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Microplanktic assemblages (sarcodines and alveolates) in the central and southeastern Aegean Sea (NE Mediterranean)

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Spatial changes in the structure of microplanktic assemblages (sarcodines and alveolates) in the surface waters of coastal regions in the central and southeastern Aegean Sea were estimated during late summer to early autumn. Tintinnidae (Ciliophora), as well, Acanthometridae (Radiolaria) and Globiderinidae (Foraminifera) exhibited a higher abundance in the central Aegean Sea, compared to that in the more oligotrophic southeastern area of the same sea. Multivariate analysis revealed that the samples from the eastern Cretan Sea (South Aegean Sea) were highly distinguished from all the others and showed the highest densities of polycystines (Radiolaria), specifically of the families Thalassicollidae, Thalassosphaeridae, Sphaerozoidae (Collodaria), as well as of Actinommidae (Spumellaria) and Theoperidae (Nassellaria). In addition, the families Ceratiaceae and Prorocentraceae (Dinoflagellata) were more abundant in the southeastern than in the central Aegean Sea. It is indicated that the hydrographic conditions prevailing in the eastern Cretan Sea affected the structure of the microplanktic community in the surface layer. It is proposed that the assemblage of the identified radiolarian families belonging to Collodaria, Spumellaria (S) and Nassellaria (N), with a high S/N ratio, could be used as biological proxy of weak upwelling systems in the warm stratified waters of the oligotrophic eastern Mediterranean.

Key words: Eastern Mediterranean, microplankton, sarcodines, alveolates, abundance, oligotrophic ecosystems.

INTRODUCTION

The Aegean Sea has been characterized as oligotrophic, like the whole eastern Mediterranean Sea (Krom et al., 1991). It is generally accepted that the degree of oligotrophy increases along an easterly gradient in the Mediterranean, which is clearly reflected in a general quantitative reduction of vertical fluxes (Heussner and

Monaco, 1995). In the eastern regions of the Mediterranean, waters remained stratified throughout most of the year and presumably pico- and small nanoplankton play a most important role in the primary production (Li et al., 1993; Ignatiades et al., 1995). In such oligotrophic ecosystems, microzooplanktic rather than mesozooplanktic organisms are expected to be the main herbivores (Calbet and Landry, 2004). In an oligotrophic ecosystem, the microplankton community is expected to be characterized by a high diversity among the protest primary and secondary producers as well as

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predators (Margalef, 1994). Furthermore, protozoan communities in the eastern Mediterranean includes picophagous species, which feed mostly on bacteria, as well as nano- and microphagous species, which generally feed on protists (Hausmann et al., 2002).

In addition, acquisition of phototrophy through maintenance of algal endosymbionts or algal organelles is common among aquatic phagotrophic protists (Stoecker et al., 2009). Most protists with acquired phototrophy are mixotrophic; they combine heterotrophy and phototrophy, and so we need to go beyond traditional concepts of 'plant' and 'animal' functions to progress in our understanding of aquatic microbial ecology. Acquired phototrophy occurs primarily among radiolarians, foraminiferans, ciliates and dinoflagellates, and is crucial in the sarcodines (radiolarians and foraminiferans) to their contributions to carbonate, silicate, strontium, and carbon flux in subtropical and tropical oceans, particularly in oligotrophic regions (Caron et al., 1995; Michaels et al., 1995; Dennett et al., 1999; Stoecker et al., 2009). On the other hand, a high percentage of dinoflagellates that bear chloroplasts also contain food vacuoles and therefore, dinoflagellates, in general, are included in the microzooplankton along with the animal-like protists by several authors (Jyothibabu et al., 2003). Microzooplankton is an important component of the diet of mesozooplankton, which is in turn consumed by larval fish (Hunter, 1981). Furthermore, there is now growing evidence that fish larvae directly eat protozoa of microplankton, particularly the alveolates (ciliates and dinoflagellates) (Figueiredo et al., 2005). Thus, the abundance and composition of sarcodines and alveolates in microplankton may have important implications to fisheries of both pelagic and benthic organisms.

