



# Vertical distribution and diel migration of zooplankton and micronekton in Polcevera submarine canyon of the Ligurian mesopelagic zone (NW Mediterranean Sea)



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## ABSTRACT

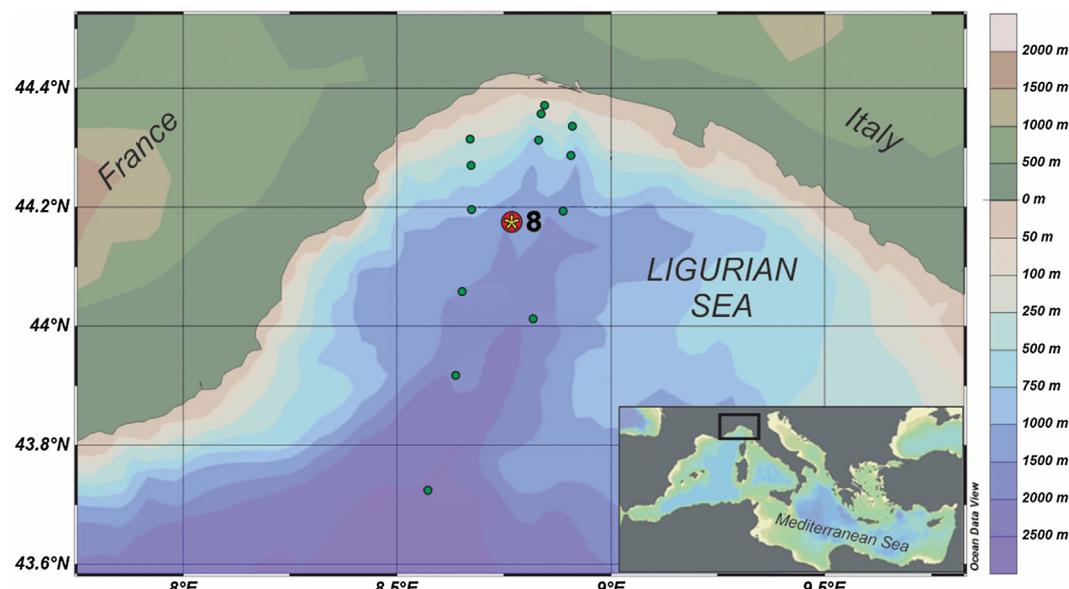
Changes in the composition and biomass distribution of deep-living zooplankton over wide gradients of depth (0–1300 m) have been analyzed in the Central Ligurian Basin (Northwestern Mediterranean Sea), seeking the environmental variables responsible for these changes. Spring vertical distribution (early May 2013) and diel vertical migration (DVM) of some key species of macroplankton and micronekton communities were studied every 6 h during a 24 h cycle. The hauls, performed with the multiple opening/closing 230 µm BIONESS net system, made possible a detailed description of the vertical distribution of twenty-three species: one siphonophore, one pyrosomid, one salp, three pteropods, four amphipods, one mysid, eight euphausiids, two decapods, two fishes. Cluster analysis performed on major species of macroplankton and micronekton community assemblage mainly highlighted the presence of four well defined assemblages, based on the depth range in the water column: 0–60 m, 60–100 m, 100–600 m and from 600 to 1300 m. During daytime, vertical distributions of biomass exhibited similar profiles, with maxima in the 0–60 m layer. Highest abundances were recorded between 20–40 and 40–60 m depth, at midnight and in the morning. The highest values of both biodiversity and number of species were found in a deeper layer comprised between 400 and 600 m. Most of the species showed similar distributions throughout the sampled area, either with typical non-diel-migrating characters such as the euphausiid *Stylocheiron longicorne* and the fishes *Cyclothona braueri* and *C. pygmaea*, or with clear diel-migrant behaviour (e.g. the siphonophore *Chelophyses appendiculata* and the euphausiid *Euphausia krohnii*). Some species (e.g. *Vibilia armata*, *Phronima sedentaria*, *Scina crassicornis*, *Salpa fusiformis*, *Cavolinia inflexa*, *Gennadas elegans*) exhibited a bimodal vertical distribution that could be attributed to different causes able to influence and modify their vertical migration. The lower values of chlorophyll concentrations found in the present study in the month of May corresponds to the transition period from a mesotrophic system to a rather oligotrophic one. Temperature and chlorophyll were the variables that principally influenced the distinction between shallow (0–60 m) and deep communities. Below 60 m depth, the dissolved oxygen and salinity become the most important variables affecting the zooplankton community.

## 1. Introduction

Marine organisms are linked to each other by complex trophic webs. Zooplankton is a key contributor to the ocean biological pump, and is

expected to play a crucial role in channeling phytoplankton production through grazing and transferring of organic matter through diel vertical migration (DVM, Longhurst, 1976, 1985). In the mesopelagic realm, non-migratory animals remain in deep water layers, and use the energy

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**Fig. 1.** Study area where zooplankton was sampled during the BioLig cruise in the Ligurian Sea (May 2013) (black dots). Location of the time-series station 8 (\*) for the BIONESS survey in this study.

transported from the epipelagic zone via physical or biological conveyor system (Gorsky et al., 1991, 2002; Stemmann et al., 2008; Peña et al., 2014). In daytime, several zooplankton and micronekton groups forming the Deep Scattering Layers (DSL) are located at a depth of 400–600 m (Sameoto, 1982; Olivar et al., 2012; Cartes et al., 2013), but during nighttime they split into a component that rises towards the surface and another that remains stationary. Euphausiids, pelagic shrimps and midwater fishes, in addition to siphonophores, are the main component of the DSL (Olivar et al., 2013; Battaglia et al., 2016). They are distributed worldwide (Reid et al., 1991; Nishikawa et al., 2001) and for this reason may support key biological processes in meso- and bathypelagic trophic webs (Cartes et al., 2008).

Within the micronekton, mesopelagic fish dominate the mesopelagic zone of all oceanic regions (Kloser et al., 2009; Young et al., 2015), moreover they are important components in several oceanic ecosystem models since they feed on zooplankton (Christensen et al., 2009). The typical pattern of the DVM of zooplankton consists of an ascent during dusk and descent during dawn with shallow residence at night and deep residence in daytime (Marshall, 1960; Andersen and Sardou, 1992; Timonin, 1997; Taki, 2008). Predator avoidance, food availability and metabolic capacity modify patterns of DVM in many zooplankton taxa (Buchholz et al., 1995). Bottom topography and geomorphology, and oceanographic features are important constraints for zooplankton distribution and aggregation. Often, some species aggregate near the water-bottom interface (so-called “near bottom-zooplankton”) (Cartes et al., 2010; Guglielmo et al., 2011) and close to thermohaline fronts (Lopez Garcia et al., 1994). The Mediterranean Sea has been considered oligotrophic since Jespersen (1923). However, several studies have shown occasional high primary production in limited areas (Margalef, 1985; Estrada, 1996). The Ligurian Sea is one of the productive upwelling systems of the western Mediterranean Sea and hosts several marine mammal species (Forcada et al., 1996; Panigada et al., 1999). Euphausiids and copepods dominate the mesozooplankton communities in this region and are an important trophic link between primary producers and higher trophic levels (Andersen et al., 2001a, b, 2004). The main pelagic crustacean in this region is primarily the northern krill *Meganyctiphanes norvegica* (Wiebe and D'Abromo, 1972; Andersen et al., 1998) that, together with squids and small fishes, are important elements in the diets of top predators including fin whales (Panigada et al., 1999).

Micronekton is a key faunal group, forming multiple trophic

linkages between meso/macro zooplankton and top predators in all oceans. Previous studies on the micronekton and macroplankton ecology of the western Mediterranean Sea have largely concerned specific taxonomic groups such as euphausiids (Casanova, 1970, 1974), pelagic crustacean decapods (Casanova, 1977), pteropods (Rampal, 1967, 1975), or the hydromedusa *Solmissus albescens* (Benovic', 1973). At the same time and for the following years standing stock and specific composition, seasonal abundance, vertical distribution/migration, and feeding habits of particular animal taxa of mesopelagic zooplankton and micronekton communities have been the focus of a number of studies in the western Mediterranean (see Andersen et al., 1998, 2001a, b, 2004; Kovalev et al., 2003 and references therein). More recently, several studies on mesopelagic realm functioning have been carried out, focusing on both short-term and seasonal time frames (see Cartes et al., 2013; Bozzano et al., 2014; Clavel-Henry, 2015; Olivar et al., 2017 and references therein). However, in comparison to neritic zooplankton (see Licandro and Ianez, 2000; Fernandez de Puelles et al., 2007; Molinero et al., 2008 and references therein), the biology and ecology of deep micronekton community, including trophic pathway, distribution patterns, and even biomass, have not been intensively studied. With regard to our study area of the Ligurian Sea, a strong contribution to the knowledge of the diversity, vertical distribution and daily migration of the main key species forming the trophic structure of the mesopelagic environment was given by Valerie Andersen and her research group (Andersen and Sardou, 1992; Andersen et al., 1992; Sardou and Andersen, 1993; Andersen and Sardou, 1994, Sardou et al., 1996; Andersen et al., 1998, 2001a,b, 2004; Andersen and Prieur, 2000).

The objectives of this study were to determine changes in the vertical diel distribution and migration patterns (DVM) of the major mesozooplankton groups (excluding copepods), macroplankton and micronekton in the upper 1300 m of the water column, in a selected station of the northern Ligurian Sea open waters. Abundance, biomass and community structure were also investigated, and the relative importance of some actively vertically migrating dominant species of crustaceans, gelatinous taxa and mesopelagic fishes was assessed. In addition, structure of water column to estimate the influence of temperature, salinity, oxygen and fluorescence on the vertical distribution of different species was examined.

**Table 1**

Tows, sampling strata and astronomic data for a daily cycle (LT, Local Time) at a fixed station 8 done with a BIONESS multinet (230 µm) in the Ligurian Sea open waters (Polcevera canyon) during the BioLig Cruise in May 2013.

Tows	Date	Bottom depth (m)	Starting position			Ending position			Daily cycle	
			Lat N	Long E	LT (+ 2)	Lat N	Long E	LT (+ 2)		
8C	04/05/2013	1400	44.18028°	8.77138°	09:47	44.11024°	8.74810°	11:19	01:32	Morning
8 D	04/05/2013	1500	44.17562°	8.76916°	16:47	44.10414°	8.74304°	18:22	01:35	Afternoon
8 A	03/05/2013	1639	44.17928°	8.76746°	22:03	44.11464°	8.75436°	23:31	01:28	Night
8B	04/05/2013	1457	44.17674°	8.77158°	04:12	44.10838°	8.74498°	05:44	01:32	Before Sunrise

Sampled layers: 1300–1000; 1000–800; 800–600; 600–400; 400–200; 200–100; 100–80; 80–60; 60–40; 40–20; 20–0.

## 2. Material and method

### 2.1. Study area

The region of interest of the Biolig Cruise is the Ligurian Sea. In particular the St. 8 sampled with BIONESS (Fig. 1) is located just downstream from the confluence of the two main currents both flowing northward along each side of northern Corsica: the Tyrrhenian Current, which intrudes into the basin through the Corsica Channel, and the West Corsica Current (WCC). Both veins feed a well-defined cyclonic circulation moving westward along the upper part of the continental slope of the Ligurian-Provençal region up to the Catalan Sea (Astraldi et al., 1990; Astraldi and Gasparini, 1992). This dominant large scale hydrodynamical year-round feature involves both the Modified Atlantic Water (MAW) in the uppermost layer and the Levantine Intermediate Water (LIW) below it (Astraldi et al., 1994; Millot, 1999). With the progressing of the spring season, the Tyrrhenian outflow reduces its strength and is nearly absent in summer, when the Ligurian-Provençal Current is almost exclusively composed of waters coming from the WCC (Astraldi et al., 1994). In May, the intermediate situation in the region of confluence is still characterized by the dominant presence of Tyrrhenian waters exiting from the Corsica Channel with a mesoscale eddy structure resulting in a less organized downstream current over the Ligurian shelf (Astraldi et al., 1994).

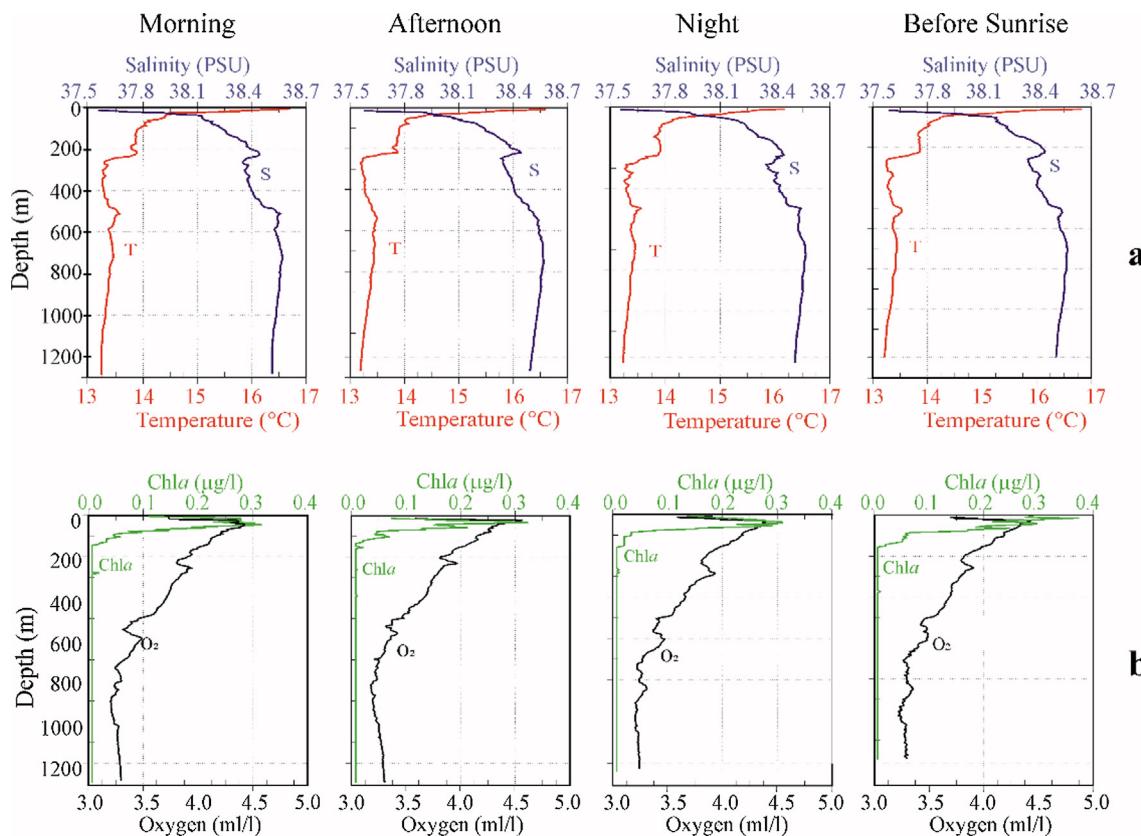
### 2.2. Sampling procedure

Zooplankton samples were collected during the BioLig - Biodiversity, ecosystem functioning and pelagic-benthic coupling in Ligurian submarine canyons-oceanographic cruise carried out in the open Ligurian Sea (northwestern Mediterranean) from April 30th to May 07, 2103 on board the Italian R/V Minerva Uno. All biological samples were taken by the BIONESS (Sameoto et al., 1980), a multinet of 1 m<sup>2</sup> mouth area equipped with 12 horizontally arranged nets (230 µm mesh size) that opened sequentially. The BIONESS system was equipped with a multiparametric probe (SBE 911plus, Seabird Electronics) and a fluorescence sensor (Seapoint Chlorophyll Fluorometer, Seapoint Sensors) mounted on its frame, which simultaneously to the biological samples recorded temperature, salinity, oxygen, and fluorescence (directly transformed into Chla equivalent). Rough data of depth (m), temperature (°C), salinity (PSU), and fluorescence (as Chla) were processed with the ODV software to obtain vertical profiles in real time. Flow velocity and filtration efficiency were monitored by internal and external flowmeters (GO2031H). The BIONESS was deployed at low

speed along an oblique path to the maximum desired depth and towed at a speed from 1 to 3 ms<sup>-1</sup>. In this study, BIONESS sampling over a 24-hour cycle was performed at the selected station BIOL8 (44°0.103180'N, 08°0.460720'E) in the Polcevera canyon, in the Ligurian Sea open waters (Fig. 1). Zooplankton and micronekton were repeatedly sampled approximately every six hours, in order to study their daily vertical migration (DVM). A total of 44 samples was collected in May 3–4, 2013 in several strata between the surface and 100–350 m from the seabed, along a 0–1300 m water column transect. The volume of water filtered in each layer varied between 43 and 372 m<sup>-3</sup>, according to the thickness of the sampled layer. In the uppermost 100 m depth, the sampled layers were 20 m of thickness, and between 100 and 1300 m the layer thickness increased to 100 and 200 m. During each tow, a total of 11 depth intervals was sampled. During the first downcast, the physical structure of the water column, the thermocline, oxycline and halocline depths, and the depth and thickness of the Deep Chlorophyll Maximum (DCM) layer were analysed in order to decide upon the sampling layers. Overall, the following vertical scheme was applied: 0–20, 20–40, 40–60, 60–80, 80–100, 100–200, 200–400, 400–600, 600–800, 800–1000, 1000–1300 m. To help compensate for the lack of replicate tows and to increase the precision of the samples, the duration of each tow was about 1.5 h, ranging in length about 2500–3500 m, according to the rationale discussed by Wiebe (1972). The sampling data are summarized in Table 1. On board, the samples were preserved in a 5% buffered formaldehyde and sea water solution. It was cloudy during the 24 h cycle and the moon was in its new phase (<http://stardate.org/nightsky/moon>). Sunrise and sunset times were 06:12 and 20:32 (GMT + 2:00), respectively. Samplings started at 09:47 h (GMT + 2:00, Morning, MO), at 16:47 h (GMT + 2:00, Afternoon, AF), at 22:03 h (GMT + 2:00, Night, NI) and 04:12 h (GMT + 2:00, Before Sunrise, BS).

### 2.3. Zooplankton and micronekton abundance and biomass

In the laboratory, mesozooplankton (excluding copepods that constitute a separate paper in this volume) and micronekton taxonomic identification and abundance and biomass quantification were performed. From each of the stratified oblique samples, the large animals between 1 and 10 cm were removed, identified into higher taxonomic groups and total numbers were determined. In this study, adult and juveniles euphausiids, pyrosomids, mesopelagic fish, cephalopods, and some deeper hydromedusae, siphonophores, amphipods, pteropods, mysids and pelagic decapods, were identified at species level, according



**Fig. 2.** Day-night vertical distribution of (a) temperature ( $^{\circ}$ C) and salinity (PSU) (b) chlorophyll a ( $\mu$ g/L) and oxygen ( $\mu$ g/L) based on Sea-bird 11 plus BIONESS profiles.

to: (a) euphausiids: Casanova (1974), Mauchline and Fisher (1969), Brinton et al. (2000) (b) pteropods: Rampal (1975) (c) amphipods: Chevreux and Fage (1925), Vinogradov et al. (1996) (d) pelagic decapods: Bouvier (1922), Hansen (1922).

