Coccolithophore communities in the Gulf of Manfredonia (Southern Adriatic Sea): data from water and surface sediments

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ABSTRACT: Living coccolithophore distributions from the Gulf of Manfredonia (Southern Adriatic Sea) were investigated and compared with the coccolith assemblages in the underlying surface sediments. In total, 55 samples from 13 stations in four transects collected at the end of October 2000 were analyzed to determine spatial and vertical distribution of individual taxa in the coastal environment. At all stations, the maximum coccosphere densities were between 10m and 30m of water depth (maximum values were ~4x10^4 coccospheres per litre of seawater). Coccolithophore absolute abundances show a vertical stratification and spatial variation, as well as variable species diversity, increasing from the coast to the open sea and decreasing with depth. Different coccolithophore communities are recorded in the shallow and deep photic zone. *Emiliania huxleyi*, *Syracosphaera* spp., *Rhabdosphaera* spp., *Coronosphaera* spp., *Umbellosphaera tenuis* and holococcolithophores are present mainly in the surface waters, above the thermocline between 25-30m depth. In the deeper water samples, there is a significant increase in coccospheres of *Florisphaera profunda*. The coccolithophore cell density variability is compared with in situ measurements of environmental parameters (temperature, salinity, nitrates and phosphates). Cell densities of all dominant taxa are most highly correlated with temperature variability. The low correlations of cell densities with nitrates and phosphates may be caused by insufficient sampling resolution, nutrient levels close to detection limits, or both. The comparison of the living assemblage with surface sediment records shows significant differences in the presence and abundance of some species. The recognised fossil record in the surface sediments is mainly represented by Cretaceous-Pleistocene reworked species, showing stronger dynamic processes at the bottom, such as terrigenous input and resuspension, than phytoplankton growth. Most marked correspondence between living and fossil assemblages has been found in the deeper and open sea sediments.

INTRODUCTION

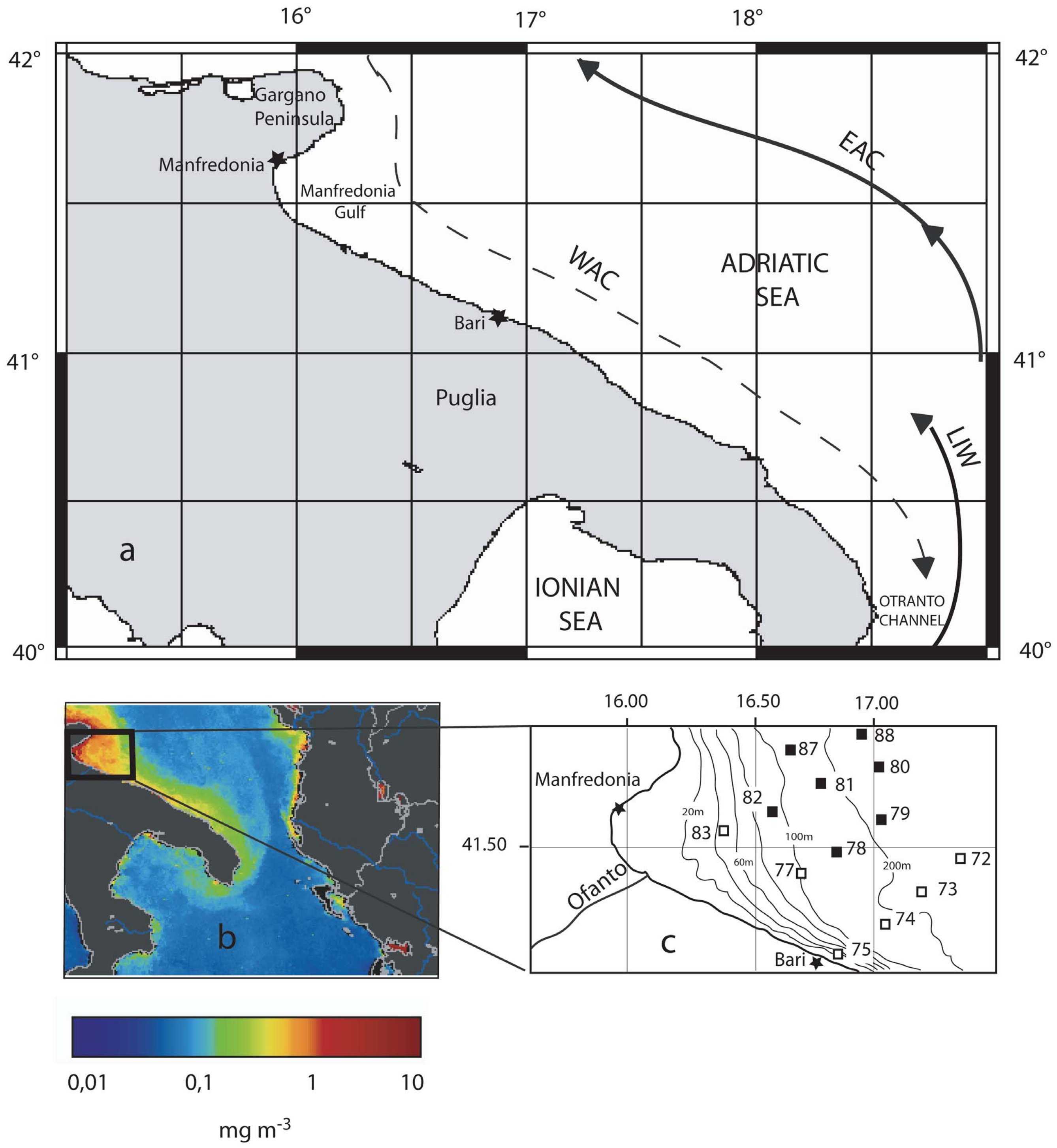
Coccolithophores are marine unicellular haptophytes, covered by calcium carbonate shields called coccoliths. Many coccolithophore taxa have specific ecological preferences, and horizontal and vertical distributions in the photic zone due to relative availability of nutrients and different levels of salinity, temperature, light and stratification of water mass in the photic zone (Okada and McIntyre 1973; 1977; 1979; Winter et al. 1994; Hagino et al. 2000; Takahashi and Okada 2000; Andruleit and Rogalla 2002; Andruleit et al. 2003; Noël et al. 2004).

Several are the previous studies that have been conducted in the Mediterranean Sea. Borsetti and Cati (1972, 1976, 1979), reviewed the taxonomy of the living coccolithophore in the Tyrrhenian Sea. Other studies in the eastern Mediterranean have shown that coccolithophores are the dominant phytoplankton group producing carbonate (Knappertsbusch 1993; Ziveri et al. 1995; Malinverno et al. 2003; Triantaphyllou et al. 2004). Cros and Fortuño (2002) showed how, this phytoplanktonic group is one of the most important in the Mediterranean Sea, because it is represented by a high number of living species, both heterococcolith-bearing species and holococcolith-bearing species.

However, studies on present coccolithophore ecology and distribution in the Southern Adriatic Sea are scarce. The present study provides the first data set on coccolithophore distribution collected in the Gulf of Manfredonia (South Adriatic) during the cruise Interreg I Italia-Albania in October 2000. Goals of this research are to improve the knowledge of coccolithophore productivity and ecology, in order to clarify the relationship of this phytoplanktonic group with the physical and chemical characteristics of waters. Linear correlations between water chemical or physical parameters and total coccolithophore abundance have been calculated. The Shannon-Weaver, and Dominance diversity indices have also been computed in order to interpret the distribution pattern and ecology of living communities. A comparison of the present coccolithophore communities with the fossil record in the underlying surface sediments is also provided.

DESCRIPTION OF THE AREA

The Gulf of Manfredonia is situated in the western part of Southern Adriatic Sea (text-fig. 1a). To the North it is delimited by the Gargano Peninsula which morphologically marks the northern border of the Southern Adriatic. The Gulf is characterized by limited circulation and high sedimentation rate (Damiani et al. 1988; Bianchi and Zurlini 1984) which, from the coastal to offshore area, mainly consists of clay, sandy clay and clayey sand (Loiacono et al. 2002). The Gulf of Manfredonia represents a transition zone between the Middle Adriatic circulation and the Southern circulation which presents Ionian Sea characteristics, such as oligotrophic water condition (Damiani et al. 1988). Recent investigations about surface circulation and current measurements in the Adriatic Sea confirm a cyclonic



TEXT-FIGURE 1
a: General surface water circulation in the Southern Adriatic Sea and location of the studied stations (map create by http://www.aquarius.geomar.de/omc/make_map.html). LIW: Levantine Intermediate Water; EAC: Eastern Adriatic Current; WAC: Western Adriatic Current.
b: Monthly chlorophyll-a concentration in October 2000 in the sampling region (http://marine.jrc.cec.eu).
c: Location of the stations. The filled squares represent the stations in which both water and surface sediment samples were available for this research. The empty ones represent the stations in which the water samples were available. The stars represent the two towns Manfredonia and Bari.

TABLE 1
Location of the stations, with the data of temperature, salinity, the phosphates, the nitrates, the total coccolithophore standing crop (cells/l) and the coccoliths/gram of sediment.

