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Mesozooplankton distribution on a transect from the Gulf of Aden to the central Red Sea during the winter monsoon

Mesozooplankton
Copepoda Calanoida
Vertical distribution
Red Sea
Gulf of Aden

Mésozooplancton
Copépodes calanoïdes
Distribution verticale
Mer Rouge
Golfe d'Aden

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ABSTRACT

Quantitative mesozooplankton samples were taken at five locations on a transect from the Gulf of Aden to the central Red Sea during March 1979. The horizontal and vertical distribution of the species was clearly related to hydrographic features. In the Red Sea, the zooplankton standing stock decreased from south to north. Contrary to earlier reports, the largest zooplankton standing stock in both the southern and central Red Sea seems to occur in winter due to the import of organisms from the Gulf of Aden with the surface current. Above the shallow Hanish Sill, that separates the Gulf and Red Sea deep waters, the plankton fauna was dominated by the epipelagic calanoid copepod, *Eucalanus crassus.* This species had apparently originated in coastal areas of the Gulf of Aden and, together with other imported species, died off in the Red Sea near 16°N. Between about 16° and 19°N, the zooplankton standing stock exhibited a rather large decrease, coinciding with a conspicuous change in plankton structure. While at about 16°N, many moribund *Eucalanus crassus* were still present in the meso- and bathypelagic zones, imported organisms obviously did not change the structure of the zooplankton in the deeper water of the central Red Sea. This area was characterized by interzonal calanoid copepod species with strong affinities for distinct, vertically separated habitat zones which appear to exist throughout the year. These affinities were less pronounced to the south.

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RÉSUMÉ

Distribution du mésoplancton le long d'une radiale entre le Golfe d'Aden et la Mer Rouge durant la mousson d'hiver

Des échantillons quantitatifs de mésozooplancton ont été prélevés le long d'une radiale en 5 stations entre le Golfe d'Aden et le centre de la Mer Rouge en mars 1979. Les espèces se répartissent horizontalement et verticalement en suivant les caractéristiques hydrologiques. Dans la Mer Rouge, la biomasse de zooplancton diminue du sud vers le nord. Contrairement aux données antérieures, c'est en hiver que la biomasse de zooplancton est la plus abondante dans le sud et au centre de la Mer Rouge, en raison de l'apport d'organismes du Golfe d'Aden par le courant superficiel. Au-dessus du seuil de Hanish qui sépare les eaux profondes du golfe et celles de la Mer Rouge, la faune planctonique est dominée par le copépode calanoïde épilagique *Eucalanus crassus.* Cette espèce semble provenir des zones côtières du Golfe d'Aden et, avec d'autres espèces allochtones, disparaît dans la Mer Rouge vers 16°N. Entre 16 et 19°N approximativement, la biomasse de zooplancton présente une diminution assez forte, coïncidant avec une variation manifeste dans la structure du plancton. Alors que vers

16°N on trouve encore des *Eucalanus crassus* dans les zones méso- et bathypélagiques, la structure du zooplancton n'est à l'évidence pas modifiée par l'apport d'autres organismes dans l'eau profonde du centre de la Mer Rouge. Cette région est caractérisée par des espèces de copépodes calanoïdes à étagement vertical bien délimité, et qui sont présentes tout au long de l'année. Ce caractère est moins marqué au sud.

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INTRODUCTION

Comparative taxonomic studies show that the overwhelming majority of zooplanktonic species in the Red Sea are obviously of Indopacific origin (Delalo, 1966; Casanova *et al.*, 1973; Godeaux, 1973; Kimor, 1973; Weigmann, 1974; older literature reviewed by Halim, 1969). However, while the hydrographic exchange pattern of Red Sea and Gulf of Aden waters was investigated during numerous research programs (*vide* Morcos, 1970; Jones, Browning, 1971; Khimitsa, Bibik, 1979), no research cruise had previously been undertaken primarily to analyze the plankton exchange.

Quantitative data on the numerical vertical distribution and composition of Red Sea zooplankton were reported by Schmidt (1973), Kimor and Golandsky (1977), and de Almeida Prado-Por (1983) for the Gulf of Aqaba, by Gordeyeva (1970) for the northern and central Red Sea, and, in more detail, by Weikert (1980 *a;* 1981; 1982) for the central Red Sea. A preliminary publication comparing the plankton in the northern, central, and southern Red Sea was provided by Weikert (1980 *b*), which included some results of the present investigations. Aside from these results, only very general information about the southern part of the Red Sea had been available from zooplankton charts of the Indian Ocean area (IOBC, 1968; 1970 *a; b*), and some isolated biomass values had been reported (Delalo, 1966; Ponomareva, 1968; Wishner, 1980).

This paper presents the results of the first comprehensive quantitative survey of the horizontal and vertical distribution and taxonomic composition of the mesozooplankton, as well as some relevant environmental parameters, along a transect from the Gulf of Aden through the southern part of the Red Sea to about 21°N. It provides information about the effects on the Red Sea zooplankton at various locations due to the import of organisms from the Gulf of Aden during the winter monsoon, when the hydrographic circulation pattern is most favourable for this import.

MATERIAL AND METHODS

During the MESEDA 2 program (Metalliferous Sediments Atlantis II Deep), which was initiated by the Saudi-Sudanese Red Sea Joint Commission, Jeddah, zooplankton sampling stations along a transect from the Gulf of Aden to the central Red Sea were visited by the R. V. "Valdivia" in March 1979. Figure 1 shows the locations of the stations, and Table 1 provides some relevant information about each.

Methods of plankton sampling and treatment corresponded to those reported by Weikert (1980 *a; b*; 1982). A multiple opening and closing net with a 0.5 m × 0.5 m mouth opening, equipped with five nets of 300 μm mesh size, was employed for vertical tows. By opening a net, the preceeding one is automatically closed. The depth is determined by a remote pressure meter, and net operations are controlled from aboard the ship *via* a one-conductor cable. The towing speed was about 50 m/min. A detailed description of the device and a discussion of its sampling characteristics were provided by Weikert and John (1981).

The vertical sampling intervals at the deep water stations were 50 m from the surface to 450 m, 150 m from 450 to 1 050 m, and 200 m below 1 050 m. Above the shallow Hanish Sill, the depth ranges sampled were 0-20, 20-40, 40-50, 50-80, and 80-130 m for the first profile; the second one included the ranges 0-15, 15-40, 40-60, 60-80, and 80-130 m. A total of 125 samples were analyzed.

The plankton was preserved in a 4% formaldehyde-seawater solution buffered with hexamethylenetetramine. The numbers of organisms presented do not include exoskeletons and animals that were obviously dead prior to collection. Most of these were remains of copepods, and the criteria of Wheeler (1967) and Weikert (1977) served for distinguishing the non-living from the living specimens. Radiolarians were also excluded from the counts, as were contaminants of the deep water samples that had definitely originated in the surface layers.

The biomass wet weight of samples was determined using the method of Tranter (1962). Coelenterates and salps larger than about 0.5 cm and crustaceans longer than about 1.5 cm were removed before weighing.

In addition to the plankton sampling, one profile of temperature, salinity, and oxygen concentration was obtained at each location. Reversing thermometers were used in the Gulf of Aden. The temperature profiles in the Red Sea were recorded by a bathysonde. Salinity and oxygen concentrations were determined by titration of hydrocast samples, the Winkler method being employed for oxygen.

