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Coccolithophorid distribution in the Ionian Sea and its relationship to eastern Mediterranean circulation during late fall to early winter 1997

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[1] The distribution of coccolithophorid assemblages is analyzed from water samples collected in the photic zone of the middle Ionian Sea during a cruise of R/V *Urania* in November–December 1997. Coccolithophorids are an important phytoplankton group in the oligotrophic eastern Mediterranean, and their coccoliths make an important contribution to the sediments of this area, being also widely used for paleoclimatic and paleoceanographic reconstructions. Nevertheless, studies on extant coccolithophorids ecology and distribution in the eastern Mediterranean are limited and mostly related to surface waters: this study, even if restricted to a single period of the year, provides the first detailed analysis of species distribution throughout the photic zone, with relation to the main local physicochemical parameters. During the investigated period, the area is characterized by the presence of a surface mixed layer, reaching a depth of 25 to 90 m. Below this layer, a marked thermo- and halocline is developed. Coccolithophorids are the dominant phytoplankton group in the investigated samples and reach concentrations up to 2×10^4 coccospheres per liter of seawater. The species assemblage is that typical of the subtropical latitude, with a general high species diversity and a well-defined depth distribution. It is in fact possible to recognize an upper photic zone assemblage, dominated by *E. huxleyi* and characterized by higher concentration and species diversity and a lower photic zone where typically deep-living species (i.e., *F. profunda*, *G. flabellatus*) are present. These two zones are separated by a transition layer, where species of both zones are represented and new ones appear. Such vertical distribution appears to be strictly related to the local hydrology, with the zone boundaries rising and falling as a function of the location of the isotherms. In particular the first significant occurrence of *F. profunda* from surface to the deep photic zone corresponds with the start of the thermocline. Comparison of present plankton data with the surface sediment record, although displaying a consistent pattern of species assemblage, shows some differences in the presence and relative abundance of some species (*G. oceanica*): this can be related to seasonal as well as interannual variations in the pattern and intensity of surface circulation in the investigated area. **INDEX TERMS:** 4855 Oceanography: Biological and Chemical: Plankton; 4815 Oceanography: Biological and Chemical: Ecosystems, structure and dynamics; **KEYWORDS:** eastern Mediterranean Sea, coccolithophorids, ecology, phytoplankton

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1. Introduction

1.1. Coccolithophorids

[2] Coccolithophorids are pelagic unicellular golden-brown algae that are widely distributed in the world oceans.

The different assemblages of their species reflect the distribution of major water masses [e.g., *McIntyre and Bé*, 1967; *Okada and Honjo*, 1973] and, even if some of them reach high abundance in particular eutrophic conditions at high latitudes, they usually also dominate the phytoplankton standing stock in the oligotrophic central gyres of the oceans. Their assemblage composition in the world oceans reflects the horizontal pattern of water masses and can be

Table 1. Location of the Sampling Stations, Sampling Time, and Weather Conditions During Sampling

Station	Area	Latitude, N	Longitude, E	Bottom Depth, m	Date	Time	Meteo Conditions
SIN97-N02	Ionian Abyssal Plain	35° 47.85'	17° 30.04'	4044	20/11/97	23.00	6
SIN97-N03	Ionian Abyssal Plain	35° 47.89'	19° 42.00'	3169	21/11/97	13.00	5
SIN97-N04	Mediterranean Ridge	35° 16.96'	21° 24.92'	3354	22/11/97	1.30	4
SIN97-N05	Mediterranean Ridge	35° 41.04'	22° 31.52'	4574	25/11/97	23.40	7
SIN97-N08	Mediterranean Ridge	34° 52.38'	21° 07.30'	2537	30/11/97	3.10	7/8
SIN97-N09	Ionian Abyssal Plain	34° 14.76'	19° 11.28'	3896	30/11/97	18.50	7/8
SIN97-N10	Mediterranean Ridge	35° 44.70'	20° 31.78'	3122	05/12/97	11.00	3/4
SIN97-N11	Ionian Abyssal Plain	35° 46.88'	18° 26.21'	4056	08/12/97	13.00	6/7
SIN97-N12	Ionian Abyssal Plain	35° 37.43'	17° 14.00'	4126	09/12/97	22.35	2/3

used to define the ecological characteristic and the latitudinal boundaries of an investigated area.

[3] Coccolithophorids are a major phytoplankton group in the oligotrophic eastern Mediterranean Sea; they dominate over diatoms during most of the year, being particularly successful in low nutrient levels. Furthermore, they contribute significantly to the carbonate export production in this area; in fact their calcareous skeletal remains, the coccoliths, dominate the carbonate flux throughout the year and can constitute a significant part of the bottom sediments of this basin.

1.2. Description of the Area

[4] The eastern Mediterranean is a semienclosed basin, whose only contact with the Atlantic Ocean is through the western Mediterranean via the Sicily Strait and the Gibraltar Strait. In the last decade the eastern Mediterranean has experienced severe modifications in its circulation pattern, involving surface, intermediate and deep water masses [e.g., Roether et al., 1996; Lascaratos et al., 1999; Klein et al., 1999; Malanotte-Rizzoli et al., 1999]. The Ionian basin displayed some changes in the surface circulation, in particular with slight shifting and intensification of the Atlantic-Ionian Stream and the Mid-Ionian Jet [Malanotte-Rizzoli et al., 1999]. Moreover, the strong modifications in the deep layers caused an uplifting of the previous middepth water masses and a rising of the nutricline, which, at some places in the Ionian Sea, reached depths of 100–150 m, possibly penetrating the euphotic layer [Klein et al., 1999]. A strong influence on primary productivity levels is thus a potential effect in areas where such water mass shifting was more pronounced.

[5] This paper presents data on coccolithophorid distribution in the photic zone of the central Ionian Sea during late fall-early winter 1997 in relation to the main local hydrographic conditions.

2. Materials and Methods

2.1. Sampling

[6] Water samples were collected during a cruise of the R/V *Urania*, in November–December 1997 in the Ionian Sea. The sampling was planned to obtain a regular grid of samples along two transects, oriented W-E and SW-NE, and at fixed depths, from the surface to the base of the photic zone. Nine locations were investigated; surface waters were sampled at a finer vertical resolution than the deeper ones, to better assess phytoplankton spatial variability. Sample locations are shown in Figure 1 and Table 1.

[7] Samples were collected with 10-L Niskin bottles mounted on a G.O. Rosette; a Seabird 911 plus CTD was used to define the correct sampling depth and to obtain the main physical and chemical parameters of the water column (temperature, salinity, dissolved oxygen, water transparency, turbidity). CTD data are plotted in Figure 2 and are displayed in section for the two transects (Figure 3).

[8] Once on-board, water samples were immediately filtered on 47 mm diameter - 0,45 μm pore size filters using a low-vacuum filtration system. Both Millipore[®] cellulose acetate and Nucleopore[®] polycarbonate filters were used, and subsequently observed with Polarized Light Microscope (PLM) and Scanning Electron Microscope (SEM) respectively. Filters were not rinsed after filtration, as often suggested in preparation techniques [Kleijne, 1991; Knappertsbusch, 1990], to avoid any pH variation or carbonate under-saturation, which could cause coccolith-carbonate dissolution. Filters were then oven dried and stored in plastic petri dishes at 4°C and in the dark, to avoid bacterial growth.

2.2. Analyses

[9] Quantitative sample analyses were performed using light polarized microscope at 1250 \times , while only selected samples (i.e., samples which displayed a suitable particle density on filters) were subsequently analyzed with a SEM (Cambridge Stereoscan 360) to better identify small coccolithophorid species.

[10] In the LM analysis, the concentration of different phytoplankton groups was assessed at selected depths, by counting a filter area of about 20 mm² along radial transects on a slice of filter mounted on a cover glass. To assess evenness of particle distribution on the filters, a uniformity test was performed on randomly selected samples. As regards coccolithophorids, a different number of coccospheres was counted in each sample (60 to 1000) depending on their concentration; as a result, a different portion of the filter area (from a minimum of 6 up to 23 mm²) was screened. The total phytoplankton and coccolithophorid concentration was then calculated and expressed as n/l (number of coccospheres per liter of seawater).

[11] For SEM analysis, a small portion of filter was mounted on an 8 mm-diameter stub with a graphite adhesive tape and coated with gold. Only coccolithophorids were analysed; for each sample 300 to 600 coccospheres were counted; the relative abundance of each species was calculated and compared with the LM results.

