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Zooplankton community dynamics in the N. Aegean front (E. Mediterranean) in the winter-spring period

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Abstract

Zooplankton community composition was studied in the North Aegean frontal area in the winter-spring period along a trophic gradient ranging from the less saline and cold modified Black Sea water to the high salinity and warm waters of Levantine origin. Samples were collected in the upper 100 m of three stations positioned along this gradient using three nets with different mesh sizes (45 µm, 200 µm and 500 µm) in order to have a holistic view of metazooplankton seasonal dynamics. Community composition (all sizes) presented smoother seasonal succession and higher diversity along the gradient of increasing oligotrophy and salinity. The temporal variability of community composition revealed significant changes in the January-April period as well as gradual decrease of diversity index values at the station positioned within the front. The major characteristic at this station was the abrupt increment and dominance of *Centropages typicus* in April, especially within the layer occupied by the modified Black Sea water. Significant difference in community composition between March and April was a common feature in the whole study area and for all zooplankton fractions, though not of the same strength. The inflow of Black Sea water and the trophic gradient were found to be important factors for the observed temporal variability and its spatial differentiation, while changes in phytoplankton and protozoa abundance and community composition could account for seasonal succession in species dominance.

Keywords: Copepods, Winter-spring, Size fractions, N.Aegean, Mediterranean.

Introduction

Water exchange between adjacent basins through straits significantly affects local ecosystems through the physical-chemical-biological characteristics of the water, which control several processes. Among the straits and channels joining the Mediterranean Sea with the adjacent marine areas, the Dardanelles Strait is of particular interest due to the great differences in water characteristics between the adjacent basins, the low saline and eutrophic Marmara Sea and the saline and oligotrophic Aegean Sea. In the northeastern part of the Aegean Sea, the inflowing modified Black Sea water (BSW) meets waters of Levantine origin (LW), resulting in the formation of the North Aegean strong thermohaline front at the exit of the Dardanelles Strait. The former water mass occupies the upper 20-30 m resulting in permanent stratification of the water column in terms of salinity and temperature (Zervakis & Georgopoulos, 2002). Plankton communities, food web structure and carbon flow seem to respond to the northeast Aegean Sea (NEA) hydrology (Pitta & Giannakourou, 2000; Ignatiades *et al*., 2002; Siokou-Frangou *et al.,* 2002; Frangoulis *et al.,* 2010). Based on satellite data analysis, NEA was classified as an intermittently blooming area, characterized by maxima in chlorophyll values in February-March (D'Ortenzio & Ribera d'Alcala, 2009).

Regarding mesozooplankton, both standing stock and species composition were found to be different in the above region, at horizontal and vertical scale, in relation to hydrology. Total mesozooplankton biomass and abundance values are almost one order of magnitude higher in the BSW layer than in the LW layer. In addition, distinct species assemblages were depicted in the waters occupied by BSW, from those occupied by LW, independently of the season (Isari et *al*., 2006; Zervoudaki *et al*., 2006; Siokou-Frangou *et al*., 2009). Interestingly, species composition in the BSW layer revealed a gradual and significant differentiation from the west Marmara Sea towards NEA (Zervoudaki *et al*., 2011), suggesting that the transport of mesozooplankters by BSW in NEA could not be the major factor for the observed distinction of the assemblages in NEA. BSW low salinity does not seem to delimit species distribution in NEA, since the dominant copepod and cladoceran species in the area affected by BSW are not totally absent in the waters of Levantine origin (Siokou-Frangou *et al*., 2009). In contrast, the hypothesis of BSW influence on mesozooplankton through the carried nutrient load (inorganic and organic) and their impact on the dynamics of phytoplankton and microheterotrophs (prey of mesozooplankton) seems to be more plausible. NEA revealed higher primary and bacterial production values compared to the rest of the north Aegean Sea (Siokou-Frangou *et al.*, 2002). In summer 2004, the entrapped BSW in the Samothraki anticyclonic gyre of the NEA was characterized by phytoplankton, microheterotrophs and mesozooplankton composition dissimilar to that observed in the surrounding waters (Isari *et al.,* 2007).

Though the influence of the entering BSW on the spatial distribution of mesozooplankton is rather well documented, no information is available regarding its possible influence on the seasonal dynamics of mesozooplankton. Moreover, there is a lack of information on zooplankton seasonal succession in the entire north Aegean Sea. The study of seasonal variability is a key factor for a better understanding of ecosystem functioning (Huskin *et al.,* 2006; Tommasi *et al.,* 2013). Zooplankton seasonality is of particular interest in NEA since the area is known for its high fishery production (Papaconstantinou, 2005). Knowledge of the zooplankton seasonal cycle is important for understanding the physical forcing influence, through zooplankton community structure, on upper trophic levels whose recruitment depends on the match-mismatch of their seasonal cycles with that of their prey (Cushing, 1990; Beaugrand *et al.,* 2003). In addition, water mass intrusions with variable characteristics can mask the seasonal variability of zooplankton by introducing superimposed variability (Calbet *et al.,* 2001).

The present study aims at filling this gap, investigating the dynamics of zooplankton community composition in the North Aegean frontal area during the winter-spring period, when significant changes in the autotrophic biomass are observed in the entire Mediterranean Sea (D'Ortenzio & Ribera d'Alcala, 2009). Similarities or not in community seasonal variability will be examined between areas covered by different water masses. Moreover, different size fractions of metazooplankton were studied using nets with 45 μm, 200 μm and 500 μm mesh size, in order to have a representative capture and, thus, a better view of the entire metazooplankton seasonal dynamics.

Materials and Methods

Study area

Zooplankton samples were collected within the MEDEX project on board R/V AEGAEO on 4 December 2009, 26 January 2011, 10 - 11 March 2011, 14 - 15 April 2011 and 12 - 13 May 2011. The one year gap between the first and second cruise was due to logistic problems. Sampling was performed at three stations MD1, MD2, MD3 positioned along the thermohaline front at the exit of the Dardanelles Strait (Fig. 1).

During all cruises the upper 10 m layer of station MD1 was occupied by BSW and/or by the formed halocline, characterized by mean integrated salinity from 33.70 (May 2011) to 38.32 (December 2009) and tem-

