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Coral Communities on a Seaward Reef Slope, Fanning Island[1]

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ABSTRACT: The coral community on a 1 × 100 meter long vertical section of the leeward ocean reef slope at Fanning Island was quantitatively investigated with SCUBA and a quadrat transect technique. Forty-seven species of corals were noted, and coral cover averaged over 60 percent on the transect. Common coral species were restricted to certain depth regimes, which resulted in pronounced vertical zonation. The community as a whole could be objectively divided into three assemblages with respect to depth. The deepest assemblage (30 to 35 m) was characterized by low coral cover, small average colony size, and high species diversity. Some of the species were specialized types not found elsewhere on the transect. Environmental conditions appeared stable with respect to wave action but suboptimal with respect to light and sediment cover. At intermediate depths (20 to 25 m) the coral assemblage showed higher cover and larger average colony size, but lower diversity values due to dominance by a few species. Environmental conditions appeared to be both optimal and stable, with biological interactions determining the nature of the assemblage. At shallow depths (8 to 15 m) the assemblage showed slightly lower cover, moderately higher diversity, and moderately smaller average colony size. Wave action may periodically disrupt the environment, which is otherwise optimal for coral development. In the shallowest environments near shore reef substrates are dominated by coralline algae, and corals are rare. Environmental conditions are probably both suboptimal and unstable, resulting in the inhibition of coral development. The structure and probable factors controlling the structure of the Fanning coral community are similar to those of other reef slope communities recently studied, particularly those in the Red Sea.

THE EVOLUTION of a reef follows a sequence in which reef slopes must first form and grow before the reef flats can develop. Environmental conditions on reef flats are quite different from those on the deeper slopes and it is not surprising that community composition and structure are correspondingly different. Nevertheless, most generalizations regarding the ecology of reef communities have been derived from the study of reef flats. Because of the inaccessibility and risk involved, the study of ocean reef slopes has been largely neglected.

The purpose of this investigation was to gain a better understanding of the forces that control the community structure of corals on an ocean reef slope at Fanning Island (3° N, 159° W). Corals are the dominant benthic organisms on many of the leeward ocean reefs of the atoll. Recently coral communities on reef slopes have been quantitatively assessed by Porter (1972*a*, *b*, *c*) in Panama and by Loya (1972) in the Red Sea. The Fanning Island site is subjected to more wave activity than the other two regions. Other common reef organisms, including fish, algae, and echinoderms, also were investigated on the Fanning site (Chave and Eckert, this issue; Tsuda 1973; Maragos et al. 1973; and Townsley and Townsley 1973).

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METHODS

The study reef was located 400 m north of English Harbor Pass (transect 3, fig. 1, Chave and Eckert, this issue). A transect was established perpendicular to the depth contours of the reef slope. The coral community was measured with a contiguous quadrat technique. From these data, estimates of abundance, size, diversity, pattern, evenness, zonation, distribution, and ordination of the corals were extracted. An attempt was made to correlate patterns of community structure with physical and biological factors.

The reef tract surveyed was 100 meters long and 1 meter wide with the upper end (quadrat no. 100) located at a depth of 8 m and the deeper end (quadrat no. 1) located at 36 m. All investigations were carried out with SCUBA during a series of dives conducted from anchored skiffs. A 100-meter-long polypropylene rope of 1/4-inch diameter with small lead markers at 1-meter intervals was paid out along the transect and tied to the reef with strands of wire. Numbers stamped on each of the markers corresponded to quadrat numbers. It was originally planned to run a parallel transect some distance down the reef, but weather and logistics prevented this. Identification of most of the corals was made on sight. Unidentified species were assigned code names, and samples of these corals were later identified in Hawaii. I have described elsewhere in this issue a reference collection of all corals from Fanning Island. The entire transect was also photographed with color-slides film and a Nikonos II underwater camera mounted on a rigid frame. Each photograph covered a constant area of the transect. The photographs were used as checks against data acquired by the quadrat method and they also provided a baseline for future planned studies.

The quadrat consisted of a frame 1 meter on a side and subdivided by wires into a grid of 100 squares of equal area. Beginning at one end of the transect, the quadrat was centered over the line between the lead reference markers. Quadrat number and depth were read and recorded on underwater writing slates. The abundance of coral was estimated by counting the number of squares occupied by each coral colony. Similar estimates of sediment cover were also recorded *in situ*. The quadrat was then placed over the 2nd meter interval and the above procedures repeated until the entire transect of 100 quadrats was surveyed.

I choose the contiguous quadrat method because I have used it in the past (Maragos 1972) and have found it to be an efficient means of acquiring data when time in the field is limited. Quadrat sampling can acquire the same kind and amount of data as line intercept methods, but a smaller dimension of the reef is covered. Because a major consideration in this study was to examine data variations along both large and small intervals of the reef, it was necessary to choose a method that could conveniently provide information on both. The quadrats were all contiguous and allowed their grouping (pooling) in order to facilitate investigation of data at a variety of sampling dimensions. Unfortunately, this study was carried out before the recent studies of Porter (1972*a*, *b*, *c*) and Loya (1972) were available for review. These authors employed similar line intercept methods. More consideration will be given to using comparable methods in the future, since one of the basic problems in the comparative investigations of reefs has been the lack of standardization of sampling procedures (Stoddart 1969, 1972).

The quadrat data were used to compute a variety of descriptive parameters. Topography and steepness of slope were computed from the depth information. Coral abundance data were expressed as percent cover. The distribution of each coral species was plotted with respect to quadrat number (i.e., depth) and provided the basis for the zonation studies. A size index of the corals was computed from the ratio of total cover to the number of colonies for each quadrat. Because many colonies were not entirely within the boundaries of the frame, this measure is only an approximation of true colony size (area). The quadrat abundance data for each of the common species were also subjected to pattern analysis using the index of dispersion (Greig-Smith 1964), which is simply the ratio of the variance to the mean abundance for a group of N samples of equal size. This index can be statistically tested to determine whether distributions are significantly random, even, or

