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Mesozooplankton in the open Black Sea: Regional and seasonal characteristics



Elena G. Arashkevich ^{a,*}, Kremena Stefanova ^b, Vinko Bandelj ^c, Ioanna Siokou ^d, Tuba Terbiyik Kurt ^e, Yesim Ak Orek ^f, Florin Timofte ^g, Alexander Timonin ^a, Cosimo Solidoro ^c

^a Shirshov Institute of Oceanology RAS, 36 Nakhimovsky pr, 117977 Moscow, Russia

^b Institute of Oceanology (BAS), Department of Marine Biology and Ecology, P.O. Box 152, Varna 9000, Bulgaria

^c OGS – Ist. di Naz. Oceanografia e di Geofisica Sperimentale, B.go Grotta Gigante-Briščiki 42/c, 34010 TS, Italy

^d Institute of Oceanography, Hellenic Centre for Marine Research (HCMR), Anavyssos, Greece

^e Faculty of Fisheries, University of Çukurova, Sarıçam, 01330 Adana, Turkey

^f Middle East Technical University, Institute of Marine Sciences (METU-IMS), P.O. Box 28, 33731 Erdemli, Mersin, Turkey

^g National Institute for Marine Research and Development "Grigore Antipa", Constantia, Romania

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ABSTRACT

Coordinated cruises conducted in the Black Sea offshore waters in spring and autumn 2008, within the framework of European project SESAME, allowed the obtainment of a quasi-synoptic picture of the mesozooplankton standing stock and community composition. A clear spatial difference in total abundance was observed in spring with higher values over the slope than over the deep basin, due to the development of the fast boundary current. In autumn, standing stock was lower than in spring; weakening of the boundary current and extensive eddy formation caused small-scale variability in mesozooplankton distribution and intensification of the exchange between the different parts of the sea. In both seasons, copepods comprised the bulk (62–95%) of mesozooplankton biomass. Community composition variability was tested for the first time using data obtained from the entire basin; the application of neural network analysis (Self-organizing Maps) revealed a rather homogenous picture of community composition. The development of cladocerans in autumn resulted in the differentiation of the slope areas from the deep basin. Mass development of the heterotrophic dinoflagellate *Noctiluca scintillans* was observed in the western and north-western areas in autumn. No change in standing stock values and community composition seem to have occurred since 2000 in the north-eastern region.

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1. Introduction

The Black Sea is a deep basin (maximum depth 2200 m) with narrow shelves (except the north-western shelf), characterized by permanent anoxia below the sharp halocline. The depth of the oxic/anoxic boundary varies at temporal and spatial scales within the 100-200 m depth interval, depending on the water dynamics (Murray et al., 1991; Tugrul et al., 1992; Vinogradov and Nalbandov, 1990). Water circulation is dominated by a boundary current, whose instability stimulates crossshelf water exchange and lateral mixing (Ozsoy and Unluata, 1997; Sur et al., 1994). The Black Sea is a nearly enclosed basin; water exchange with the Mediterranean Sea is restricted through the Turkish Straits System. The north-western and western regions are more eutrophic than the eastern one, due to the Danube runoff (Humborg et al., 1997; Yunev et al., 2005), while the south-western region is influenced by the Mediterranean waters penetrating through the Bosphorus (Kovalev et al., 1998a). The limited exchange with the World Ocean and the small thickness of the oxygenated layer, make the Black Sea ecosystem very sensitive to the influence of external forcing. In the Black Sea, the pattern of the spatial distribution of mesozooplankton is highly dependent on water dynamics (Arashkevich et al., 2002b; Ozsoy and Unluata, 1997; Sur et al., 1994; Zatsepin et al., 2003).

During the last decades, the pelagic community of the Black Sea revealed dramatic changes due to several biotic and abiotic pressures. Eutrophication (Humborg et al., 1997; Yunev et al., 2005), overfishing (Daskalov, 2002), climate variability (Oguz et al., 2006), and the development of the non-indigenous ctenophores *Mnemiopsis leidyi* and *Beroe ovata* (Kideys et al., 2005) were the main pressures and their effects on the ecosystem have been discussed extensively from different perspectives. In the early 90s, the abrupt decrease in mesozooplankton biomass reflected the deep changes occurring at the different levels of the pelagic food web; this was associated with top-down and bottom-up controls, enhanced by a cooling climate (Kideys, 2002; Kovalev et al., 1998b; Oguz, 2005).

A limited number of studies have been performed at basin scale in the last decades (Gruzov et al., 1994; Shushkina et al., 1987; Vinogradov et al., 1991). The survey carried out in August–September 1989 offered the best coverage of the basin and revealed biomass differences along the west–northeast axis (Vinogradov et al., 1991). In contrast, the data

^{*} Corresponding author. Tel.: +7 499124 7749; fax: +7 499124 5983. *E-mail address:* aelena@ocean.ru (E.G. Arashkevich).

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obtained in different seasons during the 1992–93 period from the northern half of the sea did not confirm any longitudinal difference in mesozooplankton abundance (Gruzov et al., 1994). However, some species revealed high sub-mesoscale spatial variability. Both Vinogradov et al. (1991) and Gruzov et al. (1994) emphasized the changes in zooplankton composition after the introduction of *M. leidyi*. The recent sub-basin scale studies in the western area (Moncheva et al., 2010; Stefanova et al., 2005) and in the north-eastern area (Arashkevich et al., 2008; Vinogradov et al., 2005) revealed a recovery of zooplankton communities as compared with the early 90s. In spite of the interannual variations in the propagation of species populations, a gradual increase of mesozooplankton biomass seems to be occurring in the western and north-eastern offshore areas.

Coordinated cruises were conducted in the Southern European Seas, in spring and autumn 2008, within the framework of European project SESAME. Mesozooplankton was studied in the Mediterranean Sea (Mazzocchi et al., in this issue) and in the Black Sea, in order to obtain a quasi-synoptic picture of the mesozooplankton standing stock and community composition in the offshore waters of both seas. The purpose of this study is to produce an overall picture of the mesozooplankton spatial distribution in the Black Sea, in terms of total abundance and biomass, community composition and structure. The study is based on samples collected at 39 stations positioned in the offshore waters; similarity among stations, as regards community composition was tested by multivariate analysis, an approach used for the first time in a study covering the entire Black Sea offshore waters. The results will also define the present state of the Black Sea mesozooplankton community in comparison with previous years.

2. Materials and methods

2.1. Data collection

SESAME cruises were performed in spring (April) 2008 and in autumn (September–October) 2008. Zooplankton samples were collected at 36 stations in spring and at 31 stations in autumn. Stations were positioned over the continental slope with bottom depths from 100 to 1900 m, and over the deep basin with bottom depth >2000 m. (Fig. 1, Table 1). Vertical hauls of nets were performed within the entire oxic zone (extending from the surface down to the depth of sigma theta = 16.2)



Fig. 1. Map of zooplankton stations sampled in spring (A) and autumn (B) 2008.

Table 1

Mesozooplankton sampling stations in the Black Sea in spring and autumn 2008, date, time, and net. J-180 – Juday net (0.1 m² mouth area, 180 μ m mesh size); N – Nansen net (0.385 m² mouth area, 100 μ m mesh size); J-150 – Juday net (0.1 m² mouth area, 150 μ m mesh size); J-200 – Juday net (0.1 m² mouth area, 200 μ m mesh size); WP2 (0.25 m² mouth area, 200 μ m mesh size).

