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Vertical structural patterns of deep-living zooplankton in the NE Atlantic, the Levantine Sea and the Red Sea: a comparison

Deep-living zooplankton Vertical distribution patterns NE Atlantic Eastern Mediterranean Red Sea

> Zooplancton profond Distribution verticale Atlantique Nord-Est Méditerrranée orientale Mer Rouge

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ABSTRACT

Full-depth profiles of zooplankton numerical abundance and major taxa composition are presented with special attention to the dominant copepod fauna, for directly comparable data sets from sites to a depth of 4 300 m in the Levantine and Red Seas, which are also compared with the deep mid-latitude NE Atlantic. Copepods showed highest proportions of calanoids, cyclopoids sensu lato and harpacticoids in the 333 μ m net subsurface samples from the Atlantic. Among the calanoids as the predominant group, there was a distinctly disproportionate, extended and depth-related sequence of zonal dominance by one single species of a family each at mesopelagic and bathypelagic depths in the Levantine Sea and the Red Sea. The mass occurrence of dormant Eucalanus monachus specimens in the Levantine Sea can be related to the presence of mesoscale gyres. The coexistence of resulting mosaic-like mesoscale communities of a "boreal" and a "tropical" design distinguishes the Levantine from the Red Sea, where eddies obviously do not significantly influence the relative proportions of dominant species of the deep-living mesozooplankton. Hence, on a larger scale, the open Red Sea seems to be the more stable system, hydrographically as well as ecologically, with the exception of its northern and southern ends where increased environmental variability affects the basic faunistic structures of deep-living mesozooplankton.

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RÉSUMÉ

La distribution verticale et la composition du zooplancton vivant en profondeur dans l'Atlantique nord-oriental, le bassin levantin et la Mer Rouge. Une comparaison

Dans ce travail sont présentés des profils complets de l'abondance numérique du zooplancton et de la composition de ses principaux groupes (avec une attention spéciale à la fraction dominante des copépodes), fondés sur des séries de données directement comparables, récoltées à un niveau de profondeur situé entre 4300 m et la surface dans le bassin levantin et la Mer Rouge, par rapport à l'Atlantique nord-oriental. Les copépodes montrent les proportions les plus élevées en cala-noïdes, en cyclopoïdes au sens large et en harpacticoïdes dans les récoltes de sub-surface effectuées dans l'Atlantique au moyen d'un filet de 333 μ m de vide de maille. Dans le bassin levantin et en Mer Rouge, aux différents niveaux méso- et bathypélagiques, dans le groupe numériquement le plus important des calanoïdes

s'observe une domination zonale d'une seule espèce d'une famille, nettement hors de proportion, étendue et liée à la profondeur. La grande quantité d'individus inactifs de *Eucalanus monachus* peut être mise en relation avec l'existence de gyres à moyenne échelle. La coexistence de communautés en mosaique de nature boréale et tropicale oppose le bassin levantin à la Mer Rouge où les tourbillons n'exercent manifestement pas d'influence significative sur les proportions relatives des espèces principales du mésozooplancton profond. D'où, dans une échelle plus grande, la Mer Rouge semble être un système plus stable tant aux points de vue hydrologique qu'écologique, sauf à ses extrémités septentrionales et méridionales où la variabilité accrue de l'environnement affecte les structures fondamentales de la faune profonde.

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INTRODUCTION

The Mediterranean and the Red Seas are semi-enclosed deep sea basins. A shallow sill at the entrance of the basins allows little exchange with adjacent waters, and this is largely confined to the surface regime. Due to the arid climate, with high insolation and a rate of evaporation which is not compensated by land runoff or by precipitation, temperatures and salinities are high throughout the water column. For a closer look at the hydrographic parameters and the water exchange processes at the entrance of the basins, the reader is referred to Miller *et al.* (1970), Morcos (1970), Maillard and Soliman (1986), Guibout (1987), Armi and Farmer and *vice versa* (1988), for example.

The deep water bodies of the two basins are almost uniform. In the easternmost Mediterranean, the Levantine Sea, temperature and salinity are ~ 13.6°C and > 38.65, respectively (review by Malanotte-Rizzoli and Hecht, 1988), while the deep Red Sea has the most anomalous conditions ($\geq 21.5^{\circ}$ C, > 40.5, *e. g.* Morcos, 1970). In the deep open ocean, the temperature decreases bathymetrically to about 3-4°C at 4000 m. Consequently, in the basins, the deviation from the open ocean increases with depth, from about 1°C at 200 m to 10°C at 4000 m in the Levantine Sea. In the Red Sea, the respective anomalies are even higher, *i. e.* from about 10°C at 200 m to 18.5°C at 2000 m.

True deep-sea species are virtually absent from the plankton of the Mediterranean and Red Seas (see literature cited both in Scotto di Carlo et al., 1984 and Weikert, 1987, respectively). This may be related both to, the anomalous hydrography of the seas and to their Pleistocene history. Most of the biota appear either to have been extinguished during the last glaciation period in the eastern Mediterranean, or to have survived in scant species assemblages in the Red Sea at local sites (Por, 1989), but the latter conclusion lacks hard data for the metazoan plankton (e. g. Weikert, 1987). The resulting deficient population in the bathypelagic zone of the two basins causes a significantly stronger decrease of zooplankton with depth in comparison to the world ocean (Weikert and Trinkaus, 1990). This feature is discussed by means of directly comparable data sets from the basins and the NE Atlantic (Weikert and Koppelmann, in prep.).

No comparison as yet exists between the Levantine Sea and the Red Sea concerning the basic structure of deepliving zooplankton. Using precisely that material, we focus on the major individual constituents of the semi-enclosed basins with reference to the Atlantic site. With the example of the calanoid copepods as the most abundant mesozooplankton group, a broad view of spatial abundance patterns in the basins is provided, which allows general conclusions to be drawn concerning the character of the basins' ecological systems and may stimulate further study of their functioning.

MATERIAL AND METHODS

Sampling and analysis

Zooplankton was collected during three cruises of the RV Meteor in the NE Atlantic, the Levantine basin (Eastern Mediterranean) and the central Red Sea. A 1 m² MOC-NESS (Multiple Opening/Closing Net and Environmental Sensing System; Wiebe et al., 1985) equipped with nine black nets of 333 µm mesh aperture was employed for oblique tows. Discrete samples were taken at a speed of about two knots: from 0 to 450 m at 50 m intervals (in the Levantine basin, the upper 100 m were fished by one step), 450 to 1050 m at 150 m intervals, 1050 to 2250 m at 200 m intervals, and every 250 m below 2250 m. In the Levantine Sea and at one station in the NE Atlantic, 500 m intervals were chosen below 3000 m. We only considered mesozooplankton, which is defined opportunistically to be smaller than 5 mm (Weikert and Trinkaus, 1990), and purged the samples of carcases according to the methods of Wheeler (1967) and Weikert (1977). Larger organisms such as euphausiids, decapods and chaetognaths were excluded to reduce bias due to net avoidence. The counts were standardized to 1000 m³ of filtered water. Detailed information on the evaluation and preservation of the material has been published elsewhere (Weikert and Trinkaus, 1990; Koppelmann and Weikert, 1992). Note that the fauna smaller than about 1 mm in size, which is dominated by cyclopoid copepods, is not quantitatively sampled by the mesh size used (e. g. Böttger, 1987). The major copepod categories were arranged according to the traditional groups Calanoida, Harpacticoida and Cyclopoida s. l. (incl. Misophrioida, Siphonostomatoida, Mormonilloida, Cyclopoida s. str. and Poecilostomatoida).

