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Community structure and species diversity of hermatypic corals at Eilat, Red Sea*

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Abstract

This study investigates the community structure of reef-building corals in terms of species composition, zonation and diversity patterns, as well as possible factors affecting the observed distributions. The study was carried out by a series of line transects run underwater with SCUBA apparatus from the reef flat to a depth of 30 m. The reefs of Eilat are of the fringing type, with scleractinian corals as the most important hermatypic organisms. The different zones of the reef are analyzed on the basis of topographical characteristics of the reef, as well as from the numerical data on abundance and living coverage, using cluster analysis of all transects surveyed. The present knowledge concerning species diversity is reviewed and analyzed in the context of hermatypic coral data. Three different diversity indices (the species count, SIMPSON's index and SHANNON and WEAVER's index) were calculated for estimating the diversity obtained on different zones of the reef. It was found that there is a successive increase in diversity of hermatypic corals from shallow water to a depth of 30 m. Species diversity and living coverage of corals were significantly greater in steeper zones as compared to flatter zones of the reef. A possible explanation for this phenomenon is the accumulation of sediments in the flat zones. It is proposed that the severe and unpredictable nature of the reef flat may account for low abundance and living coverage of corals. It is also proposed that deep-water species which do not invade shallow water are species which have developed high specialization to their local environment. The idea that light intensity is a significant factor in calcium-carbonate deposition by scleractinian corals is supported by field measurements of individual colonies at different depths.

Introduction

This work discusses the community structure of reef-building corals in terms of species composition, zonation and diversity patterns, as well as possible factors affecting the observed distributions. The quantification of these aspects has been very poor in the literature. Most studies of coral-reef ecology have been limited to general descriptions of zonation patterns of the corals, or to determination of the environmental tolerances of constituent coral species. The present work attempts to provide a better quantitative basis for some generalizations concerning the organization and community structure of these organisms. This work has been carried out in the northern part of the

Gulf of Eilat, Red Sea, in the nature reserve of the Eilat coral-reefs. Publications on meteorological and hydrographical research of the northern part of the Gulf include those of ASHBEL (1951, 1963), OREN (1962) and FRIEDMAN (1968).

A coral reef constitutes probably the most complex community of the marine environment. It is actually an association of several thousand species of different kinds of animals which occupy various ecological niches. A correspondingly complex community on dry land is, perhaps, the tropical-rain forest. Corals constitute the basic framework and substrate for many other organisms which penetrate the skeletal mass (sponges, polychaetes, sipunculides, bivalves and gastropods). Corals also provide shelter for many fishes as well as various species of polychaetes, crustaceans, molluscs and echinoderms. It is, therefore, of primary interest to obtain an adequate understanding of the coral-community structure as the first step for a better understanding of the complex interspecific relations between corals and other organisms living in close association with them. This study is a description of the structure of a coral community; i.e., the distribution, arrangement and abundance of different coral species are presented with reference to such features as depth, reef topography, sedimentation and light intensity, which are the major factors considered in this work.

This study presents a descriptive analysis of zonation patterns and community organization of the scleractinian corals, based on numerical analysis of species abundance. The numerical description is based upon several currently employed techniques and methods used by both terrestrial and aquatic biologists. The approach taken for the coral-species diversity-analysis is similar to that of HAIRSTON and BYERS (1954) in their soil arthropods studies, i.e., the preliminary identified species are assigned code numbers and are used later for a more careful analysis by a qualified taxonomist. The first, preliminary, systematic list of the scleractinian corals of Eilat was published by LOYA and SLOBODKIN (1971). The entire collection was identified by Professor J. W. WELLS of Cornell University, to whom I am very grateful.

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The reef framework

Coral reefs are built primarily by hermatypic corals of the order Scleractinia (VAUGHAN and WELLS, 1943). The hermatypic, or reef-building corals, are characterized by their intense calcifying activity and remarkable ability to construct massive skeletal structures of calcium carbonate.

WAINWRIGHT (1965) makes an important distinction between structural reefs and coral communities. In structural reefs, corals actively contribute, by skeletal accumulation, to the topographical development of the reef; a coral community, on the other hand, is an assemblage of reef organisms "growing on a substratum other than that of their own recent production, in shallow tropical seas." This distinction, originally drawn in the Southern Red Sea, has been shown to be applicable to many other reef areas (STODDART, 1969). The present work deals with this framework, and specifically with the scleractinian corals comprising the coral-reef community.

GOREAU (1969) defined fringing reef as a coral reef growing hard upon a coastline, with little or no lagoon other than, perhaps, a shallow moat, and a more or less well developed reef table. The reefs of Eilat are of the fringing type with scleractinian corals as the most important hermatypic organisms (LOYA and SLOBODKIN, 1971). Although, in some reefs, scleractinian corals are quantitatively less important as sources of skeletal material than many other groups of organisms, the term "coral reef" still holds because it is the skeleton-building capacities of the scleractinian corals which create the framework of the reef structure (STODDART, 1969). GOREAU (1963, 1969) stresses the great significance of coralline algae as contributors to the reef sediments. In Eilat, however, skeletons of green algae were not observed in the sediment samples studied by FRIEDMAN (1968), and it was, therefore, concluded that they play a minor role in the reef framework.

FISHELSON (1968) notes some "coral feeders" and possible reef destroyers in Eilat, the most important groups of which are the parrot fishes (Scaridae), the wrasses *Coris angulata* and *C. lunula*, and trigger fishes of the genera *Rhinecanthus* and *Balistes*. Other reef destroyers may be the pencil sea-urchin *Heterocentrotus mammilatus* and the sponge *Cliona*. In the Caribbean Sea, GOREAU and HARTMAN (1963) stressed the importance of boring sponges as principal reef destroyers. Below 25 to 30 m, the boring sponges in the Jamaican north coast reefs are so active that they cause more reef destruction than all other erosional factors combined.

Acanthaster planci, which has been reported as a major predator of scleractinian corals in the southern Red Sea (GOREAU, 1964), and which causes heavy destruction of Guam's coral reefs (CHESHER, 1969), seems to be very rare in Eilat. Very few specimens of

the crown of thorns sea star have been seen thus far by all the investigators working on the coral reef of Eilat.

Although this study is concerned essentially with the reef-building corals, it is of interest to note that some non-reef building, or ahermatypic species, are often found underneath large colonies in tunnels and crevices, especially within the Sinai reefs. These corals may become quite common in certain restricted areas, as in the Ras Muhammad underwater caves in the southern tip of the Sinai peninsula. Their abundance, however, in terms of aggregate biomass or living coverage, is negligible as compared to the hermatypic corals.

Methods

A review of different methods used in quantitative studies and of the problems involved at the level of sampling unit and field recording is provided by STODDART (1969). The very few quantitative studies performed on coral reefs have used different sizes of quadrats on different reefs. Table 1 lists these studies, their location, quadrat size and investigators (after STODDART, 1969).

Detailed work has been confined to accessible shallow reef flats, while fore-reef slopes have been neglected. Some of these studies record the number of species or genera per quadrat and their relative coverage, but, in general, most of them have no usable quantitative data. Quantitative quadrat sampling seems to be applicable on reef flats, as reported from these studies. However, many technical problems arise when the same method is used on reef slopes, where the bottom topography in many cases is very complex. After considering different terrestrial methods for studying plant communities (GREIG-SMITH, 1964), we tried line transects which seemed to be most applicable for a comparative study of the different reef zones (LOYA and SLOBODKIN, 1971).

The line transects were run underwater with SCUBA apparatus, at three stations in the nature reserve of the Eilat coral reefs. A total of 84 transects were surveyed at Eilat. Each transect was 10 m long, i.e., 840 m of reef were measured and recorded. The transects were run along depth contours parallel to the shore, at fixed intervals of 1 m on the reef flat and 5 m on the fore-reef slope. For the purpose of this work, an individual was defined as any colony growing independently of its neighbors (i.e., whenever an empty space was recorded between two adjacent colonies). In cases where an individual colony was clearly separated into two or more portions by the death of the intervening parts, the separate parts were considered as one individual. Any coral species which underlay the line was recorded and its projected length on the line was measured to the nearest centimeter. The data was recorded to a maximum depth of 30 m. In the case of two or more colonies growing one above the

Table 1. *Quadrat studies on various reefs. (After STODDART, 1969)*

Location	Quadrat size	Author
(A) Continuous quadrats on transects		
Low Isles, Great Barrier Reef	3 × 6 ft	MANTON (1935)
Bikini, Marshalls	No frame, transect 20 ft. wide	EMERY et al. (1954) HIATT (1957)
Arno, Marshalls		
Seaward reef	50 × 50 ft	
Lagoon reef	100 × 100 ft	
Alacran	30 × 30 ft	KORNICKER and BOYD (1962)
Abaco, Bahamas	12 × 24 ft	STORR (1964)
Addu, Maldives	10 × 10 ft	STODDART et al. (1966)
(B) Sample quadrats on transects		
Murray Island, Torres Straits	50 × 50 ft	MAYOR (1918)
Aua, Pago Pago, Samoa	24 × 24 ft	MAYOR (1924)
Oahu, Hawaii	Not stated	EDMONDSON (1928)
Eniwetok	20 × 20 ft	ODUM and ODUM (1955)
(C) Sample area quadrats		
Iwayama Bay, Palao	1 × 1.5 ft	ABE (1937)
Spanish Harbor, Florida	5 × 5 ft	KISSLING (1965)

other and underlying the transect, the projected length of the largest colony was recorded for the coverage analysis and the length and species of all overlapping colonies, which underlay the line, were recorded for the coral species diversity analysis.

It was found that line transects were highly efficient for information recorded per time spent underwater, which is certainly the most critical factor in deep-water study. Problems which arise from complex bottom topography are also avoided, since a line may be put along depth contours, while quadrat sampling is much more complicated to handle in an underwater situation. Moreover, the amount of information derived from line transects is for many purposes as useful as that derived from quadrat sampling-techniques.

One of the most serious technical problems in this study was that the identification of many species is almost impossible underwater. Whenever confronted with the slightest doubt concerning the species of a certain coral underlying the transect, a small piece was chopped off and put into a plastic bag carrying an identification number. Later, the coral samples were bleached clean, with concentrated solution of KOH, for purposes of identification and preservation.

Color photographs were taken with a Nikonos II camera with a flash attachment. For close-ups, a Rolleiflex camera in a Rollimarine underwater case was used. At the beginning of the study, photographs at 1 m intervals along a transect were taken. The idea was to measure living coverage of different species on the photographs and thus to save time underwater. However, many small species, as well as species which typically grow beneath other colonies

did not show up in the photographs. In addition, the identification of many species of *Acropora*, *Porites*, *Favia*, *Favites*, *Montipora* and others was impossible from the photographs only. It was therefore necessary to carry out the measurements and identification of the coral species as described above.

Results

General characteristics

Since the present work involved deep diving, it was very important to determine the smallest sample size (i.e., smallest transect length) appropriate for the purposes of this work. At 30 m depth, the maximum amount of time permitted for work is about 30 min (avoiding long decompression time). I tried, therefore, by random sampling of transects at different depths, to estimate how many meters of a line transect must be examined before there was no significant increase in the number of species added with a new meter of the line; in other words, we are interested in finding the sample size where the species start accumulating at a decreasing logarithmic rate. By plotting the cumulative number of species as a function of meter number along the transect, it was found that the resulting curve levelled off after 9 to 10 m of the line had been recorded; therefore, the chosen length of the transect was 10 m. Fig. 1 plots the average number of species recorded in the different zones of the reef as a function of meter number along the transect; i.e., each point along each curve represents the average number of species recorded for all transects surveyed at a particular zone. Table 2 specifies the total number of meters

pooled for this analysis, by gradually increasing the sample size in the different zones of the reef. Fig. 1 demonstrates clearly that, after 9 to 10 m of line transect, the five curves that represent different zones of the reef level off.

The same analysis was performed with the diversity values obtained from the different zones of

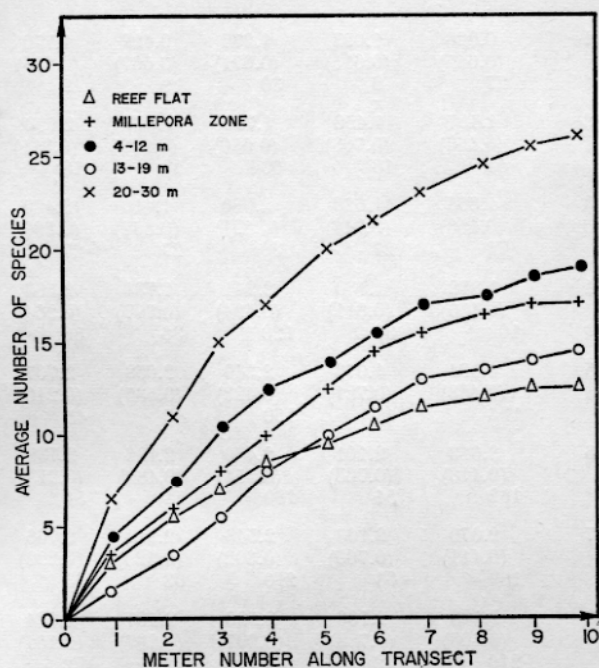


Fig. 1. Cumulative number of hermatypic coral species as a function of meter number along a line transect

the reef. Fig. 2 plots the average values of H'_N (SHANNON and WEAVER's, 1948 species diversity index) as a function of meter number along the transect. Here, after 5 m of line transect, all the curves level off; i.e., there is no significant increase in species diversity or information recorded beyond meter No. 5 along the transect. The standard deviations and number of meters pooled at each zone are given in Table 3.

It should be pointed out that, in both Figs. 1 and 2, the average values obtained for the mean number of species and the mean H'_N values were different in the different zones of the reef; that is, the 10 m line provides full information for all zones, despite the fact that the diversity differs from zone to zone. Had the species clustered more, for example, it might have been necessary to use a longer line; but, as indicated before, this is not the case. It is concluded, therefore, that 10 m of line transect were an appropriate and "safe" sample size for the purposes of this study.