Depending on the total sample abundance, the remaining portion of the sample with animals of the mesozooplankton was split a number of time with a Motoda sample splitter (Motoda, 1959) and if necessary with a Stempel pipette. One of the fractions, of 200–400 animals, was classified and counted at lower taxonomic levels. In many samples taken in the deeper layers the count of individuals was carried out on the whole volume. In this paper, we present abundance estimates of the organisms standardized to number of individuals per  $m^2$  for the entire sampled water column (0–1300 m) and 0–60 m, 60–200 m, 200–600 m, 600–1300 m integrated strata and as ind. per 1000  $m^3$  for each sampled layer. Samples were split by a Folsom splitter, so that 500 mL sub-samples of each sampled layer were analyzed, in order to measure the total biomass as Wet Mass (WM) and Dry Mass (DM). Before the biomass analysis, all large specimens were excluded, sorted, measured (TL mm) and weighed (WM). Samples were filtered on 200  $\mu$ m gauze and rinsed with distilled water. Then, the entire sample was wet weighed and the same sample was dried at 60° C for 24 h. according to Lovegrove's method (1966). In this paper, we present biomass estimates of the organisms standardized to mg WM per  $m^3$  and mg DM per  $m^3$  at each layer for vertical distribution patterns and as mg WM per  $m^2$  and mg DM per  $m^2$  of the entire sampled water column (0–1300 m), and 0–60 m, 60–200 m, 200–600 m, 600–1300 m integrated strata, for standing stock measurements.

#### 2.4. Identification of diel patterns

To assess the vertical partitioning of the species by daytime and nighttime abundances (DVM), the weighted mean depth (WMD) of each

adult and juveniles was calculated according to the equation:  $WMD = \Sigma(ni \times zi \times di) / \Sigma(ni \times zi)$ , where  $ni$  is the number of individuals per 1000  $m^3$  in the  $i$  layer,  $di$  is the depth of a sample  $i$  (centre of the depth interval, e.g., 30 m for a 20–40 m depth layer), and  $zi$  the thickness of the layer (Barange, 1990; Andersen and Sardou, 1992). To evaluate the migration range amplitude (dz) between day and night WMDs, differences resulting from MO (09:47–11:19) and NI (22:03–23:31) samples were calculated.

#### 2.5. Multivariate analysis and correlation with environmental parameters

Differences in species composition among the different layer depths and time were investigated through cluster analysis on Bray-Curtis similarity matrix. Prior to this analysis the abundance data were transformed using square root. As the cluster analysis showed an evident vertical stratification, the permutation multivariate analysis of variance (PERMANOVA) was used to evaluate if the community assemblages of each cluster differed significantly, and if these significant differences were maintained even in the four sampling periods. A crossed sampling design was used, with two factors: “time”, fixed with four levels (“before sunrise”, “morning”, “afternoon” and “night”), and the factor “depth layer”, fixed and orthogonal to “time”, with four deep layer levels (“0–60”, “60–100”, “100–600” and “600–1300”). Diversity indices and similarity percentage analysis (SIMPER) were produced in order to describe in detail the zooplankton community in the study area, and which species most contributed to similarity inside each cluster group in the four different time. Moreover, distance-based Redundancy Analysis (dbRDA) was used to describe the correlation between zooplankton species and environmental variables (temperature, salinity, dissolved oxygen and chlorophyll a). All analysis were performed using Plymouth Routines in Multivariate Ecological Research (PRIMER) software (Clarke and Warwick 1995) in

conjunction with the Windows PERMANOVA + module (Anderson et al., 2008).

### 3. Results

#### 3.1. Environmental variables

The temperature and salinity profiles of the sampled water column are shown in Fig. 2a. Values recorded by the BIONESS revealed a marked vertical thermohaline structure, highlighting the different water masses along the profile. The warmer and less salty water masses from the surface until the pycnocline (about 5–20 m depth), featured typical values of the spring Tyrrhenian MAW ( $T \approx 16.09 - S \approx 37.63$ , Vignudelli et al., 2000). Beneath it, an intermediate layer extending to approximately 250 m exhibits colder waters ( $T \approx 13.8-14^{\circ}\text{C}$ ) characterized by an increasing salinity (from 38.1 to 38.45) that reflect the ongoing mixing processes with the resident winter MAW in the Ligurian Sea. Below, the layer 250–500 m is occupied by the Levantine Intermediate Water (LIW) coming from the Tyrrhenian (through the sill of the Corsica Channel, depth 450 m). This LIW is more mixed and characterized by a T in the range 13.2–13.4 °C (LIW coming from WCC is colder,  $T \approx 12.8^{\circ}\text{C}$ ). The layer from 500 m to the maximum sampled depth is occupied by the Deep Mediterranean Water (DMW) ( $T \approx 13.25-13.30^{\circ}\text{C}$ ; salinity  $\approx 38.40-38.45$ ). Diurnal change in temperature were observed in the upper 20 m layer, with a maximum value at the NI (Table S1). Thermocline and halocline layers seemed to be slightly thick during daytime with respect to nighttime. No significant differences were observed among time samplings showing the same vertical water structure, and a very stable pycnocline. Oxygen and fluorescence BIONESS profiles were shown in Fig. 2b. During this period, the fluorescence values were lower (0.01–0.38 mg m<sup>-3</sup> Chla). No significant differences in the amplitude of the chlorophylla layer during the day and night samplings were shown: 5–80 m during daytime (average MO-AF: 0.09–0.04 mg m<sup>-3</sup>), 5–90 m in the NI (0.20–0.06 mg m<sup>-3</sup>) and slightly deeper in the BS (5–100 m; 0.18–0.01 mg m<sup>-3</sup>) (Table S1). During early May, a main Deep Chlorophyll Maximum (DCM1) was recorded within the thermocline and below the pycnocline (20–30 m) reaching average values of 0.36 mg m<sup>-3</sup>. Another peak value (DCM2) at about 50 m (0.31 mg m<sup>-3</sup>) was found in the MO. From 150 m depth, the Chla concentration (of about 0.01 mg m<sup>-3</sup>) was uniformly mixed throughout the entire water column. In the nighttime the amplitude of the oxycline is deeper than in daytime.

#### 3.2. Biomass and abundance

Day and nighttime vertical distribution of both total zooplankton biomass (expressed as Wet Mass and Dry Mass) and total abundance are shown in Fig. 3. Biomass values were higher at NI than during the MO, showing a daily integrated means for the entire sampled water column of 82,628 and 61820 mg WM m<sup>-2</sup>, and 11,092 and 8674 mg DM m<sup>-2</sup>, respectively (Table S2). In the upper 200 m layer, the average integrated biomass was  $24603 \pm 11364$  WM m<sup>-2</sup> and  $3386 \pm 1562$  DM m<sup>-2</sup>, with almost double NI values compared to the MO. During daytime similar biomass profiles were detected (Fig. 3 and Table S2), with the greatest values in the 0–60 m sampled layers and slightly higher in the MO rather than in the AF (20–0 m: average MO-AF 228.2 mg WM m<sup>-3</sup> and 43.7 mg DM m<sup>-3</sup>; 40–20 m: average 151.0 mg WM m<sup>-3</sup> and 22.9 mg DM m<sup>-3</sup>; 60–40 m: 104.2 mg WM m<sup>-3</sup> and 9.9 DM mg m<sup>-3</sup>). At NI the biomass profile shows a marked increase in the values in the layer between the surface and 100 m depth, with the maximum recorded at 0–20 m and a decreasing but rather high trend. In the BS the value at 0–20 m was still quite high, while between 40 and 200 m very similar values were found. The integrated biomasses recorded during MO and AF showed almost similar values both in the 0–60 m and 200–600 m layers. A peak value at 0–60 m in the NI was

observed, while at BS time the biomass was uniformly distributed in the 20–200 m layer (Table S2).

The highest concentration of individuals was always found in the 0–60 m layer (Table S2), with a weighted average almost similar among the four daily hauls. The highest values of abundance were recorded between 0 and 20 m depth, with higher peaks at dark hours. The average number of individuals in the entire water column varies from a minimum of 589,002 ind.m<sup>-2</sup> (BS) to a maximum of 1,009,152 ind.m<sup>-2</sup> in the MO. During daytime, the vertical distribution of the total zooplankton (Fig. 3) is quite similar, even if an increase in abundance is noticed already in the AF starting from 200 m depth.

#### 3.3. Major zooplankton groups

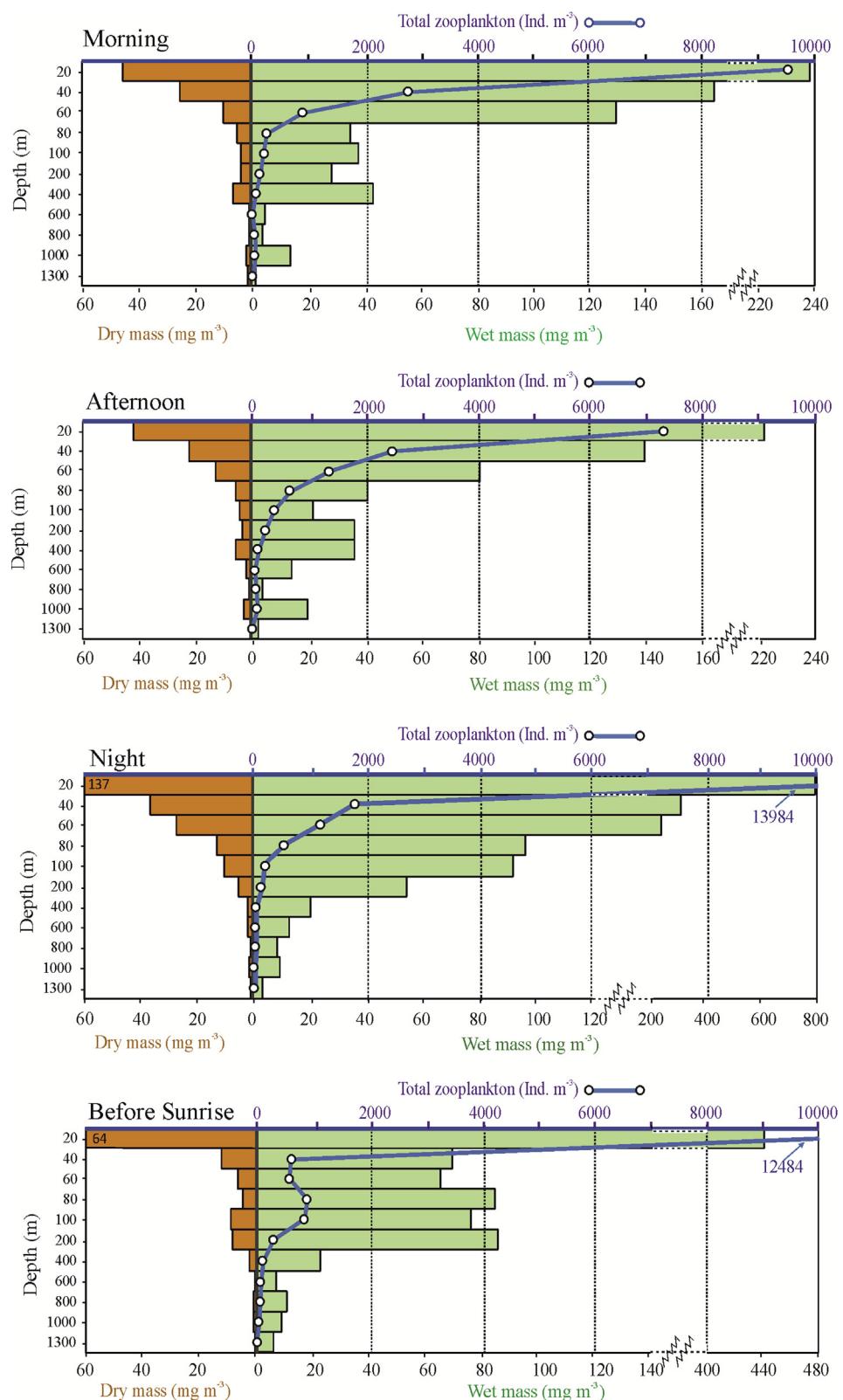
Over 23 taxa were identified from the BIONESS tows during this study. Temporal variations of abundance at MO and NI times and weighted mean depth (WMD) of major taxa were shown in Table S3. Copepods represented the dominant group of total mesozooplankton abundance, both by day and by night (97.4% and 98.5%, respectively), followed by euphausiid larval stages furcilia (1.1% and 0.6%), chaetognaths (0.2% and 0.1%), ostracods (around 0.1% in both day and night), and hydromedusae (less than 0.1% in both day and night). Other non-copepod holoplanktonic groups showed higher abundances during the day (calyptopis, pteropods, siphonophores). In contrast, only adult euphausiids displayed higher individual numbers at night (3202 ind. m<sup>-2</sup>). Salps and several other taxa were less than 0.2% of the total zooplankton abundance.

The vertical distribution of pelagic polychaetes group can be seen in Figure S1. In the MO the community was concentrated in the lower mesopelagic zone between 100 and 600 m, showing an abundance peak in the 100–200 m layer depth and a second poorer concentration of individuals at greater depth. A very strong diel migration at nighttime was evident, with highest concentration found in the epipelagic layer (20–40 m) in the NI time). Maximum abundance values were detected within the NI thermocline (5–15 m) and just above the main DCM (32 m, see Table S1). Day-night WMDs (346 m and 41 m, respectively) demonstrates that this group can be considered a very strong migrant. WMD values gave a mean migration amplitude of 305 m (Table S3).

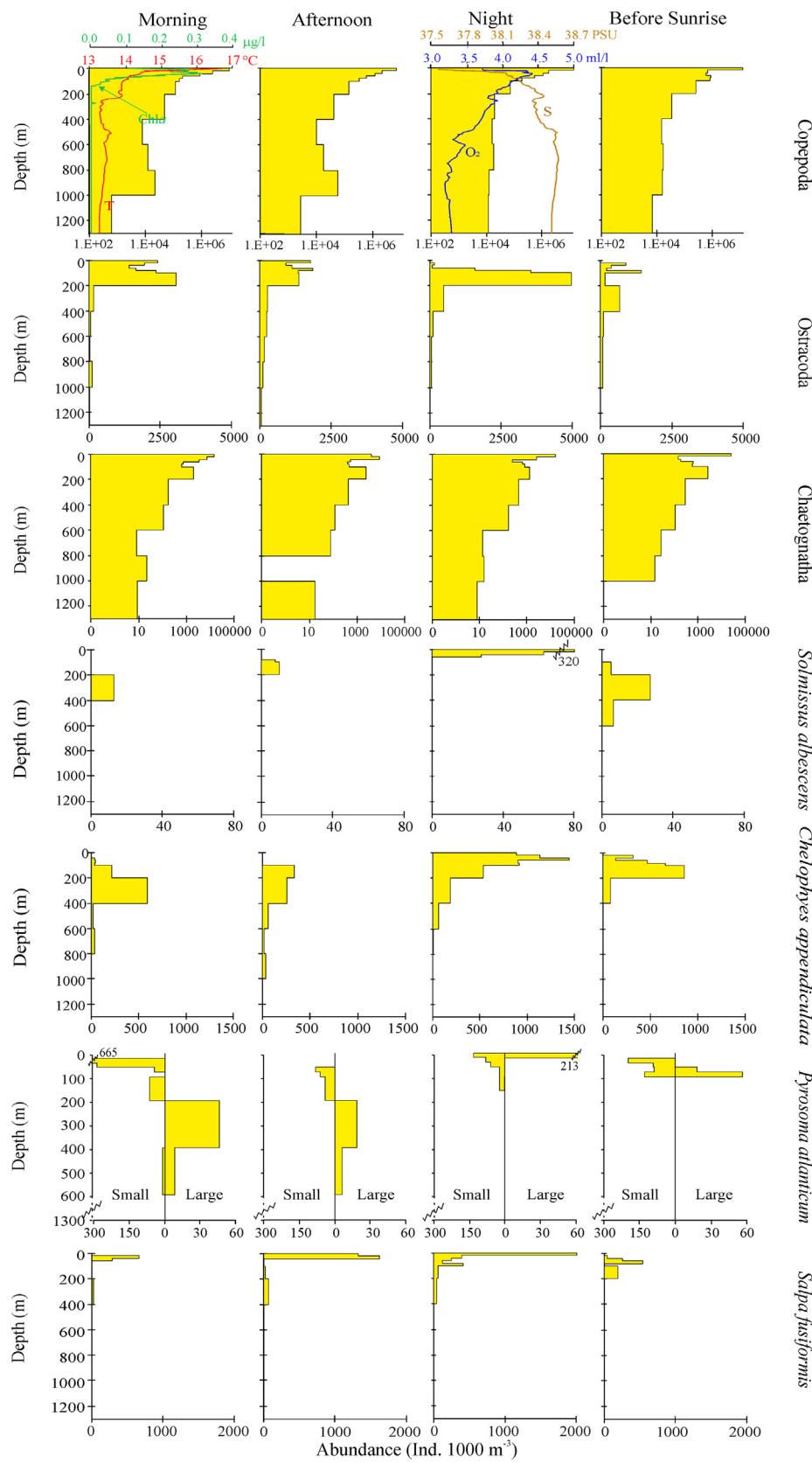
Copepods represent the major group in terms of abundance in the entire sampled water column, at day and nighttime. Daily vertical distribution of the entire copepod community shows a similar day-night trend (Fig. 4; Table S3). The highest concentrations of individuals were always detected in the top 100 m with an average day-night value of 2588 ind.m<sup>-3</sup> with a peak of MO abundance in the 0–20 m layer. Vertical night migration resulted in an increase of about 30% in copepod abundance in the top 20 m. Very similar day-night WMDs (54 and 51 m, respectively) show that very few species of copepods perform extensive vertical migrations, while most of them do not migrate or are weakly migratory. More details on the specific composition and on the vertical distribution and daily migration of this group of crustaceans are available in the paper of Zagami et al. (in this volume).

Ostracods always occupied the entire water column between the surface layer and 1000 m depth (Fig. 4). Highest day and night concentration of individuals were recorded between 100 and 200 m, although most of the young specimens were concentrated in the top 100 m layer (Table S3). Another part of the deeper community remains confined between 400 and 1000 m maintaining low abundance values during the daily cycle.

Chaetognaths community occupied the entire water column between the surface layer and the maximum sampled depth (Fig. 4). A similar vertical pattern distribution at day and nighttime was found, with highest abundance values always found on the surface layer, with a gradual decrease in the number of individuals with depth was detected. The standing crop values during the MO were almost double (2245 ind. m<sup>-2</sup>) of those recorded during the NI (Table S3). In the upper 100 m, chaetognaths concentrated in the top 20 m with average



**Fig. 3.** Day-night vertical distribution of total biomass ( $\text{mg WM per m}^{-3}$  and  $\text{mg DM per m}^{-3}$ ) and zooplankton abundance ( $\text{Ind m}^{-3}$ ) sampled by BIONESS hauls in the Ligurian Sea. For the biomass measurements all individuals of the pyrosomid *Pyrosoma atlanticum*, mysid *Eucopia unguiculata*, pelagic decapods *Gennadas elegans* and *Sergestes arcticus*, cephalopods *Heterotheuthis dispar* and *Rossia macrosoma* and mesopelagic fish *Cyclothona braueri*, *C. pygmaea*, *Lobianchia dofleinii*, *Electrona rissoii* and *Lampanyctus crocioides* species were excluded.