Although Aegean Sea is considered as oligotrophic, some relatively eutrophic areas do exist. For example, Stergiou et al. (1997) estimated that nutrient concentrations as well as plankton and benthos abundance and/or productivity are all by one order of magnitude higher in the N-NW than in the S-SE Aegean Sea. The Cretan Sea in the southernmost basin of the Aegean Sea is thought to be among the few marine ecosystems that could be characterized as strongly oligotrophic through long periods of the year (Ignatiades, 1998; Psarra et al., 2000). Apart from the low nutrient levels, impoverished phytoplankton populations and low mesozooplankton standing stocks were recorded (Gotsis-Skretas et al., 1999). A significant retention of vertical biogenic particle flux has been recorded in the Cretan Sea, since microzooplanktic communities (phaeodarians and foraminiferans) rapidly decreased net sedimentation from the photic layer, by ingesting and repackaging liable particles several times during descent, and thus restricting food supply to benthic organisms (Wassmann et al., 2000). The high water column temperatures in the Cretan Sea further enhance the decomposition rate of organic matter.

However, Duineveld et al. (2000) argued that benthic-pelagic coupling does exist in the Cretan Sea, although the amplitude of the seasonal signal is small. Circulation pattern is rather complex in the Aegean Sea, where water masses with different characteristics enter and may get uplifted in some areas, enriching surface with nutrients and enhancing primary productivity (Psarra et al., 2000; Tselepides et al., 2000). As a result, significant spatial differences in the abundance and structure of pelagic and benthic communities are generated (Psarra et al., 2000; Duineveld et al., 2000).

Distribution of microzooplanktic species is partly controlled by temperature and hydrographic structures and their interrelations on water mass fertility; some species are characteristic of upwelling systems and/or of fertile areas (Venec-Peyre and Caulet, 2000). Despite that microzooplanktic organisms play an important role in the biogenic matter fluxes in the oligotrophic systems, and may also serve as biological signatures (Boltovskoy, 1999), little is known about their distribution and abundance in the Aegean Sea, but emphasis has been given mainly on phytoplankton and mesozooplankton (Stergiou et al., 1997). Furthermore, studies on microzooplankton have been performed in relatively eutrophic gulfs (Kormas et al., 1998; Mihalatou and Moustaka-Gouni, 2002), but not in the islands and particularly in the more oligotrophic southeastern part of the Aegean Sea.

The aim of the present study was to estimate the abundance of radiolarians, foraminiferans, tintinnids and dinoflagellates in the surface waters of coastal areas in the central and southeastern Aegean Sea during the stratification period. We tried to evaluate spatial changes in the structure of their communities (on family level) based on perturbations in the productivity levels and hydrographic features aforementioned. Furthermore, the possible role of certain microplanktic taxa in the microbial loop and bentho-pelagic coupling is discussed. The results of this study are the first ones carried out on the study area and could be used in the future as a useful tool for comparison purposes, among other regions of the Mediterranean basin.

