Willis, Bette Lynn (1987) ***Morphological variation in the reef corals Turbinaria esenterina and Pavona cactus: synthesis of transplant, histocompatibility, electrophoresis, growth, and reproduction studies.*** **PhD thesis, James Cook University.**

CHAPTER 2. SPECIES DESCRIPTIONS AND THE DISTRIBUTION OF MORPHS IN RELATION TO THE PHYSICAL ENVIRONMENT

2.1 Introduction

Morphological variation in scleractinian corals has presented many difficulties for defining taxonomic boundaries within the order. Early taxonomists, constrained by incomplete collections and lack of field data, generally resolved uncertain affinities between specimens by assigning them to separate species. However, many recognised the limitations of their classifications and decried the lack of ecological and environmental information available to them. Quelch (1886) was one of the first to comment: "Observations and experiments on individual species of Reef-Corals are sadly needed in order to bring to light the influence of local conditions upon them....". Bernard (1896) questioned whether clearly defined species would ever be identified in the Scleractinia: "It seems to me certain that we are rapidly nearing the time when our ever-increasing collections, revealing as they do the infinite grades of variation presented by living organisms ... will compel us to break loose from the restraint of the Linnean 'species'". He eventually abandoned the Linnean binomial nomenclature in favour of the 'local form' as a taxonomic unit. Bernard's controversial scheme was never accepted and in 1907, Vaughan defined a species as "a group of individuals connected among themselves by intergrading characters and separated by distinct lacunae from all other individuals or groups of individuals". Nevertheless, Vaughan recognized that before species could be confidently identified, variation in corals would have to be studied in nature, with and without experiment, and in controlled conditions in aquaria. He concluded (Vaughan, 1907) "...until these studies are made it will not be possible to understand variation in the Madreporaria. Until variation is understood the systematic work must be more or less unreliable."

Until the 1970's coral taxonomists maintained the traditional accordance between growth form and species, but continued the plea for ecological studies of variable corals. Crossland (1952) summarized the general approach to variability thus, "These forms and others may later be proved, by experiment and observation on the reef to be only ecological variations, but, until that is done, they must be kept apart." With the advent of S.C.U.B.A., more recent systematists (eg. Wijsman-Best, 1972; Veron and Pichon, 1976; Wallace, 1978) have been able to correlate morphological variablity with different environmental regimes through extensive underwater observations. Accordingly, taxonomic definitions of species in corals have been expanded to include 'ecomorphoses' (Laborel, 1970) or 'ecomorphs' (Veron and Pichon, 1976), defined by the latter authors as "intraspecific skeletal variations phenotypically and/or genotypically determined in response to specific ecological conditions".

Despite advances in the understanding of what constitutes a coral species, overlap in skeletal characters is still found among presently-defined species, and uncertainties remain within many genera (eg. *Turbinaria* (Veron and Pichon, 1980) and *Acropora* (Veron and Wallace, 1984)). Thus, skeletal studies, even in conjunction with environmental observations, have currently reached the limits of their ability to resolve species. Lang (1984) has reviewed a comprehensive range of biological characters and chemical techniques which could be used to augment skeletal characters. What becomes clear is that detailed studies of individual problematic species or species groups are necessary to advance further our understanding of species within the Scleractinia.

In the present study, two inshore, foliaceous species of corals, *Turbinaria mesenterina* (Lamarck, 1816) and *Pavona cactus* (Forskal, 1775), were chosen as subjects of separate studies because of the extreme variability of their coralla. The term 'species', in reference to these two corals, will henceforth refer to taxonomic descriptions of *T. mesenterina* and *P. cactus* in Veron and Pichon (1980). In *T. mesenterina* patterns of morphological variation may be readily associated with environmental gradients, whereas most of the morphological variation in *P. cactus* may be found within seemingly uniform biotopes (Veron and Pichon, 1980). The apparent contrast in the environmental pattern of morphological variation between the two species, made them attractive for study from an evolutionary viewpoint, particularly as both patterns have developed in similar environments (described in 2.3).

With the exception of Jaubert's studies (1977, 1981) of *Synaraea convexa*, growth form variation within a foliaceous species of coral, has not been the subject of extensive study before. Most previous studies of growth form variation have been preoccupied with the flattening of hemispherical colonies with depth, notably of the Caribbean corals, *Montastrea annularis* and *Porites astreoides* (Goreau, 1959, 1963; Barnes 1973; Roos, 1967; Dustan, 1975; Graus and Macintyre, 1976, 1982; Brakel, 1983). These studies have stimulated much thought on the growth and calcification process in corals (Goreau, 1959, 1963; Barnes, 1973; Graus and Macintyre, 1976) and the physiological relationship between the coral and its symbiotic zooxanthellae (Dustan, 1979, 1982). However, other growth forms exhibit a similar flattening response with depth (eg. Wallace, 1978; Veron, 1981; Kuhlman, 1983; Fricke and Meischner, 1985) and may not utilize the same mechanism. There are potentially important insights to be gained from studying variation and growth processes in different forms of corals.

The variation in growth form of *Pavona cactus* (foliaceous to branching) does not readily fall into any pattern previously investigated. Branching corals, particularly within the genera *Acropora* and *Pocillopora*, have been observed to vary in thickness and the number of branches in response to both depth and degree of exposure to hydrodynamic energy (Wood Jones, 1907; Goreau 1963; Maragos, 1972; Veron and Pichon, 1976; Graus *et al.*, 1977; Bottjer, 1980; Oliver *et al.*, 1983). However, Veron and Pichon (1980) commented that variation in *P. cactus* occurred in the absence of an identifiable environmental gradient, but as no measurements were taken, this requires clarification.

Most observations of variation in corals are not accompanied by actual measurements of the physical environment. Of those studies which have measured environmental parameters, few have quantified more than two. The recent study by Oliver *et al.* (1983) is the major exception. Therefore, a further objective of the present study was to characterize the habitats of the different growth forms of *T. mesenterina* and *P. cactus*. Experimental studies have shown that temperature affects coral growth rates (Jokiel and Coles, 1977), and also that temperature, salinity, and light may act synergistically (Coles and Jokiel, 1978). Light has been implicated in most studies where the flattening of growth form has been documented (Roos, 1967; Jaubert, 1977). Numerous studies have recorded the effect of high sedimentation on coral growth (reviewed in Brown and Howard, 1986), and discussed morphological adaptations to reduce its impact (Hubbard and Pocock, 1972; Lasker, 1980). Water motion is also known to affect coral growth rates (Jokiel, 1978) and growth forms (as cited above). Moreover, hydrodynamic energy has been identified as a controlling agent in coral community zonation schemes based on both characteristic species (Rosen, 1975; Geister, 1977) and growth forms (Pichon, 1978). Therefore, these five physical parameters (temperature, salinity, light, sedimentation and localized water turbulence) were identified as the environmental variables most likely to affect growth form in *Turbinaria mesenterina* and *Pavona cactus*. Accordingly, monitoring schemes were designed to collect comparative data on the characteristic habitats of the different morphs of *T. mesenterina* and *P. cactus*.

2.2 Descriptions of Study Species

2.2.1 Morphological Variation in *Turbinaria mesenterina*

The only major revision of the genus *Turbinaria* since Bernard's in 1896, has been completed recently by Veron and Pichon (1980) based on specimens from the Great Barrier Reef, Eastern Australia. The following discussion of the variation in colony morphology of *T. mesenterina* is based on specimens from Magnetic Island (for location see 2.3) which conform to descriptions of *T. mesenterina* given by Veron and Pichon (1980).

Large colonies (>30cm in diameter) from intertidal and shallow biotopes may be readily separated from those from deeper biotopes through comparisons of the degree of convolution of fronds (Veron and Pichon, 1980). In shallow water, colonies have highly folded, vertically directed laminae which may form 'chimneys' (Figure 1a). Chimneys are formed when laminae fold completely upon themselves producing an upward growing cylinder. Polyps may be located on either the interior or the exterior of the cylinder, but polyps are generally found on the latter, more exposed surface. This form of the species will be referred to as the 'convoluted form' (Figures 1a, 2a).

Laminae become progressively more horizontal and less folded as depth increases, culminating in the 'plate form' (Figure 1b) at depths greater than 4m in turbid biotopes. Laminae may form horizontal tiers or even whorls in large colonies (Figure 2b). The growing margins of plate colonies are often wavy in older colonies, but the central axis of growth is never vertically-directed.

A continuum of variation exists between the contorted, upright laminae of the convoluted form and the flatter, horizontal laminae of the plate form. Colonies whose morphology falls between the extremes of the range will be referred to as 'intermediate' in form.

Small colonies (<10cm in diameter) from all depths tend to be uniformly vase or crater-like in shape, and are attached to the substratum by a stalk of undifferentiated coenosteum. Colonies of all forms may attain diameters of two to three metres, though the convoluted form is more commonly represented in the upper size ranges, presumably because the interlocking structure of this form provides a more stable base preventing dislodgement (Figure 2a). Stalks supporting the free-standing laminae of the plate form often become asymmetrically positioned as the colony encounters obstacles to growth in one direction (Figure 2b). Thus this form may become unstable with increased growth. If dislodged and overturned, colonies generally die (pers. observation).

FIGURE 1

Representative growth forms of *Turbinaria mesenterina.*

Top photograph (A): The convoluted morph. Upright, highly folded laminae and some vertical 'chimneys' are shown. Corallite size and degree of immersion vary with the topography of the colony. Corallites in hollows are smaller and more immersed than those on unfolded surfaces. (Colony 30cm in diameter. Collected: Nelly Bay, 1m).

Bottom photograph (B): The plate morph. The typically horizontally-directed laminae of this morph are shown. Corallites generally are regular in size and spacing, and incline towards the growing margins of the colony. (Colony 30cm in diameter. Collected: Nelly Bay, 4m).

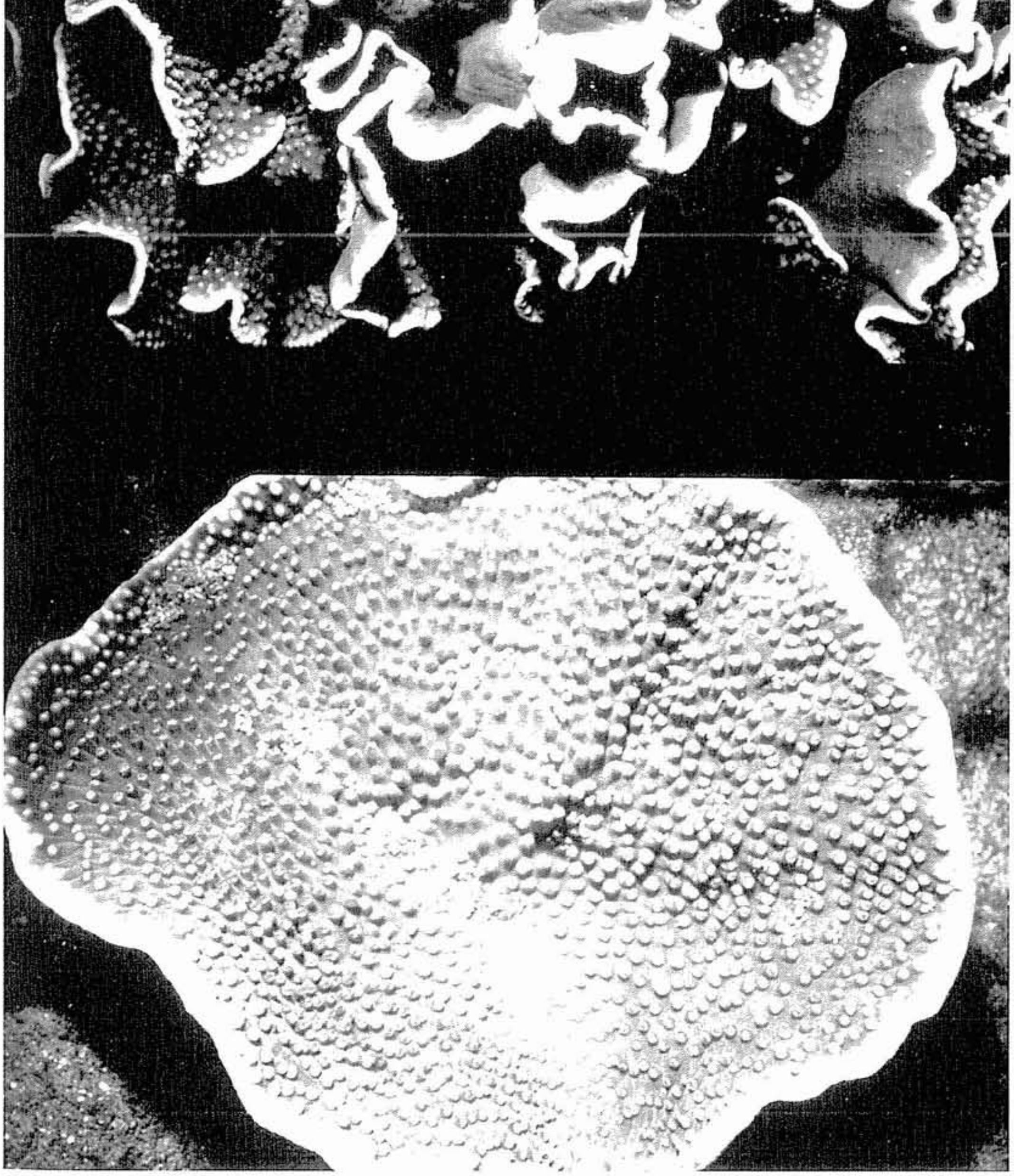
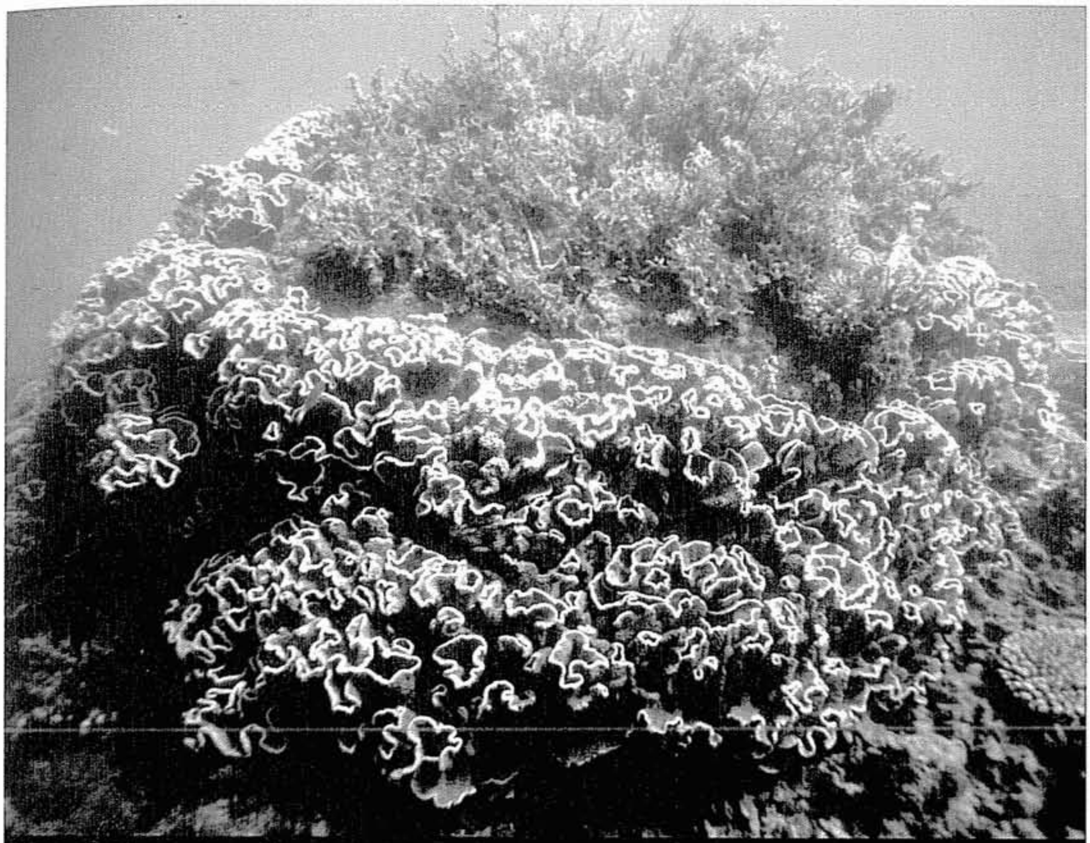


FIGURE 2

Growth forms of *Turbinaria mesenterina*:
Large *in situ* colonies at Nelly Bay, Magnetic Island.

