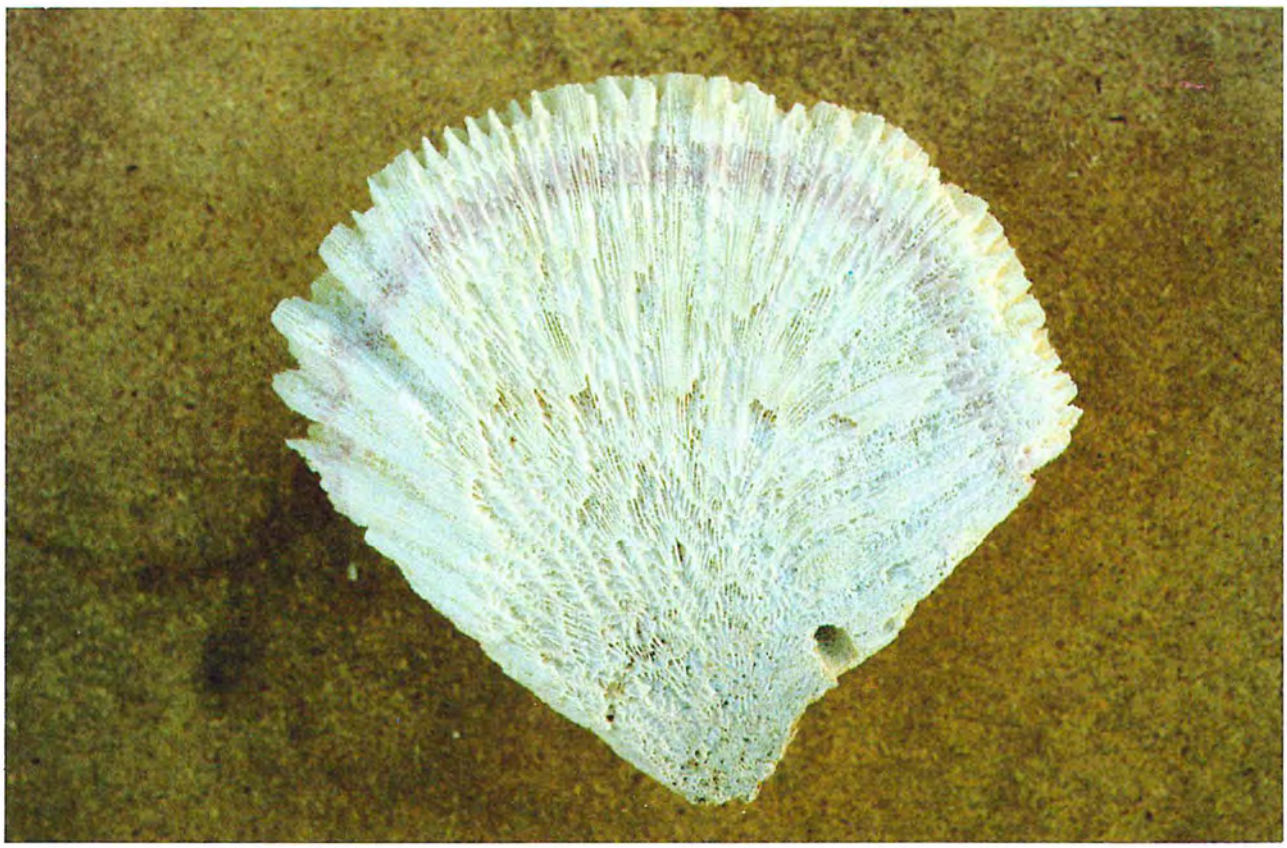


Figure 3.1 Photographs of bleached corals showing alizarin stain incorporated into the skeleton. New growth is measured from the stain to the tips or outer edge of the skeleton: (a) *Acropora formosa,* (b) *Platygyra daedalea.*

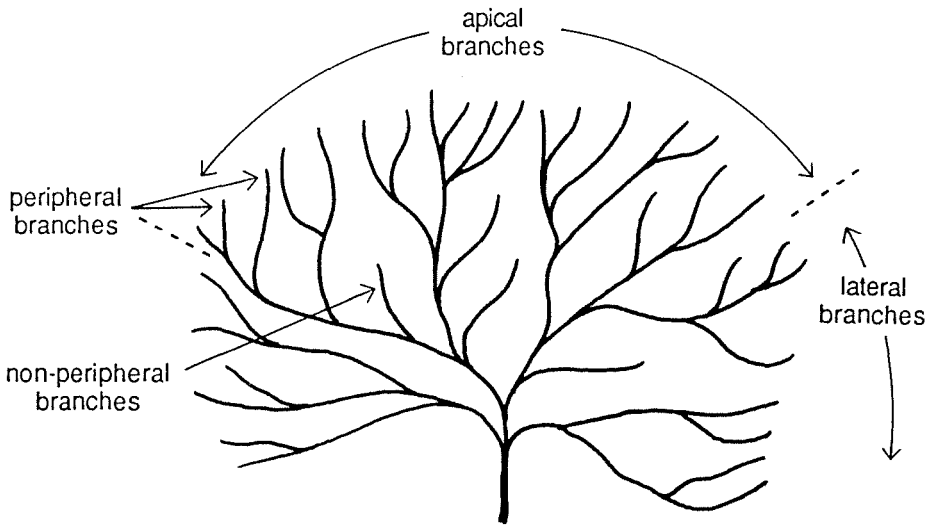


Figure 3.2 Diagram of a coral colony showing the coral branch sampling criteria (peripheral, apical branches) used in this study for arborescent species.

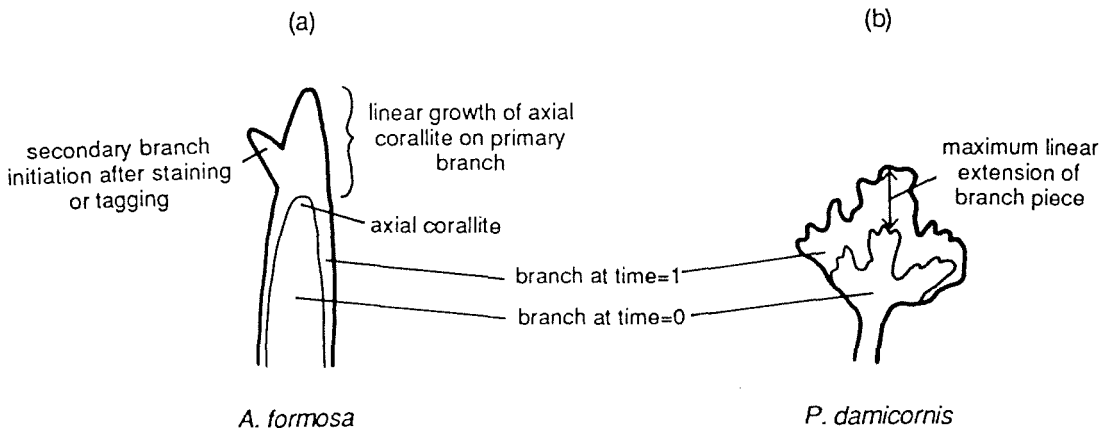


Figure 3.3 Coral branch measuring criteria used in this study showing (a) linear skeletal extension of the axial, apical corallite of an *Acropora formosa* branch and (b) maximum linear skeletal extension of a *Pocillopora damicornis* branch piece.

tips were selected for measurement. Branches outside this quadrant (lateral branches) were abraded occasionally during the staining process and brown, zooxanthellae-bearing tips have been shown to be non-growing (Oliver, 1984).

At the completion of each growth period the branches were brought back to the laboratory, immersed in chlorinated water for 24 hours, rinsed, and dried in an oven for three to four hours. A small hack saw was used to cut each branch to the stain line and the extension of each axial corallite on each primary branch of *Acropora formosa* was measured to 0.1 mm with vernier calipers. Secondary branches were not included (Fig. 3.3a). The maximum extension of each branch piece for *Pocillopora damicornis* (Fig. 3.3b) and *Acropora hyacinthus* was measured . Thus growth rates are the mean for growing branches as specified and not for the overall colony. Colonies of similar initial size/age (*Acropora formosa* , 0.5 - 0.7 m diameter; *Pocillopora damicornis*, 0.3 - 0.5 m diameter; *Acropora hyacinthus*, 0.6 - 0.8 m diameter) were selected to minimise possible deterministic effects on the growth of these species (see Buddemeier and Kinzie, 1976).

Tagging of individual branches

Growth measurements of *Acropora formosa* and *Acropora hyacinthus* were also made by tagging branches with uniquely numbered, plastic ties (80 mm x 4 mm) and using the same criteria for branch selection and measurement as described above. This was necessary at site 1 because of the persistent surge which made conventional staining techniques impossible in rough conditions. Branches of *Acropora formosa* were tagged approximately 50 mm from the growing tip. Similarly ten equally spaced tags were placed approximately 110 mm from the growing radial tips on colonies of *Acropora hyacinthus* . A strip of yellow 'Day Glo' with the colony

identification number and date of tagging was attached to the base of each colony, which was then photographed. All branches were measured underwater to 0.1mm with vernier calipers and recorded on a plastic sheet. The lengths of curved branches of *Acropora formosa* were estimated with two measurements.

Projected area by photography

Changes in projected areas of *Acropora hyacinthus* were measured by photographing colonies through a calibrated perspex grid (1.02 m x 1.02 m x 0.006 m; grid lines 0.1 m apart; Fig. 3.4). Metal spikes (0.3 m long, 6 mm diameter) were driven into the centres of colonies of *Acropora hyacinthus* and the grid was placed over the spike and rested gently onto the colony to avoid crushing any polyps (negative buoyancy of the grid was < 0.5 kg). A 1.5 kg lead weight and a lead sheet displaying the site, date and colony number were used to prevent the grid from moving. In rough conditions additional stability was provided by a diver holding one corner (Fig. 3.4). Each colony was then photographed from directly above, at a height of about 2.5 m, with a Nikonos IVA camera fitted with a 28 mm wide angle lens using 400 ASA Kodak Ecktachrome film.

Following development of the film, each slide was projected onto a wall to approximately 50% of actual size and the outline of the colony and a calibration area from the superimposed grid traced onto paper. The projected area (p) of the colony was then calculated using a digitizer (Summagraphics Corp., U.S.A.). For approximately circular coral colonies, changes in radial skeletal extensions (Δ r) were determined by calculating radii from the formula:

$$\Delta r = r_1 - r_0 = \sqrt{(p_1/\pi)} - \sqrt{(p_0/\pi)}$$

where p_0 and p_1 are the projected surface area at time = 0 and 1 respectively.

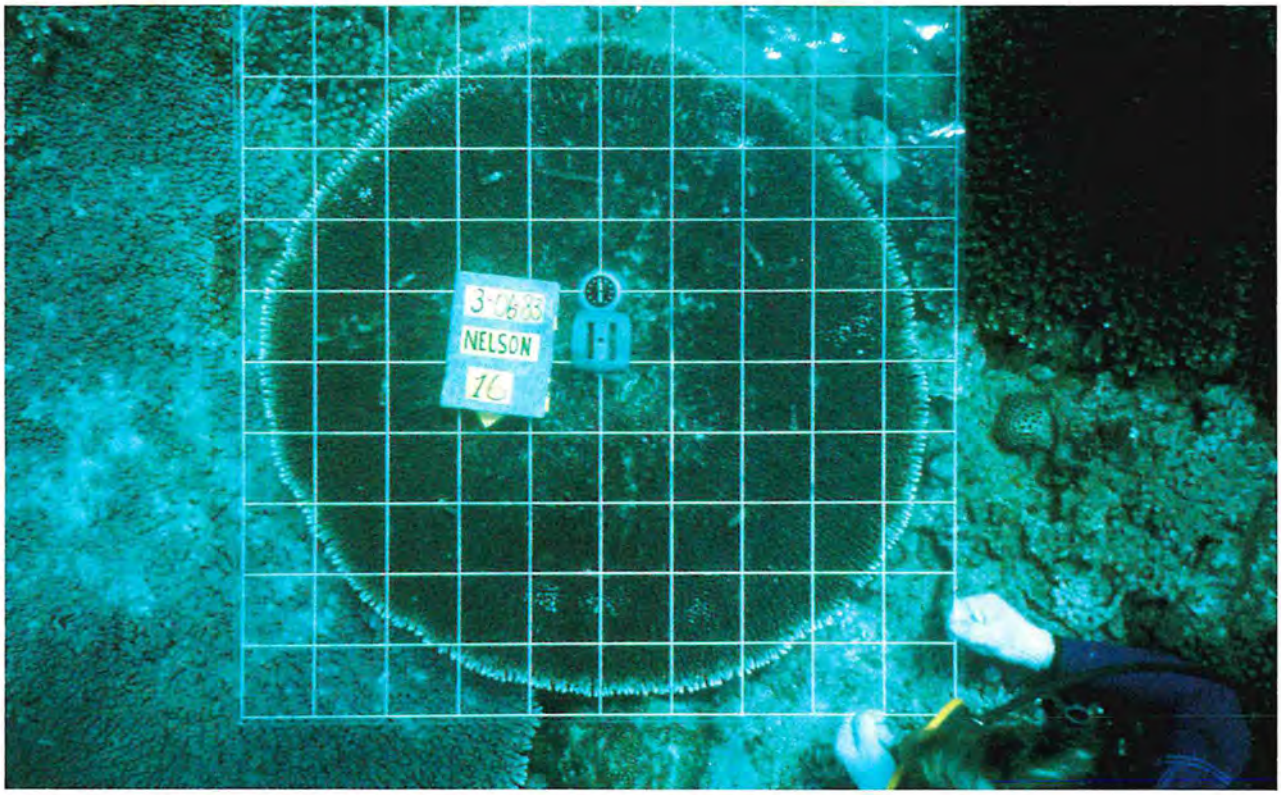


Figure 3.4 Photograph of a colony of *Acropora hyacinthus* and a calibrated grid used to estimate growth rates from increases in colony projected area. Grid squares are 0.01 m^{-2}.

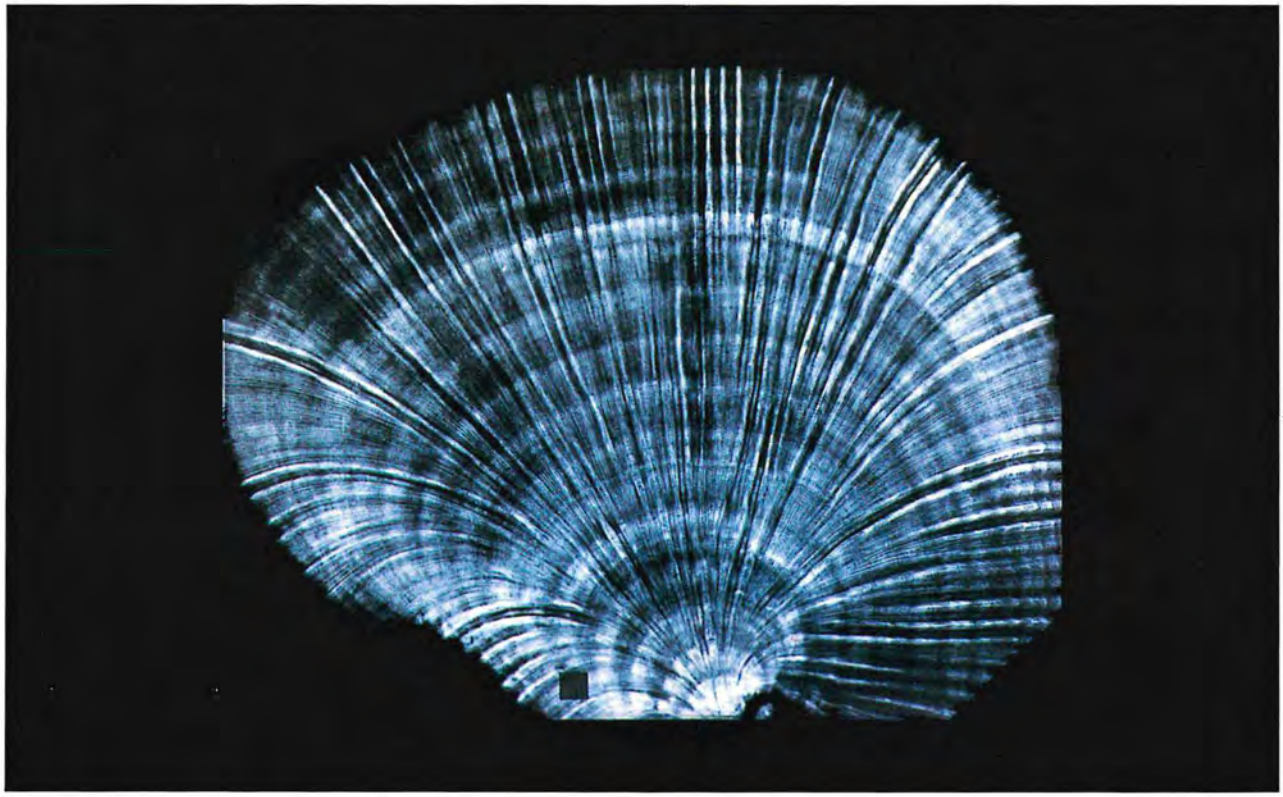


Figure 3.5 Photograph of an X-radiograph negative of a 14 year old colony of *Platygyra daedalea* showing the annual couplets of high (light band) and low skeletal density (dark band). Square at bottom is 10 mm by 10mm.

This formula assumes the coral colonies are circular, and so calculated growth rates are integrated for whole colonies.

Retrospective coral growth by radiography

Colonies of the massive coral *Platygyra daedalea* (0.1 - 0.3 m diameter) were collected from site 4, a fringing reef on the eastern side of Elphick Nob (Fig. 2.1) in water less than 2 m below datum. In the laboratory the colonies were immersed in fresh water for 12-18 h, then rinsed with a jet of water and oven dried at 80^{0} C for about 24 hours.

The X-radiographic techniques employed were similar to those reported by Buddemeier *et al.* (1974). Vertical slices approximately 8 mm thick were cut through the centre and the maximum vertical dimension of the coral colonies with a 0.4 m diamond rock saw. Each coral slice was then 'X-rayed' by technicians of the Radiography Department, Curtain University of Technology, Perth, Western Australia.

The developed X-ray negatives showed alternate light and dark bands representing variations in skeletal density (Fig. 3.5). Each pair of light and dark bands represents an annual increment in linear growth (Knutson *et al.*, 1972). X-ray negatives of colonies with clearly defined bands were laid on a light table under a transparent overlay. The distance between alternate dark (low density) bands along the axis of maximum growth were marked on the overlay ($\pm$ 0.5 mm). Distances between marks were measured with a digitizer (Summagraphics Corp. U.S.A.) to 0.1mm. These measurements represent estimates of maximum annual vertical skeletal extension for each colony.

Attempts were made initially to use a scanning microdensitometer to determine the distance between successive bands of high and low density more precisely but these attempts were unsuccessful because of continued instrument malfunction.

3.2.2 Evaluation of Experimental Manipulation

Optimal number of branch measurements per colony of *Acropora formosa*

A colony of *Acropora formosa* about 0.7 m in diameter was stained at site 2. After 41 days, 60 branches were collected, cleaned, measured and the growth rate for each branch was calculated. The coefficients of variation (standard deviation/mean) for different sample sizes (2, 5, 10, 15, 20, 30, 60) were calculated. All samples except n = 60 were selected randomly. This procedure was repeated 4 times and the mean of the coefficient of variation for each group (n = 5) of branches was calculated.

Frequency distribution of growth rates of *Acropora formosa*

Five colonies of *Acropora formosa* were stained at site 2. After 64 days, 108 branches were collected (approximately equal numbers from each colony), cleaned and measured.

Inter-colony variation

Acropora formosa

Seven branches per colony on 8 colonies of *Acropora formosa* were tagged at site 1 and the distance from the tag to the tip of the axial corallite measured. After 40 days the measurements were repeated. Branches which had grown within about 20 mm of another colony of a different species were measured but not included in the estimates of growth rate. Four and five colonies of *Acropora formosa* at sites 2 and 3 respectively were stained and approximately 20 branches per colony were collected, cleaned and measured after 90 (site 2) and 47 days (site 3).

Acropora hyacinthus

Six colonies of *Acropora hyacinthus* were tagged (10 tags per colony) at site 1. After 41 days each measurement was repeated (excluding damaged portions).

Pocillopora damicornis

Four colonies were stained at site 1 and after 82 days about 25 branch pieces per colony were collected, washed and the maximum growth of each piece was measured.

The effect of branching on the growth of *Acropora formosa*

Forty two branches of *Acropora formosa* were tagged at site 1 in September 1982. Tags were placed above any secondary branches and about 50 mm from the growing tips and the distance from the tag to the tip of the axial corallite measured. These measurements were repeated in October and December, 1982 and in January, 1983 and any secondary branching above the tag was noted. The growth rates of branched and unbranched axial corallites were compared for the periods before, during and after branching.

The effect of the staining on coral growth

Mean branch growth for n consecutive periods (x_i, i=1 to n) was determined from a total of 30 - 40 branch measurements from 4 to 5 colonies stained at the beginning of each growth period. The cumulative mean growth (X) of these colonies (multiple stain) was calculated from $X = \Sigma x_1 + x_2 + \ldots x_n$. The mean branch growth for the overall period (X_o) was determined from the mean growth of about 30 branches from 4 to 5 colonies stained once at the beginning of the first period and collected at the end of the final period (n).

The cumulative growth of corals over the consecutive periods (X) (ie multiple stain) was compared to the growth over the entire period (X_0) (ie single stain) for 6 trials for *Acropora formosa* and 4 for *Pocillopora damicornis* .

The effect of tagging on growth of *Acropora formosa*

Seventy branches of *Acropora formosa* were tagged on September 15, 1982 at site 1 and the distance from the tag to the tip of the axial corallite was measured. In addition about 70 branches of *Acropora formosa* within about 3 m of the tagged branches were stained on September 20,1982. Thirty five days later 48 tagged branches were remeasured and the mean growth rate calculated. In addition, 27 stained branches were collected, cleaned and mean growth rate calculated. On the same day an additional 30 branches of *Acropora formosa* were stained. On December 7, 1982 twenty three stained branches were collected and 38 tagged branches were remeasured and mean growth rates for the previous period calculated.

Five colonies of *Acropora formosa* were stained at site 2 on September 14, 1982. Twenty five branches on one of these colonies stained the previous day, were tagged and measured on September 15, 1982. On October 26, 15 tagged branches and 29 stained branches were collected from this colony and remeasured. In addition, 34 branches from the other four colonies (approximately equal numbers from each colony) were collected on the same day.

Precision of tagged measurements above and below water

Thirteen tagged branches were measured *in situ* underwater, collected and remeasured above water.

Comparison of methods for estimating the radial extension of *Acropora hyacinthus*

At site 1, ten tags were attached at approximately equal distances apart on one almost circular colony of *Acropora hyacinthus* at site 1 and radial branch growth was measured over 3 consecutive growth periods. Increases in projected area were measured photographically on the same colony over the same 3 growth periods. Computed radial extensions were then calculated on the assumption that this colony was circular. Three different nearby colonies of *A hyacinthus* were stained and growth estimates for two of the above three periods were obtained by collecting pieces from each colony, and measuring the increase in radial extension from the stain line.

3.2.3 Statistical treatment

Parametric (Students' t - test (t), Paired t - test (t_p)) and the non - parametric analogues of these tests (Mann - Whitney U - test (MW), Wilcoxon paired sample test (W_p); Snedecor & Cochran, 1978) were performed on all data to test for significant differences between sample means. Parametric and non parametric tests were run in parallel on all data with agreement in all cases. To test whether a series (>2) of means (eg inter - colony variation) were significantly different a Model 1, 1-way ANOVA was performed. If a significant difference existed the mean/s likely to be causing the differences were extracted and the ANOVA was then repeated on the remaining means until no significant difference was recorded. This procedure determined which mean values, if any, were different from the rest.

In tests where single mean values (integrated colony growth rate) were compared to a sample mean (as in the comparison of the 3 methods for measuring the radial extension of *Acropora hyacinthus*) a significant

difference was assumed if the single mean value was outside the 95% confidence interval of the sample mean.

3.3 RESULTS AND DISCUSSION

3.3.1 Optimal number of branch measurements per colony of *Acropora formosa*

All measurements have some variability due to systematic errors or inaccuracies in the method of measurement and to non-systematic errors such as the 'natural' or inherent variability of the subject (eg different growth rates of coral branches on the same colony). Providing the appropriate methods and criteria of measurement are chosen carefully, and kept to rigorously, systematic errors can be ignored. The non-systematic errors must be quantified if measurements are to be reproducible, and are often a function of the sample size. In this study the coefficient of variation (standard deviation divided by the mean) of different sample sizes has been used to estimate this inherent variability.

The mean coefficient of variation from n= 5 to n=60 varies slightly from 0.14 to 0.19 and suggests that the inherent variability in the growth rate of branches of *Acropora formosa* can be reduced to a relatively constant value (ie CV ~ 0.16) if between about 7 or more branch measurements are made for any one coral colony growth estimation (Fig. 3.6). In this study an average of approximately 30 to 40 branch measurements from 4 to 5 colonies were used to estimate mean growth rates during a particular period. The mean coefficient of variation for *Acropora formosa* for all growth periods at the three sites and the coefficient of variation for 63 branches collected after 383 days supports these conclusions (Fig. 3.6).

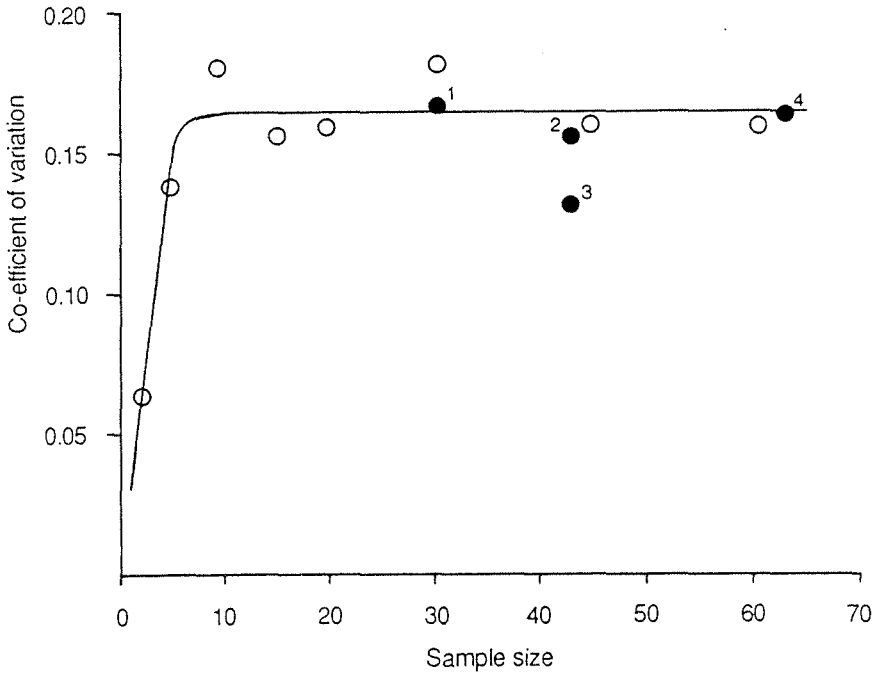


Figure 3.6 Variation in the mean coefficient of variation for different sample sizes of *Acropora formosa* branches grown over 41 days (open circles).
1, 2, 3 represent the mean coefficient of variation for the growth of *Acropora formosa* branches for all growth periods for sites 1 (12 growth periods; mean number of branch measurements =29), 2 (10 growth periods; mean number of branch measurements =43) and 3 (10 growth periods; mean number of branch measurements =43), and 4 is the coefficient of variation for 383 days growth of 63 branches of *Acropora formosa* at site 2.

3.3.2 Frequency distribution of growth rates for *A.formosa*

The frequency distribution of the linear extension of 108 branches of *Acropora formosa* were normally distributed ($X^2 = 5.593$, p (X^2) > 0.05) (Fig. 3.7). On the basis of these results, samples used in estimating the growth of branches in this study were considered to be normally distributed and therefore the use of parametric statistics was justified. However because modern statistical packages on computers often use a common input file for different statistical tests, little extra effort is required to perform the equivalent non-parametric statistics. Throughout this study this was done as a check on the parametric tests.

3.3.3 Inter-colony variation

Acropora formosa

A one-way ANOVA showed that a significant difference ($F = 2.80$, $p < 0.05$) in growth rate existed when all 8 colonies at site 1 were analysed. However when colony #6 was excluded there was no significant difference in growth rate between the remaining 7 colonies (Fig. 3.8a). At site 2 a significant difference ($F = 3.20$, $p < 0.05$) in growth rate existed when all colonies were included. However, when colony #2 was excluded, no significant difference occurred (Fig. 3.8b). At site 3 there was no significant difference in growth rate between the 5 colonies (Fig. 3.8c).

Acropora hyacinthus

A one-way ANOVA on all 6 colonies showed a significant difference ($F = 35.46$, $p < 0.0001$) in mean growth rates between the six colonies. Colonies 9, 10 and 16 were not significantly different from each other and there was no significant difference in mean growth rate between colonies 17, 18, and 19 (Fig. 3.9a).

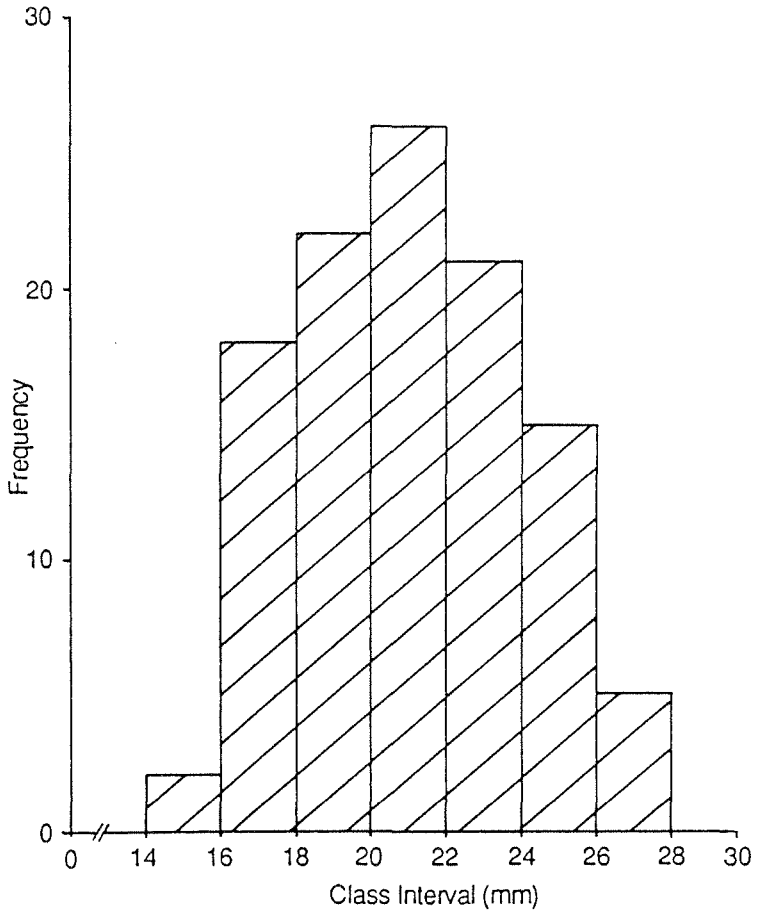


Figure 3.7 Frequency distribution of the growth of 108 branches from 5 colonies of *Acropora formosa* at site 2.

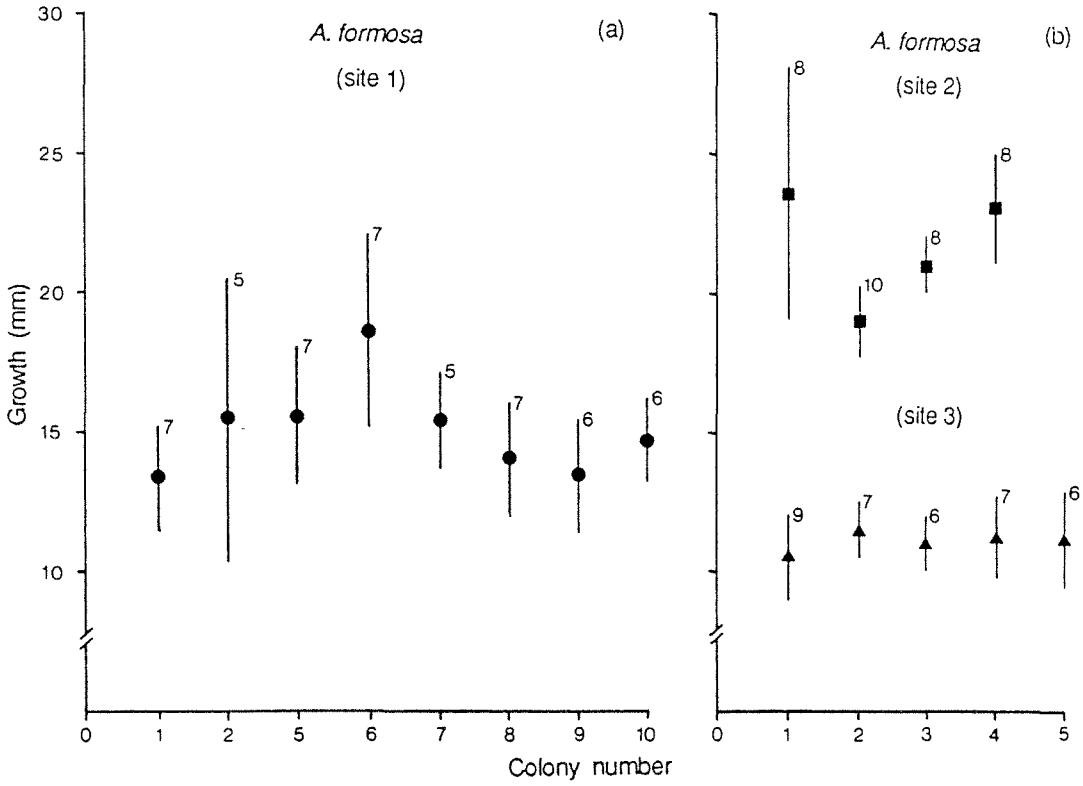


Figure 3.8 Inter-colony variation in the mean growth rate of *Acropora formosa* .

Error bars are 95% confidence intervals and (n) is the number of branch measurements per colony; (a) site 1: September 15 to October 25, 1982; (b) site 2: July 28 to October 26, 1982; site 3: July 29 to September 14,1982.

Pocillopora damicornis

A one-way ANOVA on all 4 colonies (2, 5, 8, 10) showed a significant difference ($F = 3.74$, $p < 0.02$) in growth rate. However when colony #8 was excluded, there was no significant difference between the remaining 3 colonies (Fig. 3.9b). The cumulative growth at site 1 of three colonies of *Pocillopora damicornis* measured over 9-10 months are shown in Figure 3.9c and indicate that the growth rates of these colonies over this period were similar.

These data suggest that inter-colony variability in mean growth rate of apical branches of *Acropora formosa* and *Pocillopora damicornis* is low over these periods and that a sample mean of 30 - 40 measurements from 4 - 5 colonies will provide a reproducible estimate of the mean growth rates of the apical branches of the surrounding colonies of the same species. *Acropora hyacinthus* exhibits more inter-colony variation in radial branch extension than the other two species. Colonies 9, 10 and 16 were approximately circular (see colony 16 in Fig. 3.4) while colonies 17, 18 and 19 were irregular. Irregular shaped colonies of this species are often related to past mechanical damage or inter-specific competition for space with nearby coral species, and these factors may have contributed to the lower growth rate of the 3 irregular colonies and the apparently higher inter-colony variability in growth rate of this species.

In summary, these data suggest that, at a particular site, the variations in the intraspecific growth rates of corals selected in this study were due largely to mechanical damage rather than intrinsic differences in metabolic parameters. The cumulative growth of 3 colonies of *P damicornis* over an extended time period support this conclusion, as this species appeared to be least affected by mechanical damage of the three species studied at site 1.

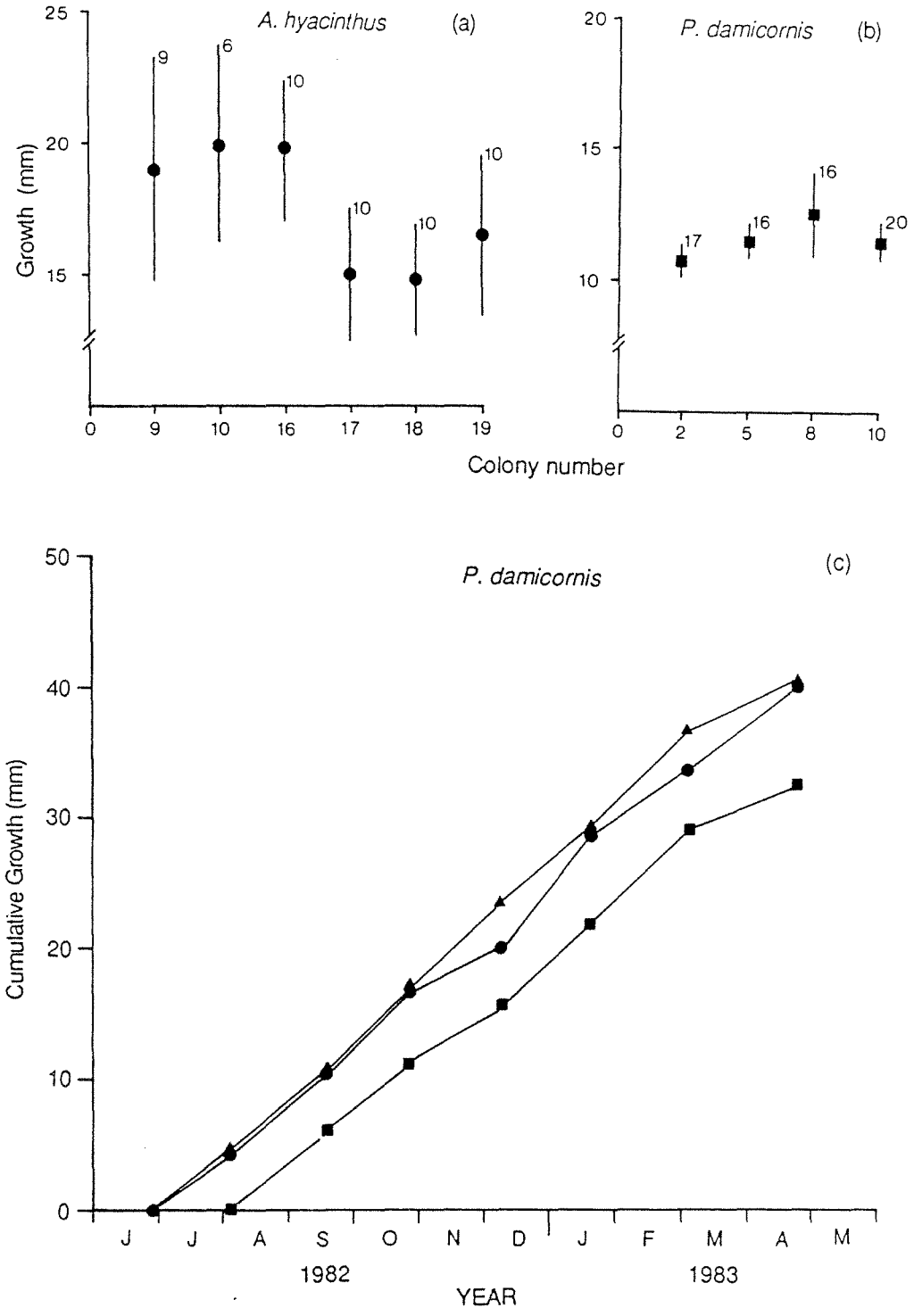


Figure 3.9 Inter-colony variation in the mean growth rate of (a) *Acropora hyacinthus* and (b) *Pocillopora damicornis* at site 1.
Error bars are 95% confidence intervals and (n) is the number of measurements per colony; (a) January 19 - March 1,1983; (b) September 17 - December 8,1982.
(c) the cumulative growth of 3 colonies of *Pocillopora damicornis* at site 1.

