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Mesozooplankton distribution from Sicily to Cyprus (Eastern Mediterranean): I. General aspects

Mesozooplankton
Distribution
Eastern Mediterranean Sea

Mésozooplancton
Répartition
Méditerranée orientale

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ABSTRACT

The first synoptic basin-wide oceanographic survey in the Eastern Mediterranean Sea was carried out in October-November 1991 within the framework of the international programme POEM-BC (Physical Oceanography of the Eastern Mediterranean - Biology, Chemistry). Mesozooplankton samples were collected at 32 stations in the Sicily Channel, Ionian Sea, Cretan Sea, Cretan Passage, Rhodes area and central Levantine Sea. Vertical hauls were taken from four discrete depth layers in the upper 300 m water column. The gross features of the mesozooplankton communities, at the phyla, class or order level, are described. Depth-integrated abundances showed high homogeneity within each region, with the highest and lowest values recorded in the Sicily Channel (mean: 200 ind. m^{-3}) and in the Cretan Sea (mean: 45 ind. m^{-3}), respectively. Strong vertical gradients in zooplankton distribution were evident at all stations, the 0-50 m layer being the richest in numbers, whereas numbers sharply decreased at 100 m depth. Copepod relative abundances accounted for approximately 80% of the total zooplankton numbers, while ostracods (6.4%), chaetognaths (4.2%), appendicularians (4%) and pteropods (1.7%) followed in rank order. It seems that the zooplankton distribution is not always influenced by local meso-scale dynamics, but only when the physical forcing is strong and persistent over time, as in the Rhodes gyre area.

RÉSUMÉ

Répartition du mésozooplancton entre la Sicile et Chypre (Méditerranée orientale) : I. Aspects généraux.

La première campagne océanographique synoptique à l'échelle de la Méditerranée orientale a été réalisée en octobre-novembre 1991 dans le cadre du programme international POEM-BC (Océanographie physique, biologie et chimie de la Méditerranée orientale).

Des échantillons de mésozooplancton ont été collectés en 32 stations situées dans le canal de Sicile, la mer Ionienne, la mer de Crète, le détroit de Crète, les zones nord-occidentale (Rhodes) et centrale de la mer du Levant. Des pêches verticales ont été réalisées entre la surface et quatre profondeurs situées dans les 300 premiers mètres de la colonne d'eau. Les principales caractéristiques des communautés mésozooplanctoniques sont décrites au niveau des phyla, des classes ou des ordres. Les abondances intégrées sur la profondeur montrent une grande homogénéité au sein de chacune des régions. Les valeurs maximales et minimales ont été enregistrées respectivement dans le canal de Sicile (moyenne de 200 ind. m^{-3}) et dans la mer de Crète (moyenne de 45 ind. m^{-3}). De forts gradients verticaux dans la distribution verticale du zooplancton sont observés à toutes les stations. Le nombre d'individus est maximal dans la couche de 0-50 m et décroît fortement à 100 m. Les Copépodes représentent environ 80 % du nombre total d'individus zooplanctoniques, alors que les abondances relatives des Ostracodes, des Chaetognathes, des Appendiculaires et des Ptéropodes sont respectivement de 6,4 %; 4,2 %; 4 % et 1,7 %. Il semble que la distribution du zooplancton n'est pas toujours influencée par la dynamique locale à méso-échelle, sauf quand le forçage physique est fort et persiste dans le temps, comme dans la région du gyre de Rhodes.

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INTRODUCTION

Only recently has the Eastern Mediterranean Sea (EMED) attracted the interest of marine scientists, and most of the new studies have focused on the physical oceanography of the basin. Under the auspices of the international programme POEM (Physical Oceanography of the Eastern Mediterranean), detailed research on the circulation in the EMED has been conducted since 1985 (Robinson *et al.*, 1991; POEM group, 1992 and references therein). The main hydrological feature of the EMED is the mesoscale dynamics, characterized by complex patterns of cyclonic and anticyclonic gyres linked by jets and current segments, most of them being permanent or interannual structures (Robinson *et al.*, 1987). Some of the permanent mesoscale structures have been shown to heavily influence the local dynamics, affecting the distribution of nutrients and, as a consequence, the biological activity. The cyclonic circulation enriches the euphotic zone through the upwelling of nutrient-rich deep waters. Higher values in comparison with the surrounding areas were recorded in the Rhodes gyre for chlorophyll *a* (Salihoglu *et al.*, 1990), and in the Cyprus eddy for primary production (Krom *et al.*, 1992), for bacterial numbers and production as well as abundance of heterotrophic nanoplankton (Zohary and Robarts, 1992). On the other hand, downwelling processes occur in the anticyclonic areas, leading to an impoverishment of the surface waters. This is the case of the anticyclonic eddies surrounding the Rhodes gyre, where the nutricline fell to 250-300 m and the primary production was half of the value in the central part of the Rhodes gyre, during the same period (Salihoglu *et al.*, 1990).

The Mediterranean Sea is considered to be one of the most impoverished marine regions and the Eastern Basin is the most oligotrophic area. With very low chlorophyll concentrations, the EMED is classified as a "marine desert" (Azov, 1991). Notwithstanding the ecological interest of this basin, the literature on its pelagic biological domain is limited. In particular, data on zooplankton communities in the EMED are from different periods and areas. In some cases, only qualitative information is given and quantitative data are not easily comparable due to different sampling techniques and mesh size employed (Greze, 1963; Delalo, 1966; Pavlova, 1966; Kimor and Berdugo, 1967; Moraitou-Apostolopoulou, 1972; Siokou-Frangou *et al.*, 1990). During recent years, most studies mainly focused on the vertical distribution at a single or a few stations (Vaissière and Seguin, 1988; Weikert and Trinkhaus, 1990; Scotto di Carlo *et al.*, 1991; Pancucci-Papadopoulou *et al.*, 1992; Weikert and Koppelmann, 1993).

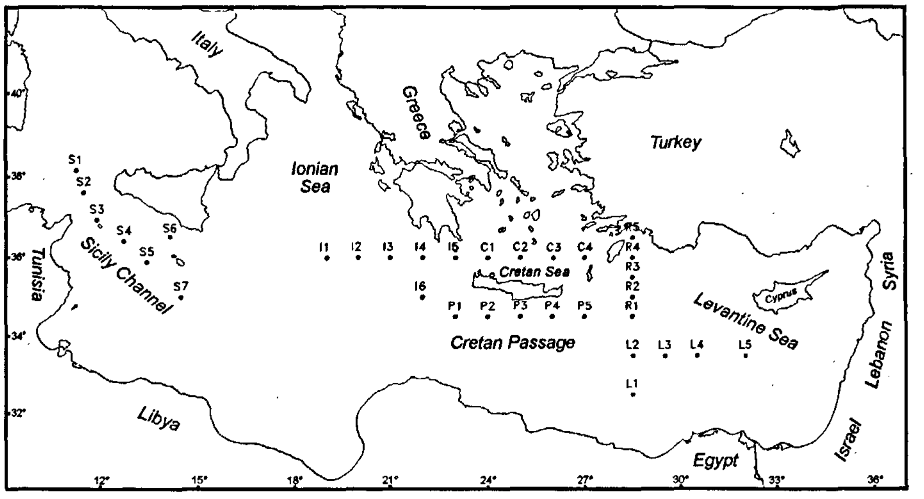
In the frame of the POEM-BC (Biology and Chemistry) programme, coordinated international cruises were carried out throughout the EMED in October-November 1991. They provided the first basin-wide synoptic survey, collecting information spanning from physics to zooplankton ecology. In this paper, which is the first of two complementary papers on mesozooplankton in this area, we present total abundances and group composition analysed in 123 uniformly collected samples. The aim of this study is to contribute to a better understanding of the pelagic ecosystem in the EMED.