Top photograph (A): A large colony of the convoluted morph (2m diameter). Laminae are predominantly vertically oriented, and are highly folded. (Nelly Bay, 1m)

Bottom Photograph (B): Large, tiers of plate colonies (between 0.5 and 1.0m in diameter). Laminae are predominantly horizontally oriented. (Nelly Bay, 4m)



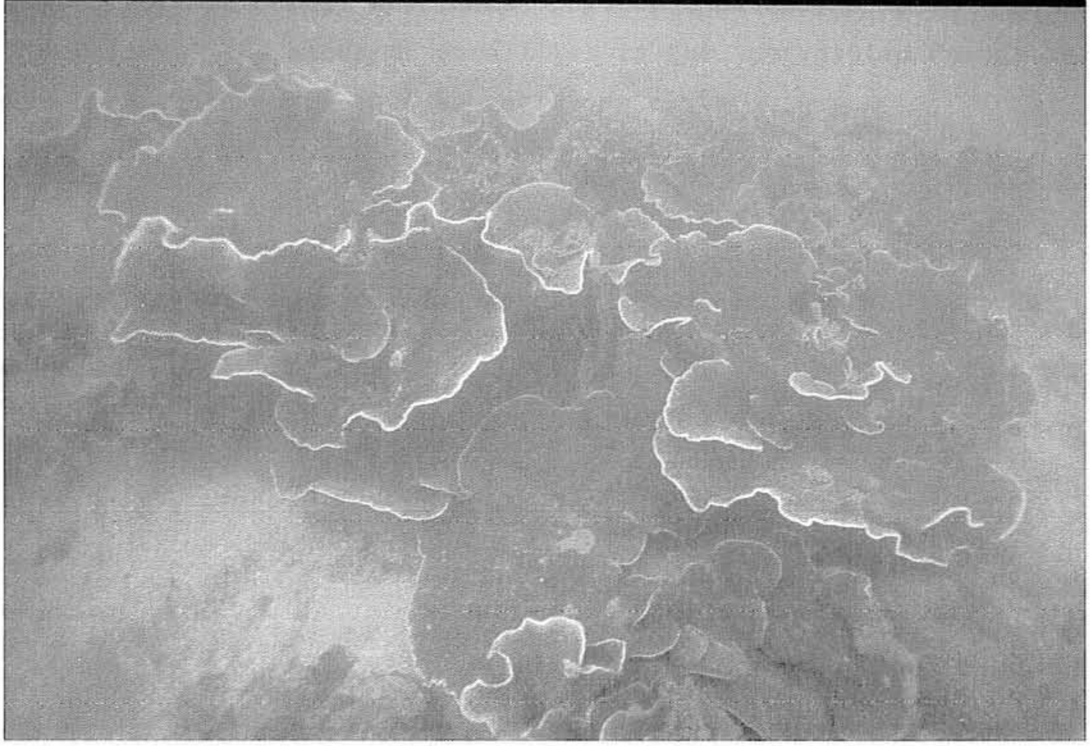
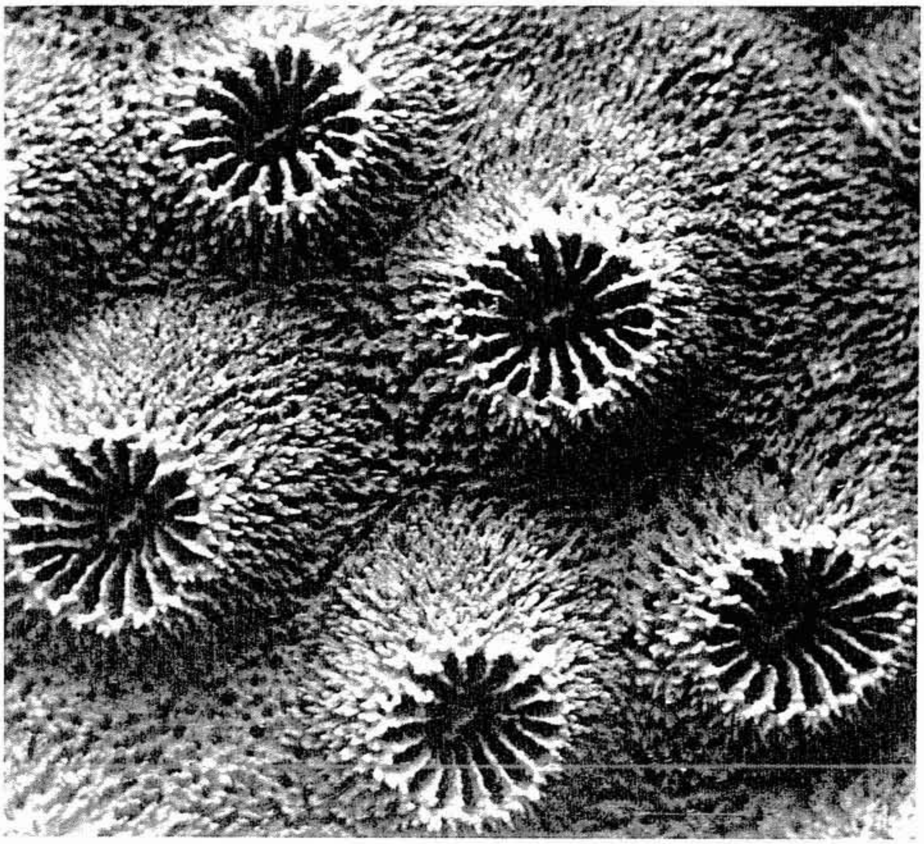


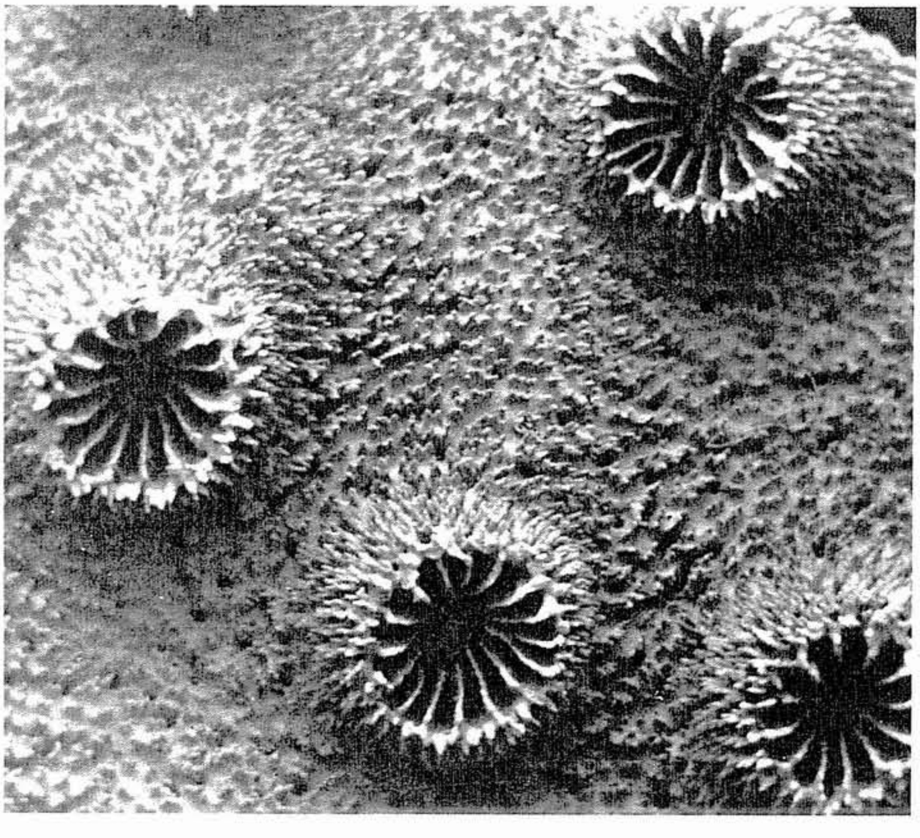
FIGURE 3

Scanning electron micrographs
of corallites of two growth forms of *Turbinaria mesenterina*.

In colonies of both the convoluted form (Top **photograph (A)**) and plate form (**Bottom photograph (B)**), corallites are similar in size, and typically have between 12 and 20 septa. Three orders of septa are seen in some corallites, the third order not extending as far towards the columella as the first two. The columella is ridge-like, in both specimens figured, but may be dome-like in either form. The bases of corallites in the convoluted colony are more conical in shape than those in the plate colony.

Specimens were spatter coated with gold and photographed in 30 KV Backscatter Mode on an ETEC Autoscan. Magnification (A,B): x 20





Variability in internal corallite architecture spans the same range in all growth forms of *T. mesenterina* (Figure 3). However, variability in corallite shape differs among forms. Thecae of shallow water colonies may be heavily calcified, especially at the base of the thecae, producing conical-shaped corallites. Thecae in deep water colonies tend to be more lightly and evenly calcified producing regular, cylindrical corallites. In both forms, there is a tendency for corallites to be more heavily calcified and conical in the centre of the colony as colony size increases. Although differences between forms have parallels within individual colonies, the plate form never approaches the degree of thickening of corallite structures that the convoluted form may attain.

2.2.2 Morphological Variation in *Pavona cactus*

The following descriptions of morphological variation in *Pavona cactus* are based on specimens collected from Eclipse Island (for location see section 2.3). A similar range in variation has been observed on other reefs, including Lizard and Yorke Island reefs and Big Mary Reef in the northern Great Barrier Reef region. Contrary to reports by Veron and Pichon (1980), individual colonies examined from these areas were found to express only one growth form. Where one seemingly large colony expressed two growth forms, *in situ* examination of tissue contact between branches representing the two forms, always revealed a zone of histoincompatibility (see Chapter 4 for further descriptions of rejection zones). This suggests the branches, were from two genotypically distinct colonies.

Colonies of *Pavona cactus* are composed of upright fronds. The term 'frond' was chosen to describe the upright portions of colonies because it denotes an essentially two-dimensional structure, which is compressed in one of the vertical planes of growth. Although fronds from all growth forms are bifacial in the distal, growing margins of the colony, fronds vary in the thickness of their basal portions and in their pattern of branching (frond thickness is measured perpendicular to the plane of compression). The term 'branch' more aptly describes upright structures which are multifacial towards the older, basal parts of the colony. However, the term frond will be used in all cases to emphasize that all upright structures are bifacial in areas of new growth.

The 'columnar form' (Figure 4b and 5b) has robust fronds which are greater than 10mm in thickness in the lower portions of the colony. Although fronds are compressed in one plane when newly formed at the growing margins of the colony, they become rounder towards the base of the colony as subsequent calcification obscures their initial bifacial nature. Branching is generally di- or trichotomous, although the growing edge may divide into 5 or more branches. Branching occurs at intervals greater than 50mm, and at angles which maximize spacing between fronds. Fronds are separated by less than 50mm at their distal edges and living tissue is found along their entire length, from the growing margins to the point of attachment.

Colonies of the 'convoluted form' (Figures 4a and 5a) consist of tightly packed, highly anastomosed fronds. Branching is similar to that described for the columnar form, but fronds are never more than 2mm thick, even at their bases. Fronds expand in width as they grow upwards so that they frequently come into close proximity, and often fuse. The high density of fronds in this form inhibits light penetration and water circulation into the interior of the colony. Thus the basal and central portions of the colony (i.e. at distances >100mm from the growing edge) are dead.

There are a range of intermediate forms (Figures 4c and 4d) which approach the convoluted form at one end of the morphological continuum but which are separated by a gap from the columnar form. Fronds of intermediate colonies remain compressed along their entire length, as in the convoluted form, and never approach the round, multifacial state of the columnar form. However, frond spacing in intermediate forms completes the range between the extremes of the convoluted and columnar forms.

Corallite structures (Figure 6) are constant in number and shape for all growth forms of *Pavona cactus* (Veron and Pichon, 1980;

FIGURE 4

Representative growth forms of *Pavona cactus*: Skeletal specimens.

