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Seasonal variations of abundance and live/dead compositions of copepods in Mersin Bay, northeastern Levantine Sea (eastern Mediterranean)

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Abstract: The seasonality of abundance and live/dead compositions of copepods was studied in the northeastern Mediterranean Sea. Zooplankton, chlorophyll-a, and PO₄ sampling was performed on a monthly basis from March 2006 to February 2007 at both a coastal station and an open water station. At the coastal station, high phytoplankton biomass was driven by PO₄ input from the Lamas River. On annual average, copepod abundance was 53,075 and 140,227 ind. m⁻² at the coastal and open water stations, respectively. The most common copepod taxa were *Oithona similis*, *Euterpina acutifrons*, *Labidocera* spp., *Oncaea media*, and *Temora* spp. at the coastal station, and *Oncaea media*, *Labidocera* spp., *Lucicutia* spp., *Farranula* spp., *Oithona similis*, and *Microsetella* spp. at the open water station. At the coastal station, dead copepods did not exceed 7% of the population; on annual average, 2.6% of the copepods were dead. At the open water station, on average 10.6% of the copepod population appeared dead; the percentages of dead copepods reached 29.5% in April and 21.7% in May 2006, suggesting that the copepod community suffered higher nonpredatory mortality at the open water station than at the coastal station, especially in the spring.

Key words: Zooplankton, copepods, carcasses, Mediterranean Sea

1. Introduction

The main drivers of seasonality of primary producers are irradiance, temperature, and nutrient availability. In the Mediterranean Sea, nutrient availability especially limits phytoplankton production (Azov, 1991; Krom et al., 1991). Anti-estuarine circulation of the Mediterranean does not allow the accumulation of nutrients in the deeper layers; therefore, external nutrient sources such as atmosphere deposition and riverine runoff become very important for the ultra-oligotrophic eastern Mediterranean (Sioguo-Frangou et al., 2010, and references therein). In the Mediterranean Basin, the highest nutrient concentrations at the surface are usually observed during winter mixing (Fernandez de Puelles et al., 2003; Ediger et al., 2005; Eker-Develi et al., 2006). In addition to the winter mixing process, active frontal regions, deep-convection areas, wind-induced upwelling events, and river runoff may also induce nutrient enrichment (Sioguo-Frangou et al., 2010). Surface chl-a distribution derived from SeaWiFS data shows that the more productive areas in the Mediterranean Sea are the coastal and continental shelf areas (D'Ortenzio and Ribera d'Alcala, 2009). Coastal areas have variable

hydrographic characteristics and are seasonally exposed to different intensities of anthropogenic and terrestrial influences, which in turn may result in variable population structures and production of the organisms in coastal areas.

The seasonality of zooplankton in the Mediterranean Sea is compounded by local variability (Siokou-Frangou, 1996; Gaudy and Champalbert, 1998; Fernandez de Puelles et al., 2003) and interannual variabilities related to the hydrography of the area (Krsinic et al., 2007; Molinero et al., 2009). In Saronikos Gulf, maximum zooplankton abundance was observed during summer until early autumn and also partially in spring, which was related to temperature and hydrography (Siokou-Frangou, 1996). Similarly, in the Gulf of Naples, the maximum was observed during summer and the minimum was in winter (Mazzocchi and Ribera d'Alcala, 1995). In the waters around the Balearic Islands, three peaks were observed, in March, May, and September, related to the hydrographic regime of the region (Fernandez de Puelles et al., 2003). In İskenderun Bay, NE Mediterranean, spring and autumn peaks in mesozooplankton abundance were defined, and

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related to temperature and salinity (Kurt-Terbyik and Polat, 2012). Uysal and Shemeleva (2012) have shown that seasonality in the copepod community is driven mainly by temperature in the shelf waters of Mersin Bay. Comparison of zooplankton time-series data from six stations in the Mediterranean Sea has highlighted the dominance of local climatic and anthropogenic drivers on coastal zooplankton dynamics (Berline et al., 2012). In the region near the Lamas River, Mersin, riverine input has a strong influence on nutrients and plankton, especially in spring (Tuğrul et al., 2005; Eker-Develi et al., 2006; Yılmaz Zenginer and Beşiktepe, 2010). The response of planktonic organisms to dust deposition and P addition (Pasternak et al., 2005; Psarra et al., 2005; Thingstad et al., 2005) was studied in the eastern Mediterranean. Pasternak et al. (2005) observed rapid feeding and egg production response of mesozooplankton communities following P addition in a mesoscale Lagrangian experiment carried out in the ultraoligotrophic Cyprus Eddy in the eastern Mediterranean Sea. Thus, we expect to see similar responses to the natural nutrient enrichment by the Lamas River in the studied area.

Seasonal variability of environmental conditions can affect the survival of organisms. There is increasing evidence that zooplankton carcasses are prevalent in the marine environment resulting from different causes of nonpredatory mortality, such as senescence, toxins, diseases, and food limitations (Tang and Elliott, 2014; Tang et al., 2014). Exclusion of carcasses can lead to significant errors in understanding zooplankton population dynamics and related ecological processes (Elliott and Tang, 2011a). Globally, nonpredatory mortality can account for 25%–33% of the total mortality among marine epipelagic copepods (Hirst and Kiørboe, 2002). Traditional zooplankton sampling ignores the live/dead status of the animals because examining individual zooplankters for vital signs is time-consuming and often impractical in field studies. The

recently improved Neutral Red vital staining method allows researchers to easily and quickly quantify zooplankton carcasses in field samples (Elliott and Tang, 2009). In Chesapeake Bay, high percentages of dead *Acartia tonsa* nauplii and copepodites were observed in summer and early fall concurrent with and after the peak annual abundance (Elliott and Tang, 2011b). In marine environments, generally there are high numbers of carcasses in polluted areas (Kulikov, 1990; Pavlova and Melnikova, 2011) and in deep layers (Vinogradov et al., 1998). Despite the many studies conducted in the eastern Mediterranean, there have been limited investigations on the seasonality and ecology of copepods in the northeastern part of the Levantine Sea. In addition to the copepod checklist reports (Uysal et al., 2002), the seasonality of zooplanktonic organisms (Yılmaz Zenginer and Beşiktepe, 2010) and copepod species has been studied only recently (Kurt-Terbyik and Polat, 2012; Uysal and Shmeleva, 2012), and no studies have included live/dead copepod compositions in the region. In the present study, abundances, taxonomic compositions, and live/dead copepod compositions in both open and coastal waters in relation to environmental variables were examined to enhance our understanding of the seasonality of copepods in this food-limited environment in the eastern Mediterranean Sea. We predicted that the zooplankton community would be different between the open water station and the coastal station in terms of abundance, composition, and live/dead proportions.

