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**SPECIES-NUMBERS RELATIONSHIPS IN AN ASSEMBLAGE
OF REEF-BUILDING CORALS: McKEAN ISLAND, PHOENIX ISLANDS**

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ABSTRACT

Species-numbers relationships in the McKean Island assemblage of reef-building corals were investigated to discover how they changed along environmental gradients of the reef. For the purposes of the study, two gradients were identified — a complex depth gradient and a wave exposure gradient.

Sampling was carried out by means of point samples along three randomly located transects, each extending from the buttress and surge channel region across the two reef terraces and down the deep reef slope to a depth of 26 m. A total of 49 species in 21 genera of hermatypic scleractinians and 2 species of hermatypic hydrozoans were encountered.

The greatest number of species was found inhabiting the shallow terraces. Evident was a reduction in the numbers of species present below the sharp increase in reef slope at approximately 18 m.

Percent cover of living coral decreased with increasing exposure to surge and waves.

Significant heterogeneity in the coral assemblage was observed along the depth gradient, and a surprisingly large, but not statistically significant, heterogeneity also existed along the exposure gradient. Three times as many species were present over all segments of the exposure gradient as over similar segments of the depth gradient.

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Most species were represented by small numbers of individuals; only a few had high abundances. Species diversity was lowest on the least exposed portion of the exposure gradient sampled and at mid-depths along the depth gradient.

Zonation and spatial aggregation for single species populations of corals are suggested by variance-to-mean ratios in excess of one for 3 of the 9 species tested and by the position of most samples below the Hurlbert (1971) expected line.

A hypothesis is outlined for the organization of atoll seaward reef coral assemblages. Wave and surge action is suggested as the principal organizing factor.

INTRODUCTION

It is the purpose of this paper to explore certain static aspects of the organizational complexity of an assemblage of hermatypic corals. Examined in particular are how numbers of species, compositional similarity, species diversity, and spatial pattern (collectively referred to as species-numbers relationships) change along environmental gradients of the reef studied. The assemblage studied occupies a portion of the subtidal seaward reef of a Central Pacific atoll.¹

The two gradients identified for the study are herewith defined. The depth gradient, a complex gradient (*sensu* Whittaker, 1967), is perpendicular to depth contours and extends from the base of the surge channel and buttress area at its shallow end to the steep reef slope below the 10 fathom (18 m) terrace at its deep end (Figure 1). Environmental variables judged to be important along this gradient are wave surge (or water movements in general), abrasion, light, plankton supply, and sedimentation. The exposure gradient is an atoll-encircling gradient in intensity of wave action (Figure 1).

This study is neither the first nor the most extensive to attempt either description or analysis of the differences in species-numbers relationships accompanying differences in the coral reef environment. Such observations date at least from Darwin (1889). The ecological surveys of Mayor (1918, 1924), Baker (1925), Manton (1935), and Abe (1937), depicting the zonation of coral species as the result of the varying degree to which corals are adapted for withstanding extremes of temperature and salinity, and of exposure to sedimentation and air,

¹ Financial support was provided by Scripps Institution of Oceanography.

laid the groundwork from which much modern reef ecology springs. A plethora of zonation studies has followed, mostly qualitative and many confined to reef flats and shallow protected areas. In his review of coral reefs, Stoddart (1969) lists an entire page of such studies, and there have been more since.

Going beyond descriptions of species zonation and its possible cause, the works of Loya (1972), Porter (1972), Grigg and Maragos (1974), Maragos (1974b), and Connell (in prep.) have attempted to relate assemblage characteristics determined from species-numbers relationships to environmental factors and ecological theory. Such studies are important in that they may provide insight into community structure, identify non-obvious interspecific associations, suggest important variables for manipulative experiments designed to explore ecosystem controls, offer empirical evidence for the test of theory, and provide the information necessary to predict the consequences of perturbation of the reef ecosystem.

The particular significance of the present study is that it was carried out in the "mare incognitum" of Wells (1954, 1957). This is the region of active upward and seaward progradation that gives any coral reef its cohesiveness and persistence.

DESCRIPTION OF THE STUDY AREA

A quantitative study of the reef-building coral assemblage at McKean Island ($3^{\circ}36'S$; $174^{\circ}08'W$) in the Phoenix Islands was undertaken during a brief visit in the summer of 1968. The atoll is slightly egg-shaped with a long axis of only some 1250 m (Figure 2). Such a small size means that there is no truly well protected lee, because the refraction of even moderate tradewind swell causes waves to break around the entire perimeter of the atoll. Mean tidal range is approximately 76 cm, winds are predominantly east and northeast trade winds, rainfall is on the order of 50 cm or less annually, and typhoons are extremely rare (Wiens, 1962).

The lagoon is filled, consisting presently of a salty guano and fine calcium carbonate mud flat. The mud flat is covered at high tides by a few centimeters of water that percolate through the atoll structure and flow in and out of the "lagoon" through several "springs" in the southeastern corner. The flat is surrounded by rubble ridges more or less filled with sand and small amounts of guano. Vegetation is sparse and low. Large numbers of sea birds use the island for nesting and roosting. The seaward shore along the western side of the island is backed by a high sandy beach used for nesting by the green sea turtle, *Chelonia mydas*. Around the remainder of the island the shore is backed by steep rubble ramparts (Figure 3). These ridges

are highest along the northern shore, reaching heights of some 5 m.¹ There is a clear series of three of these ridges around the northern portion of the island, indicating that since the attainment of present sea level some 4,000 years ago (Shepard, 1963) there have been at least three episodes (or single events) of extremely high waves to strike McKean Island.

On the east and south sides of the atoll the reef flat is quite smooth, carpeted with a thick algal turf, and normally kept wet even during low tides by wave run up. Around the northern side there is a shallow moat (maximum depth approximately 1 m at low tide) between the seaward reef margin and the rubble ridge. This moat contains large quantities of coral fragments and scattered small colonies of living coral. The reef flat is narrower along the west side, has a very few widely scattered blocks of reef material deposited on it, lacks a dense algal turf as wave action is reduced, but has occasional colonies of living coral in the pools in its uneven surface. The entire reef margin consists of buttresses and surge channels with no prominent algal ridge at any point.

The small size of McKean Island made a series of spot dives and surveys from the surface around the entire atoll feasible. A remarkable abundance of the grey reef shark, *Carcharhinus amblyrhynchos*, inhibited carrying out a continuous underwater survey. A sharp increase in slope at approximately 18 m or 10 fathoms is clearly defined throughout with the exception of an area in the south-west where a more irregular, stepwise slope prevails. The region of the sharp increase in slope received the most attention during these extra-limital dives. A shallower change in slope between 8 and 10 m found on many Pacific atolls (W.A. Newman and J.R. Curray, unpublished) was much more difficult to distinguish and was not discernable at all on the southwestern portion of the reef. The deeper portions of the reef terraces in the northeast were covered with coral rubble encrusted with calcareous algae, with only scattered colonies of living coral (Figure 4a). The amount of living coral increased to the south and west, and the amount of rubble decreased rapidly. The reef slope below 18 m and the deeper portion of the terrace were covered with luxuriant coral growth in the south and west (Figure 4b). The shallower terrace area had scattered coral growth in the northeast, east, and south. The coverage by living corals was greatest in the west. In the northwest a considerable extent of dense alcyonacean growths was present. Fish were abundant everywhere.

¹ These ridges are not unlike the ramparts reported by Maragos *et al.* (1974) from Funafuti formed during a rare typhoon strike. Similar ridges are also present at Fanning and at Christmas in the Line Islands (W.A. Newman, pers. comm., and Gallagher, 1970).

STUDY METHODS

Three transect lines of weighted 0.25 in. (0.635 cm) hard lay cotton were laid from the base of the buttresses and surge channels, across the seaward terraces, and down the outer reef slope to a depth of 26 m. The location of the initial transect was chosen arbitrarily as the most exposed point where, in the first day of field work, wave surge would not prohibit work in shallow water. Subsequent transects were located by running in a northerly direction (increasing exposure) along the reef in a small outboard-powered rubber boat for a number of seconds between 30 and 90 drawn from a table of random numbers. The distances between transects were never measured, but the overall distance between the first and last was an estimated 400 m. The approximate locations of these transects are shown in Figure 2.

The transect lines were marked at 1 m intervals. An ordinary wooden pencil was used to define a point sample below each mark. This procedure may be considered a systematic sample with a random start (Cochran et al., 1954). When a point overlaid living coral, a sample was collected for purposes of positive species identification. Only by examination under light and scanning electron microscopes could the various species of massive *Porites* and tuberculate *Montipora* be distinguished. Literature used for species identifications is given in an appendix. The primary data acquired by the sampling, which was performed with the aid of SCUBA, were the number of species and the number of individuals per species present.¹ These assemblage characteristics, and others computed or deduced from them, were then compared along the two nearly perpendicular environmental gradients (depth and exposure).

For analysing how species-numbers relationships change along the environmental gradients of exposure and depth, the sample points are grouped into two classes - transects and depth intervals, of three

¹ In the strictest sense what was recorded was the number of "hits" rather than the number of individuals. This arises since colonies of several massive species may attain dimensions greater than 1 m and a few branching species may form thickets greater than 1 m in extent. For the McKean Island study, the only problem area was at depths greater than about 15 m where it was not always possible to be certain in defining the limits of massive, shelving colonies of *Porites*. Since such cases arose only two or three times in the sampling, the number of "hits" in this study may safely be referred to as the number of individuals.

sampling units each. Limits of the depth intervals were chosen to correspond to the terrace topography widely observed on seaward reefs of Pacific atolls, as these might represent habitat boundaries. Depth Interval 1 extends from the base of the buttress and surge channel system, found at depths between 1 and 2 m along the section of reef studied, to the slight change in slope between 8 and 10 m. Depth Interval 2 extends from the lower limit of Depth Interval 1 to the rather sharp break in slope at approximately 18 m. Depth Interval 3 extends from the lower limit of Depth Interval 2 down the steep deep reef slope to a depth of 26 m (Figure 1). Data for the depth intervals were obtained by pooling the points within each depth interval from each transect.

ANALYSIS TECHNIQUES AND RESULTS

A total of 49 species of hermatypic scleractinians representing 21 genera was found at McKean Island. Of this total, 36 species in 16 genera were encountered along the transects. The remainder were collected during the circum-atoll series of dives. Two species of the hermatypic hydrozoan *Millepora* were also present, one of which occurred under the transects. A list of species and their distribution in the samples is given in Table 1a and b.

Since Depth Interval 3 (the deepest) contains so many fewer sample points than any of the other sample units, it is necessary to demonstrate a sampling adequacy at least comparable to the other sample units before any meaningful interpretation can be made. This may be accomplished by comparing the relative shapes of the curves of cumulative number of species versus total numbers of individuals curves for the three depth intervals (Figure 5). These curves were constructed by successively adding the numbers of new species and total individuals from the segments of each of the transects lying within each particular depth interval. They appear to be a family of curves in which individuals of previously recorded species enter increasingly larger samples more frequently than do individuals of new species. This suggests that all three curves may be approaching plateaus, indicating relatively complete sampling. Depth Interval 1 (the shallowest) appears to have the poorest fit. Corroborating the suggestion of the plateauing of the Depth Interval 3 cumulative species-individuals curve is the paucity of additional species found in deep water during the series of dives all around the atoll (Table 1b).

