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Deep-sea meiofaunal and foraminiferal communities along a gradient of primary productivity in the eastern Mediterranean Sea

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SUMMARY: Benthic metazoa and stained foraminifera (>32 μm) were studied in relation to prevailing environmental parameters in the Aegean Sea (Sporades Basin and Cretan Sea) and Levantine Basin (Ierapetra Basin) during the METEOR Cruise 40 Leg 3 (December 1997–January 1998). The sampling stations differed in nutrient contents, which were indicative of the oligotrophy of the eastern Mediterranean Sea. Meiobenthic abundance decreased significantly with depth and the total standing stock in the top 6 cm sediment layer was significantly higher at the northern stations (204–231 ind./10 cm²). In the abyssal Ierapetra Basin, the abundance for all meiobenthic taxa was minimal (10–26 ind./10 cm²). Nematodes and foraminifera were dominant and accounted together for 79–93% of the total abundance. All taxa were concentrated near the surface of the sediment and only nematodes showed a deeper penetration into the sediments in the Sporades Basin. Concentrations of chloroplastic pigments, total organic carbon and total organic nitrogen were higher in the Sporades and Ierapetra Basins than in the Cretan Sea, reflecting: (a) the different productivity levels and, thus, the higher food availability in the former than in the latter; (b) the seasonal accumulation of organic matter from the euphotic zone down to the abyssal trenches; and (c) the transportation of large amounts of sediment and organic matter in the Sporades and Ierapetra Basins, which are located at the mouth of submarine canyons, through riverine inputs, flush flooding, sediment failure and dense shelf water cascading. Meiofaunal abundances in the Aegean Sea were positively correlated with chlorophyll *a*, phaeopigments and chloroplastic pigment equivalent (CPE), and were not correlated with any of the remaining sediment descriptors, thus indicating the dependence of meiofauna on food availability.

Keywords: meiofauna, foraminifera, deep sea, oligotrophy, eastern Mediterranean Sea.

RESUMEN: COMUNIDADES DE MEIOFAUNA Y FORAMINÍFEROS DE MUCHA PROFUNDIDAD A LO LARGO DE UN GRADIENTE DE PRODUCCIÓN PRIMARIA EN EL MEDITERRÁNEO ORIENTAL. – Durante la campaña METEOR 40/3 (diciembre 97-enero 98) se estudiaron los metazoos bentónicos y foraminíferos teñidos (>32 μm) en relación a parámetros ambientales persistentes en el mar Egeo (Cuencas de Sporades y mar de Creta) y cuenca Levantina (cuenca de Ierapetra). Las estaciones muestreadas se diferenciaron por el contenido en nutrientes, y fueron indicativas de oligotrofia en el este del Mediterráneo. La abundancia del meibentos disminuyó significativamente con la profundidad; y el total de la población en los primeros 6 cm de sedimento fue significativamente más alto en las estaciones del norte (204–231 ind./10 cm²). En la cuenca abisal de Ierapetra, la abundancia de todos los taxa del meibentos fue mínima (10–26 ind./10 cm²). Los nemátodos y foraminíferos fueron dominantes y representaron el 79–93% de la abundancia total. Todos los taxa se concentraron cerca de la superficie del sedimento y solamente los nemátodos mostraron una penetración más profunda en la cuenca de Sporades. Las concentraciones de pigmentos cloroplásticos, carbón orgánico total y nitrógeno orgánico total fueron más altas en las cuencas de Sporades y Ierapetra que en el mar de Creta, reflejando: (a) los diferentes niveles de productividad y la mayor disponibilidad de alimento en el primero que en el segundo, (b) la acumulación estacional de materia orgánica desde la zona eufótica hacia los canales abisales y (c) el transporte de grandes cantidades de sedimentos y materia orgánica en las primeras áreas, que se encuentran en la boca de cañones submarinos, a través de los influjos de ríos, arrastre por inundaciones, fallos de sedimentos y cascadas de aguas densas de plataforma. Las abundancias de la meiofauna en el mar Egeo estuvieron positivamente correlacionadas con la clorofila *a*, los feopigmentos y pigmentos cloroplásticos equivalentes y no estuvieron correlacionados con ningún otro descriptor del sedimento, indicando la dependencia de la meiofauna de la disponibilidad de alimento.

Palabras clave: meiofauna, foraminíferos, mar profundo, oligotrofia, Mediterráneo oriental.

