Vol. 495: 91–104, 2014
doi: 10.3354/meps10562

MARINE ECOLOGY PROGRESS SERIES
Mar Ecol Prog Ser

Published January 9

Mesozooplankton carbon requirement in the southern Adriatic Sea: vertical distribution, diel and seasonal variability, relation to particle flux

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ABSTRACT: Mesozooplankton plays a role in particulate organic carbon (POC) remineralisation from the pelagic sinking POC flux down the water column. The vertical distribution (to 1000 m depth), diel variability (during a 24 h cycle) and seasonal differences of the mesozooplankton carbon requirement (µg C g^{-1} d^{-1}), estimated by measuring the activity of the electron transport system, were investigated at a fixed station in the southern Adriatic Sea during November 2006 and April 2007. To estimate the quantitative role of zooplankton in the carbon loss that occurs during organic particle sinking, the zooplankton carbon requirement was compared with organic carbon vertical fluxes measured using a sediment trap. Zooplankton abundance, biomass and community composition were investigated along with the diel vertical distribution of euphausiid migrating groups and the relative importance of crustaceans and gelatinous taxa to the potential community carbon requirement. Day/night zooplankton carbon requirement differences in the upper 100 m were shown in both sampling periods. They were not at all correlated to the vertical distribution pattern of euphausiids but were attributable to the amount of non-living specimens and/or the ratio between gelatinous and crustacean taxa. The mean metabolic requirement in the sampled layers of the water column was lower in November than in April, ranging from 0.02 to 9.10% and from 0.07 to 31.86%, respectively, of the measured carbon losses. In the epi- and mesopelagic zones, the total percent contributions of mesozooplankton respiration to organic carbon losses were 0.18 and 18.45%, respectively, in November and 1.41 and 87.27%, respectively, in April. The higher remineralisation percentages detected in April compared to November could be linked to seasonal differences that involve higher primary production, zooplankton biomass, vertical amount of sinking POC flux and more intense heterotrophic metabolism, which take place mainly in the mesopelagic layer in each period.

KEY WORDS: Mesozooplankton · Euphausiids · Carbon requirement · ETS · Sinking POC flux · Adriatic Sea

INTRODUCTION

The oceans play a key role in mitigating atmospheric carbon dioxide (CO_2) increases by absorbing and storing 30 to 50% of man-made CO_2, produced by the burning of fossil fuel. If the oceans did not sequester any CO_2, atmospheric levels would be much higher than the current level (IUCC 1993). Upon dissolution in water, CO_2 forms a weak acid that reacts with carbonate anions and water to form bicarbonate (Falkowski et al. 2000). The capacity of the oceanic carbonate system to buffer changes in

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CO_2 concentration is finite and depends on the addition of cations from the relatively slow weathering of rocks. Because the rate of anthropogenic CO_2 emissions is several orders of magnitude greater than the supply of mineral cations, the ability of the surface oceans to absorb anthropogenic CO_2 will inevitably decrease as the atmospheric concentration of the gas increases (Kleypas et al. 1999, Falkowski et al. 2000, Langdon et al. 2000). This is especially true over the time scale of millennia. Biological processes contribute to the absorption of atmospheric CO_2 into the ocean. Phytoplankton photosynthesis lowers the partial pressure of the gas in the upper ocean and thereby promotes the absorption of CO_2 from the atmosphere. Approximately 25% of the carbon fixed in the upper ocean sinks into the interior (Falkowski et al. 1998, Laws et al. 2000), where it is oxidised through heterotrophic respiration, raising the concentration of dissolved inorganic carbon. Particulate organic carbon (POC) transformed from inorganic carbon by biological activity in the epipelagic realm partly sinks to greater depths, where it can be stored for hundreds or even thousands of years. Approximately 90% of POC is remineralised as it sinks through the water column, and heterotrophic consumption results in a decreasing flux of this organic material with depth, mainly between 100 and 1000 m (Martin et al. 1987). The consumption of organic particles represents the 'carbon demand/requirement' of heterotrophs along the water column. This carbon consumption represents a 'carbon loss' for the ocean interior, leaving only an average of 10% exported POC to reach the sea bottom. The largest part (90%) is consumed, remineralised or, once transformed into new prokaryotic biomass (Azam et al. 1983), transported towards higher trophic levels (Berger et al. 1989, Koppelmann et al. 2000, Koppelmann & Frost 2008). In addition, the mesozooplankton actively pumps gases and nutrients from the ocean surface to the deep; in this way, it plays a key role in building the organic particles into new biomass (Koppelmann et al. 2000).

The mesozooplankton carbon requirement from the sinking carbon flux can be estimated by evaluating respiratory electron transport system (ETS) activity (Packard 1971, King & Packard 1975, Owens & King 1975, Båmstedt 1979, 1980, Bidigare et al. 1982), using a respiratory quotient to convert respiratory oxygen consumption rates to CO_2 production rates that represent the carbon demand for zooplankton respiration (Hirch et al. 2009). This respiration proxy is used in biological oceanography to assess plankton metabolism (Hernández-León & Gomez 1996, La Ferla et al. 2003). The ETS, nearly ubiquitous in mitochondrial membranes, can be used as an indicator of organic matter remineralisation, as it consists of a complex chain of cytochromes, flavoproteins and metabolic ions that transport electrons from catabolised foodstuffs to oxygen. The rate-limiting step of the system is the oxidation of the coenzyme Q-cytochrome B complex, and it can be measured by its reaction with the artificial electron acceptor 2-(p-iodophenyl)-3-(p-nitrophenyl)-5-phenyl tetrazolium chloride (INT) (Packard 1971). Many papers have shown good correlation between ETS activity and *in vivo* respiration, so that ETS activity can be used as a proxy of micro- and mesozooplankton respiration rates (Packard et al. 1974, Kenner & Ahmed 1975, Owens & King 1975, Devol & Packard 1978, Gómez et al. 1996, La Ferla et al. 1999, Packard & Christensen 2004, Packard & Gómez 2008, 2013, Martínez et al. 2010, Maldonado et al. 2012).

To provide new insights into the quantitative role of mesozooplankton in the carbon loss during POC sinking in open waters, we investigated the vertical distribution (to 1000 m depth) and the diel (during a 24 h cycle) and seasonal variability of the mesozooplankton carbon requirement (µg C g wet mass^{-1} d^{-1}), calculated from ETS activity measurements, at a fixed station in the southern Adriatic Sea. The carbon requirement was then compared to vertical carbon fluxes, measured using a sediment trap (Steinberg et al. 1998, 2000, Boyd & Newton 1999, Buesseler et al. 2007). In addition, mesozooplankton abundance, community composition and biomass were investigated along with the vertical distribution pattern and relative importance of crustaceans and gelatinous taxa and focusing on vertically migrating groups of euphausiids.