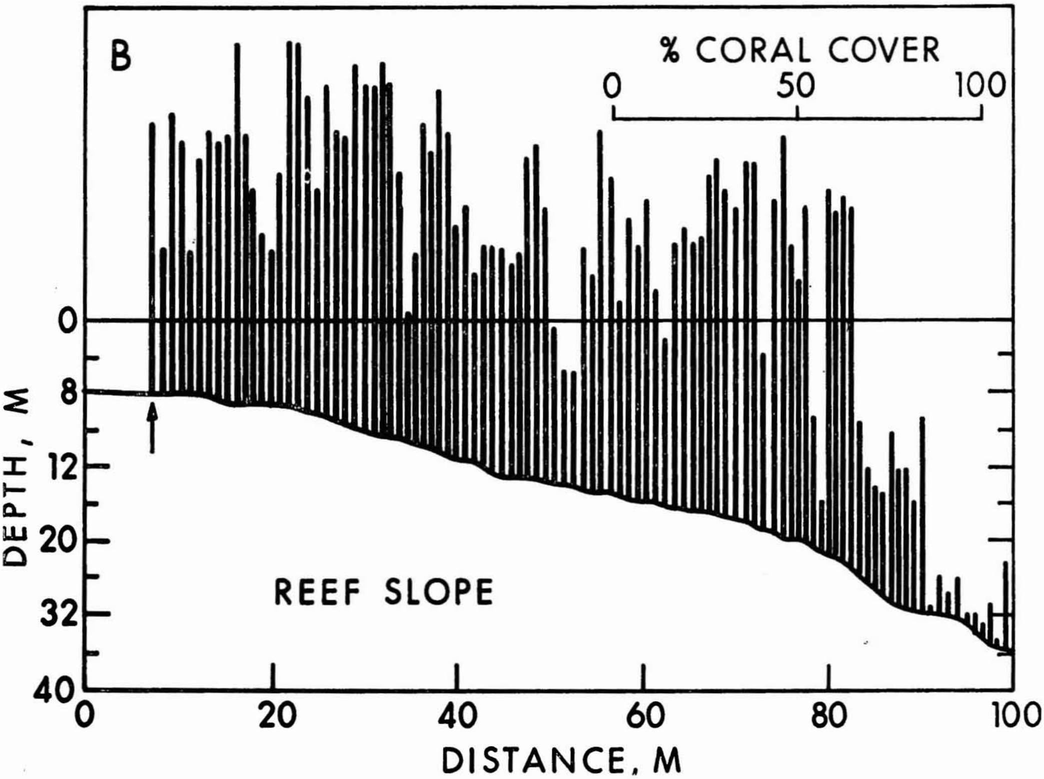

FIG. 1. Bathymetry of reef slope and coral abundance. Percent cover plotted for each of 100 quadrats. No vertical exaggeration. Arrow designates the location of the upper end of the transect (quadrat no. 100).

aggregated. For each species, the index was computed within a range of quadrats where the species was commonly found. The quadrat data also provided the estimates of species richness; that is, the number of species per unit area and a measure of diversity. The Shannon-Weaver (1949) index H_c' was computed using

$$H_c' = \Sigma p_i l_n p_i$$

where p_i is the proportion (percent cover) of the "ith" species in a sample and l_n refers to the natural logarithm. This index is also a measure of diversity but differs from species richness in that it also considers the relative proportion of each species as well as the number of species. When the abundance of all species in a sample is the same, H_c' is at a maximum. The ratio of the observed H_c' to the maximum value of H_c' is called the evenness index (Pielou 1966). Presumably this index is a good measure of dominance. When one or a few species in a sample are much more abundant than the rest, the evenness index is low.

The coral abundance data for individual quadrats were subjected to dendrograph analysis (McCammon and Wenninger 1970). The analysis graphically determines the relative similarities among groups of variables. A dendrograph was computed on the individual quadrats to determine whether the transect could be objectively divided into discrete zones. This examination also provided a basis for determining the maximum number of quadrats that could be pooled at regular intervals along the transect.

Analysis of the relative differences in the above properties along the transect was the major consideration of this study. Since many of these expressions are dependent on sample size, comparisons were made only between groups of quadrats or transect intervals of equal size. The criterion for the determination of the minimum sampling interval corresponding to maximum diversity values (see Loya 1972) was not considered because it was not important to determine the absolute values of some of the parameters.

RESULTS

Bathymetry of the transects is indicated in Fig. 1. The slope of the reef is gradual and consistent. At small intervals (± 1 meter) substrate relief is irregular. The lack of large scale relief is due in part to the poor development of a spur and groove system on this reef, a feature more common along windward slopes. The upper end of the transect terminates on the outer edge of a broad shelf (in 8 meters of water), which gradually shoals toward the shoreline located 200 meters landward. Although the outer edge of this deep reef "flat" is not distinct, long period swells generate noticeably stronger surge currents here before passing overhead and breaking onshore. Surge currents inhibited sampling in shallow water and were a primary reason for abandoning a shoreward extension of the transect. Qualitative surveys showed that coral cover and colony size diminish while coralline algae abundance increases toward shore and shallow water. In the surf zone the pink coralline algae *Porolithon* dominates substrate cover. Large, overturned colonies of *Acropora reticulata* and abundant, old, eroded shingle formed from the skeletons of these corals indicate that at times wave action must be severe along this coast (Gallagher 1970, Gallagher et al. 1971).

The deep end of the transect was located at the bottom of the reef slope at a depth of 36 m near the upper edge of a sand talus which appears to extend to great depths. In the marginal zone between reef and sand are isolated rubble fragments to which corals are frequently attached. Sand is rare above depths of 30 m (quadrat no. 15). Hard substrate and live coral covered 99 percent of the transect above this point. Normally, the deep reef environment is not subjected to much wave surge. Water is extremely transparent at all areas of the transect, and both vertical and horizontal visibility usually approached 50 m or more.

A species list of the transect corals and a summary of their abundance, distribution, and pattern are presented in Table 1. The reef tract was judged to be the most diverse and flourishing with respect to corals of any area at Fanning. At least 47 species were present within the boundaries of the transect. These included 40 scleractinian hermatypes, one milliporinid hermatype, three alcyonaceans, two stylasterinids, and one antipatharian. About 60 percent of the hermatypic coral species of Fanning (Maragos, this issue) were present.

Live coral cover on the reef was high (Figs. 1 and 2), averaging over 60 percent. Excluding the sand zone at the bottom, coral cover approached 75 percent along the reef slope. Corals are locally rare on the deep slope, presumably because of the lack of suitable substrates for larval attachment. Harrigan (1972) has shown that coral larvae (planulae) do not settle on sediment particles the size of sand or smaller. Elsewhere on the transect, coral abundance was both high and variable (Fig. 1). Pooling the quadrats into larger groups tended to reduce variability between groups (Figs. 1 and 2).

Pattern analysis on coral abundance data showed trends of patchiness for most of the species (Table 1). Only for two corals, *Porites* (*S.*) *vaughani* and *Pavona clavus*, was there an indication of random or even distributions. Both of these corals are small encrusting forms which occupy crevices and local dead patches between larger colonies. This habitat type is fairly common along the reef and may be randomly distributed. By maintaining small dimensions, both *Porites* and *Pavona* may be occupying a habitat that is limited in space but commonly distributed throughout the reef even in areas where larger corals predominate.

The Shannon-Weaver diversity index computed for the individual quadrats showed wide fluctuations but tended to become smoothed out when progressively larger groups of quadrats were compared (Figs. 2 and 3). It has been suggested (Porter 1972*b*, *c*; Kinzie 1970) that local variations in substrate relief can affect diversity values. Data were sufficient to test this hypothesis. Diversity values for each of the 50 quadrat pairs were pooled into one of three classes, depending on steepness of slope within

