

DIFFERENTIATION IN CORAL POPULATIONS

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INTRODUCTION

The extensive and seemingly continuous range of morphological variation found within some groups of corals has created recurrent problems whose history was summarized by Yonge (1963). The original practice of describing each morphological form as a separate species was replaced towards the end of the nineteenth century by belief in the existence of a relatively few species in which a variety of growth forms were induced by different environmental conditions (e.g., Wood-Jones, 1907). This latter view was criticized in its turn by those who found a purely environmental explanation inadequate and suggested that genetic components were also involved (e.g., Crossland, 1931; Stephenson and Stephenson, 1933; Boschma, 1948). Current opinions were expressed by Yonge (1968) when he said "The final form of any coral is clearly the consequence both of genetic constitution and of environment," a conclusion which is still based largely on field observations. Although a need for experimental approaches has been recognized for a long time (e.g., Crossland, 1931), and although transplanting experiments were being conducted over 60 years ago by Vaughan (1910), no comprehensive experimental study of variation within any coral group has been published.

This paper presents the first data from a continuing series of experiments examining variation within a subgroup (*Isopora*) of the genus *Acropora*. The major objectives of this study are:

- a. To describe patterns of variation in morphological and physiological characters, and also of variation among intra- and inter-specific interactions;
- b. to assess the relative values of environmental and genetic contributions to these phenotypic characters;
- c. to relate patterns of variation to the environments normally occupied by the animals, and to identify important selective factors in each habitat;
- d. to examine the demographic consequences of phenotypic variation, and to compare the ecological and genetical structures of populations in different habitats;

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- e. to evaluate the evolutionary relationships within the group.

I am studying corals from five habitats near Heron Island at the southern end of the Great Barrier Reef. I chose Isoporan corals within the genus Acropora for this study because they are morphologically variable with massive, encrusting, branching and platelike forms; because these corals are widely distributed across the Heron Island reef, occurring in all habitats from close inshore to the bottom of the slope; and because Isoporan corals are usually relatively abundant, in some habitats being the dominant corals. Isoporan corals are easily recognized because they lack the single, enlarged apical corallites so characteristic of other Acropora. Instead, their apical corallites usually occur in clusters and tend to be rather similar in size and form to the other corallites (Brook, 1893). In this paper I only consider certain aspects of growth, survival, and intraspecific interactions during the first summer of the study. The experiments described in this paper are continuing.

MATERIALS AND METHODS

Sites

The locations of experimental sites and the names used to identify them are shown in Figure 1. I chose these particular sites because:

- a. They appeared to be very different from each other, both physically and biologically;
- b. each site seemed to be representative of a different, widely-distributed habitat type;
- c. the Isoporan coral fauna seemed to be dominated by a different morphological form at each site.

Except for the lagoon, the habitats extend more or less concentrically around the island so that any transect running over the reef from the island will cut across at least four habitats. In fact, many transects with an easterly component in their directions would also include the lagoon. Interpretation of the data is simplified when the sites are assumed to be positioned in a linear fashion along a transect such as that shown in Figure 2, an arrangement which is followed for the rest of this paper.

The experimental sites are described briefly in Table 1, which summarizes the apparent differences in physical and biological properties which were considered when selecting the sites. Quantitative data on these and other environmental components are being gathered in a continuing survey and monitoring program. On the crest, corals grow as a thin encrusting sheet over a hard limestone pavement, but at the other