MATERIALS AND METHODS

Mesozooplankton sampling

Mesozooplankton was collected at the AM1 fixed station (17° 45' E, 41° 50' N; 1150 m depth) in the southern Adriatic Sea (Fig. 1) during the VECTOR-AM1 (14–21 November 2006) and VECTOR-AM3 (10–17 April 2007) oceanographic cruises on board the RV 'Universitatis'. These cruises were developed as part of a large, national interdisciplinary project, the **V**uln**E**rability of the Italian coast area and marine ecosystems to **C**limatic changes and **T**heir r**O**le in the Mediterranean ca**R**bon cycles (VECTOR), which involved many scientific operative units in Italy

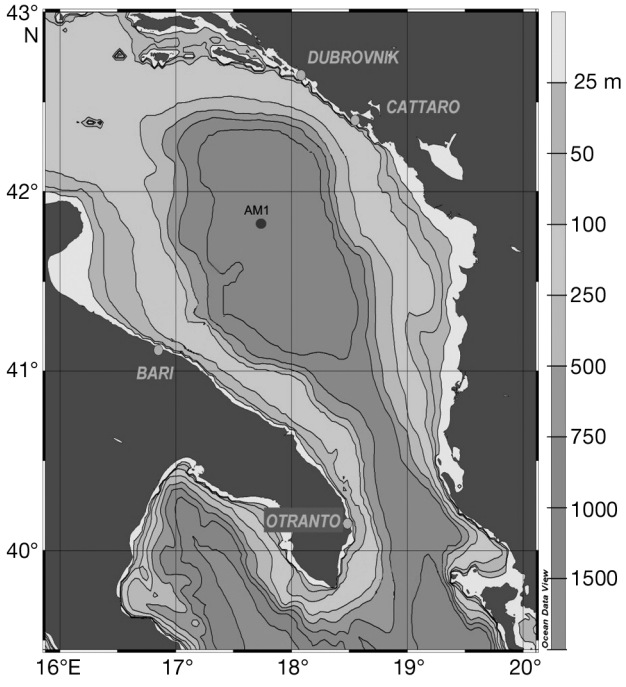

Fig. 1. Zooplankton sampling Stn AM1 in the southern Adriatic Sea during the VECTOR AM1 cruise (14–21 November 2006) and VECTOR AM3 cruise (10–17 April 2007)

(http://vector.conismamibi.it/) from 2006 to 2010. Mesozooplankton samples were collected using an electronic multinet (Bedford Institute of Oceanography Net and Environmental Sampling System, BIONESS; Sameoto et al. 1980) on 17 November 2006 and on 13–14 April 2007. The BIONESS had a 1 m^2 mouth area and was equipped with 11 horizontally arranged nets (200 µm mesh size) that opened sequentially. It was towed at a speed of about 2 knots using a conductor cable that transmitted and received information from the vessel. For both cruises, samples were collected from the surface to 1000 m depth 4 times during a 24 h cycle (morning, 06:00 h; midday, 12:00 h; afternoon, 18:00 h; and midnight, 24:00 h). Each deployment required about 3 h. The local sunrise/sunset times were 06:40 h/16:29 h and 06:13 h/19:29 h (GMT+1) for November 2006 and April 2007, respectively. The BIONESS was equipped with a multiparametric probe Sea Bird 911 Plus and a Seapoint fluorometer to continuously record temperature, salinity, oxygen and fluorescence. Fluorescence was measured and calculated as equivalent µg chl *a* l^{-1}. The conventional unit (F) for *in vivo* fluorescence in the range of 0 to 5 volts corresponds to 0 to 50 mg m^{-3} for chl *a* with a resolution of 0.1 mg m^{-3} and an accuracy variability of less than 10%. Rough data on water depth (m), temperature (°C), salinity and fluorescence were processed with Ocean Data View software to obtain vertical profiles in real time. Two flow meters installed internally and externally to the net measured the filtered volume and the filtration efficiency. At each sampling time, the BIONESS was deployed vertically to the maximum depth of 1000 m, and the physical structure of the water column; thermocline, pycnocline and halocline depths; and depth and thickness of the deep chlorophyll maximum (DCM) layer were analysed during the first downcast. Standardised sampling intervals were 1000–800, 800–600, 600–400, 400–300, 300–200, 200–100, 100–80, 80–60, 60–40, 40–20 and 20–0 m (for the midnight collection of April 2007, the net was not closed at the 60 m depth, so the more superficial layer is 80–0 m). On board, each 2 l collected sample from each sampling layer was split into 2 separate aliquots of 1 l each using a Folsom splitter. One (1 l) aliquot was filtered on a 200 µm mesh sieve, and the filtered material was diluted in 10 ml of filtered seawater and immediately frozen in liquid nitrogen for subsequent analysis of ETS activity. The second (1 l) aliquot was preserved in 4% formaldehyde-seawater solution buffered with sodium tetraborate (Steedman 1976) for the subsequent ecological qualitative/quantitative analyses, as described in 'Materials and methods: Mesozooplankton abundance and biomass'. A total of 85 frozen samples in 10 ml of seawater and 85 preserved samples, 1 l each, were used for this study.

ETS activity and carbon requirement

In the laboratory, the potential respiration and, consequently, the carbon requirement of mesozooplankton were estimated on frozen samples (after water removal) from ETS activity measurements in accordance with the method of Packard (1971) modified by Kenner & Ahmed (1975), and calculated using the following equation:

$$\mathrm{ETS}_{\mathrm{assay}}\ (\mu l\ O_2\ g\ wet\ wt^{-1}\ h^{-1}) = A_{\mathrm{corr}} \times H \times S \times 60/1.42 \times W \times f \times t \quad (1)$$

where A_{corr} is the absorbance of the sample at 490 nm corrected for blank and reagents, H is the homogenate volume (ml), S is the reaction mixture volume (ml), 60 converts minutes to hours, 1.42 is the conversion factor of INT-formazan into O_2 (µl), W is the wet mass (g) of the incubated sample, f is the volume (ml) of the homogenate in the assay and t is the incubation time (min). The samples were incubated at 20°C, but all activities were recalculated for *in situ* temper-

ature using the Arrhenius equation, assuming an activation energy (E_a) of 13.2 kcal mol^{-1} for bathypelagic mesozooplankton (Packard et al. 1975):

$$ETS_{in\ situ}\ (\mu l\ O_2\ g\ wet\ wt^{-1}\ h^{-1}) = ETS_{assay} \times e^{((Ea/R \times (1/T assay - 1/T in\ situ))} \quad (2)$$

where R is the gas constant, T_{assay} is the temperature of the assay and $T_{in\ situ}$ is the *in situ* temperature at the time and depth of sampling.

The oxygen consumption rate per hour was converted into carbon requirement, normalised by mesozooplankton wet biomass unit and by day, expressed as µg C g wet wt^{-1} d^{-1} and assuming a respiratory quotient of 0.85 (King et al. 1978), using the following equation:

$$ETS_{assay}\ (\mu g\ C\ g\ wet\ wt^{-1}\ d^{-1}) = ETS_{assay}\ (\mu l\ O_2\ g\ wet\ wt^{-1}\ h^{-1})\ 0.85 \times 12 \times 24/22.4 \quad (3)$$

where 12 is the weight (g) of 1 mol of carbon, 24 converts hours to days and 22.4 is the gas volume mol^{-1}. Carbon demand can be used as an index of minimum food requirement when assimilation efficiency and growth are not taken into account (Ikeda et al. 2000, Hirch et al. 2009).

To relate the potential oxygen consumed measured throughout the ETS methodology to *in situ* respiration, the typically assumed ETS:respiration ratio (0.5) for natural mesozooplankton assemblages was used (Kenner & Ahmed 1975, King & Packard 1975). Packard (1971) suggested that ETS activity, as measured by INT reduction in homogenates, can be used as a reliable index of *in situ* oxygen consumption. The values computed for the respiration:ETS ratio are reasonable assuming that the ETS activity measures the maximum uptake rate (V_{max}) of electron transfer.

