Vertical distribution and ecology of living coccolithophores in the marine ecosystems of Andros Island (Middle Aegean Sea) during late summer 2001*

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ABSTRACT: Living coccolithophores were collected in August 2001, at different photic depths (0-120 m), form 8 stations along a transect in the gulf of Korthi (Andros island). The analysis of the vertical distribution of coccolithophores certified high differentiation in density and diversity, as well as in the species composition at different depth levels. As a result, the photic zone is separated into three distinct sub-zones: upper (0-25 m depth), middle (45-60 m depth) and lower (90-120 m depth). The total cell density varies between 14.7x10^3 cells/l and 1.9x10^3 cells/l, and is usually higher in the upper and middle photic zone, while in the lower photic zone it gradually decreases. The highest species richness (max=34 taxa) was observed at the middle photic zone. *Emiliania huxleyi*, *Rhabdosphaera clavigera* and holococcolithophores preferred the upper photic zone. On the contrary, in the lower photic zone, the presence of *Florisphaera profunda* and *Algirosphaera robusta* becomes important, making up the typical deep community. *Umbellosphaera tenuis* is an additional important component of the summer heterococcolithophore nannoflora, especially in the middle photic zone. The studied coastal marine coccolithophore communities indicate that temperature and availability of nutrient concentrations are the most important controlling factors controlling their vertical distribution.
Key-words: *Living coccolithophores, vertical distribution, coastal environments.*

ΠΕΡΙΛΗΨΗ: Η δειγματοληψία των σύγχρονων κοκκολιθοφόρων πραγματοποιήθηκε τον Αύγουστο του 2001, σε διαφορετικά βάθη της ευφωτικής ζώνης (0-120 m), από 8 καθορισμένους σταθμούς στον κόλπο του Κορθίου (Νήσος Άνδρος). Η ανάλυση της κατακόρυφης κατανομής των κοκκολιθοφόρων πιστοποίησε διαφοροποίηση στην περιεκτικότητα, στην ποικιλότητα, όπως και στη σύνθεση των ειδών στα διάφορα επίπεδα βάθους. Ως εκ τούτου, η ευφωτική ζώνη διαχωρίστηκε σε τρεις επιμέρους υποζώνες: ανώτερη (0-25 m βάθος), ενδιάμεση (45-60 m βάθος) και κατώτερη (90-120 m βάθος). Οι τιμές περιεκτικότητας των κοκκολιθοφόρων κυμαίνονταν μεταξύ των 14.7x10^3 cells/l και 1.9x10^3 cells/l, με υψηλότερες τιμές στην ανώτερη και στην ενδιάμεση και χαμηλές στην κατώτερη ευφωτική ζώνη. Η μεγαλύτερη αφθονία ειδών (max=34 taxa) παρατηρήθηκε στην ενδιάμεση ευφωτική ζώνη. Τα είδη *Emiliania huxleyi, Rhabdosphaera clavigera*, όπως και τα ολοκοκκολιθοφόρα παρουσιάζουν προτίμηση στην ανώτερη ευφωτική ζώνη. Από την άλλη πλευρά, στην κατώτερη ευφωτική ζώνη, η παρουσία του είδους *Florisphaera profunda* και η αύξηση της αφθονίας του είδους *Algirosphaera robusta* πιστοποιούν συνάθροιση βαθιών υδάτων. Ένα άλλο σημαντικό είδος ανάμεσα στα ετεροκοκκολιθοφόρα της θερινής περιόδου είναι η *Umbellosphaera tenuis*, η οποία προτιμά για διαβίωση την ενδιάμεση υποζώνη. Η μελέτη των κοινοτήτων των κοκκολιθοφόρων από τα παράκτια οικοσυστήματα κατέδειξε ότι η θερμοκρασία και οι περιεκτικότητες των θρεπτικών στοιχείων αποτελούν τους πιο σημαντικούς παράγοντες για το διαχωρισμό των υποζωνών της ευφωτικής ζώνης.
Λέξεις-κλειδιά: *Σύγχρονα κοκκολιθόφορα, κατακόρυφη κατανομή, παράκτια περιβάλλοντα.*

INTRODUCTION

Coccolithophores are unicellular marine biflagellate golden-brown algae, which at least at some points in their life cycle, produce and bear minute calcium carbonate plates called coccoliths. Two structurally very different types of coccoliths, heterococcoliths and holococcoliths, formed by different types of biomineralisation, are recognizable. The heterococcoliths are formed by crystal units of variable shape and size, and their biomineralisation occurs intracellularly (MANTON & LEEDALE, 1969). The holococcoliths are formed of numerous minute crystallites that appear to get calcified extracellularly (ROWSON *et al.*, 1986). The coccoliths make an important contribution to translocation of the inorganic carbon produced in pelagic areas to the ocean floor and thus to the sedimentary archive. Since they are biologically formed and sediment forming, coccoliths are extremely valuable for stratigraphic and paleoceanographic purposes, especially in reconstructing the past productivity in the oceans.

Coccolithophores form the base of the oceanic food web and hence they play an important role in marine ecosystems. Due to their capacity to control ocean-atmosphere carbon dioxide exchange, they participate actively in the formation of the climate system (BERGER *et al.*, 1989; WESTBROEK *et al.*, 1993; ROST & RIEBESELL, 2004). The composition and distribution of living cocco-

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* Κατακόρυφη κατανομή και οικολογία των σύγχρονων κοκκολιθοφόρων από τα θαλάσσια οικοσυστήματα της νήσου Άνδρου (κεντρικό Αιγαίο πέλαγος) κατά το τέλος της θερινής περιόδου του 2001

lithophores are directly dependent on the climatic and oceanographic conditions of the oceans.

The living coccolithophores in the Mediterranean Sea waters present a high number of species (e.g. KNAPPERSTBUSCH, 1990; KLEIJNE, 1991, 1992, 1993; ZIVERI *et al.*, 2000; CROS *et al.*, 2000; CROS & FORTUÑO, 2002; SAUGESTAD & HEIMDAL, 2002; TRIANTAPHYLLOU *et al.*, 2002; 2004a; 2004b; TRIANTAPHYLLOU & DIMIZA, 2003; MALINVERNO *et al.*, 2003) with a strong seasonal variability and regional patchiness. The oligotrophic character of the Mediterranean Sea, as well as the high seasonality in sea surface temperatures, solar radiation, nutrient concentrations and in the circulation of surface water masses affect the content, the abundance of species and the productivity of living coccolithophores in general. Therefore, it is important to understand the role of coccolithophores in different marine ecosystems of Mediterranean Sea.

The main goal of the present study is to determine the cell density, diversity and investigate the species composition and summer vertical ecology and distribution of living coccolithophore communities in coastal environments (Andros island, middle Aegean Sea, E. Mediterranean). Understanding the distribution and ecology of these species is therefore of interest for both to paleoceanography and to environmental studies.

OCEANOGRAPHIC SETTING

The complex circulation of the Aegean Sea is due to many factors, such as: the geographical distribution of the various island chains, the irregular bottom topography throughout the region, the inflow of the cooler and lower salinity Black Sea waters, the river outflows from the mainland and the seasonal changes in the meteorological conditions. The surface water circulation is incorporated, in general, into an anti-clockwise gyre system during winter, similar to that in the Adriatic, Ionian, Tyrrhenian and Alboran Seas (LACOMBE & TCHERNIA, 1972). In summer, water movement is essentially towards the south (POULOS *et al.*, 1997) (Fig. 1).

The general counter-clockwise gyre is complicated by mesoscale cyclonic and anticyclonic circulation (POULOS *et al*., 1997). This area is influenced by a persistent thermocline with distinct periods of summer and early autumn water column stratification and intense winter mixing period.

The annual maximum Sea Surface Temperature (SSTs) in the Aegean Sea occur around August/ September (>24 °C); minimum values (<15 °C) are reached in winter (POULOS *et al*., 1997; TRIANTAPHYLLOU *et al*., 2004b). Sea Surface Salinity (SSS) varies seasonally, ranging from less than 31.0 psu to more than 39.0 psu. Temperature and salinity increase to the south.

