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Regional and seasonal characteristics of epipelagic mesozooplankton in the Mediterranean Sea based on an artificial neural network analysis

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ABSTRACT

The cruises conducted in the spring and autumn of 2008 in the frame of the European project SESAME represented the first coordinated surveys that allowed acquiring a quasi-synoptic picture of epipelagic mesozooplankton in most regions of the Mediterranean Sea. Seasonal differences were recorded in biomass, total abundance, and community composition and structure. In both seasons, it did not appear a clear west-east decreasing gradient in total standing stock, but rather regional discontinuities. However, west or east preferences were observed in the distribution of some zooplanktonic groups and copepod species. An artificial neural network analysis (SOM) identified, in both seasons, a clear mesozooplankton regionalization, which resembled the autotrophic regimes based on color remote sensing data. The correspondence between the distribution of zooplankton communities and the trophic regimes appeared more precise in spring, when the increased concentration of chlorophyll *a* makes the Mediterranean Sea a more heterogeneous environment, but it was still visible in the more uniform oligotrophic autumn conditions. Three distinct types of mesozooplankton communities seem to flourish in the investigated regions: the first type is the most widespread and thrives in the "non-blooming" areas, the second type occurs in the "intermittently-blooming" areas, and the third type is a characteristic of areas with recurrent and intense phytoplankton blooms. Overall, the well defined regionalization of mesozooplankton that appears from our results corroborates the view of the Mediterranean Sea as a mosaic environment, as previously emerged from the analyses of different biological compartments.

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1. Introduction

The Mediterranean Sea is a large semi-enclosed basin characterized by high diversity of its marine biota (Coll et al., 2010). Despite the extension of this sea within a narrow latitudinal range, numerous biogeographic sectors have been identified based on the distribution of benthic and nektonic communities (Bianchi and Morri, 2000). A zonation of the Mediterranean Sea based on the time-series of chlorophyll *a* (chl *a*) concentration from satellite images was recently proposed by D'Ortenzio and Ribera d'Alcalà (2009). The close link observed between the structure of the chl *a* seasonal cycle and the extent of phytoplankton biomass accumulation lead these authors to infer that the observed spatial patterns likely reflect also different trophic regimes, i.e., different food web functioning and structures. Considerable diversity and spatial variability appear also in the plankton communities of the open epipelagic Mediterranean Sea (reviewed by Siokou-Frangou et al., 2010), including mesozooplankton that are key elements of the pelagic food webs.

Zooplankton in the open Mediterranean Sea are characterized by a general scarcity of biomass and abundance and by the overall dominance of small-sized (≤1 mm) animals (Siokou-Frangou et al., 2010 and references therein). A less clear picture emerges in terms of community spatial patterns. An eastward decrease of standing stock was observed across the basin for both microzooplankton (Dolan et al., 2002) and mesozooplankton (Siokou-Frangou, 2004), though a recent survey revealed such gradient in metazooplankton abundance but not biomass (Nowaczyk et al., 2011). Minutoli and Guglielmo (2009) did not observe significant differences in total mesozooplankton abundance between the western and the eastern sectors of the Mediterranean Sea whereas

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they measured a significant eastward increase in carbon consumption calculated by ETS, which was related to changes in sea water temperature. In some cases, distinct seasonal or spatial patterns at basin scale were observed in species and/or group distribution (e.g., Brugnano et al., 2010; Fonda Umani et al., 2010; Gaudy et al., 2003; Hure et al., 1980; Mazzocchi et al., 2003; Nowaczyk et al., 2011; Siokou-Frangou et al., 1997), suggesting that differences in community structure may be indicative of distinct functioning of the pelagic system.

An open question therefore remains in our understanding of mesozooplankton distribution in the Mediterranean Sea, i.e., whether the observed patterns in abundance and composition result from a continuous gradual change (the west–east gradient hypothesis) or they emerge with patchy characters because of marked regional discontinuities. This is not a trivial question. The features of mesozooplankton distribution should be linked to the lower trophic levels and influence the top consumers, thus reflecting and shaping structure and functioning of the pelagic systems. However, sometimes biological plasticity may determine stability and resilience in mesozooplankton communities even in highly variable conditions, thus uncoupling it from the environmental dynamics (Mazzocchi et al., 2012). A better depiction of the mesozooplankton distribution in terms of standing stock and community structure may improve our comprehension of the overall trophic and biogeochemical features of the Mediterranean Sea. Such issue, however, can be properly addressed only by large-scale synoptic cruises that survey extensively the whole basin. This approach has been applied in the past to deep zooplankton (Scotto di Carlo et al., 1991) but only in a few cases to epipelagic zooplankton, which have been investigated only in the Eastern Basin (Mazzocchi et al., 1997) or, more recently, during trans-Mediterranean cruises with a limited number of stations along transects (Minutoli and Guglielmo, 2009; Nowaczyk et al., 2011; Siokou-Frangou, 2004).

The cruises conducted in the spring and autumn of 2008 in the SESAME project represented the first coordinated surveys that allowed acquiring an extensive and quasi-synoptic picture of epipelagic mesozooplankton in most Mediterranean regions. In the same periods as the cruises in the Mediterranean Sea, surveys were also conducted in the Black Sea, for parallel zooplankton investigations in the two communicating but very different basins (Arashkevich et al., in this issue). Aim of the SESAME cruises was to assess the current status of the Southern European Seas through an analysis of newly collected physical, chemical and biological data at basin scale for a better understanding and modeling of their pelagic system also in relation to global changes.

We present here a synthetic overview of the Mediterranean epipelagic mesozooplankton based on the analysis of standing stock and composition in the integrated 0–200 m water column. Moreover, in consideration of the extension of our data set, we did attempt to verify whether spatial patterns would emerge from the mere zooplankton distribution that might compare to the trophic regimes inferred from color remote sensing data (D'Ortenzio and Ribera d'Alcalà, 2009). To this aim, we performed a classification of the samples by using an unsupervised artificial neural network analysis on zooplankton community composition. This analysis also returned an ordination of the cluster of samples and offered a synthesis and graphical representation of the space–time variability of the original data set, so favoring the comparison with the classification based on remote sensing data.

2. Materials and methods

2.1. Sampling

Mesozooplankton communities were investigated in the late winter–early spring (spring henceforth) and late summer–early autumn (autumn henceforth) of 2008 during the Sesame-WP2 cruises, which were conducted by five countries to survey most of the Mediterranean regions (Fig. 1, Table 1). Samples were collected at different times of the day, but mostly (93%) during light hours (Table 1) in three discrete layers (200–100 m, 100–50 m, 50–0 m) by vertical tows performed with a closing WP2 net (57 cm diameter, 200 μm mesh). In the Atlantic, Gibraltar, Alboran Sea, and at a few stations in the Ionian, Aegean and northwest Levantine seas, the entire 0–200 m layer was sampled by a single haul (in the Gibraltar Strait, due to the strong current, the bottom of the sampled layer was slightly shallower) (Table 1 in supplementary material). Due to the frequent malfunctioning of flowmeters in various cruises, the filtered water volumes ($V = AxL$, m^3) were calculated by taking into account the area of the net mouth (A, m^2) and the length of the released wire (L, m) (Sameoto et al., 2000). The final thickness of the sampled layer (ΔD, m) and the depth limits of the layer ($\Delta L = L_i - L_f$, m) were computed considering the wire angle α ($\Delta D = \Delta L \cos \alpha$). After the tow, the net was carefully washed, and the sample was split in two halves by using the Hunstman beaker technique (Van Guelpen et al., 1982). Half sample was used fresh for biomass measurements as dry mass and carbon content; the other half sample was fixed and preserved in a seawater-buffered formaldehyde solution (4% final concentration) for later determination of composition and abundance. In the present study, we report only about mesozooplankton in the integrated 0–200 m water column at 73 stations, therefore excluding the shallower stations (Table 1 in supplementary material).

2.2. Biomass

The fresh half sample was sieved in succession through 1000 μm, 500 μm, and 200 μm mesh to obtain three size fractions (>1000 μm, 500–1000 μm, and 200–500 μm). Each size fraction was re-suspended in a small volume of filtered sea water and drained by vacuum filtration on GF/C filters (25 or 47 mm diameter, pre-combusted at 400 °C for about 24 h and weighted), after a quick final rinse with distilled water to eliminate the salts of seawater (Postel et al., 2000). Each filter was then placed in a small plastic Petri dish and dried in the oven at 60 °C for 4–5 h. At each station, two additional filters without material were rinsed with distilled water and dried to be considered as blank filters. The dried filters were folded and stored at −20 °C until further processing. In the laboratory on land, the GF/C filters were thawed, dried in the oven at 60 °C for 24 h or longer until completely dry, and weighed on an electronic microbalance. Size fractionation could not be performed on samples collected in the Atlantic, Strait of Gibraltar, Alboran and Aegean seas, as well as on few samples collected in the Ionian and Levantine seas (Table 1 in supplementary material). The carbon content of size-fractionated mesozooplankton samples from the Italian and Greek cruises was successively determined by CHN analyzer (Postel et al., 2000).

2.3. Taxonomic composition and abundance

The fixed half sample was concentrated to remove the formaldehyde, and the organisms were suspended in graduate cups with filtered seawater or tap water for analysis. After thorough mixing, sub-samples were taken with a wide-bore pipette or with a Folsom plankton splitter and analyzed in Bogorov or Dolffus chambers under a dissecting stereomicroscope. Finally, rare species were searched in the rest of the sample. Taxonomic classification was performed according to common criteria established during a pre-cruise inter-calibration workshop held in Athens in May 2008. Copepods were identified at species level whenever possible while other groups were mainly identified at higher taxonomic levels. The common taxonomic list and dataset used for the statistical analysis comprised a total of 200 zooplankton taxa. We did not consider the organisms smaller than 200 μm (e.g., microzooplankters) because not efficiently collected by our nets.

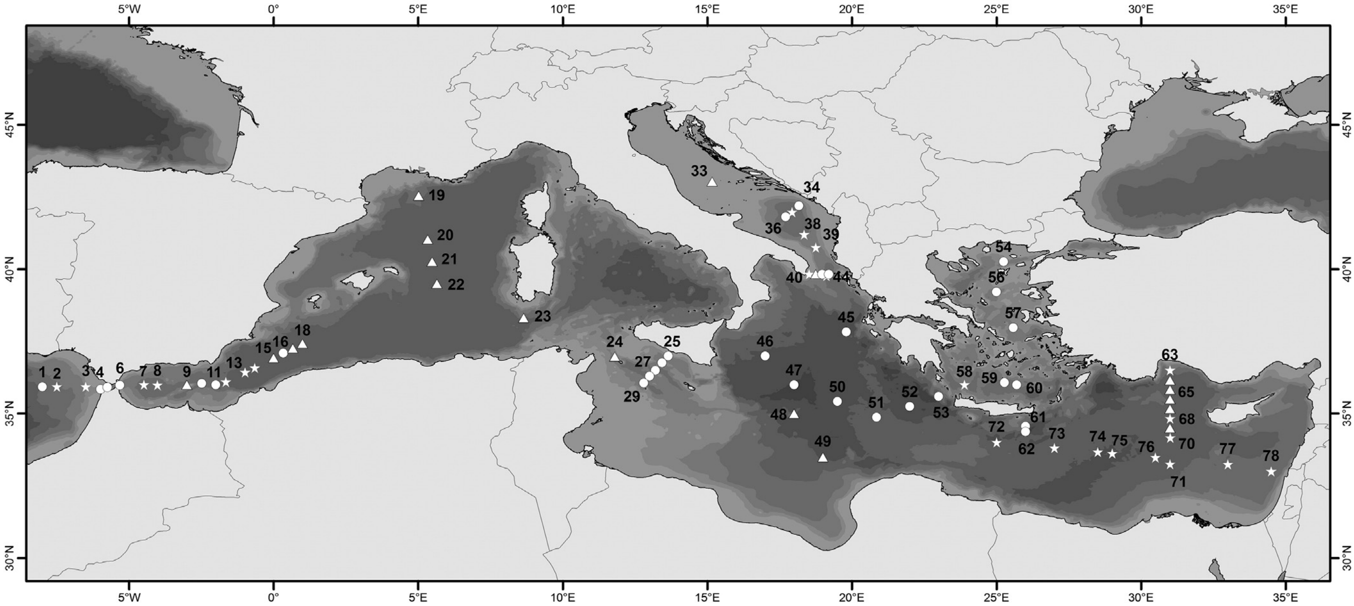

Fig. 1. Mesozooplankton stations sampled in the Mediterranean Sea during the SESAME cruises in 2008, in spring (triangles) or autumn (stars), or in both seasons (circles).

