

<b>FACIES</b>	<b>37</b>	<b>183-194</b>	<b>Pl. 41-42</b>	<b>5 Figs.</b>	<b>6 Tab.</b>	<b>ERLANGEN 1997</b>
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## **Bivalve Distribution on Coral Carpets in the Northern Bay of Safaga (Red Sea, Egypt) and its Relation to Environmental Parameters**

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KEYWORDS: ZOOXANTHELLATE BIVALVES – SUSPENSION FEEDERS – CORAL ASSEMBLAGES– BIVALVE HABITATS – ENVIRONMENTAL GRADIENT – SUSPENSION LOAD – SUBSTRATE – LIGHT – GIANT OYSTERS – NORTHERN RED SEA – RECENT

### **SUMMARY**

Bivalve assemblages on coral carpets in the Northern Bay of Safaga do not form distinct associations, but gradually shift in faunal composition. The taxonomic shift is accompanied by continuous variations in bivalve density and percentage of living individuals as well as by a change of coral associations and potential bivalve habitats. The gradual lateral change of associations is best documented by *Tridacna maxima* and jewel box clams (Chamoidea) and is probably due to variations of the suspension load in the water column. High suspension loads in the water column are additionally indicated by 'giant oysters' (extremely large individuals of *Hyotissa hyotis*) and striking agglomerates of *Lopha cristagalli*. The vertical differentiation is best documented by the decrease of the zooxanthellate *Tridacna maxima* and is probably due to the depth-dependent light penetration in the water column, which is attenuated in areas of high suspension load.

### **1 INTRODUCTION**

Ecological studies dealing with bivalves are generally rare in the Indo-Pacific (for a detailed review see MORTON, 1983b) and information on subtidal faunal differences in response to physical parameters is available for a few regions only. MASTALLER (1978) for example reported reduced mollusc species diversity and lower numbers of individuals in areas with low water exchange, high sedimentation rates and turbid waters in the region of Port Sudan. KAY & SWITZER (1974) associated mollusc distribution patterns in Fanning Island lagoon (Republic of Kiribati, central Pacific) with clear and turbid water areas. SHEPPARD (1984) stated for the Chagos Archipelago, that mollusc distributions on hard substrates parallel those of corals with respect to diversity and

separate along depth or depth-related parameters. TAYLOR (1968) recorded a zonation parallel to the shoreline in response to a variety of environmental factors around Mahé, Seychelles.

Within a wide ranging study of mollusc distributions on hard substrates in the northern Bay of Safaga, a variety of mollusc associations was recognised (ZUSCHIN & PILLER, in press). The dominating type of hard substrate in this area are coral carpets (PILLER & PERVESLER, 1989) which show spatially changing coral assemblages and a distinct distribution pattern (RIEGL & PILLER, 1997).

The present study on bivalves was conducted in the 'southwest channel' of the northern Bay of Safaga (PILLER & PERVESLER, 1989) (Fig. 1) and was designed to answer the following questions:

1. Do bivalve assemblages change laterally and with water depth?
2. Do bivalve assemblages on coral carpets represent distinct associations or do they gradually merge into one another?
3. Which bivalve taxa are group diagnostic and suitable to recognize faunal shifts?
4. Which environmental factors are responsible for differences in the bivalve fauna of coral carpets?
5. Are bivalve assemblages linked with coral assemblages?

### **2 MATERIAL AND METHODS**

Lateral distribution patterns were studied by comparing the bivalve assemblages of 5 sample locations in similar water depth (6-10 m). This relatively narrow depth range reduces the influence of depth and depth-related factors. The distribution in different water depth (10 m versus 20 m and 9 m versus 15 m) was studied at two sampling sites.

The study was limited to bivalves due to the low number of encountered gastropods. Some boring bivalves (e.g.,

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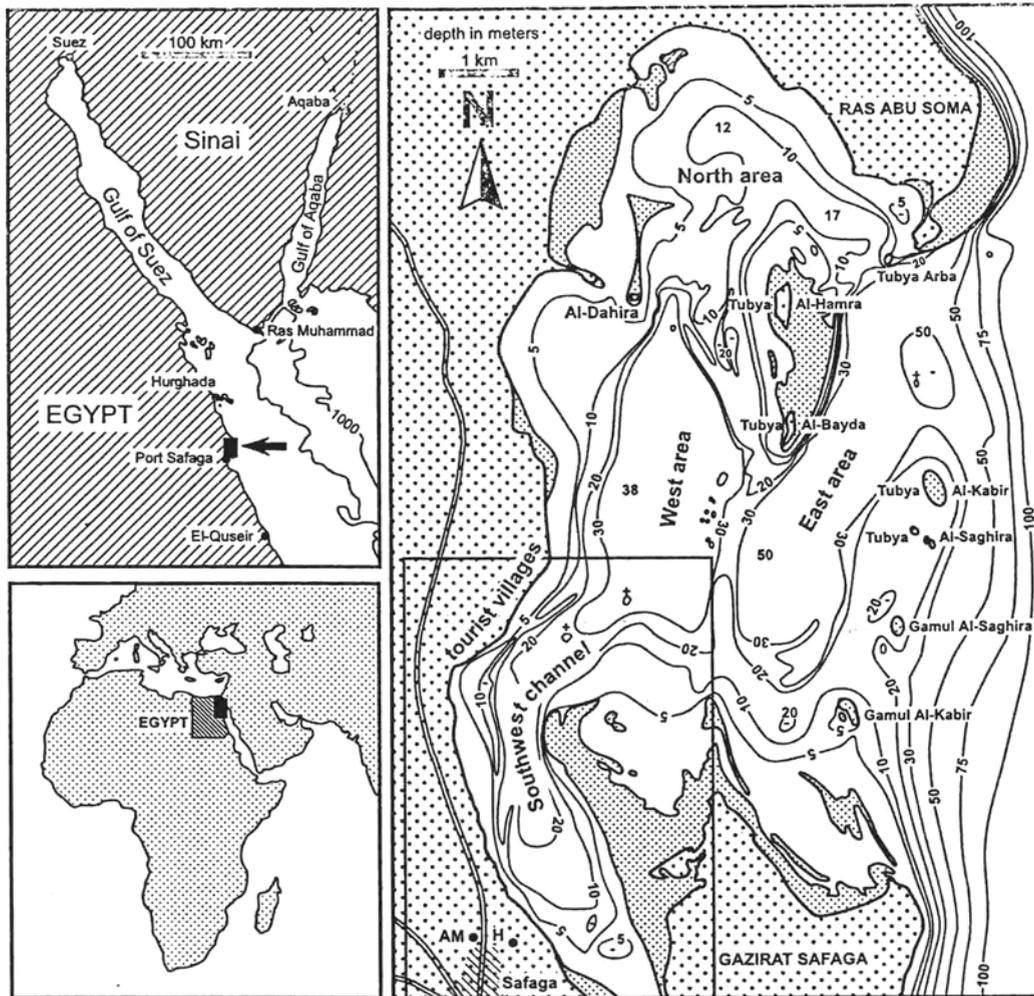


Fig. 1. Location map of the Northern Bay of Safaga, Red Sea. Coarse stippled areas in right figure are land, fine stippled areas are tidal flats; the rectangle in lower left corner represents the area shown in Figs. 2 and 5.

gastrochaenids, lithophagins) have been excluded from the quantitative data collection due to the difficulty of clearly identifying them from the surficial appearance of their bore holes. A qualitative study on boring bivalves was already presented by KLEEMANN (1992).

