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Composition, bathymetric and temporal differentiation of zooplankton in an oligotrophic area (South Aegean Sea)

Composition, différenciation bathymétrique et temporelle du zooplancton dans une zone oligotrophe (sud de la mer Égée)

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ABSTRACT

Moraitou-Apostolopoulou M., S. Zervoudaki, K. Kapiris - Composition, bathymetric and temporal differentiation of zooplankton in an oligotrophic area (South Aegean Sea). Mar. Life, **10** *(1-2) : 43-55.*

Zooplankton samples (horizontal: 3-0 m and vertical, 300-100 m, 100-0 m) were collected during four seasonal cruises (March, June, September and December 1994) in the South Aegean Sea. The total numbers of mesozooplankton varied from 5.5 to 1,721 ind.m^{-3}. The 3-0 m water layer proved the richest with a mean of 769 ind.m^{-3}, whereas the 300-100 m layer was the poorest with a mean of 221 ind.m^{-3}. The 100-0 m layer occupied an intermediate position with a mean of 658 ind.m^{-3}. When zooplankton abundance is expressed as dry weight some differences are noticed compared to the pattern observed when the number of individuals is taken into consideration. Thus, the layer 100-0 m present the highest biomass values in almost all samples. This is due to the abundance in this layer of large planktonic forms such as chaetognaths, appendicularians and crustacean larvae. No clear pattern of spatial differentiation seems to exist between the studied areas. The mesozooplankton assemblages are dominated by copepods that form 72% of the total number of zooplanktonic individuals. Among all other zooplankton groups, only chaetognaths (8%), cladocerans (5%) and appendicularians (4%) are of some quantitative importance. Sixty copepod species were identified throughout the whole water column (0-300 m). The surface layer showed the greatest diversity with 54 species, 46 species were identified in the 100-0 m layer and 34 in the 300-100 m layer. The surface and the 100-0 m layer presented similar copepod species composition. The main species were: Clausocalanus furcatus, Oithona plumifera, Calocalanus pavo *followed by* Farranula rostrata, Mecynocera clausi *and* Lucicutia flavicornis. *The deep layer (300-100 m), characterized by poverty in planktonic organisms, is dominated by* Lucicutia flavicornis *followed by* Oithona plumifera, Farranula rostrata *and* Pleuromamma gracilis. *The complicated hydrography of the area, where cyclonic gyres prevail, and the seasonal changes of environmental parameters are the main factors regulating the zooplankton distribution. Zooplankton populations show pronounced quantitative seasonal differences and seem to depend on picoplankton as a food resource*

RÉSUMÉ

Moraitou-Apostolopoulou M., S. Zervoudaki, K. Kapiris – [Composition, différenciation bathymétrique et temporelle du zooplancton dans une zone oligotrophe (sud de la mer Égée)]. Mar. Life, **10** *(1-2) : 43-55.*

Des échantillons de zooplancton (traits horizontaux (3-0 m) et verticaux (300-100 m, 100-0 m)) ont été collectés au cours de quatre campagnes océanographiques saisonnières (mars, juin, septembre et décembre 1994) au sud de la mer Égée. Les concentrations totales en mésozooplancton varient entre 5,5 et 1 721 ind.m^{-3}. La couche superficielle était la plus riche (moyenne : 769 ind. m^{-3}) et la couche profonde la plus pauvre (moyenne : 221 ind.m^{-3}). C'est dans la couche 100-0 m que l'on observe les valeurs de biomasse les plus élevées pour presque tous les échantillons. Ceci est dû à l'abondance des grands organismes planctoniques dans cette couche (chaetognathes, appendiculaires et larves de crustacés). Aucun modèle clair de différenciation spatiale entre les zones échantillonnées n'apparaît. Les assemblages mésozooplanctoniques sont dominés par les copépodes qui représentent 72% de la communauté zooplanctonique totale. Parmi les autres groupes du zooplancton, seuls les chaetognathes (8%), les cladocères (5%) et les appendiculaires (4%) présentent une importance quantitative. Dans l'ensemble de la colonne d'eau, 60 espèces de copépodes ont été identifiées. Les eaux de surface présentent la plus grande diversité spécifique avec 54 espèces. 46 espèces ont été identifiées dans la couche 100-0 m et 34 dans la couche 300-100 m. La surface et la couche 100-0 m présentent des compositions spécifiques similaires avec, principalement, les espèces suivantes : Clausocalanus furcatus, Oithona plumifera, Calocalanus pavo *suivies de* Farranula rostrata, Mecynocera clausi *et* Lucicutia flavicornis. *La couche profonde (300-100 m), caractérisée par une pauvreté en organismes planctoniques, est dominée par* Lucicutia flavicornis *suivie de* Oithona plumifera, Farranula rostrata *et* Pleuromamma gracilis. *L'hydrographie complexe de la zone, marquée par la circulation cyclonique, ainsi que les variations saisonnières des paramètres environnementaux constituent les facteurs principaux régulant la distribution du zooplancton. Quantitativement, les populations zooplanctoniques montrent une variabilité saisonnière prononcée et semblent dépendre de la ressource alimentaire constituée par le picoplancton.*

INTRODUCTION

The Mediterranean Sea is a semi-enclosed basin displaying several peculiarities compared with typical oceanic environments: negative water balance, lack of tides and a temperate to subtropical gradient from North to South. Among the most important characteristics is the nutrient deficiency with a West-East gradient creating an oligotrophic, and even ultra-oligotrophic, environment at its Eastern end. The Eastern Mediterranean is a very interesting area both from the hydrological and the biological points of view (Furnestin, 1979; Unesco, 1984).

The Aegean Sea occupies a strategic position in the Mediterranean Basin and is of great importance due to its morphology, hydrology and the clearly pronounced heterogeneity of its ecological characters. This heterogeneity gives rise to two ecologically distinct areas, the North and the South Aegean Sea, and to a variety of biotopes. Although the south part of the Aegean Sea has been studied more than the North, the state of our knowledge is far from adequate to offer a basis for an understanding of the composition and functioning of pelagic ecosystems.

Studies on spatial, bathymetric and temporal variability of zooplankton communities are important for a better understanding of the functioning of oligotrophic ecosystems. The aim of the present study is to provide information on the occurrence, seasonal cycle and bathymetric and spatial differentiation of the zooplankton in the South Aegean Sea and the Cretan Straits.

This work is part of the MAST PELAGOS programme of the EC (Contract MAS2CT93-0059) and presents the results of the study of zooplankton samples collected during four seasonal cruises.

MATERIAL AND METHODS

Mesozooplankton samples were collected at five stations during four seasonal cruises (March, June, September and December 1994). The samplings took place in the South Aegean Sea in the area North of Crete (station 50 and 59) and in the straits of the Cretan Arc (station 32, 23, 80) (figure 1). Mesozooplankton sampling was performed with a WP2 net (200 µm mesh aperture size). At every station horizontal and vertical (100-0, 300-100 m) hauls were performed. In order to eliminate differences attributable to nychthemeral migrations, samples were taken between 10.00 h and 14.00 h.

The volume of the filtered sea-water was estimated by a flowmeter (Hydrobios). Samples were preserved with 4% buffered formaldehyde-sea water solution. Depending on zooplankton abundance, identification and counting of organisms were performed on the entire sample or to a fraction (up to 1/4). Copepods were identified to species level. Minor taxa were referred to as groups.

Quantitative estimation of zooplankton has been done by measuring: (a) the number of individuals per cubic meter (ind.m^{-3}) and (b) the dry weight (mg.m^{-3}).