MATERIALS AND METHODS

A multi-vessel quasi-synoptic survey (POEM-BC-O91) was conducted in October-November 1991. Oceanographic data (physical, chemical and biological) were acquired on a grid of stations covering a major area of the EMED. Details of the above procedures are reported elsewhere (POEM Scientific report # 9, 1993). Mesozooplankton quantitative samples were collected at 32 stations in the Sicily Channel (Italian vessel R/V *Minerva*), eastern Ionian Sea, Cretan Sea, Cretan Passage (western Levantine Sea), Rhodes area (north-western Levantine Sea) (Greek vessel R/V *Aegaio*) and in the central Levantine Sea (Israeli vessel R/V *Shikmona*) (Fig. 1). The stations were located along transects chosen on the basis of the known circulation patterns, some of them in areas with permanent hydrological features. The scheme of the sampling design is presented in Table 1. Zooplankton samples were collected in the upper 300 m of the water column. Vertical hauls were taken at a speed of 1 m s^{-1} from four depth layers (0-50 m, 50-100 m, 100-200 m, 200-300 m) using a closing WP-3 net (113 cm mouth diameter, 200 μm mesh aperture). Replicated samplings were not performed. Due to malfunction of the closing mechanism during the hauls, the following layers were not sampled: 200-300 m at St. L1 and 100-200 m at St. L3; at St. S7 quantitative samples were only taken at the 0-50 m and 0-300 m layers. For each tow, the volume (m^3) of filtered water ($V = A \times \Delta L$) was

Figure 1

Map of the Eastern Mediterranean (EMED) and stations sampled during the POEM-BC-O91 cruise.



estimated taking into account the area of the net mouth (A) and the difference in winch readings (L_i-L_f). The thickness of the sampled layer (ΔD) and the depth limits (L_i, L_f) were computed taking into account the wire angle α ($\Delta D = \Delta L \cos \alpha$). Particular care was taken in maintaining wire angles always below 10-15°. For this reason, we report in the figures the nominal values of layer limits. The net was carefully rinsed after each haul. Samples were fixed immediately after collection and preserved in a 4% buffered-formaldehyde sea-water solution. All specimens were identified and counted in an aliquot (1/4) of the entire sample for the rich surface (0-50 m) collections, using the HML beaker technique (Van Guelpen *et al.*, 1982). The counts were performed on the entire sample for all deeper collections. Zooplankton data classified at the phyla, class or order level are presented.

Table 1

Station data for the POEM-BC-O91 cruise in the Eastern Mediterranean. Station names are the official codes; station numbers have been arbitrarily chosen here for conciseness, and to reflect a geographical criterion (W-E and S-N direction).

Location *Vessel*	Station name	Station number	Date	Lat. N	Long. E	Sonic depth (m)	Local time
Sicily Channel	5003	S7	6 Oct.	35°00.35	14°28.75	509	0010
R/V Minerva	5302	S6	7 Oct.	36°30.71	14°00.05	611	0050
	82	S5	7 Oct.	35°52.29	13°25.29	784	0900
	75	S4	9 Oct.	36°24.63	12°43.44	1267	0015
	56	S3	13 Oct.	36°55.96	11°53.78	561	2105
	47	S2	17 Oct.	37°36.96	11°29.51	742	1615
	38	S1	18 Oct.	38°09.37	11°15.18	449	1300
Ionian Sea	25307	I5	15 Oct.	36°00.00	23°00.00	910	1600
R/V Aegaio	26203	I4	16 Oct.	36°00.00	22°00.00	3340	0900
	26102	I3	17 Oct.	36°00.00	21°00.00	3140	0300
	26002	I2	17 Oct.	36°00.00	20°00.00	3190	1000
	36903	I1	18 Oct.	36°00.00	19°00.00	3500	0030
	25202	I6	19 Oct.	35°00.00	22°00.00	3200	1100
Cretan Passage	24303	P1	26 Oct.	34°30.00	23°00.00	2600	0200
R/V Aegaio	24405	P2	28 Oct.	34°30.00	24°00.00	2100	0400
	24502	P3	6 Nov.	34°30.00	25°00.00	1920	1000
	24603	P4	6 Nov.	34°30.00	26°00.00	3000	1700
	24702	P5	7 Nov.	34°30.00	27°00.00	1550	1200
Rhodes area	24830	R1	7 Nov.	34°30.00	28°30.00	2400	0200
R/V Aegaio	25817	R2	8 Nov.	35°00.00	28°30.00	2750	0800
	25810	R3	9 Nov.	35°30.00	28°30.00	3500	1000
	26811	R4	9 Nov.	36°00.00	28°30.00	4350	1600
	26804	R5	11 Nov.	36°30.00	28°30.00	800	1400
Cretan Sea	26704	C4	12 Nov.	36°00.00	27°00.00	2500	0500
R/V Aegaio	26605	C3	12 Nov.	35°59.00	26°02.00	1050	1800
	26502	C2	13 Nov.	36°00.00	25°00.00	1500	0400
	26404	C1	13 Nov.	36°00.00	24°00.00	1200	1600
Levantine Sea	72	L5	5 Nov.	33°30.00	32°00.00	1950	1200
R/V Shikmona	76	L4	7 Nov.	33°30.00	30°30.00	2550	0700
	78	L3	7 Nov.	33°30.00	29°30.00	2850	1640
	80	L2	8 Nov.	33°30.00	28°30.00	3100	0030
	83	L1	8 Nov.	32°30.00	28°30.00	2800	1530

In order to assess similarities among stations in zooplankton communities, non-metric multidimensional scaling (MDS) was employed according to Field *et al.* (1982). Group abundances (ind. m^{-3}) were subjected to square root transformation and the Bray-Curtis similarity matrix was used.

The study area

Hydrological meso-scale features observed during the present cruise were the broad cyclonic area between Rhodes and Cyprus islands (comprising two or three cyclonic centres, including the Rhodes gyre), and the anticyclonic gyres Pelops (in the eastern Ionian Sea, south-west of Peloponnisos), Ierapetra (south-east of Crete) and Mersa Matruh (along the Egyptian coast) (Fig. 2). In addition, one cyclonic gyre in the Cretan Sea and one in the Sicily Channel were recorded (Budillon *et al.*, 1994; Yacobi *et al.*, 1995; A. Theocharis, pers. comm.).

The Sicily Channel connects the Eastern and Western Mediterranean, playing a crucial role in the water mass exchange between the two basins. In this region, the circulation is characterized by a two-layer system flowing in opposite directions: the surface Atlantic water (AW) eastward and the Levantine intermediate water (LIW) westward. The LIW is a steady structure in the hydrology of the Sicily Channel. In contrast, the surface flow displays meanders with high spatial and temporal variability (Manzella *et al.*, 1988; Moretti *et al.*, 1993). Relatively intense local phenomena such as cyclonic and anticyclonic gyres were frequently observed from the satellite imagery (Le Vourch *et al.*, 1992); most of them seem to be wind-induced (Piccioni *et al.*, 1988). During the present cruise, the surface AW occupied the upper 100 m layer over the entire Channel, and entered the Ionian Sea north of the Malta Island (Budillon *et al.*, 1994). The core was indicated by a salinity minimum of about 37.5 in the 30-50 m layer, particularly evident in the Tunisia sector. The LIW occupied the column down to the bottom. Its core was centred in the 250-300 m layer and was signed by a salinity maximum of 38.8 at the easternmost stations and 38.75 at the western exit of the Channel (Fig. 3). The pattern of dynamic height anomaly at 10/150 db showed the presence of a large cyclonic gyre in the central part of the Sicily Channel, related to upwelling of water from intermediate layers. This was also detectable in the dome-shaped distribution of physical parameters and oxygen data (Budillon *et al.*, 1994; Conversano *et al.*, 1996).

In the central EMED (eastern Ionian, Cretan Sea, Cretan Passage and Rhodes area), the main water masses are: the Modified Atlantic Water (MAW), characterized by a salinity minimum (37.5) in the upper 50 m layer; the LIW (14.5 °C, 38.9), whose range varies greatly down to 1000 m in areas of intense circulation features. Furthermore, the hydrography and circulation are characterized by complex structures whose spatial and seasonal variability was extensively examined by Theocharis *et al.* (1993). The north-western Levantine is greatly influenced by the presence of the Rhodes gyre, which is also one of the major sites of formation of the LIW. The outstanding circulation feature in the Ionian Sea is the persistent and strong Pelops anticyclonic gyre. In the Cretan Sea, the hydrography shows high spatial and temporal variability according to the season; the autumnal circulation is characterized by the existence of a large-scale cyclonic gyre (Zodiatis, 1993). The main water masses in the regions sampled during the POEM-BC-O91 cruise could also be identified at some representative zooplankton stations, as shown in Figure 3.

The physical structure of the water masses in the central and southern Levantine Sea during the POEM-BC-O91 cruise is reported by Yacobi *et al.* (1995). The upper layer from the surface to 35 m depth was occupied by the warm, high salinity Levantine Surface Water (LSW) (22 °C, 39.4). Below that, a narrow layer of AW (38.82) between 35 and 75 m, and the LIW (39.10) were recorded. This homogeneous pattern was disrupted only at the boundaries of the Ierapetra eddy, where the limit between LSW and AW occurred at about 200 m.

