

AN INFORMATION ANALYSIS APPROACH TO ZONATION  
PATTERNS OF THE CORAL GENUS ACROPORA  
ON OUTER REEF BUTTRESSES

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INTRODUCTION

The coral genus Acropora poses formidable problems for both taxonomists and ecologists. Most skeletal features usually used in coral taxonomy are reduced or absent in this genus. A high degree of morphological versatility is attained by means of an axial branching pattern, where a central polyp increases in length and buds off radial polyps from its sides. Any radial polyp has the potential to become axial itself, and to introduce a secondary branching situation. The relative importance of secondary branches is highly variable and commonly the growth form pattern is dominated by the side branches rather than a main stem, a situation superficially similar to that seen in Angiosperm plants (Vermeij, 1974).

With such a flexible growth scheme, adaptive solutions might be made by the individual colony as well as by the species, and the task of determining even morphological species limits within the Acropora has not yet been accomplished. The situation still existing is basically that described for corals in general by Hoffmeister (1925): "Ordinarily, if we think a specimen is far enough removed from a recognized and described type to suite our own personal views, we give it another specific name."

In the Great Barrier Reef Province, this genus dominates the coral cover of the reef front. In reefs of the central Great Barrier, which are without an algal rim, the most luxuriant and diverse Acropora assemblages are usually along the south-western to southern reef front. These give an impression of some structural zonation patterning, possibly determined in terms of colony shapes. One of these reefs ("Big Broadhurst" Reef, 147°44'E; 18°15'S) (see Figure 1) was chosen as the study area. The reef buttresses here support an Acropora assemblage of such abundance that other genera are almost entirely excluded (see plates 1, 2 and 3). I was interested to see how the reef buttresses might be defined in terms of the patterns of Acropora distribution and abundance, and whether particular characteristics of the Acropora present might be responsible for the patterns.

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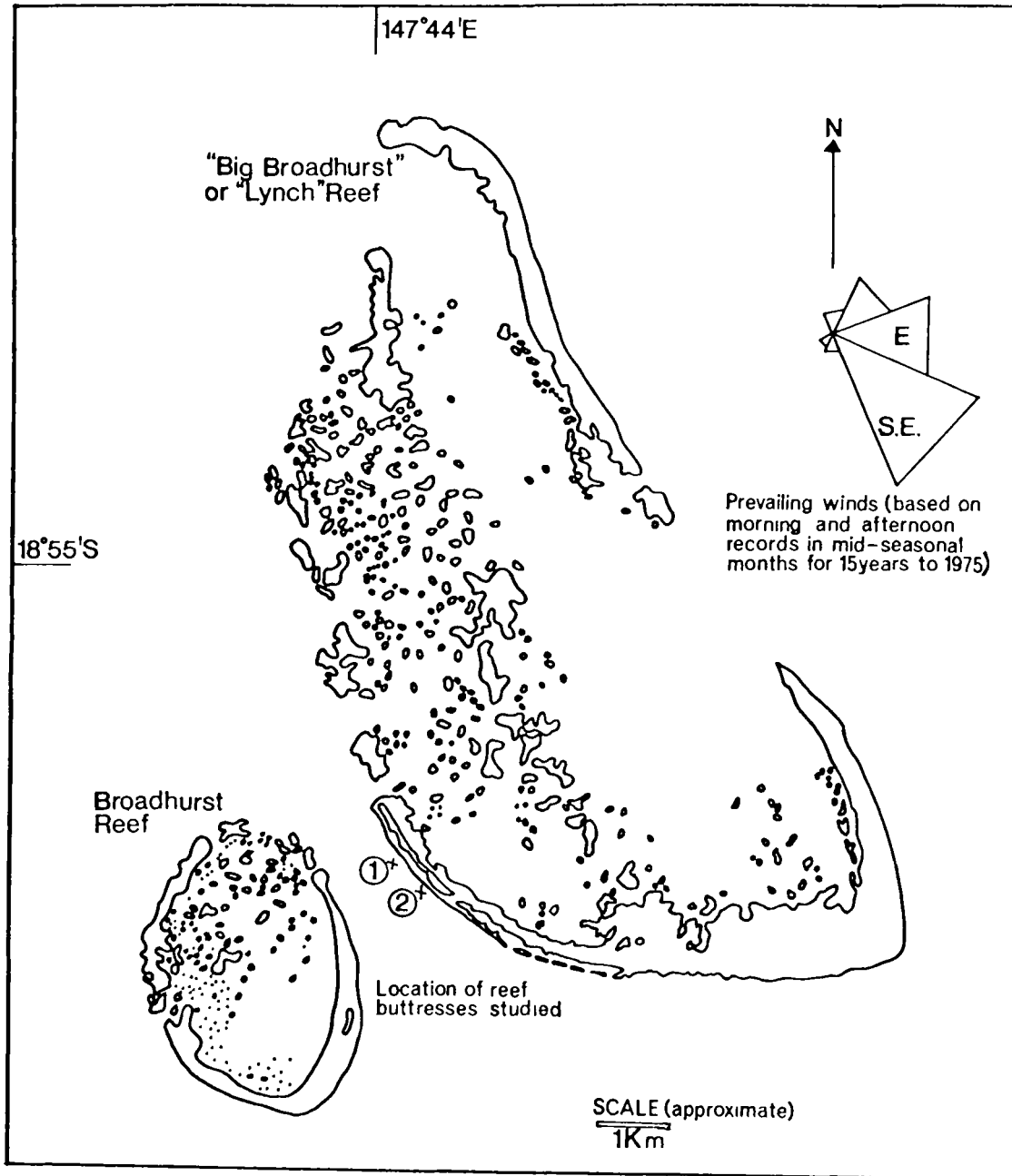


Figure 1. Map of study area, with crosses indicating positions of first and second reef buttresses studied.

## METHODS

Two reef buttresses about 400 m apart were studied, using the line transect method adapted from plant community methods by Loya (1972). Line transects of 10 m length and marked in meter sections were run parallel to the reef front on these buttresses, at 1 m intervals. The transect series began on the outer reef flat, 12 m before the beginning of the drop-off, and proceeded outwards across the flat and down the reef slope until no more Acropora were encountered (see Figure 2). Values are given in parentheses for those transects in which the transect number was altered for computer analyses. Transects devoid of corals were not used in the analyses.