2.4. Data analysis

When not from a direct 0–200 m tow, the data from each sampled depth layer were firstly referred to the water volume unit (1 m^3) and then integrated and referred to 1 m^2 over the 0–200 water column for both biomass (g m^{-2}) or abundance (ind. m^{-2}) according to the formula: $I = (x \cdot a + y \cdot b + z \cdot c)$ where I is the integrated value (e.g., ind. m^{-2}); x, y, and z are the values in the unit volume (e.g., ind. m^{-3}) in each of the three depth layers; a, b, c are the heights (m) of the three depth layers.

Log-transformed values of mesozooplankton biomass (as dry mass, DM) and total abundance were analyzed with a one way ANOVA for evaluating differences among regions, and the Least Significant Difference Test was employed for comparison among regions, which were considered significantly different at $p < 0.01$.

To obtain an objectively derived typology of epipelagic mesozooplankton, the community composition at 66 stations (Table 1) was analyzed with the Self-Organizing Map (SOM). We used the SOM toolbox (Vesanto et al., 1999) for Matlab that was developed by the Laboratory of Information and Computer Science in the Helsinki University of Technology (http://www.cis.hut.fi/projects/somtoolbox). This analysis excluded seven stations in the Levantine Sea where only biomass data were available (Table 1 in supplementary material).

SOM is a neural network unsupervised iterative numerical algorithm (Kohonen, 2001) for non-linear projection and ordination of multidimensional data onto a lower dimensional (usually 2D) lattice. SOM is based on multi-dimensional similarity among data. It has several advantages compared to other numerical classification techniques, e.g., it does not rely on any particular a priori assumption on dataset structure and the global ordination on the map is not affected by the presence of outliers. The original data are classified in a number of clusters, called map units, and for each map unit a vector represents the set of samples associated to it (Solidoro et al., 2007). During the iterative learning process, areas (i.e., groups of vectors, with each vector representing a group of samples) with similar values in many parameters (i.e., relative abundance of taxa) emerge on the SOM, so that map units representing samples with similar compositions are close to each other onto the 2D map space. Guidelines for the choice of size and geometry of the map suggest using a number of map units intermediate between the number of original samples and the expected number of clusters. A two-step procedure that applies classical hierarchical or partitive clustering methods to map units (Bandelj et al., 2008; Solidoro et al., 2007) can give an even better representation of the important features of original data. SOM has already been successfully applied in ecology (Bandelj et al., 2008; Giraudel and Lek, 2001; Lek and Guégan, 1999; Park et al., 2004).

The original mesozooplankton abundances were first transformed with the Hellinger transformation (Legendre and Gallagher, 2001) in order to prevent the “double zero” problem (Legendre and Legendre, 1998), and then analyzed with the SOM toolbox routines. The maps were built by using linear initialization of map unit vectors, sequential learning algorithm and other parameters at the default SOM toolbox values. The map units were then clustered following the Ward's minimum variance method (Legendre and Legendre, 1998).

To identify the species assemblages that characterize each cluster, the Indicator Value index (IndVal, Dufrêne and Legendre, 1997) was applied on the original abundance values. The IndVal index combines the species relative abundance (the so-called specificity, A_{jk}) with the species relative frequency of occurrence within a given group of observations (the so-called fidelity, B_{jk}):

$$\mathrm{IndVal}_{jk} = A_{jk} \times B_{jk} \times 100.$$

A_{jk} is the ratio between the mean abundance of the species j in the observations of the group k and the sum of the mean abundance of the species j in all groups:

$$A_{jk} = \frac{\mathrm{Nsp}_{jk}}{\mathrm{Nsp}_{+k}}.$$

B_{jk} is the ratio between the number of observations in the group k where the taxon j is present and the total number of observations in k:

$$B_{jk} = \frac{\mathrm{Nobs}_{jk}}{\mathrm{Nobs}_{+k}}.$$

The IndVal analysis identifies the most characteristic species in each cluster not only on the basis of their highest abundance but also on their occurrence at the stations grouped in that cluster. Therefore, the IndVal

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Table 1
Mesozooplankton stations sampled during the SESAME cruises in the spring (late February–mid April) and autumn (late August–mid October) of 2008. Station codes have been assigned here according to station positions along the west-east direction. The station original names and coordinates, and mesozooplankton parameters are reported as supplementary material (Suppl. Table 1). Stations n. 30, 31, 32, 37, 40 in the Adriatic Sea and st. 55 in the Aegean Sea were not considered in the present study because shallow (≤150 m).

Region	Station code	Bottom depth, m	Spring date	Local time	Autumn date	Local time	R/V — country
Atlantic (ATL)	1	1691	14 Apr	5:54	27 Sep	13:54	*Regina Maris/Garcia del Cid* — SP
	2	1225			28 Sep	6:08	
Strait of Gibraltar (GBL)	3	463			26 Sep	16:12	
	4	355	13 Apr	15:03	26 Sep	10:32	
	5	260	13 Apr	11:54	26 Sep	7:29	
	6	800	13 Apr	7:20			
Alboran Sea (ALB)	7	1244			25 Sep	16:55	
	8	1292			24 Sep	18:24	
	9	200	8 Apr	8:20			
	10	1819	8 Apr	12:23	22 Sep	15:51	
	11	1847	8 Apr	0:00	22 Sep	11:10	
	12	2107			22 Sep	3:40	
	13	2593			21 Sep	13:15	
	14	2630			21 Sep	6:22	
	15	2658	9 Apr	12:19			
	16	2672	9 Apr	15:24	20 Sep	9:08	
	17	2701	9 Apr	18:33			
	18	2764	1 Apr	13:45			*Urania* — IT
Gulf of Lion–Algerian Basin (LION–ALG)	19	1909	4 Apr	15:30			
	20	2637	5 Apr	8:55			
	21	2808	5 Apr	17:10			
	22	2840	30 Mar	10:10			
	23	1893	29 Mar	12:30			
Strait of Sicily (SIC)	24	536	20 Mar	9:45			
	25	465	17 Mar	13:00	8 Sep	11:15	
	26	326	17 Mar	18:40	8 Sep	16:10	
	27	1733	18 Mar	17:00	9 Sep	16:55	
	28	841	18 Mar	14:15	9 Sep	11:15	
	29	866	18 Mar	8:20	9 Sep	7:15	
Adriatic Sea (ADR)	33	251	20 Feb	7:10	14 Oct	17:30	
	34	1051	24 Feb	15:40	10 Oct	7:30	
	35	1219			10 Oct	12:00	
	36	1191	23 Feb	16:55	10 Oct	16:45	
	38	1046			9 Oct	16:30	
	39	850			9 Oct	9:40	
	41	369	26 Feb	11:20			
	42	891	26 Feb	7:00	8 Oct	14:48	
	43	1069	25 Feb	21:40	8 Oct	4:45	
Ionian Sea (ION)	44	1047			21 Sep	9:20	
	45	3470	2 Mar	14:55	20 Sep	6:30	
	46	3426	8 Mar	12:45	18 Sep	7:20	
	47a	4037	4 Mar	12:05	19 Sep	6:50	
	47b	3983	22 Mar	19:00	28 Aug	13:00	*Aegaeo* — GR
	48	2850	5 Mar	2:05			*Urania* — IT
	49	3027	6 Mar	12:45			
	50	3126	23 Mar	13:00	28 Aug	21:45	*Aegaeo* — GR
	51	2700	27 Mar	10:15	29 Aug	10:00	
	52	3347	28 Mar	0:00	30 Aug	8:00	
	53	2122	28 Mar	8:50	30 Aug	17:00	
Aegean Sea (AEG)	54	1550	4 Apr	11:30	7 Sep	15:00	
	56	797	3 Apr	18:10	6 Sep	10:15	
	57	729	3 Apr	8:15	5 Sep	18:10	
	58	1203			3 Sep	13:10	
	59	1700	2 Apr	11:45	4 Sep	12:30	
	60	1283	1 Apr	16:40	4 Sep	3:30	
Levantine Sea (LEV)	61	2591	30 Mar	12:00	1 Sep	8:00	
	62	4000	31 Mar	1:30	31 Aug	17:00	
	63	1550			18 Oct	13:20	*Bilim2* — TR
	64	2400	5 Apr	17:30			
	65	2400	5 Apr	13:15			
	66	2200	5 Apr	9:00			
	67	2500	3 Apr	7:00			
	68	2600			19 Oct	8:30	
	69	2400	3 Apr	15:35	19 Oct	12:05	
	70	2440			19 Oct	17:05	
	71	2468			20 Oct	8:15	
	72	2566			12 Sep	11:30	*Shikmona* — IL
	73	2449			11 Sep	16:30	
	74	2738			10 Sep	17:30	
	75	3036			10 Sep	13:00	
	76	2529			9 Sep	14:20	
	77	1609			8 Sep	13:30	
	78	1439			7 Sep	15:00	

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index is highest when all individuals of a species are found in a single group of observations and when the species occurs in all observations of that group. Only taxa with IndVal > 25% and highly significant in both statistical tests proposed by Dufrêne and Legendre (1997) were considered characteristic of the clusters.

2.5. Environmental data

The distribution of seawater temperature and salinity during the cruises was obtained from the CTD casts and is represented here, for each station, by the depth averaged values in the whole 200 m layer and by the values recorded at 5 m and 200 m depths (Fig. 2). Spatially averaged profiles of temperature and salinity for each of the surveyed areas are provided as supplementary material.

The surface chl *a* concentration from satellite images was considered as a proxy of the general distribution of autotrophic biomass over the whole Mediterranean Sea during our surveys. Daily satellite data products were downloaded from the GlobColour Project (http://www.globcolour.info/) and the chl *a* estimates were calculated with the Garver, Siegel, Maritorena (GSM) semi-analytical algorithm (Maritorena and Siegel, 2005; Maritorena et al., 2002) and averaged over each of the two sampling periods.

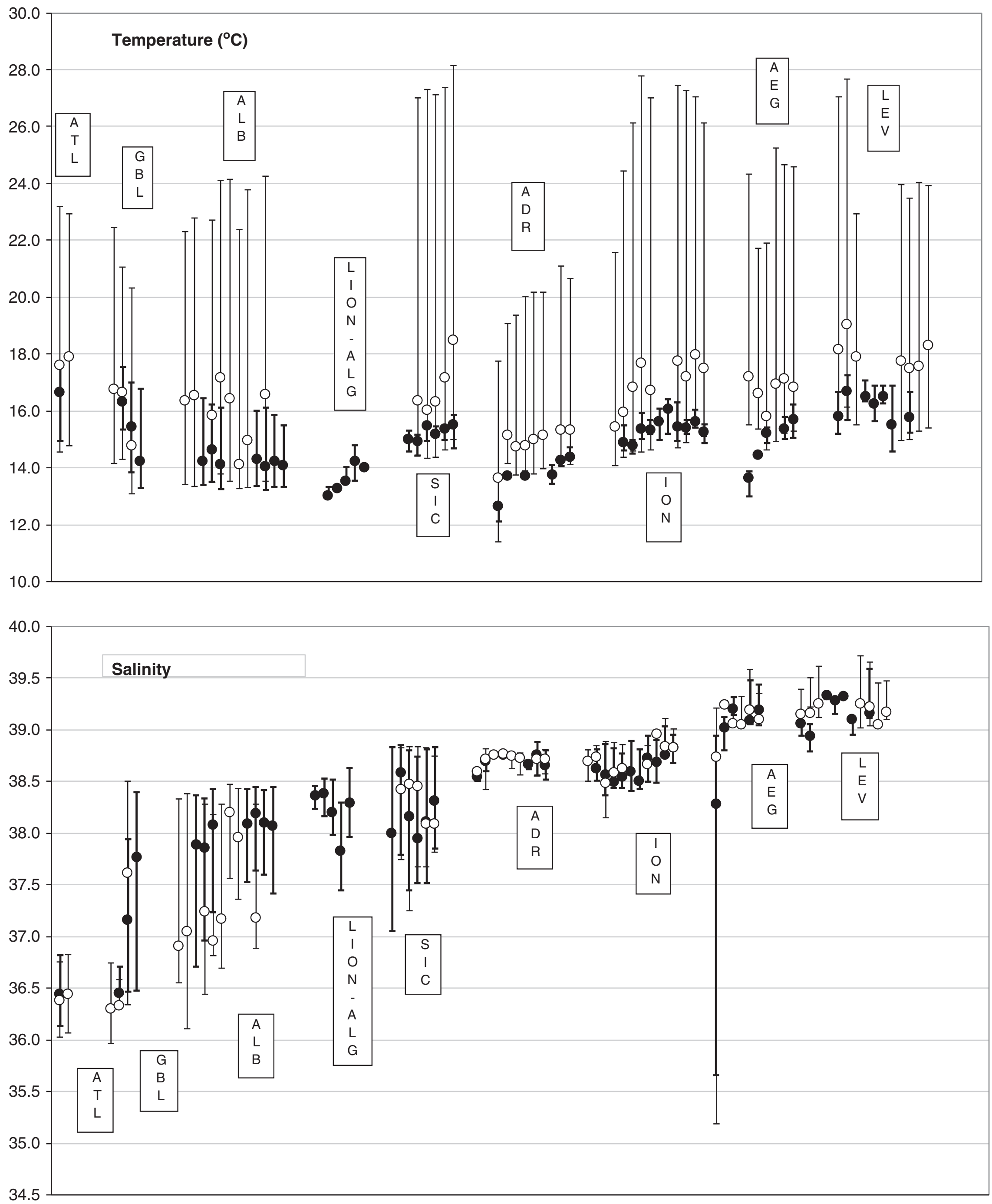

Fig. 2. - Depth averaged values of temperature (upper panel) and salinity (lower panel) in the 0–200 m water column as recorded by the CTD casts at the spring (●) and autumn (○) stations in 2008. Bars indicate temperature and salinity measured at 5 m and 200 m depths. ATL, Atlantic; GBL, Strait of Gibraltar; ALB, Alboran Sea; LION–ALG, Gulf of Lion–Algerian Basin; SIC, Strait of Sicily; ADR, Adriatic Sea; ION, Ionian Sea; AEG, Aegean Sea; LEV, Levantine Sea.