Using a  $1/4 \text{ m}^2$  aluminium square frame, the coral carpets were studied at 5 sample localities. At each locality the location of the first frame was selected randomly, with the following frames being positioned in an adjoining line. In mixed hard / loose substrates, frames were only taken from hard substrate. For the lateral bivalve distribution the investigated area per locality varied from  $2.25 \text{ m}^2$  to  $12 \text{ m}^2$  in water depths from 6-10 m (Fig. 2, Table 1). At sample locations 2 and 3, additional sampling was carried out in the same way in 20 m and 15 m water depth respectively to study vertical mollusc distributions (Fig. 2, Tab. 2).

Bivalves were identified in situ. Poor states of preservation and/or difficulties in identification prevented differentiation of Chamoidea, Spondylidae and Ostreoidea (except: *Lopha cristagalli*) to the species level for the quantitative treatment. Generally, the taxonomy of these three groups is highly questionable, with most of the studies in fact mainly describing ecophenotypes (OLIVER,

1992, 1995). Due to the dominance of one phenotype in the area of investigation, spondylids are summarized under *Spondylus marisrubri sensu lato*. The large oysters at sample location 5 were identified as *Hyotissa hyotis* for descriptive reasons. Apart from the taxonomic status, all bivalves were separated into living and dead specimens. The statistical analyses (using the SPSS 6.1.3 program package), however, were applied to the living specimens only.

The lateral bivalve distribution was classified by a cluster analysis using Ward's method (squared Euclidian distances). Data transformation of species proportions was performed by the arcsine root method (HOHENEGGER, 1996), retaining linearity of data scales (FLEISS, 1973; HOHENEGGER, 1995; LINDER & BERCHTOLD, 1976). Two discriminant analyses were performed with the absolute frequencies of every sampled frame after elimination of missing values, one analysis with the groups according to the sample locations and one with the groups according to the clustering. The results were very similar and are therefore shown only for the groups according to the sample locations. Depth-dependent differences were statistically investigated by discriminant analyses with the groups from the

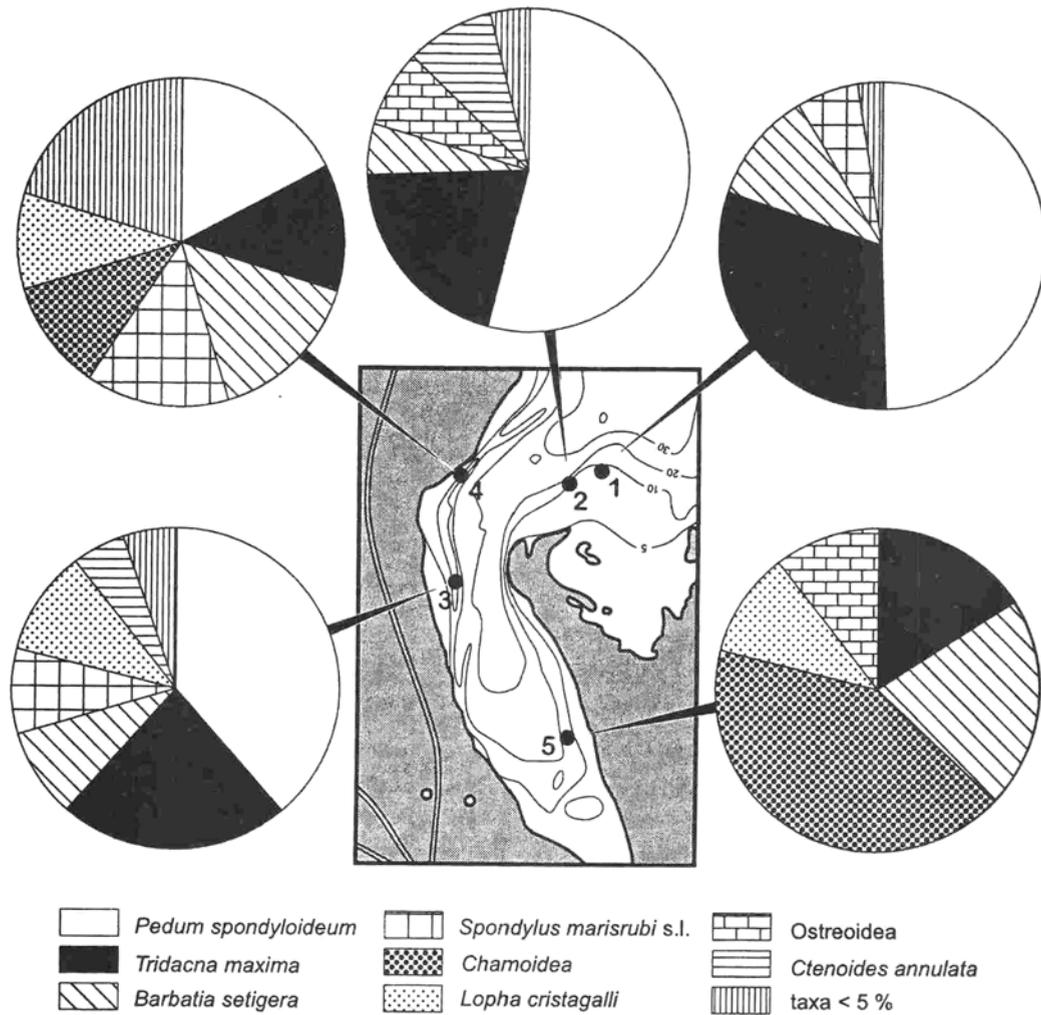


Fig. 2. Composition of the bivalve fauna at sampling sites 1-5 in the 'southwest channel'. The pie diagrams clearly reflect the lateral shift in composition.

shallower and deeper settings. Generally the interpretation of the statistical results is based on the 5% confidence interval.

### 3 RESULTS

#### 3.1 Coral carpets and sample locations

All sample locations represent coral carpets in the 'southwest channel' of the northern Bay of Safaga. The 'southwest channel' was chosen due to the occurrence of different coral carpets (RIEGL & PILLER, 1997) and due to the presence of an obvious, although weak, southward directed water current (PILLER & PERVESLER, 1989). This current is related to the general current pattern inside the bay and is reinforced by the funnel-shape of the channel and a constant shallowing to the south. This narrowing and shallowing of the bay also produces a distinct concentration of suspended matter.

Sampling site 1 is situated on the northwestern flank of Gazirat Safaga and represents a *Porites* carpet dominated by *P. columnaris* and *P. lutea*, both in predominantly columnar growth form (Pl. 41/1). This growth form pro-

duces numerous cavities providing room for a diverse invertebrate fauna.

Sampling sites 2 and 3 represent faviid carpets (RIEGL & PILLER, 1997). Location 2 (compare PILLER & PERVESLER, 1989, fig. 6, profile A 14) is, similar to site 1, at the northwestern flank of Gazirat Safaga, although it lies closer to the entrance of the 'southwest channel'. Site 3 (compare PILLER & PERVESLER, 1989, fig. 6, profile A 9) is in the southern part of the 'southwest channel' immediately after the direction of the channel turns from NE-SW to NNW-SSE. This carpet is located at a submarine ridge facing eastward in the direction of the axial part of the channel and westward towards an elongated depression. Data collecting was carried out in the shallowest portion of the ridge. It is a highly diverse faviid assemblage producing a rugged surface morphology due to highly variable growth forms (Pl. 41/2).