Examined sites

Most station data except those for the Red Sea are reported elsewhere (Weikert and Trinkaus, 1990; Koppelmann and Weikert, 1992) and will not be repeated in detail. Table 1 summarizes the haul data of the cruises. Information on the hydrography in the studied areas is omitted since only gross structures of the zooplankton are examined. Details on the hydrography at the Levantine site can be found in Weikert and Trinkaus (1990). The setting in the Red Sea compared well to a previous situation at the same site as described by Böttger (1987). Mittelstaedt *et al.* (1986) treated in detail the hydrography in the Atlantic *Biotrans* area for the years 1982-1985.

The NE Atlantic material was gathered in April/May 1988 in the *Biotrans* area (47°N, 20°W; Pfannkuche *et al.*, 1990) and somewhat to the northeast, at a European Community (EC) station (48°50'N, 16°30'W). From the *Biotrans* site, one-day profiles from the surface to 3300 m and one-and-a-half night profiles from 10 to 4460 m were available. The day profile from the EC station extended from 150 to 4 000 m. The deepest hauls commenced about 200 m from the bottom.

In the Levantine Sea, sampling was above a 4 250 m deep trough south off Crete ($34^{\circ}20$ 'N, $26^{\circ}00$ 'E). One and a half day profiles and two and a half night profiles were available from January 1987, commencing about 200 m from the seabed. The volumina filtered by the nets were recalculated using an improved calibration factor of the flowmeter (Koppelmann, 1990). Therefore, the zooplankton concentrations in the present study are approximately 18.5 % higher (standard deviation 2.9 %) than the data given by Weikert and Trinkaus (1990). In contrast with the previous study, individuals greater than 5 mm (many chaetognaths, some polychaetes and a few copepods and pteropods), in addition to other crustacean taxa, salps and coelenterates, were completely excluded.

In the central Red Sea $(21^{\circ}23'N, 38^{\circ}04'E)$, the profiles were 100 m close to the floor of the axial graben. One-day profile from the surface to 1 650 m and one-and-a-half night profiles from 0 m to 1950 m were analyzed. In order to obtain data over an extended depth range, a third deep haul was taken from a southern location at 19°40'N, 38°42'E, where the sounding was 2 400 m. Sampling took place between 24-29 July 1987, *i. e.* during the SW-monsoon.

RESULTS

Standing crops of major zooplankton groups

Copepods were the dominant major taxon at all sites and comprised nearly 90 % of the total zooplankton standing crop in the water column in both the NE Atlantic and the Levantine basin (Tab. 2). In the central Red Sea, copepod abundance

Table 1

Station data. B = Biotrans-area, NE Atlantic. E = European Community station, NE Atlantic. L = Levantine basin, eastern Mediterranean Sea. R = central Red Sea. * Filtered volume estimated by a geometric formula (Beckmann, 1988).

Date	Local time	Cruise Area	Depth/m
11.04.88 11.04.88 13.04.88 14.04.88 17.04.88 17.04.88 22.04.88* 04.05.88* 05.05.88* 06.05.88	$\begin{array}{r} 00:40 & - & 01:22\\ 13:41 & - & 17:45\\ 21:32 & - & 23:49\\ 02:57 & - & 03:50\\ 00:48 & - & 02:50\\ 11:18 & - & 14:09\\ 13:48 & - & 14:31\\ 10:18 & - & 14:30\\ 12:55 & - & 15:35\\ 14:00 & - & 14:32\\ 00:08 & - & 00:23\\ \end{array}$	M6/7,B M6/7,B M6/7,B M6/7,B M6/7,B M6/7,B M6/7,E M6/7,E M6/7,E M6/7,B	1650 - 3600 1450 - 3300 400 - 1650 10 - 400 400 - 1650 0 - 1650 0 - 450 1850 - 4000 400 - 1650 1850 - 450 2750 - 4460
14.01.87 14.01.87 15.01.87* 15.01.87* 18.01.87* 18.01.87* 19.01.87* 20.01.87* 20.01.87 21.01.87	$10:40 - 11:23 \\ 15:23 - 17:40 \\ 2:58 - 5:39 \\ 14:03 - 16:26 \\ 2:40 - 05:32 \\ 15:46 - 19:44 \\ 23:06 - 23:54 \\ 3:58 - 6:37 \\ 14:25 - 15:20 \\ 21:20 - 22:00 \\ 2:38 - 5:02 \\ 18:00 - 21:44 \\ \end{bmatrix}$	M5/1,L M5/1,L M5/1,L M5/1,L M5/1,L M5/1,L M5/1,L M5/1,L M5/1,L M5/1,L M5/1,L	$\begin{array}{rrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrr$
24.07.87 25.07.87 25.07.87 25.07.87 25.07.87 25.07.87 29.07.87	21:56 - 23:38 2:01 - 2:53 5:18 - 7:11 10:32 - 11:17 13:57 - 16:55 12:40 - 18:32	M5/5,R M5/5,R M5/5,R M5/5,R M5/5,R M5/5,R	900 - 1950 0 - 350 350 - 1450 0 - 400 400 - 1650 750 - 2250

was less and did not exceed some 70 %. Here, in turn, ostracods (10.4-5.1 %) and the collecting group "remainder" (8.4-12.2 %) were more abundant than in the Levantine basin (ostracods 4.0-4.3 %; remainder 2.3-3.6 %) and the NE Atlantic (ostracods 6.4-6.5 %; remainder 1.3-5.4 %). The remainder comprised chaetognaths, polychaetes and molluscs. The relative abundance of the malacostracans was virtually similar in all regions, ranging from 3.2 to 4.6 %.

Distinct day/night differences were obvious for the copepods, ostracods and the remainder in the upper 100 m at the sites in the NE Atlantic and central Red Sea (Tab. 2). This may indicate nocturnal upward migration of the former two groups from the underlying layers. But such a suggestion needs to be supported by species-specific analyses, because the overall integrals of both the copepods and ostracods were also larger by night, except the copepod standing crop in the Red Sea. For the remainder, both the standing crops in the top 100 m and the mesopelagic zone were higher by day, as was their total crop in the water column. In the Levantine Sea, neither the individual standing crops of total zooplankton (Weikert and Koppelmann, in prep.) nor those of the major taxa provided support for diel vertical migration, thereby corroborating the results presented by Weikert and Trinkaus (1990).

Vertical distribution of major copepod taxa relative to total zooplankton

Calanoids were the main copepod constituents of the total zooplankton throughout the water column at the sites (Fig. 1). At all depths, they comprised 50-80 % of the fauna, reaching

Table 2

Standing crops of the main zooplankton groups (specimens/ m^2). RA = Relative abundance to the total zooplankton standing crop.