INTRODUCTION

Deep-sea sediments are food-limited environments, in which benthic communities depend strongly on the amount of organic matter reaching the sea floor (Rowe, 1983; Thiel, 1983; Gooday and Turley, 1990). Since primary production decreases with distance from shore and energy transfer to the sea floor also decreases with increasing water depth, benthic standing stock and biomass also decrease towards more oligotrophic regions and at greater depths (Thiel, 1975). This relationship applies not only to the larger benthic organisms but also to all benthic size classes, including meiofauna, macrofauna and the deposit-feeding megafauna (Thiel, 1983; Lampitt *et al.*, 1986; Sibuet *et al.*, 1989; Vincx *et al.*, 1994). Regarding meiofauna, there is growing evidence that food availability in particular is one of the major factors affecting their abundance and distribution (Thiel, 1983; Gooday *et al.*, 1992; Danovaro *et al.*, 2000; Soltwedel, 2000).

In the eastern Mediterranean, which is one of the most oligotrophic areas in the world (Psarra *et al.*, 2000), low productivity rates combined with enhanced organic matter decomposition (due to warm deep waters of 13–14°C) reduce the organic carbon flux to deeper waters. In addition, during certain periods of the year, energy flow and mineralisation processes in the water column are completely regulated by small unicellular organisms, which form the microbial loop and are responsible for the accumulation of DOC in the water column, further minimising the energy transfer to the deeper waters and the benthos (Wassmann *et al.*, 2000). Moreover, analyses of organic matter quality in the eastern Mediterranean indicate that the labile fraction of the organic matter, which may be readily available to meiofaunal organisms, decreases sharply with increasing water depth (Danovaro *et al.*, 1999). As a consequence, meiofaunal abundances and biomasses at bathyal and abyssal depths in the eastern Mediterranean are generally very low (Danovaro *et al.*, 1995; Tselepidis and Lampadariou, 2004; Tselepidis *et al.*, 2004; Lampadariou and Tselepidis, 2006), usually 2 to 25 times lower than those of the more productive western basins (de Bovée *et al.*, 1990). Exceptions to this general pattern are the high meiofaunal abundances found in abyssal trenches (Tselepidis and Lampadariou, 2004), and the higher abundances found in areas with seasonally or spatially higher production rates and areas with increased terrigenous organic

matter inputs (Danovaro *et al.*, 2000; Lampadariou and Tselepidis, 2006).

Starting in 1987, a series of expeditions in the eastern Mediterranean with the R/V *Meteor* was carried out [METEOR 5 (1987); METEOR 25 (1993); METEOR 40 (1998)] with the general aim of investigating the structure and function of deep-sea benthic communities under highly oligotrophic conditions and warm deep-sea waters. Preliminary results from these expeditions showed that the eastern Mediterranean is an event-driven system which largely depends on lateral transport combined with terrestrial runoff rather than on pelagic production (Kröncke *et al.*, 2003; Tselepidis and Lampadariou, 2004). Here we report on the response of meiobenthic communities (both metazoans and foraminiferans) from the METEOR 40 expedition to: (1) the contrasting food supply of two areas with comparable depths, the Sporades Basin (1230 m deep) versus the Cretan Sea (1840 m deep); and (2) the prevailing environmental conditions in the abyssal Ierapetra Basin (southeast of Crete, Levantine Basin, 4260 m).

MATERIAL AND METHODS

Sampling procedure

Sediment samples were collected from eight stations in the Aegean Sea and Levantine Sea during the R/V *Meteor* Cruise no 40, leg 3 in December 1997–January 1998 (Fig. 1). The physical and chemical parameters of the sediment, as well as the characteristics of the macrofaunal, viral and bacterial communities, have been presented elsewhere (Danovaro and Serresi, 2000; Kröncke *et al.*, 2003). Three stations were sampled in the Sporades Basin (1230 m deep, North Aegean Sea), three in the Ierapetra Basin (4260 m deep, Levantine Sea) and two in the Cretan Sea (1840 m deep, South Aegean Sea) (Table 1).

Undisturbed sediment samples were collected using a multiple corer with 63.5 cm² core tubes. Samples for chloroplastic pigments, total organic carbon (TOC) and total organic nitrogen (TON) analyses were collected by subsampling from the multiple-corer and were sliced into 6 sediment layers (0–0.3, 0.3–1, 1–2, 2–4, 4–6 and 6–10 cm). Each layer was homogenised and stored at –22°C for later laboratory analysis. For the grain size analysis, surface sediments (0–5 cm) were sub-

