

Abstract

The diversity and distribution of metazooplankton across the Mediterranean Sea was studied along a 3000 km long transect from the eastern to the western basins during the BOUM cruise in summer 2008. Metazooplankton were sampled using both a 120 μm mesh size bongo net and Niskin bottles at 17 stations. Here we report on the stock, the composition and the structure of the metazooplankton community. The abundance was 4 to 8 times higher than in several previously published studies, whereas the biomass remained within the same order of magnitude. An eastward decrease in abundance was evident, although biomass was variable. Spatial (horizontal and vertical) distribution of metazooplankton abundance and biomass was strongly correlated to chlorophyll-*a* concentration. In addition, a clear association was observed between the vertical distribution of nauplii and small copepods and the depth of the deep chlorophyll maximum. The role of environmental factors is also discussed. Cluster analysis allowed us to define a regionalization of the Mediterranean Sea based on the abundance and diversity of metazooplankton. We found a north-south distinction in the western basin and a longitudinal homogeneity in the eastern basin. The Sicily Channel appeared as an intermediate region. The specific pattern of distribution of remarkable species was also described.

1 Introduction

Although the Mediterranean Sea represents only $\sim 0.82\%$ of the total surface of the global ocean, it is the largest quasi-enclosed sea and is considered as one of the most complex marine environments and marine biodiversity hot spots (Margalef, 1985; Bianchi and Morri, 2000; Coll et al., 2010). The marine Mediterranean biota is composed of endemic and migrant species of Atlantic and Red Sea origins, with cosmopolitan species and species linked to the complex geologic history of the Mediterranean Sea (Tethyan, Pliocene origins or glacial inter-glacial periods) (Furnestin, 1968;

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Bianchi and Morri, 2000). Based on remote sensing-estimated phytoplankton biomass and several other physical and biological parameters (i.e. the 72 most abundant zooplankton species), Longhurst (1998) described the Mediterranean Sea as a composite subtropical oligotrophic environment but ascribed it to a single bioprovince. Nevertheless, other studies provide evidence of several biogeographic regions. Based essentially on marine biodiversity, Bianchi and Morri (2000) distinguished ten major biogeographic sectors. Bianchi (2004) then specified two additional sectors: the southern Tyrrhenian Sea and the southern Aegean Sea. Finally a thirteenth biogeographic sector was defined: the Strait of Messina, a small biogeographic region where local endemism is present (Bianchi, 2007). D'Ortenzio and Ribera d'Alcalà (2009) proposed a regionalization based on a 10-year time series of satellite images of sea surface chlorophyll-*a* resulting in seven clusters which can be regrouped as "coastal regions", "blooming areas", "intermittently blooming areas" and "non blooming areas".

The entire Mediterranean Sea is oligotrophic with a strong eastward gradient in nutrient deficiency which reaches ultra-oligotrophic conditions in the Levantine Basin (Krom et al., 1991; Ignatiades, 2005; Moutin and Raimbault, 2002). This nutrient deficiency results in weak phytoplankton biomass and primary production (reviewed in Siokou-Frangou et al., 2010). The same pattern has also been reported for the mesozooplankton abundance (Dolan et al., 2002; Siokou-Frangou, 2004; Minutoli and Guglielmo, 2009) but not for the biomass (reviewed in Siokou-Frangou et al., 2010). In addition, the west-east decrease in abundance emerges from one survey running through the Sicily Channel into the Levantine Basin (Mazzocchi et al., 1997). Nevertheless, only a handful of studies have described metazooplankton standing stock and diversity throughout the Mediterranean Sea (Dolan et al., 2002; Siokou-Frangou, 2004; Minutoli and Guglielmo, 2009; Siokou-Frangou et al., 2010) and they highlight an overall scarcity with the presence of hot spots of abundance located in the northwestern Mediterranean, the Catalan Sea, the Algerian Sea and the Aegean Sea (reviewed in Siokou-Frangou et al., 2010, Fig. 17). In contrast to the generalized oligotrophy, several mesoscale hydrodynamic structures are known to enhance nutrient concentration,

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and therefore, biological activities. In the Mediterranean Sea, such structures exist like river plumes (i.e. Rhône, Po and Nile) (Cruzado and Velasquez, 1990; Revelante and Gilmartin, 1992), frontal regions (i.e. Almeria-Oran region, north Balearic-Catalan region and northeast Aegean Sea) (Estrada and Salat, 1989; L'Helguen et al., 2002; Zervoudaki et al., 2006) and deep convection areas (i.e. Gulf of Lion, South Adriatic eddy, Rhodes eddy) (Lévy et al., 1998; Gacic et al., 2002; Azzaro et al., 2007). In turn, these mesoscale features can impact the distribution and diversity of metazooplankton occurring both in the western basin (Ibanez and Bouchez, 1987; Pinca and Dallot, 1995; Youssara and Gaudy, 2001; Riandey et al., 2005; Molinero et al., 2008; Licandro and Icardi, 2009) and in the eastern basin (Mazzocchi et al., 2003; Siokou-Frangou, 2004; Pasternak et al., 2005; Zervoudaki et al., 2006; Siokou-Frangou et al., 2009). Moreover, in these frontal systems, turbulence is increased and has an impact on the structural and functional characteristics from plankton communities to the whole ecosystem (Margalef, 1997; Franks, 2001; Saiz et al., 2003; Alcaraz et al., 2007).

The BOUM experiment (Biogeochemistry from the Oligotrophic to the Ultraoligotrophic Mediterranean) was conducted in order to obtain a better representation of the interactions between planktonic organisms and the cycle of biogenic elements in the Mediterranean Sea, considering scales from the single process to the whole basin. Here, we describe first the stock represented by the metazooplankton community and define its structure and its composition across the Mediterranean Sea (both in the western and eastern basins) through a synoptic survey in summer. Then, we define the role of the environmental factors in the spatial and vertical distribution of the zooplankton. Finally, we attempt to define a regionalization of the metazooplankton based on both its abundance and its specific composition in the Mediterranean Sea.

2 Materials and methods

2.1 Cruise track and sampling

A 3000 km transect across the Mediterranean Sea was conducted during the BOUM cruise from 18 June to 20 July 2008 on board the RV *Atalante*. The cruise run eastward from the Ionian Basin (IB) to the Levantine Basin (LB) from 18 to 29 June; then switched to a westward direction. After a transit period of three days, sampling continued from the Ionian Basin through the Sicily Channel (SC), the Algero-Provencal Basin (APB) to the Rhône River Plume (RRP) (Fig. 1). Sampling strategy consisted in short-stay stations (~2–3 h) every 100 to 200 km and long-stay stations (4 days: stations A, B and C) located in the centre of important hydrological features (anticyclonic eddies) (see Moutin et al., 2011, for more details). Location of the sampling stations is presented in Fig. 1 and Table 1.

Zooplankton was collected within the upper 200 m layer (100 m at st 17 and 27) using Bongo nets (60 cm mouth diameter) fitted with 120 μm mesh size and mounted with filtering cod ends. Vertical hauls were done at a speed of 1 m s^{-1} . Due to wire time constraints sampling was performed at different times of day and night. The length of time spent at stations A, B and C allowed us to collect zooplankton 3 times at noon and 4 times at midnight, on consecutive days.

Immediately after collection, the content of one of the two nets was preserved in 4% buffered formaldehyde with seawater solution for later species determination, staging and sizing of the whole metazooplankton community.

Samples from the second net were split in two parts (Motoda splitter). The first half was immediately collected onto a GF/F filter, placed in a Petri dish, and then deep frozen in liquid nitrogen for further gut content analysis. The second half of the sample was processed immediately to estimate biomass (see below).

