CHAPTER 3. RECIPROCAL TRANSPLANT STUDIES: PHENOTYPIC PLASTICITY VERSUS PHENOTYPIC STABILITY

3.1 Introduction

Intraspecific morphological variation may arise in a variety of ways. Species may be phenotypically plastic, with genotypes expressing one of a range of possible phenotypes in response to the environment encountered (Wright, 1931). Alternatively, intraspecific variation may arise if individuals are phenotypically stable (*sensu* Bradshaw, 1965), but the species is genetically polymorphic. Genotypes of such species express the same phenotype despite variation in environmental conditions, but genetically distinct morphs are maintained within populations. Thirdly, it has been suggested that variation may be due to phenotypic instablity (Bradshaw, 1965). In this case the variation is nongenetic, but its seemingly random nature makes it difficult to identify an environmental cause. Phenotypic instability may reflect phenotypic plasticity in response to unperceived microhabitat differences, or random events during development, but the term will be used here to denote unexplained morphological variation.

The sources of intraspecific variation may be complex, and all three mechanisms may contribute to morphological variation in a particular trait (Jones *et al.*, 1977). Moreover, phenotypic plasticity is itself a genetically controlled trait (Jain, 1978), and therefore genotypes may differ in their capacity to vary their phenotypes (Schlicting and Levin, 1984). Further complexity is introduced because extreme or harsh environments may modify morphological expression. To distinguish non-adaptive, stress-induced morphological responses from phenotypic plasticity of growth form, a species will be considered to be phenotypically plastic if it exhibits major morphological variation in response to environmental conditions which are not marginal for the growth or survival of that species. Also for the purposes of the present

discussion, phenotypic plasticity will refer exclusively to morphological plasticity.

Theoretically, the different mechanisms underlying morphological variation should have different consequences for the distribution of genotypes within populations. If it is assumed that individual genotypes of phenotypically stable species may be adapted to specific biotopes as suggested by Van Valen (1965), then each genotype should settle and survive in only a narrow range of biotopes in comparison to plastic genotypes. Such predictions have not been tested for corals, and the hypothesis has been contradicted in a recent study of a plant species (Garbutt *et al.*, 1985). Further research to compare the fitness of genotypes between phenotypically plastic and stable species is needed. Little is known about phenotypically instable species and the implications of this strategy for the distribution of genotypes are unclear.

Although it is often speculated that variability of growth form in corals reflects phenotypic plasticity, experimental evidence is sparse. In many non-manipulative studies of individual species, colonies from different habitats have been compared, and correlations between morphological variation and environmental gradients suggested, particularly with respect to gradients of light and hydrodynamic energy (Wood Jones, 1907; Stephenson and Stephenson, 1933; Yonge, 1935; Goreau, 1963; Roos, 1967; Veron and Pichon, 1976, 1980, 1982; Veron *et al.*, 1977; Jaubert 1981; Brakel, 1983; Fricke and Schuhmacher, 1983; Veron and Wallace, 1984; Fricke and Meischner, 1985). Similar distributional studies have correlated variation in corallite features with environmental gradients (Wijsman-Best, 1974). These studies demonstrate that morphological trends, such as the flattening of colony shape with increased depth, are widespread. However, it is not possible to distinguish the underlying mechanism through direct observational methods, as correlations observed between growth forms and specific biotopes could reflect either genetic polymorphism within a phenotypically stable species or environmentally-induced phenotypic plasticity. In the former case, correlations would reflect selection for specific genotypes at the settlement stage (cf. Potts, 1978). Demonstration of the ability of an organism to change its

morphology, clearly separates phenotypic plasticity from genetically-determined phenotypic variability. If the morphological response varies consistently with an identifiable environmental parameter, plasticity may also be distinguished from phenotypic instability.

Reciprocal transplant techniques have been used extensively to illustrate phenotypic plasticity, with respect to physiological and morphological traits, in plants (Turesson, 1922; Clausen *et al.*, 1940; Turkington and Harper, 1979; Ashmun and Pitelka, 1985; Schmid, 1985). However, when the present project was initiated, clear experimental evidence of phenotypic plasticity in corals was lacking. Attempts to demonstrate it date back to Vaughan's (1911, 1914) pioneering work in manipulative ecology. Although changes in growth form were recorded, the results of these studies were unclear because controls were not maintained at the source depth and only one colony of each species was transplanted into a different biotope. A major problem in undertaking transplant experiments with corals is the length of the experimental period required to produce enough growth to be able to detect changes in colony morphology. Previous experimental studies of growth form variation in corals have generally involved the transplantation of colonies to different habitats for periods less than one year (Stephenson and Stephenson, 1933; Roos, 1967; Maragos, 1972), or for periods that have resulted in inadequate growth to test for the presence of phenotypic plasticity of growth form (Dustan, 1979). Based on relatively short-term evidence of this type, Stephenson and Stephenson (1933) and Dustan (1979) both concluded that growth forms were primarily genetically defined, although they attributed small modifications in growth form to environmental influences. In a major long-term transplant study, Potts (1978) also concluded that morphological variation in *Acropora palifera* did not reflect phenotypic plasticity. Following the initiation of this project, experimental evidence of phenotypic plasticity has been presented for a massive coral (Graus and Macintyre, 1982). Although it was demonstrated that colonies could modify their morphology, the results of this study were again weakened by the lack of rigour in the experimental design. Shallow-to-deep transplants did not involve the same depths, the same reefs, or the same years as the reciprocal

deep-to-shallow transplants, and there were no controls for the latter transplants. A second recent study (Oliver *et al.*, 1983) has shown that branch initiation frequency is a plastic response in the branching coral *Acropora formosa*.

The objective of the study described in this chapter, was to investigate the basis of the extensive morphological variability in the scleractinian corals, *Turbinaria mesenterina* and *Pavona cactus*. Both species have moderate growth rates (Chapter 5), and thus were suitable for transplantation. Surveys of growth form distributions (Chapter 2) identified common growth form-biotope associations. To test for phenotypic plasticity, adult colonies representing the two morphological extremes of each species, were reciprocally transplanted between biotopes. Ideally, juvenile colonies should be included in transplant studies to control for possible constraints on the ability of an adult colony to change its form, either through commitment to an existing form or through physiological adaptation. This problem is addressed for *T. mesenterina* in Chapter 5, through the analysis of changes in growth form with size, but the lack of juveniles of *P. cactus* (Chapter 2) precluded either approach for this species. Several skeletal features of adult colonies were identified which differed between morphs. Analyses of these features, before and after transplanting, were used to determine whether colonies changed their morphology in response to the new environment. An ancillary objective was to determine how the growth process is modified in phenotypically plastic species. Further morphometric analyses were used to determine which changes in growth patterns were responsible for the plasticity. Finally, the survival and growth of individuals in different environments were compared, and related to the morphological strategy employed by the species, to assess the niche breadth of phenotypically plastic versus phenotypically stable genotypes. The fitness of a genotype is ultimately determined by its reproductive efficiency in contributing offspring to the following generations (Dobzansky *et al.*, 1977). However, growth and survival are components of fitness which affect reproductive success (Ayala and Kiger, 1984) and because they can be measured more easily, they are often used to estimate fitness (*eg.* Silander, 1979; Potts, 1984a).

3.2 Materials and Methods

3.2.1 Reciprocal Transplants

Turbinaria mesenterina: A total of 48 colonies were involved in a reciprocal transplant study of the plate and convoluted morphs of *T. mesenterina* between the deep and shallow stations at site A, Nelly Bay (Figure 8, Chapter 2). Colonies selected for transplantation were 20 to 30cm in diameter and thus had well-defined growth forms. Two equal-sized fragments were collected from each source colony of the convoluted morph, one for a control to be maintained at the depth of origin, and one for transplantation to the deep station. Plate colonies for control-transplant pairs could only be matched for general size and shape because of the lack of suitably large colonies for splitting. The twelve pairs of each morph were initially transported to their respective control stations (*i.e.* the depth at which the morph naturally occurred) for recovery from the collecting procedure before transplantation. Two methods were used to attach colonies to steel mesh grids at each station. Colonies with stalks were attached with three perspex strips bolted together in a triangle which firmly gripped the stalk. Those with appropriate topography were wired directly to racks with plastic coated wire. All colonies were allowed to recover for a period of three months before further manipulation, so that any broken surfaces could be repaired.

To distinguish between skeletal growth before and after transplantation, all colonies were stained with alizarin red S by releasing a solution of the stain into plastic bags enclosing each colony. Colonies were exposed to a solution of approximately 10ppm for 6 hours and remained attached to racks throughout this procedure. One colony of each morph was collected at this stage to verify that staining had occurred. To reduce trauma, a further 2 weeks elapsed before the final transplantation. In April 1981, one colony from each convoluted pair was transplanted to the deep station, and conversely, one colony from each plate pair was transplanted to the shallow station. All transplants and controls

were photographed initially and then yearly until their retrieval in November 1984. All photographs were taken with a Nikonos IVA with a 28mm lens fitted with a close-up lens and attached framer. Spirit levels were attached to two adjacent sides of the framer in order to ensure that all photographs were taken in the horizontal plane, and a metal scale included to facilitate subsequent comparisons of photographic records. Racks were cleared of algal growth on bimonthly visits to the site, and records made of each colony's general health. Immediately prior to collection, all colonies were sampled for electrophoretic (Chapter 4) and histological examinations. Following collection, they were bleached in dilute calcium hypochlorite solution. Where necessary, the alizarin stain line was exposed by grinding away surface skeletal layers with an angle grinder.

