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# Composition of the deep Red Sea macro- and megabenthic invertebrate fauna. Zoogeographic and ecological implications

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Abstract: To date 96 macro- and megabenthic invertebrate species are known from the Red Sea at depths exceeding 500 m. A table listing these species together with bathymetric and zoogeograhic information as well as relevant literature is presented. The results of the faunistic research indicate that the deep Red Sea invertebrate fauna is basically Indo-Pacific with a high degree of endemism (at least about 30% of total fauna). Another tendency is that of subduction: the same species or genera occur at much grater depths in the Red Sea than in the adjacent Indian Ocean. Recent investigations of the deep Gulf of Aden benthic invertebrate fauna has revealed the existence of endemic deep Red Sea species within the outflow of Red Sea water south of the Straits of Bab el Mandeb. With this the deep Red Sea endemics appear to be endemic for the respective water masses rather than for the basin.

## Introduction

The deep Red Sea is a peculiar environment as it is the warmest deep-water body of the world's oceans. Below 200 m it is homoiothermic, measuring 21.5° C - 22° C down to the greatest depths (SIEDLER 1969, MORCOS 1970). It is therefore astonishing that it has not been subject to more interest by biological oceanographers. TÜRKAY (1986a) listed all expeditions up to that time that have collected benthic fauna. Recently, a few more campaigns have been carried out (Tab. 1). The present paper summarizes the published and some of the unpublished information on the composition of the fauna in depths exceeding 500 m and discusses the zoogeographic and ecological significance of these findings.

Most of the species known from the deep Red Sea and listed here have been collected during the expeditions of the Austrian/Hungarian vessel S.M.S. "Pola" (1895-98) as well as during the expeditions MESEDA I-III (1977-81) with the R.V. "Sonne" and R.V. "Valdivia", and MINDIK (1987) with the R.V. "Meteor". Some scattered findings were made by other expeditions but do not have the same significance as the former ones. The significance of the "Pola" expeditions can best be judged by the fact that about half of the fauna known today was already collected during these early endeavours. Station maps of these most extensive collecting efforts are given in Fig. 1. More details on the narratives and general results have been published by POTT (1898, 1899), FUCHS (1901), THIEL (1980, 1987), THIEL et al. (1985, 1986, 1987), THIEL & WEIKERT (1984), and TÜRKAY (1986b).

Tab. 1: List of expeditions with biological research in the deep Red Sea.

| Expeditions with benthic sampling in the deep Red Sea | | |
|---|---|---|
| S. M. S. *POLA* | 1.X.1895-18.V.1896 | Northern Red Sea (S to Jeddah) |
| S. M. S. *POLA* | 4.IX.1897-24.III.1898 | Southern Red Sea (S of Jeddah), some stations in the northern part |
| H. E. M. S. *MABAHISS* | 6.-18.IX.1933, 16.-17.V.1934 | 13 stations in total in the Red Sea |
| H. E. M. S. *MABAHISS* | 18.XII.1934-14.II.1935 | 33 stations between Tiran and Abu el Kizan |
| R. V. *VITYAZ* | 6.X.1959-28.IV.1960 | 3 Red Sea stations during cruise no. 31 |
| R. V. *AKADEMIK A. KOVALEVSKI* | 3.XII.1961-3.III.1962, 28.IX.-12.XII.1963, VIII.-X.1966 | 100 Red Sea stations, only 13 deeper than 200m |
| R. V. *METEOR* | X.-XI.1965 | 15 Red Sea stations, only 5 deeper than 200m |
| R. V. *MENELIK* and R. V. *JEHUDA AMBESSA* | 1965, 1966 | Gulf of Aqaba, 17 stations deeper than 200m |
| R. V. *SONNE* | X.-XI.1977 | Central Red Sea |
| R. V. *VALDIVIA* | IV.1979 | Central Red Sea |
| R. V. *PROFESSOR ŠTOKMAN* | 29.XI.1979-15.III.1980 | Exact number of samples not published |
| R. V. *VALDIVIA* | III.1981 | Central and northern Red Sea |
| R. V. *METEOR* | 31.I.-17.III.1987 | Central Red Sea, Bab el Mandeb, also Gulf of Aden |
| R. V. *METEOR* | 3. - 22. III. 1995 | All Red Sea regions, 50-2000m, also Gulf of Aden |

