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Mesozooplankton carbon requirement in the Tyrrhenian Sea: its vertical distribution, diel variability and relation to particle flux

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ABSTRACT: Mesozooplankton consumes an important fraction of particulate organic matter sinking down the water column in all oceans. We investigated the vertical distribution (down to 2000 m depth) and diel variability (during a 24 h cycle) of the mesozooplankton carbon requirement (µg C g^{-1} d^{-1}), estimated by measuring the activity of the electron transport system (ETS), at a fixed station in the open southern Tyrrhenian Sea. To estimate the quantitative role of zooplankton in carbon losses occurring during organic particle sinking, zooplankton carbon demand was compared with organic carbon vertical flux (measured using the ^{234}Th:^{238}U disequilibrium method). Zooplankton abundance, biomass and community composition were also investigated, as were the vertical distribution of diel migrant species and the relative importance of crustaceans and gelatinous taxa. A distinct day-night variation of carbon demand in the upper 300 m of the water column was observed, with the highest values encountered during dark hours. The high values estimated in sunset samples were most likely due to the presence or dominance of the calanoid copepod *Pleuromamma gracilis*. Mesozooplankton were responsible for 13.2% and 8.8% of carbon losses in the meso- and bathypelagic zones, respectively. These results reflect the trophic status of the southern Tyrrhenian Sea, which is typically less oligotrophic than the central and eastern Mediterranean Sea.

KEY WORDS: Mesozooplankton · Carbon requirement · Electron transport system · Particulate organic carbon sinking flux · POC sinking flux · Tyrrhenian Sea

INTRODUCTION

The oceans play a pre-eminent role in the global carbon cycle, as they can store 50 times more CO_2 than the atmosphere. Up to 98.5% of pre-industrial CO_2 is in fact stored in the ocean, whereas only 1.5% is preserved in the atmosphere, because of the high solubility of CO_2 (30 times higher than that of oxygen) and because of the hydrolysis reaction it undergoes to form carbonate and bicarbonate ions (Marinov & Sarmiento 2004). Carbon cycling in the oceans is controlled mainly by 2 processes: CO_2 dissolution into seawater (the so-called physical pump) and incorporation into phytoplankton biomass (the so-called biological pump). Dissolved CO_2 is then transferred from the upper layers of the ocean to the sea floor by sinking currents, where it can be stored for hundreds to thousands of years. Eventually, mixing and upwelling phenomena can bring back CO_2-enriched deep waters to the ocean surface.

Primary production in the relatively thin upper layer of the sea fuels the heterotrophic metabolism in the dark ocean (Burd et al. 2010). Once incorporated into phytoplankton biomass, carbon enters the planktonic grazing food web: protists and animals eat the phytoplankton, then leading up to fish and

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large marine mammals. Faeces, dead organisms and their remains (i.e. detrital particles) and prokaryotes, together with phytoplankton exudates, sink deeper into the ocean's interior, providing food to planktonic heterotrophs and, once landed on the sea floor, to the deep-sea benthos (Fabiano et al. 2001, Vanucci et al. 2001). A relatively small fraction of the sinking material is eventually buried and stored in sediments for up to millions of years (Middelburg & Meysman 2007). Most of the reduced carbon in and below the sea floor is thus used by animals and heterotrophic prokaryotes, and returned as CO_2 to the deep ocean, as part of the global carbon cycle.

Particulate organic matter (POM) cycling in the ocean's interior is controlled by the interaction of physical, chemical and biological forces (see Koppelmann et al. 2004). Approximately 90% of POM is remineralised as it sinks through the water column: heterotrophic consumption results in decreasing fluxes of organic material with increasing water depth, with the largest loss of material generally observed between 100 and 1000 m depth (Martin et al. 1987).

The consumption of organic particles represents the carbon demand or requirement by heterotrophs. Carbon consumed by heterotrophs in the water column is subtracted from the organic particle vertical flux, thus representing a carbon loss for the ocean's interior. Only an average 10% of POM exported from the upper photic ocean reaches the sea bottom: the remaining 90% is therefore consumed, remineralised or, once transformed into new prokaryotic biomass (through the microbial loop; Azam et al. 1983), redirected towards higher trophic levels (Berger et al. 1988, Koppelmann et al. 2000, Koppelmann & Frost 2008).

Mesozooplankton, namely planktonic metazoans 200 to 2000 µm in size, actively feed on POM (Longhurst 1991, Halsband-Lenk et al. 2003, Minutoli & Guglielmo 2009). Diel vertical migration (DVM) of mesozooplankton is one of the most important movements of biomass in the ocean (Longhurst 1976). The active carbon transport from the ocean surface to the deep sea mediated by the mesozooplankton, hypothesised by Vinogradov (1962), reinforces the biological pump for the net transport of organic and inorganic matter through the pycnocline (Longhurst et al. 1989, 1990).

A specific and highly sensitive technique to evaluate the mesozooplankton carbon requirement from the carbon sinking flux consists of measuring the electron transport system (ETS) activity (Packard 1971, King & Packard 1975, Owens & King 1975, Båmstedt 1979, 1980, Bidigare et al. 1982). 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 ETS is the coenzyme Q-cytochrome *b* complex oxidation, that can be measured after the reaction of the complex with the artificial electron acceptor 2-(*p*-iodophenyl)-3-(*p*-nitrophenyl)-5-phenyl tetrazolium chloride (INT) (Packard 1971). This reaction is influenced by various factors, such as temperature, salinity and sexual stage (Torres et al. 1979, Ikeda & Fay 1981, Raymont 1983, Schalk 1988), even if adaptations to environmental conditions are possible (Anraku 1964, Musayeva & Shushkina 1978, Båmstedt 1980, Hirche 1984). Several papers have shown a good correlation between ETS activity and *in vivo* respiration (Packard et al. 1974, Kenner & Ahmed 1975, Owens & King 1975, Devol & Packard 1978), so that ETS activity can be used as an estimate of mesozooplankton respiration rates.

To provide new insights into the role of mesozooplankton in the carbon loss during POM sinking in open waters, we investigated the vertical distribution (down to 2000 m depth) and diel variability (during a 24 h cycle) of the mesozooplankton carbon requirement (µg C g wet wt^{-1} d^{-1}) at a fixed station located in the open southern Tyrrhenian Sea. To estimate the quantitative role of zooplankton in carbon losses occurring during particle sinking, the mesozooplankton carbon demand, estimated using ETS activity measurements, was related to vertical carbon fluxes, measured by the ^{234}Th:^{238}U disequilibrium method. Mesozooplankton abundance, biomass and community composition were also investigated, as were the vertical distribution and the relative importance of crustaceans, gelatinous taxa and vertically active migrating species.

