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Vertical structure of small metazoan plankton, especially non-calanoid copepods.
II. Deep Eastern Mediterranean (Levantine Sea)

Metazoan
Non-calanoid copepod
Oncaea
Levantine sea

Métazoaire
Copépode non-calanoïde
Oncaea
Mer Levantine

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ABSTRACT

The abundance and vertical distribution of micrometazoans sampled with fine nets of 0.05 mm mesh size were studied in different regions of the Eastern Mediterranean Sea down to a maximum depth of 1850 m. Significant east-west differences in biomass, total metazoan abundance and/or species composition of non-calanoid copepods were not recorded. The vertical gradient for total plankton biomass and abundance of major taxa was more or less consistent, showing no secondary maximum at intermediate water layers. The copepods were dominated by poecilostomatoids (genus *Oncaea*) which accounted for about 50 % of total copepod numbers in the water column. The greatest relative abundance of poecilostomatoids (up to 80 %) was found in the mesopelagic zone, at 100 m to 1050 m. In the epipelagic zone, calanoids were most numerous, however. In the bathypelagic zone below 1050 m depth, harpacticoids (*Microsetella* spp.) were next in abundance to poecilostomatoids. More than 56 non-calanoid species were recovered of which 28 belonged to the genus *Oncaea*. Dominant *Oncaea* species in the epi- and upper mesopelagic zone were *O. zernovi*, *O. ivlevi* and *Oncaea* sp. K. Below 450 m and down to the deepest stratum sampled *Oncaea longipes* and *Oncaea* sp. 1 were most abundant. No *Oncaea* species had its main population centre in the bathypelagic zone. The results are compared with published data on micrometazoans in other tropical oceans (*e.g.* Red Sea, Arabian Sea) and the absence of a true bathypelagic microcopepod fauna in the Eastern Mediterranean is discussed. Similar to the Red Sea, the dominance of individual species among non-calanoids appears to be less pronounced than that reported for calanoids in the meso- and upper bathypelagic zones of the Eastern Mediterranean.

RÉSUMÉ

Structure verticale des micro-métazoaires (copépodes non-calanoïdes) dans le bassin Levantin de la Méditerranée.

L'abondance et la distribution verticale des micro-métazoaires ont été étudiées dans des différentes régions de la Méditerranée orientale jusqu'à une profondeur de 1850 m. L'échantillonnage a été effectué avec des filets à plancton de 0,05 mm de vide de maille. En ce qui concerne la répartition de la biomasse, de l'abondance totale des métazoaires, et de la composition par espèces des copépodes non-calanoides, il n'existe aucune différence entre les secteurs est et ouest de la région étudiée. Le gradient vertical de la biomasse et de l'abondance des principaux groupes systématiques est plus ou moins régulier, n'ayant pas de maximum secondaire aux profondeurs intermédiaires. Les copépodes sont dominés par les poecilostomatoides (genre *Oncaea*), lesquels comprennent environ 50 % des copépodes de la colonne d'eau. L'abondance relative la plus importante des poecilostomatoides (jusqu'à 80 %) est trouvée dans la zone mésopélagique entre 100 m and 1050 m. Les calanoides sont quand même plus nombreux en zone épipélagique. Dans le zone bathypélagique au-dessous de 1050 m, les harpactioides (*Microsetella* spp.) sont secondes en abondance après les poecilostomatoides.

Au total, plus de 56 espèces et groupes systématiques non-calanoides ont été recueillis, dont 28 appartiennent au genre *Oncaea*. Les espèces principales d'*Oncaea* dans les zones épipélagique et mésopélagique supérieures sont *O. zernovi*, *O.ivlevi* et *Oncaea* sp. K. Au-dessous de 450 m jusqu'à la couche la plus profonde, *O. longipes* et *Oncaea* sp. 1 sont les plus abondantes. Aucune espèce d'*Oncaea* n'a sa population centrée principalement dans la zone bathypélagique. Les résultats sont comparés avec les données publiées sur les micro-métazoaires d'autres eaux tropicales (par exemple en Mer Rouge et en Mer d'Arabie), et l'absence d'une vraie faune bathypélagique de microcopépodes en Méditerranée orientale est discutée. De même qu'en Mer Rouge, la dominance d'espèces individuelles dans les zones mésopélagique et bathypélagique supérieures en Méditerranée orientale semble moins prononcée dans le cas des non-calanoides que ce qui est cité dans la littérature pour les calanoïdes.

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INTRODUCTION

Second to the Red Sea, the Eastern Mediterranean has the most extreme hydrographic conditions in the meso- and bathypelagic zone, characterized by a constant and relatively high temperature of 13.6 °C and a salinity of about 38.6 (*see* Malanotte-Rizzoli and Hecht, 1988, for a review). Consequently, a strong impoverishment of the deep-sea fauna is found in this area. Only a few true deep-sea species can survive the unusual environmental conditions (*e.g.* Băcescu, 1985) and they are only partly replaced by submerging mesopelagic species (Scotto di Carlo *et al.*, 1984; Gaudy, 1985; Weikert and Trinkaus, 1990).

Most previous studies on the quantitative composition of the deep sea plankton fauna in the Eastern Mediterranean were based on sampling with nets of mesh sizes equal to or larger than 0.2 mm (Trinkaus, 1988; Pancucci-Papadopoulou and Siokou-Frangou, 1988; Weikert, 1990; Weikert and Trinkaus, 1990; Scotto di Carlo *et al.*, 1991; Pancucci-Papadopoulou *et al.*, 1990, 1992; Weikert and Koppelmann, 1993), which cannot sample quantitatively the numerous microcopepods smaller than 1 mm in size. A few studies were conducted with somewhat finer nets of about 0.15 mm mesh size (Greze, 1963; Delalo, 1966; Greze *et al.*, 1982), but they considered mainly higher taxonomic categories and provided only qualitative aspects for some microcopepod species (*see* also Kimor and Wood, 1975).

Fine mesh-net studies (equal to or smaller than 0.1 mm mesh size) from other tropical oceanic regions, such as the Sargasso Sea, the Red Sea and the Arabian Sea, have shown that the microcopepod fauna is dominated by non-calanoid genera and species (Böttger, 1982, 1985; Böttger-Schnack, 1987, 1994; Cowles *et al.*, 1987). This is in contrast to the larger copepod size-fraction, where calanoids prevail. One important group within the microcopepod community is the poecilostomatoid genus *Oncaea*, which is presumably the most speciose taxon among marine pelagic microcopepods (Malt, 1983; Böttger-Schnack, 1994). Species of *Oncaea* have rarely been considered in marine plankton studies so far, due to the methodological difficulties in sampling and identifying these small species. Studies in the Red and Arabian Seas down to 1650 or 1850 m depth have provided first insights in the species composition and vertical distribution of the total *Oncaea* fauna in these areas (Böttger-Schnack, 1988, 1990 *a*, *b*, 1992, 1995, in press; Böttger-Schnack *et al.*, 1989). For the Red Sea, a comparison with published data on the species composition of calanoids in the mesopelagic zone suggested that the dominance of individual species within the *Oncaea* community was less pronounced than that reported for the (larger) calanoids, thereby indicating a higher diversity of the small species (Böttger-Schnack, 1988).

Compared to other regions of the world ocean, the number of microcopepod species in the Mediterranean Sea is quite well known. The list of copepod species provided by Kovalev and Shmeleva (1982) for the Mediterranean is the most comprehensive known from tropical/subtropical regions. Many small *Oncaea* species have first been described from the Adriatic Sea by Shmeleva (1966, 1968, 1969, 1979). Quantitative information on these small species, however, has only rarely been provided (Shmeleva, 1964) and the species composition in the easternmost parts of the Mediterranean is poorly understood altogether, except for the Lebanese waters (Malt *et al.*, 1989).

The present study reports on the qualitative and quantitative composition of small metazoans sampled with fine nets of 0.05 mm mesh size in different regions of the Eastern Mediterranean (Levantine Sea) down to a maximum depth of 1850 m. Special attention is paid to the species

Table 1

Sampling data of 0.055 mm mesh nets during METEOR Cruise 5 in the Eastern Mediterranean Sea.
*D = Day; N = Night; A = Abundance and taxonomic composition of metazoans; B = Biomass; * = 20 m intervals*

Region / Geographical position of research area		**Station no.**	**Date 1987**	**Time**	**Depth range sampled (m)**	**Total water depth (m)**	**Parameters investigated**
I. CRETE							
N	E						
34° 17’	25° 50’	1	14.1.	D	0- 450	4300	B
34° 30’	26° 30’	3 a	–”–	D	0- 250		B
		3 b	–”–	D	0- 100*		B
		21	17.1.	D	450-1850		A, B
		23	18.1.	D	0- 250		A, B
		25	–”–	N	0- 200*		B
		26	19.1.	N	250- 450		B
		31	20.1.	D	250- 450		A, B
		34	–”–	N	450-1850		A, B
		35	–”–	N	0- 450		A, B
		36 a	21.1.	N	0- 250*		B
		36 b	–”–	N	450-1850		B
II. CYPRUS							
N	E						
34° 08’	31° 57’	43	24.1.	N	0-450	2530	B
34° 07’	31° 55’	44	–”–	D	0-450		A, B
III. ISRAEL							
N	E						
32° 15’	33° 40’	52	27.1.	N	0-1050	1390	B
32° 35’	34° 08’	53	–”–	D	0- 100*		B
		54	–”–	D	0-1050		A, B

composition of non-calanoid copepods. Preliminary results on the microcopeod assemblage based on higher taxonomic categories (suborders, genera), have already shown that poecilostomatoid genus *Oncaea* constitutes an important part of the community, dominating especially in the meso- and bathypelagic zones (Böttger-Schnack, 1994). The results are compared with published data obtained by the same sampling device in other tropical oceanic areas, such as the Red Sea and the Arabian Sea (Böttger-Schnack, 1994, 1995, in press). By comparing the results with previously published data on the larger calanoid copepod fauna sampled simultaneously with nets of 0.3 mm mesh size (Trinkaus, 1988; Weikert and Trinkaus, 1990; Weikert and Koppelmann, 1993), differences in the dominance of individual species between the two size-fractions of copepods will be demonstrated.

MATERIAL AND METHODS

During METEOR Cruise 5 (MINDIK) zooplankton samples were taken in the Eastern Mediterranean Sea between January 14 and 27, 1987 (Weikert, 1988). The three research areas were located (I) SE off Crete, (II) SW off Cyprus and (III) near the coast of Israel (Fig. 1). A multiple opening-closing plankton net (Weikert and John, 1981) with a mouth area of 0.25 m^2 equipped with five nets of 0.055 mm mesh size was used to sample consecutive depth strata at vertical hauls down to a maximum depth of 1850 m. The depth of the net was determined by the length of the towing wire, the hauling speed was 0.5 m s^{-1}. A total of 11 vertical series were taken, at least one daytime and one night-time in each of the three areas (Tab. 1). The deep daytime series off Crete was composed of shorter profiles from different days (Stns. 21, 23 and 31). The samples off Cyprus covered the upper 450 m of the water column only. Samples were taken at 50 m intervals between 0 to 450 m, at 150 m intervals between 450 to 1050 m and at 200 m intervals between 1050 to 1850 m. In the top 100 or 200 m, three additional sampling series were taken at 20 m intervals (Tab. 1). No clogging of the net was observed; assuming a filtration efficiency of 100 %, the volumes filtered ranged between 5 m^3 (20 m intervals) to 50 m^3 (200 m intervals).

