

Summer distribution of micro- and small mesozooplankton in the Red Sea and Gulf of Aden, with special reference to non-calanoid copepods

Ruth Böttger-Schnack

Institut für Meereskunde an der Universität Kiel, Düsternbrooker Weg 20, D-24105 Kiel, Germany

ABSTRACT: From the Gulf of Aden along a transect to the central-northern Red Sea the abundance and taxonomic composition of metazoan plankton was studied during the southwest monsoon period (summer 1987). Samples were taken with 0.055 mm mesh nets down to a maximum depth of 1050 m. In the epipelagic zone, a distinct decrease in total plankton abundance was observed from south to north, which was much more pronounced in biomass (by a factor of up to 10) as compared to numbers (by a factor of 2). This could partly be explained by differences in the taxonomic and/or size composition of the planktonic fauna. Among non-calanoid copepods, 40 out of 75 species or taxa investigated decreased in abundance from south to north. Sixteen of these species were completely absent in the central-northern area. Nineteen species or taxa, however, showed the opposite feature of a higher abundance in the central-northern Red Sea. The stations were grouped according to similarities in the taxonomic composition of non-calanoid copepods in the epipelagic zone. The following 3 geographical regions could be separated: (1) Gulf of Aden and Strait of Bab al Mandab; (2) southern Red Sea; and (3) central-northern Red Sea. In the meso- and bathypelagic zones, regional differences were not evident. The results are discussed in relation to hydrographic conditions during summer 1987.

KEY WORDS: Small mesozooplankton · Red Sea · South-north differences · Vertical distribution · Non-calanoïd copepods · *Oncaea*

INTRODUCTION

Micrometazoans smaller than 1 mm in size form a group of organisms that has only rarely been considered in studies on oceanic zooplankton communities. Böttger (1985, 1987) reviewed the earlier literature, and few studies have been added in subsequent years (Roman et al. 1985, Cowles et al. 1987). The ecological importance of this size fraction as potential prey for adult and larval fish (e.g. Arthur 1977, Govoni et al. 1986, Kellermann 1990, Kinzer et al. 1993) and larger invertebrates (e.g. Kimmerer 1984) is well known and it is only recently that their importance for the grazing impact on phytoplankton has been pointed out (Morales et al. 1991, 1993).

Copepods form the most important taxon among pelagic oceanic micrometazoans. In this size category, they are not only represented by numerous developmental stages, but also by a great number of extremely

small species. In samples of larger mesh sizes, calanoid copepods usually dominate in variety as well as in total biomass and number (e.g. Weikert 1982, Beckmann 1984). In small mesh net samples, however, non-calanoïd taxa have been found to be the most important group at least by numbers (Gordeyeva 1970, Star & Mullin 1981, Böttger 1985, 1987, Cowles et al. 1987). The relative importance of these non-calanoïds has been found to increase strongly with increasing depth (Böttger 1985, 1987). This is mainly due to the poecilostomatoid genus *Oncaea* that contains a great number of very small mesopelagic species (Böttger-Schnack 1990a, b). The numerical dominance of *Oncaea* in meso- and bathypelagic zones seems to be a typical feature for tropical/subtropical areas (Böttger-Schnack 1994), but has also been observed in other regions (Schnack et al. 1985, Metz 1993).

In the Red Sea, recent studies with 0.1 mm mesh nets have given first insights into the taxonomic composi-

tion and vertical distribution patterns of cyclopoid and poecilostomatoid copepod species in the central and northern area (Böttger-Schnack 1988, 1990a, b, 1992, Böttger-Schnack et al. 1989). These studies were restricted to the upper 450 m and to the autumn and winter (northwest monsoon) periods. Methodologically important was the result that adults of the smallest *Oncaea* species, which are in the size range 0.2 to 0.3 mm, could not be sampled quantitatively even with nets of 0.1 mm mesh size (Böttger 1985). Seasonal differences in the results on the taxonomic composition of cyclopoids and poecilostomatoids in the central Red Sea (Böttger-Schnack 1990b) were difficult to interpret due to a lack of corresponding data from the southern Red Sea. It is known that the species composition in the central area is influenced by an inflow of plankton species from the Gulf of Aden during winter and spring (Halim 1969, Weikert 1980, 1987). Compared to results for the calanoid fauna in the central Red Sea (Weikert 1982), non-calanoids showed a less-pronounced dominance of single species in the upper mesopelagic zone (Böttger-Schnack 1988). Whether this difference can also be observed further down in the water column is not known, as corresponding investigations in the lower meso- and bathypelagic zones are lacking.

According to its productivity, the Red Sea has been divided latitudinally into 2 main subregions, whose limits are located at about 18° N (Weikert 1987, 1988a). The northern part is less productive and has a less diverse fauna than the southern part, whose surface layers are influenced by a regular inflow of nutrients and planktonic organisms from the Gulf of Aden. The system is depending on the monsoon-driven water exchange through the shallow Strait of Bab al Mandab (Halim 1969, 1984, Morcos 1970, Kimor 1973). During winter (October to May), surface water from the Gulf of Aden flows northwards into the Red Sea. This is compensated for by an outflow of Red Sea water at greater depth (Siedler 1968, Morcos 1970, Edwards 1987). During summer (late June to early October), the wind direction over the southern part of the Red Sea is reversed and the 2 existing layers at Bab al Mandab are superimposed by a surface current flowing southwards from the Red Sea into the Gulf (Morcos 1970, Maillard & Soliman 1986).

A great number of taxonomic and zoogeographical observations have been reported on the invasion and northern extension of Gulf zooplankton into the Red Sea (see Halim 1969 and Weikert 1987 for a review of the literature), but only limited quantitative information is available on the abundance and community structure of southern Red Sea plankton as it is effected by the water exchange with the Gulf of Aden. Mostly, the studies were conducted during winter and spring, when the inflow from the Gulf is greatest (Delalo 1966,

Beckmann 1984, unpubl.). For the summer season, only a few data on zooplankton abundance are available from the southern Red Sea (Rudyakov & Voronina 1967, Ponomareva 1968). All these data are based on samples with nets of 0.2 or 0.3 mm mesh size, which cannot sample quantitatively the numerous small metazoans.

The present study addresses this specific gap in the knowledge about Red Sea plankton and reports on the abundance and taxonomic composition of the small metazoan plankton caught with nets of 0.055 mm mesh size. The samples were taken in summer 1987 during the southwest monsoon period along a transect from the Gulf of Aden to the central and northern Red Sea (23° N) down to a maximum depth of 1050 m. Special attention is given to the species abundances and vertical distributions of non-calanoid copepods, in order to supplement the present knowledge which is mainly restricted to calanoids in the southern parts of the Red Sea. For the central Red Sea, the new results from summer are compared with published data from other seasons to provide further information on seasonal variation in the abundance of medium-sized non-calanoids in this area.

MATERIAL AND METHODS

During RV 'Meteor' Cruise 5 (MINDIK) zooplankton samples were collected between July 11 and August 6, 1987, on a transect from the Gulf of Aden to the northern Red Sea (Fig. 1). Maximum sampling depth was 1050 m. The research work was conducted in territorial waters of the Sudan, North Yemen and Djibouti; investigations in the northern Red Sea beyond Sudanese territorial waters were not permitted (Weikert 1988b). A total of 23 sampling series (Table 1) were grouped geographically into 5 different regions (Fig. 1): A, Gulf of Aden; B, Bab al Mandab; C, southern Red Sea; D, Central Red Sea; and E, northern Red Sea. Samples were taken of vertical hauls during day and night with a multiple opening-closing plankton net. The sampler had a mouth area of 0.25 m² (Weikert & John 1981), and was equipped with 5 nets of 0.055 mm mesh size. The depth of the nets was determined by a pressure recorder; the limits of the depth strata sampled varied only a few meters from preset values. The sampled depth ranges were generally resolved by 50 m steps down to 450 m and by 150 m steps between 450 and 1050 m. Total ranges of 250 m or less were taken by 20 m steps in the upper 100 m and by 25 or 50 m steps below 100 m. In the Gulf of Aden, 2 sampling series from the upper 250 m were resolved by 50 m steps only. No clogging of the net was observed; assuming a filtration efficiency of 100%,

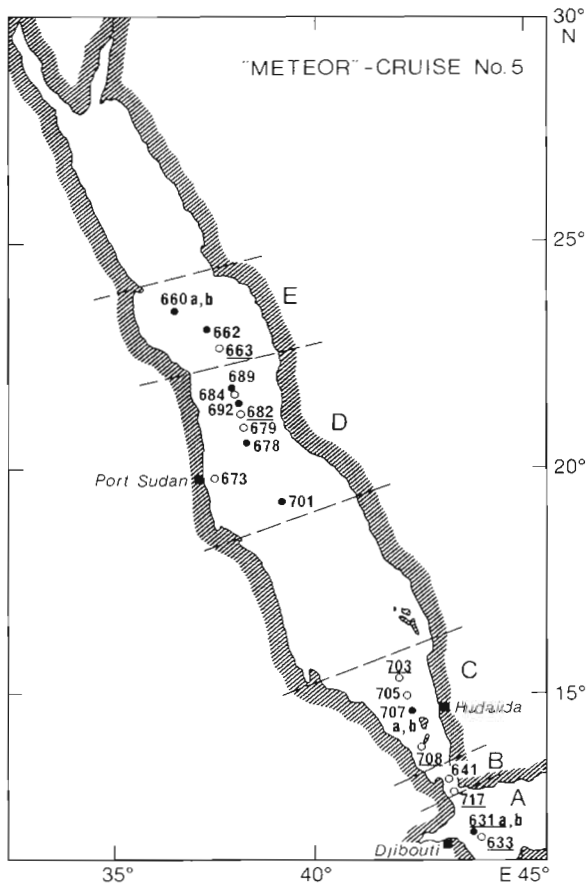


Fig. 1. Plankton sampling stations in the Red Sea and Gulf of Aden during summer 1987. (○) Daytime samples; (●) nighttime samples. A: Gulf of Aden; B: Bab al Mandab; C: southern Red Sea; D: central Red Sea; E: northern Red Sea. Those 7 stations which were selected for a detailed analysis of zooplankton abundance and taxonomic composition are underlined

the volumes filtered ranged between 5 m³ (20 m intervals) and 37.5 m³ (150 m intervals). Plankton samples were fixed in a 4% formaldehyde-seawater solution buffered with hexamethylene tetramine (2% by weight). For sorting and further storage the plankton samples were transferred into a preservation fluid containing 5% propylene glycol, 0.5% propylene phenoxetol and 94.5% filtered seawater (Steedman 1976) after 2 yr of fixation.