MATERIALS AND METHODS

Sampling

Mesozooplankton was collected at a fixed station named 'VTM' in the southern Tyrrhenian Sea off Naples (39° 30′ 00″ N, 13° 30′ 00″ E; 3450 m depth) during the 'TM3' oceanographic cruise on board the RV 'Universitatis', carried out from 19 to 23 April 2007 (Fig. 1). This cruise was carried out in the framework of a large national project named VECTOR (VulnErability of Coasts and marine Italian

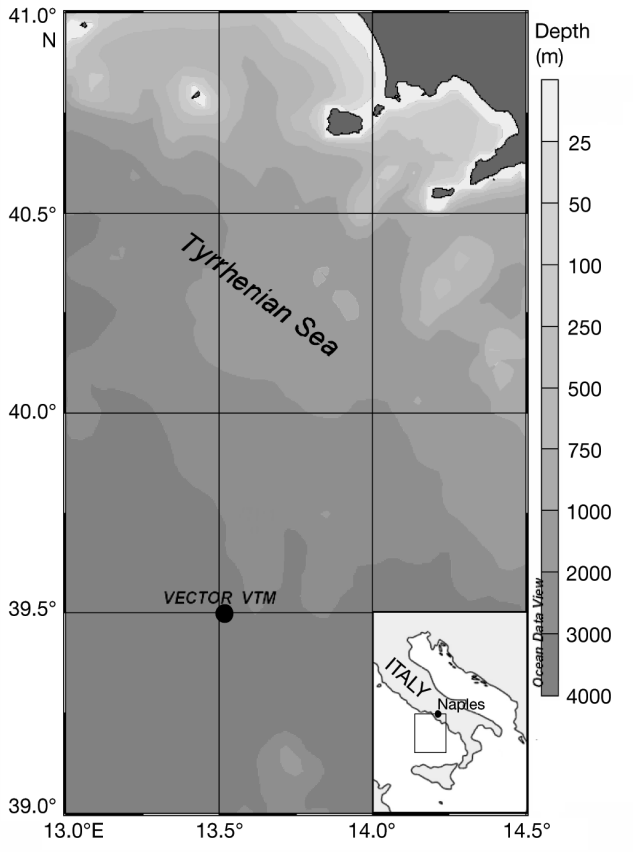

Fig. 1. Zooplankton sampling station VTM in the Tyrrhenian Sea during the 'VECTOR TM3' cruise (19–23 April 2007)

ecosystems to climaTic changes and their rOle in Mediterranean caRbon cycle) from 2006 to 2010 that included many Italian scientific operative units and investigated a large number of topics (http://vector-conisma.geo.unimib.it/). Samples were collected using the electronic multinet BIONESS (Bedford Institute of Oceanography Net and Environmental Sampling System; Sameoto et al. 1980) on 20 April 2007. The sampling instrument has a 1 m^2 mouth area, with 12 horizontally arranged nets (200 µm mesh size) which can be sequentially opened and closed, and is towed at a speed of about 2 knots through a conductor cable that transmits and receives information from the vessel. Samples were collected from the surface down to 2000 m depth, 4 times during a 24 h cycle. Samplings started at 06:00 h (morning), 12:00 h (midday), 18:00 h (afternoon) and 24:00 h (midnight) and, at each time, took about 5 h. The BIONESS system was equipped with a multiparametric probe Sea-Bird 911 Plus and a Seapoint fluorometer which continuously recorded temperature (T), salinity (S), oxygen and fluorescence. Fluorescence was measured and calculated as equivalent µg chl *a* l^{-1} (where chl *a* is chlorophyll *a*). The conventional unit (F) for *in vivo* fluorescence in the range of 0 to 5 V 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 <10%. Rough data of water depth (m), temperature (°C), salinity and fluorescence were processed with ODV software to obtain vertical profiles in real time. Two flowmeters installed inside and outside the net allowed the measurement of the filtered water volume and the filtration efficiency. At each sampling time, the BIONESS was deployed vertically down to the maximum depth of 2000 m, 2 times, for collecting mesozooplankton. During the first downcast, the physical structure of the water column, the thermocline, pycnocline 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. Standardised sampling intervals were 2000–1600, 1600–1400, 1400–1200, 1200–1000, 1000–800, 800–600, 600–400, 400–300, 300–200, 200–100 and 100–0 m for the deep haul, and 100–80, 80–60, 60–40, 40–20 and 20–0 m for the shallow haul. On board, a 2 l sample from each sampling layer was split, using a Folsom splitter, into 2 separate aliquots of 1 l each. A 1 l aliquot was filtered on a 200 µm mesh sieve, diluted in 10 ml of seawater and immediately frozen in liquid nitrogen for subsequent analysis of the ETS. The second 1 l aliquot was preserved in a 4% formaldehyde-seawater solution buffered with sodium tetraborate (Steedman 1976) for the subsequent taxonomic and quantitative analyses, as described below. The integrating samples 0–2000, 100–0 and 0–100 m from any time sampling were not used for the present study. A total of 60 frozen samples in 10 ml of seawater and 60 preserved samples of 1 l were used for the present study.

Vertical carbon flux quantification

Thorium fluxes and residence times were evaluated at 100 m depth by another operative unit involved in the same synoptic cruise (Dr. A. Schirone, Enea, La Spezia, Italy), assuming that thorium scavenging in this environment is mainly due to association with biogenic particles. The disequilibrium of ^{234}Th:^{238}U is commonly used to trace scavenging processes (Buesseler et al. 1992). ^{234}Th is a particle-reactive, naturally occurring radionuclide, produced in the water column by the decay of ^{238}U. After production, thorium can be scavenged onto particles and removed from the water column in association with them. The extent of the disequilibrium between ^{234}Th

and ^{238}U is an effective tracer of scavenging processes and particle residence times in coastal waters and in the upper ocean. Due to its short half-life (24.1 d), ^{234}Th can be used to trace scavenging processes on time scales varying from a few to about 100 d. Assuming steady state and negligible advection, the ^{234}Th-normalised particulate organic carbon (POC) export flux is defined as the product of the flux of ^{234}Th and the POC:^{234}Th ratio of sinking particles.

Particulate and dissolved ^{234}Th were pre-concentrated by filtration of large volumes of water (700 to 1000 l) using battery-powered *in situ* pumps. Seawater was pumped at a flow rate of 8 to 10 l min^{-1} through a prefilter (10 µm, Nitex) to collect suspended particles, then a polypropylene cartridge (0.5 µm) to retain the particulate matter and 2 MnO_2-impregnated cartridges (1 µm, polypropylene), in series, to extract dissolved thorium.

The particles collected with prefilters were then sonicated, divided in 3 aliquots and collected with 3 pre-combusted GF/F filters of 25 mm diameter. One filter was used for ^{234}Th evaluation on sinking particles by direct beta-counting. The other 2 filters were used for POC measurements, with a CHN Elemental Analyzer (Hedges & Stern 1984), thus allowing calculation of the POC:^{234}Th ratio.

