

Vertical distribution and population structure of *Macrosetella gracilis* (Copepoda: Harpacticoida) in the Red Sea in relation to the occurrence of *Oscillatoria* (*Trichodesmium*) spp. (Cyanobacteria)

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ABSTRACT: *Macrosetella gracilis* is closely associated with the epipelagic filamentous cyanobacteria *Oscillatoria* (*Trichodesmium*) spp., which serve as food for adults and as a substrate for the non-pelagic juveniles. Plankton sampling in the Red Sea in 1980–81, using a multiple opening-closing net with 0.1 mm mesh, revealed *M. gracilis* populations from the surface to the deepest stratum sampled (1650 m). Their population biology was investigated in the central and northern Red Sea, and included analysis of ontogenetic composition and size distribution, sex ratio and percentage of egg-bearing females. By relating population structure differences to variations in the abundance of *Trichodesmium* spp. at the surface, a hypothetical life cycle for the copepod could be proposed: (1) Reproduction takes place only in surface waters during blooms of *Trichodesmium* spp. (2) Short-term, diurnal vertical migrations are not apparent. (3) At the surface and in the lower meso- and bathypelagic zone, the female population consists mainly of small specimens; in the upper part of the oxygen minimum zone, at 300 to 450 m, long-lived large, non-reproductive females are congregated. The significance of these midwater populations in the life cycle of *M. gracilis* is discussed under 2 alternative assumptions: (a) the copepods survive periods of *Trichodesmium* spp. scarcity in a resting phase, or (b) the part of the population in deep waters is moribund. The unusually deep occurrence of *M. gracilis* may have some significance for the nutrient cycle in these waters.

INTRODUCTION

Massive blooms of the marine filamentous cyanobacteria *Oscillatoria* (*Trichodesmium*) spp. are a characteristic feature in Red Sea surface waters (Carpenter 1983). For tropical marine plankton communities, the *Trichodesmium* blooms have a 2-fold significance. (1) The cyanobacteria use molecular nitrogen as an additional nitrogen source (Goering et al. 1966) and thereby become an important primary producer in oligotrophic marine areas, as in the Red Sea. Naqvi et al. (1986) estimated that nitrogen fixation by *Trichodesmium* may contribute 6% to total primary production in this area. (2) The dense mats of *Trichodesmium* filaments that drift on the sea surface serve as a substrate for a specific association of organisms. Members of this community include bacteria and phytoplankters, such as the dinoflagellate *Peridinium trochoideum* and diatoms of the genus *Nitzschia*, as well as the hydroid *Pelagiana trichodesmiae* (Borstad & Borstad 1977). The harpac-

ticoid copepod *Macrosetella gracilis* Dana, 1848 is the largest and phylogenetically most advanced member of this microcommunity yet discovered. *Trichodesmium* filaments serve as food for the adults (Roman 1978) and as a substrate for the non-pelagic juveniles, which grasp the filaments by their hook-like appendages (Björnberg 1965).

The relative abundance of *Macrosetella gracilis* within the total copepod community of tropical seas is poorly known. Michel & Foyo (1977) reported it as one of the 10 most common copepod species in the Caribbean Sea, where *Trichodesmium* blooms can be observed regularly (Borstad & Borstad 1977, Corredor 1977, Carpenter 1983). It accounted for about 1% of the total number of copepods, excluding nauplii, sampled with 0.1 mm mesh nets in the upper 2000 m. This is somewhat lower than the corresponding value (3%) in the upper 1650 m in the Red Sea found by Böttger (1987).

The nauplii of *Macrosetella gracilis* have been sam-

pled in plankton nets only in cases when *Trichodesmium* blooms were occurring (Krishnaswamy 1951, Tokioka & Bieri 1966). The vertical range of the habitat of these juveniles is determined by the vertical extension of the bloom. This can be quite variable, ranging from a few centimetres (Devassy et al. 1978) to several metres (Belogorskaya 1970, Bryceson 1980), but is generally restricted to surface waters.

The occurrence of later copepodids and adults is not restricted to the surface. They have been found in the Atlantic Ocean to a depth of 1750 m (Grice 1963, Owre & Foyo 1964) and Weikert (1982) has also reported its occurrence in deep waters of the Red Sea. It is still unknown whether a relationship exists between surface populations and deep water specimens of *Macrosetella gracilis* and if so what the nature of relationship may be. Existing information on the vertical distribution and migration is rather scarce (Moore & Foyo 1963, Roehr & Moore 1965) and insufficient to prove any hypothesis on this question. There is no information at all available on possible seasonal or production-related differences in the depth distribution of *M. gracilis* populations. The ontogenetic composition and sex ratio of surface and deep water populations are also unknown.

This lack of information may be mainly due to the facts that mesh sizes of about 0.3 mm, as frequently used in marine zooplankton investigations (Roehr & Moore 1965), are not adequate for quantitatively sampling this very slender copepod species (Böttger 1985), and that finer mesh net sampling in pelagic regions has generally been restricted to the upper 200 m.

The present paper is based on samples taken with 0.1 mm mesh nets. It considers the population structure and vertical distribution of *Macrosetella gracilis* in the upper 450 m of the central and northern parts of the Red Sea during autumn and winter. Some preliminary information is also included on the deeper layers, down to 1650 m. All developmental stages of the copepod have been included in the analysis, although the smallest nauplii may not have been sampled quantitatively. Several population parameters, such as ontogenetic composition, sex ratio, size and percentage of egg-bearing females are used to characterize different *M. gracilis* populations in the region studied. By correlating the findings with regional and seasonal variations in the abundance of *Oscillatoria (Trichodesmium) spp.*, a general outline of this copepod's life cycle is proposed.

MATERIAL AND METHODS

Zooplankton samples were collected from the RV 'Valdivia' in the northern Red Sea, above the Kebrit

Deep, between 9 and 15 October 1980; and in the central Red Sea, above the Atlantis II Deep, between 15 October and 8 November 1980, and between 21 and 24 February 1981. The geographical locations are shown in Fig. 1. A single reference station, situated north of the Kebrit Deep, was sampled on 9 October 1980.

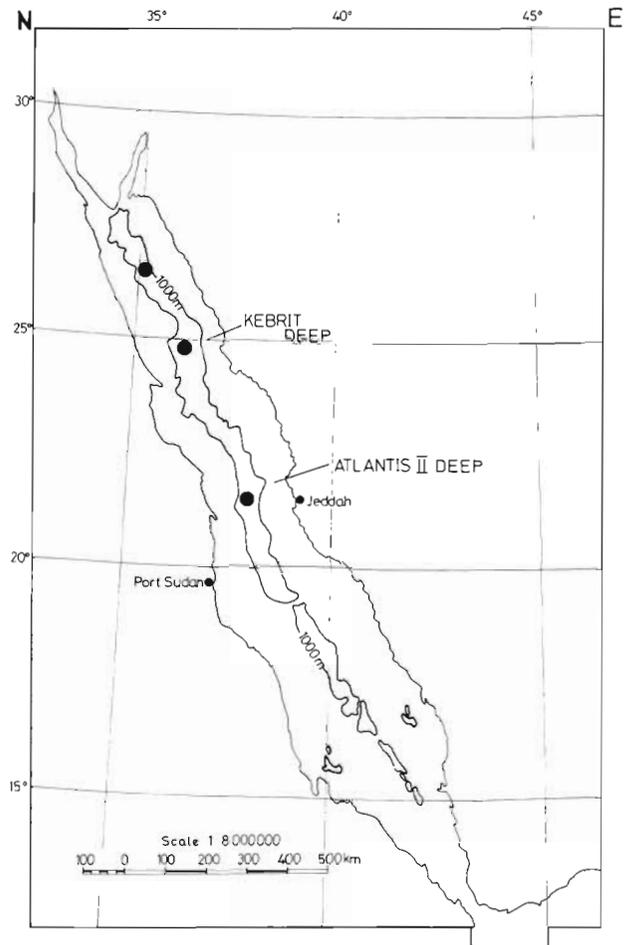


Fig. 1. Plankton sampling stations in the Red Sea during Meseda 3, 1980–81

The sampling was part of a multi-disciplinary environmental research program, Meseda 3 (Thiel et al. 1986). A multiple opening-closing net with a mouth area of 0.25 m² (Weikert & John 1981) equipped with 5 nets of 0.1 mm mesh was towed vertically at a speed of 0.5 m s⁻¹. The depth of the net was determined by the length of the towing wire during the sampling in October and November and by a depth-pressure recorder in February. As the wire angle was less than 10°, the actual depth limits of the vertical strata sampled varied less than ± 3 m from the preset values.

