

Copepods
Eastern Mediterranean Sea
Offshore distribution

Copépodes
Méditerranée orientale
Répartition

Mesozooplankton distribution from Sicily to Cyprus (Eastern Mediterranean): II. Copepod assemblages

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ABSTRACT

Mesozooplankton samples were collected during October-November 1991 in the Eastern Mediterranean Sea from four discrete depth layers in the upper 300 m water column and were analysed at copepod species level. Differentiation of species composition with depth was clear, suggesting the existence of an epipelagic (0-100 m) and a mesopelagic (100-300 m) community. Correspondence analysis revealed similarities among areas for the 0-50 m layer, due to the dominance of *Clausocalanus furcatus* and *Oithona plumifera*. Dissimilarities among areas appeared below 50 m and increased with depth, discriminating between different copepod assemblages. These dissimilarities appear to be related to different hydrological features (cyclonic gyres or anticyclonic gyres) prevailing in the basin, rather than to the geographical position of stations and/or to water masses distribution.

RÉSUMÉ

Répartition du mésozooplancton entre la Sicile et Chypre (Méditerranée orientale) : II. Peuplements de copépodes.

Des échantillons de mésozooplancton ont été prélevés en octobre et novembre 1991 en Méditerranée orientale, dans quatre couches d'eau des 300 premiers mètres. La composition des espèces révèle la présence d'une communauté épipelagique (0-100 m) et d'une communauté mésopélagique (100-300 m). L'analyse des correspondances indique des analogies entre les régions, dans la couche 0-50 m, où dominent *Clausocalanus furcatus* et *Oithona plumifera*. Au-delà de 50 m, les peuplements de copépodes se différencient d'une région à l'autre, en raison des caractéristiques dynamiques du bassin (tourbillons cycloniques ou anticycloniques), plutôt que de la position géographique des stations ou de la répartition des masses d'eaux.

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INTRODUCTION

The Mediterranean Sea has been compared with a miniature ocean (Estrada *et al.*, 1984), but it displays several peculiarities that distinguish it from the typical oceanic environment: it is a semi-enclosed basin with negative water balance, lack of tides and a temperate to sub-tropical gradient from north to south (Gaudy, 1985; Kiortsis, 1985). A west-east gradient in nutrient deficiency creates an oligotrophic environment (Margalef, 1984) that is even ultra-oligotrophic in its easternmost part, the Levantine Sea (Berman *et al.*, 1984).

The species composition of copepods in the Eastern Mediterranean has been studied in fragmentary fashion in space and in time (Greze, 1963; Pavlova, 1966; Delalo, 1966; Moraitou-Apostolopoulou, 1972; Kimor and Berdugo, 1967). An attempt was recently made to relate zooplankton distribution with the hydrology in some parts of the basin (Christou *et al.*, 1990; Siokou-Frangou *et al.*, 1990; Pancucci-Papadopoulou *et al.*, 1992).

The role of mesozooplankton in the pelagic ecosystem of the Eastern Mediterranean and the influence of hydrology thereupon were included among the subjects of the POEM-BC (Physical Oceanography of Eastern Mediterranean – Biology, Chemistry) project. The study of the general structure of the zooplanktonic communities throughout area during autumn 1991 (POEM-BC-091 synoptic cruise) revealed low variability of group abundance and composition within the basin, and the influence of some permanent hydrological features on the zooplankton vertical distribution (Mazzocchi *et al.*, 1997). Copepods constituted by far the most important fraction

of zooplankton in the area; they are analysed in detail in the present study in order to contribute to the knowledge of the copepod community structure and to determine the existence or otherwise of similarities within a large area of the Eastern Mediterranean Sea, based on uniformly and simultaneously collected samples.

MATERIALS AND METHODS

Mesozooplankton samples were collected in four discrete layers (0-50 m = A layer, 50-100 m = B layer, 100-200 m = C layer, 200-300 m = D layer) at 32 stations positioned along transects in the Sicily Channel, the Ionian and Cretan Seas, the Cretan Passage (western Levantine Sea), the Rhodes area and the central Levantine Sea (Fig. 1). Sampling was performed by vertical hauls using a closing WP-3 net (200 μ m) (Tranter and Fraser, 1968). Details of sampling strategy and counting methods are given in Mazzocchi *et al.* (1997). Copepods already dead at time of collection and exoskeletons were identified according to the criteria given by Weikert (1977) and counted separately.

An estimation of species diversity was made using the Shannon-Wiener formula (Shannon and Weaver, 1963) only on adult copepods. Differences between areas in respect of diversity index values were tested using the analysis of variance separately for each layer. The dominance of the two first species was estimated according to the formula proposed by Hulburt (1963). Correspondence analysis (Benzecri, 1979) was employed in order to seek similarities among sites and/or layers and for the discrimination of fauna assemblages characterizing layers and areas.

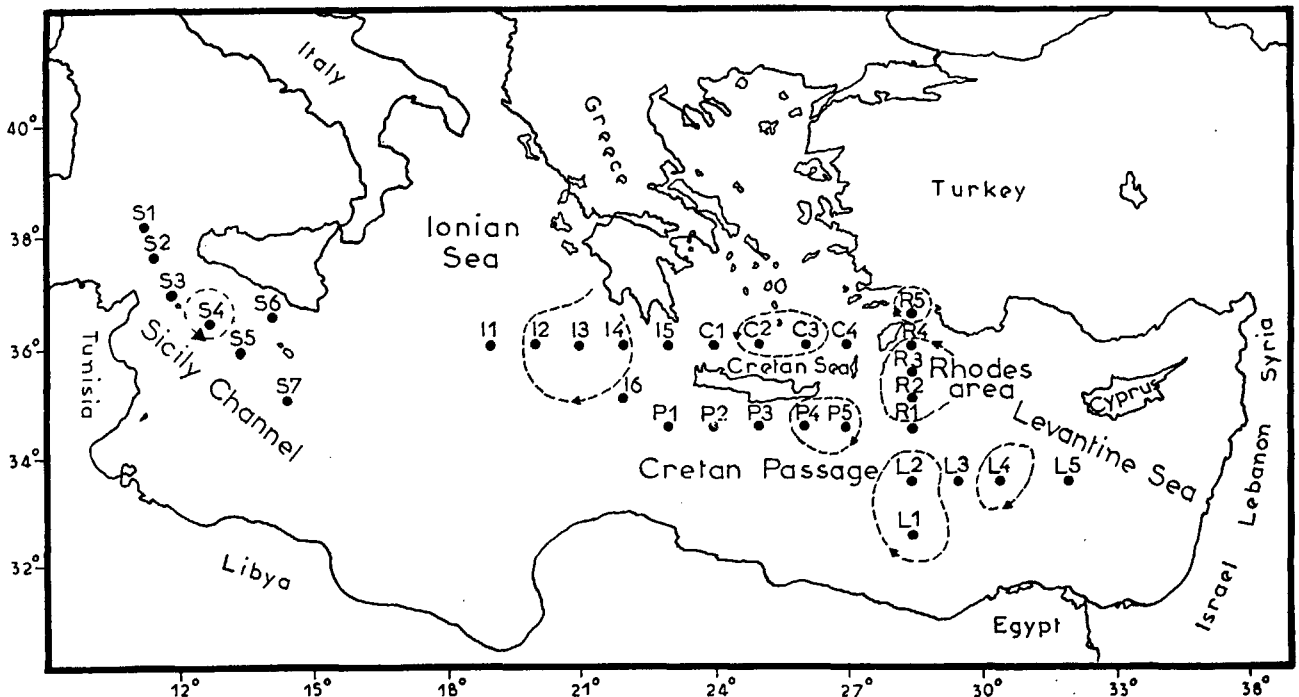


Figure 1

Location of sampling stations with schematic configuration of the main hydrological features during the October-November 1991 cruise in the Eastern Mediterranean. (see Fig. 2 in Mazzocchi *et al.*, 1997, for names of the gyres and more details).