The terms "epi-, meso-, and bathypelagic zone" are used for the depth ranges 0-100, 100-750, and below 750 m, respectively, as defined by Weikert (1982) for the central Red Sea. Data calculated for the upper 1 050 m in the Red Sea (Tables 2 through 7) are

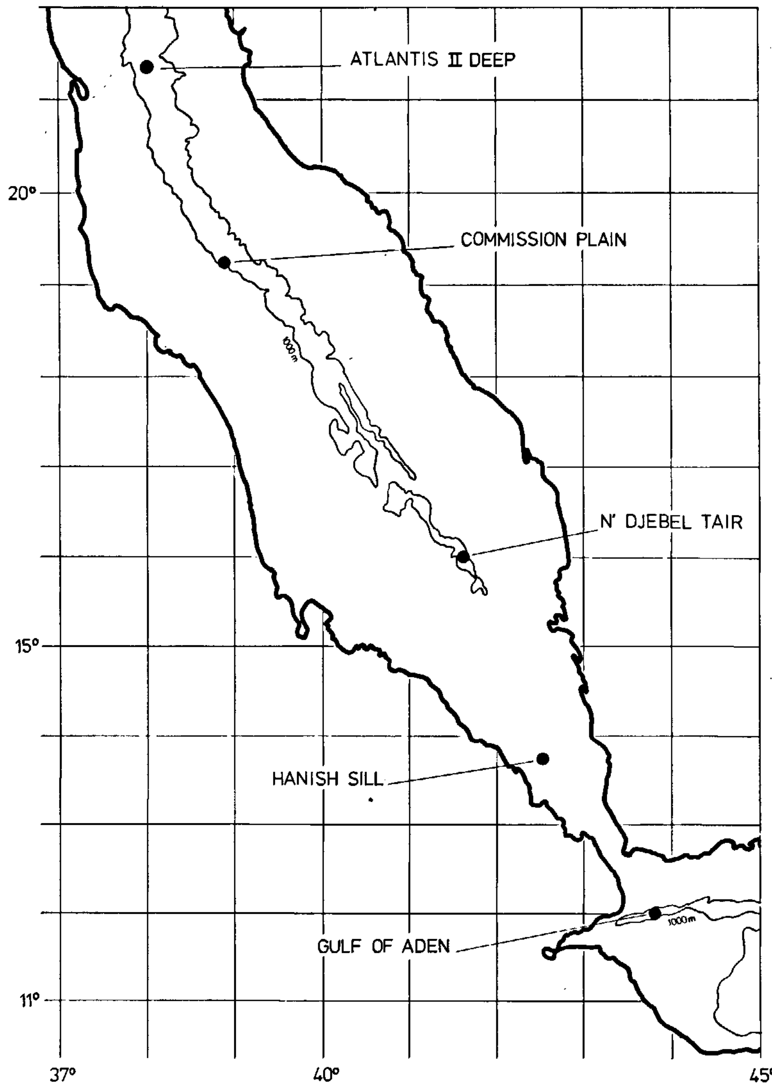

Figure 1
Sites of investigations in the Gulf of Aden and the Red Sea during March 1979.

assumed to be representative for the entire water column, as below this range, population densities are negligible. The Hanish Sill is not included in the term "Red Sea proper" as used below.

RESULTS

Temperature, salinity, and oxygen concentration (Fig. 2)

At all stations investigated, the surface layer had a warmer temperature and lower salinity than the deeper water.

In the Gulf of Aden, a sharp thermocline extended from 100 to 150 m. A distinct salinity gradient appeared between the depths of 400 and 500 m. Between 500 and 800 m, maximum salinity values for the whole water column were detected, and temperatures were warmer than in the adjacent layers.

Above the shallow Hanish Sill, the sharpest gradients of both temperature and salinity occurred from about 70 to 100 m.

At the Red Sea deep water stations, the surface layer was separated by a thermocline from a homogeneous deep water body. The thermocline extended from about

Table 1
Station list.

No.	Location	Lat. N	Long. E	Date	Sampling time of profiles	Sampling range (m)	Water depth total (m)
5	Gulf of Aden	12°00.6'	43°48.2'	16/3	16.24-17.17	0.1 050	1 200
14	Hanish Sill	13°44.5'	42°31.7'	17/3	20.29-20.34	0-130	137
					20.51-20.56	0-130	
17	N'Djebel Tair	16°00.6'	41°38.2'	18/3	15.00-16.37	0-1 050	1 673
21		16°01.3'	41°37.3'		23.18-23.57	0-450	
30		16°01.2'	41°37.2'	19/3	15.47-17.14	450-1 450	
41	Commission Plain	19°14.9'	38°53.8'	21/3	13.55-18.00	0-1 250	1 912
44		19°14.8'	38°52.7'	22-23/3	23.09-02.08	0-1 250	
49		19°13.9'	38°54.1'	23/3	11.38-14.50	0-1 250	
52	Atlantis II Deep	21°22.0'	38°03.9'	24/3	12.51-16.27	0-1 250	2 122
60		21°20.5'	38°04.9'	25-26/3	23.59-02.35	0-1 450	

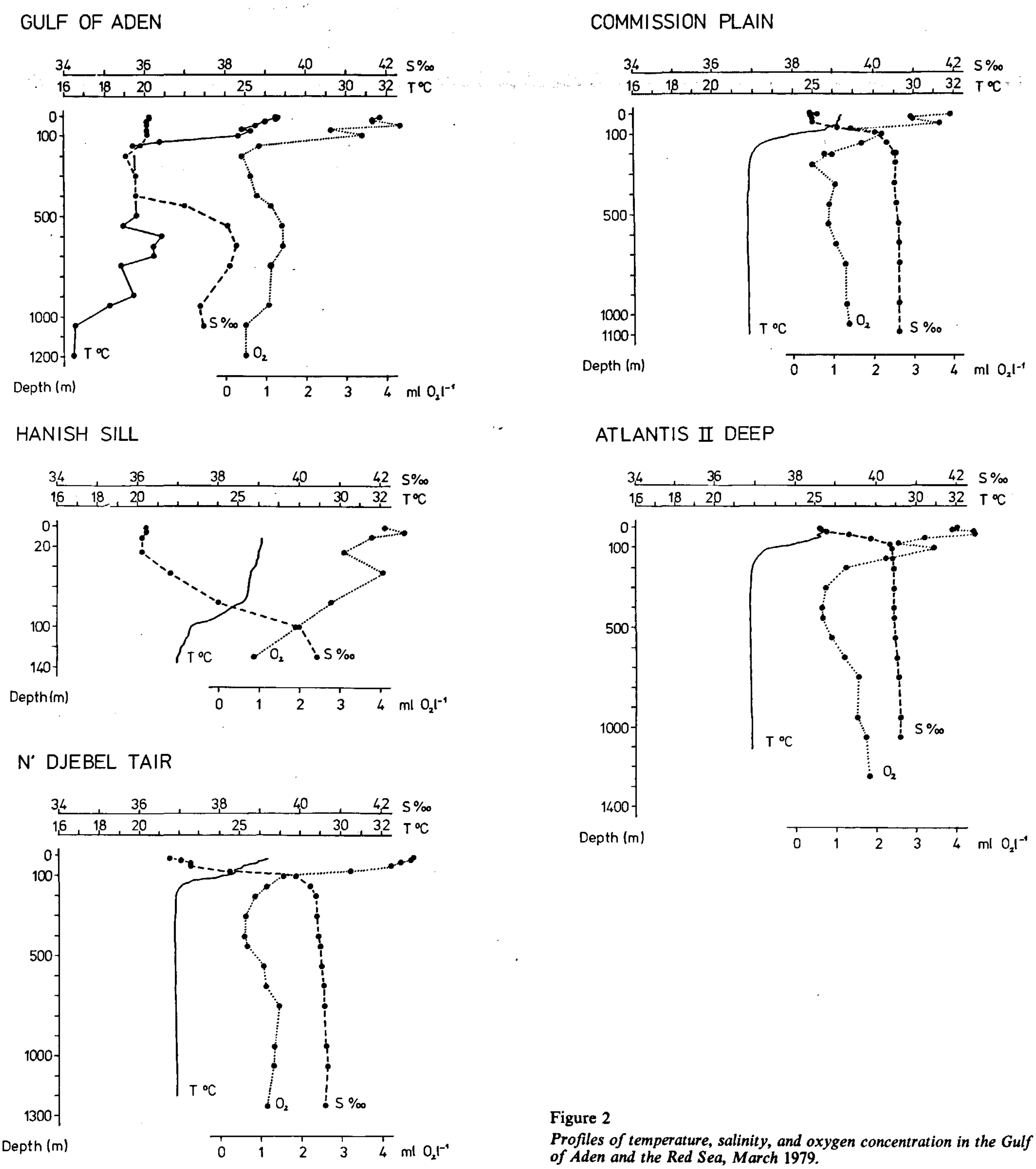

Figure 2

Profiles of temperature, salinity, and oxygen concentration in the Gulf of Aden and the Red Sea, March 1979.

70 to 150 m at N'Djebel Tair and the Commission Plain and from 50 to 100 m at the Atlantis II Deep. Salinity gradients were sharpest from 50 to 100 m at N'Djebel Tair and the Commission Plain and from 20 to 80 m at the Atlantis II Deep.

In contrast to the Gulf of Aden, rather constant thermohaline conditions prevailed from about 200 to below 1 000 m. The temperature (21.7-21.9°C) and salinity (40.4-40.7 ‰) of this deep water body were distinctly higher than at corresponding depths in the Gulf.

The oxygen profiles revealed a well-oxygenated surface layer at all locations. Subsurface peaks of oxygen concentration were found everywhere except at N'Djebel Tair. They occurred at a depth of 50 m, and in the Gulf of Aden, Commission Plain, and Atlantic II Deep areas, additional peaks were observed at 100 m.