Pavona cactus: The convoluted and columnar morphs of *Pavona cactus* were reciprocally transplanted between sites C and E at Eclipse Island (Figure 10, Chapter 2), among four depths at site C (1.5m, 3m, 6m, 9m), and among three depths at site E (1.5m, 3m, 6m). Because of the gradual incline of the reef slope at site E, a 9m station could not be located within a reasonable working distance. The 3m station at site E (northern reef slope) was the control station for the convoluted morph and the 6m station at site C (western reef slope) was the control station for the columnar morph. The 1.5m and 9m stations were included to determine how environments beyond their natural depth range might affect morphological expression in these two morphs. Although the 1.5m and 9m stations represented extreme environments for the convoluted and columnar morphs, the intermediate form could be found at these depths, and thus these stations were within the normal depth range of the species. Transplant procedures for *P. cactus* were similar to those described above for *Turbinaria mesenterina*.

One or more colonies from five separate patches of each of the convoluted and columnar morphs were stained with alizarin red S. Patches were located adjacent to each morph's control station, and colonies within each patch were assumed to be clonemates (see Chapter 4). Following a one week recovery period, the stained colonies from each patch were subdivided into 5 to 7 fragments. Fragments were randomly assigned to the 7 transplant stations. In

cases where a patch yielded fewer than 7 fragments, fragments were assigned to the northern slope stations first. Each fragment was between 10cm and 25cm in mean radius, and is henceforth referred to as a colony. A total of 30 colonies per morph were used to achieve at least 3 replicates at each of the 7 stations. The lower dead portions of each colony were firmly fastened to the vertical sides of plastic-covered metal racks with plastic cable-ties, and the racks tied to the substratum. Colonies were transplanted to the northern slope stations in January and to the western slope stations in March 1980. All colonies were recovered in May 1982, 26 to 28 months later.

3.2.2 Morphometric Analyses: *Turbinaria mesenteria*

Convolution Index (Plate Morph): The most obvious difference between the two morphs of *Turbinaria mesenterina* is the degree of folding of the colony edges. In order to quantify differences between transplants and controls of the plate morph at the end of the 3.5 year period, a convolution index was devised. The shape of the plate morph approximates an open cone, which is attached to the substratum at its apex (Figure 16).

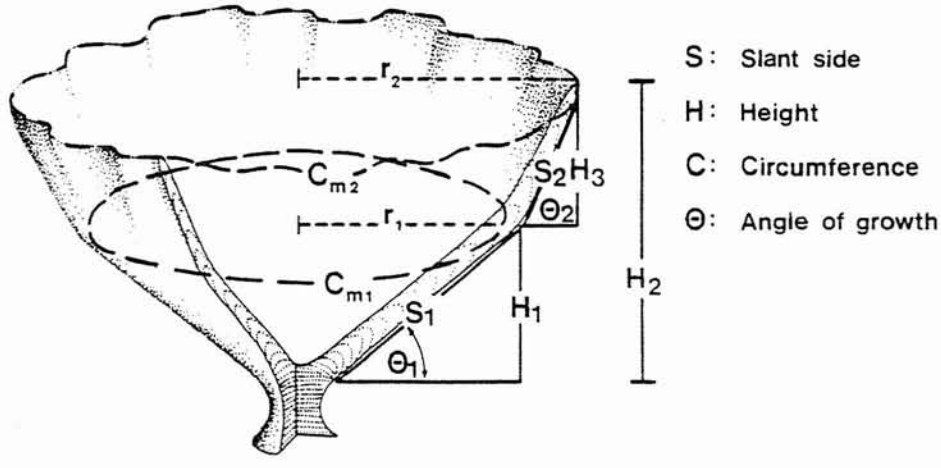


FIGURE 16. Morphometric measurements for the plate morph of *Turbinaria mesenterina*. C_m, Measured Circumference; H, Height; S, Slant side length; Θ, Angle of growth; r, radius of cone; 1, measurement before transplanting; 2, final measurement.

A series of parameters (Figure 16) were measured on the cone defined by the alizarin stain line (i.e. initial cone before transplanting) and compared to measurements at the end of the transplant period (final cone). The convoluted morph could not be compared in this manner because the alizarin stain line was inaccessible on centrally-positioned laminae, due to the complexity of the convolutions.

The measured circumference of the cone before transplanting (C_{m1}) was determined by laying a thread along the alizarin stain line. A thin layer of petroleum jelly created a sticky surface so that the thread clung to the contours of the colony. Measurement of the final circumference along the edge of the colony (C_{m2}) used the same procedure. C_{m2} would be expected to be larger than C_{m1} simply through allometric considerations. Therefore the following measurements were made to calculate predicted circumferences (C_p) for before and after comparisons.

Twenty points were evenly-spaced around both C_{m1} and C_{m2}. The height (H) of each point above the central corallum depression was measured while the colony was supported in a horizontal position. The means, $\overline{H}_1$ and $\overline{H}_2$ were calculated, and $\overline{H}_3$ determined by subtraction. Using a flexible tape, the length of the slant side (S) of each initial and final cone was measured from the centre of the corallum depression to each of the 20 positions spaced around C_{m1} and C_{m2}. The predicted circumference (C_p) for a cone with the measured mean height and slant side length was then calculated, substituting the trigonometic identity for r (calculated mean radius):

$$C_p = 2\pi r, \qquad r = \sqrt{S^2 - H^2}$$

The ratio of the measured circumference to the predicted circumference provided an index (I) of how much longer (i.e. convoluted) the edge was than expected for a standard cone with unfolded edges:

$$I_{convolution} = C_m / C_p$$

This index was thus independent of the size of the colony and Mann-Whitney tests were used to compare the degree of convolution

both between colonies (controls versus transplants) and within colonies (before versus after transplanting) of the plate morph. Where a colony had grown asymmetrically, so that it no longer completely encircled the stalk (Figure 17E), the portion of a cone remaining was determined and C_p multiplied by that percentage.

Angle of Growth: The angle of corallite addition was compared for plate colonies of *T. mesenterina* before and after transplanting, using Hotelling's test for paired samples of angles (Zar, 1984). The angle of growth (θ) was calculated trigonometrically:

$$\theta = \sin^{-1}(H/S)$$

The original cone shape of convoluted colonies is altered as the colony grows, so the above H and S measurements were not applicable. Moreover, the stain line was inaccessible because of the closely packed nature of the convoluted lamellae, so it was not possible to measure the initial angle of growth. However, an angle measuring device was constructed to measure the final growth angle. The device had a fixed arm with an attached spirit level (to allow it to be maintained in a horizontal orientation) and a short moveable arm which pivoted at one end of the fixed arm. The pivot point was positioned on the edge to be measured. The fixed arm was then held horizontal and the short arm rotated until it was parallel with the colony surface. The angle formed between the two arms was measured with a protractor. The angle of growth was measured at 30 points evenly dispersed over the surface of each colony. These were located by placing a quadrat with 5 by 6 adjustable divisions on the surface of each colony and marking a point on the edge nearest each grid intersection. Final growth angles were compared between the 2 experimental groups with Watson's 2-sample test (Zar, 1984).

Linear Extension: The alizarin stain also provided a time line from which the amount of linear growth that occurred during the transplant period could be measured. A flexible tape was laid along the surface of the corallum perpendicular to the stain line, and the distance from the stain to the edge of the corallum measured in millimetres. Twenty measurements of linear extension were made using the point distributions outlined above for the plate morph. Twenty of the 30 points used in growth angle measurements for

convoluted colonies were randomly selected for linear extension measurements. The effects of growth form, transplant depth, and colony on linear extension rates, were assessed in a 3-factor analysis of variance performed using the MANOVA routine of SPSS (Hull and Nie, 1981). Morph and depth were treated as fixed factors and colony as a random factor. Expected mean squares and F-ratios were determined as per methods outlined in Winer (1962).

3.2.3 Morphometric Analysis: *Pavona cactus*

Frond Spacing: In *Pavona cactus*, the distance between frond tips was selected as an indicator of colony morphology. A quadrat was positioned over each colony, and the divisions (6 x 5 rows) adjusted individually for each colony's size and shape. The colony tip nearest each of the 30 intersection points of the grid was marked. The distance between each marked tip and its nearest neighbour was then measured. The effects of reef slope, depth (the two transplant variables, fixed factors), growth form (fixed factor), and colony (random factor) on frond spacing, were assessed in a 4-factor analysis of variance using the MANOVA routine of SPSS (Hull and Nie, 1981). Expected mean squares and F-ratios were determined as per methods outlined in Winer (1962).

Linear Extension: Linear extension rates were used to give a rough indication of the amount of growth which had occurred during the transplant period. Linear growth was measured along the midline of fronds, generally parallel to septo-costae. Although ongoing skeletal growth continued to increase the thickness of columnar fronds, the alizarin stain line was visible when the frond was backlit with a point light source focussed through fibre optics. However, growth is highly irregular in all dimensions in the columnar form, and net growth must take into account variation in branch initiation rates, in rates of increase in diameter, and in the shape of fronds. Therefore, linear extension rates were determined only as an approximate indication of fitness of genotypes at the transplant and control sites.

3.3 Results

3.3.1 Survival and Growth of Transplants: *Turbinaria mesenterina*

Survival: Of the original twelve pairs of colonies collected per morph, 10 pairs survived the initial manipulations and staining and were transplanted to either the deep or shallow station (Table 4). Losses in the initial period resulted from dislodgement of colonies from racks during periods of rough seas. A further 5 colonies were dislodged during the transplant period, primarily at the shallow station (Table 4). Three colonies died for reasons other than dislodgement. Of these, two were convoluted colonies transplanted to the deep station. These colonies visibly declined during the first year, and were dead within 12 months of transplanting. In contrast, the third colony, a plate control, died in the third year between two of the monthly field trips having exhibited no prior signs of ill health.

