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Research paper

Distribution of large *Emiliania huxleyi* in the Central and Northeast Atlantic as a tracer of surface ocean dynamics during the last 25,000 years

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ABSTRACT

The coccolithophore species *Emiliania huxleyi* is characterized by a wide range of sizes, which can be easily distinguished in the light microscope. In this study we have quantified the abundance of large (coccoliths >4 µm in maximum length) *E. huxleyi* specimens during the last 25 kyr in sedimentary records from eleven cores and drill sites in the NE Atlantic and W Mediterranean Sea, to prove its usefulness in the reconstruction of water mass dynamics and biostratigraphic potential.

During the Last Glacial Maximum this large form, a cold-water indicator, was common in the NE Atlantic and Mediterranean, and its regional variation in abundance indicates a displacement of the climatic zones southwards in agreement with the development of ice sheets and sea ice in the Northern Hemisphere during this period. On the other hand, the gradient between northern and southern surface water masses in the Subtropical Gyre appears to have been more pronounced than at present, while the Portugal and Canary Currents were more intense. In the western Mediterranean basin temperatures were cooler than in the adjacent Atlantic, provoking a quasi-endemism of these specimens until the end of Heinrich Event 1. This may have been due to a restriction in the communication between the Atlantic and Mediterranean through the Strait of Gibraltar, the arrival of cold surface water and the amplification of cooling after the development of ice sheets in the Northern Hemisphere.

During the deglaciation, large *E. huxleyi* specimens decreased in abundance at medium and low latitudes, but were still numerous close to the Subarctic region during the Holocene. In transitional waters this decrease to present day abundances occurred after Termination Ib.

The abrupt change in abundance of this large *E. huxleyi* form is proposed as a new biostratigraphic event to characterize the Holocene in mid- to low-latitude water masses in the North Atlantic, although this horizon seems to be diachronous by 5 kyr from tropical to subarctic regions, in agreement with the gradual onset of warm conditions.

1. Introduction and objectives

Emiliania huxleyi (Lohmann) Hay and Mohler is the most abundant extant coccolithophore species and has dominated assemblages for 73 kyr, although the first specimens occur at 290 kyr (Lourens et al., 2004), having evolved from the genus *Gephyrocapsa*. Variations in its abundance and ratio with other species have been widely used as biostratigraphic markers (e.g. Martini, 1971; Bukry, 1973; Thierstein et al., 1977; Gartner, 1977).

E. huxleyi is a cosmopolitan species (McIntyre and Bé, 1967; Geitznauer et al., 1977; Okada and McIntyre, 1979; Winter, 1985), and is able to live within a broad range of sea-surface temperature (SST) and salinity conditions (e.g. McIntyre et al., 1970; Bukry, 1974; Winter et al., 1979; Winter, 1982). It is found in the entire photic zone (Okada and Honjo, 1973), with higher abundances in nutrient-rich subpolar waters (McIntyre and Bé, 1967; Okada and Honjo, 1973; Gard, 1993; Brand, 1994; Flores and Marino, 2002; Gravalosa et al., 2008; Backman et al., 2009), as well as along the border of subtropical oceanic gyres, in equatorial and coastal upwelling regions, and in outer shelf areas (Winter, 1985; Verbeek, 1990; Brand, 1994, Baumann et al., 2000; Giraudeau et al., 2000).

Several authors have studied morphological variations of this taxon, observing a positive correlation between abundance of large (>4 µm) forms of *Emiliania* (sometimes referred as *Emiliania pujoseae* Verbeek or *E. huxleyi* var. *pujosiae* (Verbeek) Young and Westbroek 1991 ex Medlin and Green) and cold oceanographic features or environments (Hagino

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et al., 2005), pulses in SSTs at orbital level (Weaver and Pujol, 1988; Flores et al., 1993, 1997; Esposito, 1999; Weaver et al., 1999), or to monitor changes at millennial and submillennial scales (Colmenero-Hidalgo et al., 2004; Sierro et al., 2005; Mejía Molina et al., 2006) during the last climatic cycle in the Northern Hemisphere.

Taking into account its usefulness as a stratigraphic and paleoecological marker (Flores et al., 1997; Colmenero-Hidalgo et al., 2002), we have compiled data of the temporal and spatial distributions of this large *E. huxleyi* (LE) form in the North Atlantic from the Last Glacial Maximum (LGM) up to the late Holocene. These data are used to determine any synchroneity during this time interval, to reconstruct and monitor the displacement of surface water masses, and to investigate the relationship between fossil abundance patterns and oceanographic features such as the Arctic Front (AF).

2. Core locations and oceanographic setting

Samples from eleven sedimentary records in the Subtropical, Central and North-East Atlantic and in the Western Mediterranean have been analyzed (Fig. 1; Table 1), covering a transect from tropical areas to polar regions, and the Western Mediterranean Sea.

IMAGES Calypso piston core MD03-2705 was obtained during the DUST Expedition on board the *R/V Marion Dufresne* from a seamount off the Mauritanian coast (18° 05′N; 21° 09′W; 3085 m water depth) located on a submarine ridge connecting the Cape Verde Archipelago to the African margin. This area is directly affected by the Canary Current (CC), the eastern branch of the Subtropical North Atlantic Gyre.