Characteristic of the vertical oxygen concentration distribution in the Gulf of Aden and the Red Sea proper was an oxygen minimum layer in the mesopelagic zone. Minimum concentrations were recorded at 200 m in the Gulf (0.39 ml O_2/l), at 250 m in the Commission

Plain area (0.49 ml O_2/l), and at 400 m at N'Djebel Tair (0.61 ml O_2/l) and the Atlantis II Deep (0.67 ml O_2/l). The most distinct oxygen concentration gradients were detected from about 100 to 150 m in the Gulf of Aden, from 50 to 100 m at N'Djebel Tair and the Commission Plain, and from 30 to 80 m at the Atlantis II Deep. Above the Hanish Sill, the oxygen concentration decreased rapidly below about 50 m all the way to the bottom at 137 m.

Distribution of organisms and biomass

At all locations investigated, plankton profiles indicated a rapid decrease within the upper 150 m of the water column that largely coincided with the decreasing temperatures and oxygen concentrations (Fig. 2 and 3).

In contrast to the Gulf of Aden, there was a secondary peak of plankton concentrations in the mesopelagic zone of the Red Sea proper. During daytime, concentrations of organisms and biomass in this zone were higher than at night, indicating the occurrence of diurnal vertical migrations of midwater species (Fig. 3).

In the Gulf of Aden and above both the Commission Plain and the Atlantis II Deep, a secondary planktocline was generally observed between 450 and 600 m (Fig. 3). In one profile from the Commission Plain area obtained at about noon, the planktocline appeared between 600 and 750 m. At N'Djebel Tair, however, the decrease below the secondary maximum was more gradual. At this site, the largest meso- and bathypelagic plankton concentrations occurred.

Along the transect from the Gulf of Aden into the Red Sea, the zooplankton abundance varied significantly (Tab. 2). The stations in the Gulf of Aden and at N'Djebel Tair were characterized by large standing stocks: 79 000 and 83 000 specimens with a biomass of 24 and 20 g wet weight were collected beneath 1 m^2 from the surface to 1 050 m. Above the shallow Hanish Sill, the standing stock in the entire 130 m water column included comparable numbers of organisms (77 000 specimens beneath 1 m^2), and its biomass (32 g wet weight) was even greater (Tab. 2). At this station, the densest zooplankton concentrations of all, in terms of organisms and biomass, were found (Fig. 3).

Considerably less plankton than at the above locations was detected in the areas of the Commission Plain and the Atlantis II Deep: only 30 000 to 50 000 zooplankters with wet weights of 9 to 12 g were found below 1 m^2 in the upper 1 050 m of the water column (Tab. 2).

Distribution patterns of mesozooplankton components

Calanoida, Cyclopoida, Ostracoda, and Chaetognatha were the main taxa represented in the mesozooplankton at all stations. They accounted for 77% of organisms inhabiting the water column from the surface to 1 050 m in the Gulf of Aden and 83-85% of the corresponding number in each of the Red Sea areas investigated (Tab. 3).

The relationship between ostracod relative abundance and depth in the Gulf of Aden was opposite to that in the Red Sea proper. In the Gulf, the percentage of ostracods among the total number of organisms decreased from the epi- to the bathypelagic zone, while it increased in the Red Sea (Tab. 3).

The relative abundance of cyclopoid copepods decreased with depth in both areas (Tab. 3). Among this group, the genera *Oithona* and *Oncaea* were most abundant within all depth ranges sampled. In the epipelagic zone, *Corycaeus, Copilia,* and *Sapphirina* occurred in relatively

Table 2
Mesozooplankton standing stock below 1 m^2 at different locations in the Gulf of Aden and the Red Sea during March 1979.

	Depth range (m)	Gulf of Aden	Hanish Sill (0-130 m)	N'Djebel Tair		Commission Plain		Atlantis II Deep	
				day	night	day*	night	day	night
Biomass (g wet weight)	0-100	13.5	a. 32.9 b. 30.5	6.8	11.5	a, 3.8 b. 5.1	4.4	4.9	7.6
	100-750	9.4	——	11.6		a. 6.4 b. 4.5	3.7	3.8	4.4
	750-1 050	0.8	——	1.6		a. 0.5 b. 0.8	0.5	0.4	0.3
	total 0-1 050	23.7	——	20.0		a. 10.6 b. 10.4	8.6	9.1	12.3
Total number of organisms	0-100	51 900	a. 77 600 b. 75 900	44 100	59 800	a. 17 700 b. 33 200	21 900	27 000	26 400
	100-750	26 100	——	36 400		a. 10 700 b. 14 700	10 300	9 000	5 500
	750-1 050	1 000	——	2 900		a. 1 500 b. 1 600	1 400	1 200	600
	total 0-1 050	79 000	——	83 400		a. 29 900 b. 49 500	33 600	37 100	32 500
Number of calanoid copepods	0-100	19 400	a. 42 500 b. 38 300	21 000	40 000	a. 5 500 b. 14 100	10 000	11 800	9 700
	100-750	15 700	——	27 400		a. 4 900 b. 6 400	3 400	3 900	1 600
	750-1 050	800	——	2 400		a. 800 b. 1 000	900	700	300
	total 0-1 050	35 900	——	50 800		a. 11 300 b. 21 600	14 200	16 400	11 600

* Profile *a:* a bloom of big salps was found (2 660 specimens per 100 m^3 in the 0-50 m layer), which had dispersed one day later in Profile *b* (290 specimens per 100 m^3 in the 0-50 m layer). These salps were not considered in the above biomass values.

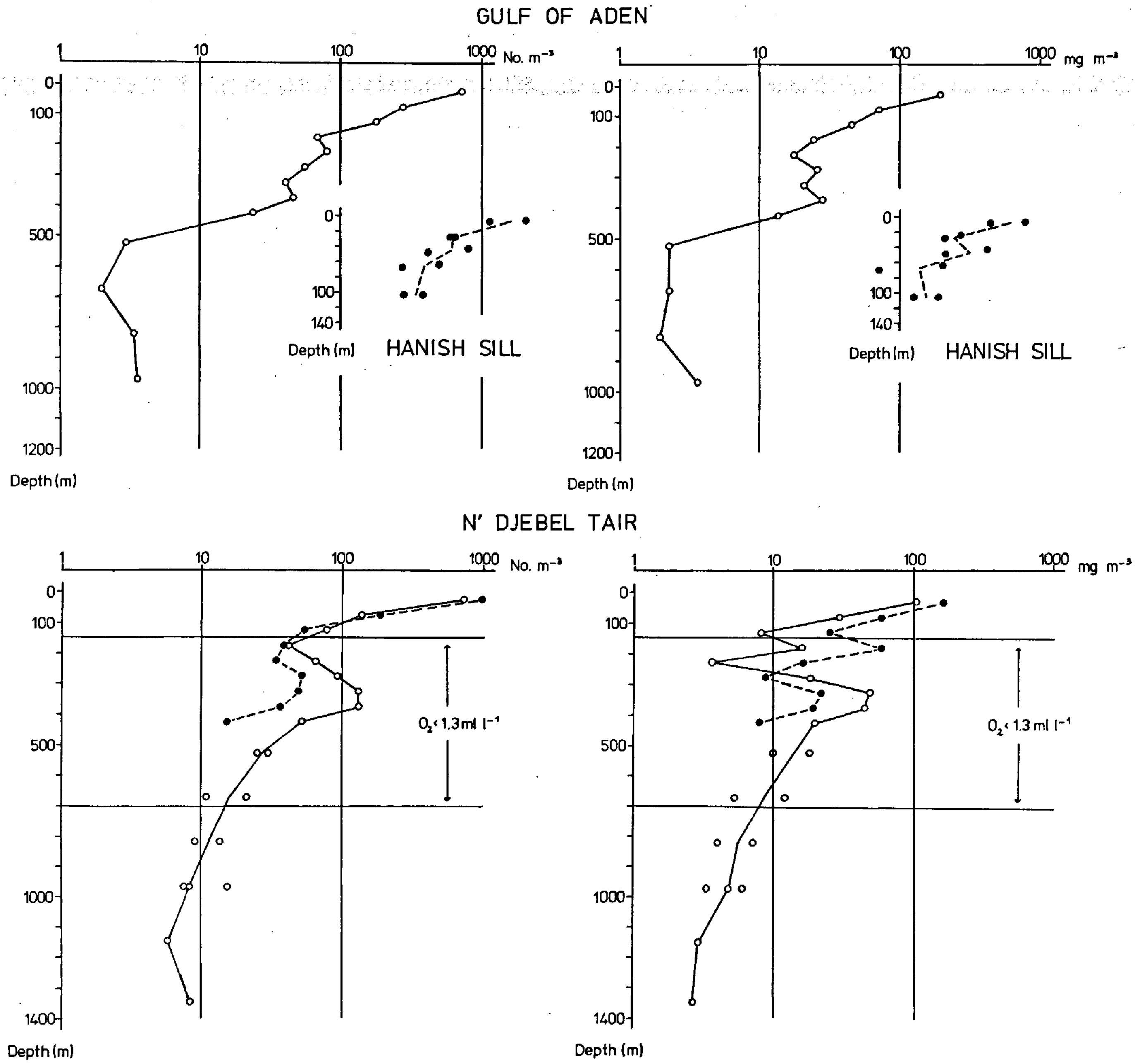

Figure 3
Vertical distribution of mesozooplankton at different locations in the Gulf of Aden and the Red Sea during March 1979. Left: numbers of organisms/m³; right: biomass wet weight/m³. Broken lines: night samples; solid lines: day samples.

large numbers, and the last two mentioned were restricted to this zone.

