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A Middle Pleistocene Northeast Atlantic coccolithophore record: Paleoclimatology and paleoproductivity aspects

F.O. Amore [a,*], J.A. Flores [b], A.H.L. Voelker [c,d], S.M. Lebreiro [e], E. Palumbo [a], F.J. Sierro [b]

[a] *DSBGA, Università del Sannio, Via dei Mulini 59a, 82100 Benevento, Italy*
[b] *Universidad de Salamanca, Departamento de Geología, Salamanca, Spain*
[c] *LNEG, Unidade de Geologia Marinha, 2610-143 Amadora, Portugal*
[d] *CIMAR Associated Laboratory, 4050-123 Porto, Portugal*
[e] *IGME, Geological and Mining Institute of Spain, OPI, Global Change, 28003 Madrid, Spain*

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ABSTRACT

Changes in paleoclimate and paleoproductivity patterns have been identified by analysing, in conjunction with other available proxy data, the coccolithophore assemblages from core MD03-2699, located in the Portuguese margin in the time interval from the Marine Isotope Stage (MIS) 13/14 boundary to MIS 9 (535 to 300 ka). During the Mid-Brunhes event, the assemblages associated with the eccentricity minima are characterised by higher nannoplankton accumulation rate (NAR) values and by the blooming of the opportunistic genus *Gephyrocapsa.* Changes in coccolithophore abundance are also related to glacial–interglacial cycles. Higher NAR and numbers of coccoliths/g mainly occurred during the interglacial periods, while these values decreased during the glacial periods. Superimposed on the glacial/interglacial cycles, climatic and paleoceanographic variability has been observed on precessional timescales. The structure of the assemblages highlights the prevailing long-term influence of the Portugal (PC) and Iberian Poleward (IPC) Currents, following half and full precession harmonics, related to the migration of the Azores High (AH) Pressure System. Small *Gephyrocapsa* and *Coccolithus pelagicus braarudii* are regarded as good indicators for periods of prevailing PC influence. *Gephyrocapsa caribbeanica, Syracosphaera* spp., *Rhabdosphaera* spp. and *Umbilicosphaera sibogae* denote periods of IPC influence. Our data also highlights the increased percentages of *Coccolithus pelagicus pelagicus* during the occurrence of episodes of very cold and low salinity surface water, probably related to abrupt climatic events and millennial-scale oscillations of the AH/Icelandic Low (IL) System.

1. Introduction

The ecological factors that mainly act on the distribution and structure of coccolithophore assemblages are light, the salinity and temperature of water masses, nutrient availability, terrigenous inputs, and water turbidity (McIntyre and Bé, 1967; Samtleben and Schröder, 1992; Giraudeau et al., 1993; Winter and Siesser, 1994; Samtleben et al., 1995; Takahashi and Okada, 2000; Andruleit et al., 2003, 2005; Hagino et al., 2005; Andruleit, 2007). These factors are connected to changes in paleoceanographic and paleoclimatic conditions. Thus the variations in the structure of calcareous nannoplankton assemblages are tools used to investigate paleoceanographic and paleoclimatic changes (e.g., Flores et al., 2003; Baumann and Freitag, 2004; Giraudeau et al., 2004; Baumann et al., 2005; Rogalla and Andruleit, 2005) and the development of the Earth's climate system. Coccolithophores also release CO_2 during the intracellular calcification process and use light energy to convert CO_2 into organic molecules. Through these processes, known as the 'biological carbon pumps' (Rost and Riebesell, 2004), coccolithophores contribute to the CO_2 exchanges between seawater and the atmosphere. Therefore, similar to the foraminiferal fragmentation index (Le and Shackleton, 1992; Becquey and Gersonde, 2002), the reconstruction of coccolith preservation and coccolithophore productivity can be used to evaluate changes in biogenic carbonate preservation and the relationship to variations in carbonate export, biogenic productivity, ocean circulation, and biogeochemistry.

In this study we use coccolithophore assemblages to reconstruct the climate signal and productivity patterns during the mid-Brunhes. Our study area is the Iberian margin, an area known for its good preservation of the record of millennial-scale climate variability for the last several climatic cycles (e.g., de Abreu et al., 2003; Martrat et al., 2007; Voelker et al., 2010). Significant paleoclimatic changes and sea surface temperature (SST) variations occurred during the last 0.6 Ma (McManus et al., 1999; Martrat et al., 2007; Voelker et al., 2010; Rodrigues et al., 2011) influencing North Atlantic Deep

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* Corresponding author: Tel.: +39 824 323633; fax: +39 824 23013.
E-mail addresses: f.amore@unisannio.it (F.O. Amore), flores@usal.es (J.A. Flores), antje.voelker@lneg.pt (A.H.L. Voelker), susana.lebreiro@igme.es (S.M. Lebreiro), epalumbo@unisannio.it (E. Palumbo), sierro@usal.es (F.J. Sierro).

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Water formation and contributing to the related paleoceanographic evolution. During this period, the global climate system underwent a climatic transition: the Mid-Brunhes Event (MBE). The global MBE event is centred around 400 ka (Jansen et al., 1986) and the interval from MIS 11 to MIS 9 (420–300 ka) is considered to be one of the warmest periods during the Pleistocene. Larger continental ice sheets, lower sea level and lower atmospheric CO_2 concentrations characterised the interglacial periods before the MBE compared to the more recent interglacials (Yin and Berger, 2010). The MBE is also characterised by the largest amplitude change in $\delta^{18}O$ in the global ocean preceded by a significant negative $\delta^{13}C$ shift and by generally high carbonate concentrations (and high productivity), with intervals of high carbonate dissolution in the deep ocean. Under steady state conditions, global increase in pelagic carbonate production, probably linked to nutrient availability and upwelling intensity, could have altered ocean geochemistry leading to an increase in dissolution. This increase in carbonate production was most likely linked to the proliferation of *Gephyrocapsa*, a genus of coccolithophores, which intensive calcification could have greatly altered marine carbonate chemistry (Barker et al., 2006) by creating a carbonate-ion undersaturation that led to increased dissolution (Baumann and Freitag, 2004).

Here we present the first mid-Brunhes record for the structure of coccolithophore assemblages and their absolute and relative abundances in the Portuguese upwelling system. We combine these data with the $CaCO_3$ record and with previously published data for SST, ice-rafted debris (IRD) amounts, and planktonic $\delta^{18}O$ and $\delta^{13}C$ isotopes (Voelker et al., 2010; Rodrigues et al., 2011). Our main objectives are:

- to describe the Middle Pleistocene climate variability for the Portuguese margin and to investigate if and how this climate variability influenced the structure of coccolithophore assemblages;
- to investigate the orbital and suborbital-scale productivity variations in the Portuguese upwelling system between the MIS 13/14 boundary and MIS 9 (535 ka to 300 ka).

Finally, we relate these climatic variations to changes in regional surface water circulation patterns, and to the migration of Intertropical Convergence Zone (ITCZ) and Azores High (AH) Pressure System.

2. Oceanographic setting

Calypso piston core MD03-2699 (39°02.20′N, 10°39.63′W) was retrieved from the Estremadura promontory north of Lisbon from a water depth of 1895 m (Fig. 1). The studied core is located between the northern Iberian Margin, which is mostly influenced by rather subpolar water masses, and the southern margin, which is affected by the subtropical water masses from the Azores current. Thus the core location offers the opportunity to document changes resulting from both subpolar and subtropical gyre behaviour (Voelker et al., 2010). Modern hydrographic conditions in the area are influenced by the Portugal Current (PC) system whose waters are mainly derived from the intergyre zone of the North Atlantic, a region of weak circulation limited in the north by the North Atlantic Current and to the south by the Azores Current (Pérez et al., 2001; Bischof et al., 2003). The PC system is also influenced by the neighbouring Canary and Azores Currents (Pérez et al., 2001). During summer, this current system is characterised by the southward flowing PC and by the upwelling filaments that form off the capes along the western Iberian margin such as Cape Roca. During winter, the PC is displaced further offshore by the Iberian Poleward Current (IPC) (Fig. 1), which transports the warm subtropical surface and subsurface waters, formed at the Azores front, northward to the site (Peliz et al., 2005). The underlying water masses of the PC system originate from about 200 m to 300 m by a northward moving layer of subtropical origin, i.e., the subtropical Eastern North Atlantic Central Water (ENACW), and from about 300 m to 400 m by the subpolar ENACW moving south (Ambar and Fiuza, 1994; Fiuza et al., 1998; Peliz and Fuiza, 1999). The Mediterranean Outflow Water dominates from depths of 400 m to approximately 1300 m. The Northeast Atlantic Deep Water, characterised by a very low temperature and salinity (Bischof et al., 2003), lies beneath the Mediterranean Outflow Water.

Current upwelling in this area is most likely related to the migration of the Azores High (AH) pressure System. This subtropical high-pressure system migrates northward during spring/summer, which results in strong northerly winds. The AH is significantly weaker in fall and winter months (Maze et al., 1997; Coelho et al., 2002). During summer, the strong winds cause the upwelling of colder, nutrient-rich waters from depths of 100 m to 300 m along the coast of the Iberian Peninsula. These nutrient-rich waters feed filaments that can extend more than 200 km offshore (Sousa and Bricaud, 1992). During winter, the dominant northward winds suppress the upwelling conditions and favour downwelling (Smyth et al., 2001). However, upwelling of a smaller magnitude than during the spring/summer, produced by northerly winds blowing across the shelf, can also occur in autumn or winter (Relvas et al., 2007; de Castro et al., 2008).

3. Material and methods

3.1. Age model

We present a study of Calypso piston core MD03-2699 (39°02.20′N, 10°39.63′W) in order to reconstruct the climate signal and the productivity patterns in the central area of the Portuguese margin. The oxygen isotope stratigraphy and three coccolithophore biostratigraphic events (Table 1) provided the stratigraphic constraints. The age model for core MD03-2699 is based on the correlation of its benthic oxygen isotope record (Fig. 2; Voelker et al., 2010; Rodrigues et al., 2011) with the record of ODP Site 980 (McManus et al., 1999; Flower et al., 2000). The age model is supported by three coccolithophore biostratigraphic events: the Last Occurrence (LO) of *Pseudoemiliania lacunosa*, the First Common Occurrence (FCO) of *Gephyrocapsa caribbeanica* and the First Occurrence (FO) of *Helicosphaera inversa* (Fig. 2). The LO of *P. lacunosa*, dated at about 460–440 ka (Raffi et al., 2006), occurs at 1895 cm corresponding to 452.47 ka (Table 1). The FCO of *G. caribbeanica,* equivalent to the progressive increase in *G. caribbeanica* percentage with values above 50–70% and dated at about 560–540 ka (Flores et al., 2003; Baumann and Freitag, 2004), is found at 2450 cm/ 546.39 ka (Table 1). The FO of *H. inversa*, dated at 510 ka (Sato et al., 1999), is identified at 2170 cm, corresponding to 514.94 ka (Table 1). The age of each sample between age control points was calculated by linear interpolation. The age of the studied interval ranges from the lowest sample that has an age of 535 ka, i.e., near the MIS 13/14 boundary, to MIS 9 (300 ka).