The oligotrophic character of the Aegean Sea is well recognized (IGNATIADES, 1998; PSARRA *et al*., 2000). However, it is more distinct in the South which is influenced, by the thermocline. The northern Aegean Sea, which is influenced by Black Sea waters, is relatively eutrophic. Chlorophyll concentrations are generally low; the lowest concentrations occurring during summer. In the northern Aegean Sea, diatoms are the most abundant components of the phytoplankton (LYKOUSIS *et al*., 2002), whereas in the south where primary production is mainly influenced by the input of Saharan dust in the water column, coccolithophores and flagellates are prevalent

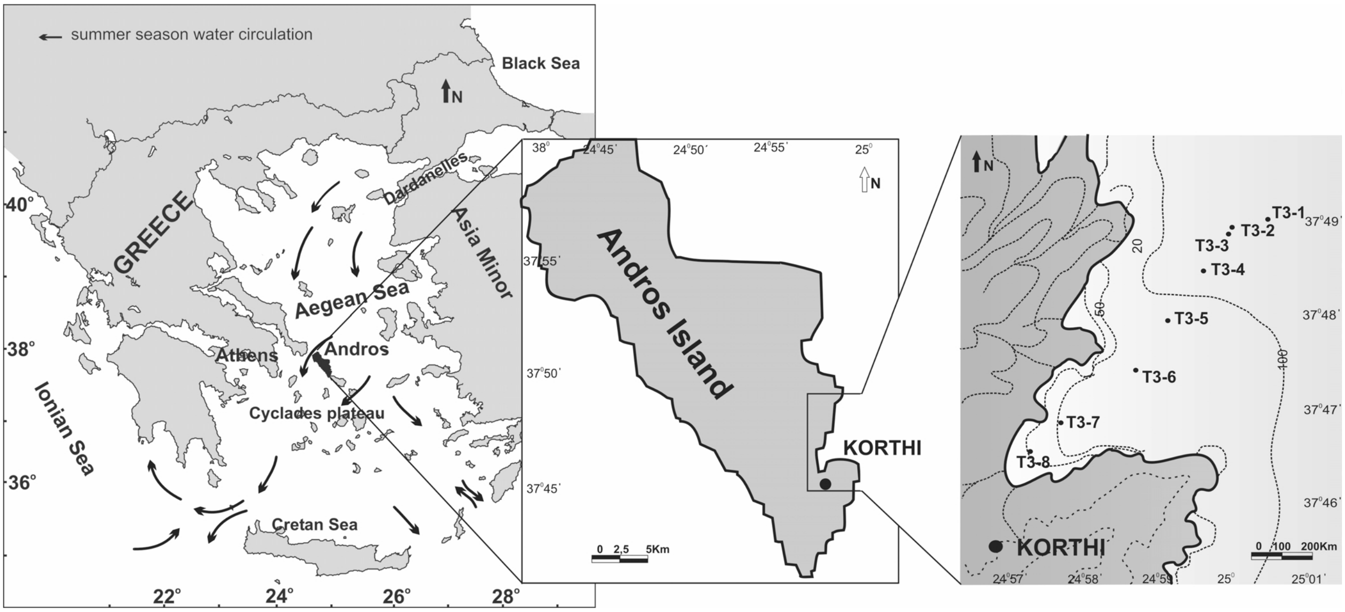


Fig. 1. Map of the study area with generalized summer current patterns (based on data from LACOMBE & TCHERNIA, 1972; THEOHARIS & GEORGOPOULOS, 1993; POULOS *et al*., 1997) and location of the sampled stations at southeastern Andros island.

(Ziveri *et al*., 2000; Triantaphyllou *et al*., 2004b).

The Cyclades Plateau is a morphologically complex marginal platform in the Middle Aegean Sea, shallower than 250 m depth and with numerous outcropping islands. Andros is one of the bigger islands in the northern Cyclades (Fig. 1). The study area concerns the gulf of Korthi, which is located at the southeastern end of the island (Fig. 1).

MATERIAL AND METHODS

Thirty six water samples were collected on August 21st, 2001, from 8 stations along a transect towards the gulf of Korthi (southeastern Andros Island) (Fig. 1). The weather conditions were excellent, providing the development of high stratification in the water column. The samples were collected at selected depths, using a single oceanographic Hydro-bios bottle. Surface water was sampled with a bucket. For each sampling depth, 1,5l of seawater was filtered on Millipore cellulose nitrate filters (47 mm diameter, 0,45 mm pore size), using a vacuum filtration system. Salt was removed by washing the filters with about 2 ml of bottled drinking water. The filters were open dried and stored in plastic Petri dishes. A piece of each filter approximately 8x8 mm was attached to a copper electron microscope stub using a double-sided adhesive tape and coated with gold. The filters were examined in a Jeol JSM 5600 Scanning Electron Microscope (SEM) and all the individual coccolithophore specimens occurring on the examined filter piece were identified and counted. The working magnification was 1200x throughout the counting procedure. The absolute abundances of coccolithophore cell densities (number of cells/l) was calculated following the methodology of Jordan & Winter (2000), by scaling up the raw counts from a known scanned area, using the equation: $A=NxS/V$, where N is the number of cells of a species on the whole piece of filter, S the scaling factor (area of the whole filter/area of scanned filter piece), V the volume of the sea water filtered (l) and A the absolute abundance of the species in cells/l.

Identification and taxonomy of species is primarily based on the recent syntheses of Cros & Fortuño (2002), Young *et al*. (2003) and Jordan *et al*. (2004), but older literature was also extensively consulted. e.g. Perch-Nielsen (1985), Kleijne (1993), Jordan & Kleijne (1994), Winter & Siesser (1994), Jordan *et al*. (1995), Young & Bown (1997), Aubry (1984-1999), Cros (2001).

Data analysis

The ecological measures were calculated using the Past.exe 1.23 software package (Hammer *et al*., 2001), including species richness (S), Dominance (D) and Shannon–Wiener diversity index (H'). The indices were calculated for each sample in order to estimate and better interpret the structure of coccolithophore communities off Andros Island. The dominance index (Simpson, 1949) was calculated to express the abundance of the most common species as a fraction of the total number of individuals. Species richness is the total number of species observed in a sample, whilst the Shannon Wiener Diversity index measures heterogeneity evaluation, which means the distribution of individuals in the different species (Magurran, 1988).

Vertical distribution of coccolithophore species has been plotted using Surfer (version 6.0) software package.

Multivariate statistical analyses [Q-mode and R-mode Hierarchical Cluster Analysis (HCA) and Nonmetric Multi-dimensional Scaling analysis (NMDS)] were performed using SPSS (version 10.1) statistical software. Analyses were carried out in order to evaluate coccolithophore ecology in the photic zone dwelling at the coastal environments off-Andros Island. R-mode cluster analysis (centroid linkage method; distance metric is 1-Pearson correlation coefficient) was used to determine species associations and to assess the ecological affinity among different groups. The R-mode HCA, applied to 14 taxa with higher occurrence and higher cell densities. The Q-mode cluster analysis (Bray-Curtis average linkage) was used to estimate similarities in species composition between the samples. All the 36 samples were considered for this analysis. Additionally, all samples were plotted onto one nonmetric multi-dimensional scaling plot. In this plot samples with the greatest similarity will be plotted closest together, and the axes of NMDS plot represent arbitrary units. The success of the MDS is measured by stress value.

RESULTS

Coccolithophore cell density and ecological indices

Coccolithophores were present in all the studied samples and dominated the phytoplankton communities. *Emiliania huxleyi*, Rhabdosphaeraceae and *Syracosphaera* spp. were highly abundant everywhere. Holococcolithophore communities sometimes reach more than 50 % of the total standing crop, and apparently tend to increase towards shallower environments (Triantaphyllou *et al*., 2002). Cell densities of heterococcolithophore and holococcolithophore species recorded in the studied area are presented in Table 1.