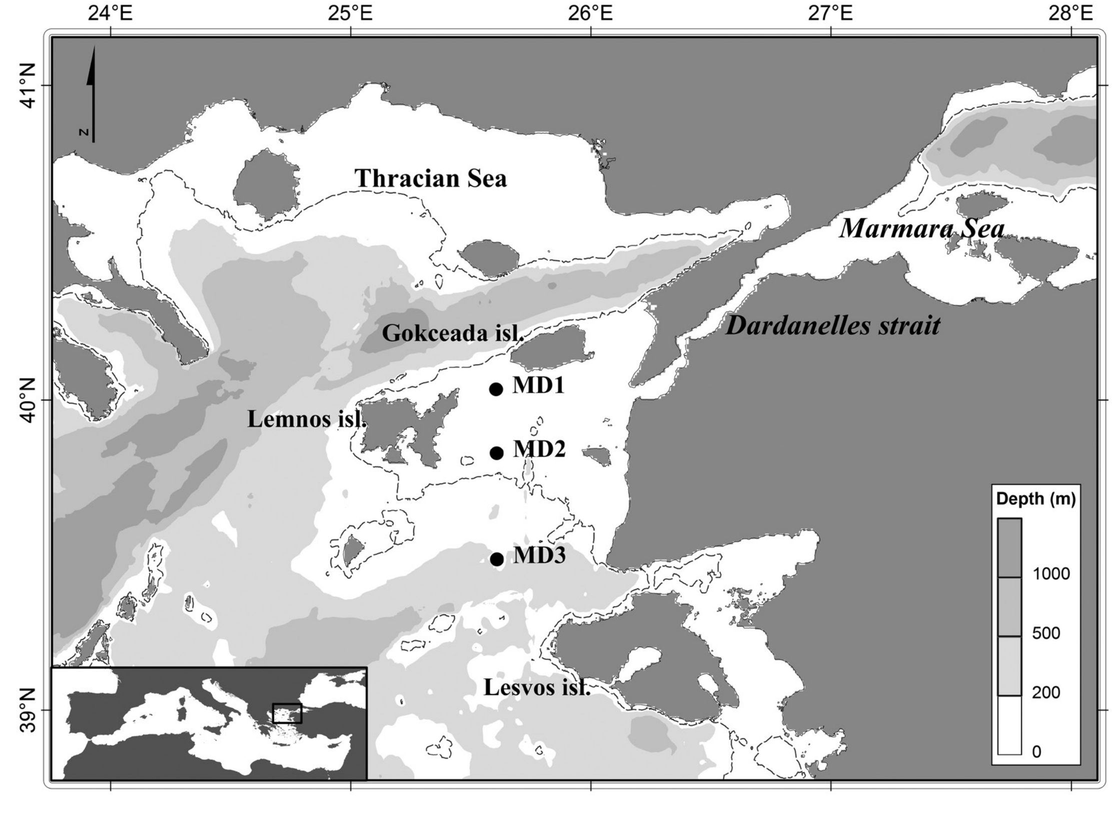


Fig. 1: Sampling stations in the North Aegean Sea.

perature from 12.26 °C (March 2011) to 17.76 °C (December 2009). In the lower layer, mostly characterized by the strong halocline, the relevant values varied between 37.39 (January 2011) and 38.98 (December 2009) and from 13.88 °C (March 2011) to 18.34 °C (December 2009). The presence of BSW in the upper layer resulted in an inverse weak thermocline (BSW was colder than LW) (Peliz, 2013). At station MD2, a very weak halocline was detected at 40-50 m depth, except in April 2011 when the halocline was important. In the upper 40 m mean integrated salinity values varied between 37.69 (April) and 39.09 (December and May), while temperature was low in March (13.62 °C) and high in December (18.56 °C). The entire water column at station MD3 was occupied by LW and temperature was homogeneously distributed in the upper 100 m layer (Peliz, 2013). In this layer, mean integrated salinity varied between 38.9 (January 2011) and 39.2 (December 2009), and temperature from 15.3 °C (April) to 18.8 (December). Chlorophyll α values decreased from MD1 to MD3 and peaked strongly in March at MD1 and MD2 (upper 20 m), whereas at MD3 a very weak peak was observed mostly in the upper 30 m in April (Peliz, 2013).

Zooplankton sampling and elaboration of data

Sampling of zooplankton was done using three nets with different mesh size: 45 μm (WP2 net), 200 μm (WP2 net), 500 μm (WP3 net). The 45 μm and 200 μm mesh size nets were towed vertically at two discrete layers (upper and lower layer) according to the physical structure of the water column as revealed by the in situ examination of CTD profiles (Peliz, 2013). At station MD1 (depth 67 m), the layers were 0-10 m and 10-60 m. At station MD2 (depth 87 m), the upper layer was from the surface to 30-50m and the second layer until close to the bottom. At station MD3 (depth 300 m), the layers were 0-50 m and 50-100 m. Double oblique hauls were performed using a WP3 500 μm mesh size net, equipped with a flowmeter, towed at a speed of 2 knots, from the surface until 50 m depth (one layer was sampled in all stations). At station MD1, samples were collected between 08:30 and 12:00; at station MD2, between 13:00 and 15:00 and at station MD3, between 20:00 and 23:00.

All samples were split in two halves by Folsom Splitter on board and one subsample was deep frozen for biomass estimation (Frangoulis *et al.*, in prep.), while the other one was fixed with 4% buffered formalin for taxonomic identification. Taxonomic identification was performed microscopically on the subsamples collected by 200 μm mesh size net (small mesozooplankton) and 500 μm net (large mesozooplankton). The samples collected using a 45 μm mesh size net (thereafter called samples of micrometazooplankton) contained an important amount of detritus, phytoplankton and protozooplankton and their microscopic analysis proved to be very laborious. As a compromise, the animals of the above samples were identified by image analysis, though at higher taxonomic level than with the microscopic analysis (due to the lower resolution of the images compared to microscopic observation). For the image analysis, a subsample was scanned at a resolution of 4800 dpi using an Epson Perfection 4990 Photo scanner (using a similar scanning method to Bell & Hopcroft [2008]). The images obtained were used to determine zooplankton abundance by image analysis (Image-pro plus 6.0) at group level (e.g. copepods, nauplii, appendicularians etc.).

In order to depict temporal differences in the community composition of small and large mesozooplankton, hierarchical clustering and non-metric multidimensional scaling (MDS) were applied (Clarke & Warwick, 1994) using the PRIMER 5 software. Copepod and cladoceran species, and other group abundance data were square root transformed; the Bray-Curtis similarity index was used and the group average method was applied. Copepod species diversity was estimated through the Shannon-Wiener diversity index (H') (Shannon & Weaver, 1963). Possible relationships between the most abundant copepod and cladoceran species and other groups at each layer with environmental variables were explored using Canonical Correspondence Analysis (CCA) (Ter Braak, 1986). A permutation test has been implemented (1000 permutations), in order to check the linearity of the relationships between the sites/species data and the sites/variables data, with 5% significance level. Taxa abundance data were $\log_{10}$-transformed and the XLSTAT 2013 software package was used. The environmental variables used were: temperature (T) and salinity (S) (measured by CTD), salinity difference between the upper and lower limit of the layer (DS) and chlorophyll α (Psarra, personnal communication). Mean integrated values over the layer where zooplankton was sampled were calculated and these values of the environmental parameters were used in the CCA.

Results

Micrometazooplankton

Microcopepods (i.e. copepods captured by the 45 μm mesh size net) overall dominated (40-90% of total micrometazooplankton), followed by nauplii (8-59%) at all stations; both groups were generally more abundant in the upper than in the lower layer. Their abundance values were higher in January 2011 than in December 2009, attaining maxima values at station MD1 (Fig. 2). Their numbers strongly declined in March 2011, especially the numbers of nauplii at stations MD2 and MD3. In April 2011, a recover of both group (microcopepods and nauplii) abundance was found in the upper layer of all stations and maxima values were recorded at MD3. A parallel increase was observed in the lower layer except at MD1. At MD2, in both layers, the maxima values of the