3.2. Coccolithophore slide preparation and counting methods

Slides for coccolith analyses were prepared using the technique described by Flores and Sierro (1997). A total of about 200 samples from core MD03-2699 collected at a sample interval of approximately 5 to 10 cm, yielding an average age resolution of about 1 to 2 ka, were analysed. Because of a lower sedimentation rate, a lower age resolution occurs mainly in MIS 12.

A quantitative analysis, considering both coccoliths/g and percentages of selected species, was conducted using a light microscope at 1250× magnification. At least 300 specimens larger than 3 μm were counted per slide in a varying number of fields of view. In the same fields, a separated count of specimens smaller than 3 μm was performed in order to quantify the absolute and percentage values of all taxa (Figs. 3, 4). The taxonomic concept of Raffi et al. (1993) and Flores et al. (1999, 2000) for the gephyrocapsids was followed. The large to medium-sized *Gephyrocapsa*, such as *Gephyrocapsa oceanica*,

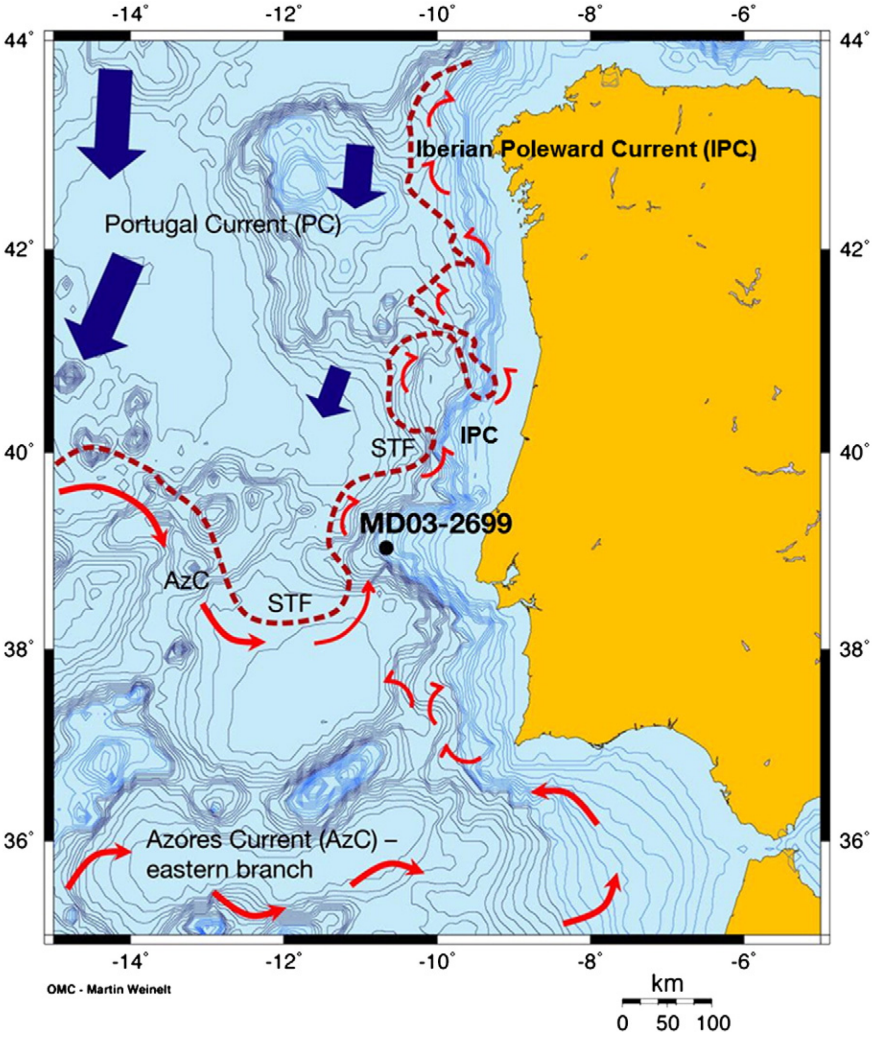


Fig. 1. Core location and modern oceanic circulation scheme off Portugal with major surface water currents. Modified after Peliz et al., 2005; Voelker et al., 2010.

Gephyrocapsa margereli and *G. caribbeanica* were counted separately. All small species of the genus, with placoliths <3 μm long, were grouped as small *Gephyrocapsa* (mainly *G. aperta*). *Syracosphaera* spp. mainly includes specimens of the species *Syracosphaera pulchra* and *Rhabdosphaera* spp. mostly specimens of *Rhabdosphaera clavigera*. The other species of these genera were not distinguished and were counted together in their corresponding genus, because they did not show a different paleoecological behaviour. A complete list of the identified taxa is given in the Appendix A.

3.3. Coccolithophore abundance and ecological proxies

The estimation of coccoliths/g (Fig. 5a) allowed us to calculate the NAR (number of coccoliths/cm^2/ka; Fig. 5a). Following previous studies (Steinmetz, 1994 and references therein; Su, 1996; Baumann et al., 2000; Lopez-Otalvaro et al., 2008), the NAR was used as a coccolithophore paleoproductivity proxy. On the basis of the available literature, we also used the small *Gephyrocapsa* group, *G. oceanica* and *Coccolithus pelagicus braarudii* as paleoproductivity proxies. The small *Gephyrocapsa* group encompasses opportunistic species of the upper photic zone (Gartner et al., 1987; Gartner, 1988; Okada and Wells, 1997), indicating eutrophic conditions (Gartner et al., 1987; Gartner, 1988; Takahashi and Okada, 2000; Colmenero-Hidalgo et al., 2004; Maiorano et al., 2009) in surface waters of upwelling areas (Gartner, 1988; Okada and Wells, 1997; Takahashi and Okada, 2000). *G. oceanica* prefers high fertility and upwelled waters of low latitudes (Mitchell-Innes and Winter, 1987; Fincham and Winter, 1989; Kleijne et al., 1989). The species has also been reported to favour

Table 1
List of coccolithophore events: depth, age evaluation and correlation to marine oxygen isotope (MIS). LO = Last occurrence; FCO = First Common Occurrence; FO = First Occurrence.

Depth (cm)	Event	Age (ka) (this study)	MIS	References
1895	LO *Pseudoemiliania lacunosa*	452,47	12	Raffi et al. (2006)
2170	FO *Helicosphaera inversa*	514,94	12	Sato and Takayama 1992 Sato et al., 1999 Chiyonobu et al., 2006
2450	FCO *Gephyrocapsa caribbeanica*	546,39	14	Flores et al. (2003) and Baumann and Freitag (2004)

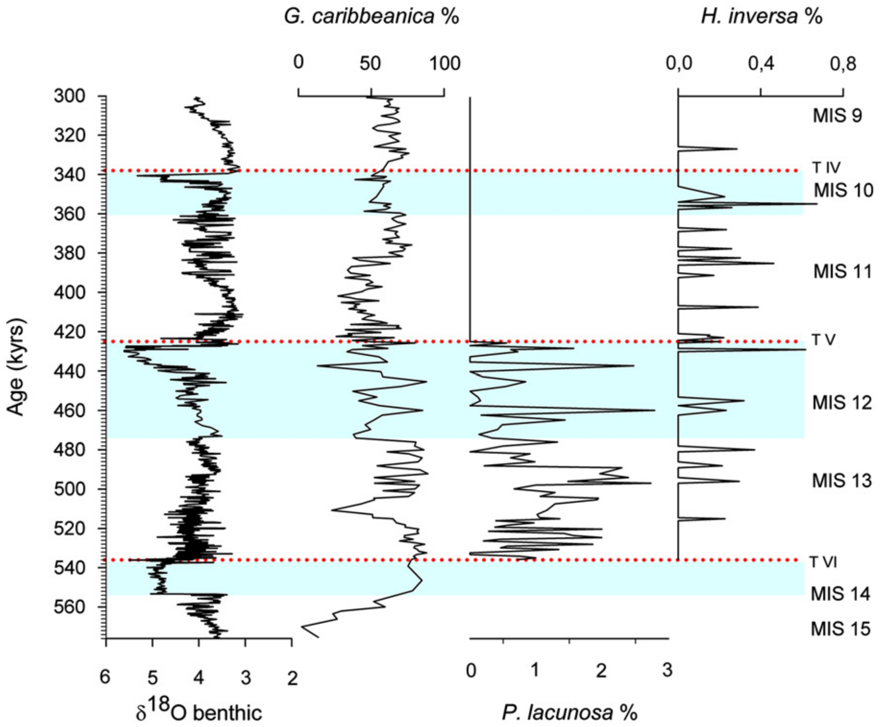


Fig. 2. The oxygen isotope stratigraphy and the coccolithophore biostratigraphic events of *Gephyrocapsa caribbeanica, Pseudoemiliania lacunosa* and *Helicosphaera inversa.* Blue bars indicate glacial isotope stages 12 and 10. T IV, V and VI refer to Terminations IV, V and VI.

low salinity conditions (Kleijne, 1993; Jordan and Winter, 2000). Off western Iberia, the presence of *C. pelagicus braarudii* is linked to changes in the intensity and/or position of non-glacial upwelling. This subspecies acts as a tracer of oceanic fronts, at the outer limits of the areas where turbulence is moderate (Cachão and Moita, 2000; Parente et al., 2004).

The species indicative of cold water masses are *G. margereli,* a transitional/subpolar species (Bréhéret, 1978), and *Coccolithus pelagicus pelagicus,* a subspecies living on the border of subarctic biogeographic province (McIntyre and Bé, 1967; Roth, 1994; Winter et al., 1994). According to the available literature on the ecological features of coccolithophores (McIntyre and Bé, 1967; Bréhéret, 1978; Roth, 1994; Winter et al., 1994; Wells and Okada, 1997; Flores et al., 1999), we propose the sum of the percentages of *C. pelagicus pelagicus* and *G. margereli* as a cold-water proxy (Fig. 3).

