



Primary productivity variability on the Atlantic Iberian Margin over the last 70,000 years: Evidence from coccolithophores and fossil organic compounds

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[1] This study analyzes coccolithophore abundance fluctuations (e.g., *Emiliania huxleyi*, *Gephyrocapsa* specimens, and *Florisphaera profunda*) in core MD01-2444 sediment strata retrieved at the Iberian Margin, northeastern Atlantic Ocean. Coccolithophores are calcareous nannofossils, a major component of the oceanic phytoplankton, which provide information about past ecological and climatological variability. Results are supported by data on fossil organic compounds (sea surface temperatures, alkenones, and *n*-hexacosan-1-ol index) and geochemical analyses (benthic $\delta^{13}\text{C}_{\text{cc}}$ and planktonic $\delta^{18}\text{O}_{\text{cc}}$ isotopes). Three scenarios are taken into account for this location at centennial-scale resolution over the last 70,000 years: the Holocene and the stadial and interstadial modes. The different alternatives are described by means of elements such as nutrients; upwelling phenomena; temperatures at surface and subsurface level; or the arrival of surface turbid, fresh, and cold waters due to icebergs, low sea level, increased aridity, and dust. During the Holocene, moderate primary productivity was observed (mainly concentrated in *E. huxleyi* specimens); surface temperatures were at maxima while the water column was highly ventilated by northern-sourced polar deep waters and warmer subsurface, nutrient-poor subtropical waters. Over most of the last glacial stadials, surface productivity weakened (higher *F. profunda* and reworked specimen percentages and lower diunsaturated and triunsaturated C_{37} alkenones); the arrival of cold Arctic surface waters traced by tetraunsaturated C_{37} peaks and large *E. huxleyi*, together with powerful ventilated southern-sourced polar deep waters, disturbed, in all likelihood, the delicate vertical equilibrium while preventing significant upwelling mixing. Finally, during the last glacial interstadials (lower *F. profunda* percentages, nonreworked material, and higher diunsaturated and triunsaturated C_{37} alkenones) a combined signal is observed: warm surface temperatures were concurrent with generally low oxygenation of the deep-sea floor, moderate arrival of northern-sourced deep waters, and subsurface cold, nutrient-rich, recently upwelled waters, probably of polar origin; these particular conditions may have promoted vertical mixing while enhancing surface primary productivity (mainly of *Gephyrocapsa* specimens).

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1. Introduction

[2] Greenland and Antarctica ice records provide invaluable information on past atmospheric composition changes [e.g., *North Greenland Ice Core Project members*, 2004; *Spahni et al.*, 2005] while paleontological and biogeochem-

ical data from sediment cores with high sedimentation rates are unique tools for investigating the role of biota in past climate variability [e.g., *Bard et al.*, 2000; *Bond et al.*, 1992; *Shackleton et al.*, 2000]. Both kinds of paleoarchives find a common focal point in the Iberian Margin. The Northern Hemisphere midlatitude location of the Iberian Margin made it as a key site for studying the north-south polar climate system connection and the reorganization of the Atlantic Ocean's surface and deep circulation [*Martrat et al.*, 2007]. Additionally, previous studies demonstrated that this area recorded Dansgaard-Oeschger-like high-frequency climatic variations and represented the southernmost boundary of iceberg transport and ice-rafted detritus (IRD) accumulation [*Lebreiro et al.*, 1996; *Bard et al.*, 2000; *Schönfeld and Zahn*, 2000; *Shackleton et al.*, 2000; *Thouveny et al.*, 2000; *Pailler and Bard*, 2002; *de Abreu et al.*, 2003; *Schönfeld et al.*, 2003; *Vautravers and Shackleton*, 2006; *Martrat et al.*, 2007]. The

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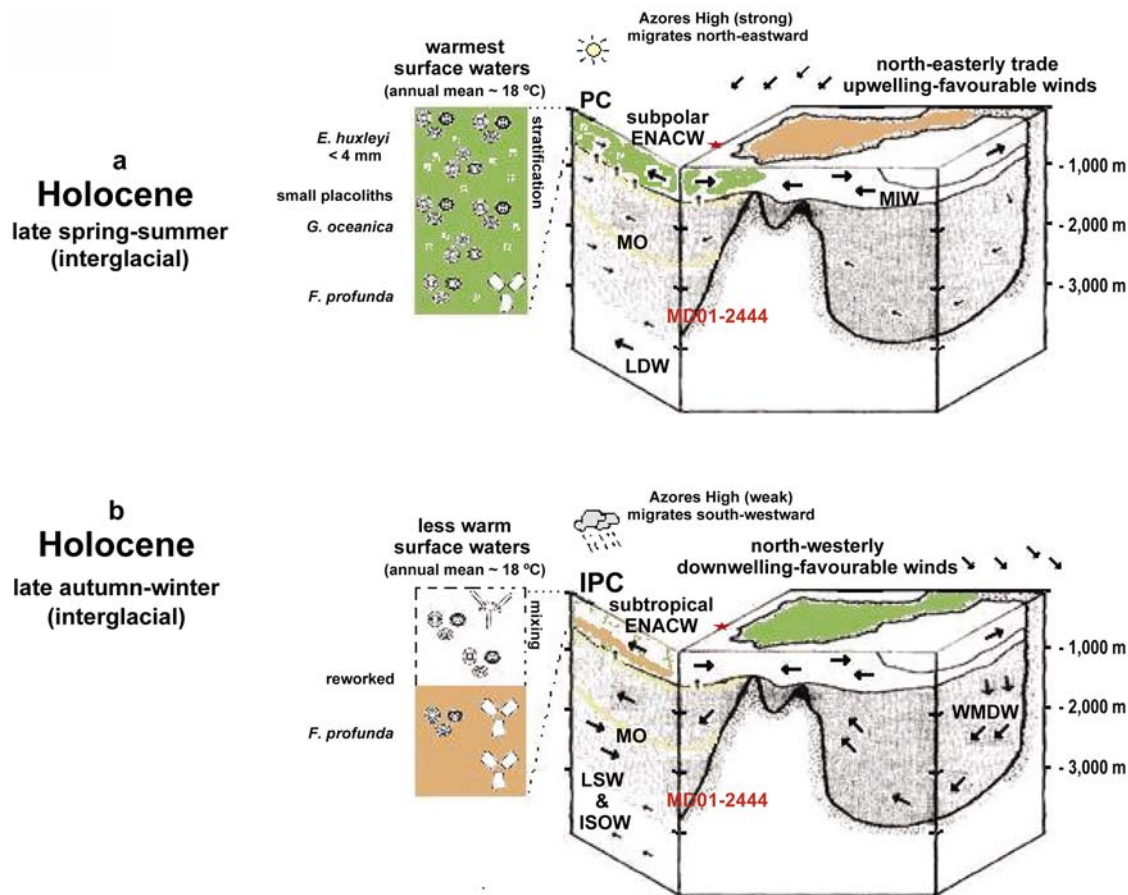


Figure 1

melting of icebergs at these latitudes could have affected even Mediterranean Sea circulation during a number of the last glacial episodes [Sierro *et al.*, 2005].