TABLE 4. Mortality of *Turbinaria mesenterina* colonies transplanted to either a shallow (1m), or deep (4m) station at Nelly Bay, Magnetic Island between April 1981 and November 1984.

NUMBER OF COLONIES:	PLATE MORPH		CONVOLUTED MORPH		TOTAL
	Control (Deep)	Transplant (Shallow)	Control (Shallow)	Transplant (Deep)	
Transplanted	10	10	11	12	43
Dislodged	1	2	2	0	5
Dead	1	0	0	2	3
Surviving	8	8	9	10	35

Linear Extension Rates: Colonies grew 50 to 90 mm in radius in 3.5 years, approximately doubling the size of smaller ones. Table 5 presents mean annual linear extension rates for the 16 cases where both members of the pair survived for the entire transplant period.

TABLE 5. Mean annual linear extension rates (mm/year) of *Turbinaria mesenterina* colonies transplanted to either a shallow (1m), or deep (4m) station at Nelly Bay, Magnetic Island. Mean annual rates were based on a 3.5 year period. N=20 for each colony.

Morph	Pair No.	CONTROLS		TRANSPLANTS	
		Mean Linear Extension	95% C.I.	Mean Linear Extension	95% C.I.
		DEEP STATION		SHALLOW STATION	
PLATE	1	21.3	±0.89	18.4	±0.72
	2	16.9	±1.30	18.9	±0.75
	3	18.4	±1.34	18.3	±0.98
	4	18.9	±1.08	15.7	±0.65
	5	16.6	±1.22	15.0	±0.76
	6	19.9	±1.36	18.0	±0.83
	7	17.8	±1.34	16.6	±1.47
	8	16.3	±0.78	15.7	+1.14
PLATE MEAN:		18.3	±0.46	17.1	±0.38
		SHALLOW STATION		DEEP STATION	
CONVOLUTED	10	18.5	±0.86	16.3	±0.85
	11	17.4	±1.54	17.3	±0.91
	12	16.2	±0.68	14.7	±1.07
	13	22.2	±1.54	15.2	±1.10
	14	19.3	±0.81	16.4	±1.03
	15	15.5	±1.40	15.5	±1.05
	16	23.4	±0.86	13.7	±1.02
	17	19.1	±1.11	12.4	±1.08
CONVOLUTED MEAN:		18.9	±0.55	15.2	±0.40

Linear extension rates were compared in a 3-factor, partially hierarchal analysis of variance (Table 6), where the factors 'experimental treatment' (control versus transplant) and 'morph' were orthogonal. The third factor, 'pair number', was nested within morph, though crossed with experimental treatment. Experimental treatment and morph were fixed factors, whereas pair number was treated as a random factor. Before proceeding with the ANOVA, the variances of the data were tested and found to be homogeneous ($C(19,32)=0.064$, $p=.12$) using Cochran's test for homogeneity of variances (Hull and Nie, 1981).

TABLE 6. Three-factor partially hierarchical analysis of variance for linear extension rates of *T. mesenterina*. Colonies were involved in a reciprocal transplant study between a shallow (1m) and a deep (4m) station at Nelly Bay, Magnetic Island.

Source of Variation	DF	Mean Square	F	Sign. of F
Within cells	608	78.42	-	-
Morph*	1	392.19	0.28	0.604
Exp'tl Regime**	1	16514.06	13.18	0.003*
Pair No. w Morph	14	1395.16	17.79	0.000*
Exp'tl Regime by Morph**	1	2768.06	2.21	0.159
Exp'tl Regime by Pair No. w Morph	14	1253.06	15.98	0.000*

* Mean square tested against mean square of 'Pair No. w Morph'.
** Mean square tested against mean square of 'Exp'tl Regime by Pair No. w Morph'.
* Significant.
w 'nested within'.

Linear extension rates did not differ significantly between morphs (Table 6). However, significant differences were found in linear extension rates between experimental regimes, with linear extension rates being lower for transplants than for controls in all but two cases (Table 5). Thus the convoluted morph grew more rapidly at the shallow station (convoluted control station), whereas the plate morph grew fastest at the deep station (plate control station). Significant differences were found between colony pairs. Assuming that conditions were uniform for colonies at each station,

such differences presumably reflect genetic differences between source colonies. The experimental regime by pair number interaction was also significant, indicating that members of each pair did not always react to the two experimental regimes in the same manner. This interaction term reflects in particular, the one case where the transplant grew faster than the control colony, and the three cases where transplants grew at the same rate as, or close to the rate of, control colonies (Table 5).

Although growth rates of transplanted colonies were slower than those of control colonies in the 3-factor ANOVA, differences between experimental regimes were not statistically significant in a separate, 2-factor ANOVA (experimental regime by pair no.) of linear extension rates involving only the plate morph (Exp'tl Regime: $p=0.078$; Pair No.: $p=0.098$; Exp'tl Regime by Pair No.: $p<.0005$). A similar 2-factor ANOVA for the convoluted colonies indicated that there were significant differences between experimental regimes for this morph (Exp'tl Regime: $p=0.022$; Pair No.: $p=0.772$; Exp'tl Regime by Pair No.: $p=.000$). Because linear extension rates were only marginally slower for transplants of the plate morph, differences between the control and transplant groups were not significant in the 2-factor ANOVA. However, when plate morph linear extension rates were combined with those of the convoluted morph, the greater differences between control and transplant extension rates of the convoluted colonies weighted the means in the direction of significant differences.

3.3.2 Morphometric analysis: *Turbinaria mesenterina*

Photographs of control and transplanted colonies of *Turbinaria mesenterina* taken before and after transplantation, show typical effects of the 2 depth treatments on the plate morph (Figure 17) and on the convoluted morph (Figure 18). Control colonies of the plate morph tended to maintain a relatively horizontal direction of growth, so that after 3.5 years, colonies were simply enlarged versions of their original growth forms (cf. Figures 17a, 17b). In

FIGURE 17

Representative colonies of the plate morph of *Turbinaria mesenterina*, before and after transplanting to a shallow station (1m) at Nelly Bay, Magnetic Island.

Each pair of photographs shows the initial growth form of the colony in May 1981 (left column) and the final growth form of the same colony in December 1984 (right column). All photographs were taken underwater with the lens framer held in a horizontal orientation. Scale bars represent 5cm and are the same length for each pair of photographs. Thus growth during the 3.5 year period may be visualized. Photos are composites.

Top pair: (A & B) Control colony transplanted to rack at source depth (4m). No change in growth form has occurred.

Middle pair: (C & D) Transplanted colony. Increased folding and angle of growth visible in D.

Bottom pair: **(E & F)** Transplanted colony. Increased folding and angle of growth visible in F.

