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Aurélie Pénaud, F. Eynaud, A. Voelker, F. Marret, J. L. Turon, et al.. Hydrological processes affecting the subtropical NE Atlantic (34-38° N) over the last 30 ka: Evidence from phyto- and zooplankton assemblages. 2011. hal-00589629

HAL Id: hal-00589629

<https://hal.science/hal-00589629>

Preprint submitted on 24 Oct 2011

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This discussion paper is/has been under review for the journal Biogeosciences (BG).
Please refer to the corresponding final paper in BG if available.

Hydrological processes affecting the subtropical NE Atlantic (34–38° N) over the last 30 ka: evidence from phyto- and zooplankton assemblages

A. Penaud^{1,2}, F. Eynaud², A. Voelker³, F. Marret⁴, J. L. Turon², L. Rossignol², D. Blamart⁵, and T. Mulder²

¹Domaines Océaniques, UMR 6538, IUEM-UBO, 29280 Plouzané, France

²EPOC, Université de Bordeaux 1, UMR 5805, 33405 Talence, France

³LNEG, Unidade de Geologia Marinha, Estrada da Portela, Zambujal, 2610-143 Amadora, Portugal

⁴School of Environmental Sciences, University of Liverpool, Liverpool, L69 7ZT, UK

⁵Laboratoire des Sciences du Climat et l'Environnement (LSCE), Orme des Merisiers, Centre de Saclay, 91191 Gif sur Yvette Cedex, France

Received: 11 February 2011 – Accepted: 22 February 2011 – Published: 7 March 2011

Correspondence to: A. Penaud (aurelie.penaud@univ-brest.fr)

Published by Copernicus Publications on behalf of the European Geosciences Union.

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New dinocyst analyses were conducted on core MD99-2339 retrieved from the central Gulf of Cadiz. Dinocyst and foraminiferal assemblages from this core are combined with existing data off SW Portugal and NW Morocco to investigate past hydrological and primary productivity regimes in the subtropical NE Atlantic Ocean over the last 30 ka. Our results have revealed highest upwelling intensity during Heinrich Stadial 1 (HS 1) and the Younger Dryas and weaker upwelling cells during the Last Glacial Maximum and HS 2, off the SW Iberian and NW Moroccan margins. Similar assemblages between Cadiz and Morocco and distinct species off Portugal were observed during the cold climatic extremes that punctuated the last 30 ka. This pattern has been linked to the occurrence of a hydrological structure between SW Iberia and Cadiz during the last glacial period, probably similar to the modern Azores Front. This front was probably responsible locally for heterotrophic dinocysts found in the Gulf of Cadiz during the last glacial period, even if this sector is not conducive to upwelling phenomena by Ekman transport. Regional reconstructions of paleo-sea-surface temperatures using dinocyst and foraminiferal transfer functions, as well as alkenones, are also discussed and depict coherent scenarios over the last 30 ka. However, some mismatches are observed between the different quantitative reconstructions such as during HS 1 in the Gulf of Cadiz and during the LGM at the three core locations.

1 Introduction

Eastern boundary current systems are associated to major coastal upwelling characterized by high marine planktonic productivity (e.g., Hagen, 2001). A complex spatial distribution of planktonic organisms is observed in these systems, tightly coupled to intensity gradients which structure the upwelling zone (Margalef, 1978; Jacques and Tréguer, 1986; Smayda and Trainer, 2010). These rich and fragile coastal ecosystems are key areas to understand the link between the biological pump and climate

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at present, but also in the past. Sedimentological archives from these domains provide detailed records of primary productivity changes through time (e.g., Berger et al., 1978). However, numerous oceanographic and paleoceanographic studies point to a large heterogeneity in the dynamic response of upwelling to climate changes (e.g., Agnihotri et al., 2003). Indeed, even within a same coastal upwelling system, as for instance off the coasts of Portugal and NW Africa, opposite responses in terms of periods of increased upwelling phenomena have been detected (e.g., Bertrand et al., 1996; Eberwein and Mackensen, 2008; Voelker et al., 2009; Salgueiro et al., 2010). Testing the response of upwelling dynamics (modality and intensity) to high-frequency climate variability is therefore of major interest; it further allows better constraining the function of productive areas as biodiversity spots, as well as potential sources or sinks of CO₂ during rapid environmental changes.

Greenland Stadials (GS) including Heinrich Stadials (HS, following Sánchez-Goñi and Harrison, 2010) have previously been observed in marine climate records worldwide (e.g., Voelker et al., 2002; Hemming, 2004; Clement and Peterson, 2008). Their impact on the paleohydrology off NW Morocco (core MD04-2805 CQ; Fig. 1) has previously been discussed with a special emphasis on past regimes of primary productivity (Penaud et al., 2010). This multiproxy study allowed to integrate responses in dinoflagellate cyst (dinocyst), planktonic foraminifera, alkenone, and stable isotope data to past abrupt climatic changes, and to highlight changes in past upwelling intensity. It demonstrated abrupt decreases of sea-surface temperatures (SST) in phase with intense northern hemispheric ice-sheet decays (i.e. HS 1 and 2), as well as intensified upwelling conditions during the last deglaciation and especially during HS 1.

The present study aims at better understanding hydrological processes affecting the subtropical NE Atlantic from the end of Marine Stage 3 to the Holocene period. New micropaleontological data acquired in the central Gulf of Cadiz (core MD99-2339, 35.9° N; Fig. 1), derived from the analysis of dinocyst and planktonic foraminifera fossil communities, are integrated with previous analysis conducted on two cores retrieved further south off the NW Moroccan Margin (MD04-2805CQ, 34.5° N; Fig. 1) and further north

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off the SW Iberian Margin (SU-8118, 37.8° N; Fig. 1). Several objectives have guided us through this study:

1. To document the potentiality of the dinocyst proxy in the reconstruction of past sea-surface environments from the subtropical North-Eastern Atlantic, both considering index species as well as using transfer functions. Actually, dinocyst studies in subtropical areas are less frequent than those performed in northern basins of the North Atlantic.
2. To test, in subtropical latitudes, the robustness of quantitative paleotemperature reconstructions inferred from a multi-proxy approach (i.e. dinocysts, foraminifera and alkenones). The direct comparison, in the same cores, of these reconstructions offers a way to test the capability of these proxies to detect coherent climatic signals (according to the robustness of the quantifications or to different biotic responses), thus constituting the best way to discuss their reliability.
3. To characterize the migration of the hydrological fronts during abrupt climatic changes over the last 30 ka; the study sites representing a north-south transect allowing us to illustrate the latitudinal transfer of the climatic variability.
4. To monitor the upwelling behaviour and the associated dynamics of the planktonic communities off NW Morocco and Portugal during abrupt and millennial-scale climatic events.

2 Modern regional setting

The sedimentary sequences used for this study were collected in the subtropical North-Eastern Atlantic (Fig. 1), and are each representative of a unique hydrologic regime. The reader is referred to Eynaud et al. (2009), Voelker et al. (2009) and Penaud et al. (2010) for a detailed description of these hydrographical settings. Hereafter are listed key features regarding our synthesis.

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The so-called Portugal-Canary eastern boundary upwelling system is the result of the interaction of the north-eastern trade winds, blowing alongshore (e.g., Pearce, 1991; Hagen, 2001; Mann and Lazier, 2005; McGregor et al., 2007) and dependent on the seasonal migrations of the Azores High coupled to the Intertropical Convergence Zone dynamics (Hsu and Wallace, 1976), with the Canary Current (CC; Fig. 1), which flows southward between 32 and 28° N. At present, seasonal wind-driven coastal upwelling is active mainly from late May/early June to late September/early October (e.g., Haynes et al., 1993; Aristegui et al., 2005; Peliz et al., 2005). Eastern North Atlantic Central Water (ENACW) and partially Mediterranean Outflow Water (MOW) are the sources of the upwelled waters (Sánchez and Relvas, 2003).

Wind-driven coastal upwelling along the Algarve coast in the Northern Gulf of Cadiz is restricted to episodes with strong northerly winds (Sanchez and Relvas, 2003). Furthermore, the Gulf of Cadiz is influenced by Portuguese and Moroccan coastal currents and an extension of the Azores Current (AC; Fig. 1), flowing eastward at about 35° N. The AC coincides with the Azores Front (AF), marking the north-eastern boundary of the North Atlantic subtropical gyre, south of the Azores Islands. Today, the AF is located at the latitude of the Gulf of Cadiz in the open Atlantic Ocean but does not penetrate into the Gulf of Cadiz (Rogerson et al., 2004). The AF corresponds to a zone of strong hydrographical transition between European and African surface water masses, both in terms of sea-surface temperature (SST) (thermal transition of about 4 °C; Gould, 1985) and in terms of vertical structure of the water column (Fasham et al., 1985). Moreover, it is locally characterized by intense upwelling cells (Rudnick, 1996; Alves and de Verdière, 1999; Alves et al., 2002).

Below subtropical waters, water mass stratification is characterized by North Atlantic Central Water between 100 and 600 m, MOW between 600 and 1700 m (Knoll et al., 2002; Llinas et al., 2002), and the North Atlantic Deep Water below 1700 m. Annual SSTs are comprised between 18 and 19 °C at the SW Iberian Margin and Gulf of Cadiz, and between 19 and 20 °C off NW Morocco (WOA 2005; Locarnini et al., 2006). Annual sea-surface salinities are approximately 36.2–36.4 throughout the year at the

three study sites (WOA 2005; Antonov et al., 2006).

