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CHAPTER 5. GROWTH STRATEGIES LEADING TO MORPHOLOGICAL VARIATION

5.1 Introduction

Studies of coral growth and calcification have been a major focus in coral reef research. Past studies have been concerned primarily with: determining growth rates for individual species (reviewed in Buddemeier and Kinzie, 1976; Bak, 1976; Gladfelter *et al.*, 1978; Hubbard and Scaturo, 1985; Gomez *et al.*, 1985 and many others); the importance of light in enhancing calcification (Goreau, 1959; Vandermeulen *et al.*, 1972; Chalker and Taylor, 1975; Rinkevich and Loya, 1984; Barnes, 1985); environmental factors affecting growth rates (reviewed in Buddemeier and Kinzie, 1976; Glynn, 1977; Jokiel and Coles, 1977; Jokiel, 1978; Coles and Jokiel, 1978; Jokiel, 1980; Dodge and Lang, 1983; Wellington and Glynn, 1983; Kendall *et al.*, 1985 and others) and more recently, the seasonality of growth within populations (*eg.* Oliver *et al.*, 1983; Wellington and Glynn, 1983; Gladfelter, 1984; Loya, 1985). There have been relatively fewer studies dealing with the relationship between growth and colony morphology in corals, and these have concentrated on massive (Goreau, 1963; Roos, 1967; Barnes, 1973; Macintyre and Smith, 1974; Graus and Macintyre, 1982; Foster, 1983) and branching (Oliver *et al.*, 1983, Oliver, 1984) species.

In Chapter 3, variation in morphology of transplanted colonies of the foliaceous corals, *Turbinaria mesenterina* and *Pavona cactus*, was analysed. Significant differences were found in convolution indices between morphs of *T. mesenterina*, and in frond spacing between morphs of *P. cactus*. In order to determine how these differences in colony morphology originated, growth of different components of the colony was examined. There are two major growth processes that determine the shape of fronds in *P. cactus*: linear extension (*i.e.* the budding of new corallites along the growing margins of the frond), and increase in thickness (*i.e.* the deposition of calcium carbonate on existing corallite structures at right angles to the plane of linear extension). The shape of laminae in colonies of *T. mesenterina* is determined primarily by factors relating to the process of linear extension. A third aspect of the growth process in corals involves increase in density through internal calcifi- cation (Oliver *et al.*, 1983). This process contributes primarily to the structural integrity of the colony, and only indirectly to the morphology of the colony, and has not been fully addressed in the present study. Analyses of changes in growth form with size provide another means of exploring the relationship between colony growth and morphology.

The major objective of the present study was to analyse growth strategies in highly variable foliaceous corals to isolate factors contributing to morpholgical variation. For each of the corals, *Turbinaria mesenterina* and *Pavona cactus*, growth parameters such as linear extension rates, angle of corallite addition, and thickness of corallite structures, were quantified. Comparisons were then made between morphs to determine which factors contributed most to the observed differences in form. Changes in these parameters with increase in colony size were analysed for specimens of *T. mesenterina*. Most small colonies of *P. cactus* are asexual in origin (Chapters 2 and 4), so studies of growth in small colonies would not provide further information on growth processes affecting morphological variation in this species. In discussions of growth in *P. cactus*, two stages in the calcification process are distinguished. Primary calcification will refer to the creation of new corallites along the margins of fronds (either along their tips or lateral edges), and is thus equivalent to the process of linear extension. Secondary calcification will refer to the deposition of calcium carbonate on pre-existing corallite structures: in other words, the process of infilling (*sensu* Gladfelter, 1983), and also the process whereby frond thickness is increased (equivalent to radial growth, *sensu* Oliver *et al.*, 1983).

Skeletal extension rates may vary independently of total calcium carbonate accretion either daily (Barnes and Crossland, 1980; Gladfelter, 1983), or seasonally (Gladfelter, 1984). Nevertheless, this parameter was chosen as a measure of colony growth because it relates directly to the shape of colonies in these two species, and because it may be equated with the acquisition of space, an ecologically important aspect of growth. Studies of coral growth have shown that the rate of linear extension within a species may decrease with depth (Buddemeier *et al.*, 1974; Dustan, 1975; Bak, 1976; Highsmith, 1979; Hubbard and Scaturo, 1985; Huston, 1985), increase with depth (Bak, 1976; Neudecker, 1977; Wellington, 1982; Oliver *et al.*, 1983), or be independent of depth (1985). Linear extension rates of *Turbinaria mesenterina* and *Pavona cactus* were measured to determine firstly, whether overall rates of extension differed between deep and shallow colonies in a manner which might give rise to morphological differences. For example, one possibility suggested by the greater thickness of columnar fronds of *P. cactus* in comparison to convoluted fronds, is that linear extension along frond edges is slower, but radial increase is greater in this form. Secondly, rates of linear extension were measured to determine whether variation in seasonal patterns of growth existed between morphs. Thirdly, linear extension rates were determined to provide the basis for interpreting demographic data, such as the age at which colonies reach reproductive maturity (see Chapter 6). Finally, as most growth studies have involved either branching or massive species of corals, a further objective was to provide basic growth rate data for foliaceous species, which comprise a significant proportion of coral reef communities.

5.2 Materials and Methods

5.2.1 Alizarin Red S Staining Technique

Alizarin Red S was first introduced as a technique for determining linear extension rates by Barnes (1972), and its toxicity has since been investigated by Dodge *et al.* (1984). The latter study concluded that the stain might affect short term determinations of growth rates because it temporarily inhibits growth, but that the lag was neglible when growth periods were measured in weeks. The stain is incorporated into the skeleton of corals during growth (Lamberts, 1978), and thus may be used to produce a visible line at a known time. Skeletal extension subsequent to the incorporation of the stain is then measured from this line. In the present study, colonies were stained *in situ* by releasing a concentrated vial of alizarin solution inside large plastic bags enclosing each colony. Colonies were exposed to concentrations of approximately 10 ppm for 4 to 6 hours, and collected 4 to 8 weeks later for measurement.

5.2.2 Sampling Programme: *Turbinaria mesenterina*

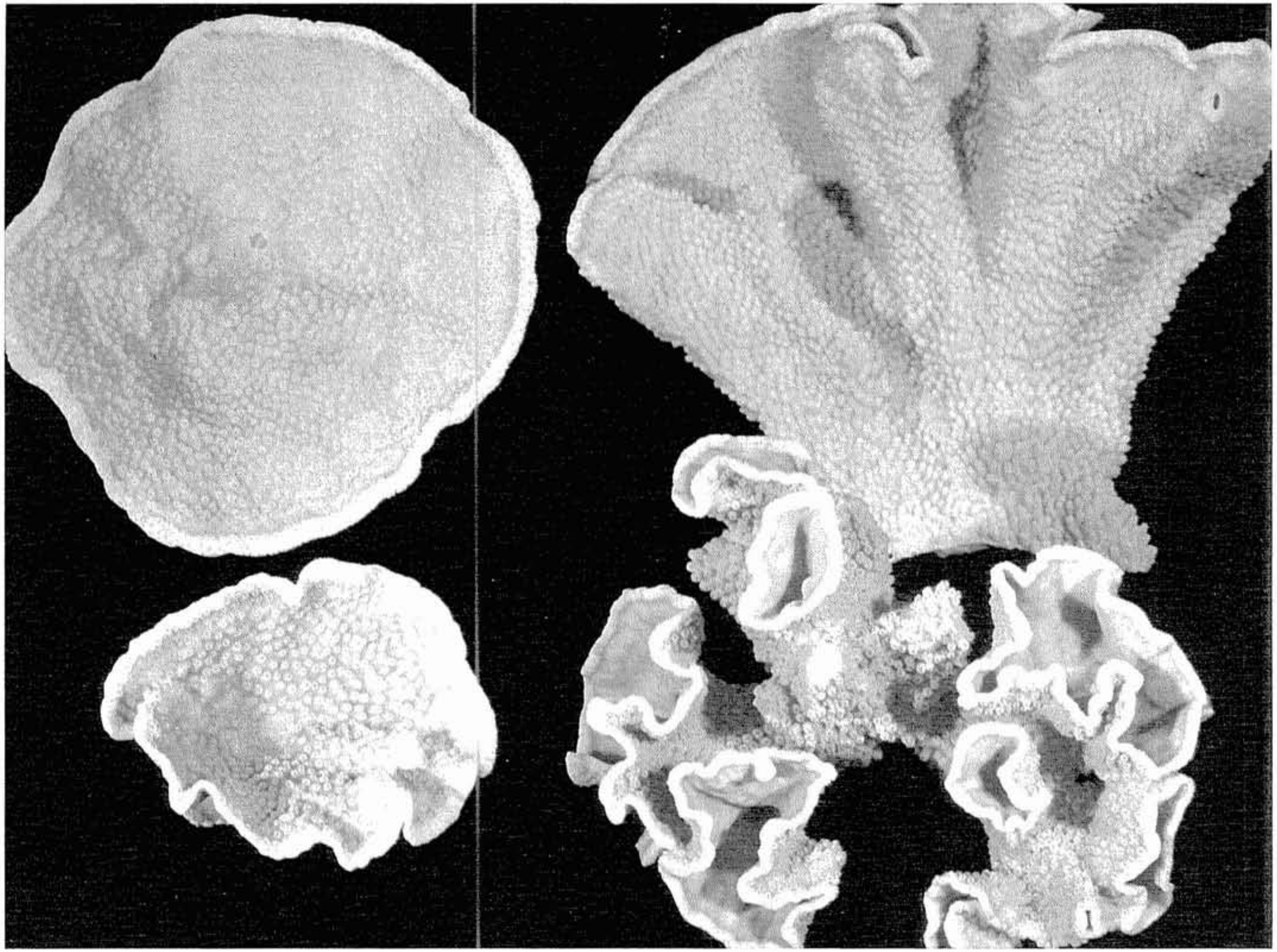
Between May 1981 and May 1983, colonies of both the plate and convoluted morphs of *Turbinaria mesenterina* were sampled at regular intervals. Every 6 to 8 weeks, portions of 5 adult colonies (>100 cm diameter) and 10 reproductively immature colonies (<20 cm diameter, Chapter 6) were stained with alizarin at both the shallow and deep stations (Figure 10, Chapter 2). At the same time, those stained on the previous trip were collected. Figure 25 shows typical specimens of mature and immature colonies, collected 2 months after staining. Adult colonies were large enough (1.5-2.0m diameter) to sustain repeated sampling (approximately 15cm^2 stained for each collection) and the same 5 convoluted and 5 plate colonies were used