The cartridges were ashed in the laboratory at 450°C and the ash obtained was sealed in plastic containers for gamma counting. ^{234}Th activity was calculated from the 63.3 keV emission peak, using an HPGe detector with a carbon fibre window. The calibration was performed by a certified ^{234}Th:^{238}U source with the same geometry and density. The accuracy of the results was checked by analysing standard reference materials. Thorium activities were corrected for extraction efficiency (E) using:

$$E = 1 - \mathrm{MnB/MnA} \quad (1)$$

where MnA and MnB are the activities measured in the first and second MnO_2 cartridge, respectively. The results were decay-corrected and divided by the volume filtered. All samples were counted within 1 mo from the date of sampling. The mean efficiency of the MnO_2 cartridges was 88 ± 5%. ^{238}U concentration was estimated by its relationship to salinity (Pates & Muir 2007). A box model was used to estimate the rate of thorium scavenging and removal by sinking particles (Savoye et al. 2006). The data obtained were used to calculate the organic carbon sinking flux, integrated over the whole water column investigated (2000 m). The organic carbon flux measured at 100 m depth was extrapolated to the depth (z) at the beginning and end of each zooplankton sampling interval by applying the following equation (Martin et al. 1987):

$$J_z = J_T/(z/T)0.858 \quad (2)$$

where J_z is the flux at depth z and J_T is the flux measured at depth T. The differences between the upper and the lower values gives a measure of the losses of organic carbon from the sinking POC-flux in each depth interval.

Mesozooplankton abundance and biomass

From each 1 l sample, subsamples (from 1/10 to 1/25 of the original sample, in relation to total abundance), obtained using a Stempel pipette, were observed under a stereomicroscope (Leica Wild M10). The whole 1 l sample was checked for the identification of rare species and for micronekton. All organisms were counted and classified at higher taxonomic levels, whereas diagnosis at the species level was carried out only for the most abundant taxa (e.g. copepods, euphausiids, cladocerans, chaetognaths). Data were normalised to the total volume filtered and expressed as ind. m^{-3}.

To better interpret the ETS data, attention was paid to the abundance of crustaceans and gelatinous taxa, to their relative importance, as well as to the distribution in the water column of vertically migrating species, with a focus on life stages of euphausiids (but not on the calyptopis stage; Marschoff et al. 1989, Stuart & Pillar 1990).

For the biomass estimates, a sub-aliquot of 250 ml from each sample was obtained using a Folsom splitter and was filtered onto a 200 µm net, and the retained animals were wet-weighed on an analytical balance according to Tranter (1962). Mesozooplankton biomass was expressed as mg wet wt m^{-3} of filtered seawater.

ETS activity

In the laboratory, the potential respiration and carbon demand of mesozooplankton was estimated from ETS activities measurements according to Packard (1971), Kenner & Ahmed (1975), Owens & King (1975), Koppelmann et al. (2000, 2004) and Koppelmann & Weikert 2003 and calculated using the following equation:

$$\mathrm{ETS_{assay}}\ (\mu l\ O_2\ g\ wet\ wt^{-1}\ h^{-1}) = A_{corr} \times H \times S \times 60/1.42 \times W \times f \times t \quad (3)$$

where A_{corr} is the absorbance of the sample at 490 nm corrected for blank and reagents, H is the homogenate volume (in ml), S is the reaction mixture volume (in ml), 60 converts minutes to hours, 1.42 is the conversion factor of INT-formazan into O_2 (in µl), w is the wet weight of the incubated sample (in g), f is the volume of the homogenate in the assay (in ml) and t is the incubation time (in min). The samples were incubated at 20°C, but the activities were adjusted for *in situ* temperature, assuming an activation energy (Ea) of 13.2 kcal mol^{-1} for bathypelagic mesozooplankton (Packard et al. 1975) and using the Arrhenius equation:

$$ETS_{in\ situ}\ (\mu l\ O_2\ g\ wet\ wt^{-1}\ h^{-1}) = ETS_{assay} \times e^{[Ea/R \times (1/T_{assay} - 1/T_{in\ situ})]} \quad (4)$$

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 hourly oxygen consumption rate was converted into daily carbon demand, expressed as µg C g wet wt^{-1} d^{-1}, assuming a respiratory quotient of 0.85 (King et al. 1978) and using the following equation:

$$ETS_{assay}\ (\mu g\ C\ g\ wet\ wt^{-1}\ d^{-1}) = ETS_{assay}\ (\mu l\ O_2\ g\ wet\ wt^{-1}\ h^{-1}) \times 0.85 \times 12 \times 24/22.4 \quad (5)$$

where 12 is the weight (in g) of 1 mol C, 24 converts hours to days and 22.4 is the gas volume mol^{-1} (l).

To interface the oxygen consumed measured throughout the ETS methodology to *in situ* respiration, the ETS:respiration ratio for natural mesozooplankton assemblages is typically assumed to be 0.5 (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 respiration:ETS are correct assuming that the ETS activity is measured at or near the V_{max} of electron transfer.

