# Zooplankton vertical distribution in relation to the hydrology in the NW Levantine and the SE Aegean seas (spring 1986)

Zooplankton
Vertical distribution
Mesoscale circulation
Eastern Mediterranean Sea

Zooplancton
Répartition verticale
Circulation à moyenne échelle
Mer Méditerranée orientale

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ABSTRACT

Zooplankton composition and vertical distribution, and its relation to the hydrological regime are studied in the NW Levantine and SE Aegean Seas. The area is characterized by intense sub-basin and mesoscale variability. Various gyres and eddies as well as currents and jets affect the vertical and horizontal transport of the identified water masses. Furthermore, in late winter LIW is generated exclusively in this region of the Eastern Mediterranean, mainly in the Rhodes cyclonic gyre and to a lesser extent in the Cretan Sea. Generally, zooplankton density and taxa numbers decreased with depth. Four groups of copepod species were distinguished according to their vertical distribution: epipelagic, epi-mesopelagic, mesopelagic and bathypelagic. From 0-500 m, the community was dominated by small cyclopoids (Oncaea, Oithona, Corycaeus, Corycella), while the calanoid *Eucalanus monachus* was extremely dominant below 1000m. Herbivores were dominant in the upper layers, normally decreasing with depth. At the station located in the anticyclonic flow region close to the Asia Minor coast, their percentages remain high, even down to deeper layers, where some cladoceran, siphonophor and appendicularian specimens were present. These phenomena can be attributed to the downwelling which occurs within the eddy field that transports coastal waters, rich in detritus, to the deeper layers. Conversely, downwelling processes in the offshore oligotrophic region lead to zooplankton paucity in deeper layers. Hierarchical clustering and MDS grouped the samples collected in the upper layer of all stations according to the flow of the Asia Minor Current in the whole area. Zooplankton vertical distribution seems to be more influenced by temperature limits than by the thermocline or halocline position.

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RÉSUMÉ

Répartition verticale du zooplancton en relation avec l'hydrologie du nord-ouest de la Mer du Levant et du sud-est de la Mer Égée (printemps 1986)

La composition du zooplancton, sa répartition verticale et ses relations avec le régime hydrologique ont été étudiées au nord-ouest de la Mer du Levant et au sud-est de la Mer Égée. La région est caractérisée par une forte variabilité aux échelles synoptique et moyenne. Certains tourbillons et vortex, ainsi que des courants et des «jets», affectent les transports horizontal et vertical des masses d'eau

identifiées. En fin d'hiver, l'eau intermédiaire levantine est formée exclusivement dans cette partie de la Méditerranée orientale, principalement dans la région du tourbillon cyclonique de Rhodes, et à un moindre degré dans la Mer de Crète. En général, la densité zooplanctonique et le nombre des taxa décroissent lorsque la profondeur augmente. Quatre groupes d'espèces de copépodes sont distingués selon leur répartition verticale : épipélagique, épi-mésopélagique, mésopélagique et bathypélagique. La communauté de la couche 0-500 m est dominée par des petits cyclopoïdes (Oncaea, Oithona, Corycaeus, Corycella), tandis que le calanoïde *Eucalanus monachus* est extrêmement dominant au-dessous de 1 000 m. Les herbivores dominent dans les couches supérieures, et leur nombre décroît lorsque la profondeur augmente. Dans la station située dans l'anticyclone proche de la côte d'Asie Mineure, leur pourcentage reste élevé, même dans les couches profondes. Au même point, quelques individus de cladocères, siphonophores et appendiculaires ont été trouvés en profondeur. Ces faits sont dus à un enfoncement dans le tourbillon anticyclonique qui transporte en profondeur les eaux côtières, riches en détritus. A l'inverse, le processus d'enfoncement induit au large une pauvreté en zooplancton dans les couches profondes. L'analyse hiérarchique et le cadrage multidimensionnel ont permis de regrouper des échantillons collectés dans la couche superficielle dans toutes les stations, en relation avec le courant d'Asie Mineure dans la région. La répartition verticale du zooplancton semble être plus influencée par les valeurs limites de la température que par la position de la thermocline ou de l'halocline.

## INTRODUCTION

The NW Levantine Basin and the SE Aegean Sea constitute a very interesting research field, from both the hydrological and the biological points of view (UNESCO, 1984; 1985; Furnestin, 1979). The NW Levantine is bounded to the north by the southern Turkish coasts and communicates with the Aegean Sea through the eastern straits of the Cretan Arc (Rhodes, Karpathos and Kasos). It is characterized by the Rhodes Basin reaching to a depth of 4 433 m.

The eastern part of the Cretan Sea and the Dodekanissos Islands are included in the SE Aegean. This area is characterized by an extended shallow plateau in the eastern part and two deep basins (depths down to 2 500 m) in the Eastern Cretan Sea.

The water masses present in the NW Levantine basin and the SE Aegean during winter are : Deep Water (DW), Levantine Intermediate Water (LIW) and North Atlantic Water (NAW) (Hopkins, 1978; Unluäta, 1986).

The DW in the Levantine Basin is characterized by a temperature of 13.6°C and a salinity of 38.7 with a slight range of fluctuation in depths exceeding 1 500 m. On the other hand, the deep waters in the SE Aegean Sea show seasonal and temporal variability even at great depths, being warmer (~14.5°C) but saltier (~38.8) and slightly denser than the Levantine DW (Wüst, 1961; Miller, 1963). The LIW is a saline water mass that significantly affects the hydrology of the entire Mediterranean Sea. Its core fluctuates from 50 to 600 m. During the formation period (late winter) it can be detected even in the surface layer. Temperature and salinity values observed in the LIW range between 14.5-

16.5°C and 38.9-39.1 respectively (Theocharis *et al.*, 1986; Georgopoulos *et al.*, 1989).

Between the two water masses lies a thick transient layer characterized by a gradual decrease in temperature and salinity with depth.

The signature of the NAW is a subsurface salinity minimum, which is located in the area of the NW Levantine and SE Aegean from 20 m to more than 100 m during the warm period of the year. In winter, the quantities of NAW entering the NW Levantine decrease significantly, leading to the conclusion that this water mass disappears during the cold period (Hopkins, 1978; Unluäta, 1986). Recent measurements taken in the framework of the POEM programme (1986-1989) indicate that even in winter NAW intrudes into the Levantine basin, carried by the Mid-Mediterranean Jet that meanders along the latitude 34-34° 50 N. During this period NAW is detected in the surface layer (Theocharis, 1989).

High temperature and salinity values, even in deep waters, compared with those of the Atlantic Ocean and the Levantine Intermediate Water (LIW) formation processes in the Eastern Mediterranean (*e. g.* Rhodes gyre), create environmental conditions which give a particular character to the zooplankton communities. On the other hand, very significant differences in abundance between surface and deeper layers (zooplankton almost absent below 1 000 m depth: Pancucci-Papadopoulou and Siokou-Frangou, 1988; Pancucci-Papadopoulou *et al.*, 1990) reinforce the view that the NW Levantine Sea occupies an "intermediate position between the Western Mediterranean and the world ocean on one side and the Red Sea on the other side" (Weikert and Trinkaus, 1989). Despite the intrinsic interest of this area, studies on its zooplankton are based on relati-

vely few samples collected in one or two stations, with scanty information on deep-water zooplankton (Pavlova, 1966; Delalo, 1966; Moraitou-Apostolopoulou, 1972; Moraitou- Apostolopoulou and Kiortsis, 1973; Kimor and Berdugo, 1967; Kimor and Wood, 1975; Pasteur *et al.*, 1976; Scotto di Carlo and Ianora, 1983; Weikert and Trinkaus, 1989).

The present work deals with the study of the zooplankton communities existing in the areas, as well as their distribution in relation to the hydrological regime and water circulation.

## MATERIALS AND METHODS

POEM-2-86 cruise was undertaken by the Greek POEM Group in late-March early-April 1986 within the framework of the international POEM programme ("Physical Oceanography of the Eastern Mediterranean"). CTD hydrological data were collected from a large number of stations with almost nominal spacing of 0.5° in latitude and longitude (Fig. 1 *a*, 1 *b*) and especially in the NW Levantine and the Eastern Cretan Seas from a higher resolution grid. In addition, zooplankton was sampled from six
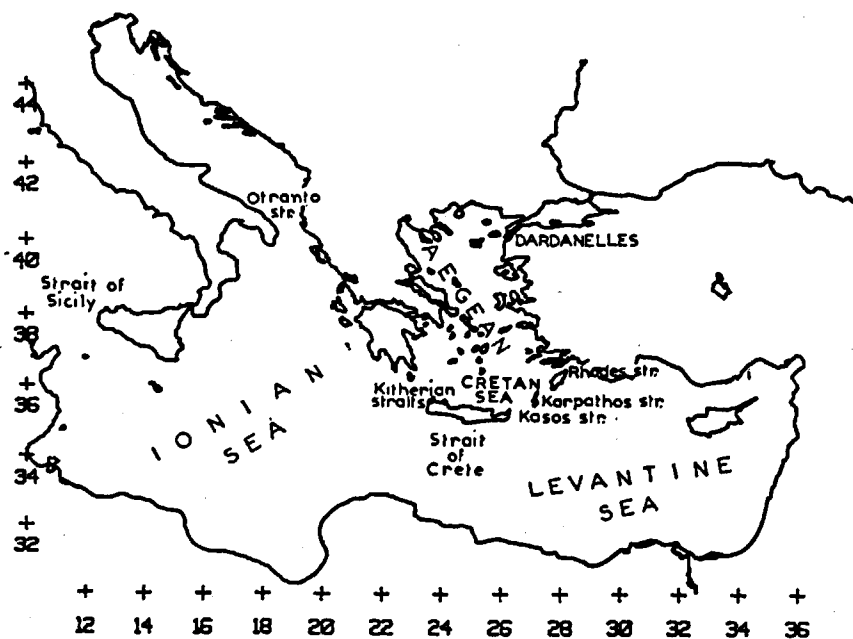


EASTERN MEDITERRANEAN

Figure 1 *a*

Geography of the Eastern Mediterranean Sea.