MATERIALS AND METHODS

Microplankton (20 to 200 μm) was sampled from sixteen stations at coastal areas in the central and southeastern Aegean Sea in 1994, during late summer to early autumn (Figure 1, Table 1). The bottom depth of these stations ranged from 12 to 100 m and the samples were collected by NISKIN bottle at depth of 10 to 30 m (Table 1). Specimens were preserved by adding borax buffered formalin to a final concentration of 2% immediately after sampling. A 2 L sample was used for protistan enumeration and identification down to family level, as in other microplankton studies in Eastern Mediterranean (Dolan et al., 2002; Kormas et al., 1998). The sample was concentrated to a volume of 100 ml by filtering through membrane polycarbonate filters (NUCLEPORE) of 5 μm diameter pore size. Filtration was performed at low pressure (250 mmHg). The organisms remaining on the filter were then very gently washed
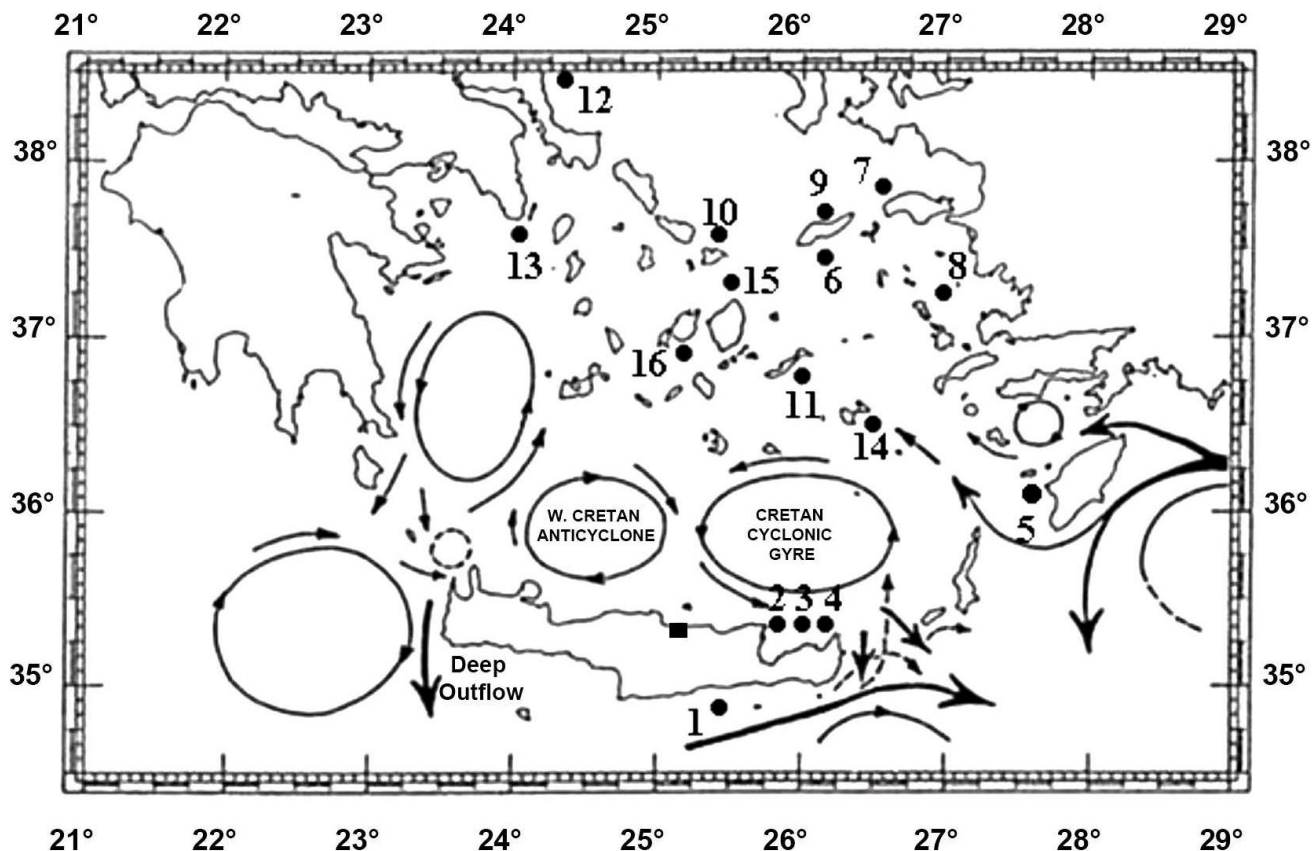
Figure 1. Sampling stations (●) in the Aegean Sea (basic map from Souvermezoglou et al., 1999) and city of Heraklion (■).

Table 1. Location, date, coordinates and sampling depth of the stations in the islands of the Aegean Sea.

Location	Date	Longitude (E)	Latitude (N)	Sampling depth (m)	Bottom depth (m)	T (°C)	S (psu)
Gaidouronisi	10/1994	25°35'46"	34°59' 56"	30	70	22.5	40
West Sitia, Crete	08/1994	25°46' 59"	35°20' 14"	20	33.5	25	39
Central Sitia, Crete	08/1994	25°59' 22"	35°12' 44"	20	37.5	25	37
East Sitia, Crete	08/1994	26°15' 26"	35°17' 58"	10	12	25.6	39
Rhodos	10/1994	27°33' 17"	36°12' 14"	10	20	23.9	42
Fourni	10/1994	26°70' 90"	37°32' 43"	30	80	23	40
Samos	10/1994	26°37' 58"	37°46' 26"	30	87.5	22	40
Lipsi	10/1994	26°45' 58"	37°24' 11"	30	67.5	22.4	40
Ikaria	10/1994	26°60' 53"	37°38' 17"	30	100	23	39
Mykonos	09/1994	25°22' 15"	37°29' 49"	10	20	22	40
Amorgos	09/1994	25°56' 12"	36°50' 48"	30	95	22.5	41
Kimi	08/1994	24°11' 55"	38°29' 39"	10	20	25.5	40
Cav°d'Oro	08/1994	24°20' 57"	37°39' 24"	10	20	25.5	37
Kalymnos	10/1994	26°26' 34"	36°33' 48"	30	55	22	40
Naxos	09/1994	25°27' 70"	37°10' 23"	30	55	23.5	41
Paros	09/1994	25°11' 40"	36°57' 39"	20	32.5	22	40