3.3.4 The effect of branching on the growth of *Acropora formosa*.

In the Dampier Archipelago branch initiation appears to occur predominantly in October to January. Oliver *et al.* (1983) found that turbulent, highly illuminated sites on the Great Barrier Reef displayed greater branch initiation than less energetic, deeper sites. This raises the possibility that spatial and temporal comparisons of growth rates of axial corallites (expressed as mm/30 days) with differential branching would be misleading if secondary branching, subsequent to staining or tagging, affects the growth of the axial corallite.

Between October 1982 - December 1983, 39% of the tagged axial corallites branched. In the period before this (September to October), the mean growth rate of the axial corallites that did not subsequently branch (x = 11.16, sd = 2.55, n = 28) was not significantly different from the mean growth rate of the axial corallites that initiated secondary branches in October to December (x = 11.26, sd = 1.95, n = 14). In the following period (October to December) the mean growth rate for these branches (x = 14.24, sd = 2.28, n = 10) was not significantly different from the unbranched axial corallites (x = 14.40, sd = 2.27, n = 13). In December 1982 to January 1983, the period after most branching occurred, growth rates again were not significantly different (Fig.3.10). For the entire period from September 1982 to January 1983, the mean growth of apical corallites that did not initiate secondary branches (x = 58.4 mm, sd = 13.3, n = 9) was not significantly different from the growth of apical corallites that did initiate new branches (x = 61.4 mm, sd = 12.8, n = 13) during this period. Damage and loss of tagged branches account for the decline over time in the numbers used in these analyses.

These data suggest that the growth of the axial corallite is not significantly affected by secondary branch initiation, and that it is valid to

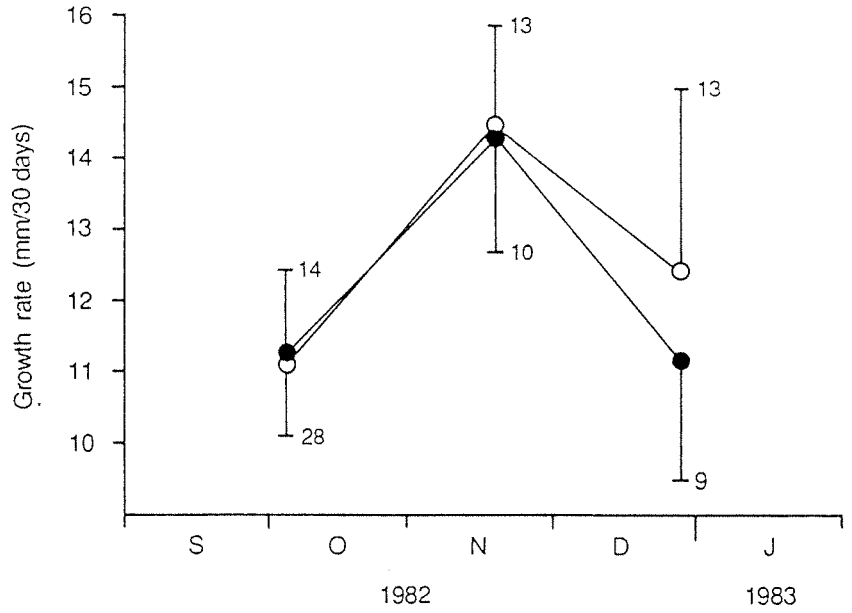


Figure 3.10 The effect of branching on the mean growth rate of axial, apical corallites of *Acropora formosa.*
Error bars are 95% confidence intervals and (n) is the number of measurements; (○) unbranched axial corallites; (●) branched axial corallites.

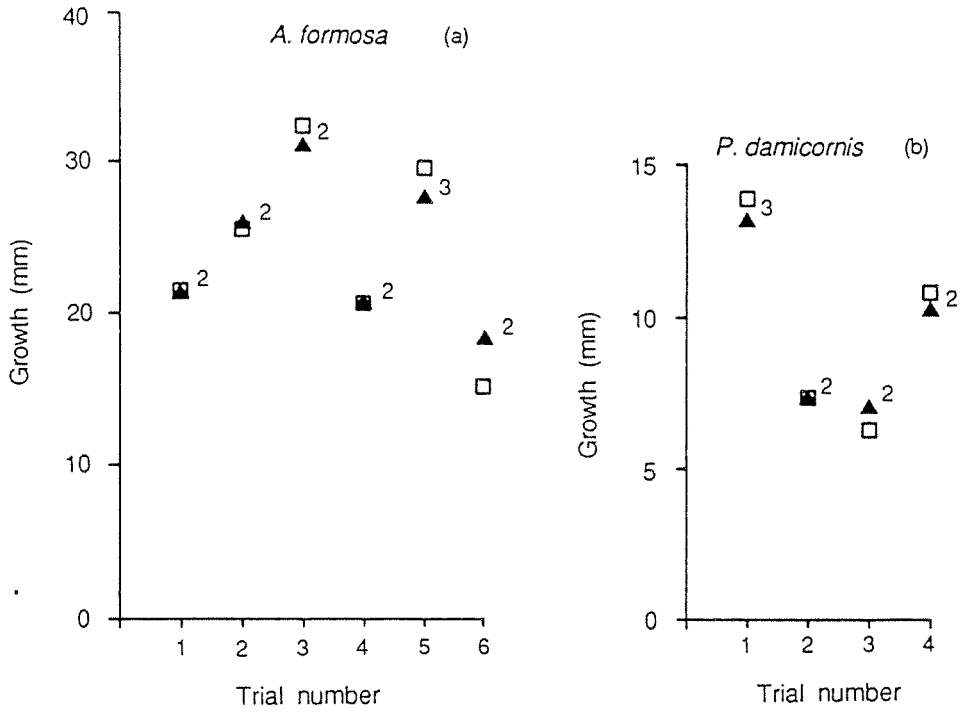


Figure 3.11 The effect of the staining procedure on the mean growth of (a) *Acropora formosa* and (b) *Pocillopora damicornis* .
(▲) cumulative growth after (n) stainings over (n) periods; (□) growth over the same period after a single staining.

make spatial and temporal comparisons of growth rates of the axial corallite between sites and times with differential branching.

3.3.5 The effect of staining on coral growth

The use of alizarin red S (sodium alizarin sulphonate) to stain the skeleton deposited by living coral was developed by Barnes (1970, 1972). Although this technique has been employed extensively, in the field and under controlled laboratory conditions (Buddemeier & Kinzie, 1976) to estimate coral growth, few studies to date have investigated the effect of the staining procedure on coral behaviour, physiology, skeletal chemistry, or growth. Lamberts (1978) has suggested that it can be mildly toxic to corals.

During *in situ* staining, coral colonies were exposed to alizarin concentrations of about 10 mg l^{-1} for 3 - 6 hours as well as increased levels of suspended sediment caused by divers, restricted water flow, mechanical abrasion and possibly oxygen depletion. A laboratory study on the effects of alizarin red S on the calcification rates of the hermatypic coral *Diploria strigosa* (Dana), found significant depressions in calcification for up to 6 days following exposure to a concentration of 10 mg l^{-1} for 24h (Dodge, 1984). Glynn and Stewart (1973) compared the extension rate of five colonies of *Pocillopora* determined by alizarin staining and of five others determined by field photographic records and reported no significant difference. Reed (1981) reported no significant difference in the extension rate of *Oculina varicosa* corals determined by staining and by reference to plastic ties fixed to colonies.

In this study there was no significant difference in branch growth between the sum of the mean growth over consecutive periods (X) and the mean growth for the overall period (X_0) for *Acropora formosa* (Fig. 3.11a) or *P.damicornis* (Fig. 3.11b), suggesting that the skeletal extension of *Acropora*

formosa and *Pocillopora damicornis* was not significantly affected by the enclosure and subsequent staining procedures. This conclusion is based on the assumption that if the staining procedure significantly affected the growth of these species then colonies stained once would exhibit different growth rates over the same time interval compared to colonies subjected to multiple stainings. The mean annual growth rate of 63 branches of *Acropora formosa* (x = 78.5 mm, sd = 13.8) stained once at the beginning of the study period at Conzinc Island (383 days) was not significantly different to the mean cumulative annual growth of branches (x = 85.8 mm, sd = 15.6) measured over nine consecutive sampling periods at the same site, and supports the above conclusion.

3.3.6 The effect of tagging on the growth of *Acropora formosa*

Shinn (1966) placed rubber bands over branches of the Atlantic staghorn coral *Acropora cervicornis* as a reference point to estimate linear branch extension and, as 'relative' growth rates of transplanted coral branches were being investigated, the effect of the rubber bands was not considered. Oliver *et al.* (1984) tagged branches of *Acropora formosa* and found that the growth rate of individual branches was related to the distance of the tag from the growing tip.

In this study branch growth rate (expressed as mm/30 days) was not significantly correlated with the initial distance (ID) of the tag from the growing tip for either *Acropora formosa* (ID=49 mm, sd=9, n=70 ; r = -0.223, n = 52) or *Acropora hyacinthus* (ID=113 mm, sd=18, n=60 ; r = -0.233, n = 52). Charuchinda and Hylleberg (1984) used plastic-coated wire tags fixed about 30 mm from the tips to measure linear extension of *Acropora formosa* and found that lowest growth rates occurred after tagging. However they suggest this was not due to the effect of the tags.

Tagged branches of *Acropora formosa* at site 1 and site 2 showed a reduction in growth rate in the period (about 40 days) immediately after the tags were applied (Fig. 3.12). At site 1 mean growth rate of tagged branches ($x = 11.20$, $sd = 2.32$, $n = 48$) was significantly lower ($t = -4.16$, $v = 73$, $p < 0.05$) than untagged branches ($x = 13.69$, $sd = 2.80$, $n = 27$). At site 2 during the same period the mean growth rate of tagged branches ($x = 3.43$, $sd = 1.44$, $n = 15$) was significantly lower ($t = -5.709$, $v = 42$, $p < 0.05$) than the mean growth rate of untagged branches ($x = 6.47$, $sd = 1.78$, $n = 29$). In the following period at site 1 the mean growth rate of tagged branches ($x = 14.46$, $sd = 2.22$, $n = 38$) was not significantly different from untagged branches ($x = 14.50$, $sd = 1.76$, $n = 23$) (Fig. 3.12).

The tabular acroporiid *Acropora hyacinthus* was tagged about 110 mm from the growing radial branch tip. Because of the reticulate nature of branching in this species and the fact that the distance from the tag to the growing edge was being measured rather than individual branches it was assumed that tagging did not affect radial extension. This assumption appears to be valid as the comparison of the three techniques (stain, tag and photographic) used to estimate radial extension of this species show comparable growth rates (Fig. 3.13). A lack of obvious retardation of the growing edges adjacent to the tags provide additional evidence to support this assumption.

The data from the tagging experiments at Conzinc Island (site 2) and Nelson Rocks (site 1) indicate that growth of tagged branches of *Acropora formosa* was significantly reduced following application of the tags. Mean growth rate of the tagged branches was 82% and 53% of the growth rate of untagged (stained) branches at sites 1 and 2 respectively. The disparity between the growth inhibition at the two sites was probably due to the lower growth rates (ie calcification rates) at site 2.

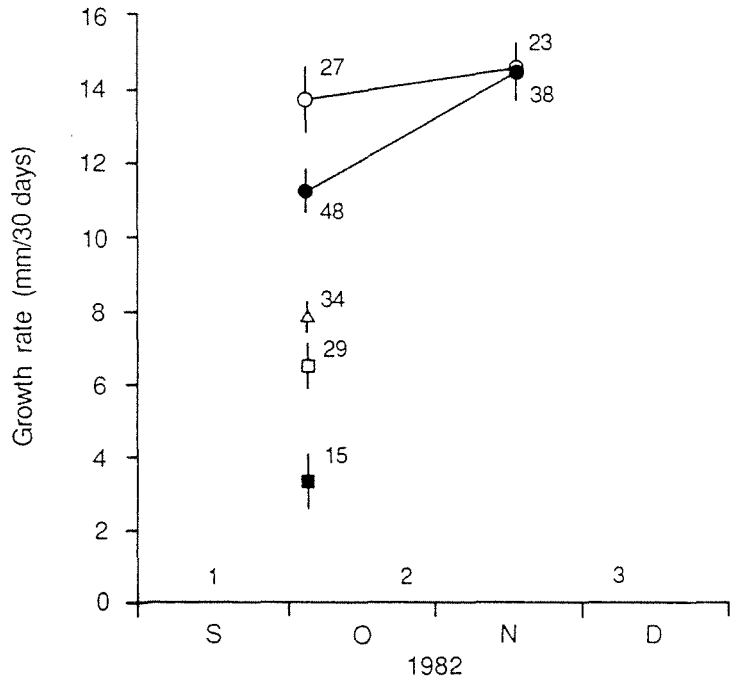


Figure 3.12 The effect of tagging on the mean growth rate of *Acropora formosa* at sites 1 and 2.
Error bars are 95% confidence intervals and (n) is the number of measurements; (○) stained and (●) tagged branches on colonies at site 1; (□) stained and (■) tagged branches on the same colony at site 2; (△) mean of 4 colonies stained at site 2; 1, initial stain and tagging; 2, remeasure tagged branches, collect stained branches; 3, remeasure tagged branches, collect stained branches.

When a tag is applied to the coral branch the corallites on the branch are crushed causing death of the underlying polyps and a break in the confluent coenosarc. This will prevent possible translocation of photosynthetic products to the growing tip (Oliver *et al.*, 1983) and may cause retardation of growth. Another possibility is that metabolic energy is directed at repairing the 'injury' caused by the tag rather than into extension of the tip. Within 3 - 4 days calcium carbonate was observed on the edges of the tag and after about 30-40 days the tag was completely covered with zooxanthellae-bearing calcium carbonate. Following the 'calcifying' of the tags and the consequent 'reconnection' of the coenosarc the growth of the tagged branches returned to 'normal' and appeared to be unaffected by the presence of the tags.

These data indicate that if coral growth is estimated by the application of tags then 'normal' growth rates will be reduced until tags have calcified over. The period of growth retardation will depend on the size of the tag and the growth rate at the time of tag application.

3.3.6 Precision of measuring tagged branches above and below water.

The 'growth' of tagged branches measured underwater was significantly greater (t_p = -2.811, $p < 0.01$) than the same branches measured above water by about 0.6 mm and where necessary, adjustments were made in the lengths recorded underwater.

3.3.7 Comparison of methods for measuring the radial growth of *Acropora hyacinthus*

The mean radial extension rates of 1 colony (#9) of *Acropora hyacinthus* measured by the use of 10 tags were not significantly different from the mean radial extensions of 3 adjacent colonies of *Acropora*

hyacinthus measured by staining over the same periods at site 1. The integrated radial extension rates of this colony (#9) as computed from increases in projected area over the same three periods were about 1 mm/30 days less than the rates estimated by either tagging on the same colony or by staining adjacent colonies. However in February 1983 radial extension rates as measured by the use of tags was not significantly different from the rates computed from projected increases in area (Fig. 3.13). The discrepancies between the estimates from tagging and projected surface area can probably be explained by the different nature of the measurements (the mean of 10 individual branch piece measurements as compared to an estimate of integrated radial increase for the whole colony) and the obviously incorrect assumption that colony 9 was perfectly circular. However these results suggest that these methods for measuring radial extension rates on approximately circular colonies of *Acropora hyacinthus* provide comparable estimates. While measuring increases in radial extension by photographic means provides a quick and reproducible method to estimate the growth of a whole colony, it also provides information on other aspects of the ecology of this species such as mechanical damage and recovery as well as data on inter-specific competition.

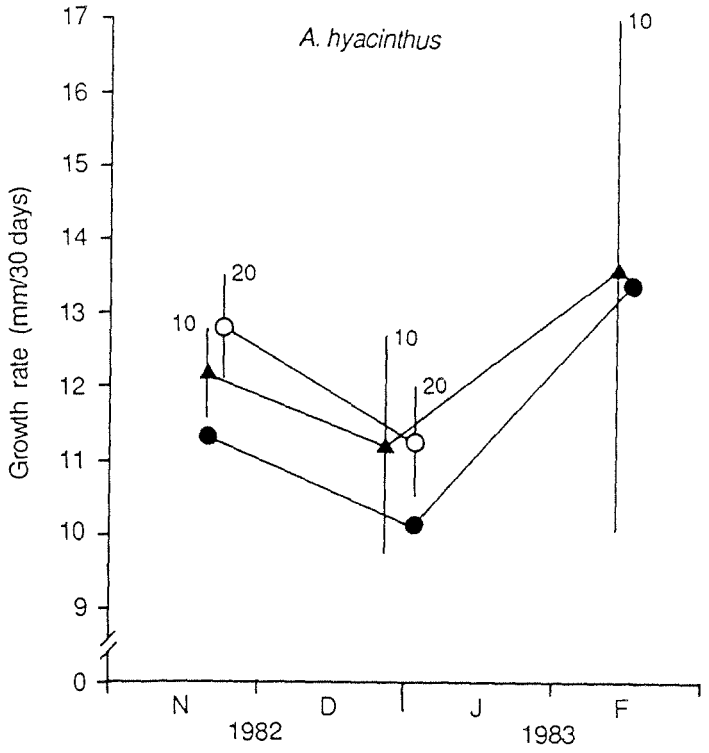


Figure 3.13 Comparison of methods to estimate the increase in the rate of radial extension of *A. hyacinthus* .
Error bars are 95% confidence intervals and (n) is the number of measurements; (●) from increases in projected area by calibrated photograhic methods and (▲) from tagging branches on the same colony and (O) by staining of 3 adjacent colonies.

CHAPTER FOUR

EFFECTS OF ENVIRONMENTAL FACTORS ON CORAL GROWTH

4.1 INTRODUCTION

Physical factors including temperature, salinity, light, sedimentation and chemical parameters including nutrients and pH are important to the growth and survival of corals (eg Buddemeier and Kinzie, 1976; Gladfelter, 1985). In Chapter Two, information was presented on the temporal and spatial variation of selected aspects of the physical environment of inshore and offshore coral reefs in the Dampier Archipelago. Chemical parameters were not investigated as part of this study, although some nutrient data have been collected for the Dampier Archipelago (Chiffings, pers. comm.). As these data suggested that spatial and temporal variability in nutrients in the archipelago is low, it was felt that it would be more profitable to examine the hypothesis that physical factors were the main determinants of coral growth in this area.

Seasonal trends in temperature, salinity and water clarity occurred at all sites whereas seasonal differences in sediment deposition were evident at the inshore sites but not at the offshore site. Environmental conditions at sites 2 and 3 were similar throughout the study period apart from sediment deposition rates which were considerably higher at site 3 during November 1982 to March 1983. These high rates coincided with nearby dredging activities. The main spatial differences in environmental conditions occurred between the two inshore sites and the offshore site. Temperatures were lower in 'summer' and higher in 'winter' at the offshore site and water clarity and PPFD were generally higher although sediment deposition and salinity were lower.

Four species of corals were selected for study. *Acropora hyacinthus* and *Pocillopora damicornis* were selected because they are common on many reefs in the Dampier Archipelago, *Acropora hyacinthus* being particularly predominant on the peripheral, seaward reefs. *Acropora formosa* was selected because it could be found in sufficient quantities at the three study sites: a necessary attribute for extended studies of spatial comparisons of coral growth. An additional advantage in the selection of *Acropora formosa* and *Pocillopora damicornis* was that these species were studied by Crossland (1981) at the Abrolhos Islands (Fig. 1.1) and thus would allow latitudinal comparisons of the growth of these species in Western Australia. Furthermore both of these species have been studied extensively in different parts of the world (see Table 4.6) and therefore would also provide a geographical perspective on the growth of these corals in the Dampier Archipelago. The massive coral *Platygyra daedalea* was selected because this species is ubiquitous in the Dampier Archipelago and preliminary work indicated that this species displayed satisfactory skeletal density band formation. The retrospective growth data obtained for this species may be also useful in the future as baseline data for longer-term work in this region.

This chapter considers spatial and temporal variations (intra-year and inter-year) in the growth of the selected species. The growth of the staghorn coral *Acropora formosa* was investigated at three sites to assess spatial differences and the growth of *Acropora hyacinthus* and *Pocillopora damicornis* was studied at site 1 to assess intra-annual or 'seasonal' variation in coral growth. Inter-year variations in annual growth of the massive coral *Platygyra deadalea* were measured retrospectively by examining skeletal density bands revealed by x-radiography and compared to 'real-time' estimates of annual growth (measured by staining) between

March 1982 and April 1983. It was assumed that comparisons of inter-year growth over about 10 years would indicate the degree of environmental stability that has prevailed at this site and, by extrapolation, at site 1 about 5 km away (Fig. 2.1). Furthermore, comparisons of the retrospective growth data with the 'real time' estimates were made to help decide how 'typical' the period March 1982 to April 1983 was in relation to the previous 10 or so years, so enabling results of the intensive coral growth studies at site 1 to be viewed from a longer perspective.

Correlations between the observed variations in coral growth and the physical factors known to influence coral growth and survival were sought and possible causal factors identified. Growth rates measured during 1982 and 1983 were considered not only in relation to the long term (~10 y) perspective, but also in comparison with growth rates of the same species in other geographical localities.

4.2 MATERIALS AND METHODS

4.2.1 Study Sites

Coral growth studies were undertaken at sites 1, 2, 3 and 4 (Fig. 2.1), of which sites 1, 2 and 3 have been described in section 2.2.1. Site 4 was located on a shallow (~1-2 m below datum), fringing reef on the eastern side of Elphick Nob. This site is characterised by clear water and low sediment deposition rates, and is well protected from swell waves. The benthic community consists of a diverse assemblage of corals including large colonies of *Porites*, *Goniopora* and *Platygyra* spp. as well as large colonies of *Acropora hyacinthus* and *Acropora formosa*.

4.2.2 Coral Growth

The methods chosen for measuring coral growth are presented in detail

in Chapter 2. However, in general approximately 30 - 40 branches from up to 8 colonies (mean was 4-5) were measured per 'growth' or 'sampling' period to provide an estimate of mean growth for *Acropora formosa* at sites 1, 2 and 3. In the case of *Pocillopora damicornis* at site 1 an average of 91 branch piece measurements from 4 - 8 colonies were made to estimate mean growth for each sampling period. Between 2 and 10 colonies of *Acropora hyacinthus* were used to estimate mean growth, the large variation in number of colonies used being due to frequent damage of experimental colonies by wave action at this site. Tagging of *Acropora formosa* was necessary at site 1 after October 1982 because of the persistent surge which made conventional staining techniques unsuitable.

4.2.3 Environmental factors and statistical treatment

Methods for measuring the environmental factors used in this study are presented in detail in Chapter 2, and the statistical treatment used here was identical, where applicable, to that outlined in section 2.2.3.

4.3 RESULTS

4.3.1 Intra - annual or seasonal variation

Acropora formosa

The seasonal variation in mean linear extension of apical branches of *Acropora formosa* at site 1 is shown in Figure 4.1. A minimum mean growth rate of 7.5 mm per 30 days occurred in July 1982 and was 52% of the maximum rate, 14.6 mm per 30 days, which occurred in November 1982. Reduced growth rates occurred in December 1982 and March 1983 coinciding with extensive damage to experimental colonies by wave action associated with tropical cyclones. The minimum growth rate in 1983 was measured

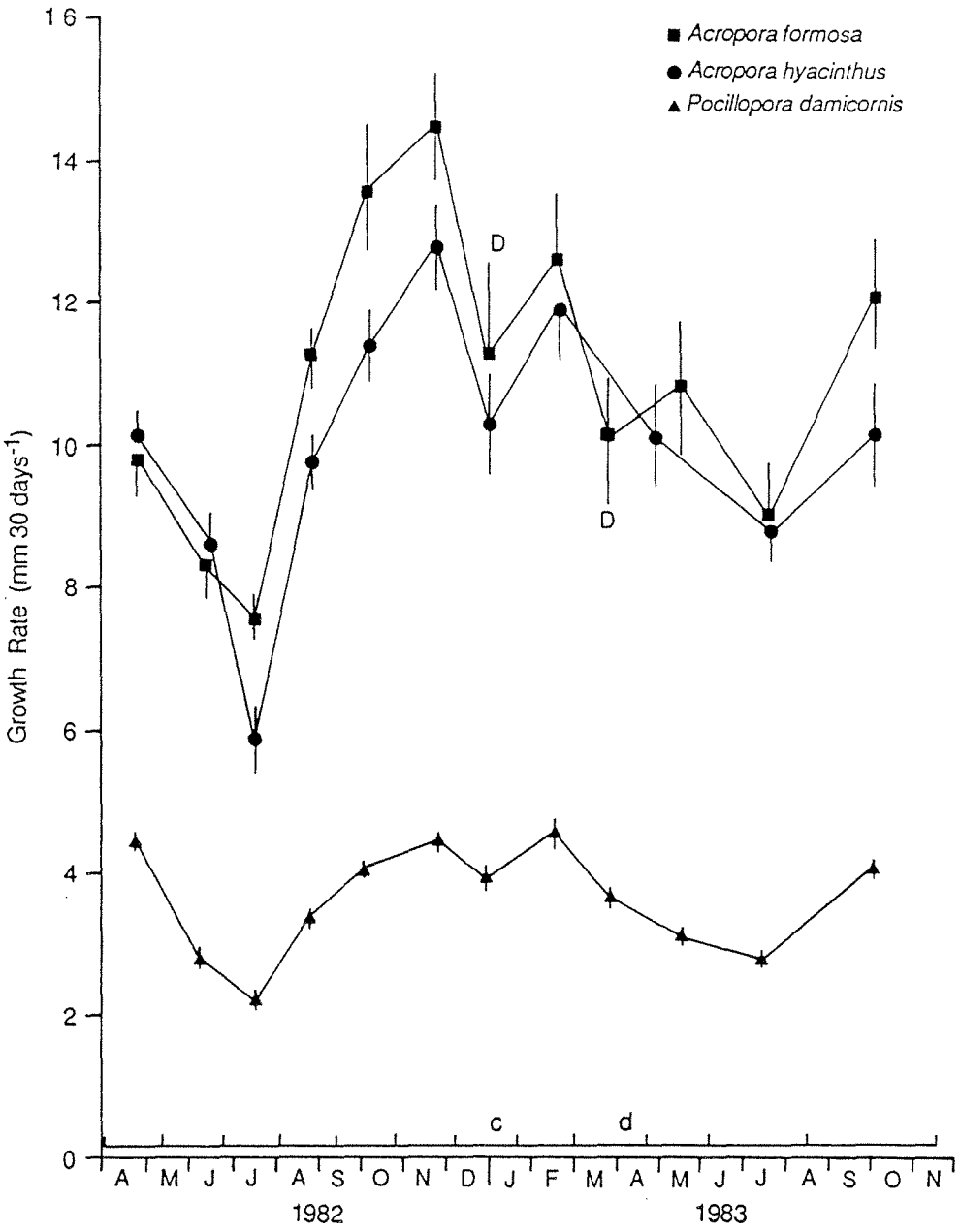


Figure 4.1 Seasonal variation in growth of *Acropora formosa, Acropora hyacinthus* and *Pocillopora damicornis* at site 1.
Error bars are 95% confidence intervals. (D) damage to experimental colonies (c) T.C. Jane, January 7-9 (d) T.C. Lena, April 7-8.

over a longer period (75 days) than in 1982 (35 days). Mean growth rates during 'summer' (x=12.37, sd=1.61, n=6) were significantly higher (t=3.256, p=0.0086, df=11) than during 'winter' (x=9.49, sd=1.45, n=6).

Acropora hyacinthus

The pattern of seasonal variation in growth rate of *Acropora hyacinthus* during the study period was similar to *Acropora formosa* Maximum growth occurred in November and minimum in July 1982 with a marked reduction during December 1982 (Fig. 4.1). Mean growth rates in 'summer' (x=11.32, sd=1.21, n=5) were significantly higher (t=2.898, p=0.0199, df=9) than in 'winter' (x=9.62, sd=1.70, n=5).

Pocillopora damicornis

The variation in the mean maximum extension of branches of *Pocillopora damicornis* followed a similar seasonal pattern to *Acropora formosa* and *Acropora hyacinthus* although growth rates were lower and considerably less variable (Fig. 4.1). A minimum growth rate of 2.2 mm per 30 days occurred in July 1982 and was 47% of the maximum value of 4.7 mm per 30 days, which occurred in February 1983. Growth rates from October 1982 to February 1983 were relatively constant: around 4 mm per 30 days (Fig. 4.1), although a reduction in growth rate occurred in December 1982, again during a period when a cyclone occurred. Mean growth rates of *Pocillopora damicornis* during 'summer' (x=4.14, sd=0.31, n=6) were significantly greater (t= 2.921, p=0.015, df=11) than during 'winter' (x=3.14, sd=0.78, n=6).

4.3.2 Inter-annual variation in growth of *Platygyra daedalea*

The mean maximum annual growth rate of *Platygyra daedalea* in

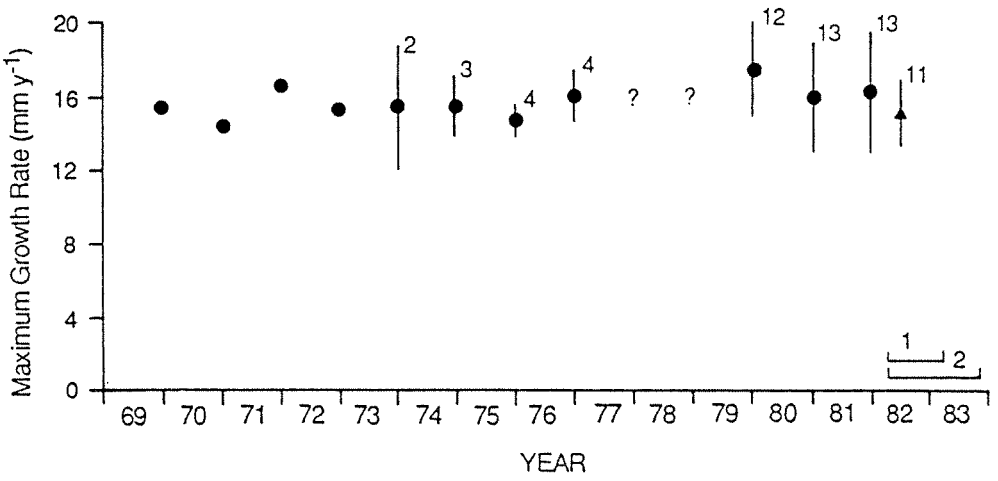


Figure 4.2 Inter-annual variation in the mean maximum vertical growth of *Platygyra daedalea* at site 4 between 1969 and 1983. Error bars are 95% confidence intervals. (●) by X-radiography; (▲) by staining; (n) number of colonies; (1) period of growth studies of *A. formosa* at sites 1, 2 and 3 and *Platygyra daedalea* at site 4; (2) period of temporal coral growth studies at site 1.

1979/1980 (n=12), 1980/1981 (n=13) and 1981/1982 (n=13), as determined from negatives of x-radiographs of vertical slices of these colonies, was not significantly different from the mean maximum vertical growth of 11 colonies of *Platygyra daedalea* between April 1,1982 and April 1, 1983 (x=15.0 mm, sd=1.9), as determined by the extension of the skeleton above the top of the stain line. In addition, the mean maximum annual growth rate for each year from about June 1969 to June 1977 was not significantly different to the measured growth between April 1982 and April 1983 (Fig. 4.2). Density bands from about June 1977 to June 1979 were unclear and omitted from the analyses.

4.3.3 Spatial variation in the growth of *Acropora formosa*

The growth of *Acropora formosa* at the three sites between March 1982 and November 1983 is summarised in Figure 4.3. Apart from June 1982, growth rates at the offshore site (1) were always higher than at the inshore sites (2 and 3). The inshore sites had similar growth rates until September 1982; after this date growth rates diverged sharply. Extensive damage, presumably by cyclonic wave action, occurred at site 1 in March 1982 when all experimental colonies were lost. Damage to experimental colonies also occurred at site 3 during this period and at site 1 during December 1982 and March 1983. Maximum growth rates at all sites occurred in November and minima during July 1982. The statistics in Table 4.1 indicate that significant differences in coral growth of *Acropora formosa* occurred between sites and seasons.

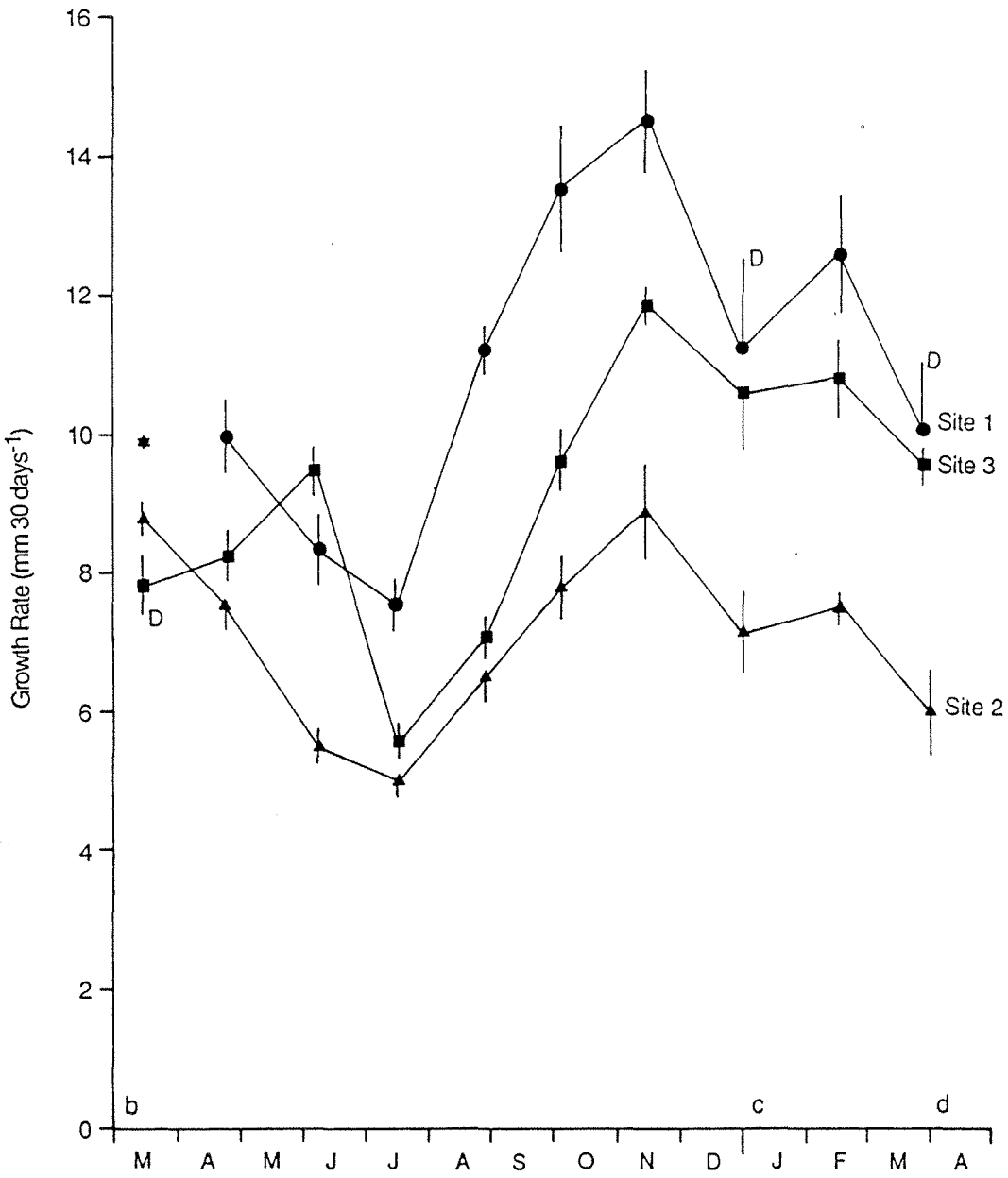


Figure 4.3 Spatial variation in the mean growth of *Acropora formosa* at sites 1, 2 and 3.
Error bars are 95% confidence intervals. (D) damage to experimental colonies; (*) all experimental colonies lost at site 1; (b) T.C. Ian, March 5-6; (c) T. C. Jane ,January, 7-9; (d) T. C. Lena, April 7-8.

Table 4.1 Summary of ANOVA of the growth of *Acropora formosa* at sites 1, 2 and 3 during 'summer' and 'winter'.

Source of variation	DF	SS	MS	F	p
Seasons	1	49.25	49.25	28.40	<0.0001*
Sites	2	68.65	34.32	19.79	<0.0001*
Seasons x sites	2	4.50	2.25	1.30	0.2977
Residual	18	31.21	1.73		
Total	23				

* significant at the 0.05 probability level

During 'winter' coral growth rates at sites 1 and 3 and at the two inshore sites (2 and 3) were not significantly different. However significant differences in mean coral growth existed between sites 1 and 2 (t=3.14, p=0.02, df=7). During 'summer' significant differences existed between the sites (F=23.44, p=0.0003, df=11). Mean growth rates at site 1 (x=13.0, sd=1.4, n=4) were significantly higher (t=6.468, p=0.0006, df=7) than at site 2 (x=7.84, sd=0.76, n=4) and at site 3 (x=10.75, sd=0.94, n=4; t=2.68, p=0.036, df=7). In addition, growth rates at site 3 were significantly greater (t=4.80, p=0.003, df=7) than at site 2.

4.4 DISCUSSION

4.4.1 Intra - annual or seasonal variation

Temporal variation in coral growth showed similar seasonal trends for all species with minimum growth rates coinciding with periods of low seawater temperatures (21° -22° C) and maximum growth rates for *Acropora formosa* (at all sites) and *Acropora hyacinthus* (site 1) occurring during

moderate temperatures (27°-28° C). Maximum growth rates for *Pocillopora damicornis* coincided with maximum mean temperatures (29°-30° C). Table 4.2 summarises the results of the statistical tests between the growth of the three coral species and the environmental parameters during 'summer' and 'winter' at site 1. The low seasonal variability in seabed irradiance (PPFD), sediment deposition and salinity at site 1 in contrast to the marked seasonality in seawater temperatures suggests that the intra-annual or 'seasonal' variation in the growth of these coral species is more likely to be causally related to seawater temperatures than to these other factors.

Table 4.2 Summary of statistical tests for environmental parameters and coral growth at site 1.
ns, not significantly different; > or <, significantly greater or less than at the 0.05 probability level

Parameter	'summer' 'winter'
Seawater temperature	>
Salinity	>
Sediment deposition	ns
Computed PPFD	ns
Wave energy	ns
Maximum wave height	ns
Growth of *Acropora formosa*	>
Growth of *Pocillopora damicornis*	>
Growth of *Acropora hyacinthus*	>

The relationship between coral growth and seawater temperature is clearly positive at all sites (Fig. 4.4 a, b, c; Fig. 4.5 a, b). The correlation coefficients in Table 4.3 are consistent with the suggestion that coral growth was causally related to seawater temperature during May to November (non-cyclone season) and that other factors were causing the variation in coral growth during December to April (cyclone season).