Plankton samples were fixed in a 4 % formaldehyde-sea water solution buffered with hexamethylenetetramine (2 % by weighing). The pH of the fixation fluid was regularly checked and ranged between 7 and 8. For sorting and further storage, samples were transferred into a preservation fluid containing 5 % propylene-glycol, 0.5 % propylene-phenoxetol and 94.5 % filtered sea water (Steedman, 1976).

Total plankton biomass was determined from all samples by wet weight measurements as described by Böttger (1982). Single large organisms > 1 cm (fishes, large crustaceans and single medusae) were weighed separately. For numerical abundance and taxonomic composition of metazoan organisms, the two deep sampling series (one daytime and one night-time each) taken down to 1850 m depth near Crete were evaluated and one daytime series each

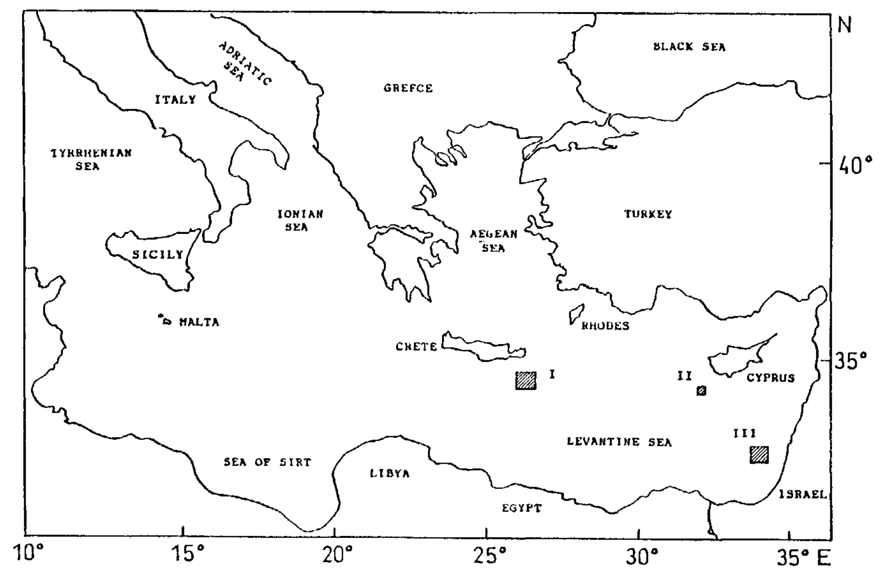

Figure 1

Location of plankton sampling areas in the Eastern Mediterranean Sea in January 1987. Area I = off Crete; Area II = off Cyprus; Area III = off Israel. (adapted from Weikert and Trinkaus, 1988)

from the two other subregions, covering the upper 450 m (Cyprus) or 1050 m (Israel) of the water column. Samples were divided into two size fractions by filtration through a 0.3 mm mesh gauze. In the fraction of larger organisms all individuals were counted, whereas for abundant smaller organisms only subsamples of *ca.* 500 to 1000 individuals were enumerated. For details of the subsampling methods see Böttger-Schnack (1985, 1990 *a*). Medium-sized species of non-calanoid copepods (between 0.6 and 0.8 mm body length) that were present in both size fractions as well as some of the less abundant small species were counted from total samples.

Quantitative analysis was carried out under a stereomicroscope at a magnification of 25 x to 75 x. Metazoan plankters were identified to major taxonomic groups (usually orders) and counts were made of four different size categories: < 0.2 mm, 0.2 - 0.4 mm, 0.4 - 1.2 mm, and > 1.2 mm. Among the Copepoda, nauplii and copepodids I - VI (including adults) were counted separately. Copepodids I - VI were usually separated into the six suborders Calanoida, Cyclopoida, Poecilostomatoida, Harpacticoida, Siphonostomatoida, and Mormonilloida following the classification of Huys and Boxshall (1991). A more detailed taxonomic analysis was carried out for the five non-calanoid copepod suborders, which were identified to genera and in many cases to species. Females, males, and in some cases, late juveniles, were counted separately. Of the Poecilostomatoida, all species of Oncaeidae and Sapphirinidae as well as species of the corycaeid genera *Agetus, Corycaeus, Farranula* and *Urocorycaeus* were identified. Several unidentified small species, belonging to the genera *Onychocorycaeus* and *Ditrichocorycaeus,* as well as the unidentified juveniles of all corycaeid genera were grouped under "*Corycaeidae* spp.". The group of unidentified sapphirinids and oncaeids, on the other hand, consists mainly of unidentified juveniles of the given species. The identification of *Oncaea* species was based on Shmeleva (1969), Malt (1983) and Böttger-Schnack and Boxshall (1990). Not all species of *Oncaea* have yet been identified and some of them are probably new; but being morphologically distinct they were all included as separate forms in the analysis. Of the Oithonidae, the genus *Paroithona* and the two smallest *Oithona* species, *O. nana* and *O. simplex,* were always counted separately, except for their smaller juvenile stages (< CIV), which are grouped together with the remaining *Oithona* species under "Oithonidae spp.". *Saphirella*-like copepods, which were distinguished according to Gooding (1988) and Itoh and Nishida (1991), were counted separately. Empty copepod exoskeletons, as well as specimens that displayed an advanced degree of internal disintegration (carcasses) were separated according to the criteria given by Wheeler (1967), Weikert (1977) and Böttger-Schnack (1990 *a*) and are not included in the abundance data.

Vertical profiles of temperature and salinity were measured with a CTD-system (Multisonde, ME, Kiel). Results are provided by Trinkaus (1988).

RESULTS

Environmental data

Hydrographic conditions in the Eastern Mediterranean during the sampling period in January 1987 (winter) were typical for the season (*see* Trinkaus, 1988, for a review of the literature). Near Crete, surface temperature and salinity were 16.5 °C and 38.7 and increased somewhat near Cyprus to 17.2 °C and 39.5, respectively (Fig. 2). Near Israel, temperature and salinity values were similar or slightly lower than those observed near Cyprus (*see* Weikert, 1988). A subsurface salinity maximum occurred at 150 to 200 m depth, which was most pronounced near Crete; it can be interpreted as a weak intermediate salinity maximum, which develops in the south-eastern part of the Levantine Sea during summer and autumn and spreads out to the west at a depth of 200 to 300 m (*e.g.* Wüst, 1960; Morcos and Moustafa-Hassan, 1976; Özsoy *et al.,* 1989).

The isothermal surface layer had a depth of about 30 to 60 m near Crete and about 80 m near Cyprus (Fig. 2) and Israel (Weikert, 1988). Below 200 m, temperatures decrea-

Table 2

Biomass (wet weight in g 1 m^{-2}) in different vertical zones of the Eastern Mediterranean Sea during January 1987. Values in brackets include the weight of single large organisms > 1 cm.

** = Depth range 0 – 200 m; ** = Sample 250 – 300 m missing; D = Day; N = Night; – = No data.*

Region / Station nos.	Depth (m)										
	0-100 m		100-250 m		250-450 m		450-1050 m		1050-1850 m		Total
	D	N	D	N	D	N	D	N	D	N	D+N
CRETE											
1	2.7	–	1.25 (2.3)	–	0.47	–	–	–	–	–	
3a	2.1	–	0.78	–	–	–	–	–	–	–	
3b	2.5	–	–	–	–	–	–	–	–	–	
21/23/31	1.7	–	1.2	–	0.50	–	1.3 (1.6)	-	0.42 (0.62)	–	
25	–	2.7 (3.4)	–	1.6	–	–	–	–	–	–	
26/36	–	2.4		1.9	–	0.58	–	1.7 (2.1)	–	–	
34/35	–	3.3		0.75	–	0.66	–	0.90	–	0.60	
Mean	2.2	2.8	1.1	1.4	0.49	0.62	1.3	1.3	–	–	
Total Mean	2.5		1.2		0.55		1.3		0.51		6.1
CYPRUS											
43	1.4	–	1.0	–	0.88	–	–	–	–	–	
44	–	1.9	–	1.4	–	0.46	–	–	–	–	
Total Mean	1.7		1.2		0.67		–		–		–
ISRAEL											
52	–	2.3 (2.4)	–	0.59	–	0.82	–	0.38 (0.58)	–	–	
53	2.0	–	–	–	–	–	–	–	–	–	
54	2.0 (2.1)	–	1.0	–	0.58	–	0.52	–	–	–	
Total Mean	2.1		1.0		0.70		0.45		–		4.1
Mean for all stations	2.2		1.15		0.60		1.0		0.51		5.5

sed by some two to three degrees Celsius down to 500 m depth, below which lies the homogeneous deep water mass of the Eastern Mediterranean, which is characterized by its constant temperature (13.6 °C) and salinity (*ca.* 38.65) (Malanotte-Rizzoli and Hecht, 1988). Oxygen concentrations were not determined during the present study, but according to Weikert and Trinkaus (1990), neither abrupt gradients nor a well-developed oxygen minimum zone have so far been reported from the Eastern Mediterranean (*cf.* Pollack, 1951; Malanotte-Rizzoli and Hecht, 1988).

Vertical distribution of biomass and total metazoan abundance

Total plankton biomass averaged 5.5 g wet weight beneath 1 m^2 in the 1850 m water column (Tab. 2). Within the upper 450 m, regional differences between the three regions were not indicated by the present data. In the 450 to 1050 m depth layer, however, biomass values were lower by one-half in the easternmost part (Israel) as compared to the west (Crete) (Tab. 2). Night-time biomass values in the upper 100 m tended to be higher than those taken during the day, indicating some diurnal vertical movement of zooplankton from deeper layers, but the ranges of values from day and night overlapped (Tab. 2, Fig. 3). The abundance of micrometazoans in the 1850 m water column averaged 180000 individuals beneath 0.25 m^2 (Tab. 3). As for biomass, no obvious differences in abundance and vertical distribution between day and night and between the three regions were indicated within the upper 450 m (Fig. 4, Tab. 3). Maximum concentrations of plankton biomass and metazoan numbers were always found in the uppermost

Table 3

Abundance of total metazoans (individuals beneath 0.25 m^2) in different vertical zones of the Eastern Mediterranean Sea.
D = Day, N = Night; – = no data

Region	Time	Depth (m)					Total
		0-100	100-250	250-450	450-1050	1050-1850	0-1850
Crete	D	110 000	27 000	20 000	23 000	2 800	
	N	100 000	34 000	17 500	15 000	3 300	
Cyprus	D	88 000	40 500	17 000	–	–	
Israel	D	110 000	70 000	14 000	9 400	–	
Mean		100 000	42 000	17 000	16 000	3 050	180 000
Percentage distribution		56	24	9.5	8.9	1.7	100

