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Structure of Africa's Southernmost Coral Communities

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STRUCTURE OF AFRICA'S SOUTHERNMOST CORAL COMMUNITIES

B. Riegl, M. H. Schleyer, P. J. Cook and G. M. Branch

ABSTRACT

The structure of Africa's southernmost coral communities, which grow on submerged fossil dune and beachrock systems and do not form true coral reefs, was quantitatively investigated by means of line transects and phototransects. None of the typical geomorphological reef-zones such as lagoons, reef crests or reef slopes were developed. A uniform community structure, differentiated only into two major community-types with three subcommunities, was found. Shallow reefs were dominated by alcyonaceans and differed from scleractinian dominated deep reefs. A high proportion of alcyonaceans was found in shallow communities (40–60%). Subcommunities, which were found on most reefs, were an alcyonacean dominated "reef-top" community in areas of low sedimentation, dominated by the genera *Sinularia* and *Lobophytum*, and a scleractinian dominated "gully" community (predominantly *Montipora* and *Faviidae*), in areas of high sedimentation. A deep sponge-dominated subcommunity existed on the deepest outcrops. The lower limit for most coral growth was between 35 and 40 m.

The southernmost reef coral communities on the African continental coast are situated along the Maputaland coastline in northern Natal, South Africa, at 27°50′S. This rates them among the southernmost true reef coral communities found anywhere in the world (the southernmost being at Lord Howe Island, off Australia at 31°33′S).

The substrata are not true coral reefs but fossilized and submerged dune and beachrock systems (Ramsey and Mason, 1990). The reefs do not reach the surface and lack most geomorphological traits typical of true coral reefs, which normally lead to differentiation of coral communities (Stoddart, 1969; Loya, 1972; Done, 1982; Sheppard, 1982). None of the usual features (lagoons, reef crests or steep reef slopes) are developed, thus resulting in relatively homogenous topographic conditions over most of the hard bottom area covered by corals. The major topographical features are gullies and associated small drop-offs, perpendicular to the dominant direction of the swells.

Both the geographical location of these reefs and the rather unusual geomorphological setting make an analysis of their coral communities worthwhile. No quantitative information about coral community structure is yet available.

This study provides information about 1) coral cover and abundance, 2) community differentiation on a macro (inter-reef) and micro (within-reef) scale and 3) within and between reef diversity (4) the major environmental factors influencing these southernmost coral communities in Africa.

Material and Methods

Data were collected using the line transect method with continuous transect recording (Loya, 1978), combined with phototransects. The ideal length of the transects was tested prior to sampling by means of a species-per-area curve (Loya, 1978) and resulted in an ideal transect length of 10 m. Due to the large and morphologically uniform area covered by corals, several randomly chosen sample sites were investigated per reef. At each sample site a series of 10 parallel transects with a spacing of 1 m was recorded. Depth of transects varied between 9 and 35 m. Five to seven sample sites per reef were surveyed in the Central and Southern Reef Complexes, one in the Northern Reef Complex. Phototransects, covering areas of 4 × 10 m each, were also taken, from which it was possible to gain further line-transect information. The scale of the photographs was determined using markings on a transect

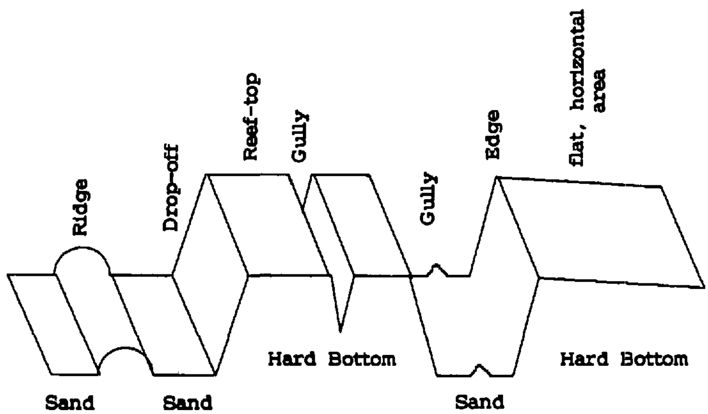

Figure 1. Explanation of terms used to describe the position of transects on the reefs. The situation is idealized and not to scale.

line, which was visible in each photograph. Coral intercepts on the transect line were measured using a ruler, the data were then multiplied by the scale of the photographs to obtain an estimate of the actual intercept distances.

Intercepts of corals, other major invertebrate groups, such as sponges and ascidians, and sand and unoccupied rock were recorded. Unoccupied rock was defined as lacking macroalgae or invertebrates.

The position of each transect on the reefs, i.e., whether it was located on a flat horizontal area, a ridge, a drop-off, a gully-edge or inside a gully, was recorded. The terminology used is illustrated in Figure 1.

One hundred seventy-one transects were recorded on five reefs (Fig. 2).

Root-root transformed data were subjected to correspondence analysis and agglomerative, hierarchical cluster analysis using the Bray-Curtis Dissimilarity Index, grouping by group average (Digby and Kempton, 1987). Then to ordination by Multidimensional scaling (MDS), using the same distance matrix as for the classification. Environmental variables were superimposed on MDS groupings to visualize their influence on species grouping (Warwick and Clarke, 1993; Agard et al., 1993). Dominant species were measured by their contribution to the average Bray-Curtis dissimilarity between groups (Field et al., 1982).

The Shannon-Weaver diversity index H′ (Loya, 1972; Pielou, 1975) and its evenness measure (Pielou, 1975) as well as Simpson's Alpha as a dominance measure (Brower and Zar, 1977) were used.

Sedimentation rates were measured using open topped tubes of 11-cm bore, each of which projected by 15 cm from rectangular vinyl containers (20 × 10 cm) that served to accumulate sediments settling in the tube. Suspended sediment in the water was sampled with 5-liter sampler bottles with simultaneously closing lids on both ends.

Study Area.—Coral communities grow on submerged fossil dune or beachrock systems (Ramsey and Mason, 1990) from about 100 to 1,000 m off-shore. The topography of the reefs is mostly flat, with numerous gullies and occasional drop-offs of rarely more than 6 m (Fig. 2, Ramsey and Mason, 1990). The area covered by these outcrops varies from a few hundred square meters to several square kilometers.

The depth range varies from 6–10 m shallowest depth to about 35–40 m (Two-Mile Reef, Red Sands Reef). The average slope of the dune face is less than 5°. Flat dunes and deep beachrock outcrops (Four-Mile Reef, Kosi Reef) occur between 18 and 24 m; shallow beachrock platforms (Nine-Mile Reef) between 6 and 18 m with a steep drop-off between 12 and 18 m parallel to the shoreline.

The outcrops were separated into (1) higher-lying, largely sediment free areas, (2) shallow gullies and depressions with little resident sediment but high debris and sediment movement in heavy seas, and (3) deep gullies with large amounts of resident sediment.

The Maputaland coastline is exposed to open oceanic swells of the SW Indian Ocean. Tidal range is between 1 m at neaps and 2 m at spring tides (Schumann and Orren, 1980).