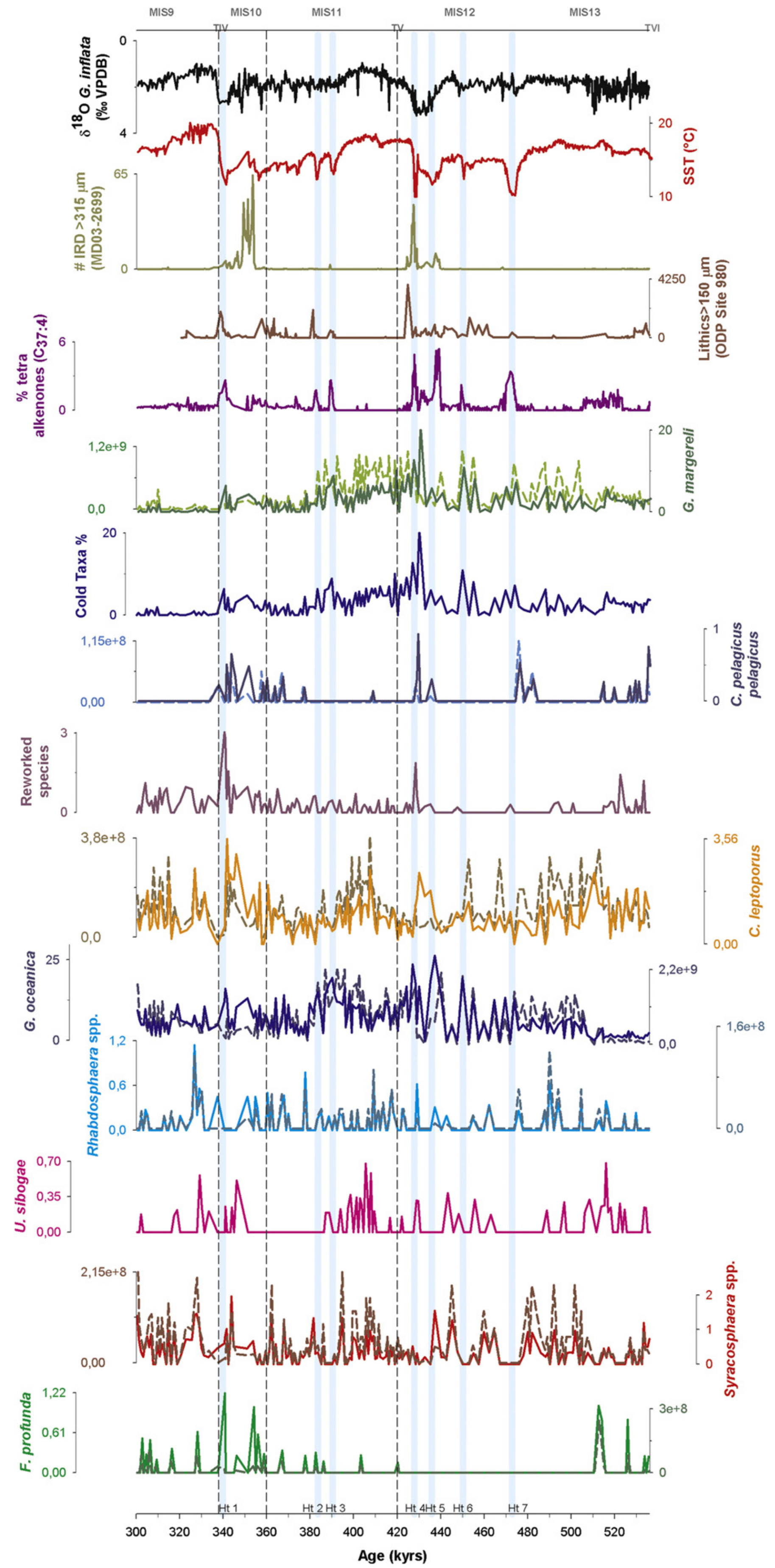
Syracosphaera spp. is regarded as a warm water indicator by Weaver (1983), Jordan et al. (1996), and Flores et al. (1999). The genus has also been reported as a typical taxon of high productive areas (Estrada, 1978; Giraudeau, 1992). Silva et al. (2008) and Beaufort and Heussner (2001) assert that *S. pulchra* is an autumn species, resisting to moderate turbulence, and capable of increasing in abundance from August to November. According to previous authors (Giraudeau, 1992; Wells and Okada, 1997; Flores et al., 1999; Broerse et al., 2000; Hagino and Okada, 2006; Silva et al., 2008), *Rhabdosphaera clavigera* and *Umbilicosphaera sibogae* are also considered very sensitive to high sea-surface temperature and salinity, revealing the presence of warm and more stratified waters. The cumulative percentage of *Syracosphaera* spp. (Fig. 3), *U. sibogae* (Fig. 3) and the species of the genus *Rhabdosphaera* (Fig. 3) is considered in this study as a warm-water proxy (Fig. 4).

Higher abundance of lower photic zone dweller, *Florisphaera profunda,* is associated with deep stratification conditions and a deep nutri-thermocline position (Okada and Honjo, 1973; Molfino and McIntyre, 1990; Wells and Okada, 1997; Flores et al., 2000).

3.4. Preservation

Dittert et al. (1999) calculated the ratio of *Emiliania huxleyi* to *Calcidiscus leptoporus* (CEX) as an index of carbonate dissolution and as a proxy of the lysocline position. Boeckel and Baumann (2004) suggested a preservation index (CEX′) based on *E. huxleyi* and *Gephyrocapsa ericsonii* versus *C. leptoporus*. To better quantify the effect of carbonate dissolution on calcareous nannoplankton assemblages, a Dissolution Index (DI) is provided (Fig. 3). Because the FAD of *E. huxleyi* occurs above the studied interval, the calculated DI is based on the following ratio: DI = small *Gephyrocapsa*/(small *Gephyrocapsa* + *C. leptoporus*). Small-sized *Gephyrocapsa* (<3 μm), like *E. huxleyi*, are relatively easily dissolved forms (Roth, 1994; Flores et al., 2003), conversely *C. leptoporus* is a very solution-resistant form. Based on the ratio of easily dissolved and more resistant forms, this index is comparable to CEX and CEX′ but applicable for a wider temporal range. High values of DI (close to 1) indicate good preservation while low values reveal poor preservation.

Following Flores et al. (2003), we also distinguish the following four categories to describe the preservation (Fig. 3) of coccoliths: Good (10), for samples which show little or no evidence of dissolution and/or secondary overgrowth of calcite, and have fully preserved diagnostic characters. Moderate (8), for samples which show dissolution and/or secondary overgrowth with partially altered primary morphological characteristics. Despite this, nearly all specimens can be identified at the species level. Poor (6), for samples which show severe dissolution, fragmentation, and/or secondary overgrowths. Primary features are destroyed, and many specimens cannot be identified at the species or the generic level. Barren (4), for samples which show absence of coccoliths. Three additional categories between good and moderate, moderate and poor, and poor and barren, i.e., with intermediate features, were introduced to refine the pattern. In order to test the reliability of the semi quantitative evaluation of preservation, which is less time consuming, the preservation and DI records were correlated.


MIS9
MIS10
MIS11
MIS12
MIS13
TIV
TV
TVI
δ18O G. inflata (‰ VPDB)
0
4
SST (°C)
20
10
IRD >315 μm (MD03-2699)
65
0
Lithics>150 μm (ODP Site 980)
4250
0
% tetra alkenones (C37:4)
6
0
G. margereli
1,2e+9
0,0
20
0
Cold Taxa %
20
0
C. pelagicus pelagicus
1,15e+8
0,00
1
0
Reworked species
3
0
C. leptoporus
3,8e+8
0,0
3,56
0,00
G. oceanica
25
0
2,2e+9
0,0
Rhabdosphaera spp.
1,2
0,6
0,0
1,6e+8
0,0
U. sibogae
0,70
0,35
0,00
Syracosphaera spp.
2,15e+8
0,00
2
1
0
F. profunda
1,22
0,61
0,00
3e+8
0
Ht 1
Ht 2
Ht 3
Ht 4
Ht 5
Ht 6
Ht 7
300
320
340
360
380
400
420
440
460
480
500
520
Age (kyrs)