Area	Station code	Latitude N	Longitude E	Sonic depth	Spring	Spring Autumn Net	Autumn		Net	R/V, country
				(m)	Date	Time	Date	Time	(spring/autumn)	
W	1	43°22.00	29°00.00	95	17 Apr	12:38	30 Sep	15:40	J-200	Akademik, BG
	2	43°10.00	28°40.00	93	19 Apr	14:35	3 Oct	16:20	J-200	
	3	43°10.00	28°50.00	366	19 Apr	08:02			J-200	
	4	43°10.00	29°00.00	1200	17 Apr	17:12	3 Oct	08:45	J-200	
	5	43°10.00	29°10.00	1550	18 Apr	17:14	2 Oct	10:30	J-200	
NW	6	43°49.84	30°08.08	100	8 Apr	09:20	10 Sep	10:30	N/J-150	Mare Nigrum, RO
	7	43°45.80	30°11.98	150	8 Apr	14:00	9 Sep	11:00	N/J-150	
	8	43°42.90	30°13.42	500	9 Apr	13:00	8 Sep	09:20	N/J-150	
	9	43°38.54	30°17.14	1000	10 Apr	11:00	8 Sep	16:30	N/J-150	
	10	43°24.48	30°25.76	1500	11 Apr	10:50	7 Sep	10:00	N/J-150	
WC	11	42°58.00	29°29.00	>2000	18 Apr	07:12	1 Oct	08:40	J-200	Akademik, BG
	12	43°01.15	30°40.52	>2000	11 Apr	16:20	7 Sep	17:00	N/J-150	Mare Nigrum, RO
	16	42°29.35	30°59.76	2200	13 Apr	12:30	6 Sep	11:10	N/J-150	
	14	42°00.08	30°11.90	>2000	23 Apr	07:50	8 Oct	08:55	WP2	Bilim-2, TR
	15	42°24.01	30°51.85	2176	23 Apr	14:50			WP2	
	13	43°12.05	32°11.94	>2000	24 Apr	06:40	9 Oct	12:40	WP2	
EC	17	43°11.89	35°23.91	2093			10 Oct	15:30	WP2	
	18	43°07.26	36°13.30	2203	25 Apr	12:00			WP2	
	19	42°53.63	36°29.70	2158			11 Oct	07:40	WP2	
	20	42°35.99	36°23.97	2118			11 Oct	11:30	WP2	
	21	42°18.06	36°18.18	1483			11 Oct	17:30	WP2	
	22	43°53.53	37°30.37	2000	20 Apr	14:40	23 Sep	08:00	J-180	Akvanavt, RU
	23	43°39.88	37°20.53	>2000	20 Apr	19:40	23 Sep	12:00	J-180	
	24	43°25.15	37°9.612	>2000	20 Apr	23:30	23 Sep	16:20	J-180	
	25	43°11.83	36°59.41	>2000	21 Apr	11:00	23 Sep	23:10	J-180	
	26	43°12.03	36°59.97	2183	25 Apr	18:25	-		WP2	Bilim-2, TR
	27	43°04.17	37°23.89	>2000	21 Apr	16:50			J-180	Akvanavt, RU
	28	42°54.66	37°49.93	>2000	21 Apr	21:00			J-180	
	29	42°45.85	38°13.87	>2000	22 Apr	01:00	24 Sep	10:30	J-180	
	30	42°37.37	38°38.05	>2000	22 Apr	07:30			J-180	
	31	42°29.51	39°00.13	>2000	22 Apr	11:00	24 Sep	19:00	J-180	
	32	42°49.47	39°12.55	2000	22 Apr	16:00	25 Sep	00:30	J-180	
NE	33	44°07.59	37°40.81	1900	20 Apr	09:20	22 Sep	21:00	J-180	Akvanavt, RU
	34	44°14.95	37°46.58	1700	20 Apr	06:40	-		J-180	
	35	44°21.58	37°51.43	1000	20 Apr	04:20	22 Sep	17:30	J-180	
	36	44°30.82	37°55.92	510	19 Apr	22:30	22 Sep	13:10	J-180	
E	37	43°06.06	39°23.16	1800	22 Apr	21:40	25 Sep	03:20	J-180	Akvanavt, RU
	38	43°19.93	39°33.52	1700	23 Apr	07:50	25 Sep	08:10	J-180	
	39	43°28.27	39°37.75	900	23 Apr	09:50	25 Sep	10:30	J-180	

Table 2

Individual weights of the Black Sea zooplankton taxa (WW – wet weight (mg/ind.), DW – dry weight (µg/ind.), C – organic carbon (µg C/ind.), L – total body length (mm), T – trunk length (mm), S – source, FGS – formula of geometric similarity).

Taxon	WW	S (WW)	DW	S (DW)	С	S (C)
Calanus euxinus, CV–VI	$WW = 0.0255 * L^3$	1	0.26 WW * 10 ³	14	0.4 DW	2
C. euxinus, CI–IV	$WW = 0.0255 * L^3$	1	0.2 WW * 10 ³		0.4 DW	2
Pseudocalanus elongatus	$WW = 0.03 * L^3$	1	0.2 WW * 10 ³	2	0.4 DW	2
Paracalanus parvus	$WW = 0.03 * L^3$	1	0.2 WW * 10 ³	2	0.4 DW	2
Acartia tonsa	$WW = 0.0235 * L^3$	1	$0.2 WW * 10^3$	2	0.4 DW	2
A. clausi	$WW = 0.0235 * L^3$	1	$0.2 WW * 10^3$	2	0.4 DW	2
Centropages ponticus	$WW = 0.035 * L^3$	1	0.2 WW * 10 ³	2	0.4 DW	2
Oithona similis			0.003	3	0.4 DW	2
Calanoida nauplii	$WW = 0.0758 * L^3$	1	0.2 WW * 10 ³	4	$C = 4.906 * L^{2.505}$	4
Penilia avirostris	0.02	FGS	4	2	1.6	2
Evadne spinifera	0.3	FGS	6	2	2.4	2
Pseudevadne tergestina	0.3	FGS	6	2	2.4	2
Pleopis polyphaemoides	0.025	FGS	5	2	2	2
Balanidae nauplii	0.025	FGS	5	2	2	2
Bivalvia larvae	0.007	FGS	1.4	2	0.56	2
Gastropoda larvae	0.01	FGS	2	2	0.8	2
Polychaeta larvae	0.0015	FGS	0.3	2	0.12	2
O. dioica		FGS	$DW = 0.018 * T^{2.49}$	5	0.5 DW	6
Parasagitta setosa	$WW = 0.0018 * L^{3.08}$	7	$DW = 0.1595 * L^{3.08}$	8	$C = 0.0473 * L^{3.14}$	8
Pleurobrachia pileus	$WW = 4/3^* \pi^* (L/2) * (W/2)^2$	FGS	$DW = 28.84 * L^{2.65}$	9, 10	3.4 DW	11
Noctiluca scintillans	0.023	FGS			0.31	12, 13

References: 1 – Chislenko (1968); 2 – Hagen (2000); 3 – Richter (1994); 4 – Rey et al. (2001); 5 – Paffenhofer (1976); 6 – Gorsky et al. (1988); 7 – Båmstedt (1981); 8 – Conway and Robins (1991); 9 – Hirota (1972); 10 – Reeve and Baker (1975); 11 – Hoeger (1983); 12 – Miyaguchi et al. (2006); 13 – Tada et al. (2000), 14 – Arashkevich (unpublished data).

and at discrete layers at most stations; in this study, the results are integrated for the entire oxic zone. Five different types of planktonic nets were used: a Juday net with 0.1 m² mouth area and 180 μ m mesh (Russia), a Nansen net with 0.385 m² mouth area and 100 μ m mesh (Romania, spring), a Juday net with 0.1 m² mouth area and 150 μ m mesh (Romania, autumn), a Juday net with 0.1 m² mouth area and 200 μ m mesh (Bulgaria), and a WP-2 net with 0.25 m² mouth area and 200 μ m mesh (Turkey) (Table 1). An intercalibration exercise was performed in April 2009 within the framework of SESAME and all the above nets were tested. Total mesozooplankton abundance values were found to decrease with increasing mesh size, from 150 μ m to 200 μ m. The 100 μ m mesh net (Nansen net) underestimated total abundance due to clogging (D. Altukhov, personal communication).

