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Summer mesozooplankton distribution in coastal waters of central Greece (eastern Mediterranean). II. Species assemblages

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Mesozooplankton distribution was investigated over an intensive grid of 124 stations in coastal and pelagic waters of central Greece (eastern Mediterranean) during July 1998. The complex topography of the area consisted of various semi-enclosed gulfs as well as open-sea areas and provided excellent fieldwork for determining species assemblages, their relationships to environmental parameters and the distribution and abundance patterns of the copepod species.

Three coastal and one pelagic group of stations were revealed by cluster analysis. Inverse analysis of species affinities defined distinct 'coastal' and 'pelagic' species assemblages. All coastal areas were dominated by a small number of species (e.g. *Penilia avirostris*, *Podon* spp., *Ctenocalanus vanus*, *Paracalanus parvus* and *Centropages typicus*) all belonging to the 'coastal' assemblage. Differences among these coastal areas were mainly due to small changes in relative abundance of a common-species list. On the contrary, pelagic stations were characterized by higher species diversity, low dominance and the presence of characteristic epipelagic and mesopelagic species of the Mediterranean Sea (e.g. *Calocalanus* spp., *Haloptilus longicornis*, *Lucicutia flavicornis*, *Mecynocera clausi*, *Farranula rostrata*, *Mesocalanus tenuicornis* and *Oncaea mediterranea*).

The observed differences in taxonomic composition and abundance of zooplankton were related to the marked differences in salinity values observed between the eastern and western part of the surveyed area. Bathymetry, temperature and fluorescence were also related with the inshore–offshore gradient of the zooplankton community observed in the pelagic areas as well as with the discrimination of the zooplankton communities of the various semi-enclosed gulfs of the region.

INTRODUCTION

In the Mediterranean Sea—especially in the eastern part—basic information on zooplankton community structure and species-composition changes in different marine environments is still needed to better understand the way this basin is functioning. Little information is available for the spatial differentiation of mesozooplankton communities in relation to environmental parameters in the Mediterranean Sea. For both western and eastern basins it has been observed that hydrology (temperature and salinity), topography, eutrophication–pollution, hydrodynamic structure (fronts, gyres, eddies) as well as food availability can influence the distribution of zooplankton (Siokou-Frangou & Papathanassiou, 1991; Pancucci-Papadopoulou et al., 1992; Kouwenberg, 1994; Mazzochi & Ribera d'Alcala, 1995; Pinca & Dallot, 1995; Ragosta et al., 1995; Siokou-Frangou et al., 1997; Siokou-Frangou et al., 1998).

The surveyed area consisted of various enclosed and semi-enclosed bays and gulfs as well as open-sea areas, thus comprising an excellent field for the study of pelagic–coastal interaction and its influence on the composition of zooplankton communities. The present paper is the second part of a broad scale study describing the composition, abundance and distribution patterns of mesozooplankton in the area of central Greece during summer. In the first part of the analysis (Ramfos et al., 2005), the environmental conditions as well as mesozooplankton abundance and group composition were considered. The most prominent characteristics of the surveyed area (Figure 1A) were its complex topography, the east–west difference in salinity, the differences in abundance and biomass between the open-sea areas and semi-enclosed gulfs and the marked variability in the distribution patterns of the major zooplankton groups.

In this paper, we present the results of the analysis concerning the structure and distribution patterns of the assemblages of copepods and cladocerans which comprised the bulk of total mesozooplankton (>90% in most stations). It involves the definition of communities, their composition, the dominant or indicator species, the major distribution patterns, and, where possible, the principal characteristics of the water column that control these patterns.

MATERIALS AND METHODS

Sample collection and analysis

Mesozooplankton sampling was carried out from 6 to 22 July 1998 off the coasts of central Greece (eastern Mediterranean). The sampling grid was based on transects spaced approximately 8 nautical miles apart and stations located at 8 nautical mile intervals on each transect (Figure 1B). A total of 124 zooplankton samples was

