



Palaeohydrological changes over the last 50 ky in the central Gulf of Cadiz: complex forcing mechanisms mixing multi-scale processes

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Abstract. New dinoflagellate cyst (dinocyst) analyses were carried out at high resolution in core MD99-2339, retrieved from a contouritic field in the central part of the Gulf of Cadiz, for the Marine Isotope Stage (MIS) 3 interval, allowing for discussion of palaeohydrological changes over the last 50 ky in the subtropical NE Atlantic Ocean. Some index dinocyst taxa, according to their (palaeo)ecological significance, shed light on significant sea-surface changes. Superimposed on the general decreasing pattern of dinocyst export to the seafloor over the last 50 ky, paralleling the general context of decreasing aeolian dust fertilization, a complex variability in dinocyst assemblages was detected at the millennial timescale. Enhanced fluvial discharges occurred during Greenland Interstadials (GIs), especially GI 1, 8 and 12, while enhanced upwelling cell dynamics were suggested during the Last Glacial Maximum and Heinrich Stadials. Finally, during the early Holocene, and more specifically during the Sapropel 1 interval (around 7–9 ka BP), we evidenced a strong decrease in dinocyst fluxes, which occurred synchronously to a strong reduction in Mediterranean Outflow Water strength and which we attributed to an advection of warm and nutrient-poor subtropical North Atlantic Central Waters. Over the last 50 ky, our study thus allows for capturing and documenting the fine tuning existing between terrestrial and marine realms in North Atlantic subtropical latitudes, in response to not only the regional climate pattern but also monsoonal forcing interfering during precession-driven Northern Hemisphere insolation maxima. This mechanism, well expressed during the Holocene, is superimposed on the

pervasive role of the obliquity as a first major trigger for explaining migration of dinocyst productive centres in the NE Atlantic margin to the subtropical (temperate) latitudes during glacial (interglacial) periods.

1 Introduction

Marginal and semi-enclosed seas, continental shelves, and especially upwelling cells or river mouths are marine regions characterized by high primary productivity conditions. They play an important role as a carbon sink and thus significantly contribute to CO₂ storage. In this context, the North Atlantic is the major contributor to atmospheric CO₂ sequestration (Sabine et al., 2004; Takahashi et al., 2009), especially in high latitudes, even if uncertainties remain in the calculated amount stored by coastal regions (e.g. Flecha et al., 2012). Disregarding abiotic processes, CO₂ storage evolution is itself substantially governed by continental and marine primary producers through biological carbon fixing, export and fossilization. The majority of ocean primary production comes from micro-phytoplanktonic organisms (mostly diatoms, coccolithophores and dinoflagellates; Falkowski and Raven, 1997), mainly in coastal upwelling systems and in temperate and subpolar regions, with these micro-organisms being extremely sensitive to climate changes at seasonal and interannual timescales. In this study, we targeted a major component of the modern phytoplanktonic biomass, the dinoflagellate group. About 15 % of living dinoflagellate

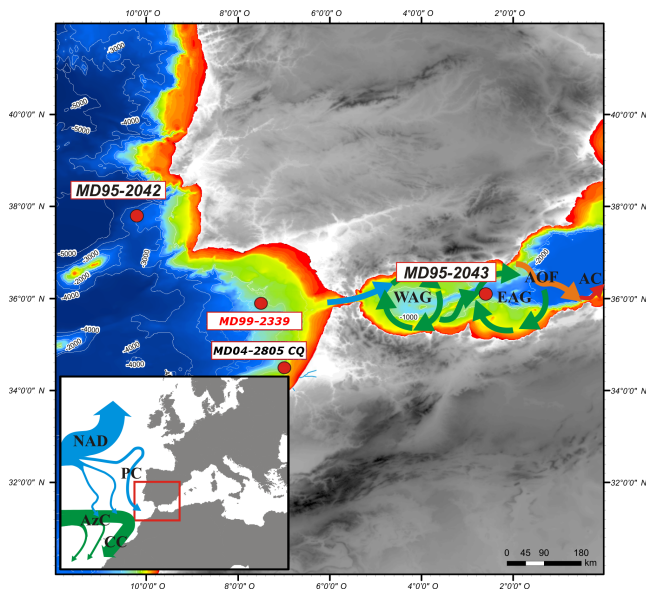


Figure 1. Area of interest with major sea-surface features. Study core MD99-2339, as well as other cores discussed in the paper, is located on the large map, which also depicts the bathymetry of the study area and the major surface currents within the Alboran Sea. WAG: Western Alboran Gyre; EAG: Eastern Alboran Gyre; AOF: Almeria–Oran Front; AC: Algerian Current. The small map on the left presents large-scale North Atlantic currents, with the North Atlantic Drift (NAD), the Portugal Current (PC) flowing southward from 45 to 30° N, the Azores Current (AzC) derived from the southern branch of the Gulf Stream and flowing eastward to the Gulf of Cadiz at about 35° N, and the Canary Current (CC) fed by both the AzC and the PC. Together, these currents form the Eastern Boundary Current of the North Atlantic subtropical gyre.

species form highly resistant resting cysts (dinocysts) after sexual reproduction (Dodge and Harland, 1991; Head, 1996; Dale, 1996) whose modern distribution is tightly coupled to sea-surface physico-chemical characteristics (nutrient availability, temperature, sea-ice cover duration, salinity or light penetration; Rochon et al., 1999; Marret and Zonneveld, 2003; de Vernal et al., 2001, 2005; de Vernal and Marret, 2007; Zonneveld et al., 2013). Dinocysts recorded in marine sediments thus enable qualitative as well as quantitative discussion of past surface environments, with their preservation being furthermore high in comparison to other fossilisable planktonic groups suffering from dissolution issues of authigenic silica and carbonates (e.g. de Leeuw et al., 2006).

The central Gulf of Cadiz is a place of low present-day marine productivity, with a moderate ability to store CO₂ and CH₄ (e.g. Huertas et al., 2006, 2009; Flecha et al., 2012). However, this might not have been the case in the past due to the potential migration of proximal productive centres (e.g. Portugal and Moroccan upwelling centres) at long-term orbital timescales (glacial–interglacial cycles) as well as at millennial sub-orbital ones (i.e. the well-known

Greenland Interstadial (GI)–Greenland Stadial (GS) cycles; Dansgaard et al., 1993; Grootes et al., 1993). In fact, it has been demonstrated that productivity changes in this region involve complex hydrographical dynamics, including upwelling (Abrantes, 1991, 1992) and river inputs, and are also probably additionally forced by Mediterranean–Atlantic exchanges (Rogerson et al., 2012; Ivanovic et al., 2013). Our study aims to explore how these changes may have impacted dinoflagellates, here viewed as an index planktonic group, so as to understand complex patterns and couplings of palaeo-hydrological and palaeo-productivity changes over the last 50 ky in the subtropical NE Atlantic. Large environmental shifts which have characterized the studied period are known to be well expressed and preserved in the Gulf of Cadiz sedimentological archives (e.g. Sierro et al., 2005; Voelker et al., 2006, 2015; Toucanne et al., 2007; Peliz et al., 2009; Rogerson et al., 2010, 2012; Bahr et al., 2014, 2015; Hernandez-Molina et al., 2014), thus providing an ideal case study for our purposes. Different configurations of Mediterranean–Atlantic exchanges were also taken into account regarding their potential impacts on MD99-2339 dinocyst surface proxies. For this paper, we focus on the palaeohydrographical response of the Gulf of Cadiz during Marine Isotope Stage (MIS) 3 to extend previous studies that extensively documented the last glacial–interglacial transition (e.g. Rogerson et al., 2004; Turon et al., 2003; Penaud et al., 2010). We also consider the Northern Hemisphere palaeoclimatological changes within a broader subtropical climate context, including the Mediterranean Basin (Bahr et al., 2015).

2 Surface and deep hydrography of the Gulf of Cadiz

The study area is located on the eastern part of the North Atlantic’s subtropical gyre, directly adjacent to the Strait of Gibraltar (< 14 km width, < 300 m depth), the latter of which channelling water-mass exchanges between Atlantic waters at the surface and saltier/denser Mediterranean Outflow Waters (MOW) at depth. This area thus couples the convergence of critical water masses regarding the Atlantic Meridional Overturning Circulation (AMOC) with a semi-permanent upwelling regime, itself connected to the larger dynamic cells off NW Africa.