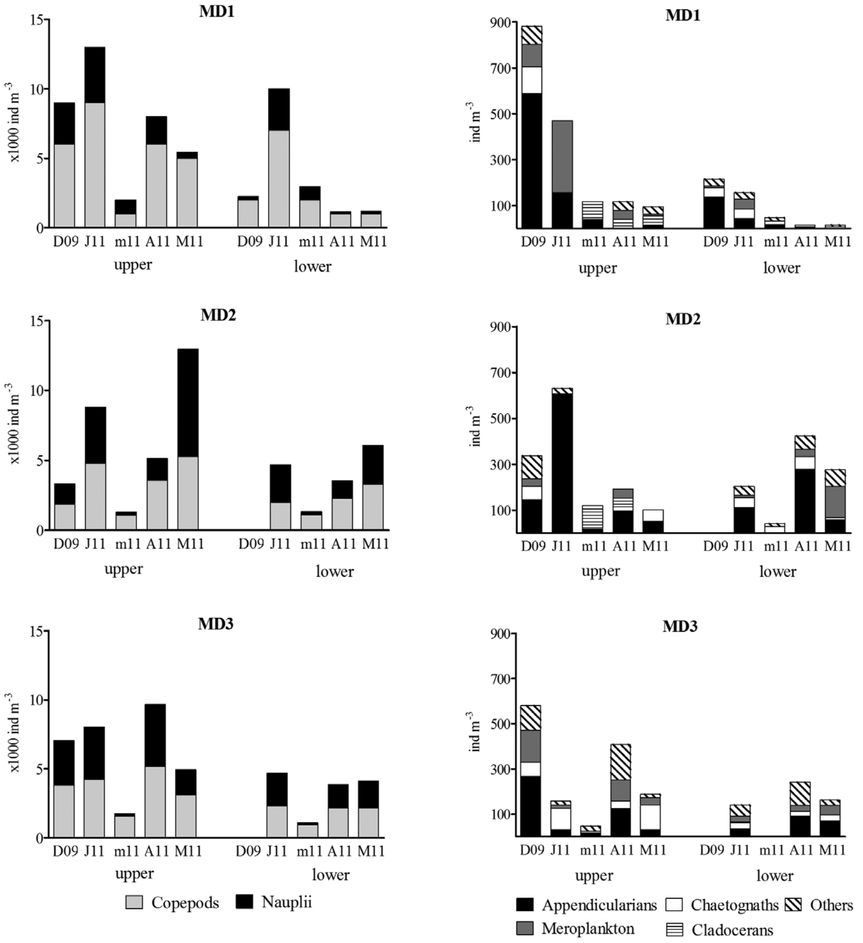


Fig. 2: Abundance (ind. m^{-3}) of micrometazooplankton groups.

study period were detected in May. Among other groups, the presence of appendicularians was noticeable in December 2009 at station MD1 and MD3, and in January 2011 at station MD2. Cladocerans were the third group in rank order only in March and in the upper layer of MD1 and MD2. Young chaetognaths were mostly found in December (MD1, MD2), January and May (MD3).

Small mesozooplankton (captured by the 200 μm mesh size net)

Copepods were dominant in both layers of all stations during the entire study period (Fig. 3). Their abundance varied more or less similarly: increase from December to January, strong decline in March (minima at all stations) followed by a considerable increment of values in April and May. In the upper layer of station MD1, *Clausocalanus* copepodites and *Oithona* copepodites were the first dominant taxa in December and January; their abundance considerably increased in the latter month (Table 1). The relative abundance of appendicularians and chaetognaths was important in December and January (Fig. 3). In March, the community was highly dominated by *Paracalanus parvus,* followed by the cladoceran *Evadne nordmanni* (28% of small mesozooplankton). In April, *Centropages typicus* (adults and copepodites) dominated the community (representing 73% of copepods) and it was still dominant in May, though with lower numbers than in April. Similar changes between months in community composition were observed in the lower layer, where the abundance of *Ctenocalanus vanus* was very important.

In the upper layer of MD2, in December, *Calocalanus* spp. (mostly *C. pavoninus* and *C. pavo*), *Mecynocera clausi* and *Oithona* copepodites were abundant (Table 1); chaetognaths and appendicularians were the second and third group respectively in rank order (Fig. 3). *Clausocalanus* copepodites dominated in January and *P. parvus* in March, the latter species accompanied by *E. nordmanni*. The community in April was characterized by the high abundance of *C. typicus* and *C. vanus,* while *P. parvus* peaked in May. Considering the lower layer, *C. vanus* and *Oithona* copepodites were abundant from January till May 2011, accompanied by *Clausocalanus* copepodites (Table 1).

At station MD3, in both layers, *Clausocalanus* copepodites, *C. vanus* and *M. clausi* were abundant in December 2009 (Table 1). The first two taxa together with *Oithona* copepodites dominated from January till May 2011 though with different rank order; their abundance values increased from March to May. The relative abundance of

Table 1. Dominant species abundance (ind. m^{-3}) of small mesozooplankton (collected by 200 μm mesh size net). D=December 2009, J=January 2011, m=March 2011, A=April 2011, M=May 2011.

Station	MD1									
Layer	**Upper layer**					**Lower layer**				
	D	J	m	A	M	D	J	m	A	M
Copepods										
Acartia clausi	0	154	35	107	154	0	197	35	66	86
Nannocalanus minor	45	14	0	0	0	7	0	0	0	0
Mesocalanus tenuicornis	6	26	0	0	0	6	69	3	54	80
Calocalanus spp.	39	33	3	0	9	14	53	7	7	52
Centropages typicus	12	31	19	2039	1505	0	48	45	653	323
Clausocalanus paululus	0	5	1	3	0	6	10	3	2	11
Clausocalanus pergens	0	2	0	22	0	1	4	0	34	55
Clausocalanus copepodites	54	268	5	195	15	14	124	8	346	69
Ctenocalanus vanus	14	12	25	13	25	34	153	61	155	254
Farranula rostrata	11	0	0	0	0	5	7	0	0	3
Mecynocera clausi	30	24	2	0	0	11	49	3	7	39
Oithona setigera	1	0	0	0	0	14	0	3	15	30
Oithona copepodites	54	137	6	6	12	21	76	10	39	155
"*Oncaea media* group"	26	5	8	3	28	5	20	10	59	30
Paracalanus parvus	18	52	228	307	231	3	110	177	371	149
Pleuromamma copepodites	0	0	0	0	0	1	18	6	2	6
Temora stylifera	12	59	0	0	0	0	83	0	0	0
Cladocerans										
Evadne nordmanni	0	14	148	13	16	0	0	44	0	0

Station	MD2									
	Upper layer					**Lower layer**				
	D	J	m	A	M	D	J	m	A	M
Copepods										
Acartia clausi	0	33	14	45	35		1	0	35	4
Nannocalanus minor	7	3	5	0	3		1	1	0	9
Mesocalanus tenuicornis	1	7	3	19	10		25	5	27	31
Calocalanus spp.	41	15	10	31	28		11	6	65	64
Centropages typicus	0	6	11	317	242		0	3	188	36
Clausocalanus paululus	16	2	1	10	3		5	6	8	7
Clausocalanus pergens	1	1	8	35	9		3	6	5	12
Clausocalanus copepodites	23	111	27	146	63		26	15	60	72
Ctenocalanus vanus	22	70	50	251	200		63	34	239	367
Farranula rostrata	16	2	0	2	10		0	0	3	25
Mecynocera clausi	32	11	1	2	12		9	3	8	33
Oithona setigera	3	1	2	3	17		5	9	21	32
Oithona copepodites	24	54	23	58	330		47	18	100	180
"*Oncaea media* group"	4	54	37	80	12		1	3	81	66
Paracalanus parvus	3	88	218	129	401		18	3	19	72
Pleuromamma copepodites	0	1	1	5	0		37	9	8	11
Temora stylifera	3	12	2	2	0		3	0	0	0
Cladocerans										
Evadne nordmanni	0	0	33	5	0		0	1	0	0

(continued)