[12] For the analyses, phytoplankton cells other than coccolithophorids were lumped together at group level; separate diatom valves were counted as half a cell. With regard to coccolithophorids, the classification system of

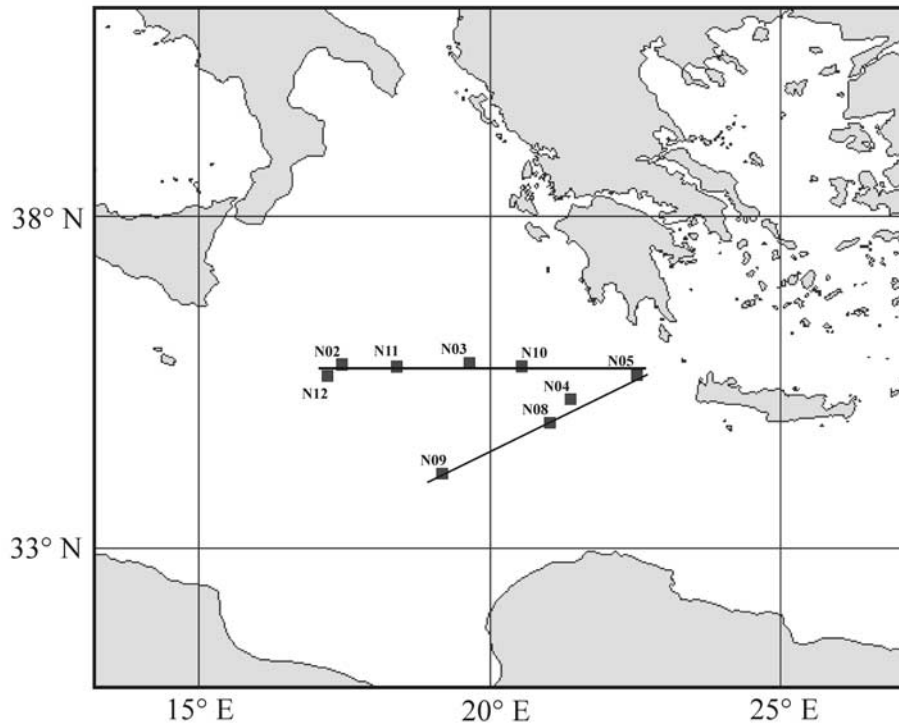


Figure 1. Map of the Ionian Sea with sample locations indicated.

Jordan and Kleijne [1994] was followed, which includes all the calcifying members of the Prymnesiophyceae in the Coccolithophorales [Schiller, 1925], subdividing 12 families of heterococcolithophorids and one of holococcolithophorids. This scheme is maintained even if recent work has showed the relation of some holococcolithophorid species with eterococcolith-bearing ones [Cros *et al.*, 2000]. Much

work still has to be done to establish all the hetero-holo correspondences (and to assess their reliability), so the temporary maintenance of the holococcolith names should avoid a possible confusion. In LM observation, small coccolithophorid species were grouped together and counted as a family or as a genus; SEM identification was done based on *Winter and Siesser* [1994] for heterococco-

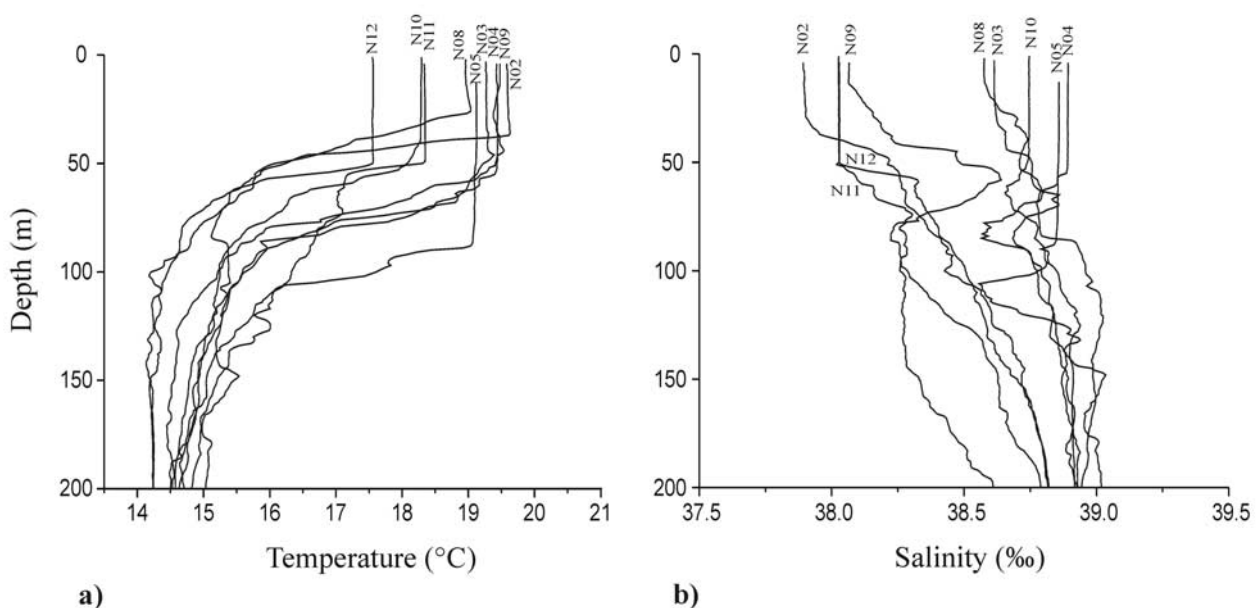


Figure 2. CTD profiles of the investigated stations: (a) temperature and (b) salinity.

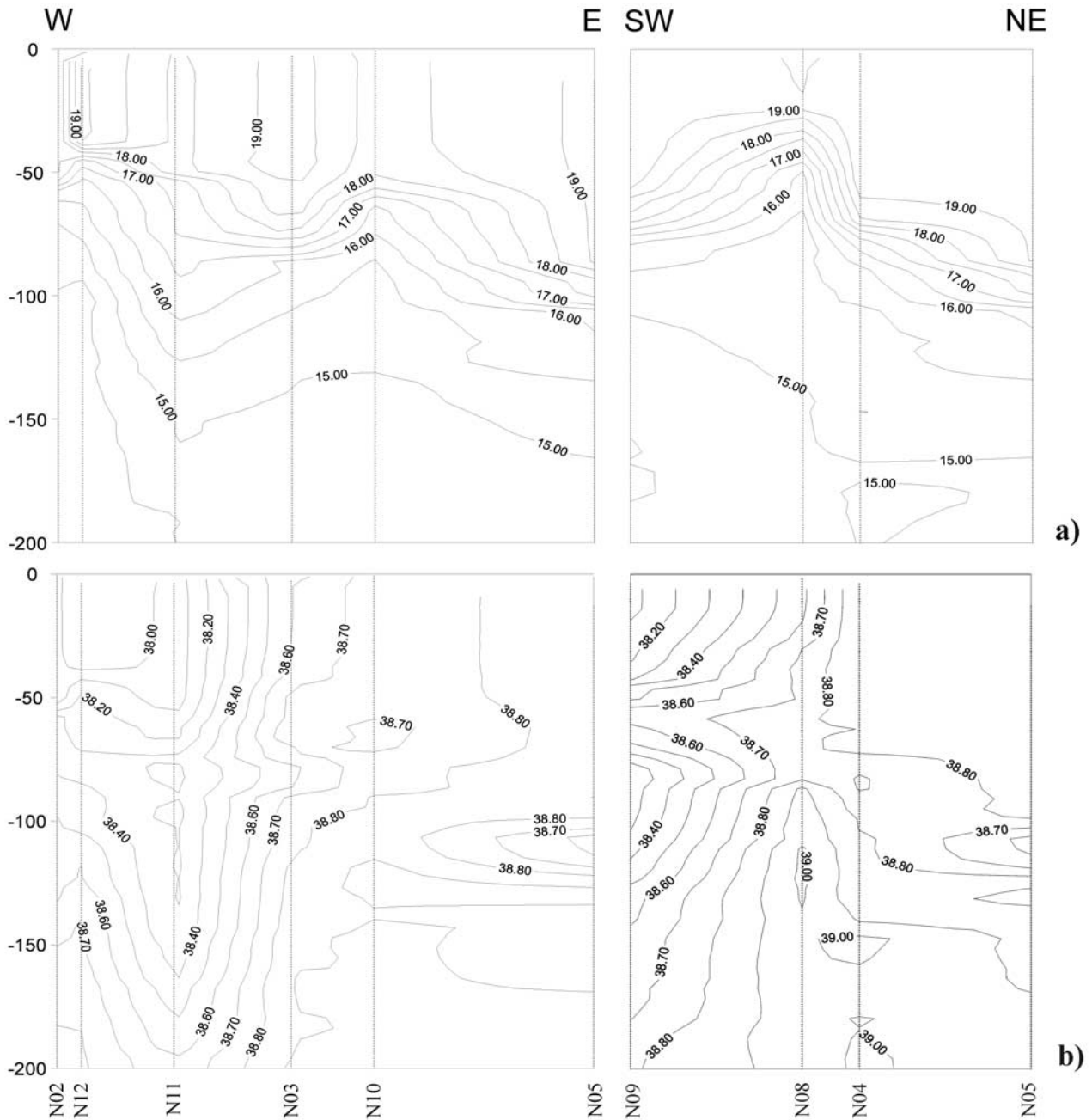


Figure 3. Correlation of CTD data along the two profiles investigated with water sampling: (a) temperature and (b) salinity.

lithophorids, Kleijne [1993], Cros *et al.* [2000], and Cros [2000] for *Syracosphaera* species, Kleijne [1991] for holococcolithophorid species.

[13] General counting criteria were followed for coccolithophorids: incomplete coccospheres which displayed more than half of their coccoliths, disaggregated coccospheres with all their coccoliths in the immediate vicinity and collapsed coccospheres with inside-out coccoliths were counted as one specimen; dithecate and/or dimorphic coccospheres were counted as one specimen even when only endothecal and/or ordinary coccoliths were present; exothecal and/or apical coccoliths alone were not considered, as

well as complete coccospheres within larger aggregates (mainly faecal pellets).