Table 4.3 Correlation coefficients for the relationship between seawater temperature and coral growth.
(r_a) between March 1982 and November 1983 ; (r_b) between May 1 to November 30 for both years; and (r_c) between December 1 and April 31 for both years; (n) number of growth periods.

Species	Site	n	r_a	p	n	r_b	p	n	r_c	p
A. formosa	1	12	0.49	>0.10	8	0.81	<0.02*	4	0.64	>0.20
A. formosa	2	10	0.69	<0.03*	5	0.94	<0.02*	5	0.67	>0.20
A. formosa	3	10	0.64	<0.05*	5	0.95	<0.02*	5	0.22	>0.50
P. damicornis	1	12	0.82	<0.002*	8	0.80	<0.02*	4	-0.06	>0.50
A. hyacinthus	1	11	0.72	<0.01*	8	0.77	<0.05*	3	0.92	>0.05

*, significant at the 0.05 probability level.

A number of possible explanations may be advanced for the variation in coral growth during the December to April period. Cyclonic wave activity, high (>30° C) seawater temperatures, increased sediment deposition and turbidity (due in part to the widespread occurrence of the planktonic blue-green alga, *Trichodesmium erythraeum* ; Creagh, 1985) all occur during December to April in the Dampier Archipelago. In addition, as shown in a

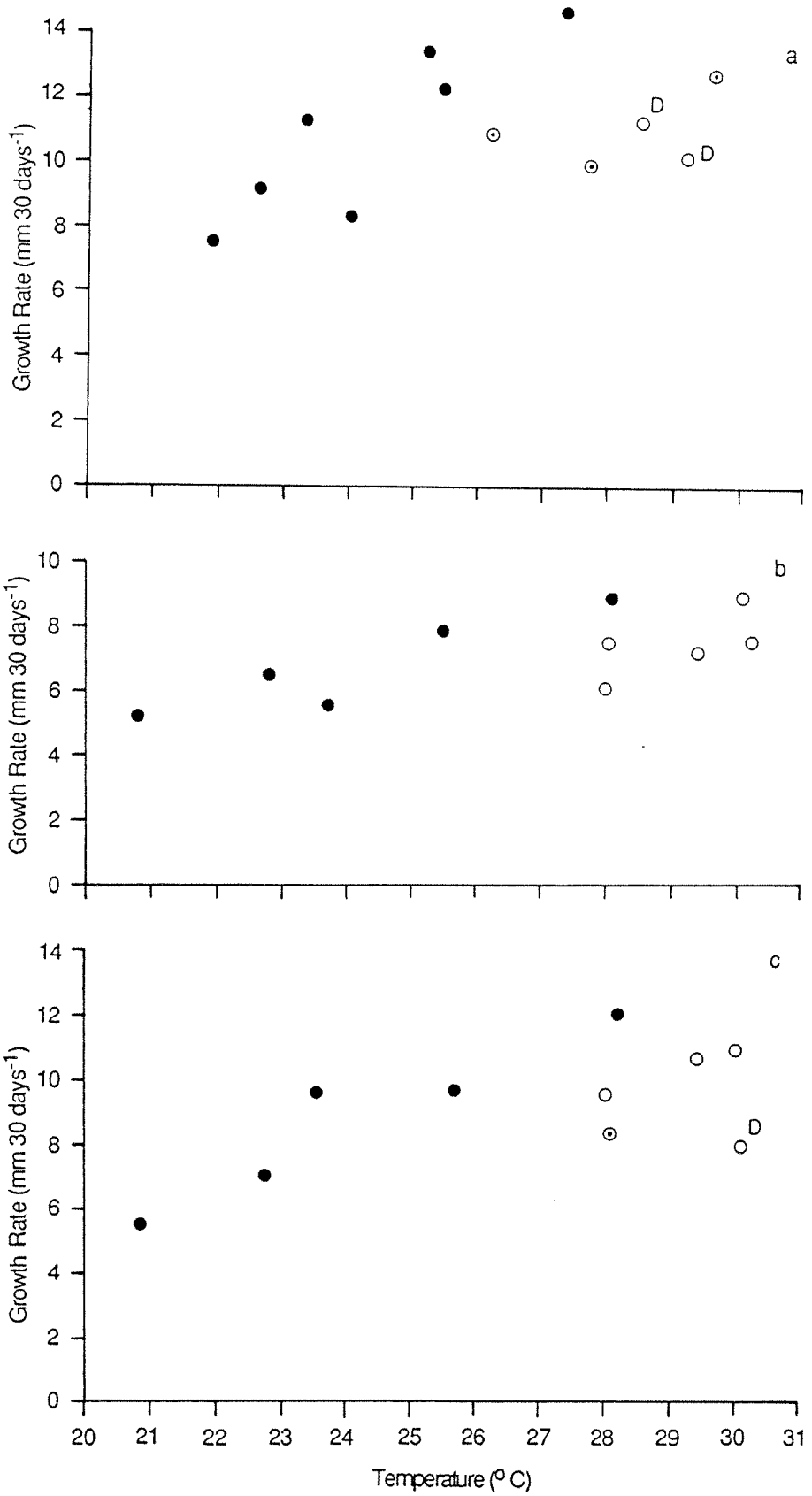


Figure 4.4 Relationship between mean growth rate of *Acropora formosa* and mean seawater temperature at sites 1 (a), 2 (b) and 3(c).
(D) damage to experimental colonies; (●) data from May 1 to November 30; (○) data from December 1 to April 31; (⊙) growth rate for the period following damage to experimental colonies.

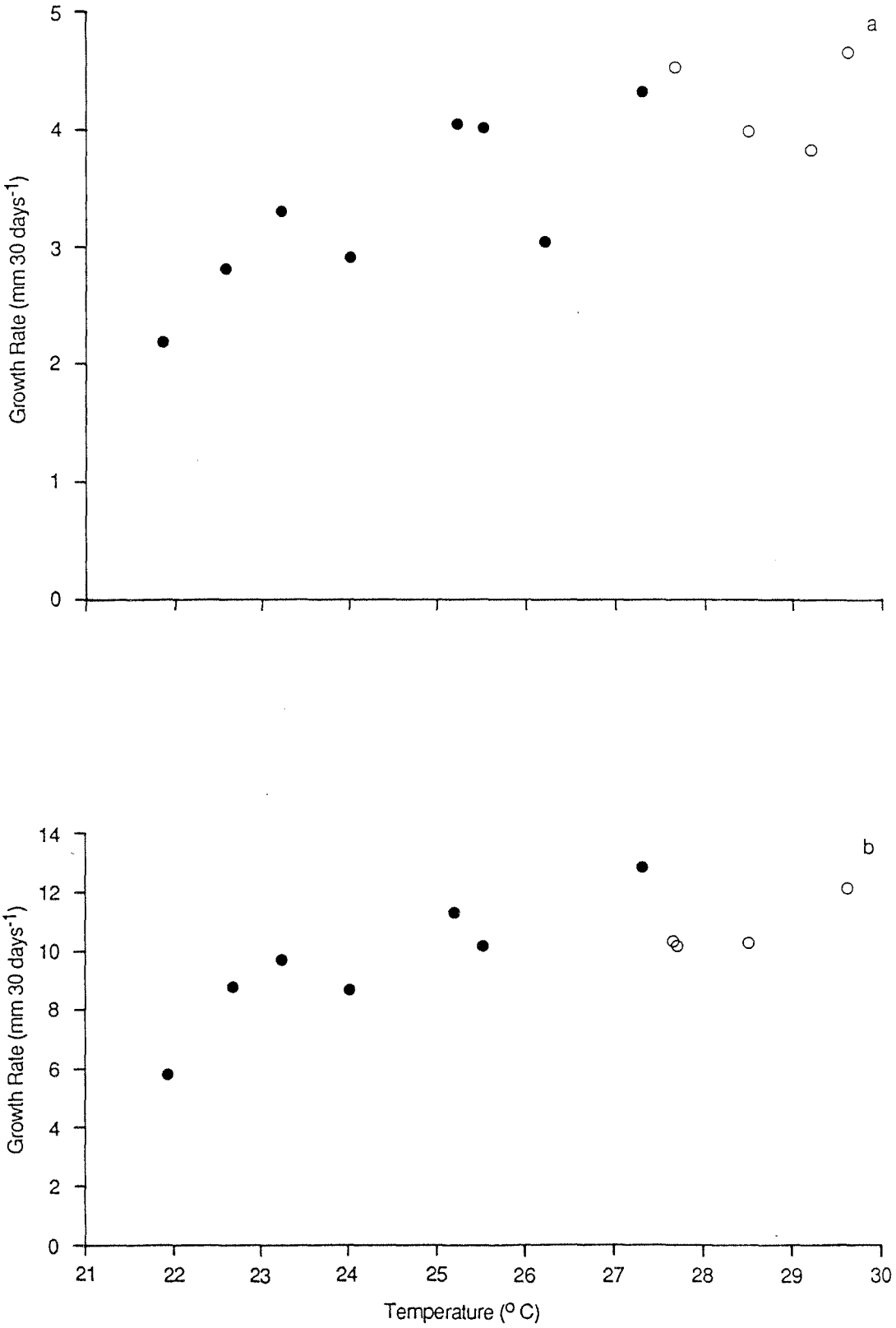


Figure 4.5 Relationship between mean growth rate of (a) *Pocillopora damicornis* and (b) *Acropora hyacinthus* and seawater temperature at site 1.
(●) data from May 1 to November 30; (○) data from December 1 to April 31.

later chapter, the period from December to March each year in the Dampier Archipelago is one of major reproductive activity for spawning coral species such as *Acropora formosa* and *Acropora hyacinthus*. These factors may have caused, independantly or synergistically, the observed variation in the growth of these corals.

For example, although sea temperatures were significantly lower, the growth rates of *Acropora formosa* and *Acropora hyacinthus* at site 1 in November 1982 were significantly higher than in December 1982. Conversely, the growth rates of *Acropora formosa* at site 1 during February and May 1983 were significantly higher than during March 1983 when mean seawater temperatures were similar (in March) and significantly lower (in May). The reduced growth rates of *Acropora formosa* at site 1 in December 1982 and in March 1983 coincided with the occurrence of tropical cyclones (Fig. 4.1), suggesting that reductions in growth were related to these events and not to seawater temperatures. Mechanical damage, again coinciding with cyclonic wave action, also occurred in March 1982 (Fig. 4.3); all colonies of *Acropora formosa* were extensively damaged at site 1 and some were damaged at site 3.

Although branches which were obviously damaged (ie usually identified by branch diameter discontinuities) were not included in the estimation of mean growth rates, there was still a marked reduction in growth of the measured 'undamaged' branches during these periods. These 'reduced growth rates' may be the result of unseen damage to fragile branch tips that reform before the branches are remeasured. Extremely high rates of sediment deposition occur during cyclones (Fig. 2.8) and the large pieces of coral rubble found in sediment traps and on colonies of *Acropora hyacinthus* up to about 2 m above the seabed at site 1 in March/April 1983, following Tropical Cyclone Lena, indicate that during these events large

quantities of coral rubble are mobilised. This raises the possibility that the reduced growth rates of apparently undamaged branches of *Acropora formosa* and *Acropora hyacinthus* may have been due to abrasion of the delicate apical corallites of these fragile species by coral rubble mobilised during cyclones. Observations on the damage and repair of branches of *Acropora formosa* support this supposition. Tips of peripheral, lateral branches of this species were often damaged during the staining process (see 3.2.1) and subsequent observations showed that branch tips were completely reformed within a week . This suggests that branches may be damaged during a cyclone, but are repaired before remeasurement takes place, thereby resulting in reduced mean linear growth of 'undamaged' branches for that period.

This suggestion is supported by comparison with growth rates of *Pocillopora damicornis*, of which a particularly robust form occurs on the seaward reefs in the Dampier Archipelago. Experimental colonies of this species appeared undamaged at site 1 during the same periods and maintained relatively constant growth rates during December 1982 to April 1983. Correlations of growth rates between *Pocillopora damicornis* and *Acropora formosa* increased from r=0.74 (n=12) to r=0.96 (n=8) when growth rates measured from December 1982 to April 1983 (the period when damage occurred to *Acropora formosa* colonies) were omitted.

Although mean seawater temperatures at site 1 during December 1982 to April 1983 were higher than during August to November 1982, growth rates of *Acropora formosa* and *Acropora hyacinthus* were generally lower. Although the reduced growth in December 1982 and March 1983 was probably due to mechanical damage the growth rate of *Acropora formosa* during February 1983 (ie when a cyclone did not occur and there was no obvious damage to the experimental colonies) was significantly lower than

in October and November 1982. In contrast, the growth rate of *Pocillopora damicornis* was significantly higher in February 1983 than in November 1982. Possible explanations for these differences could be different temperature optima for the growth of these species, residual effects following mechanical damage to the more fragile *Acropora* species and the different modes of reproduction for *Pocillopora damicornis* and the *Acropora* species.

Gladfelter (1984) found that the seasonal variation in the growth rate of *Acropora cervicornis* , a species closely related to *Acropora formosa*, was not significantly related to seawater temperature in a study where temperatures were always above 26° C. Clausen and Roth (1975) found that the maximum growth rate of *Pocillopora damicornis* at Enewetok had two temperature optima, 27° C and 31° C. Different temperature optima may also partially explain the higher correlation for the entire study period between growth and seawater temperature for *Pocillopora damicornis* than for the two *Acropora* species (Table 4.3).

Incidences of bleaching (expulsion of zooxanthellae) were observed at all sites in February/March 1982, 1983 and at site 2 in March 1984; maximum seawater temperatures during February/March 1983 were 31.2°, 31.9° and 32.7° C for sites 1,2 and 3 respectively. The expulsion of zooxanthellae can be triggered by stress (Goreau, 1964; Bak,1978) and Yap and Gomez (1981) attributed reduced growth rates of *Acropora pulchra* in the Philippines, to the effect of supra-optimal sea (>30° C) temperatures. Furthermore, Neudecker (1981) found the growth rates of *Acropora formosa* and *Pocillopora damicornis* colonies were lower than controls when colonies were transplanted into an area affected by a thermal effluent (4-6° C above ambient) and that the slower growing *P. damicornis* was more tolerant of thermal enrichment than *A. formosa*. The presence of bleached

colonies during periods of high temperatures at site 1 where sediment deposition was generally low, suggests that these temperatures may be supra-optimal for growth of these species, and may have contributed to the lower growth rates of *Acropora hyacinthus* and *Acropora formosa* during February 1983.

In most cases the Pocilloporidae and Acroporidae have different modes of reproduction and this may also influence growth rates. *Pocillopora damicornis* is commonly a planulating species (ie. fertilisation and larvae development occur internally followed by release of planulae larvae) which breeds intermittently throughout the year (Fadlallah, 1983) and this is likely to be the mode of reproduction for this species in the Dampier Archipelago. In contrast, *Acropora formosa* and *Acropora hyacinthus* are broadcasting species (Table 5.1); that is they shed gametes once a year with fertilisation and subsequent larval development occurring externally. In the Dampier Archipelago, mass spawning of broadcasting species takes place on a few nights about the third quarter of the moon in March. The gametogenic cycle of the Acroporidae occurs over an approximately nine month period (Wallace, 1985; Babcock *et al.* 1986) and this appears to be the case on Western Australian reefs (Simpson, unpublished data) with a rapid increase in ooycyte diameter and spermatogenesis during the month before spawning (Wallace, 1985; Simpson, unpubl data). Although the apical and radial polyps of extending branch tips of many *Acropora* on the Great Barrier Reef are sterile (Wallace, 1985), the growth of *Acropora* in the months preceding spawning may be reduced by the increased level of reproductive activity in the rest of the colony diverting translocated metabolic energy away from extension of the sterile branch tips. Loya (1985) found the ratio of summer to winter growth rates of sexually mature colonies of *Stylophora pistillata* to be lower than sexually immature colonies and

suggested this was due to reproductive activity diverting energy away from growth. Furthermore, the growth rate of *Montipora digitata* was lowest during September, coinciding with a rapid enlargement of spematagonia (Heyward and Collins, 1985). In contrast, the withdrawal of resources normally allocated for reproduction, into growth has also been documented when colonies are reduced below a critical size (Kojis and Quinn, 1985). These data suggest that reproductive activity may have an effect on growth (and vice versa in certain cases) and may partly explain the lower growth rates of *Acropora* in December to April in comparison to October to December.

This conclusion is supported by the lower mean daily growth rate of *Platygyra daedalea* at site 4 during a period of assumed reproductive activity, compared to the inferred average daily growth rate during an assumed non-reproductive period. The mean daily growth of 7 colonies of *Platygyra daedalea* between September 20, 1982 to April 19, 1983 (corresponding closely to the annual period of gametogenesis for this species on Western Australian reefs; Simpson, unpupl. data) was 0.035 mm d^{-1}, and was significantly lower ($t=-2\text{-}176$, $p<0.03$) than the annual mean daily growth rate (0.041 mm d^{-1}) of 11 colonies of the same species from March 31, 1982 to April 19, 1983. Assuming the 11 colonies stained in March 1982 grew at similar rates, during September to April, to the 7 colonies stained in September 1982, and all were reproducing, then the mean daily growth rate of this species during the assumed period of reproductive activity was 73% of the inferred growth rate (0.048 mm d^{-1}), during the assumed non-reproducing period (March to September 1982). Considering that in all the other species studied, growth in 'summer' was greater than in 'winter', it is suggested that the lower growth rates of *Platygyra daedalea* during September to March was due partly to the increase in reproductive activity

during this period.

Maximum growth rates of *Acropora formosa* and *Acropora hyacinthus* at site 1 occurred in November 1982 coinciding with near maximum computed PPFD. From October 1982 light levels at this site declined as a result of increased light attenuation (caused by the presence of *Trichodesmium erythraeum* and seasonal changes in the amount of sediment suspended in the water), to a minimum in February 1983. These lower PPFD levels coincided with increased growth rates of *Acropora formosa* and *Acropora hyacinthus* at this site in November 1982, followed by reduced growth rates of these species in January and February 1983. Maximum growth of *Pocillopora damicornis* in February 1983 at this site coincided with minimum light levels. Similarly at sites 2 and 3, sharp decreases in PPFD during October and November, 1982 coincided with increases in the growth rate of *Acropora formosa* at these sites. Although PPFD at site 2, from November 1982 to March 1983, was either higher or similar to levels at site 3, growth rates of *Acropora formosa* at site 2 were significantly lower and was more likely due to elevated sediment deposition rates at this site as a result of nearby dredging activities. The conflicting trends between PPFD and coral growth outlined above, suggest that light-availability did not significantly influence the temporal patterns of growth of these species during December 1982 to March 1983.

Further evidence to support this conclusion can be found in a parallel study by Crossland (1981) on the growth of *Acropora* cf *formosa* and *Pocillopora damicornis* at the Abrolhos Islands (Fig. 1.1). He suggested that temperature was the primary determinant factor for skeletal growth rate and that light-availability was a secondary or modifying influence on coral growth. Mean global radiation for the Abrolhos between 1971-75 was higher in summer and lower in winter than mean global radiation recorded at

Dampier during this study (Figure 2.9b). This and the shallower depth (2-3 m) and generally clearer water at the Abrolhos site suggest that the differences in overall light levels between the site in the Abrohos and site 1 in the Dampier Archipelago during 1982-83 were minimal yet annual growth rates of both species were over 3X greater at the Dampier Archipelago (Table 4.6). In contrast, mean monthly temperatures at the Abrolhos range from about 20-24° C (Crossland, 1981) whereas at site 1 during 1982-83, mean temperatures ranged from 22-30° C. These data provide further evidence that seawater temperature is the primary determinant factor for the seasonal coral growth patterns observed in the Dampier Archipelago.

It therefore appears that seawater temperatures, mechanical damage, supra-optimal sea temperatures, the effect of increased reproductive activity, and the metabolic cost of sediment rejection were possible influences, to varying degrees, on the temporal variation of growth of the *Acropora* species during this study. However, the data suggest that temporal variation in the growth of *Acropora formosa* and *Acropora hyacinthus* during the periods from May 1 to November 30 (ie when sea temperatures are below about 27° C) were primarily related to seawater temperatures whereas the major cause of variation in the growth of these species at site 1 from December 1 to April 30 (ie during the cyclone season) was the frequency and severity of damage to these species by cyclonic waves. In contrast, the growth of *Pocillopora damicornis* appears to be causally related to sea temperatures throughout the year with 67% (ie. r^2=0.67) of the seasonal variation in growth being explained by the seasonal variation in temperature .

The temporal trends in coral growth at these sites are consistent with published seasonal variations observed in staghorn corals, in locations where minimum temperatures are below 26° C (eg Shinn, 1966; Crossland,

1981; Oliver *et al.* 1983; Oliver, 1985).

4.4.2 Inter - annual variation in the growth of *Platygyra daedalea*

The mean maximum annual growth of 11 colonies of *P. daedalea* measured from April 1982 to April 1983 was not significantly different from the mean maximum annual growth, determined retrospectively from x-radiographs, of other colonies of the same species for the preceding ten years, excluding the period from about June 1977 to June 1979 for which reliable data were not available. This suggests that environmental conditions at site 4 during April 1982 to April 1983 were generally similar to those which prevailed during most of the preceding ten year period. Extending this logic to site 1 (about 5 km away; Fig 1.2) suggests that the intensive coral growth studies conducted at site 1 during 1982 and 1983 were carried out in conditions that could be defined broadly as 'normal' and that the results of these studies provide an estimate of 'typical' seasonal variation in the growth of these species.

4.4.3 Spatial variation in the growth of *Acropora formosa*

A summary of the differences in coral growth and in environmental parameters measured at three sites during 'summer' and 'winter' is shown in Table 4.4.

Table 4.4 Summary of statistical tests of the environmental parameters and growth of *Acropora formosa* at sites 1, 2 and 3. (ns, not significantly different; > or <, significantly greater or less than at the 0.05 probability level)

		'Summer'			'Winter'		
Parameter	Sites	1-2	1-3	2-3	1-2	1-3	2-3
Temperature		ns	ns	ns	ns	ns	ns
Salinity		<	<	ns	<	<	ns
Sediment deposition		<	<	>	ns	ns	ns
Computed PPFD		ns	>	ns	ns	ns	ns
Wave energy		>	>	-	>	>	-
Coral growth		>	>	<	>	ns	ns

Spatial differences in coral growth rate and in the environmental parameters were minimal during April to August 1982. During 'winter' mean coral growth rates were not significantly different at the inshore sites (2 and 3) and there was no significant difference between these sites in any of the environmental parameters measured. During 'winter' growth rates of *Acropora formosa* at site 1 were generally higher than at the two inshore sites although there was no significant difference in mean seawater temperature, sediment deposition and PPFD between these sites. The higher rate of growth of *Acropora formosa* at site 1 during 'winter' may be due to the generally higher temperatures (minimum 20.4^{o} C) at this site in comparison to sites 2 (minimum 19.1^{o} C) and 3 (minimum 18.6^{o} C).

In 'summer' mean growth rates of *Acropora formosa* were significantly different between all sites with site 1 > site 3 > site 2. Mean seawater

temperatures (all sites) and PPFD (sites 1 and 2; sites 2 and 3) were not significantly different although PPFD at site 1 was significantly higher than at site 3. Sediment deposition in 'summer' was significantly different between all sites with site 1 < site 3 < site 2. Although mean PPFD levels were relatively low at the three sites during 'summer', these levels are unlikely to be limiting growth of this species (Chalker and Dunlap, 1983), suggesting that differences in growth rate of *Acropora formosa* between the three sites in 'summer', were due to effects of differences in sediment deposition rates rather than differences in light-availability.

Past studies elsewhere have shown that high rates of sediment resuspension and sedimentation reduce coral growth (Dodge *et al.* 1974; Dodge and Vaisnys, 1977; Hudson, 1981) especially that of branching, foliose and tabular species (see Endean, 1976; Hudson *et al.* , 1982; Kendall *et al.* 1984).

To examine the relationship between the spatial variation in growth of *Acropora formosa* and the physical parameters considered to influence growth of this species, correlations were sought between differences in coral growth between the three sites and differences in selected environmental variables, for 6 growth periods between June 30, 1982 and March 10, 1983. This removes the temporal (seasonal) component and assumes that the growth response of this species to seawater temperature is the same at all sites. Significant negative correlations were obtained between coral growth and total and refractory sediment deposition rate (Table 4.5).

Table 4.5 Correlation coefficients for differences in the growth of *Acropora formosa* and environmental variables between sites 1, 2 and 3 for 6 growth periods from June 1982 and March 1983.

Variable	n	r	p
Sediment deposition (Total)	18	-0.613	<0.008*
Sediment deposition (Refractory)	18	-0.660	<0.004*
Seawater temperature	18	0.062	0.805
Salinity	18	-0.436	0.070
Computed PPFD	18	0.287	0.249

*, significant at the 0.05 probability level

The relationship between difference in growth of *Acropora formosa* and difference in refractory sediment deposition rate (Fig. 4.6) has been approximated by the third order polynomial equation :

$$Y= 0.5441-0.1357x+0.0011x^2-0.000003x^3; \quad r=0.73$$

The effects of sediment resuspension and sediment settling on reef corals are mainly associated with removal of sediment from the surface of the live coral, and reduced photosynthesis caused by lowered light-availability. Sediment is removed from the surface of corals actively and passively. Active (energy consuming) removal of sediment by corals is achieved by the secretion of mucus which is then removed by the action of waves and current. Thus sediment settling on a coral may reduce growth by diverting energy normally available for growth to the production of mucus for sediment removal. Low light levels may also cause a decrease in the photosynthetic products translocated to the growing branch tip thereby causing a reduction in linear growth.

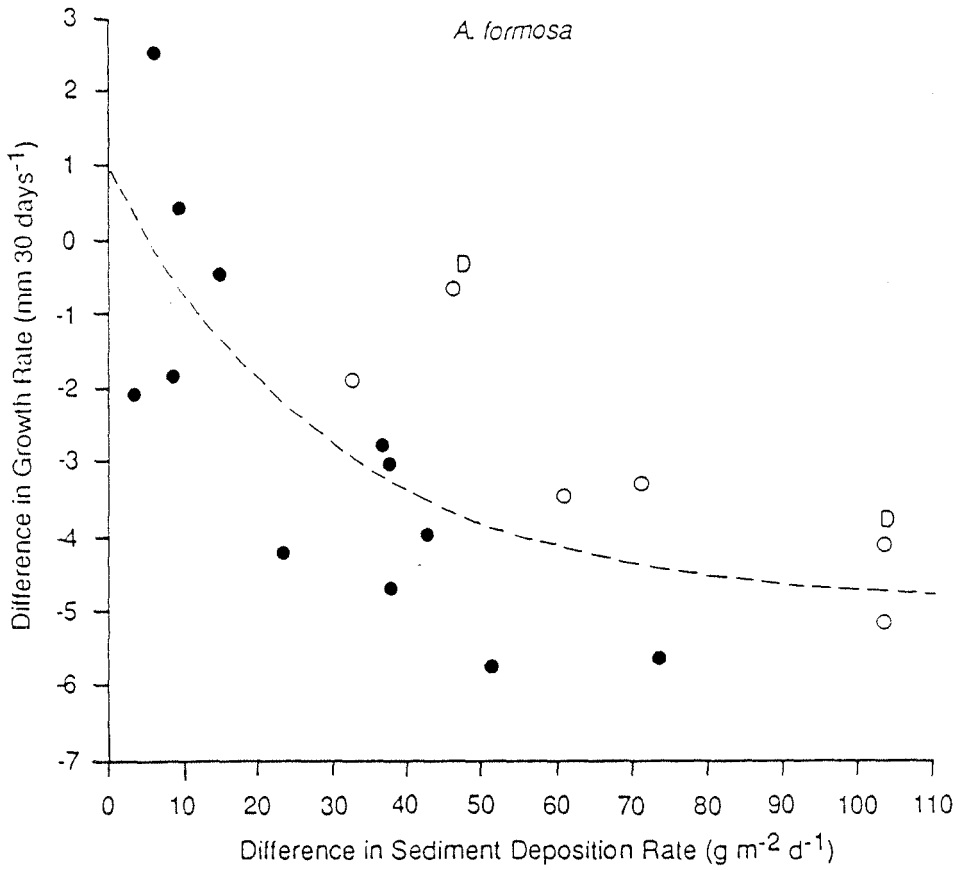


Figure 4.6 Relationship between differences in mean growth rate of *Acropora formosa* and corresponding differences in mean sediment deposition rate between June 30, 1982 and March 2, 1983 for sites1, 2 and 3.
(D) damage to experimental colonies; (●) data from June 30 to November 30, 1982; (○) data from December 1,1982 to March 2, 1983.

Computed PPFD at sites 2 and 3, were not significantly different during December 1982 to February 1983 whereas sediment deposition rates (refractory fraction) were significantly greater and coral growth rates significantly less at site 2 than at site 3. These data suggest that the difference in coral growth between these two sites in December and February was due to the metabolic cost of sediment rejection rather than by reduced photosynthesis. This conclusion assumes that the computed mean PPFD is an accurate estimation of actual PPFD: an assumption supported by actual PPFD measured by data loggers deployed at sites 1 and 2 over a 11 day period in November 1983 (Fig. 2.14).

During November 1982 to March 1983 high total sediment deposition rates (>259 g m-2 d-1) were recorded at site 2 and coincided with dredging and dumping activities in the vicinity of this site during this period. In April 1983 experimental colonies of *Acropora formosa* at this site were recorded as appearing 'unhealthy' (patchy loss of zooxanthellae throughout the colony) and by March 1984 many of the arborescent *Acropora* colonies on this reef were dead. From approximate maximum colony size (2 m diameter) and growth rates (0.1 m y^{-1}) it is concluded that these colonies had survived at least 10 years. This supports the conclusion that the observed coral mortality was caused by a rare (>10 y) event, which, in the Dampier Archipelago, could be the dredging and dumping activities that occurred in the vicinity of site 2 and 3 from November 1982 to February 1983.

4.4.4 Annual growth rates

In a review on coral growth, Buddemeier and Kinzie (1978) suggested that if deep-living and clearly stressed corals are excluded, then the range of linear growth for massive corals was between 4 to 20 mm y^{-1}. They suggest under optimum conditions maximum 'normal' growth is 10-15 mm y^{-1} and

average 'normal' growth about 10-12 mm y^{-1} for most massive species. For staghorn coral species they suggest an upper limit of branch extension at 200 mm y^{-1}.

The mean annual growths of *Acropora formosa* and *Pocillopora damicornis* at site 1 and *Platygyra daedalea* at site 4 are shown in comparison to the same or similar species from other geographical localities in Table 4.6. The comparison suggests that the growth rate of corals in the Dampier Archipelago is high. The exception is *Acropora formosa* , which has moderately high annual growth rates in comparison with other localities. However the annual growth rate for this species in the Dampier Archipelago may be an underestimate because of the frequent damage by wave action at site 1.

Table 4.6 Comparison of annual growth rates of three species of scleractinian corals in the Dampier Archipelago with other localities.

Species	Annual growth (cm y^{-1})	Locality	Source
Acropora formosa			
	18.5	Samoa	Mayor (1924)
	~8.0	Thailand	Charuchinda and Hylleberg (1984)
	4.0	Abrolhos Is.	Crossland (1981)
	~16.0	Great Barrier Reef	Oliver *et al.* (1983)
	13.7	Dampier Arch.	This study
Pocillopora damicornis			
	3.6	Gibraltar	Stephenson and Stephenson (1933)
	2.4	Gibraltar	Manton (1935)
	2.8	Samoa	Mayor (1924)
	3.9	Panama	Glynn (1977)
	1.4	Abrolhos Is.	Crossland (1981)
	3.6-6	eastern Pacific	Richmond (1985)
	4.5	Dampier Arch.	This study
Platygyra spp.			
	~0.5-1.2	15 localities	Weber and White (1974)
	~1.5-1.6	Dampier Arch.	This study

CHAPTER FIVE

CORAL REPRODUCTION AND MASS SPAWNING

5.1 INTRODUCTION

A review by Fadllalah (1983) on the reproduction of scleractinian corals shows that most research, before 1980, dealt with species which are fertilised internally and have been observed to release planula larvae. This emphasis led to the generalisation that vivipary, in this instance planulation, is the typical mode of reproduction in hermatypic corals and occurs intermittently throughout the year. Recent findings have shown that many species release gametes which are fertilised externally and develop outside the parent colony (Rinkevich and Loya, 1979; Szmant-Froelich *et al.* 1980; Bothwell, 1981; Kojis and Quinn, 1981,1982a,1982b; Harriot, 1983; Babcock, 1984). Further work by Harrison *et al.* (1983, 1984) have invalidated the generalisation of vivipary in scleractinian corals, and more coral species are now known to spawn gametes (broadcasting species) than to brood planulae (brooding species). Additionally, the spawning of many broadcasting species appears to be synchronous and confined to a single, brief annual period (Harrison *et al.* 1984).

Multispecific, synchronous spawning, or 'mass spawning', of scleractinian corals has been observed on the Great Barrier Reef (GBR), during late spring to early summer (October - December) since 1981 (Harrison *et al.* 1983, 1984; Willis *et al.* 1985; Babcock *et al.* 1986), and occurs predominantly on the third to sixth nights after a full moon, during a period of rising sea temperatures (Babcock *et al.* 1986). Offshore reefs appear to spawn exactly 1 lunar month later than inshore reefs, and synchronous spawning has been recorded between reefs separated by as much as 5^{o} of latitude (Babcock *et al.*

1986). At present, 133 species of scleractinian corals on the Great Barrier Reef (of a total of 356) are known to spawn during this period: it has been postulated that ' .... it is likely that the majority of corals on the Great Barrier Reef participate in the annual mass spawning phenomenon ' (Willis *et al.* 1985).

This chapter describes a coral spawning event that was observed, fortuitously, in the Dampier Archipelago during March 1984, and a second mass spawning of corals observed at the same reef, in March 1985. Observations during March 1985 confirmed the coral mass spawning phenomenon in the Dampier Archipelago, documented some of the species involved and characterised aspects of the physical environment during the spawning period. Findings from subsequent studies (in 1986 and 1987) of coral mass spawning on other Western Australian reefs are also summarised. In this chapter 'mass spawning' is defined as the multispecific, synchronous release of gametes by scleractinian corals, 'spawning period' refers to the few days on which mass spawning occurs each year, and 'breeding season' refers to the season (for example spring in the Great Barrier Reef) in which mass spawning occurs.

These are the first recorded observations of mass spawning of scleractinian corals in the Indian Ocean, the first recorded in autumn rather than late spring to early summer, and the first recorded outside the Great Barrier Reef Province. Environmental data collected during the spawning periods in 1984 and 1985 are presented. Possible causal factors determining the timing of mass spawning of scleractinian corals are discussed. Implications for management of coral reefs, in the Dampier Archipelago and elsewhere in Western Australia, are outlined.

5.2 MATERIALS AND METHODS

5.2.1 Study sites

To determine the timing, mode, and spatial extent of scleractinian coral reproduction in the Dampier Archipelago, coral species were studied at 3 sites designated 5, 6 and 7 in Figure 2.1. Site 5 is on an inshore subtidal fringing reef about 2 m below chart datum (hereafter referred to as datum) on the north side of Conzinc Island and is characterised by turbid water in summer, weak currents, and intermittent, moderate long period wave action caused by tropical cyclones (during December to April). Site 6 is on an intertidal reef about 1.7 m above datum on the eastern side of Keast Island. This site is typified by turbid water, strong currents and is protected from swell by adjacent islands. Site 7 is on the reef crest at Hamersley Shoal (about 0.5 m above datum), an offshore reef with predominantly clear water, weak currents and constant swell activity.

5.2.2 Reproductive status and spawning records

Polyp reproductive status was determined either by examination of freshly broken pieces of live coral in the field (Fig. 5.1a) or under a dissecting microscope in the laboratory (Fig. 5.1b). The presence of pigmented eggs was used as a criterion for reproductive maturity (Harrison *et al.* 1984).

In order to determine the reproductive status of selected coral species in the Dampier Archipelago at the time of mass spawnings on the Great Barrier Reef, corals (28 species, 60 colonies) were collected at site 6 on November 12 and 13, 1984 (dates of mass spawning on the offshore reefs on the Great Barrier Reef in 1984) and examined for the presence of mature eggs. *In situ* assessment of the reproductive status of various acroporiid and faviid species were also made at site 5 on November 12, 1984. On October17, 1985 (less than three weeks before the dates of mass spawning at inshore reefs on the Great

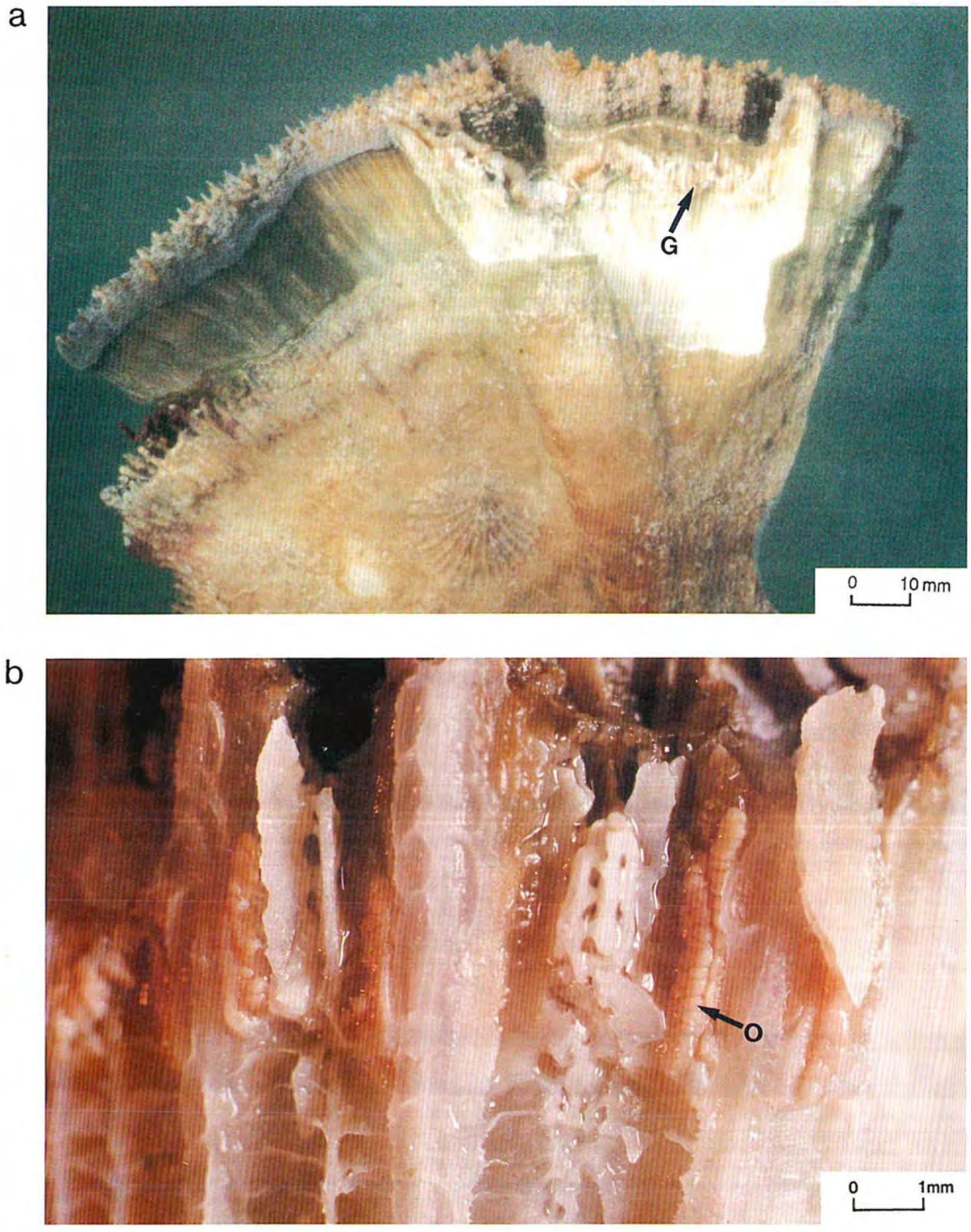


Figure 5.1 (a) Polyp of *Lobophyllia hemprichii* split through the centre exposing gonads (G). Photograph: C J Simpson.
(b) polyps of *Platygyra sinensis* split through the centre exposing gonads containing pigmented ooyctes (O). Photograph: C J Simpson.