Table 1 *(continued)*

Station	MD3									
	Upper layer					**Lower layer**				
	D	J	m	A	M	D	J	m	A	M
Copepods										
Acartia clausi	3	0	0	0	2	0	0	0	0	0
Nannocalanus minor	20	4	0	8	10	55	5	0	6	3
Mesocalanus tenuicornis	10	7	5	13	2	17	11	3	15	72
Calocalanus spp.	65	38	23	61	78	47	31	7	3	95
Centropages typicus	0	1	0	8	20	0	1	0	1	8
Clausocalanus paululus	30	9	20	27	20	50	6	10	19	28
Clausocalanus pergens	1	1	0	10	12	2	3	2	4	8
Clausocalanus copepodites	75	91	38	89	120	62	68	37	88	38
Ctenocalanus vanus	37	83	52	225	309	62	100	43	156	133
Farranula rostrata	22	6	2	33	46	58	6	3	13	46
Mecynocera clausi	65	29	10	36	35	74	22	15	22	56
Oithona setigera	0	1	5	27	11	14	13	14	38	36
Oithona copepodites	30	68	61	141	238	3	59	27	138	136
"*Oncaea media* group"	20	46	9	68	64	6	12	8	24	51
Paracalanus parvus	0	53	0	10	101	0	38	0	0	10
Pleuromamma copepodites	1	8	20	31	2	20	11	14	68	28
Temora stylifera	8	12	0	0	1	2	22	0	0	3
Cladocerans										
Evadne nordmanni	0	0	0	0	0	0	0	0	0	0

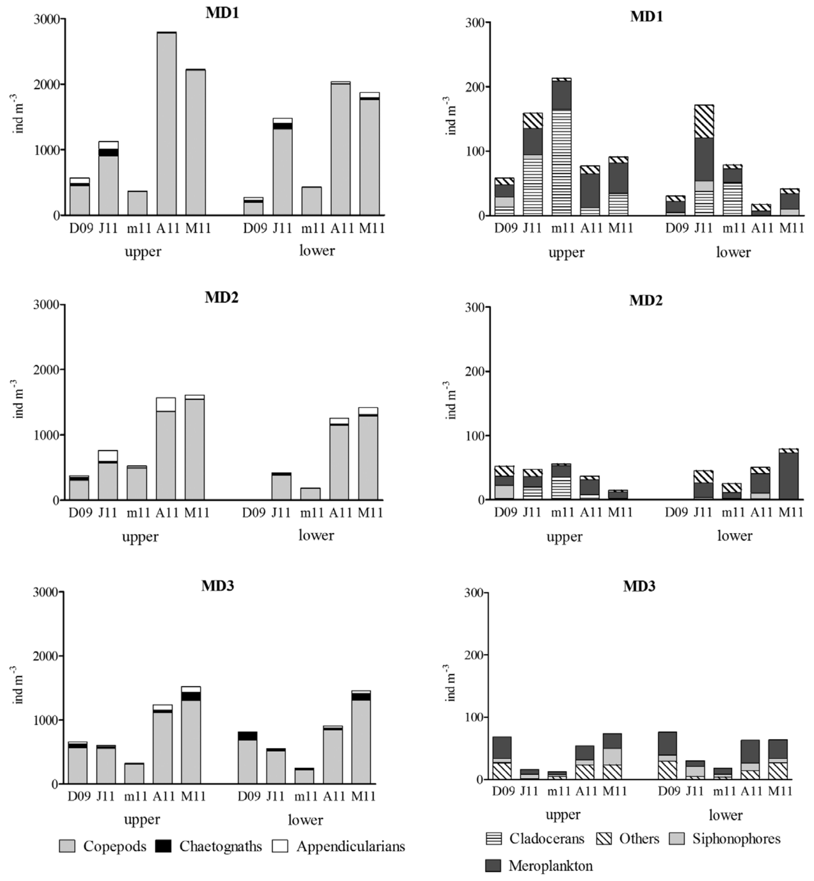


Fig. 3: Abundance (ind. m^{-3}) of small mesozooplankton groups (collected by 200 μm mesh size net).

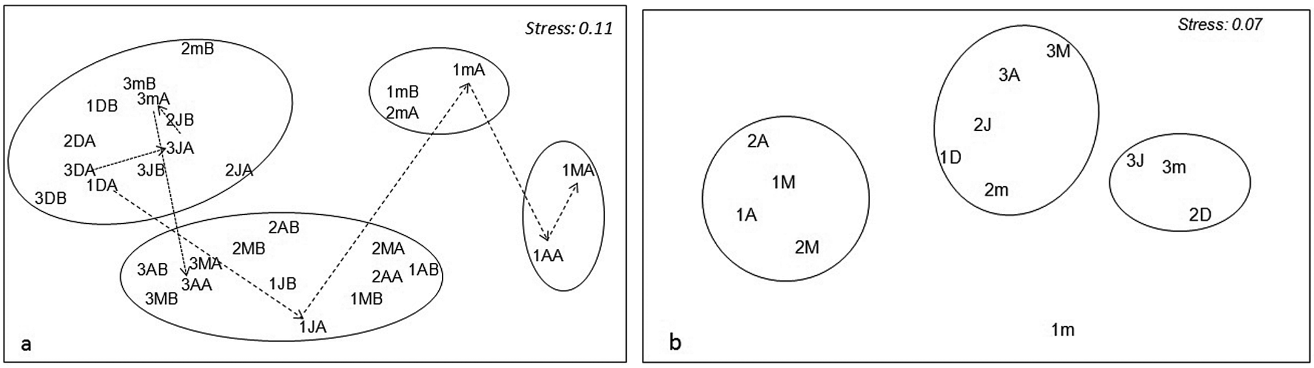
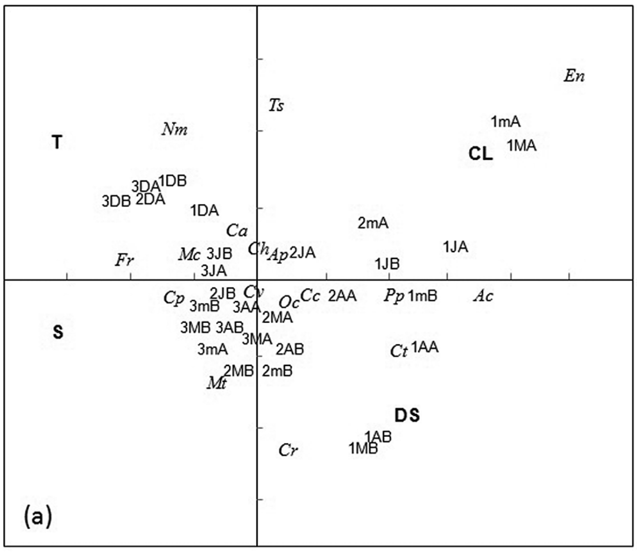


Fig. 4: (a) MDS plot of small mesozooplankton samples (collected by 200 μm mesh size net). 1, 2, 3 = stations MD1, MD2, MD3, D=December 2009, J=January 2011, m=March 2011, A=April 2011, M=May 2011, A=upper layer, B=Lower layer. Example 1DA=sample collected in the upper layer of station MD1 in December 2009. Cycles include samples belonging to the same group (derived from hierarchical clustering). Dashed line arrows link samples collected during each month in the upper layer of station MD1. Dotted line arrows link those collected in the upper layer of station MD3. (b) MDS plot of large mesozooplankton samples (collected using a 500μm mesh size net). Letters and numbers as above.

chaetognaths was overall higher at MD3 than at the other stations; in contrast, very few cladocerans were encountered (Fig. 3). The list of all copepod and cladoceran species collected by 200 μm mesh size net is provided in the supplementary material (online edition only).

The above described temporal changes and spatial differences in the community composition of small mesozooplankton resulted in the distinction of four groups of samples by hierarchical clustering and in the mapping of samples in the MDS plot (Fig. 4a). At 53% similarity level, the samples collected at all stations and layers in December constitute the first group, together with samples collected at MD2 in January (both layers) and in March (lower layer), as well as at MD3 (both layers) in December, January and March. The second group includes the samples collected at MD1 in January (both layers), April and May (lower layer) at MD2 and at MD3 (both layers) in April and May. The samples gathered in March at MD1 (both layers) and at MD2 (upper layer) constitute the third group. Finally, a small group includes the samples of MD1 upper layer in April and May. A very interesting result of the applied multivariate analyses is the similarity (53%) between the December 2009 and January 2011 samples for all stations, despite the one year difference between the relevant cruises.