[3] Core MD01-2444 retrieved from the Atlantic Iberian Margin (Figure 1) has been intensively investigated by means of high-resolution planktonic foraminifera, stable isotopes, pollen, and biomarker analyses [Vautravers and Shackleton, 2006; Martrat *et al.*, 2007; Skinner and Elderfield, 2007; Skinner, 2008; Margari *et al.*, 2010]. In this study, quantitative data on coccolithophores are presented and discussed at centennial-scale resolution over the last 70,000 years. Coccolithophores, as a major component of oceanic phytoplankton, may well offer useful indications on surface water mass changes, with particular emphasis on primary productivity variations. For example, *Florisphaera profunda* dwells within the lower photic zone of stratified subtropical waters, and its relative abundance (or ratios with other coccolithophores) has been used in a large range of paleoceanographic investigations [Castradori, 1993; Jordan *et al.*, 1996; Kinkel *et al.*, 2000; Sprovieri *et al.*, 2003; Di Stefano and Incarbona, 2004; Prabhu and Shankar, 2005; Incarbona *et al.*, 2008a, 2008b] in the Indian Ocean, Atlantic Ocean, and Mediterranean Sea [Beaufort *et al.*, 1997, 2001; Henriksson, 2000; Beaufort *et al.*, 2001; Incarbona *et al.*, 2008c]. Literature

suggests that *F. profunda* is a productivity proxy at low to middle latitudes of the North Atlantic Ocean when the upper photic zone is nutrient depleted and its production enhances in comparison with other coccolithophorid species [Molfino and McIntyre, 1990a, 1990b; McIntyre and Molfino, 1996; Broerse *et al.*, 2000; Flores *et al.*, 2000; Henriksson, 2000; Beaufort and Heussner, 2001; Haidar and Thierstein, 2001; Sprengel *et al.*, 2002; Colmenero-Hidalgo *et al.*, 2004; Kameo *et al.*, 2004].

[4] In this study, a detailed evaluation of the *F. profunda* and other floral assemblages (e.g., geophycocapsids, warm water taxa, or reworked specimens) is presented in order to confirm their ecological preference and meaning as paleo-indicators in the Iberian Margin. The results are discussed together with a variety of fossil organic compounds found in the same core strata: (1) the alkenone sea surface temperature profile (U_{37}^k SST), used for definition of the Iberian Margin interstadials (IMI) and stadials (IMS) observed; (2) diunsaturated and triunsaturated alkenones, which form part of the autochthonous biomass synthesized by coccolithophores; (3) the relative proportion of tetraunsaturated C_{37} alkenone to the sum of C_{37} alkenones, indicative of cold surface waters; and (4) the relative proportion of *n*-hexacosanol ($C_{26}OH$) to the sum of $C_{26}OH$ plus *n*-nonacosane (C_{29}), which is a

chemical proxy reflecting ventilation of the deep-sea floor at the core location, since both compounds have the same vascular terrestrial plant origin but differ in their resistance to degradation by oxygenation [Martrat, 2007; Martrat et al., 2007].

2. Study Area

[5] Iberian Margin surface hydrography is part of the complex North Atlantic eastern boundary current of the Azores, where the North Atlantic Current (NAC) is connected to the Azores Current (AC) by means of the slow equatorward Portugal Current (PC); the fast, seasonally reversing Iberian Poleward Current (IPC); the western Iberia winter front; and other meandering structures [Álvarez-Salgado et al., 2003; Pérez et al., 2001; Peliz et al., 2005; Relvas and Barton, 2002, 2005; Relvas et al., 2007; Sánchez and Relvas, 2003; Sánchez et al., 2007; Schiebel et al., 2002a; van Aken, 2000a, 2000b, 2001]. The Mediterranean outflow (MO) flows at intermediate depths, while different percentages of northern-sourced North Atlantic deep water (NADW) and southern-sourced Antarctic Bottom Water (AABW) occupy the lowermost part of the water column [Skinner et al., 2003; van Aken, 2000a, 2000b, 2001] (Figure 1).

[6] A close link has been observed between present-day surface phytoplankton distribution, surface temperatures in

the area, and atmospheric patterns [Lopes et al., 2009; Oliveira et al., 2009; Henson et al., 2009]. Although caution is required when attributing climate variability on a regional scale to the North Atlantic Oscillation [Gil et al., 2006; Sánchez et al., 2007], the intensity and position of the more stable Azores anticyclone cell could modulate a nonlinear response in diffused seasonal upwelling phenomena along the western Iberian Margin [Peliz et al., 2005].

[7] In late spring through summer, the Azores High strengthens while the axis of maximum moisture transport and the predominant storm track extend to the north and east (Figure 1a). This results in decreased precipitation over southern Europe and northwestern Africa [Trouet et al., 2009], attracting strong trades which produce coastal upwelling up to 200 km from the shore while enhancing the availability of nutrients and phytoplankton biomass accumulation in the western Iberian Margin [Álvarez et al., 2005; Fiúza, 1983; Moita, 2001; Moita et al., 2003; Sánchez et al., 2007, 2008]. The water upwelled to the surface originates from either subpolar ($>45^{\circ}\text{N}$, recently upwelled, cold, nutrient-rich, and fresh) or subtropical ($<45^{\circ}\text{N}$, warmer, nutrient-poor, less ventilated, and saltier) branches of the eastern North Atlantic Central Water, subsurface components of the PC system, and the IPC [Álvarez-Salgado et al., 2003; Pérez et al., 2001; Rios et al., 1992]. In late autumn through winter, the Azores High is weak and offers protection from north-

Figure 1. The Iberian Margin during Holocene characteristic (a) late spring through summer upwelling-favorable seasons and (b) late autumn through winter downwelling-favorable periods. Location of core MD01-2444 is marked for reference. A permanent antiestuarine exchange occurs between the Mediterranean Sea and the Atlantic Ocean at the Straits of Gibraltar: surface salinities are lower than deep water salinities [Bray et al., 1995]. The large-scale circulation in the northeastern Atlantic is dominated by two basin-scale currents: the North Atlantic Current extension to the north of the Iberian Peninsula (48°N – 53°N) and the Azores Current south of Iberia (centered around 34°N – 35°N). The subsurface components of these water masses are also referred to as the eastern North Atlantic Central Water (ENACW) of subpolar origin ($>45^{\circ}\text{N}$; recently upwelled, nutrient-rich, cold, and fresh; between 4°C and 12°C ; 35.66‰ – 34.96‰) and the ENACW of subtropical provenance ($<45^{\circ}\text{N}$; nutrient-poor, less ventilated, warmer, and saltier; $>12.2^{\circ}\text{C}$; 35.66‰) [Rios et al., 1992]. The two gyres are connected by means of the slow equatorward advection Portugal Current (PC) and the fast, seasonally reversing Iberian Poleward Current (IPC) or Portugal Coastal Countercurrent [Álvarez-Salgado et al., 2003]. During late spring through summer, stratification is initiated, surface waters flow southward, subsurface subpolar ENACW is in the north, and subtropical ENACW is in the south. During late autumn through winter, the subtropical high shifts southward, greater amounts of rainfall reach the Mediterranean, and the surface circulation reverses, transporting subtropical ENACW northward. The upper mixed layer depth in the IPC domain progressively increases from 20 m in early autumn (maximum surface temperatures $>20^{\circ}\text{C}$) to 150 m in late winter (SST $<14^{\circ}\text{C}$) [Álvarez-Salgado et al., 2003]. A western Iberian winter front separates colder waters to the north along 40°N , and meandering extensions of the Azores Current eastern branch are formed at around 35°N (not shown) [Peliz et al., 2005]. The main intermediate and deep water mass at the western Iberian Margin is the recirculating northeast Atlantic deep water (NEADW), which includes four main end-members: (1) Labrador seawater (LSW), a relatively fresh and cold intermediate and deep water mass formed in the Labrador Sea through winter convection; (2) Iceland-Scotland overflow water (ISOW), a deep water mass derived from Nordic seawater mixed with LSW and with entrained subpolar intermediate water; (3) Mediterranean outflow seawater (MO), a relatively warm and very saline water mass circulating at intermediate depths (e.g., 13°C ; $>38\text{‰}$; between 500 and 1500 m), which is the result of merging waters, mainly between the warmer and salty Mediterranean intermediate water (MIW) and the cold, dense western Mediterranean deep water (WMDW) where, during severe winters, northwesterly winds blowing over platform zones cause surface waters to downwell (e.g., in the Gulf of Lions); and (4) lower deep water (LDW), a southern-sourced abyssal water mass derived from Antarctic Bottom Water (AABW). For example, below 3000 m, recirculating modern NEADW comprises $\sim 47\%$ LDW, $\sim 27\%$ ISOW, $\sim 23\%$ LSW, and $\sim 3\%$ MO. These percentages changed during the geological past (Figure 5), describing changes in local dominance of northern-sourced North Atlantic deep water (NADW) versus southern-sourced AABW [Martrat et al., 2007]. Description from Di Stefano and Incarbona [2004], Peliz et al. [2005], Skinner et al. [2003], Relvas and Barton [2002, 2005], Relvas et al. [2007], Stanley et al. [1975], Stanley [1978], and van Aken [2000a, 2000b, 2001].

westerly winds, making them weaker, while a northward IPC develops and downwelling occurs (Figure 1b) [Relvas et al., 2007; Sánchez et al., 2008]. Additionally, although the phytoplankton biomass during summer upwelling has been quantified as at least 1 order of magnitude greater than in winter, upwelling also occurs during autumn or winter under northerly winds blowing at the shelf [deCastro et al., 2008; Relvas et al., 2007]. Diatoms and coccolithophores are the most important contributors to upwelling and nonupwelling conditions, respectively [Abrantes and Moita, 1999; Cachão and Moita, 2000; Gil et al., 2006, 2007]. Apart from upwelling, buoyant, low-salinity plumes from rivers (Tagus, Douro, Minho, and smaller rivers and lagoons) play a major role in this ecosystem behavior [Peliz et al., 2005; Santos et al., 2007].

