



HAL
open science

Distribution of epipelagic metazooplankton across the Mediterranean Sea during the summer BOUM cruise

A. Nowaczyk, F Carlotti, Delphine Thibault, M. Pagano

► To cite this version:

A. Nowaczyk, F Carlotti, Delphine Thibault, M. Pagano. Distribution of epipelagic metazooplankton across the Mediterranean Sea during the summer BOUM cruise. *Biogeosciences*, 2011, 8 (8), pp.2159-2177. 10.5194/bg-8-2159-2011 . hal-02008131

HAL Id: hal-02008131

<https://hal.science/hal-02008131v1>

Submitted on 3 Aug 2020

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.



Distributed under a Creative Commons Attribution - NoDerivatives 4.0 International License

Distribution of epipelagic metazooplankton across the Mediterranean Sea during the summer BOUM cruise

A. Nowaczyk, F. Carlotti, D. Thibault-Botha, and M. Pagano

Aix-Marseille Université, UMR6535, INSU-CNRS – Laboratoire d’Océanographie Physique et Biogéochimique, Centre d’Océanologie de Marseille, Campus de Luminy, Case 901, 13288 Marseille, France

Received: 14 March 2011 – Published in Biogeosciences Discuss.: 22 March 2011

Revised: 29 July 2011 – Accepted: 1 August 2011 – Published: 9 August 2011

Abstract. The diversity and distribution of epipelagic 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 in the upper 200 m layer 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 distinction between the communities of the eastern and western basins was clearly explained by the environmental factors. The specific distribution pattern of remarkable species was also described.

1 Introduction

Although the Mediterranean Sea represents only ~0.82 % of the total surface of the global ocean, it is the largest quasi-enclosed sea composed of two large basins, the eastern and the western basins, separated by the Strait of Sicily, which are subsequently divided in several sub-basins. It could be assimilated to a mini-size ocean with continental shelves, deep basins and trenches. The surface circulation is driven mainly by the inflow of Atlantic water through the Strait

of Gibraltar, its signature being modified as it travels eastward. The Mediterranean is displaying deep water mass formation sites which have shown large modifications through time (Pinardi and Masetti, 2000; Millot and Taupier-Letage, 2005; and review by Bergamasco and Malanotte-Rizzoli, 2010). It is a hot spot for marine biodiversity (Margalef, 1985; Bianchi and Morri, 2000; Coll et al., 2010) with a marine biota composed of endemic and allochthonous species of Atlantic and Red Sea origins (Furnestin, 1968; Bianchi and Morri, 2000). This ecosystem is overall oligotrophic, but paradoxically, significant production do occur which sustain large fisheries and marine mammals communities (Coll et al., 2010; Würtz, 2010). This “maxi-size laboratory” can be then considered as one of the most complex marine environment (Meybeck et al., 2007).

As a whole, the Mediterranean Sea is characterized by a strong eastward gradient in nutrients, phytoplankton biomass and primary production (reviewed in Siokou-Frangou et al., 2010) with ultra-oligotrophic conditions being found in the Levantine basin (Krom et al., 1991; Ignatiades, 2005; Moutin and Raimbault, 2002). From a handful of studies, a similar pattern has also been reported at the basin scale for mesozooplankton abundance (Dolan et al., 2002; Siokou-Frangou, 2004; Mazzocchi et al., 1997; Minutoli and Guglielmo, 2009) but no synoptic view through the western and eastern basins was run to confirm this trend. Moreover, no clear pattern was highlighted for the biomass which presents several hot spots located in the north-western Mediterranean, the Catalan Sea, the Algerian Sea and the Aegean Sea (reviewed in Siokou-Frangou et al., 2010). Currently, the existing datasets are not yet sufficient to get a comprehensive understanding of the metazooplankton distribution in the Mediterranean Sea.

Indeed, many field studies have been realised at regional scales and have highlighted the impact of mesoscale features on the distribution and diversity of metazooplankton in both Mediterranean basins (Ibanez and Bouchez, 1987; Pinca and



Correspondence to: A. Nowaczyk
(antoine.nowaczyk@univmed.fr)

Dallot, 1995; Youssara and Gaudy, 2001; Mazzocchi et al., 2003; Siokou-Frangou, 2004; Pasternak et al., 2005; Riandey et al., 2005; Fernandez de Puelles et al., 2004, 2007; Zervoudaki et al., 2006; Molinero et al., 2008; Licandro and Icardi, 2009; Siokou-Frangou et al., 2009). Mesoscale hydrodynamic structures are known also to enhance nutrient concentrations, and therefore, plankton patchiness stimulating trophic transfers towards large predators.

The BOUM experiment (Biogeochemistry from the Oligotrophic to the Ultra-oligotrophic 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 across the western and eastern basins through a 3000 km survey. Our main goal here was to improve our knowledge on the role of planktonic metazoan (metazooplankton hereafter; Sieburth et al 1978) in the biogeochemical cycle in such an open oligotrophic ecosystem by coupling standing stock estimations (abundance, biomass, and size classes) and metabolic measurements. The presentation of this work is carried out in two steps. The structural investigation is presented here and the functional part will be presented in another manuscript (Nowaczyk et al., 2011). Therefore, the present study investigates the metazooplankton community spatial distribution (vertical and horizontal) including small-size copepods (nauplii and different copepodite stages) often neglected in previous studies. Finally, we attempt to define the links between the spatial distribution of metazooplankton and the environmental characteristics.

2 Materials and methods

2.1 Cruise track and environmental parameters

2.1.1 Cruise transect

A 3000 km transect across the Mediterranean Sea was conducted during the BOUM cruise from 18 June to 20 July 2008 on board the French N.O. *L'Atalante* (Fig. 1). The cruise run eastward from the Ionian basin (IB) to the Levantine basin (LB) from 18 June 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). Sampling strategy consisted in 27 short-stay stations (~2–3 h) distributed ~100 km apart and long-stay stations (4 days: stations A, B and C) located in the centre of important hydrological features (anticyclonic gyres) (see Moutin et al., 2011 for more details). Location of the sampling stations is presented in Fig. 1 and Table 1. Physico-chemical parameters and phytoplankton were sampled at all stations whereas the metazooplankton, ciliates and heterotrophic nanoflagellates (HNF) were samples every other stations.

2.1.2 Sampling and analysis of environmental parameters

Vertical profiles of temperature, conductivity and oxygen were obtained using a Sea-Bird Electronic 911 PLUS CTD. Nutrients, chlorophyll, ciliates and HNF were sampled using Niskin bottles. Ammonium and phosphate concentration were immediately measured on board with an auto-analyzer (Bran+Luebbe auto-analyseur II) according to the colorimetric method as fully described in Pujo-Pay et al. (2011). Total chlorophyll-*a* was measured by the fluorimetric methods following a methanol extraction (Herbland et al., 1985). HNF samples were filtered onto black nucleopore filters and stained with DAPI (Porter and Feig, 1980) and stored at -20°C on board until analysis, then enumerated using LEITZ DMRB epifluorescence microscope. Ciliates samples were fixed in 2% Lugol's iodine-seawater solution, stored at 4°C and counted using an inverted microscope. These two methods were fully described in Christaki et al. (2011). The same method was used for nanophytoplankton and diatoms identification. The particular organic matter was determined according to the wet oxydation procedure described by Raimbault et al. (1999).

2.2 Zooplankton

2.2.1 Sampling strategy

Zooplankton was collected within the upper 200 m layer (100 m at st. 17 and 27) using double Bongo nets (60 cm mouth diameter) fitted with $120\ \mu\text{m}$ mesh size and equipped with filtering cod ends. Vertical hauls were done at a speed of $1\ \text{m s}^{-1}$. No flowmeters were available but special care was taken while sampling to keep the cable vertical. Volume sampled by the net was then reported to the depth of the tow and the opening surface of the net ($0.28\ \text{m}^2$). 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 cod-end content of the first net was kept fresh and split into two parts with a Motoda box. The first part was processed immediately for biomass measurements. The second half of the sample was collected onto a GF/F filter, placed in a Petri dish, and then deep frozen in liquid nitrogen for further ingestion rates measurements (Nowaczyk et al., 2011). The cod-end content of the second net was directly preserved in 4% buffered formalin-seawater solution for later taxonomic identification and abundance measurements. Discrete sampling was also performed to study vertical distribution of copepod nauplii and small copepods from water samples collected with the CTD/rosette. At each selected depth, the content of a 12 L Niskin bottle was gently collected onto a $20\ \mu\text{m}$ mesh net and fixed in a 2% Lugol's iodine-seawater solution. Seven

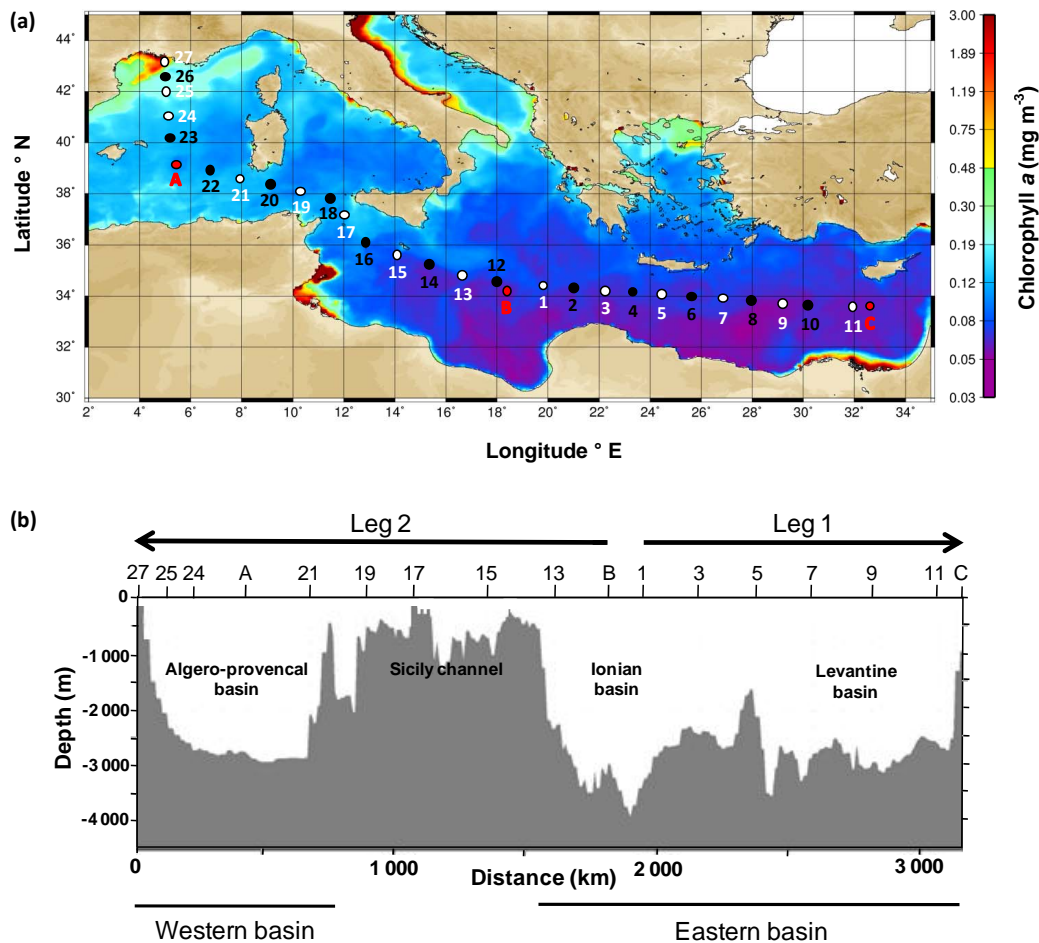


Fig. 1. (a) Location of sampling stations superimposed on a SeaWiFS composite image of the sea surface integrated chlorophyll-*a* concentration (permission to E.Bosc) during the BOUM transect (16 June–20 July 2008). Short-stay stations where zooplankton was sampled (white) and not sampled (black) and long-stay stations (red). (b) Bottom depth and geographic areas along the transect.

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.