Top Left Photograph (A): The convoluted morph (25cm diamter). Fronds are thin, bifacial, and densely packed. Frequent anastomosis produces a rigid framework to support the relatively fragile growing margins of the colony. (Eclipse Island: 3m, northern reef slope)

Top Right Photograph (B): The columnar morph (35cm high). Fronds are thick and rounded. Branches are widely spaced and anastomosis is rare. (Eclipse Island: 4m, western reef slope)

Bottom Left (C) and Right (D) Photographs: Examples of intermediate forms of *P. cactus* (22cm and 20cm diameter respectively). Fronds are more widely spaced and the growing margins less folded than fronds of the convoluted form. However, in cross section, fronds remain essentially bifacial and never approach the rounded condition of the columnar form. (Eclipse Island: 3m, northern and western reef slopes)

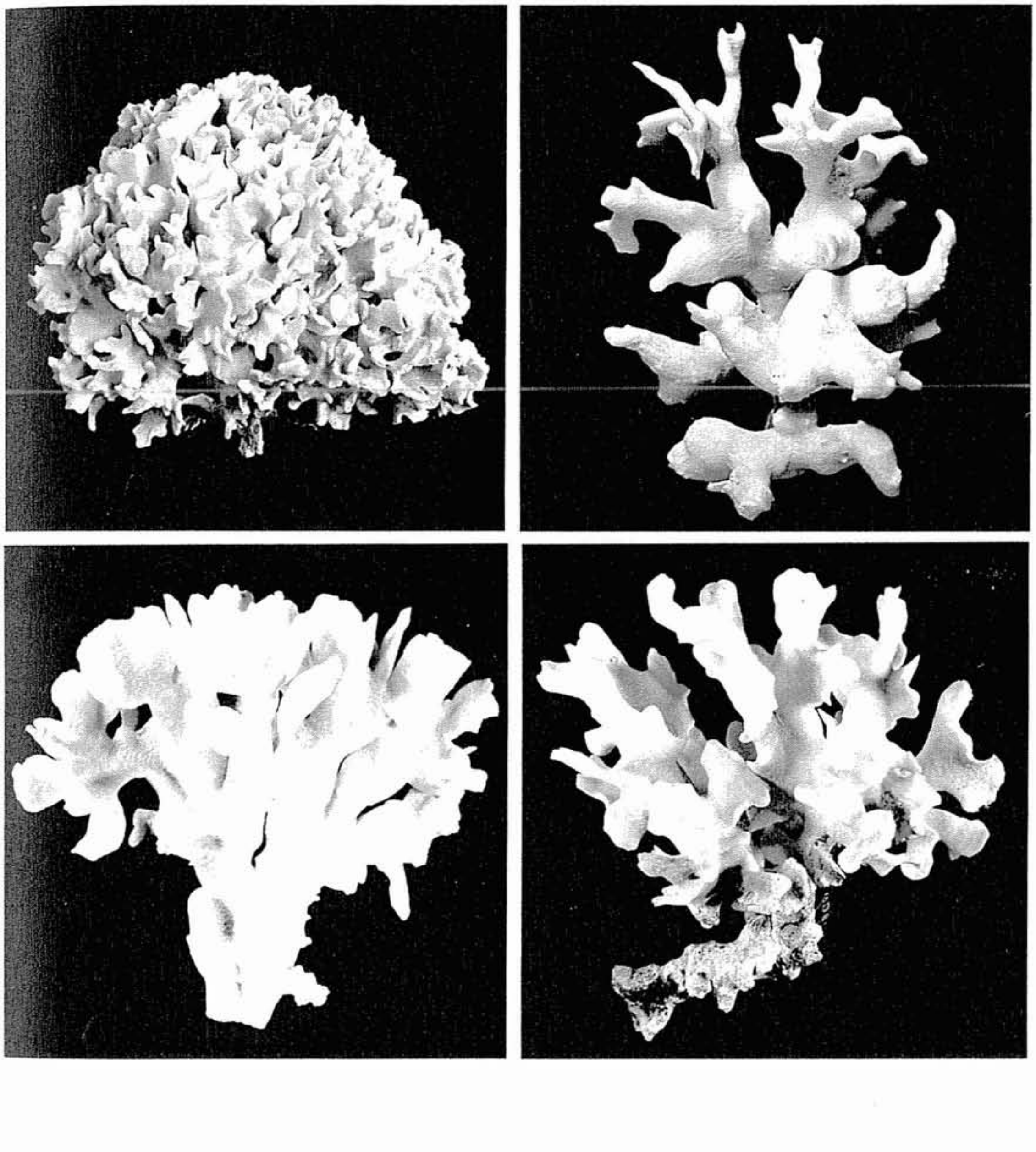


FIGURE 5

Growth forms of *Pavona cactus*: *in situ* colonies at Eclipse Island.

Top Photograph (A): Small colonies of the convoluted morph surrounded by the more open, less fluted fronds of intermediate morphs. Living tissue extends only 2-4cm towards the interior of the colony in the convoluted form. Living tissue may reach the substratum in intermediate colonies, depending on spacing between fronds. (Eclipse Island: 2.5m, northwestern reef slope.)

Bottom Photograph (B): A large stand of the columnar morph. Fronds are robust, and living tissue extends to the substratum. (Eclipse Island: 3.5m, western reef slope)

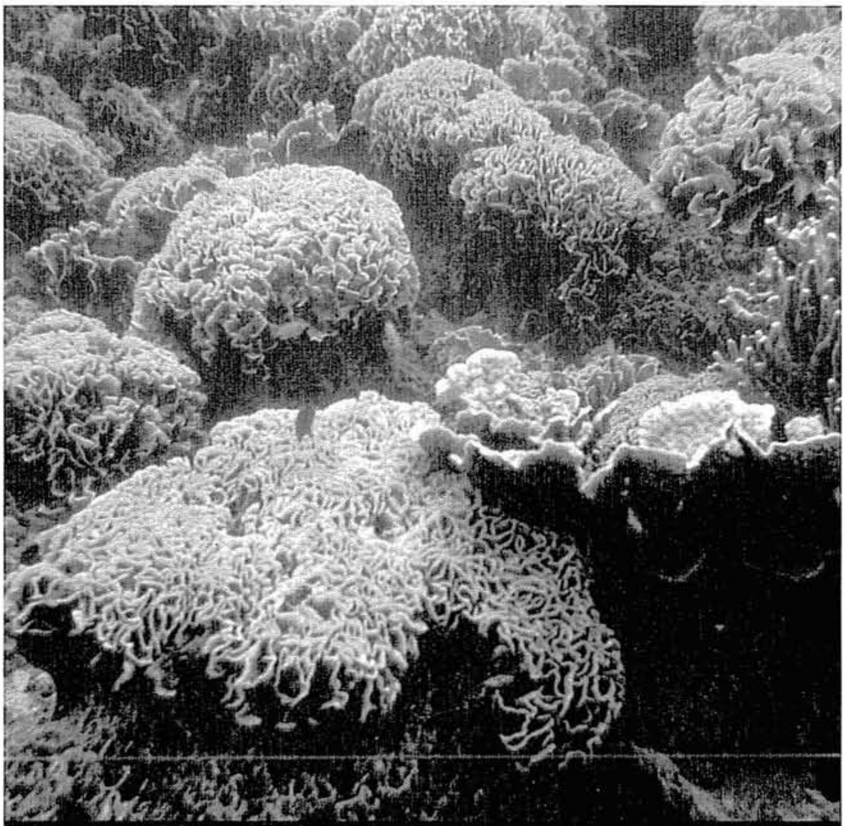


FIGURE 6

Scanning electron micrographs
of corallites of two growth forms of *Pavona cactus*.

Corallites in all forms are athecate so that it is impossible to define boundaries between them. Septo-costae run between adjacent calices, generally perpendicular to the growing margin of the frond. The 6 to 8 septo-costae of the first order usually reach the columella, whereas second order septo-costae do not. Septo-costae in all forms have lateral bead-like granulations or vepreculae.

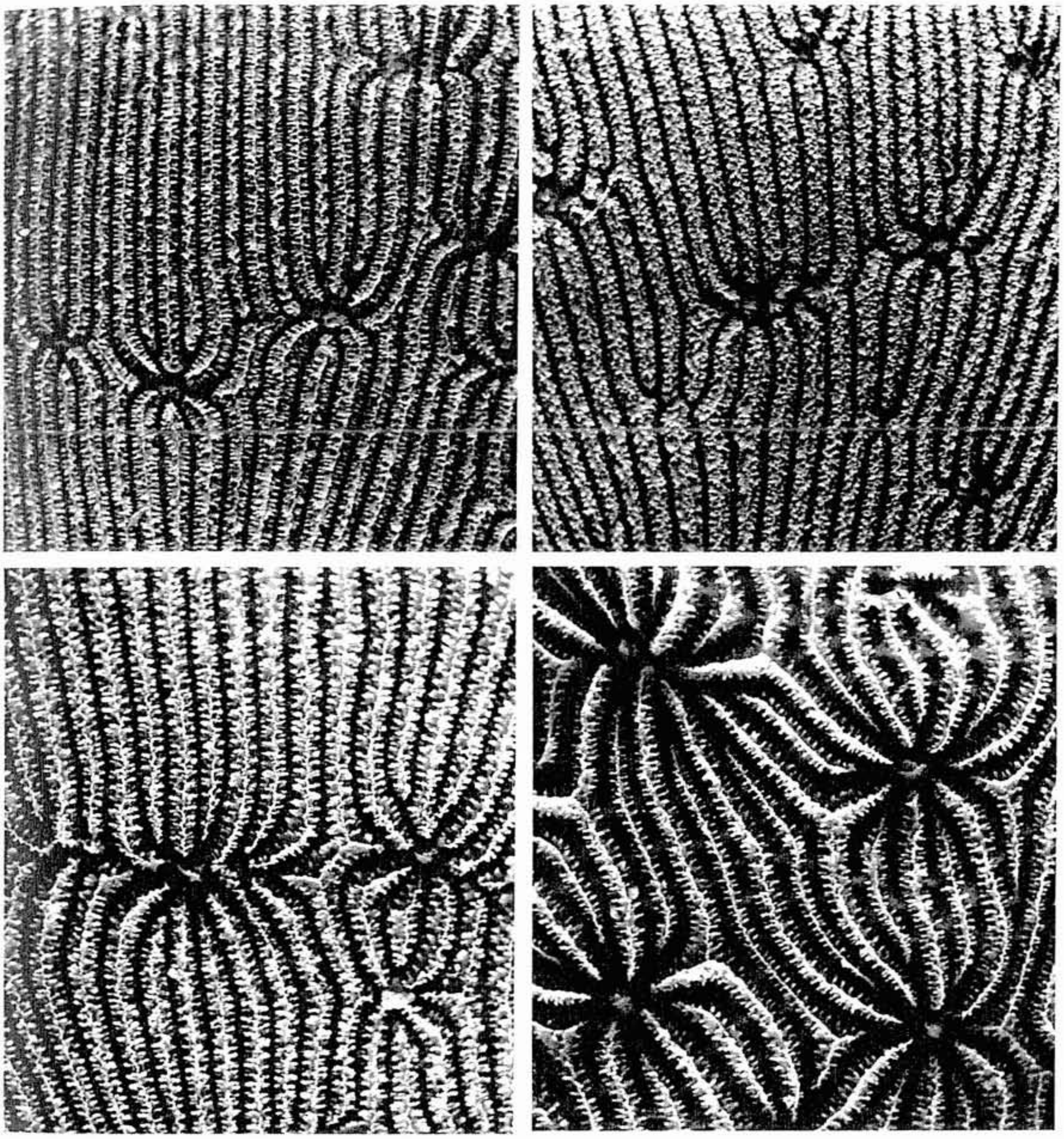
Top Left Photograph (A): Convoluted morph, corallites 1cm from growing margin of frond.

Top Right Photograph (B): Convoluted morph, corallites 4cm from growing margin of frond. Septo-costae are approximately the same distance apart, but appear thicker at this level, because spaces between lateral granulations have been filled in.

Bottom Left Photograph (C): Columnar morph, corallites 1cm from growing margin of frond. The size and spacing of corallites is similar to those in A.

Bottom Right Photograph (D): Columnar morph, corallites 4cm from the growing margin of frond. Septo-costae are farther apart at this level, but generally equivalent in thickness to those in C.

Specimens were spatter coated with gold and photographed in 30KV Backscatter Mode on an ETEC Autoscan. Magnification (A-D): x 20

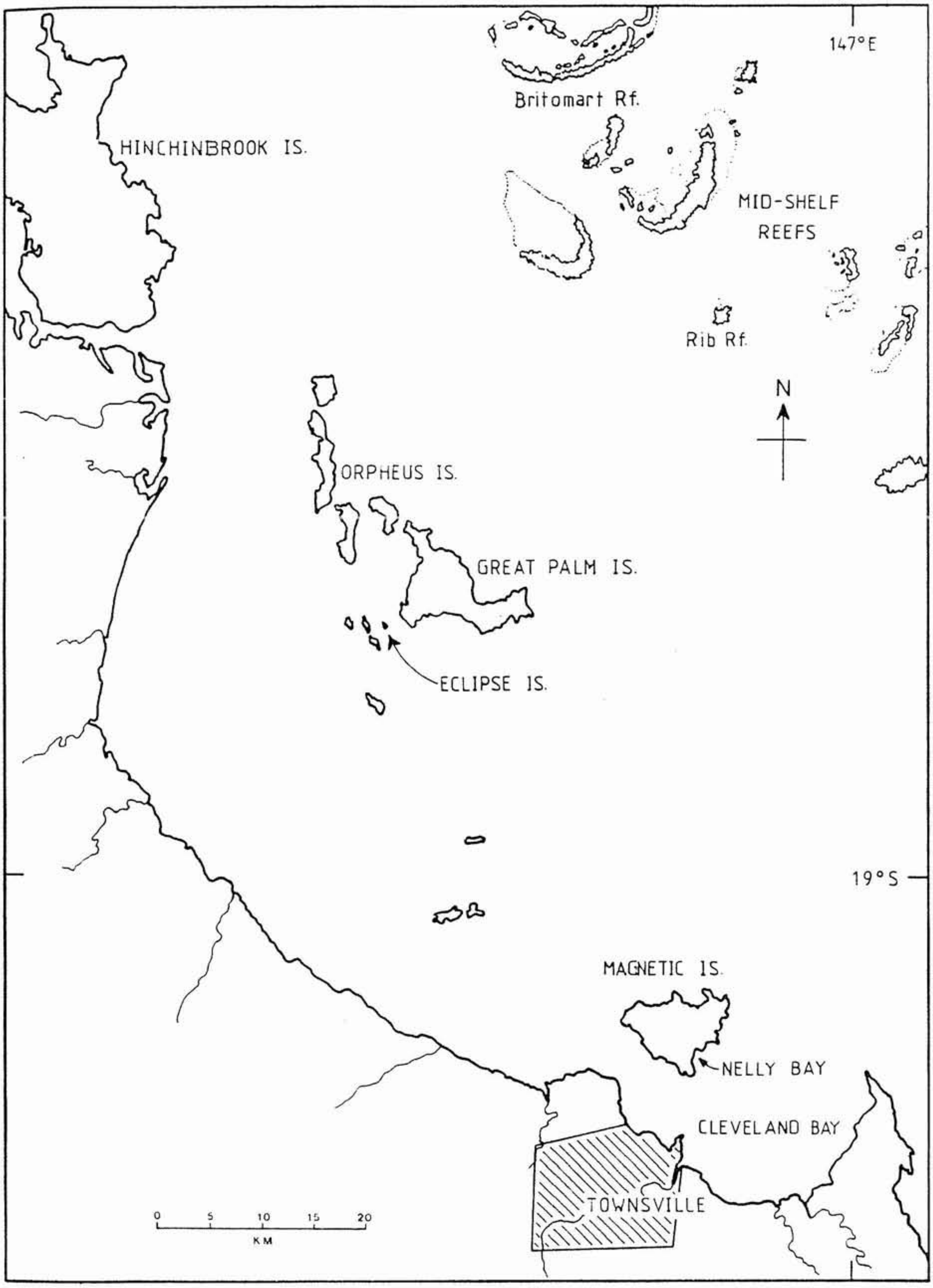


this study). However, the average size and spacing of calices differ between the convoluted and columnar forms. In general, calice size and spacing remain constant and small along the length of the frond in the convoluted form, but both dimensions increase towards the base of columnar fronds. The spacing between septo-costae follows a similar pattern. In contrast, the thickness of septo-costae increases towards the base of convoluted fronds (compare Figures 6a and 6b), whereas it tends to remain constant along the length of columnar fronds (compare Figures 6c and 6d). These differences are illustrated further in Figure 31.