Discrete sampling was also performed to study vertical distribution of copepod nauplii and small copepods through the water column. Water samples were collected with the CTD/rosette. At each selected depth, one whole 12 L Niskin bottle was gently sieved

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through a 20 μm mesh size before being fixed in a 2% Lugol's iodine-seawater solution. Seven depths were sampled between the surface and 200 m depth at stations A, B and C and only to a depth of 150 m at short-stay stations. The sampling depths were distributed according to the deep chlorophyll maximum depth.

2.2 Zooplankton community characteristics

2.2.1 Biomass measurement

The subsample for bulk biomass measurement was filtered onto pre-weighted and pre-combusted GF/F filter (47 mm) which was quickly rinsed with distilled water and dried at 60 °C for 3 days onboard. Dry-weight of samples was calculated from the difference between the final weight and the weight of the filter; and biomass (mg DW m^{-3}) was extrapolated from the total volume sampled by the net. In addition, to determine the carbon and nitrogen content, dried samples were grinded, homogenized then split into 3 equal fractions ($\sim 0.8\text{--}1$ mg DW), placed in tin caps and analyzed with a mass spectrometer (INTEGRA CN, SerCon).

2.2.2 "Classic" microscopic approach

Once back to the lab, taxonomic determination was made using a LEICA MZ6 dissecting microscope. Very common species were sub-sampled (1/32 or 1/64), with whole sample being counted for uncommon or larger organisms. Identification was made down to species level and developmental stage when possible. Sex determination was also done on the most abundant species. Species/genus identification was made according to Rose (1933), Trégouboff and Rose (1957) and Razouls et al. (2005–2011).

2.2.3 Digital imaging approach using the Zooscan

After homogenization, a fraction of each sample containing a minimum of 1000 particles was placed on the glass plate of the ZooScan. Special care was taken to separate

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the organisms, one by one manually with a wooden spine, in order to avoid overlapping. Each image was then run through ZooProcess plug-in using the image analysis software Image J (Grosjean et al., 2004; Gorsky et al., 2010). Several measurements of each organism were then computerized. Organism size is given by its equivalent circular diameter (ECD) and can then be converted into biovolume, assuming each organism is an ellipsoid (more details in Grosjean et al., 2004). The lowest ECD detectable by this scanning device is 300 μm . To discriminate between aggregates and organisms, we used a training set of about 1000 objects which were selected automatically from 35 different scans. Each image was classified manually into zooplankton or aggregates and each scan was then corrected using the automatic analysis of images.

The size spectrum of each sample was then measured using the NB-SS calculation (Yurista et al., 2005; Herman and Harvey, 2006) where biovolume is converted into wet weight ($1 \text{ mm}^3 = 1 \text{ mg}$). The slope of NB-SS linear regression for each sample gives information on the community size-structure. Low negative slopes, close to zero, reveal high percentages of large organisms while high negative slopes are linked to higher percentages of small organisms (Sourisseau and Carlotti, 2006).

2.3 Statistical analysis

One way Anova was used to examine spatial variation on zooplankton density between the geographic areas.

A plot classification diagram of percentage similarity (Bray-Curtis Index) between samples was constructed using complete linkage (Field et al., 1982). Rare species (<10% occurrence) were ignored. All multivariate analyses were conducted using PRIMER software (Clarke and Warwick, 1994). Indicator species for each cluster were identified using the SIMPER routine within PRIMER. Analyses were performed on the whole zooplankton community (74 taxa) and on the copepod community (54 taxa).

Pearson correlation and stepwise multiple regression analysis were conducted in order to explain the variability in zooplankton distribution. Relationships were tested between zooplankton parameters (abundance, biomass) and physical (temperature,

salinity), chemical (oxygen), and biological (Chlorophyll-*a*, heterotrophic nanoflagellates, nanophytoplankton, diatoms, ciliates, PON, POP and N/P) parameters. Variables were $\log(x + 1)$ transformed when normalized tests failed.

Abundance and biomass differences between day (3 samplings) and night values (4 samplings) were analyzed using paired t-tests.

3 Results

3.1 Characterization of the study area

The cruise took place during the stratified period. Details on the chemical, biological and physical environmental conditions are presented in Pujó-Pay et al. (2010), Crombet et al. (2011), Moutin et al. (2011). Briefly, the Eastern Basin, sampled during the first leg, showed a surface layer (0–20 m) with temperatures above 22 °C and reaching 27 °C at station C. Intermediate waters (60–200 m) displayed temperatures between 15 and 18 °C, with warmer waters eastwards. Along the westward transect (second leg), temperatures within the surface layer remained very high (>25 °C) as far as the Sicily Channel. Salinity was much higher in the eastern basin and in particular from station 5 eastwards, where it remained above 39 down to 200 m. Associated with the increasing trend in oligotrophy from west to east, chlorophyll-*a* vertical distribution showed the deepening of the deep chlorophyll maximum (DCM) from 50 m at station 25, down to 80 m at station 19, to 100 m at station 3 and to 120 m at station C. The chlorophyll-*a* values of the DCM ranged from 0.237 to 1.14 $\mu\text{g L}^{-1}$.

3.2 Total abundance and biomass distribution

Zooplankton abundance based on microscopic counts (Fig. 2a) varied over the five geographic areas (RRP, APB, SC, IB and LB), with values (mean \pm sd) of 2053, 1455 \pm 384, 1499 \pm 722, 1208 \pm 650, 934 \pm 75 ind m^{-3} , respectively. No significant

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copepod community (Table 2). *Euterpina acutifrons* and meroplanktonic larvae are very common in neritic and coastal waters (e.g. st 17 and 27).

Less abundant copepod species also displayed interesting geographical distribution. *Corycaeus* spp. was less abundant in a large part of the western basin. *Mecynocera clausi*, *Lucicutia flavicornis*, *Haloptilus longicornis* and *Pareucalanus attenuatus* (Fig. 3f, g, h and j, respectively) were clearly characteristic species of the eastern basin being absent or with a very low occurrence in the western basin. *Acartia* species were located throughout the Mediterranean Sea (Fig. 3e). However, *A. negligens* replaced *A. clausi* in the north part of the occidental Mediterranean (st 27 and 25) and at station 19. Both adult and copepodite stages of *Cosmocalanus darwini* (Fig. 3i) were found in both basins.

Non-copepod holoplanktonic species, mainly appendicularians, ostracods, pteropods and chaetognaths, made up $8.7 \pm 2.0\%$ of the metazooplankton community while meroplanktonic species were scarce ($0.4 \pm 0.4\%$) except at the RRP (4.1%). Cladocerans (Fig. 3l) were absent in the central sector of the oriental basin. Appendicularians (Fig. 3k) were 3 to 10 times more abundant at the “coastal” stations than in the rest of the study area.

3.4 Cluster analysis

Zooplankton and copepod communities displayed at least 57.72% and 63.9% similarity, respectively (Fig. 4). There was no distinction between IB and LB on the basis of either the zooplankton or the copepod communities. Eddies B and C formed a distinct subgroup. These two eddies were characterized by high abundance of echinoderm larvae (5.7 ind m^{-3}) while *Ctenocalanus* spp. were most abundant at the other stations (5.8 ind m^{-3}). Within the APB, community structure showed a clear north-south difference due to the higher abundance of *Centropages typicus* (10.7 ind m^{-3}) in the northern part and of chaetognaths (13.92 ind m^{-3}) in the southern part. The SC stations showed variable communities. In particular, the copepod community found at the stations located on the outskirts of the Sicily Channel (st 19 and 15, respectively)

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presented a stronger similarity (~76%) to the stations located in the nearest basin, while the communities at station 17 and at the RRP station were similar. The high abundance of *Euterpina acutifrons* in these two latter stations explained for 10% of this grouping.