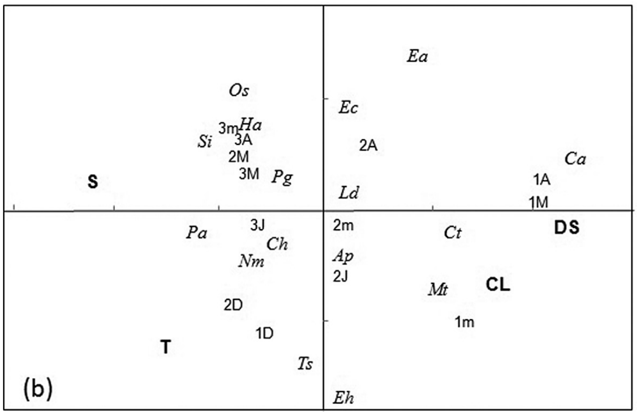


Fig. 5: (a) CCA of small mesozooplankton samples (collected by 200 μm mesh size net) and environmental parameters. 1, 2, 3 =stations MD1, MD2, MD3, D=December 2009, J=January 2011, m=March 2011, A=April 2011, M=May 2011, A=upper layer, B=Lower layer. Example 1DA=sample collected at the upper layer of station MD1 in December 2009. S= salinity, T= temperature, CL= chlorophyll a, DS= salinity difference within layer. *Ac= Acartia clausi, Ap= Appendiclarians, Ca= Calocalanus spp., Cc= Clausocalanus* copepodites, *Ch=* chaetognaths, *Cp= Clausocalanus paululus, Cr= Clausocalanus pergens, Ct= Centropages typicus, Cv= Ctenocalanus vanus, En= Evadne nordmanni, Fr= Farranula rostrata, Mc=Mecynocera clausi, Mt=Mesocalanus tenuicornis, Nm= Nannocalanus minor, Oc= Oithona* copepodites, *Pp=Paracalanus parvus, Ts=Temora stylifera.* (b) CCA of large mesozooplankton samples (collected using a 500 μm mesh size net) and environmental parameters. Letters and numbers of stations, parameters and species as above. *Ea= Eucalanus attenuatus, Ec= Eucalanidae* copepodites, *Eh= Euchaeta* copepodites, *Ha= Haloptilus longicornis, Os= Oithona setigera, Pa= Pleuromamma abdominalis, Pg= Pleuromamma gracilis, Si=* siphonophores.

According to CCA results, the first axis (69% of total variance) was positively related to chlorophyll *α*, and negatively to salinity and temperature (Fig. 5a). The permutation test revealed that the sites/species data were linearly related to the sites/variables data (p value < 0.05). The second axis (21% of total variance) was negatively related to salinity as well as to the salinity difference within layers. *E. nordmanni, C. typicus, A. clausi, P. parvus* were related to high chlorophyll *α* values, characterizing the upper layer of station MD1 in the period January-May, when the layer was occupied by the low saline BSW. *Farranula rostrata, Nannocalanus minor, Lucicutia flavicornis, M. clausi* were related to the high salinity and very oligotrophic LW present in December at stations MD2 and MD3 (both layers). *Clausocalanus pergens, C. typicus, Oithona setigera* seem to be favored by the presence of a strong halocline in the lower layer of station MD1 in April and May.

All samples collected at MD3 were projected at short distances in the negative part of the first axis, related to high salinity and temperature values of LW and very low chl *α* values. In contrast, MD1 samples were discriminated along the first axis, thus along a gradient of salinity, temperature and chl *α*; the December samples were related to high salinity and temperature LW with low chl *α*, whereas the upper layer samples of the period March-May were related to the less saline and cold BSW with high chl *α*. Finally, samples collected at MD2 were less differentiated in relation to salinity and temperature, and they were projected between those of MD1 and MD3, suggesting an intermediate position between MD1 and MD3 as regards community composition and environmental parameters.

Very high values of the diversity index for small copepods were found in December at all stations and layers (4.41 to 4.61 bits ind.$^{-1}$) (Fig. 6). From January onwards, diversity index values were consistently lower at station MD2 and even more so at MD1 compared to MD3. In the upper layer of MD1, the value was lower in January than in December and then declined considerably by April (1.11 bits ind.$^{-1}$). A similar temporal pattern was observed in the lower layer, but the decrease was less important than in the upper layer (min 2.80 bits ind.$^{-1}$ in April). At MD2, the diversity index values revealed an overall decline in the upper layer from January to May, whereas values were higher in the lower layer and the temporal pattern was slightly modified. Diversity varied within a small range of values in both layers of station MD3 (3.80 to 4.72 bits ind.$^{-1}$) and without any clear temporal pattern.

Large mesozooplankton (captured by the 500 μm mesh size net)

Large copepods, the dominant group, followed the same temporal pattern at all stations characterized by low abundance values in March and a considerable increase in April-May (Fig. 7). *C. typicus* (only adult specimens were captured by 500 μm net) was the most abundant species at station MD1 during the whole study period and peaked in April-May (Table 2). It was accompanied by *N. minor* and *Euchaeta* copepodites in December, *Pleuromamma gracilis*, *Mesocalanus tenuicornis* in March and *Calanus helgolandicus* in April-May. The abundance of large chaetognaths was noticeable in December, while large larvae of decapods and euphausiids were found in significant numbers in April-May (Fig. 7).

Among the few specimens collected at station MD2 in December, the presence of *N. minor* was important (Table 2); *T. stylifera* and *M. tenuicornis* were dominant in January, whereas in March *C. typicus* was the first species in rank order. The latter species together with C. *helgolandicus* were very abundant in April and the community was characterized by the significant contribution of large siphonophores (Fig. 7). *C. typicus* peaked in May, representing 83% of copepods.

At station MD3, *Pleuromamma gracilis* was dominant in the period January-May, accompanied by *N. minor*, except in March when *Haloptilus longicornis* was quite abundant (Table 2). Large chaetognaths, siphonophores, larvae of decapods and euphausiids were encountered in significant numbers in April-May (Fig. 7). Among the copepods found at this station, the presence of *Centropages furcatus* is noticeable since it is considered an alien species in the N. Aegean Sea (Siokou *et*

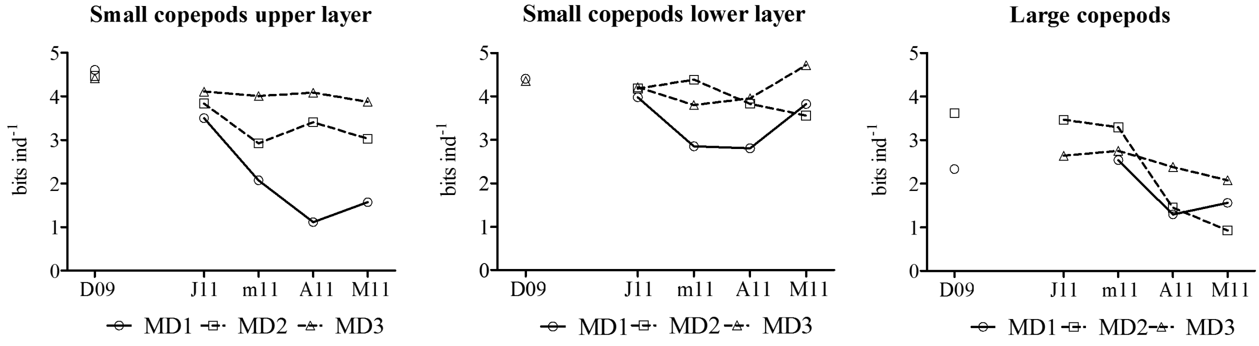


Fig. 6: Shannon-Wiener diversity index variability of small copepods (collected using a 200 μm mesh size net) and large copepods (collected using a 500 μm mesh size net).