3 Material and methods

3.1 Age models

5 Core MD04-2805 CQ (34.52° N, 7.02° W, 859 m depth, and 7.72 m long), mainly characterized by homogenous hemipelagic clays, was retrieved at about 40 km off the Moroccan coast, in relative shallow environments of the North-Western African Margin. The stratigraphical framework of core MD04-2805 CQ (Penaud et al., 2010) is based on six AMS ^{14}C dates and correlation of the planktonic $\delta^{18}\text{O}$ data with the one from the well-dated core MD99-2339 (Voelker et al., 2006), both derived from the planktonic foraminifer *Globigerina bulloides*.

10 Core MD99-2339 (35.89° N, 7.53° W, 1170 m depth, 18.54 m long) was retrieved in a contourite field (Habgood et al., 2003) from the Eastern Gulf of Cadiz and allows to trace the MOW dynamics over the last 47 000 yr (Voelker et al., 2006). The stratigraphy of core MD99-2339 (Voelker et al., 2006) is based on 20 AMS ^{14}C dates and on three control points correlated with the GISP2 chronology (Grootes and Stuiver, 1997).

15 Core SU-8118 (37.78° N, 10.18° W, 3155 m depth, 7 m long) was retrieved from the South-Western Iberian Margin, near the Tagus Abyssal Plain. This sedimentary sequence is mainly composed of homogeneous clays with two discrete peaks of ice-rafted debris (IRD) recorded around 260–290 cm (15.2–16.2 cal. ka BP) and 500–520 cm (22.6–23.4 cal. ka BP) corresponding with HS 1 and HS 2, respectively (Turon et al., 2003). The stratigraphy of this core is established on the basis of 22 AMS ^{14}C dates (Bard et al., 2000) and planktonic $\delta^{18}\text{O}$ data derived from the planktonic foraminifer *G. bulloides* (Bard et al., 1987, 1989).

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3.2 Dinocyst analysis

Dinocyst analyses were previously carried out on cores MD04-2805 CQ (Penaud et al., 2010) and SU-8118 (Turon et al., 2003).

Core MD99-2339 was subsampled at the EPOC laboratory (“Environnements et Paléoenvironnements OCéaniques”, Bordeaux1 University, France). Each subsample of 8 cm³ was weighed, dried overnight and then weighed again to obtain dry weight. Subsamples were then washed through a 150 µm sieve and the fraction smaller than 150 µm was used for palynological preparation and analysis. Sixty-five samples were analysed over the last 30 ka. The preparation technique followed the protocol described by de Vernal et al. (1999) and Rochon et al. (1999), slightly modified at the EPOC laboratory (Castera and Turon, cf. http://www.epoc.u-bordeaux.fr/index.php?lang=fr&page=eq_paleo26). For each sample, an average of 300 dinocyst specimens was identified and counted using a Leica DM 6000 microscope at 400 × magnification. Dinocyst taxonomic identification is conform to Fensome et al. (1998) and Fensome and Williams (2004), and dinocyst assemblages were described by the percentages of each species calculated on the basis of the total dinocyst sum including unidentified modern taxa and excluding pre-Quaternary specimens.

Maximal relative abundances of *Lingulodinium machaerophorum* in core MD99-2339 reach nearly 85% during the Bölling/Alleröd and this species shows an average of 55% of the total dinocyst assemblage throughout the whole record. For this reason, we have systematically counted 100 dinocysts excluding *L. machaerophorum* in order to obtain a statistically correct image of dinocyst assemblages. *Brigantedinium* spp. includes all spherical brown cysts as their crumbled aspect makes them difficult to identify to species level. Cysts of *Protoperidinium nudum* are grouped with the species *Selenopemphix quanta* and noted as *S. quanta* in this study.

Calculation of absolute abundances of dinocysts is based on the marker grain method (de Vernal et al., 1999; Mertens et al., 2009): aliquot volumes of *Lycopodium* spores were added to each sample before chemical treatment in order to estimate palynomorph concentrations (number of dinocysts cm⁻³).

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3.3 SST reconstructions

3.3.1 Dinocyst SST reconstructions

We used two transfer functions based on the Modern Analogue Technique (MAT) to reconstruct dinocyst SST on the three cores. The MAT principally uses the statistical distance between fossil (paleoceanographic record) and current (modern database) assemblages. The calculation of past hydrological parameters relies on a weighted average of the SST values of the best modern analogues found (minimum and maximum number of analogues imposed in the transfer functions are 5). The maximum weight is given for the closest analogue in terms of statistical distance. The reader is referred to Guiot and de Vernal (2007) for a review of theory of transfer functions and to de Vernal et al. (2001, 2005) for a step by step description of the application of transfer functions to dinocysts, including discussion about the degree of accuracy of the method.

The first transfer function used in this work (cf. de Vernal et al., 2005; GEOTOP website: http://www.unites.uqam.ca/geotop/monographie_n940/eng/index.shtml) is derived from a modern database comprising 60 dinocyst species and 940 stations from the North Atlantic, Arctic and North Pacific oceans and their adjacent seas, including the Mediterranean Sea, as well as epicontinental environments such as the Estuary and Gulf of St. Lawrence, the Bering Sea and the Hudson Bay. The transfer function ($n = 940$) is run under the “3Pbase” software (Guiot and Goeury, 1996). Hydrological parameters are systematically calculated on the basis of the 5 best analogues found by the transfer function. An index “Dmin”, provided by the software “3PBase”, allows testing the reliability of the reconstructions. This index describes, for each sample analyzed, the distance between the closest analogue found by the transfer function and the fossil assemblage. A threshold value is calculated from the calibration of the database for the identification of non-similar or very bad analogues. The similarity between the modern data and the fossil record is considered significant below the threshold value of 71.72 (cf., de Vernal et al., 2005). With the $n = 940$ transfer function implemented with the “3PBase” software (i.e. 3PBase-940), we present February and August mean

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sea-surface temperatures (SST, with prediction errors of $\pm 1.2^\circ\text{C}$ and $\pm 1.8^\circ\text{C}$, respectively).

The second, and most recent, transfer function was presented at the workshop “Quantitative treatments for paleoceanographical reconstructions based on dinocyst assemblages” (Dino8 meeting, Montréal, May 2008). The modern database has been expanded and comprises $n = 1189$ surface samples (cf. Radi and de Vernal, 2008, or the GEOTOP website: http://www.unites.uqam.ca/geotop/paleoceanographicDatabase/monographie_n1171/eng/index.shtml; the full $n = 1189$ database is still unpublished) and 63 dinocyst species, and is run within the “R version 2.7.0” software (R Development Core Team, 2008; <http://www.r-project.org/>). Hydrological parameters are calculated on the basis of the best analogues (maximum of 5) found by the transfer function. For each sample analyzed, the distance between the 5 analogues and the fossil assemblage is calculated and, above a threshold value, the software “R” does not consider analogues found by the transfer function, leading occasionally to non analogue configurations. With the $n = 1189$ transfer function implemented with the “R” software (i.e. R-1189), we discuss February/winter and August/summer SST reconstructions with prediction errors of $\pm 1.2^\circ\text{C}$ and $\pm 1.6^\circ\text{C}$, respectively.

3.3.2 Foraminiferal SST reconstructions

In the same way, we used two transfer functions based on the MAT to reconstruct foraminiferal SST on the three cores. Calculation of past SST relies on a weighted average of the SST values of the best 5 modern analogues found systematically.

In the first transfer function, February and August SST have been estimated using the MAT transfer function derived from Pflaumann et al. (1996) which relies on a modern database of 692 modern assemblages (only Atlantic stations) improved during the MARGO project (Kucera et al., 2005). Fossil assemblages are compared to the modern ones, based on the relative abundances of species for which no transformation has been done (no weight given artificially to species by logarithmic transformation for

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instance). In this paper, we present February and August mean SST, with a prediction error of $\pm 1.2^\circ\text{C}$ and $\pm 1.4^\circ\text{C}$, respectively. More information can be found in the compilation of Kucera et al. (2005) for a critical review of the accuracy of the method. It is worth noting that SST reconstructions have already been published for core MD99-2339 with the SIMMAX program and a modern database including 1020 Atlantic modern analogues (Voelker et al., 2006). Our results obtained with the transfer function “ $n = 692$ ” have been compared and show exactly the same values. However, since we have used the transfer function “ $n = 692$ ” for cores MD04-2805 CQ (SST published in Penaud et al., 2010) and SU-8118, we have chosen to apply the same procedure for the three cores.

The second, and most recent, transfer function has been developed at EPOC laboratory (“Environnements et Paléoenvironnements OCéaniques”, Bordeaux1 University, France). The MAT (e.g., Kucera, 2007) is run under the “R” software using a script first developed for dinocyst transfer functions (http://www.cerege.fr/IMG/pdf/ECCOR_StatRAvr08.pdf). The modern database relies on a modern database of 1007 modern assemblages and is derived from the ones developed separately for the North Atlantic and the Mediterranean Seas during the MARGO project (Kucera et al., 2005; Hayes et al., 2005). These databases were merged together to offer a larger set of analogues for subtropical reconstructions over the last glacial period notably (Eynaud et al., 2009; Matsuzaki et al., 2011). Modern hydrological parameters were requested from the WOA 2008 database using the tool developed during the MARGO project (<http://www.geo.uni-bremen.de/geomod/staff/csn/woasample.html>). This method allows the reconstruction of annual and seasonal (winter, spring, summer and fall) SST. In this paper, we present winter and summer mean SST with a prediction error of $\pm 1.2^\circ\text{C}$ and $\pm 1.3^\circ\text{C}$, respectively, and annual SST with a prediction error of $\pm 1.1^\circ\text{C}$ (Eynaud et al., 2009; Matsuzaki et al., 2011).