Sampling site 4 is in the northern part of the 'southwest channel' at the western margin directly in front of the beach of the tourist villages (compare PILLER & PERVESLER, 1989, fig. 6, profile A 11). It represents a depauperate faviid carpet (RIEGL & PILLER, 1997) (Pl. 41/3) which is located

on the steep slope inclined against the channel axis. The coral assemblage is dominated by massive species with only few branched colonies in between. Space coverage of live corals is distinctly lower than at locations 2 and 3; areas with dead colonies predominate.

Sampling site 5 is the southernmost studied site (Fig. 2). It is situated in that area of the channel where the profile is already relatively flat (compare PILLER & PERVESLER, 1989, fig. 6, profile A 5). The data collecting site is east of the channel axis on generally relatively smooth bottom topography. It represents a *Sarcophyton* carpet (RIEGL & PILLER, 1997), although the sampling site itself is close to the eastern margin of the carpet, where it starts to disintegrate into coral patches which rise 1 - 2 m above the sea floor (Pl. 41/4). The most obvious constituents of this assemblage are soft coral colonies of the genus *Sarcophyton*. These are accompanied by scleractinians of mostly small colony size. An obvious feature is the relatively high abundance of fungiids.

### 3.2 Bivalves

According to various habitat classifications (HADFIELD, 1976; MORTON, 1983a; TAYLOR 1971) and personal field observations the encountered bivalves belong to borers in living corals (*Pedum spondyloideum*), encrusters of dead corals or other hard substrates (Chamoidea, Ostreidea, Spondylidae), crevice-dwellers of living and/or dead coral colonies (*Barbatia setigera*, *Chlamys livida*, *Ctenoides annulata*, *Isognomon legumen*, *Lima lima*, *Streptopinna saccata*), and reef associates (*Tridacna maxima*).

#### 3.2.1 Lateral distribution

The taxonomic composition shows distinct differences at the 5 sampling sites (Tab. 1). Sampling sites 1, 2 and 3

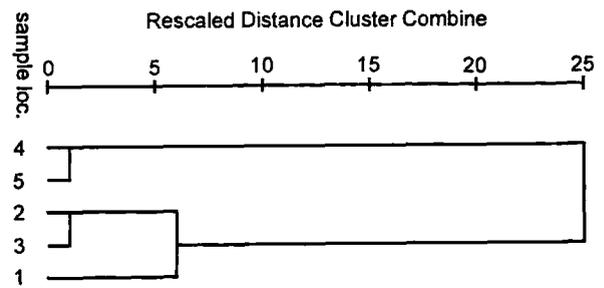


Fig. 3. Dendrogram of the cluster analysis (Ward's method).

are dominated by *Pedum spondyloideum* (Pl. 42/1) and *Tridacna maxima* (Pl. 42/2). Station 4 shows a variety of taxa with similar abundances. Sampling site 5 is dominated by Chamoidea.

Overall densities decrease continuously from station 1 to 5, with station 1 having a considerably higher density than all others. A similar decrease is reflected in the percentage of living individuals, with sample point 5 having a much lower percentage of living individuals than all others. Sample point 4, which has a low bivalve density, exhibits the highest number of bivalve taxa and highest diversity indices and is the only station with direct anthropogenic influence (tourist villages).

The cluster analysis yielded 3 groups. Stations 4 and 5 and stations 2 and 3 are grouped together; sampling site 1 remains alone, but with a close relation to the cluster containing stations 2 and 3 (Fig. 3).

The two discriminant analyses show similar results: In both analyses the variables *T. maxima*, *P. spondyloideum* and Chamoidea provide the best univariate discrimination; the values of all other taxa are insignificant. Both discriminant analyses have two significant canonical discriminant functions (Tab. 2), which show a strong overlap and scattering of the groups (Fig. 4). The ordinations of