Temperature (T) and salinity (S) recorded at the surface of the water column.

into a 100 ml settling chamber using a fine tipped glass pipette and some water which run through the filter. For settling (2 days), the

Utermöhl method (Utermöhl, 1958) was used. The counting was performed by using an inverted-phase microscope. The
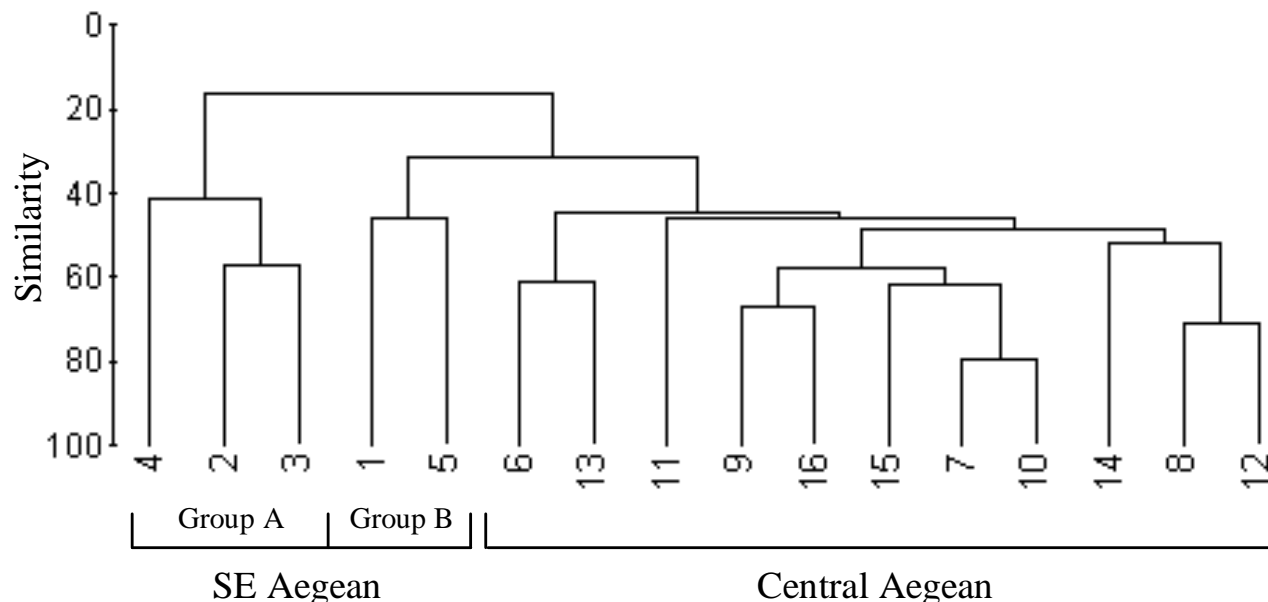
Figure 2. Bray-Curtis similarity indices of the abundance of microplanktic families at 16 stations in southeastern and central Aegean Sea. Dendogram using group averaged clustering. Group A: stations in eastern Cretan Sea; Group B: the other stations in SE Aegean Sea.

Table 2. Average abundance of microplanktic families (cells l^{-1}) collected in Aegean Sea.

Families	SE Aegean	Central Aegean				
	Av. Abund	Av. Abund	Av. Diss	Diss/SD	Contrib%	Cum%
Tintinnidae	1.00	11.55	12.18	2.35	15.50	15.50
Thalassicollidae	18.80	0.09	12.09	1.65	15.38	30.88
Thalassosphaeridae	15.60	0.45	10.42	1.38	13.26	44.14
Prorocentraceae (10^3)	3.40	0.55	7.45	1.16	9.48	53.62
Sphaerozoidae	4.80	0.09	5.76	0.84	7.32	60.95
Ceratiaceae (10^3)	4.40	0.18	5.46	1.02	6.94	67.89
Actinommidae	6.00	0.00	4.67	0.72	5.94	73.83
Acanthometridae	0.40	1.45	4.57	0.83	5.81	79.64
Globigerinidae	0.20	0.91	3.78	1.01	4.81	84.45
Dinophysiaceae (10^3)	0.60	0.18	3.24	0.77	4.12	88.57
Theoperidae	1.00	0.18	2.60	0.66	3.31	91.88

SIMPER analysis showing discrimination of the samples in central and SE Aegean Sea. Av. Abund: average abundance, Av. Diss: average dissimilarity between all pairs of inter-group samples, Diss/SD: dissimilarity/standard deviation of contribution, Contrib%: percentage contribution, Cum%: cumulative percentage.

classification of microplankton is presented according to Systema Naturae 2000 (Brands, 2000), except that of Radiolaria Polycystinae that follows the scheme proposed by Boltovskoy (1999).