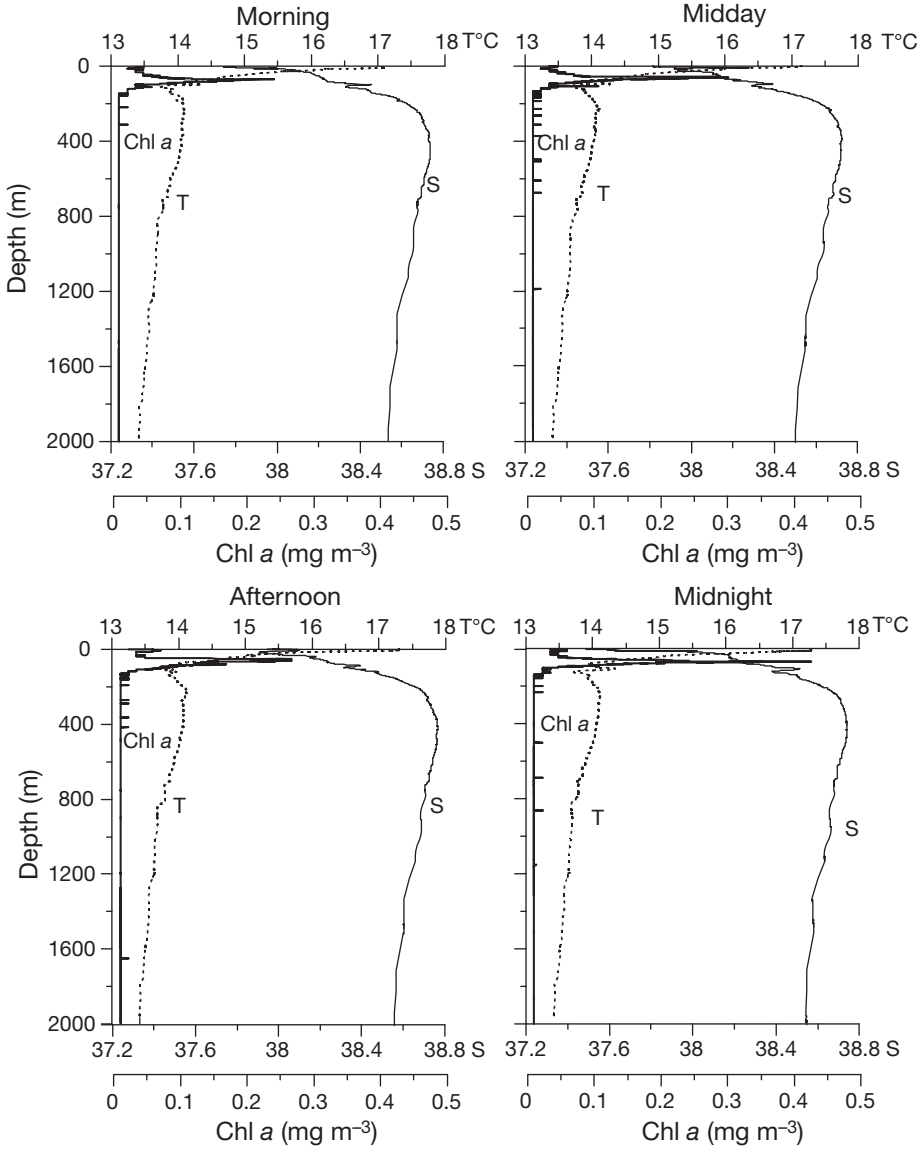

Fig. 2. Vertical profiles of temperature (T), salinity (S) and chl *a* concentration during the 4 sampling times

RESULTS

Environmental conditions

Profiles of water properties (T, S, chl *a*) collected during BIONESS hauls were used to obtain an overall hydrographical picture of the sampling station during the 24 h cycle. During all 4 sampling times, T and S showed similar vertical distribution patterns (Fig. 2). A typical stratified spring situation, with warmer waters at the surface (17.3°C in the layer 0 to 20 m) and a thermocline at about 150 m depth, were observed. Below the

thermocline and down to the maximum sampling depth, the temperature was about 14°C. The salinity showed values around 38, with less salt water occupying the upper 300 m of the water column. Chl *a* concentrations showed the same vertical distribution pattern at all sampling times: the maximum value was consistently observed at about 80 m depth and concentrations became almost undetectable below 150 m depth. Concentration of chl *a* was higher during the night (0.43 mg m^{-3} at midnight).

Mesozooplankton abundance, biomass and community composition

The total number of identified taxa (n = 26) remained constant at each sampling time. The total zooplankton weighted abundance, calculated summing up all counted specimens and dividing them by the total volume of filtered seawater, was 18.07, 16.47, 8.09 and 18.31 ind. m^{-3} in the morning, midday, afternoon and midnight, respectively (Table 1). Over the entire sampling period, copepods were the dominant taxon (representing 79 to 91% of the total abundance, at midday and in the morning, respectively). Copepod abundance varied from 7.15 ind. m^{-3} (afternoon) to 16.41 ind. m^{-3} (morning). The total number of copepod species identified was 67, 71, 70 and 75 in the morning, midday, afternoon and midnight samples, respectively.

Table 1. Mean weighted abundances (ind. m^{-3}) of total zooplankton, crustaceans and gelatinous taxa identified in the whole water column sampled during the 4 sampling times. ad+juv: adults plus juveniles

	Morning 06:00 h	Midday 12:00 h	Afternoon 18:00 h	Midnight 24:00 h
Zooplanktonic taxa				
Total zooplankton	18.070	16.470	8.090	18.310
Crustaceans				
Amphipoda	0.012	0.025	0.007	0.043
Calyptopis	0.074	0.233	0.060	0.082
Cladocera	0.001	1.392	0.235	1.604
Copepoda	16.410	12.940	7.150	14.800
Copepoda nauplia	0	0	0.002	0
Decapoda	0.001	0.002	0.002	0.001
Exuvie Decapoda	0	0.001	0.001	0.001
Euphausiacea ad+juv	0.044	0.018	0.023	0.050
Euphausiacea nauplia	0.014	0.004	0	0.029
Exuvie Euphausiacea	0.007	0.004	0.002	0.002
Furciliae	0.044	0.086	0.032	0.090
Isopoda	0	0	0.001	0.002
Misidacea	0.001	0	0	0
Ostracoda	0.410	0.436	0.180	0.449
Total	17.019	15.141	7.695	17.154
Gelatinous taxa				
Doliolida	0.030	0.082	0.007	0.047
Ephirae	0.001	0.017	0.002	0.048
Idromedusae	0.004	0.016	0.005	0.001
Salpae	0.001	0.004	0	0
Siphonophora	0.387	0.403	0.152	0.224
Total	0.424	0.521	0.165	0.320

Overall, both crustaceans and gelatinous mesozooplankton taxa represented relatively invariant fractions (92 to 95% and 1.7 to 3.2%, respectively) of the total mesozooplankton abundance. For the entire water column, the abundance ratio between gelatinous and crustacean taxa ranged from 1:29 to 1:53. Similar ratios were observed also in the upper 300 m of the water column (Table S1 in the supplement at www.int-res.com/articles/suppl/m446p091_supp.pdf), a layer in which the daily differences in carbon demand was evidenced.

Looking at the most important group in DVM, the highest abundance of euphausiids (adult + juvenile + furcilia stages) was observed at midnight in the upper 300 m of the water column, which was also true when considering adults plus juveniles and furcilia stages separately (213.4 and 465 ind. 1000 m^{-3} respectively) (Fig. 3). The abundance and frequency of total euphausiids in the 15 water column layers are reported in Table S2 in the supplement. Overall, 10 euphausiid species were found. *Euphausia krohni* was always the most abundant euphausiid species, representing from 38 to 55% of the total euphausiid abundance, with the exception of the afternoon sample, where *Nematoscelis megalops* became the most

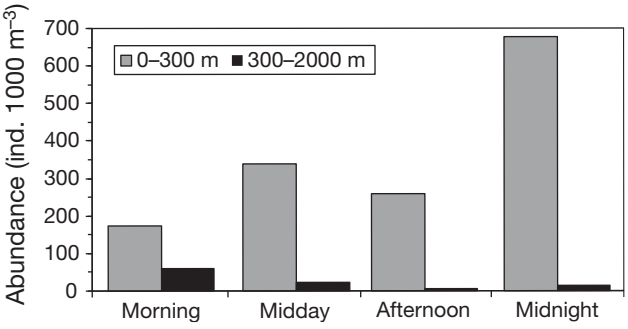

Fig. 3. Mean weighted abundance of euphausiid (adult + juvenile + furcilia stages) in the 0–300 m and 300–2000 m layers of the water column during the 4 sampling times

abundant species (44% of the total euphausiid abundance). *E. brevis*, *E. krohni*, *E. hemigibba*, *N. megalops* and *Thysanopoda aequalis* showed a clear daily migratory behaviour, whereas *N. atlantica*, *Stylocheiron abbreviatum*, *S. longicorne* and *Thysanoessa gregaria* did not vary their vertical distribution over the entire study period.