The 10 m transect length was necessitated by the shape of the buttresses, which have, as well as a frontal face, a less-defined face dropping to the floor of the surge channel at about 10 m from the reef top. A 10 m transect length was the maximum at which a uniform depth would be maintained for the whole sample in some sections of the slope.

Each transect was worked in the following way: each Acropora colony under the line was identified with a field name, measured, and a piece of the colony collected. The field identification was useful as a cross-check in later laboratory identification.

In the laboratory the cleaned skeletal specimens were examined for morphological continuities, and identified from the literature with the aid of accumulated comparative material and type material on loan.

A total of 41 "species" could be differentiated on the basis of morphological continuity and similarity in some live characteristics. Each of these was given a code number, appended if possible with an identification. It was highly probable on my evidence that the colonies in each of these groups were members of a single population. A second sorting lumped together those "species" which, despite certain discontinuities, I consider may prove to be single species. This group, "the lumped species," had 27 members.

The material was then reclassified in terms of the shape of the colony, expressed as 11 shape categories, then in terms of the structure of the radial corallites, expressed in nine categories.

### Coding

Each transect could now be described in terms of the members present and their abundance (in terms of extent under the line). This information could be sorted by hand or by computer.

### Sorting

A set of classificatory and ordination programs was run on the transects. The diversity measure was an information statistic which used the abundance data. The classificatory program, now in general

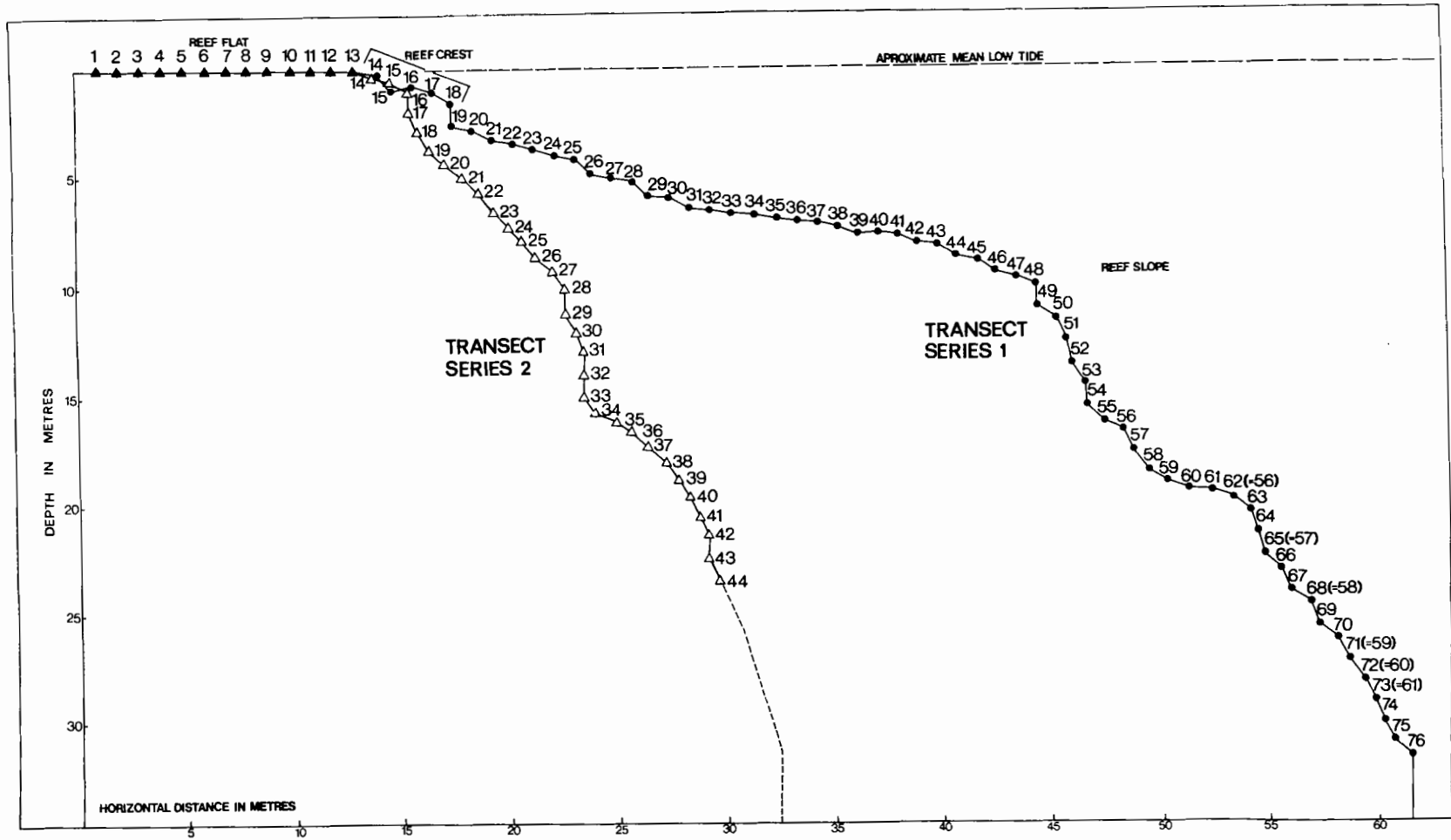


Figure 2. Profiles of the two buttresses studied. Numbers represent transect positions. Bracketed numbers are given where the transect number was altered for the programs.

use in Australia, is referred to as CENTPERC 2 (see Dale, Lance, and Albrecht, 1971). The ordination program, code-named GOWER, sorts the information content of each transect into seven coordinates and plots the first three of these (Gower, 1966). Both programs were analysed by further programs ("GROUPER" and "GOWERCORE"), which assess the contribution of the various characters to the result. These programs were chosen and run by Mike Dale, of CSIRO Division of Tropical Agronomy, Brisbane. In addition to these normal (i.e., R-type) analyses, an inverse (i.e., Q-type) package of the same programs was run for the first series "unlumped species." The program devised by Williams and Lambert (1961) was used (see also Sneath and Sokal, 1973, p. 436).

## RESULTS

### The Ordination Programs

Ordination methods probably allow a less artificial result than classifications, which assume groupings of some sort must be obtained (Greig-Smith, 1964, p. 158). The ordinations for all categories in this study gave a similar pattern: when consecutive transect-numbers were joined an overall horseshoe-shaped curve resulted (see Figures 3 & 4). This result is classically obtained with ordination of serially-arranged samples (e.g., for temporal series in archaeology, Kendall, 1971). The curve indicates the non-linear nature of the data. A strong disjunction can be seen in the pattern in the first axis. All of the reef flat values are highly negative, reef crest values (i.e., transects to either side of transect 12) tend to be low negative, and reef slope values are positive. In the second axis a slight disjunction is related to abundance.