3. Results

3.1. Hydrological Data

[14] Measured CTD data, shown in Figure 2, display the presence of a surface mixed layer, developed at all stations, characterized by temperatures around 19 deg, slightly lower in the stations sampled later in the year (see satellite SST data of Figure 4a). Salinity is typical of the Modified Atlantic Water, markedly lower than in subsurface layers

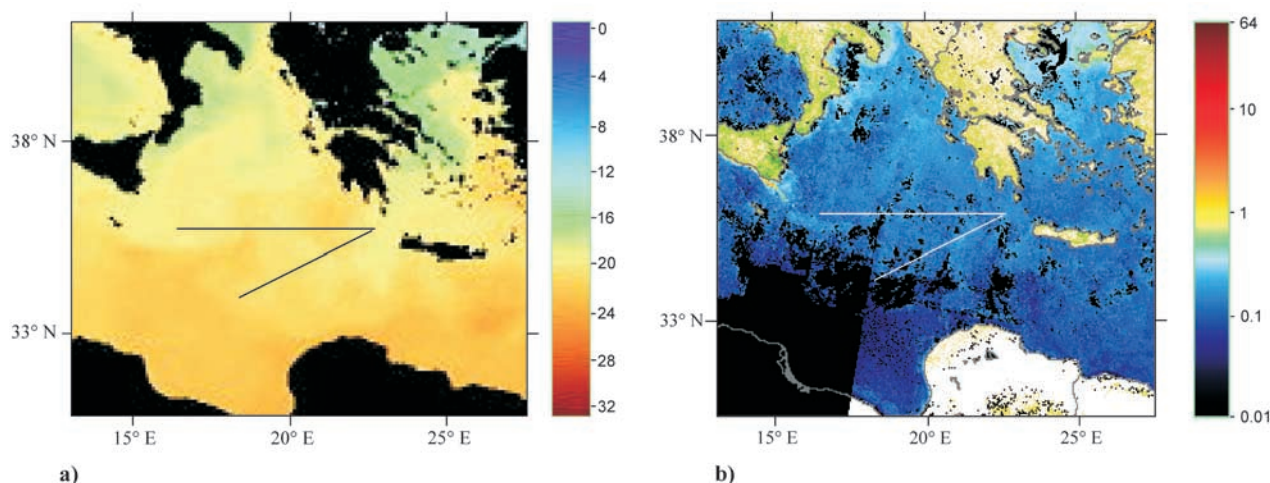


Figure 4. Sea surface maps of the eastern Mediterranean from satellite data and location of the two transects: (a) monthly SST from 15 November to 15 December 1997 (from DLR EOWEB, Earth Observation Information Service of the German Remote Sensing Data Center (DFD), <http://eoweb.dlr.de:8080/servlets/welcome>), scale bar: °C; and (b) monthly chlorophyll-a concentration in November 1997 (SeaWiifs image processed from the Marine Environment Unit (ME) - Space Applications Institute (SAI), <http://me-www.jrc.it>); scale bar: Chl-a mg/m^3 .

(37.9% to maximum 38.8% in the eastern most stations). The mixed layer reaches a mean depth of 50 m, varying between stations, from 25 to 90 m as a function of the surface circulation pattern and of wind mixing. Below this mixed layer, a strong seasonal thermo- and halocline is developed. The bottom of the thermocline is commonly located at around 100 m.

3.2. Total Coccolithophorid Standing Stock

[15] Coccolithophorids constitute the majority of the phytoplankton assemblage ($>3 \mu\text{m}$ fraction) at all stations:

only a few diatoms, calcareous dinocysts, silicoflagellates and other Chrysophytes (*Meringosphaera mediterranea*) were recovered in the investigated samples. The relative abundance of different phytoplankton groups at different depths is shown in Figure 5.

[16] A total of 69 heterococcolithophorid (plus six varieties) and 37 holococcolithophorid species were recovered (listed in Appendix A) in the investigated samples. During the sampling period coccosphere concentration was generally low. Along the two investigated transects the total abundance is always greater in the upper 25 m of the water

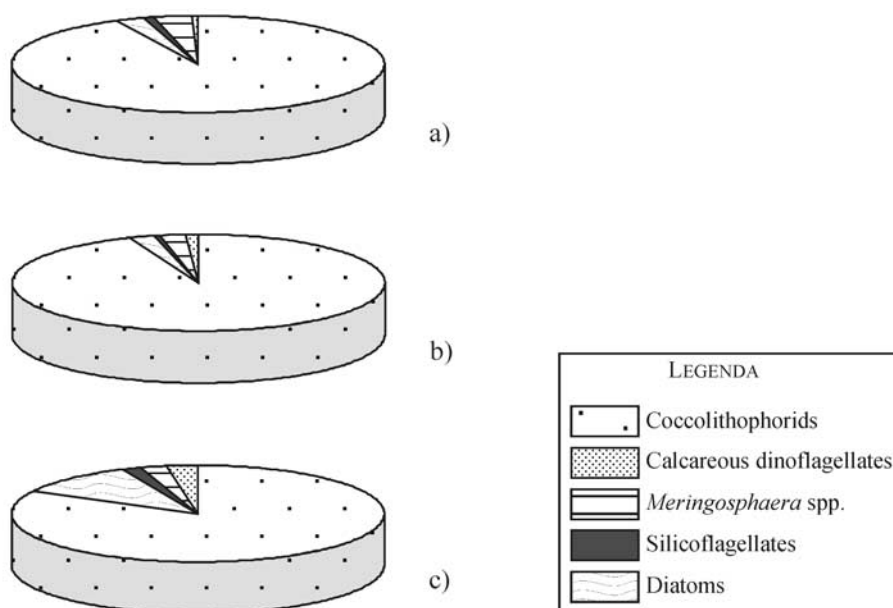


Figure 5. Relative abundance of different phytoplankton groups at different depths in the photic zone, correlated among all nine analysed stations: (a) 5, (b) 25, and (c) 80 m.

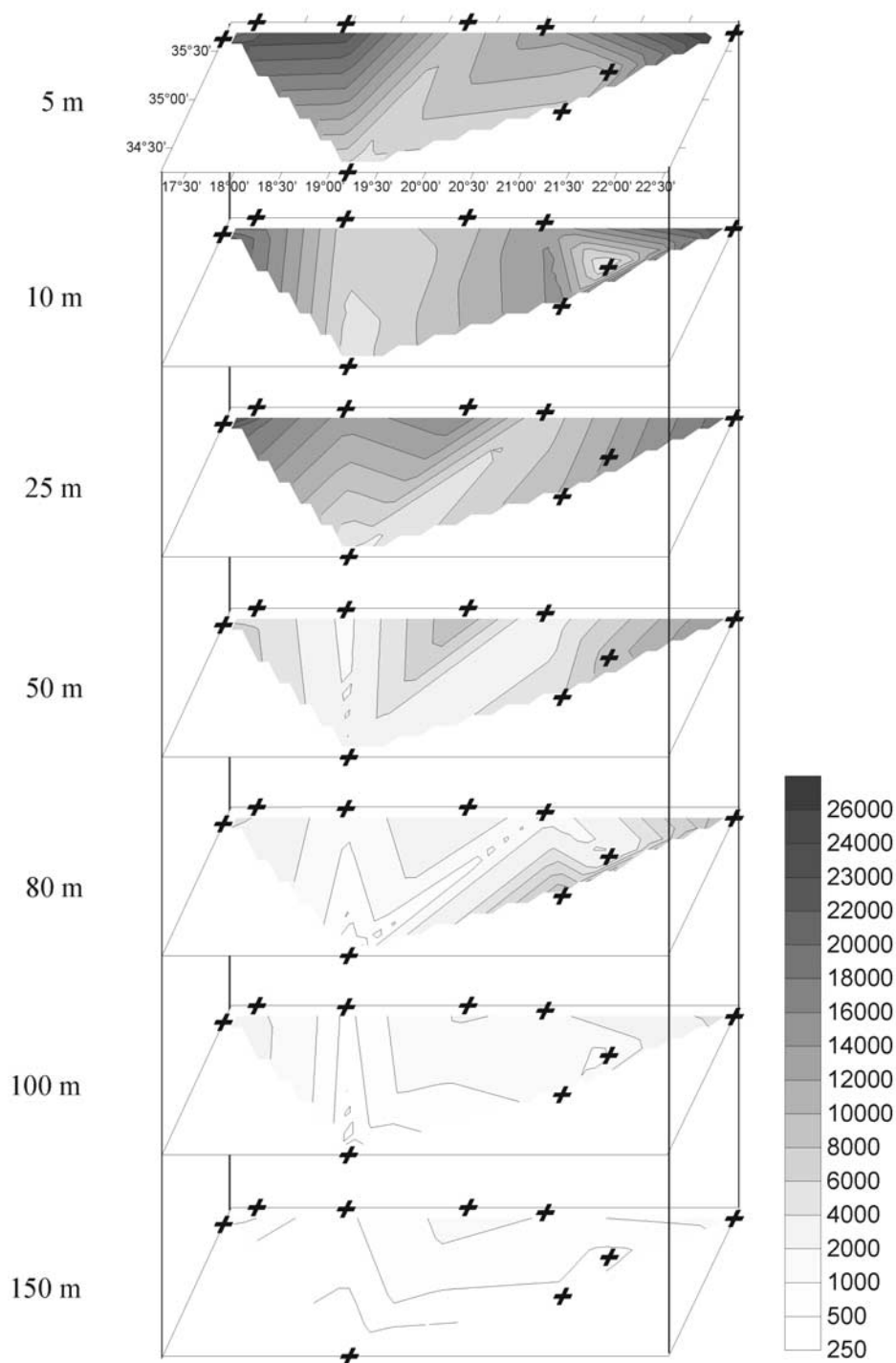


Figure 6. Total coccolithophorid concentration at different depths in the photic zone. Black crosses, samples location along the two profiles; scale bar: number of coccospheres/L.