Depth/m	Cope Day	poda Night		acoda Night		costr. Night		inder Night		tal Night
0 - 100	5391	15493	271	511	965	983	677	137	7304	17124
RA	19.5	41.3		1.4	3.5	2.6	2.4	0.4	26.4	45.7
100 - 1050	15346	15208	1324	1709	236	205	832	337	17738	
RA	55.4	40.5	4.8	4.6	0.8	0.5	3.0	0.9	64.0	
1050 - 2250	2098	2053	102	101	9.9	12.5	20.8	18.8	2231	2185
RA	7.6	5.5	0.4	0.3	<0.1	<0.1	<0.1	<0.1	8.0	5.8
2250 - 4000	393	522	41.9	66.7	4.0	29.1	3.0	3.5	442	621
RA	1.4	1.4	0.2	0.2	<0.1	0.1	<0.1	<0.1	1.6	1.7
4000 - 4500 RA		103 0.3		17.2 <0.1		1.3 <0.1		0.9 <0.1		122 0.3
Total	23228	33379	1739	2405	1215	1231	1533	497	27715	37511
RA	83.9	89.0	6.4	6.5	4.3	3.2	5.4	1.3	100.0	100.0

NE Atlantic

Levantine Basin

Depth/m	Cope	poda	Ostra	acoda	Mala	costr.	Rema	inder	Tot	tal
	Day	Night	Day	Night	Day	Night	Day	Night	Day	Night
0 - 100	5972	5040	318	209	326	352	209	463	6825	6064
RA	31.7	32.0	1.7	1.3	1.7	2.2	1.1	2.9	36.2	38.5
100 - 1050	10486	8364	419	340	269	201	220	94.8	11394	9000
RA	55.6	53.2	2.2	2.2	1.4	1.3	1.2	0.6	60.4	57.3
1050 ~ 2250	447	379	60.0	64.3	55.5	91.0	5.9	11.4	568	546
RA	2.4	2.4	0.3	0.4	0.3	0.6	<0.1	0.1	3.0	3.5
2250 - 4000	59.7	96.1	9.5	14.1	1.6	3.7	7.3	1.8	78.1	116
RA	0.3	0.6	<0.1	0.1	<0.1	<0.1	<0.1	<0.1	0.4	0.7
Total	16965	13879	807	627	652	648	442	571	18865	15726
RA	89.9	88.2	4.3	4.0	3.4	4.1	2.3	3.6	100.0	100.0

central Red Sea

Depth/m	Cope	poda	Ostr	acoda	Mala	costr.	Rema	inder	TO	tal
	Day	Night	Day	Night	Day	Night	Day	Night	Day	Night
0 - 100	6265	9169	305	1274	334	765	2088	1564	8992	12772
RA	27.6	43.0	1.3	6.0	1.5	3.6	9.2	7.3	39.6	59.9
100 - 1050	10061	5695	1964	1848	584	209	672	220	13281	7972
RA	44.3	26.7	8.6	8.7	2.6	1.0	3.0	1.0	58.5	37.4
1050 - 2250	309	478	122	85.3	2.7	2.7	5.6	8.3	439	574
RA	1.4		0.5	0.4	<0.1	<0.1	<0.1	<0.1	1.9	2.7
Total RA	16635 73.3		2391 10.4	3207 15.1	921 4.1	977 4.6	2766 12.2		22712 100.0	21318 100.0

The night profile extends to 1950 m only.

some 90 % as a maximum in the central Red Sea at 1 350 to 1 650 m and in the Levantine Sea as well, where peak values occurred at 400 to 800 m and below 3 250 m. Minimum percentages (30 to 50 %) were found in the NE Atlantic between 50 and 200 m, but with that exception, the calanoid share of the zooplankton in the water column appeared to vary less when compared to the sites in the landlocked basins.

The density of cyclopoids s. l. in the water column was least in the Levantine basin, varying between less than 1 % and 9 %, depending on depth.

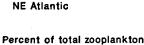
In the central Red Sea, cyclopoids s. l. accounted for approximately 20 % of the mesozooplankton in the upper 300 m. Among this copepod group, the poecilostomatoid genera Oncaea, Sapphirina and Copilia were found to have their highest abundances in the top 100 m, whereas Corycaeus, Lubbockia and the cyclopoids s. str., Oithona, were abundant down to 500 m. Between 300 and 1 300 m, the shares of cyclopoids s. l. had diminished to 1 %, but at greater depths, there was an increase up to 10 %, probably due to contamination of mainly Corycaeus species.

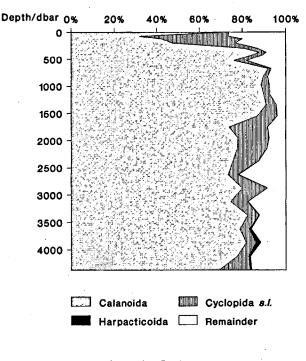
At the site in the NE Atlantic, the relative amount of cyclopoids s. l. (up to 40 %) was highest in the upper 300 m, primarily due to poecilostomatoids (Oncaea) and cyclopoids s. str. (Oithona). In the lower mesopelagic and bathypelagic zones the percentages were less but still higher in comparison with the sites in the Levantine and Red Seas (~ 5-15 % vs. < 1 % and 1-3 %, respectively). This feature can be attributed to the appearence of Mormonilla spp. and Conaea rapax, which attained high numbers at 500 to 3 000 m (up to 70 specimens/1000 m³) and at 700 to 2500 m (up to 140 specimens/1 000 m³), respectively. Below 2 000 m, the obligate bathypelagic Benthomisophria spp. and Hyalopontius spp. appeared in addition to other - probably contaminant - cyclopoids.

Harpacticoids were not found at the Levantine site. In the central Red Sea, their relative abundance, as represented by *Macrosetella gracilis*, was too small (< 0.1%) to be delineated for the upper 1200 m. In the NE Atlantic, harpacticoids (*Macrosetella* spp., *Microsetella* spp. and *Aegisthus* spp.) held a similar small share of less than 1% throughout the upper 2000 m. At greater depths, *Aegisthus* spp. were found in increasing numbers of 30 specimens/1000 m³, and the relative abundance of harpacticoids was around 2%.