2. Materials and methods

2.1. Physico-chemical parameters

Monthly sampling was done from March 2006 to February 2007 at a coastal station (36°33.5'N, 34°15.6'E; ~20 m depth) and an open water station off Erdemli (36°26'N, 34°21'E; ~200 m depth) (Figure 1) aboard the R/V Lamas (Middle East Technical University). Sampling was not done in October 2006 due to severe weather conditions.

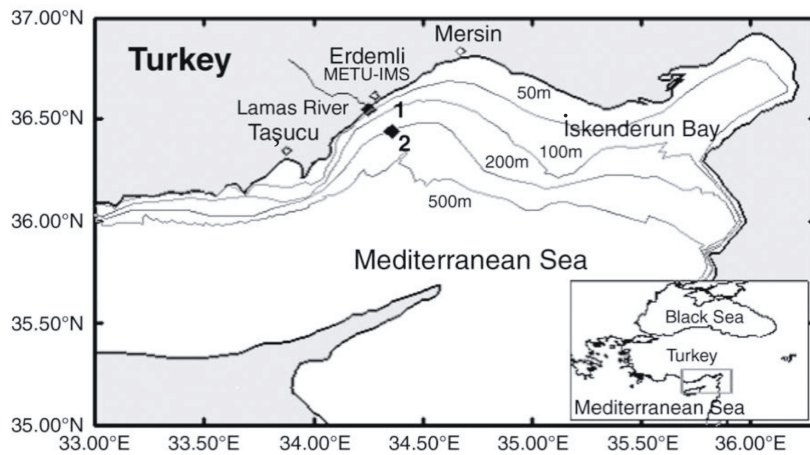


Figure 1. Locations of the sampling stations.

Water temperature and salinity were recorded using a multiparameter probe (Seabird SBE 19 plus). Due to technical problems, we lost the CTD data from August at the coastal station. Water samples for chlorophyll-a (chl-a) and PO_4 measurements were collected from the upper 4 m with a 5-L Niskin water bottle. For chl-a measurements, samples were filtered onto Whatman (GF/F) filters and analyzed fluorometrically (Hitachi F 3000 fluorometer) after 90% acetone extraction. Ten-milliliter water samples were stored at -20°C until measurement of inorganic PO_4 using a Technicon Model multi-channel auto analyzer (Murphy and Riley, 1962).

2.2. Zooplankton sampling

Zooplankton samples were collected vertically from 5–7 m above the bottom to the surface using a Nansen closing net with a 70-cm mouth diameter and 100- μm mesh size. Tow depth was always corrected for wire angle. Samples were taken between 0830 and 1200 hours. Haul speed was $<0.5\text{ m s}^{-1}$ to avoid artifact mortality (Elliott and Tang, 2009). Duplicate tows were carried out each time, and the net was thoroughly rinsed between tows. Zooplankton from the first tow were stained with Neutral Red for sorting live/dead copepods according to Elliott and Tang (2009): 1.5 mL of Neutral Red stock solution (10 g L^{-1}) was added to 1000 mL copepod sample volume and allowed to stain for 15 min; the sample was then rinsed with alkaline filtered seawater (pH 9) into a container for preservation (10 mL 37% formaldehyde per 100 mL sample volume). Samples were kept in a refrigerator until counting. Samples were counted within 3 days of staining using a stereomicroscope with a dark field. Before counting, 1 mL of acetic acid/sodium acetate mixed solution for every 50 mL sample volume was added to acidify the samples. A subsample was taken from each bottle, and around 700–3000 individuals (nauplii + copepodites + adults) were counted as live (stained bright red) or dead (unstained or light pink). Zooplankton from the second tow were preserved with borax-buffered formaldehyde (5% final concentration) in 250-mL bottles for abundance and taxonomic identification. After observing a high percentage of dead copepods in April at the open water station, beginning in May 2006, 2 discrete strata (~195–100 m and 100 m–surface) were sampled to investigate the vertical distribution of dead copepods at this station. In the laboratory, formaldehyde-preserved zooplankton samples were subsampled using a Folsom splitter; around 300–400 individuals were enumerated and identified. Dominant calanoid copepods were classified to genus; cyclopoid copepods were identified to the species level.

2.3. Statistical analyses

Similarities among samples were estimated by using the Bray–Curtis similarity index, and clustering of samples was performed using group average linkage. Abundances

were transformed using $\log(X + 1)$ function to reduce bias caused by dominant species. SIMPER analysis was applied to evaluate species contributions to similarity among groups obtained by cluster analysis. Adult and copepodite stages were taken into consideration in the analyses. The Shannon–Wiener index (H') was used to analyze biodiversity among the adult copepods. Primer v5 was used for all of these analyses (Clarke and Gorley, 2006). The relationships between environmental variables and copepod abundance and percentage of dead specimens were explored by Pearson correlation.