Having a system of systematic transects running parallel to each other and parallel to the shore at three stations, it was important to test for homogeneity of the data recorded at the different stations (Table 4). The purpose of this analysis was to discover whether several transects surveyed at similar zones, but different stations, might be lumped together into one

Table 2. *Hermatypic corals at Eilat, Red Sea. Cumulative average values of number of species recorded along line transects of 10 m. First number: average species number; second number (in parentheses): standard deviation; third number: total number of meters pooled for calculations*

Meter No.	Back reef and reef flat	Millepora zone	Depth (m)		
			3-12	13-19	20-30
1	3.19 (1.84) 27	3.44 (1.67) 9	4.50 (2.61) 30	1.44 (2.13) 9	6.67 (1.87) 9
2	5.41 (2.36) 54	6.22 (3.60) 18	7.43 (3.89) 60	3.44 (3.57) 18	11.22 (3.19) 18
3	6.93 (2.77) 71	8.00 (4.58) 27	10.47 (4.21) 90	5.56 (3.57) 27	15.11 (4.11) 27
4	8.37 (3.27) 108	9.89 (5.49) 36	12.33 (4.89) 120	7.78 (4.24) 36	17.00 (4.50) 36
5	9.37 (3.49) 135	12.67 (5.94) 45	13.83 (5.19) 150	10.00 (4.44) 45	20.22 (4.71) 45
6	10.56 (3.51) 162	14.44 (7.04) 54	15.27 (5.17) 180	11.33 (4.42) 54	21.33 (4.92) 54
7	11.44 (3.47) 189	15.33 (6.96) 63	16.87 (5.04) 210	12.89 (2.76) 63	22.78 (5.07) 63
8	11.96 (3.61) 216	16.33 (7.89) 72	17.70 (5.00) 240	13.33 (2.60) 72	24.33 (4.69) 72
9	12.67 (3.70) 243	17.00 (8.49) 81	18.67 (4.74) 270	14.11 (2.67) 81	25.67 (3.74) 81
10	13.00 (3.65) 270	17.56 (8.73) 90	19.80 (4.96) 300	15.22 (3.27) 90	26.67 (3.87) 90

sample, thus increasing the sample size (the number of transects surveyed within the same zone). A model II analysis of variance (SOKAL and ROHLF, 1969) was applied to the data recorded at the three stations (Table 4). This analysis takes account of the variance within and between stations. The critical F values are given in Table 4 and compared with the calculated F values. It is shown that the different statistics

measured at the three stations were homogeneous, i.e., there was no significant ($P > 0.05$) added variance component for each statistic tested. The conclusion, therefore, is that one may lump transects surveyed at the same zone of different stations into one sample. Thus, it is possible to compare several groups of transects surveyed at a certain depth range to another group of transects surveyed at different depths or zones of the reef. The analysis of zonation and species diversity patterns was performed on this basis, from the numerical data of relative abundance and living coverage of the coral species.

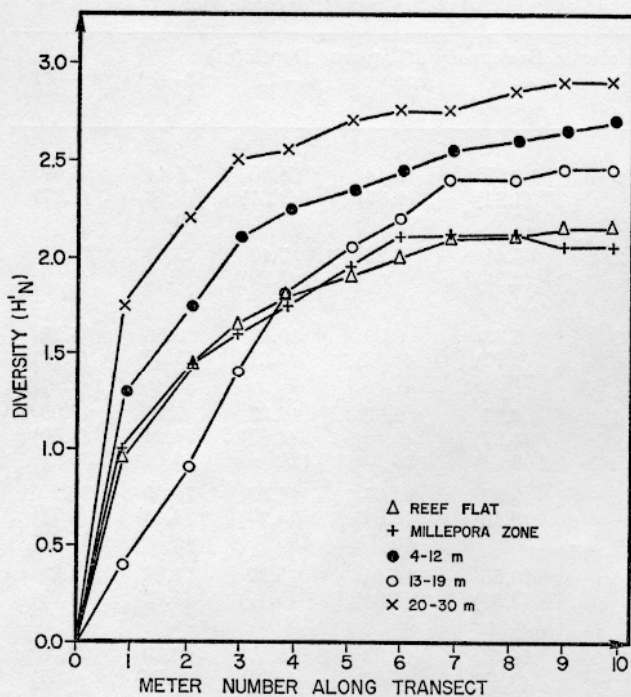


Fig. 2. Cumulative number of SHANNON and WEAVER's (H'_N) index of diversity as a function of meter number along a line transect

Table 3. *Hermatypic corals at Eilat, Red Sea. Cumulative average values of SHANNON and WEAVER's index of diversity (H'_N). Calculations made on line transects of 10 m each. First number: average H'_N value; second number (in parentheses): standard deviation; third number: total number of meters pooled for calculations*

Meter No.	Back reef and reef flat	Millepora zone	Depth (m)		
			3-12	13-19	20-30
1	0.926 (0.645) 27	1.023 (0.615) 9	1.277 (0.671) 30	0.422 (0.667) 9	1.770 (0.285) 9
2	1.457 (0.463) 54	1.450 (0.708) 18	1.750 (0.650) 60	0.877 (0.913) 18	2.190 (0.311) 18
3	1.665 (0.453) 71	1.620 (0.741) 27	2.080 (0.591) 90	1.410 (0.867) 27	2.489 (0.290) 27
4	1.812 (0.450) 108	1.730 (0.811) 36	2.241 (0.494) 120	1.781 (0.797) 36	2.563 (0.264) 36
5	1.904 (0.458) 135	1.973 (0.781) 45	2.349 (0.423) 150	2.058 (0.535) 45	2.707 (0.246) 45
6	2.013 (0.418) 162	2.101 (0.763) 54	2.450 (0.354) 180	2.196 (0.489) 54	2.738 (0.213) 54
7	2.079 (0.411) 189	2.108 (0.765) 63	2.543 (0.302) 210	2.381 (0.225) 63	2.766 (0.222) 63
8	2.106 (0.408) 216	2.106 (0.788) 72	2.586 (0.297) 240	2.407 (0.207) 72	2.834 (0.154) 72
9	2.147 (0.406) 243	2.069 (0.838) 81	2.629 (0.253) 270	2.458 (0.185) 81	2.885 (0.136) 81
10	2.158 (0.392) 270	2.028 (0.856) 90	2.676 (0.257) 300	2.517 (0.222) 90	2.915 (0.122) 90

Table 4. *Single classification analysis of variance. Species diversity indices (F values of hermatypic corals), recorded in transects from 3 areas at Eilat, Red Sea. H'_N : SHANNON and WEAVER's diversity index; D_N : SIMPSON's diversity index; H'/H'_{max} : PIELOU's "evenness" measurement; for further explanation see "Species diversity" section*

Statistic	Lagoon	Table	Millepora zone	Depth (m)			
				3-7	8-11	13-19	20-25
Degrees of freedom	(2,3)	(2,18)	(2,6)	(2,14)	(2,10)	(2,6)	(2,6)
Critical $F_{0.05}$ values	9.55	3.55	5.14	3.74	4.10	5.14	5.14
Number of species	0.77	0.41	1.36	1.22	0.87	0.23	2.34
Number of colonies	0.78	0.87	0.03	1.01	0.71	0.09	0.18
Living coverage (cm)	7.18	0.92	0.50	0.24	0.54	0.07	0.27
Diversity H'_N	1.55	1.05	3.00	0.42	0.16	0.33	0.37
Diversity D_N	2.25	1.25	4.06	0.00	0.00	0.00	0.00
"Evenness" H'/H'_{max}	1.98	1.40	4.10	2.50	0.00	0.38	0.05

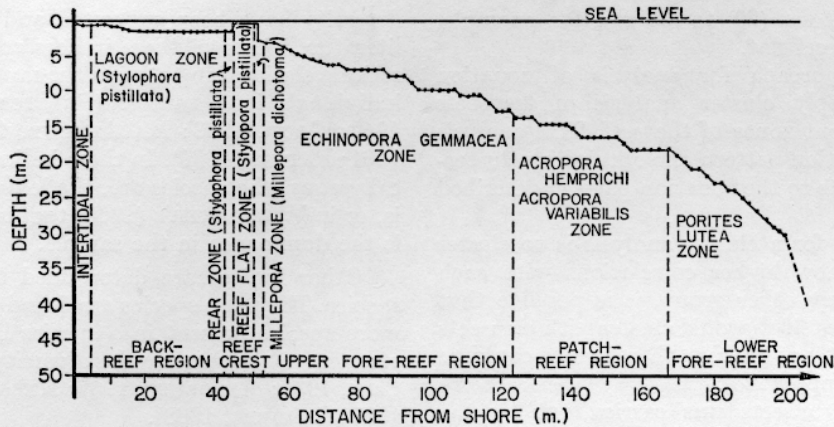


Fig. 3. Reef-profile perpendicular to the shore, at nature reserve of Eilat. Each black dot represents depth measurement. Distance between two adjacent measurements is 2 m. Note differences in steepness of slope in different reef zones. Steepest reef zones are upper *Echinopora gemmacea* zone (3 to 7 m) and *Porites lutea* zone (> 20 m). Lower *E. gemmacea* zone (8 to 12 m) and *Acropora hemprichi* - *A. variabilis* zone (13 to 19 m) are characterized by wide and flat terraces. Between depth of 30 to 45 m, lower fore-reef forms angle of 80° to 90°. The living reef ends in Eilat at depths of 45 to 50 m

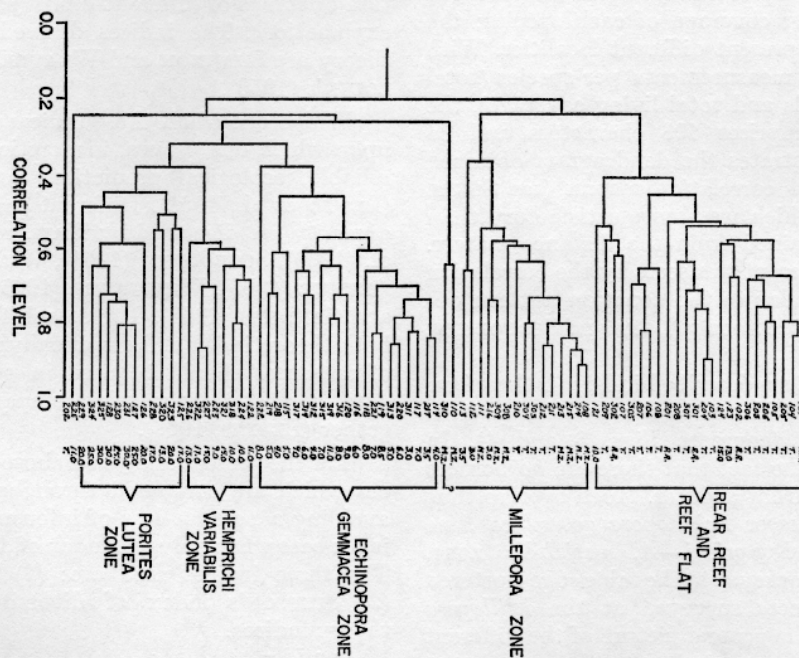


Fig. 4. Cluster analysis of 84 transects run at nature-reserve area of coral reef at Eilat. Phenogram computed from correlation matrix based on 198 "characters" (see explanation in text). Similarity scale is shown as abscissa. Numbers at tips of phenogram correspond to transect code numbers. Column to right of transect code numbers indicates depth or zone where each transect was recorded. R. R. rear reef; T. table reef; M. Z. *Millepora* zone. Brackets indicate different zones of reef as obtained from cluster analysis

Zonation patterns

The relationship of zones in the Eilat coral reefs was discussed in a previous paper (LOYA and SLOBODKIN, 1971). The different zones and regions were named according to their most conspicuous faunal or topographical characteristics (see GOREAU, 1959). The zonation pattern described previously was based on top-

ographical characteristics, as well as relative abundance and living coverage of different species (see Fig. 3). Thus, the reef flat, for example, was described as a separate zone from the rear reef, or the *Millepora* zone, since it is clearly different in its topographical characteristics. According to the zonation analysis described previously, there was no chance of including

the *Porites lutea* zone (20 to 30 m), for example, together with the reef flat.

A different approach for analysis of zonation patterns is to apply cluster analysis of transects surveyed at different zones of the reef. This analysis compares the zonation pattern one obtains by clustering similar transects to the zonation pattern described previously.

Since the basis for a cluster analysis is to cluster transects which show higher correlations with each other than with any other group, it is possible that transects surveyed at 30 m would cluster with transects from the reef flat. It is of interest, therefore, to compare the two different approaches.

Clustering of transects was carried out by the unweighted pair-group method using arithmetic averages (SOKAL and SNEATH, 1963). The NT-SYS programs developed by Dr. J. F. ROHLF and J. KISHPAUGH (State University of New York at Stony Brook) were used for the cluster analysis computations. The "characters" measured were the relative abundance and living coverage of each species; the different transects represent different localities. With 99 species and two measurements per species (total number of individuals and total living coverage), the resulting matrix comprises 198 characters and 84 localities. Fig. 4 illustrates the dendrogram obtained by using the 84×84 correlation matrix (see SOKAL and ROHLF, 1962) which was more satisfactory than the dendrogram obtained from the distance matrix. The clustering of different transects by the correlation matrix was very similar to the zonation pattern obtained and described previously (LOYA and SLOBODKIN, 1971).

The zonation pattern described in Fig. 4, therefore, provides supporting evidence to the zonation pattern previously described (compare Figs. 3 and 4). In addition, it clarifies the fact that there are no borders separating one zone from another. Much overlap thus exists between the lower *Echinopora gemmacea* zone and the *Acropora hemprichi*—*A. variabilis* zone. Similarly, transects surveyed at the table edge clustered together with transects surveyed at the *Millepora* zone. Nevertheless, the general picture of the different zones of the reef is very similar to the one drawn before.

Species diversity indices

The measurement of species diversity in a certain ecosystem may refer to the number of species assembled, or it may be a more complex measure which takes into account the respective number of individuals.

The first important attempt to interpret animal community structure from the relationship between the number of individuals and the number of species obtained by sampling was that of FISHER et al. (1943). These authors predicted a negative binomial distribution of abundance. Since then, several indices of

diversity have been suggested and used in ecological literature. Some of these indices are based on a theoretical relationship between the number of species and individuals in a sample (PRESTON, 1948; SIMPSON, 1949; GOOD, 1953; MACARTHUR, 1957; WHITTAKER, 1961; PATEN, 1962). In these indices, the less numerically equal the species are, the less diverse the sample is, or in WHITTAKER's (1965) terminology, the greater is the dominance in the sample.