Regional differences among standing crops of dominant calanoid families

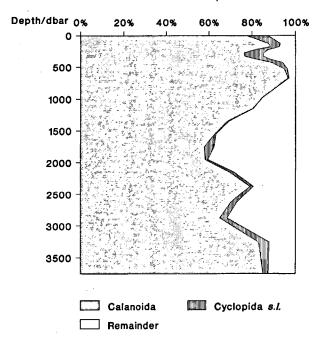
Metridinidae consistently dominated at the NE Atlantic and central Red Sea sites. Of this family, the genus *Pleuromamma* comprised some 30 % of the regional total calanoid crops (Tab. 3). In the NE Atlantic *Metridia* spp. ranked next (16.6 %), while this genus was not present at





Levantine Basin

Percent of total zooplankton



either the Red Sea or the Levantine Sea sites. Heterorhabdidae (10.5 %) and Calanidae (6.0 %) were also notable groups in the Atlantic. In the Red Sea, the standing crops of Calanidae (12.7 %), Scolecitrichidae (11.4 %), Augaptilidae (8.5 %) and Lucicutiidae (5.9 %) ranked next to Metridinidae. At the Levantine site, Augaptilidae and Eucalanidae were dominant, comprising 27.5 % and 23.8 %, respectively, of the total standing crop of calanoids. Candaciidae showed higher percentages at the Levantine and Red Sea sites (0.8 and 2.3 %, respectively) than in the

Central Red Sea

Percent of total zooplankton

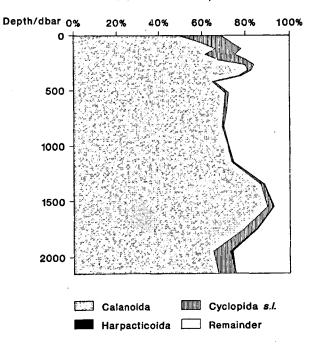


Figure 1

Relative numerical contribution of Calanoida, Cyclopoida s. 1., and Harpacticoida to the total zooplankton at the deep sites in the NE Atlantic, the Levantine Sea and the central Red Sea. Note the different scales for the sites.

NE Atlantic and were distributed in increased absolute and relative numbers in the bathypelagic zone.

A number of families, endogenous in the NE Atlantic, were not found in the Levantine basin, and even more of them were absent from the central Red Sea. For example, Arietellidae and Bathypontiidae, in addition to the genus *Metridia* spp., were found in neither basin, while Aetideidae were absent from the central Red Sea.

Figure 2 depicts the abundance of the principal calanoid families in relation to the total calanoid counts at the sites according to depth. In the NE Atlantic, Metridinidae abounded throughout the water column, reaching almost 70 % at 150 to 1650 m. Heterorhabdidae showed a bimodal distribution pattern with relative amounts of some 25 % at 250 to 450 m and up to 35 % at 1450 to 2500 m. Bathypontiidae (only female *Foxtonia barbatula*) were exclusively found below 2000 m and contributed up to 10 % to the calanoid counts.

In the Levantine basin, three families accounted for 90 % of the calanoid fauna over large distances in the water column: Augaptilidae at 100 to 300 m, Eucalanidae in the lower mesopelagic and upper bathypelagic zones at 450 to 1 450 m, and Lucicutiidae at 2 050 to 4 000 m.

In the central Red Sea, Calanidae, Lucicutidae (mainly *L. fla-vicornis*, *L. ovalis*), Eucalanidae and Augaptilidae were abundant, with 15 to 35 % to the total calanoid bulk in the subsampled epipelagic and upper mesopelagic zones (50 to 200 m). Metridinidae comprised up to 75 % between 250 and 900 m. Below 900 m, Scolecitrichidae accounted for approximately

Table 3

Relative abundance of calanoid taxa to the total calanoid standing crop over the whole water column at the sites in the NE Atlantic (0-4500 m), the Levantine basin (0-4000 m) and the central Red Sea (0-2250 m). N = not found, ? = not found or not distinguished, A = absent, including information from literature (Levantine basin: Scotto di Carlo et al., 1984; Greze, 1963; Red Sea: Delalo, 1966; Halim, 1969; Beckmann, pers. comm.).

Taxa	NE Atlantic	Levantine Basin	' Central Red Sea
Calanidae	6.0	4.3	12.7
Eucalanus spp.	0.1	23.8	2.2
Rhincalanus nasutus	0.6	N	4.8
Mecynocera clausi	<< 0.1	0.6	0.2
Calocalanus spp.	?	0.1	0.5
Spinocalanidae	?	0.2	N
Aetideidae	2.1	1.1	N
Euchaetidae	2.9	1.8	4.7
Phaenna spinifera	N	N	< 0.1
Cephalophanes spp.	< 0.1	A	A
cf. Scolecithrichidae	1.4	0.5	11.4
Metridia spp.	16.6	A ·	A
Pleuromamma spp.	30.5	4.6	32.9
Centropages spp.	0.2	0.1	1.5
Lucicutia spp.	2.8	6.8	6.8
Heterorhabdidae	10.6		N
Heterorhabdus spp.		0.7	
Augaptilidae	0.7	27.9	8.4
Arietellidae	0.2	?	N
Candaciidae	0.1	0.8	2.3
Pontellidae	?	?	< 0.1
Foxtonia barbatula	0.1	A	A
Acartia spp.	N	0.3	3.8
Unidentified	25.1	26.4	7.7
Numbers/m ²	19 974	15 841	14 854

40-50 % of the calanoids, and Lucicutiidae attained a secondary peak of abundance (~15 %) at 900 to 1650 m.

Taxonomic and age structures in dominant subsurface calanoid families of the basins

NE Atlantic

As analyzed for the Metridinidae by one profile, *Pleuromamma gracilis* comprised 57 % of the genus, but

NE Atlantic

accounted for only 37 % of the standing crop of the family and 58 % of the counts in the layer of maximum abundance at 350 to 600 m, respectively. However, the quantitative species-specific study of dominant families is still at an early stage, and the reduced dominance of a single species in the families' standing crop, which is unlike the situation in the semi-enclosed basins as shown below, needs to be examined more thoroughly.

Levantine Sea

Augaptilidae were dominated by *Haloptilus longicornis* which accounted for about 99 % of the total counts (Tab. 4). Juveniles (day-night: 70 and 74 %) dominated over females (21 %) and males (5 and 8 %) at all depth intervals throughout the water column (Tab. 4, Fig. 3).

Figure 4 illustrates the day and night distribution of *H. longicornis* together with that of *H. acutifrons* and *H. ornatus*. The rare species (Tab. 4) *H. angusticeps*, *H. mucronatus*, *Euaugaptilus hecticus*, *Augaptilus longicaudatus* and some unidentified singular augaptilid specimens are neglected.

Peak concentrations of *H. longicornis*, amounting to 30,000 specimens/1 000 m³, were encountered at 100 to 150 m, comprising about 88 % of the calanoids in this layer. Below 200 m the numbers decreased rapidly in the day and night profiles (Fig. 3) and tended to be irregular below 1 000 m (Fig.

4). The appearance of *H. ornatus* coincided with the maximum abundance of the former species, whereas *H. acuti-frons* was found consistently between 900 and 2 050 m (Fig. 4). No diel vertical migrations seemed to exist; the Spearman rank correlation (Sachs, 1978) showed a significant coherency (P < 0.002) between the day and night patterns of each of the species.

Among the Eucalanidae, three species were found in decreasing order of abundance: Euchalanus monachus, E.

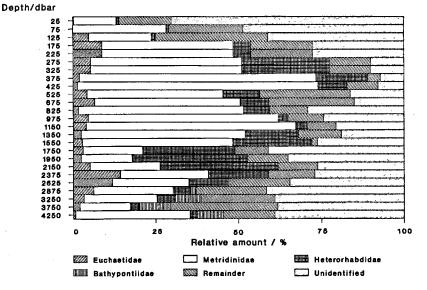


Figure 2



Relative abundance of the principal calanoid families above the bathyal sites in the NE Atlantic, the Levantine Sea and the Red Sea. Above 1000 m only day data were used.