The mesozooplankton carbon requirement, expressed as µg C m^{-3} d^{-1}, for the entire mesozooplanktonic community for each water column layer, was calculated by multiplying the biomass value (g wet wt m^{-3}) and the estimated carbon requirement (µg C g^{-1} d^{-1}) (Hirch et al. 2009).

Mesozooplankton abundance and biomass

Each whole 1 l fixed sample was first checked to separate all the larger specimens (>1 cm). Depending on the apparent mesozooplankton abundance in each sample, either the whole sample or subsamples (1/10 to 1/25, obtained using a Stempel pipette) were observed under a stereomicroscope (Leica Wild M10). Finally, the whole sample was observed for the identification of rare species. All organisms were counted and classified at higher taxonomic levels, whereas diagnosis at the species level was carried out for euphausiids (copepod abundance, composition and diel vertical distribution will be described in another study; R. Minutoli et al. unpubl.). Data were normalised to the total volume filtered and expressed as ind. m^{-3}, except for euphausiids, which were expressed as ind. 1000 m^{-3} due to their low abundance. The mean weighed abundance, as ind. m^{-3} for the entire water column, was calculated, summing all the counted specimens of the 11 layers and diving by the total volume of filtered seawater from the maximum sampled depth to the surface. The mean weighed abundance was similarly calculated for total zooplankton and for each taxonomic group.

To better interpret the ETS data, attention was given to the abundance and relative importance of crustaceans and gelatinous taxa (Doliolida, Ephirae, Idromedusae, Salpae, Siphonophora) as well as to the distribution in the water column of vertically migrating taxa, the euphausiids, except those in the calyptopis stage (Marschoff et al. 1989, Stuart & Pillar 1990).

For the biomass estimates, a 250 ml aliquot obtained from the 1 l sample with a Folsom splitter was wet weighed on an analytical balance in accordance with Tranter (1962), and the biomass was expressed as mg wet mass m^{-3} of filtered seawater.

Settling particulate matter

Downward particle fluxes were measured by another operative unit involved in the same synoptic cruises (CNR-ISMAR, Bologna, Italy). A mooring line equipped with 2 sediment traps (Technicap PPS3/3, 0.125 m^2 collection area, 12 collecting cups), temperature and conductivity recorders and current meters was deployed at Stn AM1. One sediment trap was deployed below the euphotic zone at 168 m water depth, and the other sediment trap, used for this study, was deployed at 1174 m water depth. To prevent organic matter degradation, the collecting cups of the sediment traps were filled with a 5% formalin solution in filtered (0.2 mm) seawater. After recovery, samples were stored at 4°C until processing in the laboratory, following the recommendations of Heussner et al. (1990). Samples were first wet sieved with a 1 mm nylon net to retain the largest swimming organisms, and then the smaller organisms were manually removed under a dissecting microscope. The samples were accurately divided into several subsamples using a precision wet splitter (Turchetto et al. 2012), and to measure the content of organic

carbon (C_{org}), the subsamples were filtered through pre-combusted 25 mm Whatman GF/F filters, which were stored at −20°C until analysis. Then, the filters were treated with 1.5 M HCl to eliminate the inorganic carbon. Finally, they were analysed with a Fisons NA 2000 CHN elemental analyser.

The C_{org} content data were used to calculate the sinking organic carbon flux integrated over the 1000 m water column. The flux measured at 1174 m depth was extrapolated to the depth at the beginning and end of each zooplankton sampling interval by applying the Martin equation (Martin et al. 1987):

$$J_z = J_T/(z/T)^{0.858} \quad (4)$$

where J_z is the flux at depth z and J_T is the flux measured at depth T. The difference between the upper and the lower values give a measure of the loss of organic carbon from the sinking POC flux in each depth interval. This same equation has been used for calculating the microplankton carbon flux in the Gulf of Maine (Packard & Christensen 2004) and the zooplankton-associated carbon flux in the tropical northeastern Atlantic Ocean (Packard & Gómez 2013).

Data analysis

The carbon demand results obtained were statistically analysed with a 1-way ANOVA to highlight potential significant differences among the 4 sampling times inside each sampling month and with a 2-way ANOVA, considering November 2006 and April 2007 data together, to determine if the carbon demand values showed significant differences between sampling months and within each sampling time between the 2 months. Results were considered significant when $p < 0.05$.

RESULTS

Environmental conditions

In the southern Adriatic Sea, it is normally possible to distinguish several water masses such as the Levantine Intermediate Water (LIW), the Adriatic Deep Water (AdDW), the North Adriatic Deep Water and the Middle Adriatic Dense Water (Cardin et al. 2011). The southern Adriatic Sea is one of the few places in the world known to be an area of dense water formation, where winter vertical convection or deep-water formation processes destroy density barriers throughout the water column (Cardin et al. 2011). These processes allow efficient mixing and exchange of properties between the upper, intermediate and deep layers, leading to oxygenation of the abyssal waters, and thus the Adriatic Sea is claimed to be a source of the Eastern Mediterranean Deep Water (Malanotte-Rizzoli 1991).

Available profiles of water properties (temperature, T, °C; salinity, S; chl *a*, mg m^{-3}) recorded during our BIONESS hauls were used to depict the hydrographical scenario at the sampling station during the 24 h cycle in November 2006 (Fig. 2) and in April 2007 (Fig. 3). The autumnal (Nov.) and spring (Apr.)

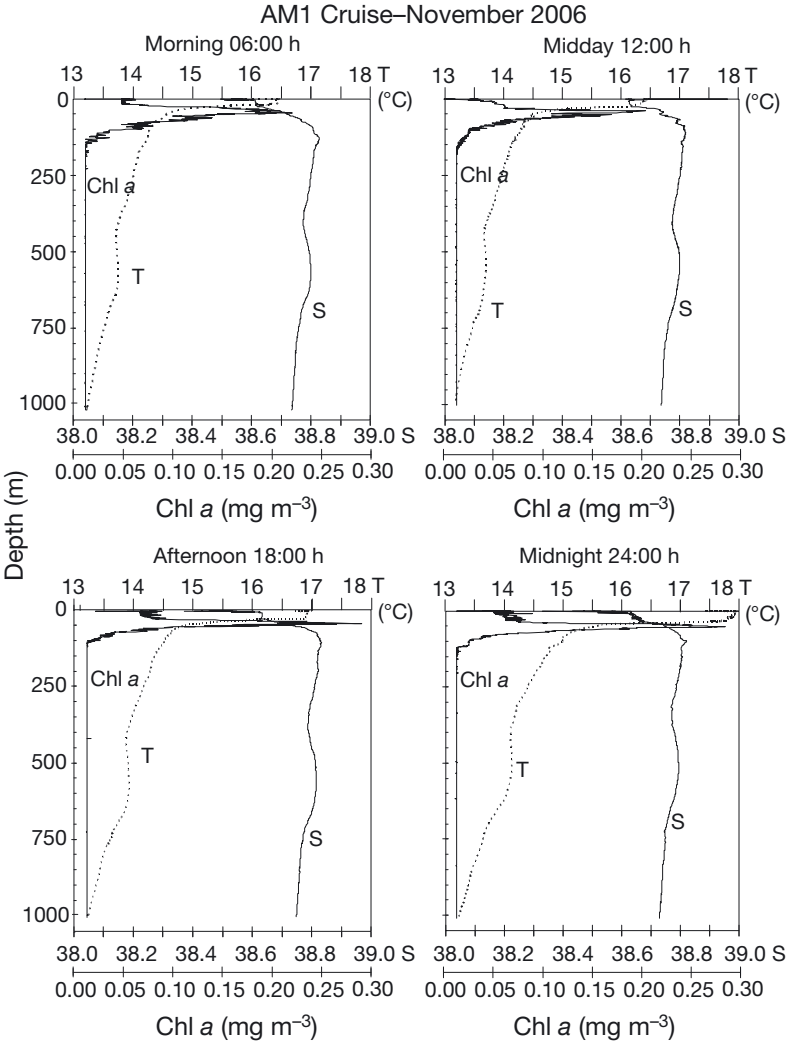

Fig. 2. Vertical profiles of temperature (T, °C), salinity (S) and chl *a* (mg m^{-3}) during a 24 h sampling cycle in November 2006