The Primer statistical software package was used to perform multivariate analysis on the abundance data (Clarke and Warwick, 1994). A hierarchical cluster analysis based on the Bray-Curtis similarity index was calculated after log transformation of data. The dendrograms were formed with the grouping average method, and analysis of similaritie (ANOSIM) was used for testing the significance of grouping. In order to determine discriminating species, the similarity percentage (SIMPER) analysis was performed.

RESULTS

Multivariate analysis on the abundance data of microplanktic organisms (sarcodines and alveolates) revealed a clear separation (average dissimilarity = 78.58) of the samples collected in the central and southeastern Aegean Sea (Figure 2). The ANOSIM test proved that the samples of these two regions differed significantly (R = 0.811, p = 0.1%). The SIMPER routine (Table 2) showed that Tintinnidae (phylum: Ciliophora, class: Spirotrichea) contributed (15.5%) the most to the

Table 3. Average abundance of microplanktic families (cells l^{-1}) collected in SE Aegean Sea.

Families	Group A	Group B				
	Av. Abund	Av. Abund	Av. Diss	Diss/SD	Contrib%	Cum.%
Thalassosphaeridae	26.00	0.00	17.64	5.69	23.30	23.30
Thalassicollidae	30.67	1.00	14.23	2.29	18.79	42.09
Sphaerozoidae	8.00	0.00	9.69	1.23	12.79	54.88
Ceratiaceae (10^3)	6.67	1.00	6.68	1.80	8.82	63.69
Actinommidae	9.67	0.50	6.40	0.93	8.45	72.14
Prorocentraceae (10^3)	4.00	2.50	5.90	1.41	7.79	79.93
Theoperidae	1.67	0.00	3.42	0.65	4.51	84.44
Dinophysiaceae (10^3)	0.33	1.00	3.15	1.16	4.15	88.60
Tintinnidae	0.67	1.50	2.28	1.11	3.01	91.61

SIMPER analysis showing discrimination of the samples in two groups. Group A: stations in eastern Cretan Sea; Group B: the other stations in SE Aegean Sea. Av. Abund: average abundance, Av. Diss: average dissimilarity between all pairs of inter-group samples, Diss/SD: dissimilarity/standard deviation of contribution, Contrib%: percentage contribution, Cum%: cumulative percentage.

average dissimilarity, being less abundant in the SE Aegean Sea. Acanthometridae (phylum: Radiozoa, subphylum: Radiolaria, class: Acantharea) and Globigerinidae (phylum: Foraminifera, class: Foraminifera) also displayed a reduced abundance in the SE Aegean Sea.

Furthermore, the stations (2, 3 and 4, Sitia bay) in the eastern Cretan Sea (Group A) were distinguished (average dissimilarity = 75.74) from the other in the SE Aegean Sea (Group B), and even more from those in the central Aegean Sea (average dissimilarity = 85.29). The discriminating families that contributed cumulatively 88.6% to the average dissimilarity between Groups A and B (Table 3) belonged to the classes Polycystinea (phylum: Radiozoa, subphylum: Radiolaria) and Dinophyceae (phylum: Myzaozoa, infraphylum: Dinoflagellata). The assemblage of polycystines (Order Collodaria: Thalassicollidae, Thalassosphaeridae and Sphaerozoidae, Order Spumellaria: Actinommidae, Order Nassellaria: Theoperidae) showed the highest densities in the stations of Group A. Dinoflagellates were more abundant in the stations of SE Aegean Sea and specifically Ceratiaceae and Prorocentraceae in the Group A, while Dinophysiaceae in the Group B.