**Fig. 4.** Temporal abundance distribution per sampling layer of three major zooplankton groups (copepoda, ostracoda, chaetognatha, ind 1000 m<sup>-3</sup>) and *S. albescens*, *C. appendiculata*, *P. atlanticum* and *S. fusiformis* species (ind 1000 m<sup>-3</sup>) sampled by BIONESS multinet during the BioLig cruise 2013 in the Ligurian Sea.

values almost similar between day and nighttime.

Appendicularians represent a more constant component in open-water zooplankton. They accounted for about 0.04% of the total spring zooplankton abundance, reaching mean values of abundance in the entire sampled water column of 384 ind. m<sup>-2</sup> and 232 ind. m<sup>-2</sup> at MO and NI, respectively (Table S3). The whole community occupies the 0–200 m layer, with the greatest individuals abundance between 40 and 60 m (Fig. S1). A very weakly upwards vertical migration was detected during day-nighttime (WMDs 62 m and 51 m; dz = 11 m).

By day, decapod larvae standing crop values were more higher than by night ones. They were distributed in the top 80 m, with higher densities between 0 and 20 m depth (Fig. S1). During nighttime, the community shows a deeper distribution than the light period, with an upper part of the community concentrated in the water column between 80 and 100 m. A much larger WMD value observed at NI than in the MO (224 m and 34 m, respectively) highlights a possible downward migration with an amplitude of 189 m (Table S3).

The rare individuals of meso- and bathypelagic fish larvae were collected only in the nighttime, which suggests that they were captured during nocturnal migration, being the habitat of this species deeper than the limit of our catches by the BIONESS. No marked differences between day and night standing crops of fish larvae were found (Table S3). By day, the larvae showed a preference for a very narrow depth range concentrating in the top 20 m in the AF (Fig. S1). At the nighttime, the larvae were distributed slightly deeper (between 40 m and 60 m) where DCM concentration values were more deeper (30–70 m) compared to the daytime. Very few individuals of mesopelagic fish larvae occupied the 400–600 m layer.

#### 3.4. Major taxa of macroplankton and micronekton

In the present study, vertical distribution for the following four groups was described: hydromedusae (1 species), siphonophores (1 species), pyrosomids (1 species) and salps (1 species). Most of the whole hydromedusae community (9.4% of the Total Macroplankton plus Micronekton Communities, TMMC) showed little or no evidence of nighttime vertical migration (Figure S1; Table S3). During the day the community occupies the layer between the surface and 400 m, but most of the individuals are concentrated between 40 and 60 m, below the thermocline and within the DCM. Vertical distribution and day-night migration were described for the deep-water hydromedusa *Solmissus albescens* (Fig. 4; Table 2). In the MO it was mainly found between 200 and 400 m (WMD = 300 m), while in the AF it already occupies the layer between 100 and 200 m. A mean standing crop of 2.6 and 16.4 ind. m<sup>2</sup> were found, by MO and NI respectively. At NI the animals were concentrated in the upper 80 m (WMD = 15.8 m), performing an extensive DVM of 284 m.

By daytime the whole siphonophores community (21.9% TMMC) occupied the entire sampled water column; (Fig. S2; Table S3), showing the maximum concentration of individuals between 100 and 80 m. During the NI a main upper community was concentrated in the 60–40 layer depth and a deeper community until 1000 m depth. The most abundantly caught siphonophore species, *Chelophysa appendiculata*, showed a clearly migration pattern (Fig. 4; Table 2). By MO, this species was caught between 100 and 1000 m depth (155 ind. m<sup>-2</sup>) with a maximum concentration of individuals in the 200–400 m layer (WMD = 303 m). At NI, *C. appendiculata* was concentrated in the upper 100 m, with a more abundant number of individuals than the day (WMD = 148 m), performing a moderate migration of 155 m as amplitude and generally reaching the surface layer.

By day, the population of *Pyrosoma atlanticum* (0.3% TMMC) showed a deeper peak of large colonies (about 5 cm long and 1 cm wide) between 200 and 400 m (Fig. 4; Table 2). A well-marked vertical migration was found after sunset with the population concentrated in the top 20 m of the water column. DVM values give a mean migration amplitude of 320 m for the large colonies. By MO, few-millimeter-long

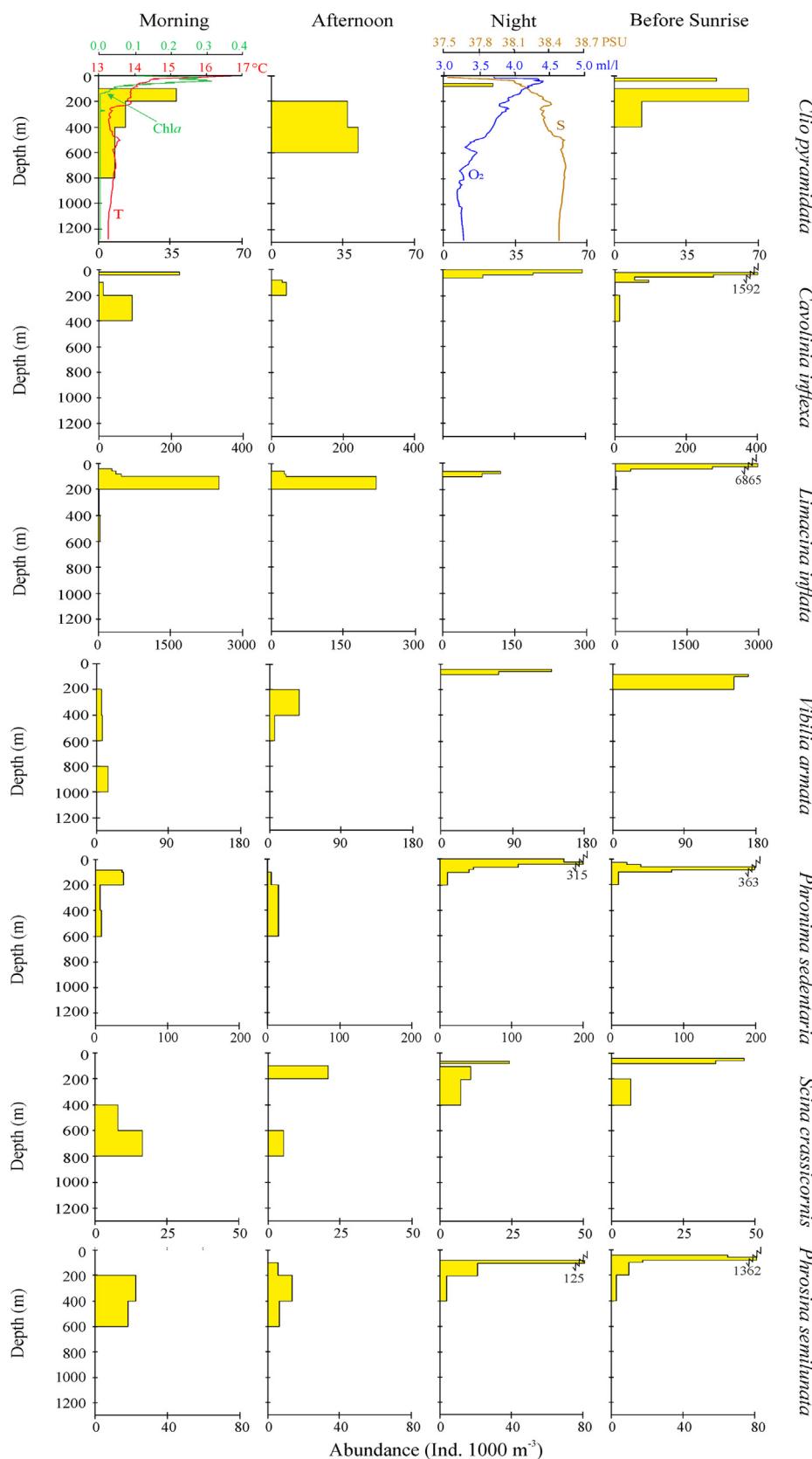
**Table 2**

Average standing crop of macroplankton and micronekton species (ind. m<sup>-2</sup>) and average Weighted Mean Depth (WMD) with amplitude of the migration dz (m), for the entire sampled water column recorded at day and night samples.

Species	Ind. m <sup>-2</sup>		WMD		dz
	Morning	Night	Morning	Night	
<b>Hydromedusae</b>					
<i>Solmissus albescens</i> (Gegenbaur, 1857)	2.6	16.4	300	15.8	284
<b>Siphonophora</b>					
<i>Chelophysa appendiculata</i> (Eschscholtz, 1829)	155	352	303	148	155
<b>Pteropoda</b>					
<i>Limacina inflata</i> (d'Orbigny, 1834)	340	9.6	153	78.1	75.1
<i>Clio pyramidata</i> (Linnaeus, 1767)	9.0	1.4	343	70.0	273
<i>Carolina inflexa</i> (Lesueur, 1813)	41.2	31.5	242	22.6	220
<b>Amphipoda</b>					
<i>Scina crassicornis</i> (Fabricius, 1775)	3.9	4.1	635	210	425
<i>Vibiliia armata</i> (Bovallius, 1887)	5.2	11.0	658	56.9	601
<i>Phronima sedentaria</i> (Forskål, 1775)	9.0	31.5	246	42.7	203
<i>Phrosina semilunata</i> (Risso, 1822)	6.4	7.5	390	143	248
<b>Euphausiacea</b>					
<i>Thysanopoda aequalis</i> Hansen, 1905	9.5	27.3	300	84.2	216
<i>Meganyctiphanes norvegica</i> (M. Sars, 1857)					
Large	8.3	12.4	455	22.6	432
Small	81.9	2172	148	10.8	137
<i>Euphausia krohnii</i> (Brandt, 1851)					
Large	7.1	63.2	300	41.9	258
Small	15.4	443	300	14.8	285
<i>Euphausia brevis</i> Hansen, 1905	7.1	6.2	300	53.6	246
<i>Euphausia hemigibba</i> Hansen, 1910	17.8	22.3	300	70.7	229
<i>Nematoscelis megalops</i> G.O. Sars, 1883					
Large	27.9	50.2	311	206	104
Small	131	81.8	311	176	135
<i>Nematoscelis atlantica</i> Hansen, 1916	0.0	7.4	–	281	–
<i>Stylocheiron longicornis</i> G.O. Sars, 1883	16.6	21.1	223	155	68.3
<i>Stylocheiron abbreviatum</i> G.O. Sars, 1883	5.9	32.2	259	85.2	174
<i>Stylocheiron maximum</i> Hansen, 1908	0.0	5.0	–	500	–
<b>Decapoda</b>					
<i>Gennadas elegans</i> (S.I. Smith, 1882)	2.6	4.1	500	391	109
<i>Sergestes arcticus</i> Krøyer, 1855					
Large	3.9	1.4	300	50.0	250
Small	2.6	6.9	150	10.0	140
<b>Mysidacea</b>					
<i>Eucopia unguiculata</i> (Willemoes-Suhm, 1875)	11.6	10.5	939	754	185
<b>Salpida</b>					
<i>Salpa fusiformis</i> Cuvier, 1804	95.4	144	127	67.9	58.9
<b>Pyrosomida</b>					
<i>Pyrosoma atlanticum</i> Péron, 1804					
Large	10.3	8.2	330	10.0	320
Small	98.0	12.3	89.9	88.0	1.9
<b>Fish</b>					
<i>Cyclothone braueri</i> Jespersen & Tåning, 1926	83.8	79.5	372	469	97.2 <sup>r</sup>
<i>Cyclothone pygmaea</i> Jespersen & Tåning, 1926	19.3	20.6	954	980	26.4 <sup>r</sup>

r = reverse migration.

small colonies (about 4–6 mm) were distributed between sub-surface waters and 200 m depth (Fig. 4), showing a peak in the 20–40 m layer. In the AF they appear slightly deeper, thickening between 100 and 200 m, while at nighttime small and large colonies occupies the same upper layers until a few hours before dawn. By day a large population of *Salpa fusiformis* (3.5% TMMC) was concentrated in the upper layer between 20 and 40 m and very few individuals were caught between 400 and 600 m (Fig. 4). Three hours after sunset, the surface population move upward reaching a maximum peak in the 0–20 m layer, whereas deeper population did not move up and down on a nycthemeral basis.



**Fig. 5.** Temporal abundance distribution per sampling layer of *C. pyramidata*, *C. inflexa*, *L. inflata*, *V. armata*, *P. sedentaria*, *S. crassicornis* and *P. semilunata* species (ind 1000 m<sup>-3</sup>) sampled by BIONESS multinet during the BioLig cruise 2013 in the Ligurian Sea.

Day-night WMDs (127 m and 68 m, respectively) demonstrates that *S. fusiformis* can be considered as weak migrant. DVM values gave a mean migration amplitude of 59 m (Table 2).

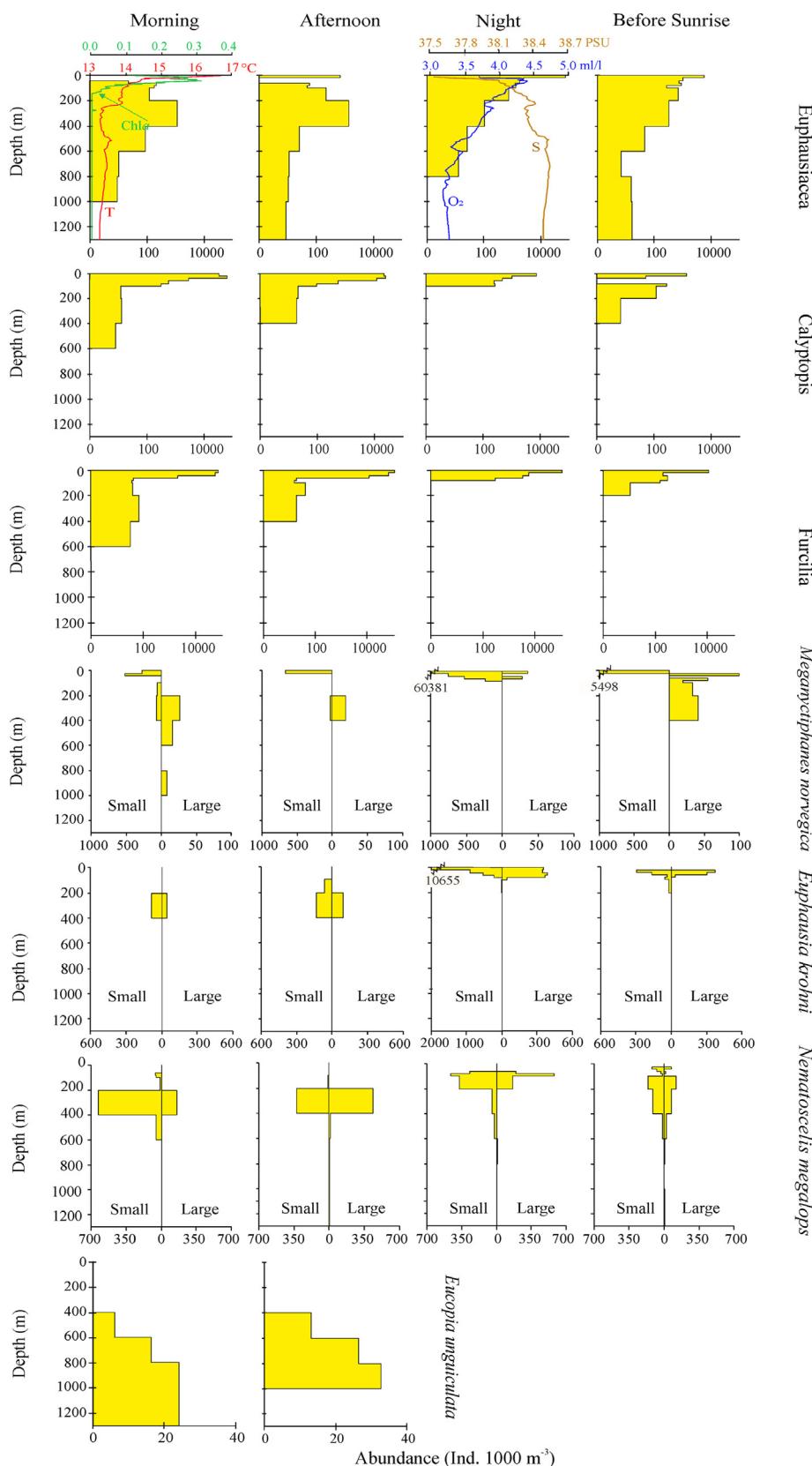
Pteropods (6.6% TMMC) are well represented, both for the total number of individuals in the community and in the number of species. By day the community was distributed between the surface layer and 600–800 m depth, with an abundance peak at 100–200 m (Figure S2). After sunset, an upward migration of the whole community was evident, with a concentration of individuals in the uppermost 100 m of the water column. The highest surface peak persists until just before dawn, while a large part of the community migrates deeper. WMD values (170 m and 36 m by day and night, respectively) gave a mean migration amplitude of 75 m for the all pteropods community (Table S3). The three pteropod species that will be taken into consideration in this study showed daily variable vertical distribution and migration (Fig. 5; Table 2). By MO, *Clio pyramidata* (2.3%) was distributed in the 100–800 m water column showing a peak of abundance between 100 and 200 m (Fig. 5). In the AF, population concentrated in the 200–600 m layer, while three hours after sunset *C. pyramidata* it was concentrated in a very thin layer between 80 m and 100 m depth, performing a DVM of 273 m as amplitude. From the increase of individuals in the surface layer, we can assume that the population continues to migrate after midnight and remains in the sub-surface waters in dark conditions without moon, before starting to migrate towards its deepest diurnal habitat. By MO, maximum abundances of adult *Cavolinia inflexa* (16.7%) were found in the 400–600 m layer, while the young specimens occupy a thin layer between 20 and 40 m (Fig. 5). From the AF a first migration of the deepest population was evident, showing a concentration of a small number of individuals between 100 and 200 m. Upward migration continues during night until the two populations of young and adults mix, concentrating in the layer between the surface and 100 m. After midnight the number of individuals increases until a few hours before dawn, showing the young individuals concentrated in their surface habitat (20 and 80 m), while a part of the adult population is already in its mesopelagic habitat (200–400 m). By our data, only adult *C. inflexa* perform a DVM of 220 m in amplitude (Table 2). The standing crop values of *Limacina inflata* (81.0%) were much higher by day than at night (Table 2). Most of the sized population of *L. inflata* found in the upper layers was youngest individuals. During the day its remains confined in the layer between 40 and 200 m, with a peak of individuals between 100 and 200 m (Fig. 5). After sunset the upward migration begins upwards and after midnight the population concentrated in the 0–60 m layer with a peak of total abundance at 0–20 m up to 20 times higher than those recorded during the day. A DVM of about 75 m of amplitude has been calculated.