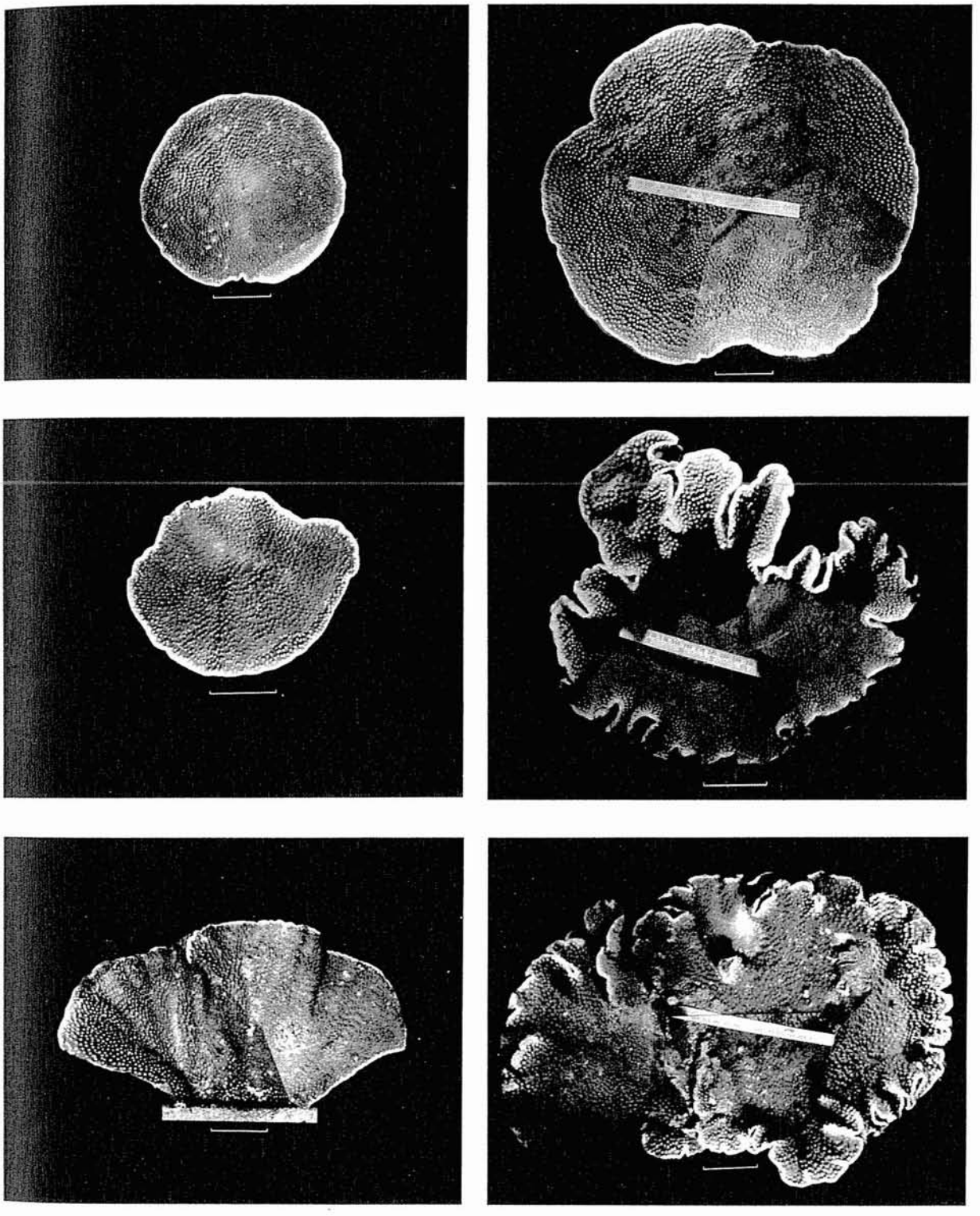


FIGURE 18

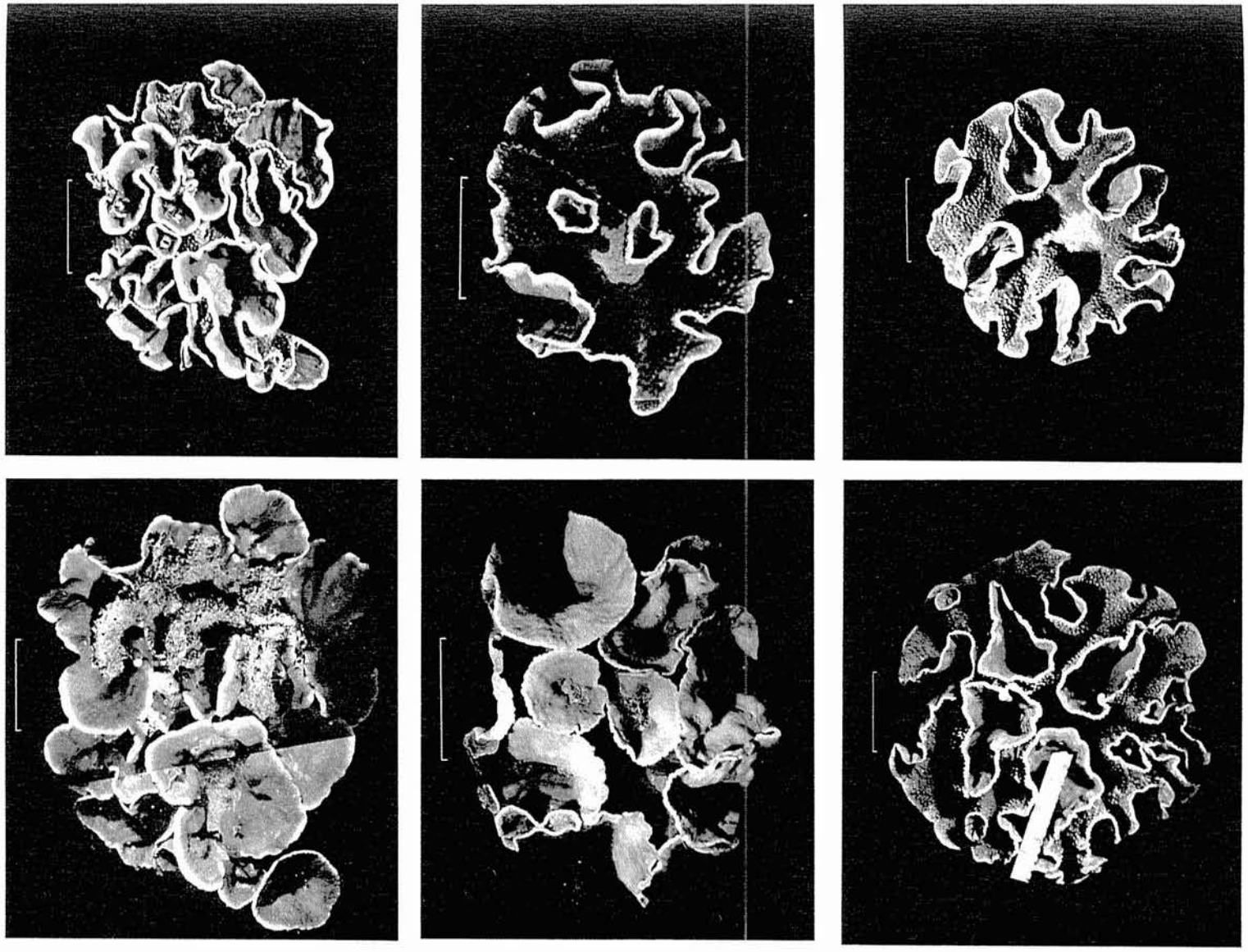
Representative colonies of the convoluted morph of *Turbinaria mesenterina*, before and after transplanting to a deep station (4m) at Nelly Bay, Magnetic Island.

Each pair of photographs shows the initial growth form of the colony in May 1981 (left column) and the final growth form of the colony in November 1982 (right column). All photographs were taken underwater with the lens framer held in a horizontal orientation. Scale bars represent 5cm and are the same length for each pair of photographs. Thus growth during the 1.5 year period may be visualized. Photos are composites.

Top Pair: (A & B) Control colony transplanted to rack at source depth (1m). No change in growth form has occurred.

Middle pair: (C & D) Transplanted colony. A flattening response due to a decreased growth angle is visible in D.

Bottom pair: (E & F) Transplanted colony. A flattening response due to a decreased growth angle is visible in F.



contrast, the axis of growth generally became more vertically directed and the edges more folded, in plate colonies transplanted to the shallow station (cf. Figures 17c, 17d and 17e, 17f). Growth of all control colonies of the convoluted morph continued to have a strong vertical component throughout the 3.5 years. This produced increased folding of the laminae, and chimneys or funnels when folded edges were isolated in the interior of the colony as a result of continued growth (cf. Figures 18a, 18b). Growth of convoluted colonies transplanted to the deep site tended to become more horizontally-directed. This initially led to the formation of horizontal lips throughout the colony, as previously upright surface features changed their direction of growth. Many of these lips subsequently grew together and either fused (Figure 18d) or reverted to vertical growth following contact. Abnormal forms were sometimes created because of geometric constraints imposed by morphology existing prior to transplantation. For example, polyps are normally located on the upper surfaces of colonies or on the outer, vertical surfaces of 'chimneys', but the flattening of funnel-like formations caused all polyps ultimately to face downwards (Figure 18d). Curiously, this occurred in many cases where it would have seemed possible to avoid the inversion of polyps by preferentially extending those sections of the colony which were initially more horizontally-directed (cf. Figures 18c, 18d and 18e, 18f).

Convolution index: Prior to testing whether morphological changes following transplantation were significant, statistical tests were applied to determine whether morphological differences existed between colonies before transplantation. A Mann-Whitney U test was used to determine whether the initial convolution indices of the plate colonies (Table 7) differed between the control and transplant groups. A non-parametric test was required because the data consisted of ratios (indices were calculated as the ratio of the measured circumference to the predicted circumference). Two transplants (pair no. 9) were included in this and the following analyses, although they were not from the same colony and both had been collected early following dislodgement. The Mann-Whitney test does not require paired data, and both colonies had been exposed for at least 70% of the total time period. The test showed that convolution indices were the same in both groups before

transplanting (U=46.5, $U_{.05(2),9,9}$=64, p>.05). Separate 1-tailed tests were then used to determine whether the convolution indices were greater following transplanting in each experimental group. These tests indicated that final convolution indices were not greater than initial ones in the control group (U=59, $U_{.05(1),9,9}$=60, p>.05). However, they were significantly greater in the transplant group (U=81, $U_{.05(1),9,9}$=60, p<.001), indicating that edges of these colonies were much longer than predicted for cones of the measured height and slant side length. Edges of transplanted, plate colonies were thus more folded than controls, to accommodate the porportionally greater increase in edge length.

TABLE 7. Comparison of initial and final convolution indices (CI) of plate colonies of *Turbinaria mesenterina*, involved in reciprocal transplant studies between a shallow (1m) and deep (4m) station at Nelly Bay, Magnetic Island.

PAIR NO.	CONTROLS			TRANSPLANTS		
	$CI_{initial}$	CI_{final}	CI	$CI_{initial}$	CI_{final}	CI
1	1.10	1.22	0.12	1.20	3.46	2.26
2	1.11	1.08	-0.02	1.06	1.62	0.56
3	1.09	1.30	0.21	1.29	1.98	0.69
4	1.12	1.55	0.43	1.18	1.76	0.58
5	1.14	1.57	0.43	1.39	1.99	0.60
6	1.83	1.96	0.13	0.96	3.90	2.84
7	1.46	2.13	0.67	1.23	3.97	2.74
8	1.35	2.90	1.55	1.12	3.05	1.93
9*	1.44	1.43	-0.01	1.24	3.01	1.77

* Colonies not members of the same original pair and had been dislodged and collected 2.5 to 3 years after transplantation.