Total plankton biomass, including phytoplankton and detritus, was determined for all samples from 23 series by wet weight as described by Böttger (1982). Individual large organisms (>1 cm), mostly fishes or large crustaceans, were weighed separately and have not been included in the present evaluation. For 2 surface samples in the central Red Sea (Stn 682: 0–50 m; Stn 692: 0–20 m) only the larger plankton fraction (>0.3 mm) was weighed, because large amounts of gelatinous material clogged the fine gauze filters. Fila-

mentous cyanobacteria (*Trichodesmium* spp.) occurred regularly in the samples, but no bloom conditions were encountered (see Böttger-Schnack 1991 for details). In the northern Red Sea (Stns 662 and 663) large numbers of diatoms (*Rhizosolenia* spp.), which were infected by the endosymbiotic cyanobacteria *Richelia intracellularis*, and dinoflagellates were noted in the surface samples. No phytoplankton correction was employed on the biomass data. Based on earlier observations (Böttger 1987), the share of phytoplankton in the total plankton biomass was assumed to be low in 0.05 mm mesh net samples.

For numerical abundance and taxonomic composition of the zooplankton, including the species abundance of non-calanoïd copepods, the samples of 7 series have been evaluated, 1 at least from each of the 5 regions (Table 1, Fig. 1). Except for the Gulf of Aden, only daytime samples were enumerated in order to eliminate differences due to diurnal vertical migration. In the central-northern Red Sea (Regions D and E), 2 sampling series down to 1050 m were enumerated (Stns 663 and 682); in the southern Red Sea (Region C) 1 deep series down to 1050 m from the oceanic area (Stn 703), and 1 shallow series from the neritic area was evaluated (Stn 708, Fig. 1). In the Strait of Bab al Mandab, at the southern entrance of the Red Sea, samples from August (Stn 717) were chosen. In the Gulf of Aden, daytime series covered the upper 100 m only. To enlarge the considered vertical range for this region, 1 nighttime series down to 250 m was enumerated (Stn 631a) in addition to 1 daytime series (Stn 633).

For numerical analysis, samples were divided into 2 size fractions by filtration through 0.3 mm mesh gauze. In the larger fraction usually all organisms were counted. For abundant smaller organisms only subsamples of ca 500 to 1500 individuals were enumerated. Subsamples of the smaller size fraction were taken with a 4-quarter splitter as described by Böttger (1985). Replicate counts showed no significant differences between the 4 quarters of the splitter (chi-squared test, $p < 0.05$). Some medium-sized copepod species, which were present in both fractions (e.g. *Faranula* spp.), as well as less abundant small species were counted from the total samples. The quantitative analysis was made under a stereomicroscope at a magnification of 25× or 75×. Metazoan plankters were identified to major taxonomic groups (usually orders); among the Copepoda, nauplii and copepodids were counted separately. Empty copepod exoskeletons as well as specimens that showed an advanced degree of internal disintegration (carcasses) were distinguished according to the criteria given by Wheeler (1967), Weikert (1977) and Böttger-Schnack (1990a) and were counted separately.

Table 1. Station list for sampling conducted in 1987. *Series selected for evaluation of metazoan abundance and composition. D: day; N: night; -: no plankton sampling; H: hydrographic profiles taken

Stn	Date	Time	Plankton sampling depth (m)	Hydrographic profile?	Total water depth (m)	Geographic position (°N, °E)
628	Jul 10	-	-	H	1340	12° 42.2', 48° 27.2'
*631a	Jul 11	N	0–250		1400	11° 55.5', 43° 37.9'
631b	Jul 11	N	0–250		1240	
*633	Jul 11	D	0–100		1330	11° 56.9', 43° 46.8'
641	Jul 12	D	0–220		245	12° 39.5', 42° 14.5'
660a	Jul 18	N	0–1050		1300	23° 39.6', 36° 36.8'
660b	Jul 18	N	0–100		1200	
662	Jul 20	N	0–1050		2200	23° 06.1', 37° 14.7'
*663	Jul 20	D	0–1050	H	1200	22° 58.4', 37° 19.4'
673	Jul 22	D	0–450		690	19° 43.8', 37° 29.1'
678	Jul 24	N	0–1050		2100	20° 39.0', 38° 12.5'
679	Jul 24	D	0–450		1950	20° 58.9', 38° 06.6'
*682	Jul 25	D	0–1050		1890	21° 13.9', 38° 05.7'
684	Jul 26	D	0–100		2000	21° 24.9', 38° 02.7'
689	Jul 27	N	0–1050		1350	21° 27.4', 37° 57.7'
692	Jul 27	N	0–100		1860	21° 19.2', 38° 06.1'
699	Jul 30	-	-	H	1200	19° 00.0', 39° 13.1'
701	Jul 30	N	0–1050		1200	19° 02.6', 39° 06.8'
*703	Aug 3	D	0–950	H	970	15° 34.8', 41° 54.9'
705	Aug 4	D	0–450		530	14° 56.0', 42° 00.2'
707a	Aug 5	N	0–250		280	14° 20.6', 42° 23.1'
707b	Aug 5	N	0–250		280	
*708	Aug 5	D	0–175	H	190	13° 40.0', 42° 37.4'
*717	Aug 6	D	0–245	H	250	12° 32.0', 43° 24.5'

Copepodids were generally separated into the 6 suborders (Calanoida, Cyclopoida, Poecilostomatoida, Harpacticoida, Siphonostomatoida and Mormonilloida) following the scheme of Huys & Boxshall (1991). A more detailed taxonomic analysis was carried out for the 5 non-calanoid suborders, which were identified to genera, subgenera and in most cases to species. Females and males were always counted separately and in some cases late juveniles were separated as well. Of the Oithonidae (Cyclopoida) only the 3 smallest species, *Oithona nana*, *O. simplex* and *Paroithona* spp. were counted. It is assumed that most sampled specimens of *Paroithona* belong to *P. pacifica*. However, in view of the identification problems (Ferrari & Böttger 1986) only the genus is given in this case. Among the corycaeids, a selection of 9 species, belonging to the genera *Agetus*, *Corycaeus*, *Farranula*, and *Urocorycaeus* were included in the regional comparison. Several unidentified species belonging to the genera *Onychocorycaeus* and *Ditrichocorycaeus*, as well as unidentified juveniles of all 6 genera were grouped under 'Corycaeidae spp.' The group of unidentified sapphirinids and oncaeids, on the other hand, consisted mainly of unidentified juveniles of the given species. The identification of *Oncaea tregoubovi* at the southernmost stations (Stns 631, 633, 708 and 717) remained uncertain, because the characteristic stout median furcal setae were broken in all cases.

Environmental data that were determined at the time of the plankton sampling (Table 1), were taken from a data report by Verch et al. (1989a, b). Temperature and salinity profiles were taken with a Multisonde (ME, Kiel, Germany), and dissolved oxygen was determined from water samples by the Winkler method.

RESULTS

Environmental data

For each of the 5 regions, a typical vertical profile of temperature, salinity and dissolved oxygen is provided in Fig. 2. The surface layer always had a warmer temperature and a lower salinity than the deeper water. Surface temperatures ranged between 29 and 33°C; sharp temperature gradients occurred between 30 to 60 m in the central-northern Red Sea, and even shallower, at ca 20 m, in the southern area. Surface salinity decreased from 39.5 ppt in the central-northern Red Sea to 37.5 ppt in the south and consequently the halocline, situated between 50 and 100 m, became considerably stronger from north to south. Beneath 200 m, the homogeneous deep water is found in the Red Sea, which is characterized by its constant and relatively high temperature (21.6°C) and salinity (40.5 ppt).

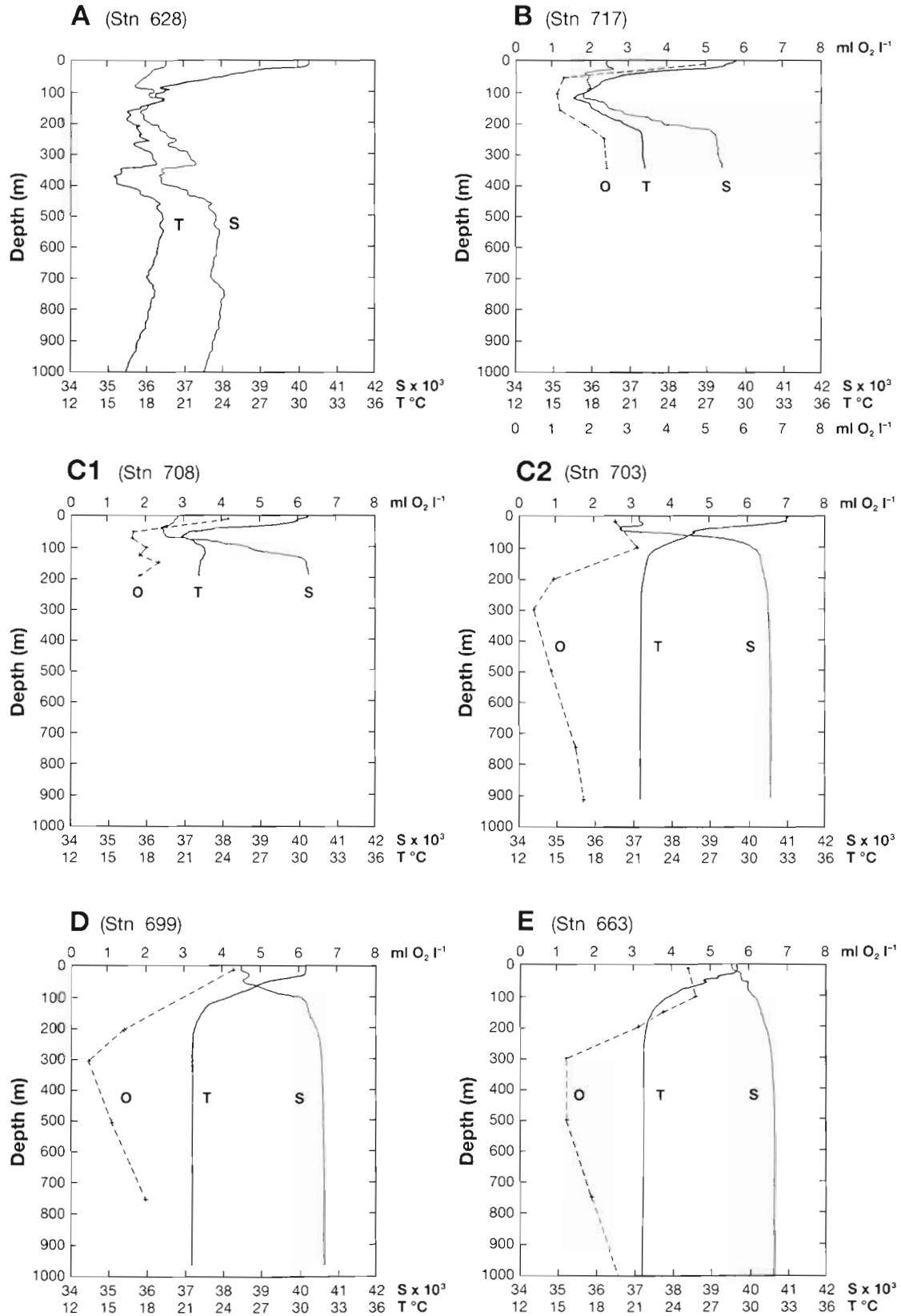


Fig 2. Vertical profiles of temperature (T), salinity (S, in ppt) and dissolved oxygen (O) in the 5 regions. A: Gulf of Aden; B: Bab al Mandab; C: southern Red Sea (C1: shallow; C2: deep); D: central Red Sea; E: northern Red Sea

