

Distribution of mesozooplankton resting eggs in seabottom sediments of Thermaikos gulf (NW Aegean Sea, Greece) and possible effects of sediment resuspension

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Abstract

The distribution of mesozooplankton resting eggs was studied in the bottom sediments of Thermaikos Gulf (Aegean Sea, Greece), within the framework of the EU project INTERPOL; possible effects of sediment resuspension, due to physical forcing (storm events) and/or to anthropogenic activity (trawling) on the egg assemblages were investigated. Sediment core slices of 2 cm height were collected down to 10 cm depth at 6 stations (from water depth ranging from 25 to 60 m); mesozooplankton samples from the water column were obtained simultaneously. Sampling was performed in September 2001 (before trawling activities and without storm events), in late October 2001 (after the start of the trawling activities) and in February 2002 (after 120 days of intensive trawling activities and the stormy season). The total abundance of eggs was higher at stations located close to the rivers' mouths, with the muddy sediments of the bed and the water column rich in zooplankters, than at stations located at greater depths and with muddy-sand bed sediments. At the former stations, the vertical distribution of resting eggs has revealed a trend of homogenisation within the sediment column, from September to February; this is related probably to sediment resuspension. At the latter stations, no clear temporal variability in the vertical distribution was detected. The eggs found in the bottom sediments of Thermaikos Gulf were assigned to 16 morpho-types. Amongst these, eggs assigned to *Paracartia latisetosa* and *Labidocera wollastoni* (as well as one type called as "Calanoida 3"), were found to be dominant at all the stations and during all the sampling periods, both as full and empty eggs.

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1. Introduction

Some copepod species of temperate coastal areas, as well as all cladocerans and rotifers are able to produce resting eggs (*sensu* Marcus, 1996) to

overcome an unfavourable season; this, for most species, is the winter (see the reviews of Onbé, 1991, for cladocerans; Marcus, 1996 and Mauchline, 1998, for copepods). This life cycle trait has been considered recently as common in neritic plankton (Giangrande et al., 1994; Marcus and Boero, 1998; Rubino et al., 2000). Copepods of the superfamily Centropagoidea (which comprises the families

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Acartiidae, Centropagidae, Temoridae, Pontellidae, all present in the study area) are the only resting egg producers in coastal areas (Lindley, 1992; Mauchline, 1998).

Resting eggs, as with other particles of a similar size (70–250 µm), accumulate in the bottom sediments of confined coastal areas (e.g., harbours, lagoons, or protected bays), characterised by low hydrodynamic conditions (Belmonte et al., 1995; Marcus and Boero, 1998). Here they compete numerically with organisms of the meiofauna within the surface sediment layer (Pati et al., 1999). The concentration of resting stages per surface unit decreases typically with the distance from the coast and water depth (Marcus, 1995; Rubino et al., 2000).

The vertical distribution of eggs in the sediment has been investigated elsewhere (Marcus et al., 1994; Viitasalo and Katajisto, 1994; Belmonte et al., 1995, 1999). The pattern identified is considered as complicated by the fact that it depends mostly upon the sediment structure (laminated or mixed), since the surface sediments are possibly affected by biotic (animals) and/or abiotic (turbulence) resuspension events (Giangrande et al., 2002). Apart from the first centimetres of sediment (which could be affected by biotic and abiotic processes), the deepest portion of the sediment column hosts generally a few resting eggs which represent a “bet hedge investment” (*sensu* Philippi and Seger, 1989) of species, implying a long-time diapause (e.g. see Marcus et al. 1994; Hairston et al., 1995).

The distribution and abundance of resting eggs has been supposed to be a critical factor influencing the overall distribution, seasonal population dynamics, and long-term variations in the abundance of copepods, cladocerans and rotifers (Marcus, 1984; Uye, 1985; Viitasalo, 1992). Hatching of the eggs may be regulated by seasonally varying conditions (e.g. temperature) (Marcus, 1989), whereas the oxygenation of deep water layers affects probably the accumulation/hatching rates of sunken resting eggs, due to the inhibition power of hypoxia on the egg hatching (Lutz et al., 1992; Viitasalo and Katajisto, 1994). A crucial point for their hatching is their vertical distribution within the sediment, since eggs do not hatch whilst buried. Therefore, mechanisms that lead to the uncovering of buried eggs (e.g sediment resuspension, bioturbation) are important (Marcus, 1996). Resuspension of sediments by episodic storm events leads, probably, also to the resuspension of eggs (Marcus, 1990). La-

boratory experiments have shown that, after resuspension, eggs may be reburied or remain at the water/sediment interface, depending upon their settling velocity relative to that of the surrounding sediment particles (Marcus and Taulbee, 1992). Nevertheless, no information is available from in situ studies on the effects of mechanical sediment resuspension on the vertical egg distribution.