Angle of growth: Calculated initial and final mean angles of growth of plate colonies, and measured final mean angles of growth of convoluted colonies are shown in Table 8. Although the data were measured in degrees, standard errors (S.E.) were calculated as if the data were measured on a linear scale. Linear statistics are

TABLE 8. Mean initial and final growth angles (θ) of *Turbinaria mesenterina* colonies involved in reciprocal transplant studies between a shallow and deep station at Nelly Bay, Magnetic Island. Data are: Mean (±S.E.). Plate morph: Pairs 1-9, (N=20). Convoluted morph: Pairs 10-18 (N=30). *: not from same pair.

PAIR NO.	CONTROLS $\theta_{initial}$	CONTROLS θ_{final}	CONTROLS $\Delta\theta$	TRANSPLANTS $\theta_{initial}$	TRANSPLANTS θ_{final}	TRANSPLANTS $\Delta\theta$
1	28.0 (±2.66)	26.2 (±3.44)	-1.8	37.1 (±3.08)	45.8 (±3.63)	8.7
2	20.7 (±1.42)	29.7 (±1.69)	9.0	19.6 (±1.31)	41.0 (±3.51)	21.4
3	20.5 (±1.64)	35.6 (±3.12)	15.1	21.5 (±2.38)	28.5 (±3.71)	7.0
4	14.8 (±1.00)	23.2 (±5.14)	8.4	12.2 (±2.35)	35.1 (±4.02)	22.9
5	1.6 (±0.84)	0.7 (±2.67)	-0.9	5.3 (±1.77)	32.4 (±3.65)	27.1
6	5.4 (±2.86)	12.7 (±4.95)	7.3	8.2 (±0.61)	18.9 (±4.98)	10.7
7	15.5 (±1.48)	21.3 (±2.71)	5.8	12.1 (±0.82)	31.9 (±3.07)	19.8
8	29.7 (±1.90)	40.6 (±4.51)	10.9	14.8 (±2.34)	36.9 (±4.29)	22.1
9*	9.6 (±2.36)	23.7 (±3.24)	14.1	17.7 (±4.27)	30.3 (±4.03)	12.6
10	-	71.5 (±3.02)	-	-	48.2 (±4.27)	-
11	-	68.5 (±2.83)	-	-	41.6 (±5.62)	-
12	-	68.2 (±4.11)	-	-	43.0 (±4.36)	-
13	-	71.1 (±2.67)	-	-	52.1 (±3.29)	-
14	-	67.9 (±3.66)	-	-	45.1 (±4.69)	-
15	-	62.5 (±4.05)	-	-	49.1 (±4.33)	-
16	-	75.8 (±2.58)	-	-	40.6 (±3.65)	-
17	-	69.0 (±3.38)	-	-	41.7 (±4.19)	-
18*	-	70.2 (±2.79)	-	-	41.9 (±3.39)	-

appropriate for data from circular distributions where the measurement scale is a portion of a circle less than 90° (Zar, 1984). In this case the range of growth angles spanned less than 90° for each individual colony. However, where comparisons were made between colonies, data spanned more than a 90° range. Therefore in the following analyses, tests designed for circular distributions were employed.

To compare initial mean angles between the two experimental groups of plate colonies, Watson's nonparametric 2-sample test for circular data was used (Zar, 1984). The data were first converted to an appropriate form using Batschelet's modification for second-order data (ie. data being compared are means of means). This test indicated that the initial mean angles were not significantly different between the control and transplant groups of plate colonies (U^2=0.086, $p>.2$). Hotelling's parametric test for paired samples of angles and second order data (Zar, 1984) was then used to test whether the angle of growth had changed at the end of the 3.5 year period within each experimental group. The paired data were the initial and final mean angles of growth of each colony. No significant differences were found between mean angles before and after transplanting in the control group ($F=2.54$, $.25>p>.10$). This test confirmed that plate colonies at the deep station continued to extend linearly at the same angle of growth, thus maintaining their original growth forms (Figure 18b). In contrast, highly significant differences were found between mean angles in the transplant group ($F=36.51$, $p<.001$). The angle of growth became more vertically directed in all cases. It changed sharply approximately 5-10mm beyond the stain line in some cases (Figures 17D and 17F), whereas in others the transition to the new angle of growth was gradual.

Since the initial mean growth angles could not be measured or calculated for convoluted colonies, only the final growth angles were compared. Watson's 2-sample test indicated that final mean angles were significantly different between controls and transplants (U^2=0.370, $p<.002$). In all cases, the mean growth angle was less for colonies transplanted to the deep station than for control colonies maintained at the shallow station, indicating that colonies were flattening in response to the depth change.

3.3.3 Survival and Growth of Transplants: *Pavona cactus*

Survival: All colonies of *P. cactus* at the 3m and 6m stations, on both the northern and western reef slopes, survived the 2.5 year period with minimal evidence of ill-effect. However both morphs did poorly at stations beyond their natural depth range (Table 9a). A slow decline for both convoluted and columnar colonies at the 1.5m station on the northern reef slope began approximately two months after transplanting. At the end of February 1980, all colonies at this station were bleached (i.e. tissue appeared white because of the expulsion of zooxanthellae, a response usually associated with stress (Glynn *et al.*, 1985)). Only the upper surfaces of colonies bleached, suggesting that a uni-directional factor such as light might have triggered the response. By early April, most colonies were recovering, as judged by the return of darker pigmentation associated with the presence of zooxanthellae. However, by November most colonies were still pale and dead patches colonized by algae had developed on all columnar colonies and two convoluted colonies. Two colonies of each morph subsequently died and the remaining three columnar colonies sustained substantial tissue loss. The three remaining convoluted colonies recovered completely with minimal tissue loss.

Western reef slope transplants were established after bleached colonies were recovering. Only unbleached corals were transplanted, hence the higher survival rates of colonies at the 1.5m western slope station. The death of one convoluted colony at the 9m station occurred gradually over a long time period, though bleaching was not observed. Similar bleaching was observed in non-transplanted colonies of *P. cactus* and in several other species of corals during late February 1980. Bleaching was observed at all depths, though it was generally restricted to colonies at the shallow end of the range within each species (*i.e.* for *P. cactus*, bleaching affected convoluted colonies at 2m and columnar colonies at 3.5m). Recovery following the 1980 bleaching was generally complete. All *in situ* colonies of *P. cactus* returned to normal pigmentation with no tissue loss by June. No bleaching was observed in 1981, but more bleaching was observed in February 1982. Only a few colonies of *P. cactus*

TABLE 9a. Mortality of colonies of the convoluted morph of *Pavona cactus* transplanted to one of four depths on two reef slopes at Eclipse Island, Great Barrier Reef, for a period of 2.3 years.

DEPTH	NO. TRANSPLANTED		NO. DEAD		TOTAL NO. DEAD
	North Slope	West Slope	North Slope	West Slope	
1.5m	5	5	2	1	3
3.0m*	5	3	0	0	0
6.0m	5	3	0	0	0
9.0m	-	4	-	1	1
Total	15	15	2	2	4

* Control Station

TABLE 9b. Mortality of colonies of the columnar morph of *Pavona cactus* transplanted to one of four depths on two reef slopes at Eclipse Island, Great Barrier Reef, for a period of 2.3 years.

DEPTH	NO. TRANSPLANTED		NO. DEAD		TOTAL NO. DEAD
	North Slope	West Slope	North Slope	West Slope	
1.5m	5	5	2	0	2
3.0m	5	3	0	0	0
6.0m*	5	3	0	0	0
9.0m	-	4	-	0	0
Total	15	15	2	0	2

* Control Station

were affected, though these did not include any of the transplants or any of the resident colonies which had been bleached in 1980. Recovery was variable among species. Bleaching was patchy in *P. cactus*, *Echinopora lamellosa*, and *Millepora sp.* and recovery was complete in these species. Most colonies of afflicted *Acropora* spp. and *Goniopora* sp. slowly declined in general appearance and ultimately died.

Linear Extension: All colonies grew substantially during the different depth and reef slope treatments, with mean linear extensions of at least 70mm being recorded at the 3m and 6m stations over the 2.5 year period. Columnar colonies which were bleached at the northern 1.5m station, grew between 30 and 40mm. Only minimum extension rates could be determined for convoluted colonies, because the alizarin stain line was generally either obscured or eroded. Bioerosion of the stain line occurred following the death of fronds in the region of staining, due to the displacement of these portions of the fronds towards the interior of the colony as a result of continued growth. Thus, virtually all of the living portions of convoluted colonies at the time of collection, represented growth which had occurred during the 2.5 years.

3.3.4 Morphometric Analysis: *Pavona cactus*

Final growth forms of representative colonies of the two morphs, transplanted to the four stations located within the natural depth distributions of these morphs, are shown in Figure 19. In all cases, colonies transplanted to these two depths closely resembled colonies maintained at each morph's control station. Spacing between fronds and frond thickness were the two major factors used to evaluate similarity. Those colonies which survived transplantation to the 9m station on the western reef slope, also closely resembled the controls. However, surviving convoluted and columnar colonies transplanted to the 1.5m stations appeared to have greater frond densities than controls.