3. Material and Methods

[8] Sediment core MD01-2444 (37°33'68"N, 10°08'53"W; 2637 m below sea level; Figure 1) is constituted of nannofossil clay, with rare levels slightly enriched in detrital carbonate and quartz grains. Calcareous nannofossil analyses were carried out by observation with a polarized microscope at about 1000X magnification. Rippled smear slides were prepared following the standard procedure [Bown and Young, 1998] on residue smaller than 63 μm . At least 300 specimens within the entire assemblage plus a variable number of *Florisphaera profunda* platelets were analyzed (mean of 516 coccoliths for the sample). Percentage values of taxa were calculated without including *F. profunda* specimens in the assemblages. Quantitative data were collected on more than 20 taxonomic units, generally following the taxonomic concepts of living coccolithophores of Young et al. [2003]. Gephyrocapsids were identified to a species level when they were at least 3 μm long, whereas smaller specimens were grouped into the "small *Gephyrocapsa*" taxonomic unit. Similarly, "small placoliths," which are hardly identifiable at a specific level, include *Reticulofenestra* spp. and, in all probability, *Emiliania huxleyi* and *Gephyrocapsa* specimens with slight diagenetic problems, i.e., etched T-shaped elements and broken bridges. Because of their very rare abundance and their common ecological preference, *Calciosolenia* spp., *Discosphaera tubifera*, holococcoliths, *Oolithotus* spp., *Rhabdosphaera* spp., *Syracosphaera pulchra*, the dinoflagellate *Thoracosphaera heimii*, *Umbellosphaera* spp., and *Umbilicosphaera foliosa* were grouped under "warm water taxa" [Winter et al., 1994; Young, 1994; Andrulic et al., 2003; Boeckel and Baumann, 2004]. The percentage of reworked specimens (taxa belonging to older stratigraphic levels and coccoliths affected by severe etching and/or overgrowth) was contrasted against no fewer than 300 coccoliths. The abundance of *F. profunda* was contrasted against the remaining coccoliths [after Molfino and McIntyre, 1990a, 1990b; McIntyre and Molfino, 1996; Beaufort et al., 1997].

[9] The MD01-2444 site is located a few kilometers from the Cape San Vicente upwelling area, where the net primary production between September 1997 and April 2007 was, for example, 221.3 g C m⁻² yr⁻¹ (calculated for the closest pixel of 9 × 9 km to the location of the core; [\[oregonstate.edu/ocean.productivity/index.php\]\(http://web.science.oregonstate.edu/ocean.productivity/index.php\)\). Unfortunately, the formula obtained by Beaufort et al. \[1997\] to quantify productivity appears to be unsuitable for the Iberian Margin. In samples external to their particular calibration set, the formula matched other primary productivity estimators only qualitatively \[Beaufort et al., 2001\], e.g., with alkenone concentration or organic carbon \[Rostek et al., 1997\]. Further specific data from the Mediterranean region \[Incarbona et al., 2008c\] and other settings are clearly required before discussing the quantitative aspect of productivity results. In this study, the comparison between *F. profunda* and the total alkenones preserved in the same strata enabled at least qualitative extension of the meaning of this coccolithophore taxon.](http://web.science.</p>
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[10] The organic fossil compounds were isolated and quantified at the Department of Environmental Chemistry at the Institute of Environmental Assessment and Water Research. Briefly, sediment samples were freeze-dried and extracted by sonication using dichloromethane. The extracts were hydrolyzed with 6% potassium hydroxide in methanol and derivatized with bis(trimethylsilyl)trifluoroacetamide. They were analyzed with a Varian gas chromatograph model 3400 equipped with a septum programmable injector and a flame ionization detector. Selected samples were examined by gas chromatography-mass spectrometry for confirmation of compound identification and evaluation of possible coelutions.

[11] In order to search for the dominant frequencies recorded in signals of *F. profunda*, the amount of reworked calcareous nannofossils, and diunsaturated and triunsaturated (C_{37:2+3}) and tetraunsaturated (C_{37:4}) alkenones over time, an ensemble of power spectral methodologies was applied. Time series analysis for unequally sampled signals was carried out using REDFIT, spectral analysis software [Schulz and Mudelsee, 2002] based on a modified version of the Lomb-Scargle periodogram [Lomb, 1976; Scargle, 1982]. A first-order autoregressive process was performed by REDFIT software to estimate the red noise and hence the confidence levels at which periodicities can be considered significant. Classical spectral analysis methods for unevenly sampled records, including REDFIT, assume that the signals analyzed are stationary in time. To analyze nonstationary signals, where frequency components evolve and change over time, the Foster's wavelet analysis algorithm is preferred [Foster, 1995, 1996a, 1996b, 1996c]. This considers the wavelet analysis for a fixed localization, concentrating on the age and period as a suitable weighted projection onto three trial functions, providing the weighted wavelet Z transform and the weighted wavelet amplitudes.

4. Results

[12] The floral data (this study), the *Globigerina bulloides* $\delta^{18}\text{O}_{\text{cc}}$ and $\delta^{13}\text{C}_{\text{cc}}$ curves [Shackleton et al., 2000; Vautravers and Shackleton, 2006], and the organic matter profiles [Martrat et al. 2007; Martrat, 2007] are presented following the chronological framework and stratigraphical events of Martrat et al. [2007], on the basis of a combination of ¹⁴C accelerator mass spectrometry dates and a Monte Carlo statistical correlation between Iberian Margin U₃₇^K SST and

