Trophic relationships of zooplankton in the eastern Mediterranean based on stable isotope measurements

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Abundance and stable isotope composition of large and small mesozooplankton were analyzed in samples taken with 333 and 100 μm nets, respectively, at four sites in the eastern Mediterranean down to 4200 m depth in October 2001. Large mesozooplankton (333 μm nets) was sieved into five size fractions, and the $\delta^{13}C$ and $\delta^{15}N$ values of the fractions were measured as well as the $\delta^{15}N$ values of total small mesozooplankton (100 μm nets) and specific mesozooplankton taxa. These measurements allow insights into the source of the diet and the trophic level relative to sinking and suspended particulate organic matter. Overall, biomass and abundance of zooplankton was low, reflecting the oligotrophic character of the eastern Mediterranean. Stable nitrogen isotope values of mesozooplankton were low (1–4‰) and close to zero in suspended particles at the surface. This indicates that the fixation of atmospheric nitrogen probably contributes to the N-pool in the eastern Mediterranean. Such low values were also found in sinking particles in deep waters and in most zooplankton size classes. However, suspended particles and mesozooplankton in the size class 0.5–1 mm, which was primarily composed of the deep-sea species Lucicutia longiserrata, showed higher values at depths below 1000 m. There is some indication that L. longiserrata was able to utilize the suspended particle pool in the deep eastern Mediterranean.

INTRODUCTION

The eastern Mediterranean is an ultra-oligotrophic ocean (Dugdale and Wilkerson, 1988) with little fishery yield and a limited influence on the global carbon cycle. However, it is an important region for monitoring ecological processes due to its relatively simple pelagic community structure (Koppelmann and Weikert, 2007). Local peculiarities such as increased temperature and salinity in the deep water, low food levels and the shallow sill at the Strait of Gibraltar result in "true" deep-sea species being rare (Scotto di Carlo *et al.*, 1991), and that the deep-sea is occupied by only few species that are able to deal with the environmental conditions of the eastern Mediterranean.

Two decades ago, significant changes in hydrography occurred in the eastern Mediterranean. An extended dry period between 1988 and 1993 and exceptional cold winters in 1987 and 1992–1993 led to the formation of high-density water in the Aegean Sea (Roether *et al.*, 2007). This dense water flowed out through the Cretan Arc Straits as Cretan intermediate water and Cretan deep water (CDW) into the Ionian and Levantine Basins, which replaced the formerly Adriatic water in the deep interior of the basins and probably lifted the nutricline partly into the euphotic zone (Klein *et al.*, 1999). In 1995, the entire bottom layer of the Levantine Basin was replaced with CDW. In the Ionian Sea, the CDW had reached the Straits of Sicily and Otranto

(Theocharis *et al.*, 2002). The total outflow of Aegean water into the eastern Mediterranean basins has been estimated to be around $2.3 \times 10^{14} \, m^3$ between 1988 and 1995 (Roether *et al.*, 2007), corresponding to a mean rate of $\sim 1 \times 10^6 m^3 s^{-1}$. This phenomenon has been named the eastern Mediterranean transient (EMT). The changes were associated with a drastic change in zooplankton abundance and composition in the deep water column (Weikert *et al.*, 2001), co-occurring with the highest flow rate with over $3 \times 10^6 m^3 s^{-1}$ in 1993 (Roether *et al.*, 2007). Although this extreme hydrographical situation was not observed after 1995, since then, the outflowing CDW was no longer dense enough to reach the bottom of the Ionian and Levantine Basins (Theocharis *et al.*, 2002), effects within the zooplankton assemblage were still visible in 1999 and 2001 (Koppelmann and Weikert, 2007) and in the Rhodes Basin in 2006 (Denda, 2008). "True" bathy-pelagic species, such as *Lucicutia longiserrata*, showed higher concentrations in these years than before the EMT, probably influencing the trophic system (Koppelmann and Weikert, 2007). However, knowledge about trophic relationships in the deep waters of the eastern Mediterranean is still very limited.

Such environmental changes occurred simultaneously at several places in the northern hemisphere in the years 1989 and 1990, causing regime shifts. Greene and Pershing (Greene and Pershing, 2007) hypothesized that a bottom-up, climate-driven regime shift has taken place in the northwest Atlantic during the 1990s, causing changes in the phytoplankton and zooplankton assemblage. Alheit *et al.* (Alheit *et al.*, 2005) reported changes in the phyto- and zooplankton community of the North Sea and central Baltic Sea, which also affected the fish stocks and were probably related to a shift in the North Atlantic Oscillation in the late 1980s. Also regions along the eastern boundary of the North Pacific were affected by regime shifts at the same time (Breaker, 2007). Tian *et al.* (Tian *et al.*, 2008) analyzed the effect of the late 1980s regime shift in the Japan/East Sea and found a shift in the demersal fish assemblage composition, abundance and distribution with several years lag relative to the time of change. Even mesopelagic fish species were affected in this region by the observed regime shift (Fujino *et al.*, 2007).

For a better understanding of processes and changes in the environment, it is important to understand the trophic structure of a system. Stable isotopes are a tool to study aquatic food webs since heavier isotopes are enriched within the food web by the organism relative to the diet (Michener and Schell, 1994; Fry, 2006). Stable nitrogen isotopes determine the trophic level (TL) of organisms (Minagawa and Wada, 1984; Hobson

and Welch, 1992), while stable carbon isotopes can be used to track the diet of organisms since there is little fractionation between ^{13}C and ^{12}C ($\sim 1‰$) from prey to predator (France and Peters, 1997). Therefore, the isotopic signature of an organism provides integrated information about its feeding habits over longer time periods. In this paper, we evaluate $\delta^{13}C$ and $\delta^{15}N$ values of zooplankton size classes and $\delta^{15}N$ values of abundant species in order to gain insights into the trophic structure and its interactions in the deep eastern Mediterranean.

METHOD

Sampling

Sampling was conducted at four stations (Fig. 1) in the Levantine Basin of the eastern Mediterranean on cruise M51/2 of RV *Meteor* in October 2001 (Koppelmann *et al.*, 2003a). Mesozooplankton samples were taken by oblique hauls (towing speed: 2 knots) with a $1 \, m^2$-double multiple opening and closing net and environmental sensing system (MOCNESS) (Wiebe *et al.*, 1985) equipped with 18 nets of $333 \, \mu m$ mesh aperture (large mesozooplankton) and 2 nets of $100 \, \mu m$ mesh size (small mesozooplankton), which can be sequentially opened and closed at defined depths. The system was equipped with conductivity (Seabird SBE 4), temperature (Seabird SBE 3S) and depth sensors.

Four full depth profiles (0–4200 m) were taken at the main site south of Crete (Table I) and additional single profiles were conducted NE of the Kaso Strait, and SW and SE of Cyprus at discrete depth intervals (Tables I and II). Veering and heaving speed of the winch was $0.5 \, m \, s^{-1}$. The heaving speed was reduced to $0.2–0.3 \, m \, s^{-1}$ when the net passed the 450 m depth to
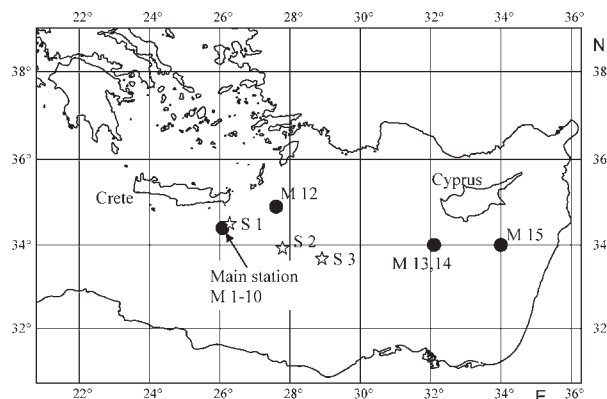
Fig. 1. Sampling sites in the eastern Mediterranean. M, MOCNESS hauls; S, water bottle samples for the analysis of suspended particles. S1 is also the position of the sediment trap stations.

Table I: Station data

Region	Haul	Date	Sampling time UTC		Latitude	Longitude	Water depth (m)	No. of samples	Sampled depth range	Remarks
			Start	End						
Crete	MOC-D-01	26 October 2001	22:27	01:30	34°22.45′ N	25°55.73′ E	4285	17	1250–0 m	B, T
Crete	MOC-D-02	27 October 2001	07:31	11:46	34°19.91′ N	26°08.47′ E	4241	16	10 mab–1250 m	B, T
Crete	MOC-D-03	27 October 2001	19:10	23:15	34°18.81′ N	26°08.49′ E	4270	16	4200–1250 m	B, T
Crete	MOC-D-04	28 October 2001	04:12	07:15	34°18.88′ N	26°08.34′ E	4264	17	1250–0 m	B, T
Crete	MOC-D-05	28 October 2001	10:07	13:10	34°19.34′ N	26°08.28′ E	4263	17	1250–0 m	only B
Crete	MOC-D-06	28 October 2001	15:57	18:49	34°19.33′ N	26°08.25′ E	4261	17	1250–0 m	only B
Crete	MOC-D-07	29 October 2001	01:20	05:37	34°19.52′ N	26°03.04′ E	4261	15	10 mab–1250 m	only B
Crete	MOC-D-08	29 October 2001	15:44	19:56	34°18.97′ N	26°05.66′ E	4285	16	10 mab–1250 m	only B
Crete	MOC-D-09	30 October 2001	04:02	08:25	34°18.62′ N	26°03.58′ E	4285	9	4250–0	only S
Crete	MOC-D-10	31 October 2001	00:52	05:18	34°18.80′ N	26°03.51′ E	4285	9	4250–0	only S
NE-Kaso	MOC-D-12	31 October 2001	23:46	01:09	34°55.11′ N	27°35.07′ E	1571	18	1250–0 m	B, T; 450–0 m S
SW Cyprus	MOC-D-13	2 November 2001	15:33	16:15	34°00.65′ N	32°03.22′ E	2537	9	450–0 m	B, T, 450–0 m (1/2 S)[a]
SW Cyprus	MOC-D-14	2 November 2001	21:23	01:00	34°04.04′ N	32°07.29′ E	2660	16	10 mab–450 m	B, T
SE Cyprus	MOC-D-15	3 November 2001	16:14	18:41	34°00.00′ N	34°00.44′ E	2121	17	1850–0 m	B, T, 200–0 m (1/2 S)[a]

The number of samples corresponds with Table II. B, biomass; T, taxonomy; S, stable isotopes. UTC + 2 h = local time. mab, meters above bottom.
[a]Half of the samples in the indicated depth range were used for biomass and taxonomic analyses, half were used for stable isotope analyses.