Frond Spacing: Comparisons of final mean frond spacing between control and transplant colonies and between morphs (Table 10), were tested in a 4-factor, partially hierarchal analysis of variance (Table 11). The factors 'morph' (convoluted versus columnar), 'slope' (western versus northern), and 'depth' (1.5m, 3m, 6m) were fixed and orthogonal. 'Colony' (3 levels) was random and nested within each of the other factors. Although replicate colonies from the same patch were assigned to each station, differential

FIGURE 19

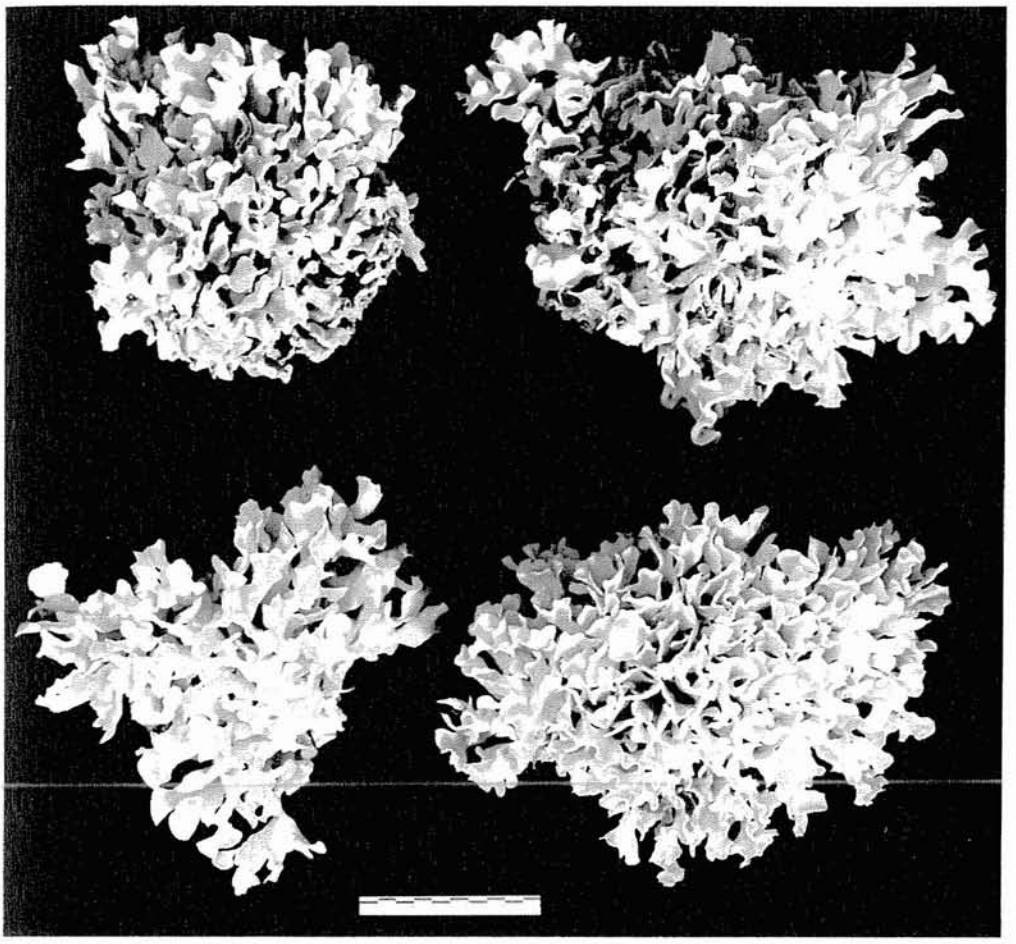
Final growth forms of colonies for both the convoluted (A) and columnar (B) morphs of *Pavona cactus*, following transplantation to two depths and two reef slopes at Eclipse Island, Great Barrier Reef.

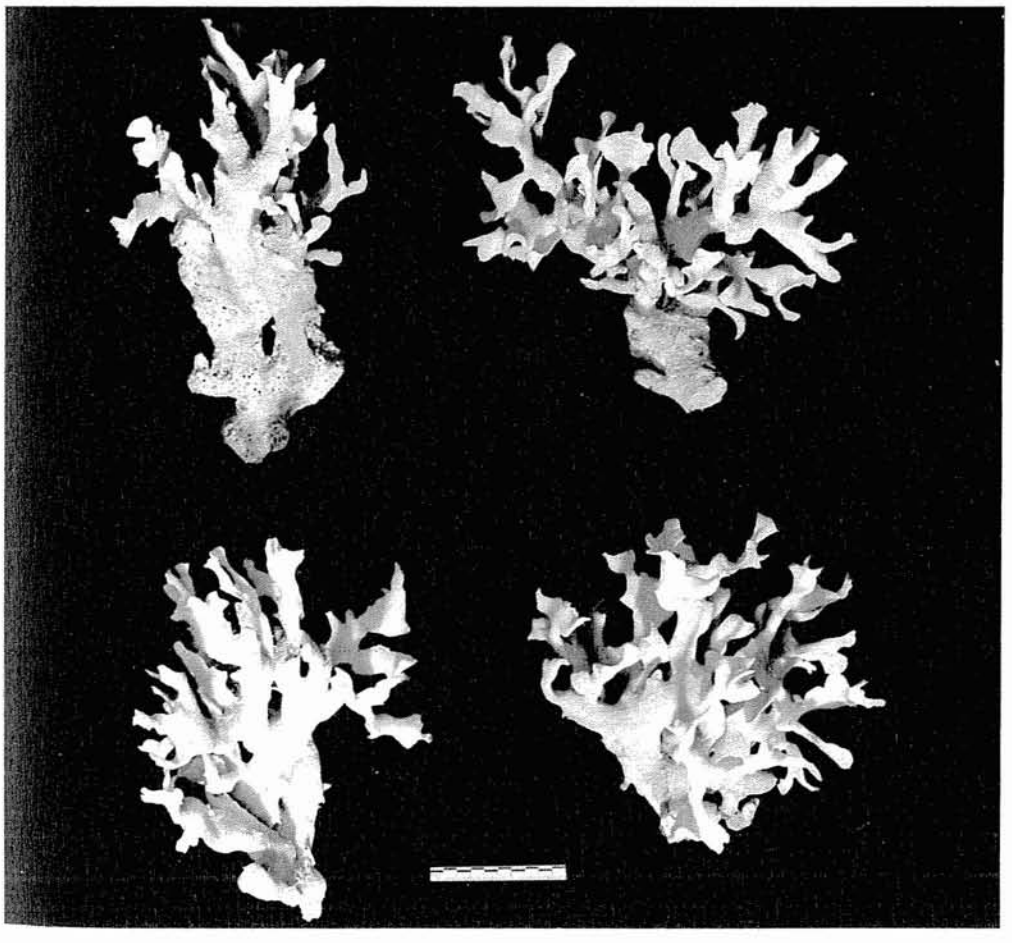
Colonies of *P. cactus* photographed 2.3 years after transplantation (following collection and bleaching). Scale bars represent 10cm.

Top (A): Representative colonies of the convoluted morph.
Bottom (B): Representative colonies of the columnar morph.

The four colonies pictured in each of 19A and 19B were transplanted to the following stations:

Upper left: 3m station, northern reef slope (convoluted control)
Upper right: 3m station, western reef slope
Lower left: 6m station, northern reef slope
Lower right: 6m station, western reef slope (columnar control)





survivorship between stations meant that colony could not be treated as orthogonal with depth and slope. Where more than three colonies per morph survived at a station, three were randomly selected for analysis. Depth was partitioned so that the effects of reciprocal transplantation between the two control depths (3m and 6m stations) could be kept separate from exposure to an extreme depth (1.5m station). The variances of the untransformed data were found to be heterogeneous according to Cochran's test for homogeneity of variances, but were equal when the square-root transformation was applied (C(29,36)=0.053, p=0.066).

TABLE 10. Mean distance (D) between fronds (mm) for convoluted and columnar colonies of *Pavona cactus*. Colonies were involved in reciprocal transplant studies between two reef slopes (northern and western) and four depths at Eclipse Island, Great Barrier Reef, for a period of 2.3 years. N=30.

	CONVOLUTED MORPH				COLUMNAR MORPH			
	Northern		Western		Northern		Western	
Depth (m)	D	95% C.I.	D	95% C.I.	D	95% C.I.	D	95% C.I.
	7.8	±1.18	9.8	±1.52	20.4	±3.83	25.7	±4.37
1.5	9.5	±1.53	10.9	±1.41	22.2	±3.11	24.9	±2.65
	11.0	±1.23	9.9	±1.15	19.9	±3.15	23.9	±2.81
	15.4	±1.97	11.4	±1.63	35.5	±4.88	32.4	±3.35
3.0	11.2	±1.45	8.4	±1.22	33.5	±3.87	32.1	±3.86
	11.8	±1.63	16.7	±2.40	24.9	±2.82	33.3	±4.10
	13.6	±1.72	15.4	±2.25	31.3	±4.25	30.7	±3.80
6.0	13.4	±1.91	14.4	±2.31	29.2	±3.41	35.9	±4.04
	8.6	±1.43	7.6	±0.85	26.0	±3.84	25.8	±2.66
	-	-	14.8	±2.40	-	-	26.9	±4.12
9.0	-	-	8.2	±1.10	-	-	33.9	±4.35
	-	-	16.2	±2.24	-	-	29.5	±4.04

Control stations: (values are boldfaced)
Convoluted Morph - 3.0m station on Northern Reef Slope
Columnar Morph - 6.0m station on Western Reef Slope

Convoluted and columnar colonies of *P. cactus* did not change their respective growth forms when transplanted reciprocally between two reef slopes nor when transplanted to the 3m and 6m stations (*i.e.* Depth 1 factor not significant, Table 11). However, the effect of depth on frond spacing differed significantly between the 1.5m station and the average of the 3m and 6m stations (*i.e.* Depth 2 factor was significant). Although the nested factor, colony, was significant, indicating that variation in frond spacing existed between colonies of each morph, variation between morphs was significant over and above this variation. None of the first or second order interaction effects were significant. In summary, colonies of the convoluted and columnar morphs differed significantly in frond spacing. They did not change their growth forms when transplanted into the habitat of the other morph, but they were capable of slight modifications in form when transplanted into an extreme habitat.