The routine program sampled the upper 450 m of the water column at 50 m intervals. A total of 27 vertical series were evaluated, 10 series each from the Atlantis

II Deep and the Kebrit Deep, and 1 series from the northern reference station during autumn, plus 6 vertical series from the Atlantis II Deep during winter. Equivalent numbers of day and night samples were taken at each of the permanent stations. Samples at the northern reference station were collected during the night. Daytime samples were collected between 03:00 and 17:00 h (local time) in the Kebrit Deep area and between 11:00 and 15:00 h in the area of the Atlantis II Deep. The night-time samples were taken between 03:00 and 05:00 h and between midnight and 04:00 h. In autumn 1980 additional samples were taken in the Atlantis II Deep area from the upper 100 m at smaller, 20 m intervals, and from the deeper water layers down to 1650 m at larger intervals. In the upper 100 m, 3 vertical series were taken during the day and 2 at night. Between 450 and 1050 m, 2 series of samples were taken at 150 m intervals, one during the day and one at night. Between 1050 and 1650 m 1 night-time series at 200 m intervals was collected. Depending on the strata sampled and assuming a filtration efficiency of 100 %, the volumes filtered ranged from 5 m³ (20 m intervals) to 50 m³ (200 m intervals).

Samples were fixed in a 4 % formaldehyde-seawater solution buffered with hexamethylene tetramine. For sorting and storage, they were transferred into a preservative of 5 % propylene glycol, 0.5 % propylene phenoxetol, and 94.5 % filtered seawater (Steedman 1976). Copepods were counted under a stereomicroscope. In most cases, the entire sample was counted. Females, males, copepodids and nauplii were counted separately. The number of egg-bearing females was noted in each sample, but only data from the night-time series will be considered here. The daytime samples had been fractionated through larger-sized mesh gauze earlier, so that some of the females lost their egg sacs, which could not be identified in the samples. Empty exoskeletons and copepods showing an advanced degree of internal disintegration (carcasses) were counted separately and are not included in the abundance data.

Due to fixation, most of the copepods were slightly bent, so the size measurements include some uncertainties. In the present study, only females were considered for sizing and were grouped into 2 classes: < 1.2 mm and > 1.2 mm (anterior tip of prosome to end of caudal rami). A more precise analysis of the size frequency distribution was made on a limited number of individuals (Böttger-Schnack 1989 [companion article]). Females contained various numbers of small 'oil droplets', which possibly serve as a means of fat storage. From each region and season, 50 to 100 females were selected from samples of the epipelagic and mesopelagic zone to determine the degree of fullness with oil droplets.

The occurrence of *Trichodesmium* filaments was semiquantitatively estimated in all 0.1 mm mesh net samples and was categorized as 'none', 'very few', 'few' or 'many'. A more precise abundance estimate was made for samples of the uppermost 0 to 50 m or 0 to 20 m depth range at the Atlantis II Deep during autumn 1980. Samples taken in February, and those taken in the northern Red Sea, contained only very few filaments. In each of these 2 cases quantitative evaluation of filaments was restricted to 1 arbitrarily selected surface sample for comparison. The numbers of filaments were estimated from small subsamples, between 1/200 and 1/6000 of the entire net sample. The subsamples were filtered through membrane filters with 0.45 µm pores, stained with a 4 % eosine and 1.4 % aniline solution, and counted under a microscope at 100× magnification. The number of filaments actually counted ranged from 20 to 500 per subsample.

For the entire water column, temperature profiles were obtained using a multisonde. Salinity and dissolved oxygen were determined from water samples during October and November 1980, but in February, a multisonde was used. The profiles were plotted using the mean values of usually 2 or 3 data sets at each of the permanent stations. In the Kebrit Deep, the temperature profile was derived from a single vertical series. At the northern reference station, no environmental data were obtained.

RESULTS

Environmental data

At all 3 stations 2 water masses, characteristic for the Red Sea, were evident: a warm surface layer with reduced salinity extending to a depth of 100 to 150 m and a deeper water mass with constant temperature and salinity down to about 2000 m (Fig. 2). In October and November 1980, sharp temperature gradients between 50 and 100 m separated the isothermal and isohaline deep water mass (21.7°C and 40.5×10^{-3} S) from a thin zone of surface water at temperatures of 28 to 30°C and salinities of 39.5×10^{-3} S in the central Red Sea and 39.7×10^{-3} S in the north. In February 1981, surface temperatures in the central Red Sea had cooled to 24°C. The temperature in the upper 100 m remained almost constant, but beneath this depth, it gradually decreased. The salinity profiles showed a marked gradient between 80 and 130 m. This was more pronounced than during autumn (Fig. 2). Oxygen concentrations in the surface zone were high (4 to 5 ml O₂ l⁻¹), but decreased sharply below 100 m. Minimum values of < 1.3 ml O₂ l⁻¹ were found in the central Red Sea between 300 and 600 m (Fig. 2). In the northern Red Sea (Kebrit Deep), the oxygen minimum zone was

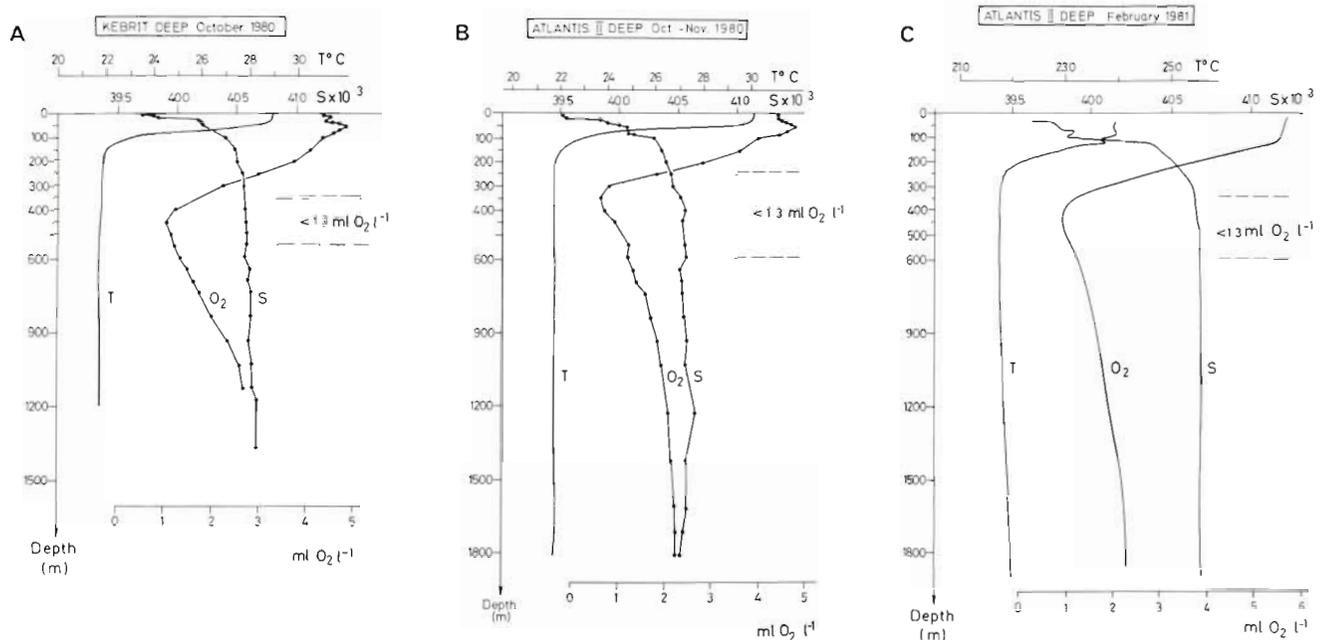


Fig. 2. Vertical profiles of temperature (T), salinity (S), and dissolved oxygen (O_2) in the northern (Kebrat Deep) and central Red Sea (Atlantis II Deep). (Modified from Lange et al. 1981)

situated deeper, and the minimum oxygen concentrations were somewhat higher than in the central part, as commonly found in the Red Sea (Morcos 1970).

Trichodesmium spp.

Filaments of *Trichodesmium* were encountered in the upper 50 or 20 m depth zone at all 4 sampling stations, but mostly at low abundance values, in the range of 10^4 to 10^5 filaments m^{-2} . A bloom of *Trichodesmium* occurred in the Atlantis II Deep area in autumn 1980. Abundance values varied considerably during the 3 wk sampling period, from about 10^4 to 10^8 filaments m^{-2} (Fig. 3).

Highest numbers of *Trichodesmium* were always present in the uppermost net samples. During bloom conditions, single filaments were found down to 450 m. Contamination of the closed nets during hauling through the dense surface patches cannot be ruled out, though this should not have been very significant. In the Kebrat Deep area, solitary filament bundles were present in the net samples to a depth of 150 m.