Results

Space Utilization, Diversity and Between-reef Differentiation.—Scleractinia occupied slightly more space than Alcyonacea (Table 1); together they dominated

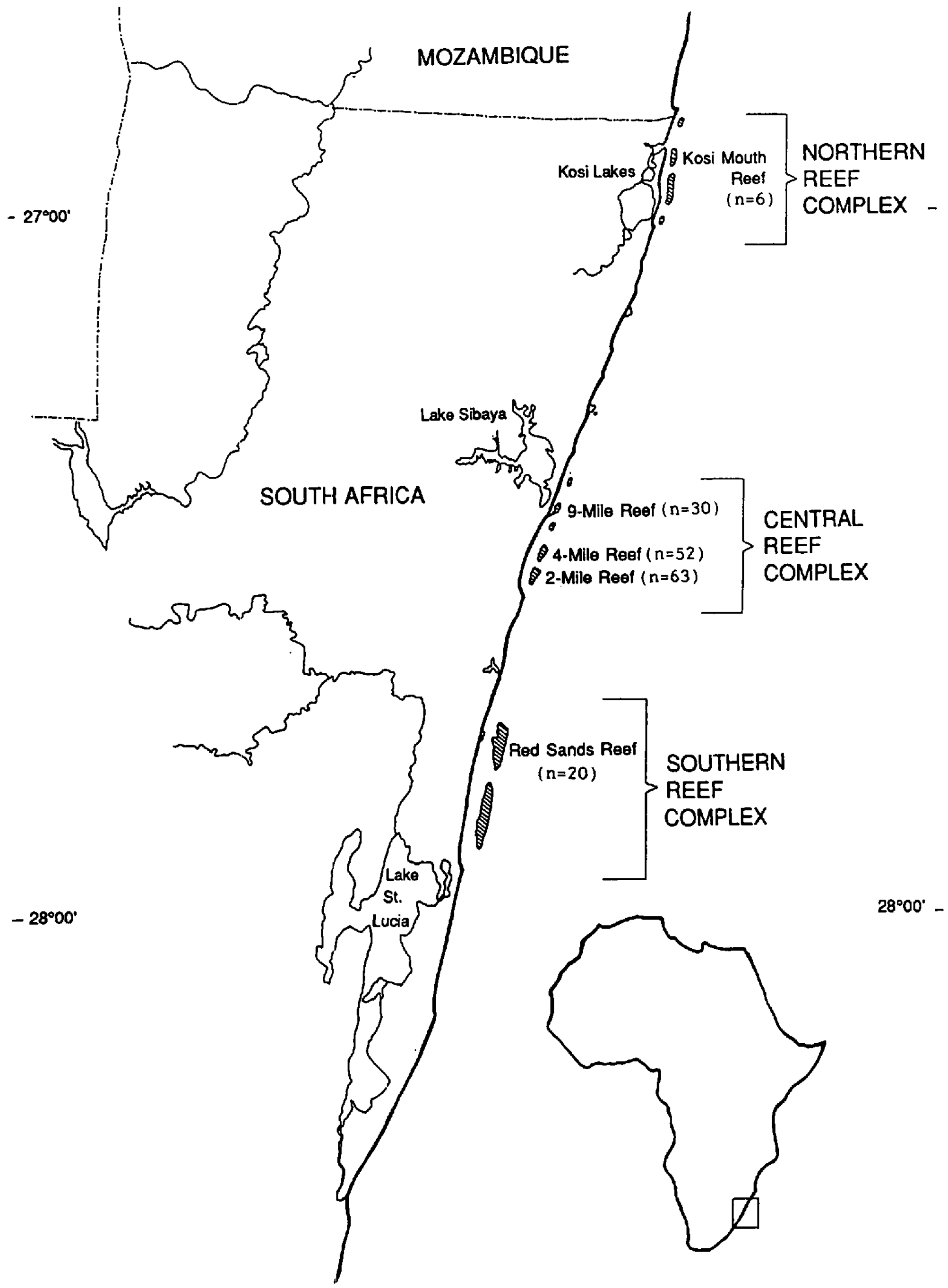

Figure 2. Location of the Maputaland reef complexes in northern Natal, South Africa. Community analysis was performed on selected reefs indicated by their local name. "n" is the number of transects taken on the reefs.

Table 1. Space utilisation by the major invertebrate categories on the Maputaland reef complexes expressed as percent share of total living animal coverage as calculated from intercepts on the line transects

	Total	Kosi	9-Mile	4-Mile	2-Mile	Red Sands
Alcyonacea	41.8 ± 7.8	35.3 ± 20.3	54.1 ± 27.9	34.8 ± 15.9	43.1 ± 23.2	41.7 ± 18.1
Scleractinia	50.5 ± 11.5	62.1 ± 19.2	38.6 ± 24.1	63.4 ± 17.1	45.1 ± 21.3	43.2 ± 16.5
Sponges	5.7 ± 4.8	0.08 ± 1.60	5.6 ± 11.1	1.7 ± 2.9	10.0 ± 17.9	10.9 ± 14.0
Ascidians	3.7 ± 3.9	1.7 ± 2.8	1.9 ± 6.6	0.03 ± 0.2	2.1 ± 4.5	3.7 ± 6.5
Total cover	57.4 ± 14.8	76.3 ± 8.1	53.6 ± 19.6	67.9 ± 20.8	50.3 ± 22.6	38.9 ± 13.2

most benthic communities. Among the scleractinia the Acroporidae covered most space overall (16.2%), followed by the Faviidae (13.8% of total scleractinian coverage, Table 2). Among the soft-corals *Lobophytum* (20.6%) and *Sinularia* (16.3%) were dominant (Table 2).

Correspondence analysis of all transects showed a clear differentiation into two groups which showed considerable overlap (Fig. 3).

A clear tendency for separation of transects obtained from deep, flat reefs between 18 and 24 m (Four-Mile Reef, Kosi Mouth Reef) and reefs with a greater depth gradient from 6 to 34 m (Red Sands Reef, Two-Mile Reef, Nine-Mile Reef) was apparent.

The horizontal axis 1 represented the ratio of scleractinian to alcyonacean coverage (scleractinian dominance on the negative axis, alcyonacean dominance on the positive axis), axis 2 represented the non-coral component (e.g., increasing sponge, ascidian and sea-fan coverage along the positive axis). Reefs separated well along these axes (Fig. 3), which is also illustrated by Tables 1 and 2.

The most diverse coral community was encountered on Four-Mile Reef ($H' = 2.24 \pm 0.36$) followed by Red Sands Reef ($H' = 2.14 \pm 0.25$) and Kosi Bay Reef ($H' = 2.11 \pm 0.36$). The least diverse communities were found on Two-Mile and Nine-Mile Reefs ($H' = 2.01 \pm 0.36$, $H' = 2.01 \pm 0.33$ respectively). Diversity differences between the reefs were significant (ANOVA, $F = 4.13$, df: 4, 165, $P = 0.032$).

As reef type appeared to be an important differentiation factor for community structure, one representative area for each reef type was sampled in detail in the Central Reef Complex and evaluated separately.

Within-community Differentiation—the Deep Outcrops.—Representative areas for this substratum type were sampled at Four-Mile Reef.

Scleractinians of the genera *Acropora* and *Montipora* were dominant (Tables 1, 2).