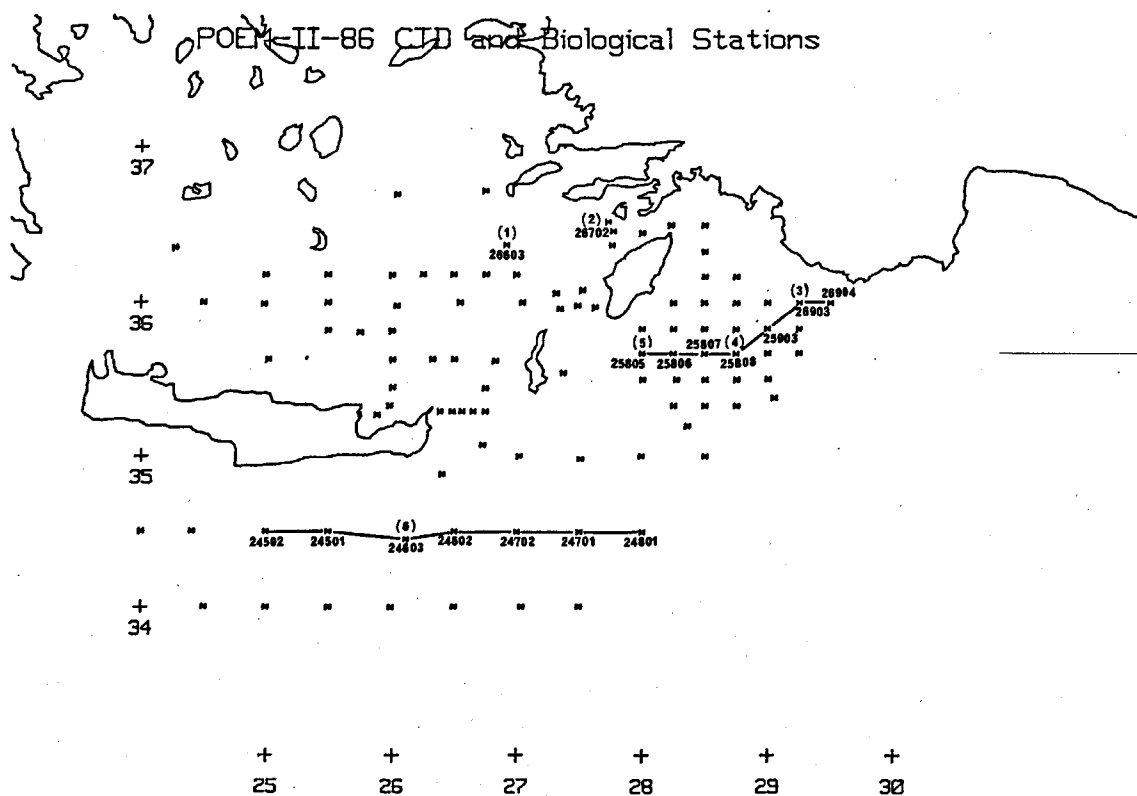Géographie de la Méditerranée orientale.



Figure 1 *b*

Sampling stations of physical parameters and zooplankton.

Stations d'échantillonnage des paramètres physiques et du zooplancton.

Table 1

*Station coordinates, date and time of zooplankton sampling.*

Coordonnées des stations, date et heure d'échantillonnage du zooplancton.

| Station | 1 | 2 | 3 | 4 | 5 | 6 |
|---|---|---|---|---|---|---|
| Latitude | 36 21 50 | 36 26 20 | 36 00 00 | 35 40 00 | 35 40 00 | 34 27 00 |
| Longitude | 26 55 50 | 27 45 00 | 29 15 00 | 28 45 00 | 28 00 00 | 26 07 00 |
| Date | 26/3/86 | 11/3/86 | 29/3/86 | 28/3/86 | 3/4/86 | 10/4/86 |
| Hour | 9.00 | 14.00 | 10.00 | 12.00 | 14.00 | 15.30 |

intervals, followed by three-point interpolation to nominal depths (every decibar). For an optimal estimation of the circulation pattern, the CTD data were analysed objectively using an isotropic homogeneous and steady correlation function of the form (Carter and Robinson, 1987):

$$C (r) = [1 - (r/a)^2] \exp [- 1/2 (r/b)^2], \, r^2 = x^2 + y^2$$

where $a$ is the zero crossing correlation length scale and $b$ the e-folding scale.

Zooplankton sampling was performed by vertical hauls of a 200 μm WP-2 closing net. The number and thickness of the sampled layers from the bottom to the surface varied among

Figure 2

*Objective analysis map of the geopotential anomaly of the 50 dbar surface relative to 700 dbar.*

Carte du relief dynamique tracée par analyse objective de la surface de 50 dbar par rapport à la surface 700 dbar.
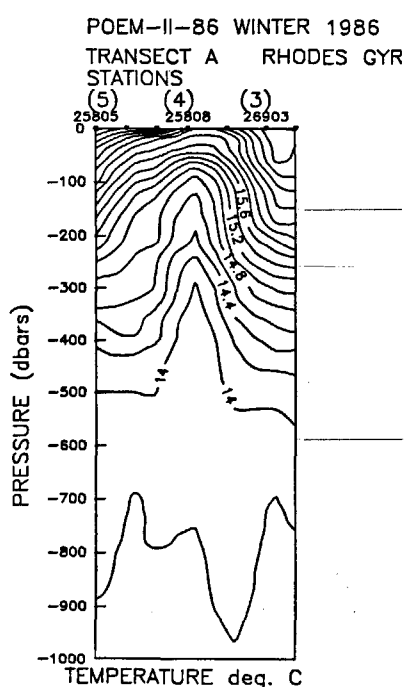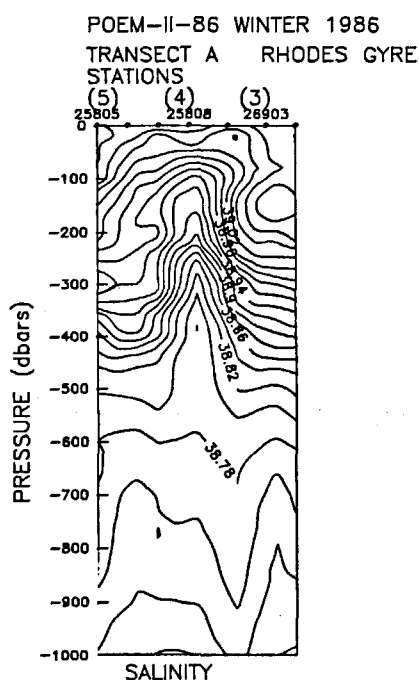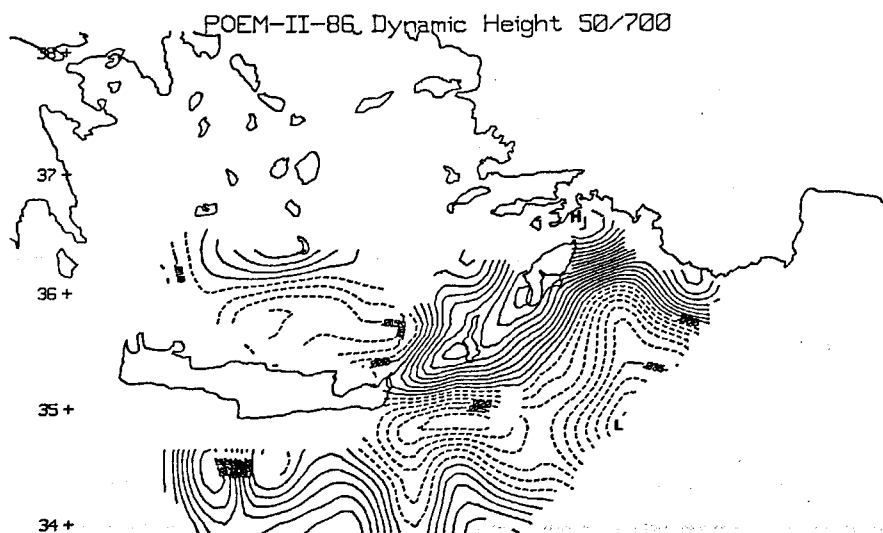


POEM-II-86. Dynamic Height 50/700



POEM-II-86 WINTER 1986
TRANSECT A    RHODES GYRE
STATIONS
(5)   (4)   (3)
25805  25808  26903
SALINITY



POEM-II-86 WINTER 1986
TRANSECT A    RHODES GYR
STATIONS
(5)   (4)   (3)
25805  25808  26903
TEMPERATURE deg. C

Figure 3 *a, b*

*Section of: a) temperature; and b) salinity across Rhodes Gyre.*

Coupe verticale de : a) la température ; et de b) la salinité à travers le tourbillon cyclonique de Rhodes.

stations (Fig. 1 *b*, Tab. 1), in the area of the NW Levantine and SE Aegean Sea.

CTD data were collected using an SBE-profiler at a rate of 33 scans/s, averaged on board by software over one-second interval, thus obtaining measurements at about 0.7 dbar

stations, specially in the upper layers, due to the special sampling procedure; in fact, samples were collected according to the distribution of the physical parameters of the water column provided by the CTD-cast: *i. e.* at each station the sampled layers were chosen above (layer A), into (layer

B) and below the thermocline or the halocline (layer C) up to 1 000 m and the last layer (layer D) below 1 000 m depth. Zooplankton samples were preserved in a 4 % formaldehyde seawater buffered solution. Qualitative and quantitative analysis was performed on the entire sample.

Hierarchical clustering, multidimensional scaling (MDS) (Field et al., 1982) and multiple correspondence analysis (MCA) (Benzécri et al., 1973) were applied to the data, in order to verify affinities between sites and/or layers and relationships between biotic and abiotic parameters. Similarity among stations was measured using the Bray and Curtis similarity index and samples were grouped by the group average sorting method in order to produce dendrograms, after square-root transformation of the data. In order to clarify the contribution of species in the formation of the groups the similarities terms analysis (Simper) was applied. Eventual relationships between zooplankton and hydrology were analysed applying multiple correspondence analysis to zooplankton abundances, temperature and salinity values simultaneously. In this case, biological and physical data were transformed into three classes, indicated as 1 for low, 2 for median and 3 for high densities (taxa) or values (temperature and salinity).

## RESULTS

### Hydrology

The analysis of the CTD data revealed an intense eddy field activity in the area under study. The objective analysis map of the dynamic height (Fig. 2) shows the predominance of sub-basin and mesoscale cyclonic and anticyclonic eddies and gyres, as well as intense currents influencing to a
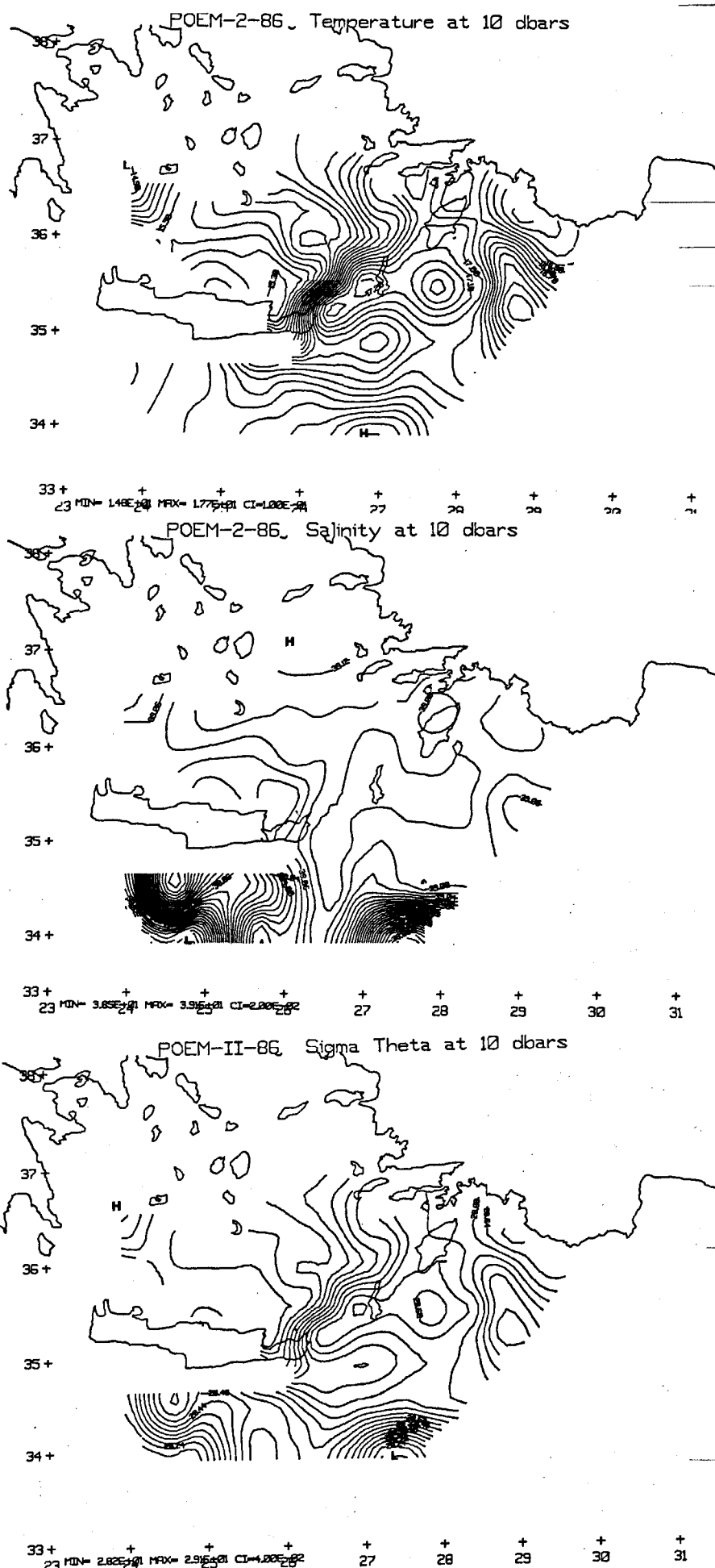
Figure 4 a, b, c