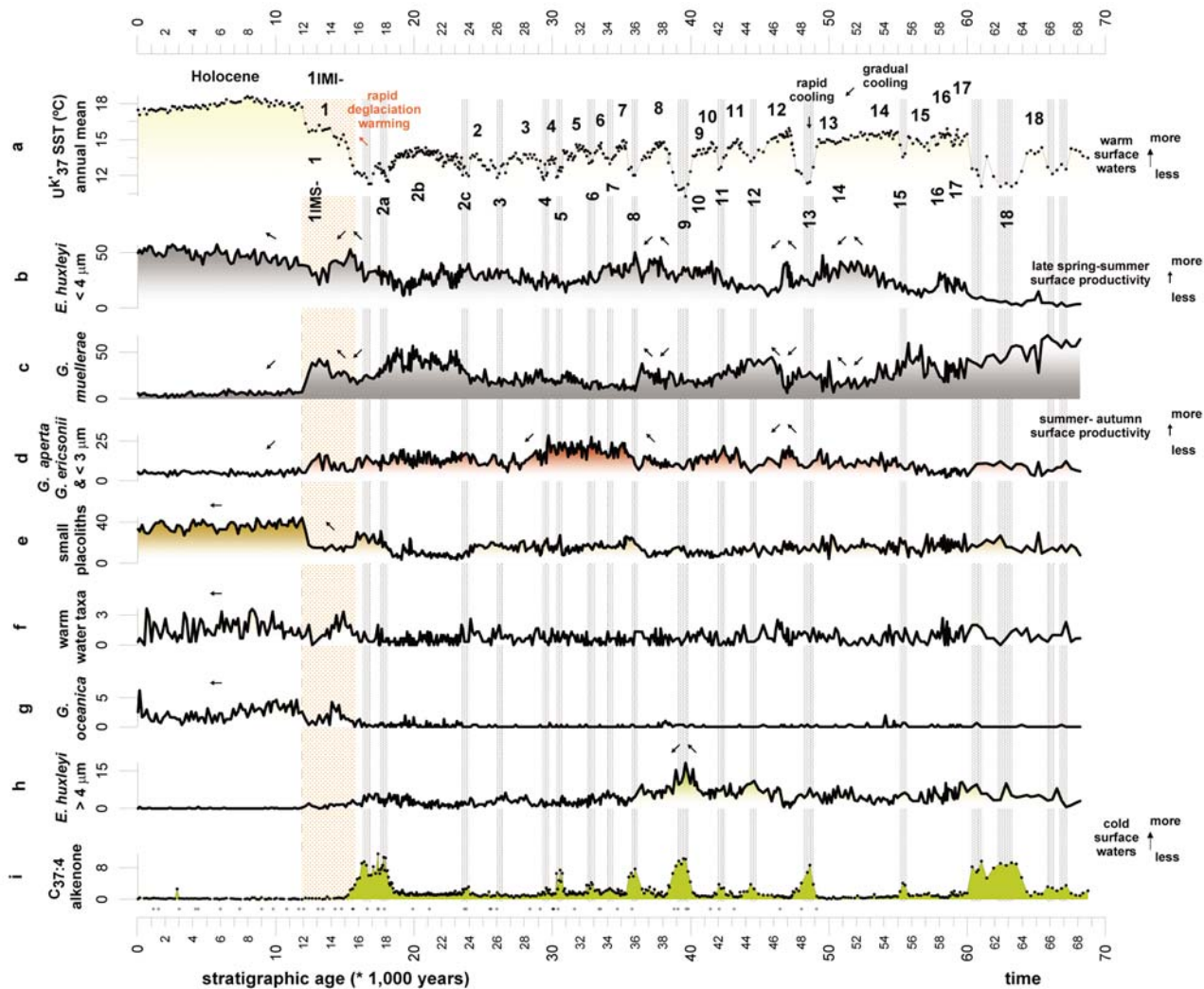


Figure 2. Down-core variations of calcareous nannofossil taxa and groups over the last 70,000 years. (a) The stadial-interstadial designation follows the sea surface temperature oscillations (U_{37}^k SST) and Iberian Margin interstadials and stadials over the first climate cycle (1IMI and 1IMS, respectively) [Martrat et al., 2007]. Calcareous nannofossil assemblages are dominated by small and medium-sized placoliths: (b) *E. huxleyi*, (c) *G. muellerae*, and (d) small *Gephyrocapsa* (<3 μm , mainly *Gephyrocapsa aperta* and *Gephyrocapsa ericsonii*). (e) Small placoliths, including *Reticulofenestra* spp. and likely *E. huxleyi* and *Gephyrocapsa* specimens with slight diagenetic problems. (f) Warm water taxa, specimens of rare abundance but common ecological preference, e.g., *Calciosolenia* spp., *D. tubifera*, and *Oolithotus* spp., and (g) *G. oceanica*, significant only in the deglaciation (area in yellow) and the Holocene. (h) Large *E. huxleyi* (>4 μm), which appear to be linked to the synthesis of the (i) tetraunsaturated C_{37} alkenone [Martrat et al., 2007], indicative of cold surface waters (areas in gray).

reference isotopic profiles from polar ice (Figures 2a and 3a (left)). An increase in the tetraunsaturated alkenone percentages characterizing last glacial stadials is used as an indicator of very cold surface waters at the core location (areas in gray, Figures 2i and 3f).

[13] A total of 495 samples has been analyzed for coccolithophores, and a total of 489 has been analyzed for biomarkers; the mean resolution of the record is approximately 138 ± 74 years. Calcareous nannofossil assemblages are dominated by small and medium-sized placoliths (*E. huxleyi*,

Gephyrocapsa muellerae, and small *Gephyrocapsa*; Figures 2b, 2c, and 2d) and by platelets of *F. profunda* (Figure 3c), as already seen in other Quaternary studies on the Iberian Margin and closer areas [Cachão and Moita, 2000; Colmenero-Hidalgo et al., 2004; Parente et al., 2004]. Warm water taxa and *Gephyrocapsa oceanica* become more significant only in the uppermost part of the record, with values of up to about 5% and 10%, respectively (Figures 2f and 2g). Other taxa, such as *Calcidiscus leptoporus*, *Coccolithus pelagicus*, *Helicosphaera* spp., *Pleurochrysis* spp., *Pontosphaera* spp., and *Syracosphaera*