DISCUSSION

Tintinnidae may constitute one major component of marine planktic ciliates, as they can respond quickly to phytoplankton pulses composed mainly of nanoplankton (Psarra et al., 2000). The abundance of tintinnids in the Aegean Sea, estimated in this study, was much lower than that reported for eutrophic regions in the Atlantic (Dolan and Gaggegos, 2001). Dolan et al. (2002) referred that the concentrations of tintinnids declined from west-to-east, between the Moroccan upwelling system and the oligotrophic eastern Mediterranean, paralleling declines

in primary production and increases in the depth of the chlorophyll maximum layer. The average abundance of tintinnids in the central Aegean Sea (late summer to early autumn) can be compared to that recorded (September) in the central basin (35 to 38°N, 8 to 18°E) of the Mediterranean (10 to 20 cells l^{-1}) (Dolan et al., 2002). The densities of tintinnids in the SE Aegean Sea are within the levels (frequently <5 cells l^{-1}) recorded during summer to early autumn in the coast (north Libanon) of the eastern-most (35°E) basin of the Mediterranean (Abboud-Abi, 2002). The decline in the abundance of tintinnids from the central to the south Aegean Sea seems to be influenced by the north-south gradient of increasing oligotrophy, deepening on the chlorophyll maximum layer in this sea (Ignatiades et al., 2002; Stergiou et al., 1997).

Foraminifera occupy circum-global latitudinal climatic provinces (Stoecker et al., 2009) with densities varying from <1 to >100 m^3 cells (Caron and Swanberg, 1990). The family Globigerinidae contains spinose species, which live mainly in the photic zone; most of them host symbiots and prefer a carnivorous diet (tintinnids, copepods, etc.) (Hemleben et al., 1989; Boltovskoy, 1999). Globigerinidae showed a higher density in the central than southeastern Aegean Sea, probably due to a relatively increased availability of their prey, such as tintinnids. In the eastern Mediterranean (north Libanon), at latitudes similar to those of the SE Aegean Sea, the foraminiferal densities in the surface layer were lower than 0.5 cell l^{-1} during summer to early autumn (Abboud-Abi, 2002).

Acantharea and Polycystinea represented Radiolaria in the surface waters of the Aegean Sea. Phaeodarians (Radiolaria) were not found in this study probably because they are typically deep-water animals, usually peaking in both abundance and diversity below 200 m (Boltovskoy, 1999; Wassmann et al., 2000).

Acantharians are common in tropical/subtropical oceans and are generally restricted to the illuminated

upper layer (Caron and Swanberg, 1990; Boltovskoy, 1999). Algal symbionts are found nearly in all acantharian species, including all members of the family Acanthometridae (Febvre et al., 2000). Acantharian densities ranged from 4 to 7 cells l^{-1} in the equatorial Atlantic and North Pacific central gyre and up to 30 cells l^{-1} in the more eutrophic southeastern Atlantic, although lower (<1 cell l^{-1}) or higher (50 cells l^{-1}) densities have been reported (Febvre et al., 2000; Boltovskoy, 1999; Stoecker et al., 2009). The values obtained in this study for the abundance of Acanthometridae are found at the lower limits of this range, probably due to the oligotrophy of the Aegean Sea, particularly in its southeastern part. In the latter, acantharians showed densities as those recorded (0.3 cell l^{-1}) in the surface waters of the highly oligotrophic Levantine Sea (Abboud-Abi, 2002). It has been shown that acantharians consumed mostly tintinnids in the surface waters of the oligotrophic Sargasso Sea (Swanberg, 1979), and this seems also to be verified in the Aegean Sea.

The polycystine radiolarians Thalassicollidae, Thalassosphaeridae, and Sphaerozoidae belong to Collodaria, an Order lacking a skeleton, or provided only with scattered spicules (Boltovskoy, 1999, Anderson et al., 2000). The family Sphaerozoidae includes colonial species that form colonial gelatinous masses (Swanberg, 1979). Due to their fragility, members of this Order preserve poorly or not at all in net plankton samples, and information on their distribution is limited (Ignatiades et al., 1995; Swanberg, 1979; Dennett et al., 2002). It seems that they have tropical/subtropical distribution ranges in the three major oceans (Dennett et al., 2002; Swanberg, 1979; Yuasa et al., 2005; Rogers and De Deckker, 2007). Collodaria (for example, *Physematium, Sphaerozoum, Collozoum* and *Thalassicolla*) have commonly been found in oligotrophic regions of the Atlantic, particularly in the Sargasso and Caribbean Seas (Swanberg, 1983; Swanberg and Anderson, 1985). In the Mediterranean, Collodaria have been studied many years ago (Swanberg, 1979; Haeckel, 1887), but have received little attention until recently (Abboud-Abi, 2002).