### The Classificatory Programs

Results of these are expressed as a series of dendrograms in Figure 5. The expectation from these programs is that any zonation patterns will be shown up by the strength of grouping amongst neighboring transects. In addition, grouping amongst adjacent transect-groups will give an indication of a sequential pattern in the zonation.

Both phenomena occur. The contents of the groups are of primary interest, and the arms of the dendrograms are, of course, free-swinging around the points of fusion. In the figures these are allowed to fall as far as possible into positions which will best indicate any sequential pattern in the results:

- a. It will be seen in all cases that a strong reef flat grouping (transects 1 to 9 or 10) occurs.
- b. Transects on either side of the reef crest line (transect 12) are capricious, but tend to associate more with reef flat transects than with those below. These transects have attributes from both the reef flat and reef slope, and no corals exclusively occur here.

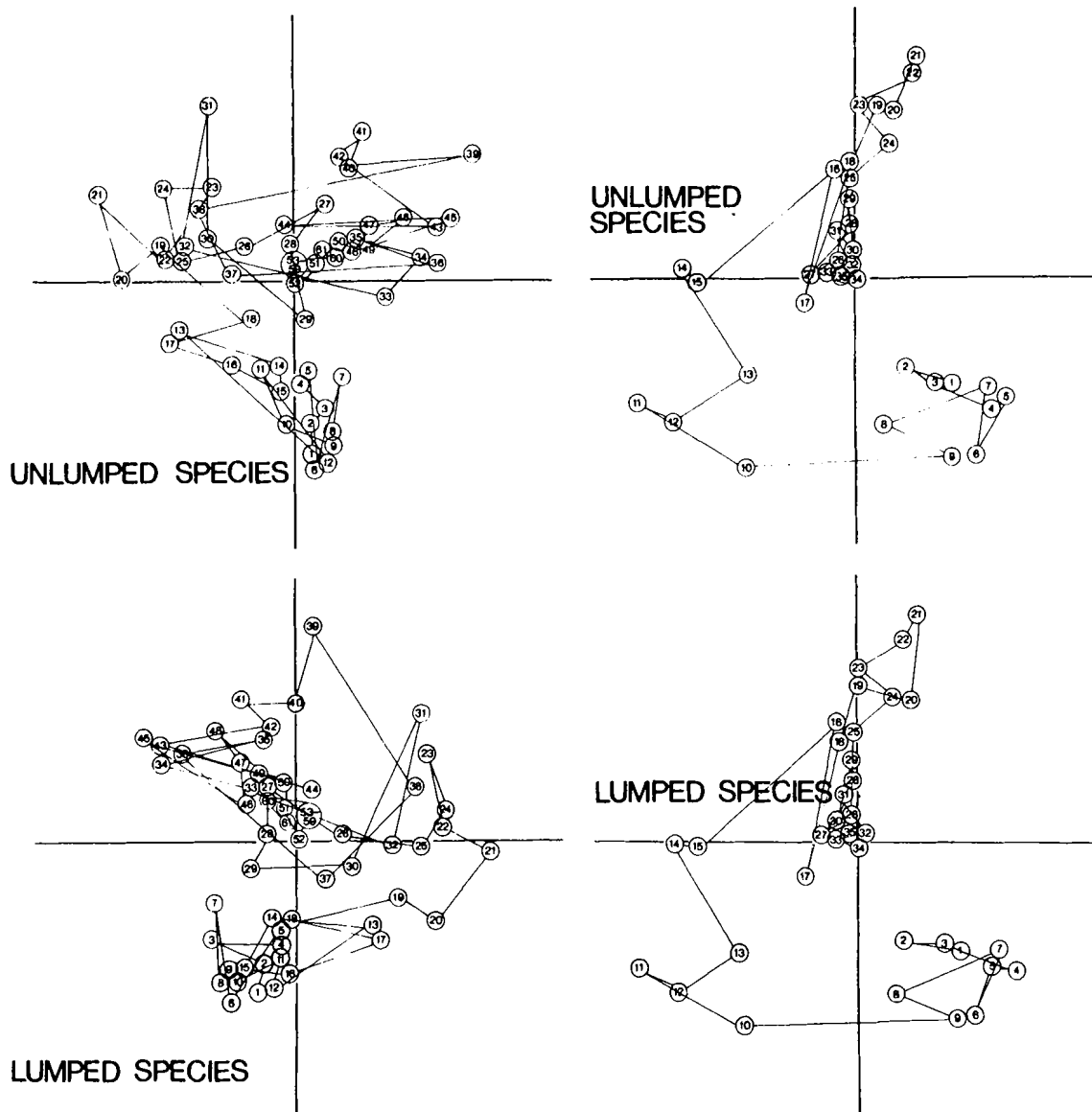


Figure 3. Ordination along first two axes for unlumped and lumped species categories: left side series 1, right side series 2. Circled numbers represent transects (sites). Consecutive site numbers are joined by a straight line.