stations	depth at the bottom (m)	depth of the sampling	date of the sampling	longitude	latitude	temperature (°C)	salinity (‰)	phosphates (µg/l)	nitrates (µg/l)	total standing crop (cells/L)	coccoliths/gr of sediment
72		0	29/10/2000	17,41738	41,45968	19,54	38,72	4,68	8,94	3,30E+04	
		10				19,53	38,68	3,98	8,80	3,01E+04	
		30				16,70	38,68			3,20E+03	
		60				14,77	38,60			6,80E+03	
		100				14,37	38,76	5,12	32,68	6,69E+03	
		150				14,08	38,80			1,31E+03	
73		0	29/10/2000	17,25150	41,35157	19,87	38,65	2,33	7,30	2,84E+04	
		10				19,81	38,72			4,25E+04	
		30				17,10	38,71	4,61	15,01	2,90E+04	
		60				15,19	38,71			1,64E+02	
		100				14,74	38,70			4,83E+02	
		150				14,50	38,82			7,92E+02	
74		0	29/10/2000	17,08383	41,24673	19,84	38,46	1,26	12,78	3,59E+04	
		10				19,84	38,58	15,87	17,31	3,59E+04	
		30				18,84	38,58			3,41E+04	
		63				15,32	38,72	5,05	22,94	1,88E+03	
		100				14,48	38,68	1,58	7,20	2,39E+03	
75		0	29/10/2000	16,92402	41,16003	19,68	38,70	2,78	23,85	1,20E+04	
		10				19,69	37,60	3,11	12,74	8,73E+03	
		28				19,61	37,59	5,88	27,34	3,67E+02	
77		0	29/10/2000	16,71522	41,37417	19,47	38,65	0,10	39,59	8,54E+03	
		10				19,37	37,81	4,02	21,15	1,20E+04	
		30				17,57	38,19	5,16	28,05	1,71E+04	
		60				15,45	38,60			4,18E+01	
78		0	29/10/2000	16,88312	41,48315	19,87	37,62	3,48	0,80	1,55E+04	
		10				19,88	38,58	5,88	23,33	1,71E+04	
		30				16,65	38,60			3,24E+04	
		60				15,27	38,50	6,64	25,18	2,02E+03	
	123	surface sediment									1,09E+08
79		30	29/10/2000	17,07465	41,59092	17,35	38,68	5,37	17,30	1,22E+04	
		60				15,10	38,63			4,01E+04	
		100				14,92	38,67			2,26E+03	
		150				14,55	38,75	0,82		1,54E+03	
	392	surface sediment									1,20E+08
80		0	30/10/2000	17,02855	41,77308	20,55	37,44	7,71	19,67	4,73E+04	
		10				20,55	38,64	8,03	14,41	2,04E+04	
		60				15,01	38,60			8,38E+03	
		100				14,61	38,72			9,70E+03	
		150				14,24	38,82			1,37E+03	
	711	surface sediment									7,53E+08
82		0	30/10/2000	16,60402	41,61795	19,43	38,70	2,47	4,00	1,77E+04	
		10				19,47	38,15	15,81	23,79	2,72E+04	
		30				16,74	38,18			7,29E+03	
	86	surface sediment									3,40E+08
81		0	30/10/2000	16,81887	41,71062	20,49	38,52	3,11	13,63	1,23E+04	
		10				20,49	38,63	11,57	24,34	1,36E+04	
		30				18,50	38,63	6,91	34,21	2,24E+04	
		60				15,33	38,64			2,21E+03	
		100				14,90	38,67			2,57E+03	
	139	surface sediment									7,21E+07
83		0	29/10/2000	16,38405	41,53673	19,76	37,50	5,56	9,17	7,15E+03	
		10				19,76	37,42			7,85E+03	
88		0	30/10/2000	16,91528	41,89193	20,25	38,52	3,54	29,18	2,65E+04	
		10				20,22	38,63	7,32	29,41	2,96E+04	
		30				16,88	38,62			1,46E+04	
		60				15,15	38,66			1,10E+04	
	444	surface sediment									
87		0	30/10/2000	16,68310	41,82225	19,43	38,74	2,59	7,53	2,71E+04	
		10				19,45	38,17			1,70E+04	
		30				17,14	38,26	30,61	36,14	3,19E+04	
		60				14,40	38,58			6,83E+02	
	109	surface sediment									1,49E+08

circulation in the Southern sub-basin (Poulain 2001; Kovacevic et al. 1999) characterized by seasonal variability (Poulain 1999; Artegiani et al. 1997).

The principal surface currents of the southern Adriatic Sea are represented in text-figure 1a. The Western Adriatic Current (WAC) connects the northern and southern ecosystem and affects the biogeochemical properties of the whole western Adriatic basin. The Southern Adriatic open waters, however, show clearly oligotrophic characteristics and the nutrient supply to the euphotic zone depends strongly on the vertical stratification/mixing processes (Vilicic et al. 1989). The Adriatic Sea mean surface flow is globally cyclonic due to its mixed positive-negative estuarine circulation forced by buoyancy input from the rivers (mainly the Po River) and by strong air-sea fluxes resulting in loss of buoyancy and dense water formation. The Eastern Adriatic Current (EAC) flows along the eastern side from the eastern Strait of Otranto to as far north as the

TABLE 2
Data distribution of the two indices applied, Shannon-Weaver, Dominance.

Shannon-Weaver													
stations	87	88	83	82	81	80	77	78	79	75	74	73	72
depth (m)													
0	0,83	1,58	2,00	1,68	0,87	1,06	1,38	1,45		1,66	1,86	2,11	2,06
10	0,82	1,54	2,17	1,70	0,84	1,88	1,09	1,22		1,85	2,13	1,87	1,92
30	0,19	1,19		1,26	1,00		1,43	0,52	1,90	0,00	1,03	1,52	1,80
60	1,21	1,56			1,50	1,96	0,00	1,67	1,37		1,16	1,10	1,81
100					1,77	0,59			1,30		1,44	0,90	0,98
150						1,84			1,29			1,34	1,37
Dominance													
stations	87	88	83	82	81	80	77	78	79	75	74	73	72
depth (m)													
0	0,56	0,36	0,16	0,27	0,60	0,55	0,41	0,42		0,28	0,27	0,18	0,21
10	0,57	0,38	0,16	0,25	0,63	0,21	0,54	0,48		0,20	0,21	0,26	0,24
30	0,91	0,38		0,41	0,55		0,34	0,80	0,20	1,00	0,52	0,33	0,19
60	0,34	0,34			0,32	0,20	1,00	0,26	0,40		0,47	0,34	0,30
100					0,25	0,77			0,45		0,33	0,47	0,61
150						0,24			0,36			0,34	0,33

Istrian Peninsula. A return flow (the WAC) is seen flowing to the southeast along the western coast (Poulain, 1999, 2001). The Mediterranean Levantine Intermediate Water (LIW), is a source of nutrients in the southern sub-basin and it enters the Adriatic from the Ionian Sea through the Otranto Channel (Zavatarelli et al. 1998).

The Adriatic Sea is characterized by a close coexistence of coastal-eutrophic and open-oligotrophic conditions, mainly in relation to the surface current circulation (Zavatarelli et al. 2000). In particular, the Southern Adriatic open waters are known to have oligotrophic characteristics (Vilicic et al. 1989), although the nutrient supply to the euphotic zone strongly depends on the vertical stratification/mixing processes. text-figure 1b shows the monthly chlorophyll-a concentration in October 2000 in the sampling region (http://marine.jrc.cec.eu) that appears to be slightly higher in respect to the adjacent areas. Furthemore, the biogeochemical properties of the Gulf waters are affected by nutrient inputs from the southward coastal current (WAC), and from the nearby terrestrial source (Spagnoli et al. 2004), which is mainly due to river runoff from the Ofanto river (Fig 1c) (Spagnoli et al. 2005).

MATERIALS AND METHODS

Water samples for nutrient and coccolithophore analysis as well as the CTD data were collected at the same time, during the cruise of N/O ITALICA in October 2000. The sampling was planned to obtain a regular grid along four transects oriented S-E - N-W, perpendicular to the shoreline. In total, 55 samples from 13 stations in four transects (text-fig. 1c) were investigated. Water samples were taken at several depth intervals (table 1) with a rosette sampler (24 bottles of 12l).

At 7 stations the underlying surface sediments were taken from box-cores (text-fig. 1c).

Hydrographic and nutrient sample processing

Depth profiles of temperature (T°) and salinity (‰) were measured using a SBE 9/11 profiler, and were carried out at the same time as the water sampling (Spezie et al. 2002) (table 1). Water samples for nutrients (nitrates and phosphates) were also collected at the same time. However, it should be noted that it was not always possible to collect the data at the same sampling depth for all the parameters. In the table 1 the white spot indicates that no data were recovered. The water samples for the nutrients were stored in 500ml PET bottles and frozen at –20°C. The spectophotometry used to detect nutrients was a PERKIN-ELMER UV/VIS double grating monocromator (190 – 900 nm) version lambda 16, and provides spectral band passes of 0.25, 1, 2, and 4 nm (Frache et al. 2002). In text-figure 2a and b, all the available data are displayed. The contour maps, which display all water parameters, are obtained by using the inverse distance to power gridding method (triangulation with linear interpolation), a weighted average interpolator. This was done with Surfer Version 8.

Coccolithophore sample processing and analysis

For the coccolithophore analysis, a fixed quantity of sea water (5l) was immediately filtered on board, on cellulose acetate filters (47mm diameter, 0.45 micron pore-size), using a low-vacuum filtration system. Filters were then oven dried and stored in petri-dishes.

For the Scanning Electron Microscope (SEM) analyses a piece of each filter was attached to a stub using a double sided adhesive tape and coated with gold. For the Light Microscope (LM) analysis a piece of filter from each water sample has been placed between a cover slip and a glass slide. The surface sediment samples for the coccolith analysis were prepared using a combined dilution/filtering technique as described by Andruleit (1996).

Data presented in this paper derive from quantitative analyses performed on water and sediment samples, using a Zeiss Polarised Light Microscope at a magnification of 1560x.

Few selected water samples were qualitatively analyzed by Scanning Electron Microscope (SEM HITACHI S-3500N and PHILIPS 2000WX). Isolated coccoliths in the water samples were not considered in this study. The numbers of the coccolithophore species (cells/l), was calculated following the methodology of Jordan and Winter (2000) by scaling up the raw counts from a known scanned area. The formula used was:

$$A=N*S/V$$

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 water filtered (litre) and A, the absolute abundance of the species in cells/l.