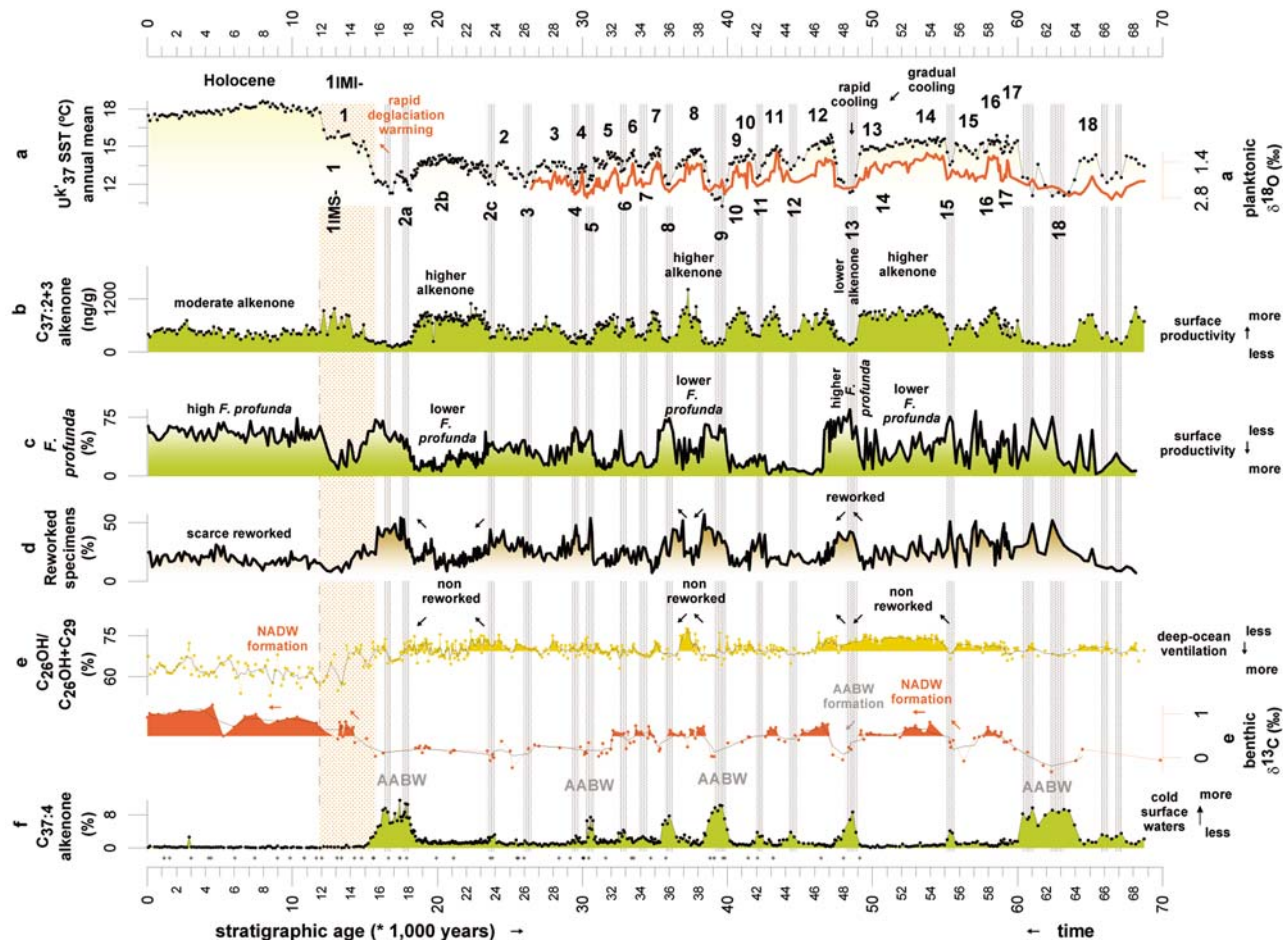


Figure 3. Down-core variations of *F. profunda* and reworked specimens versus geochemical isotopes and fossil organic proxies. (a) U_{37}^k SST (left axis) [Martrat et al., 2007] and planktonic *G. bulloides* $\delta^{18}O_{cc}$ (right axis) profile [Vautravers and Shackleton, 2006]. (b) Diunsaturated and triunsaturated C_{37} alkenone amounts and (c) *F. profunda* relative abundances; they present a moderate inverse correlation, which suggests differing productivity behavior between the surface and the deeper level of the photic zone. (d) Calcareous nannofossil reworked specimens. (e) The relative proportion of *n*-hexacosanol ($C_{26}OH$) to the sum of $C_{26}OH$ plus *n*-nonacosane (C_{29}), which is a chemical proxy reflecting ventilation at the core location: high and low percentages of the $C_{26}OH$ ratio correspond to low and high deep ocean ventilation, respectively. The benthic $\delta^{13}C_{cc}$ record in core MD95-2042, which reflects the influence of both hemispheres, is shown on the right axis: typical values of NADW and AABW are about 1.1‰ and 0.5‰, respectively. This indicator shows depleted values documenting entrances of AABW in the North Atlantic during glacials and within the short-term cooling stages of interglacial marine isotope stages [Martrat et al., 2007]. (f) The percentage of heptatriatetraenone ($C_{37:4}$) to total alkenone, indicative of Arctic surface waters at the core location (areas in gray) [Martrat et al., 2007].

histrica, have rarely been found and constitute a largely subordinate part of the assemblages. Reworked specimens show remarkable abundance fluctuation, ranging, for example, from 19% during the Holocene up to 54% during IMS-2a or 52% in IMS-18 and only around 14% during IMI-8 or 7% in IMI-1 or IMI-7 (Figure 3d). Diunsaturated and triunsaturated alkenones oscillate throughout the record, with rapid and abrupt changes across the glacial and stable behavior observed during the Holocene, ranging from 400 $ng\ g^{-1}$ during the Holocene up to, for example, around 1000 $ng\ g^{-1}$ over IMI-14 [Martrat, 2007] (Figure 3b). This relative abun-

dance of nannofossil taxa and diunsaturated and triunsaturated alkenones is available as auxiliary material.¹

5. Discussion

5.1. Paleoproductivity

[14] Since many of the major species are eurythermals, on the whole, coccolithophores flourish, displaying high

¹Auxiliary materials are available in the HTML. doi:10.1029/2008PA001709.

diversity throughout a wide range of surface water temperatures, estimated in core MD04-2444 with both the foraminifera (planktonic $\delta^{18}\text{O}_{\text{cc}}$) and alkenone (U_{37}^k SST) paleothermometers (Figures 2a, 3a (left axis), and 3a (right axis)). *E. huxleyi* is a cosmopolitan, eutrophic species, mainly concentrated in late spring through summer, and its presence could be considered as a tracer of turbid, cold, and nutrient-enriched polar upwelled waters (e.g., during IMI-12 and IMI-8, Figures 2b and 2d). *G. muelleriae* is a transitional species indicative of colder climate, mainly during late summer through autumn, and, while dominant during a number of stadials (e.g., during IMS-18, IMS-13, IMS-12, and IMS-2b), it also appears during the final gradual decreasing temperature trend of interstadials (IMI-12). The alternating dominance between *E. huxleyi* and *G. muelleriae* results from an evolutionary adaptation [Bollmann et al., 1998; Incarbona et al., 2009] and might explain why the abundance of this latter species appears to vary irrespective of absolute SST (Figure 2c).

[15] In order to further qualitatively characterize paleoproductivity, it is essential to make an in-depth evaluation of other variables such as coccolithophore biomass ($C_{37:2+3}$, Figure 3b), ventilation patterns, and the provenance of deep waters at the core location (*n*-hexacosanol index and $\delta^{13}\text{C}_{\text{cc}}$ benthics, Figures 3e (left axis) and 3e (right axis)). Stratification features at the core location are provided by *F. profunda* relative abundance (Figure 3c), reworked specimens (Figure 3d), and increases in the relative proportions of the tetraunsaturated alkenone (Figures 2i and 3f), which in some way appear to be linked to the presence of the largest morphotype of *E. huxleyi* ($>4 \mu\text{m}$) (Figure 2h).

[16] $C_{37:2+3}$ alkenones originate from the autochthonous biomass synthesized by blooming species of coccolithophores (*E. huxleyi* and *Gephyrocapsa* spp.), thus tracing productivity in the area [Prahl et al., 1993; Rostek et al., 1993; Villanueva et al., 1998; Pailler and Bard, 2002; Moreno et al., 2004; Zhao et al., 2006]. Their distribution pattern in core MD01-2444 supports conclusions on productivity reached on the basis of *F. profunda* relative abundance (Figure 3c): high values were recorded during the Holocene (up to 74%), which is associated with the warmest SST values [Martrat et al., 2007]; the highest values were observed during the stadials (e.g., ~85% during IMS-13); and the lowest concentration was observed during interstadials (e.g., ~15% during IMI-8). There is a general correspondence between maxima $C_{37:2+3}$ alkenone amounts and lower percentages in *F. profunda* along the studied section of core MD01-2444. Both proxies were constantly anticorrelated, peak by peak, particularly during the last glacial (Figures 3b and 3c). In particular, diunsaturated and triunsaturated alkenone minima are recorded during the coldest intervals and represent independent evidence of significant productivity drops over the last glacial period (e.g., IMS-18, IMS-15, IMS-13, IMS-9, IMS-8, IMS-5, IMS-4, IMS-3, and IMS-2a). Nevertheless, the statistical anticorrelation between *F. profunda* percentages and diunsaturated and triunsaturated alkenone amounts is moderate ($R = -0.44$, $n = 494$). At least two explanations are given for this relatively low correlation index: noise in the data and complex interplay of factors.

[17] 1. The standard error on the counting of *F. profunda* averages 3.8%, which is very low in comparison with the change detected in the major transitions, i.e., from a stadial to an interstadial and vice versa (usually between 20% and 60%). Absolute alkenone concentration errors are below 10% (i.e., below 40 ng g^{-1} during the Holocene or below 100 ng g^{-1} over some specific events in the last glacial). Both errors might affect the correlation parameter, particularly within any cold or warm relatively stable period, e.g., the Holocene. However, this circumstance is not likely to have repercussions on the largest fluctuations and the rapid climate variability. If *F. profunda* percentages and alkenone values are averaged through some of the most important long phases, the correlation index becomes higher and significant.