At Bab al Mandab, a thin, warm surface layer with a temperature of 30°C and a salinity of 36.5 ppt lay on top of cooler and less saline water at 60 to 180 m depth during both sampling dates in July and August (Fig. 2). Beneath was the deep water of the Red Sea, which is characterized by constant temperature and salinity (see above). Current velocity profiles pointed out an inflow of stratified Gulf waters at the surface, which is compensated for by outflowing Red Sea waters at greater depths (E. Mittelstaedt pers. comm.; see also Weikert 1988b). In the Gulf of Aden, the thermocline extended from 25 to 90 m; salinity at the surface was similar to that in the Strait of Bab al Mandab (36.5 ppt) and increased gradually with depth to ca 38 ppt below 500 m (Fig. 2).

Dissolved oxygen concentrations in the surface zone were high (4 to 5 ml O₂ l⁻¹) and decreased sharply below 100 m depth. Minimum values of <1.5 ml O₂ l⁻¹ were found between 200 and 600 m depth in the northern and central Red Sea and even shallower, at ca 100 m, in the southern area (Fig. 2). At Bab al Mandab minimum oxygen concentrations occurred between 30 and 180 m. In the Gulf of Aden, no oxygen measurements were available for the sampling period. According to Beckmann (1984, unpubl.) minimum oxygen values of <0.4 ml O₂ l⁻¹ are found in this area between 150 and 500 m.

Total plankton biomass

Table 2 summarizes the biomass values of total 0.055 mm mesh net plankton in the 5 regions investigated during the summer survey; the results are grouped into 4 vertical zones as defined by Weikert (1982): epipelagic (0–100 m), upper mesopelagic (a) O₂-gradient (100–250 m), (b) O₂-minimum-zone (250–450 m) and lower meso-/upper bathypelagic (450–1050 m). In the Strait of Bab al Mandab minimum oxygen concentrations were seen as shallow as 60 m (Fig. 2); for comparison, however, the vertical integration of biomass values in this region was done in the same manner as at all other sites.

Day-night differences. Biomass differences between day and night within each region were usually minor in the 4 vertical depth zones (Table 2) and statistically not significant (central Red Sea, Region D, 0–100 m, Mann-Whitney *U*-test, $p > 0.1$). However, the upper limit of biomass values in the epipelagic zone was generally higher during the night than during the day (Table 2), indicating some upward vertical migration of larger zooplankters from deeper layers.

South-north differences. For regional comparison of plankton biomass, only the epipelagic zone (0–100 m) will be considered, since the largest data set was avail-

able for this zone. Within the central-northern Red Sea, no significant differences in plankton biomass were found between the 3 northernmost (Region E) and the central (Region D) stations (Mann-Whitney *U*-test, $p < 0.1$). Thus, Regions D and E are treated together in the following comparison. Between the central-northern and the southern Red Sea plankton biomass increased significantly by a factor of 2 to 3 (Mann-Whitney *U*-Test, $p < 0.05$; Table 2). In the southern Red Sea and in the Gulf of Aden biomass values were similar (ca 15 g m⁻²), whereas exceptionally high biomass values of 30 to 50 g m⁻² occurred at Bab al Mandab. These were about 5 to 10 times higher than in the north.

Vertical distribution. Maximum biomass values always occurred in the epipelagic zone, at 0–100 m (Table 2, Fig. 3). Within this depth zone, maximum biomass concentrations were generally found above or near the strong thermocline, from 0 to 40 m (80 m) (Fig. 3). A secondary peak in biomass concentration found in the 80 to 100 m layer at Bab al Mandab during July was caused by a high number of medium-sized medusae and non-copepod crustaceans, which were not present during August.

Below the epipelagic zone, biomass concentrations rapidly decreased with depth by 1 to 2 orders of magnitude to minimal values of 1 to 10 mg m⁻³ in all depth layers below 450 m (Fig. 3). The vertical gradient in total plankton biomass between the epipelagic and the adjacent 100–250 m depth layer was stronger in the subregions of the Red Sea (by a factor of 3 to 4) than in the Gulf of Aden and the Strait of Bab al Mandab (by a factor of 2) (Table 2).

Total metazoan composition and abundance by number

South-north differences. The numerical abundance of total metazoans and major metazoan taxa in the 4 depth zones is shown in Table 3 for the 6 locations investigated. In the epipelagic zone, total abundance by number was in general higher in the southern Red Sea and at Bab al Mandab as compared to the central-northern area (by a factor of 2). This south-to-north decrease was lower, however, than that of total biomass based on a larger number of stations. In the Gulf of Aden, total abundance values were similar to those found in the central-northern Red Sea.

Copepoda were the dominant taxa at all stations investigated, contributing 84 to 92% to the total number of metazoans in each of the 4 depth zones sampled (Table 3). Nauplii and copepodids I to VI shared similar proportions of 30 to 50% of the total each. Appendicularians and molluscs ranked second

Table 2. Biomass of 0.055 mm mesh net plankton (g wet wt beneath 1 m²) in the Gulf of Aden and in different regions of the Red Sea during summer 1987. Stations are listed in geographical order from south to north. D: day; N: night; -: no data

Region Stn	Time:	0-100 m		100-250 m		250-450 m		450-1050 m		Total D+N
		D	N	D	N	D	N	D	N	
Gulf of Aden (A)										
631a		-	13	-	8.1	-	-	-	-	
631b		-	13	-	6.6	-	-	-	-	
633		16	-	-	-	-	-	-	-	
Mean		16	13	-	7.4	-	-	-	-	
Total mean		14.5		7.4		-		-		22
Bab al Mandab (B)										
641		57	-	17	-					
717		35	-	10	-					
Mean		46	-	13	-					
Total mean		46		13						59
Southern Red Sea (C)										
708		22	-	6.4 ^a	-					
707a		-	19	-	3.0					
707b		-	14	-	3.5					
705		8.0	-	3.1	-	3.5	-			
703		15	-	2.0	-	2.6	-	4.6 ^b	-	
Mean		15	16.5	3.8	3.3	3.0	-	4.6 ^b	-	
Total mean		16		3.0		3.0		4.6 ^b		27
Central Red Sea (D)										
701		-	9.2	-	2.6	-	1.8	-	3.9	
673		3.7	-	1.3	-	1.0	-	-	-	
678a		-	4.2	-	1.4	-	2.8	-	1.6	
678b		-	4.0	-	-	-	-	-	-	
679		5.5	-	1.7	-	1.6	-	-	-	
682		3.7	-	1.5	-	1.1	-	1.3	-	
692		-	7.3	-	-	-	-	-	-	
684		-	5.8	-	1.7	-	3.7	-	2.5	
689		5.5	-	-	-	-	-	-	-	
Mean		4.6	6.1	1.5	1.9	1.2	2.7	1.3	2.7	
Total mean		5.3		1.7		2.0		2.0		11
Northern Red Sea (E)										
663		8.7	-	1.7	-	1.9	-	2.5	-	
662		-	11	-	3.1	-	1.7	-	1.6	
660a		-	7.1	-	1.7	-	1.3	-	2.1	
660b		-	7.0	-	-	-	-	-	-	
Mean		8.7	8.3	1.7	2.4	1.9	1.5	2.5	1.9	
Total mean		8.5		2.0		1.7		2.2		14

^aDepth range 100-175 m; ^bdepth range 450-950 m

or third, with percentages of mostly 2 to 4%; higher relative abundances were found for these 2 groups in the shallow region of the southern Red Sea (Stn 708), where they contributed 8% each to the total numbers. Molluscs at this station consisted mainly of bivalve larvae, whereas at all other sites peropod larvae (mainly *Limacina* spp. and *Creseis* spp.) dominated. The group 'other crustaceans' consisted of larval and adult euphausiids, amphipods, decapods, cladocerans, isopods, and individual mysids, as well as larval cirripeds. Unusual ascothoracid larvae as described by Boxshall & Böttger-Schnack (1988) and several

types of Hansen's γ -larvae (Crustacea: Maxillopoda: Facetotecta; see Grygier 1987) were found at all stations investigated, the latter showing maximum abundances in the Strait of Bab al Mandab (2 to 5 ind. m⁻³ at 100 to 200 m). Individual nauplii of another type of ascothoracids, which were tentatively identified as Petrarciidae (Grygier 1993), were found in the central and southern Red Sea. The group 'other metazoans' consisted mainly of meroplanktic larval forms (see below) as well as of fish and *Branchiostoma* larvae, turbellarians and individual insects (*Halobates*).