More specifically, sea-surface waters from the Gulf of Cadiz are influenced by several currents, including the Portuguese and Moroccan coastal currents, a branch of the Azores Current (AzC; Fig. 1) flowing eastward at 35° N (Peliz et al., 2009), and the MOW, which feeds the Canary Current (CC; Fig. 1) to the south and also contributes to the generation of the AzC. In the open ocean only, the AzC coincides with the Azores Front (AF), forming a strong hydrographical barrier at the northeastern boundary of the Atlantic subtropical gyre marked in terms of both temperature gradients (about 4 °C; Gould, 1985) and the vertical structure of the water column (Fasham et al., 1985). This front is locally

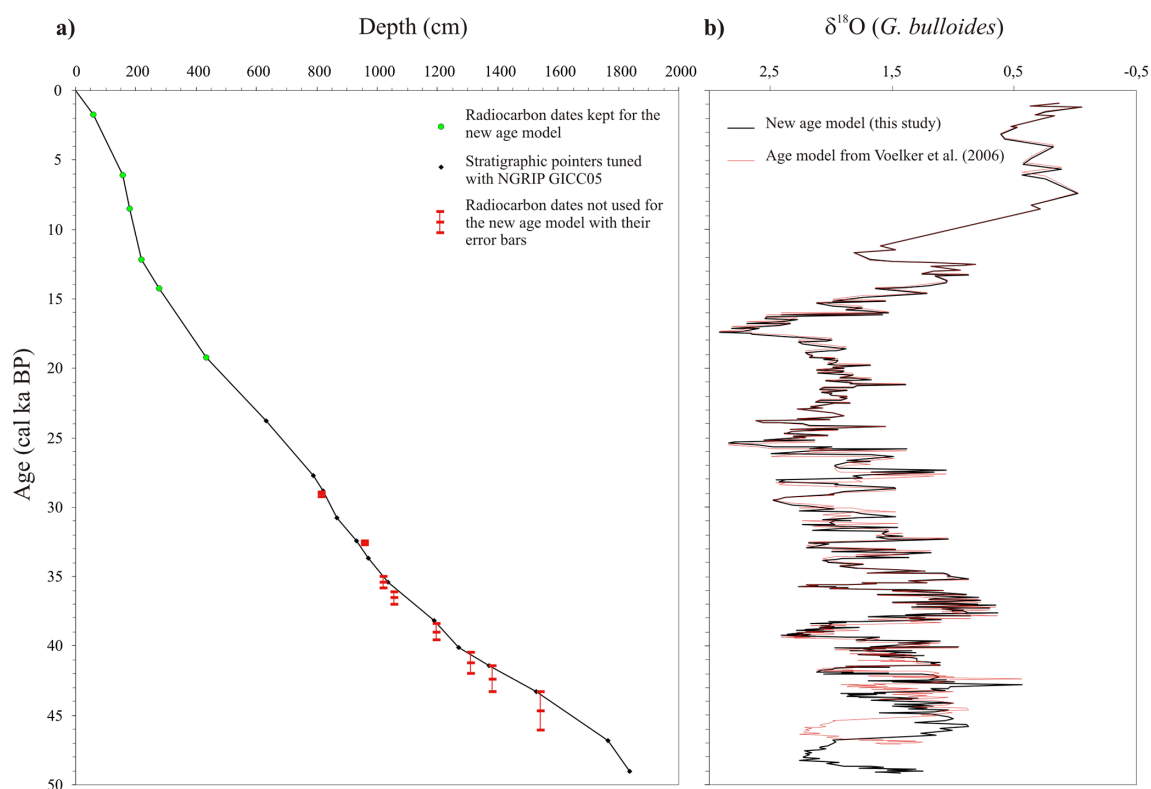


Figure 2. (a) Age–depth model for core MD99-2339 (all symbols are explained in the figure), allowing for comparison of (b) the new age model (this study: planktonic $\delta^{18}\text{O}$ monospecific record in black) with the first published one (Voelker et al., 2006: planktonic $\delta^{18}\text{O}$ record in red).

characterized by intense upwelling cells and thus higher sea-surface productivity (Rudnick, 1996; Alves and de Verdière, 1999; Alves et al., 2002). At present, the AF does not penetrate into the Gulf of Cadiz, where the upper 50 m sea-surface waters are generally depleted in nutrients (Navarro and Ruiz, 2006). The Gulf of Cadiz is thus today moderately responsible for CO_2 storage (e.g. Huertas et al., 2006, 2009; Flecha et al., 2012), and this oligotrophic regime is mainly due to surface inflow of relatively nutrient-depleted Atlantic water, while nutrient-richer conditions are found at depth as remnant Antarctic Intermediate Waters (Cabeçadas et al., 2002, 2003).

On the northeastern shelf of the Gulf of Cadiz, it has been demonstrated that present-day river discharges (freshwater inputs from large rivers such as the Guadiana, Tinto–Odiel and especially the Guadalquivir on the southern Iberian margin), in combination with meteorological conditions (incident irradiance, strong winds), strongly impact phytoplankton biomass (Huertas et al., 2006). More specifically, turbidity-plume and chlorophyll-concentration dynamics shed light on enhanced primary productivity conditions related to fluvial discharges occurring during rainy seasons, and especially during negative modes of the North Atlantic Oscillation (NAO; Caballero et al., 2014). The central Gulf of Cadiz is, conversely, rather subject to fluvial influ-

ences from NW Moroccan rivers (especially from the Sebou River and additional northern African small distributaries) for which plumes spread over a large coastal area (Warrick and Fong, 2004). Additionally, the wind pattern is highly significant for sea-surface biological processes within the Gulf of Cadiz (Navarro and Ruiz, 2006): the wind-related mixing phenomenon cumulates with the wind-driven coastal upwelling regime, active mainly from late May/early June to late September/early October in the Portugal–Canary system (e.g. Haynes et al., 1993; Aristegui et al., 2005; Peliz et al., 2005). This seasonal upwelling functioning is itself dependent on seasonal migrations of the Azores High coupled to the Intertropical Convergence Zone dynamics (Hsu and Wallace, 1976). Over the last 30 ky, evidence of extremely close palaeohydrological patterns between the central Gulf of Cadiz and the NW Moroccan margin supports the idea of similar forcing acting on both of these subtropical areas of the NE Atlantic margin (Penaud et al., 2011a).

Water masses from our study area are structured as follows: Surface Atlantic Waters, between the surface and 100 m water depth, overlay North Atlantic Central Waters, found between 100 and 700 m. Deep MOW are divided into two main branches centred at around 800 and 1200 m water depths, as well as at 500 m in the continental shelf (Ambar

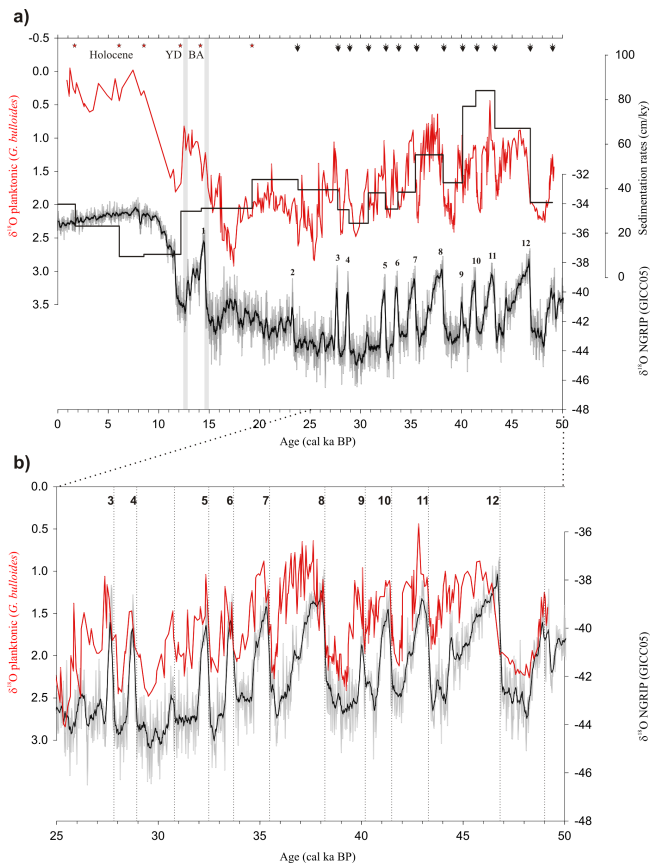


Figure 3. Comparison, against age (new age model from this study), between the planktonic $\delta^{18}\text{O}$ monospecific record of core MD99-2339 (red curve; Voelker et al., 2006) and the NGRIP $\delta^{18}\text{O}$ according to the GICC05 timescale (Svensson et al., 2008). (a) Red stars show the six radiocarbon dates retained for the chronology of core MD99-2339, and dark arrows show the 13 pointers used to tune the $\delta^{18}\text{O}$ data of core MD99-2339 to the NGRIP chronology, by considering GI onsets for core MD99-2339 (numbers 1 to 12 in the figure) according to GI onset chronology established in Wolff et al., (2010). Sedimentation rates, calculated between different pointers of core MD99-2339, are also highlighted by the dark histogram. YD: Younger Dryas; BA: Bölling–Alleröd. (b) A close-up of the 25–50 ka BP interval allows for better consideration of the pointers selected (dotted vertical lines) for this new age model.

and Howe, 1979; Ambar et al., 2002). North Atlantic Deep Waters are found below 1500 m (Alvarez et al., 2005).

3 Material and methodology

3.1 Marine cores integrated within the study: chronostratigraphy

Core MD99-2339 (35.89° N, 7.53° W; 1170 m water depth; 18.54 m length; Fig. 1) was recovered from a contouritic field (Habgood et al., 2003) by the R/V *Marion Dufresne* during the 1999 International Marine Global Change Studies V (IM-

AGES V-GINNA) cruise (Labeyrie et al., 2003). It covers the last 45 ky according to its published age model (Voelker et al., 2006), which is based on 20 AMS ^{14}C dates and three $\delta^{18}\text{O}$ control points tuned to the GISP2 chronology (Grootes and Stuiver, 1997).