[18] 2. *F. profunda* could respond not only to nutrients as a proxy for productivity but, as many organisms, to a variety of factors. The literature assumes that when percentages of *F. profunda* increase, productivity in the upper photic zone collapses. Upwelling is apparently not strong enough to reach the surface because the nutricline remains deep or upwelling simply does not occur, thereby jeopardizing the bloom of superficial eutrophic taxa. The MD01-2444 data indicate that the bloom of *F. profunda* occurs during stadials. In the Mediterranean its behavior is the opposite. *F. profunda* percentages clearly increase at the beginning of interstadials, not during stadials [Colmenero-Hidalgo, 2004; Colmenero-Hidalgo et al., 2004; M. Sprovieri et al., unpublished data, 2009]. This particular difference could give clues as to the particular factors affecting *F. profunda* percentages in the Atlantic. Thus, it may well be that during stadials, upwelling or the nutricline positions are not the only factors which affect the signal observed. *F. profunda* is a tropical taxon; it cannot survive in temperatures colder than 10°C and prefers stratified tropical subsurface waters. The presence of surface stratified, turbid, fresh, cold waters due to icebergs, low sea level, floods, increased aridity, and dust could affect the more superficial species while increasing the survival possibilities of *F. profunda*, which dwells at a greater depth. Even warm temperatures at the subsurface level [Flückiger et al., 2006; Peck et al., 2006, 2008; Rogerson et al., 2004; Shaffer et al., 2004], warmer in the Atlantic than in the Mediterranean, must not be discarded.

[19] Stadial intervals, specifically, the periods indicated above, were characterized by abundance of large *E. huxleyi* ($>4 \mu\text{m}$), particularly around the coldest stadial IMS-9 (Figures 2a and 2h), concurrent with a prominent increase in the number of lithics (IRD) over 150 mm g^{-1} of dry sediment [Vautravers and Shackleton, 2006]. These observations are in line with previous studies in the Mediterranean Sea and the Atlantic Ocean [Colmenero-Hidalgo et al., 2002, 2004; Sierro et al., 2005]. Additionally, during the last glacial, reworked calcareous nannofossil specimens show a surprising correlation with both *F. profunda* relative abundance and $C_{37:2+3}$ alkenones ($R = 0.58$ and $R = -0.47$, respectively; $n = 420$ samples). For instance, erosion was more efficient during low-stand phases (e.g., IMS-13, IMS-9, IMS-5, IMS-2c, and IMS-2a; Figures 3a (left axis) and 3d) when continental margins received an increased supply of sediments from land and the MO was flowing deep [Schönfeld and Zahn, 2000].

Recent studies suggest that evolution of the sea level record was similar to Antarctic-style climate variations: apparently, sea level rose during Northern Hemisphere stadial-to-interstadial transitions and dropped at the end of the interstadials [Siddall et al., 2003; Rohling et al., 2004, 2009]. Inconsistent or even opposing behavior between reworked calcareous nannofossil specimens and sea level fluctuations disqualifies the latter as the modulator of their abundance in the Iberian Margin. Other mechanisms such as enhanced runoff increase are hardly reliable given that the vegetation pattern was tightly linked to steppic-dominant pollen assemblages over these stadial phases [Sánchez Goñi et al., 2000; Roucoux et al., 2001, 2005]. One possible explanation for the reworked calcareous nannofossil profile is the difference in productivity levels. A dramatic weakening of upwelling activity could lead to a drop in coccolithophore blooming, fully consistent with the above considerations on productivity levels traced by *F. profunda* and $C_{37:2+3}$ alkenone abundance values.

[20] The last glacial period recorded six distinctive episodes of IRD discharge into the North Atlantic Ocean, known as Heinrich (H) events, repeating approximately every eight millennia [Heinrich, 1988; Bond et al., 1992]. A recent study carried out on seven cores along the North Atlantic and focused on H1 and H4 demonstrated that surface primary productivity decreased, probably because of a strong water column stratification induced by icebergs [Nave et al., 2007]. The same result, i.e., a primary productivity decrease at the time of the Heinrich events, is evident in different climate-ecosystem model simulations [Schmittner, 2005; Menviel et al., 2008]. However, disturbance in the Iberian Margin upwelling system and the arrival of Arctic waters occurred more frequently than the classical H events cycle. *F. profunda*, reworked calcareous nannofossils, and diunsaturated, triunsaturated, and tetraunsaturated C_{37} alkenones show similar periodicity, centered at about 3000 years, significant between about 25,000 and 50,000 years before present (Figure 4). This periodicity has commonly been found in Atlantic Ocean and Greenland ice core records [Moreno et al., 2005, and references therein] and is linked to the Dansgaard-Oeschger cycles in which the importance of the prolonged duration of interstadials 8 and 12 is assumed. Nevertheless, the repetitive pattern of observed oscillations does not necessarily imply strict periodicity. Climate periodicities published on the last climate cycle must be considered separately from stochastic resonance or from a simple alias of a very powerful annual cycle [Ganopolski and Rahmstorf, 2002; Meeker et al., 2001; Schulz and Mudelsee, 2002; Wunsch, 2000; Wunsch and Gunn, 2003]. It must be emphasized that their pervasive manifestation is far from being proved [Alley et al., 2003; Ditlevsen et al., 2007; Braun et al., 2008, 2009].

[21] A separate issue is the moderate Holocene primary productivity. This circumstance has already been observed in other studies [Abrantes, 1991; Paillet and Bard, 2002]. Interestingly, the warming of water masses and oligotrophy throughout the last deglaciation are clearly traceable by a relative increase in warm water taxa and *G. oceanica* (Figures 2f and 2g), which are today a common component of low-latitude assemblages [Winter et al., 1994; Haidar and Thierstein, 2001; Boeckel and Baumann, 2004; Ziveri et al., 2004; Baumann et al., 2005]. *F. profunda* sustained at high relative proportion (Figure 3c), together with significant increase in small placoliths (up to 45%, Figure 2e), suggests that warmer, intermediate, nutrient-poor subtropical waters have been modulating productivity for the last 11,500 years.

5.2. Climatic Forcing of the Upwelling System Variations

[22] Productivity variations in the Iberian Margin during the last glacial-interglacial cycle are still an open issue. In this study, coccolithophore abundance fluctuations and closely related organic compounds are evaluated at centennial time resolution. Three modes are taken into account. First, during the Holocene surface temperatures were at maxima (U_{37}^k SST annual mean $\sim 18^\circ\text{C}$), moderate primary productivity was observed (mainly concentrated in *E. huxleyi* specimens), and the water column was highly ventilated by northern-sourced polar deep waters and subsurface, nutrient-poor, relatively warm subtropical waters, mainly during winter (Figure 1). The MO flowed between 500 and 1500 m [Rogerson et al., 2006], and upwelling occurred during summer and was moderate given that winds during an interglacial period are not as strong as during a glacial period. Second, in the interstadial mode (Figure 5a) lower *F. profunda* percentages, nonreworked material, and higher diunsaturated and triunsaturated C_{37} alkenones point to a combined signal; that is, relatively warm surface temperatures (annual mean $\sim 15^\circ\text{C}$) were concurrent with generally low oxygenation of the deep-sea floor and moderate arrival of northern-sourced deep waters. However, intermediate, cold, nutrient-rich recently upwelled waters, probably of polar origin, were also present. The MO flowed at a depth of between 500 and 2000 m [Rogerson et al., 2006]. These particular conditions may have promoted vertical mixing while enhancing surface primary productivity (mainly of *Gephyrocapsa* specimens). Finally, during the stadial mode (Figure 5b) surface temperatures were cold (annual mean $\sim 12^\circ\text{C}$) and surface productivity weakened (higher *F. profunda* and lower diunsaturated and triunsaturated C_{37} alkenones); in all likelihood, the arrival of cold Arctic surface waters (tetraunsaturated C_{37} peaks and large *E. huxleyi*), together with powerful ventilated southern-sourced polar deep waters, disturbed the delicate vertical

Figure 4. Wavelet spectral analyses of *F. profunda*, reworked calcareous nannofossils, tetraunsaturated C_{37} alkenones, and diunsaturated and triunsaturated C_{37} alkenones. On the left side of each analysis is the bias-corrected power spectrum (REDFIT) of the unevenly sampled signals. The green and black dashed lines indicate the 95% and 80% confidence levels, respectively. The dashed red line indicates the first-order autoregressive theoretical red noise spectrum. Spectral bandwidth equals 5.825×10^{-5} . Foster's wavelet transforms of the three considered signals, in which the thick green and black dashed contours designate the 95% and 80% confidence levels.