Thermaikos Gulf (NW Aegean Sea—Greece) (Fig. 1) is a semi-enclosed elongated shelf area, connecting with the deep part of the North Aegean Sea at its far southern end. Several circulation-forcing mechanisms (wind and surface heating/cooling, riverine buoyancy input, intrusion of Aegean waters) contribute to the formation of the circulation structures and the associated variability. Hence, despite its semi-enclosed morphology, the Gulf is a very hydrodynamically energetic area (Kontoyiannis et al., 2003). Three major rivers (Axios, Aliakmonas, and Pinios) flow into the area. The northern part of the area, together with the zone offshore of the western coastline, are covered by fine-grained sediments with a low percentage of sand (<10%) (Karageorgis and Anagnostou, 2001). The elevated nutrient inputs from the rivers, as well as urban and industrial runoff, are the main causes of eutrophication of the inner gulf (Gotsis-Skretas and Friligos, 1990). Mesozooplankton abundance and biomass has been found to decrease from the inner to the outer part of the Gulf; they vary seasonally, presenting high values in early spring and low values during summer (Siokou-Frangou and Papathanassiou, 1991; Siokou-Frangou et al., 2003). Among the zooplankters, the copepods *Acartia clausi*, *Centropages typicus*, *C. ponticus* and the cladocerans *Evadne spinifera*, *E. tergestina*, *Penilia avirostris*, *Podon polyphemoides* were found to be dominant (Siokou-Frangou and Papathanassiou, 1991). All the above species are known to produce resting eggs (Sazhina, 1968; Onbé, 1991; Mauchline, 1998) used probably as a survival strategy in the area. Thermaikos Gulf is submitted to intense trawling from October to May (Stergiou et al., 1997) and storm events are common during winter (Tragou et al., this volume), resulting probably in sediment resuspension in the shallower parts of the gulf.

Within the framework of the EU project INTERPOL, an attempt was made to study the abundance and distribution of mesozooplankton resting eggs in the sediments of Thermaikos Gulf, and likewise to investigate the possible effects of sediment

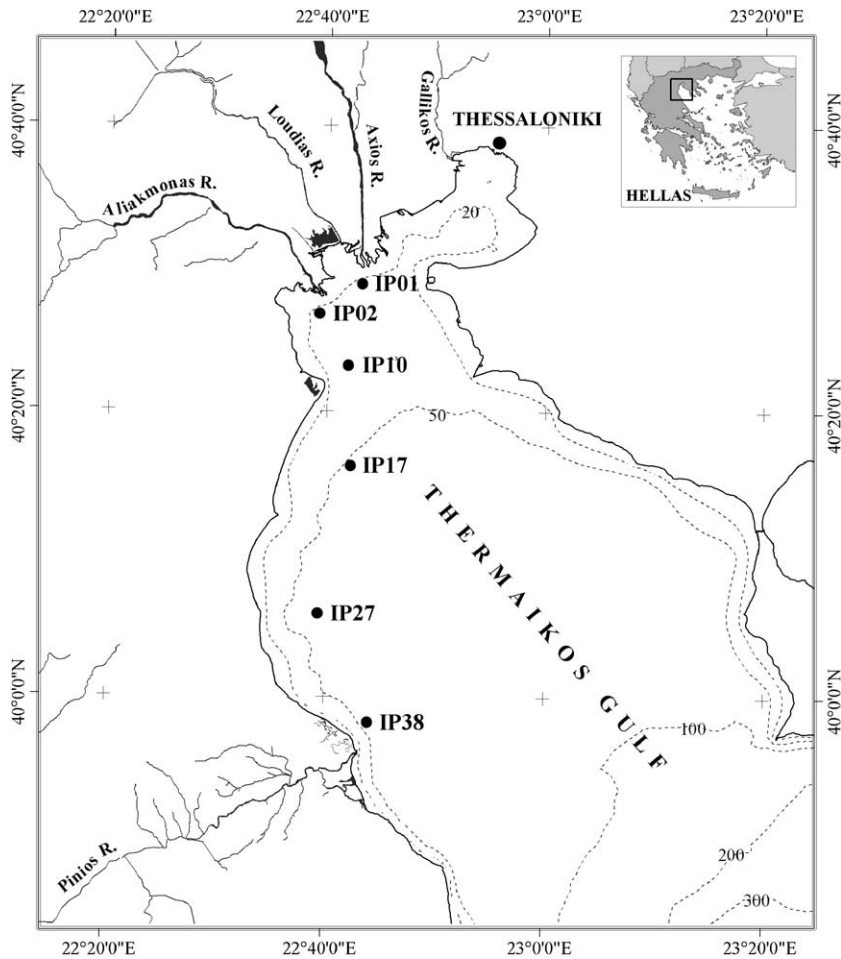


Fig. 1. The location of sampling stations in Thermaikos Gulf (bathymetry in metres).

resuspension, due to storm events and/or trawling procedures, on the egg banks of the study area. The present study is a first survey of zooplankton resting eggs in Greek marine coastal waters.

2. Material and methods

In order to evaluate the effects of sediment resuspension on the consistency and the composition of resting egg assemblages on the seabed of Thermaikos Gulf, integrated sampling of plankton/sediment was carried out in late September 2001 (end of the non-trawling period and, generally, without storm events), in late October 2001 (three weeks after trawling was permitted) and in late February 2002 (following intensive trawling activities and the stormy season).