3.5 Discrete sampling

The discrete depth sampling within the top 200 m collected small-sized copepods and nauplii. The community of small copepods was composed of adult and copepodite stages of *Oithona* spp., *Oncea* spp., *Corycaeus* spp., *Macrosetella/Microsetella* spp., and copepodite stages of *Clausocalanus/Paracalanus* spp. Distinct spatial patchiness was observed in the distribution of both nauplii and small copepods throughout the Mediterranean Sea (Fig. 5). The depth of the maximum nauplii density matched that of small copepods for most stations excepting at two stations (24 and 7). A west-east deepening of the density maximum was observed with depths ranging from 25 m to 90 m in the western part and from 100 m to 135 m in the eastern part. Integrated nauplii abundance was 1.4 (st 24) to 3.1 (st 7) times higher than that of small copepods. The eastern basin showed an overall lower integrated abundance than the western basin and the SC for both nauplii and small copepods. Integrated values of nauplii and small copepods obtained using bottles sampling were on average 140 times and 5 times higher than for samples collected with nets.

3.6 Zooplankton community size structure

Zooplankton abundance results obtained with the two counting methods. The automatic recognition system ZooScan (ZC) and the more classical dissecting microscope (MC) (Fig. 6) showed a significant linear regression with $ZC = 1.447 MC + 146.25$ ($R^2 = 0.70$, $p < 0.001$, $n = 20$). The lower detection limit for the ZooScan is 300 μm ECD, which led to an underestimation of the total number of organisms counted by ~35% ± 15.8 when compared to the microscopic technique. Nevertheless, the overall

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spatial distribution of the metazooplankton density was similar between the two methods (Figs. 2a and 7). Biovolume (ZooScan determinations, data not shown) and biomass (Fig. 2b) also shown similar spatial variations. The ZooScan allowed us to characterize the metazooplankton distribution in terms of size classes (Fig. 8). Abundance and NB-SS slopes did not show any clear relationship between the five geographic areas ($p > 0.05$). Nevertheless, the NB-SS slopes showed clear basin scale differences, with significantly lower slope in the eastern basin (IB + LB) than in the western basin (APB) ($p = 0.032$), indicating a higher relative abundance of large organisms (>2 mm; i.e. *Haloptilus longicornis* and *Pareucalanus attenuatus*) (Fig. 4h, j).

3.7 Day-night variation

The impact of diel migrations of organisms >300 μm ECD was studied within the three eddies (Fig. 8). The zooplankton abundance was significantly higher ($\sim 17\%$; $p < 0.001$) during the night, corresponding to a significant increase in biomass of $\sim 40\%$ ($p < 0.001$). This variation was mainly explained by medium- (500–1000 μm) and large-sized (>1000 μm) organisms ($p < 0.05$).

The C/N ratio was stable on the whole (3.82 ± 0.26 , $n = 21$) but decreased slightly during the night in spite of there being no significant difference between day and night samples.

3.8 Relationships between metazooplankton and environmental factors

No significant correlations between the different physico-chemical variables (temperature, salinity and oxygen) and the net metazooplankton abundance or biomass were found, while discrete abundance of nauplii and small copepods were significantly correlated with oxygen level (Table 3). All metazooplankton parameters – both integrated and discrete data – were strongly correlated with chlorophyll-*a* concentrations (Fig. 9). Discrete abundance of nauplii and small copepods was strongly correlated with nanophytoplankton diatoms and POP concentrations. PON concentration was the

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only variable showing a significant relationship with both the net and discrete metazooplankton data.

Chlorophyll-*a* was included in all multiple regression models for biomass and integrated or discrete abundance (Table 4). Nanoplankton were selected as an explanatory variable in the model for integrated metazooplankton abundance as well as heteroflagellates in the models for integrated abundance of nauplii (HNF > 10 µm) and small copepods (total HNF).

4 Discussion

4.1 Metazooplankton community composition

The zooplankton composition recorded during the BOUM transect is in general agreement with the published data on the Mediterranean (Siokou-Frangou et al., 1997; Gaudy et al., 2003; Pasternak et al., 2005; Riandey et al., 2005) The overall metazooplankton community was dominated by copepods. *Clausocalanus/Paracalanus* spp. and *Oithona* spp. were the dominant genera, as is generally observed (Gallienne and Robins, 2001; Gaudy et al., 2003; Peralba and Mazzocchi, 2004; Zervoudaki et al., 2007). Nevertheless, during the BOUM cruise, the presence of the subtropical copepod species *Cosmocalanus darwini* was reported for the first time in the Mediterranean Sea, and was observed in both the western and eastern basins. We found copepodite stages as well as adult females, indicating the reproductive success of this species. This species is common in the Red Sea (Razouls et al., 2005–2011; web site) and is expected to undergo lessepsian dispersion in the Mediterranean Sea. Nevertheless, this species showed a higher abundance in the south part of the western Mediterranean, particularly in the SC, suggesting an Atlantic origin. However, to our knowledge this species has never been recorded in the Eastern Atlantic (Razouls et al., 2005–2011; web site).

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4.2 Metazooplankton abundance and biomass

4.2.1 Westward gradient

Our study confirms the westward decrease of zooplankton abundance across the Mediterranean which has also been observed during other cruises conducted from June–September (Dolan et al., 2002; Siokou-Frangou, 2004; Minutoli and Guglielmo, 2009). The same trend was also observed in terms of abundance during one survey conducted through the SC and into the LB (Mazzocchi et al., 1997). The biomass distribution did not show any specific pattern along the BOUM transect but can be characterized as having generally high variability with higher values in a few regions, as has previously been observed (Champalbert, 1996; Alcaraz et al., 2007; Siokou-Frangou et al., 2010). Several species of metazooplankton showed a clear distribution pattern across the Mediterranean Sea, enabling us to define characteristic species for the western and eastern basins. For example, *Haloptilus longicornis* and *Pareucalanus attenuatus* are principally located in the eastern basin. The relative abundance in this region of these two large-sized copepod species partly explains the lower NB-SS slope, and indicates a higher relative abundance of large organisms.

4.2.2 Effect of mesoscale hydrodynamic structures on metazooplankton distribution

Mesoscale circulation and hydrodynamic structures are known to affect the mesozooplankton community structure (Youssara and Gaudy, 2001; Zervoudaki et al., 2006; Alcaraz et al., 2007; Molinero et al., 2008; Siokou-Frangou et al., 2009; Hafferssas and Seridji, 2010). Stations A, B and C were located at the centre of anticyclonic eddies characterised by a clear downwelling (Moutin et al., 2011). Both metazooplankton and copepod communities within the B and C eddy formed a distinct subgroup from the other stations sampled in the IB-LB region. Nevertheless, no specific community composition was found in eddy A located in the APB.