Estimation of species diversity was calculated using the Shannon Index, whereas the species predominance was calculated using the Simpson dominance Index. In order to assess similarities in zooplankton communities between stations, we have used the methods of classification and ordination according to Field *et al.* (1982). The raw data, mesozooplankton species density and group composition were subjected to square root transformation. The Bray-Curtis similarity matrix was used for the computation. With classification we have clustering of samples as dendrograms.

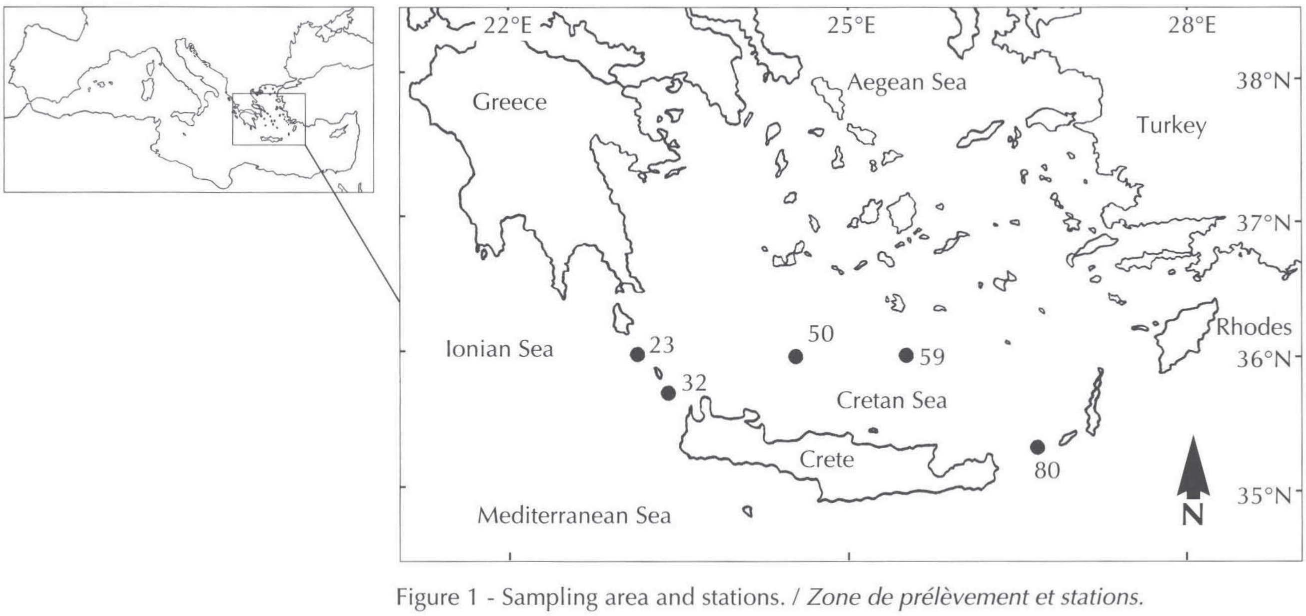

Figure 1 - Sampling area and stations. / *Zone de prélèvement et stations.*

Table I – Identified species of zooplankton in the studied area. / *Espèces zooplanctoniques identifiées dans la zone d'étude.*

Calanus helgolandicus Claus, 1863
C. tenuicornis Dana, 1849
C. minor Claus, 1863
C. gracilis Dana, 1849
Calocalanus pavo Dana, 1849
Eucalanus monachus Giesbrecht, 1888
E. attenuatus Dana, 1849
E. pavo
Clausocalanus mastigophorus Claus, 1863
C. jobei Frost et Fleminger, 1968
C. paululus Farran, 1926
C. lividus Frost et Fleminger, 1968
C. pergens Farran, 1926
C. arcuicornis Dana, 1849
C. furcatus Brady, 1883
C. arcuicornis (fem.)
C. arcuicornis (mal.)
C. parapergens Frost et Fleminger, 1968
C. juveniles
Paracalanus parvus Claus, 1863
Mecynocera clausi I.C. Thompson, 1888
Scolecithrix bradyi Giesbrecht, 1888
Aetideus armatus Boeck, 1872
A. giesbrechti
Lucicutia flavicornis Claus, 1863
Pleuromamma gracilis Claus, 1863
P. abdominalis Lubbock, 1856
Temora stylifera Dana, 1849
Centropages typicus Kröyer, 1849
Chiridius poppei Giesbrecht, 1892
Candacia ethiopica Dana, 1849
C. bispinosa Claus, 1863
C. longimana Claus, 1863
C. armata Boeck, 1872
C. simplex
C. juveniles
Acartia clausi Giesbrecht, 1889
Phaena spinifera Claus, 1863
Oncaea media Giesbrecht, 1891
O. venusta Philippi, 1843
O. mediterranea Claus, 1863
Euterpina acutifrons Dana, 1847
Oithona plumifera Baird, 1843
O. tenuis Rosendorn, 1917
O. nana Giesbrecht, 1892
O. setigera Dana, 1849
O. juveniles
Copilia mediterranea Claus, 1863
Corycaeus brehmi Stener, 1910
C. clausi F. Dahl, 1894
C. giesbrechti F. Dahl, 1894
C. limbatus Brady, 1883
C. typicus Kröyer, 1849
Diaixis pygmaea T. Scott, 1899
Farranula rostrata Claus, 1863
Sapphirina sp.
Clytemnestra sp.
Ratania flava Giesbrecht, 1892
Lubbockia squillimana Claus, 1863
Microsetella rosea Dana, 1847

RESULTS

The identified species of zooplankton (table I), its occurrence, seasonal cycles, bathymetric distribution and spatial differentiation are shown in figure 2 (ind.m^{-3}) and figure 3 (dry weight, mg.m^{-3}).

A clear seasonal pattern characterizes the occurrence of zooplankton with maximum mean values in September (803 ind.m^{-3}) and December (563 ind.m^{-3}) declining to minimum values in March (103 ind.m^{-3}) and June (180 ind.m^{-3}).

The surface (0-3 m) layer proved the most dense (769 ind.m^{-3}), the 300-100 m layer seemed to be the poorest (221 ind.m^{-3}) whereas the 100-0 m layer presented intermediate but similar to surface values (658 ind.m^{-3}). Differences in the bathymetric distribution of the zooplankton density of the two upper layers were observed between the sampling periods. Thus the highest zooplankton densities are recorded in the surface layer in September and December and in the 100-0 m layer in March and June. Consequently the higher zooplankton densities occur in the surface layer during September and December, with the exception of station 50.

When zooplankton abundance is expressed as biomass values (dry weight) the seasonal and bathymetric distribution of zooplankton shows some differences. Thus, the 100-0 m layer presents for most samplings the highest biomass values, whereas March becomes the richest sampling period. This is due to the abundance of some large zooplanktonic forms such as chaetognaths, siphonophores, salps, appendicularians and crustacean larvae.

Concerning the spatial distribution of zooplankton in the sampling area, no clear pattern of quantitative differentiation is apparent between the 5 stations. Only during the June cruise the 300-100 m layer presented a regular quantitative increase from the West to the East. Furthermore, due to the complicated hydrography of the area some peculiarities in the quantitative distribution of zooplankton are also noted. For example, in June, station 32 is the richest for the surface layer and the poorest for the 300-100 m layer. Station 80 in March and June is one of the poorest stations for the surface layer while the 100-0 m layer was the richest of all stations.

Zooplankton composition data, pooled in all stations and seasons, in dominant groups is presented in figure 4. Copepods dominated the mesozooplankton assemblages in all zooplankton samples. The contribution of copepods to the total zooplankton community in the four cruises was: March: 75.6%; June: 71.4%; September: 70.5% and December: 72.5% of the total density.