Other indices are determined by the number of species. The more species are found in a sample, or the more species present in a species list for a given environment, the greater the diversity (GLEASON, 1922; CAIN, 1938; MARGALEF, 1957; HESSLER and SANDERS, 1967; SANDERS, 1968).

The third group of indices are derived from information theory. Information theory provides the basis for measuring the diversity of animal populations, since it is related to the amount of confusion one experiences upon trying to comprehend a collection of things of different kinds (see below for further explanation). The indices derived from information theory are SHANNON and WEAVER's (1948) and BRILLOUIN's (1956).

Which one of all these indices is the best depends upon which one proves, in practice, to give the most reliable, ecological predictions and greatest insight (LOYD et al., 1968). Different indices of community diversity are discussed by HAIRSTON (1959), ODUM et al. (1960), SLOBODKIN (1961), WILLIAMS (1964), MACARTHUR (1965), WHITTAKER (1965), MCINTOSH (1967) and SANDERS (1968). The search for criteria proceeds both theoretically and empirically; however, a variety of measures should be used in presenting ecological data, so that they may be compared and studied together (LEVINS, 1966).

For the present analysis I chose three different indices which are compared throughout the study, thus avoiding a possible loss of information, as frequently is the case when only one index of diversity is analyzed. The three indices used are: (1) The species count; (2) SIMPSON's index of diversity; (3) information theory indices.

Table 5 summarizes the values obtained for the different diversity indices used, as well as the total number of colonies, number of species and living coverage recorded per transect.

The species count

The simplest measure of species diversity is a count of the number of species found in a sample. The two principal drawbacks of species counts are that they fail to take account of species abundance and that they depend upon sample size (MACARTHUR and MACARTHUR, 1961; PRESTON, 1962). However, after repeated sampling, a relatively complete list of

Table 5. Numbers of species and of colonies, living coverage and species diversity indices calculated for each transect at the coral reef at Eilat, Red Sea. H'_N : SHANNON and WEAVER's index of diversity (Eq. 6); H'_C : SHANNON and WEAVER's index of diversity (Eq. 9); H'/H'_{max} : PIELOU's "evenness" measurement (Eq. 8); H_N : BRILLOUIN's index of diversity (Eq. 5)

Station 1									
Transect No.	Zone (depth, m)	No. of species	No. of colonies	Cover (cm)	H'_N	H'_C	H'/H'_{max}	D_N	H_N
101	R. R. ^a	9	43	305	1.447	1.491	0.659	0.641	1.222
102	R. R.	13	47	447	2.025	2.135	0.790	0.808	1.712
103	T. ^a	10	27	201	1.818	1.763	0.790	0.765	1.448
104	T.	9	23	183	1.787	1.569	0.814	0.760	1.401
105	T.	13	40	339	2.009	2.044	0.783	0.806	1.662
106	T.	10	42	482	1.949	1.927	0.846	0.819	1.663
107	T.	16	41	370	2.470	2.491	0.891	0.894	2.033
108	T.	18	39	306	2.742	2.744	0.949	0.927	2.222
109	M. Z. ^a	11	65	750	1.244	1.327	0.519	0.489	1.056
110	M. Z.	21	47	712	2.867	2.486	0.942	0.933	2.353
111	M. Z.	25	80	954	2.818	2.654	0.875	0.918	2.433
112	3.0	13	36	461	2.332	2.199	0.909	0.881	1.917
113	3.5	18	80	821	2.581	2.479	0.893	0.904	2.274
114	4.0	22	52	532	2.800	2.426	0.906	0.919	2.319
115	5.0	22	53	493	2.772	2.728	0.897	0.918	2.302
116	6.0	18	45	424	2.628	2.375	0.909	0.909	2.169
117	7.0	13	47	412	2.347	2.227	0.915	0.888	1.999
118	8.0	17	40	281	2.681	2.596	0.946	0.921	2.191
119	8.5	20	59	620	2.587	2.282	0.864	0.889	2.185
120	9.0	26	75	610	2.999	2.814	0.921	0.935	2.565
121	10.0	16	26	170	2.665	2.568	0.961	0.923	2.043
122	11.0	23	53	392	2.932	2.799	0.935	0.937	2.429
123	13.0	14	28	234	2.465	2.241	0.934	0.898	1.938
124	15.0	15	21	141	2.624	2.482	0.969	0.921	1.944
125	17.0	20	45	305	2.729	2.589	0.911	0.911	2.229
126	20.0	26	64	396	3.041	2.957	0.933	0.944	2.557
127	25.0	23	67	562	2.746	2.854	0.876	0.907	2.334
128	30.0	28	106	880	2.877	2.864	0.863	0.915	2.534

Station 2									
Transect No.	Zone (depth, m)	No. of species	No. of colonies	Cover (cm)	H'_N	H'_C	H'/H'_{max}	D_N	H_N
201	R. R.	11	58	694	1.855	1.916	0.774	0.785	1.620
202	R. R.	9	44	731	1.660	1.332	0.756	0.747	1.424
203	T.	13	36	311	2.259	2.244	0.881	0.869	1.856
204	T.	12	57	413	1.728	1.772	0.695	0.741	1.491
205	T.	10	45	328	1.887	1.880	0.819	0.787	1.616
206	T.	5	17	138	1.300	1.314	0.808	0.671	1.025
207	T.	9	28	287	1.986	1.999	0.904	0.842	1.625
208	T.	13	35	431	2.352	2.245	0.917	0.888	1.928
209	T.	16	44	371	2.575	2.512	0.929	0.912	2.144
210	T.	18	57	431	2.546	2.523	0.881	0.898	2.165
211	T.	21	64	518	2.759	2.585	0.906	0.922	2.356
212	T.	16	51	514	2.534	2.052	0.914	0.905	2.148
213	M. Z.	10	52	697	1.247	1.660	0.542	0.507	1.044
214	M. Z.	8	79	997	0.740	0.888	0.356	0.297	0.634
215	M. Z.	16	72	971	1.680	1.984	0.606	0.614	1.427
216	3.0	10	29	254	2.082	1.994	0.904	0.856	1.699
217	3.5	18	55	609	2.382	1.913	0.824	0.852	2.006
218	4.0	22	81	736	2.824	2.726	0.914	0.929	2.467
219	5.0	20	54	556	2.780	2.547	0.928	0.927	2.344
220	6.0	17	50	534	2.540	2.212	0.897	0.901	2.136
221	7.0	11	23	280	2.246	2.123	0.937	0.881	1.751
222	8.0	24	59	644	2.928	2.743	0.921	0.933	2.450
223	9.0	25	55	392	3.002	2.983	0.933	0.941	2.483
224	10.0	20	56	304	2.620	2.518	0.875	0.907	2.209
225	11.0	18	24	182	2.810	2.551	0.972	0.934	2.093
226	13.0	12	13	78	2.458	2.355	0.989	0.911	1.681
227	15.0	17	44	361	2.500	2.434	0.882	0.893	2.066
228	17.0	16	26	170	2.665	2.602	0.961	0.923	2.043
229	20.0	20	40	213	2.838	2.664	0.947	0.933	2.286
230	25.0	26	93	731	2.861	2.823	0.878	0.924	2.504
231	30.0	27	129	766	2.797	2.750	0.849	0.916	2.512

Table 5 (continued)

Station 3

Transect No.	Zone (depth, m)	No. of species	No. of colonies	Cover (cm)	H'_N	H'_c	H'/H'_{max}	D_N	H_N
301	R. R.	15	47	541	2.360	2.264	0.872	0.875	1.985
302	R. R.	11	38	367	2.073	2.041	0.865	0.848	1.740
303	T.	15	38	438	2.390	2.127	0.882	0.880	1.954
304	T.	17	43	387	2.536	2.357	0.895	0.902	2.093
305	T.	15	37	429	2.468	2.280	0.911	0.898	2.015
306	T.	16	51	382	2.542	2.553	0.917	0.900	2.149
307	T.	11	27	314	2.223	2.019	0.927	0.875	1.779
308	M. Z.	16	43	604	2.230	2.376	0.804	0.812	1.825
309	M. Z.	15	63	668	2.197	2.257	0.811	0.830	1.901
310	M. Z.	36	99	980	3.238	3.091	0.904	0.943	2.790
311	3.0	14	47	512	2.260	2.006	0.856	0.866	1.912
312	4.0	27	72	579	2.961	2.944	0.899	0.934	2.518
313	5.0	23	73	667	2.742	2.336	0.875	0.911	2.357
314	6.0	24	117	872	2.776	2.639	0.873	0.918	2.490
315	7.0	16	30	247	2.401	2.309	0.866	0.864	1.873
316	8.0	24	62	440	2.844	2.657	0.895	0.924	2.394
317	9.0	26	84	856	2.986	2.911	0.916	0.939	2.589
318	10.0	17	36	201	2.717	2.555	0.959	0.927	2.187
319	11.0	30	69	653	3.059	3.078	0.899	0.936	2.563
320	13.0	9	18	151	1.985	1.702	0.903	0.827	1.502
321	15.0	16	31	277	2.557	2.525	0.922	0.905	2.018
322	17.0	18	33	273	2.677	2.621	0.926	0.915	2.110
323	20.0	27	77	520	2.938	2.888	0.891	0.930	2.516
324	25.0	29	91	704	3.122	3.018	0.927	0.946	2.709
325	30.0	34	116	945	3.010	2.936	0.854	0.929	2.646

* For explanation to symbols see legend to Fig. 4.

species can usually be obtained, even if no accurate estimate of individuals per species is available.

Fig. 11 is a histogram of the average number of species recorded per transect in the different zones of the reef. In contrast to many reports from other reefs (WELLS, 1954, 1957; STODDART, 1969) — where significant decreases in the number of coral species with depth have been reported — a successive increase in the number of species with depth was recorded at Eilat (see the "Light intensity" section and the "Discussion" for further interpretation). The *Acropora hemprichi* — *A. variabilis* zone (12 to 19 m) is the only exception to this scheme; a significantly lower number of species per transect was recorded in this zone, as compared to the adjacent shallower and deeper zones (*t* tests, $P < 0.05$).

The intercorrelations between the number of species recorded per transect and the other indices of diversity are discussed separately in the sections dealing with each particular index.

Simpson's index of diversity

SIMPSON (1949) introduces his "measure of concentration" as follows: "Consider an infinite population such that each individual belongs to one of Z

groups, and let $\pi_1 \dots \pi_Z$ ($\sum \pi = 1$) be the proportions of individuals in the various groups. Then λ defined as $\sum \pi^2$ is a measure of the concentration of the classification. It can take any value between $1/Z$ and 1, the former representing the smallest concentration or largest diversity possible with Z groups, and the latter complete concentration, all the individuals being in a single group. λ can be simply interpreted as the probability that two individuals chosen at random and independently from the population will be found to belong to the same group."

An unbiased estimator of λ is provided by SIMPSON as:

$$L = \frac{\sum_{i=1}^Z n_i(n_i-1)}{N(N-1)} \quad (1)$$

where the n_i is the number of individuals of the i th species in a sample of N . If N is reasonably large, the equation reduces essentially to:

$$\lambda = \sum_{i=1}^Z \left(\frac{n_i}{N}\right)^2 \quad (2)$$

and this is the form commonly used, for example by WHITTAKER (1965) in his study of land-plant communities. In this form of the index, λ equals unity if

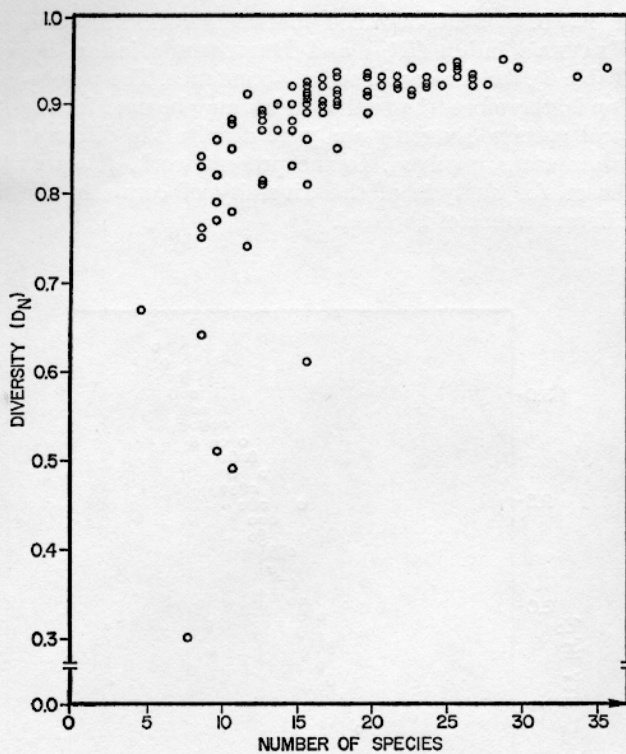


Fig. 5. Relationship between SIMPSON'S diversity index (D_N) and number of species recorded per transect

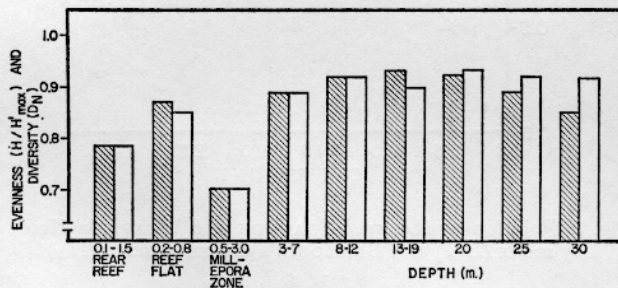


Fig. 6. PIELOU'S "evenness" index (H'/H'_{max} ; hatched columns), and SIMPSON'S diversity index (D_N ; white columns), calculated for different zones of reef

only one species is present in the sample, while SHANNON and WEAVER'S index H'_N (Eq. 6) equals zero in this case. If all the individuals are equally distributed among the species, $\lambda = 1/z$ and H'_N is at its maximum of $\log_e S$ (where S is the number of species).