column (Figures 6 and 7a), and maximum values can be found either at the surface or slightly below, in the range of $1-2 \times 10^4$ coccospheres/L (maximum values of $2-3 \times 10^4$ at 25 m in station N2). Concentration gradually decreases with depth, reaching $1-2 \times 10^3$ coccospheres/L at 100–150 m and near-zero values at 200 m. The concentration profiles are rather similar at all stations, and in general a decreasing trend in total abundance can be observed in a

NE-SW direction, that is toward the middle of the basin. Surface waters commonly display a higher species richness, while species number decreases with depth along with species concentration. *Emiliania huxleyi* and *Florisphaera profunda* are dominant species throughout the investigated samples, while other common species are, with decreasing abundance, *Rhabdosphaera clavigera*, *Umbellosphaera tenuis*, *Gladiolithus flabellatus*, *Algirosphaera robusta*,

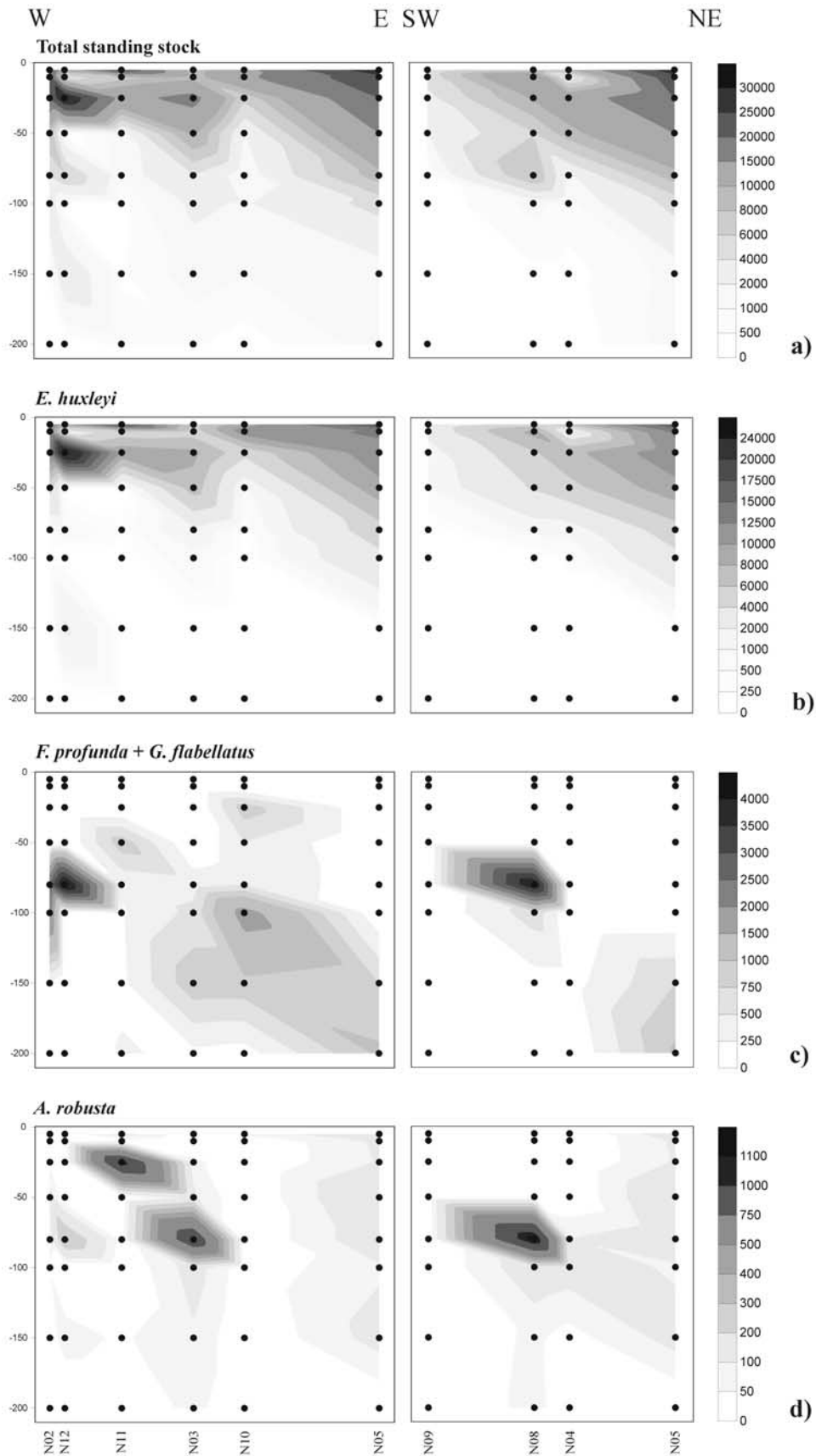


Figure 7. Total concentration of different coccolithophorid species along the two investigated transects: (a) total concentration, (b) *E. huxleyi*, (c) *F. profunda* + *G. flabellatus*, (d) *A. robusta*, (e) *R. clavigera*, (f) *S. pulchra*, (g) *U. tenuis*, and (h) total holococcolithophorids. Scale bar: number of coccopheres/L.

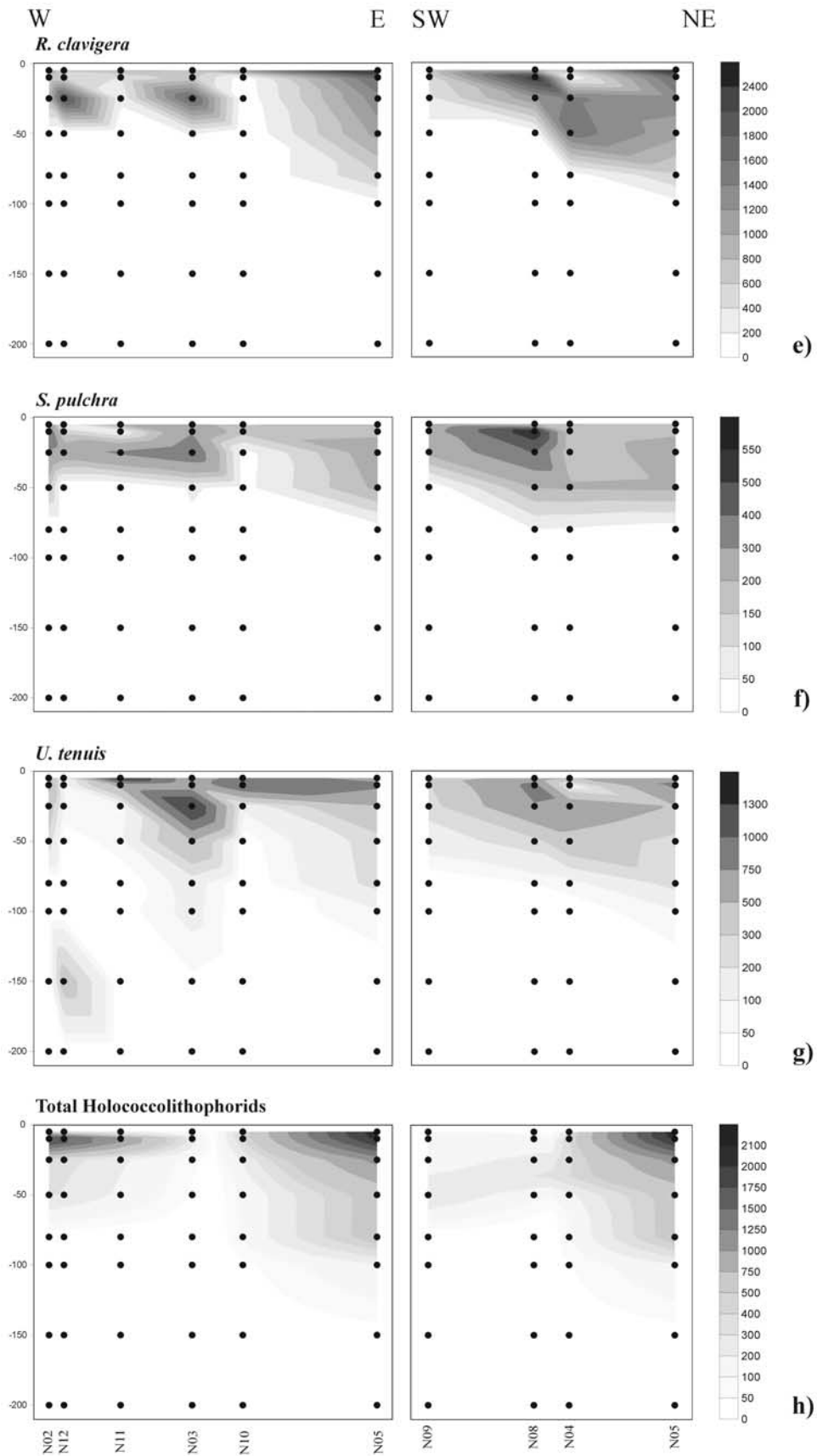


Figure 7. (continued)

and *Syracosphaera pulchra*. The assemblage at 200 m depth usually contains only *E. huxleyi*, whose coccospheres probably derive from sinking cells of disaggregating faecal pellets or other agglutinates: such samples were therefore excluded from the calculation of relative abundance.