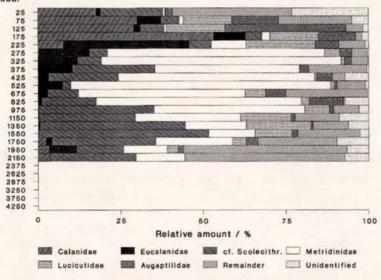
DEEP-LIVING ZOOPLANKTON INTEROCEANIC COMPARISON

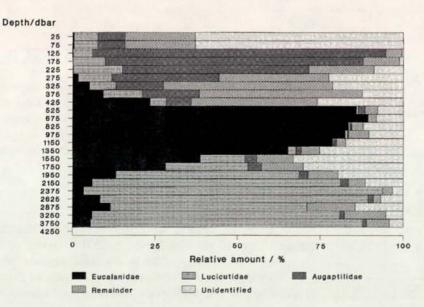
Table 4

Standing crop (specimens/m²) of augaptilid taxa (Haloptilus, Euaugaptilus and Augaptilus) over the 4000 m water column at the Levantine site. In parentheses: the relative abundance of adults and juveniles refers to the respective species standing crop, the percentage of the latter to the total crop of Augaptilidae.

Taxa	Male		Juvenile	Total	Male		ight Juvenile	Total
H. longicornis	370 (8.5)	915 (20.9)	3088 (70.6)	4373 (98.9)	235 (5.3)	924 (21.0)	3243 (73.7)	4402 (98.9)
H. acutifrons	0.4	2.4 (42.1)	2.9 (50.9)	5.7 (0.1)	0.1 (2.2)	1.8 (40.0)	2.6 (57.8)	4.5
H. ornatus	9.1 (34.3)	4.9	12.5 (47.2)	26.5	0.6	4.1 (16.7)	19.8 (80.8)	24.5
H. angusticeps	0.0	0.0	0.0	0.0	0.0	0.0	0.3	0.3
H. mucronatus	4.1	0.0	0.0	4.1 (0.1)	0.0	0.0	0.0	0.0
E. hecticus	2.8 (28.0)	0.5	6.7 (67.0)	10.0 (0.2)	0.8	1.6 (12.9)	10.0 (80.6)	12.4 (0.3)
A. longicaudatus	1.9 (41.3)	0.0	2.7 (58.7)	4.6	0.9	0.8 (18.2)	2.7 (61.4)	4.4 (0.1)
Unidentified	0.6	2.3 (59.0)	1.0 (25.6)	3.9 (0.1)	0.0	0.0	2.9	2.9 (0.1)
Total	389	925	3114	4428	237	932	3281	4451

Central Red Sea





Levantine Basin

attenuatus and E. crassus. E. monachus formed about 99 % of the standing crop. The main distribution of the species was between 450 and 900 m, while the congeners resided at slightly shallower depths, thereby extending into the upper concentration range of E. monachus (Fig. 5). No day/night differences in the vertical distribution of E. monachus seemed to exist either for the total population or the sexes and copepodid stages (Fig. 6; Spearman rank correlation, P < 0.005). Copepodid V stages dominated the standing crop and comprised 57 % of the specimens during the day and 67 % during the night. Males, females and CIV stages shared the remaining percentages in decreasing order, and males outnumbered females by a factor of two (Fig. 7).

The dominance of Lucicutiidae at depths greater than 2050 m (Fig. 2) was due to a single species, Lucicutia longiserrata (Tab. 5), which was exclusively collected in the bathypelagic zone, i. e. below 1250 m (Fig. 8). Juveniles (day: 71.1 %, night: 78.5 %) outnumbered females (day: 17.0 %, night: 12.3 %) and males (day: 11.9 %, night: 9.3 %). Figure 8 also shows the copepodid distribution of the species which abounded at 2000 to 2500 m in both the day and night samples, amounting up to 70 and 90 specimens/1000 m³ respectively. The mean concentration depth of juveniles, however, was found to be deeper when compared to that of the adults (2600 m vs. 2200 m: Logit analysis, Rudyakov, 1982).

Two other large species, L. pera and L. curta, were encountered between 600 and 2050 m and 400 and 1450 m, respectively. Small species such as L. clausii and L. ovalis, which have not yet been fully analyzed for their species-specific depth dis-

Depth/dbar

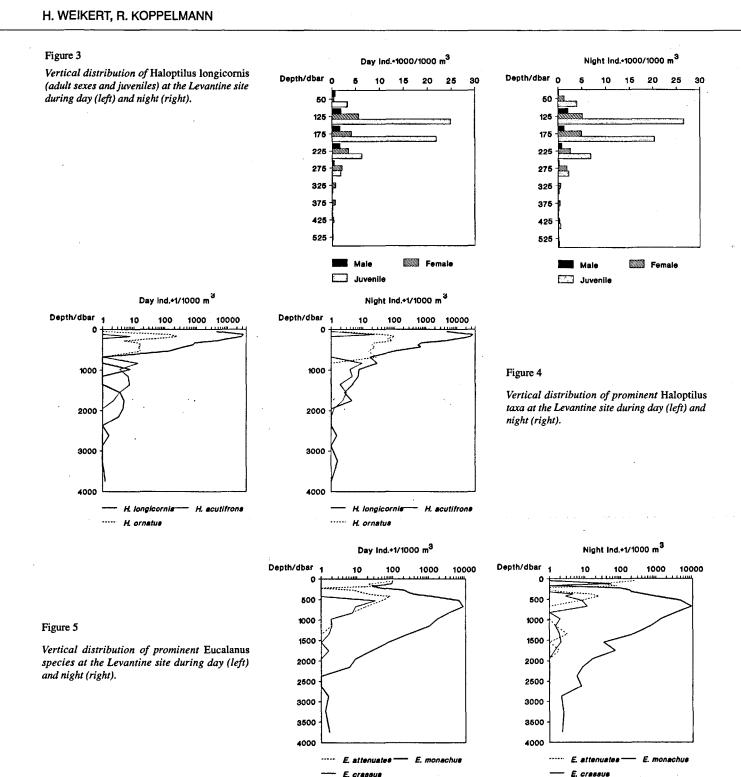


Table 5

Standing crop of Lucicutia species below 1050 m at the Levantine site. RA = relative abundance.

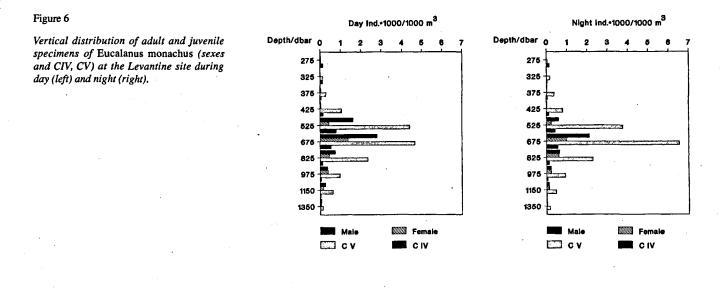
	D	ay	Nig	ht
	Ind./m ²	RA	Ind./m ²	RA
L. longiserrata	66.0	90.3	103.5	94.7
L. curta	0.4	0.5	0.5	0.5
L. pera	2.4	3.3	1.7	1.6
L. clausi	1.0	1.4	0.5	0.5
L. spp.	3.3	4.5	3.1	2.9
Total	73.1	100	109.3	100

tribution, were congregated in the upper 600 m of the water column. Their erratic numbers at greater depths point to contamination, so that the total standing crop in Table 5, which is based on the *Lucicutia* counts from the bathypelagic zone, is probably overestimated. *L. longiserrata* contributed some 90 % to these numbers.

