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The Structure of Coral Communities at Hurghada in the Northern Red Sea

BERNHARD RIEGL & BRANKO VELIMIROV

Institut für Allgemeine Biologie, Währingerstr.17, 1090 Wien, Austria.

With 8 figures and 3 tables

Key words: Coral community structure, Red Sea, *Scleractinia*, coral reef, diversity.

Abstract. The community structure of hard and soft corals, with an emphasis on hard corals, was determined by means of line-transects on 9 on- and off-shore reefs of different type and different wave exposure in the Northern Red Sea near Hurghada in Egypt. Coral communities were found to differentiate along a horizontal wind- and wave-exposure gradient. Exposed communities were dominated by *Acropora* species, sheltered communities by *Porites* species, and semi-exposed communities by *Millepora* species. Also, vertical within-reef zonations following a depth gradient were observed; these were unique for each exposure-determined community type. Average transect diversity was highest on semi-exposed reefs, lowest on sheltered reefs. Reef slopes were more diverse than other reef zones. The observed community structure was compared with data from the literature, and widely distributed, roughly comparable hard and soft coral communities were identified.

Problem

Most recent studies of Red Sea reef systems were made in the northern Gulf of Aqaba and the central part of the Red Sea, in the latter area concentrating on reefs in Sudan and Saudi-Arabia (LOYA, 1972; MERGNER & SCHUHMACHER, 1974, 1985 a,b; SCHUHMACHER & MERGNER 1985; MONTAGGIONI *et al.*, 1986; HEAD, 1987; SHEPPARD & SHEPPARD, 1991). The two regions are geographically distant and therefore climatic differences exist (EDWARDS, 1987; SCHUHMACHER & MERGNER, 1985). While the climatic and oceanographic conditions in the Gulf of Aqaba are characterized by extreme temperature variations from winter to summer, coupled with a changeable wind regime, the central Red Sea has a more constant climate, and the water body has a more constant temperature (EDWARDS, 1987).

Comparisons of reefs in different Red Sea localities yielded varying results. MERGNER & SCHUHMACHER (1985 a,b) and SCHUHMACHER & MERGNER (1985) compared Gulf of Aquaba's coral communities with central Red Sea coral communities in Sudan and found differences in average coral size and in species diversity, both being greater in the central Red Sea. SHEPPARD & SHEPPARD (1991) and SHEPPARD *et al.* (1992) compared reefs along the Arabian Red Sea coast and described 13 communities from different reef environments which diversified along

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a north-south gradient. Their results indicate that certain community types can always be found in specific environments.

As only very little quantitative information is available on coral communities along the African coast between the northern gulfs and the central Red Sea (KLEEMANN, 1992), we tested whether communities similar to those reported as being widespread on the Arabian side by SHEPPARD & SHEPPARD (1991) and SHEPPARD *et al.* (1992) can be found in this region. We also investigated similarities to communities described from other parts of the Indo-Pacific.

The present paper is a study on coral community structure on a number of shallow shelf reefs off Hurghada (Al Ghardaqa), Egypt. This area is considered to be a geological and climatic transition zone between the northern gulfs and the main basin of the Red Sea (ROBERTS, 1985; EDWARDS, 1987).

The aims of the study were 1) to determine coral cover and abundances as indicators of possible community differences on reefs with different exposure to wind and waves; 2) to examine whether zonation patterns can be defined and to quantify the importance of zone-determining species; 3) to estimate changes in species richness and diversity between zones. This approach should allow the detection of possible community differences between exposed and sheltered reefs, as well as between shallow and deep reef zones. It should also allow comparison with other described coral communities from the Red Sea and the Indo-Pacific Ocean.

Material and Methods

1. Sampling procedure and statistics

Data were collected using the line transect method (LOYA, 1978). The ideal transect length was previously tested by plotting the cumulative number of recorded coral species as a function of transect length. The species per area curve levelled off after 8 m to 10 m transect length. A 10 m transect length was therefore chosen.

A total of 137 transects were obtained from 9 localities. The transects were positioned parallel to each other and perpendicular to a vertical gradient along the reef extending from shoreward to seaward. The 10 m transects were repeated in 1 m depth intervals from the waterline to the fore reef area. Adequate replication was provided by repeated transect sampling in each depth and by pooling the data from reefs in similar exposure and of similar geomorphology. Three coverage types were recorded: coverage by hard corals, by soft corals, and the amount of bare substratum, *e.g.*, substratum uncolonized by any sessile macro-invertebrates or macro-algae. The intercept values of each of the coverage types on the transect rope were determined, as was the numerical frequency of coral colonies.

Hard corals were identified according to CHEVALIER (1971, 1975), VERON & PICHON (1976, 1982), VERON *et al.* (1977), WALLACE (1978), SCHEER & PILLAI (1983), and VERON & WALLACE (1984). Species of uncertain identity were sampled and compared to museum specimens or photographs of specimens from the collections of the Zoological Museum of the University of Tel Aviv, the Museum national d'histoire naturelle in Paris, the Institut für Paläontologie and the Institut für Allgemeine Biologie in Vienna. Soft corals were only identified to generic level.

For the analysis of horizontal and vertical zonation, a binary dataset along with a quantitative dataset of intercept values were used. In the latter, the variables were standardized by their standard deviation in order to achieve scale independence (DIGBY & KEMPTON, 1987). Data were subjected to agglomerative hierarchical cluster analysis using the Ward method of linkage with the City-Block (Manhattan) distance measure (DIGBY & KEMPTON, 1987). A critical distance of 15 was chosen for the designation of final clusters used in further analyses, as distances above or below this value did not yield interpretable clusters. Diversity was expressed as MARGALEF's index (MAGURRAN, 1988).

$$D \doteq (S-1)/\ln N$$

where N is the total number of individuals and S the total number of species.

The more frequently used SHANNON-WEAVER Index (LOYA, 1972; MERGNER & SCHUHMACHER, 1985 a,b; SCHUHMACHER & MERGNER, 1985) was not used in this study due to its sample-size dependence (SOTAERT & HEIP, 1990); this would have resulted in biased results due to the relatively small sample-size yielded by each transect. MARGALEF'S index is also easier to calculate and to understand (MAGURRAN, 1988; SOTAERT & HEIP, 1990).