The distribution of sample points, numbers of coral species, dominance, and a biased measure of percent living coral coverage are summarized in Table 2. The sampling indicates a decrease in the number of species with depth but little if any change over the range of the exposure gradient sampled.

The values for percent living coral coverage can be ignored except for the trends they suggest: decreasing coverage with increasing exposure but no discernable change along the depth gradient. It was, however, my subjective impression that coverage was lower along the shallowest portions of the transects. An upward bias has been introduced into the coverage values by the use of a sample point with finite dimensions (Grieg-Smith, 1964).

The similarity of species composition along the depth and exposure gradients was studied by comparing the numbers of species shared by pairs of sample units within sampling classes. This was done statistically by determining the probability that any two samples drawn from a randomly distributed population should be as or more similar than those actually obtained by sampling natural field populations. The formula for a single event (sample pair) is given by Glime and Clemons (1972).

Since the frequencies of the various species making up the total assemblage affect their chances of entering samples, it was necessary to include this distribution in the determination of probabilities of number of shared species. To do this, samples containing the numbers of species observed in the field samples were iteratively drawn at random (with replacement) by computer from the overall frequency distribution and sample pairs compared as to the number of shared species. The probabilities of observing given numbers of shared species were determined from these sample comparisons. These individual probabilities were summed to give the probability of observing as many or more shared species. Such probabilities for the McKean Island samples are given in Table 3. The numbers of species shared between each of the three possible transect pairs do not differ significantly from random expectation at the 5% level. However, in all three cases the number shared is on the "too few" side. Both Depth Intervals 2 and 3 have significantly too few species in common with Depth Interval 1, but do not themselves differ from random expectation. Too few shared species means differences in the species composition for portions of the assemblage being compared. In the actual field sampling, 15 species were found in common between all transects, but only 5 were common to all depth intervals. There is greater compositional similarity between transects than between depth intervals.

Changes in relative abundance along the depth and exposure gradients were explored by computing the degree of concordance in the rankings of species abundances for the sample units within each sampling class. Agreement in the rankings of the transect abundances of the 7 most common species and the depth interval abundances of the 5 species found in all three depth intervals, as well as for all species, was compared using Kendall's coefficient of concordance (Tate and Clelland, 1957). The coefficients of concordance are presented in Table 4. There is greater than 95% certainty that

the transect rankings for all species are correlated, but not when only the most abundant species are considered separately. There is no significant agreement at the 5% level in the ranks of species from the depth intervals, even when only those species found at all depths are considered. The relative abundances of the various coral species are, at best, only slightly more alike between the transects than between depth intervals.

Species diversity (number of species, heterogeneity, and evenness or dominance) was explored using several different approaches. First, several indices that incorporate both the number of species present and the numbers of individuals per species as a summary statistic were calculated and ranked for each sample unit within each sampling class. These indices were 1 - Simpson's index (SI^*), the Shannon-Wiener function (H'), the standard deviation about the mean (SD), and the number of moves index (NM) (Fager, 1972). Subsequently, each of these indices was scaled (see Fager, 1972, for methods) and ranked. The results of these calculations and rankings are presented in Table 5a and b. Next the antilogarithm of H' [$\text{Exp}(H')$], the reciprocal of Simpson's index ($1/\sum p_i^2$) and the ratio of these two expressions ($R\ 1:2$, a measure of evenness or dominance) were calculated and are presented (after Peet, 1974) in Figure 6. Also, the actual sampling distributions are presented in Figure 7 as histograms of numbers of individuals per species versus species rank order for each sample unit in each sampling class. Dominance was further measured by calculating the minimum number of species needed to furnish 50% of the individuals contained in a sample unit (Fager, unpublished). This is most conveniently expressed as a percentage (given in Table 2). It is the trends in diversity along environmental gradients, as expressed in the rankings of Table 5b, the graphs of Figures 6 and 7b, and the species counts and dominance of Table 2, that are taken as of interest here rather than any actual calculated values. The outcome of the diversity analysis is contained in the discussion section.

Segments of the environmental gradients considered in this study were sampled with differing intensities, resulting in samples of different sizes. Hurlbert (1971) has presented a method of computing the expected number of species to be found in a sample of n individuals selected at random (without replacement) from a collection containing N total individuals and S total species. If such a computation is made for a series of sample sizes (n 's) and these values are plotted and connected by a line, the numbers of species observed in small samples may be compared to the numbers of species found in large samples by noting their respective locations relative to the expected line. This was done for the sample units of this study using the pooled composite of all samples as the collection. Figure 8 illustrates the result. It may be noted from this figure that Depth Interval 3 (the smallest sized sample) departs less in absolute magnitude and proportionally the

same from the expected line as Depth Interval 2 (the largest sized sample). This offers additional objective support to the earlier contention that the Depth Interval 3 sample may reasonably be considered adequate.

It may also be noted from the figure that only one point lies above the expected line, all the rest fall below, but most are quite close to it. Unfortunately with only three sample units per sampling class all three could be expected on the basis of chance alone to be located on one side or the other of the expected line 12.5% of the time (using a binomial distribution with p and q both equal to 0.5). Thus it is not possible to assess the significance of the observed frequencies of sample unit positions above or below the line with any confidence greater than about 90%. However the observed distribution of samples about the line, most having fewer species than expected, suggests that the coral assemblage is characterized by at least moderate spatial aggregation (Hessler and Jumars, 1973, explain the reasoning involved) along both environmental gradients.

DISCUSSION

Biogeography

The closest localities to McKean Island for which the hermatypic scleractinian faunas are relatively well known are Canton (also in the Phoenix Islands) and Fanning Island — roughly 650 km northeast of McKean in the Line Islands. Seventy-four species in 28 genera have been reported from Canton (P. Jokiel and J. Maragos, pers. comm.), and 69 species in 26 genera have been reported from Fanning (Maragos, 1974a). Three additional genera are reported (Maragos, pers. comm.) from Christmas Island, also in the Line Islands. Wells (1954) and Stehli and Wells (1971) place both the Phoenix and Line Islands within the boundaries of their 20 and 30 isopangeneric lines. The 21 genera reported here for McKean Island further suggests that at the generic level observations in this region are approaching completeness. All of the McKean genera are present elsewhere in the Phoenix or Line Islands.

The extremely small size of McKean Island, its relatively isolated location, the generally short duration of pelagic coral larval stages, and the occurrence of catastrophic environmental disturbances — such as wave storms — make it seem quite likely that temporal disequilibria occur in extinction and immigration rates (see MacArthur and Wilson, 1967, for a discussion of island size and isolation in island biogeography.) Using the Canton and Fanning faunas as references, genera of hermatypic scleractinians likely to have species represented by at least a few individuals from time to time at McKean, but not observed there in 1968, are *Stylophora*,

Astreopora, Coscinaraea, Pachyseris, Herpolitha, Leptoria, Echinophyllia, and Merulina.

Number of species

Wells (1957) has presented a general curve depicting a sharp decrease in the number of hermatypic coral species with depth. This curve was constructed from data collected at Bikini, Marshall Islands, and the steepness of the decline in numbers of species with depth certainly reflects the heavy sampling bias towards reef flats and shallow lagoon areas. Probably the most extensive and complete data on the depth distribution of hermatypic corals have been provided by Goreau and Wells (1967) for the north coast of Jamaica. Of the 48 hermatypic species they list, 36 have a distribution whose "optima" includes the depth interval 0 to 10 m, 26 include the interval between 10 and 20 m, and 22 have "optima" extending to depths greater than 20 m. The pattern of decreasing numbers of species along the complex depth gradient is similar even if the "maximum" and "minimum," rather than the "optimal," distributional limits are used: 42, 38, and 34 species for the respective depth intervals.

Sampling done on the seaward reef of McKean Island suggests that the number of species present there decreases only slightly with depth until the sharp increase in reef slope characteristic of Pacific atolls is encountered at approximately 18 m. At about that portion of the environmental gradient there is a reduction in the number of species present.

No one had ever challenged Wells's (1957) generality of a decrease in the number of hermatypic coral species with depth until Loya (1972) claimed that his study at Eilat showed "a successive increase in the number of species with depth." However, what Loya actually showed was that on the scale of 10 m line transects species density (number per unit of transect length) increased with depth. Maragos (1974b) arrived at a similar conclusion of high species richness at the deep end of his Fanning Island transect for the same reason. Hiatt (1957) first pointed out that all quantitative studies of coral assemblages up to and including his own employed fixed sample areas (same size quadrats) throughout and therefore measured densities on a particular scale. Stoddart (1966), Davies *et al.* (1971), Loya (1972), Porter (1972), Grigg and Maragos (1974), and Maragos (1974b) have all done likewise since.

Loya (1972) does give total species numbers for the reef flat (34) and the portion of the reef deeper than 20 m (59). No numbers are given in that paper for the intervening subtidal segments of the depth gradient. However, in an earlier paper (Loya and Slobodkin, 1971) dealing with the same reef at Eilat, a table similar to that presented by Goreau and Wells (1967) is given. Treating the distributional data in Loya and Slobodkin's table in the same manner as that of Goreau and

Wells, the distribution of numbers of hermatypic species is 77, 46, and 36. "Optimum" range is all that they give. The 77 species found in shallow water (0-10 m) is still greater than the 59 from deep water (>20 m) reported in Loya's 1972 paper. Sampling of an intensity comparable to that performed in Jamaica by T.F. Goreau and his associates would seem in order for both Fanning and McKean Islands before the final word on how the number of hermatypic coral species changes with depth can be spoken. Meanwhile, although Wells's (1957) curve may be too steep, the generality that the number of hermatypic coral species and the suitability of the environment for their growth decreases with depth on a reef appears to remain valid.

The exposure gradient

Changes in coral assemblage composition and characteristics along an axis paralleling the trends or faces of reefs have received very little attention in the past. Depending on size, shape, and location of any particular reef, environmental conditions may be similar for many kilometers or they may change rather rapidly. The principal factor of environmental change along or around the trend of an atoll reef is considered here to be exposure to wave action. Grigg and Maragos (1974) advance a similar hypothesis for their reef studies around the island of Hawaii. For the myriad zonation schemes determined for coral reefs to be meaningful, some measure of variation in species composition and relative abundances along the environmental gradient paralleling the reef trend must be made.

In a study of the reef front of Aldabra, Barnes *et al.* (1971) presented a figure depicting variation in the zonation pattern they determined. Their qualitative zonation scheme was based on coral growth forms, restricted species of hermatypic corals, and the presence of other distinctive taxonomic groups of benthos. Even though there is considerable variation in their scheme, that they were able to recognize similar zones over such a wide range of environmental conditions (their survey circled the entire atoll) seems remarkable. The lack of determination of species-numbers relationships however makes comparison with the McKean study impossible.

Having a series of systematic transects running parallel to each other and parallel to the shore at three stations, Loya (1972) tested for homogeneity of the data recorded at the different stations. Using an analysis of variance procedure, he found that means for the number of species, number of colonies, living coverage, and diversity (all per transect) for each of the various zones enumerated were not significantly variable between the three stations. Unfortunately neither of the papers dealing with this study (Loya and Slobodkin, 1971, and Loya, 1972) reveal how the stations were selected or how they were spaced. It is surmised from locality descriptions and

figures in those two papers, however, that no strong environmental gradients are to be expected along the extent of any one of the Eilat fringing reefs. The results of Loya's (1972) analysis is then gratifying in that those assemblage characteristics analysed did not change significantly along an axis where environmental change was probably negligible.¹

It should be added that all fringing reefs near Eilat are not necessarily alike in terms of species zonation. Mergner (1971) describes a rather considerably different zonation pattern for reefs there.