## Composition of the invertebrate fauna

Tab. 2 contains a list of all macro- and megabenthic Red Sea invertebrates recorded to date from depths exceeding 500 m. In total, 96 species are now known to occur below that depth. In most animal groups the collected material has been studied and the species numbers show a certain stability. There are, however, still some taxa with a potential beyond the known species numbers. More than 200 species of Mollusca have been identified from depths below 400 m (R. JANSSEN, pers. comm.). Notwithstanding the fact that many forms are represented by dead shells only, this material, still under study, will certainly substantially increase the number of known species. Asteroids have also not been studied up to now, but only very few species in this group have been collected.

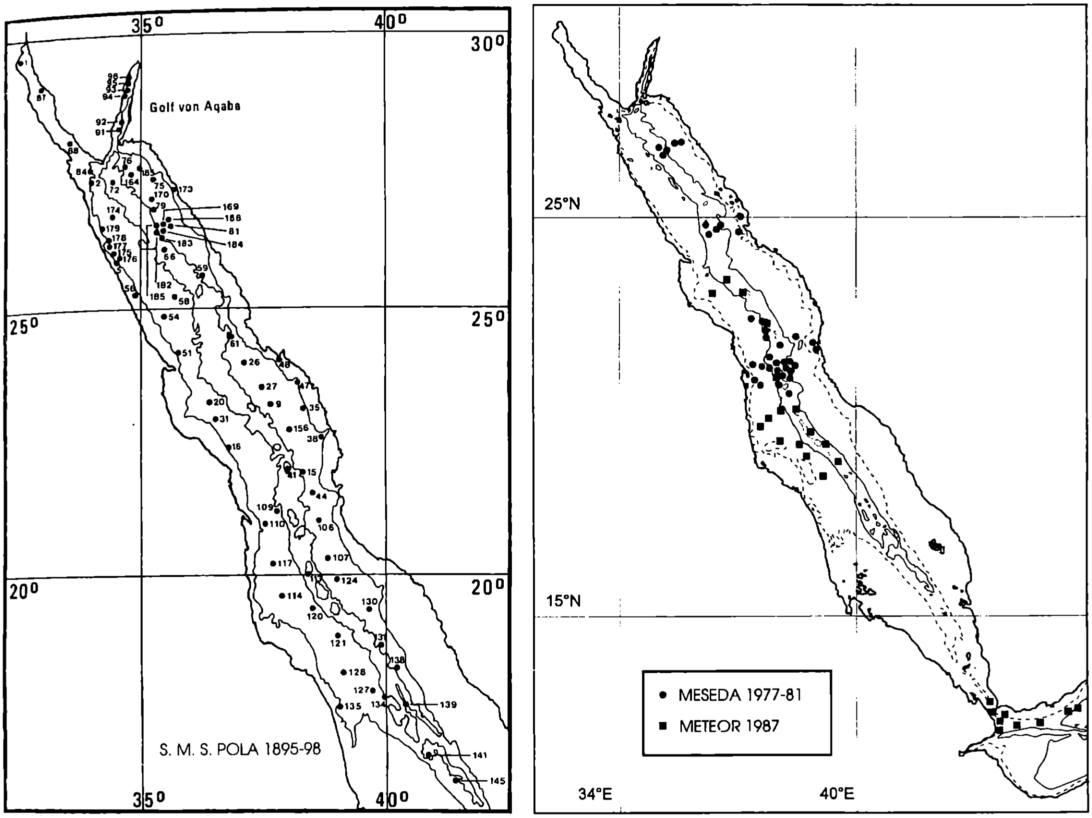


Fig. 1: Station maps of: a) S. M. S. "Pola"; b) MESEDA and "Meteor-5".

The number of species known only from the deep Red Sea is high and equals 39 (i. e., ca. 41 %). This percentage is lower than the one given by TÜRKAY (1986b: 234) based on earlier knowledge of the fauna, which was about 56 %. It is, however, still true that the faunal composition is very peculiar with reference to the world's oceans. Even if more of these species become known from the adjacent Indian Ocean in the future, a ratio of about 30 % endemics may be a realistic figure. In this connection there is one important point to note: a number of the endemics have proved to be attached to the warm deep Red Sea water rather than to the Red Sea basin (cf. infra).