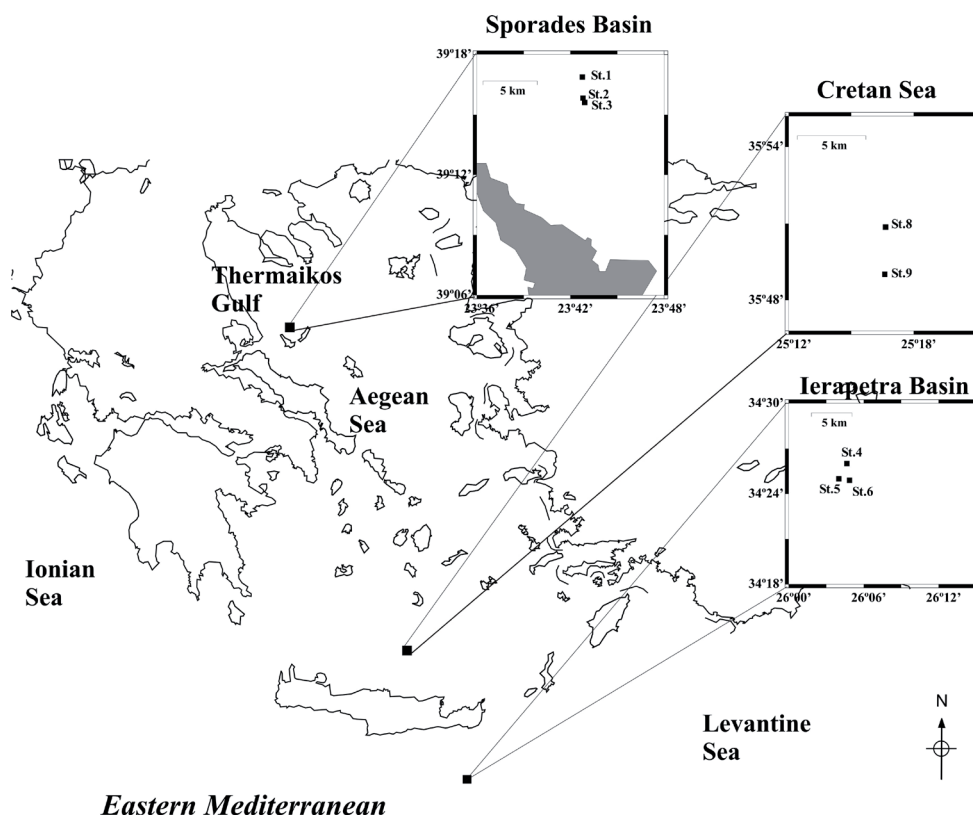


FIG. 1. – Sampling area and location of stations (Sporades Basin: stations 1, 2, and 3; Cretan Sea: stations 8 and 9; Ierapetra Basin: stations 4, 5, and 6).

TABLE 1. – Station list for the three sampling areas (Temp.: sediment temperature; Eh: redox potential at 1 cm depth; MD: median diameter of the sediment; σ_1 : sediment sorting coefficient; S&C: percentage of silt and clay).

	Stations	Latitude (N)	Longitude (E)	Depth (m)	Temp. (°C)	Eh (mV)	MD (mm)	σ_1	S&C (%)
Sporades Basin	1	39°16.53'	23°42.46'	1250	13.0	461	0.012	2.4	99.4
	2	39°15.50'	23°42.48'	1221	13.1	526	0.010	2.1	99.2
	3	39°14.97'	23°42.55'	1224	13.1	528	0.003	2.7	99.4
Ierapetra Basin	4	34°26.01'	26°03.99'	4157	13.9	466	0.011	1.0	99.9
	5	34°25.00'	26°04.00'	4260	13.8	508	0.006	1.7	96.2
	6	34°24.54'	26°04.52'	4261	13.8	503	0.020	1.6	98.2
Cretan Sea	8	35°49.01'	25°15.97'	1840	14.2	439	0.028	1.6	96.4
	9	35°50.52'	25°15.99'	1840	13.7	471	0.005	1.0	98.2

sampled from the cores and stored at -22°C for later analysis.

For meiofaunal analyses, three replicate samples which were sliced into 6 sediment layers (0-1, 1-2, 2-4, 4-6 and 6-10 cm) were collected. Immediately after slicing, they were placed for 15 min. in a MgCl_2 solution for tissue relaxation and then fixed with a neutralised formaldehyde solution to a final concentration of 4%.

Redox Potential (Eh) of the sediment was measured (in mV) on board immediately after sampling (at 1 cm intervals down to 20 cm sediment depth) with the use of calibrated combined

electrodes (Russell pH, Scotland, type no. CMPT 11/280/SA1.5).

Analytical procedures

Chlorophyll *a* and phaeopigment concentrations were determined with a TURNER 112 fluorometer (Lorenzen and Jeffrey, 1980) and using 90% acetone extractant. Phaeopigments were estimated by acidification with 0.1N HCl. The fluorometer was calibrated using an acetone extract of pure chlorophyll *a* from the algae *Anacystis nidulans* obtained from SIGMA. Chloroplastic pigment

TABLE 2. – Mean abundance (individuals per 10 cm² ± SD) of all meiobenthic taxa in the top 6 cm of the sediments. Others include taxa (Tardigrada, Tanaidacea, Oligochaeta, Echinodermata, Mollusca, Nemertina and Sipuncula) which occurred only occasionally and in very low numbers.