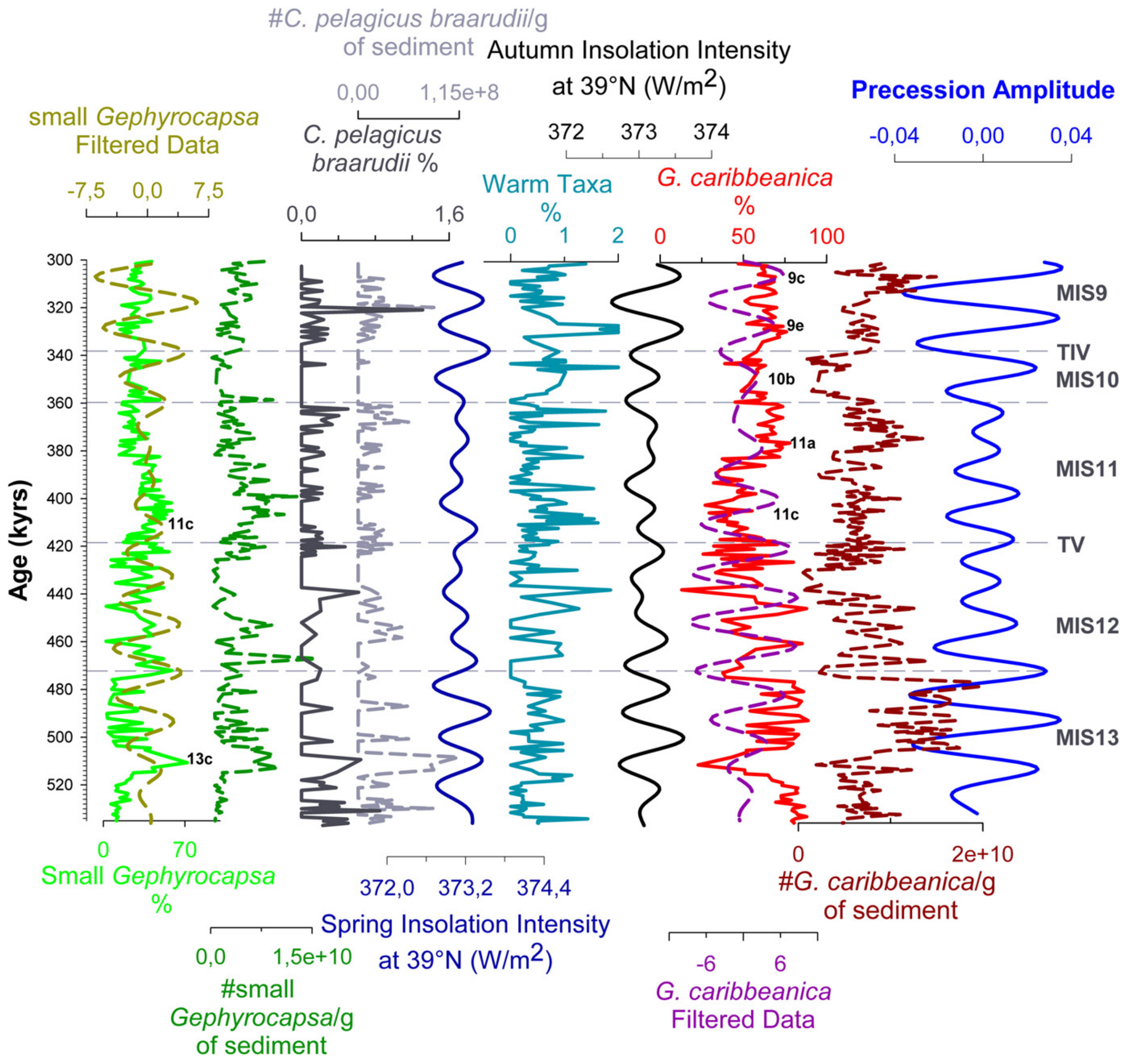


Fig. 4. Small *Gephyrocapsa* %, absolute abundance (N°coccoliths/g of sediment) and filtered data. *Coccolithus pelagicus braarudii* % and absolute abundance (N°coccoliths/g of sediment). Spring insolation intensity at 39°N (W/m^2). Sum of Warm taxa (*U. sibogae*, *Rhabdosphaera* spp. *Syracosphaera*) %. Autumn insolation intensity at 39°N (W/m^2). *G. caribbeanica* %, absolute abundance (N°coccoliths/g of sediment) and filtered data. Precession amplitude (Berger and Loutre, 1991). Substages (e.g. 11c), reported in Voelker et al. (2010), are indicated on small *Gephyrocapsa* and *G. caribbeanica* curves.

Reworked Neogene and Paleogene calcareous nannofossils (Fig. 3) were observed along the core.

3.5. Sediment geochemistry

The calcium carbonate ($CaCO_3$) content (Fig. 5a) was determined from 2 mg of dried, ground and homogenised total sediment, using the CHNS-932 Leco element analyser of the Marine Geology Laboratory at LNEG. The values are based on three repeated analyses (with precision ±0.5) and the sample resolution varies from 2 cm to 5 cm. The $CaCO_3$ is dominantly of biogenic origin (coccoliths and foraminifers).

3.6. Statistical analyses

Statistical analyses in the time domain have been performed on productivity proxies and on percentage data of selected species. Matlab software using the "crosscorr", a cross-correlation function, was used to perform the analyses. The sample cross correlation, a

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Fig. 3. Total (N°coccoliths/g of sediment, dashed lines) and relative abundances (%, solid lines) of selected coccolithophore species. *G. inflata* $\delta^{18}O$ (‰VPDB; Voelker et al., 2010). Sum of cold taxa (*G. margereli*, *C. pelagicus pelagicus*) %. The ODP Site 980 relative proportion ice-rafted detritus (IRD) > 150 µm (McManus et al., 1999). Reworked species %. The MD03-2699 core relative proportion IRD > 315 µm (; Voelker et al., 2010; Rodrigues et al., 2011). Tetra alkenones ($C_{37:4}$) % (Rodrigues et al., 2011). SST (°C; Rodrigues et al., 2011). Horizontal dashed black lines indicate the subdivision of Marine Isotope Stage (MIS) from 13 to 9; T IV, V and VI refer to Terminations IV, V and VI. Ht 7 to 1 are referred to Heinrich-type events identified by Rodrigues et al. (2011).

mathematical function (implemented in Matlab Toolbox), is used to determine a possible relation between two time series that are equally spaced in time. For this reason, we interpolated all proxy records using the same time vector that was reconstructed on the basis of a constant sample period (2.138 kyr) estimated from the best resolution for coccolithophore assemblages (on the basis of time vector length – number of data points – sedimentation rate and maximum and minimum values of the time vector). In the input arguments of this function the default of number of STandard Deviations of the sample cross-correlation (nSTDs) is approximately the 95% confidence interval. The cross-correlation function is assessed on the basis of the correlation coefficients, which indicate the amplitude of the correlation (with values from 0 to 1), and the lag, which indicates the delay between the two time series (Buccianti et al., 2003). Negative correlation coefficient values indicate that the two time series are in phase opposition. Positive values indicate that the two time series are in phase. The delay is evaluated by multiplying the lag by the sample period (Table 2; Fig. 6). The bound values in respect to the correlation are also reported. The bounds are two-element vectors indicating the approximate upper and lower confidence bounds, assuming that Series 1 and Series 2 are completely uncorrelated.

Fourier series analysis (Fig. 5a) was used on the primary productivity record (number of coccoliths/g).

The significance of spectral peaks and the time variability of the major frequencies have been estimated using the algorithm developed by Torrence and Compo (1998) applied to warm taxa (sum of *Syracosphaera spp., Rhabdosphaera spp.* and *U. sibogae*), small *Gephyrocapsa* and *G. caribbeanica*. Morlet Mother Wavelet Analysis has been used and attention has been given to interpret the results within the Cone of Influence (COI), the region of the spectrum where errors could occur because of the padding of zero (Torrence and Compo, 1998). Spectral analyses have been applied to the evenly spaced data (2.138 kyr; Fig. 7). The series of small *Gephyrocapsa* and *G. caribbeanica* were band-pass filtered (Fig. 4) for the precession frequency range (0.04–0.05 1/kyr) using the "filtfilt" Matlab function.

Insolation intensity at 39°N has been estimated using the formula proposed by Berger (1978). The obtained values have been extended to the astronomical seasonal (summer, spring and autumn) duration (Figs. 4, 5) using the methods proposed by Loutre et al. (2004).

4. Results

Coccolithophore abundances were used to reconstruct environmental conditions off the Portuguese margin from MIS 13 to MIS 9. Absolute and relative abundances of coccoliths are shown in Figs. 3, 4.

G. caribbeanica (Fig. 4) and the small *Gephyrocapsa* group (up to 70%; Fig. 4) are the major contributors to the NAR and decreases in the abundances of these taxa coincide with lower NAR values (Fig. 5a). The other main taxa are *G. oceanica* (up to 26%; Fig. 3) and *G. margereli* (up to 20%; Fig. 3). *P. lacunosa* (Fig. 2), *C. leptoporus* (Fig. 3), *C. pelagicus pelagicus* (Fig. 3), and *C. pelagicus braarudii* (Fig. 4) also contribute to the assemblages. *F. profunda* (Fig. 3) occurs sporadically and has very low values (0, 5–1%) in the assemblages.

G. caribbeanica dominates the assemblages from 546.39 ka (MIS14) upwards showing percentages >50% (Fig. 2). The highest *G. caribbeanica* percentages were recorded during MIS 13, reaching values of more than 80% (Fig. 4). The abundance of this species alternates with that of the small *Gephyrocapsa* group (Fig. 4) that occurred continuously and reveals percentages from 20% to 40%. This group tends to show higher percentages during interglacial periods, particularly in the first part of MIS 11 and during MIS 13.