3. Results

3.1. Seasonal variability of environmental conditions

Surface water temperature (average of the upper 4 m) at the coastal station began to increase by April (Figure 2a), and thermal stratification was observed in June at 6–11 m. The surface temperature ranged between 16.5 (February) and 29.1 (September) $^\circ\text{C}$, and the surface salinity (average of upper 4 m) ranged between 35.6 (April) and 39.6 (September) (Figure 2a). At this station, spring and summer chl-a peaks coincided with the PO_4 maximum (Figure 2a). During the springtime chl-a maximum (April), runoff from the nearby Lamas River reduced the salinity to 36.2 in the upper 4 m (Figure 2a). During the summer peaks of chl-a and PO_4 in August, we unfortunately did not have CTD data, but the river plume was clearly visible based on its color. A negative significant correlation was observed between salinity and PO_4 (Pearson correlation, $r = -0.823$, $P < 0.002$). Chlorophyll-a correlated positively with PO_4 (Pearson correlation, $r = 0.904$, $P < 0.001$), but negatively with salinity (Pearson correlation, $r = -0.855$, $P < 0.002$). No correlation was found between chl-a and temperature.

At the open water station, the surface water temperature and salinity ranges were 16.8–29.6 $^\circ\text{C}$ (February–August) and 38.9–39.7 $^\circ\text{C}$ (April–August), respectively (Figure 2b). The water column showed a seasonal cycle of stratification and mixing. Vertical mixing of the water column was observed in January–April when chl-a concentrations were relatively high (Figure 2b). The thermocline was usually well established by May, and maximal thermal stratification occurred during July, August, and September. Throughout the year, PO_4 concentrations were very low, and mostly at the detection limit level of 0.02 μM . There was a weak negative correlation between chl-a and surface water temperature ($r = -0.585$, $P = 0.058$), but no correlation was found with salinity and PO_4 .

3.2. Copepod abundances and taxonomic compositions

Zooplankton abundance varied seasonally from 17,000 (February) to 227,781 (June) ind. m^{-2} at the coastal station (Figure 3). Peak zooplankton abundances appeared 1–2 months after the spring and summer chl-a maxima, suggesting recruitment fueled by phytoplankton

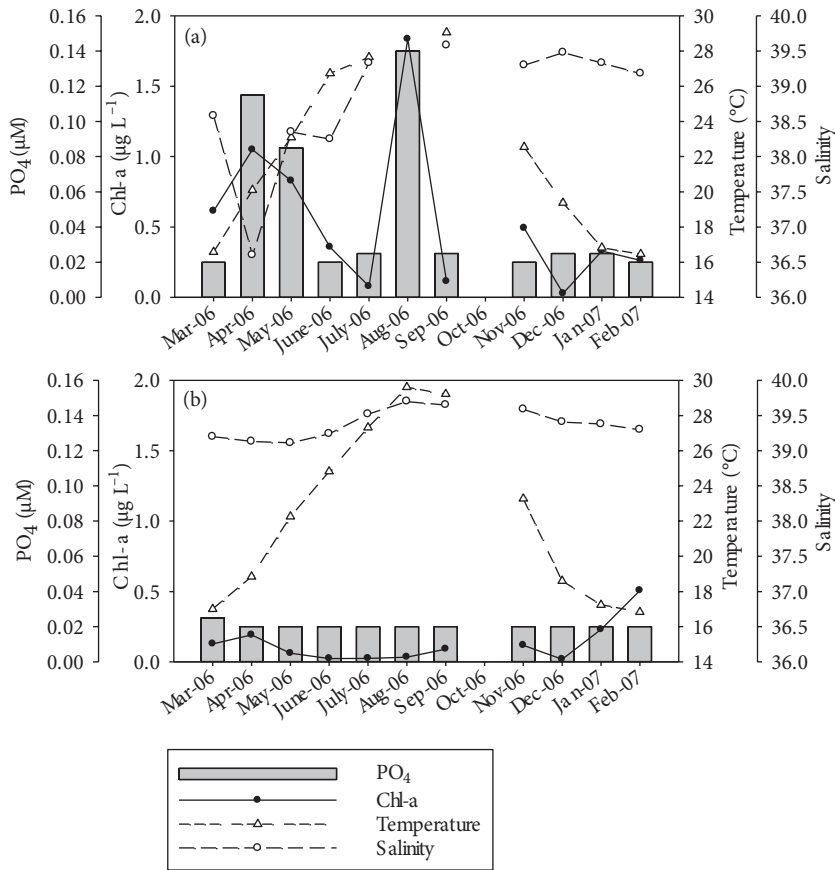


Figure 2. Monthly values of temperature, salinity, PO₄, and chl-a concentrations at the coastal (a) and the open water stations (b).