TABLE 1

ABUNDANCE, DISTRIBUTION, AND PATTERN OF CORALS FOUND IN TRANSECT, FANNING ISLAND, JULY AND AUGUST 1972

SPECIES	ABUNDANCE (PERCENTAGE OF COVER)	NUMBER OF QUADRATS	INDEX OF DISPERSION
All corals	62.38	100**	5.93
Acropora abrotanoides (Lam.)	0.01	1‖	‡
Acropora humilis (Dana)	1.03	9**	‡
Acropora nasuta (Dana)	0.17	3#	‡
Acropora reticulata (Brook)	6.97	52**	16.29
Acropora syringodes (Brook)	0.14	5‖	‡
Astreopora listeri Bernard	0.09	2#	‡
Cirripathes sp.†	0.04	4#	‡
Distichopora violacea (Pallas)†	0.01	1‖	‡
Echinophyllia aspera (Ell. & Sol.)	0.51	22#	1.97
Favia speciosa (Dana)	0.28	8**	‡
Favia speciosa cf. *F. s. puteolina* (Dana)	0.44	23**	‡
Favia stelligera (Dana)	9.35	75**	11.00
Favites abdita (Ell. & Sol.)	0.12	6**	‡
Fungia fungites (Linn.)	0.02	2‖	‡
Fungia (*Pleuractis*) *scutaria* Lam.	0.29	18**	‡
Fungia (*Verrillofungia*) *concinna* Verrill	0.75	29**	3.18
Herpolitha limax (Esper)	0.09	2#	‡
Hydnophora microconos (Lam.)	0.28	8**	‡
Leptastrea purpurea Dana	1.97	28**	8.74
Leptoseris sp.	0.06	2#	‡
Leptoseris mycetoseroides Wells	0.01	1#	‡
Lobophyllia costata (Dana)	5.99	38**	18.41
Merulina ampliata (Ell. & Sol.)	0.09	5#	‡
Millepora platyphylla H. & E.	3.95	34**	15.34
Montipora hoffmeisteri Wells	0.08	3**	‡
Montipora patula Verrill	0.01	1#	‡
Montipora socialis Bernard	0.32	4‖	‡
Montipora verrilli Vaughan	0.75	27**	‡
Pachyseris speciosa (Dana)	0.08	5**	‡
Parahalomitra robusta (Quelch)	0.03	1#	‡
Pavona clavus (Dana)	0.49	29**	1.72§
Pavona gigantea Verrill	0.23	12#	‡
Pavona varians Verrill	3.32	66**	7.92
Pavona (*Pseudocolumnastraea*) *pollicata* Wells	0.54	11#	‡
Platygyra lamellina (Ehr.)	0.31	18**	‡
Platygyra sinensis (M. Ed. & H.)	0.07	5#	‡
Plesiastrea versipora (Lam.)	0.19	10‖	‡
Pocillopora eydouxi M. Ed. & H.	1.01	13**	‡
Pocillopora meandrina Dana	5.80	72**	6.36
Pocillopora molokensis Vaughan	0.06	1#	‡
Porites lobata Dana	0.16	4#	‡
Porites (*Synaraea*) *vaughani* Crossland	0.36	32**	0.57§
Psammocora verrilli Vaughan	0.12	7**	‡
Sarcophyton sp.*	7.47	25#	30.64
Stylaster elegans Verrill†	0.02	2‖	‡
Stylophora mordax (Dana)	6.34	61**	8.58
Unidentified alcyonarian (no. 1)*	1.19	7#	‡
Unidentified alcyonarian (no. 2)*	0.76	17**	22.50

* Ahermatypic corals.
† Soft corals.
‡ Data insufficient for calculations.
§ Pattern not significantly clumped at $P = 0.05$ level.
‖ Confined to depths less than 18 meters.
Confined to depths of 18 meters or more.
** Found in both zones.

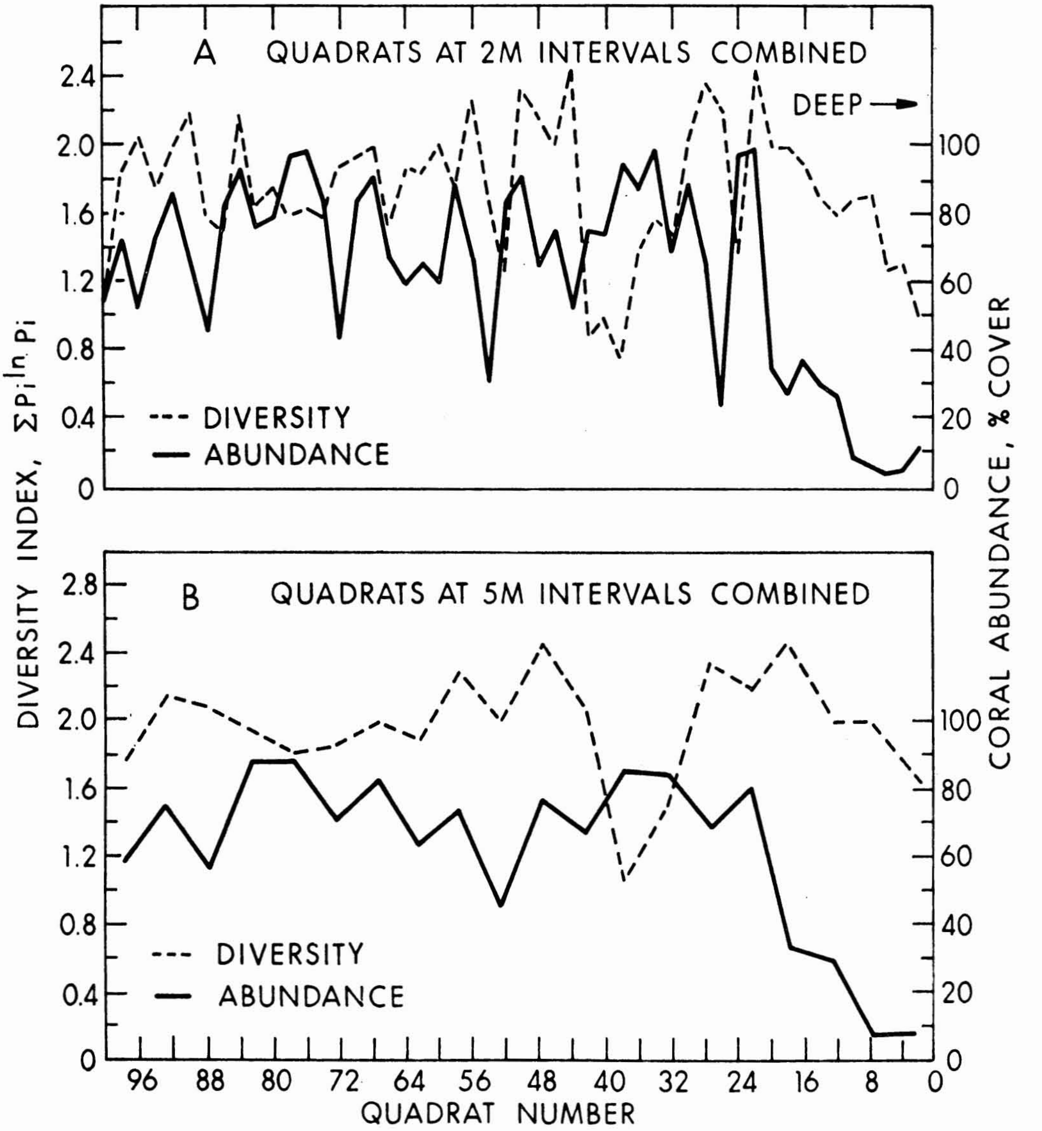

FIG. 2. Coral abundance and the Shannon-Weaver diversity index plotted as a function of transect location (depth). *A*, values based on pooling of contiguous pairs of quadrats; *B*, values based upon pooling of contiguous groups of five quadrats.

each interval, and then were subjected to analysis of variance (Table 2). Species richness, diversity indices, and evenness indices were significantly or nearly significantly higher on steep reef slopes than were those values obtained from moderate or flat slopes. These findings may indicate that corals preferentially settle on steep reef slopes, but that dominance is correspondingly reduced in such environments. However, it is also important to note that depth and slope showed partial but significant correlation along the transect (Table 2). Hence, the significantly greater diversities on steep slopes may be due in part to the effect of depth.