Classification of transects gave four distinct groups (Fig. 4). The dominant

Table 2. Space utilisation by the major scleractinian and alcyonacean families and genera on the Maputaland reef complexes expressed as percent share in total living coverage calculated from intercepts on the line transects

	Total	Kosi	9-Mile	4-Mile	2-Mile	Red Sands
Acropora	35.1%	9.9%	25.2%	25.2%	6.2%	4.9%
Montipora	5.8%	3.5%	7.6%	7.6%	9.7%	2.6%
Faviidae	9.2%	15.4%	15.1%	15.1%	12.1%	17.2%
Sinularia	5.3%	25.8%	11.8%	11.8%	27.7%	11.1%
Lobophytum	27.7%	23.3%	13.6%	13.6%	16.7%	21.8%

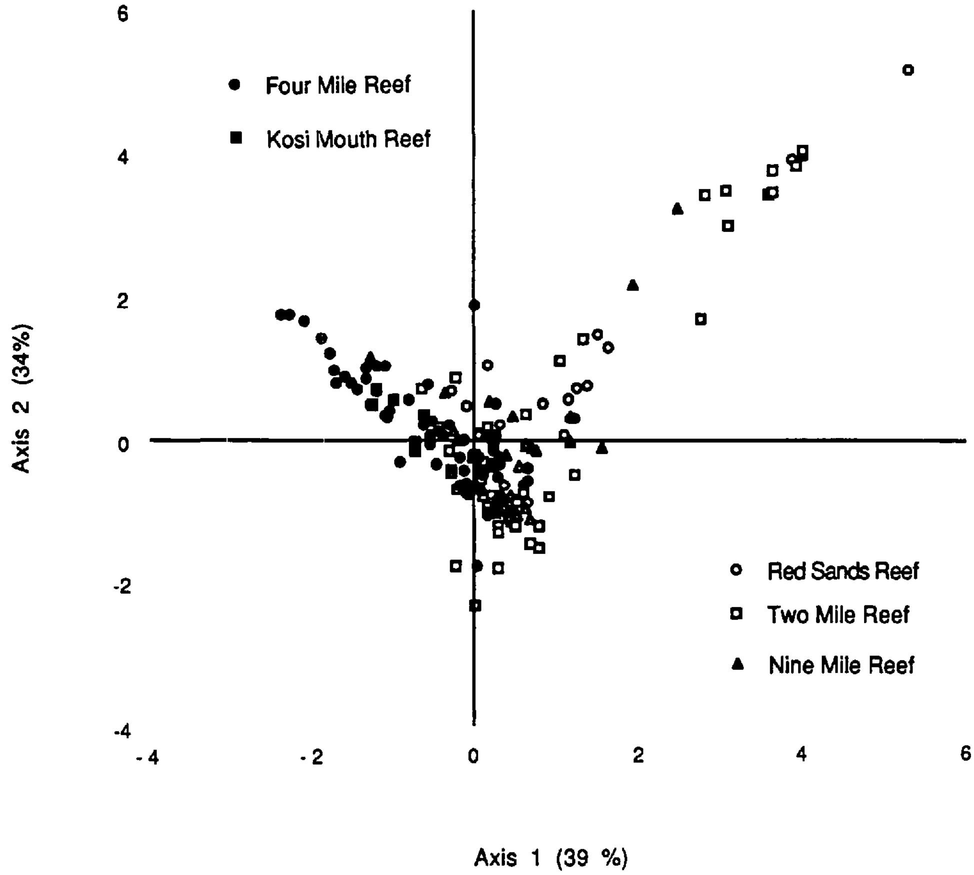

Figure 3. Ordination by correspondence analysis of all transects obtained from five reef sites in Northern Natal. Two distinct clusters are formed, suggesting two different community types.

species as well as the species responsible for the separation of clusters are given in Table 3. No species could be counted as a "perfect indicator," i.e., being exclusive to only one cluster (Field et al., 1982). Ordination by MDS (Fig. 5) gave essentially the same results as the classification.

Superimposing environmental variables onto the ordination plot (Fig. 6a–e) illustrated the most important substratum and environmental factors.

Group A was dominated by scleractinians. The dominant corals were *Acropora clathrata* forming solid, tabular or vasiform plates of up to 1.5-m diameter, and *Acropora austera* with an open arborescent branching pattern, forming monospecific thickets up to several meters in diameter. The horizontal projection of the platelike *A. clathrata* colonies on the transect line frequently formed a canopy over adjacent colonies thus creating areas of greater than 100% surface cover. Group A comprised transects from horizontal, flat parts of the reef (Fig. 6d) with high coral coverage (Table 3, Fig. 6a–e), low diversity and evenness and high dominance (Table 4), which gave a clear picture of the importance of the dominant species.

Group B showed mixed dominance by alcyonaceans and scleractinians, with alcyonaceans being slightly more important (genera *Sarcophytum, Lobophyton,*

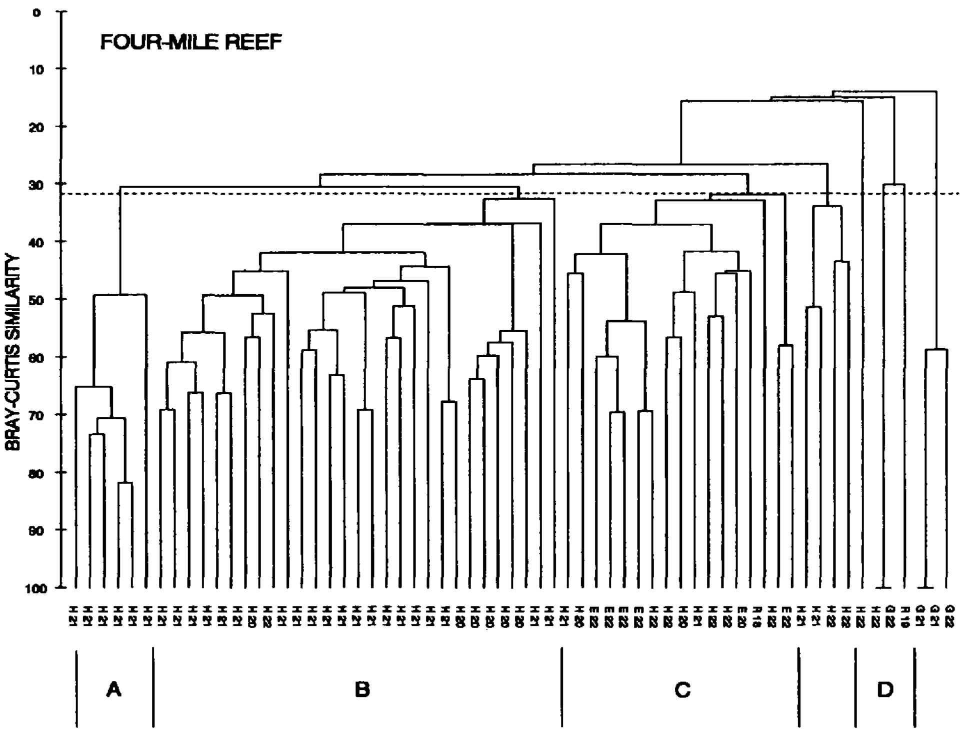

Figure 4. Differentiation of the coral community on the deep outcrops (Four-Mile Reef) as obtained by classification of quantitative data of all transects. Four main groups (A–D) were distinguished at an arbitrary similarity level of 31% (y-axis). Species responsible for within-group similarity and between-group dissimilarity are given in Table 4. Transects are coded, characterizing their position on the reef. H = flat, horizontal area, G = gully, E = gully-edge, R = ridge, the number stands for depth in meters (H22: transect from horizontal area, 22-m depth).

Sinularia). Of all groups, B and A were the most similar (average dissimilarity = 69.8%), and shared one of the indicator species, the scleractinian *A. austera* (Table 3). Group B was also a community of the flat, horizontal parts of the reef (Fig. 6d) with high coral cover, diversity and evenness, coupled with low dominance (Table 4), which indicated a very heterogeneous community.