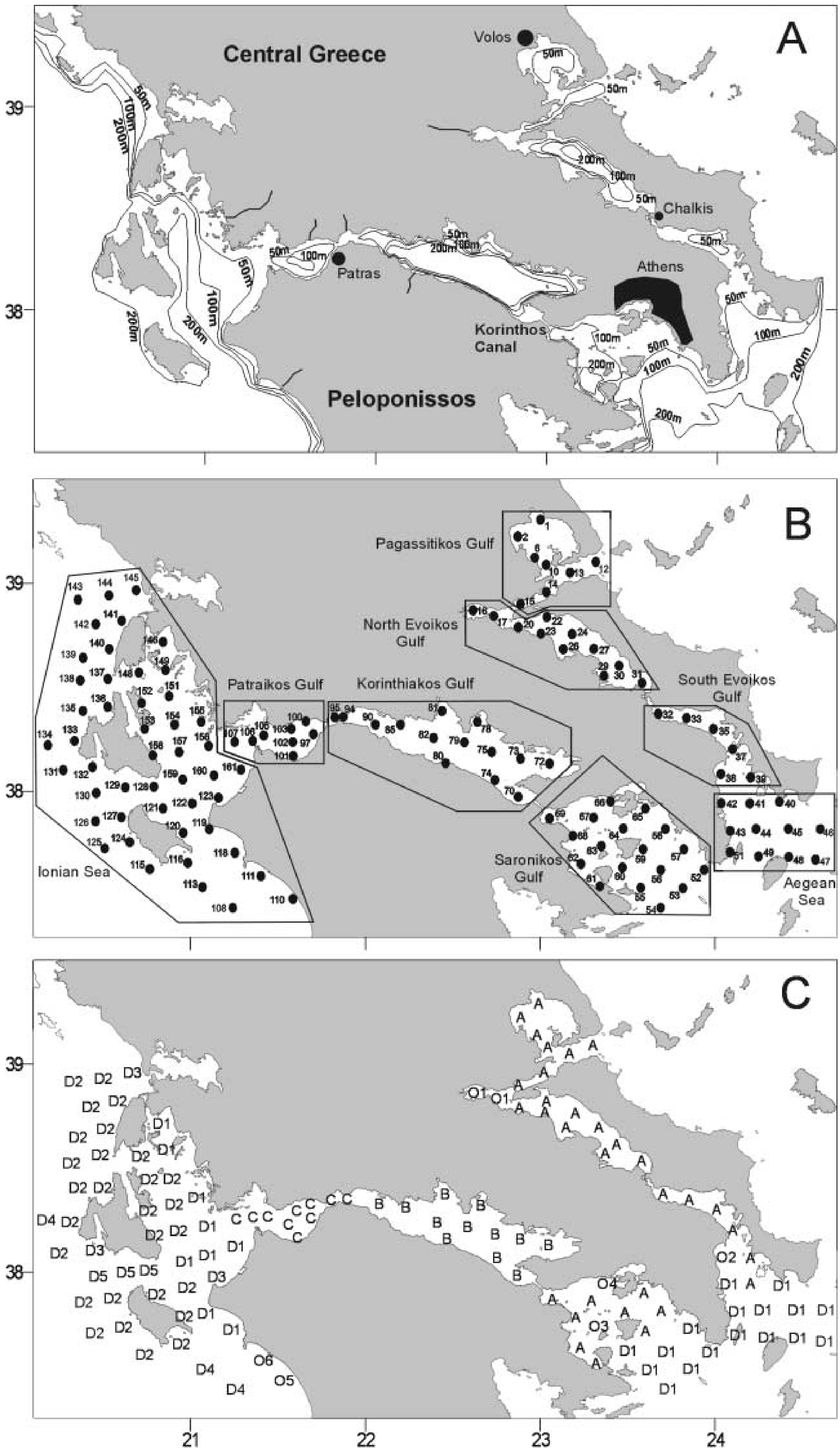

Figure 1. Maps of the surveyed area showing (A) the topography of the surveyed area; (B) the sampling stations and sub-regions referred to in the text; and (C) the geographical distribution of station groups defined by cluster analysis. O1–O7: 'outlier' stations not grouped in any of the major station groups.

collected. At each station, a WP2 net (mesh size 200 μm) was vertically towed in the upper 200 m of the water column or from near the bottom to the surface if station depth was less than 200 m. Hydrographic sampling (temperature, salinity and fluorescence profiles) was also performed at each station. More details on sampling methods as well as laboratory analysis of the samples are provided in Ramfos et al. (2005). Copepods and cladocerans were identified to the lowest possible taxonomic group (genus or species level). Copepods were the dominant group in the collections and cladocerans were particularly abundant in some coastal areas (Ramfos et al., 2005). Both accounted for almost 90% of total zooplankton in most stations.

Multivariate analysis

A species by sampling site matrix, expressed as abundance values (ind m^{-2}), was analysed using both cluster analysis and non-metric multidimentional scaling (nMDS) (Clarke & Warwick, 1994). All copepod (adults and copepodites separately) and cladoceran taxa were included in the matrix. Data were transformed using the [$\log_{10}$(x+1)] transformation. Hierarchical agglomerative clustering was carried out first, using the Bray–Curtis similarity index coupled with group average linkage. The data set was subsequently subjected to nMDS ordination after the removal of the 'outlier' sites identified by the cluster analysis. Outlier sampling sites may bias or dominate the ordination, often compressing the distribution of the remaining sites (Hosie & Cochran, 1994).

Ordination scores produced by the nMDS were compared by multiple regression analysis with various environmental parameters to determine which of these parameters may best explain the zooplankton distributions (Kruskal & Wish, 1978; Hosie & Cochran, 1994). In the regression analysis the nMDS scores were treated as the independent variables and each environmental parameter as the dependent variable. This method was selected because it is not based on an a priori ecological hypothesis such as other methods (e.g. canonical analysis, non-parametric methods), it is not affected by parameter inter-correlations and does not remove the variance explained by previously used variables (Somarakis et al., 2002). By comparing the coefficient of determination of each parameter the variable that explained best the plankton distribution could be determined. Regression lines and their directions were plotted in the nMDS graphs according to Kruskal & Wish (Kruskal & Wish, 1978): the direction of maximum correlation of each regression line is at an angle ϕ_r with the rth MDS axis. The direction cosine, or regression weight c_r, of that angle is given by the formula:

$$c_r = b_r / \sqrt{b_1^2 + b_2^2} \quad (1)$$

where b_1 and b_2 are the coefficients from the multiple regression $a + b_1 x_1 + b_2 x_2$ and x_1 and x_2 are the scores in the first and second MDS axis respectively. The parameters examined were haul depth, temperature and salinity at the surface mixed layer (SML) and bottom layer (BL), thermocline depth, integrated fluorescence and