Macrosetella gracilis

Populations of *Macrosetella gracilis* were present in the sampled depth range at all stations considered during this study. Total abundance, vertical distribution and population structure, however, varied considerably among stations and sampling dates. Highest

concentrations were found in the central Red Sea (Atlantis II Deep) in autumn 1980, during *Trichodesmium* bloom conditions. Only on this occasion were juveniles (nauplii and copepodid stages I to V) encountered. Results are thus presented for this period first and taken as a basis to feature the specific differences at the remaining surveys.

Central Red Sea, October and November 1980

Both juvenile and adult stages were mainly concentrated in the uppermost 50 or 20 m depth interval sampled (Table 1). Beneath this surface zone, juveniles were found irregularly and in low numbers only. Adults were less confined to the surface waters. On the average only two-thirds of the males and one half of the females inhabiting the upper 450 m of the water column were caught in the 0 to 50 m interval (Table 1a). But within the upper 100 m zone (Table 1b), where samples were taken at close intervals, about 80% of the adults and almost 100% of the juveniles were caught in the 0 to 20 m surface layer. Thus, numbers per m^2 obtained from 50 or 20 m surface samples appeared to be roughly comparable and were combined for the following analysis.

Within the surface zone (0 to 50 m and 0 to 20 m), the abundance of *Macrosetella gracilis* stages showed a substantial variation. Total ranges of values are given in Table 1. The time sequence of the data, as presented in Fig. 3, did not indicate any systematic day-night

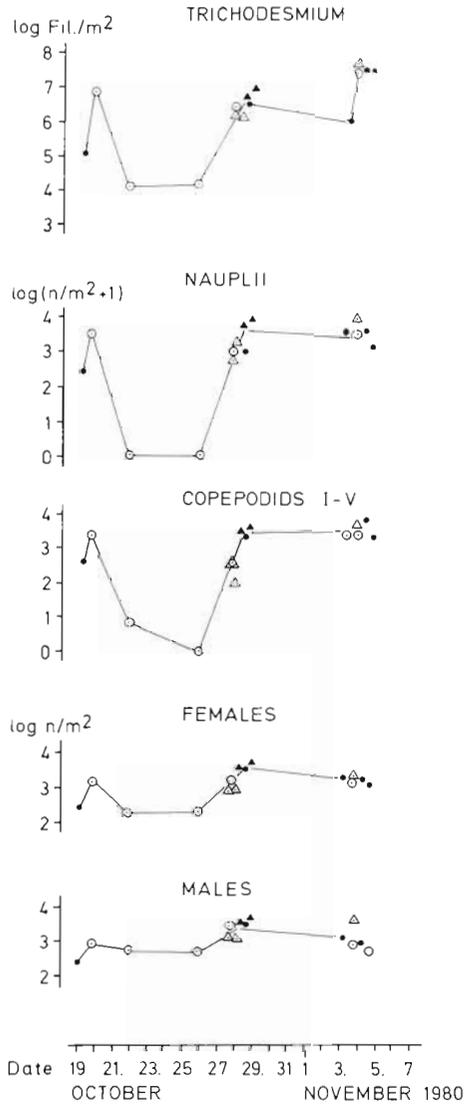


Fig. 3. Temporal variation in the abundance of *Trichodesmium* spp. filaments and *Macrosetella gracilis* juveniles and adults beneath 1 m² in the upper 50 m (●, ○) or 20 m (▲, △) in the Atlantis II Deep during October and November 1980. Solid symbols: night; open symbols: day. Note logarithmic scale

differences. Rather, the dominating feature was exceptionally low abundance values on 2 out of 15 sampling dates. The differences were most pronounced for juvenile stages. These were caught as single specimens only on these 2 dates, whereas adults were present in numbers of about 700 m⁻² at the same time. On all other dates, juveniles outnumbered adults on average by a factor of about 4.

The variation in the abundance of *Macrosetella gracilis* at the surface appeared to be closely related to changes in the abundance of *Trichodesmium* filaments, which were exceptionally rare on the same 2 sampling dates (Fig. 3). Spearman rank correlation coefficients (*r*) proved to be highly significant (*p* < 0.01) for both juvenile groups – nauplii (*r* = 0.70) and copepodids I to V (*r* = 0.78) – and for females (*r* = 0.61). For males, the variation was less pronounced and the correlation with *Trichodesmium* abundance was statistically significant at the 5% level only (*r* = 0.48).

In the 50 to 450 m depth range, compared to the surface layer, the variation of abundance values was generally less pronounced among sampling dates (see ranges in Table 1). The occurrence of juveniles was strongly related to the surface conditions – the abundance sequences in both depth ranges closely parallel each other (Fig. 4). For adults, on the other hand, there was no indication for any correlation with the surface population or with *Trichodesmium* conditions. A complete picture of the variation in the vertical distribution pattern is given in Fig. 5 for males and 2 size groups of females. The concentration of males decreased more or less continuously with depth and towards the end of the sampling period, whereas for females in total, some irregular layering was indicated beneath the surface zone, without any general trend over time. Large females (> 1.2 mm), however, showed a conspicuous and consistent pattern, with minimum concentrations between 50 and 250 m and a secondary maximum in the range 250 to 450 m (Fig. 5).

Table 1. *Macrosetella gracilis*. Abundance of juveniles and adult beneath 1 m² (a) in the upper 450 m (a) and (b) in the upper 100 m above the Atlantis II Deep during October and November 1980. \bar{x} : arithmetic mean; R: range; *n*: number of sampling series

Depth (m)	Juveniles (Nauplii + copepodids)		Adults		Males	
	<i>n</i>	\bar{x}	\bar{x}	R	\bar{x}	R
(a) Upper 450 m						
0–50	10	4200	1400	(190–3800)	1300	(280–3700)
50–450	10	235	1400	(1200–2100)	740	(260–1500)
0–450	10	4400	2800	(1400–5000)	2000	(980–4400)
(b) Upper 100 m						
0–20	5	7300	2850	(800–5000)	3300	(1000–7200)
20–100	5	180	670	(500–970)	600	(380–950)
0–100	5	7400	3500	(1600–5600)	3900	(1800–7900)

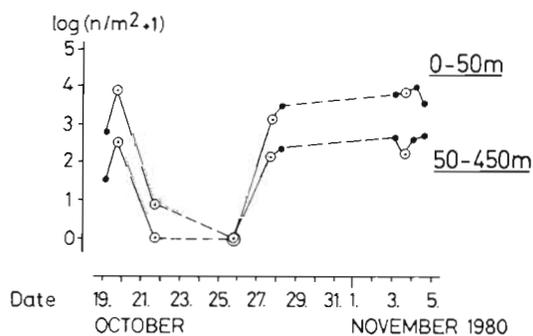


Fig. 4. *Macrosetella gracilis*. Number of nauplii and copepods I to V beneath 1 m² in the upper 50 m and 50 to 450 m in the Atlantis II Deep during October and November 1980. Solid symbols: night; open symbols: day. Note logarithmic scale

Among females, small specimens were generally dominant. On average, individuals < 1.2 mm accounted for 75 % of all females in the upper 450 m. This proportion varied among profiles over the wide range of 50 to 90 %. Within the surface layer, the proportion of small females was regularly above 70 %, (with one exception only), and within the depth of the secondary maximum of large females it was in the range 50 to 70 %.

Size differences were also apparent in the percentage of females bearing eggs. In the surface zone 34 % of small females carried egg sacs, as compared to only 19 % of large females, giving an average of 31 % for all females. In the vertical profile low numbers of egg-

bearing females were also found regularly down to 150 m, and single specimens were collected as deep as 450 m. The sex ratio was, on average, well balanced at the surface, but varied between 2:1 and 0.3:1 females to males at high and low *Trichodesmium* concentrations, respectively.

The restricted number of sampling profiles going down to 1650 m revealed that *Macrosetella gracilis* populations beneath 450 m consisted mainly of females (Table 2a). Males and juveniles combined accounted for only 5 % of all individuals sampled in this extended depth range. Juveniles were caught irregularly and may have entered the samples as contaminants from the surface waters. Males were regularly present but decreased in abundance toward greater depths. The female population was not reproductive at these depths. Only one egg-bearing specimen was found, which may also have been introduced as a contaminant. The proportion of large females (> 1.2 mm) decreased with increasing depth. Between 1050 and 1650 m, nearly all individuals were smaller than 1.2 mm (Table 2b).

Central Red Sea, February 1981

In winter 1981, the population of *Macrosetella gracilis* in the central Red Sea consisted exclusively of adults. One single nauplius was caught at 400 to 450 m. Females were predominant, accounting for 90 % of the total number of copepods in the upper 450 m (Table

Table 2. *Macrosetella gracilis*. Population structure in various habitat zones within the upper 1650 m of the water column above the Atlantis II Deep during autumn 1980.