Group C was more scleractinian dominated than any other cluster, some of its scleractinian indicators being uncommon or absent in all the other samples (e.g., *Montipora danae, M. tuberculosa,* Table 3). There was still a strong alcyonacean component (*Lobophytum venustum, Sinularia*). This community was restricted to the periphery of flat, horizontal areas of the reef and gully edges (Fig. 6d), with less coral coverage than the other groups. It was the most diverse group with highest evenness and lowest dominance (Table 4).

Group D was strongly alcyonacean dominated (Table 3). It was from the flat, horizontal areas of the reef (Fig. 6d) with high coral coverage, high diversity and evenness coupled with low dominance (Table 4).

The remaining transects, which did not fall within any distinct cluster, were all situated in gullies. They are loosely referred to as a "gully-subcommunity." They had the highest dissimilarity to all other groups and were also dissimilar to one another. All of them had low coral coverage ($\bar{x}$ = 21.3 ± 7.4%, Fig. 6a), little

Table 3. Species causing within group similarity and between group dissimilarity in the coral community on Four-Mile Reef. Species are listed in descending order according to their contribution to average Bray-Curtis similarity within groups or dissimilarity between groups. The numbers are cumulative values for contribution to average Bray-Curtis similarity or dissimilarity.

Four-Mile Reef			
Group A		Differences between groups A & B	
1) *Acropora clathrata*	22.2%	1) *Stereonephthya* sp.	6.1%
2) *Acropora austera*	40.2%	2) *Oulophyllia crispa*	11.4%
3) *Stereonephthya* sp.	53.8%	3) *Sarcophyton* spp.	16.4%
4) *Oulophyllia crispa*	66.2%	4) *Acropora clathrata*	21.4%
5) *Lobophytum* sp. 4	76.3%	5) *Acropora tenuis*	25.5%
Group B		Differences between groups B & C	
1) *Sarcophyton* spp.	17.5%	1) *Acropora tenuis*	3.6%
2) *Lobophytum venustum*	27.3%	2) *Acropora austera*	7.3%
3) *Acropora tenuis*	34.9%	3) *Sarcophyton* spp.	10.8%
4) *Acropora clathrata*	42.2%	4) *Favites pentagona*	14.3%
5) *Sinularia gyrosa*	49.4%	5) *Acropora clathrata*	17.6%
Group C		Differences between groups A & C	
1) *Favites pentagona*	11.4%	1) *Acropora austera*	6.2%
2) *Lobophytum venustum*	20.5%	2) *Stereonephthya* sp.	11.1%
3) *Montipora danae*	27.4%	3) *Acropora clathrata*	15.6%
4) *Montipora tuberculosa*	33.7%	4) *Favites pentagona*	19.6%
5) *Sinularia gyrosa*	39.7%	5) *Lobophytum* sp. 4	23.5%
Group D		Differences between groups A & D	
1) *Lobophytum patulum*	18.3%	1) *Acropora austera*	7.7%
2) *Sarcophyton* spp.	35.9%	2) *Acropora clathrata*	12.9%
3) *Lobophytum* sp. 4	47.6%	3) *Stereonephthya* sp.	18.6%
4) *Lobophytum depressum*	56.4%	4) *Oulophyllia crispa*	22.8%
5) *Echinophyllia aspera*	64.6%	5) *Sarcophyton* spp.	26.9%
Differences between groups B & D		Difference between groups C & D	
1) *Lobophytum venustum*	4.1%	1) *Lobophytum patulum*	4.5%
2) *Lobophytum patulum*	7.9%	2) *Lobophytum* sp. 4	8.9%
3) *Lobophytum* sp. 4	11.7%	3) *Lobophytum venustum*	12.7%
4) *Acropora tenuis*	15.4%	4) *Montipora danae*	15.9%
5) *Acropora austera*	19.1%	5) *Sarcophyton* spp.	19.1%

free rock ($\bar{x}$ = 13.3 ± 8.81%, Fig. 6b), but high percentages of sand cover ($\bar{x}$ = 63.5 ± 17.84, Fig. 6c).

All the mentioned subcommunities occupied the same depth range (between 18 and 24 m). Depth therefore had no influence on coral community differentiation (Fig. 6e).

The subcommunities tended to intergrade to a certain extent, with the "gully subcommunity" being particularly ill-defined. Nevertheless, a typical pattern of *Acropora* dominated flat parts (either by branching *A. austera* or tabular *A. clathrata*), which intergraded with *Sarcophyton* dominated areas and markedly different edge and gully areas, dominated by *Montipora* and *Lobophytum*, emerged.

Within-community Differentiation—the Fossil Dunes.—While the deep outcrops generally lacked a depth stratification, this was not the case on the large fossil dunes, which were sampled at Two-Mile Reef.

The clusters shown in the dendrograms in Figure 7 and the MDS plot in Figure 8 were identical. Dominant species in each cluster and species responsible for the differentiation of clusters are given in Table 5.

The subcommunity in cluster A was characterized by sponges, sea fans of the

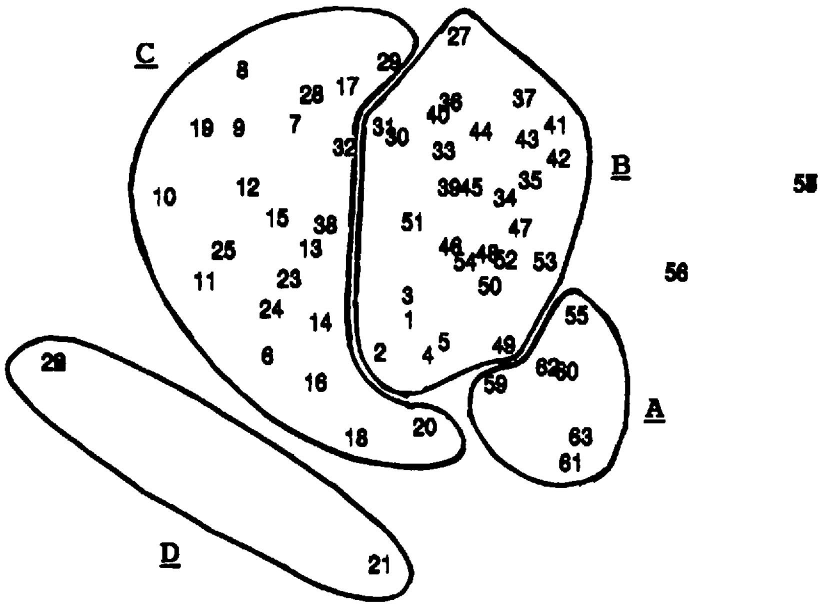

Figure 5. Ordination of the Four-Mile Reef transects in two dimensions using multi-dimensional scaling on the same similarity matrix as Figure 4. The groups obtained by the dendrogram were superimposed onto the ordination plot by encircling each cluster of transects.

genus *Acabaria* and various ascidians. Sponges were the dominant community members, occupying 20–70% of the total living coverage. Living cover in each transect was generally very low (18–28%) as was diversity and evenness, but dominance was high (Table 6). This subcommunity was typically only found in depths greater than 25 m (Fig. 9e). Some scleractinians, such as *Podabacia crustacea* and *Diaseris distorta,* were only recorded in this subcommunity. Other typical corals of the deep association were *Coscinaraea monile* and *Oulophyllia crispa.* Sea fans of the genus *Acabaria* as well as whip corals (*Ellisellidae* sp.) were common.