Table II: MOCNESS hauls: sampled depth intervals

Haul	Sampled depth intervals (m)
MOC-D-01	1250[a],1250,1250–1050–900–750–600–450–400,(450–400[a])–350–300–250–200–150–100–50–0
MOC-D-02	4200[a],4200,4200–4000–3750–3500–3250–3000–2750,(3000–2750[a])–2500–2250–2050–1850–1650–1450–1250
MOC-D-03	4200[a],4200,4200–4000–3750–3500–3250–3000–2750,(3000–2750[a])–2500–2250–2050–1850–1650–1450–1250
MOC-D-04	1250[a],1250,1250–1050–900–750–600–450–400,(450–400[a])–350–300–250–200–150–100–50–0
MOC-D-05	1250[a],1250,1250–1050–900–750–600–450–400,(450–400[a])–350–300–250–200–150–100–50–0
MOC-D-06	1250[a],1250,1250–1050–900–750–600–450–400,(450–400[a])–350–300–250,200–150–100–50–0
MOC-D-07	10 mab[a],10 mab,10 mab–4000–3750–3500–3250–3000,(3000–2750[a]),2500,2500–2250–2050–1850–1650–1450–1250
MOC-D-08	10 mab[a],10 mab,10 mab–4300–3750–3500–3250–3000–2750,(3000–2750[a])–2500–2250–2050–1850–1650–1450–1250
MOC-D-09	4250–3500–3000–2500–2000–1500–1000–500–250–0
MOC-D-10	4250–3500–3000–2500–2000–1500–1000–500–250–0
MOC-D-12	1250–1050–900–750–600–450–400–350–300–250–200–100–50–0; left nets: 450–150–100–50–0 (stable isotopes)
MOC-D-13	450–400–350–300–250–200–150–100–50–0
MOC-D-14	10 mab,10–50 mab,50 mab,50–100 mab–2500–2250–2050–1850–1650–1450–1250–1050–900–750–600–450
MOC-D-15	1850–1650–1450–1250–1050–900–750–600–450–400–350–300–250–200–150–100–50–0

mab, meters above bottom.
[a]100 μm net.

increase the water volume sampled in the smaller 50 m intervals. The ascent rates were between 9 and 16 m min^{-1}. The mean filtered volumes per net were 300 m^3 in the upper 450 m, 700 m^3 between 450 and 1050 m, and 900 m^3 below 1050 m. Upon recovery of the MOCNESS, the nets were rinsed with seawater, and fractions of the samples (see below) were prepared for stable isotope analyses; the remaining plankton was preserved in a 4% formaldehyde–seawater solution buffered with sodium tetraborate (Steedman, 1976) for biomass and taxonomic analyses. The samples taken in the upper 400 m at the Kaso Strait and SW of Cyprus and from the upper 200 m SE of Cyprus were split directly on board. One-half was fixed in formaldehyde for taxonomic and biomass analyses and the other half

was used for stable isotope analyses. Small mesozooplankton samples were only taken at the Crete site. Sampling was conducted from 400 to 450 m (two day and two night samples), at 1250 m (four samples), from 2750 to 3000 m (four samples) at 4200 m (two samples) and at 10 m above the bottom (two samples). Day and night samples were not separated below 1000 m since diel differences are negligible at these depths.

Biomass and taxonomic analyses

In the laboratory, the preserved large mesozooplankton samples for biomass determination and taxonomic analyses were sieved in fractions of 0.3–0.5, 0.5–1, 1–2, 2–5 and >5 mm. After placing the fractions in 70%

ethanol for 30 s and drying them on tissue paper, the material was wet weighed on an analytical balance. This method allowed a subsequent taxonomic analysis. Especially in the deep-sea, the samples were too small to be split for a more precise dry weight determination. After weighing, the samples were transferred into a sorting fluid composed of 0.5% propylene-phenoxetol, 5.0% propylene glycol and 94.5% fresh water (Steedman, 1976).

The fractionated large mesozooplankton and the small metazoan plankton were sorted into taxonomic groups and counted. Protozoans (e.g. foraminiferans, radiolarians and tintinnids) were not included in the counts. Rich large mesozooplankton samples were split according to Kott (Kott, 1953). If there were <30 individuals from a taxonomic group, the respective counts were made from the total sample. Carcasses, discriminated according to Weikert (Weikert, 1977), and Siphonophora, which break into pieces in the nets and are supposed to belong to the size fraction >5 mm, were excluded from the counts. Small mesozooplankton samples were divided into two size fractions by filtration through a 0.3 mm mesh gauze. All individuals in the larger fraction were counted, whereas only subsamples of 500–1000 individuals were enumerated in the smaller fraction. Methods of subsampling and taxonomic identification were the same as described by Böttger-Schnack (Böttger-Schnack, 1997).

Biomass and abundance data were standardized to a volume of 1000 m^3. To enable the plotting of data with zero values on a logarithmic scale, "+1" was added. The term "standing stock" stands for the numerical quantity in the water column below 1 m^2 (Ind. m^{-2}) of the whole water column or a given depth range.

Stable isotope measurements

Directly upon recovery of the MOCNESS, the 333 μm mesozooplankton samples solely for stable isotope measurements (MOC-D-09 and MOC-D-10), additional samples from the Kaso Strait (from layers in the 0–450 m depth range) and split samples from SW (from layers in the 0–400 m depth range) and SE (from layers in the 0–200 m depth range) Cyprus (Table I) were sieved into fractions as described above, rinsed with filtered fresh water, frozen, freeze-dried at −40°C and ground without any additional treatment. Measurements of carbon and nitrogen isotope ratios (δ^{13}C and δ^{15}N) were performed with a Thermo Finnigan/Costech Delta-Plus Advantage Mass Spectrometer with a Costech EAS Elemental Analyzer. The analytical error of this method is ≤0.1‰. Stable isotope values are expressed in δ-notations as parts per thousand (‰), where R is the

ratio of ^{13}C/^{12}C and ^{15}N/^{14}N and the standard is peedee belemnite and atmospheric nitrogen, respectively:

$$\delta^{13}C \text{ or } \delta^{15}N[‰] = ((R_{\text{sample}}/R_{\text{standard}}) - 1) \times 1000.$$

To obtain δ^{15}N values of the selected taxa, the dominant Calanoida species (*Haloptilus longicornis*, *Eucalanus monachus*, *L. longiserrata*) were sorted out of the fresh samples from integrated hauls over a wide depth range and treated as described above or put on pre-combusted GF/F filters (*H. longicornis*) and analyzed (Koppelmann *et al.*, 2003b).

The δ^{15}N values of the selected taxa of large mesozooplankton and fractions of total small mesozooplankton were measured from preserved samples. The small mesozooplankton samples were stored in formaldehyde, and the selected taxa had been stored in formaldehyde and sorting fluid (see above). Mullin *et al.* (Mullin *et al.*, 1984) and Kaehler and Pakhomov (Kaehler and Pakhomov, 2001) stated that storing samples in formaldehyde has little influence on the δ^{15}N values. We tested the effects of storing the zooplankton in formaldehyde and sorting fluid using material taken at the Crete site (Table III). Four integrated samples from the surface to 1250 m depth and six samples from the surface to 4250 m depth were analyzed. The samples were stored frozen from October 2001 till April 2002, then one-half of the sample was prepared for stable isotope measurements as stated above. The other half was stored in formaldehyde buffered with sodium tetraborate for 10 months before measuring the δ^{15}N values. The formaldehyde samples showed slight, but significantly (paired t-test $P = 0.007$) higher values (mean 0.35‰) than the frozen samples (Table III). To test the effect of storage in sorting fluid, one integrated sample from the surface down to 4250 m which was stored in formaldehyde buffered with sodium tetraborate for 5 years was split into 10 aliquots. Five aliquots were stored in sorting fluid for 3 weeks. Then, the δ^{15}N content of all subsamples was measured as described above. Storing the material in sorting fluid will increase the δ^{15}N value by 0.16‰ (Table III). The difference between the samples was significant: paired t-test $P = 0.048$. To summarize, conservation of the material in formaldehyde and sorting fluid will increase the δ^{15}N values by 0.51‰. This value was subtracted from the measurements of selected species, which were pooled from different nets (Table IV). A value of 0.35‰ was subtracted from the small mesozooplankton measurements, which were not stored in sorting fluid.

Table III: $\delta^{15}N$-comparison of preservation methods

Sample depth	Frozen	Formaldehyde	Formaldehyde − frozen	Sample depth	Formaldehyde	Sorting fluid	Sorting fluid − formaldehyde
0–1250	4.30	4.22	−0.08	0–4250	3.82	3.96	0.14
0–70 mab	4.06	4.20	0.14	0–4250	3.41	3.78	0.37
0–4200	4.23	4.56	0.33	0–4250	3.56	3.69	0.13
0–1250	3.84	4.16	0.32	0–4250	3.81	3.89	0.08
0–1250	3.76	4.17	0.41	0–4250	3.66	3.72	0.06
0–1250	4.40	4.83	0.43				
0–10 mab	2.93	3.90	0.97				
0–10 mab	2.09	2.70	0.61				
0–4250	4.16	4.66	0.50				
0–4250	4.40	4.28	−0.12				
Mean	3.82	4.17	0.35		3.65	3.81	0.16
Std	0.75	0.58			0.17	0.11	

For explanation see text. mab, meters above bottom; Std, standard deviation.