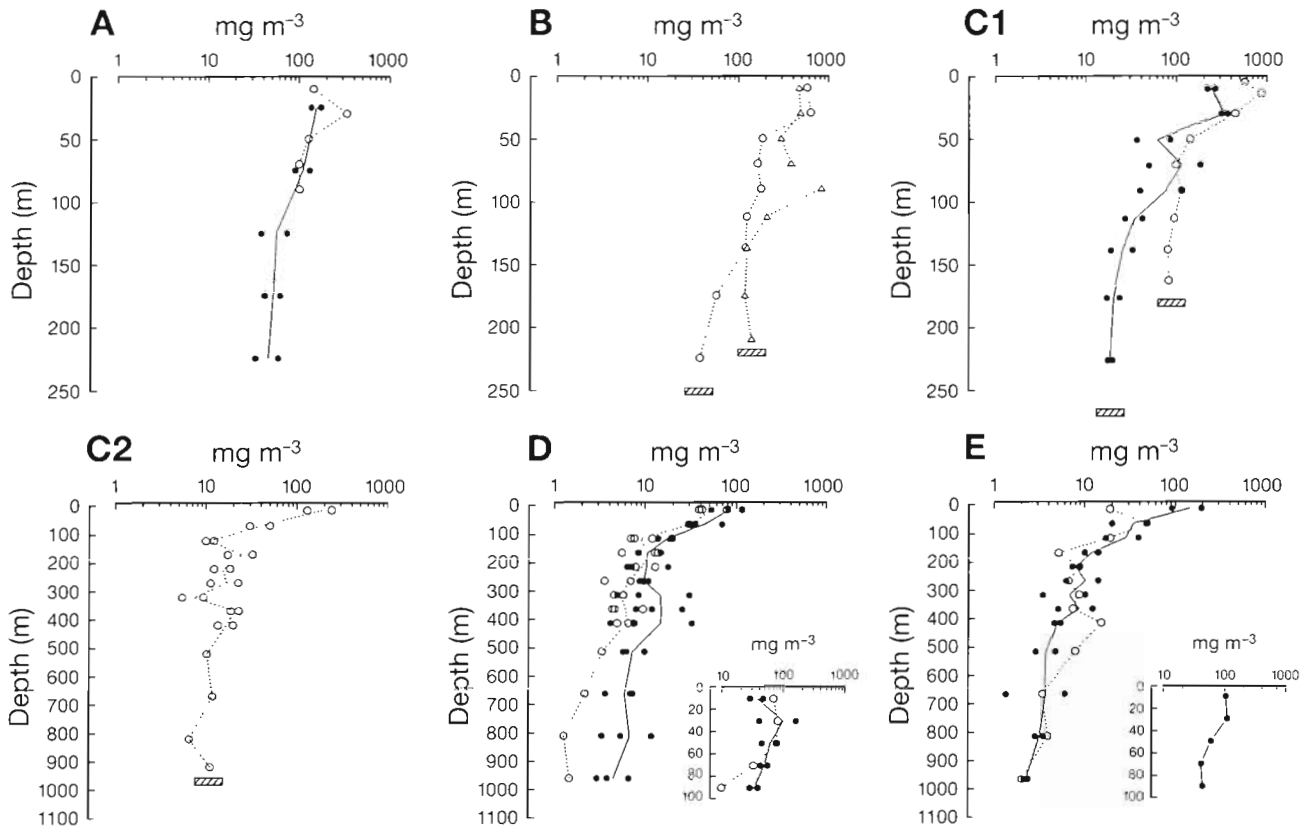


Fig. 3. Vertical distribution of total plankton biomass in the 5 regions. A: Gulf of Aden; B: Bab al Mandab sampled only during the day on July 12 (Δ) and August 6 (\circ); C: southern Red Sea (C1: shallow; C2: deep); D: central Red Sea; E: northern Red Sea. (\circ) Daytime; (\bullet) nighttime. Dashed and solid lines indicate arithmetic means. Note the logarithmic scale. (zzzz) Bottom

Table 3. Abundance of metazoan taxa (individuals beneath 0.25 m^2) in different regions of the Red Sea and in the Gulf of Aden during summer 1987. D: day; N: night; -: no data

Taxon	Gulf of Aden		Bab al Mandab	Red Sea			
	Stn: 631	633		Shallow	Deep	Central	North
	Time: N	D	D	708	703	682	663
				D	D	D	D
Copepodids I–VI							
0– 100 m	130000	84000	140000	305000	190000	80000	68000
100– 250 m	35000	–	27000	91000 ^a	31000	21000	23000
250– 450 m	–	–	–	–	33000	13000	14000
450–1050 m	–	–	–	–	26000 ^b	11000	9800
Copepod nauplii							
0– 100 m	85500	97000	210000	180000	160000	100000	87000
100– 250 m	11000	–	17000	22000 ^d	13000	22000	24500
250– 450 m	–	–	–	–	12000	7600	7200
450–1050 m	–	–	–	–	29000 ^b	17500	12000
Medusae							
0– 100 m	260	170	28	55	630	620	340
100– 250 m	6	–	33	18 ^a	12	30	58
250– 450 m	–	–	–	–	1	25	12
450–1050 m	–	–	–	–	0 ^b	5	3

Table 3 (continued)

Taxon	Gulf of Aden		Bab al Mandab	South		Red Sea	North	
	Stn: Time:	631 N	633 D	717 D	Shallow 708 D	Deep 703 D	Central 682 D	663 D
Siphonophores								
0– 100 m		14	67	110	41	100	280	230
100– 250 m		8	–	32	6 ^a	4	5	20
250– 450 m		–	–	–	–	3	5	11
450–1050 m		–	–	–	–	20 ^b	6	33
Ostracods								
0– 100 m		1000	1250	2500	800	640	170	26
100– 250 m		1000	–	2100	900 ^a	1100	730	510
250– 450 m		–	–	–	–	1100	630	290
450–1050 m		–	–	–	–	1100 ^b	920	760
Other crustaceans								
0– 100 m		450	390	1450	710	400	240	140
100– 250 m		140	–	510	530 ^a	190	30	55
250– 450 m		–	–	–	–	115	13	38
450–1050 m		–	–	–	–	63 ^b	19	19
Molluscs								
0– 100 m		12000	8100	17000	33000	11000	11000	9900
100– 250 m		430	–	2700	25000 ^a	530	440	390
250– 450 m		–	–	–	–	550	200	250
450–1050 m		–	–	–	–	700 ^b	270	345
Appendicularians								
0– 100 m		9300	16000	19000	45000	20000	4600	8050
100– 250 m		380	–	730	1400 ^a	160	350	2100
250– 450 m		–	–	–	–	110	36	64
450–1050 m		–	–	–	–	97 ^b	32	9
Thaliaceans								
0– 100 m		780	170	1150	150	1700	9	145
100– 250 m		0	–	22	0 ^a	0	0	31
250– 450 m		–	–	–	–	0	0	0
450–1050 m		–	–	–	–	1 ^b	0	0
Chaetognaths								
0– 100 m		2700	2700	2400	3300	6100	1500	2000
100– 250 m		84	–	350	1050 ^a	230	250	260
250– 450 m		–	–	–	–	175	58	110
450–1050 m		–	–	–	–	125 ^b	34	130
Polychaetes								
0– 100 m		610	1100	3000	1750	1750	110	340
100– 250 m		940	–	1600	2400 ^a	360	620	490
250– 450 m		–	–	–	–	140	380	380
450–1050 m		–	–	–	–	180 ^b	105	120
Other metazoans								
0– 100 m		690	830	1400	890	570	110	88
100– 250 m		520	–	1200	240 ^a	240	24	56
250– 450 m		–	–	–	–	310	69	16
450–1050 m		–	–	–	–	110 ^b	46	31
Total metazoans								
0– 100 m		250000	210000	405000	570000	400000	200000	175000
100– 250 m		50000	–	53000	140000 ^a	46000	46000	51000
250– 450 m		–	–	–	–	47000	22000	23000
450–1050 m		–	–	–	–	57000 ^b	30000	23000

^aDepth 100–175 m; ^bdepth 450–950 m

Most of the separated metazoan taxa followed the south-to-north decrease in number observed for total metazoans (Table 3). For only a few taxa, such as chaetognaths, salps and medusae, was no consistent south-to-north gradient evident (Table 3). The greatest decrease in abundance was noted for ostracods, polychaetes, and for the group 'other metazoans': varying by a factor of 5 to 10 from south to north. The occurrence of larval bryozoans, brachiopods and anthozoans, which were included in this group, was restricted to the southern area only. Anthozoan larvae dominated total plankton biomass at the southern shallow station (Stn 708), and large numbers of gelatinous zooplankton occurred at Bab al Mandab during August; both taxa increased the observed total plankton biomass, but contributed little to total number of metazoans.

Vertical distribution. Maximum concentrations of total metazoans were always found in the upper 20 or 50 m depth layer. Values ranged between 10^4 and 10^5 ind. m^{-3} according to the region sampled; they decreased by about 2 orders of magnitude to mini-

imum values of 100 to 200 ind. m^{-3} in the 900 to 1050 m layer (Fig. 4). In the deep oceanic regions of the Red Sea, a small secondary maximum was situated between 150 (200 m) and 400 m depth, in the upper part of the oxygen minimum zone (see Fig. 2). In the shallow region of the southern Red Sea (C1) the vertical distribution of total metazoan abundance differed from all other sites: below the very high surface concentrations of nearly 100 000 ind. m^{-3} in the upper 20 m, above the shallow thermocline, nearly homogeneous concentrations of about 5000 to 10000 ind. m^{-3} were found down to the bottom at 175 m (Fig. 4).

Total copepodids

Among copepodids I to VI, the 3 suborders Calanoida, Cyclopoida and Poecilostomatoida dominated, together accounting for 80 to 95% of the total numbers (Table 4). Harpacticoida mostly ranked fourth, Siphonostomatoida were present in very low percent-