2.3 General Descriptions of Study Areas

Sites at Nelly Bay and Eclipse Island (Figure 7) were selected for study because of the abundance of *Turbinaria mesenterina* and *Pavona cactus*, respectively, on these two reefs. Both are inshore fringing reefs surrounding continental islands in the central Great Barrier Reef region. Nearshore fringing reefs in this region have been described as thin veneers which have developed on unconsolidated, terrigenous sediments by Hopley *et al.* (1983). In their terminology (referring to the zone in which sediments accumulate), the reef at Nelly Bay is a 'bayhead' reef, whereas at Eclipse Island the reef is the 'leeside sand spit' type.

Although Eclipse Island is farther from the coast than Nelly Bay (27km and 8km respectively), both reefs are influenced by the mainland. In comparisons with mid- and outer-shelf reefs, nutrient and sediment loads are increased (Walker and O'Donnell, 1981; Wolanski and Jones, 1981) and salinities decreased during the wet season (associated with monsoonal rains and occasional cyclones, primarily between January and March). As well as local terrigenous inputs, both reefs may be affected by river plumes discharged during the rainy season and carried northward in longshore currents (Wolanski and Jones, 1981). Probably of greater significance though, are wind-driven bottom resuspension processes which characterize Cleveland Bay (Figure 7) and probably most of the


147°E
Britomart Rf.
HINCHINBROOK IS.
MID-SHELF
REEFS
Rib Rf.
N
ORPHEUS IS.
GREAT PALM IS.
ECLIPSE IS.
19°S
MAGNETIC IS.
NELLY BAY
CLEVELAND BAY
TOWNSVILLE
0 5 10 15 20
KM

coastal areas of the Great Barrier Reef lagoon (Walker and O'Donnell, 1981). For all these reasons, nearshore fringing reefs including those at Nelly Bay and Eclipse Island, may be classified as turbid water reefs in cross-shelf comparisons. Inner-shelf turbid water reefs were found to have the lowest species diversity in Done's (1982) cross-shelf study of coral community structure in the central Great Barrier Reef region.

Nelly Bay: Nelly Bay is located on the southeastern shore of Magnetic Island (Figure 7) and is therefore exposed to the easterly and southeasterly winds which prevail for most of the year. Although partially in the lee of Cape Cleveland, there is sufficient fetch (25km) across Cleveland Bay to produce short period waves, commonly to 1m in height. Swell is also diffracted around the headlands into Nelly Bay.

The Nelly Bay fringing reef (Figure 8) is approximately 200m wide, and may be subdivided into two major reef zones: an extensive reef flat zone between 0m and 1m above datum, and a reef slope zone which reaches a maximum depth of 6m below datum. The inner portions of the reef flat dry during extreme low water spring tides. (Mean tidal range is 2.27m for spring tides and 0.59m for neap tides (Qld. Dept. Harbours and Marine, 1986).) The base of the reef slope merges into a bottom zone of fine, sandy mud with coral outcrops continuing but decreasing in frequency for approximately 100m.

The coral assemblages in Nelly Bay are impoverished in comparison to communities farther offshore. Approximately 69 species were recorded from Geoffrey Bay, which is immediately adjacent to Nelly Bay, in a line transect survey by Bull (1977). Qualitative comparisons of the coral community between these two bays suggests that Nelly Bay has even lower species diversity than Geoffrey Bay. The reef flat coral assemblage is dominated by the ramose coral *Montipora digitata* and small colonies of *Porites* and *Goniastrea*. In summer, the fleshy macroalga, *Sargassum sp.*, competes strongly for space and attains high percentage cover over the outer reef flat and upper reef slope areas (Morrissey, 1980). The most abundant species on the reef slope include *Turbinaria mesenterina*, foliose *Montipora* species, and arborescent *Acropora*

FIGURE 8

Geomorphology of Nelly Bay, Magnetic Island, and location of Site A.

The fringing reef at Nelly Bay and adjacent mainland are pictured. At Nelly Bay, sediments have accumulated against the island in an embayment to produce a 'bayhead type reef'. Adjacent Cleveland Bay reaches a maximum depth of 10m below datum.

rf - reef flat (unconsolidated rubble); **rs** - reef slope; **bs** - beach sand; **sa** - sedimentary accumulation zone; **A** - study site A.


N
sa
bs
rf
rs
A

species (primarily *A. formosa*). Coral outcrops on the floor of the bay consist mainly of massive *Porites*, *Turbinaria*, and small faviids.

Eclipse Island: The fringing reef at Eclipse Island (Figure 9) is narrow and steep on all sides of the island except to the north. In the region of the northwestern projection, the reef flat and reef slope areas extend for approximately 700m. The prevailing southeasterlies break along the eastern face of the projection, leaving the northern and western slopes relatively protected. However, water exchange is high on all aspects of the Eclipse Island reef because frequent southerlies entrain northerly water flow past these 'protected' slopes. Also, superimposed on the wind-generated surface water flow, subsurface currents average 0.3k in a southerly direction in the vicinity of the Palm Island Group (E. Wolanski pers. comm.).

Tide ranges are virtually identical to those described for Nelly Bay. A large proportion of the extensive reef flat area dries during low spring tides, though a network of small pools and drainage channels always traps some seawater. The macroalgae, which characterize the reef flat and upper reef slope at Nelly Bay, are largely replaced by the Alcyonaria: *Lobophytum*, *Sinularia* and *Sarcophyton spp.*

Coral assemblages of the northern leeside reef at Eclipse Island are much more complex than those at Magnetic Island. The progression of community types around the reef are all types described within Done's (1982) Class III communities of sheltered habitats. Although the Palm Island reefs are inner-shelf in terms of location, in terms of coral diversity, they lie somewhere between mid-shelf (highest) and inner-shelf (lowest: Done, 1982) reefs, due to the oceanographical and topographical complexity of the area (Veron and Pichon, 1976).

FIGURE 9

Geomorphology of Eclipse Island and adjacent reef.

The 'leeside sandspit type' fringing reef at Eclipse Island (*i.e.* built on sediments accumulated behind the island). Maximum depths of approximately 28m occur between Eclipse Island and adjacent islands within the Palm Island Group.

m - mangroves; **irf** - inner reef flat (sand, coral debris, dead microatolls); **orf** - outer reef flat; **rs** - reef slope; **ss** - sand spit.


N
rs
orf
irf
ss
m

2.4 Materials and Methods

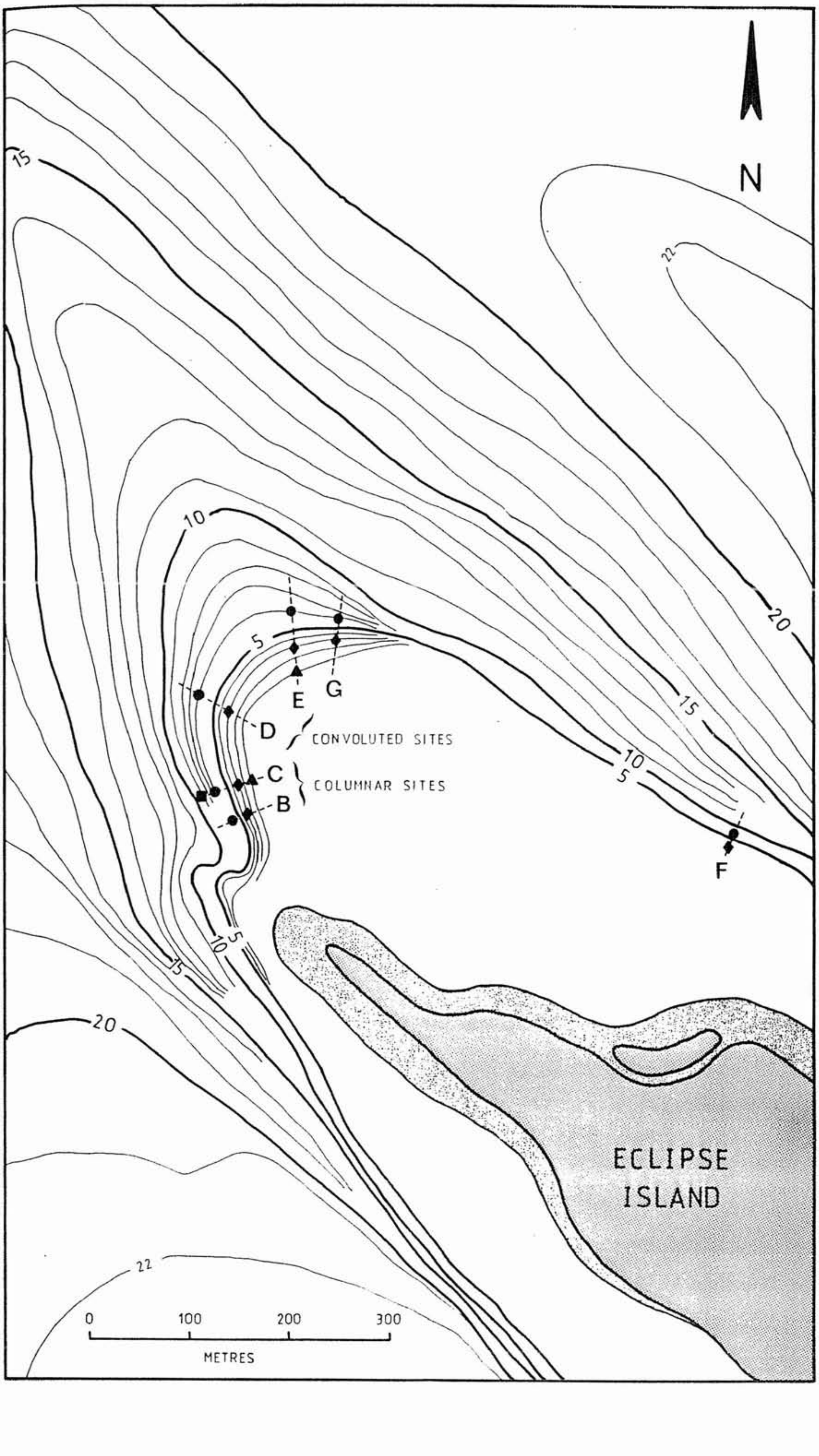
2.4.1 Location of Study Sites

In the following descriptions, the term 'site' will be used to describe the general location of a study area as it relates to its position along the reef slope. At each 'site', a deep and a shallow 'station' were established down the reef slope.

Nelly Bay: Site A was positioned towards the southern end of the fringing reef in Nelly Bay (Figure 8). *Turbinaria mesenterina* is abundant along much of the length of the reef, so the actual site was selected for the presence of convenient landmarks which could be aligned for site relocation. At site A, a shallow station was located at the top of the reef slope (depth: 1m below datum) and a deep station 60m down the slope at its base (depth: 4m below datum). These stations were located within areas where the convoluted and plate morphs, respectively, of *T. mesenterina* were most abundant (see results of survey in 2.5.1).

Eclipse Island: Sites B to F identify study areas spaced around the northern leeside reef at Eclipse Island (Figure 10). Sites B and C were located on its steep western slope, 30m apart, towards either end of a continuous stand of the columnar form of *Pavona cactus*. Sites D and E were located on the gentle northwestern and northern slopes of the reef, respectively, in areas where the convoluted form was abundant (see results of survey 2.5.1). Although site F (eastern reef slope), was located beyond the range of *P. cactus*, it was included as an exposed site for comparative studies of the hydrodynamic and sedimentary regimes of the leeside reef at Eclipse Island.

Shallow and deep reef slope stations were established at depths of 3m and 6m below datum, for all six sites. These stations were located near the top and approximately three-fifths of the way down the reef slope. The 3m stations corresponded to the depth contour


N
15
22
20
15
10
5
E
G
D
CONVOLUTED SITES
C
COLUMNAR SITES
B
10
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F
5
10
15
20
22
0
100
200
300
METRES
ECLIPSE ISLAND

at which the convoluted form was most abundant, and similarly, the 6m stations corresponded to the depth at which the columnar form was most abundant. The distance between each set of stations was greatest at sites D and E because of the gentle slope of the reef to the north. A 'reef crest' station (1m below datum) was established at sites C and E, and a 'bottom of the reef slope' station (9m below datum) at the steeper site C, where such depths were attained within reasonable distances.

2.4.2 Surveys of Growth Form Distributions

Initial surveys of populations of *Turbinaria mesenterina* and *Pavona cactus* at the two study reefs were conducted to determine whether a correlation between growth form distribution and either, depth gradient (both reefs) or reef slope orientation (Eclipse Island) could be established empirically. The method used to survey the distribution was largely dictated by the configuration of the reef.

Nelly Bay: At Nelly Bay where the reef essentially parallels the shore, a measuring tape was laid perpendicular to the reef edge and down the length of the reef slope, through an area dominated by *Turbinaria mesenterina*. At a distance of 0m and 60m along the tape, 50m transects were laid approximately perpendicular to the tape, but the angle was modified to approximate the selected depth contours. The two transects followed the 1m and 4m depth contours. At 1m intervals along these two transects, the growth form of the colony nearest the tape (within 2m limits), and greater than 30cm in diameter (lower size limit for growth form expression) was recorded.

Eclipse Island: At Eclipse Island a much larger reef area was surveyed. After a preliminary search of the study area, a stake was embedded in the reef flat, such that a semi-circle described with the stake as its centre, covered the northern reef slope and those parts of the eastern and western slopes where *Pavona cactus* was found. Ten measuring tapes varying between 50 and 100m in length were laid from the central stake in a radiating pattern following compass bearings. Bearings were spaced at regular intervals between 204° and 036°. The nine sectors defined by the tapes (=radii of the semi-circle) were then subdivided into working units. This was done by laying a further 4 to 5 tapes in arcs between the 2 sides of each sector, at increasing distances from the central stake.