The overall range of the chlorophyll *a* concentrations in the upper 200 m of the water column was 0.01-0.33 $\mu g\ l^{-1}$ at the zooplankton stations (M. Montresor, O. Gotsis-Skretas and K. Pagou, unpublished data). In the Levantine Sea, the chlorophyll *a* range was 0.01-0.42 $\mu g\ l^{-1}$ (Yacobi *et al.*, 1995). The mean values within each basin spanned from 0.08 $\mu g\ l^{-1}$ in the Cretan Passage to 0.12 $\mu g\ l^{-1}$ in the Ionian Sea, this latter value being close to the overall mean measured in the western Ionian Sea during the same survey (Rabitti *et al.*, 1994). The pattern of vertical distribution of

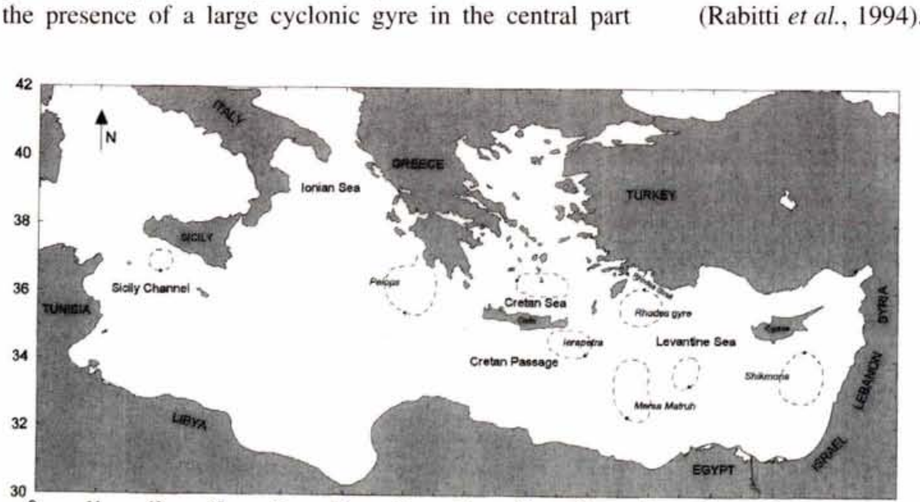


Figure 2

Map of the EMED showing the main gyres observed during the POEM-BC-O91 cruise.

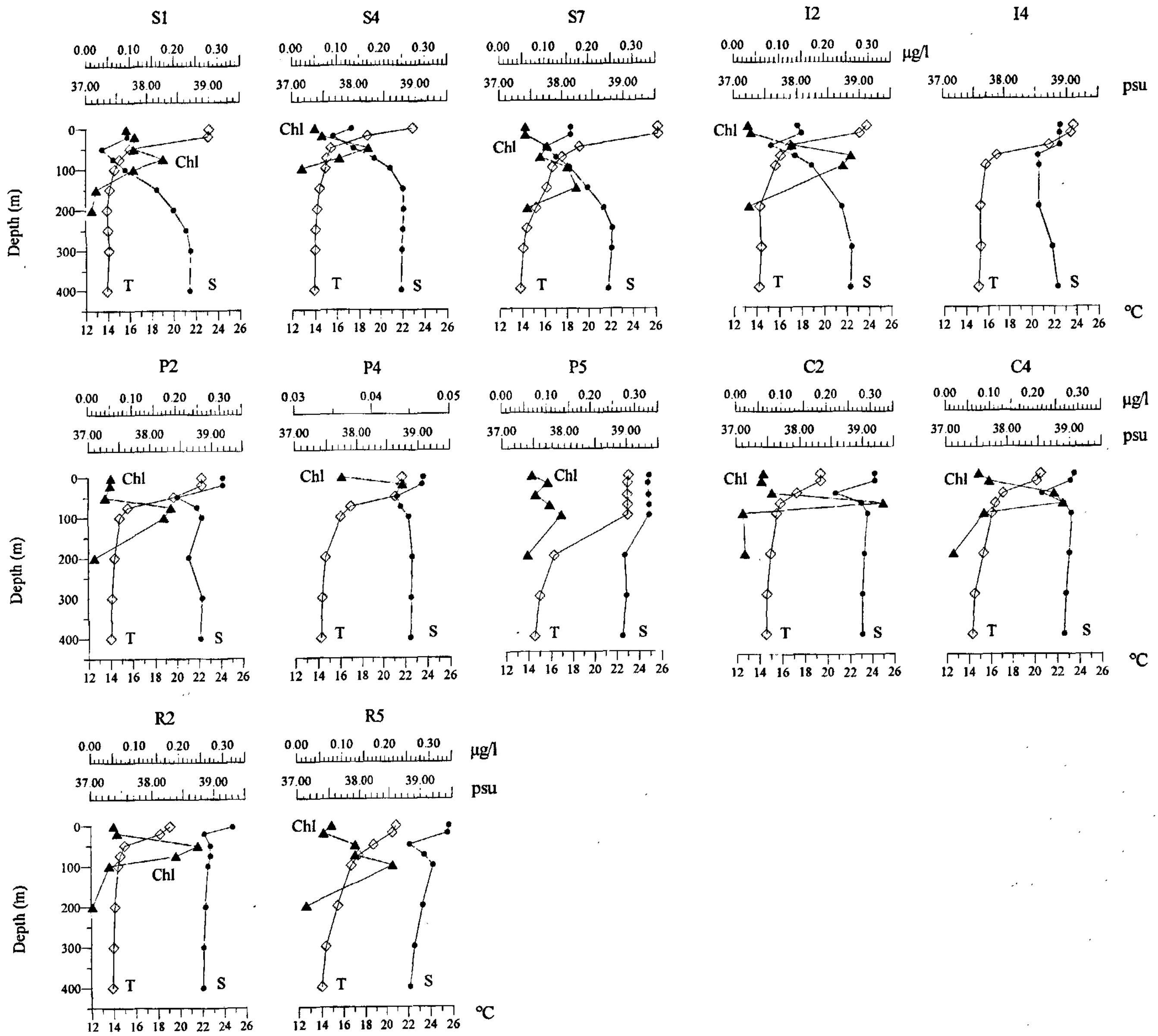


Figure 3

Temperature (T), salinity (S) and chlorophyll a *(Chl* a*) profiles at some representative zooplankton stations during the POEM-BC-O91 cruise in the EMED.*
S1, S4, S7: Sicily Channel; I2, I4: Ionian Sea; P2, P4, P5: Cretan Passage; C2, C4: Cretan Sea; R2, R5: Rhodes area. For the profiles in the central Levantine Sea, see Yacoby et al. *(1995).*

chlorophyll *a* was consistent throughout the EMED. A clear deep chlorophyll maximum (DCM) generally occurred at 75-100 m depth (Fig. 3). In the Levantine Sea, the DCM was located at 90-110 m depth (Yacobi *et al.,* 1995). This seems to confirm the deepening of the DCM in the Mediterranean in an eastward direction, as already observed by Berland *et al.* (1988).

RESULTS

Total zooplankton spatial distribution

Depth-integrated abundances (0-300 m) showed a spatial pattern, with the highest and lowest values in the westernmost and central regions, respectively (Fig. 4). The mean value recorded in the Sicily Channel was almost one order of magnitude higher than in the other areas (200 ± 47 ind. m^{-3}). The lowest values were obtained in the Cretan Sea (45 ± 11 ind. m^{-3}), while slightly higher abundances were recorded in the Cretan Passage (56 ± 6 ind. m^{-3}), in the Ionian Sea (62 ± 16 ind. m^{-3}), in the Rhodes area (66 ± 16 ind. m^{-3}), and especially in the central Levantine Sea (89 ± 12 ind. m^{-3}). General consistency in quantities among stations was evident within each area. Only at St. I5 in the Ionian Sea and at St. S7 in the Sicily Channel did depth-integrated abundances exceed by more than 50% the mean values for each transect (Fig. 4). One-way ANOVA results revealed no significant differences within areas but showed significant differences between areas ($F = 31.726$; $P < 0.001$; 5 d.f.). The Tukey test indicated a difference in total abundances between the Sicily Channel and all other areas, while the Cretan Sea and Cretan Passage differed from the central Levantine Sea.

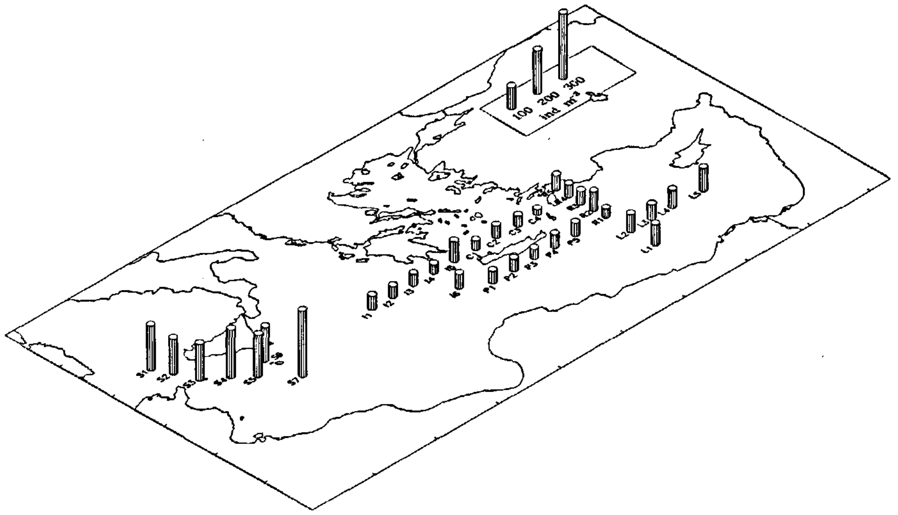


Figure 4

Depth-integrated values (0-300 m) of total zooplankton abundances (ind. m^{-3}) at each of the sampling sites. For each region, the mean abundance and its standard deviation are given in the text.