	Sporades Basin						Ierapetra Basin				Cretan Sea					
	St.1	SD	St.2	SD	St.3	SD	St.4	SD	St.5	SD	St.6	SD	St.8	SD	St.9	SD
Nematoda	142 ± 80		184 ± 52		143 ± 46		10 ± 5		15 ± 4		18 ± 6		51 ± 32		88 ± 74	
Foraminifera	46 ± 19		37 ± 9		47 ± 10		1 ± 1		5 ± 1		5 ± 1		14 ± 1		28 ± 28	
Copepoda	21 ± 2		18 ± 2		20 ± 2		0 ± 0		3 ± 1		4 ± 1		8 ± 1		6 ± 2	
Nauplii	6 ± 3		8 ± 2		8 ± 5		0 ± 0		0 ± 0		1 ± 0		3 ± 2		2 ± 3	
Polychaeta	5 ± 1		6 ± 2		8 ± 2		0 ± 0		0 ± 0		0 ± 0		2 ± 1		2 ± 1	
Turbellaria	3 ± 1		2 ± 1		1 ± 1		0 ± 0		0 ± 0		0 ± 0		1 ± 0		0 ± 0	
Kinoryncha	1 ± 0		0 ± 0		2 ± 1		0 ± 0		0 ± 0		0 ± 0		0 ± 0		1 ± 1	
Ostracoda	2 ± 0		1 ± 1		2 ± 1		0 ± 0		0 ± 0		0 ± 0		1 ± 0		0 ± 0	
Others	2 ± 1		2 ± 1		5 ± 4		0 ± 1		0 ± 0		1 ± 2		1 ± 1		1 ± 0	
Total	228 ± 99		258 ± 59		235 ± 30		11 ± 6		23 ± 5		29 ± 5		80 ± 35		127 ± 108	

equivalents (CPE) were considered as the sum of chlorophyll *a* and phaeopigments content.

TOC and TON concentrations were measured with a Perkin Elmer CHN 2400 analyser (Hedges and Stern, 1984).

Grain size analysis was performed according to Buchanan (1984). The median diameter (MD) and the graphic sorting coefficient (σ_1) of the sediments were calculated after Folk (1966). The silt-clay percentage fraction was also calculated.

Meiofaunal analyses

In the laboratory, meiobenthic samples were stained with Rose Bengal solution (0.5 g l⁻¹) and sieved through a 32 μ m mesh. The fauna retained on the 32 μ m mesh was extracted by triplicate centrifugation in Ludox TM (density 1.15 g cm⁻³). All meiobenthic metazoans and soft-shelled foraminiferans in the supernatant, as well as the stained hard-shelled foraminiferans from the residual sediment, were counted and identified to major taxa using a WILD stereomicroscope.

Statistical analyses

Differences in environmental and faunal parameters were assessed by one-way analysis of variance (one-way ANOVA), followed by pairwise comparisons based on the Tukey honest significant difference test (Tukey HSD). The nonparametric Kruskal-Wallis test was used when data did not meet the assumption of normality or equality of variances after being log-transformed. Spearman's rank correlation coefficient was used to assess the relationships between meiofaunal and

abiotic descriptors. Non-metric multidimensional scaling (MDS) ordination was based on the Bray-Curtis similarity and square-root transformed abundance data. Univariate and multivariate analyses were performed with the STATISTICA 6.0 and the PRIMER version 6.1.3 (Clarke and Warwick, 1994) packages, respectively.

RESULTS

Sediment characteristics and changes in Redox potential

Silty superficial sediments characterised all investigated stations (Table 1). Median grain size ranged from 0.003 mm (Station 3, Sporades Basin) to 0.028 mm (Stations 8 and 10, Cretan Sea). The silt and clay fraction varied on average from 96% (Station 8, Cretan Sea) to 99% (Stations 1, 2, 3, Sporades Basin). Northern stations (1, 2 and 3, Sporades Basin) were characterised by a sorting coefficient (σ_1) higher than 2. Redox potential (Eh) in the top 1 cm sediment layer was relatively high at all stations, ranging from 461 to 528 mV in the Sporades Basin, from 439 to 471 mV in the Cretan Sea and from 466 to 508 mV in the Ierapetra Basin. Sediment temperature was relatively constant at all stations, ranging between 13 and 14°C.