In this study, the stratigraphical framework of core MD99-2339 was re-considered for its older part, where radiocarbon dates exhibited large error bars (between 200 years around 900 cm and 1400 years at 1500 cm; Voelker et al., 2006; Fig. 2) and inconsistencies with the regional North Atlantic stratotype NGRIP GICC05 timescale (Svensson et al., 2008; Austin and Hibbert, 2012; Austin et al., 2012; Rasmussen et al., 2014). This revision was furthermore motivated by the comparison of this new dinocyst MIS 3 record to that of core MD95-2043 (Alboran Sea; 36.14° N, 2.62° W; 1841 m water depth; 36 m length; Penaud et al., 2011b; Fig. 1). Such an approach is validated by previous works conducted on the southern Iberian margin, where the stratigraphy of palaeoclimatological reference sites was constructed using a similar tuning to Greenland ice records (e.g. Shackleton et al., 2000; Bard et al., 2004). However, this event-based stratigraphy (i.e., Austin and Hibbert, 2012) prevents any definitive conclusion about latitudinal leads and lags from being established, as well as any evaluation of intra-hemispheric propagation velocities of climatic perturbations. To build the revised age–depth model (Fig. 2), we chose to keep six radiocarbon dates (Voelker et al., 2006; Figs. 2 and 3) younger than 20 ka BP (until around 600–700 cm; mean errors of 60 years) that we calibrated to calendar years with the CALIB 7.1 program using the Marine13 calibration data (Stuiver and Reimer, 1993; Reimer et al., 2013). Below 700 cm, we tuned the planktonic monospecific $\delta^{18}\text{O}$ record (*G. bulloides*) of core MD99-2339 (13 pointers; Figs. 2 and 3) to the NGRIP ice-core GICC05 chronology, considering synchronous sea-surface warmings in the Gulf of Cadiz with the onsets of GI 3 to 12, respectively (Wolff et al., 2010). As a result, Heinrich Stadial (HS; Barker et al., 2009; Sánchez-Goñi and Harrison, 2010) 5 (HS 5) is dated around 48 ka BP in our revised age model rather than 45–46 ka BP (Voelker et al., 2006; Fig. 2). Sedimentation rates show a general decreasing trend from 60–90 cm ky^{-1} around 40–45 ka BP to 10–40 cm ky^{-1} across the Holocene (Fig. 3).

3.2 Dinoflagellate cyst analysis

3.2.1 Laboratory procedure and microscopic observation

A total of 161 samples were analysed for their dinocyst content every 10 cm on average, representing a sample resolution of around 300 years ($\sigma = 210$) for the whole of core MD99-2339, using an Olympus BX50 microscope at 400× magnification (75 slides from 0 to 740 cm/0 to 27 ka BP; Penaud et al., 2011a; 86 slides from 750 to 1844 cm/27 to 49 ka BP: this study). The preparation technique followed the

Table 1. Modern distribution versus past occurrences (MD99-2339 record) for selected major dinocyst species found in the fossil assemblage (see Fig. 5).

Dinocyst species	Present-day ecology	Occurrence in core MD99-2339 (Fig. 5) and palaeo-ecological interpretation
<i>Lingulodinium machaerophorum</i> (opportunistic/temperate)	Temperate to tropical euryhaline species, often found in stratified waters (fjords, bays, estuaries; e.g. Dale et al., 1999), and interpreted as a proxy for fluvial discharges to the ocean (Zaragosi et al., 2001; Gonzales et al., 2008; Mertens et al., 2009; Holzwarth et al., 2010; Penaud et al., 2011b). Modern centres of distribution located along the Atlantic Eastern Boundary Current with a maximum representation observed at the Strait of Gibraltar outlet (Marret and Zonneveld, 2003) and close to river mouths in general (Mertens et al., 2009).	Observed all along the record with maximal percentages identified during GI 12, GI 8, GI 1 and the late Holocene. Interpreted as a strong signal for run-off and fluvial-related nutrients, as well as strong surface stratification in the Gulf of Cadiz during these intervals.
<i>Operculodinium centrocarpum</i> (opportunistic/temperate)	Cosmopolitan, cold to temperate (low percentages in tropics) species that has often been linked to nutrient-enriched waters and waters such as the North Atlantic Drift (Wall et al., 1977; Harland, 1983), through its distribution in the modern dinocyst database (Rochon et al., 1999), but also regarding its past temporal occurrences in North Atlantic sediments (Turon, 1984; Eynaud et al., 2004; Penaud et al., 2008).	Pattern close to that of <i>S. mirabilis</i> . Potential witness of increased Atlantic surface water inflow into the Gulf of Cadiz. Interestingly, the couple <i>S. mirabilis</i> – <i>O. centrocarpum</i> is succeeded by <i>Impagidinium</i> species twice during MIS 1 warmer intervals, with a clear bipartite structure evidenced during the BA as well as during the Holocene.
<i>Impagidinium</i> spp. (<i>I. patulum</i> , <i>I. aculeatum</i> , <i>I. paradoxum</i> , <i>I. sphaericum</i> , <i>I. striolatum</i>) (warm group)	Temperate to tropical full-oceanic species (except <i>I. pallidum</i>) typically characteristic of tropical/subtropical (20 to 35° N) oligotrophic environments (Wall et al., 1977; Turon, 1984; Marret and Zonneveld, 2003; Bouimetarhan et al., 2009) without large inter-seasonal fluctuations in SST/SSS (Vink et al., 2000). Highest abundances found in regions with SST above 20–25 °C (winter-summer SST; summer SST above 15 °C) and SSS around 35–36.	Strong increases during MIS 1 and especially at the start of GI 1 and during the early Holocene. Interpreted as an imprint for the installation of warm oligotrophic conditions in the Gulf of Cadiz through warm and nutrient-poor advection of subtropical North Atlantic Central Water through the Azores Current.
<i>Spiniferites mirabilis</i> (warm group)	Characterizes temperate to tropical environments and extends as far south as 10° N, with high abundances found today along the European margin in the Bay of Biscay (Rochon et al., 1999). Not observed from sites with summer SST below 12 °C and found in fully marine environments characterized by SSS above 28.5 (Marret and Zonneveld, 2003).	Significant increases during MIS 3 GI and BA, as well as highest values recorded during the Holocene.
<i>Spiniferites delicatus</i> <i>Spiniferites bentorii</i> (warm group)	A relatively high number of <i>Spiniferites</i> species, including <i>S. delicatus</i> and <i>S. membranaceus</i> (as well as <i>O. israelianum</i>), characterize the equatorial zone, also often found at the vicinity of upwelling cells (Marret and Zonneveld, 2003). <i>S. delicatus</i> highest relative abundances are observed at sites with SST exceeding 25 °C throughout the year, and forms a prominent part of associations in regions with SSS exceeding 31, as well as above 34 (Marret and Zonneveld, 2003).	Occurs especially during MIS 3, with significant drops related to all HS, alternating with <i>L. machaerophorum</i> higher percentages, and attesting to the warm/productive character of the subtropical study area during MIS 3 GI.
<i>Operculodinium israelianum</i> (warm group)	Temperate to tropical (SST above 24 °C) species characterizing fully marine sites as well as coastal waters (Wall et al., 1977; Harland, 1983), and tolerating a broad range of nutrient concentrations (Marret and Zonneveld et al., 2003). Can be related to a typical signal of high-salinity environments (Morzadec-Kerfourn et al., 1990; Marret and Zonneveld, 2003).	Typical signature found during the LGM, with, however, weak percentages, suggesting the relatively warm/saline character of the study area during MIS 2, especially between 16 and 24 ka BP.
<i>Nematosphaeropsis labyrinthus</i> (cold group)	Cosmopolitan species able to tolerate a wide variety of environments (Marret and Zonneveld, 2003), including areas where up to 12 months of sea-ice cover prevail (de Vernal et al., 2001). Also considered a typical open-ocean species and predominantly found in cold to cool waters between 45 and 65° N in the North Atlantic Ocean (cf. Rochon et al., 1999), and recorded today with maximum abundances around the British Isles and in the NW Atlantic. Possibly related to nutrient-enriched waters (Devillers and de Vernal, 2000).	Typical signature, being mainly related to cold GS, such as HS1 or the YD, but also occurs during some GIs recorded between HS4 and HS 5. This species would suggest cool/eutrophic conditions.
<i>Spiniferites elongatus</i> /cysts of <i>Pentaparsodinium dalei</i> (cold group)	Both taxa have their highest relative abundances in temperate to cold regions and decreasing percentages of these species along the Northern Hemisphere subtropical front, constituting a “physical” barrier for these taxa, today typically reflecting the transition from temperate to subtropical waters (Marret and Zonneveld, 2003)	Across HS4, strongest percentages of cysts of <i>P. dalei</i> attest to important coolings.
<i>Spiniferites lazus</i> (cold group)	Restricted to fully marine, coastal regions of western Europe (with low occurrences) and distributed within a broad range of temperature and nutrient concentrations, in areas with SSS exceeding 30. Arctic to temperate, inner to outer neritic species (Harland, 1983), not recorded from sites where SSS is reduced (e.g. Wall and Dale, 1973; McMinn, 1991; de Vernal et al., 1994; Nehring, 1994; Ellegaard, 2000; Persson et al., 2000).	MIS 3 to MIS 2 transition marks a strong shift from the earlier HS characterized by the association of cyst of <i>P. dalei</i> – <i>B. tepikiense</i> (HS5–HS4–HS3) to younger HS characterized by the association <i>S. elongatus</i> – <i>S. lazus</i> (HS 2 and HS1).
<i>Bitectatodinium tepikiense</i> (cold group)	Characterizes strong thermal, seasonal contrasts with freezing winter SST and enhanced surface water stratification (Sánchez-Goni et al., 2000; Turon et al., 2003; Combourieu-Nebout et al., 2002; Penaud et al., 2011a, b).	Across HS5, HS 4 and then HS3, decreasing percentages of <i>B. tepikiense</i> , in parallel with decreasing <i>L. machaerophorum</i> , may confirm a decreasing stratification trend through time over each HS.
<i>Brigantedinium</i> spp. (heterotrophic)	Cosmopolitan species that can dominate cyst associations from coastal to oceanic sediments of the North Atlantic, the western equatorial Atlantic, and the coastal upwelling along the western African margin. Found within a broad range of temperatures, salinities and nutrient concentrations (Marret and Zonneveld, 2003). However, in this group distribution of the heterotrophic species seems largely controlled by their food requirements and some authors suggest a relationship with high surface productivity (e.g. Lewis et al., 1990; Dale and Fjellsafi, 1994; Marret, 1994; Biebow, 1996; Targarona et al., 1999; Zonneveld et al., 2001).	Especially found with maximal percentages during the LGM, but also during HS4. Across the LGM, <i>Brigantedinium</i> has been previously related to the presence of a front within the Gulf of Cadiz at that time, probably similar to the modern Azores Front, which may have enhanced primary productivity through frontal upwelling cells (Rogerson et al., 2004, 2010; Penaud et al., 2011a). A strong seasonal pattern during HS4 would also be confirmed by the significant occurrence of <i>B. tepikiense</i> , while cysts of <i>P. dalei</i> attest to extremely cold SST during this interval (cf. also Patton et al., 2011).
<i>Selenopemphix nephroides</i> / <i>Selenopemphix quanta</i> / <i>Trinovantedinium applanatum</i> (coastal heterotrophics)	Even if distributed within a broad range of temperature, salinity, or nutrient concentration, these characterize estuarine to neritic environments (Harland, 1983) and are often found in western African upwelling and the equatorial margin (Dodge and Harland, 1991; Wall et al., 1977). Highest occurrences of <i>S. nephroides</i> , a temperate to tropical and fully marine species, characterize mesotrophic/eutrophic coastal environments (Marret and Zonneveld, 2003).	Grouped as “coastal heterotrophic species” in this study. Especially found during GI–GS cycles of MIS 3, and strongly decrease after 30 ka BP, although slightly rising again during the Late Holocene. Contrary to <i>Brigantedinium</i> , these species (especially <i>S. nephroides</i>) are absent during HS in the Gulf of Cadiz.