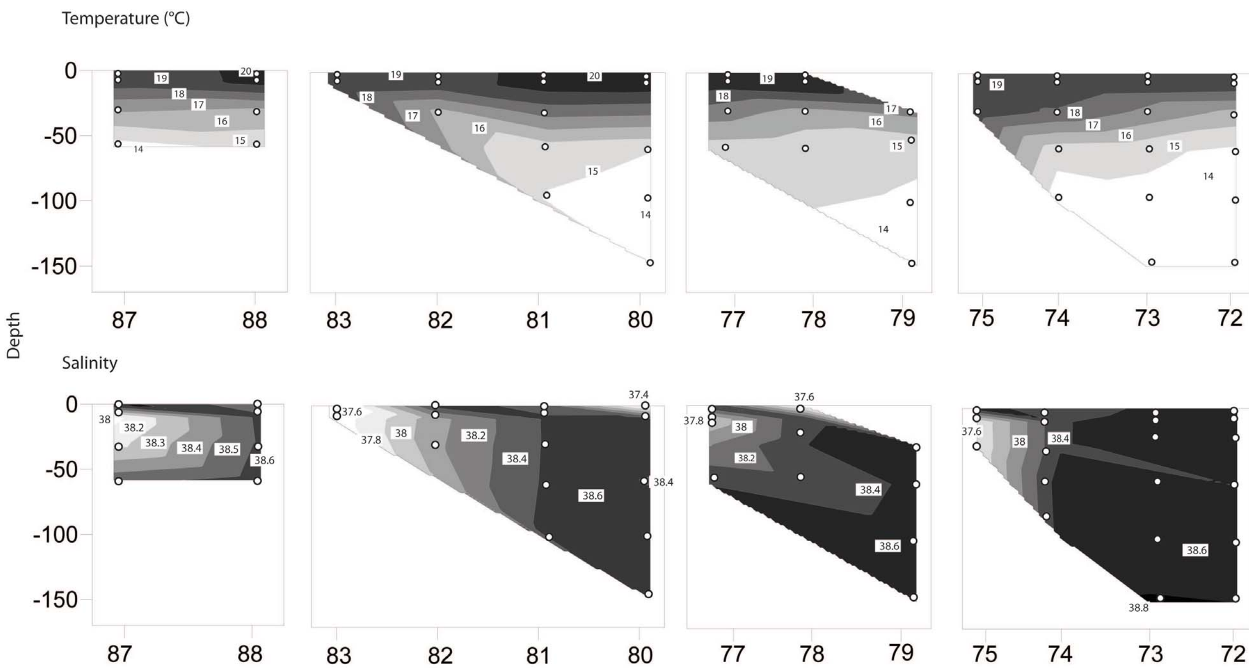


Figure 2a

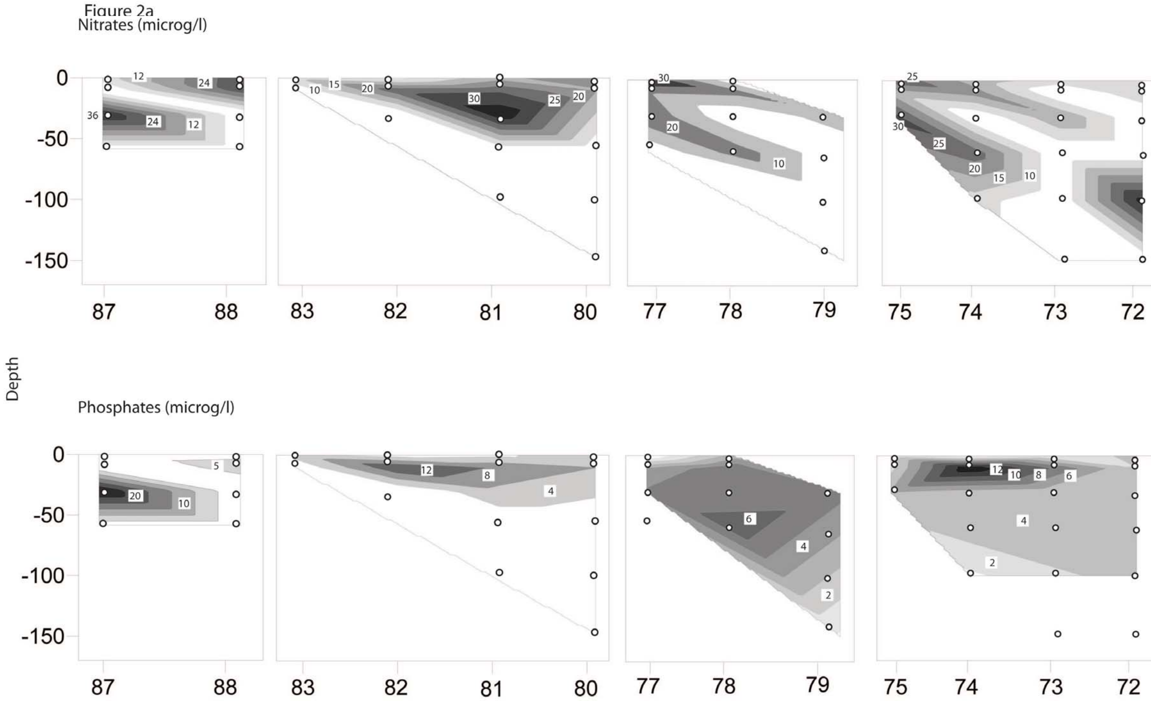
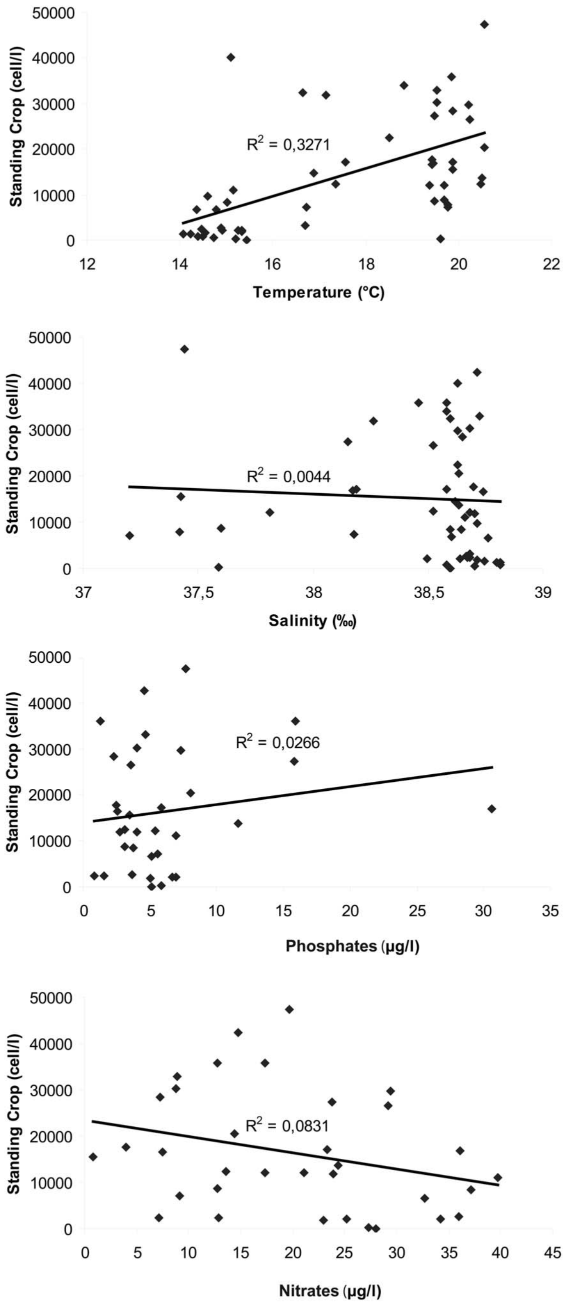
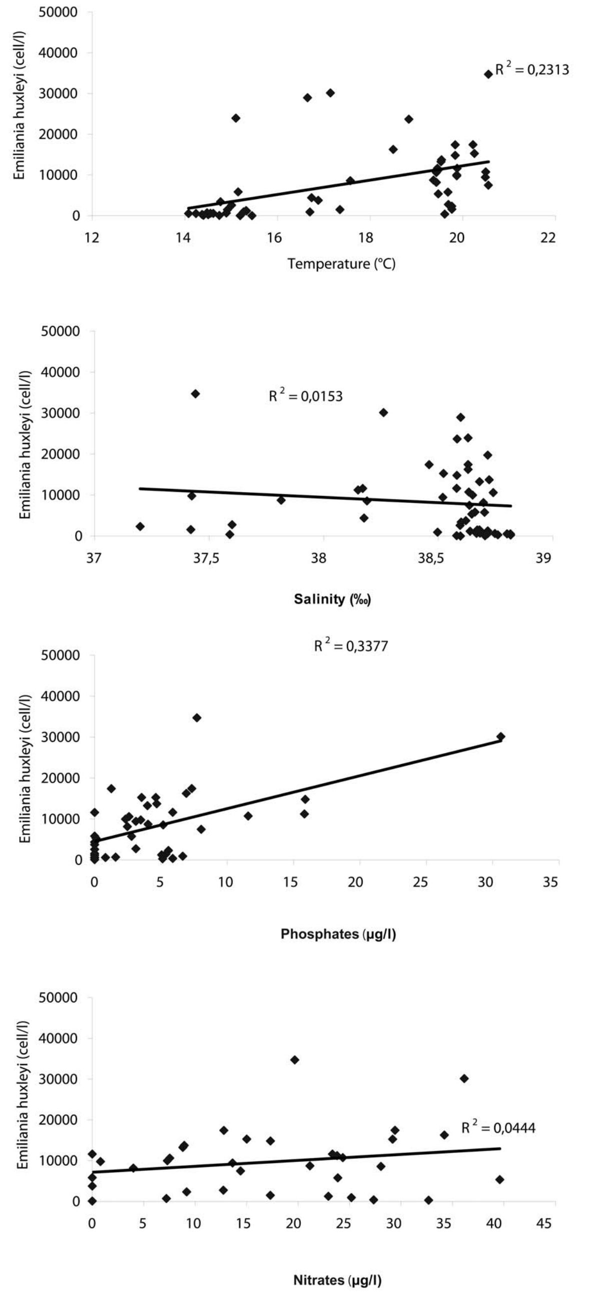


Figure 2b

TEXT-FIGURE 2a and b
Spatial distribution of temperature, salinity, and nitrate and phosphate levels in the four transects analyzed. The empty dots indicate the depth of sampling for each stations.



TEXT-FIGURE 3a
Scattered plots between the physical/chemical parameters of the waters and the standing crop (3a), absolute total abundances of *Emiliana huxleyi* (3b), *Syracosphaera* spp. (3c) and of *Florisphaera profunda* (3d).

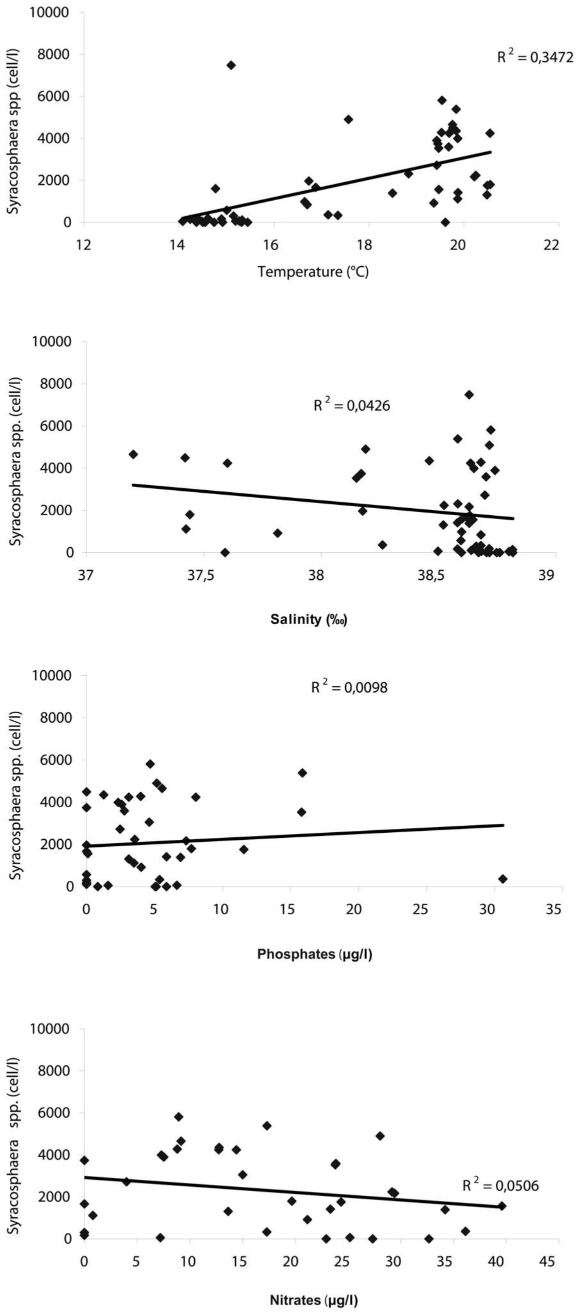


TEXT-FIGURE 3b
Scattered plots between the physical/chemical parameters of the waters and the absolute total abundance of *Emiliana huxleyi*