Distribution and structure of meiobenthos and relationships with the environment

Standing stock of the total meiobenthos in the top 6 cm sediment layer varied significantly (Kruskal Wallis Test, $P < 0.01$) among stations, decreasing

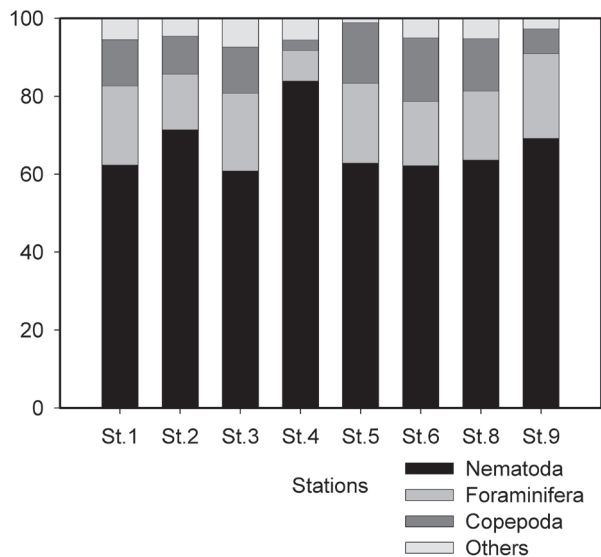


FIG. 2. – Average contribution (%) of different groups to the total meiobenthos in the three study areas.

sharply with increasing depth. The highest values were recorded in the Sporades Basin (228-258 ind./10 cm²), while in the abyssal Ierapetra Basin, the abundance of all meiobenthic taxa was very low (11-29 ind./10 cm²) (Table 2).

Nematodes and foraminifera were the most abundant groups, accounting together for 79-92% of the total meiofaunal abundance (Table 2, Fig. 2). Nematodes were the dominant taxon at all the stations examined (61-84%), with abundances ranging from 10±5 (St. 4, Ierapetra Basin) to 184±52 ind./10 cm² (St. 2, Sporades Basin). Foraminifera were the second most abundant taxon, accounting for 8-22%. Their abundance ranged from 1±1 (St. 4, Ierapetra Basin) to 47±10 ind./10 cm² (St. 3, Sporades Basin). Harpacticoid copepods (including nauplii) contrib-

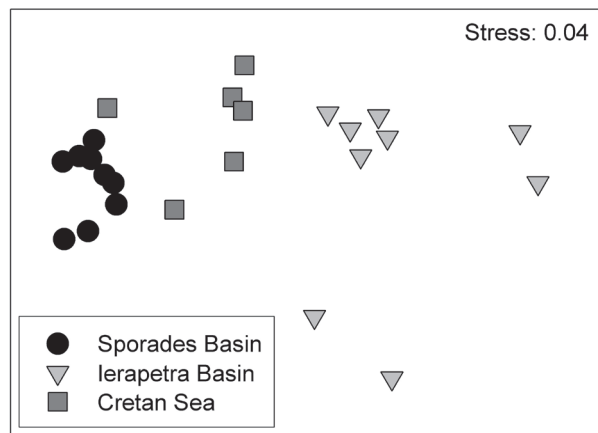


FIG. 4. – Non-parametric multidimensional scaling (MDS) ordination of replicate samples from the three sampling areas.

uted 3-16% to the total abundance and polychaetes accounted for less than 4% (Table 2). Turbellarians and kinorhynchans represented always less than 2% of the community. The remaining taxa (i.e. nemertins, molluscs, ostracods and other minor groups) contributed together approximately 3.5% to the total meiobenthos (Table 2).

As a general rule, all meiobenthic groups were concentrated in the top 1 cm layer of the sediment, the only exception being nematodes, which showed a much deeper penetration in the sediment in the Sporades Basin (Fig. 3).

Samples from the same basin were grouped closely together in the MDS plot (Fig. 4), the only exception being 9c (Cretan Sea), which lay close to the Sporades Basin stations. The main grouping factors were depth and Eh (BIOENV: R=0.82), as the shallower Sporades Basin was clearly separated from the much deeper Ierapetra Basin (one-way ANOSIM, *P*<0.001).