The absolute abundance of the total calcareous nannoplankton varied between $14.7x10^3$ cells/l (Stn T3-1, 45 m depth) and $1.9x10^3$ cells/l (Stn T3-1, 120 m depth), whereas heterococcolithophores varied between $9.3x10^3$ cells/l (Stn T3-5, 45 m depth) and $1.5x10^3$ cells/l (Stn T3-3, 0 m) (Table 1). The total standing crop of heterococcolithophores is characterized by a negative correlation with

TABLE 1

Local and temporal position of samples collected on August 21st, 2001, sampling depth, coccolithophore total standing crop, heterococcolithophore and holococcolithophore cell densities.

Station	Longitude Latitude	Water depth (m)	Total standing crop ($x10^3$ cells/l)	Heterococcolithophores ($x10^3$ cells/l)	Holococcolithophores ($x10^3$ cells/l)
T3-1	37°49.02´N 25°00.52´E	0	4,1	2,6	1,5
		5	13,4	12	1,4
		15	12,7	7,5	5,2
		45	14,7	7,4	7,3
		90	6,8	6,4	0,4
		120	1,9	1,8	0,1
T3-2	37°48.80´N 25°00.03´E	0	8,7	6,5	2,2
		5	12,6	8,2	4,4
		15	11,1	7,2	3,9
		45	5,9	5,3	0,7
		90	3,4	2,9	0,5
T3-3	37°48.77´N 24°59.97´E	0	3,1	1,5	1,5
		5	6,7	3,7	3,0
		15	13,6	8,7	5,0
		45	7,4	4,6	2,8
		90	3,7	2,9	0,8
T3-4	37°48.47´N 24°59.68´E	0	3,7	2,9	0,8
		5	8,5	5,7	2,8
		15	10,3	5,9	4,4
		45	11,3	6,8	4,5
		60	5,9	4,8	1,1
T3-5	37°47.93´N 24°59.33´E	0	2,5	1,9	0,6
		5	7,3	4,1	3,2
		15	6,0	4,1	1,9
		45	13,6	9,3	4,3
T3-6	37°47.40´N 24°58.75´E	0	8,4	5,9	2,5
		5	10,4	5,0	5,4
		15	11,2	6,9	4,2
		45	2,0	2,0	0,0
T3-7	37°46.67´N 24°57.73´E	0	4,2	2,7	1,5
		5	8,3	5,2	3,1
		15	8,9	4,3	4,6
		25	7,9	3,3	4,6
T3-8	37°46.57´N 24°57.38´E	0	7,8	4,5	3,3
		5	12,0	6,4	5,6
		7	8,3	4,6	3,7

sea bottom depth. The highest species richness (34 taxa) was observed at Stn T3-5, 45 m depth and the lowest (5 taxa) at Stn T3-6, 45 m depth. Boxplots of average values and standard errors are shown in figure 2 determining vertical zonation of ecological indices. The Shannon diversity index is obviously relatively higher at 45 m depth (Fig. 2) in the water column. On the contrary, at 120 m depth, high values of the dominance index (H′=0.27) are followed by decreased Shannon diversity (H′=1.74) and species richness (34 taxa).

Coccolithophore distribution

33 heterococcolithophore species have been identified in the studied assemblages. All heterococcolithophore species encountered are listed alphabetically with full citations in Appendix A. The two most abundant heterococcolithophore species are *Emiliania huxleyi* and *Rhabdosphaera clavigera*, with more or less negatively correlated abundances, which together with the holococcolithophores actually dominate the communities. *E. huxleyi* was found at all depths in this study. It shows maximum cell density ($5.5x10^3$ cells/l) at Stn T3-2, 15 m depth, whereas *R. clavigera* becomes respectively minimum and generally decreases in abundance below 45 m (Fig. 3). The family Rhabdosphaeraceae is generally represented by several species (*Acanthoica acanthifera*, *A. quattrospina*, *Discosphaera tubifera*, *Palusphaera vandelli*, *Rhabdosphaera xiphos*), but with low cell densities. *Umbellosphaera tenuis* becomes a significant component of nannoflora at 45 m depth (Fig. 3). The presence of *Florisphaera profunda* and *Algirosphaera robusta* is distinct at 90 and 120 m depth. At this depth (Stn T3-1), *Calciosolenia brasiliensis* presents maximum cell density ($0.5x10^3$ cells/l). Finally, the genus *Syracosphaera* is relatively well represented in the studied heterococcolithophore communities, appearing with several species (Table 2). *Syracosphaera histrica* is the most abundant species of this genus, followed by *S. pulchra*, *S. molischii* and *S. halldalii*.

R-mode HCA (Fig. 4) distinguishes three main groups

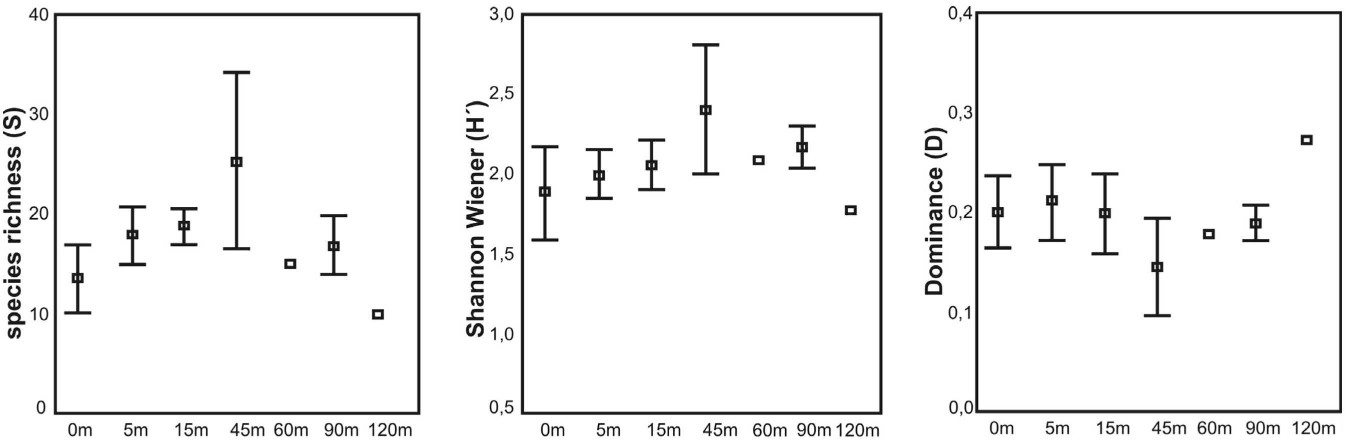


Fig. 2. Box plots of ecological indices between coccolithophore floras.