The seaward reef of McKean Island with its changing exposure to tradewind generated waves presents a situation rather different from that at Eilat.² Because of the small size of the atoll this gradient is noticeable over distances as small as a hundred meters or so, as judged by changes in heights of breaking waves.

The lack of a trend in the number of species found along the exposure gradient may result from there being no real changes in the number of species inhabiting the relatively narrow segment of the gradient sampled. Two other possible explanations are available. First, some species found shallow where exposure is low may be found deeper, but perhaps in reduced abundance, where exposure is greater. Or, second, there may be a regular faunal replacement series along the exposure gradient. On the first alternative the McKean data are certainly insufficient; the second will be treated in following discussion sections.

Percent cover

The decrease in percent coverage of living coral with an increase in exposure to waves may result from physical breakage and removal of corals by strong surge and wave action and also possibly from greater competition with coralline algae. Grigg and Maragos (1974) also

¹ It does not necessarily follow from Loya's (1972) analysis that the coral assemblage is homogeneous in terms of its species and their relative abundances, but only that the summary statistics computed from his data are not significantly variable between stations.

² Munk and Sargent (1954) used a local wind rose to compute the wave power distribution around Bikini Atoll. Such a gradient in wave exposure may then be deduced from the local wind rose for McKean Island given in Wiens (1962, p. 143).

arrive at a similar conclusion for reefs around the island of Hawaii. Both of these factors should operate more strongly in shallow water. On the other hand, the decrease in coverage observed may be the result of either a gradation in the degree of coral destruction during the last catastrophic disturbance to strike McKean Island, or differential rates of recovery since such events, or both. The major obstacle to a firm answer is a lack of sampling (or observation) over a sufficient time span rather than any spatial deficiencies in the sampling program.

For the same reasons as above I would have expected lower coral coverage on the shallow portion of the depth gradient than on deeper segments. My subjective impression was that this was probably the case. However the numbers for percent living coral generated during the study are so similar for all three depth intervals that it is not sound to offer them as verification of that expectation. The changes in living coral coverage with depth reported by Loya (1972) are of little help here due to differences in reef topography and physical environments between the areas studied. Maragos (1974b) reports, like the McKean study, a qualitative impression of relatively low coral coverage in water shallower than 8 m at Fanning Island in an environment not too unlike that sampled at McKean Island.

Compositional similarity

The modification of Glime and Clemons' (1972) statistical approach to measuring compositional similarity, incorporating species abundances, is a measure of assemblage homogeneity. It was surprising that the numbers of species shared between pairs of transects is less than expected. All probabilities are well below 0.50, the level expected of species occur at random in the samples (Table 3). In fact, Transects 1 and 2 border on being significantly different from each other at the 5% level. Thus, while the number of species found along each transect is quite uniform (25, 27, and 21), the kinds present appear to change somewhat even along the rather narrow segment of the exposure gradient sampled.

The depth intervals also have too few shared species. The shallowest depth interval is significantly different from both the deeper depth intervals (Table 3). The shallowest depth interval appears to be distinctly different from deeper depths in the composition of its coral fauna. While the two deeper intervals are not significantly different at the 5% level, they too are on the side of fewer than expected shared species. Thus heterogeneity in the coral assemblage is more strongly indicated when proceeding along the depth gradient.

Concordance coefficients calculated for the sample units allow a more detailed look into the nature of the differences in compositional similarity. The high degree of concordance observed in

the transect rankings should not be taken as being in disagreement with the heterogeneity along the exposure gradient suggested by the shared species method, but may be used to clarify the nature of that heterogeneity. The significant concordance in the transect rankings of all species stems mainly from the large number of tied ranks amongst the rare species, most of which are represented by only one or two colonies (Table 1). Differences in concordance are therefore largely precluded.

The lack of significant concordance in the rankings of the seven most common species indicates that the more common species show moderate variations in abundance along the portion of the exposure gradient sampled. This suggests that it is not only the presence or absence of uncommon species within the sample units that constitutes the coral assemblage heterogeneity along the exposure gradient but also the changes in relative abundance of the most common species.¹

Compositional changes in the coral fauna along the depth gradient are much more striking. Not only were fewer species found in common between the three depth intervals than between the three transects, but the absolute and relative abundances of those species held in common by the depth intervals varied considerably. Even the presence of considerable numbers of species with abundances of only one or two individuals was not sufficient to obscure both the restricted distributions of some of the moderately abundant species and the rather large changes in relative abundance of the widely distributed ones.

I consider the concordance analysis and the shared species method to give consistent results. Both are needed to make the pattern of assemblage heterogeneity clear. Along the exposure gradient there were a moderate number of widespread species whose relative abundances changed moderately over the portion of the gradient sampled. There were a large number of species found in low abundance, but the magnitude of the sampling was insufficient to conclude whether or not these were widespread along the gradient. Changes in species composition and relative abundance were much more marked along the complex depth gradient. Only a few species appeared to be ubiquitous along it, and their relative proportions usually changed between depth intervals. Fewer still were found in large enough numbers, but only over a limited extent of the depth gradient, to suggest restricted depth distributions. Again, most species were not present in the samples in sufficient abundance to determine the extent of their distributions.

¹ The degree of heterogeneity or concordance observed is relative to the scale of sampling and thus is best used for comparative purposes only.

Diversity

Preston (1969) observed that "every naturalist from Darwin downwards has felt aggrieved that a few species are very common and most are rare." Abe (1937), for the corals inhabiting a small lagoon reef at Palau, and Loya and Slobodkin (1971) for a collection from the fringing reef at Eilat, both present curves of species rank order versus numbers of individuals per species that have shapes virtually identical with that of the McKean coral fauna shown in Figure 7a. Data presented by Mayor for Murray Island (1918) and Samoan (1924) reef flats also indicate that species with high abundance are a minority. If the species pooling in his studies is taken into account the agreement with other studies improves. Hermatypic corals as a group appear to fit the general pattern noted by Preston.

Species diversity, its evolution, maintenance, and consequences has surely become an involved topic. Several older theories on the evolution of high species diversity required long-term stable (constant) environments (reviewed by Pianka, 1966). Additionally, diversity has been said to relate to community productivity, integration, evolution, niche structure, competition (McIntosh, 1967), and habitat complexity (Kohn, 1971). Further, Slobodkin and Sanders (1969) have theorized on the relationship between species diversity and environmental variability, unpredictableness and harshness. In this discussion coral species diversity is taken as a measure of environmental favorability for coral growth and as a measure of how well each species is doing relative to all others in its habitat. High numbers of species are considered positively related to environmental favorableness; low distributional skew means all species present are doing very nearly equally well.¹ The observed diversity pattern may then be correlated with changing physical conditions along environmental gradients.

Peet (1974), in the most recent review of the concept and measurement of species diversity, has discussed the various components comprising the concept and the methods employed in their measurement. He has also discussed the mathematical properties and interpretive limitations of the various measuring techniques. I wish to retain a dual concept approach; that is, species diversity is comprised of both a species "richness" and an "evenness" component.

Look first at the rankings for the unscaled diversity indices SI^* , H' , SD , and NM (numbers in parentheses in Table 5b). These are all indices classed as heterogeneity indices by Peet (1974) as they use various mathematical procedures in an attempt to summarize into a single statistic both the number of species in a sample and the distribution of individuals among species. As discussed by Fager

¹ A potential problem not dealt with here would be the analogous situation of lumping trees, shrubs, and herbs in the calculation of diversity of terrestrial plant communities.

(1972), Hill (1973), and Peet (1974), these indices are sensitive to different aspects of these two components of diversity. Although these indices may pertain to slightly different questions about diversity (Fager, 1972), the choice of which one to use is largely arbitrary, and their lack of agreement in ranking samples suggests a tenuousness for hypothesis construction that would be better avoided.

Scaling these indices before ranking them improves their agreement somewhat. This probably results because, as pointed out by Grigg (pers. comm.) and Peet (1974), scaling in the manner proposed by Fager (1972) converts all the indices to measures emphasizing the evenness of the distribution of individuals among species. That is, the scaling procedure places each calculated index value on a scale relative to the values possible for maximum and minimum distribution skew for each sample. In the case under study here all four scaled indices do agree on which sample unit in each sampling class has the most uneven distribution (Transect 1 and Depth Interval 2), but they do not agree in discriminating between the others. As the choice of which index to use is still arbitrary (and they do not agree in the ranking of samples) and the units of expression have questionable biological meaning (bits, moves, or probabilities), I prefer to avoid their use just as the unscaled indices.

Graphical presentation of the sampling distribution (Figure 7b) shows the relationship between the number of species present and the distribution of individuals among them without losing or obscuring any of the information content of the original sampling. When coupled with the dominance calculations (given in Table 2), the graphic plots can be used to describe the diversity patterns along the environmental gradients of exposure and depth.

It can be readily noted from Figure 7b that Transect 1 has the most highly skewed distribution among the transects. Transect 1 also shows high calculated dominance (it takes only roughly 8% of the species present to furnish 50% of the individuals in the sample) and a high species count. Transects 2 and 3 have essentially the same number of species as does Transect 1, but they both show considerably greater evenness in their distributions. This pattern of maintained high numbers of species but decreasing dominance (or increasing evenness) with increasing exposure to wave action suggests that where the coral assemblage is exposed to a higher average level of wave action from either tradewind swell or large, long-period storm waves relatively fewer species are able to monopolize available space. Thus coral diversity may be enhanced by greater exposure to waves. Both Mayor (1918) and Grigg and Maragos (1974) invoke essentially this same hypothesis to explain the nature of the coral distributions they observed.

The graphical plots of the depth intervals show Depth Interval 2 to have the greatest distributional skew among the depth intervals,

but at the same time this depth interval has a high species count. Depth Intervals 1 and 3 show nearly equivalent evenness with the dominance calculations suggesting that Depth Interval 3 is less dominated. Depth Interval 1, however, has a greater number of species than Depth Interval 3 and a number comparable to that of Depth Interval 2 and thus is the most diverse of the depth intervals. This pattern of species diversity suggests again that that portion of the environmental gradient in shallow water subject to a relatively constant and high wave energy level is prevented from having space highly monopolized by a few species. It further suggests that an assumed long-term constancy of the deep reef environment may be quite amenable to a rather equitable division of resources and that the sharp increase in reef slope at about 18 m represents a possible environmental threshold beyond which a greatly reduced number of hermatypic coral species find conditions favorable for growth and survival.

The methodology developed by Peet (1974) for studying species diversity was also employed in this study to check its agreement with the results of the graphical plots of the sample distributions. The overall shape of the Exp (H') curves are similar to those of the species counts. This was to be expected as H' is primarily sensitive to the number of species present (Fager, 1972) or, if you will, changes in the number of rare species (Peet, 1974). The index $1/\sum p_i^2$ is more sensitive to changes in abundance of the more common species (Peet, 1974), and the plots of it in Figure 6 show changes similar to those seen in the distributional plots of Figure 7b. The ratio of Exp (H') to $1/\sum p_i^2$, a measure of dominance or evenness (Hill, 1973; Peet, 1974) agrees with the distributional plots and the dominance calculations except for the relative dominance of Depth Intervals 1 and 3. The particular attractiveness of this procedure according to Peet (1974) lies in the nature of the response of the two diversity indices and the suggestion that their units (species) are both the same and ecologically meaningful. At this point their calculation appears to be unnecessary as the graphical plots of the sample distributions and the dominance calculations give at least as satisfactory results, without concealing the information contained in the actual sample distributions, without problems of "units," and without problems of interpretation.