The volume of filtered sea water was estimated from the area of the net mouth and the length of the released wire. In the Russian cruises, the volume of filtered water was estimated using a flow meter (Digital Flowmeter Model 23.091, KC Denmark). The samples were immediately fixed with buffered formaldehyde (4% final concentration of seawater-formaldehyde solution).

Temperature and salinity data were collected by CTD deployed at each station down to 500 m prior to mesozooplankton sampling. In order to estimate in situ chlorophyll-*a* concentration, water samples were collected at selected depths according to the CTD profile and the in situ fluorometric readings. Water was filtered through GF/F filters and chlorophyll-*a* concentration was measured spectrophotometrically in acetone extracts. The data obtained were kindly provided by SESAME



Fig. 2. Map of the satellite derived Chl-*a* concentrations averaged for the period of spring (upper) and autumn (lower) cruises in 2008. Chl-*a* was estimated from Globcolour Merged SeaWiFs, MODIS and MERIS Sensor Data (GSM semi-analytical algorithm). Figure by A. Banks (HCMR, Heraklio, Greece).

participants (see Acknowledgments section) for all stations except those positioned in the north-western Black Sea.

In order to have a view of the chlorophyll-*a* (Chl-*a*) distribution over the entire Black Sea, figures on surface chlorophyll-*a* concentration from satellite images, averaged for the sampling periods, were kindly provided by A. Banks. Daily satellite data products were downloaded from the Globcolour Project. These data were then geographically subsetted for the Black Sea using the ESA BEAM software and processed and visualized using MATLAB programs and software. The chlorophyll-*a* estimates have been calculated with the Garver, Siegel, Maritorena (GSM) semianalytical algorithm (Maritorena and Siegel, 2005; Maritorena et al., 2002) and averaged over the periods indicated.

2.2. Laboratory analyses of mesozooplankton

In the laboratory, mesozooplankton were counted in subsamples (1/2 to 1/32 depending on the amount of specimens) obtained by Stempel pipette (Bulgaria, Romania, Russia) or by Folsom splitter

(Turkey). Analysis of mesozooplankton samples for the study of species composition and abundance was performed in a Bogorov chamber under a dissecting stereo-microscope. Mesozooplankters were determined at species level and at age stages for copepods and size classes for chaetognaths and ctenophores. Mesozooplankton biomass in terms of carbon was estimated based on the individual weight of organisms (Table 2). Biomass and abundance values were standardized to g C m⁻² and 10³ × ind. m⁻², respectively. Organisms less than 200 μ m (nauplii of copepods *Paracalanus parvus* and *Oithona similis*) were not considered in the above analyses.

Taking into account the geographic position of the stations and their location over the slope or over the deep basin, we distinguished the following areas: West (W) is located over the western slope of the Black Sea, North-West (NW) is located over the north-western slope, East (E) is located over the eastern slope and North-East (NE) is located over the north-eastern slope. The area West-Center (WC) is located in the western part of the deep basin and the area East-Center (EC) is located in the eastern part of the deep basin. In most figures, the mean



Fig. 3. Distribution of total mesozooplankton abundance integrated over the entire oxic zone of the Black Sea (without Noctiluca scintillans) in spring (A) and autumn (B) 2008.



Fig. 4. Distribution of mesozooplankton abundance (A) and biomass (B) in the different areas of the Black Sea in spring and autumn 2008. Numbers under *x*-axis indicate the mesh size of the used net. The average values for each area are reported with the standard error bars.

values over areas are presented. Due to the use of different mesh size nets, average values obtained in the same areas by different mesh sizes are presented separately. Although no published results are available for the intercalibration exercise with the nets used, an attempt will be made to compare the results considering available literature.

2.3. Statistical analysis

Significance of differences among areas regarding total abundance and biomass values was tested by ANOVA (p < 0.01). In order to test similarities among stations, as regards species and group composition, and to identify characteristic features in species distribution, we used self-organizing maps (SOM). SOM has already been successfully applied in ecology (Bandelj et al., 2008; Giraudel and Lek, 2001; Lek and Guégan, 1999; Park et al., 2004). SOM is a neural network unsupervised iterative numerical algorithm (Kohonen, 2001) used 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. The multi-dimensional data are classified in a number of map units. These map units can be seen as clusters, grouping a certain set of the samples. Each map unit is described by a codebook vector, which represents the original data associated to the map unit. During the iterative learning process, areas with similar values in many parameters emerge on the SOM, so that map units with similar vectors are close to each other in the 2D dimensional map area. 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. In this study, the



Fig. 5. Mean percentage contribution of zooplankton groups to total abundance (A, B) and total biomass (C, D) in the oxic column of the Black Sea in spring (left) and autumn (right) 2008. Numbers under x-axis indicate the mesh size of the net used.

vertically integrated zooplankton abundances were analyzed using SOM.

The original zooplankton abundances were firstly 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 for MATLAB 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 quantization error (QE) (Kohonen, 2001) and the topographic error (TE) (Kiviluoto, 1996), both measures of the SOM's quality, were used in selecting the optimum map size and topology. The map units were clustered with the Ward's minimum variance method. The number of clusters to interpret was chosen in accordance with the ANOVA tests of significance, while significant differences between mean values of taxa across the clusters were tested with a post-hoc comparison, using Tukey's Unequal N HSD test (Spjøtvoll and Stoline, 1973).

Samples collected in the north-western area during spring were not considered in these analyses since they were collected with a Nansen 100 µm mesh net. This net captures higher numbers of small size animals compared to large mesh size nets (e.g., 200 µm) and it was clogged in spring 2008, which probably accounts for an underestimation of abundance (Evans and Sell, 1985; Hernroth, 1987).

3. Results

3.1. Environmental conditions

During spring, the temperature in the surface layer (upper 5 to 11 m) increased from 9 to 10 °C in NW (sampling on 8–11 April) to 10–11.5 °C in W (sampling on 18–19 April) and 13–14 °C in WC (sampling on 23–24 April). In E and NE areas temperatures varied between

12 and 14 °C and decreased in the EC area (sampling on 19–23 April). The above differences could be due to the sampling dates. Although the formation of the thermocline had started in April, it could be easily destroyed by wind forcing. The lower boundary of oxygenated zone (sigma-theta = 16.2) was at depths of 102–124 m over the deep basin and deepened down to 160–190 m over the continental slope.

In autumn, in the eastern part of the sea, the warm $(24-25 \ ^{\circ}C)$ upper mixed layer was about 20 m thick at most stations, while in the western part this layer was cooler $(19-20 \ ^{\circ}C)$ and deeper (down to $25-32 \ m$ depth). A sharp thermocline (temperature dropped by about $1.5 \ ^{\circ}C$ per meter), separated the upper mixed layer and cold intermediate water. The location of sigma-theta = 16.2 varied between 111 and 182 m among stations, and its position was deeper mostly over the deep basin.

The general distribution of phytoplankton biomass during spring and autumn 2008 is given in Fig. 2, where the surface chlorophyll-*a* (Chl-*a*) concentration, according to the satellite images, averaged over the sampling periods, is presented (figures by A. Banks). In spring, maximum values of autotrophic biomass were observed at the northwestern continental shelf. Chlorophyll-*a* concentration decreased over the slope and the deep basin of the western part of the sea (areas NW, W, WC) and even further east (area EC). Exceptionally, values seemed to be quite high over the NE and E areas. In autumn, the entire Black Sea was rather homogenous in terms of Chl-*a*, with the exception of the high values observed over the north-western continental shelf.