In depths less than 20 m the coral community followed the differentiation of the substratum into flat areas and gullies as could be seen in the overlay of substratum characteristics over the MDS plot (Fig. 9). Cluster A comprised only transects from flat horizontal, deep areas with uniform, moderate percentage of sand on the substratum. Clusters B and C were from the shallower areas of the reefs, with less uniform percentage of sand but higher living coverage (Fig. 9a–e).

Cluster B was dominated by alcyonarians (*Sinularia leptoclados, S. dura, Lobophytum venustum* and *L. patulum*). Overall, *Sinularia* was the dominant genus. Space utilization by scleractinians and alcyonaceans did not differ significantly (t-test, $P < 0.05$) and total living coverage was relatively low (Table 6). Diversity and evenness were the highest of the three transects groupings, dominance was the lowest (Table 6).

Cluster C comprised transects from gullies and gully-edges (Fig. 9d). Average Bray-Curtis similarity within the group was 31.5%. Scleractinians occupied significantly more space than alcyonaceans (t-test, $P < 0.05$), a clear dominance, however, was not observed. The dominant species were the alcyonaceans *Lo-*

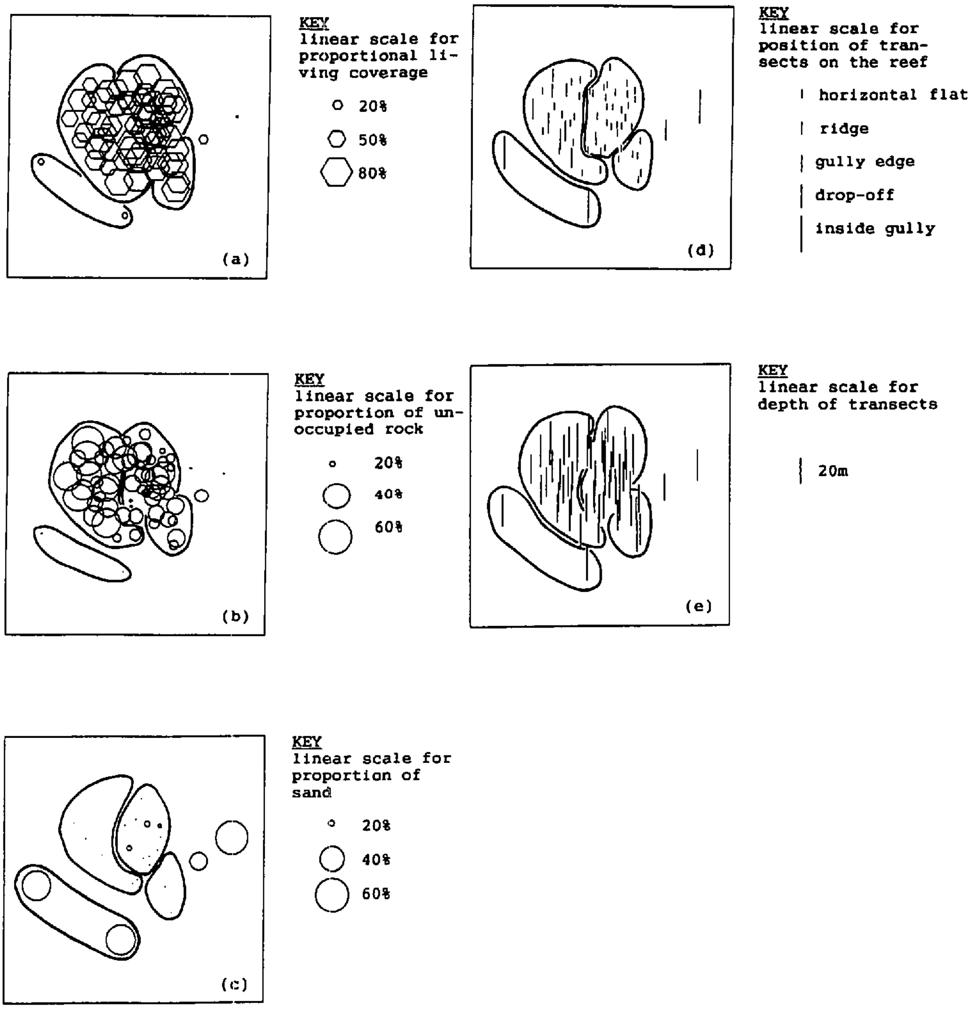

Figure 6. Relation of transect groups to general community and substrate characteristics. The clusters in the MDS plots are the same as in Figure 5. At each sample point a) the hexagons are proportional in diameter to average coral coverage. b) Circles proportional in diameter to the proportion of unoccupied hard substratum. c) Circle diameter proportional to the proportion of sand in each transect. d) Relation of groups to topography: Each line length symbolizes a particular geomorphological area from which the samples were taken. e) line lengths indicate the depth of each sample.

bophytum patulum, L. depressum and *Sinularia dura* and the scleractinians *Favites pentagona* and *Montipora tuberculosa.* All these species were also typical in the "gully-cluster" on Four-Mile Reef. The group was characterized by relatively low coral coverage and the highest percentage of sand in any subcommunity on Two-Mile Reef (Table 6, Fig. 9c). Within sandy gullies corals were limited to the often strongly sloping or near vertical walls or to hard substratum projecting above the sand. Diversity and evenness were high, dominance low (Table 6).

The coral community was thus divisible in shallow areas (6–25 m) into a "reef-top subcommunity" (dominated by alcyonaceans of the genera *Sinularia* and *Lobophytum*) a gully-subcommunity (dominated by alcyonaceans of the genus *Lobophytum* and scleractinia of the genera *Montipora* and *Favites*) and a "deep-reef

Table 4. Summary statistics characterizing the clusters obtained in Figure 3 (values are mean and standard deviation)

	Four-Mile Reef			
	Group A	Group B	Group C	Group D
Diversity	1.69 ± 0.22	2.29 ± 0.22	2.49 ± 0.19	2.30 ± 0.12
Evenness	0.39 ± 0.05	0.53 ± 0.04	0.57 ± 0.04	0.53 ± 0.02
Dominance	0.25 ± 0.08	0.13 ± 0.03	0.10 ± 0.02	0.12 ± 0.03
% Scleractinia	63.2 ± 9.41	60.7 ± 16.1	66.5 ± 16.9	56.2 ± 5.85
% Alcyonaria	27.6 ± 8.38	37.4 ± 15.1	32.3 ± 315.5	43.7 ± 5.85
% Porifera	9.2 ± 10.7	1.88 ± 2.98	1.33 ± 2.19	0
% Others	0	0	0	0
% Total living cover	79.9 ± 6.96	77.5 ± 11.5	65.8 ± 12.7	66.2 ± 14.9
% Rock	20.1 ± 6.69	22.1 ± 10.9	31.7 ± 15.4	31.3 ± 10.6
% Sand	0	0.36 ± 1.84	2.52 ± 9.76	0

subcommunity" in depths greater than 25 m (dominated by sponges, ascidians and sea-fans). The "*Sinularia-Lobophytum* reef-top" subcommunity and the gully subcommunity shared the same depth range (8–14 m) with the latter occupying less space due to its confinement to gullies.