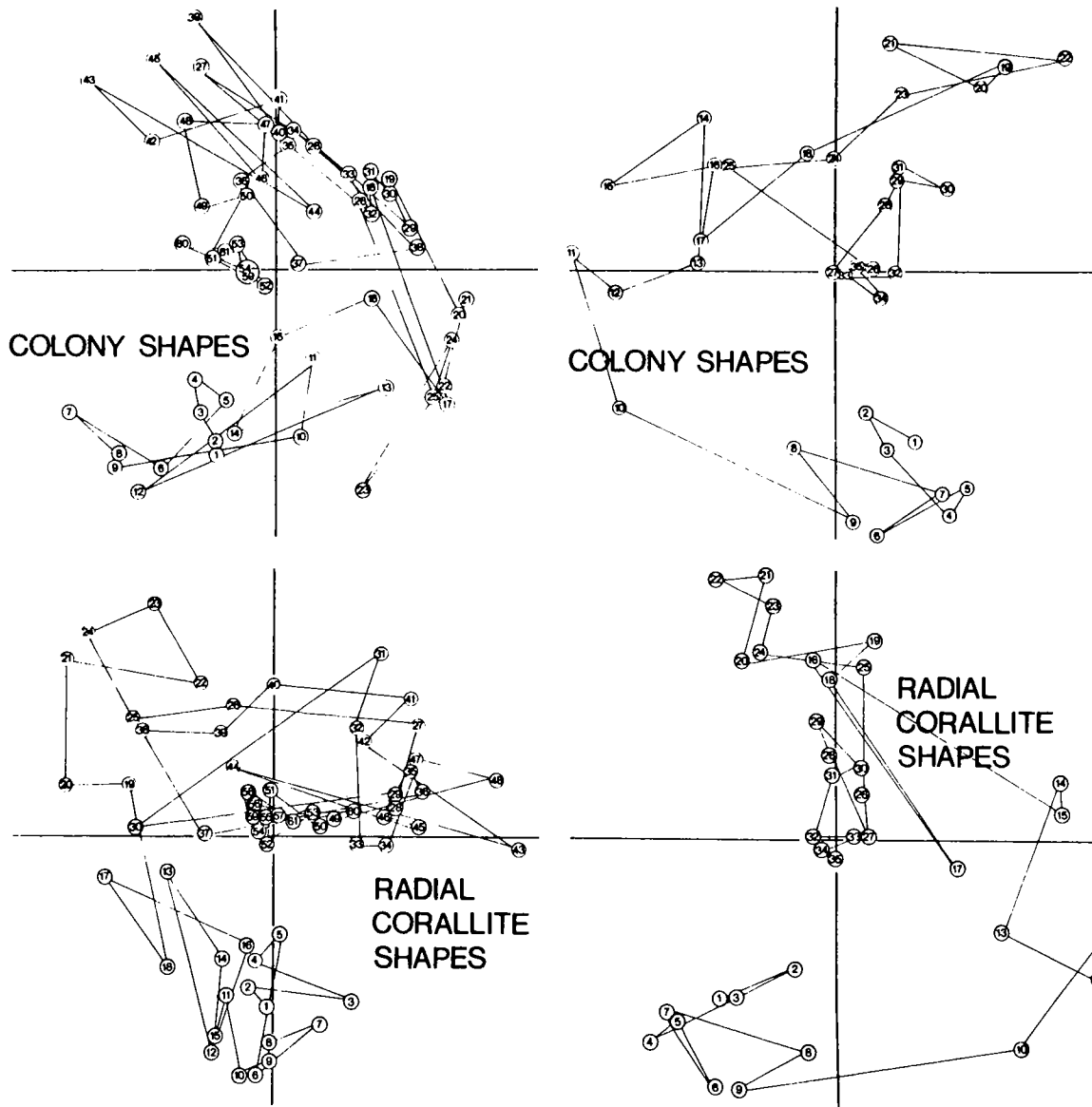


Figure 4. Ordination along first two axes for colony shapes and radial corallite shapes categories: left side series 1; right side series 2. Circled numbers represent transects (sites). Consecutive site numbers are joined by a straight line.

- c. In some cases, particularly the first two programs for transect series 2, transects at the bottom of the series (near transect 35) group with those in the crest zone. This phenomenon can be attributed to low information content, the almost-empty transects being accepted into the dendrogram where they will least upset the grouping procedure.
- d. In the first series, the groupings within the reef slope zone always include one very large group.

#### The Inverse Program

"Inverse analysis" is a term coined by Williams and Lambert (1961) to describe the classification of species into groups by manipulation of quadrat data. Results of the inverse classification and ordination are given in Figure 6. These results reflect the patterns of the normal analyses as well as categorizing the species. In the classification, it will be seen that:

- a. Two subgroupings occur, one being compact and containing all reef slope species.
- b. The almost ubiquitous species 5, 35 and 4 form unique groups, which then cluster loosely with common reef flat-crest species 6, 8, 10, 11, 40, 41.
- c. Most of the reef slope species cluster very closely into a single group, which also includes the reef flat species 9, 12, 29 (which occur only once). In fact all "rare" species have been attracted into this very large group. Being low in abundance, they behave in the inverse program in an analogous manner to transects low in diversity in the normal analysis (Williams and Lambert, 1961).

In the ordination program, a horseshoe-shaped curve occurs, incorporating all except species high in abundance through most of the samples (species 5, 35, 4). Reef flat-crest species occur as negative on the first axis, and the bulk of the reef slope species cluster together near the center of the axis. The singling out of the ubiquitous species is to be expected in a program sensitive to abundance.

#### Hand Sorting of Material

The results can also be portrayed in the form of a simple hand-sorted matrix. Figures 7 and 8 display this technique for the "unlumped species" category. In these the disjunction can be seen between transects on the reef flat (above dotted line) and reef slope (below). Some species are almost ubiquitous, but most are restricted either above or below the crest line, with some extension (mainly from above