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3. Results

3.1. Spatial variability of temperature, salinity and chlorophyll *a*

In spring, the depth averaged temperature ranged from 12.66 °C in the Adriatic Sea (st. 33) to 16.67 °C in the Levantine Sea (st. 62) (Fig. 2). Temperature was quite homogenous in the 200 m water column in all areas (Fig. 1 in supplementary material), with the exception of the Atlantic site, the Strait of Gibraltar and the Alboran Sea where the vertical distribution was more variable, with a difference up to 3.49 °C between the 5 m and 200 m depths (Fig. 2). In autumn, the depth averaged temperature ranged from 13.64 °C in the Adriatic Sea (st. 33) to 19.04 °C in the Levantine Sea (st. 62) with the same spatial patterns as in spring (Fig. 2). However, as expected, the ranges of temperature within the 200 m water column were larger in autumn, due to the heat accumulation in the upper layers (Fig. 2 in supplementary material). The highest values (>27 °C at 5 m depth) were recorded in the Strait of Sicily and at some stations in the Ionian and Levantine seas. In all areas, the temperature values in the upper 30 m were >20 °C, with the exception of few stations in the Adriatic Sea.

The distribution patterns of salinity in both seasons showed the lowest values at the Atlantic stations (from 36.03 to 36.83) and then a gradual increase eastward (Fig. 2), with the highest values (>39) in the Aegean Sea and in the Levantine Sea (Figs. 3, 4 in supplementary material). Exceptionally low values of salinity were recorded at 5 m depth in both seasons (35.66 in spring and 35.19 in autumn) at the northernmost station of the Aegean Sea (st. 54), a clear indication of the presence of the modified Black Sea water at this station.

The distribution of surface chl *a* differed remarkably between the two seasons (Fig. 3). In spring, high chl *a* values were visible in a large area of the north-western Mediterranean, in the western Alboran Sea, and in the north-eastern Aegean Sea. The Algerian Basin, south Adriatic Sea, north-western Ionian Sea, and a small area east of Crete Island had less chl *a* than the above areas but more than the open Ionian and Levantine seas. A clear north-south gradient of chl *a* concentration appeared in the Aegean Sea. In autumn, the whole Mediterranean Sea displayed very low surface chl *a*, with a small increase only in the western Alboran Sea.

3.2. Mesozooplankton standing stock

Mesozooplankton biomass was generally higher and more spatially variable in spring than in autumn, without clear gradients in the west-east or north–south directions. In spring (Fig. 3), the highest value occurred in the Gulf of Lion–Algerian Basin (3.52 g DM m^{-2}, st. 20) and the minimum in the Strait of Gibraltar (0.18 g DM m^{-2}, st. 4). In autumn (Fig. 3), the highest and lowest values were recorded in the Aegean Sea (0.99 g DM m^{-2}, st. 54) and in the Strait of Gibraltar

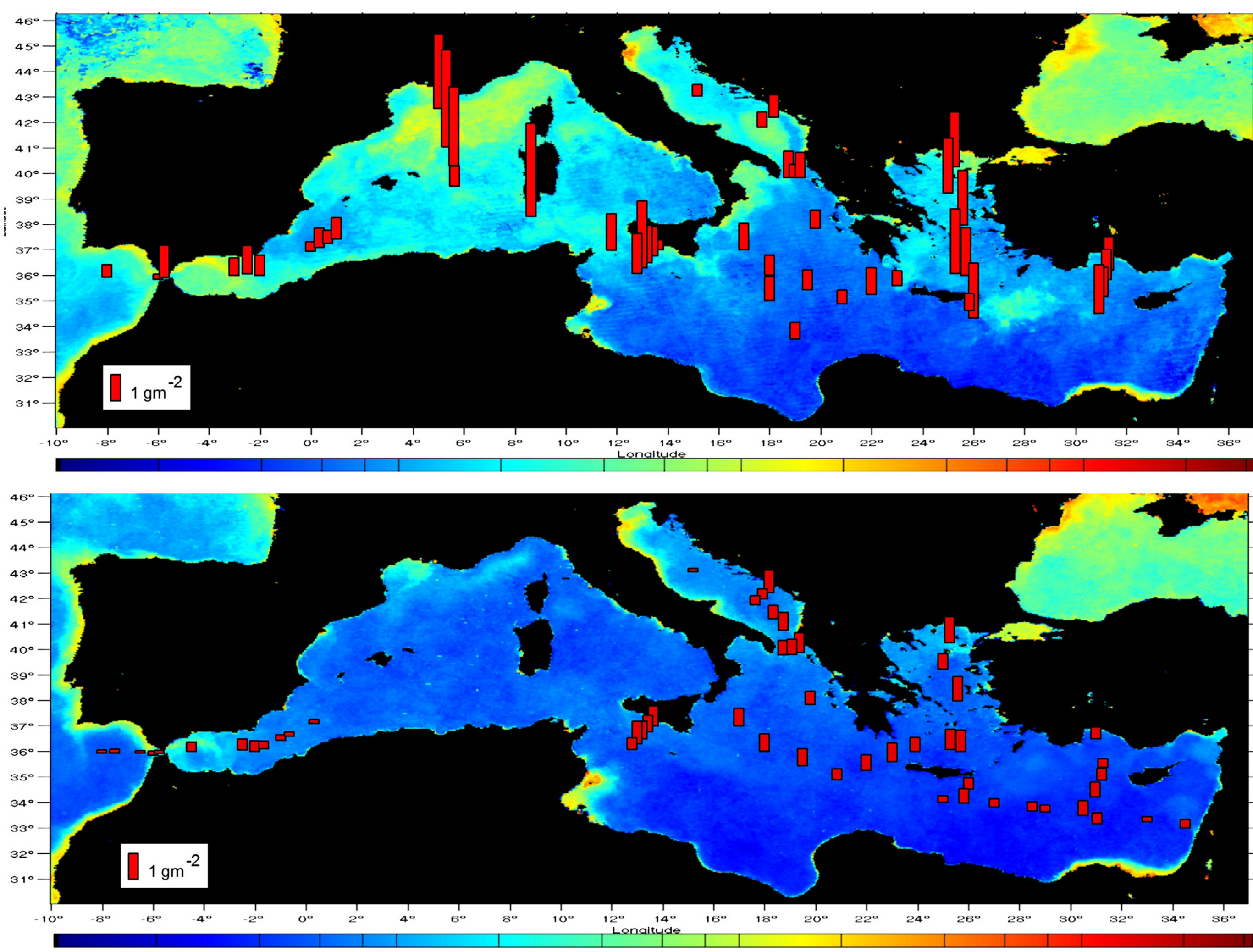

Fig. 3. Maps of the satellite derived chlorophyll-*a* concentration (mg m^{-3}) averaged for the period of spring (upper panel) and autumn (lower panel) cruises in 2008. Columns represent the distribution of mesozooplankton biomass (dry mass, g m^{-2}) integrated in the 0–200 m water column. The chl *a* concentration was estimated from Globcolour Merged SeaWiFs, MODIS and MERIS Sensor Data (GSM semi-analytical algorithm).

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(0.08 g DM m^{-2}, st. 3), respectively. When averaged by regions, total biomass (Fig. 4) showed the highest spring values in the Gulf of Lion–Algerian Basin (mean 2.63 ± 0.50 g DM m^{-2}) and in the Aegean Sea (mean 2.0 ± 0.10 g DM m^{-2}), regions that were significantly richer in mesozooplankton dry mass than all other areas ($p < 0.0001$). Biomass values in the Adriatic, Alboran and Ionian seas were significantly lower than those in the Levantine Sea and in the Strait of Sicily ($p < 0.0001$). In autumn, the Strait of Sicily, the Adriatic, the Ionian and the Aegean seas presented significantly higher biomass (range of mean values 0.53–0.77 g DM m^{-2}) than the westernmost regions (range of mean values 0.13–0.28 g DM m^{-2}) and the Levantine Sea (0.03–0.46 g DM m^{-2}) ($p < 0.0001$). The seasonal signature in dry mass appeared clearly in all regions, with the exception of the Adriatic and the Ionian seas, where quantitative differences between spring and autumn were very small.

Total carbon content in spring ranged between 0.24 ± 0.03 g C m^{-2} in the Ionian Sea and 0.82 ± 0.15 g C m^{-2} in the Gulf of Lion–Algerian Basin (Fig. 5a); in autumn, it ranged between 0.15 ± 0.02 g C m^{-2} in the Adriatic Sea and 0.22 ± 0.02 g C m^{-2} in the Ionian Sea (Fig. 5b). The contribution of three size fractions to total mesozooplankton carbon content varied among regions and seasons. In spring, the relative importance of the smallest animals (200–500 μm) decreased gradually from the western to the eastern regions, with a corresponding increase of the largest organisms (>1000 μm); the medium size (500–1000 μm) individuals contributed more in the eastern than in the western regions (Fig. 5a). In autumn, an opposite pattern was observed, with the smallest size fraction contributing more eastward, while the medium and large size fractions did not reveal a clear spatial pattern (Fig. 5b). Overall, large mesozooplankters contributed more in spring than in autumn.

Similarly to biomass, total mesozooplankton abundance was, on average, higher in spring ($123.4 \times 10^3 \pm 17.5 \times 10^3$ ind. m^{-2}) than in autumn ($73.1 \times 10^3 \pm 4.7 \times 10^3$ ind. m^{-2}). Seasonal differences were highest in the Strait of Gibraltar and in the Adriatic Sea (Fig. 6). In contrast with the general pattern, mesozooplankton were slightly more abundant in autumn than in spring in the Ionian Sea and in the Strait of Sicily. In spring, the abundance was significantly higher in the Adriatic Sea, Gulf of Lion–Algerian Basin and Strait of Gibraltar than in the other regions ($p < 0.0001$), as well as in the Alboran and Aegean seas than in the Ionian Sea ($p < 0.0001$). The highest value was measured in the Gulf of Lion (688.1×10^3 ind. m^{-2}, st. 21) and the lowest in the Ionian Sea (20.2×10^3 ind. m^{-2}, st. 51). In autumn, abundance was significantly lower in Atlantic, Strait of Gibraltar and Levantine Sea compared to the other regions ($p < 0.0018$). The highest abundance occurred in the Adriatic Sea (173.2×10^3 ind. m^{-2}, st. 39) and the lowest in the Strait of Gibraltar (16.6×10^3 ind. m^{-2}, st. 3).

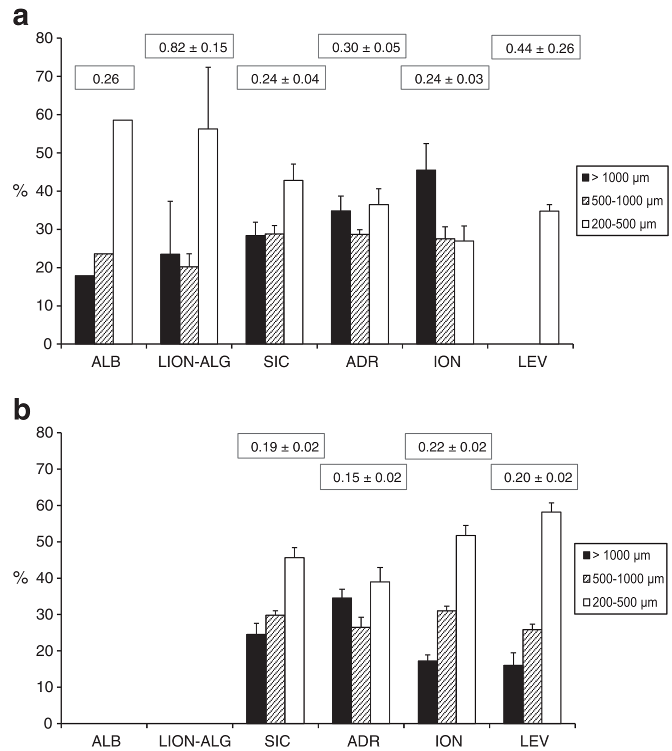

Fig. 5. Total mesozooplankton carbon content (g C m^{-2}) integrated in the 0–200 m water column as regionally averaged values (±standard error) and corresponding percentage contribution (columns ± standard error) of three size fractions (black, >1000 μm; stripped, 500–1000 μm; white, 200–500 μm) in (a) spring and (b) autumn. Regional codes as in Fig. 2.