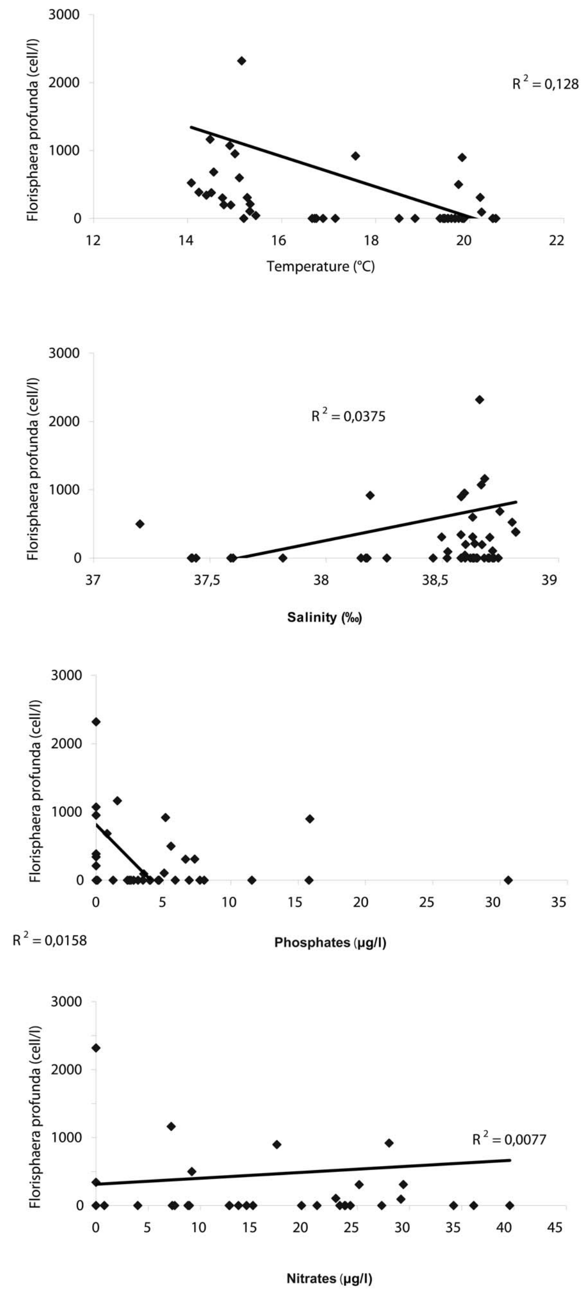
The counts performed on sediment samples were expressed in terms of numbers of specimens per gram of dry sediment as total coccolith concentration (absolute abundance), and in terms of species percentage (relative abundance).

In the water and sediment samples, the recognized coccolithophore species with low concentrations were grouped together at genus level. Taxonomy of the taxa follows Young et al. (2003), and Jordan et al. (2004). All the recognized taxa in the water samples are listed in Appendix A. The Cretaceous-Pleistocene species recognized in the sediment samples, have been grouped in the Reworked group. The total coccolithophore absolute abundances of the water and the total coccolith abundances of the sediment samples are displayed in table 1.

Scatter plots between the chemical and physical parameters of the waters and the total absolute abundances of important spe-



TEXT-FIGURE 3c
Scattered plots between the physical/chemical parameters of the waters and the absolute total abundance of *Syracosphaera* spp.



TEXT-FIGURE 3d
Scattered plots between the physical/chemical parameters of the waters and *Florisphaera profunda.*

cies in the assemblages were performed and displayed in text-figure 3a, b, c, d. These plots provide very useful information about possible relationships between the bivariate variables that otherwise could have been difficult to grasp. Furthermore, correlation coefficients were computed.

Diversity indices were calculated on the quantitative data of living communities to better interpret the spatial distribution and ecological preference of the taxa within the water column. In particular, diversity values for each sample were determined with the Shannon-Weaver Index and Dominance using PAST (PAleontology Statistic) software (Hammer et al. 2001). Thus, we were concerned with identifying the ecological preferences of both individual species and the entire assemblage. These statistical data are presented in table 2 and they were mapped using Surfer Version 8, obtaining contour maps, and represented in text-figure 4.

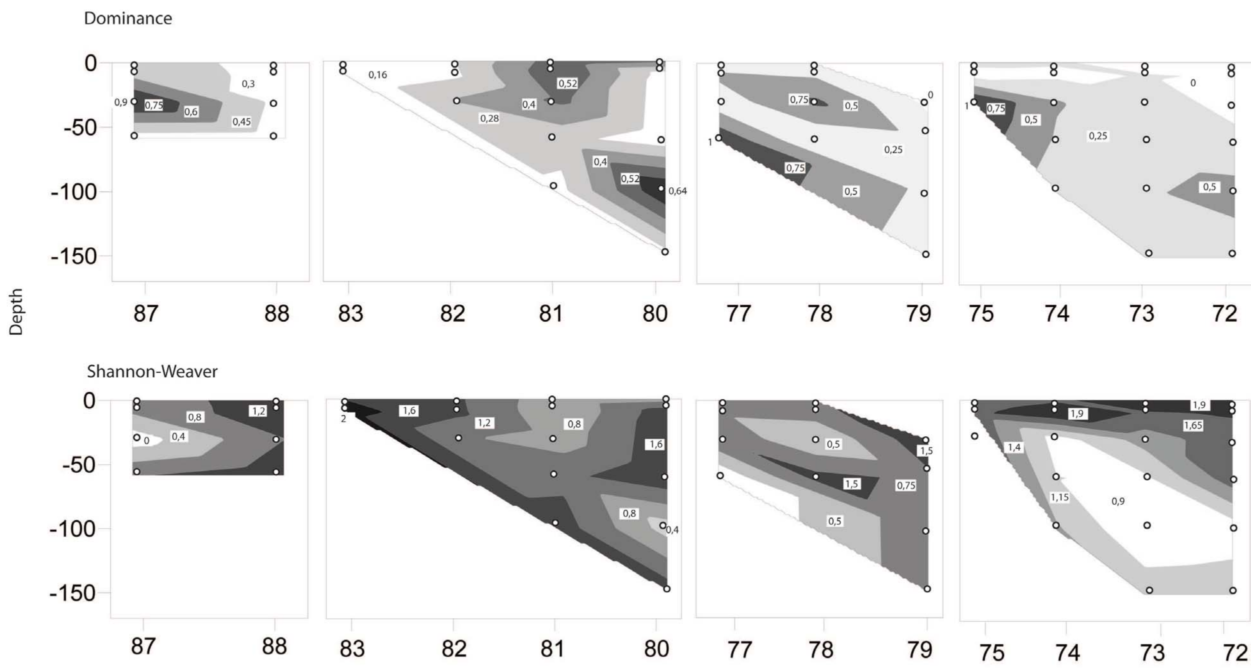


Figure 4

TEXT-FIGURE 4
Spatial distribution of Shannon-Weaver and Dominance.

RESULTS

Hydrological and nutrient data

The temperatures at all stations are variable (text-fig. 2a) with a mean value of 19°C. A decreasing trend may be clearly observed from surface to deeper waters. Salinity increases from the shore to the open sea (37.4‰ to maximum of 38,8‰) and from shallow to deeper water, with higher values (38.75-38.82 ‰) below 120m of depth (text-fig. 2a).

The whole area is characterized by the presence of a seasonal thermo and halocline limit. The thermocline is commonly located at around 25-30m (Spezie et al. 2002). In text-figure 2b the nutrient values are displayed. In general, nitrates are commonly more abundant upon reaching the major depths with an increase from the station relatively close to the shore to the open sea (medium value 20μg/l). Highest nitrate values are recorded in the subsurface water with lower salinity values observed at the more proximal stations. Phosphates show major variability near the stations relatively close to the shore and the values recovered are commonly 10μg/l.

Coccolithophore standing crop

A total of 48 species (38 HET and 10 HOL) were recovered in the analysed samples. Along the four transects, the total abundance is highest in the uppermost 30m of the water-column (table 1). Maximum values can be found either at the surface or slightly below, in the range of 3×10^4 cells/l. The concentration profiles in general show gradual decrease with depth and an increasing trend from close to the shore to the open sea stations. In text-figure 3a, are shown the scatter plots. Scatter plots of total coccolithophore cell densities and environmental parameters were used to check whether there were any dominant ecological controls. From our data coccolithophores occurred in different environmental conditions. There are slight positive correlations (R^2 between 0.2 and 0.3) between water temperature and absolute abundances. There is not, however, a clear correlation between the environmental parameters and the absolute abundances.

Coccolithophore species distribution

Coccolithophore profiles from all the stations are plotted in text-figure 5a and b. The assemblages are dominated by *Emiliania huxleyi* (~15×10^3 cells/l). Its concentration drives the observed pattern of total coccolithophore distribution throughout the water column in all the investigated area. Other important taxa are *Syracosphaera* spp. (reaching ~7×10^3 cells/l, in the station 79) and *Umbellosphaera tenuis* (reaching ~7×10^3 cells/l, in the station 88). *Umbellosphaera tenuis* seems to be more abundant at 30m and 60m of depth in all the four transects in the more open sea stations. *Rhabdosphaera* spp. is presents especially in the upper part of the photic zone (mean value ~ 3×10^3 cells/l) *Florisphaera profunda,* a deep dwelling species, reaches higher cell densities (from 1×10^3 to 8×10^3 cells/l) in the more open sea stations between 100 and 150m of water depth where it may be dominant over the rest of the assemblage. Surface waters show a higher species richness in the southern transect. We provided scatter plots between the ecological parameters and *Emiliania huxleyi*, *Syracosphaera* spp. and *Florisphaera profunda* (text-fig. 3b, c, d) since they were the major part of the assemblages. There are slight positive correlations (R^2 ~ 0.2) between water temperature and absolute abundances of all these species and groups. It should also be noted that there is a slight correlation between phosphates and *Emiliania huxleyi* (R^2~ 0.3). The Shannon-Weaver index usually decreases with depth, as well as the species richness (table 2, text-fig. 4). Exception to the general trend are the stations 83, 81 and 80. The Shannon-Weaver index shows abrupt variations which have an opposite pattern with respect to the Dominance values.