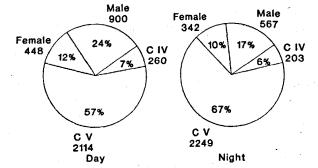
Central Red Sea

The increased relative abundances of Calanidae and Eucalanidae in the subsampled 50-200 m layer, which approximated the range of the thermohalocline, was due to the sharp diminution of individual copepods and zooplankton in general (Weikert and Koppelmann, in prep.). As previously

DEEP-LIVING ZOOPLANKTON INTEROCEANIC COMPARISON







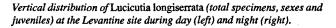
shown (Weikert, 1980 a; b; 1982), the prominently involved Calanus tenuicornis and Rhincalanus nasutus attained their maximum concentrations at different layers: C. tenuicornis elsewhere in the top 100 m depending on day-time and R. nasutus in the midwater oxygen minimum zone. In contrast with the above studies, part of the population of R. nasutus was in an active life-phase: copepodids younger than stages VI and V made up 60 % of the standing crop, mainly distributed at shallower depths at 200 to 300 m along the strong oxygen gradient, while the concentration peak of older stages coincided with minimum values between 400 and 450 m.

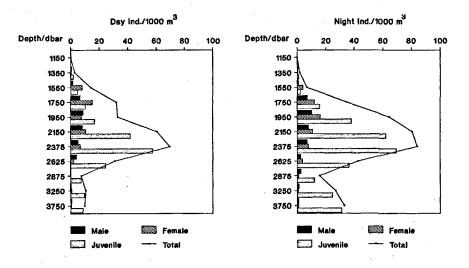
Haloptilus longicornis was abundant in the upper mesopelagic zone of the central Red Sea and, much as it did at the Levantine site (Fig. 2), it caused the dominance of Augaptilidae at 100 to 150 m (Fig. 9). However, the species was less "important" in this layer when compared to the Levantine site, with respect to both its numerical (~10,000 specimens/1000 m³) and percentage contributions (near to 40 %) to the calanoid fauna. Also, the standing crops of H. longicornis, and thus that of the family (Tab. 6), were less by an order of magnitude when compared to the Levantine counts (Tab. 4). As a further difference, female H. longicornis (day-night: 54.4 and 59.4 %) dominated the standing crop



Standing crop (specimens/m²) of Eucalanus monachus (sexes and juveniles) over the 4000 m water column at the Levantine site during day (left) and night (right).

Figure 8





over juveniles (35.8 and 39.1 %) and males (4.8 and 6.5 %). Bathymetrically, the species abounded at 50 to 150 m: females were dominant in the 50-100 m layer, but at 100 to 150 m juveniles outnumbered the adults (Fig. 10).

The standing crops of H. acutifrons and H. ornatus (Tab. 6) were markedly larger in absolute and relative numbers as compared to the Levantine site (Tab. 4). Like their Mediterranean counterparts, these species as well as H. longicornis showed a significant coherency in their day and night patterns (Fig. 9; rank correlation, P < 0.013). A comparable result was obtained for H. (?) plumosus (Fig. 9), while Euaugaptilus hecticus and an unidentified species were too sparsely recorded to be tested (Tab. 6).

Figure 9

Table 6

Taxa

H. longicornis

H. acutifrons

H. cf. plumosus

H. ornatus

H. sp.

E. hecticus

stages)

(all sexes and

Vertical distribution of prominent Haloptilus taxa at the central Red Sea site during day (left) and night (right).

Standing crop (specimens/m²) of augaptilid taxa (Haloptilus and

Euaugaptilus) over the 2250 m (day) and 1950 m (night) water column

in the central Red Sea. In parentheses: the relative abundance of sexes and juveniles refers to the respective species standing crop, the percenta-

Female

543

0.0

17.7

(54.4)

Day

Juvenile Total

999

(79.6)

(1.4)

0.0

17.7

(1.4)

1255

391

0.0

(39.1)

ge of the latter to the total crop of Augaptilidae.

Male

64.9

(6.5)

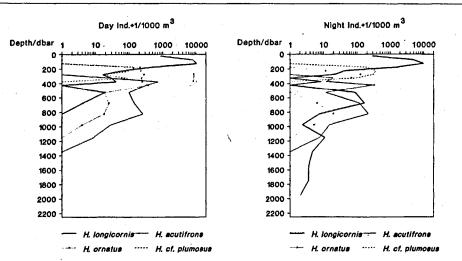
1.0

(0.7)

0.0

0.0

0.0



The concentration maxima were as follows: *H. longicornis* 10,000 specimens/1000 m³ at 50 to 200 m; *H. (?) plumo-sus* 200 specimens/1000 m³ at 150 to 350 m; *H. ornatus* 200 specimens/1000 m³ at 250 to 900 m; and *H. acutifrons* 500 specimens/1000 m³ at 350 to 1050 m (Fig. 9).

Pleuromamma indica constituted the predominant Metridinidae in the central Red Sea. Within the 250 to 1050 m zone of overall dominance (Fig. 2), juveniles were confi-

> ned mostly to the 250 to 300 m depth by day and adults to the 450 to 600 m depth, with peak abundances up to 37,000 and 13,500 specimens/1000 m³, respectively. At night, most juveniles migrated into the upper 100 m with a maximum concentration of 28,000 specimens/1000 m³ in the top 50 m. Adults were then most abundant in the contiguous 50-100 m layer where they attained 19,000 specimens/1000 m³ and outnumbered the juveniles.

> The composition of the standing crop was (day and night values given separately): juveniles, 50 and 38 %; females, 31 and 40 %; males, 19 and 22 %. In total, the results confirm the diel and spatial abundance patterns reported previously by Weikert (1980 *a*; *b*; 1982) and Beckmann (1984) for the entire Red Sea basin.

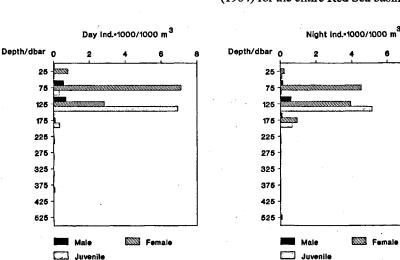


Figure 10

Vertical distribution of Haloptilus longicornis (sexes and juveniles) at the central Red Sea site during day (left) and night (right).