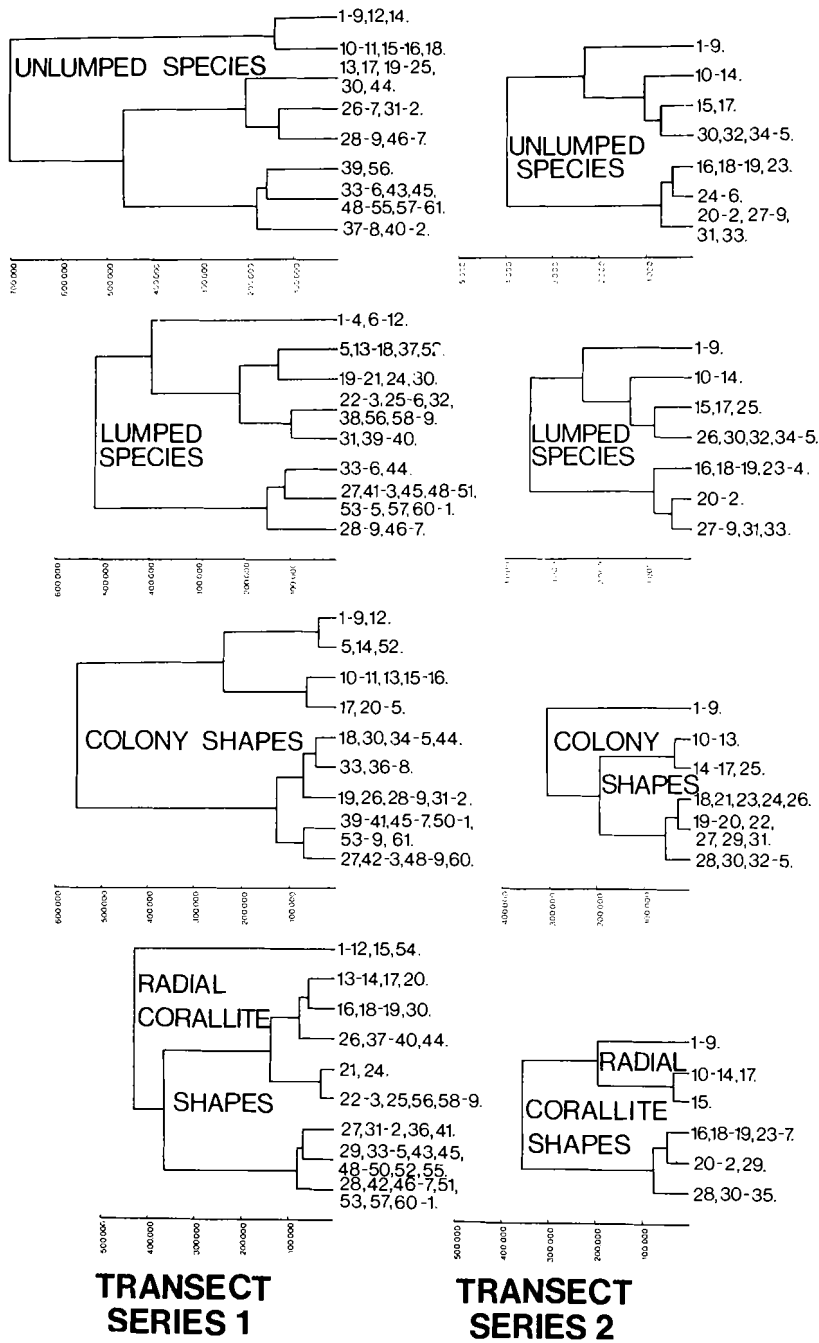


Figure 5. Results of the classificatory programs expressed as dendrograms. Numbers at sides of dendrograms represent sites (transects). Scales indicate information levels.

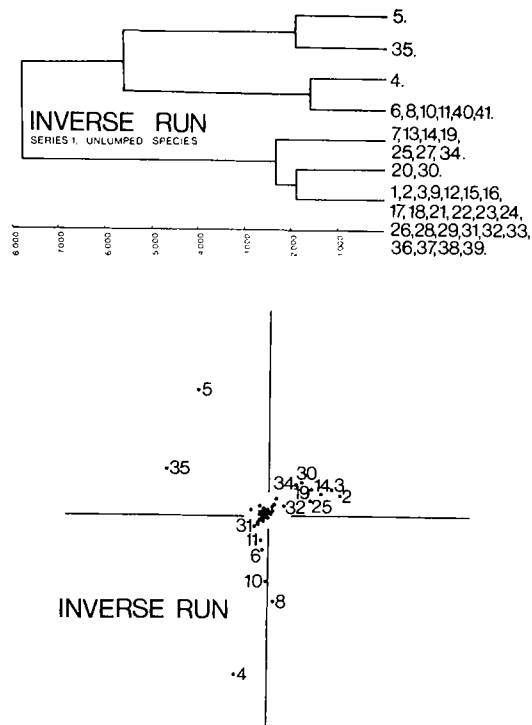
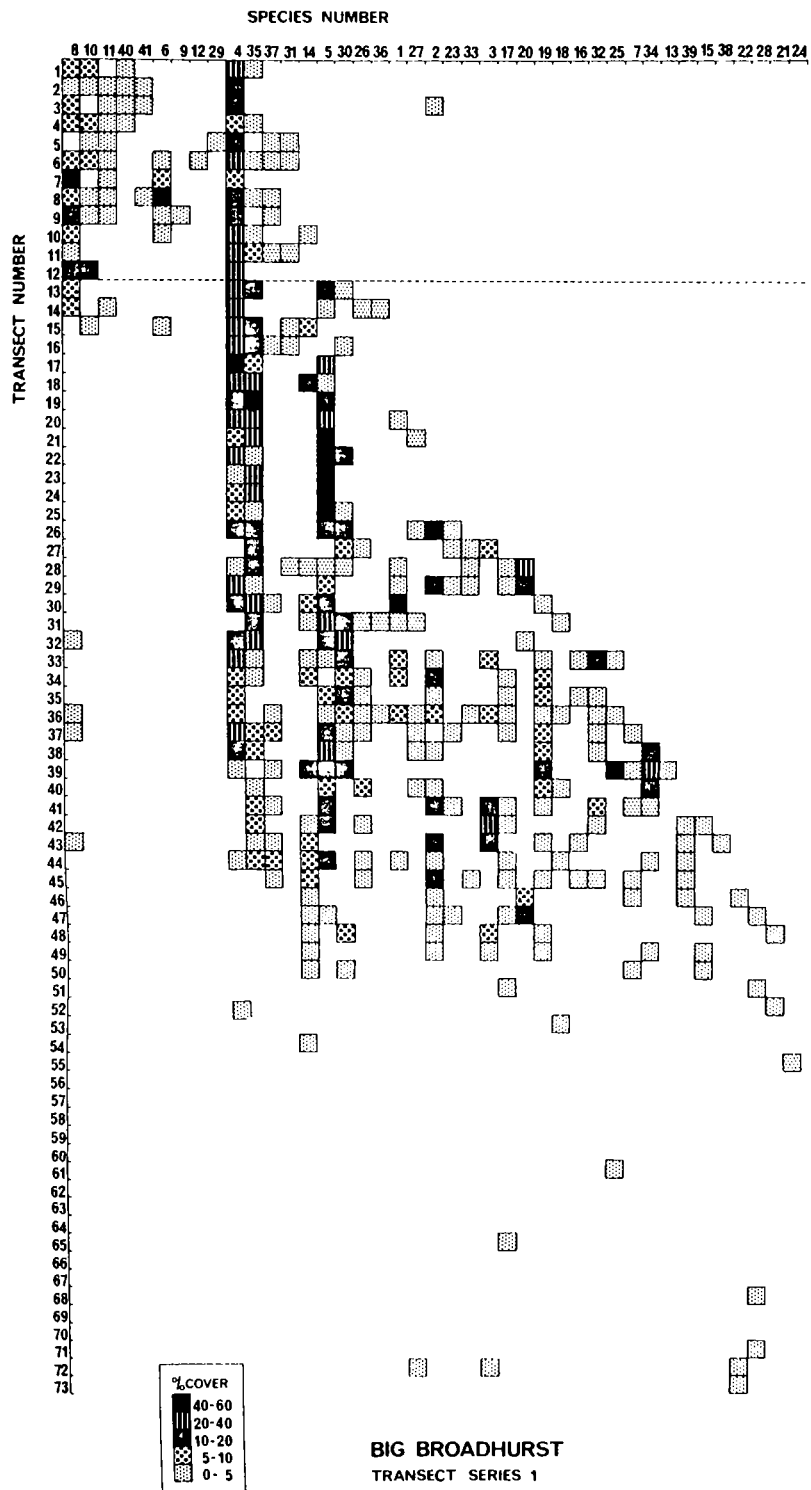


Figure 6. Results of inverse analyses of "unlumped species": dendrogram and ordination. Numbers represent individual species. In the ordination, closely aggregated points in the centre of the axes are left unnumbered. Scale in dendrogram indicates information levels.