The densities of the shelled polycystines are typically around 0.3 to 1 cells l^{-1}, but values exceeding 50 cells l^{-1} have been recorded in some productive areas (Boltovskoy, 1999; Caron and Swanberg, 1990). In the eastern Cretan Sea, polycystines exhibited high densities (76 cells l^{-1}), whereas their majority (86%) belonged to Collodaria including colonial gelatinous polycystines (8 cells l^{-1}). For the latter, underwater video recordings revealed densities up to 13 cells l^{-1} in the central North Pacific (Dennett et al., 2002). In the oligotrophic Levantine Sea (north Libanos), the densities of polycystines in the plankton net tow samples (55 µm mesh size) were usually lower than 1 cell l^{-1} during spring to early autumn, and maximum values (up to 6 cells l^{-1}) were due to proliferation of one or two species belonging to colonial Collodaria, *Sphaerozoum* spp. and

Collozoum sp. (Abboud-Abi, 2002). Similarly, the densities of the polycystines encountered in this study for the samples collected by Niskin bottles were around 1 cell l^{-1} in most of the stations.

The enhanced abundance of polycystines in the stations (Group A) of the eastern Cretan Sea (northeastern of the city Helaklion), may be attributed to the multiscaled circulation pattern and the complex hydrographic structure prevailing in the Cretan Sea, which links with the NW Levantine Sea and the SE Ionian Sea. Within this basin, circulation is dominated by a mesoscale dipole; an anticyclone in the West and a cyclone in the East (Georgopoulos et al., 2000). The intrusion (at intermediate depths of 200 to 700 m) of the Trans Mediterranean Water (TMW) from the east has important implications to this system, because it is a water mass that is older and comparatively richer in nutrients (Souvermetzoglou et al., 1999). The persistent mesoscale dipole circulation can act as a pump, upwelling TMW into the euphotic zone and transporting it southward up to the shelf. This creates a persistent water flow (jet) in a SE and ESE direction that inhibits offshore transport of material (Tselepides et al., 2000). As a result, an offshore increase in oligotrophy has been observed (along a transect that extended north of the city Heraklion) from a coastal ecosystem with consistently higher standing stock and productivity rates, to a more stressed oligotrophic pelagic environment (Psarra et al., 2000).

Plankton studies on shelled polycystines have shown that in the surface oceanic waters, nassellarians usually exceed spumellarians in abundance (Boltovskoy et al., 1993), although slightly in the oligotrophic southern Sargasso Sea (Spaw, 1979). This was true in this study for the samples of the central Aegean Sea. Actinommidae dominated the shelled spumellarians in the Aegean Sea, as in the Sargasso Sea (Spaw, 1979). This family has an important biostratigraphic role with species that are included in radiolarian upwelling assemblages (Benson, 1966; Nigrini, 1991). In the shelf of the eastern Cretan Sea, Actinommidae exhibited an important abundance of around 10 cells l^{-1}. It seems that in the warm stratified waters of the Cretan Sea, spumellarians (S) respond more than nassellarians (N) to the weak upwelling systems, resulting in high S/N ratios. Benson (1966) found in the sediments of the Gulf of California that the S/N ratios increased under coastal upwelling conditions, while it decreased (<1) under open oceanic upwelling conditions resulting in high diatom production.

All colonial polycystines, and most of the solitary ones, possess photosynthetic symbionts that are commonly dinoflagellates (Swanberg, 1983; Stoecker et al., 2009; Caron et al., 1995). The exploitation of a symbiotic relationship may account in part for the high abundance of the polycystines observed in the eastern Cretan Sea. However, their predator activity seems to also play a

considerable role, particularly that of the families Thalassosphaeridae and Sphaerozoidae (Swanberg, 1983; Swanberg et al., 1986). In *Physematium muelleri* (Thalassosphaeridae), a highly opportunistic predator collected in the Caribbean and Sargasso Seas, the most common large prey identified were silicoflagellates (42%) or dinoflagellates (63%), respectively, as well as tintinnids and copepods (Swanberg et al., 1986).

Dinoflagellates showed increased densities in the southeastern than central Aegean Sea, as it is characteristic in the oligotrophic waters during summer (Krom et al., 1991; Jyothibabu et al., 2003; Stoecker et al., 2009). The enhanced abundance of polycystines in the eastern Cretan Sea, and particularly that of collodarians, coincided with the highest densities of dinoflagellates observed in this study. Unexpectedly high levels of phytoplankton, dominated by dinoflagellates, have been recorded during the summer of the same year (July to August 1994) in stratified waters at the shelf of the Cretan Sea (north of Heraklion), attributed to the TMW intrusion (Psarra et al., 2000). It seems that an enrichment in nutrients of the surface waters under vertical stability resulted in higher densities of the dinoflagellates that belonged to the families Ceratiaceae and Prorocentraceae, in the stations located in the Cretan Sea (Group A) compared to the other in the southeastern Aegean Sea (Group B). Furthermore, Silva et al. (2009) inferred that dinoflagellates dominated phytoplankton under persistent and weak upwelling events in stratified waters.

