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Zooplankton respiratory Electron Transport System (ETS) activity in the Mediterranean Sea: spatial and diel variability

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ABSTRACT: The zooplankton community plays a key role in biological carbon binding activity in the epipelagic marine ecosystem. The activity of the Electron Transport System (ETS), located in the mitochondrial membrane, is a specific and highly sensitive method to determine respiration rates and thus evaluate zooplankton carbon requirements. The present study focuses on the geographical distribution of zooplankton carbon demand and its day/night variability (measured over a 24 h period) in the top 200 m of the water column at 10 sampling stations throughout the Mediterranean Sea, from the Strait of Gibraltar to the Isle of Rhodes. To interpret the ETS data, species composition, abundance, and biomass (in mg wet weight m^{-3}; mg wet wt m^{-3}) of zooplankton were investigated. Oxygen consumption (µl O_2 g^{-1} h^{-1}) rates were recalculated for measured *in situ* temperatures, converted into carbon demand and expressed as µg C g wet wt^{-1} d^{-1}. The carbon requirements per unit zooplankton biomass indicated spatial, geographical and day/night differences in the Mediterranean Sea. The data revealed an increasing gradient from the Strait of Gibraltar to the easternmost station near the Isle of Rhodes, going from a mean value of 240 866 to 419 344 µg C g wet wt^{-1} d^{-1}. The relationship between zooplankton ETS activity and sea surface temperature was analysed. At all stations, ETS activities, and thus carbon demand, were higher in samples collected between sunset and sunrise than in those collected during daytime. This was related to actively migrating organisms that mediate the vertical transport of material in the sea.

KEY WORDS: Electron Transport System · Oxygen consumption · Carbon consumption · Zooplankton · Mediterranean Sea

INTRODUCTION

The accumulation and segregation of CO_2 in the ocean has been a main topic of the international scientific community for many years. Carbon can be bound in the epi- and mesopelagic zones for months to several years (Koppelmann et al. 2000). All abiotic and biotic compartments in the ocean are involved in the transport and/or transformation of carbon. Among all these processes, the formation of particulate organic matter (POM) in the upper ocean plays a key role. The primary source of POM in the ocean is autotrophic, carbon-fixing phytoplankton organisms (Bradford-Grieve et al. 2001). POM cycling in the ocean's interior is controlled by the interaction of physical, chemical and biological forces (Koppelmann et al. 2004). Many taxa use POM as a food source, thus decreasing the total amount. In fact, only 10% reaches the seafloor, while the main part is consumed, remineralized, and converted into new biomass (Berger et al. 1988, Koppelmann et al. 2000).

Among the consumers, a key role in carbon binding activity is played by the mesozooplankton community (Smith 1982, 1987, Sasaki et al. 1988, Longhurst 1991, Lampitt 1992, Steinberg et al. 1997, Koppelmann et al. 2000, Christiansen et al. 2001, Yamaguchi et al. 2002,

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Halsband-Lenk et al. 2003). The net contribution to remineralization (respiration) consists of ingestion minus defecation, growth and excretion (Lampitt 1992).

The determination of respiration rates based on electron transport system (ETS) activities is a specific and highly sensitive method to estimate the zooplankton carbon requirement and thus the proportion of carbon removed from the sinking flux (Packard 1971, King & Packard 1975, Owens & King 1975, Bamstedt 1979, 1980, Bidigare et al. 1982). The ETS, nearly ubiquitous in living organisms and located in the mitochondrial membranes, consists of a complex chain of cytochromes, flavoproteins and metabolic ions that transport electrons from catabolized foodstuffs to oxygen. The rate-limiting step is the oxidation of the coenzyme Q-cytochrome B complex, which can be measured by its reaction with the artificial electron acceptor 2-(p-iodophenyl)-3-(p-nitrophenyl)-5-phenyl tetrazolium chloride (Packard 1971). This enzymatic transport is influenced by various factors such as temperature, salinity, and sexual stage (Torres et al. 1979, Ikeda & Hing Fay 1981, Raymont 1983, Schalk 1988), even if acclimatization to environmental conditions is possible (Bamstedt 1980, Hirche 1984). High or low ETS values in zooplankton may indicate growing or declining populations, respectively, or the beginning or end of a phytoplankton bloom the zooplankton is feeding on. In fact, the relationships between respiratory activity and growth, reproduction, crowding and starvation have long been demonstrated (Schalk 1988). More than one study has shown a good correlation between ETS activity and *in vivo* respiration (Packard et al. 1974, Kenner & Ahmed 1975b, Owens & King 1975, Devol & Packard 1978).

Geographical and seasonal differences in zooplankton respiratory activity in oceans have also been demonstrated (Marshall & Orr 1956, Conover 1959, Conover & Corner 1968, Gaudy 1973, Marshall 1973, Raymont 1983, Schalk 1988). However, data on ETS activities in mesozooplankton and micronekton of the Mediterranean Sea are scarce. The only region that has been investigated is the Levantine Sea near Crete, where only the ETS activity of deeper zooplankton was measured but the diel cycle was not analyzed (Halsband-Lenk et al. 2003, Koppelmann & Weikert 2003, Koppelmann et al. 2004).

The present study focuses on geographical differences in zooplankton carbon demand and its diel variability at 10 stations, from a reference station in the Atlantic near the Strait of Gibraltar to the Isle of Rhodes in the Mediterranean Sea. To interpret the ETS data, the relative species composition, abundance and biomass were investigated and the relationships between ETS activity (oxygen and carbon demand) and composition and/or abundance of zooplankton and temperatures of the basins were determined.