The locations of colonies within each sector were mapped using the tapes, along the radii and arcs of the sectors, to provide co-ordinates for major features. This was done for the three growth forms of *P. cactus* as well as other dominant species of coral. At 0.5m depth intervals the distance along each radius was recorded, and used in conjunction with compass bearings from the central stake to superimpose the semi-circle on a bathymetric chart of Eclipse Island.

2.4.3 Temperature and Salinity

On each visit to the study reefs, temperature and salinity data were collected from the deep and shallow stations at site A (Nelly Bay) and site E (Eclipse Island). Field trips were designed to be 4 weeks apart, but actual intervals between trips were dictated by the weather, and ranged up to 8 weeks. Seawater temperature readings were taken with a 0-50°C mercury thermometer. Maximum-minium thermometers were also tied permanently to the substratum at the four stations. Following each reading, fouling organisms were removed and the maximum-minimum markers relocated to ambient temperature.

500ml plastic sample jars were used to collect seawater samples at the four stations for salinity determinations. Maximum-minimum salinity data were collected with a sampling device described by Walker (1980). The upright and inverted bottles were clamped between steel brackets fixed to a stake at each station. The bottles were taped with black electrical tape to occlude light and changed every 4 to 8 weeks. All salinity determinations were made using an Autolab inductive salinometer (model 601-MKIIIB).

2.4.4 Light Profiles

Li-Cor aerial and underwater (model LI-192SB) quantum sensors, connected through calibrated calconnectors to a LI-185B quantum meter, were used to take instantaneous measurements of irradiance in the photosynthetically active range (PAR). Light profiles were collected on 2 different days at each reef. Surface PAR was measured with the aerial sensor. The underwater sensor was then lowered through the water column above the deep stations at sites A and E, on a bracket designed to maintain it in a vertical position. PAR (μ Einsteins/m^2/s) was recorded at 1m depth intervals.

The attenuation coefficient, k, was calculated as the slope of the straight line, for each graph of depth versus ln(% surface PAR). Attenuation coefficients calculated in the present study were compared to those calculated in a year long study by Walker and O'Donnell (1981) in Cleveland Bay, to provide a more detailed characterization of the underwater light environment.

2.4.5 Sedimentation Regimes

The downward flux of particles settling on corals was compared among stations and sites, by placing three replicate sediment traps upright on the substratum at each location. Replicate traps were placed at the deep and shallow station at site A (Nelly Bay), and at sites B to F around the Eclipse Island reef. The traps were positioned so that the height of the open mouth of each trap approximated the height of nearby colonies.

Sediment traps were designed to prevent resuspension and subsequent loss of trapped particles in moderately turbulent conditions. Hargrave and Burns (1979) and Gardner (1980) recommended cylindrical traps with aspect (height:width) ratios greater than 5, to maximize residence time of particles within the traps. Traps were made from 3cm (inside diameter) opaque PVC tubing cut to 30cm lengths, giving an aspect ratio of 9 after a rubber stopper had been inserted to form the bottom of the trap. The cylinders were dipped in marine antifouling paint to inhibit the growth of sessile organisms on the inside of the trap. Small vials, which leached copper sulphate solution, were also placed in the traps to create an inimical environment for small fish (but see results 2.5.4). The three replicate traps were firmly wedged into PVC bases, which were 40cm apart and fixed to the corners of a triangular steel plate. Sediment traps were collected every 6 to 8 weeks. During collection, a rubber stopper was inserted into the mouth of each trap to prevent loss of sediment on ascent.

Within 24 hours of collection, the contents of each trap was washed into a preweighed, shallow, wide-mouthed container. Following settling of the sediment 5 to 7 days later, the water was siphoned off and replaced with clean freshwater to remove salts from the mixture. The contents of the traps were washed twice in this manner and the remaining sediment oven-dried to constant weight at 60°C.

To determine the organic and carbonate content of sediment samples from the two reefs, three subsamples from each reef were heated in a muffle furnace, first to 550°C and subsequently to 1000°C. The proportion of organic matter in the sample was determined as the percent ignition loss at the lower temperature. Similarly, the amount of carbonate in the sediment was determined as the percent weight loss after heating to 1000°C (Dean, 1974).

2.4.6 Localized Water Turbulence

The turbulent flow of water in the vicinity of each of the stations was qualitatively compared via calculation of dissolution rates of plaster of Paris. Plaster of Paris is sparingly soluble in seawater and both 'plaster spheres' (Muus, 1968) and 'clod cards' (Doty, 1971) have been used as turbulence indicators. Clod cards were constructed as per details given by Doty (1971) and exposed during a preliminary survey of the Eclipse Island reef. Plaster spheres were used subsequently because of the uniform surface they presented in all directions for dissolution, and the longer period over which they could be used to integrate water movement.

Moulds, 60mm in diameter, were constructed of surgical gauze and latex carpet glue for casting the plaster spheres. Upon drying the moulds were moderately flexible so that when set, the plaster spheres could be removed easily through a midline slit in the mould. A plaster of Paris mixture (Doty, 1971) was poured into the moulds, and 10cm weighed lengths of brass brazing rod inserted to provide a means of attaching the plaster spheres to stakes underwater. An engraving gun with an attached rod was used to vibrate the mixture to remove pockets of trapped air. The plaster spheres were dried at 60°C until consecutive weighings gave constant results. Variation in weight between plaster spheres within a single batch (*i.e.* enough spheres for one complete trial) was less than 5% of the mean total weight.

Three plaster spheres were attached to steel rods at deep and shallow stations at site A, Nelly Bay, and sites B to F, Eclipse Island. Three control plaster spheres were placed in a large, sealed bucket at the deep stations at sites A and B. Plaster spheres were collected 48 to 72 hours later, rinsed briefly in freshwater, dried, and reweighed to determine weight loss. Weight losses of control spheres represented dissolution rates in still water at ambient field temperatures and salinities, and were used to calibrate each batch of plaster spheres.

2.5 Results

2.5.1 Surveys of Morph Distributions

Nelly Bay: The line transect survey of *Turbinaria mesenterina* in Nelly Bay confirmed preliminary observations that the convoluted and plate morphs have different depth distributions. With one exception, all colonies greater than 30cm in diameter were convoluted on the shallow transect (N=50), and all colonies on the deep transect were plate-like (N=47). The single odd colony on the shallow transect was intermediate in form. *T. mesenterina* was abundant at these depths, and there were only 3 1-metre intervals along the deep transect where a colony could not be found within 2m of the tape. Observations over the whole study area showed that transitional forms occurred between 1m and 4m. At depths shallower than 2m they tended towards the upright, wavy fronds of the convoluted form but were more laminar at depths greater than 3m.

A few deviations from the above pattern of variation with depth were found in widespread observations. Plate colonies were found in shallow, shaded habitats, such as slight overhangs in gulleys, or the bases of large (>2m diameter) colonies. Also, large, shallow colonies of *T. mesenterina* were often convoluted in the upper portions of the colony, but had platelike, horizontal laminae near the substratum.

Eclipse Island: The columnar form of *Pavona cactus* was confined to the steeply inclined (20°) western reef slope at Eclipse Island. It occurred as a continuous monospecific stand, dominating an area approximately 30m along the reef slope between sites B and C, and 11m down the reef slope, between 3.5m and 7m below datum. Colonies of the intermediate form were also present in this area, but in much lower numbers.

The convoluted form was found on the northwestern and northern reef slopes from 2m to 4m below datum. The slope is generally less than 5° in this region, so the actual area involved was extensive (the distance down the reef slope between these two depth contours was approximately 25m). This form occurred as isolated colonies up to 2m in diameter, rather than as continuous stands. Intermediate colonies were always found within 1m of convoluted colonies, so that no area could be exclusively associated with the convoluted form. Together the convoluted and intermediate forms visually dominated the scleractinian assemblages on these slopes, with the intermediate form being the more abundant of the two.

Intermediate forms were found throughout the depth and reef slope distributions of the species and were relatively more abundant than either columnar or convoluted forms. This form extended approximately 12m further along the western reef slope towards the island than the columnar form (*i.e.* past site B), and approximately 20m further along the eastern slope than the convoluted form (*i.e.* to site G). Its depth distribution ranged from 1m to 9m below datum. In several areas intermediate colonies formed stands up to 5m in diameter. This form often grew beside colonies of either the convoluted or columnar forms. The intermediate form of *P. cactus* was regularly associated with either *Porites cylindrica* or *Millepora spp.* In both cases the fronds of *Pavona cactus* overgrew the base of the associated coral but did not grow above the level of its branches. No colonies which could be identified as juveniles resulting from sexual reproduction were observed throughout the survey area.

2.5.2 Temperature and Salinity

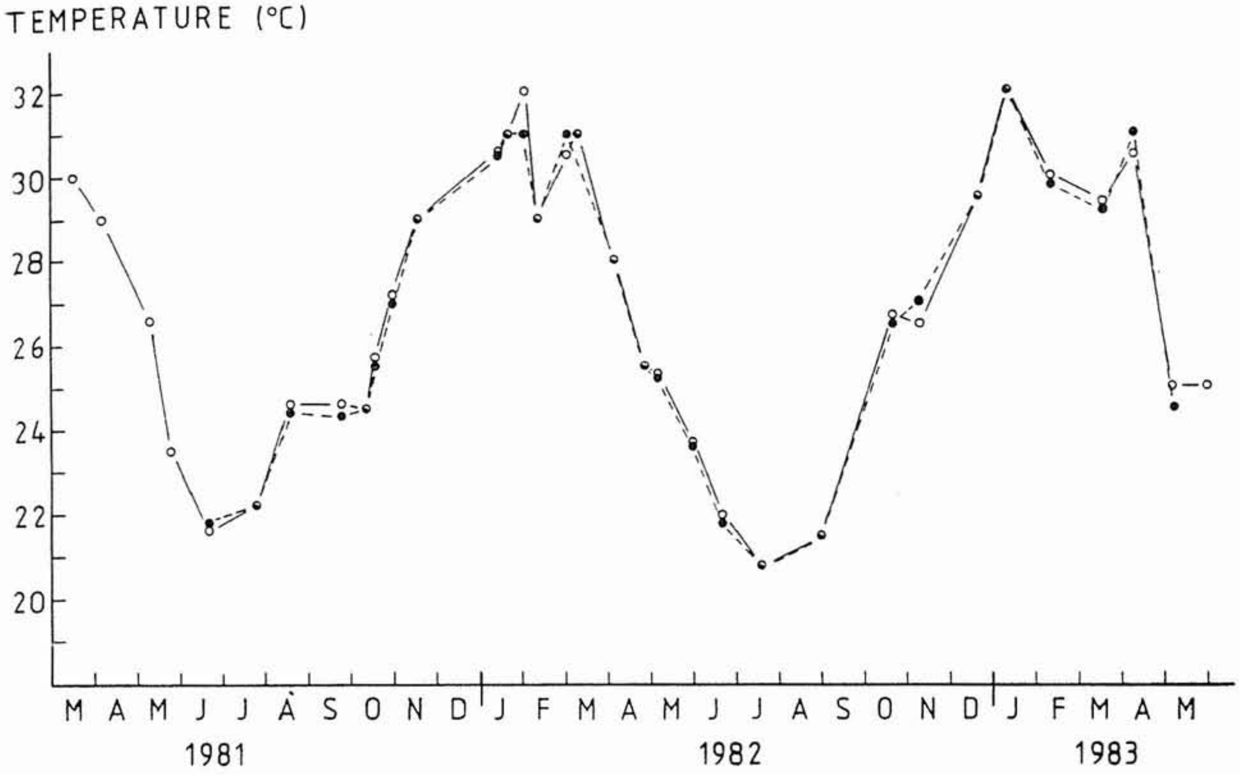
Nelly Bay: Seawater temperatures over two years at Nelly Bay (Figure 11a) and Eclipse Island (Figure 12a) showed strong seasonal trends at all stations. At both reefs maximum temperatures occurred between January and March and minima between June and August. The temperature range recorded in instantaneous readings over 2 years at Nelly Bay (20.8°-32.0°C) was greater than that at Eclipse Island (21.8°-30.6°C). Although records at the two reefs overlapped for only 9 months, comparisons of maxima and minima between the two

FIGURE 11

Seasonal patterns of temperature and salinity
at Nelly Bay, Magnetic Island.

Each point represents a single reading. Temperatures were recorded between 10:00 and 14:00 hours.

O——O Shallow station records (1m), Site A.
●---● Deep station records (4m), Site A.