2.2.2 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 in an oven at 60 °C for 3 days onboard. Dry-weight (mg) 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. Once back on land, carbon and nitrogen contents were measured. Dried samples were grinded, homogenized then split into 3 equal fractions (~0.8–1 mg DW), placed in tin caps and analyzed with a mass spectrometer (INTEGRA CN, SerCon).

2.2.3 Microscope counts

Taxonomic identification and counts of zooplankton were done back in the land laboratory using a LEICA MZ6 dissecting microscope. Very common taxa were counted in subsamples (1/32 or 1/64), and the whole sample was examined for either rare species and/or large organisms (i.e. euphausiids, amphipods). Identification of the copepods community 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). Holoplankton organisms other than copepods as well as meroplankton were identified down to taxa levels.

2.2.4 Digital imaging approach using the Zooscan

After homogenization, another fraction of each preserved sample containing a minimum of 1000 particles was placed

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

Station ID	Latitude (°N)	Longitude (°E)	Bottom depth (m)	Region	Date	Sampling time (h:min)	Distance to the coast (km)
27	43°12	4°55	106	Rhône River Plume	7/18/08	23:10	14
25	41°59	5°00	2267	Algero-Provencal Basin	7/18/08	11:40	140
24	41°05	5°03	2659		7/18/08	01:05	130
A day	39°05	5°21	2798		7/15/08	11:30	120
A night	39°05	5°21	2786		7/15/08	23:30	120
21	38°37	7°54	2055		7/11/08	06:30	58
19	38°05	10°13	556	Sicily Channel	7/10/08	11:30	91
17	37°10	12°00	117	''	7/09/08	13:50	82
15	35°40	14°06	588	''	7/08/08	19:00	33
13	34°53	16°42	2097	Ionian Basin	7/08/08	01:30	240
B night	34°08	18°26	3007	''	7/04/08	01:45	260
B day	34°08	18°26	3197	''	7/05/08	11:55	260
1	34°19	19°49	3210	''	6/21/08	05:00	210
3	34°10	22°09	2382	''	6/22/08	01:15	140
5	34°02	24°29	2616	Levantin Basin	6/22/08	19:00	110
7	33°54	26°50	2780	''	6/23/08	13:25	135
9	33°45	29°10	3033	''	6/24/08	07:30	270
11	33°34	31°56	2514	''	6/25/08	04:30	135
C day	33°37	32°39	798	''	6/27/08	14:55	110
C night	33°37	32°39	817	''	6/27/08	23:35	110

on the glass plate of the ZooScan. Organisms were carefully separated 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 (Normalized Biomass Size Spectrum) 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 Data analysis

Nauplii abundance presented here only concern the discrete bottle sampling and not the integrated dataset as they have been under-sampled even with a fine mesh bongo.

Based on both microscope and ZooScan abundance and biomass datasets, one way Anovas were used to examine differences among geographic areas and paired t-tests were run to study the diel variations at the long-stay stations. Only one day and one night samples were counted and taxonomic composition described at each of these 3 stations. Thus, day-night comparison was assessed using paired t-test on the 6 data points. In order to reduce variability among stations, normalization was done by dividing each data by the maximum value of the pair.

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), biogeochemical (oxygen, PON, POP and particular N/P ratio), and biological (Chlorophyll-*a*, heterotrophic nanoflagellates, nanophytoplankton, diatoms, and ciliates) parameters. Regarding Niskin bottle sampling, small copepods and nauplii variability was study at discrete depth scale but also integrated over the upper 200 m.

Metazooplankton abundance and biomass variability assessment was on the other hand performed from the net sample data. Variables were $\log(x + 1)$ transformed when normalized tests failed.

The spatial variability of the environmental parameters and the metazooplankton community characteristics was assessed using multivariate analysis performed with ADE4 software (Thioulouse et al., 1997). The same environmental variables as in the correlation analysis (see above) was used but we added the mixed layer depth, and DIN, DIP, DON and DOP concentrations; we limited the metazooplankton community to the 74 more representative taxa (>10% occurrence). A principal component analysis (PCA) was performed on the environmental parameters, and a factorial correspondence analysis (COA) on the metazooplankton characteristics. The results of these two analyses were then associated through a co-inertia analysis (Dolédéc and Chesel, 1994). A cluster classification (percentage similarity, Bray-Curtis Index) was run on the observation (stations) scores from the first factorial plane using complete linkage and multidimensional scaling analysis (MDS) with PRIMER 6.0 software (Clarke and Warwick, 1995). The significance among groups was then tested using a non parametric MANOVA (PERMANOVA plug-in for PRIMER).

3 Results

3.1 Characterization of the study area

The cruise took place during the stratified period. The Eastern basin, sampled during the first leg, showed a surface layer (0–20 m) with temperature above 22 °C and up to 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), temperature 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 (Fig. 4a). The chlorophyll-*a* values at the DCM ranged from 0.237 at 100 m (st. 4) to 0.897 $\mu\text{g L}^{-1}$ at 75 m (st. 20). Ciliate standing stock decreased also from west to east and maximum values were located as well as at the depth of the DCM; nevertheless ciliate abundance displayed high variability between stations. Mixotrophic ciliates represented an appreciable amount of the ciliate biomass (Christaki et al., 2011). More details on the chemical, biological and physical environmental conditions are presented in Pujopay et al. (2011), Crombet et al. (2011), Moutin et al. (2011).

3.2 Zooplankton abundance and biomass distribution

Zooplankton abundance in the upper 200 m layer estimated from the microscope counts (Fig. 2a) varied over the five geographic areas (RRP, APB, SC, IB and LB), with values (mean \pm sd) of 1948, 1286 ± 409 , 1407 ± 687 , 1031 ± 492 and 872 ± 93 ind m^{-3} , respectively. No significant spatial differences were found between these five areas (Anova, $p > 0.05$). However, the general trend showed higher abundances in the western basin than in the eastern basin. Open water stations located in the western basin presented significantly ($p < 0.05$) higher abundance than those of the LB, but not to those in the entire eastern basin, due to the high abundance at station 13 (1901 ind m^{-3}). Abundance was higher at the stations located in coastal regions (st. 27) and in the centre of the SC (st. 17) than in open water, with the lowest abundance located at station 3 (732 ind m^{-3}). As for the total abundance pattern, nauplii and small copepods abundance did not show any significant differences between the five geographic areas ($p > 0.05$) (Fig. 2b). Nevertheless, at the basin scale, only small copepods abundance presented a significant higher abundance ($p < 0.05$) in the western basin (4450 ± 2035 ind m^{-3}) than in the eastern basin (2627 ± 340). In addition, in the western basin, a clear northward increase in both the nauplii and small copepods abundance with values ranging from 20 929 (st. 27) to 6620 ind m^{-3} (st. 21) was observed while it was not clear for the total abundance.

Zooplankton biomass (mg DW m^{-3}) was weakly but significantly correlated with abundance (ind m^{-3}) ($R^2 = 0.298$, $n = 20$, $p < 0.01$). Biomass displayed large spatial variability, with the values ranging from 3.2 mg DW m^{-3} (st. 19) to 10.4 mg DW m^{-3} (st. 17), equivalent to 1.2 to 4.6 mg C m^{-3} and 0.33 to 1.35 mg N m^{-3} , respectively (Fig. 2c, d). Station 7 displayed a low abundance but a rather large biomass, which can be explained by the presence of large amphipods. A clear increase of DW biomass occurred northward in the APB (st. 21 to st. 27), but no clear pattern was observed in the other regions. In addition, no significant spatial differences were found between the five geographic areas (Anova, $p > 0.05$). Mean zooplankton carbon and nitrogen contents represented $36.3 \pm 3.7\%$ and $9.6 \pm 1.2\%$ of the DW respectively. Zooplankton C/N ratio was fairly constant (mean: 3.78 ± 0.29) with values ranged from 3.35 to 4.37 at station 15 and 5, respectively.

3.3 Metazooplankton community composition and distribution

Over 74 taxa were identified from net tows during this study (Table 2) with 56 genera/species of copepods, 6 taxa of meroplankton and 12 taxa of holoplankton. Nauplii were present in the net samples but this technique, even when using a 120 μm mesh net, did underestimate their real abundance, which was confirmed by the comparison with the integrated abundance obtained with the Niskin bottle sampling

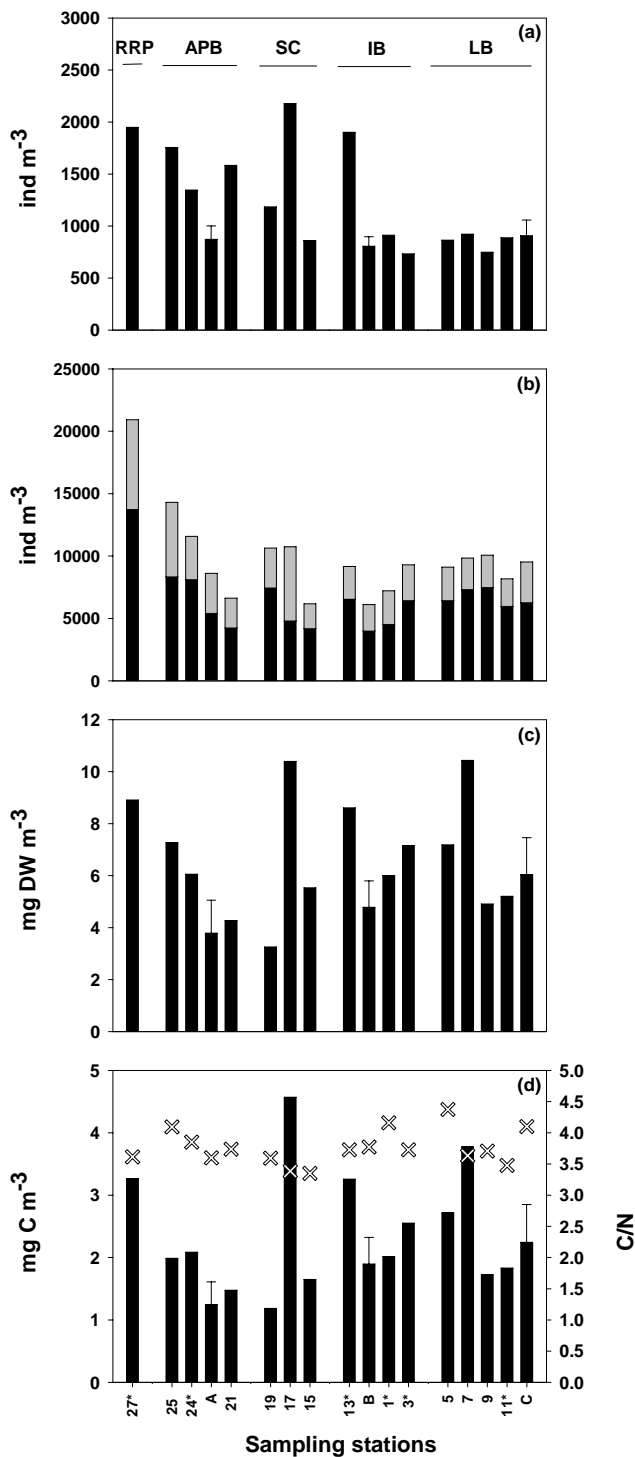


Fig. 2. Spatial distribution of zooplankton integrated abundance obtained by net sampling (a) and by Niskin bottle (b) including nauplii (black) and small copepods (grey), biomass as dry weight (c) and as carbon (d) with C/N ratio (cross). Mean and standard deviation for stations A, B and C. (*) night sampling. See text for details on the five Mediterranean areas.

(see Sect. 3.4) and were given in Table 2 for information purpose only. Copepods represented $90.4 \pm 3.0\%$ of total metazooplankton abundance and were dominated by 4 taxa: *Clausocalanus/Paracalanus* spp., *Oithona* spp., *Oncaea* spp. and *Macrosetella/Microsetella* spp. which represented $\sim 80\%$ of the copepod community. The three first taxa were evenly distributed along the transect but presented a local higher abundance (Fig. 3a, b, c), whereas *Macrosetella/Microsetella* spp. were 7 times more abundant in the western than in the eastern Mediterranean Sea (Fig. 3e). *Euterpina acutifrons* and meroplanktonic larvae were very common in neritic and coastal waters (e.g. st. 17 and 27 in Table 2). With the exception of one or two stations, *Corycaeus/Farranula* spp. and *Oncaea* spp. populations were the only taxa dominated by adult stages (50 to 80%).