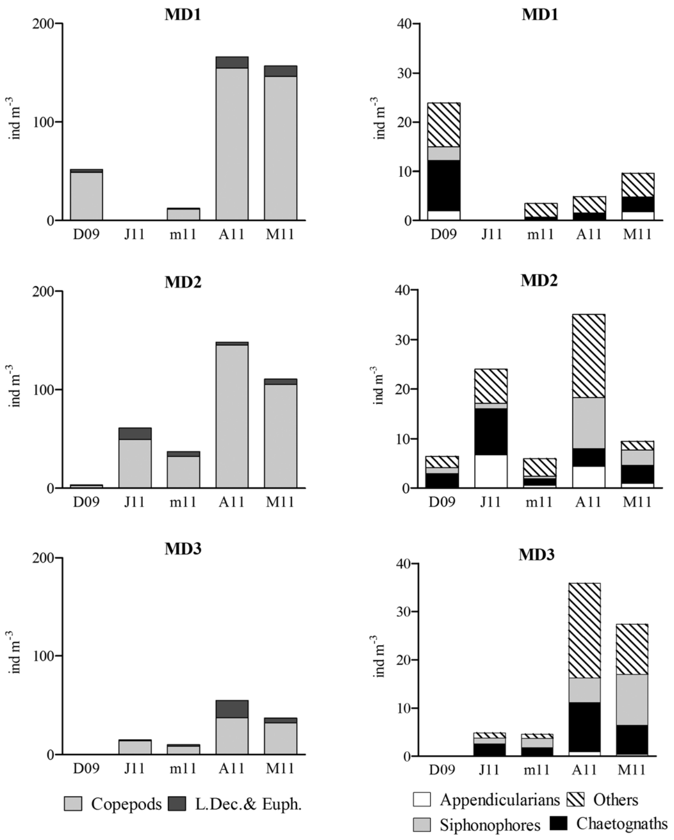


Fig. 7: Abundance (ind. m^{-3}) of large mesozooplankton groups (collected using a 500 μm mesh size net). L.Dec & Euph=Larvae of decapods and euphausiids.

Table 2. Dominant species abundance (ind m^{-3}) of large copepod species (collected by 500 μm mesh size net). D=December 2009, J=January 2011, m=March 2011, A=April 2011, M=May 2011.

	MD1				**MD2**					**MD3**			
	D	m	A	M	D	J	m	A	M	J	m	A	M
Calanus helgolandicus	0.3	0.3	52.1	48.5	0.0	4.5	3.4	62.3	0.8	0.0	0.0	0.0	0.0
Nannocalanus minor	9.2	0.1	0.5	0.8	0.7	4.8	3.2	0.9	3.5	1.2	0.5	4.3	5.5
Mesocalanus tenuicornis	3.6	0.7	4.1	8.8	0.0	7.3	3.4	1.3	0.3	1.1	0.6	2.2	0.0
Candacia simplex	0.9	0.1	0.0	0.3	0.0	0.0	0.5	0.0	0.0	0.0	0.0	1.4	0.3
Candacia copepodites	0.5	0.0	0.0	0.3	0.0	2.5	0.2	0.2	0.0	0.1	0.0	0.2	0.7
Centropages typicus	20.9	5.0	94.0	80.5	0.0	3.3	8.8	68.4	88.3	0.1	0.0	0.5	0.6
Eucalanus attenuatus	0.0	0.1	1.6	0.5	0.0	0.6	0.0	2.2	0.1	0.2	0.2	1.4	0.4
Subeucalanus crassus	0.0	0.0	0.2	0.0	0.0	0.3	0.0	1.8	0.0	0.1	0.0	0.0	0.0
Eucalanidae copepodites	0.0	0.0	0.6	0.5	0.1	2.4	0.0	4.2	1.1	0.0	0.0	1.0	1.7
Euchaeta acuta	0.0	0.0	0.2	0.8	0.0	0.0	0.2	0.0	1.4	0.0	0.0	0.0	0.0
Euchaeta copepodites	7.3	0.0	0.5	1.3	0.1	0.6	0.2	0.9	0.0	0.1	0.0	0.0	0.8
Haloptilus longicornis	0.3	0.0	0.0	0.3	0.0	1.2	0.3	0.5	0.0	0.2	1.7	1.2	0.0
Oithona setigera	0.0	0.0	0.0	0.3	0.0	0.9	0.3	0.0	7.4	0.0	0.2	0.0	0.0
Pleuromamma gracilis	0.7	1.9	0.5	2.6	0.1	5.8	6.0	0.0	0.4	6.6	3.6	20.4	16.9
Temora stylifera	1.8	0.0	0.2	0.0	0.1	7.9	1.6	0.5	0.3	0.3	0.0	0.0	0.0

al., 2013). The list of all copepod and cladoceran species collected by 500 μm mesh size net is provided in the supplementary material.

The groups distinguished at 49% similarity level by hierarchical clustering are shown in the MDS plot (Fig. 4b). The first group includes the samples collected at MD2 in December and at MD3 in January and March; the samples of MD1 and MD2 in April and May constitute the second group, while the third one includes the samples of MD1 in December, MD2 in January and March, and MD3 in April and May. The first axis of the CCA (63% of total variance) was positively related to the salinity difference within layers and negatively to salinity and temperature (Fig. 5b); the second axis (21% of total variance) was negatively but weakly related to temperature. *C. helgolandicus* and *C. typicus* were related to the less saline BSW and the resulting strong halocline present at station MD1 in April and May. *Pleuromamma abdominalis, O. setigera, N. minor* and siphonophores characterized the homogenized and saline LW at station MD2 in December and May and at station MD3 in the period January-May. The samples of station MD3 are projected very closely, while the opposite is obvious for stations MD1 and MD2. The permutation test indicated that the sites/species data were not linearly related to the sites/variables data; the p-value is just above the threshold we had chosen (0.05 against 0.072). Therefore, the conclusions might not be as obvious.

The highest values of the Shannon-Wiener diversity index for large copepods were found at station MD2 in December, January and March (3.29-3.61 bits ind.$^{-1}$), followed by a decrease in April and May when the minimum value was calculated (0.93 bits ind.$^{-1}$) (Fig. 6). At station MD1, values were overall lower than at the other stations; the seasonal pattern was more or less similar to that at MD2, except for the slight increment of diversity between April and May. A smooth decline of the index values was observed after March at station MD3.

Discussion

The temporal variability of zooplankton community composition in the North Aegean frontal area during the winter-spring period was investigated in the present study and an attempt was made to discern the influence of environmental variability. The use of three different mesh size nets aimed at a more representative capture of metazooplankton, since each net captures only a certain size fraction of metazooplankton organisms and undersamples organisms above or below that range. The analysis of different size fraction community samples provided an almost holistic aspect of metazooplankton variability, despite the different method used for the analysis of samples obtained with the 45 μm mesh size net, resulting in different taxonomic level compared to the other fractions. Interestingly, the small mesozooplankton samples collected at all three stations in December 2009 and in January 2011 revealed more than 53% similarity, and the large mesozooplankton more than 49%, despite the one year difference between the relevant cruises. Based on this finding, it is assumed that the December 2009 results are part of the same annual cycle as the 2011 cruise results.