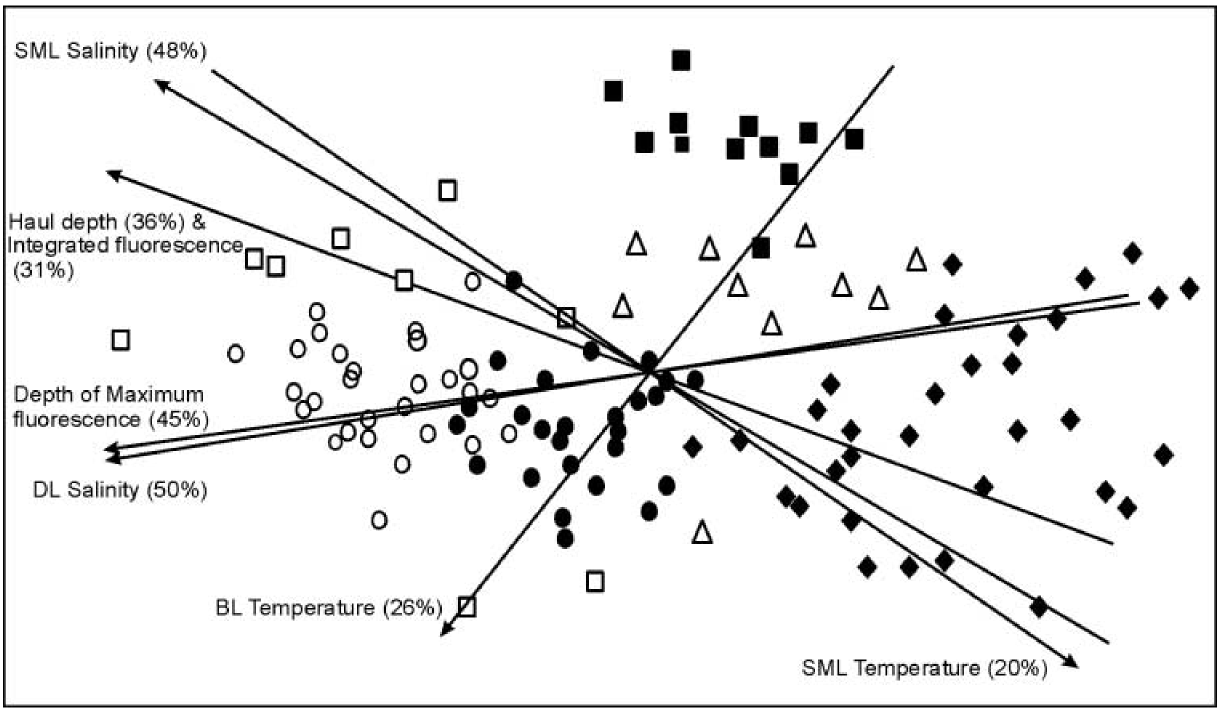

Figure 2. Ordination plot of the sampling site comparison using nMDS and Bray–Curtis similarity index. Respective cluster groups are superimposed and presented with different symbols. Significant multiple regressions between ordination scores and environmental parameters are also shown, as well as the fraction (%) of the variance of the zooplankton data explained by the parameters. Stress value was 0.17. ◆, Group A; ■, Group B; △, Group C; ●, Subgroup D1; ○, subgroup D2; □, subgroups D3–D5. SML, surface mixed layer; BL, bottom layer.

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Table 1. *Multiple regression analysis between various parameters and the nMDS scores for two-axis ordination of sampling sites.*

Variable	X	Y	Adjusted R^2	F
Haul depth	0.914	0.406	35.94	33.26***
SML temperature	−0.970	−0.244	19.97	15.23***
SML salinity	0.816	0.579	47.69	52.97***
BL temperature	0.549	−0.836	26.15	20.30***
BL salinity	0.986	−0.164	49.64	54.24***
Integrated fluorescence	0.916	0.401	30.82	26.62***
Depth of maximum fluorescence	0.984	−0.181	45.05	48.14***
Thermocline depth	—	—	—	0.02 n.s.

X, Y, are the direction cosines (regression weights).
SML, surface mixed layer; BL, bottom layer; n.s., not significant.
*, $P<0.05$; **, $P<0.01$; ***, $P<0.001$.

depth of maximum fluorescence (see Ramfos et al., 2005 for definition of parameters).

The data set was also subjected to inverse analysis to define dominant species affinities. This analysis also involved cluster analysis using the Bray−Curtis index and group average linkage. Only abundant taxa (relative abundance >4% in at least one site) were included in this data matrix (Clarke & Warwick, 1994). Data were standardized according to Clarke & Warwick (Clarke & Warwick, 1994).

One way analysis of variance (ANOVA) was performed on $[\log(x+1)]$ transformed values to test for differences in abundance of the dominant species, among the groups defined by the cluster analysis. The Student−Newman−Keuls (SNK) test was used to define homogenous groups.

Finally, the copepod community diversity was assessed using the ($\log_2$) Shannon−Wiener information index (H'). Data on adult copepods were only used for this analysis.

RESULTS

Sampling site differences

Cluster analysis identified four major groups of stations (Groups A, B, C and D) and seven 'outlier' stations at the 62% similarity level (Figure 1C). At a higher similarity level (69%), Group D could be further divided into two large (D1 and D2) and three smaller subgroups (D3, D4, D5). The seven outlier stations (all inshore stations which were near river mouths or disturbed areas—see below) differed markedly from all others. These stations had very low diversity and/or high dominance of certain copepod

Table 2. *Mean abundance values (ind m^{-2}), analysis of variance (F) and Student–Newman–Keuls (SNK) multiple range tests for dominant zooplankton species (copepod adult species, copepodites [cops.] and cladoceran taxa) in station groups defined by the cluster analysis (Figure 1C). Groups with highest abundance are shown in bold. Species groups defined in the inverse analysis of dominant taxa (Figure 4) are also presented (I–IV).*

Species	Species group	Group A	Group B	Group C	Group D1	Group D2	F	P
Podon spp.	I	**8819**^{a}	1323^{b}	663^{b}	1393^{a,b}	163^{c}	15.02	***
Centropages spp. cops.	I	**2779**^{a}	42^{c}	95^{b}	**2089**^{a}	800^{b}	27.27	***
Paracalanus parvus	I	**3546**^{a}	862^{b}	**1770**^{a}	**1297**^{a}	463^{b}	14.65	***
Clausocalanus spp. cops.	I	**8061**^{a}	3931^{b}	1955^{c}	**8114**^{a}	3673^{b}	12.32	***
Paracalanus spp. cops.	I	**6856**^{a}	2203^{a,b}	**4795**^{a}	2070^{a,b}	1141^{b}	7.96	***
Centropages typicus	I	**814**^{a}	61^{c}	287^{z,b}	**707**^{a}	198^{b}	14.96	***
Oithona spp. cops.	I	10063^{a,b}	**13355**^{a}	7002^{b}	9202^{a,b}	8805^{a,b}	2.99	**
Oncaea spp. cops.	IV	302^{c}	**3644**^{a}	318^{b,c}	337^{b}	318^{b}	9.21	***
Ctenocalanus vanus	I	**1505**^{a}	**1912**^{a}	**1416**^{a}	**830**^{a}	377^{b}	5.48	***
Lucicutia spp. cops.	II	4^{c}	**1308**^{a}	90^{b}	164^{b}	**1183**^{a}	65.95	***
Penilia avirostris	I	53454^{a,b}	**81695**^{a}	9600^{b}	1529^{c}	127^{d}	86.58	***
Ctenocalanus vanus cops.	I	**4463**^{a}	**5271**^{a}	**3469**^{a}	1887^{a,b}	603^{b}	8.16	***
Calocalanus sp. A	II	179^{b}	**795**^{a}	0^{c}	**490**^{a}	**436**^{a}	19.86	***
Corycaeus brehmi	I	1047^{a,b}	**1287**^{a}	**1381**^{a}	545^{a,b}	274^{b}	3.16	**
Farranula rostrata	II	389^{b}	163^{b}	**406**^{a}	**1305**^{a}	**669**^{a}	12.2	***
Haloptilus spp. cops.	II	0^{c}	20^{c}	8^{c}	284^{b}	**2849**^{a}	105.3	***
Mesocalanus tenuicornis cops.	II	211^{c}	179^{b,c}	216^{c}	893^{a,b}	**866**^{a}	12.87	***
Mecynocera spp. cops.	II	44^{c}	156^{b}	200^{b}	**509**^{a}	**1149**^{a}	35.27	***
Calocalanus pavo cops.	II	14^{d}	76^{c}	132^{b}	**543**^{a}	**875**^{a}	41.14	***
Oncaea mediterranea	II	160^{b}	86^{b}	87^{b}	**445**^{a}	**1064**^{a}	22.59	***
Calocalanus spp. cops.	II	344^{b}	216^{b}	**1735**^{a}	**2192**^{a}	**2780**^{a}	28.06	***
Clausocalanus jobei	III	184^{b}	7^{c}	14^{c}	**705**^{a}	197^{b}	21.19	***
Clausocalanus males	III	**979**^{a}	145^{b,c}	109^{c}	**880**^{a}	164^{b}	12.24	***
Temora stylifera cops.	I	2211	4313	3360	2555	1860	2.62	n.s.
Evadne spp.	I	3035	2622	962	1088	1061	0.8	n.s.
Oncaea media	I	1541	1049	1696	1672	864	0.76	n.s.
Oithona plumifera	I	1426	824	1240	769	696	0.72	n.s.
Corycaeus spp. cops.	I	521	1148	770	533	571	2.29	n.s.
Clausocalanus furcatus	III	1187	108	154	1414	150	2.01	n.s.