Sampling was performed at six stations: IP01 (30 m), IP02 (27 m), IP10 (41 m), IP17 (55 m), IP27

(64 m), IP38 (50 m) (Fig. 1). Stations IP01, IP02 and IP38 are located in front of the Axios, Aliakmonas, and Pinios river mouths, respectively. No sampling was performed at Station IP02, in October 2001. Station IP17 was not affected by trawling activities during the study period, since a multiparametric buoy was anchored at this station and the site was too deep for the surface waves to cause any sediment resuspension (Tragou et al., *this volume*); therefore Station IP17 may be considered as a “control site”.

Two cores of bottom sediment (9 cm diameter) were collected with a Multiple-corer, of Bowers and Connelly type. Each core was extruded at 2 cm intervals, down to a depth of 10 cm; each slice was divided in two parts. Half of the first core slice was pooled together with that of the second core, constituting the analysed sample for the determination of egg abundance and species

composition at each layer. The other half parts of the slices were used for taxonomy and for hatching experiments in order to confirm eggs taxonomy. All the samples were kept in plastic boxes, at 4 °C and in dark.

In the laboratory, each sample was washed into a 500 ml beaker with 0.45 μm -filtered seawater. Samples used for egg abundance were sonicated for 1 min, with a Vibra Cell 72405 sonicator; they were filtered over 200 and 40 μm plankton screens. For the determination of the empty and full egg abundance, the material on the screens was washed with seawater and transferred to a counting apparatus, for identification under a dissecting microscope. “Empty” eggs were considered those, which were damaged (very few eggs), or empty because they were hatched. The identification into species level of the eggs was based upon the existing published literature (Sazhina, 1968; Grice and Gibson, 1981, 1982; Onbé, 1985; Belmonte et al., 1995; Belmonte, 1992; Della Tommasa et al., 2000; Rubino et al., 2000). Experiments for hatching were performed on different egg morphotypes, collected at selected stations. The samples were filtered over 40 μm plankton screens and the remaining material on the screens was added to tubes containing a saturated solution (1/1) of sucrose and distilled water; they were centrifuged at 3000 rpm, for 5 min (Onbé, 1978). After centrifugation, the material remaining in suspension was washed through a 40 μm sieve and transferred to a counting apparatus, for identification under a dissecting microscope. Different egg types were sorted and transferred to wells containing seawater; they were incubated at the ambient temperature of Thermaikos Gulf (13–17 °C). The wells were checked daily by inverted microscope, to identify the hatched forms. Measurements of egg diameter were performed using an image analyser system (Image Pro Plus). About 300 eggs of different morphotypes were used for hatching tests; these were incubated for 110 days.

In parallel to the sediment sampling, mesozooplankton samples were collected from the water column at each of the above-mentioned stations, by vertical hauls of a WP-2 net (200 μm).

Differences between stations and months, regarding the total abundance of eggs in the 0–10 cm sediment column, were tested by two-way ANOVA; any differences were considered as significant at $p < 0.05$. The Tukey test was employed, for comparison between stations or months.

3. Results

Eggs of copepods, cladocerans and rotifers, were found at all stations studied; however, their abundance varied during the sampling periods. In September, their total abundance in the 0–10 cm sediment depth varied from 979 eggs m^{-2} (IP17) to 15,679 eggs m^{-2} (IP38) (Fig. 2). An increase of egg abundance was observed in October at all of the stations except at IP38, when the values varied