Sediment piston core GeoB 5546 was obtained during the *R/V Meteor* Cruise M42-4 at 27°32′N, 13°44′W from 1070 m water depth off Cape Yubi (NW Africa). Today this area also lies under the influence of the CC. In addition, this area is influenced by trade wind-driven coastal upwelling during the boreal summer.

IMAGES Calypso piston core MD95-2037 (37° 05′N, 32° 01′W; 2159 m water depth), was obtained from the Central North Atlantic, southwest of the Azores archipelago in the Subtropical region, influenced by the Azores Current (AC), a relatively warm branch of the Subtropical Gyre, during the IMAGES I Cruise on board the *R/V Marion Dufresne*.

Gravity core SU90-08 (43° 41′N, 30° 24′W; 3080 m water depth) was obtained during the PALEOCINAT I Cruise in 1990 on board the *R/V Le Suroît* on the western flank of the mid-oceanic ridge. The north-

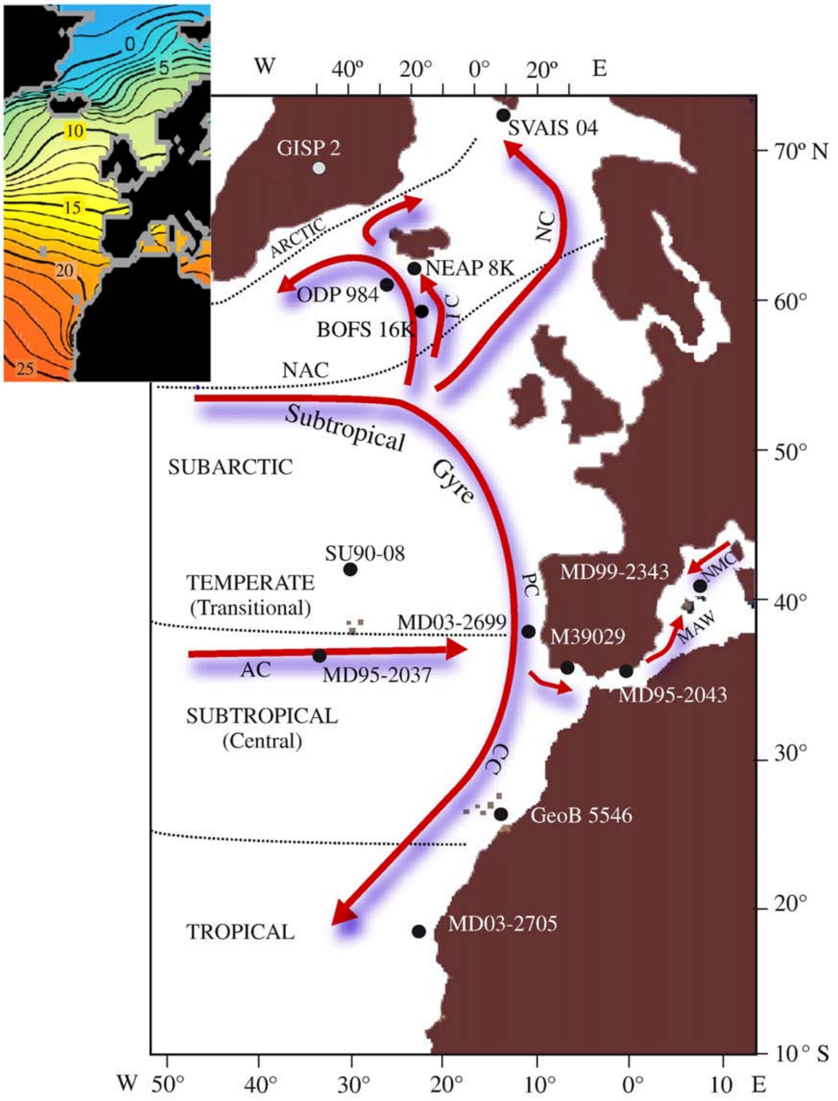

Fig. 1. Site location, main oceanographic features, coccolithophore biogeographic regions (after McIntyre and Bé, 1967) and Sea Surface Temperatures (top-left graph, SST distribution after Locarnini et al., 2006). NAC: North Atlantic Current; IR: Irminger Current; NC: Norway Current; PC: Portugal Current; NASW: North Atlantic Surface Waters; MAW: Modified Atlantic Waters; NMC: North Mediterranean Current; CC: Canary Current.

Table 1
Core location, age model references and main oceanographic features.