(a) Standing stock of juveniles and adults: mean numbers ($N m^{-2}$) beneath 1 m² and percentages (%) in given layers. *n*: number of sampling series

Depth (m)	<i>n</i>	Females		Males		Juveniles		Ratio adults:juv.	Ratio females:males
		$N m^{-2}$	%	$N m^{-2}$	%	$N m^{-2}$	%		
0-50	10	1400	(35)	1300	(62)	4200	(93)	0.6 : 1	1 : 1
50-450	10	1400	(35)	740	(35)	240	(5)	10 : 1	2 : 1
450-1050	2	710	(17)	60	(3)	72	(2)	11 : 1	12 : 1
1050-1650	1	510	(13)	4	(<2)	-	-	-	130 : 1
0-1650		4000	(100)	2100	(100)	4500	(100)	1.4 : 1	2 : 1

(b) Standing stock of small (< 1.2 mm) and large (> 1.2 mm) females. For abbreviations, see Table 2a

Depth (m)	<i>n</i>	< 1.2 mm		> 1.2 mm		Ratio < 1.2 : > 1.2 mm
		$N m^{-2}$	%	$N m^{-2}$	%	
0-50	10	1100	(34)	270	(34)	4 : 1
50-450	10	1000	(31)	430	(56)	2 : 1
450-1050	2	640	(20)	72	(9)	13 : 1
1050-1650	1	500	(15)	4	(<1)	130 : 1
0-1650		3300	(100)	780	(100)	4 : 1

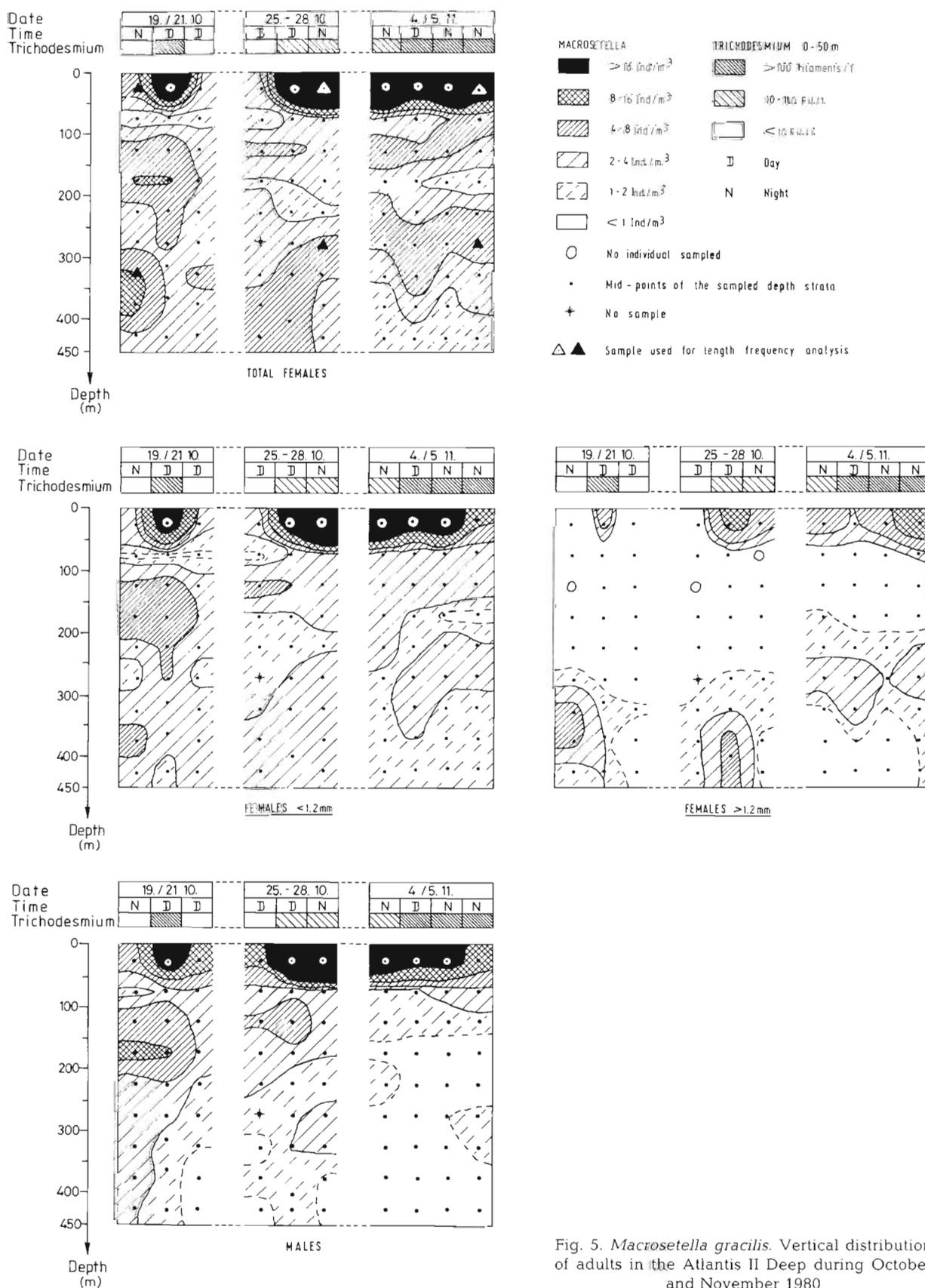


Fig. 5. *Macrosetella gracilis*. Vertical distribution of adults in the Atlantis II Deep during October and November 1980

Table 3. *Macrosetella gracilis*. Temporal and regional variation in abundance beneath 1 m² in the upper 450 m. (a) Atlantis II Deep, February 1981; (b) Kebrit Deep, October 1980, (c) northern reference station, October 1980. \bar{x} : Arithmetic mean; R: range; n: number of sampling series

Depth (m)	n	Females		Males		Juveniles	Ratio females: males
		\bar{x}	R	\bar{x}	R		
(a) Atlantis II, Feb 1981							
0–50	6	70	(32–140)	30	(12–44)	–	2:1
50–450	6	2100	(1700–2600)	260	(180–360)	(–) ^a	8:1
0–450	6	2200	(1700–2800)	290	(190–390)	–	8:1
(b) Kebrit, Oct 1980							
0–50	10	100	(44–140)	130	(64–200)	–	0.8:1
50–450	10	350	(260–400)	64	(36–96)	(–) ^a	5:1
0–450	10	450	(370–520)	200	(140–260)	–	2:1
(c) Northern, Oct 1980							
0–50	1	8		40		–	0.2:1
50–450	1	340		180		–	2:1
0–450	1	350		220		–	1.6:1

^a Solitary find

3a). Comparing autumn 1980 and February 1981, the standing stock of females was at the same level, while the standing stock of males was one order of magnitude lower in winter 1981.

The vertical distribution of males was not very consistent, but showed a generally increased concentration with depth (Fig. 6). Values of > 1 ind. m⁻³ were only found below 200 m and mostly between 300 and 400 m. The sex ratio of females to males shifted with increasing depth in favour of the females, from a mean ratio of 2:1 in the upper 50 m to a mean of 10:1 below 300 m.

Females showed a more distinct deep concentration maximum at 300 to 400 m, which was consistent during day and night and for both size groups (Fig. 6). Larger females (> 1.2 mm) congregated almost exclusively in the deep concentration maximum, whereas smaller females also showed some irregular concentrations above 300 m. The size composition of the females correspondingly changed abruptly at 250 m. In the pooled samples from the deeper layers of each profile, individuals > 1.2 mm accounted for 40 to 60 % of total females, compared to only 4 to 9 % above 250 m. Egg-bearing females were collected sporadically between the surface and 150 m. Egg-bearing females in surface samples made up 3 % on average, which is very low compared to the 10 times higher value observed in autumn.

Northern Red Sea, October 1980

At the Kebrit Deep (24°N) and the northern reference station (26°N, Fig. 1), sampled in autumn 1980,

the populations of *Macrosetella gracilis* consisted almost exclusively of adults (Table 3b, c). In the upper 450 m, the range of variation in the total standing stock was much lower in the Kebrit Deep area than in the central Red Sea during the same season (Table 1). Females predominated, accounting for > 70 % of adults. Total numbers of *M. gracilis* and the size composition of females from the single northern reference station were similar to those from the Kebrit Deep, but distribution patterns differed considerably.

In the Kebrit Deep area, males were concentrated mainly in the upper 50 m (Fig. 7), with a mean abundance of 2.6 ind. m⁻³. A small secondary maximum was found at 350 to 450 m. Females showed the same general distribution pattern with 2 concentration maxima, of which the deep maximum was however much more pronounced (Fig. 7). Mean concentration in both peaks was 2 to 3 ind. m⁻³ and this pattern was consistent during both day and night. Large females (> 1.2 mm) dominated. They congregated preponderantly at greater depths, whereas the majority of the smaller females were concentrated in the upper 50 m (Fig. 7). Egg-bearing females were regularly found in the upper 50 m and occasionally egg-bearing individuals descended as deep as 150 m. At the surface about 16 % of females carried eggs. A size-related difference was not apparent in this case. The sex ratio of females to males averaged 0.8:1 in the surface zone and increased to 7:1 at 350 to 450 m.