MATERIALS AND METHODS

Field sampling. Samples were taken during the second and third legs of the TRANSMED oceanographic cruise (28 May to 28 June 2007) from Cadiz in the North Atlantic, through the Strait of Gibraltar and the western and eastern Mediterranean, to the Isle of Rhodes (Fig. 1). This expedition was part of the large Italian project VECTOR (VulnErability of the Italian coastal area and marine ecosystems to Climatic changes and Their rOle in mediterranean caRbon cycles). During the second leg (28 May to 12 June 2007), the

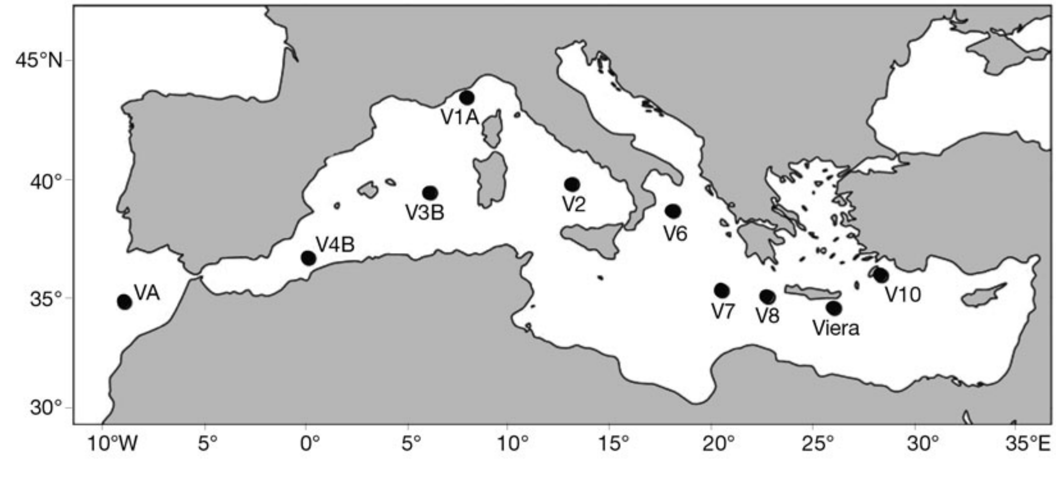

Fig. 1. Zooplankton sampling stations in the Mediterranean Sea during the second and third legs of the TRANSMED oceanographic cruise 28 May to 28 June 2007

upper 200 m of the water column were sampled 4 times during a 24 h cycle (06:00, 12:00, 18:00, 24:00 h) at 5 stations (VA, V4B, V3B, V1A, V2) in the western Mediterranean (WM) in order to study the change in zooplankton composition caused by diel vertical migrations and its potential relation with the obtained ETS values. At Stn V3B, only 3 samplings were carried out. During the third leg (12 to 28 June 2007), the upper 200 m of the water column were sampled at 5 stations (V6, V7, V8, Viera, V10) in the eastern Mediterranean (EM); however, during this cruise only 3 samplings were carried out over the 18 h available at each station, except at Stn V10 where it was possible to carry out 4 samplings. All sampling details are summarized in Table 1. If the actual time of sampling differed greatly from the intended sampling time, this is indicated to avoid misinterpretation of results.

A total of 35 samples were collected vertically using the 1 m^2 Indian Ocean standard net (IOSN) with a mesh size of 335 µm. A flow meter (Hydro Bios) was connected to the net to measure the volume of seawater filtered by the net. On board, each sample was split into 2 aliquots of 1 l: one aliquot was filtered through a 335 µm mesh sieve and immediately frozen in liquid nitrogen for the ETS measurements; the other was preserved in 4% formaldehyde–seawater solution, buffered with sodium tetraborate (Steedman 1976), for the ecological qualitative and quantitative analyses.

Environmental parameters at the sampling stations were measured with a CTD SBE911 equipped with primary sensors for conductivity (mS), temperature (°C), depth (m), fluorescence (V), and dissolved oxygen (ml l^{-1}).

Electron Transport System analysis. In the laboratory, ETS activity (as amount oxygen per gram wet weight per hour, µl O_2 g wet wt^{-1} h^{-1}) as a measure of potential respiration and carbon demand was determined for the 35 frozen samples according to Packard (1971), Kenner & Ahmed (1975a), Owens & King (1975), Koppelmann et al. (2000, 2004), and calculated by the following equation:

$$\mathrm{ETS}_{\mathrm{assay}} = A_{\mathrm{corr}} \times H \times S \times 60/1.42 \times W \times f \times t \qquad (1)$$

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 volume of the reaction mixture in

Table 1. Sampling details of the western and eastern leg of the 'VECTOR TRANSMED' cruise. Samples were taken at: morning 06:00 h; midday 12:00 h; afternoon 18:00 h; midnight 00:00 h. If the time of sampling differed, the exact time is given in parentheses

Stn Sampling run	Sampling date (DD/MM/YY)	Latitude N	Longitude W	Sampling time (h)
Eastern Mediterranean				
VA				
1	29/05/07	35° 00′ 02″	08° 20′ 02″	Midday
2	29/05/07	34° 59′ 96″	08° 20′ 04″	Afternoon
3	30/05/07	35° 00′ 02″	08° 20′ 03″	Midnight
4	30/05/07	34° 59′ 86″	08° 19′ 96″	Morning (09:00)
V4B				
1	01/06/07	36° 29′ 99″	00° 59′ 98″	Morning
2	01/06/07	36° 29′ 93″	00° 59′ 85″	Midday
3	01/06/07	36° 30′ 01″	00° 59′ 97″	Afternoon
4	01/06/07	36° 29′ 90″	00° 59′ 94″	Midnight
V3B				
1	03/06/07	39° 18′ 74″	06° 04′ 07″	Afternoon
2	04/06/07	39° 18′ 79″	06° 04′ 17″	Morning
3	04/06/07	39° 19′ 91″	06° 02′ 57″	Midday
V1A				
1	05/06/07	43° 29′ 98″	08° 00′ 01″	Afternoon
2	06/06/07	43° 30′ 00″	08° 00′ 08″	Midnight
3	06/06/07	43° 29′ 99″	07° 59′ 96″	Morning
4	06/06/07	43° 30′ 04″	07° 59′ 39″	Midday
V2				
1	08/06/07	39° 29′ 99″	13° 00′ 01″	Midnight
2	08/06/07	39° 29′ 99″	13° 00′ 13″	Midday
3	08/06/07	39° 29′ 93″	13° 00′ 06″	Afternoon (20:00)
4	08/06/07	39° 29′ 93″	12° 59′ 99″	Midnight
Western Mediterranean				
V6				
1	14/06/07	38° 29′ 42″	17° 60′ 00″	Midday
2	14/06/07	38° 29′ 21″	17° 59′ 45″ E	Afternoon
3	14/06/07	38° 29′ 36″	17° 59′ 36″ E	Midnight
V7				
1	16/06/07	35° 07′ 48″	20° 52′ 19″	Morning (08:30)
2	16/06/07	35° 08′ 10″	20° 51′ 52″	Midday
3	16/06/07	35° 08′ 23″	20° 54′ 19″	Afternoon (20:00)
V8				
1	17/06/07	34° 52′ 17″	22° 33′ 53″	Midday
2	17/06/07	34° 50′ 16″	22° 39′ 40″	Afternoon
3	17/06/07	34° 49′ 07″	22° 42′ 37″	Afternoon (20:30)
Viera				
1	24/06/07	34° 24′ 48″	26° 04′ 52″	Midday
2	24/06/07	34° 24′ 14″	26° 05′ 29″	Afternoon
3	24/06/07	34° 25′ 20″	26° 05′ 31″	Midnight (22:00)
V10				
1	22/06/07	35° 57′ 13″	28°19′ 19″	Midnight (22:00)
2	22/06/07	35° 55′ 30″	28°19′ 17″	Midnight
3	23/06/07	35° 57′ 12″	28°19′ 19″	Morning (08:30)
4	23/06/07	35° 56′ 18″	28°19′ 12″	Midday