Table 1

Depth-integrated abundances (ind. m^{-3}) of live (A) and dead (D) copepods, all stations, October-November 1991, Eastern Mediterranean.

	S1	S2	S3	S4	S5	S6
A	160.8	125.4	136.5	177.7	165.2	127.9
D	14.6	14.0	30.5	17.2	44.0	10.0
	I1	I2	I3	I4	I5	I6
A	49.7	42.7	31.4	27.9	59.5	36.3
D	11.7	17.2	20.5	13.1	2.9	7.3
	C1	C2	C3	C4		
A	25.8	33.2	29.0	18.3		
D	2.9	0.4	0.6	8.4		
	P1	P2	P3	P4	P5	
A	28.5	39.7	24.7	35.6	25.6	
D	11.1	21.2	3.2	5.2	12.4	
	R1	R2	R3	R4	R5	
A	28.0	60.7	25.6	44.6	41.5	
D	6.5	10.6	20.2	19.5	6.8	
	L1	L2	L3	L4	L5	
A	78.5	68.2	60.5	71.4	96.0	
D	2.9	2.1	1.9	3.0	7.8	

RESULTS

General aspects

Copepods were the dominant group and their relative abundances on total zooplankton ranged from 45.49% and 98.54% (Mazzocchi *et al.*, 1997). Their percentages were generally higher in the Cretan Sea (mean values per layer: 84.52 to 93.31%) and lower in the Rhodes area (mean values per layer: 70.23 to 84.92%). Depth-integrated abundances (ind. m^{-3}) are given in Table 1 for each station for live and dead copepods. Copepods were more abundant in the Sicily Channel (max. 178 ind. m^{-3} , St. S4) and less abundant in the Cretan Sea (min. 18 ind. m^{-3} , St. C4). The abundances decreased sharply with depth (Table 2), a pattern particularly evident below 50 m in the Rhodes area (Fig. 2).

The percentage of dead copepods increased generally with depth. Higher values were found at the 100-200 m and 200-300 m layers in the Rhodes area (St. R3: 75%, St. R4: 89%). In the upper layer, high values were recorded in the Sicily Channel and especially at station S5. Dead copepods were relatively more abundant in the Ionian Sea (I2, I3, I4), in the Cretan Passage (P1, P2, P5) and in the Rhodes area (R3, R4), whereas their presence was negligible in the central Levantine Sea.

Table 2

Mean (AVG) and standard deviation (SD) values for total copepod abundances (ind. m^{-3}) in each region and each depth layer sampled in October-November 1991 in the Eastern Mediterranean.

Layer	Sicily Channel		Ionian Sea		Cretan Sea		Cretan Passage		Rhodes area		Levantine Sea	
	AVG	SD	AVG	SD	AVG	SD	AVG	SD	AVG	SD	AVG	SD
A (0-50 m)	458.68	76.60	153.75	42.28	101.29	31.72	166.54	23.03	228.02	92.27	187.25	43.50
B (50-100 m)	237.13	32.72	72.78	24.17	64.83	37.75	52.58	19.94	47.01	21.39	93.34	21.70
C (100-200 m)	72.29	44.81	24.28	7.82	18.43	1.74	13.71	11.32	13.50	12.86	50.49	3.81
D (200-300 m)	40.48	12.01	8.60	3.55	16.16	4.08	6.03	1.79	8.18	8.53	30.64	6.40

Copepods

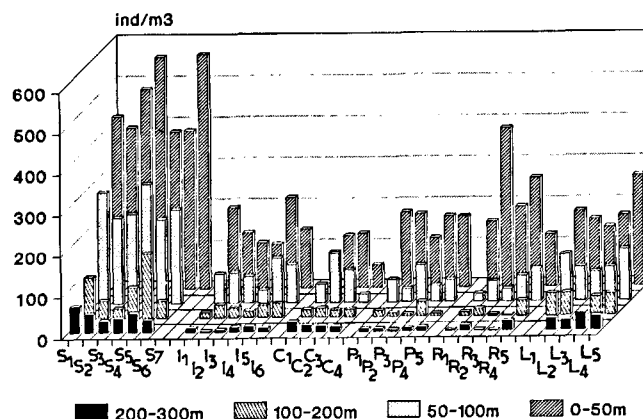


Figure 2

Distribution of total copepod abundances (ind. m^{-3}), October-November 1991, Eastern Mediterranean.

Community structure

Species number, diversity and dominance

With regard to the integrated column (0-300 m), a total of 141 species was identified; 126 species were found in the Sicily Channel, 104 in the Ionian Sea, 85 in the Cretan Sea, 91 in the Cretan Passage, 89 in the Rhodes area and 95 in the central Levantine Sea. The decreasing number of species from the Sicily Channel to the Cretan Sea was more evident in the 100-200 m layer (Fig. 3). Variability of the species number within areas was greater in the Cretan Passage and in the Rhodes area. Generally, fewer species were found in the 200-300 m layer than in the ones above.

Diversity index values varied between 4.63 bits ind^{-1} (St. S3, C layer) and 1.76 bits ind^{-1} (St. P1, D layer) (Fig. 3). Diversity was generally higher in the B or in the C layer. The variability of diversity values was greater within than between areas (ANOVA, $P > 0.05$).

The dominance of the first two species was always higher in the A layer (28% to 66%). High dominance values were also found in the D layer of the Sicily Channel, the Ionian Sea, the central Levantine Sea and the Cretan Passage. In the latter area (D layer), extremely high values were recorded (max 83%). Conversely, dominance was low in the B layer of all areas and especially in the Cretan Passage (24% to 30%).

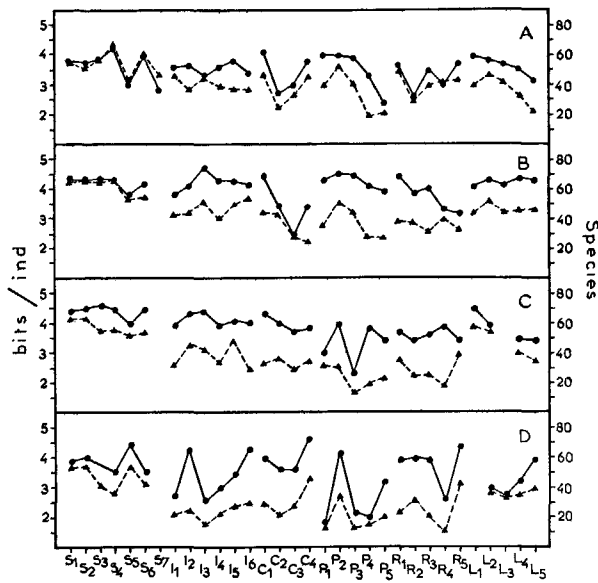


Figure 3
 Fluctuations of species number (dashed line) and diversity (solid line), at each station and for each of the sampled layers (A-D), October-November 1991, Eastern Mediterranean.