The vertical distribution pattern of *Macrosetella gracilis* observed at the northern reference station differed from that near the Kebrit Deep in 2 main features (Table 3c): (1) males congregated at greater depths

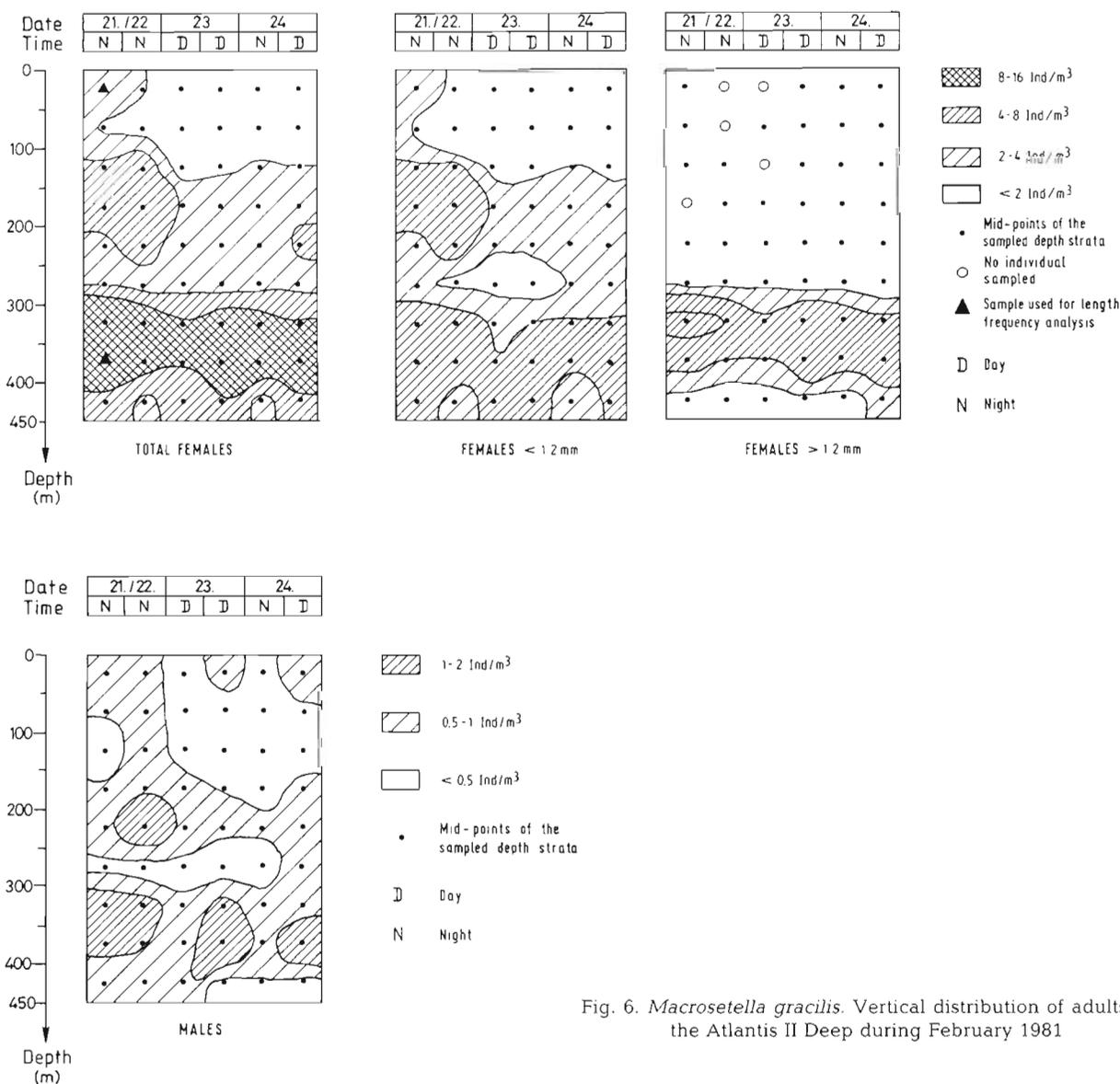


Fig. 6. *Macrosetella gracilis*. Vertical distribution of adults in the Atlantis II Deep during February 1981

below 300 m; (2) there was also no surface maximum for females; they were concentrated at 350 to 450 m (2.5 ind. m^{-3}) and were mainly large ($> 1.2 \text{ mm}$). Females with egg sacs were found irregularly between 50 to 300 m. The sex ratio of females to males shifted from 0.2:1 in the upper 50 m to 2:1 at 350 to 450 m.

Oil droplets in female *Macrosetella gracilis*

The quantity of oil droplets in female *Macrosetella gracilis* was regularly considered during the present analysis as an obvious special feature that might be related to the condition of the stock. Results from all stations and for different *Trichodesmium* situations are summarized in Fig. 8. Generally, more oil droplets were

found in individuals from deeper water layers than in those from the surface zone. However, individuals taken at the surface during highest concentrations of *Trichodesmium* (Atlantis II Deep, Fig. 8C), also contained many oil droplets.

DISCUSSION

Population structure and life cycle of *Macrosetella gracilis* in the Red Sea

When resolving the vertical structure of a plankton population by the use of closing net samples, the possibility of contamination of deep samples by surface organisms has to be considered. For the sampling

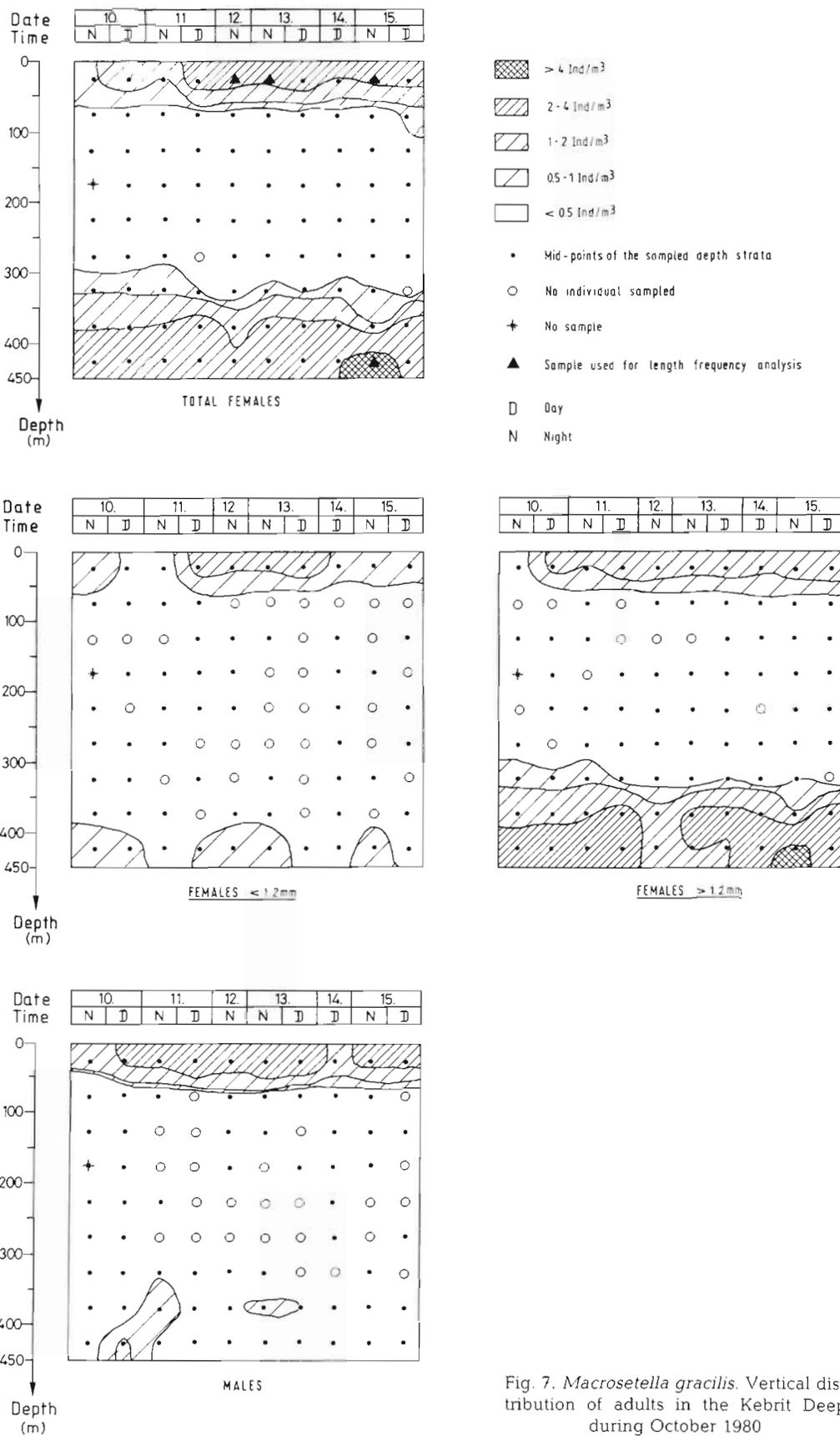


Fig. 7. *Macrosetella gracilis*. Vertical distribution of adults in the Kebrit Deep during October 1980