Less abundant copepod species also displayed interesting geographical distribution. The genera *Corycaeus/Farranula* and *Calocalanus* spp. were less abundant in a large part of the western basin (Fig. 3d and Table 2). *Mecynocera clausi*, *Lucicutia flavicornis*, *Haloptilus longicornis*, *Pareucalanus attenuatus* and *Subeucalanus monachus* (Fig. 3g, h, i, k, l 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. 3f). However, *A. clausi* replaced *A. negligens* in the north part of the western Mediterranean (st. 27 and 25) and at station 19 (Table 2). The subtropical copepod species *Cosmocalanus darwini* (Fig. 3j) was found in the two basins and is reported here for the first time in the Mediterranean Sea. Both adult and copepodite stages were collected.

Non-copepod holoplanktonic species, mainly appendicularians, ostracods, pteropods and chaetognaths, made up $9.3 \pm 2.0\%$ of the metazooplankton abundance while meroplanktonic species were scarce ($1.0 \pm 1.4\%$) except at the RRP (4.3%). Cladocerans (Fig. 3n) were absent in the central sector of the eastern basin. Appendicularians (Fig. 3m) were 3 to 10 times more abundant at stations 27 and 17 than in the rest of the transect. It is also interesting to note that station C presented a high abundance (up to 11.6 ind m^{-3}) of echinoderm larvae (Asteroidae).

Spatial impact of the mesoscale features, the anticyclonic gyres, when compared to the neighbouring stations was more or less obvious (see Table 2 and Fig. 3). *Clausocalanus/Paracalanus* spp. were 2 to 4 times less abundant at stations A and B than at the adjacent stations, and only 1.5 less abundant at station C than at station 11. *Mecynocera clausi* and *Corycaeus/Farranula* spp. were on the other hand more abundant in the gyres than in the neighbouring stations especially obvious for the gyre B and C.

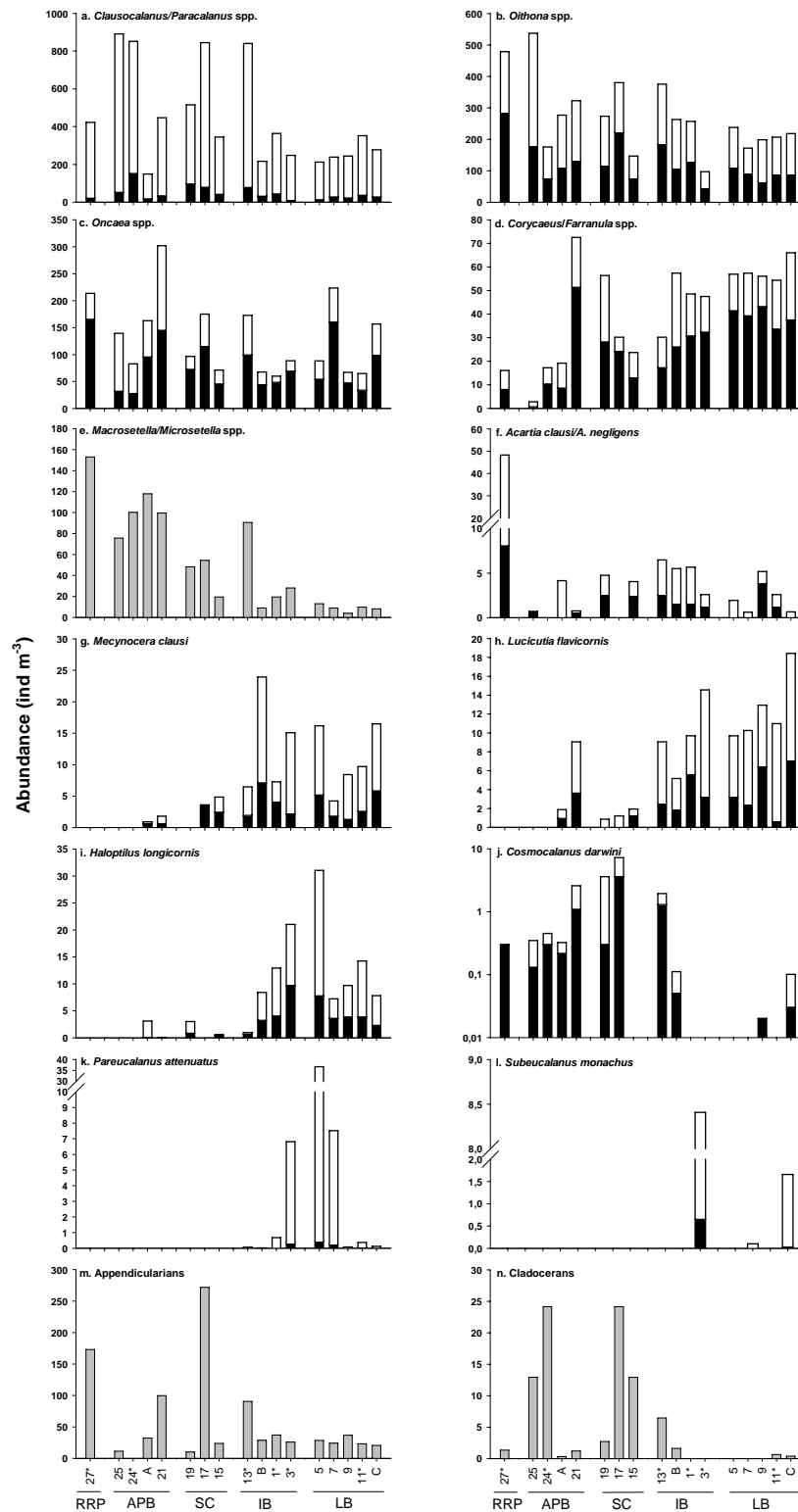


Fig. 3. Spatial distribution of the important zooplankton species across the Mediterranean transect: **(a)** *Clausocalanus* spp. and *Paracalanus* spp., **(b)** *Oithona* spp., **(c)** *Oncaea* spp., **(d)** *Corycaeus* spp. and *Farranula* spp., **(e)** *Macrosetella* spp. and *Microsetella* spp., **(f)** *Acartia clausi* and *Acartia negligens*, **(g)** *Mecynocera clausi*, **(h)** *Lucicutia flavicornis*, **(i)** *Haloptilus longicornis*, **(j)** *Cosmocalanus darwini*, **(k)** *Pareucalanus attenuatus*, **(l)** *Subeucalanus monachus*, **(m)** Appendicularians and **(n)** Cladocerans. Copepodit (white), adult (black) and undifferentiated (grey) stages. (*) night sampling. Mean for stations A, B and C between day and night sampling. Note: logarithmic scale in panel (j).

Table 2. Mean integrated abundance (\pm standard deviation) in the upper 200 m depth of total zooplankton, copepods, other holoplankton and meroplankton and percentage abundance 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	Symbole	Rhône river plume	Algero Provencal basin	Sicily channel	Ionian basin	Levantin basin	Algero Provencal eddy	Ionian eddy	Levantin eddy
Total (ind m ⁻³)		1948	1561 \pm 205	1407 \pm 687	1181 \pm 630	855 \pm 75	872 \pm 129	806 \pm 92	906 \pm 151
Copepods (ind m ⁻³)		1636	1457 \pm 229	1230 \pm 519	1073 \pm 570	771 \pm 83	773 \pm 110	742 \pm 74	828 \pm 134
Other holoplankton (ind m ⁻³)		228	102 \pm 107	173 \pm 184	107 \pm 59	81 \pm 19	90 \pm 28	60 \pm 20	69 \pm 13
Meroplankton (ind m ⁻³)		83.6	2.4 \pm 3.7	3.6 \pm 1.9	1.3 \pm 1.1	2.7 \pm 1.8	9.4 \pm 9.2	4.0 \pm 1.7	9.4 \pm 4.4
Nauplii* (ind m ⁻³)		105	67 \pm 54	92 \pm 35	128 \pm 128	74 \pm 18	64 \pm 18	100 \pm 15	67 \pm 7
Copepods (%)		84.0	93.3	87.4	90.8	90.2	88.6	92.1	91.4
<i>Clausocalanus/Paracalanus</i> spp.	CIPa	21.7	46.8	40.4	41.0	30.6	17.1	26.9	30.5
<i>Oithona</i> spp.	Oi	24.6	22.1	19.0	20.6	23.8	31.7	32.6	24.1
<i>Oncaea</i> spp.	On	10.9	11.2	8.1	9.0	12.9	18.6	8.4	17.3
<i>Macrosetella/Microsetella</i> spp.	MiMa	7.9	5.9	2.9	3.9	1.0	13.5	1.1	0.9
<i>Corycaeus/Farranula</i> spp.	CoFa	0.8	2.0	2.6	3.6	6.6	2.2	7.1	7.3
<i>Acartia clausi</i>	Acl	2.5	< 0.1	0.1	0.0	0.0	0.0	0.0	0.0
<i>Acartia negligens</i>	Ane	0.0	< 0.1	0.1	0.4	0.3	0.5	0.7	0.1
<i>Calanus helgolandicus</i>	Che	< 0.1	0.1	0.0	0.0	0.0	< 0.1	0.0	0.0
<i>Calocalanus pavo</i>	Cpa	0.0	0.0	0.4	1.3	0.9	0.0	0.4	0.5
<i>Calocalanus</i> spp.	Ca	0.4	0.4	1.0	2.6	2.5	1.5	4.1	2.3
<i>Candacia</i> spp.	Cd	0.1	< 0.1	0.1	0.1	0.1	< 0.1	< 0.1	< 0.1
<i>Centropages typicus</i>	Cty	0.2	0.3	1.4	< 0.1	0.0	0.0	0.0	0.0
<i>Cosmocalanus darwini</i>	Cda	< 0.1	0.1	0.3	0.1	< 0.1	< 0.1	< 0.1	< 0.1
<i>Ctenocalanus vanus</i>	Cva	2.1	0.0	0.6	0.8	0.8	0.0	0.0	0.0
<i>Eucalanus hyalinus</i>	Ehy	0.0	0.1	< 0.1	< 0.1	< 0.1	< 0.1	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>	Eac	4.1	0.0	0.1	0.4	0.0	0.0	0.0	0.0
<i>Haloptilus</i> spp.		0.0	< 0.1	0.1	1.0	1.8	0.4	1.0	0.9
<i>Lucicutia</i> spp.		0.0	0.2	0.1	0.9	1.3	0.2	0.7	2.1
<i>Mecynocera clausi</i>	Mcl	0.0	< 0.1	0.2	0.8	1.1	0.1	3.0	1.8
<i>Mesocalanus tenuicornis</i>	Mte	< 0.1	< 0.1	0.0	< 0.1	0.0	< 0.1	< 0.1	0.0
<i>Nannocalanus minor</i>	Nmi	3.3	0.7	5.5	0.0	0.3	0.4	1.3	0.0
<i>Neocalanus gracilis</i>	Ngr	0.0	< 0.1	< 0.1	0.2	0.1	0.1	0.1	< 0.1
<i>Pareucalanus attenuatus</i>	Pat	0.0	0.0	0.0	0.2	1.3	0.0	< 0.1	< 0.1
<i>Pleuromamma abdominalis</i>	Pab	0.0	0.2	0.0	0.1	< 0.1	0.2	< 0.1	< 0.1
<i>Pleuromamma gracilis</i>	Pgr	0.6	0.1	0.2	0.4	0.1	0.4	0.1	< 0.1
<i>Scolecithricella</i> spp.	Sa	0.4	0.0	0.2	0.2	< 0.1	0.0	0.6	0.3
<i>Scolecithrix</i> spp.	Sx	0.0	0.0	< 0.1	0.2	0.8	0.0	0.1	0.4
<i>Spinocalanus</i> spp.	Sp	0.6	< 0.1	0.8	< 0.1	0.3	< 0.1	0.2	0.1
<i>Subeucalanus monachus</i>	Smo	0.0	0.0	0.0	0.2	< 0.1	0.0	0.0	0.0
<i>Temora stylifera</i>	Tst	< 0.1	< 0.1	< 0.1	0.3	0.3	0.0	0.0	0.1
other copepods		3.5	3.0	3.0	2.3	3.1	1.7	3.7	2.7
Other holoplankton (%)		11.7	6.6	12.3	9.1	9.5	10.3	7.4	7.6
Appendicularians	AP	8.9	2.4	7.2	4.3	3.3	3.7	3.6	2.3
Chaetognaths	CH	0.2	0.5	0.6	1.9	1.3	1.0	0.6	0.4
Cladocerans	CL	0.1	0.8	0.9	0.2	< 0.1	< 0.1	0.2	< 0.1
Doliolids	DO	0.0	< 0.1	0.0	< 0.1	0.3	0.0	0.0	0.0
Euphausiids/Mysids	EU MY	0.6	< 0.1	0.1	0.1	< 0.1	0.1	0.1	< 0.1
Ostracods	OS	< 0.1	2.3	0.8	1.2	3.0	3.7	1.4	2.7
Polychaetes	PO	0.5	0.3	0.1	0.4	0.3	0.8	0.1	0.2
Pteropods	PT	1.0	0.2	2.0	0.5	1.1	0.6	1.3	0.6
Salps	SA	< 0.1	0.0	0.4	0.1	0.0	< 0.1	< 0.1	< 0.1
Siphonophores	SI	0.4	< 0.1	0.2	0.3	0.1	< 0.1	0.1	0.9
Others		< 0.1	< 0.1	< 0.1	0.1	0.1	0.4	< 0.1	0.4
Meroplankton (%)		4.3	0.2	0.2	0.1	0.3	1.1	0.5	1.0
Decapod larvae	DE	0.1	0.1	< 0.1	0.0	< 0.1	0.0	< 0.1	< 0.1
Echinoderm larvae	EC	0.8	< 0.1	< 0.1	0.0	0.1	0.0	0.3	1.0
Fish eggs		0.1	< 0.1	< 0.1	< 0.1	< 0.1	< 0.1	< 0.1	< 0.1
Fish larvae	FI	< 0.1	< 0.1	< 0.1	< 0.1	0.1	0.1	< 0.1	< 0.1
Jellyfishes	JE	0.2	< 0.1	0.1	0.1	< 0.1	0.9	0.1	< 0.1
Lamellibranch larvae	LA	3.1	0.1	0.1	0.0	0.1	0.1	< 0.1	0.0

