Changes in calcareous nannofossil assemblages during the Mid-Pleistocene Revolution

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1. Introduction

The Mid-Pleistocene Revolution (MPR) represents the period when the climate-forcing signal in the geological record changed from the dominant 41-kyr cyclicity of obliquity to the 100-kyr cyclicity of eccentricity (Berger and Jansen, 1994). It is also considered a transitional and gradual process (Mid-Pleistocene Transition, Berger et al., 1993; Mudelsee and Stattegger, 1997), characterized by global changes in the climate system, including lower global temperatures, increased global ice volume, and lower seawater temperatures (Shackleton et al., 1990). The timing of the transition is still under debate, being variously interpreted as starting as early as 1500 kyr and ending as late as 600 kyr (Prell, 1982; Ruddiman et al., 1989; Mudelsee and Schulz, 1997; Rutherford and D’Hondt, 2000; Raymo et al., 2004). During this important climate transition significant modifications in the global thermohaline circulation occurred, involving changes in the production of North Atlantic Deep Water (NADW), an oxygenated and nutrient-poor water mass (Oppo and Lehman, 1993), which plays a vital role in the ventilation
of the world's deep ocean. Significantly weaker formation of NADW occurred during the Mid-Pleistocene glaciations: this has been associated with an increase of global aridity and a decrease of atmospheric CO₂ (Raymo et al., 1997; Shackleton, 2000), during glacial times (Barnola et al., 1987; Jouzel et al., 1993), in turn related to decreased deep oceanic circulation, and enhanced biological activity (Broecker, 1982; Knox and McElroy, 1984; Broecker and Peng, 1989; Sigman and Boyle, 2000). Weaker NADW production may have caused dramatic stagnation of deep-water circulation since MIS 24 (Schmieder et al., 2000) and chemical stratification of water masses, as revealed by vertical benthic δ¹³C gradients in the North Atlantic (Oppo et al., 1995; Raymo et al., 1997; Flower et al., 2000) and in the Pacific and Indian oceans (Keigwin, 1987; Duplessy et al., 1988; Kallen et al., 1988). The δ¹³C values during glacial periods were lower in the deeper waters (>2500 m) than in upper waters (Boyle, 1988, 1990; Curry et al., 1988; Raymo et al., 1997), possibly due to tectonic processes (Raymo et al., 1988; Raymo, 1994) and/or to the northward expansion of the deep Southern Ocean Water, which has low δ¹³C values and higher nutrient content (Raymo et al., 1990; Oppo and Lehman, 1993; Bertram et al., 1995; Kleiven et al., 2003). Variations in the mode of oceanic circulation during glacial–interglacial periods modified the vertical nutrient distribution (Boyle, 1988) and affected the benthic and planktic assemblages. In particular, phytoplankton primary productivity changed as a result of variable nutrient availability during glacial and interglacial periods, playing a critical role via the biological pump on sequestration of carbon in the deep ocean and on atmospheric CO₂ levels and climate variations (Knox and McElroy, 1984; Broecker and Peng, 1989; Sigman and Boyle, 2000).

The response of marine phytoplankton communities to the Mid-Pleistocene environmental fluctuations is poorly known. Coccolithophores are a major constituent of modern marine phytoplankton; they are abundant and widespread in the oceans with many taxa sensitive to changes in the properties of the surface water masses such as temperature, salinity, turbidity and nutrient content. Moreover, coccolithophores play key roles in biogeochemical cycles, thus affecting the surface ocean CO₂ balance. Despite the increasing documentation of the ecological preferences of modern coccospheres, this group has been little used for Pleistocene paleoclimatic and paleoceanographic reconstruction when compared with other plankton groups.

This study examines changes in calcareous nannofossils in order to determine their response to global climate variation during the Mid-Pleistocene Revolution. The analyses focus on the interval belonging to the Mid-Pleistocene Transition according to Raymo et al. (2004), between about 1200 and 600 kyr, from MIS 35 to 15, in high-quality and temporally well-constrained deep-sea cores at the North Atlantic DSDP Site 607 and Mediterranean ODP Site 967. Site 607, recovered at 3427 m on the western flank of the Mid-Atlantic Ridge and located at the core depth of NADW today (Fig. 1), is ideally located to record the relative strength of NADW production during the Pleistocene (Raymo et al., 1990). Site 967, recovered at 2564 m, is situated in the eastern Mediterranean (Fig. 2), a basin that was affected by modifications in Mediterranean thermohaline circulation during the Pleistocene (Rossignol-Strick et al., 1982; Rossignol-Strick, 1983). The study of these two sites allows us to compare the response of the calcareous nannofossil assemblage in a semi-enclosed basin and in the open ocean during global paleoclimatic
changes. Diversity indices were calculated, and Principal Component Analysis were performed on the quantitative data set, in order to improve the interpretation of nannofossil abundance changes and enhance knowledge of the ecological preferences of nannofossil taxa. Finally, spectral analysis has been performed on the nannofossil abundance variations in order to extract possible Milankovitch periodicities.

2. Oceanographic setting

NADW formation is tied to the flow of warm saline surface waters to the North Atlantic and Nordic Seas in the Gulf Stream and the associated North Atlantic Drift. The NADW forms north of 60° (Fig. 1), mainly in the Greenland and Labrador Seas (Kellogg, 1987; Hay, 1993), as surface waters cool and increase in salinity due to evaporation and heat loss, thus creating a dense water mass that moves southward at depth (>2 km) carrying saline water to the South Atlantic and other ocean basins. Three components of NADW are distinguishable: the upper Labrador Sea Water enters the NADW between 1600 and 2500 m depth; the lower Denmark Strait Overflow Water is cold and relatively fresh flowing below 3500 m in the NADW. The third component (N-E Atlantic Deep Water) originates in the Greenland Sea, leaving the basin between Iceland and Scotland; it is warmer and salty because it entrains higher density Mediterranean water and Labrador Sea Water, and sinks between 2500 and 3500 in the NADW. This thermohaline circulation, involving the movement of warm salty water to high latitude of North Atlantic, the formation of NADW and the exit of water masses from the North Atlantic, is considered a conveyor belt whose strength varied on glacial and interglacial time scales during the Pleistocene (Broecker and Denton, 1989; Broecker, 1991; Imbrie et al., 1993). At the present day, the nutrient-poor and oxygenated NADW (Oppo and Lehman, 1993) fills the deep northern and tropical Atlantic, whereas, during the last glacial maximum (LGM), this deep-water mass was replaced by nutrient-rich (high δ13C) Southern Ocean Water (SOW) (Boyle and Keigwin, 1982, 1987; Oppo and Fairbanks, 1987; Duplessy et al., 1988; Curry et al., 1988; Oppo and Lehman, 1993; Oppo et al., 1995). Many studies have suggested that NADW was still produced during Pleistocene glaciations but reached depths lower than 2 km (Curry et al., 1988; Oppo and Lehman, 1993; Zhan et al., 1997; Venz et al., 1999; Kleiven et al., 2003), thus producing a water mass stratification as revealed by benthic foraminifera bathymetric δ13C gradient (Flower et al., 2000). Within this framework, Site 607 lies in water that is predominantly NADW today.