*Objective analysis maps of: a) temperature; b) salinity; and c) potential density distribution at surface (10 dbar).*

Répartition par analyse objective de : a) la température ; (b) la salinité ; et c) la densité potentielle en surface (10 dbar).
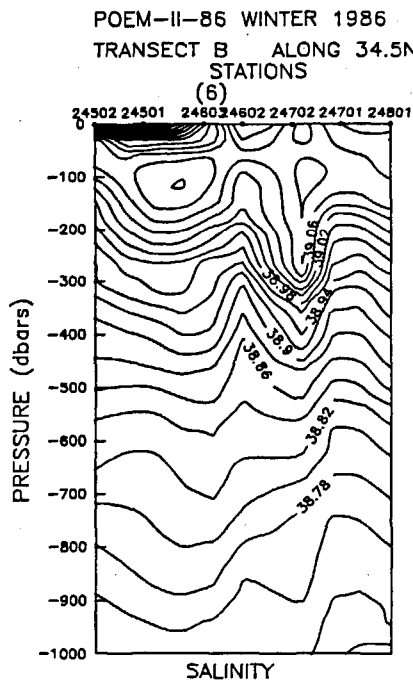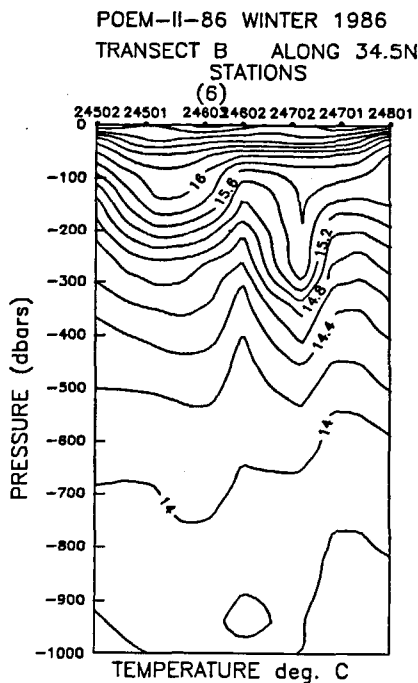
POEM—II—86 WINTER 1986
TRANSECT B ALONG 34.5N
STATIONS
(6)
24502 24501 24602 4602 24702 24701 24801

PRESSURE (dbars)

TEMPERATURE deg. C

POEM—II—86 WINTER 1986
TRANSECT B ALONG 34.5N
STATIONS
(6)
24502 24501 24602 4602 24702 24701 24801

PRESSURE (dbars)

SALINITY

Figure 5 *a, b*

*Section of: a) temperature; and b) salinity along 34° 5 N.*

Coupe verticale de : a) la température ; et b) la salinité le long de 34° 5N

considerable extent the vertical and horizontal transport of the existing water masses respectively.

The three major circulation features are the Rhodes gyre and two meandering currents, namely the Asia Minor Current (AMC) and the Mid-Mediterranean Jet (MMJ). Some mesoscale features may also be detected: the anticyclonic eddies close to the Asia Minor coasts (namely the Rhodes strait and Anaximander anticyclones), as well as those developed on either side of the MMJ and the meandering current in the Cretan Sea (Fig. 2), which also play an important role in the hydrology of the area (Georgopoulos *et al.*, 1989; Theocharis *et al.*, 1988; Theocharis, 1989).

The large multicentred cyclonic Rhodes gyre to the east and southeast of Rhodes island extended, during the cruise period, to the southeast of Crete. The doming vertical structure within the gyre field which is maintained down to 1 000 dbar indicates an upwelling of relatively colder, less saline and denser waters from deeper layers (Fig. 3 *a*, 3 *b*). In particular, waters from 250 dbar depth are transported up to the surface layer, enriching these waters with nutrients, while the intermediate depths are occupied mostly by the

Table 2

*Distribution of taxonomic groups (%) and total zooplankton density (ind/$m^3$).*

Distribution des groupes taxonomiques(%) et de la densité totale du zooplancton (ind/$m^3$)).

| Depth range Groups (%) | STATION 1 | | STATION 2 | | | STATION 3 | | | | STATION 4 | | | | STATION 5 | | | STATION 6 | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 0-50 | 50-450 | 0-250 | 250-550 | 550-700 | 0-100 | 100-500 | 500-1000 | 1000-2500 | 0-50 | 50-250 | 250-1000 | 1050-3000 | 0-150 | 150-550 | 580-1100 | 0-80 | 80-300 | 300-1000 |
| Siphonophors | 0.49 | 0.07 | 1.07 | 0.41 | 0.00 | 1.04 | 2.42 | 0.00 | 20.00 | 0.49 | 0.38 | 0.36 | 10.00 | 0.28 | 0.00 | 0.00 | 0.61 | 0.70 | 0.11 |
| Medusae | 0.43 | 0.02 | 0.18 | 0.05 | 0.00 | 0.33 | 0.43 | 1.10 | 0.00 | 0.64 | 0.13 | 0.06 | 0.00 | 0.03 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| Polychaets | 1.32 | 1.26 | 0.61 | 0.41 | 3.25 | 1.30 | 0.00 | 1.10 | 6.67 | 0.23 | 1.11 | 0.79 | 0.00 | 0.53 | 0.47 | 1.72 | 0.93 | 0.95 | 0.81 |
| Cladocerans | 0.10 | 0.00 | 0.06 | 0.00 | 0.00 | 0.00 | 0.00 | 5.49 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| Ostracods | 3.43 | 10.92 | 1.22 | 6.24 | 6.49 | 3.86 | 13.71 | 0.00 | 3.33 | 0.02 | 5.45 | 6.46 | 10.00 | 5.01 | 26.98 | 5.17 | 2.39 | 13.96 | 7.47 |
| Copepods | 80.80 | 79.99 | 69.21 | 89.21 | 81.17 | 76.57 | 73.36 | 73.63 | 53.33 | 87.75 | 78.37 | 85.44 | 77.50 | 85.75 | 62.33 | 68.97 | 78.32 | 76.79 | 84.15 |
| Chaetognaths | 4.65 | 4.27 | 5.13 | 2.25 | 1.30 | 2.66 | 4.19 | 7.69 | 6.67 | 3.03 | 2.23 | 0.97 | 0.00 | 4.26 | 6.51 | 1.72 | 9.96 | 4.49 | 4.40 |
| Heteropods | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.04 | 0.14 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| Pteropods | 1.72 | 0.35 | 0.16 | 0.20 | 0.00 | 2.44 | 0.92 | 2.20 | 0.00 | 0.25 | 0.47 | 1.09 | 0.00 | 1.03 | 0.93 | 1.72 | 0.61 | 0.00 | 0.21 |
| Appendicularians | 4.68 | 1.57 | 21.04 | 0.66 | 1.30 | 10.49 | 3.34 | 8.79 | 10.00 | 0.56 | 0.61 | 0.00 | 0.00 | 0.81 | 0.00 | 0.00 | 4.61 | 1.22 | 0.00 |
| Salps | 0.03 | 0.02 | 0.00 | 0.00 | 0.00 | 0.16 | 0.14 | 0.00 | 0.00 | 0.02 | 0.13 | 0.00 | 0.00 | 0.03 | 0.00 | 0.00 | 0.14 | 0.09 | 0.43 |
| Doliolids | 0.89 | 0.02 | 0.30 | 0.00 | 0.00 | 0.16 | 0.00 | 0.00 | 0.00 | 6.34 | 8.34 | 1.63 | 0.00 | 1.13 | 0.00 | 0.00 | 1.36 | 0.64 | 0.00 |
| Crustaceans | 1.19 | 1.13 | 0.30 | 0.51 | 6.49 | 0.67 | 0.99 | 0.00 | 0.00 | 0.51 | 1.19 | 2.72 | 0.00 | 1.00 | 2.33 | 12.07 | 0.75 | 0.86 | 1.77 |
| Mollusca larvae | 0.00 | 0.00 | 0.59 | 0.05 | 0.00 | 0.08 | 0.07 | 0.00 | 0.00 | 0.00 | 1.54 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.14 | 0.00 | 0.05 |
| Echinoderms larvae | 0.16 | 0.00 | 0.11 | 0.00 | 0.00 | 0.10 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| Icthyoplankton | 0.10 | 0.11 | 0.02 | 0.00 | 0.00 | 0.04 | 0.14 | 0.00 | 0.00 | 0.16 | 0.06 | 0.48 | 0.00 | 0.13 | 0.47 | 8.62 | 0.18 | 0.31 | 0.59 |
| Others | 0.00 | 0.26 | 0.00 | 0.00 | 0.00 | 0.06 | 0.14 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 2.50 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| TOTAL DENSITY | 202.13 | 44.97 | 87.35 | 25.39 | 4.05 | 189.28 | 13.94 | 0.73 | 0.08 | 381.10 | 127.45 | 8.88 | 0.08 | 83.48 | 1.72 | 0.36 | 140.00 | 55.50 | 9.13 |

Figure 6

*Vertical distribution of zooplankton density.*

Distribution verticale de la densité du zooplancton.
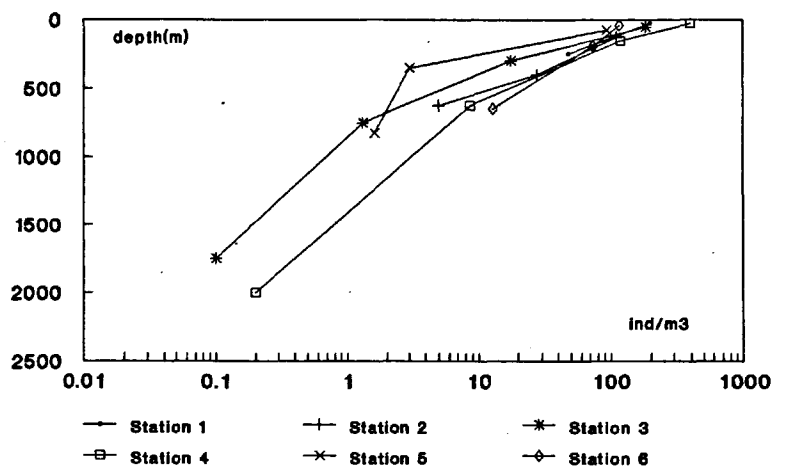