The ordering of samples (or assemblages or communities) from the graphical plots is largely a subjective decision and hence may not always be clear cut. Where samples cannot be distinguished as to the more diverse on the basis of distributional plots, it probably is not safe to say they differ in diversity regardless of the method of measurement used. All of the methods currently used to measure species diversity are sample size dependent (Hill, 1973; Peet, 1974). Only in the graphical approach does this problem appear surmountable. This may be done through replicate sampling to verify the number, kinds, and relative frequencies of the species involved (Scanland, in prep.). This study begs to be repeated employing such a sampling design.

There have been three other studies recently of the diversity of hermatypic coral assemblages. All three studies employed the Shannon-Wiener function (H') as the diversity index for comparison. Loya (1972) reported an increasing trend in diversity (per 10 m of transect length) with depth for a fringing reef at Eilat. He also reported that at the 5% significance level there were no differences in diversity between stations (within zones only). Porter (1972) reported that diversity per 10 m transect reached a high level at a depth of 5 m and remained relatively high to the base of a lagoon reef in the San Blas Islands off the Caribbean coast of Panama. He also reported a trend of increased diversity values on "cliff edges." Maragos (1974b) reports highest diversity (per 10 m² of area) on the deepest segment (30-35 m) of his transect on the leeward seaward reef of Fanning Island, lowest diversity on the intermediate portion (20-25 m), and intermediate diversity at the shallow end (8-15 m).

The lack of agreement between the results, and to some degree also the hypotheses advanced to explain the patterns observed, of the McKean study and those of Loya, Porter, and Maragos may stem from several factors. The physical environment, particularly wave action and geological structure, of the reefs studied by Loya in the Gulf of Eilat and by Porter in the San Blas Islands are quite different from that at McKean, although the Fanning reef studied by Maragos may be somewhat comparable. Both Porter and Maragos used a measure of coral cover rather than individuals as the importance value for their diversity calculations.¹ The diversity (H') and evenness (H'/H'_{max}) indices used in each of these other studies are primarily sensitive to changes in the rare species only (Fager, 1972; Peet, 1974) and pay little attention to the concentration of dominance. Diversity values in each of the other three studies, unlike the McKean study, are reported in terms of fixed sized sample areas. Hopefully in the not too distant future some sort of common ground for sampling procedure and data analysis can be found so that generalizations regarding the structure of hermatypic coral assemblages can be realistically compared.

¹ Loya (1972) used both individuals and coverage as importance values for calculating H' and found them strongly correlated. In addition to Loya's suggestion that this linear relationship showed that there were no significant differences in the sizes of the corals within a transect, that correlation may also have resulted from the distribution of cover closely matching that of individuals by chance and most likely from the fact that the same number of species was involved in each set of calculations. (H' shows extreme sensitivity to just the number of species involved (Fager, 1972.) Thus diversity based on individuals or coverage may or may not be equivalent.

Spatial Pattern

Spatial aggregation for single species populations of hermatypic corals along an environmental gradient parallel to depth is implied in the many determinations of reef "zones." Similarly, circumscribed species distributions have been referred to along an exposure gradient; for example, the differences in species present on windward and leeward seaward reefs (Wells, 1954). These propositions imply that any given species occupies only a limited range of the environment, the very basis of gradient analysis.

Likewise, the position of all three depth interval samples below the Hurlbert (1971) expected line suggest aggregation, or zonation, along the depth gradient. At best this offers limited statistical support for the zonation of corals with depth. The indirect gradient analysis technique of ordination employed by Loya (1972) provides a much stronger quantitative verification of zonation along the depth gradient. Maragos (1974b) also utilized an ordination procedure to show zonation.

Since the exposure gradient is generally much less steep (environmental conditions are assumed to change less rapidly per unit of distance) than the depth gradient, relatively similar environmental conditions may prevail for relatively large distances on many reefs. This makes the determination of patchy distributions for populations of coral species within arbitrary habitats lacking steep physical environmental gradients feasible and an inherently interesting feature of assemblage organization.

The relationship of the McKean transect samples to the Hurlbert (1971) expected line suggests a small degree of aggregation present in the coral assemblage when viewed along the exposure gradient. That a few of the more common species have variance-to-mean ratios in excess of one (Table 6) supports the aggregation hypothesis in the McKean Island assemblage.

There are now several reports in the literature concerning patterns of spatial distribution of hermatypic corals within limited habitats. Lewis (1970) reported highly aggregated distributions for three of the four species he studied on the reef crest of a Caribbean fringing reef. He states that the causes of such contagious distributions are under investigation, but suggests they are biological. He appears to reject heterogeneity of microhabitats, as the zone studied seemed to be physically homogeneous. Maragos (1974b) measured spatial pattern for several species (12) within a range of quadrats where each species was commonly found. He reports aggregated distributions for most of those species.

Stimson (1974) has determined an underdispersed pattern for *Pocillopora meandrina* in shallow water areas in Hawaii where it was virtually the only coral species present. He hypothesizes that this

pattern probably results from larval settling behaviour.

On the reef flat at Heron Island near the southern end of the Great Barrier Reef, Grassle (1973) has found four species of hermatypic corals and several other invertebrates and algae to have patchy distributions on several scales. He suggests that this patchiness is a small scale response to the environment.

The aggregation present along the exposure gradient at McKean Island could result from such microhabitat differences as variations in exposure to waves, scour, sedimentation, and light that would lead to differential mortality rates or larval settling behaviour. It is also conceivable that interspecific aggressive behaviour might play a role. Clarification of the degree of aggregation exhibited by even a modest portion of the coral fauna inhabiting a relatively homogeneous reef environment other than the reef flat and the factors that lead to it must await a larger study properly designed to reveal spatial patterns.

CONCLUSIONS

The relative depauperateness of the McKean Island coral fauna probably results from a combination of very small island size, relative isolation, limited powers of coral larval dispersal, and catastrophic disturbances. The figures of 51 species in 22 genera of hermatypes are consonant with known biogeography.

Two gradients were studied at McKean — depth and horizontal exposure to wave action. The distribution of numbers of species appears to fit Wells's (1957) generality of a decline with increasing depth. The reduction seems most noticeable across the rather sharp increase in reef slope found at approximately 18 m. This reduction may result from changes in environmental variables, such as light, circulation, sedimentation, and plankton supply; reef topography; and/or biological interactions. The sampling at McKean revealed no changes in the numbers of species along the exposure gradient.

The McKean data are rather weakly suggestive of a decrease in living coral coverage with increasing exposure to wave action along both environmental gradients. Corals being broken free or damaged by strong surge and waves and space competition with coralline algae are possible explanations for such a pattern.

Comparisons of compositional similarity reveal the following characteristics of species and population distributions in the McKean coral assemblage: 1) Most species occur in relatively low abundances; these may or may not be widespread. 2) There are a moderate number of relatively abundant and widespread species along the exposure gradient;

there are considerably fewer such species along the depth gradient. 3) There are a small number of relatively abundant species that show restricted distributions along the depth gradient. This last group constitutes a break in faunal composition that separates that portion of the reef shallower than 10 m from the remainder. The average depth of surf base is the environmental factor implicated.¹ There must be a small suite of highly surge resistant species living in this shallow, more intensely wave and surge-swept habitat.

Graphical analysis, a simple dominance calculation, and various diversity indices were used to explore species diversity in the coral assemblage. The least exposed portion of the exposure gradient sampled appeared to be the least diverse. The middle segment of the depth gradient appeared to be the least diverse portion of that gradient. Along the exposure gradient it is the degree of dominance that appears to change rather than species richness. Along the depth gradient mid-depths are rich in species, but dominance is relatively high; shallow depths are also rich in species, but are dominated less; deep depths are less rich in species, but show greater evenness in species abundances.

Results of both the shared species comparisons and the positions of the depth interval samples relative to the Hurlbert (1971) line imply a degree of zonation in the coral assemblage with depth. Variance-to-mean ratios of common species and the positions of the transect samples relative to the Hurlbert (1971) line suggest at least a small degree of spatial aggregation in the McKean coral assemblage along the exposure gradient. Zonation with depth simply reflects the changing adaptive capabilities of the various species to relatively rapidly changing environmental conditions. Since the exposure gradient at McKean is subjectively less steep than the depth gradient, aggregation along it may reflect microhabitat differences although biological interactions cannot be ruled out.

Drawing upon knowledge of coral biology, the nature of the coral reef physical environment, observed coral assemblage species-numbers relationships, and aspects of ecological theory, I offer the following hypothesis for the organization of assemblages of reef building corals on atoll seaward reefs.

Shallow, subtidal, frequently wave-swept reef environments — the physiologically optimal region for coral growth — should have high temporal predictability, high temporal variability, and a high, steady rate of space production. But survival of individual colonies may be unpredictable. The result might be an arrested successional stage in

¹ Surf base is the depth at which hard rock erosion ceases to occur (Bascom, 1964). For normal tradewind generated swell this depth lies between 7 and 9 m.

which there are many species found in rather equitable numbers, with at least a few restricted to such environments.¹

Mid-depth environments should have relatively low temporal predictability, high temporal variability, and a fluctuating rate of space production due to irregular, unpredictable occurrences of heavy surge. Thus, while many species may persist, the assemblage is likely to be highly dominated a good deal of the time. This portion of the environmental gradient may be considered transitional, with very few species restricted to it, and in varying stages of succession depending on how much time had elapsed since the last space-creating episode.

Deep reef environments, perhaps slightly less favorable but no more variable physiologically than shallow water, may remain quite constant for lengthy periods of time and be disturbed only at great, but unpredictable, intervals by such events as particularly devastating typhoons or massive *Acanthaster* swarms. The number of species would be reduced and space utilized in an equitable manner. Only here may coral-coral competitive interactions be of any importance to coral assemblage organization. Deep reef assemblages, and perhaps some lagoon reef ones located in regions of low or zero typhoon frequency, are probably the only hermatypic coral assemblages reaching a true climax. Figure 8 summarizes this hypothesis.

Segments of the depth gradient where these various conditions prevail are likely to be displaced toward shallower depths only where the exposure gradient includes a long-term, well protected lee.

It is here suggested, as it has been by others (particularly Storr, 1964), that the organization of most coral assemblages is principally under the control of the physical factor of wave and surge action.

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APPENDIX

Literature utilized in the identification of the McKean corals.

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Table 1a. Hermatypic coral species observed at McKean Island and their distribution in the samples.

1b. Additional hermatypic coral species collected during the McKean Island study and the depth intervals where found.

Growth form abbreviations are as follows: B, branching; E, encrusting; M, massive; SM, submassive; U, unattached; and F, foliaceous.

Literature utilized in the identification of the McKean corals is given in the appendix.