Species composition

In general, the contribution of cyclopoids and poecilostomatoids to the copepod community of the Eastern Mediterranean was important (Table 3). In the Sicily Channel, they accounted for up to 37% (St. S1, A layer) and 40% (St. S5, B layer) of total copepods, respectively, and in the Ionian Sea up to 49% (St. I6, A layer) and 35% (St. I1, B layer).

Clausocalanus furcatus and *Oithona plumifera* were the most abundant species (Table 3). The cores of their populations were restricted to the upper layer (0-50 m) throughout the studied area, with mean values of relative abundance 29% and 14% respectively (Fig. 4a). Higher abundances of *C. furcatus* were recorded in the Sicily Channel and in the Rhodes area, (max. 201 ind. m⁻³ at St. R2, 0-50 m layer). *O. plumifera* was more abundant in the Sicily Channel and Ionian Sea (mean values 97 ind. m⁻³ and 32 ind. m⁻³, respectively). The congeneric species *Oithona setigera* was abundant between 50 m and 200 m, and its relative abundance varied spatially (2.2%-25%) but without any clear trend (Figs. 4b, c, d).

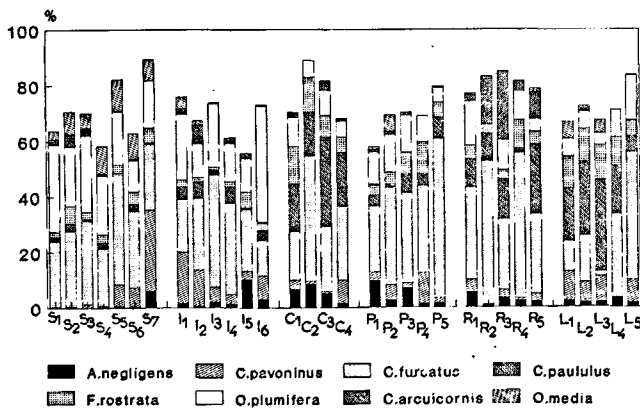


Figure 4a
 Relative abundances (%) of main copepod species in the A (0-50 m) layer, October-November 1991, Eastern Mediterranean.

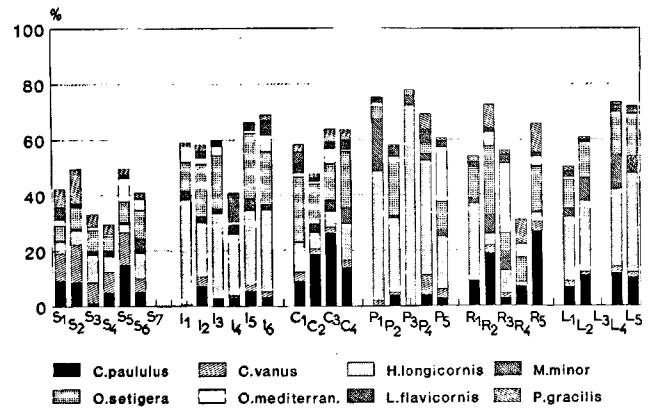


Figure 4c
 Relative abundances (%) of main copepod species in the C (100-200 m) layer, October-November 1991, Eastern Mediterranean.

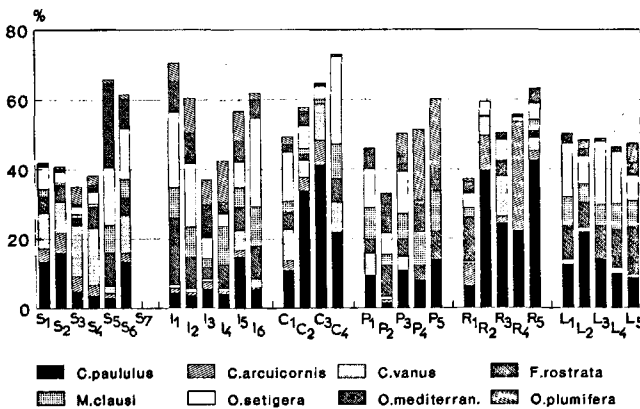


Figure 4b
 Relative abundances (%) of main copepod species in the B (50-100 m) layer, October-November 1991, Eastern Mediterranean.

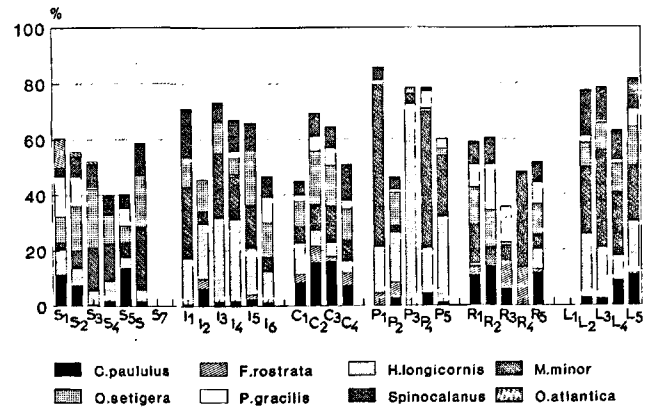


Figure 4d
 Relative abundances (%) of main copepod species in the D (200-300 m) layer, October-November 1991, Eastern Mediterranean.

Table 3

Mean relative abundance (%) of dominant copepod species, October-November 1991, Eastern Mediterranean. A = 0-50 m, B = 50-100 m, C = 100-200 m, D = 200-300 m.