**Figure 7.** Hand-sorting of distribution and abundance of "unlumped species" category for the gradual-slope buttress. (transect series 1). Dotted line marks position of reef-crest transect

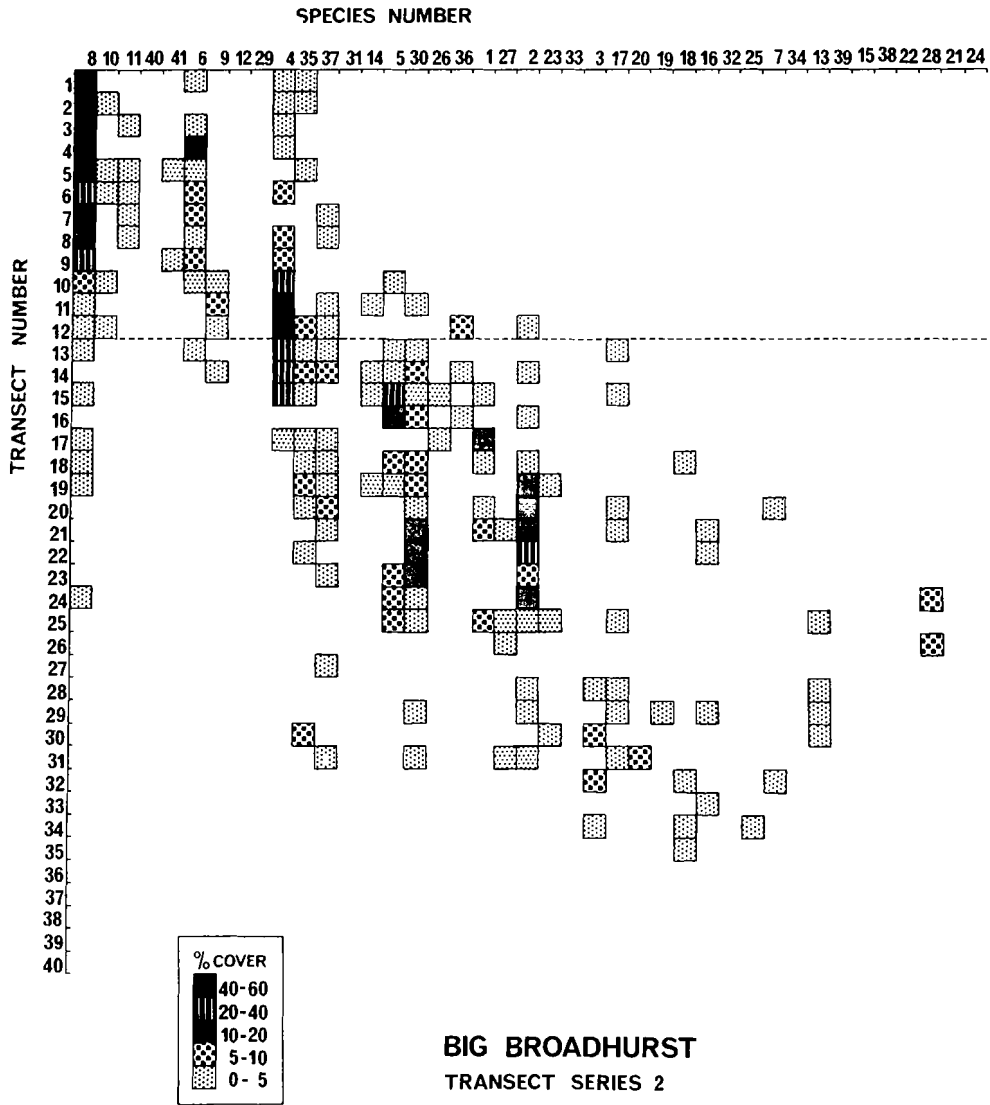


Figure 8. Hand-sorting of distribution and abundance of "unlumped species" category for the steep-slope buttress (transect series 2). Dotted line marks position of reef-crest transect.

downwards) into an area around the line. This reef crest area has no unique species; this area might be regarded as a zone of overlap, a transition zone, or an ecological zone in its own right.

In the reef slope zone the hand-sorting appears to show two different patterns: in the first series (gradual reef slope) a sequential increase in the number of species present, with little dropping-out of species; in the second series (steep reef slope), a gradual change in assemblage with almost constant species-numbers. In both series, transects from about 20 m and below are almost or completely devoid of corals. A similar pattern was seen in hand-sortings for all the categories. The pattern was weakest in the "radial corallite shape" data; only two shapes are unique to the reef slope, and none are unique to the flat.

#### DISCUSSION

Even when the terms of reference include only a single coral genus, the outer reef poses a complex pattern of situations. It may be heuristically useful to define some of these situations with a "jigsaw-solving" approach as units for separate examination, in order to remove some of the non-linearity from the pattern. The units and the methods used to study them do not need to be directly comparable in order to contribute to an understanding of the overall pattern. From this study, four units emerge: three definable as reef localities (from the results of normal analysis), and one as a coral group (from the inverse analysis). They are:

1. The outer reef flat; it more or less coincides with the low tide mark and its physical environment includes variables dependent on the tidal cycle as well as gradients related to horizontal distance from the reef crest. This area supports a number of Acropora species which do not invade the reef slope, and colonies here are either corymbose or flexible-indeterminate forms. The latter can adapt to limits imposed by the tidal level by a low growth profile, which in some cases effectively mimics a corymbose growth form. In this study only the outer 12 m of reef flat was included, and indications are that this included area is the "tail end" of a serial reef flat assemblage.