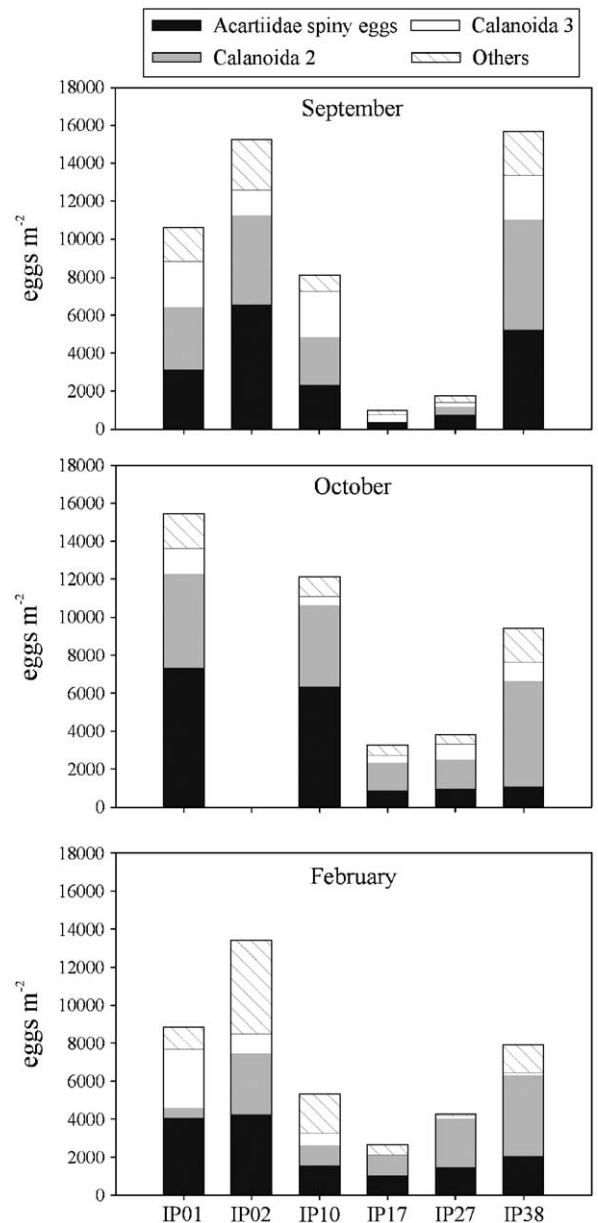


Fig. 2. Distribution of egg abundance in the sediments of Thermaikos Gulf.

between 3265 eggs m^{-2} (IP17) and 15,453 eggs m^{-2} (IP01). In contrast, egg numbers were lower in February compared to previous sampling months: 2612 eggs m^{-2} (IP17) to 13,442 eggs m^{-2} (IP02) (Fig. 2). During almost all of the periods, higher abundances were encountered at Stations IP01, IP02, followed by those at stations IP38 and IP10; the lowest values were recorded at Stations IP17 and IP27. Differences between the stations were statistically significant ($p = 0.0013$) and, according to the Tukey test, the egg abundance values were significantly higher at Stations IP01, IP02, IP38 than at IP17 and IP27; similarly, egg abundances at Station IP10 were significantly higher than at Station IP27. The observed differences among sampling periods were not significant ($p = 0.2602$). The average value of the empty/full ratio varied between 1 in September, 0.78 in October and 1.28 in February. Regarding the total abundance of copepods (only species known to produce resting eggs) and cladocerans within the water column, higher values were generally identified at Station IP02 (with an average value over all the periods of 1057 ind m^{-3}), than at the other stations (Fig. 3).

The vertical distribution of eggs in the sediment column from 0–10 cm, did not follow the same pattern at all of the stations and during all the sampling periods. Stations IP01, IP10 and IP38 have revealed some similarities regarding the vertical distribution of eggs. In September (before trawling), a general decrease of eggs was observed from the surface layer to the deepest one; conversely in October (the start of the trawling period), the decreasing pattern was not so clear and differences

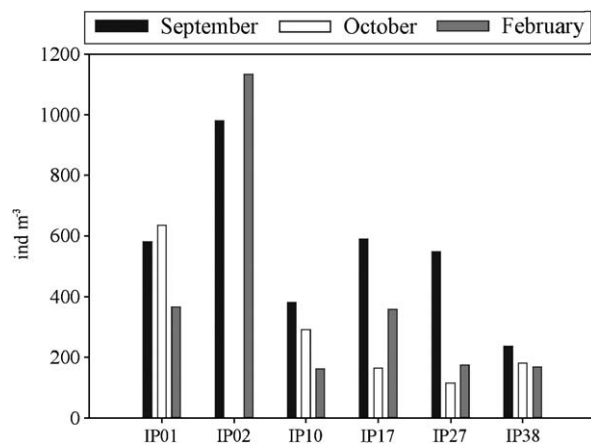


Fig. 3. Total abundance of copepods (only species known to produce resting eggs) and cladocerans within the overlying water column of Thermaikos Gulf.

between the layers were less important. Finally, in February (after 120 days of intense trawling and the stormy season) the egg distribution amongst the layers was more or less homogenised (Fig. 4). As for Station IP02, a decrease of egg numbers with depth was also observed in September; however the pattern was inverted in February. It should be noted that, at Stations IP17 and IP27 the abundance of eggs was found generally to be decreasing with sediment depth, during September and February; no clear pattern was obvious in October (Fig. 4).

The eggs found in the bottom sediments of Thermaikos Gulf were assigned to 16 morphotypes. Amongst these, spiny eggs of Acartiidae as well as two types named as “Calanoida 2” and “Calanoida 3” were found to be dominant at all of the stations and during all of the sampling periods, both as full and empty eggs (Table 1); they represented, respectively, 35%, 34% and 14% of all eggs encountered in the sediments. Eggs of the cladocerans *Evadne* spp., *Podon* spp. and *Penilia avirostris* were common in the sediments. Interestingly, eggs of the copepods *A. clausi* and *C. typicus*, which according to the literature are not classifiable as diapausal on a morphological basis but rather as quiescent eggs, were found only rarely.

Eggs of Acartiidae (spiny), “Calanoida 2” and “Calanoida 3”, *Evadne* spp., *Podon* spp., *P. avirostris*, *A. clausi* and *C. typicus* were incubated for hatching. Nauplii were born after 50–80 days from eggs of “Calanoida 2” (Fig. 5); one egg of *Centropages typicus* hatched one nauplius, after 3 days of incubation. Further, *Podon* spp. juveniles hatched from eggs incubated over 70 days.