For ANOVA P values: *, $P<0.05$; **, $P<0.01$; ***, $P<0.001$; n.s., not significant. ^{a,b,c,d}, SNK test homogenous groups ($a>b>c>d$).

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species: Stations 16 and 17 (O1) were characterized by the high dominance of the copepod species *Centropages ponticus* (54% in Station 16) and *Paracalanus parvus* (61% in Station 17) as well as by the low species number present in this area (seven and nine species respectively). *Clausocalanus furcatus* and the copepodites of the genus comprised as much as 50% of the total copepod abundance in Station 38 (O2). *Acartia clausi* and its copepodites was the dominant species in Stations 63 (O3) and 66 (O4) with relative abundance 31% and 71% respectively. Finally, Stations 110 (O5) and 111 (O6) were characterized by the high dominance of *P. parvus* (33% and 36% respectively) as well as by the exclusive presence of the copepod species *Isias clavipes* (10% and 4% respectively). These seven sites were excluded from all subsequent analysis.

Group A comprised the neritic stations of the eastern part of the study area, i.e: Pagassitikos, North Evoikos, South Evoikos and the inner part of Saronikos Gulf (Figure 1C). Group B included all sites in the Korinthiakos Gulf, except two in its western part which were grouped

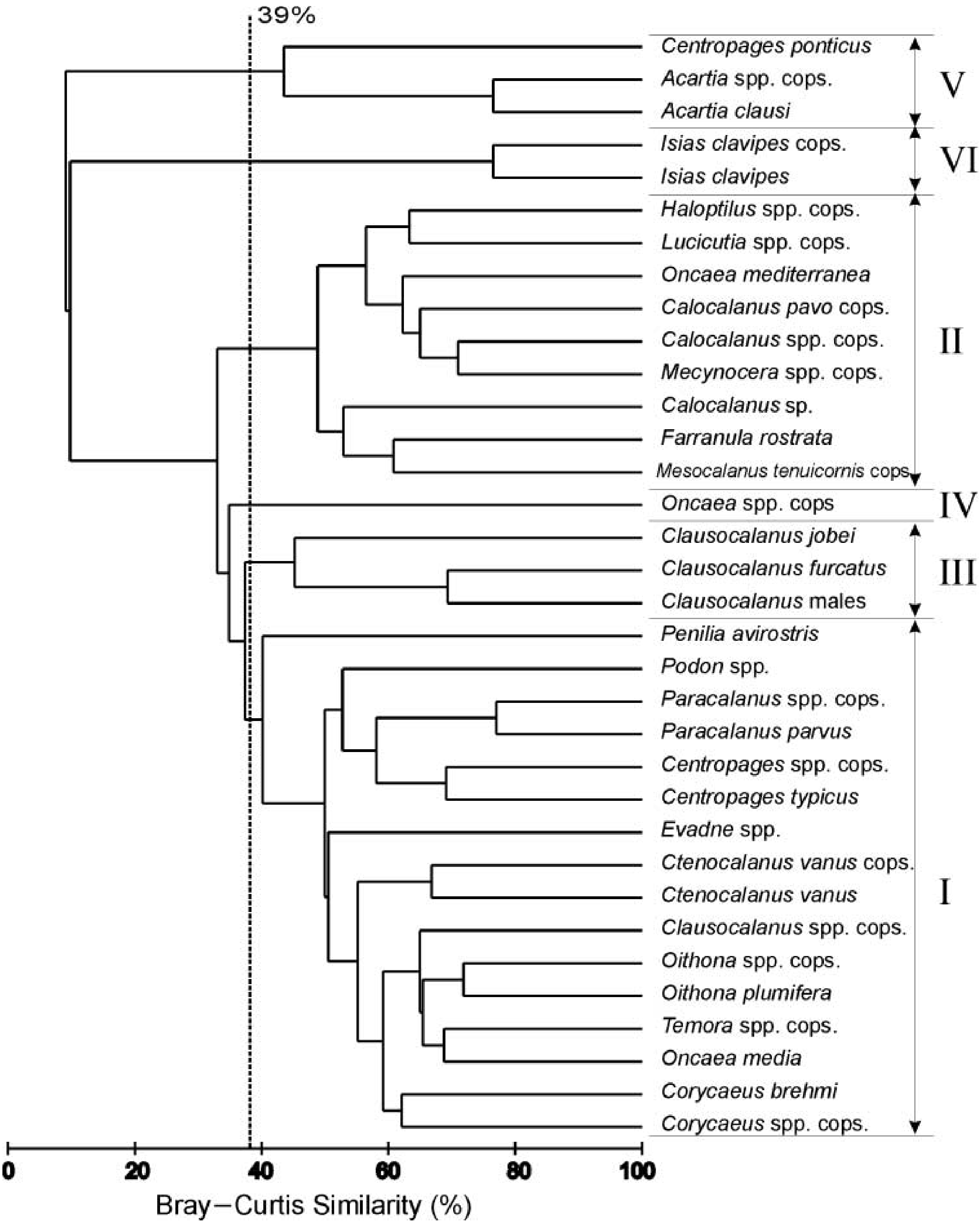

Figure 3. Dendrogram showing inverse analysis, comparing dominant species. Cops, copepodites.