The semi-enclosed Mediterranean basin exchanges water, salt, heat, and nutrients with the North Atlantic Ocean. The nutrient-rich and low salinity Atlantic surface waters flow eastward through the Gibraltar Strait (Fig. 2). Flowing eastwards, the surface waters increase in salinity due to strong evaporation, and decrease in nutrient content due to consumption by primary producers. Winter cooling and evaporation of surface waters combine to form dense Mediterranean Intermediate Water (MIW), which spreads between 150 and 600 m below the surface layer (Wust, 1961; Malanotte-Rizzoli and Hecht, 1988). MIW flows westward increasing its nutrient content and finally exits the Strait of Gibraltar below the surface Atlantic water. Ventilation of deeper waters of the basin (Eastern Mediterranean Deep Water and Western Mediterranean Deep Water) is ensured by dense thermally-driven waters forming in the Gulf of Lions and in the Aegean and Ionian seas. The thermohaline Mediterranean circulation was modified during Pleistocene monsoonal maxima driven by
astronomical variations (precessional minima and eccentricity maxima), thus determining unventilated or anoxic deep conditions and sapropel deposition (Rossignol-Strick et al., 1982; Rossignol-Strick, 1983). The investigated Site 967 is located in an area bounding the formation area of Intermediate Water masses (Fig. 2).

3. Age models

The age models adopted here utilise orbitally tuned targets. The age model of Raymo et al. (2004) was used at Site 607. In this age model $\delta^{18}O$ data from the benthic foraminifera Cibicidoides and Uvigerina of Ruddiman et al. (1989), have been tuned to the Shackleton et al. (1990) target record. The data have been linearly interpolated to a uniform 3-kyr spacing and smoothed with a five-point running mean (Raymo et al., 2004). This provides a clear pattern of global climate changes in the $\delta^{18}O$ record and enables an easier comparison with the main nannofossil assemblage variations. Glacial stages were labelled according to Ruddiman et al. (1989).

The age model for Site 967 is from Kroon et al. (1998) and was established by a combination of astronomical calibration of the sapropel record and the stable oxygen isotope stratigraphy. The planktonic $\delta^{18}O$ record at Site 967 documents global climate changes; it shows large amplitude fluctuations mainly caused by variations in surface water temperature and salinity, predominantly influenced by eccentricity, obliquity, and precessional related orbital fluctuations (Kroon et al., 1998). The age models adopted in the present study are almost equivalent between the two different sections and are well comparable with the recent isotope chronology of Lourens (2004). Main references of studied sites are shown in Table 1.

4. Sampling and analyses

A total of 263 samples were analysed in the interval across MIS 35 to 15. According to the different sedimentation rates, ranging from about 25–40 m/Ma at both sites, sample spacing varied between 10 and 20 cm, in order to obtain approximately one sample per 2–5 kyr. Frequently, the samples used for oxygen isotope analysis (Ruddiman et al., 1989; Kroon et al., 1998) have also been investigated in this study.

Simple smear slides were prepared from unprocessed samples according to standard technique (Bown and Young, 1998) and analysed under a polarized light microscope at a magnification of 1000×. Quantitative data were collected by counting about 300 nannofossils $>4 \mu$m in size. Nannofossils $<4 \mu$m in size were not included in these counts, since small placoliths always dominate the assemblages and so abundances of the other taxa would have not been well represented. Additionally, in order to evaluate abundances of Florisphaera profunda and small placoliths $<4 \mu$m in size, a supplementary count of 300 specimens of the total nannofossil assemblages was performed, as suggested by Matsuoka and Okada (1989) and Castradori (1993). The abundance of each taxon has been plotted as a percentage of the selective count. Quantitative abundances of calcareous nannofossils at the same sites can be also found in Maiorano and Marino (2004), where only selected marker species have been considered per unit area. Numerical data of the $>4 \mu$m assemblage were performed using PAST (PAleontology STatistic) software (Hammer et al., 2001), in order to estimate the Shannon–Weaver index (diversity and dominance). In addition Principal Component Analysis was carried out on this assemblage, using SPSS software version 10. The measure of diversity is based on a count on genus level, or on species when a sole species is recorded within a genus (Pseudoemiliania lacunosa, Calcidiscus leptoporus, Cocolithus pelagicus s.l., Neospaera coccolithomorpha, Braarudosphaera bigelovii); this allows comparison of homogeneous taxonomic units in order to identify the main changes in the relative richness and dominance of the assemblages. Patterns of diversity and of the factor with maximum variance have been plotted and interpreted in terms of paleoclimatic and paleoceanographic changes. The ecological preferences of the observed taxa are discussed in Appendix A.

The quantitative data of selected calcareous nannofossil species, the PCA Factor with maximum variance and Shannon–Weaver Index fluctuations were processed by spectral analysis using the AnalySeries program of Paillard et al. (1996). The spectral analysis and the filtering (Gaussian band-pass filters) procedures are based on the standard approach of Jenkins and Watt (1968) and Weedon (1991), which make it possible to highlight the harmonic structure of the obtained signal and offers the opportunity to filter the original time series in selected frequency bands. This technique was developed to identify, in climate-sensitive records, cyclic alternations correlatable with variations of the same order recognised in the astronomical target curves.

5. Results

5.1. Changes in the nannofossil abundances

The studied interval corresponds to MIS 35 to 15 across the small Gephyrocapsa and P. lacunosa zones. Quantitative

<table>
<thead>
<tr>
<th>Studied sites</th>
<th>Location, latitude, longitude</th>
<th>Previous calcareous nannofossil studies</th>
<th>Oxygen isotope stratigraphy</th>
<th>Sapropel stratigraphy–insolation cycle</th>
<th>Age model</th>
</tr>
</thead>
</table>
Fig. 3. Abundance patterns of selected calcareous nannofossils at Site 607 and correlation with \( \delta^{18}O \) stratigraphy. Shaded bands represent glacial cycles. Quantitative data are % abundances in a count of 300 total nannofossils >4 \( \mu \text{m} \) in size. Last common occurrence (LCO) of \( R. \text{asanoi} \) and re-entry of medium \( \text{Gephyrocapsa} \) (reemG = first occurrence of \( \text{Gephyrocapsa omega} >4 \mu \text{m} \)) are indicated according to Maiorano and Marino (2004) and this study.
Fig. 4. Abundance patterns of selected calcareous nannofossils at Site 607 and correlation with δ¹⁸O stratigraphy. Shaded bands represent glacial cycles. Quantitative data are % abundances in a count of 300 total nannofossils >4 μm in size. Last common occurrence (LCO) of R. asanoi and re-entry of medium Gephyrocapsa (reemG = first occurrence of Gephyrocapsa omega >4 μm) are indicated according to Maiorano and Marino (2004) and this study.
abundances of the most significant calcareous nannofossils through the succession of glacial and interglacial intervals are shown in Figs. 3–8.