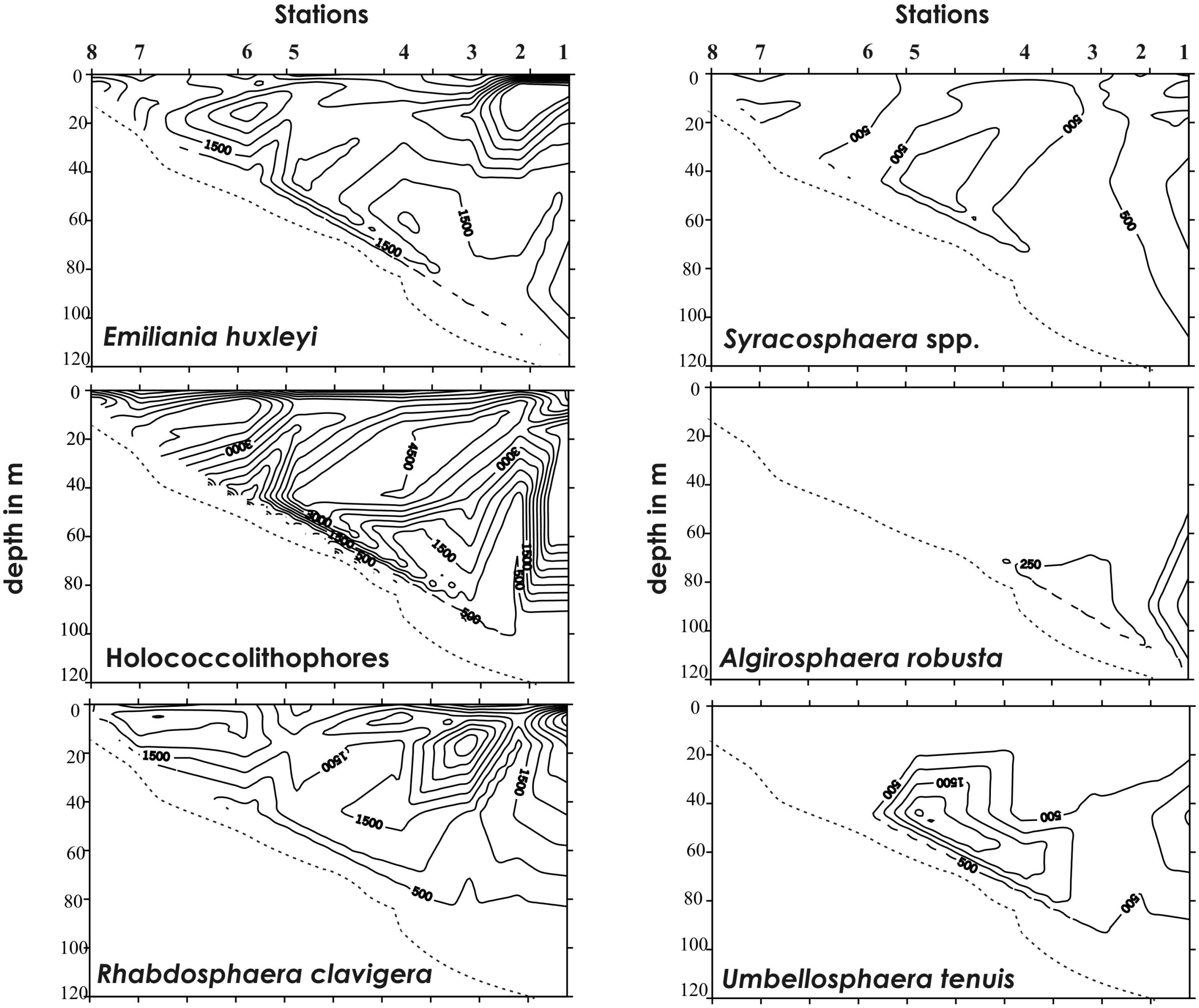


Fig. 3. Vertical distribution (cells/l) of *Emiliania huxleyi*, *Rhabdosphaera clavigera*, *Algirosphaera robusta*, *Umbellosphaera tenuis*, *Syracosphaera* spp. and holococcolithophores.

of species: Rhabdosphaera clavigera Group consists of holococcolithophores, *R. clavigera*, *E. huxleyi*, *S. histrica*, *S. pulchra*, *S. halldalii* and *R. xiphos*, Umbellosphaera tenuis Group is represented by *U. tenuis*, *A. quattrospina*, *D. tubifera* and *S. molischii* and Florisphaera profunda Group includes *F. profunda*, *A. robusta* and *C. brasiliensis*.

In general, *Rhabdosphaera clavigera* group dominates throughout the photic zone contributing 50–100 % to the total coccolithophore abundance, followed by *Umbellosphaera tenuis* group (ranging between 0-33 %) and *Florisphaera profunda* group (ranging between 0-29 %).

Coccolithophore vertical variation in the photic zone

A Q-mode HCA was applied to determine the degree of similarity in coccolithophore communities between the studied samples, intending to describe the possible relationship between coccolithophore distributional patterns. The resulting dendrogram of Q-mode HCA (Fig. 5) revealed four distinct clusters. The relationship among sample of the four groups was also estimated using a NMDS plot. *Stress* values (0.15) provide a potentially useful 2-dimensional picture (Fig. 5).

The results of statistical analysis show four discrete sub-zones between 0-120 m: surface layer (SL) at 0 m depth, upper photic zone (UPZ) ranging between 5-25 m depth, middle photic zone (MPZ) ranging between 45-60 m depth and lower photic (LPZ) zone ranging between 90-120 m depth.

Surface layer: The cluster includes samples characterized mainly by the *Rhabdosphaera clavigera* group (95.52 % on average; Fig. 6) with low frequencies of the other two

Station	(m)	*A. acanthifera*	*A. quattrospina*	*A. robusta*	*A. unicornis*	*C. leptoporus*	*C. brasiliensis*	*C. cristatus*	*C. binodata*	*C. mediterranea*	*D. tubifera*	*E. huxleyi*	*F. profunda*	*G. ericsonni*	*G. oceanica*	*H. carteri*	*M. adriaticus*	*P. vandelii*	*P. galapagensis*	*R. clavigera*	*R. xiphos*	*S. anthos*	*S. corolla*	*S. dilalata*	*S. halldalii*	*S. histrica*	*S. lamina*	*S. molischii*	*S. nana*	*S. nodosa*	*S. ossa*	*S. pulchra*	*S.* sp. type K	*U. tenuis*
T3-1	0											963								1252	96							96		96		96		
	5							110				5174								5284					220	550		110		110		440		
	15		83						83			3302							83	3138					25	83						330		165
	45	59	59	59				178	59		118	1482								2016	296		59		652	415		59				119		1601
	90		73	1321			587					2496					293			220				73		73		147				147	73	440
	120			180			60					900	300				60					180					60			60				60
T3-2	0						110		110			1321								341	220				330	330					220	220		110
	5								72			5419						72		1879					144						144	361		72
	15											5491							96	915	96				48	144		144			48	96		48
	45							57		57	57	1713		114	57			57		1598					57	171		285				114	57	856
	90			60			180	60			120	1381	60						60	120	120	60							60	120			60	360
T3-3	0											660								660	11													11
	5							94				1038								2170					94	94						188		
	15			116		116	116					3121								4624					116	231						116		116
	45			66	66	66					66	1651		132	264	132		66		859	66			66	132	66		132						660
	90		83	413								1404	83							248			83											578
T3-4	0											1321								1453														132
	5											1387						462		2929						308		308				308		
	15							128			128	2440		128						1413	514					385		128				385		257
	45	110			110		110			110		1431		330	110			220		1651					110	110						110		220
	60			110							110	881			220			110		1321	110									110				1872
T3-5	0											743								908						165					83			
	5							53	53			2470						53		998					53			158			53	158		53
	15	96										2119								1686					48	96			48					
	45		294		73						147	2642		73	220	73		147	147	1395			73	73	367	294		294		147	73	73		2642
T3-6	0							96				2312							193	2312					385	193		193				96		
	5											1604						94		2548					189	189		94				283		
	15			64			64	64				3404								2505	64		64		64	193		64		64	64	128		128
	45											428			86					171												171		342
T3-7	0											771								1541						289						96		
	5											1156							83	3138	83				413	83						83		83
	15											826								2312					165	495				165		330		
	25			94			94					944								849	94				377	189						189		377
T3-8	0											1156							96	2601	96				96	289						193		
	5					96		96			96	2601						96	96	2548						289					96	289		
	7											2220								1295					370	185		185				185		185

TABLE 2
Heterococcolithophore species (cell/1) at the sampled stations.