Growth form	Species	Depth						Total
		Transects			Intervals			
		1	2	3	1	2	3	
B	<i>Pocillopora setchelli</i> Hoffmeister	2	0	0	2	0	0	2
B	<i>P. verrucosa</i> (Ellis & Solander)	1	2	0	0	2	1	3
B	<i>P. elegans</i> Dana	0	2	0	0	2	0	2
B	<i>P. damicornis</i> (Linnaeus)	0	1	0	1	0	0	1
B	<i>Acropora variabilis</i> (Klunzinger)	2	0	0	2	0	0	2
B	<i>A. humilis</i> (Dana)	2	0	0	0	2	0	2
E-F	<i>Montipora verrilli</i> Vaughan	4	9	7	16	4	0	20
F	<i>M. sp. cf. M. aequi-tuberculata</i> Bernard	4	2	0	1	5	0	6
E	<i>M. granulata</i> Bernard	2	1	1	1	3	0	3
E	<i>M. informis</i> Bernard	4	2	2	8	0	0	8
E-SM	<i>M. socialis</i> Barnard	0	1	0	0	1	0	1
SM	<i>M. venosa</i> (Ehrenberg)	0	0	1	1	0	0	1
E	<i>Pavona varians</i> Verrill	0	3	1	3	1	0	4
M	<i>P. clivosa</i> Verrill	0	1	0	0	0	1	1
E	<i>Psammocora nierstraszi</i> van der Horst	0	0	1	1	0	0	1
U	<i>Halomitra phillippinensis</i> Studer	1	0	0	0	0	1	1
U	<i>Parahalomitra robusta</i> (Quelch)	0	1	0	0	1	0	1
M	<i>Porites lobata</i> Dana	1	3	4	3	2	3	8
M	<i>P. solida</i> (Forsk.)	0	1	2	0	1	2	3
M	<i>P. lutea</i> Milne-Edwards & Haime	7	3	2	3	5	4	12
M	<i>P. australiensis</i> Vaughan	0	0	4	0	3	1	4
M	<i>P. fragosa</i> Dana	1	1	5	0	0	7	7
E-SM	<i>P. superfusa</i> Gardiner	0	1	0	1	0	0	1
M	<i>P. lichen</i> Dana	18	11	9	12	24	2	38
E	<i>P. (Synaraea) hawaiiensis</i> Vaughan	2	0	0	1	1	0	2
M	<i>Favia stelligera</i> (Dana)	13	19	4	12	18	6	36
M	<i>F. pallida</i> (Dana)	0	1	0	0	1	0	1
M	<i>Favites pentagona</i> (Esper)	1	0	0	1	0	0	1
M	<i>Plesiastrea versipora</i> (Lamarck)	2	3	1	5	1	0	6
M	<i>Platygyra daedalea</i> (Ellis & Solander)	1	0	1	0	0	2	2
B	<i>Hydnophora rigida</i> (Dana)	3	11	5	2	17	0	19
M	<i>H. microconos</i> (Lamarck)	1	1	1	1	2	0	3
M	<i>Leptastrea purpurea</i> (Dana)	1	1	1	3	0	0	3
M	<i>L. transversa</i> Klunzinger	2	2	1	1	4	0	5
M	<i>Cyphastrea microphthalma</i> (Lamarck)	2	3	5	10	0	0	10
F	<i>Echinopora lamellosa</i> (Esper)	45	3	17	5	50	10	65
M	<i>Millepora platyphylla</i> Hemprich & Ehrenberg	2	9	0	11	0	0	11
Totals		124	98	75	107	150	40	297

b. Extra-limital Species

Growth Form	Species	Depth Interval
B	<i>Pocillopora eydouxi</i> Milne-Edwards & Haime	2
B	<i>Acropora cymbicyathus</i> (Brook)	reef flat
B	<i>A. hyacinthus</i> (Dana)	2 and 3
B	<i>A. sp. cf. A. abrotanoides</i> (Lamarck)	2
F	<i>Pavona minuta</i> Wells	1
M	<i>P. clavus</i> (Dana)	1
SM	<i>P. (Polyastra) sp.</i>	1 and 2
F	<i>Leptoseris mycetoseroides</i> Wells	1
U	<i>Fungia (Pleuractis) scutaria</i> Lamarck	2
U	<i>F. (Verrillofungia) concinna</i> Verrill	2
M	<i>Favites abdita</i> (Ellis & Solander)	2
M	<i>Lobophyllia costata</i> (Dana)	2
F	<i>Turbinaria irregularis</i> Bernard	1
B	<i>Millepora murrayi</i> Quelch	reef flat

Table 2. Distribution of sample points, numbers of species, dominance, and percent living coral. Numbers in parentheses following the number of species are the number of species found only in that particular sampling unit when each sampling class is considered separately. Dominance is expressed as 100 minus the minimum percentage of species required to yield 50% of the individuals present. High dominance exists when only a small percentage of the species present are needed to constitute 50% of the individuals present.

Sample Unit	No. of Points	Coral	Non-coral	No. of Species	Dominance	% Living Coral
Transect 1	127	124	3	25 (6)	92	97.6
Transect 2	111	98	13	27 (7)	85	89.1
Transect 3	101	75	26	21 (3)	81	74.3
Depth Interval 1	127	107	20	25 (11)	83	84.3
Depth Interval 2	167	150	17	22 (5)	91	89.8
Depth Interval 3	44	40	4	12 (4)	79	90.9

Table 3. Probabilities and cumulative probabilities of as many or more shared species within sample unit pairs. For each sample unit pair comparison, the number of species in each and the number shared between them is also given.

Transects 1 and 2

Species in 1 = 25 Species in 2 = 27 Observed No. Shared Species = 18

No. Shared Species	Probability	Cumulative Probability
18	.06	1.00
19	.26	.94
20	.16	.68
21	.24	.52
22	.16	.28
23	.10	.12
24	.02	.02
25	.00	.00

Depth Intervals 1 and 2

Species in 1 = 25 Species in 2 = 25 Observed No. Shared species = 14

No. Shared Species	Probability	Cumulative Probability
15	.06	1.00
16	.10	.94
17	.34	.84
18	.18	.50
19	.26	.32
20	.06	.06
21	.00	.00
22	.00	.00

Transects 2 and 3

Species in 2 = 27 Species in 3 = 21 Observed No. Shared Species = 17

No. Shared Species	Probability	Cumulative Probability
15	.02	1.00
16	.04	.98
17	.26	.94
18	.30	.68
19	.28	.38
20	.10	.10
21	.00	.00

Depth Intervals 1 and 2

Species in 2 = 22 Species in 3 = 12 Observed No. Shared Species = 8

No. Shared Species	Probability	Cumulative Probability
8	.18	1.00
9	.24	.82
10	.26	.58
11	.22	.32
12	.10	.10

Transects 1 and 3

Species in 1 = 25 Species in 3 = 21 Observed No. Shared Species = 16

No. Shared Species	Probability	Cumulative Probability
14	.02	1.00
15	.08	.98
16	.24	.90
17	.36	.66
18	.18	.30
19	.06	.12
20	.06	.06
21	.00	.00

Depth Intervals 1 and 3

Species in 1 = 25 Species in 3 = 12 Observed No. Shared Species = 5

No. Shared Species	Probability	Cumulative Probability
8	.04	1.00
9	.16	.96
10	.48	.80
11	.26	.32
12	.06	.06

Table 4. Rank orders of abundance for the 7 most common species, all of which are present along all 3 transects, and the 5 species common to the 3 depth intervals with coefficients of concordance (w) for these rankings as well as for all the species. All W's have been corrected for ties.

Seven Most Common Species (present along all transects)	Rank Order of Relative Abundance		
	Transect 1	Transect 2	Transect 3

<i>Porites lichen</i>	2	2.5	2
<i>Echinopora lamellosa</i>	1	6	1
<i>Favia stelligera</i>	3	1	6
<i>Montipora verrilli</i>	5	4	3
<i>Hydnophora rigida</i>	6	2.5	4.5
<i>Porites lutea</i>	4	6	7
<i>Cyphastrea microphthalma</i>	7	6	4.5

W for the 7 most common species = 0.43 0.10 < p < 0.20

W for all species by transects = 0.65 p < 0.01

Species Common to All 3 Depth Intervals	Rank Order of Relative Abundance		
	Dpth.Intv.1	Dpth.Intv.2	Dpth.Intv.3

<i>Echinopora lamellosa</i>	3	1	1
<i>Favia stelligera</i>	1.5	3	2
<i>Porites lichen</i>	1.5	2	5
<i>Porites lutea</i>	4.5	4	3
<i>Porites lobata</i>	4.5	5	4

W for the 5 species in common = 0.56 0.10 < p < 0.20

W for all species by depth intervals = 0.42 p = 0.27

Table 5a. Scaled and unscaled values of the following diversity indices:
 SI* = 1 minus Simpson's Index, H' = Shannon-Wiener function, SD = standard deviation,
 NM = Number of Moves Index.

b. Rankings for the various diversity indices. Ranks in parentheses are for unscaled values.

a.

		SI*		H'		SD		NM	
		unscaled	scaled	unscaled	scaled	unscaled	scaled	unscaled	scaled
Trans 1:	S = 25, N = 124	0.167	0.782	2.379	0.602	9.249	0.533	962	0.190
Trans 2:	S = 27, N = 98	0.079	0.898	2.800	0.732	4.360	0.681	682	0.261
Trans 3:	S = 21, N = 75	0.088	0.894	2.631	0.752	3,842	0.674	379	0.298
Dpth 1:	S = 25, N = 107	0.073	0.926	2.771	0.773	4.468	0.728	683	0.306
Dpth 2:	S = 22, N = 150	0.164	0.821	2.259	0.632	11.533	0.577	1070	0.204
Dpth 3:	S = 12, N = 40	0.119	0.871	2.179	0.753	2.902	0.641	103	0.331

b.

Index	Transects			Index	Depth Intervals		
	1	2	3		1	2	3
SI*	3 (1)	1 (2)	2 (3)	SI*	1 (3)	3 (1)	2 (2)
H'	3 (3)	2 (1)	1 (2)	H'	1 (1)	3 (2)	2 (3)
NM	3 (1)	2 (2)	1 (3)	NM	2 (2)	3 (1)	1 (3)
SD	3 (3)	1 (1)	2 (2)	SD	1 (2)	3 (1)	2 (3)

Table 6. Spatial pattern of the more common and widespread species along the exposure gradient. At the 5% level of significance the three species marked with an asterisk are clumped, while none of the others depart from random.