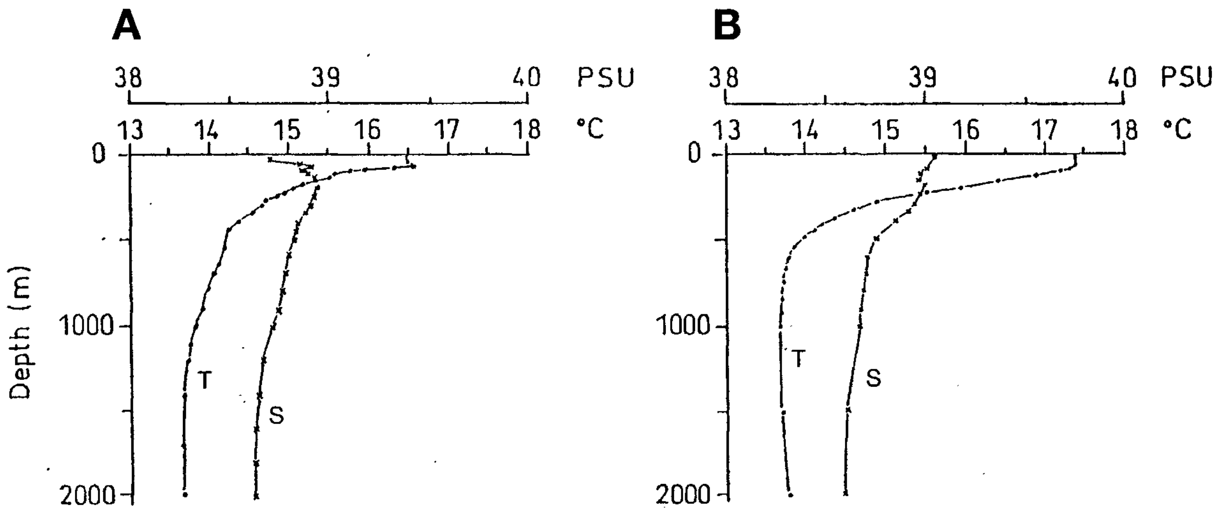

Figure 2

Vertical profiles of temperature (T) and salinity (S) in the Eastern Mediterranean off Crete (A) and off Cyprus (B). (adapted from Trinkaus, 1988)

depth stratum, 0 to 50 m, accounting on average for 30 mg wet weight m^{-3} and 5000 individuals m^{-3} (Figs. 3, 4). Below the upper 50 m, concentrations decreased more or less constantly by two and three orders of magnitude to minimum values of less than 0.5 mg m^{-3} and *ca.* 10 individuals m^{-3} for biomass and for metazoan numbers, respectively, at all depth layers below 1200 m. Between 200 and 600 m, the vertical gradient in biomass and numbers was less pronounced and in some cases (Israel) a strong variation between adjacent depth layers was found, but no secondary maximum became apparent in this depth layer (Fig. 3, 4). The size composition of micrometazoans showed a decrease in the proportion of smallest organisms < 0.2 mm with increasing depth, whereas the proportion of organisms in the largest size class (> 1.2 mm) tended to increase (Tab. 4).

On average, the top 450 m of the water column contained 72 % of the plankton biomass and 90 % of the total numbers of micro- metazoans. The bathypelagic zone below 1050 m, on the other hand, contained 9 % of plankton biomass, but only < 2 % of the total number of metazoans.

Composition and vertical distribution of metazoan taxa

Copepoda were the dominant group accounting for more than 90 % of the total number of metazoans in the 1850 m water column (Tab. 5). Nauplii and copepodids I-VI (including adults) were present in similar proportions in the upper 100 m, but with increasing water depth the percentage of nauplii declined considerably (Tab. 5), particularly in the size class < 0.2 mm. Appendicularians were second in abundance, accounting for 2 % to 4 % of the total numbers in the 1850 m water column. Molluscs and ostracods ranked next. The vertical gradient by numbers between the upper 100 m and the adjacent 100-250 m depth layer was most pronounced for molluscs (by a factor of 20) as well as for appendicularians, chaetognaths, copepod nauplii, and salps (by a factor of 5 to 8). As for total metazoans (Fig. 4), no secondary maximum was observed in the mesopelagic zone for any of the major taxa. The group "other crustaceans" consisted of larval and adult euphausiids, amphipods, cryptoniscid isopods and decapods. Decapods were numerically dominated by penaeid nauplii and zoea larvae, which were especially abundant between 750 to 1450 m. The group "other metazoans" consisted mainly of fish larvae, individual turbellarians as well as some totally unidentified small larval forms. In the mesopelagic zone, between 450 and 750 m, the gonostomatoid fish *Cyclothone braueri*, a common mesopelagic species, occurred quite regularly in the samples, accounting for most of the biomass of large organisms in that layer (*see* Tab. 2).

Table 4

Size composition of micrometazoans in different vertical zones of the Eastern Mediterranean. Percentage values of four different size groups of the total numbers (see Table 3) in a given depth layer.

$\bar{x}$ = weighted mean; R = Range; N = number of sampling series

Depth (m)	Size range:	< 0.2 mm		0.2-0.4 mm		0.4-1.2 mm		> 1.2 mm	
	N	$\bar{x}$	R	$\bar{x}$	R	$\bar{x}$	R	$\bar{x}$	R
0-100	4	55	51-59	31	27-38	13	11-16	0.75	0.6-1.0
100-250	4	42	33-47	45	33-50	12	11-13	1.3	0.9-1.4
250-450	4	33	28-36	53	52-55	13	11-15	1.2	0.8-1.6
450-1050	3	32	30-33	57	55-58	9.2	7.8-11	1.7	0.8-2.0
1050-1850	2	31	30;31	54	49;58	13	9.3;18	2.0	1.1-3.0

Taxonomic composition and vertical distribution of copepods, especially non-calanoids

The microcopepod fauna was dominated by poecilostomatoids, which accounted for between 40 % and 50 % of the total number of copepods in the 1850 m water column (Tab. 6). Calanoids accounted for about 25 % of all copepods, with cyclopoids, harpacticoids and mormonilloids ranking next. Siphonostomatoids, represented by *Pontoeciella abyssicola*, occurred as solitary finds only. The group "Copepoda varia" includes some very small juvenile forms of uncertain taxonomic status.

The copepod composition changed considerably according to water depth (Tab. 7). In the epipelagic zone (0 to 100 m), calanoids and poecilostomatoids were most abundant, accounting on average for 44 % and 34 % of all copepods; cyclopoids and harpacticoids ranked next. In the upper and lower mesopelagic zone, between 100 and 1050 m, poecilostomatoids dominated, accounting for 50 % to 80 % of all copepods. The relative importance of mormonilloids was highest in the 250 to 450 m depth layer, where they contributed 12 % to total copepod density. In the bathypelagic zone, at 1050 to 1850 m, poecilostomatoids remained dominant, but harpacticoids increased significantly in relative importance (Tab. 7).

A total of 56 non-calanoid species were identified during the present study (Tab. 8 *a*, 8 *b*). The number of species could have been higher, had all species of oithonids and corycaeids been identified. The greatest number of species, 28, was found in the genus *Oncaea*, which accounted for one-half of all species identified. The vertical distribution patterns of non-calanoid species differed only little between day and night and between the three regions investigated (Figs. 5, 6). Thus, the community structure of non-calanoids, given for five different vertical layers was similar at all stations and in all regions investigated. This is examplified in Table 9, presenting individual results for dominant poecilostomatoid species. The pooled data are listed for each depth layer in Table 8 *a* and 8 *b*.

Poecilostomatoida

Oncaeids accounted for between 92 % and 99 % of the total numbers of poecilostomatoids in the different vertical layers (Tab. 8 *a*). Corycaeids and sapphirinids were mainly confined to the epipelagic zone. Of the 28 distinguishable *Oncaea* species, eight could not be assigned to any of the described *Oncaea* species and may possibly be new to science. Two of them, *Oncaea* sp. K and *Oncaea* "ivlevi/K", are also known from the Red Sea and were morphologically characterized by Böttger-Schnack (1992, 1995). For the remaining six unidentified *Oncaea* species, a short morphological diagnosis of the females and sizes of both sexes are given in Table 10. However, in some cases, these morphological characteristics did not allow for separation of *Oncaea* sp. 5 and sp. 6, and consequently they were partly counted together in a single group (*Oncaea* sp. 5 + 6, *see* Tab. 8 *a*).

Dominant species in the 1850 m water column were *Oncaea zernovi* and *Oncaea* sp. 1, accounting on average for 12 % and 9 %, respectively, of total poecilostomatoid numbers (Tab. 8 *a*). Other abundant species, each accounting for more than 1 % of total poecilostomatoid density were (in order of decreasing abundance) *O. ivlevi*, *O. longipes*, *O. ovalis* + *bathyalis*, *Oncaea* sp. K, *O. vodjanitskii*, *O. tregoubovi*, *O. mollicula*, *O. minor* and *Oncaea* sp. 5.

Of the 28 *Oncaea* species recorded, 13 were concentrated mainly in the upper 100 m or 250 m and can be regarded as epipelagic in the broad sense. Except for *Oncaea zernovi* and *O. media* f. *minor*, however, all epipelagic species had their main population centre below the uppermost (0-50 m) depth layer (Fig. 5). Six *Oncaea* species occurred primarily in the upper mesopelagic zone, between depths of 200 m and 450 m and three species were concentrated in the lower mesopelagic zone, at 450 to 1050 m (*Oncaea longipes*,

Table 5

Mean abundance (individuals beneath 0.25 m^2) of major metazoan taxa in different vertical zones of the Eastern Mediterranean Sea. N = number of sampling series

Depth (m)	0-100	100-250	250-450	450-1050	1050-1850	Total 0-1850
N	(4)	(4)	(4)	(3)	(2)	
Copepodids I-VI	42500	26000	13000	14000	2000	97000
Copepod nauplii	54500	15000	3700	3800	810	77000
Medusae	19	20	9	2	2	52
Siphonophores	50	14	4	3	1	70
Ostracods	460	280	140	90	51	1000
Other Crustaceans	60	32	16	85	64	255
Molluscs	1100	74	41	23	26	1300
Appendicularians	4000	900	150	72	30	5200
Salps	23	4	0	0	2	30
Chaetognaths	200	45	23	11	3	290
Polychaetes	100	82	64	43	25	310
Other metazoans	11	28	34	27	8	110
Total metazoans	100000	42500	17000	18000	3050	180000

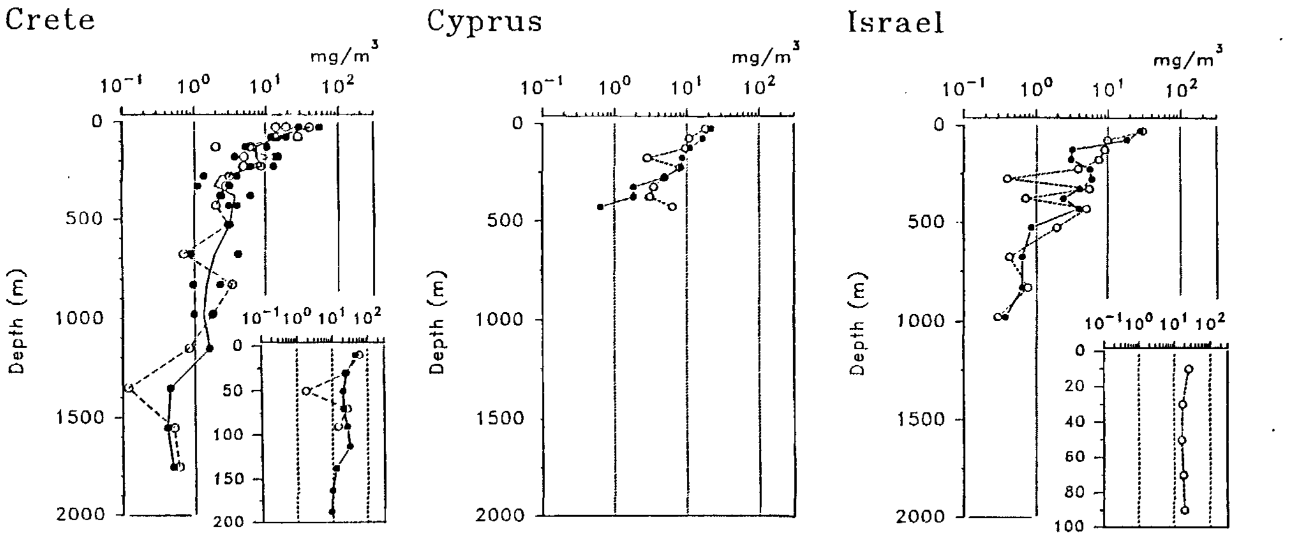

Figure 3

Vertical distribution of total plankton biomass (wet weight) in different regions of the Eastern Mediterranean. Open symbols = daytime samples, solid symbols = night-time samples. Note the logarithmic scale.