Dinophysiaceae includes species that carry out required phototrophy, by sequestering plastids or multiple organelles from their algal prey, mainly cryptophytes, or indirectly from their ciliate prey *Myrionecta rubra,* and form blooms usually associated with upwelling mixing events with nutrient delivery (Stoecker et al., 2009). This family did not follow the increase of Ceratiaceae and Prorocentraceae in the shelf of the eastern Cretan Sea, probably due to the stability of water column during summer. Ciliates have shown close relationships to pico- or nanoplankton abundance in the Aegean Sea (Kormas et al., 1998; Mihalatou and Moustaka-Gouni, 2002). Tintinnidae and Dinophysiaceae showed a lower abundance in the stations of Group A than B in the southeastern Aegean Sea. This might be attributed to a relatively reduced availability of their favorable prey, but competitor interactions or predator activity should not be disregarded.

Polycystines, particularly Collodaria, dominated sarcodines and overwhelmed tintinnids in the eastern Cretan Sea. The density of Globigerinidae and Acanthometridae was similar between the two groups of stations in the southeastern Aegean Sea, although they consume a wide range of prey almost similar to that of polycystines. Thus, competitive interactions may also play an important role in the enhanced abundance of polycystines in the eastern Cretan Sea. Furthermore, in

polycystines, there is evidence that some dinoflagellate symbionts produce sterols, which could render the host less vulnerable to predators or diseases (Stoecker et al., 2009). It seems that mixotrophy gives polycystines a competitive advantage over strict heterotrophic or other mixotrophic animal-like protists.

Polycystines appear to play a diverse and important role in the microbial loop of the eastern Cretan Sea. It has been shown that polycystines constitute a significant fraction of the total primary production in the surface waters of certain oligotrophic regions, even the colonial Collodaria that are usually ignored (Caron et al., 1995; Dennett et al., 2002). Present results indicate that the mixotrophic polycystines may be associated with the unexpectedly high levels of primary production recorded in the coast of the Cretan Sea during July to August 1994 (north of Heraklion) (Psarra et al., 2000). Furthermore, a significant contribution of polycystines in the total microbial biomass and the vertical flux of biogenic matter from the surface waters have also been suggested, particularly as far as the colonial Collodaria is concerned (Stoecker et al., 2009; Caron et al., 1995; Michaels et al., 1995). Thus, a participation of polycystines in the bentho-pelagic coupling detected (Duineveld et al., 2000) in the Cretan Sea (along a transect north of Heraklion) could be expected. In addition, during the surveys of this study, sponges (Porifera) were collected concomitantly from the seabed, and the demosponge *Spongia officinalis* was numerous at the eastern Cretan Sea and scarce in all the other stations (Castritsi-Catharios et al., 2011).

Present results showed that polycystine radiolarians constitute an important component of the microplankton in the surface waters of the Aegean Sea, particularly in the Cretan Sea. It is concluded that the hydrographic features and the episodic pulses of nutrients in the surface waters at the coast of the eastern Cretan Sea, due to the intrusion of the TMW, its upwelling, the SE direction of the mesoscale jet and the eastern eddy, could affect the structure of the microplanktic community in the highly oligotrophic southeastern Aegean Sea. It is proposed that the assemblage of the radiolarian families belonging to Collodaria, Spumellaria (S) and Nassellaria (N), with a high S/N ratio in the surface layer could be used as biological proxy of weak upwelling systems in the warm stratified waters of the oligotrophic eastern Mediterranean. Venec-Peyre and Caulet (2000) inferred that interpretation of planktic foraminiferal assemblages in terms of changes in the intensity of productivity and/or upwelling conditions is not easy as in the case for radiolarian assemblages.

The potential contribution of Collodaria in the oligotrophic ecosystems of the eastern Mediterranean should not be disregarded in biogeographical, biogeochemical and bioproductivity studies. Further research on the taxonomic composition, abundance and biomass of microplankton, especially in marine regions where they have been hitherto ignored, such as the

Aegean Sea, could assess the larval fish recruitment. In addition, it could improve the knowledge concerning the abundance and distribution of certain benthic organisms like sponges, since microplankton may be included among their main food resources (Ribes et al., 1999), apart its potential role in the vertical fluxes.

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