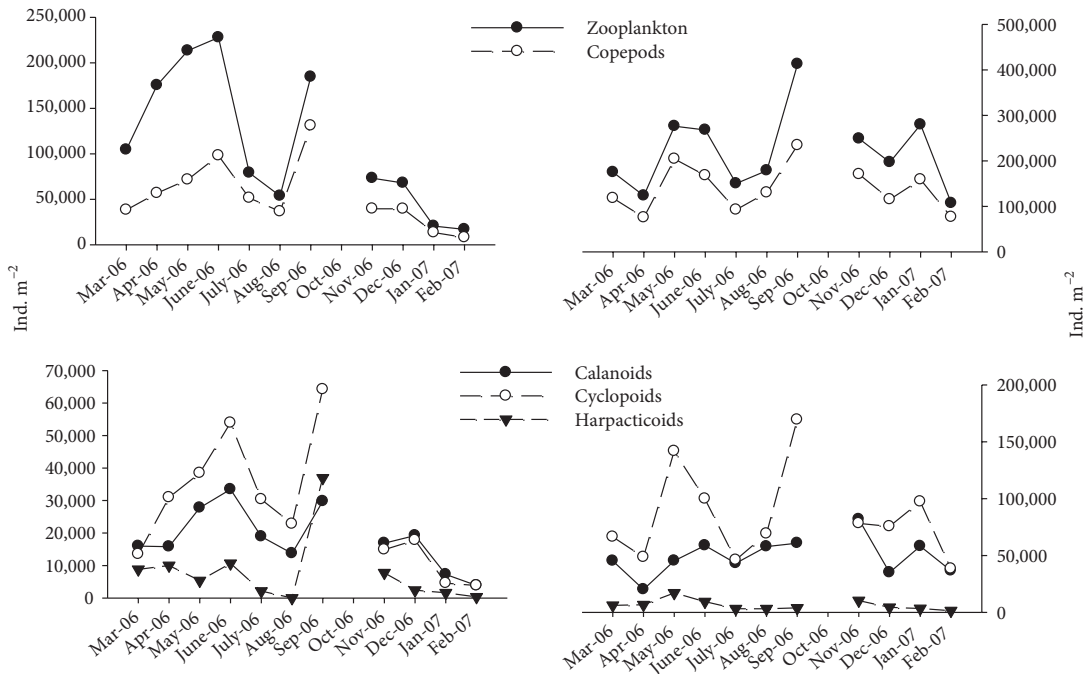


Figure 3. Monthly abundances of zooplankton and copepods, and total calanoid, cyclopoid, and harpacticoid copepods at the coastal (left) and open water (right) stations.

production. Zooplankton abundance was significantly correlated with temperature (Pearson correlation, $r = 0.683$, $P < 0.05$, excluding August due to missing temperature data).

On annual average, copepods (copepodites + adults) comprised 48% of the total zooplankton abundance. Other dominant groups were cladocerans, appendicularians, cyprid larvae, polychaeta larvae, pteropods, and chaetognaths; their contributions to the total zooplankton abundance were 13.5%, 8%, 4%, 1.7%, 0.8%, and 0.6%, respectively. Copepod nauplii and protozoans were important contributors to the total zooplankton abundance (11% and 6.9%, respectively), although they were not efficiently collected by the 100- μ m mesh net.

The abundance of copepods ranged from 8061 (February) to 130,945 (September) ind. m^{-2} , with an annual average of 53,075 ind. m^{-2} (Figure 3). Peak copepod abundances coincided with peak zooplankton abundances in June and September.

Cyclopoid (adult + copepodite) copepods were the most abundant group in spring and summer, comprising 34% (January) to 62% (August) of all copepods (Figure 3). Harpacticoids showed low abundance throughout the year, representing less than 20% of total copepods, except in March (23%) and September (28%) (Figure 3). Copepod nauplii were abundant in spring and early summer (Figure 4). Nauplii abundances could have been underestimated because of the relatively large mesh size

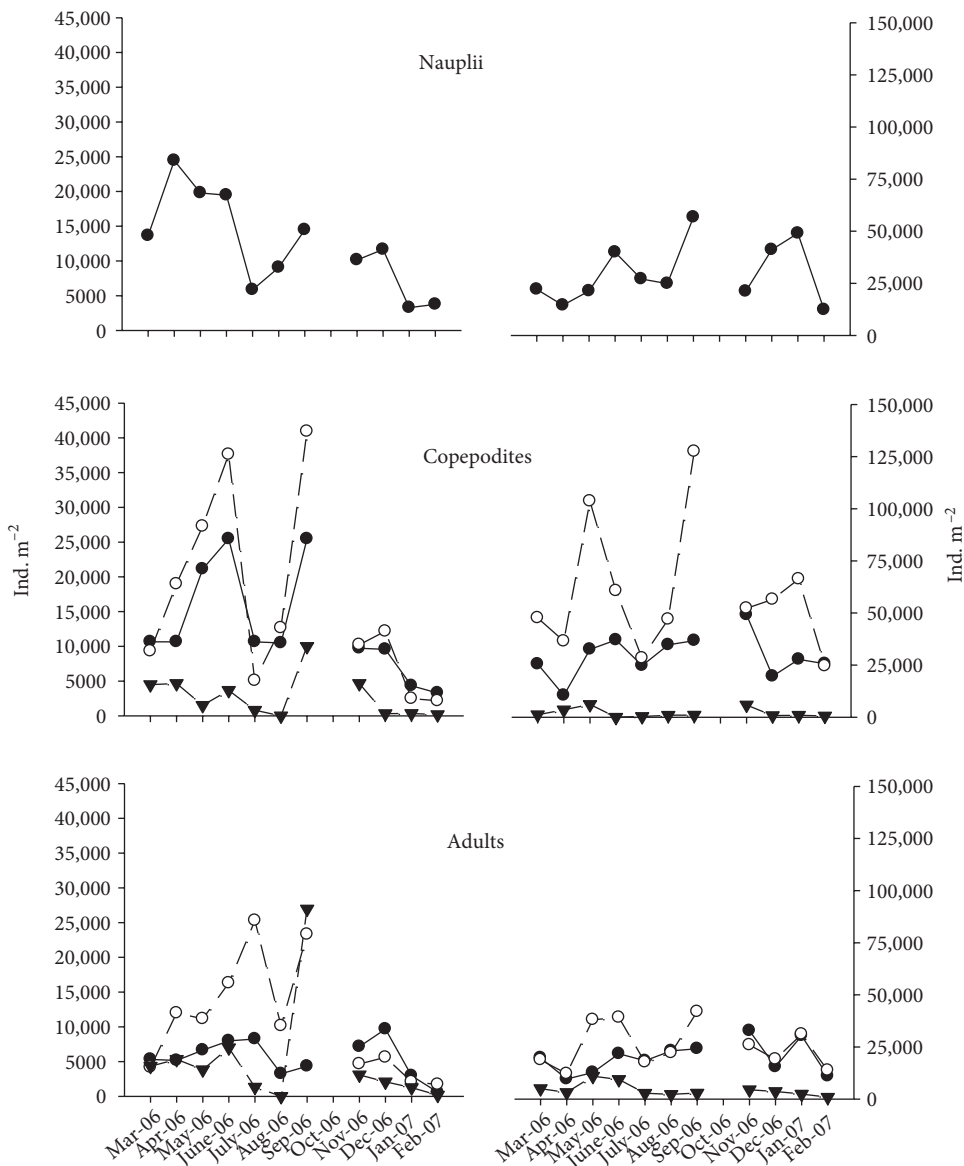


Figure 4. Monthly abundances of nauplii, copepodites, and adults of calanoid (●), cyclopoid (○), and harpacticoid (▲) copepods at the coastal (left) and the open water (right) stations.