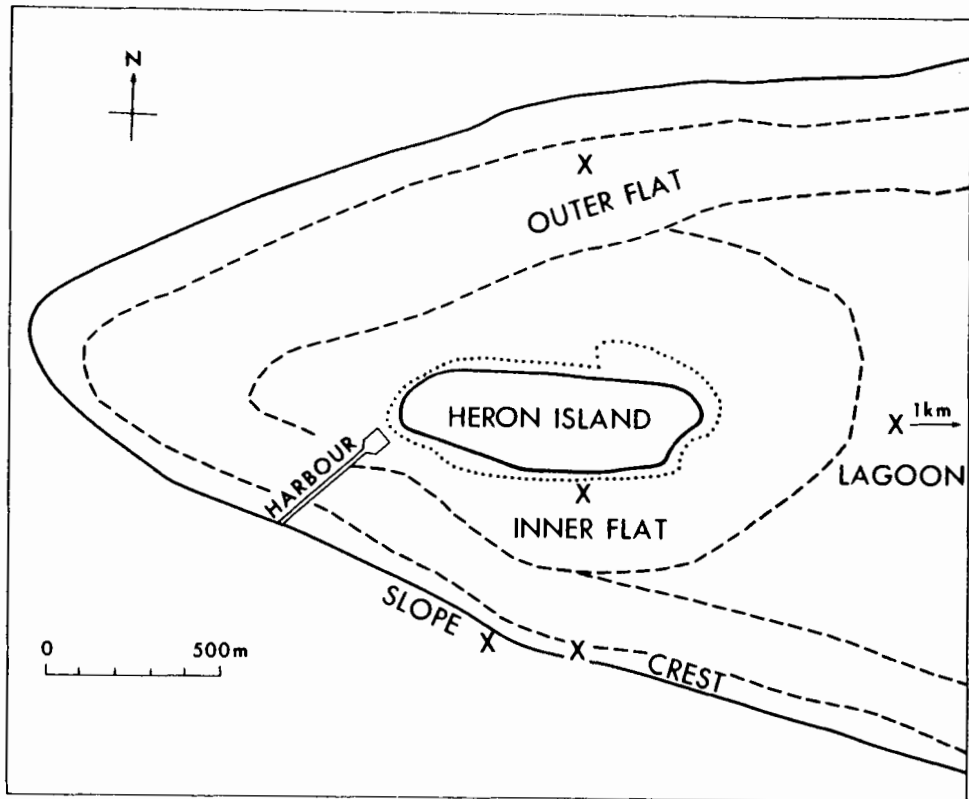


Figure 1. Map of western part of Heron Island reef showing locations (X) of experimental sites and approximate distributions of major habitats.

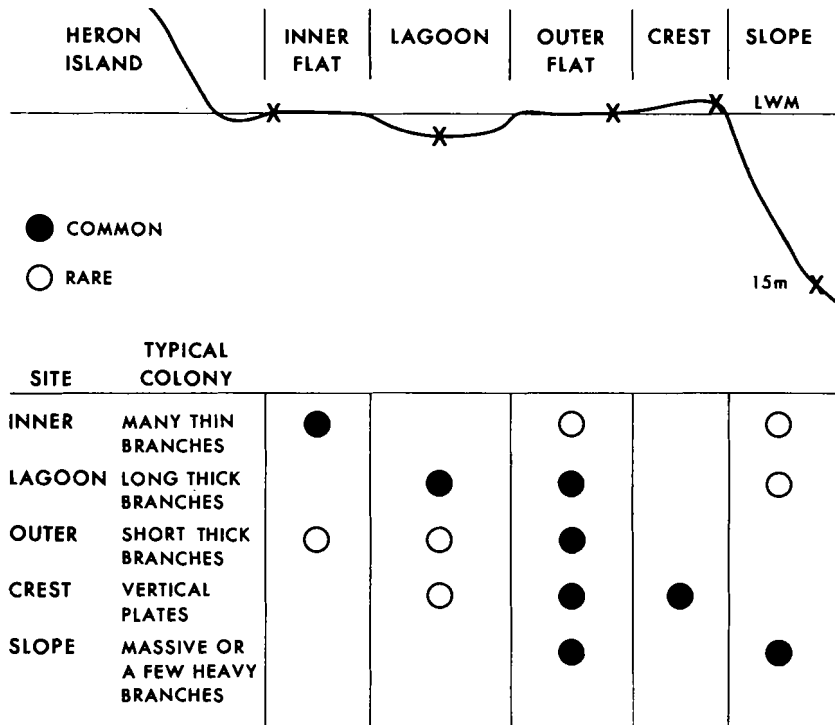


Figure 2. Stylized profile showing experimental sites arranged along an hypothetical linear transect (not to scale). Table summarizes distributions of chief morphological forms of Isoporan corals.

Table 1. General physical and biological characteristics of the experimental sites.