3.3.3 Alkenone SST reconstructions

SST changes were previously reconstructed with the alkenone unsaturation ratios on cores MD04-2805 CQ (Penaud et al., 2010) and SU-8118 (Bard et al., 2000).

In this study, we compare dinocyst and foraminiferal SST reconstructions obtained on these two cores with two different calibrations converting the C_{37} alkenone unsaturation data ($U_{37}^{K'}$) in terms of SST. First temperature estimates are based on a culture calibration ($SST = (U_{37}^{K'} - 0.039)/0.034$; Prahl et al., 1988), equivalent to a global core-top compilation (Müller et al., 1998). Additional temperature estimates calculated from a regional calibration, based on $U_{37}^{K'}$ measured in modern sediments from the NE Atlantic (Rosell-Melé et al., 1995), is also used in this study ($SST = (U_{37}^{K'} - 0.186)/0.026$; Weaver et al., 1999).

4 Dinocyst assemblages from core MD99-2339 through time

Dinocyst analysis in core MD99-2339 shows concentrations varying between 1600 and 13 500 cysts cm^{-3} , with values being the highest at the transition between the Bölling-Alleröd (B/A) and the Younger Dryas (YD) (Fig. 2). The average dinocyst concentration in the whole sedimentary record is 5900 cysts cm^{-3} .

From the beginning to the end of the sequence, assemblages are dominated by *Lingulodinium machaerophorum* and *Brigantedinium* spp. (Fig. 2). *Brigantedinium* spp. were present during the whole glacial period and decreased abruptly at Termination IA (transition between HS 1 and the B/A) while *L. machaerophorum* strongly expanded, with relative abundances of this latter species reaching 80% during the B/A and 70% during the Holocene (Fig. 2). This is consistent with the current distribution of this taxon which shows the highest abundances off Portugal and around the Strait of Gibraltar with modern values reaching 80% (Rochon et al., 1999). Concerning *Brigantedinium* spp., it is important to keep in mind that this species can be linked to better preservation under

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preanoxic or anoxic bottom conditions (Combourieu-Nebout et al., 1998; Zonneveld et al., 2001; Kodrans-Nsiah et al., 2008).

The species occurring during cold intervals (HS and YD) are represented by *Bitectatodinium tepikiense*, *Spiniferites lazus*, *Spiniferites elongatus*, *Trinovantedinium applanatum* and *Nematosphaeropsis labyrinthus*. Warmer periods (Last Glacial Maximum: LGM, B/A, and Holocene) are mainly characterized by increases of *Spiniferites mirabilis*, *Impagidinium* species (*I. aculeatum*, *I. paradoxum*, *I. patulum*, *I. sphaericum*, *I. strialatum*), *Spiniferites bentorii*, and *Spiniferites delicatus* (Fig. 2). These occurrences are very similar to those found off the NW Moroccan Margin over the last 30 ka (Penaud et al., 2010). More details on the present-day ecology of the species, discussed later in this manuscript, can be found in Penaud et al. (2010).

5 Temperature records: convergences and discrepancies

5.1 The different transfer functions applied to dinocysts and foraminifera

For each core, dinocyst SST reconstructions obtained from the two transfer functions (3PBase-940 and R-1189) for the months of February and August are compared on the same graph (Fig. 3). Differences between the results of the two transfer functions cannot be due to the different software used and result from the expansion of the dinocyst database. Indeed, in order to overcome this potential bias on our quantitative data, we have tested the “3PBase” software with the $n = 1189$ database and the results were exactly similar to those obtained from the “R” software. However, we chose to apply the same statistical methods as those applied in previous paleoenvironmental reconstructions (3PBase-940; de Vernal et al., 2005) and those recommended at present (R-1189; Dino8 meeting, Montréal, May 2008).

For the three cores, differences between SST values obtained with “R” and “3PBase” are generally lower than or equal to the error bars (Fig. 3). However, “3PBase” provides data in a systematic way while “R” provides a discontinuous record, particularly

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for core SU-8118 (Fig. 3). The index “Dmin” provided by the two transfer functions (Fig. 3) represents the minimum distance between the closest analogue and the fossil assemblage found by each transfer function. Concerning the transfer function 3PBase-940, the similarity between modern and fossil data is judged significant below the Dmin value of 71.72 and, beyond this value, analogues found by the transfer function are considered less reliable (cf. de Vernal et al., 2005). However, this transfer function considers the 5 analogues without removing any of the worst ones. The transfer function R-1189 makes a selection of the different analogues found and, above a threshold value, the transfer function R-1189 does not consider some of the analogues found. This can lead to non-analogue configurations for a fossil sample when the minimum distance of the closest analogue exceeds the threshold value. In summary, the data provided by the two transfer functions are rather similar, and the reconstructions provided by the transfer function R-1189 allow us to distinguish better the critical periods when the results are less reliable.

Quantitative reconstructions derived from the two foraminiferal transfer functions are not directly comparable since the reconstructed parameters are not exactly the same. The transfer function PaleoToolBox-692 only provides February and August SST reconstructions while the transfer function R-1007 provides annual and seasonal-mean (i.e. winter, spring, summer and fall) SST reconstructions. However, the comparison of winter vs. February SST values on the 664 common stations from the North Atlantic databases ($n = 1007$ vs. $n = 692$) generates a mean difference of 0.26°C (with a maximum difference of 1.95°C). For the summer vs. August SST values, the mean difference is 0.37°C (with a maximum difference of 1.1°C). These values are within the range of the error bars of the reconstructions and therefore encourage us to compare the two sets of reconstructions.

The results show that monthly or seasonal reconstructions are extremely close for the three Atlantic cores (Fig. 4). Using an Atlantic database or the most complete database with 1007 stations (including Mediterranean sites) does not alter the SST values obtained. This is particularly interesting because we can, in the following

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discussion, compare February and August dinocyst SST ($n = 940$) with winter and summer foraminiferal ones ($n = 1007$), and we also can compare the annual foraminiferal SST estimates ($n = 1007$) with the alkenone data available for cores SU-8118 and MD04-2805 CQ. This will give us the opportunity to discuss paleotemperature records obtained with three different proxies, and very limited sedimentary archives illustrate such a complete SST dataset in subtropical latitudes (cf. Bard, 2001).

5.2 SST multiproxy compilation

5.2.1 Dinocysts vs. foraminifera

When comparing reconstructions from both micropaleontological proxies on the three cores, one can note that winter and summer SST values are closer than February and August ones (Fig. 5). Closer, and probably more reliable, seasonal reconstructions may be due to the enlargement of the databases ($n = 1189$ dinocysts and $n = 1007$ foraminifera) providing a wider choice of analogues, and to the fact that R-1189 does not consider “bad” analogues for its calculations. Largest discrepancies between dinocyst and foraminiferal SST are observed for February and August reconstructions, and especially during the LGM on the NW Moroccan and SW Iberian Margins (offset of about 2–4°C between dinocyst and foraminiferal estimates), and during HS 1 in the Gulf of Cadiz (offset around 8°C), with dinocysts generally indicating warmer SST (Fig. 5).

Beyond the accuracy of the reconstructions, two hypotheses can be put forward with respect to this observation. Either the dinocyst and/or foraminiferal SST are less reliable, or, the discrepancy reflects an ecological bias. Dinocysts are indeed produced by dinoflagellates (phytoplankton group) with shallow living depths (photic zone) while planktonic foraminifera (zooplankton group) can migrate deeply in the water column with living depths ranging from 0 to 1000 m. Dinoflagellates, being found in shallower water, would thus record warmer SST. Various biases between different micropaleontological reconstructions can thus occur in relation to water masses or productivity

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and to the ecological strategy (depth of habitat, growth seasons) of phytoplankton vs. zooplankton organisms (de Vernal et al., 2005).

Moreover, de Vernal et al. (2006), in an attempt of re-evaluating LGM sea-surface conditions with various proxies including dinocysts, foraminifera and alkenones, previously demonstrated that LGM SSTs show significant differences depending upon the proxy used for reconstruction. Discrepancies between the different techniques especially marks the eastern boundary currents (de Vernal et al., 2006). It is thus expected to record discrepancies off NW Africa and SW Iberia.

Discrepancies between dinocysts and foraminifera may also result from glacial upwelling microfossil assemblages (Kucera et al., 2005; de Vernal et al., 2006). Indeed, *Brigantedinium* spp. are particularly dominant throughout the glacial in the three cores (cf. Fig. 7) and their present-day occurrence shows a multimodal temperature preference since they are observed in sub-arctic/arctic waters (Rochon et al., 1999) as well as along continental margins subjected to upwelling phenomena (Gaines and Elbrächter, 1987; Biebow, 1996; Marret and Zonneveld, 2003). This taxon thrives particularly in nutrient-rich sea-surface waters but no clear correlation was found between *Brigantedinium* spp. and the conditions of temperature or salinity. Indeed, the weaknesses of our LGM estimates may come from this bias induced by heterotrophic taxa such as *Brigantedinium* cysts.