Satellite-derived data on Chl-*a* distribution were in good agreement with in situ measurements. In spring, in the surface layer of WC and EC, Chl-*a* values varied between 0.2 and 0.4 mg m⁻³, while maximum values $(0.7-1.3 \text{ mg m}^{-3})$ were observed at 30–50 m depth. High values were measured at the surface of the W, NE and E areas $(1.5-2.0 \text{ mg Chl m}^{-3})$. There was a typical nearshore–offshore decreasing trend and deepening of Chl-*a* maxima. In autumn, in situ analyses



Fig. 6. Mean percentage contribution of major species to total copepod abundance (A, B) and biomass (C, D) in the oxic column of the Black Sea in spring (left) and autumn (right) 2008. Numbers under *x*-axis indicate the mesh size of the net used.



Fig. 7. Copepod age structure and abundance integrated for the entire oxic zone of the Black Sea in spring (left) and autumn (right) 2008. (A–B) – *Calanus euxinus*, (C–D) – *Pseudocalanus elongatus*, and (E–F) – *Acartia clausi*. The average values of copepodite stages and adults for each area are reported with the standard error bars for total abundance. Numbers under *x*-axis indicate the mesh size of the net used.

revealed homogenous distribution of surface Chl-*a* concentrations $(0.3-0.6 \text{ mg m}^{-3})$ across the sea. In most areas, deep maxima values $(0.8-2.2 \text{ mg m}^{-3})$ were detected at shallower depths compared to spring, at 20–30 m depth.

3.2. Mesozooplankton total abundance and biomass

In spring, total mesozooplankton (referring only to metazoans) abundance varied from 85×10^3 ind. m⁻² (station 21) to $830 \times$ 10^3 ind. m⁻² (station 39). A noticeable increase of abundance was observed at the stations located over the continental slope of all areas, while low numbers were encountered over the deep basin (Fig. 3A). Considering the abundance values averaged over each area and with the same mesh size net, the highest value $[(489 \pm 181) \times$ 10^3 ind. m⁻²] was observed in area E (Fig. 4A). Comparing values obtained from the same mesh size net by ANOVA, average total abundance in W was significantly higher than in WC (200 µm mesh) and it was higher in NE and E than in EC (180 µm mesh). Biomass distribution does not reflect that of total abundance; max value was found at station 35 (5.4 g C m⁻²) and min at station 7 (0.4 g C m⁻²). High average values were recorded both over the slope (NE: 3.8 g C m^{-2} and E: 4.0 g C m $^{-2}$) and over the deep basin (WC sampled by 200 μm mesh size net: 3.2 g C m^{-2}) (Fig. 4B). Comparing the values obtained by the same net, no significant differences appeared among the relevant areas.

In autumn, total abundance was 1.2–3.1 times lower than in spring in most areas except in WC where zooplankters were more abundant than in spring. Low numbers of animals were encountered at some stations of areas EC and NE (min 46×10^3 ind. m⁻² at station 17) (Fig. 3B). Generally, mesozooplankton was more abundant in the western part of



Fig. 8. Distribution of cladoceran species in spring (A) and autumn (B) 2008. The average values for each area of the basin are reported with the standard error bars. Numbers under *x*-axis indicate the mesh size of the net used.

the Black Sea than in the eastern one (Fig. 4A), and differences were significant between WC and EC (200 μ m mesh net was used in both areas). Biomass values were 1.6 to 3.7 times lower than in spring over most of the basin (Fig. 4B); values varied between 0.26 g C m⁻² (station 6) and 3.2 g C m⁻² (station 24). Considering average values in each area, biomass was higher in NE than in the other areas, but no significant differences were detected among values obtained with the same mesh size.

3.3. Mesozooplankton group and species composition

In spring, the Black Sea mesozooplankton was by far dominated by copepods (Fig. 5, left panel), which made up 80-93% of total abundance and 66-86% of total biomass. Chaetognaths contributed significantly to biomass only (12-31%); their share in total abundance did not exceed 1%. The presence of appendicularians was important, especially in W and NW areas, followed by cladocerans, and meroplankton. The contribution of the latter group was higher in NW, NE and E (areas over the slope). Ctenophores contributed only in terms of biomass from 0.5 to 3%. The picture changed in autumn (Fig. 5, right panel) due to the higher contribution of cladocerans in terms of abundance; in NW and WC (sampled by 150 µm mesh net) their relative abundance attained 75% and their contributions to biomass were 24% and 18% respectively. In NE and E the presence of cladocerans was guite important (up to 34%), while in EC they represented only 4% of the abundance in the samples collected by 200 µm mesh net (Fig. 5B). The relative abundance of copepods was decreased respectively, although they represented more than 70% of biomass (Fig. 5D). The relative abundance of chaetognaths was more important than in spring (up to 10%), but they contributed less to total biomass (2-5%), due to the decrease of the size of individuals. Exceptionally, some large specimens were found in W and chaetognath biomass represented 16% of total mesozooplankton. Appendicularians were present mostly in W (11%) but their contribution to biomass was negligible (less than 1%).

Only nine species of copepods were found during the investigated period, and among them, Acartia tonsa, Pontella mediterranea, Anomalocera patersoni were encountered occasionally. In spring, Calanus euxinus made a very high contribution to biomass (70–94%), but low in terms of abundance (6-16%) (Fig. 6, left panel); a westeast increasing trend of total population abundance was observed, from 4×10^3 (W) to 44×10^3 ind. m⁻² (E) (Fig. 7A). Pseudocalanus elongatus was the first dominant species in terms of relative abundance in all areas (50-65%), but the second in terms of biomass (Fig. 6, left panel); it was more abundant over the slope (W, E, NE) than over the deep basin (Fig. 7C). Although Acartia clausi was more abundant above the slope (i.e., W, NE and E) than over the deep basin (Fig. 7E), its relative abundance (9-18%) did not reveal a clear spatial pattern (Fig. 6A). The contribution of Paracalanus parvus was quite significant as regards abundance (4-31%), especially in the NW and WC areas (Fig. 6A). The presence of Oithona similis was very low (relative abundance less than 1%) and exclusively in the W, E and NE areas.

During autumn *A. clausi* was the first dominant species in terms of abundance, representing 35–63% of copepods, but without a clear spatial pattern (Fig. 6B). In all areas, except in E, the *A. clausi* population was 1.5–3 times more abundant in autumn than in spring (Fig. 7E, F). A great seasonal difference was also observed in the abundance of *P. elongatus*, with decreasing abundance from spring to autumn (Fig. 7C, D); during the latter season its share varied between 7 and 33% (Fig. 6B). The contribution of *C. euxinus* to total copepod abundance was more important than in spring (10–28%) (Fig. 6B), although the abundance of the population was lower than in spring (Fig. 7A, B). This species was the major component of copepod biomass, except for area W where the contribution of *A. clausi* was significant (Fig. 6D). The relative abundance of *P. parvus* was lower than in spring (0.2–8.8%) and the species was more important to the spring that over the deep basin than over the slope (Fig. 6B), in contrast to the spring pattern. The presence



Fig. 9. *Parasagitta setosa*. Size structure and abundance integrated for the entire oxic zone of the Black Sea in spring (A) and autumn (B) 2008. The average values of different size classes (mm) for each area of the basin are reported with the standard error bars for total abundance. Numbers under *x*-axis indicate the mesh size of the net used.

of *O. similis* and *Centropages ponticus* was noticed mostly in the areas EC, E and NE (Fig. 6).