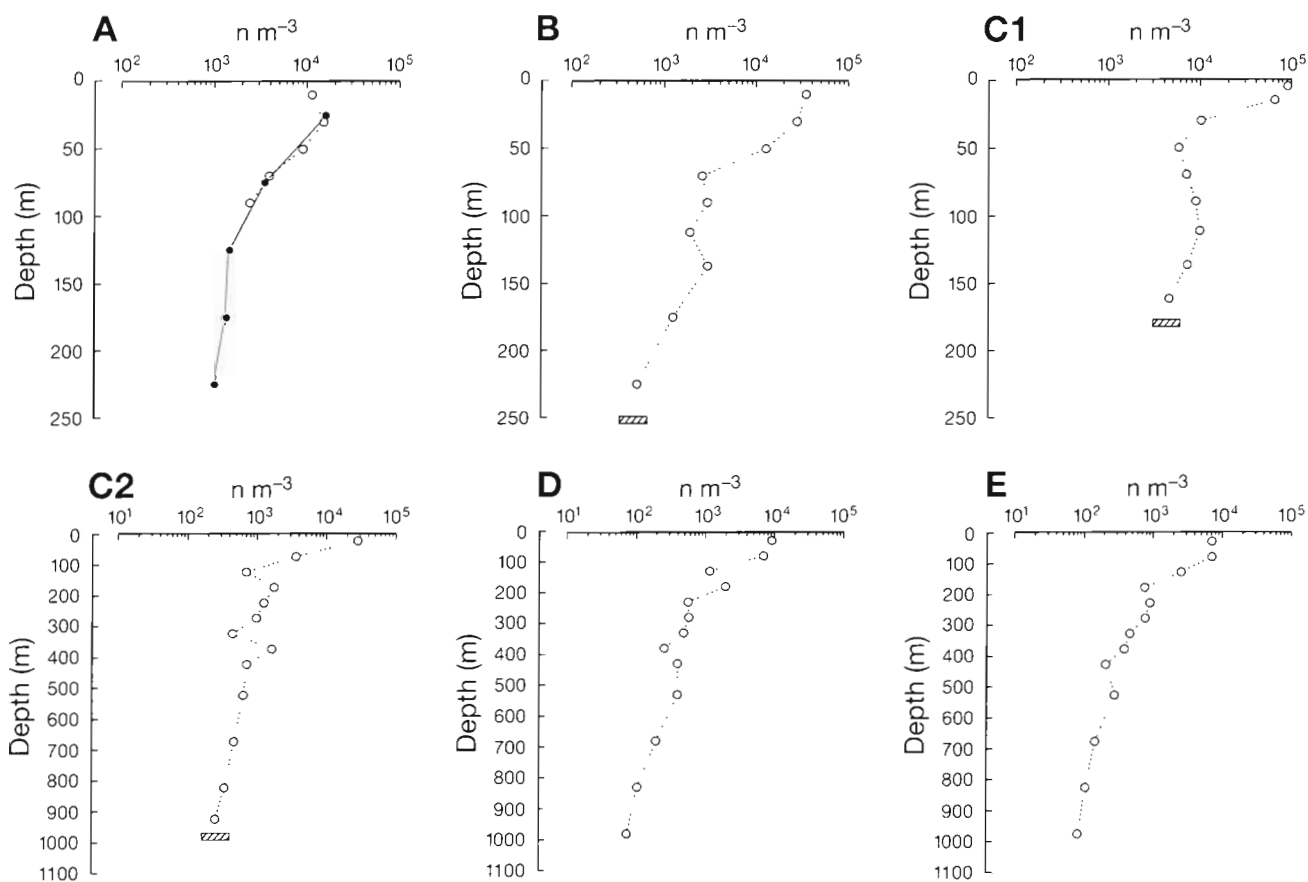


Fig. 4. Vertical distribution of total metazoan abundance in the 5 regions during daytime, except for Gulf of Aden (A) data which include nighttime series. B: Bab al Mandab; C: southern Red Sea (C1: shallow; C2: deep); D: central Red Sea; E: northern Red Sea. (▨) Bottom

Table 4. Abundance (individuals beneath 0.25 m²) of copepod suborders in the Gulf of Aden and different regions of the Red Sea during summer 1987. Daytime values unless otherwise indicated. 0: no individuals; -: no data

Copepod suborder	Gulf of Aden		Bab al Mandab	South		Red Sea Central	North
	Stn: 631 (Night)	633		Shallow 708	Deep 703		
Calanoida							
0- 100 m	50000	25000	43500	36000	36000	28000	22000
100- 250 m	8800	-	4400	7400 ^a	3800	3300	3400
250- 450 m	-	-	-	-	1750	975	920
450-1050 m	-	-	-	-	1800 ^b	770	1100
Cyclopoida							
0- 100 m	46500	24000	35000	220000	54000	20000	20000
100- 250 m	3200	-	5700	29000 ^a	3200	5100	5300
250- 450 m	-	-	-	-	380	500	500
450-1050 m	-	-	-	-	415 ^b	250	310
Poecilostomatoida							
0- 100 m	30000	29000	55000	25500	54500	21000	16000
100- 250 m	19000	-	16000	30500 ^a	21000	12000	12000
250- 450 m	-	-	-	-	29000	11000	12000
450-1050 m	-	-	-	-	22000 ^b	9000	7900
Siphonostomatoida							
0- 100 m	6	5	11	9	75	78	73
100- 250 m	2	-	0	42 ^a	0	25	40
250- 450 m	-	-	-	-	0	14	10
450-1050 m	-	-	-	-	0 ^b	41	15
Harpacticoida							
0- 100 m	6500	5300	8100	19000	50000	9700	9200
100- 250 m	1800	-	2200	24000 ^a	3100	1250	1900
250- 450 m	-	-	-	-	1200	650	550
450-1050 m	-	-	-	-	1550 ^b	780	420
Mormonilloida							
0- 100 m	2	33	370	65	0	0	0
100- 250 m	1600	-	960	16 ^a	1	0	0
250- 450 m	-	-	-	-	17	0	0
450-1050 m	-	-	-	-	4 ^b	0	0

^aDepth 100-175 m; ^bdepth 450-950 m

ages only (<1%). The occurrence of Mormonilloida was restricted to the Gulf of Aden and southern Red Sea; they were absent in the central-northern part (Table 4).

In the epipelagic zone, calanoids, cyclopoids and poecilostomatoids were usually present in similar percentages, each group including 20 to 35% of all copepodids. In the shallow region of the southern Red Sea, however, cyclopoids (*Oithona* and *Paroithona*) contributed over 70% to the total numbers, whereas calanoids amounted to less than 20% at this station (Stn 708) and at the adjacent deep water station (Stn 703) in the southern Red Sea. Below the epipelagic zone, the proportion of poecilostomatoids (mainly *Oncaea*) strongly increased: in the 100-250 m layer they mostly contributed more than 50% to all copepodids, and in the 2 meso- and bathypelagic

zones between 250 and 1050 m depth they were strongly dominant, with more than 80% of all copepodids (Table 4). Regional differences were usually minor in these depths below the epipelagic zone; only at the more shallow station in the southern Red Sea did harpacticoids (mainly *Microsetella*) account for a large proportion (26%) of all copepodids in the 100 to 250 m depth layer.

Non-calanoïd copepodids

South-north differences in general. Table 5 presents an overview of the abundance of non-calanoïd copepod species or genera at the 6 stations investigated and their relative percentages within the respective suborder. The number of species would have been higher if

Table 5. Abundance (individuals beneath 0.25 m²) of non-calanooid copepod species or genera in the Gulf of Aden and different regions of the Red Sea during summer 1987. shall.: shallow; D: day; N: night. Sex/Stage: F, females; M, males; 1, late juveniles; 2, early juveniles; 3, various juveniles. 0: no individuals; +: present, but species not evaluated quantitatively; *species not present in the central-northern Red Sea

Species, Sex, Stage	Strn: Sampling depth (m): Time:	Gulf of Aden	Bab al Mandab	Red Sea			
		631 0–250 N	717 0–245 D	South, shall. 708 0–175 D	South, deep 703 0–950 D	Central 682 0–1050 D	North 663 0–1050 D
Cyclopoida, total		46500	40000	240000	58000	26000	26000
Oithonidae							
* <i>Dioithona rigida</i> Giesbrecht	F M	+	+	+	+	0	0
* <i>Oithona brevicornis</i> Giesbrecht	F M	+	+	+	+	0	0
<i>O. nana</i> Giesbrecht	F M 1	5000	5750	34000	11000	41	290
<i>O. simplex</i> Farran	F M 1	5400	4300	58000	16000	5400	6300
<i>Paroithona</i> sp.	F M 1	3400	4300	10000	2700	4250	5300
<i>Oithona</i> spp.	F M 3	33000	25500	140000	29000	16000	14000
Unidentified cyclopoids	2	0	17	190	0	8	0
Poecilostomatoida, total		50000	71000	56000	125000	52000	50000
Oncaeidae, total		44000	62000	48000	120000	49000	45000
<i>Lubbockia aculeata</i> Giesbrecht	F M 1	0	0	0	28	12	6
<i>L. squillimana</i> Claus	F M 1	0	0	2	18	135	155
<i>Lubbockia</i> spp.	2	0	0	1	160	140	140
* <i>Oncaea</i> sp. AD	F M	510	620	380	0	0	0
<i>O. atlantica</i> Shmeleva	F M	23	650	630	74	480	250
<i>O. clevei</i> Früchtl	F M	580	690	235	2400	29	9
<i>O. conifera</i> Giesbrecht small form	F M	1100	310	1	40	235	265
<i>O. dentipes</i> Giesbrecht form A	F	84	350	330	190	1300	1200
* <i>O. dentipes</i> form B	F	91	140	8	1	0	0
<i>O. dentipes</i> form A	M	160	360	1200	170	440	555
<i>O. hawii</i> Böttger-Schnack & Boxshall	F	130	270	115	670	150	210
<i>O. ivlevi</i> Shmeleva	F M	1700	2400	7500	2600	11000	8900
<i>O. ivlevi</i> /sp. K (unidentified)	F M	260	2500	0	0	0	0
<i>Oncaea</i> sp. K	F M	3300	430	2400	13000	2300	3300
<i>O. media</i> Giesbrecht f. <i>minor</i>	F M	3000	5300	1000	480	1400	2000
<i>O. media</i> f. <i>major</i>	F M	99	100	36	3	26	250
<i>O. mediterranea</i> Claus	F M	170	255	135	760	120	110
<i>O. minuta</i> Giesbrecht	F	39	75	95	75	390	430
<i>O. ovalis</i> Shmeleva	F M	420	510	33	5800	3700	3500
<i>O. platysetosa</i> Boxhall & Böttger	F M	6	160	87	12	110	100
<i>O. rufa</i> Boxhall & Böttger	F	0	1	2	145	41	25
* <i>O. subtilis</i> Giesbrecht	F	3000	3300	440	1	0	0
* <i>O. subtilis/dentipes</i> form B	M	7600	5000	2400	5	0	0
<i>O. tregubovi</i> Shmeleva	F M	580	17	48	19000	5500	6200
<i>O. umerus</i> Böttger-Schnack & Boxshall	F	150	160	230	540	220	260
<i>O. venusta</i> Philippi f. <i>venella</i>	F M	500	1400	110	140	66	210
* <i>O. venusta</i> f. <i>typica</i>	F M	29	19	0	4	0	0
<i>O. vodjanitskii</i> Shmeleva & Delalo	F M	53	240	300	120	525	450
<i>O. zernovi</i> Shmeleva	F M	7300	7400	8300	17000	5400	5100
<i>Oncaea</i> spp. (form group <i>vodjanitskii/atlantica/platysetosa</i>)	F M	5	36	22	7	15	0
<i>Oncaea</i> spp. (form group <i>hawii/minuta/umerus</i>)	M	315	690	350	1000	1400	390
<i>Oncaea</i> spp. (mainly juveniles)	F M 3	12500	28500	22000	56000	14000	11000
<i>Pachos</i> sp.	1	0	0	0	0	0	1
Corycaeidae, total		5000	5300	540	3200	2300	4100
<i>Corycaeus</i> (<i>Agetus</i>) <i>limbatus</i> Brady	F M 1	30	13	12	1	120	180
* <i>C. crassiusculus</i> Dana	F M	44	0	0	0	0	0
<i>C. speciosus</i> Dana	F M	6	17	0	5	22	21
<i>Farranula carinata</i> Giesbrecht	F M	270	75	1	17	275	900
<i>F. gracilis</i> Dana	F M	0	0	0	0	12	23
<i>F. rostrata</i> Claus	F M	360	44	0	13	935	930
<i>Farranula</i> sp.	F	16	0	0	0	0	4
* <i>Urocorycaeus furcifer</i> Claus	F M	120	420	39	0	0	0
<i>Corycaeidae</i> spp., adults	F M 3	130	290	320	690	27	160
<i>Corycaeidae</i> spp., juveniles	F M 3	4000	4500	170	2450	930	1900