Table IV: $\delta^{15}N$-values (‰) of specific mesozooplankton taxa from the Crete site

	This study			Koppelmann *et al.* (2003b)		
Species	$\delta^{15}N$	Range	Depth (m)	$\delta^{15}N$	Range	Depth (m)
Oithona spp.	2.15		50–100			
Corycaeus spp.	3.34		50–100			
Siphonophora	2.87		50–100			
Lucicutia ovalis	2.36		50–100			
Lucicutia gemina	2.98		100–150			
Chaetognatha	4.69		150–200			
Haloptilus longicornis	5.42	0.19	200–300	3.42	0.46	0–400
Lucicutia flavicornis	1.85	0.02	200–300			
Ostracoda	3.11	0.16	200–300			
Pleuromamma spp.	2.18	0.09	350–600			
Euchaeta spp.	4.14	0.15	350–600			
Fishlarvae	3.42		450–600			
Eucalanus monachus	6.13	0.17	600–1050	6.89		0–2750
Scaphocalanus spp.	7.67	1.73	1050–1650			
Lucicutia longiserrata	11.92	0.24	3000–4000	8.59		0–2750

Values from this study were corrected for conservation bias (−0.51‰, see text).

Table V: $\delta^{15}N$ values (‰) of suspended particles from three sites in the eastern Mediterranean

Depth (m)	Station S1 34°26.54′N 26°11.51′E	Station S2 33°55.44′N 27°44.45′E	Station S3 33°40.00′ N 29°00.00′E
0	0.76	0.43	1.19
35			0.45
45		1.74	
65	1.60		
200	1.33	7.92	0.87
1000	7.37	8.49	6.19
3067			7.82
3626	7.26		

Table VI: $\delta^{15}N$ values (‰) of sinking particles from three moorings in the eastern Mediterranean

Coordinates	Deployment period	Trap depth (m)	$\delta^{15}N$ (‰)
34°25.90′N 26°10.75′E	30 January 1999 to 13 April 1999	2720	2.17
34°26.50′N 26°11.40′E	5 November 2001 to 1 April 2002	2560	1.19
34°26.63′N 26°11.58′E	30 January 2007 to 22 August 2007	1508	0.68
34°26.63′N 26°11.58′E	30 January 2007 to 22 August 2007	2689	0.76

Suspended and sinking particulate organic matter

The $\delta^{15}N$ values of suspended particulate organic matter (POM) were measured in water samples from different depths at three stations (Fig. 1 and Table V) east of Crete. The material was taken with a rosette sampler in January 2007 during Meteor cruise 71/3. Volumes of 37–74 L (depending on total suspended matter concentrations) were immediately filtered on precombusted and tared GF filters (diameter: 47 mm; pore size ∼0.7 μm). Filters were subsequently dried at 40°C overnight and stored dry and cool until analysis for stable nitrogen isotopes via isotope ratio mass spectrometry (Thermo Finnigan Delta Plus XP) in the home laboratory. The stable isotopic composition of sinking POM caught in sediment traps was analyzed by the same analytical method. The samples were taken in 1999 (Koppelmann *et al.*, 2003c), 2001/2002 (Warnken, 2003) and 2007 in the eastern Mediterranean at stations close to the Crete site (Table VI).

RESULTS

Hydrography

Surface temperatures and salinities at all four stations ranged between 20.7 and 23.7°C and 39.2 and 39.3 PSU, respectively, in the upper 25 m (Fig. 2). The mixed layer extended down to 130 m at the Crete site, 70 m at the Kaso and SE Cyprus sites, and 50 m at the SW Cyprus site. A distinct salinity minimum was observed at the lower border of this zone, which, however, was less developed at the Kaso site. At the Crete and Cyprus sites, the drop was 0.6 PSU, but at the Kaso site it was only 0.15 PSU. Deep-water temperatures and salinities were relatively stable below 500 m, ranging around 13.5°C and 38.7 PSU at all sites.

Large mesozooplankton size distribution

Generally, most of the animals (>40%) belonged to the sieve fraction of 0.5−1 mm at all sites with highest
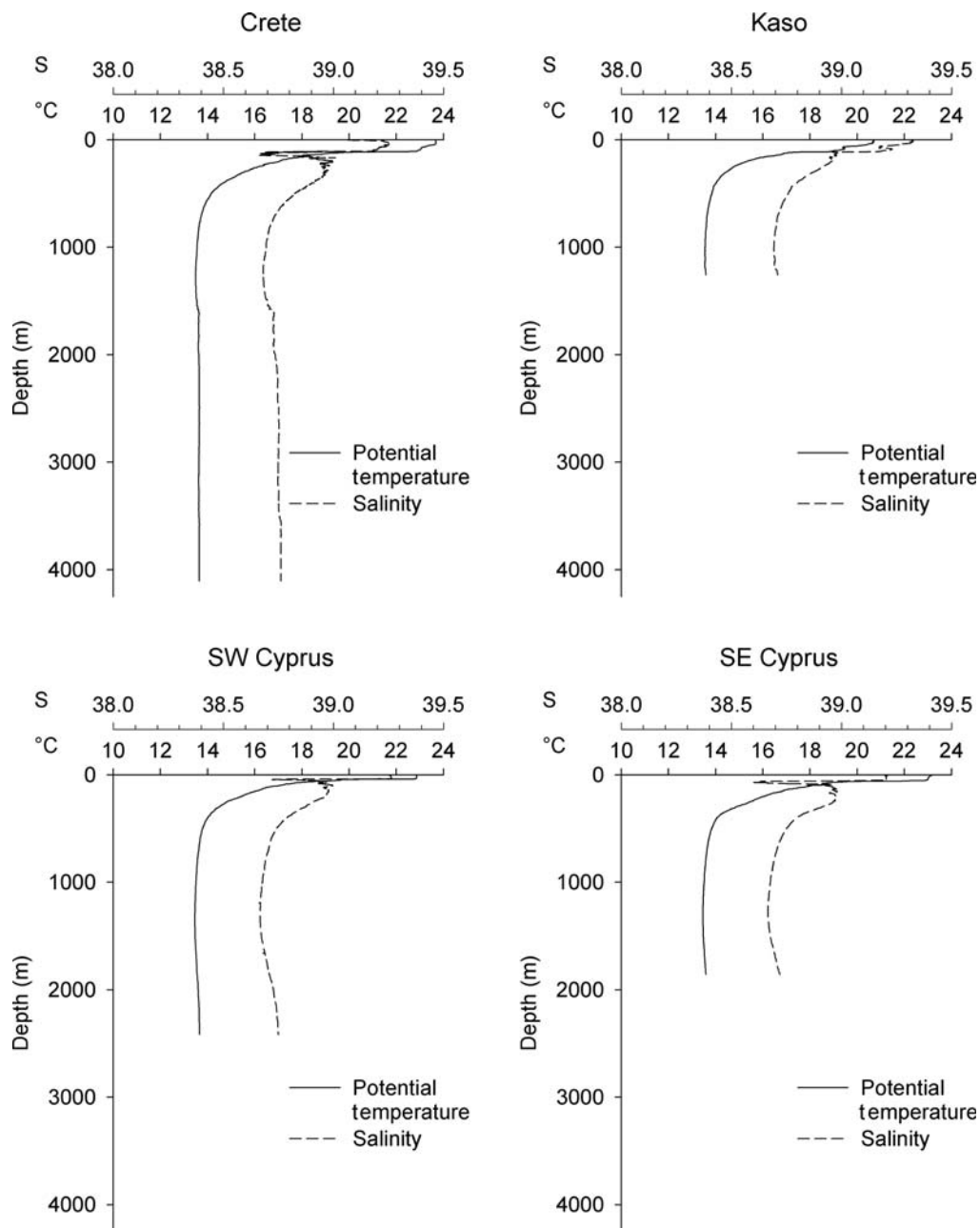
Fig. 2. Hydrography at the four sampling sites in the eastern Mediterranean.

relative concentrations below 1000 m; i.e. in the bathy-pelagic zone (>60%). The only exception was between 1050 and 1850 m SE of Cyprus, where a higher relative amount belonged to the sieve fraction of 1–2 mm (Fig. 3). The largest size fraction (2–5 mm) was of minor numerical importance, but in terms of biomass, this size fraction gained in relative importance (Fig. 4). However, in deep waters at the Kaso Strait (<1050 m) and at the Crete site (<2500 m), the 0.5–1 mm fraction dominated the biomass standing stock with nearly 50%.