Barrier Reef) selected acroporiid and faviid coral species were tagged at site 6 and 20 samples were collected and examined for the presence of pigmented eggs.

To assess the taxonomic extent of coral reproduction during March 1985, corals were sampled randomly before (at sites 5, 6 and 7; 46 species, 139 colonies) and after (at sites 5 and 6; 43 species, 86 colonies) the dates of mass spawnings and their reproductive status assessed. During the 2 nights of mass spawning, coral species observed releasing gametes were sampled for identification. Additionally, corals at site 5 (*Acropora formosa* , *Acropora hyacinthus*, *Acropora* cf *danai* , *Acropora* cf *grandis* , *Acropora tenuis* , *Astreopora* cf *myriophthalma* , *Favites pentagona* , *Platygyra daedalea* , *Galaxea fascicularis* , *Turbinaria mesenterina*) and site 6 (*Acropora formosa*, *Acropora hyacinthus*, *Acropora aspera*, *Acropora sp.1*, *Favites abdita*, *Favia pallida*, *Goniastrea retiformis*, *Platygyra sinensis*) were tagged and later sampled on March 13, 19 (site 5) and March 14, 15 and16 (site 6).

To determine whether corals in an aquarium would spawn simultaneously with *in situ* corals, pieces of 6 species (*Galaxea fascicularis*, *Favites abdita*, *Platygyra daedalea*, *Acropora hyacinthus*, *Leptoria phrygia*, *Acropora millepora*) were removed from the reef, at site 6, at 1300h on March 14, 1985 and maintained in an aquarium under a natural photoperiod and at ambient seawater temperatures (29 ^{o}C $\pm$ 2 ^{o}C) until March 18.

Spawning of corals in the field was determined directly by observation of gamete release *in situ* (Fig. 5.2a), the appearance of eggs on the sea surface, or inferred from the disappearance of mature gametes in sequential samples from tagged colonies. In the laboratory, spawning was inferred by the appearance of gametes in the aquarium. The approximate size range of floating eggs was estimated from photographs (15X) of eggs collected and preserved in 10% formalin seawater during the mass spawnings on March 15,

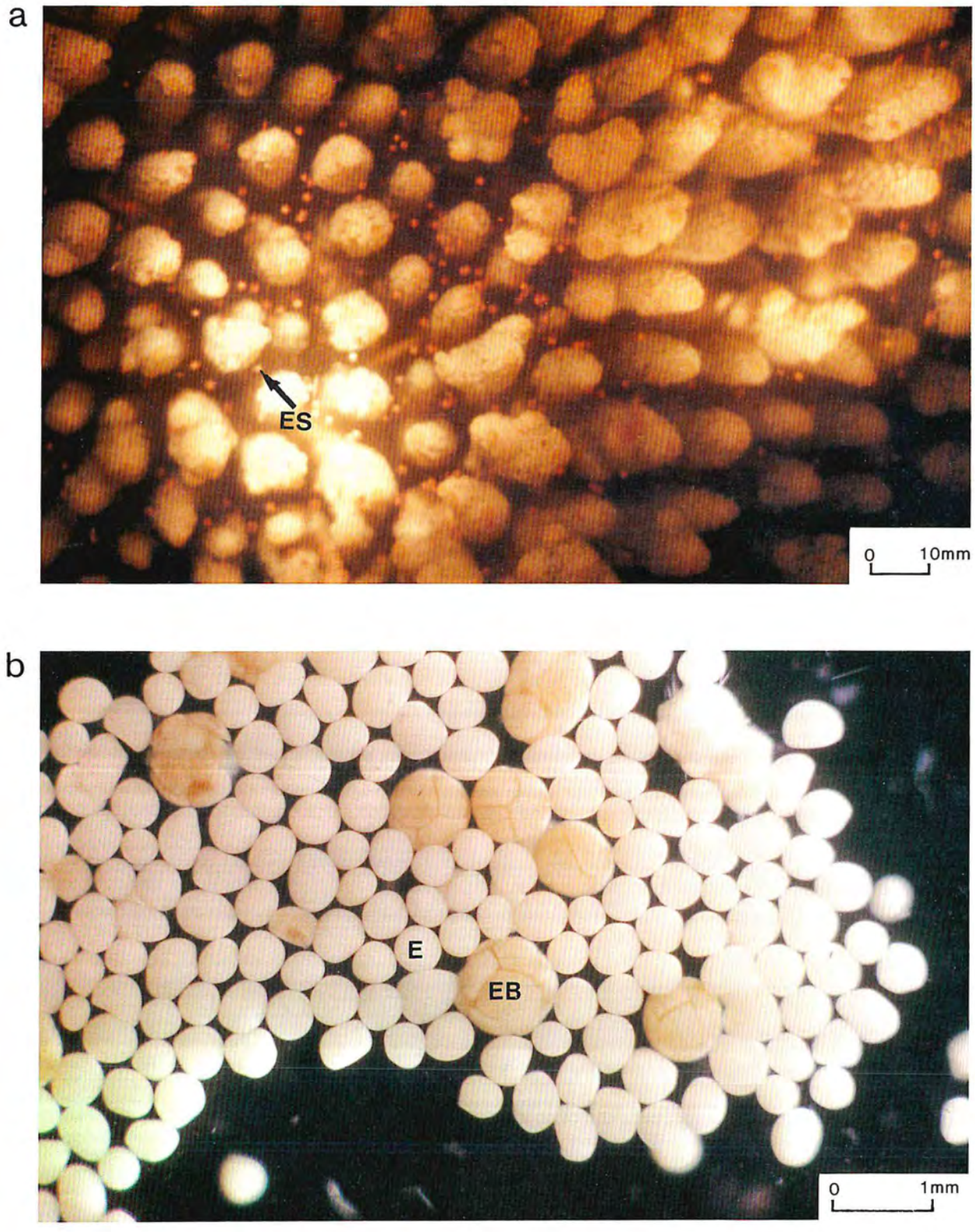


Figure 5.2 (a) *in situ* spawning of *Acropora millepora* showing the release of buoyant egg and sperm bundles (ES) between 2010h-2100h on March 15, 1985 at Keast Island reef. Photograph: C J Simpson;
(b) unfertilised eggs (E) and egg bundles (EB) collected from the sea surface at Keast Island reef between 2000h-2050h on March 16, 1985; colour of eggs at the time of collection was mainly pink. Photograph: E I Paling.

1985 (Fig. 5.2b). The maximum diameter of 50 eggs was determined with a digitizer (Summagraphics Corp. USA).

5.2.3 Environmental data

Data loggers (Windrift Instruments, WA) recording (15 minute sampling interval) instantaneous measurements of depth (± 0.05 m), seawater temperature (± 0.02 ^{o}C) and bottom irradiance (± 5%) were deployed during the spawning periods in 1984 and 1985. Also salinity (± 0.05 $^{o}/_{oo}$) and seawater temperature were measured during March and November in 1984 and in March 1985 with a Yeo - Kal Model 605 temperature - salinity meter. The times of sunset and moonrise were recorded on the nights of March 15, 16 and 17, 1985.

5.3 RESULTS

5.3.1 Taxonomic extent

Twenty-seven species of scleractinian corals were found (directly and indirectly) to release gametes between March 13-19. Eighteen species were observed, *in situ* , releasing gametes on two consecutive nights after the full moon in March 1985. One species (*Acropora florida*) spawned on both nights. Spawning in a further 9 species was inferred from the disappearance of mature eggs in sequential samples from tagged colonies (Table 5.1). No species were observed to release planulae. About 70% (32 species) of all corals sampled before March 15, at sites 1, 2 and 3, contained mature eggs. A similar survey at sites 1 and 2 after March 16, found 23% (10 species) with mature eggs. Six of these species (*Acropora* cf *clathrata*, *Astreopora* cf *myriophthalma*, *Favia matthaii*, *Favia stelligera*, *Goniastrea palauensis*, *Platygyra lamellina*) contained low numbers of eggs, the remainder (*Montastrea valenciennesi*, *Moseleya latistellata*, *Galaxea fascicularis*,

Table 5.1 List of coral species sampled in the Dampier Archipelago during November 1984 and March 1985.

Colonies containing pigmented eggs (total number sampled); * - low number of eggs in samples; ** - high number of eggs in samples.
Spawning species : S - *in situ* spawning observed at site 6 between 2010h-2100h on March 15,1985; S^* - *in situ* spawning observed between 2010h-2100h on March 15,1985 and between 2000h-2020h on March 16,1985 at site 6; S^2 - spawned at site 6 between 1430h on March15 and 1545h on March 16,1985 (inferred from the disappearance of eggs in consecutive samples) ; S^1 - spawned at site 5 between 1000h on March 13 and 1400h on March 19,1985 (inferred from the disappearance of eggs in consecutive samples).

	Nov. 12-13 1984	March 12-14 1985	March 15-16 1985	March 17-20 1985
Sites	6	5,6,7	5,6	5,6
Days after full moon	3-4	5-7	8-9	10-13
ACROPORIDAE				
Acropora formosa	0(5)	12(13)	S	0(8)
A. hyacinthus	0(3)	19(19)	S	0(4)
A. florida	0(3)	3(3)	S^*	0(1)
A. tortuosa	-	3(3)	-	-
A. cf clathrata	-	4(5)	-	1(1)*
A. attstella	0(1)	-	S	-
A. cf danai	-	3(3)	S^1	0(1)
A. tenuis	0(1)	2(2)	S^1	0(2)
A. cf nasuta	0(2)	0(2)	S	0(1)
A. millepora	0(2)	3(3)	S	0(1)
A. cf microphthalma	0(1)	1(1)	-	-
A. aspera	0(1)	1(1)	S^2	0(4)
A. cf grandis	-	11(11)	S^1	0(3)
A. spicifera	0(1)	1(1)	-	-
A. verweyi	0(1)	1(1)	-	-
A. pulchra	-	1(1)	S^1	0(1)
A. anthoceris	-	2(2)	-	-
A. cf robusta	-	0(1)	-	-
Acropora sp.1	-	1(1)	S^2	-
Astreopora gracilis	0(2)	1(1	S	-
A. cf myriophthalma	-	4(4)	-	1(1)*
Montipora verrucosa	-	0(1)	-	0(1)
M. hispida	0(2)	-	S	0(2)

table continued next page

Table 1 continued:

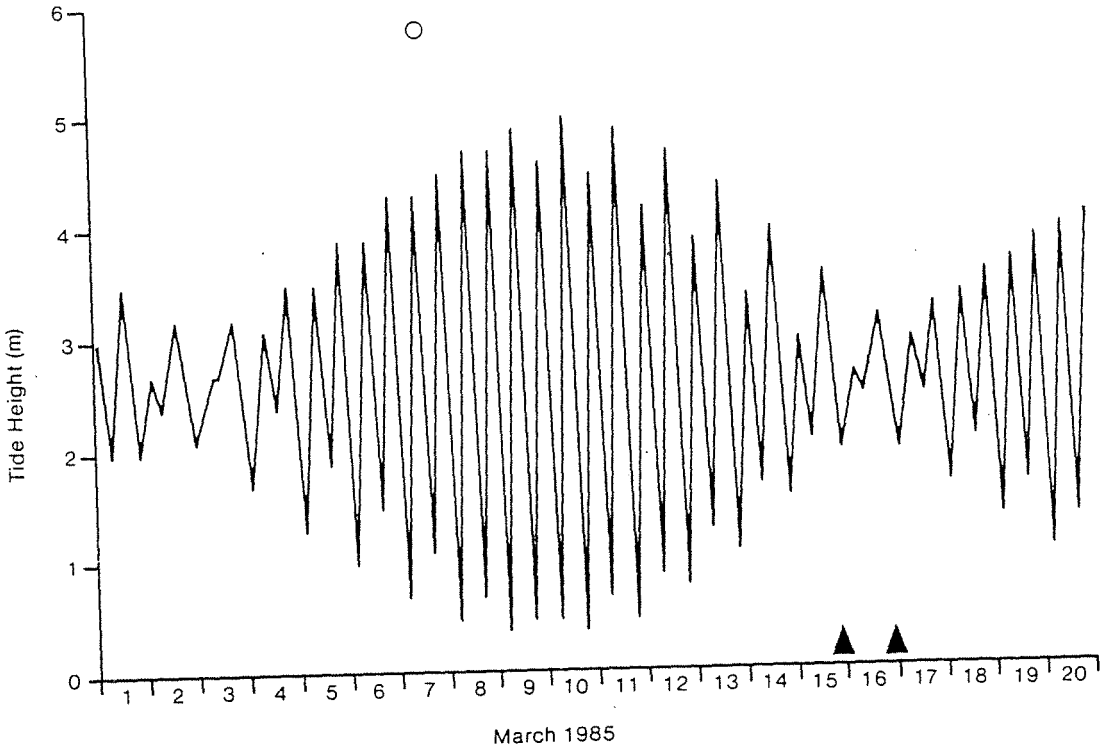
FAVIIDAE				
Caulastrea tumida	0(2)	-	-	0(2)
Cyphastrea serailia	0(1)	1(3)	-	-
Favia pallida	-	1(1)	S[2]	0(1)
F. matthaii	-	-	-	1(2)*
F. stelligera	-	1(1)	-	1(3)*
Favites abdita	0(4)	4(4)	S	-
F. cf *rotundata*	-	0(1)	-	0(1)
F. pentagona	-	3(3)	S[1]	-
F. halicora	-	-	S	-
F. lexuosa	-	-	-	0(1)
Goniastrea palauensis	-	-	-	1(1)*
G. retiformis	0(3)	1(1)	S	0(6)
G. aspera	-	-	S	0(2)
Leptoria phrygia	0(2)	3(3)	-	0(1)
Montastrea curta	-	-	-	0(1)
M. magnistellata	0(1)	-	S	-
M. valenciennesi	-	2(2)	-	1(1)**
Platygyra daedalea	0(2)	5(5)	S[1]	0(5)
P. sinensis	0(4)	6(6)	S	0(5)
P. cf *pini*	-	1(1)	S	-
P. lamellina	-	-	-	1(1)*
Leptastrea cf *pruinosa*	-	-	-	0(2)
Moseleya latistellata	0(1)	-	-	1(1)**
OCULINIDAE				
Galaxea astreata	-	1(2)	-	-
G. fascicularis	0(3)	1(1)	-	2(3)**
MERULINIDAE				
Merulina ampliata	0(1)	-	S	-
Hydnophora exesa	-	0(2)	-	0(1)
H. microconos	-	-	-	1(1)**
MUSSIDAE				
Lobophyllia hemprichii	0(5)	6(6)	S	0(2)
PECTINIIDAE				
Echinophyllia aspera	-	1(1)	-	0(1)
AGARICIIDAE				
Pavona decussata	0(1)	0(3)	-	0(2)
THAMNASTERIIDAE				
Psammocora digitata	-	0(1)	-	-
FUNGIIDAE				
Fungia fungites	-	0(1)	S	0(1)
PORITIDAE				
Goniopora minor	-	-	-	0(2)
G. tenuidens	-	0(1)	-	0(1)
Porites heronensis	0(2)	0(2)	-	0(2)
P. lutea	0(3)	0(5)	-	-
P. lobata	-	0(3)	-	0(1)
DENDROPHYLLIIDAE				
Turbinaria mesenterina	-	0(1)	-	0(2)

Hydnophora microconos) having high numbers of mature eggs.

In total, 62 species of scleractinian corals were sampled between March 12-20, 1985 and 46 species (74%) were found to contain ripe gonads. Five species that did not contain eggs (*Caulastrea tumida, Favia flexuosa, Montastrea curta, Leptastrea* cf *pruinosa, Goniopora minor*) were only sampled after the observed spawning periods. At sites 5, 6 and 7, 62%, 83% and 57% (respectively) of the species sampled before March 15 contained mature eggs. Furthermore, as the presence of pigmented eggs (using a dissecting microscope) was used as the criterion for reproductive maturity, the results for dioeceous species with small polpys (eg *Porites* spp., *Turbinaria* sp.) in Table 5.1, should be interpreted with caution as eggs/testes in these species are sometimes difficult to see. In addition, on March 14 at site 7, 10 colonies of *Acropora hyacinthus*, the dominant species at the site, were all found to contain mature eggs. Of the 46 species found to contain ripe gonads, 8 families of scleractinia were represented, although most species were confined to two families, Acroporidae (21 species) and Faviidae (18 species). Of the 27 species found to release gametes during this period 5 families of scleractinia were represented: Acroporidae (14), Faviidae (10), Merulinidae (1), Mussidae (1) and Fungiidae (1). Mature gonads were not observed in the coral samples collected at site 6 on November 12 and 13, 1984 (Table 5.1) or in samples collected in October 1985.

5.3.2 Day of spawning

Coral spawnings occurred at site 6 on March 25 and 26, 1984. In 1985, scleractinian corals were observed at site 6 to be spawning on the nights of March 15 (18 species) and March 16 (1 species). These dates, in both years, occurred on the eight and ninth nights after the full moon in March (Fig. 5.3). During March 1984, observations were not made on the seventh or tenth nights after the full moon. In 1985, the eight tagged species at site 6 all



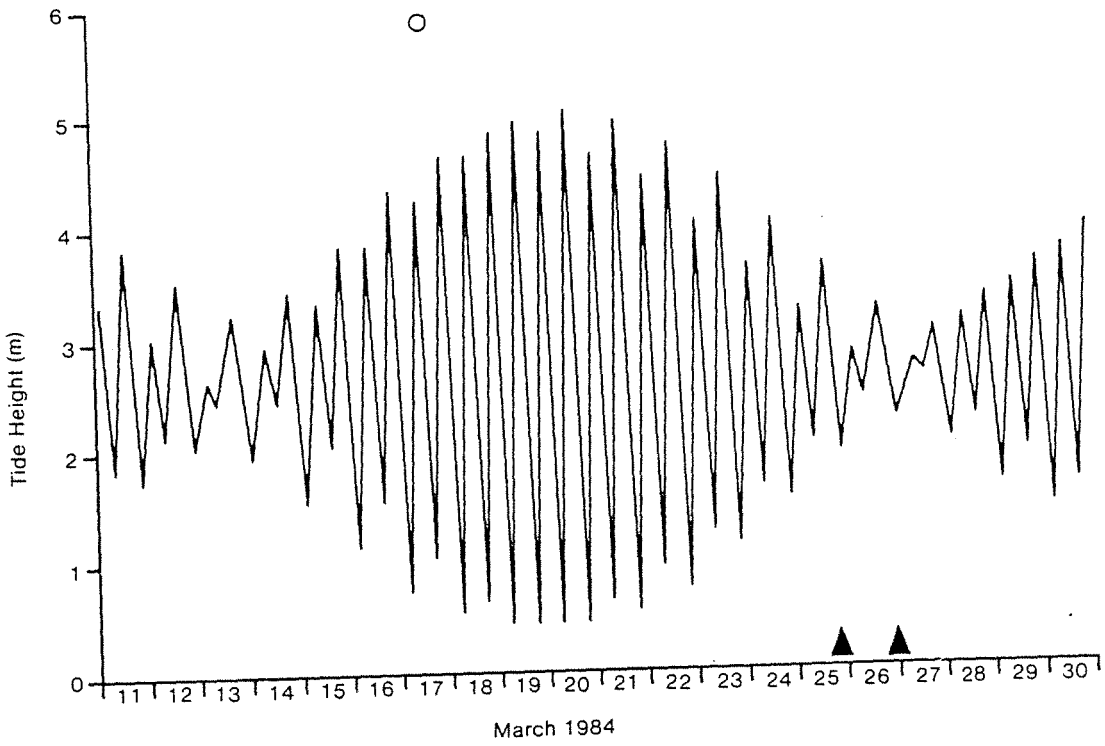


Figure 5.3 Predicted astronomical tide height , date of full moon (○), and dates of mass spawning (▲) for the Dampier Archipelago during March in 1984 and 1985.

spawned between 1430h on March 15 and 1545h on March 16 (Table 5.2).

Table 5.2 Reproductive status of tagged corals at Keast Island reef during March 1985: (+), eggs present; (-), eggs absent; (n), number of colonies.

SPECIES	n	14/3/85 1200	15/3/85 1430	16/3/85 1545
ACROPORIDAE				
A. formosa	3	+	+	-
A. hyacinthus	1	+	+	-
A. aspera	1	+	+	-
Acropora sp.1	1	+	+	-
FAVIIDAE				
Favites abdita	1	+	+	-
Favia pallida	1	+	+	-
Goniastrea retiformis	1	+	+	-
Platygyra sinensis	3	+	+	-

The corals kept in an aquarium from 1300h on March 14 spawned between 1900h and 2000h on March 15 (D. M. Gordon, pers. comm.). At site 6, observations were also maintained from 1700h to 2230h on March 17. No spawning was observed during this period.

5.3.3 Hour of spawning

The sudden appearance of large quantities of eggs (predominantly pinkish-red) floating on the sea surface in 1984 was first noticed at 1925h on March 25. On the following night spawning began at about 1930h. When observations ceased at 2200h on both nights, large numbers of floating eggs were still visible. The timing and duration of the mass spawning events observed in 1985, in relation to tide height, diel light cycles, sunset and

moonrise are shown (Fig. 5.4). On March 15, the first eggs (pink) were observed at 1900h. Between 1900h - 1940h many *Acropora* colonies were observed releasing gametes. Between 2010h - 2100h, 18 species were observed spawning (Table 5.1). Spawning activity appeared to peak (maximum number of eggs on the surface) between 2000h - 2100h, and by 2140h only a few eggs were visible on the sea surface. On March 16, pink egg bundles were first observed at 1923h. Between 2000h - 2020h only 1 species of *Acropora* was observed spawning. Most of the observed eggs were pink or red, although green and white eggs were also present indicating that other unidentified coral species were also spawning. Spawning activity appeared to peak between 2030h - 2100h, and by 2200h only a few eggs were visible.

A swarming of polychaete worms, predominantly rag-worms (Polychaeta: Nereididae), occurred simultaneously with the coral mass spawning in both years. *Eunice* cf *australis* was present although less abundant. The epitokous (reproductive) stage of these worms emerged following the appearance of coral eggs on the sea surface. On the night of March 17,1985 (the night after the two consecutive nights of mass spawning) polychaete swarming was not observed.

5.3.4 Spawning behaviour and egg size

The form of spawning most commonly observed on the two nights was the slow extrusion of gametes through the polyp mouth (Type I as described by Babcock *et al.* 1986). Size of preserved coral eggs was 356um - 661um (mean = 505um). No fertilized coral eggs were detected in samples collected during the mass spawnings on March 15 or16 in 1985.

5.3.5 Environmental data

Environmental data collected during the spawning periods in 1984 and

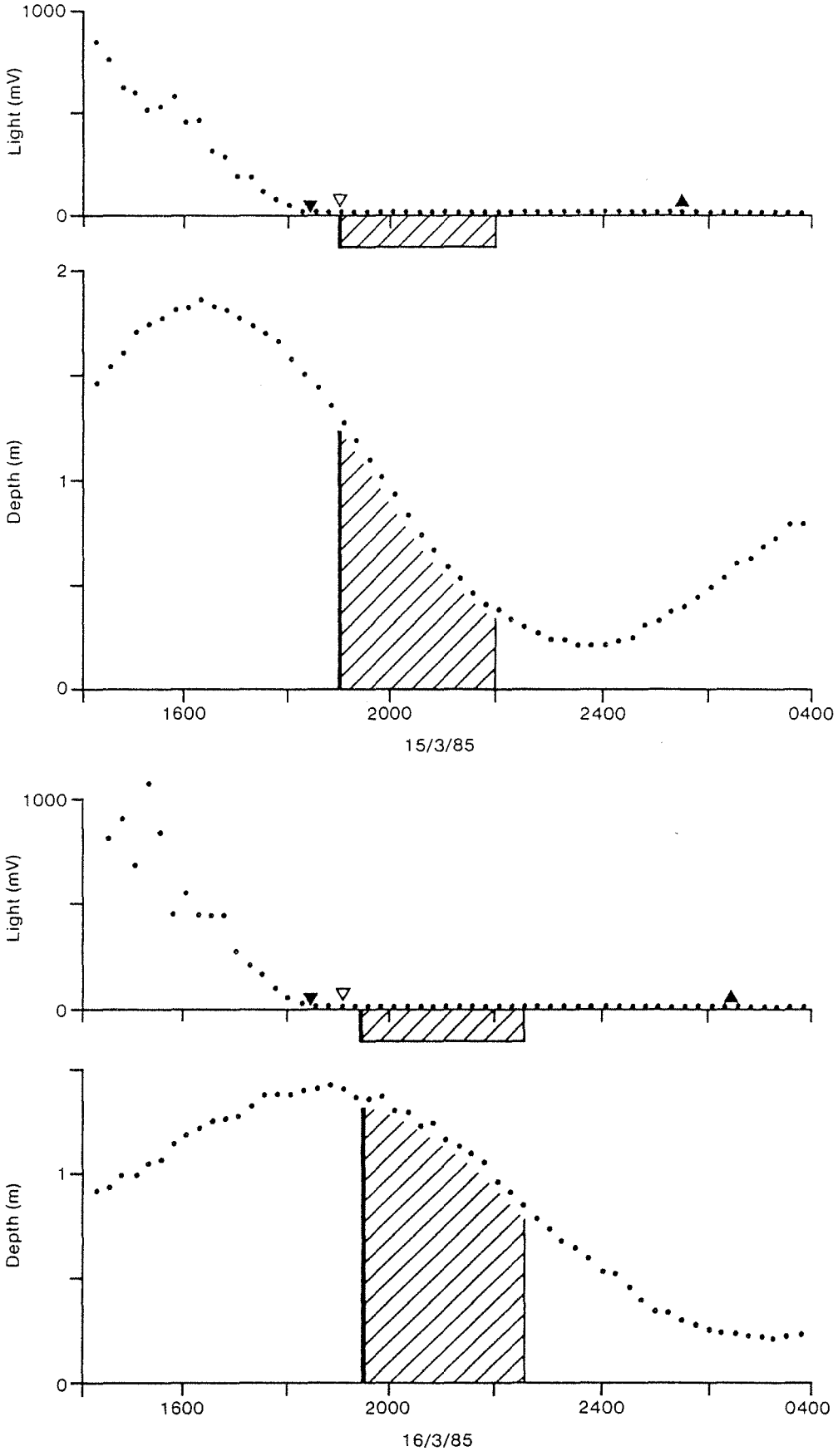


Figure 5.4 Bottom irradiance, depth, and period of mass spawning (shaded) at Keast Island reef on consecutive days in March 1985. (▼) sunset ; (▲) moonrise ; (▽)1st night value.

1985 are summarised in Figures 5.5 and 5.6. The full moon occurred at 1810h on March 17, 1984 and at 1014h on March 7, 1985. The time of moonrise on the nights of March 15/16, 16/17, 17/18, 1985 occurred at approximately 0130h, 0220h, 0310h respectively. Sunset occurred at about 1825h on March 14 - 17, 1985. At 1845h, on these nights, recorded irradiance levels were still above night values. The first night values were recorded at 1900h.

In the Dampier Archipelago, spring and neap tides occur 2 - 4 days and 8 - 10 days respectively after the full moon (Fig. 5.3). At site 6, the eighth to tenth days after the full moon during March 1984 (Fig. 5.5c), and the eighth and ninth days after the full moon during March 1985 (Fig. 5.6c) were the only days during the spawning periods that this reef was not exposed. Similarly in 1986, this occurred on the 7-10 days after the full moon in March. In all cases, the first night of major spawning in the Dampier Archipelago coincided with the first night after the full moon in March that this reef was not exposed. On March 15, 1985 (the first date of mass spawning), high water occurred at 1615h. The tide began to ebb approximately 45 minutes later and low water occurred at 2345h. On the following day, a high water occurred at 1845h and the tide began to ebb at approximately 1910h with low water occurring at 0245h on March 17 (Fig. 5.4).

Temperature records show that the corals on this reef were subject to large (>4 ^{o}C) diel variations in seawater temperatures during the spawning period in 1985 (Fig. 5.6a). A warming trend also occurred with a minimum of 27.0 ^{o}C, at 2300h on March 12, and a maximum of 32.5 ^{o}C, at 1445h on March 17. During the equivalent period in 1984, temperatures varied from 31.3 ^{o}C on March 23 to 27.6 ^{o}C on March 27. Mean temperatures during the two successive periods of mass spawning in each year were 29.3 ^{o}C and 29.4 ^{o}C in 1985 and 30.5 ^{o}C and 28.8 ^{o}C in 1984. Salinities at site 6 during the spawning

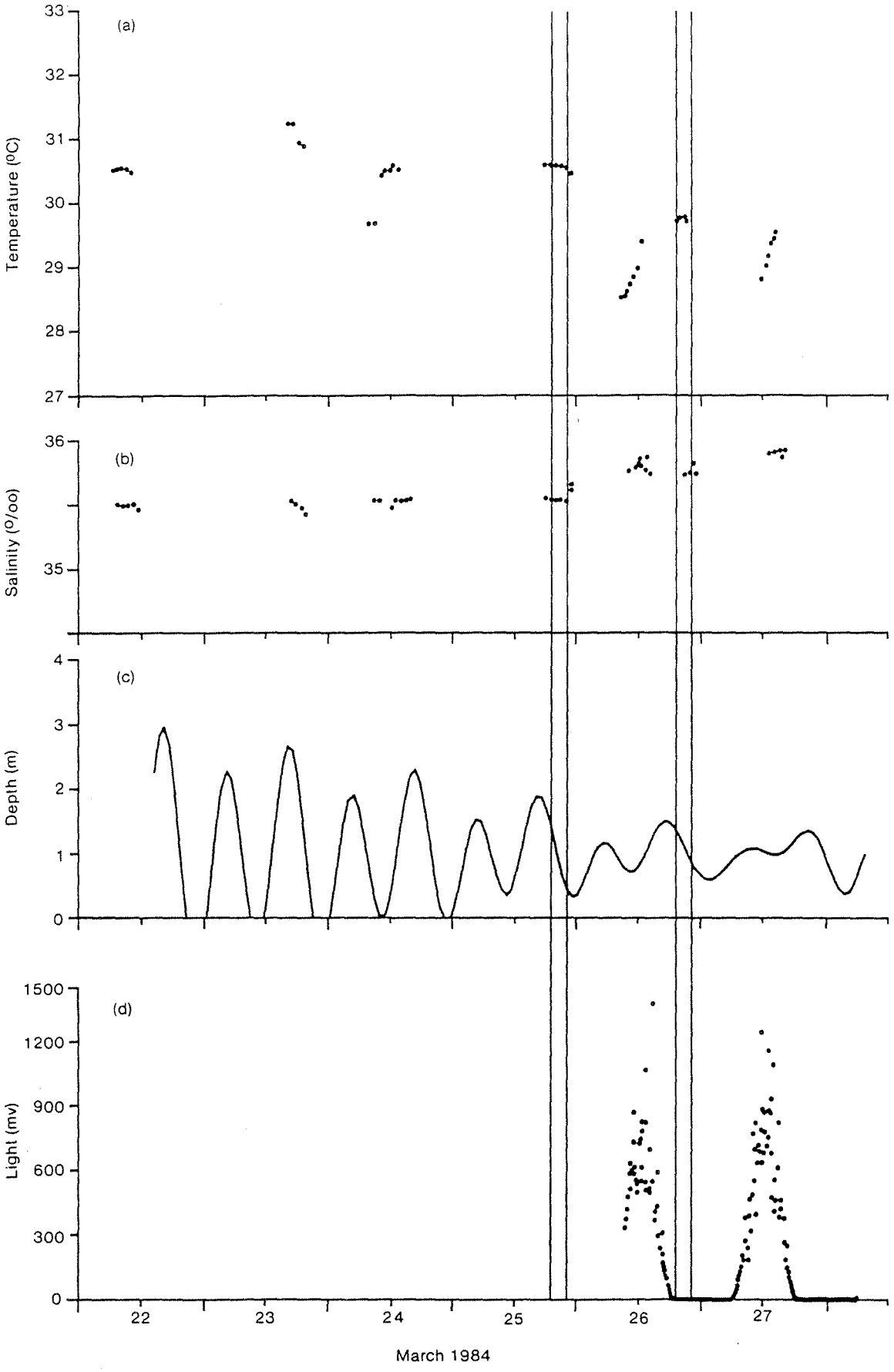


Figure 5.5 Environmental data recorded during the spawning period at Keast Island reef in 1984. Periods of mass spawning are marked. Depth was determined from tide tables (Anon.,1983) and depths recorded *in situ* from 0900h on March 26 to 0700h on March 28.

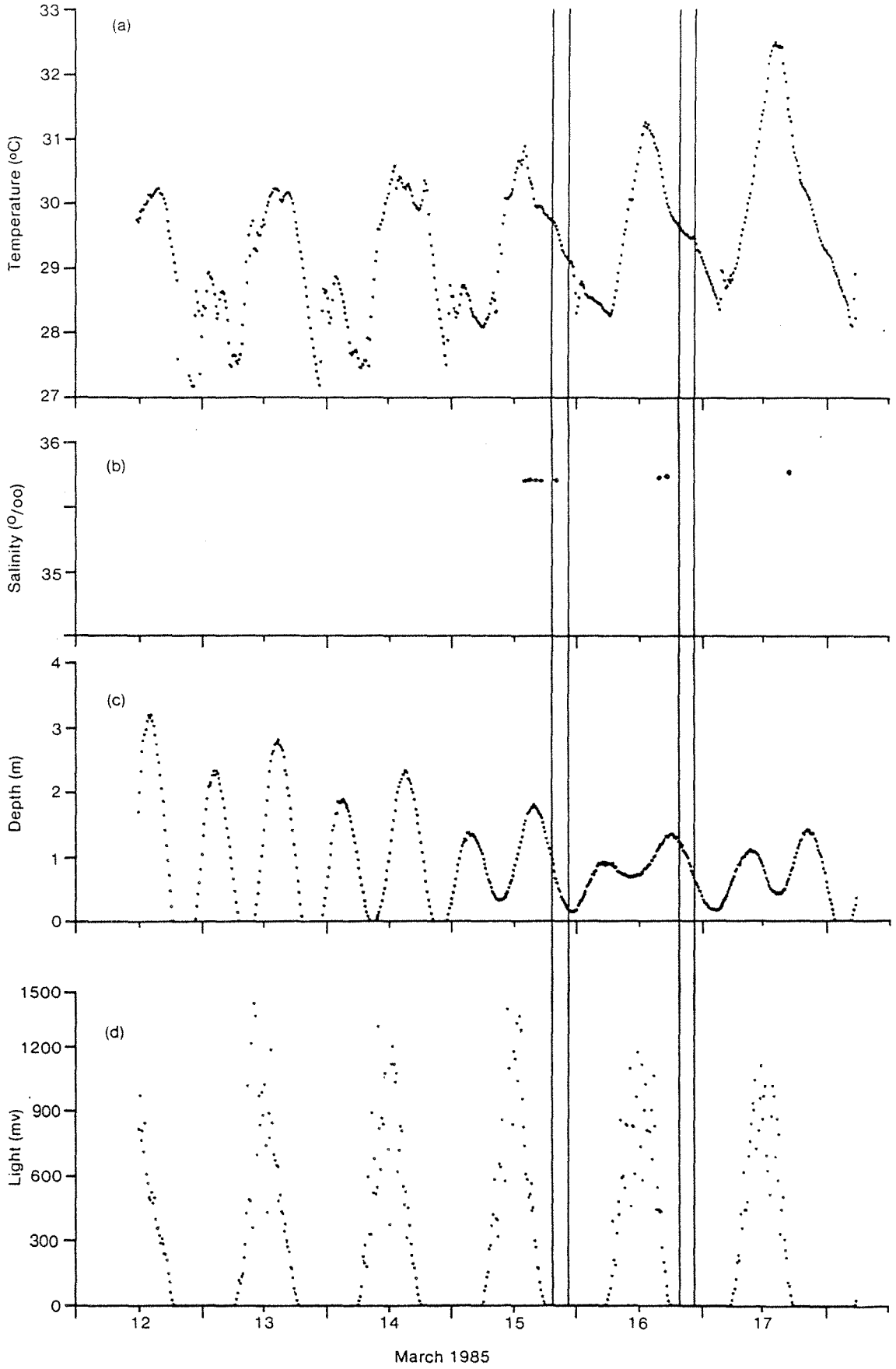


Figure 5.6 Environmental data recorded during the spawning period at Keast Island reef in 1985. Periods of mass spawning are marked.

periods were 35.5 $^{o}/_{oo}$- 36.0 $^{o}/_{oo}$ in both years (Figs 5.5b, 5.6b).

5.3.6 Summary of coral mass spawning studies in 1986 and 1987

In 1986, coral mass spawning at the Dampier Archipelago was predicted to occur on April 3 and 4 (Simpson, 1985b). In March 1986, systematic surveys of corals were carried out at the Dampier Archipelago and at Coral Bay on the Ningaloo Reef (Fig. 1.1), to determine whether corals on these reefs, approximately 500-600 km apart, spawned synchronously as predicted by Simpson and Masini (1986). Mass spawning in both areas occurred mainly on April 2 and 3 or on the 7th and 8th night after the full moon in March (the full moon occurred on March 26 th), although some spawning occurred on April 1 and 4. These dates were 13 lunar months after the 1985 mass spawnings in the Dampier Archipelago. Over 350 colonies, comprising about 75 species, were sampled and the majority spawned over this period. Tide height and seawater temperatures were also recorded during the spawning periods at both locations. Spawning in both locations occurred during neap, nocturnal, ebb tides.

Preliminary studies of gametogenesis of selected acroporiid, faviid and mussid species on the Ningaloo Reef, between October 3, 1985 and April 8, 1986 indicate that the gametogenic cycle of these species is similar to and about 4-5 months out of phase with the same or similar species on the Great Barrier Reef (eg Marshall and Stephenson, 1933; Kojis and Quinn, 1981, 1982a, 1982b; Harriot, 1983; Babcock, 1984; Wallace, 1985). Oocyte diameters of acroporiid, faviid and mussid species collected from the Abrolhos Islands (Fig.1.1) and Ningaloo Reef in late February and March 1986 were similar in colour and size, suggesting that these species were at similar stages of reproductive maturity. Histological sections of the Abrolhos samples collected in late March (about 1 week before the predicted spawning dates on

the reefs at the Dampier Archipelago and the Ningaloo Reef) revealed mature oocytes and testes. These data suggested that coral spawning at the Abrolhos takes place at about the same time as the tropical reefs in Western Australia. These data are currently being prepared for publication (Simpson, in preparation).

Table 5.3 Summary of coral mass spawning observations in Western Australia during March 1987. Temperatures are monthly means (from Pearce, 1986); s = predominantly semi-diurnal tides; d = predominantly diurnal tides.