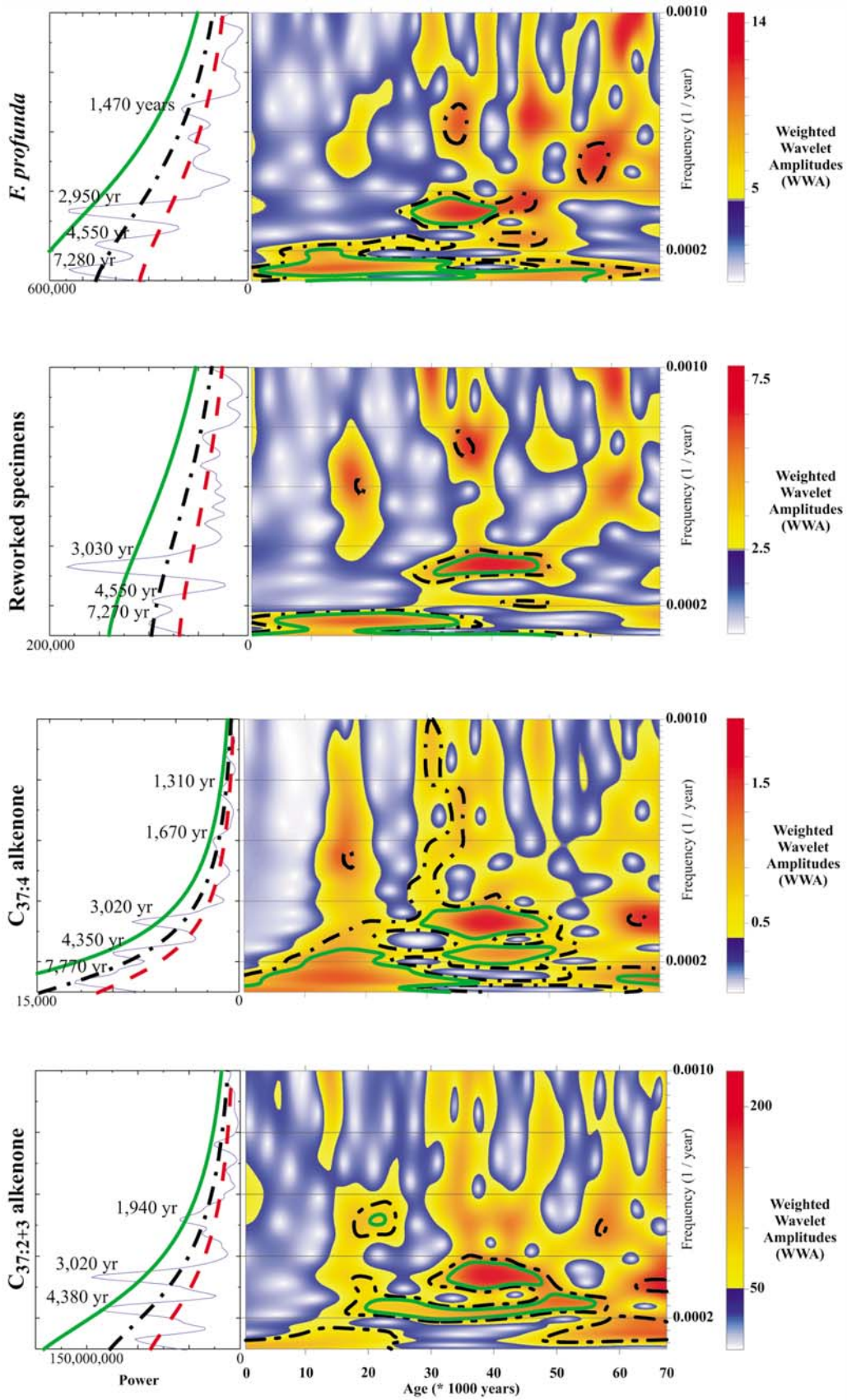


Figure 4

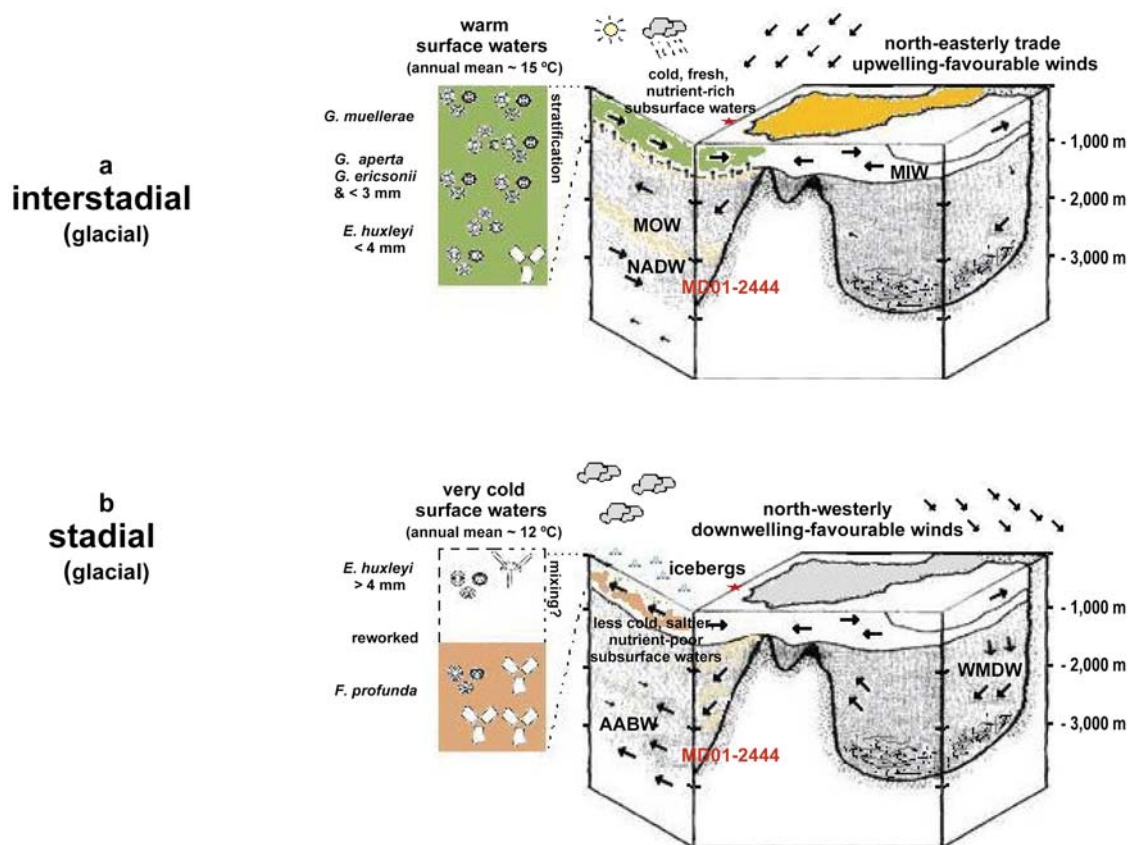


Figure 5. The Iberian Margin during the glacial (a) interstadial and (b) stadial scenarios. Location of core MD01-2444 is marked for reference. During interstadials, lower *F. profunda* percentages, nonreworked material, and higher diunsaturated and triunsaturated C_{37} alkenones point to a combined signal: relatively warm surface temperatures were concurrent with generally low oxygenation of the deep-sea floor, moderate arrival of northern-sourced deep waters, and intermediate, cold, nutrient-rich recently upwelled waters, probably of polar origin. Thus, surface primary productivity (mainly of *Gephyrocapsa* specimens) increased; the MO flowed between 500 and 2000 m below sea level. During stadials, surface productivity weakened (higher *F. profunda* and lower diunsaturated and triunsaturated C_{37} alkenones); in all likelihood, the arrival of cold Arctic surface waters (tetraunsaturated C_{37} peaks and large *E. huxleyi*), together with powerful ventilated southern-sourced polar deep waters, disturbed the delicate vertical equilibrium while preventing significant upwelling mixing. The main MO flow core during these cold events reached greater depths, between 1000 and 2000 m (higher reworked specimens), and warmer subsurface, nutrient-poor subtropical waters penetrated eastward.

equilibrium while preventing significant upwelling mixing. The main MO flow core during these cold events reached greater depths between 1000 and 2000 m [Schönfeld and Zahn, 2000; Toucanne et al., 2007] and, while it was then perhaps unable to pass over the Tagus slope (Horseshoe Seamount), may have allowed the Azores Current eastward penetration, i.e., subsurface, nutrient-poor, relatively warm subtropical waters [Peliz et al., 2005; Rogerson et al., 2005, 2006; Voelker et al., 2006].