Species	Distribution			\bar{x}	s^2	s^2/\bar{x}	χ^2	p
<i>Montipora verrilli</i>	4	9	7	20/3	12/3	0.60	1.20	.50<p<.75
<i>Porites lobata</i>	1	3	4	8/3	7/3	0.88	1.76	.25<p<.50
<i>Porites lutea</i>	7	3	2	12/3	21/3	1.75	3.50	.10<p<.25
<i>Porites lichen</i>	18	11	9	38/3	67/3	1.76	3.52	.10<p<.25
<i>Favia stelligera</i> *	13	19	4	36/3	171/3	4.75	9.50	.005<p<.01
<i>Hydnophora rigida</i>	3	11	5	19/3	52/3	2.74	5.48	.05<p<.10
<i>Cyphastrea microphthalma</i>	2	3	5	10/3	3/3	0.30	0.60	.50<p<.75
<i>Echinopora lamellosa</i> *	45	3	17	65/3	1372/3	21.6	43.2	p<.005
<i>Millepora platyphylla</i> *	2	9	0	11/3	67/3	6.09	12.18	p<.005

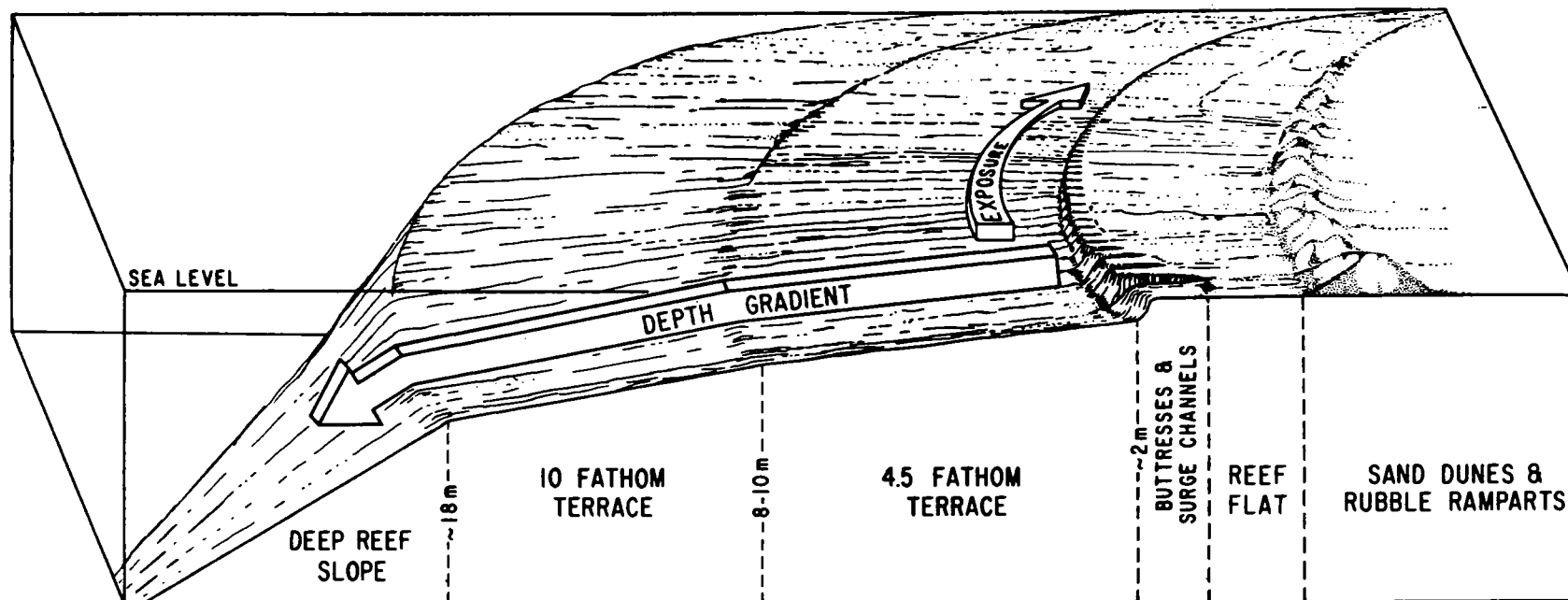


Figure 1. A generalized three-dimensional cut-away view of the seaward reef of an Indo-Pacific atoll located in trade wind regions. Terrace structure and environmental gradients are labeled. Prevailing wind would be from the upper right.

3°35'S+

+

McKEAN ISLAND

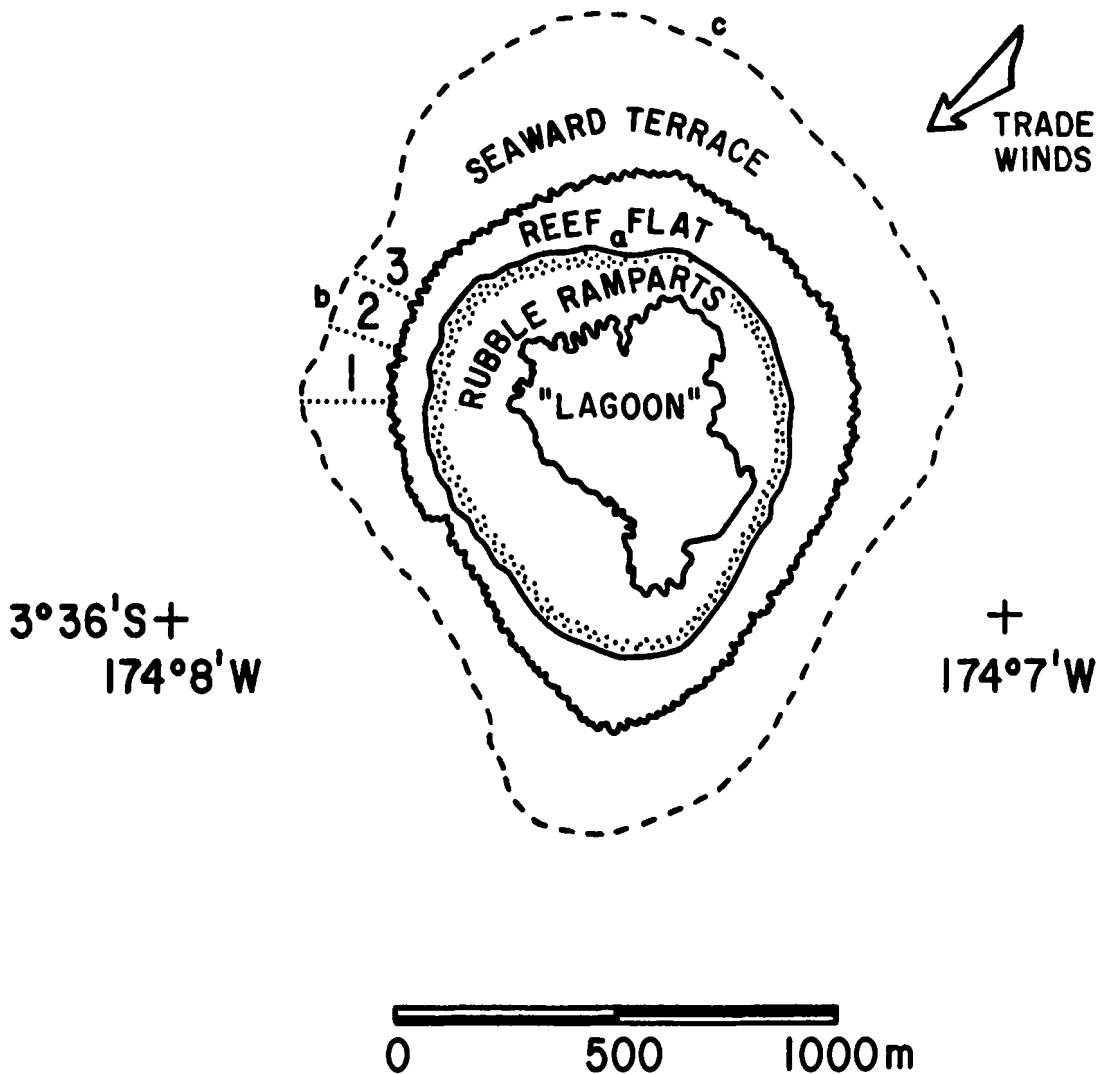


Figure 2. Plan view of McKean Island showing approximate location of the three transects. The contour indicated represents the 20 m contour. This figure was redrawn from HO Chart 83037. The lower case letters a, b, and c refer to the locations of the following two figures.



Figure 3. Rubble ridges along the northern shore of McKean Island. Here the ramparts reach a height of some 5 m. This photograph was taken at the point marked "a" on Figure 2.

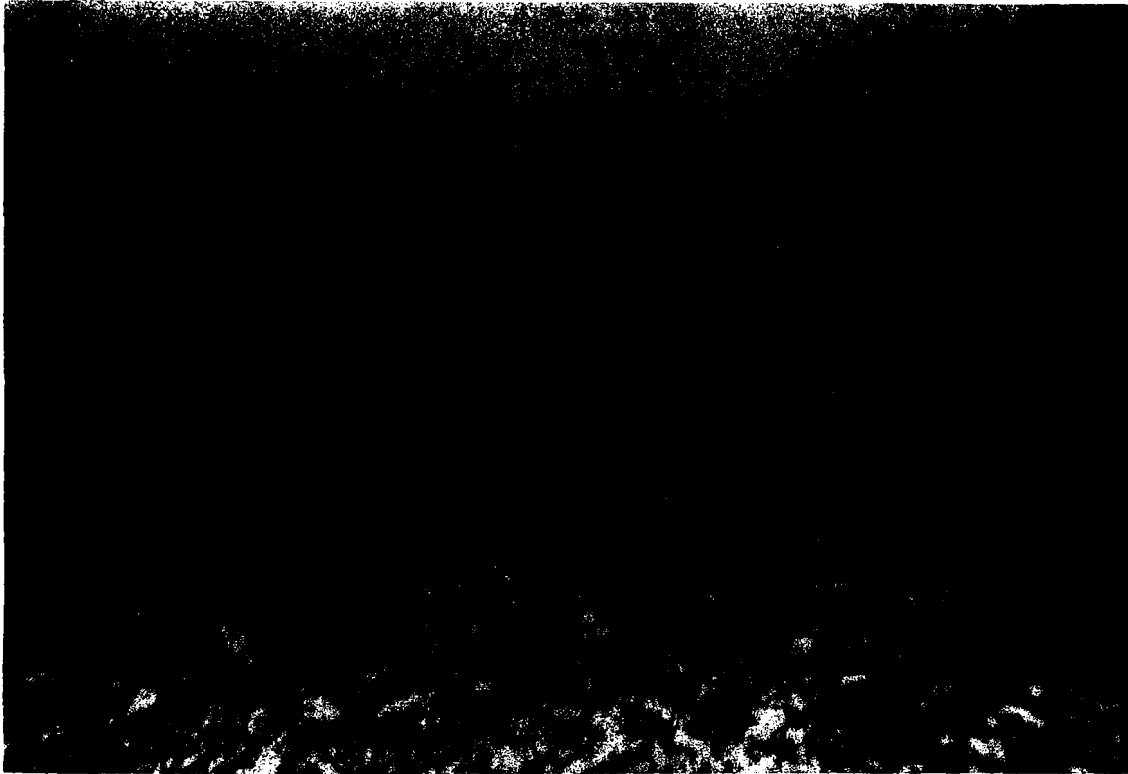


Figure 4a. Region of the sharp break in reef slope in the northeastern sector of the reef. At this point virtually all living coral has been stripped from the reef and only rubble remains. This photograph was taken at the point marked "c" on Figure 2.