Location	Latitude (° S)	Tide range (m)	Temp range (° C)	Dates of main spawning	Days after full moon in March	Type of observation
Koolan Is.	16	>10/s	31-24	23, 24	8, 9	*in situ*
Dampier Arch.	20	~5/s	30-22	23, 24	8, 9	*in situ* photo
Lowendal Is*	20	~4/s	30-23	23, 24	8, 9	*in situ*
Ningaloo Reef	23	<2/s	27-23	23, 24	8, 9	*in situ* photo
Abrolhos Is.	28-29	~1/d	24-20	25, 26	10, 11	*in situ* photo

* Approximate tide and temperature data only.

In March 1987 a systematic survey of corals was conducted at the Abrolhos Islands to determine if and when coral mass spawning occurred. Tide and seawater temperature data were also recorded during this period. About 80 species were sampled and the majority of these spawned with most spawning occurring on March 25 and 26 (Table 5.3). These data are currently being prepared for publication (Simpson *et al.* in preparation). In addition to

this intensive study, observers were stationed at different locations along the coastline to determine the extent of latitudinal synchrony of coral spawning in Western Australia. A summary of these observations is given in Table 5.3.

The observations for the Lowendal and Koolan Islands should be considered as unconfirmed, although the descriptions supplied by the observers suggest that spawning of corals did occur. In all cases simultaneous swarmings of marine worms, presumably polychaetes, were also reported, although at the Abrolhos Islands the relative adundance of these worms during spawning appeared to be considerably lower than I observed on tropical reefs in previous years.

5.4 DISCUSSION

5.4.1 General

Following the observation of spawning events on two consecutive nights in March 1984, a mass spawning of scleractinian corals was predicted to occur 12 synodic months (1 synodic month=1 lunar month=29.53 days) later, after dark, and on the eighth and ninth nights after the full moon.

The accuracy of this prediction confirmed the phenomenon of mass spawning of scleractinian corals in the Dampier Archipelago, and suggested that the observed spawning events in March 1984 were mass spawnings of corals. Furthermore, this also suggests that a predictable, brief, annual period of multispecific, synchronous spawning by scleractinian corals occurs in late summer, early autumn in the Dampier Archipelago. The presence of mature eggs in many species of corals and in many colonies of the same species, at widely separated reefs, suggest that this is a major reproductive effort in the Dampier Archipelago .

Although 27 species of corals were found (directly and indirectly) to have spawned, a high proportion (74%) of the coral species sampled during March 12 to 20, 1985, contained mature eggs. This, and comparisons with the

species composition of the mass spawnings on the Great Barrier Reef (Babcock *et al.* 1986), suggest that many more of the 209 species of scleractinian corals found in the Dampier Archipelago (Appendix I) are likely to be involved in mass spawning. The total absence of mature eggs in the corals sampled in the Dampier Archipelago on November 12 and 13, 1984, and on October 17, 1985, and the observed mass spawning in March 1985 confirm that the mass spawning of corals on the Great Barrier Reef and in the Dampier Archipelago are not synchronised, and support findings on the Great Barrier Reef that the observed mass spawnings are an annual event. The presence of high numbers of apparently mature eggs in some non-acroporiid species after the nights of mass spawning in 1985 suggest that these species may have spawned at a later date (ie a 'split' spawning occurred). 'Split' spawnings have been observed at Magnetic Island on the Great Barrier Reef in 1981 and 1984 (Willis *et al.* 1985). Subsequent studies in 1986-87 at the Dampier Archipelago on other coral reefs in Western Australia support the above conclusions.

5.4.2 Comparisons with mass spawnings on the Great Barrier Reef

Many characteristics of the mass spawnings observed on the east and west coasts of Australia are similar. Most species spawn after a full moon, on 2 - 3 consecutive nights, during a period of neap tides and for 3 - 4 hours between sunset and moonrise. In addition, spawning appears to be an annual event, in both locations, and most species observed to spawn or contain ripe gonads during March 1985 at the Dampier Archipelago, and at other Western Australian coral reefs in 1986 and 1987, are known spawning species on the Great Barrier Reef (Harrison *et al.* 1984; Willis *et al.* 1985; Babcock *et al.* 1986; Table 5.1; Simpson, in preparation; Simpson *et al.* in preparation). Time elapsed between consecutive annual mass spawnings in 1983-84, 1984-85 and

1985-86 on the Great Barrier Reef, and 1984-85, 1985-86 and 1986-87 at the Dampier Archipelago, was 12, 13 and 12 synodic months respectively (Willis *et al.* 1985; Babcock *et al.* 1986; Babcock, pers. comm.; this Chapter). The colours, general buoyancy (Babcock *et al.* 1986; this Chapter) and size range (Marshall and Stephenson, 1933; Kojis and Quinn, 1981, 1982a, 1982b; Harriot, 1983; Babcock, 1984; Wallace, 1985; this Chapter) of mature eggs, and the most common spawning behaviour also appear to be similar (Babcock *et al.* 1986; this Chapter). The synchronous spawning of corals kept in aquaria with *in situ* corals (Harrison *et al.* 1984; this Chapter), the manipulation of the hour of spawning by altering the photoperiod of corals kept in aquaria (Babcock, 1984, Simpson, in preparation) and the possibility that a 'split' spawning occurred during 1985 in the Dampier Archipelago consistent with the 'split' spawning observed at Magnetic Island in 1984 (Willis *et al.* 1985; this Chapter) are further similarities.

The seasonal timing of the mass spawnings, and as a consequence, the different environmental conditions that exist during the periods of gametogenesis and spawning are, therefore, the most significant differences that exist between both locations; for example, mass spawning on the Great Barrier Reef occurs after a period of rapidly rising sea temperatures and at temperatures well below the mean maxima for these locations (Babcock *et al.* 1986; Fig. 5.7a). In contrast, spawning at the Dampier Archipelago occurs after a period of high, relatively constant temperatures and coincides with the period of maximum temperatures (Fig. 5.7a, b). At Ningaloo Reef and the Abrolhos Islands spawning also occurs during a period of maximum temperatures, following a gradual rise in the previous months (Fig. 5.7b; Simpson *et al.* in preparation; Crossland, 1981). Spawning at maximum temperatures has been documented for tropical corals (eg Wyers, 1985; Heyward, 1986) and for the temperate species *Astrangia danae* (Szmant-

Froelich *et al.* 1980).

A further difference is that mass spawning occurs on different nights after a full moon (Babcock *et al.* 1986; Table 5.3) and although the state of the tide is similar (ie, on or just before neap tides; Fig. 5.8 a, b), the periods of darkness between sunset and moonrise will be different due to the later rising of the moon (about 50 minutes) on successive nights.

5.4.3 Environmental factors co-related with the timing of spawning

Korringa (1947) listed annual sea temperature changes, monthly tidal or moonlight cycles and diel light or tidal cycles as the factors that determine the timing of reproduction in marine invertebrates. Babcock *et al.* (1986) suggest that ' ... the synchrony, predictability and brevity of the mass coral spawning appear to be linked to successive environmental cues which operate on increasingly fine time scales: annual sea temperature patterns, monthly lunar or tidal cycles, and diel light cycles'. Environmental conditions (for example, annual sea temperature cycles), at a given location, can vary markedly from year to year (see Babcock *et al.* 1986, Fig. 2.3) and as a result it is unlikely that the timing of reproduction is a response to exogenous factors alone. Olive and Garwood (1983) suggest that all reproductive cycles have an endogenous component. Willis *et al.* (1985) made a preliminary analysis of the mass spawning phenomenon on the Great Barrier Reef since 1981, and have identified lunar and diel light cycles as zeitgebers for spawning synchrony.

Annual rhythms

(i) Sea temperature cycles

Korringa (1947) suggests that '... most probably temperature conditions preponderate in establishing the breeding season' in marine animals.

Babcock *et al.* (1986) suggest that the seasonal variation in sea temperatures, on the Great Barrier Reef, may influence gametogenic cycles in corals and state that mass spawning of corals occurs after a period of rapidly rising sea temperatures in spring. They state that the corals on the inshore reefs on the Great Barrier Reef, spawn 1 lunar month earlier than corals on the offshore reefs and suggest that, because of an earlier and more rapid rise in sea temperatures at the shallower, inshore reefs, temperature is a possible proximal factor in determining the timing of the spawning season. Kojis and Quinn (1981) have associated seawater temperature changes with annual periodicity of spawning in scleractinian corals and also suggest that the spawning of corals at Lord Howe Island, where spring sea temperatures are lower (by over 4 ^{0}C) than in the Dampier Archipelago, is delayed until January due to a later rise in seawater temperatures.

Seawater temperatures in the Dampier Archipelago showed a pronounced seasonal pattern and comparisons with Magnetic Island (Babcock *et al.* 1986) during spring to early summer in 1982 indicate that the differences were generally less than 1^{0} C yet the spawning season is about 5 months out of phase (Fig. 5.7a). This difference is markedly less than the diurnal variation in sea temperature in the Dampier Archipelago, which can exceed 4^{0} C on shallow reefs (Fig. 5.6a). In contrast annual patterns of seawater temperature at the Dampier Archipelago, Ningaloo Reef and the Abrolhos Islands and are all markedly different yet corals on these reefs spawn synchronously or within a few days of each other (Fig. 5.7b; Table 5.3).

It could be argued that the reproductive physiology of corals is unlikely to be controlled by an inflexible gametogenic response to temperature (see Loya, 1983) and instead, corals evolve different responses to temperature at different locations with temperature remaining the major proximate cue for determining the timing of spawning. Although the data presented above

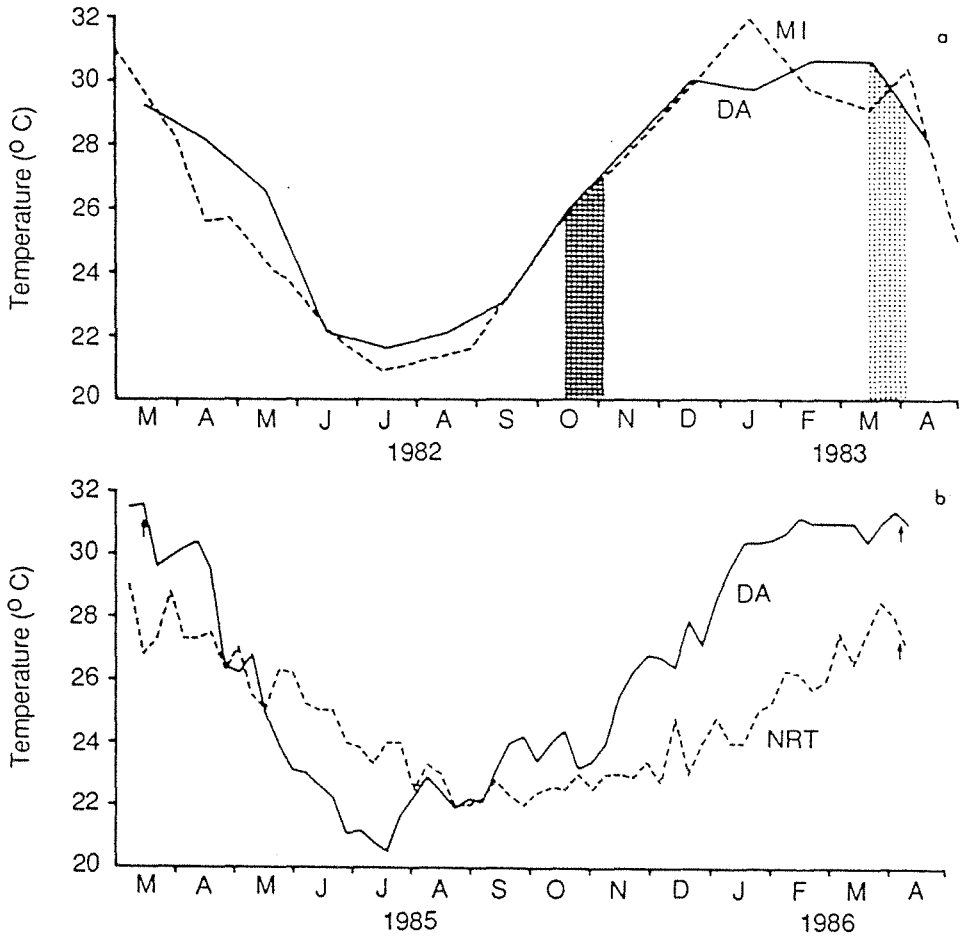


Figure 5.7 (a) Annual seawater temperature patterns and asynchronous breeding seasons of corals at Magnetic Island (MI, dark shade) and the Dampier Archipelago (DA, light shade); (b) annual seawater temperature patterns and synchronous periods of coral mass spawning (arrows) at the Dampier Archipelago (DA) and the Ningaloo Reef tract (NRT).
Data for the Dampier Archipelago for (a) are from monthly means and (b) from weekly means. Data for Magnetic Island are from Babcock *et al.* (1986) and for the Ningaloo Reef tract from weekly means.

suggest that sea temperature is not a proximal cue in determining the timing of the breeding season of scleractinian corals on a geographical scale, it may influence the final maturation of gametes on a local scale and explain the difference in the timing of spawning on inshore and offshore reefs on the Great Barrier Reef. However, the inter-year variability in sea temperatures on the Great Barrier Reef and at the Dampier Archipelago (Babcock *et al.* 1986; Fig. 2.3) and the high, relatively constant temperatures in the Dampier Archipelago during the 4 months before spawning, in contrast to the rising temperatures during the equivalent period on the Great Barrier Reef, Ningaloo Reef and at the Abrolhos Islands suggest that this may not be the case. Furthermore, the apparent immaturity (ie lack of pigmented eggs) of gametes in some corals (in some cases within the same colony) days before the March spawning at Coral Bay in 1987 (J Cary, R Masini, pers. comm.) and the presence of a spawn 'slick', at the same location, on 8th day after the full moon in April 1987 (M Forde, pers. comm.) indicate that spawning in part of the coral population at this location was 'delayed' by 1 lunar month. This delay appears unlikely to be the result of 'atypical' environmental conditions which presumably would have affected the entire coral population.

The apparent similarity to the highly predictable spawning rhythm of the Pacific palolo worm, *Eunice viridis*, in Samoa, where sea temperatures are equable throughout the year (Korringa,1947), is further evidence that annual sea temperatures alone may not determine the breeding season in tropical marine invertebrates that reproduce in brief, annual periods. Furthermore, Johannes (1978) states that seawater temperature does not appear to play a key (cf proximal) role in the timing of spawning of coastal tropical marine teleosts and cites examples where the collective spawning peaks, at different locations, occur during periods of minimum, maximum and intermediate sea temperatures.

(ii) Wind and current cycles

Mass spawning of corals in spring to early summer on the Great Barrier Reef and in autumn on Western Australian coral reefs, coincide approximately with periods of calms associated with changes in seasonal wind patterns. During November, winds on the central Great Barrier Reef change from the southeast trade winds that predominate during March to November to the northwest monsoons that occur from December to February (Pickard *et al.* 1977; Williams *et al.* 1984). In the Dampier Archipelago, winds from the west and southwest (monsoons) predominate from September to March and change to the southeast trades from March to August (Hollaway and Nye, 1985).

Approximately coincident with the change in wind patterns at both locations is a change in large scale water circulation patterns. Some evidence suggests that a unidirectional, poleward flow of surface water occurs in late spring to early summer along the northern and central Great Barrier Reef and this pattern remains until about March/April when more complex patterns occur and persist until November (Pickard *et al.* 1977; Williams *et al.* 1984). On the west coast of Australia a unidirectional, poleward flow of surface water (the Leeuwin Current) occurs during autumn and early winter (Cresswell and Golding, 1980; Legeckis and Cresswell, 1981; Thompson and Cresswell, 1983; Thompson, 1984; Hollaway and Nye, 1985). This current is strongest during March to June with the speed and direction of the surface water being more variable during the remainder of the year (Hollaway and Nye, 1985).

These periods of relative calm, coinciding approximately with changes in large-scale water circulation patterns, appear to occur annually in each location and at the approximate time of the breeding season of scleractinian corals. Might these events be significant in the evolution of the timing of

mass spawning, even if they do not provide the mechanism which is the environmental cue responsible for triggering the mass spawning event? The existence of an endogenous annual rhythm, interacting with environmental cues within the breeding season (ie lunar/tidal/light cycles), as a result of factors related to similar meteorologic/oceanographic events in both locations, but at different times of the year, may explain the difference in the timing of the breeding season of corals on the east and west coasts of Australia. Thus the breeding seasons of corals on the Great Barrier Reef and on Western Australian reefs may be a reflection of spawning patterns of 'ancestral' corals further north that were dispersed southward by different circulation patterns that occurred at different times of the year.

The timing of peak periods of reproductive activity in many tropical, coastal teleosts has been found to coincide with periods of calms (Basheerudin and Nayar, 1962; Bapat, 1955; Prasad, 1958). Watson and Leis (1974) suggest that the spring and autumn reproductive peaks in some Hawaiian marine fishes is an adaptation to changes in the local current patterns that occur at these times of the year. Johannes (1978) found collective spawning peaks in 13 out of 18 locations (5 locations had insufficient data to draw conclusions) to occur at times of the year when prevailing winds or prevailing currents are the weakest.

Lunar rhythms

The spawning of corals on Western Australian coral reefs in 1984-87 occurred around the third quarter of the moon in March. On the Great Barrier Reef most species spawn in the week following full moons in October and November. These data suggest that within the breeding season corals respond to lunar periodicity. Lunar periodicity has been previously recorded in both brooding (eg Lewis, 1974; Richmond and Jokiel, 1984) and spawning

(Kojis and Quinn, 1981,1982a; Harriot,1983; Babcock, 1984; Harrison *et al.* 1984; Willis *et al.* 1985; Wallace, 1985; Babcock *et al.* 1986) coral species.

Tidal rhythms

Babcock *et al.* (1986) suggest that ' ...the release of gametes occurs after nightfall following the first full moon subsequent to the maturation of gonads'. If this were so, spawning would be expected to occur on the same nights after the full moon irrespective of the geographical location. This does not happen. Most species spawn on the third to fifth nights after the full moon on the inshore reefs of the central Great Barrier Reef (Fig. 5.8b), and on the fourth to sixth nights after the full moon on the offshore reefs (Babcock *et al.* 1986). In the Dampier Archipelago and on the Ningaloo Reef spawning appears to occur mainly on 7-10 nights after the full moon (Fig. 5.8a) and 10-11 nights after the full moon at the Abrolhos Islands.

Tidal records (Anon.,1984) for Townsville (for inshore reefs), Bugatti Reef (for offshore reefs) on the Great Barrier Reef and depth logger records for the Dampier Archipelago and Ningaloo Reef indicate that spawning coincides with the occurrence of neap tides. At the Abrohos Islands spawning appears to occur as the neap cycle begins (Simpson *et al.* in preparation). These data suggests that following the occurrence of the full moon within the breeding season the mass spawning of corals is synchronised by a tidal rhythm. Thus the nights after the full moon that major spawning takes place appear to be the result of local adaptation to tide patterns.

Many marine organisms display a tidal rhythm in reproductive behaviour (Korringa, 1947). In particular, the Pacific palolo worm, *Eunice viridis* , which also spawns during a brief period each year, displays a similar tidal periodicity (ie, spawns on neap tides) following the first full moon within the breeding season (Caspers, 1984).

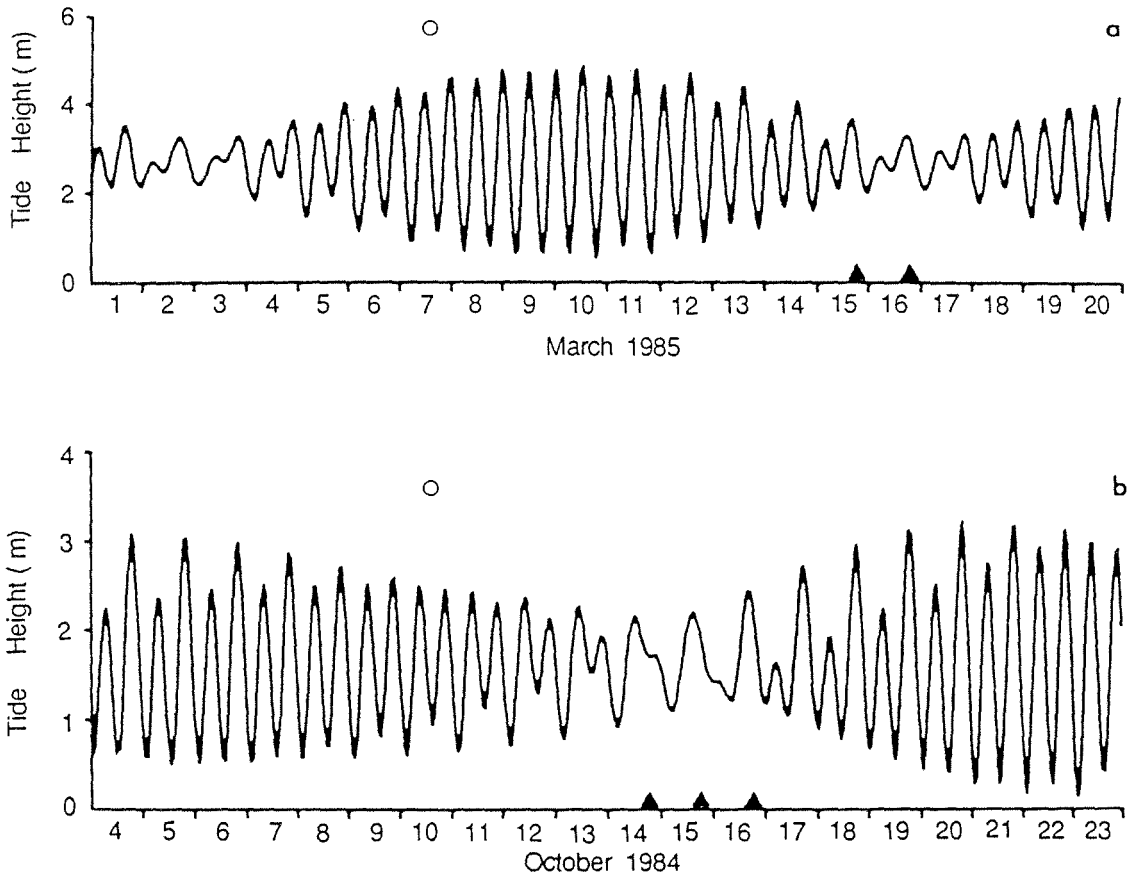


Figure 5.8 Predicted astronomical tide height, date of full moon (○) and dates of major mass spawning (▲) at (a) the Dampier Archipelago and (b) Magnetic Island.

Daily rhythms

In the Dampier Archipelago, the release of gametes on March 15, 1985 coincided with the onset of darkness during a falling tide. On the following night, spawning commenced about 10 minutes after the onset of the ebb tide during darkness (Fig. 5.4). In 1987 at a site at the Abrolhos Islands, most species spawned on March 25 and 26. Spawning occurred mainly from 2030-2130h on March 25 and from 2130-2230h on March 26 and began about 1 hour after high water on these nights (about 1930h and 2020h respectively; Simpson *et al.* in preparation). The difference in the timing of spawning was not apparently due to different species spawning on separate nights as different colonies of many species spawned on both nights. These data indicate that the spawning period displays lunar periodicity, subsequent to gonad maturation but that the specific time of *in situ* spawning may be influenced by a tidal rhythm, interacting with the light/dark cycle. Thus observed differences in the timing of *in situ* spawning at night, therefore, may be related to phase differences in the tides.

Evidence to support the possible influence of tides may be seen from the timing of spawning of many corals on the Great Barrier Reef. Harrison *et al.* (1984) and Babcock *et al.* (1986) have shown that many acroporiid and faviid corals at Magnetic Island spawn 2 - 4 hours after sunset. This period coincides approximately with high water and an ebbing tide in Townsville (Anonymous, 1982). Observations by the author at Magnetic Island on November 1, 1985 noted that many acroporiid corals appeared to spawn between 2100h-2200h. Predicted high tide at Townsville on November 1, 1985 occurred at 1958h (Anonymous,1984). Further evidence can be seen in the timing of spawning of *Goniastrea favulus* in two locations on the Great Barrier Reef. This faviid coral spawns during daylight (1600h-1800h) at

Heron Island (Kojis and Quinn, 1981a) but after dark on reefs near Townsville where tides are at least 30 minutes later (Babcock *et al.* 1986).

The reproductive swarming of the polychaete worm, *Eunice viridis*, on Tutuila reef in Samoa, also starts at the end of the nocturnal flood tide, at about 0030h (Caspers, 1984). This timing, in relation to the state of the tide, is identical to the swarming of polychaete worms in the Dampier Archipelago and is additional evidence to support the importance of tides in determining the nocturnal time of spawning.

5.4.4 Possible ultimate cues determining the timing of spawning

The precise timing of mass spawning during periods of relative calm, after a full moon, over neap tides, on an ebbing tide, and after dark is an unusual and significant feature of the mass spawning phenomenon. The synchronous spawning of gametes within populations of a single species has the obvious advantage of promoting cross fertilization. Many marine invertebrates employ this reproductive strategy (Korringa, 1947) and, in particular, the spawnings of the crinoid, *Comanthus japonica* (Kubota, 1980), and the Pacific palolo worm, *Eunice viridis* (Caspers, 1984), are well documented examples of predictable, synchronized spawning that occur for a few days each year.

The advantages of multispecific synchronous spawning are less clear. Harrison *et al.* (1984) suggest that epidemic spawning of many species would increase the chances of survival for planktonic larvae by satiating predators and filter feeders. The general buoyancy of propagules and the timing of spawning during darkness would also reduce predation by benthic filter feeders and visual feeders respectively. Predation by planktivorous fishes such as the blue sprat, *Spratelloides robustus*, which was observed eating coral eggs (subsequently confirmed by gut analysis) in the Dampier

Archipelago, increased when lights were shone on the water during spawning and supports the hypothesis that nocturnal spawning reduces gamete wastage due to predation.

Spawning on an ebbing tide would facilitate the flushing of propagules to deeper, offshore waters and may also be related to the need to reduce the threat of predation from the many planktivores that occur in shallow coral reef communities (*sensu* Johannes,1978).

Babcock *et al.* (1986) suggest that spawning on low tides may be related to the advantage of reducing the dispersal of gametes prior to fertilization and Stimson (1978) proposed that the reproduction of shallow water reef corals during low tides facilitates the retention of planulae near the natal reef. In addition, Kojis and Quinn (1982b) suggested that the propagules of the faviid corals *Favites abdita* and *Leptoria phrygia* are likely to remain in the vicinity of the natal reef because spawning of these two corals takes place on neap tides.

Mills *et al.* (1986) has shown that the net excursion of water during the week of neap tides in the Dampier Archipelago can be an order of magnitude greater than during the week of spring tides (Fig. 5.9). This is a result of the decreased influence of the tidal (oscillatory) current component and the relative increase of the wind-driven (non-oscillatory) current component. Thus, spawning on neap tides is more likely to disperse (periods of wind being more likely than periods of calm during the days following spawning) rather than retain larvae in the vicinity of the natal reef and may be an adaptation for increasing the dispersal of the ensuing adults. Similarly, Johannes (1978) states that, in relation to considerable year to year variation in recruitment of some tropical marine fishes, ' ..... it might prove revealing to compare the relative strength of the prevailing currents and winds during years of high and low recruitment'.

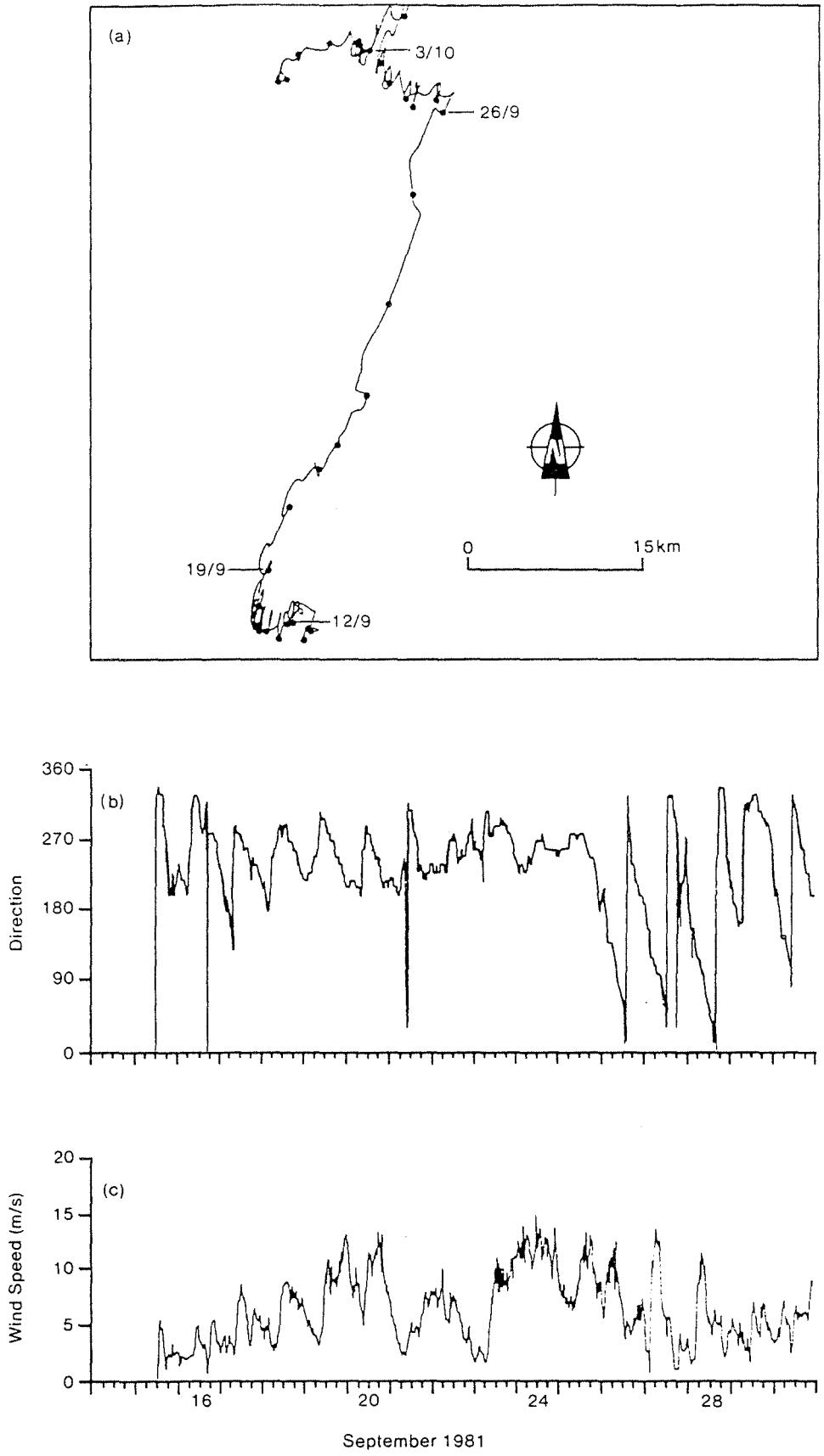


Figure 5.9 (a) Continuous vector plot of current speed and direction at 7 m depth recorded near site 3 (from Mills*et al.* 1986).
(b) wind direction and (c) speed recorded at Conzinc Island (Mills and Pitt, 1985). Full moon occurred on September 14, and neap tides on September 23, 1981.

The positive, rather than negative, buoyancy of the propagules, the low level of endemism of coral species found on isolated shelf atolls such as the Rowley Shoals (15°-16 °S, 119° E) and the similarity of the coral fauna on regionally separate Western Australian coral reefs (for example, Ningaloo Reef and the Abrolhos Islands ; J E N Veron, pers. comm.) also support the hypothesis that coral larvae can have an extended pelagic phase.

Willis *et al.* (1985) postulate that different populations of corals reach, concurrently, a state of reproductive maturity to take advantage of favourable environmental conditions for larval development. The occurrence of periods of relative calm weather that follow mass spawning events on the east and west coasts of Australia support this hypothesis. In addition, Coles (1985) has shown that settlement of planula of *Pocillopora damicornis* increased as a result of exposure to elevated temperatures with maximum settlement occuring after exposure to 33.5° C and less at lower temperatures. In Western Australia spawning and presumably settlement, at all reefs documented so far, occurs during periods of maximum temperatures. Assuming that settlement of planulae of other coral species show a similar temperature effect, it may be possible that this also, ultimately influences the seasonal timing of mass spawning.

5.4.5 Management implications of mass spawning

Timing and mode of reproduction

The timing and mode of reproduction in scleractinian corals is of fundamental importance to the management of coral reefs. The risks to the annual reproductive effort of corals that breed in brief, annual periods is greater than to species that breed intermittently throughout the year. If a wide range of species reproduce synchronously, and the reproductive propagules are mostly buoyant, the entire reproductive effort of a reef is

vulnerable to certain sea surface perturbations. This was clearly demonstrated at Magnetic Island, on the Great Barrier Reef, in November, 1981 when a heavy rain squall coincided with a multispecific synchronous spawning event. Harrison *et al.* (1984) state 'propagules on the surface were destroyed, probably by reduced salinity, thereby negating the entire reproductive effort of those corals for the year.'

The full moon preceding spawning, occurs 10-12 days earlier in successive years (Fig. 5.3; Willis *et al.* 1985). To maintain reproductive seasonality spawning must be delayed at some stage. Willis *et al.* (1985) suggest that this occurs every three years (that is, when the full moon is approximately 1 synodic month earlier) and that 13 synodic months will elapse between consecutive spawnings involving adjustment years. Additionally, spawning in the year preceding this adjustment is 'split' over two periods following consecutive full moons. The presence of mature eggs in corals, mainly non-acroporiid species, after the spawning periods in March 1985 and the apparent lower number of eggs observed on the sea surface in 1985 suggest that 1985, in the Dampier Archipelago, may have been a 'split' spawning year. If this is correct then 13 synodic months will elapse before the 1986 spawning in the Dampier Archipelago and the reproductive effort of corals will be at risk for two brief periods in 'split' spawning years.

Possible effects of 'stress' on coral reproduction

The gametogenic cycle of some scleractinian corals ranges on the Great Barrier Reef from about 4 months for some faviid species to about 9 months for some acroporiid species (Babcock *et al.* 1986). If the duration of gametogenesis is similar in the Dampier Archipelago, then November to March each year is a period of major reproductive effort. This is also a period of natural environmental extremes with some evidence (ie , bleaching) that

some coral species are under stress (see Chapter 4). Prolonged high sea temperatures (>30 ^{o}C) and high levels of sediment deposition (on some inshore reefs) occur during this period each year (see Chapter 4). Thus, it is possible that the tolerance of corals on some reefs in the Dampier Archipelago to human environmental perturbations may be lower than at others. Additional environmental stress, such as sedimentation from dredging operations, may lower the fecundity of corals due to energy for reproduction being diverted to cope with the 'stress', for example to actively reject sediment. Kojis and Quinn (1984) have shown that fecundity in the brooding species *Acropora palifera* is inversely related to sedimentation, turbidity, depth and high seawater temperatures and suggest that reduced fecundity of corals as a response to human environmental perturbations, may be useful as a biological indicator of sub-lethal stress on coral reefs.

Distribution of coral reefs in the Dampier Archipelago in relation to recruitment

Babcock and Heyward (1986) have shown that in general , for 19 species of scleractinian corals that spawned on the Great Barrier Reef in 1983, fertilization occurred less than 2 hours after spawning, mobile planulae had developed within 1-3 days and that settlement, if planulae were transferred to aquaria, occurred 4-7 days after spawning. For these species, at least, the direction and net excursion of water, for the 4-7 days after spawning, will influence recruitment (supply of planulae) to the parent and other local reefs. In the Dampier Archipelago, the movement of water during this period will be influenced largely by the wind speed and direction. In the week following spawning in 1984 winds were predominantly from the east, and in 1985 from the west. Under these conditions, the net excursion of water would be southward into Mermaid Sound (Fig. 1.2) in 1984 and northward out of

Mermaid Sound in 1985 (D. A. Mills, pers. comm.). If larval development times are similar in the Dampier Archipelago, planulae from the 1984 spawning are therefore more likely to have settled on reefs within the archipelago than in 1985. During years when planulae are carried out to sea and presumably do not settle on reefs within the archipelago, the relative contribution to overall recruitment by the less extensive, but more diverse, inshore reefs (eg site 5) increases due to their further proximity from the open ocean. In areas, such as the Dampier Archipelago, where a high proportion of the live corals occur as extensive reefs on the seaward periphery of the archipelago and where the planulae from these reefs may often be carried out to sea, these inshore reefs may be providing a high proportion of the recruits for the reefs within the archipelago. If this hypothesis is correct, the preservation of these inshore coral communities may be more critical to the maintenance of the coral reefs in the Dampier Archipelago than are the offshore reefs.

Location of coral reefs in the Dampier Archipelago in relation to recruitment

The location of reefs in relation to local water circulation at the time of spawning will influence the level of recruitment to these reefs. 'Downstream' reefs are likely to receive more planulae than 'upstream' reefs. This interdependence or otherwise of reefs is related to the ability of coral reefs to recover from natural (for example *Acanthaster* infestations or cyclonic wave damage) or human disturbances.

Low recruitment may partly explain the low cover of live coral on Sailfish Reef (Table 1.3; Fig. 1.2). Prior to 1975 extensive coral communities flourished on this reef (L. M. Marsh, pers. comm.). During 1972-1974, reefs at Kendrew Island (Fig. 1.2), at the south-western end of Sailfish Reef, were 'infested' by the crown-of-thorns starfish, *Acanthaster planci* , (Wilson and

Marsh,1974;1975). Marsh (1978) attributes the decline in coral communities on these reefs to the effects of this 'infestation' and cyclonic wave damage that occurred in February,1975. Either of these events, or a combination of both, may have caused the apparent reduction in live coral on Sailfish Reef. In contrast, Hamersley Shoal has a high cover of live coral on parts of the upper seaward reef slope (Fig. 1.2; Tables 1.3; 6.1). The possible 'unfavourable' location of Sailfish Reef in relation to larval recruitment may partly explain the slow recovery of this reef and suggests that different reefs in a given locality may vary considerably in ability to recover from perturbations. The degree of interdependence of reefs is important in determining the location and size of 'sanctuaries' or 'seed' areas essential for the maintenance of coral communities.

5.4.6 Mass spawning and the Leeuwin Current

During autumn and winter a unidirectional, poleward flow of water of tropical origin, the Leeuwin Current, occurs along the Western Australian coastline. Observations on the southern part of the Australian North-West Shelf, between January 1982 and July 1983, indicate that the flow of the Leeuwin Current in this region is strongest between March and June (Hollaway and Nye,1985). Cresswell and Golding (1980) suggested '.....it may be an important factor in the movements of various planktonic larvae '.

As noted above, coral mass spawning during autumn in the Dampier Archipelago, approximately coincides with the initiation of this current. Planula larvae that have been transported out to sea may be dispersed southward by this current. Data on the maximum longevity of coral planulae in the laboratory (Harrison *et al.* 1984) and surface (20 m) speeds of the Leeuwin Current from satellite tracked drogues (CSIRO, unpublished data), suggest that some coral reefs in Western Australia may be interrelated on a

regional scale and may explain the occurrence of 4 genera of reef building corals near Esperance (33 ^{o} S, 122 ^{o} E) (Table 1.1). In addition, the dispersal of larvae from tropical reefs (eg Ningaloo Reef) via the Leeuwin Current, may partly explain the existence of the extensive high latitude coral reefs at the Abrolhos Islands (28^{o} S-29^{o} S). These reefs are exceptionally diverse for this latitude: 37 genera have been identified (Wilson and Marsh,1980), and the reefs support an extensive commercial rock lobster fishery (Johannes *et al.*1983). At the end of last century, Saville-Kent (1897) suggested that the corals found at the Abrolhos Islands may have been carried there by a southward flow of tropical water. The autumn timing of mass spawning of scleractinian corals in the Dampier Archipelago, approximately coincident with the onset of the Leeuwin Current, provides the first scientific evidence to support this hypothesis.