Numerically, the calanoid copepods constituted the most important mesozooplankton group at all stations. Their relative abundance generally tended to increase with depth, except at night in the Red Sea proper, when it was higher in the epipelagic zone than in the mesopelagic (Tab. 3).

Two calanoid families, Metridiidae and Eucalanidae, displayed remarkable patterns of horizontal and vertical distribution (Tab. 4, 5, and 6), as described below.

Metridiidae

The most abundant member of the Metridiidae in the Gulf of Aden and above the Hanish Sill was *Pleuromamma indica* Wolfenden. In the Gulf, at least some specimens of *Pleuromamma xiphias* Giesbrecht, *Pleuromamma gracilis* (Claus), and *Metridia* sp. were found, while in the Red Sea, *Pleuromamma indica* was the only metridiid. This species formed a considerable proportion of the zooplankton at N'Djebel Tair and decreased to the north in both relative and absolute abundance (Tab. 4 and 5).

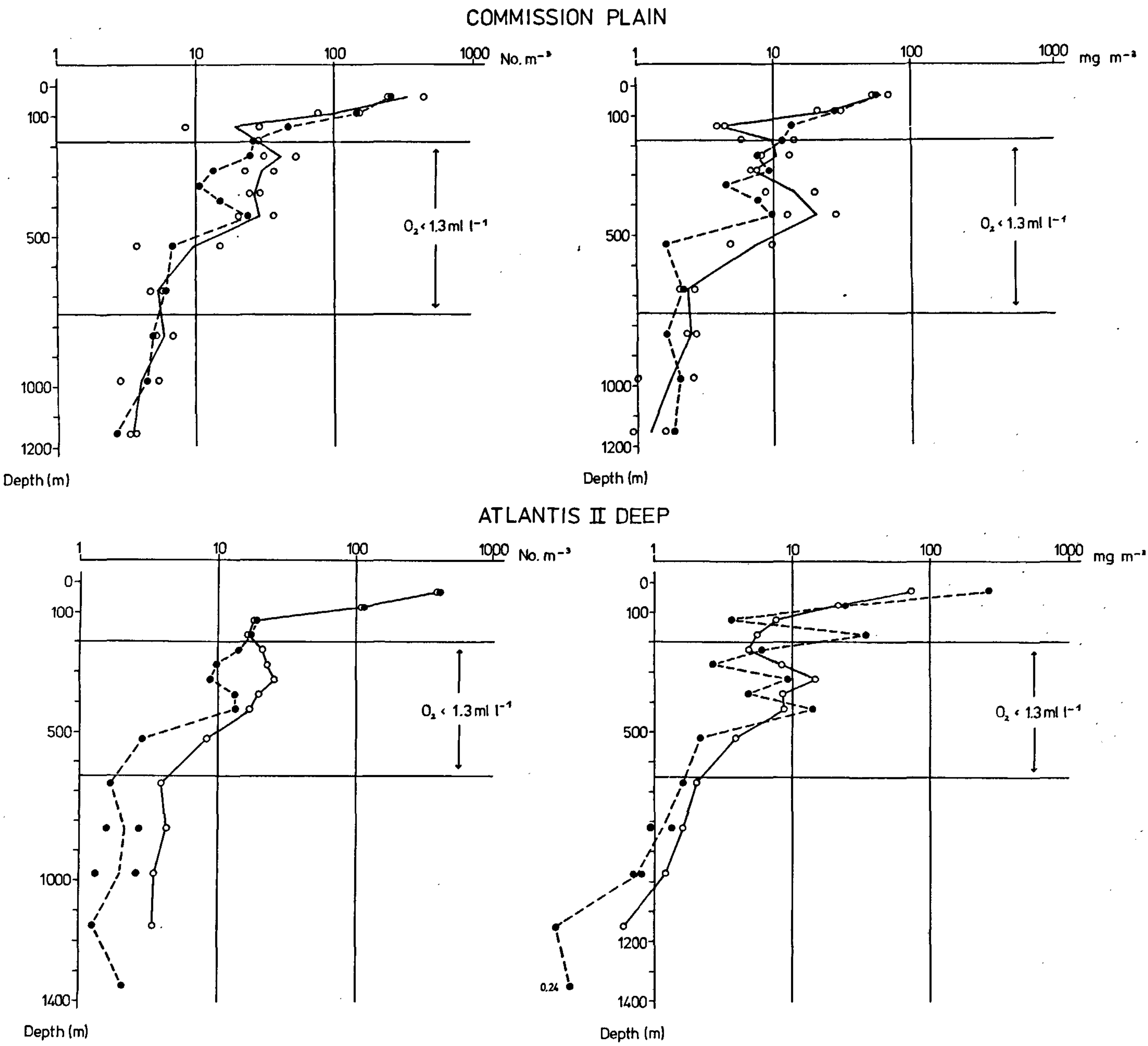

Table 3

Percentages of the main taxa in the whole zooplankton at different locations in the Gulf of Aden and the Red Sea during March 1979.

	Depth range (m)	Gulf of Aden	Hanish Sill (0-130 m)	N'Djebel Tair day	N'Djebel Tair night	Commission Plain day	Commission Plain night	Atlantis II Deep day	Atlantis II Deep night
Calanoida	0-100	37.3	52.3	47.4	67.0	38.7	45.6	43.9	36.6
	100-750	60.1	——	75.1		44.8	32.9	43.6	30.4
	750-1 050	79.6	——	83.0		57.3	61.8	64.4	47.4
	total 0-1 050	45.4	——	60.7		41.4	42.4	44.4	35.8
Cyclopoida	0-100	17.8	9.2	18.3	15.1	35.1	25.8	26.6	17.2
	100-750	17.4	——	5.9		19.5	25.3	25.2	23.5
	750-1 050	2.7	——	1.4		9.1	4.2	8.0	13.7
	total 0-1 050	17.5	——	12.3		29.1	24.7	25.7	18.2
Ostracoda	0-100	7.2	13.2	3.0	2.0	1.0	2.8	1.7	2.5
	100-750	5.6	——	6.7		15.3	16.0	11.1	10.2
	750-1 050	2.7	——	6.7		25.9	27.6	11.1	17.0
	total 0-1 050	6.6	——	4.8		6.6	7.9	4.3	4.0
Chaetognatha	0-100	9.7	8.7	6.8	4.4	8.9	9.3	11.0	24.1
	100-750	3.5	——	4.2		7.3	13.4	6.8	18.3
	750-1 050	5.1	——	2.8		2.5	3.9	6.9	10.5
	total 0-1 050	7.6	——	5.5		8.1	10.3	9.8	22.9

Table 4

Percentages of Metridiidae and Eucalanidae among the total number of calanoid copepods at different locations in the Gulf of Aden and the Red Sea during March 1979. Values for the genus Eucalanus *in parentheses.*

	Depth range (m)	Gulf of Aden	Hanish Sill (0-130 m)	N'Djebel Tair		Commission Plain		Atlantis II Deep	
				day	night	day	night	day	night
Metridiidae	0-100	2.2	4.8	1.3	33.5	0.4	22.8	0.4	11.2
	100-750	32.2	——	68.5		46.7	30.5	33.7	22.8
	750-1 050	0.5	——	16.4		26.0	20.7	21.0	40.7
	total 0-1 050	15.3	——	37.9		17.8	24.5	9.2	13.5
Eucalanidae	0-100	38.8	37.2		4.8	9.5	1.0	8.4	8.8
	100-750	36.3	——	9.4		1.4	2.6	5.0	8.9
	750-1 050	75.9	——	8.0		0	0	0.5	2.1
	total 0-1 050	38.6	——	32.1		6.2	1.3	7.2	8.6
		(34.8)	(37.1)	(9.7)		(5.7)	(0.9)	(5.0)	(7.2)