Species	Sicily Channel				Ionian Sea				Cretan Sea				Cretan Passage				Rhodes area				Levantine Sea			
	A	B	C	D	A	B	C	D	A	B	C	D	A	B	C	D	A	B	C	D	A	B	C	D
CALANOIDA																								
<i>Acartia negligens</i>	1.02	0.00	0.00	0.00	3.13	0.30	0.18	0.29	5.44	0.84	1.99	5.12	4.44	1.02	0.40	0.46	2.87	0.16	0.60	2.84	2.15	0.24	0.17	0.00
<i>Calocalanus pavoninus</i>	6.68	1.32	0.52	0.24	8.65	1.82	0.29	0.49	3.26	0.27	0.16	0.11	4.69	2.02	0.18	0.00	2.14	0.29	0.32	0.45	7.14	2.54	0.26	0.16
<i>Clausocalanus arcuicornis</i>	1.58	3.45	1.77	1.36	1.53	1.24	0.27	0.73	1.28	3.38	1.46	0.72	0.45	0.16	0.11	0.14	11.48	10.44	1.82	3.48	0.13	0.00	0.22	0.89
<i>Clausocalanus furcatus</i>	27.54	0.98	0.68	0.22	25.59	1.11	0.91	1.61	28.42	0.48	0.97	4.21	36.06	0.33	0.00	0.22	38.44	0.82	1.63	2.51	21.19	0.88	0.27	0.00
<i>Clausocalanus paululus</i>	1.53	9.05	7.30	5.93	3.66	6.33	3.66	2.13	21.03	27.04	16.96	11.85	4.68	8.76	2.22	1.70	12.16	27.07	12.99	8.58	20.28	13.42	9.93	6.27
<i>Clausocalanus pergens</i>	0.29	6.75	3.93	5.03	0.00	0.15	0.33	0.80	0.74	6.70	3.15	3.59	0.00	0.20	0.00	0.25	0.74	6.93	2.39	2.74	0.45	0.07	0.00	0.08
<i>Ctenocalanus vanus</i>	2.19	10.56	9.18	4.50	0.03	2.00	1.49	0.94	0.38	8.22	2.47	0.83	0.22	2.24	2.59	0.29	0.04	4.53	1.51	0.29	0.56	1.00	1.79	0.79
<i>Haloptilus longicornis</i>	0.01	0.12	6.26	5.99	0.12	2.85	27.82	20.78	0.04	0.45	8.93	6.70	0.09	3.05	41.22	30.92	0.00	0.91	9.10	1.69	0.11	1.27	28.16	17.10
<i>Lucicutia flavicornis</i>	0.26	0.39	1.07	0.51	1.27	1.62	3.65	2.45	0.13	1.61	3.44	1.75	1.52	2.07	2.57	2.65	0.17	1.32	1.52	0.50	0.58	0.62	1.80	2.90
<i>Mecynocera clausi</i>	0.39	3.06	0.57	0.05	2.35	8.09	0.60	0.42	0.88	4.10	0.09	0.20	2.71	8.18	0.35	0.21	0.09	1.19	0.08	0.20	1.87	6.97	0.20	0.01
<i>Paracalanus denudatus</i>	1.54	0.04	0.00	0.01	3.74	0.52	0.11	0.42	1.89	0.43	0.16	0.10	3.49	0.69	0.16	0.35	0.40	0.09	0.09	0.69	2.27	1.17	0.13	0.00
<i>Pleuromamma abdominalis</i>	0.29	0.21	1.27	2.79	0.31	2.31	1.93	2.32	0.11	3.65	5.01	1.91	1.24	1.42	1.09	0.65	0.03	1.76	1.89	0.07	0.02	0.22	0.53	0.78
<i>Pleuromamma gracilis</i>	0.39	1.51	5.19	5.38	0.50	1.99	1.04	1.89	1.76	2.71	3.22	4.18	0.25	0.56	1.38	2.22	0.57	3.66	6.25	9.04	0.00	0.73	0.88	2.83
<i>Spinocalanus</i> spp	0.00	0.00	0.36	6.95	0.00	0.00	0.90	8.78	0.04	0.30	3.67	8.36	0.05	0.00	0.34	2.01	0.00	0.00	3.20	4.95	0.00	0.00	1.17	12.32
Sum	55.35	55.36	56.92	54.96	64.32	49.05	64.13	61.20	73.36	74.54	64.90	62.50	72.41	59.06	74.03	58.17	81.49	74.76	58.29	53.85	68.43	49.79	63.90	54.57
CYCLOPOIDA																								
<i>Oithona plumifera</i>	21.19	1.94	0.14	0.18	21.09	7.46	1.82	1.44	7.86	0.99	2.25	1.68	10.75	9.22	0.00	0.00	8.66	0.17	2.31	1.79	8.61	1.59	0.00	0.00
<i>Oithona setigera</i>	1.11	7.72	7.30	13.56	0.12	13.71	18.78	11.97	2.25	12.34	17.83	13.66	0.65	5.86	7.80	3.83	0.18	3.94	13.49	7.85	0.38	12.82	13.54	10.58
Sum	25.25	18.95	17.75	20.11	25.98	25.37	21.59	13.81	12.42	14.88	22.20	16.75	14.14	16.49	8.22	3.83	9.77	7.91	18.89	14.86	13.61	23.96	17.03	12.37
POECILOSTOMATOIDA																								
<i>Farranula rostrata</i>	3.75	5.39	1.69	0.17	2.64	9.07	0.88	0.97	9.78	3.36	1.76	3.70	6.56	6.12	1.29	2.00	4.90	3.88	2.44	5.74	10.39	10.28	1.84	0.22
<i>Oncaea media</i>	7.75	8.58	6.12	3.02	1.57	2.31	0.36	1.02	0.23	0.77	0.28	0.56	1.58	0.61	0.16	1.55	0.44	0.41	0.00	0.13	2.43	5.62	0.51	0.48
<i>Oncaea mediterranea</i>	1.42	6.06	2.90	0.85	1.43	6.96	3.30	0.94	0.77	1.77	2.34	2.16	1.45	7.68	4.69	2.28	0.07	1.96	7.82	2.81	0.57	2.18	0.46	0.87
Sum	18.17	23.79	19.22	9.24	9.43	24.39	9.18	5.98	14.04	10.08	8.23	10.94	13.36	23.89	11.60	10.34	8.65	16.21	17.80	14.91	16.84	24.70	8.89	4.92
MORMONILLOIDA																								
<i>Mormonilla minor</i>	0.00	0.00	1.63	10.91	0.00	0.00	2.73	15.06	0.00	0.00	3.10	8.86	0.00	0.20	5.57	27.03	0.00	0.02	3.16	13.01	0.00	0.47	7.54	25.57
HARPACTICOIDA																								
	0.09	0.53	0.68	0.86	0.03	0.09	0.15	0.28	0.13	0.16	0.03	0.06	0.04	0.29	0.20	0.07	0.05	0.93	1.51	2.61	0.20	0.17	0.12	0.21

Haloptilus longicornis was found below 100 m and revealed high fluctuations, its mean abundance was amounting to 14 ind. m⁻³ in the C layer of the central Levantine Sea and to 1 ind. m⁻³ in the same layer of the Rhodes area. The presence of *Clausocalanus paululus* was quite important in the 0-200 m layer, especially in the Levantine Sea. *Farranula rostrata* occurred mainly in the 0-100 m layer (mean relative abundance in the studied area: 6%). The relative abundances of *Mormonilla minor* and *Spinocalanus* spp. were very important in the 200-300 m layer (mean percentages 16% and 7%, respectively) attaining 58% and 18% of total copepods, but their numbers were generally low (max. 9 ind. m⁻³ and 4.6 ind. m⁻³, respectively).

In the 0-50 m layer, the eight most abundant species (*C. furcatus*, *O. plumifera*, *F. rostrata*, *Acartia negligens*, *Calocalanus pavoninus*, *C. paululus*, *Oncaea media* and *Clausocalanus arcuicornis*) represented at least 60% of the total copepods at almost all stations (Fig. 4a). The contribution of the eight most abundant species was lower for the 50-100 m layer, especially in the Sicily Channel (St. S1 to S4), where species such as *C. paululus*, *Mecynocera clausi*, *O. setigera*, *C. arcuicornis*, *Ctenocalanus vanus*, *Oncaea mediterranea*, *F. rostrata* and *O. plumifera* accounted for almost 40% of the total copepods (Fig. 4b). A similar pattern was found in the 100-200 m layer, where *C. paululus*, *O. setigera*, *C. vanus*, *O. mediterranea*, *H. longicornis*, *Lucicutia flavicornis*, *M. minor* and *Pleuromamma gracilis* constituted the most abundant species (Fig. 4c). The prominent abundance of *H. longicornis* in the Ionian Sea, the Cretan Passage and the Levantine Sea is evident in comparison with the other areas. A similar spatial difference is also clear for the 200-300 m layer, where the contribution of the dominant species (*C. paululus*, *O. setigera*, *F. rostrata*, *P. gracilis*, *H. longicornis*, *M. minor*, *Spinocalanus* spp. and *Oithona atlantica*) varied mainly between 40 and 70% (Fig. 4d).