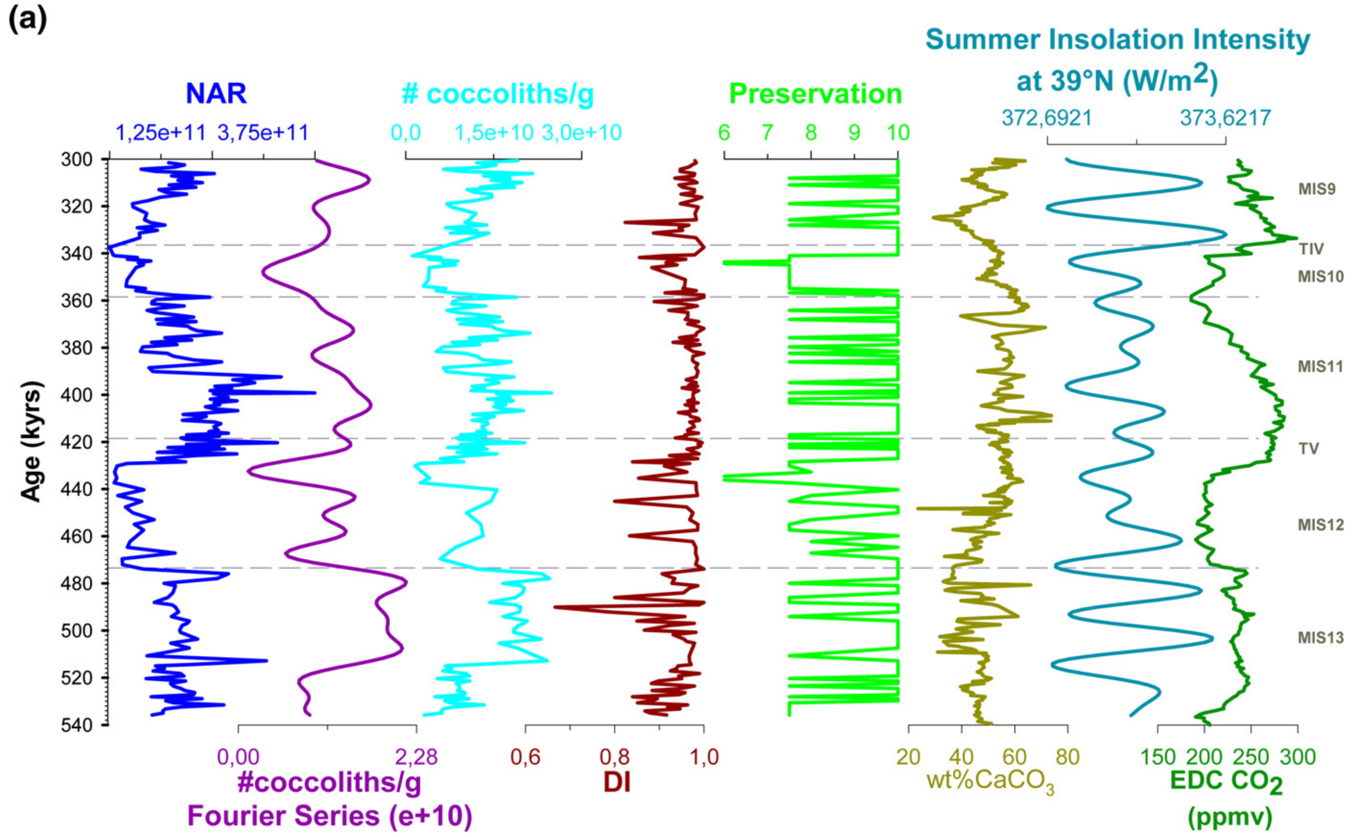

Fig. 5. (a) NAR; N°coccoliths/g Fourier Series; Total abundance of coccoliths (N°coccoliths/g of sediment); DI (ratio of small-sized *Gephyrocapsa%* and the sum of small-sized *Gephyrocapsa%* and *C. leptoporus%*). Preservation (10 = little or no evidence of dissolution and/or secondary overgrowth of calcite, with fully preserved diagnostic characters; 4 = absence of coccoliths). $CaCO_3$ wt.%. Summer insolation intensity at 39°N (W/m^2); EPICA Dome C CO_2 (ppmv; Siegenthaler et al., 2005); (b) Eccentricity Amplitude (Berger and Loutre, 1991); Significant coccolithophore assemblages of eccentricity maxima and minimum.

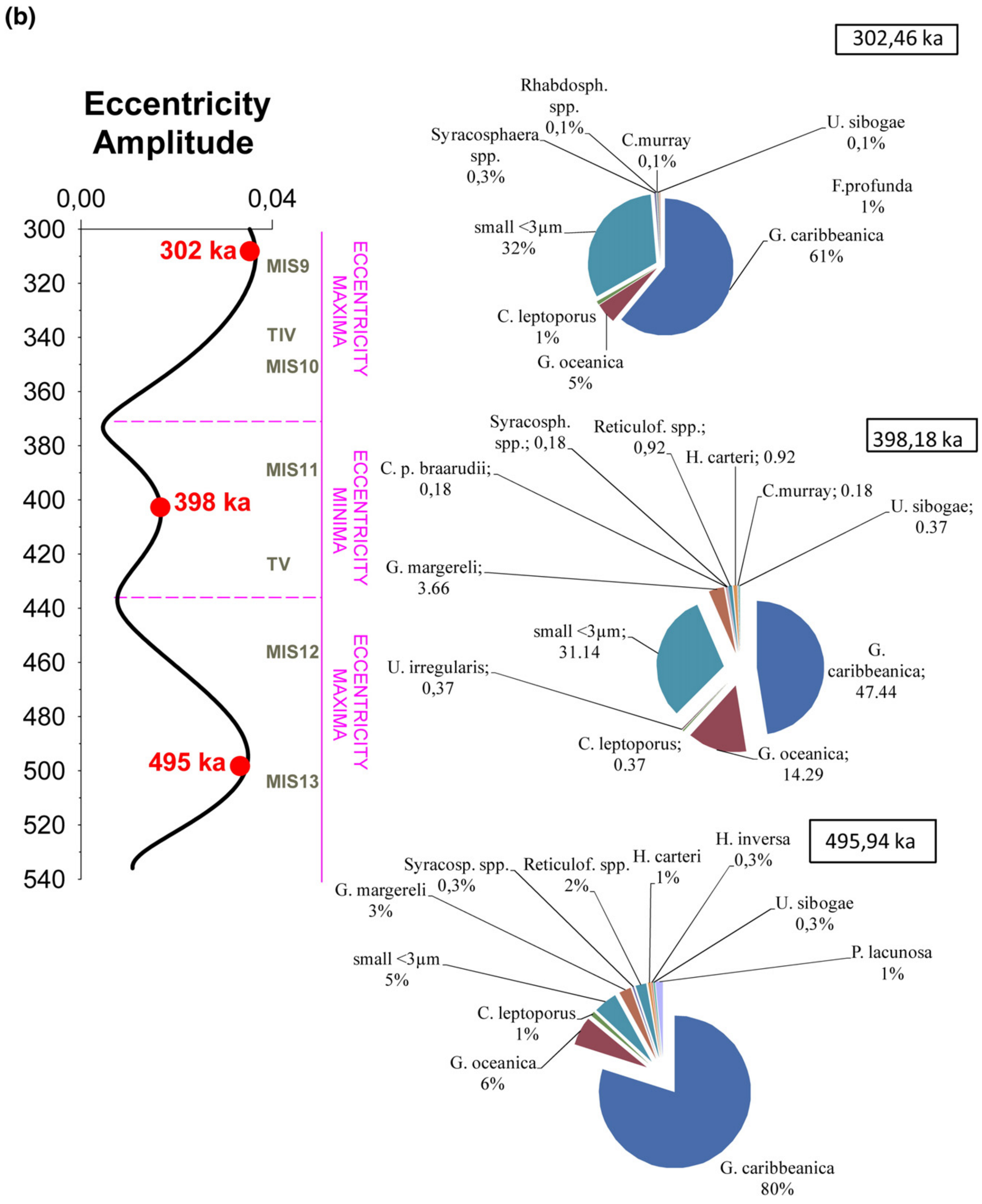

Fig. 5 (*continued*).

G. margereli (Fig. 3) is recorded with percentages up to 20%, with higher values during MIS 12 and stadial events.

C. pelagicus pelagicus, *C. pelagicus braarudii*, and *Coccolithus pelagicus azorrinus* have been distinguished. The percentage record of *C. pelagicus pelagicus* agrees well with the planktonic $\delta^{18}O$ and SST fluctuations with continuous and high values during MIS 10 and during Heinrich-type (Ht) ice-rafting events 4, 5 and 7 of MIS 12 (Fig. 3). *C. pelagicus braarudii* (Fig. 4) shows slightly higher percentages during MIS 13c (512 ka–505 ka), coinciding with maxima of coccoliths/g (Fig. 5a), NAR (Fig. 5a) and low wt.% $CaCO_3$ (Fig. 5a). *C. pelagicus azorrinus* occurs sporadically. *C. leptoporus* (Fig. 3) reveals values ranging from 0.5% to 3.5%. This species shows higher percentages during the interglacial intervals, but some peaks are also recorded just prior to the terminations.

Table 2
Correlation coefficients, indicating the amplitude of the correlation (with values from 0 to 1); the offset, indicating the delay in ka, evaluated multiplying the LAG by the sample period. The 95% significance corresponds to correlation coefficients values of ±0.18.

Variables	Corr coefs	LAG	Offset (kyrs)
G. caribbeanica% − DI	−0.57	0	0
C. leptoporus% − DI	0.43	0	0
SST(°C) − warm taxa%	0.19	0	0
SST(°C) − cold taxa%	−0.3	0	0
C. pelagicus pelagicus % − IRD	0.47	1	1.278
$C_{37:4}$ − *C. pelagicus pelagicus%*	0.24	1	1.278
DI-preservation	0.24	0	0

Two significant changes occurred in the coccolithophore abundance and assemblages during glacial MIS 12. The first event, recorded at the MIS 13/12 boundary, is marked by a reduction of NAR (Fig. 5a) and number of coccoliths/g (Fig. 5a). A second minimum in both records occurred between 435 and 429 ka in conjunction with lower percentages of *C. pelagicus braarudi* (Fig. 4) and the highest percentages of *G. margereli* and *C. pelagicus pelagicus* (Fig. 3). A similar minimum in coccolithophore abundance is observed at the end of glacial MIS 10, which started with high NAR values, followed then by a reduction (Fig. 5a).

The onsets of MIS 11 and MIS 9 are associated with increased values of paleoproductivity indices, as reflected by the rising trends of number of coccoliths/g (Fig. 5a) and NAR (Fig. 5a). A clear decrease in these paleoproductivity indices characterises the end of MIS 11. An increase in the percentages of reworked specimens (Fig. 3) occurred around Termination IV (339 ka), i.e., the glacial–interglacial transition from MIS 10 to MIS 9. This period is also characterised by a small NAR increase, a pattern similar to the one observed during Termination V.

In the DI and preservation records (Fig. 5a) the lowest values occurred mainly when proliferation peaks of *G. caribbeanica* (Fig. 4) are recognised during the glacial and interglacial periods. The cross correlation between *G. caribbeanica* and the DI indicates a negative correlation with no time lag (Table 2; Fig. 6). A negative correlation without offset is also observed for *C. leptoporus* and DI (Table 2; Fig. 6). The DI and the preservation records (Figs. 5a, 6) show similar trends, with a positive correlation coefficient with no time lag (Table 2; Fig. 6). Cross-correlations between percentages of tetra alkenones, SST and IRD (Fig. 3) with selected coccolithophore taxa were performed in the time domain. SST are negatively related to the percentages of cold-water taxa and *C. pelagicus pelagicus* and positively related to percentages of warm taxa (Table 2; Fig. 6). Moreover, percentages of *C. pelagicus pelagicus* are positively related to percentages of tetra alkenones at a lag = 1 and to IRD at a lag = 1 (Table 2; Fig. 6).

Spectral analyses applied to *G. caribbeanica,* warm taxa and small *Gephyrocapsa* (Fig. 7) show peaks for the 19–21 and ~10 kyr-cycles reaching or overcoming the 95% level of confidence. The major time variability of these cycles is observed between 505 and 430 ka for warm taxa and *G. caribbeanica* and throughout the time window for small *Gephyrocapsa* with an interruption between 430 and 405 ka. Filtered time series estimated on selected taxa have been compared with spring and autumn insolation intensity (respectively SInI and AInI) at 39°N. A good correspondence of *G. caribbeanica* with the AInI and small *Gephyrocapsa* with SInI has been observed (Fig. 4).