During the day the amphipod community was distributed throughout the water sampled column, showing the maximum concentration of individuals in the 0–100 m layer (mostly very young individuals of *Hyperia* spp.) with highest abundances in the top 20 m (Figure S2; Table S3). Only for 4 species of deep water amphipods the vertical distribution and the day-night migration will be reported. *Vibiliia armata* (20.5%) was found in all samples at depths of from 50 and 1000 m. The data suggests that *V. armata* exists in a thick zone ranging from 200 to 1000 m during the day and from 40 to about 80 m at night (Fig. 5). It appears that in the AF the entire population moves upward some 400 m, and in the NI all the population was concentrated in the sub-surface layer A DVM of about 601 m of amplitude has been calculated (Table 2). *Phronima sedentaria* (51.3%) was collected in all samples at depths of from the surface to 1000 m. During daytime was found at depths ranging from about 100 to 600 m, with the greatest concentration about 100 and 200 m (Fig. 5). The entire population appears concentrated between the surface and 200 m and remains in this layer for a long time in the dark, reaching maximum values of abundance between 20 and 40 m before midnight and between 60 and 80 m up to three hours after midnight. A DVM of about 204 m of

amplitude has been calculated (Table 2). A few individuals associated with salps in surface were noted. *Scina crassicornis* (10.3%) occurred during vertical hauls ranging between 100 and 800 m (Fig. 5). This species displayed a unique pattern of vertical migration. At morning-time the entire population was concentrated between 400 and 800 m. It appears that only the upper portion of the population moves upward some 400 m at AF (still with the day-light) concentrating in the 100–200 m layer, while the deeper members remained rather stable at 600–800 m. The deepest portion of the population move at night and three hours after the sunset all the population was concentrated in the mesopelagic layer where it remains up to three hours before dawn, resulting in an absence of individuals at great depths during the dark hours. A DVM of about 425 m of amplitude has been calculated (Table 2). *Phrosina semilunata* (17.9%) occupies the layer between 200 and 600 m during daytime, moving upwards already in the AF light hours (Fig. 5). At NI it continues to migrate to the surface, not reaching the surface layer and concentrating between 80 and 100 m, even if a small part of the population remains in the deepest layer between 200 and 400 m. This nocturnal migration pattern remains almost the same until a few hours before sunrise, when the maximum abundance of 1362 ind.1000 m<sup>-3</sup> is reached. *P. semilunata* was essentially represented by young specimens. A DVM of about 248 m of amplitude has been calculated (Table 2).

Mysids constitutes less than 0.1% of the entire zooplankton community (Table S3) and 0.3% of the TMMC. During the day, the community occupies the layer between 200 m and the maximum sampled depth, with an evident increase of individuals deeper than 600 m (Figure S2). During the night, the deepest part of the community makes a moderate upward migration (108 m as amplitude), but not above 400 m. Also the upper part of the community (possibly young specimens) detaches from the deeper one performing a moderate DVM of 100 m, occupying the layer 100–200 m. Among mysids, *Eucopia unguiculata* was the largely dominant deep-water mysid species caught in this study. By day, its vertical distribution was restricted to deepest mesopelagic zone from 400 m to 1300 m (Fig. 6, Table 2, WMD 939 m). Individuals abundance increase with depth reaching maximum values at 1000–1300 m (27 ind.1000 m<sup>-3</sup>). Overnight, only a part of deeper individuals performed a moderate DVM of amplitude of about 185 m, while the upper part of the population does not move from the diurnal depth of 400 m.

In the present study, the dominant micronekton on the slope other than siphonophora, and hydromedusae, were euphausiids (50.6% TMMC). At daytime, all the community was distributed between 40 m and 1000 m, with a peak of abundance at 200–400 m (Fig. 6). During the AF, the vertical distribution pattern remains almost similar, but the total abundance in the total sampled water column was double in respect to the MO (323 and 153 ind. m<sup>-2</sup>, respectively). After sunset, deeper species migrate upwards in the surface layers and most of the community was concentrated in the first 100 m, while both non- and weak-migrant species are distributed in the deepest layers up to 800 m. During the NI, the abundance in the overall sampled water column reached the maximum values of 3202 ind. m<sup>-2</sup>. The highest peak in the top 20 m remains until just before dawn although with much lower abundance values, while a large part of the community migrates deeper. WMD value give a mean migration amplitude of 285 m for the all euphausiids community (Table S3). Day-night distribution and migration of euphausiid larval stages (calyptopis and furcilia) they can be observed in Fig. 6. Most of the larvae were concentrated in the top 60 m, during day and nighttime. By day, a similiar vertical distribution was observed both stages being distributed between the surface layer and 600 m and 400 m depth, respectively (Table S3). Already in the afternoon the two populations move upwards concentrating in the top 100 m at the NI time and maintaining the furcilia a higher number of individuals compared to the calyptopis (4408 and 363 ind. m<sup>-2</sup>, respectively). Three hours after sunset, highest concentration in the first 40 m of both larvae stages were found. Morning and NI average



**Fig. 6.** Temporal abundance distribution per sampling layer of euphausiacea, calyptopis and furcilia groups (ind 1000 m<sup>-3</sup>) and *M. norvegica*, *E. krohnii*, *N. megalops* and *E. unguiculata* species (ind 1000 m<sup>-3</sup>) sampled by BIONESS multinet during the BioLig cruise 2013 in the Ligurian Sea.

abundances in the entire sampled water column, WMDs and migration amplitudes of all euphausiid species were reported in Table 2. During daytime, the euphausiid community was essentially represented by large and small *Nematoscelis megalops* (48.5%), *Meganyctiphanes norvegica* (27.4%), and *Euphausia krohni* (6.7%). By NI, the order of abundance changes being large and small *M. norvegica* (74.2%), *E. krohni* (17.2%), and *N. megalops* (4.5%). The most abundant species. Most larger individuals of different *M. norvegica* size classes showed a daytime distribution between 200 and 600 m (WMD = 455 m, Table 2; Fig. 6), with only a small part of population in the deeper layer. Already in the AF the whole population makes a migration towards the upper mesopelagic layers, concentrating between 200 and 400 m. At NI, most small and large individuals were caught in the upper layers, and all the population was concentrated between the surface and 40 m, with higher values in the top 20 m (Table 2). The vertical migration amplitudes were 432 m and 137 m for large and small individuals, respectively. Patterns of vertical distribution showed that during the MO and the AF different size classes of *E. krohni* was distributed in the layer 200–400 m (WMD = 300 m). At nighttime the large population performed an extensive DVM of 258 m as mean amplitude, migrating as a compact unit from 200 to 400 m by day to the upper 100 m (Fig. 6). A high concentration of individuals in this layer has been shown for a long period of darkness and up to a few hours before dawn, when a weak downwards migration it begins. The smallest specimens show almost the same behavior as large ones, both in the vertical distribution and in the amplitude of upward migration at night (DVM = 285 m), but with a high peak of individuals about 25 times higher than the value recorded for the largest individuals in the 0–20 m layer. In the MO, *N. megalops* showed the maximum density between 200 and 400 m, with the remaining small population down to 800 m (Fig. 6; WMD = 311 m). *Nematoscelis megalops* shows a clear weak migratory behaviour. By darkness, there was a slight migration upward. A large part of the population of both size classes moves towards and three hours after sunset concentrated in the layer between 100 and 200 m. Larger individuals show the highest peak of abundance between 80 and 100 m, while small individuals show high values in a thicker layer. A small part of the population remains confined at highest depth. Amplitudes of upward migration for both large and small individuals were 104 m and 135 m, respectively (Table 2).

By day, pelagic decapods were uniformly distributed between 100 m and 600 m (Fig. 7; WMD = 334 m, Table S3). In the AF the vertical distribution pattern observed during the day extends in depth from 600 m up to the maximum sampled depth. After sunset, the vertical distribution was clearly bimodal: the upper mesopelagic species migrate upwards showing a peak around 20–40 m while both non- and weak-migrant species they are distributed in the deepest layers down 600 m. Before sunrise a large part of the community migrates deeper. Average WMDs give a mean migration amplitude of 289 m for the whole decapod community (Table S3). The average standing crop was significantly higher at night ( $18 \text{ ind. m}^{-2}$ ) than by day ( $7 \text{ ind. m}^{-2}$ ). By day, *Gennadas elegans* occurred between 400 and 600 m depth (Fig. 7, WMD = 500 m Table 2), while in the AF the population appeared partitioned in the entire water column between 200 m and 1300 m. Individuals abundance increase with depth, reaching the maximum values in the 800–1000 m layer. By NI, a part of the population remains steady 600–800 m, while the majority migrate towards the superficial layers (WMD = 391 m), concentrating between 100 and 80 m stratum. *G. elegans* appeared as an extensive migrator performing a mean displacement of 288 m. Few hours before sunrise, the population has already made a large migration to the deeper layers, separating in a more superficial part between 200 and 600 m) and a deeper part between 800 and 1000 m. By day, small and large *Sergestes arcticus* occurred between 100 and 200 m and 200–400 m, respectively (Fig. 7, WMDs 150 m and 300 m, respectively, Table 2). In the AF, young specimens and adults occupy the same layer between 200 and 400 m. At NI all the sized population was concentrated in the upper layer between 20 and

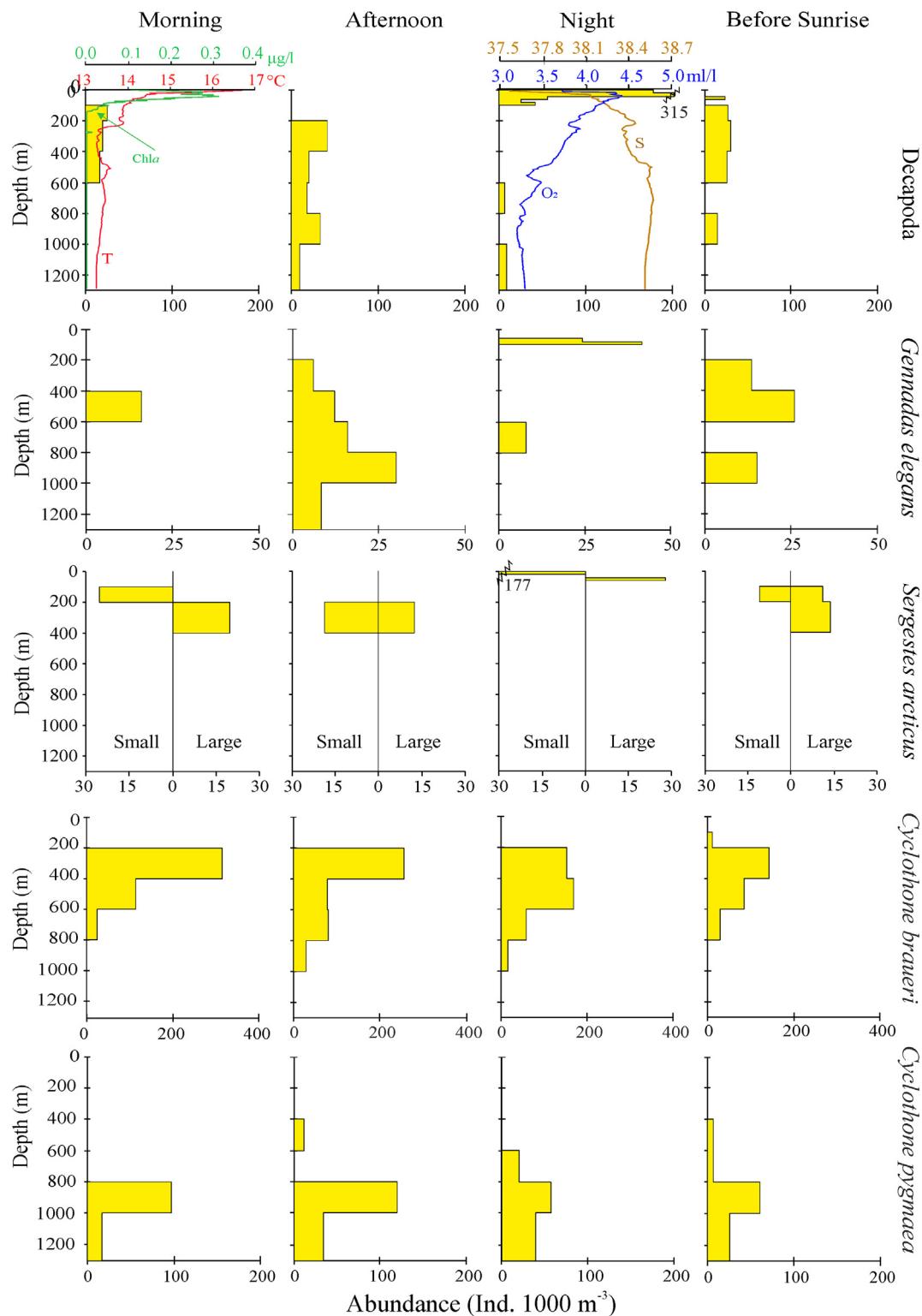
40 m and 40–60 m, for the small and large specimens, respectively. *Sergestes arcticus* performed DVM with mean amplitude of 140 m and 250 m for juvenile and adults, respectively (Table 2).

A total of 593 adult mesopelagic fish were collected, 468 were *Cyclothona braueri*, 122 were *C. pygmaea*, one was *Lobianchia dofleini* (tow 8A, 800–1000 m), one *Electrona risso*, and one *Lampanyctus crocodilus* (both tow 8B, 100–200 m). During the MO *C. braueri* population was distributed between 200 and 600 m (73.8% at 200–400 m, and 21.5% at 400–600 m) with some animals as deep as 800 m (4.6%, Fig. 7). In the AF 200–400 m and 400–600 m layers showed the same shape and almost individual percentages (56.9% and 18.0% respectively), while the abundance increases in the layer 600–800 m (20.8%) and a lower percentage is added in the deepest layer 800–1000 m (4.2%). At NI 81% of the population of *C. braueri* was located in the 200–600 m layer, the remaining 19% of the population was found between 600 and 1000 m. Its preferential depth was regular during time (WMD of 372 m by day and 469 m at night). Thirty-six percent of the population did no migrate vertically at night, but remained at the day time depths. Going deeper, *C. braueri* was replaced by *C. pygmaea* which was also no-migrant. Its maximum abundance was always observed between 800 and 1000 m, with a lower part of the population observed below 1000 m (Fig. 7). A WMD of 954 m by day and 980 m at night were observed. Few individuals have been caught in the 400–600 m layer at the AF and before sunrise (Fig. 7). The abundance of *C. braueri* and *C. pygmaea* caught during the day and night (84 and 80 ind.  $\text{m}^{-2}$ ; 19 and 21 ind.  $\text{m}^{-2}$ , respectively) were very similar. This demonstrated that avoidance of the BIONESS by fish are negligible.

Only two species of cephalopods were found during nighttime: two specimens of *Heteroteuthis dispar* at 100–200 m depth and one specimen of *Rossia macrosoma* at 400–600 m.

### 3.5. Data processing

Cluster analysis performed on major species of macroplankton and microneuston community assemblage mainly highlighted the presence of 4 clusters of samples, grouped according to the sampling depth along the water column: from surface to 60 m (cluster A), from 61 to 100 m (cluster B), from 101 to 600 m (cluster C) and from 601 to 1300 m (cluster D) (Fig. 8a). Cluster analysis performed on each layer depth showed a change in zooplankton assemblage among the 4 different sampling times, with the exception of the layers between 100 and 600 m, where the pattern was not explained by sampling time (Fig. 8b). Differences encountered by cluster analysis were confirmed by PERMANOVA test (Table 3). Moreover, SIMPER analysis showed the species that mainly contributed to the similarity of each time group (Table 4). Table 5 show the diversity indices of the planktonic community. The highest values of biodiversity were found in the deep layers between 100 and 600 m. In this layer the highest number of species was also found. Fig. 9 showed the constrained classification produced by dbRDA analysis. The first two axis explain 27% of total variance, and the 87% of the fitted model. Environmental covariates significantly influence the zooplankton species distribution (Table 3). The axis 2 of dbRDA analysis captured the existing variance among the community living between 0 and 600 m depth. Temperature and chlorophyll were the environmental variables mainly correlated with this axis, and were the variables that principally influenced the distinction between “shallow community” (0–60 m, high values of temperature and chlorophyll) characterized by adults of *Meganyctiphanes norvegica*, and adults and juveniles of *Euphausia krohni*, and “deep community” (below 60 m, low values of temperature and chlorophyll) characterized by *Stylocheiron longicornis*, *Chelophysa appendiculata* and juveniles of *Nematoscelis megalops*. Below 60 m depth, the temperature parameter reached low values, and was constant in all water column. The axis dbRDA 1 captured the existing variance between two group, the community living above 600 m depth and the community living below 600 m depth. The dissolved oxygen and salinity become the most important variables



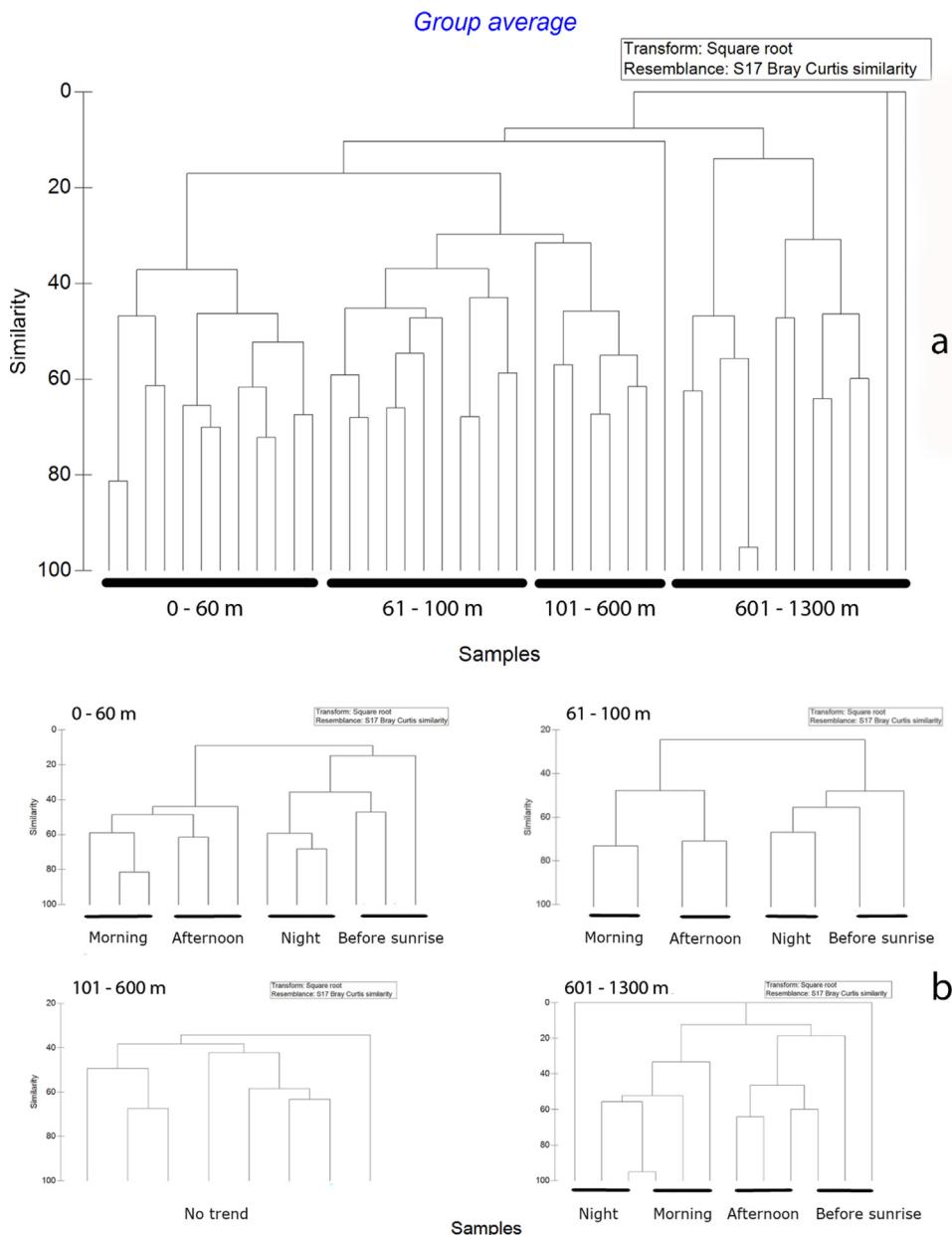
**Fig. 7.** Temporal abundance distribution per sampling layer of the decapoda group (ind 1000 m<sup>-3</sup>) and *G. elegans*, *S. arcticus*, *C. braueri* and *C. pygmaea* species (ind 1000 m<sup>-3</sup>) sampled by BIONESS multinet during the BioLig cruise 2013 in the Ligurian Sea.

affecting the zooplankton community living between these two deep strata. *Eucopia unguiculata* was the species that showed highest value of Pearson correlation with dbRDA1, living in the deep strata below 600 m.