Table 5

Vertical distribution of Pleuromamma indica *Wolfenden in the Red Sea proper during March 1979 given as individuals per 100 m³.*

a.) N'Djebel Tair

Depth range (m)	Females		Males		Juveniles		Relative abundance of *Pl. indica* (percent of total number of organisms)		
	day	night	day	night	day	night	day	night	
0-50	0	5 003	0	3 117	375	16 768	0.5	24.8	
50-100	0	1 598	0	96	180	991	1.3	14.1	
100-150	0	120	0	16	789	80	10.1	4.0	
150-200	0	16	0	0	1 639	152	39.2	4.3	
200-250	0	24	0	0	4 286	376	65.2	11.7	}
250-300	160	16	136	8	5 507	1 591	60.8	30.8	}
300-350	272	47	1 798	71	6 961	1 639	68.5	35.2	} <0.85 ml O_2/l
350-400	3 778	116	1 865	216	3 658	456	70.6	21.3	}
400-450	2 295	128	303	38	638	128	61.8	19.1	}
450-600	200		422		132		26.8		
600-750	29		368		37		25.3		
750-900	15		157		16		15.3		
900-1 050	16		59		8		13.5		

b.) Commission Plain

Depth range (m)	Females		Males		Juveniles		Relative abundance of *Pl. indica* (percent of total number of organisms)		
	day	night	day	night	day	night	day	night	
0-50	0	236	0	433	16	1 056	0.1	6.2	
50-100	0	811	0	662	64	1 339	0.8	17.7	
100-150	0	280	0	8	32	32	3.7	6.5	
150-200	0	88	0	0	64	0	2.2	3.2	
200-250	0	40	0	16	735	48	22.5	4.0	}
250-300	8	8	112	0	853	192	41.1	14.6	}
300-350		0		8		202		19.7	}
350-400	112	8	80	0	192	88	14.9	6.3	} <1.3 ml O_2/l
400-450	623	112	152	32	184	96	24.7	9.7	}
450-600	37	37	29	56	3	13	18.2	15.5	}
600-750	11	21	155	131	21	11	31.5	26.9	}
750-900	11	5	96	88	35	3	20.3	18.8	
900-1 050	0	13	16	11	3	3	6.5	6.0	

c.) Atlantis II Deep

Depth range (m)	Females		Males		Juveniles		Relative abundance of *Pl. indica* (percent of total number of organisms)		
	day	night	day	night	day	night	day	night	
0-50	8	338	0	226	24	677	0.1	3.0	
50-100	8	402	0	189	48	347	0.5	8.3	
100-150	0	16	0	0	8	16	0.4	1.7	
150-200	0	0	8	0	72	8	4.9	0.5	
200-250	0	0	0	0	528	0	24.5	0	}
250-300	0	0	39	0	520	32	23.9	3.3	}
300-350	0	0	79	0	228	152	11.5	17.1	}
350-400	0	8	0	24	200	256	10.0	21.7	} <0.85 ml O_2/l
400-450	40	16	8	8	136	144	10.6	12.5	}
450-600	133	5	43	0	16	8	23.2	4.7	}
600-750	11	0	35	13	24	0	17.8	8.1	
750-900	16	4	59	42	8	10	19.5	26.3	
900-1 050	3	6	16	14	3	2	6.2	11.6	

Table 6
Standing stock of some species of Eucalanidae at different locations in the Gulf of Aden and the Red Sea during March 1979 (number below 1 m²).

	Depth range (m)	Gulf of Aden	Hanish Sill (0-130 m)	N'Djebel Tair		Commission Plain		Atlantis II Deep	
				day	night	day	night	day	night
	0-100	0	a. 7 052	a. 274	a. 308	a. 6	a. 4	0	0
Eucalanus			b. 697	b. 8	b. 0	b. 0	b. 0		
crassus	100-750	a. 48	——	a. 1 671		a. 10	a. 20	0	0
Giesbrecht		b. 4		b. 4		b. 0	b. 4		
a. total indiv.	750-1 050	a. 20	——	a. 772		0	0	0	0
b. mature females		b. 0		b. 2					
Eucalanus	0-100	400	167	461	432	168	55	136	180
attenuatus	100-750	40	——	8		6	16	4	8
(Dana)	750-1 050	52	——	0		0	0	0	0
	0-100	636	5	0	0	2	0	16	0
Eucalanus	100-750	676	——	20		8	4	12	0
elongatus (Dana)	750-1 050	16	——	8		0	0	0	0
Rhincalanus	0-100	268	25	4	0	0	0	8	0
nasutus	100-750	540	——	38		32	32	99	92
Giesbrecht	750-1 050	500	——	16		0	0	0	0
Rhincalanus	0-100	12	4	0	4	0	0	0	0
cornutus	100-750	16	——	18		0	0	0	0
Dana	750-1 050	0	——	0		0	0	0	0
Mecynocera	0-100	12	0	0	0	50	12	243	66
clausi	100-750	0	——	0		6	8	20	8
Thompson	750-1 050	0	——	0		0	0	0	2

In the Red Sea proper, *Pleuromamma indica* undertook diurnal vertical migrations (Tab. 5). It congregated in the epipelagic zone at night and in the mesopelagic zone during the day. A comparison of the migration patterns of both sexes and juveniles revealed that copepodids were concentrated in the upper part of the oxygen minimum layer during the day, while the adults preferred greater depths.

A small fraction of the adults and copepodids did not join in the upward nocturnal migration and rested in deeper layers at night. Among the females, the proportion of non-migratory individuals was found to be the smallest. These observations were made at all sites investigated in the Red Sea proper (Tab. 5).

Eucalanidae

The family Eucalanidae played an important role in the planktonic community of the Gulf of Aden and above the Hanish Sill. Moving northward in the Red Sea, a decrease in absolute and relative abundance was observed (Tab. 2 and 4).

The species of this family exhibited different patterns of horizontal or vertical distribution (Tab. 6).

Eucalanus crassus Giesbrecht was restricted in its regional distribution almost exclusively to the areas of the Hanish Sill and N'Djebel Tair. Nearly all mature females collected were found above the Sill. At both sites, the species occurred in great numbers, accounting for averages of 17.5% of all calanoid copepods above the Hanish Sill and 5.4% at N'Djebel Tair (Tab. 2 and 6). A peculiarity at N'Djebel Tair was that many of these individuals were found below 300 m. The highest concentrations of *E. crassus* in the water column were detected from 450 to 750 m, and it accounted for 24.0 to 30.8% of all calanoids in the depth ranges sampled below 450 m. At this site, specimens of *Eucalanus crassus* showed signs of lethal degeneration. The colour of the animals was deep yellow, and body substances had extruded from the mouths of several individuals collected below 450 m.

Eucalanus attenuatus (Dana) was collected at all locations, mainly in the epipelagic zone.

Eucalanus elongatus (Dana) was found to be abundant in the Gulf of Aden, while above the Sill and in the Red Sea proper, it was rare. The species can be regarded as a preponderantly epipelagic one at the Gulf station with decreasing abundance from the surface to deeper waters: 408 of the 676 individuals below 1 m² in the depth range from 100 to 750 m (Tab. 6) were collected between 100 and 200 m. In the Red Sea proper, *Eucalanus elongatus* tended to submerge. Adult specimens were caught exclusively in the mesopelagic zone.

Rhincalanus nasutus Giesbrecht occurred in the Gulf of Aden in all depth ranges (Tab. 6). One peculiarity not apparent in Table 6 is that 47% of the standing stock from 100 to 750 m in the Gulf was found between 100 and 150 m. In this layer, the highest concentration of *Rhincalanus nasutus* in the water column was observed (504 specimens per 100 m³, corresponding to 2.7% of the total number of organisms). Between 900 and 1 050 m, a second maximum concentration of 245 specimens per 100 m³ occurred, corresponding to 70% of the total number of organisms.

In the Red Sea, *Rhincalanus nasutus* was much less abundant and had clearly submerged. There were no detectable diurnal vertical migrations, and the species was restricted exclusively to the range between 200 and 450 m at the Commission Plain and between 300 and 450 m at the Atlantis II Deep. Only a single juvenile specimen was collected in the epipelagic zone of the Red Sea proper (Tab. 6).