TABLE 11. Four-factor analysis of variance of frond spacing in transplants of *Pavona cactus*. 'Morph', 'slope', and 'depth' factors were orthogonal, and 'colony' was nested within each of these factors. Depth effects were partitioned: 'Depth 1' tested the effects of the 3m versus 6m stations, and 'Depth 2' tested the effect of the 1.5m station versus the average of the 3m and 6m stations on frond spacing.

Source of Variation	DF	Mean Square	F	Significance of F
Within cells	1044	0.64		
Colony w (Depth, Slope and Morph)	24	3.84	5.98	0.00**
Morph+	1	994.96	259.32	0.00**
Slope+	1	6.43	1.67	0.21
Depth (1)+	1	1.71	0.44	0.51
Depth (2)+	1	80.74	21.04	0.00*
Morph by Slope+	1	4.80	1.25	0.27
Morph by Depth (1)+	1	0.39	0.10	0.75
Morph by Depth (2)+	1	12.99	3.39	0.08
Slope by Depth (1)+	1	1.43	0.37	0.55
Slope by Depth (2)+	1	2.30	0.60	0.45
Morph by Slope by Depth (1)+	1	0.19	0.01	0.95
Morph by Slope by Depth (2)+	1	0.04	0.01	0.92

\+ Tested against mean square of 'Colony w Depth, Slope and Morph'
w 'Nested within'
* Significant
** Highly significant

3.4 Discussion

The present study has shown that genotypes of *Turbinaria mesenterina* were morphologically plastic in their response to depth-related environmental changes. Both morphs changed their form consistently in a direction that led them to resemble resident colonies, when transplanted reciprocally between their respective depths. Hence, the morphological response of *T. mesenterina* represents phenotypic plasticity rather than phenotypic instability. It is not possible to separate the depth-related effects of light and water motion solely on the basis of this transplant study. However, for reasons outlined in Chapter 2, it is suggested that genotypes were responding primarily to differences in light intensity.

In contrast, genotypes of the convoluted and columnar morphs of *Pavona cactus* did not change their morphology over a 2.3 year period, when transplanted reciprocally between two reef slopes and two depths. However, when they were transplanted into the extreme upper depth range of the intermediate morph, some modification of growth form occurred, although they did not come to resemble either each other, or the intermediate morph. Hence, adult colonies of *P. cactus* are phenotypically stable when transplanted into each other's habitat, but exposure to an extreme environment, which affects colony growth and survival, may result in abnormal forms. Observations of extremely stunted, thickened colonies of the convoluted form in close proximity to the alcyonacean, *Sinularia flexibilis* (Appendix 1), suggests that colony form may also be modified in an extreme 'biological environment', possibly as a result of allelochemical effects (Sammarco *et al.*, 1983).

The ability to vary the expression of growth form, has obvious advantages for the survival of sessile organisms dispersed through planktonic larval stages, and living in environments which are unstable or heterogeneous, especially if physical factors vary over relatively small scales (Jackson, 1979). Phenotypic plasticity has been shown to have adaptive value in plant species where such

disruptive selection operates either spatially or temporally (Bradshaw, 1965), but its presence as a morphological strategy in corals has been largely assumed. There is abundant evidence of morphological variation in corals, but as outlined in section 3.1, this does not necessarily reflect phenotypic plasticity. Other attempts to demonstrate phenotypic plasticity have generally produced negative or conflicting results. A recent transplant study of *Acropora formosa* (Oliver *et al.*, 1983) is the only clear exception. Studies involving only 1 or 2 colonies per species (Vaughan 1911, 1924; Yonge, 1935; Roos, 1967; Maragos, 1972) have provided anecdotal evidence of change, though the lack of controls weakens the interpretation of these results. The flattening of colonies of *Montastrea annularis* has been an oft-quoted example of morphological change in response to decreasing light intensity (Goreau, 1963; Barnes, 1973). When Dustan (1979) tested *M. annularis* for phenotypic plasticity in a 2-year transplant experiment, he reported that colonies of this species had a small capacity to change their form. Moreover, he distinguished two ecotypic races of zooxanthellae in the depth range of the species, and suggested that differences were primarily genetically determined. However, in a 3-year study of the same species, Graus and Macintyre (1982) reported that 7 colonies transplanted to varying depths consistently resembled resident colonies from the same depth, concluding that morphological variation was environmentally induced. In the only other long-term test of phenotypic plasticity, Potts (1978, 1984a) reported minor evidence of phenotypic plasticity in *Acropora palifera* and *Acropora cuneata*, and suggested that complex regimes of disruptive selection operated in the early life history stages to select for specialized genotypes, thus maintaining high levels of genetic variation in these two species. Thus, no clear picture emerges from previous research, and it is not yet possible to assess the extent to which phenotypic plasticity is employed as a morphological strategy by corals. The present study further emphasizes that morphological variability within coral species may be accomplished through different evolutionary pathways.

Studies of individual corallite architecture have provided evidence that different morphological strategies operate at this

level as well. Foster (1979) demonstrated that features such as the thickness of thecae, septa and columellae are phenotypically plastic in *Montastrea annularis* and *Siderastrea siderea* in a reciprocal transplant study. Foster also concluded that the degree of phenotypic plasticity varied among species, with the former species being more plastic than the latter. However, the relationship between corallite dimensions (with the possible exception of thecae thickness in *Montastrea annularis*) and colony shape in these species remains obscure (Foster, 1983). Brakel (1977) used cluster analysis to conclude that there was a continuum of genetic variation in a number of corallite structures within the genus *Porites*, which made it extremely difficult to resolve taxonomic species through morphological analyses. In arriving at this conclusion Brakel equated all within-colony corallite variation to non-genetic variation, assuming that this could be attributed to microhabitat differences. This ignores the possibility of other sources of phenotypic instability, particularly where variation is randomly dispersed over the colony. Furthermore, recent evidence suggests that genetic chimeras are possible, either through somatic mutation (Whittam and Slobodchikoff, 1981) or through juvenile fusion (Hidaka 1985). Brakel concluded that complex patterns of genetic variation existed within the genus, but reciprocal transplant studies would provide further insights into the 'species problem' in *Porites*. Other examples of within-colony corallite variation (Veron, 1981) may represent phenotypic plasticity in response to microhabitat variation (occurs over scales as small as centimetres (Antonovics *et al.*, 1971)), phenotypic instability, or somatic mutations.

The evolution of phenotypic plasticity within a species appears to be extremely advantageous for individual genotypes. However, as pointed out by Jackson (1979), problems may arise if the morphological response to short term environmental conditions commits the colony to a shape which is disadvantageous in the long term. The response of the convoluted morph of *Turbinaria mesenterina* in the present study suggests how such a situation could arise. Although transplanted colonies of this morph were able to flatten the angle of growth in response to lowered light conditions, constraints imposed by pre-existing colony shape resulted in the polypary

surface facing downwards. This orientation does not represent a normal condition, and such colonies subsequently suffered extensive tissue loss. Although it could be argued that genetically-defined, inflexible genotypes could also give rise to inappropriate growth forms, it could be advantageous to persevere with a genetically programmed form which is inappropriate under conditions of juvenile growth, but highly successful in the adult stage. For example, the ambient light regime may be perceived quite differently by small and large colonies because of differences in colony height with respect to nearby competitors. Therefore it would be important that patterns of colony growth were not established in the first few years that would constrain adult growth under changed environmental conditions. Evaluation of the extent to which phenotypic plasticity is employed as a morphological strategy among coral species, remains an important question in understanding evolutionary processes within this order, but further manipulative studies are required before such questions can be resolved.

The fitness of phenotypically plastic genotypes of *Turbinaria mesenterina* in different environments was assessed by comparing survival and growth rates between control and transplant colonies. An electrophoretic survey (Chapter 4) established that all source colonies involved in the transplant study represented distinct genotypes. Genotypes of the plate morph survived equally well at both transplant stations and grew only marginally slower at the shallow station (possibly as a result of a growth lag following transplantation). The two transplant stations represent the limits of the depth distribution of the species at Nelly Bay. Thus, in terms of growth and survival, it appears that genotypes which are phenotypically plastic may be equally fit throughout the depth distribution of the species, undoubtedly conferring some advantage on individuals with this propensity. Convoluted genotypes sustained greater losses among deep station transplants than among shallow station controls. Colonies also grew significantly slower at the deep station, suggesting that although shallow, convoluted genotypes were morphologically plastic, they were less fit at greater depths. Lowered survivorship and growth of convoluted genotypes at the deep station, appeared to reflect impediments to morphological change imposed by pre-existing surface features of this morph.

It may be postulated that genotypes of phenotypically plastic species should display greater fitness when transplanted to a new habitat, than genotypes of phenotypically stable species. Although it would be desirable to compare a number of measures of fitness between the two species, it was not possible to measure growth meaningfully for *Pavona cactus*. A qualitative comparison of survival rates and general health suggests that phenotypically stable genotypes of *Pavona cactus* did poorly when transplanted too far from their normal depth range, though still within the depth limits of the species. Specifically, the columnar genotype (see chapter 4), which is normally found between 3.5m and 7m, did poorly when transplanted to the 1.5m stations. Convoluted genotypes, which are normally found between 2m and 4m, did poorly when transplanted to the 1.5m, and 9m stations. Thus this study supports theoretical predictions of fitness for phenotypically plastic and stable species. However, further tests of fitness involving juveniles are required before it can be concluded that other factors, such as commitment to growth form or physiological adaptation, did not affect adult survival.