5. Discussion

5.1. Coccolithophore evidence for paleoproductivity and surface water variations

Recent sediments along the Portuguese margin are very rich in coccolithophorids (Abrantes and Moita, 1997). This group has important blooms in poorly productive warm waters but is also a consistent component of mature upwelling communities during late summer–autumn, when conditions of reduced turbulence but nutrient-rich

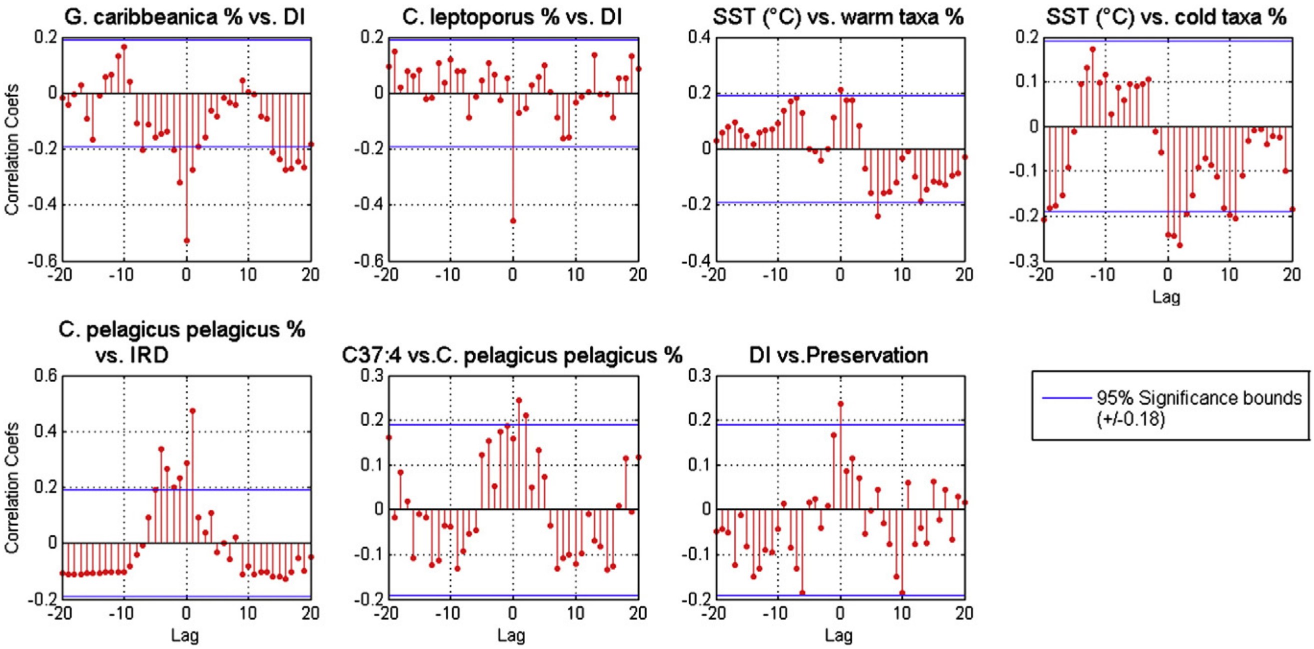

Fig. 6. Correlograms indicating cross correlations between: *G. caribbeanica* % and DI; *C. leptoporus* % and DI; SST (°C; Rodrigues et al., 2011) and sum of warm taxa (*U. sibogae*, *Rhabdosphaera* spp., *Syracosphaera*) %; SST (°C; Rodrigues et al., 2011) and sum of cold taxa (*G. margereli*, *C. pelagicus pelagicus*) %; C. *pelagicus pelagicus* and IRD > 315 μm (MD03-2699; Voelker et al., 2010; Rodrigues et al., 2011); Tetra alkenones ($C_{37:4}$) % (Rodrigues et al., 2011) and *C. pelagicus pelagicus* %; DI and Preservation. X-label of all plots indicates LAG (delay between two time series) while y-label correlation coefficients. Blue upper and lower lines in correlograms indicate 95% significance bounds corresponding to correlation coefficients values of ±0.18. LAG, maxima correlation coefficient values and offset are reported in Table 2.

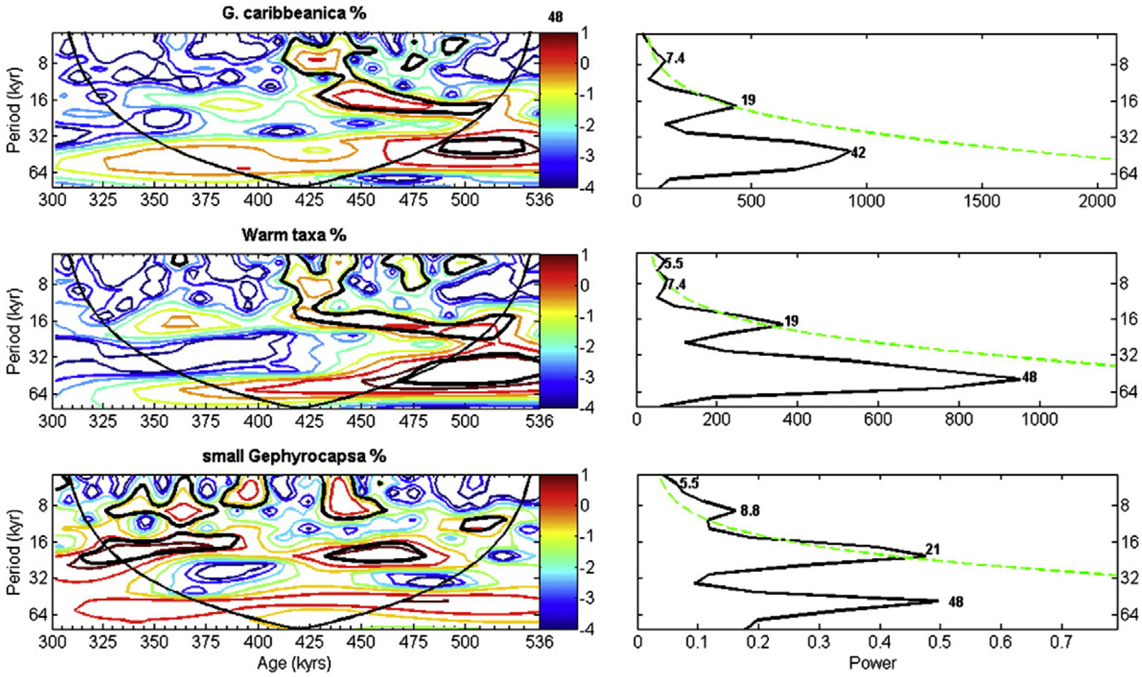

Fig. 7. Wavelet power spectra and periodograms of *G. caribbeanica* %, sum of warm taxa (*U. sibogae*, *Rhabdosphaera* spp., *Syracosphaera*) %, small *Gephyrocapsa* %. The green dotted line in the periodograms and bold black lines in wavelet powerspectra represent the 95% significance level.

waters occur (Winter, 1985; Mitchell-Innes and Winter, 1987; Giraudeau, 1992; Wefer and Fisher, 1993; Ziveri et al., 1995). Nowadays, the geographic distribution of coccolithophore assemblages marks the nutrient-enriched waters upwelled during summer (Moita, 1993) off the Portuguese coast. Coccolithophore abundance in the water column is highest in summer (Abrantes and Moita, 1997) and associated with persistent and weak upwelling events, occurring during the short period of transition from upwelling to downwelling events (Silva et al., 2009; Moita et al., 2010). During the winter, concentrations of the same order of magnitude as the summer maxima are only present in minor patches along the south-western and southern coasts.

The temporal succession of coccolithophore assemblages in core MD03-2699 is complex and reflects the superimposition of long and short-term changes in this hydrographically complex area, where environmental variables strongly interact and where the coccolithophore ecology is still incompletely understood. Nowadays the seasonal coastal upwelling, mainly controlled by northerly winds, is the major productivity driver on the Portuguese margin, together with the continental-fresh water input through the Tagus River, which is controlled by precipitation over the Iberian Peninsula. In our study different species of coccolithophores are used as proxies for productivity and salinity changes, resulting from upwelling and river input variability.

Currently, the maximum abundances of small *Gephyrocapsa* species, *C. pelagicus braarudii* and *G. oceanica,* are observed in highly productive conditions, throughout the upwelling season (Giraudeau, 1992; Young, 1994; Ziveri et al., 1995; Bollmann, 1997; Broerse et al., 2000; Cachão and Moita, 2000; Hagino et al., 2000; Barcena et al., 2004; Rogalla and Andruleit, 2005; Silva et al., 2008), and these species are therefore considered good proxies for elevated coastal productivity generated by upwelling and high nutrient availability. In particular small *Gephyrocapsa* and *C. pelagicus braarudii* are considered as good proxies of periods during which the Portuguese Current (PC) prevailed and show higher abundances during the first part of MIS 13 and MIS 11, during MIS 12 and for *C. pelagicus braarudii* during MIS 9d.

Syracosphaera spp., *R. clavigera* and *U. sibogae*, regarded as warm water indicators and thus good proxies of periods during which the Iberian Poleward Current (IPC) prevailed, show higher abundances during the interglacial periods of MIS 13, 11 and 9 and during the warm events of MIS 12 conform with the observations of Voelker et al. (2010) and Rodrigues et al. (2011). Abundances, however, fluctuated, pointing to varying hydrographic conditions during the interglacial periods (Fig. 3). Furthermore, *U. sibogae* is more present during MIS 13c, contemporary with lower percentages of *Syracosphaera* spp. and also *G. oceanica*, than during MIS 13a, indicating that hydrographic conditions differed during these two warm periods, with slightly warmer conditions during MIS 13c. Also *G. caribbeanica* is reported to prefer warm water conditions and is well represented during the periods of prevailing IPC influence. Episodes during which the water column became more stratified and a reduction in nutrient supply occurred in the surface waters are highlighted by peaks of *F. profunda* (Fig. 3), which is regarded as a deep-photic species occurring below oligotrophic surface waters, out of phase with *Syracosphaera* spp. (Fig. 3).

The assemblage structure highlights the alternately prevailing influence of the PC and IPC, over time (Fig. 8c, d) that nowadays is linked to the migration of the Azores High (AH) pressure System and related changes in the wind regime occurring at seasonal time scale. The weaker the equatorward wind-stress, the larger is the IPC's transport, whereas a reversal of the IPC flow only occurs if the equatorward wind stress is sufficiently strong (Haynes and Barton, 1990). So during periods when the IPC-related coccolithophorid species dominated the assemblages in the studied interval, the equatorward wind-stress was probably reduced.