Mecynocera clausi Thompson was absent above the Hanish Sill and at N'Djebel Tair, rare in the Gulf of Aden and at the Commission Plain, and obviously more abundant above the Atlantis II Deep (Tab. 6). This species occurred mainly in the epipelagic zone.

Four other species of the genus *Eucalanus* which have not yet been identified were observed. They also appeared mainly in the upper 100 meters, both in the Gulf of Aden and in the Red Sea, and they decreased in abundance from south to north.

The abundances of various other taxa, not yet mentioned, at each of the locations investigated are presented in Table 7. Three main groups can be distinguished based on the distribution pattern, and at least one species of the Eucalanidae was included in each of these groups (Tab. 6):

— taxa which were abundant at the Gulf station and showed a sharp decrease in abundance to the north. They were rare or even absent above the Commission Plain or the Atlantis II Deep. These comprise the foraminiferan, *Globorotalia menardii* (d'Orbigny); *Mormonilla* sp. (Copepoda Cyclopoida); and copepod nauplii (especially *Eucalanus*). *Eucalanus attenuatus* and *E. elongatus* can be included in this group;

— taxa that were distinctly more abundant above the Hanish Sill than at all other sites, such as Cirripedia larvae, Malacostraca, Ostracoda (Tab. 3), and among the Eucalanidae, *Eucalanus crassus;*

— taxa that were distinctly more abundant above the Hanish Sill than at all other sites, such as Cirripedia larvae, Malacostraca, Ostracoda (tab. 3), and among the Eucalanidae, *Eucalanus crassus;*

— taxa that were relatively abundant in the Red Sea proper and rare or absent above the Hanish Sill. They included the calanoid copepods *Haloptilus acutifrons* (Giesbrecht), *Haloptilus longicornis* (Claus), *Lucicutia paraclausi* Park, and among the Eucalanidae, *Mecynocera clausi.* These species preferred specific depth ranges within the water column: *Lucicutia paraclausi* occurred only below 300 m at the Red Sea deep water stations. *Haloptilus acutifrons* was restricted to the 100 to 450 m range at the Gulf station, and to the 200 to 900 m range in the Red Sea proper. *Haloptilus longicornis* was most densely concentrated where sharpest gradients in oxygen concentrations occurred, that means from 100 to 150 m in the Gulf (360 specimens/100 m^3) and from 50 to 100 m at N'Djebel Tair (30 specimens/100 m^3), the Commission Plain (640 specimens/100 m^3; median value), and the Atlantis II Deep (700 specimens/100 m^3). The total standing stock of *Haloptilus longicornis* was relatively low above the Hanish Sill and at N'Djebel Tair and increased in the Red Sea from south to north, while that of *Lucicutia paraclausi* was largest at N'Djebel Tair and decreased to the north. *Haloptilus acutifrons* was most abundant above the Commission Plain (Tab. 7). *Lucicutia paraclausi* seemed to be absent from the Gulf of Aden, but eight specimens of *Lucicutia clausi* (Giesbrecht) were collected there between 50 and 250 m. In the Red Sea, only one juvenile that might be assigned to *L. clausi* was found at N'Djebel Tair between 900 and 1 050 m.

Table 7

Occurrence of various taxa (not mentioned in Tables 3 through 6) at different locations in the Gulf of Aden and the Red Sea during March 1979. Standing stock given as individuals in the water column below 1 m^2 (deep water stations: 0-1 050 m).

	Gulf of Aden	Hanish Sill	N'Djebel Tair	Commission Plain	Atlantis II Deep
Globorotalia menardii (d'Orbigny) (foraminifera, epipelagic)	820	106	118	0	0
Coelenterata	3 004	2 524	3 325	756	800
Tomopteris sp. (polychaeta)	168	350	299	144	115
Bivalvia larvae (epipelagic)	432	471	141	47	92
Pteropoda Euthecosomata	640	381	473	229	420
Mormonilla sp. (Cop. Cyclopoida)	732	2	2	0	0
Haloptilus acutifrons (Giesbrecht) (Cop. Calanoida)	48	2	68	228	88
Haloptilus longicornis (Claus) (Cop. Calanoida)	428	10	41	419	611
Lucicutia paraclausi Park (Cop. Calanoida)	0	0	496	170	68
Copepoda nauplii	3 460; much *Eucalanus*	232	128	32	18
Cirripedia larvae (nauplii, cypris)	40	652	73	8	0
Malacostraca	1 712	4 568	1 928	904	888

DISCUSSION

Reliability of the data

Although the data set is limited, this analysis allows some general conclusions to be drawn on the relationship between the mesozooplankton distribution and the hydrographic conditions in the area investigated.

The general vertical zooplankton distribution pattern in each sampling profile from the Red Sea proper was similar to that observed during extensive investigations in the Atlantis II Deep area in November 1977 (Weikert, 1982). This similarity was particularly well exemplified by the strong affinities of interzonal calanoid copepod species (*Pleuromamma indica, Rhincalanus nasutus, Haloptilus* spp., and *Lucicutia paraclausi*) to distinct, vertically separated habitat zones in the water column during both March and November. The vertical sequence of habitat zones (a: warm and least saline surface layer, b: zone of thermo-, halo-, and oxyclines, c: homogeneous thermohaline conditions below 200 m to the bottom, d: oxygen minimum layer in the mesopelagic zone) is maintained throughout the year, at least in the southern and central parts of the Red Sea (Morcos, 1970). Thus, the results presented here appear to reflect consistent, typical features rather than random movements.

Indications of the degree of horizontal zooplankton patchiness in the Red Sea are provided by duplicate hauls and several series of replicate samples:

At locations where more than one vertical series of samples were taken at about the same time of day, individual values recorded for identical depth layers differed only slightly, in most cases (Hanish Sill, meso- and bathypelagic zone of the Red Sea proper; Fig. 3, Tab. 2), and similar vertical profiles were obtained.

A statistical analysis of the replicate sample series from different depth ranges at the Atlantic II Deep, obtained during November 1977 and over a three day period in June 1979, revealed a much lower horizontal zooplankton variability in the deeper water than in the surface layers (Tab. 8). Moreover, the horizontal patchiness in the deep water was rather low compared to that found by Angel *et al.* (1982) at a depth of 1 000 m in the North Atlantic Ocean at about 42°N, 17°W. Because of the uniform environmental conditions in the Red Sea below 200 m throughout the year (Morcos, 1970), a relatively even distribution of mesopelagic species is assumed to exist permanently. It should be noted that there are no true bathypelagic zooplankton species in the Red Sea (Weikert, 1982). Year-to-year fluctuations are also apparently very small (*see* below).

It may be concluded that even a few profiles taken in the Red Sea, or at least in its deep southern and central parts, can yield results representative for a large area and a long time. Within the relatively unstable epipelagic zone, however, an increased zooplankton variability (Tab. 8) may be induced by blooms (Tab. 2) and has to be considered.

Hydrography

The water exchange between the Red Sea and the Gulf of Aden exhibits two characteristic seasonal patterns (Morcos, 1970; Jones, Browning, 1971). A two-layer model is typical for the winter monsoon period, which lasts from October through April. Warm and less saline Gulf of Aden water flows into the Red Sea at the surface, whereas the denser Red Sea water penetrates into the Gulf of Aden between depths of 500 and 1 000 m. During the summer monsoon (May through September), the upper surface current reverses sometime after June, forming a circulation pattern resembling a three layer model which is characterized by an inflow of water from the Gulf into the Red Sea at intermediate depths between countercurrents both at the surface and near the bottom. This circulation system is responsible for the formation of a cold water layer in the southern Red Sea. A temperature inversion at a depth of about 100 m is produced that lasts from late summer to late fall (Jones, Browning, 1971).

The patterns of hydrographic parameters (Fig. 2) clearly reflected the two layer model during the winter monsoon. The profiles can be regarded as typical for this time of the year, although there are some differences in specific details from the patterns described in the literature (Morcos, 1970; McGill, 1973). The tongue of Red Sea water in the Gulf of Aden could be detected from about 400 to 1 000 m.

Subsurface peaks in oxygen concentration above the Hanish Sill, the Commission Plain, and the Atlantis II Deep might be normal for the Red Sea, as they have also been described by Grasshoff (1969) and Weikert (1980 *b;* 1981; 1982).

Table 8

Estimates of deviation factors for single observations from the mean values in the Atlantis II Deep area, central Red Sea, indicating the 95% confidence intervals (derived from logarithmically transformed data).