used for sampling (cf. Elliott and Tang, 2011a). A large population of cyclopoid copepodites (especially *Oithona* spp. and *Oncaea* spp.) occurred in May–June (Figure 4b), which apparently matured into adults in July (Figure 4). Continuous spawning by adult cyclopoid copepods may explain the increase in copepodite abundance again in August and September. During the winter time, calanoids were the dominant copepod group, except in February when calanoids and cyclopoids together accounted for 48% of all copepods (Figure 3). The contributions of adult *Acrocalanus* spp. and *Labidocera* spp. to the calanoids were high in December and January (Table 1; Figure 4). In September, adult harpacticoids (*Euterpina acutifrons*) dominated the adult copepod community (Table 1). Abundances of copepodites and adults of both calanoids and cyclopoids were correlated only with temperature ($r \geq 0.644$, $P < 0.05$); only adult harpacticoids were correlated with temperature ($r = 0.65$, $P < 0.05$).

A total of 48 adult copepod taxa were observed at the coastal station, and the diversity index (Shannon–Wiener $-\log_e$) was highest (2.64) in November and December, and lowest (1.54) in July. Five adult copepod taxa were the most common regardless of season: *Oithona similis*, *Euterpina*

acutifrons, *Labidocera* spp., *Oncaea media*, and *Temora stylifera*. The cyclopoid copepod *O. similis* was abundant throughout the year with its maximum abundance in July. *Oncaea media* was abundant in spring and early autumn (Table 1). On annual average, *O. similis* and *O. media* made up about 25% and 6% of all adult copepods, respectively. Among the calanoids, the genus *Labidocera* was abundant in summer, late autumn, and winter, while *T. stylifera* was dominant in spring and early summer. Two harpacticoid copepod species were observed in the samples: *Euterpina acutifrons* and *Microsetella* spp. *Euterpina* (adult + copepodites) was the dominant harpacticoid species; it reached high abundance in September (35,606 ind. m^{-2}). Among the abundant adult copepods, only *O. similis* showed a positive significant correlation with temperature (Pearson correlation, $r = 0.69$; $P < 0.03$), whereas the others were not correlated with temperature, salinity, or chl-a.

At the open water station, zooplankton abundance varied between 106,861 (February) and 412,635 (September) ind. m^{-2} (Figure 3). Three main peaks were observed, the highest being in September. Starting in May 2006, zooplankton samples were collected from 2 depth strata: 100 m–surface and 195–100 m. On

Table 1. Common copepod species abundance (ind. m^{-2}) at the coastal station.

	Mar. 06	Apr. 06	May 06	Jun. 06	Jul. 06	Aug. 06	Sep. 06	Nov. 06	Dec. 06	Jan. 07	Feb. 07
<i>Acartia</i> copepodites		1165								42	85
<i>Acartia</i> spp.	1165	1997	166	499		166	333		416	125	
<i>Acrocalanus</i> copepodites					532			582	208	749	113
<i>Acrocalanus</i> spp.	166				1065	416	333	333	936	1206	
<i>Labidocera</i> copepodites	2163	1331	1331	2163	3461	3494	8486	1082	2496	1414	622
<i>Labidocera</i> spp.	2995	1498	1830	1498	4792	1497	1331	3078	4784	957	311
<i>Temora</i> copepodites	832	1997	7654	3660	799			499	832		28
<i>Temora</i> spp.	166	1331	4492	2995	266	416	499	749	936		
<i>Oithona</i> copepodites	5491	12146	26954	18136	2130	8569	22961	6822	4576	541	962
<i>Oncaea</i> copepodites	3827	5491		17803	2396	4076	17304	749	6136	1955	509
<i>Oithona hamata</i>	666	1498	166	2496		1082	1497				
<i>Oithona plumifera</i>			1331	1498	799		2995			166	85
<i>Oithona similis</i>	666	3827	5824	8319	21031	5657	6323	666	1560	1248	651
<i>Oithona simplex</i>						1581	3494	915	416		
<i>Oncaea media</i>	832	4326	1830	1498	799	998	3993	250	624	374	198
<i>Euterpina</i> copepodites	4492	3827		1664	799		8652	2662	104	333	170
<i>Euterpina acutifrons</i>	3993	3827	2329	6988	799		26954	2829	1768	1206	170
<i>Microsetella</i> spp.	333	1498	1497		532			250	312	42	

annual average, ~70% of the zooplankton were found in the upper layer. No correlation was observed between zooplankton abundance and any of the environmental variables measured. Copepods (64%), copepod nauplii (13.7%), appendicularian (5%), protozoan (5%), thaliacea (3%), chaetognaths (2%), ostracods (1.4%), and cladocerans (0.7%) were the main contributors to the total zooplankton. Copepod abundance ranged from 75,372 (April) to 234,104 (September) ind. m⁻², with an annual average of 140,227 ind. m⁻² (Figure 3). On annual average, >70% of the nauplii, copepodites, and adults were found within the upper 100 m. Among the copepods, cyclopoids were dominant for most of the year, comprising 46%–72% of the total copepod abundance (Figure 3). Copepod nauplii were abundant in summer and winter (Figure 4). Copepodites comprised 53% of all developmental stages (nauplii + copepodites + adults), and among the copepodites, cyclopoid species were the most common (average 64% of all copepodites; Figure 4). Adult stages comprised 30% of all copepods, among which calanoid, cyclopoid, and harpacticoid accounted for 41%, 51%, and 9% of all adults, respectively (Figure 4).

A total of 63 adult copepod taxa were observed at the open water station. The diversity index was highest (3.32) in July and lowest (2.69) in May. Six adult copepod taxa were the most common at the open water station: *Oncaea media*, *Labidocera* spp., *Lucicutia* spp., *Farranula* spp., *Oithona similis*, and *Microsetella* spp., and their abundances varied by seasons (Table 2).