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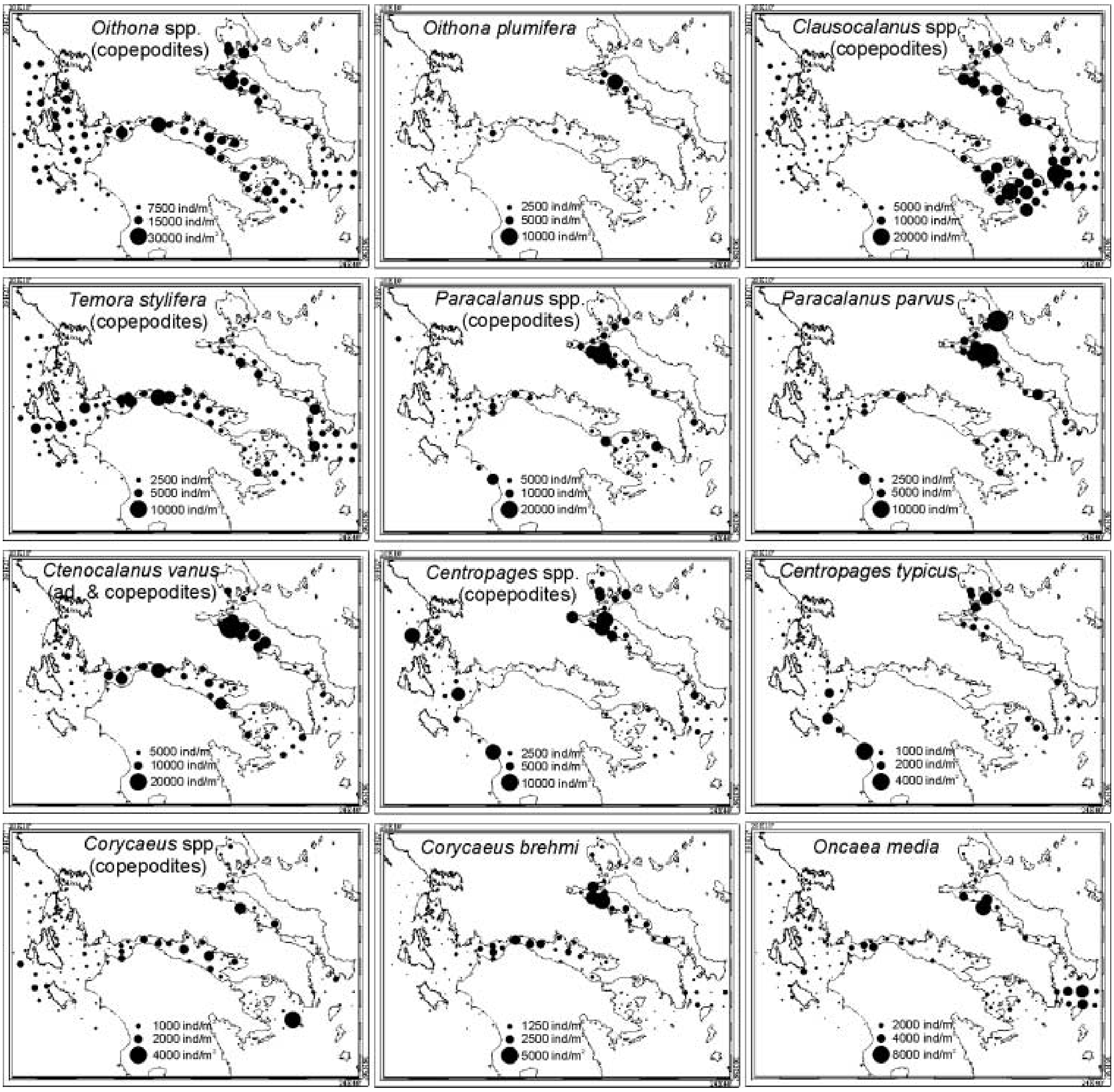

Figure 4. Distribution and abundance (ind m^{-2}) of the copepod species comprising the 'coastal' assemblage. Pooled abundance of a species (adults+copepodites) is presented when identification of copepodites was possible to the species level.

with the Patraikos Gulf sites. The latter formed Group C. Finally, Group D consisted of all pelagic stations of the Ionian Sea, the Aegean Sea and the outer part of Saronikos Gulf. Subgroup D1 comprised most coastal stations in the Ionian and all stations in the Aegean Sea and the outer part of Saronikos Gulf. Subgroup D2 consisted of most deep stations in the Ionian Sea and subgroups D3 and D5 included stations with depths less than 150 m (i.e. Stations 123, 128, 129, 130, 132 and 145). Subgroup D4 included deep stations at the western and southern limits of the surveyed area (i.e. Stations 108, 113, 134).

The nMDS ordination showed that the four major groups defined by the cluster analysis were quite distinct. Group C (Patraikos Gulf) was positioned in-between the three other groups (Figure 2), implying an intermediate community structure. An inshore–offshore trend was also evident for Group D. The shallower stations of subgroup D1 were placed closer to Group A than the deeper stations of subgroup D2.