Coccolith assemblages in the surface sediments

The absolute coccolith species concentrations are displayed in text-figure 6a. The relative abundance within the different species and group data, have been plotted without the reworked part of assemblage in text-figure 6b. The coccoliths recorded in the surface sediments are well preserved. Concentrations greater than $7x10^8$ coccoliths/g occur in the sediment recovered at the more deep and open sea stations 88 (-450m) and 80 (-700m). The lower abundances were found in station 81 with a value of ~$7x10^7$ coccoliths/g of sediment (text-fig. 6a; table 1). The large component of the coccolith sediment assemblages belonging to the Reworked Group, are represented by taxa belonging to the Cretaceous-Pleistocene interval.

While standing crop and taxonomic composition of the coccolithophore communities appeared to be well diversified, the nannoflora preserved in the studied surface sediments presents a different pattern with less diversification in the assemblages (text-fig. 6b). *Emiliania huxleyi* is the most abundant species in the stations approaching the open sea (Stations 80, 88). *Syracosphaera* spp. and *Helicosphaera* spp. are recorded in all the sediment samples. *Helicosphaera* spp. have an high mean abundance (~ 55%). *Calcidiscus leptoporus* is present with a mean value of ~15%. Both these last two species are rarely found in the living assemblages. *Rhabdosphaera* spp. are present just in the northern stations of the transects. Holococcolithophores have only been found in station 88, with very low abundance.

DISCUSSION

Spatial and vertical distribution of the coccolithophore communities

The standing crop abundances and the number of recognized species are in agreement with previous studies carried out in the Mediterranean Sea, as well as in the Otranto Strait and in the Ionian Sea (Kleijne 1991; Knappertbusch 1993; Malinverno et al. 2003). In general the mean maximum value observed in this area, is ~$1x10^4$ cell/l during the same season as our samples (Kleijne 1991; Knappertbusch 1993; Malinverno et al. 2003).

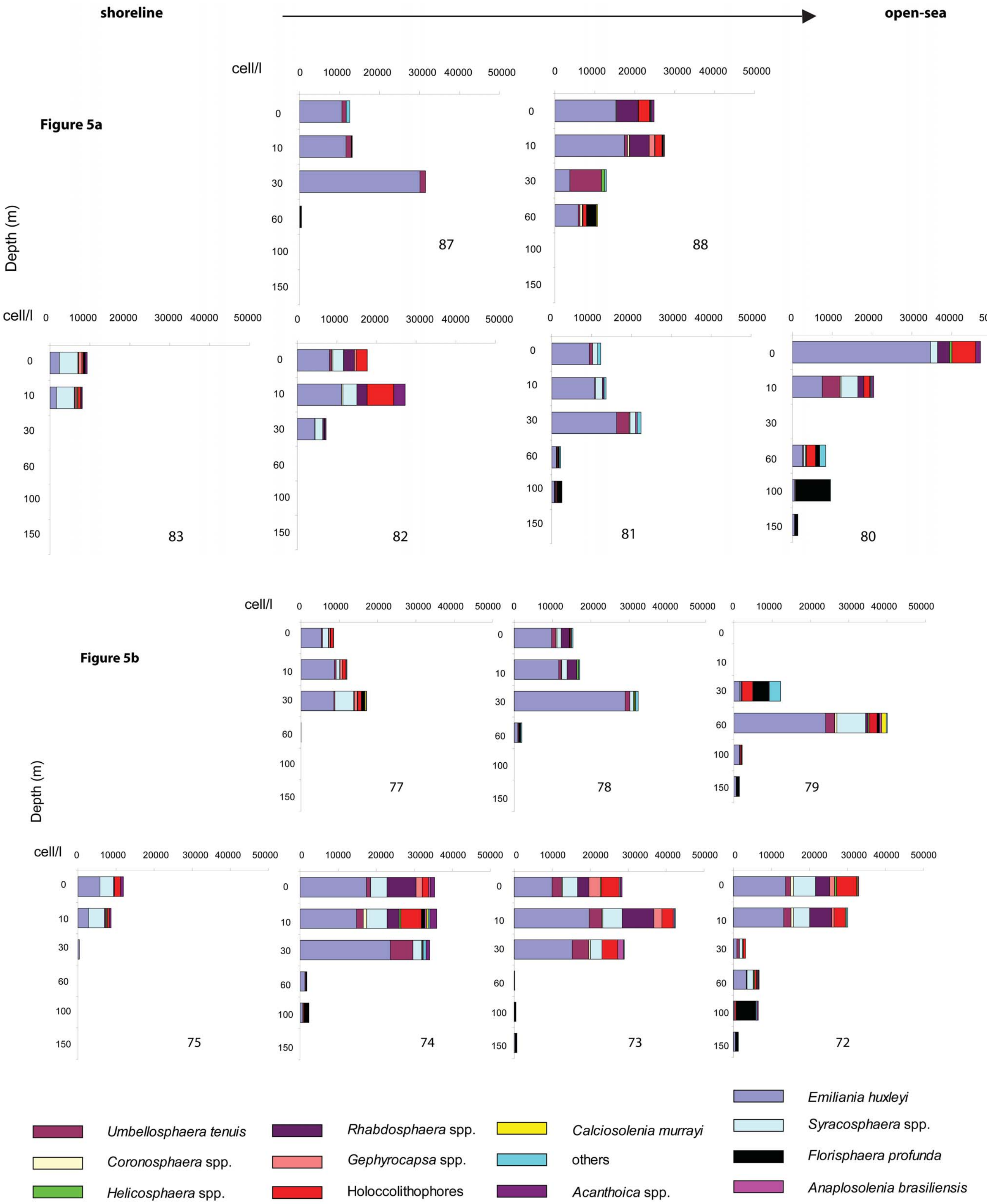
A general increase both in number of total coccolithophore cells as well as in richness of the assemblages is recognizable from close to the shore to the open sea, and from the northern to the southern transect. *Emiliania huxleyi*, already well known for its cosmopolitan characteristics, is always present and abundant especially in the upper 30m of the water column. It is possible to identify two main layers in the photic zone (text-fig. 5a and b) characterized by different species composition assemblages, an upper photic-zone assemblage (UPZ) and a lower photic-zone (LPZ) with respect the depth of 30m.

The UPZ assemblage in addition to high numbers of *Emiliania huxleyi*, is characterized by the greatest species diversity and by a large number of species belonging to the genera *Rhabdosphaera*, *Syracosphaera*, and *Coronosphaera* (text-fig. 5a and b). Also *Umbellosphaera tenuis* and holococcolithophores have been found in the UPZ. *Umbellosphaera tenuis*, known to live both in the upper (McIntyre and Bé 1967; Winter et al. 1994; Haidar and Thierstein 2001) and middle photic zone (Winter et al. 1994), is only a surface species in the study area. This species was also recovered as upper photic zone species in the southeast subtropical Indian Ocean (Takahashi and Okada 2000), in the Caribbean Sea (Jordan and Winter 2000), and in the Ionian Sea (Malinverno et al. 2003). Holococcolithophores characterizes the very upper part of the water column in agreement with previous results from Mediterranean area (Malinverno et al. 2003). However, the species diversity for this group in the Gulf of Manfredonia is not as high as documented by previous findings in the Mediterranean Sea. Triantaphyllou et al. (2002) in the coastal waters of Andros Island (South Greece) and Kleijne (1993) in the eastern part of the Mediterranean, found higher species diversity in the holococcolithophore assemblages sampled during the summer season. The lower holococcolithophore diversity recovered in the Gulf of Manfredonia may be linked to the different timing of the sampling. The high abundances of *Syracosphaera* spp. and *Rhabdosphaera* spp. recorded in the upper photic zone of the investigated area are in agreement with several previous studies (Honjo and Okada 1974; Winter et al. 1994; Takahashi and Okada 2000; Weaver and Pujol 1988; Flores et al. 1997; Colmenero-Hidalgo et al. 2002; Andruleit et al. 2003; Saugestad and Heimidal 2002; Malinverno et al. 2003). Both *Syracosphaera* spp. (especially *Syracosphaera pulchra*) (Boeckel and Baumann 2008) and *Rhabdosphaera* (especially, *Rhabdosphaera clavigera*) (Haidar and Thiersten 2001) are considered warm and oligotrophic taxa. Warmer and stratified oligotrophic waters are preferred by *Umbellosphaera tenuis* (Okada and McIntyre 1973; Kleijne et al. 1989; Hagino and Okada 2006). Ecological preferences of *Coronosphaera* spp. are not well documented in the literature. It, inhabits the UPZ in the Manfredonia area, showing ecological preference for surface waters.