Dominant species displayed distinct distribution patterns throughout the year at the two stations. At the coastal station, *Oncaea media* abundance peaked in spring (April) and in late summer (September). At the open water station, its primary peak was in May and its secondary peak was in January. *Labidocera* spp. showed 2 peaks in July and September at the coastal station, and in May–June and November–December at the open water station. Peak abundance of *Oithona similis* was observed in July at the coastal station, but it was not found during the summer (July, August, September) at the open water station.

Cluster analysis performed on the abundance data set of adult and copepodite stages of copepods showed four groups at 54% similarity level (Figure 5): group D included samples collected in the open water station except during

Table 2. Common copepod species abundance (ind. m⁻²) at the open water station.

	Mar. 06	Apr. 06	May 06	Jun. 06	Jul. 06	Aug. 06	Sep. 06	Nov. 06	Dec. 06	Jan. 07	Feb. 07
<i>Centropages</i> copepodites		660	1307	18444	2780	6257	3820	1160			2620
<i>Centropages</i> spp.	1159	660		2842	1020	3208	1840	500	1102		1996
<i>Labidocera</i> copepodites	2992	200	2360	6605	7440	12276	2160	5160	4142	2640	2746
<i>Labidocera</i> spp.	2338	1500	4797	4782	3000	2732	6160	9660	5320	7874	2412
<i>Lucicutia</i> copepodites	2655	2160		1313	2820		5500	3000	893	2560	1082
<i>Lucicutia</i> spp.	7162	2320	585	1313	1460	3881	5160	6980	3116	10255	2370
<i>Temora</i> copepodites	673	840	7391	4567	1160	653		4820	323		708
<i>Temora</i> spp.	337	1500	2262	2940	340	79	340	3820	152	1232	166
<i>Farranula</i> copepodites	1664	160	2360	4939	1260	1327	2320	2660	1520	6334	1664
<i>Farranula</i> spp.	1346	1320	1073	5958	3500	1168	7660	2500	1197	5234	2206
<i>Oithona</i> copepodites	29621	16980	50076	31321	11820	25047	59060	26960	23237	34686	9110
<i>Oncaea</i> copepodites	14810	16480	49823	21423	11620	18434	60740	16480	28063	21660	12894
<i>Oithona hamata</i>	2338	1340	2789	4292	700	158	6820				
<i>Oithona similis</i>	4488	500	2379	4939				3660	5795	4570	5574
<i>Triconia conifera</i>		820	1814	9859	1680	2475	3140	2160	1064	307	2204
<i>Oncaea media</i>	666	1332	17963	7909	2478	5718	5158	4826	1685	7581	
<i>Oncaea venusta</i>	1833		78		1460	1742	7320		95		666
<i>Euterpina</i> copepodites		2160						2820	627	940	84
<i>Euterpina acutifrons</i>	2487	660	2945	1627				200	2204	1134	250
<i>Microsetella</i> spp.	2001	2160	7820	7762	2700	2237	1500	2500	1406	1264	624

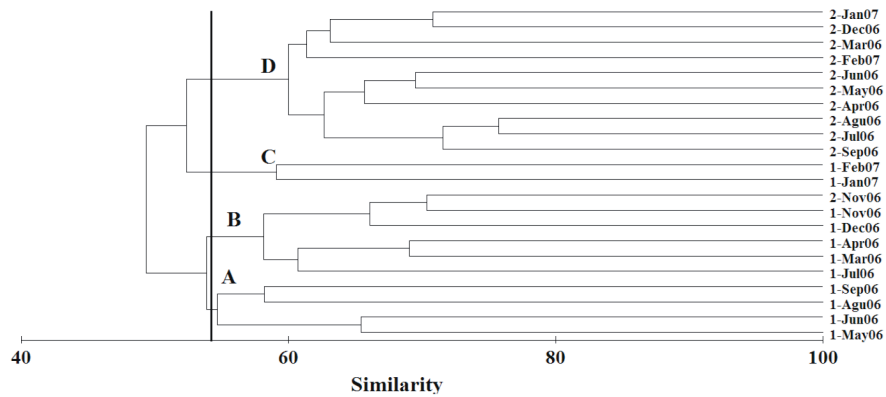


Figure 5. Cluster diagram of abundance data sets of monthly sampling based on the Bray-Curtis similarity matrix (1 represents coastal station, 2 represents open water station).

November, when the species assemblage was more similar to group B. Group B generally included spring and autumn samples from the coastal station. The high similarity between group B and the copepod assemblages in November at the open water station probably resulted from the lateral intrusion of the water masses at that time of the year. Group C included January and February samplings from the coastal station. Group A included samples collected at the coastal station during summer with the exception of the July sample, which had similar species assemblages to group B. The average similarity within group A was 57.1%, and this percentage was attributed to the first 7 taxa, including *Oithona similis*, *Oncaea media*, *Labidocera* spp., and their copepodite stages. In addition to these taxa, the contribution of coastal species *Euterpina acutifrons* and the copepodites was important for group B and C; the epi- and mesopelagic copepods *O. plumifera*, *Lucicutia* spp., and *Farranula* spp., and their copepodites were included in group D (Table 3). Dissimilarity analysis between coastal and open water species assemblages showed that the species which are likely to be good discriminators were *Euterpina acutifrons* and *Temora* spp. as coastal and neritic species, and *Lucicutia* and *Farranula* as open water genera.

3.3. Live/dead composition of copepods

At the coastal station, total dead copepods including nauplii (unstained by Neutral Red) did not exceed 7% of the population (nauplii + copepodites + adults). On annual average, 2.6% of the copepods were dead (Figure 6a). In contrast, 10.6% of the copepods were dead on average at the open water station; a high number of copepod carcasses were observed in April and May 2006, accounting for 29.5% and 21.7% of the population, respectively (Figure 6a). Overall, there was a significantly higher percentage of dead copepods at the open water station than at the coastal station (Mann-Whitney U-test, $P < 0.01$). At the

open water station, zooplankton samples were collected from two depth intervals (100–0 m and 195–100 m) beginning in May 2006. Total copepod abundance was significantly higher in the upper layer (t-test, $P < 0.02$), but the percentage of dead copepods was higher in the deeper layer (Figure 6b). No significant correlation between live/dead copepod percentages and environmental variables (surface chl-a, surface temperature, depth integrated temperature, and salinity) was found.