* Nauplii abundance is given only for information and is not included in the total abundance.

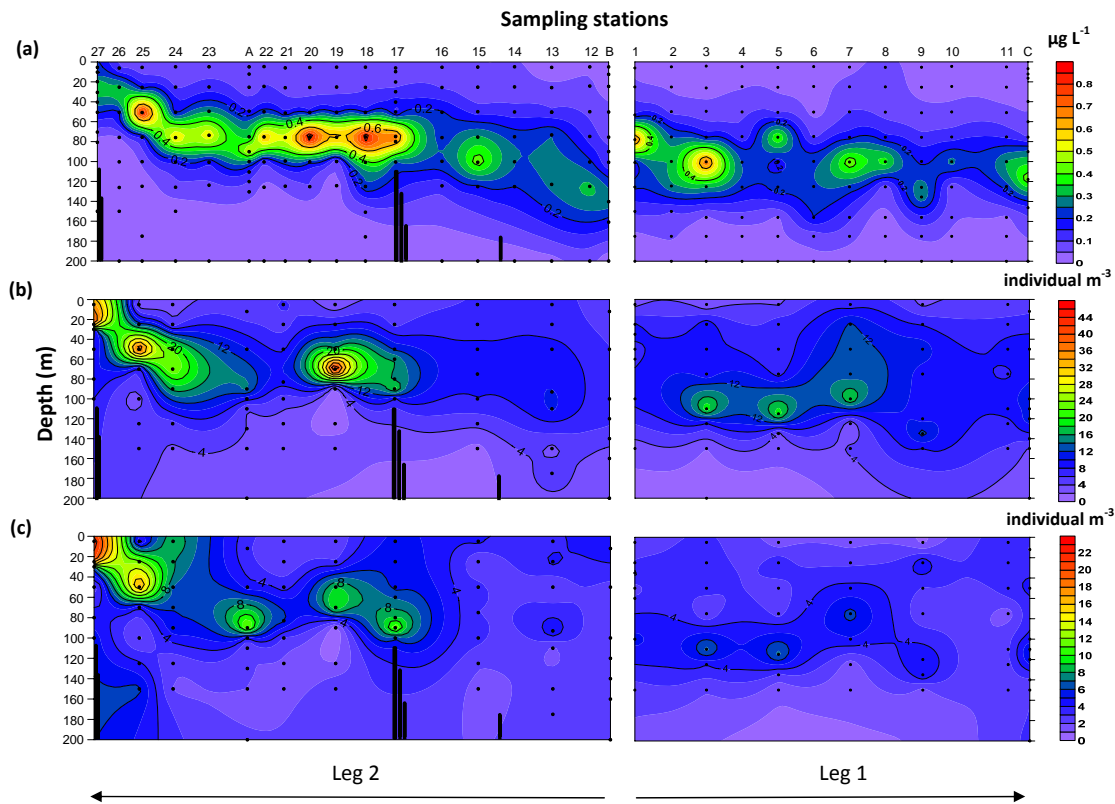


Fig. 4. Spatial distribution of chlorophyll-*a* concentration (a), copepods nauplii (b) and small copepods (c) within the upper 200 m layer across the Mediterranean Sea. Bottom depth in black.

3.4 Discrete sampling

The discrete depth sampling within the top 200 m collected small-sized copepods (<1 mm) and nauplii. The community of small copepods was composed of adult and copepodite stages of *Oithona* spp., *Oncaea* spp., *Corycaeus/Farranula* 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. 4). The depth of the maximum nauplii density matched that of small copepods for most stations with the exception of stations 7 and 24. An eastward deepening of the depth of the highest abundance was observed from 25 m to 90 m in the western basin and from 100 m to 135 m in the eastern basin. Nauplii abundance was integrated over the upper 200 m except at st. 17 and 27 where depth range was limited to 100 m. Integrated abundance ranged from 4177 ind m⁻³ (st. 15) to 13 729 ind m⁻³ (st. 27). It 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 104 times and 4 times higher, respectively, than for samples collected with nets.

3.5 Zooplankton size structure

The automatic recognition system ZooScan (ZC) and the dissecting microscope (MC) (Fig. 5) showed a significant linear regression with $ZC = 0.50 MC + 169.93$ ($R^2 = 0.69$, $p < 0.001$, $n = 20$). The lower detection limit for the ZooScan is 300 µm ECD, which led to an underestimation of the total number of organisms counted by $\sim 33 \pm 15.9\%$ (corresponding to $35.4 \pm 14.9\%$ when nauplii were computed) when compared to the microscope technique. This underestimation corresponded to the fraction <300 µm ECD equivalent to a copepod with a total length of 500 µm. No clear pattern between the five geographic areas or between the western and eastern basins were found for this single size fraction ($p > 0.05$). Nevertheless, the overall spatial distribution of the metazooplankton abundance was similar between the two methods (Figs. 2a and 6). Biovolume (ZooScan determinations, data not shown) and biomass (Fig. 2c) also shown similar spatial variations. Abundance and NB-SS slopes (Fig. 6) 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; such as

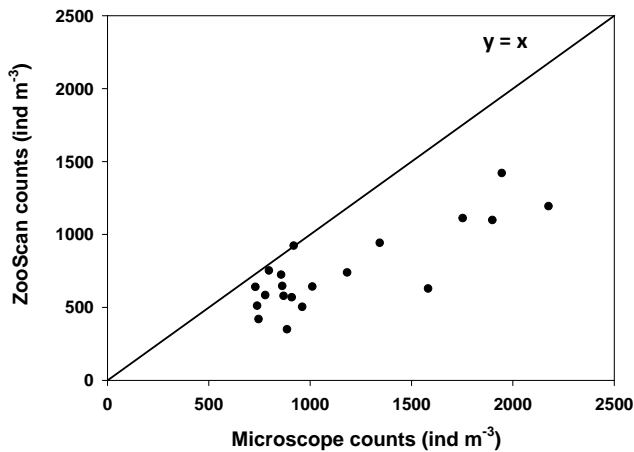


Fig. 5. Comparison between microscope and ZooScan counts for all stations sampled with the Bongo net.

Haloptilus longicornis, *Pareucalanus attenuatus* and *Subeucalanus monachus*) (Fig. 3i, k, l).

3.6 Day-night variation

At the three long-stay stations, significant higher abundance ($\sim 17\%$; $p < 0.001$) and biomass ($\sim 40\%$; $p < 0.001$) of organisms $> 300\ \mu\text{m}$ ECD observed at night highlighted the impact of the diel vertical migration on the structure of the community (Fig. 7). This increase was mainly explained by medium (500–1000 μm) and large-sized ($> 1000\ \mu\text{m}$) organisms. Several specific taxa displayed higher night abundance within the upper 200 m. This included the copepods *Euchirella messinensis* and *Neocalanus gracilis* ($p < 0.05$), *Pleuromamma abdominalis* and *P. gracilis* ($p < 0.01$), as well as other taxa such as euphausiids, fish larvae ($p < 0.001$), pteropods and doliolids ($p < 0.05$).

The C/N ratio was overall stable (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.

3.7 Relationships between metazooplankton and environmental parameters

No significant correlations between the different physico-chemical variables (temperature, salinity and oxygen) and the net metazooplankton abundance or biomass were found, while abundance of nauplii and small copepods from discrete samples were significantly correlated with oxygen level (Table 3). All metazooplankton parameters – both integrated and discrete data – were strongly correlated with chlorophyll-*a* concentrations (Fig. 8). Discrete abundance of nauplii and small copepods was strongly correlated with nanophytoplankton, diatoms and POP concentrations. PON concentration was the only variable showing a significant relationship with both the net and discrete metazooplankton data.

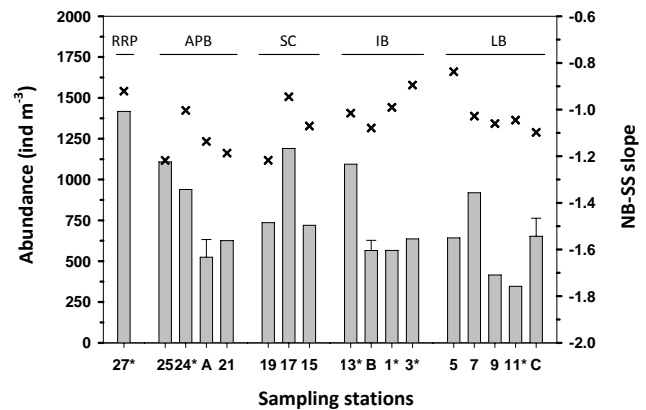


Fig. 6. Spatial distribution of mesozooplankton abundance (vertical bar) from the ZooScan counts and values of NB-SS slope (dark cross) along the BOUM transect. Mean values and standard deviations for stations A, B and C between day and night sampling. (*) night sampling. See text for details on the 5 regions.

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 $> 10\ \mu\text{m}$) and small copepods (total HNF).