In both sections the major component of the calcareous nannofossil assemblage is represented by placoliths <4 μm (Figs. 3–5), among the nannofossils >4 μm, Reticulofenestra spp., medium Gephyrocapsa, P. lacunosa are the most abundant taxa. Other common taxa are C. leptoporus and Helicosphaera spp. Abundances generally lower than 10% are recorded for Umbilicosphaera spp., Syracosphaera spp., Rhabdosphaera spp., Oolithotus spp. On the other hand F. profunda, C. pelagicus s.l., and Pontosphaera spp. are minor components of the nannofossil assemblage having abundances consistently lower than 7%. Calciosolenia spp., Scyphosphaera spp., N. coccolithomorpha, and Thoracosphaera spp. are very rare (percentage lower than 1%) or absent and therefore their abundance patterns are not shown.

At Site 967 (Figs. 6–8) the calcareous nannofossil assemblage is mostly represented by the extinct species P. lacunosa, medium Gephyrocapsa, F. profunda, Rhabdosphaera spp., and Syracosphaera spp. Additional common taxa are Reticulofenestra spp., Umbilicosphaera spp., C. leptoporus, Calciosolenia spp., Helicosphaera spp. Minor components are Pontosphaera spp., C. pelagicus s.l., Oolithotus spp. A few taxa such as Ceratolithus spp., Scyphosphaera spp. and B. bigelowii are very rare and scattered in the assemblage.

In both sections some of the taxa show short-term variations, sometimes clearly related to glacial–interglacial cycles. The pattern of medium Gephyrocapsa observed above its well-known temporary disappearance interval, ending in stage 29 at Site 607 (this study) and 25 at Site 967 (Maiorano and Marino, 2004), generally shows a positive correlation with interglacial stages (Figs. 3 and 6) and particularly with MIS 25, 23, 21, and 19.

At Site 607 C. leptoporus, Umbilicosphaera spp., Syracosphaera spp., Rhabdosphaera spp., and Oolithotus spp., have higher abundances during interglacial stages, especially in the upper part of the record, MIS 21–15 (Fig. 3). These taxa do not clearly show a relation with oxygen isotope fluctuations at Site 967 (Fig. 6), with the exclusion of Umbilicosphaera spp. which shows positive correlation with interglacial episodes, particularly in the interval MIS 21–15, when the taxon is recorded in higher relative abundance. Syracosphaera spp. and Rhabdosphaera spp. are more abundant taxa in the Mediterranean site (Fig. 6), with percentages up to 30–40%, than in the Atlantic section (percentages lower than 5–8%) (Fig. 3).

The abundance of Helicosphaera spp. does not show a clear relation to glacial–interglacial stages at either site (Figs. 4 and 7). At Site 607 a sharp increase is noted from MIS 21 upward (Fig. 4). Helicosphaera spp. are more abundant in the Mediterranean section with percentages generally of about

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**Fig. 5.** Abundance patterns of small placoliths and Florisphaera profunda at Site 607 and correlation with δ18O stratigraphy. Shaded bands represent glacial cycles. Quantitative data are % abundances on 300 specimens of the total nannofossil assemblage. Last common occurrence (LCO) of R. asanoi and re-entry of medium Gephyrocapsa (reemG = first occurrence of Gephyrocapsa omega >4 μm) are indicated according to Maiorano and Marino (2004) and this study.
Fig. 6. Abundance patterns of selected calcareous nanofossils at Site 967 and correlation with δ¹⁸O and sapropel stratigraphy. Shaded bands represent glacial cycles. Quantitative data are % abundances in a count of 300 total nanofossils >4 μm in size. Last common occurrence (LCO) of *R. asanoi* and re-entry of medium *Gephyrocapsa* (reemG = first occurrence of *Gephyrocapsa omega* >4 μm) are indicated according to Maiorano and Marino (2004).
Fig. 7. Abundance patterns of selected calcareous nanofossils at Site 967 and correlation with δ¹⁸O and sapropel stratigraphy. Shaded bands represent glacial cycles. Quantitative data are % abundances in a count of 300 total nanofossils >4 μm in size. Last common occurrence (LCO) of R. asanoi and re-entry of medium Gephyrocapsa (reeG = first occurrence of Gephyrocapsa omega >4 μm) are indicated according to Maiorano and Marino (2004).
15–20% and with peaks reaching 60%; in the Atlantic site the genus has percentages mainly lower than 5%, with a few peaks up to 20%.

The pattern of the extinct *P. lacunosa*, at Site 607, reveals high abundances during the glacials MIS 24, 20 and 16, showing the highest values during MIS 16 (Fig. 4). On the other hand, in the Mediterranean section, where the species is more abundant, several abundance peaks of the species are recorded in the warmer periods with the highest abundance at the bottom of MIS 21 (Fig. 7). At Site 607, *Reticulofenestra* spp. (*R. minutula*, *R. asanoi*, *Reticulofenestra* sp., see Appendix A) are the major component of the assemblage in the lower cores of the site up to bottom of MIS 21 (Fig. 4), when an abrupt decrease is recorded. This pattern is also observed from MIS 23–22 to MIS 18 at Site 967 (Fig. 7).

The patterns of *Calciosolenia* spp. and *Pontosphaera* spp. do not show apparent relationship with glacial–interglacial stages at either site. *Calciosolenia* spp. are relatively more abundant in the Mediterranean section (Fig. 6) than in the Atlantic section. *C. pelagicus* s.l. is mainly represented by *C. pelagicus braarudii* in the Atlantic site (Fig. 4), showing distinct peaks in abundance in the cold glacials MIS 18 and 16. In the Mediterranean section the taxon primarily consists of *C. pelagicus pelagicus* while *C. pelagicus braarudii* mainly occurs at MIS 16 (Fig. 7). *C. pelagicus azorinus* is virtually absent at both sites. The small placolith group (essentially *Gephyrocapsa* spp. <4 µm) shows abundance fluctuations at both sites (Figs. 5 and 8). Strong short-term shifts in the abundance characterize the upper MIS 25 to MIS 22/21. No simple relationship can be observed with respect to glacial–interglacial cycles, even though small placoliths seem to increase in several interglacial episodes.