3.3. Coccolithophorid Species Distribution and Community Structure

[17] Within the investigated samples, *E. huxleyi* is the most common species: it is present at all depths but usually dominates the upper layers, reaching up to 80% of the assemblage while it gradually decreases with depth. Its concentration (Figure 7b) drives the observed pattern of total coccolithophorid distribution throughout the water column in all the investigated area. *F. profunda* is a deep dwelling species, reaching higher abundances, up to 3.5×10^3 coccospheres/L, between 50 and 150 m. It is not present at the surface, and it generally peaks just below the beginning of the thermocline, where it becomes dominant over the rest of the assemblage (Figure 8). It is always accompanied by *G. flabellatus* (plotted together in Figure 7c) and by other minor taxa (see later). Also *A. robusta* has a similar distribution, even if it is sometimes present in surface water and it reaches maximum abundance at slightly shallower depths.

[18] *R. clavigera* (both var. *clavigera* and var. *styliifera*) and *U. tenuis* have higher concentration in the surface samples down to 25–50 m depth (Figures 7e and 7g): the same pattern is displayed by *S. pulchra* (Figure 7f) and by other *Syracosphaera* species, even with lower abundance, and by a number of minor taxa belonging to the genera *Pontosphaera*, *Scyphosphaera*, *Acanthoica*, *Anacanthoica*, *Cyrtosphaera*, *Discosphaera*, *Coronosphaera*, and by all the holococcolithophorid species. As a result, surface waters show a much higher species diversity than the deeper ones, where the assemblage is dominated by few specialized taxa.

[19] Some other minor species are *Michaelsarsia adriaticus* and *elegans*, *Ohiaster* spp., *Calciosolenia murrayi* and *Anoplosolenia brasiliensis*; these species are typically found in subsurface waters. *Helicosphaera* species are occasionally found at all depths, but in general, they display low abundance.

4. Discussion

4.1. General Phytoplankton and Coccolithophorid Distribution

[20] For the present work, only larger than 3 μm fraction phytoplankton cells, with hard cell coverings, were considered: picoplankton, which are known to be a very important contributor to primary productivity in such oligotrophic pelagic environments as the eastern Mediterranean [Azov, 1986], were not taken into account. The sampling period (late November-early December) coincides with deeply oligotrophic conditions in the Ionian Sea: the summer thermocline is still maintained but a surface mixed layer is already developed, due to the presence of strong autumn winds, with lower temperatures than the summer season (mean SST around 19°C). No in situ nutrient and primary production data are available for the study period, but chlorophyll concentration, measured from satellite sensors (see Figure 4b), appears to be very low in the entire pelagic

Ionian Sea, as is usual in this area throughout most of the year [Barale et al., 1999]. Comparison with previous literature data in this area [Rabitti et al., 1994] shows a much larger contribution of coccolithophorids with respect to dinoflagellates and diatoms in the presently investigated samples. In particular dinoflagellates, which are usually widespread in oligotrophic environments [Estrada, 1985], show very scarce abundance; diatoms show in general a slight increase in relative abundance with depth within the photic zone.

[21] Previous investigations on coccolithophorids in the eastern Mediterranean are mostly restricted to early taxonomic work (see Winter et al. [1994] for a review) and distribution studies in surface waters [Kleijne, 1991], while a detailed survey through the entire photic zone was only done, for the whole Mediterranean, during two cruises in 1986 and 1988 [Knappertsbusch, 1993], but also in this case the spatial coverage was quite sparse in the Ionian Sea. Therefore a comparison with previous distribution data can give only a rough estimate of possible variations in time of coccolithophorid standing stocks and species composition.

[22] Total coccolithophorid abundance during the study period is quite low when compared to other oceanic settings at northern latitudes where coccolithophorids can form large blooms, but it falls within the range of the oligotrophic subtropical Atlantic, where a mean concentration of 2.1×10^4 coccospheres/L [Okada and McIntyre, 1979] is detected. Such concentration is also in accordance with previous investigations at the same location: in fact, Knappertsbusch [1993] found maximum values of 1×10^4 coccospheres/L in the subsurface Ionian Sea in late summer (September/October), while higher values up to 6×10^4 coccospheres/L were detectable in late winter (February/March).

[23] The coccolithophorid assemblage recovered during this study is, at a wide scale, that typical of the subtropical zone in the Atlantic Ocean [McIntyre and Bé, 1967; Okada and McIntyre, 1979] and coincident with the transitional zone in the Pacific [Okada and Honjo, 1973; Okada and McIntyre, 1977]. This is in fact the zone of the Atlantic that is in contact with the Mediterranean basin through the Strait of Gibraltar. This biogeographic zone is characterized by high abundance of *E. huxleyi*, followed by species of the Coccolithaceae, Pontosphaeraceae, Rhabdosphaeraceae, Syracosphaeraceae, and Holococcolithophorids [Jordan and Chamberlain, 1997], with a general high species richness and a well-developed deep photic-zone community. The high number of species recovered in surface waters during this study is in accordance with previous data obtained through surface sampling in this area [Kleijne, 1991]: in particular, a high number and density of holococcolith-bearing species is recovered in the upper meters, that is typical for deeply oligotrophic environments.

[24] The main difference from this general biogeographic distribution pattern is the very low concentration of *Gephyrocapsa oceanica* and of all the Gephyrocapsid group found in this study and also revealed by Knappertsbusch [1993] for the two investigated time periods. These species were instead found to be quite abundant in the western Mediterranean basin in late winter [Knappertsbusch, 1993]: their occurrence was therefore related to the eastward flowing Atlantic surface water, with the Sicily Strait acting as an

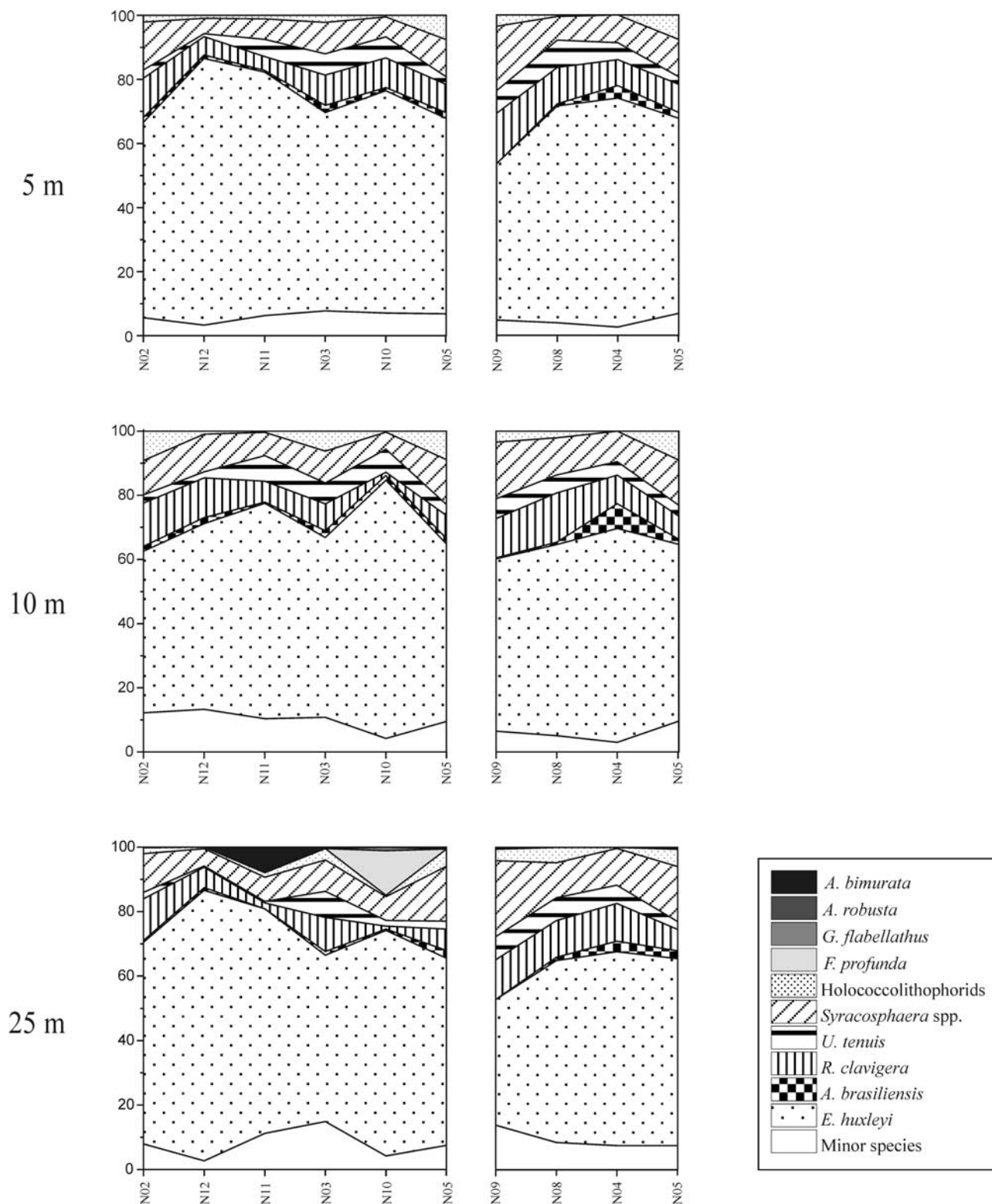


Figure 8. Relative abundance of the major coccolithophorid species in the investigated samples at different depths in the photic zone.

ecological barrier to the transport of Atlantic plankton communities. However, *Gephyrocapsa* species were detected, with low abundance, in some sediment trap samples from the Ionian Sea [Ziveri *et al.*, 2000], and they are present in the bottom sediments of this area [Knappertsbusch, 1993;

Malinverno *et al.*, 2000], possibly indicating significant seasonal or interannual variations in the strength of the Atlantic surface current and/or the maintenance of its physicochemical and biological characteristics during eastward flow.