#### 4. Discussion

##### 4.1. Vertical patterns and day-night migrations

WMD of different macroplankton and micronekton species were reported in Figs. 10–11. Highest values of *Solmissus albescens* abundance found in this study are in agreement with Goy et al. (1989) that



**Fig. 8.** a-b. Dendogram obtained after cluster analysis applied on Bray Curtis similarity matrix (a) on macroplankton and micronekton species abundance data sets of all depth intervals at each sampling time (b) on each selected deep stratum.

reported in winter and spring its maximum abundance. Our data confirm the extensive vertical migration of the entire compact population as been reported previously by different authors (Andersen et al., 1992; Sardou and Andersen, 1993, 1996). Our data agree with Benovic's (1973) results that *Solmissus* never reached the 0–100 m level at full moon, while at periods of low moonlight intensity individuals were even found near the surface (Fig. 10a). *Chelophyes appendiculata* was the prevailing siphonophore in this study confirming the results of previous findings (Franqueville, 1971; Sardou et al., 1996; Andersen et al., 2001a). Also the day-night WMDs (Fig. 10a) and a moderate migration pattern of *C. appendiculata* found in this study are in agreement with other authors (Andersen et al., 1992, 2001b; Sardou and Andersen, 1993; Andersen et al., 1998). Its importance throughout the sampled water column and particularly in the superficial layer at night was confirmed by the results of the SIMPER analysis (Table 4). *Salpa fusiformis* was the most abundant species found in the present study. In general, our data on its vertical distribution behaviour agree with the results of Franqueville (1971) and Sardou and Andersen (1993). The

very small calculated DVM value seems indicates *S. fusiformis* as a non- or weak migrant (Tsuda and Nemoto, 1992) and that the bulk of the population did not move up and down on a nycthemeral basis (Laval et al. 1992). During the darkness and before sunrise this species reaches the DCM layer (Fig. 10a).

The extensive DVM of *Pyrosoma atlanticum* has previously been reported by Andersen et al. (1992) and Andersen and Sardou (1994) showing, that amplitude of the migration increased with the size of the colonies, from 90 m for the 3 mm-length colonies up to 760 m for the 51 mm-length ones. Its results agree with our findings. The largest colonies reach the surface at night within both the thermocline and the DCM1 (Fig. 10b).

The three pteropod species caught here are known to perform more or less extensive migration (Sardou and Andersen, 1993; Sardou et al., 1996). As shown in the present study by the large number of young individuals found in the surface layer in the DCM layer (Fig. 10c), our results in the Ligurian Sea in May 2013 agree partly with Rampal's conclusions that in the Mediterranean *L. inflata* performs large

**Table 3**

(Top) Results of PERMANOVA used to test the effects of bathymetric stratum and time on the structure of the macroplankton and micronekton species assemblage. (Bottom) Results of Distance based redundancy analysis.

PERMANOVA						
Variable	df	MS	Pseudo-F	P(perm)		
time	3	5110	2.72	0.0001		
cluster	3	12625	6.72	0.0001		
ti x cl	9	5201	2.77	0.0001		
Res	28	1879				
Total	43					
Distance based redundancy analysis						
Variable	df	SS(trace)	Pseudo-F	P		
Prop.	Cum. Prop.					
temperature	1	15415	4.71	0.0001	0.10	0.10
salinity	1	16774	5.17	0.0001	0.11	0.21
chlorophyll a	1	15130	4.61	0.0001	0.10	0.31
oxygen	1	28181	9.48	0.0001	0.18	0.49

bathymetric displacements, that the adult population has a deeper habitat and that reproduction is important not only in the autumn–winter period, but also in spring (Rampal, 1967; Sentz-Braconnat, 1968). Its importance throughout the sampled water column and particularly in the surface layer in the dark hours at night and before sunrise, was

**Table 5**

Diversity indices of the macroplankton and micronekton communities. Species number, total individuals, species richness (Margalef Index) and Pielou's evenness of the four of samples labeled with water mass which they refer.

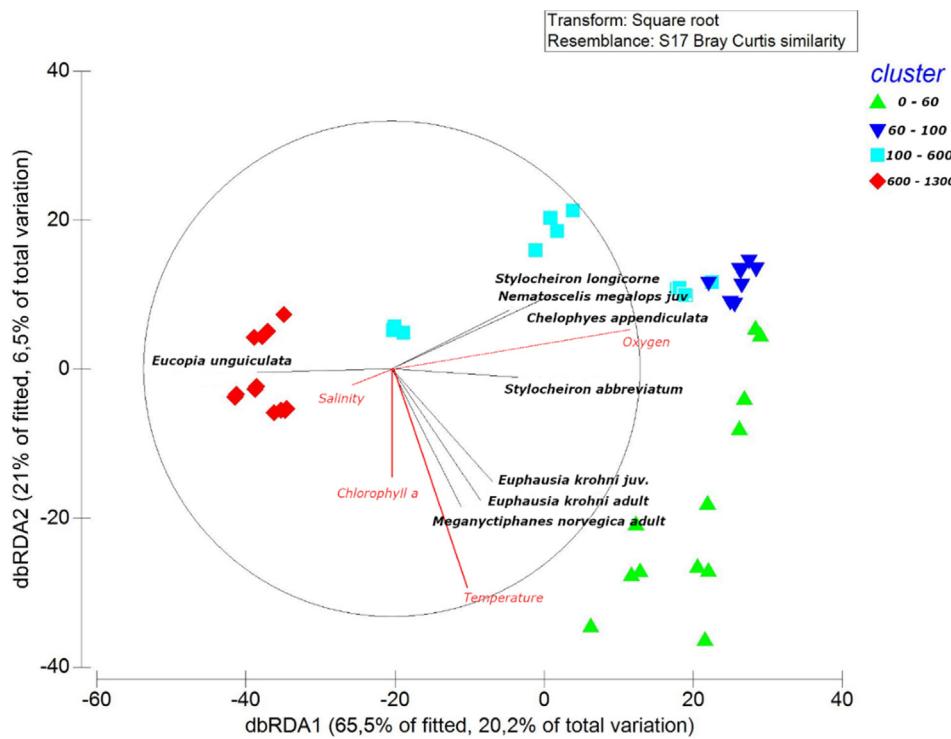
	Total species	Total individuals	Species richness (Margalef)	Pielou's evenness	Deep stratum
Morning	14	133	2.65	0.91	A
Afternoon	9	67	1.91	0.93	
Night	11	102	0.84	0.84	
Before sunrise	11	111	0.74	0.74	
Morning	12	99	2.39	0.85	B
Afternoon	13	78	2.75	0.93	
Night	12	93	2.42	0.88	
Before sunrise	12	99	2.39	0.86	
Morning	18	104	3.66	0.83	C
Afternoon	21	83	4.52	0.91	
Night	15	82	3.17	0.89	
Before sunrise	24	123	4.78	0.91	
Morning	7	14	2.29	0.90	D
Afternoon	4	9	1.34	0.84	
Night	3	6	1.64	0.82	
Before sunrise	3	4	1.39	0.94	

confirmed by the results of the SIMPER analysis (Table 4). In the Ligurian Sea, *Cavolinia inflexa* was observed only in the spring seasons: upper 300 m in April 1986 (Laval et al., 1989), between 250 and 450 m

**Table 4**

SIMPER analysis: contribution (%) of the most macroplankton and micronekton representative species to similarity among groups by Cluster Analysis.

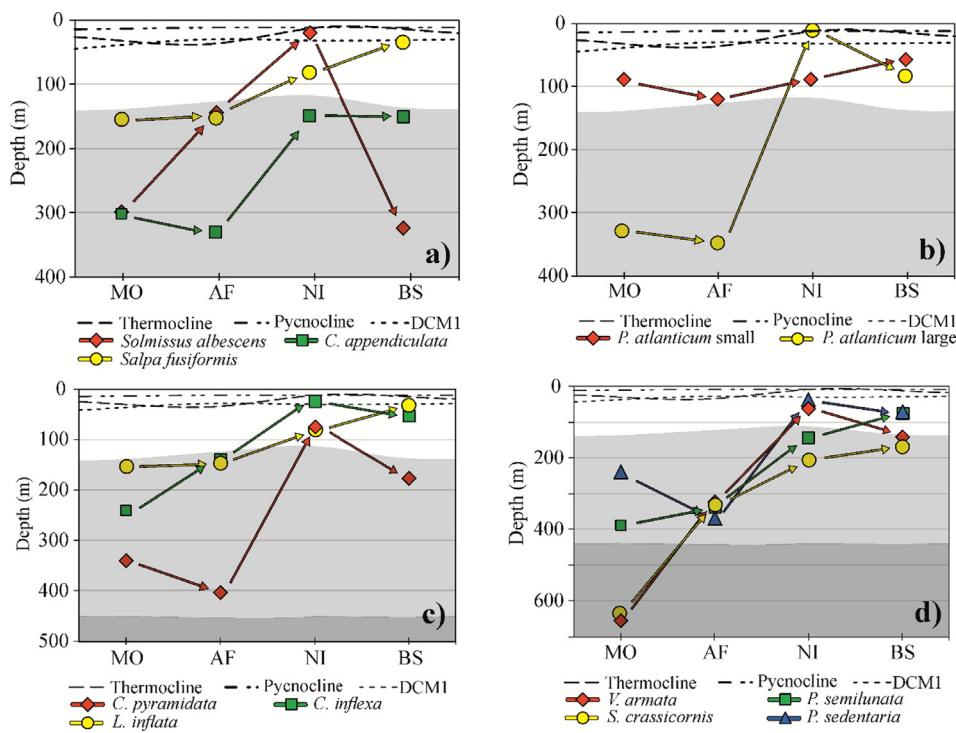
Cluster	Time	Specie	Abundance	Contrib%	Cum.%
0–60	Morning	<i>Euphausia krohnii</i> Ad	19.15	21.37	21.37
0–60	Morning	<i>Meganyctiphanes norvegica</i> Juv	22.03	20.77	42.14
0–60	Morning	<i>Euphausia krohnii</i> Juv	22.59	20.19	62.33
0–60	Afternoon	<i>Euphausia krohnii</i> Ad	14.24	29.47	29.47
0–60	Afternoon	<i>Euphausia krohnii</i> Juv	12.02	24.68	54.14
0–60	Afternoon	<i>Nematoscelis megalops</i> Juv	8.51	20.12	74.26
0–60	Night	<i>Chelophyes appendiculata</i>	33.84	49.89	49.89
0–60	Night	<i>Cavolina inflexa</i>	15.40	19.60	69.49
0–60	Night	<i>Phronima sedentaria</i>	13.88	18.26	87.76
0–60	Before Sunrise	<i>Limacina inflata</i>	48.68	69.89	69.89
0–60	Before Sunrise	<i>Cavolina inflexa</i>	18.86	15.01	84.90
0–60	Before Sunrise	<i>Chelophyes appendiculata</i>	9.93	10.62	95.51
60–100	Morning	<i>Nematoscelis megalops</i> Juv	20.38	27.06	27.06
60–100	Morning	<i>Limacina inflata</i>	20.46	26.74	53.80
60–100	Morning	<i>Nematoscelis megalops</i> Ad	18.41	17.72	71.52
60–100	Afternoon	<i>Euphausia hemigibba</i>	12.35	22.54	22.54
60–100	Afternoon	<i>Stylocheiron abbreviatum</i>	12.12	19.08	41.63
60–100	Afternoon	<i>Stylocheiron longicorne</i>	7.82	13.81	55.43
60–100	Night	<i>Chelophyes appendiculata</i>	30.13	48.78	48.78
60–100	Night	<i>Limacina inflata</i>	10.08	14.85	63.63
60–100	Night	<i>Stylocheiron longicorne</i>	7.69	12.05	75.68
60–100	Before Sunrise	<i>Chelophyes appendiculata</i>	23.77	43.42	43.42
60–100	Before Sunrise	<i>Phronima sedentaria</i>	14.41	19.49	62.90
60–100	Before Sunrise	<i>Cavolina inflexa</i>	8.57	14.75	77.65
100–600	Morning	<i>Chelophyes appendiculata</i>	14.34	22.67	22.67
100–600	Morning	<i>Salpa fusiformis</i>	9.28	19.96	42.63
100–600	Morning	<i>Limacina inflata</i>	19.81	14.39	57.02
100–600	Afternoon	<i>Chelophyes appendiculata</i>	14.08	35.00	35.00
100–600	Afternoon	<i>Salpa fusiformis</i>	7.39	14.78	49.78
100–600	Afternoon	<i>Nematoscelis megalops</i> Ad	5.33	11.47	61.25
100–600	Night	<i>Chelophyes appendiculata</i>	14.77	73.55	73.55
100–600	Night	<i>Nematoscelis megalops</i> Juv	10.88	10.80	84.35
100–600	Night	<i>Meganyctiphanes norvegica</i> Ad	3.05	5.77	90.12
100–600	Before Sunrise	<i>Limacina inflata</i>	3.64	17.17	17.17
100–600	Before Sunrise	<i>Nematoscelis megalops</i> Ad	9.16	16.61	33.78
100–600	Before Sunrise	<i>Solmissus albescens</i>	3.37	15.42	49.20
600–1300	Morning	<i>Europia unguiculata</i>	4.66	87.17	87.17
600–1300	Morning	<i>Chelophyes appendiculata</i>	2.84	12.83	100.00
600–1300	Afternoon	<i>Gennadas elegans</i>	4.13	77.27	77.27
600–1300	Afternoon	<i>Chelophyes appendiculata</i>	3.45	22.73	100.00
600–1300	Night	<i>Europia unguiculata</i>	3.60	100.00	100.00
600–1300	Before Sunrise	<i>Nematoscelis megalops</i> Ad	2.02	100.00	100.00



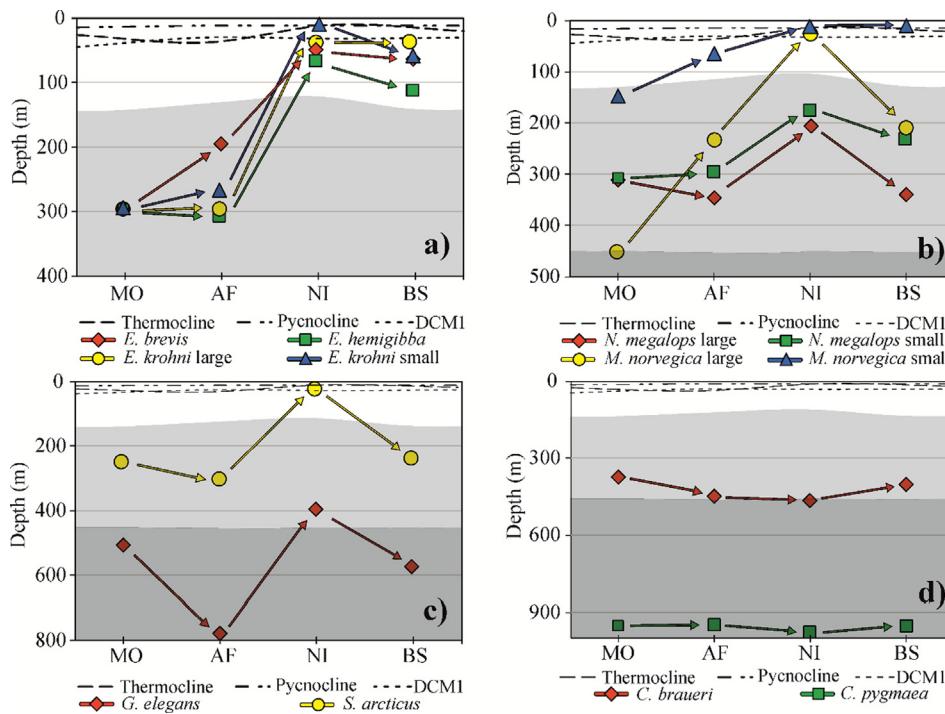
**Fig. 9.** Constrained classifications by distance-based Redundancy Analysis (db-RDA) ordination diagram of the macroplankton and micronekton species. The red arrows indicate significant explanatory variables, from a set of environmental descriptor (chlorophyll, temperature, oxygen and salinity). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

in April 1990 (Sardou and Andersen, 1993) and 200–400 m in this study. The large number of young individuals of *C. inflexa* found in the surface layer at night (Fig. 10c) were confirmed by SIMPER analysis (Table 4) and agree with the conclusions of Sardou et al. (1996) that the breeding period extends from April to June. There are still many uncertainties about the deepest bathymetric level that this species can reach during the day: 1000 m according to Rampal (1975), 550–700 m according to Sardou and Andersen (1993). Our data suggest that adult

*C. inflexa* live during the day at a maximum depth of 400 m. It seems that this species performs a DVM of 220 m as amplitude that is in agreement with the DVM of 150–250 m found by Sardou et al. (1996) in April. After midnight the population concentrated in the 20–60 m between DCMs (Fig. 10c). Our results suggest that *Clio pyramidata* performs a day-night migration broader than the two previous species, that is in agreement with BIONESS data of Sardou and Andersen (1993) and close but not very comparable with the findings of Franqueville (1970,



**Fig. 10.** WMD of (a) *S. albescens*, *C. appendiculata*, *S. fusiformis* (b) small and large *P. atlanticum* (c) *C. pyramidata*, *C. inflexa*, *L. inflata* (d) *V. armata*, *P. semilunata*, *S. crassicornis*, *P. sedentaria* at fixed station 8 in the Ligurian Sea, Spring 2013. Shaded grey area indicates dissolved oxygen concentration below 4.0 mLO<sub>2</sub>L<sup>-1</sup>.