CHAPTER SIX

COMMUNITY METABOLISM

6.1 INTRODUCTION

In Chapter Four organism level studies were conducted to infer which environmental factors were important to the growth and survival of corals in the Dampier Archipelago as well as providing a geographical perspective. This chapter presents the results of system or community level studies in the Dampier Archipelago. Kinsey (1979, 1983a, 1985) proposed the concept of a worldwide 'standard metabolic performance' for different components of 'typical unperturbed' coral reefs. For example, he proposes that the metabolic performance of the 'standard' reef-flat is:

$$P = 7 \pm 1;\ P/R = 1 \pm 0.1;\ G = 4 \pm 1$$

where P is the rate of gross photosynthesis (g C m^{-2} d^{-1}); R is the rate of community respiration (g C m^{-2} d^{-1}) and G is the rate of net calcification (kg $CaCO_3$ m^{-2} y^{-1}) and suggests that departure from these 'standards' may provide an '...excellent basis for checking for the effects of stresses and perturbations'. He cites a number of examples where a marked departure from 'standard' metabolic performance was the response to different perturbations and, in some instances, was associated with obvious changes in community structure. In others, these responses were readily detectable before any visual change in community composition was apparent.

These studies were undertaken to determine the level of organic productivity and calcification on two 'typical' reefs in the Dampier Archipelago and to compare the metabolic performance of these reefs to reefs worldwide, as well as providing baseline data for future studies. The work described below was carried out on two reef types: an offshore barrier

reef, Hamersley Shoal, and a protected, inshore reef near Keast Island (Fig. 1.2). Inorganic (ie net calcification) and organic (ie production and respiration) carbon flux were estimated during November 1983 and March 1984 at Hamersley Shoal and in March and July 1984 at Keast Island reef.

Initially it had been intended to estimate community metabolism in "summer" and "winter" at both reefs and average these to provide annual estimates of primary production and calcium carbonate production on two reef types in the Dampier Archipelago. However, conditions at Hamersley Shoal were often unsuitable for flow respirometry studies because of the exposed nature of this reef. Nevertheless, the data obtained in November 1983 and March 1984 at this site, allow some temporal and spatial comparisons to be made.

In the past the basic technique for measuring primary production and respiration on coral reefs has been flow respirometry (Lewis, 1977) which was pioneered by Odum (1956) and involved measuring changes in the oxygen content of water as it flowed across a reef. While the method is precise, it provides only an indirect estimate of carbon flux and requires a knowledge of the community metabolic quotients RQ ($\Delta CO_2 / \Delta O_2$) and PQ ($\Delta O_2 / \Delta CO_2$) to convert oxygen flux to carbon flux. These quotients are not readily available and depend on the biological characteristics of the reef in question (see Kinsey, 1985). Further disadvantages of this method in open flow systems is that corrections must be made for oxygen exchange with the atmosphere, and monitoring of oxygen flux alone does not provide any information on the net flux of inorganic carbon (ie precipitation or dissolution of calcium carbonate).

More recently an indirect method for measuring CO_2 flux has been developed and used extensively in estimating community metabolism of coral reefs (Kinsey, 1972; Smith, 1973; Smith and Preset, 1974; Smith and

Jokiel, 1975; Smith and Key, 1975; Smith, 1978; Smith and Kinsey, 1978). The method is now well established and involves the measurement of pH, total alkalinity, temperature and salinity and has a number of advantages over the monitoring of oxygen to estimate community metabolism: (1) It is a direct measure of carbon flux, (2) CO_2 is not readily exchanged with the atmosphere and (3) it allows carbon flux to be partitioned into organic (production and respiration) and inorganic carbon flux (net calcification). These advantages in an open flow system more than offset the higher precision of the oxygen monitoring technique. A concise account of the methodologies and contemporary and past directions of systems-level research on coral reefs is presented by Kinsey(1985).

6.2 MATERIALS AND METHODS

6.2.1 Study Sites

Hamersley Shoal

Hamersley Shoal is a barrier reef that lies on the seaward periphery of the eastern side of the Dampier Archipelago (site 7, Fig. 1.2). The 20 m contour lies about 500 m seaward of Hamersley Shoal and the seabed rises sharply to the reef crest, which at its highest is 0.7 m above datum. The lagoon east of Hamersley Shoal is generally less than 2 m below datum and between 3 to 4 km wide with a predominantly sandy bottom interspersed with *Porites* "bommies" and occasional patches of macroalgae, predominantly *Sargassum* spp. The study area ranged in depth from 1.0 m below datum on the seaward slope to 0.6 m above datum on the reef crest and was about 250 m wide (Fig. 6.1). Mean live coral cover over the study area was about 46% ranging from about 78% on the upper seaward reef slope to about 4% on the back reef (Table 6.1), consisting predominantly of *Acropora* spp. (Table 6.2), especially the tabular coral *A. hyacinthus*. Other

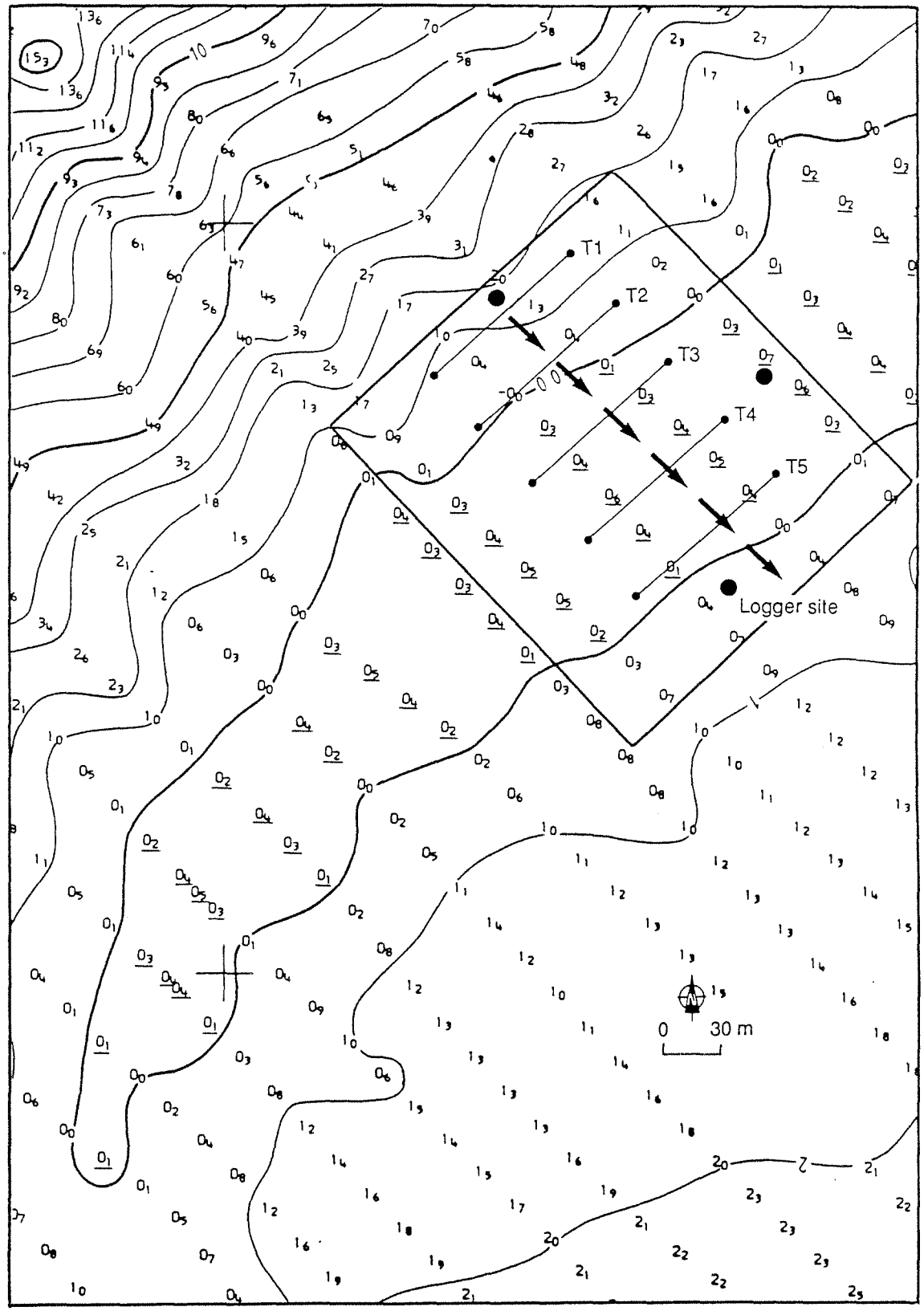


Figure 6.1 Bathymetric map of Hamersley Shoal showing the study area and location of marker buoys (●), depth logger site and coral cover transects. Depths underlined are reef heights above chart datum. Arrows show typical surface current directions during flood tides.

photosynthetic organisms are predominantly algal turfs which occur on coral rubble mainly on the reef crest and back reef areas (Transects 3, 4 and 5 in Fig. 6.1). Water clarity is generally high and sediment deposition low although turbidity plumes from the intertidal area south of Legendre Island (Fig.1.2) occasionally cover this reef. Tidal currents in the vicinity of Hamersley Shoal are low (Fig. 1.3) and current meter records in 6 m depth on the seaward reef slope between November 2 - 17, 1983 indicate that current speeds respectively were generally less than 0.1 m s^{-1} and rarely exceeded 0.2 m s^{-1} (Mills *et al.* 1985). During flood tides surface waters are driven over the shoal and into the lagoon (Fig. 6.2) presumably by a combination of tidal action, wind forcing and wave pumping whereas the deeper (>5 m) waters are deflected and run parallel to Hamersley Shoal (Mills *et al.* 1985; Fig. 6.2). Figure 6.1 shows typical surface current direction during a flood tide at Hamersley Shoal. Under certain flood tide conditions, especially during strong easterly winds and neap tides, surface waters can flow westward across Hamersley Shoal, that is, from the lagoon to the ocean.

Table 6.1 Percentage of live coral cover for 5 transects at sites 6 and 7 and was estimated as the proportion of live coral intersecting a 100 m transect (after Loya, 1978).

Transect number	Hamersley Shoal	Keast Island
1	78.4	61.2
2	69.7	35.9
3	47.2	24.2
4	29.1	45.6
5	3.9	14.6

Keast Island

The Keast Island "transect" is located on an intertidal reef on the

Table 6.2 Common coral species occurring at the study sites.

Keast Island	Hamersley Shoal
Acropora hyacinthus	*Acropora hyacinthus*
A. formosa	*A. formosa*
A. florida	*A. florida*
A. cf clathrata	*A. cf clathrata*
A. danai	*A. latistella*
A. tenuis	*A. tenuis*
A. millepora	*A. cf microphthalma*
A. cf nasuta	*A. aspera*
A. cf microphthalma	*A. spicifera*
A. aspera	*A. pulchra*
A. cf grandis	*A. danai*
A. verweyi	*A. austera*
A. pulchra	*A. nobilis*
Astreopora gracilis	*A. valida*
Montipora hispida	*A. digitifera*
Caulastrea tumida	*A. nasuta*
Cyphastrea serailia	*A. cytherea*
Favia pallida	*A. stoddarti*
Favites abdita	*A. millepora*
F. pentagona	*A. horrida*
F. halicora	*A. solitaryensis*
Goniastrea retiformis	*A. polystoma*
Leptoria phrygia	*A. anthoceris*
Montastrea magnistellata	*Favia stelligera*
Platygyra daedalea	*Favites flexuosa*
P. sinensis	*Favites halicora*
P. cf pini	*Galaxea astreata*
Pocillopora damicornis	*Platygyra cf pini*
Porites heronensis	*P. sinensis*
P. lutea	*Porites lutea*
P. lobata	*Pocillopora damicornis*
Fungia fungites	*P. eydouxi*
Galaxea astreata	
G. fascicularis	
Goniopora tenuidens	
Lobophyllia hemprichii	
Merulina ampliata	
Pavona decussata	

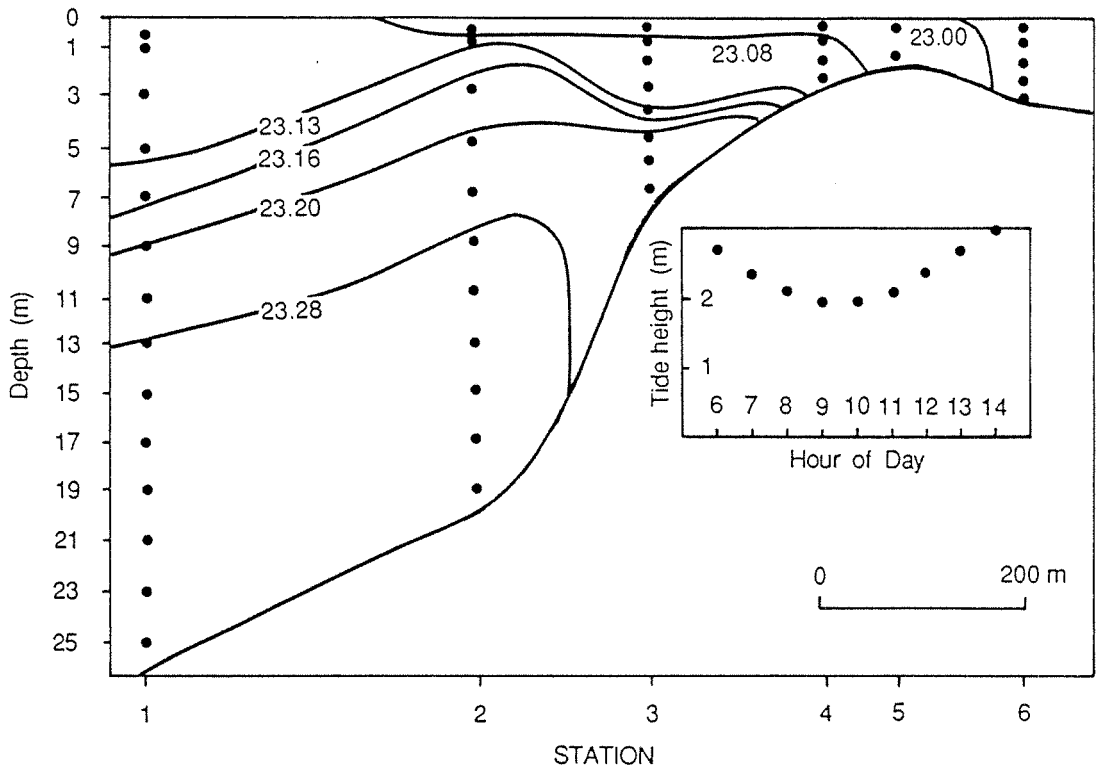


Figure 6.2 Hydrographic section through Hamersley Shoal showing density contours (∂_t values) on a flood tide (Inset) on November 13, 1983 between 1220h and 1258h. Stations 4 and 6 are the upstream and downstream marker buoys in Figure 6.1

eastern side of the island and is protected from swell by surrounding islands (site 6, Fig. 1.2). The study area was about 700 m long although most "transect runs" were located in the southern half of the study area, with a mean reef height above datum of 1.65 m (Fig. 6.3) . The benthic community consists predominantly of a diverse assemblage of corals with a mean live coral cover of about 36% (Table 6.1), consisting mainly of acroporiid and faviid species (Table 6.2), algal turf and coralline algae. During November to March small stands of *Sargassum* spp. occur at either end of the transect and "die off" during the winter. Water clarity is lower than at Hamersley Shoal due to higher levels of suspended sediment. Currents are tidally driven with peak speeds exceeding 1 m s^{-1} and water depths ranging from 0-3.5 m. Current direction during flood tides is shown in Figure 6.3, and ebb tidal flow is in the opposite direction.

2.2.2 Flow respirometry

Benthic community metabolism of the two reefs in the Dampier Archipelago was estimated using flow respirometry techniques as described by Marsh and Smith (1978), Kinsey (1978) and Smith and Kinsey (1978). This method involves tracing the physical and chemical history of cells of water flowing over a reef, by sampling at the beginning (upstream) and end (downstream) of each "transect run". During "transect runs" surface water samples (0- 0.5 m depth) were obtained with a 5 litre Nisken bottle at upstream and downstream "stations" determined by the location of drogues (0.7 m^2 trivane drogue or a 20 litre plastic drum filled with water and containing a 100 mm diameter polystyrene float and a 1.5 kg diving weight) or fluorescein dye patches.

Each sample pair was measured for pH, total alkalinity, temperature and salinity. Approximate drogue paths were determined from the positions

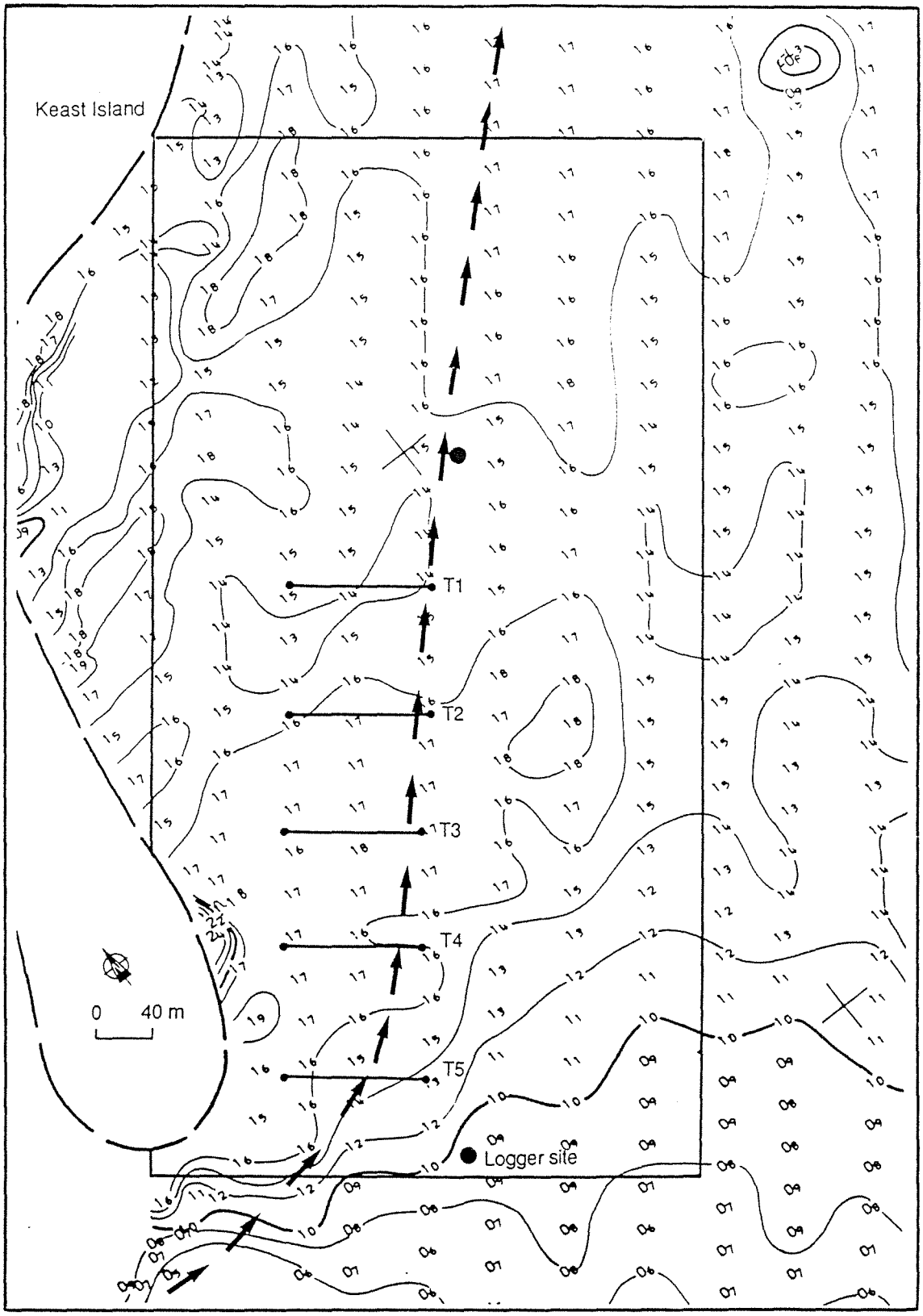


Figure 6.3 Bathymetric map of Keast Island reef showing the study area and location of marker buoys (●), depth logger site and coral cover transects. All depths are reef heights above chart datum. Arrows show typical surface current directions during flood tides.

of the upstream and downstream "stations" relative to marker buoys of known position (Figs 6.1, 6.3). "Transect runs" did not necessarily begin or end at the same location and ranged in duration from 10 - 90 minutes. A difference in salinity greater than 0.1 $^{o}/_{oo}$ (ie two times the instrument error) between the upstream and downstream samples resulted in a "transect run" being rejected on the basis that different cells of water were sampled. At Hamersley Shoal and Keast Island "transect runs" were carried out on flood tides and on flood and ebb tides respectively. Because of the large tidal amplitude (~ 5 m) in the Dampier Archipelago "transect runs" were confined generally to periods just after (Hamersley Shoal, Keast Island) or just before (Keast Island) low water when mean depth in the study areas were generally less than about 2 m. "Transect runs" were carried out at different times day and night over an approximately 2 week period to produce a composite diel curve during each "season".

The net flux (F_x) of a substance in the water was determined by multiplying the change in concentration (C) between the beginning and end of a "transect run" by the average depth (D) and dividing by the duration (T) of each "run":

$$F_x = D\,(C_0 - C_1) / T.$$

6.2.3 Chemical Measurements

pH

pH was measured with a high-resolution millivolt meter (Windrift Instruments, WA: Model 721) and a Ross combination glass electrode. Duplicate samples of unfiltered seawater for pH measurement were taken from the Nisken bottle by allowing 120 ml glass culture tubes to overflow by about 3x their volume. Care was taken to avoid trapping air bubbles in the tubes which were then capped and placed in a dark, insulated water bath at

near ambient sea temperatures. At the completion of a "transect run" the upstream and downstream replicates were measured alternatively for pH and temperature within about 5 minutes of collecting the downstream sample. This delay in measurement allowed the downstream replicates to equilibrate to the same temperature as the upstream replicates. Measurement of pH up to 3 hours after collection was not significantly different to the pH of the same samples measured immediately after collection. Samples were measured within 0.2° C of each other and field pH's were calculated by adjusting measured pH's by -0.01 pH unit per ° C temperature difference between the *in situ* sea temperatures at the time of collection and the water bath temperature.

Total alkalinity (TA)

Using a calibrated acid dispenser in the laboratory, 8.7 ml of 0.01 M hydrochloric acid was placed carefully in preweighed 60 ml glass culture tubes, reweighed to 0.01 g (Sartorious 5012 M) and sealed with teflon lined tops and stored in darkness in polystyrene tube holders. In the field approximately 29 ml of seawater was collected in a calibrated syringe from glass culture tubes filled with seawater from the Nisken bottle as described above for pH measurement. Using an in-line 0.45 um GF/C glass-fibre filter the seawater was filtered and placed carefully in the acid tubes which were resealed and replaced in their container. Four replicates per water sample were processed within 10 minutes of collection.

In the laboratory the tubes were cleaned externally to remove salt accumulation, equilibrated to ambient laboratory air temperature and reweighed. All 8 tubes per "transect run" were then thoroughly shaken, placed in a water bath and bubbled simultaneously with CO_2- free, water saturated air for 5 minutes (see Smith and Kinsey, 1978), allowed to stand for

a further 5 minutes to equilibrate to a constant temperature and then measured for pH and temperature. The volumes of the seawater and acid samples were calculated from their weight divided by their density. The density of each seawater sample was calculated from the *in situ* temperature and salinity and the density of the acid (0.01 M HCL was assumed to have the density of distilled water) was calculated from *in situ* temperature only. The total alkalinity was calculated from the following formulae:

$$TA = 1000/V_S * V_aM - 1000/V_S(V_S+V_a) * a_H/f$$

where V_S and V_a are the volume of seawater and acid respectively, M is the molarity of the acid, a_H is hydrogen ion activity ($a_H = 10^{-pH}$) and f is an empirical constant (Culberson *et al.* 1970; Kinsey, 1978). The modifications described above of the method of Anderson and Robinson (1946) to measure the total alkalinity of seawater enable a standard error of about 0.001 meq l^{-1} for 4 replicates to be achieved consistently. A computer program was written to perform the necessary computations (Appendix IV).

6.2.4 Physical Measurements

Depth

The study areas at Hamersley Shoal and Keast Island were surveyed by the Australian Survey Office and bathymetric maps prepared in relation to chart datum (Figs 6.1, 6.3). Using these data and the approximate path of each "transect run" (determined in relation to marker buoys in known positions), the mean reef height of each "transect run", in relation to datum was calculated. Automatic depth recorders (Windrift Instruments, WA) were installed at known locations in relation to the bathymetric maps (Figs 6.1, 6.3).

The mean depth of each "transect run" was determined from the following formula:

Mean depth of "transect run" = (Ht. of logger site in relation to datum) - (Ht. of "transect run" in relation to datum) + (Depth recorded by logger)

where reef height above and below datum is positive and negative respectively. For example if the logger was installed at at 1.2 m below datum and recorded a mean depth of 3.5 m during a "transect run" over part of the reef which had a mean height above datum of 0.6 m, then the mean "transect run" depth would be:

$$\text{Mean depth} = (-1.2) - (+0.6) + 3.5 = 1.7\text{m}.$$

Hourly tide heights recorded *in situ* at Keast Island and Hamersley Shoal were found to be closely correlated with simultaneous tide heights recorded near No Name Rocks (Fig. 1.2) by Woodside Offshore Petroleum Pty Ltd. In the absence of *in situ* depth measurements the tide heights recorded near No Name Rocks were used in conjunction with the bathymetric maps and drogue paths to determine mean "transect run" depth.

Environmental Parameters

Seawater temperature ($\pm$ 0.1^{0} C) and salinity ($\pm$0.05%) was recorded with a Yeo-Kal salinity - temperature bridge (Model 605) at the beginning and end of each "transect run". At the beginning of each day the sensor was immersed in 0.01 M HCl to clean the platinum electrode to minimise instrument drift and at least 1 sample per day was taken and later analysed for salinity on an inductive salinometer as a calibration check.

Seabed irradiance was recorded automatically by light loggers (Mcilwraith Instumentation Pty., Ltd., Tas.; Windrift Instruments, WA). A light sensor (Megatron Ltd., UK) calibrated against a Li-Cor Integrating Quantum Sensor (LI 192S) and a Li-Cor Underwater Quantum meter (LI-188B) was used in both instruments. At Hamersley Shoal light was recorded in

November 1983 as 15 minute integrated measurements and as instantaneous measurements (every 15 minutes) at Keast Island during March and July 1984. Instrument malfunction caused complete loss of irradiance and sea temperature data recorded automatically at Hamersley Shoal during March 1984. Cloud cover was estimated as percentage cover without regard to the type of cloud present.

6.2.5 Community metabolism

Total Carbon Dioxide (TCO_2)

Total carbon dioxide (TCO_2) was calculated by a computer program (Appendix V) using pH, total alkalinity, temperature and salinity and the equations presented by Smith and Kinsey (1978). The dissociation constants for carbonic acid, boric acid and Henry's Law coefficient for CO_2 in seawater were calculated as a function of temperature and chlorinity of the seawater sample. Changes in CO_2 due to gas exchange across the sea / air interface were not corrected for as these are considered to be insignificant (~2%) compared to changes caused by the benthic communities (Smith, 1981).

Calcification

The term calcification is used here to denote net calcification (ie precipitation minus solution) and is used synonomously with inorganic carbon flux. The rate of calcification (ie Flux $_{CaCO3}$) is related stoichiometrically to the total alkalinity by the relationship: Flux $_{CaCO3}$ = Flux $_{TA}/2$ (Smith and Marsh, 1973; Smith and Kinsey, 1978). Changes in total alkalinity can be caused by the assimilation of nitrogen and sulphate reactions but these are considered to be insignificant compared to CO_2 induced changes (Kinsey, 1978).

Carbon Flux

The flux of carbon occurs through the inorganic ($\Delta CO_2{}^C$) and organic ($\Delta CO_2{}^P$) carbon cycles. The flux of organic carbon was calculated as total carbon flux minus the inorganic carbon flux. All are in units of m mol m^{-2} h^{-1} and are multiplied by 0.012 (organic C) and 0.1 (inorganic C) to convert to g C m^{-2} h^{-1}. The annual estimate of calcification (G) is expressed as kg $CaCO_3$ m^{-2} y^{-1}. The mean hourly net photosynthetic rate (p) during the day and the mean hourly respiration rate (r) during the night were calculated from the area under the line of best fit of a three point running average curve through the raw data. Community respiration (R) is the mean hourly rate times 24 h (R=24 x r) and assumes that r is constant over a diurnal cycle, and gross production (P) is the mean hourly net photosynthetic rate plus the respiration rate times the hours of daylight (h_d): (P=(p+r) x h_d). The P:R ratio is used to define the degree of autotrophic self-sufficiency, that is if P:R <1 then the community is heterotrophic and is either importing organic carbon or consuming organic carbon stored within the community but if P:R >1 then the community is autotrophic and either exporting or storing organic carbon. The net gain or loss of organic carbon (E) is defined as E = P - R. The daily net calcification rate is the mean hourly daylight rate (C_d) times the hours of daylight plus the mean hourly night rate (C_n) times the hours of night. The mean hourly net calcification rates are calculated as for p and r. Means for summer and winter were averaged to provide annual estimates of calcification and organic carbon metabolism for the Keast Island reef. Data for Hamersley Shoal was insufficient to construct useful diel curves or annual estimates but are used qualitatively to compare spatial and temporal trends in community metabolism between the two reef types.

In this study organic carbon flux was assumed to be caused primarily by the benthic communities and not by phytoplankton which, in the past,

has been assumed to be trivial by comparison (eg Lewis 1977, Kinsey, 1983a, Atkinson and Grigg, 1984), although as Kinsey (1985) points out, in some cases phytoplankton production can contribute up to 10% of very active reef-flat communities (ie >10% 7 gC m^{-2} d^{-1}). However these high production rates were often associated with phytoplankton blooms (not present at these sites during this study), whereas more 'typical' rates of phytoplankton production in coral reef systems are considereably lower (Kinsey, 1985).

6.3 RESULTS AND DISCUSSION

6.3.1 Carbon Flux

Organic ($\Delta CO_2{}^P$) and inorganic ($\Delta CO_2{}^C$) carbon fluxes for Hamersley Shoal (November 1983 and March 1984) and Keast Island (March and July 1984) are shown in Figures 6.4, 6.5, 6.6, and 6.7. Negative and positive fluxes indicate that CO_2 has been consumed and produced respectively. In general all figures show that CO_2 is consumed during the day through the organic and inorganic carbon cycle due to community photosynthesis and calcification repectively whereas at night CO_2 is produced by community respiration. In general calcification and photosynthesis increase during the morning and maxima occur between 1000 h and 1400 h followed by a decline in the late afternoon. In general net calcification during darkness was zero, although in "winter" some nighttime "transect runs" at site 6 indicate calcification occurred. Table 6.3 summarises gross and net community metabolism measured at Keast Island reef during March ("summer") and July ("winter") 1984.

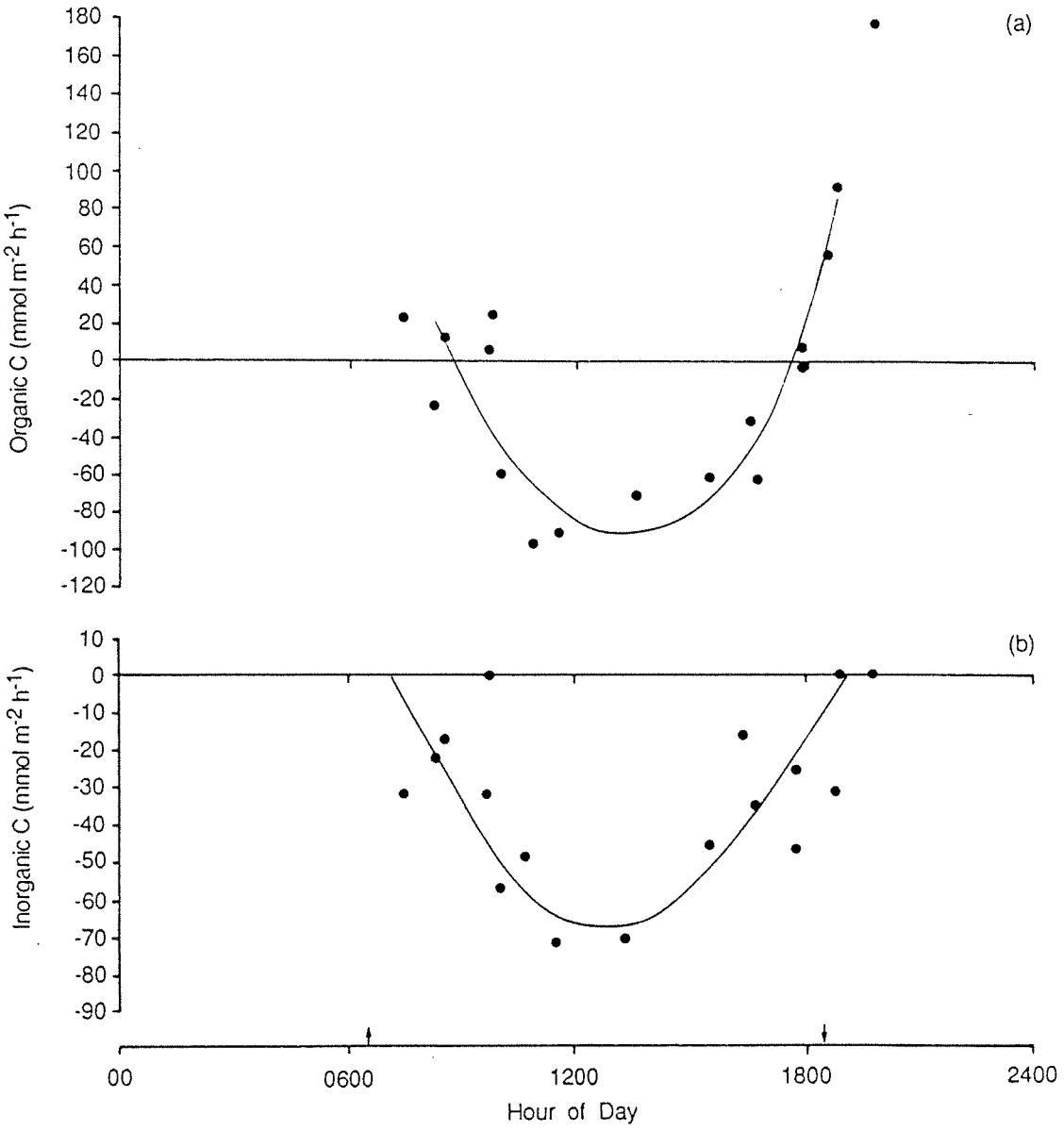


Figure 6.4 (a) Diurnal curve for organic carbon flux at Hamersley Shoal in November 1983. (b) Diurnal curve for inorganic carbon flux at Hamersley Shoal during November 1983. Curves were constructed by sampling during flood tides between November 7 to 16. Arrows indicate time of sunrise and sunset.

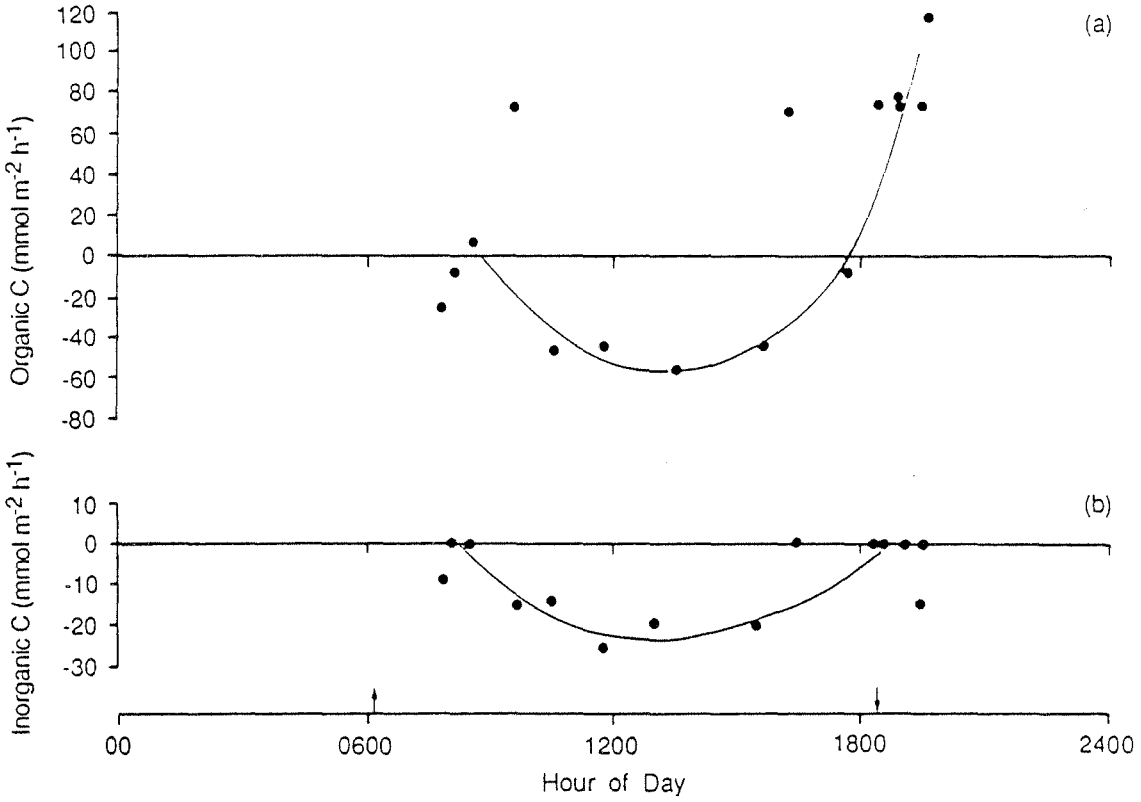


Figure 6.5 (a) Diurnal curve for organic carbon flux at Hamersley Shoal during March 1984.
(b) Diurnal curve for inorganic carbon flux at Hamersley Shoal during March 1984.
Curves were constructed by sampling during flood tides between March 12 to 27.
Arrows indicate time of sunrise and sunset.