Almost all of the parameters examined explained an amount of variation in the nMDS ordination (Table 1, Figure 2). Thermocline depth was the only parameter that did not show a significant relationship with the ordination scores. Based on relative angles of intersection, variables could be grouped into: (a) bottom layer temperature (BL), being the only parameter related to the separation of Group B (Korinthiakos Gulf which comprised sites with low BL temperature); and (b) all other significant parameters mainly related to the separation of Groups A and D. As mentioned above, Group A comprised most of the neritic stations of the eastern part of the surveyed area while Group D, comprised pelagic stations of the Aegean and Ionian Seas. Surface and bottom layer salinity explained most (48% and 50% respectively) of data variation, with increasing values from Group A towards Group D (Figure 2). Group A included most stations that were under the influence of the less saline Black Sea waters. Haul depth, total fluorescence

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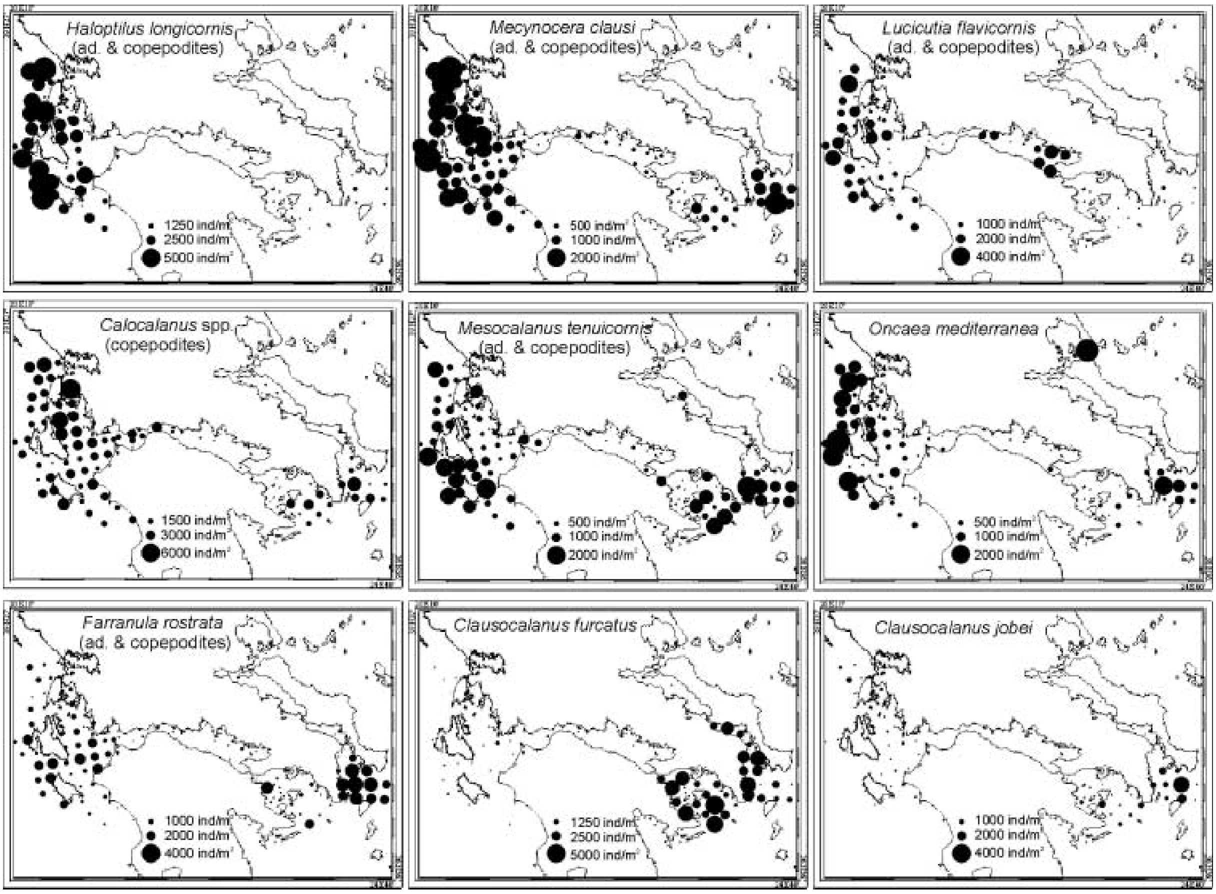

Figure 5. Distribution and abundance (ind m^{-2}) of the copepod species comprising the 'pelagic' assemblage. Pooled abundance of a species (adults+copepodites) is presented when identification of copepodites was possible to the species level.

and depth of maximum fluorescence also increased towards a similar direction. Surface-layer temperature increased in the opposite direction (Group A). These results were in general agreement with the horizontal distribution of these parameters in the surveyed area (Ramfos et al., 2005).

Species assemblages

Only 15 out of 86 adult copepod species as well as 15 copepodite taxa, were defined as 'dominant' (>4% of relative abundance in at least one site). Moreover, three cladoceran genera were also dominant in the samples. Inverse analysis of the data matrix for the dominant species defined six groups at the 39% similarity level (Figure 3).

Group I included the species that showed maximum abundance values in stations of Groups A, B and C (stations of the semi-enclosed gulfs) and therefore could be labelled as the 'coastal assemblage' (Table 2). The copepodites of the genera *Oithona*, *Clausocalanus*, *Temora* and *Corycaeus*, as well as the cladoceran genus *Evadne*, which were present all over the surveyed area (Table 2), were most abundant in the semi-enclosed gulfs and were therefore grouped within the 'coastal assemblage'. This group also included the taxa *Penilia avirostris*, *Podon* spp., adults and copepodites of *Ctenocalanus vanus*, *Paracalanus parvus* and *Centropages typicus* as well as adults of *Oncaea media*.

Group II included the species that showed maximum abundance values in stations of Group D (pelagic stations of the Ionian and Aegean Seas) and especially in subgroup D2 (offshore stations of the Ionian Sea). This Group could therefore be labelled as the 'pelagic assemblage' (Table 2). Copepodites of the genera *Calocalanus*, *Haloptilus*, *Lucicutia* and *Mecynocera* along with the species *Farranula rostrata*, *Calocalanus pavo*, *Mesocalanus tenuicornis* and *Oncaea mediterranea* comprised this assemblage.