The spatial variability patterns of the abundance values of the spiny eggs of Acartiidae, together with the “Calanoida 2” and “Calanoida 3” eggs, were similar to that of the total abundance of eggs during all the sampling periods: high abundance values were found at Stations IP01 and IP02 while low values were detected at Stations IP17 and IP27 (Fig. 2). It is noteworthy that eggs of rotifers were found exclusively at Stations IP01, IP02, IP38, which are located close to the rivers’ mouths.

Average values of full eggs over all the stations have shown a decrease from October to February for the Acartiidae spiny eggs (Table 1). The abundance of eggs of “Calanoida 2” increased from September to October, followed by a decrease in February; no variability was detected for “Calanoida 3”. The increased ratio of empty/full eggs of the Acartiidae spiny eggs, in October and February

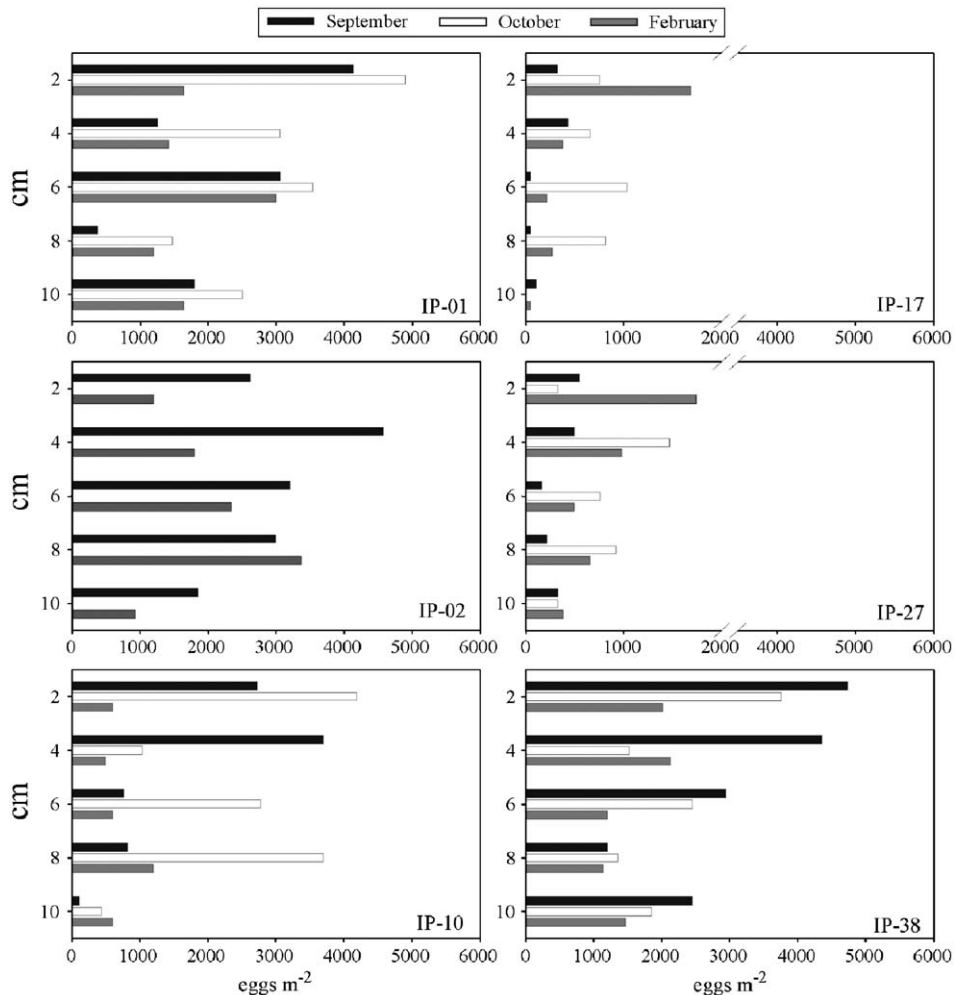


Fig. 4. Vertical distribution of egg total abundance in the sediments of Thermaikos Gulf.

compared to September, could lead to the assumption that hatching occurred in the October–February period. For “Calanoida 2”, the lower ratio empty/full in October than in September suggests an enrichment of the egg bank. The increased ratio in February could be due to the egg hatching.

In September and October, the water column community was dominated by the copepods *Paracalanus parvus*, *Clausocalanus furcatus* and the cladoceran *P. avirostris*, accompanied by the cladoceran *Evadne spinifera*, and the copepod *Oncaea media* (Table 2). *A. clausi* (adult females representing 6% of the population, with 93% were copepodids) and *P. polyphemoides* were found to be dominant in the inner part of the Gulf (Stations IP01, IP02 and IP10) during February; whereas

P. parvus and *Ctenocalanus vanus* dominated in the outer part of the Gulf. Adults of *Paracartia latisetosa*, *Acartia negligens*, and *Paracartia grani* (family Acartiidae) were found in September and/or in October, in very low numbers. *Centropages typicus* was numerically scarce during all the sampling periods; *C. ponticus* and *Evadne tergestina* decreased from September to February. Few specimens of the cladocerans *Evadne nordmanni* and *Podon intermedius* were detected in the water column.