The main features of the composition of the zooplankton community for the three water layers are given below.

In the surface layer the density of the copepod group varied from 9.5 ind.m^{-3} (March) to 1,105.4 ind.m^{-3} (September). The cladocerans are the second group in abundance, whith maximum values (340.7 ind.m^{-3} and 324.6 ind.m^{-3}), at stations 80 and 59 of the September cruise respectively. The presence of this group is low during the remaining cruises. The third group in abundance are the chaetognaths showing the highest density in December (123.6 ind.m^{-3}), and low numbers for the other seasons. The appendicularians are the next group in abundance forming a maximum during December (53.52 ind.m^{-3}). Finally ostracods present an almost regular

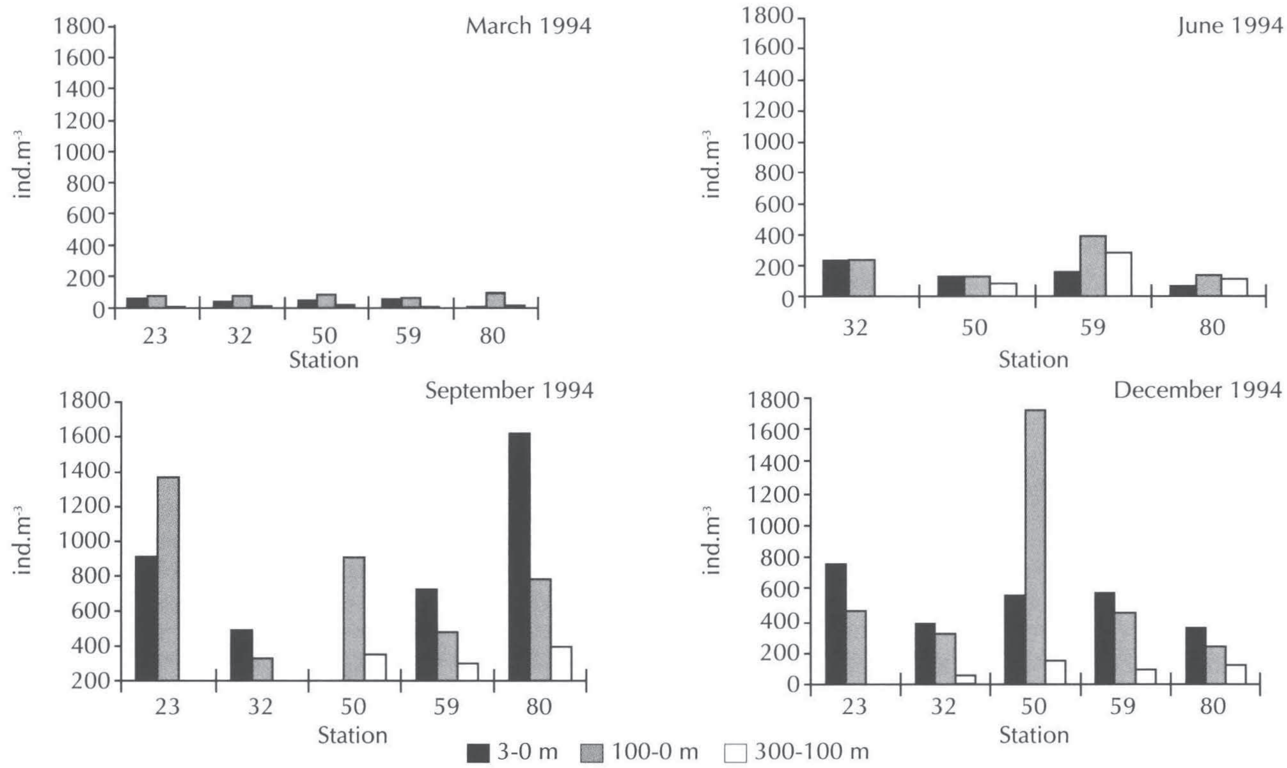

Figure 2 - Seasonal cycles, bathymetric distribution (3-0 m, 100-0 m, 300-100 m) and spatial differenciation of total zooplankton (ind.m^{-3}). / *Cycles saisonniers, distribution bathymétrique (3-0 m, 100-0 m, 300-100 m) et différenciation spatiale du zooplancton total (ind.m^{-3}).*

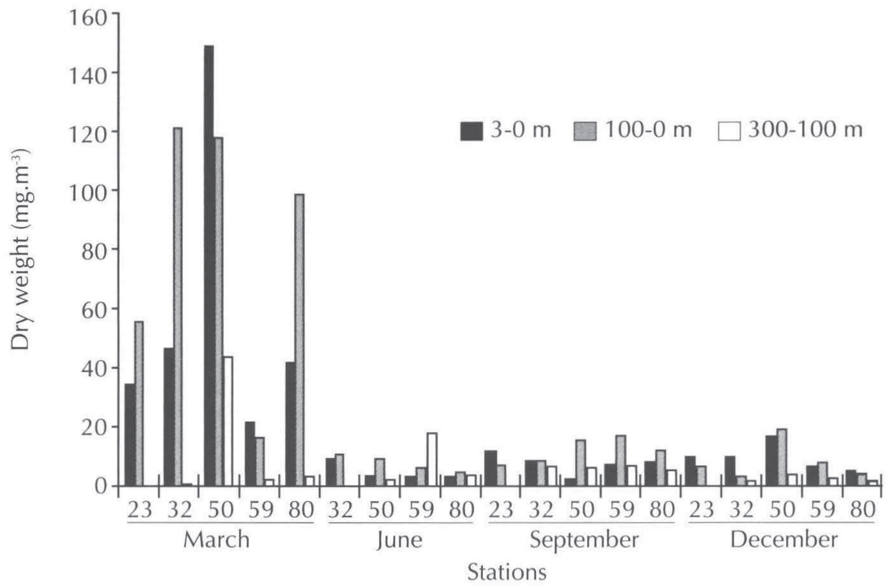

Figure 3 - Sampling stations' seasonal cycles, bathymetric distribution (3-0 m, 100-0 m, 300-100 m) and spatial differentiation of total zooplankton (ash free dry weight, mg.m^{-3}). *Cycles saisonniers des stations de prélèvement, distribution bathymétrique (3-0 m, 100-0 m, 300-100 m) et différenciation spatiale du zooplancton total (poids sec, mg.m^{-3}).*

distribution at all stations, with mean densities between 0 and 23.54 ind.m^{-3} (December). The mean percentages of abundance of these groups for this water layer are: copepods 72.42%; cladocerans 10.31%; chaetognaths 7.25%; appendicularians 3% and ostracods 1.41% (figure 4).