During the study period, microcopepod (copepodites and adults collected using the 45 μm net) and nauplii abundance followed similar seasonal patterns at each station. Abrupt changes within a wide range of values were observed at stations MD1 and MD2, especially in the upper layer, covered by the modified BSW at the former station. In contrast, the temporal variability of the above taxa was less important at the deeper station MD3. Strong but not parallel fluctuations of microcopepods and nauplii abundance and at weekly intervals were observed in the December-May period in the Bay of Blanes-NW Mediterranean Sea- (Calbet *et al.,* 2001). Seasonal variability was found to be weaker at deeper than at shallower areas of the Mediterranean Sea, especially if the former were affected by the intrusion of offshore water masses (Fernández de Puelles *et al.,* 2003; Siokou-Frangou, 1996). In spite of the differences we observed between stations regarding the abundance and relative abundance of microcopepods and nauplii, they presented some similarities in their temporal pattern at all stations. The observed high values in January and May could be supported by the simultaneous peak of nano- and microphytoplankton abundance (Peliz, 2013). Maxima of nauplii in January and of small size copepods in January and April were also detected in the Bay of Blanes, but no correlation was found between the above groups and chlorophyll *α* values (Calbet *et al.,* 2001). In contrast, in the North Adriatic Sea the increasing trend of nauplii from December to May was significantly correlated with nano- and microphytoplankton abundance (Kršinić *et al.,* 2007). Seasonal variability of nauplii and microcopepods in NEA was rather similar to that of small and large copepods (collected by the 200 μm and 500 μm nets respectively). The minima values of nauplii and microcopepods in March, at all stations, coincided with the lowest abundance values of small and large sized copepods. A decline of food availability could have occurred between January and March, affecting metazooplankton dynamics, since bacteria, phytoplankton cells and protozoa abundance values were found to be lower in March compared to January (Peliz, 2013; Giannakourou *et al., 2014).* Maxima values of nauplii and all size fractions of copepods coincided only at station MD2. Discrepancies in the peaks between nauplii and microcopepods and copepods >200 μm were observed in the Cantabrian Sea (López *et al.,* 2007) and in the north Adriatic Sea (Kršinić *et al.,* 2007). Knowledge of the lower taxonomic composition of microcopepods and nauplii could elucidate their seasonal patterns and relationships with their autotrophic and heterotrophic prey.

Small appendicularians (collected using the 45 μm net) revealed important variability at MD1 and MD2: their abundance was very low when copepods were dominated by medium and large sized species (*C. typicus, C. helgolandicus*). Sommer *et al.* (2003) hypothesized that appendicularian population dynamics may be controlled by common calanoid copepods in the Baltic Sea. Copepods are known predators of the larval stages of appendicularians (Gorsky & Fenaux, 1998; López-Urrutia *et al.,* 2003). Differences in the size of phytoplankton and protozoans could also account for the observed changes in appendicularian abundance.

According to the hierarchical clustering results, the community composition of small mesozooplankton was very similar between stations and layers of NEA in December. The very oligotrophic conditions in the whole study area in December, the weak presence of BSW in the upper layer of MD1 and the absence of this water mass at the other two stations (Peliz, 2013) could account for the observed homogeneity, as confirmed also by CCA. Community composition did not change significantly at stations MD2 and MD3 between December and March (except in the upper layer of MD2 in March). In contrast, at station MD1, sequential changes in community composition were observed from January to April 2011 (as revealed also by the large distance between months in the MDS plot-Figure 4a), due to shifts in the dominant species. Interestingly, large mesozooplankters also revealed an important change between March and April related to the considerable increase of *C. typicus* and *C. helgolandicus* abundance. Similar but less acute changes in the community composition of small and large mesozooplankton also occurred at station MD2 from January to April. Variability of small mesozooplankton was smoothest at station MD3 (small distances between months in the MDS plot) with the only significant difference detected between March and April-May for both layers. This difference was probably due to modifications in the abundance and/or the rank order of the copepod species found during the entire study period than to changes in dominant species. In contrast, the observed important change in large mesozooplankton between March and April at MD3 should be related to the increment of large chaetognaths, siphonophores, decapods and euphausiid larvae in April and May.

The dominant species relevant to the above abrupt changes at station MD1 (*A. clausi, P. parvus, C. typicus, C. helgolandicus, E. nordmanni*) have previously been found to be abundant in winter and spring in the north Aegean Sea (Moraitou-Apostolopoulou, 1985; Tarkan, 2000; Zervoudaki *et al.*, 2006; Siokou-Frangou *et al.,* 2009). Among them, *A. clausi*, *C. typicus, P. parvus,* have revealed recurrent seasonal patterns in several Mediterranean coastal areas (Cataletto *et al.,* 1995; Christou, 1998; Fernández de Puelles *et al*., 2009; Mazzocchi *et al.,* 2011). According to Mazzocchi *et al.* (2011), the phenology of copepods depends mainly on their life histories, while their maxima abundance values are affected by local conditions. Moreover, in coastal waters, mesozooplankton composition and abundance reveal profound temporal-spatial variability related to that of hydrological properties (Roman *et al.,* 2005). This seems to be true at station MD1, always positioned within the thermohaline front, which is submitted to lateral advection and to temperature and salinity variability, according to the seasonality of circulation and the involved water masses (BSW and Levantine water) characteristics (Poulos *et al.,* 1997; Zervakis & Georgopoulos, 2002). Seasonal variability of BSW volume, the nutrients concentration and characteristics (organic/inorganic and stochiometry) (Polat & Tugrul, 1996; Tugrul *et al.,* 2002) should affect primary and bacterial production, phytoplankton and the composition of microbial communities (Peliz, 2013; Giannakourou *et al*., 2014) and indirectly control the abundance and composition of zooplankton through a bottom-up effect (Verheye & Richardson, 1998). The influence of the different water masses and their physical and trophic (in terms of chl α) characteristics, was clearly confirmed by the CCA results, since salinity, temperature and chl α accounted for the formation of the first axis of the small mesozooplankton samples analysis. Salinity together with the strength of the halocline also accounted for the differentiation of the large mesozooplankton samples.

The influence of the environment on the seasonal dynamics of community composition is more evident as regards the dominant species that revealed very important variability. The development of the *E. nordmanni* population in the upper layer of MD1 and MD2 in March, should be related to the simultaneous high abundance of large diatoms (and the resulting high chl α values) (Peliz, 2013), since this species was found to select large diatoms actively (Katechakis & Stibor, 2004). This relationship was confirmed by the CCA results. In contrast, this cladoceran was not found at station MD3 where large diatoms did not prevail; in addition, the depth of the latter station (300 m) is unfavorable for cladoceran population development, which depends on the hatching of resting eggs (Egloff *et al.,* 1997).