FIGURE 25

Representative skeletons from immature and adult size classes of *Turbinaria mesenterina*, stained with Alizarin Red S.

Colonies were collected from Nelly Bay, Magnetic Island, 1.5 months after they had been stained with Alizarin Red S. Growth during the period is represented by the white skeleton extending beyond the central stained skeleton. Viewing the page sideways:

Top left photograph (A):	Deep, immature colony from the 10-20cm size class (4m).
Top right photograph (B):	Adult colony of the plate morph (4m).
Bottom left photo (C):	Shallow, immature colony from the 5-10cm size class (1m).
Bottom right photo (D):	Adult colony of the convoluted morph (1m)



throughout the programme. They represented a random sample of the adult population at each depth. The immature colonies were selected haphazardly on each trip (the whole colony was collected each time), but were located within 10m of both the deep and shallow stations. The immature colonies included 5 corals from two size classes (5-10cm and 10-20cm in diameter) at each depth. Thus, extension rates could be calculated for different size classes for age determinations. The diameters of immature colonies were measured along the contours of the colony and calculated as the mean of 2 diameters at right angles to each other. All colonies were bleached in dilute calcium hypochlorite solution to reveal the stain line.

5.2.3 Growth Analyses: *Turbinaria mesenterina*

Linear Extension: Rates of linear extension were measured using a dissecting microscope with an ocular micrometer. Linear growth was measured to the nearest 0.1mm at thirty points evenly spaced around the periphery of adult colonies. The points were located by progressively subdividing the edge length into halves for plate colonies, and by use of a grid with 5 by 6 adjustable rows (measuring points located at grid intersections) for convoluted colonies. New polyps bud primarily along the edges of the colony, thus increasing the diameter of the colony (plate morph) or the height of laminae (convoluted morph). Therefore, linear extension was measured along the contours of the colony, perpendicular to the stain line at each point. The precise axis of growth was determined by positioning the cross in an ocular micrometer over each point, so that the x-axis of the cross defined the tangent to the stain line and the y-axis defined the growth axis. The same procedure was used to measure linear extension in immature colonies. However, because colonies were much smaller, growth was measured at only 12 points evenly spread around the edge of each colony. Linear extension rates for each interval were standardized to a 60 day growth period, as the average sampling interval was closer to 2 months than 1 month. Growth rates were then compared between morphs, size classes and months using analysis of variance (MANOVA routine of SPSS: Hull and Nie, 1981). Expected mean squares and F-ratios were calculated as per methods outlined in Winer (1962). Annual linear extension rates and their 95% confidence limits were calculated from the sum of the non-standardized means and variances of all growth intervals for 2 one-year periods.

Angle of Growth: The mean angle of growth was determined for 64 immature colonies (12 measurements per colony) using the methods described in Chapter 3 (section 3.2.2). Colonies measured were a subset of immature colonies used in studies of linear extension, and consisted of 16 colonies from each of 2 size classes (5-10cm and 10-20cm diameter) and 2 depths (1m and 4m). The subset included four colonies randomly selected from each 'sizeclass-depth' category for each of 4 growth intervals spanning the second year of the study. Mann Whitney tests were used to compare angles of growth between deep and shallow immature colonies within each size class. A non-parametric test was used because angular data do not conform to assumptions of normality required for parametric tests based on linear distributions. Growth angles of immature colonies were compared to the final growth angles of adult colonies calculated for each control group of transplants (N=9) in Chapter 3 (Section 3.3.2).

Convolution Index: A convolution index was determined for each of the 64 immature colonies used in angle of growth determinations. Convolution indices were calculated as the ratio of the measured circumference to the predicted circumference as per methods outlined in Chapter 3 (Section 3.2.2). A Mann Whitney test was used to compare convolution indices between deep and shallow colonies within each size class. A non-parametric test was used because the data consisted of ratios, which have non-normal distributions. Convolution indices of immature colonies were compared to the initial index calculated for all plate colonies (n=18) involved in the reciprocal transplant study (Chapter 3, Section 3.3.2).

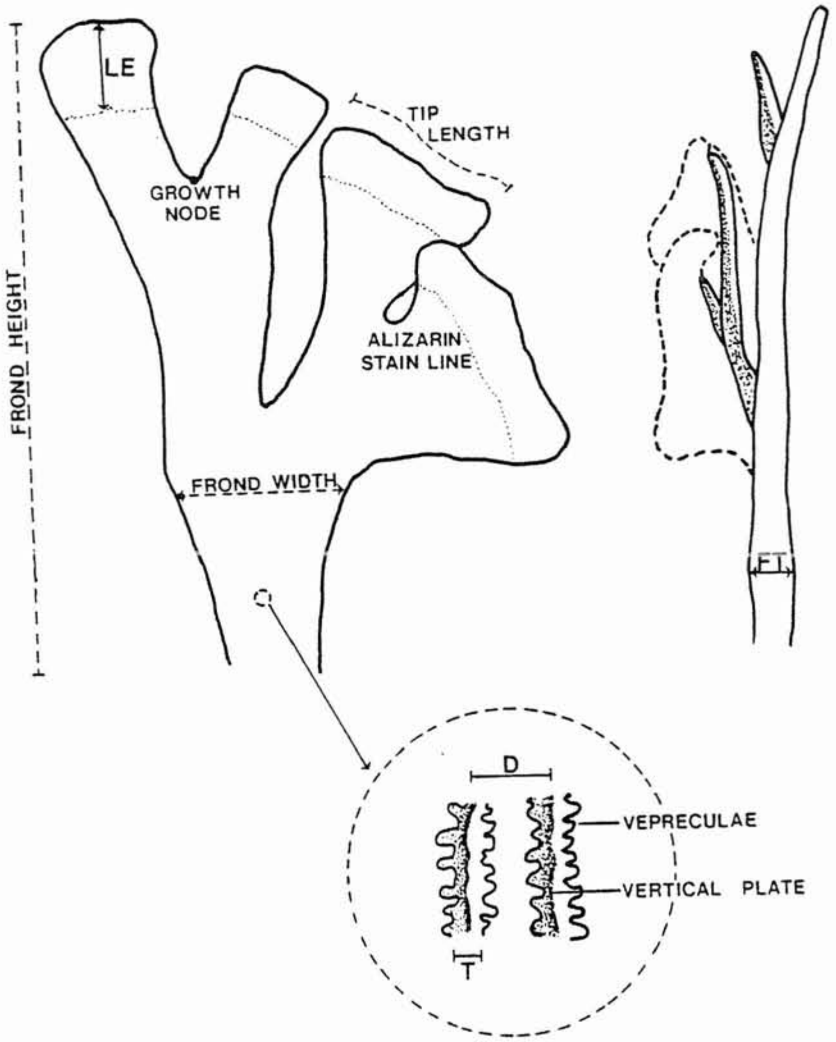
5.2.4 Sampling Programme: *Pavona cactus*

Convoluted and columnar colonies of *Pavona cactus* were sampled at regular intervals between September 1979 and March 1981. Three colonies of each growth form were stained every 4 to 8 weeks, and those stained on the previous trip were collected. Columnar colonies were located within 10m of the deep station at site D or E, and convoluted colonies were located within 15m of the shallow station at site B or C. Following collection, colonies were bleached in dilute calcium hypochlorite solution.