Vertical profiles of zooplankton distribution displayed strong gradients along the water column, the 0-50 m layer being the richest in terms of abundance (Fig. 5). In this layer, mean abundances ranged from 108 ind. m^{-3} (Cretan Sea) to 551 ind. m^{-3} (Sicily Channel). The highest value of surface total abundance was recorded in the easternmost part of the Sicily Channel (752 ind. m^{-3}, St. S7), while the lowest was recorded in the Cretan Sea (60 ind. m^{-3}, St. C4). Mean abundances decreased below the 100 m depth, and reached the lowest values in the 200-300 m

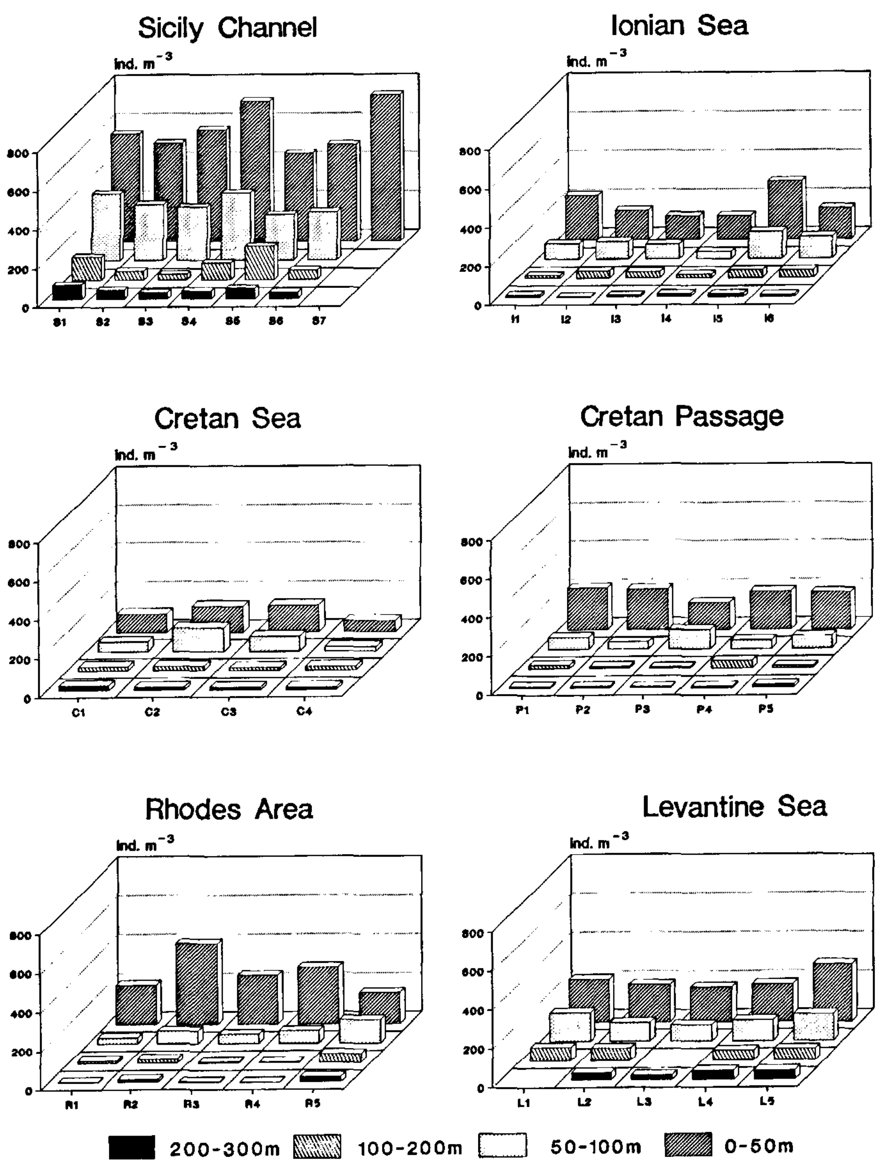


Figure 5

Distribution of total zooplankton abundances (ind. m^{-3}) both in horizontal and vertical scales in each of the regions explored in the EMED during the POEM-BC-O91 cruise.

layer. In the deepest layer, the extreme low value (1.4 ind. m^{-3}) characterized St. R4 in the Rhodes area. The pattern of vertical distribution of total abundances was different among areas (Fig. 5). In the Rhodes area and in the Cretan Passage, the surface abundances were by far the highest when compared to the other layers; the ratio of total zooplankton numbers in the upper 100 m to those in the 100-200 m layer was 9.6 and 7.5, respectively, in comparison with 2.8-5 in the other regions. At most of the stations in the Rhodes area, surface numbers represented more than 80% of the standing stock in the whole water column, whereas the 200-300 m layer accounted for only 3% of the total column values. However, St. R5 differed from the other stations by having higher densities below 50 m. In the other regions, the decrease of zooplankton standing stock with depth was smoother; in the central Levantine and Cretan Sea, the 200-300 m layer accounted for about 10% of the numbers present in the whole water column.

Two-way ANOVA showed significant differences of the total zooplankton abundances between layers ($F=172.31$; $P<0.001$; 3 d.f.) and between areas ($F=33.64$; $P<0.001$; 5 d.f.). Significant interactions of depth on area were also revealed ($F=2.55$; $P<0.05$; 15 d.f.), suggesting differences among areas in terms of vertical distribution patterns. In order to determine whether the variability in the vertical distribution could be attributable to zooplankton diel vertical migrations, a two-way ANOVA test between depth ranges and day/night samples was performed. No significant differences ($F=0.034$; $P>0.05$; 1 d.f.) between day/night samples were detected.

Group composition

Copepod abundances accounted for some 80% of the total zooplankton collected during the present cruise, followed by ostracods (6.4%), chaetognaths (4.2%), appendicularians (4%) and pteropods (1.7%). Polychaetes (0.7%), siphonophores (0.5%), euphausiids (0.4%), medusae and cladocerans (0.3%) occurred with lower density values. The mean values of total zooplankton abundances and taxa composition are reported in Table 2 for each transect. Horizontal and vertical distributions are shown in detail for some of the major groups (Figs. 6-10).

Copepods clearly dominated the zooplankton assemblages. Their numbers ranged from 1 to 571 ind. m^{-3} in all the samples combined, minimum and maximum values being recorded in the Rhodes area (St. R4, 200-300 m) and in the Sicily Channel (St. S7, 0-50 m), respectively. They generally accounted for more than 70% of total zooplankton (Fig. 6) and only in 15 out of 123 samples was their percentage lower; it declined to 45.5% at St. P5 in the 100-200 m layer (where ostracods reached 22%). Copepods showed generally a slight decrease in relative abundances with depth but in the Sicily Channel this trend was not observed, since they still accounted for 83% in the 200-300 m layer. A detailed study of the copepods at species level was performed by Siokou-Frangou *et al.* (1997).

Ostracods contributed significantly to overall zooplankton (Fig. 7). Their relative abundances were consistent throughout the sampled areas, showing a slight but constant increase with depth. In the Cretan Passage, they comprised up to 10% of the total zooplankton (mean for all stations),

Table 2

Distribution of the taxonomic groups (%) and of the total zooplankton (mean abundances as ind. m^{-3} and ind. m^{-2}) in each of the areas sampled during the POEM-BC-O91 cruise in the Eastern Mediterranean.

	Sicily Channel	Ionian Sea	Cretan Sea	Cretan Passage	Rhodes aera	Levantine Sea
Medusae	0.34	0.34	0.07	0.05	0.17	0.86
Siphonophora	0.17	0.87	0.12	0.93	0.41	0.65
Ctenophora	0.01	0.00	0.00	0.01	0.00	0.02
Heteropoda	0.04	0.00	0.01	0.00	0.00	0.02
Pteropoda	2.07	0.56	1.00	2.32	2.94	1.37
Mollusca larvae	0.01	0.00	0.00	0.01	0.00	0.02
Polichaeta	0.56	0.47	0.26	1.07	0.88	0.82
Cladocera	0.42	0.53	0.09	0.13	0.46	0.02
Copepoda	81.83	79.11	88.57	77.21	74.68	82.91
Ostracoda	5.43	6.55	4.27	9.61	6.61	5.57
Euphausiacea	0.08	0.81	0.20	0.77	0.41	0.16
Decapoda larvae	0.34	0.05	0.00	0.06	0.01	0.40
Decapoda (*Lucifer*)	0.08	0.03	0.03	0.20	0.02	0.01
Mysidacea	0.00	0.05	0.02	0.02	0.00	0.00
Isopoda	0.04	0.00	0.06	0.15	0.00	0.05
Amphipoda	0.18	0.17	0.05	0.47	0.31	0.12
Chaetognatha	2.43	8.09	3.22	5.86	3.53	1.52
Echinodermata larvae	0.04	0.03	0.01	0.01	0.01	0.03
Appendicularia	5.49	2.04	1.90	0.78	9.44	4.17
Pyrosomida	0.01	0.00	0.00	0.00	0.01	0.01
Doliolida	0.02	0.17	0.03	0.11	0.04	0.20
Salpida	0.25	0.01	0.01	0.01	0.03	1.06
Pisces eggs + larvae	0.15	0.11	0.07	0.09	0.05	0.03
Total zooplankton (ind. m^{-3})	264	79	55	70	89	114
Total zooplankton (ind. m^{-2})	60003	18701	13490	16827	19867	23097