	Experimental Site				
	Inner Flat	Lagoon	Outer Flat	Crest	Slope
Approx. distance from base of beach rock (m)	25	2,000	600	500	550
Approx. depth at LWS (m)	0.25	1.0	0.5	0.0	13.0
Wave action	slight	slight	medium	heavy	none
Major water mass	lagoonal	lagoonal	oceanic	oceanic	oceanic
Silting	heavy	heavy	slight	none	heavy
Light intensity	high	high	high	high	low
Daily physical fluctuations	high	low	medium	high	low
Coral cover	low	low	medium	high	high
Coral diversity	low	medium	high	high	high
Macroscopic algal standing crop	heavy	slight	medium	none	none
Calcareous algal standing crop	slight	slight	medium	heavy	slight
Borer infestation of corals	slight	slight	heavy	medium	heavy

four sites, masses of live and dead coral project above a sandy bottom. At all sites except the slope, the tops of some corals may be exposed at low tide, and the depths given in Table 1 for the inner flat, lagoon, and outer flat indicate the amount of water covering the sand, not the coral.

Corals

During the preliminary surveys I came to recognize five fairly distinct morphological classes of Isoporan corals, although many intermediate forms also exist. The lower part of Figure 2 is a table which summarizes the distribution of these forms at the experimental sites. Each form is most abundant at one particular site (shown by the diagonal of the table), and I have regarded each form as characteristic of the site where it is most abundant; I am using the name of that site to identify the form of coral. Most forms also occur at one or more other sites, at relatively low frequencies (usually <5% of the Isoporan corals). The outer flat is unique, because all forms are present and relatively common. What I call the outer flat form is simply the most abundant (about 40-50%).

The chief morphological differences among the corals at each site are summarized below:

- Inner Flat: orange-brown; branches frequently and irregularly with many incipient branches on sides; bases of branches tend to fuse giving a massive center to colony; relatively small tubular corallites.
- Lagoon: yellowish-brown; branches infrequently and regularly (10-20 cm apart); branches remain separate and of similar diameter (about 2 cm); relatively small, thick-walled corallites adpressed to branch.
- Outer Flat: usually greenish-brown; similar to lagoon form but branches more frequently (less than 10 cm apart); corallites tend to be thinner-walled and more closely packed.
- Crest: dark orange-brown; encrusting basal plate produces thick vertical plates after base exceeds 10-20 cm diameter; small, closely-packed corallites adpressed to sides of plates.
- Slope: dark purplish-brown; massive cones or a few heavy branches; relatively large, well-spaced thick-walled corallites, tending to become tubular.

Transplanting techniques

Small pieces of coral (about 5 cm long) broken from a large colony were mounted in shallow polyvinyl chloride (P.V.C.) cups (8 cm diameter, 3 cm deep). Each cup was filled with quick-setting concrete made from finely sieved coral sand, cement, seawater and "Sealwall Rapid Setter for Cement" (Sealwall Trading Co. Pty. Ltd., Sydney); as temperatures and water content of the sand changed, the proportions were altered to give a mixture which set in 5-10 minutes. The broken end of the coral was pushed into the concrete just before it set, and the concrete was leveled to form a smooth, horizontal surface flush with the edge of the cup. As soon as the surface was hard to the touch, the cups were placed in a shallow protected place on the inner reef flat for 24 hours while the concrete cured. Corals were rarely out of water for more than 10 minutes.

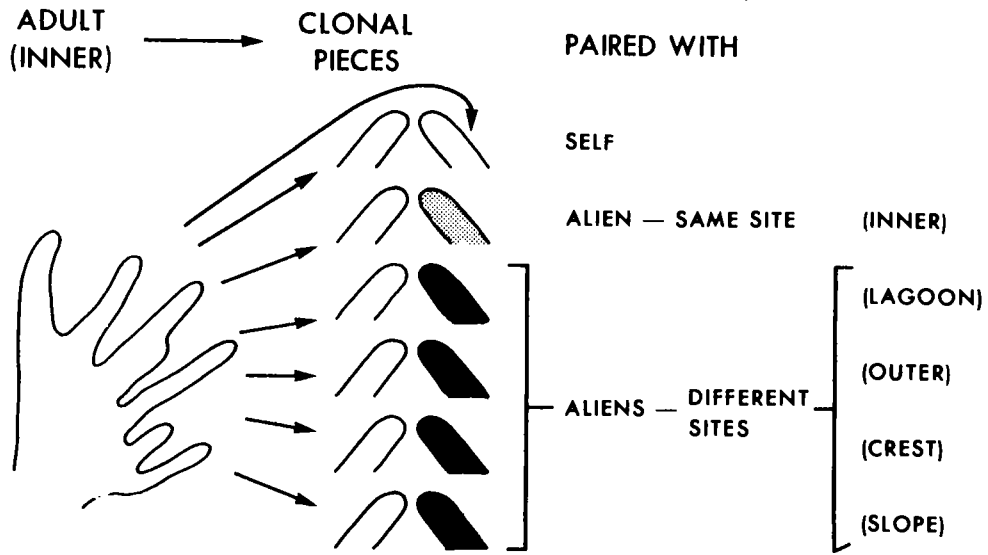
The cups are mounted at the intersections of square grids made from a steel mesh (6 mm rods welded at 20 cm centers) normally used for reinforcing concrete. Each grid holds nine cups attached by two bolts projecting from the bottom of each cup. At the crest site, each grid is fastened to a smooth patch of bare limestone by steel straps attached to long bolts embedded in the rock. At the other sites, four grids are held on a 120x120 cm steel frame, bolted onto four heavy concrete blocks which raise the frame 10-15 cm above the sand. All metal parts are mild black steel and not treated in any way to prevent rusting or corrosion, neither of which are yet serious problems after 18 months of submersion.