TEMPERATURE (°C)
32
30
28
26
24
22
20
M
A
M
J
J
A
S
O
N
D
J
F
M
A
M
J
J
A
S
O
N
D
J
F
M
A
M
1981
1982
1983

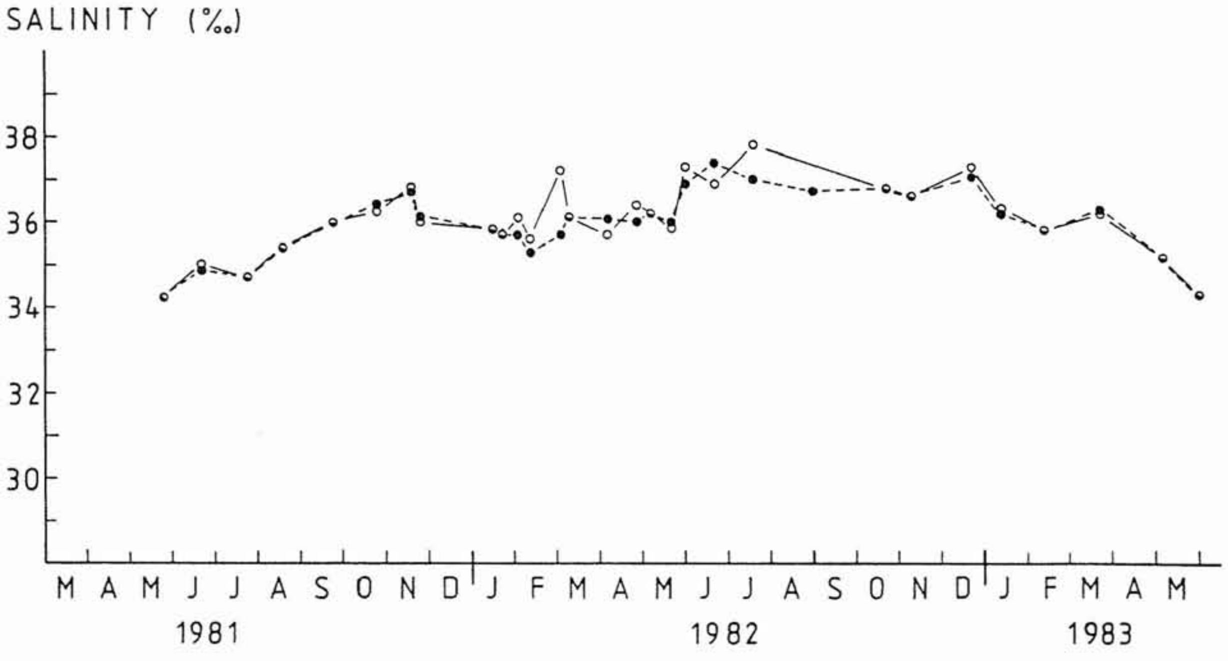
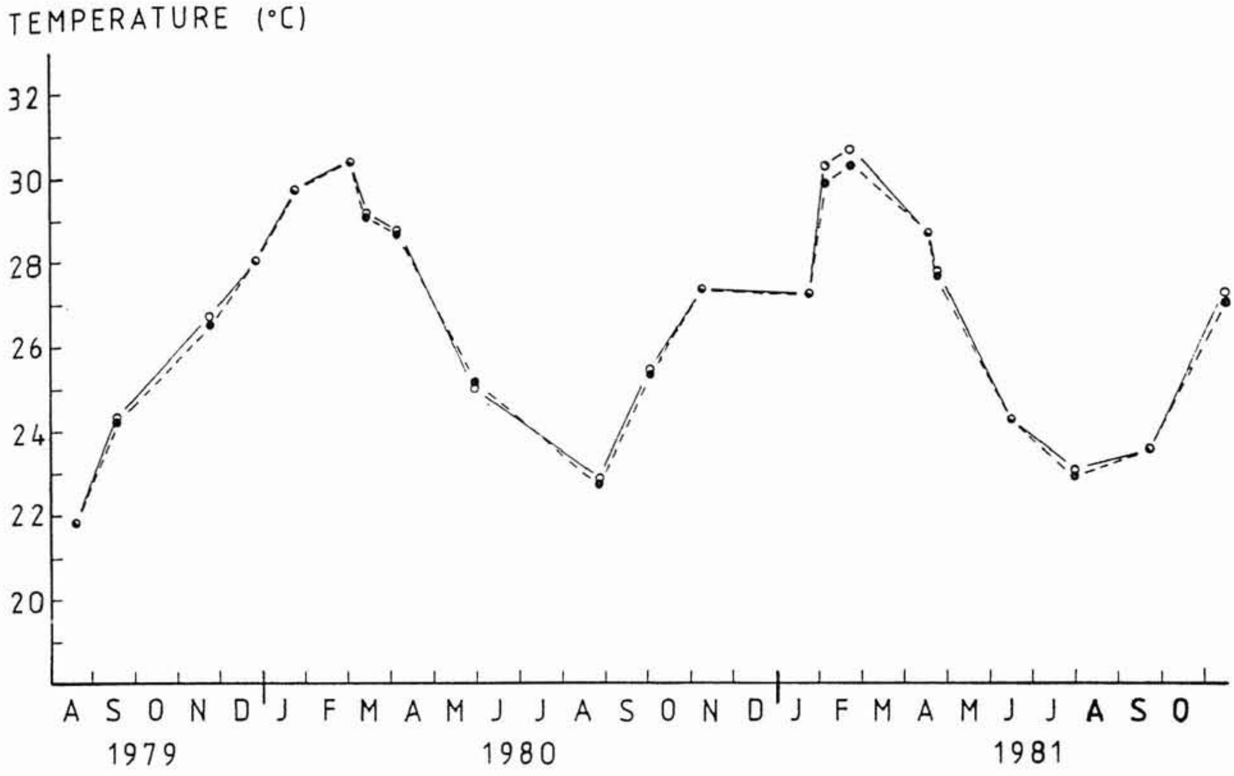

SALINITY (‰)
38
36
34
32
30
M
A
M
J
J
A
S
O
N
D
J
F
M
A
M
J
J
A
S
O
N
D
J
F
M
A
M
1981
1982
1983

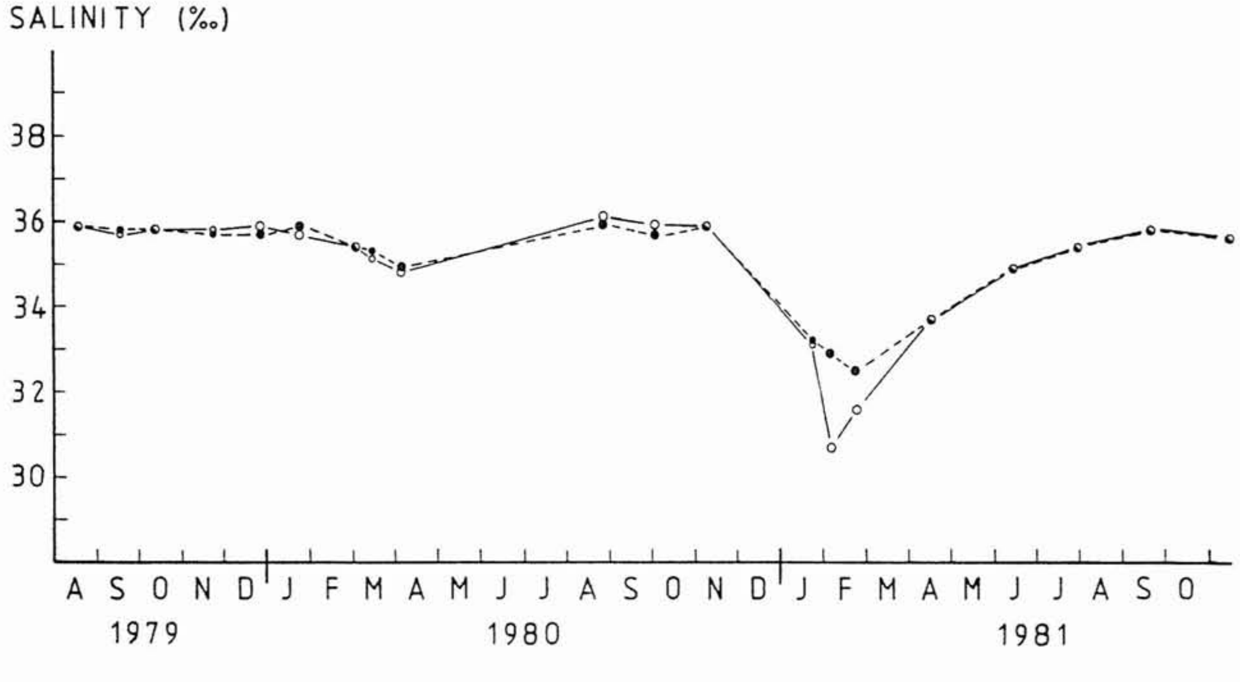
FIGURE 12

Seasonal patterns of temperature and salinity
at Eclipse Island, Great Barrier Reef.

Each point represents a single reading. Temperatures were recorded between 10:00 and 14:00 hours.

O——O Shallow station records (3m), Site E.
●---● Deep station records (6m), Site E.


TEMPERATURE (°C)
32
30
28
26
24
22
20
A S O N D J F M A M J J A S O N D J F M A M J J A S O
1979
1980
1981


SALINITY (‰)
38
36
34
32
30
A S O N D J F M A M J J A S O N D J F M A M J J A S O
1979
1980
1981

sites during the overlap period, support the general statement. Although the sampling resolution was somewhat coarse, there was a general trend for the winter/spring seawater temperature rise to begin in July at Nelly Bay, approximately 1 month earlier than the beginning of the rise at Eclipse Island.

Seasonal patterns in salinity (Figures 11b, 12b) were not as well-defined as temperature patterns. Minima occurred between February and May. However, the intensity of the minima was variable between years, reflecting variation in annual rainfall recorded in the region (Walker, 1981). The maximum-minium salinity apparatus did not retain the extreme ranges of salinity experienced at the stations, due to diffusion processes which operated over the long sampling intervals. However, a greater proportion of the range was recorded through this method than through spot samples. Despite this qualification, wide salinity ranges were recorded at both reefs (Nelly Bay: 30.2 -37.8%.; Eclipse Island: 30.0 -36.1%.). Nelly Bay experienced the highest salinities after a long, dry period in 1982.

Comparisons of these physical parameters at each site revealed only minor differences between deep and shallow stations. Spot temperatures at the Nelly Bay deep and shallow stations (Figure 11a) differed by less than 0.2°C over the two year period, except in one sample. In February, 1982 temperatures were 1.0°C higher at the shallow station. Including maximum and minimum recordings, corals at the shallow station in Nelly Bay experienced a range of 13.2°C (19.3-32.5°C). Corals at the deep site experienced a slightly lower range (19.3-31.5°C).

Eclipse Island: At Eclipse Island the two stations varied by less than 0.2°C for all readings except in February, 1980, when temperatures were 0.4°C higher at the shallow station (Figure 12a). Including maximum and minimum recordings, corals at the shallow station experienced a 10.6°C range (21.0-31.6°C). Those at the deep station experienced a 10.4°C range (20.8-31.2°C).

Differences in spot salinity recordings between stations were less than 0.4%. at both reefs, except on two occasions. Disparities of 0.8‰ and 2.5‰ were recorded during the dry 1982 summer-winter period at Nelly Bay (Figure 11b). However, the increased salinities at the shallow site were only 0.4‰ higher than the maximum recorded at the deep site. Disparities of 2.9‰ and 0.8‰ were recorded during the 1980 rainy season at Eclipse Island (Figure 12b). The decreased salinities at the shallow station were 1.8‰ lower than the minimum salinity recorded at the deep station.

2.5.3 Light Profiles

Nelly Bay: Water transparency at Nelly Bay was variable throughout the study period as judged by horizontal visibility underwater. An attenuation coefficient (k) of $0.34m^{-1}$ was calculated for a light profile taken in January, 1985 (Figure 13A), when seas were slight and underwater visibility high for Nelly Bay. During such optimal conditions, shallow station corals experience 61% of surface PAR, and deep station corals 21%, assuming extreme low spring tides. Percentages would decrease at higher tides to a potential minimum of 16% and 6% of surface PAR (calculated for a tide of 3.8m, the maximum high tide recorded in Townsville over the past 15 years, Qld. Dept. Harbours and Marine, 1986).

The calculated attenuation coefficient is within the range of attenuation coefficients ($0.25-0.35m^{-1}$) found by Walker and O'Donnell (1981) during January, 1977 at a site in the middle of Cleveland Bay (values cited were interpreted from Figure 2 in their paper). In their year long study, attenuation coefficients varied between 0.145 and $2.25m^{-1}$ at their Cleveland Bay site, and correlated well with sea state. Assuming that conditions do not differ grossly between years, nor across a distance of approximately 12km from the middle of Cleveland Bay to Nelly Bay, the attenuation coefficient calculated in the present study represents near optimal light penetration at Nelly Bay. Under the conditions of poorest light penetration recorded by Walker and O'Donnell (1981), corals at the shallow station would experience 8.9% of surface PAR and those at the deep station 0.01% at low tides.

FIGURE 13

Light (PAR) profiles
at Nelly Bay, Magnetic Island and Eclipse Island.

All profiles were recorded at mid-day during slight seas and sunny conditions.

A Nelly Bay:

- ● February 1980, Site A
- o January 1985, Site A
  - Fitted curve for January 1985 recordings

Attenuation coefficient: $0.34m^{-1}$

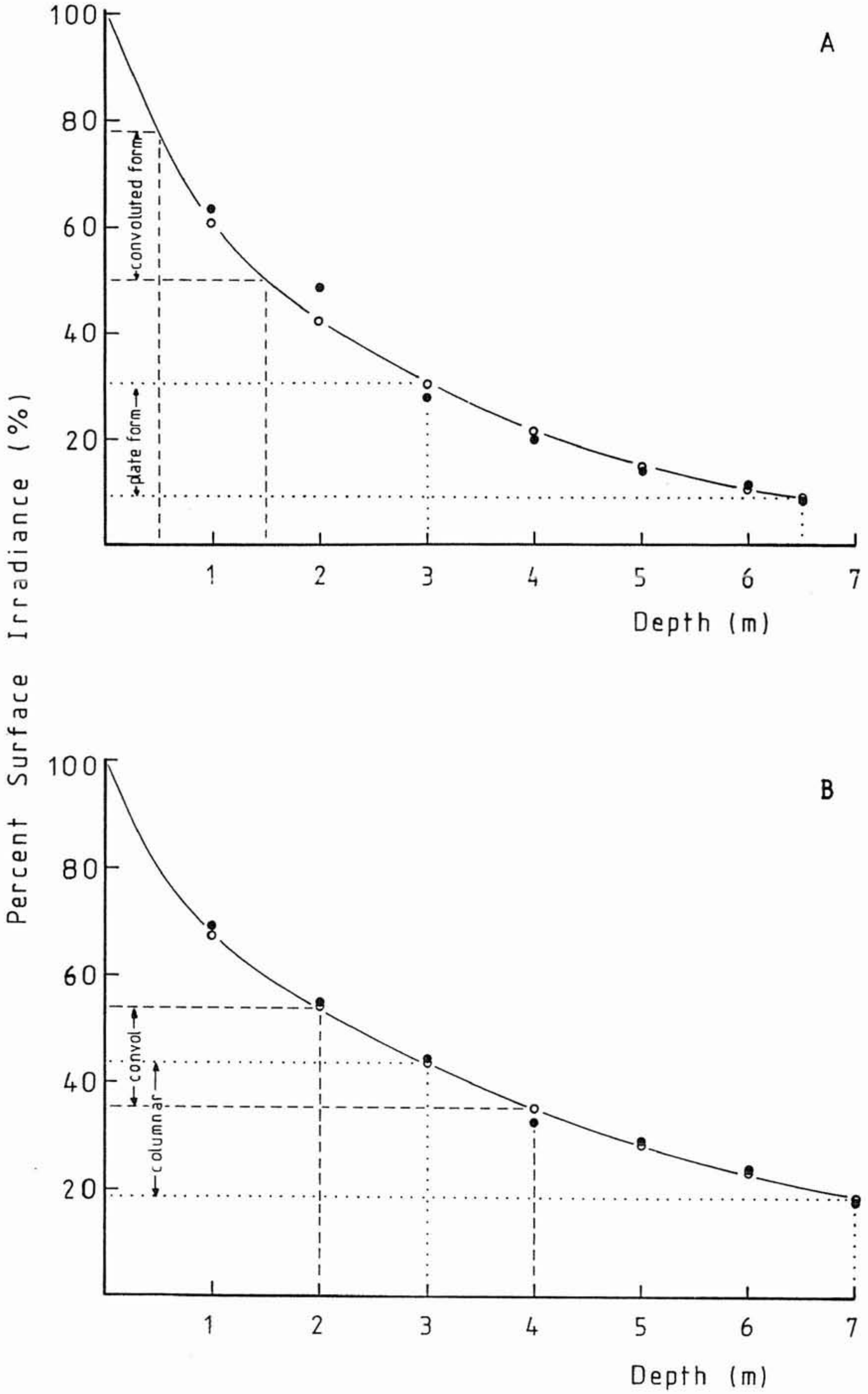
Depth distributions of the convoluted and plate morphs of *Turbinaria mesenterina* are shown relative to datum.