In general, data from Fig. 2 show no visual or consistent correlation of diversity with coral

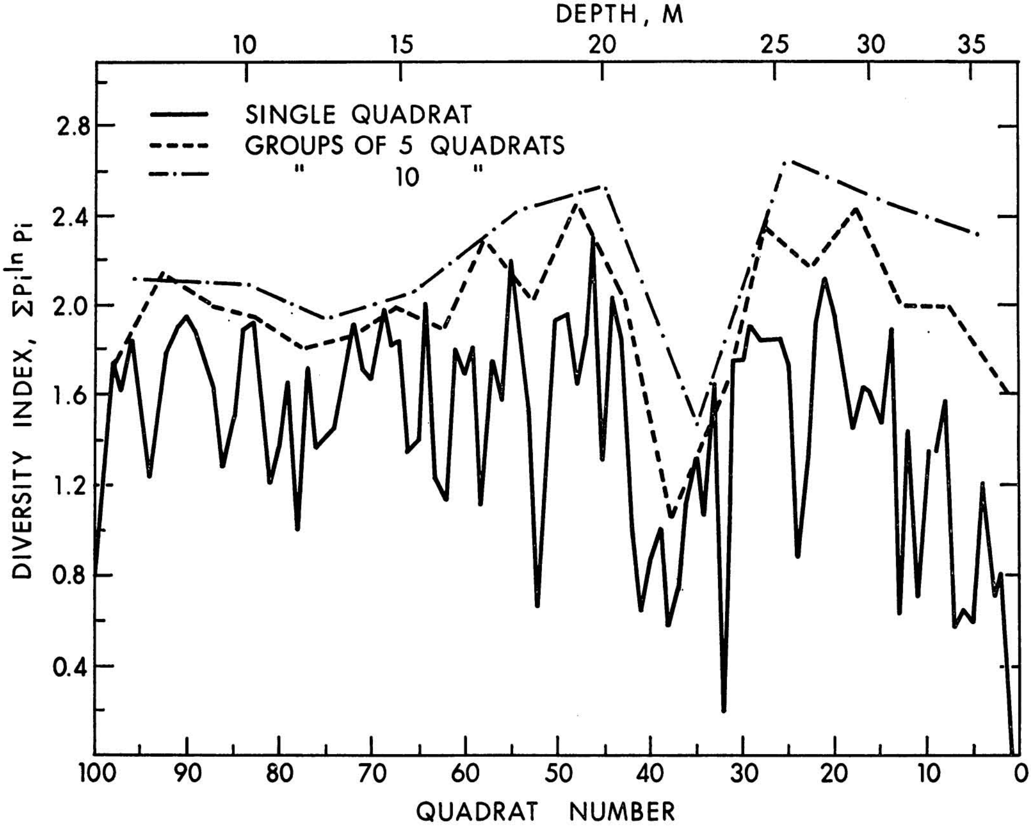

FIG. 3. The Shannon-Weaver diversity index plotted as a function of transect location (depth) for individual quadrats, for groups of 5 quadrats, and for groups of 10 quadrats. Data for groups of 2 quadrats are found in Fig. 2 and are omitted here due to crowding.

abundance, which would imply that each parameter is controlled by different sets of factors. Pooling the quadrats into larger groups tended to smooth out small scale variations, but large scale variations in diversity and abundance persisted even when large groups of quadrats were analyzed (Fig. 3). One area of the transect between quadrats 30 to 40 showed significantly lower diversity values than did adjacent regions (Table 3). This suggests that dominance of the substrate is probable because coral cover is high. The situation is different for the bottom 20 quadrats of the transects which as a group also showed significantly lower diversity indices (Table 3). However, pooling the quadrats into successively larger groups resulted in a greater increase of diversity at the deep end of the reef relative to other regions (Fig. 3). The increase was so great that the diversity values at the deep end were higher than elsewhere when contiguous groups of 10 quadrats are compared. This zone also coincides with that of high sediment cover and low coral abundance. Diversity may be low in small sample sizes because the number of corals encountered were few. Combining quadrats substantially raised the apparent diversity because there is a larger proportion of new species added, none of which dominates the others. Thus, over large sampling areas (that is, groups of 10 quadrats), coral populations at the deep end of the transect are characterized by high diversity and greater heterogeneity as compared to other areas of the transect (Fig. 3). Loya (1972) noted higher coral diversities at the bottom of reef slopes, and Porter (1972*b*, *c*) noted lower values at the

TABLE 2

A. A List of the Slopes for Each Quadrat on the Transect

1–2—B	27–28—C	53–54—A	79–80—B
3–4—B	29–30—C	55–56—C	81–82—B
5–6—C	31–32—B	57–58—B	83–84—B
7–8—C	33–34—B	59–60—A	85–86—A
9–10—C	35–36—A	61–62—C	87–88—A
11–12—B	37–38—B	63–64—B	89–90—A
13–14—B	39–40—A	65–66—A	91–92—A
15–16—C	41–42—A	67–68—C	93–94—A
17–18—C	43–44—B	69–70—B	95–96—A
19–20—C	45–46—A	71–72—B	97–98—A
21–22—C	47–48—B	73–74—A	99–100—A
23–24—C	49–50—A	75–76—B	
25–26—C	51–52—A	77–78—B	

Note: Numbers refer to quadrat number. A, slope less than 15° (flat); B, slope 20° to 30° (moderate); C, slope greater than 45° (steep). Correlation between slope and depth = 0.57 and is significant at $P = 0.01$.

B. Analysis of Variance Results: Slope Comparisons

PARAMETER	TYPE OF COMPARISONS	PROBABILITY
Species Richness	Steep, moderate slopes	.018
	Steep, flat slopes	.019
Shannon-Weaver Diversity Index	Steep, moderate slopes	.009
	Steep, flat slopes	.032
Evenness Index	Steep, moderate slopes	.055
	Steep, flat slopes	.087

Note: Summary of probabilities of occurrence based upon analyses of variance to determine whether coral diversity values at 2-meter intervals on steeper reef slopes are significantly different from those on moderate or flat slopes. Steep is defined here as greater than a 45° slope, moderate is 20° to 30°, and flat is 15° or less. The parameters tested measure various aspects of coral diversity and include species richness, Shannon-Weaver index, and the Pielou evenness index.

bottom of his study reef where coral cover ends.

Essentially the same trends were noted for the species richness comparisons (Fig. 4). Greater variability is evident for smaller sampling increments. Again the transect region between quadrats 30 to 40 showed a consistent "low" at all size comparisons. At the deep end, species richness also showed greater increases than those for other regions of the transect when comparisons involved progressively larger numbers of pooled quadrats. These observations suggest that the same factors control both species richness and the Shannon-Weaver function. Porter (1972*c*) also postulated that both these expressions are simultaneous properties of the coral community.