3.3. Group and species composition

Ten taxonomic groups accounted for >99% of total mesozooplankton abundance in each of the surveyed regions (Table 2). Seven groups, i.e., copepods, ostracods, cladocerans, appendicularians, thaliaceans, cnidarians + ctenophors, chaetognaths, represented the bulk communities, followed by malacostracans, molluscs and polychaetes. In spring, communities were by far dominated by copepods, especially in the western regions (>91%); the only exception was represented by the Alboran Sea where the contribution of appendicularians and thaliaceans (mainly doliolids), and cladocerans (*Podon intermedius*, *Penilia avirostris*, *Evadne spinifera*) was important. In autumn, copepods

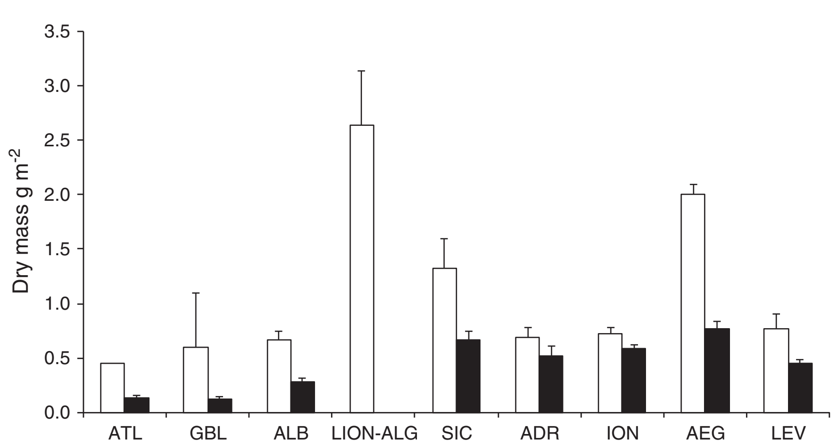

Fig. 4. Mesozooplankton biomass (dry mass, g m^{-2}) integrated in the 0–200 m water column as regionally averaged values (±standard error) in spring (white) and autumn (black). Regional codes as in Fig. 2.

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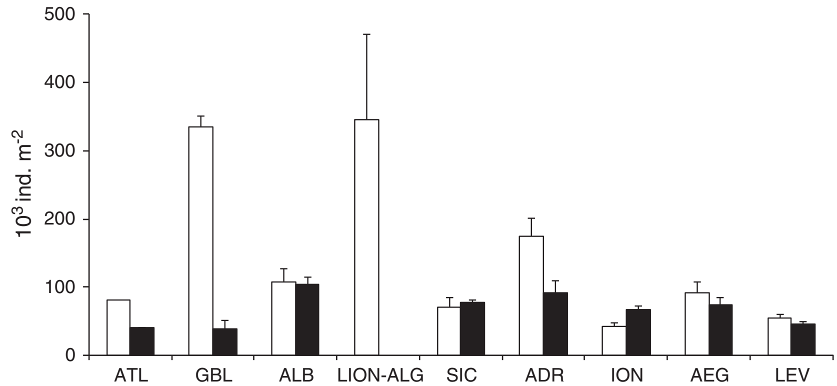

Fig. 6. Mesozooplankton abundance (10^3 ind. m^{-2}) integrated in the 0–200 m water column as regionally averaged values (±standard error) in spring (white) and autumn (black). Regional codes as in Fig. 2.

occurred with lower percentages than in spring, followed by cladocerans, appendicularians, ostracods and chaetognaths. Cladocerans were particularly important in the Alboran Sea (up to 45.1% at st. 14) and in the Aegean Sea (28.8% at st. 54), with the dominant species *P. avirostris* followed by *E. spinifera* and *Pseudoevadne tergestina*. A few groups showed a longitudinal gradient in their contribution to total mesozooplankton abundance (Table 2). Ostracods increased their share eastward, while the opposite pattern was presented by larger crustaceans (e.g., malacostracans) and by appendicularians (only in autumn). Gelatinous predators like cnidarians and ctenophors were slightly more important in the eastern regions in spring and more equally important over the whole Mediterranean in autumn.

Copepods were represented by at least 170 identified species. The bulk of most abundant species (Table 3) accounted for 93.0% and 91.9% of total copepod abundance in spring and autumn, respectively. In both seasons, the copepod assemblages were numerically dominated by small-sized (≤1 mm) individuals, namely juveniles (mainly copepodites CIII–CV) of Clausocalanidae (*Clausocalanus*+*Ctenocalanus* + *Pseudocalanus*, the latter genus occurring only in the Adriatic Sea) and of *Oithona*. Overall, the two groups contributed almost similarly in autumn (mean 17.8 ± 1.4% and 12.3 ± 0.8%, respectively), while the former prevailed over the latter in spring (23.2 ± 2.1% and 8.2 ± 0.5%, respectively). Clausocalanidae juveniles were relatively less important in the westernmost regions, while Oithonidae juveniles had quite similar contribution in all regions. In a rank order of relative abundance, a few species followed with more or less similar share in all regions and both seasons: *Oncaea* "*media* group" (*Oncaea media* + *Oncaea curta* +*Oncaea scottodicarloi* + *Oncaea waldemari*) females, *Paracalanus* spp. juv., *Paracalanus parvus* adults, *Oithona* (*Oithona atlantica* + *Oithona longispina* + *Oithona setigera*) females, *Corycaeus* spp. juv. (Table 3). A group of species had higher percentage contribution in spring than in autumn: *Clausocalanus pergens*, *Clausocalanus arcuicornis*, *Centropages typicus* and *Ctenocalanus vanus*. *C. pergens* was very important in the Gulf of Lion–Algerian Basin and its contribution in the Aegean Sea decreased from north to south. A different group of copepods prevailed in autumn: *Calocalanus* spp.,

Table 2
Spatially averaged percentage contribution of main groups (%) and total zooplankton abundance (10^3 ind. m^{-2}) in the 0–200 m water column, in each of the regions surveyed in the spring and autumn of 2008. The general average was calculated on data at the single stations. ATL, Atlantic; GBL, Strait of Gibraltar; ALB, Alboran Sea; LION–ALG, Gulf of Lion–Algerian Basin; SIC, Strait of Sicily; ADR, Adriatic Sea; ION, Ionian Sea; AEG, Aegean Sea; LEV, Levantine Sea.

	ATL	GBL	ALB	LION–ALG	SIC	ADR	ION	AEG	LEV	General average
Spring										
Copepods	91.88	91.28	75.29	94.37	83.59	84.23	85.35	84.72	82.49	84.42
Ostracods	0.00	0.36	1.73	0.52	1.62	2.34	3.02	2.64	3.21	2.12
Cladocerans	0.87	0.23	3.29	0.00	0.03	0.00	0.00	0.07	0.11	0.53
Malacostracans	0.58	4.86	1.78	1.56	1.50	2.55	0.99	1.13	1.04	1.59
Molluscs	0.00	0.36	1.15	0.16	1.08	0.50	0.87	0.84	0.85	0.77
Chaetognaths	1.45	0.61	1.45	0.17	1.62	0.68	1.67	4.96	3.88	1.92
Salps	0.00	0.00	0.46	0.76	1.43	0.07	1.09	0.32	0.26	0.63
Doliolids	0.29	0.00	3.06	0.00	0.20	1.56	1.27	0.43	1.99	1.14
Appendicularians	3.19	1.61	9.17	2.34	2.68	4.61	3.19	1.40	3.00	3.81
Jelly (Cnidarians + Ctenophores)	1.45	0.46	1.45	0.03	5.78	2.36	2.03	1.78	2.03	2.15
Polychaetes	0.00	0.04	0.63	0.08	0.37	0.54	1.10	0.46	0.50	0.55
Total zooplankton (10^3 ind. m^{-2})	80.72	334.18	107.92	346.28	70.65	175.03	42.77	91.55	54.26	123.36
Autumn										
Copepods	76.20	82.59	53.61		85.35	85.31	87.12	72.43	88.10	78.02
Ostracods	1.58	2.37	0.85		2.29	1.59	2.91	2.42	5.73	2.48
Cladocerans	1.62	2.02	25.92		1.16	0.73	1.08	8.90	1.25	6.46
Malacostracans	1.36	1.37	0.87		0.71	1.05	0.72	0.51	0.39	0.80
Molluscs	1.36	0.69	2.34		2.11	1.88	1.94	1.72	0.87	1.82
Chaetognaths	3.18	1.65	3.48		1.22	3.07	2.20	3.57	1.14	2.53
Salps	0.22	0.12	0.06		0.23	0.08	0.11	2.61	0.07	0.40
Doliolids	0.91	0.24	2.37		0.63	0.42	0.11	0.14	0.15	0.72
Appendicularians	9.73	4.82	7.54		4.96	2.67	1.74	3.95	0.63	4.03
Jelly (Cnidarians + Ctenophores)	3.17	1.64	1.73		0.83	1.68	1.40	1.99	0.98	1.56
Polychaetes	0.45	0.56	0.63		0.43	0.95	0.57	0.80	0.56	0.66
Total zooplankton (10^3 ind. m^{-2})	40.57	39.08	103.46		77.15	91.32	67.68	73.67	45.36	77.66

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Table 3
Spatially averaged percentage contribution (%) of species and genera to total copepod abundance (10^3 ind. m^{-2}) in each of the regions surveyed in the spring and autumn of 2008. Only taxa with a general contribution > 0.5% to total copepod abundance in at least one of the two seasons are reported here. For each species, the whole population (adult females and males, and copepodites) is considered, when not differently indicated. Legend: juv., copepodites; n.i., not identified at genus/species level; f. adult females; m. adult males; ad., adult females + males.