Depth range (m)	Species, species group	Number of samples	Estimate of deviation factor for 95% conf. int.	Origin of data used for computation
0-150	Acartiidae	8	10.99	Unpublished data from Weikert, November 1977
	Calanus tenuicornis	8	8.55	
	Calocalanus spp.	8	1.80	
	Candaciidae	8	1.51	
	Centropagidae	8	5.25	
	Undinula vulgaris	8	21.49	
0-750	*Pleuromamma indica*, females	6	1.69	Weikert, 1980 (only night samples)
	Pl. indica, males	6	1.66	
400-600	*Rhincalanus nasutus*	11	1.56	Unpublished data from Weikert, November 1977
750-900	Calanoida	10	1.52	Personal data, June 1979
	Ostracoda	10	1.57	
	Total number of organisms	10	1.43	
900-1 050	Calanoida	10	2.20	Personal data, June 1979
	Ostracoda	10	1.83	
	Total number of organisms	10	1.58	

The characteristic oxygen minimum layer in the Red Sea proper extended in autumn from 350 to 650 m, and its oxygen concentrations ranged from 0.9 to 1.3 ml O_2/l (Weikert, 1980*a;* 1982). During the present investigations, it was located closer to the surface, and the minimum concentration was lower (Fig. 2).

The Red Sea as a whole exhibits unusual environmental conditions, particularly in its high salinity and the unique phenomenon of temperatures as high as 22°C in the deep water (Morcos, 1970). These features, in combination with the low oxygen concentration at intermediate depths, make the habitat an extreme one for the pelagic community (Weikert, 1980*a*).

Vertical and horizontal distribution of organisms and biomass

In the surface layers of the Red Sea proper, the most rapid decrease in the abundance of plankton with depth was observed between 50 and 100 m and coincided largely with the sharpest vertical gradients of temperature and oxygen concentration (Fig. 2 and 3). A similar coincidence of plankto-, thermo-, and oxyclines was detected by Weikert (1982) at the Atlantis II Deep in November 1977. He found this zonation in the water column to occur from about 100 to 150 m, deeper than in March 1979.

Weikert (1982) found the ratio of the number of organisms in the upper 100 m to those in the 100 to 200 m layer and the corresponding ratio for biomass to be significantly higher in the Atlantis II Deep than in other oligotrophic, tropical regions of the World Ocean. His assumption that the strong affinity of zooplankton for the epipelagic zone is a characteristic of the central Red Sea is corroborated by the data obtained in the Red Sea in March 1979 (Tab. 9). Thus, the entire Red Sea Deep basin south of about 22°N is distinguished by this kind of plankton distribution from other oceanic regions.

(Fig. 3) may be due to the intrusion of plankton-poor Red Sea water. Exuviae and specimens which were obviously dead prior to collection comprised 53.5% of the total calanoid specimen counts from 450 to 1 050 m. The corresponding proportion from the surface to 450 m in the Gulf was only 3.1%.

The number of species in the Red Sea zooplankton decreases from south to north (Halim, 1969; Kimor, 1973). A similar decrease was also quantitatively established for biomass distribution, as revealed by comprehensive studies of the southern, central, and northern Red Sea (Delalo, 1966; Ponomareva, 1968), and for the distribution of both biomass and numbers of organisms between about 20 and 27°N (Gordeyeva, 1970).

The data reported by Delalo (1966) may be best compared with the present results from the Red Sea proper (Tab. 2 and 10), since they were obtained using 330 µm nets during the winter monsoon. However, Delalo generally reported higher values, apparently due to his somewhat different methods. He may not have removed large organisms from the samples before the determination of biomass.

The rather sudden decrease in plankton abundance between N'Djebel Tair and the Commission Plain area (Tab. 2) was also indicated by the data of Delalo (1966), who found a greater difference between the southern and the central parts of the Red Sea than between the central and northern regions.

Distribution of prominent species

The calanoid copepod, *Pleuromamma indica,* was the most conspicuous migratory species in the Red Sea zooplankton. Juveniles congregated nearer the surface than adults during daylight hours, and the males sought a higher level than the females, which are larger. This situation is common among vertically migrating

Table 9
Ratios of the number of organisms and biomass (wet weight) in the upper 100 m to those in the 100 to 200 m layer at different locations in the Red Sea proper.

		N'Djebel Tair March 1979	Commission Plain March 1979	Atlantis II Deep March 1979	Atlantis II Deep Nov. 1977	Other oceans (from Weikert, 1982)
Numbers of organisms	day	7.3:1	a. 9.2:1 b. 10.0:1	15.5:1	4.7:1-13.4:1	———
	night	12.8:1	5.7:1	14.6:1	5.2:1-11.7:1	———
Biomass	day	5.6:1	a. 4.1:1 b. 11.4:1	7.4:1	4.0:1-15.8:1	0.7:1-3.4:1
	night	2.7:1	3.5:1	3.9:1	4.8:1-17.3:1	

The existence of a second planktocline in the mesopelagic zone above the Commission Plain and the Atlantis II Deep (Fig. 3) also seems to be a typical feature. It was observed in November 1977 above the Atlantis II Deep between 450 and 600 m (Weikert, 1982), the same depth range at which it was found during this investigation in most profiles.

The rapid decrease in the concentration of living plankters between 450 and 600 m in the Gulf of Aden zooplankters (Longhurst, 1981), and the migration patterns of both sexes and of juveniles (Tab. 5) coincided exactly with those described by Weikert (1980*a*). Weikert found that in the Atlantis II Deep area, a significantly larger percentage of females than males undertook migrations and suggested this phenomenon to be related to a difference in the body surface to volume ratio.

During daylight hours, *Pleuromamma indica* congregates

Table 10
Zooplankton standing stock below 1 m² in terms of biomass and numbers of organisms (in parentheses) in the southern and central Red Sea during different months.

Months of investigations	Authors; methods	Southern Red Sea	Central Red Sea
December-March	Delalo (1966) 330 µm; biomass determined as wet weight	0-100 m: 10.5 g 0-800 m: 23.1 g	0-100 m: 8.1 g 0-800 m: 16.1 g
February	Weikert (1981) 300 µm; biomass determined as wet weight		Atlantis II Deep: 0-100 m: 7.0 g (35 200) 0-1 850 m: 15.8 g (51 100)
March	this study	N'Djebel Tair: 0-100 m: 6.8 and 11.5 g (44 100 and 59 800) 0-1 050 m: 20.0 g (83 400) biomass concentration per 100 m³; 900-1 050 m: N'Djebel Tair 0.5 g Commission Plain 0.2 g	Atlantis II Deep: 0-100 m: 4.9 and 7.6 g (27 000 and 26 400) 0-1 050 m: 9.1 and 12.3 g (37 100 and 32 500) biomass concentration per 100 m³; below 1 000 m: 0.02 g
May-June	Ponomareva (1968) 180 µm; biomass determined as displ. volume	0-100 m: 30-50 ml	0-100 m: <30 ml
June	Weikert (1980 *b*) 315 µm; biomass determined as wet weight		Atlantis II Deep: 0-1 050 m: 9.0 g(34 000)
June	Wishner (1980) 183 µm; biomass determined as wet weight	biomass concentration per 100 m³; 800-1 100 m: about 17°26'N: 0.1 g	biomass concentration per 100 m³; below 1 000 m: 0.01 g
October	Gordeyeva (1970) 330 µm; biomass determined as wet weight		0-100 m: 5.9 g (63 500)
November	Weikert (1982) 300 µm; biomass determined as wet weight		Atlantis II Deep: 0-100 m: 2.7 g (19 900) 0-1 850 m: 5.3 g (29 900)

in the oxygen minimum layer. Below 900 m, its abundance is clearly reduced. The species is known to thrive at oxygen concentrations much below 1 ml O_2/l in the Arabian Sea and northern Indian Ocean, and it is abundant as deep as 1 400 m or more (Vinogradov, Voronina, 1961; Haq *et al.*, 1973). Weikert (1982) suggested that a lack of food possibly prevents large standing stocks of *Pleuromamma indica* from dwelling the bathypelagic zone of the Red Sea.

A comparison of the data from the Atlantis II Deep area obtained during the present study with those of Weikert (1982) shows that the absolute and relative abundances of *Pleuromamma indica* were larger in November 1977 (from 0-1 700 m: 2 140 specimens below 1 m², corresponding to 18.7% of the total number of Calanoida) than in March 1979 (from 0-1 050 m: 1 560 specimens below 1 m², corresponding to 11.1% of the total number of Calanoida; mean values calculated from Tables 2 and 5). This may be attributed to seasonal fluctuations. The lower relative abundance of the species in March might be due largely to the increased occurrence of other, preponderantly epipelagic species which had been driven from the Gulf of Aden to the north in the surface layer. The genus *Eucalanus*, which can be regarded as an indicator for the incoming water mass (Halim, 1969; Weikert, 1980 *b*), comprised 5.0 and 7.2% of the standing stock of calanoid copepods in the Atlantis II Deep during March 1979 (Tab. 4), while in November 1977, it contributed only 0.2% to the total number of Calanoida (Weikert, 1982).