In order to compare SIMPSON'S index to SHANNON and WEAVER'S index, SIMPSON'S index was changed to the following form:

$$D_N = 1 - \sum_{i=1}^s p_i^2 \quad (3)$$

Table 6. The coral reef at Eilat, Red Sea. Matrix of correlation coefficients for species diversity indices and other statistics. For further explanation see Table 5

No of species	No of colonies (cm)	Cover (cm)	H'_N	H'_C	H'/H'_{max}	D_N	H_N
1.00							
0.72	1.00						
0.49	0.84	1.00					
0.84	0.35	0.09	1.00				
0.86	0.41	0.13	0.92	1.00			
0.36	-0.19	-0.40	0.78	0.68	1.00		
0.58	0.07	-0.17	0.90	0.82	0.94	1.00	
0.89	0.51	0.25	0.98	0.94	0.69	0.85	1.00

using the same notation as used for SHANNON'S index, i.e., p_i is the proportion of individuals of species i ($i = 1, 2, \dots, s$). D_N is the revised expression for SIMPSON'S index of diversity. In this form, D_N has a different interpretation. It measures the probability that two specimens picked at random from a sample belong to different species. In this form, D_N equals zero if only one species is found in the sample, as does H'_N . The advantage of using D_N is in its sensitivity to the distribution of individuals among the species: in a sample where one species is significantly more abundant than other species, the probability that two specimens picked at random would belong to different species is very low. Thus, D_N is very similar in its outcome to PIELOU'S (1966c) H'/H'_{max} (Eq. 8). The correlation between the two indices is very high, $r = 0.94$, (Table 6), as expected, while a relatively low correlation $r = 0.58$, is obtained with the species count. In fact, after the first 10 to 12 species are encountered along a transect, D_N reaches its maximum value (Fig. 5), which means that this index is insensitive to the relative contribution of the rare species encountered along a transect. Fig. 6 is a histogram of the average values obtained for D_N (Eq. 3) and H'/H'_{max} (Eq. 8), as a function of depth (standard deviations and number of transects surveyed at each zone are given in Table 7). The major difference between the results obtained in this histogram and the coral species diversity as described in Fig. 11, is the strikingly low values obtained in the *Millepora* zone, when D_N and H'/H'_{max} are used, while relatively higher diversity is reported when the species count is used. On the other hand, in contrast to the other indices, the values obtained for the *Acropora hemprichi-A. variabilis* zone (13 to 19 m) are very high, and do not differ significantly from the values obtained in the adjacent shallower and deeper zones. The low values of D_N and H'/H'_{max} obtained for the *Millepora* zone, indicate clear dominance of one species (see WHITTAKER, 1965), *Millepora dichotoma*. In the *A. hemprichi-A. variabilis* zone, on the other hand, there is no clear dominance of one species; the distribution of colonies

among the different species in this zone is much more even, as reflected in the relatively high numerical values obtained for H'/H'_{\max} and D_N . The conclusion from Fig. 6 is that the rear reef, reef flat and *Millepora* zone are characterized by a relatively more marked dominance compared to all other zones below a depth of 3 m.

Diversity indices derived from information theory

PIELOU (1966b) states that diversity is equated with the amount of uncertainty which exists regarding the species of an individual selected at random from a population. The more species there are and the more nearly even their representation, the greater the uncertainty and hence the greater the diversity. "Information content" is a measure of uncertainty, and thus a reasonable measure of diversity.

MARGALEF (1957) proposed to measure the species diversity of a collection of organisms by the information content of the collection. Thus, if a collection contains N individual organisms belonging to S species, with N_i in the i th species ($i = 1, 2, \dots, s; \sum_i N_i = N$), the information content according to BRILLOUIN (1956) is:

$$B = \log_e \frac{N!}{N_1! N_2! \dots N_s!} \text{ information units} \quad (4)$$

The diversity per individual would be (following PIELOU's 1966c notation):

$$H_N = \frac{1}{N} \log_e \frac{N!}{N_1! N_2! \dots N_s!} \text{ information units/individual} \quad (5)$$

Alternatively, SHANNON and WEAVER's (1948) formula may be used:

$$H'_N = - \sum_{i=1}^s p_i \log_e p_i \text{ information units} \quad (6)$$

where $p_i = N_i/N$ is the proportion of the total number of individuals (N) belonging to the i th species (N_i). The units of H depend upon the base of the logarithm, which is largely a matter of choice. The commonest logarithm bases used are Base 2 or Base e , and the information units are "bits" or "nits" respectively (LLOYD et al., 1968). In the present study, Base e is used for calculating the different diversity indices.

PIELOU (1966b, c) clarifies the different uses of the two measurements. Whether to use H_N (Eq. 5) or H'_N (Eq. 6) depends upon whether one regards the collection as an entity to be studied for its own sake, or as a representative sample from some much larger parent population, whose diversity is to be estimated. The assumptions involved in using H'_N are that all the species in the parent population are represented in the sample and that the "parent population" is a homogeneous entity. To measure the species diversity of a biological collection, PIELOU advises the use of H_N rather than H'_N (PIELOU, 1966a, b, c, 1969). In the present study, both measurements are computed for comparative analysis (Fig. 7). A very high correlation

of $r = 0.98$ was obtained between SHANNON and WEAVER's index (H'_N) and BRILLOUIN's index, H_N (Table 6), for the coral species abundance. The conclusion is, therefore, that either index may be used for the coral species diversity analysis, despite the different assumptions involved. In the present work, H'_N was chosen for analysis of the diversity of corals in the different zones of the reef.

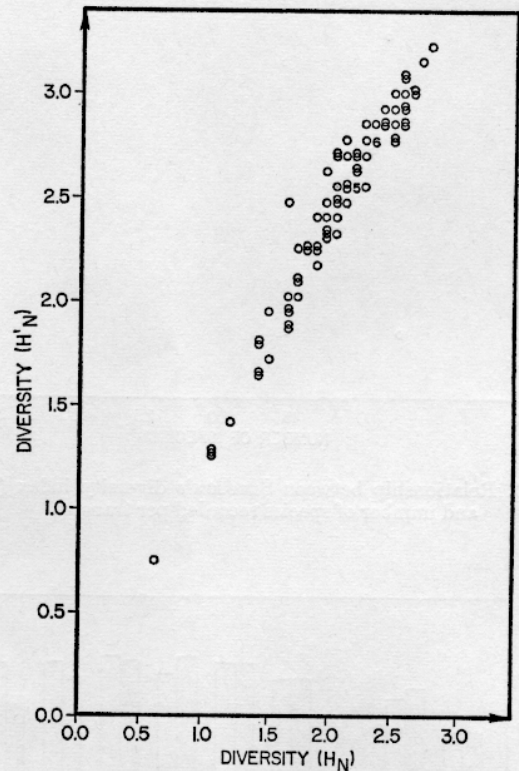


Fig. 7. Relationship between SHANNON and WEAVER's diversity index (H'_N) and BRILLOUIN's diversity index (H_N)

It should be noted that, if all S species in a sample are equally common, each has a proportion of $1/S$ of the total. Thus, the measure

$$H' = - \sum_{i=1}^s p_i \log_e p_i$$

takes the value:

$$H'_{\max} = -S \left(\frac{1}{S} \log_e \frac{1}{S} \right) = \log_e S \quad (7)$$

Thus, the measure of equally common species is simply the natural logarithm of the number of equally common species.

The evenness index (PIELOU, 1966a, c) was also computed in the present study. This measure is:

$$J' = H' (\text{observed}) / H'_{\max} \quad (8)$$

which compares the observed distribution of individuals among species to the value H' would take, if the same number of individuals were apportioned as evenly as possible, among the same number of species.

Another measure of "evenness" is that of LLOYD and GHELARDI (1964), which uses the term "equitability". These authors use MACARTHUR's (1957) type (1) distribution as a yardstick for comparing the observed diversity values. In the present work, PIELOU's "evenness" (Eq. 10) was adopted (see Fig. 6) rather than LLOYD and GHELARDI's "equitability" [consult

the results stresses the relatively low importance of the rare species, which have only a minor influence on both components H'_N and H'/H'_{max} and, consequently, on the index of diversity. SAGAR and HASLER arrive at this conclusion after plotting H'_N and H'/H'_{max} as a function of the number of species per sample. In both cases, insignificant correlations were obtained. In the present work, however, a high correlation was observed between the number of species recorded per transect and H'_N ($r = 0.84$) and a relatively much lower correlation with H'/H'_{max} ($r = 0.36$).

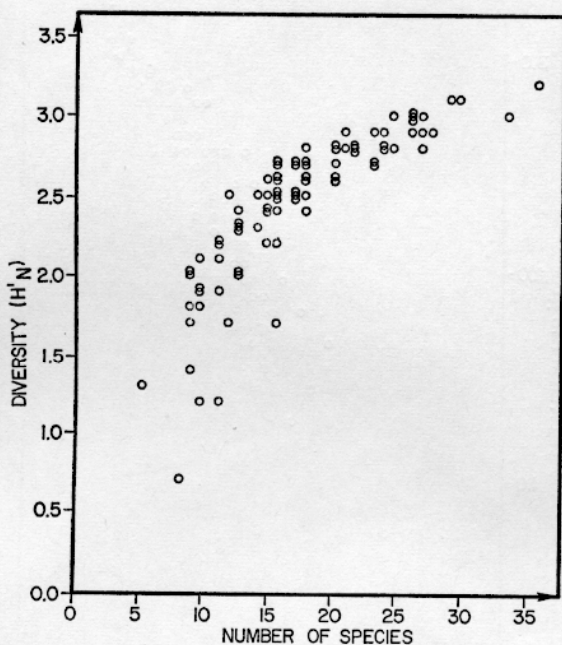


Fig. 8. Relationship between SHANNON and WEAVER's index of diversity (H'_N) and number of coral species recorded per transect

SHELDON (1969)], for comparative analysis of equitability indices).

The relationship between SHANNON and WEAVER's (H'_N) index of diversity and the number of species recorded per transect is presented in Fig. 8. H'_N increases sharply with increase in number of species, and tends to plateau after about 25 to 30 species per transect are recorded. The question is what causes this levelling off of H'_N ?

As pointed out before, an increase in the number of species and/or increase in tendency toward more equal distribution of individuals among species can result in higher values of H'_N . SAGAR and HASLER (1969) noted little effect on H'_N after the 10 to 15 most abundant species were encountered in lacustrine phytoplankton communities. Their interpretation of

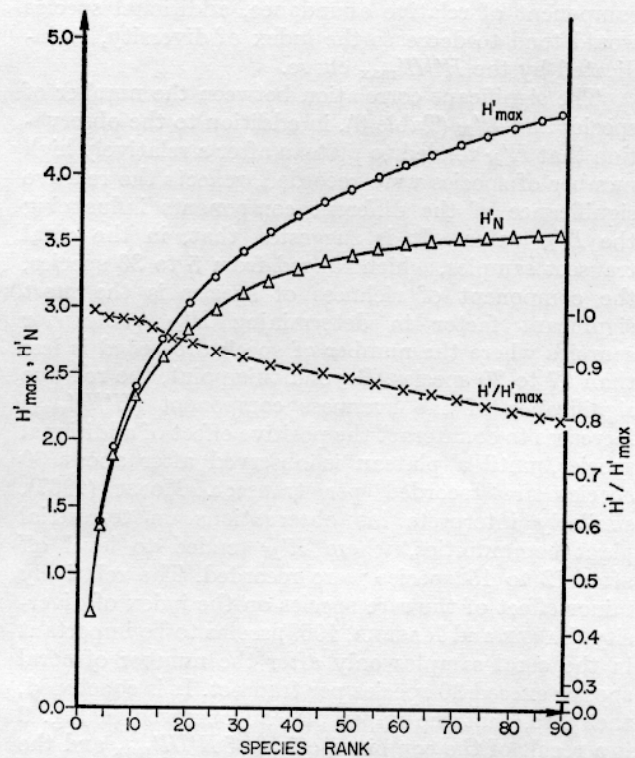


Fig. 9. Response of H'_N , H'/H'_{max} and H'_{max} to sequential incorporation of ranked species

Another way to check the effect of species richness on the diversity index, is to note the changes in the different indices as all species are incorporated from a sample; that is, the species are ranked in order of abundance and consecutively incorporated into H'_N beginning with the most abundant species. SAGAR and HASLER (1969) use this method to illustrate their interpretation of the small contribution to the diversity index of the rare species. Fig. 9 illustrates this manipulation for the coral samples. H'_N , H'/H'_{max} and H'_{max} are plotted against the ranked species in order of abundance. In this graph, the greatest change in H'_N occurs with the incorporation of roughly the

first 15 species. Then, a relatively smaller change occurs between 15 to 30 species, and from this point onward the curve tends to plateau. H'_{\max} continues to rise as more species are added. However, the greatest change in H'_{\max} occurs with the incorporation of roughly 20 to 25 species; H'/H'_{\max} decreases continuously with the incorporation of more species. The greatest change in H'/H'_{\max} values occurs when 20 to 25 species are incorporated. Fig. 9 illustrates a possible interpretation of the levelling off of H'_N . Acting through the component of species richness, additional species would tend to increase the index of diversity for the community. In opposition, and acting on the component of relative abundance, additional species would tend to decrease the index of diversity, as indicated by the H'/H'_{\max} curve.

The significant correlation between the number of species and H'_N (Table 6), in addition to the observation that H'_N tended to plateau after a relatively high number of species were recorded, reflects the relative significance of the different components influencing the H'_N values. It is suggested that, in the coral transect samples, which ranged from 5 to 36 species, the component of richness of species is the most significant factor in determining H'_N values for samples where the number of species recorded is less than 17 to 20 species. Beyond this point, the relative significance of the evenness component (H'/H'_{\max}) increases to counteract the positive effect of additional species, until a plateau is observed after about 30 species are recorded per transect. MONK (1967), similarly interprets his observations on terrestrial plant communities, where H'_N tended to level off after 12 to 15 species were recorded. The relatively minor effect of the rare species on the index of diversity (SAGER and HASLER, 1969) seems to be important in the coral samples only after the number of coral species exceed 30 species per transect. It is concluded, therefore, that the upper plateau observed in Fig. 9 is a result of the combined effect of H'/H'_{\max} and the rare species component (See also Fig. 8).