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While looking at the copepod assemblage of the east Mediterranean Sea, Siokou-Frangou et al. (1997) indicated several dissimilarities between the cyclonic and anti-cyclonic eddies but only for the subsurface layer (50–100 m). Their main hypothesis was that differences in chlorophyll-*a* concentration (with the highest concentration observed in the cyclonic eddy) were driving the mesozooplankton community structure. In our study, the three eddies displayed a weak decrease in term of chlorophyll-*a* concentration but a clear deepening of the DCM when compared to adjacent stations. In turn, eddies B and C displayed higher abundance of echinoderm larvae (*Asteroidae*), and of the copepods *Mecynocera clausi* and *Nannocalanus minor* while lower abundance of the copepods *Ctenocalanus* spp. and *Pareucalanus attenuatus* are reported. During a synoptic study in the Algerian basin covering both cyclonic and anticyclonic eddies, Riandez et al. (2005) showed, as well, that the deepening of the chlorophyll-*a* in the anticyclonic eddies seems to promote calanoïd copepods. In addition, anticyclonic eddies could act as hydrodynamic trap maintaining non motile zooplankton as echinoderm larvae (Pedrotti and Fenaux, 1996).

4.2.3 Comparison of mean values

Mean integrated abundance values for nauplii and small copepods obtained from discrete samplings were ~100 times and 4 times higher, respectively, than values from vertical bongo net (120 µm) sampling. This is in agreement with a study conducted in the Cyprus Eddy (Pasternak et al., 2005) where small copepods collected with Niskin bottle were 8 times more abundant than when collected with a 180 µm mesh size net. Zooplankton abundance values recorded with bongo nets during the BOUM transect were 4 to 8 times higher than in several previously published studies (Mazzocchi et al., 1997; Siokou-Frangou et al., 1997; Pasternak et al., 2005; Riandey et al., 2005), whereas biomass values were of the same magnitude. Strong discrepancies with previously recorded abundance arise mainly from the use of different sampling mesh sizes (>120 µm in previous studies). Mesh size is a very important factor in the evaluation of metazooplankton abundance (Calbet et al., 2001; Turner, 2004). Large organisms are

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caught with a greater efficiency using 500 μm nets, while small organisms are sampled significantly better using 80 μm mesh size (Bourdillon, 1964). The mesh width also affects the hydrodynamic properties of the plankton net and consequently the filtering efficiency (Thibault et al., 1994; Turner, 2004). Zervoudaki et al. (2006) reported an increase in abundance of 2 to 20 times when smaller organisms (45–200 μm) were considered during sampling in frontal areas of the Aegean Sea. The most pronounced differences were observed for copepod nauplii, copepodites and adults of small organisms such as *Oithona* spp., *Oncea* spp. and *Macrosetella/Microsetella* spp. It is therefore clear that abundance is significantly higher when sampling is performed with an 80 μm mesh size, but no concomitant increase in biomass has been shown (Thibault et al., 1994; Gaudy et al., 2003), probably due to the low specific weight of small organisms.

4.3 Diel vertical migration: incidence on observed spatial patterns

During the BOUM cruise, clear diel vertical migration of medium and large organisms (>500 μm ECD) explains the difference in numbers and biomass at the station A, B and C. Large organisms like carnivorous copepods (*Euchaeta* spp.), omnivorous copepods (*Euchirella* spp., *Pleurommama* spp.), other predators (fish larvae, siphonophores), herbivorous (pteropods) and other omnivorous (euphausids, ostracods) species were more abundant in the upper 200 m at night, as has already observed in other studies dedicated to the observation of diel vertical migrations (Andersen et al., 1998, 2004, 2001; Riandey et al., 2005).

Such day-night variations can partly explain the variability observed between all stations, where sampling was conducted at different times of the day. This variability source appeared to be less marked in abundance data (17% variations between mean day and night values) than in biomass data (40%).

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4.4 Vertical distribution in relation with the DCM

In the Mediterranean Sea, the bulk of epipelagic mesozooplankton is generally concentrated within the upper 100 m (Scotto di Carlo et al., 1984; Weikert and Trinka, 1990; Brugnano et al., 2010) and mainly within the upper 50 m in the western basin (Mazzocchi et al., 1997) and in the Ligurian Sea (Licandro and Icardi, 2009). In this study, the bulk of both nauplii and small copepods was located at depths down to 120 m in the Levantine Basin. A patchy vertical distribution of small-sized zooplankton was observed throughout the Mediterranean Sea, mainly driven by the deep chlorophyll maximum (DCM) depth. Clear association between vertical distribution of epipelagic mesozooplankton and DCM has previously been shown during the stratified period in summer (Alcaraz, 1985, 1988; Alcaraz et al., 2007).

4.5 Role of environmental factors to explain vertical and horizontal distribution

During the BOUM cruise, the maximum depth for nauplii abundance did not always match the DCM, indicating that other factors could also impact their vertical distribution. The potential role of temperature revealed by the multiple regression analysis is in agreement with Koski et al. (2011). Nauplii and small copepod vertical distributions were also correlated with oxygen, PON and POP, but these variables are indirectly linked to phytoplankton abundance through photosynthesis, respiration and organic composition. Their distribution was also associated with heterotrophic nanoflagellates and ciliates, suggesting a link with the microbial loop, which is known as a potential food source for small planktonic organisms (Calbet and Saiz, 2005; Henriksen et al., 2007).

The horizontal distribution of the metazooplankton in terms of abundance and biomass was also mainly driven by chlorophyll-*a*. Our study establishes empirical relationships (linear regression) between metazooplankton abundance or biomass and chlorophyll-*a* concentration throughout the Mediterranean Sea. Horizontal distribution of the abundance of nauplii, small copepods and metazooplankton was correlated

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with the distribution of HNF $>10\mu\text{m}$, total HNF and nanophytoplankton respectively. These correlations can illustrate size-selective predator-prey relationships. The affinity of nauplii for small motile prey such as HNF was evidenced experimentally by Henrikzen et al. (2007), that of small copepods for phytoplankton and microheterotrophs (Nakamura and Turner, 1997; Zervoudaki et al., 2007) and of metazooplankton for nanophytoplankton (Pinca and Dallot, 1995; Gaudy and Youssara, 2003; Alcaraz et al., 2007; Zervoudaki et al., 2007) is also well known.

4.6 Eco-regionalization

D'Ortlenzo and Ribera d'Alcalà (2009) proposed a regionalization of the Mediterranean Sea based on a 10-year time series of satellite images of sea surface chlorophyll-*a*. As mesozooplankton distribution is associated with chlorophyll-*a*, one can wonder if there is a link between our regional patterns for zooplankton abundance (see Fig. 2) or metazooplankton or copepod communities (Fig. 4) and the regional pattern described by D'Ortlenzo and Ribera d'Alcalà (2009) (see their Fig. 4). In the western basin these authors observed a clear north-south chlorophyll-*a* gradient with a northern blooming area, an intermittently-blooming central area and a non blooming area in the south. We find similar spatial patterns for zooplankton biomass, and for zooplankton and copepod communities. More specifically, in the western basin, the IB and the LB were grouped together as a non blooming region. Homogeneity between these two basins was also observed in BOUM for zooplankton, except at station 13 where high zooplankton abundance was observed. Interestingly, this high abundance corresponded to high concentrations of nanophytoplankton (984 Cell mL^{-1}), which was perhaps linked to a margin effect (border between SC and IB). Finally, in D'Ortlenzo and Ribera's (2009) study, the SC was defined as a non blooming region with intermediate characteristics between the southwestern and eastern basins. Intermediate characteristics were also shown for zooplankton, abundance, biomass and community in the BOUM transect. More particularly, in the SC central part (st 17, 117 m bottom depth) showed similar characteristics to the RRP (st 27, 106 m bottom depth) and can

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thus be classified as coastal. In summary, the synoptic view of the mesozooplankton community, its abundance and its biomass distributions show very similar patterns to the regionalization obtained by D'Ortiz and Ribera d'Alcalà (2009). Bianchi's (2007) study based on marine diversity (mainly benthos) identified thirteen biogeographic sectors in the Mediterranean Sea. The four clusters identified in our study for zooplankton or copepod communities (RRP, APB north, APB south and IB + LB: Fig. 4) match this classification. As discussed above, the SC not classified in Bianchi's study, appears also as an intermediate zone, as suggested by the difficulty in fixing a precise boundary between the western and eastern basins (Pérès and Picard, 1964; Giaccone and Sortino, 1974; Bianchi and Morri, 2000; Costagliola et al., 2004).