Regional variations in evenness (H'/H max) are plotted for selected size increments in Fig. 5. Again the transects region between quadrats 30 to 40 shows lower values (that is, higher dominance), although evenness estimates were also low in other areas of the transect. The fact that dominance in most areas of the transect did not result in a reduction of diversity or species richness suggests dominance by corals within the 30 to 40 quadrat range was more severe, resulting in the exclusion or reduced abundances of other species. At opposite ends of the transect, evenness indices were higher and indicate a lack of relative dominance. Both abundant sediment and reduced sunlight could account for the greater evenness values at the deep end while wave and, possibly, storm activity may prevent dominance at the shallow end of the transect. Grigg and Maragos (1974) have presented a similar hypothesis to explain the relatively high community diversity of reef corals along exposed coasts in Hawaii.

The abundance of common colonial and

TABLE 3

ANALYSIS OF VARIANCE RESULTS: DEPTH COMPARISONS

PARAMETER	TRANSECT INTERVALS UPON WHICH COMPARISONS ARE BASED (QUADRAT NO.)	PROBABILITY
Species Richness	0–10, 10–20	< .001
	10–20, 20–30	.121
	20–30, 30–40	.004
	30–40, 40–50	.004
Percentage of Coral Cover	0–10, 10–20	< .001
	10–20, 20–30	< .001
Size Index	0–10, 10–20	.044
	10–20, 20–30	.039
	20–30, 30–40	.004
Evenness Index	0–10, 10–20	.068
	10–20, 20–30	.887
	20–30, 30–40	.011
Shannon-Weaver Diversity Index	0–10, 10–20	.012
	10–20, 20–30	.140
	20–30, 30–40	.002
	30–40, 40–50	.012

NOTE: Summary of probabilities of occurrence based upon analyses of variance to determine whether coral diversity, size, and abundance values within selected intervals of the transect differ significantly from those of adjacent zones. The three measures of diversity used here included species richness, evenness index, and the Shannon-Weaver diversity index. Each interval comprises a group of 10 contiguous quadrats.

solitary corals is plotted as a function of transect location (depth) in Figs. 6 and 7. These diagrams show pronounced overlapping vertical zonation among the corals. Dives to either side of the transect line indicated the zonation pattern persisted for considerable distances along the reef face.

Lobophyllia costata and *Sarcophyton* sp. are the dominant corals of the region between quadrats 30 to 40, a zone previously showing significantly reduced values of species richness, diversity indices, and evenness indices. Individual colonies of both species are spread out over large areas of the reef. Hence, these colonies can effectively exclude other corals and reduce diversity. *Lobophyllia* is a mussid coral with large polyps; according to Lang (1970) and Connell (in press), such forms are more likely to rank high among the competition-predation hierarchy of corals inhabiting a reef. The possibility exists that predation by *Lobophyllia* may aid the coral in achieving dominance, an idea that will be investigated in future studies. *Sarcophyton*, on the other hand, is a soft coral characterized by a continuous spongy "corallum" that seemingly smothers other corals by growing over them. The alcyonacean may be capable of rapid growth and this may help in achieving local dominance.

Several varieties of unattached, solitary corals were found principally in depressions between larger corals and frequently stacked upon each other. Although these corals were not as common as some of the colonial forms, their capacity to move and live unattached to the substrate may enable solitary forms to be less affected by competition for space by other common and sessile colonial corals.

A correlation matrix based upon the data of each quadrat was generated and formed the basis for the dendrograph in Fig. 8. The analysis shows that the transect quadrats may be objectively subdivided into a seriesof discrete clusters, each of which characterizes a certain depth regime. Loya (1972) used a similar approach to describe coral community zonation in the Red Sea. In my study, each association roughly encompassed groups of 10 quadrats or greater. There are seven smaller clusters (Fig. 8) which appear to be portions of the three major regions of the transect. One major zone encompasses quadrats mostly on the upper half of the transect (quadrats 50 to 100). Another major zone appears to be located at the bottom of the transect between quadrats 0 to 20. The final major zone includes quadrats 20 to 50 located at moderate depths along the transect.

The quadrat data and dives in shallow water indicated that only seven species were confined to shallow regions of the reef, while 17 of the total of 47 species recorded were confined to the deep areas of the transect (below 18 m). The greatest number of species (23) was found both above and below a depth of 18 m (Table 1). The greater number of both total and unique forms in deeper water suggests that the environment there is more favorable for the coexistence of corals than it is in shallower waters.

Analysis of the index of average size (Fig. 9) indicates that the smallest colonies existed at

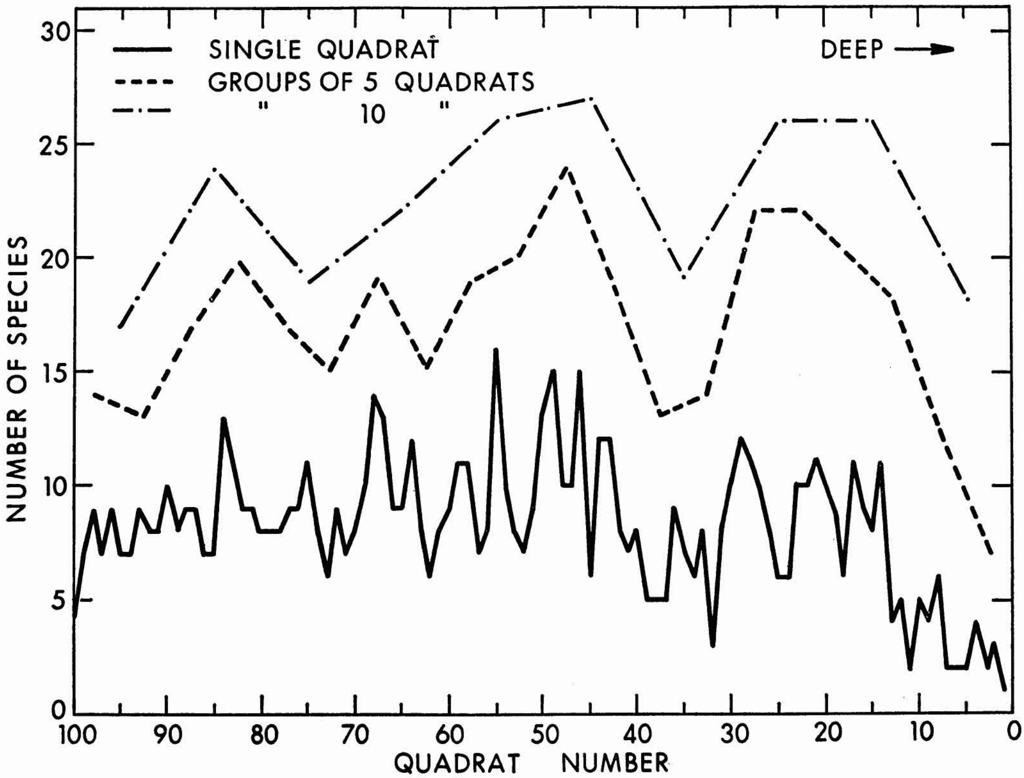

FIG. 4. Species richness plotted as a function of transect location (depth) for individual quadrats, for groups of 5 quadrats, and for groups of 10 quadrats.

the deep end of the reef where sediment and light conditions presumably are suboptimal. The largest colonies predominate within the 30 to 40 quadrat range and support the hypothesis that the larger colonies of both *Lobophyllia* and *Sarcophyton* may physically exclude other corals. Colonies along the remainder (shallower portion) of the transect were generally of moderate size.