protocol described by de Vernal et al. (1999) and Rochon et al. (1999), slightly modified at the EPOC laboratory (Castera and Turon, http://www.epoc.u-bordeaux.fr/index.php?lang=fr&page=eq_paleo_pollens), including chemical treatments (cold HCl: 10, 25 and 50 %; cold HF: 45 and 70 %) and sieving through single-use 10 μm nylon mesh screens. The final residue was then mounted between slide and coverslip with glycerine jelly coloured with fuchsin.

For each analysed sample, a minimum of 300 dinocyst specimens were systematically identified following the taxonomy in Fensome and Williams (2004) and Fensome et al. (2008). High occurrences of the species *Lingulodinium machaerophorum* (nearly monospecific in some cases but typical for the area today) forced us to additionally count 100 dinocysts outside this species for each palynological slide in order to obtain statistically robust dinocyst results (Fatela and Taborada, 2002). Dinocysts can be expressed in percentages and also in concentrations (number of specimens per cubic centimetre of dry sediments), which are calculated through the marker grain method (Stockmarr, 1971; de Vernal et al., 1999; Mertens et al., 2009). This consists in adding aliquot volumes of *Lycopodium* spores before the palynological treatment in each sample, with these exotic spores being counted in parallel with fossil palynomorphs. One can argue that there might be a relationship between concentrations and granulometry (increasing/decreasing concentrations vs. increasing clays–fine silts/coarser silts–fine sands; Wall et al., 1977), especially in a contouritic environment. However, it is important to note that only fine silts have been sampled for palynological analysis. Furthermore, given that cyst concentrations are the combined results of sedimentation rates, grain size and productivity, we also calculated flux rates (number of cysts $\text{cm}^{-2} \text{ky}^{-1}$). We do not have enough time marker points to calculate flux rates for every single short event separately, but, at least on a multi-millennial timescale, dinocyst fluxes may provide a better insight into dinocyst export to the seafloor, and perhaps also indirectly into dinoflagellate productivity in surface waters.

3.2.2 Dinocyst indexes and statistical treatments of dinocyst results

Warm/cold ratio

The present-day ecology of many of the recovered species is well known from their surface sediment distribution in the North Atlantic (e.g. Turon, 1984; Rochon et al., 1999). Furthermore, latitudinal (SST changes) and inshore–offshore (eutrophic–oligotrophic conditions) gradients are mainly responsible for dinocyst distribution in modern sediments (Marret and Zonneveld, 2003; Zonneveld et al., 2013). A qualitative thermic index, “warm/cold” (W/C), which has previously been used to qualitatively address SST variations (Turon and Londeix, 1988; Versteegh, 1994; Combourieu-

Nebout et al., 1999; Eynaud et al., 2016), was calculated for core MD99-2339 (cf. Table 1).

Heterotrophic/autotrophic ratio

Most dinoflagellate species are mixotrophic, and strict autotrophic dinoflagellates (phototrophic organisms) are rare. However, previous investigations have discussed heterotrophic cysts, i.e. derived from dinoflagellates with a strict heterotrophic strategy of nutrition, as being indirectly related to food resources, and especially diatoms, as has commonly been shown in upwelling areas (Wall et al., 1977; Lewis et al., 1990; Marret, 1994; Biebow, 1996; Zonneveld et al., 1997a, 2001; Targarona et al., 1999; Bouimtarhan et al., 2009; Penaud et al., 2011a). This is especially true for *Protoperidinium* species, including *Brigantedinium* and *Selenopemphix* species, thus indirectly signing periods of higher surface water productivity. In the following sections of the paper, we will refer these taxa as “heterotrophics”, with “coastal heterotrophics” being more specifically used for *Selenopemphix* species (*S. quanta* and *S. nephroides*; Table 1). A ratio of heterotrophics to autotrophics (H/A) can be also addressed that simply takes into account “strict” heterotrophic occurrences vs. the other dinocyst taxa identified in fossil assemblages.

Diversity statistics

Taxonomical diversity in study samples was quantified through a variety of statistical analyses using the “Past version 1.75b” software (Hammer et al., 2001); most of these indexes are explained in Harper (1999). Here, we calculated the number of taxa per sample (S); the dominance (D), which ranges from 0 (all taxa are equally present) to 1 (one taxon dominates the community completely); and Margalef’s richness index: $(S-1)/\ln(n)$, where n is the number of individuals counted in each sample.

Quantitative estimates of past sea-surface parameters

We used the modern analogue technique (MAT) based on the statistical distance between fossil (palaeoceanographic record) and current (modern database) assemblages (de Vernal et al., 2001, 2005; Guiot and de Vernal, 2007). The dinocyst transfer function used (Radi and de Vernal, 2008) is derived from a modern database comprising 67 dinocyst species and 1492 stations from the North Atlantic, Arctic and North Pacific oceans and their adjacent seas, and is run using R version 2.7.0 software (R Development Core Team, 2008; <http://www.r-project.org/>). The calculation of past hydrological parameters relies on a weighted average of the values obtained for a maximum of five best modern analogues for fossil assemblages, with the maximum weight being given for the closest analogue (i.e. minimal statistical distance, or “Dmin”). If Dmin reaches a maximal threshold value, the R software will consider no analogue, thus leading occasionally to non-analogue configurations. Here, we discuss win-