71.1 75.0 57.5 134 0.0 34.5 36.6 (56.2) (43.1)(10.7) (48.5) (51.5)(6.9) 31.6 39.4 47.5 86.9 0.0 17.7 13.9 (45.3) (56.0) (44.0) (3.1) (6.9) (54.7)0.0 17.5 17.5 0.0 0.0 47.8 47.8

0.0

Male

41.6

(4.8)

Night

Juvenile

309

0.3

(35.8)

Total

864

(84.0)

(4.6)

0.3

(<0.1)

14.5

(1.4)

1029

Female

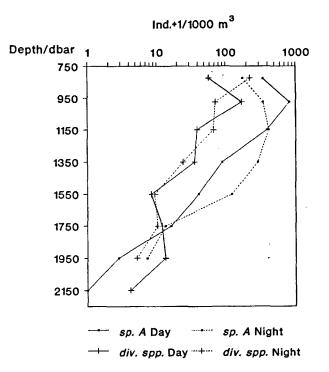
513

0.0

14.5

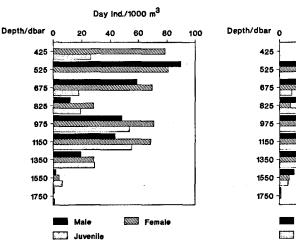
(59.4)

172





Vertical distribution of Scolecitrichidae (species A and others, spp.) below 750 m at the central Red Sea site.



Α number of unidentified yet Scolecitrichidae governed the calanoid standing crop in the bathypelagic zone (Fig. 2). The species A (Fig. 11) was dominant with 80 % among the family below 750 m. Juvenile stages prevailed by day and night (day, night both 46 % vs. females: 43 and 47 %, and males: 11 and 7 %, respectively). Maximum abundances of species A and the remainder were found in the 150 m-intervals from 750 to 1050 m (Fig. 11). The data do not indicate vertical migration.

Lucicutia paraclausi contributed only 0.9 % to the calanoid standing crop in the Red Sea, but its population is noteworthy as the species belongs to the few abundant deep-sea calanoids in the Red Sea. In addition, it is the only deep-living member of Lucicutiidae there (Weikert, 1982; Beckmann, 1984). The distribution pattern was similar by day and by night and bimodal with concentration maxima around 600 and 1100 m (Fig. 12). Among the copepodid stages, juveniles tended to abound at the depth of the deeper concentration peak.

DISCUSSION

Principal structural differences in the deep-living zooplankton population of the basins

Even slight differences in mesh size caused drastic taxonomical changes in our zooplankton samples, corroborating particularly designed studies (e. g. Barnes and Tranter, 1965; Nichols and Thompson, 1991). This is in contrast to the merely minor effects on the slope and the shape of the total zooplankton profiles (Weikert and Koppelmann, in prep.). A first comparison of 333 μ m Mocness samples and 300 μ m samples with a vertically towed multiple opening/closing net, MCN (Weikert and John, 1981) which were taken during the same period at the same site in the central Red Sea, showed a marked decrease of the calanoid copepod counts in the less coarse MCN samples in relative numbers compared with those of the cyclopoids and har-

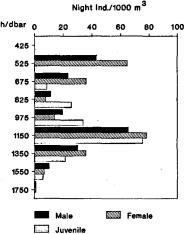


Figure 12

Vertical distribution of Lucicutia paraclausi (sexes and juveniles) at the central Red Sea site below 400 m during day (left) and night (right).

Table 7

Standing crop and relative abundance (RA) of the "traditional" major copepod groups in the upper 1050 m of the central Red Sea calculated from different mesh sizes of a single profile each.

	MOCNESS,	333 μm	MCN, 300 µm			
	Ind./m ²	RA/%	Ind./m ²	RA/%		
Calanoida	14 474	88.7	13 604	65.9		
Cyclopoida s.l.	1 840	11.3	6 448	31.2		
Harpacticoida	12	< 0.1	604	2.9		
Total	16 326	100.0	20 656	100.0		

pacticoids (Tab. 7). According to Bernhard *et al.* (1973), this tendency may also reflect a reduced loss of small individuals through the net mesh due to the lower towing speed of the MCN (*ca.* 1 kn vs. 2 kn of the Mocness). This is despite the fact that the shift of the proportions is in agreement with the prominent role of in the small size groups of Red Sea copepods which was reported for fractionized 100 μ m MCN samples from the central area (Böttger, 1987).

Our directly comparable data set identified striking interoceanic differences concerning the relative abundance of the main constituents of the zooplankton, the copepods, and their gross composition at different taxonomical levels. Copepods were numerically most abundant in the NE Atlantic, where they consistently accounted for 85 to 90 % of the total zooplankton in subsurface waters. Ultimately, this high percentage was mainly due to the outstanding calanoid group, but cyclopoids s.l. were also more important throughout the water column than in the Red Sea and the Levantine Sea (Fig. 1). Compared to the Atlantic, cyclopoids showed a distinct minimum in their relative abundance in intermediate layers, from 400 to 1 450 m in the Red Sea and from 600 to 1450 m in the Levantine Sea. According to 100 mm mesh size samples from the upper 1000 m in the central Red Sea (Böttger, 1985; 1987), this pattern reflects inversely related changes in relative size with depth in these taxa: it increased in calanoids but decreased in cyclopoids, mainly due to the dominance of small Oncaea species in the latter group. The biological implications have yet to be understood. A possible explanation may be differential predation. Grice et al. (1980) found in enclosed ecosystem experiments that the copepod Corycaeus anglicus was not preyed upon by ctenophores as were other copepods of similar size.

Harpacticoids were absent from our samples in the Levantine Sea. Though rare, their relative abundance in both the other seas increased with depth, starting at 1450 m in the Red Sea and at 3250 m in the Atlantic. In the Atlantic, the distribution was bimodal due to the depth-limited occurrence of a number of polyspecific genera, whereas in the Red Sea *Macrosetella gracilis* was the sole harpacticoid in our samples which was spread throughout the water column (*e. g.* Böttger-Schnack and Schnack, 1989). Note, however, that the scant findings of harpacticoids in the two basins were operational; finer-sized nets yielded a number of small species (Delalo, 1966; Böttger, 1985).

Depth-related zonal dominances of a single species in the low-latitude ocean are well-known but from rather narrow zones (e. g. Longhurst, 1985), mainly from mesopelagic depths (Longhurst, 1981) and often associated with oxygen minimum layers (e. g. Alldredge et al., 1984; Vinogradov and Shushkina, 1982). Mesopelagic and, probably, bathypelagic dominances over an extended range of some hundreds of metres, as observed for the two basins, are typical of the boreal ocean (e. g. Ostvedt, 1955; Hattori, 1989) and attributed to instable ecosystems in general. Most likely, the reestablishment of the ecosystems in the basins towards an equilibrium is still in progress after the last species' emergence during the Pliocene glaciation. A condensed niche partitioning by additional links in the food web (e. g. Por, 1978; McGowan and Walker, 1979) may result in an overall more mature system.

The Lessepsian migration, faciliated by the artificial connection via the Suez Canal, exemplifies the free carrying capacity at least of the Levantine Sea. This permits the coexistence of endogenous Atlantic and immigrant Indo-Pacific faunas without the extinction of the former (Por, 1978). Well adapted to high temperatures and salinities, the Red Sea biota invade the almost tropical hydrographic setting (Oren, 1957) of the Levantine surface layer and add to a fauna of a subtropical-tropical design (Por, 1981; Bacescu, 1985). As observed in fishes, competition may lead to resource allocation and/or vertical habitat displacement of the local species to cooler subsurface layers (Por, 1978; Stergiou, 1988; Golani, 1988). By their provenance from the temperate Atlantic fauna living at the entrance of the Strait of Gibraltar, the allied local species in the Mediterranean are adapted to temperatures below 20°C. This value demarcates the annual surface isotherm which hydrographically encloses the Levantine Sea (Por, 1978).