ml, the factor 60 converts min to h, 1.42 is the conversion factor of INT-formazan into O_2 as 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. To determine *in situ* ETS activities ($ETS_{in\ situ}$, µl O_2 g wet wt^{-1} h^{-1}), all activities were recalculated for *in situ* temperatures using the Arrhenius equation, assuming an activation energy (Ea) of 13.2 kcal mol^{-1} for bathypelagic zooplankton (Packard et al. 1975):

$$ETS_{in\ situ} = ETS_{assay} \times e^{((Ea/R \times (1/T_{assay} - 1/T_{in\ situ}))} \quad (2)$$

where R is the gas constant, T_{assay} is the temperature of the assay and $T_{in\ situ}$ is the *in situ* temperature of the sampled sea water layers.

The rate of oxygen consumption per hour was converted into carbon demand per day, expressed as µg C g wet wt d^{-1}, assuming a respiration factor of 0.85 (King et al. 1978, Koppelmann et al. 2000):

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

where 12 is the weight of 1 mol C (g), the factor 24 converts h into d and 22.4 is the volume (in l) of 1 mol oxygen.

Table 2. Oxygen and carbon consumption rates (determined by electron transport system activity) of zooplankton collected in the 0 to 200 m layer during the 24 h cycle. See station and sampling time details in Table 1. If the time of sampling differed, the exact time is given in parentheses

Stn	Sampling run	Oxygen demand			Carbon demand		Sampling time
		(µl O_2 g^{-1} h^{-1}) Measured	*In situ*	(µmol O_2 g^{-1} h^{-1})	(µg C g^{-1} h^{-1})	(µg C g^{-1} d^{-1})	
Western Mediterranean							
VA	1	27.59	17.99	0.80	8.19	197	Midday
	2	28.69	18.71	0.84	8.52	204	Afternoon
	3	45.75	29.84	1.33	13.59	326	Midnight
	4	33.14	21.61	0.96	9.84	236	Morning (09:00)
V4B	1	49.29	27.41	1.22	12.48	299	Morning
	2	43.77	24.34	1.09	11.08	266	Midday
	3	41.28	22.96	1.02	10.45	251	Afternoon
	4	60.05	33.39	1.49	15.21	365	Midnight
V3B	1	41.21	25.02	1.12	11.39	273	Afternoon
	2	56.04	34.03	1.52	15.49	372	Morning
	3	42.83	26.01	1.16	11.84	284	Midday
V1A	1	45.20	23.76	1.06	10.82	260	Afternoon
	2	64.63	33.97	1.52	15.47	371	Midnight
	3	53.53	28.14	1.26	12.81	307	Morning
	4	41.10	21.60	0.96	9.84	236	Midday
V2	1	52.94	31.14	1.39	14.18	340	Midnight
	2	41.87	24.63	1.10	11.21	269	Midday
	3	43.78	25.75	1.15	11.73	281	Afternoon (20:00)
	4	54.39	31.99	1.43	14.57	350	Midnight
Eastern Mediterranean							
V6	1	42.77	27.45	1.23	12.50	300	Midday
	2	40.18	25.80	1.15	11.75	282	Afternoon
	3	51.37	32.98	1.47	15.02	360	Midnight
V7	1	47.76	31.65	1.41	14.41	346	Morning (08:30)
	2	49.37	32.72	1.46	14.90	357	Midday
	3	57.22	37.91	1.69	17.26	414	Afternoon (20:00)
V8	1	61.65	39.27	1.75	17.88	429	Midday
	2	60.32	38.42	1.71	17.49	420	Afternoon
	3	63.34	40.34	1.80	18.37	441	Afternoon (20:30)
Viera	1	45.63	34.56	1.54	15.74	378	Midday
	2	47.99	36.35	1.62	16.55	397	Afternoon
	3	50.86	38.52	1.72	17.54	421	Midnight (22:00)
V10	1	65.70	42.51	1.90	19.36	464	Midnight (22:00)
	2	66.56	43.07	1.92	19.61	471	Midnight
	3	51.58	33.38	1.49	15.20	365	Morning (8:30)
	4	53.35	34.53	1.54	15.72	377	Midday

The ratio for converting measured ETS activities to *in situ* oxygen consumption for natural zooplankton assemblages is 0.5 (Kenner & Ahmed 1975a,b, King & Packard 1975, Hernandez-Leon & Gomez 1996, Koppelmann et al. 2000). Packard (1971) and Packard & Richards (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 R:ETS are reasonable, assuming that the ETS activity is measured at or near the V_{max} of electron transfer.

Zooplankton abundance and biomass. Qualitative and quantitative analyses were carried out on the 35 preserved samples. To determine total zooplankton abundances, subsamples of 1/10 to 1/25 of any 1 l sample were taken and sorted under a stereomicroscope (Leica Wild M10). The entire sample was sorted for the identification of rare species and micronekton. All organisms of each taxon were counted and classified at higher taxonomic levels, while species-level identification was carried out only for the main groups, including copepods, cladocerans, euphausiids, and chaetognaths. All data were reported as total abundance in 2 l, divided by the volume of seawater filtered during net tows, and expressed as ind. m^{-3}.

For the biomass analysis, a 250 ml subsample from each 1 l sample was obtained using a Folsom Splitter and wet weighed according to the method of Tranter (1962). Biomass values were expressed as mg m^{-3} of filtered seawater.

RESULTS

Spatial patterns in carbon demand

Oxygen consumption (µl O_2 g^{-1} h^{-1}) as measured by ETS activity, recalculated for *in situ* temperature and subsequently converted into carbon demand (µg C g^{-1} d^{-1}) of zooplankton in all samples collected in the 0 to 200 m layer during the 24 h cycle are shown in Table 2.