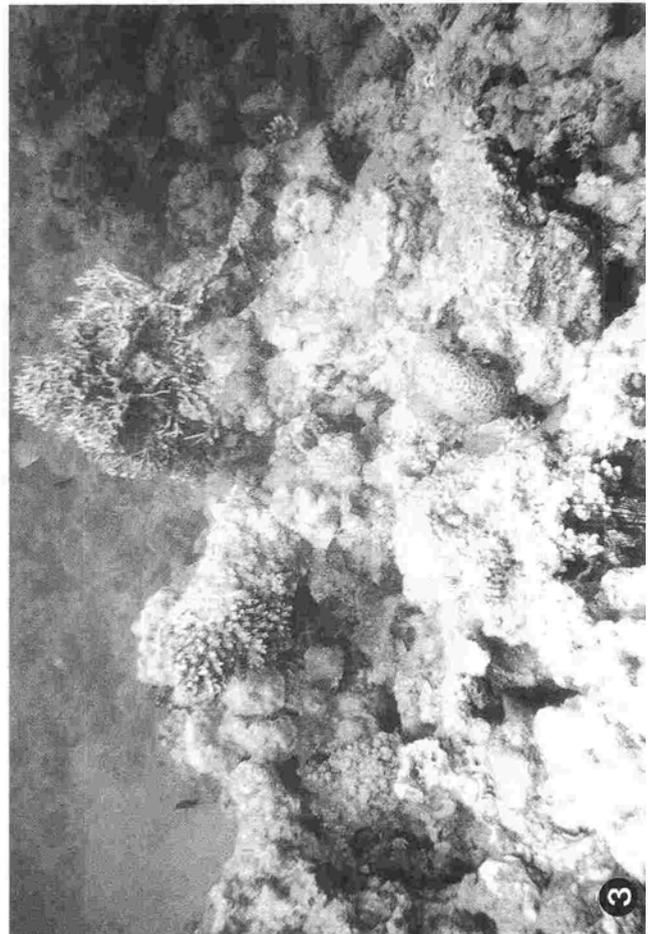
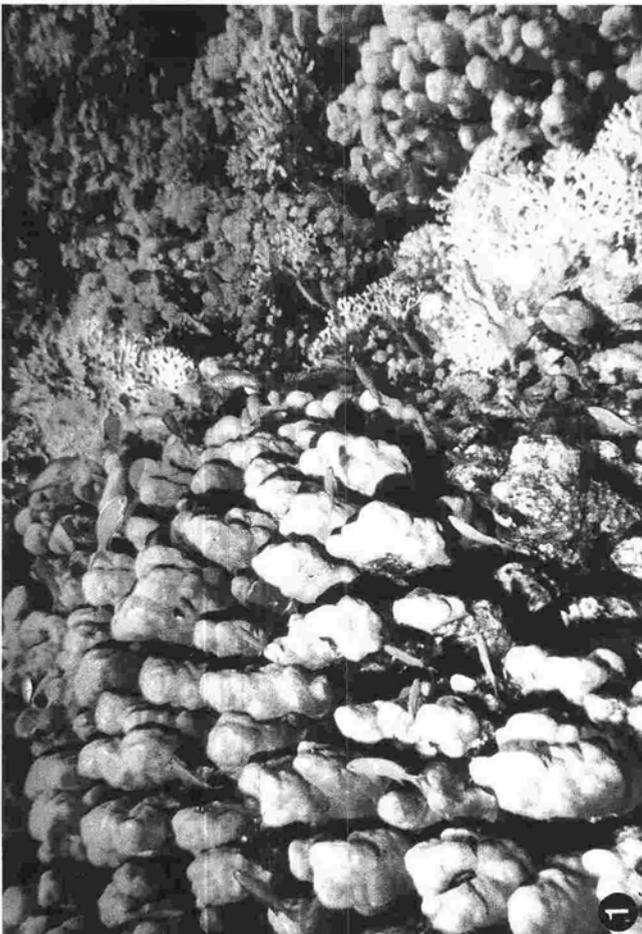
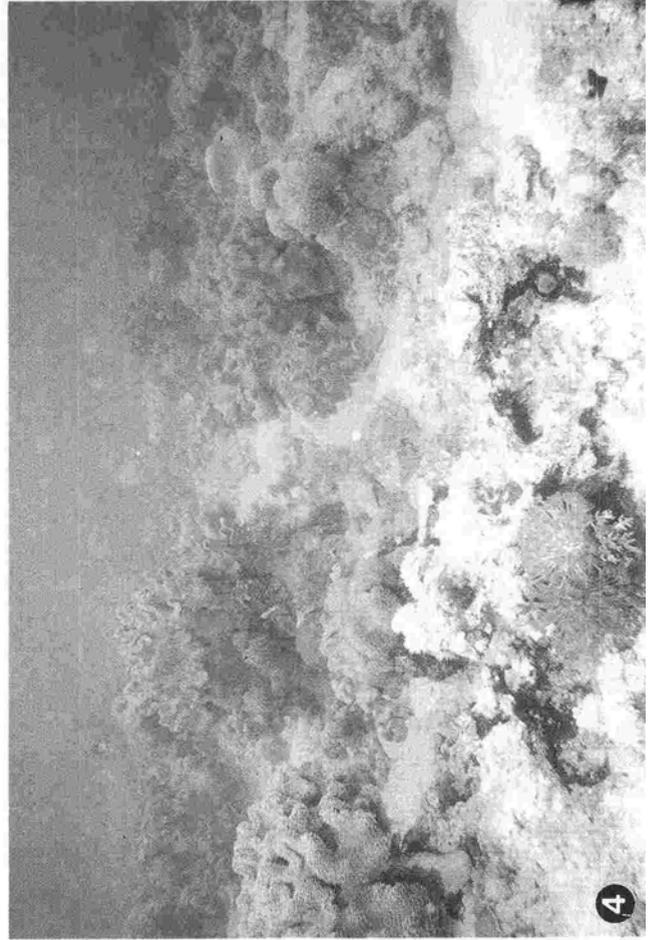
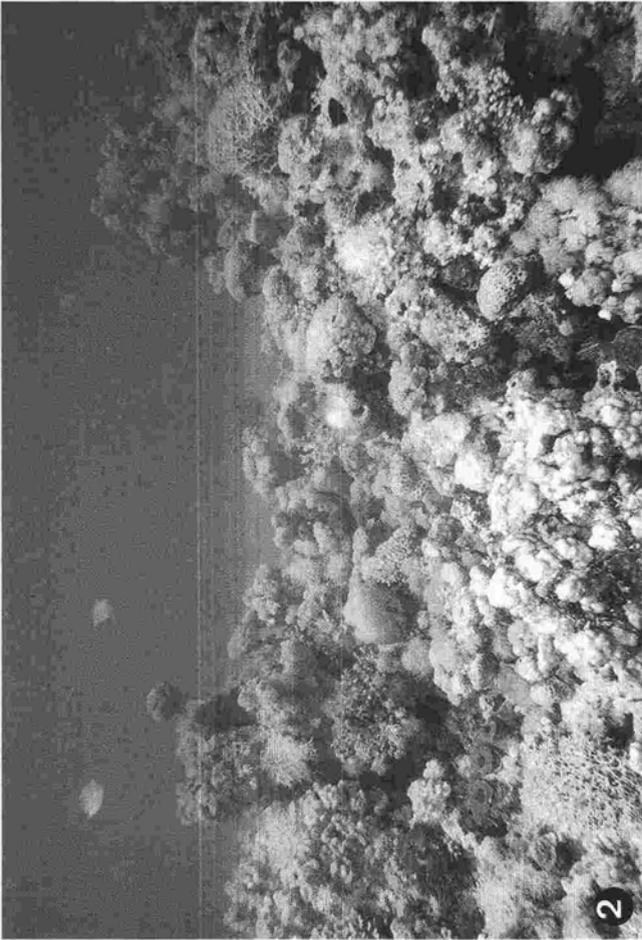
Plate 41 Coral carpets of the northern Bay of Safaga, Red Sea, Egypt. Classification of coral carpets according to RIEGL & PILLER (1997).

Fig. 1. Dense *Porites* carpet clearly dominated by *P. columnaris* and *P. lutea*. Besides *Porites*, *Millepora* and *Acropora* colonies are also present. The deep depressions between the columnar growth form of *Porites* offer abundant space for bivalve settlement. Sampling site 1, 9 m depth.

Fig. 2. Well-developed faviid carpet with high scleractinian diversity (*Goniastrea pectinata*, various *Favia* and *Favites*, *Seriatopora hystrix*, *Stylophora pistillata*, *Porites solida*) and typical rugged surface topography. Besides scleractinians, soft corals (xeniids) are also abundant. The heterogeneous surface and rugged topography provide many niches for molluscs, as visible by *Pedum spondyloideum* in *Porites solida* (foreground center) and two large *Tridacna maxima*. Sampling site 2, 10 m depth.

Fig. 3. Depauperate faviid carpet with only few live scleractinian corals (*Acropora loripes*, *Echinopora gemmacea*, *Porites solida*), one *Millepora dichotoma* colony, and a high amount of dead hard substrate. The *Millepora* colony shows no preferred orientation, reflecting the weak current. Sampling site 4, 7 m depth.

Fig. 4. *Sarcophyton* carpet with high spatial coverage by colonies of this soft coral. Besides *Sarcophyton*, xeniids are also abundant (foreground, center left). The relatively small bases of the *Sarcophyton* colonies leave wide areas of dead hard substrate for bivalves. Note the typical high suspension load in the water column. Sampling site 5, 6 m depth.