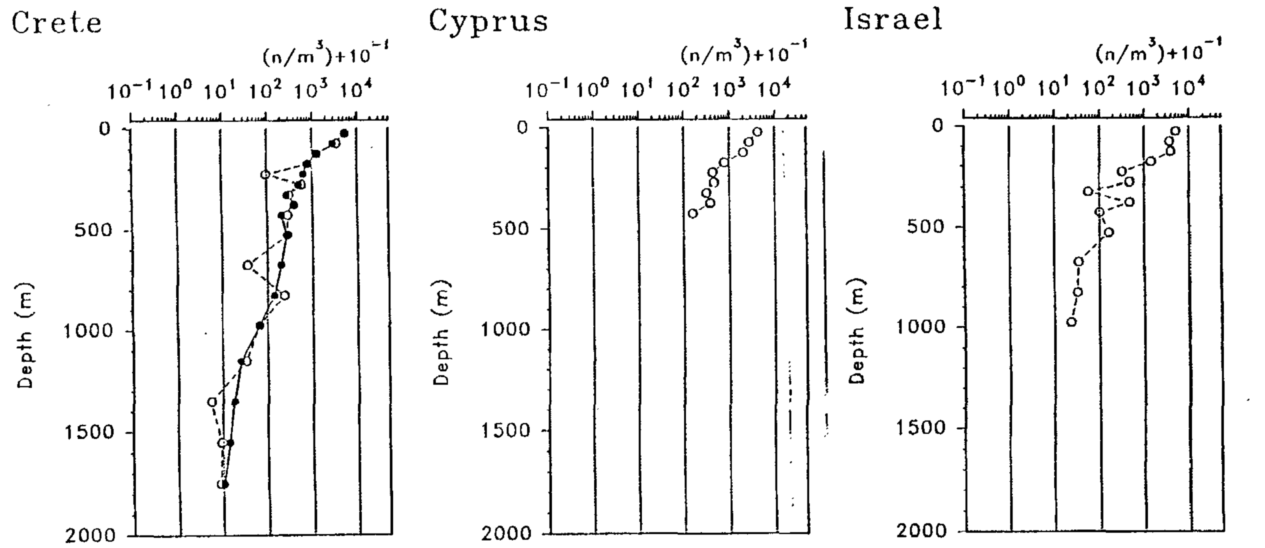

Figure 4

Vertical distribution of total metazoan numbers in different regions of the Eastern Mediterranean. Symbols as in Figure 3.

Oncaea sp. 1 and *Oncaea* sp. 7). The remaining six species, including the combined group of *O. ovalis* + *bathyalis*, had a broad vertical range, covering two or more habitat zones. No *Oncaea* species had population centres in the bathypelagic zone, below a depth of 1050 m (Tab. 8 *a*; Fig. 5).

The quantitative composition of poecilostomatoids differed considerably between depth strata (Tab. 8 *a*). In the epi- and upper mesopelagic zones (0 - 450 m) *O. zernovi* was dominant, accounting for 11 to 16 % of total poecilostomatoid numbers. In the upper 250 m, *O. ivlevi* was secondmost abundant, but it decreased rapidly below that depth. Other important poecilostomatoids in the epipelagic zone (0 - 100 m) were three *Oncaea* species and *Farranula rostrata*, each accounting for more than 1 % of total poecilostomatoids. In the 250 to 450 m depth layer, *Oncaea* sp. K was similar in abundance to *O. zernovi.* Eight other *Oncaea* species each contributed more than 1 % to total poecilostomatoids in that layer (Tab. 8 *a*). Of these, *O. mollicula*, *O. ovalis* + *bathyalis*, and *O. tregoubovi* were the most important.

In the lower mesopelagic zone (450 - 1050 m), the species composition of poecilostomatoids changed substantially. *Oncaea* sp. 1 was highly dominant, accounting on average for 36 % of total poecilostomatoids (Tab. 8 *a*). Secondmost abundant was *O. longipes* (18 %). Another 6 *Oncaea* species each accounted for more than 1 % of total poecilostomatoid numbers in that layer. In the bathypelagic zone (1050 - 1850 m), *O. longipes* and *Oncaea* sp. 1 remained

Table 6

Composition of copepods by suborders (% = percentage of the total numbers) in different regions of the Eastern Mediterranean Sea.

D = Day; N = Night; n = total number of copepods beneath 0.25 m²

Region	Crete		Cyprus	Israel
	D	N	D	D
Depth (m)	0-1850	0-1850	0-450	0-1050
n	95 000	100 000	76 000	95 000
%				
Calanoida	26	25	27	30
Cyclopoida	12	13	16	15
Poecilostomatoida	51	51	40	46
Siphonostomatoida	-	0.01	0.01	< 0.01
Harpacticoida	8.0	8.0	15	5.1
Mormonilloida	3.7	3.3	2.4	3.1
Copepoda, varia	0.16	0.34	0.23	0.5

the dominant species, but their ranks changed. The relative abundance of *O. longipes* was similar to that in the overlying depth layer, whereas that of *Oncaea* sp. 1 decreased greatly. Maximum concentrations of both species in the bathypelagic zone occurred in the uppermost part, at 1050 - 1250 m (Fig. 5). Another ten *Oncaea* species had relative abundances of more than 1 % of total poecilostomatoids each in the bathypelagic zone (Tab. 8 *a*). The occurrence of epipelagic species, such as *O. ivlevi*, in the deep samples has to be interpreted with caution, however, since a possible contamination of the nets cannot be excluded for these very small species.

Cyclopoida

Paroithona was the dominant cyclopoid genus, accounting for 40 % of total cyclopoid numbers in the 0 to 1850 m water column (Tab. 8 *b*). If the smaller, unidentified juvenile stages of this genus had been included, the density would have been even higher. Due to difficulties in species discrimination (Nishida and Marumo, 1982; Ferrari and Böttger, 1986) *Paroithona* spp. were not identified. It is conceivable that several species were sampled since at least two species, *P. parvula* and *P. pulla*, have been reported from the Eastern Mediterranean (Delalo, 1966; Kovalev and Shmeleva, 1982). The main part of the *Paroithona* spp. population was concentrated in the lower epi- or uppermost mesopelagic zone, at 100 to 250 m (Table 8 *b*), but considerable numbers were found even down to 600 m depth (Fig. 6). As a consequence, the relative importance of *Paroithona* spp. increased strongly with depth, from about 20 % of total cyclopoids in the epipelagic zone to over 40 % and up to 90 % in the deepest zones. Of the two *Oithona* species investigated, *Oithona simplex* was far more abundant than *O. nana*, contributing about 6 % to total cyclopoids. Both *Oithona* species were mainly confined to the upper 250 m (Tab. 8 *b*), but maximum concentrations of *O. simplex* occurred deeper than those of *O. nana* (Fig. 6).

Harpacticoida

Harpacticoid copepods consisted almost exclusively of *Microsetella* spp., which had maximum concentrations in the upper 250 m (Tab. 8 *b*) and decreased rapidly by about one order of magnitude between 250 and 350 m (Fig. 6). Below 500 m, they were present in fairly constant concentrations down to 1250 m depth, and showed only slight reductions in the deeper layers. The remaining five harpacticoid species occurred as solitary finds. Of these, *Euterpina acutifrons* and *Distioculus minor* (formerly *Miracia minor*, see Huys and Böttger-Schnack, 1994) were found only in the easternmost region near Israel.

Mormonilloida

Of the two *Mormonilla* species known (Boxshall, 1979), only one, *M. minor*, occurred in the area studied. The

Table 7

Mean abundance (individuals beneath 0.25 m²) of copepod suborders in different vertical zones of the Eastern Mediterranean Sea, and abundance of copepod carcasses.

N = number of sampling series

Depth (m)	0-100	100-250	250-450	450-1050	1050-1850	Total 0-1850
N	(4)	(4)	(4)	(3)	(2)	
Calanoida	19000	3900	1200	940	240	25000
Cyclopoida	5300	5400	1500	670	90	13000
Poecilostomatoida	15000	13000	7800	11000	1000	47000
Siphonostomatoida	2	3	< 1	0	0	5
Harpacticoida	3600	2700	800	840	540	8500
Mormonilloida	29	840	1500	660	130	3100
Copepoda, varia	150	62	19	67	20	320
Total Copepods	42500	26000	13000	14000	2000	97000
Copepod carcasses	3400	3750	3700	4500	1400	17000

population consisted mainly of juveniles and females, whereas males were very rare (Tab. 8 *b*). Juvenile and male *Mormonilla* have not been recorded until very recently from tropical marine areas (Huys *et al.* 1992; Böttger-Schnack, 1995, in press), which can be ascribed to inadequate sampling methods. The main population core of *M. minor* in the Eastern Mediterranean was situated between 200 and 450 m (Fig. 6). In this depth layer mormonilloids also had their maximum relative abundance to the total copepod community (Tab. 7).