A significant problem which arises in species diversity studies, is the relative size or biomass of the individuals of different species. Most diversity studies to date have been restricted to mixed populations composed of similar sized individuals, i.e., diversity studies on gastropods (KOHN, 1959, 1967, 1968), cladocerans (WHITESIDE and HARMSWORTH, 1967; GOULDEN, 1969a, b), benthic forameniferans (BUZAS and GIBSON, 1969) planktonic foraminiferans (BERGER and PARKER, 1970), terrestrial arthropods of caves (POULSON and CULVER, 1969), fish (SHELDON, 1968), lizards (PIANKA, 1967), frogs, lizards and snakes (LLOYD et al., 1968), and birds (MACARTHUR and MACARTHUR, 1961; MACARTHUR, 1964; RECHER, 1969). In some cases, however, SHANNON and WEAVER's diversity index was little sensitive to relative abundance but sensitive to relative biomass (DICKMAN,

1968; WILHM, 1968). To remedy this situation, WILHM and DICKMAN independently modify SHANNON and WEAVER's index (Eq. 6), so that p_i is defined in terms of relative biomass rather than relative abundance. MONK et al. (1969), facing similar problems in a stratified oak-hickory community, determine the diversity by pooling all the data used to estimate diversity of each stratum.

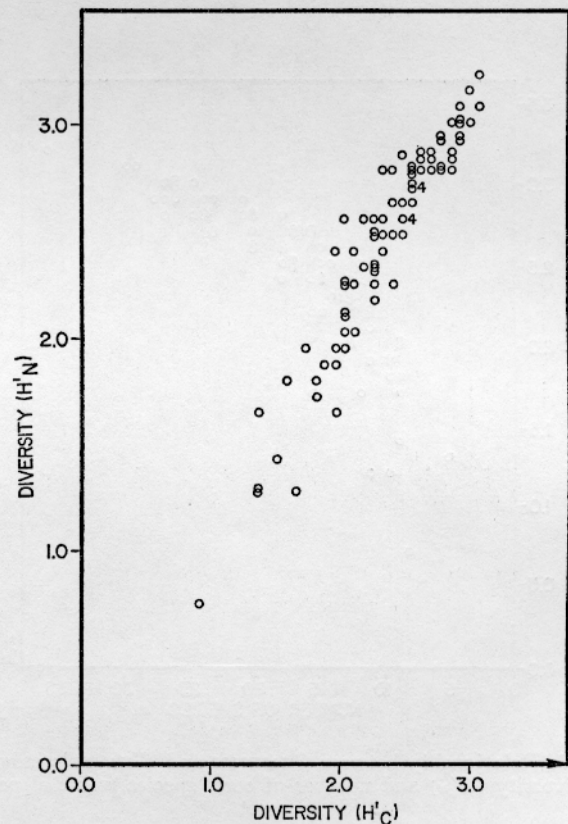


Fig. 10. Relationship between SHANNON and WEAVER's diversity index as computed from relative abundance of corals (H'_N), and same index when computed from relative living coverage of corals (H'_C)

For the coral transect samples, SHANNON and WEAVER's index of diversity was calculated both from the relative abundance (H'_N), and from the relative living coverage (H'_C) (Table 5). Thus, SHANNON and WEAVER's diversity index (Eq. 6) may be modified to:

$$H'_C = - \sum_{i=1}^s p_i \log_e p_i \quad (9)$$

where p_i is the living coverage proportion of the i th species in the sample. The correlation between H'_N and H'_C (Table 6) is highly significant ($r = 0.95$). The

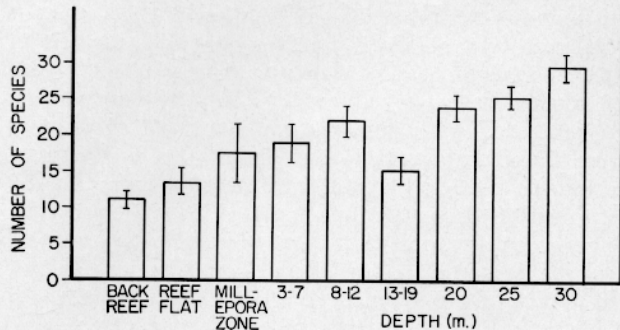


Fig. 11. Average number of species per transect as function of depth

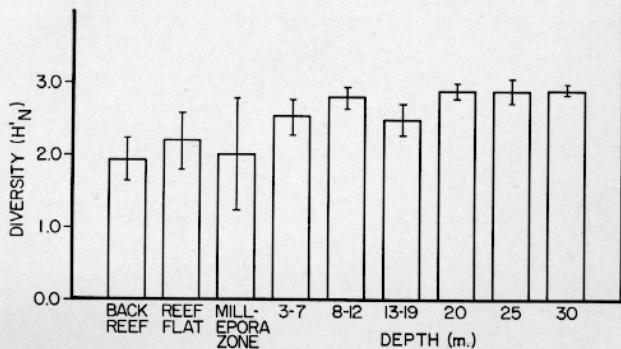


Fig. 12. SHANNON and WEAVER's index of diversity (H'_N) as function of depth

linear relationship between H'_N and H'_C (Fig. 10) indicates that there are no significant differences in the sizes of the corals within a transect. That is not to say that there are no changes in relative coral sizes between the different zones of the reef, as discussed in the next section. The high correlation between H'_N and H'_C also means that either measurement, number of colonies or living coverage, may be used for comparative studies of coral species diversity in different areas.

Fig. 12 is a histogram of H'_N in the different reef zones, and in general, is similar to Fig. 11, where the species count is used (see also Table 7). A more careful examination, however, reveals some differences between the two histograms. The most significant change is in the *Millepora* zone, where considerably lower diversity was estimated by using H'_N as an index, than was obtained by using the species count. The reason for the decrease in H'_N values in the *Millepora* zone, as compared to the reef flat, is probably due to the low evenness which has been discussed before. On the other hand, the H'_N values for the lower *Echinopora gemmacea* zone (8 to 12 m) and the *Porites lutea* zone (20 to 25 m) do not differ significantly (t tests, $P > 0.05$), while a significant increase (t tests, $P < 0.05$) was observed in the values of the species count (S) between the two zones. The observed plateau in the H'_N values has been discussed previously.

In conclusion, the two histograms indicate clearly the relatively lower species diversity in the *Acropora hemprichi*-*A. variabilis* zone (13 to 19 m). A possible explanation for this result is given in the "Discussion".

Table 7. Averages and standard deviations (in parentheses) of various statistics measured on the coral reef at Eilat, Red Sea

Location	Number of transects	Number of species	Number of individuals	Cover (%)	H'_N	H'/H'_{max}	D_N
Back reef	6	11.33 (2.34)	46.17 (6.68)	51.41 (17.32)	1.904 (0.323)	0.786 (0.078)	0.784 (0.088)
Table reef	21	13.48 (3.86)	40.10 (11.84)	36.06 (10.21)	2.231 (0.386)	0.869 (0.063)	0.851 (0.070)
<i>Millepora</i> zone	9	17.56 (8.73)	66.67 (17.97)	81.47 (15.76)	2.029 (0.856)	0.706 (0.206)	0.705 (0.235)
3-7 m	17	18.12 (4.86)	55.53 (23.33)	52.87 (18.07)	2.556 (0.255)	0.894 (0.028)	0.898 (0.027)
8-12 m	13	22.00 (4.32)	53.69 (18.00)	44.19 (21.72)	2.833 (0.164)	0.923 (0.033)	0.927 (0.015)
13-19 m	9	15.22 (3.27)	28.78 (10.91)	22.11 (9.15)	2.518 (0.222)	0.933 (0.034)	0.900 (0.029)
20 m	3	24.33 (3.79)	60.33 (18.77)	37.63 (15.44)	2.939 (0.101)	0.924 (0.029)	0.936 (0.007)
25 m	3	26.00 (3.00)	84.00 (14.80)	66.73 (9.26)	2.913 (0.190)	0.894 (0.030)	0.925 (0.020)
30 m	3	29.66 (3.78)	117.00 (11.53)	86.36 (9.06)	2.894 (0.108)	0.854 (0.008)	0.919 (0.008)

Light intensity, number of species and colony size

The attenuation of light with depth (Fig. 13) was measured by a cadmium sulphide light-meter. Light intensity is reduced by about 75 to 85% from the surface to 12 m. Thus, species living in the first 10 to 12 m are in a zone of sharp change in light intensity, with small changes in depth, while deep-water species are subjected to a less dramatic change. It must be mentioned that the change of light intensity of different wave lengths does not follow this pattern, since the longer wave lengths of visible light are lost first, while the blue light penetrates deeper.

WELLS (1957) discusses different factors affecting coral species distribution with depth. He comes to the conclusion that the number of species of reef corals is controlled by light intensity and radiant energy rather than by oxygen supply or temperature: "Even where oxygen supply and temperatures are favorable, reef corals will not flourish except in relatively shallow depths where radiation and light values are high. This is, of course, a result of the restrictive effect of the symbiotic zooxanthellae in the tissues of hermatypic corals." WELLS reports approximately 55% decrease in the number of coral species at Bikini Atoll at a depth of 10 m as compared to very shallow water, and about 70% decrease in the number of species at a depth of 30 m. The attenuation of light with depth at Bikini Atoll is very similar to that at Eilat. In Eilat, however, there is a successive increase in the number of species to a depth of 30 m. At the *Acropora hemprichi*—*A. variabilis* zone (13 to 17 m), there is a significant decrease in the number of species. The reason for this decrease, however, does not seem to be light intensity (see "Discussion" below). At Eilat, the number of species in deep water (30 m) is more than twice as many as in very shallow water (rear reef and reef flat, see Fig. 13).

It is suggested that light intensity and radiant energy may have a critical effect on coral-species abundance only below a certain depth, which may vary from reef to reef according to the local visibility. The present study proves that, at least until a depth of 30 m, light is not a limiting factor in coral-species abundance. A similar conclusion was drawn from an identical study by the late Professor T. F. GOREAU and myself in the Jamaican reefs (unpublished data). In Jamaica, a decrease in the number of species was observed only below a depth of about 40 m. A detailed study of the different light-wave lengths and their influence on coral growth and distribution may be needed in order to draw more accurate conclusions on the distribution of corals with depth.

Another aspect to be considered is the role of light in growth of coral colonies. In a series of papers, GOREAU (GOREAU and GOREAU, 1959, 1960a; GOREAU, 1961a, b) has clearly demonstrated, using calcium-45 and carbon-14 as radioactive tracers and conducting ex-

periments *in situ*, that calcification in a series of representative corals is, on the average, ten times greater in light than in darkness. The rate of uptake of calcium was even reduced by about 50% on cloudy as compared with sunny days. No such differences were found in ahermatypic corals or in hermatypes which had been deprived of zooxanthellae by prolonged exposure to darkness. The work of GOREAU provides experimental proof that the zooxanthellae are an essential factor in reef formation. According to GOREAU, the effect of photosynthesis by the zooxanthellae in the tissues is to increase the speed with which CO₂ produced in metabolism is removed and so to assist in the production of calcium carbonate.

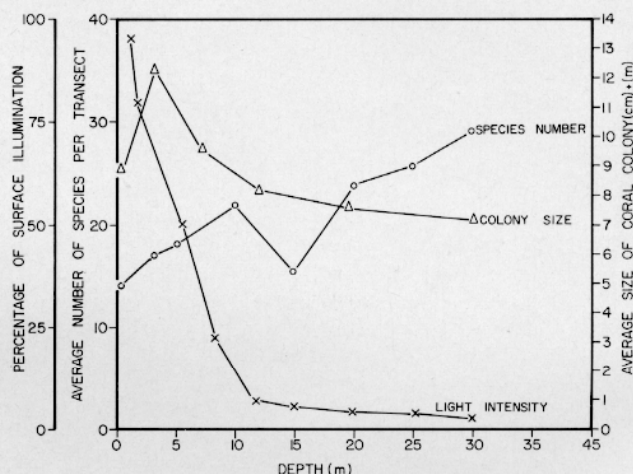


Fig. 13. Light attenuation with depth, average number of species per transect and average-colony size in different zones of reef (see text for explanation and Tables 7 and 8)

One of the conclusions which may be drawn from GOREAU's studies is that there may be a reduction in average colony size with depth. Since dramatic attenuation of light with depth occurs in the first 10 to 12 m, one would expect significant changes in colony size in this range, so that, on an average, smaller colonies would be found in deeper water.

Since the present work involved counting and measuring individual colonies along a transect, it was possible, to some extent, to measure the size distribution of several species with depth. It has been shown (Fig. 10) that, within a transect, there were no significant differences in the sizes of the most abundant coral species. It is possible, therefore, to calculate the size of an average colony for the different zones of the reef. The average-colony sizes, their standard errors and the number of colonies counted at each zone are given in Table 8.

Table 8. *Hermatypic corals at Eilat, Red Sea. Average colony-size at different depths (first number); standard errors (second number); and total number of colonies measured at each zone (third number)*

Species code No.	Species name	Reef table	<i>Millepora</i> zone	Depth (m)			
				3—7	8—12	13—19	20—30
2	<i>Stylophora pistillata</i>	7.29 (3.26) 181	8.43 (3.18) 16	8.88 (3.93) 35	9.09 (3.57) 43	10.03 (4.61) 26	7.75 (2.37) 16
12	<i>Montipora lobulata</i>	—	15.06 (9.60) 30	8.65 (5.51) 41	7.85 (3.49) 21	8.33 (4.67) 6	8.26 (4.73) 71
23	<i>Acropora variabilis</i>	11.20 (3.88) 29	14.22 (6.20) 9	11.35 (6.48) 59	11.93 (6.67) 63	11.21 (7.58) 23	9.90 (4.78) 32
24	<i>Acropora hemprichi</i>	14.20 (10.43) 10	18.81 (14.74) 11	10.72 (7.53) 83	8.42 (4.43) 49	7.21 (3.90) 33	9.00 (5.51) 77
53	<i>Porites lutea</i>	15.88 (12.76) 27	16.80 (8.98) 5	4.81 (3.73) 11	5.23 (3.22) 21	5.09 (3.12) 15	6.45 (4.25) 105
70	<i>Platygyra lamellina</i>	6.90 (4.09) 44	14.85 (10.76) 7	8.65 (3.61) 20	7.13 (4.43) 30	7.26 (2.97) 26	6.48 (3.70) 29
83	<i>Echinopora gemmacea</i>	16.91 (10.08) 23	12.96 (9.90) 29	13.70 (12.50) 125	9.18 (6.12) 66	5.16 (3.05) 6	8.17 (3.58) 34
Average colony		8.99 (7.95) 842	12.22 (9.10) 600	9.52 (9.06) 944	8.23 (7.23) 698	7.68 (5.33) 259	7.28 (4.45) 772

It may be argued that "average colony" has no biological meaning, since different species may have different patterns of size distribution with depth. On the other hand, the average-colony size may indicate some pattern which the average colony exhibits with depth. The size distribution of several species is calculated and discussed below. The actual measurement of large number of colonies does not serve as a direct proof of possible patterns of size distribution with depth, nevertheless, these measurements can suggest which of the species should be chosen in order to carry out more direct studies on the influence of light intensity on deposition of calcium carbonate by corals.