The first factorial plane of the co-inertia analysis explained 69% of the variance, with 52% by the first axis. In both systems (“Environment” and “Zooplankton”), the three same groups of stations were observed (Fig. 9). Besides, the segregation obtained with the MDS analysis, based on the observation scores of the 2 first axes of both systems, showed the same grouping (not shown). The first group was composed of all stations located in the western basin, except for st. A, and the western stations in the Sicily Channel (st. 19 and 17). The second group comprised all the stations located in the eastern basin except for st. 13. The third group was composed of the eastern station in the SC (st. 15), the eastern station in the IB (st. 13) and the anticyclonic gyre A. The first group was characterized by high values of nutrients, chlorophyll-*a*, nanophytoplankton and ciliates (Fig. 9a) and the second group by elevated temperature and salinity and high diatoms concentration. In the “Zooplankton” system, the first group was mainly identified by the copepods *A. clausi*, *C. typicus* and *Calanoides carinatus* while the second group by the copepods *A. setosus*, *L. squilimana* and *H. longicornis* (Fig. 9c, d). In both systems the third group of stations occupied an intermediate position on the factorial plane. Other taxa (appendicularians, pteropods, polychetes, the calanoid copepods *Clausocalanus/Paracalanus* and the cyclopoid and poecilostomatoid copepods *Oithona* and *Oncaea*) were located near the barycentre. The relationship between the normalized coordinates of the stations on the first

Table 3. Simple correlation analysis between zooplankton parameters and environmental factors: significance degree of p values. Integrated water column zooplankton abundance (ind m^{-3}) and biomass (mg DW m^{-3}) were obtained from net sampling ($n = 20$); discrete abundance of nauplii and small copepod (ind m^{-3}) was issued from Niskin bottles ($n = 111$ to 140).

Variable	Symbole	Net Biomass	Abundance				
			Net Total	Integrated		Discrete depths	
				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

* = $p < 0.05$; ** = $p < 0.01$; *** = $p < 0.001$, underlined stars mean negative correlation; ns: not significant.

axis of both systems (“Environment” and “Zooplankton”) which reflects the degree of association between zooplankton and environment was highly significant ($R^2 = 0.89$).

4 Discussion

4.1 Pattern of metazooplankton abundance and biomass along the BOUM transect

Zooplankton abundance values recorded, when using 120 μm bongo nets, during the BOUM transect, were 4 to 8 times higher than in previously published studies (Mazzocchi et al., 1997; Siokou-Frangou 2004; Gaudy et al., 2003; Pasternak et al., 2005; Riandey et al., 2005), whereas biomass were of the same magnitude. Strong discrepancies with previously recorded abundance may arise from (1) the use of different sampling mesh-size (120 μm during BOUM and >120 μm in all previous studies) and (2) differences in sampling periods. Mesh size is a very important factor in the evaluation of metazooplankton abundance (Calbet et al., 2001; Turner, 2004). Zervoudaki et al. (2006) reported in a frontal area of the Aegean Sea, an increase of 2 to 20 times in abundance when smaller organisms (45–200 μm) were considered. The most pronounced differences were observed for copepod nauplii, copepodites and adults of small organisms such as *Clausocalanus/Paracalanus* spp., *Oithona* spp., *Oncaea* spp. and *Macrosetella/Microsetella* spp. Therefore it is clear that abundance is significantly higher when sampling is

performed with a 80 μm mesh size, but concomitant increase in biomass is not obvious (Thibault et al., 1994; Gaudy et al., 2003) probably due to the fact that small organisms have a low specific weight. According to the seasonal pattern of zooplankton production in temperate oceanic areas (Harvey, 1955), our abundance should be intermediate between maximum late spring values and vernal minimum values. Nevertheless, for the seasonal period (June–July), our values (700–2500 ind m^{-3}) recorded in the 0–200 m layer with a 120 μm net were higher than that of Siokou-Frangou (2004; 50–900 ind m^{-3}) recorded in the upper 100 m with a 200 μm mesh net. This discrepancy highlights the difficulty when comparing different zooplankton datasets and the lack of common protocols.

The present work contributed to widening the characterization of the zooplankton distribution in the Mediterranean Sea. Our synoptic survey through the western and eastern basins confirms the eastward decrease of zooplankton abundance that has already been reported during other trans-Mediterranean surveys (Mazzocchi et al., 1997; Dolan et al., 2002; Siokou-Frangou, 2004; Minutoli and Guglielmo, 2009). In contrast, the biomass distribution did not show any large scale trend with average ($\sim 6.3 \text{ mg DW m}^{-3}$) and maximal ($\sim 10.4 \text{ mg DW m}^{-3}$) values similar between regions, in agreement with biomass data compilations for various Mediterranean regions (Champalbert, 1996; Alcaraz et al., 2007; Siokou-Frangou et al., 2010). The apparent paradox between the trend in abundance and no trend in biomass might be explained by difference in size-spectra between the

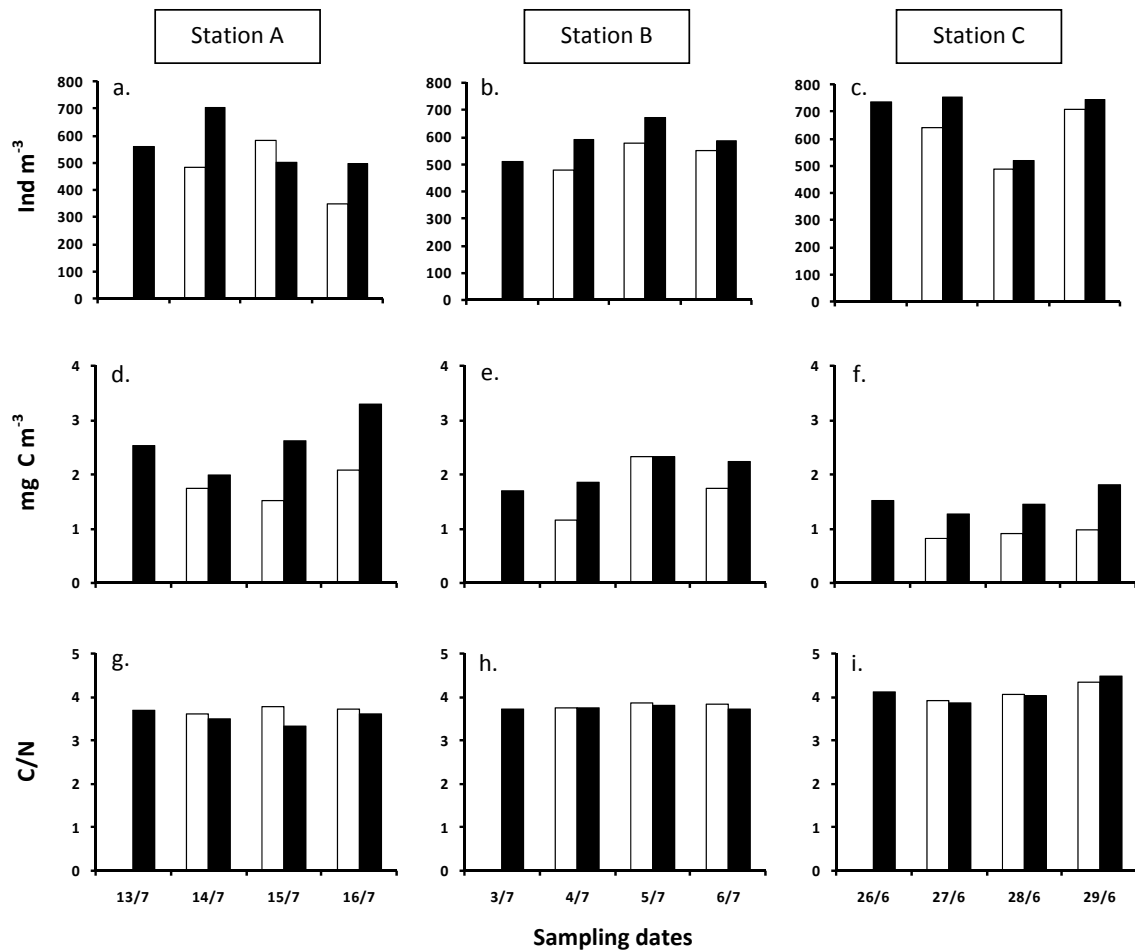


Fig. 7. Impact of sampling time (day: white; night: black) on zooplankton abundance integrated in the upper 200 m (ZooScan counts) (a, b, c), carbon biomass (d, e, f) and C/N ratio (g, h, i) at stations A, B and C.

eastern and western basins. The presence of a few dominant large species, such as *Haloptilus longicornis*, *Pareucalanus attenuatus* and *Subeucalanus monachus* in the eastern basin, or the large amphipod *Phronima sedentaria* at station 7 could explain high local biomass. For example, the contribution of the three large copepod species to the total biomass was estimated, using length-weight relationship (Webber and Roff, 1995; Hopcroft et al., 2002) to be 1.7 % (st. 13), 24.3 % (st. 3) and 30.5 % (st. 5). Therefore, large organisms contributed to the low NB-SS slopes observed in the eastern basin (see Fig. 6). In contrast in the western basin, high abundance was linked with the predominance of small organisms such as *Oncaea* spp. and *Macrosetella/Microsetella* spp. This higher abundance of small organisms was confirmed by the Niskin bottle sampling.

In the western basin metazooplankton and small copepods abundances as well as the total biomass displayed a North-South decreasing gradient. D'Ortlenzo and Ribera d'Alcalà (2009) reported also this clear north-south gradient in the lower trophic level (chlorophyll-*a* levels) with a “northern

blooming area”, an “intermittently-blooming central area” and a “non blooming area” in the south.

The high biomass and abundance variability between stations potentially arises from day-night variations, because sampling was conducted at different times of the day. When comparing day-night samplings at the three long stay stations, diel variation led to an increase of 17 % in term of abundance and over 40 % in term of biomass due to increasing numbers of medium and large organisms (>500 μ m ECD) at night as already observed in studies dedicated to the diel migration (Andersen et al., 1998, 2001, 2004; Riandey et al., 2005). Variability in zooplankton abundance and biomass could also be explained by the 3 identified anticyclonic gyres characterized by a clear downwelling (Moutin et al., 2011) with, as consequence, a deepening in nutrients (Pujo-Pay et al., 2011) and low phytoplankton and microzooplankton biomass (Christaki et al., 2011; Crombet et al., 2011). On the other hand, freshwater and terrestrial mineral input from the Rhône River (Cruzado and Velásquez, 1990) could explain high nutrient levels and high phytoplankton

Table 4. Equation parameters of the multiple linear regression models using forward stepwise method explaining the zooplankton parameters distribution. Integrated zooplankton abundance (ind m^{-3}) and biomass (mg DW m^{-3}) were obtained from net sampling ($n = 20$); discrete abundance of nauplii and small copepod (ind m^{-3}) was issued from Niskin bottles ($n = 111$ to 140). Symbols of variables are described in Table 3.

	Beta	Beta standard error	<i>P</i> -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
Discrete nauplii abundance			
$R^2 = 0.56$; adjusted $R^2 = 0.54$; $F = 31.51$; $P < 0.001$			
Constant	-12.79	2.22	
O2	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

and metazooplankton biomass in the river plume area (st. 27), as already evidenced by Gaudy et al. (2003). Variability resulted also probably from local hydrodynamic conditions linked to the bottom topography. The station 17 was very shallow with bottom depth ~ 100 m and presented typical characteristic of a coastal stations with high values of chlorophyll, high abundance of metazooplankton and a neritic community. This was also reported in other neritic areas of the western basin such as the Balearic Sea (Fernandez de Puellas et al., 2004, 2009). Station 13 located over the margin area

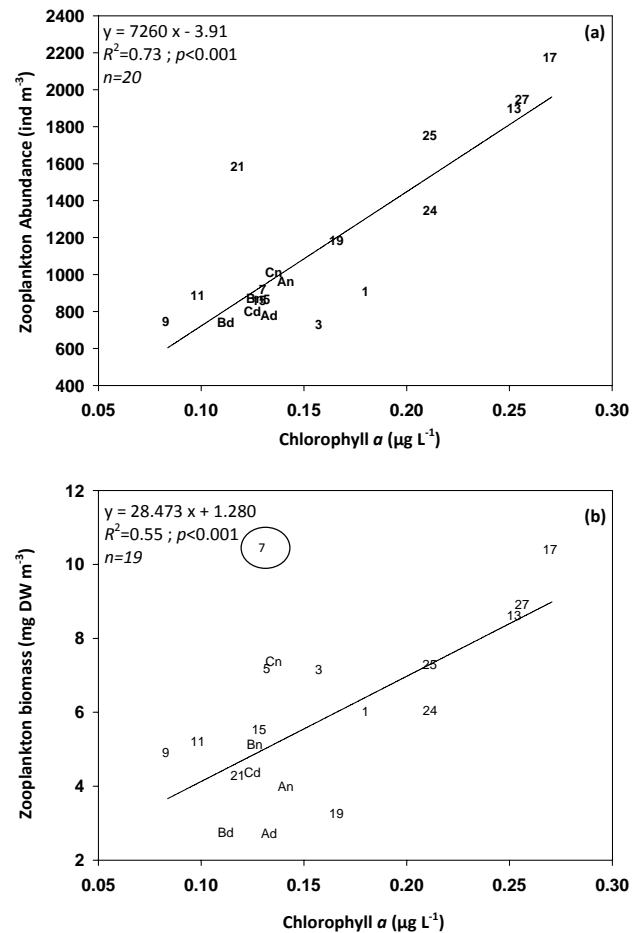


Fig. 8. Relationship between chlorophyll-*a* concentration ($\mu\text{g L}^{-1}$) and zooplankton abundance (a) (microscope counts) and net zooplankton biomass (b) across the whole Mediterranean Sea. For A, B and C stations, day sampling (*d*) and night sampling (*n*). See Table 1 and Fig. 1 for localization of stations. Note: st. 7 biomass value was removed from the analysis.