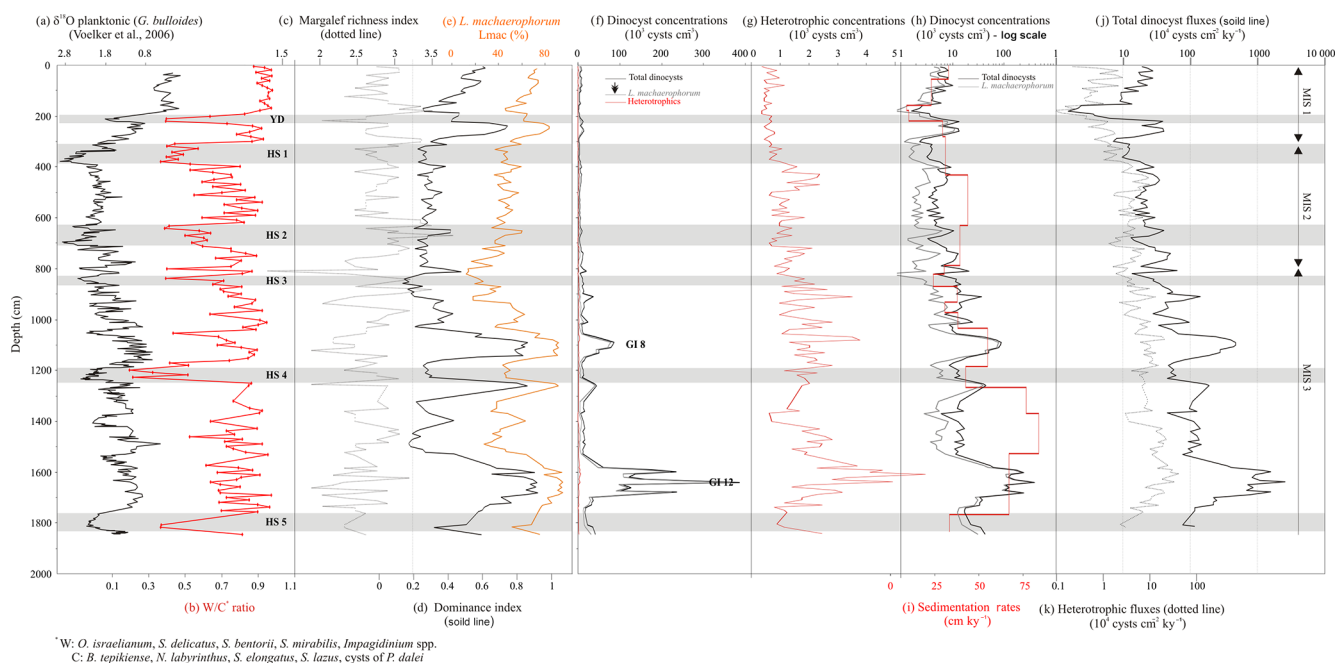


Figure 4. Data from core MD99-2339 compared to depth (cm). $\delta^{18}\text{O}$ planktonic monospecific record of core MD99-2339 (a; Voelker et al., 2006) is presented in parallel with the W/C qualitative index of surface temperatures (b). Diversity indexes (species richness according to the Margalef index, c, and dominance, d) are drawn in parallel with percentages of the major species *L. machaerophorum* (e). Different calculations of dinocyst concentrations (f, g) are represented on a linear scale, while (h) illustrates total dinocyst and *L. machaerophorum* concentrations on a logarithmic scale, compared with sedimentation rates (i) and dinocyst fluxes (j). GI: Greenland Interstadial. Grey bands indicate Heinrich Stadials (HS) and the Younger Dryas (YD).

ter/summer SST with prediction errors of $\pm 1.2^\circ\text{C}/\pm 1.6^\circ\text{C}$, respectively; winter/summer SSS, with prediction errors of $\pm 2.1^\circ\text{C}/\pm 2.3^\circ\text{C}$, respectively; and primary productivity reconstructions with prediction error of 57 g C m^{-2} .

4 Main dinocyst results across the last 50 ky in the Gulf of Cadiz

4.1 Dinocyst diversity, concentrations, and fluxes

A total of 40 taxa were identified, with an average diversity of 20 main species. Considering the whole dinocyst assemblage, increased total diversity (Fig. 4c) generally appears anti-correlated with decreased dominance (Fig. 4d); this index is essentially explained by *Lingulodinium machaerophorum* percentages through time (Fig. 4e) that oscillate between 30 and 90%. *L. machaerophorum* is commonly considered as a typical index species for stratified waters (Table 1; Zaragosi et al., 2001; Penaud et al., 2009; Holzwarth et al., 2010), thus probably indicating enhanced fluvial inflows. Since core MD99-2339 is located in the major flow path of the lower limb of the MOW, and in a position also corresponding to the major limb of the MOW during the LGM (Rogerson et al., 2011), one can speculate whether the palaeoceanographical record has been disturbed by MOW plume hydro-

dynamics or advection by sedimentological processes (i.e. downslope transport). A large increase in monospecific assemblages (when dominance is close to 1) will generally tend to reduce diversity and conversely (dominance close to 0 reflecting an equidistribution of different species when the diversity is maximum). Based on the obvious anti-correlation depicted in Fig. 4 (diversity vs. dominance), we argue for an autochthonous assemblage where species, and especially *L. machaerophorum*, reflect an in situ signal linked to changing sea-surface conditions.

Total dinocyst concentrations are generally low (less than $30\,000\text{ cysts cm}^{-3}$), with the exception of two large maxima, centred on GI 8 and GI 12, showing higher values (between $100\,000$ and $400\,000\text{ cysts cm}^{-3}$; Fig. 4f). A general trend of decreasing concentrations is then observed throughout the record with lower values observed during the early to mid-Holocene (between 1000 and $10\,000\text{ cysts cm}^{-3}$) and especially at the very start of the Holocene ($1500\text{ cysts cm}^{-3}$; at $150\text{--}200\text{ cm}$), following the cold interval of the Younger Dryas (YD; Fig. 4f). Also, minimum concentration values recorded during MIS 3 are comparable to maximum values recorded during the following MIS 2 and MIS 1. The general trend described above closely matches the one of the sedimentation rates (Fig. 4h) and thus also accounts for extremely high dinocyst fluxes to the seafloor during MIS 3 (Fig. 4j), compared to the last deglaciation and the Holocene.

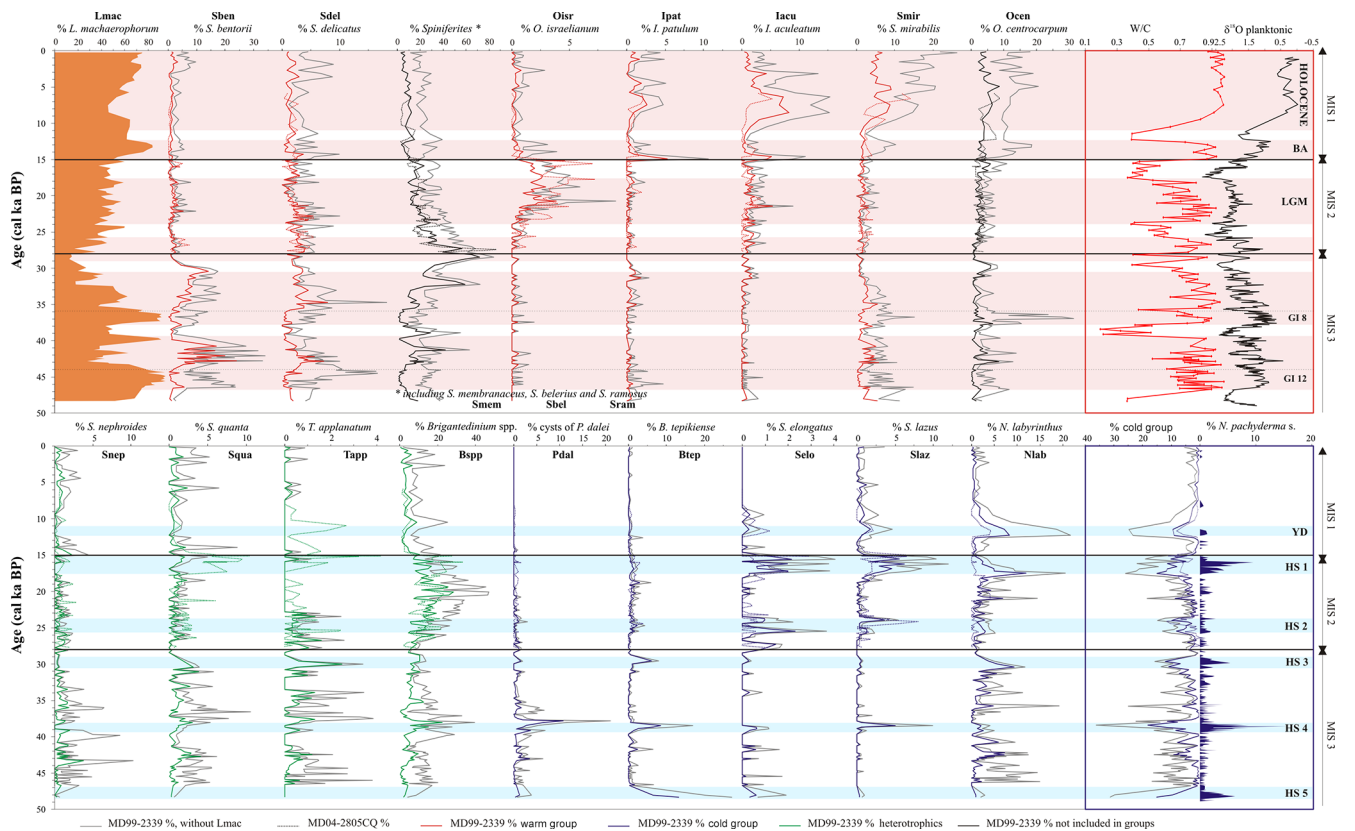


Figure 5. Data from core MD99-2339 against age (cal ka BP): major taxa occurring with values higher than 2% in dinocyst assemblages from core MD99-2339 (0–48 ka BP; 0–1854 cm). Red, blue and green respectively indicate the “warm”, “cold”, and “heterotrophic” groups. W/C: warm to cold ratio. The trends shown in grey are calculated by excluding *Lingulodinium machaerophorum* from the main dinocyst sum, while coloured curves (colours explained in the figure) depict the whole assemblage considering all species. MD04–2805 CQ dinocyst data are also represented over the 28 ka BP so as to illustrate similarities between the assemblages from the central (MD99-2339, this study) and southern (MD04-2805 CQ; Penaud et al., 2011a) Gulf of Cadiz. Pink bands indicate warmer intervals (including BA, Bölling–Alleröd; LGM, Last Glacial Maximum; and GI, Greenland Interstadial) and blue bands indicate colder events (HS, Heinrich Stadials; YD, Younger Dryas).