For examination, the grids are collected and brought into shallow water on the inner flat near the laboratory. As required, the cups are removed from the grids, sessile organisms and silt are scraped from the cups and concrete, and the cups are placed in large, aerated tanks in the laboratory.

INTERACTIONS BETWEEN DIFFERENT FORMS

This experiment was designed to see whether certain forms of coral "recognized" other forms as being different, by responding with morphological changes in the region of contact as the two corals grew together. Four large, morphologically typical colonies were collected at each site and brought back to the laboratory. Each colony was broken into eight genotypically identical pieces suitable for transplanting. The pieces were arranged in pairs, and each pair was concreted into a single cup with their growing tips in contact.

Figure 3 illustrates the basic design of the experiment, using an inner flat colony as an example. As a control, two pieces of the same colony were concreted together to provide the interaction of that colony with a piece known to be phenotypically and genotypically identical. Secondly, one piece was paired with a piece from a different, but morphologically similar, colony from the same site. Finally, one piece was paired with a colony from each of the four other sites. Theoretically



DESIGN : 5 SITES × 4 ADULTS × 6 PAIRINGS

START : MARCH 1975 — CONTINUING

Figure 3. Summary of the design of an experiment examining the interactions between Isoporan corals. An inner flat colony is used as an example.

there could be 30 possible pairings in the complete design (5 with self, 25 with aliens). However, the experimental design for aliens was symmetrical about the major diagonal (Table 2), so the ten treatments below the diagonal were not set up as separate pairings. Initially there were four replicates of each of the 20 pairings used; I discarded eight pairings before the experiment began, because one or both corals appeared adversely affected by the concreting. Horizontal and vertical photographs were taken of each pair, and on 25 March 1975 the remaining 72 pairs were placed on two frames at the inner flat site. On 24 June 1975, all the corals were healthy except for one pair which had been dislodged, possibly by a turtle.

In the controls (paired with self) the two pieces fused together indistinguishably wherever they came into contact, but there were no signs of any changes in either growth rates or normal growth patterns of either piece. However, when a coral was placed in contact with an alien, both corals usually responded, (A) by rapid differential growth towards the other coral in the region of contact, and (B) by the production of abnormal skeletal tissue in the region of contact. The responses of all interactions between alien corals are summarized in Table 2. The table is symmetrical about the major diagonal, because each piece was considered firstly with respect to its origin and secondly as the alien for the other member of the pair. Only the signs of some interactions change across the diagonal.

There were two qualitatively distinct categories of abnormal growth. The commonest, called "Fill" in Table 2, was formed when both corals filled the space between them by growing towards each other. Frequently, both corals grew about equally, so that the plane of contact lay more or less in the middle of the original space. The surface of the zone of abnormal growth along the contact varied in width (2-5 mm), color and texture. Often the surface was smooth, but it sometimes contained large pores and small corallites. The line of contact, when visible, varied from a thin line to a deep groove.

The second interaction involved the overgrowth of one coral by the other. The overgrowth consisted of a thin layer of skeleton covered with normal corallites except for a smooth zone 2-5 mm wide along the advancing edge. Usually there was very little growth by the subordinate coral in the area of contact. Overgrowth occurred chiefly in those pairings which included a crest coral, and in every one of these cases the nature and direction of overgrowth was clearly visible. Some overgrowth also occurred in pairings between two similar corals from the same site, but in these cases it was not always easy to distinguish overgrowth from filling.