5.2.5 Growth Analysis: *Pavona cactus*

Linear Extension: Rates of linear extension were measured using a dissecting microscope with an ocular micrometer. Linear extension was measured to the nearest 0.1mm at 10 points evenly spaced along the growing margins of fronds. The number of fronds on each specimen ranged between 3 and 10, so measuring points were located by visually dividing the total frond length per specimen into 10 equal intervals. In regions of active growth, septo-costae are laid down parallel to the direction of growth, and thus were used to define the axis of growth for linear extension measurements (Figure 26). Both lateral and vertical growth occurs near the tips of fronds. However, lateral growth was irregular and difficult to define. Therefore, measuring points were located at least 5mm from the lateral margins of fronds, and measurements represented growth in the vertical direction. Linear extension rates for each interval were standardized to a 30 day growth period. Growth rates were compared between morphs and months using analysis of variance (MANOVA routine of SPSS: Hull and Nie, 1981). Annual linear extension rates and their 95% confidence limits were calculated from the sum of the non-standardized means and variances of all growth intervals between January 1st 1980 and January 1st 1981.

FIGURE 26. Morphometric measurements of *Pavona cactus*. A frond, with an inset showing portions of 2 septo-costae, and a 'lateral' view at right angles are figured. LE: Linear Extension; FT: Frond Thickness; D: Distance between septo-costae; T: Thickness of septo-costae.



Morphometrics: In order to ascertain how growth differed between the convoluted and columnar forms of *P. cactus*, frond thickness (FT), septo-costae thickness (T), and septo-costae spacing (D) were measured for each morph (Figure 26). Figure 6 (Chapter 2) shows further details of corallite structure in this species. Measurements of each growth parameter were made at distances of 0.75cm and 4.0cm from the tip of all fronds. In addition, measurements were made at 8cm, 12cm and 16cm from the tip of columnar branches. At distances greater than 4cm, convoluted fronds do not support living tissue, because of the dense, closely packed nature of fronds within the colony. Measurements were not made on areas where growth had ceased. Thus, the most distant measurements on convoluted fronds were made at 4.0cm from their tips.

The majority of new polyps are budded along the distal edges and lateral margins of fronds. Thus individual fronds extend predominantly in one plane. However, fronds do increase in thickness (growth perpendicular to the plane of linear extension, Figure 26), especially those of the columnar morph. Thickness was recorded to the nearest 0.1mm, and measured in the centre of fronds at 4cm intervals down their length, using calipers. Measurements were made on 30 fronds, randomly selected from those collected for linear extension studies, for each morph.

Corallite structures were compared between the two morphs to determine if the sites of secondary calcification differed. Septo-costae form the major structures of corallite architecture in *P. cactus*, and their thickness and spacing down the length of fronds provides an indication of growth subsequent to the process of linear extension. A septo-costa consists of a thin, vertical plate running between two adjacent calices, and bead-like granulations (vepreculae), which cover the lateral surfaces of the plate. Septo-costae thickness (T) is considered here to be the width of the vertical plate excluding the vepreculae (Figure 26), and is therefore an indicator of the degree of infilling between vepreculae that has occurred since the vertical plate was laid down. It was measured to the nearest 0.1mm using an ocular micrometer. The thickness of five contiguous septo-costae were measured at each distance, on 10 fronds from each morph.

Septo-costae spacing (D) was determined by measuring the distance between 5 adjacent septo-costae (Figure 26) and dividing by 4. Distances were measured from the tip of the first to the tip of the fifth vertical plate using an ocular micrometer, and recorded to the nearest 0.1mm. Five determinations were made at each tip distance for 30 fronds of each morph.

5.2 Results

5.3.1 Growth Analyses: *Turbinaria mesenterina*

Linear Extension Rates (Adult Colonies): Mean linear extension rates for adult colonies of the plate and convoluted morphs of *T. mesenterina* are shown in Figure 27. A three-factor partially hierarchal analysis of variance (Table 21) tested for differences in rates of extension between months (10 levels), depths (2 levels), and colonies (5 levels). The factors 'months' and 'depth' were fixed and orthogonal. The factor 'colony' was random and nested within depth, though crossed with months. 'Morph' is synonymous with the depth factor, as the convoluted morph occurs only at the shallow station and the plate morph only at the deep station (Chapter 2). Because differences in growth form cannot be distinguished in the immature size classes collected from the two depths (Chapter 2), and the objective of the analysis was to compare growth rates between morphs, the two terms, 'depth' and 'morph', will be retained and used interchangeably. Although the variances of the data were heterogeneous for both the untransformed linear extensions (Cochran's C(29,100)=0.035, P<0.001) and for logarithmic and square root transformations (P<0.001 in both cases), all F ratios were either highly significant or highly non-significant (Table 21). Analysis of variance is robust to departures from homogeneity of variances (Winer, 1962; Underwood, 1981; Zar, 1984), and as none of the F ratio tests were close to the selected level of significance (0.05), it was considered that the conclusions were not spurious.

Linear extension rates differed significantly between months and between colonies. The interaction between these two factors was also significant, indicating that individual colonies sampled throughout the 2 year period did not grow consistently faster or slower than other colonies sampled. Figure 27 shows that the significant difference in linear extension between months may be interpreted as seasonality in growth rates. High growth rates

FIGURE 27

Mean linear extension rates for the convoluted and plate morphs of *Turbinaria mesenterina*, Magnetic Island.

Colonies were collected from Nelly Bay, Magnetic Island, approximately two months after having been stained with Alizarin Red S. Shown are the means ± their 95% confidence intervals. The growth interval for each mean is indicated above the X-axis. N=150 for each sample.

●—● Mean linear extension of the convoluted morph.
O---O Mean linear extension of the plate morph.