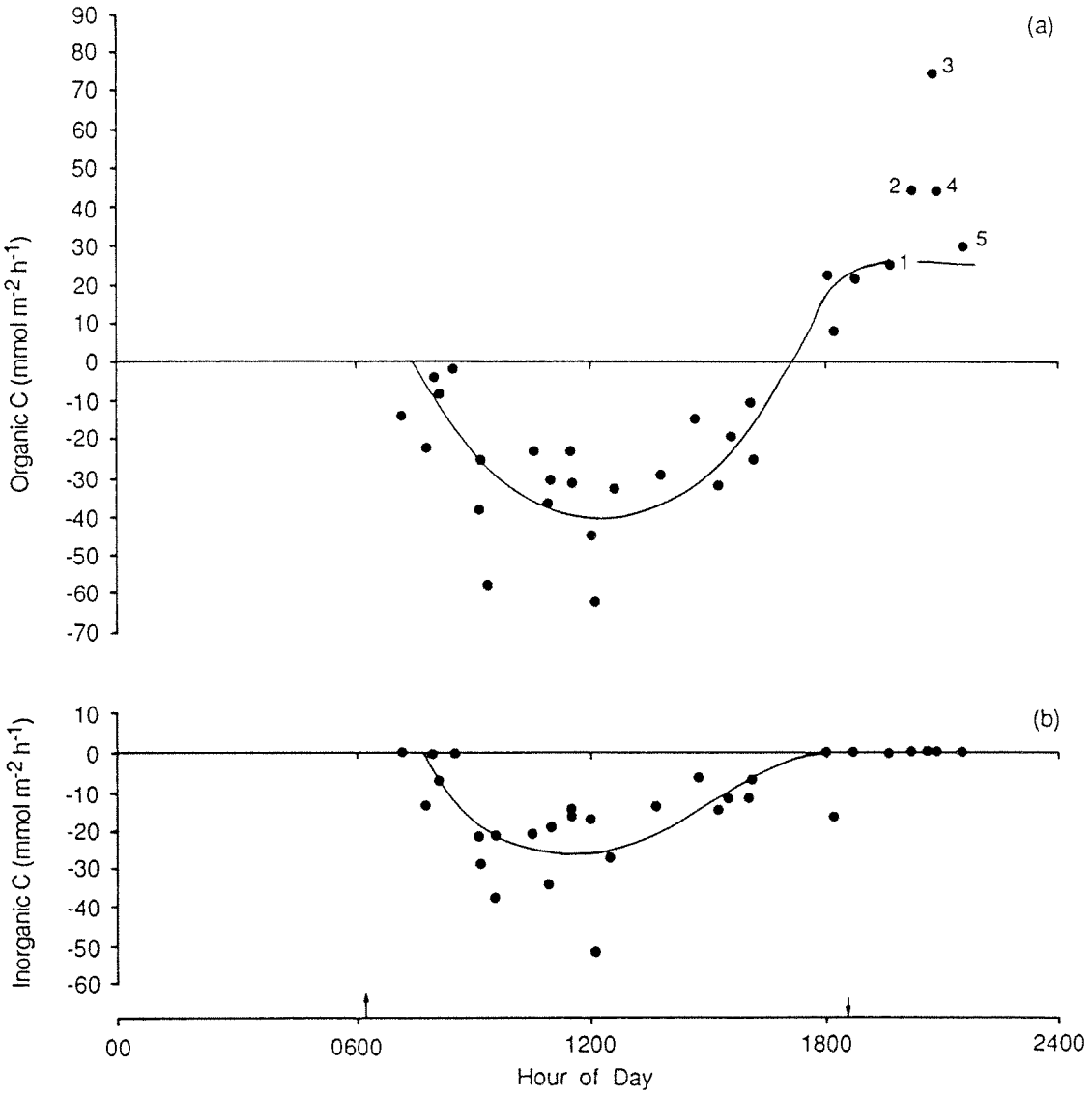


Figure 6.6 (a) Diurnal curve for organic carbon flux at Keast Island reef during March 1984. 1, 2, 3 are estimates of r on successive "transect runs" on March 25; 4, 5 are successive estimates of r on March 26.
(b) Diurnal curve for inorganic carbon flux at Keast Island reef during March 1984. Curves were constructed by sampling during flood and ebb tides between March 12 to 27. Arrows indicate time of sunrise and sunset.

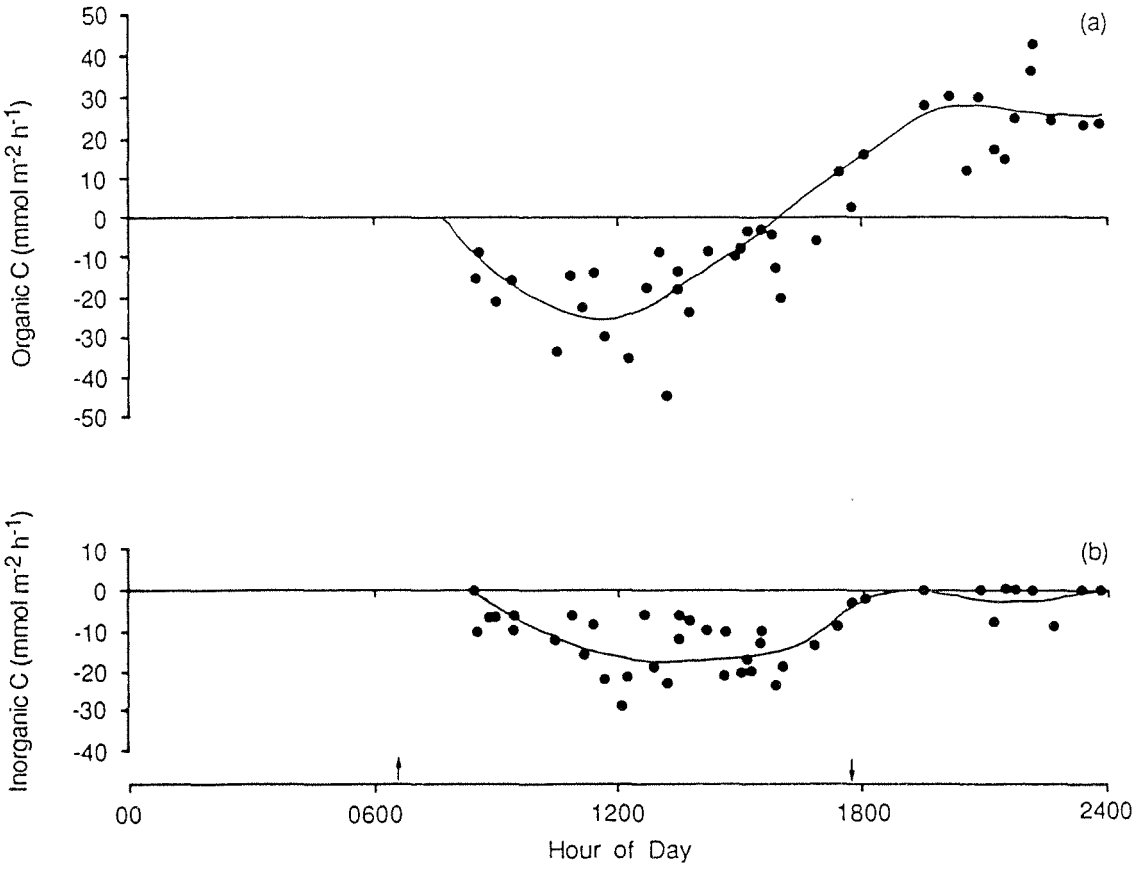


Figure 6.7 (a) Diurnal curve for organic carbon flux at Keast Island reef during July 1984. (b) Diurnal curve for inorganic carbon flux at Keast Island reef during July 1984. Curves were constructed by sampling during flood and ebb tides between July 13-28. Arrows indicate time of sunrise and sunset.

Table 6.3 Seasonal estimates of mean community metabolism parameters at Keast Island reef-flat during 1984.

	"Summer"	"Winter"	Average
Inorganic C metabolism			
$\Delta CO_2{}^c$ m mol m^{-2} h^{-1} (kg $CaCO_3$ m^{-2} y^{-1})	-15 (6.8)	-11 (4.6)	-13 (5.7)
Organic C metabolism			
$\Delta CO_2{}^P$ m mol m^{-2} d^{-1} (g C m^{-2} d^{-1})			
Gross production (P)	-591 (7.1)	-371 (4.5)	-481 (5.8)
Respiration (R)	672 (8.1)	504 (6.0)	588 (7.0)
Net production (E=P- R)	81 (-1.0)	133 (-1.5)	107 (-1.2)
P : R	0.9	0.7	0.8

Gross production in "summer" was 7.1 g C m^{-2} d^{-1} and respiration was 8.1 g C m^{-2} d^{-1} resulting in a P:R of 0.9. In "winter" gross production was 4.5 g C m^{-2} d^{-1} and respiration was 6.0 g C m^{-2} d^{-1} giving a P:R of 0.7. Net calcification in "summer" was 6.8 kg $CaCO_3$ m^{-2} y^{-1} and 4.6 kg $CaCO_3$ m^{-2} y^{-1} in "winter" giving an annual average of 5.7 g $CaCO_3$ m^{-2} y^{-1}. The annual average for P was 5.8 g m^{-2} d^{-1} and for R was 7.0, resulting in an average P:R of 0.8.

These values for P, R and G conform reasonably well to published values for extensive coral/ algal reef flats as described by Kinsey (1985; Table 6.4) although the overall P:R of 0.8 is lower than for the standard reef flat which is, generally, in autotrophic balance with a P:R of unity. The "winter" P:R of 0.7 for the Keast Island reef is comparable to the P:R of other similar reefs during "winter" and although the "summer" P:R increased to 0.9 it is lower than the mean of 1.1 for 7 locations of similar reef types reported by Kinsey (1985; Table 6.5).

A number of explanations for this difference are possible. Firstly this reef may, in fact, be heterotrophic throughout the year and secondly, while the P:R value determined during March is obviously a reflection of the trophic balance of the reef at the time of measurement it may not be

Table 6.4 Published values for community metabolism in reef-flat coral / algal zones (from Kinsey, 1985).

Reference	Location	P	R	P/R	G
		(g C m^{-2} d^{-1})			(kg $CaCO_3$ $m^{-2}y^{-1}$)
Sargent and Austen (1949)	Rongelap	4	3.5	1.1	
Odum and Odum (1955)	Enewetak	10	10	1.0	
Kohn and Helfrich (1957)	Kauai	7.9	7.6	1.0	
Qasim *et al.* (1972)	Laccadives	6.2	2.5	2.5	
Kinsey (1972)	One Tree Is.				4.6
Smith (1973)	Enewetak	6	6	1.0	4.
Smith and Marsh (1973)	Enewetak	6	6	1.0	
Kinsey and Domm (1974)	One Tree Is.	7.5	6.8	1.1	
Marsh (1974)	Guam	7.2	6.6	1.1	
LIMER Team (1976)	Lizard Is.				4.
Sournia (1976)	Moorea	7.2	8.4	0.9	
Kinsey (1977)	One Tree Is. DK13	7.2	7.4	1.0	4.6
Kinsey (1979)	Lizard Is. A2	7.8	8.9	0.9	4.6
Kinsey (1979)	Lizard Is. D1	7.0	5.8	1.2	3.1
Sournia *et al.* (1981)	Moorea	17	17	1.0	0.5
Atkinson and Grigg (1984)	French Frigate Shoals	~6.5	~4	~1.6	~6.5
Barnes and Deveraux (1984)	Rib Reef	8.8	7.6	1.2	3.5
Kinsey (1983b)	Rib Reef line reef	5.7	8.4	0.7	
Pichon and Morrissey (1985)	Tulear (Madagascar)	19	11	1.7	1.9
This study	Dampier Arch.	5.8	7.0	0.8	5.7

Table 6.5 Seasonality in community metabolism for shallow reef-flat areas (from Kinsey, 1985).

Reference	Location	Season	P	R	P/R	G
			($g\ C\ m^{-2}\ d^{-1}$)			($kg\ CaCO_3 m^{-2} y^{-1}$)
Kohn and Helfrich (1957)	Kauai fringing reef (22° N)	S	8.3	7.6	1.1	
			(1.1)	(1.0)		
		W	7.7	7.6	1.0	
Kinsey and Domm (1974)	One Tree Is. patch reef (23° S)	S	4.1	3.8	1.1	
			(2.4)	(1.6)		
		W	1.7	2.4	0.7	
Kinsey (1977)	One Tree Is. reef-flat (23°S)	S	9.0	7.9	1.1	5.0
			(2.5)	(1.5)		(1.3)
		W	3.6	5.3	0.7	4.0
Kinsey (1979)	Lizard Is. reef-flat (23° S)	S	9.7	11.8	0.8	3.3
			(2.4)	(3.1)		(1.4)
		W	4.1	3.8	1.1	2.4
Kinsey (1979)	Kaneohe Bay fringing reef (21° N)	S	11.0	15.1	0.7	10.0
			(2.0)	(2.5)		(1.3)
		W	5.5	6.4	0.9	7.9
Smith (1981)	Abrolhos Is coral shoal (29° S)	S	21.0	19.6	1.1	18.3
			(1.7)	(1.4)		(3.9)
		W	12.1	14.4	0.8	4.7
Atkinson and Grigg (1984)	French Frigate Shoals reef-flat (25° N)	S	8.5	4.9	1.8	10.2
			(2.0)	(1.9)		(3.6)
		W	4.3	2.6	1.7	2.8
This study	Dampier Arch. reef-flat (20° S)	S	7.1	8.1	0.9	6.8
			(1.6)	(1.4)		(1.5)
		W	4.5	6.0	0.7	4.6

representative of a mean "summer maximum". The data obtained at Hamersley Shoal during November 1983 and March 1984 support the latter suggestion. Figures 6.4 and 6.5 show that the maximum hourly rate of net photosynthesis (p_{max})at Hamersley Shoal in November 1983 was about 1.1 g C m^{-2} h^{-1} whereas in March p_{max} was about 0.6 g C m^{-2} h^{-1}. Similarly the maximum daytime hourly rate of net calcification (c_{max}) was about 7.0 and 3.0 g $CaCO_3$ m^{-2} h^{-1} in November and March respectively. Although the data, especially in March 1984, are insufficient to be conclusive it appears that in general inorganic and organic carbon flux at this reef was significantly higher in November 1983 than in March 1984.

This conclusion is supported by the growth rates of *Acropora hyacinthus* (the dominant coral species on the upper reef slope at Hamersley Shoal) and *Acropora formosa* at Nelson Rocks between February 1982 and November 1983 where March growth rates were approximately 80 % and 70 % respectively of November growth rates (see Fig. 4.1).

The apparent decrease in community metabolism during March 1984 may be due to a number of factors. Firstly sea temperatures in the Dampier Archipelago are maximal during the latter half of March and the first week in April (see Fig. 3.2) and temperatures over 30° C can occur for periods of several weeks (Mills *et al.* 1986). Bleaching of corals was observed at Keast Island in March 1985 and 1986 during periods when maximum temperatures reached 32.5 and 33.3° C respectively. There are many reported instances of corals expelling zooxanthellae at temperatures above 30° C and this is generally considered a sign of "stress" (see Chapter 4). Loss of zooxanthellae, which has also been observed at these temperatures at other sites in the Dampier Archipelago (see Chapter 4), may significantly reduce gross production on a coral-dominated reef resulting in reduced P and therefore, a lower P:R value.

The second possibility is that R was elevated by a period of high reproductive activity that occurred on this reef during March 1984. On March 25, 1984 three consecutive estimates of r were 26 (1930 h), 44 (2015 h) and 74 (2040 h) m mol CO_2 m^{-2} h^{-1} and on the following night r was 44 m mol CO_2 m^{-2} h^{-1} at 2045 h and 30 m mol CO_2 m^{-2} h^{-1} at 2130 h (Fig. 6.6). These "transect runs" all occurred during different stages of a coral mass spawning event that occurred on these two nights. In the Dampier Archipelago this phenomenon involves many species of corals spawning synchronously for about 3 hours after dark and includes a simultaneous reproductive swarming of polychaete worms (see Chapter 5). Coral eggs first appeared about 30 minutes after sunset at about1700 h. By 1930 h (ie during the first "transect run" that night) scattered coral eggs and a few polychaete worms were present. By 2000 h (ie during the second "transect run") the water was covered with red and pink coral eggs, the number of polychaete worms had increased markedly and schools of the blue sprat *Spratteloides robustus* were observed eating the coral eggs. The density of coral eggs and the swarming of polychaetes appeared to peak between 2030 h and 2100 h (ie during the third "transect run"). On the following night the first "transect run" was approximately equivalent to the second "transect run" of the night before in relation to the stage of coral spawning. By 2130 h on this night relatively low densities of coral eggs and polychaetes were present.

The estimate of r measured on the "low activity transect runs" (ie first "transect run" on the night of March 25 and the second "transect run" on March 26) have been included in estimating R for this period whereas r measured during the three "high activity transect runs" have been excluded. The subjective nature of this selectivity and the paucity of estimates of r other than during spawning times makes the estimate of R for this period rather tenous and may result in an over estimation of this parameter

resulting in a lower P:R value.

The implications of these data raise a number of important questions. Firstly although r is obviously elevated during actual spawning and was probably largely due to the activity of the polychaete worms, the question remains of whether R measured during the period (weeks, months?) before or after the spawning season is "typical" of a "summer" value when making annual estimates of community matabolism from 2 data points (ie "summer" and "winter") and highlights the need to consider the influence of other biological processes, such as reproduction, on community metabolism. Secondly coral gonads increase rapidly in size in the month before spawning indicating that large amounts of energy are required for gametogenesis during this period. This may result in coral dominated reefs becoming increasingly heterotrophic as the amount of energy required for reproductive processes increases. Loya (1985) found that linear growth rate of sexually immature colonies of *Stylophora pistillata* was greater in summer than winter whereas in general sexually mature colonies showed no significant difference between summer and winter growth rates. He suggests that increased reproductive activity of *S. pistillata* during summer was partly responsible for the relatively lower growth rates of sexually mature colonies in summer. Although this species is a planulating species with a markedly different mode of reproduction than the mostly spawning species found at sites 6 and 7, this study provide further evidence (see Chapter 4.4.2) that reproductive processes of corals may significantly influence growth rates and therefore coral-dominated community metabolic parameters.

Thus additional man-made "stress" at a time of high reproductive activity may be more detrimental than at less critical (ie less heterotrophic) times in the life cycle of corals. This combination of events may have led to the sudden decline and eventual death of an *Acropora* dominated reef in the

Dampier Archipelago during 1983-1984 following a period of dredging operations between November 1982 and February 1983 (see Chapter 4).

6.3.2 Seasonality

Gross production and respiration at Keast Island in "winter" was about 63 % and 74 % of the "summer" values respectively and net calcification decreased from 6.8 kg $CaCO_3$ m^{-2} y^{-1} in "summer" to about 4.6 kg $CaCO_3$ m^{-2} y^{-1} in "winter"; a decrease of about 32 %. In a summary on seasonality in community metabolism Kinsey (1985) has stated that in general there appears to be a two- fold difference in P and R between summer and winter and that the variation in seasonality appears to be inversely proportional to latitude. In contrast seasonal differences in net calcification appear to be correlated with latitude, increased seasonality occurring at higher latitudes (Table 6.5). No explanation for these opposing trends is offered. Although the data presented here for the Dampier Archipelago conform approximately to these generalizations further speculation is pointless in view of the preceding discussion, although it is interesting to note the seasonal ratio of P and R for the Dampier Archipelago reef (1.6 and 1.4) are similar to the ratios of 1.7 and 1.4 found by Smith (1981) at the Abrolhos Islands (Table 6.5) .

Environmental data collected at both sites are shown in Figures 6.8 to 6.11. Lower light intensity and sea water temperature in "winter" were the major seasonal differences in the measured environmental conditions during March and July. At the Keast Island reef maximum noon seabed light intensities on a cloudless day were 1700 μ mol m^{-2} s^{-1} in March and 1250 μ mol m^{-2} s^{-1} in July (Figs 6.10e, 6.11 e) whereas mean seawater temperature was about 30° C (range: 27.5 - 31.4° C) in March and about 21° C (range: 18.0 - 22.8 ° C) in July (Figs 6.10b, 6.11b).

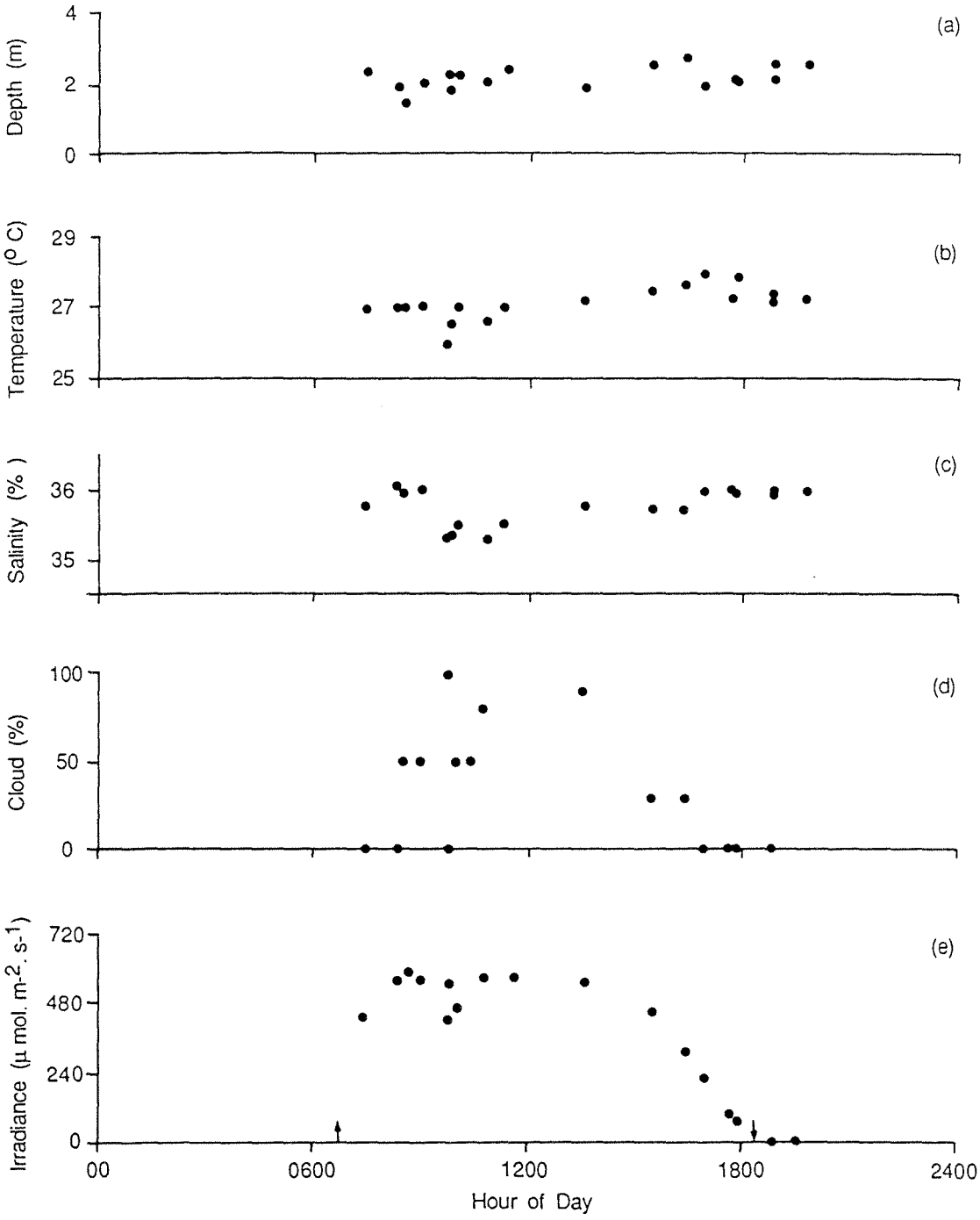


Figure 6.8 Environmental data recorded for each "transect run" at Hamersley Shoal between November 7 to 16, 1983. Arrows indicate time of sunrise and sunset. Light values are typical values on a cloudless day in November 1983, 0.7 m above the seabed at the logger site (Fig. 6.1).

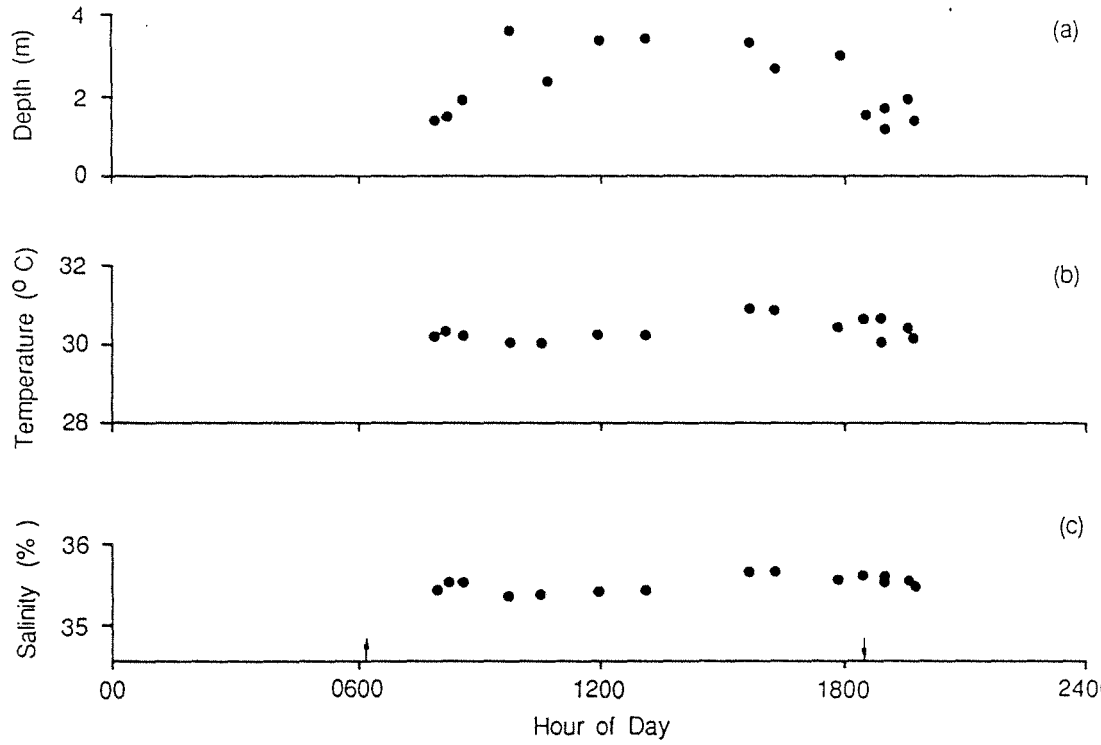


Figure 6.9 Environmental data recorded for each "transect run" at Hamersley Shoal between March 12 to 27, 1984.

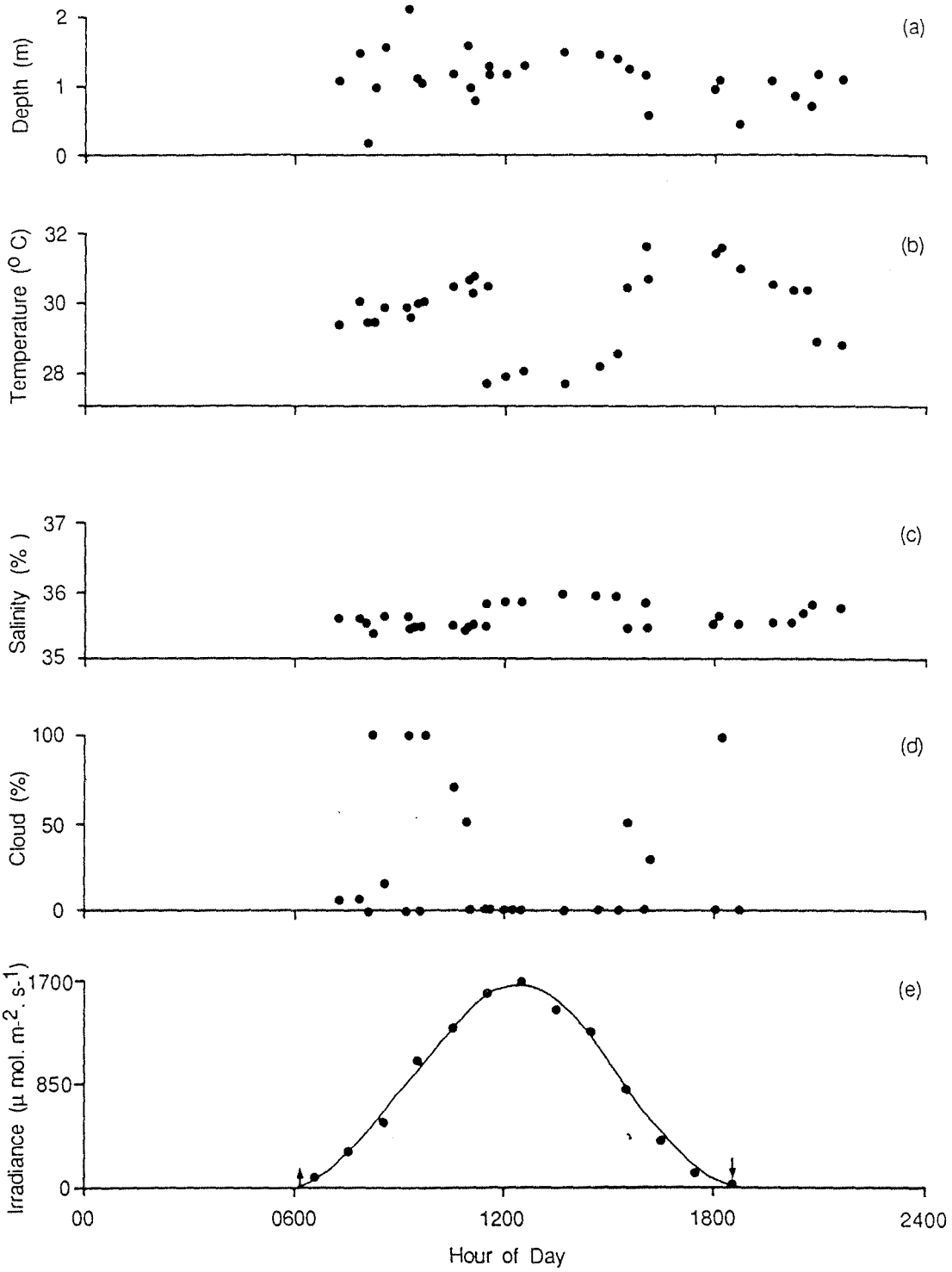


Figure 6.10 Environmental data recorded for each "transect run" at Keast Island reef between March 12 to 27, 1984. Arrows indicate time of sunrise and sunset. Light values are typical values on a cloudless day in March 1984, 0.2 m above the seabed at the logger site (Fig. 6.3).

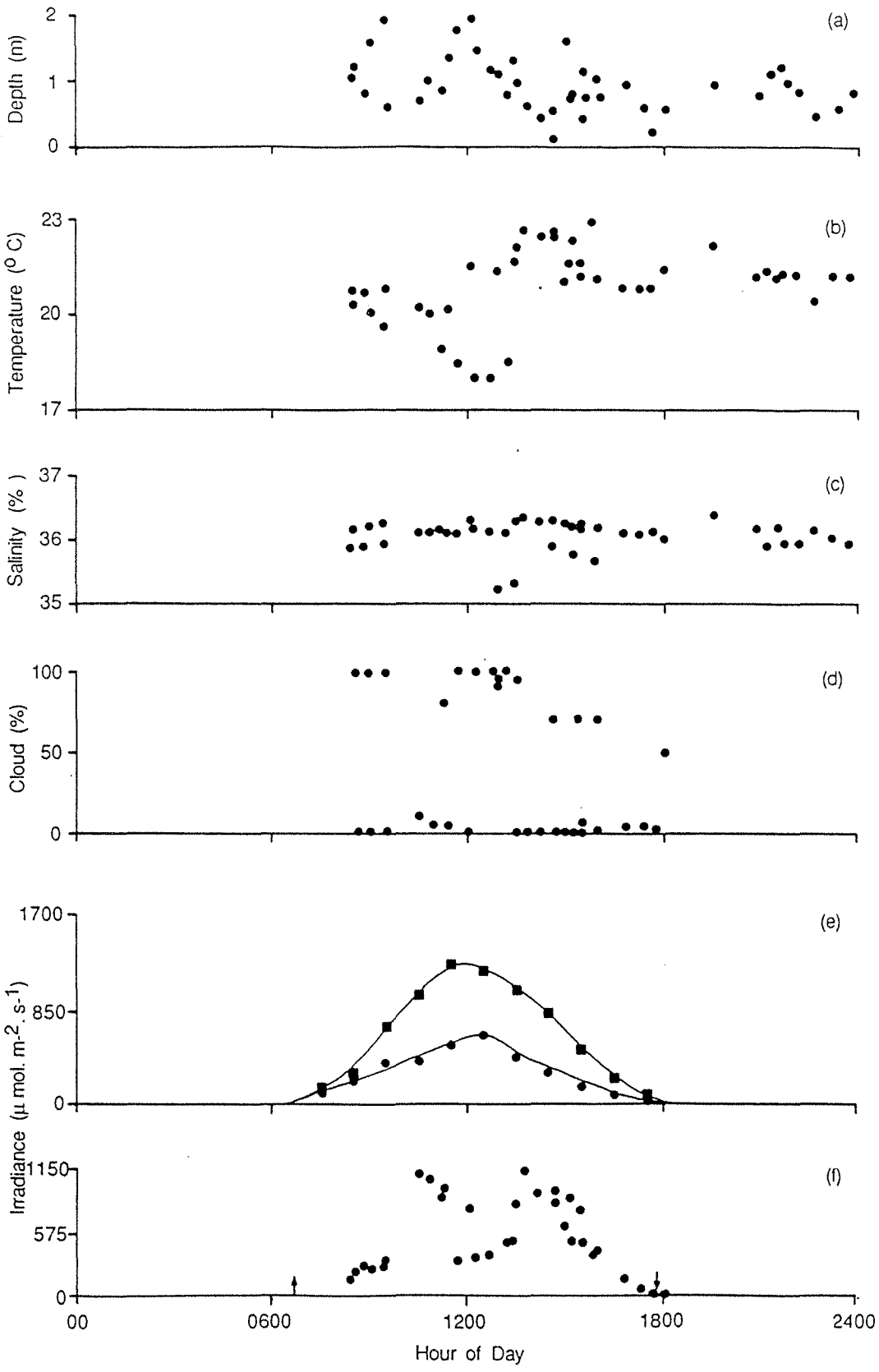


Figure 6.11 Environmental data recorded for each "transect run" at Keast Island reef between July 3 to 17, 1984. Arrows indicate time of sunrise and sunset. Light values in (e) are typical values on (■) cloudless day and (●) high cloud in July 1984, 0.2 m above the seabed at the logger site (Fig. 6.3).

Variation in P, R and G measured at Keast Island during "summer" and "winter" may be related to the seasonal variation in temperature and light availability but the data are insufficient to ascribe specific causes. In general net hourly production and net calcification rates at Keast Island in July show a positive relationship to light intensity. Barnes and Devereux (1984) using a continuous logging, Lagrangian method of data acquision found, for the first time, that reef-flat hourly production and net calcification rates could be described mathematically in terms of light intensity. Non-automated methods are unlikely to be able to discern these relationships because of the low density and the high variability of the data when diel cycles are constructed over extended periods.

6.3.3 Short term variability

The variability observed in the community metabolism data may be due to several possibilities. Firstly, part of the observed variation may be due to real differences between sampling occasions. Individual "transect runs" at a site do not necessarily characterise one particular section of the benthic community due to variations in current direction caused by different combinations of wind, water depth and current speed. Thus diel cycles of community metabolism constructed over several days under these varying conditions will characterise the metabolism of a relatively heterogeneous area of reef and this heterogeneity may be reflected as scatter in the data. The high resolution studies of Barnes (1983b) and Barnes &Devereux (1984) where changes in community metabolism were correlated to changes in benthic community structure, and in this study, where changes in community respiration rates coincided with an observable biological event (ie coral spawning) support the suggestion that these variations are not wholly "noise". The lower scatter in the data from Hamersley Shoal (Figs

6.4, 6.5) may be due to the higher degree of similarity of the benthic community between "transect runs" at this site as a result of a more pronounced zonation, normal to the reef crest, of the benthic community.

Variations in the data may also caused by short term fluctuations in the physical environment. In general environmental conditions at the Hamersley Shoal study site were considerably less variable in the short term than at Keast Island due to the proximity of the open ocean and greater mean depth. For example seawater temperatures at Hamersley Shoal and Keast Island varied by $<2^{o}$ C and $>4^{o}$ C respectively during the March study period (Figs 6.9b, 6.10b). Furthermore seabed irradiance at a particular time of the day can also vary considerably from day to day depending upon the water depth and clarity and the amount of cloud. Figure 6.11e shows the effect of cloud on seabed irradiance at Keast Island on July 7 (high cloud cover) and on July 8 (low cloud cover) with mean irradiance levels during daylight hours increasing from 289 μ mol m^{-2} s^{-1} to 641 μ mol m^{-2} s^{-1} respectively.

At Keast Island most "transect runs " were carried out at water depths between 0-2 m with an average depth of about 1 m (Figs 6.10a, 6.11a). Water samples were taken in the top 0.5 m on the assumption that changes in water chemistry at the seabed level are mirrored in the surface water (ie the water is well mixed vertically). Dye studies conducted under different tide and wind conditions at Keast Island indicate that vertical mixing throughout the water column is rapid under conditions of high current and/or wind speed irrespective of the depth but is significantly less under conditions of low current and low wind speed. These experiments indicate that the degree of vertical mixing at this site is probably directly related to the amount of turbulance and suggests that the assumption of a chemically homogeneous water column, under conditions of laminar flow, becomes increasingly tenuous as depth increases, introducing further errors into estimates of

community metabolism.

The flux of material is directly proportional to the mean "transect run" depth (MTD) and therefore the precision of measurement of this parameter directly influences the calculated flux. At Keast Island MTD ranged from 0.2 - 2.0 m and thus the percentage error varied by an order of magnitude. Many studies of material flux have estimated MTD by taking a series of depth measurements along each "transect run" by graduated pole or lead line (eg Smith, 1981; Atkinson and Grigg, 1984) . The error in these methods will depend upon the uniformity of the substrate: that is the degree of "roughness" of the seabed. Although the method used to estimate MTD in this study is possibly an improvement on these techniques, albeit more costly, there remains an inherent error in the measurement of mean transect depth which will cause variation in the data.

The data presented here for the Keast Island reef support the theory of modality of metabolic performance of reefs worldwide and suggest that seasonal variation in organic productivity and calcification occurs on coral-dominated reefs in the Dampier Archipelago. Comparisons between the offshore reef at Hamersley Shoal, and the inshore reef at Keast Island suggest that as expected, differences in metabolic performance occurs between different reef types in the Dampier Archipelago. Community metabolism data for the Keast Island reef suggest that overall this reef may be heterotrophic and therefore importing carbon. However, as discussed above this conclusion depends largely on the influence of other key biological processes on community metabolic parameters. Further discussion is presented in Chapter Seven.

CHAPTER SEVEN

GENERAL DISCUSSION AND CONCLUSIONS

7.1 The Dampier Archipelago marine environment

The Dampier Archipelago lies on the inner part of the North West Shelf and swell waves impinge persistently on the outer reefs from the west in winter and periodically from the northwest in summer when tropical cyclones occur. These cyclones occur from December to April and can generate large waves which have a destructive influence on the coral communities in the archipelago. Winds from the west and southwest predominate during September to March and change to the southeast trades during April to August. During the changeover of these seasonal wind patterns, periods of light and variable winds are common. Tides are semi-diurnal with a maximum spring amplitude of 4.9 m.

From an oceanographic point of view, the coastal waters off Western Australia are unique because of the presence of a poleward, warm current that flows down the coastline during autumn and winter. This is opposite to most eastern boundary currents which are generally cold, equatorward currents.

The photic zone of inshore waters in the Dampier Archipelago is generally less than 20 m whereas in the adjacent offshore waters on the inner northwest shelf, it can be over 50 m. The proximity of the open ocean modifies the physical environment of the outer reefs on the periphery of the archipelago. Blooms of the blue-green alga, *Trichodesmium erythraeum* are common during December to April.