"Transient Mediterranean Waters". Deep Mediterranean waters (T = 13.7°C, S = 38.7) can be detected below 1 000 dbar (Fig. 3 *a*, 3 *b*)

Along the periphery of the Rhodes gyre meanders the intense Asia Minor Current, the western part of which can be detected in the area of the NW Levantine. Branches of this current intrude into the SE Aegean and the Cretan Sea, through the eastern straits of the Cretan Arc, significantly affecting the South Aegean hydrology. The waters transported by the AMC and its branches are characterized by high salinity, relatively high temperature and relatively lower density and nutrient concentration (Fig. 4 *a*, 4 *b*, 4 *c*). The intensity of the AMC decreases with depth, maintaining the same circulation pattern down to approximately 500-600 dbar (Theocharis, 1989). Important temperature and salinity gradients occur across the current, separating the waters of the dome of the Rhodes gyre from the waters entrapped in the anticyclonic flow regions. Waters of high temperature (T > 16.5°C) and salinity (S > 39.10), which constitute the signature of the LIW core water, are trapped within the anticyclones and transported down to 100-200 dbar (Fig. 3 *a*, 3 *b*).

The mid-Mediterranean Jet flows eastward occupying the northern part of the Strait of Crete (Fig. 2). The circulation pattern induced remains intense down to 150-200 dbar (Theocharis, 1989). From the horizontal and vertical (Fig. 4 *b*, 5 *b*) salinity distribution, it is inferred that this jet carries considerable amounts of the relatively less saline Modified Atlantic Water from the Ionian towards the Levantine basin. Patches of core LIW (S up to 39° 20) are incidentally trapped in the accompanying mesoscale anticyclones on either side of the jet.

## ZOOPLANKTON

### Total density and taxonomic group composition

Zooplankton densities in the different layers and the relative percentage composition of taxonomic groups are presented in Table 2, while density distributions for each station are plotted in Figure 6, on a logarithmical scale *versus* depth. Maximum values were recorded in the upper layers, followed by a sharp reduction with depth, especially below 1 000 m, where only 0.1 to 0.2 ind./m$^3$ were found. It must be noted that virtually all zooplankton was concentrated in the upper 500 m. A slight differentiation was observed locally: the neighbouring stations 5 and 4 presented the
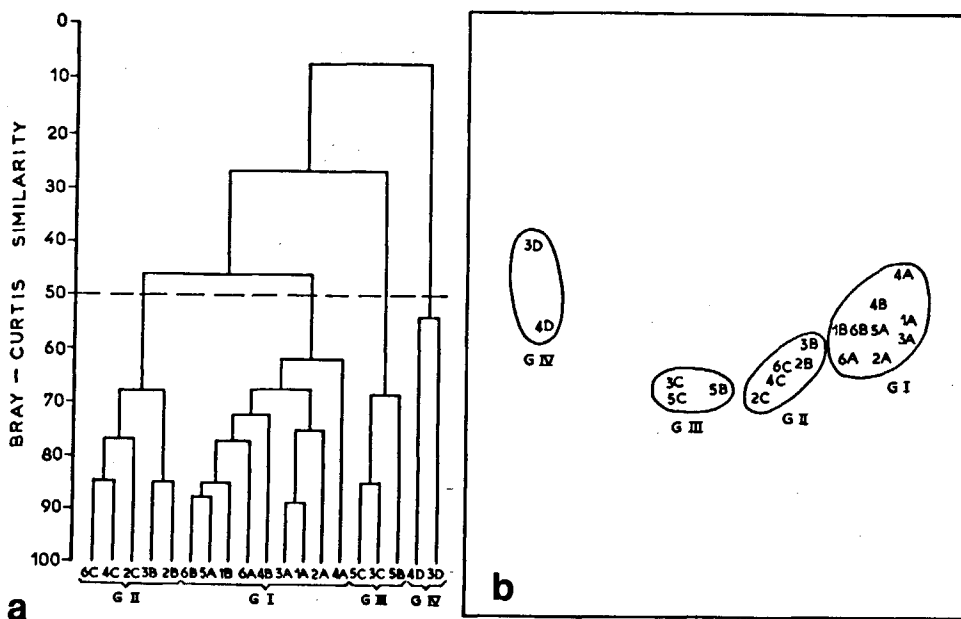


a                    b

Figure 7 *a*

*Dendrograms issued from the hierarchical clustering of zooplankton samples based on taxonomic groups composition.*

Dendrogrammes issus de l'analyse hiérarchique des échantillons du zooplancton, basée sur la composition en groupes taxonomiques.
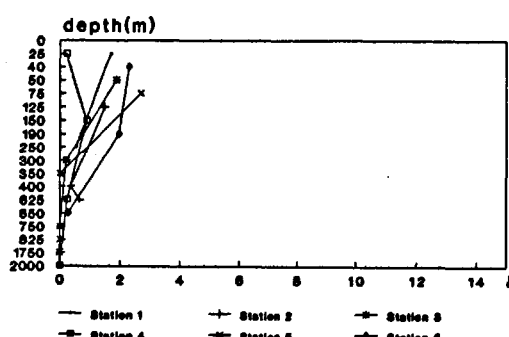
Figure 7 *b*

*MDS plot of samples based on taxonomic groups composition.*

Cadrage multidimensionnel des échantillons, basé sur la composition en groupes taxonomiques.

## Corycella rostrata



**a**
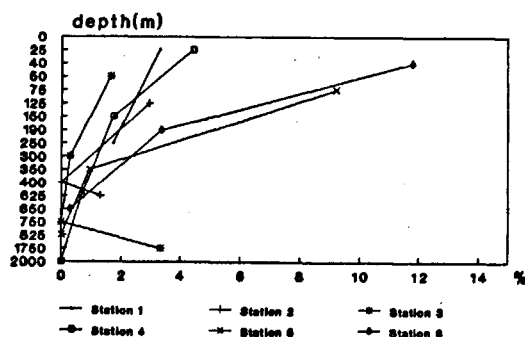
## Corycaeus typicus



**a**

Figure 8 *a, b, c, d*

*Vertical distribution of the main copepod species: a) epipelagic species; b) epi-me-sopelagic species; c) mesopelagic species; d) bathypelagic species.*
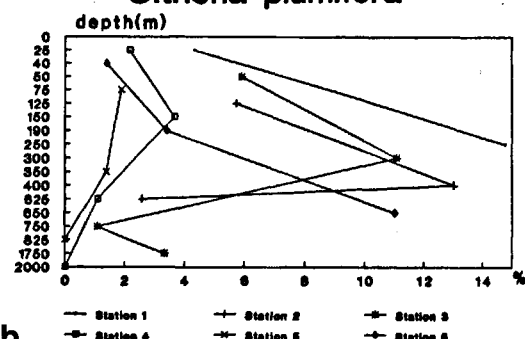
Distribution verticale des espèces abondantes des copépodes : a) espèces épipélagiques ; b) espèces épimésopélagiques ; c) espèces mésopélagiques ; d) espèces bathypélagiques.
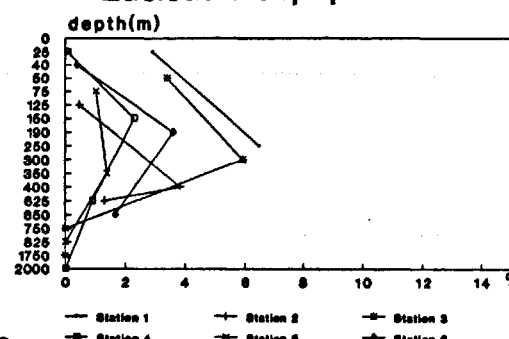
## Oithona helgolandica
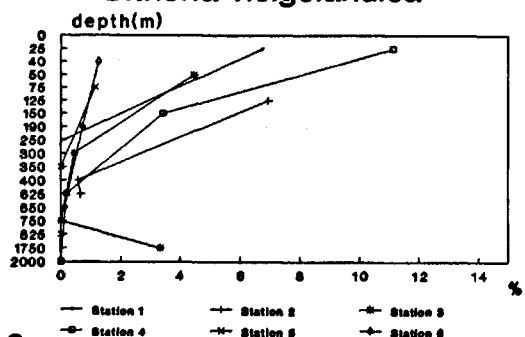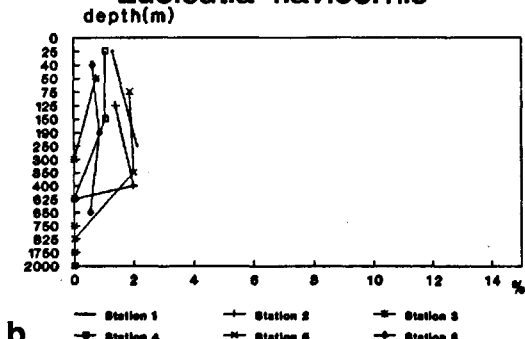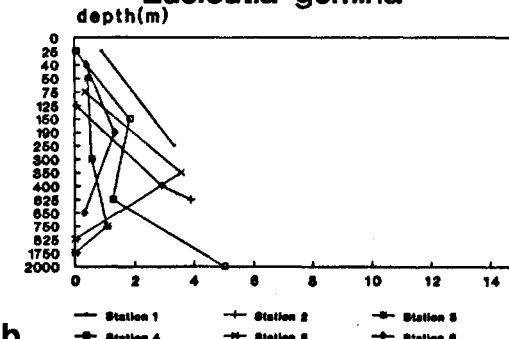


**a**

## Clausocalanus furcatus



**a**
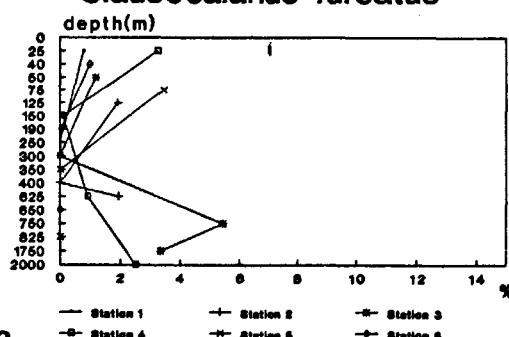
## Oithona plumifera



**b**

## Lucicutia copepodits



**b**

## Lucicutia flavicornis



**b**

## Lucicutia gemina



**b**

lower and higher densities respectively throughout the water column.