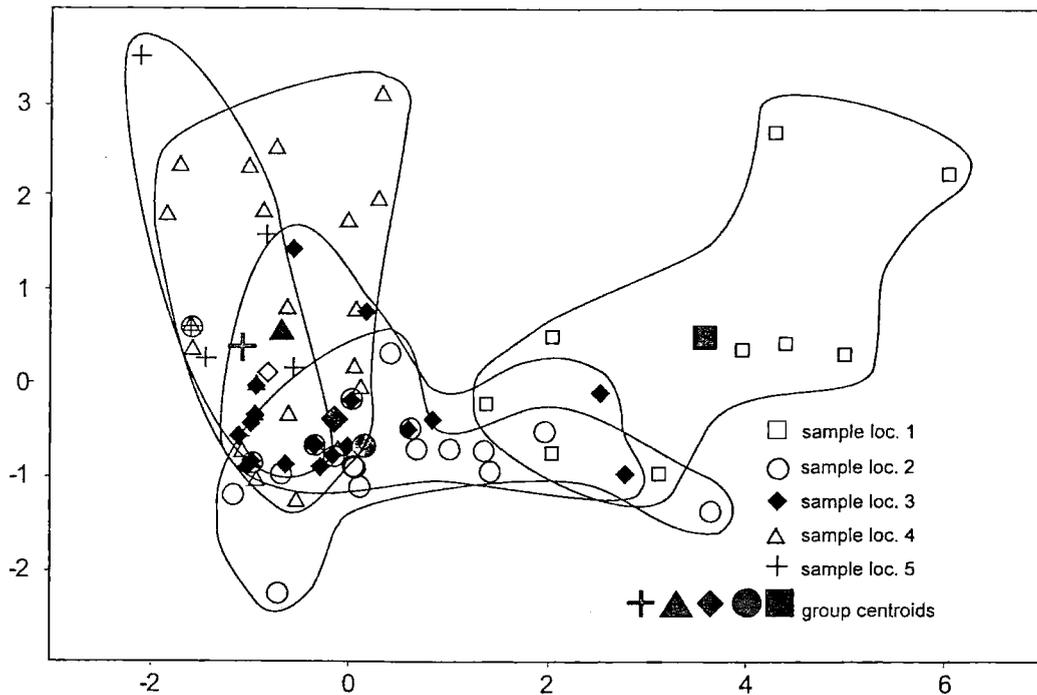


Fig. 4. Discriminant analyses using the two significant canonical discriminant functions. The bivalve fauna shows distinct scattering within sampling sites and strong overlap between locations.

both analyses take the form of a horseshoe, which indicates the dependence on only one dominant ecological gradient expressed in the primary function (DIGBY & KEMPTON, 1987).

### 3.2.2 Distribution in different water depth

The distribution of bivalves in different water depth is characterised by similar trends at both sampling sites (Tab. 3). Regarding the taxonomic composition, the shallower settings are dominated by *Pedum spondyloideum* and *Tridacna maxima*, the deeper settings by *Pedum spondyloideum* only (Fig. 5). The percentage of living individuals decreases slightly with depth and the diversity indices are lower in the deeper areas (except the Margalef Index at station 2). The bivalve densities are lower in the deeper areas, with sample location 2 showing a much stronger decrease.

The discriminant analyses show a significant differ-

ence between the shallow and the deep sites at station 2 (indicated by the canonical discriminant function), which is based on *Tridacna maxima* by best univariate discrimination. The shallow and the deep sites at station 3, in contrast, exhibit no statistically significant difference in taxonomic composition (Tab. 5).

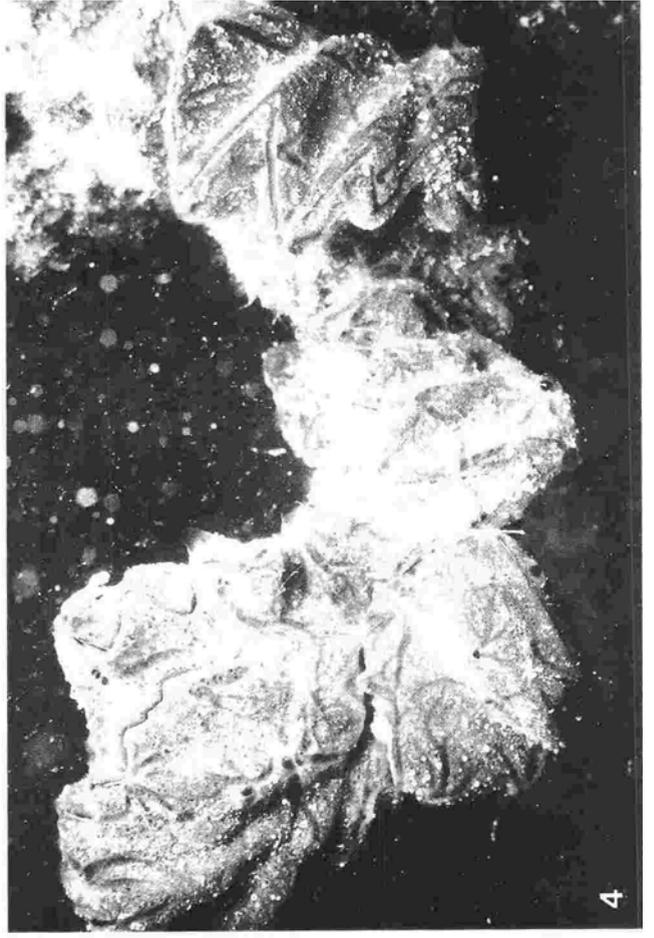
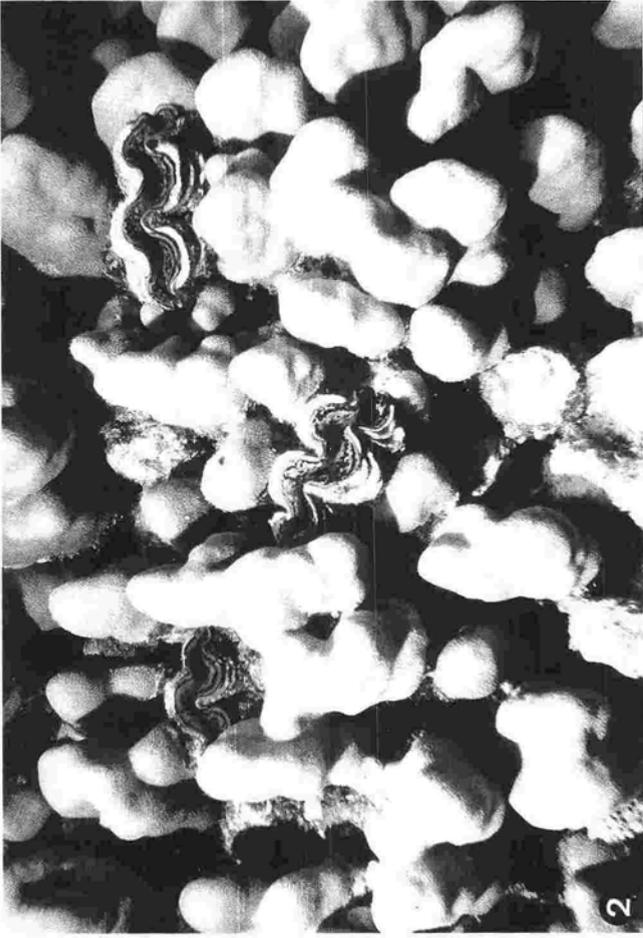
## 4 DISCUSSION

A total of 12 bivalve taxa were counted at the 5 sample locations. Most belong to the order Pteriomorpha (Tab. 6). Apart from *T. maxima*, which uses various food sources (FANKBONER & REID, 1990), all observed taxa are exclusively suspension feeders (after MORTON, 1983a).

The bivalve distribution pattern and its statistical analysis indicate a distinct change of bivalve assemblages which is best documented by *T. maxima*, *P. spondyloideum* and Chamoidea in lateral direction and by *T. maxima* in different water depth.

