## Long-term fluctuations of coral communities at Aqaba and on Sanganeb-Atoll (northern and central Red Sea) over more than a decade

#### Langzeituntersuchungen über mehr als eine Dekade an Korallenvergesellschaftungen bei Aqaba und am Sanganeb-Atoll (nördliches und zentrales Rotes Meer)

by

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#### Abstract

Quantitative analyses of coral communities had been carried out on test squares in a fore reef area of a fringing reef near Aqaba (northern Red Sea) and on inner and outer reef slopes on Sanganeb-Atoll (central Red Sea) in 1976 (MERGNER & SCHUHMACHER, 1981) and 1980 respectively (MERGNER & SCHUHMACHER, 1985a). Further investigations at Aqaba in 1989 and on Sanganeb in 1991 yielded information on the growth and mortality of individual colonies as well as data on long-term fluctuations of community parameters. Near Aqaba, data of the test square U-7 (5 x 5 m in size) at a depth of some 10 m showed that significant changes occurred in the composition of the coral reef community between 1976 and 1989: xeniid soft coral colonies completely disappeared during this time. In total, 112 species of Cnidaria including 88 Scleractinia were found in the test square in 1976 and 1989. The diversity (H' = 3.23 in 1989–H' = 3.42 in 1976, based on Cnidaria-coverage) compared to the highest in the world. On Sanganeb-Atoll coral communities of four test squares (TQ-IV) of 5 x 5 m were analyzed. The data of 1991 for four TQs comprised a total of 3034 colonies of 130 species of stony corals, soft corals and hydrocorals, among them 86 species of Scleractinia. A mean diversity of H' = 2.80 in 1991 and H'= 2.58 in 1980 (based on Cnidaria-coverage) was recorded. The comparison of the qualitative analyses of the Sanganeb TQs in 1980 and 1991 proved the constancy of the coral communities. The analysis of the TQs near Aqaba and on Sanganeb-Atoll, however, showed significant differences when compared latitudinally. On Sanganeb-Atoll the data suggest that the stable abiotic conditions support a relative constancy of the coral communities in the reef areas studied, whereas near Aqaba considerable alterations become evident over a decade. Higher fluctuations of abiotic conditions (light, temperature) near the boundary of the geographical reef belt as well as grazing by sea urchins may account for retarded regeneration after occasional disturbances.

#### Zusammenfassung

Quantitative Analysen von Korallengemeinschaften sind in Testquadraten im Vorriff eines Saumriffes bei Aqaba (nördliches Rotes Meer) und an inneren und äußeren Riffhängen des Sanganeb-Atolls (mittleres Rotes Meer) im Jahr 1976 (MERGNER & SCHUHMACHER, 1981) bzw. 1980 (MERGNER & SCHUHMACHER, 1985a) durchgeführt worden. Erneute Untersuchungen bei Aqaba im Jahre 1989 bzw. am Sanganeb-Atoll im Jahre 1991 lieferten nicht nur Informationen bezüglich Zuwachs und Lebenserwartung von individuellen Kolonien, sondern auch bezüglich Langzeit-Schwankungen abstrakter Kenngrößen dieser Besiedler-Gemeinschaften. In Agaba zeigen die Daten des Testquadrates U-7 (5 x 5 m; in 10 m Tiefe) bedeutende Veränderungen in der Zusammensetzung der Korallengemeinschaft zwischen den Jahren 1976 und 1989. Kolonien der Xeniidae-Weichkorallen verschwanden vollständig in diesem Zeitraum. Insgesamt wurden 112 Arten von Cnidaria bzw. 88 Scleractinia-Arten im Testquadrat während der Untersuchungsdaten gefunden. Die Diversität (H' = 3.23 in 1989 bzw. H' =3.42 in 1976, basierend auf der Cnidaria-Bedeckung) gehört zu den höchsten Werten weltweit. Die Korallengemeinschaften des Sanganeb-Atolls wurden in vier Testquadraten (5 x 5 m Größe; ca. 10 m Tiefe) analysiert. Die Daten von 1991 betreffen 3034 Kolonien von 130 Arten Steinkorallen, Weichkorallen und Hydrokorallen, unter ihnen 86 Arten von Scleractinia, bezogen auf alle vier TQs. Die Diversität liegt im Mittel bei H' = 2.80 in 1991 bzw. H' = 2.58 in 1980, basierend auf der Cnidaria-Bedeckung. Der Vergleich der qualitativen Analysen der Sanganeb TQs in den Jahren 1980 und 1991 belegt eine