Another important feature observed in a number of animal groups is their bathymetric ranges. Comparing the depth ranges of species common to the Red Sea and the adjacent Indian Ocean shows that 35 of 56 (i.e., 62.5 %) species occur at much greater depths in the Red Sea. The same applies to the genera of Red Sea endemics, but to a lesser extent. This phenomenon is easily explained by the high bottom-water temperatures which allow warm-water elements to inhabit greater depths than elsewhere.

Generally spoken, the deep Red Sea invertebrate fauna has typical Indo-Pacific features, with a high degree of endemism and a strong tendency towards submergence. As already stated by BALSS (1929) and TÜRKAY (1986b), typical cold-adapted, oceanic deep-sea organisms such as large siliceous sponges, as well as deep-sea decapod genera such as *Polycheles* or *Geryon,* are missing altogether. This makes the faunal assemblage a very peculiar one.

KLAUSEWITZ (1994) reported on the vertical distribution of the deep-sea fishes of the Red Sea and obtained very similar results. Of 13 species recorded from depths below 700 m, 4 (i.e., 31 %) are only known from the Red Sea. Of the remaining 9 species common with the Indian Ocean, 7 (i.e., 78 %) live at greater depths.

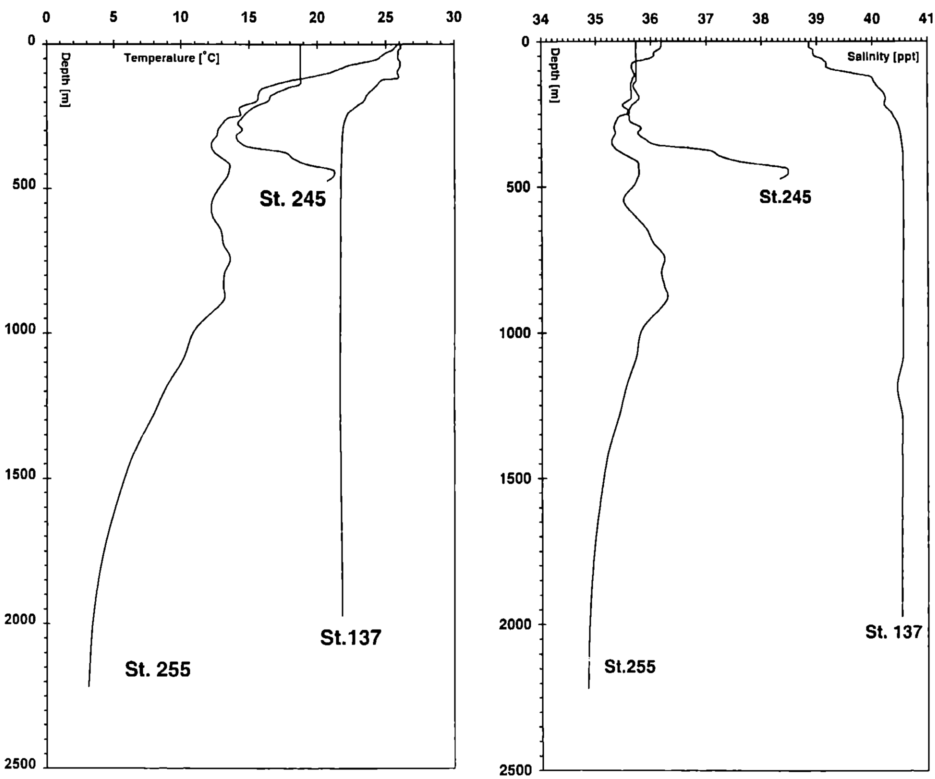


Fig. 2: Examples of temperature (left) and salinity (right) profiles taken during the expedition "Meteor-5" from the central Red Sea (Stat. 137), innermost Gulf of Aden (Stat. 245), and central Gulf of Aden (Stat. 255). In both cases the warm and saline Red Sea outflow is detectable at Stat. 245. -- After VERCH et al. (unpubl. report), redrawn.