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Table 1. Position and characteristics (latitude, longitude, bottom depth, geographical region, date and time) of the zooplankton sampling stations during the BOUM cruise.

Station ID	Latitude (° N)	Longitude (° E)	Bottom depth (m)	Region	Date	Sampling time (h:min)
27	43°12	4°55	106	Rhône River Plume	7/18/08	23:10
25	41°59	5°00	2267	Algero-Provencal Basin	7/18/08	11:40
24	41°05	5°03	2659	"	7/18/08	01:05
A day	39°05	5°21	2798	"	7/15/08	11:30
A night	39°05	5°21	2786	"	7/15/08	23:30
21	38°37	7°54	2055	"	7/11/08	06:30
19	38°05	10°13	556	Sicily Channel	7/10/08	11:30
17	37°10	12°00	117	"	7/09/08	13:50
15	35°40	14°06	588	"	7/08/08	19:00
13	34°53	16°42	2097	Ionian Basin	7/08/08	01:30
B night	34°08	18°26	3007	"	7/04/08	01:45
B day	34°08	18°26	3197	"	7/05/08	11:55
1	34°19	19°49	3210	"	6/21/08	05:00
3	34°10	22°09	2382	"	6/22/08	01:15
5	34°02	24°29	2616	Levantin Basin	6/22/08	19:00
7	33°54	26°50	2780	"	6/23/08	13:25
9	33°45	29°10	3033	"	6/24/08	07:30
11	33°34	31°56	2514	"	6/25/08	04:30
C day	33°37	32°39	798	"	6/27/08	14:55
C night	33°37	32°39	817	"	6/27/08	23:35

Table 2. Average abundance obtained by microscopic counts of total zooplankton, copepods, other holoplankton and meroplankton and percentage of the major species and taxa within each category, for the different regions. Unidentified copepods and copepods <0.1% were grouped as other copepods. Amphipods, isopods and gelatinous larvae were grouped as others.

Taxa	Rhône River Plume	Algero Provencal Basin	Sicily Channel	Ionian Basin	Levantin Basin	Algero Provencal Eddy	Ionian Eddy	Levantin Eddy
Total (ind m ⁻³)	2053	1629	1499	1309	929	935	906	974
Copepods (ind m ⁻³)	1741	1524	1323	1201	845	836	842	896
Other holoplankton (ind m ⁻³)	233	104	175	108	82	98	61	69
Meroplankton (ind m ⁻³)	78.4	1.4	2.3	0.5	2.4	1.5	3.4	9.1
Copepods (%)	84.8	93.5	88.2	91.7	90.8	89.1	92.6	92.0
<i>Clausocalanus/Paracalanus</i> spp.	20.6	44.8	37.9	37.0	28.1	15.9	23.9	28.4
<i>Oithona</i> spp.	23.3	21.2	17.8	18.6	21.9	29.6	29.0	22.5
<i>Oncaea</i> spp.	10.4	10.7	7.6	8.2	11.9	17.4	7.5	16.1
<i>Macrosetella/Microsetella</i> spp.	7.5	5.6	2.7	3.5	1.0	12.6	1.0	0.8
<i>Corycaeus</i> spp.	0.8	1.9	2.5	3.2	6.0	2.1	6.3	6.8
<i>Acartia</i> spp.	2.4	0.0	0.2	0.4	0.3	0.4	0.6	0.1
<i>Calanus helgolandicus</i>	<0.1	0.1	0.0	0.0	0.0	<0.1	0.0	0.0
<i>Calocalanus</i> spp.	0.4	0.4	1.3	3.6	3.2	1.4	4.0	2.6
<i>Candacia</i> spp.	<0.1	<0.1	<0.1	<0.1	0.1	<0.1	<0.1	<0.1
<i>Centropages typicus</i>	0.2	0.3	1.3	<0.1	0.0	0.0	0.0	0.0
<i>Cosmocalanus darwini</i>	<0.1	<0.1	0.2	<0.1	<0.1	<0.1	<0.1	<0.1
<i>Ctenocalanus</i> spp.	2.0	0.0	0.5	0.7	0.7	0.0	0.0	0.0
<i>Eucalanus hyalinus</i>	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.0
<i>Euchaeta</i> spp.	0.2	0.1	0.1	0.2	<0.1	<0.1	<0.1	<0.1
<i>Euterpina acutifrons</i>	3.3	0.0	0.1	0.3	0.0	0.0	0.0	0.0
<i>Haloptilus</i> spp.	0.0	<0.1	0.1	0.9	1.7	0.3	0.9	0.8
<i>Lucicutia</i> spp.	0.0	0.2	0.1	0.8	1.2	0.2	0.6	1.9
<i>Mecynocera clausi</i>	0.0	<0.1	0.2	0.7	1.0	0.1	2.6	1.7
<i>Mesocalanus tenuicornis</i>	<0.1	<0.1	0.0	<0.1	0.0	0.0	0.0	0.0
<i>Nannocalanus minor</i>	3.1	0.6	5.2	0.0	0.2	0.3	1.1	0.0
<i>Neocalanus gracilis</i>	0.0	0.0	0.0	0.2	0.1	0.1	0.1	0.0
<i>Pareucalanus attenuatus</i>	0.0	0.0	0.0	0.2	1.2	0.0	0.0	0.0
<i>Pleuromamma</i> spp.	0.6	0.2	0.2	0.4	0.1	0.5	0.1	<0.1
<i>Scolecithricella</i> spp.	0.4	0.0	0.1	0.2	<0.1	0.0	0.5	0.3
<i>Scolecithrix</i> spp.	0.0	0.0	<0.1	0.1	0.7	0.0	0.1	0.3
<i>Spinocalanus</i> spp.	0.6	<0.1	0.7	<0.1	0.3	<0.1	0.1	0.1
<i>Subeucalanus monachus</i>	0.0	0.0	0.0	0.2	0.0	0.0	0.0	0.0
<i>Temora stylifera</i>	<0.1	<0.1	<0.1	0.3	0.2	0.0	0.1	0.1
other copepods	3.4	2.9	2.9	2.9	2.9	1.6	3.3	2.5
nauplii	5.1	3.8	6.1	9.8	6.2	4.2	6.8	6.9
Other holoplankton (%)	11.1	6.3	11.6	8.2	8.8	9.6	6.6	7.0
Appendicularians	8.4	2.3	6.8	3.9	3.1	3.5	3.3	2.1
Chaetognaths	0.2	0.5	0.5	1.7	1.2	1.0	0.6	0.4
Cladocerans	0.1	0.8	0.9	0.2	<0.1	<0.1	0.2	<0.1
Doliolids	0.0	<0.1	0.0	<0.1	0.3	0.0	0.0	0.0
Euphausiids/Mysidaceans	0.5	<0.1	0.1	0.1	<0.1	0.1	0.1	<0.1
Ostracods	<0.1	2.2	0.7	1.1	2.8	3.5	1.3	2.5
Polychetes	0.4	0.3	0.1	0.3	0.3	0.7	0.1	0.2
Pteropods	1.0	0.2	1.9	0.5	1.0	0.6	1.2	0.6
Salps	<0.1	0.0	0.3	0.1	0.0	<0.1	<0.1	<0.1
Siphonophores	0.4	<0.1	0.2	0.3	0.1	<0.1	0.1	0.8
Others	<0.1	<0.1	<0.1	0.1	0.1	0.3	<0.1	0.4
Meroplankton (%)	4.1	0.1	0.2	0.1	0.3	1.0	0.4	1.0
Decapod larvae	0.1	0.1	<0.1	0.0	<0.1	0.0	<0.1	<0.1
Echinoderm larvae	0.8	<0.1	<0.1	0.0	0.1	0.0	0.3	0.9
Fish eggs	0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	0.0
Fish larvae	<0.1	<0.1	<0.1	<0.1	0.1	0.1	<0.1	0.0
Jellyfishes	0.1	0.0	0.1	0.1	0.0	0.9	0.1	0.0
Lamellibranch larvae	2.9	<0.1	0.1	<0.1	0.1	0.1	<0.1	0.0