Copepod carcasses

Empty copepod exoskeletons and carcasses are not included in the abundance data presented above, but were counted from the samples at the same time as the living fraction. The relative proportion of carcasses and empty exoskeletons increased with depth. They contributed about 10 % of all copepods in the epipelagic zone, but 20 and 40 % respectively in the meso- and bathypelagic zones below 250 m depth (Tab. 7). Table 11 lists the proportion of dead copepods to the total number of dead and living individuals for selected non-calanoid species and genera. Species not listed in this table were found as living individuals only or were very rare. Many of the numerically dominant species in the different vertical depth zones, such as *Oncaea* sp. 1, *O. ivlevi*, *O. ivlevi*/K, *O. longipes* and *O. tregoubovi*, had high proportions of dead individuals, which on average accounted for 20 to 40 % of all individuals for a given species. Dominant species exhibiting a low proportion of dead individuals were *Oncaea* sp. 7 and *Farranula rostrata.*

DISCUSSION

Biomass and metazoan abundance

The vertical gradient in total plankton biomass (wet weight) found during the present study was significantly less pronounced than that of total metazoan density. On average, only 60 % of total biomass was concentrated in the upper 200 m and a considerable proportion was found in the lower mesopelagic and the bathypelagic zones (20 and 10 %, respectively). The corresponding values for total metazoan abundance were only 4.5 % and 1.5 % for these two strata. A possible explanation for this discrepancy may be a general increase in the size of plankton organisms with depth, as has been suggested by Trinkaus (1988) for the Eastern Mediterranean, based on 0.3 mm mesh net samples (*see* also Scotto di Carlo *et al.*, 1984). For the micrometazoans investigated during the present study the proportion of larger organisms (> 1.2 mm) in fact increased with depth: they contributed 0.6 % to the total metazoan density in the epipelagic zone, but over 1 % and up to 3 % in the meso- and bathypelagic zones, respectively. Another important point worth considering is the amount of dead copepods (carcasses) and empty exoskeletons, which were included in the biomass measurements, but not in the abundance data. As the proportion of dead individuals strongly increases with depth (Tab. 7; *see* also Pancucci-Papadopoulou *et al.,* 1992), biomass values from deeper layers might be grossly overestimated compared to those from shallower depths.

Comparable data on the abundance and vertical distribution of micrometazoans are not available for the Eastern Mediterranean Sea. Comparison with larger zooplankton organisms sampled simultaneously with 0.3 mm mesh nets (MOCNESS with 1 m^2 opening area) in the area off Crete (Trinkaus, 1988; Weikert and Trinkaus, 1990) shows that the abundance of small metazoans is 30 times higher (average for the 0 to 750 m depth layer). This ratio is similar to values reported for these two mesh sizes in other marine areas (Gordeyeva, 1970; Böttger, 1987). The biomass values of the fine-mesh net plankton in the upper epipelagic zone (0-100 m: 2.5 g wet weight beneath 1 m^2) were similar to those obtained with the larger mesh size (2.2 g beneath 1 m^2, Weikert and Trinkaus, 1990). In the lower epi- and mesopelagic zones (100 - 750 m), however, the biomass obtained by the smaller mesh nets was lower by a fact of two compared to the larger mesh size. In this depth zone, no secondary zooplankton maximum was observed for micrometazoans, which contrasts the results of Weikert and Trinkaus (1990). According to Trinkaus (1988), the secondary maximum of zooplankton at intermediate layers was mainly caused by a large calanoid copepod, *Eucalanus monachus,* which might not have been sampled quantitatively by the small mesh size used during the present study. In fact, the numbers of *Eucalanus* spp. (mainly *E. monachus*) sampled simultaneously in the 1850 water column off Crete were much lower in the fine-mesh nets (day: 1800 , night: 1640 individuals per 1 m^2) as compared to the large-mesh nets (5000 and 4800 individuals per 1 m^2, respectively; Weikert and Trinkaus, 1990). Beside the different mesh sizes used for the two studies, this discrepancy may be explained by the different sampling strategies (sampling gear, hauling type and speed, filtered volume).

Regional differences in plankton biomass or metazoan abundance and composition between the western and eastern parts of the Levantine Sea were not evident during the present study. This is in concordance with previous results on zooplankton and phytoplankton densities in this area Pasteur *et al.,* 1976; Pancucci-Papadopoulou and Anagnostaki, 1989; Pagou and Gotsis-Skretas, 1990). It is also in agreement with Gaudy (1985), who compared the total numbers of mesozooplankton organisms (mesh size 0.2 mm) from different regions in the Mediterranean and did not record a general west east trend calculated on a yearly average. The results contrast, however, with previous results of Trinkaus (1988), who reported a reduction of plankton abundance from the west (Ionian Sea) to the east (Cyprus) for larger zooplankton sampled with 0.3 mm mesh size. The author states, that between Crete and Cyprus, the decrease in total zooplankton was mainly brought about by a strong reduction in *Eucalanus* (mainly *E. monachus*) numbers in mesopelagic layers (450 - 900 m). The conspicuous dominance of *E. monachus* off Crete has been attributed to the occurrence of local eddies occurring in that area (Weikert and Koppelmann, 1993). During the present study, plankton samples off Cyprus

Table 8*a*

Taxonomic composition of non-calanoid copepods in different vertical zones of the Eastern Mediterranean Sea. Completely identified species are listed in alphabetical order; putative species and species groups are given subsequently.

Abbreviations are: n = individuals beneath 0.25 m^2; N = number of sampling series; F = Females, M = Males, 1 = Late juveniles; 2 = Early juveniles, 3 = Various juveniles.

Depth (m) N	Sexes/ Stages	0-100 (4) n	100-250 (4) n	250-450 (4) n	450-1050 (3) n	1050-1850 (2) n	TOTAL 0-1850 n
POECILOSTOMATOIDA							
Oncaeidae							
Oncaea conifera	FM	4.5	8.5	5.0	6.3	0	24
O. dentipes	FM	270	41	10	0	0	325
O. ivlevi	FM	1800	1800	62	40	24	3750
O. longipes	FM	18	56	100	1900	180	2300
O. media f. *minor*	FM	240	46	5.3	3.0	0	290
O. media f. *major*	F(M)	7.3	1.3	0	0	0	8.5
O. mediterranea	FM	76	13	3.0	5.3	2.0	99
O. minima	FM	0	300	16	17	6.0	340
O. minor ?	FM	32	640	21	16	22	730
O. minuta	F	9.3	24	4.0	4.0	0	41
O. mollicula	FM	32	92	690	11	20	840
O. ornata	FM	0	1.8	12	35	2.5	51
O. ovalis+bathyalis	FM	44	650	585	760	48	2100
O. shmelevi	FM	0	4.8	25	34	2.0	66
O. similis	F	1.3	4.8	8.8	14	0	29
O. subtilis	FM	110	0	13	2.7	4.0	130
O. tregoubovi	FM	0	250	530	470	28	1300
O. umerus	FM	29	53	4.5	2.7	0.5	89
O. vodjanitskii	FM	770	850	54	24	12	1700
O. zernovi	FM	2400	2500	850	140	61	5900
Oncaea "ivlevi/K"	FM	0	350	5.0	9.3	10	380
Oncaea sp. K	FM	16	830	890	13	50	1800
Oncaea sp. 1	FM	2.0	16	360	4000	76	4400
Oncaea sp. 4	F	4.5	28	2.0	4.0	0	39
Oncaea sp. 5	FM	0	56	280	300	26	665
Oncaea sp. 6	FM	2.0	74	170	91	33	370
Oncaea sp. 5+6	FM	1.0	20	0	16	4.0	41
Oncaea sp. 7	FM	3.0	2.0	68	320	8.0	400
Oncaea sp. 8	F	15	100	33	4.0	0	160
Oncaea minuta+sp. 8	M	28	100	18	1.3	0	150
Oncaea spp.	(FM)3	7700	4000	3000	2600	390	18000
Lubbockia aculeata	1	0	0	0.3	0	0	0.3
L. minuta	F	0	0.3	0.5	0	0	0.8
L. petersoni	FM	0	1.3	7.0	2.0	0	10
L. squillimana	FM1	9.5	3.0	0.5	0.3	0	13
L. spp.	(F)2	21	29	11	13	0	73
Total		14000	13000	7800	11000	1000	46500
Corycaeidae							
Agetus flaccus	FM	2.0	0.3	0	0	0	2.5
A. limbatus	FM	16	2.0	0.3	0	0	18
A. typicus	FM	26	1.5	0.3	0	0	28
Corycaeus clausi	F	1.3	0	0	0	0	1.3
Farranula rostrata	FM	280	2.5	2.0	12	0.5	300
Urocorycaeus furcifer	FM	4.0	2.8	1.3	0.7	0.5	9.2
Corycaeidae spp.	FM3	620	36	2.8	6.3	0	660
Total		950	45	6.8	19	1.0	1000
Sapphirinidae							
Copilia mediterranea	FM	0	0	0.3	1.0	0	1.3
C. mirabilis	FM	0.5	0.3	0	0	0	0.8
Sapphirina auronitens	F	0	0.3	0	0	0	0.3
S. metallina	FM	11	1.3	0.3	0.3	0	13
Sapphirina sp.	FM	1.5	2.3	0	0	0	3.8
Vettoria granulosa	FM	10	12	1.5	1.7	0	25
V. longifurca	FM	0	0	0	0.3	0	0.3
V. parva	FM	20	21	0.8	0	0	42
Vettoria sp.	3	2.0	14	4.5	5.3	4.0	30
Total		44.5	51	7.3	8.6	4.0	116
Unidentified poecilostomatoids	3	18	22	6.0	0	9.0	55
TOTAL POECILOSTOMATOIDA		15000	13000	7800	11000	1000	47500

Table 8*b*

Taxonomic composition of non-calanoid copepods in different vertical zones of the Eastern Mediterranean Sea. Completely identified species are listed in alphabetical order; putative species and species groups are given subsequently.

Abbreviations are : n = individuals beneath 0.25 m^2*; N = number of sampling series; F = Females; M = Males; 1 = Late juveniles; 3 = Various juveniles*

Depth (m)		**0-100**	**100-250**	**250-450**	**450-1050**	**1050-1850**	**TOTAL 0-1850**
N		**(4)**	**(4)**	**(4)**	**(3)**	**(2)**	
		n	**n**	**n**	**n**	**n**	**n**
CYCLOPOIDA							
Oithona simplex	FM1	500	260	30	1.3	4	790
O. nana	FM1	99	16	0	0	0.5	120
Paroithona spp.	FM1	1000	2400	1000	600	38	5100
Oithonidae spp.	FM3	3650	2700	450	65	39	6900
Saphirella-like	3	18	22	6	0	9	55
TOTAL		5300	5400	1500	670	90	13000
SIPHONOSTOMATOIDA							
Pontoeciella abyssicola	FM3	1.8	3.3	0.3	0	0	5.3
HARPACTICOIDA							
Clytemnestra rostrata	FM3	1.0	0.3	0.5	2.7	0.5	4.9
C. scutellata	FM	1.3	0.8	0	0	0	2.0
Distioculus minor	F	0.3	0	0	0	0	0.3
Euterpina acutifrons	FM3	5.3	0	0	1.3	0	6.6
Macrosetella gracilis	FM	0.5	1.0	0	0	0	1.5
Microsetella spp.	FM3	3600	2700	800	840	540	8500
TOTAL		3600	2700	800	840	540	8500
MORMONILLOIDA							
Mormonilla minor	F	4.8	96	430	215	60	800
	M	0	9.0	6.5	3.0	0	19
	3	24	730	1050	440	70	2300
TOTAL		29	840	1500	660	130	3100

covered only the upper 450 m of the water column, and thus the stock of *Eucalanus* was missed in that area.