Regarding the age structure of the dominant copepod species, in both periods the older copepodites (CIV–CV) and adults dominated the *C. euxinus* population (Fig. 7A, B) contributing to total abundance of 55–99% in spring and 82–95% in autumn. The number and share of the young stages (CI–CIII) did not seem to be related to the mesh size of the nets used. In spring, the CI–CIII stages were relatively abundant in the NE, EC, and E areas only (20–45%) and in autumn, their share varied between 6% (NW) and 17% (NE). In spite of the great difference in the abundance of *P. elongatus* among areas, the population age structure was quite similar over the sea in both seasons (Fig. 7C, D) with almost



Fig. 10. *Oikopleura dioica*. Abundance integrated for the entire oxic zone of the Black Sea in spring and autumn 2008. The average values for each area of the basin are reported with the standard error bars. Numbers under *x*-axis indicate the mesh size of the net used.

equal proportions of the older stages (CV–CVI) and the younger ones (CIII–CIV). The contribution of CI–CII was negligible, even when sampling was carried out with 100 and 150 µm mesh size nets. In both seasons, the adults had a significant share in the population abundance: 30–46% in spring and 30–49% in autumn. Similarly, the *A. clausi* adults made a significant contribution to total abundance: 33–64% in spring and 30–55% in autumn. The share of copepodites I–II did not exceed 10%, and copepodites CIII–IV and CV contributed with almost equal proportions (Fig. 7E, F).

In spring, cladocerans were represented almost solely by one species, *Pleopis polyphemoides* (Fig. 8A). A few numbers of *Penilia avirostris* were found only at one station of area W. The population of *P. polyphemoides* was distributed unevenly across the basin. A big difference in abundance was observed within the western Black Sea: values were one order of magnitude higher in W than in NW and in WC. In the eastern Black Sea, a large variability within each area was observed. During autumn, *P. avirostris* dominated the cladoceran community, constituting 50–80% of the total cladoceran abundance. Abundance values were high in areas NW and WC where a 150 µm mesh was used (Fig. 8B). The

abundance of *Pseudevadne tergestina* and *Evadne spinifera* was low in all areas, especially in EC. Finally, very low numbers of *P. polyphemoides* were found in the western Black Sea, and its abundance was negligible in the eastern part.

The spring population of *Parasagitta setosa* consisted mainly of largesized (>16 mm in body length) animals, while the autumn population was dominated by small (<10 mm) specimens (Fig. 9). The seasonal change in structure from the large-size-domination to the small-sizedomination was accompanied by an increase in abundance in autumn compared to spring. In spring, the population was distributed quite evenly across the sea (except the low abundance observed in NW). Overall, there was a west–east decreasing trend of abundance in autumn.

Although the abundance of *Oikopleura dioica* was generally higher in spring than in autumn, seasonal differences were significant (ANOVA, p < 0.01) in the W area only, where the highest abundance was also reported (Fig. 10).

During the studied periods, meroplankton included the larvae of four benthic groups: bivalves, cirripeds, gastropods and polychaetes.



Fig. 11. Distribution of Noctiluca scintillans abundance (cells m⁻²) integrated for the entire oxic zone of the Black Sea in spring (A) and autumn (B) 2008.



Fig. 12. Results of the self-organizing map (SOM) for spring zooplankton. Dendrogram on map units (upper) and ordination of samples on the SOM (lower). Each sample is indicated by the sampling site and station code (see Table 1). Clusters are shown with white/gray shades and corresponding numbers.

In spring, the meroplankton was strongly dominated by bivalve larvae (80–100% of abundance) followed by polychaetes. Two other groups were encountered occasionally and made up 0–4% of meroplankton abundance. Polychaete and gastropod larvae were more abundant in area W as compared to other areas. Total meroplankton abundance was significantly higher over the slope $[(11–17) \times 10^3 \text{ ind. m}^{-2} \text{ in}$ the W and NW and $(33–44) \times 10^3 \text{ ind. m}^{-2}$ in the NE and E], than in the deep areas (up to $6 \times 10^3 \text{ ind. m}^{-2}$). In autumn, meroplankton was significantly less abundant than in spring. Over the slope, their numbers were higher $[7 \times 10^3 \text{ ind. m}^{-2} \text{ in the W and } (3–4) \times 10^3 \text{ ind. m}^{-2}$ in the NE and E], than in the deep areas (<1.8 × 10^3 ind. m^{-2}). Bivalves were still an important group (30–70% of total meroplankton) and the share of gastropods was noticeably higher in the western part of the basin than in the eastern one, irrespective of the net used.

Noctiluca scintillans is a particular component of the Black Sea mesozooplankton, since it is not metazoan. Therefore, it was not included in the estimated total mesozooplankton abundance and biomass values of this study, but its spatial distribution is presented separately herein. In both seasons, the spatial distribution of *N. scintillans* was extremely heterogeneous (Fig. 11). The numbers differed by orders of magnitude even at neighboring stations. In spring, the species

was generally more abundant in the NW, W and WC areas than in EC, E and NE, despite the use of different nets. Mass development of *N. scintillans* was observed in autumn in NW and W (Fig. 11b), where abundance values exceeded that of metamesozooplankters. In the other areas, the abundance of *N. scintillans* was almost two orders of magnitude lower. In terms of carbon biomass, *N. scintillans* never exceeded 10% of the mesozooplankton biomass in both seasons.

3.4. Self-organizing maps (SOM)

The SOM applied to spring mesozooplankton data resulted in a 4×6 map (QE = 0.130, TE = 0.000). The uppermost row of map units, dominated by all samples from the area W, is separated by empty units from the rest of the map (Fig. 12). The lower part of the map is characterized by EC samples, which are projected mainly along the bottom and bottom left part of the map. The EC samples represent 12 out of 28 samples of the spring dataset, and 11 of them are found in the lower part of the map. Most probably, their presence has an overwhelming effect on the ordination and clustering of the SOM.

ANOVA test was significant for the grouping in 2, as well as for the grouping in 3 clusters. Not surprisingly, the first partition on the SOM separated cluster 2 in the uppermost row from the rest of the map units (Fig. 12). Cluster 2 groups all the W samples along with one from each of the NE, the EC and the WC areas. The huge lower part of the map is divided in cluster 3, which occupies the bottom right corner of the map and in cluster 1, which includes the rest of the central and bottom left part of the map: cluster 3 consists mainly of samples collected over the deep basin of the Black Sea (EC, WC). The Tukey's HSD posthoc comparison among the mean values of mesozooplankton abundance in the clusters revealed that in spring only 6 out of 15 species showed significant differences across the clusters (Table 3). At the first level of partition, cluster 2 is characterized by significantly higher abundances of the cladoceran P. polyphemoides, gastropod and polychaete larvae, and the appendicularian O. dioica. This can also be seen at the second level of partition, where clusters 1 and 3 have much lower abundances compared to cluster 2 of these species. Only the difference

Table 3

Tukey's HSD post-hoc comparison among zooplankton mean values across clusters for the spring dataset. In italics are significant (p < 0.05) differences between pairs of clusters means. m = mean cluster abundance.

Partition in 2 clu	isters Clus	ter 1	Cluster 2		
Pleopis polyphen Cluster 1	noides m =	= 1190 ind.m ⁻²	$m = 17,056$ ind. m^{-2}		
Gastropoda la	rvae m =	= 0 ind. m ⁻²	$m = 164$ ind. m^{-2}		
Cluster 1		2	0.00836		
Polychaeta lar	vae m =	$= 59 \text{ ind. m}^{-2}$	$m = 1574$ ind. m^{-2}		
Cluster I Oikoplaura dia	ica m –	- 5038 ind m^{-2}	0.00600 m - 33.293 ind m ⁻²		
Cluster 1	icu 111 –	- 5556 md, m	0.00016		
Partition in	Cluster 1	Cluster 2	Cluster 3		
3 clusters					
Pleopis	$m = 985$ ind. m^-	m = 17,056 ind. m	$m^{-2} m = 1668 \text{ ind. } m^{-2}$		
polyphemoides	;				
Cluster 1		0.00259	0.98955		
Cluster 2			0.01210		
Gastropoda	$m = 0$ ind. m^{-2}	$m = 164 \text{ ind. } m^{-2}$	$m = 1$ ind. m^{-2}		
larvae		0.02477	0.00083		
Cluster 1 Cluster 2		0.02477	0.99982		
Polychaeta $m = 75$ ind		$m = 1574 \text{ ind } m^{-1}$	$^{-2}$ m = 22 ind m ⁻²		
larvae	in <i>i</i> o mai m				
Cluster 1		0.01965	0.99577		
Cluster 2			0.03856		
Oikopleura	m = 7205 ind. m	$^{-2}$ m = 33,293 ind. m	$m^{-2} m = 2981 \text{ ind. } m^{-2}$		
dioica					
Cluster 1		0.00025	0.77226		
Cluster 2			0.00024		

between clusters 2 and 3 for gastropod larvae, while important, is not statistically significant.