As regards the composition, a total of 19 taxonomic groups was found, with a maximum of 17 at station 3 in the layer 0-250 m and a minimum of 4 at station 4 (layer D, from 1 000 to 3 000 m). A decrease with depth in the number of the taxonomic groups was observed, especially below 500 m. Copepods were by far the dominant component of the samples, their percentage varying bet-

ween 64 % (station 3, layer D) and 92 % (station 5, layer C). Their importance mostly increased with depth, except for some cases, where they decreased in the second layer because of the ostracod maximum. The latter group always occurred with higher values in the layers B and C. It is interesting to note the abrupt decrease of the copepod percentage in the deep layer of station 3 (1 000-2 500 m) accompanied by the relatively important presence of five other groups (Siphonophora, Appendicularia,

## Oncaea media



b

## Oncaea mediterranea



b

## Pleuromamma gracilis



c

## Pleuromamma copepodits



c

## Haloptilus longicornis



c

## Eucalanus monachus



d
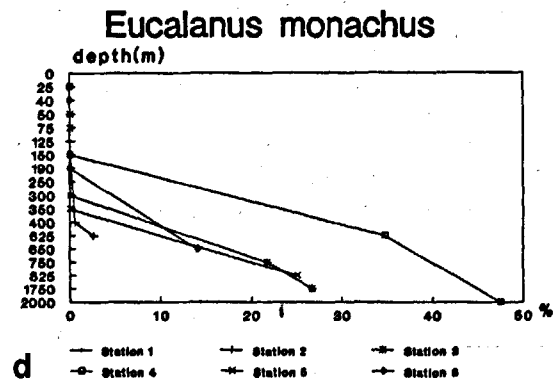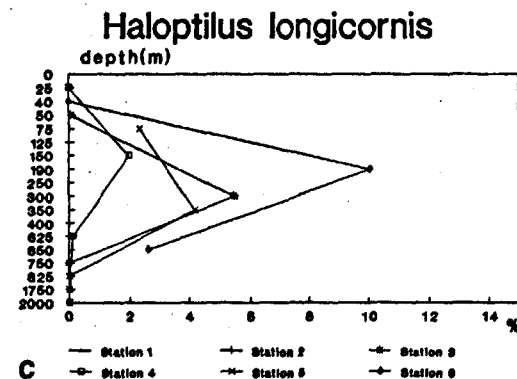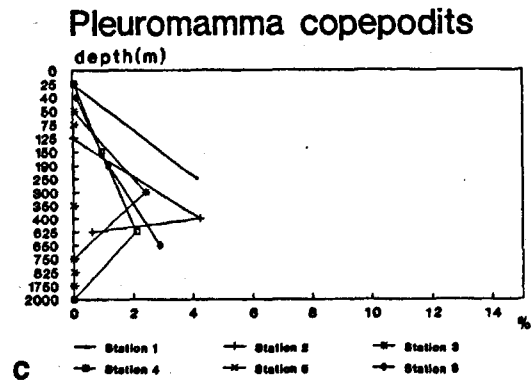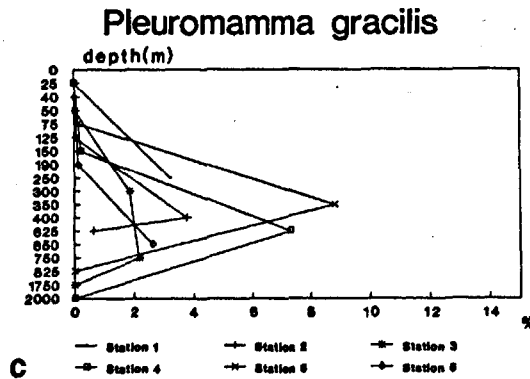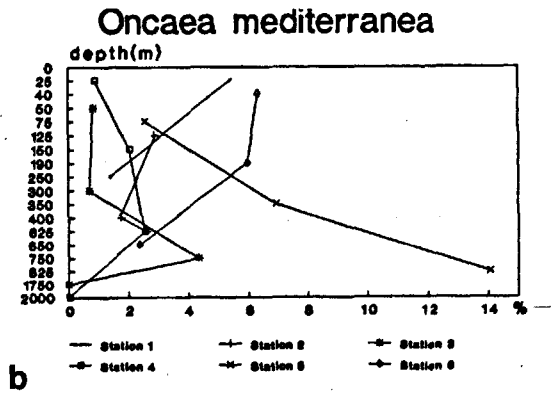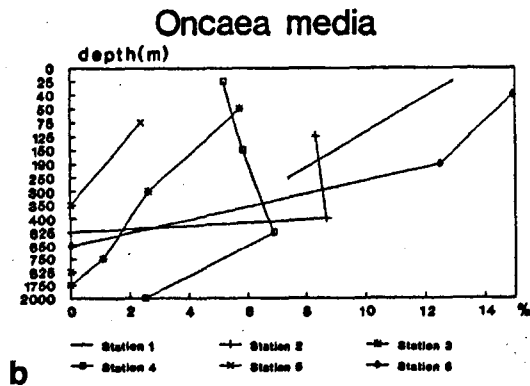
Chaetognatha, Ostracoda and Polychaeta), as well as the presence, in layer C (500-1 000 m) of the same station, of few *Penilia avirostris* specimens, while other cladocerans were almost absent from all the samples.

Among the other plankters, chaetognaths were constantly present in relative large numbers (up to 9.96 %) throughout the water column, although their contribution decreased with depth. Appendicularians occurred mainly in the upper layers and were important at stations 3 and 2, accounting for 21 % of the total zooplankton in the upper layer of station 2; doliolids were found to be quite important only at station 4 (6.34 % in layer A and 8.34 % in the layer B). The remaining taxonomic groups contributed very little to the overall zooplankton density or were rare.

Analysis by hierarchical clustering (Fig. 7 *a*) and multidimensional scaling (Fig. 7 *b*) revealed four groups of samples: group I includes the first layer (A) of all stations and the second layer (B) of stations 1, 4 and 6, grouping together zooplankton from 0 to 450 m depth; group II includes layer B of stations 2 and 3 and layer C of stations 2, 4 and 6, while group III includes layer B of the station 5 and layer C of stations 3 and 5. The last two groups include

zooplankton up to 1 000 m; their differentiation seems to be due to the lower abundances of samples 5B, 5C and 3C (group III) in comparison with those of the other stations as well as to the presence of the identical, very low, copepod abundance. Group IV includes only two samples, 3D and 4D (up to 2 500 and 3 000 m depth respectively) having the lower abundance values. The positioning of all samples according to depth ranges along the X axis should be noted.

### Copepod species composition

A total of 110 copepod species was identified. Furthermore, copepodite stages belonging to 27 genera were found, while few specimens remained unidentified. The abundances of the 30 main copepod species are reported in Table 3: richness of species composition was observed in the two upper layers (A and B), while a decrease with depth was observed, reaching 6 species in the deepest layer, below 1 000 m. Even though one or two species constitute the bulk of the deep copepod population, as is obvious from Table 3, copepod species can be distinguished in four groups according to their vertical distribution:

Table 3

*Distribution of main copepod species (ind/m³).*

Distribution des espèces abondantes de copépodes (ind/m³).