Tab. 2: List of macro- and megabenthic invertebrates recorded from the Red Sea in depths of more than 500 m.

| Animal group/ Species | Bathymetric range a: in Red Sea b: outside Red Sea | Bathymetric range of genus or next relatives of Red Sea endemites | Literature |
|---|---|---|---|
| Porifera | | | SCHULZE 1901 |
| *Aulocystis grayi polae* | a: 490-868m<br>b: — | Genus: 82-659m | IJIMA 1927 |
| *Tretocalyx polae* | a: 341-820m<br>b: — | Genus: 549m | |
| Scyphozoa Coronatae<br>*Nausithoe thieli* | a: 763m<br>b: — | Living polyps to abt. 400m | JARMS 1990 |
| Madreporaria | | | MARENZELLER 1907 |
| *Balanophyllia rediviva* | a: 490-900m<br>b: 258m | | GARDINER & WAUGH 1938<br>ZIBROWIUS pers. comm. |
| *Dendrophyllia fistula* | a: 299-900m<br>b: 31-485m | | SCHEER & PILLAI 1983 |
| *Javania insignis* | a: 164-825m<br>b: 52-100m | | |
| *Polycyathus conceptus* | a: 732-805m<br>b: 80-229m | | |
| *Rhizotrochus typus* | a: 130-780m<br>b: ? shallow water | | |
| *Trochocyathus virgatus* | a: 512-978m<br>b: 15-275m | | |
| Actinaria | | | RIEMANN-ZÜRNECK 1983 |
| *Halcurias sudanensis* | a: 517-1121m<br>b: — | Genus: 55-800 | RIEMANN-ZÜRNECK pers. comm. |
| Annellida Polychaeta | | | ROSENFELDT 1989 |
| *Chloeia viridis* | a: 740-785m<br>b: 9-500m | | |
| *Eunoe depressa* | a: 747m<br>b: 5-350m | | |
| *Polyodontes maxillosus* | a: 1424-1987m<br>b: 18-450m | | |
| *Eupanthalis kinbergi* | a: 836m<br>b: 20-500m | | |
| *Peisidice aspera* | a: 588-1977m<br>b: 27-459m | | |
| *Bhawania goodei* | a: 757m<br>b: 0-300m | | |
| *Anaitides madeirensis* | a: 487-757m<br>b: 0-1200m | | |
| *Synelmis albini* | a: 831m<br>b: 0-2500m | | |
| *Micronereides capensis* | a: 601m<br>b: 183m | | |
| *Progoniada regularis* | a: 831m<br>b: 196-5023m | | |
| *Onuphis (Nothria) conchylega* | a: 747-1977m<br>b: 5-4020m | | |
| *Eunice (Eunice) tubifex* | a: 588-601m<br>b: 5-255m | | |
| *Lumbrineriopsis paradoxa* | a: 487-836m<br>b: 14-2802m | | |
| *Poecilochaetus serpens* | a: 601m<br>b: 20-1469m | | |
| *Heterospio longissima* | a: 507m<br>b: 30-4950m | | |
| *Prionospio steenstrupi* | a: 831-1424m<br>b: 2-5007m | | |
| *Cossura longocirrata* | a: 757m<br>b: 10-6487m | | |

 