2. Study area

Nine different reef localities ranging from the Straits of Gubal (Gulf of Suez) to Abu Hashish Island, south of the Egyptian town Hurghada (Al Ghardaqa), were sampled (Fig. 1). These reefs can be classified as patch reefs (locality: Patch Reefs, 20 transects), ridge reefs (GUILCHER, 1988; localities: Shaab el Erg, 12 transects, Shaab Rur umm Qamar, 12 transects), platform reefs (locality: Shaab Abu Rimathi, 15 transects), island fringing reefs (localities: Gubal saghir, 17 transects, Giftun saghir, 27 transects, Shaab

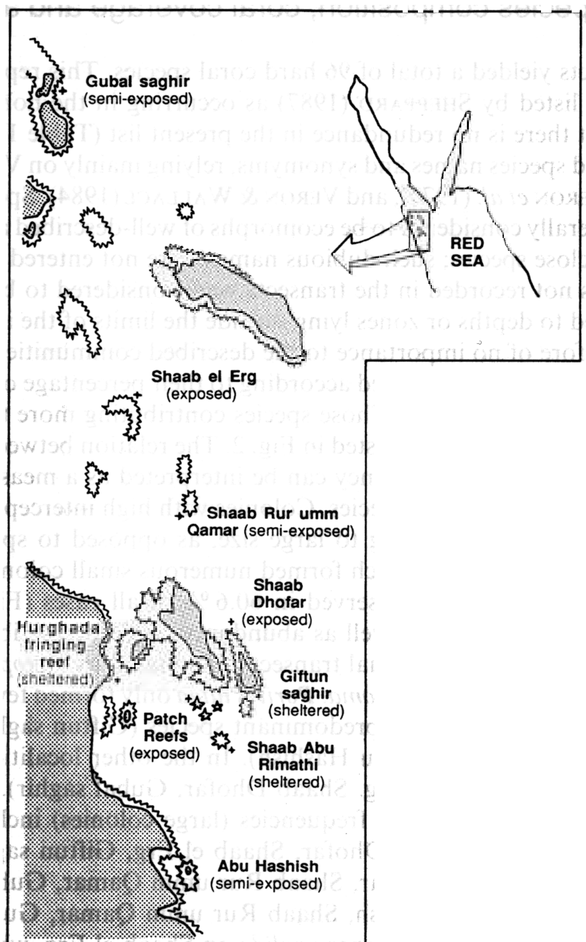


Fig. 1. The Northern Red Sea with the studied reefs. Locations of sample sites are indicated by a cross.

Dhofar, 11 transects, Abu Hashish, 12 transects) and mainland fringing reefs (locality: Hurghada fringing reef, 11 transects). The localities are situated on a N-S gradient roughly parallel to the shoreline. Only reef slopes and fore reef areas with comparable morphology were sampled.

The oceanographic and climatic conditions in the area are very constant (SHEPPARD *et al.*, 1992). Most of the year, winds blow from NW with an average speed of 10 knots (ROBERTS, 1985). In winter, eastward travelling depressions can cause winds to change direction to SE or S (EDWARDS, 1987). This very constant wind regime gives rise to a differentiation between exposed windward and mostly sheltered leeward reef sides (SCHUHMACHER & MERGNER, 1985; MERGNER & SCHUHMACHER, 1985 a,b).

Exposed coral communities were sampled at Shaab el Erg, the Patch Reefs, and Shaab Dhofar. Sheltered communities were sampled at Giftun saghir, Shaab Abu Rimathi, and the Hurghada fringing reef. Shaab Rur umm Qamar, Abu Hashish, and Gubal saghir are semi-exposed localities. These coral communities are largely sheltered from direct wind- and wave impact. The high current velocities encountered here could be expected to persist for most of the year due to the geological and oceanographic setting (ROBERTS, 1985).

Results

1 Species composition, coral coverage and abundance

The 137 transects yielded a total of 96 hard coral species. This represents 72 % of the 134 species listed by SHEPPARD (1987) as occurring in the northern Red Sea. We assume that there is no redundance in the present list (Table 1), as we tried to eliminate invalid species names and synomyms, relying mainly on VERON & PICHON (1976, 1982), VERON *et al.* (1977), and VERON & WALLACE (1984). Species of dubious status were generally considered to be ecomorphs of well-described and established, taxonomically close species; such dubious names were not entered into the species list. The species not recorded in the transects were considered to be rare, solitary, and/or restricted to depths or zones lying outside the limits of the investigated reef areas and therefore of no importance to the described communities.

In each locality, corals were listed according to their percentage of total recorded intercept and colony frequency. Those species contributing more than 5 % of the total value in either category are listed in Fig. 2. The relation between proportional intercept and proportional frequency can be interpreted as a measure of the size/frequency distribution of these species. Colonies with high intercept but low abundance were those species growing to large size, as opposed to species with high abundance but low intercept, which formed numerous small colonies. High intercept and low abundance was observed in 60.6 % of all cases (Fig. 2). Cases in which both highest intercept as well as abundance could be ascribed to the same species were observed for individual transects dominated by *Acropora hyacinthus*, *Porites lutea*, and *Millepora dichotoma*. *Porites lutea* only formed few large colonies in the localities where it was the predominant species (Giftun saghir, Shaab Abu Rimathi, to a lesser extent at Abu Hashish). In the other localities, it tended to form small colonies (Shaab el Erg, Shaab Dhofar, Gubal saghir). Species whose intercepts were higher than their frequencies (large colonies) included *Acropora hyacinthus* (Patch Reefs, Shaab Dhofar, Shaab el Erg, Giftun saghir), *Acropora valida* (Patch Reefs, Shaab Dhofar, Shaab Rur umm Qamar, Gubal saghir), and *Millepora dichotoma* (Abu Hashish, Shaab Rur umm Qamar, Gubal saghir). An exception was the hard coral *Acropora valida* on Shaab el Erg, where it was very frequent but formed small colonies.

Table 1. Systematic list of all scleractinia, hermatypic hydrozoa and octocorallia species encountered in 137 transects in the Northern Red Sea near Hurghada.