Site	Location	Longitude	Latitude	Water depth (m)	Age-model	Oceanographic feature	Mean SST (°C) WOA05
MD03-2705	Senegal/Mauritania	21°09 W	18°05′N	3085	Jullien et al. (2007)	Subtropical Gyre Canary C.	22
GeoB 5546	Morocco/Canary Islands	13°44′W	27°32′N	1070	Kuhlmann et al. (2004)	Subtropical Gyre Canary C	20
MD03-2699	Portuguese Margin	10° 39′W	38°38′N;	1865	Rodrigues et al. (in press)	Subtropical Gyre Portugal C.	18
MD95-2043	Alboran (Mediterranean)	02°37′W	36°08′N	1841	Cacho et al. (1999)	MAW	20
MD99-2343	Minorca (Mediterranean)	04°01′E	40°29′N	2391	Sierro et al. (2005)	MAW/NMW	20
M39029-7	Gulf of Cadiz (N Atlantic)	8°13′W	36°02N	1917	Colmenero-Hidalgo et al. (2004)	Subtropical Gyre Portugal C.	19
MD95-2037	North Atlantic	32°01′W	37°05′N	2159	Labeyrie et al. (2005)	Subtropical Gyre Azores C.	19
SU90-08	Azores (N Atlantic)	30°24′W	43°41′N	3080	Grousset et al. (1993)	Subtropical Gyre Central	16
ODP 984	Bjorn Drift (N Atlantic)	24°.02′W	61°25′N	1648	Praetorius et al. (2008)	NAC	9
NEAP 8K	NE Atlantic	23°54′W	59°48′N	2360	Barker et al. (2004)	NAC	9
SVAIS04	Norwegian–Greenland Sea	13°54′W	74°457N	1839	Colmenero-Hidalgo et al. (2009)	Arctic	3

flowing, relatively cold surface waters of the Subtropical North Atlantic Gyre dominate this area within the Temperate (Transitional) region.

IMAGES Calypso piston core MD03-2699 was collected from the Estremadura Spur north of Lisbon along the Iberian Margin (38° 38′N, 10° 39′W; 1865 m water depth) during the PICABIA Expedition on board the *R/V Marion Dufresne*. Gravity core M39029-7 (36°02 N, 8°13 W; 1917 m water depth) was obtained by the *R/V Meteor* from the outer zone of the Gulf of Cadiz. The relatively cold Portugal Current (PC), linked to the Subtropical North Atlantic Gyre, characterize the surface waters of this Transitional (Temperate) region.

IMAGES Calypso core MD95-2043 (36° 08′N, 2° 37′W; 1841 m water depth), was obtained from the Alboran Sea, Western Mediterranean, between the anticyclonic gyres fed by the Atlantic surface waters during the IMAGES I Cruise on board the *R/V Marion Dufresne*.

IMAGES Calypso piston core MD99-2343 was obtained from a sediment drift north of the island of Minorca, in the Northwestern Mediterranean Sea (40° 29′N, 04° 01′E; 2391 m water depth) during the IMAGES V Expedition on board the *R/V Marion Dufresne*. The surface water in this region is mainly controlled by the Modified Atlantic Water (MAW), which is linked with the Subtropical North Atlantic Gyre, but also influenced by the Northern Mediterranean Current (NMC) generated in the Mediterranean basin.

Piston core NEAP 8K (59° 48′N, 23° 54′W; 2360 m water depth) and ODP Site 984 (61° 25′N, 24° 02′W, 1648 m water depth) were obtained from the Bjorn Drift (North Atlantic) during *RRS Charles Darwin* Cruise 88 (NEAPACC) and ODP Leg 162 on board the *JOIDES Resolution*, respectively. This area is influenced by the North Atlantic Current (NAC), which is the northern branch of the Subtropical North Atlantic Gyre in the Subarctic region, and particularly by its warm branch the Irminger Current (IR).

Piston core SVAIS04 (74° 45′N, 13°54′W, 1839 m water depth) was obtained from the Storfjorden Trough-mouth fan, located south of the Svalbard Archipelago in the Norwegian–Greenland Sea, during the SVAIS Expedition on board the *BIO Hespérides*. This site is influenced by the relatively warm Norwegian Current (NC), the northern branch of the NAC in the northern part of the Subarctic Zone, close to the Arctic region.

3. Materials and methods

For all locations, except GeoB 5546, NEAP 8K and ODP Site 984, samples used for nannofossil counts were prepared following the methodology of Flores and Sierro (1997). With this method, a weighed amount of dry sediment is diluted in a volume of buffered water. A small fraction is extracted with a micropipette and dropped onto a petri-dish, which has been previously filled with more buffered water and has a cover slide in the bottom. After one day of settling the cover is imbued in Canada balsam. Around 500 coccoliths were counted in each sample, using a Leica DMRXE polarized light microscope at 1250× magnification to calculate percentages. Forms of *E. huxleyi*, such as specimens larger than 4 µm and smaller than 4 µm in size, were considered separately. For this operation a micrometer eye-piece was used, although some samples were studied using microphotographs captured with the Leica QWin Pro software. Routine scanning electron microscope (SEM) analyses were performed on Zeiss DSM 940 and Hitachi H-3000 microscopes in order to estimate the preservation state of specimens. However, it should be noted that for core SVAIS04 the total coccoliths considered for the counting analysis was significantly reduced due to the low coccolith abundance in the samples of this high-latitude sediment record (sometimes even barren in coccoliths).

For ODP Site 984 and core GeoB 5546, samples were prepared using a combined dilution/filtering technique as described by Andruleit (1996) and modified by Boeckel et al. (2006). Identification of *E. huxleyi* specimens was made using a Zeiss DMS 940A SEM. Around 500 coccoliths per sample in different transects were counted, estimating the percentage of LE.