(slope between SC and IB) was also a site where local enhancement can be observed.

Globally, the horizontal distribution of the metazooplankton in terms of abundance and biomass was mainly driven by the chlorophyll-*a* concentration (Tables 3, 4 and Fig. 9). Our study established empirical relationships (linear regression) between metazooplankton abundance or biomass and chlorophyll-*a* concentration throughout the Mediterranean Sea. Chlorophyll-*a* (and subsequently zooplankton) distribution was mainly driven by the eastward gradient in oligotrophy which is a consequence of the thermohaline circulation and the nutrient inputs from rivers (Krom et al., 1991; Ignatiades, 2005; Moutin and Raimbault, 2002; D'Ortenzio and Ribera d'Alcalà, 2009).

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 Trinkaus, 1990;

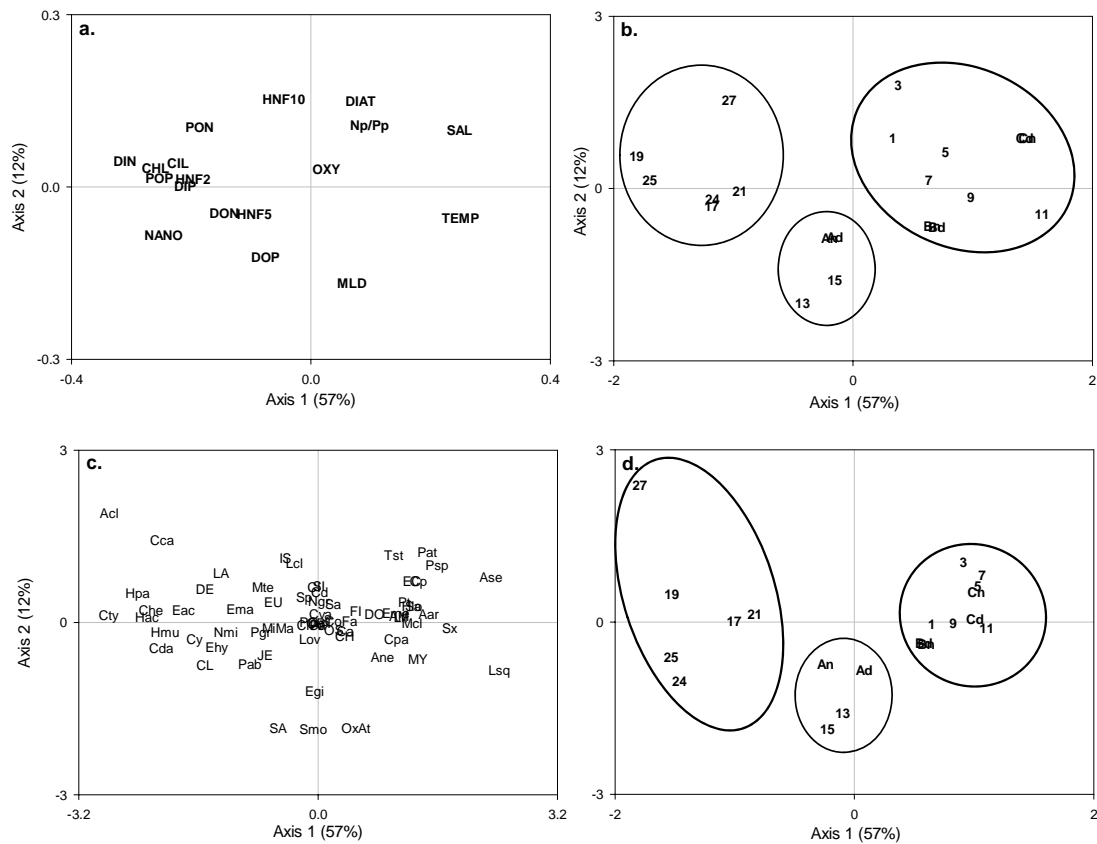


Fig. 9. Co-inertia analysis: plots of the environmental variables (a) and the stations (b) in the “Environment” system and plot of the taxa (c) and the stations (d) in the “Zooplankton” system. Circles corresponded to cluster group tested with non parametric MANOVA. Mixed Layer Depth (MLD), *Aetideus armatus* (Aar), *Arietellus setosus* (Ase), *Calanoides carinatus* (Cca), *Clytemnestra* spp. (Cy), *Copilia* spp. (Cp), *Euaetideus giesbrechti* (Egi), *Euchaeta marina* (Ema), *Euchirella messinensis* (Eme), *Haloptilus acutifrons* (Hac), *H. longicornis* (Hlo), *H. mucronatus* (Hmu), *Heterorabdus papilliger* (Hpa), *Lubbockia squilimana* (Lsq), *Lucicutia clausi* (Lcl), *L. flavicornis* (Lfl), *L. ovalis* (Lov), *Phaenna spinifera* (Psp), *Sapphirina* spp. (Sa), Amphipods (AM), Cirriped larvae (CI), Isopods (IS), *Oxygyrus/Atlanta* spp. (OxAt) and *Pterotrachea* spp. (Pt). Other abbreviations as in Tables 2 and 3.

Brugnano et al., 2010) and mainly within the upper 50 m in both the eastern basin (Mazzocchi et al., 1997) and the Ligurian Sea (Licandro and Icardi, 2009). Here, the bulk of both nauplii and small copepods presented a patchy vertical distribution (down to 120 m) 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 summer stratified period (Alcaraz, 1985, 1988; Alcaraz et al., 2007; Sabatés et al., 2007). Higher grazing activity by copepods is also often associated with DCM as demonstrated by increased phaeophorbide concentration (Latasa et al., 1992). Here, the nauplii abundance vertical distribution showed a maximum matching the DCM except at a few stations where temperature at the maximum nauplii concentration was $\sim 15^{\circ}\text{C}$. The multiple regression analysis confirmed the combined effort in the search for the optimal food availability (DCM) and the best thermal conditions for development (Chinnery and Williams, 2004; 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). Horizontal distribution of the abundance of nauplii, small copepods and metazooplankton was correlated with the distribution of HNF $> 10\ \mu\text{m}$, total HNF and nanophytoplankton respectively. The affinity of nauplii for small motile prey such as HNF was evidenced experimentally by Henriksen et al. (2007), that of small copepods for phytoplankton and microheterotrophs (Nakamura and Turner, 1997; Zervoudaki et al., 2007) and of metazooplankton for nanophytoplankton performed at different season of the year (Pinca and Dallot, 1995; Gaudy and Youssara, 2003; Alcaraz et al., 2007; Zervoudaki et al., 2007) is also well

known. Finally physical forcing can also affect vertical distribution as shown by Andersen et al. (2001), with nauplii of copepods and euphausiid being influenced by a deepening of the mixed layer and a dilution of the phytoplankton biomass in the water column following a wind event.

4.2 Pattern of zooplankton assemblages in relation with environmental parameters

The zooplankton composition recorded during the BOUM transect was in general agreement with the published data on the Mediterranean Sea community (Siokou-Frangou et al., 1997, 2010; Gaudy et al., 2003; Pasternak et al., 2005; Riandey et al., 2005). The overall metazooplankton community was dominated by copepods and especially by small size species (<1 mm). *Clausocalanus/Paracalanus* spp. and *Oithona* spp. were the dominant genera, as is generally observed (Gaudy et al., 2003; Peralba and Mazzocchi, 2004; Zervoudaki et al., 2007).

We found a clear distinction in taxonomic composition between the western and the eastern basins mainly driven by ecological characteristics. Several copepods species showed a clear eastward pattern. For example, *Macrosetella/Microsetella* spp., *Acartia clausi* and *Centropages typicus* were more abundant in the western basin; while, *Calocalanus pavo*, *Corycaeus/Farranula* spp., *Haloptilus longicornis*, *Lucicutia flavicornis*, *Mecynocera clausi* and *Pareucalanus attenuatus* were present mainly in the eastern basin. The spatial distribution of most species reported here has been confirmed by Siokou-Frangou et al. (2010). Other taxonomic groups presented also a clear spatial pattern. Cladocerans were nearly absent from the eastern basin, which may be also explained by the difference in the sampling dates between the two basins (>2 weeks). Indeed, these organisms are known to display explosive growth over very short time-periods linked to their parthenogenetic reproduction (Christou and Stergiou, 1998; Atienza et al., 2007, 2008). The distance to the coast could also explain local high abundance, such as in the Sicily Channel, of these organisms, known to have a neritic affinity (Fernandez de Puelles et al., 2007). These differences in the percentage contribution of some important species to the whole copepod assemblage might reflect differences in species biogeography, but might also be indicative of different associations between structural and functional features. In the co-inertia analysis (Fig. 9), the eastern basin was characterized by high diatoms concentration associated with higher abundance, compared to other stations, of large-size herbivorous copepods i.e. *Pareucalanus attenuatus* (st. 5 and 7) and *Subeucalanus monachus* (st. 13) both restricted to the eastern basin. High abundance of these copepods also corresponded to hot spots of biogenic silicon dominated by the microphytoplankton *Chaetoceros* spp. in the eastern basin (Crombet et al., 2011). *Subeucalanus monachus* has already been reported in high abundance in the Rhodes cyclonic gyre where nutrients rich

waters have been upwelled leading to high phytoplankton biomass dominated by large diatoms (Siokou-Frangou et al., 1999). One novelty observed during the BOUM cruise is the presence of *Cosmocalanus darwini* reported for the first time in the Mediterranean Sea, both in the western and eastern basins. We found copepodites stages as well as females indicating the reproductive success of this species. However, it is difficult to conclude about its origin in the Mediterranean Sea. This species is common in the Red sea (Razouls et al., 2005–2011; web site) and is expected to undergo lesseptian dispersion but this species was found in lower abundance in the eastern basin than in the western basin.

On the other hand, the western basin was characterized by high nutrient concentrations, high abundance of nanophytoplankton and small and medium (<1.5 mm prosome length) herbivorous/omnivorous copepods (i.e. *Acartia clausi*, *Centropages typicus*, *Euterpina acutifrons*). The association of these small copepods species with nanophytoplankton-rich conditions has already been demonstrated in the Mediterranean (Pinca and Dallot, 1995; Gaudy and Youssara, 2003; Alcaraz et al., 2007; Zervoudaki et al., 2007).

Mesoscale hydrodynamic structures could also play an important role in the variability of zooplankton abundance and community structure. Anticyclonic gyres displayed lower abundance of metazooplankton and less marked vertical distribution than neighbouring stations where higher chlorophyll concentration at the DCM was observed. These gyres showed a metazooplankton community characterized by lower *Clausocalanus/Paracalanus* (herbivorous) and more *Corycaeus/Farranula* spp. (omnivorous) that could reflect changes in food availability (increase in oligotrophy, lower chlorophyll concentration) (Legendre and Rassoulzadegan, 1995).