B Eclipse Island:

- ● March 1980, Site E
- o May 1982, Site C
  - Fitted curve for May, 1982

Attenuation coefficient: $0.21m^{-1}$

Depth distributions of the convoluted and columnar morphs of *Pavona cactus* are shown relative to datum.


A
B
Percent Surface Irradiance (%)
100
80
60
40
20
convoluted form
plate form
convol
columnar
1
2
3
4
5
6
7
Depth (m)
Depth (m)

Eclipse Island: Light profiles recorded at Eclipse Island are shown in Figure 13B. The attenuation coefficient of $0.21m^{-1}$ calculated for the May 1982 profile, was lower than that found at Nelly Bay, and approached optimal light penetration recorded by Walker and O'Donnell (1981) in Cleveland Bay. Underwater visibility was average for Eclipse Island during these measurements. Therefore, these data support general observations of consistently greater water clarity throughout the year at Eclipse Island, than at Nelly Bay. Under the measured conditions, corals would experience 44% of surface PAR at shallow stations and 23% at deep stations during extreme low tides. At extreme high tide (3.8m above datum) these percentages would be reduced to 19.8% and 10.5%. Although no light data are available for the Palm Island area for comparisons with the present study, underwater visibility records suggest that water transparency was much more consistent throughout the year at Eclipse Island than at Nelly Bay.

2.5.4 Sedimentation Regimes

Nelly Bay: The mean amounts of sediment collected during sampling intervals at Nelly Bay are shown in Figure 14. One of the three replicate traps per station often collected an amount of sediment inconsistent with the other two traps, or occasionally was found on its side. If 2 values were within 2.0g of each other but the third differed by more than 15.0g, then the third value was excluded from calculations of the mean. The irregular value was always lower than the other two, and it is possible that small blennies were living in the traps causing the discrepancy. On the three occasions that a blenny was actually observed in a trap, the amount of sediment collected in that trap was less than 0.12g. Values from these three traps were also discarded. Standard deviations associated with the means were generally high, especially where the results from only 2 sediment traps were availabe (Figure 13). The coefficient of variation ranged between 0.6% and 53.6%.

No consistent seasonal pattern was observed at Nelly Bay over the two year period that the traps were exposed. At both stations, sediment accumulation was greatest during the July-August period in 1982, and corresponded to a period of consistently moderate to strong southeasterlies.

Although annual patterns were inconsistent, the amount of sediment collected in traps at Nelly Bay was greatest at the shallow station for 11 of the 12 intervals for which comparative data were collected (Figure 14). A paired t-test, comparing sediment accumulation between the deep and shallow stations during each sampling interval, showed that the mean amount of sediment collected was significantly different between the two depths ($t=4.214$ with 11 df, $p<0.002$).

Eclipse Island: Sediment accumulation over a one year period at sites B to F (Eclipse Island) is shown in Figure 15. Means for each station are based on the contents of either 2 or 3 of the replicate traps, depending on circumstances similar to those described above for the Nelly Bay traps. As site F was difficult to access, sediment traps were not collected on a regular basis. During the two periods that sediment traps were exposed at all 5 sites, the amount of sediment accumulated was greatest at site F for both the deep and shallow stations. The amount of sediment collected was greatest at all sites and depths, during the March-April sampling interval in 1982.

A 2-factor ANOVA, testing for the effects of site and depth on the mean amount of sediment accumulated, was performed using the 4 time periods as replicates. Neither site ($F=0.207$ with 3x24 df, $p>0.5$) nor depth ($F=0.003$ with 1x24 df, $p>0.5$) was found to affect sediment accumulation significantly. The interaction effect was also not significant ($F=0.105$ with 3x24 df, $p>0.5$). Therefore, sedimentation regimes at the deep stations of sites B and C, where the columnar form was most abundant, were virtually indistinguishable from sedimentation regimes at the shallow stations of sites D and E, where the convoluted form was most abundant.

FIGURE 14

Rates of sediment accumulation at Nelly Bay, Magnetic Island.

Each histogram represents mean sediment accumulation (± S.E.) over a standardized 56 day sampling interval (mean duration of all intervals). Actual sampling intervals are shown above each pair of histograms. N=3 (or 2 where histograms are marked with an * (see text)).

unstipled: Shallow station (1m), Site A.
stipled: Deep station (4m), Site A.

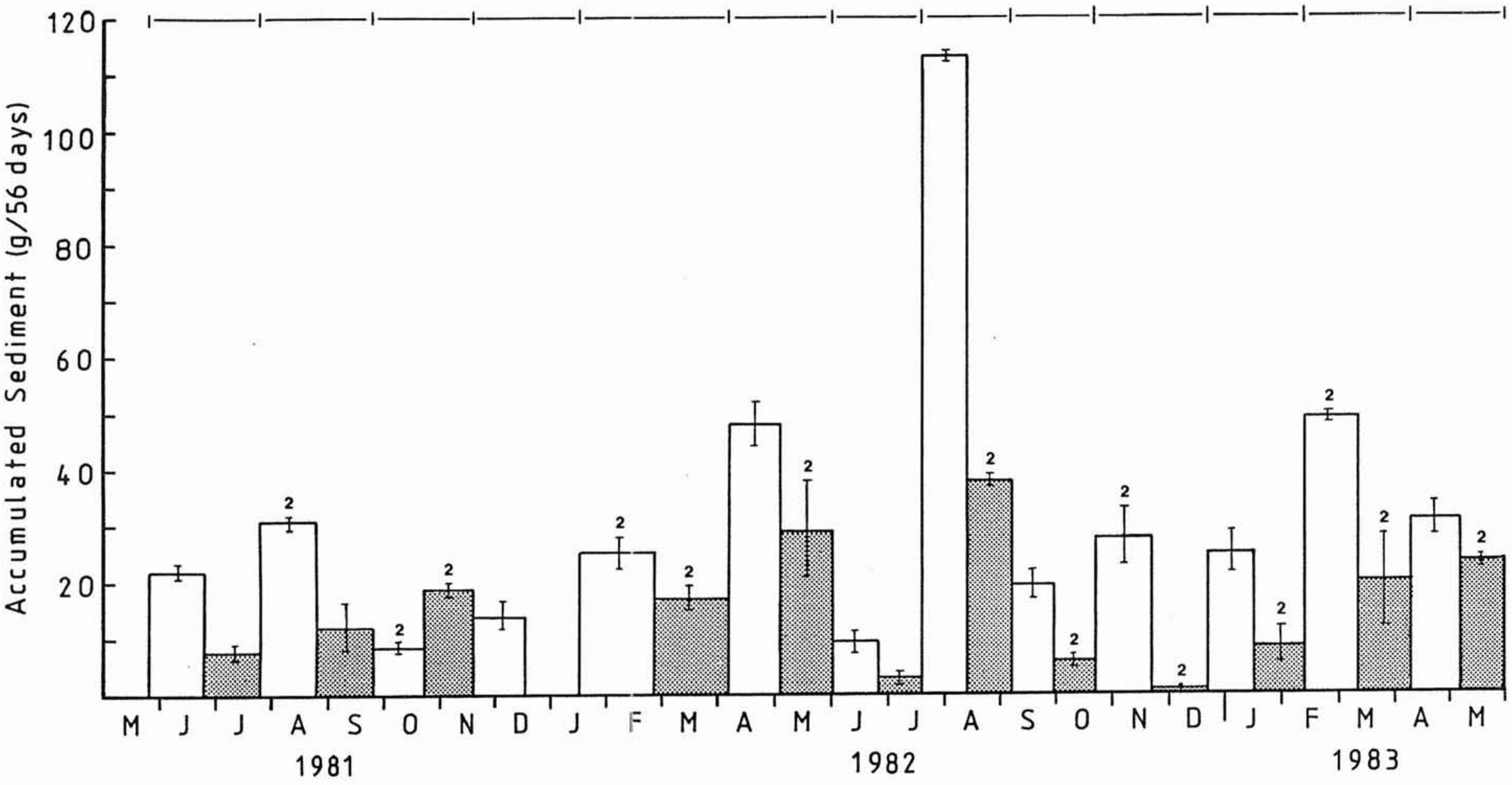
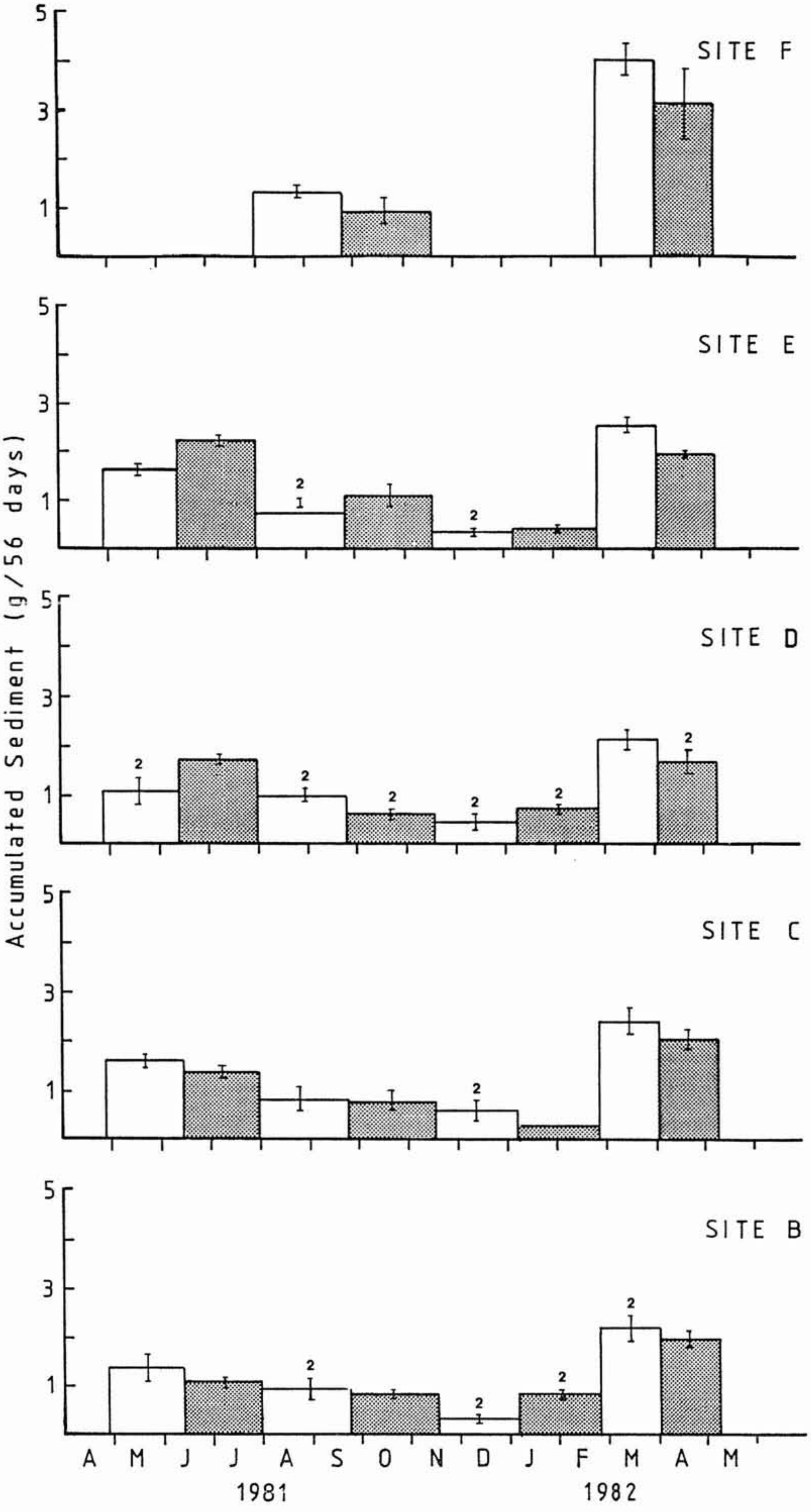

Accumulated Sediment (g/56 days)
120
100
80
60
40
20
M
J
J
A
S
O
N
D
J
F
M
A
M
J
J
A
S
O
N
D
J
F
M
A
M
1981
1982
1983
2

FIGURE 15

Rates of sediment accumulation at Eclipse Island.

Each histogram represents mean sediment accumulation (± S.E.) over a standardized 56 day sampling interval (mean duration of all intervals). Each pair of histograms spans the actual sampling interval. N=3 (or 2 where intervals are marked with an * (see text)).

unstipled: Shallow stations (3m), Sites B to F.
stipled: Deep stations (6m), Sites B to F.


Accumulated Sediment (g/56 days)
SITE F
SITE E
SITE D
SITE C
SITE B
5
3
1
2
A
M
J
J
A
S
O
N
D
J
F
M
A
M
1981
1982

Organic content: The amount of sediment collected in traps at the shallow Nelly Bay station was an order of magnitude greater than the amount collected in traps at Eclipse Island (comparisons based on standardized 56 day periods). The composition of the sediment also differed between the two reefs. The organic content of the sediments at Eclipse Island was double that of the Nelly Bay sediments (Table 1). However, carbonates comprised a much greater proportion of the sediment at Nelly bay than at Eclipse Island.

TABLE 1. Muffle furnace determination of the organic (100-550°C % loss) and carbonate (550-1000°C % loss) content of sediment subsamples (n=3).

Reef	Percent Ignition Loss 100-550°C	95% C.L.	Percent Ignition Loss 550-1000°C	95% C.L.
Nelly Bay	4.63	±0.38	34.67	±1.59
Eclipse Is.	10.17	±0.63	9.0	±1.27

2.5.5 Localized Water Turbulence

Nelly Bay: The mean weight losses of plaster spheres, during two exposure periods at site A in Nelly Bay, are presented in Table 2. During the first period, the spheres experienced 5-10kt southeasterlies and slight seas. During the second period seas were moderate to rough with 15-20kt southeasterlies. Although three plaster spheres were positioned at each station, in several cases (indicated by asterisks) weight loss of one of the three was substantially greater than the other two. Such values were discarded. As discussed by Doty (1971), it was assumed that the occasional deviant weight losses were the result of solid pieces flaking off the spheres.

TABLE 2. Mean weight losses and diffusion indices for plaster spheres exposed at Nelly Bay (Site A) during calm and rough periods. N=3 (where means marked with an *, N=2).