Large mesozooplankton biomass and abundance

Mesozooplankton biomass and abundance of the sum of fractions <5 mm were similar at all sites investigated at the surface, ranging around 20 000 mg 1000 m^{-3} and 70 000 Ind. 1000 m^{-3} (Fig. 5). There was a steady decrease in biomass and individual counts down to 1000 and 1500 m depth, with minimum values between 200–600 mg 1000 m^{-3} and 200–600 Ind. 1000 m^{-3}, respectively. An exception was observed at the Kaso site; here an elevated biomass and abundance was observed around 1000 m.
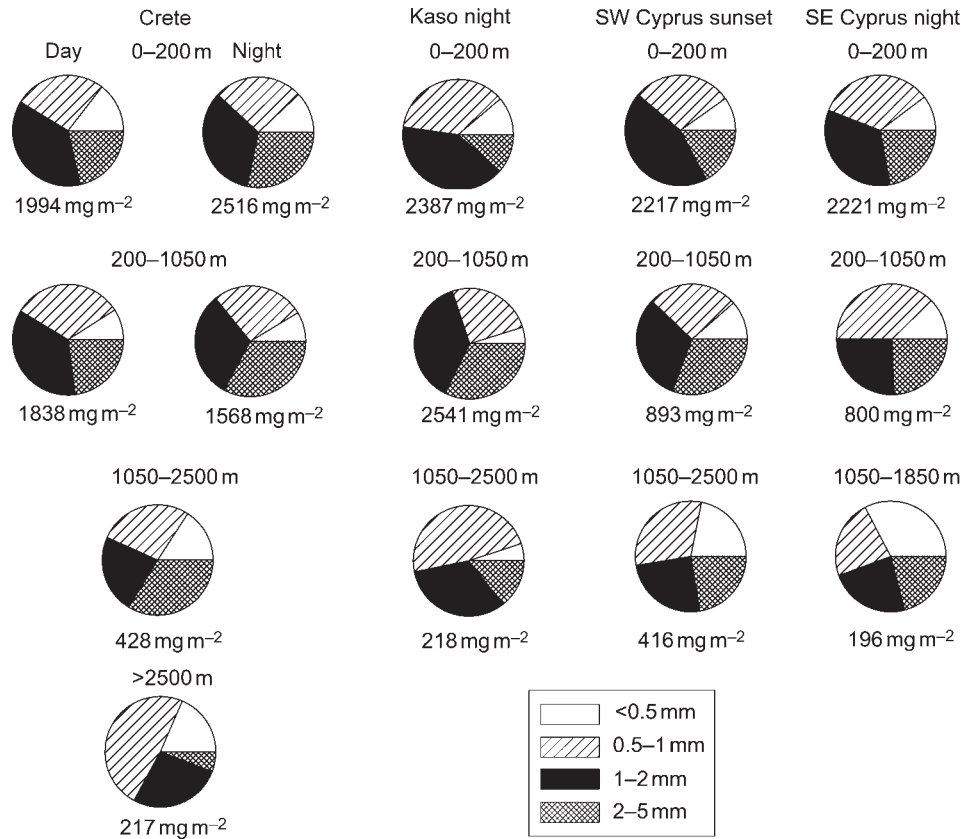
Large mesozooplankton composition

Calanoid copepods dominated the mesozooplankton assemblage with >50% at all sites, indicating slightly increasing relative abundances with increasing depth. Non-calanoid copepods seemed to be more important in terms of relative abundance in the upper 500 m (up to 35%). Ostracods were a constant and abundant component throughout the water column (10–15%). Like chaetognaths, their relative abundance was higher between 250 and 450 m at all sites (Fig. 6).

In the upper 150 m, some calanoid taxa such as *Acartia* spp, *H. longicornis*, *Clausoclanus* spp. and *Pleuromamma gracilis* were found in high numbers, with relative abundances higher than 3% of the total zooplankton either during the day or during the night. At around 300 m, however, *H. longicornis* dominated the calanoid copepod community with >80% (Fig. 7). At depths around 1000 m, *E. monachus* was the dominant taxon at the Crete, Kaso and SW Cyprus sites. This species was also responsible for the increase in biomass and abundance at these depths at the Kaso site. SE of Cyprus, *E. monachus* was of minor importance; at this site *Scaphocalanus* spp. and *Spinocalanus abyssalis* were
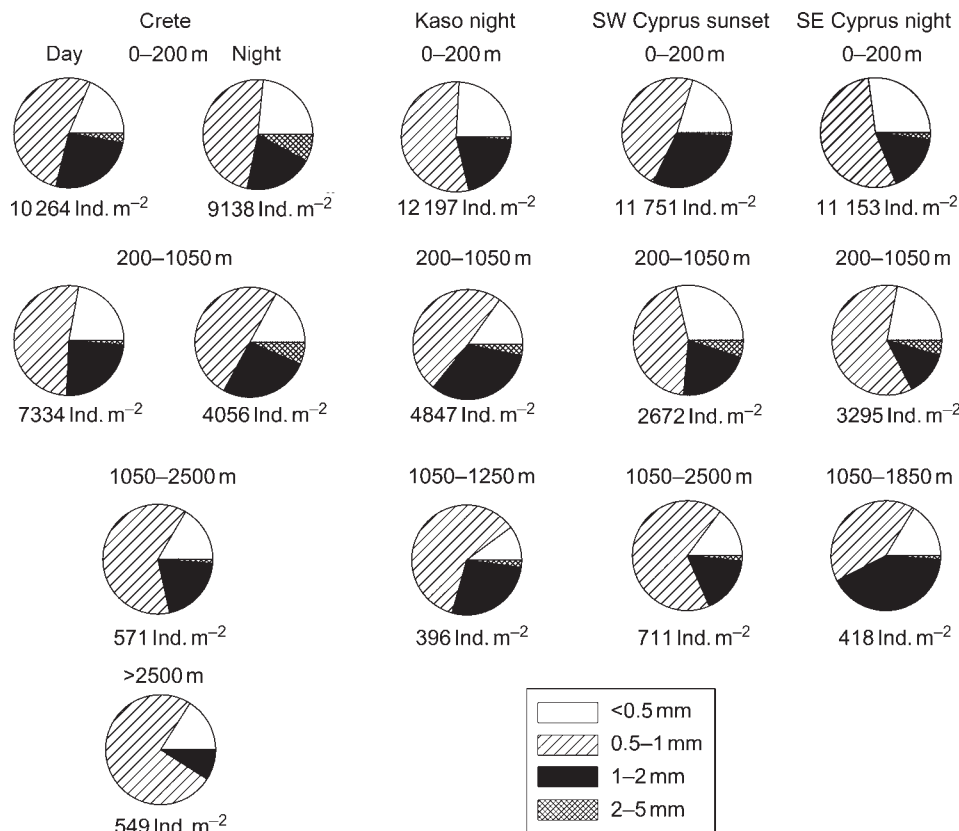
Fig. 3. Relative size composition of large mesozooplankton (333 μm mesh size) individuals in different depth zones at the four sampling sites in the eastern Mediterranean.
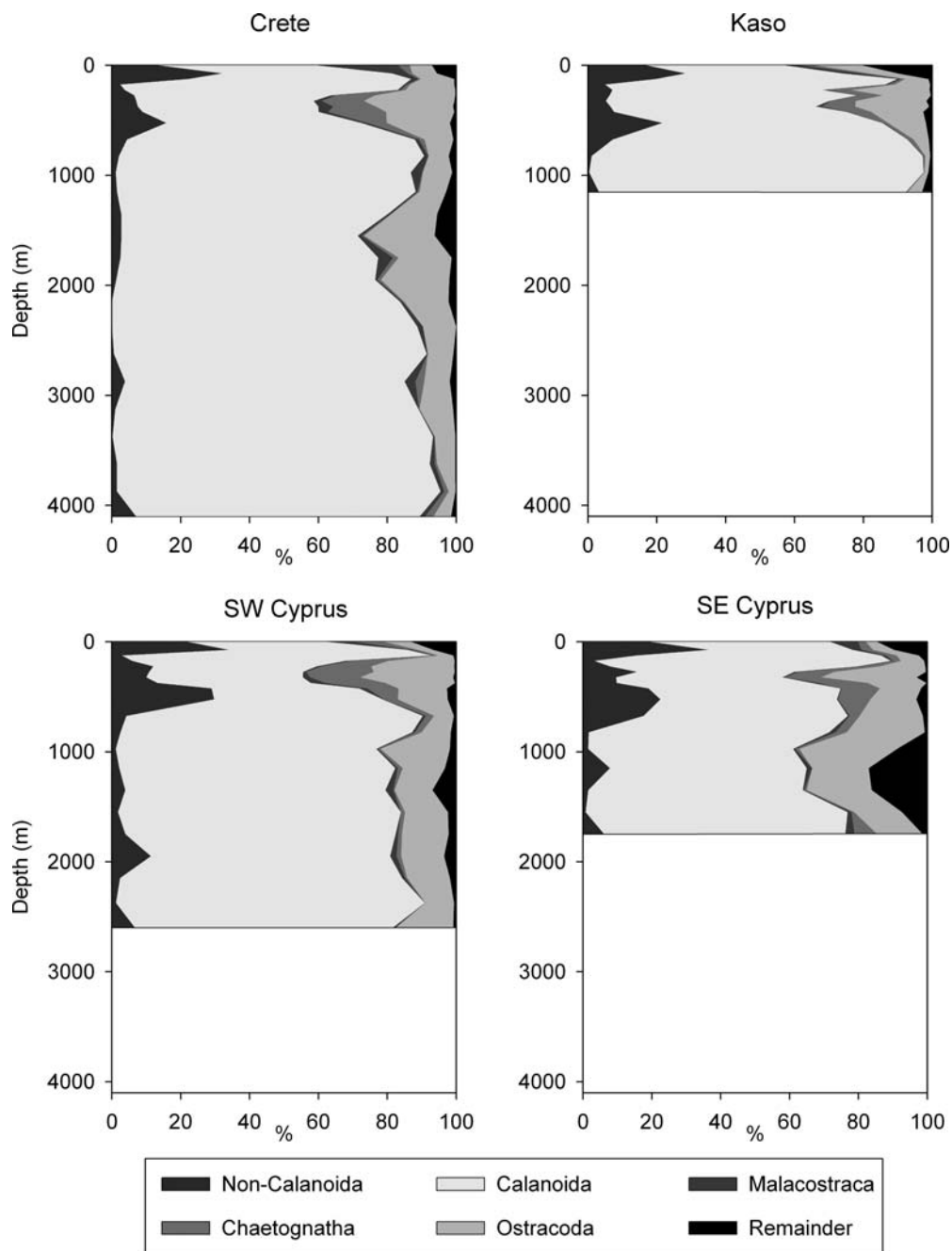
Fig. 4. Relative size composition of large mesozooplankton (333 μm mesh size) biomass in different depth zones at the four sampling sites in the eastern Mediterranean.
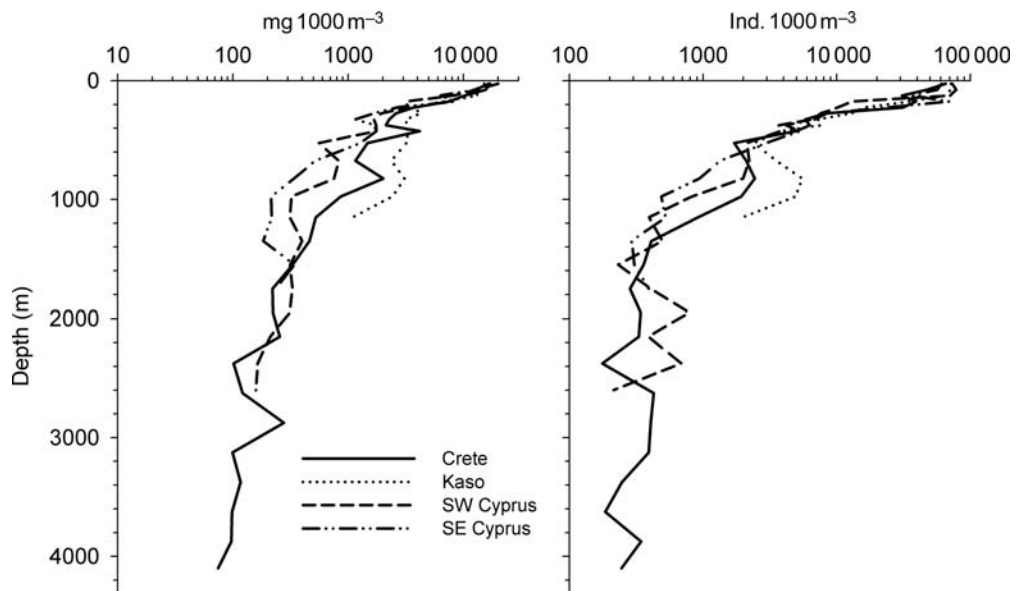
Fig. 5. Vertical distribution of large mesozooplankton (333 μm mesh size) biomass and numbers at the four sampling sites in the eastern Mediterranean.