1) *Psammocora nierstraszi* VAN d. HORST
2) *P. haimeana* MN.E. & H.
3) *Stylocoeniella guentheri* (BASSET-SMITH)
4) *Stylophora pistillata* (ESPER)
5) *Seriatopora caliendrum* EHRBG.
6) *S. hystrix* DANA
7) *Pocillopora damicornis* (L.)
8) *P. verrucosa* (ELL. & SOL.)
9) *Astreopora myriophthalma* LAM.
10) *Montipora venosa* (EHRBG.)
11) *M. tuberculosa* (LAM.)
12) *M. verrucosa* (LAM.)
13) *M. monasteriata* (FORSK.)
14) *M. spumosa* (LAM.)
15) *M. circumvallata* (EHRBG.)
16) *M. danae* (MN.E. & H.)
17) *Acropora hyacinthus* (DANA)
18) *A. cytherea* (DANA)
19) *A. tenuis* (DANA)
20) *A. nasuta* (DANA)
21) *A. valida* (DANA)
22) *A. horrida* (DANA)
23) *A. pharaonis* (DANA)
24) *A. valenciennesi* (MN.E. & H.)
25) *A. humilis* (DANA)
26) *A. gemmifera* (BROOK)
27) *A. loripes* (BROOK)
28) *A. hemprichi* (EHRBG.)
29) *A. capillaris* (KLUNZ.)
30) *Pavona varians* VERRILL
31) *P. cactus* (FORSK.)
32) *P. decussata* (DANA)
33) *P. maldivensis* (GARDINER)
34) *Leptoseris yabei* (PILLAI & SCHEER)
35) *Gardineroseris planulata* DANA
36) *Pachyseris rugosa* (LAM.)
37) *P. speciosa* (DANA)
38) *Coscinaraea monile* (FORSK.)
39) *Siderastraea savignana* MN.E. & H.
40) *Fungia fungites* L.
41) *F. scutaria* LAM.
42) *F. klunzingeri* DOEDERLEIN
43) *F. echinata* (PALLAS)
44) *Podabacia crustacea* (PALLAS)
45) *Goniopora planulata* (EHRBG.)
46) *G. stokesi* MN.E. & H.
47) *Synaraea rus* (FORSK.)
48) *Porites lutea* MN.E. & H.
49) *Porites solida* FORSK.
50) *P. columnaris* KLUNZ.
51) *P. nodifera* KLUNZ.
52) *Alveopora daedalea* (FORSK.)
53) *Favia speciosa* (DANA)
54) *F. pallida* (DANA)
55) *F. favus* (FORSK.)
56) *F. helianthoides* WELLS
57) *F. stelligera* (DANA)
58) *Favites abdita* (ELL. & SOL.)
59) *F. complanata* (EHRBG.)
60) *F. halicora* (EHRBG.)
61) *F. flexuosa* (DANA)
62) *F. pentagona* (ESPER)
63) *Goniastrea retiformis* (LAM.)
64) *G. pectinata* (EHRBG.)
65) *Platygyra deadalea* (ELL. & SOL.)
66) *Leptoria phrygia* (ELL. & SOL.)
67) *Hydnophora microconos* (LAM.)
68) *H. exesa* (PALLAS)
69) *Leptastrea bottae* (MN.E. & H.)
70) *L. transversa* KLUNZ.
71) *L. purpurea* (DANA)
72) *Cyphastrea serailia* (FORSK.)
73) *C. microphthalma* (LAM.)
74) *Echinopora gemmacea* (LAM.)
75) *E. hirsutissima* (MN.E. & H.)
76) *E. horrida* (DANA)
77) *E. lamellosa* (ESPER)
78) *Plesiastrea versipora* (LAM.)
79) *Montastrea curta* (DANA)
80) *Galaxea fascicularis* (L.)
81) *Acanthastrea echinata* (DANA)
82) *Lobophyllia corymbosa* (FORSK.)
83) *L. hemprichii* (EHRBG.)
84) *Echinophyllia aspera* (ELL. & SOL.)
85) *Mycedium elephantotus* (PALLAS)
86) *Merulina ampliata* (ELL. & SOL.)
87) *M. scabricula* (DANA)
88) *Plerogyra sinuosa* (DANA)
89) *Gyrosmilia interrupta* (EHRBG.)
90) *Turbinaria mesenterina* (LAM.)
91) *Tubastrea coccinea* (EHRBG.)
92) *Dendrophyllia micranthus* (EHRBG.)
93) *Millepora dichotoma* (FORSK.)
94) *M. platyphylla* HEMP. & EHRBG
95) *M. exaesa* (FORSK.)
96) *Tubipora musica* (L.)

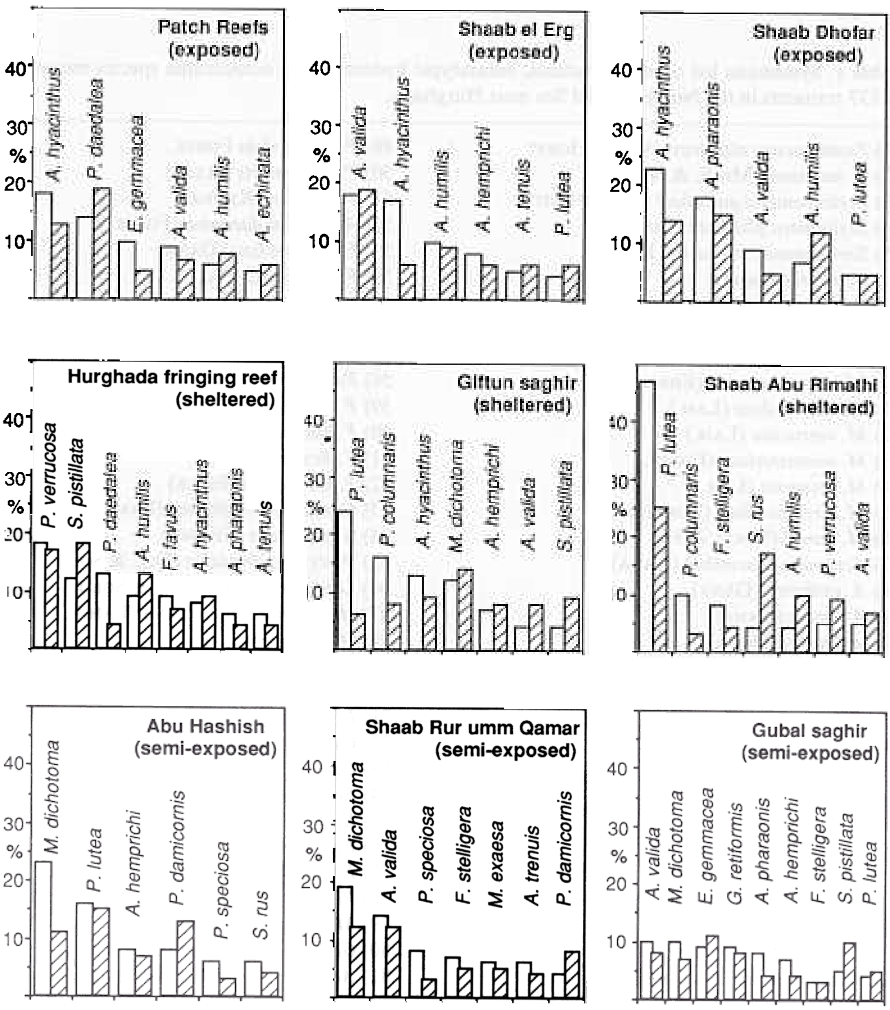


Fig. 2. Species dominance showing percentage of total intercept (white columns) and of total colony frequency (hatched columns) of hard corals occupying more than 5 % of either total intercept or total colony number in each locality. Sequence of species is according to importance of proportional intercept. Abbreviations: A = *Acropora*, E = *Echinopora*, F = *Favia*, G = *Goniastrea*, M = *Millepora*, P = *Porites* in *P. lutea*, *P. columnaris*, P = *Pocillopora* in *P. verrucosa*, P = *Platygyra* in *P. daedalea*, S = *Stylophora* in *S. pistillata*, S = *Synaraea* in *S. rus*.