## Plate 42 Typical bivalves living on coral carpets in the Northern Bay of Safaga, Red Sea, Egypt

- Fig. 1. *Pedum spondyloideum* in *Cyphastrea microphthalmia*, showing the high densities of this bivalve in host corals. Depauperate faviid carpet, sampling site 4, 6 m depth.
- Fig. 2. Three individuals of *Tridacna maxima* intergrown with a *Porites columnaris* colony. *Porites* carpet, sampling site 1, 9 m depth.
- Fig. 3. The 'giant oyster' *Hyotissa hyotis* growing on a dead hard substrate. The oyster is surrounded by colonies of *Sarcophyton*. Two *Chama* individuals grow close to the base of *H. hyotis*. *Sarcophyton* carpet, sampling site 5, depth 6 m.
- Fig. 4. An aggregate formed by at least 7 individuals of *Lopha cristagalli*; note typical overgrowth by sponges. The aggregate originates from dead coral rock. Note the high suspension load preferred by these bivalves. Faviid carpet, sampling site 4, depth 6 m.



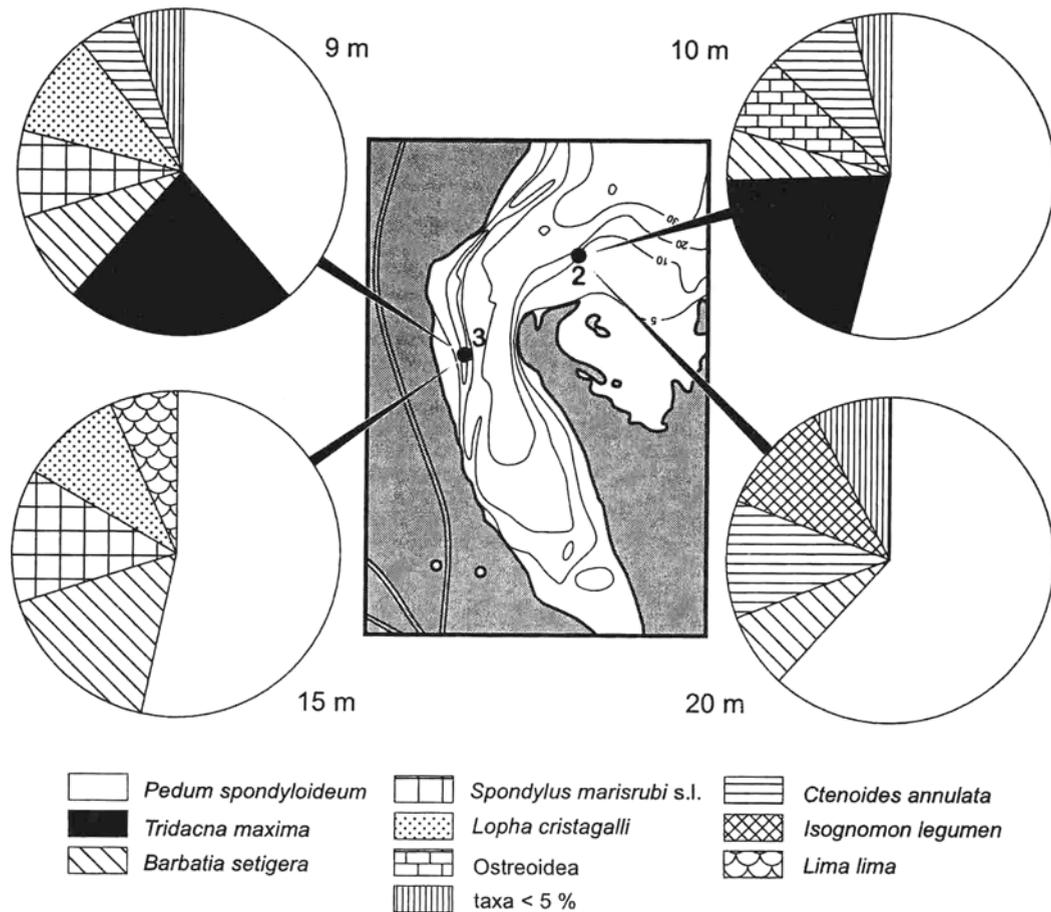


Fig. 5. Composition of the bivalve fauna at sampling sites 2 and 3 in different water depths.

The results of the discriminant analyses on the lateral bivalve distribution suggest a gradual change of the faunal composition due to one dominant ecological gradient. Based on observations during long-term fieldwork (since 1986) in all seasons, the environmental parameter most likely responsible for lateral bivalve distributions is the varying suspension load of the water column. The latter, which was visible as clearly different water transparency at the respective sites, may originate from a variety of sources (e.g., POM of seagrass, coral-expelled zooxanthellae, coral mucus, zooplankton, phytoplankton) and generally increases from N to S along the channel due to accumulation in the main current (PILLER & PERVESLER, 1989) and during the course of the day. This general pattern of suspension transport is locally modified at sample location 4, due to its current-protected position and anthropogenic influence (tourist villages).

The bivalve distribution in different water depth suggests a dependence on the depth-related light penetration of the water column. Differences between stations 2 and 3 are explained by smaller water depth differences between the shallower and the deeper setting at station 3 and a suspected higher suspension load at station 3, which obscures a depth-related effect. However, applying a 10% confidence interval would reveal *T. maxima* as significant discriminator also at station 3.

All tridacnids are restricted to the Indo-Pacific, *Tridacna*

*maxima* being the species with the widest distribution (ROSEWATER, 1965) and with reported densities of up to 63 individuals/m<sup>2</sup> (SALVAT, 1969). According to YONGE (1980) *T. maxima* has the ability to penetrate substrates (preferentially mechanically but probably supported by chemical boring) and is byssally attached throughout life. In the area of investigation, however, large specimens of *T. maxima* were occasionally observed without byssus-attachment but lying free on the substrate. Generally, tridacnids are considered to be opportunistic bivalves which draw food material from several sources including filter feeding, uptake of dissolved matter through their epidermis, photosynthates released by endosymbiotic zooxanthellae, and the intracellular digestion of senescent endosymbiotic zooxanthellae (FANKBONER & REID, 1990). They probably obtain greatest metabolic benefits from the photosynthates produced by their zooxanthellae (GOREAU et al., 1973). Their ecological success in coral-reef waters is due to their association with the endosymbiotic zooxanthellae (YONGE, 1980), because tropical reefs are notoriously impoverished in mineral nutrients and plankton (YONGE, 1975). The tridacnids have essentially the same ecological needs as zooxanthellate corals, namely shallow, intensely illuminated water and high temperature. Their occurrence is consequently limited to coral reef areas, where they are confined to shallower water depth than zooxanthellate corals (YONGE 1974).