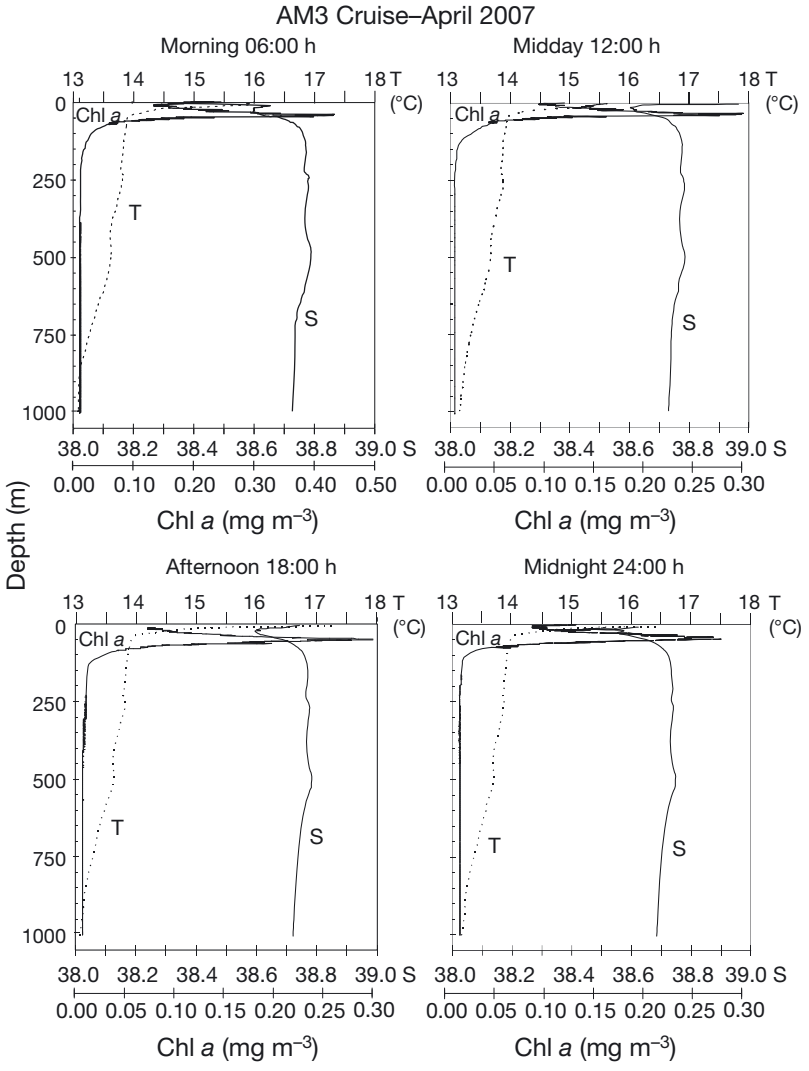

Fig. 3. Vertical profiles of temperature (T, °C), salinity (S) and chl *a* (mg m^{-3}) during a 24 h sampling cycle in April 2007

vertical profiles were quite similar. Temperature showed the same vertical trend in both months and during all 4 sampling times, with warmer waters at the surface, a thermocline at about 50 m depth and temperatures decreasing to 13°C at the maximum sampling depth. A slight warming around 500 m depth was detected during the 24 h cycle in autumn. Above 50 m depth, higher temperatures were detected in the afternoon and midnight collections compared to the morning and midday collections, in both study periods (Figs. 2 & 3). Salinity was lower in the surface layers (mean: 38.72 and 38.68 in November and April, respectively) than in the deep layers (no significant differences between months; mean: 38.77 in the 100–800 m depth layer and 38.73 in the 800–1000 m depth layer). Chl *a* concentration showed the same vertical distribution pattern in each month and during the entire 24 h cycle of investigation. Maximum chl *a* values (DCM) occurred at about 40 m. Chl *a* was almost undetectable below 150 m depth. Higher concentrations (though with different peaks, 0.29 and 0.49 mg chl *a* m^{-3} in November and April, respectively) always occurred during the afternoon collection (Figs. 2 & 3).

Mesozooplankton abundance, community composition and biomass

The total number of identified taxa during the 4 sampling times remained almost constant between autumn and spring (23 and 26, respectively).

In the autumnal scenario, the total zooplankton weighed abundances for the entire water column were 8.99, 9.32, 7.19 and 7.14 ind. m^{-3} in the morning, midday, afternoon and midnight collections, respectively (Table 1). Crustacean taxa represented different fractions of the total mesozooplankton abundance during the 24 h cycle, ranging from 56 to 86% in the midday and midnight collections, respectively. Within this subphylum, copepods were the dominant taxon, representing from 50% (morning) to 80% (midnight) of the total abundance. This translates as an integrated value for the entire water column from 4.46 to 5.66 ind. m^{-3} in numerical abundance. Gelatinous taxa represented similar values in the afternoon and at midnight, 0.7 and 0.9%, respectively. The abundance ratio between gelatinous and crustacean taxa ranged from 1:70 (morning) to 1:115 (midnight).

In spring, the total zooplankton weighed abundances for the entire water column were 40.06, 45.07, 43.68 and 33.80 ind. m^{-3} in the morning, midday, afternoon and midnight collections, respectively (Table 1). Over the entire 24 h cycle, copepods were the dominant taxon, representing more than 70% of the total abundance at all 4 sampling times and ranging from 24.37 to 33.25 ind. m^{-3}. Both crustaceans and gelatinous mesozooplankton taxa represented similar fractions during the 24 h cycle (ranging from 83 to 88% in midday and afternoon and 0.4 to 1.3% in midnight and midday, respectively) of the total mesozooplankton abundance. The abundance ratio

Table 1. Mean weighed abundances (ind. m^{-3}) of total zooplankton, crustaceans and gelatinous taxa identified in the entire water column at Stn AM1 during the 4 sampling times in November 2006 and April 2007