Concerning the 100-0 m layer (figure 4), the percentage of copepods remained practically the same (73.2%). The abundance of this group varied between 41.5 ind.m^{-3} (March) to 1,258 ind.m^{-3} (December). The second group in abundance are the chaetognaths (7.6%), the density of which ranged from 0 ind.m^{-3} (March) to 106.7 ind.m^{-3} (December). The next group in abundance are the

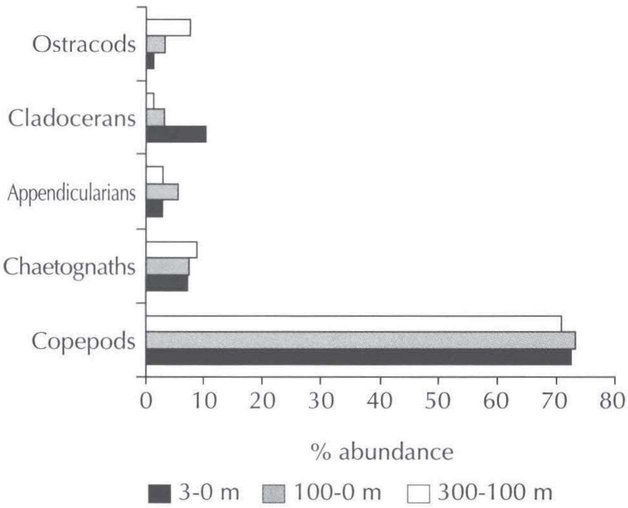

Figure 4 - Zooplankton composition of dominant groups in the three water layers in all seasons. / *Composition zooplanctonique des groupes dominants dans les trois couches d'eau et pour toutes les saisons.*

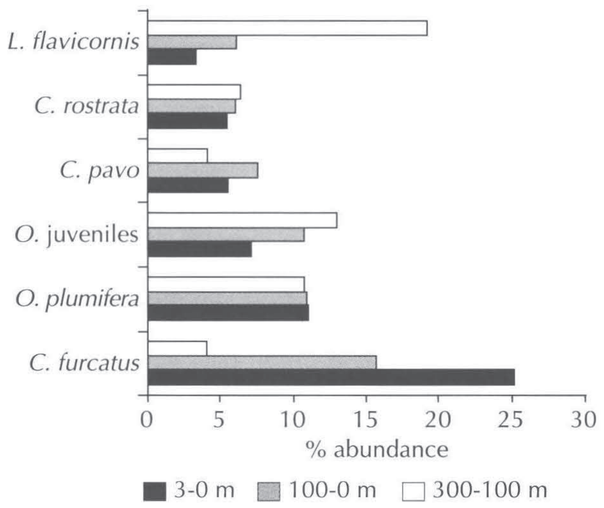

Figure 5 - Copepod composition of dominant species in the three water layers in all seasons. / *Composition en espèces de copépodes dominantes dans les trois couches d'eau et pour toutes les saisons.*

appendicularians (5.75%). The presence of this group varied between 0.54 ind.m^{-3} (March) and 6.6 ind.m^{-3} (December). The cladocerans follow with a mean percentage of 3.2%. The maximum density of cladocerans was during the September cruise (72.22 ind.m^{-3}). The last of the important mesozooplankton groups is the ostracods (3.12%) with densities fluctuating from 0.25 ind.m^{-3} (March) to 40.46 ind.m^{-3} (December).

Concerning the deep layer (300-100 m) copepods continue to dominate the mesozooplankton, accounting for 70.8% of the total zooplankton numbers. The abundance of the group varied from 8.33 ind.m^{-3} (March) to 320.8 ind.m^{-3} (September). The second group in abundance are the chaetognaths (8.86%), the density of which varied between 0.016 ind.m^{-3} (March) to 66.61 ind.m^{-3} (September). The next group are the ostracods (7.65%) and the last most numerous groups are the fish larvae, with a mean percentage of 4.42%. All other zooplankton groups presented much lower numbers (figure 4).

Sixty copepod species were identified throughout the water column (0-300 m). The surface layer showed the greatest diversity with 54 species, 46 species were identified in the 100-0 m layer and 34 in the 300-100 m layer. Copepod composition in dominant species is presented in figure 5.

As copepods constitute the main part of the zooplankton community they have been more intensively studied and identified to species level. From the 60 species identified only a few could be characterized as important on the basis of their numbers. These copepod species are: *Clausocalanus furcatus, Oithona plumifera, Calocalanus pavo, Farranula rostrata, Mecynocera clausi, Acartia negligens, Lucicutia flavicornis, Oncaea media, Oncaea mediterranea, Temora stylifera, Eucalanus monachus* and *Pleuromamma gracilis* (figures 6, 7, 8).

Copepod diversity (figure 9) varied from 0.276 to 1.581 for the surface layer, from 0.267 to 1.967 for the 100-0 m layer and from 0.538 to 1.167 for the 300-100 m layer For all water layers copepod diversity was greatest in September, being more stable in the other sampling months. Exceptionally low diversity was recorded at station 80 at 100-0 m in March.

The values for dominance (figure 9) of the first two species varied from 1.516 to 2,925 for the surface (dominant species: *Clausocalanus furcatus, Oithona plumifera*), from 0.647 to 1,443.1 for the 100-0 m (*Clausocalanus furcatus, Oithona plumifera*) and from 0.002 to 101.34 for the 300-100 m layer (*Lucicutia flavicornis, Oithona plumifera*).

According to the pattern of vertical distribution of copepod species, for all sampling periods wide differentiation was observed between the samples of the 100-0 m layer and those of the 300-100 m layer.

The copepod assemblages of the surface layer are dominated by *Clausocalanus furcatus* (1,419