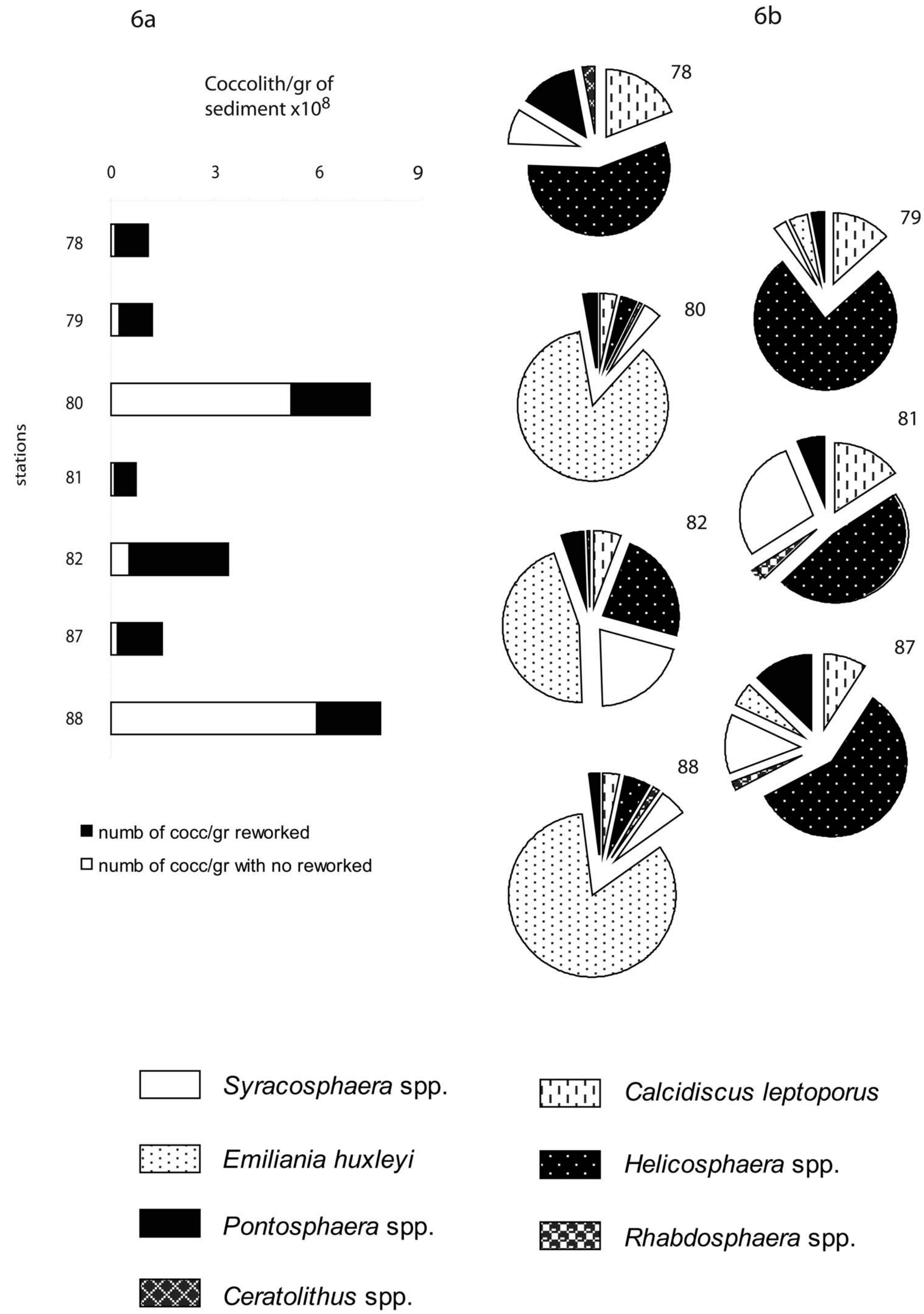
We did not recognize a peculiar assemblage characterizing the middle photic zone as found in previous studies (Malinverno et al. 2003), probably because it is well developed in summer, when the surface stratification is usually better pronounced (Malinverno et al. 2003). In the LPZ assemblages the most important species is *Florisphaera profunda*. The higher abundance of *Florisphaera profunda* does not reveal any significant relation to the nitrates and phosphate patterns (text-figure 3d). We can not exclude the fact that in the Gulf of Manfredonia turbidity and lower light intensity may represent additional control factors on the distribution of this species, as observed by Ahagon et al. (1993), in the north-western margin of the Pacific Ocean.

Calcidiscus leptoporus s.l. (including here *C. leptoporus* and *C. quadriperforatus*) and *Helicosphaera* spp were rarely found in the living assemblages (fig.5a and b). The low presence in the living assemblages could mean a different bloom timing of these species with respect to the sampling period. Also, the gephyrocapsid group and in particular *Gephyrocapsa oceanica*, are present with very low concentrations in few stations. This result is consistent with previous results from adjacent areas (Knappertsbusch 1993; Malinverno et al. 2003). In contrast gephyrocapsids have been recovered especially in the western part of the Mediterranean basin, which is probably linked to the lower surface salinity Atlantic water that characterizes that area (Knappertsbusch, 1993; Malinverno et al. 2003).

The coccolithophore assemblages in the Gulf of Manfredonia show that the vertical species distribution is mostly related to the position of the thermocline but can fluctuate slightly as a function of the main physical parameters that characterize the photic zone. This is in agreement with the results by Knapperts-



TEXT-FIGURE 5a and b
Comparison of the different composition of the coccolithophore distribution along the column water in each transects, during the sampling. Note that the distance within the stations is in proportion to the real location of the stations.



TEXT-FIGURE 6a
Total coccolith abundance (coccoliths/gram of sediment) recovered in each stations analyzed.

TEXT-FIGURE 6b
Relative percentage of the different coccolith specimen or genus recognized in the surface sediments.

busch (1993) who suggested that regional patchiness and temporal variability dominate the distribution of coccolithophores.

Text-figure 3 shows that there is a slight correlation between the temperature and total coccolithophore abundances, while the relationship between abundance and salinity, as well as nitrates and phosphates are uncorrelated. The low correlation with the nutrients could be explained because the sampling is based just in a single season, and thus influenced by particular local effects. For example it could be the geographic localization of the stations and the presence of seasonal cyclonic or anticyclonic gyres in the Gulf, which are mainly linked to N-NW and S-SE winds (Simeoni 1992). However, the most relevant indications derived by diversity indices pattern are coherent with the recognition of an UPZ assemblage and LPZ one. The higher values of Shannon-Weaver index (table 2; text-fig. 4) at shallower depths are in agreement with the composition of the assemblage in UPZ, where k-selection taxa (*Syracosphaera*, *Rhabdosphaera*, *U. tenuis*, holococcolithophore group), which prefer more stable condition (Dodd and Stanton 1981; Hallock 1987; Brand 1994; Young 1994; Bown et al. 2004), benefit from relatively warmer, oligotrophic and stratified waters. The Dominance index shows an expected opposite pattern (table 2; text-fig. 4). Specifically, the Dominance has higher values when *Emiliania huxleyi* are more abundant thus supporting the known r-selection life strategy of these taxa.

Comparison of the plankton community with the sediment assemblage

The assemblages recovered in the surface sediments do not have an obvious correlation with the abundance of the living species recorded in the water samples. The direct comparison of the living assemblage with surface sediment records (fig.6a and b) shows differences in the presence and abundance of some taxa. The main difference is a larger number of species in the water samples, also with the presence of delicate species along the water column that are not preserved in the sediments. The results agree with previous studies that compared the living assemblages with the surface sediments in the Mediterranean Sea (Knappertsbusch 1993; Malinverno et al. 2003), and revealed that the assemblage preserved in the sediment are quite difficult to compare with the living assemblages.

The presence in surface sediments of species that are rarely found in the water samples, such as *Helicosphaera carteri* and *Calcidiscus leptoporus* s.l., is remarkable. The same results were also found in several studies in the North Atlantic (Baumann et al. 1999, 2000; Sprengel et al. 2000; Balestra et al. 2004). The presence/absence of these species has been explained as different bloom timing with respect to the period of water sampling, or because of advective transport from other zones into the study area. Another explanation could be the different life stages of these two species. In our case, it may be that the hetero-phase stage had a different timing with respect to that of the water sampling. Nevertheless, in the living assemblages the holococcolithophore-stage of *Calcidiscus leptoporus*, and of *Helicosphaera carteri* were found. The holococcolithophore phases are least resistant to dissolution, thus it is extremely difficult to recover them in the sediments. In contrast, since *Helicosphaera carteri* and *Calcidiscus leptoporus* are considered dissolution-resistant species (Knappertbusch 1993; Baumann et al. 2000; Boeckel and Baumann 2008) in the fossil record, their relative abundance in the sediment may represent a passive enrichment in the assemblages, also possibly affected by reworking phenomena (Findlay 1998). Similar suggestions are inferred in the Balearic Sea where higher abundances of *Helicosphaera* spp. and *C. leptoporus* are recorded in the sediment sample with higher terrigenous component due to the influence of Ebro River runoff (Cros 1995). Loubere et al. (2004) also consider the species to be a “heavy” taxon. In the Gulf of Manfredonia, the sediment recovered from the two open and deeper sea stations 88 and 80, shows assemblages characterized by the major presence of the species found in the overlying living community. The abundant presence of species found in the living community in these two stations suggests a lower intensity of bottom dynamic processes and thus a minor influence of reworked coccoliths at these sites. Reworked species are a major component of the surface sediments, and are more abundant in the stations closest to the shore (text-fig. 6a), in relation to the larger influence of terrigenous input from terrestrial source (Spagnoli et al. 2005).

SUMMARY

The distribution of the living and fossil coccolithophore species in the Gulf of Manfredonia during the late fall reveals quite different assemblages in relationship to the various depths, and provide the following results.

1) A total of 48 species were recovered in the analyzed samples. Maximum total numbers of up to of $3x10^4$ cells/l are found in the uppermost 30m of the water column. The recovered living assemblage is mainly characterized by the presence of *Emiliania huxleyi*, *Syracosphaera* spp. and *Umbellosphaera tenuis*. In the deeper samples the presence of *Florisphaera profunda* increases.

2) There is no clear correlation between the environmental parameters and absolute abundance, except than with the temperature.

3) Different composition of coccolithophore communities were recognized in the UPZ and the LPZ in relation to the thermocline depth, which was situated at ~25-30m. *Rhabdosphaera* spp., *Coronosphaera* spp., *Umbellosphaera tenuis* and *Syracosphaera* spp., as well as holococcolithophores, are related to the upper part of the water column that is characterized by warmer, oligotrophic and stratified conditions. In the deeper water samples, below the thermocline, *F. profunda* dominates the communities. *F. profunda* peaks when nutrient content is moderate,

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PLATE 1
Light microscopy.