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Table 3. Simple correlation analysis between zooplankton parameters and environmental factors: significance degree of p-values (* $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$, ns: not significant). Net metazooplankton biomass (mg DW m^{-3}) and abundance (ind m^{-3}) ($n = 20$) and integrated and discrete depths abundance of small copepod and nauplii (ind m^{-3}) from Niskin bottles ($n = 111$ to 140).

Variable	Symbole	Abundance					
		Net biomass		Integrated		Discrete depths	
		Net biomass	Net total	Small copepods	Nauplii	Small copepods	Nauplii
Temperature	TEMP	ns	ns	ns	ns	ns	ns
Salinity	SAL	ns	ns	ns	ns	ns	ns
Oxygen	OXY	ns	ns	ns	ns	***	***
HNF 2–5 μm	HNF2	ns	ns	ns	ns	ns	ns
HNF 5–10 μm	HNF5	ns	ns	ns	ns	*	**
HNF >10 μm	HNF10	ns	ns	ns	**	ns	ns
HNF total	HNFT	ns	ns	*	ns	ns	**
Nanophyto.	NANO	ns	***	ns	ns	**	***
Diatoms	DIAT	ns	ns	ns	ns	***	***
Chlorophyll- <i>a</i>	CHL	**	***	***	**	***	***
Ciliates	CIL	ns	ns	ns	ns	*	*
Part. Org. Phos.	POP	ns	*	ns	ns	***	***
Part. Org. Nitr.	PON	*	ns	*	*	***	***
N/P particular	Np/Pp	ns	ns	ns	ns	ns	ns

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Table 4. Equation parameters of the multiple linear regression models using forward stepwise method explaining the zooplankton parameters distribution. Net metazooplankton biomass (mg DW m⁻³) and abundance (ind m⁻³) ($n = 20$) and integrated and discrete depths abundance of nauplii and small copepod (ind m⁻³) from Niskin bottles ($n = 111$ to 140). Symbols as in Table 3.

	Beta	Beta standard error	P-level
Integrated nauplii abundance $R^2 = 0.53$; adjusted $R^2 = 0.47$; $F = 8.61$; $P = 0.003$			
Constant	3.63	0.08	
HNF10	0.27	0.09	0.008
CHL	3.15	1.22	0.021
Integrated small copepods abundance $R^2 = 0.57$; adjusted $R^2 = 0.51$; $F = 9.82$; $P = 0.002$			
Constant	3.10	0.12	
CHL	4.17	1.14	0.002
HNFT	0.32	0.14	0.039
Integrated metazooplankton abundance $R^2 = 0.75$; adjusted $R^2 = 0.71$; $F = 21.89$; $P < 0.001$			
Constant	1.87	0.3	
NANO	0.37	0.14	0.016
CHL	3.4	1.48	0.036
Integrated metazooplankton biomass $R^2 = 0.55$; adjusted $R^2 = 0.49$; $F = 9.18$; $P = 0.002$			
Constant	-19.84	6.77	
CHL	6.24	1.52	< 0.001
SAL	12.70	4.21	0.009
	Beta	Beta standard error	P-level
Discrete nauplii abundance $R^2 = 0.56$; adjusted $R^2 = 0.54$; $F = 31.51$; $P < 0.001$			
Constant	-12.79	2.22	
O ₂	5.58	0.86	< 0.001
CHL	2.29	0.36	< 0.001
TEMP	1.01	0.37	0.007
Discrete small copepods abundance $R^2 = 0.32$; adjusted $R^2 = 0.31$; $F = 17.97$; $P < 0.001$			
Constant	1.20	0.08	
CHL	1.33	0.35	< 0.001
PON	1.97	0.59	0.001

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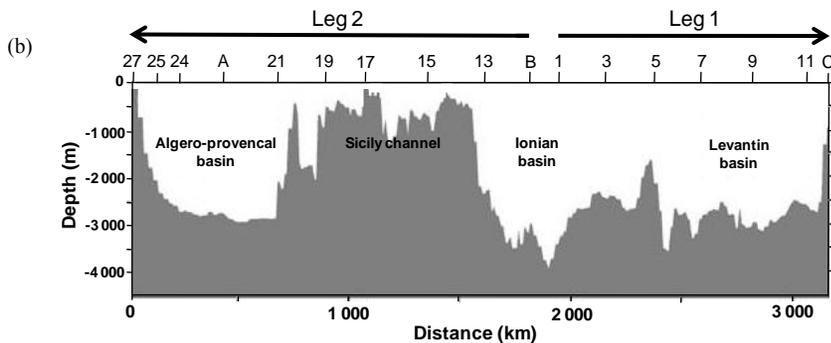
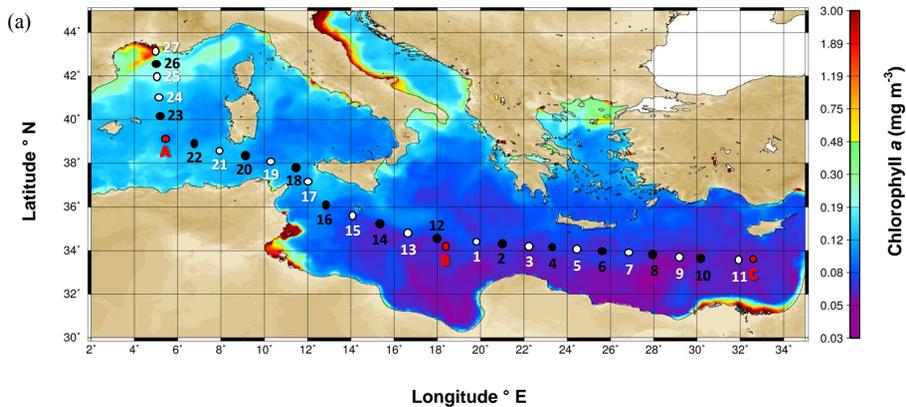


Fig. 1. Location of sampling stations **(a)** superimposed on a SeaWiFS composite image of the sea surface chlorophyll-*a* concentration integrated (permission to E. Bosc) during the BOUM transect (16 June–20 July 2008). Zooplankton sampling stations (white), stations with other parameters sampling (black), long-stay stations (red). Bottom depth and geographic areas **(b)** along the transect.