5.2.2 Transfer functions vs. alkenones

Alkenone-derived SST from cores SU-8118 (Bard et al., 2000) and MD04-2805 CQ (Penaud et al., 2010) have previously been compared with ice-core records, demonstrating a close linking between SSTs in the subtropical NE Atlantic and temperature developments over the wider North Atlantic region, including Greenland. Here, we show two reconstructions of alkenone derived-SST based on two different calibrations. It is obvious that using the regional NE Atlantic calibration (Weaver et al., 1999) or the culture calibration (Prahl et al., 1988) does not change both SST patterns (Fig. 6). Largest offsets between both calibrations are observed at the SW Iberian Margin and

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represent small differences of less than 1.5 °C (Fig. 6). Therefore, selecting one instead of the other equation will not alter the following discussion.

Dinocyst and foraminiferal-based SST reconstructions for both cores match peak to peak with the SSTs derived from alkenones, showing minimum values during HS and the YD (Fig. 6). Furthermore, the alkenone-based SST, which records an annual signal of temperature, fluctuates in between the temperature range given by seasonal dinocyst and foraminiferal SST reconstructions (Fig. 6). The foraminiferal transfer function $n = 1007$ also provides annual SST reconstructions that can directly be compared with the alkenone signal. One can note that annual SST values reconstructed with both proxies are very close, except during HS 1 where foraminifera provide 5 °C colder temperatures than alkenones do. This supports the fact that SST reconstructions during HS 1 in the Gulf of Cadiz may also be over-estimated. This trend of foraminiferal SST towards colder estimates during Greenland Stadials, and especially during HS, was previously observed on the SW Iberian Margin and in the Alboran Sea between 25 and 50 ka BP, with significant SST anomalies between 4 and 7 °C (Penaud et al., 2011). Since alkenones are synthesized by coccolithophorids which are single-celled algae, protists and phytoplankton such as dinoflagellates, we can assume that they both give a more robust signature of sea-surface hydrological changes, while foraminifera may yield a bias towards colder SSTs, especially during GS. However, it will be crucial to understand if this finding reflects a real ecological strategy of foraminifera (different depths of habitat following different seasons) or a problem associated with the transfer function.

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6 Paleohydrological changes affecting the NE Atlantic over the last 30 ka

6.1 Compilations of SST data through time

6.1.1 Last Glacial Maximum

The LGM is the period of the last glacial period characterized by maximum extension of polar ice caps and minimum mean global sea-level (Mix et al., 2001). High resolution studies have called into question the CLIMAP paleoclimate quantifications (CLIMAP Project Members, 1981), including the perennial sea-ice cover in the northern basins (e.g., Pflaumann et al., 2003; Kucera et al., 2005; de Vernal et al., 2006). Today, many studies indicate an active North Atlantic Drift during the LGM and SSTs relatively warm in comparison with the two surrounding Heinrich Stadials (HS 1 and HS 2) (Sarnthein et al., 1995; Eynaud, 1999; de Vernal et al., 2000, 2001, 2005, 2006; Zaragosi et al., 2001; Boessenkool et al., 2001; de Abreu et al., 2003; Kucera et al., 2005; Penaud et al., 2009; Eynaud et al., 2009, 2011).

In our study, we find increases of the temperate to tropical *Impagidinium* dinocyst species and *S. mirabilis*, these species being quasi-absent from the surrounding HS (Fig. 7). These taxa suggest a warming of sea-surface waters. This is in agreement with temperature reconstructions obtained during the LGM showing mean SSTs higher than those recorded during the surrounding HS and close to present-day and B/A temperature estimates (if considering the warmer LGM excursions; Fig. 5, Table 1). Indeed, some oscillations with amplitudes ranging from 2 to 4°C, observed in SST records derived from foraminifera and dinocysts, suggest that the LGM was not a completely stable period (Fig. 5), consistent with previous studies carried out in the temperate Atlantic Ocean (Zaragosi et al., 2001; Mojtahid et al., 2005; Voelker et al., 2009; Eynaud et al., 2011). Our resolution allows us to identify at least three warmer periods around 18.5, 20.5 and 22 ka (Fig. 5).

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6.1.2 Heinrich stadials

During HS, armadas of icebergs invaded the North Atlantic Ocean (e.g., Heinrich, 1988; Bond et al., 1992), causing great sea-surface cooling and freshening up to the subtropical latitudes off Portugal (e.g., Lebreiro et al., 1996; Baas et al., 1997; Zahn et al., 1997; Cayre et al., 1999; Bard et al., 2000; Turon et al., 2003; de Abreu et al., 2003; Eynaud et al., 2009). Cold sea-surface waters likely invaded latitudes of the Eastern Subtropical Atlantic via the Portugal Current and were then spread by the Canary Current (Zhao et al., 1995; Plewa et al., 2006).

On the three cores, HS are noted by significant SST decreases (Fig. 5) linked to a significant drop in warm species (dinocyst species *Impagidinium* spp. and *S. mirabilis*; Fig. 7) and the development of polar to subpolar species (dinocysts *B. tepikiense* and *S. lazus*, and foraminifera *N. pachyderma* s. and *T. quinqueloba*; Fig. 8). These periods are marked by very low February dinocyst and foraminiferal SSTs on the SW Iberian Margin (around 4–6°C). Further south, at 315 km (central Gulf of Cadiz) and 460 km (NW Moroccan Margin) from the SW Iberian Margin, HS 1 and 2 are identified by warmer SSTs with February SSTs reaching 9–11°C off NW Morocco (Fig. 5). When only considering dinocyst SST, HS 1 and 2 however appear to be colder at the NW Moroccan Margin than in the Gulf of Cadiz (Fig. 5). Indeed, in the Gulf of Cadiz, HS 2 is characterized by consistent and relatively warm dinocyst and foraminiferal February SSTs of 12–14°C, and HS 1 shows an ambiguous pattern with February dinocyst estimates close to 13–14.5°C and foraminiferal ones close to 6–8°C. This raises the question of the validity of the obtained reconstructions for this sector during HS 1. The peak of *N. pachyderma* s. reaching 5 to 10% of the total foraminiferal assemblage during HS 1 seems to be responsible for the switch of the transfer function towards extremely cold SST values (Fig. 8). Furthermore, dinocysts and foraminifera show only large offsets higher than error bars for the different reconstructions during HS 1 (Fig. 5), and dinocyst reconstructions are reliable according to the statistical distance calculated between fossil and modern assemblages (Fig. 5). We suggest that, for the

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Gulf of Cadiz, cold foraminiferal estimates during HS 1 may be over-estimated. This observation needs however confirmation through other paleotemperature records based on different proxies.

6.1.3 Younger dryas

The YD can be assimilated to an HE if the hydrological disturbance associated with this cold climatic event is considered (HE 0, Andrews et al., 1995).

In our study, this interval is clearly marked, in the three sedimentary sequences, with a decline of thermophilous species (Fig. 7), a decrease of *L. machaerophorum* percentages (Fig. 7) and the development of species dominating today polar to sub-polar environments (Fig. 8). The YD is characterized by February SST of about 8–10 °C off Portugal (15.5 °C today), while further south (Cadiz and Morocco), it is characterized by warmer February SST of 13–14 °C (16.5 °C today) (Fig. 5). This represents a mean anomaly of minus 3 and 7 °C regarding to present-day SSTs in the areas of Portugal and Cadiz-Morocco, respectively.

6.1.4 Holocene and Bölling-Alleröd

The Holocene and B/A are characterized by the development of temperate to tropical species *S. mirabilis* and *Impagidinium* spp., however with lower percentages during the B/A than during the Holocene (Fig. 7). Dinocyst, foraminifera, and alkenone derived-SST reconstructed during the Holocene (until 5 ka BP) from cores retrieved off Portugal and NW Morocco and in the Gulf of Cadiz are consistent, given the method's uncertainties, with those characterizing these areas today (WOA 2005; Locarnini et al., 2006; Fig. 5). February and August SST are around 15 °C and 20–21 °C for the areas of Portugal and Cadiz-Morocco, respectively (Fig. 5). Comparison of dinocyst vs. foraminiferal reconstructions show consistent values except for the Gulf of Cadiz for the interval younger than 11 ka BP. This discrepancy is partly due to a lack of resolution in the foraminiferal record, with no data available between 11 and 7 ka BP (Fig. 5).