Four smaller species-groups were also defined by the cluster analysis (Figure 3), comprising species with higher abundance in specific areas. Group III included the species *Clausocalanus furcatus*, *Clausocalanus jobei* and males of the genus *Clausocalanus*, which were most abundant in

Table 3. *Mean values and standard deviations (SD) of Shannon–Wiener diversity index (H′) and the number of adult copepod species (S) for different groups and subgroups defined by the cluster analysis (Figure 1C).*

	H′		S		Number of stations
	Mean	SD	Mean	SD	
Group A	3.10	0.50	17.5	4.6	31
Group B	3.54	0.21	19.3	3.7	12
Group C	3.56	0.23	22.9	2.8	10
Subgroup D1	3.98	0.31	27.0	4.8	26
Subgroup D2	4.38	0.17	32.9	2.9	28

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the sub-regions of the Aegean Sea, South Evoikos and Saronikos Gulfs. Group IV included the copepodites of the genus *Oncaea*, which were most abundant in the Korinthiakos Gulf. Groups V and VI included the species *Centropages ponticus* and *Acartia clausi* (very abundant in the outlier Stations O1 and O4 respectively) and *Isias clavipes* (abundant in the outlier Stations O5 and O6).

The distribution and abundance of the copepod species comprising the 'coastal' (Group I) and the 'pelagic' assemblage (Group II) are presented in Figures 4 and 5 respectively.

Copepod diversity

A total of 86 copepod species was found in the study area. The number of species at each site ranged from 7 to 38. The Shannon–Wiener (H′) diversity index ranged from 1.65 to 4.84. The lowest values were observed in the outlier stations (near ports or river mouths) and the highest in the pelagic areas of the Ionian Sea. The mean values of H′ were lower in Groups A, B and C (semi-enclosed gulfs) and higher in subgroups D1 and D2 (pelagic areas of the Ionian and Aegean Seas) (Table 3).

DISCUSSION

According to the zooplankton community structure the surveyed area could be divided into four distinct sub-regions (Figure 1): the neritic of the eastern part, the pelagic of the eastern and western part and, finally, the gulfs of Korinthiakos and Patraikos.

The zooplankton community of the neritic eastern part of the study area (Group A) was dominated by a small number of species all belonging to the 'coastal' assemblage (Table 2, Figure 4). The copepod species *Paracalanus parvus*, *Centropages typicus* and *Temora stylifera* as well as the cladoceran *Penilia avirostris* and *Podon* spp., have often been reported as common species of the coastal Mediterranean (Kouwenberg, 1994; Mazzocchi & Ribera d'Alcala, 1995), exhibiting clear seasonal cycles with maximum abundance during the warm months (Siokou-Frangou, 1996; Christou, 1998). Scotto di Carlo & Ianora (1983) state that in coastal areas of the Mediterranean Sea, the bulk of the zooplankton population comprises a relatively small number of species (about ten) throughout the year. The same statement was made by Mazzocchi & Ribera d'Alcala (1995) for the Gulf of Naples. The low diversity index (H′) values observed for Group A in the present study can be attributed to the high abundance values of a small number of species in the respective areas. Similar diversity values have also been reported for other coastal areas of the Mediterranean (Siokou-Frangou & Papathanassiou, 1991; Jamet et al., 2001).

The presence of the less saline Black Sea Water (BSW, Ramfos et al., 2005) seemed to be the main environmental factor related to the definition of Group A (Figure 2). Salinity has often been considered as one of the main environmental factors affecting zooplankton composition (Christou, 1998; Valdes & Moral, 1998). Temperature of the surface layer also seemed to contribute to the east–west separation of sampling sites, but to a lesser extent, since the differences in temperature values were less pronounced. Temperature is known as one of the main environmental factors affecting the seasonal evolution of zooplankton communities (Siokou-Frangou et al., 1998; Valdes & Moral, 1998).

The zooplankton community of the Aegean and Ionian Seas (stations of Group D) was dominated by species of the 'pelagic assemblage' (Table 2, Figure 5) characterized by the species *Haloptilus longicornis*, *Lucicutia flavicornis*, *Mecynocera clausi*, *Oncaea mediterranea*, *Mesocalanus tenuicornis*, *Farranula rostrata* and *Calocalanus pavo*. These species have been considered as indicative of the offshore water masses in the eastern Mediterranean (Stergiou et al., 1997), either as epipelagic (e.g. the species *Mecynocera clausi*, *F. rostrata*, *C. pavo*) or mesopelagic species (e.g. the species *H. longicornis*, *L. flavicornis*, *O. mediterranea*) (Scotto di Carlo et al., 1984; Paffenhofer & Mazzocchi, 2003). The distribution of mesopelagic species seemed to be restricted by station depth, being almost absent in the shallower stations of the Ionian and Aegean Seas (subgroup D1). The occurrence of these species only in the deep stations of the area is due to the combination of their mesopelagic character and migratory behaviour.

Haul depth was one of the main factors explaining the differentiation between the pelagic subgroups D1 (more inshore) and D2 (offshore). The lower abundance of mesopelagic species as well as the higher abundance of neritic species (e.g. *Paracalanus parvus*, *Ctenocalanus vanus*, *Centropages typicus*, *Penilia avirostris*) characterized the shallower stations of D1. The latter species were not strictly associated with the neritic environment (as also stated by Scotto di Carlo et al. (1984) for the offshore Mediterranean waters) but could also be found in offshore waters. High-density values have been reported for the aforementioned species in pelagic stations of a frontal area in the north Aegean Sea and their dominance was attributed to the favourable environmental conditions and the higher productivity of the region (Christou & Zervoudaki, 2000).

The mesozooplankton community was very similar between the pelagic stations of the Ionian and the Aegean Seas (Group D), two practically separated water masses. This observation is consistent with the suggestion of a homogenous surface layer (0–100 m) in all pelagic areas of the eastern Mediterranean caused mainly by the dominance of two species *Clausocalanus furcatus* and *Oithona plumifera* (Siokou-Frangou et al., 1997). Although the copepodites of these two genera were abundant in our pelagic samples, the resemblance of the communities between the Ionian and Aegean Seas could be attributed not only in these species but also in other abundant species such as *Mecynocera clausi*, *Calocalanus* spp., *Mesocalanus tenuicornis* and *Farranula rostrata*.

The zooplankton communities of Saronikos and South Evoikos Gulfs are known to be influenced by the Aegean Sea water masses (Siokou-Frangou et al., 1984; Siokou-Frangou et al., 1998). The obvious intrusion of the Aegean Sea water into these gulfs seemed to follow the 100 m isobath (Ramfos et al., 2005). The influence of this water was obvious in the zooplankton community as all stations in these sub-areas, with depth greater than 100 m, had a clear pelagic character.