Although *F. profunda* is rare in the calcareous nannofossil assemblage at the Atlantic site, important short-term fluctuations characterize MIS 24 to MIS 22/21 (Fig. 5); at Site 967 significant shifts are observed through MIS 22 and 21 (Fig. 8). A general opposite trend can be observed between the patterns of small placoliths and *F. profunda* at the Atlantic site. This negative correlation is also observed at Site 967, mainly through MIS 36–26.

### 5.2. Measure of diversity and Principal Component Analysis

At Site 607, a distinct change in the Shannon–Weaver index (H) occurs at the MIS 22/21 transition (Fig. 9): a minimum in the diversity is observed at MIS 22, and a sharp increase is recorded from MIS 21 upward. At Site 967, a sharp decrease in diversity characterizes the bottom of MIS 21 (Fig. 10), followed by a recovery within MIS 21, testifying a reasonable similarity with the Atlantic site. The pattern of diversity is different in the two sections: at Site 607 the index has slightly lower values and a more distinct trend through time; it fluctuates between 0.8 and 1.6 below MIS 22, and between 1.6 and 2 above MIS 22 (Fig. 9). At Site 967 it consistently ranges between 1.2 and 2,
throughout the section (Fig. 10). The trend of dominance reflects changes in diversity in both sections; maximum dominance values, recorded at minimum diversity in the nannofossil assemblage at MIS 22/21, correspond to dominance of *Reticulofenestra* spp. at Site 607, and of *P. lacunosa* at Site 967.

Principal Component Analysis allows an interpretation of the complex patterns of nannofossil changes at the Mid-Pleistocene Transition. At both sites only Factor 1 is discussed, since Factor 2 has a very low variance (<14%) and therefore is of uncertain interpretation. At Site 607 the first component (Factor 1) accounts for 23% of the variance and it is positively loaded mainly by *Umbilicosphaera* spp. and *C. leptoporus* with negative loadings for *Reticulofenestra* spp. (Table 2). Factor 1 seems to discriminate between taxa (see Appendix A) indicative of warm, oligotrophic and stratified water masses (*Umbilicosphaera* spp. and *C. leptoporus*), and of mixed and high productive cool waters (*Reticulofenestra* spp.). The Factor 1 score plot (Fig. 9) shows short fluctuations below MIS 22 and significantly more positive values, together with high amplitude changes, from MIS 21 upwards. This pattern seems unrelated to the LCO of *Reticulofenestra asanoi* and to the drop in abundance of *Reticulofenestra* sp. at MIS 23/MIS 22/21, and of medium *Gephyrocapsa* (reemG = first occurrence of *Gephyrocapsa* omega–4 μm) at MIS 22/21. The minimum in diversity occurring at these times is also accompanied by a decrease of dissolution-resistant coccoliths, such as medium *Gephyrocapsa* and *C. leptoporus* (Figs. 3 and 6), and by a dominance of eutrophic taxa (*P. lacunosa* and *Reticulofenestra* spp.) (Figs. 4 and 7) and therefore it may be interpreted as due

5.3. Dissolution of calcareous nannofossil assemblages

Although dissolution is more intense during glacial periods in both the Atlantic Ocean (Curry and Lohman, 1986; Meyers and Diester-Haas, 1987; Diester-Haas and Rothe, 1987; deMenocal et al., 1997) and the Mediterranean Sea (Vázquez and Zamarreño, 1993), the calcareous nannofossil preservation, which generally varies from moderate to good at both sites, does not show clear differences in dissolution status between glacial and interglacial stages. This could be supported by the pattern of Shannon–Weaver index, which does not show minima during the glacial periods, as would be expected from a dissolution effect, with the exception of MIS 22 or 22/21. The minimum in diversity occurring at these times is also accompanied by a decrease of dissolution-resistant coccoliths, such as medium *Gephyrocapsa* and *C. leptoporus* (Figs. 3 and 6), and by a dominance of eutrophic taxa (*P. lacunosa* and *Reticulofenestra* spp.) (Figs. 4 and 7) and therefore it may be interpreted as due...
to a primary ecological response of the nannofossil assemblage rather than to dissolution.

5.4. Spectral analyses

In order to understand the short-term fluctuations occurring in the calcareous nannofossil assemblages, in terms of astronomical forcing and paleoceanographic changes during the Middle Pleistocene Revolution, power spectral analysis and filtering procedures have been attempted. Few data are available on orbital periodicity in the calcareous nannofossil record during the Pleistocene, and they mainly focus on *F. profunda*, revealing Milankovitch periodicities (Molfino and McIntyre, 1990; Bassinot et al., 1997; Beaufort et al., 2003). The power spectral analysis (calculated according to the Blackman–Tukey method with a Tukey window), suggests that the fluctuations observed in most of the taxa (*C. leptoporus*, *F. profunda*, *P. lacunosa*, medium *Gephyrocapsa*, *Syracosphaera* spp. and *Rhabdosphaera* spp.), Factor 1 and Shannon–Weaver Index from both sites (Fig. 11), yield significant peaks mainly in the obliquity (41-kyr) frequency bands. The 100-kyr periodicity is also present in the *C. leptoporus*, *P. lacunosa* and medium *Gephyrocapsa* power spectra. *F. profunda* and *C. leptoporus* are the only two records showing significant spectral variance occurring at the frequency of 23-kyr at Site 967 (Fig. 11). These results indicate that the quasi-periodic oscillations observed in the variations of calcareous nannofossil assemblage and characteristics of surface waters (Factor 1) are largely controlled by these orbital parameters. However, other distinct peaks in the spectra do not correspond to the primary Milankovitch frequencies (Fig. 11).