The SOM analysis of the autumn dataset resulted in a map of 4×8 map units (QE = 0.189, TE = 0.032). The samples from the NW area are grouped in the left upper corner (Fig. 13). The samples from the W area are all very similar and projected on one map unit. The EC samples are scattered all over the map, except in the upper left corner. The samples from the E, NE and WC areas are very different and projected way apart one from one another on the map. Yet, with the exception of the NW and W samples, the mesozooplankton populations seem quite homogenous all across the Black Sea.

This finding is also confirmed by the results of clustering (Fig. 13, upper panel), with all partitions, up to 4 clusters, being significant in ANOVA. The first partition is between the upper part of the map (cluster 1) and the lower part of the map (cluster 2). At the next partition, the upper part of the map is further divided between cluster 1 (upper left corner), with all NW samples and 2 WC samples, and cluster 3 (along the right border) comprising 3 map units with 3 EC and 1 NE sample. The lower part of the map is further partitioned in cluster 2 along the right bottom corner, with several EC and WC samples. Cluster 4, roughly the bottom left quarter of the map, groups together the five very similar W samples along with some samples mainly from the EC



Fig. 13. Results of the self-organizing map (SOM) for autumn zooplankton. Dendrogram on map units (upper) and ordination of samples on the SOM (lower). Each sample is indicated by the sampling site and station code (see Table 1). Clusters are shown with white/ gray shades and corresponding numbers.

and E areas. Notably, clusters 2 and 3 group the majority of data sampled over the deep basin while clusters 1 and 4 group the majority of samples collected above the continental slopes. Tukey's HSD post-hoc comparison (Table 4) revealed that the differentiation between clusters in autumn is due to 5 out of 17 identified species. At the first level of partition in 2 clusters, the upper part of the map is characterized by the high values of cladocerans P. avirostris, P. tergestina and E. spinifera, while the lower part of the map shows low values of these cladocerans and high values of copepod *P. elongatus*. At the second level of partition, P. avirostris and P. tergestina show significant differences in abundances, which are high in cluster 1 and low in clusters 2 and 3. E. spinifera abundances can only differentiate cluster 2 from clusters 1 and 3. At the third level of partition with 4 clusters, cluster 1 is strongly characterized by high abundances of P. avirostris and P. tergestina compared to the rest of the clusters, while cluster 2 is significantly different from all other clusters because of high abundances of P. elongatus. E. spinifera shows significantly high abundance in cluster 1 and significantly low abundance in clusters 2 and 4.

4. Discussion

4.1. Mesozooplankton abundance and biomass

The use of different types of nets was an important deficiency for the study of spatial variability. However, sampling using the same mesh size in certain areas or parts of them, allowed a comparison among areas. Namely, area W and part of areas WC and EC were sampled by 200 µm mesh nets, while areas E and NE and part of area EC were sampled by 180 µm mesh net. For both nets, a similar spatial pattern was observed in spring with higher values of total mesozooplankton abundance over the slope than over the deep basin. This pattern could be related to environmental factors. In this period, the areas positioned over the slope (W, NW, E, NE) were characterized by higher chlorophyll-a concentration than those positioned over the deep basin (WC, EC). The increased phytoplankton biomass in area E could account for the observed maximum mesozooplankton abundance. The development of the fast boundary (Rim) current over the continental slopes around the sea (A. Zatsepin, personal communication), could result in an increase of mesozooplankton abundance over the slope. Accumulation of surface living zooplankters (A. clausi, P. parvus, O. dioica as well as the younger stages of P. elongatus and C. euxinus) was attributed to this cyclonic contour-like circulation, whereas large animals inhabiting the deep layer (e.g., adults of C. euxinus, P. setosa) were not affected. Interestingly, the difference between areas over the slope and over the deep basin was observed, irrespective of the net used (i.e., different mesh sizes). It has already been noted that intensification of the Rim current leads to an increase in the abundance of the upper-dwelling zooplankters and reduced cross-shelf exchange (Arashkevich et al., 2002a,b).

Biomass distribution did not reflect that of total abundance, apparently due to the difference in size structure among areas. Indeed, areas WC and EC (all nets used) revealed increased biomass due to the very important contribution of large animals (*C. euxinus*) in contrast to areas NE and E where small-sized animals were relatively more abundant as mentioned above. Exceptionally, the NW area, where a 100 µm net was used and small-sized zooplankters dominated, revealed the lowest biomass. Dominance of small-sized animals in samples collected by fine mesh size nets has been commonly observed (Evans and Sell, 1985; Hernroth, 1987). When comparing results obtained in different areas using the same mesh size, the relatively higher contribution of small-sized zooplankters over the slope (areas W, NE, E) than over the deep basin (areas WC, EC) is noteworthy. The former areas were characterized by the increased abundance of small copepodites and nauplii.

Total abundance followed a different spatial pattern in autumn, since zooplankters were more homogenously distributed over the slope and the deep basin (for areas sampled with the same net). During this period, circulation was characterized by a weakening of the Rim current and by extensive formation of eddies from small to mesoscale size (A. Zatsepin, personal communication). This resulted in high station-to-station (small scale) variability in mesozooplankton distribution and facilitated the exchange between the continental slope and the deep basin. Indeed, no important differences were observed between slope and deep basin areas; in contrast, a west-east decrease was evident, especially between areas WC and EC. During the survey carried out in August-September 1989 and covering almost the entire Black Sea, a clear decreasing trend for biomass was observed from nearshore to offshore waters (Vinogradov et al., 1991). In addition, the values observed in the western part of the Black Sea were higher than in the eastern part (Vinogradov et al., 1991). In contrast, the data obtained during different seasons of 1992-93 in the northern Black sea did not confirm a longitudinal difference in mesozooplankton abundance (Gruzov et al., 1994).

According to the results of intercalibration, total mesozooplankton abundance values were found to decrease with increasing mesh size, from 150 μ m to 200 μ m, in parallel with a decline in the number of small-sized (<0.5 mm) organisms. Clogging of the Nansen net (100 μ m mesh size) caused undercatching of zooplankton (D. Altukhov, personal communication). Consequently, mesozooplankton abundance in the areas where a 200 μ m mesh size was used (areas W, WC and EC), could be expected to be higher than the values found during this study. However, abundance of small zooplankters was similar in the samples collected with the 150 μ m, 180 μ m, and 200 μ m mesh size nets during the periods investigated by SESAME cruises. Moreover, the proportion of small zooplankters was only 11–25% of total mesozooplankton abundance in spring and 8–20% in autumn, and the values of these proportions did not depend on mesh size. In terms of biomass, the share of the small-sized fraction was negligible (0.2–3% of total biomass) in both seasons. Due to clogging of the Nansen net, abundance and biomass might be underestimated in areas NW and WC in spring 2008. Clogging was considered to lead to underestimation of zooplankton abundance (Evans and Sell, 1985; Hernroth, 1987).