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|---|---|---|---|
| *Cossura soyeri* | a: 601m<br>b: 3-1050m | | |
| *Notomastus (Notomastus) latericeus* | a: 601-1977m<br>b: 0-7216m | | |
| *Myriochele heeri* | a: 977-1424m<br>b: 8-5441m | | |
| *Terebrellides stroemi* | a: 1549m<br>b: 0-7587m | | |
| *Monorchos philippinensis* | a: 747-757m<br>b: 1449m | | |
| *Vermiliopsis infundibulum* | a: 757-1554m<br>b: 0-4020m | | |
| Crustacea Stomatopoda<br>*Kempina zanzibarica* | <br>a: 490-804m<br>b: 118-212m | | MANNING 1981 |
| Crustacea Amphipoda<br>*Ichnopus teretis* | <br>a: 1869m<br>b: — | <br>Genus: predom. shallow water | ANDRES 1981<br>ANDRES pers. comm.<br>BARNARD & KARAMAN 1991<br>LOWRY & STODDART 1992 |
| *Socarnopsis allectus* | a: 1544m<br>b: — | Genus: 0-170m | |
| *Pseudamaryllis nonconstricta* | a: 731-1544m<br>b: 335-390m | | |
| Crustacea Isopoda<br>*Cirolana meseda* | <br>a: 456-2148m<br>b: — | | HOBBINS & JONES 1993 |
| *Cirolana bisulcata* | a: 600-2148<br>b: — | | |
| *Natatolana insignis* | a: 731-1825m<br>b: 155-201m | | |
| *Argathona hirsuta* | a: 731-740m<br>b: — | | |
| Crustacea Decapoda Natantia<br>*Pleoticus steindachneri* | <br>a: 212-2061m<br>b: 472-479m | <br>Genus: 2-1362m | CROSNIER 1986, 1987, 1988, 1995<br>GOY 1986<br>BRUCE 1992 |
| *Parapenaeus fissuroides erythraeus* | a: 430-1672m<br>b: 472-479m | other ssp.: 65-399m | |
| *Metapenaeopsis erythraea* | a: 212-600m<br>b: — | | |
| *Parapandalus adensameri* | a: 732-1090m<br>b: — | Genus: 50-1300m | |
| *Parapandalus* cf. *narval* | a: 341-910m<br>b: — | *narval*: 100-400m | |
| *Parapandalus spinipes* | a: 732-805m<br>b: 110-366m | | |
| *Periclimenes pholeter* | a: 0-1972m<br>b: Shallow water | | |
| *Pontocaris pennata* | a: 212-902m<br>b: 20-274m | | |
| *Engystenopus spinulatus* | a: 650-690m<br>b: 247m | | |
| Crustacea Decapoda Reptantia<br>*Munida dispar* | <br>a: 212-900m<br>b: — | <br>Closest relatives: 214-390m | TÜRKAY 1986<br>MCPHERSON & BABA 1993<br>GUINOT 1989 |
| *Paguristes calvus* | a: 490-804m<br>b: 122m | | |
| *Paguristes incomitatus* | a: 1043-1134m<br>b: 75-300m | | |
| *Catapaguroides pectinipes* | a: 112-588m<br>b: — | Genus: 16-2200m | |
| *Nematopagurus helleri* | a: 890-2148m<br>b: — | Genus: 20-800m | |

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|---|---|---|---|
| *Solitariopagurus profundus* | a: 1310-1995m<br>b: — | New genus, closest relatives unknown | |
| *Ethusa* sp | a: 779-801m<br>b: — | Genus: shallow water to 1830m | |
| *Ebalia nobilii* | a: 733-1175m<br>b: — | Relations within genus unclear | |
| *Nursia dimorpha* | a: 212-800m<br>b: — | Genus: shallow water to 97m | |
| *Pariphiculus coronatus* | a: 800m<br>b: 135-1080m | | |
| *Calappa* cf. *pustulosa* | a: 363-785m<br>b: 83-100m | | |
| *Achaeus erythraeus* | a: 341-1554m<br>b: — | Closest relative: 38-100m | |
| *Charybdis acutidens* | a: 363-1203m<br>b: — | spp. of *Ch. miles*- group: 20-ca. 200m | |
| *Viaderiana meseda* | a: 1092-1113m<br>b: — | Shallow coral reef genus | |
| *Carcinoplax* sp. aff. *monodi* | a: 562m<br>b: — | Genus with broad bathymetric distrib. | |
| *Typhlocarcinops serenei* | a: 363-601m<br>b: — | Genus: 36-141m | |
| Mollusca Bivalvia<br>*Lyonsia intracta* | a:535-1082m<br>b: — | Deep sea genus | STURANY 1899<br>KNUDSEN 1967<br>R. JANSSEN pers. comm. |
| *Cuspidaria steindachneri* | a: 314-1308m<br>b: 106-132m | | |
| *Cuspidaria brachyrhyncha* | a: 375-2160m<br>b: — | Deep sea genus | |
| *Cardiomya alcocki* | a: 490-1424m<br>b: 240-1134m | | |
| *Pseudoneaera thaumasia* | a: 439-1082m<br>b: 247m | Deepwater genus | |
| *Limopsis elachista* | a: 490-588m<br>b: 75-292m | | |
| *Amussium siebenrocki* | a: 490-588m<br>b: 292m | | |
| Mollusca Gastropoda<br>*Murex forskoehlii* | a: 50-920m<br>b: 0-67m | | STURANY 1903<br>R. JANSSEN pers. comm. |
| *Fusinus bifrons* | a: 490-900m<br>b: 472-479m | Only St. 287 | |
| *Nassarius siquijorensis* | a: 314-690m<br>b: subtidal-450m | Genus: wide bathymetric range, | |
| *Nassarius munda* | a: 332-800m<br>b: — | most species littoral, closest relatives of | |
| *Nassarius sporadica* | a: 535m<br>b: — | Red Sea species not determined to date | |
| *Nassarius lathraia* | a: 439-748m<br>b: — | | |
| *Mitra gonatophora* | a: 562-700m<br>b: — | Genus as *Nassarius* | |
| *Vexillum castum* | a: 58-800m<br>b: depth unknown | Genus: wide bathymetric range | |
| *Ancilla "cinnamomea"* | a: 490-588m<br>b: shallow water | Identification wrong, min. 2 spp. involved | |
| *Columbella erythraeensis* | a: 535m<br>b: — | Genus predominantly in | |
| *Columbella nomanensis* | a: 690m<br>b: — | shallow water, some deep species | |
| *Conus tegulatus batheon* | a: 212-800m<br>b: — | Nominate ssp. sublittoral | |