Comparison with published data on small-mesh net plankton in various tropical and subtropical regions shows that biomass values in the Eastern Mediterranean were in the same order of magnitude as those recorded in the southern, less productive part of the Sargasso Sea (Böttger, 1982; multiple opening-closing net, mesh size 0.1 mm, 0 - 200 m). Similarly, micrometazoan abundances in the Eastern Mediterranean were in the upper range of values found in the southern Sargasso Sea (Böttger, 1982; Apstein net, mesh size 0.05 mm, 0 - 100 m). Compared to data from the Red Sea and Arabian Sea sampled by the same sampling device (Böttger-Schnack, 1995, in press) values of plankton biomass and micrometazoan abundance in the upper 100 m in the Eastern Mediterranean were only half as high as those found in the less productive central part of the Red Sea and up to one order of magnitude lower than in the Arabian Sea. This confirms the oligotrophic conditions of the Eastern Mediterranean, which have been reported on before by several authors (Furnestin, 1979; Weikert and Trinkaus, 1990; Pancucci-Papadopoulou *et al.*, 1992). In the three mesopelagic zones between 100 and 1050 m, however, zooplankton numbers and biomass in the Eastern Mediterranean Sea were similar or even higher than those in the Arabian Sea, where the extremely low oxygen concentrations cause a strong reduction of the zooplankton fauna (Böttger-Schnack, 1994, in press). Compared to the mesopelagic zone in the Red Sea (Böttger-Schnack, 1995), on the other hand, biomass values were lower by one-half in the Eastern Mediterranean, whereas the abundance of micrometazoans was similar in both areas. Below 1050 m, biomass and abundance values in the Eastern Mediterranean are again much lower as compared to the Arabian Sea, due to the unusual increase in zooplankton below the oxygen minimum in this latter area, the causes of which have been discussed by Böttger-Schnack (1994). For the Red Sea, no corresponding data on deep-sea micrometazoans are yet available. Preliminary data obtained by one single vertical profile down to 1650 m depth in the Red Sea (Böttger-Schnack, unpublished data) exhibited only very low micrometazoan abundances, similar to those from the Eastern Mediterranean. In this respect, the abundance and vertical distribution of total micrometazoans in the Eastern Mediterranean show a great similarity to the Red Sea, but differ considerably from the Arabian Sea, where the large oxygen minimum zone causes an unusual distribution pattern of the zooplankton fauna.

Species of *Oncaea*

Twenty-eight *Oncaea* species were found in the Eastern Mediterranean Sea during the present study. The number of species is higher than has been reported so far in the literature for this area. Kovalev and Shmeleva (1982) listed a total of 37 *Oncaea* species for the entire Mediterranean Sea, only twelve of which were represented in the easternmost part (Levantine Sea). Malt *et al.* (1989) studied the yearly cycle of the *Oncaea* fauna near the Lebanese coast down to 600 m depth and found a total of 18 *Oncaea* species, several of which were represented by solitary finds, however. Of the 20 *Oncaea* species named during the pre-

Table 9

Poecilostomatoid species percentages of the total number of pecilostomatoids per 0.25 m² in different vertical layers of the Eastern Mediterranean Sea. Only the most abundant 6 to 8 species are listed.

—— = no data; D = Day; N = Night.

Depth Zone	**Region**							
	Crete (D)		**Crete (N)**		**Cyprus (D)**		**Israel (D)**	
0 – 100 m		%		%		%		%
	Oncaea zernovi	18	*Oncaea ivlevi*	20	*Oncaea zernovi*	13	*Oncaea zernovi*	17
	O. ivlevi	12	*O. zernovi*	16	*O. ivlevi*	11	*O. ivlevi*	6.4
	O. vodjanitskii	3.0	*O. vodjanitskii*	10	*O. vodjanitskii*	7.4	*O. dentipes*	2.9
	O. dentipes	1.5	*Farranula rostrata*	3.2	*O. dentipes*	2.4	*Farranula rostrata*	2.5
	O. media f. *minor*	1.3	*O. media* f. *minor*	1.6	*O. media* f. *minor*	1.9	*O. media* f. *minor*	1.5
	Farranula rostrata	1.2	*O. dentipes*	0.9	*O. subtilis*	1.0	*O. vodjanitskii*	1.2
Total poecilostomatoids (no. per 0.25 m²)		18000		15000		11000		14000
100 - 250 m		%		%		%		%
	Oncaea zernovi	23	*Oncaea zernovi*	23	*Oncaea ivlevi*	23	*Oncaea zernovi*	19
	Oncaea "*ivlevi*/K"	11	*Oncaea* sp. K	19	*O. vodjanitskii*	18	*O. ivlevi*	18
	O. ovalis+ *bathyalis*	8.9	*O. minor* ?	9.1	*O. zernovi*	12	*O. vodjanitskii*	5.6
	O. minor ?	6.8	*O. ivlevi*	5.8	*O. ovalis*+ *bathyalis*	3	*Oncaea* sp. K	4.9
	O. ivlevi	5.4	*O. ovalis*+ *bathyalis*	5.2	*O.* "*ivlevi*/K"	2.6	*O. ovalis*+ *bathyalis*	4.2
	O. minima	2.8	*O. tregoubovi*	3.9	*O. minor* ?	1.6	*O. minor* ?	3.4
	Oncaea sp. K	2.8	*O. minima*	3.7	*O. minima*	1.1	*O. minima*	1.9
Total poecilostomatoids (no. per 0.25 m²)		6700		12000		12000		18000
250 - 450 m		%		%		%		%
	Oncaea zernovi	11	*Oncaea* sp. K	13	*Oncaea zernovi*	12	*Oncaea* sp. K	15
	Oncaea sp. K	9.0	*O. zernovi*	9.5	*O. mollicula*	9.3	*O. zernovi*	12
	O. tregoubovi	8.5	*O. mollicula*	9.0	*Oncaea* sp. K	8.8	*O. mollicula*	9.4
	O. mollicula	7.9	*O. ovalis*+ *bathyalis*	8.7	*O. tregoubovi*	6.4	*O. ovalis*+ *bathyalis*	7.8
	O. ovalis+ *bathyalis*	7.5	*O. tregoubovi*	6.1	*O. ovalis*+ *bathyalis*	5.7	*Oncaea* sp. 1	5.9
	Oncaea sp. 5	6.0	*Oncaea* sp. 5	5.5	*Oncaea* sp. 1	3.8	*O. tregoubovi*	5.2
Total poecilostomatoids (no. per 0.25 m²)		9600		8300		6900		6400
450 - 1050 m		%		%		%		%
	Oncaea sp. 1	31	*Oncaea* sp. 1	38	——		*Oncaea* sp. 1	46
	O. longipes	17	*O. longipes*	20			*O. longipes*	11
	O. ovalis+ *bathyalis*	7.4	*O. ovalis*+ *bathyalis*	6.5			*O. ovalis*+ *bathyalis*	7.0
	O. tregoubovi	4.4	*O. tregoubovi*	4.0			*O. tregoubovi*	5.0
	Oncaea sp. 5	4.0	*Oncaea* sp. 5	2.5			*Oncaea* sp. 8	3.3
	Oncaea sp. 8	3.2	*Oncaea* sp. 8	2.5			*O. ivlevi*	1.6
Total poecilostomatoids (no. per 0.25 m²)		13000		15000				4900
1050 - 1850 m		%		%				
	Oncaea longipes	30	*Oncaea longipes*	10	——		——	
	Oncaea sp. 1	6.4	*Oncaea* sp. 1	7.8				
	Oncaea sp. 5	4.7	*Oncaea* sp. K	7.8				
	O. zernovi	2.9	*O. zernovi*	7.8				
	O. ovalis+ *bathyalis*	2.6	*O. ovalis*+ *bathyalis*	5.9				
	Oncaea sp. 8	1.6	*Oncaea* sp. 6	4.4				
Total poecilostomatoids (no. per 0.25 m²)		770		1300				

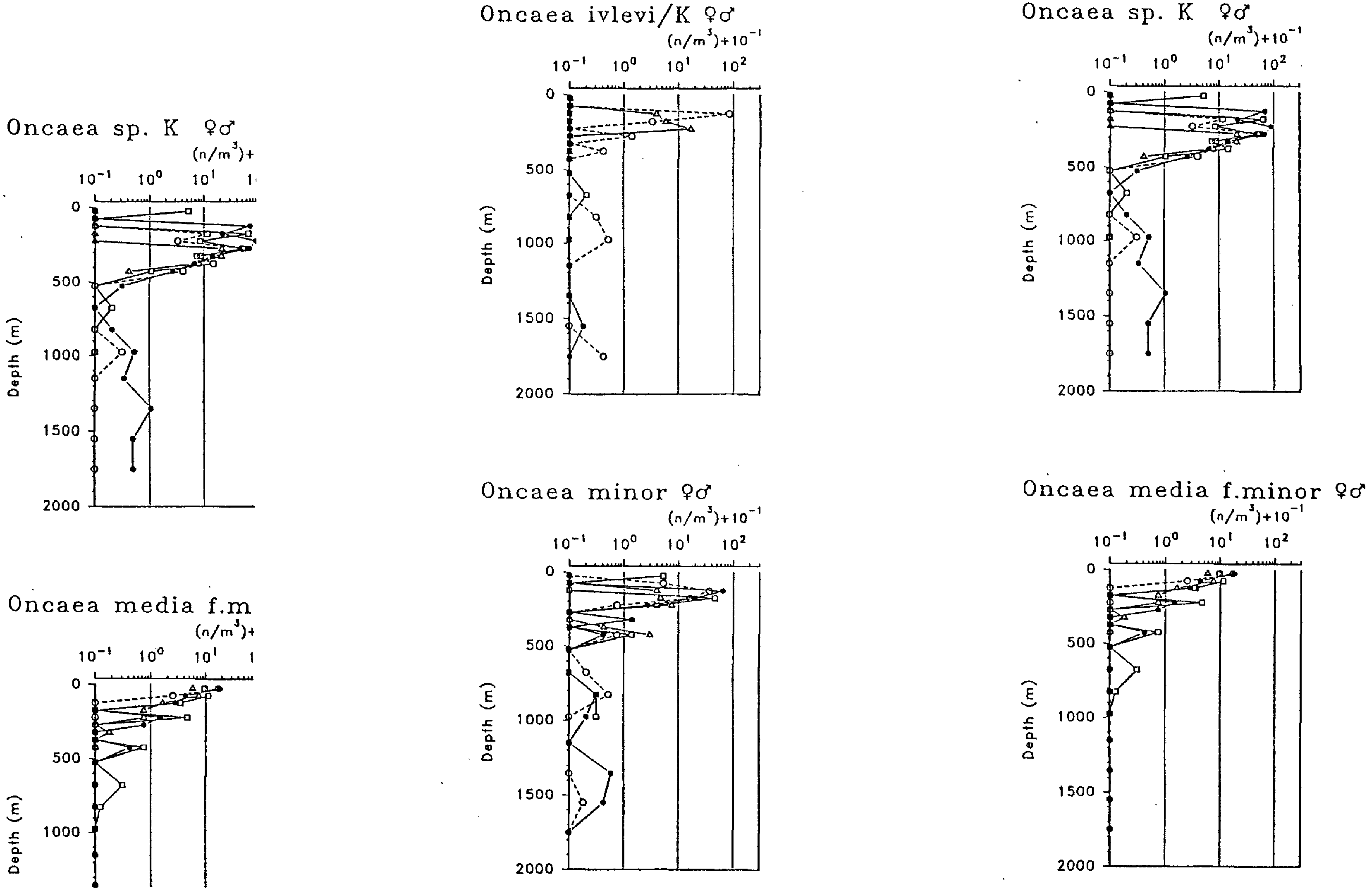
Oncaea sp. K ♀♂
(n/m³)+
Oncaea media f.m
(n/m³)+
Oncaea ivlevi/K ♀♂
(n/m³)+10⁻¹
Oncaea minor ♀♂
(n/m³)+10⁻¹
Oncaea sp. K ♀♂
(n/m³)+10⁻¹
Oncaea media f.minor ♀♂
(n/m³)+10⁻¹
10⁻¹
10⁰
10¹
10²
0
500
1000
1500
2000
Depth (m)