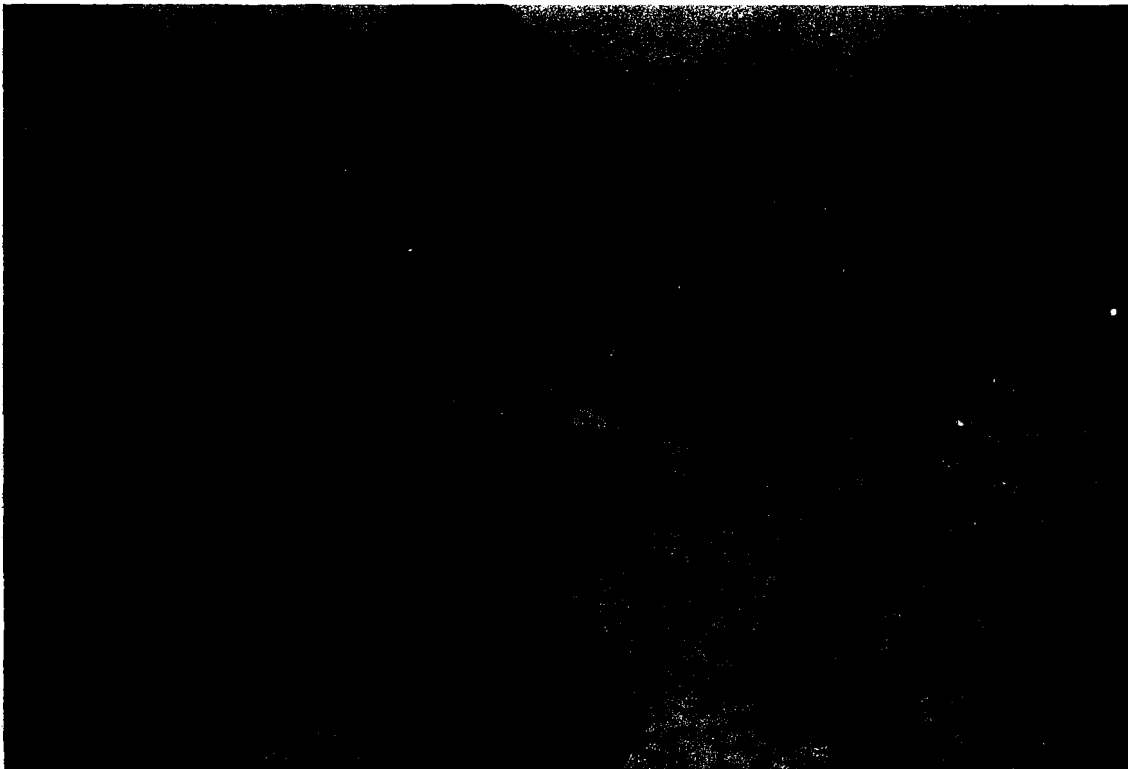


Figure 4b. Region of the sharp break in reef slope in the area of the transects. The abundance of large, shelving colonies of such species as *Porites solida*, *P. lutea*, *P. australiensis*, and *P. fragosa* can clearly be seen. This photograph was taken at the point marked "b" on Figure 2.

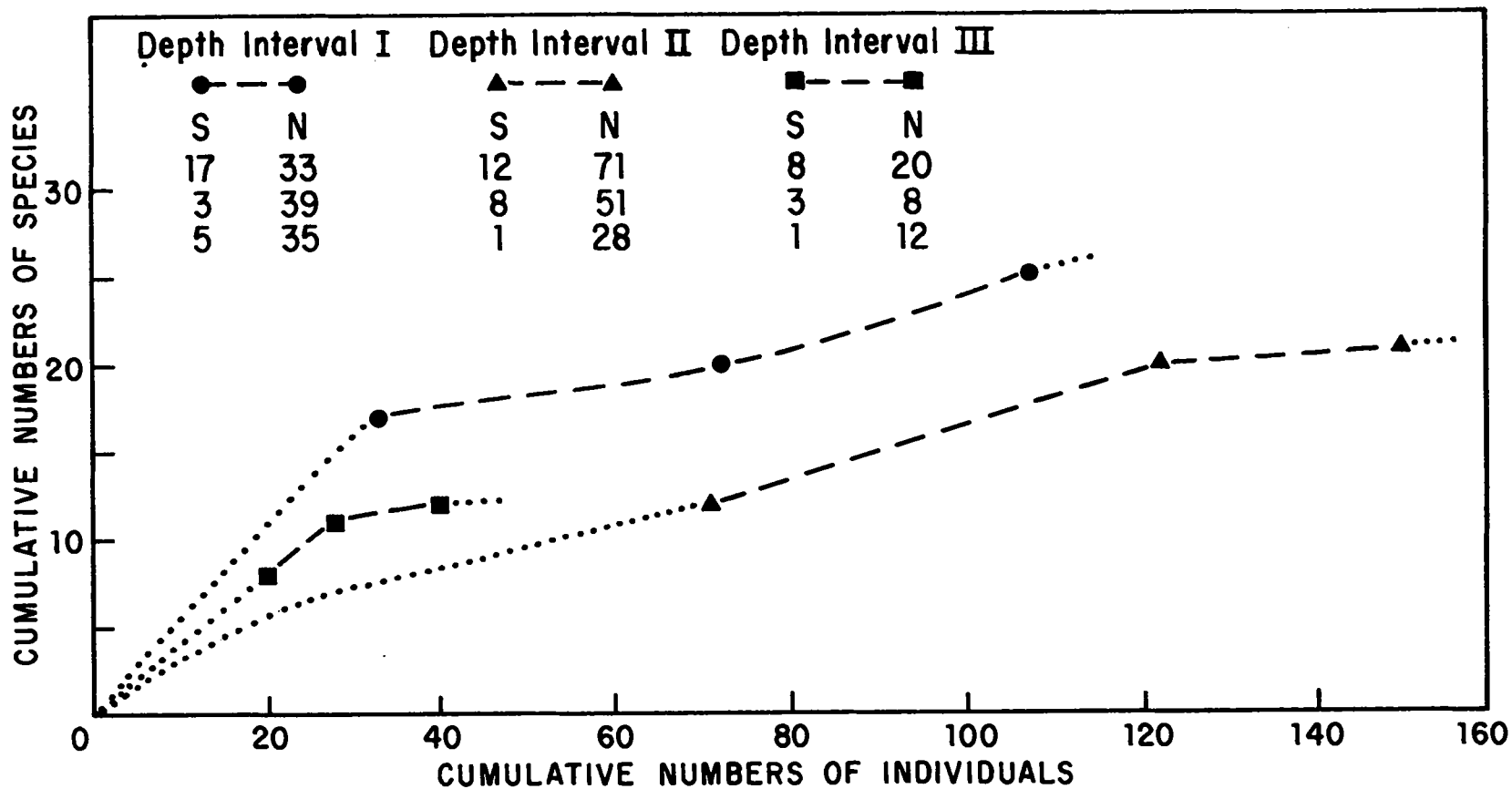


Figure 5. Plots of the cumulative numbers of species against the cumulative numbers of individuals for each of the depth intervals. These curves were constructed by successively adding new species and total individuals from the segments of each transect within each depth interval in the order of Transects 1, 2, and 3.

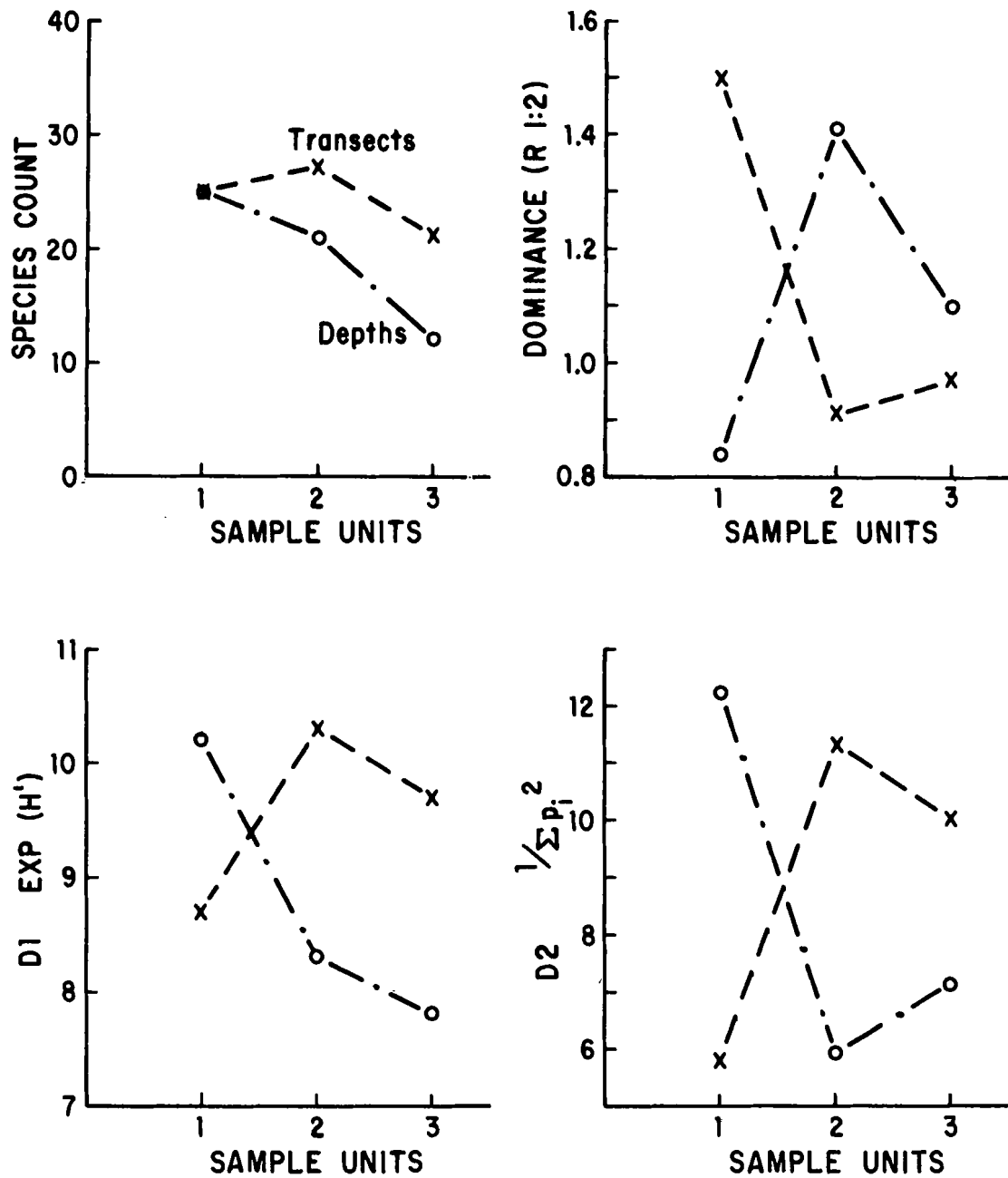


Figure 6. Plots of the species counts and Hill's diversity numbers as proposed by Peet (1974) for use in species diversity studies.