Some species with moderate abundance displayed a clear horizontal variation. *O. atlantica* (C and D layers) and *Acartia danae* (A layer) were found only in the Sicily Channel. The congeneric species *A. negligens* (Fig. 4a) appeared only at station S5 and eastward to the central Levantine Sea. *C. pavoninus*, the major species of Calocalanidae, was quite important in the upper layer except in the Sicily Channel and the Rhodes area (Fig. 4a). The presence of *O. media* (Fig. 4a) and *C. vanus* (Figs. 4b, c) was prominent in the Sicily Channel mainly above 200 m, while the latter species occurred in low numbers in the 100-200 m layer of the Cretan Sea, the western Cretan Passage and the Rhodes area. *Clausocalanus pergens* was virtually restricted to the Sicily Channel, the Cretan Sea and the Rhodes area (Fig. 5). In the latter area, and mainly at the central stations (R2, R3, R4), the abundance of *C. arcuicornis* (mean value 28 ind. m⁻³) was considerable. On the other hand, *Centropages typicus* was found only in the 0-100 m layer of the above-mentioned stations (max: 6 ind. m⁻³), as well as in the same layer of stations S2, S3 and S4 in the Sicily Channel.

C.pergens

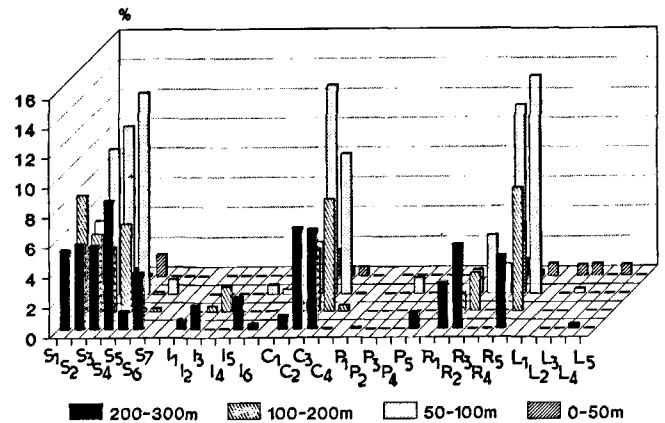


Figure 5

Distribution of *Clausocalanus pergens*, October-November 1991, Eastern Mediterranean.

Similarities among stations, areas and layers

In the plane of the first two axes of the correspondence analysis (which express 35% of the total variance), short distances are generally observed among all samples collected in the A layer (Fig. 6a). Distances among stations become greater with depth, suggesting a greater differentiation with depth, mainly in the C and D layers. This differentiation exists between, as well as within areas.

Samples collected below 50 m from the Sicily Channel, the Cretan Sea and the Rhodes area, are positioned "higher" along the second axis than those of the central Levantine Sea, Ionian Sea and Cretan Passage. Along the same axis, samples collected between 50 and 300 m at station R1 are positioned "lower" than those collected at the other Rhodes area stations. The sample collected in the D layer at station R4 is positioned apart from the other samples of the same layer, due perhaps to the extreme paucity in copepod numbers. For the B, C and D layers, shorter distances are observed among samples from the Sicily Channel, the Rhodes area and the Cretan Sea and among samples collected in the Ionian and central Levantine Seas and in the Cretan Passage. Samples collected in the D layer of the Ionian and Levantine Seas and Cretan Passage are well distinguished from the samples collected in the same layer in the other areas; this could be due to the dominance of *M. minor* and *Spinocalanus* spp. (Fig. 6b), since these species and samples are positioned at the extremity of the "cloud" of samples.

Samples from the upper (A) to the lower (D) layer are positioned successively along the first axis, which is correlated to depth ($r^2=0.791$, $P<0.001$) and temperature ($r^2=0.639$, $P<0.001$). Along the second axis, samples collected in the B layer of the Sicily Channel, Rhodes area and Cretan Sea are opposed to the samples collected in the C and D layer of the central Levantine Sea and the Cretan Passage. The trophic status of each layer and area may account for these differences, since this axis is correlated to chlorophyll *a* concentrations ($r^2=0.3901$, $P<0.001$). It is worth mentioning that day and night

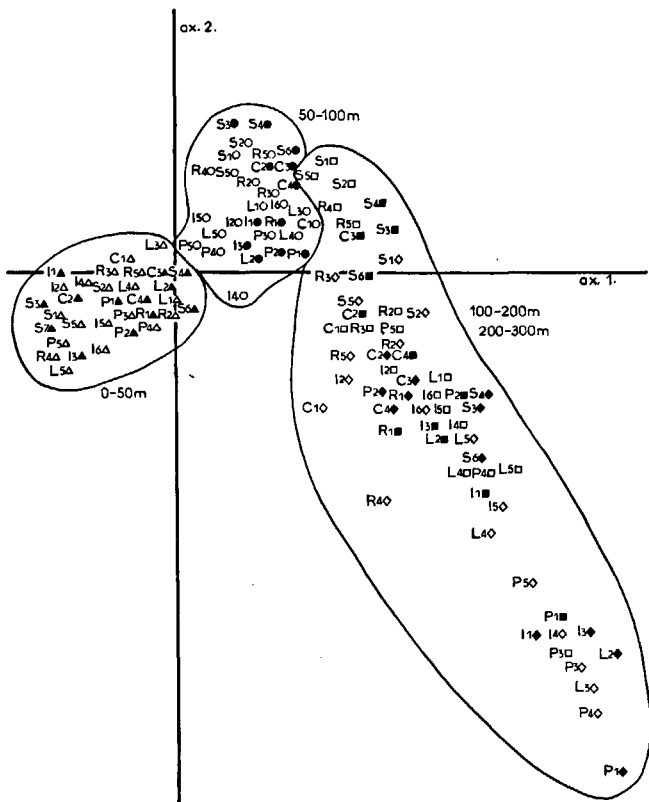


Figure 6a

Correspondence analysis (1 × 2 plane), projection of samples, October–November 1991, Eastern Mediterranean.

△ = 0–50 m, day; ▲ = 0–50 m, night; ○ = 50–100 m, day; ● = 50–100 m, night; □ = 100–200 m, day; ■ = 100–200 m, night; ◇ = 200–300 m, day; ◆ = 200–300 m, night.

samples were projected close to each other (Fig. 6a), suggesting that no significant difference was produced in the species composition by nocturnal migration.

Since the similarity among the total surface samples was due to the abundance of *Clausocalanus furcatus* and *Oithona plumifera*, the correspondence analysis was also performed excluding these two species. In the issued plane of the two first axes (which express 30% of the total variance), the projection of the samples (Fig. 7a) and species (Fig. 7b) collected below 50 m is similar to that of Figures 6a and 6b. On the other hand, a spatial differentiation of the surface layer samples along the second axis is evident. The order of station positioning along this axis was: Rhodes area, Sicily Channel (except station S7), Cretan Sea, central Levantine Sea, Ionian Sea, Cretan Passage and station S7. This positioning reflects the similarity among the areas: the Rhodes area exhibited greater similarity with the Sicily Channel and the Cretan Sea, and less with the Cretan Passage and the Ionian Sea.

Species assemblages

In the plane of the first two axes of the correspondence analysis (Fig. 6b), the following species assemblages could be distinguished, related to the areas and/or to the layers.