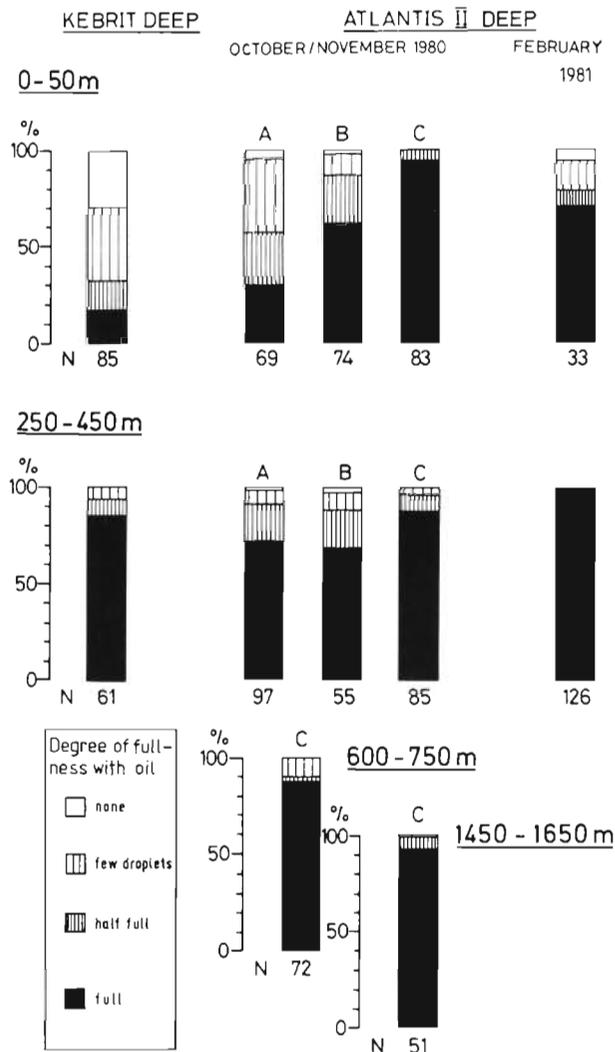


Fig. 8. *Macrosetella gracilis*. Degree of fullness with oil droplets observed in females from various water depths. N: number of individuals examined. A, B, C: various densities of *Trichodesmium* filaments in the upper 50 m; A = 4 filaments l^{-1} , B = 70 filaments l^{-1} , C = 650 filaments l^{-1}

device used in the present study. Weikert & John (1981) presented some quantitative assessment on this problem and indicated small contamination effects only, using a larger mesh size of 0.3 mm. Reducing the mesh size, and thus the sizes of organisms considered, might in principle increase the contamination problem. However, in the present study, distinct differences were observed between surface and deep water populations. Contamination obviously had no severe effect on the sampling results, however for organisms caught sporadically and in low numbers only, depth allocation remains uncertain.

In general, the population structure of *Macrosetella gracilis* during autumn and winter differs substantially within the Red Sea. *Trichodesmium* appears to be the key factor governing the ontogenetic composition, the size distribution of adults, the sex ratio, and the percentage of reproductive females. The details presented under 'Results' are schematically summarized in Fig. 9, which serves as a basis for some generalization and discussion of principle features of the population biology of this species in the Red Sea. In the following, the paragraph numbering corresponds to the numbering of populations of *M. gracilis* in Fig. 9.

(1) Reproduction of *Macrosetella gracilis* populations is restricted to sea surface layers and depends on *Trichodesmium* bloom conditions. Only within these blooms do the pseudopelagic nauplii and copepodids find the substrate of filaments they need for their development. The abundance of the copepod within the bloom is correspondingly high. Female and male copepods are present in almost equal numbers, and a large proportion of the females carry egg sacs. On average small females (< 1.2 mm) are more numerous and have a higher percentage of egg-bearers than larger females.

(2) In the water column beneath a *Trichodesmium* bloom, the population consists mainly of adults. The sporadic occurrence of juveniles remains uncertain, as some of these small individuals may also have entered the closed sampling nets during hauling through the densely populated patches of *Trichodesmium*. Males are less abundant than females at this depth. The difference in sex ratio between surface and deeper layers may indicate a lower survival rate of males at greater depths. Alternatively, a greater downward flux of females seems possible. Also within the group of females, larger specimens (> 1.2 mm) seem to move down more rapidly or survive longer at greater depths than smaller ones, as their proportion increases with depth. The passive sinking velocity of copepods has been found to vary between 36 and 720 $m d^{-1}$ (Parsons et al. 1977). Thus, it seems possible that these copepods sink to a few hundred meters within a very short time. The possible retarding effect of the long, thin body form of *Macrosetella gracilis* on its sinking velocity has not been investigated, however.

(3) Without a *Trichodesmium* bloom, as in February 1981, no surface population of *Macrosetella gracilis* develops. Females > 1.2 mm congregate in the upper part of the oxygen minimum at a depth of 300 to 400 m. The abundance of smaller females also increases with depth, but shows no strong tendency to congregate at a certain depth. Males are rare in this winter situation and juveniles are no longer present. A small percentage of females is still carrying egg-sacs in the near-surface water down to 150 m, but juveniles cannot

develop successfully, because sufficient amounts of *Trichodesmium* are lacking. It can be presumed that the autumn population of *M. gracilis* is still present in the following winter. After reproduction in *Trichodesmium*-rich surface waters, the adults congregate at greater depth just above the oxygen minimum zone. The ecological significance of this behaviour will be discussed in the next section.

Regional differences observed in the vertical distribution pattern of *Macrosetella gracilis* can be summarized and interpreted as follows (cf. Fig. 9):

(4) Regarding the midwater population present at depths of more than 300 m, the autumn situation in the northern Red Sea (Kebrit Deep) looks similar to the winter situation in the central Red Sea, when no *Trichodesmium* bloom was noticed. It is a small population, characterized by a low proportion of males and a lack of juvenile stages. The dominance of large females, however, is much more pronounced in the Kebrit Deep. The aggregation of large females is found ca 100 m deeper than in the central area, which corresponds to the regional differences in the depth of the oxygen minimum zone (Fig. 2). Thus, it may be assumed that the decreasing oxygen concentrations act as a stimulus that prevents larger females from descending further.

(5) In Kebrit Deep, the surface population of *Macrosetella gracilis* is completely separated from the population at midwater depths. It resembles Population (1) found in the central Red Sea during the *Trichodesmium* bloom with respect to sex ratio and size composition of females. However, this northern population is less numerous than Population (1) and has a lower mean percentage of egg-bearing females. Juvenile stages are not present, and *Trichodesmium* is scarce. This surface population of *M. gracilis* may be part of an expanding Population actively reproducing within a *Trichodesmium* bloom nearby. Such a bloom may well be missed during a survey because of the very patchy distribution of *Trichodesmium*. Alternatively, the observed Population (5) may be interpreted as part of an old surface population after bloom conditions have disappeared. It may have been separated from the related deep population by drift processes.