Table 5 (continued)

Species, Sex, Stage	Stn: Sampling depth (m): Time:	Gulf of Aden	Bab al Mandab	Red Sea			
		631 0-250 N	717 0-245 D	South, shall. 708 0-175 D	South, deep 703 0-950 D	Central 682 0-1050 D	North 663 0-1050 D
Sapphirinidae, total		370	110	70	135	130	120
* <i>Copilia lata</i> Giesbrecht	F M	0	6	0	0	0	0
<i>C. mirabilis</i> Dana	F M 1	20	23	2	63	23	66
<i>C. quadrata</i> Dana	F	0	0	0	4	0	0
<i>Copilia</i> spp.	2	4	0	0	18	1	1
* <i>Sapphirina intestinata</i> Giesbrecht	F M	0	2	0	1	0	0
<i>S. metallina</i> Dana	F M 1	8	5	0	4	26	43
<i>S. nigromaculata</i> Claus	F M	0	8	0	2	0	1
<i>S. opalina</i> Dana	F M	0	4	0	1	0	1
* <i>S. ovatolanceolata-gemma</i> Dana	F M	0	2	0	0	0	0
<i>Sapphirina</i> spp. (mainly juveniles)	F M 3	7	18	2	4	53	6
* <i>Vettopia granulosa</i> Giesbrecht	F M	0	18	66	0	0	0
<i>V. parva</i> Farran	F M	2	14	0	4	8	5
<i>Vettopia</i> spp.	3	330	7	0	34	17	1
<i>Saphirella</i> -like copepodids	2	380	3300	6000	1700	83	790
Unidentified poecilostomatoids	3	770	990	150	2900	780	130
Harpacticoida, total		8300	10000	43000	56000	12000	12000
<i>Clytemnestra rostrata</i> Brady	F M 1	4	6	1	0	0	3
<i>C. scutellata</i> Dana	F M 1	150	30	120	8	8	3
* <i>Euterpina acutifrons</i> Dana	F M 3	6	1500	140	260	0	0
<i>Macrosetella gracilis</i> Dana	F M 1	380	60	1100	3000	110	470
<i>Microsetella norvegica</i> Boeck	F M 3	7800	8700	42000	53000	12000	11500
<i>M. rosea</i> Dana	F M 3						
* <i>Miracia minor</i> Scott ^a	F M	3	6	1	0	0	0
Unidentified harpacticoids (mainly <i>Longipedia</i> spp.)	3	8	2	2	64	1	10
Siphonostomatoida, total		8	11	51	75	160	140
<i>Pontoeciella abyssicola</i> T. Scott	F M 3	6	10	51	75	160	130
<i>Ratania flava</i> Giesbrecht	F M 1	2	1	0	0	1	7
Mormonilloida							
* <i>Mormonilla minor</i> Giesbrecht	F M 3	1600	1300	81	22	0	0

^a Synonymus with *Distiocolus* (gen. nov.) *minor* (see Huys & Böttger-Schnack in press)

all species of *Oithona* and the smaller Corycaeidae could have been identified. Of the 75 species or groups listed in Table 5 about one-half (ca 40) decreased in number from south to north; 16 of these taxa were completely absent in the central-northern area. Moreover, for several *Oithona* and *Oncaea* species different morphs or size variants occurred in the Gulf of Aden and the southern Red Sea that were not found in the central-northern area (Table 6). For *Oithona* species, the identity of these morphs was verified (F. Ferrari pers. comm.), but for *Oncaea* species they are not yet recorded in the taxonomic literature.

The strongest regional trends in abundance were observed for *Oncaea subtilis*, *Mormonilla minor* and *Euterpina acutifrons*. The numbers of these species decreased from south to north by more than 3 orders of magnitude (Table 5). Differences of at least one order of magnitude were noted for another 7 species. Opposite to the general trend, an increase in abundance

from south to north was observed for 19 non-calanoid species or groups (Table 5). Among these, 2 general groups were apparent:

(1) Species which showed a more or less constant increase in numbers from south to north within the Red Sea, and which were rare or absent further south in the Gulf of Aden. These include *Lubbockia squillimana*, *Oncaea rufa*, *Farranula gracilis*, *Sapphirina metallina* and *Pontoeciella abyssicola*.

(2) Species which occurred in minimal numbers in the southern Red Sea, but exhibited higher values to the south (in the Gulf of Aden - Bab al Mandab area) as well as to the north (in the central-northern Red Sea). These include *Oncaea conifera*, *O. media* f. *major*, *Farranula carinata* and *F. rostrata*.

Copepod carcasses and empty exoskeletons were comparably low in abundance among the non-calanoid species during summer. In most cases, less than 10% of the total standing stock of a given species

Table 6. Occurrence of different forms or size variants among non-calanoid copepod species in the Red Sea during summer 1987. +: present; (+) solitary finds; -: not present

Species/forms	Central-northern Red Sea	Southern Red Sea
Oithonidae		
<i>Oithona nana</i> typical form	+	+
plumosa form	-	+
form A	-	+
<i>O. simplex</i> typical form (short)	+	+
long form	-	+
Oncaeiidae		
<i>Oncaea dentipes</i> form A	+	+
form B	-	+
<i>O. ivlevi</i> typical form	+	+
small form	(+)	+
<i>O. hawaii</i> typical form	+	+
long form	-	+
<i>O. venusta</i> forma <i>typica</i>	-	+
forma <i>venella</i>	+	+

in the upper 1050 m were dead. The only exception was *Oncaea* sp. K, which had a fairly high proportion of dead individuals throughout the entire region studied (10 to 29%). Some of the southern species, such as *Oncaea venusta* f. *typica*, were found in the central Red Sea as empty exoskeletons only. Species which were mainly concentrated in the north such as *O. tre-goubovi*, were found with high proportions of carcasses in the southern Red Sea.

Epipelagic zone (0–100 m). Regional differences in the non-calanoid fauna were most pronounced in the epipelagic zone. Based on the similarity in species composition among stations within this depth zone (Tables 7 & 8) 3 different regions could be distinguished:

(1) The Gulf of Aden and the Bab al Mandab area, where the 3 small oithonid species investigated were more or less equally abundant, each accounting for 7 to 13% of the total cyclopoids (Table 7). Among the poecilostomatoids, *Oncaea subtilis* strongly dominated. When assuming that most of the males of '*subtilis/dentipes* sp. B' belong to *O. subtilis*, this species amounted to 14 to 27% within the group (Table 7). *O. zernovi* and *O. media* f. *minor* ranked second and/or third, each accounting for 7 to 15% of all poecilostomatoids. Among harpacticoids, *Euterpina acutifrons* was especially abundant in the Strait of Bab al Mandab, accounting for 19% of this group in that area.

(2) The southern Red Sea, where 2 *Oithona* species dominated, *O. simplex* and *O. nana*, each contributing about 15 to 25% within the cyclopoids (Table 7). Among poecilostomatoids, *Oncaea zernovi* and *O. ivlevi* were dominant, with a relative abundance of 10 to 20% of the total. In this area, the proportion of *Oncaea* spp. juveniles was conspicuously high (Table 8).

(3) The central-northern Red Sea, where the relative abundance of *Oithona nana* was strongly reduced and *O. simplex* and *Paroithona* spp. were the dominant cyclopoid species, each sharing about 20% within this

Table 7. Abundance (individuals beneath 0.25 m²) of selected small oithonid species in the Gulf of Aden and different regions of the Red Sea during summer 1987. D: day; N: night. shall.: shallow; F, females; M, males; 1: late juveniles. 0: no individuals; -: no data

Species, Sex, Stage	Gulf of Aden		Bab al Mandab	Red Sea			North D
	Stn: 631 Sampling time: N	633 D	717 D	South, shall. 708 D	South, deep 703 D	Central 682 D	
<i>Oithona nana</i> FM 1							
0– 100 m	4900	2400	4300	29000	11000	9	270
100– 200 m	96	-	1400	4700 ^a	100	32	24
200– 450 m	-	-	-	-	100	0	0
450–1050 m	-	-	-	-	35 ^b	0	4
<i>Oithona simplex</i> FM 1							
0– 100 m	5400	3200	4200	54000	16000	5100	5900
100– 200 m	0	-	110	4600 ^a	140	220	310
200– 450 m	-	-	-	-	72	8	48
450–1050 m	-	-	-	-	66 ^b	24	24
<i>Paroithona</i> spp. FM 1							
0– 100 m	2050	2350	2700	5800	960	2700	1450
100– 200 m	1300	-	1600	4300 ^a	1700	1500	1700
200– 450 m	-	-	-	-	16	56	160
450–1050 m	-	-	-	-	10 ^b	44	40

^a Depth 100–175 m; ^b depth 450–950 m

Table 8. Abundance (individuals beneath 0.25 m²) of dominant *Oncaea* species and *Oncaea* spp. juveniles in the Gulf of Aden and different regions of the Red Sea during summer 1987. Species are listed in alphabetical order. shall.: shallow. F, females; M, males; 3: juveniles. D: day; N: night. 0: no individuals; -: no data