Taxon	AM1 Cruise (November 2006)				AM3 Cruise (April 2007)			
	Morning	Midday	Afternoon	Midnight	Morning	Midday	Afternoon	Midnight
Zooplanktonic taxa								
Total zooplankton	8.987	9.323	7.195	7.137	40.058	45.067	43.684	33.799
Crustacean								
Amphipoda	0.019	0.022	0.012	0.008	0.100	0.159	0.043	0.047
Calyptopis	0.001	0	0.002	0	0.001	0.563	0.574	0.449
Copepoda	4.456	4.841	4.724	5.666	29.507	33.247	31.158	24.370
Decapoda	0.001	0.001	0.003	0.003	0.032	0.045	0.069	0.086
Decapoda larvae	0.001	0.005	0.001	0.0005	0.010	0.009	0.003	0
Euphausiacea ad+juv	0.107	0.030	0.077	0.078	1.955	1.027	3.726	1.580
Furciliae	0.014	0.033	0.085	0.009	0.348	0.183	0.260	0.246
Isopoda	0.006	0.004	0.004	0	0.001	0	0	0.002
Ostracoda	0.505	0.305	0.531	0.371	1.662	2.377	2.729	2.745
Total	5.111	5.240	5.439	6.135	33.614	37.609	38.562	29.525
Gelatinous								
Doliolida	0	0	0.0004	0.005	0.012	0 .012	0.001	0
Ephirae	0	0	0	0	0.008	0.199	0.001	0
Idromedusae	0	0.041	0.033	0.029	0.119	0.114	0.106	0.023
Salpae	0.020	0	0.006	0	0.001	0.005	0	0.002
Siphonophora	0.053	0.029	0.024	0.019	0.255	0.278	0.249	0.121
Total	0.073	0.070	0.064	0.053	0.395	0.610	0.357	0.146

between gelatinous and crustacean taxa ranged from 1:62 (midday) to 1:202 (midnight).

Considering the focused diel vertical migratory group in the 0–100 and 100–1000 m layers of the water column, in autumn, the highest abundance of euphausiids (adults + juveniles + furcilia stages) was observed in the afternoon between 0 and 100 m (434.62 ind. 1000 m^{-3}), whereas the lowest was observed at midday between 100 and 1000 m (33.23 ind. 1000 m^{-3}) (Fig. 4a). In spring, the highest abundance of euphausiids was observed in the afternoon between 0 and 100 m (17 396.89 ind. 1000 m^{-3}), whereas the lowest occurred at midnight between 100 and 1000 m (215.86 ind. 1000 m^{-3}) (Fig. 4b).

The abundance (ind. 1000 m^{-3}) for all identified euphausiid species and the relative percentage frequency in the 11 water column layers investigated for each sampling time are reported separately for both sampling periods in Tables S1 & S2 in the Supplement at www.int-res.com/articles/suppl/m495p091_supp.pdf. Overall, 9 euphausiid species were found in the 2 sampling periods. In both autumn and spring, *Euphausia krohni, Nematoscelis megalops* and *Stylocheiron longicorne* were the 3 most abundant euphausiid species, followed by *E. hemigibba* and *E. brevis* in November 2006 and by *S. abbreviatum* and *E. hemigibba* in April 2007. *E. brevis, E. krohni, E. hemigibba* and *Meganyctiphanes norvegica* showed a clear daily migratory behaviour, whereas *N. megalops, S. abbreviatum, S. longicorne, S. maximum* and *Thysanopoda aequalis* did not vary their vertical distribution over the entire study periods.

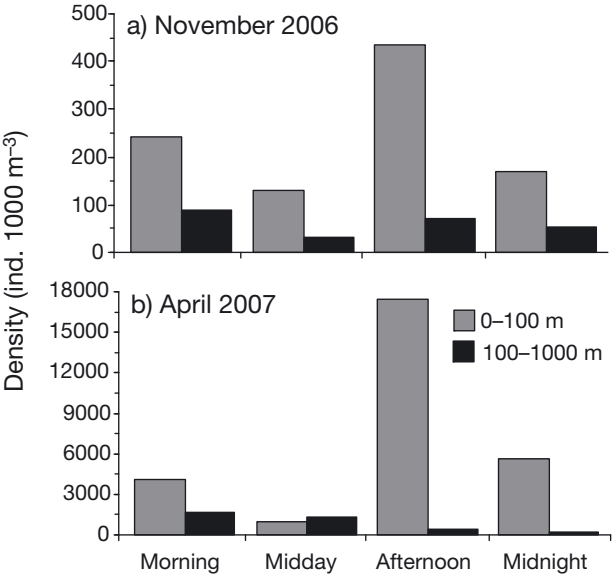

Fig. 4. Euphausiid (adults + juveniles + furcilia stages) mean abundance (ind. 1000 m^{-3}) for the 0–100 and 100–1000 m layers during a 24 h cycle in (a) November 2006 and (b) April 2007. Note the difference in abundance scale

Considering the vertical distribution of zooplankton wet weight biomass (mg m^{-3}), in autumn, the highest biomass values of the 4 sampling times were detected in the uppermost layers during dark hours, specifically in the upper 20 m at midnight (31 mg wet wt m^{-3}) and in the afternoon (25.24 mg wet wt m^{-3}) (Fig. 5a). In April, the highest biomass was also detected during dark hours, in the 60–40 m layer in the afternoon (176.61 mg wet wt m^{-3}) followed by the 80–0 m layer at midnight (145.03 mg wet wt m^{-3}) (Fig. 5b). Overall, during the entire sampling cycle in both months, mesozooplankton biomass decreased with increasing water depth, except for midday collections.

Zooplankton carbon requirement

Table 2 shows the mesozooplankton carbon requirement separately for the 4 hauls (morning, midday, afternoon and midnight) carried out over the 24 h investigation cycle for the November 2006 and April 2007 collections. Differences between the 2 sampling periods were observed and statistically validated (2-way ANOVA; df = 1, 3, $F = 9.72$, p = 0.01). In the 0–100 and 100–1000 m layers of the water column, the zooplankton carbon requirement was mostly higher in April (Fig. 6a,b). The mean value for all samples collected for each sampling period was 153 µg C g^{-1} d^{-1} in November 2006 compared to 209 µg C g^{-1} d^{-1} in April 2007.

The vertical distribution pattern of carbon requirement revealed differences between the daily and nightly collections inside each sampling month but showed the same diel trend in both sampling months without significant differences (2-way ANOVA; df = 1, 3, $F = 0.27$, p = 0.84). In the 0–100 m layer, the zooplankton carbon requirement was characterised by higher mean values during the morning and at midnight compared to the midday and afternoon collections for both months sampled (Fig. 6a) (1-way ANOVA; df = 3, $F = 8.56$, p = 0.01 for November 2006 and $F = 20.74$, p = 0.01 for April 2007). In the 100–1000 m layer, very similar carbon requirements were calculated for the 4 hauls of each 24 h collection cycle (1-way ANOVA; df = 3, $F = 1.50$, p = 0.29 for November 2006 and $F = 0.76$, p = 0.53 for April 2007), except for the midday haul of November 2006, which showed a higher mean demand than the other 3 hauls (Fig. 6b).