The only completely unpredictable responses were those between crest and outer flat corals which included both filling and overgrowth, and also involved what appeared to be the only example of aggression by means of extra-coelenteric digestion such as that described by Lang (1973).

Table 2. Growth responses of two alien corals placed in contact at the Inner Flat experimental site from March to June 1975. Numbers are the total numbers of colonies from that origin which gave a particular response. (Responses: NIL = no visible response; FILL = both corals grew into the space between them; OVER + = coral spread over the surface of the other; OVER - = coral was covered by the other; AGGRES + = extra-coelentric digestion of other; AGGRES - = digested by other.)

Origin of Coral	Paired with Coral from:				
	Inner Flat	Lagoon	Outer Flat	Crest	Slope
Inner Flat	2 FILL 1 OVER + 1 OVER -	4 FILL	4 FILL	1 OVER + 3 OVER -	2 FILL
Lagoon	4 FILL	4 FILL	2 FILL	3 OVER - 1 NIL	3 FILL
Outer Flat	4 FILL	2 FILL	3 FILL 1 OVER -	2 FILL 1 OVER - 1 AGGRES +	2 FILL 1 OVER +
Crest	3 OVER + 1 OVER -	3 OVER + 1 NIL	2 FILL 1 OVER +	3 FILL 1 OVER -	4 OVER +
Slope	2 FILL	3 FILL	2 FILL 1 OVER -	4 OVER -	2 FILL 1 OVER + 1 NIL

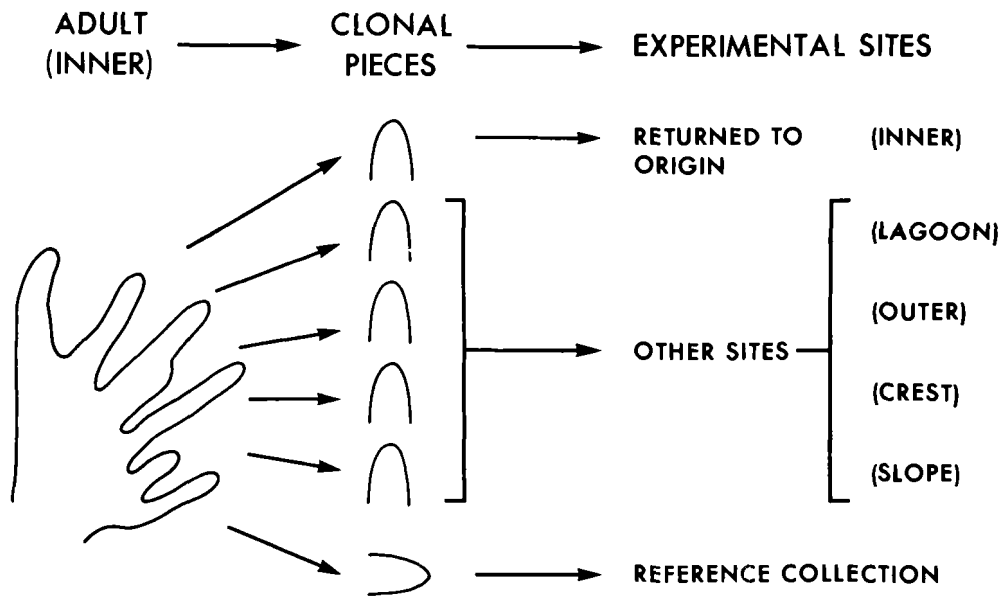
All the corals readily distinguished between a piece of themselves and all other corals, and they also seemed able to recognize several classes of alien corals. These data support the view (e.g., Hildemann, 1974) that recognition systems analogous to immunological systems in higher organisms exist among corals and suggest that the various forms of coral may be genetically different.

GROWTH AND SURVIVORSHIP

This experiment was designed to assess the relative contributions of genetical and environmental factors influencing a variety of phenotypic characters of ecological importance. This paper only considers some of the survivorship and growth data, but morphological changes and interactions with other organisms are also being examined. Some aspects of reproduction will be considered later. In the basic design (summarized in Figure 4), 20 colonies were collected from each site (referred to as "origins"). Each colony was broken into five genotypically identical pieces which were mounted in separate cups before transplanting to the "experimental" sites. One piece was returned to the origin, and one piece was transferred to each of the other four sites. A sixth piece was preserved as a permanent reference specimen. The first transplants were made in April 1974, but the design was not completed until November 1974 when the crest site was established.