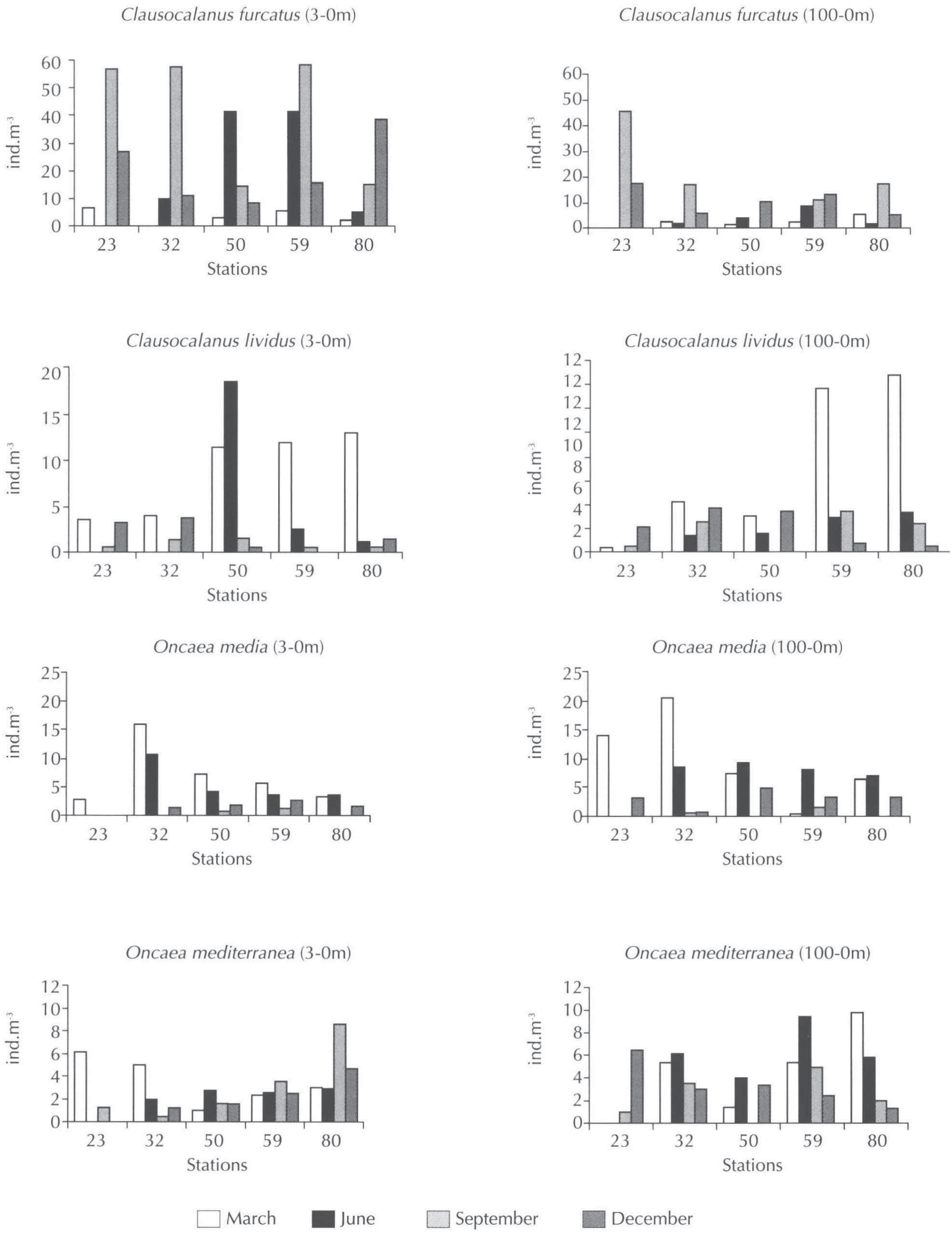

Figure 6 - Bathymetric and temporal fluctuations of *Clausocalanus furcatus, C. lividus, Oncaea media* and *O. mediterranea* abundance in all seasons. / *Fluctuations bathymétriques et temporelles de l'abondance de* Clausocalanus furcatus, C. lividus, Oncaea media *et* O. mediterranea.

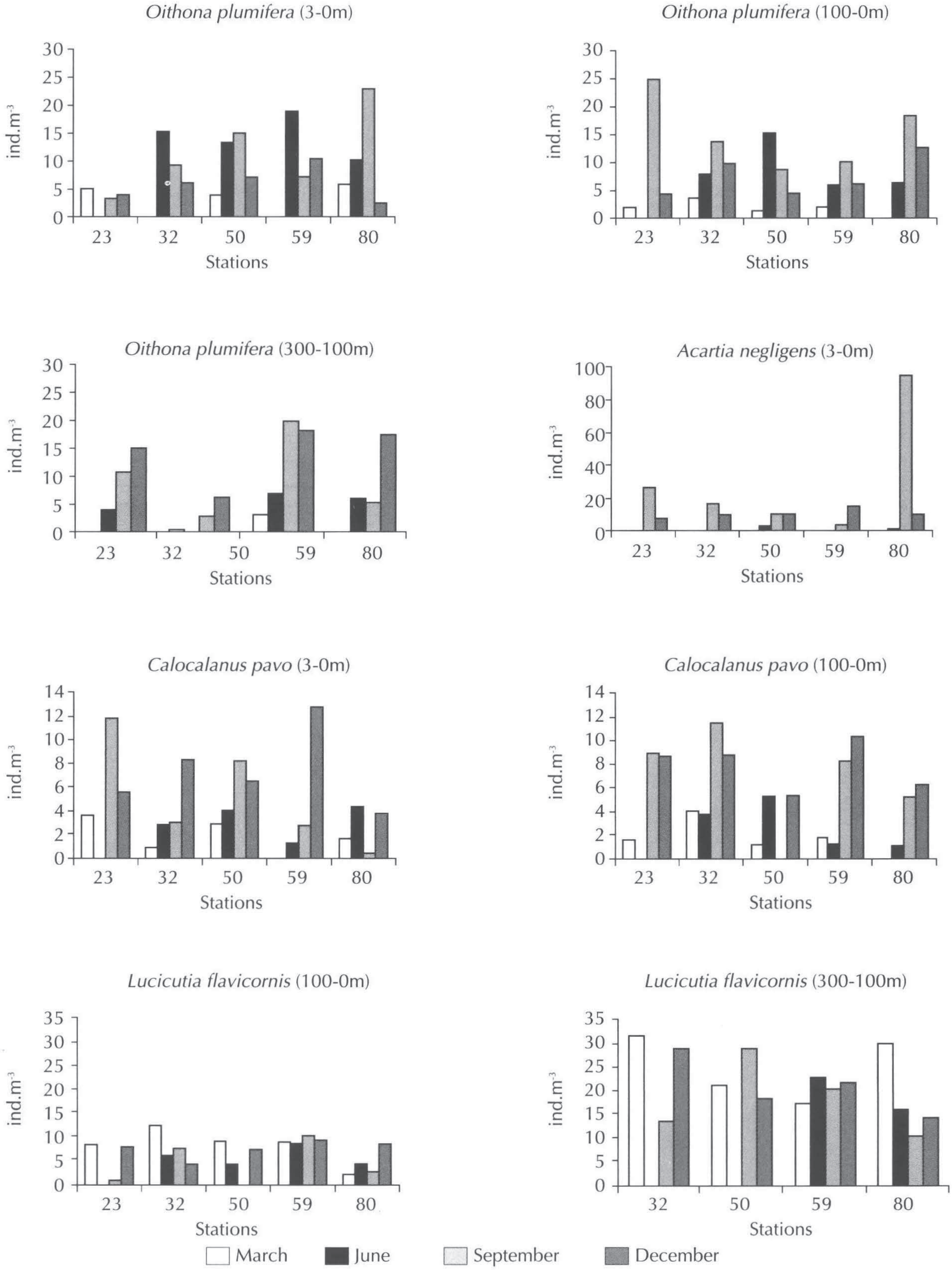

Figure 7 - Bathymetric and temporal fluctuations of *Oithona plumifera, Acarcia negligens, Calocalanus pavo* and *Lucicutia flavicornis* abundance in all seasons. / *Fluctuations bathymétriques et temporelles de l'abondance de* Oithona plumifera, Acarcia negligens, Calocalanus pavo *et* Lucicutia flavicornis.