Differences in species composition between the fringing reef and the off-shore reef localities were suggested by cluster analysis using presence/absence data. The dendrogram (Fig. 3) shows the highest dissimilarity among these two locality groupings. According to our transects, a total of 32 species were exclusive to either on-shore or off-shore localities. Species exclusive to the fringing reefs belonged to the genera *Astraeopora*, *Montipora*, *Fungia*, *Goniopora*, and *Gardineroseris*. Species found only in off-shore localities were *Hydnophora exesa*, *Echinophyllia aspera*, and *Dendrophyllia micranthus*. The windward off-shore localities had 11 species which were not shared with the leeward localities (*Psammocora nierstraszi*, *Seria-*

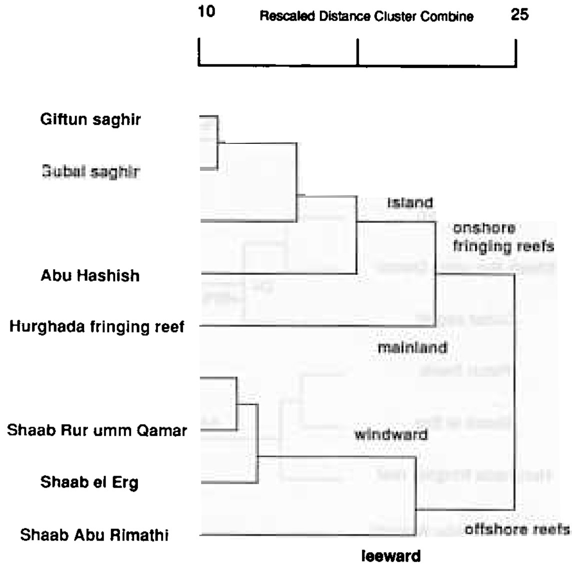


Fig. 3. Dissimilarity in species composition between the localities. Dendrogram obtained from a binary data set using the Bray-Curtis nonmetric dissimilarity index.

topora hystrix, *Acropora nasuta*, *A. loripes*, *Montipora danae*, *Pavona decussata*, *P. cactus*, *Pachyseris speciosa*, *P. rugosa*, *Fungia fungites*, *Fungia klunzingeri*), while the mainland fringing reef in Hurghada was distinguished from the island fringing reefs by the exclusive presence of only one species (*Goniopora* sp.).

2. Horizontal differentiation

In order to test for similarities in community structure among the localities, the quantitative intercept data sets were pooled for each locality and subjected again to cluster analysis (Fig. 4). The two main clusters, formed by dichotomy D1, were communities characterized by either a high (>40 %) or a low (<40 %) *Acropora* share. Dichotomy D2 was generated by the importance of the proportional intercept of *Porites lutea*, separating reefs with >40 % *Porites* share from reefs with <40 % *Porites* share. Dichotomy D4, in the <40 % *Porites* cluster, was caused by the actual ranking of the dominant species in the cluster, *Millepora dichotoma* (compare Fig. 2). In the >40 % *Acropora* grouping, dichotomy D3 generated two further clusters. One comprised reefs with only *Acropora* dominance, the other was a reef with *Pocillopora* dominance (compare Fig. 2).

The major clusters occurred at a critical distance of 15 (rescaled City Block metric) and grouped the reefs into four community types. This grouping was identical with the observed exposure of the localities, as designated in Fig. 1. The clusters were therefore considered to contain discrete natural communities.

The three exposed localities were dominated by *Acropora* species (48.5 ± 14.2 % of total hard coral coverage) and species of the soft coral *Sinularia* (39.2 ± 10.8 % of total soft coral coverage).

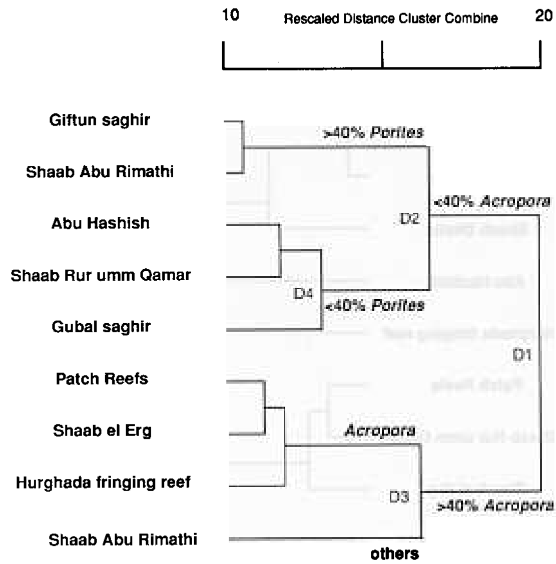


Fig. 4. Similarity of community types between the localities. Dendrogram from pooled intercept values of hard corals in each locality. Distance on ruler is rescaled City-Block (Manhattan) metric.

The fringing reef in Hurghada was similar to these reefs as it was also characterized by a high *Acropora* share (40.1 % of total hard coral intercept); the hard coral species with highest numerical frequency, however, were *Pocillopora damicornis* and *Stylophora pistillata* (Fig. 2). The dominant soft corals in this locality were *Sarcophyton* species (30.6 % of total soft coral intercept).

The two sheltered localities were clearly dominated by the hard coral *Porites* (49.1 ± 10.5 %) and soft corals of the family *Xeniidae* (43.5 ± 9.0 %). The three semi-exposed localities were characterized by elements from the exposed as well as the sheltered communities, a unique feature being the comparatively high contribution of the hydrozoan *Millepora dichotoma* (19.4 ± 6.3 %). The dominant soft corals were also of the family *Xeniidae* (33.7 ± 9.4 %). Despite these patterns, the percentage of coverage by hard corals, soft corals, and bare substratum was not significantly different among the community types (ANOVA, $F = 1.86$, $df = 2, 6$, $P > 0.05$, Table 2).

3. Vertical differentiation

A vertical differentiation of the three basic community types into species zones, which alternated with depth, was suggested by further cluster analysis. In this case, the intercept data for all transects of the localities grouped into the community types exposed, sheltered, and semi-exposed were used. The fourth community type, observed only in the Hurghada fringing reef, was not examined for depth zonation, as the reef did not extend below one meter depth.

The respective dendrograms are given in Fig. 5a,b,c; again, a critical distance of 15 (rescaled City Block metric) was chosen for the designation of zone clusters. All

Table 2. Percentage of total intercept of hard corals, soft corals, and bare substratum in each sampled locality. Values are means and standard deviations. l.i. = living intercept, i. = intercept.

	living intercept hard corals	living intercept soft corals	intercept of bare substratum
patch reefs	36.8±3.4	23.6±4.1	39.5±4.4
Shaab el Erg	60.9±4.9	16.6±3.8	22.5±3.5
Shaab Dhofar	46.4±9.9	0.9±0.6	52.8±9.9
Hurghada fringing reef	35.7±4.5	8.9±2.1	55.4±4.4
Giftun saghir	49.9±5.9	12.5±3.1	36.1±4.8
Shaab Abu Rimathi	82.2±3.5	1.1±0.9	15.8±3.5
Abu Hashish	41.2±4.9	12.8±3.7	45.8±6.1
Shaab Rur umm Qamar	41.1±5.8	8.5±2.2	50.8±5.1
Gubal saghir	57.3±3.1	9.4±1.3	33.9±2.5