	sample location 1	sample location 2	sample location 3	sample location 4	sample location 5
Coral assemblages	<i>Porites</i> carpet	faviid carpet	faviid carpet	depauperate faviid carpet	<i>Sarcophyton</i> carpet
water depth	9 m	10 m	9 m	6 m - 9 m	6 m - 7 m
sampled area	2.25 m <sup>2</sup>	8 m <sup>2</sup>	6 m <sup>2</sup>	12 m <sup>2</sup>	5.25 m <sup>2</sup>
indiv./m <sup>2</sup>	36.00	9.75	9.50	5.33	3.62
% living individuals	92	96	84	78	43
number of taxa	5	7	8	12	5
diversity indices					
Simpson	0.65	0.66	0.78	0.90	0.77
Margalef	0.91	1.38	1.73	2.64	1.36
Information	1.22	1.37	1.71	2.26	1.46
Taxa	ind./m <sup>2</sup> %	ind./m <sup>2</sup> %	ind./m <sup>2</sup> %	ind./m <sup>2</sup> %	ind./m <sup>2</sup> %
<i>Barbatia setigera</i>	4.00 11.11	0.50 5.13	0.83 8.77	0.83 15.63	0.76 21.05
<b>Chamoidea</b>	<b>0.00 0.00</b>	<b>0.25 2.56</b>	<b>0.00 0.00</b>	<b>0.58 10.94</b>	<b>1.52 42.11</b>
<i>Chlamys livida</i>	0.00 0.00	0.00 0.00	0.00 0.00	0.08 1.56	0.00 0.00
<i>Ctenoides annulata</i>	0.89 2.47	0.88 8.97	0.50 5.26	0.25 4.69	0.00 0.00
<i>Isognomon legumen</i>	0.00 0.00	0.00 0.00	0.17 1.75	0.25 4.69	0.00 0.00
<i>Lima lima</i>	0.00 0.00	0.00 0.00	0.00 0.00	0.25 4.69	0.00 0.00
<i>Lopha cristagalli</i>	0.00 0.00	0.00 0.00	1.00 10.53	0.50 9.38	0.38 10.53
Ostreoidea	0.00 0.00	0.75 7.69	0.00 0.00	0.08 1.56	0.38 10.53
<b><i>Pedum spondyloideum</i></b>	<b>17.78 49.38</b>	<b>5.25 53.85</b>	<b>3.67 38.60</b>	<b>0.92 17.19</b>	<b>0.00 0.00</b>
<i>Spondylus marisrubi s.l.</i>	2.22 6.17	0.00 0.00	0.83 8.77	0.75 14.06	0.00 0.00
<i>Streptopinna saccata</i>	0.00 0.00	0.13 1.28	0.33 3.51	0.17 3.13	0.00 0.00
<b><i>Tridacna maxima</i></b>	<b>11.11 30.86</b>	<b>2.00 20.51</b>	<b>2.17 22.81</b>	<b>0.67 12.50</b>	<b>0.57 15.79</b>

Tab. 1. Basic data for all 5 sample locations with respect to lateral bivalve distribution. Bold letters indicate the statistically significant taxa according to the discriminant analysis. Classification of coral carpets according to RIEGL & PILLER (1997).

	Wilks' Lambda	F	Sig	Func 1	Func 2
<i>Barbatia setigera</i>	0.92	1.89	0.1195	0.3816	0.4949
<b>Chamoidea</b>	<b>0.77</b>	<b>6.79</b>	<b>0.0001</b>	<b>-0.2605</b>	<b>1.4456</b>
<i>Chlamys livida</i>	0.97	0.58	0.6789	-0.3288	2.2737
<i>Ctenoides annulata</i>	0.96	0.93	0.4528	0.3978	-0.2170
<i>Isognomon legumen</i>	0.95	1.20	0.3146	-0.2420	1.1820
<i>Lima lima</i>	0.92	1.87	0.1218	-0.3724	3.1667
<i>Lopha cristagalli</i>	0.96	1.00	0.4120	0.1088	0.1350
Ostreoidea	0.95	1.21	0.3128	0.1508	-0.3488
<b><i>Pedum spondyloideum</i></b>	<b>0.74</b>	<b>7.74</b>	<b>0.0000</b>	<b>0.3446</b>	<b>-0.0125</b>
<i>Spondylus marisrubi s.l.</i>	0.92	2.05	0.0941	0.4009	0.8110
<i>Streptopinna saccata</i>	0.98	0.48	0.7489	0.2462	0.0972
<b><i>Tridacna maxima</i></b>	<b>0.59</b>	<b>1.55</b>	<b>0.0000</b>	<b>0.9709</b>	<b>0.1843</b>

Fcn	Eigen value	% of Var	Can Corr	After Fcn	Wilks' Lambda	Chi <sup>2</sup>	Sig
1	1.6113	71.63	0.79	0	0.22	129.130	<b>0.000</b>
2	0.30	13.52	0.48	1	0.57	48.024	<b>0.044</b>
3	0.26	11.48	0.45	2	0.74	25.593	0.179
4	0.08	3.38	0.27	3	0.93	6.187	0.721

Tab. 2. Discriminant analyses using absolute frequencies of bivalve data at each sample location with respect to lateral bivalve distribution: data of the univariate statistics, the unstandardized canonical discriminant function coefficients and the canonical discriminant functions. Bold letters indicate statistically significant taxa.

In addition to these restrictions in general distribution, the present study shows that local variations in suspension load in the surroundings of a subtropical coral reef area fundamentally influence the occurrence of *T. maxima*. Due to its association with zooxanthellae, the bivalve is also a powerful tool for the indication of water depth differences in coral reef areas.

The coral-boring *Pedum spondyloideum* (Pl. 42/1) is a host-specific bivalve, associated with a variety of scleractinians (preferentially *Montipora* spp.) in the north-

ern Red Sea (KLEEMANN, 1990). KLEEMANN (1990) reports higher densities of *P. spondyloideum* in the west area of the northern Bay of Safage and especially at the channel entrance and correlates them not only with suitable host corals on well-developed coral carpets, but also with the higher nutrient contents of slowly flowing bay waters. Our results initially suggested a decrease of *P. spondyloideum* in the channel due to an increasing suspension load of the water column. In fact, however, the decrease of *P. spondyloideum* rather reflects the decrease of suitable host

	sample location 2				sample location 3			
	shallower setting		deeper setting		shallower setting		deeper setting	
coral assemblage	faviid carpet		faviid carpet		faviid carpet		faviid carpet	
water depth	10m		20 m		9m		15m	
sampled area	8m <sup>2</sup>		6m <sup>2</sup>		6m <sup>2</sup>		4m <sup>2</sup>	
indiv./m <sup>2</sup>	9.75		4.34		9.50		7.50	
% living individuals	96		90		84		81	
number of taxa	7		6		8		5	
diversity indices								
Simpson	0.66		0.61		0.78		0.68	
Margalef	1.38		1.53		1.73		1.18	
Information	1.37		1.25		1.71		1.31	
Taxa	ind./m <sup>2</sup>	%						
<i>Barbatia setigera</i>	0.50	5.13	0.33	7.69	0.83	8.77	1.25	16.67
Chamoidea	0.25	2.56	0.00	0.00	0.00	0.00	0.00	0.00
<i>Chlamys livida</i>	0.00	0.00	0.17	3.85	0.00	0.00	0.00	0.00
<i>Ctenoides annulata</i>	0.88	8.97	0.50	11.54	0.50	5.26	0.00	0.00
<i>Isognomon legumen</i>	0.00	0.00	0.50	11.54	0.17	1.75	0.00	0.00
<i>Lima lima</i>	0.00	0.00	0.00	0.00	0.00	0.00	0.50	6.67
<i>Lopha cristagalli</i>	0.00	0.00	0.00	0.00	1.00	10.53	0.75	10.00
Ostreoidea	0.75	7.69	0.00	0.00	0.00	0.00	0.00	0.00
<i>Pedum spondyloideum</i>	5.25	53.85	2.67	61.54	3.67	38.60	4.00	53.33
<i>Spondylus marisrubi</i> s.l.	0.00	0.00	0.00	0.00	0.83	8.77	1.00	13.33
<i>Streptopinna saccata</i>	0.13	1.28	0.00	0.00	0.33	3.51	0.00	0.00
<i>Tridacna maxima</i>	2.00	20.51	0.17	3.85	2.17	22.81	0.00	0.00

Tab. 3. Basic data of sample locations 2 and 3 with respect to bivalve distribution in different water depth.