1 *Rhabdosphaera clavigera,* St. 79, 30m, XP

2 *Syracolithus dalmaticus,* St. 79, 30m, XP

3-4 *Umbilicosphaera foliosa,* St. 81, 10m, 3 XP, 4 PL

5 *Umbellosphaera tenuis,* St. 87, 0m, XP

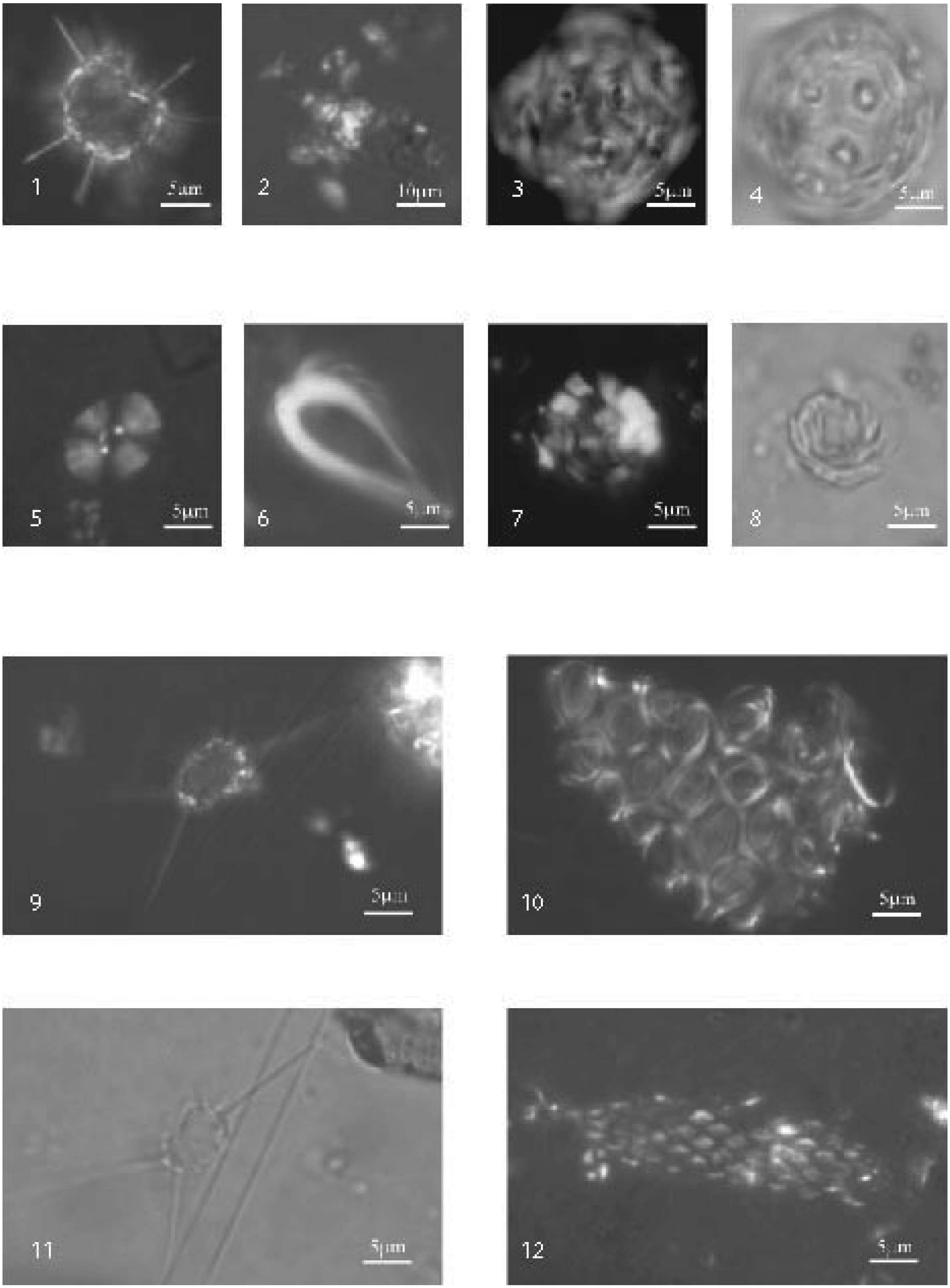
6 *Ceratolithus cristatus,* St. 79, 60m, XP

7-8 *Florisphaera profunda,* St. 79, 30m, 7 XP; 8 PL

9,11 *Acanthoica quattrospina,*St. 79, 60m, 9 XP, 11 PL

10 *Syracosphaera pulchra,* St. 87, 0m, XP

12 *Calciosolenia murrayi,* St. 80, 60m, XP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suggesting a possible positive relationship with other water parameters including high turbidity and low light intensity.

4) The Shannon-Weaver index and the Dominance have opposite patterns. In general, the Dominance has higher values when *E. huxleyi* is more abundant, thus supporting the known r-selection life strategy of these taxa.

5) The fossil record in the surface sediments is mainly represented by Cretaceous-Pleistocene reworked species. There is not a clear correlation between the living communities and the autochthonous sediment assemblages. This is especially the case in samples closer to the coast where re-suspension at the bottom of sea floor and reworking phenomena can be more intense. In the sediment located far from the coast for instance at the two station 80 and 88, the more consistent correspondence between living and fossil assemblages suggests that inorganic input and reworked species are less important in these open sea conditions.

6) *Helicosphaera carteri*, *Calcidiscus leptoporus* and *Emiliania huxleyi*, are the most abundant coccoliths in the sediment. *Helicosphaera carteri*, and *Calcidiscus leptoporus* are quite rare in the living community, and thus they can be considered dissolution-resistant and heavier taxa, able to enrich the sediment in a passive way. Another explanation could be related to the different timing of the life stages of these two species.

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PLATE 2

Light microscopy.

1 *Calciosolenia brasiliensis,* St. 79, 60m, XP

2 *Calcidiscus leptoporus,* (HET and HOL), St. 87, 0m, XP

3-4 *Syracosphaera* sp., St. 87, 0m, 3 XP, 4 PL

5 *Rhabdosphaera clavigera,* St. 78, 60m, XP

6 *Scyphosphaera apsteini*, St. 78, 0m, XP

7 *Coronosphaera binodata,* St. 78, 30m, XP

8 *Alisphaera* sp., St. 79, 60m, XP

9 *Syracosphaera pulchra*, HOL (*Calyptrosphaera oblonga*), St. 79, 60m, XP

10 *Scyphosphaera apsteini,* St. 79, 60m, XP

11 *Umbellosphaera tenuis*, St. 81, 0m, XP

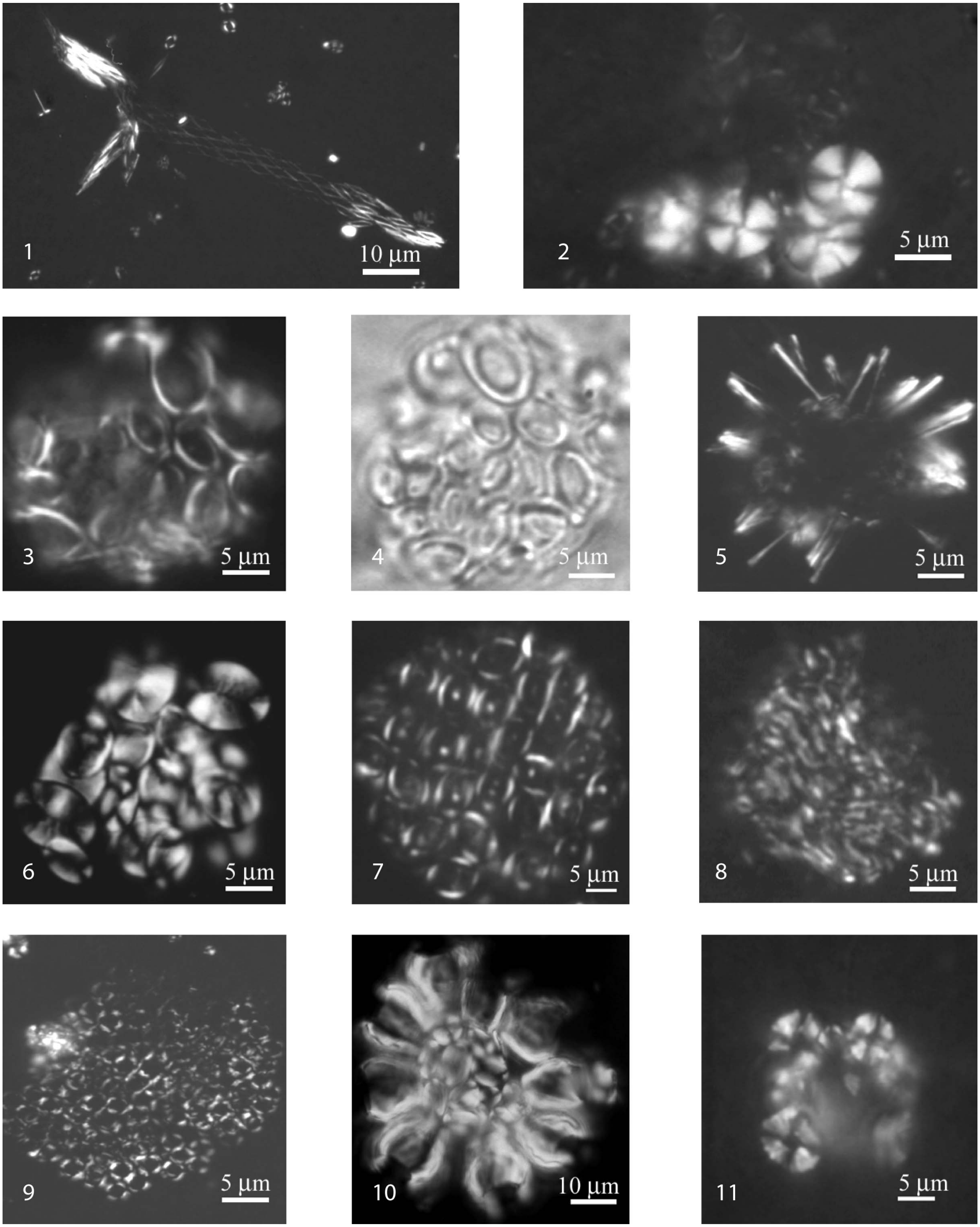
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PLATE 3

Scanning electron microscopy.