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6.2 Paleoproductivity conditions through time

6.2.1 Duality *L. machaerophorum* – *Brigantedinium* spp.

Dinocyst assemblages from the three study areas are dominated by the taxa *L. machaerophorum* and *Brigantedinium* spp. (Fig. 7). Profiles of these two species are furthermore almost identical between the Gulf of Cadiz and the Moroccan Margin, with the dominance of *Brigantedinium* spp. during the glacial period until the end of HS 1 (Termination IA; Fig. 7), then followed by a sharp decrease of *Brigantedinium* spp. replaced by a strong development of the species *L. machaerophorum*. At the SW Iberian Margin, the switch between these two taxa occurred at the end of the YD (Termination IB; Fig. 7). Moreover, we note that the percentages of *Brigantedinium* spp. were always much higher at the SW Iberian Margin, and vice versa for *L. machaerophorum* which exhibited maximum relative abundances at the NW Moroccan Margin and central Gulf of Cadiz (Fig. 7). In all cases, for the three studied areas, there existed a duality between these two taxa which had previously been described for the MIS 5 substages at the SW Iberian Margin (Eynaud, 1999; Eynaud et al., 2000). *L. machaerophorum* is a species mostly occurring in neritic environments, close to the Strait of Gibraltar and including the Portuguese coast, representing today 80% of the total dinocyst assemblage (Marret and Zonneveld, 2003). This taxon has often been associated with relatively warm and stratified water masses (Marret and Zonneveld, 2003), and particularly off NW Africa, where highest abundances of this taxon have been linked to periods of relaxation of upwelling cells (Bouimetarhan et al., 2009). In contrast, *Brigantedinium* spp. are formed by heterotrophic dinoflagellates whose nutrition is mainly characterized by diatoms (e.g., Wall et al., 1977; Gaines and Elbrächter, 1987; Matsuoka, 1987; Lewis et al., 1990). The occurrence of these cysts in significant proportions in dinocyst assemblages has often been linked to nutrient-rich sea-surface waters, such as areas affected by permanent upwelling (Marret, 1994; Biebow, 1996; Dupont et al., 1998; Zonneveld et al., 2001; Radi and de Vernal, 2004; Sprangers et al., 2004). Furthermore, when comparing *Brigantedinium* spp. percentages on core SU-8118 with

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summer export productivity obtained on the twin core MD95-2042 (Salgueiro et al., 2010; Fig. 9), the same trend of decreasing productivity is noted on both sedimentary sequences over the last 30 ka. These preliminary observations based on dinocyst from heterotrophic dinoflagellates suggest a general intensification of primary productivity in this sector likely reflecting the intensification of upwelling cells during the last glacial period, echoing previous studies carried out along the Iberian Margin (e.g., Abrantes, 2000; Lebreiro et al., 1997; Voelker et al., 2009; Salgueiro et al., 2010).

6.2.2 Significance of *S. quanta* and *T. applanatum* occurrences

Particularly intense upwelling conditions prevailing off NW Morocco during HS 1 were derived from a various set of proxies (Penaud et al., 2010). Among these tracers, high planktonic $\delta^{13}\text{C}$ values and expansions of heterotrophic taxa (especially *S. quanta* and *T. applanatum*; Fig. 7) suggested high primary productivity in surface waters. In addition, increased concentrations of *Pinus* pollen, likely representing a component of the Southern European vegetation (Agwu and Beug, 1982; Hooghiemtra et al., 2006), suggested stronger north-eastern trade winds (Marret and Turon, 1994; Penaud et al., 2010).

In this study, we show that, off the SW Iberian Margin, *S. quanta* and *T. applanatum* also increased substantially during HS 1 and Termination IA (TIA), but also characterized the YD with relative abundances as high as during HS 1 (Fig. 7). Similar to the Moroccan Margin, percentages of these species decreased during the LGM, and especially during HS 2. By analogy with observations made off NW Morocco (Penaud et al., 2010), these taxa thus allow us to discriminate between periods of intensification of upwellings at the SW Iberian Margin. It suggests relatively weak upwelling cells during HS 2, and particularly intensified upwelling cells during HS 1 on the NW Moroccan and SW Iberian Margins as well as during the YD along the Portuguese coast. *S. quanta* and *T. applanatum* did not occur significantly in the Gulf of Cadiz during HS 1 and the YD (Fig. 7). In the subtropical North-Eastern Atlantic, these species may be restricted to neritic areas affected by coastal upwelling, as suggested previously off NW Africa

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(Wall et al., 1977; Marret and Turon, 1994; Penaud et al., 2010). However, the profile of *Brigantedinium* spp. recorded within core MD99-2339 is very close to the one in the Moroccan core (Fig. 7), suggesting higher concentration of nutrients during the last glacial period in the Gulf of Cadiz as well. Processes other than coastal upwellings may thus be involved to explain the occurrence of *Brigantedinium* spp. in the Gulf of Cadiz, as an indirect proxy of paleoproductivity, such as frontal upwellings (cf. Voelker et al., 2009).

6.2.3 Influence of the Azores Front on the local paleohydrology

Rogerson et al. (2004) studied the migration of the AF, over the last 30 000 yr, with two cores located in the Gulf of Cadiz and at the SW Iberian Margin (MD95-2042). Based on the planktonic foraminifer *G. scitula*, this study shows that the AF, a robust element characterizing sea-surface circulation in the Atlantic, penetrated into the Gulf of Cadiz during the YD and before 16 000 yr. *G. scitula* is a temperate to subpolar species (Thunnell, 1978) which mainly grows in environments characterized by seasonal vertical mixing within the water column (Thunnell and Reynolds, 1984; Eguchi et al., 1999; Kuroyanagi et al., 2002, Rogerson et al., 2004) and which is found in high abundances along the AF (Schiebel et al., 2002a, b). Rogerson et al. (2004) thus interpreted periods of relative high abundances of *G. scitula* as intervals of active upwellings in the Gulf of Cadiz, rather due to the presence of the AF in this area than to coastal upwelling processes. Indeed, the AF is at present locally associated with intense upwelling cells (Rudnick, 1996; Alves and de Verdière, 1999; Alves et al., 2002). We have thus tested this hypothesis with our data by comparing the profiles of *G. scitula* in cores MD04-2805 CQ, MD99-2339 and SU-8118. We show that high percentages of this species mainly characterized the LGM (Fig. 8), with no significant differences being observed between the 3 sites, over the last 30 000 yr. However, the AF represents today a strong thermal gradient of around 4 °C (Gould, 1985), and, if the AF was present in the Gulf of Cadiz during the last glacial, it should have resulted in drastic hydrological changes

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between core MD04-2805 CQ located further south and core SU-8118 located further north from site MD99-2339.

When comparing the profiles of *N. pachyderma* (s) and *T. quinqueloba* from the three sedimentary sequences (Fig. 8), a strong gradient of decreasing temperature is well demonstrated by a significant decrease of relative abundances of these two species from the SW Iberian Margin up to the NW Moroccan Margin, during the YD and HS 1. This decline is particularly important with regard to *N. pachyderma* (s), whose occurrence fades abruptly between the SW Iberian Margin and the Gulf of Cadiz. The foraminifer *T. quinqueloba* shows high relative abundances during the YD and HS 1 at the SW Iberian Margin and also decreases towards southern latitudes. However, significant percentages of this species are still recorded in the Gulf of Cadiz and off the SW Iberian Margin during the YD and HS 1 (Fig. 8). Today, this species is found in high latitudes and becomes abundant in transitional domains to polar water masses. This species prefers cool environments characterized by low vertical temperature gradients and low stratification. Van Leeuwen (1989) considers *T. quinqueloba* as an indicator of upwelling episodes off Angola and Meggers et al. (2002) include this species among the taxa related to upwelling filaments in the Canary Islands region. The observation of *T. quinqueloba* during the YD and HS 1 thus suggests periods of increased upwelling influence on the three study sites. This is consistent with observations made earlier from heterotrophic dinocysts (*S. quanta*, *T. applanatum* and *Brigantedinium* spp.).

The profile of the foraminifer *N. pachyderma* s. is particularly similar to that of the dinocyst *B. tepikiense*. The SW Iberian Margin is indeed characterized by the occurrence of the subpolar taxon *B. tepikiense* during HS 1 and HS 2 (20–30%) and during the YD (5%). This species has also been observed previously further north in the Bay of Biscay (47° N) with higher percentages up to 30–40% during HS 1 and 2 (Zaragosi et al., 2001; Penaud et al., 2009). At the NW Moroccan Margin and Gulf of Cadiz, this subpolar taxon occurred in very low percentages during HS (3% maximum) and the YD, while the species *S. lazus* is clearly identified with abundances close to 10 and 5% during HS and the YD, respectively (Fig. 8). Unlike *B. tepikiense* whose ecological affinity

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for subpolar water masses and high seasonal contrast has already been the subject of numerous paleoenvironmental interpretations in the North Atlantic and Mediterranean Sea (e.g., Turon and Londeix, 1988; Sánchez-Goñi et al., 1999; Eynaud et al., 2000; Combourieu-Nebout et al., 2002; Turon et al., 2003; Penaud et al., 2008, 2009, 2011), *S. lazus* is identified here for the first time as a marker of HS from the latitude of the Gulf of Cadiz to the NW Moroccan Margin.

Nematosphaeropsis labyrinthus is another dinocyst taxon whose percentages on the three cores illustrate the southward shift of the bioclimatic belts during the last glacial period and the YD. This species occurs at the transition between the LGM and HS 1 as well as during the YD (Fig. 8). During the YD, there is a gradient from north to south, between 38 and 34° N, with percentages around 20% off the Iberian Margin, 10% in the central Gulf of Cadiz and 5% off Morocco (Fig. 8). This decreasing gradient in percentages from the Portuguese to the NW Moroccan Margin may reflect a latitudinal climate trend associated with the YD impact in the subtropical North-Eastern Atlantic that goes conform to the reconstructed SST (Fig. 8). It should be mentioned that further north in the Bay of Biscay, around 47° N, Zaragosi et al. (2001) and Penaud et al. (2009) found this species with percentages of 15 and 30%, respectively, during the B/A. They, however, also noted a percentage decrease during the YD, time interval when cysts of *Pentapharsodinium dalei* expanded. It is therefore interesting to see that, north of the Iberian Peninsula, *N. labyrinthus* characterizes the warm event of the last deglaciation (B/A), while at the latitudes of our study, i.e. in subtropical areas of the North-Eastern Atlantic and also in the western Mediterranean (Turon and Londeix, 1988), this species characterizes the cold event of the last deglaciation (YD). Eynaud (1999) suggested a migration of this species from the Bay of Biscay to more southern latitudes due to the climatic deterioration during the YD. Our study thus confirms a general southward shift of the bioclimatic belts, even affecting the Moroccan Margin, while the magnitude of this cold episode is low compared to that associated with HS.