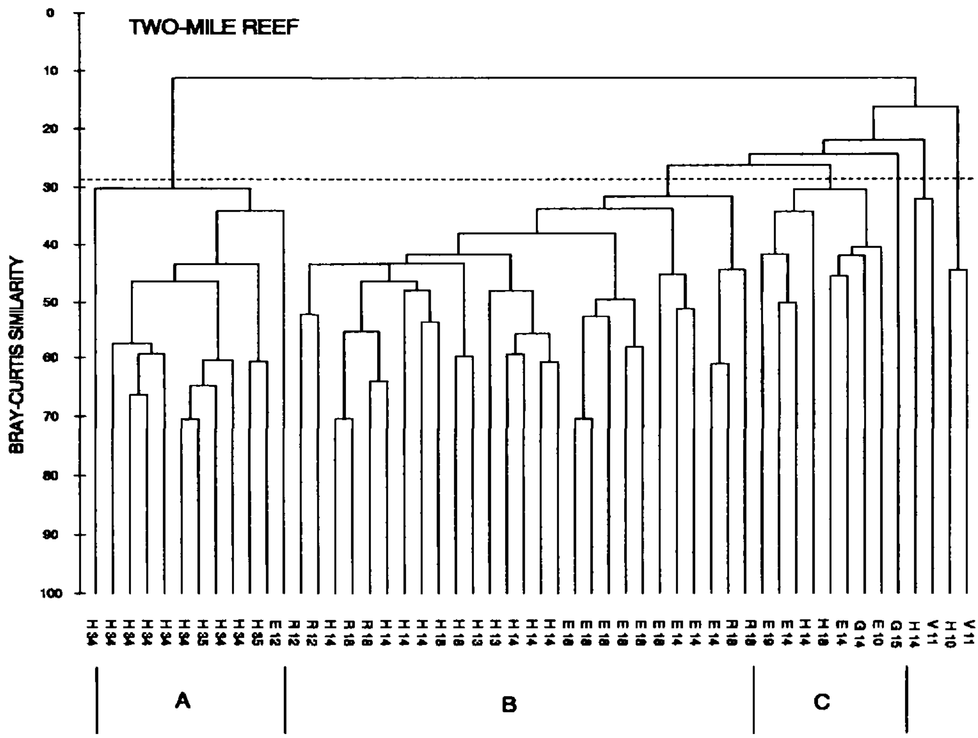

Figure 7. Differentiation of the coral community on a typical fossil dune (Two-Mile Reef) in the Central Reef Complex, as obtained by classification of root-root transformed intercept data. Clustering algorithm was the same as in Figure 4. At an arbitrarily chosen distance of 29% similarity four main groups were distinguished, three of which were well grouped together and one very dissimilar to all others. Species responsible for within-group similarity and between-group dissimilarity are given in Table 5. Transects are coded to characterize their position on the reefs; R = Ridge, G = Gully, E = Edge, H = flat, horizontal area, the number gives the depth in meters.

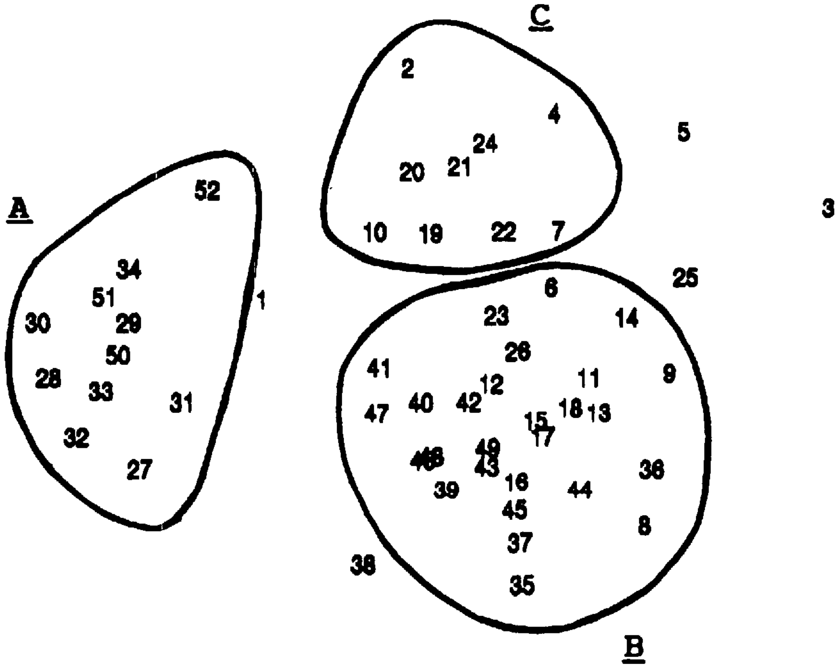

Figure 8. Ordination of the Two-Mile Reef transects in two dimensions using multi-dimensional scaling on the same similarity matrix as Figure 7. The groups obtained by the dendrogram were superimposed onto the ordination plot by encircling each cluster of stations.

Table 5. Species causing within-group similarity and between-group dissimilarity in the coral community on Two-Mile Reef. Species are listed in descending order according to their contribution to average Bray-Curtis similarity within groups or dissimilarity between groups (numbers are cumulative values for contribution to average Bray-Curtis similarity or dissimilarity)

Two-Mile Reef			
Group A		Differences between groups A & B	
1) Sponges	36.4%	1) *Sinularia* sp. 2	6.4%
2) Gorgonians	51.4%	2) Sponges	11.5%
3) Ascidians	62.5%	3) *Lobophytum venustum*	16.3%
4) *Podabacia crustacea*	72.2%	4) *Sinularia leptoclados*	20.8%
5) *Coscinaraea monile*	84.3%	5) *Sinularia dura*	24.5%
Group B		Differences between groups B & C	
1) *Sinularia gyrosa*	19.1%	1) *Montipora tuberculosa*	4.4%
2) *Lobophytum venustum*	30.1%	2) *Sinularia gyrosa*	8.7%
3) *Sinularia leptoclados*	46.7%	3) *Sinularia leptoclados*	12.8%
4) *Sinularia dura*	46.7%	4) *Lobophytum venustum*	16.5%
5) *Sarcophyton* spp.	54.4%	5) *Acropora clathrata*	20.2%
Group C		Differences between groups A & C	
1) *Lobophytum depressum*	16.4%	1) Sponges	6.1%
2) *Favites pentagona*	30.1%	2) *Montipora tuberculosa*	11.5%
3) *Montipora tuberculosa*	43.2%	3) *Lobophytum depressum*	15.8%
4) *Sinularia gyrosa*	50.2%	4) *Sinularia gyrosa*	19.8%
5) *Favia favus*	56.8%	5) Gorgonians	23.3%

Table 6. Summary statistics characterizing the clusters obtained in Figure 6 (values are mean and standard deviation)

	Two-Mile Reef		
	Group A	Group B	Group C
Diversity	1.59 ± 0.35	2.13 ± 0.26	1.51 ± 0.19
Evenness	0.37 ± 0.08	0.49 ± 0.05	0.35 ± 0.04
Dominance	0.34 ± 0.12	0.16 ± 0.05	0.28 ± 0.07
% Scleractinia	40.5 ± 24.8	55.3 ± 17.7	33.3 ± 4.90
% Alcyonaria	14.3 ± 8.44	44.4 ± 18.1	28.0 ∓ 30.8
% Porifera	36.5 ± 21.7	0	26.3 ± 22.9
% Others	7.6 ± 6.87	0.28 ± 0.75	12.3 ± 18.0
% Total living cover	23.4 ± 15.6	55.6 ± 15.6	43.6 ± 9.71
% Rock	59.6 ± 13.9	32.5 ± 9.33	56.3 ± 9.71
% Sand	17.5 ± 10.1	16.9 ± 22.6	0

General Community Characteristics.—The overlay plots on the MDS ordinations (Figs. 6, 9) showed that the substratum characteristics with the strongest influence on community structure were (a) the location of the samples (whether they were on flat areas or in gullies) and (b) depth. Proportion of sand within the community was generally closely linked to the location of the samples, being highest in the gullies.