| | STATION 1 | | STATION 2 | | | STATION 3 | | | | STATION 4 | | | | STATION 5 | | | STATION 6 | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 0-50 | 50-450 | 0-250 | 250-550 | 550-700 | 0-100 | 100-500 | 500-1000 | 1000-2500 | 0-50 | 50-250 | 250-1000 | 1050-3000 | 0-150 | 150-550 | 580-1100 | 0-80 | 80-300 | 300-1000 |
| *Calocalanus pavoninus* | 5.33 | 0.27 | 1.47 | 0.21 | 0.03 | 0.23 | 0.00 | 0.00 | 0.00 | 16.39 | 2.40 | 0.00 | 0.00 | 0.76 | 0.00 | 0.00 | 2.00 | 0.17 | 0.00 |
| *Calocalanus styliremis* | 4.93 | 0.23 | 1.84 | 0.00 | 0.00 | 2.88 | 0.00 | 0.00 | 0.00 | 1.10 | 0.04 | 0.01 | 0.00 | 0.92 | 0.00 | 0.00 | 1.30 | 1.12 | 0.00 |
| *Clausocalanus furcatus* | 1.53 | 0.00 | 1.67 | 0.00 | 0.08 | 2.19 | 0.00 | 0.04 | 0.00 | 12.39 | 0.12 | 0.08 | 0.00 | 2.88 | 0.00 | 0.00 | 1.35 | 0.02 | 0.00 |
| *Clausocalanus jobei* | 0.67 | 0.01 | 0.33 | 0.00 | 0.00 | 0.08 | 0.00 | 0.01 | 0.00 | 3.69 | 14.15 | 0.04 | 0.00 | 4.16 | 0.00 | 0.00 | 5.55 | 0.44 | 0.00 |
| *Clausocalanus mastigophorus* | 1.13 | 0.06 | 0.58 | 1.00 | 0.00 | 0.46 | 0.02 | 0.00 | 0.00 | 3.37 | 0.04 | 0.02 | 0.00 | 0.55 | 0.00 | 0.01 | 0.85 | 0.02 | 0.01 |
| *Clausocalanus parapergens* | 0.07 | 0.00 | 0.00 | 0.00 | 0.00 | 0.85 | 0.00 | 0.00 | 0.00 | 0.55 | 0.00 | 0.00 | 0.00 | 0.03 | 0.00 | 0.00 | 1.60 | 2.10 | 0.00 |
| *Clausocalanus paululus* | 2.33 | 0.35 | 1.17 | 0.81 | 0.00 | 0.46 | 0.03 | 0.00 | 0.00 | 0.55 | 0.50 | 0.02 | 0.00 | 0.18 | 0.00 | 0.00 | 0.00 | 0.00 | 0.16 |
| Cop. *Clausocalanus* | 25.73 | 7.01 | 18.09 | 4.99 | 0.68 | 0.00 | 3.46 | 0.14 | 0.01 | 156.16 | 24.17 | 0.92 | 0.00 | 27.87 | 0.14 | 0.00 | 0.45 | 0.29 | 1.12 |
| Cop. *Calanus* | 2.60 | 0.23 | 0.30 | 0.21 | 0.03 | 8.38 | 0.16 | 0.00 | 0.00 | 3.22 | 1.80 | 0.00 | 0.00 | 0.60 | 0.00 | 0.00 | 2.50 | 0.66 | 0.00 |
| Cop. *Lucicutia* | 5.87 | 2.91 | 0.41 | 0.97 | 0.05 | 6.42 | 0.82 | 0.00 | 0.00 | 0.24 | 2.92 | 0.08 | 0.00 | 0.86 | 0.02 | 0.00 | 0.55 | 2.00 | 0.15 |
| Cop. *Pleuromamma* | 0.00 | 1.86 | 0.00 | 1.08 | 0.03 | 0.08 | 0.34 | 0.00 | 0.00 | 0.16 | 1.24 | 0.19 | 0.00 | 0.03 | 0.00 | 0.00 | 0.15 | 0.66 | 0.26 |
| *Corycaeus typicus* | 3.40 | 0.24 | 1.30 | 0.09 | 0.03 | 3.54 | 0.03 | 0.00 | 0.00 | 0.78 | 1.12 | 0.02 | 0.00 | 2.25 | 0.00 | 0.00 | 3.20 | 1.08 | 0.02 |
| *Corycella rostrata* | 6.67 | 0.78 | 2.58 | 0.00 | 0.05 | 3.12 | 0.04 | 0.00 | 0.00 | 16.86 | 2.20 | 0.06 | 0.00 | 7.69 | 0.02 | 0.00 | 16.50 | 1.86 | 0.02 |
| *Ctenocalanus vanus* | 0.80 | 0.40 | 0.41 | 0.47 | 0.05 | 0.65 | 0.05 | 0.00 | 0.00 | 0.71 | 5.20 | 0.01 | 0.00 | 0.68 | 0.00 | 0.00 | 0.00 | 0.22 | 0.02 |
| *Eucalanus monachus* | 0.00 | 0.00 | 0.00 | 0.14 | 0.11 | 0.00 | 0.01 | 0.16 | 0.02 | 0.08 | 0.02 | 3.09 | 0.04 | 0.00 | 0.00 | 0.10 | 0.00 | 0.00 | 1.29 |
| *Euchirella rostrata* | 0.00 | 0.13 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.01 | 0.00 | 0.00 | 0.04 | 0.01 | 0.00 | 0.00 | 0.02 |
| *Heterorhabdus papilliger* | 0.40 | 0.00 | 0.06 | 0.08 | 0.03 | 0.00 | 0.01 | 0.00 | 0.00 | 0.08 | 0.28 | 0.07 | 0.00 | 0.08 | 0.00 | 0.00 | 0.20 | 0.07 | 0.04 |
| *Heterorhabdus spinifrons* | 0.13 | 0.00 | 0.00 | 0.00 | 0.00 | 0.08 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.01 | 0.00 | 0.00 | 0.00 |
| *Haloptilus longicornis* | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.15 | 0.76 | 0.00 | 0.00 | 0.00 | 2.54 | 0.01 | 0.00 | 1.96 | 0.07 | 0.00 | 0.00 | 5.58 | 0.24 |
| *Lucicutia flavicornis* | 1.87 | 0.06 | 0.05 | 0.00 | 0.00 | 0.85 | 0.00 | 0.01 | 0.00 | 0.16 | 0.06 | 0.00 | 0.00 | 0.29 | 0.00 | 0.00 | 0.85 | 0.47 | 0.05 |
| *Lucicutia gemina* | 2.60 | 2.40 | 1.22 | 1.25 | 0.16 | 1.38 | 0.08 | 0.00 | 0.00 | 4.00 | 3.62 | 0.11 | 0.00 | 1.57 | 0.10 | 0.00 | 0.55 | 0.75 | 0.03 |
| *Oithona helgolandica* | 13.60 | 0.04 | 4.31 | 0.14 | 0.03 | 7.85 | 0.06 | 0.00 | 0.00 | 42.35 | 4.34 | 0.02 | 0.00 | 0.94 | 0.00 | 0.00 | 1.75 | 0.39 | 0.01 |
| *Oithona plumifera* | 8.73 | 6.65 | 5.00 | 3.31 | 0.11 | 11.15 | 1.54 | 0.01 | 0.00 | 8.31 | 4.68 | 0.10 | 0.00 | 1.57 | 0.02 | 0.00 | 1.95 | 1.90 | 1.00 |
| *Oncaea conifera* | 0.00 | 0.44 | 0.16 | 0.52 | 0.00 | 0.54 | 0.18 | 0.00 | 0.00 | 0.00 | 0.02 | 0.24 | 0.00 | 0.00 | 0.03 | 0.00 | 0.15 | 0.34 | 0.12 |
| *Oncaea media* | 26.07 | 3.34 | 7.28 | 2.21 | 0.00 | 10.85 | 0.37 | 0.01 | 0.00 | 19.69 | 7.42 | 0.61 | 0.00 | 1.99 | 0.00 | 0.00 | 20.90 | 6.93 | 0.00 |
| *Oncaea mediterranea* | 10.93 | 0.63 | 2.52 | 0.44 | 0.11 | 1.62 | 0.10 | 0.03 | 0.00 | 3.45 | 2.58 | 0.23 | 0.00 | 2.14 | 0.12 | 0.06 | 8.85 | 3.31 | 0.22 |
| *Oncaea notopus* | 0.00 | 0.02 | 0.08 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.02 | 0.06 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.40 |
| *Oncaea* sp. | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.03 | 0.04 | 0.05 | 0.05 | 0.17 |
| *Paracalanus denudatus* | 4.60 | 0.14 | 1.11 | 0.09 | 0.00 | 3.96 | 0.00 | 0.00 | 0.00 | 3.69 | 0.14 | 0.00 | 0.00 | 1.73 | 0.00 | 0.00 | 5.55 | 0.08 | 0.00 |
| *Pleuromamma abdominalis* | 0.00 | 0.41 | 0.00 | 0.22 | 0.00 | 0.04 | 0.10 | 0.00 | 0.00 | 0.00 | 0.02 | 0.15 | 0.00 | 0.00 | 0.13 | 0.01 | 0.00 | 0.02 | 0.11 |
| *Pleuromamma gracilis* | 0.00 | 1.45 | 0.02 | 0.96 | 0.03 | 0.04 | 0.26 | 0.02 | 0.00 | 0.00 | 0.28 | 0.65 | 0.00 | 0.10 | 0.15 | 0.00 | 0.00 | 0.08 | 0.24 |
| *Scaphocalanus similis* | 0.20 | 0.47 | 0.11 | 0.47 | 0.16 | 0.35 | 0.03 | 0.00 | 0.00 | 0.00 | 0.72 | 0.08 | 0.00 | 0.21 | 0.00 | 0.01 | 0.00 | 0.25 | 0.03 |
| *Spinocalanus* sp. | 0.00 | 0.31 | 0.00 | 0.27 | 1.18 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.14 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.36 | 0.30 |

a) the first group (Fig. 8 *a*) included species with maximum abundance between 0 and 200 m, such as *Corycella rostrata* (relative percentage between 1.65 and 11.79 %), *Oithona helgolandica* (from 1.13 to 11.1 %), *Corycaeus typicus*, *Clausocalanus furcatus*, *C.arcuicornis*, *C. jobei*, *Paracalanus denudatus* and *Calocalanus pavoninus*;

b) the relative frequency of the second group species was higher between 0 and 500 m (Fig. 8 *b*). This group included species abundant in the studied area, such as *Oncaea media* (relative frequency between 2.38 and 14.93 %),
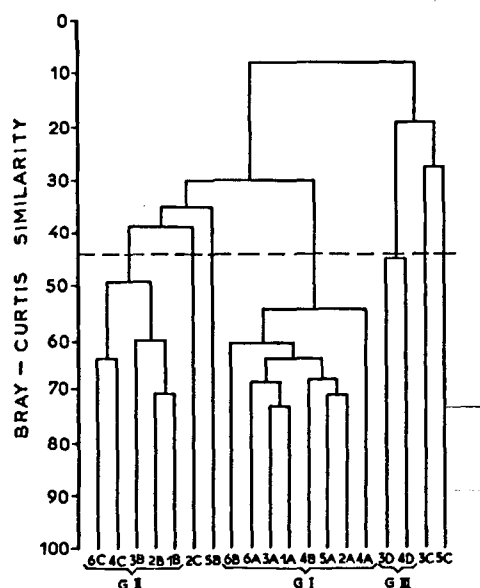
Figure 9 a

*Dendrograms issued from hierarchical clustering of samples, based on copepod species and other groups composition.*

Dendrogrammes issus de l'analyse hiérarchique des stations, basée sur la composition en espèces de copépodes et autres groupes.



Figure 9 b

*MDS plot of samples, based on copepod species composition and other taxonomic groups.*

Cadrage multidimensionnel des échantillons, basé sur la composition en espèces de copépodes et autres groupes.

*Oithona plumifera* (between 1.39 and 14.77 %), *Oncaea mediterranea* (between 1.40 and 14.06 %) and a great number of copepodite stages of *Clausocalanus* (7.87 to 33.39 %). Some other species presented the same distribution but lower abundance: *Lucicutia flavicornis*, *L. gemina*, *Lucicutia* copepodites (1.30 to 6.47 %), *Neocalanus gracilis*, *Ctenocalanus vanus* and *Euaetideus giesbrechti*;

c) the third group included subsurface and intermediate species, with a maximum abundance from 150 to 700 m (Fig. 8 c). Strong migrants occurred, such as *Pleuromamma gracilis* and copepodites of the genus, as well as other species: *Haloptilus longicornis*, *Scaphocalanus similis*, *Spinocalanus* sp.

d) the last group included species abundant between 500 and 3 000 m. *Eucalanus monachus* (from 2.60 up to 47.5 % below 1 000 m, Fig. 8 d) was found in relatively high numbers in the area, together with many exoskeletons of the species. Other rare specimens of this group belonged to *Euchirella messinensis*, *E. rostrata* and to an unidentified species of *Oncaea*.

**Statistical analysis**

Hierarchical clustering (Fig. 9 a) applied to both copepod species and the other taxonomic groups revealed the same general feature as the dendrograms for the taxonomic groups. Three groups may be distinguished at the level of 45 % similarities, while samples 5B, 5C, 2C and 3C were not grouped. The same general picture was given by the MDS (Fig. 9 b), where the latter four samples were plotted in scattered positions. Results obtained with SIMPER clarify the
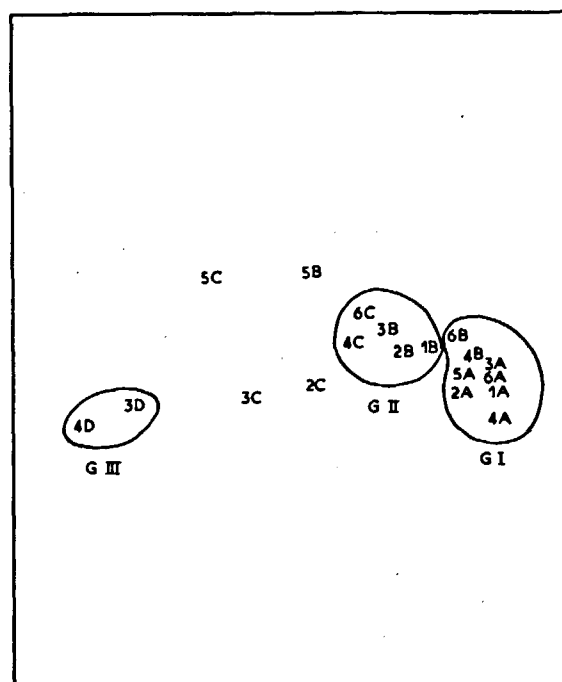
preceding analyses, giving the contribution of each taxon in the grouping of stations. Thus, group I (samples 1A, 2A, 3A, 4A, 5A, 6A, 4B, 6B) was characterized by the important contribution of chaetognaths, appendicularians, the copepod species *Oithona helgolandica*, *Corycella rostrata*, *Corycaeus typicus*, *Paracalanus denudatus*, *Mecynocera clausi*, *Oncaea media* and copepodites of the genera *Lucicutia* and *Clausocalanus*.

Group II (samples 1B, 2B, 3B, 4C, 6C) was characterized by an important contribution of chaetognaths, ostracods, *Oithona plumifera*, *Oncaea media*, *Oncaea mediterranea*, copepodites of the genera *Lucicutia* and *Pleuromamma*, *Pleuromamma gracilis* and *Pleuromamma abdominalis*. We must point out that layer B of stations 4 and 6 was clustered in the first group, as they are limited down to 300 m. Samples 1B and 6B, although neighbouring in the MDS plot, belong in different clustering groups because they have more similar qualitative than quantitative composition.