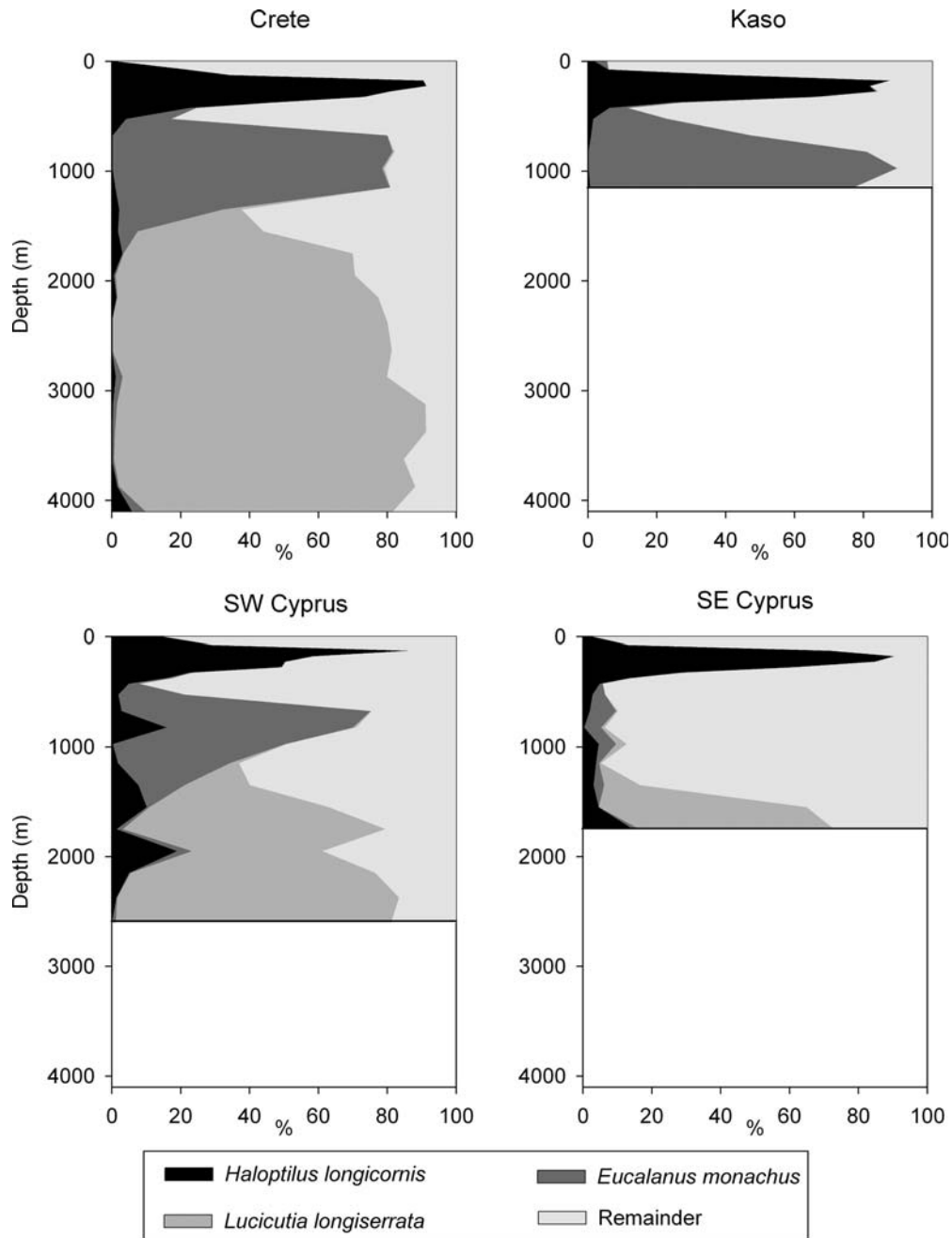**Fig. 6.** Relative taxonomic composition of large mesozooplankton (333 μm mesh size) throughout the water column at the four sampling sites in the eastern Mediterranean.

more important in the calanoid copepod community. *Lucicutia longiserrata* dominated the greater depths below 1500 m as indicated at the sites of Crete, SW Cyprus and SE Cyprus. This species contributed with 45–73% to the 0.5–1 mm size fraction at these sites, with highest values of over 80% at around 3000 m at Crete (see also Koppelmann and Weikert, 2007). At the Kaso site, the water depth was not deep enough to detect this bathypelagic species.
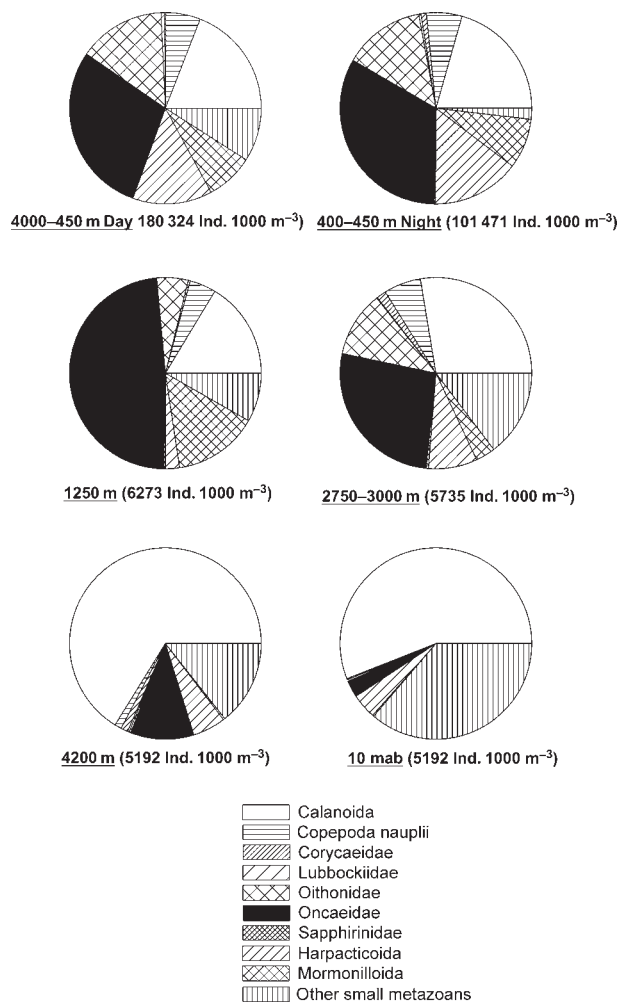
Small mesozooplankton composition

The small mesozooplankton community at the site south of Crete consisted in the upper 3000 m depth

Fig. 7. Relative composition of main calanoid copepods sampled by 333 μm mesh size throughout the water column at the four sampling sites in the eastern Mediterranean.

ranges mainly of non-calanoid copepods ($\geq 50\%$), and these were dominated by Oncaeidae (Fig. 8). The proportion of calanoids ranged from 16 to 28%, and noncopepods (mainly ostracods, pteropods and polychaete larvae) shared between 6.5 and 15%. Copepod nauplii were less abundant (4–6%). A day/night change in composition was not apparent in the 400–450 m zone; however, the day concentration of the small metazoan assemblage was higher than the night concentration by a factor of 1.8. At 1250 m, Oncaeidae contributed an especially high portion with 40–50%, and also the proportion of mormonilloids was higher than above and below. Near to the bottom, the relative abundance of calanoids had increased to >60%, they were dominated by small species of Discoidae and juveniles of an unknown taxonomic status. The small mesozooplankton

4000–450 m Day 180 324 Ind. 1000 m⁻³)   400–450 m Night (101 471 Ind. 1000 m⁻³)

1250 m (6273 Ind. 1000 m⁻³)   2750–3000 m (5735 Ind. 1000 m⁻³)

4200 m (5192 Ind. 1000 m⁻³)   10 mab (5192 Ind. 1000 m⁻³)

- Calanoida
- Copepoda nauplii
- Corycaeidae
- Lubbockiidae
- Oithonidae
- Oncaeidae
- Sapphirinidae
- Harpacticoida
- Mormonilloida
- Other small metazoans

Fig. 8. Relative composition of small mesozooplankton (100 μm mesh size) individuals in different depth zones at the Crete site in the eastern Mediterranean. Day and night data are separated for the 400–450 m depth zone only. Abundance values in brackets represent averages from four samples at the 1250 and 2750–3000 m depth ranges and from two samples at other depths.

abundance was low at 4200 m (372 Ind. 1000 m⁻³). Ten meters above the bottom, again higher concentrations of metazoan plankton were found (5192 Ind. 1000 m⁻³). Non-calanoid copepods contributed only 8% of the concentration, calanoids 56% and the non-copepods 36%. The latter group consisted mainly of small larvae of polychaetes.