Total dinocyst concentrations are mainly explained by *L. machaerophorum* alone (Fig. 4h), showing the crucial role of this species regarding dinocyst export to the seafloor from the last glacial to present in this subtropical NE Atlantic area. While heterotrophics represent a minor component of total dinocyst concentrations all along the core (Fig. 4g), it is interesting to note that both heterotrophic and *L. machaerophorum* concentrations/fluxes reveal the same decreasing trend along the record (Fig. 4j). Previous studies have revealed contrasted patterns between brown heterotrophic and *L. machaerophorum* cysts. Their apparent conflict is discussed at long timescales on the southern Iberian margin area in Eyraud et al. (2000, 2016).

4.2 Dinocyst species reflecting qualitatively main palaeohydrological changes

Present-day ecologies of major species found in MD99-2339 assemblages are listed in Table 1 with their major past occur-

rences in the fossil record. The detailed examination of the qualitative thermic index “warm/cold” (W/C; Table 1; Fig. 5; cf. Sect. 3.2.2 of this paper), compared with the planktonic $\delta^{18}\text{O}$ curve (*G. bulloides*) of core MD99-2339 (Voelker et al., 2006), shows that millennial-scale climate variability related to the GS/GI cycles is clearly captured by our fossil record thus confirming the robustness of reconstructed surface environments through dinocyst assemblages in the central Gulf of Cadiz.

Specific percentages, calculated relative to the total dinocyst assemblages but also vs. a total that excludes *L. machaerophorum*, reveal that trends with or without *L. machaerophorum* are similar (Fig. 5). Peak occurrences are, however, better expressed when *L. machaerophorum* is omitted from the main palynological sum. Figure 5 furthermore includes the published data from core MD04-2805 CQ (Fig. 1) over the last 28 ky (Penaud et al., 2010; dotted lines in Fig. 5). Obvious correlation between surface conditions recorded off the NW Moroccan coast (Marret and

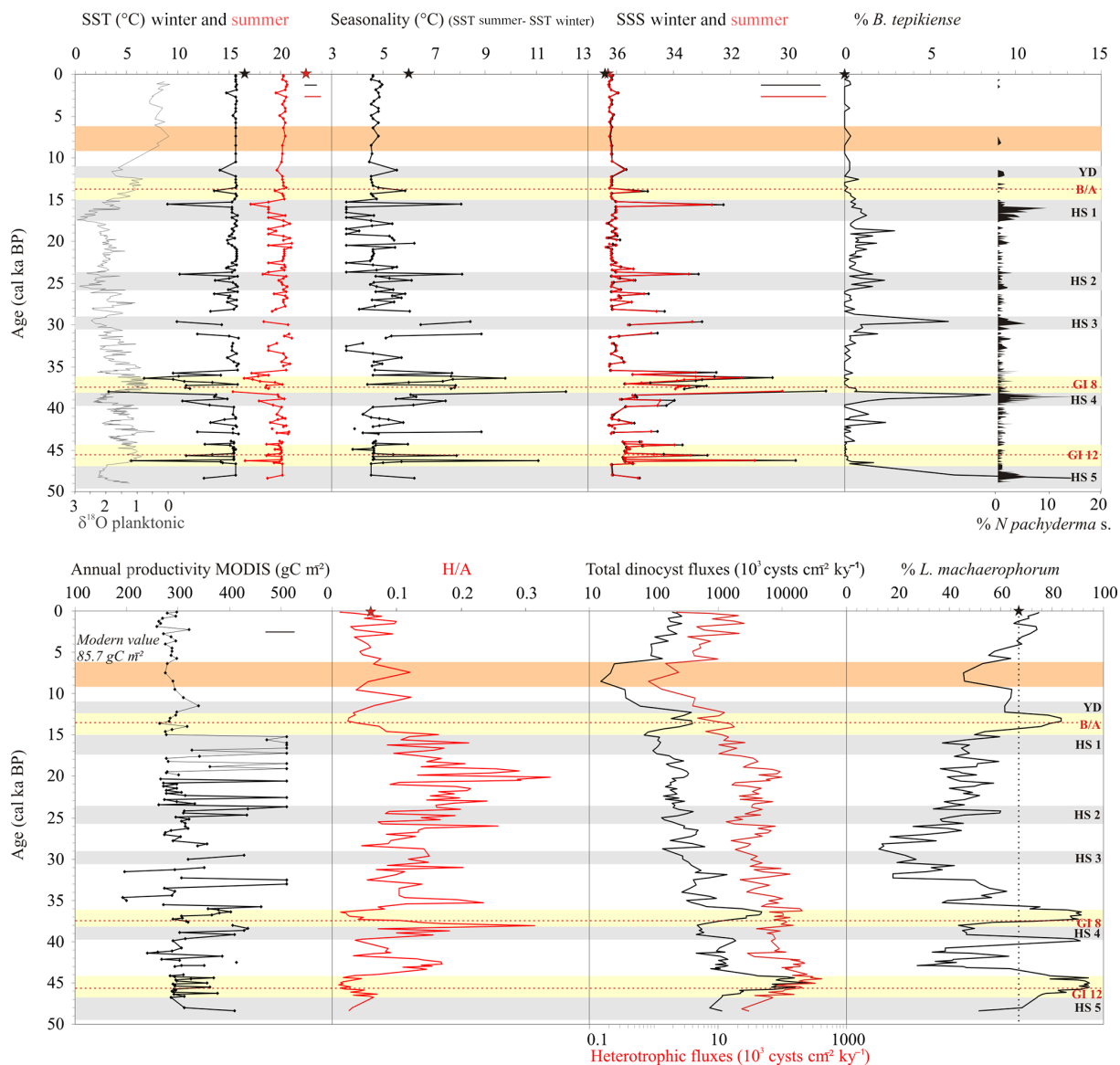


Figure 6. Data from core MD99-2339 against age (cal ka BP). $\delta^{18}\text{O}$ planktonic monospecific record and *N. pachyderma* (s.) percentages from core MD99-2339 (Voelker et al., 2006) in parallel with dinocyst transfer function results ($n = 1492$; Radi and de Vernal, 2008); winter and summer sea-surface temperature (SST) and sea-surface salinity (SSS), as well as seasonality (SST summer–SST winter) and annual productivities. Total dinocyst and heterotrophic fluxes are also depicted with the ratio *H/A* for “heterotrophics / autotrophics”, and percentages of two species: *L. machaerophorum* as a species index for higher surface stratification linked with increased palaeo-river discharges and *B. tepikiense* as a species index for thermal seasonal contrasts. Stars on each graph indicate present-day values for dinocyst percentages and hydrological parameters recorded in modern sediments and overlying surface waters, respectively, at the coordinates of analogue “A184” in the modern dinocyst database (34.32° N, 7.02° W; <http://www.geotop.ca/fr/bases-de-donnees/dinokystes.html>): SST winter of 16.48 °C and SST summer of 22.47 °C, SSS winter of 36.35 and SSS summer of 36.33, mean annual productivity of 85.7 g C m⁻², and percentages of *L. machaerophorum* of 65.27 % and *B. tepikiense* of 0 %.

Turon, 1994; Penaud et al., 2010) and in the central part of the Gulf of Cadiz may be due to the same dynamics governing palaeohydrological changes in this sector (Penaud et al., 2011a). More specifically, heterotrophics are never dominant among studied assemblages (Fig. 5). Heterotrophics are well known to be sensitive to oxic conditions (e.g.

Combourieu-Nebout et al., 1998; Zonneveld et al., 1997b; Kodrans-Nsiah et al., 2008), and the fact that *Brigantidium* percentages increased during GS (i.e. periods with relatively well-oxygenated bottom waters related to MOW dynamics) may be an argument for a negligible effect of oxidation processes on species-selective degradation after cyst depo-

sition at our study site. Significant occurrences of some selected species (Table 1; Penaud et al., 2011a), and especially coastal heterotrophics (*S. quanta* and *S. nephroides*; Fig. 5), will thus indirectly reflect varying regimes of mesotrophic–oligotrophic conditions in the Gulf of Cadiz over the last 50 ky.

5 Mechanisms behind dinocyst changes at orbital and sub-orbital timescales in the Gulf of Cadiz

Portuguese–Moroccan upwelling dynamics are of particular interest since planktonic populations are directly linked there to frontal areas and upwelled nutrient-enriched waters. At the Quaternary timescale, biodiversity increases have previously been observed during glacial periods, as a probable consequence of an enhanced functioning of upwelling cells (Abrantes, 1988, 1991; Targarona et al., 1999; Penaud et al., 2011a) and strong biodiversity modifications have been related to abrupt climate changes such as cold GS and especially HS (Lebreiro et al., 1997; Eynaud et al., 2000; Voelker et al., 2006; Penaud et al., 2011a, b) with a total restructuration of the water column. Understanding mechanisms underlying the complex pattern of palaeo-productivity changes at orbital as well as millennial timescales thus includes considering a wide range of external and internal forcing, i.e. varying conditions in terms of sea level, insolation, wind stress, water-mass exchanges at the Strait of Gibraltar, iceberg or fluvial discharges, and frontal upwelling cells, all of which are more or less interconnected at different timescales.