Simper analysis revealed that the discrimination of sample 2C was due to the presence of *Spinocalanus* sp., *Monacilla typica* and *Scaphocalanus similis*. Samples 2C and 5B are neighbouring in the MDS plot, having the same density values and *Clausocalanus* copepodites and ostracods in common. The 5B sample, although positioned near group II, was not clustered in this group because of the general low density values and the low number of taxonomic groups. Samples 5C and 3C had in common only the abundance of *Eucalanus monachus* with no other common species, while their grouping in the MDS plot related to taxonomic groups (Fig. 7 b) could be attributed to their identical number of groups and ind/m$^3$.

Group III included the deeper samples 3D and 4D which were differentiated because of the abundance or the presence of *Eucalanus monachus*.

In order to investigate relationships among physical parameters (temperature, salinity) and zooplankton composition, both sets of data were analysed by multiple correspondence analysis. Data were transformed in three classes of abundance for taxa or of values for physical parameters. The first axis (Fig. 10) separates: a) samples 1A, 2A, 3A, 4A, 5A, 6A, 4B, characterized by the high density of *Clausocalanus furcatus*, *Corycella rostrata*, *Oncaea media*, *Calocalanus pavoninus*, *Paracalanus denudatus*, *Oncaea mediterranea*, *Lucicutia flavicornis*, *Ctenocalanus vanus*, *Oithona plumifera*, chaetognaths, appendicularians, ostracods and copepodites of *Clausocalanus*, accompanied by high values of temperature and salinity; b) samples 3C, 5C, 5B, 3D, 4D characterized by the median abundance of *Eucalanus monachus* and the low density of a very few species, accompanied by low temperature and salinity values. Along the second axis, all the above samples are separated from samples 1B, 2B, 6B, 3B, 2C, 4C, 6C, which are characterized by high density of *Pleuromamma gracilis*, *Pleuromamma* copepodites, *Haloptilus longicornis*, *Eucalanus monachus*, *Euchirella rostrata*, median density of *Lucicutia gemina*, *L. flavicornis*, *Oncaea media* and accompanied by median values of temperature and salinity.
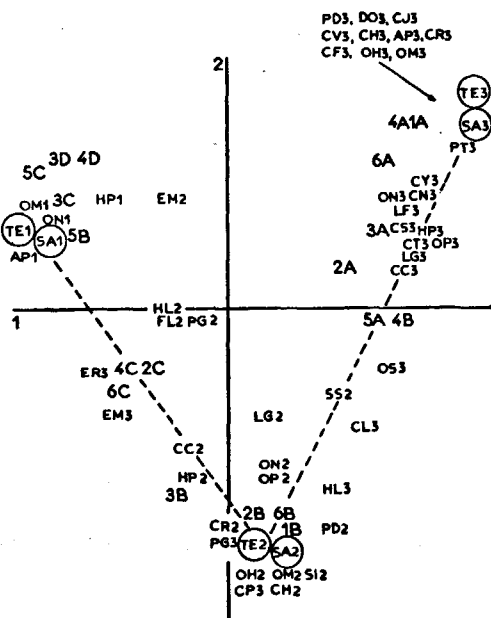


Figure 10

*Multiple correspondence analysis based on zooplankton composition, temperature and salinity data. TE = temperature; AP = appendicularians; SA = salinity; CH = chaetognaths; CF = C. furcatus; CV = C. pavoninus; OH = O. helgolandica; PT = pteropods; OP = O. plumifera; LF = L. flavicornis; CR = C. rostrata; OP = O. plumifera; CJ = C. jobei; OS = ostracods; PD = P. denudatus; LG = L. gemina; DO = doliolids; EM = E. monachus; OM = O. media; CL = Lucicutia copepodits; ON = O. mediterranea; CC = Clausocalanus copepodits; HL = H. longicornis; HP = H. papilliger; 1, 2, 3 = low, median and high density or values.*

Analyse des correspondances multiples basée sur la composition du zooplancton et les données de température et salinité.

Both samples and taxa are positioned along a "horse-shoe" figure. The first axis seems to express salinity and temperature and also depth, while the second axis expresses the opposition between extreme and median temperature and salinity values.

Corresponding hierarchical clustering ($x^2$ distance) revealed three main groups of samples. The first group comprises 1A, 4A, 6A, 3A, 2A, 5A, 4B; the second group contains 1B, 6B, 2B, 3B, 2C, 4C, 6C (the latter two samples constitute a sub-group); the third group contains 3C, 5B, 5C, 3D, 4D. This grouping of samples is slightly different from that already reported (Fig. 9 *a*), based on the Bray and Curtis similarity index. The discrepancies encountered are due to the differing approaches of these two clustering methods.

In the plane of the first two axes, along the "horse-shoe" figure, we can distinguish within the group of layer A, two sub- groups: a) those samples taken from the narrow surface layer (maximum 80 m) (1A, 4A, 6A) characterized by the abundance of taxa with narrow distribution (epipelagic: *Clausocalanus furcatus*, *Corycella rostrata*, *Oithona helgolandica*, *Calocalanus pavoninus*, Siphonohora, Appendicularia, Doliolidae); b) those samples collected from a wide surface layer (maximum 250 m, 3A, 2A, 5A, 4B), characterized by taxa with wider distribution (epi-mesopelagic: *Oncaea mediterranea*, *Calocalanus styliremis*, *Ctenocalanus vanus*, *Oithona plumifera*, *Lucicutia flavicornis*, *L. gemina*, *Lucicutia* copepodites, Ostracods). The latter group is positioned closer to the group of the B samples, characterized by taxa of strict mesopelagic distribution (*Pleuromamma gracilis*, *Pleuromamma* copepodites, *Haloptilus longicornis*). Continuing along the "horse-shoe" figure, samples 4C, 6C and 2C, in the wide depth range (250-1 000 m), are positioned between B samples and the other C samples (3C, 5C). Thus, it seems that there is a gradient of samples and taxa along the "horse-shoe" figure, expressing the depth gradient. In addition, species and taxa vertical distribution are confirmed by this analysis.

## Trophic structure

An investigation was made of the vertical distribution of zooplankton on the basis of food requirements. The exact differentiation of zooplankton in "strict" trophic classes seems to be more practical than reliable, because planktonic groups normally regarded as mainly herbivores may include carnivorous species; in addition, many copepod species may change their food requirements according to age or food availability. The complexity increases if we take into account the capacity of many species to supplement a predominantly carnivorous diet with the consumption of small particles, often of detrital material. This capacity may play an important role in survival in oligotrophic areas or in the deeper layers. Such overlapping, of course, can create difficulties in zooplankton ordination in distinct classes, because the same organism may, according to its environment and food supplies, be included in a different trophic level by different authors.
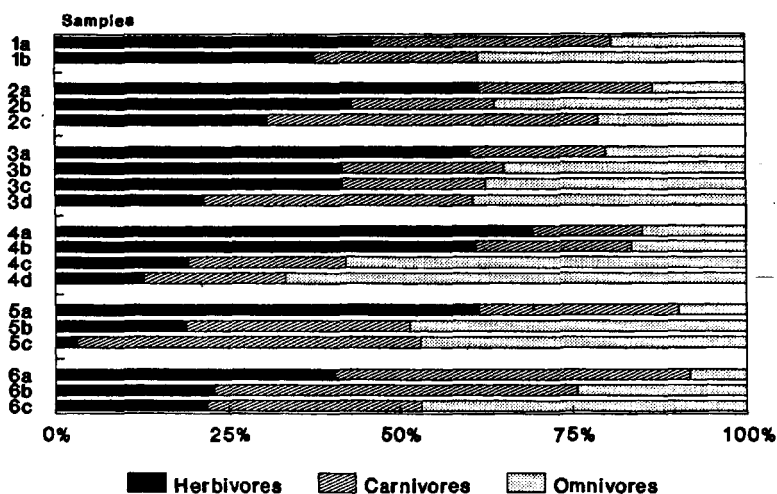
Figure 11

*Trophic structure of zooplankton communities.*

Structure trophique des communautés zooplanctoniques.

However, according to the available literature (Tregouboff and Rose, 1957; Greze, 1963; Greze et al., 1982; Bileva et al., 1982; Raymont, 1983; Longhurst, 1985; Paffenhöfer, 1983; Sameoto, 1984; Bradford and Chapman, 1988), zooplankters were classified in three classes: herbivorous, carnivorous and omnivorous, depending on their main trophic requirements. The vertical distribution for each class (relative percentage) is given in Figure 11. For a small number of organisms, however, this ordination was not possible, either because of their wide trophic spectrum or because of inadequate information. Herbivores were dominant in the upper layer, except for station 6: their presence was significant even in the deeper layers, normally decreasing with depth. For station 3, however, their percentage remains high, up to 2 500 m. As for the omnivores, they were dominant in 1B, 4C, 4D, 5B, 6C, with percentages generally increasing with depth, up to 65 % in the layer 1 000-3 000 m of station 4. Carnivores, on the other hand, were always present in large numbers, specially in the deeper layers, but were also the dominant group in the upper layers (A and B) of station 6 (up to about 50 %).

DISCUSSION

It is generally accepted that the Mediterranean Sea is relatively poor in plankton, as compared with the Atlantic open ocean (Furnestin, 1979). Comparison of data from different sources, however, seems to be difficult because of the different sampling methods used. For the Levantine Sea, zooplankton abundance data either concern the epizooplankton (Pasteur et al., 1976), or samples were collected with different mesh-size nets (Delalo, 1966; Weikert and Trinkaus, 1989). As for the neighbouring seas, we can only compare data coming from the South Aegean and Ionian Seas (Pancucci-Papadopoulou and Anagnostaki, 1989), the South Mediterranean (Porumb et al., 1981) and the Tyrrhenian Sea (Scotto di Carlo et al., 1984), as these authors used similar mesh-size nets. Zooplankton density does not differ significantly in the Levantine, Southern Aegean and Eastern Ionian Seas (Pancucci-Papadopoulou and Anagnostaki, 1989), ranging between 27 and 90 ind/m$^3$ for the layer 0-500 m and from 15 to 44.5 ind/m$^3$

for the layer 0-1 000 m. Results from the Southern Mediterranean Sea (Porumb et al., 1981) showed higher values (310 ind/m$^3$) for the layer 0-400 m during spring, results considered by Gaudy (1985) to be similar to certain areas of the Western Mediterranean. Weikert (1982) reported analogous values in the Red Sea (mean abundance values from 0-100 m about 200 ind/m$^3$) but these results were obtained using a 330 μm mesh-size net.

It is of interest to stress that the higher zooplanktonic density is observed at station 4, where the cyclonic doming structure is developed and carries waters rich in nutrients to the surface (Souvermezoglou, pers. comm.). High densities of zooplankton in the upper layers are also reported by Delalo (1966) in the northern Levantine and are attributed to the cyclonic gyre in the area. On the other hand, in the related anticyclone (station 5), zooplankton has a lower density because surface waters poor in nutrients move downward trapped by the anticyclonic flow region. Station 3, although situated inside the Anaximander anticyclone, presented higher densities than station 5, which has similar hydrological conditions. This fact could be related to the influence of the neighbouring Asia Minor coast resulting in the water enrichment in detritus (Pagou, pers. comm.). It must be noted that at all stations a sharp decrease of zooplankton is observed with depth, especially below 1 000 m, as reported also by Weikert and Trinkaus (1989) in the same region.