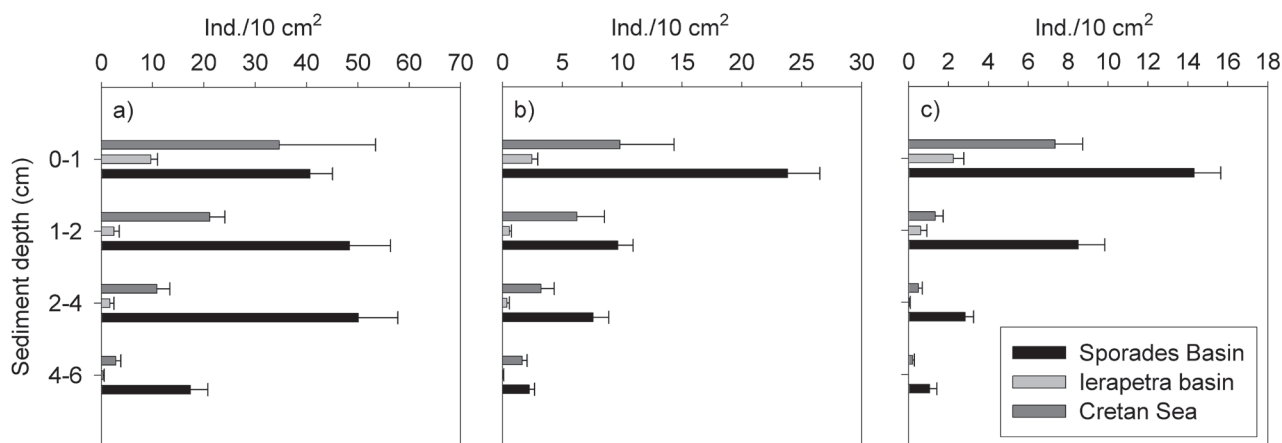


FIG. 3. – Mean vertical (individuals per 10 cm² ± SE) of (a) nematodes, (b) foraminifera and (c) copepods (adults and nauplii) at the three sampling areas.

TABLE 3. – Spearman correlation coefficient between environmental variables and meiobenthic groups (TOC: total organic carbon; TON: total organic nitrogen; Chl *a*: chlorophyll *a*; Phaeop.: phaeopigments; CPE: chloroplastic pigments equivalent; Temp.: sediment temperature; Eh: redox potential; MD: median diameter of the sediment; $\sigma 1$: sediment sorting coefficient; S&C: percentage of silt and clay).

	TOC	TON	TOC/TON	Chl <i>a</i>	Phaeop.	CPE	Chl. <i>a</i> /CPE	Depth	Temp.	Eh	MD	$\sigma 1$	S&C
Nematoda	0.76*	0.74*	-0.81*	0.33	0.52	0.45	-0.52	-0.90**	-0.77*	0.38	-0.31	0.66	0.19
Foraminifera	0.69	0.67	-0.74*	0.26	0.55	0.45	-0.62	-0.83*	-0.81*	0.29	-0.33	0.73*	0.26
Copepoda	0.74*	0.71*	-0.69	0.26	0.60	0.48	-0.62	-0.80*	-0.75*	0.07	-0.07	0.76*	0.21
Nauplii	0.74*	0.71*	-0.76*	0.33	0.48	0.40	-0.50	-0.87**	-0.67	0.33	-0.24	0.76*	0.21
Polychaeta	0.74*	0.71*	-0.76*	0.33	0.48	0.40	-0.50	-0.87**	-0.67	0.33	-0.24	0.76*	0.21
Turbellaria	0.75*	0.72*	-0.68	0.28	0.59	0.47	-0.59	-0.84**	-0.73*	0.01	0.02	0.67	0.25
Kinoryncha	0.36	0.40	-0.69	0.02	0.28	0.14	-0.54	-0.70	-0.82*	0.34	-0.68	0.52	0.55
Ostracoda	0.63	0.63	-0.76*	0.17	0.39	0.27	-0.61	-0.90**	-0.69	0.17	-0.24	0.75*	0.34
Others	0.79*	0.69	-0.57	0.62	0.62	0.60	-0.19	-0.73*	-0.66	0.38	-0.10	0.72*	0.45

* $P \leq 0.05$; ** $P \leq 0.01$

Most meiobenthic groups were negatively correlated with depth, while nematodes, copepods, nauplii, polychaetes and turbellaria were positively correlated with total organic carbon and nitrogen (Table 3). A significant positive correlation between the sorting coefficient of the sediment and most groups, with the exception of nematodes, turbellaria and kinorynchs, was also found (Table 3).

DISCUSSION

In the present study, several trends regarding the distribution patterns of meiofaunal communities under the highly oligotrophic conditions of the eastern Mediterranean are evident. Meiofaunal abundances significantly decreased with increasing water depth. They were also much higher in the northern (Sporades) compared to the southern (Cretan and Ierapetra) basins, with average abundances in the Sporades Basin being almost double than those in the Cretan Sea (215-93 ind./10 cm², respectively) and 10 times higher than the extremely low values found in the southernmost Ierapetra Basin (10-26 ind./10 cm²). Meiofauna abundances were also much lower below the surface of the sediments and only nematodes showed a deeper penetration in the sediments in the Sporades Basin, following the vertical profiles of phaeopigments and bacteria.