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weitgehende Konstanz der Korallengemeinschaften. Im latitudinalem Vergleich hingegen offenbarte die Analyse der TQs bei Aqaba und am Sanganeb-Atoll deutliche Unterschiede. Die Daten für das Sanganeb-Atoll weisen darauf hin, daß stabile Umweltbedingungen eine relative Konstanz in den untersuchten Riffabschnitten gewährleisten, während bei Aqaba beträchtliche Veränderungen innerhalb einer über zehnjährigen Periode offensichtlich werden. Größere Schwankungen von abiotischen Bedingungen (Licht, Temperatur) nahe der Grenze des geographischen Riffgürtels sowie Weidedruck durch Seeigel scheinen für eine verzögerte Regeneration nach gelegentlichen Störungen verantwortlich sein.

#### 1. Introduction

Coral reef communities are dynamic. The space occupied by hermatypic organisms, by ahermatypic organisms and open space are continuously changing. In order to identify the extent of such fluctuations, we recorded quantitatively the benthic composition of fore reef areas at different positions on a latitudinal gradient over a time span of more than ten years.

Three underlying questions are:

1. If species composition does change qualitatively and quantitatively, do higher community characteristics, such as diversity, remain unchanged or vary in the same degree? Is a "trend" visible?

2. Can life history traits be recognized?

3. Do the geographically different community structures reflect a latitudinal gradient?

The 2270 km long basin of the Red Sea stretches from the tropics to the northern outpost of reef development in the Indopacific at the tip of the Gulf of Aqaba. Therefore seasonal differences in illumination and temperature can be expected to be more pronounced in the northern than in the central Red Sea and even reach the subsistence minimum of reef-building corals.

MERGNER & SCHUHMACHER (1981, 1985a) had already provided detailed quantitative analyses of the community composition on the fore reef at Aqaba for the year 1976 and on the outer and inner reef slopes of Sanganeb-Atoll in the central Red Sea for the year 1980; repeat investigations of these areas in 1989 (MERGNER et al., 1992) and 1991 respectively yielded a second "snapshot" of these particular sections of the reef.

The distance between the two localities allows the hypothesis of the "dynamic equilibrium model" (HUS-TON, 1979) to be tested. According to that hypothesis, a high diversity is maintained as long as the frequency of disturbance and speed of recovery are in equilibrium. The temperature (five degrees higher at Sanganeb than at Aqaba) and the geographically determined high amount of illumination should favour a more rapid recovery on Sanganeb than at Aqaba resulting in larger colonies and fewer species per area.



Figure 1: Map of the Red Sea, including isotherms (January – May) and the locations of study sites A = Aqaba and B = Sanganeb-Atoll. After SCHUHMACHER & MERGNER (1985a).

#### 2. Study site and time

The coral reefs of the northern Gulf of Aqaba are among the most northerly ones in the world at a latitude of  $29^{\circ} 30'$ N. The test area, a square of 5 x 5 m, is on the middle fore reef about 150 m off the Marine Science Station at Aqaba (Figs. 1A and 2), in the coastal fringing reef at a depth of 10 m. The bottom slopes at a gradient of about 20 %. This area is characterized by a regime of moderate illumination and current conditions. Previous studies of the sublittoral biota of the 25 km Jordanian coastline (MERGNER & SCHUHMACHER, 1974) had revealed that this area was a representative section of the fore reef least disturbed by man.

Fig. 2 shows details of the reef south of the various ports of Aqaba and the location of the 25 m<sup>2</sup> square (called U–7) in the fore reef. The Sanganeb-Atoll is located in the central Red Sea at a latitude of  $19^{\circ} 45'$  N and  $37^{\circ} 26'$  E (30 km off Port Sudan; Figs. 1B and 3).