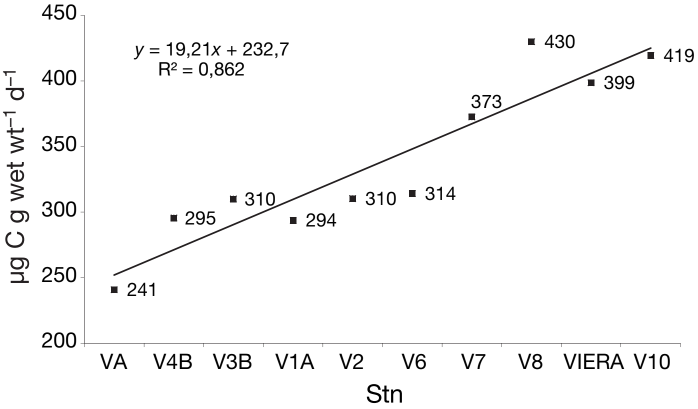

Fig. 2. Mean carbon consumption (µg C g^{-1} d^{-1}), calculated by electron transport system activity, per gram wet weight of mixed 0 to 200 m depth zooplankton from all sampling stations

The biochemical analyses showed differences in mean carbon consumption rates between the samples from western and eastern stations. In fact, the mean value of the 19 samples collected in the western sector was 290 µg C g^{-1} d^{-1}, compared to 387 µg C g^{-1} d^{-1} in the 16 samples collected in the Levantine Basin. Mean values for the different sampling times at each station are reported in Fig. 2. An increasing gradient in carbon demand from a mean value of 241 µ Cg^{-1} d^{-1} at the Strait of Gibraltar to 419 µg C g^{-1} d^{-1} at the easternmost station near the Isle of Rhodes was detected, with a significant R^2 value of 0.86 for the regression line (Fig. 2) (ANOVA $p < 0.5$ %, $F = 2.32$; Table 3).

Trends for carbon demands per unit biomass of zooplankton in all morning, midday, afternoon and midnight samples, which showed the same profile of the mean, are reported in Fig. 3. The values in the samples collected in the WM ranged from a minimum of 197 µg C g^{-1} d^{-1} in the midday samples from Stn VA to a maximum value of 372 µg C g^{-1} d^{-1} for the morning sampling, before sunrise, at Stn V3B. The station showing the lowest minimum mean value was VA (241 µg C g^{-1} d^{-1}), while that with the mean highest ETS value during the different times in 24 h, was V2 (311 µg C g^{-1} d^{-1}), off Naples in the Tyrrhenian Sea. Among the zooplankton samples collected during the Levantine leg, data ranged from a minimum value of 282 µg C g^{-1} d^{-1}, for the afternoon zooplankton sampling at Stn V6 to a maximum value of 471 µg C g^{-1} d^{-1} for the midnight sampling at Stn V8. The station that showed the lowest minimum mean value of ETS activity was V6 (314 µg C g^{-1} d^{-1}), while that with the highest mean value was V8 (429.94 µg C g^{-1} d^{-1}), similar to the easternmost V10 (419 µg C g^{-1} d^{-1}).

Table 3. Differences in electron transport system activity between western and eastern Mediterranean and among sampling groups, as determined by ANOVA

Source	Deviance Sums of squares	df	Variance Mean squares	F	p (%)
Between means	102125.3	9	11347.3	2.32	$p < 0.5$
Within Time samplings	25068.9	3	8356.3	3.15	$p < 0.1$
Error	26320.6	19	1385.3		
Total	153514.8	31			

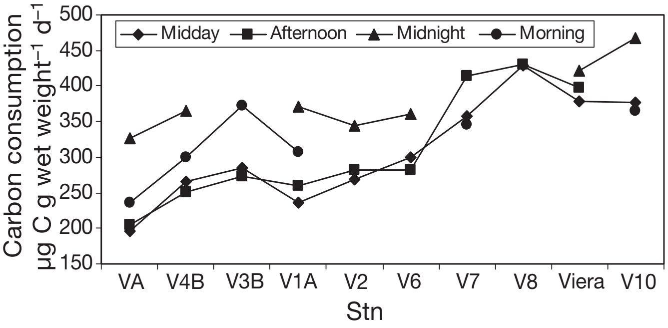

Fig. 3. Carbon consumption, calculated by electron transport system activity, plotted separately for morning (06:00 h), midday (12:00 h), afternoon (18:00 h) and midnight (00:00 h) zooplankton samples (where the time sampling differed, this is reported in Table 1)

ANOVA, applied to groups of data for the 4 sampling occasions, showed a statistically significant west–east trend for all sampling times, with an *F*-value of 3.15 ($p < 0.1\%$) (Table 3).

Diel variability

The ETS analyses indicated diel differences in zooplankton distribution in the 0 to 200 m water layer (Table 2). Higher values were found in the samples collected between sunset and sunrise at all stations, compared to those taken during the day. For example, the carbon requirement of samples from the westernmost Stn VA (out of the Strait of Gibraltar) was 326 µg C g^{-1} d^{-1} in the midnight sample compared to 197 µg C g^{-1} d^{-1} in the sample taken at midday; at the easternmost Stn V10 (near Rhodes), the carbon requirement of the midnight sample was 471 µg C g^{-1} d^{-1} compared to 377 µg C g^{-1} d^{-1} in the midday sample.

Zooplankton composition and abundance

Table 4 shows the results of the qualitative and quantitative analyses of the samples taken at midday at all 10 sampling stations. Concerning general taxonomic composition, the western stations showed the same mean value of identified taxa (17) as the eastern stations, with the highest number (22) observed at Stn VA and the lowest (13) at Stn V1A.