Since wide disagreement exists in defining when the possible transition from 41-kyr forcing up to 100-kyr could have occurred, floating spectral analyses were performed in

![Fig. 10. Correlation between δ¹⁸O stratigraphy, pattern of diversity (H), dominance (D) and score plot of Factor 1 at Site 967. Shaded bands represent glacial cycles. Last common occurrence (LCO) of *R. asanoi* and re-entry of medium *Gephyrocapsa* (reemG = first occurrence of *Gephyrocapsa* omega > 4 μm) are indicated according to Maiorano and Marino (2004).](image-url)

### Table 2

<p>| Loadings of calcareous nannofossil taxa on the first principal component at Site 607 and Site 967 |
|---------------------------------|---------------------------------|---------------------------------|---------------------------------|</p>
<table>
<thead>
<tr>
<th><strong>Matrix of component Site 607</strong></th>
<th><strong>Factor 1</strong></th>
<th><strong>Matrix of component Site 967</strong></th>
<th><strong>Factor 1</strong></th>
</tr>
</thead>
<tbody>
<tr>
<td><em>P. lacunosa</em></td>
<td>0.344</td>
<td><em>P. lacunosa</em></td>
<td>-0.727</td>
</tr>
<tr>
<td>Medium <em>Gephyrocapsa</em></td>
<td>0.451</td>
<td>Medium <em>Gephyrocapsa</em></td>
<td>-0.151</td>
</tr>
<tr>
<td><em>Helicosphaera</em> spp.</td>
<td>0.579</td>
<td><em>Helicosphaera</em> spp.</td>
<td>0.536</td>
</tr>
<tr>
<td><em>Reticulofenestra</em> spp.</td>
<td>-0.887</td>
<td><em>Reticulofenestra</em> spp.</td>
<td>-0.574</td>
</tr>
<tr>
<td><em>C. leptoporus</em></td>
<td>0.668</td>
<td><em>C. leptoporus</em></td>
<td>0.484</td>
</tr>
<tr>
<td><em>Syracosphaera</em> spp.</td>
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<td><em>Syracosphaera</em> spp.</td>
<td>0.721</td>
</tr>
<tr>
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<td>0.777</td>
<td><em>Umbilicosphaera</em> spp.</td>
<td>0.035</td>
</tr>
<tr>
<td><em>Rhabdosphaera</em> spp.</td>
<td>0.264</td>
<td><em>Rhabdosphaera</em> spp.</td>
<td>0.671</td>
</tr>
<tr>
<td><em>Calciosolenia</em> spp.</td>
<td>0.372</td>
<td><em>Calciosolenia</em> spp.</td>
<td>0.220</td>
</tr>
<tr>
<td><em>Pontosphaera</em> spp.</td>
<td>-0.035</td>
<td><em>Pontosphaera</em> spp.</td>
<td>0.545</td>
</tr>
<tr>
<td><em>Oolithotus</em> spp.</td>
<td>0.517</td>
<td><em>Oolithotus</em> spp.</td>
<td>0.205</td>
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<tr>
<td><em>N. coccolithomorpha</em></td>
<td>0.443</td>
<td><em>Scyphosphaera</em> spp.</td>
<td>0.596</td>
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<tr>
<td><em>Scyphosphaera</em> spp.</td>
<td>0.314</td>
<td><em>B. bigelowii</em></td>
<td>0.201</td>
</tr>
<tr>
<td><em>C. pelagicus</em> pelagicus</td>
<td>-0.066</td>
<td><em>Ceratolithus</em> spp.</td>
<td>0.223</td>
</tr>
<tr>
<td><em>C. pelagicus</em> braarudii</td>
<td>0.230</td>
<td><em>C. pelagicus</em> pelagicus</td>
<td>0.535</td>
</tr>
<tr>
<td>Method: Principal Component Analysis</td>
<td>Method: Principal Component Analysis</td>
<td>Method: Principal Component Analysis</td>
<td>Method: Principal Component Analysis</td>
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several time windows, on selected climate-sensitive records from both sites. The results seem to suggest that ~1200–~850 kyr and ~850–~575 kyr time intervals represent the two possible windows where the 41-kyr–100-kyr transition could occur. In the present study we report only data from site 967 where this change seems almost clear in few taxa (Fig. 12): the power spectra of *P. lacunosa*, *C. leptoporus* and *Syracosphaera* spp. data performed in the two selected time windows 1200–850 kyr and 850–575 kyr, revealed significant peaks in the 41-kyr and 100-kyr frequency bands, respectively (Fig. 12). Finally Gaussian band-pass filtering has been applied to extract the 41-kyr frequency component from selected calcareous nannofossils, Factor 1 and Shannon Index time series and to compare them with the stable isotope stratigraphy (Fig. 13). Visual comparison of the time series suggests a general good relationship between the obliquity component of the climate proxies, in terms of ecological signature, and the standard δ¹⁸O target curves for Site 607 and Site 967. The main discrepancies are present in the Mediterranean Site 967 where the calcareous nannofossil taxa are not completely in agreement with the δ¹⁸O record in the whole studied time interval. This may be related to an additional non-astronomical forcing which controls the climatic system (regional component).

6. Discussion

The quantitative analyses point out few differences in the taxonomic composition of the calcareous nannofossil assemblage between the Atlantic and the Mediterranean sites. *Syracosphaera* spp. and *Rhabdosphaera* spp. are significantly more abundant in the Mediterranean section, which may be a response to warmer and more oligotrophic condition in the surface waters; this observation is in agreement with the higher abundances of these extant taxa in the Eastern Mediterranean (Knappertsbusch, 1993). Moreover, higher diversity values and higher abundance of *F. profunda* at Site 967 also suggest the more oligotrophic aspect of the eastern Mediterranean.
Mediterranean Sea with respect to Atlantic water masses during the Pleistocene. Although there are no data on the ecological preference of the extinct *P. lacunosa*, and only few data are known on the ecology of *Calciosolenia* spp., the significantly higher abundance and stronger fluctuations of these taxa in the Mediterranean site may suggest a possible relation with higher variability in salinity and nutrient content, due to the changeable paleoceanographic conditions during Pleistocene rhythmic sapropel deposition in the eastern Mediterranean. In fact, peaks in abundance of *Calciosolenia* spp. and increase of *P. lacunosa* have been recently recorded within sapropel layers (Negri et al., 2003; Flores et al., 2005).

Despite the different composition of calcareous nannofossil assemblages between the two sections, the variations through time seem to reflect modifications in the characteristics of water masses in both sites, as evidenced by abundance patterns of selected taxa, pattern of Factor 1 and diversity. These variations are mainly controlled by the obliquity 41 kyr periodicity and therefore primarily reflect climate signal and glacial–interglacial cycles. Few taxa (*C. leptoporus*, *P. lacunosa*, *Syracosphaera* spp.) record the 41–100 kyr periodicity transition at around 850 kyr, at MIS 22/21.

Obliquity-related variations in the benthic δ¹⁸O records from the open ocean have been interpreted to reflect changes in global ice volume (e.g. Shackleton et al., 1990, 1995; Raymo et al., 1989; Tiedemann et al., 1994). Obliquity-related variations in the Mediterranean δ¹³C record have been interpreted in a similar way (Lourens and Hilgen, 1997), but in this case the signal is amplified due to regional changes in sea-surface salinity and/or temperature (Hilgen et al., 1993). According to these data the strong power at the 41–kyr periodicity, occurring in the calcareous nannofossil variations from Site 967, is consistent with the assumption that the eastern Mediterranean climate (during the Pleistocene) was considerably affected by changes in northern hemisphere climate (Lourens et al., 1996a,b; Kroon et al., 1998) and references therein, when Arctic ice sheets expanded rapidly.