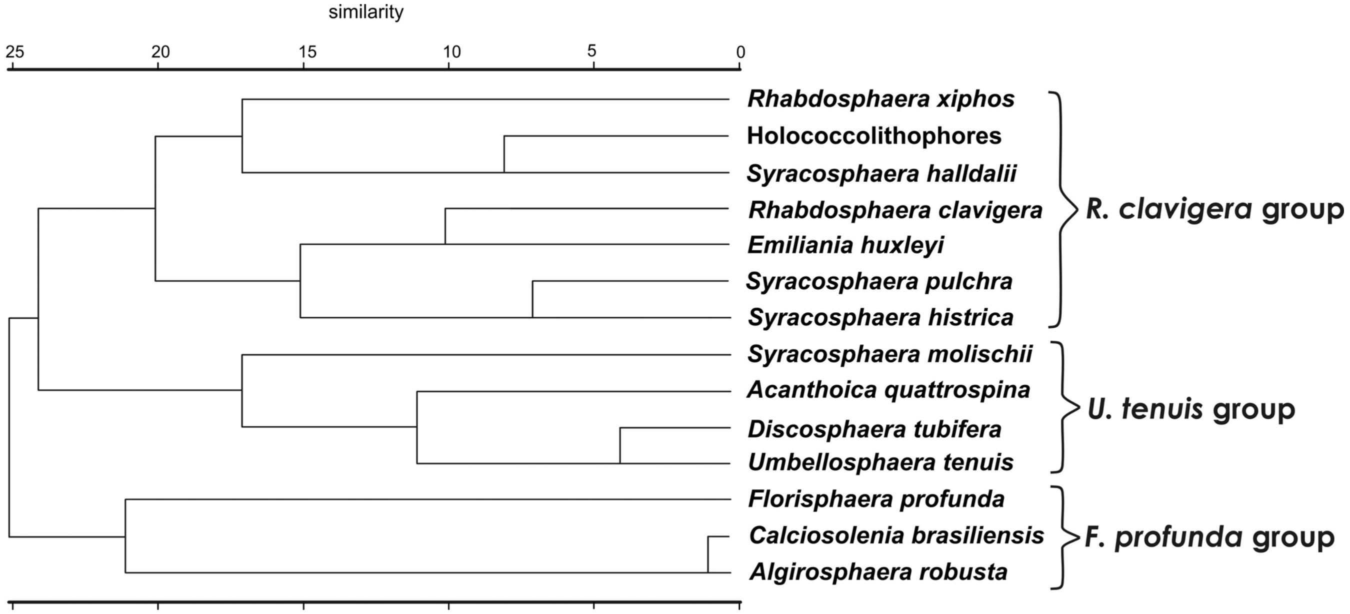


Fig. 4. R-mode hierarchical cluster analysis (centroid linkage method, distance metric is 1-Pearson correlation coefficient) based on the cell densities of the statistically important coccolithophore species.

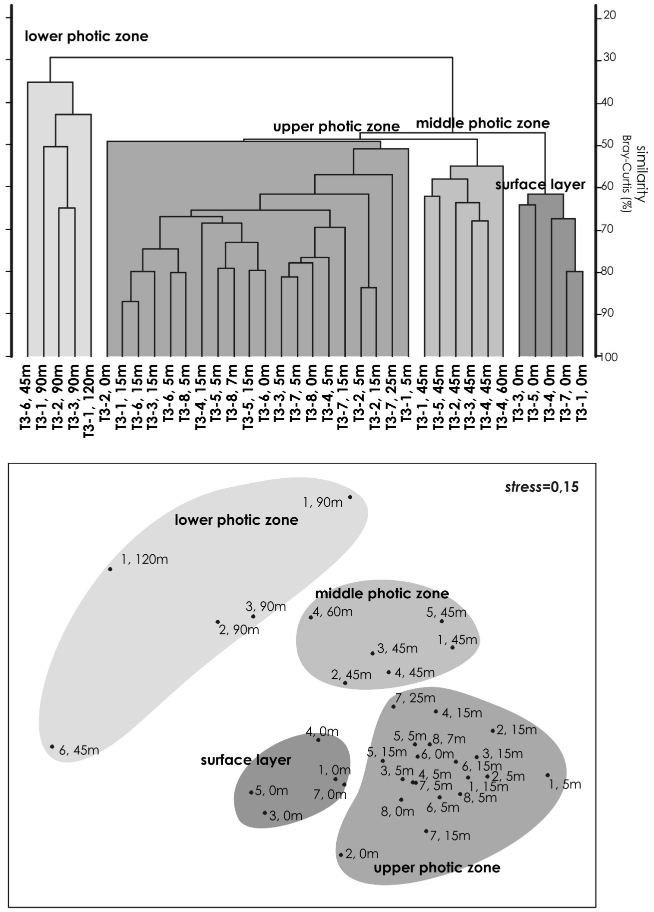


Fig. 5. Dendrogram resulting from a Q-mode hierarchical cluster analysis (Bray-Curtis average linkage) and nonmetric multi-dimensional scaling diagram of coccolithophore samples, based on a correlation matrix of species cell densities.

groups or remnant species.

Upper photic zone: The cluster contains samples characterized mainly by the *Rhabdosphaera clavigera* group (95.78 % on average; Fig. 6). In general, *Rhabdosphaera clavigera* group corresponds to the Surface layer and Upper photic zone clusters, which may actually be considered as a single level. The difference in the coccolithophore communities between the Surface layer and the Upper photic zone clusters is most possible due to coccolithophore cell densities and species richness (Fig. 2, Table 1). Both factors are slightly decreasing in the Surface layer because of the unstable physical conditions in coastal zone, but the coccolithophore communities are remarkably similar. Therefore, when plotted on the nonmetric multidimensional scaling plot, the samples of the Surface layer are very close to samples of the Upper photic zone (Fig. 5).

Middle photic zone: The cluster consists of the samples with the most prominent species richness and Shannon Wiener diversity index. The middle photic zone is dominated by *Rhabdosphaera clavigera* group (74.75% on average), but it differs from the other clusters by having the peak relative abundance of *Umbellosphaera tenuis* group (16.88 % on average; Fig. 6).

Lower photic zone: The cluster includes samples that are characterized by high values of the dominance index, low coccolithophore cell densities and species richness. In this layer, the decrease of *Rhabdosphaera clavigera* group (57.10 % on average) and *Umbellosphaera tenuis* group (11.92 % on average) are followed by a peak of relative abundance of *Florisphaera profunda* group (20.77 % on average; Fig. 6).

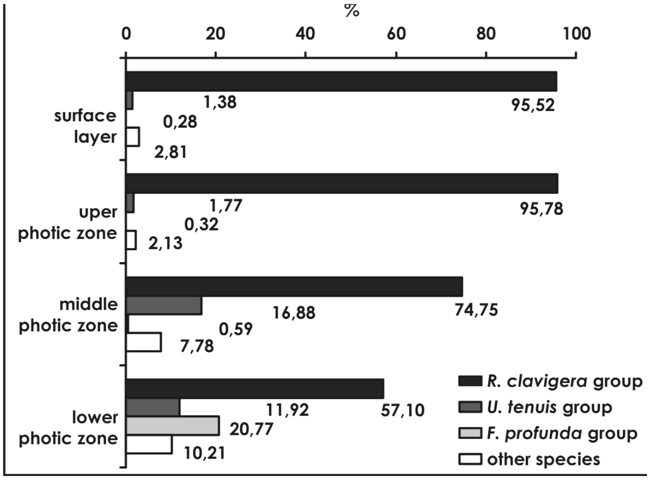


Fig. 6. Vertical distribution of photic zone coccolithophore groups in Andros coastal environments.

DISCUSSION

Coccolithophores have a world wide distribution in the ocean photic zone, but prefer warm, low productivity regions (Honjo & Okada, 1974). Therefore, they are the dominant primary producers in the oligotrophic eastern Mediterranean Sea (Knappertsbusch, 1990; Ziveri *et al.*, 1995; Malinverno *et al.*, 2003; Triantaphyllou *et al.*, 2004b).

The species composition, in the summer period off the southeastern coast of Andros island (gulf of Korthi) is very similar to communities previously described from other parts of the eastern Mediterranean Sea (Knappertsbusch, 1990; Kleijne, 1993; Malinverno *et al.*, 2003). Communities' structure was characterized by high values of the species richness and relatively increased Shannon diversity index. This implies full development of the populations and better representation of all the species in the communities. The summer Shannon diversity values of the Andros coastal environments were as high as those documented for the Mediterranean Sea by Kleijne (1993), indicating a remarkable diversity in the middle Aegean Sea.