4. Discussion

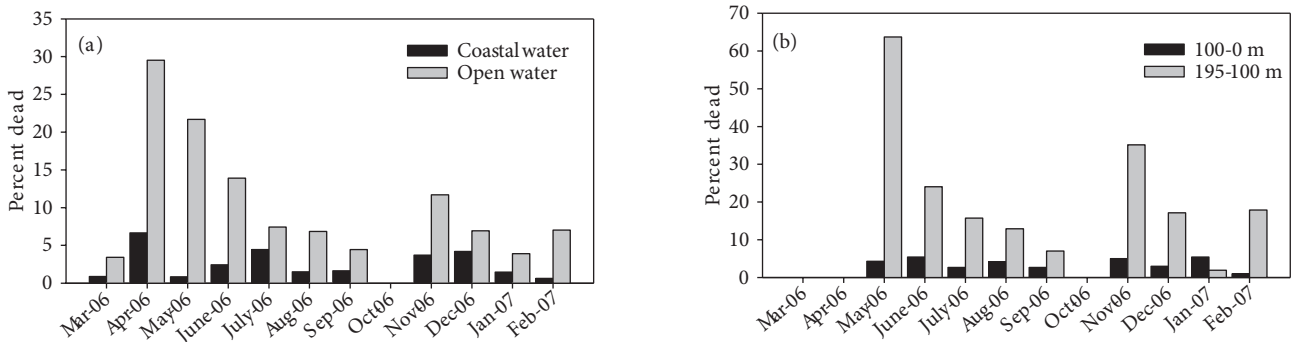
4.1. Seasonal variability of environmental parameters and copepod composition

In the eastern Mediterranean, primary production is controlled mainly by limiting nutrients, especially PO_4 (Krom et al., 1991; Zohary and Robarts, 1998; Thingstad et al., 2005). At the coastal station, high phytoplankton biomass was supported by PO_4 input from the Lamas River in April and August, and as expected, copepods responded by increasing their abundance 1 month after the spring and summer chl-a peaks. At the coastal station, food limitation may explain the low copepod abundance in the winter, whereas the low abundance in midsummer (July–August) may have been caused by a combination of food scarcity and high predation, when a high abundance of fish larvae was present in this area (Yeşim Ak Örek, personal communication). Ak Örek et al. (2007) observed a high abundance of scombrid larvae, which feed on copepods (Conway et al., 1999), at this station in June 1999 and July 2000.

The open water station was not influenced by the river, and both PO_4 and chl-a concentrations remained low for most of the year. Atmospheric deposition is a significant source of nutrients for the eastern Mediterranean Sea (Herut et al., 1999; Koçak et al., 2010). It has been shown that atmospheric deposition of PO_4 is important in the

Table 3. SIMPER analysis: Percent contribution of the most represented species and copepodite stages (cutoff 70%) to similarity among cluster groups. AS = average similarity for each group.

Cluster groups	A	B	C	D
Species	AS: 57.05	AS: 61.08	AS: 59.12	AS: 62.33
<i>Oithona</i> spp. copepodite	11.50	8.29	8.43	8.32
Unidentified calanoid copepodite	10.50	8.70	10.84	6.88
<i>Oithona similis</i>	10.08	5.58	8.86	2.22
<i>Labidocera</i> spp. copepodite	8.14	6.23	8.75	4.95
<i>Labidocera</i> spp.	7.62	7.09	7.14	4.94
<i>Oncaea media</i>	7.44	4.98	6.13	3.49
<i>Temora</i> spp.	6.15	4.43		
<i>Oithona hamata</i>	5.56			
<i>Oncaea</i> spp. copepodite	4.78	7.13	8.28	8.16
<i>Euterpina acutifrons</i>		6.03	5.78	
<i>Temora</i> spp. copepodite		5.41		
<i>Euterpina</i> spp. copepodite		4.99	5.78	
<i>Microsetella</i> spp.		4.25		3.83
<i>Acrocalanus</i> spp. copepodite			4.91	
<i>Lucicutia</i> spp.				4.22
<i>Corycaeus</i> spp. copepodite				4.15
<i>Farranula</i> spp.				4.00
<i>Farranula</i> spp. copepodite				3.44
<i>Triconia conifera</i>				2.75
<i>Oithona plumifera</i>				2.56
<i>Lucicutia</i> spp. copepodite				2.46
<i>Centropages</i> spp.				2.20

**Figure 6.** Percentage of dead copepods at the coastal and open water stations (a), and the percentage of dead copepods at 0–100 and 100–195 m at the open water station (b).

northern Levantine basin. It is estimated that the yearly atmospheric deposition is around 3 orders of magnitude higher than that supplied by the Lamas River (Koçak et al., 2010).

The literature suggests that productivity of copepods is mainly controlled by temperature and food resources (Vidal, 1980; Durbin et al., 1983). In the present study, positive correlations between temperature and abundance

of copepodites and adults of calanoids and cyclopoids were observed at the coastal station but not at the open water station. At the coastal station, instead of a direct coupling with chl-a, copepodite abundances for all three copepod groups were significantly correlated with chl-a with a 1-month delay (Pearson product moment correlation, $P < 0.05$). This suggests that the generation time of the copepods is around 1 month during the sampling period, which is a factor of ca. 1–2 longer than expected under optimal growth conditions at similar temperatures (Gillooly, 2000), and indicative of food limitations in situ (Bakker and van Rijswijk, 1987; Breteler and Schogt, 1994).