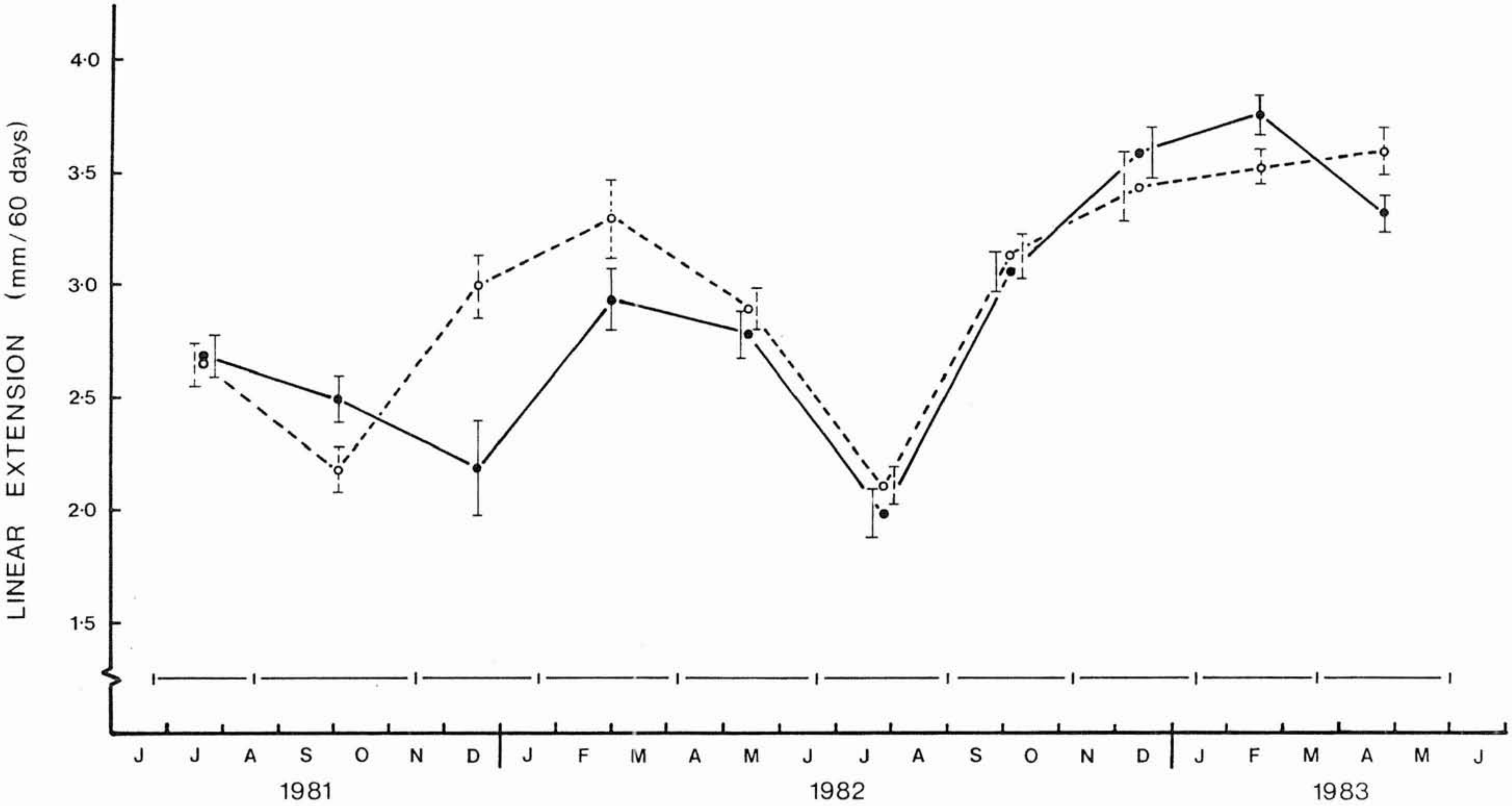

LINEAR EXTENSION (mm / 60 days)
4·0
3·5
3·0
2·5
2·0
1·5
J
J
A
S
O
N
D
J
F
M
A
M
J
J
A
S
O
N
D
J
F
M
A
M
J
1981
1982
1983

TABLE 21. Three-factor, partially hierarchal analysis of variance of linear extension rates for adult colonies of *Turbinaria mesenterina*. Stained colonies were collected at intervals of approximately 2 months, between June 1981 and June 1983 from Nelly Bay, Magnetic Island.

Source of Variation	DF	Mean Square	F	Sign. of F
Within cells	2899	0.2938		
Months+	9	82 4673	11.104	<0.001•
Depth++	1	6.7267	0.357	0.57
Colony w Depth	8	18.7581	63.848	<0.001•
Months by Depth+	9	7.5901	1.022	0.43
Months by Colony w Depth	72	7.4272	25.280	<0.001•

\+ Tested against mean square of 'Months by Colony w Depth'
++ Tested against mean square of 'Colony w Depth'
• Significant F ratio
w 'Nested within'

occurred during the summer months from January to March in both years at both depths, and low growth rates in the July-August period in 1982.

Linear extension rates did not differ significantly between the two depths, indicating that growth rates (based on this measure) did not differ between the convoluted and plate morphs of *T. mesenterina*. Although the interaction term, 'month by depth' was also not significant, Figure 27 shows that a substantial difference in extension rates occurred between the two depths in the summer of 1981/82 (15 November to 21 January interval). Shallow colonies had their lowest growth rates for the year during this period, while deep colonies were approaching their highest growth rates. This low growth rate in summer is anomalous when compared to seasonal trends for the second year at the shallow station, and for both years at the deep station. Observations of bleaching in other species during this same period may be significant in explaining the low, shallow, growth rates. Extensive bleaching was first observed for other species of corals at Nelly Bay on 15 January 1982. Bleaching was not observed on 24 November 1981, and must have been initiated at some time between these two field trips. Those most affected included foliose species of *Montipora*, staghorn and digitate species of *Acropora*, and *Pocillopora* sp. Although no colonies of *T. mesenterina* appeared bleached, the extent of bleaching in other species suggests that conditions may have been sub-optimal for growth.

Linear Extension Rates (Immature Colonies): Figure 28 presents linear extension rates for the two immature size classes at the shallow station (Figure 28A) and at the deep station (Figure 28B). Extension rates of adult colonies from Figure 27 are also included to aid comparisons between size classes. Strong seasonality in extension rates is evident for the two immature size classes. Growth minima occurred during winter (June to August interval) in 1982. Maxima occurred during the November to January interval in each year, at both depths and for both size classes. A 4-factor analysis of variance of linear extension rates (Table 22) showed that the differences in growth rates between months were highly significant.

Table 22. Four-factor, partially hierarchal analysis of variance of linear extension rates for immature colonies of *Turbinaria mesenterina*. Stained colonies were collected at intervals of approximately 2 months between August 1981 and June 1983 from Nelly Bay, Magnetic Island.

Source of Variation	DF	Mean Square	F	Sign. of F
Within cells	1584	0.4293		
Main Effects:				
Months^{+}	8	92.2819	30.78	<0.001*
Depth^{+}	1	269.3206	89.82	<0.001*
Size^{+}	1	61.7102	20.58	<0.001*
Colony w (Size, Depth and Months)	108	2.9986	6.98	<0.001*
First Order Interactions:				
Months by Depth^{+}	8	11.3250	3.78	0.001*
Months by Size^{+}	8	2.2592	0.75	0.64
Depth by Size^{+}	1	2.8586	0.95	0.33
Second Order Interactions:				
Months by Depth by Size^{+}	8	1.7582	0.59	0.79

$^{+}$ Tested against mean square of 'Colony w (Size, Depth and Month)

* Significant

w 'Nested within'

FIGURE 28

Mean linear extension rates of immature and adult size classes of *Turbinaria mesenterina*, Magnetic Island.

Colonies were collected from Nelly Bay, Magnetic Island, approximately 2 months after they had been stained with Alizarin Red S. Shown are the means ± their 95% confidence intervals for each growth interval. Growth intervals are indicated above the X-axis. N=60 for each sample of the immature size classes. Mean linear extension rates of the adult size class from Figure 27 (without their confidence intervals), have been included for size class comparisons.

Top Graph (A): Linear extension rates at the shallow station (1m):
●—● 5-10cm size class;
0---0 10-20cm size class;
◆—◆ >100cm size class.

Bottom Graph (B): Linear extension rates at the deep station (4m):
●—● 5-10cm size class;
0---0 10-20cm size class;
◆—◆ >100cm size class.

In the analysis of variance (Table 22), the factors 'months', 'depth', and 'size' were fixed and orthogonal. 'Colony' was random and nested within all levels of the other three factors. Variances of the untransformed data were heterogeneous (Cochran's C(11,144)= 0.031, P<.001), but for the same reasons as those outlined above for mature growth rates, the general conclusions were considered to be valid.

All of the main effects were highly significant. In contrast, only one of the higher interaction effects was significant. Therefore, although there were significant differences in extension rates between colonies, there were still significant differences between months, depths and size classes over and above inter-colony differences. Figure 28 shows that linear extension rates of the 10-20cm size class were greater than those of the 5-10cm size class. Also, in all cases within the immature size classes, linear extension rates were greater for deep water corals than for shallow water corals. The significance of the interaction term, 'Months by Depth', reflects the more rapid decrease in growth rates of colonies in both size classes at the shallow station in the February-March period of 1982. This period coincided with records of bleaching in other species.

When data for the adult colonies are included, the two major trends in the immature growth rate data are obscured. Linear extension rates did not continue to increase with the increased size of adult colonies. Secondly, as described above, the trend of increased growth with depth found for immature colonies was not found in the adult size class.

Although growth rates of immature colonies at the shallow station were lower than those at the deep station during the summer of 1981/82, they were not as depressed as those of shallow water, adult colonies during this period. Observations of seasonal changes in the abundance and height of the macroalgae, *Sargassum*, may be relevant for understanding differences in growth depression between the size classes at the shallow station. Young plants of *Sargassum* become visible in August, reach their peak in February, and are reduced to holdfasts by May. During peak growth they reach heights of 1-2m, dominating the upper reef slope at Nelly Bay during the summer months and shading smaller colonies. The adult colonies of *T. mesenterina* sampled during the study were all greater than 1m in height, and thus too large to have been effectively shaded by *Sargassum*.

Annual Linear Extension Rates: Annual linear extension rates for each size class at each depth are summarized in Table 23. Rates were determined for both years of the study and averaged to give a mean annual linear extension rate for each 'size class-depth' category. The lowest growth rates were recorded in year 1 (1981-82) for all of the shallow size classes. Year 1 included the bleaching period observed in the summer of 1981-82. In contrast, the highest growth rates were recorded in year 1 for deep, immature colonies.

Table 23. Mean annual linear extension rates (mm/year) at two depths for three size classes of *Turbinaria mesenterina*. Data are means ± 95% confidence limits. N=60 for each sample of the immature size classes (5-10, 10-20cm in diameter). N=150 for each sample of the adult size class.