The mechanism by which colonies of *Turbinaria mesenterina* are able to vary their phenotypic response is related to the angle at which new polyps were added at the growing edge of the colony. The plane of polyp addition, or growth angle, clearly became more horizontal in convoluted colonies transplanted to the deep station. Conversely, the growth angle became more vertical in plate colonies transplanted to the shallow station. This latter change in angle was often visible as an upward bend in the corallum immediately distal to the alizarin stain line and preceding the beginnings of increased folding of the colony. Examining the vertically directed response in more detail: it can be assumed that budding along the edge of a colony continued to increase its circumference. However, the radius would not continue to increase at a commensurate rate, because the direction of colony growth changes and is predominantly upwards rather than outwards. This causes the edges of transplanted plate colonies to fold in order to accommodate the changed radius to circumference ratio. In much the same way, *in situ* shallow colonies, which are generally cone-shaped when less than 20cm in diameter, convolute because of predominantly vertical growth. It is

concluded that where light intensities are high, zooxanthellae are able to adapt to the degree of self-shading introduced by steeper growth angles. Moreover, the folded nature of the colony increases canopy development. Jokiel and Morrissey (1986) have demonstrated that canopy development increases the efficiency of energy utilization at potentially saturating light intensities, and thus provides a mechanism for photoadaptation to high light intensities. The response of convoluted colonies transplanted shallow-to-deep is the inverse of this process. As growth becomes more horizontal, budding along the circumference of the colony can be fully accommodated without the need for the edges to fold. Thus as laminae become progressively more horizontal, they become less convoluted.

Differences in the rate of budding also occur between morphs, as there are more polyps per cm^2 in the convoluted form (Section 6.3.3, Chapter 6) despite the equivalence in rates of linear extension. However, the relationship between rate of budding and the observed changes in growth angle following transplantation is unclear. To explain the observed changes, rate of budding would have to increase both, in plate colonies transplanted deep-to-shallow to accomplish increased folding, and in convoluted colonies transplanted shallow-to-deep to account for the flattening response (a lower growth angle would increase the circumference to surface area ratio). As growth angles decreased consistently with depth, it seems unlikely that rate of budding could determine colony morphology in *T. mesenterina*. Although it is possible that increased budding frequency may lead to convolutions in shallow water colonies over and above convolutions caused by changes in the angle of growth, further morphometric analyses are required to clarify the role of budding rate in determining colony morphology in this species.

Most previous analyses of growth form variation between species (Porter, 1976) and within individual species (Goreau, 1963, Barnes, 1973; Dustan, 1975), have emphasized the importance of differences in the surface area to volume ratios (SA/V) between growth forms, and the relationship between this ratio and light intensity. Porter (1976) argued that species with small polyps and high SA/V

ratios (branching and foliaceous forms) should be better suited for autotrophy whereas species with large polyps and low SA/V ratios (massive forms) would be better suited for heterotrophy. Moreover, he suggested that high SA/V ratios should be selected for whenever incident light energy could support the extra tissue, because of associated increased fecundity. Goreau (1963) hypothesized that discrepancies between skeletal and tissue growth processes at reduced light levels would lead to greater reductions in skeletal mass than in tissue surface area, and hence to the flattening of hemispherical colonies of *Montastrea annularis*. He reasoned that, whereas coral calcification is enhanced by light (Goreau, 1959) because of its close link with the photosynthetic process of symbiotic zooxanthellae (corroborative evidence subsequently provided by Vandermeulen *et al.*, 1972; Chalker, 1981; Barnes, 1982, 1985), tissue growth may be dependent on heterotrophic nutrition and be relatively independent of light. Thus, if tissue growth were faster than skeletal accretion, the colony would be forced to spread laterally. Barnes (1973) modified and developed this idea, hypothesizing that poorly illuminated colonies reached a critical radius at very small colony sizes, and were unable to support the low SA/V ratios typical of massive colonies. The critical radius was defined as the point at which skeletal accretion was insufficient to meet the demand for increase in the radius of curvature required to permit the insertion of new polyps. Thus ultimately, new polyps could only be added at the edges of the colony, leading to the flattened morph. Although Barnes immediately qualified his assumptions on the manner in which tissue and skeletal growth were integrated in an addendum, he upheld his basic tenets.

Evidence of photoadaptation of the photosynthetic process in *Pavona praetorta* subsequently led Wethey and Porter (1976) to question the existence of depth restraints on the calcification process. However, further work on translocation in light and shade-adapted colonies of *Stylophora pistillata* (Falkowski *et al.*, 1984) has shown that the amount of photosynthetic translocate assimilated is lower in deep than shallow colonies and that the translocate is nitrogen-deficient, hence of limited value for coral tissue growth. Therefore, although evidence exists to link calcium carbonate accretion with photosynthesis, the exact nature of the

coupling has yet to be clearly elucidated (see also Rinkevich and Loya, 1984). Moreover, skeletal growth in species of *Acropora* has been shown to involve separate processes of extension and infilling which may operate independently (Barnes and Crossland, 1980; Gladfelter, 1983; Oliver, 1984). Thus early analyses of morphological variation were based on relatively simple models of growth processes in corals. More recently, Graus and Macintyre (1976, 1982) have used computer simulations to demonstrate that flattening of hemispherical colonies of *Montastrea annularis* may be explained by changes in maximum corallite angle, intercorallite spacing, growth rates, and density with decreased light intensity. However, they still found it necessary to incorporate a miniumum increase in surface area, which was added peripherally at low light intensities, representing the discrepancy between tissue and skeletal growth.

Morphological changes recorded in colonies of *Turbinaria mesenterina* shed further light on the relationship between tissue and skeletal growth, and on processes controlling colony growth. Although this study supports previous suggestions that the flattening of colonies with increased depth is a response to maximize the exposure of polyps to light (Roos, 1967; Dustan, 1975; Graus and Macintyre, 1976), two lines of evidence suggest that the morphological response to light does not result from photosynthetically linked changes in calcification rates. Firstly, since colonies of *Turbinaria mesenterina* consist of essentially two-dimensional sheets or laminae, changes in growth form were not associated with changes in SA/V ratios. Thus discrepancies between tissue and skeletal growth do not need to be invoked to explain the change from convoluted to platelike. Secondly, new polyps are budded almost exclusively along the edges of the colony. Therefore the rate of polyp addition is directly related to the rate of linear extension in this species. Since linear extension rates were not significantly different between control colonies of the two morphs, photosynthetically-linked differences in calcification rates at different depths do not produce the different growth forms. It is suggested that new polyps are budded at the periphery of the colony at angles which are directly related to the intensity of light. If it can be assumed that growth in corals is coordinated at the level

of the colony, then it is possible that new polyps will bud at angles which introduce self-shading, only when light intensities are sufficient to counteract this effect. Thus steep growth angles (as measured from the horizontal) are only possible in high light conditions, and represent an optimal strategy for maximizing stratification of the photosynthetic tissues. This is directly analogous to the multilayer strategies of growth which are possible at high light intensities in tropical tree communities (Horn, 1971). Conversely, under low light conditions, only low growth angles occur. Although the angle of growth is linked to the zooxanthellae's requirement for light, the morphological change occurs in response to a threshold requirement for light rather than to a rate-controlled step in the calcification process. A recent study on *Galaxea fascicularis* by Hidaka and Yamazato (1982) provides corroborative evidence for this view of the direct role of light. When small portions of a single, isolated polyp were shielded, they found that buds were formed only on surfaces directly exposed to light. They suggested that light itself was necessary to induce budding, irrespective of its associated photosynthetic role. The greater branching frequency of shallow-water transplants in comparison to deep-water transplants of *Acropora formosa* (Oliver *et al.*, 1983) could also be interpreted as a direct response to light, though an indirect photosynthetic response linked to the calcification process cannot be ruled out in this case. Positive phototropism in the direction of colony growth has been demonstrated for branching (Kawaguti, 1937) and massive (Wellington, 1982) corals. This differs from the mechanism described here for *T. mesenterina*. Colony growth was not directed towards light at low intensities. Rather, the change in the growth angle represents a photoadaptive response to maximize the utilization of light energy.

In summary, this study demonstrated firstly, that morphological variation in corals has evolved via at least two distinct pathways. Adult colonies of *Turbinaria mesenterina* are phenotypically plastic. In contrast, adults of *Pavona cactus* are phenotypically stable, indicating that morphological variation is not environmentally induced in this species. Either behavioural selection at the settlement stage, or historical differences in patterns of settlement and mortality might be responsible for the present distribution

of morphs of *P. cactus*. As discussed in section 2.6, the lack of clear environmental separation between morph distributions favours the latter explanation. Secondly, this study demonstrated that deep-water genotypes of a phenotypically plastic species had greater fitness (in terms of growth and survival) when transplanted into the upper depth range of the species, than genotypes of a phenotypically stable species. Such evidence supports theoretical predictions of fitness for these two morphological strategies. However, shallow water adult colonies of the plastic species, *T. mesenterina*, were shown to be maladapted for low light conditions, illustrating a potential hazard of this strategy for sessile organisms living in an environment which changes with respect to life history stage, or through time. Finally, it is suggested that morphological change in *T. mesenterina*, involves a co-ordinated colony response to light and represents a photoadaptative response to control stratification of photosynthetic tissues. The orientation of colony growth is controlled directly by light intensity, irrespective of how light intensity affects photosynthetically-linked rates of calcification.