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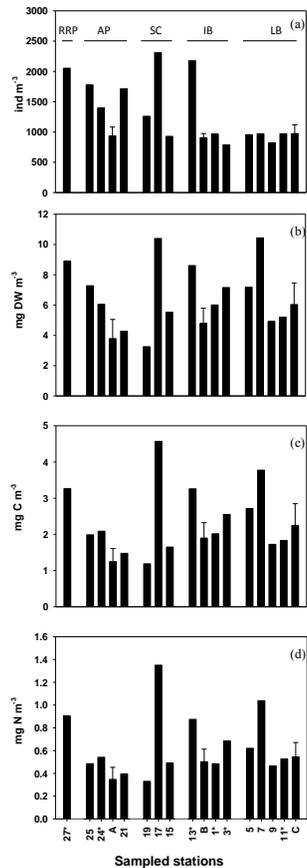


Fig. 2. Zooplankton abundances **(a)** and biomass expressed in terms of dry weight **(b)**, carbon **(c)** and nitrogen **(d)** at the different stations over the five geographic areas. Mean and standard deviation for stations A, B and C. (*) night sampling.

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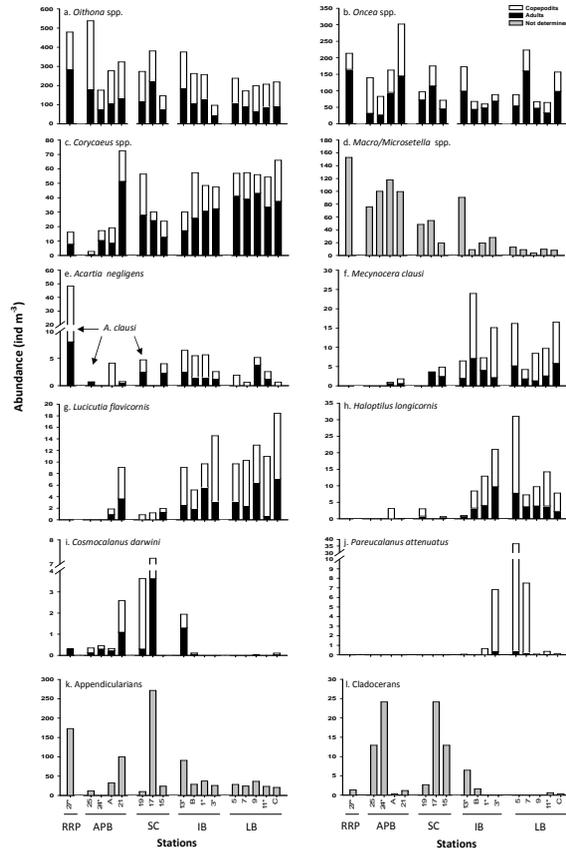


Fig. 3. Spatial distribution of the important zooplankton species across the Mediterranean transect: **(a)** *Oithona* spp., **(b)** *Oncea* spp., **(c)** *Corycaeus* spp., **(d)** *Macrosetella* spp. and *Microsetella* spp., **(e)** *Acartia clausi* and *Acartia negligens*, **(f)** *Mecynocera clausi*, **(g)** *Lucicutia flavicornis*, **(h)** *Haloptilus longicornis*, **(i)** *Cosmocalanus darwini*, **(j)** *Pareucalanus attenuatus*, **(k)** Appendicularians and **(l)** Cladocerans. (*) night sampling. Mean abundance for stations A, B and C.

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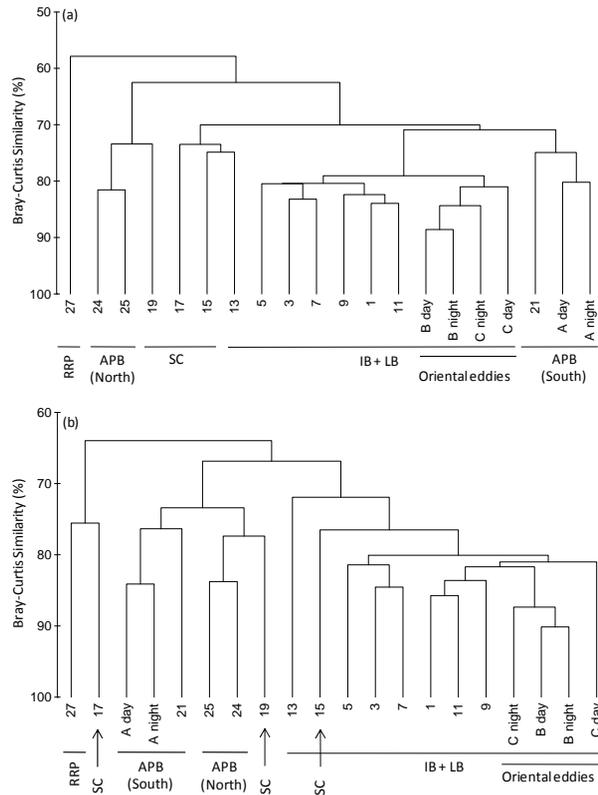


Fig. 4. Bray-Curtis similarity cluster based on $\text{Log}(X + 1)$ transformed zooplankton **(a)** and copepod **(b)** communities along the transect. RRP: Rhone River Plume, APB: Algero-Provencal Basin, SC: Sicily Channel, IB: Ionian Basin and LB: Levantine Basin.

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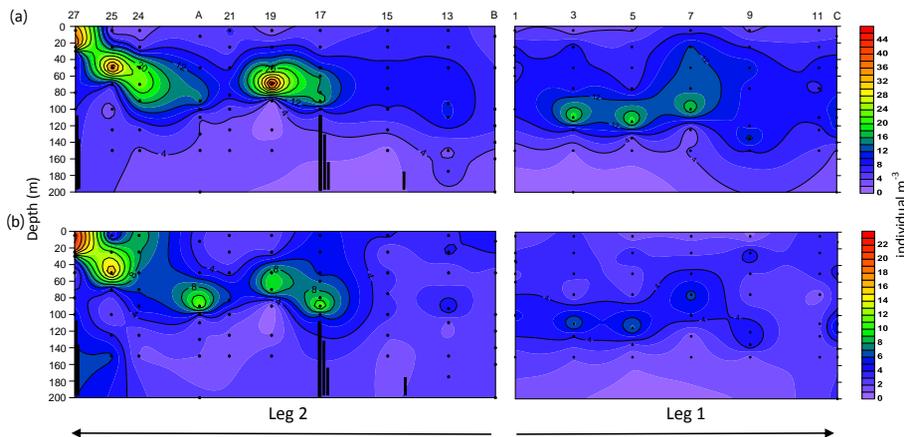


Fig. 5. Spatial distribution of copepods nauplii **(a)** and small copepods **(b)** within the first 200 m depth across the Mediterranean Sea. Bottom depth in black.