Wind Speed	Station	Mean Weight Loss	95% C.L.	Mean Diffusion Index
5-10kt	shallow	66.8	±0.531	5.5
	deep	52.0	±0.661	4.3
	controls	12.2*	±1.68	
15-20kt	shallow	85.7	±3.74	28.7
	deep	57.1*	±7.05	19.0
	controls	3.0*	±0.13	

Weight losses were greatest at the shallow station during both the relatively calm and rough periods. In order to compare weight loss between the two periods, a diffusion index (Doty, 1971) was calculated (mean weight loss per station divided by the mean weight loss of control spheres during the interval). This index shows the degree to which diffusion or dissolution in the vicinity of the spheres was enhanced over still water conditions. The diffusion indices given in Table 2 suggest that localized water turbulence was much greater during the period of 15-20kt winds. However, a 2 factor ANOVA (wind speed by depth on diffusion indices) showed that there was a significant interaction effect (F= 51.707 with 1 X 8 df, $p<.001$). Consequently, neither wind speed (F=28.38 with 1X1 df, $p>0.2$) nor depth (F=2.05 with 1X1 df, $p>0.5$) was significant over and above this interaction. Therefore, although weight loss increased at both depths as wind speed increased, weight loss was so much greater at the shallow site, it obscured any actual depth effects.

Plaster spheres recorded the direction of the prevalent water motion, as well as the comparative intensity. During the rough weather exposure period, spheres were more 'weathered' on two opposing sides of the sphere than elsewhere on their surface. Thus, the original spherical shape became flattened, with the long cross-sectional axis pointing in a southeast-northwest direction.

TABLE 3. Mean weight losses and diffusion indices for clod cards (exposed for 48 hours during northwesterlies) and plaster spheres (exposed for 72 hours during southeasterlies) at Eclipse Island. N=3 (where means marked with an *, N=2).

		SHALLOW STATION			DEEP STATION		
Wind Speed and Direction	Site	Mean Weight Loss (g)	95% C.L.	Mean Diffusion Index	Mean Weight Loss (g)	95% C.L.	Mean Diffusion Index
5-10 kt north-westerly	B	8.5*	±2.48	1.82	5.7	±0.29	1.21
	C	10.9	±1.28	2.34	6.9	±0.81	1.48
	E	11.0	±0.66	2.35	6.7	±0.73	1.44
	F	7.7*	±0.50	1.64	6.1*	±1.31	1.30
	G	8.6*	±2.66	1.83	5.7*	±0.66	1.22
	Control	-	-	-	4.7	±0.40	-
5-10 kt south-easterly	B	44.0	±0.43	1.61	34.7*	±6.46	1.27
	C	42.6*	±8.75	1.56	35.0*	±7.79	1.29
	D	44.8	±1.95	1.64	37.2*	±5.28	1.37
	E	52.1	±2.36	1.91	42.0	±3.08	1.54
	F	66.0	±5.46	2.42	56.8	±3.96	2.09
	Control	-	-	-	27.3	±1.33	-

The prevalent water motion over the 55 hour period was therefore in the same direction.

Eclipse Island: Weight loss results for plaster spheres exposed at Eclipse Island during the winter southeasterlies, and for clod cards exposed during the summer northwesterlies, are given in Table 3. Despite three attempts, plaster sphere results were not obtained during the northwesterly period. (Problems included fish grazing and a cyclone which completely eroded all spheres.)

As the results from the two experimental periods were not directly comparable, a 2 factor ANOVA (site by depth) was performed on weight loss separately for each of the two periods. In both cases site affected weight loss significantly (southeasterlies: F=139.3 with 4X20 df, $p<0.001$; northwesterlies: F=165.2 with 4X20 df, $p<0.001$). Depth also affected weight loss significantly (southeasterlies: F=146.1 with 1X4 df, $p<0.001$; northwesterlies: F=179.8 with 1X4 df, $p<0.001$). There were no significant interaction effects (southeasterlies: F=0.48 with 4X20 df, $p>0.5$; northwesterlies: F=0.88 with 4X20 df, $p>0.5$).

Weight loss was consistently greatest at the shallow site, indicating greater water movement at 3m than at 6m. However, the site of greatest water movement differed between the two periods. During the southeasterlies, site F experienced greatest turbulence at both depths, followed by site E. Sites B, C and D experienced very similar conditions as measured by the plaster spheres. In contrast, during the north/northwesterlies, sites C and E experienced greatest water movement, with sites B, G, and F experiencing lower but relatively similar water movement regimes.

2.6 Discussion

Documentation of the range (*i.e.* continuous or discontinuous) of morphological variation within a species provides a starting point for interpreting the basis of the variation. Growth form variation in *Pavona cactus* lacked the continuity of transitional forms found between the morphological extremes of *Turbinaria mesenterina*. In *T. mesenterina*, the change from highly folded, vertical laminae to horizontal plates proceeded through a clear progression of intermediate growth forms. In contrast, although there was a clear progression in growth form from the convoluted end of the morphological range of *P. cactus* through colonies having intermediate forms, the intermediate range did not merge with the columnar form. Variation included thin, bifacial, densely-packed fronds in the convoluted form and thick, multifacial, widely spaced branches in the columnar form. However, a gap occurred in the morphological continuum between the bifacial condition of the convoluted and intermediate forms and the multifacial condition of the columnar form.

The pattern of growth form distribution in relation to the physical environment, provides further information on factors affecting colony morphology. Growth form variation in *T. mesenterina* was clearly related to depth and virtually no overlap occurred between the convoluted and plate forms. In contrast, the morphological extremes of *P. cactus* overlapped in their depth distributions. Whereas, intermediate forms of *T. mesenterina* occupied depths transitional between the two extreme forms, intermediate forms of *P. cactus* co-occurred with both of the extreme forms. Moreover, intermediate colonies of *P. cactus* extended to habitats both shallower than convoluted colonies and deeper than columnar colonies of the species. Although the average depth of the convoluted form of *P. cactus* was shallower than that of the columnar form, the overlap in the ranges of the two extreme forms, and the lack of any depth constraints on the distribution of the intermediate forms, suggest that depth-related environmental factors do not play a major role in morphological variation in this species.

Comparisons of growth form distributions with reference to along-reef position, also highlight differences between the two species. All forms of *T. mesenterina* could be found on a single transect perpendicular to the reef edge, regardless of where the transect was positioned along the Nelly Bay fringing reef. However, the convoluted and columnar forms of *P. cactus* were confined to separate areas of the Eclipse Island reef. These areas differed in their orientation to the prevailing southeasterlies and in substrate slope. The intermediate forms of *P. cactus* could not be identified with any specific along-reef position transitional between the distributions of the other two forms, but could be found throughout all orientations and substrate slopes.

The above analyses of the continuity of growth form variation, and of reef slope distribution patterns, suggests that variation in *T. mesenterina* is correlated with an environmental factor, whereas variation in *P. cactus* occurs independently of measurable environmental gradients. Analyses of environmental parameters associated with the depth gradient at Nelly Bay, revealed that seawater temperature and salinity patterns differed only marginally between the deep and shallow stations. It is considered unlikely that such differences are functional in determining colony morphology in *T. mesenterina*. Predictably, light, sediment accumulation, and water turbulence all decreased significantly between the two stations.

Light has been implicated as the controlling factor in theoretical discussions of the flattening of hemispherical colonies of *Montastrea annularis* with depth (Goreau, 1959, 1963; Barnes, 1973; Graus and Macintryre, 1976), and in experimental studies involving *Porites astreoides* (Roos, 1967) and *M. annularis* (Graus and Macintyre, 1982). Light has been shown to enhance calcification (Goreau, 1959) through its stimulation of photosynthesis in the symbiotic zooxanthellae of corals (Vandermuelen *et al.*, 1972; Chalker, 1981; Barnes, 1982, 1985). Jaubert (1977) also suggested that light was the controlling factor in the change of *Synaraea convexa* from branching to platelike with depth. Studies of chlorophyll concentration from the associated zooxanthellae of *S. convexa* colonies at different depths (Jaubert, 1981), provided the evidence for this conclusion. While colonies of *S. convexa* were able to respond morphologically to decreased light levels, chlorophyll concentrations remained relatively constant over the depth interval. Increase in chlorophyll concentration, which is associated with increased light harvesting capability, was greatest over depth intervals where light attenuation was significant but morphological change minimal between the colonies tested. In particular, chlorophyll concentration increased rapidly with depth at the lower limit of the species' depth distribution once all possible morphological responses to low light levels had been exhausted.

Optimal morphological strategies for coping with extremes in water motion and sedimentation have been suggested from single factor studies of these environmental parameters. Laboratory investigations of the hydromechanics of coral skeletons (Chamberlain and Graus, 1975) indicate that large colonies with thick, widely spaced branches are adapted to high energy areas. Conversely tightly branched colonies are characteristic of low energy conditions, because they act as solid bodies above threshold current velocities, causing water flow to circumvent the colony rather than penetrate it. In general, to minimize stress from increasing hydrodynamic energy, morphological adaptations proceed from thin-branched forms to thick-branched forms, or alternatively, to small hemispherical and finally encrusting forms (Graus *et al.*, 1977). The low profiles and large attachment areas of the latter forms effectively minimize hydraulic stress. Branching corals may minimize hydraulic bending forces by decreasing the angle of branching and growing into the direction of the prevailing current (Graus *et. al*, 1977; Schuhmacher and Plewka, 1981). Optimal morphological strategies for sediment removal include branching and massive forms (Hubbard and Pocock, 1972). In the former instance sediment falls through openly branched networks, whereas in the latter case, sediment rolls off convex surfaces.

Although single factor studies are extremely useful in developing theories of growth form variation, in general, most recognize that morphological trends are complex responses controlled by a suite of physical and biological factors. Brakel (1983) has suggested that the depth-related morphological trends of massive species are more complex than previously thought. In growth form distribution surveys, he found that conditions of high turbulence, as well as low light, set an upper limit to colony height. Thus, both hemispherical and flattened forms of *Porites astreoides* could be found in high light, low wave energy situations, but only flattened colonies were found in high energy regimes, regardless of the light regime. Oliver *et al.* (1983) has also suggested that both light intensity and water motion are operational in controlling the depth-related decrease in the number and density of branches in *Acropora formosa*.

The flattening of laminae with depth in *T. mesenterina* could potentially be related to the concurrent decrease in light, water motion, and/or sedimentation at Nelly Bay. Although the results of growth form surveys alone, cannot conclusively distinguish between these alternatives, it is useful to evaluate the likely impact of each of these three parameters for purposes of defining further studies. High wave energy conditions are not found at Nelly Bay due to its sheltered, inshore position. Therefore the occurrence of tightly packed laminae of the convoluted form in shallow water is consistent with Chamberlain and Graus's (1975) predictions of tightly branched colonies in low energy conditions. Although water motion did decrease with depth, most hydrodynamic specializations in morphology involve adaptation to high energy regimes. It is unlikely that the truncated hydrodynamic gradient at Nelly Bay might alone be responsible for the striking morphological change observed over the 3m depth interval. Moreover, platelike forms of *Montipora* co-occurred with the convoluted form at the shallow station, suggesting that hydrodynamic energy did not exclude this form from these depths. Periodic major disturbances, particularly cyclones, may be more important in determining growth form distributions on a longer time scale. However, although Collins (1978) reported that many colonies of *Turbinaria* were overturned in Nelly Bay during cyclone Althea in 1971, damage was reasonably uniform throughout the depth range of this species (Collins, pers. comm). Therefore even major disturbances may not define two distinctive hydrodynamic regimes at Nelly Bay.

Growth forms of *T. mesenterina* do not appear to be adapted to maximize sediment shedding, which is surprising in a species which typically inhabits turbid water reefs, with extremely high rates of sediment accumulation. The growing margins of the platelike form are generally higher than the centre of the colony, so that sediment may be trapped in the central depression. Similarly, sediment tends to be trapped in the crevices between the upright laminae of the convoluted form. The convoluted form appears to cope with this problem by sacrificing the lower portions of the colony, though this could equally be due to decreased water motion or light penetration. Kelly (1982) reported that in laboratory experiments, small, cuplike colonies of *T. mesenterina* had a relatively poor capacity to remove the mud fraction, which was found to comprise 71% of the sediment load at 1.4m in Geoffrey Bay. Although field observations confirm that small amounts of sediment occasionally accumulate in the central hollow of plate colonies, this form flourished despite the high rates of sedimentation at Nelly Bay. It is possible that this form relies on water movement to supplement behavioural sediment rejection. It may also be speculated that in the relatively higher sedimentation regime of the shallow station, the hemispherical outline of large, convoluted colonies enhances the passive rolling of sediment over the colony surface, and that valleys between the upright laminae direct the falling sediment. Similarly, the downward directed folds of smaller colonies may provide channels for passive and active rejection processes. Thus, neither morphological strategy appears to be as effective as branching or hemispherical forms in high sedimentation regimes, but both forms may have compromised their ability to shed sediment in response to a more dominating factor.

Depth-related decrease in light intensity created the most marked environmental gradient at Nelly Bay. Porter (1976) described highly foliaceous corals as having one of the most efficent forms at intercepting light, as not all light energy can be effectively captured in one plane when light intensity is high, due to saturation of the photosynthetic apparatus. Conversely, in low light levels, plating forms were described as optimally suited for light interception. These predictions agree well with the observed variation in growth form with depth in *T. mesenterina*. Moreover, observations of plate-like colonies in shallow, shaded habitats provide corroborative evidence that light is more controlling than water motion in this species. However, colony morphology represents a net response of the coral to its environment. Although circumstantial evidence suggests that light is of primary importance, it is more than likely that morphological responses are highly complex, and that all three factors have placed constraints on growth form expression.

Empirical observations suggest that growth form variation in *Pavona cactus* is not depth-related. However, convoluted and columnar forms occurred in separate along-reef sites. Of the environmental parameters monitored, water movement and sedimentation were the only factors which would be likely to vary between these sites at Eclipse Island. However, neither of these factors showed site-dependent patterns. Sediment accumulation was consistently equal at all sites where the two growth forms were found. Patterns in water movement were inconsistent among sites, and depended on wind direction. Thus site C, a columnar site, was closest in water movement to site B (the second columnar site) during southeasterlies, but was closer to site D (a convoluted site) during north/northwesterlies. Significantly, the greatest differences were found between sites where the same growth form occurred. The lack of any consistent environmental pattern detected in relation to the site-dependent distribution of growth forms of *P. cactus*, suggests that these environmental parameters are not major controlling factors in growth form distribution within this species. It is possible that microhabitat differences in substrate slope, or some other unmeasured parameter, may influence growth form distributions. Microhabitat differences in soil type have been found to influence distributions over scales measured in centimeters in plants (Antonovics *et al.*, 1971). However, it is equally possible that distributions may simply reflect historical differences in settlement and/or mortality patterns.

Although correlations between growth form variation and environmental gradients are a useful starting point for exploring factors which might control growth form variation, they do not prove that such gradients induce variation. The basis of the manifested variability may involve one of several mechanisms. These alternatives are examined in the next chapter.