The abundance and species composition of migrant copepods did not vary among sampling times. Among these, specific attention was paid to the distribution of strong migrating species, like *Paraeuchaeta acuta*, *Pleuromamma gracilis* and *Pleuromamma abdominalis*, in terms of weighted abundance in the water column layers 0–300 m and 300–2000 m during the 4 sampling times (Table 2). *Pleuromamma gracilis* was always the most abundant species, representing from 80 to 96% of total abundance. With the exception of the morning sample, it was followed in decreasing order by *Pleuromamma abdominalis* and *Paraeuchaeta acuta*. In the upper 300 m of the water column, characterised by diel variations in the ETS activity values, the abundance of *Paraeuchaeta acuta* and *Pleuromamma abdominalis* did not show variations among the 4 sampling times (Fig. 4). In contrast, the abundance of *Pleuromamma gracilis* in the morning (3.68 ind. m^{-3}) and at midnight (2.56 ind. m^{-3}) was much higher than at midday (0.49 ind. m^{-3}) and in the afternoon (0.93 ind. m^{-3}).

Table 2. Mean weighted abundance of strong migrant copepod species (ind. m^{-3}) above and below 300 m depth during the 4 sampling times. Freq is the occurrence frequency of each species over the total abundance in the whole water column (0–2000 m)

	0–300 m	300–2000 m	Total specimens	Freq (%)
Morning (06:00 h)				
Paraeuchaeta acuta	0.0033	0.0315	0.024	2.33
Pleuromamma abdominalis	0.0196	0.0201	0.020	1.91
Pleuromamma gracilis	3.6791	0.0974	1.002	95.76
Midday (12:00 h)				
Paraeuchaeta acuta	0	0.0027	0.002	1.19
Pleuromamma abdominalis	0.1181	0.0008	0.031	18.39
Pleuromamma gracilis	0.4865	0.0143	0.138	80.43
Afternoon (18:00 h)				
Paraeuchaeta acuta	0.0344	0.0005	0.008	3.30
Pleuromamma abdominalis	0.1212	0	0.025	11.03
Pleuromamma gracilis	0.9295	0.0031	0.195	85.67
Midnight (24:00 h)				
Paraeuchaeta acuta	0.0057	0.0060	0.006	0.85
Pleuromamma abdominalis	0.2540	0.0118	0.069	9.95
Pleuromamma gracilis	2.5655	0.0217	0.623	89.21

Generally, during the entire sampling period, mesozooplankton biomass decreased with increasing water depth. The highest values of mesozooplankton wet-weighed biomass were found in the 60–80 m layer of the water column at all sampling times, with the exception of the afternoon sample, in which the highest biomass was observed in the 20–40 m layer (Fig. 5). In the upper 300 m of the water column, a progressive increase in zooplankton biomass was observed, from 80 mg wet wt m^{-3} in the morning and midday samplings, to 140 and 170 mg wet wt m^{-3} in the afternoon and midnight samplings, respectively.

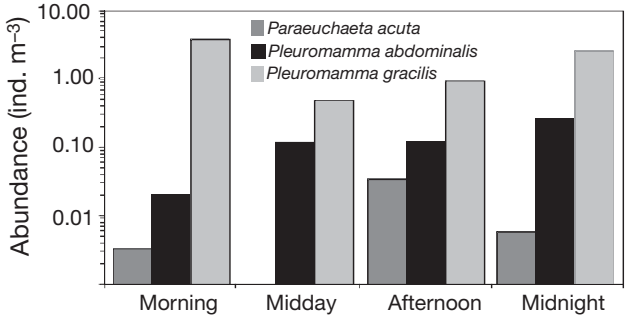

Fig. 4. Mean weighted abundance of strong migrant copepod species in the upper 300 m of the water column during the 4 sampling times (*y*-axis in log scale)

Zooplankton carbon requirement

Mesozooplankton carbon demand during the 4 hauls (morning, midday, afternoon and midnight) showed a different vertical distribution pattern from diurnal to nocturnal hours (Table 3).

Mesozooplankton carbon requirement below 300 m depth remained almost constant during all sampling times, with the exception of the midday sampling, when values were slightly higher than at all other sampling times (Fig. 6). Mean values of mesozooplankton carbon requirement in the upper 300 m of the water column were 279, 142, 153 and 270 µg C g^{-1} d^{-1} in the morning, midday, afternoon and midnight samples, respectively. Below 300 m depth, mesozooplankton carbon requirement was 160, 200, 166 and 165 µg C g^{-1} d^{-1}, respectively.

Carbon requirement in the 0–2000 m water column layer, normalised per mesozooplankton wet biomass

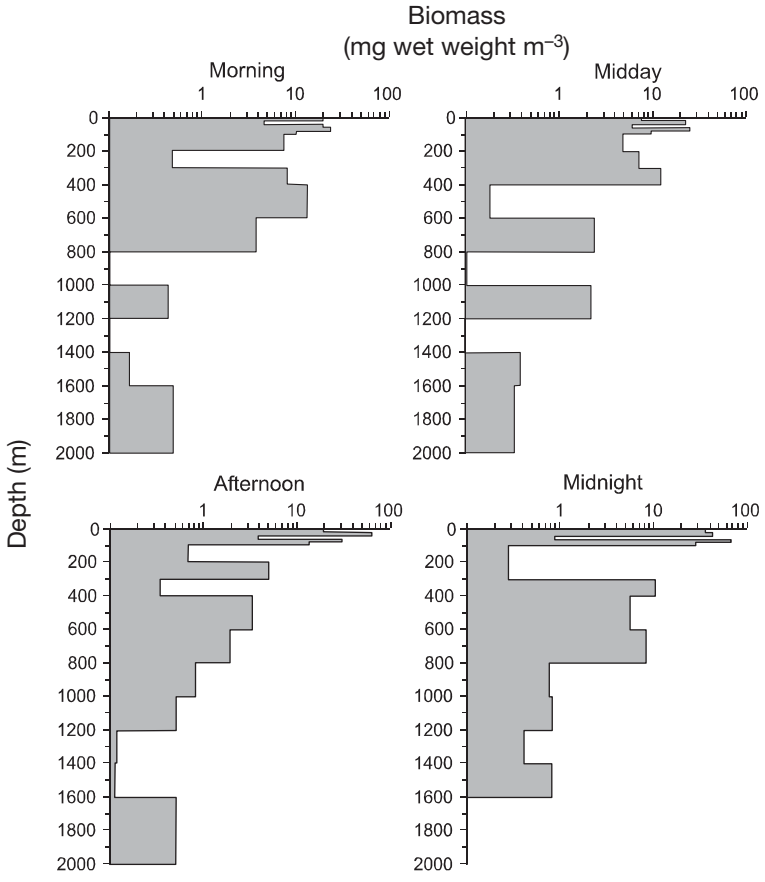

Fig. 5. Vertical distribution of mesozooplankton wet weight biomass down the sampled water column during the 24 h cycle (*x*-axis in log scale)