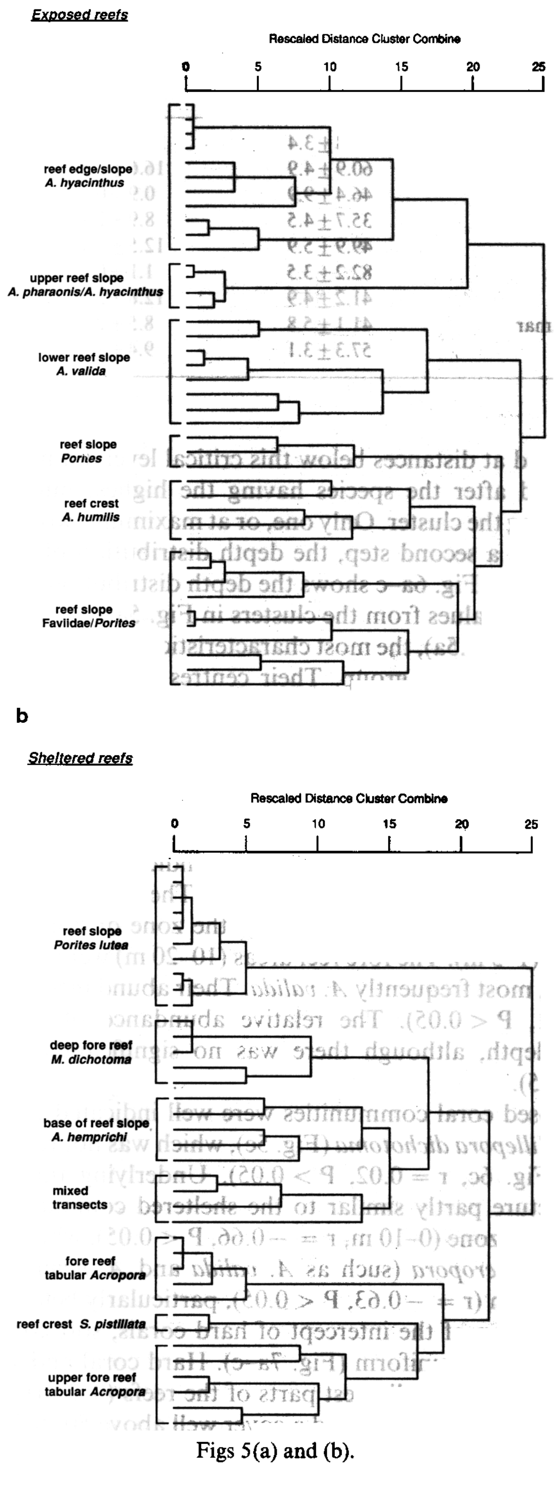
sub-clusters formed at distances below this critical level did not prove useful. The zones were named after the species having the highest intercept values in the transects composing the cluster. Only one, or at maximum two, species were chosen for this purpose. In a second step, the depth distribution of the most important species was examined. Fig. 6a–c shows the depth distribution of those species with the highest intercept values from the clusters in Fig. 5a–c.

On exposed reefs (Fig.5a), the most characteristic hard corals belonged to species of the *Acropora hyacinthus* group. Their centres of abundance were reef edges and upper reef slopes (1.5–7 m). Their importance declined with depth (Fig. 6a, $r = -0.89$, $P < 0.05$). Exposed reef slopes bore very heterogenous communities, usually dominated by other *Acropora* species (such as *A. valida*), *Porites* species (*P. lutea*, *P. solida* and *Faviidae*, particularly *Favia stelligera*, which was characteristic on these reefs (Figs 2e 5a).

Sheltered coral communities (Fig. 5b) were indicated by a clear dominance of *Porites* species, mainly *P. lutea* and *P. solida*. The degree of *Porites* dominance declined with depth ($r = -0.85$, $P < 0.05$), the zone of dominance being on the upper reef slopes (1–5 m). The fore reef areas (10–20 m) were dominated by tabular *Acropora* species, most frequently *A. valida*. Their abundance increased with depth (Fig.6b, $r = 0.81$, $P < 0.05$). The relative abundance of *Millepora dichotoma* increased with depth, although there was no significant correlation (Fig. 6b, $r = 0.59$, $P > 0.05$).

The semi-exposed coral communities were well indicated by the dominance of the hydrozoan *Millepora dichotoma* (Fig. 5c), which was not restricted to any depth zone (1–25 m, Fig. 6c, $r = 0.02$, $P > 0.05$). Underlying this dominance was a community structure partly similar to the sheltered communities. *Porites* dominated in the shallow zone (0–10 m, $r = -0.66$, $P < 0.05$), while branching, corymbose, and tabular *Acropora* (such as *A. valida* and *A. hemprichi*) became more important with depth ($r = -0.63$, $P < 0.05$), particularly below 13 m.

The depth variation of the intercept of hard corals, soft corals, and bare substratum was remarkably uniform (Fig. 7a–c). Hard coral and soft coral coverage was generally low on the shallowest parts of the reefs (0–2 m). On the reef slopes (1–12 m), hard corals rapidly reached a cover well above 50 %. They then declined sharply towards the base of the reef slopes at approximately 10 m depth. Here,


Exposed reefs
Rescaled Distance Cluster Combine
0 5 10 15 20 25
reef edge/slope
A. hyacinthus
upper reef slope
A. pharaonis/A. hyacinthus
lower reef slope
A. valida
reef slope
Porites
reef crest
A. humilis
reef slope
Faviidae/Porites
b
Sheltered reefs
Rescaled Distance Cluster Combine
0 5 10 15 20 25
reef slope
Porites lutea
deep fore reef
M. dichotoma
base of reef slope
A. hemprichi
mixed
transects
fore reef
tabular Acropora
reef crest S. pistillata
upper fore reef
tabular Acropora

Figs 5(a) and (b).

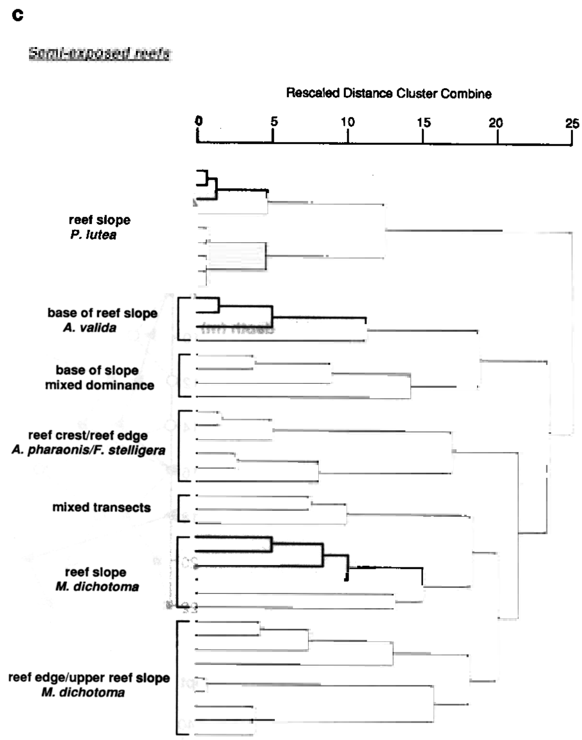


Fig. 5. Classification of all transects. a. Exposed reefs (Shaab el Erg, Patch Reefs, Shaab Dhofar), b. sheltered reefs (Giftun saghir, Shaab Abu Rimathi), c. semi-exposed reefs (Gubal saghir, Shaab Rur umm Qamar, Abu Hashish). Distance on ruler is rescaled City-Block (Manhattan) metric.

soft coral coverage increased, but remained generally lower than the hard coral cover. The amount of bare substratum greatly increased in the fore reef areas (below 10 m), and in most instances sand was the dominant substratum type.