	Spring									Autumn							
	ATL	GBL	ALB	LION–ALG	SIC	ADR	ION	AEG	LEV	ATL	GBL	ALB	SIC	ADR	ION	AEG	LEV
Calanoida																	
Acartia spp.	1.9	6.6	0.4	0.4	0.5	0.1	0.3	0.2	0.1	3.2	5.0	1.2	1.1	2.9	2.7	0.6	1.1
Calanidae juv. n.i.	0.0	0.9	0.3	0.2	0.5	1.2	0.3	0.0	0.0	1.2	0.8	1.3	2.4	1.4	1.0	0.0	0.0
Calanoida juv. n.i.	3.7	2.2	2.6	0.1	1.1	13.7	0.5	2.7	2.6	0.0	1.2	0.3	0.4	4.3	0.8	1.4	0.4
Calanus helgolandicus	0.6	1.8	2.0	0.0	0.0	0.4	0.0	0.7	0.0	3.4	1.5	5.0	0.0	0.2	0.0	0.0	0.0
Calocalanus contractus f.	0.0	0.0	1.5	0.0	0.8	0.9	0.4	0.7	0.7	1.6	1.3	1.9	0.8	1.8	0.5	2.7	0.9
Calocalanus pavo f.	7.4	1.1	0.3	0.0	0.2	0.0	0.2	0.3	0.4	1.9	0.2	2.0	0.2	0.2	1.0	1.0	0.5
Calocalanus pavoninus f.	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.2	2.5	0.0	0.2	1.3	0.3	0.6	0.3	0.7
Calocalanus spp. n.i.	1.2	0.9	1.9	1.2	0.9	1.2	1.8	0.3	2.3	3.3	3.0	2.1	1.9	3.4	4.5	4.3	4.0
Calocalanus styliremis f.	0.0	1.1	0.6	0.7	0.5	1.5	0.7	1.0	2.0	2.3	1.1	1.9	0.5	2.4	0.7	0.1	0.6
Candacia spp. juv.	0.0	0.1	2.9	0.0	0.2	0.4	0.6	0.4	0.4	0.0	0.8	0.6	0.3	0.1	0.1	0.1	0.3
Centropages typicus	0.0	1.5	3.8	6.0	0.9	0.0	0.0	12.3	0.0	0.0	0.0	0.0	0.1	0.0	0.2	0.5	0.0
Clausocalanus arcuicornis f.	12.3	4.1	8.2	0.9	2.7	1.5	0.8	0.8	0.4	1.6	2.1	3.7	2.3	0.3	0.4	0.3	0.2
Clausocalanus furcatus f.	2.5	0.4	2.6	0.0	0.2	0.7	1.6	0.1	1.0	1.5	0.9	3.2	7.3	0.7	8.0	4.8	6.2
Clausocalanus jobei f.	0.6	0.4	0.1	0.2	0.7	1.2	0.4	1.1	0.6	0.3	0.0	0.1	0.4	0.3	0.1	0.2	0.5
Clausocalanus parapergens f.	0.0	1.1	0.2	0.3	0.8	1.1	1.0	1.3	0.7	0.1	0.5	0.0	0.2	1.2	0.3	0.1	0.2
Clausocalanus paululus f.	0.0	0.0	0.8	2.3	3.8	5.7	6.8	0.9	3.2	0.0	1.6	0.1	2.9	2.9	1.2	0.3	4.4
Clausocalanus pergens f.	0.0	0.0	1.4	16.5	3.6	4.2	1.1	1.9	0.1	0.0	0.0	0.4	2.4	2.0	0.4	1.4	0.1
Clausocalanus spp. m.	5.6	1.1	1.0	4.6	2.4	1.1	1.0	1.2	0.5	0.0	0.4	0.5	2.5	1.8	2.2	1.4	1.2
Clausocalanus + *Ctenocalanus* + *Pseudocalanus* juv.	8.6	11.7	13.6	43.5	30.8	16.6	30.7	15.0	17.0	6.5	7.9	7.7	29.6	22.4	24.0	12.3	19.7
Ctenocalanus vanus ad.	0.6	0.9	0.5	0.9	3.2	2.3	0.8	3.8	1.1	0.0	0.0	0.3	0.7	0.5	0.3	0.6	0.3
Euchaetidae juv.	0.0	0.0	0.2	0.1	1.3	2.2	1.5	1.1	0.4	0.3	0.0	0.0	0.2	1.4	0.5	0.5	0.2
Haloptilus longicornis	0.0	0.0	0.3	0.0	1.6	0.9	6.0	1.6	3.6	1.2	1.2	0.0	0.5	2.0	4.9	10.9	10.1
Lucicutia flavicornis ad.	1.2	1.8	2.1	0.0	0.4	0.4	1.2	0.9	1.9	3.6	1.6	0.0	0.1	0.4	0.6	0.6	1.3
Lucicutia spp. juv.	0.0	0.0	0.1	0.0	0.8	1.4	2.0	2.0	2.6	1.0	2.1	0.0	0.5	2.2	1.8	3.0	2.9
Mecynocera clausi	5.6	0.9	0.3	0.0	0.9	0.6	2.3	1.3	2.2	4.1	2.6	2.9	0.5	3.2	3.2	3.0	4.1
Mesocalanus tenuicornis	1.9	0.0	0.2	0.0	0.2	0.1	0.2	1.6	1.0	2.2	0.5	0.1	0.4	0.0	0.6	2.1	0.5
Nannocalanus minor	0.6	0.6	0.7	0.0	0.5	0.1	0.4	0.3	0.5	0.7	0.7	1.0	3.0	1.5	0.8	0.8	0.3
Paracalanus denudatus ad.	0.0	0.0	0.0	0.0	0.1	1.1	1.6	0.7	3.0	1.8	0.0	0.0	0.1	0.1	0.5	0.3	2.3
Paracalanus nanus ad.	0.0	1.5	0.7	0.3	1.1	0.7	0.3	0.7	1.0	0.3	0.0	0.1	0.2	0.2	0.3	0.1	0.6
Paracalanus parvus ad.	1.2	15.0	8.7	2.4	0.1	0.4	0.0	0.1	0.2	4.2	5.0	5.5	0.1	0.3	0.3	4.2	0.0
Paracalanus spp. juv.	1.9	9.5	8.0	3.6	0.4	2.5	0.4	0.2	0.9	2.9	2.3	5.5	0.3	2.1	0.5	1.2	0.7
Pleuromamma gracilis	0.0	0.0	0.7	0.1	0.1	0.3	1.9	1.5	1.1	0.3	0.3	0.5	0.1	0.1	0.3	0.3	0.1
Pleuromamma spp. juv	3.1	0.0	2.5	0.2	2.7	3.2	1.8	1.1	3.3	0.0	0.0	0.0	2.4	1.1	1.3	0.4	2.2
Temora stylifera	0.0	2.5	2.8	0.0	0.0	0.0	0.0	0.9	0.5	0.3	0.5	2.3	0.2	1.1	3.2	3.5	1.5
Cyclopoida																	
Oithona atlantica + *O. longispina* + *O. setigera* f.	1.2	1.5	0.8	0.2	3.0	1.1	2.1	5.1	4.6	2.5	1.5	2.8	2.8	1.9	2.0	1.8	2.8
Oithona plumifera f.	0.0	0.7	0.1	0.0	0.4	0.8	0.1	0.4	1.1	4.9	2.5	1.5	2.2	0.8	1.6	1.1	1.1
Oithona similis f.	0.0	0.0	0.3	5.0	4.5	1.8	0.3	3.3	0.2	0.0	0.0	0.0	1.9	1.6	0.2	0.2	0.2
Oithona tenuis f.	0.0	0.0	0.0	0.0	0.1	0.0	0.0	0.1	0.2	2.9	0.0	1.5	0.4	0.0	0.1	0.0	0.5
Oithona spp. juv.	13.0	5.3	7.6	6.2	7.0	10.5	6.1	11.3	10.3	13.2	15.3	13.9	9.9	16.1	9.5	14.4	8.0
Corycaeus (*Agetus flaccus* + *A. limbatus* + *A. typicus*) ad.	0.0	0.0	0.0	0.1	0.8	0.6	1.7	0.6	1.0	0.6	0.2	0.3	0.6	0.3	1.1	0.8	0.5
Corycaeus spp. juv.	3.1	1.4	2.1	0.2	1.8	1.7	2.7	1.3	3.2	2.1	2.5	1.0	1.5	1.5	2.6	1.4	3.6
Farranula spp.	0.0	1.0	0.2	0.0	1.2	0.7	4.6	3.4	5.0	1.8	1.4	0.8	2.3	1.0	2.6	3.4	1.8
Oncaea curta + *O. media* + *O. scottodicarloi* + *O. waldemari* f.	8.6	10.7	7.0	0.6	6.8	5.8	2.0	5.0	4.9	4.0	10.6	8.3	2.4	2.0	1.5	2.3	2.5
Oncaea mediterranea f.	1.2	5.1	2.1	0.0	0.5	0.4	0.6	0.8	0.7	0.0	0.5	1.4	0.4	0.2	0.3	0.7	0.7
Oncaeidae n.i.	0.0	0.0	0.4	0.3	2.1	1.6	2.4	2.6	2.6	5.4	11.4	7.4	2.1	1.2	1.7	2.7	2.4
Mormonilloida																	
Mormonillidae	0.0	0.0	0.2	0.1	1.1	1.0	0.7	0.3	0.7	0.0	0.0	0.0	0.9	1.9	0.9	0.6	0.9
Total copepods (10^3 ind. m^{-2})	80.7	334.2	107.9	346.3	70.7	175.0	42.8	91.6	54.3	30.9	32.8	55.3	65.7	76.8	58.7	50.7	39.9

Clausocalanus furcatus, *Mecynocera clausi* and *Temora stylifera*. In the spatial scale, *P. parvus*, *Calanus helgolandicus*, oncaeids, *C. pergens* and *C. arcuicornis* were more important in the western regions and in the Aegean Sea. *Clausocalanus paululus*, *C. furcatus*, *Haloptilus longicornis*, *Lucicutia* spp. (in spring), *Pleuromamma* spp. (in autumn), *Corycaeus* spp., and *Farranula* spp. contributed more in the eastern regions.

3.4. Self-organizing maps (SOM) and cluster analysis

The SOM non-linear ordination analysis returned a map of 5 × 7 units for the spring dataset (Fig. 7) and a map of 4 × 9 units for the autumn dataset (Fig. 8). A partitioning in 5 clusters was identified in each of the two seasonal datasets, based on the levels of diversity between clusters in the spring and autumn dendrograms and on visual inspection of clusters on the spring and autumn maps. In both maps, stations from the same region were projected on the same map unit or on neighboring map units, with few exceptions as mentioned below.

3.4.1. Spring

The first partition of map units of the spring SOM was broadly between eastern and western Mediterranean regions (Fig. 7). Stations from the western Mediterranean Sea (Strait of Gibraltar, Alboran Sea and Gulf of Lion–Algerian Basin) and the Atlantic were projected along the bottom border and the left side of the map, while stations

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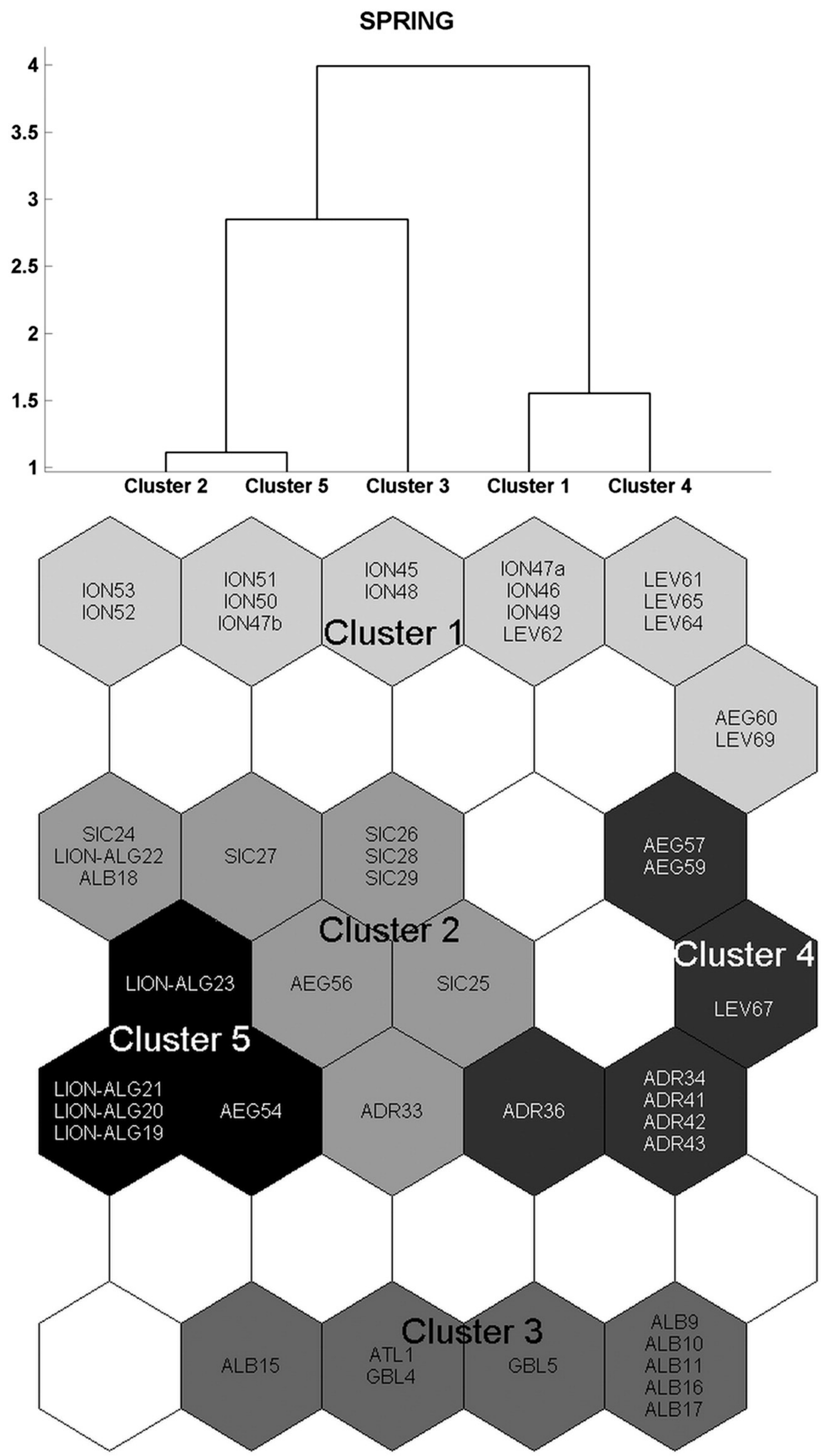