The corals are being examined at approximately three monthly intervals. At each examination they are photographed under standard conditions, the area of dead coral is recorded, and the positions of boring organisms are mapped. Finally, the volume is measured by displacement. The coral is lowered upside down into a cylinder of water so that the edge of the cup rests on the edge of the cylinder. The coral is removed and excess water is allowed to drip back into the cylinder, which is sealed with a flat plastic plate. The cylinder is then refilled through a small hole in the plate using a self-filling 10 cc syringe, and the amount of water required to refill the vessel is the volume of the coral. This method gives results repeatable to within 0.2-0.4 cc.

The data presented here came from the period beginning in November 1974 and ending in late June 1975. This more or less corresponds to the entire summer growth period at Heron Island, because in 1974 there was no measurable growth between June and November. Table 3 summarizes the preliminary analysis of growth data. Within each row the performance of the same set of genotypes derived from a single origin can be compared across the five experimental sites. The final value in each row is the average performance of that array of genotypes in all habitats, and these values can be used to rank the performance of the various forms with respect to origin. Thus corals from the inner flat and lagoon grew relatively fast whereas slope corals grew slowly in all habitats where sufficient individuals survived to give adequate data. Growth of other forms was intermediate.



DESIGN : 5 ORIGINS × 20 COLONIES × 5 EXPERIMENTAL SITES

START : APRIL — NOVEMBER 1974 — CONTINUING

Figure 4. Summary of the design of a reciprocal transplant experiment examining growth and survivorship of Isoporan corals in five habitats. An inner flat colony is used as an example.

Table 3. Mean increase in volume (%) from November 1974-June 1975 of cloned transplants from each origin. Sample sizes are given in parentheses.

Coral Origin	Experimental Site					Mean Growth (Origin)
	Inner Flat	Lagoon	Outer Flat	Crest	Slope	
Inner Flat	49(18)	66(18)	101(23)	52(18)	35(7)	66
Lagoon	58(19)	76(23)	89(26)	60(7)	33(7)	71
Outer Flat	41(17)	56(20)	73(22)	36(6)	34(9)	53
Crest	44(21)	54(22)	74(20)	58(21)	45(8)	56
Slope	12(2)	30(4)	-	32(2)	-	26
Mean Growth (Habitat)	47	62	85	53	37	61

Source	Analysis of Variance				
	df	SS	MS	F	
Origin	4	21067	5266	5.97	P<.001
Site	4	83827	20956	23.76	P<<.001
Origin x site	14	11432	816	.92	P>.05
Error	331	291929	881		

Each column in Table 3 gives the average performance of the five sets of genotypes (i.e., from five origins) when growing under one set of environmental conditions. The last entry in each column is the mean growth of all forms of corals placed in that particular habitat, and comparison of the column totals provides a ranking of the overall favorability of the habitats for these corals. Among surviving corals, all forms grew fastest at the outer flat site, and slowest on the slope.

The effects of both origin and experimental site were highly significant ($P < .001$). Although experimental site contributed approximately four times more to the total variation than did the origin, the analysis of variance suggests that corals from at least some origins have growth rates different from those of the other forms.

A similar analysis of survivorship from November 1974 to June 1975 is given in Table 4, which shows a significant effect of experimental site approximately twice as strong as the effect of origin. By themselves these data are of limited value because, during this summer period, mortality was the lowest observed so far during the study. However, it is interesting that the considerably heavier mortality during the previous winter (before the design was completed) was ranked in much the same way with respect to both origin and experimental site. Therefore, my tentative conclusions are that: (A) most forms survived well at the outer flat and crest sites and poorly on the slope, and (B) corals derived from the inner flat survived well in all habitats, whereas corals from the slope survived very poorly. The missing cells and unequal sample sizes in Tables 3 and 4 are largely the results of unexpected damage to many corals which were cemented at low temperatures ($< 20^{\circ}\text{C}$) during August 1974, and do not reflect patterns of mortality under the experimental conditions. In a subsequent experiment, much larger sample sizes will be used to assess survivorship more accurately.

DISCUSSION

The interactions and the survivorship and growth data suggest that the phenotypes of the various forms differ biochemically and physiologically as well as morphologically. Possible explanations for these patterns of variation fall into four general classes which are not necessarily mutually exclusive.