The study areas were four 5 x 5 m squares at a depth of 10 m along a SSW–NNE transect across the Sanganeb-Atoll. They were situated along a line bisecting the angle between the surface current generated by the monsoon and the water movement produced by the day and night breeze. Hence the two squares facing north-east were exposed to the swell of the open sea and the lagoon respectively,

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Community parameters	Sang TQ I–IV	aneb (mean)	Aqaba test area U–7		
	1980	1991	1976	1989	
Cnidaria:					
number of colonies	666	759	2050	1541	
colony size (cm <sup>2</sup> )	189	150	52	49	
diversity (H')	2.58	2.80	3.42	3.23	
evenness $(J')$	0.64	0.67	0.74	0.73	
hermatypic corals, % of TQ	34.8	26.5	21.6	28.0	
ahermatypic corals, % of TQ	15.4	18.9	20.6	1.4	

Table 1: Comparison of community parameters (number and size of colonies, diversity, evenness) of Cnidaria between the four test areas of Sanganeb-Atoll in 1980 and 1991 (mean) and the test area U-7 near Aqaba in 1976 and 1989.

whereas the other two squares facing south-west were protected from this hydrodynamic impact.

Fig. 3 shows details of the atoll and the locations of the test squares (called TQ I–IV). Data collection at Aqaba took place during spring of 1976 and 1989.

An additional survey in spring 1982 is not considered here. The investigations on Sanganeb-Atoll were carried out during March/April in 1980 and 1991.

#### 3. Methods

The test squares U–7 at Aqaba and the TQ I–IV on Sanganeb-Atoll are each  $5 \times 5$  m in size, they are laid out



**Figure 2:** Location of the study site south of the town of Aqaba. Left: shore line with fringing reef near the Marine Science Station (hatched area: harbour facilities built in 1977/78); center and right: top plan view and profile of a transect perpendicular to the shore with test square U–7. After MERGNER & SCHUHMACHER (1981).

at a depth of approximately 10 m, marked off by nylon ropes.

The size of the Aqaba square had been determined after a precedent species/area survey as the smallest one representing all species of that reef area. The Sanganeb squares were identically sized for the sake of comparison. The colonization of the area by Cnidaria and other sessile organisms was mapped colony by colony by means of underwater drawings, photographs and video tapes. Specimens which could not be identified in situ were collected directly next to the test area and identified later. Nearly all the original nylon ropes marking the squares were located during repeat investigations. We were therefore able to remap the identical areas.

Further details of the methods used are given by MERGNER & SCHUHMACHER (1981).

Calculations of species diversity (Shannon-Wiener Index) were made using both coverage of colonies (square centimeters) and the number of colonies. These two



**Figure 3:** Map (left) and profile (right) of Sanganeb-Atoll near Port Sudan with location of test areas TQ I–IV After SCHUHMACHER & MERGNER (1985a).



**Figure 4:** Percentage of coverage of Anthozoans, Non-Anthozoans and dead substrates in the TQ U–7 near Aqaba, 1976 and 1989 (left) and in the TQs I–IV on Sanganeb-Atoll, 1980 and 1991 (right).



**Figure 6:** Percentage of scleractinian suborders in the TQ U–7 near Aqaba, 1976 and 1989 (left) and in the TQs I–IV on Sanganeb-Atoll, 1980 and 1991 (right).

measures are correlated, but, as corals are sessile organisms, both their size and their numerical presence are of ecological significance.

#### 4. Results

This report presents the data of the species concerned, number and size of colonies, living coverage, abundance, growth forms, and species diversity.

The abundance of the species recorded on each monitoring date is given in the Table 2 and in Appendix 1.

Fig. 4 shows that significant changes occurred in the composition of the coral reef community at Aqaba between 1976 and 1989: xeniid soft coral colonies completely disappeared during this time. Thus the share of the Alcyonaria in the total area decreased from 20.6 to 1.4%, whereas that of the Scleractinia increased from 21.6 to 28.0% (Fig. 5). The number of cnidarian colonies dropped from 2050



**Figure 5:** Percentage of anthozoan coverage (Alcyonaria, Scleractinia) in the TQ U–7 near Aqaba, 1976 and 1989 (left) and in the TQs I–IV on Sanganeb-Atoll, 1980 and 1991 (right).



Figure 7: Percentage of scleractinian growth forms in the TQ U– 7 near Aqaba, 1976 and 1989 (left) and in the TQs I–IV on Sanganeb-Atoll, 1980 and 1991 (right).

in 1976 to 1541 in 1989, while the mean colony size (approx. 50 cm<sup>2</sup>) remained almost constant (Tab. 1). In total, 112 species of Cnidaria including 88 Scleractinia were found in the test square on the monitoring dates in 1976 and 1989 (Appendix 1).