2. The reef slope; physical gradients are related to depth, and factors correlating with shape characteristics of the slope may be expected to be influential. Again, there is a characteristic Acropora assemblage undergoing a serial change in species and colony shape characteristics from upper to lower assemblage; in this case the study included the whole of the unit. Upper and lower sections have lower diversity than a middle section by all criteria used, and colony-shape characteristics are probably of great importance. In the deeper water transects, abundance is very low, and all species present grow

horizontally: species present include horizontally growing species which also occur in shaded shallow-water situations (Wallace, unpublished) as well as flattened modifications of other reef slope shapes (for five species in this study).

The shallow-water reef slope area in this study was dominated by a small number of species (probably six), of two very different colony shapes: large horizontal plates and indeterminate arborescent bushes. These two shapes seem to partition the available space effectively, and abundance is very high.

Between these extremes of the slope assemblages occurs a high-diversity assemblage; each species is able to attain its most distinctive form, and most of the range of variability within the genus for colony-shape and radial corallite shape is expressed. It seems likely to me that comparative study of this region for a variety of reef-slope regions may yield information on factors important to maintenance of diversity.

This part of the reef slope may not be physically any less unpredictable than other outer reef areas, when the effects of major catastrophic events such as cyclones are considered: "Groove-spur systems..removed from reef fronts" (Stoddart, 1974); "An extensive forest of staghorn Acropora...flattened...at a depth of 20 M" (Pearson, 1975). However, these intermediate depths are below the region of tidal influence, yet above the region where light is a limiting factor to coral abundance (Loya, 1972) and within the upper area of a gradual temperature and oxygen concentration gradient (Wells, 1957). A gentle slope in this region would present minimal gradation of physical factors and allow easy settlement of larvae, as well as access to a large body of nutrient-containing water; this region may well be the most benign region on the reef.

This middle region in the reef buttresses surveyed was gentle in the first case and steep in the second. On the first buttress a high diversity is developed and maintained through the 5-10 m range, with extra species being added into the components, but no species dropping out, so that in 8-10 m water depth most species except the exclusively "reef flat" species co-occur. All colony shapes except the specialized "reef flat" shapes occur, as well as all types of radial corallite. On the second buttress, no such build-up is seen: a lower diversity is maintained throughout the series, and the transects go through a gradual change in species-composition from shallow to deeper water.

I have discussed this elsewhere (Wallace, 1975) and I hope to be able to examine other reef slope shapes, pursuing the hypothesis that in the second buttress the species may be more closely indicating the physical conditions to which they are adapted. In the first set, the benign slope may allow settlement of all reef slope species, providing at least initially a high diversity which must be equated with a high potential for variety of biological interaction.

3. The third unit of interest is the area around the reef crest, from one or two meters before the beginning of the drop-off to three or four meters below. Physically, this is an intersection between the previous two very different units. Biologically it may be defined as a transition zone, with elements from the assemblages to either side. Alternatively it can be seen as a region of physical stresses, the first part of the reef to receive ocean-borne influences and subject to constant short-term disruptive features.

4. A final "unit" emerging from this study, from the inverted programs, is that of the almost-ubiquitous species and colony shapes. These cut across the zonal descriptions, although some characteristics such as colony size and site abundance may change through the series. Interestingly they do not occur in the low abundance deep-water transects. The success of these species relative to that of the remaining colonies is of interest to an understanding of both the genus and the ecological problems posed by reefs. The species belong to two shape categories: wide horizontal plates and arborescent bushes. The first shape is documented as the best light-catching shape for corals (Goreau, 1963), but these species do not occur on the part of the slope where all species flatten out. The three very abundant species pose these and other tantalizing questions and because of their abundance would be ideally suited to population sampling.

Each of the above units lends itself to a different style of hypothesis testing, and these should be explored before a synthesis is attempted.

#### ACKNOWLEDGEMENTS

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#### REFERENCES

- Dale, M. B., Lance, G. M., and Albrecht, C. 1971. Extensions of information analysis. *Aust. Comput. J.* 3(1):29-34.
- Goreau, T. F. 1963. Calcium carbonate deposition by coralline algae and corals in relation to their roles as reef builders. *Ann. New York Acad. Sci.* 109:127-167.

- Gower, J. C. 1966. Some distance properties of latent root and vector methods used in multivariate analysis. *Biometrika* 53:325-38.
- Greig-Smith, P. 1964. *Quantitative Plant Ecology*, 2nd ed. Butterworth, London, 256 pp.
- Hoffmeister, J. E. 1925. Some corals from American Samoa and the Fiji Islands. *Carnegie Inst. Washington Pap. Mar. Biol.* 22:1-90.
- Kendall, D. G. 1971. Seriation from abundance matrices. pp. 215-252, in: *Mathematics in the Archaeological and Historical Sciences*. F. R. Hodson, D. G. Kendall, and P. Tautu, eds. Edinburgh Univ. Press.
- Loya, Y. 1972. Community structure and species diversity of hermatypic corals at Eilat, Red Sea. *Mar. Biol.* 13:100-123.
- Pearson, R. G. 1975. Coral reefs, unpredictable climatic factors and Acanthaster. 2nd Crown-of-Thorns Starfish Seminar Proceedings, Brisbane, 6 Sept. 1974:131-134.
- Sneath, P. H. A., and Sokal, R. R. 1973. *Numerical Taxonomy*. Freeman, San Francisco, 573 pp.
- Stoddart, D. R. 1974. Post-hurricane changes on the British Honduras reefs: re-survey of 1972. *Proceedings of the Second International Coral Reef Symposium*. 2:473-483.
- Vermeij, G. J. 1974. Adaptation, versatility and evolution. *Syst. Zool.* 22:466-477.
- Wallace, C. 1975. Distribution patterns of the coral genus Acropora on the reef slope: a preliminary report. 2nd Crown-of-Thorns Starfish Seminar Proceedings, Brisbane, 6 Sept. 1974:81-107.
- Wells, J. W. 1957. Coral Reefs. *Geol. Soc. America. Mem.* 67:609-631.
- Williams, W. F., and Lambert, J. M. 1961. Multivariate methods in plant ecology III: Inverse association analysis. *J. Ecol.* 49:717-729.



Plate 1. Outer reef flat on first reef buttress. Dark patch on left hand side is a surge-channel opening. Acropora humilis, A. digitifera and A. valida (corymbose forms); A. decipiens (low sturdy arborescent); A. corymbosa (horizontal plate).