The position of station A in the co-inertia analysis is peculiar, highlighting the response of the zooplankton community structure to the environmental forcing. Geographically belonging to the western basin, the physical conditions prevailing at station A led to a different zooplankton composition (i.e. less *Clausocalanus/Paracalanus* spp., and more *Corycaeus/Farranula* spp. and *P. gracilis*) than other stations in the APB; therefore station A emerged on the co-inertia analysis half way between its geographical group and the group where station B and C were located. Nevertheless, the gyre located at station C did not display a lower abundance and biomass than surrounding LB stations. Its functioning could be slightly different from the two other gyres resulting in stronger ($0.441 \mu\text{g L}^{-1}$) and deeper (120 m depth) DCM. Moreover, its location close to the Cyprus coast could explain the high abundance of echinoderm larvae through the aggregation effect of the gyre (Pedrotti and Fenaux, 1996). Indeed, these structures are known to affect mesozooplankton community structure and functioning (Youssara and Gaudy, 2001; Beaugrand and Ibañez, 2002; Isla et al., 2004; Riandey et al., 2005; Hafferssas and Seridji, 2010).

In conclusion, we found a clear eastward pattern in term of metazooplankton abundance but not for the biomass which showed a high variability between stations. The causes of this variability were numerous and of different aspect. The horizontal and vertical distribution of the metazooplankton was strongly linked to the chlorophyll-*a* concentration but also to other parameters such as microzooplankton or physical forcing (i.e. stratification, temperature). These environmental parameters influenced also the species distribution and size structure of the community. It is obvious that the type and the size of the available food (nanophytoplankton and/or diatoms) should also influence the presence of smaller or larger species.

Acknowledgements. This is a contribution of the BOUM (Biogeochemistry from the Oligotrophic to the Ultraoligotrophic Mediterranean) experiment (<http://www.com.univ-mrs.fr/BOUM>) of the French national LEFE-CYBER program, the European IP SESAME and the international IMBER project. The BOUM experiment was coordinated by the Institut des Sciences de l'Univers (INSU) and managed by the Centre National de la Recherche Scientifique (CNRS). The authors thank the captain and crew of the N. O. *L'Atalante* for outstanding shipboard operations. We are grateful to M. G. Mazzocchi, M. L. Fernández de Puellas and a third anonymous referee for the time and effort which helped the authors to substantially improve the manuscript. A. N. was supported by a fellowship from the French Ministry of Higher Education and Research. We also thank O. Grosso for CHN analysis.

Edited by: C. Jeanthon



The publication of this article is financed by CNRS-INSU.

References

Alcaraz, M.: Vertical distribution of zooplankton biomass during summer stratification in the Western Mediterranean, edited by: Proceedings of the 19th European Marine Biology Symposium, P., Devon, UK, 16–21 September 1984, 135–143, 1985.

Alcaraz, M.: Summer zooplankton metabolism and its relation to primary production in the Western Mediterranean, edited by: Minas, J. H. and Nival, P., *Océanographie pélagique méditerranéenne*, *Oceanol. Acta SP 9*, 185–191, 1988.

Alcaraz, M., Calbet, A., Estrada, M., Marrasé, C., Saiz, E., and Trepát, I.: Physical control of zooplankton communities in the Catalan Sea, *Prog. Oceanogr.*, **74**, 294–312, 2007.

Andersen, V., François, F., Sardou, J., Picheral, M., Scotto, M., and Nival, P.: Vertical distributions of macroplankton and micronek-

ton in the Ligurian and Tyrrhenian Seas (northwestern Mediterranean), *Oceanol. Acta*, **21**, 655–676, 1998.

Andersen, V., Gubanova, A., Nival, P., and Ruellet, T.: Zooplankton community during the transition from spring bloom to oligotrophy in the open NW Mediterranean and effects of wind events. 2. Vertical distributions and migrations, *J. Plankton Res.*, **23**, 243–261, 2001.

Andersen, V., Devey, C., Gubanova, A., Picheral, M., Melnikov, V., Tsarin, S., and Prieur, L.: Vertical distributions of zooplankton across the Almeria-Oran frontal zone (Mediterranean Sea), *J. Plankton Res.*, **26**, 275–293, 2004.

Atienza, D., Calbet, A., Saiz, E., and Lopes, R. M.: Ecological success of the cladoceran *Penilia avirostris* in the marine environment: feeding performance, gross growth efficiencies and life history, *Mar. Biol.*, **151**, 1385–1396, 2007.

Atienza, D., Saiz, E., Skovgaard, A., Trepát, I., and Calbet, A.: Life history and population dynamics of the marine cladoceran *Penilia avirostris* (Branchiopoda : Cladocera) in the Catalan Sea (NW Mediterranean), *J. Plankton Res.*, **30**, 345–357, 2008.

Beaugrand, G. and Ibañez, F.: Spatial dependence of calanoid copepod diversity in the North Atlantic Ocean, *Mar. Ecol. Prog. Ser.*, **232**, 197–211, 2002.

Bergamasco, A. and Malanotte-Rizzoli, P.: The circulation of the Mediterranean Sea: a historical review of experimental investigations, *Adv. in Oceano. and Limnol.*, **1**, 11–28, 2010.

Bianchi, C. N. and Morri, C.: Marine biodiversity of the Mediterranean Sea: situation, problems and prospects for future research, *Mar. Pol. Bul.*, **40**, 367–376, 2000.

Brugnano, C., Bergamasco, A., Granata, A., Guglielmo, L., and Zagami, G.: Spatial distribution and community structure of copepods in a central Mediterranean key region (Egadi Islands-Sicily Channel), *J. Mar. Sys.*, **81**, 312–322, 2010.

Calbet, A., Garrido, S., Saiz, E., Alcaraz, M., and Duarte, C. M.: Annual zooplankton succession in coastal NW Mediterranean waters: the importance of the smaller size fractions, *J. Plankton Res.*, **23**, 319–331, 2001.

Calbet, A. and Saiz, E.: The ciliate-copepod link in marine ecosystems, *Aquat. Microb. Ecol.*, **38**, 157–167, 2005.

Champalbert, G.: Characteristics of zooplankton standing stock and communities in the Western Mediterranean Sea: relations to hydrology, *Sci. Mar.*, **60**, 97–113, 1996.

Chinnery, F. E. and Williams, J. A.: The influence of temperature and salinity on *Acartia* (Copepoda: Calanoida) nauplii survival, *Mar. Biol.*, **145**, 733–738, 2004.

Christaki, U., Van Wambeke, F., Lefevre, D., Lagaria, A., Prieur, L., Pujo-Pay, M., Grattepanche, J.-D., Colombet, J., Psarra, S., Dolan, J. R., Sime-Ngando, T., Conan, P., Weinbauer, M. G., and Moutin, T.: Microbial food webs and metabolic state across oligotrophic waters of the Mediterranean Sea during summer, *Biogeosciences*, **8**, 1839–1852, doi:10.5194/bg-8-1839-2011, 2011.

Christou, E. D. and Stergiou, K. I.: Modelling and forecasting the fortnightly cladoceran abundance in the Saronikos Gulf (Aegean Sea), *J. Plankton Res.*, **20**, 1313–1320, 1998.

Clarke, K. R. and Warwick, R. M.: Changes in marine communities: an approach to statistical analysis and interpretation, *Nat. Env. Res. Counc.*, UK 144 pp., 1995.

Coll, M., Piroddi, C., Steenbeek, J., Kaschner, K., Ben Rais Lasram, F., Aguzzi, J., Ballesteros, E., Bianchi, C. N., Corbera, J., Dailianis, T., Danovaro, R., Estrada, M., Frogliá, C., Galil, B.

- S., Gasol, J. M., Gertwagen, R., Gil, J., Guilhaumon, F., Kesner-Reyes, K., Kitsos, M. S., Koukouras, A., Lampadariou, N., Laxamana, E., López-Fé de la Cuadra, C. M., Lotze, H. K., Martin, M., Mouillot, D., Oro, D., Raicevich, S., Rius-Barile, J., Saiz-Salinas, J. I., San Vicente, C., Somot, S., Templado, J., Turon, X., Vafidis, D., Villanueva, R., and Voultsiadou, E.: The biodiversity of the Mediterranean Sea: estimates, patterns, and threats, *PLoS ONE*, 5(8), e11842, doi:10.1371/journal.pone.0011842, 2010.
- Crombet, Y., Leblanc, K., Quéguiner, B., Moutin, T., Rimmelin, P., Ras, J., Claustre, H., Leblond, N., Oriol, L., and Pujo-Pay, M.: Deep silicon maxima in the stratified oligotrophic Mediterranean Sea, *Biogeosciences*, 8, 459–475, doi:10.5194/bg-8-459-2011, 2011.
- Cruzado, A. and Velásquez, Z. R.: Nutrients and phytoplankton in the Gulf of Lions, *Cont. Shelf Res.*, 10, 931–942, 1990.
- D'Ortenzio, F. and Ribera d'Alcalà, M.: On the trophic regimes of the Mediterranean Sea: a satellite analysis, *Biogeosciences*, 6, 139–148, doi:10.5194/bg-6-139-2009, 2009.
- Dolan, J. R., Claustre, H., Carlotti, F., Plounevez, S., and Moutin, T.: Microzooplankton diversity: relationships of tintinnid ciliates with resources, competitors and predators from the Atlantic Coast of Morocco to the Eastern Mediterranean, *Deep-Sea Res. Pt. I*, 49, 1217–1232, 2002.
- Dolédec, S. and Chessel, D.: Co-inertia analysis: an alternative method for studying species-environment relationships, *Fresh. Biol.*, 31, 277–294, 1994.
- Fernandez de Puellas, M. L., Valencia, J., Jansa, J., and Morillas, A.: Hydrographical characteristics and zooplankton distribution in the Mallorca channel (Western Mediterranean): spring 2001, *ICES J. Mar. Sci.*, 61, 654–666, 2004.
- Fernandez de Puellas, M. L., Morillas, A., Alou Font, L., and Vicente, L.: The spatial zooplankton distribution in the North Balear front (Western Mediterranean): early spring, 2005, 38th CIESM Cong. Proc., 38, 473 pp., 2007.
- Fernandez de Puellas, M. L., Lopez-Urrutia, A., Morillas, A., and Mollinero, J. C.: Seasonal variability of copepod abundance in the Balearic region (Western Mediterranean) as an indicator of basin scale hydrological changes, *Hydrobiol.*, 167, 3–16, 2009.
- Furnestin, M.-L.: Le zooplancton de la Méditerranée (Bassin Occidental), *Essai de synthèse*, *ICES J. Mar. Sci.*, 32, 25–69, 1968.
- Gaudy, R. and Youssara, F.: Variations of zooplankton metabolism and feeding in the frontal area of the Alboran Sea (western Mediterranean) in winter, *Oceanol. Acta*, 26, 179–189, 2003.
- Gaudy, R., Youssara, F., Diaz, F., and Raimbault, P.: Biomass, metabolism and nutrition of zooplankton in the Gulf of Lions (NW Mediterranean), *Oceanol. Acta*, 26, 357–372, 2003.
- Gorsky, G., Ohman, M. D., Picheral, M., Gasparini, S., Stemmann, L., Romagnan, J. B., Cawood, A., Pesant, S., Garcia-Comas, C., and Prejze, F.: Digital zooplankton image analysis using the ZooScan integrated system, *J. Plankton Res.*, 32, 285–303, 2010.
- Grosjean, P., Picheral, M., Warembourg, C., and Gorsky, G.: Enumeration, measurement, and identification of net zooplankton samples using the ZOOSCAN digital imaging system, *ICES J. Mar. Sci.*, 61, 518–525, 2004.
- Hafferssas, A. and Seridji, R.: Relationships between the hydrodynamics and changes in copepod structure on the Algerian coast, *Zoological Studies*, 49, 353–366, 2010.
- Harvey, H. W.: The chemistry and fertility of sea waters, Cambridge Univ. Press., 224 pp., 1955.
- Henriksen, C. I., Saiz, E., Calbet, A., and Hansen, B. W.: Feeding activity and swimming patterns of *Acartia grani* and *Oithona davisae* nauplii in the presence of motile and non-motile prey, *Mar. Ecol. Prog. Ser.*, 331, 119–129, 2007.
- Herbland, A., Le Bouteiller, A., and Raimbault P.: Size structure of phytoplankton biomass in the equatorial Atlantic Ocean, *Deep-Sea Res. Pt. I*, 32, 819–836, 1985.
- Herman, A. W. and Harvey, M.: Application of normalized biomass size spectra to laser optical plankton counter net intercomparisons of zooplankton distributions, *J. Geophys. Res.*, 111, 1–9, doi:10.1029/2005JC002948, 2006.
- Hopcroft, R. R., Clarke, C., and Chavez, S. P.: Copepod communities in Monterey Bay during the 1997–1999 El Niño and La Niña, *Prog. Oceanogr.*, 54, 251–264, 2002.
- Ibanez, F. and Bouchez, J.: Anisotropie des populations zooplanctoniques dans la zone frontale de Mer Ligure, *Oceanol. Acta*, 10, 205–216, 1987.
- Ignatiades, L.: Scaling the trophic status of the Aegean Sea, eastern Mediterranean, *J. Sea Res.*, 54, 51–57, 2005.
- Isla, J. A., Ceballos, S., Huskin I., Anadón, R., and Alvarez-Marqués, F.: Mesozooplankton distribution, metabolism and grazing in an anticyclonic slope water oceanic eddy (SWODDY) in the Bay of Biscay, *Mar. Biol.*, 145, 1201–1212, 2004.
- Koski, M., Jonasdottir, S. H., and Bagøien, E.: Biological processes in the North Sea: vertical distribution and reproduction of neritic copepods in relation to environmental factors, *J. Plankton Res.*, 33, 63–84, 2011.
- Krom, M. D., Kress, N., Brenner, S., and Gordon, L. I.: Phosphorus limitation of primary productivity in the Eastern Mediterranean Sea, *Limnol. Oceanogr.*, 36, 424–432, 1991.
- Latasa, M., Estrada, M., and Delgado, M.: Plankton-pigment relationships in the Northwestern Mediterranean during stratification, *Mar. Ecol. Prog. Ser.*, 88, 61–73, 1992.
- Legendre, L. and Rassoulzadegan, F.: Plankton and nutrient dynamics in marine waters, *Ophelia*, 41, 153–172, 1995.
- Licandro, P. and Icardi, P.: Basin scale distribution of zooplankton in the Ligurian Sea (north-western Mediterranean) in late autumn, *Hydrobiol.*, 617, 17–40, 2009.
- Margalef, R.: Western Mediterranean, Key environments, Pergamon Press, Oxford, 363 pp., 1985.
- Mazzocchi, M. G., Christou, E., Fragopoulou, N., and Siokou-Frangou, I.: Mesozooplankton distribution from Sicily to Cyprus (Eastern Mediterranean): I. General aspects, *Oceanol. Acta*, 20, 521–535, 1997.
- Mazzocchi, M. G., Nervegna, D., D'Elia, G., Di Capua, I., Aguzzi, L., and Boldrin, A.: Spring mesozooplankton communities in the epipelagic Ionian Sea in relation to the Eastern Mediterranean Transient, *J. Geophys. Res.*, 108, 8114, doi:10.1029/2002JC001640, 2003.
- Meybeck, M., Dürr, H., Roussennac, S., and Ludwig, W.: Regional seas and their interception of riverine fluxes to oceans, *Mar. Chem.*, 106, 301–325, 2007.
- Millot, C. and Taupier-Letage, I.: Circulation in the Mediterranean Sea, *Handbook Environ. Chem.*, 5(K), 29–66, 2005.
- Minutoli, R. and Guglielmo, L.: Zooplankton respiratory Electron Transport System (ETS) activity in the Mediterranean Sea: spatial and diel variability, *Mar. Ecol. Prog. Ser.*, 381, 199–211, 2009.
- Molinero, J. C., Ibanez, F., Souissi, S., Bosc, E., and Nival, P.: Sur-