Samples from core NEAP 8K were prepared following the spraying and duplicate slide procedure of Henderiks and Törner (2006) and Bollmann et al. (1999). Observations were made with a Leitz polarizing light microscope (1250×), counting around 400 coccoliths to obtain relative species abundances. The relative abundance of LE was determined, in each sample, by measuring 100 individual specimens of *E. huxleyi* captured with a Leica DFC 320 digital camera.

Some small numerical discrepancies between records from close locations can be observed (Fig. 2). These are most likely due to the usage of different microscopy techniques (SEM and polarizing microscope) and to the difficulty of identifying all of the small *E. huxleyi* forms in the SEM. However, different authors point out that in these situations the general trend of the coccolithophore assemblages in selected time slices is similar (e.g. Baumann et al., 1998, 2000; Bollmann et al., 2002; Herrle and Bollmann, 2004).

The degree of preservation of the coccolithophore assemblage in the studied interval is good to moderate in all records. Partial dissolution of some elements on the distal shield and central area grill is frequent, especially in the larger forms. These problems have not hampered the measurements and counting.

4. Stratigraphy and age model

Table 1 includes a list of the publications where age models of the studied sections were presented; a brief description of the age models of all cores is given below.

The age-model for core MD03-2705 was established by Jullien et al. (2007) based on the comparison of the benthic foraminifera $\delta^{18}O$ record obtained with the SPECMAP stack record (Martinson et al., 1987). To better constrain this age model, eight AMS ^{14}C ages obtained by analysing planktonic foraminifera were corrected for reservoir ages (500 yr) and calibrated to calendar ages using Bard's polynomial relation (Bard et al., 1998).

For GeoB 5546 14 AMS ^{14}C datings and the planktonic foraminifera $\delta^{18}O$ isotopic record were used for stratigraphy (Kuhlmann et al., 2004). The AMS ^{14}C ages were corrected for a reservoir age of 400 years and were subsequently converted to calendar ages using the CALIB program (Stuiver and Reimer, 1993; Stuiver et al., 1998). In addition, the planktonic isotope record was correlated with the NGRIP $\delta^{18}O_{ice}$ record.

The stratigraphy for core MD03-2699 was constructed by Rodrigues et al. (in press) based on four AMS ^{14}C dates measured on planktonic foraminifera. The conventional AMS ^{14}C radiocarbon ages were converted into calendar ages using the marine dataset of the CALIB program (Stuiver and Reimer, 1993; Stuiver et al., 1998) and the MARINE04 calibration curve (Hughen et al., 2004).

The chronology of core MD95-2043 has been previously established by Cacho et al. (1999). A total of 17 AMS ^{14}C ages were obtained, corrected for a reservoir age of 400 yr and converted into calendar ages using the CALIB program (Stuiver and Reimer, 1993; Stuiver et al., 1998) while three extra isotopic events were dated for additional tiepoints.

Sierro et al. (2005) provided an age model for core MD99-2343 based on four AMS ^{14}C dates and several tie points with the Greenland ice core GISP2 (Grootes et al., 1993). The ages were calibrated with the standard marine correction of 408 yr and the regional average marine reservoir correction for the Western Mediterranean Sea by means of the CALIB program (Stuiver and Reimer, 1993; Stuiver et al., 1998) and the MARINE04 calibration (Hughen et al., 2004).

The stratigraphy and age model of core M39029-7 were established by Colmenero-Hidalgo et al. (2004) by making a peak to peak correlation of oxygen isotope data between this core and the nearby core M39008-3 (Löwemark, 2001), recovered from the upper slope of the Gulf of Cadiz. This latter core contains AMS ^{14}C dates and its age model has been established by Cacho et al. (2001).

The age model for MD95-2037 was established by Labeyrie et al. (2005) based on AMS ^{14}C dating analyzed on planktonic foraminifera, which were converted into calendar ages using the CALIB program.

The age model of core SU90-08 was defined by Grousset et al. (1993) through correlation to the spectral mapping SPECMAP stack (Martinson et al., 1987). Isotope stages and their limits were also recognized from magnetic susceptibility and colour reflectance data (Grousset et al., 1993; Cortijo et al., 1995).

For core NEAP 8K we used the chronology proposed by Barker et al. (2004) who recalibrated 14 radiocarbon dates in core BOFS 5K (50.7°N, 21.9°W; Manighetti et al., 1995) and cross-correlated IRD concentrations and oxygen isotope records to establish age models for cores BOFS 8K, BOFS 17K and NEAP 8K located to the North.

The chronology of ODP Site 984 was published by Praetorius et al. (2008) and was established using 18 radiocarbon dates and a correlation with the previously dated Vedde Ash layer.

The stratigraphy of core SVAIS04 is shown in Colmenero-Hidalgo et al. (2009), based on the correlation of the concentrations of coccolithophores, diatoms and dinocysts to those recorded in radiocarbon-dated cores from the Nordic Seas (Koç et al., 1993; Andruleit and Baumann, 1998). Recently obtained AMS ^{14}C ages (Lucchi et al., personal communication, 2010) confirm this preliminary age model.