The abundances recorded in this study are in accordance with those of other studies in bathyal and abyssal sediments of the eastern Mediterranean (Danovaro *et al.*, 1995; Danovaro *et al.*, 2000; Tselepides and Lampadariou, 2004; Tselepides *et al.*, 2004; Lampadariou and Tselepides, 2006) but much lower than those of other deep-sea areas with a similar water depth (Shirayama, 1984a; Soetaert *et al.*, 1991; Vincx *et al.*, 1994). This general trend

of very low meiofaunal abundances in the eastern Mediterranean is mainly related to the prevailing oligotrophic conditions and is clearly evident when the northern and southern stations of the Aegean Sea are compared. The South Aegean, one of the most oligotrophic regions of the Mediterranean Sea, is characterised by extremely low productivity rates coupled with high temperatures, strong summer stratification of the water column and minimal quantities of organic matter in bathyal sediments (Psarra *et al.*, 2000; Tselepides *et al.*, 2000). In contrast, the North Aegean is more productive, mainly due to the influx of nutrient-rich Black Sea surface waters entering through the Dardanelles Straits and riverine outflows (Poulos *et al.*, 1997). In addition to this, the deep Sporades Basin is at the south end of Thermaikos Gulf, acting as a deposition centre for sediments originating from riverine inputs and nepheloid layer detachments over the continental shelf (Lykousis and Chronis, 1989). This higher productivity of the North Aegean clearly results in high pigment concentrations in the sediment (chlorophyll *a*, phaeopigments and CPE), which in turn results in much higher meiofaunal abundances in the Sporades Basin, as can also be seen in the significant correlations between abundances and pigment concentrations. These results are in line with previous research in the area. For example, strong differences in meiofaunal standing stocks between bathyal stations of the North Aegean and stations of similar depth of the South Aegean have been reported by Lampadariou and Tselepides (2006), who also attributed them to differences in surface productivity and food input to the benthos.

The very low abundances found in the Ierapetra Basin follow the general trend of decreasing meiofauna abundance with increasing water depth (de Bovée *et al.*, 1990; Vincx *et al.*, 1994). One of the

most important factors varying with depth is the supply of organic matter to the sea floor, and the low food supply at abyssal and hadal depths results in reduced macrofaunal and meiofaunal abundance and biomass. Exceptions from the above rule are upwelling areas, characterised by high seasonal down-slope fluxes of organic matter as well as areas where—due to seafloor morphology or hydrodynamic processes—particulate organic carbon may be accumulated on the ocean floor. For example, Danovaro *et al.* (2002) reported meiofaunal densities 1 or 2 orders of magnitude higher in the Atacama Trench (7800 m deep) than in the much shallower surrounding areas (1050–1355 m deep), and Tselepides and Lampadariou (2004) reported much higher meiofaunal abundances in the Hellenic and Pliny Trenches (3744–4617 m deep) than at the shallower (<3000 m deep) nearby abyssal sites. These high values were attributed to the function of trenches as abyssal traps for particulate organic matter, as indicated by the very high phaeopigment concentrations and the enhanced activity and biomass of microbial communities (Boetius *et al.*, 1996). Food quality is another factor that may account for the lower abundances found in the Ierapetra Basin. Analysis of the biogeochemical composition of sedimentary organic matter has shown that the eastern Mediterranean is a strongly protein-depleted ecosystem and that the concentration of proteins plays a key role in determining its trophic properties (Danovaro *et al.*, 1999). In contrast, carbohydrates, which are common for oligotrophic environments, are composed mainly of refractory compounds with low degradation rates. In the Ierapetra Basin, the protein/carbohydrate ratio suggested that the quality of organic matter was very low during winter (Danovaro and Serresi, 2000). We postulate that the labile compounds from the high-quality, fresh organic matter accumulated during the summer are easily consumed, resulting in surprisingly high meiofaunal abundances. Then, the remaining organic matter during the winter is dominated by less soluble, refractory compounds behaving as an organic carbon reservoir that is difficult for benthic meiofauna to degrade, thus limiting their standing stocks until a further down-slope flux of fresh labile organic matter occurs.