- face patterns of zooplankton spatial variability detected by high frequency sampling in the NW Mediterranean. Role of density fronts, *J. Mar. Sys.*, 69, 271–282, 2008.
- Moutin, T. and Raimbault, P.: Primary production, carbon export and nutrients availability in western and eastern Mediterranean Sea in early summer 1996 (MINOS cruise), *J. Mar. Sys.*, 33–34, 273–288, 2002.
- Moutin, T., Van Wambeke, F., and Prieur, L.: Introduction to Biogeochemistry from the Oligotrophic to the Ultraoligotrophic Mediterranean (BOUM) experiment, *Biogeosciences Discuss.*, in preparation, 2011.
- Nakamura, Y. and Turner, J. T.: Predation and respiration by the small cyclopoid copepod *Oithona similis*: How important is feeding on ciliates and heterotrophic flagellates?, *J. Plankton Res.*, 19, 1275–1288, 1997.
- Pasternak, A., Wassmann, P., and Wexels Riser, C.: Does mesozooplankton respond to episodic P inputs in the Eastern Mediterranean?, *Deep-Sea Res. Pt. II*, 52, 2975–2989, 2005.
- Pedrotti, M. L. and Fenaux, L.: Distribution of echinoderm larval populations in the geostrophic frontal jet of the eastern Alboran Sea, *Oceanol. Acta*, 19, 385–395, 1996.
- Peralba, A. and Mazzocchi, M. G.: Vertical and seasonal distribution of eight Clausocalanus species (Copepoda: Calanoida) in oligotrophic waters, *ICES J. Mar. Sci.*, 61, 645–653, 2004.
- Pinardi, N. and Masetti, E.: Variability of the large scale general circulation of the Mediterranean Sea from observations and modeling: a review, *Palaeogeogr. Palaeoclimatol. Palaeoecol.*, 158, 153–173, 2000.
- Pinca, S. and Dallot, S.: Meso- and macrozooplankton composition patterns related to hydrodynamic structures in the Ligurian Sea (Trophos-2 experiment, April-June 1986), *Mar. Ecol. Prog. Ser.*, 126, 49–65, 1995.
- Porter, K. G. and Feig, Y. S.: The use of DAPI for identifying and counting aquatic microflora, *Limnol. Oceanogr.*, 25, 943–948, 1980.
- Pujo-Pay, M., Conan, P., Oriol, L., Cornet-Barthaux, V., Falco, C., Ghiglione, J.-F., Goyet, C., Moutin, T., and Prieur, L.: Integrated survey of elemental stoichiometry (C, N, P) from the western to eastern Mediterranean Sea, *Biogeosciences*, 8, 883–899, doi:10.5194/bg-8-883-2011, 2011.
- Raimbault, P., Diaz, F., Pouvesle, W., and Boudjellal, B.: Simultaneous determination of particulate organic carbon, nitrogen and phosphorus collected on filters, using a semi-automatic wet-oxidation method, *Mar. Ecol. Prog. Ser.*, 180, 289–295, 1999.
- Razouls, C., de Bovée, F., Kouwenberg, J., and Desreumaux, N.: Diversity and geographic distribution of marine planktonic copepods, <http://copepodes.obs-banyuls.fr/en>, 2005–2011.
- Riandey, V., Champalbert, G., Carlotti, F., Taupier-Letage, I., and Thibault-Botha, D.: Zooplankton distribution related to the hydrodynamic features in the Algerian Basin (western Mediterranean Sea) in summer 1997, *Deep-Sea Res. Pt. I*, 52, 2029–2048, 2005.
- Rose, M.: Copépodes pélagiques, *Faune de France*, 26, 374 pp., 1933.
- Sabatés, A., Olivar, M. P., Salat, J., Palomera, J., and Alemany, F.: Physical and biological processes controlling the distribution of fish larvae in the NW Mediterranean, *Prog. Oceanogr.*, 74, 355–376, 2007.
- Scotto di Carlo, B., Ianora, A., Fresi, E., and Hure, J.: Vertical zonation patterns for Mediterranean copepods from the surface to 3000 m at a fixed station in the Tyrrhenian Sea, *J. Plankton Res.*, 6, 1031–1056, 1984.
- Sieburth, J. M. N., Smetacek, V., and Lenz, J.: Pelagic ecosystem structure: Heterotrophic compartments of the plankton and their relationship to plankton size fractions, *Limnol. Oceanogr.*, 23, 1256–1263, 1978.
- Siokou-Frangou, I., Christou, E. D., Fragopoulou, N., and Mazzocchi, M. G.: Mesozooplankton distribution from Sicily to Cyprus (Eastern Mediterranean): II. Copepod assemblages, *Oceanol. Acta*, 20, 537–548, 1997.
- Siokou-Frangou, I., Gotsis-Skreta, O., Christou, E., and Pagou, K.: Plankton characteristics in the Aegean, Ionian and NW Levantine seas, in: *The Eastern Mediterranean as a Laboratory Basin for the Assessment of Contrasting Ecosystems*, edited by: Malanotte-Rizzoli, P., and Eremeev, V., 205–223, 1999.
- Siokou-Frangou, I.: Epipelagic mesozooplankton and copepod grazing along an east-west transect in the Mediterranean Sea, *Rap. Com. inter. Explor. Scient. Mer Méd.*, 37, p. 439, 2004.
- Siokou-Frangou, I., Zervoudaki, S., Christou, E., Zervakis, V., and Georgopoulos, D.: Variability of mesozooplankton spatial distribution in the North Aegean Sea, as influenced by the Black Sea waters outflow, *J. Mar. Sys.*, 78, 557–575, 2009.
- Siokou-Frangou, I., Christaki, U., Mazzocchi, M. G., Montresor, M., Ribera d'Alcalá, M., Vaqué, D., and Zingone, A.: Plankton in the open Mediterranean Sea: a review, *Biogeosciences*, 7, 1543–1586, doi:10.5194/bg-7-1543-2010, 2010.
- Sourisseau, M. and Carlotti, F.: Spatial distribution of zooplankton size spectra on the French continental shelf of the Bay of Biscay during spring 2000 and 2001, *J. Geophys. Res.*, 111, C05S09, doi:10.1029/2005JC003063, 2006.
- Thibault, D., Gaudy, R., and Le Fèvre, J.: Zooplankton biomass, feeding and metabolism in a geostrophic frontal area (Almeria-Oran Front, western Mediterranean), Significance to pelagic food webs, *J. Marine Syst.*, 5, 297–311, 1994.
- Thioulouse, J., Chessel, D., Dolédec, S., and Olivier, J. M.: ADE-4: a multivariate analysis and graphical display software, *Stat. Comp.*, 7, 75–83, 1997.
- Trégouboff, G. and Rose, M.: *Manuel de planctologie méditerranéenne*, Centre National de la Recherche Scientifique, 587 pp., 1957.
- Turner, J. T.: The importance of small copepods and their roles in pelagic marine food webs, *Zoological Studies*, 43, 255–266, 2004.
- Webber, M. K. and Roff, J. C.: Annual biomass and production of the oceanic copepod community off Discovery Bay, Jamaica, *Mar. Biol.* 123, 481–495, 1995.
- Weikert, H. and Trinkaus, S.: Vertical mesozooplankton abundance and distribution in the deep Eastern Mediterranean Sea SE of Crete, *J. Plankton Res.*, 12, 601–628, 1990.
- Wurtz, M.: *Mediterranean pelagic habitat: Oceanographic and biological processes*, an overview, Gland, Switzerland and Malaga, Spain: IUCN., 90 pp., 2010.
- Youssara, F. and Gaudy, R.: Variations of zooplankton in the frontal area of the Alboran sea (Mediterranean sea) in winter 1997, *Oceanol. Acta*, 24, 361–376, 2001.
- Yurista, P., Kelly, J. R., and Miller, S.: Evaluation of optically acquired zooplankton size-spectrum data as a potential tool for assessment of condition in Great Lakes, *Env. Manag.*, 35, 34–44,

- 2005.
- Zervoudaki, S., Nielsen, T. G., Christou, E., and Siokou-Frangou: Zooplankton distribution and diversity in a frontal area of the Aegean Sea, *Mar. Biol. Res.*, 2, 149–168, 2006.
- Zervoudaki, S., Christou, E. D., Nielsen, T. G., Siokou-Frangou, I., Assimakopoulou, G., Giannakourou, A., Maar, M., Pagou, K., Krasakopoulou, E., Christaki, U., and Moraitou-Apostolopoulou, M.: The importance of small-sized copepods in a frontal area of the Aegean Sea, *J. Plankton Res.*, 29, 317–338, 2007.