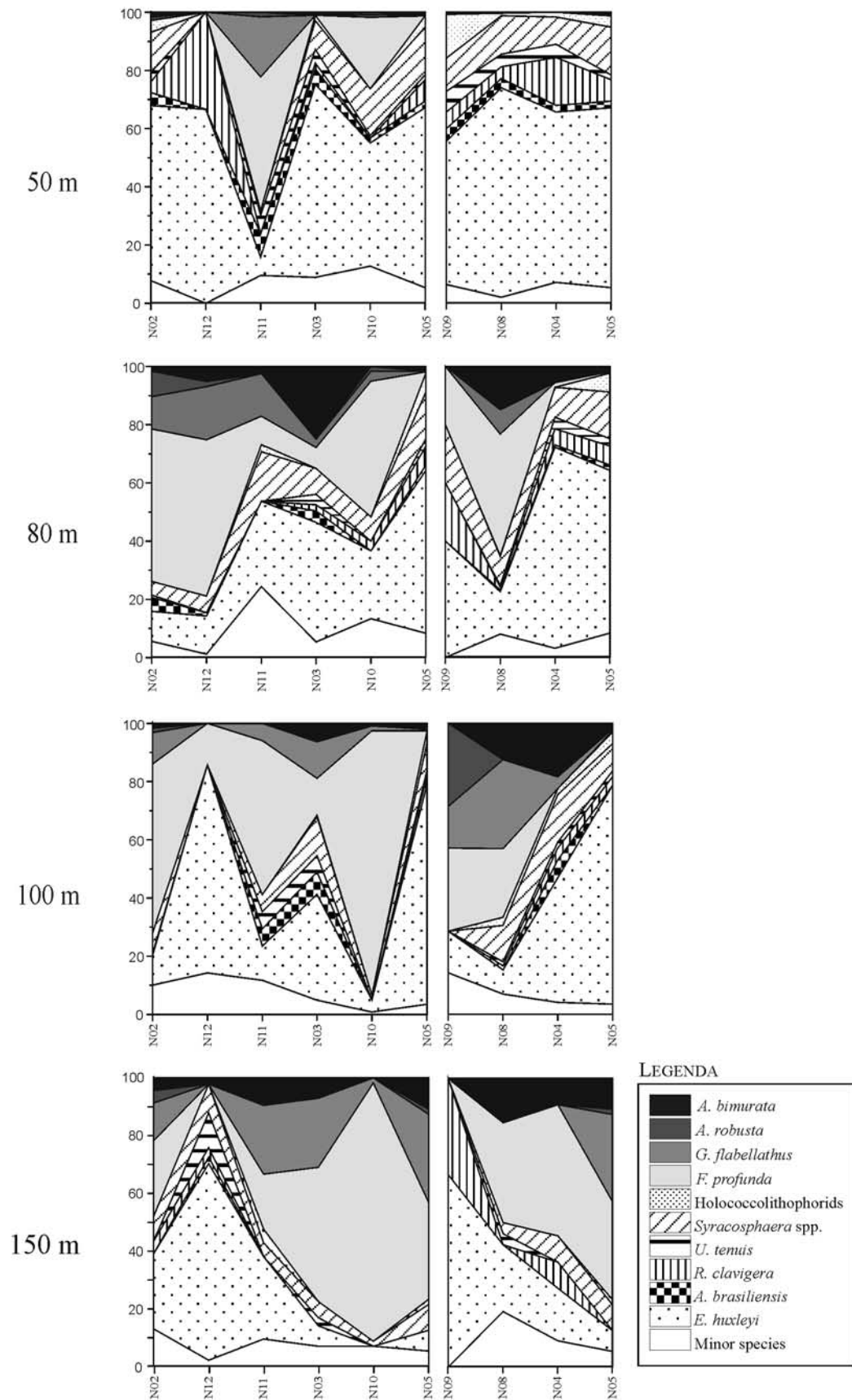


Figure 8. (continued)

4.2. Coccolithophorid Depth Distribution

[25] The most significant pattern of coccosphere distribution in this study is the depth distribution of different species, that gives rise to typical depth-related assemblages (Figure 8): these are essentially related to the physicochemical characteristics of the upper water column, and in particular to the depth of the seasonal thermocline. It is in fact possible to identify two main layers in the photic zone and a transitional one in between.

[26] The surface layer is characterized in general by the highest abundance and the greatest species diversity: *E. huxleyi* is always the dominant species and besides it there is a large number of Rhabdosphaeraea species (*R. clavigera*, *R. xiphos*, *D. tubifera*, *Acanthoica* spp.), Syracosphaeraea (several species of *Syracosphaera*, *Coronosphaera*), Umbellosphaeroidea (*U. tenuis*), and a large variety of holococcolith-bearing species. This species composition is commonly referred to as the upper photic zone (UPZ) assemblage [e.g., *Winter et al.*, 1994; *Jordan and Chamberlain*, 1997].

[27] In the lower samples investigated, the assemblage is dominated by a few deep-living species, namely *F. profunda*, *G. flabellatus*, and *A. robusta*, well known from the literature to occupy this specific niche, defined as the lower photic zone (LPZ, see for a review, *Jordan and Chamberlain* [1997]). These three species can constitute up to 80% of the entire assemblage, while *E. huxleyi*, still present, has lower absolute and relative abundance. Along with these species, some taxa of the overlying layers can be present, with low density, and some other species usually appear. Among these are *Oolithotus antillarum*, observed at the same depths in the Atlantic [*Okada and Honjo*, 1973] and in the Mediterranean [*Knappertsbusch*, 1993], *Alveosphaera bimurata*, *Hayaster perplexus*, *Papposphaera lepida* and three species of *Syracosphaera*: *S. lamina*, already mentioned at depth in the Mediterranean [*Knappertsbusch*, 1993], *S. anthos* and *Syracosphaera* type-K [sensu *Kleijne*, 1993], described from the North Atlantic but without any specific depth preference.

[28] The transition interval between these two layers is characterized by the presence of surface species, among which *E. huxleyi* is still dominant, but with a generally much lower concentration. Some typically deeper species (see above) start to be present, but their concentration is usually still low. At some stations it is possible to observe some species that are known from the literature to occupy this specific intermediate depth, the middle photic zone, MPZ [*Jordan and Chamberlain*, 1997]: these belong to the genera *Michaelsarsia*, *Ophiaster*, *Anoplosolenia*, and *Calciosolenia*. Their depth occurrence shows changes, at different sampling stations, with respect to the thermocline location in the water column.

[29] In the subtropical oceans, where such zones are usually well developed, previous studies defined at 80 and 120 m respectively the common limit between UPZ and MPZ and between MPZ and LPZ [*Winter et al.*, 1994; *Jordan and Chamberlain*, 1997]. Nevertheless, such limits are only broad indications; in fact, they can rise and fall in the photic zone over short time periods [*Jordan and Winter*, 2000], as a function of the hydrology. From the data of a previous investigation in the Mediterranean Sea [*Knappertsbusch*, 1993], it is possible to observe the main changes at different

depths in the two investigated seasons: in late summer the MPZ species were present from 50 to 100 m, while *F. profunda* became dominant in the samples at 200 m; in late winter the MPZ species were not detected and *F. profunda* started to be dominant at 100 m depth.

[30] In the present study the UPZ assemblage can generally be recognized at depth until 50 m; the only exception is seen at station N10, where some changes are detected starting from 25 m depth. A peculiar difference from common literature data is the distribution of *U. tenuis*. This species is commonly considered as a middle photic zone species, but in this study it displayed the same distribution pattern as surface species (as indicated for the southeast subtropical Indian Ocean [e.g., *Takahashi and Okada*, 2000]). The LPZ assemblage starts to be present throughout the investigated area at 50 m (25 m at station N10) but it becomes dominant usually at or below 100 m depth. We consider here as deep assemblage all the above mentioned deep species, even if some differences are observed from previous literature data: in particular, *A. robusta* seems to be slightly shifted upward with respect to the other deep species, being sometimes present, even with low absolute abundance, from the surface and displaying peak concentration at 25 m. The MPZ is not well defined: *A. brasiliensis*, a typical MPZ species [*Jordan and Chamberlain*, 1997], is actually present throughout the photic zone, while other typical MPZ species are found in samples at 25 and 50 m, but their concentration is much lower than that of other species present there. Therefore, in this study it was not possible to clearly define a MPZ depth range. This may be due to a too coarse sampling spacing or to a poorly developed MPZ assemblage due to changing hydrological conditions; in fact typical middle-depth species are commonly found with higher abundance in summer, when the surface stratification is more pronounced [*Reid*, 1980]. Therefore we cannot refer in this study to a real MPZ, but we can identify a transition assemblage, commonly located at 50 m, where surface species are still abundant and middle and deep species are present.