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|---|---|---|---|
| *Tomopleura violacea* | a: 212-535m<br>b: 5-41m | | |
| *Gemmula amabilis* | a. 212-700m<br>b: 732m | | |
| *Inquisitor "flavidulus"* | a: 212-800m<br>b: 13-327m | | |
| *"Drillia" inchoata* | a: 800m<br>b: — | Turridae listed under "*Drillia*", "*Clavus*", "*Pleurotoma*", and "*Mangelia*" are probably real deep-sea forms | |
| *"Clavus" siebenrocki* | a: 900m<br>b: — | | |
| *"Pleurotoma" nannodes* | a: 212-700m<br>b: — | | |
| *"Mangilia" pertabulata* | a: 800m<br>b: — | | |
| *Solariella illustris* | a: 212-588m<br>b: — | Genus: mainly deep water | |
| Echinodermata Ophiuroidea<br>*Ophiocirce mabahitae* | a: 468-1424<br>b: — | Genus: Littoral to 732m | BARTSCH 1983 |
| Echinodermata Echinoidea<br>*Echinocyamus crispus* | a: 490-588m<br>b: 20-120m | | M. JENSEN, pers. comm. |
| *Pericosmos akabanus* | a: 363-588m<br>b: 272-486m | | |

## Comparative notes on the deep-sea fauna of the Gulf of Aden

The Gulf of Aden deep-sea fauna has been investigated by a number of early expeditions including the German Deep-Sea Expedition with the R.V. "Valdivia" (1898-99) and the John Murray Expedition with H.E.M.S. "Mabahiss" (1933-34). The most intense research was carried out during the International Indian Ocean Expedition from 1959-1965. All published data show that typical cold-adapted organisms occur in this oceanic environment. Cruise 5 (1987) of the R.V. "Meteor" confirmed these results, but also added an observation which is important for understanding deep Red Sea endemism. While most of the stations in the inner Gulf of Aden were governed by cold water and its associated fauna, one sample (St. 287, 12°16.0'N 44°08.5'E, 472-479 m depth) taken within the range of the Red Sea deep-water outflow proved to be totally different. The measured bottom-water temperatures were clearly elevated (Fig. 2). This is in full accordance with the dynamics of water masses in the area. In fact, the haline and warm deep Red Sea water has bottom contact in the innermost Gulf of Aden, where it sinks to a depth of about 500-1000 m. As the sea floor becomes deeper, this water loses bottom contact and spreads into the free water column (SIEDLER 1968). The fauna collected from the warm-water area of the Red Sea outflow contains a number of species formerly thought to be endemics of the Red Sea basin: the gastropod *Fusinus bifrons* and the crab *Charybdis acutidens*. CROSNIER (1991) reported the Red Sea peneids *Pleoticus steindachneri* and *Parapenaeus fissuroides erythraeus* only from this station in the Gulf of Aden.