1 *Helicosphaera wallichii,* St. 81, 60m

2 *Pontosphaera syracusana*, St. 81, 60m

3 *Florisphaera profunda,* St. 80, 60m

4 *Algirosphaera robusta,* St. 80, 60m

5 *Gladiolithus flabellatus,* St. 80, 60m

6 *Emiliania huxleyi,* St. 79, 60m

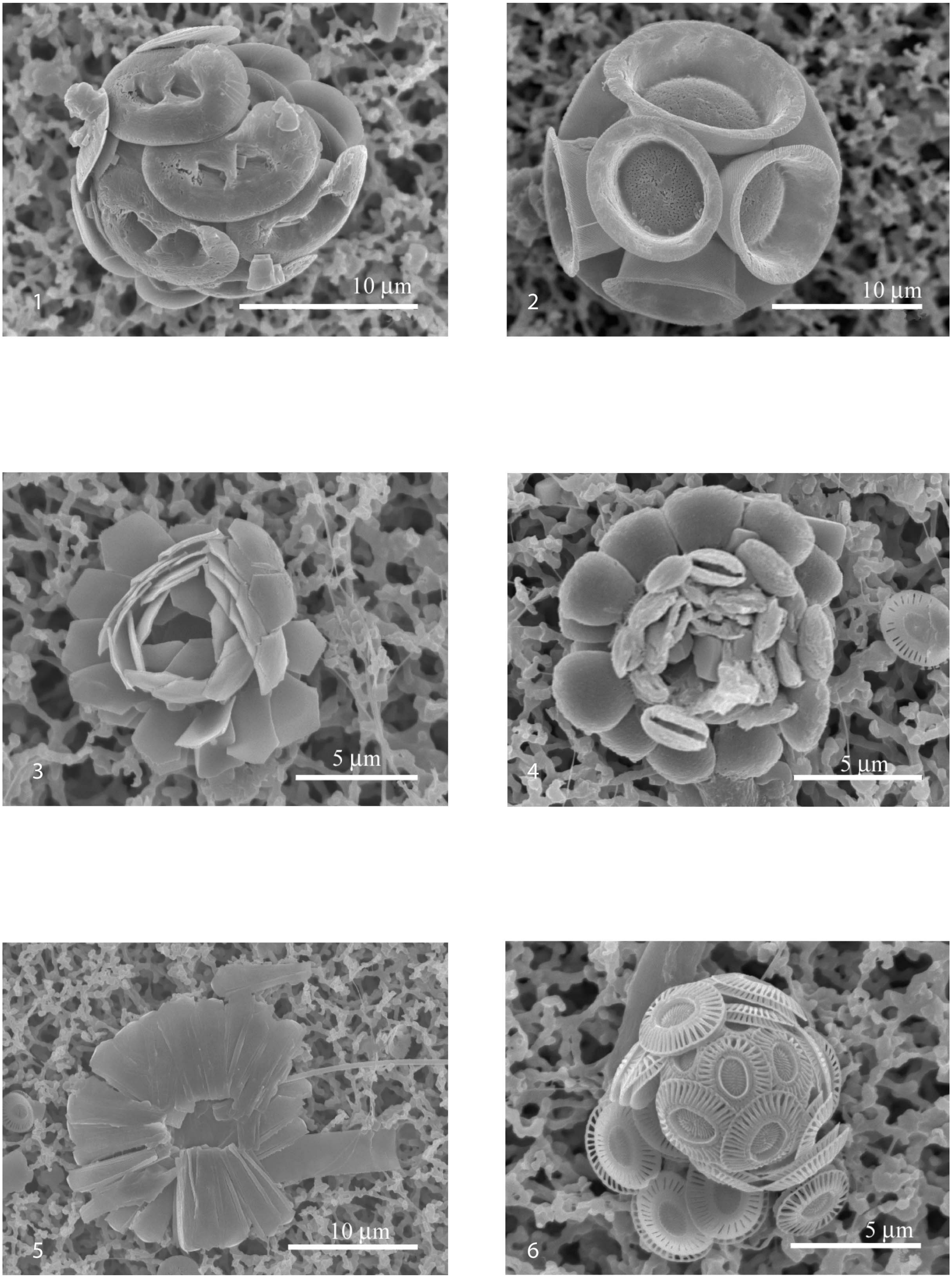
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PLATE 4

Scanning electron microscopy.

1 *Syracosphaera histrica,* St. 78, 0m

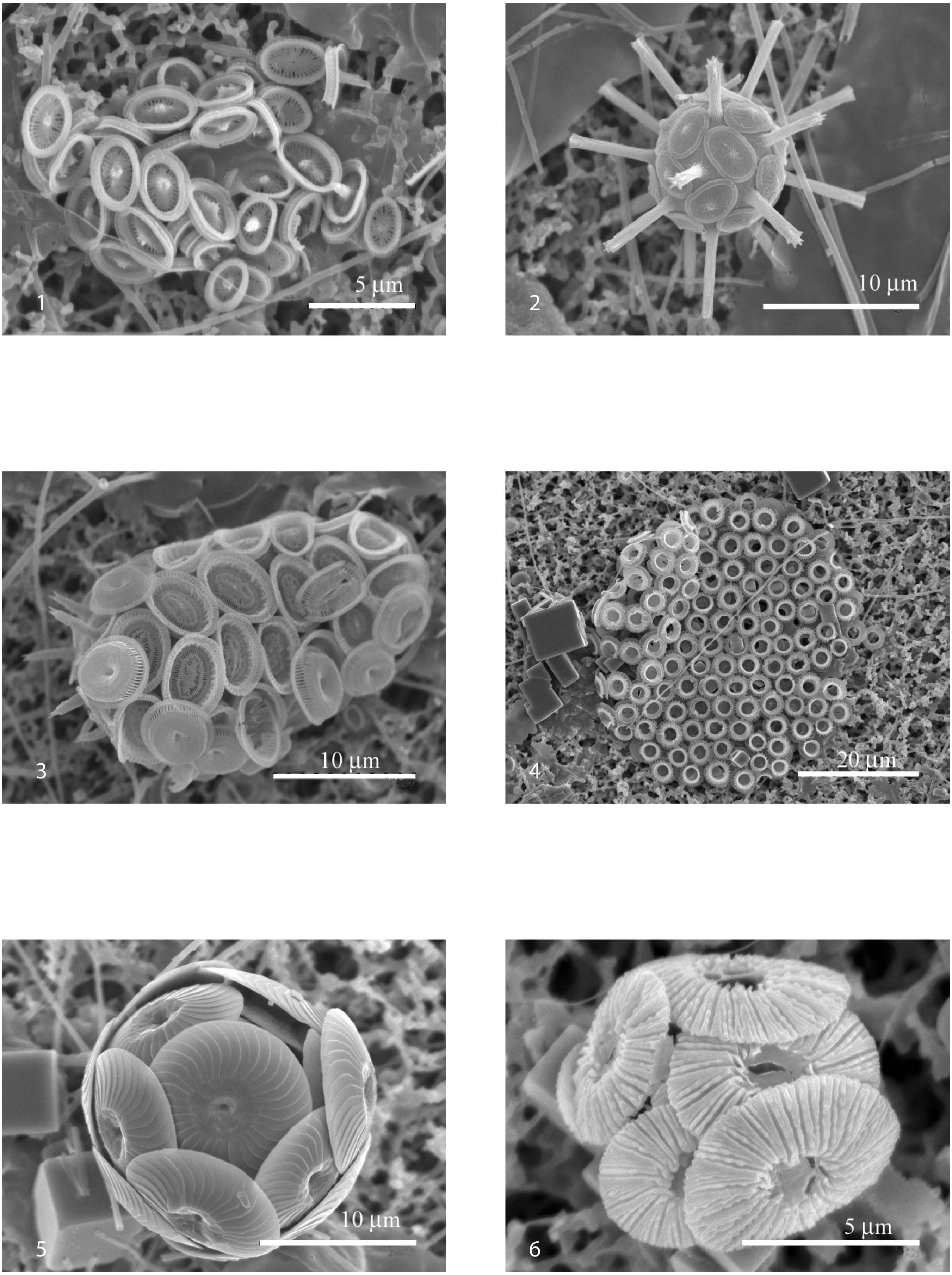
2 *Rhabdosphaera clavigera,* St. 78, 0m

3 *Syracosphaera pulchra*, St. 78, 0m

4 *Umbilicosphaera sibogae,* St. 78, 10m

5 *Calcidiscus quadriperforatus,* St. 78, 10m

6 *Umbellosphaera tenuis,* St. 81, 10m


5 µm
1
10 µm
2
10 µm
3
20 µm
4
10 µm
5
5 µm
6

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Manuscript received
Manuscript accepted

APPENDIX 1: Taxonomic List
Following Young et al. (2003); Jordan et al. (2004)

Acanthoica acanthifera Lohmann 1912 ex Lohmann 1913a
Acanthoica quattrospina Lohmann 1903
Algirosphaera robusta (Lohmann 1902) Norris 1984
Alisphaera unicornis Okada and McIntyre 1977
Calcidiscus leptoporus (Murray and Blackman 1898) Loeblich and Tappan 1978
Calcidiscus leptoporus HOL (*Crystallolithus rigidus* Gardeer 1980 in Heimdal and Gardeer 1980)
Calcidiscus quadriperforatus (Kamptner1937) Quinn and Geisen in Sàez et al. 2003
Calcidiscus quadriperforatus HOL (*Syracolithus quadriperforatus* (Kamptner 1937) Gardeer 1962)
Calciosolenia brasiliensis (Lohmann 1919) Young in Young et al. 2003
Calciosolenia murrayi Gran 1912
Ceratolithus cristatus Kamptner 1950
Coronosphaera binodata (Kamptner 1927) Gaarder in Gaarder and Heimdal 1977
Coronosphaera mediterranea (Lohmann, 1902) Gaarder in Gaarder and Heimdal 1977
Discosphaera tubifera (Murray and Blackman 1898) Ostenfeld 1900
Emiliania huxleyi (Lohmann 1902) Hay and Mohler in Hay et al.1967 var. *huxleyi*
Florisphaera profunda Okada and Honjo 1973 var. *profunda*
Gephyrocapsa oceanica Kamptner 1943
Gladiolithus flabellatus (Halldal and Markali 1955) Jordan and Chamberlain 1993b
Helicosphaera carteri (Wallich 1877) Kamptner 1954
Helicosphaera carteri HOL (*Syracolithus catilliferus* (Kamptner 1941) Borsetti and Cati 1972)
Helicosphaera carteri HOL (*Syracolithus confusus* Kleijne 1991)
Helicosphaera hyalina Gaarder 1970
Helicosphaera pavimentum Okada and McIntyre 1977
Helicosphaera wallichii (Lohmann 1902) Okada and McIntyre 1977
Holococcolithophora dentata (Kleijne 1991) Jordan et al., comb. nov.
Homozygosphaera arethusae (Kamptner 1941) Kleijne 1991
Michaelsaria elegans Gran 1912; emend. Manton et al. 1984
Ophiaster hydroideus (Lohmann 1903) Lohmann 1913b; emend. Manton and Oates 1983b
Oolithotus fragilis (Lohmann 1912) Martini and Müller 1972
Pontosphaera syracusana Lohmann 1902
Rhabdosphaera clavigera Murray and Blackman 1898
Rhabdosphaera xiphos (Deflandre and Fert 1954) Norris 1984
Reticulofenestra sessilis (Lohmann 1912) Jordan and Young 1990
Scyphosphaera apsteini Lohmann 1902
Sphaerocalyptra quadridentata (Schiller 1913) Deflandre 1952
Syracolithus dalmaticus (Kamptner 1927) Loeblich Jr. and Tappan 1966
Syracosphaera anthos (Lohmann 1912) Janin 1987
Syracosphaera anthos HOL (*Periphyllophora mirabilis* (Schiller, 1925) Kamptner 1937)
Syracosphaera bannockii (Borsetti and Cati 1976) Cros et al. 2000
Syracosphaera halldalii Gaarder in Gaarder and Hasle 1971 ex Jordan and Green 1994
Syracosphaera histrica Kamptner 1941
Syracosphaera molischii Schiller 1925
Syracosphaera prolongata Gran 1912 ex Lohmann 1913b
Syracosphaera pulchra Lohmann 1902
Syracosphaera pulchra HOL (*Calyptrosphaera oblonga* Lohmann 1902)
Umbellosphaera tenuis (Kamptner 1937) Paasche in Markali and Paasche 1955
Umbilicosphaera foliosa (Kamptner 1963 ex Kleijne 1993) Geisen in Sàez et al. 2003b
Umbilicosphaera sibogae (Weber-van Bosse 1901) Gaarder 1970