Total mean zooplankton abundances in the midday samples was higher for the western (64.17 ind. m^{-3}) compared to the eastern sector (32.43 ind. m^{-3}). The lowest abundances were found in the 3 samples taken from midday to evening at the eastern Stn V8 (15.69,

Table 4. Abundances (ind. m^{-3}) of total zooplankton, crustacean, tunicate and gelatinous taxa identified in the midday (12:00 h) collections at the 10 sampling stations. Stn details are given in Table 1

Taxa	VA	V4B	V3B	V1A	V2	V6	V7	V8	Viera	V10
Total zooplankton[a]	32.25	103.31	22.18	129.37	33.74	24.49	36.23	15.69	26.87	58.89
Crustacea										
Amphipoda	0.12	0.00	0.00	0.03	0.14	0.08	0.29	0.05	0.00	0.35
Copepoda	25.24	35.11	8.42	119.78	22.58	16.98	22.56	10.62	13.67	41.00
Copepoda nauplii	0.00	0.00	0.00	0.00	0.07	0.00	1.42	0.00	0.30	0.35
Cladocera	0.47	34.51	1.79	3.47	2.11	0.00	0.00	0.18	0.00	0.00
Decapoda	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Euphausiacea adults and juveniles	0.03	0.00	0.13	0.03	0.00	0.09	0.06	0.06	0.00	0.00
Euphausiacea nauplii	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Calyptopis	0.12	0.30	0.00	2.15	0.00	0.26	0.22	0.00	0.00	0.00
Furciliae	0.13	0.09	0.03	0.49	0.14	0.00	0.06	0.08	0.01	0.01
Misidacea	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Ostracoda	0.47	2.12	0.38	0.33	1.09	1.15	0.97	0.48	0.90	0.96
Total	26.58	72.13	10.75	126.29	26.13	18.56	25.58	11.47	14.88	42.67
Tunicata										
Appendicularia	2.13	4.54	2.31	0.99	2.58	0.88	2.54	0.54	2.00	1.84
Chaetognata	0.24	3.63	4.24	0.03	0.27	0.00	2.54	1.50	1.60	5.70
Total	2.36	8.17	6.55	1.02	2.85	0.88	5.08	2.04	3.60	7.54
Gelatinous zooplankton										
Doliolida	0.94	15.44	1.28	0.00	0.07	0.18	2.17	0.24	0.40	4.91
Idromedusae	0.35	0.91	2.18	0.16	0.75	0.08	0.15	0.00	1.20	0.35
Salpae	0.00	0.00	0.00	0.00	0.14	0.00	0.00	0.00	0.20	0.00
Siphonophora	0.83	2.72	0.77	0.49	2.31	2.30	1.19	1.08	0.60	2.54
Total	1.30	16.35	3.46	0.16	0.96	0.26	2.32	0.24	1.80	5.26

[a] Includes listed taxa as well as other taxa (e.g. Forminifera, Radiolana, Polychaeta, larvae of Mollusca, etc.)

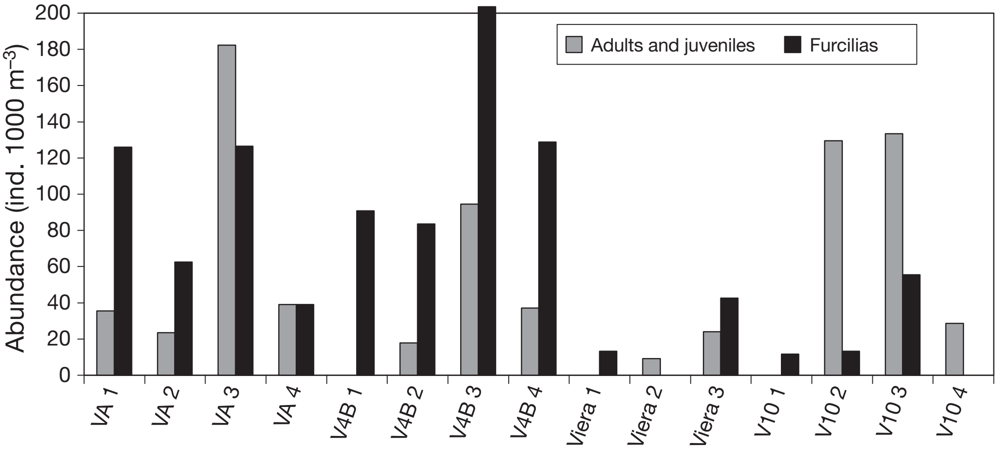

Fig. 4. Density (ind. 1000 m^{-3}) of adults and juvenile and furcilia stages of euphausiids, for zooplankton samples from Stns VA and V4B (western Mediterranean) and Viera and V10 (eastern Mediterranean) at 1: midday (12:00 h), 2: afternoon (18:00 h except Stn V10: 22:00 h), 3: midnight (00:00 h except Stn Viera: 22:00 h), 4: morning (06:00 h except Stns VA: 09:00 h and V10: 08:30 h)

20.86 and 19.92 ind. m^{-3}), and the highest occurred in the 4 samples taken over a 24 h period from the western Stn V1A (108.35, 118.86, 76.11 and 129.37 ind. m^{-3}).

Copepods were the dominant group in all 35 analysed samples, ranging from 33.99 % (midday sample at V4B) to 97.5 % (afternoon sample at V1A) of all identified zooplankton taxa. Abundances were between 6.46 ind. m^{-3} in the afternoon sample at Stn V3B and 119.78 ind. m^{-3} in the midday sample at Stn V1A. The highest number of identified copepod species at all stations was 67 at Stn V7, while the lowest was 19 at Stn V3B.

To interpret the ETS data obtained at the different stations and times, the ratio between crustaceans and gelatinous taxa and the abundances of migrant species were determined. The relative abundance of crustacea in the midday samples from all 10 stations (Table 4) ranged from 48.47 % (Stn V3B) to 97.62 % (Stn V1A) in the western compared to 55.38 % (Stn Viera) to 75.79 % (Stn V6) in the eastern sector. In contrast, the gelatinous taxa represented from 0.50 % (Stn V1A) to 19.07 % (Stn V3B) of the total zooplankton community for the western compared to 8.41 % (Stn V8) to 13.24 % (Stn V10) for the eastern sector. In the samples collected at midday, the ratio between gelatinous and crustacean taxa was almost equal across all stations, without significant differences from west (mean ratio 1:7.2) to east (mean ratio 1:7), except for Stn V1A where the total gelatinous specimens were <1 ind. m^{-3} and where the crustaceans showed the highest density of all samples collected (126.29 ind. m^{-3}).