5. Results

An overall pattern of latitudinal variation is observed along the N–S transect, with distinct changes between different time slices (Fig. 2). Abundances of LE are generally higher during the LGM and the interval corresponding to Heinrich Event (HE) 2 than later in most available records (note that this interval is not studied in Site 984, and for SVAIS04 this period is barren of coccolithophores most probably due to its proximal location to the margin of the Barents Sea ice sheet, preventing comparisons). The Mediterranean cores also show a distinct peak at HE1, while records under the influence of the Azores and Canary Currents (MD95-2037 and GeoB 5546) present highest abundances during the Bølling-Allerød (BA) to Younger Dryas (YD) interval.

In the Tropical, Subtropical and Temperate regions (with the exception of the Mediterranean sites), LE abundances are close to 10% during the LGM to HE2 interval, reaching up to 70% in the Subarctic core NEAP 8K. In a previous study, Weaver et al. (1999) showed similar proportions of LE (quoted as *E. pujoseae*) at core BOFS 16K (59°N, 23°W) (Fig. 1). In the Mediterranean cores, abundances of LE are up to twice as high as in the Atlantic at similar latitudes.

A drastic reduction in the abundance of LE occurs between HE1 and the BA period, particularly in the Mediterranean records. In general, during this interval LE disappears abruptly from the tropical region while a progressive reduction takes place in mid- to high-latitude records, with the exception of Site 984. A comparison between this Site and core NEAP 8K (situated at the same latitude but at different longitudes) shows differences of between 10 and 20% for the mentioned interval, with no obvious decrease at Site 984 until the end of the YD.

From the YD to Termination Ib (TIb) and into the Holocene, Subtropical to Temperate locations show abundance values of less than 5% of LE. One exception is the Central Subtropical core MD95-2037, where abundances increase up to 10% during certain short intervals in the deglaciation.

During the Holocene, abundances of less than 5% of LE characterize the southern records, with small exceptions at core MD03-2699 (Portuguese margin) and ODP Site 984 (Subarctic), where a peak around 8 kyr is recorded. This Site and core SVAIS04 show higher LE abundances of around 10% during the Holocene. In this northernmost record, the intervals barren in coccoliths alternate with others showing up to 10% of LE during the deglaciation.

6. Discussion

6.1. Paleobiogeography and paleoceanographic scenario

The available data on the geographical distribution of LE and its relative abundance in the North Atlantic show a close relationship with cold surface waters (Flores et al., 1993, 1997; Weaver et al., 1999; Esposito, 1999; Colmenero-Hidalgo et al., 2002; Sierro et al., 2005). In the latest Holocene, LE occurs mostly and in low proportions (below 10%) in Subarctic regions, where the annual mean temperature is always below 5 °C (Locarnini et al., 2006), while in other regions it is almost absent. Therefore a link between low SST and high LE abundances appears very probable, although at this time we cannot constrain the relationship in numerical terms. In addition, other factors such as nutrient content, salinity, and interaction with other organisms, rather than SST, may also play a role in the abundances of LE, which is not yet well understood.

6.1.1. Glacial period

During the LGM, ice sheets covered a large extent of the Northern Hemisphere (NH), reaching as far south as 55° N in West Europe and affecting ocean dynamics (e.g. Peltier, 1994; Sejrup et al., 2000; de Vernal et al., 2006) (Fig. 3). Before 16 kyr, the northernmost location (SVAIS04), placed in the south of the Svalbard Archipelago, was covered with sea ice almost all-year round (Martrat et al., 2003). The rest of the northern locations, including the Subarctic core NEAP 8K, remained free of ice at least seasonally (de Vernal et al., 2006; Backman et al., 2009). We have no data for this interval in ODP Site 984, but the record of nearby core BOFS 16K (Weaver et al., 1999) (Fig. 1) shows the highest abundances of large specimens of *Emiliania* (quoted as *E. pujoseae*) at 25 kyr. The abundances of LE observed at this latitude for the LGM suggest that SSTs were colder than those recorded in the Norwegian Sea today (Locarnini et al., 2006), in agreement with most of the proxies tested in the region (Weinelt et al., 2003; Kucera et al., 2005a,b; Lee, 2004; de Vernal et al., 2005,