4. Discussion

Egg banks in the sediments could include both resting, quiescent and subitaneous eggs. The majority of the eggs found in the sediments of Thermaikos

Table 1
Average abundance values (eggs m⁻²) over sampled stations of full and empty eggs of the taxa found in the Thermaikos Gulf sediments (0–10 cm)

Taxon	Description	Reference	September		October		February	
			Full	Empty	Full	Empty	Full	Empty
<i>Copepods</i>								
Spiny egg of Acartiidae	70 µm, spines 15–20 µm	Rubino et al. (2000)	1488	1588	1535	2101	735	1678
“Calanoida 2”	120–130 µm, spines 15–20 µm	Della Tommasa et al. (2000)	1497	1546	2135	1415	1043	1274
“Calanoida 3”	120–130 µm, spines 5 µm	Della Tommasa et al. (2000)	699	798	664	163	697	315
<i>Acartia clausi</i>	75 µm, smooth	Belmonte (1998)	18	81	90	54	109	353
<i>Centropages typicus</i>	75 µm, spines 35 µm	Rubino et al. (2000)	36	190	0	54	27	54
<i>Cladocerans</i>								
<i>Evadne spp.</i>	230–265 µm	Rubino et al. (2000)	317	380	424	239	136	163
<i>Podon spp.</i>	220 µm	Belmonte et al. (1995)	36		76		9	
<i>Penilia avirostris</i>	240–270 × 175–220 µm	Onbé (1985)	63	54	76		36	
<i>Rotifers</i>								
<i>Synchaeta sp.</i>	80 × 60 µm	Rubino et al. (2000)	127	272	0		136	325
Other rotifers	130 × 90 µm		72	244	54		27	
<i>Other taxa</i>								
Unknown 1	80 µm, spines 3.5 µm		0		54	54	54	
Unknown 2	175 µm, smooth		145	72	54	82	14	54
Unknown 3	125 µm, crispy		36	81	18	54	27	163
Unknown 4	110 µm, spines 5 µm		0	54	18		0	



Fig. 5. Egg and hatched nauplius of the morphotype “Calanoida 2” (for details see text). Scale bar: 100 µm.

Gulf can be considered as resting eggs, based upon their morphology. Hatching experiments reinforce the above classification, since very few eggs hatched even after 110 days of incubation. On a morpholo-

gical basis, only the eggs of *Acartia clausi* and *Centropages typicus* were classified as quiescent; particularly for *C. typicus*, this was also confirmed by the egg hatching after 3 days of incubation. Eggs

Table 2
Mean abundance values over sampled stations of mesozooplankton species found in the Thermaikos Gulf water column

Species (ind m ⁻³)	Month		
	September	October	February
<i>Copepods</i>			
Species known to produce resting eggs			
<i>Acartia clausi</i>	27	2.1	284
<i>Centropages typicus</i>	15	3.8	17
<i>Centropages ponticus</i>	14	1.6	—
<i>Paracartia latisetosa</i>	—	0.3	—
Species not known to produce resting eggs			
<i>Paracartia grani</i>	2	0.3	—
<i>Acartia negligens</i>	2	—	—
<i>Calocalanus spp.</i>	33	56	7
<i>Clausocalanus furcatus</i>	181	145	14
<i>Ctenocalanus vanus</i>	—	16	51
<i>Oithona plumifera</i>	55	44	27
<i>Oncaea media</i>	70	56	47
<i>Paracalanus parvus</i>	517	133	50
<i>Temora stylifera</i>	52	37	—
<i>Cladocerans</i>			
Species known to produce resting eggs			
<i>Penilia avirostris</i>	220	148.4	0
<i>Evadne spinifera</i>	128	56.4	0
<i>Evadne tergestina</i>	36	3.9	0
<i>Evadne nordmanni</i>	4	16.7	1
<i>Podon polyphemoides</i>	3	0.8	72
<i>Podon intermedius</i>	1	0.1	4

of both species were found very rarely in the sediments; similarly the abundance of adults was very low in the water column, except in February, when *A. clausi* was encountered in high numbers. The latter species, together with *C. typicus*, was found throughout almost all of the year in inner Thermaikos Gulf, reaching high numbers in the area of Stations IP01, IP02 (Siokou-Frangou et al., 2003). In addition, both species were found to be present throughout the year in the Adriatic Sea (Hure and Kršnić, 1998). Thus, we may assume that the strategy of resting egg production is not probably necessary for the perpetual presence of these species in Thermaikos Gulf.