Seasonal differences in the mesozooplankton standing stock were almost similar in all areas. In spring, total mesozooplankton biomass was 1.5-3 times higher as compared to autumn in all areas, except the NW area. In 1960-80s, the seasonal cycle of the Black Sea meso zooplankton was characterized by an autumn peak (Greze, 1979), but after an outburst of the M. leidyi population in the late 80s-early 90s, the seasonal maximum of mesozooplankton biomass shifted from autumn to spring, apparently due to top-down control (Vinogradov et al., 1992). From 1993 onward, the abundance of gelatinous predators stabilized at the moderate level (Kideys and Romanova, 2001). The population of M. leidyi gradually decreased since 1999, after mass development of the ctenophore B. ovata, a predator of M. leidyi (Vinogradov et al., 2005). Therefore, the observed decrease of mesozooplankton biomass in autumn can hardly be attributed to predation. Similarly, the observed similarity of Chl-a concentration over the deep basin, between the two seasons, does not confirm a bottom-up control of mesozooplankton. However, even with an equal Chl-a concentration, the food conditions could be different due to changes in the proportion of edible/inedible phytoplankton species. Therefore, the role of bottom-up control cannot be totally excluded for the observed autumnal decrease

Table 4

Tukey's HSD post-hoc comparison among zooplankton mean values across clusters for the autumn dataset. In italics are significant (p < 0.05) differences between pairs of clusters means. m = mean cluster abundance.

Partition in 2 clusters		Cluster 1		Cluster 2
Pseudocalanus elongatus		$m = 8066 \text{ ind. } m^{-2}$		$m = 26,434$ ind. m^{-2}
Penilia avirostris		$m = 91,923$ ind. m^{-2}		$m = 9215$ ind. m^{-2}
Evadne spinifera		m = 6420 ind. m		$m = 371$ ind. m^{-2}
Pseudoevadne tergestina Cluster 1		$m = 17,263$ ind. m^{-2}		$m = 4053$ ind. m^{-2} 0.01353
Partition in 3 clusters	Cluster 1		Cluster 2	Cluster 3
Penilia avirostris Cluster 1 Cluster 2	$m = 115,600 \text{ ind. } m^-$	2	$m = 9215$ ind. m^{-2} 0.00013	$m = 38,600 \text{ ind. } m^{-2}$ 0.01508 0.49523
Evadne spinifera Cluster 1 Cluster 2	$m = 6874$ ind. m^{-2}		$m = 371$ ind. m^{-2} 0.00209	$m = 5400$ ind. m^{-2} 0.83483 0.14113
Pseudoevadne tergestina Cluster 1 Cluster 2	$m = 23,914$ ind. m^{-2}		$m = 4053 \text{ ind. } m^{-2}$ 0.00212	$m = 2300 \text{ ind. } m^{-2}$ 0.02687 0.97295
Partition in 4 clusters	Cluster 1	Cluster 2	Cluster 3	Cluster 4
Pseudocalanus elongatus Cluster 1 Cluster 2 Cluster 3	$m = 9795 \text{ ind. } m^{-2}$	$m = 40,138$ ind. m^{-2} 0.00018	$m = 4175$ ind. m^{-2} 0.88971 0.00064	$m = 9304 \text{ ind. } m^{-2}$ 0.999771 0.00020 0.913304
Penilia avirostris Cluster 1 Cluster 2 Cluster 3	$m = 115,600$ ind. m^{-2}	$m = 13,168$ ind. m^{-2} 0.00018	$m = 38,600 \text{ ind. } m^{-2}$ 0.03031 0.76316	$m = 4274 \text{ ind. } m^{-2}$ 0.00017 0.96215 0.55886
Evadne spinifera Cluster 1 Cluster 2 Cluster 3	$m = 6874$ ind. m^{-2}	$m = 542$ ind. m^{-2} 0.00603	$m = 5400$ ind. m^{-2} 0.94177 0.26843	$m = 156$ ind. m^{-2} 0.00601 0.99675 0.20996
Pseudoevadne tergestina Cluster 1 Cluster 2 Cluster 3	$m = 23,914$ ind. m^{-2}	$m = 6793 \text{ ind. } m^{-2}$ 0.01385	$m = 2300$ ind. m^{-2} 0.04618 0.93830	$\begin{split} m &= 629 \text{ ind. } m^{-2} \\ 0.00143 \\ 0.68142 \\ 0.99650 \end{split}$

of the mesozooplankton standing stock. In 2008, the decline of total biomass in autumn was partly due to substantial biomass reduction (almost by one order of magnitude) of the chaetognath *P. setosa* in all areas. This decrease is related to its life cycle: in spring, large-sized specimens dominated the population, resulting in a large contribution to total mesozooplankton biomass. In autumn, the population consisted of small-sized animals due to intense breeding in mid-summer–early autumn (Besiktepe and Unsal, 2000), which resulted in the increase of population abundance but a decrease of biomass.

The dramatic variability in the Black Sea ecosystem observed in the last decades under the cumulative effects of nutrient enrichment, strong cooling/warming, over-exploitation of pelagic fish stocks, and population outbreak of gelatinous carnivores, have provided a basis to consider the system as being in transition, with successive regime-shifts of distinct ecological properties (Oguz and Gilbert, 2007). Regular investigation of all components of the Black Sea ecosystem is extremely important in order to "track" these perturbations. Since long-term mesozooplankton data are available only for the north-eastern region, a comparison will be attempted between the historical data and the data obtained in areas NE, E, and EC with the same mesh size nets (after conversion of the carbon biomass data of this study into wet weight (see Table 2)). It is clear that mesozooplankton biomass values obtained in 2008 were as high as those measured since 2001 (Fig. 14).

4.2. Mesozooplankton groups and species composition

In spite of sampling with different nets or mesh sizes, a similar pattern of the community main characteristics was revealed. In spring, copepods and chaetognaths comprised the main bulk of mesozooplankton biomass (more than 93%) and abundance (more than 80%). In autumn, three mesozooplankton groups, namely copepods, cladocerans, and chaetognaths formed more than 95% of total abundance and biomass. The fall of the Black Sea pelagic ecosystem in the early 90s was accompanied by drastic alterations in plankton community composition. First of all, the vital changes concerned the populations of upper-dwelling species, especially those reproducing in late summer-early autumn (M. leidyi mass development season). Thus, in 1991–1994, the populations of cladocerans shrank significantly and chaetognaths nearly vanished from the Black Sea (Vinogradov et al., 1995; Zaitsev, 1992). Restoration of the pelagic ecosystem begun in 2000 (Arashkevich et al., 2002a; Lebedeva et al., 2003; Vinogradov et al., 2005) and at present the populations of cladocerans and chaetognaths play an important role in zooplankton community yet again (Moncheva et al., 2012; Nikishina et al., 2010), similar to that observed in 1970-80s (Greze,



Fig. 14. Long-term changes in mesozooplankton biomass in the north-eastern Black Sea. Data of SouthNIRO and IBSS were redrawn from Kovalev et al. (1998b). Data of SIO RAS were re-estimated from Arashkevich et al. (2002b, 2008). SESAME data for the NE, E, and EC areas were converted to wet weight for this comparison. The average values are

reported with the standard error bars.

1979; Sorokin, 1982). The large copepod *C. euxinus* was the major component of biomass, as it has already been noted in previous studies (Vinogradov et al., 1992 and citation therein). However, *P. elongatus* and *A. clausi* were more numerous than *C. euxinus* in spring and autumn, respectively. All taxa found, except the rare ones, were encountered in all samples. This quasi-homogeneity of the mesozooplankton community in the Black Sea was confirmed by SOM analyses. The peculiarity of the Black Sea water dynamics causes intensive along- and cross-shore water mixing (Zatsepin et al., 2003), which can favor the similarity in plankton community composition.