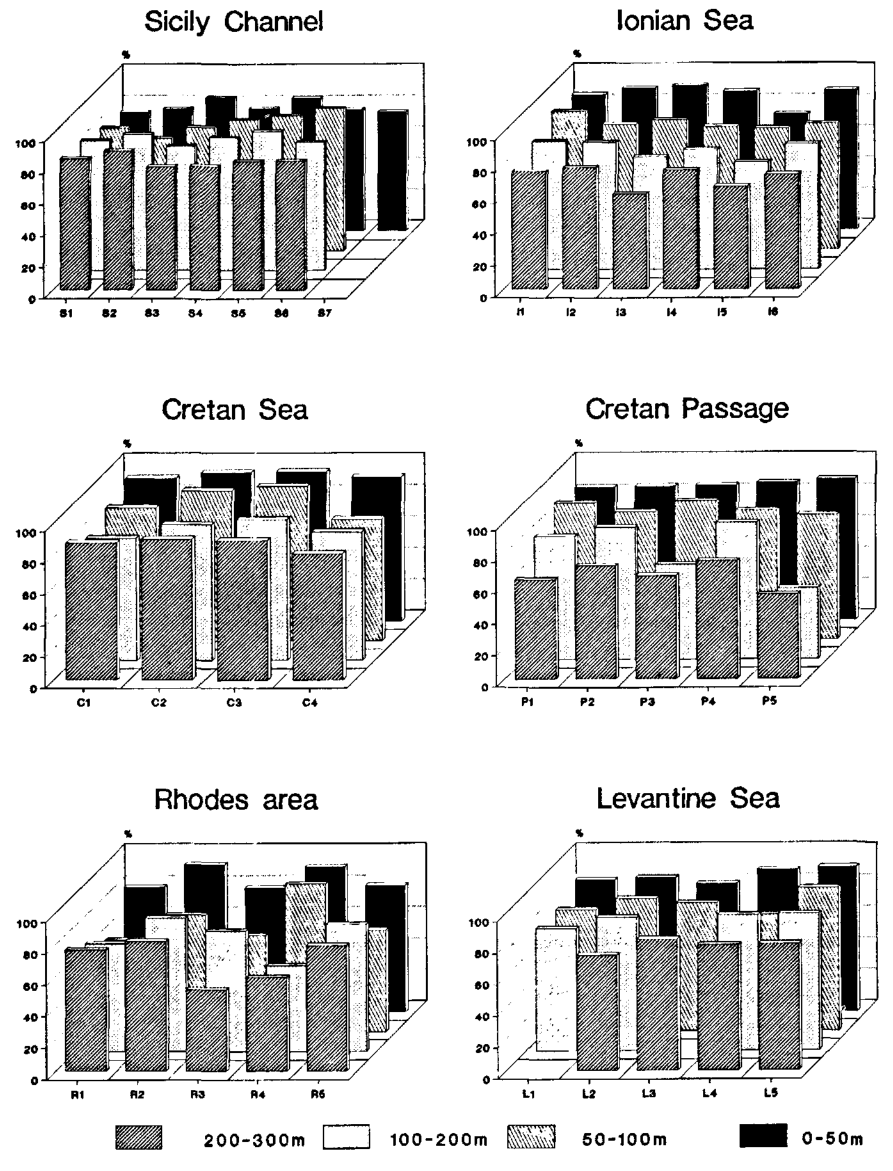


Figure 6

Distribution of the percentages of copepods on total zooplankton abundances at each station and depth layer during the POEM-BC-O91 cruise in the EMED.

while their presence was generally low in the Cretan Sea. Maximum abundace recorded was 19 ind. m^{-3} (St. R3, 0-50 m).

Chaetognaths showed higher percentages of total zooplankton in the Ionian Sea (8%) and Cretan Passage (5.9%) (Fig. 8). In other areas, they ranged from 1.6% to 3.5%, with the lowest mean values in the central Levantine Sea and Sicily Channel. Their presence was generally low in the Cretan Sea, except at station C1, the closest to the Ionian transect. A gradual increase in relative abundances with depth was observed; only at St. P3 was the percentage value noteworthy (19%) in the 100-200 m layer. Chaetognaths reached maximum density value of 48 ind. m^{-3} in the Sicily Channel (St. S4, 0-50 m).

Appendicularians were relatively abundant in the Rhodes area (9.4%), Sicily Channel (5.5%) and central Levantine Sea (4.2%), whereas in the Cretan Passage they accounted for only 0.8% of zooplankton numbers (Fig. 9). They were well represented down to the 200 m depth, but the highest densities were generally recorded in the 50-100 m layer, where they comprised on average 7.2% of total zooplankton. Maximum density was 84 ind. m^{-3} (St. S1). In the Rhodes area, at all stations but one, they showed very high percentages in the 50-100 m layer (20.2-28.4%). In the Cretan Sea, appendicularians were abundant only at St. C4, close to the Rhodes area. In the Sicily Channel, where the highest abundance was recorded (84 ind. m^{-3}, St. S1), their percentages decreased in a west-east direction.

Pteropods were represented mostly by thecosomes and showed a narrow range of mean percentages throughout the sampled areas (0.6-2.9%), with higher values generally in the surface layer. However, they showed a very variable distribution in both horizontal and vertical scales (Fig. 10). The highest density value (120 ind. m^{-3}) was recorded in the Sicily Channel (St. S7, 0-50 m), while the highest percentage (19.2%) was recorded in the Rhodes area (St. R3, 200-300 m).

Siphonophores contributed as little as 0.5% of total zooplankton in all the samples combined. The mean percentage rose slightly only in the Ionian Sea and in the Cretan Passage (0.9%). This group was much more important in the upper 100 m (0.7%) and only in the areas of higher densities did their relative abundances reach up to 4% in deeper waters (St. P5). Horizontal gradient was evident in the Cretan Passage, where percentages increased in a west-east direction.

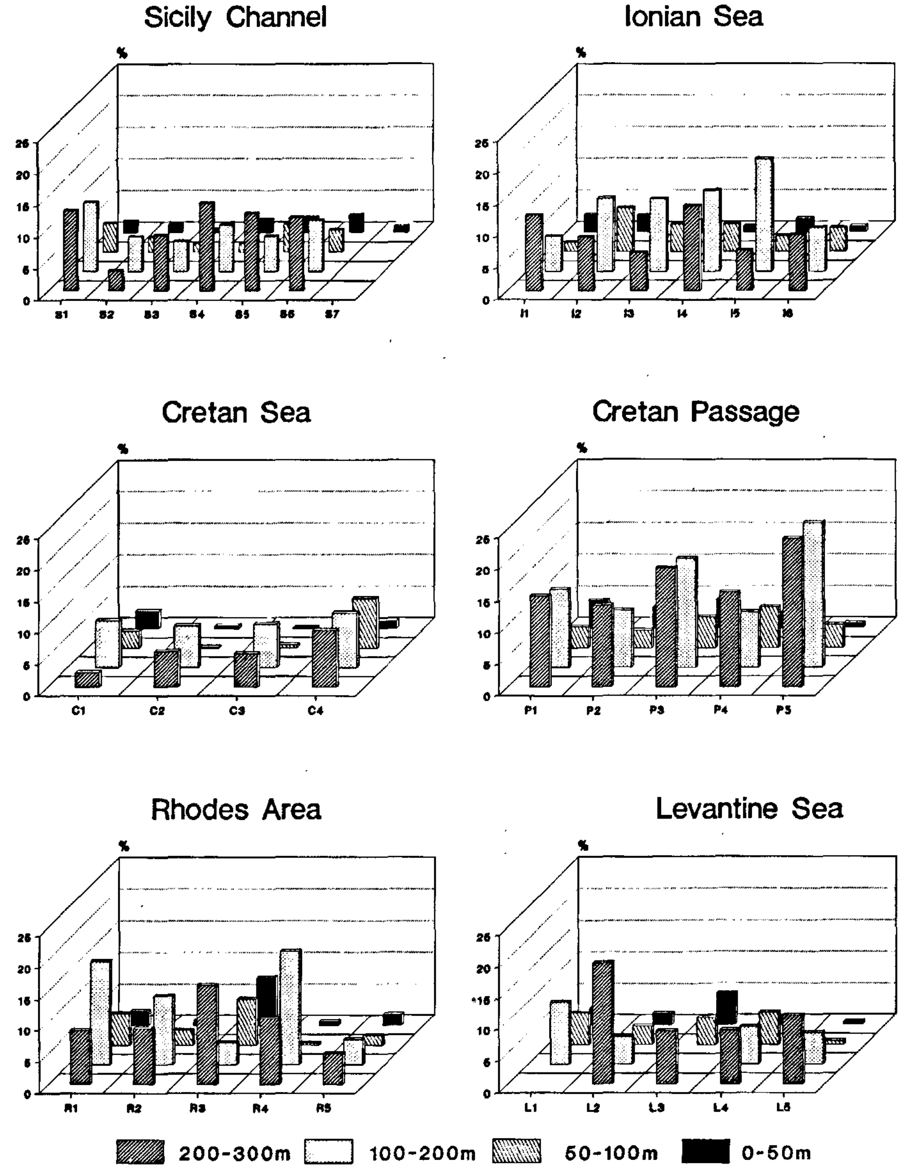


Figure 7

Distribution of the percentages of ostracods on total zooplankton abundances at each station and depth layer during the POEM-BC-O91 cruise in the EMED.