Within the Scleractinia the suborder Astrocoeniina occupied a major part of the total area, especially in 1989 (63.2% of anthozoan coverage). The corresponding figures for Faviina and Fungiina were much smaller and were subject to different changes (Fig. 6).

Fig. 7 shows that scleractinian growth forms (related to the share of Cnidaria) are dominated by branching corals (48.9%). Due to the disappearance of xeniids the total anthozoan coverage dropped from 42.2 to 29.8% (Fig. 4). In spite of the major shifts in the composition of the sessile community the species diversity is still largely maintained (H' = 3.23, compared to H' = 3.42 in 1976, based on Cnidaria-coverage).

		mean 1	976:1980		mean 1989:1991			
species	colon U-7	y size :I–IV	colony number U-7:I–IV		colony size U-7:I–IV		colony number U-7:I–IV	
Parerythropodium fulvum (7;5)	1	1.29	3.87	1	1.29	1	1	1.69
Sarcophyton ehrenbergi (8;6)	2.47	1	2.66	1	1	1.10	4.00	1
Stylophora pistillata (36 ; 25)	1	1.19	11.39	1	1	1.82	29.29	1
Seriatopora hystrix (38;24)	1	1.29	1	2.75	1	4.25	1	14.00
Acropora hemprichi (45 ; 29)	1	14.19	1	2.08	1	4.81	2.27	1
Acropora variabilis (51;33)	1	3.14	6.74	1	1	1.32	38.57	1
Montipora meandrina (56 ; 39)	1	2.19	31.00	1	1.49	1	37.45	1
Montipora venosa (60; 42)	1.68	1	2.67	1	1	4.47	2.00	1
Pavona varians (67; 49)	1	1.38	3.22	1	1	2.27	4.00	1
Favia laxa (86; 71)	1	1.85	5.60	1	1	7.23	1.60	1
Favia stelligera (90 ; 73)	1	3.43	2.40	1	1	2.44	4.86	1
Goniastrea pectinata (97 ; 79)	1	3.03	9.82	1	1	1.23	8.51	1
Goniastrea retiformis (98 ; 80)	1	2.38	6.35	1	1	2.77	2.49	1
Leptastrea bottae (103;83)	1	3.11	38.67	1	1.83	1	9.33	1
Leptastrea transversa (105 ; 85)	1.21	1	11.00	1	1.64	1	20.00	1
Cyphastrea chalcidicum (106; 62)	1	2.33	1.88	1	1	1.05	4.00	1
Cyphastrea microphthalma (107;63)	1	1.13	27.00	1	1	2.95	11.69	1
Echinopora gemmacea (109;66)	1	6.32	1.71	1	1	6.70	2.20	1
E. gemmacea var. fruticulosa (110; 67)	1	3.46	6.40	1	1	13.71	10.67	1
Galaxea fascicularis (113; 88)	1	4.47	1	1.17	1.16	1	1	1.69
Lobophyllia corymbosa (115;91)	1	5.91	1	10.75	1	1.73	1	8.50

 Table 2: Comparison of size and number of colonies between the test area U-7 near Aqaba (1976 and 1989) and the average of the four Sanganeb areas TQ I-IV (1980 and 1991)

In 1991, the data of the coral communities in the four test squares on Sanganeb-Atoll comprised a total of 3034 colonies of 130 species of stony corals, soft corals and hydrocorals, among them 86 species of Scleractinia in all four TQs (Appendix 1). The respective figures for 1980 are given in Figs. 4–7. The cnidarian cover of the four test squares ranged from 39.4 to 57.5% with a mean diversity of H' = 2.80. Each TQ contained 41–49 scleractinian species with 226 to 424 colonies. With respect to scleractinian growth forms, branching species had a mean share of 29.7%, massive corals 19.7%, encrusting corals 7.1% and solitary corals 0.3% of the total living coverage (Fig. 7). The share of Alcyonaria ranged between 2.7 and 28.9%.

The comparison of the qualitative analyses of the Sanganeb-TQs in 1980 and 1991 proved the constancy of the coral communities. However, although the mean number of colonies increased from 666 to 759, the decrease in mean colony size from 189 to 150 cm<sup>2</sup> (Tab. 1) resulted in a reduction of mean anthozoan coverage from 48.2 to 43.1% (Fig. 4). Furthermore, the share of Scleractinia decreased significantly from 32.7 to 24.1%, whereas the share of Alcyonaria sligthly increased from 15.0 to 18.4% (Fig. 5). Fig. 6 shows that all suborders of Scleractinia had lost between 3 and 5% in 1991.