1. Phenotypic plasticity: The simplest explanation is that the individuals are genetically similar, and that the observed differences are induced by local environmental conditions. It is certainly true that physiological characters are greatly influenced by environmental factors (Tables 3 and 4), and casual examination of the photographs suggests that some morphological changes have followed transplantation. However, there certainly has not been a spectacular morphological convergence among the transplants to the form normally found in each habitat: in November 1975 (19 months after transplanting began) the origin of most individuals was still obvious from their morphological appearance alone. It is difficult to explain the existence of all forms in relatively high

Table 4. Survival (%) from November 1974-June 1975 of cloned transplants from each origin. Sample sizes are given in parentheses. Sums of squares are weighted by sample sizes.

Coral Origin	Experimental Site					Mean Growth (Origin)
	Inner Flat	Lagoon	Outer Flat	Crest	Slope	
Inner Flat	95(22)	95(21)	100(23)	100(18)	100(8)	98
Lagoon	83(24)	96(22)	100(26)	83(5)	58(11)	88
Outer Flat	75(21)	83(20)	87(23)	75(6)	69(11)	79
Crest	100(22)	92(24)	95(21)	100(21)	46(13)	90
Slope	75(4)	60(5)	-	100(2)	-	73
Mean Growth (Habitat)	87	90	95	94	65	88

Source	Analysis of Variance				F	
	df	SS	MS	F		
Origin	4	16122	4031	2.40		P>.05
Site	4	32313	8078	4.81		.05>P>.01
Origin x site	14	23515	1680			

frequencies on the outer flat on the basis of phenotypic plasticity. Such an explanation would require: (A) habitat differences over a few centimeters as great as the environmental variation found over the entire Heron reef, and (B) the persistence of these microhabitat differences for many years. Alternatively, it is possible that phenotypic characters are induced at one point in the individual's development and then remain fixed for the rest of its life, but data from analogous studies (e.g., on terrestrial plants) provide no reason to expect simultaneous fixation of a wide range of morphological and physiological characters in this way. The interaction experiment suggests that the forms differ biochemically in a manner analogous to immunological interactions in higher organisms; it is particularly difficult to use phenotypic plasticity to explain biochemical differences, because molecular configurations are usually closely related to the genotype of the individual.

2. Species: The second possible explanation is that each form belongs to a different, reproductively isolated species: each species has a preferred habitat, but its range includes some habitats preferred by other species. All physiological and morphological differences, as well as the interactions between corals could then be explained largely by genotypic variation. Carden Wallace (Personal communication) of the Queensland Museum has examined much of this material and has compared a representative collection with type specimens of Isoporan corals held in European and North American collections. Following the usage of Wells (1954), the lagoon form seems to conform reasonably well to Acropora palifera forma α ; the slope form resembles A. palifera forma β ; and the crest form is similar to A. cuneata. The outer flat form seems to fit most closely to A. brueggemanni as used by Brook (1893). Unfortunately the inner flat form does not correspond well to any of the Isoporan type specimens, even though this form is commonly called Acropora cuneata by people working at Heron Island. The greatest problem with this explanation is the presence of many morphologically intermediate forms, especially on the outer flat. In particular, lagoon and outer flat forms seem to merge indistinguishably; intermediates between inner flat and crest and between outer flat and crest forms are also common; and most other possible intermediates to exist.

3. Genetic isolation: This explanation assumes that the corals in each habitat are discrete, geographically and reproductively isolated subpopulations of a single species. The differences may result from founder effects, or from long-term selective pressures. It has been suggested that coral planulae settle very rapidly after release and in the immediate vicinity of their parents (e.g., Duerden, 1902). This localized settling would enhance genetic isolation, although Connell (1973) questioned the effectiveness of limitations on the dispersal of coral larvae. However, Connell (1973) also pointed out the importance of pieces broken off existing colonies as a source of recruits within a habitat. The outer flat could either be a habitat in which all genotypes are present, or one to which larvae can disperse from all habitats. The wide distribution of similar habitats with similar forms over the Heron reef (about 8 km long), the sharp boundaries often found between

habitats, and the usual occurrence of three distinct habitats (slope, crest, outer flat) within a distance of about 100 m all tend to argue against geographic isolation.

4. Local selection: The final explanation assumes that the maximum range of genotypes will be present among settling larvae in every habitat, either as a result of genetic recombination within each habitat or by dispersal from other habitats. In each habitat, adult colonies will be those individuals which have survived selection during the present generation; they represent small subsets of the original ranges of genotypic and phenotypic variation. Different local selective pressures acting within the lifetime of most living colonies will account for the forms found in each habitat. Presumably, various selective factors will act on different phenotypic characters, or on the same characters in different ways. The existence of intermediates and the different assemblages of forms in each habitat is compatible with this explanation.