To conclude, a regional synthesis (36–42° N) on the extension of the Polar Front (PF) during the last glacial period showed that the PF oscillated around 40° N at the

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Iberian Margin during HS (Eynaud et al., 2009). The fact that the PF did not reach the latitudes of Cadiz and Morocco may explain the quasi-absence of *N. pachyderma* s. and *B. tepikiense* in both these areas. The relay of dinocyst and foraminiferal species to the south likely marks a well-defined hydrological front somewhere between 38 and 36° N, during the last glacial period and the YD, probably similar to the modern Azores Front (Rogerson et al., 2004; Voelker et al., 2009) and responsible for upwelling cells (Rudnick, 1996; Alves and de Verdière, 1999; Alves et al., 2002) in the Gulf of Cadiz as deduced from our paleoproductivity record.

7 Conclusions

This work aimed at improving our understanding of the spatial and temporal high frequency climate variability of the late Quaternary in the subtropical NE Atlantic. Combined micropaleontological (dinocysts and planktonic foraminifera) data from three sedimentary cores, distributed on a latitudinal transect from 34 to 38° N, have shown that planktonic population dynamics were very consistent over the last 30 ka, and were essentially forced by the movements of hydrological fronts in response to millennial-scale climate variability.

Despite the fact that these cores are located in a narrow geographical area, we demonstrate that microfossil assemblages from the NW Moroccan Margin and Gulf of Cadiz are very similar qualitatively but quite different from those observed northward off the SW Iberian Margin. Their response to cold extreme events (YD, HS) has highlighted a very large drop in percentages of subpolar species from the SW Iberian Margin to the Gulf of Cadiz. This strong gradient likely highlights a hydrological structure, probably equivalent to the present-day Azores Front, that separated the SW Iberian Margin from the study sites further south during the last glacial period. Furthermore, occurrences in the Gulf of Cadiz of the foraminifer *T. quinqueloba* and of heterotrophic dinocysts (*Brigantedinium* spp.) suggest higher primary productivity during the last glacial. Upwelling cannot be initiated there by Ekman transport, as it is the case along continental margins

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subjected to trade winds. Thus, we suggest that the presence of the Azores Front in the vicinity of the Gulf of Cadiz during the last glacial could be locally responsible for the occurrence of nutrient-rich water masses in this area.

Common points were highlighted between the two areas subjected to seasonal coastal upwellings (SW Iberian and NW Moroccan Margins), with increased coastal upwelling cells during HS 1 and the YD, and upwelling relaxation during the LGM and HS 2. Interestingly, core MD99-2339 (Cadiz) has also highlighted variations in the paleo-intensity of the MOW over the past 50 ka and, regarding the last 30 ka, intensifications of upwelling cells off Portugal and NW Morocco correspond to periods of higher export of the MOW. Knowing that the formation of the MOW is directly coupled to the cold and dry continental winds from Northern Europe, we could establish a link between the prevailing wind regimes above the Northern Hemisphere, upwelling cells, and formation of Mediterranean deep waters.

This study further demonstrates the great sensitivity of dinocysts in reconstructing (qualitatively as well as quantitatively) sea-surface conditions in the subtropical NE Atlantic, despite a modern dinocyst database that primarily focuses on subpolar to temperate North Atlantic areas.

Acknowledgement. Thanks to IPEV, the captain and the crew of the *Marion Dufresne* and the scientific team of the PRIVILEGE and IMAGES-GINNA cruises. We wish to thank Mr. Y. Balut for his assistance at sea and M. Castera, and O. Ther for invaluable technical assistance at the laboratory. A. V. acknowledges funding support from FCT through the MOWFADRI project. Part of this study was supported by the French CNRS.



The publication of this article is financed by CNRS-INSU.

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Table 1. Mean SST values for the warm and cold LGM excursions derived from dinocysts ($n = 940$) and foraminifera ($n = 692$), on the three cores.

Mean LGM reconstructions (°C)			Warm excursions	Cold excursions	Present
Portugal	Feb	Dinocyst	14	8.5	15.5
		Foraminifera	11.5	9.5	
	Aug	Dinocyst	20.5	12	20.5
		Foraminifera	18.5	15	
Cadiz	Feb	Dinocyst	15	14	16.5
		Foraminifera	16.5	12	
	Aug	Dinocyst	22	21	21.5
		Foraminifera	22	18	
Morocco	Feb	Dinocyst	15	14	16.5
		Foraminifera	15	11.5	
	Aug	Dinocyst	22	20.5	21.5
		Foraminifera	20.5	17.5	

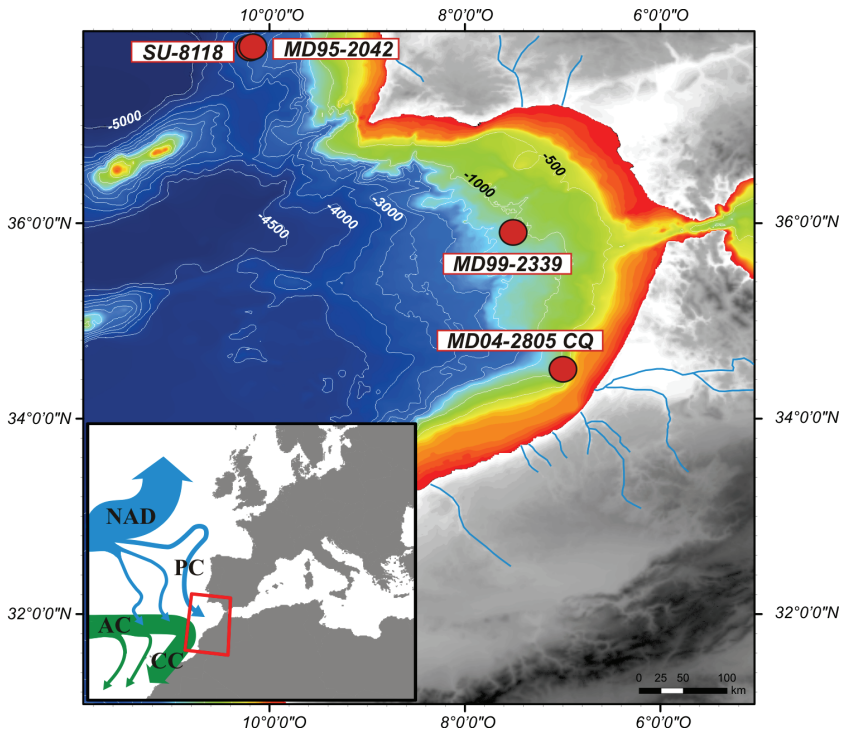


Fig. 1. Major sea-surface currents in the study area (small map): North Atlantic Drift (NAD), Portugal Current (PC) flowing southward from 45° N to 30° N, Azores Current (AC) derived from the southern branch of the Gulf Stream and flowing eastward to the Gulf of Cadiz at about 35° N, and Canary Current (CC) fed by both the AC and the PC. Together, these currents form the Eastern Boundary Current system of the North Atlantic subtropical gyre. The studied cores MD99-2339 (35.89° N; 7.53° W; 1170 m water depth), MD04-2805 CQ (34.52° N; 7.02° W; 859 m water depth), and SU-8118 (37.78° N; 10.17° W; 3155 m water depth), as well as MD95-2042 (37.80° N; 10.17° W; 3146 m water depth), are located on the bigger map, depicting also the bathymetry of the study area.

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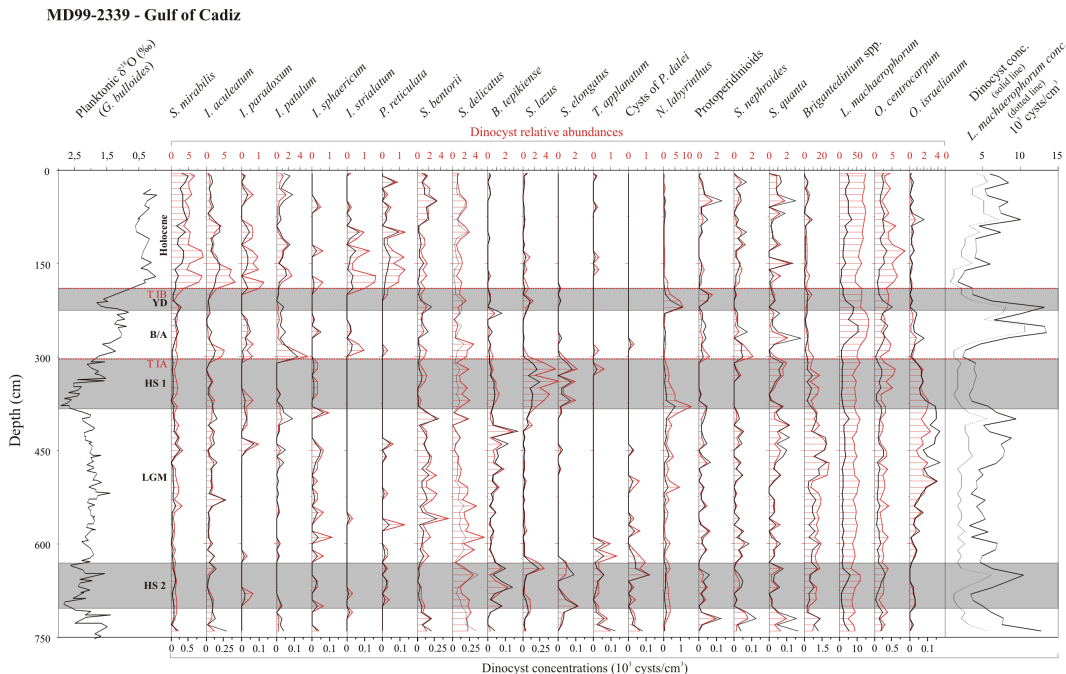


Fig. 2. Dinocyst data of core MD99-2339 (Gulf of Cadiz) vs. depth (cm). Dinocyst relative abundances and concentrations of selected species, as well as total dinocyst concentration, are displayed. The planktonic oxygen isotope curve (*G. bulloides*) provides the stratigraphical framework for the core (Voelker et al., 2006). YD: Younger Dryas; B/A: Bölling-Allerød; HS: Heinrich Stadial; LGM: Last Glacial Maximum; T1: Termination 1.