Regarding the study of migrant groups, euphausiid densities in the samples collected during the 24 h periods were determined to investigate possible correlations of migration patterns with ETS activities. Fig. 4 shows the combined densities of adults and juveniles and those of furcilia stages for every sample from the 2 western- and easternmost sampling stations. The calyptopids were not considered because they were evidently less active, restricted to the surface layer, and did not show diel vertical migration (Marschoff et al. 1989, Stuart & Pillar 1990). The analyses of euphausiids reflected vertical migration patterns. Of the selected western stations, Stn VA showed higher a density of adults and juveniles (182.33 ind. 1000 m^{-3}) and furcilias (126.43 ind. 1000 m^{-3}) at night. Similarly, at Stn V4B, high densities were found in the midnight sample (adults + juveniles 94.51 ind. 1000 m^{-3}; furcilias 203.56 ind. 1000 m^{-3}). The same was observed at the eastern stations: at Stn Viera, where all taxa showed very low total abundances, adults and juveniles (23.95 ind. 1000 m^{-3}) and furcilia stages (42.58 ind. 1000 m^{-3}) of euphausiids were most abundant in the sample collected at 22:00 h; at Stn V10, the sample with the highest density of adults plus juveniles (133.33 ind. 1000 m^{-3}) and furcilias (55.56 ind. 1000 m^{-3}) was that collected at midnight.

In Table 5, the abundances (ind. 1000 m^{-3}) and the relative percent frequencies (F%) of all sampled euphausiid species for the 2 westernmost and 2 easternmost stations are reported. Higher abundance values were found in the WM (429.74 ind. 1000 m^{-3}) with respect to the EM (324.53 ind. 1000 m^{-3}). We found 9 euphausiid species in the western basin while 8 were found in the Levantine Basin. *Stylocheiron abbreviatum* was the most abundant species in both basins, followed by *S. longicorne* and *Euphausia hemigibba* in the WM and by *E. brevis* and *E. hemigibba* in the EM.

Table 5. Euphausiid species abundances (ind. 1000 m^{-3}) in samples taken at different times at the 2 westernmost and the 2 easternmost Mediterranean stations

Western Mediterranean

Stn Time sampling	VA 1 12:00	VA 2 18:00	VA 3 00:00	VA 4 09:00	V4B 1 06:00	V4B 2 12:00	V4B 3 18:00	V4B 4 00:00	Total no. of specimens	F (%)
Thysanopoda aequalis	0.00	0.00	21.88	0.00	0.00	0.00	0.00	0.00	21.88	5.09
Euphausia krohni	0.00	0.00	21.88	0.00	14.86	0.00	0.00	7.27	44.01	10.24
E. brevis	0.00	0.00	7.29	0.00	0.00	0.00	0.00	0.00	7.29	1.70
E. hemigibba	0.00	0.00	43.76	0.00	7.43	0.00	0.00	0.00	51.19	11.91
Nematoscelis megalops	0.00	0.00	29.17	4.87	0.00	0.00	0.00	0.00	34.04	7.92
N. atlantica	0.00	0.00	14.59	0.00	0.00	0.00	0.00	0.00	14.59	3.40
Stylocheiron suhmi	5.90	0.00	0.00	4.87	0.00	0.00	0.00	0.00	10.77	2.51
S. longicorne	17.71	7.82	14.59	24.35	0.00	0.00	8.95	14.54	87.96	20.47
S. abbreviatum	11.81	15.65	29.17	4.87	14.86	0.00	8.95	72.70	158.01	36.77
Total	35.42	23.47	182.33	38.96	37.15	0.00	17.90	94.51	429.74	100.00

Eastern Mediterranean

Stn Time sampling	Viera 1 12:00	Viera 2 18:00	Viera 3 22:00	V10 1 22:00	V10 2 00:00	V10 3 08:30	V10 4 12:00	Total no. of specimens	F (%)
Thysanopoda aequalis	0.00	0.00	0.00	0.00	16.67	0.00	0.00	16.67	5.14
Euphausia krohni	0.00	0.00	0.00	0.00	16.67	9.52	0.00	26.19	8.07
E. brevis	0.00	0.00	0.00	49.82	25.00	0.00	0.00	74.82	23.05
E. hemigibba	0.00	0.00	23.95	29.89	8.33	0.00	0.00	62.17	19.16
Nematoscelis megalops	0.00	0.00	0.00	0.00	8.33	0.00	0.00	8.33	2.57
N. atlantica	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Stylocheiron suhmi	0.00	0.00	0.00	9.96	0.00	0.00	0.00	9.96	3.07
S. longicorne	0.00	9.16	0.00	9.96	8.33	0.00	0.00	27.45	8.46
S. abbreviatum	0.00	0.00	0.00	29.89	50.00	19.05	0.00	98.94	30.49
Total	0.00	9.16	23.95	129.52	133.33	28.57	0.00	324.53	100.00

Table 6. Abundances (ind. m^{-3}) of strong migrant copepod species in the samples taken at different times at the 2 westernmost and the 2 easternmost Mediterranean stations

Western Mediterranean

Stn Time sampling	VA 1 12:00	VA 2 18:00	VA 3 00:00	VA 4 09:00	V4B 1 06:00	V4B 2 12:00	V4B 3 18:00	V4B 4 00:00
Paraeuchaeta acuta	0	0	0	0	0	0	0	0
Pleuromamma abdominalis	0	0	0	0	0.01	0	0	0.02
Pleuromamma gracilis	0	0	0	0.01	0.05	0	0	0

Eastern Mediterranean

Stn Time sampling	Viera 1 12:00	Viera 2 18:00	Viera 3 22:00	V10 1 22:00	V10 2 00:00	V10 3 08:30	V10 4 12:00
Paraeuchaeta acuta	0	0	0	0	0	0	0
Pleuromamma abdominalis	0	0	0	0	0	0	0
Pleuromamma gracilis	0	0	0	0.01	0.01	0	0

Concerning copepod composition, significant differences in total density and the presence of weak migrant species were not observed between night and day. Attention was also given to strong migrant species, such as *Paraeuchaeta acuta*, *Pleuromamma gracilis* and *P. abdominalis*, to detect behaviours that might be correlated to the ETS-data trends. Table 6 reports the density of these species in the samples taken at different times at the 2 western- and easternmost sampling stations, showing higher values in nighttime samples (sunset to sunrise, 21:00 to 07:00 h).

Zooplankton biomass and related carbon requirement

The biomass values of all samples taken at all 10 stations at different times of the day are reported in Table 7.