δ^{15}N values of large mesozooplankton size classes and small mesozooplankton

In general, δ^{15}N values of large mesozooplankton were low (between 1 and 4‰), but increased slightly with increasing depth at the Crete, Kaso and SW Cyprus sites (Fig. 9). SE of Cyprus, the values were higher than

at the other sites at the surface and decreased slightly in the subsurface layer (50–100 m). Differences between size classes were minor, but the values tended to increase with increasing size class.

At the Crete site, the increase in δ^{15}N with increasing depth could be detected down to 2500 m depth, then the values decreased for the size classes 0.3–0.5, 1–2 and 2–5 mm. Only animals in the 0.5–1 mm size class showed a steady increase in δ^{15}N with increasing depth; the values were distinctly higher than the values of the other zooplankton size groups.

Small mesozooplankton δ^{15}N (Table VII) was higher than that of larger mesozooplankton in the 400–450 m depth zone both during day (8.2‰) and night (5.7‰). At 1250 m, the values were in the same range (5.0‰) for both size categories, but between 2750 and 3000 m small mesozooplankton δ^{15}N was slightly lower (4.1‰). Close to the bottom, the δ^{15}N was 6.5‰ at 4200 m and 4.2‰ at 10 m above the bottom. In the deepest samples, (10 m above the bottom) polychaete larvae (δ^{15}N 6.8‰) were partly sorted out before analysis, which may have reduced the value for total small mesozooplankton.

δ^{13}C and δ^{15}N values of large mesozooplankton

The spatial distribution of δ^{13}C and δ^{15}N values of large zooplankton showed a distinct pattern that can be grouped into three clusters (Fig. 10). At all sites, stable isotope values from epi- and mesopelagic depths ranged around 2.5 ± 1‰ in δ^{15}N. Differences in δ^{13}C, however, were clear: samples from the epipelagic and mesopelagic zones at the western sites (Crete and Kaso) and the mesopelagic zone SW of Cyprus showed lower values (mean −20.0‰, SD 0.6) than samples from the epipelagic zones (upper 200 m) at both Cyprus sites (mean −18.9‰, SD 0.7). Samples taken in the bathypelagic zone at Crete revealed a more widespread pattern: δ^{15}N values were between 2 and 12‰ depending on the depth and δ^{13}C values were between −22.5 and −18.5‰ (mean 20.4‰, SD 1.1), with generally lower values in deeper waters (see Supplementary Material online).

Vertical distribution and δ^{15}N values of specific large mesozooplankton taxa

Stable δ^{15}N values of single groups and species were measured at the Crete site (Table IV). The samples were taken at the depths of main occurrence of these taxa (Fig. 11). Like the sieve fractions of total zooplankton, the values of taxa from the samples in the upper 200 m were
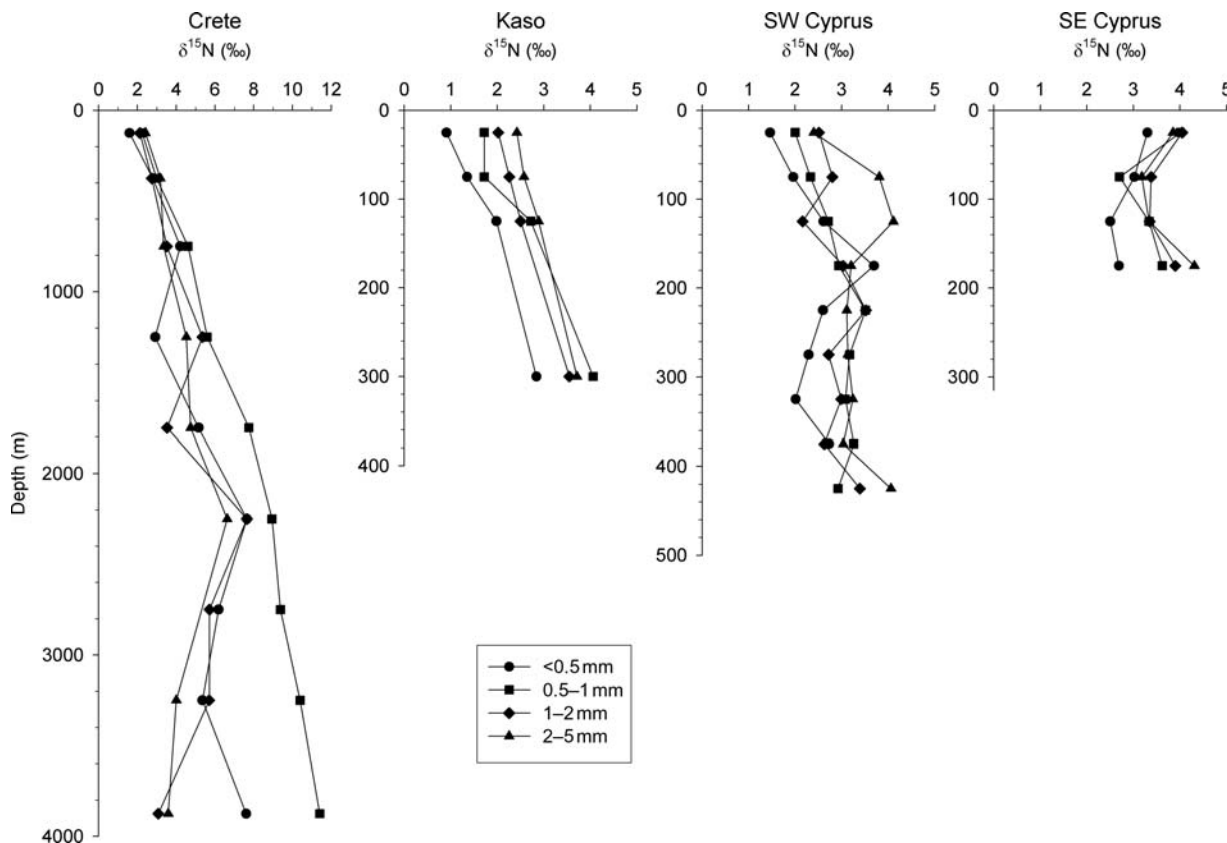
Fig. 9. Vertical distribution of δ¹⁵N values (‰) of large mesozooplankton (333 μm mesh size) size classes at the four sampling sites in the eastern Mediterranean. Mean of two values at Crete, single values at the other sites. Note the different depth scales.

Table VII: $\delta^{15}N$ values (‰) of small mesozooplankton (100 μm mesh size) taken at different depths at the Crete site

400–450 m	1250 m	2750–3000 m	4200 m	10 mab
8.14 (D)	5.45 (D)	4.95 (D)	5.57 (D)	5.43 (N)
8.30 (D)	4.99 (D)	4.13 (N)	7.50 (N)	2.96 (N)
5.68 (N)	4.63 (N)	2.62 (N)		
5.65 (N)	4.93 (N)	4.63 (N)		

Values were corrected for conservation bias (−0.35‰, see text). mab, meters above bottom; D, day sample; N, night sample.

close together, ranging between 2 and 3‰, except for *Corycaeus* spp. and chaetognaths, which were higher with 3.3 and 4.7‰, respectively. At mesopelagic depths, the δ¹⁵N ratios were somewhat higher; the values from 1.9 to 6.3‰ reflect trophic differences among the animals. Highest values were found for *Scaphocalanus* spp. and *L. longiserrata* in the bathypelagic zone.

Suspended and sinking POM

δ¹⁵N of suspended POM was most depleted in surface waters with a range of 0.43–1.19‰ (Table V). Slightly

higher values (except for station S3) were found in the chlorophyll maxima (35–65 m) while deep-sea samples, taken at 1000 m and at bathypelagic depths (3067–3626 m), were obviously higher in δ¹⁵N (6.19–8.49‰). Intermediate water values (at 200 m water depth) were similar to deep water values at station S2 (7.92‰). At stations S1 and S3, however, the values of 1.33 and 0.87‰, respectively, were similar to the values measured in the chlorophyll maximum waters. This reflects the deepening of the upper layer in the anticyclonic Ierapetra Gyre. Generally, suspended particles at all stations showed strong enrichment in δ¹⁵N in the upper layer and more or less uniform values from the transition zone down to sea floor.

Sinking POM, collected by sediment traps in the Ierapetra Deep (S1), south of Crete, showed lighter δ¹⁵N values than suspended POM from comparable depths (Table VI). Deeper traps (2560–2720 m) reported mean values of 0.76–2.17‰ during three deployments while a mean δ¹⁵N of 0.68‰ was measured in samples from a trap at 1508 m. A trend from heavier to lighter nitrogen isotopes in sinking POM was observed from 1999 to 2007.
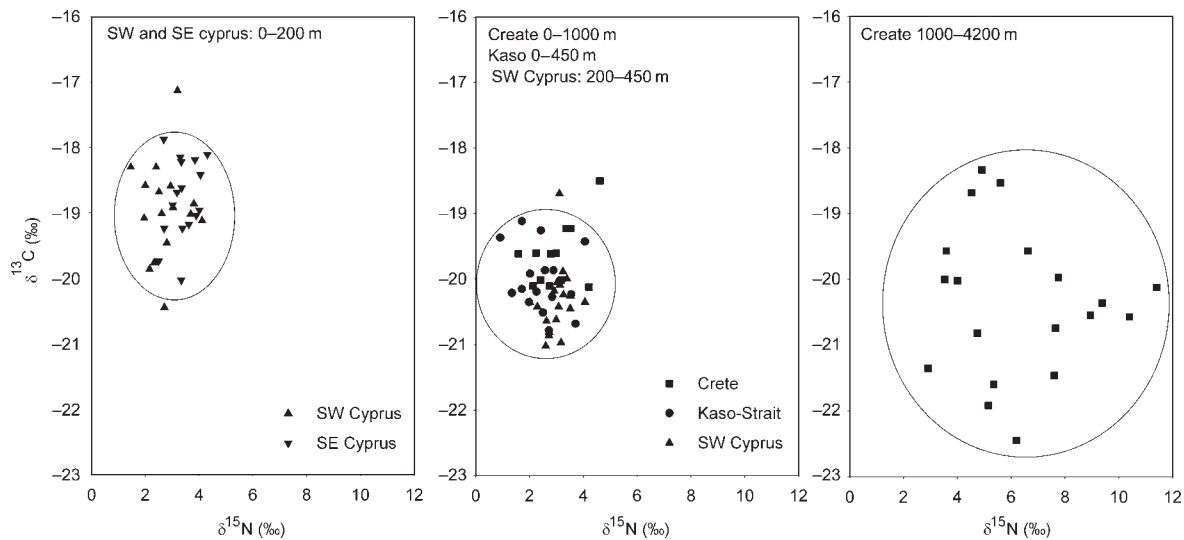
Fig. 10. $\delta^{15}N$ and $\delta^{13}C$ distribution of large mesozooplankton (333 μm mesh size) in the eastern Mediterranean arbitrary clustered into three groups. See Supplement Material online for size class and depth differentiation.