Former studies identified that many coccolithophore species prefer to live in specific depth ranges (Winter *et al.*, 1994; Jordan & Chamberlein, 1997; Jordan & Winter, 2000; Hagino *et al.*, 2000; Takahashi & Okada, 2000; Cros, 2001; Winter *et al.*, 2002; Andruleit *et al.*, 2003; Malinverno *et al.*, 2003). When investigating NW Mediterranean planktonic coccolithophores Cros (2001), showed clearly that some coccolithophore species prefer particular water depths. This feature might be related to the high stratification of Mediterranean waters in summer. Additionally Triantaphyllou *et al.* (2002) provided evidence of vertical distribution of holococcolithophore assemblages in the Aegean Sea.

In the present study we have additionally observed that the photic zone boundaries –based on coccolithophore distribution- are displaced upwards as the sea bottom depth is decreasing, possibly due to the effort of the species to get ecologically adapted to smaller heights of the water column at coastal environments. Similar results characterize also the holococcolithophore species distribution (Triantaphyllou *et al.*, 2002).

Statistical analysis allowed us to discriminate three groups of coccolithophore taxa. All three groups recognized in this region are associated with vertical zonation with specific sets of ecological properties. Below, we discuss the ecological behaviour and distribution of heterococcolithophore species for each of three groups. Syntheses of ecological data on coccolithophores show that certain associations of species characterise different environmental conditions.

Rhabdosphaera clavigera Group

The *R. clavigera* Group consists of holococcolithophores, *R. clavigera*, *E. huxleyi*, *S. histrica*, *S. pulchra*, *S. halldalii* and *R. xiphos* and represents the main feature of SL and UPZ zones.

R. clavigera is abundant in temperate to subtropical waters, while distributes in surface or near-surface water and tends to decrease in abundance with depth (Honjo & Okada 1974; Okada & McIntyre 1979; Roth & Coulbourn, 1982; Brand, 1994; Roth 1994; Haidar & Thierstein, 2001; Malinverno *et al.*, 2003). According to Brand (1994), this species grows well at low nutrient levels and does not increase its growth rate in response to elevated nutrient concentrations. *R. clavigera* is present with high absolute frequencies in the Mediterranean Sea (Kleijne, 1993) and together with *R. xiphos* show an affinity to upper water layers (Cros, 2001). Additionally, holococcolithophores are abundant in warm, oligotrophic marine environments of the Mediterranean Sea (Kleijne *et al.*, 1989; Kleijne, 1991; Cros, 2001; Triantaphyllou *et al.*, 2002; Dimiza *et al.*, 2004). *Syracosphaera* is the most diverse living coccolithophore genus and is reported to inhabit different photic layers (Jordan & Chamberlein, 1997). In this study, *S. pulchra*, *S. histrica* and *S. halldalii* seem to prefer the upper photic zone. Young (1994) included Rhabdosphaeraceae along with Syracosphaeraceae and holococcolithophores in the "miscellaneous" group of species; this group does not have an obviously distinctive biogeography, but tends to be more important in intermediate environments than in the extreme eutrophic or oligotrophic conditions, showing a tendency towards weak K-selection/efficiency maximizing (Aubry, 1992; Brand, 1994; Young, 1994; Bown *et al.*, 2004; Baumann *et al.*, 2005). *E. huxleyi* is also included in *Rhabdosphaera clavigera* Group. This species has been found over a wide range of environmental conditions, but Cros (2001) has noticed its preference for the upper-middle photic layer in the NW Mediterranean.

Umbellosphaera tenuis **Group**

U. tenuis Group consisting of *U. tenuis*, *A. quattrospina*, *D. tubifera* and *S. molischii* is mainly restricted to the MPZ.

U. tenuis is rare in surface waters but common in depth from 50 to 100 m (Honjo & Okada 1974). This species prefers tropical to subtropical waters (Okada & Mcintyre, 1979) and may dominate the summer coccolithophore flora in the Mediterranean Sea (Knappertsbusch, 1990). Kleijne (1993) stated that the presence of *Umbellosphaera* spp. indicates oligotrophic, nutrient-depleted conditions. *U. tenuis* and *D. tubifera* are counted among the umbelliforms (Young, 1994; Winter *et al.*, 2002; Hagino & Okada, 2004), a typical group of much more consistent populations (strongly K-selection). In the studied Aegean samples of the present study *U. tenuis* becomes a significant part of nannoflora at 45 m depth and continuous till 60 m. Cros (2001) found it with maximum densities around 40 m at NW Mediterranean, and therefore considered that is represents an upper-middle photic zone inhabitant. Our results reinforce Cros's (2001) findings, indicating also that the increase of this species may be correlated with a respective increase in diversity, at 45 m depth. *A. quattrospina* is present in few stations, but has a clear maximum abundance at 45m depth. Also, *S. molischii* inhabits better the 45 m depth. This is consistent with the results by Cros (2001) who reported *S. molischii* as a middle photic zone inhabitant.

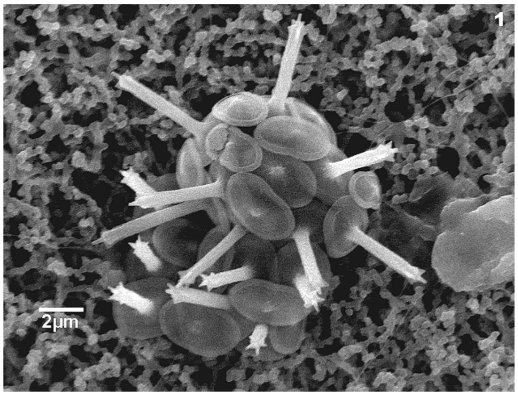
Florisphaera profunda **Group**

F. profunda Group consists of *F. profunda*, *A. robusta* and *C. brasiliensis* and dominates the LPZ.

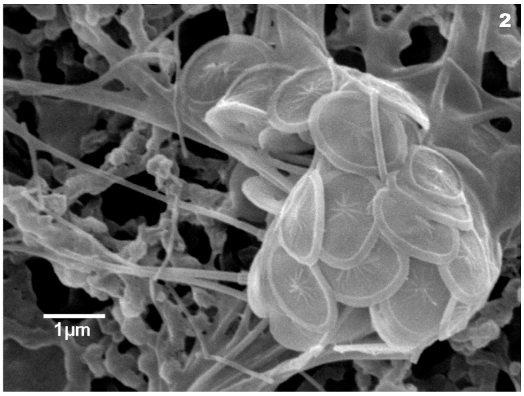
F. profunda is restricted to the lower photic zone (Okada & Honjo, 1973; Jordan & Winter, 2000), and the depth distribution of this species signals the depth of the lower photic zone. *A. robusta* and *F. profunda* are included in the floriform coccolithophores which live below the thermocline under low light and temperature conditions (Molfino & Mcintyre, 1990; Young, 1994; Winter *et al.*, 1994; Okada & Matsuoka, 1996; Takahashi & Okada, 2000; Winter *et al.*, 2002; Malinverno *et al.*, 2003). *A. robusta* is characteristic for the lower water layers (deeper than 100 m). Kleijne (1993) considered this species as an indicator for relatively cold and eutrophic conditions. Both these species become important at 90 and 120 m depth, making up the typical deep assemblage. The presence of few *A. robusta* specimens at 60, 45, 25 m, even though at 15 m depth in several stations from Andros coastal environments (Table 2) may be due to the upward displacement of the depth position of the species. In this study, *F. profunda* and *A. robusta* are associated with *C. brasiliensis*. Although the latter species only occurred in low abundance (Table 2), its higher values were found at 90 m depth showing close affinity to *A. robusta*.