The decline of Scleractinia affected all growth forms: the share of branching corals fell from 30.7 to 29.7%; massive corals from 27.6 to 19.7% and encrusting corals from

8.5 to 7.1% of total Cnidaria cover (Fig. 7).

Tab. 2 compares the Aqaba and Sanganeb squares with respect to colony size and numbers of 21 alcyonarian and scleractinian species. The ratios of the 1976–1980 comparison have been recalculated, since the data given by MERGNER & SCHUHMACHER (1985b) unfortunately include some errors. With few exceptions, the colonies of Sanganeb are larger than the Aqaba colonies which, however, are more numerous.

Furthermore, it is apparent from the data that different species of corals have undergone different types of changes in the time between the surveys. The specific life histories, however, cannot be discussed in this paper.

#### 5. Discussion

The results call for discussion of two aspects a) the reasons for and extent of changes on the spot over time and b) comparison between the two study areas. A detailed discussion of the community dynamics at Aqaba and on Sanganeb-Atoll will be provided separately. Here, the main features of development at the two sites are put side by side and compared.

The most striking feature at Aqaba is the complete disappearance of xeniid soft corals. In March 1982, SCHUH-MACHER found that all xeniids had been wiped out along the Jordanian coast. Reinvasion took place only slowly: in 1989 several xeniid species could again be recognized in the reefs at Aqaba but no colony had yet colonized the test square. The space left by xeniids was partly taken over by scleractinian corals particularly by new settlement of pioneer species such as *Stylophora pistillata*, *Acropora variabilis*, *Acropora squarrosa* and by the growth and enlargement of colonies still persisting. Nevertheless nearly 70 % of the bottom area was free in 1989 (compared to some 57 % in 1976) – most probably due to the grazing activity of a high number of *Diadema* sea urchins (7 animals per m<sup>2</sup> – KROLL pers. com.).

The squares on Sanganeb-Atoll each of which is characterized by a specific community (-"physiographische Leitarten" – MERGNER & SCHUHMACHER, 1985a) preserved these site specific characteristics, although a storm obviously had passed the atoll one or two years before the second inspection date. With no grazing sea urchins present, scleractinian corals are recolonizing the empty space but have not yet reached the same coverage as before. This can be detected from the high number of colonies, the high percentage of branching forms (including mainly pioneer types), the low mean colony size and the total scleractinian coverage in comparison with the respective data from 1980.

MERGNER & SCHUHMACHER (1985b) stressed the point that the mean diameter of colonies on Sanganeb is larger than at Aqaba. This feature generally persisted. It may be concluded that favorable conditions (especially light, temperature, lack of grazers) in the central Red Sea result in a growth rate of corals which enables them to recover rapidly after occasional catastrophes. In contrast, the growth rate at Aqaba is scarcely sufficient to overcome the high "colonization resistance" of that site. "Colonization resistance" is understood as "sum" or total effect of abiotic parameters (e.g. illumination, temperature, sedimentation) and biotic conditions (e.g. grazing pressure, fall of larvae) which prevent sessile organisms from settling with subsequent growth at the maximum rate and of the maximum extent.

The two snapshots of the community with an interval of more than a decade permit the preliminary conclusion that general community characteristics such as diversity, mean colony size and growth form, change slowly and remain distinctly different in the central Red Sea and at its northern end. A more detailed comparison of the communities is in preparation.