Species, Sex, Stage	Strn: Sampling time:	Gulf of Aden		Bab al Mandab	Red Sea			North
		631 N	633 D	717 D	South, shall. 708 D	South, deep 703 D	Central 682 D	663 D
<i>Oncaea</i> sp. AD	FM							
0- 100 m		510	610	620	100	0	0	0
100- 250 m		0	-	1	270 ^a	0	0	0
250- 450 m		-	-			0	0	0
450-1050 m		-	-			0	0	0
<i>O. dentipes</i> form A	F							
0- 100 m		16	81	240	70	83	470	190
100- 250 m		68	-	100	260 ^a	105	770	1000
250- 450 m		-	-			0	32	20
450-1050 m		-	-			2 ^b	24	6
<i>O. dentipes</i> form B	F							
0- 100 m		25	170	140	5	1	0	0
100- 250 m		66	-	0	3 ^a	0	0	0
250- 450 m		-	-			0	0	0
450-1050 m		-	-			0	0	0
<i>O. dentipes</i> form A	M							
0- 100 m		130	110	290	480	59	68	130
100- 250 m		32	-	65	710 ^a	110	350	430
250- 450 m		-	-			0	8	0
450-1050 m		-	-			1 ^b	8	0
<i>O. ivlevi</i>	FM							
0- 100 m		1400	1900	2200	3500	2400	7900	5600
100- 250 m		260	-	260	4000 ^a	170	3000	3300
250- 450 m		-	-			24	48	8
450-1050 m		-	-			10 ^b	170	24
<i>O. ivlevi</i> /sp. K	FM							
0- 100 m		130	0	540	0	0	0	0
100- 250 m		130	-	1900	0	0	0	0
250- 450 m		-	-			0	0	0
450-1050 m		-	-			0	0	0
<i>Oncaea</i> sp. K	FM							
0- 100 m		0	48	65	935	64	64	64
100- 250 m		3300	-	370	1500 ^a	4100	510	820
250- 450 m		-	-			6050	1700	2200
450-1050 m		-	-			2350 ^b	40	170
<i>O. media</i> f. <i>minor</i>	FM							
0- 100 m		850	770	300	380	5000	2800	2000
100- 250 m		160	-	330	620 ^a	81	220	380
250- 450 m		-	-			91	350	620
450-1050 m		-	-			7 ^b	28	130
<i>O. subtilis</i>	F							
0- 100 m		2700	2800	3150	84	1	0	0
100- 250 m		320	-	130	360 ^a	0	0	0
250- 450 m		-	-			0	0	0
450-1050 m		-	-			0	0	0
<i>O. subtilis</i> / <i>dentipes</i> form B	M							
0- 100 m		3450	4900	4800	1350	5	0	0
100- 250 m		4200	-	180	1100 ^a	0	0	0
250- 450 m		-	-			0	0	0
450-1050 m		-	-			0	0	0
<i>O. tregoubovi</i>	FM							
0- 100 m		130	0	1	0	64	0	130
100- 250 m		450	-	16	48 ^a	1600	130	80
250- 450 m		-	-			8700	1500	2400
450-1050 m		-	-			8400 ^b	3800	3600

(Table continued on next page)

Table 8 (continued)

Species, Sex, Stage	Gulf of Aden		Bab al Mandab	Red Sea			
	Stn: 631	633	717	South, shall. 708	South, deep 703	Central 682	North 663
	Sampling time: N	D	D	D	D	D	D
<i>O. ovalis</i> F M							
0–100 m	0	0	32	1	0	0	0
100–250 m	420	–	480	32 ^a	890	24	48
250–450 m	–	–	–	–	1600	2000	1700
450–1050 m	–	–	–	–	3300 ^b	1700	1700
<i>O. zernovi</i> F M							
0–100 m	4350	2200	4800	4500	4100	2000	640
100–250 m	3000	–	2600	3900 ^a	6000	1600	2000
250–450 m	–	–	–	–	6300	1700	2300
450–1050 m	–	–	–	–	290 ^b	100	200
<i>Oncaea</i> spp. 3							
0–100 m	7250	7800	22000	11000	36000	4550	4100
100–250 m	5200	–	6500	11000 ^a	7000	3850	2700
250–450 m	–	–	–	–	5900	2800	2200
450–1050 m	–	–	–	–	7300 ^b	2450	1650
<i>Oncaea</i> total							
0–100 m	25000	25000	48000	23000	46500	18000	12500
100–250 m	19000	–	14000	25000 ^a	21000	11000	12000
250–450 m	–	–	–	–	29500	10500	12000
450–1050 m	–	–	–	–	22000 ^b	8900	7800

^aDepth 100–175 m; ^bdepth 450–950 m

group. Among poecilostomatoids, the relative importance of *Oncaea ivlevi* is increased considerably in this area, with a share of 30 to 40% of the total number in this group. *O. zernovi*, *O. media* f. *minor*, and *O. dentipes* (form A) had relative abundances between 1 to 10% of the total. In this area, 2 *Farranula* species, *F. carinata* and *F. rostrata*, were also of some numerical importance (not mentioned in Table 8), each contributing 1 to 5% to the total number of poecilostomatoids.

Compared to these results from the epipelagic zone, regional differences were less pronounced in the deeper layers. The following 3 depth zones can be distinguished below 100 m with regard to the non-calanoid fauna.

Upper mesoepelagic zone (a) O₂ gradient (100–250 m).

The cyclopid community of this zone was dominated by *Paroithona* spp. at all oceanic sites in the Red Sea and Gulf of Aden (Table 7). In the shallow waters of the southern Red Sea and at Bab al Mandab the dominance of this species was less pronounced. Among poecilostomatoids, the proportions of *Oncaea zernovi* and *Oncaea* sp. K increased compared to those in the upper 100 m, while those of *O. ivlevi* and *O. media* f. *minor* were generally lower (Table 8). Regional differences in the composition of the dominant *Oncaea* species were generally similar to those in the upper 100 m. The mormonilloids were mainly confined to this depth zone. The finer vertical resolution of samples at

Bab al Mandab showed that adult and juvenile *Mormonilla minor* were concentrated mainly at 80 to 150 m depth, in the cooler and less saline water flowing in from the Gulf of Aden (cf. Fig. 2).

Upper mesopelagic zone (b) O₂ minimum (250–450 m).

Below 250 m depth, *Oncaea* was the dominant genus within the copepod community (see Table 4). Compared to the 2 zones above, the species composition of *Oncaea* changed considerably. Dominant forms were *Oncaea* sp. K, *O. ovalis*, *O. tregoubovi* and *O. zernovi*, each sharing between 15 and 30% of the total poecilostomatoids at the 3 stations investigated. A south-to-north decrease in the proportion of the 2 dominant species, *O. tregoubovi* and *O. ovalis*, was indicated (Table 8), but remains uncertain due to the limited data set in the southern Red Sea.

Lower mesopelagic/upper bathypelagic zone (450–1050 m).

In this depth zone, *Oncaea tregoubovi* always was the dominant species, amounting to ca 40% of all poecilostomatoids (Table 8). *O. ovalis* ranked second with percentages between 15 and 20% of the total. *Oncaea* sp. K contributed a considerable percentage (10%) to all poecilostomatoids only in the southern Red Sea. Another 2 *Oncaea* species, *O. conifera* and *O. hawaii* (not mentioned in Table 8), accounted for slightly over 1% of all poecilostomatoids in this depth layer in the central-northern Red Sea.

DISCUSSION

Hydrographic conditions during summer 1987

At the southern entrance of the Red Sea, the hydrographic regime during the southwest monsoon period is usually characterized by an outflow of surface and deep water through the Strait of Bab al Mandab, which is compensated for by an inflow of Gulf of Aden surface water at an intermediate depth (Morcos 1970, Maillard & Soliman 1986, Edwards 1987). Under these conditions the number of invading plankton species has been found to be minimal (Halim 1969, Weikert 1987). During summer 1987, however, the hydrographic condition was not typical for the season: rather, the current meter readings pointed to an inflow of stratified Gulf water at the surface, which was compensated for by an outflow of Red Sea water at greater depth (E. Mittelstaedt pers. comm.; see also Weikert 1988b). This situation is typical for the northwest monsoon period, which prevails during the greatest part of the year (Morcos 1970, Edwards 1987). Thus, the observed south-to-north differences found in the species spectrum of non-calanoid copepods during the present study are not assumed to reflect minimal (summer) values, but can be viewed as a more typical feature found during the greatest part of the year.

Horizontal distribution of epipelagic plankton

Within the central-northern Red Sea, latitudinal differences in the environmental conditions were considerable during summer 1987, showing a south-to-north increase in salinity from 38.5 to 39.5 ppt. However, no corresponding differences were found in total plankton biomass and/or metazoan abundance within this region. This observation seems to contrast with many others which have indicated lower biomass and abundance values in the northern Red Sea (22° to 25° N) as compared to the central region (Delalo 1966, Ponomareva 1968, Gordeyeva 1970, Kornilova & Fedorina 1970, Weikert 1980, 1987, Böttger 1985, Böttger-Schnack 1990b, Schneider et al. 1991, 1994, Beckmann unpubl. data). The difference may be due to the unrestricted northern extension (23° 40' N) of plankton sampling during the present study, which does not include the entire less-productive northern parts.

Between the central-northern and the southern Red Sea, however, pronounced differences were found in biomass, metazoan abundance and composition of the 0.05 mm mesh net plankton. Generally, biomass and numerical abundance of total metazoans as well as the species numbers of non-calanoid copepods were greater in the southern as compared to the central-

northern part. This corresponds to the general south-north trend reported for biomass, abundance and diversity of larger mesozooplankton (Delalo 1966, Rudyakov & Voronina 1967, Halim 1969, 1984, Kimor 1973, Weikert 1980, 1981, Beckmann 1984, Casanova 1985) and can be explained by the more hostile environmental conditions in the central and northern Red Sea, especially the increase in salinity (e.g. Morcos 1970). In the epipelagic zone, the south-to-north decrease in the numerical abundance of total metazoans was much lower than the corresponding decrease in biomass. This discrepancy is partly due to differences in the taxonomic composition: anthozoan larvae and large gelatinous zooplankton taxa (siphonophores and medusae) occurred mainly in the southern Red Sea and in the Strait of Bab al Mandab. They contributed a large proportion to the wet weight, but little to the total number of metazoans, which was dominated by small organisms <0.4 mm in size. The exceptionally high biomass values at Bab al Mandab co-occurred moreover with a high phytoplankton standing stock and primary production, which was twice as high in the Strait as compared to the adjacent areas (A. Moigis in Weikert 1988b).

Latitudinal differences in species numbers were not consistent for all non-calanoid copepod genera investigated, however. Within the genera *Oithona*, *Corycaeus*, *Sapphirina* and *Copilia*, species numbers showed a relatively strong decrease to the north, even though not all species in the first 2 genera have been identified yet. The generally high numbers of *Oncaea* species, on the other hand, decreased only slightly to the north. Out of 12 epipelagic *Oncaea* species, only 2 (*O. subtilis* and *Oncaea* sp. AD) were absent in the central-northern Red Sea. However, within *Oncaea* species and also *Oithona* species a number of form or size variants were found in the southern Red Sea, which were rare or absent in the central area. Since most of the *Oncaea* variants have not yet been described in the literature, their taxonomic status has yet to be ascertained. A recent re-examination of a form variant of *O. hawaii* from the southern Red Sea, for instance, indicated that this form should be regarded as a separate species (G. A. Boxshall pers. comm.). Also, the taxonomic status of *O. tregubovi* from the Gulf of Aden has to be clarified; in the adjacent Arabian Sea, a morphologically very similar species was found in high abundances in the epipelagic zone (Böttger-Schnack 1994). This has not been identified from the Red Sea yet, but may well be present in the Gulf. A more detailed taxonomic description of all small *Oncaea* species from the Red Sea is in progress in order to overcome difficulties in species identification and resulting problems in the ecological interpretation of data on species distribution.