Any realistic description of the causes of variation observed in Isoporan corals at Heron Island will involve some combination of the discrete explanations given above. While phenotypic plasticity certainly exists, the evidence so far suggest that its effects are relatively minor compared with those of underlying genotypic variation. More than one species may be present, but I think it highly improbable that there are five species. At present I am treating all forms as belonging to a single species Acropora palifera. Complete geographic and reproductive isolation seems unlikely; but there may well be partial isolation so that, at least in some habitats, recruits tend to come from parents within that habitat. Such a process would tend to enhance and perpetuate the effects of selection from one generation to the next. However, my tentative conclusion is that all of these processes are secondary to the effects of local selective regimes acting in every generation.

SPECULATIONS

I propose that the selective regimes are complexes of many different factors. Table 1, which lists apparent differences among the sites, also summarizes a few of the extreme conditions which may be selective factors. Not only will the factors vary from habitat to habitat, but any one factor may vary in frequency, duration, intensity and predictability of selection. To illustrate these points, I shall discuss the three most extreme sites, considering the phenotypic properties of adults from those sites, and suggesting selective regimes which could have favored them. The transplant experiment gives data on the growth and survival of each form in a range of environments. Growth can be considered primarily as a measure of the responses of a coral to the favorable aspects of its environment, while survivorship can be regarded as a measure of the ability of individuals to tolerate unfavorable conditions. Thus, the growth data in Table 3 can be used to rank the overall favorability of the five habitats, and also to rank the

abilities of the five forms to respond to favorable conditions. Similarly, Table 4 provides rankings of the habitats in terms of their adverse features, and ranks the forms on the basis of their tolerance of a range of adverse conditions.

The outer flat is generally the most favorable environment for Isoporan corals. Physical conditions seem relatively benign (Table 1), and all forms grew fastest and survived well on the outer flat. All forms normally occur on the outer flat (frequently side by side), and the simplest explanation is that this distribution is maintained by a general absence of selection; in such an environment, almost all genotypes will survive and grow well. Outer flat corals did not perform particularly well after being transplanted to other sites; indeed, even at the outer flat they did not survive or grow as well as some of the other forms. These results would be expected if even relatively unfit genotypes are likely to survive and contribute to a rather intermediate average performance.

The slope is the worst environment for Isoporan corals, with the lowest growth and survival rates for all forms. The inner flat is also an unfavorable environment, with low average growth rates and relatively poor survivorship. However, the phenotypes of corals living in these sites are very different from each other, implying that they are the products of quite different selective regimes. Corals from the slope had the lowest survival and growth rates, whereas inner flat corals grew very rapidly and survived extremely well in all habitats.

I suggest that the slope selects for a specialized phenotype which is adapted only to slope conditions and is not pre-adapted for other conditions. I propose that this specialization involves adaptation to a few very predictable, but almost continuously unfavorable factors. The slope site is close to the lower limit of Isoporan growth at Heron Island; low light intensities, heavy silt loads, and possibly limited food supplies seem to be likely adverse factors.

In marked contrast, the inner flat seems to select for generalized, all-purpose phenotypes which are pre-adapted to tolerate a wide range of adverse conditions and which are well able to exploit any favorable conditions. The most likely selective regime to produce this outcome would be one where many different adverse factors operate more or less independently, and the action of most factors is relatively unpredictable. Thus, survivors will have persisted through many different adverse conditions. It seems likely that the inner flat may experience great extremes of temperature, salinity, radiation, exposure (and dessication), low oxygen tension, silting, overgrowth by algae, and probably other factors, although it is unlikely that any of these conditions would persist for extended periods. I propose that frequent adverse events are separated by relatively short periods of good conditions, and that selection favors rapid responses to changing

conditions. To persist, individuals must be able to exploit even short periods of favorable conditions. Thus, what is simply an opportunistic response on the inner flat would result in prolonged high growth rates on the outer flat.

I must stress that these conclusions are highly speculative, based on data covering less than eight months; but they are presented now to indicate the scope of this project. Adult corals have survived selection over many years; during this time relatively rare events not yet observed in this study may have had strong cumulative effects.

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