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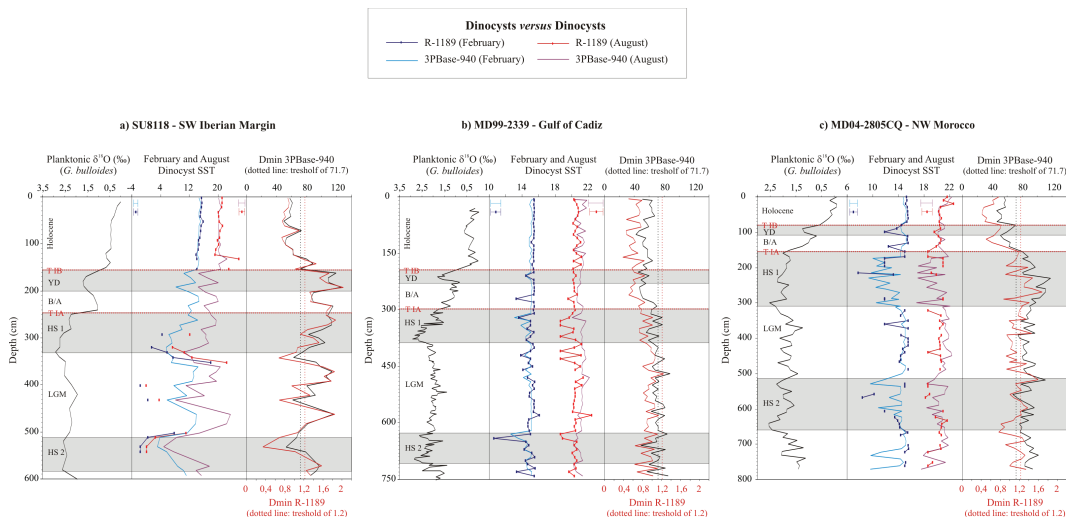


Fig. 3. SU-8118 (a), MD99-2339 (b) and MD04-2805 CQ (c). Comparison of quantitative dinocyst SST reconstructions (February and August) from 3PBase-940 and R-1189, in parallel with planktonic $\delta^{18}\text{O}$ (*G. bulloides*). Error bars are shown for the different reconstructions. Dmin, for each transfer function, represents the statistical distance between the closest analogue found by the transfer function and the fossil assemblage. Threshold values of each method are represented by dotted lines. YD: Younger Dryas; B/A: Bölling-Allerød; HS: Heinrich Stadial; LGM: Last Glacial Maximum; TI: Termination 1.

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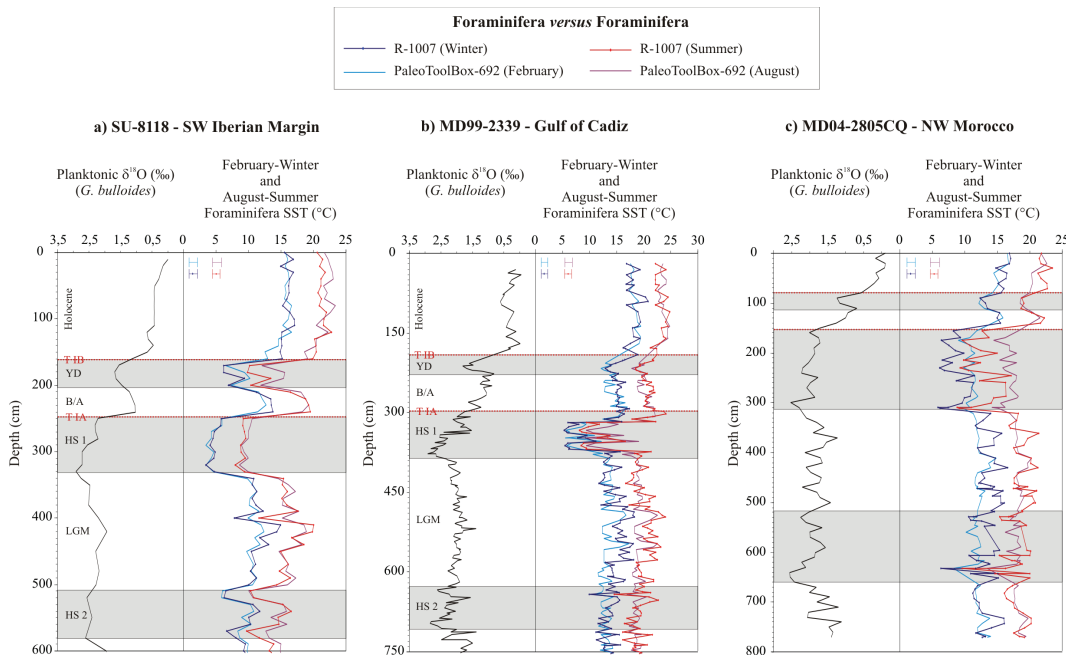


Fig. 4. SU-8118 (a), MD99-2339 (b) and MD04-2805 CQ (c). Comparison of quantitative foraminiferal SST reconstructions (February vs. winter and August vs. summer) from PaleoToolBox-692 and R-1007, in parallel with planktonic $\delta^{18}\text{O}$ (*G. bulloides*). Error bars are shown for the different reconstructions. YD: Younger Dryas; B/A: Bölling-Allerød; HS: Heinrich Stadial; LGM: Last Glacial Maximum; TI: Termination 1.

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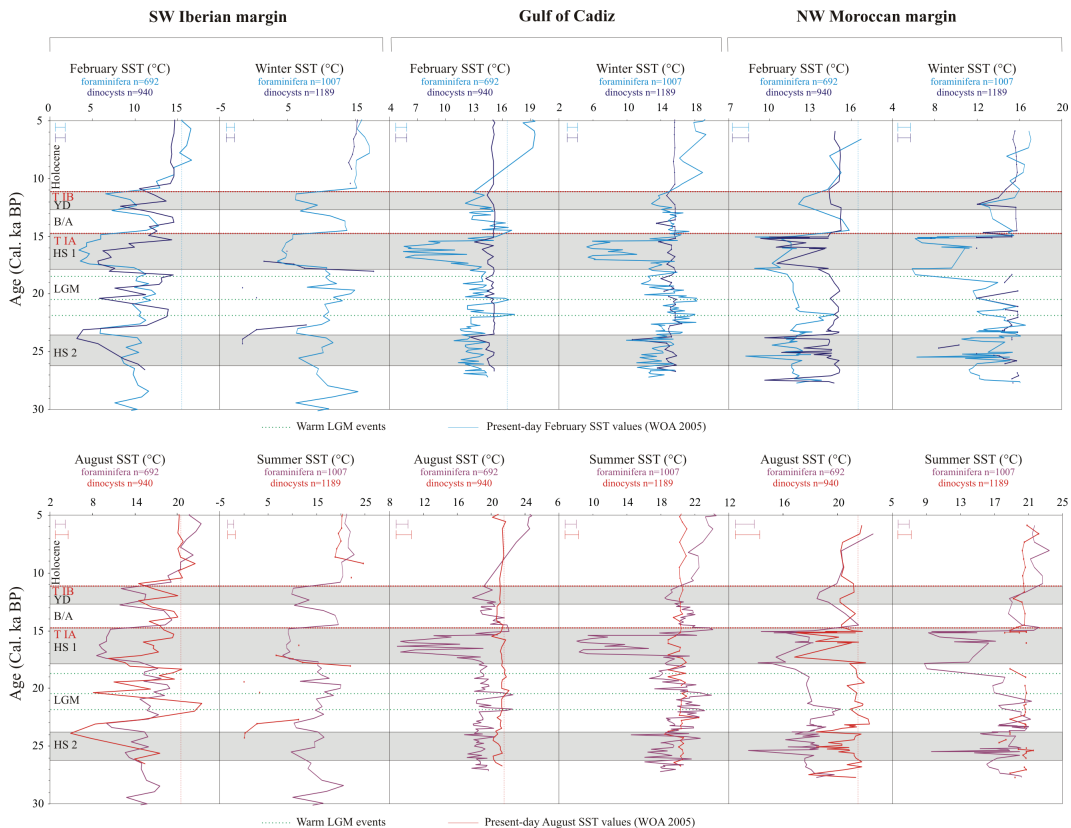


Fig. 5. Comparison of foraminiferal versus dinocyst SST reconstructions: February and August (PaleoToolBox-692-foraminifera vs. 3PBase-940-dinocysts), winter and summer (R-1007-foraminifera vs. R-1189-dinocysts). Error bars are shown for the different reconstructions. YD: Younger Dryas; B/A: Bölling-Allerød; HS: Heinrich Stadial; LGM: Last Glacial Maximum; T1: Termination 1.