Fig. 13 illustrates light attenuation with depth, average number of species, and average-colony size for the different zones of the reef. It can easily be seen that the average-colony size-curve follows the same pattern as the light-intensity curve (with the exception of the reef flat): a sharp decrease in the average-colony size from the *Millepora* zone (0.2 to 3.0 m) to a depth of 12 m, and then a much less dramatic change between 12 and 30 m. In order to test whether the changes in the average-colony size with depth were significant, *t* tests were carried out on the different averages comparing the different zones (after testing

for equality of variance). The conclusion drawn from these tests is that there is a significant decrease in the average size of the coral colonies ($P < 0.05$) between the *Millepora* zone and a depth of 12 m. However, between 12 and 30 m, there is no significant difference in the average-colony size ($P > 0.05$). This again fits very well with the curve of light attenuation with depth, and confirms indirectly GOREAU's experiments concerning the influence of light on the rate of calcium-carbonate deposition.

The reef flat exhibits the only exception to the general scheme drawn above. The average-colony size on the reef flat is significantly smaller than the average colony in the *Millepora* zone, but there is no significant difference in size when compared to colonies between a depth of 3 and 12 m. A possible explanation for the smaller colony size on the reef flat may be that the reef flat is a relatively unstable, severe and unpredictable zone compared with the deep reef. This point will be further clarified in the "Discussion" section.

A study of the colony sizes of different species can be made only on species which are abundant in all the reef zones. In order to obtain a representative sample-size of a certain species at different depths, this species should be abundant in all the reef zones. Fig. 14 plots

the average size of seven coral species which occur in all the reef zones. It can be seen that some colonies, such as *Stylophora pistillata* and *Acropora variabilis*, do not exhibit a significant decrease in size with depth. Nevertheless, the general size pattern of most of the corals is similar to the pattern drawn from the average-colony size at different depths.

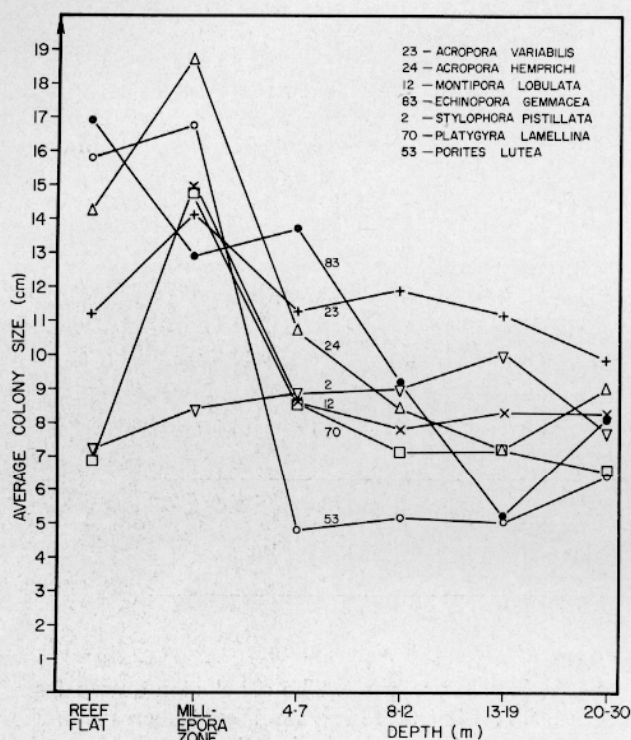


Fig. 14. Average colony size of 7 hermatypic coral species in different zones of reef (see text for explanation and Table 8)

Discussion and conclusions

The diversity concept contains at least three aspects:

- (1) Species-number diversity, i.e., number of species per a certain unit of individuals;
- (2) Species-area diversity, i.e., number of species per a certain unit of area;
- (3) Species evenness, or the apportionment of individuals among the species.

Nevertheless, the different diversity indices differ largely in their sensitivity to these aspects.

There may be good reasons to measure diversity in different ways under different circumstances, or in different taxonomic or ecological categories (see PIELOU, 1966 a, b, c), but the choice of diversity index must precede the collection of data. That is, choosing a certain index which seems appropriate for some set of data, and then drawing conclusions about diversity

from the computed values of that index is a flagrant form of a *posteriori* hypothesis construction (see COLWELL, 1969). Furthermore, using only one index may frequently cause a loss of significant information, which may result in the derivation of misleading conclusions.

The approach taken in the present study is to choose several indices, with different biological interpretations, which are also sensitive to different aspects of the diversity concept. Thus, SIMPSON's (1949) D_N and PIELOU's (1966 a, c) H'/H'_{max} indices measure how equally or unequally individuals are distributed among their species. These indices are essentially a measure of the degree of dominance in a sample. The less numerically equal the species are, the less diverse the sample is or, conversely, the greater the dominance in the sample. SHANNON and WEAVER's (1948) index (H'_N) is sensitive both to the number of species and to the degree of equal apportionment of the individuals among the species: The more species present in a sample and the more even their representation, the greater the diversity. Since "information content" is related to the amount of uncertainty or confusion one experiences upon confronting a collection of things of different kinds; it also agrees most closely, I think, with our intuitive notion of the concept "diversity".

"Information content" may also serve as a numerical basis for comparative studies of species diversity of animals of different taxa. Better insight into the interspecific relationship between different animals may be achieved by using the same criteria for comparing their abundance, biomass or relative productivity. A detailed diversity analysis of the hermatypic corals, taking into account also the most important physical parameters affecting coral distribution, may serve as a basis for comparisons and interpretations of the relative dependence on the reef framework of many other organisms which live within and between the corals. If the same factors are studied in different reef systems, applying the same diversity criteria, a better understanding of the causality and mechanisms affecting the observed distributions could be achieved.

In contrast to many descriptive studies suggesting that the number of coral species decrease significantly with depth, an opposite trend was recorded in Eilat. A significantly larger number of species per transect was recorded in deep water (20 to 30 m) compared to very shallow water (i.e., rear reef and reef flat). A comparison of species lists recorded in the two areas indicate that 26 out of 34 species found on the reef flat (i.e., 75%) also occur in deep water. On the other hand, 33 out of 59 species (i.e., 56%) which occur in deep water are completely absent from shallow water: i.e., more than half of the species present in deep water do not invade the reef flat, while only one quarter of the species on the reef table do not appear in deep water. This result ties up very well with SLOBODKIN and SANDERS' (1969) prediction that invasion of low

predictability areas by species from high predictability areas is less probable than the reverse process. Also, as JANZEN (1967) puts it, "the more predictable the environment, the smaller the change in that environment needs to be to serve as an immediate or long term barrier to dispersal." Thus, there is an increase in "fidelity" of the deep reef species to their habitat, as compared to the shallow-water species.

SLOBODKIN and SANDERS (1969) define unpredictable environments as environments in which the variances of environmental properties around their mean values are relatively high and unpredictable both spatially and temporally. According to this definition, the reef flat is unpredictable to a much larger extent than the deep-water reef. On the reef flat, physical parameters, such as water temperature and salinity, tides and wave action fluctuate more widely and in an

unpredictable manner around their means, compared to the same parameters in deeper water. The reef flat is much more "physically controlled" than the deep reef, which seems to be "biologically accommodated" (SANDERS', 1968, 1969, terminology).

It has been shown that the average-colony size on the reef flat is smaller than the average-colony size at a depth range of 3 to 12 m. It is suggested that the severity and unpredictability of the reef flat may also account for these differences; the growth of an individual colony is interfered with, or completely stopped (with the death of a colony) by the relatively harsh and unpredictable reef-flat environment.

In fact, the reef flat also fits SLOBODKIN and SANDERS' (1969) definition of "severe environment", i.e., an environment which may become completely abiotic with relatively slight environmental change.

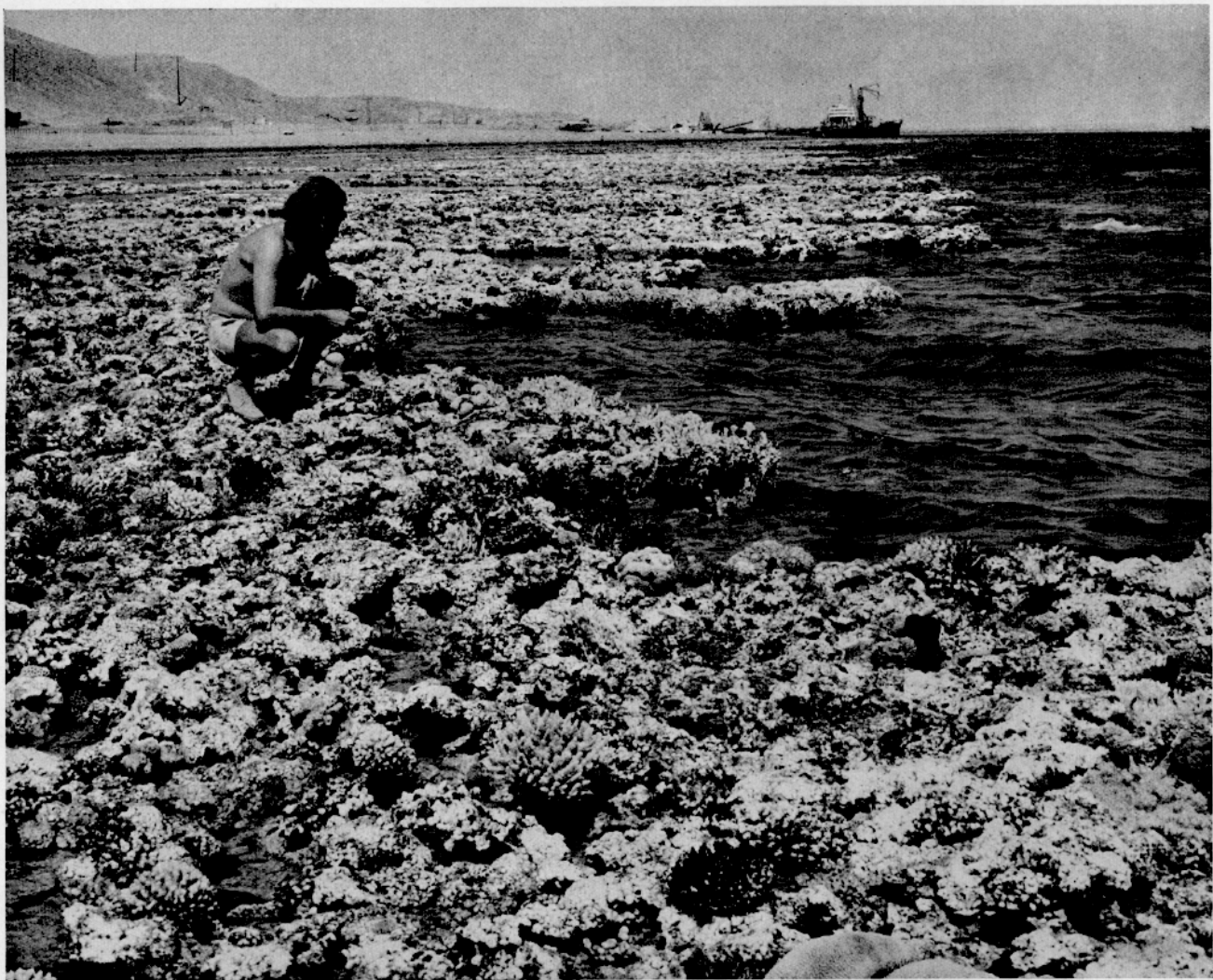


Fig. 15. Example of unpredictable nature of reef flat. Unusual circumstance of extremely low tide in the coral reef of Eilat