CONCLUSIONS

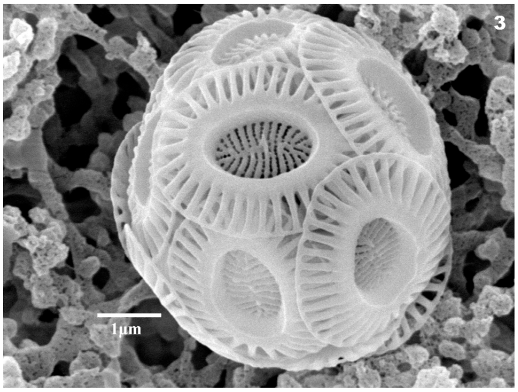
- Coccolithophore total cell densities in the marine ecosystems of Andros Island (Middle Aegean Sea) during late summer 2001, varied between 14.7x10^3 cells/l and 1.9x10^3 cells/l. Heterococcolithophores are nicely represented even in shallow coastal environments, showing quite diverse communities. In all 33 different heterococcolithophore species are recognized, of which 13 species with holococcolithophores contributed 96 % of the communities, and form distinct groups: *Rhabdosphaera clavigera* Group, *Umbellosphaera tenuis* Group and *Florisphaera profunda* Group. The depth distribution of these three groups depends mainly on the nutrient and temperature levels along the photic zone.
- The present study shows clearly that certain species prefer particular water depths in the studied coastal environments. In particular, *Rhabdospahera clavigera*, *R. xiphos* and *Emiliania huxleyi* occupy better the upper water layers. *Umbellosphaera tenuis* increases between 45-60 m depth. In this zone, other important species are *Discosphaera tubifera* and *Acanthoica quattrospina*. *Algirosphaera robusta* and *Calciosolenia brasiliensis* are distributed mainly below 90 m depth. *Florisphaera profunda* is restricted in the deeper layers. Finally, *Syracosphaera* species tend to bear vertical distribution in the water column. In particular, *Syracosphaera pulchra*, *S. histrica* and *S. halldalii* seem to prefer the upper water layers (till 25 m depth), whereas *S. molischii* inhabits better the 45m depth.
- The vertical profiles showed similar patterns between Shannon–Wiener index and species richness with peak values occurring in the middle photic zone, reflecting that higher number of species occurred by higher distribution of individuals in the different species. The dominance index is rising gradually from 45 m to 120 m depth showing an opposite pattern to Shannon –Wiener index and species richness.
- The combination of heterococcolithophore species composition, ecological indices (species richness, Shannon–Wiener diversity and Dominance) and coccolithophore concentration are used to characterize the modern photic zone environments. Three main ecological niches combined with differentiating environmental parameters have been recognized in the Aegean Sea coastal waters column; intermediate environments in the upper photic zone (0-25 m depth; *R. clavigera* Group), continuing of normal nutrification conditions in middle photic zone (45-60 m depth; *U. tenuis* Group) and higher nutrient content and low temperature in the deep photic zone (90-120 m depth; *F. profunda* Group). The studied



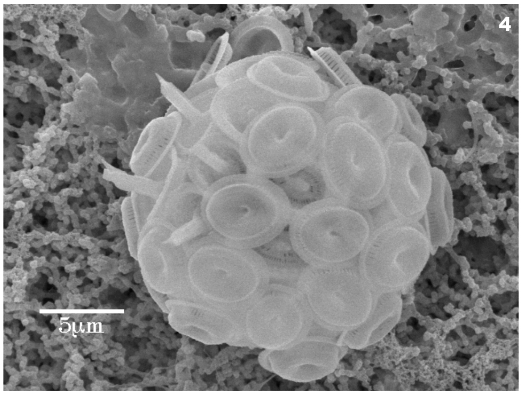
***Rhabdosphaera clavigera* sample T3-5, 15m**



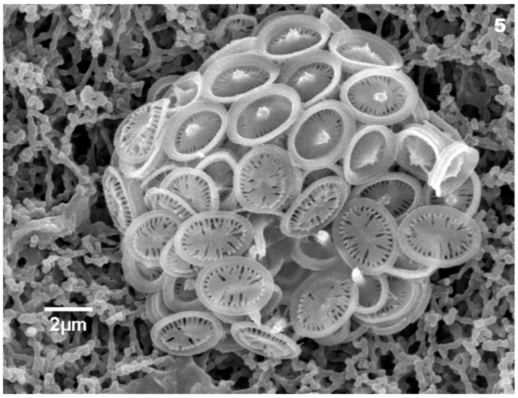
***Rhabdosphaera xiphos* sample T3-2, 15m**



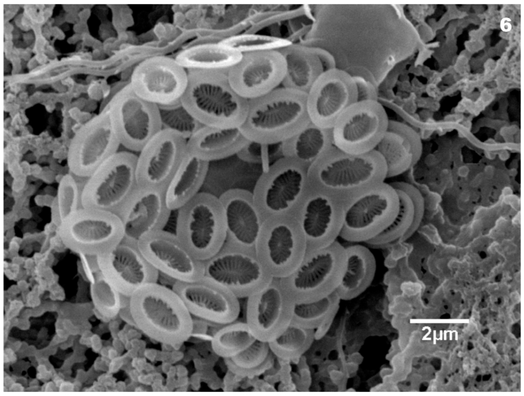
***Emiliania huxleyi* sample T3-5, 15m**



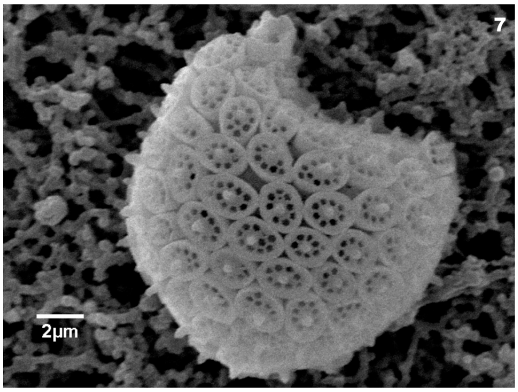
***Syracosphaera pulchra* sample T3-2, 5m**



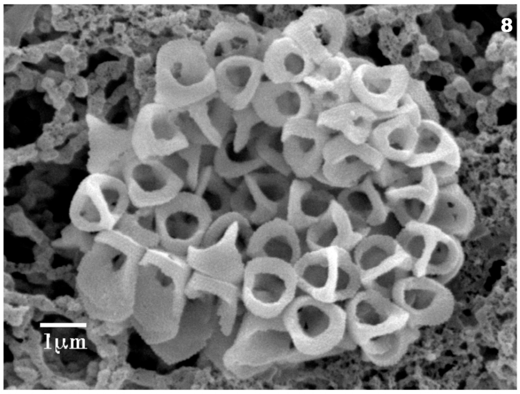
***Syracosphaera histrica* sample T3-5, 15m**



***Syracosphaera halldalii* sample T3-8, 7m**

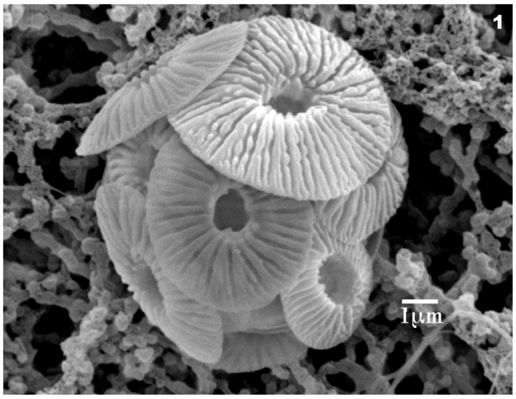


***Calyptrolithina multipora* sample T3-1, 45m**

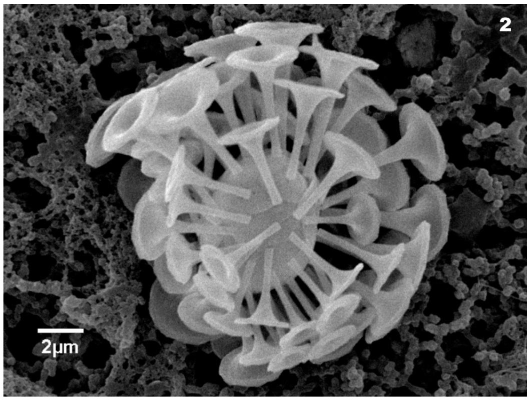


***Helladosphaera cornifera* sample T3-2, 5m**

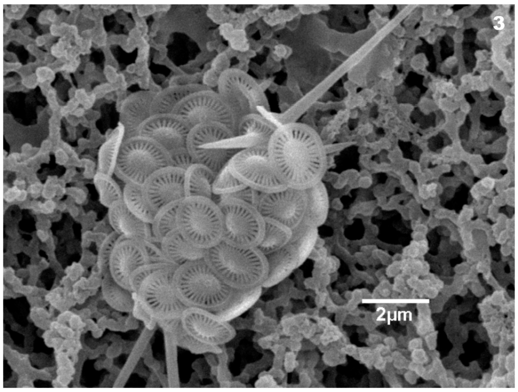
PLATE 1
1-6 Heterococcolithophore species of *Rhabdosphaera clavigera* Group. 7-8 Holococcolithophore species.