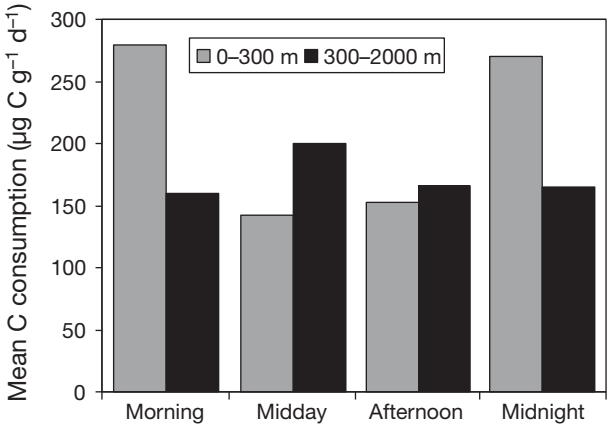

Fig. 6. Carbon requirement mean values, calculated by electron transport system activity, per gram of mixed zooplankton in the 0–300 m and 300–2000 m layers of the water column during the 4 sampling times

Table 3. Carbon demand of mesozooplankton (determined by electron transport system activity) during the 4 sampling periods from 0 to 2000 m depth. nd: not detected

Sampling	Layer (m)	*In situ* temperature (°C)	Carbon demand (µg C g^{-1} d^{-1})
Morning 06:00	0–20	15.78	397
	20–40	14.89	317
	40–60	14.43	320
	60–80	13.97	242
	80–100	13.88	261
	100–200	14.03	280
	200–300	14.08	133
	300–400	14.06	141
	400–600	13.94	179
	600–800	13.79	159
	800–1000	13.59	nd
	1000–1200	13.62	169
	1200–1400	13.48	155
	1400–1600	13.37	165
	1600–2000	13.42	151
Midday 12:00	0–20	15.46	108
	20–40	14.78	131
	40–60	14.60	177
	60–80	14.13	172
	80–100	13.84	155
	100–200	14.06	108
	200–300	14.09	142
	300–400	14.06	110
	400–600	13.91	203
	600–800	13.80	153
	800–1000	13.59	222
	1000–1200	13.61	204
	1200–1400	13.48	232
	1400–1600	13.50	239
	1600–2000	13.42	233
Afternoon 18:00	0–20	16.04	119
	20–40	15.09	116
	40–60	14.34	199
	60–80	14.13	96
	80–100	14.32	127
	100–200	14.08	137
	200–300	14.08	275
	300–400	14.07	149
	400–600	13.92	113
	600–800	13.80	109
	800–1000	13.59	246
	1000–1200	13.64	198
	1200–1400	13.46	133
	1400–1600	13.45	244
	1600–2000	13.42	137
Midnight 24:00	0–20	15.82	325
	20–40	14.93	328
	40–60	14.29	305
	60–80	13.93	218
	80–100	13.86	226
	100–200	14.07	276
	200–300	14.07	210
	300–400	14.03	100
	400–600	13.93	120
	600–800	13.80	233
	800–1000	13.67	137
	1000–1200	13.62	227
	1200–1400	13.47	197
	1400–1600	13.37	128
	1600–2000	13.42	181

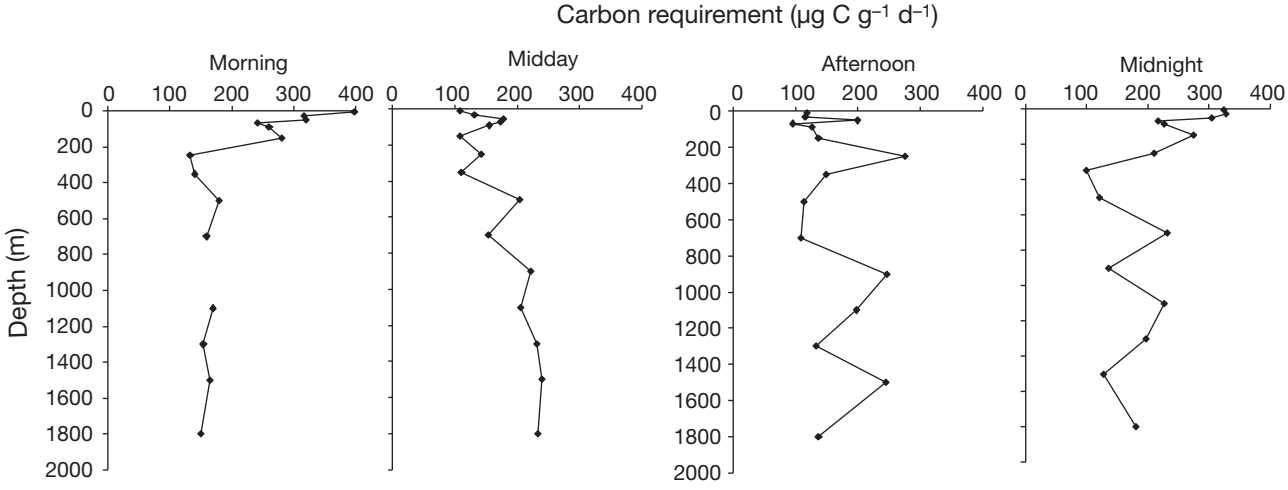

Fig. 7. Vertical diel *in situ* carbon requirement distribution from the surface to 2000 m depth during the 4 sampling times

unit, was characterised by higher values in the morning and midnight, than in midday and afternoon samples (Fig. 7).

The mesozooplankton carbon requirement, expressed as µg C m^{-3} d^{-1}, of the entire mesozooplanktonic community for each water column layer, calculated by multiplying the biomass value (g wet wt m^{-3}) by the estimated carbon demand (µg C g^{-1} d^{-1}), were analysed. During entire 24 h sampling cycle, the mesozooplankton carbon requirement showed the same vertical distribution, with the highest values consistently observed above 80 m depth during the entire sampling period (Fig. 8).