SIZE CLASS (cm)	SHALLOW (1M)			DEEP (4M)		
	Year 1	Year 2	Grand Mean	Year 1	Year 2	Grand Mean
5-10*	12.6 ±0.43	13.8 ±0.40	13.2	17.8 ±0.46	16.8 ±1.53	17.3
10-20*	13.6 ±0.41	16.0 ±0.49	14.8	20.2 ±1.53	18.7 ±1.56	19.4
>100+	16.0 ±0.29	18.8 ±0.24	17.4	16.9 ±0.29	19.0 ±0.26	18.0

* Year 1: 28/8/81 to 28/8/82
Year 2: 29/5/82 to 29/5/83

\+ Year 1: 25/6/81 to 25/6/82
Year 2: 29/5/82 to 29/5/83

Angle of Growth: Within each size class, a one-tailed Mann Whitney test was used to test the null hypothesis that the mean growth angle of shallow water corals was less than or equal to the mean growth angle of deep water corals (Table 24). A one-tailed test was used because adult convoluted (*i.e.* shallow) colonies were found to have significantly steeper growth angles than adult plate (*i.e.* deep) colonies in Chapter 3 (Section 3.3.2).

Table 24. Comparison of mean growth angles (°) between depths for three size classes of *Turbinaria mesenterina* (Nelly Bay, Magnetic Island). Data are means ± SE. N=192 for each sample of the immature size classes (5-10cm and 10-20cm in diameter). N=180 for each sample of the adult size class.

SIZE CLASS	SHALLOW (1M)		DEEP (4M)		MANN WHITNEY U' STATISTIC	
5-10cm	37.5	±2.04	37.4	±1.34	146^{+}	$P>0.1$
10-20cm	37.7	±1.27	35.6	±1.42	177^{+}	$0.025<P<0.05^{*}$
>100cm	69.4	±1.19	23.7	±3.95	81^{++}	$P<0.001^{**}$

$^{+}$ $U_{.05(1),16,16} = 173$

$^{++}$ $U_{.05(1),7,7} = 60$

* Significant

** Highly significant

The Mann Whitney tests indicated that growth angles were the same at the deep and shallow stations for very small colonies of *T. mesenterina*. However, as they approached 20cm in diameter, the growth angles of deep colonies became less steep and were significantly different from those at the shallow station in this size class. For colonies greater than 1m in diameter, differences in growth angles at the two depths were highly significant. These differences result from changes in the angle of growth between immature and adult colonies. Shallow water colonies increase their angle of growth with size, whereas deep water colonies decrease their angle of growth with size.

Convolution Index: One-tailed Mann Whitney tests were also used to determine whether changes in convolution indices with size, paralleled trends outlined above for changes in growth angle with size. Table 25 shows that the indices of small colonies of *Turbinaria mesenterina* were the same at the two depths. However, by the time shallow water colonies were 10-20cm in diameter, they had significantly greater convolution indices than deep colonies. Mean convolution indices were much the same for all three size classes at the deep station, indicating that both small and large plate colonies maintained the same ratio of measured to predicted circumferences. Indices could not be calculated for shallow, adult colonies using the same method, because the complexity of the convolutions in the larger size class obscured the original cone shape (Chapter 3, Section 3.2.2). Therefore, the mean convolution index, which increased with size in the shallow, immature size classes, undoubtedly increased further in the adult size class.

Table 25. Comparison of mean convolution indices between depths for three size classes of *Turbinaria mesenterina* (Nelly Bay, Magnetic Island). Data are means ± SE. N=16 for each sample of the immature size classes (5-10cm and 10-20cm in diameter). N=18 for the sample of the adult size class at the deep site. The index could not be calculated for the adult size class at the shallow station (see text).

SIZE CLASS	SHALLOW (1M)		DEEP (4M)		MANN WHITNEY U' STATISTIC	
5-10cm	1.42	±0.090	1.26	±0.047	172^{+}	$0.05<P<0.10$
10-20cm	1.69	±0.147	1.21	±0.043	237^{+}	$P<0.001^{++}$
>100cm	-	-	1.24	±0.047		

$^{+}$ $U_{.05(1),16,16} = 173$

$^{++}$ Highly significant

5.3.2 Growth Analysis: *Pavona cactus*

Linear Extension Rates: Mean linear extension rates for the convoluted and columnar morphs of *P. cactus* are shown in Figure 29. A three-factor partially hierarchal analysis of variance (Table 26) tested for differences in rates of extension between months (11 levels), morphs (2 levels), and colonies (3 levels). The factors 'month' and 'morph' were fixed and orthogonal. The factor 'colony' was random and nested within both morph and month, because different colonies were sampled each time. Variances of the data were heterogeneous (Cochran's C(9,66)=0.079, P<.001), but as all the significant F ratios had probabilities <0.001, it was considered unlikely that a type 1 error had been made (the major concern when variances are heterogeneous (Underwood, 1981)).

FIGURE 29

Mean linear extension rates for the convoluted and columnar morphs of *Pavona cactus*, Eclipse Island.

Colonies were collected from Eclipse Island, approximately 1.5 months after having been stained with Alizarin Red S. Shown are the means ± their 95% confidence intervals. The growth interval for each mean is indicated above the X-axis. N=30 for each sample.

O---O Mean linear extension of the convoluted morph.
●—● Mean linear extension of the columnar morph.

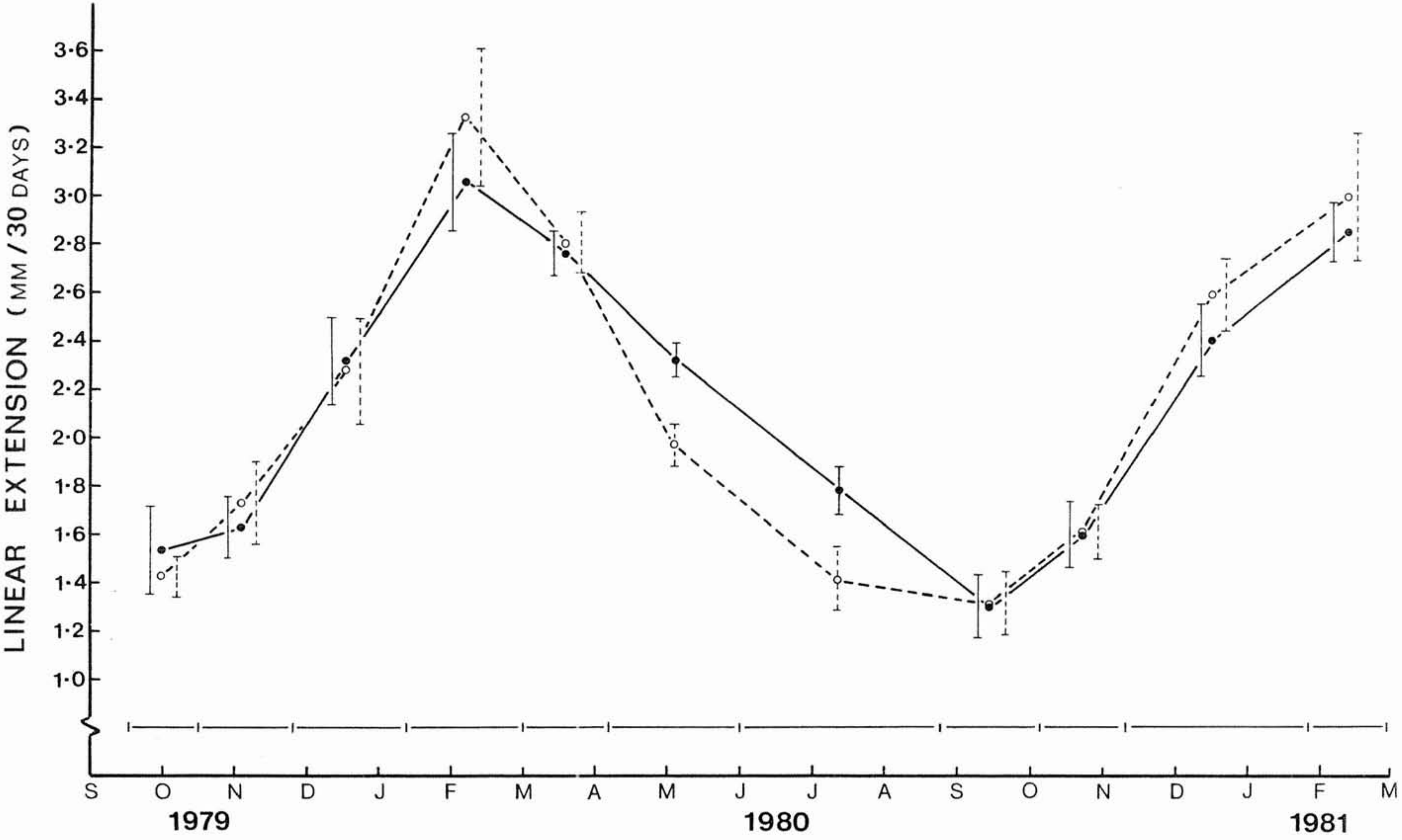

LINEAR EXTENSION (MM / 30 DAYS)
3·6
3·4
3·2
3·0
2·8
2·6
2·4
2·2
2·0
1·8
1·6
1·4
1·2
1·0
S
O
N
D
J
F
M
A
M
J
J
A
S
O
N
D
J
F
M
1979
1980
1981

TABLE 26. Three-factor, partially hierarchal analysis of variance of linear extension rates for the convoluted and columnar morphs of *Pavona cactus*. Colonies were collected at intervals of approximately 1.5 months from Eclipse Island, between September 1979 and March 1981.