Trends in the abundance of selected taxa, observed in the open ocean Atlantic Site 607, have been of major importance for unravelling significant paleoceanographic changes with respect to the semi-enclosed Mediterranean Sea. The low amplitude fluctuations noted in most of the patterns, through MIS 35–22, and the distinct higher amplitude variations from MIS 21 upwards (Figs. 3–4), can be associated with the major changes in physical and chemical features of the water masses, related to the shift toward more intense glacial conditions (Ruddiman et al., 1989). More unstable conditions in surface waters are already known during the acme interval of small *Gephyrocapsa* (small *Gephyrocapsa* Zone, MIS 38/29–25), which has been suggested as characterized by high productivity and poorly stratified surface waters (Gartner et al., 1987). In the studied sections the high amplitude, short-term, shifts of small placoliths and *F. profunda* (Figs. 5 and 8) occurring through MIS 24 to 22/21 indicate strong instability in the nutricline dynamics and in productivity of surface waters. This pattern may be the beginning of significant changes in the calcareous nannofossil assemblage as a response to the shift towards much larger north hemisphere ice sheet at the Mid-Pleistocene Transition, at around 920 kyr (Ruddiman et al., 1989; Berger and Jansen, 1994; Mudelsee and Schulz, 1997). At this transition, the amplitude of sea level fluctuations in glacial cycles increased up to 33 m (Prell, 1982; Ruddiman et al., 1989) and nutrient supply also increased from land and continental shelves (Kitamura and Kawagoe, 2006), leading to higher primary productivity (Broecker, 1982).

The minimum in diversity recorded in both sites at MIS 22 and 22/21 (Figs. 9–10) and the corresponding dominance of *Reticulofenestra* spp. at Site 607 and of *P. lacunosa* at Site 967, may reflect r-selected life strategies in eutrophic conditions (Young, 1994). A positive relation between enhanced stability of water masses, an increase in diversity and switch to k-selection life strategies is already well known (Dodd and Stanton, 1981; Hallock, 1987; Aubry, 1992; Brand, 1994; Young, 1994; Bown et al., 2004). The dominance of taxa at MIS 22/21 is recorded just above the minimum values in Atlantic δ¹³C recorded in the benthic foraminiferal tests at the base of MIS 22 (Kleiven et al., 2003; Raymo et al., 2004), possibly due also to the higher flux of organic matter at the sediment–water interface, during a major sea level fall or to the northward expansion of the deep Southern Ocean Water.

From MIS 21 upwards, the significant increase of warm oligotrophic taxa, mainly during interglacial cycles, and a general increase in diversity, seem to indicate the onset of more stable and stratified surface waters. This change in the nannofossil assemblage seems to support the hypothesis of a
weaker production or suppression of North Atlantic Deep Water during glacials (Raymo et al., 1990; Raymo et al., 1997; Venz et al., 1999), which may have been responsible for a more stratified water column, lower upwelling rate and oligotrophic surface waters.

7. Concluding remarks

Calcareous nannofossil assemblages in the studied cores show strong changes in abundance patterns that may reflect modifications in surface waters. Although the abundances of several taxa co-vary with glacial or interglacial cycles, particularly at Site 607, the Principal Component Analyses suggest that in both analysed sections the primary change (Factor 1) in the assemblage is related to stratification and nutrient content of surface waters. The quasi-periodic oscillations in the paleoenvironmental proxy data are controlled by orbital cyclicity, especially obliquity (41-kyr).

The beginning of the calcareous nannofossil changes is observed through MIS 24/22, and is marked by high amplitude fluctuations in the abundance of small placoliths and *F. profunda* suggesting strong instability in the nutricline dynamics. This is probably related to the transition from the dominant 41-kyr cyclicity to the 100-kyr cyclicity. Distinct changes in siliceous and calcareous plankton composition have been also recorded during the MPR, at MIS 24–22.
and Abelmann, 2002; Zheng et al., 2005), as due to significant modification in the surface water masses. At MIS 22/21, a minimum in diversity in both the sites and dominance of Reticulofenestra spp. at Site 607 and of P. lacunosa at Site 967 are recorded, and are interpreted as r-selected life strategies in more eutrophic conditions. From MIS 21 upwards, calcareous nannofossil changes suggest a trend towards more stable, oligotrophic and stratified surface waters which may be related to weaker production of glacial NADW. This trend is clearer in the Atlantic section than in the Mediterranean site; it cannot be excluded that within the semi-enclosed Mediterranean basin the interaction between several factors (salinity, nutrients, temperature, turbidity) and the rhythmic paleoceanographic changes related to Pleistocene sapropel deposition, may have played a more complex role in the abundance pattern of calcareous nannofossils. Preliminary results suggest that variations of few calcareous nannofossil taxa at Site 967 recorded a change from the dominant 41-kyr to 100-kyr periodicity from about 850 kyr upwards.

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Appendix A. Ecological notes

In this section we review the available data on the autecology and paleoecological significance of the identified taxa and compare these observations with the results of the present study.

C. leptoporus has been described as being characteristic of tropical to subtropical oligotrophic warm water masses and of upper and middle photic zones (McIntyre and Bé, 1967; McIntyre et al., 1970; Okada and Honjo, 1973; Blasco et al., 1980; Klejine, 1993; Winter et al., 1994; Flores et al., 1999; Baumann et al., 2004; Ziveri et al., 2004). In the eastern Mediterranean, co-variance of C. leptoporus and H. carteri has been observed (Ziveri et al., 2000). In addition, some ecological preference for eutrophic environments have been inferred (Roth and Berger, 1975; Fincham and Winter, 1989; Andruleit and Rogalla, 2002; Flores et al., 2003). C. leptoporus is one of the most dissolution-resistant species (Schneidermann, 1977) and the increase of its abundance in more fertile areas has been supposed to be related to selective dissolution occurring in organic-carbon rich sediments (Baumann et al., 2004). C. leptoporus has been shown to consist of different sub-taxa (Knappertsbusch et al., 1997; Quinn et al., 2004), although their distribution is rather complex (Ziveri et al., 2004). No subdivision into sub-taxa was attempted in this study. However, it is noteworthy that C. leptoporus is mainly represented by specimens >8 μm in size, belonging to the large morphotype of Knappertsbusch et al. (1997). In the studied sections, the ecological preferences of C. leptoporus are related to warmer, oligotrophic and stratified surface waters; the species loads positively on Factor 1 together with Syracosphaera spp. and Rhabdosphaera spp. at Site 967, and with Umbilicosphaera spp. at Site 607.