Mesozooplankton contribution to carbon losses from the sinking flux

Even though it was possible to measure the organic carbon downward flux from 20 m depth down to the maximum sampled depth, we show the results starting from 100 m depth, because the organisms in the epipelagic zone depend mainly on primary production as supported by the chl *a* maximum measured at 80 m depth, where mixing processes cannot be overlooked. During the study period, organic carbon downward flux at 100 m (58 mg C m^{-2} d^{-1}) was about 13-fold higher than that measured at 2000 m depth (4.44 mg C m^{-2} d^{-1}) (Table 4). Thus, the estimated

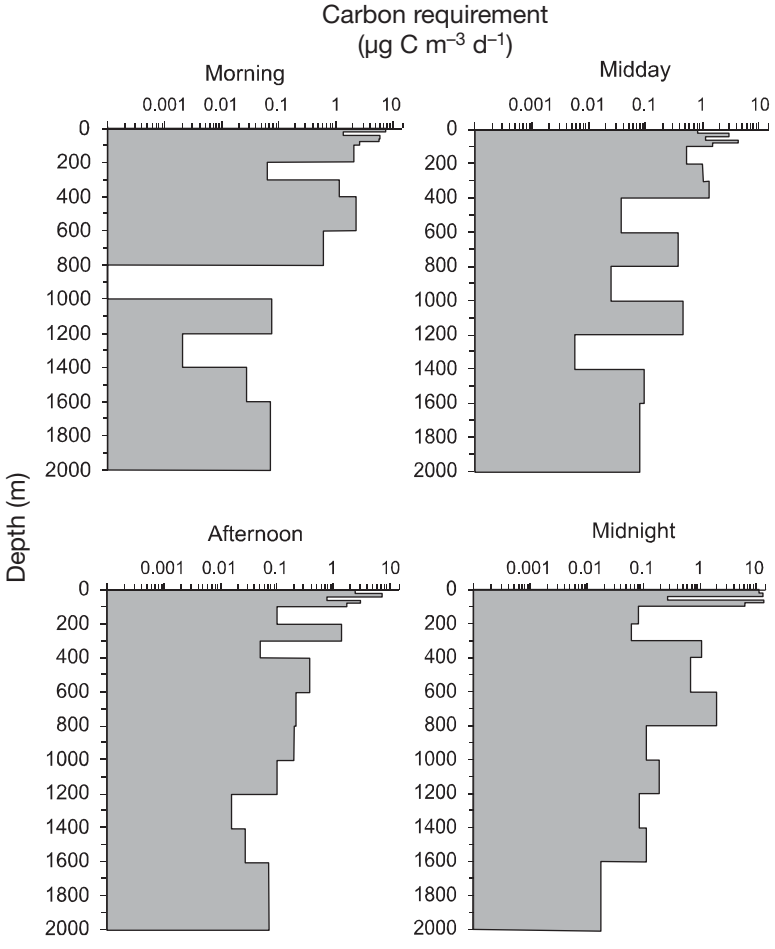

Fig. 8. Vertical distribution of mesozooplankton metabolic carbon requirements down the sampled water column during the 24 h cycle (*x*-axis in log scale)

Table 4. Sinking organic carbon flux calculated from the ^{234}Th:^{238}U disequilibrium at a fixed station in the Tyrrhenian Sea in April 2007. Calculations based on the estimated flux of 58.00 mg C m^{-2} d^{-1} at 100 m. The flux rate is extrapolated 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 the carbon losses are shown as means over the 4 sampling times

Sampling layer (m)	Sinking flux (mg C m^{-2} d^{-1})	Carbon losses (mg C m^{-2} d^{-1})	Carbon respired (µg C m^{-2} d^{-1})	Zooplankton biomass (mg wet wt m^{-2})	Zooplankton contribution (%)
100–200	58.00	26.00	69	329	0.27
200–300	32.00	9.40	64	327	0.68
300–400	22.60	4.94	90	775	1.81
400–600	17.65	5.19	173	1122	3.33
600–800	12.47	2.73	158	834	5.81
800–1000	9.74	1.70	23	89	1.34
1000–1200	8.04	1.16	41	203	3.55
1200–1400	6.88	0.85	5	29	0.63
1400–1600	6.03	0.65	13	77	2.00
1600–2000	5.37	0.94	24	145	2.60
Max. sampled depth	4.44				

carbon loss during particle descent down to 2000 m depth was about 92% (53.56 mg C m^{-2} d^{-1}) of the flux at the surface, of which the largest fraction was lost within the top 1000 m. From 1000 to 2000 m depth, the carbon loss was only 3.61 mg C m^{-2} d^{-1}.

DISCUSSION

The present study provides new information about the vertical distribution of the mesozooplankton carbon requirement down to 2000 m water depth in the open Tyrrhenian Sea, with clues about its role in the pelagic carbon flow within this pelagic ecosystem. The estimate of zooplankton respiration through ETS activity measurement represents an easy and advantageous method (Packard 1971, King & Packard 1975) which is well correlated with *in vivo* respiration rates (Packard et al. 1974, Kenner & Ahmed 1975, Owens & King 1975, Devol & Packard 1978). Since concomitant *in situ* measurements of respiration and ETS are not available for the deep sea, we could not give error values for the respiration:ETS ratio used. This relationship, as shown by Arístegui & Montero (1995), was not different with respect to other methods that measure other planktonic metabolic processes (Richardson 1991). The ETS method can therefore be useful for obtaining data on carbon requirements in bathypelagic environments below 1000 m water depth, an oceanic region very poorly investigated to date in this respect (Koppelmann & Weikert 1999, Koppelmann et al. 2000). Table 5 lists some *in situ* (Smith 1982, 1985, Smith et al. 1986) and ETS-estimated (Koppelmann et al. 2000, 2004, Hals-band-Lenk et al. 2003) respiration measurements, for the Pacific Ocean and for the Levantine and Arabian Seas, respectively.

The vertical distribution of mesozooplankton carbon requirement per unit biomass in the upper 300 m of the water column varied considerably among sampling periods, whereas it remained almost constant at deeper depths. Above 300 m depth, ETS activities in the morning and midnight samples were higher than in the midday and afternoon samples. Since the ETS activity was standardised per unit of biomass, variations in the zooplankton abundance cannot explain the observed temporal variations, though the oxygen demand is a function of body mass (Ikeda et al. 2001). Moreover, the minor changes in the community composition of mesozooplankton and in the values of the abundance ratio of gelatinous taxa over crustaceans during the different sampling times are most likely not responsible for the observed temporal variations in ETS activity. The abundance of copepod, euphausiid and decapod carcasses (about 0.01 carcasses m^{-3} for each replicate) was very low and did not show variations during the study period, suggesting that the ratio between carcasses and living specimens did not have a relevant role in controlling variations in carbon requirement estimates among sampling periods.