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Dinocysts versus foraminifera versus alkenones

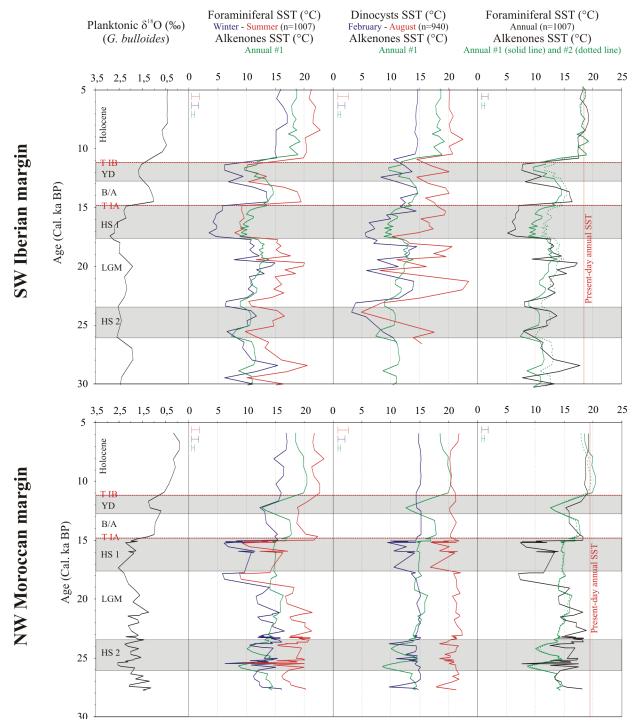


Fig. 6. SW Iberian Margin (MD95-2042) and NW Moroccan Margin (MD04-2805 CQ). Dinocyst SST reconstructions (February and August, 3PBBase-940) and foraminiferal SST reconstructions (winter, summer and annual, R-1007) are compared with SST provided by alkenones (U_{37}^k -SST). Two different calibrations have been used to convert the C_{37} alkenone unsaturation data in terms of SST: #1 corresponds to Weaver et al. (1999) and #2 corresponds to Prah et al. (1988). Error bars are shown in the figure for the different reconstructions. YD: Younger Dryas; B/A: Bölling-Allerød; HS: Heinrich Stadial; LGM: Last Glacial Maximum; TI: Termination 1.

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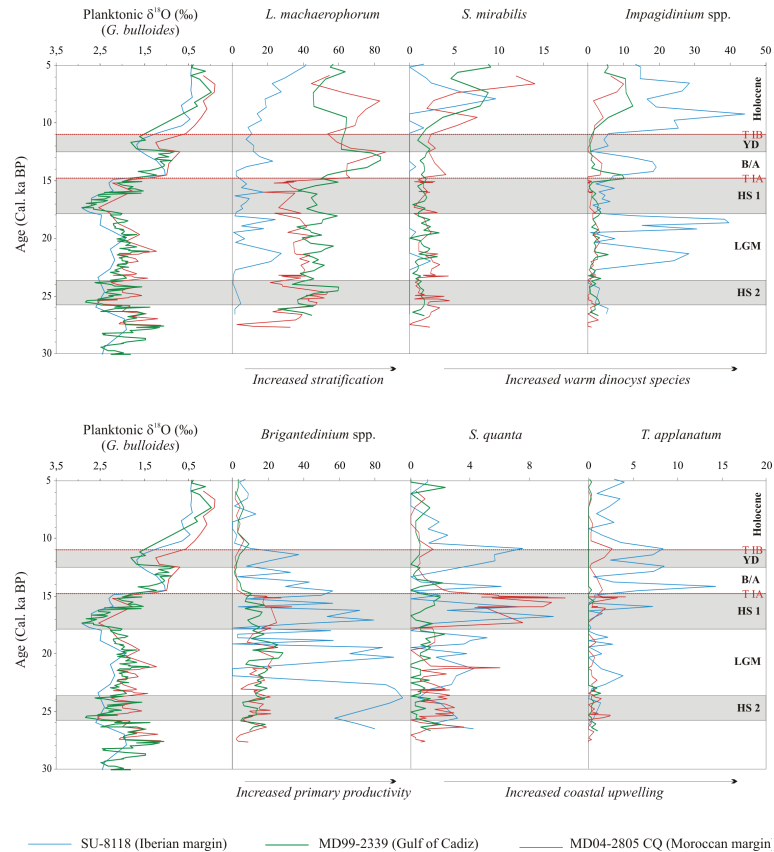


Fig. 7. Comparison of the relative abundances of selected dinocyst species on the three study cores covering the last 30 000 yr. The color code is mentioned in the figure for each core. The planktonic $\delta^{18}\text{O}$ records provide the stratigraphic framework for the three sedimentary sequences.

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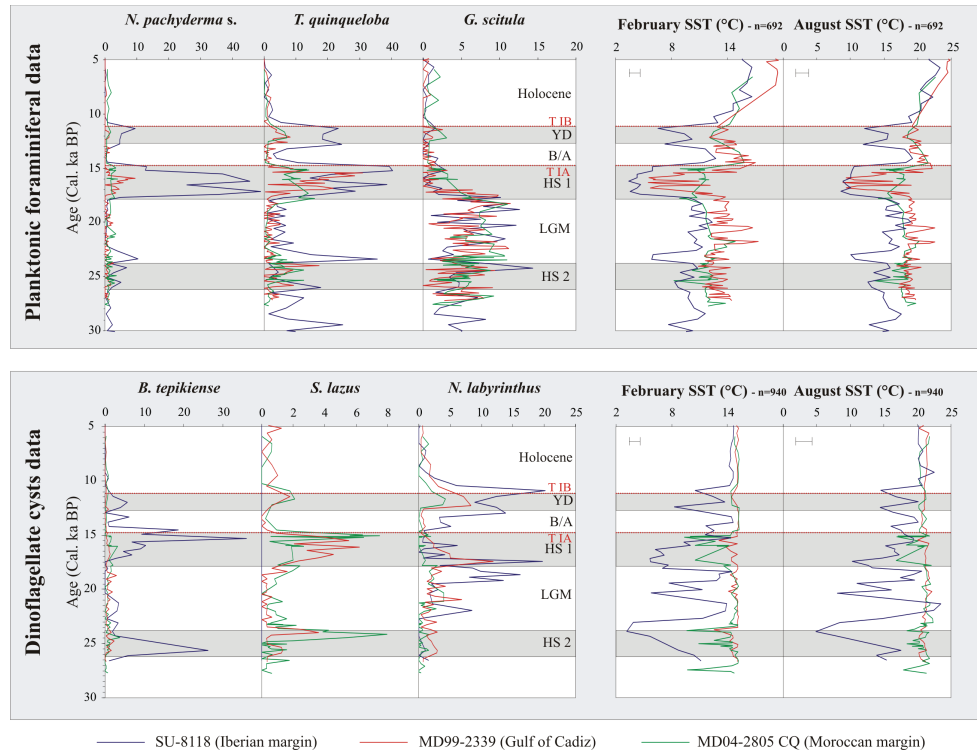


Fig. 8. On each graph, relative abundances of selected planktonic foraminiferal and dinocyst species are depicted for the three cores with the same percentage scales. These data allow materializing the hydrological front in the NE subtropical Atlantic over the last 30 ka. The color code is noted on the figure. Reconstructions of February and August SST with dinocysts and foraminifera are also shown in the figure with error bars.

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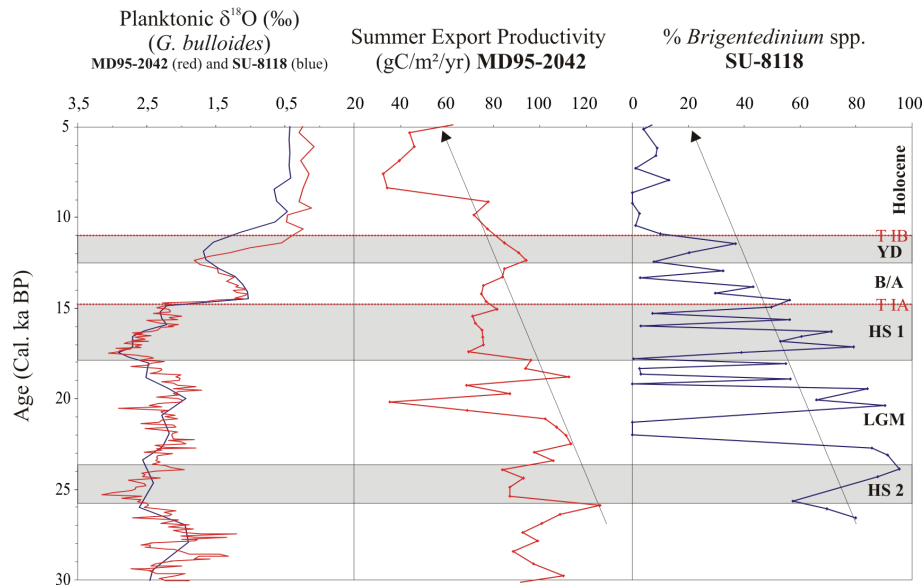


Fig. 9. Summer export productivity estimated for core MD95-2042 (Salgueiro et al., 2010) vs. relative abundances of *Brigantedinium* spp. obtained in core SU-8118 (Turon et al., 2003). The planktonic $\delta^{18}\text{O}$ records provide the stratigraphic framework for the two sedimentary sequences.