In the Mediterranean Sea, small-sized copepods are dominant in zooplankton (Calbet et al., 2001; Zervoudaki et al., 2006; Bottger-Schnack, 2011). When using the traditional 200- μm mesh size for collecting zooplankton, a considerable amount of small-sized taxa would be lost. Other studies using a finer mesh size have found a 2–20-fold increase in abundance, particularly abundance of *Oithona* sp. and *Oncaea* sp. (Calbet et al., 2001; Zervoudaki et al., 2006). In the present study, by using 100- μm size mesh, the small species became dominant: *Euterpina acutifrons* was the dominant species at the coastal station, and *Oncaea media* and *Oithona similis* were among the most abundant species at both stations. The dominance of *O. similis* in this oligotrophic water can be explained by its low metabolic needs (Castellani et al., 2005). The relatively low rates of feeding, growth, reproduction, and mortality of cyclopoids, especially for the families Oncaeidae and Oithonidae, all contribute to their ability to survive unfavorable conditions (Paffenhofer, 1993).

The seasonal cycles of environmental variables and planktonic organisms were not identical between years. Yılmaz Zenginler and Beşiktepe (2010) observed three seasonal peaks of zooplankton abundance in 2005 at the coastal station; in the present study, only two peaks were observed, in early summer and early autumn. Dominant species displayed different seasonal patterns throughout the year at the two stations, suggesting differences in water characteristics. In the present study, copepod species succession was obvious at the coastal station: the dominant *Temora* spp. in late spring/early summer were replaced by *O. similis* and *Labidocera* spp. in summer, which were replaced by *Euterpina acutifrons* at the beginning of autumn. Succession of species shows differences in different areas in the Mediterranean Sea, suggesting differences in their ecological traits (Siokou-Frangou et al., 2010).

4.2. Live/dead composition of copepods

To properly understand the ecological roles of zooplankton, it is necessary to separate the live and dead individuals, which is rarely done in conventional field sampling. To our knowledge, this is the first study to measure the live/dead compositions of copepods in the eastern Mediterranean

Sea. Because the coastal station was under the influence of freshwater runoff in April and August, there was a possibility that some copepods might have died of salinity shock. Contrary to this expectation, the surface salinity varied by less than 4 psu at the coastal station, and the percentage of dead copepods remained low throughout the year with no distinct seasonal pattern. On average, 2.6% of the copepods were dead at the coastal station, much lower than the global average for marine (11.6%–59.8%) and fresh/brackish water (7.4%–47.6%) zooplankton reported in the literature (reviewed by Tang et al., 2014).

At the open water station, we observed a higher percentage of dead individuals, averaging 10.7% throughout the year, and reaching >20% in April and May, comparable to the global average (Tang et al., 2014). The higher percentage of dead individuals suggests that the copepod community suffered higher nonpredatory mortality at the open water station than at the coastal station, especially in the spring. This may be a result of food shortages in the open water, as indicated by the low chlorophyll-a concentrations there. Food quantity and quality as environmental stressors affect both early developmental stages and adult copepods (Lopez, 1996; Koski and Breteler, 2003; Avery et al., 2008), and the success of a copepod population in a food-limited ecosystem is determined by species-specific ability to resist starvation (Koski and Breteler, 2003). For the open water station in this study, ignoring the live/dead composition would likely lead to overestimation of zooplankton recruitment and grazing impact.

Another interesting observation is that, at the open water station, the percentage of dead copepods was generally higher in the deep layer (100–195 m) than in the upper layer (0–100 m), suggesting an accumulation of carcasses below the thermocline. Upon death, zooplankton bodies tend to sink due to their higher mass density than ambient water. However, the sinking rate may decrease as a function of water column stratification, microbial decomposition, and resuspension (Kirillin et al., 2012), leading to the accumulation of carcasses in the deep layer. Large quantities of zooplankton carcasses have been observed in deep oceans and over seamounts (Genin et al., 1995; Haury et al., 1995). A study in the Japan Sea reported the accumulation of copepod carcasses just below the thermocline, where carcasses may remain for months (Terazaki and Wada, 1988). Zooplankton carcasses resulting from nonpredatory mortality may act as an important organic substrate source for microbes (Tang et al., 2009; Bickel and Tang, 2010), or become a part of the vertical flux (Ivory et al., 2014). The only relevant study in the region is that by Frangoulis et al. (2011), who compared the sinking fluxes of fecal pellets vs. zooplankton carcasses in the western Mediterranean.

In their study, carbon and nitrogen fluxes due to sinking zooplankton carcasses exceeded that of fecal pellets, except at the beginning of a phytoplankton bloom (Frangoulis et al., 2011). Zooplankton carcasses also contribute significantly to the vertical carbon flux in the oligotrophic southeastern Beaufort Sea (Sampei et al., 2009). The continuous presence of copepod carcasses in our study area suggests that sinking zooplankton carcasses could represent a persistent supply of high quality organic matter to the benthos in the northeastern Levantine basin.

The present data help fill the information gap about the annual structure and dynamics of copepod assemblages in a coastal and an open marine environment in the northeastern Mediterranean. Our data showed that PO₄ enrichment by the Lamas River is very important for the phyto- and zooplankton production in the coastal area. However, in the open water, winter–spring mixing, together with the atmospheric nutrient deposition, might be responsible for triggering an increase in planktonic organisms. Small copepods dominated both habitats. The distinct copepod species assemblages also implied different food web dynamics between the two stations: the harpacticoid copepod *Euterpina acutifrons*, which was dominant at the coastal station, is known to thrive in productive and detritus-rich waters (Diaz et al., 2003). On the other hand, the open water copepod community was

distinguished by the presence of *Farranula* spp., which belongs to the family Corycaeidae, with a characteristic large pair of eyes suggesting their role as a visual predator of other zooplankton (Gophen and Harris, 1981). Further investigation into the feeding ecology of the two copepod communities will help elucidate the trophodynamics in the region. We also showed for the first time that dead copepods were prevalent in the area, and that the percentage of dead copepods was significantly higher at the open water station, indicating the impact of nonpredatory mortality factors. These observations further highlight the need for measuring the dead zooplankton composition and the probable causes thereof for proper understanding of the Mediterranean ecosystem.

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