[31] This depth distribution is rather similar to that observed by *Knappertsbusch* [1993] in late winter (February/March 1988): in fact, even if *E. huxleyi* displays a much higher relative abundance there, the vertical distribution pattern is rather similar: *A. brasiliensis* is present throughout the photic zone, *U. tenuis* has a low relative abundance and is confined to surface samples and *F. profunda* appears with other deep species from 100 m depth.

[32] Comparison of present observations on coccolithophorid assemblages with previous data shows that the vertical species distribution is not related to fixed depths but can fluctuate as a function of the main physicochemical parameters that characterise the photic zone. In particular, the presence and location of the seasonal thermocline seems to be a major control factor. The downward extension of the UPZ assemblage coincides with the lower limit of the upper mixed layer, being shallower in correspondence with a doming of the thermocline (e.g., station N10) and deeper where the thermocline is moved downward (e.g., station N05); this limit always coincides with the first significant occurrence of deepwater species. It thus seems clear that the identified zone boundaries are shifted upward, with respect to the literature data, probably due to the early winter situation: this is also in accordance with seasonal variations observed

by *Knappertsbusch* [1993] in the same area and can explain the different depth distribution for example of *U. tenuis*. Therefore it is not only light which is the forcing factor in species depth distribution, but also some of the physicochemical parameters which are thermocline-dependent (temperature, nutrients).

[33] Finally, the thermocline depth can be related to the pattern of surface circulation at subbasin scale: surface currents determine the rise or depression of isotherms, as shown in Figure 3: this situation is well testified by coccolithophorid species depth distribution.

4.3. Coccolithophorids: Comparison Between Plankton and Sediment Records

[34] Coccoliths are a significant component of the pelagic sediments in most oceans [Milliman, 1993] and their assemblage composition is thought to reflect climatic and oceanographic conditions of the overlying photic zone. In the Mediterranean, where carbonate is well preserved, coccoliths can make an important contribution to the bottom sediments. Variations in time of species assemblages are therefore widely used for paleoceanographic reconstruction [Castradori, 1993; Negri and Giunta, 2001; Sbaffi et al., 2001], based on the ecological preferences of the observed species and their assemblage composition in surface sediments. In particular, the relative abundance of *F. profunda* is taken as an indication of surface and intermediate water mass conditions [Molfini and McIntyre, 1987].

[35] For the eastern Mediterranean, a calibration of the present bottom assemblage with the overlying water conditions is complicated by the low sedimentation rate (2 to 4 cm/kyr, depending on the area [e.g., Van Santvoort et al., 1996]) and the bioturbation activity (reaching the topmost 2 cm [e.g., Basso and Corselli, 1995]): the upper millimeters of sediments thus represent a mixing of different seasons and several years. Previous investigations [Knappertsbusch, 1993] showed that the assemblage preserved in the sediments was not easily comparable to the photic zone living assemblage of the two investigated seasons, late winter and late summer, showing different relative abundance of major species. On the other hand, the living assemblage described in the present paper, even if not representative of the whole year, is quite similar to that recorded in the bottom sediments [Knappertsbusch, 1993; Malinverno et al., 2000] as regards the major species dominance; the main differences can be recognized in a generally higher species number in water samples (with very delicate species which are probably not preserved in the bottom sediments), in the above mentioned distribution of Gephyrocapsids and in the scarce presence of *Helicosphaera* species and *Calcidiscus leptoporus*, which are a minor but constant element in bottom sediments of this area.

[36] An important way of linking living and "fossil" assemblages is given by present fluxes obtained through sediment traps: up to now, such data are available for the pelagic Ionian Sea only from 1991 to 1994 [Ziveri et al., 2000]. From these data, coccosphere and coccolith fluxes are shown to be very seasonal in the Ionian Sea and strongly variable from year to year. This depends not only on changes in surface productivity but also on the mechanism of downward transport: it is in fact possible to observe that each component's flux coincides in general with the total

mass flux. In the 3000 m sediment trap, the main fluxes are recorded about one month later than the events occurring in the overlying photic layers (coccolith fluxes are recorded slightly later than coccosphere ones). Following this calculation, the highest coccosphere and coccolith fluxes (recorded around February/March and April/May/June respectively) correspond to maximum coccolithophorid productivity/export production in January/February, while the sampling period of the data presented in this paper coincides with minimum productivity/export production conditions, also confirmed by satellite measures of chlorophyll concentration at the surface.

[37] The major species composition recorded in the sinking assemblage [Ziveri et al., 2000] reflects the pattern of surface sediments. In addition, some minor species are present: some of them are represented in the plankton community but are usually rare in the sediments (e.g., Holococcolithophorids): this is probably due to their low preservation potential. On the other hand, *H. carteri* and *Calcidiscus leptoporus*, two dissolution-resistant species [Roth and Berger, 1975], are scarce to nearly absent in the present living assemblage but occur in the bottom sediments, possibly indicating seasonal or interannual variations in surface production.

[38] Regarding *F. profunda*, its main coccolith fluxes do not show significant variations from those of other species, while its relative abundance seems to increase in late spring/early summer period (recorded at 3000 m depth in July/August) in correspondence with drops in abundance of *E. huxleyi*. The same alternation pattern of these two species is observed in water samples at similar latitudinal settings [e.g., Haidar and Thierstein, 2001], even if with some seasonal shift: this can be due to interannual variations as well as to the deposition mechanism affecting flux data in sediment trap samples. To trace variations of *F. profunda* relative abundance from the present to the fossil record, only sparse data are available. In the present plankton samples (1997), *F. profunda* is generally well represented below 50 m, and it appears to constitute 10 to 40% of the whole-photoc-zone-integrated coccosphere assemblage [Malinverno et al., 2000]: it can therefore make a potential large contribution to the bottom sediments. Its relative abundance is significantly lower in sediment traps (1991–1994), with an average of 5.3% coccolith relative abundance, while it has quite stable values around 10% of the total coccolith assemblage in the surface sediments of the whole Ionian basin. Its relative abundance rises to over 20% in the sapropel S1 interval (anoxic black layer deposited around 9–6 kyr BP [e.g., Cita et al., 1997]) and in some other sapropel layers: this variation was explained as a result of the development of a deep chlorophyll maximum, with high *F. profunda* production, due to the rising of the nutricline within the lower photic zone [Castradori, 1993].

[39] This phenomenon immediately comes to mind when considering the recent changes affecting the eastern Mediterranean. Recent studies in fact revealed that modifications in the deepwater masses caused a general uplift of the intermediate layers, leading to an upward shifting of the nutricline to 100–150 m in the northern and eastern Ionian [Klein et al., 1999]. The enhanced nutrient concentration in the lower photic zone can thus affect phytoplankton productivity and assemblage composition, and *F. profunda*

appears to be a good indicator of such changes [Molfini and McIntyre, 1987, 1990].

[40] Following these observations, a strict comparison between plankton and sediment trap data, linking surface productivity with export production, is essential for the understanding of how changes occurring in planktonic assemblages can be recorded in the bottom sediments and can thus provide further information to interpret paleoceanographic changes based on assemblages preserved in the sediments.

5. Conclusions

[41] 1. Coccolithophorids are the dominant phytoplankton group in the Ionian Sea photic zone in late autumn-early winter.

[42] 2. Coccolithophorid assemblages in the investigated area reflect the general latitudinal distribution pattern, with a well-developed surface community and a clear depth distribution.

[43] 3. The occasional presence of some species of Atlantic origin in the eastern Mediterranean can be related to variations at a seasonal/interannual/decadal scale in the intensity of surface circulation.

[44] 4. The deep photic zone community is well developed with a high number of specialized species, not only the few ones commonly indicated in the literature.

[45] 5. The vertical distribution boundaries of the deep community are strictly linked to the depth of the seasonal thermocline, which is related to the pattern of local surface circulation.

[46] 6. *F. profunda* relative abundance, commonly related to the depth of the nutricline [Molfini and McIntyre, 1987, 1990], can allow detection of the effects of recent changes of deep water masses on the pelagic surface ecosystem.

[47] Data are available from authors upon request.

Appendix A: Coccolithophorid Species List

[48] Asterisk marks species that are recorded also from surface sediments [Malinverno et al., 2000; Ziveri et al., 2000; Knappertsbusch, 1993].