DISCUSSION

Results of this study indicate that at small intervals (1 to 2 meters) along the reef there is marked variation in coral abundance, distribution, diversity, evenness, and colony size. Much of this variability may be attributed to variations in slope or substrate relief (Table 2). Accumulation of sediment in reef depressions may also promote greater heterogeneity and reduced abundance. For coral communities (Figs. 1 to 3), large size and dominance by some corals may inhibit the development of other forms and may lead to small-scale patchiness of abundance for individual species. Predation and competition for space may periodically disrupt the continued development of some corals, resulting in a community more patchy in abundance. Nonuniform larval settlement (both in space and time) and natural coral mortality are other factors that may account for small-scale patchiness. Connell (1973) has attempted to investigate some of the factors responsible for this phenomenon.

The pronounced zonation and diversity of the Fanning reef coral community suggest that a variety of strategies have evolved among corals that enable them to persist on reefs. Solitary, unattached, fungiid corals may "avoid" the effects of competition for space by being

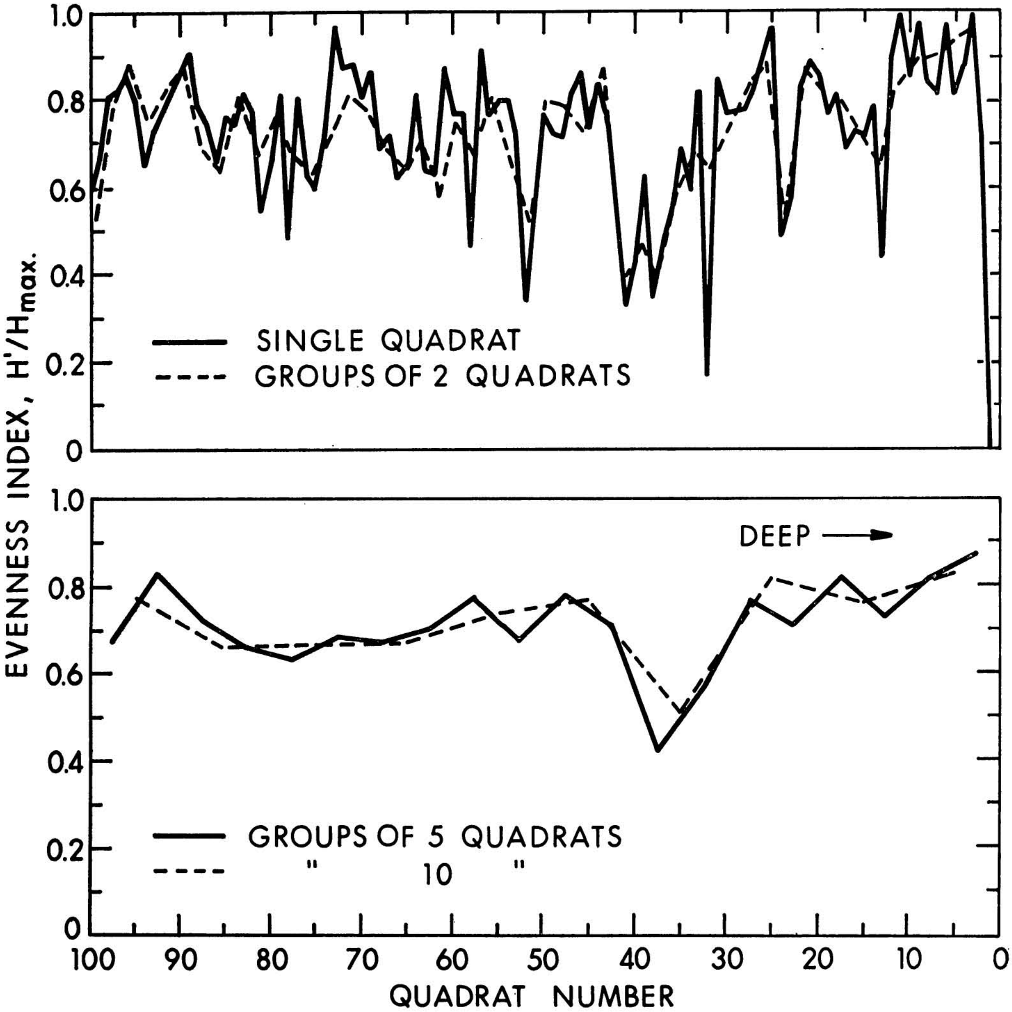

FIG. 5. Evenness index (H'/H max) plotted as a function of transect location (depth) for individual gradients, and for groups of 2, groups of 5, and groups of 10 quadrats.

able to move and live apart from the substrate. *Lobophyllia* and *Sarcophyton* grow to a large size, which results in dominance and the exclusion of other forms. Large colony size is achieved in habitats not subjected to catastrophic events such as storms, which enables continuous growth. Some corals persist by inhibiting the growth of other corals by predatory activity. Elsewhere in tropical oceans, staghorn *Acropora* (Shinn 1972, Manton and Stephenson 1935, Crossland 1938) form extensive thickets that exclude other corals by reducing light or circulation. A similar strategy applies to branching *Porites* platforms in Hawaii (Maragos 1972) and for the alcyonacean *Sclerophytum* in Samoa (Cary 1931). Other corals may exist on reefs only at small dimensions. Nevertheless, *Porites* (*S.*) *vaughani* and *Pavona clavus* achieve a common and even distribution on Fanning reef by living in the small spaces between larger colonies or upon the local dead portions of larger colonies. Elsewhere, *Pocillopora* (Maragos 1972) and *Stylophora* (Loya 1972) appear to remain on reefs as fugitive species (Hutchinson 1951).

The reef coral community at Fanning may be subjectively divided into a number of vertical