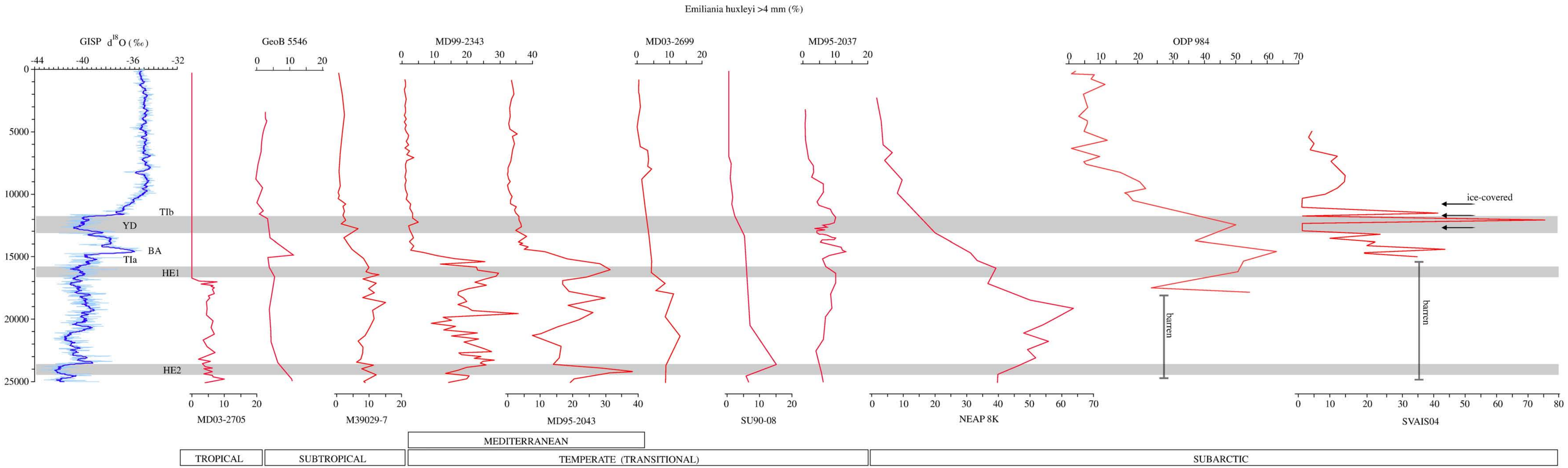

Fig. 2. Relative abundance (percentages) of *Emiliania huxleyi* >4 µm at the studied sites vs. the Greenland GISP2 $\delta^{18}O_{ice}$ record (Grootes et al., 1993). H2: Heinrich event 2; H1: Heinrich event 1; TIa: Termination Ia; BA: Bølling-Allerød; YD: Younger Dryas; TIb: Termination Ib. Present day biogeographic coccolithophore zones after McIntyre and Bé (1967).

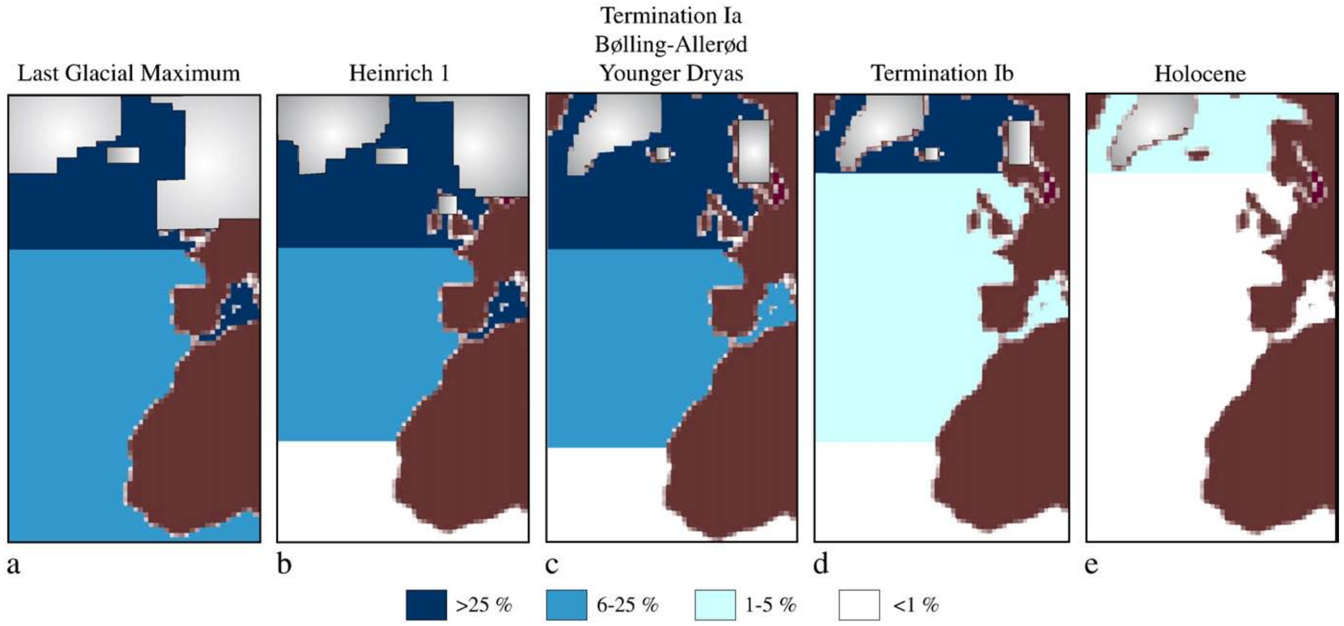

Fig. 3. Schematic distribution and relative abundances of *E. huxleyi* >4 μm in five selected time slices. Since the LGM it is noteworthy that a northward displacement of these forms occurred and that during the Holocene it became restricted to the Subarctic zone, symbolized by arrows. High concentrations during the LGM and H1 in the Mediterranean Sea are consistent with lower SSTs than in the surrounding Atlantic. Ice sheet contours modified after Peltier (1994) and Sejrup et al. (2000).

2006). Curiously, the record of LE in the Transitional, Subtropical and Tropical regions (except the Mediterranean) shows rather similar abundance values; we thus believe that a strong gradient existed between the stations north and south of approximately 50°N. In this context, abundances up to 20% of LE in the eastern North Atlantic seem to be linked to seasonal sea-ice cover, which is consistent with a winter sea-ice limit at about 55°N for this time (de Vernal et al., 2006).