The temporal variability of *C. typicus* is of particular interest, since its abundance increased one hundred fold within a month (from March to April). The observed high abundance values in April-May coincide with the seasonal cycle of the species in the Mediterranean Sea where major peaks are observed in April-June (Mazzocchi *et al.,* 2007). Most likely, the great quantity of large diatoms in March at MD1 enhanced the population growth of *C. typicus* in the March-April period; this copepod was found selecting larger phytoplankton cells among phytoplankton (Tomasini & Mazza, 1979). Interestingly, at station MD1, *C. typicus* was also very abundant in May; maintenance of the population should be supported by the increased number of ciliates in April-May (Giannakourou *et al*., 2014) and of dinoflagellates in May (Peliz, 2013). According to Calbet *et al.* (2007), this copepod prefers ciliates or dinoflagellates when both phytoplankton and microzooplankton are available, displaying inconsistent selective behaviour (Broglio *et al.,* 2004). The role of food availability for the population increment of *C. typicus* is also evident from the lower numbers encountered at station MD2 and even less at MD3, as well as from the CCA results, since the species was positively related to chl α. In addition, the availability of ciliates as food declined gradually from MD1 to MD3, especially in the upper layer (Giannakourou *et al*., 2014). The above observations are in accordance with the statement that *C. typicus* is not tolerant to starvation (Dagg, 1977). It is interesting to note that the abundance of *C. typicus* decreased slightly from April to May both at MD1 and MD2, while the opposite occurred at MD3 (though with much lower numbers than at MD1 and MD2). Di Capua & Mazzocchi (2004) noted that in open-oligotrophic waters the peak of the above species appears one month later and is much lower than in coastal waters. Changes in phytoplankton phenology have been found to affect the seasonal succession of mesozooplankton (Tommasi *et al.,* 2013); indeed, peak of chl *α* was delayed by one month at station MD3 (in April instead of March) (Peliz, 2013). The increment of *C. typicus* at MD1 in April-May in parallel to the decline of *A. clausi* abundance is remarkable; both species were found to be more or less equally abundant in April and May during previous studies in the north Aegean Sea (Zervoudaki *et al.,* 2006; Siokou-Frangou *et al.,* 2009; Siokou *et al.,* 2013). In addition, they present a parallel seasonal cycle with overlapping peaks of similar abundance in the Gulfs of Naples and Saronikos (Christou, 1998; Mazzocchi *et al*., 2011). Most likely, *C. typicus* took more advantage of the available food compared to *A. clausi* at station MD1 during the study period. According to Mazzocchi *et al.* (2011), available autotrophic food apparently acts on different phases of population development of *C. typicus* and *A. clausi,* which present different response to environmental forcing.

The increased numbers of the herbivore *C. helgolandicus* among large mesozooplankters at stations MD1 (April and May) and MD2 (April) should be also related to the availability of large diatoms in March (Peliz, 2013) and ciliates in April (Giannakourou *et al*., 2014). Its absence at station MD3 is most likely due to the paucity of phytoplankton and ciliates (Peliz, 2013; Giannakourou *et al*., 2014), since it has been found to be abundant in the less oligotrophic regions of the Mediterranean Sea (Bonnet *et al.,* 2005), especially in upwelling and frontal areas (Boucher, 1984).

Therefore, it appears that at station MD1, permanently influenced by BSW, the important change in phytoplankton community composition in March triggered the major shift in the mesozooplankton community, which occurred one month later. Tommasi *et al*. (2013) noted that the change between the winter-spring and spring-summer community occurred about two weeks after the phytoplankton bloom. The composition of the small mesozooplankton presented some differences between the upper and lower layer at station MD1; however, changes in the lower layer occurred in parallel to the upper layer, but they were not so pronounced (as shown by the shorter distances between months in the MDS plot). Differences between layers are most likely related to the strength of the halocline at MD1, as revealed by the CCA analysis. During the study period, phytoplankton and protozoa peaked mostly above or within the halocline from March to May (Peliz, 2013; Giannakourou *et al*., 2014). Metazooplankters were found to behave differently to haloclines (residence in or near the halocline, below the halocline, above the halocline), which is probably related to the distribution of biological and physical factors between strata (Lougee *et al.,* 2002). Among them, food, predators, competitors and turbulence (which affects feeding), seem to play a major role (Ambler *et al.,* 1985; Orsi & Mecum, 1986; Saiz *et al.,* 1992). Differences between layers smoothed at MD2 and even more at MD3, in accordance with the gradual homogenization of the water column.

The structure of the copepod community also differed between stations and layers and revealed a seasonal evolution. The copepod community (small and large sized) was highly diversified in December at all stations, the period of minimum influence exerted by BSW during the study period. In addition, the contribution of appendicularians and chaetognaths, which play a different role in the pelagic food web (small particle filter feeders and carnivorous predators respectively), was quite important. Based on the above, we could consider that the small and large mesozooplankton community was probably at the mature stage in (sensu Frontier, 1985) in December. The strong gradual decrease of diversity index values to the minimum value in April in the upper layer of MD1, suggests increasing instability of the environment related to the variability of hydrology (BSW influence) and phytoplankton (Peliz, 2013). In contrast, the copepod community continued to be highly diversified during the entire study period at station MD3, most probably reflecting the stability of the environment given the open and very oligotrophic character of the area. The continuous important presence of large predators (chaetognaths and siphonophores) at this station contributes to the maturity of the mesozooplankton community. The moderate changes at station MD2 apparently reflect the intermediate position of the station, between a highly variable and a stable environment. Similar spatial variability of diversity index values was also observed across the same frontal area both in September and April with lower values in the upper layer of the stations occupied by BSW (Zervoudaki *et al.,* 2006). A gradual increment of diversity index values and carnivore dominance was observed from estuaries and stratified areas towards shelf waters and deep regions (Estrada *et al.,* 2012; Rakhesh *et al.,* 2013). The latter authors suggested that such an increase in taxonomic diversity would, in turn, increase the average number of planktonic trophic links. In addition to the spatial variability of diversity index values in relation to sampling station depth, a clear seasonal variability was also discerned with high diversity index values in winter months compared to summer months, due to the important inflow of offshore waters during the former period (Siokou-Frangou, 1996). A similar seasonal pattern was observed in the north Adriatic Sea, due to the northward advection of water masses (Camatti *et al.,* 2008).

As arising from the results of the present study, the seasonal succession of zooplankton community composition (all size fractions) was spatially and temporally differentiated in the study area in relation to the variability of the abiotic and biotic parameters of this particular environment. The increasing influence of inflowing Black Sea water (as depicted by salinity variations) at the trophic state of the station closest to the Dardanelles Strait seems to be an essential factor for the observed significant differences between months in community composition and structure. Variations in the community composition of phytoplankton and protozoa should act additionally for the quick shifts in species abundance and dominance. The March-April period was found to be very crucial for zooplankton seasonality (mostly for small and large mesozooplankton) and probably for the planktonic food web of the station permanently positioned in the front. The abundance of large diatoms in March (Peliz, 2013) and the high dominance of *C. typicus* in April, accompanied by the herbivore *C. helgolandicus,* suggest the prevalence of a classical food chain in the in-between period. Considering the maintenance of the large population of *C. typicus* until May, combined with the increment of heterotrophic nanoflagellates and ciliates in April (Giannakourou *et al*., 2014), we can assume a change towards a microbial or a multivorous food web. Zooplankton temporal variability (e.g. seasonal succession, short-term changes of several properties) was found to be affected by hydrological features such as fronts and upwellings (Alcaraz *et al.,* 2004; Escribano *et al.,* 2007). Strong spatial differentiation of small mesozooplankton was depicted in the same area (Zervoudaki *et al*., 2006; Siokou-Frangou *et al*., 2009); the above findings combined with the observed seasonal patterns in the present study, suggest that zooplankton reflects an unstable environment close to the Dardanelles Strait due to the inflowing water mass. This influence was furthermore evidenced by the gradual smoothing of the temporal variability moving southwards to the deeper, very oligotrophic station, permanently covered by LW. However, changes in community composition during the March-April period, even of different strength, were a common feature for all zooplankton fractions in the entire study area, suggesting the existence of a common triggering factor. Although we have information on the differences in zooplankton community composition in the study area between spring and summer (Isari *et al.,* 2006; Zervoudaki *et al.,* 2006, Siokou-Frangou *et al.,* 2009), it appears very interesting to study the entire seasonal cycle in order to depict the degree of temporal and spatial variability in a highly diversified environment, of high interest for pelagic production. The seasonal variability in the area not affected by BSW could provide us an idea of future changes in zooplankton dynamics and consequently fisheries, in case of decreased BSW inflow in the north Aegean Sea due to climate change.

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