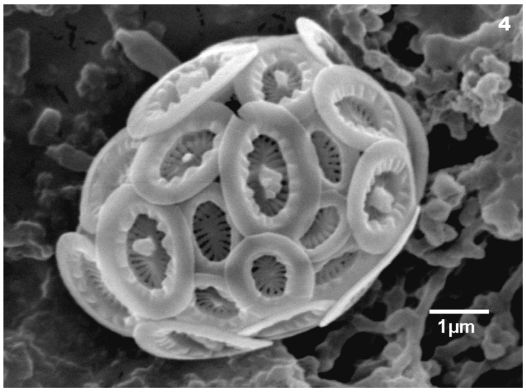
Umbellosphaera tenuis **sample T3-2, 5m**



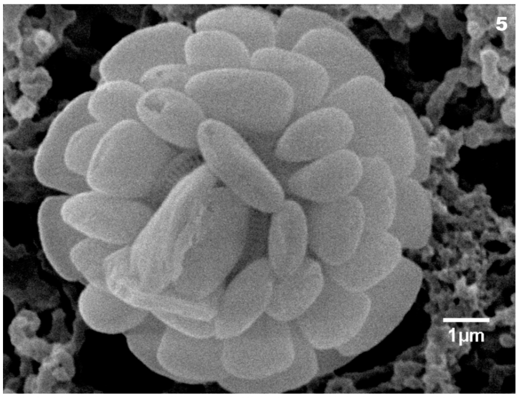
Discosphaera tubifera **sample T3-1, 45m**



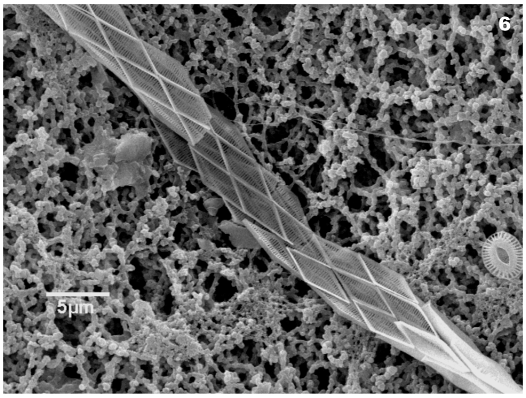
Acanthoica quattrospina **sample T3-5, 45m**



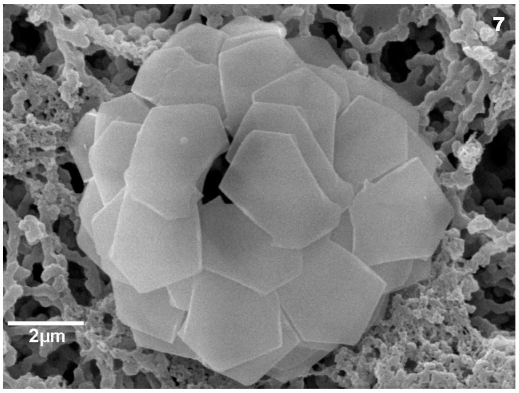
Syracosphaera molischii **sample T3-4, 5m**



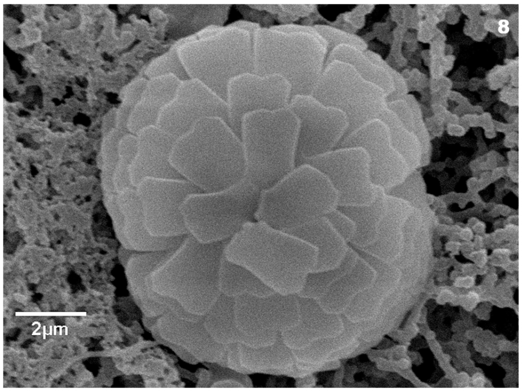
Algirosphaera robusta **sample T3-1, 90m**



Calciosolenia brasiliensis **sample T3-2, 90m**



Florisphaera profunda **sample T3-2, 90m**



Florisphaera profunda **sample T3-1, 120m**

PLATE 2
1-4 Heterococcolithophore species of *Umbellosphaera tenuis* Group. 6-8 Heterococcolithophore species of *Florisphaera profunda* Group.

communities indicate that the coccolithophore photic zone boundaries are displaced upwards as the sea bottom depth is decreasing, possibly due to the effort of the species to get ecologically adapted to smaller heights of the water column at coastal environments.

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APPENDIX A. Taxonomic list

The taxonomic list includes all heterococcolithophore taxa cited in the text and all heterococcolithophore taxa identified during the present study.

Acanthoica acanthifera Lohmann, 1912
Acanthoica quattrospina Lohmann, 1903
Algirosphaera robusta (Lohmann, 1902) Norris, 1984
Alisphaera unicornis Okada & McIntyre, 1997
Calcidiscus leptoporus (Murray & Blackman, 1898) Loeblich & Tappan, 1978
Calciosolenia brasiliensis (Lohmann, 1919) Young, 2003
Ceratolithus cristatus Kamptner, 1950
Coronosphaera binodata (Kamptner, 1927) Gaarder & Heimdal, 1977
Coronosphaera mediterranea (Lohmann, 1902) Gaarder & Heimdal, 1977
Discosphaera tubifera (Murray & Blackman, 1898) Ostenfeld, 1900
Emiliania huxleyi (Lohmann, 1902) Hay & Mohler, 1967 var. *huxleyi*
Florisphaera profunda Okada & Honjo, 1973
Gephyrocapsa ericsonii McIntyre & Be, 1967
Gephyrocapsa oceanica Kamptner, 1943
Helicosphaera carteri (Wallich, 1877) Kamptner, 1954
Michaelsarsia adriaticus (Schiller, 1914) Manton *et al*., 1984
Palusphaera vandelii Lecal 1965 emend. Norris 1984
Polycrater galapagensis Manton & Oates, 1980
Rhabdosphaera clavigera Murray & Blackman, 1898
Rhabdosphaera xiphos (Deflandre & Fert, 1954) Norris, 1984
Syracosphaera anthos (Lohmann, 1912) Jordan & Young, 1990
Syracosphaera corolla Lecal, 1966
Syracosphaera dilalata Jordan *et al*., 1993
Syracosphaera halldalii Gaarder ex Jordan et Green, 1994
Syracosphaera histrica Kamptner, 1941
Syracosphaera lamina Lecal-Schlauder, 1951
Syracosphaera molischii Schiller, 1925
Syracosphaera nana (Kamptner, 1941) Okada & McIntyre, 1977
Syracosphaera nodosa Kamptner, 1941
Syracosphaera ossa (Lecal, 1966) Loeblich & Tappan, 1968
Syracosphaera pulchra Lohmann, 1902
Syracosphaera sp. type K Kleijne (1993)
Umbellosphaera tenuis (Kamptner, 1954) Paasche, 1955