Fig. 7. Results of the Self-Organizing Map (SOM) and cluster analysis for the zooplankton spring survey in the Mediterranean Sea. Upper panel: dendrogram on map units. Lower panel: ordination of samples (0–200 m integrated data) on the SOM. Each sample is indicated by the area code and the station number (see Table 1). Clusters are shown with white/gray shades and corresponding numbers. Empty units in the map indicate major discontinuities in the dataset.

from the eastern Mediterranean Sea were clustered along the upper border and on the right side of the map. The Strait of Sicily stations were placed on the map in a more central position. The western stations appeared more heterogeneously distributed; they were distributed among Cluster 3, grouping samples from the Alboran Sea, the Strait of Gibraltar and the Atlantic, and the more similar Cluster 2 and Cluster 5. In Cluster 2, positioned in the central part of the map, all stations from the Strait of Sicily were included along with the easternmost station of the Alboran Sea (st. 18), station 22 of the Algerian Basin, station 33 of the central Adriatic and station 56 of the North Aegean Sea. Cluster 5 included most stations of the Gulf of Lion–Algerian Basin and the northernmost station of the Aegean Sea. The stations of the eastern regions were more homogenously grouped between Cluster 1 and Cluster 4: Cluster 1 grouped all Ionian

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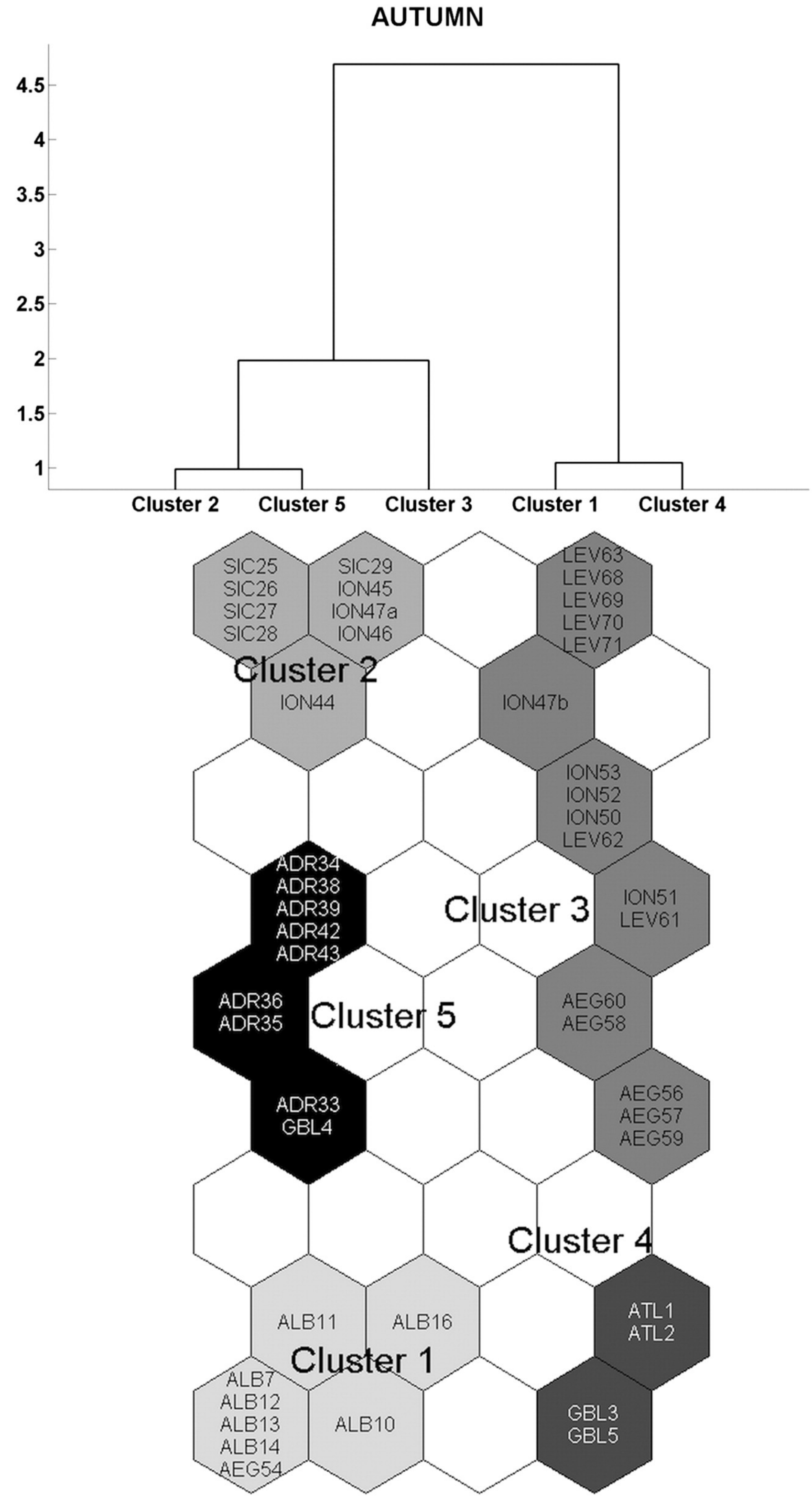

Fig. 8. Results of the Self-Organizing Map (SOM) and cluster analysis for the zooplankton autumn survey in the Mediterranean Sea. Upper panel: dendrogram on map units. Lower panel: ordination of samples (0–200 m integrated data) on the SOM. Each sample is indicated by the area code and the station number (see Table 1). Clusters are shown with white/gray shades and corresponding numbers. Empty units in the map indicate major discontinuities in the dataset.

stations, the majority of Levantine stations and st. 60 in south Aegean Sea; Cluster 4 grouped all south Adriatic stations along with st. 57 and st. 59 in the south Aegean Sea and st. 67 in the Levantine Sea.

The five clusters differed in the number of characteristic species and their IndVal values (Table 4). A small number of copepod species characterized Cluster 1, with low and quite similar IndVal values, and among them, the most abundant species were *Farranula* spp. and *H. longicornis*. Cluster 2 was characterized by the cyclopoid *Oithona decipiens* with the highest IndVal, and three species (*Triconia umerus*, *Heterorhabdus papilliger*, *Microsetella* spp.) that were recorded with

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Table 4
Zooplankton taxa that characterize the five spring clusters identified by the SOM analysis. The values of Indicator Value Index (IndVal) are reported together with relative abundance (Specificity, A_{jk}), relative frequency (Fidelity, B_{jk}) and average abundance (10^3 ind. m^{-2}) for the characterizing taxa in each cluster. For each taxon, the whole population (adult females and males, and copepodites) is considered, when not differently indicated. Legend: juv., copepodites; n.i., not identified at lower taxonomic level; f. adult females; m. adult males; ad., adult females + males.

Cluster	Taxa	IndVal	A_{jk}	B_{jk}	Avg 10^3 ind. m^{-2}
1	*Pareucalanus* spp. ad.	47.18	0.94	0.50	0.07
	Candacia bispinosa ad.	43.96	0.64	0.69	0.07
	Clausocalanus mastigophorus f.	43.29	0.46	0.94	0.21
	Haloptilus longicornis	40.47	0.40	1.00	1.73
	Farranula spp.	40.08	0.40	1.00	2.01
2	*Oithona decipiens* f.	65.20	0.82	0.80	0.03
	Triconia umerus f.	48.26	0.60	0.80	0.11
	Heterorhabdus papilliger	48.02	0.53	0.90	0.11
	Microsetella spp.	37.27	0.41	0.90	0.07
3	Cladocerans	85.89	0.97	0.89	3.33
	Clausocalanus arcuicornis f.	66.03	0.66	1.00	9.25
	Calanus helgolandicus	59.78	0.67	0.89	2.81
	Temora stylifera	58.70	0.88	0.67	3.18
	Paracalanus parvus	53.85	0.54	1.00	15.64
	Lucicutia flavicornis ad.	53.56	0.60	0.89	2.43
	Crustacean eggs and larvae n.i.	51.03	0.66	0.78	1.90
	Acartia clausi	46.86	0.84	0.56	2.68
	Oncaea curta + *O. media* + *O. scottodicarloi* + *O. waldemari* f.	46.18	0.52	0.89	11.75
	Euterpina acutifrons	43.21	0.97	0.44	0.61
	Calocalanus tenuis f.	37.29	0.84	0.44	0.91
4	*Triconia dentipes* f.	84.40	0.96	0.88	0.82
	Calanoida juv. n.i.	79.05	0.79	1.00	17.39
	Paracalanus denudatus ad.	62.37	0.62	1.00	1.51
	Echinoderm larvae	61.61	0.62	1.00	0.62
	Paracalanus aculeatus f.	60.99	0.98	0.63	0.40
	Lubbockia spp.	60.79	0.61	1.00	0.08
	Scaphocalanus spp.	57.74	0.58	1.00	0.75
	Siphonophores	57.64	0.58	1.00	3.02
	Haloptilus spp. juv.	56.45	0.75	0.75	0.55
	Lucicutia spp. juv.	51.90	0.52	1.00	2.06
	Pleuromamma spp. juv.	51.64	0.52	1.00	4.19
	Corycaeus (*Ditrichocorycaeus* + *Onychocorycaeus*) spp. ad.	51.55	0.59	0.88	0.58
	Tomopteris spp.	48.75	0.65	0.75	0.17
	Lucicutia gemina ad.	48.58	0.49	1.00	0.61
	Clausocalanus paululus f.	48.21	0.48	1.00	6.76
	Mormonilla spp.	47.81	0.64	0.75	1.21
	Calocalanus ovalis f.	47.58	0.95	0.50	0.08
	Calocalanus pavoninus f.	47.46	0.63	0.75	0.10
	Ostracods	47.25	0.47	1.00	4.29
	Haloptilus acutifrons	46.63	0.75	0.63	0.06
	Larvae n.i.	45.75	0.73	0.63	0.19
	Corycaeus (*Agetus flaccus* + *A. limbatus* + *A. typicus*) ad.	45.48	0.45	1.00	0.83
	Corycaeus (*Urocorycaeus*) *furcifer* ad.	45.24	0.45	1.00	0.55
	Euchaetidae juv.	45.16	0.45	1.00	1.64
	Clausocalanus jobei f.	44.86	0.45	1.00	1.19
	Oncaeidae n.i.	43.78	0.44	1.00	2.32
	Calocalanus plumulosus f.	41.77	0.67	0.63	0.24
	Polychaete larvae	41.02	0.41	1.00	0.73
	Temora longicornis	37.50	1.00	0.38	0.10
	Chaetognaths	35.44	0.35	1.00	2.51
	Lucicutia clausi ad.	34.66	0.55	0.63	0.05
	Anomalocera patersoni	25.00	1.00	0.25	0.01
	Euchaeta spinosa ad.	25.00	1.00	0.25	0.04
5	*Clausocalanus pergens* f.	84.53	0.85	1.00	52.93
	Oithona similis f.	80.94	0.81	1.00	19.33
	Centropages typicus	79.22	0.79	1.00	28.07
	Clausocalanus spp. m.	75.56	0.76	1.00	15.58
	Clausocalanus + *Ctenocalanus* + *Pseudocalanus* juv.	66.46	0.66	1.00	137.34
	Calocalanus plumatus f.	63.77	0.80	0.80	1.97
	Euchirella spp.	61.76	0.77	0.80	0.11
	Paracalanus spp. juv.	56.04	0.56	1.00	18.90
	Decapod larvae	55.93	0.56	1.00	2.95
	Oithona spp. m. + juv.	42.21	0.42	1.00	21.17
	Calocalanus spp. n.i.	41.81	0.42	1.00	3.16

low abundance but very high frequency. Cluster 3 was characterized by eleven taxa; among them, cladocerans had the highest IndVal value, followed by several species of abundant copepods, such as the calanoids *C. arcuicornis*, *C. helgolandicus*, *T. stylifera*, *P. parvus* and the cyclopoid *Oncaea* "*media* group". Cluster 4 had the largest number of characterizing taxa (33), which included not only copepods but also other groups like echinoderm larvae, siphonophores, polychaetes, ostracods and chaetognaths. Many of them showed low specificity but high fidelity values (Table 4). Cluster 5 was characterized by eleven taxa, and among them *C. pergens*, *Oithona similis*, *C. typicus*, juveniles and males of *Clausocalanus* had the highest IndVal values.