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#### 6. References

- HUSTON, M., 1979. A general hypothesis of species diversity. — Am. Nat. 113(1):81–101, Chicago.
- MERGNER, H., & SCHUHMACHER, H., 1974. Morphologie, Ökologie und Zonierung von Korallenriffen bei Aqaba, (Golf von Aqaba, Rotes Meer). — Helgoländer Wiss. Meeresunters., 26:238–358, Hamburg.
- MERGNER, H. & SCHUHMACHER, H., 1981. Quantitative Analyse der Korallenbesiedlung eines Vorriffareals bei Aqaba (Rotes Meer).—Helgoländer Meeresunters., 34:337–354, Hamburg.
- MERGNER, H. & SCHUHMACHER, H., 1985a. Quantitative Analyse von Korallengemeinschaften des Sanganeb-Atolls (mittleres Rotes Meer). I. Die Besiedlungsstruktur hydrodynamisch unterschiedlich exponierter Außen- und Innenriffe. — Helgoländer Meeresunters., 39:375–417, Hamburg.
- MERGNER, H. & SCHUHMACHER, H., 1985b. Quantitative analysis of coral communities on Sanganeb-Atoll (central Red Sea) comparison with Aqaba reefs (northern Red Sea). — Proc. 5<sup>th</sup> Int. Coral Reef Congr., Tahiti., 6:243–248, Tahiti.
- MERGNER, H., SCHUHMACHER, H. & KROLL, D. K., 1992. Long-term changes in the coral community of a fore reef area near Aqaba (Red Sea): 1976–1989. — Proc. 7<sup>th</sup> Int. Coral Reef Symp. Guam, 1:104–113, Guam.
- SCHUHMACHER, H. & MERGNER, H. 1985. Quantitative Analyse von Korallengemeinschaften des Sanganeb-Atolls (mittleres Rotes Meer). II. Vergleich mit einem Riffareal bei Aqaba (nördliches Rotes Meer) am Nordrande des indopazifischen Riffgürtels. — Helgoländer Meeresunters., 39:419–440, Hamburg.