	Wilks' Lambda	F	Sig.	Func 1
<i>Barbatia setigera</i>	1.00	0.05	0.818	0.5691
Chamoidea	0.97	1.29	0.262	2.8919
<i>Chlamys livida</i>	0.96	1.63	0.210	-1.1254
<i>Ctenoides annulata</i>	0.99	0.31	0.583	0.2761
<i>Isognomon legumen</i>	0.92	3.10	0.086	-0.7890
Ostreoidea	0.97	1.29	0.262	0.8072
<i>Pedum spondyloideum</i>	0.98	0.59	0.448	0.2015
<i>Streptopinna saccata</i>	0.98	0.62	0.436	2.6158
<b><i>Tridacna maxima</i></b>	<b>0.83</b>	<b>7.56</b>	<b>0.009</b>	<b>1.4653</b>
Significance of function: <b>0.0179</b>				

	Wilks' Lambda	F	Sig.	Func 1
<i>Barbatia setigera</i>	0.97	1.11	0.300	1.6527
<i>Ctenoides annulata</i>	0.97	0.92	0.344	-1.4583
<i>Isognomon legumen</i>	0.98	0.49	0.488	-4.0662
<i>Lima lima</i>	0.87	4.59	0.040	2.6815
<i>Lopha cristagalli</i>	1.00	0.00	1.000	0.2717
<i>Pedum spondyloideum</i>	0.99	0.42	0.519	0.3531
<i>Spondylus marisrubi</i> s.l.	0.98	0.50	0.483	0.4847
<i>Streptopinna saccata</i>	0.97	1.03	0.317	0.2469
<i>Tridacna maxima</i>	0.89	3.72	0.062	-0.3803
Significance of function: 0.1413				

Tab. 4. Discriminant analyses using absolute frequencies of bivalve data at sample location 2 with respect to vertical bivalve distribution: data of the univariate statistics, the unstandardized canonical discriminant function coefficients and significance of the canonical discriminant function. Bold letters indicate the statistically significant taxon.

Tab. 5. Discriminant analyses using absolute frequencies of bivalve data at sample location 3 with respect to bivalve distribution in different water depth: data of the univariate statistics, the unstandardized canonical discriminant function coefficients and significance of the canonical discriminant function.

order	superfamily	family	species	feeding strategies
Pteriomorpha	Arcoidea	Arcidae	<i>Barbatia setigera</i> (Reeve, 1844)	suspension feeder
	Pinnoidea	Pinnidae	<i>Streptopinna saccata</i> (Linnaeus, 1758)	suspension feeder
	Pterioidea	Isognomidae	<i>Isognomon legumen</i> (Gmelin, 1791)	suspension feeder
	Pectinoidea	Pectinidae	<i>Pedum spondyloideum</i> (Gmelin, 1791)	suspension feeder
			<i>Chlamys livida</i> (Lamarck, 1819)	suspension feeder
		Spondylidae	<i>Spondylus marisrubi</i> s.l. Röding, 1798	suspension feeder
		Limidae	<i>Lima lima</i> (Linnaeus, 1758)	suspension feeder
			<i>Ctenoides annulata</i> (Lamarck, 1819)	suspension feeder
		Ostreoidea	various phenotypes	suspension feeder
			<i>Lopha cristagalli</i> (Linnaeus, 1758)	suspension feeder
Heterodonta	Chamoidea		various phenotypes	suspension feeder
	Tridacnoidea		<i>Tridacna maxima</i> (Röding, 1798)	various sources

Tab. 6. Feeding strategies of the encountered bivalve taxa (after MORTON, 1983).

corals, which are interpreted to be more sensitive to the high suspension load in the channel than the bivalve. Their dominance at the deeper settings of sampling sites 2 and 3 consequently indicates the presence of host corals over a relatively broad depth range.

The heterodont Chamoidea are well-known suspension feeding and cementing colonizers of dead coral bases and other hard substrates in the Indo-Pacific (MORTON, 1983a, b; OLIVER, 1992, 1995). In the study area they occur frequently on various hard substrates, especially on *Sarcophyton* carpets (ZUSCHIN & PILLER, in press). The present investigation indicates a dominance of Chamoidea in areas with both large bare rocky surfaces and an appropriate food supply in the form of a high suspension load. The interpretation of laterally shifting bivalve assemblages due to a varying suspension load in the water column is supported by field observations: At sampling site 5, which is interpreted to exhibit the highest suspension load, some of the oysters (*Hyotissa hyotis*; Pl. 2/3) show gigantism (largest observed specimen has a dimension of 31 x 21 cm). Similar occurrences of 'giant oysters' in the northern Bay of Safaga were observed in other areas with high suspension load. *Lopha cristagalli*, despite not being a statistically significant discriminator, produces striking agglomerations at the more suspension-affected sample locations 3, 4 and 5. These agglomerations almost always show a succession: The base is provided by a dead coral colony. This is encrusted by a *Spondylus marisrubri* s.l., which is colonised by varying numbers (up to 10) of *Lopha cristagalli* (Pl. 42/4).

The gradual horizontal taxonomic shift is accompanied by a continuous decrease of both bivalve density and percentage of living individuals. The depth differences in bivalve associations mainly involve a lower bivalve density at the deeper sites, whereas the percentage of living individuals remains largely the same. These differences in taxonomic composition, density and live-dead ratios of bivalve faunas are related to complex interactions of bottom types, suspension load and water depth: Bottom types provide potential bivalve habitats, which influence the taxonomic composition and density distributions. Borers of living corals (*Pedum*), for example, disappear with decreasing scleractinian cover, whereas encrusters of dead corals and other hard substrates become dominant (Chamoidea) or striking (Ostreoidea) in areas with more bare rocky surface. The relative abundance of living and dead molluscs is intimately correlated with the presence of living scleractinians, which rapidly overgrow dead molluscs. Therefore the percentage of dead bivalve specimens is highest at sampling site 5, where nearly no scleractinians occur. Suspension load, in contrast, provides food for most bivalves, but limits the occurrence of scleractinians along with their specific habitats. *T. maxima* is an exception in that it is not related to a specific hard substrate. Based on the similar ecological needs of this bivalve and scleractinians it varies parallel with corals directly in response to suspension load and light penetration of the water column.

## 5 CONCLUSION

The investigated bivalve fauna reflects the environmental parameters through its feeding strategies and substrate preferences: the feeding strategies separate the bivalves into light-dependant and suspension-dependant organisms. The light-dependant *T. maxima* indicates very shallow and clear water conditions. The suspension-dependant bivalves indicate environmental parameters indirectly by their substrate preferences: the coral boring *Pedum spondyloideum* depends on the presence of host corals, which prefer clear water but have a less restricted depth dependence than *T. maxima*. Encrusters (Ostreoidea, Chamoidea, Spondylidae) need dead hard substrates, which are extensive in areas with high suspension load and corresponding low scleractinian cover.

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