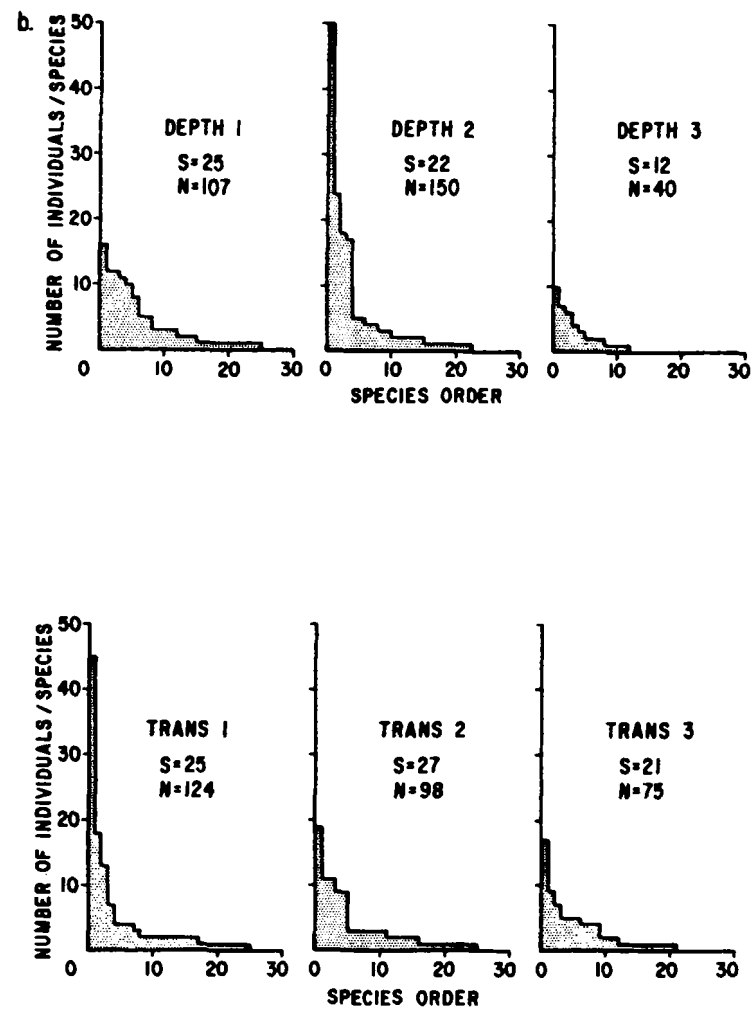
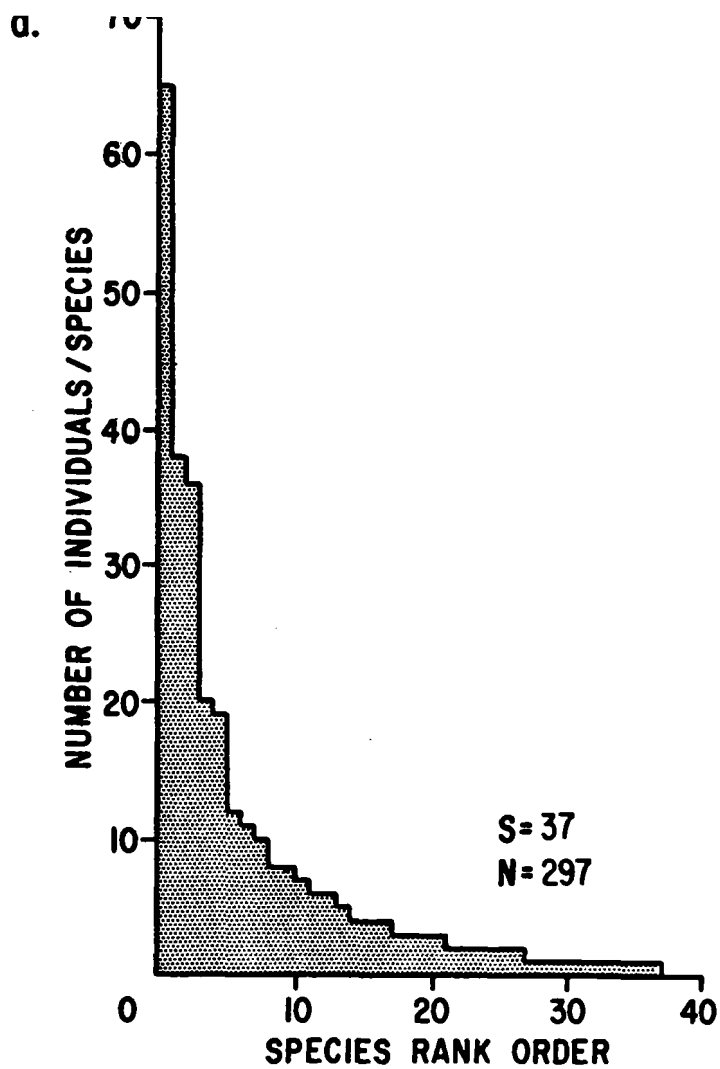


Figure 7a. Histogram of the number of individuals per species plotted against species rank order for the entire McKean Island coral collection.

Figure 7b. Histograms of the number of individuals per species plotted against species rank order for individual sample units.

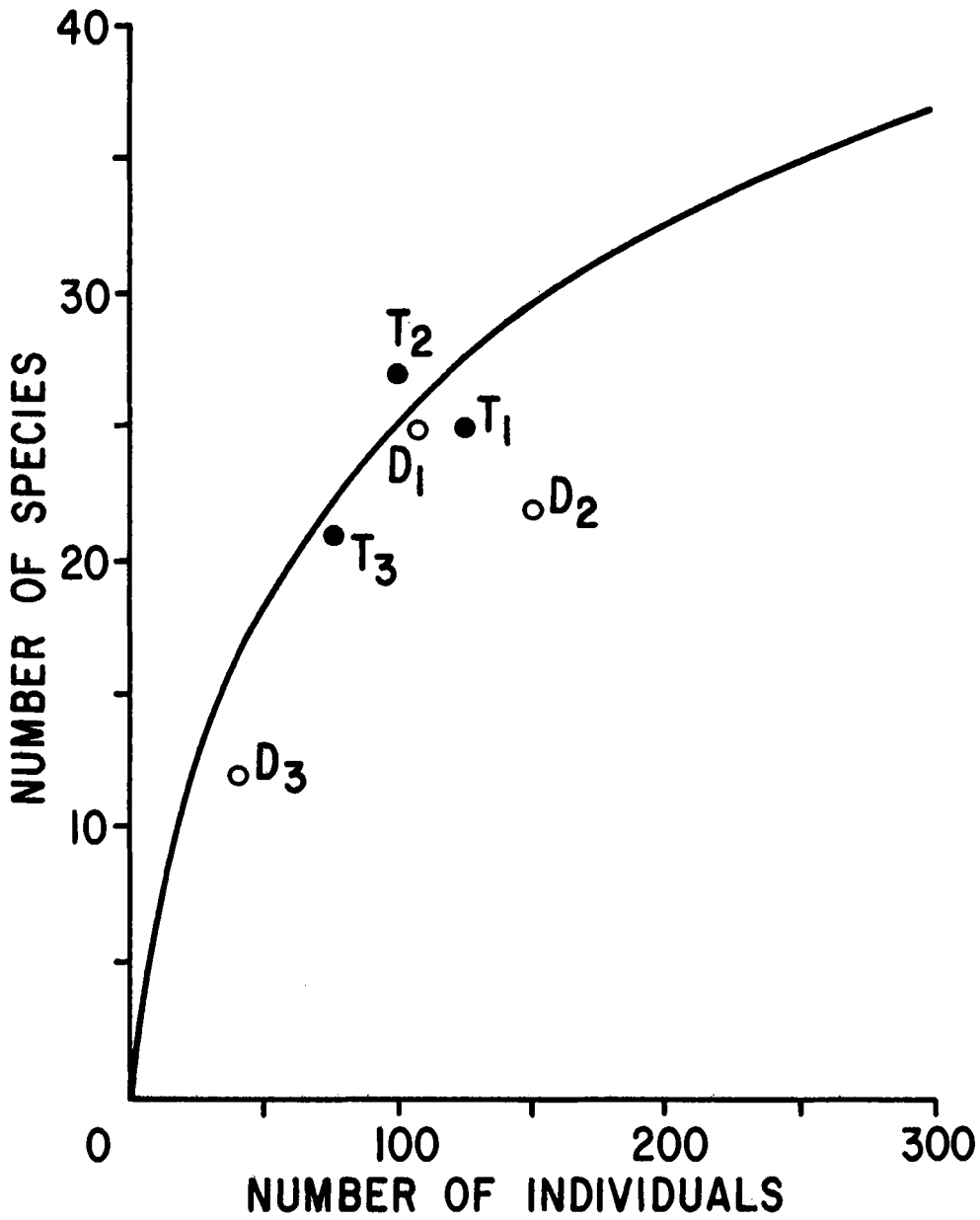


Figure 8. Distribution of the McKean samples relative to the expected number of species line calculated by the Hurlbert (1971) method.

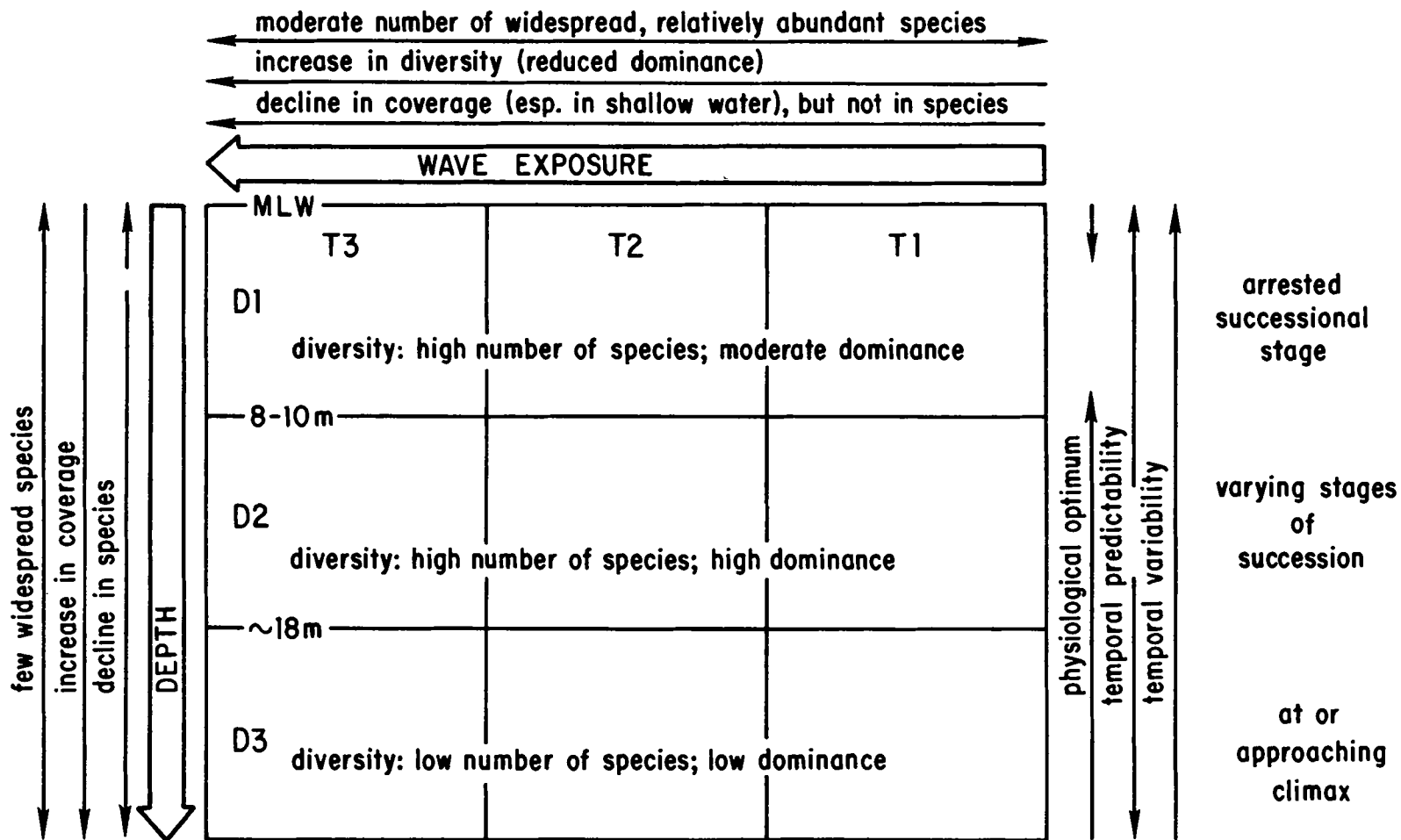


Figure 9. Graphical summary of the organization hypothesis for seaward reef coral assemblages.