Figure 5

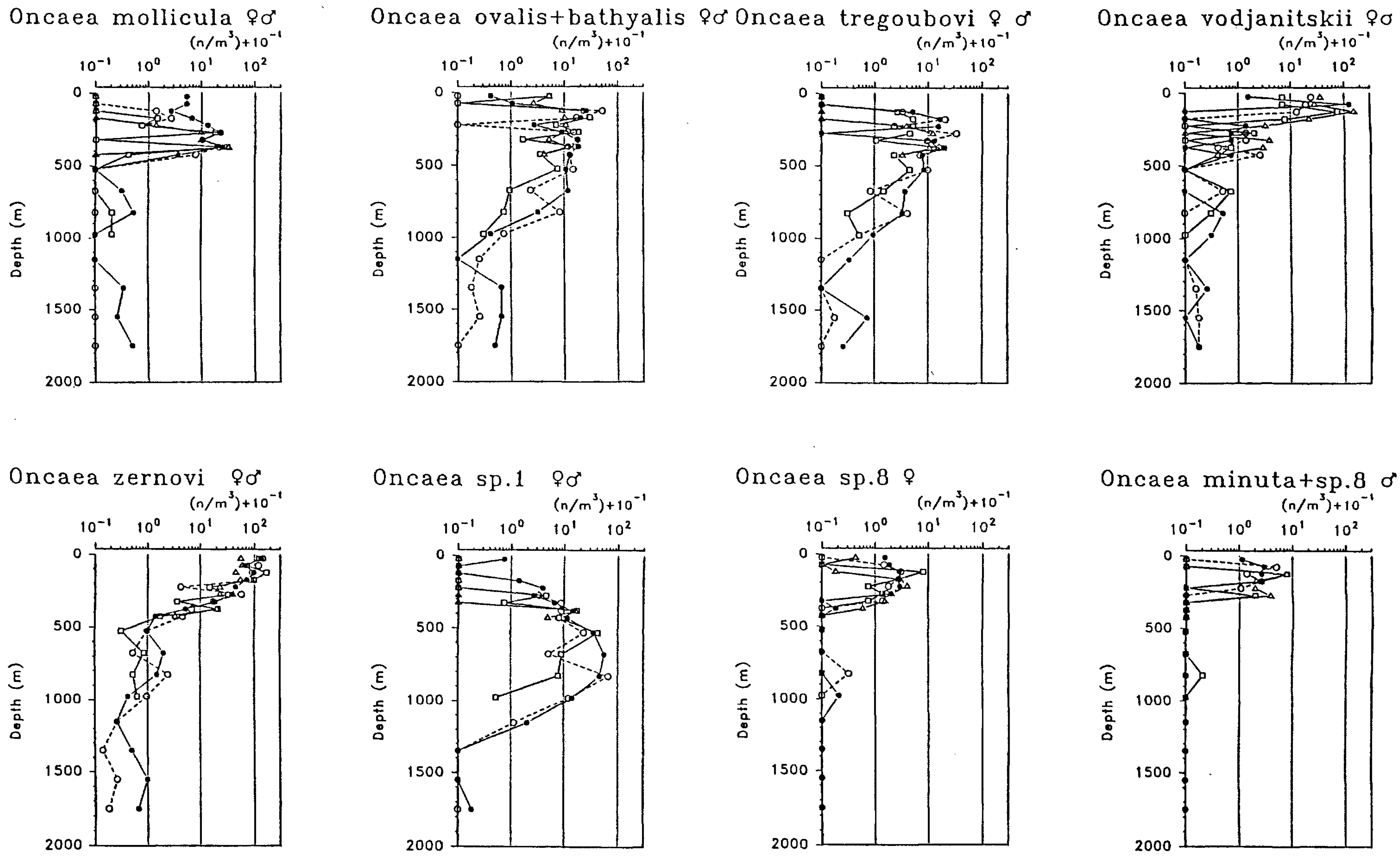

Figure 5 (continued)

Vertical distribution by numbers of selected Oncaea species in the Eastern Mediterranean. o = off Crete (day); • = off Crete (night); △ = off Cyprus; □ = off Israel.

Table 10

Morphological characterization of Oncaea species not yet identified in the Eastern Mediterranean Sea.
T2 = 2nd thoracic segment; P5 = 5th leg; c.r. = caudal ramus; Mxp = Maxilliped

Species	Size (mm) F = Female M = Male	Morphological characteristics of females	Belonging to species group
1	F: 0.28-0.38 M: 0.28	similar to *O. tregoubovi* but differences in Mxp armature and setae on c.r.	"*tregoubovi*"-group
4	F: 0.25 M: not found	similar to *O. atlantica*, but showing conspicuous dorsal protuberance ("keel") on T2	"*atlantica*"-group (see Boxshall and Böttger, 1987)
5	F: 0.36-0.40 M: 0.34-0.36	c.r. with notable expansion on dorsal surface, surrounding base of dorsal seta; dorsal setae remarkably long and resilient	"*Epicalymma*"-group (see Heron, 1977)
6	F: 0.26-0.32 M: 0.25-0.26	prosome oval-shaped, spherical genital segment	?
7	F: 0.48-0.52 M: 0.40-0.42	free segment of P5 elongate	"*notopus*"-group (see Heron, 1977)
8	F: 0.56-0.59 M: 0.48-0.50	very similar to *O. hawii*, particularly in form of genital segment; but segments of leg rami more elongate and posterior seta on free segment of P5 more robust than in typical *O. hawii*	"*similis*"-group (see Böttger-Schnack and Boxshall, 1990)

sent survey, 18 had been reported previously in the Levantine Sea (Kovalev and Shmeleva, 1982; Malt *et al.*, 1989). Four of the species reported from the western Mediterranean by Kovalev and Shmeleva (1982) (*O. longipes*, *O. minima*, *O. minor*, and *O. mollicula*) were found for the first time in the easternmost part during the present study. For *O. umerus*, this is the first report for the entire Mediterranean Sea. Eight *Oncaea* species from the present study have not so far been identified. Based on their general morphology and in view of their extremely small size and deep occurrence, it is assumed that most of them represent new species, which might be present in the western parts as well. This indicates that even the fairly well-known microcopepod fauna of the Mediterranean Sea still needs to be completed by more detailed taxonomic studies on the smallest and deep-living species.

Five oncaeid species reported by Kovalev and Shmeleva (1982) and/or Malt *et al.* (1989) from the Eastern Mediterranean were not found during the present survey. These were *Conaea rapax*, *O. pumilis*, *O. rufa*, *O. tenella* and *O. venusta*. The absence of *O. venusta* was most remarkable, since the species has a widespread distribution in subtropical and tropical regions (*e.g.* Boxshall, 1979; Malt, 1983). Malt *et al.* (1989) and Lakkis (1990) reported *O. venusta* f. *venella* all year round in low numbers near the Lebanese coast, except for February (winter), while *O. venusta* f. *typica* occurred only during April and May. Near the coast of Alexandria, *O. venusta* has been recorded in relatively high concentrations during spring and autumn, being rare during summer and winter (Dowidar and El-Maghraby, 1970 *a*). Siokou-Frangou and Papathanassiou (1989) studied the annual cycle of copepods near Rhodes (South Aegean Sea) and identified six *Oncaea* species among which *O. venusta* was not present. Similarly, Pancucci-Papadopoulou *et al.* (1992) did not report this species among the numerically dominant copepod species in the Levantine Sea during March/April (spring). However, the authors provided no complete species list, and thus *O. venusta* may have been present among the remaining *ca.* 80 species recovered. The total absence of *O. venusta* in the present winter survey in comparison with the literature data indicates the general scarcity of this species in the oceanic part of the Eastern Mediterranean. It obviously displays a seasonal cycle with lowest abundances during winter. This assumption is supported by results of Shmeleva (1963) from the southern Adriatic, where *O. venusta* was found to be superabundant during summer, but rare during the rest of the year.

Seasonal variation may also be the reason for the absence of *O. pumilis* and *O. tenella* during the present winter survey. Both species were recorded by Malt *et al.* (1989) only during September, the former being represented by a single male only, possibly indicating the very low abundance of this species. *O. pumilis* has previously been recorded only from the deep Arctic and Antarctic sectors of the Pacific as well as from the Norwegian Sea (Heron, 1977; Heron *et al.*, 1984).

O. rufa, not recorded during the present study, belongs to a group of morphologically very similar species (Böttger-Schnack and Boxshall, 1990), and has hitherto been found only in the Red and Arabian Seas (Böttger-Schnack, 1990 *a*, *b*, 1994, 1995, in press). One of the unidentified *Oncaea* species of the present study, *Oncaea* sp. 8, also belongs to this species complex, but was definitely different from *O. rufa* (*see* Tab. 10). Since Malt *et al.* (1989) gave no taxonomic description of their *O. rufa* specimens, it may well be possible that they were dealing with this new *Oncaea* species, too.

O. zernovi, which was the most important microcopepod species during the present study, has generally been recorded for the Levantine Sea before (Shmeleva, 1973; Kovalev and Shmeleva, 1982), but was completely absent in the year-round study of Malt *et al.* (1989) along the Lebanese coast. The absence of *O. zernovi* in combination with the occurrence of *O. tenella* in their study is interesting, since both species are similar in size and general habitus. The taxonomic description of *O. tenella* given by Malt *et al.* (1989) corroborates, however, the view that they were not dealing with *O. zernovi*, which was excellently redescribed by Kršinić (1988). During the present study, all specimens of *O. zernovi* belonged to the same type and there was no evidence for the presence of a second closely related species in the samples. In this context it is noteworthy that *none* of the few quantitative or semi-quantitative reports on microcopepods in the Eastern Mediterranean has reported both species simultaneously (Delalo, 1966; Malt *et al.*, 1989; Kovalev and Shmeleva, 1982; this study). Due to the difficulties in separating these small copepod species during quantitative counts, it may well be possible that both species are present in the area, but have not been separated, due to the scarcity of one of them.

The total number of 28 *Oncaea* species reported for the Eastern Mediterranean during the present study is similar to that found in the Red Sea (26 species); 15 *Oncaea* species are common to both regions (Böttger-Schnack, 1994). Compared to the Arabian Sea, where the great number of 69 *Oncaea* species is found (Böttger-Schnack, 1994, in press), the species numbers in the Eastern Mediterraenean appear to be low. The greater number of *Oncaea* species in the Arabian Sea, however, is mainly brought about by bathypelagic forms, which are lacking in the Eastern Mediterranean and the Red Seas, whereas the estimated numbers of epi- and mesopelagic species occurring between the surface and 1000 m depth appear to be similar in all three areas (Böttger-Schnack, 1994, her Tab. 2).