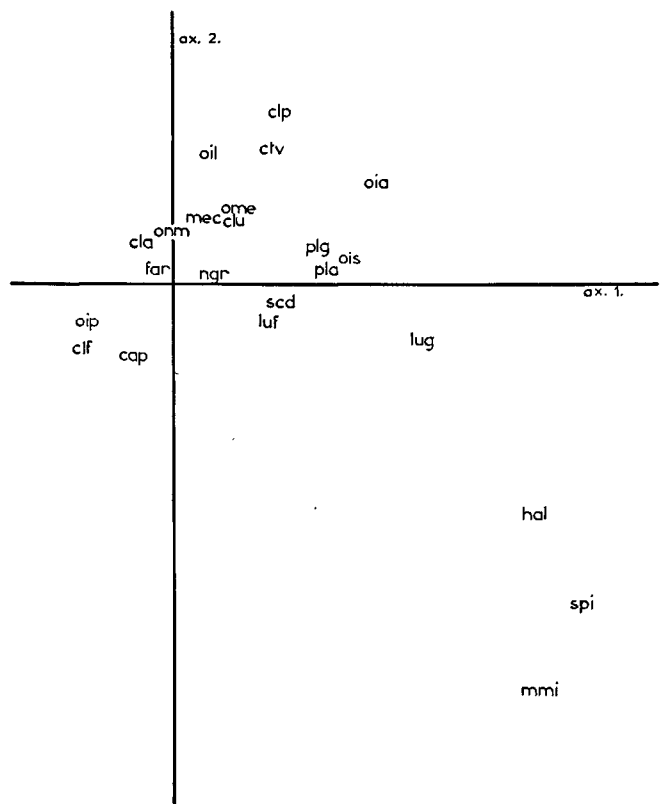


Figure 6b

Correspondence analysis (1 × 2 plane), projection of species, October–November 1991, Eastern Mediterranean.

cap = *Calocalanus pavoninus*, cla = *Clausocalanus arcuicornis*, clf = *Clausocalanus furcatus*, clp = *Clausocalanus pergens*, clu = *Clausocalanus paululus*, ctv = *Ctenocalanus vanus*, far = *Farranula rostrata*, hal = *Haloptilus longicornis*, luf = *Lucicutia flavicornis*, lug = *Lucicutia gemina*, mec = *Mecynocera clausi*, mmi = *Mormonilla minor*, ngr = *Neocalanus gracilis*, oia = *Oithona atlantica*, oil = *Oithona longispina*, oip = *Oithona plumifera*, ois = *Oithona setigera*, ome = *Oncaea mediterranea*, onm = *Oncaea media*, pla = *Pleuromamma abdominalis*, plg = *Pleuromamma gracilis*, scd = *Scolecithricella dentata*, spi = *Spinocalanus spp.*

a) The first assemblage concerns the upper layer (0–50 m) of all the areas, and is characterized by the dominance of *C. furcatus* and *O. plumifera*. These species are accompanied by *Acartia negligens*, *Farranula rostrata*, *Temora stylifera*, *Oithona tenuis*, *Oncaea media* and *Calocalanus pavoninus*.

b) The subsurface layer (50–100 m) of the Sicily Channel and some stations in the Cretan Sea and the Rhodes area is characterized by the dominance of *Clausocalanus pergens* and *Ctenocalanus vanus*, accompanied by *Calocalanus contractus*, *Oithona longispina* and *Euchaeta hebes*.

c) *Clausocalanus paululus* is the characteristic species of the subsurface assemblage in the Ionian Sea, the Cretan Passage, and the central Levantine Sea. *Lucicutia flavicornis*, *Mecynocera clausi*, *Oncaea mediterranea*, *Neocalanus gracilis*, *Scolecithricella dentata* and *Corycaeus limbatus* are species contributing to the above assemblage.

d) In the Sicily Channel as well as in the Cretan Sea and the Rhodes area, the 100–200 m and 200–300 m layers are characterized by the abundance of *Oithona setigera*,

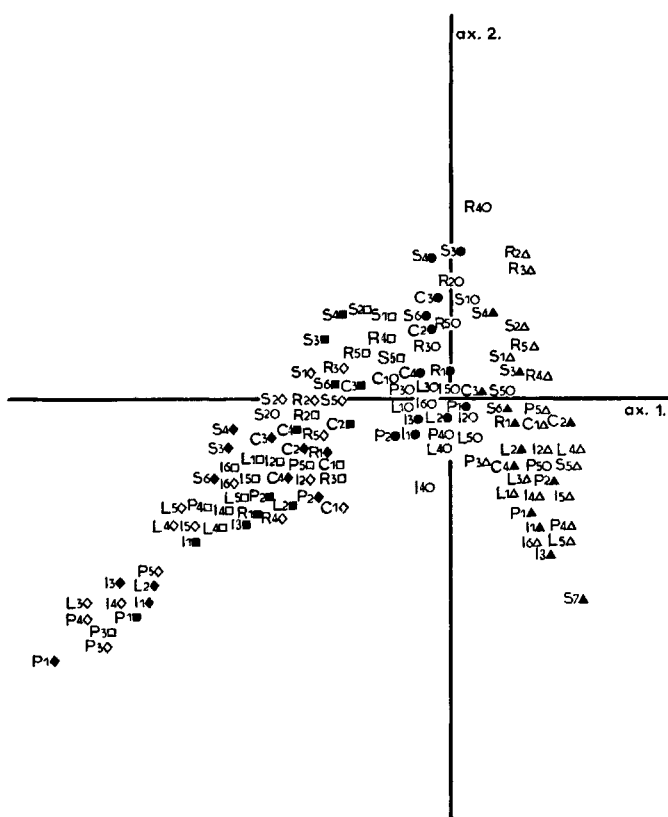


Figure 7a

Correspondence analysis without *Clausocalanus furcatus* and *Oithona plumifera* (1×2 plane), projection of samples, October-November 1991, Eastern Mediterranean. Symbols as in Figure 6a.

followed by *Pleuromamma gracilis*, *P. abdominalis*, *Heterorhabdus papilliger*, *Euaetideus giesbrechti*, *Lucicutia gemina*, *O. atlantica* and *Scaphocalanus* spp.

e) The single species characterizing the 100-200 m layer in the Ionian and central Levantine Seas and the Cretan Passage is *Haloptilus longicornis*.

f) The 200-300 m layer of the above areas is distinguished by the dominance of *Spinocalanus* spp. and *Mormonilla minor*.

DISCUSSION

The presence of copepod carcasses and exuviae was notable in the Ionian Sea, the Cretan Passage and the Rhodes area; in these regions, dead outnumbered the living fraction below 100 m. Similar values were recorded between 2000 m and 4000 m in the Sargasso Sea (Wheeler, 1967). In the 200-250 m and 400-450 m layers of the central Red Sea, the 17.5% and 25.5% of all the copepods consisted of carcasses or molted skins (Weikert, 1982). In this area, the depth ranges of increased copepod debris coincided with the upper layer of minimum oxygen saturation, suggesting an increased environmental stress in these layers. The same author (Weikert, 1977) found high numbers of copepod carcasses in the surface layer of an upwelling system off NW Africa and suggested that rapid changes in the