Despite the scarcity of the existing published literature on the resting egg taxonomy, almost 50% of the types of eggs found in the sediments of Thermaikos Gulf were attributed to a genus or a family level. The spiny eggs of Acartiidae were among the dominant taxa in the bottom sediments, at all the stations and during all the sampling periods. This morphotype could be assigned to four different species of this family: *Paracartia latisetosa*, *Acartia adriatica*, *A. italica*, and *A. tonsa*. Specimens

of the three latter species were not recorded in the water column of Thermaikos Gulf during the present, as well as during previous studies in Thermaikos Gulf (Siokou-Frangou and Papathanassiou, 1991; Siokou-Frangou et al., 2003). In contrast, few specimens (1.6 ind m⁻³) of *P. latisetosa* were found in the water column of Station IP01, in October 2001. During previous studies undertaken in the area, low numbers of this species were encountered (0.5–20 ind m⁻³, representing 0.02–1.5% of the total zooplankton), except in the region of the river mouths, where the population was found to be richer, especially during the warm season (up to 370 ind m⁻³) (Siokou-Frangou and Papathanassiou, 1991; Siokou-Frangou, unpublished data). The presence of this species was found to be more important (up to 700 ind m⁻³ representing 20% of total zooplankton) in the inner part of the Gulf—named as Thessaloniki Gulf which is a confined area—during the warm season (Siokou-Frangou and Papathanassiou, 1991). Therefore, these spiny eggs of Acartiidae could be assigned to *P. latisetosa*. We could hypothesise that the high abundance of resting eggs in the study area could be due to a lateral transport of the spawned eggs, by currents from Thessaloniki Gulf southwards. Moreover these eggs constitute probably a “bank”, for the survival of this species in the study area.

Another dominant egg morphotype was that of “Calanoida 2”, with a diameter of 120–130 µm and spines of 15–20 µm in length. Size and spine morphology allowed us to exclude their attribution to Acartiidae and to search for other producers. In contrast, *Labidocera wollastoni* and *Pontella mediterranea* are known to produce resting eggs similar in size and spiny surface (Sazhina, 1968; Grice and Gibson, 1981, 1982). The nauplii obtained from the “Calanoida 2” eggs, incubated during this study, were similar to those of *Labidocera wollastoni* (see Grice and Gibson, 1982; Sazhina, 1985 for other *Labidocera nauplii*). Based upon the above comparisons, we could assign the “Calanoida 2” eggs to *L. wollastoni*. The latter species was not collected in our water samples and has been found only very rarely during previous studies in Thermaikos Gulf (Siokou-Frangou, unpublished data); however, this is probably due to the sampling methodology (vertical hauls), which is not suitable for this hyponeustonic species. Unfortunately, the other dominant morphotype “Calanoida 3” could not be assigned to any known species.

The total abundance of eggs (both full and empty) found in the sediments of Thermaikos Gulf was generally very low, when compared to other temperate areas. The numbers encountered in the 0–10 cm sediment column ($979\text{--}15,679\text{ eggs m}^{-2}$) are one or two orders of magnitude lower than those found in the Northern California waters, where the mean numbers of the dominant species (*A. clausi*) ranged between 3.3×10^4 and 1.2×10^5 (Marcus, 1995). A maximum density of 6.7×10^4 eggs of cladocerans was detected in the Inland Sea of Japan (Onbé, 1985). Similar differences are apparent in relation to the upper sediment layer, since up to 4900 eggs m^{-2} were encountered in the 0–2 cm layer of the Thermaikos Gulf. For comparison $18\text{--}1124 \times 10^3\text{ eggs m}^{-2}$ were recorded in the upper 1 cm layer along the coastal areas of the Adriatic and Ionian Seas (Belmonte et al., 1995; Rubino et al., 2000). Only the abundance values found in the sediments of the inshore waters of the Tyrrhenian Sea ($800\text{--}7900\text{ eggs m}^{-2}$, Belmonte et al., 1995) are of same order of magnitude to those recorded in Thermaikos Gulf. The egg abundance depends probably upon a series of factors; these should be considered in addition to the numerical abundance of copepod and cladoceran species producing resting eggs in the overlaying water column. The abundance of these zooplankters during the present study and during previous studies in Thermaikos Gulf (Siokou-Frangou and Papathanassiou, 1991), was found to be lower (by almost one order of magnitude) than in the above mentioned temperate coastal areas (Marcus, 1995; Onbé, 1985; Belmonte et al., 2001). Furthermore, the resting eggs found as dominant in the sediments were produced from species, which were non-abundant in the area (*P. latisetosa*, *L. wollastoni*). In contrast, eggs of the copepod species, dominant in the water column (*A. clausi*, *C. typicus*, *C. ponticus*), were found rarely or were absent from the sediments. Amongst the factors favouring the accumulation of the resting eggs, one should refer to the hydrodynamism and the grain size which are correlated inversely (Marcus, 1996). Elsewhere positive correlations have been revealed between egg number and the proportion of silt-sized particles (Marcus and Fuller, 1989; Lindley, 1990). In the case of this study, the combination of the generally low abundance of zooplankters in the water column and of the high hydrodynamic conditions (Kontoyiannis et al., 2003), when compared to other coastal areas could be responsible for the poorness of eggs in the Thermaikos Gulf sediments.