As a result, the typical deep Red Sea fauna also occurs outside the Red Sea basin. The endemic species may thus be referred to as endemics of the Red Sea water rather than the Red Sea basin. The investigations in the Gulf of Aden showed further that the species considered to be endemic do not occur at shallower depths and have simply not been detected before. This strongly supports the peculiarity of the deep Red Sea fauna.

## Speciation problems and history of the fauna

All animal groups analysed to date show a similar differentiation between deep Red Sea and adjacent Indian Ocean. Basically four types occur:

1) Species common to both areas show that a gene flow still exists.
2) Sister species in both sea areas indicate a close relationship with few but constant differences.
3) Species within one genus in which it is not possible to detect the closest relative.
4) Genera only known from the deep Red Sea or species that are very much apart from other species in the same genus.

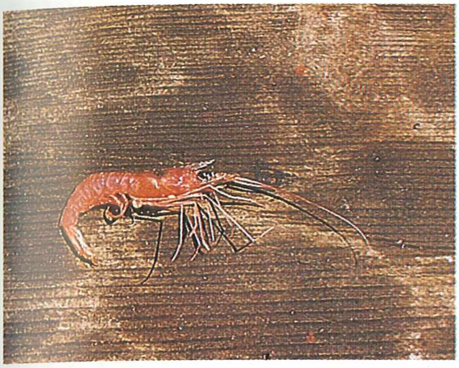
These four stages of differentiation can be understood as steps of an ongoing speciation and diversification process. They probably reflect different ages of genetic isolation, the youngest one resulting in the morphologically closest species.

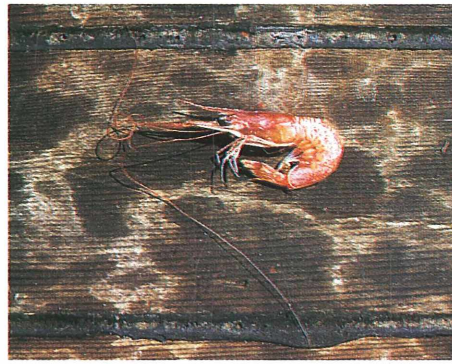
TÜRKAY (1986a) suggested that these isolation events might be the result of current reversals in the Straits of Bab el Mandeb in times of positive water balance and/or lower sea level in the ocean. This model had already been used by KLAUSEWITZ (1983) to explain the composition of the shallow-water fish fauna and has been detailed recently (KLAUSEWITZ 1989). The recent inward-directed surface current can carry larvae from the ocean into the Red Sea so that a regular gene flow can occur. The reversal, in contrast, would stop this influx and isolate the Red Sea populations. Successive events in this sense could be responsible for the gradual differentiation described above. One has to keep in mind that these isolation processes are quite recent as after its first opening towards the Gulf of Aden in the Oligocene, the Red Sea underwent a salinity crisis with evaporite formation in the Miocene and was again flooded during the Pleistocene (GIRDLER 1984, BRAITHWAITE 1987). Based on the study of foraminiferans in deep Red Sea and Gulf of Aden cores, LOCKE and THUNELL (1988) have suggested that a relative stagnation of surface water influx must have occurred in the last glacial rather than a current reversal in the Straits of Bab el Mandeb. To date it is very difficult to judge if this applies to all glacial/interglacial cycles, but a stagnation in the influx process could also isolate Red Sea populations from those of the adjacent ocean.

Another problem in explaining the composition of the deep-sea fauna has been that it must have survived after the speciation had taken place. However, dessications and/or salinity crises in the Red Sea basin were described for a number of glacialia, and such severe environmental changes have again been demonstrated recently for the last glacial/interglacial cycle by LOCKE and THUNELL (1988) and ALMOGI-LABIN et al. (1991). In the zoogeographic literature there is some controversy as to whether the Red Sea environment actually did not support marine life during these stress periods. While POR (1971, 1975) stresses that the Red Sea might have been a hypersaline environment and the fauna had to withdraw into the Gulf of Aden, ORMOND and EDWARDS (1987) and KLAUSEWITZ (1989) argue against this presumption and believe that the environmental conditions were not as harsh. In the deep sea, anoxic conditions must have occurred during at least the last deglaciation (about 12 000-8000 years ago) as shown by sapropelic layers in cores (LOCKE and THUNELL 1988). With the discovery made during "Meteor"-cruise 5 that Red Sea endemics occur outside the Red Sea basin proper but obviously dwell in the deep Red Sea water, the problem of survival of the deep Red Sea fauna across events leading to environmental stress is no longer a problem. Indeed, if the water circulation in the past was similar to recent conditions, the deep outflow would always have provided environments governed by deep Red Sea water outside the basin and the survival of the fauna would have been possible.