Source of Variation	DF	Mean Square	F	Sign. of F
Within cells	594	0.0710		
Month+	10	24.4442	38.31	<0.001**
Morph+	1	0.0191	0.03	0.86
Month by Morph+	10	0.6045	0.95	0.50
Colony w Morph w Month	44	0.6381	8.99	<0.001**

\+ Tested against mean square of 'Colony w Morph w Month'
** Very significant F ratio
w 'Nested within'

Linear extension rates of *P. cactus* differed significantly between months and among colonies, but not between the two morphs. Figure 29 shows that growth was distinctly seasonal. Colonies of both morphs had high rates of linear extension in summer (January-March) and low rates in winter (August-September). Mean annual rates of linear extension (N=30) and their 95% confidence limits were calculated to be:

27.1 ± 0.31 mm/year for the columnar morph, and
26.1 ± 0.39 mm/year for the convoluted morph.

Morphometric analysis: Fronds from the two morphs of *Pavona cactus* were very similar in thickness near their growing tips (Figure 30C). Frond thickness increased with distance away from the tip in the convoluted morph, but the greatest mean thickness attained was only 3.6mm at 4cm. At distances greater than 4cm, growth ceases in this form. Although measurements were not made in dead areas, visual inspection revealed that frond thickness was either constant or decreased (through bioerosion) at distances further towards the interior of the colony. In comparison, columnar fronds increased in thickness much more rapidly between 0.75 and 4.0cm, indicating that differences in the rates of increase in thickness exist between the two morphs. Columnar fronds continued to increase in thickness towards the base of the colony, attaining a maximum of 17.2mm.

FIGURE 30

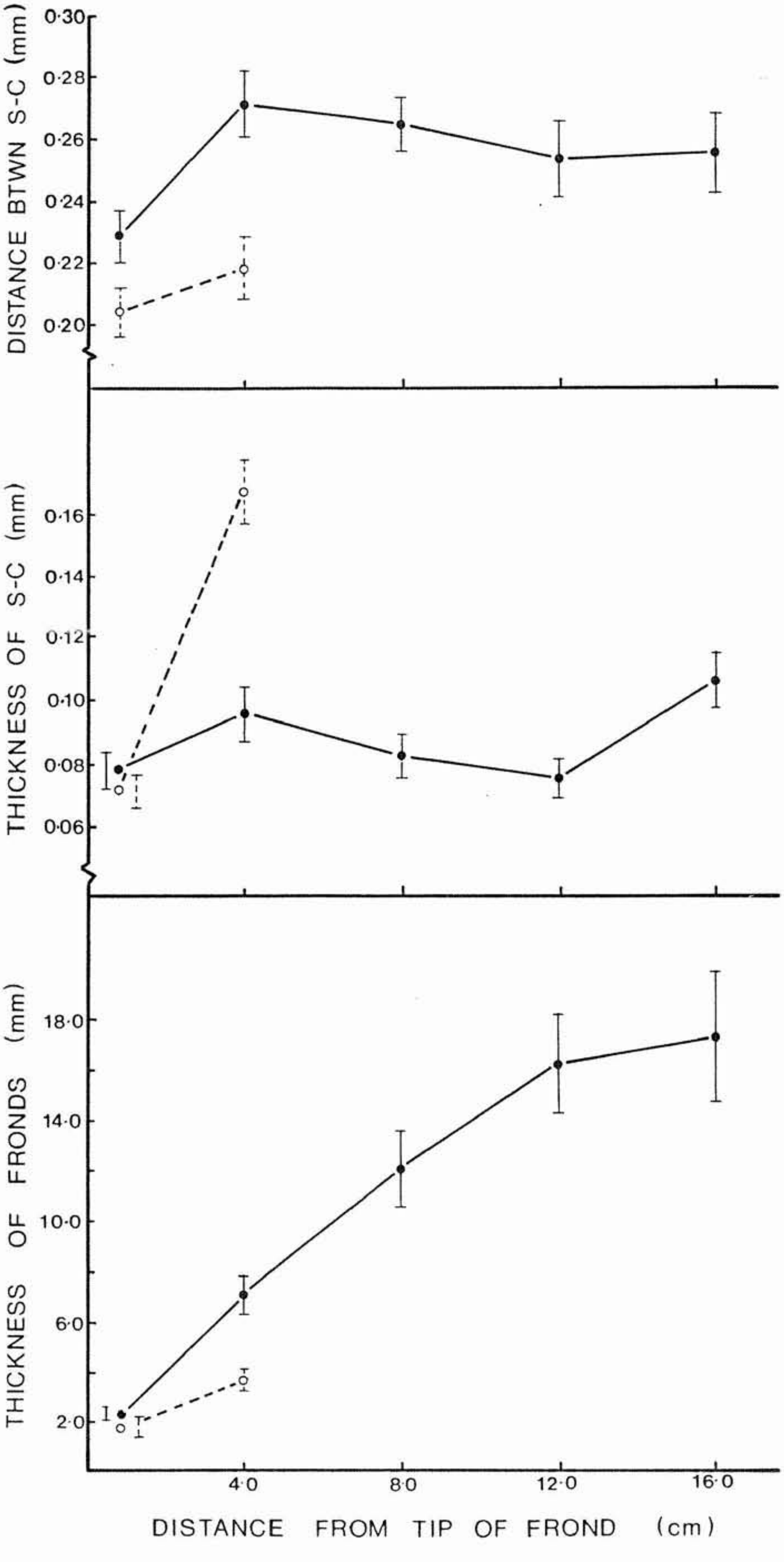
Comparison of frond and corallite structures between the convoluted and columnar morphs of *Pavona cactus*, Eclipse Island.

Shown are the means for each corallite or frond measurement ± their 95% confidence intervals. S-C: Septo-costae; 0---0: convoluted morph; ●—●: columnar morph.

A Septo-costae spacing versus tip distance. N=150 for each sample.

B Septo-costae thickness versus tip distance. N=50 for each sample.

C Frond thickness versus tip distance. N=30 for each sample.


DISTANCE BTWN S-C (mm)
0·30
0·28
0·26
0·24
0·22
0·20
THICKNESS OF S-C (mm)
0·16
0·14
0·12
0·10
0·08
0·06
THICKNESS OF FRONDS (mm)
18·0
14·0
10·0
6·0
2·0
4·0
8·0
12·0
16·0
DISTANCE FROM TIP OF FROND (cm)

Frond thickness is determined by the 'height' of septo-costae (*i.e.* by the growth of septo-costae in the plane perpendicular to the axis of linear extension). From the preceding descriptions of variation in frond thickness, septo-costae must continue to increase in height down the length of fronds in the columnar form, but not in fronds of the convoluted form. Since fronds from both morphs have similar thicknesses when they are first laid down (ie. along their distal edges) but convoluted fronds do not increase in thickness at the same rate, the question arises as to where secondary calcification is directed in the convoluted form, if it does not go towards increasing the height of septo-costae. Details of corallite architecture near the tip and at 4.0cm away from the tip of fronds, are illustrated in Figure 31, for both the convoluted and columnar morphs. Comparisons of septo-costae between morphs showed that the central vertical plates (Figure 26) were thinnest near the growing tips of fronds and had virtually the same dimensions in this region (Figure 30B). However, septo-costae more than doubled in thickness at distances of 4cm from the tips of convoluted fronds (cf. Figures 31A and 31B), whereas septo-costae remained relatively thin down the entire length of columnar fronds (cf. Figures 31C and 31D). This suggests that septo-costae in regions of primary growth (ie. near the tips of fronds) are formed in the same way for both morphs. However, once corallites have been established, secondary calcification is directed towards different aspects of the septo-costae structure in the two morphs. In the mid portions of convoluted fronds, secondary calcification is directed towards infilling the spaces between the vepreculae on the lateral surfaces of septo-costae, and thereby increasing their thickness. This type of infilling was not observed on the surface of columnar fronds anywhere along their length, although it is likely that it occurs on portions of septo-costae deeper towards the interior of the frond Thus, secondary calcification in the columnar form, is directed towards both increasing the 'height' of septo-costae and increasing their thickness, and thereby increasing the diameter of fronds.