The zooplankton biomass (mg m^{-3}) values obtained for the 2 western- and easternmost sampling stations are shown in Fig. 5a. Higher mean values were obtained for Stn V4B (15.53) and Stn V10 (9.02) compared with Stn VA (8.33) and Stn Viera (3.33). The carbon requirement of the community (µg C m^{-3} d^{-1}) at the intervals sampled was calculated by multiplying the biomass value (g m^{-3}) and the measured carbon demand based on ETS activity (µg C g^{-1} d^{-1}) (Fig. 5b). The mean values (in µg C m^{-3} d^{-1}) were: 4.55 at Stn V4B, 3.82 at Stn V10, 2.01 at Stn VA and 1.33 at Stn Viera. The highest community carbon requirements were observed in those samples that had a high carbon demand per g biomass combined with a higher total biomass.

DISCUSSION

In the present study, information on the carbon consumption (µg C g^{-1} d^{-1}) by zooplankton in the 0 to 200 m layer at different stations in the Mediterranean Sea was obtained. All 10 stations were sampled during less than 1 mo (first sampling on 29 May, last on 23 June 2007), so we consider the samples as quasi-synoptic and compare the results obtained from them.

To evaluate the role of zooplankton in the carbon flow in the pelagic ecosystem, ETS values were converted to carbon demand. The carbon requirements per unit of zooplankton biomass indicate diel and spatial geographical differences in the study area. There was a clear lower mean activity at the 5 stations in the western compared with the 5 stations in the eastern Mediterranean Sea. An increasing gradient from the Strait of Gibraltar towards the easternmost station near the Isle of Rhodes was evident. This increasing west–east gradient, validated by statistical analysis, was also observed separately for all morning, midday, afternoon and midnight samples. Considering that there were no significant differences in total zooplankton density and composition between the western and eastern sector, and that there was an almost equal ratio between gelatinous and crustacean taxa from west (mean ratio 1:7.2) to east (mean ratio 1:7), the trend in increasing carbon demand, confirmed by ANOVA, could be explained by a relationship between zooplankton ETS activity and seawater temperature. In fact, there is evidence (Packard et al. 1974, Finlay et al. 1983, Schalk 1988, Koppelmann & Weikert 2003, Koppelmann et al. 2004) of a relationship between ETS activity and environmental temperature based on the measurement of enzymatic levels at different temperatures in the lab and recalculation of ETS activity using the Arrhenius equation (Owens & King 1975). An increase by only a few degrees leads to higher enzymatic activities. It has been shown that the temperature profile from the ocean surface to deeper layers exhibits the same decreasing trend as zooplankton ETS activity (Schalk 1988). The same linear relationship had already been demonstrated by Packard et al. (1974), who reported that 90% of the differences in geographical ETS activity are due to differences in temperature. Analysing our ETS data, it is evident that the spatial distribution of ETS activity, and thus of carbon and O_2 demand, is influenced by temperature values. The mean temperature at the 5 western stations was 15.1°C with a minimum value of 13.8°C, while for the eastern stations the mean temperature was 16.8°C with a maximum value of 18.4°C. Zooplankton samples from stations with higher temperatures, as in the Levantine Basin, showed higher ETS values because metabolic activities, like the remineralization of organic material, are directly correlated with temperature.

Furthermore, among the different sampling times, ETS activity peaks were recorded in the samples taken at midnight or in the morning before sunrise, followed (in decreasing order) by afternoon and midday collections. For this reason, we hypothesize that this could be

Table 7. Biomass values (wet and dry weights, WW and DW) for the 35 collected samples

Station	Sample	WW (mg m^{-3})	DW (mg m^{-3})
VA	1	8.98	0.72
VA	2	8.79	0.91
VA	3	8.78	0.87
VA	4	6.78	0.66
V4B	1	20.09	1.69
V4B	2	16.88	1.23
V4B	3	12.78	0.84
V4B	4	12.37	1.13
V3B	1	9.76	0.73
V3B	2	7.41	0.60
V3B	3	6.99	0.59
V1A	1	8.39	1.09
V1A	2	7.04	0.87
V1A	3	6.05	0.66
V1A	4	9.01	0.98
V2	1	3.75	0.53
V2	2	4.83	0.52
V2	3	5.05	0.57
V2	4	6.20	0.59
V6	1	4.52	0.39
V6	2	2.64	0.27
V6	3	5.01	0.50
V7	1	4.18	0.62
V7	2	3.66	0.41
V7	3	4.10	0.48
V8	1	1.78	0.25
V8	2	1.78	0.24
V8	3	2.29	0.28
VIERA	1	3.92	0.44
VIERA	2	1.76	0.22
VIERA	3	4.32	0.53
V10	1	6.33	0.77
V10	2	12.78	1.13
V10	3	7.59	0.69
V10	4	9.40	1.45