5.1 Glacial fertilization control on marine surface productivity

Annual productivity quantifications calculated from dinocyst transfer function (Fig. 6), the qualitative ratio H/A , and dinocyst fluxes (total and heterotrophics) evidence higher productivities during the Late Glacial compared to the Holocene, with a sharp transition especially noted at 15 ka BP (Fig. 6). Similar decreasing palaeo-productivity at the end of the last glacial period (Voelker et al., 2009) was also previously discussed with regard to the Gulf of Cadiz in a nearby core (GeoB 9064; 35°24.91' N, 06°50.72' W; 702 m water depth) based on planktonic foraminifera-derived productivity quantifications (Wienberg et al., 2010). Glacial productivity rise is commonly attributed to a fertilization effect caused by increasing aeolian dust supply to the ocean under stronger glacial winds (Moreno et al., 2002; Bout-Roumazielles et al., 2007; Wienberg et al., 2010), combined with higher Mediterranean continental aridity (Combourieu-Nebout et al., 2002; Sánchez-Goñi et al., 2002; Bar-Matthews et al., 2003; Fletcher and Sánchez-Goñi, 2008). Also, during MIS 2, glacial productivity reconstructed in the Gulf of Cadiz through dinocyst assemblages is the highest (around 500 g C m⁻² compared to present-day values of

about 90 g C m⁻²; Fig. 6). It was suggested to be regionally due to upwelled nutrient-enriched waters linked to the occurrence of a comparable hydrographic barrier to the modern Azores Front (Rogerson et al., 2004, 2010; Voelker et al., 2009). This is also suggested in our record with enhanced *Brigantedinium* (Fig. 7) and total heterotrophic percentages (H/A ; Fig. 6) between 26 and 15 ka BP (Penaud et al., 2011a).

5.2 Orbital control on palaeo-river discharges and nutrient availability

Furthermore, when considering *L. machaerophorum* percentages vs. orbital parameters, a very close relationship to the obliquity curve becomes obvious (Fig. 7). Assuming this species as a strong fluvial-sensitive cyst (Table 1), we may suggest enhanced precipitation in the southern borderlands of the Mediterranean Basin with obliquity maxima, which account for increasing northern summer insolation. Furthermore, generally higher percentages of *L. machaerophorum* recorded between 50 and 35 ka BP coincide with extremely high total dinocyst concentrations (fluxes), while generally higher percentages of *L. machaerophorum* recorded from 15 ka BP onwards coincide with extremely low total dinocyst concentrations (fluxes; Fig. 7). As the Mediterranean Basin is subject to interference of northern and tropical latitudes, both obliquity and precession signals may be considered. These indeed represent major influences for the eastern African and western Indian summer monsoon systems (Tuenter et al., 2003) and can be evidenced, for instance, in Mediterranean palaeorecords (Lourens et al., 1996, 2001). Furthermore, Tuenter et al. (2003) discussed the fact that the combination “obliquity maxima–precession minima” (cf. MIS 1 in Fig. 7) would have a weaker effect on the African monsoon compared to the combination “obliquity maxima–precession maxima” (cf. MIS 3 in Fig. 7). This would be consistent, during MIS 1, with our recorded enhanced stratification related to lower productivities (Fig. 6), especially between 10 and 6 ka BP, and our recorded enhanced stratification during periods of higher productivities across the last glacial (Fig. 6).

Also, interestingly, similar high Gulf of Cadiz dinocyst concentrations (fluxes) and *L. machaerophorum* percentages are recorded in the northern Bay of Biscay during the mid-Holocene (Naughton et al., 2007; Ganne A., personal communication, 2016). We can assume that high nutrient availability in the Gulf of Cadiz during the last glacial may have been similarly high to modern nutrient availability in the northern latitudes of the temperate NE Atlantic (Bay of Biscay). This northward migration of palaeo-productive centres is also similar to the migration of cold-water corals, from the Gulf of Cadiz during the last glacial period to the Irish–Norwegian margins at present (Freiwald et al., 2004; Dorschel et al., 2005; Rüggeberg et al., 2007; Eisele et al., 2008; Frank et al., 2005, 2009; de Haas et al., 2009; Wienberg et al., 2009, 2010). We then suggest maxima in

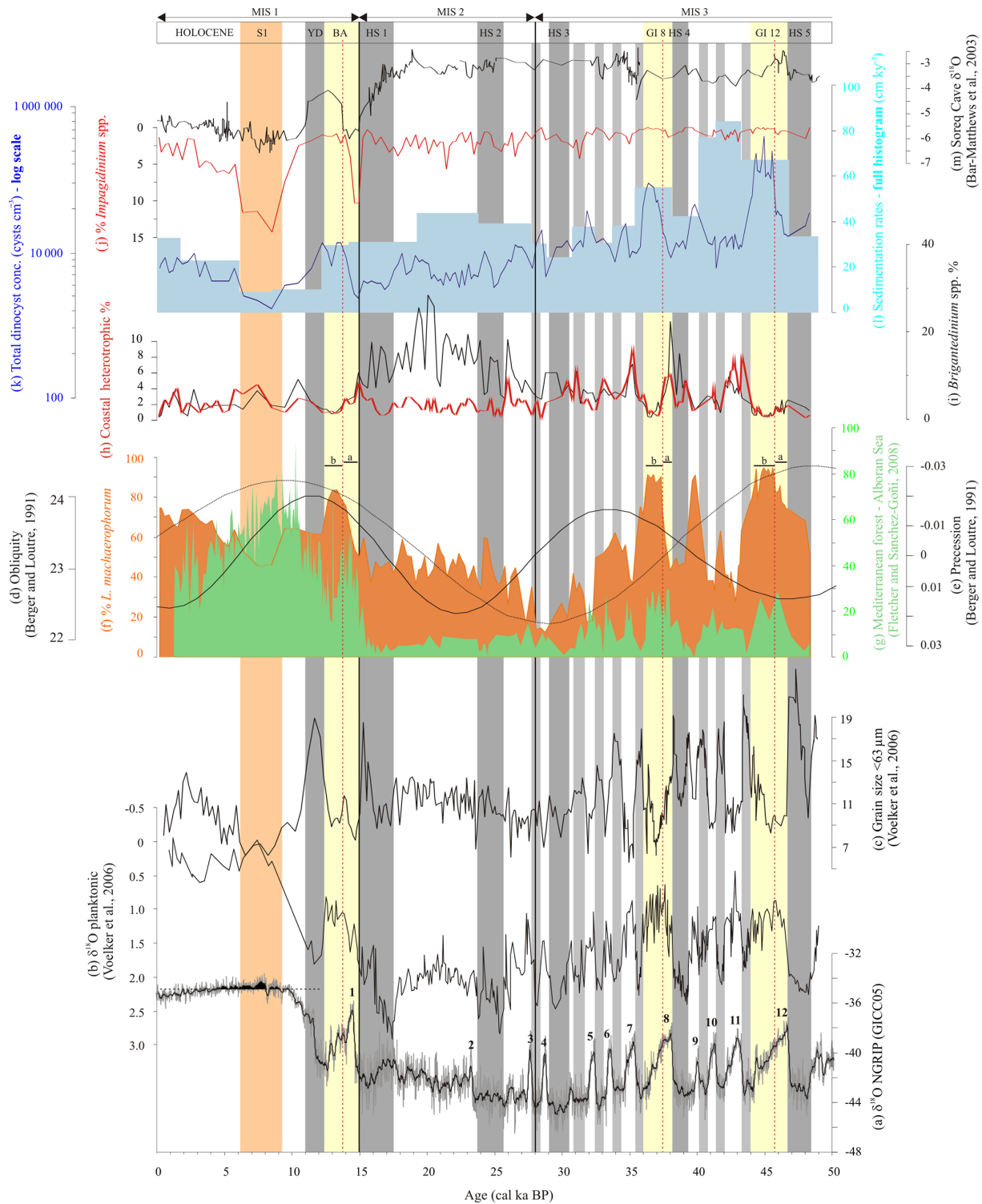


Figure 7. Greenland $\delta^{18}\text{O}$ data (a) in parallel with data from core MD99-2339: planktonic $\delta^{18}\text{O}$ (b) and mean grain size $<63 \mu\text{m}$ (c), over the last 50 ky. Dinocyst data (f, h, i, j) from core MD99-2339 are also depicted vs. western (pollen, Alboran Sea, g) and eastern ($\delta^{18}\text{O}$, Soreq Cave, m) Mediterranean records, as well as orbital parameters (d, e). Sedimentation rates (l) calculated from the new age model of core MD99-2339 echo total dinocyst concentrations (k). Greenland Interstadials (GI) 1 (Bölling–Alleröd: BA), 8 and 12 are highlighted with yellow bands and are characterized by a bipartite structure labelled “a” and “b” for the first and second phases, respectively. Grey bands indicate Heinrich Stadials (HS) and the Younger Dryas (YD). The orange vertical band indicates the time interval corresponding to Sapropel 1 (S1) formation (9.5–6.5 ka BP).