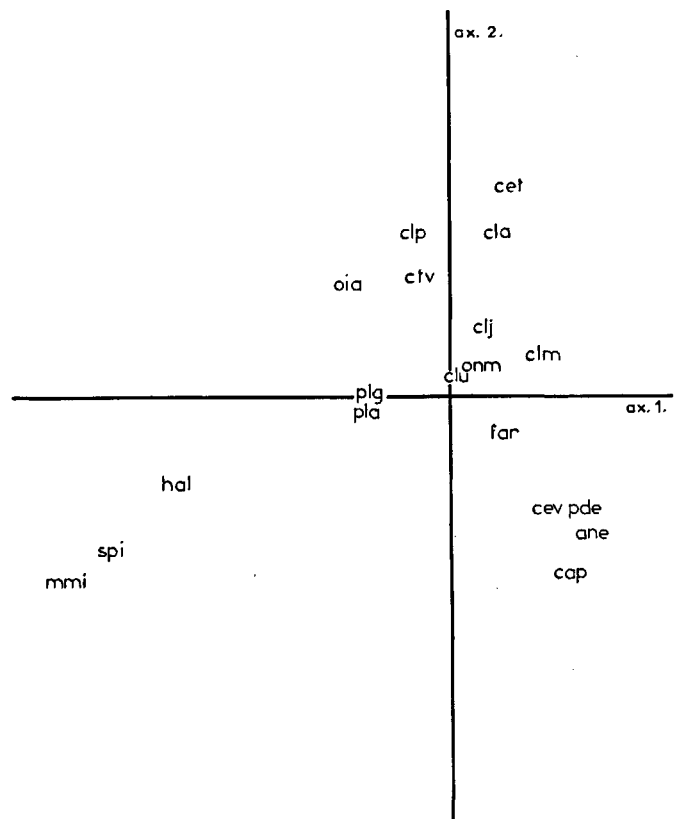


Figure 7b

Correspondence analysis without *Clausocalanus furcatus* and *Oithona plumifera* (1×2 plane), projection of species, October-November 1991, Eastern Mediterranean.

Same abbreviations as in Figure 6b and, in addition: ane = *Acartia negligens*, cet = *Centropages typicus*, cev = *Centropages violaceus*, clj = *Clausocalanus jobei*, clm = *Clausocalanus mastigophorus*, pde = *Paracalanus denudatus*.

environment caused by the pulsation of violent mesoscale upwelling resulted in an increased mortality in zooplankton. This explanation could be assigned to the increased number of carcasses in the Rhodes area, a region characterized by an important cyclonic gyre with upward movement.

The Sicily Channel was the richest area in species number, similar to the neighbouring Tyrrhenian Sea in the Western Mediterranean (Scotto di Carlo *et al.*, 1984). This richness could be attributed to its geographical position between the western and eastern basins and the resulting influences. Some species occurred exclusively in the Sicily Channel samples. Among these, the presence of *Oithona atlantica* was quite important. The absence of this species in our samples from the Ionian to the central Levantine Seas could be related to the boreal temperate character of the species (Raymont, 1983), since the Eastern Mediterranean has been shown to possess strong tropical affinities (Oren, 1957). However, this species has been referred to as inhabiting the entire Mediterranean Sea by Kovalev and Shmeleva (1982). In the Sicily Channel, *Acartiidae* were represented by *Acartia danae* and *A. clausi*, whereas *A. negligens* occurred at the two easternmost stations (S6, S7) and remained the only representative species of the family in the other areas. In the Aegean Sea, *A. clausi* was found in the northern,

and *A. negligens* in the southern part (Kiortsis, 1974). Although a decrease in species number was obvious from the Sicily Channel to the Cretan Sea, our data cannot clearly confirm the general opinion that the Eastern Mediterranean is poorer in species with respect to the western basin (Furnestin, 1979), since data obtained in the same layers of the Western Mediterranean and by the same net mesh size are not available.

Nevertheless the diversity index values were generally similar among the studied areas and lower than or equal to those estimated for the Tyrrhenian Sea (Scotto di Carlo *et al.*, 1984). The vertical pattern presented a similar trend in the western and eastern basins, since maximum values occurred in the 50-200 m layer. These higher values could be related to the increased number of species in this layer, as well as to the low dominance of species. Oceanic zooplankton communities are more diverse in oligotrophic areas (McGowan, 1974). Furnestin (1979) mentioned that with regard to copepods, diversity indices are high in the Ionian Sea (3.27 for the 0-200 m layer and 3.64 for the 200-400 m layer), where Adriatic, Levantine and Atlantic water influences converge. These values are slightly lower than those observed in the Ionian Sea during the present study. The high dominance values observed in the 200-300 m layer are due to the particular abundance of *Haloptilus longicornis* and/or *Mormonilla minor* in some stations of the Ionian Sea, the Cretan Passage and the central Levantine Sea. The unique abundance of *H. longicornis* (>80%) in the 100-300 m layer of the Cretan Passage has been also mentioned by Weikert and Trinkaus (1990).

The contribution of cyclopoids and poecilostomatoids to the copepod community was quite important. Similarly significant percentages of these copepods have been found in the Rhodes area and the SE Aegean Sea in March 1986 (Siokou-Frangou and Pancucci-Papadopoulou, 1990), as well as in Atlantic epipelagic waters (Deevey and Brooks, 1971; Chahsavari-Archad and Razouls, 1982). It should be mentioned that the contribution of cyclopoids and poecilostomatoids was lower in the Levantine Sea (near St. P4 of the present study) according to Weikert and Koppelmann (1993), a fact which should be attributed to the larger mesh size (333 μm) used. The abundance and diversity of the cyclopoid *Oithona* and the poecilostomatoid *Oncaea*, *Corycaeus* and *Farranula* support the subtropical character of Eastern Mediterranean zooplankton, since these genera are abundant in warm seas (Raymont, 1983). According to Basescu (1985), the Eastern Mediterranean is distinguished by a high percentage of thermophile tropical and subtropical elements.

Species composition was primarily differentiated according to depth; copepod assemblages characterized discrete sampled layers, each of them being dominated by different species, such as *Clausocalanus furcatus*, *Oithona setigera* or *Haloptilus longicornis*. Therefore, the assemblages distinguished can be considered as communities occupying discrete layers. The similarity between the 0-50 m and the 50-100 m layers could suggest the existence of an epipelagic (0-100 m) and a mesopelagic (100-300 m) community. In their study of copepod vertical distribution,

Scotto di Carlo *et al.* (1984) distinguished a surface (0-100 m) and a midwater (100-600 m) community in the Tyrrhenian Sea. Cummings (1983) considered depth as the primary habitat dimension for copepods. The influence of temperature is secondary, since the latter is depth-dependent, presenting more important fluctuations in the vertical than in the horizontal scale in the studied area.

The observed similarity in species composition between the day and night samples suggests no influence of nocturnal migration in the studied area. The above result is due to the absence of strong migrant species in the area, as generally reported in the Mediterranean Sea (Scotto di Carlo *et al.*, 1984). Similarity in species composition between day and night samples has been also observed in previous studies in the Eastern Mediterranean (Christou *et al.*, 1990; Siokou-Frangou *et al.*, 1990; Weikert and Koppelmann, 1993; Kehayias *et al.*, 1994) and in the Western Mediterranean (Scotto di Carlo *et al.*, 1984; Kouwenberg, 1994). No significant differentiation in total zooplankton abundance was detected between day and night samples in the studied regions (Mazzocchi *et al.*, 1997). Angel and Fasham (1974) determined vertical groupings of zooplankton in the North Atlantic using factor analysis, and observed that despite vertical migration by some of the species and some groups, the pattern was identical by day and night. Similar observations were made by Marlowe and Miller (1975) in the North Pacific.