At low-latitude stations LE percentages for the LGM were higher than those of Subarctic stations during the Holocene, suggesting that water masses SSTs south of 50°N were cooler during the LGM than today at high latitudes. One exception for this time period is MD95-2037, situated in the Subtropical region (centre of the Subtropical Gyre), where low LE abundances indicate that SSTs were relatively higher than those estimated N and E. However, this gradient is not observed at the coastal sites, including the tropical MD03-2705, where SSTs should be similar or slightly lower than SSTs in Transitional regions.

Taking into account these interpretations, for the LGM we propose that the northern branch of the NAC (Fig. 1) would have occupied a more southerly position, with the Subarctic Front (SAF) below 60°N at the same latitude as ODP Site 984 and core NEAP 8K (~25°W); however, seasonal advection in the warm ice-free season allowed the growth of *E. huxleyi* and other coccolithophore taxa, such as *Coccolithus pelagicus* (Weaver et al., 1999). At the same time, we suggest an intensification of the southern branch of the Subtropical North Atlantic Gyre, and consequently of the PC and CC. Inside the gyre, a gradient is also observed at ca. 40°N in a sector where the relatively warm Azores Current (AC) is the dominant feature. This is not the case for the cores recovered at the periphery of the Subtropical North Atlantic Gyre, close to the Iberian and Africa margins affected by more active PC and CC.

This interpretation coincides with previous studies (e.g. Calvo et al., 2001; de Vernal et al., 2006) which observed an abrupt change in the SST gradient at ~40°N, and is in good agreement with a general oceanic scenario for the Northern Hemisphere in which a weakening of the Meridional Overturning Current contributed to the enlargement of the ice sheets and the enhancement of temperature gradients between the central and northern surface water masses (e.g. Chapman and Maslin, 1999; Rahmstorf, 2002).

The records observed in the Mediterranean Sea during the LGM need some special attention, since the percentages of LE sometimes are 3–4 times larger than those recorded in the North Atlantic during the same interval. According to our hypothesis, this would be interpreted as a consequence of changing temperature gradients between both regions. Although our proxy is not calibrated to quantify SST, other data corroborate our interpretation. Cacho et al. (2001) estimated alkenone-derived SST values of 17–18 °C and 13–14 °C in the Gulf of Cadiz and Alboran Sea, respectively. Comparable data were obtained by other authors using micropaleontological techniques (e.g. Kucera et al., 2005a,b; de Abreu et al., 2003 — planktonic foraminifers; de Vernal et al., 2005 — dinocysts, in the Atlantic; Pérez-Folgado et al., 2003 — planktonic foraminifers in the Mediterranean). This observation was related to the entrance of cold waters into the Mediterranean through the Strait of Gibraltar, as well as an amplified cooling related to the atmospheric teleconnection due to the strengthening of the north-westerly winds over the north-western Mediterranean, linked to the migration of the AF during the LGM (Cacho et al., 1999, 2000; Sierro et al., 2005) (Fig. 3).

The major decrease in abundance of LE in most cores occurred during and after HE1. However, this is not the case for the Mediterranean cores as they all recorded a peak in LE abundance at ~16 kyr, indicating a significant decrease in SST. This conclusion is in agreement with the findings of Cacho et al. (2001), who calculated an SST for HE1 of ~15 °C in the Atlantic and ~10 °C for the Mediterranean. In addition, Sierro et al. (2005) suggested a maximum in iceberg melting during this interval, a process that can favour the development of LE in the relatively isolated Mediterranean. This situation produces an apparent paradox: LE remained in a quasi-endemic situation in the Mediterranean, with relative abundances similar or even higher than in the Subarctic region. We interpret this fact as a consequence of the relative isolation related with a restriction (but not closure) in the communication between the Atlantic and Mediterranean, the consequent reduction in the generation of the MAW and the amplification of the Northern Hemisphere climatic signal in this basin (Fig. 3). However, other authors (e.g. Caralp, 1988; Grousset et al., 2000) indicated a more active interchange, and Cacho et al. (2001) argued that these low SSTs could be due to an intensification in the vertical water mixing with cooler intermediate waters. Our hypothesis considers temperature to be the most relevant factor in explaining the distribution of LE, but we cannot exclude additional environmental factors affecting the distribution of the large *E. huxleyi* forms.

6.1.2. Deglaciation (YD and BA)

In the Subtropical and Temperate regions, an abrupt reduction in LE abundance took place during TIa, reaching values similar to the Holocene as early as the BA. This fall is also observed in the Mediterranean records, coincident with a larger injection of Atlantic waters through the Strait of Gibraltar due to the deglacial sea-level rise (Pérez-Folgado et al., 2003), and synchronous with warming in the Western Mediterranean (Cacho et al., 1999). The decrease of abundance in LE occurs at TIb in core SU90-08, although is not so prominent in this record. On the contrary, cores GeoB 5546 and MD95-2037, in the Subtropical and Temperate Zones, respectively, peak during the BA, and show a similar decreasing trend afterwards. This feature may be related to local dynamics linked to upwelling or the CC influence in the case of GeoB 5546, and to the Azores Front dynamics (Gould, 1985) in the case of core MD95-2037. More cores and a comparison with similar resolution are necessary to address this question.