The mesozooplankton carbon requirement, expressed as µg C m^{-3} d^{-1}, for the entire mesozooplanktonic community for each water column layer was analysed for the 2 sampling periods. Considering the entire 24 h sampling cycle, the carbon requirement of the mesozooplanktonic community follows the same vertical distribution pattern of biomass in both months, with highest values during afternoon and

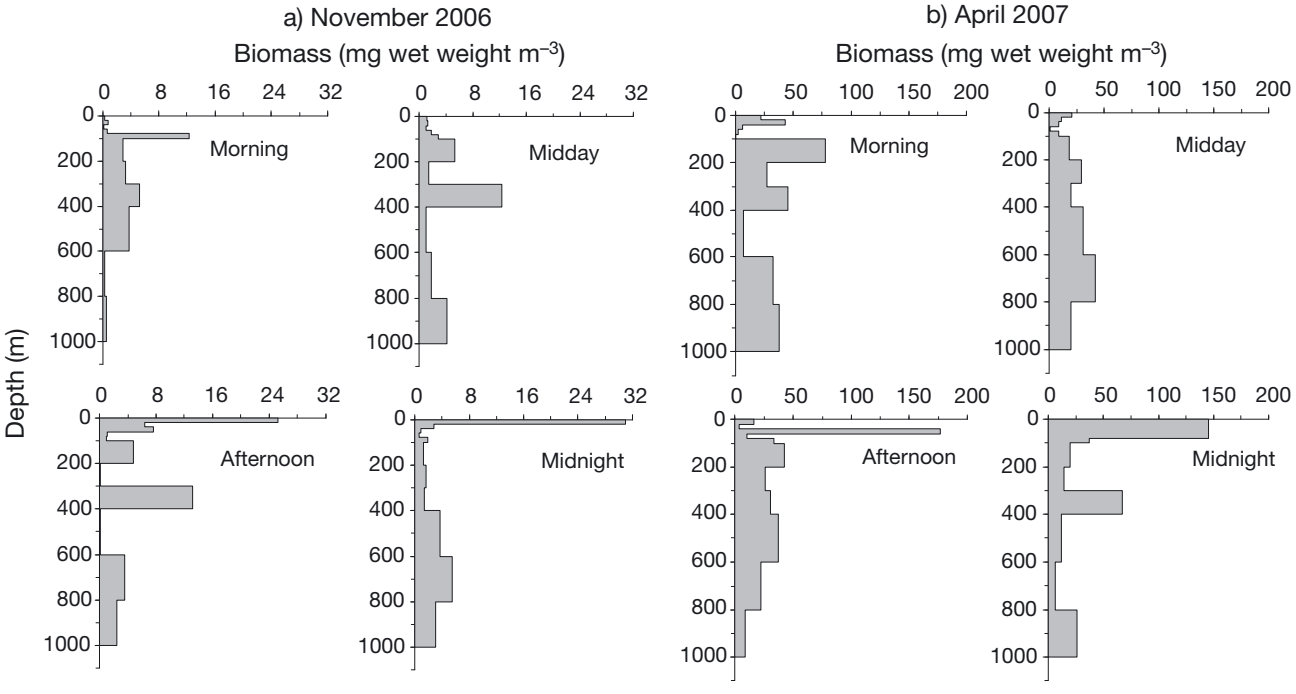

Fig. 5. Vertical distribution of mesozooplankton wet biomass (mg m^{-3}) during a 24 h cycle in (a) November 2006 and (b) April 2007. Note the difference in biomass scale

Table 2, Carbon requirement (calculated from electron transport system activity) of mesozooplankton collected from 0–1000 m depth during a 24 h cycle in November 2006 and April 2007

Sampling time	Layer (m)	Carbon demand (µg C g^{-1} d^{-1})	
		November 2006	April 2007
Morning	0–20	245	279
	20–40	248	278
	40–60	246	210
	60–80	159	249
	80–100	109	250
	100–200	94	209
	200–300	123	201
	300–400	97	218
	400–600	114	216
	600–800	154	172
	800–1000	106	164
Midday	0–20	156	172
	20–40	159	160
	40–60	160	151
	60–80	169	172
	80–100	104	225
	100–200	115	207
	200–300	153	182
	300–400	182	205
	400–600	237	202
	600–800	201	168
	800–1000	241	181
Afternoon	0–20	153	159
	20–40	173	177
	40–60	111	282
	60–80	116	298
	80–100	120	212
	100–200	102	199
	200–300	142	198
	300–400	168	188
	400–600	126	187
	600–800	136	232
	800–1000	108	233
Midnight	0–20	249	
	20–40	289	
	40–60	182	
	60–80	149	225[a]
	80–100	147	270
	100–200	141	224
	200–300	129	169
	300–400	94	188
	400–600	108	210
	600–800	92	241
	800–1000	118	209

[a]0–80 m sampling layer

midnight above 20 m depth in November (Fig. 7a) and above 80 m depth in April (Fig. 7b).

Mesozooplankton contribution to losses from the sinking carbon flux

Table 3 shows the vertical sinking carbon fluxes for the 2 different sampling periods, as well as the losses occurring in the water column and mesozooplankton contribution (%). The flux of organic carbon at 20 m in November (163.30 mg C m^{-2} d^{-1}) is half that in April (320.01 mg C m^{-2} d^{-1}). This proportion is maintained through the deep column until the maximum sampled depth, where the flux in November was only 5.69 mg C m^{-2} d^{-1} compared to 11.15 mg C m^{-2} d^{-1} in April. For both the autumn and spring periods, downward organic carbon flux in the upper 20 m of the water column was about 30-fold higher than that measured at 1000 m depth. The carbon loss during particle descent to 1000 m depth was 157.60 mg C m^{-2} d^{-1} for November and 308.85 mg C m^{-2} d^{-1} for April, which represented, in both cases, 96% of the flux at the surface. The largest fraction was lost in the top 100 m (75%).

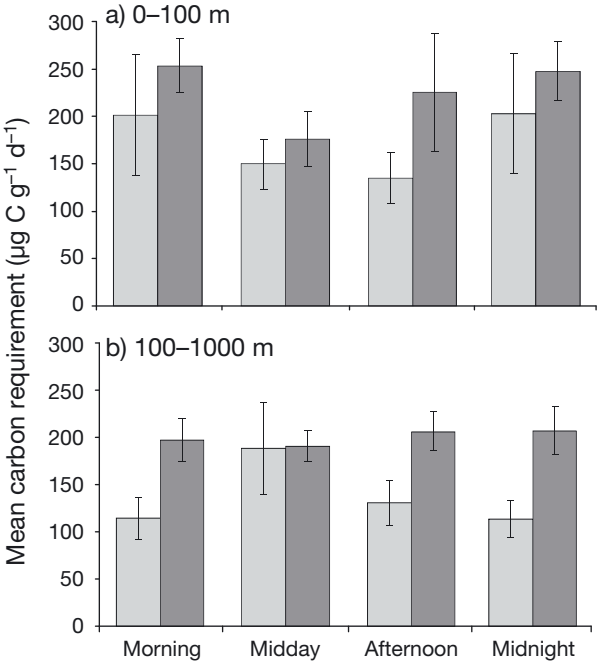

Fig. 6. Mean carbon requirement values (µg C g^{-1} d^{-1}), calculated by electron transport system (ETS) activity, per gram of mixed zooplankton (a) 0–100 m and (b) 100–1000 m during a 24 h cycle in November 2006 and April 2007

DISCUSSION

This study is the first attempt to evaluate the vertical distribution of mesozooplankton carbon requirement, its diel variability, its role in the carbon flow and potential seasonal differences in the upper 1000 m in the southern Adriatic Sea. The calculation of respiration from ETS activity (Packard 1971, King