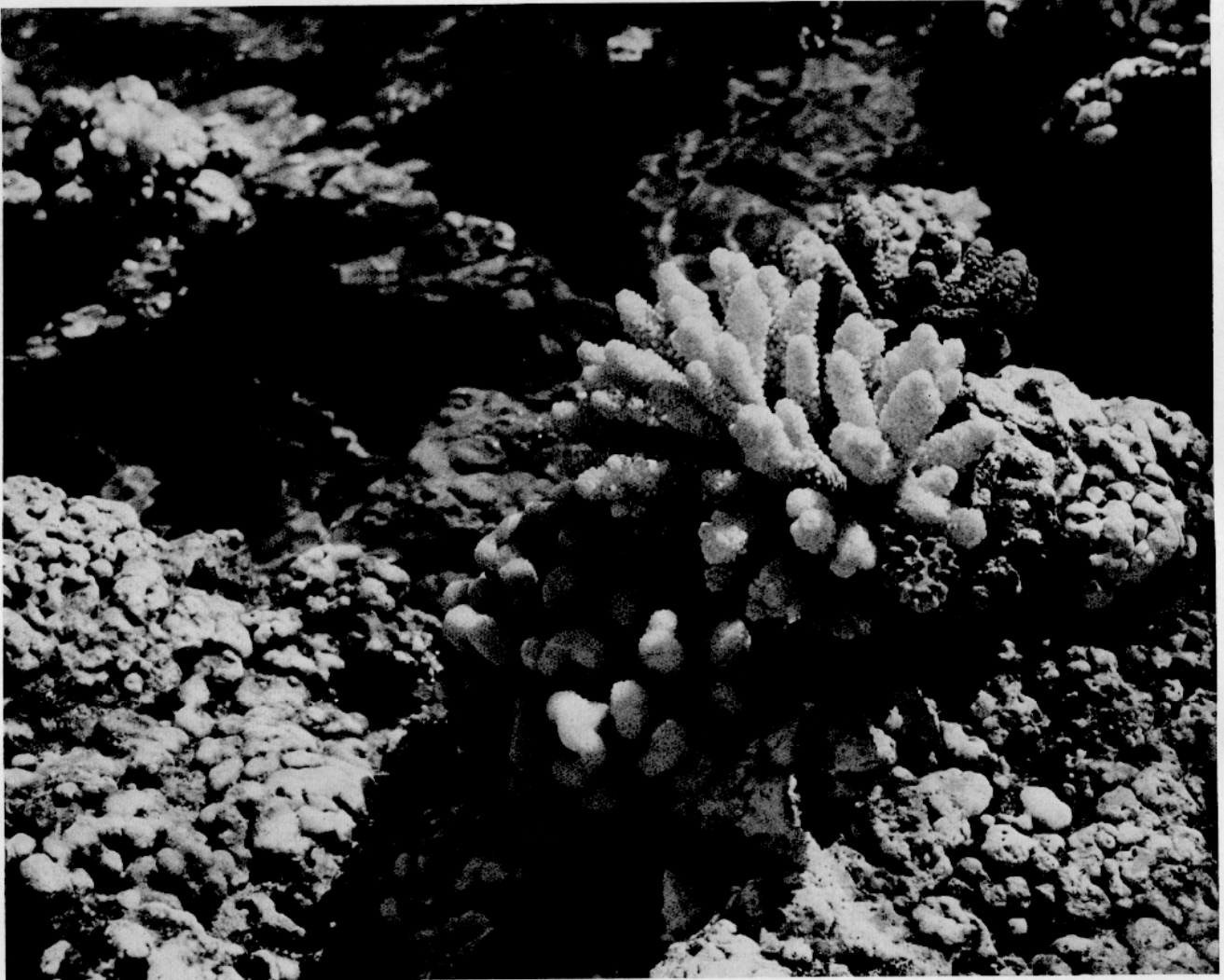


Fig. 16. Dead colonies of *Stylophora pistillata* and *Acropora variabilis* on reef flat, after the extreme low tide at Eilat

A good example of the severe and unpredictable nature of the reef flat is the very unusual circumstance of an extreme low tide (15—17 September, 1970), which was lower than any tide in Eilat during the last 5 years, at least (Fig. 15). This low tide, which was probably due to a combination of astronomical and meteorological features, completely exposed the reef flat to the air during the hottest portion of the day, and caused mass mortality among the reef flat corals (Fig. 16).

It has been shown by SLOBODKIN and SANDERS (1969) that severity and unpredictability combine in their effects, so that a severe, unpredictable environment tends to be poorer in species than either a less severe or more predictable environment. It is concluded, therefore, that the severe and unpredictable reef flat and the benign and much more predictable deep reef

fit very well to SLOBODKIN and SANDERS' assertion concerning species diversity and relative immigration to and from such areas.

Another question of interest is the relationship between environmental predictability, species diversity, and ecological specialization. PIANKA (1966) has reviewed the literature dealing with latitudinal gradients of species diversity. Several of the explanations for the diversity differences (DOBZHANSKY, 1950; KLOPFER, 1959; KLOPFER and MACARTHUR, 1960; CONNELL and ORIAS, 1964; WILLIAMS, 1964; MACARTHUR, 1965) depend upon the hypothesis that the average species of a more diverse community is ecologically more specialized, in one way or another, than the average species in a less diverse community. COLWELL (1969), testing this hypothesis on temperature and tropical arthropods, comes to the conclusion that

there is a high and positive correlation between species diversity and ecological specialization. Also, analysis of evolutionary strategy (SLOBODKIN, 1968) predicts that high specialization can evolve only with reference to highly predictable features of the environment.

The present work does not present any direct evidence concerning relative specialization in different coral species. Nevertheless, if one accepts the theoretical considerations mentioned before, combined with experimental evidence on arthropods, it may well be the case that similar relations may hold for corals. Perhaps most of the deep-water species which do not emigrate to shallow water are corals, which have developed high specialization to their local environment. Species like *Leptoseris tubulifera* and *L. fragilis*, for example, which are exclusively limited to deep water, should demonstrate narrower physiological tolerances in comparison to *Stylophora pistillata* or *Echinopora gemmacea*, which are abundant both in very shallow water and in deep water. Especially interesting in its distribution is *S. pistillata*, which is more abundant in the rear reef, reef flat and the *Acropora hemprichi*—*A. variabilis* zone (13 to 19 m) (LOYA and SLOBODKIN, 1971). These zones are relatively harsh and unpredictable compared to other zones of the reef, and are also in their early stages of succession. It is suggested, therefore, that *S. pistillata* is an example of a "fugitive species" as termed by HUTCHINSON (1951) or an "opportunistic species" as termed by other authors. *S. pistillata* is, therefore, a species which may be expected to invade temporarily vacant ecological niches or relatively harsh and unpredictable environments. If, indeed, this species is an opportunistic species as suggested, it is expected that with time, it will be eliminated from the deep reef by competition from other species. The decreasing pattern of abundance and living coverage with depth, typical of this species (with the exception of the *A. hemprichi*—*A. variabilis* zone), provides supporting grounds for the prediction that *S. pistillata* will be eliminated from the deep reef. A simple experiment to test this hypothesis would be to transplant colonies of *S. pistillata* onto the reef flat and the deep reef, together with coral species which are abundant all over the reef. If all these species are placed very close to each other, it is expected that the relative survivorship of *S. pistillata* on the reef flat will be much higher compared to its relative survivorship on the deep reef.

A deviation from the general scheme of increasing coral diversity with depth was observed in the *Acropora hemprichi*—*A. variabilis* zone (13 to 19 m), where a significantly lower species diversity and living coverage per transect were recorded (see Table 7). The *Millepora* zone (0.2 to 3.0 m), upper *Echinopora gemmacea* zone (8 to 12 m) and *Porites lutea* zone (20 to 30 m) possess the highest percentage of living coral coverage, the *A. hemprichi*—*A. variabilis* zone the poorest: the steepest zones of the reef are also the

richest in living coral coverage (Fig. 3). LOYA and SLOBODKIN (1971) postulated that sedimentation may be the main reason for this phenomena. In the steep zones of the reef, sediments are washed down by water currents and tend to accumulate in the flat zones.

Nevertheless, there are reports on some coral species which grow even in muddy environments (GOREAU and YONGE, 1968). This is, however, a special symbiotic association between a coral and a sipunculid worm which lives in a cavity under the surface of the coral and pulls the coral over the muddy surface.

It is suggested that, in areas of high sedimentation-rate on a coral reef, natural selection will favor coral species which can most successfully avoid settlement of sediment on their surface. The best strategy for a coral trying to grow in such an area is either to develop some kind of cleaning mechanism or to develop a special growth form which avoids sediment accumulation. Thus, coral species with a branching growth form would be advantageous to large and massive species, which would be exposed to a relatively rapid accumulation of sediments on their surface. In the high sedimentation-rate zone, on the coral reef of Eilat (the *Acropora hemprichi* — *A. variabilis* zone), three out of the four most abundant species are branching corals. *A. variabilis*, *A. hemprichi* and *Stylophora pistillata* are typical branching forms. *Platygyra lamellina*, on the other hand, is a typical massive species. It is predicted, therefore, that the massive *P. lamellina* has some cleaning mechanism which enables this species to withstand heavy sedimentation. This prediction is a direct result of the relative abundance of the coral species in this zone, and may easily be tested in the field, as well as in the laboratory. Mucus and ciliary cleaning have been suggested by MARSHALL and ORR (1931) and also by YONGE (1935) as possible cleaning mechanisms and have been observed in corals with large polyps.

Light intensity seems to have a minor effect in the *Acropora hemprichi* — *A. variabilis* zone (13 to 19 m), since the total living coverage, as well as the coral species diversity, increased significantly (see Figs. 11, 12, and Table 7) in the adjacent deeper zone (20 to 30 m).

It is concluded, therefore, that heavy sedimentation may be a very significant factor in determining the community structure of scleractinian corals. Thus, the relatively low abundance and living coverage of the coral species in the *Acropora hemprichi*—*A. variabilis* zone may be mainly a result of the sedimentation effect. This conclusion leads to a series of testable predictions concerning the relative survival of different coral species in areas of heavy sedimentation. By transplanting different coral species of different growth forms onto appropriate surfaces in areas of heavy sedimentation-rates, the relative survivorship of the different corals may be determined within a few weeks.

It may be assumed that the position occupied by any coral colony on the reef indicates where the initial planula (or planulae) settled. Unfortunately, very little has been done in reference to the factors influencing settlement of planulae and their relative survivorship. KAWAGUTI (1941) has shown some positive phototropism in coral planulae, but there is not, so far, any detailed information concerning these problems. Planulae of different coral species may have differences in behavioral responses to environmental factors, which may account for the differences in the regions where they settle. Thus, a great deal of the zonation pattern observed may be explained by the initial choice of settlement (if there is any) of the free planulae, with the adult colonies being adapted for life in these places. On the other hand, it is also possible that very many planulae settle and very few survive, in which case initial planulae settlement is less important in considerations of the location of coral species. The settlement of coral planulae has been studied to some extent only in the laboratory. CONNELL (in press) in a recent review of the population ecology of the reef corals, discusses the problem of larval dispersal and settlement. I would say, at the very least, that experiments in the field are needed on this subject of larval settlement for further understanding of the coral community organization.

It should be emphasized that there are other factors affecting coral growth and distribution which were not discussed in the present work; for example, interspecific competition, predation, and food availability. The availability of favorable space is another limiting factor in coral growth and diversity. If two coral colonies are very close, it is very probable that they would compete with each other for space. Thus, faster growing corals may overgrow their neighboring colonies, reduce the availability of light to these colonies, and act as physical barriers to their development. Furthermore, LANG (1970) has found that certain species extend their mesenterial filaments and digest any living coral tissue from a colony of another species which they can touch. She was also able to arrange the different coral species in an aggressive hierarchy. That is, each species attacks all others below it in the hierarchy, and is attacked by all the species ranked above it.

The "affinity" among the different coral species recorded in the present work may be determined from the data. Since the sequence of the coral species along the line transects is known, it is possible to calculate how many times species x appeared beside species y . The relative association between the different coral species will be discussed in a separate paper.

Summary

1. The community structure of hermatypic corals in the northern Gulf of Eilat, Red Sea is analyzed

from a series of line transects surveyed underwater with SCUBA. The distribution and patterns of abundance of the different coral species are presented with reference to such features as depth, reef topography, sedimentation and light intensity, which are the major factors considered in this work.

2. Coverage of living corals and coral species abundance were the characteristics used for cluster analysis of 84 transects surveyed on the reef. The dendrogram obtained describes the zonation pattern of the reef-building corals at Eilat.

3. The present knowledge concerning species diversity is reviewed and analyzed in context with the hermatypic corals community. Several diversity indices are used (the species count, SIMPSON'S index and indices derived from information theory), and compared throughout the study.

4. A successive increase in species diversity of hermatypic corals was recorded from the reef flat to a depth of 30 m. The H'_N values ranged from an average of 2.0 in the reef flat to 3.0 in deep water (20 to 30 m).

5. It is proposed that the severe and unpredictable nature of the reef flat may account for the lower abundance, smaller colony size and lower living-coral coverage on the reef flat as compared to the deep reef.

6. Light intensity does not seem to have inhibiting effects on coral species abundance to a depth of 30 m. However, the measurements of individual corals support, indirectly, the idea that light intensity is a significant factor in calcium-carbonate deposition by scleractinian corals.

7. Species diversity and living coverage of corals were significantly greater in steeper zones as compared to flatter zones of the reef. A possible explanation of this phenomenon is the accumulation of sediments in the flat zones.

8. Some field experiments are suggested and some testable predictions are made concerning sedimentation effects on different coral-growth forms, as well as the relative success of different coral species in invading different zones of the reef.

9. It is suggested that, in areas of heavy sedimentation, natural selection will favor coral species with branching growth-forms rather than massive growth-forms. It is expected that the few massive species found in this zone have evolved some cleaning mechanism.

10. *Stylophora pistillata* is suggested to be an opportunistic species, which may be expected to invade temporarily vacant ecological niches or relatively harsh and unpredictable environments on the reef.

11. The information derived from the present study is of interest in reference to further investigations and understanding of the distribution and variability of numerous organisms within and between the corals.