In the lower-latitude ocean (e. g. Vinogradov, 1968; Longhurst, 1991) and also the Red Sea (Weikert, 1982; this study) a large portion of the midwater calanoids belongs in terms of numbers and biomass to species of families comprising typical interzonal diel migrators which perform long-range migrations. At the Levantine site, this component, including micronekton animals (Weikert, 1990), was unimportant, though the number of such species is higher in copepods (Delalo, 1966; Scotto di Carlo *et al.*, 1991) when compared to the monotypic interzonal copepod fauna (*Pleuromamma indica*) of the Red Sea.

The imprint on the deep-living community of the Levantine Sea by the prominent population of *Eucalanus monachus* resembled that of winter situations in boreal/temperate open ocean and eastern boundary current regions of relaxed upwelling periods. Their mid-water zooplankton communities are then dominated by a single "phytophagous" mass species of the families Calanidae and Eucalanidae (*e. g.* review by Vinogradov, 1968). They perform seasonal vertical migrations and can hibernate in diapause at depth in the course of their life cycle (reviews by Geynrikh, 1986; Conover, 1988). The age structure of *E. monachus* (Fig. 7) and the fact that virtually all individuals were filled with oil sacs unequivocally support this view.

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The life history of this ecological group of "interzonal", seasonal migrants (using the terminology of Vinogradov, 1968 and Conover, 1988) is intimately coupled with feeding on augmenting phytoplankton populations. Recent studies in the Levantine Sea, which has long been viewed as one of the most oligotrophic water bodies (Murdoch and Onuf, 1974; Berman et al., 1984 a; b), report on short-term events of markedly increased chlorophyll and primary production due to upwelling of nutrient-rich deep water in the centres of the long-lasting mesoscale eddies off Rhodes and Cyprus (Salihoglu et al., 1990; Krom et al., 1992). At present, general information (Pancucci-Papadopoulou and Siokou-Frangou, 1988; Siokou-Frangou, 1990; Pancucci-Papadopoulou et al., 1992) and hard data (this study) on the conspicuous dominance of E. monachus are restricted to the eddy-affected areas off Rhodes (Salihoglu et al.,

1990) and our site of SE Crete (Lacombe, 1990; Price *et al.*, 1990). This may be due to the poor stratified sampling of the deep water body of the basin, since the species is common from the Western Mediterranean to the Levantine Sea (Delalo, 1966; Scotto di Carlo *et al.*, 1991). But a designed study throughout a complete annual cycle in the Tyrrhenian Sea of the Western Mediterranean did not reveal a comparable dominance of any deep-living copepod species (Scotto di Carlo *et al.*, 1984). Also, two profiles from a site SW of Cyprus outside the area from where the local eddy has been observed yielded only a small 6 % contribution of *E. monachus* to the total calanoid standing crop (Trinkaus, 1988), supporting general observations from the Rhodes region (Siokou-Frangou, 1990).

Jenkins and Goldman (1985) suggested that transient eddies and pulses of wind-induced vertical mixing enhance new production and thus, overall primary productivity in the Sargasso Sea. The seasonal upward migration of the local midwater species *Eucalanus hyalinus* reported by Deevey and Brooks (1977) seems to be another example of seasonal vertical migration of an interzonal species which lives in a warm ocean outside the limits of coastal boundary currents.

Eddies are suggested to be an important mechanism affecting the distribution and abundance of zooplankton and fishes (e. g. Wiebe et al., 1976; Tranter et al., 1980). Their species composition can contrast markedly with that of the contiguous waters (e. g. Wiebe et al., 1976; Wiebe and Flierl, 1983; Beckmann et al., 1987). However, differences in the Levantine fauna should only be displayed by a shift in the proportions of deep-living species; Scotto di Carlo et al. (1991) reported the uniform taxonomic nature of the larger-sized copepod fauna in the upper 2000 m throughout the entire Mediterranean Sea.

The spatial scales of the eddies are large in relation to the total area of the Levantine basin. Therefore, their ecological role must be significant as compared to the great oceans. Adopting the results presented by Krom *et al.* (1992), we find enhanced production in anticyclonic gyres such as that in our study area (Price *et al.*, 1990) to be limited to vertical convection in winter, "over a limited period of time" (Krom *et al.*, 1992, abstract) which contrasts with the situation of the cyclonic type near Rhodes (Salihoglu *et al.*, 1990). In the course of the year, the eddies change their geographic position, and a number of them (except the aforementioned ones) change from anticyclonic to cyclonic rotation and vice versa (Salihoglu *et al.*, 1990). This scenario should imply overall environmental instability and thus variation in plankton community structure in time and space on a mesoscale.

Mesoscale eddies also exist in the Red Sea (e. g. Quadfasel and Baudner, in press). Unlike those in the Levantine Sea, they obviously do not significantly influence the relative proportions of dominant species of the deep-living zooplankton community. This was well investigated by stratified narrow sampling with 100 and 300 µm nets along the axial trough between the basin entrance in the south and 25°N at a monthly scale of a composite annual cycle (Weikert, 1980 b; 1982; Beckmann, 1984; Böttger-Schnack, 1990). The disturbance of the uniform structure of the subsurface copepod assemblage in the southernmost part originates from the mass import of obviously moribund Eucalanus species from the Gulf of Aden (Beckmann, 1984). Calanoides carinatus, a temporary mass species in regions of coastal upwelling like the Gulf of Aden (Gapishko, 1972; 1980), has not been encountered in the Red Sea basin where, for the most part, surface temperatures seem to be too high to allow a distinct mass occurrence of "cold" water coarse filterers. This can also be concluded from the increased abundance and surfacing of the eucalanid Rhincalanus nasutus in the northernmost Red Sea in January (Kornilova and Fedorina, 1970) when the local surface temperature drops to 22°C (e. g. Morcos, 1970). In the permanently stratified larger part of the Red Sea, the species has been observed exclusivelyto exist in diapause in the oxygen minimum layer in low numbers at mesopelagic depths during most of the year (Weikert, 1980 a; b; 1982; Beckmann, 1984). Our present data, though indicating reproductive activity of the species in the central Red Sea for the first time, document a negligible overall concentration and standing crop among calanoids (Tab. 3) which has no influence whatsoever on the consistency of the basic structural pattern.

The final conclusion is that the basins exhibit distinct differences in the functioning of their pelagic systems due to the acting role of long-lasting eddies in the Levantine Sea. In general, the deep Levantine Sea system would appear to be more variable than that of the Red Sea. This is despite the fact that the deep-living zooplankton is qualitatively similar in both seas with respect to the diminished total abundance, the low number of species and the existence of subsequent, distinct depth-related zonal dominances of a one single species of a family are concerned.

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