The high diversity values observed in the pelagic regions can be attributed to the high species number in the area as well as to the absence of high dominance.

High diversity is a common feature of the oligotrophic offshore waters in the eastern Mediterranean (Siokou-Frangou et al., 1997). The main parameters corresponding to the differentiation of the pelagic community (Figure 2) were the higher salinity values, the deeper fluorescence maximum, the higher haul depth and the higher integrated fluorescence (the latter was positively correlated with haul depth). The pelagic water masses of the Greek seas (with the exception of the north-eastern Aegean), are characterized by high salinity values (Stergiou et al., 1997). The deep chlorophyll maximum, usually observed between 75 m and 120 m, is also a common feature of these oligotrophic pelagic areas (Psarra et al., 2000).

The zooplankton community structure in Korinthiakos Gulf (Group B) differed markedly from the others in the study area. Korinthiakos Gulf has unique topographical and hydrological characteristics: great maximum depth (>900 m), narrow continental shelf and restricted communication with the neighbouring Patraikos and Saronikos Gulfs. The bottom layer of the water column is completely homogenous and is characterized by high salinity (38.5–38.6 psu) and low temperature values (Poulos et al., 1996). This was also confirmed in our survey (13–14°C, Ramfos et al., 2005). Indeed, the low temperature of the water below the thermocline seemed to be the only environmental factor that explained the differentiation of the zooplankton community in Korinthiakos Gulf (Figure 2). *Penilia avirostris* was the dominant species in this Gulf as well as in all semi-enclosed basins (Ramfos et al., 2005). This species is strictly distributed above the thermocline (Christou & Zervoudaki, 2000). The great depth (>200 m) of most stations in Korinthiakos Gulf resulted in the high abundance of certain poecilostomatoid (genus *Corycaeus* and *Oncaea*) copepod species which are known to contribute significantly to total zooplankton of the deep waters (Longhurst, 1985). The almost exclusive presence of the copepod species *Oncaea conifera* in this area, as well as the absence of *Centropages typicus* further contributed to the differentiation of the Korinthiakos Gulf community. Since species of the genus *Oncaea* are certainly undersampled by our 200 μm net, it is likely that, if sampled quantitatively, they would contribute further to the characterization of communities in the surveyed area, especially the deeper sites.

Low temperature below the thermocline, especially in the enclosed basins of the North Evoikos and Korinthiakos Gulfs, may explain the high abundance of the copepod *Ctenocalanus vanus* in these gulfs (Figure 4). This species is very common in coastal waters of the eastern Mediterranean and multi-annual studies have described it as cryophilic, showing its maximum abundance during the winter months (Siokou-Frangou, 1996; Christou, 1998; Siokou-Frangou et al., 1998). It seems that *C. vanus* prefers the subsurface layer (50–100 m) and stays below the thermocline during summer (Scotto di Carlo et al., 1984; Siokou-Frangou et al., 1997; Fragopoulu et al., 2001).

It must be noted here that the stations in the western part of Korinthiakos Gulf were grouped with the Patraikos Gulf sites. This western part of the gulf is characterized by smaller depths (<100 m) communicating with Patraikos Gulf through a narrow strait with strong wind-driven and tidal currents (Drakopoulos & Lascaratos, 1998).

Patraikos Gulf has been described as the basin where mixing processes take place between the water masses of the Ionian Sea and Korinthiakos Gulf (Friligos et al., 1985). Although cluster analysis clearly separated Patraikos from all other sites (Group C), nMDS ordination positioned them in-between the three other groups (Figure 2). The dominant copepod species found in Patraikos Gulf belonged to the 'coastal' assemblage (e.g. *Clausocalanus* and *Oithona* copepodites, *Oithona plumifera*, *Oncaea media*, *Paracaluns parvus*, *Temora stylifera*, *Ctenocalanus vanus*, *Penilia avirostris*) and have been reported in the area by a previous study (Fragopoulu & Lykakis, 1990). Species abundant in Korinthiakos Gulf (*Corycaus brehmi*) or the Ionian Sea (*Farranula rostrata*, *Calocalanus* spp. copepodites) were also abundant in Patraikos Gulf, thus contributing to the transitional character of this area.

The difference in the zooplankton community structure was more or less expected for the seven stations characterized as 'outliers' in the cluster analysis. Stations 16 and 17 were located in a shallow embayment of the North Evoikos Gulf, which is strongly influenced by river outflow and has been described as a disturbed area (Christou et al., 1996). Station 66 is positioned in the most disturbed area of the Saronikos Gulf (Siokou-Frangou et al., 1998) with low copepod diversity values and high dominance of the tolerant and opportunistic copepod species *Acartia clausi* (Siokou-Frangou & Papathanassiou, 1991; Siokou-Frangou et al., 1998; Christou & Zervoudaki, 2000). Stations 38 and 63 were very shallow stations (less than 30 m) and were characterized by the dominance of the species *Clausocalanus furcatus* and *Acartia clausi* and low diversity values. Finally, the copepod species *Isias clavipes* was only abundant in Stations 110 and 111 which were also near a river mouth.

Conclusively, two major distinct species assemblages were defined by the mesozooplankton community analysis in the coastal and pelagic areas of central Greek waters: the 'coastal' assemblage characterizing the zooplankton communities of the various semi-enclosed gulfs and the 'pelagic' assemblage characterizing the open-sea stations of the surveyed area. The different community structure among the various semi-enclosed basins was mainly due to small changes in hierarchy of relative abundance of a common-species list rather than presence–absence differences. Species belonging to the 'pelagic' assemblage of the Aegean and Ionian Seas, exhibited a clear inshore–offshore gradient. Salinity and, to a lesser extent, temperature seemed to be the main environmental parameters explaining the east–west differentiation of zooplankton communities. Topography also seemed to contribute to the differentiation.

It seems that despite the differences in environmental conditions in the Mediterranean Sea, few are the abundant zooplankton species which separate the epipelagic (0–200 m) community mainly into pelagic and neritic/coastal. Cladocerans contribute in high numbers in the coastal community during summer months. Abundant copepods are epipelagic and weak mesopelagic migrators. The coastal community exhibits differentiation depending on topography, hydrology, water circulation or food availability which persists over time according to season.

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