The vertical distribution of meiofauna within the sediment has been investigated by many authors. A decrease in meiofauna abundance has been generally observed, although in some cases a maximum was found in deeper layers (Thiel, 1983 and refer-

ences therein). One of the main factors influencing the vertical penetration of meiofauna into deep-sea sediments is the oxygenation of the sediment column (Shirayama, 1984b). In more productive areas, however, food may be more important since it will penetrate deeper into the sediment due to vertical mixing and bioturbation by larger animals (Thiel, 1983; Lambshead *et al.*, 1995). In the present study, the high Eh values measured in all three areas—although not a direct measurement of oxygenation—suggest that other site-specific factors may be important for the observed vertical distribution patterns of meiofauna. In fact, the significantly deeper penetration of meiofauna in the Sporades Basin and the Cretan Sea and the relatively high abundances of nematodes in the 2–4 cm layer in the Sporades Basin clearly fit the vertical profiles of phaeopigments and bacterial density in the sediment (Danovaro and Serresi, 2000), thus suggesting that the depth of food penetration may be more important for meiofauna than oxygen (Lambshead *et al.*, 1995).

Regarding foraminifera standing stocks, data from the eastern Mediterranean are practically nonexistent. However, the densities found during this investigation, especially those from the Sporades Basin, were similar to those previously found in the western Ionian (Tselepides *et al.*, 2004) as well as in other deep-sea areas (Hughes *et al.*, 2000). Foraminifera densities at bathyal and abyssal depths are usually less than 200 ind./10 cm² (Thiel, 1975; Gooday, 1986), although much higher values have been reported from areas with a higher carbon input (Fariduddin and Loubere, 1997). Some foraminifera may rapidly and directly incorporate part of a bloom sedimentation, which suggests that they play an important role in the breakdown of fresh detrital material by benthic food webs (Moodley *et al.*, 2000). Thus, the comparison of the two major meiobenthic components (i.e. nematodes and foraminifera) suggests that both groups are similarly sensitive to food supply and that they show a similar response to carbon limitation in terms of standing stock.

In the deep-sea, short-term seasonal changes that may affect benthic populations, such as the deposition of large amounts of phytodetritus, are known to occur quite often (Tyler, 1988; Pfannkuche, 1993; Smith *et al.*, 1996). Longer time-series measurements over decadal scales, although quite rare, have also successfully attributed changes in benthic communities to temporal changes in phytodetrital fluxes (Smith and Druffel, 1998; Billett *et al.*, 2001). In

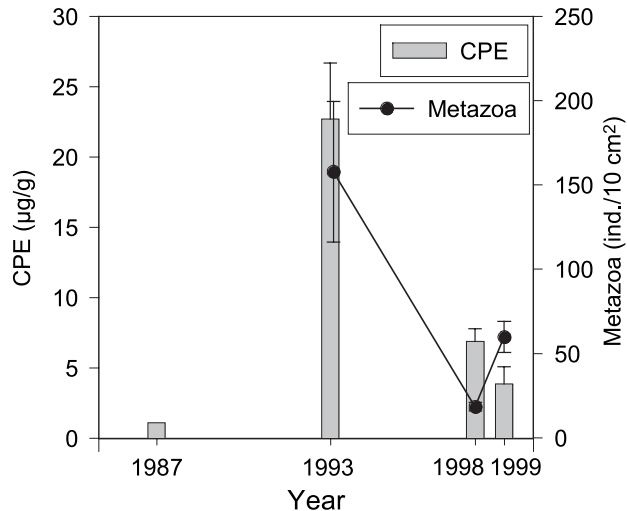


FIG. 5. – Time series measurements of chloroplasic pigment equivalent (CPE) and metazoan meiofauna abundances from different cruises in the Ierapetra Basin [1987: Meteor No 5/1 (Tselepidis and Lampadariou, unpublished data); 1993: Meteor No 25/1 (Tselepidis and Lampadariou, 2004); 1998: Meteor No 40/3 (Present study); 1999: Aegaeo Trans-Mediterranean cruise (Danovaro *et al.*, 2008)].

the eastern Mediterranean, low food availability at 4000 m in the abyssal Ierapetra Basin, as indicated by the low concentrations of CPE in 1987, was followed by very high concentrations in 1993 before dropping near to background values in 1998 and 1999 (Fig. 5). This fluctuation was probably due to a dramatic change in the hydrography of the Cretan Sea as of 1992, which caused an increasing outflow of nutrient rich water masses into the Levantine Basin (Roether *et al.*, 1996; Theocharis *et al.*, 1999). This event affected not only the abundance and composition of the planktonic assemblages (Weikert *et al.*, 2001) but also the macro- and meiobenthic communities (Kröncke *et al.*, 2003; Tselepidis and Lampadariou, 2004). The still high winter concentrations of phaeopigments in 1998 compared to 1987 may suggest that the induced changes are longer-term and also that organic material may accumulate in the Ierapetra Basin. The above results are a clear indication that the eastern Mediterranean is an event-driven system, with irregular high food ingressions into the sea floor, which plays a major role in the structure and function of benthic communities.

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