A decreasing trend in egg numbers was observed from the stations located close to the rivers' mouths to the outer part of the gulf, likewise from shallow to deeper water stations. These differences could be attributed also to the above-mentioned factors. In fact, mesozooplankters producing resting eggs were found to be more abundant in the samples collected simultaneously with the sediments, at Stations IP01 and IP02 than at the other stations. Indeed, our previous studies in the area have revealed higher abundance values in the area where Stations IP01 and IP02 are located, than in the area of Stations IP17 and IP27 (Siokou-Frangou and Papathanassiou, 1991). Nevertheless, one should have in mind that the encountered numbers of plankters in the water column are "snap-shots" in time; they vary significantly, even daily, whereas the egg "banks" represent an integration over time of the egg production in the study area. Moreover, stations located close to a river mouth are known to be rich in resting eggs (Rubino et al., 2000), such as Stations IP01, IP02 and IP38 in Thermaikos Gulf. In contrast, Stations IP17 and IP27, where decreased egg numbers were encountered, are located in greater water depth ($> 50\text{ m}$) and far from a river mouth and/or the coast; according to Marcus (1995) the abundance of resting eggs in the sediments is generally higher at smaller rather than at greater water depths. Finally, the enrichment of the egg assemblages of Stations IP01, IP02, IP10, together with that of Station IP38, could be correlated to their muddy sediments (sand content less than 4%) when compared to Stations IP17 and IP27 (sand: 5–9%) (Karageorgis, personal communication). As has been mentioned already, muddy sediment is a good indicator for resting egg presence (Marcus and Fuller, 1986).

The increase of full egg abundance in the sediments in October (due mainly to those of *L. wollastoni*) could be attributed to an enrichment from the water column. In contrast, the observed decrease of full eggs in February, together with a relative increase of empty eggs (mainly those of *P. latisetosa* and *L. wollastoni*) could be attributed to hatching. This hypothesis is not supported by the water column results, since the dominant species in the water column do not coincide with the dominant morphotypes in the sediment during any of the sampling periods (see above).

Sediment mechanical resuspension is among the factors controlling the vertical distribution of eggs in the sediment, leading probably to egg

resuspension (Marcus, 1990, 1996; Marcus et al., 1994). Trawling activity has been found to affect the seabed, even down to 15 cm in the case of muddy sediments (Krost et al., 1990). As well as resuspending sediment, trawl gear can bring about vertical redistribution of sediment layers (Jones, 1992). Heavy chain dredges could mix surface organic material, into the subsurface layers (Mayer et al., 1991); a part of the upper layer could be transported to the outer shelf (Churchill, 1989). Moreover, in the shallow areas, eggs could be resuspended also by storm events, then submitted to advection movements or to hatching (Marcus, 1996). During the present study, the bottom trawling has been considered as the main driving force of sediment resuspension in Thermaikos Gulf, whilst the benthic nepheloid layer was found to be advected horizontally (Tragou et al., *this volume*; Zervakis et al., *this volume*).

According to our results, the vertical distribution pattern of the eggs in the sediment column differed between the sampling periods at Stations IP01, IP02, IP10 and IP38: there was more or less a decrease with depth in September, a weak disturbance of the egg profiles in October and a clear homogenised distribution in February. The redistribution of eggs observed in October should be attributed to sediment resuspension by trawling activity. The frequent resuspension of the sediments, by trawlers, in the October–February period, in combination with storm events during winter, have resulted probably in the more homogenous egg profiles in the sediments observed during February. Moreover, the above stations are more affected by resuspension since, according to Karageorgis and Anagnostou (2003) this process takes place mainly near the rivers' mouths and along the western coastline of Thermaikos Gulf. One could not exclude bioturbation effects, since the conveyor-belt deposit feeder *Maldane* sp. has been found commonly in the area (Anagnostou et al., 1997), but the sediment is more deeply reworked by trawlers (15 cm–Krost et al., 1990). The impact on sediment redistribution by polychaetes has been found to be insignificant (reworking down to 4 cm), compared to the sediment reworking by waves (Giangrande et al., 2002). Nevertheless, bioturbation contributes indirectly to resuspension, by making the sea bottom more susceptible to physical resuspension events (Rhoads and Young, 1970).

Interestingly, at Stations IP17 and IP27, the vertical distribution pattern of eggs was decreasing both in September and February; in October the

pattern was not clear. Several factors could account for these findings. Trawling activities could not affect Station IP17 during the study period due to anchoring of a multiparametric buoy; moreover, according to Tragou et al. (*this volume*) no sediment resuspension could be induced by surface waves, since the site was too deep. Similarly, resuspension of sediments at Station IP27 by surface waves would occur rather rarely in relation to water depth. A different depositional velocity, between the eggs and the sand grains (which are more abundant at Stations IP17 and IP27, than at the other stations) could account for this vertical pattern. According to Marcus and Taulbee (1992) no homogenisation of the vertical egg distribution has been observed in sediments with an important sand component.

Sediment resuspension has been considered as an important factor for the hatching of resting eggs (Marcus, 1996). Our results have shown that there was a redistribution of the egg, correlated with the resuspension period from October to February (at least at most of the study stations). Moreover the finding of a higher ratio empty/full eggs, in February, could suggest that hatching occurred during this period for some of the dominant taxa of the seabed (*P. latisetosa*, *L. wollastoni*). Nevertheless, these taxa were rare, or even absent, in our water samples; therefore, the hypothesis of hatching induced by sediment resuspension cannot be supported by our results. A more frequent sampling (e.g. weekly) throughout the year could provide more information on the above question.

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