Coral communities in the Dampier Archipelago are confined to extensive reefs on the periphery of the archipelago and as small fringing or

patch reefs adjacent to islands and rocky shores. At present 209 species of scleractinian corals from 57 genera have been recorded, and this high diversity is consistent with the wide range of habitats found in the archipelago. Generic diversity is highest in the midshore regions of Mermaid Sound with abundance being highest on the offshore reefs and lowest on the inshore reefs.

7.2 Temporal and spatial variation in the physical environment

Intra-annual or seasonal variation in the physical environment of the offshore zone (ie at site 1) is summarised in Table 7.2. Seawater temperature, salinity, global radiation and wind speed were greater in 'summer' than in 'winter', although wave parameters, cloud and computed PPFD were not significantly different.

Table 7.2 Summary of statistical tests of temporal variation of environmental parameters at site 1 (data from Chapter 2). (ns, not significantly different; > or<, significantly greater or less than at the 0.05 probability level).

Parameter	'summer'	'winter'
Seawater temperature	>	
Salinity	>	
Sediment deposition	ns	
Global radiation	>	
Cloud	ns	
Computed PPFD	ns	
Wave energy	ns	
Maximum wave height	ns	
Wind speed	>	

A summary of the results of statistical tests on the spatial variation of the environmental parameters at the three study sites in 'summer' and 'winter' are presented in Table 7.1.

Table 7.2 Summary of statistical tests of the spatial variation of environmental parameters between sites 1, 2 and 3 (data from Chapter 2).
(ns, not significantly different; > or<, significantly greater or less than at the 0.05 probability level).

	'Summer'			'Winter'		
Parameter	Sites 1-2	1-3	2-3	Sites 1-2	1-3	2-3
Temperature	ns	ns	ns	ns	ns	ns
Salinity	<	<	ns	<	<	ns
Sediment deposition	<	<	>	ns	ns	ns
Water clarity	>	>	ns	>	>	ns
Computed PPFD	ns	>	ns	ns	ns	ns
Wave energy	>	>	-	>	>	-

These data indicate that the coral reefs in the Dampier Archipelago occur in two distinct hydrographic zones: an offshore and an inshore zone and that difference between these two zones is greatest in 'summer'. The offshore zone in 'winter', as represented by site 1, has clearer water, lower salinity and higher wave energy although seawater temperatures, sediment deposition rates and light availability are similar to the inshore zone. Conversely, in 'summer', salinity and sediment deposition are lower whereas

water clarity, wave energy and light are generally higher. In the inshore zone, environmental conditions under 'natural' conditions are generally similar at both sites. An exception occurred at site 2 when extremely high sediment deposition rates coincided with dredging and dumping activities.

Seawater temperatures on a shallow, well-flushed reef in the Dampier Archipelago had a annual range of >15° C with recorded extremes of 18.0° C and 33.3° C at site 6. High seawater temperatures (>30° C) can occur for extended periods during summer, and published values suggest that maximum summer temperatures are close to the upper lethal limits for corals; the presence of bleached colonies in the Dampier Archipelago during summer and winter indicate that some species, at least, are 'stressed' at both temperature extremes. On the other hand salinity values in the Dampier Archipelago are close to the optimum range for coral growth and survival and vary only slightly from the average tropical ocean salinities of 35 $^{o}/_{oo}$.

Sediment deposition rates (total) for the offshore reefs in the Dampier Archipelago averaged about 40 g $m^{-2}d^{-1}$ throughout the study period, which is consistent with published values on 'clear water' coral reefs that have a high cover of live coral. In contrast, background levels of total sediment deposition on the inshore reefs range from about 50 g m^{-2} d^{-1} in 'winter' to approximately 130 g $m^{-2}d^{-1}$ in 'summer'. Rates comparable with these 'summer' levels have been recorded in the literature as associated with reductions in coral growth, fecundity and live cover, suggesting that even small increases in the rate of sediment deposition for extended periods in 'summer' would be likely to be detrimental to corals on these reefs.

The high rates of 260 g $m^{-2}d^{-1}$ recorded at site 2 during 'summer' coincided with dredging and dumping activities, and probably caused the reduced growth observed in *Acropora formosa* and the high mortality of corals observed at this site during the subsequent 12 months. Sediment

deposition data collected at sites 1 and 3, during a period when a cyclone occurred, suggest that the rates recorded at site 2 during the dredging, are unlikely to occur naturally over a similar time period, at either the inshore or offshore reefs in the Dampier Archipelago. Under normal conditions light availability at site 1 was generally similar to the inshore sites due to a combination of clearer and deeper water at that site.

Little is known about the synergistic effects of environmental stresses on coral growth, reproduction and survival. For example, although corals may tolerate increases in sediment deposition at certain times of the year, their tolerance to the same increase during periods of high seawater temperatures and/or during periods of intense reproductive activity may be significantly lower. Furthermore, where corals exhibit signs of stress (ie expulsion of zooxanthellae) under natural conditions at certain times of the year, additional man-made stresses may have sub-lethal effects such as reduced fecundity and/or growth rates. Catastrophic effects of human purturbations on coral communities are often relatively localised and may well be insignificant in comparison to the possibly more widespread effects of sub-lethal stress; the results of which may not be evident for years.

7.3 Coral growth methods and evaluation of experimental manipulation

The data collected here concerning the growth of branches of the staghorn coral *Acropora formosa* were assumed to be normally distributed, and so the use of parametric statistics was justified. However, both parametric and non-parametric statistical analyses were carried out in parallel on all data, and the results agreed completely. About 7 or more branch measurements per colony are required to reduce the inherent variability in branch growth, when measured over a time scale of weeks, to provide a reproducible estimate of mean branch growth. In this study the

growth of arborescent species were recorded as the mean of 30-40 branch measurements from 4 - 5 colonies.

There was generally little inter- colony variation in growth, for the 3 species studied, over periods of about 40 days, but this variation increased as growth periods got longer. This variation appeared to be related more to the relative vulnerability to mechanical damage rather than intrinsic metabolic differences between colonies. It is concluded that 4-5 colonies per growth datum, under the specified sampling regime, will ensure that the mean value obtained is a reproducible estimate of the growth rate of the immediate population of the same species. Branching did not significantly reduce the growth of the axial corallite and comparisons of linear branch extension between sites with differential secondary branching are, therefore, assumed to be valid.

The staining procedure did not significantly affect the growth of *Acropora formosa* or *Pocillopora damicornis* measured over a time scale of weeks although tagging of branches of *Acropora formosa* retards growth in the period immediately following tagging if, as in this study, tags are placed relatively close to the growing branch tip. However once the tag is covered with calcium carbonate and the coenosarc is 'reconnected' growth rates return to 'normal'. The period of 'calcifying over' of the tag and the consequent period of retarded branch growth will be vary as a function of tag distance from the branch tip and the rate of coral growth (cf calcification). Measuring increases in radial extension of *Acropora hyacinthus* by tagging, staining and from increases in projected area of colonies appear to provide comparable results.

7.4 Effects of environmental factors on coral growth

The intra-annual or 'seasonal' variation in the growth of *Acropora*

formosa and *Acropora hyacinthus* was significantly related to seawater temperature between the period from May 1 to November 30. However, between December 1 to April 30, the growth of these species was not statistically related to sea temperatures. In contrast, the growth of *Pocillopora damicornis* was significantly related to seawater temperatures for the entire period (from March 1982 to November 1983) with maximum growth rates occurring at maximum mean temperatures. These correlations are consistent with the suggestion that, in the Dampier Archipelago, the growth of *Acropora formosa* and *Acropora hyacinthus* are causally related to sea temperatures in the range of about 21^{o} to 27^{o} C and that the growth of *Pocillopora damicornis* is causally related to sea temperatures at least within the measured range of 21^{o} to 30^{o} C.

Variation in the growth of the *Acropora* species and to a lesser extent, *P. damicornis*, at site 1 during December 1, 1982 to April 30, 1983 was most likely due to mechanical damage caused by wave action associated with the passage of tropical cyclones. The effects of supra-optimal temperatures and increased reproductive activity (for the *Acropora* species) are additional possible modifying influences on the temporal patterns of coral growth during this period.

Spatial variation in the growth rate of *Acropora formosa* was negatively correlated with differences in sediment deposition rate at the three study sites. In this study the direct effects of sedimentation *per se*, on growth of *Acropora formosa* , could not be separated unequivocally from the indirect effect of increased shade reducing photosynthetic rates. There was, however, some evidence to support the suggestion that differences in coral growth at these sites was attributable to the different metabolic costs of sediment rejection rather than due to the effects of reduced light availability.

The period between April 1982 and April 1983 appeared to a 'typical'

year, in relation to the majority of the preceding ten years as determined from retrospective and real-time growth rates of *Platygyra deadalea*. Therefore the growth of the coral species measured during this study at site 1 are assumed to represent 'typical' seasonal and annual growth rates. On the other hand, site 2 and site 3 (to a lesser degree) were in areas of the archipelago that were effected by dredging and dumping operations, and the growth rates of *Acropora formosa* measured are assumed to represent growth under 'abnormal' conditions. Comparisons of annual growth rates of selected species at sites 1 and 4 in the Dampier Archipelago with other geographical locations, suggest that coral growth in this area is high on a worldwide basis, and the annual growth of *Acropora formosa* and *Pocillopora damicornis* is approximately three times higher in the Dampier Archipelago than at the Abrolhos Islands.

The high sediment deposition rates measured at site 2 between December 1982 and February 1983 were probably due to nearby dredging and dumping operations and it is suggested that the high mortality of corals that subsequently occurred at this site was due to these activities.

7.5 Coral reproduction and mass spawning

Mass spawning of scleractinian corals in the Dampier Archipelago (DA) has been observed to occur mainly on the 7-9 nights after the full moon in March 1984-1987. Mass spawning on the Ningaloo Reef tract (NRT) in 1986, occurred mainly on the 7-8 nights after the full moon in March, in synchrony with the coral mass spawning in the Dampier Archipelago. In 1987, mass spawning on some tropical reefs in Western Australia (including DA and NRT) occurred mainly on the 8-9 nights after the full moon in March, and two nights later on the temperate reefs at the Abrolhos Islands. These observations and the occurrence of mature eggs in many of the coral species

sampled during March 1985 and 1986 in the Dampier Archipelago, and the results from similar studies at Ningaloo Reef and the Abrolhos Islands, suggest that many of the 283 species of scleractinian corals that occur on Western Australia reefs (Veron, 1986) may participate in the mass spawning phenomenon.

Mass spawning appears to be an annual event in the Dampier Archipelago as corals examined at other times of the year lacked mature gonads. Preliminary studies of gametogenesis at Ningaloo Reef and the Abrolhos islands support this conclusion. Mass spawning appears to be synchronised within populations (at least in part) of corals and between corals on different reefs in the Dampier Archipelago. The presence of mature eggs in some species after the dates of mass spawning in March 1985 suggest that a 'split' spawning may have occurred in 1985 (ie these species also spawned at a later date). In all cases on tropical reefs in Western Australia, mass spawning occurred on neap, nocturnal, ebb tides. At the Abrolhos Islands mass spawning occurred on nocturnal, ebb tides at the beginning of the period of neap tides.

A simultaneous emergence of epitokous (reproductive) segments of polychaete worms also occurred in all cases. In addition, observations of spawning by other marine invertebrates (eg Echinodermata, Mollusca) around the same time , suggest that many other marine invertebrates may reproduce during this period each year.

Comparisons with the mass spawnings on the Great Barrier Reef suggest that, apart from the timing, many features of the spawnings are similar. The difference in the seasonal timing of the breeding season of scleractinian corals on the east and west coasts of Australia appears to be unrelated to sea temperatures and the breeding season may be the result of an endogenous rhythm, reflecting different dispersal and spawning patterns of

'ancestral' corals. Spawning during darkness and on an ebb tide may be related to the need to reduce the chance of predation by the many planktivores that exist in shallow coral reef communities. Spawning during neap tides may be an adaptation to maximise fertilisation and for increasing the dispersal of the ensuing adults.

The autumn timing of the mass spawning of corals in the Dampier Archipelago and on other reefs in Western Australia, and the presence of a poleward flowing current in the adjacent offshore waters provide a possible mechanism for widespread dispersal of planulae larvae. This raises the possibility that there is a unidirectional gene flow between regionally separate coral reefs in Western Australia, so that the reefs are more closely interrelated than would be expected through the original expansion of the range of ancestral corals. More generally, the process provides an opportunity to maximise outbreeding.

The mass spawning of corals has been observed on the Great Barrier Reef and on temperate and tropical coral reefs in Western Australia. It is not known if it occurs elsewhere but it does not occur in the Caribbean Sea (Szmant-Froelich *et al.* 1984) or in the Red Sea (Shlesinger and Loya, 1985).

7.6 Community metabolism

Annual gross production (P) and respiration (R) of the Keast Island reef-flat community was 5.8 and 7.0 g C m^{-2} d^{-1} respectively and annual net calcification (G) was 5.7 kg $CaCO_3$ m^{-2} d^{-1}. These values fall within the range of published values for community metabolism on reef-flats in other locations. In addition these values conform reasonably well to the so called worldwide 'standard metabolic performance' of reef-flat zones of 'typical unperturbed' coral reefs. "Winter" values of P, R ang G were 63%, 74% and 68% respectively of "summer" values and fall within the range of published

values for seasonality of community metabolism on other coral reefs.

Many reef-flats appear to be in a state of autotrophic balance with annual P/R values approaching unity: that is there is no net loss or gain of energy. The annual P/R value for the Keast Island reef-flat was 0.8, suggesting that this community is heterotrophic and is importing organic carbon.

Comparisons of community metabolism parameters at Hamersley Shoal in November 1983 and March 1984 suggest that P may be lower in March and additional evidence from Keast Island in March 1984 suggest that the value of R during this period may be overestimated. Lower gross production, resulting from a reduced photosynthetic capacity of the corals (the main component of the benthic community at this site), due to the expulsion of zooxanthellae or elevated community respiration as a result of increased reproductive activity would lower the estimate of P/R for "summer" with significant effect on the overall P/R for this reef.

In overview, corals in the Dampier Archipelago had rapid growth rates on an offshore reef where environmental conditions appear to be similar to areas in other parts of the world where extensive coral communities exist. Corals on inshore reefs in the Dampier Archipelago are seasonally subjected to 'natural' conditions which independantly and/or synergistically appear to stress particular species thereby increasing their vulnerability to anthropogenic perturbations to the marine environment. Community metabolism on a reef-flat in the Dampier Archipelago conforms approximately to worldwide reef-flat 'standard metabolic performance' for 'typical unperturbed' coral reefs. The autumn breeding season and modes of reproduction of many coral species on temperate and tropical reefs in Western Australia have been determined during this study. Finally, the presence of a poleward current along the Western Australian coastline in

autumn provides a mechanism for the southward dispersal of larvae and raises the possibility that regionally separate reefs in Western Australia are biologically connected.

Coral reefs are valuable natural resources and their preservation and management deserves high priority. This work is the first detailed study of coral ecology on a tropical reef in Western Australia and has benefits in addition to purely scientific considerations, in providing information which enables informed decisions to be made about management of coral reefs in Western Australia in general, and in the Dampier Archipelago in particular.

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APPENDIX I: List of 209 scleractinian corals species from 57 genera recorded in the Dampier Archipelago (List compiled by J.E.N.Veron and L.M. Marsh). Species in bold are new records for the Dampier Archipelago which were from this study.

Acanthastrea echinata
A. lordhowensis
Acropora abrolhosensis
A. austrea
A. aculeus
A. anthoceris
A. aspera
A. cerealis
A. clathrata
A. cytherea
A. danai
A. digitifera
A.divaricata
A. florida
A. formosa
A. gemmifera
A. glauca
A. grandis
A. horrida
A. humilis
A. hyacinthus
A. latistella
A. listeri
A. microphthalma
A. millipora
A. nana
A. nasuta
A. nobilis
A. polystoma
A. pulchra
A. robusta
A. samoensis
A. sarmentosa
A. secale
A. selago
A. solitaryensis
A. spicifera
A. stoddarti
A. subulata
A. tenuis
A. tortuosa
A. valenciennesi
A. valida
A. verweyi
A. yongei
Alveopora fenestrata
Astreopora explanata
A. gracilis
A. myriophthalma
Australomussa rowleyensis
Barabattoia amicorum
Blastomussa merleti
Catalaphyllia jardinei
Caulastrea tumida
Coscinaraea columna
C. exesa
Cycloseris cyclolites
Cyphastrea microphthalma
C. serailia
Diploastrea heliopora
Duncanopsammia axifuga
Echinophyllia aspera
E. orpheensis

Echinopora hirsutissima
E. horrida
E. lamellosa
Euphyllia ancora
E. cristata
E. divisa
E. glabrescens
Favia favus
F. lizardensis
F. matthai
F. maxima
F. pallida
F. rotumana
F. speciosa
F. stelligera
F. veroni
Favites abdita
F. chinensis
F. complanata
F. flexuosa
F. halicora
F. pentagona
F. cf rotundata
Fungia concinni
F. fungites
F. repanda
F. scruposa
F. simplex
Galaxea fascicularis
G. astreata
Gardinoseris planulata
Goniastrea aspera
G. australensis
G. edwardsi
G. favulus
G. palauensis
G. pectinata
G. retiformis
Goniopora columna
G. djiboutensis
G. lobata
G. minor
G. palmensis
G. pendulus
G. stokesi
G. stutchburyi
G. tenuidens
Herpolitha limax
Heteropsammia cochlea
Hydnophora exesa
H. microconus
H. pilosa
H. rigida
Leptastrea pruinosa
L. purpurea
Leptoria phrygia
Lithophyllon edwardsi
Lobophyllia corymbosa
L. hataii
L. hemprichii
Merulina ampliata
M. scabricula
Montastrea curta
M. magnistellata
M. valenciennesi
Montipora aequituberculata
M. calcarea
M. crassituberculata

M. danae
M. digitata
M. efflorescens
M. foveolata
M. grisea
M. hispida
M. hoffmeisteri
M. incrassata
M. millipora
M. mollis
M. monasteriata
M. peltiformis
M. spongodes
M. spumosa
M. tuberculosa
M. turgescens
M. turtlensis
M. undata
M. verrucosa
Moseleya latistellata
Mycedium elephantotus
Oulophyllia bennettae
O. crispa
Oxypora lacera
Pachyseris rugosa
P. speciosa
Pavona decussata
P. explanulata
P. minuta
P. varians
Pectinia lactuca
P. paeonia
Physogyra lichtensteini
Platygyra daedalea
P. lamellina
P. pini
P. sinensis
P. verweyi
Plerogyra sinuosa
Plesiastrea versipora
Pocillopora damicornis
P. eydouxi
P. meandrina
P. verrucosa
P. woodjonesi
Podabacia crustacea
Polyphyllia talpina
Porites cylindrica
P. heronensis
P. lichen
P. lobata
P. lutea
P. murrayensis
P. rus
P. solida
Psammocora contigua
P. digitata
P. explanulata
P. haimeana
P. nierstraszi
P. profundacella
P. superficialis
Psuedosiderastrea tayamai
Scapophyllia cylindrica
Stylocoeniella guentheri
Stylophora pistillata
Symphyllia agaricia
S. recta

S. valenciennesi
Trachyphyllia geoffreyi
Turbinaria bifrons
T. conspicua
T. frondens
T. mesenterina
T. patula
T. peltata
T. reniformis
T. stellulata

Appendix II: Summary of sediment trap deployments and analyses at sites 1, 2 and 3.

(a) Sediment deposition rate and composition at site 1

Date deployed	Total No. days deployed	Total dry weight ($g\ m^{-2}\ d^{-1}$)	ORGANIC Dry weight ($g\ m^{-2}\ d^{-1}$)	%	CARBONATE Dry weight ($g\ m^{-2}\ d^{-1}$)	%	REFRACTORY Dry weight ($g\ m^{-2}\ d^{-1}$)	%
08.05.82	8.9	15.9	4.2	26.5	5.8	36.4	5.9	37.1
30.06.82	28.0	69.5	8.9	12.9	38.2	55.1	22.2	31.9
27.07.82	8.0	42.3	12.2	28.6	18.7	44.3	11.5	28.0
04.08.82	41.0	24.4	3.7	15.1	12.0	49.6	8.7	35.3
14.09.82	8.0	64.1	13.9	21.7	24.5	38.0	25.7	40.3
22.09.82	31.1	33.0	5.4	17.3	16.7	50.3	10.7	32.4
23.10.82	9.0	25.8	6.4	24.4	10.4	38.9	8.9	34.7
01.11.82	35.2	32.7	6.2	19.0	14.9	45.6	11.6	35.4
08.12.82	5.9	39.3	9.4	24.0	13.1	33.4	16.7	42.6
19.01.83	7.0	32.2	7.5	23.7	16.4	50.8	8.3	25.5
05.03.83	7.0	39.1	7.0	18.1	17.3	44.5	14.6	37.3
09.03.83	48.0	326.5	27.6	8.4	242.8	74.3	56.3	17.3
26.04.83	39.0	23.6	2.4	10.2	17.4	73.9	3.8	15.9
13.08.83	14.0	34.1	7.4	21.4	20.4	59.9	6.4	18.8

(b) Sediment deposition rate and composition at site 2

Date deployed	Total No. days deployed	Total dry weight ($g\ m^{-2}\ d^{-1}$)	ORGANIC Dry weight ($g\ m^{-2}\ d^{-1}$)	%	CARBONATE Dry weight ($g\ m^{-2}\ d^{-1}$)	%	REFRACTORY Dry weight ($g\ m^{-2}\ d^{-1}$)	%
22.06.82	8.0	21.5	4.9	22.5	4.5	18.5	12.8	59.0
30.06.82	27.9	32.3	5.3	16.2	10.7	33.9	16.1	49.9
27.07.82	8.0	25.5	6.1	23.8	11.0	42.8	8.3	33.0
04.08.82	41.0	95.3	15.1	15.8	33.0	35.0	47.0	49.0
14.09.82	8.0	146.5	21.1	14.6	51.4	35.4	74.0	49.9
26.10.82	6.0	100.0	17.1	17.1	36.0	36.0	46.7	46.9
06.12.82	7.8	263.0	32.0	12.2	115.6	43.9	115.4	43.9
19.01.83	7.0	253.1	33.7	13.3	100.2	39.6	119.1	47.1
02.03.83	7.0	268.7	32.6	11.9	123.1	45.9	113.5	42.2
19.04.83	55.0	63.1	9.5	15.0	23.2	36.6	30.6	48.4
18.08.83	9.3	46.0	10.8	23.7	17.7	38.1	17.5	38.3

APPENDIX II continued

(c) Sediment deposition rate and composition at site 3

Date deployed	Total No. days deployed	Total dry weight ($g\ m^{-2}\ d^{-1}$)	ORGANIC Dry weight ($g\ m^{-2}\ d^{-1}$)	%	CARBONATE Dry weight ($g\ m^{-2}\ d^{-1}$)	%	REFRACTORY Dry weight ($g\ m^{-2}\ d^{-1}$)	%
21.02.82	9.9	136.7	16.7	12.2	57.2	41.9	62.8	45.9
31.03.82	5.1	33.0	8.4	25.4	11.0	33.3	13.6	41.1
08.05.82	7.0	34.4	8.3	23.6	9.2	26.5	16.9	49.2
22.06.82	8.0	56.8	10.6	18.7	14.7	25.8	31.5	55.5
30.06.82	27.9	48.1	7.1	14.6	15.0	31.6	25.7	53.4
27.07.82	8.0	42.7	7.7	17.6	14.2	32.7	21.2	49.3
04.08.82	41.0	62.1	9.2	14.9	20.9	33.5	32.0	51.6
14.09.82	8.0	140.6	20.8	14.8	51.2	36.2	68.6	48.9
22.09.82	31.1	104.3	17.2	16.5	33.8	32.5	53.2	51.0
23.10.82	8.9	64.4	15.2	23.4	12.8	20.1	36.5	56.5
01.11.82	35.2	96.2	14.2	14.9	33.8	35.0	48.2	50.1
06.12.82	7.8	128.8	17.7	13.6	42.3	32.8	66.8	51.9
19.01.83	7.0	100.4	13.7	13.8	43.2	42.3	43.5	43.9
02.03.83	7.0	96.7	14.5	15.3	35.31	36.2	46.9	48.5
10.03.83	40.0	211.3	28.0	13.3	89.5	42.0	94.0	44.7

APPENDIX III: Computer program (SEDCOM) for sediment deposition computations.

```
      PROGRAM SEDCOM
      WRITE(5,1)
1     FORMAT(1H1,10X,'**** SEDIMENT PROGRAM DATA ****',5X,'MOORING
      TYPE:
     *        TAUT WIRE',5X,'TRAP X-SECT.AREA=20.3 SQ.CM',5X,'ASPECT
      RATIO=6')
10    READ(23,30)IDATE,STAT,DEPTH,XN,TIN,TOUT,DAY,TOTD
30    FORMAT(I6,A4,F3.1,F2.0,2F4.2,F2.0,F3.1)
      XD=((DAY-2.)*24.+(24.-TIN)+TOUT)/24.
      IF(IDATE.EQ.0)GO TO 100
      WRITE(5,2)IDATE,STAT,DEPTH,XN,TOTD,XD
2     FORMAT(///,4X,'DATE:',I6,2X,'STATION:',A4,2X,'HT.OFF BOTTOM(M):',
     * F4.1,2X,'REPLICATE NUMBER:',F2.0,2X,'TOTAL DEPTH:',F4.1,2X,'NO.OF
     *    DAYS:',F6.1)
      WRITE(5,50)
50    FORMAT(//,4X,'TOT.DRY WT(G)',2X,'g/m2/day',2X,'ORG.WT(G)',2X,'ORG
     *    g/m2/day',2X,'C03.WT(G)',2X,'CO3 g/m2/day',2X,'ORGANIC %',2X,'
     * CARBONATE %',2X,'REMAIN %',2X,'ORG.:CARB.')
      XM=0.
20    READ(23,40)CW,TSW,XOSW,XCSW
40    FORMAT(4F5.3)
      XF=492.61/XD
      SW=TSW-CW
      OW=TSW-XOSW
      XOW=OW*XF
      CX=XOSW-XCSW
      CW=CX*102./44.
      OP=OW/SW*100.
      CP=(CX*102./44.)/SW*100.
      RP=100.-OP-CP
      XCW=CW*XF
      SR=SW*XF
      OC=OP/CP
      WRITE(5,60)SW,SR,OW,XOW,CW,XCW,OP,CP,RP,OC
60    FORMAT(5X,F6.3,8X,F6.1,5X,F6.3,6X,F6.1,7X,F6.3,7X,F6.1,2(6X,F5.2)
     *    ,8X,F5.2,6X,F5.2)
      XM=XM+1.
      IF(XM.EQ.XN)GO TO 10
      GO TO 20
      100 STOP
      END
```

APPENDIX IV Computer program (ALK) for calculating total alkalinity.

```
      PROGRAM ALK
      WRITE(5,5)
5     FORMAT(1H1,25X,'TOTAL ALKALINITY CALCULATIONS')
2     READ(24,6)XLT,XSL,XINT,XSLT,XINTT,XMOL,XF,N
6     FORMAT(F4.2,F8.6,F7.6,F6.4,F7.4,F7.7,F2.2,I2)
      IF(XLT.EQ.0.)STOP
      WRITE(5,7)XSL,XINT,XMOL,XF
7     FORMAT(//,2X,'SLOPE=',F9.6,2X,'INTERCEPT=',F8.6,2X,'MOLARITY=',F9.
     *   7,2X,'ACTIVITY COEFFICIENT=',F3.2)
      WRITE(5,8)
8     FORMAT(/,2X,'VOL OF ACID',2X,'VOL OF SEAWATER',2X,'PH OF ACID/SEAW
     * ATER',2X,'TOTAL ALKALINITY(meq l-1)')
      M=0
1     READ(24,10)XB,XBA,XBAS,XT,XS,XMT,XPH
10    FORMAT(5F4.2,2F4.1)
      IF(XB.EQ.0.)STOP
      TM=XSLT*XMT+XINTT
      XDO=(((((-280.54253E-12*XT+105.56302E-9)*XT-46.170461E-6)*XT-7.
     *   9870401E-3)*XT+16.945176)*XT+999.83952)/(1+(16.87985E-3*XT))
      XD2=XDO/1000.
      XSO=((6.76786136E-6*XS-4.82496140E-4)*XS+0.814876577)*XS-0.0934458
     *   632
      E1=(((-1.43803061E-7*XT-1.98248399E-3)*XT-0.545939111)*XT+4.531684
     *   26)*XT
      B1=((-1.0843E-6*XT+9.8185E-5)*XT-4.7867E-3)*XT+1.0
      B2=((1.667E-8*XT-8.164E-7)*XT+1.803E-5)*XT
      E2=(B2*XSO+B1)*XSO
      XST=E1/(XT+67.26)+E2
      XD1=1.0+(XST)*.001)
      XVA=(XBA-XB)/XD2
      XVS=(XBAS-XBA)/XD1
      PHM=XSL*XPH+XINT
      TA=1000.*XVA*XMOL/XVS-(1000./XVS)*(XVS+XVA)*10**(-PHM)/XF
      WRITE(5,15)XVA,XVS,PHM,TA,XB,XBA,XBAS,XD1,XD2,XPH
15    FORMAT(6X,F5.3,8X,F6.3,13X,F6.4,16X,F6.4,20X,3(F5.2,1X),2F8.6,1X,F
     * 6.2)
      M=M+1
      IF(M.EQ.N)GO TO 2
      GO TO 1
```

APPENDIX V: Computer program (DIOX.DAT) for calculating carbon dioxide and CO_2- related variables in seawater from pH, total alkalinity, temperature and salinity.

```
      PROGRAM CACL
      READ(24,5)IHD,IHT,IPD,ICO
5     FORMAT(4I1)
      WRITE(5,9)
9     FORMAT(1H1,15X,'----------CALCULATION OF CARBON DIOXIDE AND C
     *    O2-RELATED VARIABLES IN SEAWATER----------')
      IF (IHD.EQ.1) GO TO 1
      WRITE(5,20)
20    FORMAT(1H0,2X,'STATION',4X,'DATE',4X,'DEPTH',2X,'HENRYS LAW COEFF'
     *    ,3X,'PK1C',5X,'PK2C',5X,'PK1B',5X,'PK2B',5X,'TOT CO2',2X,'SPEC ALK
     * ALINITY',1X,'CO2 PARTIAL PRESSURE')
      1 CONTINUE
      IF(IHT.EQ.1) GO TO 101
      WRITE(5,15)
15    FORMAT(1H0,2X,'STATION',4X,'DATE',4X,'DEPTH',2X,'SALINITY',2X,'TEM
     *    PERATURE',4X,'PH',4X,'TOT ALKALINITY',2X,'CHLORINITY',4X,'TOT
     *    ,4X,'SPEC ALKALINITY',4X,'PCO2')
11    READ(24,10)XT,XS,XPH,XALK
10    FORMAT(2F4.2,2F5.4)
      IF(XT.EQ.0000) GO TO 260
      IF(XS.EQ.0.OR.XT.EQ.0.OR.XPH.EQ.0.OR.XALK.EQ.0.) GO TO 250
      XTK=XT+273.
      CHL=(XS-0.03)/1.805
      ALPHA=-58.09+9050.7/XTK+22.29*ALOG(XTK/100.)+CHL*(0.05-4.67E-4*XTK
     * +9.1E-7*XTK*XTK)
      HLC=EXP(ALPHA)
      PK1C=3405./XTK+0.0328*XTK-14.71-0.192*(CHL**(1./3.))
      C1C=1./(10.**PK1C)
      PK2C=2902./XTK+0.0238*XTK-6.47-0.469*(CHL**(1./3.))
      C2C=1./(10.**PK2C)
      PK1B=2292./XTK+0.0176*XTK-3.39-0.321*(CHL**(1./3.))
      C1B=1./(10.**PK1B)
      PK2B=20.21-0.0334*XTK-0.0175*(CHL)
      C2B=1./(10.**PK2B)
      SB=2.06E-5*CHL
      HIC=(1./10.**XPH)
      BA=SB*((HIC*C1B+2.*C1B*C2B)/(HIC*HIC+HIC*C1B+C1B*C2B))*1000.
      HA=((1.0E-14-HIC*HIC)/HIC)*1000.
      CA=XALK-(BA+HA)
      TCO2=CA*((C1C*HIC+C1C*C2C+HIC*HIC)/(C1C*HIC+2.*C1C*C2C))
      SA=XALK/CHL
      PCO2=(CA*HIC*HIC)/(C1C*HLC*(HIC+2.*C2C))*1000.
      IF(IHD.EQ.1) GO TO 29
      WRITE(5,30)ID,IDATE,XD,HLC,PK1C,PK2C,PK1B,PK2B,TCO2,SA,PCO2
30    FORMAT(/ / /,4X,I4,4X,I6,4X,F4.1,6X,F7.5,7X,4(F7.4,2X),2X,F7.5,7X,F7
     *    5,10X,F7.3)
29    IF(IHT.EQ.1) GO TO 31
      WRITE(5,55)XS,XT,XPH,XALK,CHL,TCO2,SA,PCO2
55    FORMAT(1H0,30X,F5.2,6X,F5.2,5X,F6.4,5X,F6.4,9X,
     *    F6.3,6X,F7.5,9X,F7.5,4X,F8.3)
31    IF(IPD.EQ.1) GO TO 41
      WRITE(5,40)XS,XT,XPH,XALK,CHL,XTK
40    FORMAT(/3X,'SALINITY =',F5.2,2X,'TEMPERATURE =',F5.2,2X,'PH =',F5.
     * 3,2X,'TOTAL ALKALINITY =',F5.3,2X,'CHLORINITY =',F6.3,2X,'ABSOLUTE
     * TEMP =',F6.2)
41    IF(ICO.EQ.1) GO TO 250
      WRITE(5,50) C1C,C2C,C1B,C2B,HIC,CA,HA,BA
50    FORMAT(/,3X,'K1C=',F14.13,1X,'K2C=',F14.13,1X,'K1B=',F14.13,1X,'K2
     *    B=',F14.13,1X,'HIC=',F14.13,1X,'CA=',F7.5,1X,'HA=',F7.6,1X,'BA=',F
     *    7.6)
250   GO TO 101
260   STOP
      END
```

APPENDIX VI: Computer program (LIGHT) for computing photosynthetic photon flux density from global radiation, Campbell-Stokes hours of sunlight, cloud cover, daylength, light attenuation coefficient and water depth.

```
C       PROGRAM LIGHT CALCULATES AVERAGE PHOTON FLUX DENSITY FROM
        DAILY INTEGRATED
C       GLOBAL RADIATION DATA(mW.H.cm-2) THEN CALCULATES P.A.R. AT A
        SPECIFIED DEPTH
C       OF WATER OF A KNOWN EXTINCTION COEFFICIENT.
        PROGRAM LIGHT
C       READ IN SITE NUMBER CODE, LATITUDE, ALBEDO CONSTANT,
        IMMERSION EFFECT
C       CONSTANT,NUMBER OF DATA LINES
2       READ(23,10)ISI,XL,XALB,XIF,M
10      FORMAT(I1,F3.1,F4.3,F3.2,I3)
C       SETTING VALUE OF ISI=0 WILL STOP THE PROGRAM
        IF(ISI.EQ.0) GO TO 30
        IF(XL.EQ.20.5)WRITE(5,18)XL,XALB,XIF
C       WRITE HEADER DATA
18      FORMAT(1H1,   'DATA FOR DAMPIER',2X,'LATITUDE:',F4.1,' S',5X,'ALBE
     *      DO:',F5.3,5X,'IMMERSION EFFECT CONSTANT:',F4.2)
C       WRITE SITE NAME
        IF(ISI.EQ.1)WRITE(5,20)
        IF(ISI.EQ.2)WRITE(5,21)
        IF(ISI.EQ.3)WRITE(5,22)
20      FORMAT(//,1X,'SITE:NO NAME ROCKS')
21      FORMAT(//,1X,'SITE:CONZINC ISLAND')
22      FORMAT(//,1X,'SITE:NELSON ROCKS')
        WRITE HEADER TITLES FOR DATA OUTPUT
        WRITE(5,23)
23      FORMAT(/,1X,'DAY NUMBER',3X,'DEPTH',4X,'BOTTOM
        IRRADIANCE',5X,'DAY
     *      LENGTH',10X,'AIR IRRADIANCE',5X,'EXTINCTION COEFFICIENT(K)')
        WRITE(5,33)
33      FORMAT(14X,'(M)',6X,'(μ mol.m-2.s-1)',8X,'(HRS.)',10X,'(μ mol.
     *      m-2-s-1)',12X,'(m-1)')
        N=0
C       JULIAN DAY NUMBER FOR SEPTEMBER 1 is 244.
        XJD=244.
        XZ=(1.*365.-XJD)
        XZ1=(1.*365.+XZ)
        XZ2=(2.*365.+XZ)
C       READ IN GLOBAL RADIATION DATA (mW.H.cm-2),CAMPBELL/STOKES
        VALUE(H),EXTINCTION
C       COEFFICIENT(m-1),DEPTH(M),DAY NUMBER.
1       READ(23,24)XR,XC,XA,XD,XN
24      FORMAT(F4.1,F3.1,F3.2,F3.1,F3.0)
C       CONVERT DATA DAY NUMBERS INTO JULIAN DAY NUMBERS FOR
        CALCULATION OF DAY LENGTH.
        IF(XN.LE.XZ)XYN=XJD+XN
        IF(XN.GT.XZ.AND.XN.LE.XZ1)XYN=XN-(365.-XJD)
        IF(XN.GT.XZ1.AND.XN.LE.XZ2)XYN=XN-(730.-XJD)
C       CONVERT mW.H.cm-2 TO EINSTEINS.m-2.day-1
        XQA=XR*0.1656
C       CALCULATE ANGLE OF SOLAR DECLINATION(RADIANS)
        XDEC=23.430*SIN(((360.*(284.+XYN)/365.))/57.296)
        XDAN=-TAN(-XL/57.296)*TAN(XDEC/57.296)
C       CALCULATE HALF DAY LENGTH
        XDH=ACOS(XDAN)/6.283185*24.
        XDF=XDH*2.
C       CALCULATE RATIO OF P.A.R. TO GLOBAL RADIATION FROM
        CAMPBELL/STOKES DATA AND
C       DAY LENGTH
        XRA=(1.-(XC*1.0723/XDF))*0.07+0.47
```

```
      XQP=XQA*XRA
C     CONVERT E/m-2/DAY TO μmol m-2 s-1
      XQ=(XQP/(3600.*XDF))*10.**6.
C     CALCULATE REDUCTION DUE TO ALBEDO
      XQS=XQ*(1.-XALB)
C     CALCULATE REDUCTION DUE TO ABSORBTION AT SURFACE LAYER
      XQSH=XQS*(1.-XIF)
C     CALCULATE INTERCEPT
      XB=ALOG10(XQSH)
      XQDI=-XA*XD+XB
C     CALCULATE LIGHT VALUE(μmol.m-2.s-1) AT SPECIFIED DEPTH ON
      SPECIFIED DAY NUMBER
      XQD=10.**(XQDI)
      WRITE(5,25)XN,XD,XQD,XDF,XQ,XA
25    FORMAT(3X,F4.0,7X,F4.1,9X,F6.1,15X,F4.1,15X,F6.1,19X,F4.2)
      N=N+1
      IF(N.EQ.M) GO TO 2
      GO TO 1
30    WRITE(5,31)
31    FORMAT(////,1X,'DATA CONVERSION COMPLETE')
      STOP
      END
```