3.4.2. Autumn

Similarly to what was observed in spring, the main partition of the map was between the western and the eastern regions (Fig. 8). However, since the Gulf of Lion–Algerian Basin was not surveyed in autumn, the only western stations were those located in the Alboran Sea, the Strait of Gibraltar and Atlantic, all positioned on the lower part of the map, but in opposite sides. In the lower part of the map we found: on the left, Cluster 1 grouping all Alboran stations with the northernmost Aegean station (st. 54); on the right, Cluster 4 grouping together the Atlantic and Gibraltar stations. The central and upper parts of the map were partitioned in: Cluster 3, grouping all the Levantine and eastern Ionian stations with the majority of the Aegean Sea stations; Cluster 2 with all stations of the Strait of Sicily and central Ionian Sea; Cluster 5 with all south Adriatic stations and one of the Gibraltar Strait. It is noticeable that the samples collected twice at station 47 in the central Ionian Sea, at 3-weeks distance, were not clustered together: the sample collected in September (st. 47a) was positioned in Cluster 2, while the sample collected in late August (st. 47b) was included in Cluster 3. There was an increase, from August to September, in the abundance of appendicularians and adult females of *Oithona plumifera* and *Oithona atlantica* + *Oithona longispina* + *Oithona setigera*, accompanied by a decrease of *Oithona* juveniles.

The autumn zooplankton of the Alboran Sea and the north Aegean Sea (Cluster 1) were strongly characterized by the presence of cladocerans with the highest IndVal, followed by the copepods *P. parvus* and *C. helgolandicus*, and by bivalve larvae (Table 5). Cluster 2 was characterized by numerous taxa (22), but most of those with highest IndVal values had low abundance associated with high relative frequency, like the copepods *T. umerus* and *Calocalanus plumatus*, and ctenophores. *C. furcatus* and Clausocalanidae juveniles presented the highest abundances and high fidelity values in this cluster. Among the six species characterizing Cluster 3, *H. longicornis* had the highest IndVal value and highest abundance, followed by *Lubbockia* spp., *Lucicutia gemina*, *Paracalanus denudatus*, *Calocalanus plumulosus* and *Clausocalanus mastigophorus*, all with lower IndVal but generally high fidelity. Stations grouped in Cluster 4 were characterized by *Microsetella* spp., *Acartia longiremis* and *Lucicutia flavicornis*. Among the numerous taxa characterizing Cluster 5, i.e. 22 copepod species and isopods, *Triconia dentipes* and *Clausocalanus parapergens* were the two most important, though with low abundance.

4. Discussion

4.1. Seasonality

The results acquired from the SESAME coordinated cruises conducted in 2008 over an extensive area of the Mediterranean Sea highlighted a clear seasonal signature in the offshore mesozooplankton, both in standing stock and community composition and structure. Differences between the spring and autumn periods likely derived from a combination of ultimate (the biological cycles of populations) and proximate (changes in water column characteristics) factors. In both

Table 5
Zooplankton taxa that characterize the five autumn clusters identified by the SOM analysis. The values of Indicator Value Index (IndVal) are reported together with relative abundance (Specificity, A_{jk}), relative frequency (Fidelity, B_{jk}), and average abundance (10^3 ind. m^{-2}) for the characterizing taxa in each cluster. For each taxon, the whole population (adult females and males, and copepodites) is considered, when not differently indicated. Legend: juv., copepodites; n.i., not identified at lower taxonomic level; f., adult females; m., adult males; ad., adult females + males.

Cluster	Taxa	IndVal	A_{jk}	B_{jk}	Avg 10^3 ind. m^{-2}
1	Cladocerans	87.32	0.87	1.00	29.03
	Paracalanus parvus ad.	65.17	0.65	1.00	4.62
	Calanus helgolandicus	62.46	0.62	1.00	1.72
	Bivalve larvae	61.18	0.61	1.00	0.44
	Doliolids	57.91	0.66	0.88	2.22
	Paracalanus spp. juv.	48.91	0.49	1.00	2.81
	Appendicularians	42.75	0.43	1.00	7.04
	Oncaea venusta f.	42.17	0.67	0.63	0.49
	Chaetognaths	37.14	0.37	1.00	3.72
	Oithona nana f.	25.00	1.00	0.25	0.31
2	*Triconia umerus* f.	100.00	1.00	1.00	0.30
	Calocalanus plumatus f.	83.35	0.83	1.00	0.67
	Ctenophores	63.73	0.64	1.00	0.14
	Oithona vivida f.	55.56	1.00	0.56	0.03
	Scolecithricidae juv.	53.72	0.54	1.00	0.33
	Tomopteris spp.	51.07	0.66	0.78	0.03
	Pleuromamma spp. juv.	50.18	0.50	1.00	1.50
	Acartia negligens	48.60	0.49	1.00	0.72
	Calanidae juv. n.i.	46.03	0.46	1.00	1.54
	Siphonostomatoida	44.79	0.67	0.67	0.04
	Clausocalanus spp. m.	44.34	0.44	1.00	1.74
	Chiridius poppei ad.	43.50	0.98	0.44	0.02
	Clausocalanus furcatus f.	42.44	0.42	1.00	4.52
	Paracalanus nanus ad.	41.49	0.41	1.00	0.24
	Corycaeus (*Urocorycaeus*) *furcifer* ad.	41.07	0.41	1.00	0.51
	Scolecithrix bradyi ad.	40.54	0.52	0.78	0.08
	Clausocalanus + *Ctenocalanus* + *Pseudocalanus* juv.	39.12	0.39	1.00	18.45
	Heterorhabdus papilliger ad.	38.90	0.44	0.89	0.05
	Corycaeus (*Ditrichocorycaeus*+*Onychocorycaeus*) spp. ad.	37.69	0.38	1.00	0.35
	Oithona decipiens f.	37.18	0.48	0.78	0.12
	Farranula spp.	35.83	0.36	1.00	1.61
	Scolecithricella vittata ad.	34.72	0.78	0.44	0.01
	Euchirella spp.	34.22	0.77	0.44	0.02
	Triconia minuta f.	33.33	1.00	0.33	0.04
3	*Haloptilus longicornis*	60.90	0.61	1.00	4.58
	Lubbockia spp.	50.46	0.54	0.94	0.05
	Lucicutia gemina ad.	50.45	0.50	1.00	0.41
	Paracalanus denudatus ad.	49.52	0.56	0.88	0.54
	Calocalanus plumulosus f.	48.94	0.49	1.00	0.29
	Clausocalanus mastigophorus f.	46.96	0.67	0.71	0.17
4	*Microsetella* spp.	62.37	0.62	1.00	0.29
	Acartia longiremis	61.47	0.82	0.75	0.26
	Lucicutia flavicornis ad.	46.36	0.46	1.00	0.78
5	*Triconia dentipes* f.	86.71	0.98	0.89	0.46
	Clausocalanus parapergens f.	76.44	0.76	1.00	0.89
	Calanoida juv. n.i.	75.64	0.76	1.00	3.00
	Calocalanus ovalis f.	66.67	1.00	0.67	0.12
	Euchaetidae juv.	62.81	0.71	0.89	1.03
	Acartia juv. n.i.	57.24	0.57	1.00	1.54
	Clausocalanus lividus f.	56.67	0.85	0.67	0.13
	Calocalanus equicauda f.	55.56	1.00	0.56	0.06
	Isopods	54.88	0.82	0.67	0.04
	Calocalanus neptunus f.	52.13	0.78	0.67	0.27
	Euchaeta marina ad.	50.89	0.92	0.56	0.06
	Oithona similis f.	49.12	0.55	0.89	1.07
	Aetideidae juv.	49.04	0.55	0.89	0.06
	Mormonillidae	46.72	0.53	0.89	1.19
	Clausocalanus paululus f.	46.46	0.46	1.00	2.19
	Vettoria spp.	46.41	0.52	0.89	0.18
	Paracalanus aculeatus f.	44.44	1.00	0.44	0.06
	Scolecithricella ovata f.	44.44	1.00	0.44	0.03
	Haloptilus spp. juv.	41.53	0.53	0.78	0.21
	Haloptilus ornatus	33.33	1.00	0.33	0.01
	Lucicutia ovalis ad.	33.33	1.00	0.33	0.01
	Pareuchaeta hebes ad.	33.26	0.75	0.44	0.04
	Oithona spp. m. + juv.	29.88	0.30	1.00	9.91

seasons, the distribution of epipelagic mesozooplankton reflected the trophic conditions of the basins.

In spring, spots of high standing stock were recorded in regions of increased chl*a* concentration. The relationship between mesozooplankton and chl *a* was very evident in the Gulf of Lion–Algerian Basin where stations 19, 20, 21 were characterized by an intense phytoplankton bloom and the highest biomass values, while station 22 located nearby but out of the bloom revealed low biomass. Mesozooplankton seemed to respond to the availability of potential autotrophic food also in other regions with relatively high chl *a* concentration, but without coherent spatial patterns between biomass and abundance. For example, the high biomass at station 23 in the Algerian Basin was due to the occurrence of salps and large crustaceans but it did not correspond to high total abundance; the opposite was observed in the Strait of Gibraltar, where numerous small copepods (*Acartia*, *Clausocalanus*, *Paracalanus*, *Oithona*, *Oncae*a) were responsible of high abundance but low biomass.

The high mesozooplankton standing stock recorded in spring in the Gulf of Lion was likely a response to the local upwelling that typically fuels the increase of autotrophic biomass in the region (Estrada et al., 1985) and was visible from the satellite images also during our cruise. A recent review of phytoplankton distribution in the open Mediterranean confirmed the existence of a regular large bloom in late winter–spring exclusively in the north-western basin (Siokou-Frangou et al., 2010). High and very similar mesozooplankton biomass values were measured in the epipelagic layer and with the same meshed net in the Gulf of Lion in the spring of 1998 (Gaudy et al., 2003) and in the north Balearic Sea in March–April 2003 (2.6–3.6 g DM m^{-2}, Mazzocchi unpublished data). The intense late winter–spring phytoplankton bloom is reported to last in the area more than three months (Bosc et al., 2004). In 2008 it had apparently disappeared in early summer, leaving only weak traces in metazooplankton abundance during the BOUM cruise (Nowaczyk et al., 2011, their Figs. 1a, 2a). This local mesozooplankton richness appears therefore to be a typical spring and recurrent feature in the region, as a response of the whole trophic web to the phytoplankton bloom generated by deep winter convection (Lévy et al., 1998). The unexpectedly low biomass we recorded in the Alboran Sea compared to previous studies (Seguin et al., 1994; Thibault et al., 1994) might be due to the complex hydrology of the area (Allain, 1960; Millot, 1987), where mesozooplankton features appear highly variable even at short spatial scale (Youssara and Gaudy, 2001). The Adriatic Sea had higher mesozooplankton abundance than the Aegean Sea but lower biomass because in the latter region larger animals were more numerous (e.g., *C. helgolandicus*, *Mesocalanus tenuicornis*, Eucalanidae, *Pleuromamma spp.*). In autumn, the whole Mediterranean appeared more oligotrophic and uniform, and, consequently, mesozooplankton standing stock was lower than in spring and more equally distributed among regions.

In terms of composition, mesozooplankton communities were characterized, in both seasons, by high taxonomic diversity and by the dominance of small-sized copepods, i.e., the calanoids Clausocalanidae and Paracalanidae, and the cyclopoids Oithonidae and Oncaeidae. The same copepods dominated also the smaller size-fraction of metazooplankton in early summer of the same year (Nowaczyk et al., 2011). These basic features of zooplankton composition, which are also reported in other periods of the year and persist through regions and decades (Siokou-Frangou et al., 2010), together with the seasonal cycle of primary production and consumption make the Mediterranean closely resembling the subtropical Atlantic (Longhurst, 1998). Superimposed to this common background, we observed seasonal differences determined by the occurrence of copepod species conspicuous either in spring or in autumn. The seasonal partitioning is also supported by the results of previous studies conducted in the Gulf of Lion (Gaudy et al., 2003), Ligurian Sea (Andersen et al., 2001), Tyrrhenian Sea (Scotto di Carlo et al., 1984), Adriatic Sea (Hure et al., 1980), Ionian Sea (Mazzocchi et al., 2003; Ramfos et al., 2006), Aegean Sea (Siokou-

Frangou et al., 2004). Therefore, the seasonal occurrence of these copepods seems to be a robust characteristic of their annual cycle in the Mediterranean, as also shown by long-term time-series in neritic waters (Fernandez de Puelles et al., 2007, 2009; Mazzocchi et al., 2007, 2012). As an example, our data confirm that a seasonal succession among the numerous congeneric species of the abundant *Clausocalanus* occurs also in the offshore waters. The time course and spatial distribution of their populations in the open Mediterranean Sea (Fragopoulu et al., 2001; Peralba and Mazzocchi, 2004) and in the Atlantic Ocean along a latitudinal gradient (Peralba, 2008) indicate that the ranges of temperature and chl *a* under which these common congeners can persist largely overlap, but their population flourish and peak under clearly different conditions therefore suggesting differentiation in their ecological niches (Peralba et al., 2010).