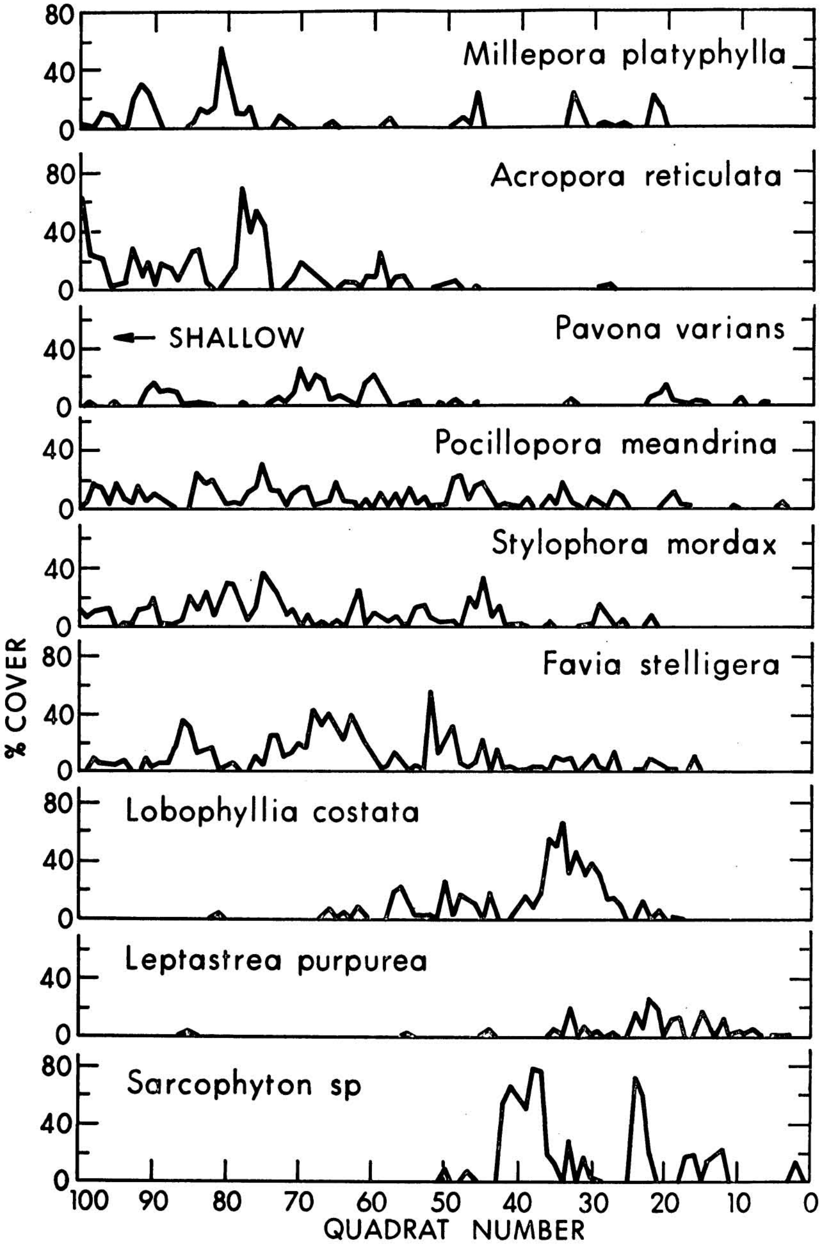

FIG. 6. The abundance of the common colonial corals plotted as a function of transect location (depth).

"zones" based upon the dendrograph and other analyses. At greatest depths on the transect, physical factors such as sediment and low-light intensity may limit both the growth and dominance of corals. However, the environment is too deep to be periodically disrupted by storm waves and therefore may allow a greater coexistence of specialized and different forms. At intermediate depths (quadrats 30 to 50), the environment may be both stable with respect to storm waves and optimal with respect to light conditions. A stable and favorable environment

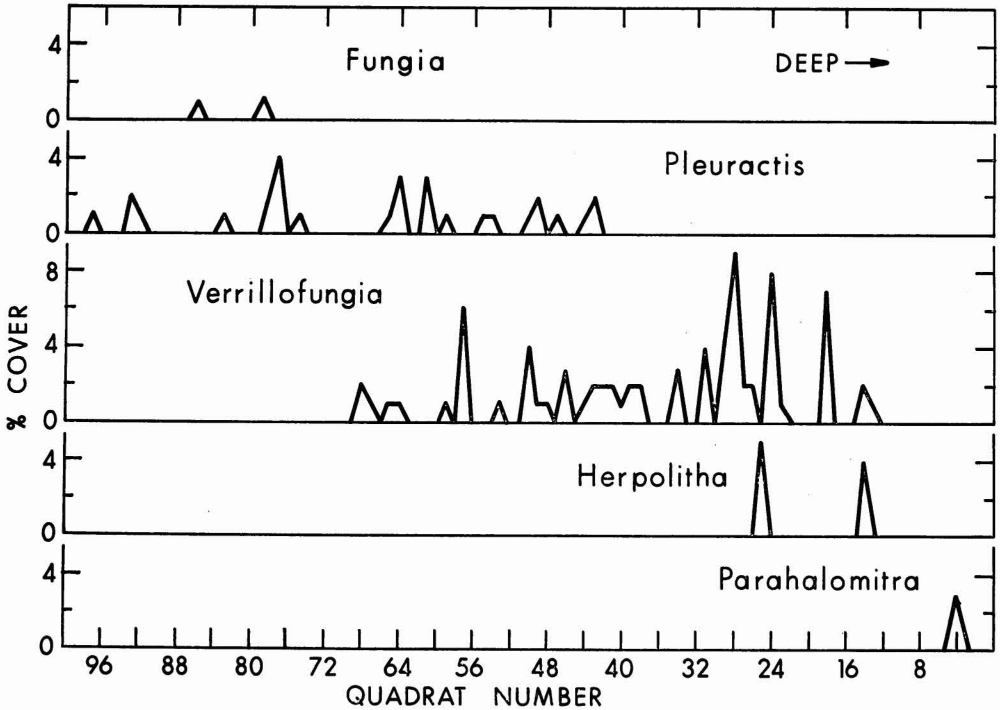

FIG. 7. The abundance of the common solitary hermatypic corals plotted as a function of transect location.

may allow biological interactions to determine the nature of the community. For example, a few forms may find conditions optimal and dominate reef substrates as do *Lobophyllia* and *Sarcophyton*. At shallower depths the environment does become periodically disrupted by wave action but light conditions are optimal for development of a variety of small forms. In the shallowest environments above the transect, breaking waves, scour, and diurnal variations in temperature, salinity, light, and exposure result in unpredictable and suboptimal conditions (see Loya 1972). The diversity and development of corals is lower there than elsewhere. The coral community is replaced by other organisms such as coralline algae.

Loya (1972) came to similar, although not identical, conclusions regarding community structure of reef corals of Eilat, Red Sea. One discrepancy was that he speculated that light is limiting to coral growth and development at moderate depths, rather than at deeper ones. He based this conclusion on a strong direct correlation of illumination intensity and average coral size for a variety of depths. His figure 13 shows that illumination underwent the greatest attenuation between depths of 2 and 10 meters. However, according to Jerlov (1968) and Holmes (1957), the greatest attenuation of solar *energy* occurs within the upper meter of the surface due to the preferential absorption of red and other long wavelengths of light by water. It is obvious then that the vertical distribution of light energy and light illumination are not the same. It seems likely that available light energy is functionally related to the biological processes of calcification and photosynthesis, and that Loya's (1972) presumed correlation of "coral growth" to illumination may be either coincidental or that his measure of colony size is not a good indicator of coral growth. Nevertheless, it seems likely that at deep depths light limits the development of corals both at the Red Sea and Fanning transect sites.