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4 5 6 7 8 9 10 11 125 12 13 126 14 15 127 16 17 18 128 19	3	SCYPHOZOA Rhizostomeae Cassiopeidae Cassiopea andromeda Stylasteridae Distichopora violacea ANTHOZOA, Octocorallia Stolonifera Tubiporidae Tubiporidae Tubipora musica Alcyonaria Alcyoniidae Cladiella pachyclados	135 28 29 30 31 136	17	Xenia sp. Heteroxenia fuscescens Anthelia fishelsoni Anthelia glauca Sympodium caeruleum Gorgonaria Melithaeidae Acabaria biserialis
5 6 7 8 9 10 11 125 12 13 126 14 15 127 16 17 18 128 19	3	RhizostomeaeCassiopeidaeCassiopea andromedaStylasteridaeDistichopora violaceaANTHOZOA, OctocoralliaStoloniferaTubiporidaeTubiporiaAlcyonariaAlcyoniidaeCladiella pachyclados	28 29 30 31 136		Heteroxenia fuscescens Anthelia fishelsoni Anthelia glauca Sympodium caeruleum Gorgonaria Melithaeidae Acabaria biserialis
5 6 7 8 9 10 11 125 12 13 126 14 15 127 16 17 18 128 19	3	Cassiopeidae Cassiopea andromeda Stylasteridae Distichopora violacea ANTHOZOA, Octocorallia Stolonifera Tubiporidae Tubipora musica Alcyonaria Alcyoniidae Cladiella pachyclados	29 30 31 136	15	Anthelia fishelsoni Anthelia glauca Sympodium caeruleum <b>Gorgonaria Melithaeidae</b> Acabaria biserialis
5 6 7 8 9 10 11 125 12 13 126 14 15 127 16 17 18 128 19	3	Cassiopea andromeda Stylasteridae Distichopora violacea ANTHOZOA, Octocorallia Stolonifera Tubiporidae Tubipora musica Alcyonaria Alcyoniidae Cladiella pachyclados	30 31 136		Anthelia glauca Sympodium caeruleum Gorgonaria Melithaeidae Acabaria biserialis
5 6 7 8 9 10 11 125 12 13 126 14 15 127 16 17 18 128 19	3	Stylasteridae Distichopora violacea ANTHOZOA, Octocorallia Stolonifera Tubiporidae Tubipora musica Alcyonaria Alcyoniidae Cladiella pachyclados	31 136		Sympodium caeruleum Gorgonaria Melithaeidae Acabaria biserialis
5 6 7 8 9 10 11 125 12 13 126 14 15 127 16 17 18 128 19	3	Distichopora violacea ANTHOZOA, Octocorallia Stolonifera Tubiporidae Tubipora musica Alcyonaria Alcyoniidae Cladiella pachyclados	136		Gorgonaria Melithaeidae Acabaria biserialis
5 6 7 8 9 10 11 125 12 13 126 14 15 127 16 17 18 128 19	3	ANTHOZOA, Octocorallia Stolonifera Tubiporidae Tubipora musica Alcyonaria Alcyoniidae Cladiella pachyclados			<b>Melithaeidae</b> Acabaria biserialis
6 7 8 9 10 11 125 12 13 126 14 15 127 16 17 18 128 19	3	Stolonifera Tubiporidae Tubipora musica Alcyonaria Alcyoniidae Cladiella pachyclados			Acabaria biserialis
6 7 8 9 10 11 125 12 13 126 14 15 127 16 17 18 128 19	3	<b>Tubiporidae</b> <i>Tubipora musica</i> Alcyonaria <b>Alcyoniidae</b> <i>Cladiella pachyclados</i>			
6 7 8 9 10 11 125 12 13 126 14 15 127 16 17 18 128 19	3	Tubipora musica Alcyonaria <b>Alcyoniidae</b> Cladiella pachyclados	32		
6 7 8 9 10 11 125 12 13 126 14 15 127 16 17 18 128 19	3	Alcyonaria Alcyoniidae Cladiella pachyclados			Clathraria rubrinodis
7 8 9 10 11 125 12 13 126 14 15 127 16 17 18 128 19		Alcyoniidae Cladiella pachyclados			ANTHOZOA, Hexacorallia
7 8 9 10 11 125 12 13 126 14 15 127 16 17 18 128 19		Cladiella pachyclados			Corallimorpharia
7 8 9 10 11 125 12 13 126 14 15 127 16 17 18 128 19					Actiniaria
7 8 9 10 11 125 12 13 126 14 15 127 16 17 18 128 19	4	<b>T T T T T T T T T T</b>			Aliciidae
8 9 10 11 125 12 13 126 14 15 127 16 17 18 128 19	4	Lobophytum pauciflorum			Triactis producta
8 9 10 11 125 12 13 126 14 15 127 16 17 18 128 19	•	Lobophytum sp.			Stoichactidae
8 9 10 11 125 12 13 126 14 15 127 16 17 18 128 19	5	Parerythropodium fulvum			Entacmaea quadricolor
9 10 11 125 12 13 126 14 15 127 16 17 18 128 19	6	Sarcophyton ehrenbergi			Heteractis aurora
10 11 125 12 13 126 14 15 127 16 17 18 128 19		Sarcophyton elegans			Scleractinia
11 125 12 13 126 14 15 127 16 17 18 128 19		Sinularia candidula			Thamnasteriidae
125 12 13 126 14 15 127 16 17 18 128 19		Sinularia dactyloclados	33		Psammocora haimeana
12 13 126 14 15 127 16 17 18 128 19		Sinularia erecta	34		Psammocora nierstraszi
13 126 14 15 127 16 17 18 128 19		Sinularia flabelliclavata		19	Psammocora profundacella
126 14 15 127 16 17 18 128 19		Sinularia gardineri		17	Astrocoeniidae
14 15 127 16 17 18 128 19		-	35	98	Stylocoeniella armata
15 127 16 17 18 128 19	7	Sinularia heterospiculata	55	70	Pocilloporidae
127 16 17 18 128 19	7	Sinularia leptoclados	36	25	-
16 17 18 128 19		Sinularia minima	30		Stylophora pistillata
17 18 128 19		Sinularia muqeblae	107	99	Stylophora prostrata
18 128 19		Sinularia notanda	137	<u> </u>	Stylophora subseriata
128 19		Sinularia polydactyla	37	23	Seriatopora caliendrum
19		Sinularia querciformis	38	24	Seriatopora hystrix
	8	Sinularia recurvata	39	20	Pocillopora damicornis
20		Sinularia schuhmacheri	40		Pocillopora verrucosa
20		Nephtheidae			Acroporidae
20	10	Nephthea albida	41	35	Astraeopora myriophthalma
		Nephthea laevis	42		Acropora capillaris
21		Dendronephthya hemprichi	43		Acropora corymbosa
	9	Dendronephthya sp.	138		Acropora digitifera
22		Stereonephthya cundabiluensis	139	27	Acropora eurystoma
23		Litophyton arboreum		28	Acropora forskali
24	11	Paralemnalia eburnea		26	Acropora granulosa
25	11	Paralemnalia thyrsoides	44		Acropora cf. haimei
25		a araichnana myrsolaes	45	29	Acropora hemprichi
129	11 12	Venjidae	45 46	30	Acropora humilis
		Xeniidae Xenia biseriata	40 47	50	Acropora hyacinthus
130 131		<b>Xeniidae</b> Xenia biseriata Xenia blumi	4/	31	Acropora pharaonis