A1. Heterococcolithophorids

- [49] **Family Calciosoleniaceae** Kamptner, 1937
 [50] *Anoplosolenia brasiliensis* (Lohmann, 1919) Deflandre, 1952 *
 [51] *Calciosolenia murrayi* Gran, 1912
 [52] **Family Coccolithaceae** Poche, 1913
 [53] *Calcidiscus leptoporus* (Murray & Blackman, 1898) Loeblich & Tappan, 1978 f. *leptoporus* *
 [54] *Hayaster perplexus* (Bramlette & Riedel, 1954) Bukry, 1973
 [55] *Neosphaera coccolithomorpha* Lecal-Schlauder, 1950 var. *coccolithomorpha* *
 [56] *N. coccolithomorpha* Lecal-Schlauder, 1950 var. *nishidae* Kleijne, 1993 *
 [57] *Oolithotus fragilis* (Lohmann, 1912) Martini & Müller, 1972 *
 [58] *O. antillarum* (Cohen, 1964) Reinhardt, in Cohen and Reinhardt, 1968

- [59] *Umblicosphaera sibogae* (Weber-Van Bosse, 1901) Gaarder, 1970 var. *sibogae* *
 [60] *U. sibogae* (Weber-Van Bosse) Gaarder var. *foliosa* (Kamptner) Okada & McIntire, 1977 *
 [61] *U. hulburtiana* Gaarder, 1970
 [62] **Family Helicosphaeraceae** Black, 1971, emend. Jafar & Martini, 1975
 [63] *Helicosphaera carteri* (Wallich, 1877) Kamptner, 1954 var. *carteri* *
 [64] *H. carteri* var. *hyalina* (Gaarder, 1970) Jordan & Young, 1990 *
 [65] *H. pavimentum* Okada & McIntire, 1977 *
 [66] **Family Noelaerhabdaceae** Jerkovic, 1970
 [67] *Emiliania huxleyi* (Lohmann, 1902) Hay & Mohler, in Hay et al., 1967 var. *huxleyi* *
 [68] *Gephyrocapsa ericsonii* McIntire & Bé, 1967/*G. ornata* Heimdal, 1973 *
 [69] *G. oceanica* Kamptner, 1943 *
 [70] **Family Papposphaeraceae** Jordan and Joung, 1990
 [71] *Papposphaera lepida* Tangen, 1972
 [72] **Family Pontosphaeraceae** Lemmermann, 1908
 [73] *Pontosphaera japonica* (Takayama, 1967) Nishida, 1971 *
 [74] *P. syracusana* Lohmann, 1902 *
 [75] *Scyphosphaera apsteinii* Lohmann, 1902 f. *apsteinii* *
 [76] *S. apsteinii* f. *dilatata* Gaarder, 1970 *
 [77] **Family Rhabdoapheraceae** Ostenfeld 1899
 [78] *Acanthoicaacanthifera* Lohmann, 1912 ex Lohmann, 1913
 [79] *A. quattropsina* Lohmann, 1903
 [80] *Algiropsphaera robusta* (Lohmann, 1902) Norris, 1984 *
 [81] *Anacanthoica acanthos* (Schiller, 1925) Deflandre, 1952
 [82] *A. cidaris* (Schlauder, 1945) Kleijne, 1992
 [83] *Cyrtosphaera aculeata* (Kamptner, 1941) Kleijne, 1992
 [84] *C. cucullata* (Lecal-Schlauder, 1951) Kleijne, 1992
 [85] *C. lecaliae* Kleijne, 1992
 [86] *Discosphaera tubifera* (Murray & Blackman, 1898) Ostenfeld, 1900 *
 [87] *Palusphaera vandeli* Lecal, 1965 emend. Norris, 1984
 [88] *Rhabdosphaera clavigera* Murray & Blackman, 1898 var. *clavigera* *
 [89] *R. clavigera* var. *stylifera* (Lohmann, 1902) Kleijne & Jordan, 1990 *
 [90] *R. longistilis* Schiller, 1925
 [91] *R. xiphos* (Deflandre & Fert, 1954) Norris, 1984
 [92] **Family Syracosphaeraceae** Lemmermann, 1908
 [93] *Alisphaera capulata* Heimdal, in Heimdal & Gaarder, 1981
 [94] *A. ordinata* (Kamptner, 1941) Heimdal, 1973
 [95] *A. spatula* Steinmetz, 1991
 [96] *A. unicornis* Okada & McIntire, 1977
 [97] *Alveosphaera bimurata* (Okada & McIntire, 1977) Jordan & Young, 1990
 [98] *Coronosphaera binodata* (Kamptner, 1927) Gaarder, in Gaarder & Heimdal, 1977 *
 [99] *C. mediterranea* (Lohmann, 1902) Gaarder, in Gaarder & Heimdal, 1977 *
 [100] *Michaelsarsia adriaticus* (Schiller, 1914) Manton et al., 1984

- [101] *M. elegans* Gran, 1912, emend. Manton et al., 1984
- [102] *Ophiaster* Gran, 1912, emend. Manton & Oates, 1983 spp.
- [103] *Syracosphaera anthos* (Lohmann, 1912) Jordan & Young, 1990
- [104] *S. bannockii* (Borsetti & Cati, 1976) Cros et al., 2000
- [105] *S. corrugis* Okada & McIntire, 1977
- [106] *S. epigrosa* Okada & McIntire, 1977
- [107] *S. delicata* Cros et al., 2000
- [108] *S. dilatata* (Heimdal, in Heimdal & Gaarder, 1981) Jordan, Kleijne & Heimdal, 1993
- [109] *S. halldalii* Gaarder, in Gaarder & Hasle, 1971 *
- [110] *S. histrica* Kamptner, 1941
- [111] *S. lamina* Lecal-Schlauder, 1951
- [112] *S. marginaporata* Knappertsbusch, 1993
- [113] *S. molischii* Schiller, 1925
- [114] *S. nodosa* Kamptner, 1941
- [115] *S. noroitica* Knappertsbusch, 1993, emend. Jordan & Green, 1994.
- [116] *S. orbiculus* Okada & McIntire, 1977
- [117] *S. ossa* (Lecal, 1966) Loeblich & Tappan, 1968
- [118] *S. prolongata* Gran, 1912, ex Lohmann, 1913
- [119] *S. pulchra* Lohmann, 1902 *
- [120] *S. rotula* Okada & McIntire, 1977
- [121] *Syracosphaera* sp. type D, *sensu* Kleijne, 1993
- [122] *Syracosphaera* sp. type G, *sensu* Kleijne, 1993
- [123] **Sub-Family Umbellosphaeroideae** Kleijne, 1993
- [124] *Gaarderia corolla* (Lecal, 1966) Kleijne, 1993
- [125] *Umbellosphaera tenuis* (Kamptner, 1937) Paasche, in Markali & Paasche, 1955 *
- [126] Incertae Sedis
- [127] *Florisphaera profunda* var. *elongata* (Okada & Honjo, 1973) Okada & McIntire, 1977 *
- [128] *F. profunda* Okada & Honjo, 1973 var. *profunda* Okada & McIntire, 1977*
- [129] *Gladiolithus flabellatus* (Halldal & Markali, 1955) Jordan & Green, 1994 *
- [130] *Polycrater galapagensis* Manton & Oates, 1980
- [131] *Ceratolithus cristatus* Norris, 1965 *
- [132] **Family Coccolithaceae** Poche, 1913
- [133] *Calcidiscus leptoporus* f. *rigidus* (Gaarder, in Heimdal & Gaarder, 1980) Kleijne, 1991
- [134] **Family Calyptosphaeraceae** Bourdreaux & Hay, 1969
- [135] *Anthosphaera fragaria* Kamptner, 1937, emend. Kleijne, 1991
- [136] *A. lafourcadii* (Lecal, 1967) Kleijne, 1991
- [137] *A. periperforata* Kleijne, 1991
- [138] *Calyptosphaera cialdii* Borsetti & Cati, 1976
- [139] *C. dentata* Kleijne, 1991
- [140] *C. heimdalae* Norris, 1985
- [141] *C. oblonga* Lohmann, 1902 *
- [142] *C. sphaeroidea* Schiller, 1913
- [143] *Calyptrolithina divergens* (Halldal & Markali, 1955) Heimdal, 1982
- [144] *C. divergens* f. *tuberosa* (Heimdal, in Heimdal & Gaarder, 1980) Heimdal, 1982
- [145] *C. multipora* (Gaarder, in Heimdal & Gaarder, 1980) Norris, 1985 *
- [146] *C. wettsteinii* (Kamptner, 1937) Kleijne, 1991 *
- [147] *Calyptrolithophora gracillima* (Kamptner, 1941) Heimdal, in Heimdal & Gaarder, 1980
- [148] *C. papillifera* (Halldal, 1953) Heimdal, in Heimdal & Gaarder, 1980 *
- [149] *Corisphaera gracilis* Kamptner, 1937
- [150] *C. strigilis* Gaarder, 1962
- [151] *C. tyrreniensis* Kleijne, 1991
- [152] *Corisphaera* sp. A Kleijne, 1991
- [153] *Daktylethra pirus* (Kamptner, 1937) Norris, 1985 *
- [154] *Gliskolithus amitakarenae* Norris, 1985 *
- [155] *Helladosphaera cornifera* (Schiller, 1913) Kamptner, 1937
- [156] *Homozygosphaera arethusae* (Kamptner, 1941) Kleijne, 1991 *
- [157] *H. spinosa* (Kamptner, 1941) Deflandre, 1952
- [158] *H. triarcha* Halldal & Markalii, 1955
- [159] *Periphyllophora mirabilis* (Schiller, 1925) Kamptner, 1937
- [160] *Poricalyptra gaarderae* (Borsetti & Cati, 1967) Kleijne, 1991
- [161] *Poritectolithus poritectun* (Heimdal, 1980) Kleijne, 1991
- [162] *P. tyronus* Kleijne, 1991
- [163] *Sphaerocalyptra adenensis* Kleijne, 1991
- [164] *S. quadridentata* (Schiller, 1913) Deflandre, 1952
- [165] *Syracolithus bicorium* Kleijne, 1991
- [166] *S. catilliferus* (Kamptner, 1941) Deflandre, 1952 *
- [167] *S. confusus* Kleijne, 1991 *
- [168] *S. dalmaticus* (Kamptner, 1927) Loeblich & Tappan, 1963 *
- [169] *S. quadriperforatus* (Kamptner, 1937) Gaarder, 1962*
- [170] *Zygosphaera amoena* Kamptner, 1937
- [171] *Z. bannockii* (Borsetti & Cati, 1976) Heimdal, 1982
- [172] *Z. hellenica* Kamptner, 1937 *
- [173] *Z. marsilii* (Borsetti & Cati, 1976) Heimdal, 1982
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