## Conclusions

The deep Red Sea is an isolated environment with a very specific fauna. This differs so distinctly from either the shallow-water fauna or the deep-sea fauna of the world's oceans that it forms an own region in the deep-sea realm. As the fauna is attached to deep Red Sea water rather than to a basin, it may be concluded that the water mass distribution plays a greater role in explaining the faunal assemblages and zoogeographic patterns of the deep sea than topographic features, as has also been demonstrated several times for shallow-water environments. A meaningful zoogeography of the deep-sea fauna is, thus, only possible if bottom-water properties are known. The deep Red Sea is an excellent example for this link between animal distribution and hydrography.





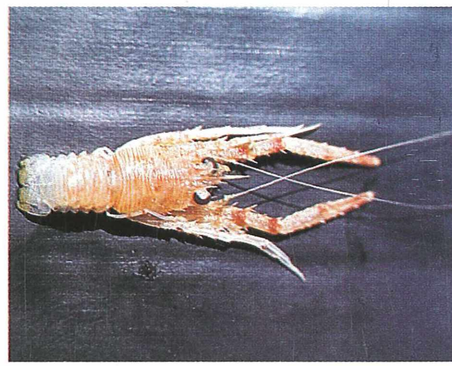
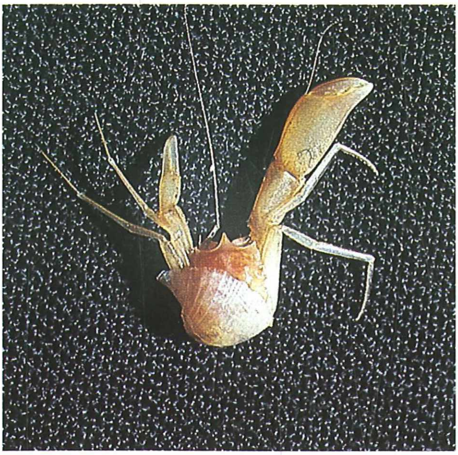


Fig. 3: *Pleoticus steindachneri* from the central Red Sea, Expedition "Valdivia" 29, station unknown.

Fig. 4: *Metapenaeopsis erythraeus* from the central Red Sea, Expedition "Valdivia" 29, station unknown.

Fig. 5: *Engystenopus spinulatus* from "Meteor" station 148 (off Port Sudan, 517-583 m depth.

Fig. 6: *Munida dispar* from "Sonne" station 36 (off Ras Abu Shagara, 490-588 m depth).



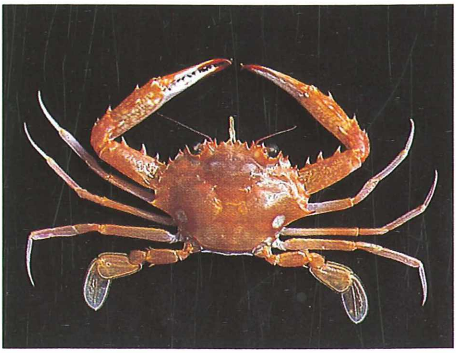


Fig. 7: *Nematopagurus helleri* from "Meteor" station 120 (Central Red Sea, 1635-1672 m depth).

Fig. 8: *Solitariopagurus profundus* from "Meteor" station 176 (Central Red Sea, 1968-1972 m depth).

Fig. 9: *Charybdis acutidens* from "Meteor" station 171 (off south Sudan, 434-469 m depth).

Fig. 10: *Achaeus erythraeus* from "Meteor" station 141 (near Port Sudan deep, 807-863 m depth).

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