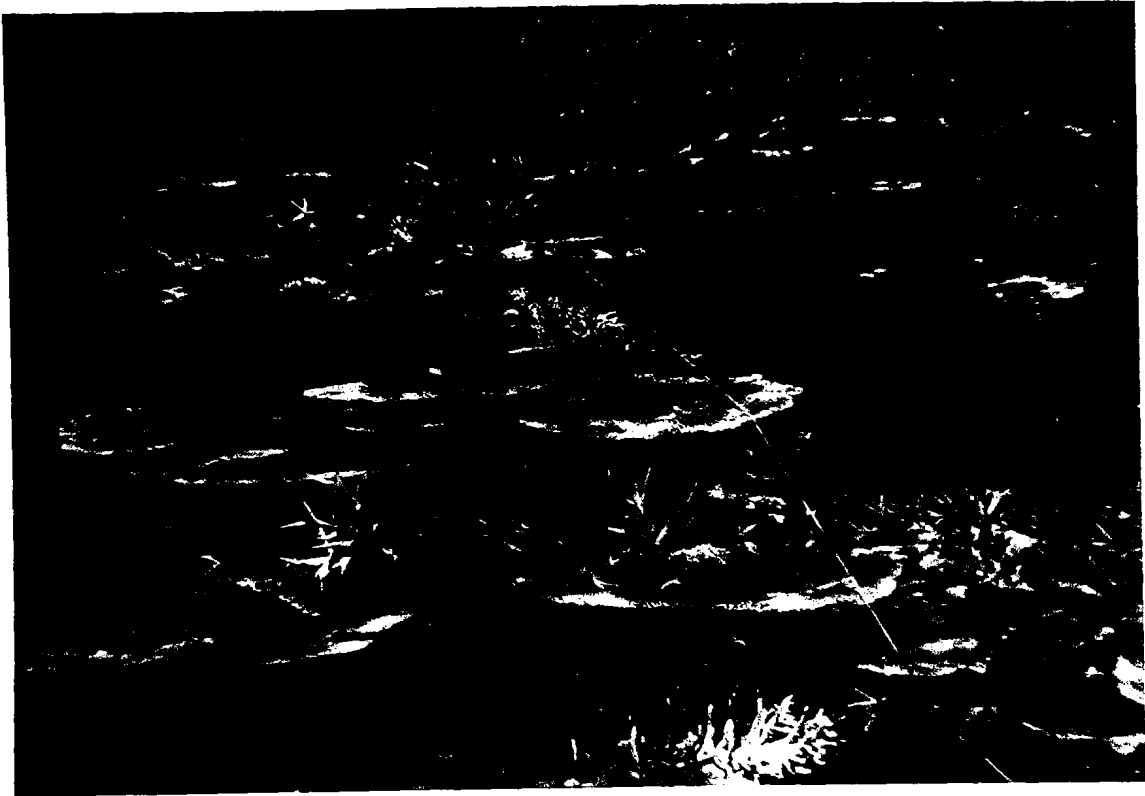


Plate 2. Upper reef slope on first reef buttress to about 7 m. Large horizontal plates of Acropora corymbosa, A. hyacinthus and A. clathrata; arborescent bushes of A. formosa, A. intermedia and an unnamed species; "bottlebrush-arborescent" A. gravida, and a new "arborescent bracket" species (in mid foreground).

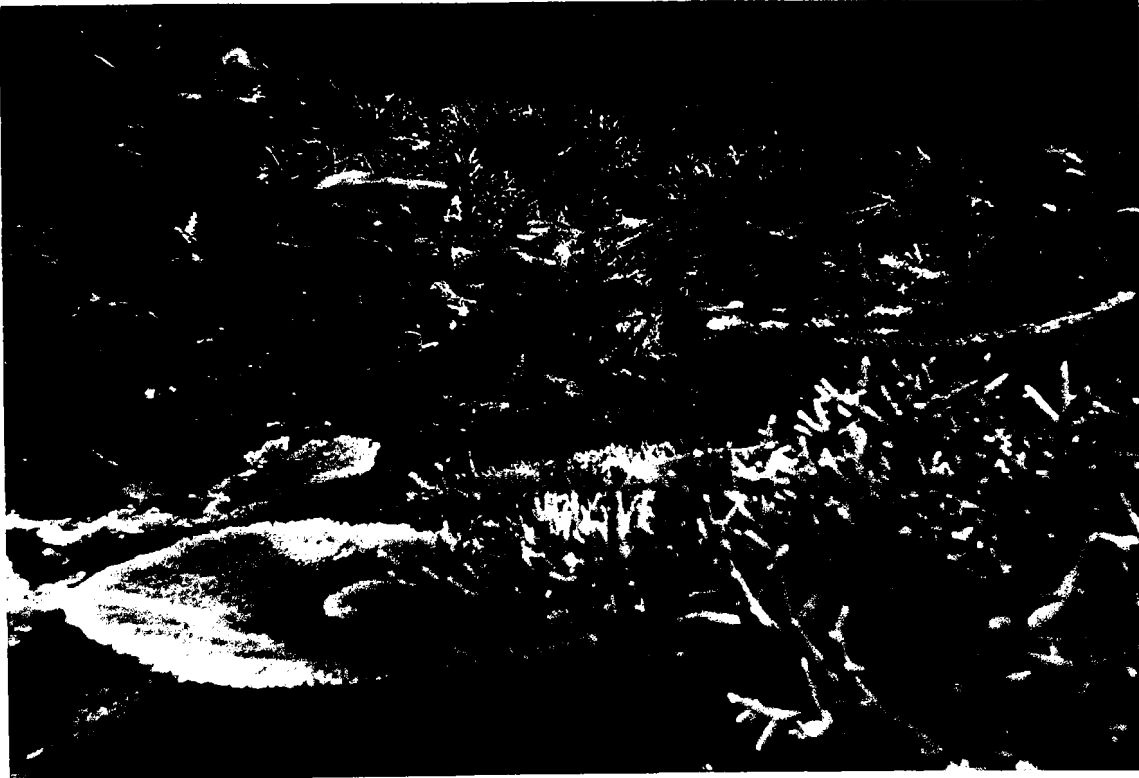


Plate 3. Close-up of high diversity assemblage on first reef buttress at about 10 m. Includes all species in plate 2 except Acropora intermedia, plus A. patula and two other species.