To determine whether secondary calcification involved the insertion of new corallites between existing ones, the mean distance between septo-costae was determined for both morphs at intervals

FIGURE 31

Scanning electron micrographs of septo-costae of *Pavona cactus*.

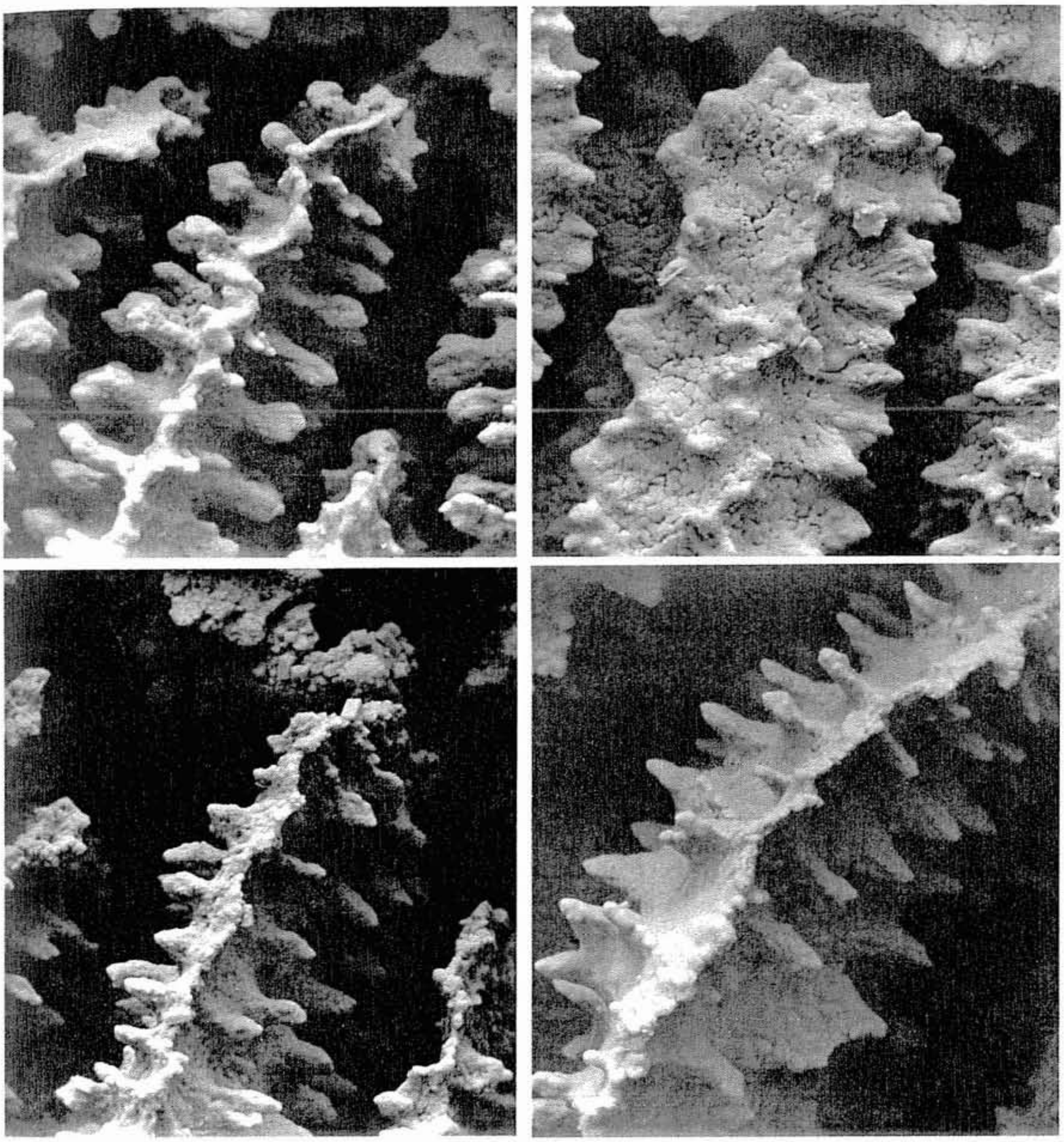
Specimens were spatter coated with gold, and photographed in 30KV Backscatter Mode on an ETEC Autoscan. Specimens were collected from Eclipse Island. Magnification A-D: x 200.

Top left photograph (A): Convoluted morph, septo-costae from a corallite 1cm from tip of frond.

Top right photograph (B): Convoluted morph, septo-costae from a corallite 4cm from tip of frond.

Bottom left photograph (C): Columnar morph, septo-costae from a corallite 1cm from tip of frond.

Bottom right photograph (D): Columnar morph, septo-costae from a corallite 4cm from tip of frond.



along the length of their fronds. It was assumed that the distance between septo-costae would increase proportionally with the increase in frond thickness if new corallites were not inserted. Conversely, if new corallites were inserted, then distances between septo-costae would remain relatively constant or decrease. Because fronds were irregularly rectangular or oval in cross section rather than circular, it was not possible to calculate trigonometrically the expected increase in septo-costae spacing with increased frond radius. However, Figure 30A shows that the distance between septo-costae was greater at 4cm than at 0.75cm from the tip of fronds in both morphs. Moreover in the tip region (<4.0cm from edge), the ratio of the increase in septo-costae spacing (D) to the increase in frond thickness (T) was approximately the same in each morph *i.e.* comparing the slopes of the graphs between Figure 30A and 30C for each morph (col, columnar; conv, convoluted):

$$\frac{\mathrm{SLOPE}_{D(col)}/\mathrm{SLOPE}_{T(col)}}{\mathrm{SLOPE}_{D(conv)}/\mathrm{SLOPE}_{T(conv)}} = 1.12$$

This evidence suggests that septo-costae merely become more widely spaced as frond thickness increases in the tip region, but does not rule out the possiblity that new corallites are inserted as frond thickness increases over the 4cm distance as well. At distances greater than 4cm from the tips of columnar fronds, septo-costae spacing becomes relatively constant. Because frond thickness continues to increase, new corallites must be inserted to maintain the constant spacing.

5.4 Discussion

Comparisons of rates of linear extension between morphs of *Turbinaria mesenterina* and *Pavona cactus*, indicated that this aspect of growth did not contribute significantly to morphological variation in either of these two species. Despite the greater thickness of columnar fronds, extension rates were the same for the convoluted and columnar morphs of *P. cactus* over a 1.5 year period. Similarly, rates of linear extension were the same for adult colonies of the convoluted and plate morphs of *T. mesenterina* over a two year period. However, extension rates were greater in deep water colonies in the smaller size classes of *T. mesenterina*. As colonies were morphologically similar or identical in small size classes, and as differences in extension rates were not maintained in the adult size class where morphological differences were greatest, it is unlikely that the process of linear extension contributes significantly to morphological differentiation in this species.

In Chapter 3 it was concluded that the degree of convolution in colonies of *Turbinaria mesenterina* was related to the angle of corallite addition. Studies of growth and form for immature colonies in the present chapter support this conclusion. Corals less than 10cm in diameter, or between 2 and 4 years in age[1], were identical at the deep and shallow stations, both with respect to their angle of growth and their convolution indices. However, at larger diameters colonies expressed distinctive growth forms. For colonies between 10 and 20cm in diameter, the angles of growth and convolution indices were significantly greater for shallow colonies than for deep colonies. These morphological trends, discernible in the 10-20cm size class, were clear in the adult size class (>100cm diameter). Two opposing patterns in the change of mean growth angle with colony size contributed to these differences: angles of growth decreased with colony size in deep water corals, but increased with colony size in shallow water corals. Decreased growth angles led to flattened plate-like morphologies, whereas increased growth angles led to folding of the colony edge to accomodate the decrease in the ratio of circumference to surface area. Morphological variation in *T. mesenterina* clearly represents a coordinated growth response by the colony to its environment,

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[1] These are probably underestimates of the age of 10cm diameter colonies, because the assumption that colonies grow at the rate calculated for the 5-10cm size class from the time of settlement is unlikely to be valid (Babcock, 1985).

i.e. phenotypic plasticity. Small colonies are morphologically indistinguishable, but through depth-dependent changes in the angle of growth, colonies achieve different growth forms. As discussed in Chapter 3, this probably represents a photoadaptive response by the colony to control the exposure of photosynthetic tissues to light.