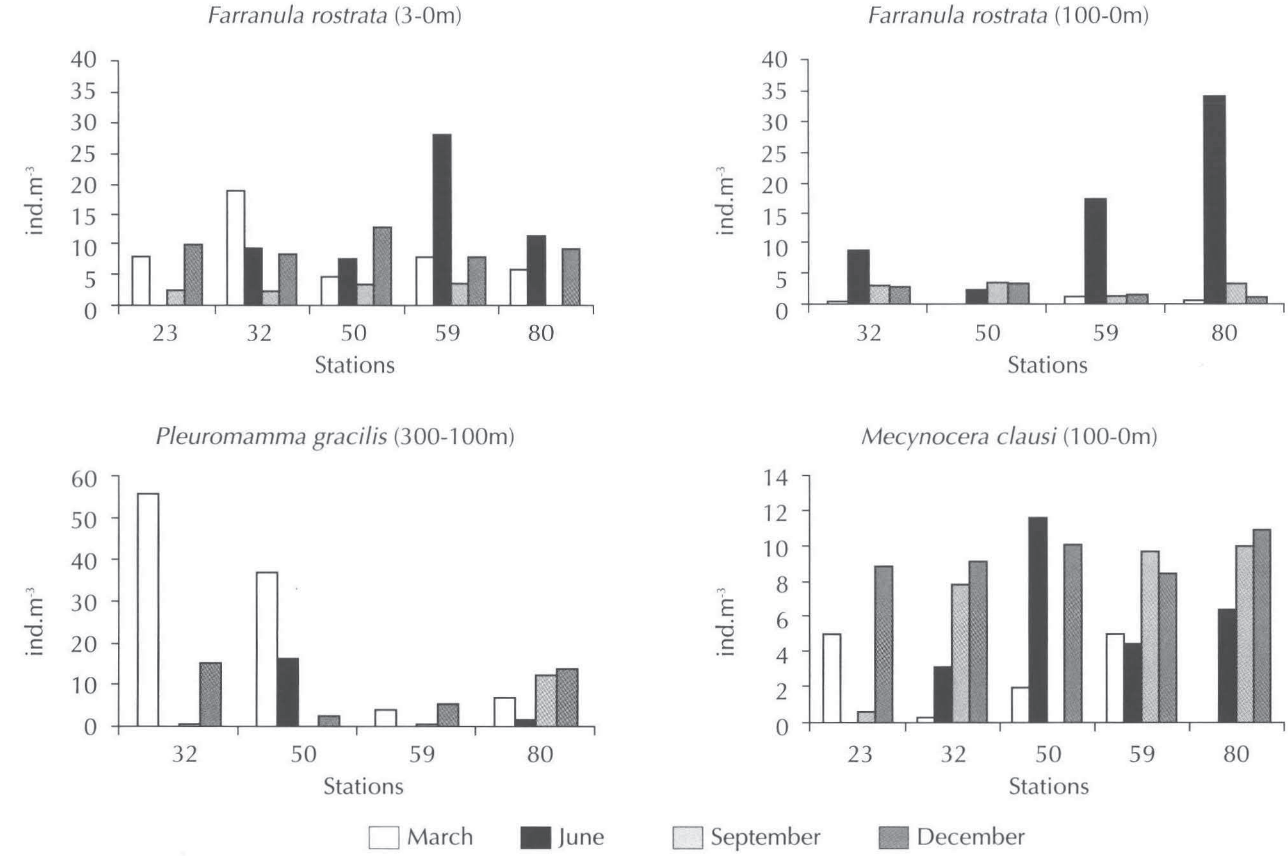

Figure 8 - Bathymetric and temporal fluctuations of *Farranula rostrata, Pleuromamma gracilis* and *Mecynocera clausi* abundance in all seasons. / *Fluctuations bathymétriques et temporelles de l'abondance de* Farranula rostrata, Pleuromamma gracilis *et* Mecynocera clausi.

ind.m^{-3}), *Oithona plumifera* (618 ind.m^{-3}), *Oithona* juveniles (400 ind.m^{-3}), *Farranula rostrata* (305.8 ind.m^{-3}), *Calocalanus pavo* (300 ind.m^{-3}), *Mecynocera clausi* (247.4 ind.m^{-3}), *Corycaeus* spp. (males) (206.2 ind.m^{-3}) and *Acartia negligens* (201.3 ind.m^{-3}).

The copepod population of the 100-0 m water layer is mainly formed by *Clausocalanus furcatus* (809 ind.m^{-3}), *Oithona plumifera* (566 ind.m^{-3}), *Oithona* juveniles (554.1 ind.m^{-3}), *Calocalanus pavo* (388.3 ind.m^{-3}), *Mecynocera clausi* (355.2 ind.m^{-3}), *Lucicutia flavicornis* (314.3 ind.m^{-3}), *Farranula rostrata* (312 ind.m^{-3}), *Oncaea mediterranea* (163 ind.m^{-3}), *Oncaea media* (155.4 ind.m^{-3}), *Temora stylifera* (121.1 ind.m^{-3}) and *Acartia negligens* (115 ind.m^{-3}).

The copepod assemblages of the surface and 100-0 m layer present similar qualitative composition.

The deep layer (300-100 m) is characterized by low species diversity and is mainly dominated by *Lucicutia flavicornis* (249 ind.m^{-3}), *Oithona* spp. juveniles (197 ind.m^{-3}), *Oithona plumifera* (148.6 ind.m^{-3}), *Farranula rostrata* (98 ind.m^{-3}), *Pleuromamma gracilis* (4.06 ind.m^{-3}), *Oncaea media* (68.06 ind.m^{-3}), *Eucalanus monachus* (61.71 ind.m^{-3}).

The similarity in copepod species composition between the surface layer and the 100-0 m water layer in the study area resulted from the dominance in both layers of *Clausocalanus furcatus* and *Oithona plumifera. Oithona plumifera* is found mainly in warmer waters but is also found in temperate regions.

In September, the richest sampling in copepods, the dominant species were *Clausocalanus furcatus* followed by *Oithona plumifera, Calocalanus pavo, Acartia negligens* and *Lucicutia flavicornis*. In December, where the second copepod maximum was observed, the dominant species was *Clausocalanus furcatus*, followed by *Oithona plumifera, Mecynocera clausi, Farranula rostrata* and *Lucicutia flavicornis*. In March the total numbers of copepods decreased and the dominant species were *Eucalanus monachus, Oncaea media, Clausocalanus lividus* and *Farranula rostrata*. Finally, in June, copepods also presented low densities and the dominant species for this sampling were *Oithona plumifera, Farranula rostrata, Oncaea media, Mecynocera clausi, Clausocalanus furcatus* and *Lucicutia flavicornis*.

Dendrograms (figure 10) produced from hierarchical clustering of samples based on zooplankton group composition were structured separately for the three water layers and for the four cruises.

Figure 10 presents the dendrogram for the surface layer (a), based on the occurrence of mesozooplankton groups. Two clusters of samples are formed at the 45% similarity level. The first one is formed by stations 59A, 32A, 50A, 23A, 80B, 50B, 59B (where A: March and B: June samplings) with similarity level varying from 62%-85%. The second includes all other stations except stations 80A and 50C (where C: September sampling), with a similarity level varying from 62%-88%.

Figure 10 shows the dendrogram for the 100-0 m water layer (b) based on mesozooplankton groups. At the 47% level two groups of stations are differentiated. Stations 80C, 50C, 23C and 59C form the first one with a similarity level varying from 81% to 86%. The second is subdivided into two clusters at the 69% level. The first subcluster includes stations 50B, 80B, 32B and 80B with a level ranging from 82% to 85%. The second includes samples 32D, 50D, 59C, 59B, 32C and 23D with a level ranging between 79% and 83%. Station 32A seems to differentiate from the other stations at the 21% level.

Figure 10 shows the dendrogram for the 300-100 m water layer (c). At the 60% level two clusters of samples are divided. The first cluster is formed by only one station (59D) while the second one is