Cladocerans accounted for only 0.3 % of total zooplankton, with a scattered distribution throughout and within regions. They were more important in the Sicily Channel (up to 4.6%) and at the northernmost station in the Rhodes transect (5.8%, St. R5). However, the highest abundance was recorded at the western station of the Ionian Sea (37 ind. m^{-3}, St. I1). Cladocerans occurred in higher numbers in the surface layer and their presence was sporadic below 50 m depth. A particular vertical distribution of this group occurred at St. R5, with percentage values of 2.5%, down to the 300 m depth.

Salps were important only in the central Levantine Sea in the 50-100 m layer (2.7%). Other taxa occurred with negligible numbers and very patchy distribution; *e.g.* the pelagic decapod *Lucifer* sp. reached 2% of total zooplankton in only three samples, collected in the Sicily Channel (St. S7, 0-50 m) and in Cretan Passage (St. P5, 0-50 m and 50-100 m).

The MDS based on depth-integrated abundances of each group showed a positioning of the stations more or less according to each geographical area, indicating dissimilarities among areas (Fig. 11*a*). Groups of stations resulting from cluster analysis (at 72% similarity level) are encircled. The Sicily Channel showed stronger differentiation from the other regions. A significant overlapping between the Ionian and Cretan Passage stations indicated some similarities between these neighbouring areas. The position of I5 apart from the other stations of the Ionian group was mainly due to the presence of cladocerans (37 ind. m^{-3}) as well as to the higher total zooplankton density (see Fig. 5). In general, the stations appear to be positioned along a horizontal gradient from higher to lower abundances, with the Sicily group on one side and the Cretan Sea group on the other. This was verified by superimposing abundances on the MDS plot (Fig. 11*b*), indicating the influence of total quantities on the position of the stations. Consequently, abundances seem to significantly affect the ordination of the stations in MDS. Copepods should not be responsible for the above differentiation patterns, being always the dominant group at all stations. By way of contrast, their presence increases the similarity among areas, since groups obtained by a second cluster analysis without copepods were distinguished at 65% similarity level (encircled in Fig. 11*c*). In the MDS

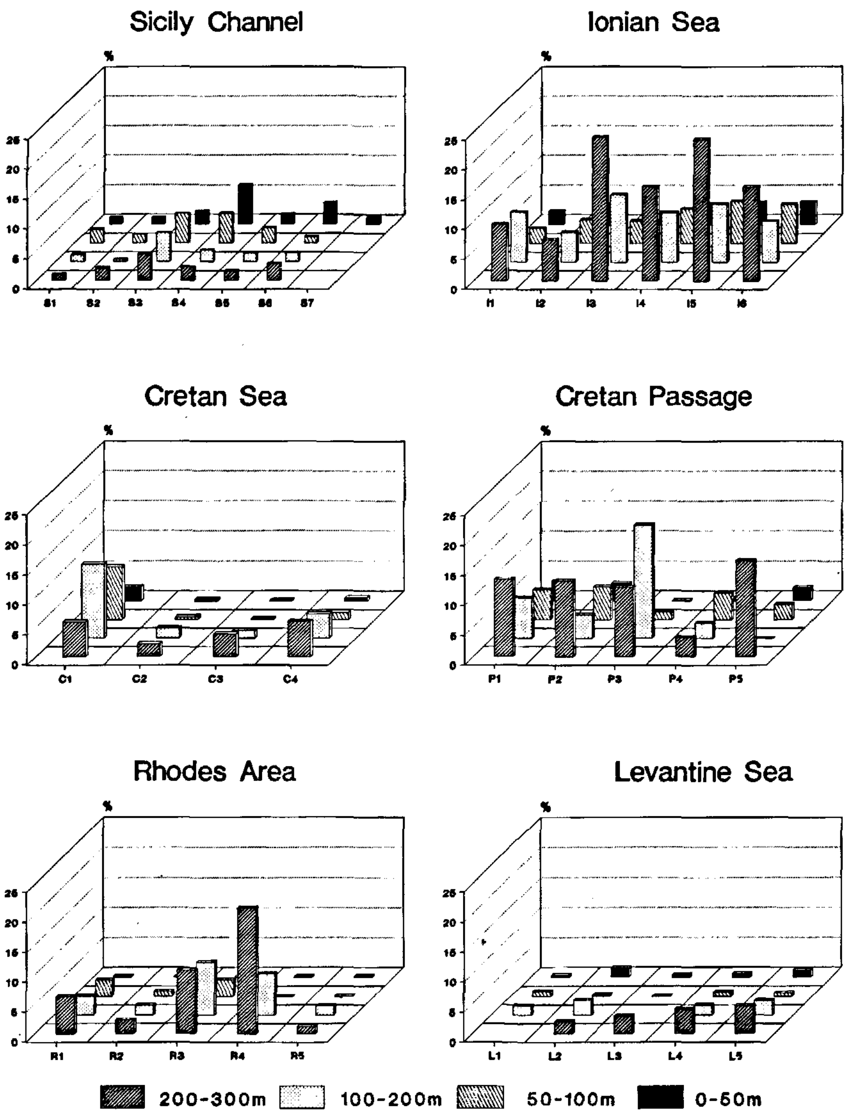


Figure 8

Distribution of the percentages of chaetognaths on total zooplankton abundances at each station and depth layer during the POEM-BC-O91 cruise in the EMED.

plot (Fig. 11*c*), the position of the stations shows a similar pattern, although distances among stations are greater. The general pattern of the above results cannot reveal any substantial influence of the local dynamics or physical forcing on zooplankton distribution.

DISCUSSION

Total zooplankton spatial distribution

The zooplankton data collected during the POEM-BC-O91 cruise are in agreement with the current opinion that the EMED is one of the most oligotrophic marine basins in the world. In the entire area, with the exception of the Sicily Channel, depth-integrated abundances were fairly low, averaging from 27.5 to 104.6 ind. m^{-3}. The values recorded fall within the ranges reported for other oligotrophic areas (Zenkevitch, 1963: total zooplankton in the tropical and North Pacific Ocean; Deevey and Brooks, 1977: copepods in the Sargasso Sea). They were also similar to those reported by Scotto di Carlo *et al.* (1984) for the Tyrrhenian Sea, which is considered poorer in zooplankton biomass when compared to the rest of the Western Mediterranean (Scotto di Carlo and Ianora, 1983). The abundances were lower than those reported for offshore waters in the Balearic Sea, Western Mediterranean (Jansa and Fernandez de Puelles, 1990). Only the Sicily Channel was strongly differentiated from the other regions, with depth-integrated values almost one order of magnitude greater than those of the other areas. In this region, the mean total abundance per square metre (end of Table 2) is similar to that of a few offshore stations sampled in the Gulf of Lions, north-western Mediterranean, in September and December 1986 (Razouls and Kouwenberg, 1993). The higher abundances in the Sicily Channel may reflect a higher productivity with respect to other areas in the open EMED, probably enhanced by the presence of bank regions, characterized by local high primary production (Greze *et al.*, 1983), or by the frequent wind-induced upwelling events recorded in the area (Piccioni *et al.*, 1988). Some weak influence of the meso-scale cyclonic gyre observed at the centre of the Sicily Channel during this study seemed to be echoed in mesozooplankton distribution at St. S4, the closest to the centre of the gyre. In this area, the abundances in the surface layer were higher than at the adjacent stations (Fig. 5); however, there was no signal of the upwelling event either in chlorophyll *a* concentrations or in DCM position.