Episodes of enhanced continental-fresh water input occurred during MIS 10 (~357–355 ka), when our data highlight a slight rise in reworked species, peaks of *G. oceanica*, *Rhabdosphaera* and *G. caribbeanica* (Figs. 3, 4). This event occurred together with a decrease of higher-plant biomarkers, and SSTs higher than 14 °C (Rodrigues et al., 2011). *G. oceanica* is usually well adapted to more coastal regions (Guerreiro et al., 2009) and relatively low salinity conditions. *Rhabdosphaera* and *G. caribbeanica* are reported to prefer

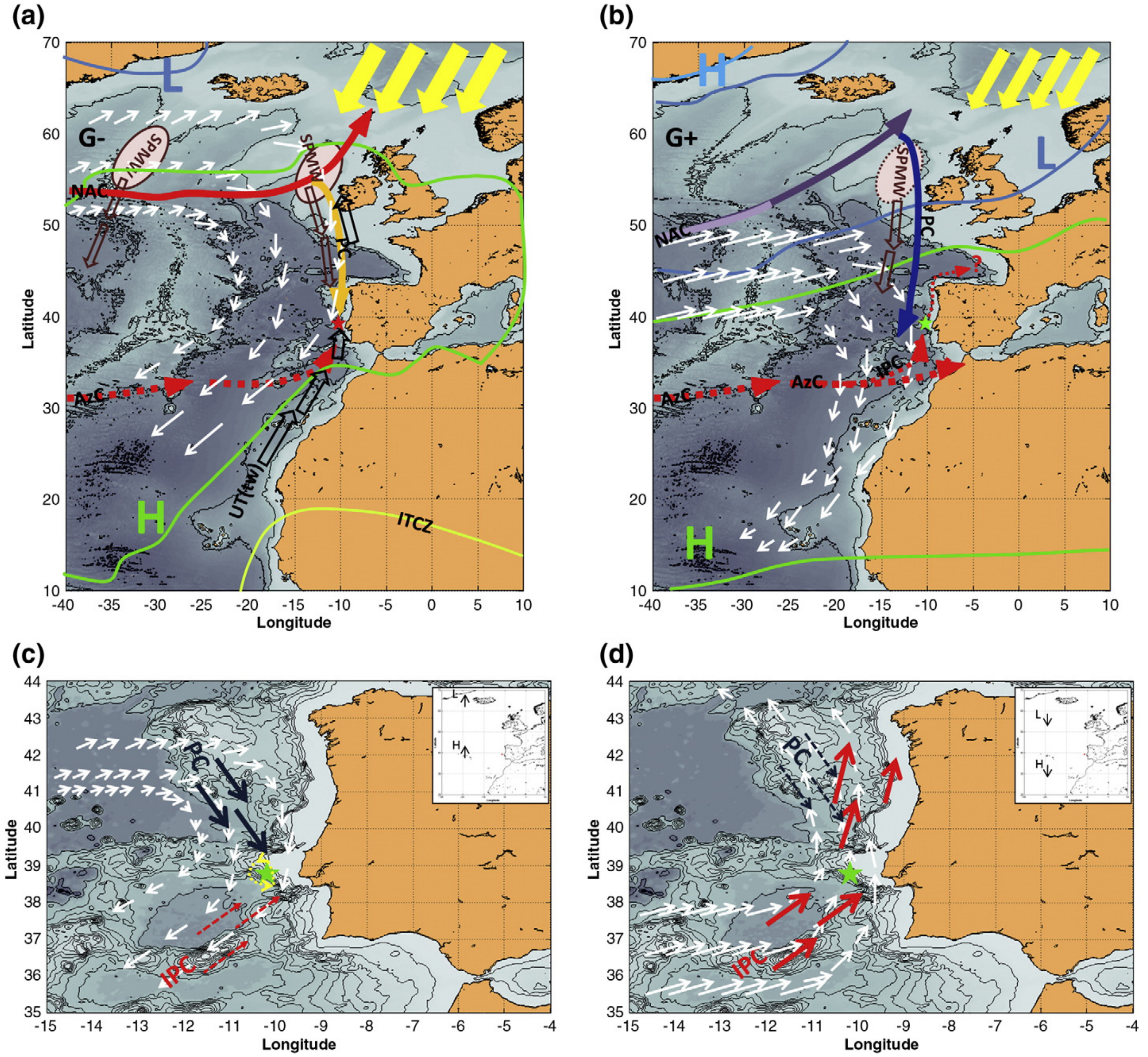

Fig. 8. (a) interglacial and (b) glacial scenarios. L = Icelandic Low. Green H = Azores High. Cyan H = Polar High. G = Pressure Gradient:"+" strong; "−"weak. ITCZ = Inter Tropical Convergence Zone. NAC = North Atlantic Current, AzC = Azores Current, IPC = Iberian Poleward Current, PC = Portugal Current; UC(tw) = Undercurrent transporting Tropical Waters, SPMW = subpolar mode waters formed in the oval region (from Voelker et al., 2010, modified). White Arrows = direction of winds; the length indicates the intensity of the winds. Yellow Arrows = Insolation Intensity at 65°N; width indicates the intensity. Paleoceanographic reconstruction at precessional time-scale: (c) PC prevailing conditions, (d) IPC prevailing conditions. White Arrows = direction of winds.

warm water conditions and are well represented during the periods of prevailing IPC influence. So our data seem to indicate further strengthening of the IPC during a period of prevailing influence of this current and the occurrence of wetter and warmer conditions. Today these conditions are observed during negative North Atlantic Oscillation (NAO) years (Sánchez et al., 2007; de Castro et al., 2011). A similar decline of continental biomarkers on the Iberian Margin is reported during MIS 11c (Rodrigues et al., 2011) and is related to less dry conditions occurring synchronously with the onset of the humid period in NW Africa (Helmke et al., 2008). Some authors (Sánchez Goñi et al., 2002; Moreno and Canals, 2004) related similar conditions, during interstadials of the Last Glacial, to the occurrence of negative NAO-type episodes at a millennial scale, however additional investigations, with increased resolution and a reduced time window, are needed to better understand these events.

5.2. Coccolithophore response to abrupt climate events

In core MD03-2699, the higher percentages values of *G. margereli* (Fig. 3), which is a transitional/subpolar species and indicative of cold water-masses (Bréhéret, 1978), occurred during the stadial events in conjunction with colder SST (Fig. 3; Rodrigues et al., 2011). The distribution pattern of *C. pelagicus pelagicus* (Fig. 3) further supports the arrival of cold surface waters. Cross correlation of this species abundance with SST indicates that it is correlated with stadial events (Table 2; Fig. 6). Cross correlation of *C. pelagicus*

pelagicus with the IRD record (Table 2; Fig. 6) suggests also a correlation with the extremely cold events identified as Ht ice-rafting events, defined by Rodrigues et al. (2011) on the base of high percentages of tetra-unsaturated alkenone ($C_{37:4}$; Fig. 3). *C. pelagicus pelagicus* is a species attributed to live on the border of the subarctic biogeographic province (McIntyre and Bé, 1967; Roth, 1994; Winter et al., 1994). During glacial times, the Polar Front shifted southward, closer to North Iberia (Eynaud et al., 2009), and this species moved southward the meridional limit of its distributional area, testifying of the arrival of subpolar water masses off western Iberia (Parente et al., 2004; Narciso et al., 2006). The time lag (LAG = 1) between $C_{37:4}$ and *C. pelagicus pelagicus* suggests that the subpolar water masses reached the site shortly before the increase of *C. pelagicus pelagicus*; the lag between *C. pelagicus pelagicus* and the IRD record, on the other hand, testifies of the subsequent arrival of IRD carrying icebergs at the site during the Ht events.

The abundance of reworked species can – at least partially – also be related to these events. One abundance maximum occurred during Ht 4 (Termination V) contemporary with maxima in *G. margereli* and *C. pelagicus pelagicus*. The increase of reworked species recorded during Termination IV is most probably related to the deglacial ice-rafting event recorded at ODP Site 980 (Fig. 3; McManus et al., 1999) that led to a major cooling at the northern (Desprat et al., 2009) and southern Iberian margin (Martrat et al., 2007; Rodrigues et al., 2011). The occurrence during these events of very cold and low salinity surface waters on the northern and southern Iberian margin (e.g., Bard et al., 2000; de Abreu et al., 2003; Martrat et al., 2007; Rodrigues et al., 2011) prevented a high surface productivity (lower NAR and number of coccoliths/g values), similar to the younger Heinrich (H1–H8 and H10–H11) events (Salgueiro et al., 2010).

5.3. Coccolithophore responses to orbital forcing

The comparison of coccolithophore assemblage data of core MD03-2699 with the planktonic δ^{18}O record (Fig. 3) indicates that higher values of NAR and number of coccoliths/g (Fig. 5a) mainly occurred during the interglacial periods and interstadial events, while the values decreased during the glacial periods and the stadial events. These changes in coccolithophore assemblages are strongly influenced by the interplay of the Earth's orbital parameters (Hays et al., 1976) that caused variability of summer insolation on the Northern Hemisphere. NH insolation maxima/minima (Ziegler et al., 2008; Ashkenazy et al., 2010; Trommer et al., 2011) determine the migration of the Intertropical Convergence Zone (ITCZ) northward/southward during interglacial and glacial periods, respectively (Chiang et al., 2003; Broccoli et al., 2006; Stoll et al., 2007; Lopez-Otalvaro et al., 2009; Tzedakis, 2010; Sepulcre et al., 2011), and the expansion/retreat of the northern latitude ice sheets on a glacial/interglacial time-scale. Higher values of coccolithophore production are observed during summer insolation maxima that correspond to minima in the precessional amplitude (Fig. 5a).

Considering the coccolithophores' response to precessional forcing and the actual seasonal succession of coccolithophore species in the area, it is possible to provide additional insights into the prevailing paleoceanographic conditions. In the periodograms, the influence of precession on *G. caribbeanica*, warm taxa and small *Gephyrocapsa* is shown (Fig. 7).

To better understand their response to this orbital forcing, these taxa have been filtered at the precession frequency band and the filtered series of small *Gephyrocapsa* and of *G. caribbeanica* reveal an alternating dominance between these groups (Fig. 4). The temporal variability of the assemblages is mainly characterised by changes in the relative abundance of the opportunistic genus *Gephyrocapsa,* which occur in response to environmental changes. In our data, maxima in the filtered record of small *Gephyrocapsa* and in the percentages of *C. pelagicus braarudii* are in phase with spring insolation intensity (Fig. 4) and are regarded as good indicators for periods of prevailing influence of the PC and for conditions near the coastal upwelling centres.