In Shaab el Erg, Shaab Rur umm Qamar, and Gubal saghir, dense hard and soft coral carpets in the fore reef areas (Fig. 5a) between 10 and 20 m occasionally exceeded the coral coverage on reef slopes.

4. Species richness, frequency, and diversity

The number of species, colonies, and the diversity index, calculated from the previous measurements, were examined along the depth gradient. The results were similar among the community type groupings (exposed, semi-exposed, sheltered). We observed significant differences (ANOVA, $F = 3.18$, $P < 0.05$) in species richness between the reef edges (0–2 m depth), the reef slopes (2–12 m) and the fore reef areas (12–19 m on semi-exposed reefs, 12–22 m on sheltered reefs, not sampled on exposed reefs). Colony frequency also differed significantly among the above-mentioned zones (ANOVA, $F = 5.55$, $P<0.01$; Fig. 8a–c). Diversities were only compared to a depth of 12 m, this being the lowest sampling limit on exposed reefs. Diversity was significantly lower on reef edges than on reef slopes (t-tests, $P<0.05$).

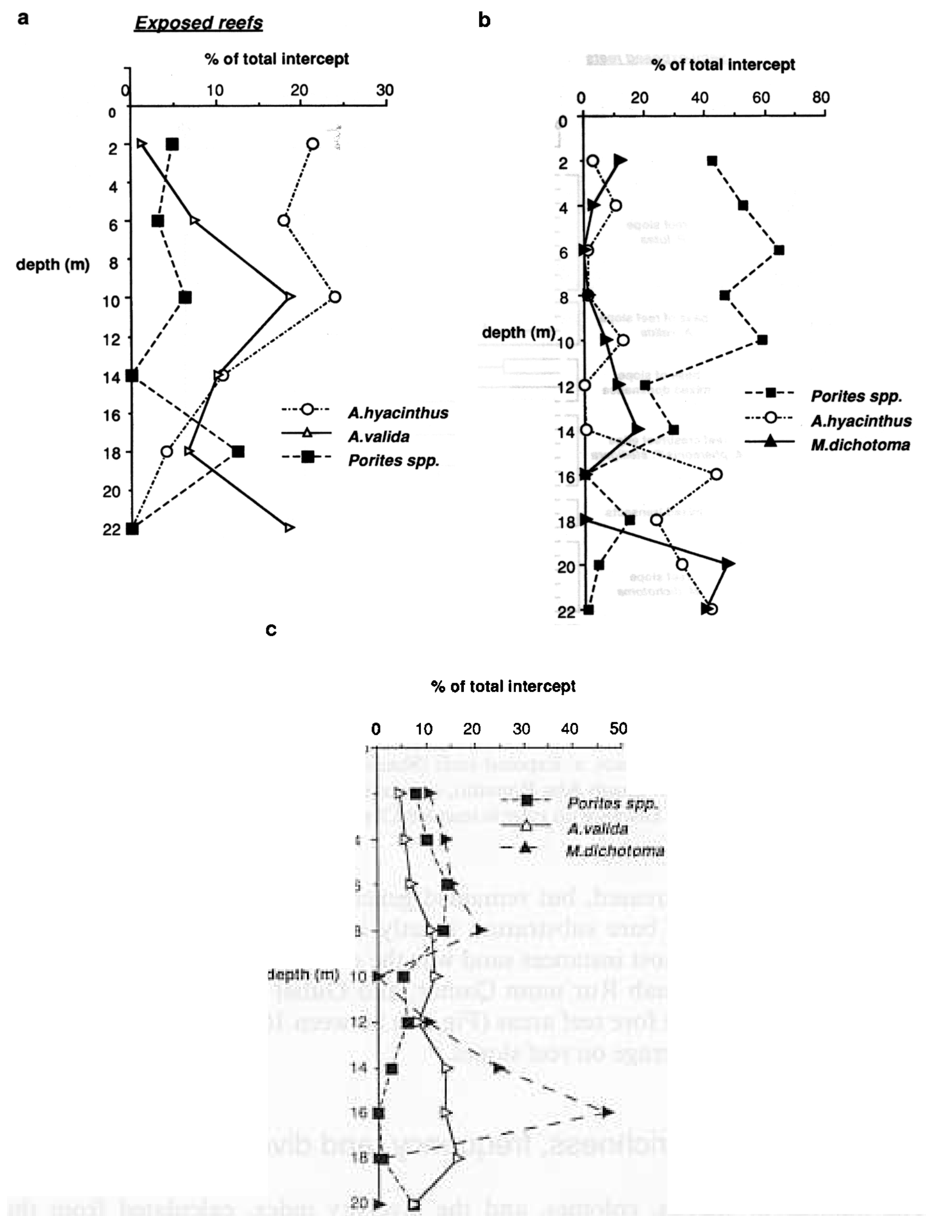


Fig. 6. Dominance of the most typical zone-characterizing species as a function of depth. a. Exposed reefs, b. sheltered reefs, c. semi-exposed reefs. Values are mean proportional coverage at each depth. Error bars were omitted for reasons of clarity.

No correlation was found between diversity and coral cover. High diversities were encountered on transects with high as well as low cover. Average transect diversity among the three community types differed significantly (ANOVA, $F = 4.13$, $P < 0.05$), being highest on semi-exposed reefs and lowest on sheltered reefs.