In higher latitudes the dominance of LE suggests that cool conditions probably remained until TIb. However, at the location of SVAIS 04 the seasonal advection of NAC may have permitted the development of LE and other coccolithophores during periods of absence of sea ice. This injection of NAC alternates with re-advances of the ice sheets, preventing a regular oceanic surface circulation, especially during the YD.

The final retreat of the Barents ice sheet occurred at the end of the deglaciation (TIb) (Martrat et al., 2003). The deglaciation is characterized by short cold episodes in the Mediterranean Sea and the Iberian margin (e.g. Renssen et al., 1996; Cacho et al., 2001). This interval coincides with an increase in atmospheric activity, observed by an increase in eolian markers (Mayewski et al., 1993) and a reduction in the accumulation of snow in Greenland (Kapsner et al., 1995). This may indicate that in the Mediterranean Sea and below 50°N in the Atlantic, LE thrived in waters characterized by conditions rather similar to the Subarctic region today, but with a mixing intensification and relative warming in the Mediterranean (Fig. 3). In latitudes higher than 50°N, the LE signal shows maxima at ODP Site 984 and pulses with the progression of ice southwards in the Subarctic core SVAIS04, characterized by barren intervals.

6.1.3. Early Holocene

During the Holocene, LE occurs only occasionally below 60°N, in relative low proportions after ~8 kyr. The peaks observed between 8 and 10 kyr are interpreted as cold pulses, previously documented both in the terrestrial record in the Scandinavian Peninsula (Baumann et al., 1995; Björck et al., 1998) and in the marine record (Cacho et al., 2001). This is especially noteworthy along the Portuguese margin and in the Subarctic zone. Unfortunately, sampling resolution and age models of some of the analyzed sites are not accurate enough, for example in the northern sector of the Subarctic region, where some peaks could correspond with this event. In the Mediterranean Sea and in low-latitude and Central Atlantic regions, this signal is not evident.

After the Climatic Optimum in the Holocene (Figs. 2 and 3) LE remains endemic in the Subarctic zone, and its record is sporadic in the northern sector of Subarctic and/or transitional regions.

6.2. Biostratigraphic implications

Large *Emiliania* in proportions >1% has been recorded since MIS 5, with significant fluctuations between MIS 4 and MIS 2 (Verbeek, 1990; Flores et al., 1993, 1997; Weaver et al., 1999; Colmenero-Hidalgo et al., 2004; Sierro et al., 2005). Its relatively large size and easily recognizable optical pattern in the light microscope are advantages for both quantitative and qualitative techniques. The decrease in abundance observed in low- and middle-latitudes during the last deglaciation, is consequently useful to identify the Holocene in marine sediments in the North Atlantic. This is a relevant event that contributes to the improvement of the resolution in the Pleistocene standard biozonations. This event has been previously used by a number of authors (Flores et al., 1993, 1997; Colmenero-Hidalgo et al., 2002; Bassetti et al., 2008), but it was not clear whether or not it was synchronous at different latitudes. Here we show that the drop in abundance occurs at ca. 16 kyr in low latitudes, ca. 11 kyr in high-latitude cores an at ca. 14 kyr in the western Mediterranean Sea (Fig. 2). So the event is diachronous by 5 kyr.

7. Conclusions

Forms of *E. huxleyi* larger than 4 μm in size can be identified as cold-water specimens. Their temporal and spatial occurrences in the North Atlantic and the Mediterranean Sea demonstrate that this form could be used as a tracer to characterize cold surface water masses conditions during the last 25 kyr.

During the LGM, large *E. huxleyi* occupied the central and northeast North Atlantic as well as the Mediterranean Sea. The development of sea ice in the Northern Hemisphere provoked a southward displacement of the climatic zones and an enhanced temperature gradient between the NAC and Central waters in the Subtropical North Atlantic Gyre. At the same time, a strong gradient in surface water temperature developed between the central Atlantic and peripheral sectors, such as the Iberian and Africa margins, as a consequence of the intensification of the PC and CC. In the western Mediterranean Sea SSTs were cooler than in the adjacent Atlantic, provoking a quasi-endemism of these organisms until the end of HE1. This may be related to a restriction in the communication between the Atlantic and the Mediterranean through the Strait of Gibraltar and the amplification of cooling via atmospheric teleconnections after the development of the Northern Hemisphere ice sheets.

During the deglaciation the LE community underwent a northward displacement interpreted as the development of a Subarctic biogeographic band similar to those recorded in the Holocene. A situation similar to present day conditions was reached after TIb in transitional waters.

Small peaks of LE are observed during the early Holocene at around 8 kyr, although sampling resolution and the accuracy of age models do not permit an exact correlation. This seems plausible for the high latitudes and along the Portuguese margin, where the PC is the most significant feature affecting the development of LE, while the event is not recorded clearly in the Mediterranean.

The abrupt change in LE abundance during the deglaciation is proposed as a new biostratigraphic event to characterize the onset of the Holocene in mid- to low-latitudes of at least the Central and North Atlantic. However, it appears to be diachronous since we found this event occurring ~ 5 kyr earlier in the tropical Atlantic in comparison to the Subarctic region.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.marmicro.2010.05.001.

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