(6) North of the Kebrit Deep, at 26°N, only one deep *Macrosetella gracilis* population was found, which resembled Population (4) of the Kebrit Deep with respect to abundance and size composition of the females. However, the large proportion of males seemed to be atypical for a midwater population of this species, according to the population structure observed farther to the south. The limited data compiled from a single

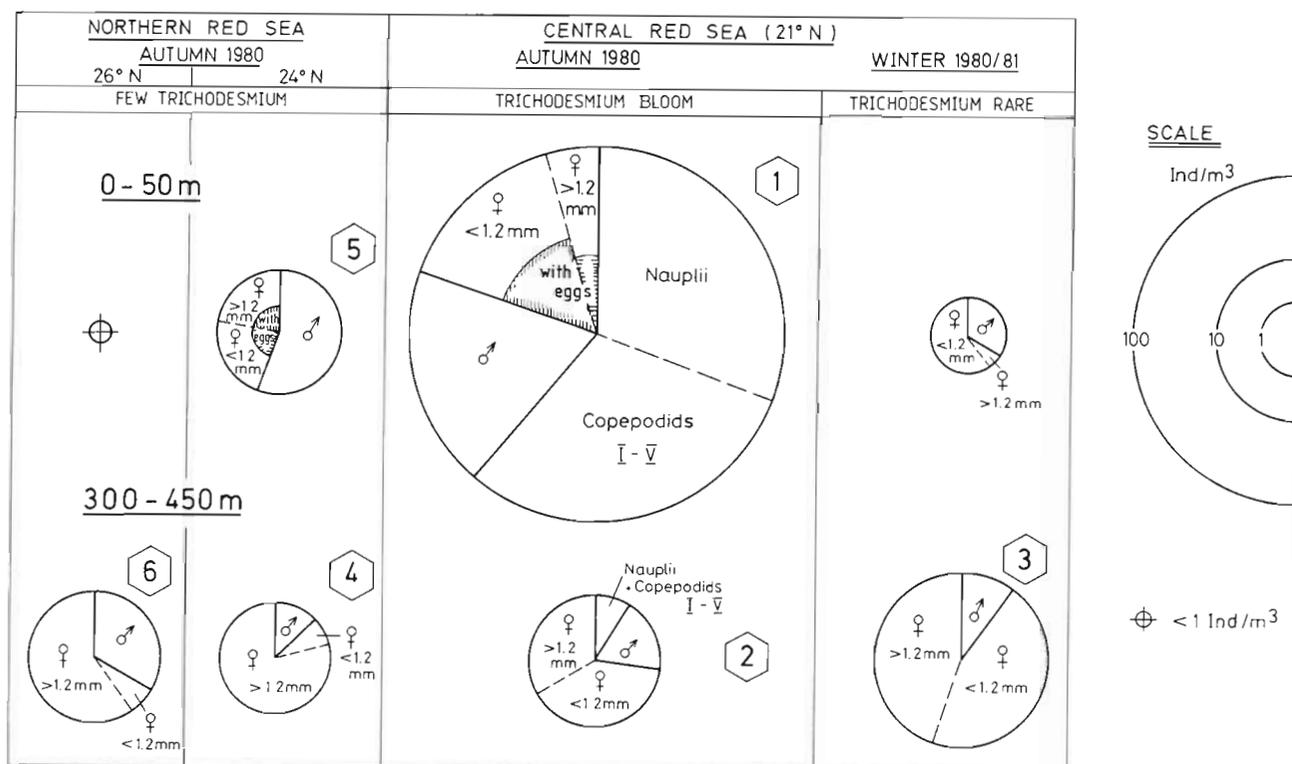


Fig. 9. *Macrosetella gracilis*. Schematic depiction of population structure in the central and northern Red Sea during autumn and winter, 1980-81. Numbers (1) to (6) refer to explanations given in the text

vertical series are insufficient for a reasonable interpretation of this regional difference in the population structure.

The results so far obtained on the population structure and vertical distribution of *Macrosetella gracilis* in the Red Sea above a depth of 450 m allow the following general conclusions:

- Reproduction of the copepod takes place only in the epipelagic zone in areas with large amounts of *Trichodesmium* spp.
- Midwater populations consist of adult *Macrosetella gracilis* only. After development in the surface zone during favourable conditions, they congregate in the mesopelagic zone in the upper part of the oxygen minimum layer. Diurnal vertical movements are not apparent.
- The midwater populations are dominated mainly by large females (> 1.2 mm) and continue to exist after conditions for reproduction are no longer favourable.

Ecological significance of midwater and deep sea populations of *Macrosetella gracilis*

The conspicuous depth distribution of *Macrosetella gracilis* raises questions concerning the function of the deep-dwelling part of the population within the life cycle of the copepod. Two explanations are presented here.

Firstly it is suggested that the midwater population represents a resting stock surviving at this depth until favourable *Trichodesmium* conditions develop again at the surface. Such resting stocks are known from a variety of calanoid copepod species, which are undergoing a 'diapause' (Alldredge et al. 1984). In the Red Sea, a deep population of *Rhincalanus nasutus*, dwelling in the oxygen minimum zone at 450 to 600 m, is also considered to be such a resting stock (Weikert 1980, 1982, Beckmann 1984). For marine harpacticoid copepod species, similar phenomena have not previously been reported. One reason for this may be that the relatively few pelagic harpacticoid species are too scarce to be sampled in sufficient numbers by traditional methods to allow a detailed investigation of their depth distribution (Boxshall 1979). Moreover, species such as *Macrosetella gracilis* and *Microsetella* spp. have not been sampled quantitatively by the commonly used 0.3 mm mesh nets. This was demonstrated by simultaneous sampling using 0.3 m and 0.1 mm mesh nets during the Meseda 3 cruise in the Red Sea. No juveniles and only one tenth of the adult *M. gracilis* were retained by the coarser mesh size (Böttger 1985).

The high number of oil droplets observed in the deep-living females indicate considerable lipid stor-

age, typical for resting stages of calanoid copepods (Conover 1962, Hirche 1983, Alldredge et al. 1984). A biochemical analysis of the *Macrosetella gracilis* specimens for physiological determinations such as protein, lipid or enzyme content is not practicable after fixation in formaldehyde. In particular, the lipid content of copepods can be greatly reduced by formaldehyde fixation (Morris 1972). The determination of metabolism, including respiration, excretion and mobility, is also possible only with living specimens. Therefore, the presence of resting stages of *M. gracilis* can only be inferred. If *M. gracilis* has an ontogenetic migration cycle only one phase of it, the downward migration, was observed during the present study. It remains to be determined whether an upward migration occurs during other periods or in other parts of the Red Sea.

Secondly, the possibility has to be considered that the deep population of *Macrosetella gracilis* is moribund. The relative percentage of carcasses among the deep population, however, was not significantly higher than that among the surface population. Furthermore, compared to the percentage of carcasses of other copepod species, that for *M. gracilis* was rather low. In view of the different distribution pattern observed for the 2 size groups of females, it may also be possible that only the population of large females (> 1.2 mm) represents a resting stock, while the smaller females are produced in surface waters for rapid reproduction and do not survive non-bloom periods.

Generally, the occurrence of *Macrosetella gracilis* in deep waters is of special importance for the nutrient cycle in the area studied. Nitrogen fixed by *Trichodesmium* spp. at the sea surface is transported into deep water by the copepod and becomes available for other planktonic organisms there after excretion or through the food web. The relative importance of *M. gracilis* within total copepods, which are the most numerous metazoan group in 0.1 mm mesh nets, was far greater in the deep sea (40%) than at the surface (2%) (Böttger 1987). It is still too early to estimate nitrogen input to the deep sea via *M. gracilis*, as important numerical data on this copepod at depths below 500 m are restricted to a few sampling series in the Red Sea. In evaluating the ecological significance of *Trichodesmium* spp. blooms in tropical pelagic areas, however, these processes will have to be taken into account.

Comparison with other pelagic areas

The abundance data for adult *Macrosetella gracilis* in the Red Sea can be compared with those from other fine mesh net sampling programs (≤ 0.1 mm mesh size) in the southern Atlantic Ocean (Calef & Grice 1966),

the Caribbean Sea (Roman 1978) and the Sargasso Sea (own unpubl. data). Usually, between zero and over 100 ind. per m² of the sea surface were counted in the upper 200 m. Extreme values of 6000 ind. m⁻² were recorded within *Trichodesmium* blooms (Calef & Grice 1966). Abundance values observed in the present study for the upper 200 m of the Red Sea varied from 120 to 8300 ind. m⁻². They are thus comparable to the more extreme values found in the Atlantic. Published information on the abundance of *M. gracilis* nauplii and copepodids is scarce. From data reported by Tokioka & Bieri (1966), a mean abundance of 1.4 nauplii m⁻² can be calculated for the upper 10 cm of the water column. For the Red Sea, much higher values have been obtained. Even when assuming an equal distribution over the upper 20 m, the average abundance of nauplii in the upper 10 cm would amount to 25 ind. m⁻². This is certainly an underestimation, because the concentrations at the surface will be higher than the average value for the upper 20 m.

Since the *in vitro* experiments of Björnberg (1965), it is known that blooms of *Trichodesmium* act as potential 'Kindergarten' for juvenile *Macrosetella gracilis*. In view of the tremendous amount of literature dealing with the mass development of these algae in tropical pelagic areas (reviewed by Carpenter 1983), the lack of any reference to the occurrence of these juvenile copepods is surprising. This omission is presumably due to the sampling methods used and not to a scarcity of the copepod. Zooplankton samples taken within *Trichodesmium* blooms have in most cases been obtained with 0.3 mm mesh nets, which do not even catch adult *M. gracilis* quantitatively (see above). The larger zooplankton organisms associated with *Trichodesmium* blooms were investigated in a long-term study along the Indian Coast (Nair et al. 1980). Unfortunately, all *Trichodesmium* filament bundles and thus any *M. gracilis* nauplii that may have been attached to them were carefully removed prior to the analysis of the zooplankton samples.