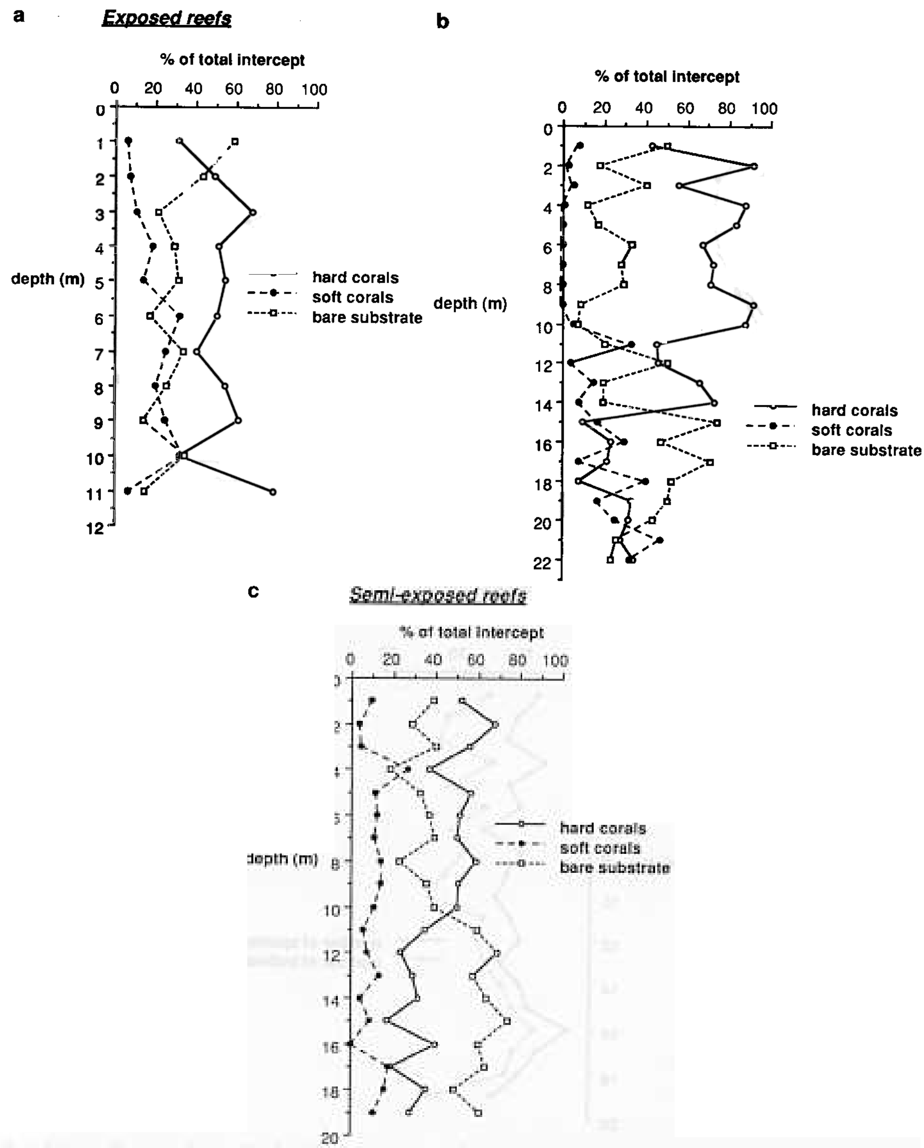


Fig. 7. Proportional intercept of hard corals, soft corals, and bare substratum. a. Exposed reefs, b. sheltered reefs, c. semi-exposed reefs. Values are mean proportional coverage at each depth. Error bars were omitted for reasons of clarity.

Discussion

The present analysis of coral community structure on various reefs in the Northern Red Sea shows how clearly coral communities can differentiate along horizontal and vertical gradients. For a general discussion of factors causing between-reef and within-reef community heterogeneity see Done (1982), Dollar (1982), Grigg (1983), Schuhmacher & Mergner (1985), and Mergner & Schuhmacher

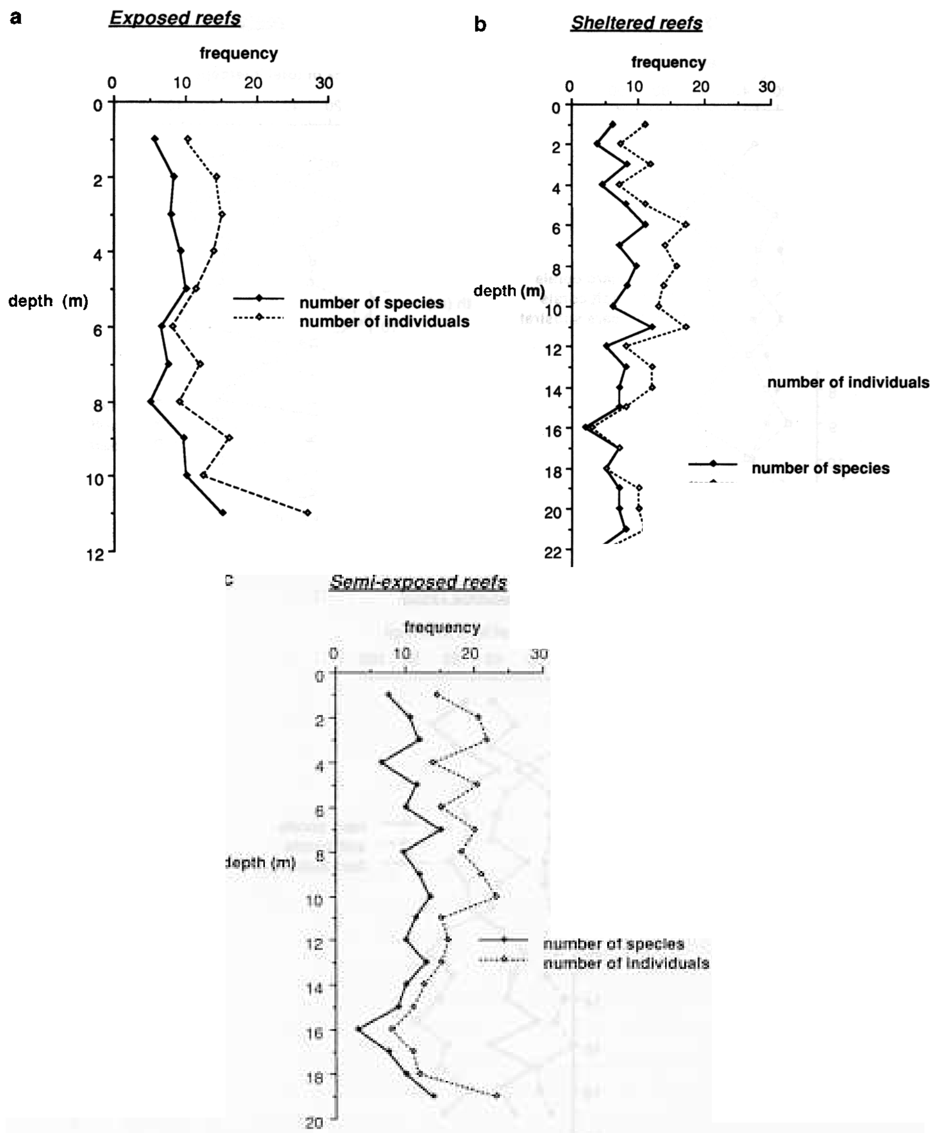


Fig. 8. Distribution of species richness and colony frequency along the depth gradient. a. Exposed reefs b. sheltered reefs, c. semi-exposed reefs. Values are mean number of species or colonies at each depth Error bars were omitted for reasons of clarity.

(1985 a,b). While DONE (1982) and DINESEN (1983) stress the importance of sedimentation for coral community differentiation, other authors stress wave action and differential hydrodynamic exposure (SCHUHMACHER & MERGNER, 1985; MERGNER & SCHUHMACHER, (1985 a,b). This point will not be further discussed, as the aim of this paper is primarily to compare community patterns rather than to formulate hypotheses about the mechanisms underlying their differentiation.

The different species composition in on-shore and off-shore reefs is surprising,

Table 3. Diversity values obtained from pooled transects for the community types 'exposed' (localities: Patch Reefs, Shaab el Erg, Shaab Dhofar), 'sheltered' (localities: Giftun saghir, Shaab Abu Rimathi), and 'semi-exposed' (localities: Abu Hashish, Shaab Rur umm Qamar, Gubal saghir). Diversity index is MARGALEF'S index.

depth	exposed	sheltered	semi-exposed
1	1.99	2.08	2.46
2	2.73	1.35	3.21
3	2.49	2.96	3.57
4	3.11	1.85	2.08
5	3.71	2.91	3.55
6	2.44	2.08	3.32
7	3.05	2.27	4.67
8	1.82	3.15	3.01
9	3.10	2.78	3.61
10	4.59	1.94	3.98
11	4.25	3.80	3.87

given the relative proximity of the reefs (120 km radius). This may reflect varying degrees of frequency of the relevant species rather than an indication of exclusive occurrence. A varying frequency of certain species in on-shore versus off-shore reefs could be a result of different larval settlement (DONE, 1982). Currents among the studied reefs are strong and driven by tides and winds. Often, tidal currents are reversive (ROBERTS, 1985). Larvae dispersing in such a water body would not achieve a high net movement, regardless of the time spent in the water column (KEOUGH, 1988). Larvae may have trouble bridging the distances among the reefs in order to establish stable populations.