The filtered percentage records of *G. caribbeanica* and the warm water species curve are in phase with autumn insolation intensity (Fig. 4). The warm water species are correlated with the SST record (Fig. 6; Table 2) suggesting a preference for higher SST. The assemblages of core MD03-2699 are characterised by a high abundance of *G. caribbeanica* (Fig. 4), in particular during MIS 13, when the high planktonic δ^{13}C values indicate fewer nutrients available in the thermocline waters (Voelker et al., 2010). For this reason, even if the paleoenvironmental meaning of *G. caribbeanica* is still a little questionable, and the potential causes of dominance could also be related to a rapid phylogenetic evolution, because this is a global and synchronous event — recorded in the Atlantic, the Pacific, the Southern oceans, and at high latitudes (Bollmann et al., 1998; Flores et al., 1999, 2003; Baumann and Freitag, 2004; Baumann et al., 2004), the species could also be influenced by environmental conditions. The interval between MIS 13 and MIS 9 shows several oscillations in the abundance of the *Gephyrocapsa* groups, superimposed on the glacial–interglacial stages, with each ca. 19–21 kyr oscillation experiencing two minor cycles of about 10 kyr, mainly recorded by the small *Gephyrocapsa* group. Thus, the oscillations follow the half and full precession harmonics found in the periodograms. The main time variability of coccolithophore assemblages, correlated to these cycles, mainly occurred between 505 and 430 kyr, as recorded by *G. caribbeanica* and warm taxa and, throughout the time window, as recorded by small *Gephyrocapsa*, with the only interruption between 430 and 405 kyr (Fig. 3). This event occurred during the eccentricity minima interval of MIS 11 when precession variability was low. A higher resolution study is needed to better understand paleoproductivity changes during this period, in order to analyse also the influence of higher frequency cycles on coccolithophore assemblages.

5.4. Coccolithophore assemblages and the Mid-Brunhes event

The studied interval is characterised by two periods of relative eccentricity maxima (536–435 ka BP and 370–300 ka BP) separated by a period of eccentricity minima during MIS 11 (Fig. 5a, b). During these periods, different structures of coccolithophore assemblages occurred at site MD03-2699. The assemblages of the MIS 11 eccentricity minimum are characterised by higher NAR values (Fig. 5a) and by blooming of the opportunistic genus *Gephyrocapsa.* Within this genus, which thrives under the more stable condition of a low eccentricity ocean (Rickaby et al., 2007), the taxa mainly represented are small *Gephyrocapsa* and *G. caribbeanica* (Fig. 4) and, subordinate, *G. oceanica* and *G. margereli* (Fig. 3). *G. caribbeanica,* in the assemblages of core MD03-2699, is the most abundant species, its dominance between ~550 and 250 ka being widely documented (Bollmann et al., 1998; Flores et al., 1999, 2003; Baumann and Freitag, 2004; Baumann et al., 2004) and associated more likely to a rapid phylogenetic evolution. However, during MIS 11, *G. oceanica* and small *Gephyrocapsa,* becoming more abundant, balanced the percentages of *G. caribbeanica*. Balch (2004) reports that the duration of the length of the day and the light intensity influence the growth of coccolithophore blooms. Rickaby et al. (2007), using data from three cores located around 0° of the western Equatorial Pacific and Equatorial and subtropical Indian Ocean, suggest that eccentricity influences phytoplankton growth rate through an interannual interplay between light intensity and length of growing season. They infer that coccolithophore blooms may occur when maximal growing season length is paired with the maximal possible orbital insolation, which can only occur when eccentricity is minimal. When eccentricity reaches amplitude minima, summer insolation in the Northern Hemisphere is marked by low variability (Loutre and Berger, 2000), and winter and summer have more or less the same length. The increase of *Gephyrocapsa* genus bloom during the eccentricity minimum period is reflected in the NAR trend. The assemblages of relative eccentricity maxima of MIS 13 and 9, instead, are associated with intermediate NAR values (Fig. 5a) and a dominance of *G. caribbeanica* (Fig. 5b). This is due to a lower contribution of small *Gephyrocapsa*, *G. oceanica* and *G. margereli* to coccolithophore blooms, which are mainly composed of *G. caribbeanica* (Fig. 4b). Because the inverse contrast in season length and insolation becomes more extreme as eccentricity increases (Rickaby et al., 2007), the dominance of *G. caribbeanica* in the assemblages of relative eccentricity maxima could be due to the fact that *G. caribbeanica*, like *E. huxleyi*, is an exceptional light-loving species.

The Mid-Brunhes Event (MBE; 600 to 200 ka), also called the Mid Brunhes Dissolution Interval (MBDI) (Barker et al., 2006), was also a period of global carbonate dissolution and represented a whole ocean shift in carbonate chemistry. Our data on *G. caribbeanica* and *C. leptoporus* (a dissolution resistant taxon) are inversely correlated with the DI (Table 2). These results indicate moderate/high dissolution episodes and could confirm the hypothesis of an influence of *G. caribbeanica* blooms in altering marine carbonate chemistry (Baumann and Freitag, 2004; Barker et al., 2006). The intensive calcification of *G. caribbeanica* caused a carbonate-ion under saturation and consequently a dissolution increase. However, because most of these dissolution episodes are recorded when high organic carbon contents are observed (Rodrigues et al., 2011), the dissolution could also be caused by metabolic CO_2 produced within the sediments by enhanced organic matter fluxes to the sea floor (Baumann and Freitag, 2004; Barker et al., 2006, and references therein). Our data of coccolithophore production shows a fair similarity with the EPICA Dome C CO_2 record (Siegenthaler et al., 2005; Fig. 5a). On geological time-scales, variation in coccolith abundance in the sedimentary record is often linked to glacial–interglacial transitions, with a predominance of coccolithophores during interglacial periods (McIntyre et al., 1972; Henrich, 1989). During glacial periods, the coccolithophores to diatoms ratio is shifted towards diatoms, which dominate the blooms. So the lower atmospheric CO_2 levels in these periods are presumably related to lower contribution of coccolithophores in respect to non-calcifying phytoplankton (Harrison, 2000; Ridgwell et al., 2002; Riebesell, 2004).

6. Conclusion

During glacial periods, because the Northern Hemisphere (NH) was less irradiated (insolation intensity), long-term ocean settings with a general persistence of cold conditions over the area occurred. This is also shown by the SST and planktonic $\delta^{18}O$ records of core MD03-2699 (Voelker et al., 2010; Rodrigues et al., 2011). The quasi-predominance of cold conditions and the occurrence of weak upwelling seasons caused unfavourable conditions for coccolithophore growth, as also supported by the total alkenone concentration data (Rodrigues et al., 2011). This suggests a long-term influence of the Portugal Current (PC) during the glacial periods on coccolithophore assemblages (Fig. 8b).

During interglacial periods, conditions opposite to the glacial stages occurred, and the quasi-predominance of warming, together with intense upwelling seasons, caused favourable conditions for coccolithophore growth (Fig. 8a). This reconstruction is in good accordance with the hydrographic model proposed by Voelker et al. (2010), who observed a strong influence of Azores Current and Iberian Poleward Current (IPC) waters during MIS 11c.

This pattern could be linked to surface current dynamics, strictly related to ocean–atmosphere settings, and to the Intertropical Convergence Zone (ITCZ) migration on a glacial/interglacial time scale. Because the ITCZ position is controlled by two major high pressure centres, the Azores High (AH) in the NH and the South Atlantic High in the Southern Hemisphere, the ITCZ migration implies the AH/Icelandic Low (IL) System shifted on glacial/interglacial time-scale. This is also confirmed by model simulations, highlighting a southward shifting of the AH/IL in the Last Glacial Maximum (LGM) relative to the pre-industrial simulation (Pausata et al., 2009).

Overprinted on this glacial/interglacial pattern, climatic and paleoceanographic variability at precessional-scale has been observed in the study area. This variability, affecting the quasi-permanent AH/IL positions, is related to the relative northward/southward migration triggered by precession (Moreno et al., 2002; Yin et al., 2009). Our results can be interpreted by the following two main scenarios:

1. PC prevalent conditions occurred when the NH spring/summer was at perihelion because there was greater warming in the NH in response to insolation. This implies that the AH moved northward (Fig. 8c). Consequently, the winds, blowing predominantly from the north, caused a persistent upwelling of cooler water. Thus, the increase in small *Gephyrocapsa* and eutrophic taxa in the coccolithophore assemblages indicate the prevailing influence of PC nutrient-rich waters (Fig. 8c) and increased productivity.
2. When the NH summer/autumn was at aphelion, the AH moved southward (Fig. 8d), causing weaker equatorward wind-stress that pushes the Azores Current northward and induces the prevailing influence of the IPC on the site (Fig. 8d). The coccolithophore assemblages reflected the increase of warm taxa and the dominance of *G. caribbeanica*.

Over-imposed on precessional variability are observed rapid switches between different modes of atmosphere circulation, probably related to millennial-scale oscillations of the AH/IL System and causing variability in wind systems together with increase/decrease of dryness.

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Appendix A. Taxonomic appendix

Calcidiscus leptoporus (Murray and Blackman, 1898) Loeblich and Tappan, 1978
Calciosolenia murrayi Gran, 1912
Coccolithus pelagicus (Wallich, 1877) Schiller, 1930
Coccolithus pelagicus ssp. *braarudii* (Gaarder 1962) Geisen et al. 2002
Coccolithus pelagicus (Wallich 1877) Schiller 1930 ssp. *pelagicus*
Florisphaera profunda Okada and Honjo, 1973
Gephyrocapsa aperta Kamptner, 1963
Gephyrocapsa ericsonii McIntyre and Bé, 1967
Gephyrocapsa caribbeanica Boudreaux and Hay, 1967
Gephyrocapsa margereli Bréhéret, 1978
Gephyrocapsa oceanica Kamptner, 1943
Helicosphaera carteri (Wallich, 1877) Kamptner, 1954
Helicosphaera hyalina Gaarder 1970
Helicosphaera inversa (Gartner, 1980) Theodoridis, 1984

Pontosphaera Lohmann, 1902

Pseudoemiliania lacunosa (Kamptner 1963) Gartner 1969

Rhabdosphaera clavigera (Murray and Blackman, 1898)

Reticulofenestra Hay, Mohler and Wade 1966

Syracosphaera Lohmann, 1902

Syracosphaera pulchra Lohmann, 1902

Umbellosphaera Paasche, in Markali and Paasche, 1955

Umbellosphaera tenuis (Kamptner, 1937) Paasche in Markali and Paasche, 1955

Umbilicosphaera Lohmann 1902

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