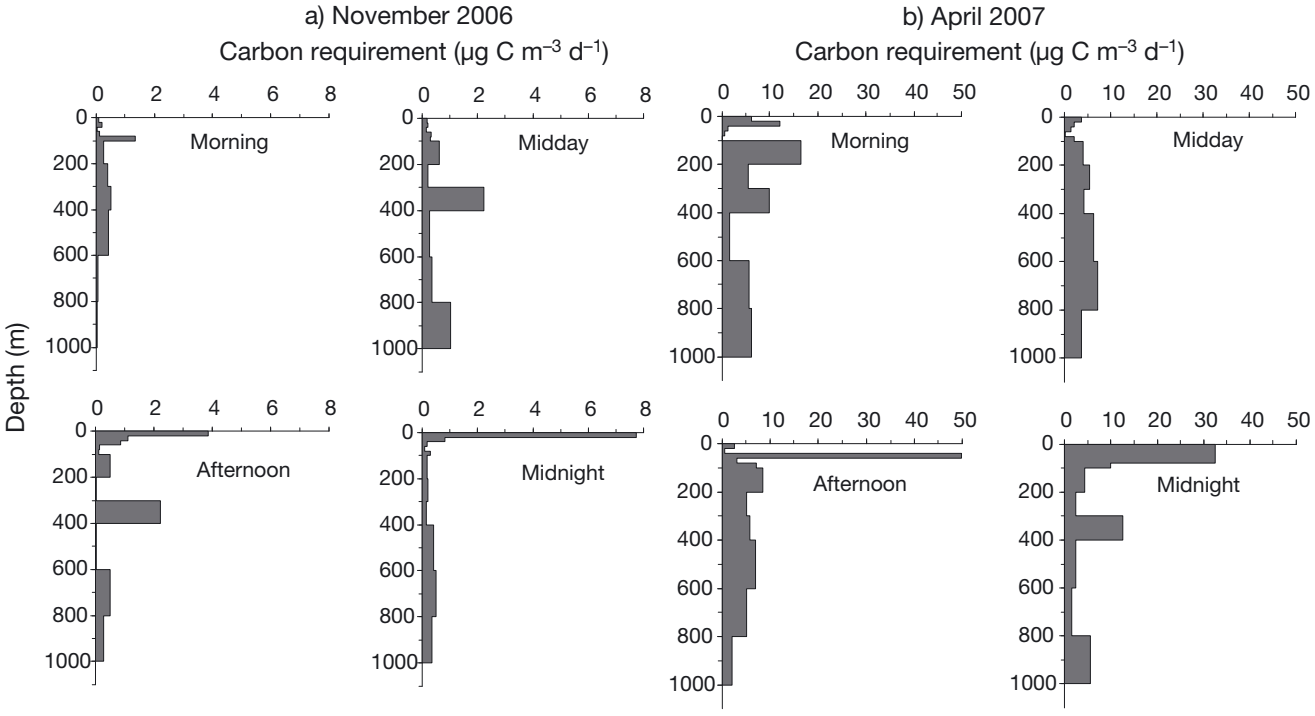

Fig. 7. Vertical distribution of mesozooplankton community metabolic carbon requirement (µg C m^{-3} d^{-1}) during a 24 h cycle in (a) November 2006 and (b) April 2007. Note the difference in carbon requirements scale

Table 3. Sinking organic carbon flux measured by a sediment trap at a fixed station in the southern Adriatic Sea in November 2006 and April 2007. The flux rate is calculated from the Martin curve to the depth of the beginning/end of each sampled layer, and the carbon losses from the sinking flux are calculated. The carbon used by mesozooplankton and its contribution to carbon losses are shown as means among the 4 sampling times. Sediment trap depth: 1174 m. Carbon organic flux: November 2006, 4.96 mg C m^{-2} d^{-1}; April 2007, 9.72 mg C m^{-2} d^{-1}

Sampling layer (m)	Sinking flux (mg C m^{-2} d^{-1})		Carbon loss (mg C m^{-2} d^{-1})		Carbon respired (µg C m^{-2} d^{-1})		Zooplankton biomass (mg wet wt m^{-2})		Zooplankton contribution (%)	
	Nov 2006	Apr 2007	Nov 2006	Apr 2007	Nov 2006	Apr 2007	Nov 2006	Apr 2007	Nov 2006	Apr 2007
0–20					59	83	289	395		
20–40	163.30	320.01	73.20	143.45	12	98	57	393	0.02	0.07
40–60	90.09	176.55	26.47	51.88	6	350	48	1278	0.02	0.67
60–80	63.62	124.68	13.92	27.27	3	26	21	94	0.02	0.10
80–100	49.71	97.41	8.66	16.97	10	97	90	402	0.12	0.57
100–200	41.04	80.43	18.40	36.06	39	830	355	3989	0.21	2.30
200–300	22.65	44.38	6.65	13.04	21	460	162	2424	0.32	3.53
300–400	15.99	31.34	3.50	6.85	128	804	807	4053	3.65	11.73
400–600	12.49	24.48	3.67	7.19	55	858	434	4336	1.50	11.93
600–800	8.82	17.29	1.93	3.78	71	980	566	5232	3.67	25.92
800–1000	6.89	13.51	1.20	2.35	109	750	513	4677	9.10	31.86
Max. sampled depth	5.69	11.15								

& Packard 1975) and correlation with micro- and mesozooplankton *in vivo* respiration rates (Packard et al. 1974, Kenner & Ahmed 1975, Owens & King 1975, Devol & Packard 1978) can be useful in calculating the ocean carbon requirement (Packard & Christensen 2004, Packard & Gómez 2013). The relationship between respiration and ETS for the microplanktonic population (<225 µm), shown by Aristegui & Montero (1995) and by Maldonado et al. (2012), is not unlike the calibration factors used as proxies for other planktonic metabolic processes, like productivity (Aristegui & Montero 1995).

The carbon requirements per unit of zooplankton biomass displayed variability in diel and seasonal vertical distribution patterns. Activities in the 0–100 m layer were higher in the sunrise and midnight samples than in the midday and afternoon samples, in both autumn and spring. Since ETS activity in the study case was standardised per unit of wet weight mass, differences in zooplankton abundance in this layer cannot explain the variation between these sampling times.

It is well known that the euphausiids, actively vertical migrating organisms that are responsible for transporting material towards the ocean interior (Longhurst 1976, Longhurst et al. 1990), feed nightly in the surface layer and excrete daily at depth, potentially supporting microbial growth in the mesopelagic zone by actively transporting dissolved and particulate organic matter (Longhurst et al. 1990, Burd et al. 2010). The entire euphausiid community, in both sampling periods, did not show marked migratory behaviour. The highest densities were observed above 100 m in the afternoon and in the 100–1000 m layer during the morning collections. The 3 *Euphausia* species and *Meganycthiphanes norvegica* showed strong migratory behaviour, whereas *Nematoscelis megalops, Thysanopoda aequalis* and the 3 *Stylocheiron* species remained consistently in the same water column layers during the entire 24 h sampling cycle in both November and April.

The autumnal carbon consumption vertical trend during the 24 h cycle seems not at all correlated to the vertical distribution pattern of euphausiids. Even if the ETS activity in the 0–100 m layer was higher in the morning and at midnight, only in the first case did the vertical distribution pattern of the enzymatic activity fit well with the vertical distribution pattern of euphausiid abundance, as previously reported (Torres et al. 1979, Schalk 1988, Minutoli & Guglielmo 2009, 2012). In fact, it is already known that dielly migrating and actively feeding zooplankton have higher respiratory activity levels than deeper-living and/or non-migrating zooplankton species (Packard et al. 1975, Schalk 1988, Hirch et al. 2009). On the other hand, in the midnight autumnal 0–100 m sampling, the high ETS activity was not associated with a high abundance of euphausiids. In this period, the amount of copepod, euphausiid and decapod carcasses showed variations during the 4 sampling times, so the ratio between carcasses and living specimens can play a role in causing variability in carbon requirement calculations. The autumnal high ETS activity in the 0–100 m layer at midnight may be linked to the very lowest abundance of carcasses detected in this layer among the 4 sampling times (0.37 carcasses m^{-3}). Changes in the community composition of mesozooplankton as an abundance ratio of crustaceans over gelatinous taxa during the different sampling times can also be responsible for this high midnight 0–100 m carbon requirement. In fact, the highest abundance of crustaceans, with their higher respiratory activity, was detected in the midnight collection.