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Literature cited

- ABE, N.: Ecological survey of Iwayama Bay, Palao. *Palao trop. biol. Stn Stud.* **1**, 217—324 (1937).
- ASHBEL, D.: Bio-climatic atlas of Israel, 151 pp. Jerusalem: Meteorological Dept., Hebrew University 1951.
- Climatic conditions of Elath. *In: "Elath": Israel Exploration Society* pp 242—256 Jerusalem: 18th Archaeological Convention, October 1963.
- BERGER, W. H. and F. L. PARKER: Diversity of planktonic Foraminifera in deep sea sediments. *Science, N.Y.* **168**, 1345—1347 (1970).
- BRILLOUIN, L.: Science and information theory, 320 pp. New York: Academic Press 1956.
- BUZAS, M. A. and T. G. GIBSON: Species diversity: benthonic Foraminifera in Western North Atlantic. *Science, N.Y.* **163**, 72—75 (1969).
- CAIN, S. A.: The species area curve. *Am. Midl. Nat. Monogr.* **19**, 573—581 (1938).
- CHESHER, R. H.: Destruction of Pacific corals by the sea star *Acanthaster planci*. *Science, N.Y.* **165**, 280—283 (1969).
- COLWELL, R. K.: Ecological specialization and species diversity of tropical and temperate arthropods. Ph. D. thesis, University of Michigan 1969.
- CONNELL, J. H.: Population ecology of reef corals. *In: The geology and biology of coral reefs*, Ed. by O. A. JONES and R. ENDEAN. New York: Academic Press. (In press).
- and E. ORLIAS: The ecological regulation of species diversity. *Am. Nat.* **98**, 399—414 (1964).
- DICKMAN, M.: Some indices of diversity. *Ecology* **49**, 1191—1192 (1968).
- DOBZHANSKY, T.: Evolution in the tropics. *Am. Scient.* **38**, 209—211 (1950).
- EDMONDSON, C. H.: The ecology of the Hawaiian coral reef. *Bull. Bernice P. Bishop Mus.* **45**, 1—64 (1928).
- EMERY, K. O., J. I. TRACEY, JR. and H. S. LADD: Geology of Bikini and nearby atolls. I. *Geology. Prof. Pap. U.S. geol. Surv.* **260** (A), 1—265 (1954).
- FISHELSON, L.: Marine biological and oceanographical research in the Red Sea, 65 pp. Final report submitted to the Office of Naval Research, Washington 1968.
- FISHER, R. A., A. S. CORBET and C. B. WILLIAMS: The relation between the number of species and the number of individuals in a random sample from an animal population. *J. Anim. Ecol.* **12**, 42—58 (1943).
- FRIEDMAN, G. M.: Geology and geochemistry of reefs, carbonate sediments, and waters, Gulf of Aqaba (Eilat), Red Sea. *J. sedim. Petrol.* **38**, 895—919 (1968).
- GLEASON, H. A.: On the relation between species and area. *Ecology* **3**, 158—162 (1922).
- GOOD, I. J.: The population frequencies of species and the estimation of population parameters. *Biometrika* **40**, 237—264 (1953).
- GOREAU, T. F.: The ecology of Jamaican coral reefs. I. Species composition and zonation. *Ecology* **40**, 67—90 (1959).
- Problems of growth and calcium deposition in reef corals. *Endeavour* **20**, 32—39 (1961a).
- On the relation of calcification to primary production in reef building organisms. *In: The biology of Hydra*, pp 269—285. Ed. by H. M. LENHOFF and W. F. LOOMS. Miami: University of Miami Press 1961b.
- Calcium carbonate deposition by coralline algae and corals in relation to their roles as reef builders. *Ann. N.Y. Acad. Sci.* **109**, 127—167 (1963).
- On the predation of coral by the spiny starfish *Acanthaster planci* (L.) in the southern Red Sea. *Bull. Sea Fish. Stn Israel* **35**, 23—26 (1964).
- Structure and ecology of the Saipan reefs in relation to predation by *Acanthaster planci* (L.), 36 pp. Marian Islands: The *Acanthaster* survey of Saipan 1969.
- and N. I. GOREAU: The physiology of skeleton formation in corals. II. Calcium deposition by hermatypic corals under various conditions in the reef. *Biol. Bull. mar. Biol. Lab., Woods Hole* **117**, 239—250 (1959).
- Distribution of labelled carbon in reef-building corals with and without zooxanthellae. *Science, N.Y.* **131**, 668—669 (1960a).
- The physiology of skeleton formation in corals. III. Calcification rate as a function of colony weight and total nitrogen content in the reef coral *Manicina areolata* (LINNAEUS). *Biol. Bull. mar. Biol. Lab., Woods Hole* **118**, 419—429 (1960b).
- and W. D. HARTMAN: Boring sponges as controlling factors in the formation and maintenance of coral reefs. *In: Mechanisms of hard tissue destruction*, pp 25—54. Ed. by R. F. SOGNAES. Washington: Publ. Am. Ass. Advmt Sci. 1963.
- and C. M. YONGE: Coral community on muddy sand. *Nature, Lond.* **217**, 421—423 (1968).
- GOULDEN, E. C.: Developmental phases of the biocoenosis. *Proc. Natn. Acad. Sci. U.S.A.* **62**, 1066—1073 (1969a).
- Temporal changes in diversity. Diversity and stability in ecological systems. *Brookhaven Symp. Biol.* **22**, 96—102 (1969b).
- GREIG-SMITH, P.: Quantitative plant ecology, 242 pp. 2nd ed. Washington, D. C.: Butterworth Inc. 1964.
- HAIRSTON, N. G.: Species abundance and community organization. *Ecology* **40**, 404—416 (1959).
- and G. W. BYERS: The soil arthropods of a field in southern Michigan: A study in community ecology. *Contr. Lab. vertebr. Biol. Univ. Mich.* **64**, 1—37 (1954).
- HESSLER, R. R. and H. L. SANDERS: Faunal diversity in the deep sea. *Deep Sea Res.* **14**, 65—78 (1967).
- HIATT, R. W.: Factors affecting the distribution of corals on the reefs of Arno Atoll, Marshall Islands. *Proc. Pacif. Sci. Congr. (9th)* **3**, 929—970 (1957).
- HUTCHINSON, G. E.: Copepodology for the ornithologist. *Ecology* **32**, 571—577 (1951).
- JANZEN, D. H.: Why mountain passes are higher in the tropics. *Am. Nat.* **101**, 233—249 (1967).
- KAWAGUTI, S.: On the physiology of reef corals. V. Trophism of coral planulae, considered as a factor of distribution of the reefs. *Palao trop. biol. Stn Stud.* **2**, 319—328 (1941).
- KISSLING, D. L.: Coral distribution on a shoal in Spanish Harbor, Florida Keys. *Bull. mar. Sci.* **15**, 600—611 (1965).

- KLOPFER, P. H.: Environmental determinants of faunal diversity. *Am. Nat.* **93**, 337—342 (1959).
- and R. H. MACARTHUR: Niche size and faunal diversity. *Am. Nat.* **94**, 293—300 (1960).
- KOHN, A. J.: The ecology of *Conus* in Hawaii. *Ecol. Monogr.* **29**, 47—90 (1959).
- Environmental complexity and species diversity in the gastropod genus *Conus* on Indo-West Pacific reef platforms. *Am. Nat.* **101**, 351—360 (1967).
- Microhabitats, abundance, and food of *Conus* on atoll reef in the Maldives and Chagos Islands. *Ecology* **49**, 1046—1061 (1968).
- KORNICKER, L. S. and D. W. BOYD: Shallow water geology and environment of Alacran reef complex, Campeche Bank, Mexico. *Bull. Am. Ass. Petrol. Geol.* **46**, 640—673 (1962).
- LANG, J. C.: Interspecific aggression within the scleractinian reef corals. Ph. D. thesis, Yale University 1970.
- LEVINS, R.: The strategy of model building in population biology. *Am. Scient.* **54**, 421—431 (1966).
- LLOYD, M. and R. J. GHELARDI: A table for calculating the "equitability" component of species diversity. *J. Anim. Ecology* **33**, 217—225 (1964).
- , R. F. INGER and F. W. KING: On the diversity of reptile and amphibian species in a Bornean rain forest. *Am. Nat.* **102**, 497—515 (1968).
- , J. H. ZAR and J. R. KARR: On the calculation of information — theoretical measures of diversity. *Am. Midl. Nat.* **79**, 257—272 (1968).
- LOYA, Y. and L. B. SLOBODKIN: The coral reefs of Eilat (Gulf of Eilat, Red Sea) Symp. zool. Soc. Lond. **28**, 117—139 (1971).
- MACARTHUR, R. H.: On the relative abundance of bird species. *Proc. natn. Acad. Sci. U.S.A.* **43**, 293—295 (1957).
- Environmental factors affecting bird species diversity. *Am. Nat.* **98**, 387—398 (1964).
- Patterns of species diversity. *Biol. Rev.* **40**, 510—533 (1965).
- and J. W. MACARTHUR: On bird species diversity. *Ecology* **42**, 594—598 (1961).
- MANTON, S. M.: Ecological surveys of coral reefs. *Scient. Rep. Gt Barrier Reef Exped.* **3**, 274—312 (1935).
- MARGALEF, D. R.: La teoría de la información en ecología. *Mems R. Acad. Cienc. Artes Barcelona* **32**, 373—449 (1957). *Transl. Information theory in ecology. Gen. Syst.* **3**, 36—71 (1959).
- MARSHALL, S. M. and A. P. OER: Sedimentation on Low Isles and its relation to coral growth. *Scient. Rep. Gt Barrier Reef Exped.* **1**, 93—133 (1931).
- MAYOR, A. G.: Ecology of the Murray Island coral reef. *Pap. Dep. mar. Biol. Carnegie Instn Wash.* **9**, 1—48 (1918).
- MCINTOSH, R. P.: An index of diversity and the relation of certain concepts to diversity. *Ecology* **48**, 392—404 (1967).
- MONK, C. D.: Tree species diversity in the eastern deciduous forest with particular reference to north central Florida. *Am. Nat.* **918**, 173—187 (1967).
- , G. I. CHILD and S. A. NICHOLSON: Species diversity of stratified oak-hickory community. *Ecology* **50**, 468—470 (1969).
- ODUM, H. T., J. E. CANTLON and L. S. KORNICKER: An organizational hierarchy postulate for the interpretation of species-individual distributions, species entropy, ecosystem evolution, and the meaning of a species-variety index. *Ecology* **41**, 395—399 (1960).
- and E. P. ODUM: Trophic structure and productivity of a windward coral reef community on Eniwetok Atoll. *Ecol. Monogr.* **25**, 291—320 (1955).
- OREN, O. H.: A note on the hydrography of the Gulf of Eilat. *Bull. Sea Fish. Res. Stn Israel* **30**, 3—14 (1962).
- PATTEN, B. C.: Species diversity in net phytoplankton of Raritan Bay. *J. mar. Res.* **20**, 57—75 (1962).
- PIANKA, E. R.: Latitudinal gradients in species diversity: A review of concepts. *Am. Nat.* **100**, 33—46 (1966).
- On lizard species diversity: North American flatland deserts. *Ecology* **48**, 333—351 (1967).
- PIELOU, E. C.: The measurement of diversity in different types of biological collections. *J. theor. Biol.* **13**, 131—144 (1966a).
- Shannon's formula as a measurement of specific diversity: Its use and misuse. *Am. Nat.* **100**, 463—465 (1966b).
- Species diversity and pattern-diversity in the study of ecological succession. *J. theor. Biol.* **10**, 370—383 (1966c).
- An introduction to mathematical ecology, 286 pp. New York: Wiley-Interscience 1969.
- POULSON, T. L. and D. C. CULVER: Diversity in terrestrial cave communities. *Ecology* **50**, 153—157 (1969).
- PRESTON, F. E.: The commonness and rarity of species. *Ecology* **29**, 254—283 (1948).
- The canonical distribution of commonness and rarity. Part I. *Ecology* **43**, 185—215 (1962). Part II. *Ecology* **43**, 410—431 (1962).
- RECHER, H. F.: Bird species diversity in Australia and North America. *Am. Nat.* **103**, 75—80 (1969).
- SAGER, P. E. and A. D. HASLER: Species diversity in lacustrine phytoplankton. I. The components of the index of diversity from Shannon's formula. *Am. Nat.* **103**, 51—59 (1969).
- SANDERS, H. L.: Marine benthic diversity: A comparative study. *Am. Nat.* **102**, 243—282 (1968).
- Benthic marine diversity and the stability-time hypothesis. Diversity and stability in ecological systems. *Brookhaven Symp. Biol.* **22**, 71—81 (1969).
- SHANNON, C. E. and W. WEAVER: The mathematical theory of communication, 117 pp. Urbana: University of Illinois Press 1948.
- SHELDON, A. L.: Species diversity and longitudinal succession in stream fishes. *Ecology* **49**, 193—198 (1968).
- Equitability indices: dependence on the species count. *Ecology* **50**, 466—467 (1969).
- SIMPSON, E. H.: Measurement of diversity. *Nature, Lond.* **163**, p. 668 (1949).
- SLOBODKIN, L. B.: Growth and regulation of animal populations, 184 pp. New York: Holt, Rinehart & Winston 1961.
- Toward a predictive theory of evolution. *In: Population biology and evolution*, pp 187—205. Ed. by R. C. LEWONTIN. Syracuse: Syracuse University Press 1968.
- and H. L. SANDERS: On the contribution of environmental predictability to species diversity. Diversity and stability in ecological system. *Brookhaven Symp. Biol.* **22**, 82—95 (1969).
- SOKAL, R. R. and F. J. ROHLF: The comparison of dendrograms by objective methods. *Taxon* **11**, 33—40 (1962).
- — *Biometry*, 775 pp. San Francisco and London: W. H. Freeman & Co. 1969.
- and P. H. A. SNEATH: Principles of numerical taxonomy, 359 pp. San Francisco & London: W. H. Freeman & Co. 1963.
- STODDART, D. R.: Ecology and morphology of Recent coral reefs. *Biol. Rev.* **44**, 433—498 (1969).
- , P. S. DAVIES and A. KEITH: Geomorphology of Addu Atoll. *Atoll Res. Bull.* **116**, 13—41 (1966).
- STORR, J. F.: Ecology and oceanography of the coral-reef tract, Abaco Island, Bahamas. *Spec. Pap. geol. Soc. Am.* **79**, 1—98 (1964).
- VAUGHAN, T. W. and J. W. WELLS: Revision of the suborders, families and genera of the Scleractinia. *Spec. Pap. geol. Soc. Am.* **44** (1943).
- WAINWRIGHT, S. A.: Reef communities visited by the Israel South Red Sea Expedition, 1962. *Bull. Sea Fish. Res. Stn Israel* **38**, 40—53 (1965).

- WELLS, J. W.: Recent corals of the Marshall Islands, Bikini and nearby atolls. Part 2, Oceanography (Biologic). Prof. Pap. U. S. geol. Surv. **260** (1), 385—486 (1954).
— Coral reefs. Mem. geol. Soc. Am. **67**, 609—631 (1957).
- WHITESIDE, M. C. and R. V. HARMSWORTH: Species diversity in chidoriid (Cladocera) communities. Ecology **48**, 664—667 (1967).
- WHITTAKER, R. H.: Estimation of net primary production of forest and shrub communities. Ecology **42**, 177—180 (1961).
— Dominance and diversity in land plant communities. Science, N.Y. **147**, 250—260 (1965).
- WILHM, J. L.: Biomass units versus numbers of individuals in species diversity indices. Ecology **49**, 153—156 (1968).
- WILLIAMS, C. B.: Patterns in the balance of nature, 324 pp. New York & London: Academic Press 1964.
- YONGE, C. M.: Studies on the biology of Tortugas corals. I. Observations on *Meandra areolata*. LINN. Pap. Tortugas Lab. **29**, 185—198 (1935).

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