DISCUSSION

During the present study, low stable nitrogen isotopes values were found in the zooplankton community (1–4‰) and in suspended POM (0–2‰) in the surface waters of the eastern Mediterranean. Similar low values reported by other authors (Sachs and Repeta, 1999; Struck *et al.*, 2001; Pantoja *et al.*, 2002) during different years and seasons strongly indicate that the production of light nitrogen is a common feature in the eastern Mediterranean. Koppelmann *et al.* (Koppelmann *et al.*, 2003c) already found low $\delta^{15}N$ values (2.0–3.1‰) of mixed zooplankton in the eastern Mediterranean surface waters in samples taken in April/May 1999. Low $\delta^{15}N$ zooplankton values of 2–5‰ were also found in the Sargasso Sea (Fry and Quiñones, 1994) and in the oligotrophic North Atlantic (0–4‰), when *Trichodesmium* spp., a nitrogen-fixing planktonic diazotroph, was present (Montoya *et al.*, 2002). In other regions of the Atlantic Ocean, where nitrate was the main N-supply for primary production, the $\delta^{15}N$ values of zooplankton were higher; e.g. 6–9‰ on Georges Bank and in the Gulf of Maine (Fry and Quiñones, 1994), 5–7‰ in zooplankton of the Atlantic Shelf off the Iberian Peninsula (Bode *et al.*, 2007) and 8–10‰ in the Southern California Bight (Mullin *et al.*, 1984) as well as in the Arabian Sea (Koppelmann and Weikert, 2000). Based on the low $\delta^{15}N$ values of zooplankton in the eastern Mediterranean, it is safe to assume that the primary food of the zooplankton (smaller zooplankton, phytoplankton and particles) has a $\delta^{15}N$ value around zero. This indicates that the whole eastern Mediterranean ecosystem is based on a nitrogen source

with low $\delta^{15}N$ values. However, spatial differences in carbon isotope values (Fig. 10) indicated that the zooplankton at the Cyprus sites has used food sources of different origin to those at the Crete and Kaso sites. However, we do not know the causes for these spatial differences. It could be possible that the carbon source has been altered by longer retention times in the easternmost part of the basin or that the discrimination of the heavier isotopes by primary producers was different in both parts of the basin due to local differences in nutrient availability.

Several authors (Sachs and Repeta, 1999; Pantoja *et al.*, 2002; Koppelmann *et al.*, 2003c) have assumed that the low $\delta^{15}N$ values in the eastern Mediterranean were caused by the fixation of atmospheric nitrogen, which is the reference standard of stable nitrogen isotope measurements. Nitrogen-fixing cyanobacteria such as *Anabaena* spp. and *Trichodesmium* spp. showed values between −2.1 and 1.0‰ (Minagawa and Wada, 1986). Indeed, nitrogen-fixing cyanobacteria such as *Synecchococcus* spp. (Li *et al.*, 1993) were found in the eastern Mediterranean. Recently, Zeev *et al.* (Zeev *et al.*, 2008) found *Richelia intracellularis*, a nitrogen-fixing cyanobacterium in the eastern Mediterranean, which provides more evidence that biological nitrogen fixation occurs in the region since this species has known nifH sequences (nifH is the marker gene which encodes nitrogenase reductase). It is known from other parts of the world that nitrogen fixation contributes substantially to "new" nitrogen supply in tropical oceans. However, the significance of this pathway is unknown in the eastern Mediterranean. Possible other explanations for the low $\delta^{15}N$ values in the eastern Mediterranean were discussed by Krom *et al.*
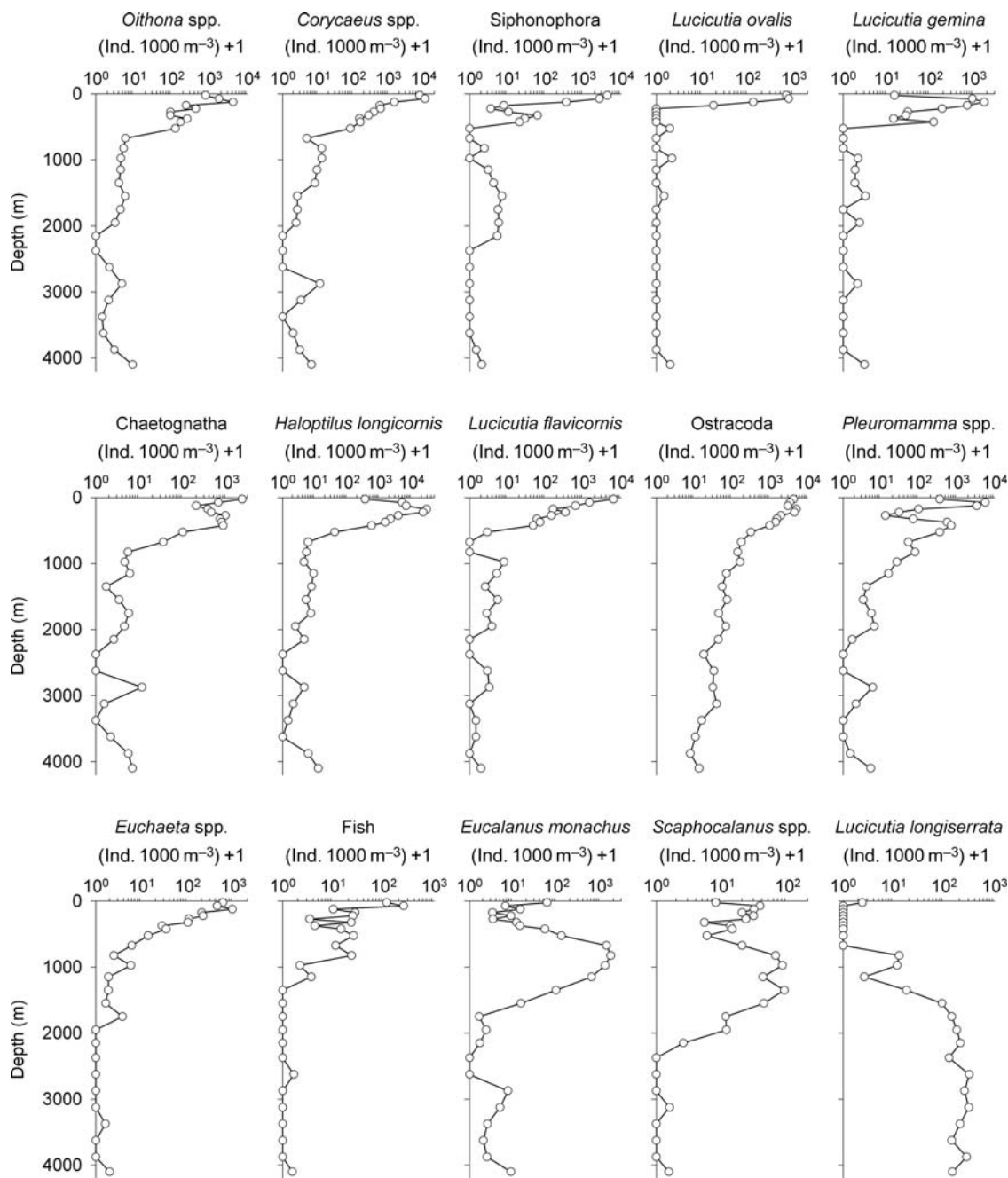
Fig. 11. Vertical distribution of specific zooplankton taxa at the Crete site.

(Krom *et al.*, 2004). The eastern Mediterranean is an ultra-oligotrophic ocean and the N:P ratio of the total input is 54, which is significantly in excess of the Redfield ratio of 16:1 (Krom *et al.*, 2004). This indicates that the system is P-limited. Krom *et al.* (Krom *et al.*, 2004) suggested alternative explanations for the low stable nitrogen values in the eastern Mediterranean. (i) In winter, when phosphate is entirely consumed, light PON of 3.5–4.0‰ but heavy nitrate of 17–20‰ remains in the

system, which caused an export of light PON. (ii) Denitrification is unimportant in the eastern Mediterranean, which causes lighter residual nitrate than the global average.