Comparisons of frond dimensions and corallite structures of *Pavona cactus* suggested that growth differed in regions of primary (areas of new growth) and secondary (areas where existing skeletal structures are modified) calcification between the convoluted and columnar morphs. Little or no difference in frond thickness, septo-costae thickness and septo-costae spacing was found between morphs in sections of colonies less than 4 months old (*i.e.* <0.75cm from frond edge), suggesting that skeletal morphogenesis is the same during the initial framework-building period of linear extension. However, substantial differences were found in all three parameters in sections of the colony which were greater than 1.5 years old (*i.e.* >4.0cm from frond tip). Therefore it is suggested that differences in the sites of secondary calcification must account for subsequent morphological differentiation.

Although fronds of both forms increased in thickness between distances of 0.75cm and 4cm from the colony edge, the greater thickness of columnar fronds indicated that differences in secondary calcification existed at the site of the septo-costae. Further morphometric analyses revealed that secondary calcification continued to increase the 'height' of septo-costae, and thereby the thickness of fronds in the columnar form. In contrast, secondary calcification was directed towards increasing the thickness of septo-costae, and thereby infilling the spaces between septo-costae, and producing a solid bifacial frond in the convoluted form. Thus, secondary calcification may be directed towards infilling septo-costae at the expense of increasing frond thickness in convoluted colonies of *P. cactus*. This infilling process undoubtedly occurs in the columnar form as well, but is not visible at the surface of the frond where septo-costae are actively increasing in 'height'.

The increase in distance between septo-costae over the first 4cm from the tips of fronds in both morphs, suggests that septo-costae merely become more widely spaced to accomodate the increase in frond thickness that occurs over this same distance. However, the relatively constant spacing between septo-costae at greater distances on columnar fronds, despite further increases in frond thickness, suggests that new corallites must be inserted to maintain the constant septo-costae spacing. In contrast, the porportional increase in septo-costae spacing with frond thickness over the entire living surface of convoluted fronds (*i.e.* approximately 4cm from the colony edge), suggests that budding of new corallites on the lateral surface of fronds does not occur in this form.

Although rates of linear extension did not differ between the two morphs, examination of many colonies indicates that linear extension occurrs along a greater length of frond tip per projected unit area of colony in the convoluted morph. Three factors contributed to this difference. Fronds in colonies of the convoluted form were more closely packed than those in columnar colonies (Chapter 3). Secondly, linear extension was not confined to the distal edges of convoluted fronds, but often occurred along their lateral margins. This also resulted in fronds spreading laterally, so that each frond in this form had a much longer edge length. Thirdly, fronds of convoluted colonies continued to extend along the entire length of their distal edges as they spread laterally. In contrast, as columnar fronds spread laterally, nodes of no growth occurred, and the frond divided dichotomously. It is suggested that energy is preferentially directed towards thickening fronds in the columnar morph, rather than towards extension along the entire length of tips. Consequently, when tip length becomes too great to maintain, the frond divides. This suggests that, of the total amount of energy available for growth, more energy is diverted towards primary calcification in the convoluted form, whereas more energy is diverted towards secondary calcification in the columnar form.

Very little is known about the rates of linear extension for foliaceous species of corals. The present study documented mean annual linear extension rates of between 1.7cm and 1.8cm for the two morphs of *Turbinaria mesenterina*, and between 2.6cm and 2.8cm for the two morphs of *Pavona cactus*. These means represent rates intermediate between those recorded for massive and branching corals.

Although linear extension rates were measured for only 3 size classes of *Turbinaria mesenterina*, the data indicated that growth rates increased as colonies became larger in the immature size range. This trend continued through to the adult size class for shallow colonies, but not for deep colonies (adult plate colonies had growth rates intermediate between those of the two immature size classes at the deep station). Oliver *et al.* (1983) suggested that linear extension rates are proportional to the colony area supporting the actively extending regions in *Acropora formosa*. The increase in linear extension rates with size of colony in the immature range supports this suggestion. The decrease in growth rate in the adult plate colonies coincided with the onset of reproductive maturity (Chapter 6). It is likely that energy allocated to growth in immature colonies is diverted to reproduction in adult colonies with subsequent reduction in the rate of linear extension. It is interesting that this pattern of decreased growth following the onset of reproductive maturity was not observed in adult colonies of the convoluted form. This may reflect the lower reproductive effort of convoluted colonies (<50% of the reproductive effort of plate colonies, Chapter 6). However, further information on rates of infilling and radial growth in the two morphs is required before this suggestion can be evaluated.

Growth was highly seasonal in both species, with rates of linear extension being highest in summer and lowest in winter. The only exception to this pattern was in the summer of 1981-82, when shallow colonies of *Turbinaria mesenterina* exhibited the lowest growth rates for the year. This period of depressed growth corresponded to a bleaching event which affected corals across the continental shelf in the vicinity of Townsville (Fisk and Done, 1985; Oliver, 1985a). Although colonies of *T. mesenterina* did not expel their zooxanthellae during this period, the widespread bleaching in other species of corals suggests that environmental conditions were suboptimal for growth.

Several theories have been advanced to explain bleaching in corals. Glynn (1984) showed that sea surface temperatures were elevated in association with a major El Ninõ event when corals on the west coast of Panama bleached in 1983. Oliver (1985a) suggested that high light intensities, high temperatures, a waterborne pathogen, or some combination of these factors operating synergistically, was responsible for the bleaching observed on the Great Barrier Reef in 1982. Fisk and Done (1985) similarly concluded that bleaching was not caused by a simple, direct effect of temperature or irradiation. In the present study, a decline in growth rate during the period of bleaching occurred only at the shallow station, suggesting that the source of stress might be depth-related. As temperature and salinity records were identical at the two depths during the period of depressed growth (Figure 11, Chapter 2: 15 November 1981 - 21 January 1982), it is suggested that light (either visible or UV) is the most likely environmental factor to have caused the anomalous growth rates. This hypothesis is further supported by evidence of growth rate maxima for small colonies of *T. mesenterina* at the same depth, during this period. Small colonies of *T. mesenterina* are shaded by the macroalgae *Sargassum* during the summer months, and thus would have experienced reduced light intensities in comparison to large colonies. The fact that small shallow colonies were apparently unaffected, verifies that neither water temperature nor salinity were in themselves affecting growth rates, as these factors would have been uniform for small and large colonies at the shallow station.

Although underwater light intensities were not recorded during this period, meteorological records provide corroborative evidence that light penetration was probably greater than the average for the month of January, due to reduced terrestrial runoff. Total rainfall in January 1982 was less than half the mean total rainfall calculated for this month from 57 years of records (1927 to 1984). Although lower rainfalls than in January 1982 have been recorded for the month of January, field observations of corals exist for only one of these other years. In 1980, rainfall in the months of January and Febru- ary was approximately half of the mean rainfall recorded for these months over 57 years, and bleaching was observed on 27th February at Eclipse Island and on 15th March at Nelly Bay (unpubl. data). It is possible that high temperatures at this time of year may interact synergistically with high light intensities, but as temperatures as high as those recorded in 1980 and 1982 are typically recorded every summer, it is suggested that temperature is not the primary causative agent of bleaching. If it is assumed that the depth-related factor responsible for the depressed growth rates in *T. mesenterina* was the same factor responsible for the bleaching in other species of corals, then it is more likely that high light intensity, either in the visible or UV portion of the spectrum, is the primary agent of bleaching.

In summary, rates of linear extension and dimensions of corallite structures in actively extending regions of the colony are the same in the two morphs of *Pavona cactus*, but differences in allocation of energy between primary and secondary calcification cause fronds to vary in thickness. Proportionally more energy is allocated to primary calcification in the convoluted form, whereas more of the total energy available is allocated to secondary calcification in the columnar form. Secondary calcification is preferentially directed towards infilling septo-costae in the convoluted form, but towards increasing the 'height' of septo-costae, inserting new corallites, as well as infilling in the columnar form. It is suggested that differences in the sites of secondary calcification, as well as in the allocation of energy to secondary versus primary calcification, reflect genetic differences between morphs. In contrast, studies of growth in small colonies of *Turbinaria mesenterina* supported previous conclusions (Chapter 3) that morphological variation results from phenotypic plasticity in the angle of corallite addition in this species. Growth rates were highly seasonal in both species, with one maximum occurring in summer and one minimum in winter. Evidence of decreased rates of linear extension in adult colonies of the plate morph of *T. mesenterina* compared to reproductively immature colonies suggests that energy is partitioned between growth and reproduction in this species. The greater decrease in growth rates of adult colonies of *T. mesenterina* at the shallow station compared to colonies at the deep station during a bleaching event (Oliver, 1985a), suggests that a depth-related factor affected growth during this period. High light intensities are implicated.