In the spring, the carbon requirement vertical trend during the 24 h cycle was also not at all correlated to the vertical distribution pattern of euphausiids. The carbon requirement in the 0–100 m layer showed higher values except for the midday sample, which in fact showed the lowest abundance of dielly migrating species characterised by higher respiratory activity. Furthermore, in the midday 0–100 m sample, the highest percentage of gelatinous taxa and its relative highest ratio over crustaceans (1:62) among the 4 sampling times, was detected. In addition, the highest total amount of non-living specimens among the 4 sampling times (1.08 carcasses m^{-3}) was observed in this layer.

Carbon demand in the 100–1000 m layer showed similar values among all 4 sampling times within each sampling period, with only a small increase in demand in the autumnal midday collection.

The increase in zooplankton biomass from morning to dark hours in both our study months has been previously reported and shown to be more complicated than a similar increase in haul efficiency at night (Hernández-León et al. 2001, Yebra et al. 2005). After sunset the larger fraction of zooplankton organisms move to the upper water column layers to feed and then return to deeper layers during the day. This results in the main zooplankton biomass being concentrated at night near surface layers (Brinton 1967, Vinogradov 1968, Mauchline & Fisher 1969, Casanova 1974, Brancato et al. 2001, Yebra et al. 2005).

The downward flux of POC is generally regarded as the most important source of organic carbon to the meso- and bathypelagic zones (Burd et al. 2010, Minutoli & Guglielmo 2012). Moored intercepting sediment traps have proven to be very useful tools to study the temporal variability of sinking matter in the deep ocean (Honjo et al. 2008, Turchetto et al. 2012). Particle fluxes collected by sediment traps can help us to better understand the biological cycles and trophic regimes and to integrate information about primary production and plankton communities over long time scales (Turchetto et al. 2012). To study mass fluxes and budgets of organic

carbon, sediment traps have been deployed in various regions of the Mediterranean Sea, but most are limited to continental margin areas, and few open-sea areas have been studied (Turchetto et al. 2012 and papers cited therein). Changes in POC flux at depth are often estimated using published regression equations rather than by direct observation, including the Martin curve (Martin et al. 1987), relating flux at depth to a known flux at a given depth. The regression between water depth and POC flux gives an estimate of the POC removed by heterotrophic consumption. In this study, the carbon flux, measured by a moored sediment trap at 1174 m depth, was calculated for the entire water column for both sampling months using the equation of Martin et al. (1987). The relative contribution of zooplankton respiration to the decrease in POC flux varies spatially, temporally and vertically, as already shown (Minutoli & Guglielmo 2009, 2012). The metabolic requirement of the mesozooplankton for each sampled layer in the studied station in the southern Adriatic Sea showed lower values in November 2006 compared to April 2007, with carbon requirements ranging from 0.02 to 9.10% and 0.07 to 31.86%, respectively.

Considering the water masses similarly in both months, the percentage of zooplankton contribution to carbon flux increases from the surface 0–100 m layer to the LIM at 100–800 m (1.87% in November 2006, 11.08 in April 2007) and is highest inside the AdDW in the 800–1000 m depth sampling layer (9.10% in November 2006, 31.86% in April 2007). Studies demonstrate that the deep waters of the southern Adriatic, like those of the Mediterranean Sea, became warmer and saltier from 1997 to 2005 because of the influence of the Eastern Mediterranean Transient climate event (Civitarese et al. 2005, Roether et al. 2007). This event modified the thermohaline cell previously originating in the South Adriatic Pit and changed the biogeochemical dynamics in the eastern Mediterranean Sea because of the spread of young and labile organic matter by lateral advection. Consequently, increasing deep respiration in the Levantine and Ionian seas and reduced remineralisation in the southern Adriatic Sea were observed (La Ferla et al. 2003, Azzaro et al. 2012). These findings suggest that mechanisms other than the sinking of particulate matter could partially justify our high carbon mesozooplankton requirement in the deeper layer.

In the epi- (0–100 m) and mesopelagic (100–1000 m) zones, higher remineralisation values always occurred in the sampled layers below 100 m depth but not in the layers above, in both November and April, with mean values of 0.04 and 0.35% for the epipelagic layer and 3.07 and 14.54% for the mesopelagic layer, respectively. The total contribution of mesozooplankton respiration to organic carbon losses in the epi- and mesopelagic realms were 0.18 and 18.45%, respectively, in autumn and 1.41 and 87.27%, respectively, in spring. These ranges are in agreement with the literature (Martin et al. 1987, Burd et al. 2010, Minutoli & Guglielmo 2012). In fact, many processes take place in the epipelagic layer, where the minimum percentage contribution of mesozooplankton respiration to organic carbon losses is evident. Most importantly, primary production, associated with the chl *a* maximum measured at about 40 m depth, replenished carbon loss to the zooplankton. The mesopelagic layer, in contrast, is characterised by heterotrophic activities and is where the largest decrease in sinking POC flux is found (Martin et al. 1987). The feeding strategies and behaviour of mesopelagic zooplankton differ from its epipelagic counterpart, and it is well known that mesopelagic zooplankton communities play different roles in the carbon binding activity in the 2 ecological zones (Koppelmann et al. 2009, Minutoli & Guglielmo 2012). Remineralisation percentages were lower in November 2006 than in April 2007 throughout the water column until the maximum sampled depth, mainly because of seasonal differences involving higher primary production, higher zooplankton biomass, higher amount of vertical sinking POC flux and, consequently, more intense heterotrophic metabolism during spring. These results support the findings of Thiel (1983), Tselepides & Eleftheriou (1992) and Minutoli & Guglielmo (2009, 2012).

In the southern Adriatic Sea, mesozooplankton contributes to carbon losses from the sinking POC flux. This loss represents an important pathway in carbon recycling processes in both the epipelagic and mesopelagic layers.

Acknowledgements. This study was undertaken in the framework of the Italian project VECTOR, led by the National Italian Consortium for Marine Science (CoNISMa) and funded by the Italian Ministry of University and Research (MIUR). Our local research unit (CoNISMa-Messina) was involved inside line 8 of the project, named the CARbon cycle in the PELagic area of the Mediterranean (CARPEL). Thanks go to Dr. S. Miserocchi (CNR-ISMAR, Bologna, Italy) for giving us the sediment trap data and to Dr. M. Pansera and L. P. Rodriguez Valdes (DiSBA-UNIME, Italy) for zooplankton abundance and biomass analyses. We are grateful to the crew of the RV 'Universitatis' for the efficient collaboration in daily and nightly collection of BIONESS biological samples.

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Editorial responsibility: Antonio Bode, A Coruña, Spain

Submitted: April 3, 2013; Accepted: September 13, 2013
Proofs received from author(s): December 7, 2013