Calciosolenia spp. The ecological affinity of calciosolenids has not been extensively-documented. They have been described as coastal or shelf taxa (Reid et al., 1978; Banse, 1994; Andruleit and Rogalla, 2002; Malinverno et al., 2003), living in the middle photic zone (Jordan and Chamberlain, 1997; Malinverno et al., 2003). Peaks in abundance of Calciosolenia spp. have been recorded within Messinian sapropel layers (Flores et al., 2005). The taxon was significantly more abundant in Site 967 than in the Atlantic Site 607; this pattern may have a relation with sapropel deposition according to Flores et al. (2005), and probably with higher nutrient content and turbidity of surface water, as suggested by Banse (1994) and Andruleit et al. (2003).

C. pelagicus s.l. has been often considered a cold-water taxon (McIntyre and Bé, 1967; Roth and Coulbourn, 1982; Samtleben and Bickert, 1990; Samtleben et al., 1995; Andruleit, 1997). High nutrient concentration and more dynamic conditions from several upwelling areas have been also related to this taxon (Blasco et al., 1980; Giraudseau and Balely, 1995; Cachao and Moita, 2000; Boeckel and Baumann, 2004). Recently, Baumann et al. (2000) and Geisen et al. (2002) documented the existence of two extant subspecies: C. pelagicus ssp. pelagicus (≪10 μm long) and C. pelagicus ssp. braarudii (≫10 μm long), the former being a subartic taxon and the latter a temperate form, related to upwelling conditions (Baumann, 1995; Baumann et al., 2000; Cachao and Moita, 2000; Parente et al., 2004; Narciso et al., 2006). More recently a third subspecies C. pelagicus ssp. azorinus (≫14 μm long) has been differentiated (Parente et al., 2004) and related to the influence of water masses from the Azores front. In both studied sites these taxa are consistently rare, so they are clearly outside their primary distribution area. Nonetheless, the increase in abundances of C. pelagicus ssp. braarudii during MIS 16 (sites 607 and 967) and 18 (Site 607) may suggest an ecological preference of the larger form for cold-water masses during the Mid-Pleistocene. The high abundance values of F. profunda during MIS 16 and 18 seems to exclude the occurrence of upwelling conditions.

F. profunda inhabits the lower photic zone (Okada and Honjo, 1973; Okada and McIntyre, 1977; Molfino and McIntyre, 1990). Its distribution seems to be limited to waters warmer than 10 °C (Okada and Honjo, 1973; Okada and McIntyre 1979). Changes in the abundance patterns of the species have been explained in terms of changes in thermocline and nutricline dynamics and in primary productivity (Molfino and McIntyre, 1990; Castradori, 1993; Jordan et al., 1996; Beaufort et al., 1997; Ziveri and Thunell, 2000). Low abundances of F. profunda are generally considered to be an indication of relatively high surface water productivity due to a shallow nutricline or upwelling. Higher values of the small placolith/F. profunda ratio have been used as an indication of higher productivity in the upper photic zone (Beaufort et al., 1997; Takahashi and Okada, 2000; Flores et al., 2000; Colmenero-Hidalgo et al., 2004). Hence, the higher abundance of F. profunda at Site 967 is likely to be a response to the more oligotrophic surface water in the eastern Mediterranean with respect to the Atlantic ocean; the anti-correlation of the species with abundance fluctuations of small placoliths in both the Atlantic and Mediterranean sections, supports the interpretation that the species is an indicator of deep nutricline and low productivity in surface waters.
Medium *Gephyrocapsa*. In the study sites medium *Gephyrocapsa* (>4 μm) are mainly composed of *G. omega*, whose ecological preferences are poorly known: a preference for warm and low salinity waters and for high nutrient conditions has been inferred in Pleistocene sediments (Maiorano and Marino, 2004). Data from the recent record indicate a warm water preference for *gephyrocapsids* having high angle bridge (McIntyre et al., 1970; Bollmann, 1997; Takahashi and Okada, 2000). Comparable environmental preferences are known for *Gephyrocapsa oceanica* Kampnemer (>3 μm); the species has proved to be a warm water taxon both in the recent (Okada and Honjo, 1973; Honjo and Okada, 1974; Geitzenauer et al., 1976; Okada and McIntyre, 1979; Klejine et al., 1989; Giraud, 1992; Jordan and Chamberlain, 1997; Jordan and Winter, 2000; Hagino et al., 2000; Findlay and Giraud, 2000; Di Stefano and Incarbona, 2004) and in the Pleistocene record (Thierstein et al., 1977; Gartner, 1988; Flores et al., 1999; Sprovieri et al., 2003). It prefers high nutrient contents (Winter, 1982; Mitchell-Innes and Winter, 1987; Gartner, 1988; Houghton and Guptha, 1991; Kink et al., 2000; Cortes et al., 2001; Andruleit and Rogalla, 2002; Boeckel and Baumann, 2004) and low salinity (Tanaka, 1991; Klejine, 1993; Knappertsbusch, 1993; Jordan and Winter, 2000; Di Stefano and Incarbona, 2004). *G. oceanica* is also considered a low latitude upwelling taxon (Mitchell-Innes and Winter, 1987; Ziveri et al., 1995; Broerse et al., 2000; Andruleit et al., 2000). However, different ecological requirements are known for *G. oceanica*: high abundances are recorded in the upper Pleistocene cold stages (Henriksson, 2000; Kink et al., 2000), and in stable waters (Gartner et al., 1987). *G. oceanica* type I (large central area) of Hagino et al. (2000) may indicate well-stratified oligotrophic waters. Moreover, coastal waters and neritic sea environments can be dominated by *G. oceanica* (Okada and Honjo, 1975; Zang and Siesser, 1986; Jordan et al., 1996; Cortes et al., 2001). In the studied sections medium *Gephyrocapsa* shows a positive relation with interglacial stages, suggesting a preference for warm surface waters. The lower abundance of this taxon in the eastern Mediterranean nean suggests a preference for lower salinity and higher nutrient conditions.