**Fig. 11.** WMD of (a) *E. brevis*, *E. hemigibba*, small and large *E. krohnii* (b) small and large *N. megalops*, small and large *M. norvegica* (c) *G. elegans*, *S. arcticus* (d) *C. braueri*, *C. pygmaea* at fixed station 8 in the Ligurian Sea, Spring 2013. Shaded grey area indicates dissolved oxygen concentration below  $4.0 \text{ mLO}_2 \text{ L}^{-1}$  (light grey) and below  $3.5 \text{ mLO}_2 \text{ L}^{-1}$  (dark grey).

1971), Rampal (1975) and Casanova (1980) who have made observations from the mesoscaphe or collected the samples by traditional non-closing nets. At night *C. pyramidata* reaches the sub-surface occupying the layer between 60 and 80 m below the DCM2 (Fig. 10c). This behaviour agree with the migration pattern suggested by van der Spoel (1973).

The more common mesopelagic species of hyperiid amphipods taken during this present study perform day-night vertical migrations, but showed different migration behaviour (Fig. 10d). Our data agree with the conclusions of Gasca (2009) that by day, *V. armata* and *S. crassicornis* live deeper (1000 m and 800 m depth, respectively) than *P. sedentaria* and *P. semilunata*. According to Macquart-Moulin (1993) highest abundances were recorded at the surface at night, but only *P. sedentaria* seems to reach the surface layer, as confirmed by SIMPER analysis (Table 4). It has been suggested in much of the earlier literature that only the young individuals of these species were ever captured near the surface and that the adults were typically taken in deep trawls. The four deep-water species appear to be distributed according to a vertical gradient of the population maximum abundance: *P. sedentaria* between 0 and 40 m, *V. armata* between 40 and 60 m, *P. semilunata* and the upper population of *S. crassicornis* between 80 and 100 m. According to the present results and previous investigations (Andersen et al., 2001b), some species showed a bimodal day distribution, but a different vertical migration pattern. *Vibiliella armata* and *P. sedentaria* displayed a unique pattern of vertical migration: the upper portion of the population remained rather stable or performed a weak migration, while the deeper dwelling members rose at night, resulting in an absence of individuals at great depths during the dark, although only the deeper part of the *V. armata* population seems to move upwards in the afternoon reaching the upper mesopelagic layer at depths ranging from 200 to 400 m. *S. crassicornis* specimens, which are often present in the superficial layers at night (Franqueville, 1971; Thurstton, 1976; Shulenberger, 1978), were frequently observed on the slop waters. *S. crassicornis* differs from the others because even if it makes an extensive migration of 425 m (this study), the upper the deepest part of the population they remain separate during the day-night migration. As reported by Macquart-Moulin (1993) the deep positive samples at night may be the result of either a descent during the dark hours or the

presence of a non-migrating portion of the population residing below the depth of perceivable light. In the Mediterranean *S. crassicornis* has been captured essentially during the night (about 80%) and reaches the sub-superficial layer (from 50 to 150 m) only at night. According to Macquart-Moulin and Patriti (1996), juvenile individuals of *Scina crassicornis* occurred during vertical hauls above bottom depths ranging between 1300 and 200 m. Another note to highlight is the persistence of the four species population in the surface layer for a long period of darkness and up to few hours before sunrise. In this time frame they reached very highest abundances and there was still no evidence of migration towards the deeper layers. In the upwelling area of the Strait of Messina, these species seemed strongly attracted by the lights of the vehicle and often followed them, swimming very quickly, with a desire for subcircular motion, for periods of time relatively long (Genovese et al., 1985).

Our results on the day/night vertical distribution and migrating behaviour of euphausiid population (Fig. 11a-b), agree both with the general remarks made by Casanova (1974) for the Ligurian Sea and with Werner and Buchholz's conclusions (2013) that differences in day and night distributions, as well as the observed migration patterns, indicated that changes in light intensity (dusk/dawn) were the proximate cue initiating up and downward migration. During the night they migrated vertically to the upper layers showing a different amplitude of migration and the biomass was quite doubled than those detected in daytime. This agrees with the findings of Brinton (1979). The three *Euphausia* species (*krohnii*, *brevis* and *hemigibba*) showed a similar migratory pattern, migrating as a compact unit from the depth of the lower mesopelagic zone (DVM of 258 m, 246 m and 229 m respectively) to the thermocline and mixed layer (Fig. 11a). At night, these species *Euphausia* aggregated at the same depth between the surface and 40 m. This consideration confirms previous results of other authors who found the same species occupy the layer from 0 to 50 m during the night (Brinton, 1979; Minutoli and Guglielmo, 2009, 2012; Minutoli et al., 2014). All other adult species have avoided the upper mixed layers. According to Andersen et al. (1998) and as confirmed by our SIMPER analysis (Table 4), the three dominant euphausiid species were *Meganyctiphanes norvegica*, *E. krohnii* and *N. megalops*. According to Casanova (1974) *M. norvegica* is exceptionally abundant in the Ligurian Sea and

constitutes about 65% of the euphausiids population. By day, small and large individuals of *E. krohni* and *N. megalops* showed a similar vertical distribution, while large *M. norvegica* live deeper than small ones. It was considered a species with a bathyplanktonic tendency, found in the Ligurian Sea below 500 (Ruud, 1936; Franqueville, 1970; Mcquart-Moulin and Leveau, 1968). *M. norvegica* appeared in the superficial and sub-superficial layers by sunset, remine in these layers during the whole night and descended by sunrise to the daytime layer of 200–500 m, and it is reported to be an important component of DSL (Jukic, 1978; Sameoto, 1982). This vertical migration was compact and performed at population level. At night, maximum numbers of small and large *M. norvegica* were caught in the 10–20 m stratum (Fig. 11b), about 20 m upper than large *E. krohni* and 180–166 m than *N. megalops* both sizes. This agrees with the general observations of Casanova-Soulier (1968); Casanova (1970, 1974); Wiebe e D'Abromo (1972) and Andersen et al. (1998) that *M. norvegica* appeared to perform DVM of variable amplitude according to the time of the year. In the present study at early May, an extensive DVM was observed for the entire population of large *Meganyctiphanes* ( $dz = 432$  m) and our results agree with Kaartvedt's observations (2010). Depending on the species, the migration strategy differs in its amplitude, day- and night-time depths and, in some species, these characteristics could be controlled by environmental and/or biological factors. Most authors (e.g. Buchholz et al., 1995; Antezana, 2009; Werner and Buchholz, 2013) clearly indicates that environmental variables, like temperature, dissolved oxygen concentration and chlorophyll strongly influence the vertical distribution of euphausiid species. According with Werner and Buchholz's conclusion (2013) *N. megalops* showed a weak migration pattern, avoided higher water temperatures and prevailed in the OMZ throughout 24 h (Fig. 11b).

Among species living in the deepest mesopelagic zone, *Eucopia unguiculata* was the largely dominant deep-water mysid species caught in this study. According to Franqueville (1971) *E. unguiculata* migrated in the upper layers but not above 400 m and referring to Andersen and Sardou (1992) and Sardou and Andersen (1993) conclusions only a few individuals performed a migration amplitude of about 200 m (185 m in this study). Casanova (1970, 1977) described the vertical distributions of *E. unguiculata* as barely affected by diel variations, while this species appeared to perform a DVM in the abyssal- and bathypelagic areas (Castelbon, 1987), as confirmed also by SIMPER analysis (Table 4).

According to the studies of Andersen and Sardou (1992), Sardou and Andersen (1993) and Andersen et al. (1998), *Gennadas elegans* is typically bathypelagic, living below 500 m by day (Franqueville, 1971) and generally at 1000 m and below (Casanova, 1980; Castelbon 1987), and performing an extensive DVM at night. *G. elegans* did not appear to migrate as a compact unit, as its night distribution was bimodal in the 60–800 m water column. In this study, *Sergestes arcticus* appears as a moderate migrant, occupying by day the lower mesopelagic zone between 100 m and 400 m (Fig. 11c). At night, all the sized population was concentrated in the upper layer. *S. arcticus* has previously been reported as a strong migrant by Casanova (1977) and Castelbon (1987). Karuppasamy et al. (2006) reported that pelagic shrimps (like *Gennadas* and *Sergestes*) formed 47% of the micronekton biomass of the DSL in eastern Arabian Sea and that catches were higher during night at 50–200 m depth than day.

*Cyclothona braueri* is the most dominant mesopelagic fish in the Mediterranean Sea (Andersen and Sardou, 1992; Cuttitta et al., 2004). The present results are in agreement with the preferential depths reported for this species in the Mediterranean sea by different previous authors (Andersen and Sardou, 1992; Gasser et al., 1998; Yoon et al., 2007; Bernal et al., 2015). Total abundance in the entire sampled water column agree with data reported by Andersen et al. (2001a). In the study of Olivar et al. (2012) the 400 m DSL appeared as a costant echotrace in which the most abundant and frequent fish was *C. braueri*, during both day and night. Most of the population was always located at the top of the LIW layer (200–400 m), where the temperature ranged between 13.2° and 13.4 °C. No animals were found between 100 and

200 m the region of warmer water (13.8–14 °C), suggesting that the fish passed through the coldest layer to feed and remain within the LIW layer. In summary, *C. braueri* did not migrated and remained in the depth of 300–600 m regardless of the day-time (Fig. 11d), though weak variations in the vertical distribution was noted by Yoon et al. (2007) and confirmed by our results. Olivar et al. (2017) found that none of the seven abundant species of Gonostomatidae of the genus *Cyclothona* displayed vertical migrations into the surface layers, and they were very abundant in the Oxygen Minimum Zone (OMZ). This last statement is in agreement with our data that *Cyclothona* lives and moves within the LIW in less oxygenated waters (3.73–3.36 mL/l O<sub>2</sub>). The WMD varied slightly with season and seems to be related with the water stratification and distribution of their preys (Cartes et al. 2010). As reported by Yoon et al. (2007), this concept reinforces our interpretation that the pattern of vertical distribution of *C. braueri* might move seasonally with that of their prey.

#### 4.2. Species relationship between temperature and DCM

In the Ligurian Sea cool and less saline water lenses can be found at intermediate depths (250–450 m depth) (Gasparini et al., 1999) as a result of cooling and mixing of the surface MAW in winter weather conditions that lead to the formation of Winter Intermediate Water (WIW). Often found in the form of coherent and isolated structures they represent an intrusion of water of surface origin into the background Ligurian water and reach the buoyancy equilibrium between the MAW and the LIW layers. The presence of such a WIW lens could explain the shape of the vertical profiles of T-S in the layer 250–500 m (see Fig. 2). Furthermore, in the area between the coast and the main westward stream of the Ligurian-Provençal Current, the common formation of intense anticyclonic eddies due to wind-stress forcing has been observed by Casella et al. (2011). As discussed in their work, these vortices are trapped between the Ligurian-Provençal Current and the coastline and have a relatively long lifetime and often remain rather still. They induce strong upwelling at their coastal side and downwelling at the open-sea side, with downward vertical velocities in the order of few tens of meters per day at a depth of 200–250 m that could further constrain or hamper vertical displacements of zooplankters.

From db-RDA analysis a close correlation between some species and environmental parameters was highlighted. In particular, two euphausiid species, large and small *E. krohni* and large *M. norvegica*, seem to be correlated with temperature and chlorophyll in the 0–60 m layer. Below this layer, salinity and oxygen variables appear to influence the distribution of some species, such as the euphausiids *S. longicornis* and small *N. megalops* and the siphonophore *C. appendiculata*. In this study carried out in the open waters of the Ligurian Sea in the first days (3–4) of May, vertical temperature gradient was < 3 °C during the daylight and < 2 °C during the darkness. These values are slightly higher than those reported by Andersen et al. (1998) in mid-April with a not well-developed thermocline. Our data on diurnal change of both temperature and fluorescence in the upper layer agree with Andersen and Prieur's (2000) short-time scale observations between 4 and 8 May. We believe that the moderate thermocline found in this study it could begin to be an important parameter in the vertical distribution of many species. Animals of all species were much more concentrated around a particular temperature or narrow temperature range and a relevant number of species were observed at similar depths. Most species were found in the cold water layer, showing a much wider distribution in deep water. Werner et al. (2012) showed that *N. megalops* is adapted to low water temperatures (5–10 °C). Southward and Barrett (1983) found that of 21 invertebrate taxa 48% moved across the thermocline of 2 °C, 33% did not move, and some species migrated through a temperature difference of 6 °C. Most migrator in this study passed through a small change in temperature and salinity, usually < 3 °C and < 1‰. Only four species occupy by day the deepest layer of Deep Mediterranean Water (DMW) between 650 and 900 m, of which two amphipods *V.*

*armata* and *S. crassicornis* migrating at night in the cold intermediate layer between 80 and 200 m, respectively, through a temperature difference of about 0.5°–0.8 °C. The decapod *G. elegans* and the mesopelagic fish *C. pygmaea* live deeper at 800–900 m, migrating the first to the LIW and the latter remaining in the DMW layer, both through a temperature difference of about 0.05 °C. Most species (15) live by day in the LIW layer between 250 and 500 m, from which they move for their vertical migrations. This community is represented in this study by six species of euphausiids, two of amphipods, two of pteropods, and one species of fish, one of decapod, one of pyrosomid, one of jellyfish and one of siphonophore. By night, two species (*S. arcticus* and *P. atlanticum*) reach the surface layer, six species (*P. sedentaria*, *S. albescens*, *C. inflexa*, *E. brevis*, *E. krohni* and large *M. norvegica*) the 30–50 m layer, five species (*P. semilunata*, *C. pyramidata*, *T. aequalis*, *E. hemigibba* and *C. appendiculata*) between 50 and 150 m and two species (*N. megalops* and *C. braueri*) between 200 and 300 m, crossing a temperature difference of about 3 °C, 1 °C, 0.6 °C and 0.02 °C, respectively. Four species (*P. atlanticum*, *S. fusiformis*, *L. inflata*, *S. longicorne* and small *M. norvegica*) live by day in the intermediate layer between 100 and 200 m, carrying out nocturnal migrations up to about 30–50 m, with the exception of *S. longicorne* which remains almost in the same layer up to 150 m. Only *M. norvegica* crosses a temperature difference of about 1.2 °C, while the other species overcome a gradient less than 0.04 °C. Some taxa such as copepods, decapod larvae or fish larvae were always found within or above the thermocline. Other groups, such as polychaetes, appendicularians, hydromedusae and small chaetognaths were also found in the thermocline at night; however, during the day a major portion of the adult chaetognaths community were found below the thermocline. About three filter-feeder (*P. atlanticum*, *S. fusiformis*, *L. inflata*), two omnivorous (*E. krohni*, *M. norvegica*) and three carnivorous species (*S. albescens*, *C. appendiculata*, *S. arcticus*) tended to concentrate within or near the base of the thermocline, particularly at night. According to Sameoto et al. (1987), no adult euphausiids were found above the thermocline during the day and those that were caught were almost entirely juveniles less than 7 mm in length, calyptopis and furcilia stages. The largest concentration of adults during the day was in the lower mesopelagic zone at a depth of 200–400 m. Sameoto (1984) found that during the day, parts of small *M. norvegica* population were found above and below the thermocline, whereas at night no animals were found below the main concentration at the base of thermocline. As stated by Mauchline (1980) and Barange (1990) the upper limit of the vertical distribution of *N. megalops* is related to the position of the thermocline and Werner and Buchholz (2013) confirmed that this species avoided the thermocline during all seasons and stayed in the Oxygen Minimum Zone (OMZ) throughout the whole diel cycles.

The sampled stations showed very low chlorophyll values, although a main DCM1 was detected at 20 m and 50 m (about 0.36 and 0.31 mg m<sup>-3</sup>Chla). Our chlorophyll maximum is much lower than that reported by Andersen and Prieur (2000) at the beginning of May (4–7) in the layer 28–32 m (2.2–2.7 mg m<sup>-3</sup>). Our results agree with the sentence of Longhurst (1976) and Sameoto (1982, 1984) that the maximum zooplankton biomass concentration (> 80%) was found above the main chlorophyll layer. Our integrated zooplankton biomass in the 0–200 m layer was a little lower than that reported by Andersen and Prieur (2000) by WP2 net, whereas average biomass value (16.9 ± 7.8 mg m<sup>-3</sup>DW) was higher or similar to those reported in several previous studies in different seasons (Razouls and Kouwemberg, 1993; Champalbert, 1996; Raybaud et al. 2008; Licandro and Icardi 2009; Siokou-Frangou et al. 2010; Nowaczyk et al. 2011; Minutoli and Guglielmo 2009, 2012; Minutoli et al. 2014, 2017). In the frontal area of the Alboran Sea, Youssara and Gaudy (2001) reported that zooplankton biomass was correlated to chlorophyll abundance. The majority of species of all trophic categories was found below the depth of the main chlorophyll layer. Most herbivore and some macroplankton filter feeder species had the majority of their concentrated population above the depth of the main chlorophyll layer. Excluding the

*Stylocheiron* and *Nematoscelis* species that are carnivorous, all euphausiids collected in this study are considered to be omnivores (Mauchline and Fisher, 1969; Mauchline, 1980; Fanelli et al., 2011). In the nighttime, *M. norvegica*, *E. krohni*, *S. fusiformis* and *L. inflata* were concentrated in the main chlorophyll layer, large *P. atlanticum*, *S. albescens* and *C. inflexa* were concentrated above the layer, *E. krohni* at the bottom of the DCM, whereas *P. sedentaria*, *V. armata*, *S. abbreviatum*, *E. brevis* and *E. hemigibba* were found below the DCM layer. Roger (1975) stated that migrating species fed for a longer period of the day than non-migrating genera such as *Stylocheiron* sp., which tended to be day feeders, and that migrating species did not show a feeding rhythm, which was contrary to the observations of Ponomareva (1971). Pelmskiy and Arashkevich (1980) found that animals at 200 m during the day fed on zooplankton, but during the night they fed on phytoplankton near the surface. Sameoto (1980) found a similar feeding pattern with *Meganyctiphanes norvegica* in the Gulf of St. Lawrence. A majority of the species had shallower mean depths at night which suggested that the biological conditions may have influenced the depths at which the various species were located. The more detailed distributions of this study showed that different species tended to occupy different layers, influenced either by the thermocline depth or chlorophyll concentration.

As highlighted by Sardou and Andersen (1993), Sardou et al. (1996) and Andersen et al. (1998), some species (e.g. *V. armata*, *P. sedentaria*, *S. crassicornis*, *S. fusiformis*, *C. inflexa*, *G. elegans*) show a bimodal vertical distribution that could be attributed to different causes such able to influence and modify their vertical migration: (a) breeding period, as for *L. inflata* and *C. inflexa* (b) presence of a non-migrating portion of the population residing below the depth of perceivable light, as for *S. crassicornis* (c) persistence of the population in the surface layer for a long period of darkness and up to few hours before sunrise at periods of low moonlight intensity, as *S. albescens* (d) avoidance of an area of possible competition or predation pressure. As reported by Sameoto (1986), an other possible explanation may be that the higher concentrations of zooplankton and phytoplankton were found at this depth layers which meant that these animals could find enough food in the lower mesopelagic zone and did not need to migrate to the euphotic zone to find food. A rain of particulate organic matter may occur below the photic layer to reach the bottom unless deep-living dwellers or daily-migrating zooplankters take advantage of this facultative food resource (Guglielmo et al., 2011). It is suggested that during low chlorophyll later spring conditions, the composition of functional groups and diet, and VDM patterns changed to take advantage of sinking particles (phytoplankton and picoplankton) in deep layers (Guglielmo et al., 2011; Zagami et al., 2011).