Midwater and deep populations of *Macrosetella gracilis* comparable to that found in the Red Sea during the present study have not yet been reported from other pelagic regions. All published information on finds of *M. gracilis* in water layers below 200 m (Grice 1963, Owre & Foyo 1964, Deevey & Brooks 1977, Boxshall 1979, Weikert 1982) are based on samples taken in 0.2 m or 0.3 mm mesh nets, which cannot catch that species quantitatively. In most cases single specimens, mainly adults, were found. Some authors assume that deep samples have been contaminated by surface organisms (Boxshall 1979). In view of the inadequate sampling methods, however, these scattered finds may also indicate that this species inhabits deep waters in other pelagic regions as well.

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LITERATURE CITED

- Allredge, A. L., Robison, B. H., Fleminger, A., Torres, J. J., King, J. M., Hamner, W. M. (1984). Direct sampling and *in situ* observation of a persistent copepod aggregation in the mesopelagic zone of the Santa Barbara Basin. *Mar. Biol.* 80: 75–82
- Beckmann, W. (1984). Mesozooplankton distribution on a transect from the Gulf of Aden to the central Red Sea during the winter monsoon. *Oceanologica Acta* 7: 87–102
- Belogorskaya, E. V. (1970). Qualitative and quantitative distribution of phytoplankton in the Red Sea and Gulf of Aden in October/November 1963. *Biol. Morja* (Kiev) 21: 133–152 (Russian)
- Björnberg, T. K. S. (1965). Observations on the development and the biology of the Miracidae Dana (Copepoda: Crustacea). *Bull. mar. Sci.* 15: 512–520
- Borstad, G. A., Borstad, L. E. (1977). The *Oscillatoria erythraea* (Cyanophyta) community of associates. In: Stewart, H. B. Jr (ed.) Cooperative investigations of the Caribbean and adjacent regions – II. FAO Fish. Rep. 200: 51–57
- Böttger, R. (1985). Untersuchungen zur Verteilung der kleinen Metazoa im Plankton des Roten Meeres, unter besonderer Berücksichtigung cyclopoider und harpacticoider Copepoden. Dissertation, University of Hamburg
- Böttger, R. (1987). The vertical distribution of micro- and small mesozooplankton in the central Red Sea. *Biol. Oceanogr.* 4: 383–402
- Böttger-Schnack, R. (1989). Body length of female *Macrosetella gracilis* (Copepoda: Harpacticoida) from various depth zones in the Red Sea. *Mar. Ecol. Prog. Ser.* 52: 33–37
- Boxshall, G. A. (1979). The planktonic copepods of the north-eastern Atlantic Ocean: Harpacticoida, Siphonostomatoida and Mormonilloida. *Bull. Br. Mus. nat. Hist. (Zool.)* 35: 201–264
- Bryceson, J. (1980). Nitrogen fixation and the autecology of *Oscillatoria erythraea* (Ehrenberg) Kuetzing, a planktonic cyanophyte from the coastal waters of Tanzania: a preliminary investigation. In: Proc. of the 'Symposium on the coastal and marine environment of the Red Sea, Gulf of Aden and tropical western Indian Ocean'. Vol. III. Khar-toum, January 9–14, 1980. The Red Sea & Gulf of Aden Environmental Programme, Jeddah, p. 471–488
- Calef, G. W., Grice, G. D. (1966). Relationship between the bluegreen alga *Trichodesmium thiebautii* and the copepod *Macrosetella gracilis* in the plankton off northeastern South America. *Ecology* 47: 855–856
- Carpenter, E. J. (1983). Physiology and ecology of marine planktonic *Oscillatoria* (*Trichodesmium*). *Review. Mar. Biol. Lett.* 4: 69–85
- Conover, R. J. (1962). Metabolism and growth in *Calanus hyperboreus* in relation to its life cycle. *J. Cons. perm. int. Explor. Mer.* 153: 190–197
- Corredor, J. E. (1977). Aspects of phytoplankton dynamics in

- the Caribbean Sea and adjacent regions. In: Stewart, H. B. Jr (ed.) Cooperative investigations of the Caribbean and adjacent regions – II. FAO Fish. Rep. 200: 101–114
- Deevey, G. B., Brooks, A. L. (1977). Copepods of the Sargasso Sea off Bermuda: species composition, and vertical and seasonal distribution between the surface and 2000 m. Bull. mar. Sci. 27: 256–291
- Devassy, V. P., Bhattathiri, P. M. A., Qasim, S. Z. (1978). *Trichodesmium* phenomenon. Indian J. mar. Sci. 7: 168–186
- Goering, J. J., Dugdale, R. C., Menzel, D. W. (1966). Estimates of *in situ* rates of nitrogen uptake by *Trichodesmium* sp. in the tropical Atlantic Ocean. Limnol. Oceanogr. 11: 614–620
- Grice, G. D. (1963). Deep water copepods from the western North Atlantic with notes on five species. Bull. mar. Sci. 13: 493–501
- Hirche, H.-J. (1983). Overwintering of *Calanus finmarchicus* and *Calanus helgolandicus*. Mar. Ecol. Prog. Ser. 11: 281–290
- Krishnaswamy, S. (1951). Development of a harpacticoid copepod *Macrosetella gracilis* (Dana). Madras Univ. J. 21(B): 2
- Lange, J., Falk, E., Zeitner, R. (1981). Meseda 3-Data hydrography: water chemistry. Tech. Rep. No. 34G, Preussag Marine Technology Dept, Hannover: 1–145
- Michel, H. B., Foyo, M. (1977). Studies of Caribbean zooplankton. In: Stewart, H. B. Jr (ed.) Cooperative investigations of the Caribbean and adjacent regions – II. FAO Fish. Rep. 200: 275–289
- Moore, H. B., Foyo, M. (1963). A study of the temperature factor in twelve species of oceanic copepods. Bull. mar. Sci. 13: 502–515
- Morcos, S. A. (1970). Physical and chemical oceanography of the Red Sea. Oceanogr. mar. biol. A Rev. 8: 73–202
- Morris, R. J. (1972). The preservation of some oceanic animals for lipid analysis. J. Fish. Res. Bd Can. 29: 1303–1307
- Nair, V. R., Devassy, V. P., Qasim, S. Z. (1980). Zooplankton and *Trichodesmium* phenomenon. Indian J. mar. Sci. 9: 1–6
- Naqvi, S. W. A., Hansen, H. P., Kureishy, T. W. (1986). Nutrient uptake and regeneration ratios in the Red Sea with reference to nutrient budgets. Oceanologica Acta 9: 271–276
- Owre, H. B., Foyo, M. (1964). Report on a collection of Copepoda from the Caribbean Sea. Bull. mar. Sci. 14: 359–372
- Parsons, T. R., Takahashi, M., Hargrave, B. (1977). Biological oceanographic processes, 2nd edn. Pergamon Press, Oxford
- Roehr, M. G., Moore, H. B. (1965). The vertical distribution of some common copepods in the Straits of Florida. Bull. mar. Sci. 15: 565–570
- Roman, M. R. (1978). Ingestion of the blue-green algae *Trichodesmium* by the harpacticoid copepod, *Macrosetella gracilis*. Limnol. Oceanogr. 23: 1245–1255
- Steedman, H. F. (1976). Examination, sorting and observation fluids. In: Steedman, H. F. (ed.) Zooplankton fixation and preservation. Monogr. on oceanogr. methodol. 4. Unesco Press, Paris, p. 182–183
- Thiel, H., Weikert, H., Karbe, L. (1986). Risk assessment for mining metalliferous muds in the deep Red Sea. Ambio 15: 34–41
- Tokioka, T., Bieri, R. (1966). Juveniles of *Macrosetella gracilis* (Dana) from clumps of *Trichodesmium* in the vicinity of Seto. Publ. Seto Mar. Biol. Lab. 14: 275–282
- Weikert, H. (1980). On the plankton of the central Red Sea. A first synopsis of results obtained from the cruises Meseda I and Meseda II. In: Proc of 'Symposium on the coastal and marine environment of the Red Sea, Gulf of Aden and tropical western Indian Ocean', Vol. III. Khartoum, January 9–14, 1980. The Red Sea & Gulf of Aden Environmental Programme, Jeddah, p. 135–167
- Weikert, H. (1982). The vertical distribution of zooplankton in relation to habitat zones in the area of the Atlantis II Deep, central Red Sea. Mar. Ecol. Prog. Ser. 8: 129–143
- Weikert, H., John, H.-C. (1981). Experiences with a modified Bé multiple opening-closing plankton net. J. Plankton Res. 3: 167–176

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