We paid particular attention to actively migrating organisms that mediate the vertical transport of material towards the ocean's interior (Longhurst 1976, Longhurst et al. 1990). Vertically migrant zooplankton and micronekton feed in surface waters and excrete at depth, potentially supporting microbial growth in the mesopelagic zone by actively transporting dis-

Table 5. Zooplankton carbon consumption data from the literature. All data were recalculated for the *in situ* temperature (~14°C) of the Tyrrhenian Sea, using the Arrhenius equation. ETS: electron transport system

Area	Depth (m)	Mesh size (µm)	Carbon consumption (µg C g wet wt^{-1} d^{-1})	Source	Notes
Levantine Sea	425 day/night	333	665/361	Koppelmann et al. (2004)	ETS
	1350		377		
	2750		860		
	4250		275		
	425 day/night	100	1242/578	Halsband-Lenk et al. (2003)	ETS
	1350		573		
	2750		310		
	4250		139		
	425 day/night	333	665/361	Halsband-Lenk et al. (2003)	
	1350		377		
	2750		860		
	4250		275		
Arabian Sea	1050	333	676	Koppelmann et al. (2000)	ETS
	2500		711		
	4000		445		
Pacific Ocean	1300	297	377	Smith (1982)	*In situ* measurement
	2615		712	Smith (1985)	*In situ* measurement
	3850		433	Smith et al. (1986)	*In situ* measurement

solved and particulate organic material (Longhurst et al. 1990, Burd et al. 2010). The total euphausiid abundance showed a typical vertical migration in the present study, with the highest densities typically observed above 100 m water depth during the dark hours. The 3 *Euphausia* species, *Nematoscelis megalops* and *Thysanopoda aequalis* all showed strong migratory behaviours, whereas *N. atlantica*, the 2 species of *Stylocheiron* and *Thysanoessa gregaria* consistently occupied the same water column layers during the entire 24 h sampling period. *Meganyctiphanes norvegica* was almost totally absent in our samples because it easily avoids the sampling device employed in the present study (Sameoto et al. 1993, Wiebe et al. 2004). The vertical distribution pattern of euphausiids does not seem to be at all correlated to the carbon consumption vertical trend during the 24 h cycle. As previously reported (Torres et al. 1979, Schalk 1988, Minutoli & Guglielmo 2009), at midday, afternoon and midnight, the vertical distribution of ETS activity in the present study resembled that of euphausiid abundance. On the other hand, in the morning, the high values of ETS activity were not associated with high euphausiid abundance. The high carbon demand observed above 300 m water depth in the morning samples is likely attributable to an actively migrant species, the calanoid copepod *Pleuromamma gracilis*, which was extremely abundant (3679 ind. 1000 m^{-3}), representing about 6% of the total mesozooplankton abundance in the same water column layer and sampling time. These results are in agreement with several previous studies which reported that in the pelagic environment, diel-migrant zooplankton have a higher respiratory activity than deeper-living and/or non-migrating zooplankton species (Childress 1969, 1971, 1975, Jannasch & Wirsen 1973, Packard et al. 1975, Jannasch et al. 1976, Torres et al. 1979).

The vertical distribution of zooplankton wet biomass increased from the morning to the dark hours, as previously reported, and not merely due to the increasing haul effectiveness at night (Hernández-León et al. 2001, Yebra et al. 2005). At night, the migrant organisms ascend for feeding, while during daylight hours, they return to deeper waters to avoid visual predators. This behaviour means that at night time, the majority of the zooplankton biomass is concentrated in the uppermost 300 m of the water column (Brinton 1967, Vinogradov 1968, Mauchline & Fisher 1969, Casanova 1974, Brancato et al. 2001, Yebra et al. 2005).

The mesh size of the net employed during the present study could have led to underestimating the abundance of some small copepod species (<0.5 mm)

and their early stages. Nevertheless, the BIONESS efficiently collects euphausiids and the migrant copepod species analysed in the present study (Herman 1992, 2001, Calbet et al. 2001).

The downward flux of POC is generally regarded as the most important source of organic carbon for the meso- and bathypelagic zones (Burd et al. 2010). Sediment traps are the most common tools for estimating sinking fluxes, though their use has many documented accuracy issues (Lee et al. 1988), especially in the upper 1000 m of the water column (Buesseler et al. 2007, Burd et al. 2010). The disequilibrium ^{234}Th:^{238}U method can be considered as a valid alternative for most of the depth intervals under scrutiny in the present study. Furthermore, the use of this method avoids the underestimation of the carbon availability at great depths, and it has been even used to correct flux data estimated using sediment traps (Scholten et al. 2001, Halsband-Lenk et al. 2003). Changes in POC flux with depth are often estimated using regression equations, including the Martin curve (Martin et al. 1987), from the literature, rather than by direct observation, relating flux at depth to a known flux at a given depth. The regression equations that relate water depth and the POC flux can be used to estimate the POC removed by heterotrophic consumption. In the present study, the carbon flux, estimated from the ^{234}Th:^{238}U disequilibrium at 100 m depth and then integrated for the entire water column using the equation suggested by Martin et al. (1987), decreased from 100 to 2000 m depth (Table 4).

The relative contribution of zooplankton respiration to the decrease in POC flux varies spatially, temporally and also vertically (Burd et al. 2010). The metabolic requirement of the mesozooplankton in the open Tyrrhenian Sea ranged from 0.27 to 5.81% of the measured carbon losses (Table 4). Higher remineralisation values occurred below 300 m depth, with a mean value of 2.75%, about 3 times higher than in the upper 300 m of the water column (0.92%). Mesozooplankton carbon requirements can be assumed to be approximately 30% of the microplankton requirements in bathypelagic environment (King et al. 1978, Packard et al. 1988), so that the majority of carbon losses are likely due to requirements by other zooplankton size classes, including microplankton and heterotrophic prokaryotes, as well as by the transfer of organic carbon into the dissolved pool (King et al. 1978, Packard et al. 1988, Koppelmann et al. 2000). In the present study, the percentage contribution of mesozooplankton respiration to organic carbon losses for the meso- and bathypelagic zones were 13.24% from 100 to 1000 m depth and 8.78% from 1000 to 2000 m depth. These results are in agreement with previous studies (Martin et al. 1987, Burd et al. 2010). In the epipelagic waters, the contribution of mesozooplankton respiration was very low (1.42%), indicating the dominance of autrotrophic processes in this upper layer of the water column. The mesopelagic layer, mostly characterised by heterotrophic activities, however accounts for the bulk of the decrease in particulate organic sinking flux (Martin et al. 1987). Below 1000 m water depth, the respiration by mesozooplankton decreases again because of the decrease in abundance values.

In the bathypelagic zone of the Arabian Sea, Koppelmann et al. (2000) estimated a mesozooplankton metabolic requirement of about 4 to 5% of the measured carbon losses. The feeding strategies and behaviour of meso- and bathypelagic zooplankton differ from their epipelagic counterparts (Wishner et al. 2000, Koppelmann et al. 2009), so that it can be inferred that meso-, bathy- and epipelagic zooplankton communities play different roles in the carbon binding activity in these 3 ecological zones along the water column.

Even if the low chlorophyll concentration, zooplankton abundance and biomass, and POM sinking flux confirmed the oligotrophic status of the open Tyrrhenian Sea, the percentage contribution of mesozooplankton to the carbon losses reflects the less oligotrophic conditions compared to the central and eastern parts of the Mediterranean Sea (Scotto di Carlo & Ianora 1983, Weikert & Trinkaus 1990, Kerhervé et al. 1999). Our results show that, in the open southern Tyrrhenian Sea, mesozooplankton may contribute to a certain extent to the carbon losses during particle descent and that their metabolism represents a relatively important pathway for carbon cycling in epipelagic waters (Thiel 1983, Tselepides & Eleftheriou 1992).

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