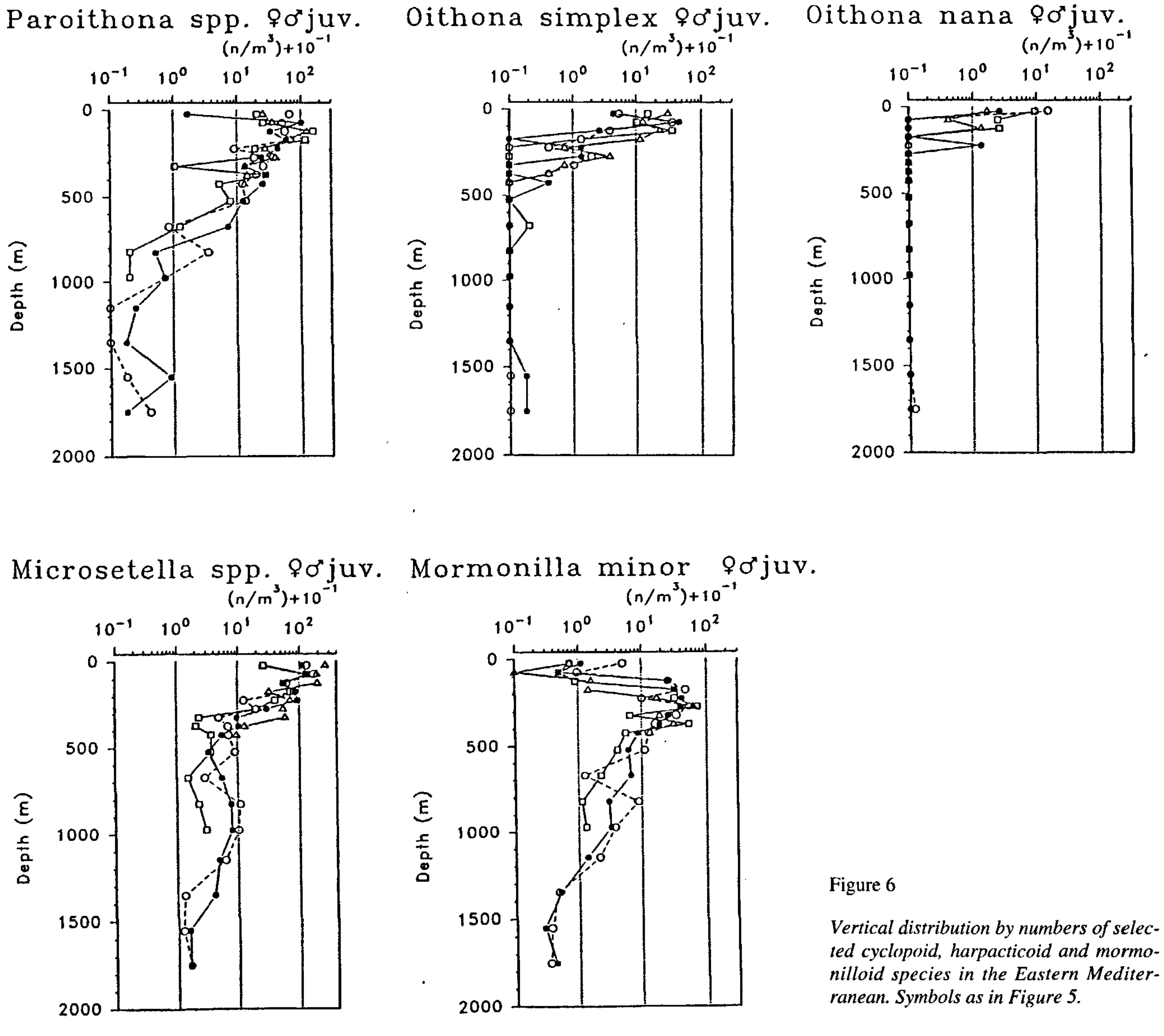

Figure 6

Vertical distribution by numbers of selected cyclopoid, harpacticoid and mormonilloid species in the Eastern Mediterranean. Symbols as in Figure 5.

Table 11

Percentage of carcasses among non-calanoid copepod species in the Eastern Mediterranean Sea. Values are relative abundances of the total number of dead and living individuals of a given species.

Pooled data ($\bar{x}$) and range (R) of four stations are listed (see Table 1). Sexes / Stages as in Table 8 a and 8 b.

Species / genera	$\bar{x}$	R
Oncaea "ivlevi/K"	40	20-94
Oncaea sp. 1	37	26-42
Oncaea sp. K	34	20-56
O. ivlevi	24	18-31
O. longipes	23	10-39
O. mollicula	23	12-38
O. minuta	21	0-52
O. tregoubovi	19	9-36
O. sp. 6	18	6-30
O. subtilis	17	3-28
O. ovalis+bathyalis	16	13-19
Oncaea sp. 5	16	8-28
O. minima	16	10-21
Paroithona spp.	16	10-22
Mormonilla minor	15	10-21
Oncaea zernovi	15	10-19
Vettoria granulosa	15	0-36
Oncaea minor ?	15	4-29
Oithona simplex	13	5-20
Oncaea media f. *minor*	12	3-23
Oncaea sp. 8	12	7-23
O. vodjanitskii	11	6-19
O. umerus	10	4-20
O. ornata	10	2-24
O. dentipes	6	5-7
Microsetella spp.	6	3-8
Oncaea sp. 7	5	2-8
Oithona nana	4	0-9
Oncaea conifera	2	0-5
O. mediterranea	2	1-4
Lubbockia squillimana	2	0-8
Agetus limbatus	2	0-7
Farranula rostrata	2	1-3
Sapphirina metallina	1	0-5
Agetus typicus	<1	0-3

Taxonomic composition of the microcopepod fauna; comparison with calanoids

Comparable quantitative data on the taxonomic composition of microcopepods in the Eastern Mediterranean have not yet been published. Previous studies reported only qualitative or semi-quantitative data, such as "common" or "rare" (Greze, 1963; Delalo, 1966; Malt *et al.* 1989; Lakkis, 1990). Compared to the copepod fauna sampled simultaneously with nets of larger (0.3 mm) mesh size (Weikert and Trinkaus, 1990), the microcopepod fauna in the Eastern Mediterranean showed a much stronger relative importance of non-calanoid species, especially of the genus *Oncaea*. This difference in copepod composition has also been noted during simultaneous sampling with 0.3 and 0.1 mm mesh nets in the Red Sea (Böttger, 1985, 1987). A relatively high proportion of non-calanoid species or taxa was also obtained in 0.2 mm mesh nets used by Scotto di Carlo *et al.* (1991) and Pancucci-Papadopoulou *et al.* (1992) and can obviously be regarded as a general characteristic of small-mesh net samples in oceanic regions (Böttger-Schnack, 1995). The relative abundance of individual *Oncaea* species within the total microcopepod community was much lower as compared to results obtained with larger-mesh nets, however. Scotto di Carlo *et al.* (1991) reported a strong dominance of *O. ornata* in the deep Eastern Mediterranean between 700 to 1400 m depth sampled with nets of 0.24 mm mesh size. It had concentrations between 50-150 ind. 1000 m^{-3} and accounted for up to 40 % of the total number of copepods. In the fine-mesh nets used during the present study, *O. ornata* was found at these depths in similar concentrations (20 - 500 ind 1000 m^{-3}). The relative abundance of this species within the microcopepod community, however, was extremely low: it accounted for less than 0.1 % of the total numbers. Dominant microcopepod species in the bathypelagic zone included a number of very small *Oncaea* species, *e.g. O. longipes* and *Oncaea* sp. 1, as well as the harpacticoid *Microsetella* spp., which is lacking in the coarser mesh sizes (Weikert and Trinkaus 1990; Scotto di Carlo *et al.* 1991; Weikert and Koppelmann, 1993) or represented by few individuals only (Scotto di Carlo *et al.*, 1984).

Compared to the larger calanoid fauna in the deep Eastern Mediterranean Sea, the dominance of individual species appeared to be less pronounced among non-calanoids. The dominant calanoid in the meso- and upper bathypelagic zone, *Eucalanus monachus*, accounted for more than 50 % of all copepods sampled by 0.2 mm mesh nets (Pancucci-Papadopoulou *et al.*, 1992) and for up to 90 % of the total calanoids in 0.3 mm mesh nets (Weikert and Koppelmann, 1993). The corresponding values for the most numerous non-calanoid species, *Oncaea* sp. 1, were 28 % (of total microcopepods) and 36 % (of total poecilostomatoids), respectively. The lower percentage may partly be due to the fact, that late juvenile stages (CIV + CV) were identified for the calanoid species, but not for the non-calanoids. Thus, the relative proportion of *Oncaea* sp. 1 might be somewhat higher if late juvenile stages were included. A reduced dominance of individual species among non-calanoids has also been observed for the extremely impoverished microcopepod fauna of the deep Red Sea (Böttger-Schnack, 1988). Therefore, it may well be possible that the results from the Eastern Mediterranean represent a more general size-dependent phenomenon among deep-sea copepods in these oligotrophic areas. By including the smaller non-calanoid copepod species, which are obviously more diverse than the (larger) calanoids, as well as by including the numerous juvenile stages, the percentage of single species in relation to the total number of copepods decreases considerably.

None of the *Oncaea* species found during the present study had its population centre in the bathypelagic zone, below 1050 m depth. This may indicate the absence of genuine deep-sea species among the non-calanoids in this quite extreme environment. This is similar to findings in the Red Sea, where the same phenomenon has been observed for *Oncaea* species and other non-calanoids (Böttger-Schnack, 1994, 1995) as well as for plankton species in general (Weikert, 1987). For the Mediterranean Sea, however, the existence of at least a few deep-sea plankton species has been demonstrated by Scotto di Carlo *et al.* (1984) and Casanova (1986). In the easternmost part, two bathypelagic calanoid species, occurring exclusively below 2000 m depth, have been found very recently by Weikert and Koppelmann (1993). In general, the non-calanoid fauna of the deep sea is not well known, since small-mesh net samples below 1000 m or 2000 m depth have rarely been obtained. A large number of *Oncaea* species occurring between 1000 and 2000 m depth have been reported by Heron (1977) and Heron *et al.* (1984) in the Antarctic and Arctic sectors of the Pacific and/or Atlantic. In the Arabian Sea, Böttger-Schnack (1994, in press) reported an extremely speciose *Oncaea* fauna in the 1050 - 1850 m layer, which contained two-thirds of all *Oncaea* species in the water column. This phenomenon, however, was attributed to the extreme oxygen minimum zone extending between 100 m to 1000 m in that area, which refrains mesopelagic species from colonizing the intermediate layers. It may not reflect the typical conditions found in most oceanic areas. Whether the deep-water *Oncaea* assemblage in the Eastern Mediterranean can be viewed as a typical feature of tropical marine areas, or whether it is more or less impoverished, can only be determined after a detailed investigation of this important small-sized copepod genus in areas with more typical environmental conditions, such as the the tropical Atlantic (Sargasso Sea) or the central gyres of the Pacific.

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