Above the Hanish Sill, an exceptionally large number of one eucalanid species, *Eucalanus crassus*, were collected. The high ratio of plankton biomass to numbers of organisms at this site (Tab. 2) can be attributed to the dominance of this relatively large organism. The species is neritic (Kasturirangan, 1963; Fleminger, 1973), and Gapishko (1971) found that it contributed up to 35% of the total plankton biomass at coastal stations in the Gulf of Aden. At the deep water station in the Gulf, *E. crassus* was rare (Tab. 6). The scarcity of nauplii and small copepodids of this species above the Hanish Sill and at N'Djebel Tair indicates that most of the specimens did not reproduce at those locations but rather in neritic areas of the Gulf of Aden.

The bottle-neck between the African and the Arabian coasts at the southern entrance of the Strait of Bab-el-Mandab has a depth of about 300 m and does not present an effective barrier between the Gulf of Aden and the Red Sea. Such a barrier, however, is formed by the much shallower Hanish Sill further to the north (*vide* Morcos, 1970). Zooplankton from the Gulf is driven northward within the surface layer during winter, but because of the proximity of the coasts in the bottle-neck zone, this plankton is expected to contain a high proportion of neritic organisms. These might find a suitable habitat above the Hanish Sill.

As in the case of *Eucalanus crassus*, the absolute and relative abundance for ostracods showed an increase above the Sill (Tab. 2 and 3). Filter feeding zooplankters apparently constituted a considerably higher proportion of the community in this area than at all other locations investigated. This assumption is supported by the low relative abundance of cyclopoid copepods (Tab. 3), most of which are regarded as predatory.

Further north, at N'Djebel Tair, *Eucalanus crassus* had decreased in relative and absolute abundance (Tab. 2 and 6). Because so many individuals of this normally epipelagic species (Fleminger, 1973) were collected below 450 m, the values for total plankton failed to reveal a sharp mesopelagic planktocline similar to that at locations further north (Fig. 3; Weikert, 1982). The signs of lethal degeneration in the deeper water layers at N'Djebel Tair may indicate that the site is near the northern border of the geographic range of *Eucalanus crassus*. Its distribution pattern in the area investigated was clearly related to topographic and circulation features.

Most of the *Eucalanus attenuatus* were observed in the upper 100 m of the water column at all locations investigated. In November 1977, however, Weikert (1982) found this species restricted to the upper part of the oxygen minimum layer above the Atlantis II Deep. This difference may indicate a seasonal vertical migration.

In the areas of the Commission Plain and the Atlantis II Deep, two calanoid copepod species exhibited a very obvious affinity for distinct layers which are avoided by other zooplankters. The same observation was made by Weikert (1982):

— *Rhincalanus nasutus* occurred exclusively in zones of minimum oxygen concentrations. In the Atlantis II Deep area, both the entire standing stock and the core of the oxygen minimum layer were found about 100 m deeper in November (Weikert, 1980*a*; 1982) than in March. The guts of the specimens were mostly empty, and Weikert (1980*a*) speculated that these copepods might be in a state of torpor or even have switched to partially anaerobic metabolism. Like *Pleuromamma indica, Rhincalanus nasutus* is also common in the oxygen minimum layer of the Arabian Sea (Vinogradov, Voronina, 1961);

— *Haloptilus longicornis* was most concentrated in the oxycline. This was also found at the Gulf of Aden station, and the species was observed by Vinogradov and Voronina (1961) in layers above the oxygen minimum layer in the Arabian Sea and the northern Indian Ocean. At the Atlantis II Deep in November, both the oxycline and the maximum concentrations of *Haloptilus longicornis* were found from 100 to 250 m (Weikert, 1982), therefore deeper than in March.

At N'Djebel Tair, the depth distribution of *Rhincalanus nasutus* is not as sharply restricted as at the other two sites above the deep basin of the Red Sea. The standing stock of *Haloptilus longicornis* was very small, so its affinity for the oxycline was much less conspicuous than elsewhere.

The distribution patterns of these two species indicate that the N'Djebel Tair station is located in a transitional area between the southernmost Red Sea, with a plankton community strongly influenced throughout the water column by the import of organisms from the Gulf of Aden during winter, and the central Red Sea, in which only the epipelagic zone indicates this import, and the plankton probably exhibits a greater stability throughout the year. This assumption is corroborated by the fact that: a) N'Djebel Tair was near the northern border of the ranges of many species which certainly had been imported from the Gulf (*Globorotalia menardii, Mormonilla* sp., and the principal species, *Eucalanus crassus;* Tab. 6 and 7); and b) particular characteristics of the vertical plankton distribution were similar to those in the central Red Sea, such as the migration pattern of *Pleuromamma indica* and the sharp decrease in the zooplankton standing stock from the surface to about 150 m (Tab. 5 and 9; Fig. 3).

Like that of *Haloptilus longicornis,* the standing stocks of *H. acutifrons, Lucicutia paraclausi,* and *Mecynocera clausi* were larger in the Red Sea proper than above the Hanish Sill or in the Gulf of Aden (Tab. 6 and 7). The assumption that all these species are independent of the import of individuals with the surface inflow from the Gulf of Aden during winter is supported by the observation of smaller standing stocks in March, at the end of winter, than in November, at the beginning (Tab. 6 and 7; Weikert, 1982).

General seasonal aspects

Zooplankton abundance and composition fluctuate seasonally in the Red Sea (Halim, 1969; Weikert, 1980*b*; 1981). Red Sea plankton, particularly in the southern part, contains more elements from the Gulf of Aden in winter than in summer, according to the species lists by Halim (1969).

The data compiled in Table 10 reveal that more plankton is present in the central Red Sea in March than in November, but still more is present in February. The total numerical abundance and biomass in the water column during March and June are similar, but there is less biomass at a depth of about 1 000 m in June in both the central and southern Red Sea.

Quantitative information on yearly fluctuations is rare. However, certain features can be expected to exhibit regular annual cycles. Zooplankton investigations at the Atlantis II Deep during November 1977 and October and November 1980 yielded very similar quantitative results (Weikert, 1981). Furthermore, data obtained in the present study and those reported by Delalo (1966) are in the same order of magnitude, as discussed above.

It is suggested that maximum zooplankton standing stocks above the central trench of the southern and central Red Sea occur in mid-winter due to the import of organisms with the surface current from the Gulf of Aden. This contradicts the views of Ponomareva (1968) and Weikert (1980*b*), who suggested that more zooplankton is present in summer than in winter. Ponomareva compared her data with those of Delalo (1966), but because she used a smaller mesh size (Tab. 10), her conclusion seems doubtful. The preliminary paper by Weikert (1980*b*) did not include any data for February; these were obtained during a later cruise.

The number of organisms found by Gordeyeva (1970) in the 0 to 100 m layer in the central Red Sea during October is greater than those reported for any other month (Tab. 10). However, her data are not directly comparable to those presented in Table 2 or reported by Weikert (1980*b*; 1981; 1982), as they include radiolarians and apparently even carcasses. Moreover, Gordeyeva's site of investigation in the central Red Sea was not located above the Red Sea's central trench but rather closer to the African coast.

According to the different patterns of water exchange between the Red Sea and the Gulf of Aden, there is a net inflow of nutrients from the Gulf into the Red Sea during summer, effected by the nutrient richness of the intermediate current. During winter, more nutrients leave the Red Sea with the bottom current than enter at the surface (Grasshoff, 1969; Khimitsa, Bibik, 1979). The plankton import from the Gulf of Aden is at its maximum in mid-winter; many species cannot adapt to the unusual Red Sea environmental conditions and die off. Certain pteropods that pass over the Hanish Sill are known to perish in this manner (*vide* Halim, 1969). It was also shown during the present study that *Eucalanus crassus*, originating from coastal areas in the Gulf of Aden, formed a considerable proportion of zooplankton at N'Djebel Tair and died off near this site. The decomposition of allochthonous zooplankton in the southern Red Sea may, to a certain extent, counterbalance the negative nutrient budget calculated for the two layer pattern of water exchange with the Gulf of Aden during winter.

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