4.2. Spatial distribution and regionalization

Our results did not reveal, either in spring or in autumn, the west–east decrease of zooplankton standing stock reported by previous studies (Dolan et al., 2002; Siokou-Frangou, 2004), although a north–south and west–east decrease was visible in the spring distribution of autotrophic biomass from the satellite images. During the summer of the same year, Nowaczyk et al. (2011) observed a longitudinal gradient in metazooplankton abundance but not in biomass. Even in the Aegean Sea, we did not record the strong north–south pattern in zooplankton biomass as reported in previous years (Siokou-Frangou et al., 1990, 2004). However, the SOM identified a broad separation between the eastern and western Mediterranean basins, both in spring and autumn, indicating a persistent differentiation between them based on mesozooplankton community composition and structure. A further successive separation emerged at regional level; in fact, a clear geographical continuity appeared among most stations grouped in the SOM clusters, in both seasons.

The results of the SOM showed that the spatial distribution of zooplankton was not significantly affected by the sampling time. This is indicated, for example, by the presence in the same map unit of both stations visited in day and night hours, or stations visited in the same day 12 h apart (e.g., sts 10 and 11 in the Alboran Sea in spring). It has been recently demonstrated that copepod vertical distribution in the Mediterranean was strongly dependent on the depth but only to a lesser extent on the time of sampling (Brugnano et al., 2012). According to Brugnano et al. (2012), the bulk of Mediterranean copepods occurring in the 2000 m water column was concentrated in the upper 200 m (>97%) during the 24 h, with only a minor difference between midday (98.6%) and midnight (99.4%). We cannot exclude the occurrence of diel vertical migration during our study. However, numerous surveys in various Mediterranean regions did not found significant day/night variations in epipelagic mesozooplankton that could be ascribed to diel vertical migrations (Ramfos et al., 2006; Siokou-Frangou et al., 1997; Weikert and Koppelmann, 1993; Weikert and Trinkhaus, 1990). This feature is attributed to the poor occurrence of strong diel migrant species in the Mediterranean Sea (e.g., Brugnano et al., 2012; Scotto di Carlo et al., 1984). The clustering highlighted by our results does therefore reflect the principal characteristics of mesozooplankton spatial distribution in the epipelagic Mediterranean Sea.

Despite the mesozooplankton dynamics develops on longer timescales than those of phytoplankton, a notable correspondence emerged between the clusters identified by SOM and the classes of trophic regimes obtained by D'Ortenzio and Ribera d'Alcalà (2009) based on spatial and temporal distribution of satellite-derived chl *a*. In spring, mesozooplankton reflected closely the environmental heterogeneity in terms of trophic conditions. The Ionian and Levantine seas (and st. 60 in the south Aegean Sea), which were grouped together (Cluster 1), presented the lowest chl *a* concentration during our cruises and were included in "non-blooming" regimes by D'Ortenzio and Ribera d'Alcalà (2009) (classes 1 and 2 in their Fig. 4). In these areas, *C. paululus*, *Lucicutia spp*., *Pleuromamma spp*., *H. longicornis* and *Farranula* spp. were abundant, with the latter two copepods characterizing the cluster. All the above mentioned species were also found in high relative abundance in the south Adriatic and south Aegean seas (cluster 4), areas that had slightly higher chl *a* concentration in spring 2008, but still belong to "non-blooming" areas (D'Ortenzio and Ribera d'Alcalà, 2009). Though positioned in the "intermittently-blooming" South Adriatic Gyre, station 36 was included in Cluster 4 but in a different cell. The structure of mesozooplankton communities seems therefore to differentiate, within the same region, between areas with different hydrological dynamics. A classical food web was assumed to prevail in the north-western Ionian Sea in the spring of 1999 (Mazzocchi et al., 2003) and a multivorous food web in the south Aegean Sea in the spring of 1997 (Siokou-Frangou et al., 2002). However, given the general dominance of picoautotrophs in the basin (reviewed by Siokou-Frangou et al., 2010) and the low ciliates biomass values apparently due to strong zooplankton grazing control (Dolan et al., 2002; Pitta et al., 2001), the above copepods should be closely linked to the microbial food web for their carbon requirements.

The stations from the Strait of Sicily were grouped together (Cluster 2) with four stations positioned in areas distant but with common features in species composition. It seems therefore that this cluster includes stations with mix features: the Strait of Sicily linking the western and eastern basins, as well as stations positioned in transition zones between regions (e.g., st. 18 between Alboran Sea and Algerian Basin) or within a region presenting gradual differentiation in environmental conditions (e.g., st. 33 in the Adriatic Sea and st. 56 in the Aegean Sea). These areas were defined as "non-blooming" class 3 by D'Ortenzio and Ribera d'Alcalà (2009). Close to this cluster, there was the group (Cluster 5) including most stations of the Gulf of Lion, st. 23 in the Algerian Basin, and the northernmost station of the Aegean Sea. The Gulf of Lion presented higher chl *a* concentration than the other regions in the spring of 2008; it is the area where the analysis of time series of satellite images indicated the occurrence of the most intense phytoplankton bloom characteristic of the western Mediterranean (D'Ortenzio and Ribera d'Alcalà, 2009). The distant st. 23 located south of Sardinia (Tyrrhenian Sea) and the northernmost station of the Aegean Sea are positioned in areas with high phytoplankton standing stock (chl *a* maps of the present study) and both areas were classified as "intermittently-blooming". Characteristic species of this cluster was the copepod *C. pergens* that is abundant in chl *a* rich environments (Peralba, 2008), *O. similis* that was encountered in high numbers in eutrophic areas of the open Atlantic Ocean (Castellani et al., 2005) and *C. typicus* that occurred in relation to spring phytoplankton blooms in the North Atlantic Ocean (Beaugrand et al., 2007). *C. typicus* is an abundant spring coastal species (Mazzocchi et al., 2007) that is found in the open Mediterranean during its peak season (Andersen et al., 2001; Gaudy et al., 2003; Hure et al., 1980; Siokou-Frangou et al., 2004); it was reported as relatively abundant in the Balearic Sea from spring until early summer in relation to upwelling waters (Fernandez de Puelles et al., 2009). *C. typicus* shows a low tolerance to starvation in comparison with other copepods, and its distribution does likely reflect the need to rely on long-lasting food supply (Calbet et al., 2007).

Finally, very distinct from all the other areas, the Atlantic stations and the westernmost Mediterranean (Gibraltar Strait and Alboran Sea) were included in a separate cluster (Cluster 3). The standing stock distribution and the mesozooplankton composition reflected the great spatial variability of the environment of these regions, as revealed in the chl *a* distribution maps of the present study and by the classification of the Alboran Sea as "intermittently-blooming" area (D'Ortenzio and Ribera d'Alcalà, 2009). These areas were distinguished because of the occurrence of cladocerans and copepod species (e.g., *C. arcuicornis*, *C. helgolandicus*, *T. stylifera*, *P. parvus*) that were uncommon or much less abundant in the rest of the open Mediterranean,

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as observed also in previous studies (Estrada et al., 1985). *C. arcuicornis* and *C. helgolandicus* occur mostly in rather rich phytoplankton conditions (Boucher, 1984; Peralba, 2008). *C. helgolandicus* inhabits mainly intermediate and deep layers of the north-western Mediterranean Sea, Adriatic Sea, and North Aegean Sea, and ascends to epipelagic waters in late winter–spring (Bonnet et al., 2005; Siokou-Frangou et al., 2010). Its presence was considered extremely rare in the Levantine Sea until it was recorded with high abundance in June 1993, probably as a consequence of changes in deep water circulation (Weikert et al., 2001).

In autumn 2008, the whole Mediterranean appeared poor in chl *a*; however, still in such condition of homogeneous oligotrophy, some correspondence persisted between mesozooplankton clusters and the spatial trophic regimes classified by D'Ortenzio and Ribera d'Alcalà (2009). The stations of the westernmost regions were all close in the SOM map but, differently from spring, they were separated in different clusters. The Atlantic and Gibraltar Strait stations (Cluster 4) were characterized by the presence of *A. longiremis*, *Microsetella* spp. and *L. flavicornis*. The high abundance of cladocerans (particularly *P. avirostris*) and the occurrence of *C. helgolandicus* resulted in the inclusion of all the Alboran stations with the north-eastern Aegean Sea (st. 54) in the same group (Cluster 1). The two areas were classified as "intermittently-blooming" and in the autumn of 2008 they were characterized by a slight increase of chl *a* concentration. The enrichment in autotrophic biomass in the former area might be related to the neighboring upwelling along the Spanish coast (Mercado et al., 2007) and in the latter area to the inflowing Black Sea water (Ignatiades et al., 2002). The high abundance of neritic species (mainly *P. avirostris* and *P. parvus*) in the Alboran Sea and in the northernmost Aegean Sea may be attributed to the close distance of those stations to the continental shelf. The abundance of *C. helgolandicus* in the epipelagic layer of the Alboran Sea during the stratification period is of particular interest since the species migrates in deeper layers in late spring–early summer and stays in diapause until winter (Andersen et al., 2001; Bonnet et al., 2005; Scotto di Carlo et al., 1984). This particular occurrence might be attributed to the upwelling occurring in the Alboran Sea.

The Strait of Sicily and western-central Ionian stations were grouped together (Cluster 2), with high level of homogeneity since for each region most stations fell within a single cell. This group of stations was dominated by *C. furcatus* and the Clausocalanidae juveniles (the juveniles of *Clausocalanus* dominated since *Pseudocalanus* was present only in the Adriatic Sea and *Ctenocalanus* had low abundance in autumn). The dominance of *C. furcatus* can be related to its capability to flourish in oligotrophic conditions (Peralba, 2008). Differently from spring, the Aegean Sea (except the northernmost station) showed a remarkable homogeneity in autumn and was grouped with the eastern Ionian Sea and the Levantine Sea (Cluster 3). This homogeneity is probably due to the absence of north–south gradient of chl *a* and the similarity of phytoplankton concentration in all three areas. This cluster was characterized by *H. longicornis*, as it was observed in spring in the Ionian and Levantine seas, but its abundance was higher in autumn. The separation between the eastern and western-central Ionian stations might be related to the presence of different water masses. In fact, in the Ionian Sea, characterized by significant sub-basin and mesoscale dynamics, the eastern area was more influenced by the Levantine Water, while the western-central section was affected by the spreading northward of the Atlantic Water (V. Kovačević and H. Kontoyiannis, pers. comm.). Unexpectedly, the two samples collected at st. 47 in the central Ionian Sea at 3-weeks distance were included in different clusters. As indicated by the higher temperature and salinity values, in August the upper 200 m layer of this station was occupied by the Levantine water, which was replaced by the Atlantic water in September. As for the spring clusters, all the above areas, from the Strait of Sicily until the Levantine Sea, were classified as "non-blooming" areas (classes 1 and 2) by D'Ortenzio and Ribera d'Alcalà (2009). Interestingly, the cluster of the south Adriatic Sea stations was positioned at close distance to the Strait of Sicily and western Ionian cluster, apparently due to the abundance of *C. furcatus*. Though within the same cluster, the stations 35 and 36 of the South Adriatic Gyre, an "intermittently-blooming" area, were separated in different cells from the other stations located in "non-blooming" areas.

5. Conclusions

In synthesis, the surveys carried out in 2008 showed that epipelagic mesozooplankton communities manifested a clear seasonal signature in structural parameters like standing stock and community composition. In both seasons, it did not appear a clear west–east decreasing gradient in total standing stock, but rather regional discontinuities. However, west or east preferences were observed in the distribution of some copepod species. The spatial regionalization identified by the mesozooplankton communities showed clear correspondences with the autotrophic regimes identified by D'Ortenzio and Ribera d'Alcalà (2009) from color remote sensing data, indicating that mesozooplankton are visibly conditioned by food availability. The match appeared particularly striking in some cases when distant stations belonging to different regions were grouped in the same cell on the SOM maps, indicating that mesozooplankton communities acquire similar characteristics not only for geographic continuity but also for common responses to similar environmental conditions and trophic regimes. The correspondence appeared more precise in spring, when the increased concentration of chl *a* makes the Mediterranean Sea a more heterogeneous environment, but they were still visible in the more uniform oligotrophic autumn conditions. This means that local characteristics at regional scale do shape the features of mesozooplankton communities likely due to the basin geo-morphology, circulation and trophic features and these regional features persist beyond the seasonal variability. Indeed, the environmental heterogeneity resulted in the distinction of three different communities in the surveyed areas. The first type is the most widespread and thrives in the ample "non-blooming" areas, the second type occurs in the "intermittently-blooming" areas, and the third type is a characteristic of areas with recurrent and intense phytoplankton blooms.

Zooplankton communities, which reflect quantity and quality of food resources, which in turn are more directly related to changes in the physical dynamics, do therefore provide an integrated picture of the regional features of the epipelagos. Overall, the well defined regionalization of mesozooplankton communities that appears from our results reinforce the view of the Mediterranean Sea as a mosaic environment already emerged from different biological compartments and perspectives.

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