There may also be a segment of the population of these species that does not migrate at all, or else some individuals may only migrate occasionally, but not every night. The largest concentration of animals was found at the same depth as the main concentration of copepods, indicating that the maximum prey concentration may be more important in determining their depth rather than the temperature, a subject dealt with in detail by Longhurst (1985). As stated by Sameoto (1986), it seems improbable that competition for food existed between species, given the limited degree of spacial overlap between the dominant species and the low number of euphausiids found even in the highest euphausiid concentrations. About 33.6% and 49.9% of the total day and night biomass per m<sup>2</sup> of mesozooplankton plus micronekton (excluding mesopelagic fish, pelagic decapods, mysids, and *Pyrosoma atlanticum*) found in the entire sampled water column (0–1300 m), was concentrated in the 0–200 m layer. At night, in the upper and lower mixed layers (0–60 m), the euphausiids wet biomass (adults plus furcilia) represents about 25–30% of the entire zooplankton biomass, which demonstrated that these animals were the dominant predators in these layers.

The lower values of chlorophyll concentrations found in the study, agree with the conclusion of DYNAPROC study (Andersen and Prieur,

2000) that in this area of the open Ligurian sea, the month of May corresponds to the transition period from a mesotrophic system to a rather oligotrophic one. In the DINAPROC study (Leg 1), no zooplankton sampling were performed during the first ten days of May and therefore no information on the mesozooplankton, macroplankton and micronekton specific composition and biomass were available (Andersen et al., 2001a, b). This study, placing itself temporally in a crucial point of DINAPROC study, could fill this lack of information and make a further contribution to better understand the dynamics of the pelagic ecosystem in the Ligurian Sea. As suggested by Andersen and Prieur (2000) the system tended to an oligotrophic state at the end of May (one month), with rapidly decreased of integrated Chl maximum and increase in regenerated production. Our low chlorophyll maximum values at the beginning of May (3–4) were about half of those found in DYNAPROC at the end of May (31), suggesting both that in 2013 the spring bloom could have started earlier in comparison to the findings of May 1995 and/or that mesozooplankton and macroplankton grazing pressure could have also played a significant role in the decrease of phytoplankton biomass, as hypothesized by Andersen and Prieur (2000). The northwestern basin is known to be subject to an intense bloom in spring, when the surface layer stabilizes (Morel and André, 1991). Bosc et al. (2004) reported that the spring bloom starts at the end of February in the Ligurian Sea and is maximum in early May. This maximum has also very variable intensity from year to year and is even virtually absent in some occasions (Bosc et al., 2004). Several studies reported that in this peculiar areas of the Ligurian Sea, the zooplankton bloom follows the peak of surface primary production recorded in February–March, with a delay of about 1 month, having higher values in April–May (Nival et al., 1975; Andersen et al., 2001a; Fanelli et al., 2009; Bozzano et al., 2014). In this study, zooplankton biomass (excluding mesopelagic fish, pelagic decapods, mysids, and *Pyrosoma atlanticum*) was slightly lower than that measured by Andersen et al. (2001a) around mid-May. This leads us to hypothesize an intense pressure of zooplankton grazing after phytoplankton post-bloom at the beginning of April (Jacques et al., 1973), which has led to a high zooplankton production, but not necessarily to an increase in biomass, as reported in the Kiorboe's revision (1993) and highlighted by Andersen and Prieur (2000). To the low phytoplankton biomass (Chla) detected in this study corresponds both a high biodiversity and a high zooplankton production in terms of copepod abundance (see Zagami et al., in this volume) in the upper 200 m layer, about seven times higher than that measured by Andersen et al. (2001a) by WP2.

Throughout the day cycle the zooplankton was well represented by filter feeders, omnivores and carnivores. Components of these three functional groups (such as copepods, appendicularians, euphausiids, calyptopis and furcilia stages, decapod larvae and fish larvae) invade and dominate the upper 60 m of the water column, both day and night. During the night, large quantities of migratory gelatinous filter-feeders and carnivores species, like siphonophores, hydromedusae, pyrosomids, chaetognaths, some amphipods, adult euphausiids and pteropods species occupy this layer. By day, the biomass is almost constant at about 17% of the overall wet biomass, whereas the values double at night. The high oxygen concentration is one of the main hydrological features of the deep Mediterranean Sea (Danovaro et al., 2010). In this study, more oxygenated waters, with values  $> 4 \text{ mL O}_2 \text{ L}^{-1}$ , occupy the MAW until about 110–140 m of water column, depending on the daily cycle. Almost 80% of the micronekton species found in this study live by day in the LIW (250–500 m) in less oxygenated waters  $< 4 \text{ mL O}_2 \text{ L}^{-1}$ , of which more than 50% are considered strong migratory that invade the most oxygenated superficial waters at night. Diversity index analysis of the zooplanktonic community (see Table 5) has highlighted that the max biodiversity and the highest number of species were found in deeper layers. The layer between 200 and 400 m contains by day the highest biomass of the mesopelagic layer (about 20%) which at night is reduced to about half. Our conclusions agree with Hargreaves's data (1985) that total micronektonic biomass was greatest at 400–500 m

during the day and greatest above 300 m and 600–900 m at night in the northeast Atlantic Ocean.

## 5. Conclusion

Most of the strong migrant species found with great abundances in our study were euphausiids, that are reported as the most important animals involved in the high carbon demand in many areas of the Mediterranean Sea (Minutoli and Guglielmo, 2009, 2012; Minutoli et al., 2014), and of other Oceans (Werner and Buchholz, 2013; Kwong, 2016). The seasonal differences in abiotic and/or biotic parameters influence the zooplankton carbon demand from the organic non-living rain that reaches the sea bottom, and therefore modulate its role in the carbon biological pump of the Mediterranean Sea (Minutoli et al., 2017). Pelagic-benthic coupling would be strengthened due to animals that suppressed their vertical daily rise to the shallow layer at nights but remained in the deep layers to feed on a rain of particulate organic matter and other non-migrant zooplankton. The changes in the observed day- and night-time distributions would be related to light distribution, and to food abundance and trophic state of the system, which were related to meteorological and physical constraints (e.g. Badcock and Merrett, 1976; Pearre, 2003; Olivar et al., 2012). Our results added further informations on the vertical distribution, biomass and day-night migration of mesozooplankton, macroplankton and micronekton in this peculiar area of the northwestern Mediterranean Sea, where the slope ecosystems with submarine canyons play an important role in the transfer of matter (Buscail et al., 1990; Puig et al., 2000; Olivar et al., 2012). According to Sardou et al. (1996) and Andersen et al. (1998, 2004), these observations underline the need for further detailed studies, with data taken concurrently on both physical and biological parameters, in order to differentiate better the effects of mesoscale physical processes and biological behaviours.

## Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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## Appendix A. Supplementary material

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.pocean.2020.102298>.

## References

- Andersen, V., Sardou, J., 1992. The diel migrations and vertical distributions of zooplankton and micronekton in the Northwestern Mediterranean Sea. 1. Euphausiids, mysids, decapods and fishes. *J. Plankton Res.* 14, 1129–1154.
- Andersen, V., Sardou, I., Nival, P., 1992. The diel migrations and vertical distributions of zooplankton and micronekton in the Northwestern Mediterranean Sea. 2. Siphonophores, hydromedusae and pyrosomids. *J. Plankton Res.* 14, 1155–1169.
- Andersen, V., Sardou, J., 1994. *Pyrosoma atlanticum* (Tunicata Thaliacea): diel migration

- and vertical distribution as a function of colony size. *J. Plankton Res.* 16, 337–349.
- Andersen, V., François, F., Sardou, J., Picheral, M., Scotto, M., Nival, P., 1998. Vertical distributions of macroplankton and micronekton in the Ligurian and Tyrrhenian Seas (northwestern Mediterranean). *Oceanol. Acta* 21, 655–676.
- Andersen, V., Prieur, L., 2000. One-month study in the open NW Mediterranean Sea (DYNAPROC experiment, May 1995): Overview of the hydrobiogeochemical structures and effects of wind events. *Deep-Sea Res. I* 47, 397–422.
- Andersen, V., Nival, P., Caparroy, P., Cubanova, A., 2001a. Zooplankton community during the transition from spring bloom to oligotrophy in the open NW Mediterranean and effects of wind events. 1. Abundance and specific composition. *J. Plankton Res.* 23, 227–242.
- Andersen, V., Cubanova, A., Nival, P., Ruellet, T., 2001b. 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.
- Andersen, V., Devey, C., Cubanova, A., Picheral, M., Melnikov, V., Tsarin, S., Prieur, L., 2004. Vertical distributions of zooplankton across the Almeria Oran frontal zone (Mediterranean Sea). *J. Plankton Res.* 26, 275–293.
- Anderson, M., Gorley, R.N., Clarke, R.K., 2008. *Permanova + for Primer: Guide to Software and Statistical Methods*. primer-E limited.
- Antezana, T., 2009. Species-specific patterns of diel migration into the Oxygen Minimum Zone by euphausiids in the Humboldt Current Ecosystem. *Prog. Oceanogr.* 83, 228–236.
- Astraldi, M., Gasparini, G.P., Manzella, G., Hopkins, T.S., 1990. Temporal variability of currents in the Eastern Ligurian Sea. *J. Geophys. Res.* 95, 1515–1522.
- Astraldi, M., Gasparini, G.P., 1992. The seasonal characteristics of the circulation in the north Mediterranean basin and their relationship with the atmospheric-climatic conditions. *J. Geophys. Res.* 97, 9531–9540.
- Astraldi, M., Gasparini, G.P., Sparnocchia, S., 1994. The seasonal and interannual variability in the Ligurian-Provençal Basin. In: La Violette, P.E. (Ed.), *Seasonal and interannual variability of the Western Mediterranean Sea. Coastal and estuarine studies*, 46. American Geophysical Union, Washington, D.C., pp. 93–113.
- Badcock, J., Merrett, N.R., 1976. Midwater fishes in the eastern North Atlantic. I. Vertical distribution and associated biology in 30°N, 23°W, with developmental notes on certain myctophids. *Prog. Oceanogr.* 7, 3–58.
- Barange, M., 1990. Vertical migration and habitat partitioning of six euphausiid species in the northern Benguela upwelling system. *J. Plankton Res.* 12, 1223–1237.
- Battaglia, P., Andaloro, F., Esposito, V., Granata, A., Guglielmo, L., Guglielmo, R., Musolino, S., Romeo, T., Zagami, G., 2016. Diet and trophic ecology of the lanternfish *Electrona rissso* (Cocco 1829) in the Strait of Messina (central Mediterranean Sea) and potential resource utilization from the Deep Scattering Layer (DSL). *J. Mar. Syst.* 159, 100–108.
- Benovic', A., 1973. Diurnal vertical migration of *Solmissus albescens* (Hydromedusae) in the southern Adriatic. *Mar. Biol.* 18, 298–301.
- Bernal, A., Olivari, M.P., Maynou, F., de Puelles, M.L.F., 2015. Diet and feeding strategies of mesopelagic fishes in the western Mediterranean. *Prog. Oceanogr.* 135, 1–17.
- Bosc, E., Bricaud, A., Antoine, D., 2004. Seasonal and interannual artibility in algal biomass and primary production in the Mediterranean Sea, as derived from 4 years of SeaWiFS observations. *Global Biogeochem. Cycles* 18 (GB1005), 1–17.
- Bouvier, E.L., 1922. *Observations complémentaires sur les Crustacés décapodes (abstraction faite des Carides) provenant des Campagnes de S.A.S. le Prince de Monaco. Rés. Camp. Sci. Monaco* 62, 1–106.
- Bozzano, R., Fanelli, E., Pensieri, S., Picco, P., Schiano, M.E., 2014. Temporal variations of zooplankton biomass in the Ligurian Sea inferred from long time series of ADCP data. *Ocean Sci.* 10, 93–105.
- Brinton, E., 1979. Parameters relating to the distribution of planktonic organisms especially euphausiids in the eastern tropical Pacific. *Prog. Oceanogr.* 8, 125–189.
- Brinton, E., Ohman, M.D., Townsend, A.W., Knight, M.D., Bridgeman, A.L., 2000. *Euphausiids of the World Ocean* (cd-room Expert System). Springer-Verlag, Heidelberg.
- Buchholz, F., Buchholz, C., Reppin, J., Fisher, J., 1995. Diel vertical migrations of *Meganyctiphanes norvegica* in the Kattegat: comparison of net catches and measurements with acoustic Doppler current profilers. *Helgolander Meeresun.* 49, 849–866.
- Buscail, R., Pocklington, R., Daumas, R., Guidi, L., 1990. Fluxes and budget of organic matter in the benthic boundary layer over the northwestern Mediterranean margin. *Cont. Shelf. Res.* 10, 1089–1122.
- Cartes, J.E., Hidalgo, M., Papiol, V., Massutí, E., Moranta, J., 2008. Changes in the diet and feeding of the hake *Merluccius merluccius* in the shelf-break of Balearic Islands (western Mediterranean): influence of the mesopelagic-boundary community. *Deep-Sea Res. I* 56, 344–365.
- Cartes, J.E., Fanelli, E., Papiol, V., Zucca, L., 2010. Distribution and diversity of open-ocean, near-bottom macroplankton in the western Mediterranean: analysis at different spatio-temporal scales. *Deep-Sea Res. I* 57, 1485–1498.
- Cartes, J.E., Fanelli, E., López-Pérez, C., Lebrero, M., 2013. Deep-sea macroplankton distribution (at 400 to 2300 m) in the northwestern Mediterranean in relation to environmental factors. *J. Mar. Syst.* 113–114, 75–87.
- Casanova-Soulier, B., 1968. Les euphausiacés de la Méditerranée. *Comm. Int. Explor. Mer Médit.* Monaco 1–62.
- Casanova, B., 1970. Répartition bathymétrique des euphausiacés dans le bassin occidental de la Méditerranée. *Revue Trav. Inst. Pêches Marit.* 34, 205–219.
- Casanova, B., 1974. Les euphausiacés de Méditerranée (Systématique et développement larvaire. Biogéographie et Biologie). In: *Thèse de Doctorat ès Sciences Naturelles*. Université Aix-Marseille I, pp. 1–380.
- Casanova, J. P., 1977. La faune pelagique profonde (zooplanton et micronekton) de la province Atlanto-Méditerranee; Aspects taxonomique, biologique at zoogeographique. Thesis, Université de Provence, pp. 1–455.
- Casanova, J.-P., 1980. Campagnes du Meteor dans l'Atlantique NE. *Siphonophores, Méduses et Thécosornes. Distribution verticale et comparaisons faunistiques avec la Méditerranée*. Meteor Forschergebn D 32, 15–32.
- Casella, E., Molcard, A., Provenzale, A., 2011. Mesoscale vortices in the Ligurian Sea and their effect on coastal upwelling processes. *J. Mar. Syst.* 88, 12–19.
- Castelbon, C., 1987. Les migrations nyctémérales du zooplancton. Déterminisme expérimental des réactions locomotrices. In: *Thèse de Doctorat ès Sciences*. Université Aix-Marseille II, pp. 1–380.
- Champalbert, G., 1996. Characteristics of zooplankton standing stock and communities in the Western Mediterranean Sea: relations to hydrology. *Sci. Mar.* 60, 97–113.
- Chevreux, Ed., Fage L., 1925. Faune de France. 9. Amphipodes. Paris, pp. 1–488.
- Christensen, V., Walters, C.J., Ahrens, R., Alder, J., Buszowski, J., Christensen, L.B., Cheung, W.W.L., Dunne, J., Froese, R., Karpouzi, V., Kaschner, K., Kearney, K., Lai, S., Lam, V., Palomares, M.L.D., Peters-Mason, A., Piroddi, C., Sarmiento, J.L., Steenbeek, J., Sumaila, R., Watson, R., Zeller, D., Pauly, D., 2009. Database-driven models of the world's Large Marine Ecosystems. *Ecol. Model.* 220, 1984–1996.
- Clarke, K.R., Warwick, R.M., 1995. Changes in marine communities: an approach to statistical analysis and interpretation. Natural Environment Research Council, U.K., pp. 1–144.
- Clavel-Henry, M., 2015. Estimates of mesopelagic fish biomass according to environmental data in the Mediterranean Sea. Thesis, Université Agrocampus Ouest, Rennes, pp. 1–40.
- Cuttitta, A., Arigò, A., Basilone, G., Bonanno, A., Buscaino, G., Rollandi, L., Lafuente, J.G., Garcia, A., Mazzola, S., Patti, B., 2004. Mesopelagic fish larvae species in the Strait of Sicily and their relationships to main oceanographic events. *Hydrobiologia* 527, 177–182.
- Danovaro, R., Company, J.B., Corinaldesi, C., et al., 2010. Deep-sea biodiversity in the Mediterranean Sea: the known, the unknown and the unknowable. *Plos ONE* 5, 1–25.
- Estrada, M., 1996. Primary production in the northwestern Mediterranean. *Sci. Mar.* 60 (Suppl. 2), 55–64.
- Fanelli, E., Cartes, J., Rumolo, E., Sprovieri, M., 2009. Food-web structure and trophodynamics of mesopelagic-suprabenthic bathyal macrofauna of the Algerian Basin based on stable isotopes of carbon and nitrogen. *Deep-Sea Res. I* 56, 1504–1520.
- Fanelli, E., Cartes, J.E., Papiol, V., 2011. Trophodynamics of zooplankton fauna on the Catalan slope (NW Mediterranean): insight from  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  analysis. *J. Mar. Syst.* 87, 79–89.
- Fernandez de Puelles, M. L., Morillas, A., Alou Font, L., Vicente, L., 2007. The spatial zooplankton distribution in the North Balearic front (Western Mediterranean): early spring, 2005. In: 38th CIESM Cong. Proc. 38, pp. 1–473.
- Forcada, J., Aguilar, A., Hammond, P., Pastor, X., Aguilar, R., 1996. Distribution and abundance of fin whales (*Balaenoptera physalus*) in the western Mediterranean sea during the summer. *J. Zool.* 238, 23–34.
- Franqueville, C., 1970. Etude comparative du macroplancton en Méditerranée nord-occidentale par plongées en soucoupe SP 350, et pêches au chalut pélagique. *Mar. Biol.* 5, 172–179.
- Franqueville, C., 1971. Macroplancton profond (invertébrés) de la Méditerranée nord-occidentale. *Tethys* 3, 11–56.
- Gasca, R., 2009. Diversity of Hyperiid Amphipods (Crustacea: Peracarida) in the Western Caribbean Sea: news from the deep. *Zool. Stud.* 48, 63–70.
- Gasparini, G.P., Zodiatis, G., Astraldi, M., Galli, C., Sparnocchia, S., 1999. Winter intermediate water lenses in the Ligurian Sea. *J. Mar. Syst.* 20, 319–332.
- Gasser, B., Payet, G., Sardou, J., Nival, P., 1998. Community structure of mesopelagic copepods (> 500 um) in the Ligurian Sea (Western Mediterranean). *J. Mar. Syst.* 15, 511–522.
- Genovese, S., Guglielmo, L., Ianora, A., Scotto Di Carlo, B., 1985. Osservazioni biologiche con il mesoscafo "Forel" nello Stretto di Messina. *Archo Oceanogr. Limnol.* 20, 1–30.
- Gorsky, G., Lins da Silva, N., Dallot, S., Laval, P., Braconnat, J.C., Prieur, L., 1991. Midwater tunicates: are they related to the permanent front of the Ligurian Sea (NW Mediterranean)? *MEPS* 74, 195–204.
- Gorsky, G., Prieur, L., Taupier-Letage, I., Stemmann, L., Picheral, M., 2002. Large particulate matter in the Western Mediterranean I. LPM distribution related to mesoscale hydrodynamics. *J. Mar. Syst.* 33, 289–311.
- Goy, J., Dallot, S., Ménard, P., 1989. Les proliférations de la méduse *Pelagia noctiluca* et les modifications associées de la composition du macroplancton gélatineux. *Oceanis* 15, 17–23.
- Guglielmo, L., Minutoli, R., Bergamasco, A., Granata, A., Zagami, G., Antezana, T., 2011. Short-term changes in zooplankton community in Paso Ancho basin (Strait of Magellan): functional trophic structure and diel vertical migration. *Pol. Biol.* 34, 1301–1317.
- Hansen, J.H., 1922. Crustacés décapodes (Sergestidae) provenant des Campagnes des yachts Hirondelle et Princesse-Alice (1885–1915). *Rés. Camp. Sci. Monaco* 64, 1–232.
- Hargreaves, P.M., 1985. The vertical distribution of Decapoda, Euphausiaceae, and Mysidae at 42°N, 17°W. *Biol. Oceanogr.* 3, 431–464.
- Jacques, G., Minas, H.J., Minas, M., Nival, P., 1973. Influence des conditions hivernales sur les productions phyto- et zooplanctoniques en Méditerranée Nord-occidentale. II Biomasse et production phytoplanctonique. *Mar. Biol.* 23, 251–265.
- Jespersen, P., 1923. On the quantity of macroplankton in the Mediterranean and the Atlantic. *Rep. Dan. Oceanogr. Exped. Mediterr.* 3, 1–17.
- Jukic, S., 1978. Contribution of the knowledge of the relationship between formation of Deep Scattering Layer (DSL) and biological components in the Central Adriatic. *Acta Adriat.* 19, 1–15.
- Kaartvedt, S., 2010. Diel Vertical Migration Behaviour of the Northern Krill (*Meganyctiphanes norvegica* Sars). *Adv. Mar. Biol.* 57, 255–275.
- Karuppasamy, P.K., Menon, N.G., Nair, K.K.C., Achuthankutty, C.T., 2006. Distribution and abundance of pelagic shrimps from the deep scattering layer of the eastern