[23] The events observed within these scenarios, i.e., the Holocene and the Iberian Margin interstadials and stadials, are defined by means of organic compounds synthesized by coccolithophores and are not intended to be exactly the same as other events described with other proxies, either from the same location or from long-distance sites. It is unfortunate

that vital, ecological, and competition factors could obscure the observations and make the response of every proxy unique. It must be emphasized that coccolithophores appear to occupy an intermediate ecological position between upwelling species (e.g., diatoms) and organisms common in nutrient-poor stratified waters (e.g., dinoflagellates) and differ from nonphotosynthetic species (e.g., most planktonic and benthic foraminifera). For example, Pailler and Bard [2002], on the basis of fossil organic compounds in the same area (37°N), argued that three productivity patterns alternated: higher productivity was associated with the last glacial interstadials, moderate productivity was observed during the Holocene, and the lowest productivity level was estimated over the most important IRD discharge episodes. Thomson et al. [2000], using diatoms from a northern site (40°N),

determined that productivity increased at the last glacial-to-interglacial transition and suggested that upwelling was probably suppressed under glacial conditions. *Vautravers and Shackleton* [2006], adopting the relative abundance of planktonic foraminifera *G. bulloides* and *Globigerina glutinata* as a straightforward proxy for the upwelling system intensity, concluded that the high and low productivity associated with the stadials and the interstadials, respectively, alternated regularly. Their conclusions coincide with other foraminifera evidence in the area [*Lebreiro et al.*, 1997; *Abrantes et al.*, 1998].

[24] Attributing the weakening/strengthening of the upwelling system during stadials/interstadials to climate forcing is not a straightforward matter, although some circumstances suggest that atmospheric and oceanic circulation play an important role. At present, increased abundance of deep-dwelling planktonic foraminifera *Globorotalia scitula* marks the northern flank of the Azores Current and Azores Front at the southern branch of the Gulf Stream, which is associated with environments exhibiting seasonal vertical mixing or upwelling at temperate latitudes [*Schiebel et al.*, 2002a, 2002b]. For example, as traced by the relative abundance fluctuations of this species and stable isotope analyses, this front penetrated eastward into the Gulf of Cadiz during the Last Glacial Maximum and the Younger Dryas (roughly, IMS-2b and IMS-1); the absence of *G. scitula* in a sediment core retrieved in this area during the Bølling-Allerød (IMI-1) [*Rogerson et al.*, 2004] points to a completely different frontal configuration, perhaps consistent with the pronounced atmospheric and oceanic reorganization of the deglaciation. Unfortunately, little information is available on how this phenomenon evolved during the oscillations of the last glacial in the Gulf of Cadiz, but peaks of *G. scitula* of the same magnitude (from 5% to 10%) occurred farther north, in core MD01-2444 [*Vautravers and Shackleton*, 2006]. Increases in this species were particularly observed toward the end of each group of interstadials, before every abrupt IRD accumulation on deep sediments. These increases occurred during times when sea surface temperatures were still warm, oxygenation of the deep-sea floor was low, *F. profunda* percentages were low, and diunsaturated and triunsaturated C_{37} values were high, i.e., higher primary productivity. These circumstances suggest an eastward migration of the Azores Current affecting the dynamics of the water column in the southern Iberian Margin during these events. This is consistent with the strengthening of the Azores anticyclonic cell estimated for the last glacial, which would have attracted intensified winds, at least on a seasonal scale during these intervals, and widened the upwelling area as far as site MD01-2444 [*Hewitt et al.*, 2001; *Pailler and Bard*, 2002] (Figure 5a).

[25] This mechanism was interrupted when the NADW formation was severely reduced or even interrupted and the transport of heat from low latitudes ceased [*Broecker et al.*, 1990; *Oppo and Lehman*, 1995; *Chapman and Shackleton*, 1998; *Rahmstorf*, 2002; *Rasmussen and Thomsen*, 2004; *Vautravers et al.*, 2004]. Paradoxically, enhanced atmospheric circulation in the Northern Hemisphere was recorded during these events [*O'Brien et al.*, 1995; *Mayewski et al.*, 1997; *Moreno et al.*, 2004]. In this context, the Iberian

Margin experienced circulation patterns which led to cold and low-saline waters from Arctic northern latitudes occupying the upper part of the water column, while deep waters of Antarctic southern origin filled the deep-sea floor [*Shackleton et al.*, 2000; *Martrat et al.*, 2007]. Despite the action of strong northerlies, the low saline level in the uppermost part of the water column disturbed the delicate equilibrium of the upwelling system and prevented any significant vertical mixing. The most severe episodes of weakening in the Iberian Margin upwelling system, as traced by *F. profunda*, diunsaturated and triunsaturated C_{37} , and reworked calcareous nannofossils, find a counterpart in increases of tetraunsaturated C_{37} alkenone percentages [*Martrat et al.*, 2007] (Figures 2i and 3f). Around 50% of the variance in the relation between the $C_{37:4}$ alkenones with reworked nannofossils and with $C_{37:2+3}$ alkenones is linearly explained ($R = 0.50$ and $R = -0.52$, respectively; $n = 495$ samples). The increase in the proportion of tetraunsaturated C_{37} alkenone is indicative of cold surface waters, possibly of Arctic provenance [*Bard et al.*, 2000; *Martrat et al.*, 2004, 2007]. Consequently, upwelling system disturbances occurred when surface polar water and iceberg armadas flowed southward as far as site MD01-2444 (Figure 5b).

[26] This study describes how the Iberian Margin upwelling system is involved in different regional-to-global climatic scenarios, mainly in terms of atmospheric patterns, e.g., Azores High, and in relation to different surface, subsurface, intermediate, and deep water mass characteristics, such as the arrival of polar cold and low-saline surface waters or the penetration of subsurface warm waters or southern-sourced deep waters at subtropical latitudes during past specific intervals. Interpretation of the results is mainly based on coccolithophore data, an abundant fossil group often underestimated in evaluation of rapid climate variability because of the lack of records studied at the fine timescale presented here.

6. Conclusion

[27] High-resolution analyses of calcareous nannofossil assemblages and fossil organic compounds shed new light on Iberian Margin productivity over the last 70,000 years. Primary productivity considerations derive from relative abundance fluctuations of the species *F. profunda*, which varies inversely to the diunsaturated and triunsaturated C_{37} alkenone amounts, the autochthonous biomass of surface coccolithophore blooming species. The relative abundance of reworked calcareous nannofossil specimens increases during glacial stadials. These proxies suggest that primary productivity was moderate during the Holocene, lower during of the last glacial stadials, and higher during most of the interstadials. Two hypotheses could explain enhanced productivity. The first hypothesis considers that the Azores Current might have penetrated eastward, affecting the southern Iberian Margin and promoting vertical mixing, as indicated by low *F. profunda* abundance and higher diunsaturated and triunsaturated C_{37} alkenone values. The second hypothesis, which by no means precludes the first one, deals with the

increase in glacial interstadial productivity levels, led by strengthened atmospheric circulation in the Northern Hemisphere; thus, the upwelling area, currently located near Cape San Vicente, would have widened as far as site MD01-2444. The arrival of cold surface water during stadials, traced by tetraunsaturated C_{37} alkenone proportions and large *E. huxleyi*, is consistent with significant reduced coccolithophore productivity; consequently, despite the action of strong northerlies, this water may have induced strong stratification, thereby preventing significant vertical mixing.

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