Loya (1972) concluded that the deeper coral communities at Eilat existed in a stable environment that facilitated more rapid evolution of new and more specialized corals. He also noted

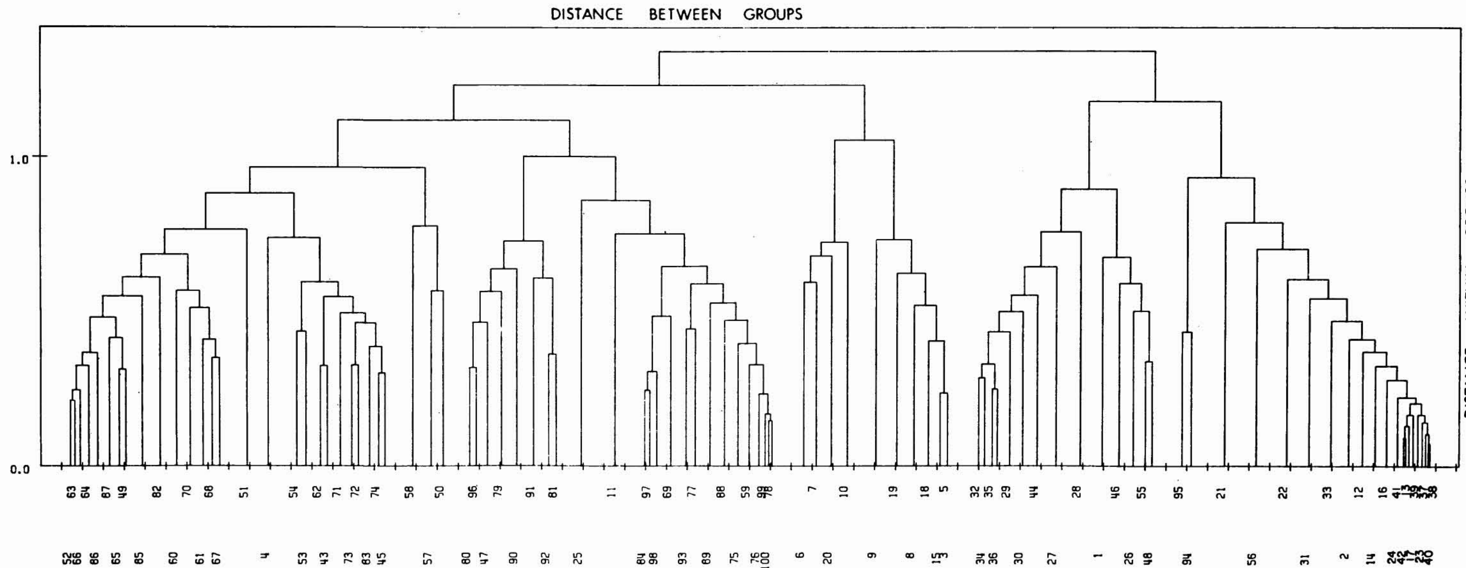

FIG. 8. Dendrograph showing associations among the individual quadrats of the transect. Numbers refer to quadrats that were enumerated sequentially, beginning at the deep end of the transect. To avoid crowding, the numbers are placed in two columns. Distance is a spatial measure of the dissimilarity between individual or groups of quadrats. The arc cosine transformation was used to convert the correlation coefficients to a measure of distance. A maximum distance of $\pi/2$ (or 1.57) corresponds to a minimum correlation of zero.

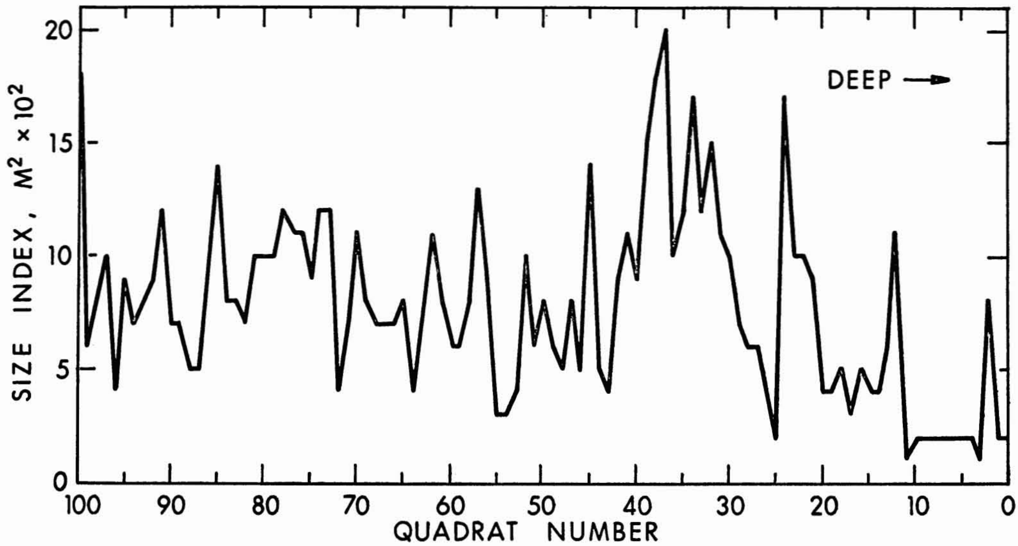

FIG. 9. The size index (an estimate of average colony area) plotted as a function of transect location (depth).

that most of the corals existing in the environment were not found in shallow water, a fact that also applies to corals on the Fanning reef slope. Specialized corals such as the solitary fungiids *Cirripathes*, *Echinophyllia*, *Pachyseris*, and *Leptoseris* were confined to deeper waters. At shallower environments at Eilat the greater unpredictability of the environment was due to extremes in tides, salinity, and temperature, as well as waves. At Fanning the upper end of the transect was not shallow enough to be affected by these factors; it seems more likely that storms and wave action take on greater significance in inhibiting the development of coral communities at shallow depths at Fanning.

Slobodkin and Sanders (1969) have postulated that environments that are both unpredictable and suboptimal show lower species diversity and evolution than environments that are either optimal or predictable. Species immigration is more likely to occur from unpredictable to optimal environments than the reverse. In this study the deepest environment showed the greatest diversity. Hence, it may be postulated that environments that are predictable and *suboptimal* are more diverse than those environments that are both predictable and *optimal*, because dominance is less likely to occur in the deeper suboptimal environment which allows greater coexistence, and, perhaps, more rapid evolution of new species.

CONCLUSIONS

1. Substrates with steep relief appear to enhance diversity and inhibit dominance by corals. Such environments may be characterized by greater habitat diversification.
2. Sediment cover appears to limit corals by restricting the amount of available substrate suitable for attachment. This has the tendency to reduce abundance and diversity of corals at small reef dimensions.
3. Growth and perhaps maximum size of corals along the deeper portions of the transect may be limited by reduced light intensities at depths greater than 30 m.
4. A combination of suboptimal light and substrate conditions at depth coupled with a predictable (wave-free) environment may have enabled a greater number of corals to coexist.
5. The structure of the coral community may be determined by biological interactions at intermediate depths. Optimal and predictable physical conditions enable some species to achieve dominance at the expense of other corals, resulting in reduced diversity.
6. At moderately shallow depths, environmental conditions are more unstable, possibly because of periodic wave damage. This has the tendency to reduce both dominance and the number of coral types.

7. Qualitative observations in shallow water indicate the environment is both unpredictable and suboptimal. Scour and mechanical stress from waves and a host of other factors may limit both the number of kinds and the abundance of corals. Coralline algae appear to find these environments more favorable than do the corals.
8. Species distribution and dendrograph analyses have indicated that coral communities of the seaward leeward reef slope at Fanning are strongly zoned and are probably very complex and mature assemblages.
9. Corals have adopted a variety of strategies enabling them to persist and dominate on reefs.
10. The phenomenon of small-scale patchiness prevails in practically all of the quantitative expressions used to describe the coral community. Potentially many factors control the local development of corals and point to the need for future studies of the phenomenon.
11. Contiguous quadrat sampling offered some unique approaches in the investigation of the ecology of reef corals. Nevertheless, studies which have employed other techniques have reached similar conclusions regarding community structure.

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