The copepod species composition of the surface layer (0-50 m) was similar throughout almost the entire Eastern Mediterranean, and resulted from the dominance of *Clausocalanus furcatus* and *Oithona plumifera*. *Clausocalanus* is a mainly surface-living genus, although some of the species can extend their vertical range to about 500 m depth (Raymont, 1983). According to Frost and Fleminger (1968), *C. furcatus* has a tropical-subtropical and circumglobal distribution. *O. plumifera* occurs widely in all three major oceans, mainly in warmer waters, but ranging into temperate regions (Raymont, 1983). Deevey (1971) found the genera *Oithona*, *Oncaea* and *Clausocalanus* to be the three numerically most important copepods in the Sargasso Sea near Bermuda, representing about 47% of the total copepod fauna. In August-September 1987, *C. furcatus* and *O. plumifera* were dominant in a major part of the Aegean Sea, in the Rhodes area and the Ionian Sea; these areas were covered by Surface Levantine Water, whose characteristics are transformed upon leaving the Rhodes area for the south Aegean and the south Ionian Seas (Siokou-Frangou *et al.*, 1990). Furthermore *C. furcatus* and *O. plumifera* dominated in late summer-autumn in coastal areas of the Mediterranean Sea, submitted temporarily to the influence of the open sea (Scotto di Carlo *et al.*, 1985; Siokou-Frangou *et al.*, 1995). In our study, these two species were found to be dominant in a large region between the islands of Sicily and Cyprus, covered by two different water masses: (a) the first 100 m of the water column in the Sicily Channel and part of the Ionian Sea (Sts. I1, I2) were occupied by the North Atlantic Water, characterized by low salinity values (Budillon *et al.*, 1994; A. Theocharis,

pers. comm.); (b) the more saline Surface Levantine Water occupied part of the Ionian Sea (Sts. I3 to I6), the Cretan Passage, the Cretan Sea, the Rhodes area (A. Theocharis, pers. comm.) and the central Levantine Sea (Yacobi *et al.*, 1995).

The distribution of zooplankton is known to depend in great measure on the physical and dynamic characteristics of the water masses (Sabates *et al.*, 1989). Differentiation between areas of the Eastern Mediterranean was observed in March 1988 due to the influence of different water masses (Christou *et al.*, 1990): the zooplankton community of the 0-100 m layer of the NE Ionian Sea (covered by the North Atlantic Water) was characterized by the dominance of *Paracalanus parvus*, *Oithona helgolandica* and *Evadne spinifera*. In the same layer the SE Ionian Sea, the Cretan Passage and the Rhodes area (covered by Levantine Intermediate Water), zooplankton was dominated by *Farranula rostrata*, *Oncaea media*, *Oncaea mediterranea* and *Paracalanus denudatus*. The results of the present study did not reveal any influence of water masses upon copepod species distribution. Regarding the surface layer, the similarity within the Eastern Mediterranean could be mainly attributed to the two widespread dominant species (*C. furcatus*, *O. plumifera*). This hypothesis is reinforced by the results of the correspondence analysis performed without *C. furcatus* and *O. plumifera*, which revealed a differentiation within the upper layer among the studied areas. The geographical position did not influence the observed distribution patterns since neighbouring areas (Sicily Channel-Ionian Sea, Rhodes area-Cretan Passage and central Levantine Sea) presented different community structures.

Correspondence analysis showed chlorophyll *a* fluctuations to be a secondary factor affecting species distribution and therefore similarities among areas. Samples collected below 50 m in the Sicily Channel, the Cretan Sea and the Rhodes area were discriminated from those collected in the Ionian Sea, Cretan Passage and central Levantine Sea due to the difference in chlorophyll *a* values, which were higher in the former areas. This difference could be related to the particular hydrological features observed in these areas (Mazzocchi *et al.*, 1997). During the present study in the Sicily Channel the Rhodes area and the Cretan Sea, predominant features are cyclonic gyres, characterized by low temperature and salinity. On the contrary, in the SE Ionian Sea, the eastern Cretan Passage and the central Levantine Sea, mainly anticyclonic gyres predominate, characterized by high temperature and salinity (Budillon *et al.*, 1994; Robinson *et al.*, 1991; Theocharis *et al.*, 1993). During the present study, only the central part of the Rhodes area (R2, R3, R4) was covered by the Rhodes cyclonic gyre (A. Theocharis, pers. comm.). In the cyclonic gyres (Rhodes area, Cretan Sea and Sicily Channel), an upward movement could variably affect biological activity and, probably, species composition. The significance of the influence of the hydrological features becomes more apparent in the Rhodes area: station R1 (Fig. 1), positioned outside the cyclonic gyre, has a species composition more similar to that of stations P5 of the Cretan Passage and L2 of the Levantine Sea (being at a distance of

1.5° or 1° from R1) than to that of station R2 (at a distance of 0.5° from R1). The influence of the Rhodes gyre during the autumn 1991 cruise was also noticed on the total zooplankton abundances (Mazzocchi *et al.*, 1997).

It would appear, therefore, that the differentiation in the copepod community structure (specially below 50 m depth) within the Eastern Mediterranean in autumn 1991 was influenced by the mesoscale hydrological structure. Hydrological features, such as fronts and eddies generated by a variety of physical processes, occur over a wide range of temporal and spatial scales, and create a succession of biological effects (Owen, 1981). At scales smaller than the large basin scale, the biological response to many physical gradients or boundaries may be manifested only as subtle changes in species composition and sometimes only as changes in the relative dominance hierarchy within a regionally ubiquitous community list (Thomas, 1992). This could be the case during the present cruise, where although no difference was observed for the presence-absence of the species among areas, their relative abundance varied.

Comparing the pattern of horizontal and vertical variation in species composition in a Gulf Stream warm-core ring, Wiebe *et al.* (1992) observed that a distinct difference in pattern existed between the ring core and the ring edge. This difference reflected in part the effects of the contrasting hydrographic variability as well as the secondary importance of diel vertical migration. Cummings (1983) observed that in the western Gulf of Mexico, the anticyclone was not distinct biologically from the cyclone, even when the latter was or was not clearly present. This observation is in contrast with our results, probably due to the difference in strength of the hydrological features. According to Weikert and Koppelman (1993), the ecological role of the Rhodes gyre must be significant when compared to the great oceans, since the spatial scale of this eddy is large in relation to the total area of the Levantine Sea.

Although the broad features of species distribution and abundances in marine plankton are undoubtedly controlled by physical factors, biotic factors such as competition and predation are critical in controlling the pattern within plankton communities (Harris, 1987). The relative importance of these two structuring mechanisms and their interactions with physical variability remains unclear. Boucher (1984) studied the respective roles of physical and biological processes in the appearance and maintenance of spatial patterns. At large spatial scales, the two causes are frequently invoked to explain observed distributions, whereas at fine scales observed spatial distributions are generally explained by dynamic features (Haury *et al.*, 1978). However, the same dynamic feature does not always produce identical biological results. The spatial distribution of copepods in relation to hydrological structure differs with species and development stage (Boucher, 1984).

It appears that the biological response of an ecosystem to variations in physical processes constitutes an important aspect of ecosystem structure because variations in production are potential disturbances which may affect species proportions (Richerson *et al.*, 1970) and the yield

available from the upper trophic levels (Cushing, 1975; Smith and Eppley, 1982). This could be very important in areas with strong hydrological features such as the Rhodes gyre. Its influence on the biological production seems to be critical (Salihoglou *et al.*, 1990; Weikert and Koppelman, 1993), especially in such an oligotrophic region as the Eastern Mediterranean. Perhaps we could consider the Rhodes gyre as an "oasis in a marine desert".

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