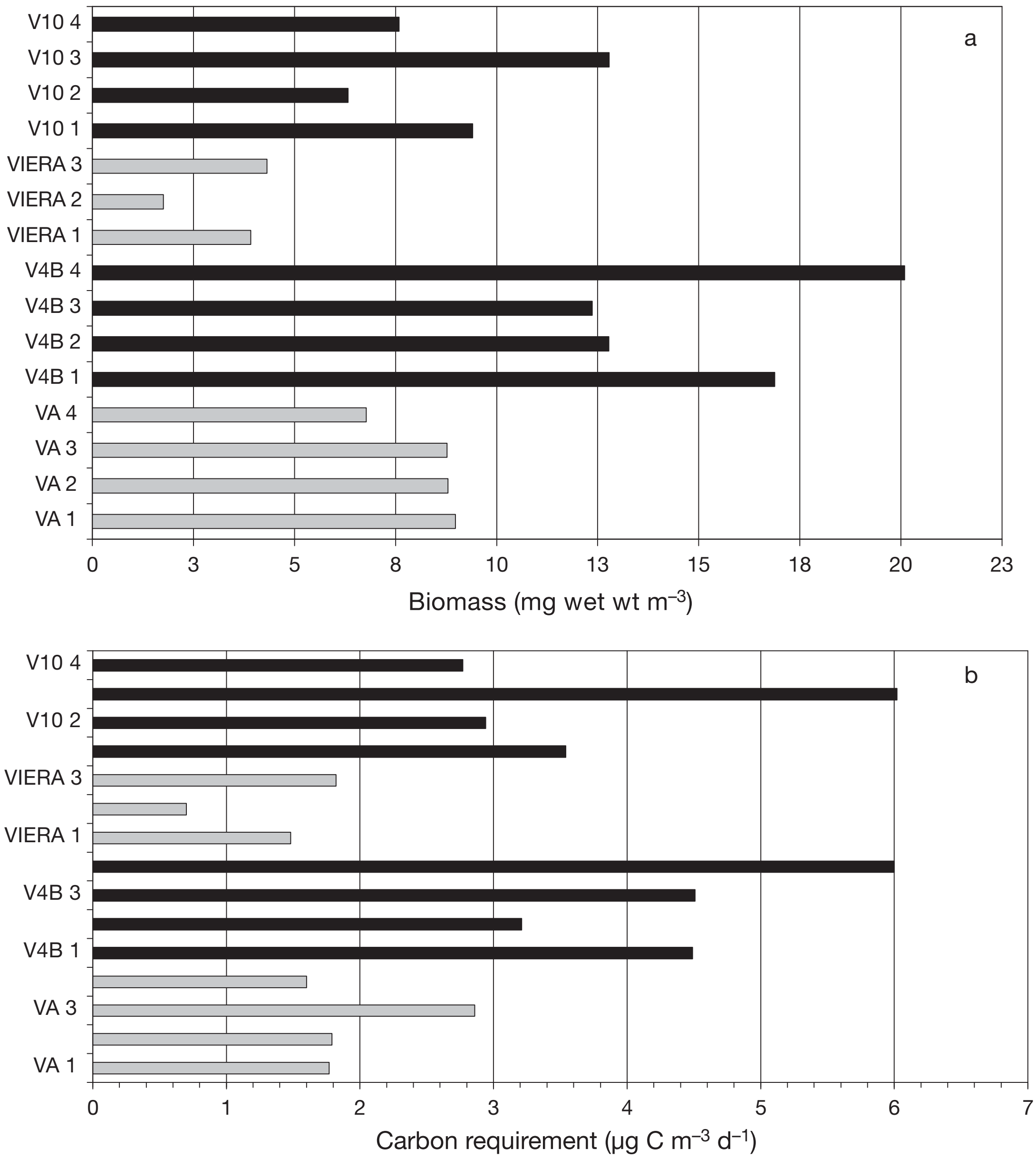

Fig. 5. Zooplankton (a) wet weight biomass and (b) metabolic carbon requirement from samples taken at 0 to 200 m depth at Stns VA and V4B (western Mediterranean) and Viera and V10 (eastern Mediterranean) at 1: midday (12:00 h), 2: afternoon (18:00 h except Stn V10: 22:00 h), 3: midnight 00:00 h except Stn Viera: 22:00 h), 4: morning (06:00 h except Stns VA: 09:00 h and V10: 08:30 h)

due to a change in composition of the layer. However, the ETS activity was standardized per g biomass, so differences only in density do not explain this phenomenon, although oxygen demand is a function of body mass (Ikeda et al. 2001). This was, therefore, probably caused by actively migrating organisms that mediate the vertical transport of material in the sea (Longhurst 1976, Longhurst et al. 1990). The euphausiid species composition analysis on the samples taken at different times revealed that adult and furcilia stages of euphausiids actively migrated from deeper layers into the top 0 to 200 m layer during nighttime, residing in the deeper layers during the day. It is well known that euphasiids show diel vertical migration, feeding in upper layers at night and returning to deeper and colder layers during the day to avoid predators (Brinton 1967, Mauchline & Fisher 1969, Vinogradov 1970, Casanova 1974, Lampert 1993, Brancato et al. 2001). In fact, in our samples, during the diel cycle, some species such as *Thysanopoda aequalis*, *Euphausia* spp. and *Nematoscelis megalops* showed a strong migratory behaviour in both basins. The small number or complete absence of specimens in morning and midday samples showed that the majority of these taxa occurred below 200 m depth at these times. In the nighttime samples, the number of individuals increased as the euphausiids concentrated in the upper layer.

The total abundance of copepod species did not differ between daytime and nighttime, which may be due to the sampled 0 to 200 m layer being too wide to study the behaviour of weak migrants such as *Corycaeus furcifer*, *Oncaea conifera*, *Heterorhabdus papilliger* or *Scolecithricella dentata* (Scotto di Carlo et al. 1984). In contrast, the strong migrant copepods, such as *Pleuromamma abdominalis*, *P. gracilis* and *Paraeuchaeta acuta*, showed a typical migratory behaviour. They were absent in the midday and afternoon samples, but present in the night collections.

Hence, mainly the euphausiids but also the copepods are responsible for the increasing ETS activity per biomass unit of zooplankton (g m^{-3} wet wt) during the day and at night (Torres et al. 1979, Schalk 1988). That migrating euphausiid species have a higher ETS activity than the deeper-living and non-migrating species in the pelagic environment has been reported previously (Childress 1969, 1971, 1975, Jannasch & Wirsen 1973, Packard et al. 1975, Jannasch et al. 1976, Torres et al. 1979).

The ratio of living to dead specimens has no relevance in our study because only a small number of dead copepods was found in 4 out of 30 samples (the highest value was 1.48% of total zooplankton abundance in the midday sample at Stn Viera).

The eastern Mediterranean Sea is a very oligotrophic region with low species richness and abundance compared to the western part and most other marine ecosystems in the world (Redfield et al. 1963, Scotto di Carlo & Ianora 1983, Dugdale & Wilkerson 1988, Weikert & Trinkaus 1990, Kerhervè et al. 1999). Based on our results, it is possible to say that the high metabolic carbon demand of the zooplankton in the eastern part of the Mediterranean Sea contributes to the carbon losses from the POC sinking flux in the water column (Koppelmann & Weikert 2003), amplifying the features of an impoverished region.

Furthermore, the higher carbon demand in the Levantine sector is not accompanied by higher primary production compared with the western sector. According to V. Saggiomo (pers. comm.), there is a decreasing trophic gradient from west to east. The total biomass (±SD) was, in fact, between 0.03 and 1.93 mg chl *a* m^{-3} (±0.33) in the western sector and between 0.03 and 0.48 mg chl *a* m^{-3} (±0.12) in the eastern sector, with primary production values between 0.04 and 3.59 mg C m^{-3} h^{-1} (±0.82) and between 0.09 and 0.57 mg C m^{-3} h^{-1} (±0.11), respectively.

The zooplankton compartment, recycling POM originating in the epipelagic layer, contributes to the decrease of material that can reach the bottom and the biotic communities that live in deeper layers (Thiel 1983, Tselepides & Eleftheriou 1992). The remaining carbon losses in the water column may be due to requirements by other size classes and/or by transfer into the dissolved organic carbon pool.

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