It is interesting to note that all the dominant species characterizing within-reef and between-reef community differences and zonations are capable of reproducing by fragmentation (MERGNER & SCHUHMACHER, 1974; HIGHSMITH, 1982). This allows them to rapidly colonize large reef areas. This situation was observed in the shallow *Acropora hyacinthus* zone on exposed reefs. In deeper reef areas, usually the bases of reef slopes, so-called secondary zones (MERGNER & SCHUHMACHER, 1974) can be formed. Here, fragments derived from the reef slopes regenerate and the species with the highest share of survivors dominates the coral community. In the study area, this process led to *Acropora valida* zones on exposed and semi-exposed reefs (Figs 5e, 6a–c). A considerable percentage of the colonies in this zone appeared to be reattached fragments, although no quantitative data were available. Due to the importance of fragmentation for the community structure we hypothesize that water movement is a key forcing factor here. Although we did not observe exactly the same communities as SHEPPARD & SHEPPARD (1991) and SHEPPARD *et al.* (1992), the Hurghada reefs were similar to their communities 2 (exposed shallow water community dominated by *A. hyacinthus*, *A. humilis*, and *Stylophora wellsi*), 3 (diverse patch reef community, no dominance), 4 (sheltered, *Porites* dominated areas), and 5 (moderately exposed *Millepora* and *Goniopora* community). Certain genera or species groups are consistently characteristic for comparable environments, not only in the Red Sea, but all across the tropical Indo-Pacific.

Exposed reefs dominated by tabular *Acropora* have been described from the central Red Sea in Sudan (MERGNER & SCHUHMACHER, 1985 a,b; HEAD, 1987), from the Indian Ocean in Chagos (SHEPPARD, 1980) and Madagascar (PICHON, 1978), from the Pacific in the Great Barrier Reef (WALLACE, 1978; DONE, 1982). In all these studies, *Acropora hyacinthus* (or closely related species like *A. cytherea*) were dominant or co-dominant corals on reef edges and upper reef slopes.

A zone comparable to the *Acropora valida* 'secondary' zone found in this study on exposed and semi-exposed reefs has also been described from Aqaba reefs (MERGNER & SCHUHMACHER, 1974). In addition, sheltered reefs totally or partially dominated by *Porites* species have been described from Sudan (MERGNER & SCHUHMACHER, 1985 a,b; HEAD, 1987), Madagascar (PICHON, 1978), Thailand (DITLEV, 1978), and the Great Barrier Reef (DONE, 1982; POTTS *et al.*, 1985).

Reefs dominated by the hydrocoral *Millepora dichotoma* have so far only been described from the Red Sea at Eilat (LOYA & SLOBODKIN, 1971; LOYA, 1972), Aqaba (MERGNER & SCHUHMACHER, 1974), Sudan (HEAD, 1987), and Saudi-Arabia (SHEPPARD & SHEPPARD, 1991). In contrast to the present findings, in Eilat and Aqaba the *Millepora dichotoma* zone is confined to the reef edges and upper reef slopes down to about 2 m (LOYA & SLOBODKIN, 1971; MERGNER & SCHUHMACHER, 1974). MERGNER (1977) describes *Millepora dichotoma* as a 'stenophot-photophil-rheophil' indicator. On the present reefs it appears to be rather a 'euryphot-rheophil' indicator: it dominated zones varying from 1–20 m depth (Figs 6 b,c). HEAD (1987) described a '*Millepora* sub-association' in the most exposed habitats of Sudan reefs, while KLEEMANN (1992) reported a similar community from the Safaga area. No such association was observed near Hurghada. However, as the Hurghada reefs are exposed to stronger swells caused by longer fetch of north winds in the Gulf of Suez (ROBERTS, 1985), it is likely that conditions on the exposed reefs as described by HEAD (1987) and KLEEMANN (1992) would have been rated as semi-exposed in the present study. Further verification of this point is necessary. In any case, *Millepora dichotoma* apparently has a wider ecological tolerance than anticipated.

The distribution of soft coral communities seems to be stable within the northern and central part of the Red Sea and partly within the Indo-Pacific. As in the present study, *Xeniidae* dominate reef slopes and fore reef areas in Eilat (LOYA, 1972), on the Sinai (BENAYAHU & LOYA, 1977, 1981), in Sudan (MERGNER & SCHUHMACHER, 1985 a,b), and the Great Barrier Reef (DINESEN, 1983). Reef crest soft coral dominance was also roughly comparable. While mainly *Sinularia* dominated reef slopes in Hurghada, BENAYAHU & LOYA (1977, 1981) report this reef zone to be dominated by *Sinularia*, *Lobophytum*, and *Sarcophyton* on the Sinai. This is similar to the situation on the Great Barrier Reef (DINESEN, 1983). It appears that soft coral communities are more plastic than hard coral communities. While the latter exhibit a remarkable constancy, this is true only to a more limited extent in soft corals. According to SHEPPARD *et al.* (1992), soft coral cover declines sharply on reefs in the southern Red Sea.

Overall, Hurhada's coral communities fit very well into a distribution scheme of reefs in similar latitudes and of similar geomorphology. When the same, or similar, coral species are present on reefs of similar morphology in a similar oceanographic setting, many features of community structure should be roughly comparable. Major deviations from such a generalized scheme could therefore only be expected on reefs which either have an entirely different species composition, which are located in extreme habitats (*e.g.*, lying outside the tropical reef belt), or which grow on completely different substrata whose geomorphology deviates from that of typical coral reefs.

Summary

In the northern Red Sea at Hurghada, coral communities differentiated along a horizontal and a vertical gradient. Hydrodynamic exposure was a major factor influencing coral community structure. Exposed windward reefs were dominated by tabular *Acropora*, semi-exposed reefs by the hydrozoan *Millepora*, and sheltered leeward reefs by massive growing *Porites*. Reef edges were dominated by tabular *Acropora* on exposed reefs, by *Millepora dichotoma* on semi-exposed reefs, and by massive *Porites* species on sheltered reefs. Reef slopes were the most diverse areas on all reefs, with varying species dominances. The fore reef areas were dominated by branching and tabular *Acropora* species.

Comparisons with data from the literature indicate that this pattern is fairly constant across the Indo-Pacific. Although different species often dominated the described reef areas (exposed, semi-exposed, sheltered) in different geographical localities, under comparable hydrodynamic exposure a certain constancy of coral community differentiation appeared to exist over wide geographical areas. This constancy was achieved by a dominance of closely related species or at least of species with a similar growth form in similar habitats.

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