### Appendix 1: Colonization by Cnidaria in the four test areas of Sanganeb-Atoll (1980 and 1991) and the test quadrat U-7 near Aqaba (1976 and 1989)

#### Appendix 1 (continued)

no [-IV	U–7	order, genus, species	no I–IV	U–7	order, genus, species
49	32	Acropora squarrosa			Faviidae
50		Acropora superba		61	Caulastrea tumida
51	33	Acropora variabilis	84	69	Favia amicorum
52	34	Acropora sp.	85	70	Favia favus
	100	Montipora edwardsi	86	71	Favia laxa
53	37	Montipora effusa	87	72	Favia pallida
54		Montipora ehrenbergi	88		Favia rotumana
55		Montipora granulosa	89		Favia speciosa
56	39	Montipora meandrina	90	73	Favia stelligera
57	40	Montipora monasteriata		74	Favia sp.
58	41	Montipora stilosa	142	75	Favites abdita
20	38	Montipora stilosa var. eilatensis	91	106	Favites complanata
59	50	Montipora tuberculosa	92	107	Favites flexuosa
60	42	Montipora venosa	93		Favites halicora
61		Montipora verrucosa		76	Favites peresi
62	43	Montipora sp.	94		Favites pentagona
02	45	Agariciidae	95		Favites rotundata
	47	Pavona cactus		77	Favites sp.
63		Pavona clavus	96	78	Goniastrea edwardsi
140	48	Pavona decussata	97	79	Goniastrea pectinata
64	40	Pavona divaricata	98	80	Goniastrea retiformis
65		Pavona explanulata		81	Goniastrea sp.
66	103	Pavona maldivensis	99	87	Platygyra daedalea
67	49	Pavona varians	143	108	Platygyra lamellina
68	102	Leptoseris mycetoseroides	144		Platygyra sinensis
00	45	Leptoseris sp.	100		Leptoria phrygia
69	44	Gardineroseris planulata	101		Oulophyllia crispa
07	46	Pachyseris speciosa		82	Hydnophora exesa
	40	Siderastreidae	102		Hydnophora microconus
70	50	Coscinaraea monile	103	83	Leptastrea bottae
/0	50	Fungiidae	104	84	Leptastrea purpurea
	51	Cantharellus doederleini	105	85	Leptastrea transversa
	52	Cycloseris sp.	106	62	Cyphastrea chalcidicum
71	52	Fungia echinata	107	63	Cyphastrea microphthalma
72	53	Fungia fungites	108	64	Cyphastrea serailia
12	54	Fungia granulosa		65	Cyphastrea sp.
141	104	Fungia horrida	109	66	Echinopora gemmacea
73	101	Fungia klunzingeri	110	67	E. gemmacea var. fruticulosa
74		Fungia scutaria	111	68	Echinopora lamellosa
<i>,</i> .	105	Ctenactis echinata			Oculinidae
75	105	Herpolitha limax	112		Galaxea astreata
.5		Poritidae	113	88	Galaxea fascicularis
76	55	Alveopora daedalea			Merulinidae
77		Goniopora minor		89	Merulina ampliata
	56	Goniopora planulata	145	109	Merulina scheeri
78		Goniopora tenuidens			Mussidae
	57	Goniopora sp.		110	Blastomussa merleti
	58	Porites (Synarea) convexa	114		Scolymia vitiensis
79	20	Porites echinulata	115	91	Lobophyllia corymbosa
80	59	Porites lutea	116	93	Lobophyllia hemprichii
81		Porites solida	117		Lobophyllia pachysepta
82		Porites (Synaraea) undulata	118	90	Acanthastrea echinata
83	60	Porites sp.	119		Symphyllia erythraea

#### SCHUHMACHER, H., KROLL, D.K. & REINICKE, G.B., Long-term fluctuations ...

#### order, genus, species no order, genus, species no I–IV U–7 I–IV U–7 96 Pectiniidae Turbinaria mesenterina Zoantharia 120 95 Mycedium elephantotus Zoanthidae Echinophyllia aspera 121 94 122 111 Oxypora lacera 123 97 Palythoa tuberculosa Caryophylliidae Antipatharia 112 Gyrosmilia interrupta Antipathidae Dendrophylliidae 124 Cirripathes sp. 146 Tubastraea aurea

#### Appendix 1 (continued)

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Zoologisch-Botanische Datenbank/Zoological-Botanical Database

Digitale Literatur/Digital Literature

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