*Helicosphaera* spp. In the study sites *Helicosphaera* spp. is mainly represented by *H. carteri*. The genus is reported as a coastal water taxon (Okada, 1992; Giraud, 1992; Ziveri et al., 1995) with a preference for low nutrient and high temperature waters (Haidar and Thierstein, 1997). *H. carteri* is known to have affinities for warm water (McIntyre and Bé, 1967; Gard and Backman, 1990; Brand, 1994; Baumann et al., 2005) and moderately elevated nutrient levels (Ziveri et al., 1995; Ziveri et al., 2000; Andruleit and Rogalla, 2002; Findlay and Giraud, 2000; Ziveri et al., 2004; Baumann et al., 2005). It seems to prefer also oligotrophic waters (Giunta et al., 2003) and peaks of the species are recorded within sapropel layers (Muller, 1985; Castradoni, 1993; Negri et al., 1999; Negri and Giunta, 2001; Negri et al., 2003). High abundances of *H. carteri* have been recorded during high productivity episodes (Pujo, 1992; Flores et al., 1995) and in upwelling regions (Estrada, 1978; Giraud, 1992). Significant peaks of *H. carteri* are also observed during glacials 2–4 (Flores et al., 1999). Lower salinity and turbid water preferences are indicated by Colmenero-Hidalgo et al. (2004). The paleoecological meaning of *Helicosphaera carteri* is therefore highly variable. In the present study, the taxon is more abundant in the eastern Mediterranean and shows a more distinct pattern at Site 607 increasing in abundance from MIS 21 upward, together with several warm and oligotrophic taxa.

*Oolithus* spp. The species *O. fragilis* and *O. antillarum* are reported as both lower and middle photic zone taxa (Okada and McIntyre, 1977; Winter et al., 1994; Takahashi and Okada, 2000). *Oolithus fragilis* has been described as a warm water species, with a preference for moderately high nutrient conditions (Roth and Coulbourn, 1982); *Oolithus antillarum* seems to show affinity to high nutrient concentrations (Zeltner, 2000; Andruleit and Rogalla, 2002). The genus shows a positive relation to interglacial stages, mainly at Site 607, suggesting a warm water preference.

Small placoliths. In the studied sites, this group is mostly represented by small *Gephyrocapsa* and rare *Reticulofenestra* spp. Small specimens of these genera are considered opportunistic taxa of the upper photic zone (Gartner et al., 1987; Gartner, 1988; Okada and Wells, 1997), whose dominances in surface waters indicate upwelling areas (Gartner et al., 1988; Okada and Wells, 1997; Takahashi and Okada, 2000) or other eutrophic conditions (Gartner et al., 1987; Gartner, 1988; Takahashi and Okada, 2000; Colmenero-Hidalgo et al., 2004; Flores et al., 2005). The extant species *R. parvula* is known to be abundant in upwelling areas (Okada and Honjo, 1973) and during late Quaternary high fertility periods (Bieker, 1989; Okada and Wells, 1997). Dominances of small placoliths have been recorded as coincident with decreases in diversity (Gartner et al., 1987; Okada and Wells, 1997). Small *Gephyrocapsa* are recorded as indicative of higher temperature in surface water (Colmenero-Hidalgo et al., 2004), and as abundant during interglacial stages (Flores et al., 1999; Henriksson, 2000) or shortly after shifts towards significant glaciations (Gartner et al., 1987). High nutrient and lower temperature conditions are also inferred for the small *Gephyrocapsa* ecological preference (Gartner, 1988). Moreover, the abundance changes of small *Gephyrocapsa* and of small reticulofenestrids have been related to fluctuations of stability or stress in the environment and their increase indicates poorer stratification of surface waters (Gartner et al., 1987). At the studied sites, small placoliths show a negative relationship with the abundance of *F. profundus*, mainly at Site 607, and higher abundance fluctuations through MIS 25–22/21, supporting ecological preference of these taxa for high productivity and instability of surface waters.

*P. lacunosa* is an extinct placolith-bearing taxon, which seems to prefer more eutrophic conditions and unstable environment. (See Factor 1); its higher abundance in the Mediterranean site may be interpreted as related to higher variability in salinity and nutrient content of surface waters.

*Reticulofenestra* spp. In the study sites *Reticulofenestra* spp. (>4 μm) include *R. asanoi*, *Reticulofenestra* sp. (sensu Maiorano and Marino, 2004) and *R. minutula*. The ecology of these taxa is unknown; a preference for lower salinity water has been inferred for *R. asanoi* and *Reticulofenestra* sp. in the early Pleistocene record (Maiorano and Marino, 2004). *Reticulofenestra* spp. are placolith-bearing taxa, which, in the modern assemblage, dominate the coastal and upwelling areas and reflect r-selected life strategies in eutrophic conditions (Young, 1994). In the Messinian sediments, Flores et al. (2005) have related abundant *R. pseudounbicitus* (>5 μm) to...
eutrophic and turbulent conditions. In the studied sections, the ecological preferences for more eutrophic and turbulent conditions are inferred for *Reticulofenestra* spp. (Factor 1), according to recent data from Flores et al. (2005).

*Rhodopsophaera* spp. are mainly represented by *R. claviger*. This group is abundant in warm and low nutrient environments (McIntyre et al., 1972; Roth and Berger, 1975; Pujos, 1992; Haidar and Thiernier, 1997; Jordan and Winter, 2000; Sprovieri et al., 2003; Baumann et al., 2004). *R. claviger* lives in the upper photic zone (Honjo and Okada, 1974; Winter et al., 1974). Its ecological preference appears ambiguous. It has been reported as a warm and oligotrophic taxon (McIntyre et al., 1972; Roth and Coulbourn, 1982; Pujos, 1992; Haidar and Thiernier, 1997; Jordan et al., 1996; Flores et al., 1999; Findlay and Giraudoue, 2000; Baumann et al., 2004; Ziveri et al., 2004). Positive relations between some *Syracosphaera* spp. and eutrophic environments have, however, also been inferred (Estrada, 1978; Giraudoue, 1992), as well as with lower salinity of surface water and increase in terrigenous input (Weaver and Pujol, 1988; Flores et al., 1997; Colmenero-Hidalgo et al., 2004). The ecological preference of the taxa at both Site 607 and Site 967 appears to be for warm, stratified and oligotrophic waters (Factor 1).

*Umbilicosphaera* spp. Most of the dataset on this group refer to *U. sibogae* s.l. and its ecological preference appears ambiguous. It has been reported as a warm water (Okada and McIntyre, 1977; Okada and McIntyre, 1979; Brand, 1994; Wells and Okada, 1996; Flores et al., 1999) and oligotrophic taxon (Giraudoue, 1992; Ziveri et al., 2004). However a positive relation with moderate to high productive waters has been also described (Roth and Berger, 1975; Andruleit et al., 2000; Flores et al., 2003). According to more recent data (Ziveri et al., 2004), *Umbilicosphaera sibogae* var. *sibogae* mostly occurs under oligotrophic conditions while *U. sibogae* var. *foliosa* prefers mesotrophic waters. In the studied sections the abundance pattern of *Umbilicosphaera* spp. (mainly *U. sibogae* var. *sibogae*) indicates preference for warmer, oligotrophic and stratified surface waters.

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