Copepod dominance in all the stations was in agreement with the data of Delalo (1966), Kimor and Berdugo (1967), Scotto di Carlo and Ianora (1983) and Moraitou-Apostolopoulou (1985) for the Eastern and the Western Mediterranean. As the mean copepod percentage was found to be about 80 %, their density seems to be in agreement with Scotto di Carlo et al. (1984).

The important contribution to the zooplankton community by ostracods and chaetognaths is also mentioned for the Tyrrhenian Sea (Scotto di Carlo et al., 1984) and the Levantine Sea (Delalo, 1966). Kimor and Wood (1975) recorded a high percentage of ostracods between 3 000 and 4 000 m east of Rhodes, as well as the presence of several phytoplankton species. This fact, according to the above authors, shows a high productivity area in one of the deepest regions of the Mediterranean Sea. As for the increase of ostracod frequency in the subsurface layer, this could be

related to their food requirement (carnivores, particle feeders; Raymont, 1983).

The presence of Siphonophora deeper than 1 000 m (station 3) was also reported by Kimor and Wood (1975) east of Rhodes, while Delalo (1966) reported their maximum values between 25 and 50 m for the Levantine Sea. The "aberrant" occasional presence of some *Penilia avirostris* specimens up to 1 000 m, as well as of appendicularians and siphonophors in the deep, could be related to the deepening of the isopleths, due to the existence of the Anaximander anticyclone. At station 5, of similar hydrological structure, no specimens of epipelagic organisms have been found, probably due to the low zooplankton abundance. On the other hand *P. avirostris* and appendicularians can adapt to another diet: according to Sorokin (1971), *Penilia* and the appendicularian *Oikopleura* are among the very few zooplankters which are capable of very fine filtration, so that even bacteria may constitute their food.

As already mentioned, zooplankton vertical distribution could be related merely to the trophic relationships among organisms. The oligotrophic character of open sea waters leads to a greater transparency of water, a greater light penetration and consequently to the possibility of phytoplankton growth at greater depths. For the Eastern Mediterranean, deep chlorophyll maximum has been observed (Kimor and Wood, 1975; Dowidar, 1984; Berman *et al.*, 1984; Kimor *et al.*, 1987; Gotsis-Skretas *et al.*, in press), coccolithophorids and monads being the most abundant components of the phytoplankton. Already Bernard (1967) had pointed out the importance of coccolithophorids in deeper layers (290-500 m) and generally in the intermediate water of the Eastern Mediterranean, characterized by high salinity values, even for its branches in the Western Mediterranean. Zore-Armanda and Pucher-Petkovic (1976) related the abundance of coccolithophorids to high salinity values in the Adriatic Sea, and attribute the phenomenon to the influence of LIW. This could explain the existence of herbivorous organisms even in the deeper layers.

On the other hand, higher temperature values lead to faster decomposition (Weikert, 1990) and this could explain the dominance, in the deep, of omnivorous and detritivorous organisms, as well as the extreme paucity of zooplankton at depths below 1 000 m. The strategic position of two stations (stations 3 and 4) from the hydrological point of view could explain the trophic structure already mentioned. The expected dominance of herbivores in the upper layers of station 4, together with the maximum zooplankton density as well as the high percentages of omnivores from 250 to 2 500 m depth, fit well with the existence of a dome in the area, with upwelling of water rich in nutrients from the deeper layers, higher quantities of phytoplankton and consequently of herbivorous zooplankters. This situation in the upper layers leads to a high concentration of particulate matter, detritus etc., food for omnivorous organisms, abundant in this station below 250 m and reaching 65 % in the layer 1 000-2 500 m. On the contrary, station 3 was located in the anticyclonic region of Anaximander, characterized by downwelling of saltier and warmer waters (Fig. 3 *a*, *b*).

As far as specific composition is concerned, the same problem related to the use of different mesh-size nets reappears in the comparison with previous studies. Kimor and Berdugo (1967), using a 200 µm net, reported that Cyclopoids such as *Oithona* sp., *Oncaea* sp., *Corycella rostrata* and *Corycaeus* spp. were found in fairly large numbers in the Levantine Sea for the layer 0-200 m, during a summer cruise. Pasteur *et al.* (1976), using the same mesh-size, also reported an abundance of several species of *Corycaeus* in the surface waters of Levantine. Moraitou-Apostolopoulou (1972) reported once more an abundance of *Oncaea mediterranea* in the southern Aegean Sea by oblique hauls in the upper 500 m. The abundance of Oncaeidae, Oithonidae and Corycaeidae is also reported in the coastal area of Rhodes (Siokou-Frangou and Papathanassiou, 1989), using again a 200 µm mesh-size net. Most species of these genera have also been reported as being of great numerical significance in the zooplankton of warmer oceans, while the maximum species diversity for Cyclopoids also appears to be in the upper layers of tropical and subtropical waters (Raymont, 1983). Deevey (1971) recorded the genera *Oithona* and *Oncaea* with the calanoid *Clausocalanus* as the three most numerically important copepods in the Sargasso Sea, near Bermuda. These results are in agreement with our findings, confirming the subtropical character of the area.

Among the epipelagic Calanoids, Kimor and Berdugo (1967) and Pasteur *et al.* (1976) recorded abundance of *Paracalanus parvus*, *Clausocalanus arcuicornis*, *Centropages kroyeri*, *C. violaceus* and *Temora stylifera*. In summer and autumn, Delalo (1966), using a finer mesh-size net, reported that, for the Levantine and Syrte Sea, in the layer 0-100 m copepods were mainly represented by *Oithona setigera*, *Oithona atlantica*, *O. decipiens*, *Paraoithona parvula*, *Calocalanus pavoninus*, *C. styliremis*, *C. pavo*, *Clausocalanus furcatus*, *C. paululus*, *C. arcuicornis*, *Calanus minor*, *C. gracilis*, *C. tenuicornis*, *Oncaea* spp. and *Corycaeus* spp. For deeper layers, Delalo's data are partly in agreement with our results, since he reported the presence, between 100 and 500 m, of the species *Ctenocalanus vanus*, *Lucicutia clausi*, *Haloptilus longicornis*, *Pleuromamma gracilis*, *Scolecithricella* spp.; the latter species were also found up to 1 000 m together with *Pleuromamma abdominalis*, *Mormonilla minor*, *Spinocalanus abyssalis* and *Temeropia mayumbaensis*. Below 1 000 m Delalo (1966) found *Eucalanus monachus*, *Gaetanus* sp., *Lucicutia simulans*.

As for the more recent results of Weikert and Trinkaus (1989), obtained near station 6 (south of Crete) we can firstly point out differences in the abundance of Cyclopoids. According to Weikert and Trinkaus (1989) Cyclopoids showed maximum abundances of 8-10 % of total copepods at 450 m, 1 850 m and below 2 500 m. On the other hand, Cyclopoids in our samples contributed up to 69 % of the total copepod population. Among them, *Oncaea* and *Oithona* were the most abundant genera in the upper 500 m. As many species of these genera are small, probably they cannot be captured in large numbers by nets of 333 µm mesh-size, such as those used by the above

authors. This mesh-size seems to be more appropriate for the capture of large species such as *Eucalanus*, *Haloptilus* and *Lucicutia*, which constituted the bulk of copepods in the Weikert and Trinkaus samples. In our case, only *Eucalanus* was found in large numbers in the same layers as they reported. The relative abundance of *Eucalanus*, irrespective of the used mesh-size, could be due to the poverty of these layers in species. All the above findings clearly indicate the difference in results using different nets, with the loss of smaller species and the preferential sampling of large specimens.

According to the model suggested by Scotto di Carlo *et al.* (1984) for vertical distribution of Mediterranean plankters, three main depth distribution zones are discernible: a surface zone, extending down to 100 m, which is also inhabited by a number of coastal forms; an intermediate zone, extending from 100 to 600 m and characterized by the paucity of strong migrants, where only *Pleuromamma gracilis* and *P. abdominalis* assume relative quantitative importance; the deep Mediterranean layer, below 600 m, characterized by the absence of bathypelagic species and their replacement by midwater species living at great depths.

The sampling method applied during the present study did not allow detailed vertical zonation analysis as the depth range of many layers was very wide (*p. e.* 250-1 000 m) according to the temperature-salinity profiles. Nevertheless the vertical distribution patterns that have been detected seem to coincide generally with the model described above. The upper and lower limits of the zones cannot be clearly defined and generally extend to greater depths: the layer of epipelagic species extends to 200 m and that of mesopelagic species to 700 m. Besides, a fourth group was defined by species which are abundant in a very broad layer from 0 to 500 m, such as *Oncaea media*, *O. mediterranea*, *Oithona plumifera*, characterized as epipelagic by Scotto di Carlo *et al.* (1984). This group of species, having epi-mesopelagic distribution in the studied area, was well defined in the plane of the first two axes of the multiple correspondence analysis (Fig. 8). The wider vertical distribution of the abundant species towards greater depths could be related to the environmental parameters of the area. The Levantine Sea has higher temperature values than the Tyrrhenian Sea (Miller *et al.*, 1970). Thus, animals could live in deeper layers if these have the appropriate temperature ranges. The presence of epipelagic species in

the deep was also reported by Wiebe *et al.* (1988) and Madhupatrap and Haridas (1990) and their presence was not considered as contaminant.

Differences in vertical distribution can also be reported for *Eucalanus monachus*, the only abundant species in the bathypelagic layer. According to Scotto di Carlo *et al.* (1984), its abundance maximum was positioned between 300-600 m depth, while in the studied area this species was found in abundance mainly below 500 m. Since species recorded in the bathypelagic layer of the Tyrrhenian Sea (*Monacilla typica*, *Temeropia mayumbaensis*, *Mormonilla minor*: Scotto di Carlo *et al.*, 1984) were not found in abundance in the studied area, we can report a difference for the deep layer between Tyrrhenian and Levantine Sea. We must not exclude the hypothesis of unsatisfactory sampling, since only two samples were taken from depths below 1 000 m, even though this difference has also been recorded (Pancucci-Papadopoulou *et al.*, 1990) for a wider area of the Eastern Mediterranean including the Ionian and NW Levantine Seas.

According to the Bray and Curtis based hierarchical clustering, the MDS and multiple correspondence analysis, the upper layer of all stations were grouped, a finding probably related to the warm and saline waters transported by the Asia Minor Current in the area of NW Levantine and SE Aegean. Even station 6, located at the borders between the mid-Mediterranean jet and the AMC, is grouped with the other stations because the surface layer is occupied by waters bearing Levantine characteristics. On the other hand, the distinction of A and B layers was not clear for all stations, suggesting that zooplankton vertical distribution does not depend strictly on the thermocline and/or the halocline positioning. As far as intermediate and deep layers are concerned, their grouping according to the statistical analysis of this study cannot be related to the circulation regime because many dynamic phenomena and structures develop in the area (water formation, cyclones and anticyclones, meandering jets and currents). Probably, a denser grid of stations in the future will clarify their relationships.

In conclusion, the vertical distribution of zooplankton seems to be influenced more by the temperature limits, than by the thermocline or halocline position in the studied area. Nevertheless, hydrological phenomena and water masses circulation seem to influence, albeit to a limited extent, zooplankton distribution, both vertical and horizontal.

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