Despite the low spatial heterogeneity of mesozooplankton composition, some species revealed clear spatial patterns within the Black Sea, although sampled with different mesh size nets. Among them, the dominant species C. euxinus and P. setosa presented opposite longitudinal abundance distribution: the former showed a west-east increase in both seasons, while the latter showed a west-east decrease in autumn, but it was distributed homogeneously in spring. According to Vinogradov et al. (1991), the population of *C. euxinus* was distributed evenly across most of the sea in early autumn 1989, with a moderate decrease of abundance in the central parts. In contrast, the distribution of C. euxinus in 1992 was characterized by the several month-to-month shifts in maximal abundance from the north-east to the north-west (Gruzov et al., 1994). In both seasons of 2008, A. clausi and P. elongatus, were more abundant at the stations located over the continental slope and almost equal in numbers in the W, NE and E areas, with few exceptions. Seasonal pulsation in abundance at the spatial scale and high submesoscale heterogeneity in the distribution of these species were observed by Gruzov et al. (1994). Apparently, the propagation of the local populations depends not only on hydrophysical forcing, but also on the timing of seasonal events - as regards phytoplankton bloom and reproduction. Hence, the species population distribution patterns should be discussed also in conjunction with seasonality. For example, the populations of two cold-water species, C. euxinus and P. elongatus, revealed an important decrease of their abundance and biomass in autumn compared to spring. This could be due to their life cycle with most active reproduction in late winter (Greze, 1979).

According to the SOM analyses, very few taxa had significantly different abundances among the clusters of stations: the copepod P. elongatus, all cladoceran species, the appendicularian O. dioica, polychaete and gastropod larvae. The majority of the stations positioned over the deep basin (areas WC, EC) were discriminated from those positioned above the western continental slope (areas W and NW) both in spring and in autumn, irrespective of the net used. In spring, discrimination among the two major clusters was due to the abundance of Podon polyphemoides, O. dioica, as well as gastropod and polychaete larvae, found almost exclusively in area W. The differences in the abundance of meroplanktonic larvae could be connected to the proximity of the wide shelf to area W, providing more space for benthic animals than the narrow shelves of areas E and NE. The relatively high abundance of appendicularians could be related to food availability. These fine filter-feeders prefer small food particles (Acuña et al., 1996) and microflagellates were an important component of phytoplankton during spring 2008 in area W (Moncheva et al., 2012).

Differences among areas were more significant during autumn, mostly due to the mass development of cladocerans. The high abundance of *P. avirostris* (accompanied by *P. tergestina* and *E. spinifera*) in area NW, resulted in the discrimination of the relevant stations as well as of the neighboring WC stations (cluster 1). In contrast, the cladoceran share in the other areas was significantly lower and this difference should be attributed to the sampling dates. In the NW and partly in WC areas, samples were collected in early September whereas in the other areas sampling was performed in late September–early October. The above cladoceran species usually appear in early August, emerging from the diapausing eggs and peak in abundance in a short time (Greze, 1979; Sorokin, 1982). Most probably, their abundance was decreased in later sampling periods in the other areas.

Interestingly, high similarity was observed among the stations of area W in autumn as it was in spring; they constituted a distinct cluster (cluster 4) and they were projected on the same map unit in both seasons. In autumn, this area was characterized by the important abundance of the copepod *P. elongatus*, which was similarly abundant at some stations of areas E and EC. On the other hand, most stations of areas EC and WC were clustered together (cluster 2), characterized by the almost absence of *P. elongatus* and cladocerans. Offshore waters do not constitute a favorable environment for the development of cladoceran populations (Egloff et al., 1997) and their occurrence is generally diminished over the deep basin of the Black Sea (Arashkevich et al., 2002a; Moncheva et al., 2010).

At some stations of area EC, located rather close to the continental slope, low abundance values were recorded for *P. avirostris*, resulting in a distinct cluster (cluster 3). During autumn 2008, weakening of the boundary current and extensive eddy formation permitted water exchange between slope and deep basin (A. Zatsepin, personal communication). The above circulation pattern facilitates mesozooplankton lateral advection and thus the spreading of the *P. avirostris* population from the slope over the deep basin, resulting in small scale variability in mesozooplankton distribution. This could also account for the inclusion of stations positioned over the slope (areas E and NE) in the clusters where stations over the deep basin (WC, EC) prevailed.

Community composition also presented some differences between the two seasons. The observed shift between P. elongatus and A. clausi is related to the difference in temperature preferences of the two species: P. elongatus prefers low temperatures and reproduces mainly in the cold season, while A. clausi is a warm-water species with a maximum reproduction rate in summer-early autumn (Greze, 1979). A similar seasonal shift was related to cladocerans, which were abundant in autumn and dominated by P. avirostris, while in spring their contribution is restricted both in numbers and in species composition (only *P. polyphemoides*). The abundance of other copepod species (*P. parvus*, O. similis, and Centropages ponticus), appendicularians and meroplanktonic larvae were also different in the different seasons. Seasonality in mesozooplankton composition was often observed over the continental slope (Konsulov, 1986; Nikishina et al., 2010; Pasternak, 1983) and no differences between this and previous studies were detected. Seasonal differences were also found over the deep basin during this study, similar to those observed by Vinogradov et al. (1992).

In autumn 2008, a strong difference between the areas was due to the mass development of the heterotrophic dinoflagellate N. scintillans in areas W and NW, where its abundance was one order of magnitude higher than in the other areas. N. scintillans is an important component of the Black Sea pelagic community (Konsulov, 1984; Sorokin, 1982; Zaika, 2005). It often forms massive blooms when its concentration can reach millions of cells per square meter, exceeding the total abundance of mesozooplankton metazoans (Konsulov and Kamburska, 1998). This omnivorous species consumes a wide range of food particles intensively, from small flagellates and coccolithophorids (<5 µm) to large diatoms, copepod eggs and nauplii (200 µm and more) (Nikishina et al., 2011) and can successfully compete for food with other mesozooplankters, thereby resulting in the reduction of their abundance. It has been suggested that *N. scintillans* blooms are related to eutrophication processes (Konsulov, 1984; Shiganova et al., 2008). However, the mass development of this species has been frequently observed not only in the eutrophicated regions but also in other parts of the basin, for example, in the south-east (Erkan et al., 2000), north-east (Gruzov et al., 1994), east-central (Arashkevich et al., 2002a) and west central (Nikishina et al., 2011) regions. Therefore, it seems that bloom events of N. scintillans are not necessarily related to eutrophication, and further investigations are needed on this issue.

5. Conclusions

Coordinated cruises conducted in the Black Sea, in spring and autumn 2008 allowed us to obtain a quasi-synoptic picture of the mesozooplankton standing stock and community composition in offshore waters. The last synoptic cruise was performed in summer 1989 and since then, the Black Sea ecosystem underwent significant changes, even regime shifts (Oguz and Gilbert, 2007). Despite the use of different mesh size nets, the results of this study revealed a spatial heterogeneity in terms of standing stock and homogeneity in terms of community composition, especially in spring. The above spatial patterns were statistically tested, providing a rather robust picture of Black Sea mesozooplankton spatial variability in two seasons. This overall picture corresponds to community composition in several areas of the Black Sea, as described in previous studies carried out during the last decade. The standing stock values measured in the northeast offshore waters of the Black Sea in 2008 do not differ from those found in the area after 2000.

The data obtained during surveys in 2008, will contribute to the evaluation of the present status of the Black Sea ecosystem through mesozooplankton, the central element of the pelagic food web. Being the intermediate link between primary producers and end-consumers, mesozooplankton may serve as an indicator of the health of the ecosystem. Future investigations will show whether the Black Sea ecosystem is really subjected to frequent regime shifts or whether the observed changes were caused by the accidental series of negative factors.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at http://dx. doi.org/10.1016/j.jmarsys.2013.07.011.

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