A significant, negative relationship existed between percentage of sand in a community and its diversity ($r = -0.77$, $P < 0.05$) and evenness ($r = -0.77$, $P < 0.05$, Fig. 10a). A positive but insignificant relationship existed between the dominance index and percentage of sand in the communities ($r = 0.47$, $P = 0.07$, Fig. 10b).

Sedimentation was linked to percentage of sand in the community, as resident sediment was resuspended during storms and settled in the same area. Maximum measured sedimentation levels in the gullies were 1.8 $kg{\cdot}m^{-2}{\cdot}h^{-1}$ in gullies and 0.7 $kg{\cdot}m^{-2}{\cdot}h^{-1}$ on the elevated parts. Maximum measured levels of sediment suspended in the watercolumn was 0.4 $g{\cdot}liter^{-1}$ in the gullies and 0.1 $g{\cdot}liter^{-1}$ on the elevated parts. Both sedimentation rates and levels of suspended sediment in the watercolumn were significantly higher in the gullies than on the elevated parts of the substratum (t-tests, $P < 0.001$, $P < 0.05$).

Diversity was significantly lower in the grouping 9–18 m than in 18–25 m. It then declined significantly again on the deep reef community, 18–35 m (ANOVA, $F = 6.27$, df: 3, 50, $P = 0.001$).

Discussion

The geomorphology of South African reef systems is different from the usual situation on most other coral reefs (Fig. 11). As the substratum underlying the coral communities in South Africa is not that of a typical coral reef, most of the morphological features found on true coral reefs are missing. South African reefs are very flat and offer a relatively uniform environment as changes in depth occur along a mild gradient. Over wide areas the substratum is not structurally complex. Despite this, the results of the present study showed clearly that there are distinct communities on different reefs and in different zones.

Differentiation occurred along a depth- and sedimentation gradient. Sedimentation is linked to depth and water motion, as surge can resuspend sediment. Almost all the sedimentation observed within the Central and Southern Reef Complexes was caused by resuspension of resident, biogenic sediments as there are

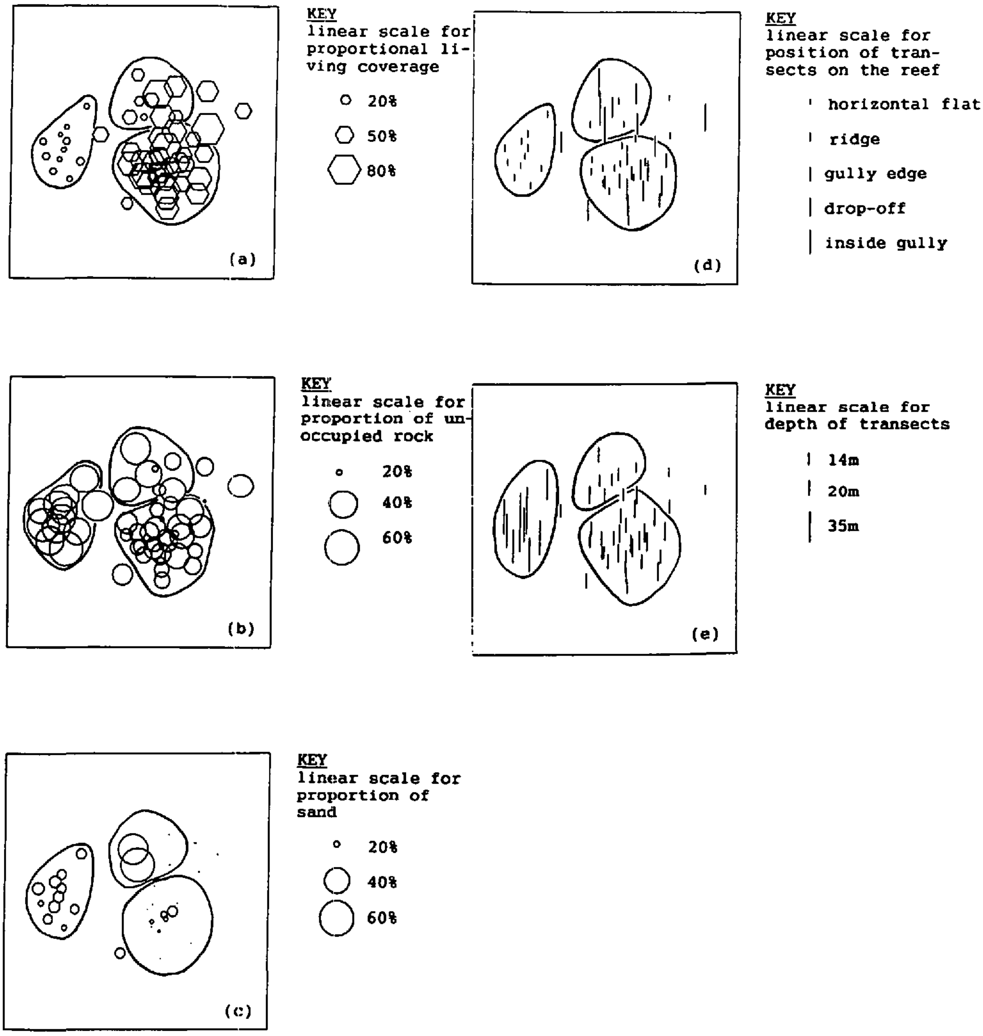

Figure 9. Relation of transect groups to general community and substrate characteristics. The clusters in the MDS plots are the same as in Figure 8. At each sample point a) the hexagons are proportional in diameter to average coral coverage. b) Circles proportional in diameter to the proportion of unoccupied hard substratum. c) Circle diameter proportional to the proportion of sand in each transect. d) Relation of groups to topography: Each line length symbolizes a particular geomorphological area from which the samples were taken. e) Line lengths indicate the depth of each sample.

no rivers importing any allochthonous sediments in this region. Strong sedimentation was not observed on the elevated parts of the reefs, where hardly any resident sediment was found. It was concentrated within the gullies, where water movement was channelled and able to resuspend the sand accumulated within these depressions.