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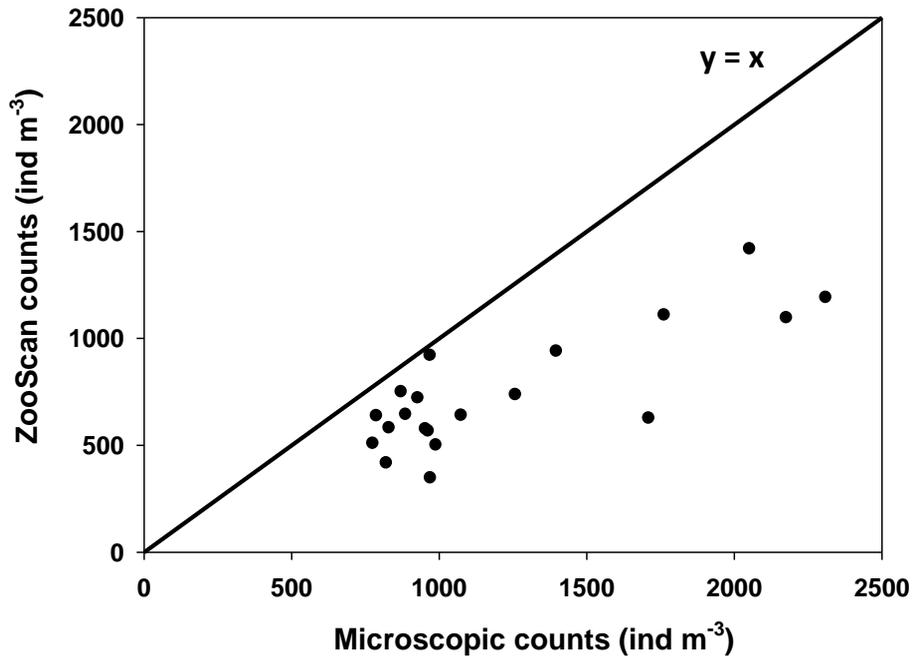


Fig. 6. Comparison between microscopic and ZooScan counts for all stations sampled with the Bongo net.

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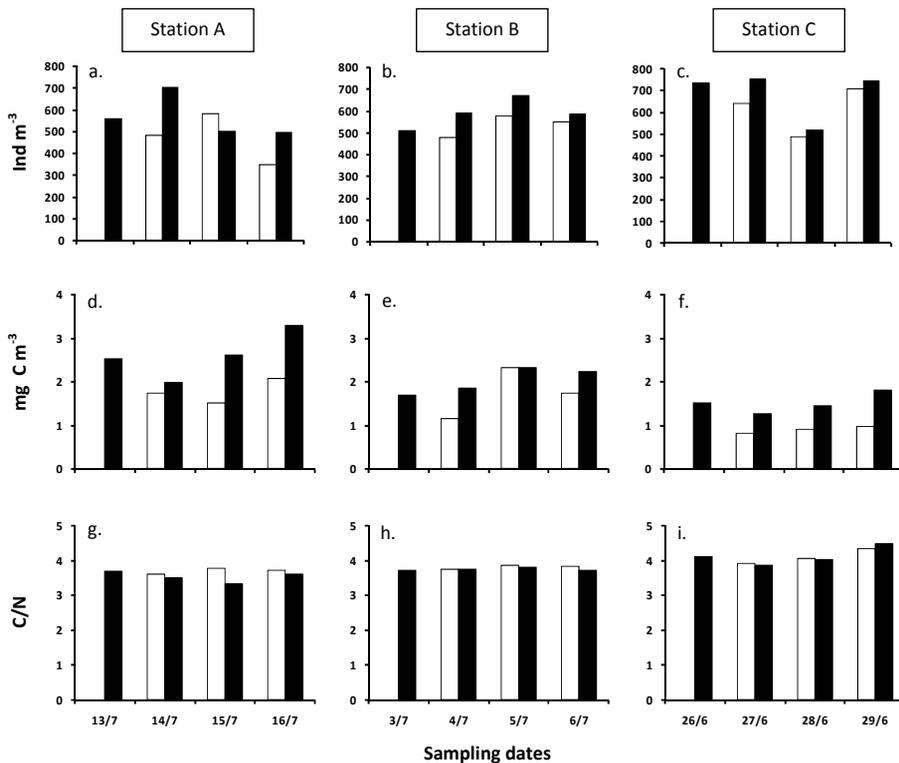


Fig. 7. Impact of sampling time (day: white; night: black) on zooplankton abundance (ZooScan counts) (a, b, c), carbon biomass (e, f, g) and C/N ratio (h, i, j) at stations A, B and C.

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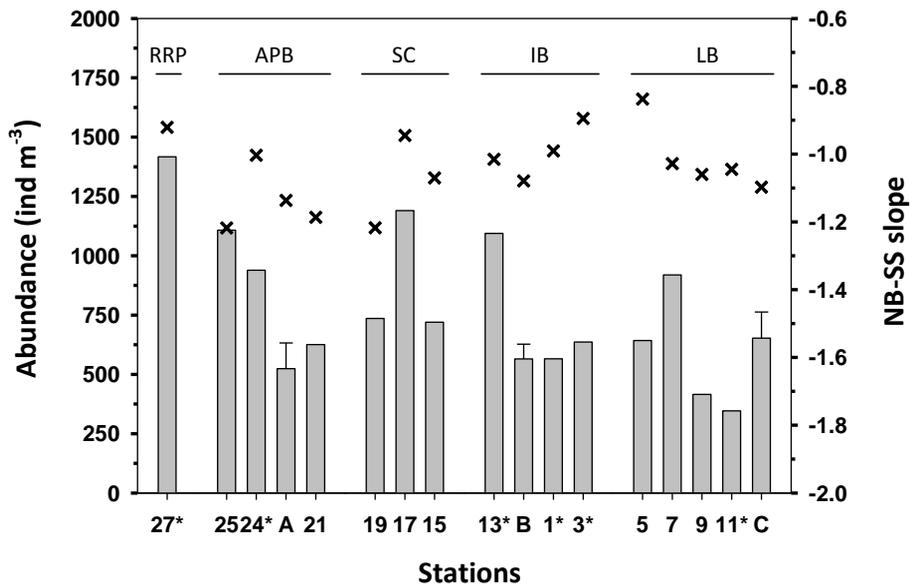


Fig. 8. Horizontal distribution of mesozooplankton abundance (vertical bar) issued from the ZooScan counts and values of NB-SS slope (dark crosses) along the BOUM transect. Mean values for A, B and C stations between day and night sampling. (*) night sampling. See Fig. 4 for details on regions.

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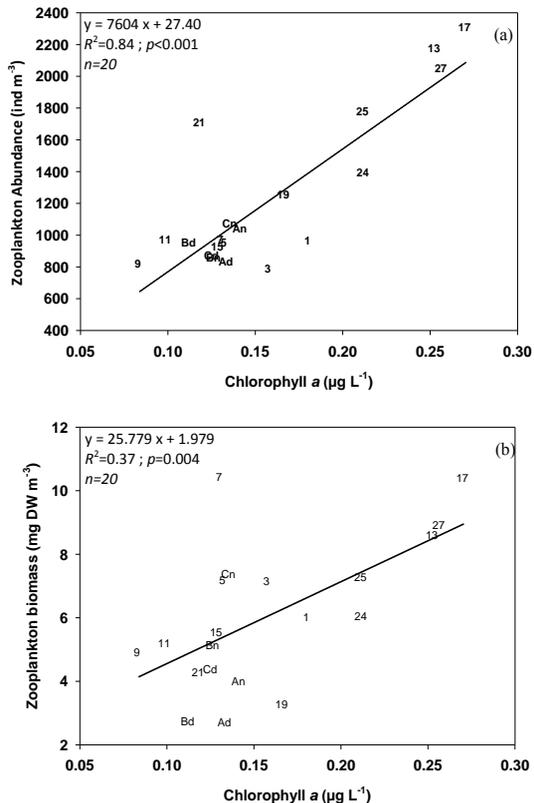


Fig. 9. Relationship between chlorophyll-*a* concentration ($\mu\text{g L}^{-1}$) and zooplankton abundance **(a)** (microscopic counts) and net zooplankton biomass **(b)** across the whole Mediterranean Sea. For A, B and C stations, day sampling (d) and night sampling (n). See Table 1 and Fig. 1 for location of stations.