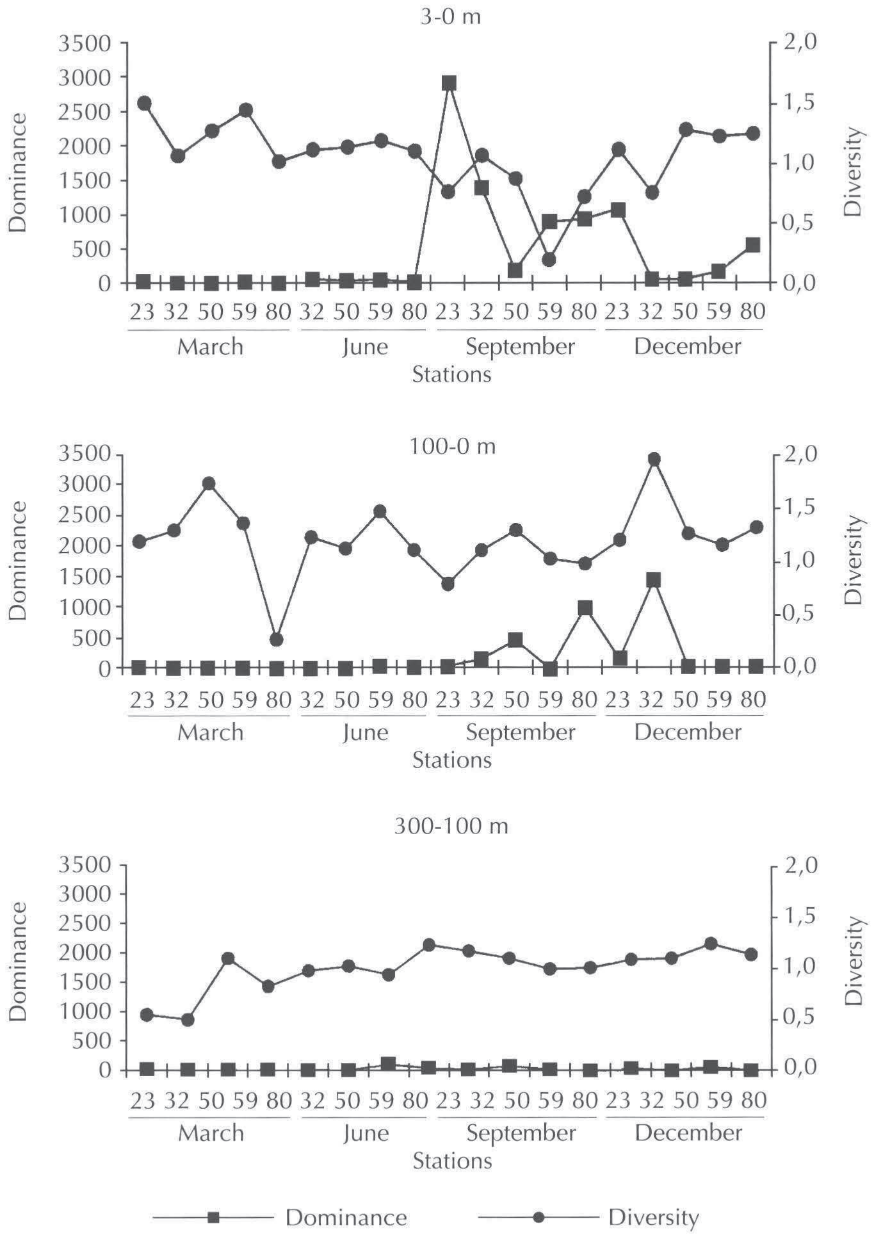

Figure 9 - Fluctuations of copepod species diversity and dominance index. / *Fluctuations des indices de diversité et de dominance des espèces de copépodes.*

subdivided into two subclusters at the level of 63%. The first subcluster is formed by stations 50C, 80C, 59B, 59C with a similarity level ranging between 79% and 87%. It was also observed that at the 70% level, samples 32A, 80A, 50A and 59A seem to differentiate from the other stations and this group of stations is joined by 32B at the 45% similarity level.

From the clustering analysis it seems that the differentiation of total zooplankton varied mainly according to the sampling period while no important spatial differentiation between the stations seems to occur.

DISCUSSION

It is generally accepted that the Mediterranean Sea is an oligotrophic marine area and that this poverty presents a decreasing gradient from the West to the East. Comparison of existing data is not easy because of the different sampling methods used and variations between authors in the quantitative estimation of zooplankton (biomass expressions or counts of numbers of plankters). Although we consider that biomass values give better quantitative estimations of zooplankton, we will use for comparison the numbers of planktonic animals as they are used by most other authors. However, it becomes clear from our results that when biomass values are taken into consideration the quantitative image of zooplankton presents differences from that given when the number of animals is calculated. This is due to the presence in some samples of rather high numbers of large planktonic forms (chaetognaths, salps, crustacean larvae).

Results on zooplanktonic abundance in the Eastern Mediterranean usually demonstrate that the area is quantitatively poor, but has strong variations. Pancucci-Papadopoulou, Anagnostaki (1989) found low zooplankton numbers ranging between 27 and 90 ind.m^{-3} (for the layer 500-0 m) in the Levantine, Southern Aegean and Eastern Ionian Seas. Mazzocchi *et al.* (1997) found that the density of zooplankton (for the 300-0 m layer) reached maximum values in the Sicily Channel (200 ind.m^{-3}) and was lowest in the Cretan Sea (45 ind.m^{-3}). Slightly higher values of abundance were recorded by the same authors for the Cretan Passage (56 ind.m^{-3}), the Ionian Sea (62 ind.m^{-3}) and the Rhodes area (66 ind.m^{-3}).

Higher zooplankton abundance has been observed in other studies. Results from the Southern Mediterranean Sea (Porumb *et al.*, 1981) showed high zooplankton values from spring samples (310 ind.m^{-3}, for the layer 400-0 m). Similar values ranging from 83.5 to 381.1 ind.m^{-3} are given by Pancucci-Papadopoulou *et al.* (1992) from samples collected from the Eastern Mediterranean (East to Crete) in spring, for the 150-0 m layer. These results are similar to those presented by Gaudy (1985) for certain areas of the Western Mediterranean.

Our results show that marked quantitative differentiation between samples that follows mainly a seasonal pattern. Mean numbers of plankton in the whole water column was low in spring and summer confirming the quantitatively poor character of the area. Plankton samples from autumn to winter are characterized by much higher numbers, not significantly different from those of the Western Mediterranean.

The strong quantitative seasonal fluctuations observed in this work give evidence that the quantitative differences observed between authors from samples in the area must be mainly attributed to the differences in the season of sampling. Most authors collected samples in only one season during an oceanographic cruise. Other sources of variation are differences in the type of nets, the time of sampling (diurnal migrations) and especially the complexity and variability of hydrographical features of the area. Multiscaled circulation patterns and complex hydrographic structures prevail in the South Aegean Sea, where a succession of cyclones and anticyclones dominate throughout the year. The general circulation does not show any significant seasonal signal (Pelagos group, 1996).

Hydrographic conditions become an important factor of plankton distribution. Thus the quantitative differences between the various stations in every sampling period do not seem to follow a clear pattern.

According to Scotto di Carlo, Ianora (1983), Mediterranean zooplankton is characterized by two abundance maxima: one in late winter or early spring and the second in autumn. Variations from this pattern have been observed: Siokou-Frangou (1996) reports that in the Saronic Gulf a very obvious zooplankton peak is apparent during the warm months.

The September and December plankton peaks of our samples are related to trophic conditions. Very low mean annual concentrations of chlorophyll a and phytoplankton have been calculated in the area (Ignatiades *et al.*, 1996), which could not support high zooplankton densities. Food chains in the area are probably based also on other sources, such as the microbial loop and carnivorous feeding.

Results of the fractionated pigments in the area (Ignatiades *et al.*, 1996) showed clearly the quantitative importance of picoplankton: The microflagellate concentrations are one to two orders of magnitude higher at each depth and station than corresponding phytoplankton densities. Their constant presence and high abundance in oligotrophic areas classify them among the most dominant and important constituents of marine plankton. The microflagellate abundance is high in summer and autumn and to a lesser degree in winter and reaches its lowest values in spring. The summer maximum probably supports the development of the noticed increased zooplankton population reported for September.