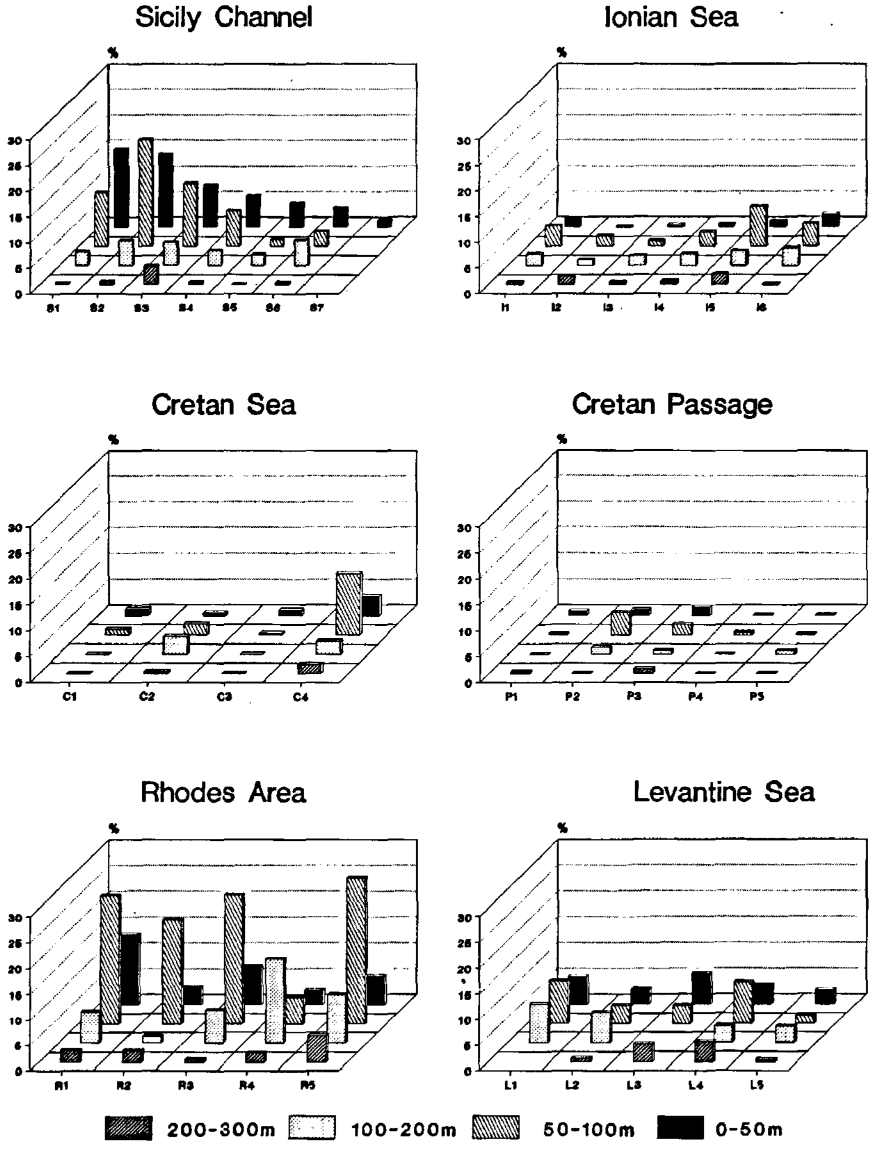


Figure 9

Distribution of the percentages of appendicularians on total zooplankton abundances at each station and depth layer during the POEM-BC-O91 cruise in the EMED.

The lowest zooplankton abundances were recorded at stations along the transect in the Cretan Sea. The extreme paucity of the pelagic fauna corresponds to the oligotrophy of this area, as shown from the nutrient data (Souvermezoglou, 1989) and chlorophyll *a* concentrations (Gotsis-Skretas *et al.*, 1993). Slightly higher total zooplankton abundances were recorded in the central Levantine Sea, as compared with those in the Cretan Sea and Cretan Passage. In this region, the lack of the deepest samples at two stations may lead to a slight overestimation of the total quantities, when depth-integrated values are taken into account. Based on the same cruise, Yacobi *et al.* (1995) observed a uniform pattern of chlorophyll *a* vertical distribution throughout the Levantine basin; this pattern differed only in the area south-east of Crete and was clearly affected by the presence of the Ierapetra anticyclonic eddy. At St. P5, located in this latter area, zooplankton did not appear to be influenced by the hydrology: the pattern of distribution resembled that observed at the other stations of the transect. On the other hand, zooplankton abundance and distribution in the Rhodes area appeared to be clearly affected by the dynamics of the meso-scale permanent gyre. Stations R2 and R4, where strong upwelling events were recorded during the sampling period, were characterized by higher zooplankton abundances in the surface layer. The Rhodes gyre is reported as a localized site of nutrient enrichment which may support higher biological activity than the surrounding areas (Salihoglu *et al.*, 1990). The influence of this gyre, increasing the zooplankton abundances at a local station, was also reported for spring 1986 by Pancucci-Papadopoulou *et al.* (1992). The same authors related a) the lower zooplankton abundances at the surface and b) the presence of epipelagic zooplankters such as the cladoceran *Penilia avirostris* and some siphonophors down to 1000 m depth layer to the anticyclonic dynamics of the Anaximander gyre, in the Rhodes area close to the Asia Minor coast (Pancucci-Papadopoulou *et al.*, 1992). During the present study, the influence of the anticyclonic downwelling was observed at St. R5, located in the Rhodes Strait, at the boundaries of the Rhodes gyre (Figs. 1, 2), where anticyclonic eddies were frequently observed (Theocharis *et al.*, 1993). Station R5 showed remarkable differences in comparison with the other stations of the same transect: the DCM was recorded

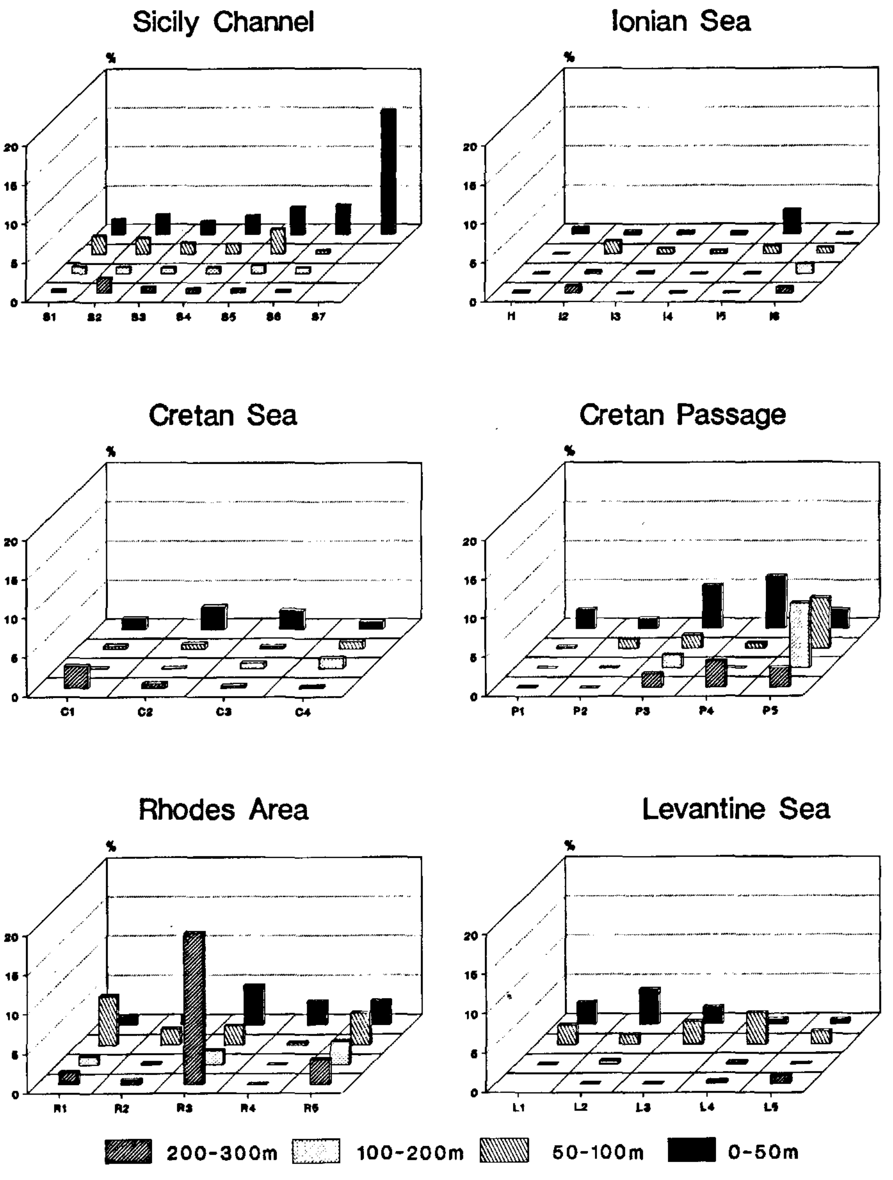


Figure 10

Distribution of the percentages of pteropods on total zooplankton abundances at each station and depth layer during the POEM-BC-O91 cruise in the EMED.

deeper (100 m) than at the neighbouring station (50-75 m); zooplankton abundances were lower at the surface, but remained higher in deep layers. Weikert and Koppelmann (1993) attributed the disproportion of copepod species in deep-living mesozooplankton (namely the mass occurrence of *Eucalanus monachus*) in the Levantine Sea to the acting role of long-lasting meso-scale gyres.