- Arabian Sea. J. Shellfish Res. 25, 1013–1019.
- Kiorboe, T., 1993. Turbulence, phytoplankton cell size, and the structure of pelagic food webs. Adv. Mar. Biol. 29, 1–72.
- Kloser, R.J., Ryan, T.E., Young, J.W., Lewis, M.E., 2009. Acoustic observations of microneuston fish on the scale of an ocean basin: potential and challenges. ICES J. Mar. Sci. 66, 998–1006.
- Kovalev, A.V., Mazzocchi, G., Kideyes, A.E., Toklu, B., Skryabin, V.A., 2003. Seasonal Changes in the Composition and abundance of zooplankton in the Seas of the Mediterranean Basin. Turk J. Zool. 27, 205–219.
- Kwong, L.E., 2016. A novel approach to estimating active carbon flux using the biomass spectra theory. MSc Thesis. Univ. Of B.C., Vancouver, B.C., pp. 1–105.
- Laval, P., Braconnor, J.-C., Carré, C., Goy, J., Morand, P., Mills, C.E., 1989. Small-scale distribution of macroplankton and microneuston in the Ligurian Sea (Mediterranean Sea) as observed from the manned submersible Cyana. J. Plankton Res. 11, 665–685.
- Laval, P., Braconnor, J.-C., Lins da Silva, N., 1992. Deep planktonic filter-feeders found in the aphotic zone with the Cyana submersible in the Ligurian Sea (NW Mediterranean). MEPS 79, 235–241.
- Licandro, P., Ibanez, F., 2000. Changes of zooplankton communities in the Gulf of Tigullio (Ligurian Sea, Western Mediterranean) from 1985 to 1995. Influence of hydroclimatic factors. J. Plankton Res. 22, 2225–2235.
- Licandro, P., Icardi, P., 2009. Basic scale distribution of zooplankton in the Ligurian Sea (north-western Mediterranean) in late autumn. Hydrobiologia 617, 17–40.
- Longhurst, A.R., 1976. Vertical migration. In: Cushing, D.H., Walsh, J.J. (Eds.), The ecology of the seas. Blackwell Scientific, Oxford, pp. 116–137.
- Longhurst, A.R., 1985. Plankton diversity and vertical structure of the upper ocean. Deep-Sea Res. 32, 1535–1570.
- Lopez Garcia, M.J., Millot, C., Font, J., Garcia Ledona, E., 1994. Surface circulation variability in the Balearic Basin. J. Geophys. Res. 9, 3285–3296.
- Lovegrove, T., 1966. The determination of the dry weight of plankton and the effect of various factors on the values obtained. In: Barnes, H. (Ed.), Some contemporary studies in Marine Sciences, London, pp. 429–467.
- Macquart-Moulin, C., Leveau M., 1968. Note préliminaire sur le macroplancton récolté en juin 1966 à partir de la bouée laboratoire. Com. Int. Explor. Mer Médit., Comité du Plancton, Bucarest 1966. Rapp. et P.V. 19, pp. 495–497.
- Macquart-Moulin, C., 1993. Répartition verticale, migrations et stratifications superficielles des Mysidacés et Amphipodes pélagiques sur les marges méditerranéenne et atlantique francaises. J. Plankton. Res. 15, 1149–1170.
- Macquart-Moulin, C., Patriiti, G., 1996. Accumulation of migratory microneuston crustaceans over the upper slope and submarine canyons of the northwestern Mediterranean. Deep. Sea Res. 43, 579–601.
- Margalef, R., 1985. Western Mediterranean. In: Key Environments. Pergamon Press, Oxford, pp. 1–363.
- Marshall, N.B., 1960. Swimbiladder structure of deep-sea fishes in relation to their systematics and biology. Discov. Rep. 31, 1–122.
- Mauchline, J., Fisher, L.R., 1969. The biology of euphausiids. Adv. Mar. Biol. 7, 1–454.
- Mauchline, J., 1980. The biology of mysids and euphausiids. Adv. Mar. Biol. 18, 1–681.
- Millot, C., 1999. Circulation in the Western Mediterranean Sea. J. Mar. Syst. 20, 423–442.
- Minutoli, R., Guglielmo, L., 2009. Zooplankton respiratory electron transport system activity (ETS) in the Mediterranean Sea: spatial and diel variability. MEPS 381, 199–211.
- Minutoli, R., Guglielmo, L., 2012. Mesozooplankton carbon requirement in the Tyrrhenian Sea: its vertical distribution, diel variability and its relation to particle flux. MEPS 446, 91–105.
- Minutoli, R., Granata, A., Brugnano, C., Zagami, G., Guglielmo, L., 2014. Mesozooplankton carbon requirement in the southern Adriatic Sea: vertical distribution, diel and seasonal variability, relation to particle flux. MEPS 495, 91–104.
- Minutoli, R., Zagami, G., Brugnano, C., Guglielmo, L., Pansera, M., Granata, A., 2017. Spring and autumn spatial distribution of zooplankton carbon requirement across the Mediterranean Sea. Chem. Ecol. 33, 352–373.
- Molinero, J.C., Ibanez, F., Souissi, S., Bosc, E., Nival, P., 2008. Surface patterns of zooplankton spatial variability detected by high frequency sampling in the NW Mediterranean. Role of density fronts. J. Mar. Syst. 69, 271–282.
- Morel, A., Andrè, J.M., 1991. Pigment distribution and primary production in the western Mediterranean as derived and modeled from Coastal Zone Color Scanner observations. J. Geophys. Res. 96, 12685–12698.
- Motoda, S., 1959. Devices of simple plankton apparatus. Mem. Fac. Fish Hokkaido Univ. 7, 73–94.
- Nishikawa, J., Nishida, S., Moku, M., Hidak, a.K., Kawaguchi, K., 2001. Biomass, Abundance, and Vertical Distribution of Microneuston and Large Gelatinous Zooplankton in the Subarctic Pacific and the Bering Sea during the Summer of 1997. J. Oceanogr. 57, 361–375.
- Nival, P., Nival, S., Thiriot, A., 1975. Influence des conditions hivernales sur les productions phyto- et zooplanctoniques n Méditerranée Nord-Occidentale. V. Biomasse et production zooplanctonique-relations phyto-zooplankton. Mar. Biol. 31, 249–270.
- Novaczky, A., Carlotti, D., Thibault-Botha, D., Pagano, M., 2011. Distribution of epipelagic metazooplankton across the Mediterranean Sea during the summer BOUM cruise. Biogeosciences 8, 2159–2177.
- Olivar, M.P., Bernal, A., Molí, B., Peña, M., Balbín, R., Castellón, A., Miquel, J., Massutí, E., 2012. Vertical distribution, diversity and assemblages of mesopelagic fishes in the western Mediterranean. Deep-Sea Res. Part I: Oceanogr. Res. Papers 62, 53–69.
- Olivar, M.P., Abelló, P., Quetglas, A., Castellón, A., Bernal, A., Molí, B., Sabatés, A., Iglesias, M., Simao, D., Massutí, E., 2013. Microneuston groups contributing to the night scattering layers in the western Mediterranean. Rapp. Comm. int. Mer Médit. 40, 728.
- Olivar, M.P., Hulley P.A., Castellón, A., Emelianov, M., López, C., Tuset, V.M., Contreras, T., Molí, B., 2017. Mesopelagic fishes across the tropical and equatorial Atlantic: Biogeographical and vertical patterns. Prog. Oceanogr. 151, pp. 116–137.
- Panigada, S., Zanardelli, M., Canese, S., Jahoda, M., 1999. How deep can baleen whales dive? MEPS 187, 309–311.
- Pearre Jr., S., 2003. Eat and run? The hunger/satiation hypothesis in vertical migration : history, evidence and consequences. Biol. Rev. 78, 1–79.
- Pelmskiy, A.G., Arashkevich, Ye.G., 1980. Quantitative characteristics of the feeding of euphausiids in the tropical part of the Pacific Ocean. Oceanology 20, 199–203.
- Peña, M., Olivari, M.P., Balbín, R., López-Jurado, J.L., Iglesias, M., Miquel, J., 2014. Acoustic detection of mesopelagic fishes in scattering layers of the Balearic Sea (western Mediterranean). Can. J. Fish. Aquat. Sci. 71, 1186–1197.
- Ponomareva, P.A., 1971. Circadian migrations and feeding rhythm of some Indian Ocean euphausiid species. Oceanologia 11, 226–231.
- Puig, P., Palanques, A., Guillen, J., García-Ladona, E., 2000. Deep slope currents and suspended particle fluxes in and around the Foix submarine canyon (NW Mediterranean). Deep-Sea Res. I 47, 343–366.
- Rampal, J., 1967. Répartition quantitative et bathymétrique des ptéropodes thécosomes récoltés en Méditerranée Occidentale au nord du 40<sup>o</sup> parallèle. Remarques morphologiques sur certaines espèces. Rev. Trav. Inst. Pêches Marit. 31, 405–416.
- Rampal, J., 1975. Les Thécosomes (Mollusques pélagiques), Systématique et évolution - Ecologie et biogéographie méditerranéennes. Thèse de Doctorat Etat, Université Aix-Marseille I, pp. 1–485.
- Razouls, C., Kouwemberg, H.M., 1993. Spatial distribution and seasonal variation of mesozooplankton biomass in the gulf of Lions (northwestern Mediterranean). Oceanol. Acta 16, 393–401.
- Raybaud, V., Nival, P., Mousseau, L., Gubanova, A., Altukhov, D., 2008. Short term changes in zooplankton community during the summer-autumn transition in the open northwestern Mediterranean Sea: species composition, abundance and diversity. Biogeosciences 5, 1765–1782.
- Reid, S.B., Hirota, J., Young, R.E., Hallacher, L.E., 1991. Mesopelagic-boundary community in Hawaii: microneuston at the interface between neritic and oceanic ecosystems. Mar. Biol. 109, 427–440.
- Roger, C., 1975. Rythmes nutritionnels et organisation trophique d'une population de crustacés pélagiques (Euphausiacea). Mar. Biol. 32, 365–378.
- Ruud, J.T., 1936. Euphausiacea. Rep. Dan. Oceanogr. Exped. 2 (D.6), 1–86.
- Sameoto, D.D., 1980. Relationships between stomach contents and vertical migration in *Meganyctiphanes norvegica*, *Thysanoessa raschii* and *T. inermis* (Crustacea, Euphausiacea). J. Plankton Res. 2, 129–143.
- Sameoto, D.D., Saroszynsky, L.O., Fraser, W.B., 1980. BIONESS, a new design in multiple net zooplankton sampler. J. Fish Res. Board Can. 3, 722–724.
- Sameoto, D.D., 1982. Zooplankton and microneuston abundance in acoustic scattering layer on the Nova Scotian slope. Can. J. Fish. Aquat. Sci. 39, 760–777.
- Sameoto, D.D., 1984. Environmental factors influencing diurnal distribution of zooplankton and ichthyoplankton. J. Plankton Res. 6, 767–792.
- Sameoto, D.D., 1986. Influence of the biological and physical environment on the vertical distribution of mesozooplankton and microneuston in the eastern tropical Pacific. Mar. Biol. 93, 263–279.
- Sameoto, D., Guglielmo, L., Lewis, M.K., 1987. Day/night vertical distribution of euphausiids in the Eastern Tropical Pacific. Mar. Biol. 96, 235–245.
- Sardou, J., Andersen, V., 1993. Microneuston and macroplankton en mer Ligure (Méditerranée): migrations nyctémérales et distributions verticales. Oceanol. Acta 16, 381–392.
- Sardou, J., Etienne, M., Andersen, V., 1996. Seasonal abundance and vertical distributions of macroplankton and microneuston in the Northwestern Mediterranean Sea. Oceanol. Acta 19, 645–656.
- Senzt-Braconnor, E., 1968. Répartition des Ptéropodes *Spiratella inflata* (d'Orbigny) et *S. trochiformis* (d'Orbigny) dans la rade de Villefranche-sur-Mer. Comm. int. Explor. Sci. Mer Médit. Rapp. et P.V. 19, 463–467.
- Shulenberger, E., 1978. Vertical distributions, diurnal migrations, and sampling problems of hyperiid amphipods in the North Pacific central gyre. Deep-Sea Res. 25, 605–623.
- Siokron-Frangou, I., Christaki, U., Mazzocchi, M.G., Montresor, M., Ribera d'Alcalà, M., Vaqué, D., Zingone, A., 2010. Plankton in the open Mediterranean Sea: a review. Biogeosciences 7, 1543–1586.
- Southward, A.J., Barrett, R.L., 1983. Observations on the vertical distribution of zooplankton, including post-larval teleosts, off Plymouth in the presence of a thermocline and a chlorophyll-dense layer. J. Plankton Res. 5, 599–617.
- Stemann, L., Prieur, L., Legendre, L., Taupier-Letage, I., Picheral, M., Guidi, L., Gorsky, G., 2008. Effects of frontal processes on marine aggregate dynamics and fluxes: an interannual study in a permanent geostrophic front (NW Mediterranean). J. Mar. Syst. 70, 1–20.
- Taki, K., 2008. Vertical distribution and diel migration of euphausiids from Oyashio Current to Kuroshio area off northeastern Japan. Plankton Benthos Res. 3, 27–35.
- Thurston, M.H., 1976. The vertical distribution and diurnal migration of the Crustacea Amphipoda collected during the SOND cruise, 1965. 11. The Hyperiidea and general discussion. J. Mar. Biol. Ass. U.K. 56, 383–470.
- Timonin, A.G., 1997. Diel vertical migrations of Calanoides carinatus and Metridia lucens (Copepoda: Calanoida) in the Northern Benguela Upwelling Area. Oceanology 37, 782–787.
- Tsuda, A., Nemoto, T., 1992. Distribution and growth of salps in Kuroshio warm-core ring during summer 1987. Deep-Sea Res. 39 (Suppl. 1), 219–229.
- van der Spoel, S., 1973. Growth, reproduction and vertical migration in *Clio pyramidata* Linné, 1767 forma lanceolata (Lesueur, 1813) with notes on some other Cavoliniidae (Mollusca, Pteropoda). Beaufortia 281, 117–134.
- Vignudelli, S., Cipollini, P., Astraldi, M., Gasparini, G.P., Manzella, G., 2000. Integrated use of altimeter and in situ data for understanding the water exchanges between the Tyrrhenian and Ligurian Seas. J. Geophys. Res. 105, 19649–19663.
- Vinogradov, M.E., Volkov, A.F., Semenova, T.N., 1996. Hyperiid Amphipods

- (Amphipoda, Hyperiidea) of the world Oceans. Douglas Siegel-Causey (ed), Science publishers, Lebanon, pp. 1–632.
- Werner, T., Huenelrage, K., Verheyen, H., et al., 2012. Thermal constraints on the respiration and excretion rates of krill, *Euphausia hansemi* and *Nematocarcinus megalops*, in the northern Benguela upwelling system off Namibia. *Afr. J. Mar. Sci.* 34, 391–399.
- Werner, T., Buchholz, F., 2013. Diel vertical migration behaviour in euphausiids of the northern Benguela current: seasonal adaptations to food availability and strong gradients of temperature and oxygen. *J. Plankton Res.* 35, 792–812.
- Wiebe, P.H., d'Abromo, L., 1972. Distribution of euphausiid assemblages in the Mediterranean Sea. *Mar. Biol.* 15, 139–149.
- Yoon, W.D., Nival, P., Choe, S.M., Picheral, M., Gorsky, G., 2007. Vertical distribution and nutritional behaviour of *Cyclothona braueri*, *Nematocarcinus megalops*, *Meganyctiphanes norvegica* and *Salpa fusiformis* in the NW Mediterranean mesopelagic zone. ICES Council Meeting Documents. F3, pp. 1–28.
- Young, J.W., Hunt, B.P.V., Cook, T.R., Llopiz, J.K., Hazen, E.L., Pethybridge, H.R., Ceccarelli, D., Lorrain, A., Olson, R.J., Allain, V., Menkes, C., Patterson, T., Nicol, S., Lehodey, P., Kloster, R.J., Arrizabalaga, H., Anela Choy, C., 2015. The trophodynamics of marine top predators: current knowledge, recent advances and challenges. *Deep-Sea Res. II* 113, 170–187.
- Youssara, F., Gaudy, R., 2001. Variations of zooplankton in the frontal area of the Alboran sea (Mediterranean sea) in winter 1997. *Oceanol. Acta* 24, 361–376.
- Zagami, G., Antezana, T., Ferrari, I., Granata, A., Sitran, R., Minutoli, R., Guglielmo, L., 2011. Species diversity, spatial distribution, and assemblages of zooplankton within the Strait of Magellan in austral summer. *Pol. Biol.* 34, 1319–1333.