Of the 16 non-calanoïd species or taxa restricted to the southern Red Sea and Gulf of Aden during the present summer survey (see Table 5), 10 have not been recorded from the central or northern areas during earlier investigations including different seasons (Delalo 1966, Halim 1969, Böttger-Schnack 1988, 1990b). Thus, they can be regarded as strictly southern species, which are transported from the Gulf of Aden into the southern Red Sea, but cannot survive in the extreme environment further north. Among the Poecilostomatoida, typical southern species were *Oncaea subtilis*, which dominated the southern fauna numerically, and *Urocorycaeus furcifer*, which was conspicuous due to its large size. Both species are not mentioned in previous records from the southern Red Sea (Delalo 1966, Halim 1969). However, *U. furcifer* is widespread in the Indian Ocean with particularly high abundances in the Gulf of Aden (Meenakshikunjamma 1974) and *O. subtilis* has recently been found in the Arabian Sea (Böttger-Schnack 1994). A further species, *Mormonilla minor*, is also assumed to belong to this group, although it was recorded from the central and northern Red Sea by Delalo (1966). However, all recent studies of larger and smaller mesozooplankton in the central and northern Red Sea (Weikert 1980, 1981, 1987, Beckmann 1984, unpubl. data, Böttger 1985) have confirmed the year-round absence of this species in the central Red Sea.

In relation to the total number of 75 species or taxa of non-calanoïd copepods investigated in the Red Sea, the number of 11 species restricted to the south appears to be comparably low. For chaetognaths, 7 out of 17 species recorded from the Red Sea have been found in the southern area only (J.-P. Casanova 1985, 1990) and for tintinnids 31 out of 108 species are restricted to this area (Halim 1969). A similar ratio was also found for the species numbers of calanoïd copepods (Halim 1969, Kornilova & Fedorina 1970), thecosome pteropods (Rampal 1988, 1990) and euphausiids (B. Casanova 1990). On the basis of the present taxonomic knowledge, this comparison indicates that non-calanoïd copepod species as compared to other zooplankton groups are to a larger part less sensitive to the strong horizontal gradients in environmental conditions observed in the Red Sea.

Four species or forms that had previously been recorded from the northern-central area during winter were not found during summer 1987 in this area: *Dioithona rigida*, *Oncaea venusta* f. *typica*, *Sapphirina ovatolanceolata-gemma*, and *Euterpina acutifrons*. These species may have been transported further north into the Red Sea due to the stronger inflow in the latter period. The difference in the occurrence of *O. venusta* f. *typica* was most conspicuous. Thus, the indicator function of this species for the extension of

the inflow from the Gulf of Aden as assumed by Böttger-Schnack (1990b) can be confirmed by the present data.

In contrast to the general south-north decrease in plankton abundances within the Red Sea, several poecilostomatoid species showed an increase from south to north, such as female *Oncaea dentipes* form A, *O. ivlevi*, *Agetus limbatus*, and *Lubbockia squillimana*. The numerical increase was most conspicuous for *Lubbockia* species, which were totally absent in samples from the Gulf of Aden (0–250 m). As *Lubbockia* species inhabit the epi- and also the mesopelagic zone in the Red Sea (Böttger-Schnack 1990a, b, this study), the limited vertical range of sampling in the Gulf may explain why none of these species were encountered in that area. However, several samples were additionally taken with a 0.1 mm mesh net from the underlying depth layer 200–500 m in the Gulf of Aden during summer 1987 (C. Hemleben in Weikert 1988b). These samples contained only 1 single juvenile specimen of *L. aculeata*, thus confirming the general scarcity of *Lubbockia* in this area. Sampling with 0.3 mm mesh nets during different seasons confirmed a general decrease in abundance for the genus *Lubbockia* from the central Red Sea to the Gulf of Aden (W. Beckmann unpubl.). *L. aculeata* and *L. squillimana* have a widespread distribution in the Indian Ocean (Stephen 1988) and their virtual absence in the Gulf of Aden is quite unexpected. Based on this observation, *Lubbockia* species in the Red Sea seem to represent isolated local populations, which are independent of a regular recruitment from the Gulf of Aden. This phenomenon has already been pointed out for several other zooplankton species, such as *Haloptilus longicornis* among calanoïd copepods (Beckmann 1984) or *Sagitta pacifica* among chaetognaths (Casanova 1985, 1986).

Oncaea ivlevi, also exhibiting a very strong numerical increase from south to north in the Red Sea, is again an epipelagic species of wider distribution in the Atlantic and the Mediterranean (Malt 1982, 1983), but has only rarely been quantitatively investigated due to its small size. In the Red Sea, it occurs mainly in the lower epipelagic zone, below the thermocline (Böttger-Schnack 1990a, b, this study). In the Arabian Sea, the typical *O. ivlevi* has not yet been found, but a closely related species, which is still unidentified, occurs in the epipelagic zone (Böttger-Schnack 1994). The presence of single exuviae of typical *O. ivlevi* in the central Arabian Sea (unpubl. data) indicate that the species may be present during other seasons or in different regions of the Indian Ocean. More complete data on the geographical distribution of *O. ivlevi* are required from the Indian Ocean, in order to assess the origin of this numerically important small oncaeid in the Red Sea.

Table 9. Seasonal differences in fine mesh net plankton biomass (g wet wt beneath 1 m², excluding single large organisms; mean for day and night) and metazoan abundance and size composition (no. of ind. × 10³ beneath 1 m², day-time values) in the upper 450 m of the central Red Sea. (n) no. of sampling series

		Summer 1987 ^a	Autumn 1980 ^b	Winter 1981 ^b
Biomass				
	Mean	10	9.1	14.5
	Range	5.9–15	6.9–13	12–20
	(n)	(9)	(10)	(6)
Metazoan abundance and size composition				
Total	Mean	1000	570	580
	Range	1000–1050	430–680	470–750
	(n)	(2)	(5)	(3)
Size groups				
< 0.2 mm	Mean	530	855	380
	Range	505–560		
0.2–0.4 mm	Mean	325	350–460	370
	Range	310–340		
0.4–1.2 mm	Mean	160	170	190
	Range	150–170		
> 1.2 mm	Mean	15.5	15	23
	Range	15–16		
			14–16	18–29
^a Mesh size 0.055 mm, this study; ^b mesh size 0.1 mm, after Böttger (1985)				

Seasonal differences in the central Red Sea

The total biomass of the fine mesh net plankton sampled in summer 1987 per standard area in the upper 450 m was similar to that obtained during earlier investigations in autumn 1980 (Böttger 1985, 1987), but significantly lower than that found during winter 1981 in the central Red Sea (Mann-Whitney *U*-test, $p < 0.05$) (Table 9). The mesh size used during the earlier investigations was somewhat larger (0.1 mm) than during the present summer survey (0.05 mm). Thus, the summer value has to be taken as an overestimation in this comparison and may, in fact, be lowest. For the autumn, Gordeyeva (1970) (mesh size 0.06 mm) reported much higher biomass values of 16 g m⁻² in the upper 500 m of the central and northern Red Sea, but her data are not directly comparable to the present biomass (wet weight) values, because a different method of biomass determination was used ('Yashnov-counting-weight method'). The seasonal comparison may be more realistic for numerical abundance values (Table 9) rather than biomass, as numbers are given by size categories and may be restricted to the size fraction of organisms quantitatively sampled by both mesh sizes used. The numbers of organisms above 0.4 mm in size confirm the general picture obtained for biomass and they indicate that the high winter values are mainly due to on the larger size fraction above 1.2 mm.

In the central Red Sea, seasonal variations in zooplankton abundance and composition are based on changes in primary production within this area but also on allochthonous influences from the southern Red Sea (Weikert 1987). This influence has been observed to be greatest during winter. An important indicator of southern inflow conditions has been found in the calanoid copepod *Eucalanus* spp., which occurs in its maximum abundance during winter and in low numbers during summer and autumn (Weikert 1980, 1987, Beckmann 1984 and unpubl. data). A corresponding seasonal pattern has also been found for a few species of non-calanoid copepods (Table 10), among which *Oncaea venusta* f. *typica* is the most important one, due to its large size. Together with *O. clevei* and *Oithona nana* they are assumed to be allochthonous organisms from the southern Red Sea.

Table 10. Seasonal variation in the abundance of non-calanoid copepod species > 0.5 mm in size in the central Red Sea. Data from autumn and winter were derived from Böttger-Schnack (1988, 1990a, b), summer values were taken from the present study. Species are listed in alphabetical order

Species showing maximum abundances during winter, but low numbers during summer and/or autumn

Oithona nana
Oncaea clevei
O. venusta f. *typica*
 f. *venella*

Species showing maximum abundances during summer and/or autumn, but low numbers during winter

Corycaeus speciosus
Farranula carinata
F. rostrata
Oncaea conifera
O. rufa

Species showing no or no consistent seasonal variation

Copilia mirabilis
Agetus limbatus
Lubbockia aculeata
L. squillimana
Oncaea dentipes form A
O. hawaii
O. media f. *minor*
 f. *major*
O. mediterranea
O. minuta
O. umerus
Sapphirina metallina
Vetтория parva

In addition, 2 other groups of non-calanoïds may be defined according to their seasonal pattern (Table 10):

(1) Species showing maximum abundances during summer and/or autumn, but low numbers during winter. This group includes 5 species (Table 10), of which the 3 corycaeid species are assumed to be independent in their population dynamics from southern inflow conditions, as they are found in the southern Red Sea in low abundances only (Table 5).

(2) Species exhibiting no or no consistent seasonal variation in abundance in the central Red Sea. This group includes the greatest number of species (Table 10). Most of them, in particular *Oncaea dentipes* form A, *Lubbockia squillimana* and *Agetus limbatus*, also do not seem to be substantially recruited from the southern Red Sea, as they were usually less abundant in that area (Table 5). Some exchange between the areas cannot be excluded for species within this group however (e.g. *Oncaea media* f. *minor*).

In summary, it can be stated that the non-calanoïd fauna above 0.5 mm in size in the central Red Sea is mainly represented by local populations. Only a few southern species seem to have any substantial seasonal influence.

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