The signal of low stable nitrogen isotope values can also be seen in deep waters, down to >4000 m depth at the Crete site, both in POM as well as in the zooplankton, though the δ^{15}N values of mesozooplankton were higher in deeper waters than at the surface.
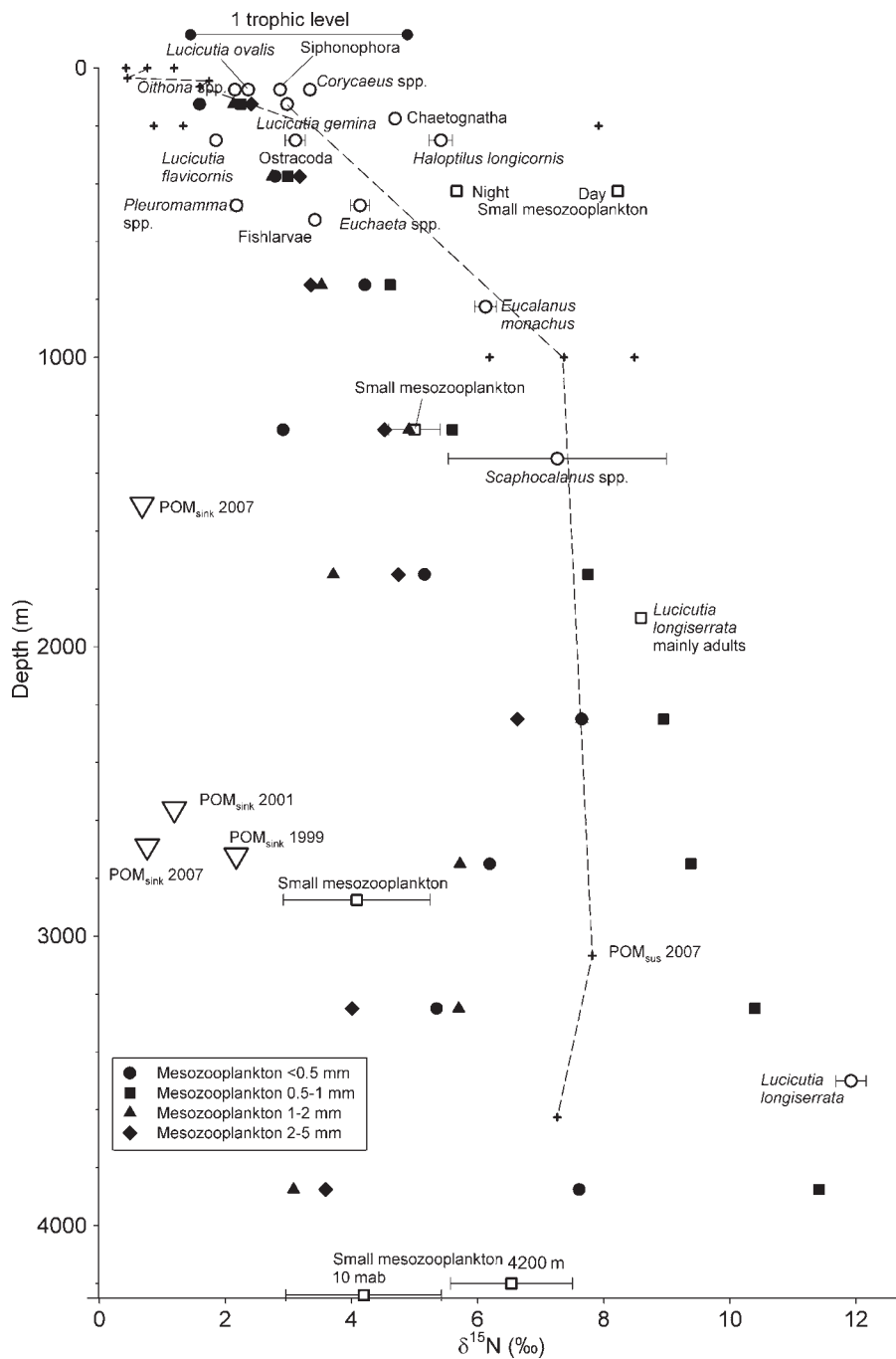
Fig. 12. $\delta^{15}N$ values (‰) of specific zooplankton taxa, small (100 μm mesh size) and large (333 μm mesh size) mesozooplankton and suspended and sinking particles at the Crete site in the eastern Mediterranean.

Polunin *et al.* (Polunin *et al.*, 2001) also found an increase in $\delta^{15}N$ of zooplankton with increasing depth in the western Mediterranean. These authors hypothesize that either more trophic steps between the consumers and the source materials exist at depth or that the source materials become enriched in ^{15}N at depth. In our study, distinctly higher values than the average zooplankton were found for *L. longiserrata*, which dominated the 0.5–1 mm size class in waters below 1500 m. Preliminary investigations by Koppelmann *et al.* (Koppelmann *et al.*, 2003b) suggested that this dominant (see Koppelmann and Weikert, 2007) "true" deep-water

species occupies a high trophic level (TL). This suggestion was based on the assumption that most deep-sea animals depend on the sinking particle flux (POM), either by direct feeding or via the food chain.

Although the increase in $\delta^{15}N$ between TLs can be variable (McCutchan et al., 2003), a mean trophic fractionation of 3.4‰ is widely applicable (Post, 2002). The TL of the different zooplankton size classes can be calculated by the following formula: $TL = (\delta^{15}N_{ZOO} - \delta^{15}N_{POM})/3.4$, where $\delta^{15}N_{ZOO}$ and $\delta^{15}N_{POM}$ are the stable isotope values of zooplankton and POM, respectively. Based on these assumptions, the TL of L. longiserrata was approximately three steps above the sinking POM since the $\delta^{15}N$ values of the sinking POM was 1.2‰ in 2001/2002 and the $\delta^{15}N$ value of L. longiserrata was 11.9‰. However, it is unknown which taxa filled the gap between the sinking particles and L. longiserrata. The larger mesozooplankton size classes and the small mesoplankton had values of 4–6‰, which are similar to a TL of 0.8–1.4 above the sinking POM. It is possible, that the still missing level was filled by other taxa, which were not investigated during the present study. A more likely explanation is that the animals had taken advantage of the suspended particle fraction, which showed $\delta^{15}N$ values around 7‰ in deep waters (Table V and Fig. 12) and/or organisms which fed on suspended particles (e.g. protozoans). Unfortunately, the values of the suspended particles (Table V and Fig. 12) were not measured concomitantly with the zooplankton, but Struck et al. (Struck et al., 2001) reported a similar depth-related trend in $\delta^{15}N$ of suspended particles in the upper 400 m at a site east of Crete in January 1998. However, the values were ~2–3‰ higher in 1998 than in 2007, indicating, similar to the sinking flux, an increase in lighter nitrogen in POM during the last decade, despite possible seasonal variations.

Lucicutia longiserrata seems to be able to utilize the suspended particle fraction in the deep-sea. Gowing and Wishner (Gowing and Wishner, 1998) showed that Lucicutia aff. L. grandis, consumed a variety of detrital particles, prokaryotic and eukaryotic autotrophs, bacteria, bacterial aggregates, microheterotrophs, virus-like particles as well as cuticle and cnidarian tissues. There is some evidence that the large numbers of E. monachus and Calanus helgolandicus observed during 1993 were transported into the deep zones of the eastern Mediterranean by the EMT (Weikert et al., 2001). Part of the population probably died in the deep water since they were not able to maintain their physiological requirements for overwintering in the relatively warm deep Levantine Sea and thus provide biomass for the nutrition of animals in this zone. Since high stocks of C. helgolandicus were not found in later years and the distribution of E. monachus was similar to the distribution before the EMT (Koppelmann and Weikert, 2007), at least the surviving C. helgolandicus may have failed to produce a generation at the surface due to a shortage of food in the oligotrophic eastern Mediterranean. The $\delta^{15}N$ values of C. helgolandicus and E. monachus were 6.6 and 6.4‰, respectively, in 1993 (Koppelmann, unpublished data). Their corpses were either consumed directly and/or decomposed by bacteria, which is in accordance with a drop in oxygen in the deep water (Klein et al., 2003). An interaction and recycling of organic matter by bacterial and viral action (Danovaro et al., 2008) can contribute significantly to the suspended particle fraction. Our results show that L. longiserrata may have taken advantage of this pathway in the eastern Mediterranean.

CONCLUSION

The processes that caused the low $\delta^{15}N$ values within the zooplankton community of the eastern Mediterranean are still not fully understood. Unlike the processes in the coastal upwelling systems (Bode and Alvarez-Ossorio, 2004) and the central North Sea (Jennings et al., 2008), seasonal variations in $\delta^{15}N$ were minor in the eastern Mediterranean, indicating that low $\delta^{15}N$ values were common throughout the year. Zooplankton at the surface was diverse, but the animals as well as the zooplankton size groups exhibited a narrow $\delta^{15}N$ range. Since stable nitrogen isotope values increase by ~3.4‰ between TLs (Post, 2002), most of the zooplankton taxa and size classes in the upper 200 m were within one TL; however, carnivorous taxa showed higher values (Fig. 12). Haloptilus longicornis was the dominant species in the subsurface zone. The $\delta^{15}N$ values for this species reflect its carnivorous feeding (Timonin, 1971). In mesopelagic depths, E. monachus accounted for ca. 40% of the 0.5–1 mm size class. The $\delta^{15}N$ value (6.1‰) of this coarse-filter feeder (Timonin, 1971) was slightly higher than the value of zooplankton in the size class of main occurrence (0.5–1 mm) between 500 and 1000 m (4.6‰), but similar to suspended particles (Fig. 12). However, feeding on suspended particles is unlikely because the $\delta^{13}C$ values of the zooplankton in the 0.5–1 mm size class (−18.5‰) was similar to the other zooplankton size classes, whereas Struck et al. (Struck et al., 2001) showed that the $\delta^{13}C$ values of suspended particles are much lower (< −25‰). Koppelmann et al. (Koppelmann et al., 2003b) reported an even higher $\delta^{13}C$ value (−14.0‰) for E. monachus, however, this was based on de-carbonized and defatted

samples. Extraction of lighter lipids will increase the $\delta^{13}C$ of an organism (Kaehler and Pakhomov, 2001). A more likely explanation is that earlier life stages of these interzonal migrators have accessed different food sources. The bathypelagic zone was dominated by the omnivorous *L. longiserrata*. This species probably fed on suspended particles as well as on remains of decomposed bodies and bacteria.

SUPPLEMENTARY DATA

Supplementary data can be found online at http://plankt.oxfordjournals.org.

ACKNOWLEDGEMENTS

FUNDING

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