The highest zooplankton abundances were detected in the 0-50 m layer, whereas the highest concentrations of chlorophyll *a* occurred mostly in the 50-100 m layer. Zooplankton standing stock often coincides with the primary production maximum (Hopkins, 1982), the latter generally occurring above the DCM (Herman, 1989). A sharp decrease, varying between areas, was evident in total zooplankton numbers below the 100 m depth. A sharp decrease within the upper 200 m has been generally observed in the oceans (*e.g.* Weikert, 1982; Longhurst, 1985; Scotto di Carlo *et al.*, 1984). This has been proposed as corresponding to the minimum oxygen layer in the Red Sea and in the south-east Arabian Sea (Weikert, 1982; Madhupratap and Haridas, 1990). Such is not the case in the EMED, since the lowest concentration of dissolved oxygen (about 180 μmol l^{-1}) were recorded in the LIW, below 400 m (Yacobi *et al.*, 1995; M. Ribera d'Alcalà, E. Souvermezoglou, pers. comm.). In the Rhodes area, the sharpest gradient observed in the vertical distribution of zooplankton abundances appears to be related to the upwelling regime prevailing in the area.

Diel vertical migrations were not found significantly to affect distribution of total zooplankton abundances in the present study. No diel vertical migration was also displayed either by any of the chaetognath species or by their developmental stages during the same cruise (Kehayias *et al.*, 1994). Also, Weikert and Koppelmann (1993) did not detect diel vertical migrations in the Levantine Sea, whereas they observed distinct day/night differences in the NE Atlantic and the central Red Sea. The present results could be due to the absence of strong migrants in the Mediterranean intermediate layers (Scotto di Carlo *et al.*, 1984; Weikert and Trinkhaus, 1990). This explanation was also suggested for the lack of significant difference between the day and night copepod samples in the north-western Mediterranean (Kouwenberg, 1994). Moreover, the spatial variability could be probably too high to detect daily

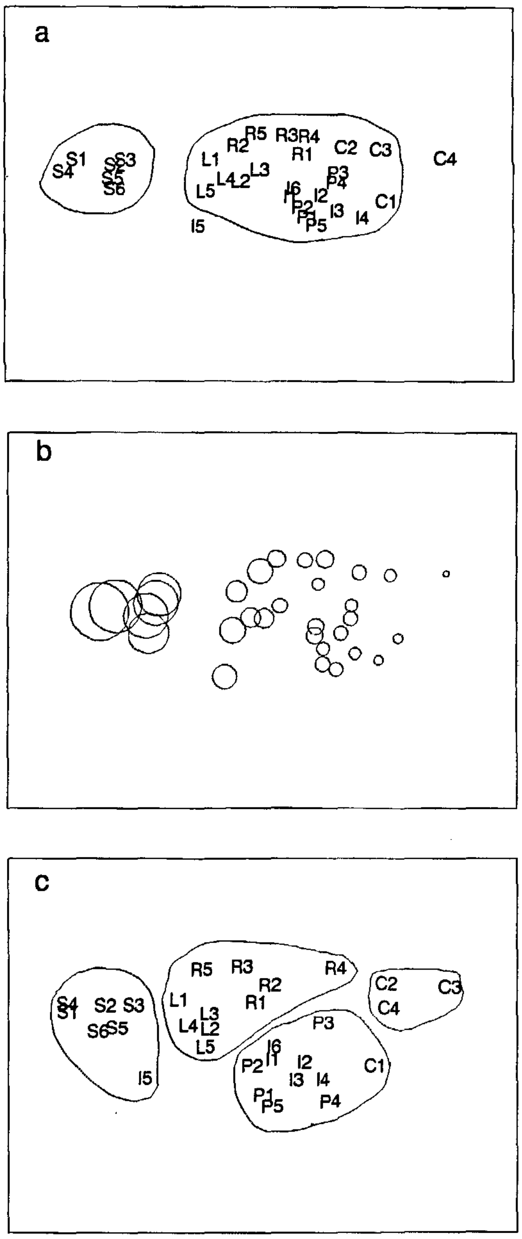


Figure 11

MDS plots of the stations sampled during the POEM-BC-O91 cruise in the EMED, based on depth-integrated abundances of the zooplankton groups. a) All the groups; b) abundances superimposed on the previous MDS plot; the largest circles represent the highest abundances and the smallest circles represent the lowest abundances; c) copepods not included.

variations within our data, since sampling resolution might not pick up subtle changes in depth distributions.

Group composition

Different patterns appear to characterize some areas as far as the distribution of the different zooplankton key-groups, other than copepods, is concerned. Chaetognaths were more important in the Ionian Sea and at the neighbouring stations of the Cretan Sea and Cretan Passage. This similarity could be attributed to water mass exchanges through Kithira Strait (Theocharis *et al.*, 1993). Chaetognaths showed low relative abundances throughout the EMED; in contrast, they have been reported to dominate the zooplankton communities at various times of the year in eutrophic regions (Reeve and Baker, 1975; Williams and Collins, 1985). The vertical distribution of chaetognath species in the central EMED regions during the POEM-BC-O91 cruise was related to the scarcity of food resources in these oligotrophic waters (Kehayias *et al.*, 1994)

Appendicularians showed higher relative abundances in the Rhodes area and in the Sicily Channel. Their higher percentage at the easternmost station of the Cretan Sea (C4, Fig. 10) could be related to the water mass exchanges between Cretan Sea and Rhodes area through the Rhodes and Kassos Straits (Theocharis *et al.*, 1993). Appendicularians are generally reported to be associated with abundant particulate organic aggregates (Alldredge, 1976) and therefore they play an important role in pelagic food webs and in the downward carbon flux (Gorsky *et al.*, 1991). Their high relative importance only in the westernmost area of the Sicily Channel and in the Rhodes area suggest that in these regions the water column was richer in particulate organic matter and generally in particles small in size. During the present cruise, Yacobi *et al.* (1995) recorded more than 90% of the chlorophyll *a* at the surface as being confined to particles <10 μm in size, more than 50% being found in particles <2 μm. The same size fractions were found to be responsible for chlorophyll *a* concentrations in the other regions of the EMED (M. Montresor, O. Gotsis-Skretas and K. Pagou, unpublished data). The high abundances of appendicularians recorded at many stations co-occurring with low numbers of chaetognaths suggest a different structure in the pelagic food webs in these areas, due to the different ecological role of these zooplanktonic groups. Salps (abundant in the central Levantine Sea) and ostracods (in the Cretan Passage) may also be important elements in pelagic environments rich in small size particles. These zooplankters seem to show no selectivity for food size and to trap fine matter other than nanoplankton and protozoans by means of mucus nets (salps) or sticky secretions of the marginal glands of the carapace (ostracods).

Cladocerans are mainly restricted to neritic surface waters, and show strong seasonality in population development, reaching very high numbers usually over short periods. *Evadne spinifera* and *E. tegestina* were the only species occurring during the present study, the latter in very scanty numbers. *Evadne spinifera*, a warm-water species, is reported to have a more oceanic distribution than other cladocerans (Raymont, 1983). This species dominates the cladocerans in offshore waters in the EMED, with the highest abundances in summer and a pronounced decline from September until disappearance in late winter (Moraitou-Apostolopoulou and Kiortsis, 1973). *Evadne* was confined to the surface layers at nearshore stations during the POEM-BC-O91 cruise. The low abundances recorded were possibly due to the ending of the seasonal cycle of this species. Cladocerans were found in a deeper layer only at St. R5 (down to 300 m depth), suggesting that zooplankton distribution at this site was affected by the downwelling of the Rhodes Strait anticyclonic gyre. The influence of hydrology on cladoceran distribution was observed also in

March 1986 by Pancucci-Papadopoulou *et al.* (1992) in the neighbouring Anaximander anticyclonic gyre.

From the results of the present study, we deduce that mesozooplankton distribution and abundance are not always affected by local dynamics, but only when the physical forcing is strong and persistent in time. The mesoscale dynamics in the EMED is quite complex and shows in most cases high temporal variability. Physical dynamics that can increase chlorophyll *a* concentrations and enhance primary productivity do not seem always to affect, in the same degree, zooplankton abundance. Due to the different temporal scales of the biological processes involved at the different levels of the food webs, the zooplankton might take advantage of the enriched waters only if the period of favourable conditions matches the cycles of the reproduction and development of the populations. In the Eastern Mediterranean, this appears to be the case only for persistent or long-lasting gyres.

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