Therefore, different coral communities existed in areas of high and low sedimentation (e.g., gullies versus high-lying, flat areas and ridges; Fig. 2). Low sedimentation "reef-top sub-communities" were always dominated by alcyonaceans (primarily *Lobophyton* and *Sinularia*), while the high sedimentation "gully sub-communities" were mostly scleractinian dominated. It is likely that the ob-

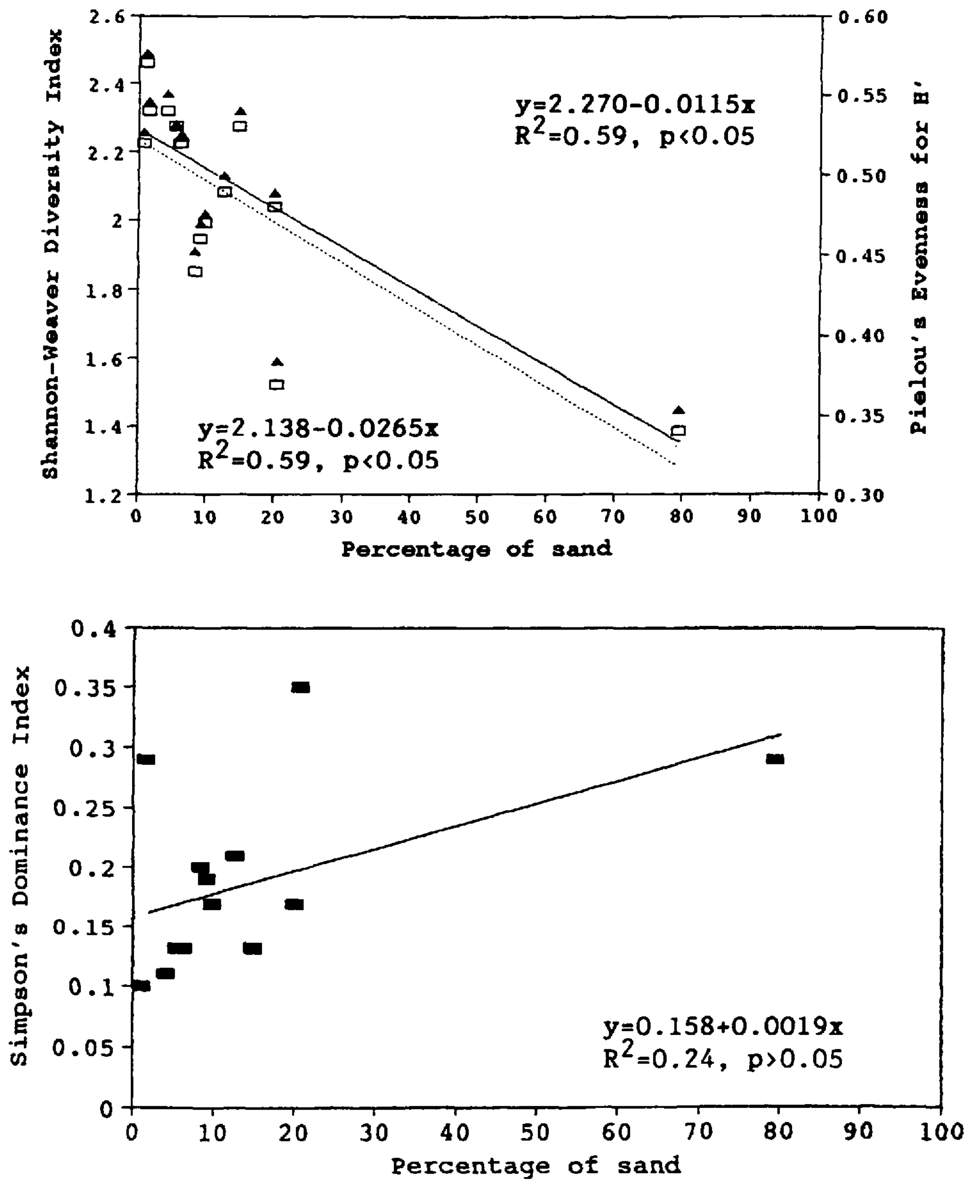

Figure 10. a, b. Correlation between the percentage of sand in the substratum within the subcommunities on all reefs and a) Shannon-Weaver diversity and evenness (dotted line and open squares: diversity, solid line and full triangles: evenness), b) Simpson's dominance index.

served preference of soft-corals for elevated areas with comparatively little sedimentation was due to them being unable to cope with long-term sedimentation. The lower diversity in gullies and areas subjected to high sedimentation suggested that only a limited number of species are able to cope with such conditions. Similar suggestions have been made by Dai (1991) to explain coral community structure in Taiwan.

Except on the deep reef, where corals did not dominate the community, light

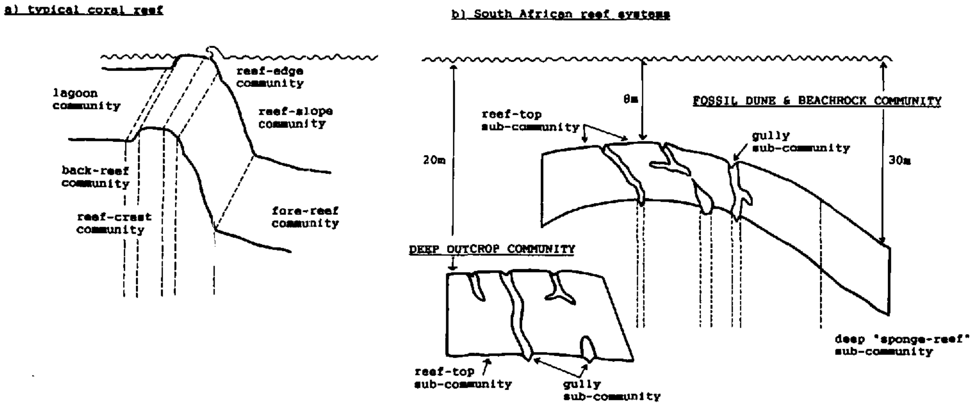

Figure 11. Idealized diagrams illustrating the main differences between South African reef systems and typical coral reefs. Depths are not to scale. The community differentiation in Figure a) is a generalization condensed from literature (Loya, 1972; Sheppard, 1982; Done, 1982; Riegl and Velimirov, in press).

levels did not have a significant influence on coral communities. Coral coverage and average colony size were higher at around 20 m depth than in shallower areas. Beyond 25 m, however, coral cover rapidly dropped to give way to dominance by non-photosynthetic organisms, like sponges, ascidians and sea-fans.

In other coral reef areas, like the Great Barrier Reef (Potts et al., 1985) and the Red Sea (Riegl and Velimirov, in press) coral size often increases up to a certain depth ("deep water gigantism," Hughes, 1984). One of the reasons why colony size increases in deeper water could be the relatively greater shelter from surge. This may also explain the distribution of the scleractinian genus *Acropora* on South African reefs. The only areas in which they dominated were in depths greater than 20 m. There, *Acropora austera* formed large, open arborescent colonies and the tabular *A. clathrata* dominated wide areas of reef. It is likely that these species are unable to survive on the shallower reefs as their shape would induce high drag and cause structural failure in high surge (Vogel, 1981). The dominant corals in the shallow areas were therefore massive (e.g., Faviidae), low branching (Pocilloporidae) or leathery (alcyonaceans).

According to Daï (1991), alcyonaceans suffer more damage in stormy seas than scleractinians in Taiwan. A similar situation was not observed in South Africa, where alcyonaceans dominated the very areas subjected to highest surge.

Some of the observed subcommunities coexisted within the same depth range and a fair amount of overlap occurred. The relative uniformity of the reef's bathymetry caused each community type to be repeatedly realized within its depth zone. Both in the shallow and the deep areas it was very apparent that gullies with "gully-subcommunities" repeatedly alternated with elevated parts of the substratum supporting "top-subcommunities."

Conclusion

South African coral communities are made up of typically Indo-Pacific coral species but do not form typical coral reefs and differentiate along gradients of water motion, sedimentation and light. Alcyonaceans dominated the areas of low sedimentation on the shallow reefs, while scleractinians with mostly massive growth form dominated the gullies, e.g., areas of high sedimentation. Branching and tabular scleractinia were dominant only on the deep reefs (around 20 m) where less surge was encountered. In the deepest areas of the reefs (>25 m) corals were rare, excluded by lack of light. The deep communities were dominated by sponges, sea fans and ascidians.

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