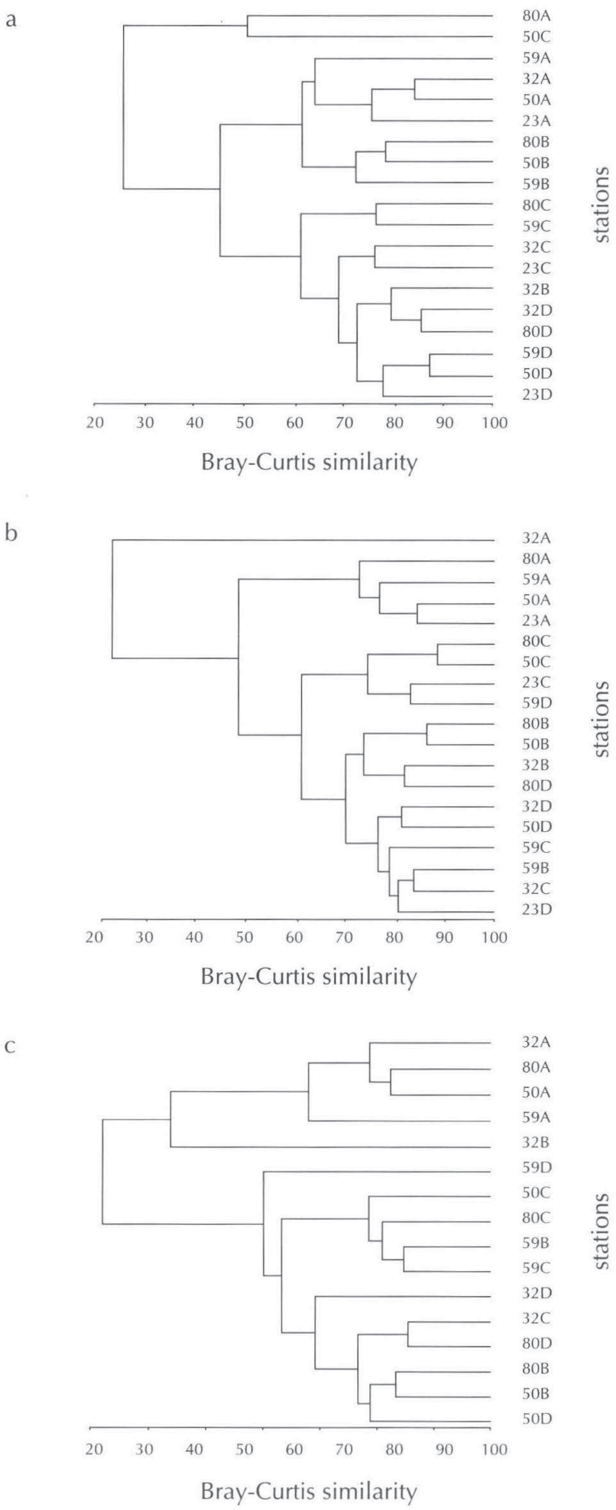

Figure 10 - Dendrograms derived from hierarchical clustering of samples based on zooplankton group composition of the three water layers (a: 3-0 m, b: 100-0 m, c: 300-100 m) in the sampling period, where A: March, B: June, C: September, D: December. / *Regroupement hiérarchique des prélèvements basé sur la composition des groupes zooplanctoniques dans les trois couches d'eau (a : 3-0 m, b : 100-0 m, c : 300-100 m), durant la période d'étude (A : mars, B : juin, C : septembre, D : décembre).*

The pattern of vertical distribution of zooplankton observed in our samples proves that the superficial layer is well populated by zooplankton. Thus, contrary to what is generally believed for the South Aegean and Cretan Arc, conditions at the sea surface are favorable for zooplankton especially in September and December when the surface layer was the most rich.

Samples from the 100-0 m layer were much richer in zooplankton than those from the 300-100 m layer where conditions are less favorable than in the upper layers. The complicated hydrography of the area and the intense water movements become important factors of vertical distribution and are related to the observed peculiarities of vertical distribution. Thus in station 80 East of Crete, an area particularly affected by the gyres, while its surface layer in March and June is one of the poorest, the 100-0 m layer proved the richest of all stations. In September, the surface layer of station 50 presents an extreme poverty level, whereas the 100-0 m layer is one of the richest. This is due to the formation of cyclonic gyres that drive water masses to deeper layers. On the other hand, during the June sampling, station 32 is the poorest for the 300-100 m layer, while it is the richest station for the surface layer. This difference is a result of a cyclonic gyre in the area driving deeper water masses to the surface layer. These phenomena affect only the deep-water stations. It is characteristic that station 23 (a shallow station not far away from station 32) is not influenced and presents normal vertical distribution (see figure 10).

The abnormalities of the vertical distribution of zooplankton groups are also reflected by the bathymetric distribution of some characteristic species. *Eucalanus monachus*, which is usually referred to as a deep-water species forms high densities in the 100-0 m layer in the present study, its density being diminished by about half at the surface and by a quarter at 300-100 m.

Copepod diversity and dominance at all stations is in agreement with previous data from the Eastern and Western Mediterranean (Delalo, 1966; Kimor, Berdugo, 1967; Moraitou-Apostolopoulou, 1972, 1985; Pancucci-Papadopoulou *et al.*, 1992, Mazzochi *et al.*, 1997). High diversity and low dominance are characteristic of a pelagic environment revealing a stable community structure.

The mean percentage of copepods calculated from our data (March: 76,52%; June: 71.4%; September: 70.5% and December: 72.5%) is in agreement with the findings of Scotto di Carlo, Ianora (1983), Pancucci-Papadopoulou *et al.* (1992) and Mazzocchi *et al.* (1997). The presence, in all March 1994 samples, of larvae of decapods seems of interest because, of all the minor plankton groups, previous authors did not report their presence. Only Kimor, Berdugo (1967) consider the decapod larvae as abundant in the Levantine basin.

The quantitative importance of chaetognaths, the second in importance of the minor zooplankton groups, is noted by Delalo (1966) for the Levantine, (Pancucci-Papadopoulou *et al.*, 1992; Mazzocchi *et al.*, 1997) for the Eastern Mediterranean. Appendicularians and ostracods are also considered by these authors as important for the Eastern Mediterranean area. Cladocerans, a usually abundant zooplanktonic group, especially in the neritic area, are scarce in our samples during the cold period and become abundant in June and especially in September when species of the genus *Evadne* constitute the second most abundant zooplanktonic group.

Comparing the specific composition of copepod assemblages with previous studies, the problem of differences in the mesh size used and/or the season of sampling is raised again. Weikert, Trinkaus (1990), using nets of 333 µm mesh size, found large species such as *Eucalanus, Haloptilus* and *Lucicutia* to constitute the bulk of copepods, while small cyclopoids such as *Oithona* and *Oncaea* form only 8-10% of total copepods. Pancucci-Papadopoulou *et al.* (1992), using mesh size of 200 µm, found that these small cyclopoids formed the 69% of the total copepod population. Kimor, Berdugo (1967), using a 200 µm mesh net, recorded small cyclopoids in fairly large numbers in the 200-100 m layer of the Levantine in summer. In our samples, although some small cyclopoids such as *Oncaea media, Farranula rostrata* and *Corycaeus limbatus* are abundant, small calanoids such as the various species of *Clausocalanus* and also large forms such as *Eucalanus monachus, Lucicutia flavicornis, Candacia ethiopica* and *Pleuromamma gracilis,* attain quantitative importance. Calanoid copepods, particularly the various species of *Clausocalanus* (*C. lividus, C. arcuicornis, C. furcatus*) and also *Mecynocera clausi, Calocalanus pavo, Oithona plumifera, Oithona* spp. juveniles, *Oncaea mediterranea* and *Temora stylifera* are numerically important.

Kimor, Berdugo (1967) and Pasteur *et al.* (1976), who have done horizontal hauls, refer to the epipelagic calanoids *Paracalanus parvus, Clausocalanus arcuicornis, Centropages kroyeri, C. violaceus* and *Temora stylifera* as the most abundant species. Differences from our data may be attributed to the season of sampling as the above authors collected samples only during summer.

The complicated hydrography of the area where cyclonic gyres prevail could be considered as an important factor of zooplankton distribution.

CONCLUSION

The mesozooplankton of the South Aegean Sea (North of the island of Crete and the Cretan straits) forms well-structured highly-diversified pelagic communities. Quantitatively the community is characterized by strong variations that seem to follow a mainly seasonal pattern while zooplankton abundance diminishes with depth. The very low concentration of phytoplankton in the area would not support the observed zooplankton densities and mesozooplankton must depend on picoplankton for food.

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