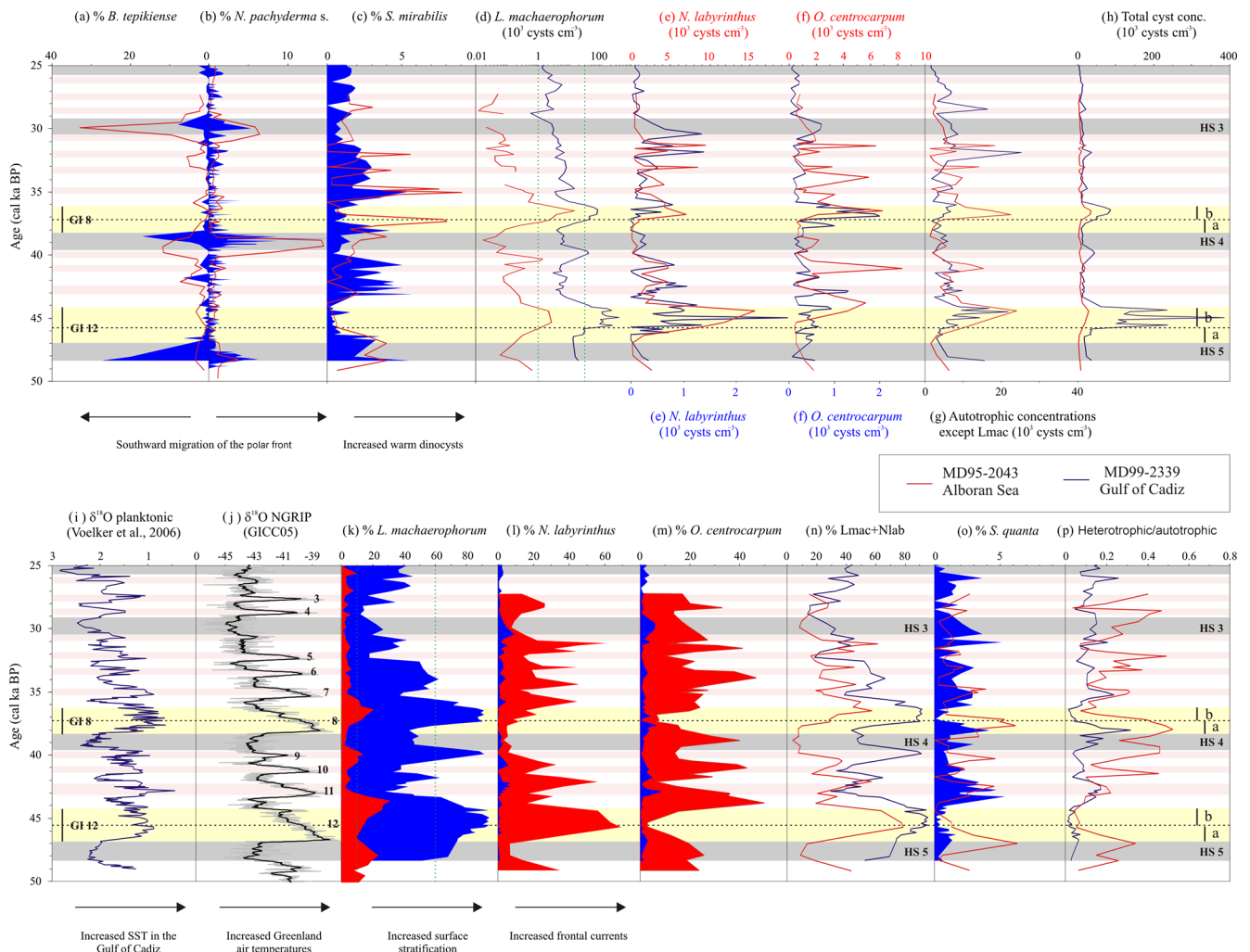


Figure 8. Comparison between dinocyst data (percentages or concentrations) as recorded from each side of the Strait of Gibraltar. Shaded blue and blue curves represent MD99-2339 data (Gulf of Cadiz, this study), while shaded red and red curves represent MD95-2043 data (Alboran Sea, Penaud et al., 2011b). Greenland Interstadials (GI) 8 and 12 are highlighted with yellow bands and are characterized by a bipartite structure labelled “a” and “b” for the first and second phases, respectively. Other GIs are highlighted with pink bands also corresponding to the numbered peaks obvious on the NGRIP curve. Grey bands indicate Heinrich Stadials (HS).

dinocyst, and perhaps phytoplanktonic organisms in general, export during glacial obliquity maxima in subtropical latitudes, when ice sheets were still well developed in the Northern Hemisphere, while interglacial obliquity maxima would preferentially stimulate phytoplanktonic growth in northern latitudes of the North Atlantic. Also, climatic changes affecting the regional freshwater inputs may also contribute to explaining those similarities between the last glacial period in the Gulf of Cadiz and the mid-Holocene in the Bay of Biscay (e.g. Sierro et al., 2000; Mikolajewicz, 2011; Bahr et al., 2015; Lofi et al., 2016). Marine surface productivity has been tentatively modelled for the Indian Ocean with simulations coupling a biogeochemical component for primary production, from 80 ka BP climate conditions to the pre-industrial state (Le Mézo et al., 2015). This modelling exercise evi-

denced the crucial role of obliquity, i.e. glacial–interglacial conditions responsible for changing oceanic circulation, as a main driver for phytoplanktonic productivities. This relationship between obliquity maxima and enhanced marine productivities has furthermore recently been evidenced in the equatorial eastern Atlantic Ocean with dinocyst data (Hardy et al., 2016).

5.3 MIS 3 and the atypical pattern of GI 8 and GI 12

5.3.1 General overview of MIS 3 pattern on either side of the Strait of Gibraltar

MIS 3 corresponds to a general stronger velocity of denser MOW export (grain-size analysis; Fig. 7). Over this period, dinocyst signals from both sides of the Strait of Gibraltar,

i.e. signals recorded from the Gulf of Cadiz (this study) and the Alboran Sea (core MD95-2043; Penaud et al., 2011b; Fig. 1), have been compared so as to qualify Mediterranean-Atlantic surface exchanges at times when MOW experienced strongest/weakest bottom current velocities (Fig. 8).

A first look at dinocyst concentrations for selected individual species (Fig. 8d, e, f) reveals extremely close patterns from either side of the Strait of Gibraltar, but with a different magnitude of values, especially when considering *L. machaerophorum* concentrations that are 10 to 100 times higher in the Gulf of Cadiz compared to the Alboran Sea (Fig. 8d). Total dinocyst concentrations are also characterized by similar temporal fluctuations but different reconstructed values; these marked value differences are only explained by *L. machaerophorum* concentrations since other “autotrophic” species show generally comparable orders of concentrations (Fig. 8g).

It is interesting to note that, even if individual species concentrations follow obviously identical oscillations, they are not as clear when considering their relative abundances (Fig. 8k, l, m). *L. machaerophorum* percentages generally dominate whole cyst assemblages all over MIS 3 in the Gulf of Cadiz, as is the case today (Rochon et al., 1999; Marret and Zonneveld, 2003; Zonneveld et al., 2013; Table 1; Fig. 8k). In the Alboran Sea, *N. labyrinthus* (cool-temperate, outer-neritic) percentages mirror those of *L. machaerophorum* (temperate, inner-neritic) in the Gulf of Cadiz (Fig. 8l), with this species hardly making up 5% of the present-day assemblage in the area. Contrary to the Gulf of Cadiz, no important river discharges are noticeable today in the Alboran Sea and the continental shelf is narrower. Primary productivity in the Alboran Sea mainly results today from the inflow of Atlantic waters through the Strait of Gibraltar, while marsh and riverine influence in coastal zones from the Gulf of Cadiz is particularly high (Macías et al., 2014). This could explain the predominance of *L. machaerophorum* in core MD99-2339, while *N. labyrinthus* will preferentially characterize MD95-2043. When these two species are summed, their percentages show obvious similar patterns in terms of both values and timing of the different recorded peaks (Fig. 8n). Combined *N. labyrinthus*–*L. machaerophorum* percentages are not clearly related to GS or GI climate conditions; however, features can be distinguished: (i) maximal values are recorded at the end of GI 8 and 12, but very low values at the start of these specific interstadials; (ii) they never occur during HS with significant percentages; and (iii) they often characterize GS climate conditions with increasing relative abundances (Fig. 8n).

5.3.2 Greenland Stadial (GS) and especially Heinrich Stadial (HS)

During GS, and especially HS, dinocyst seasonal SST reconstructions from the Gulf of Cadiz evidence a 2 to 5 °C cooling, as a consequence of the southward shift of the polar front

(e.g. Eynaud et al., 2009). This is especially true for winter SST (Fig. 6), with dry and cold winter conditions also being previously recorded in these latitudes (Sánchez-Goñi et al., 2002; Combourieu-Nebout et al., 2002; Moreno et al., 2002, 2005; Bout-Roumazielles et al., 2007). *B. tepikiense* and the polar foraminifera *N. pachyderma* (s.) attest, respectively, to enhanced seasonality (large offset between summer and winter temperatures as confirmed by dinocyst transfer function; Fig. 6) and important coolings in the interval 25–50 ka BP (Fig. 6). The combination “*N. pachyderma* (s.)–*B. tepikiense*” thus evidences in both the Gulf of Cadiz and the Alboran Sea the influx of subpolar water masses into these subtropical northeastern Atlantic latitudes (Bard et al., 2000; Sánchez-Goñi et al., 2000; Pailler and Bard, 2002; Turon et al., 2003; de Abreu et al., 2003; Vautravers and Shackleton, 2006; Eynaud et al., 2000, 2009; Salgueiro et al., 2010, 2014; Patton et al., 2011; Penaud et al., 2011a, b), also accounting for direct and strong surface connections responsible for similar planktonic species occurrences at both sides of the Strait (Fig. 8). During HS, this occurs in a context where bottom MOW experienced intermediate (and not the strongest) velocities because of the strong advection of less saline waters at the surface in the western Mediterranean Basin (Cacho et al., 2000; Sierro et al., 2005; Voelker et al., 2006; Frigola et al., 2008).

In the Gulf of Cadiz, during HS, increased annual productivity reconstructions (Fig. 6) together with increased heterotrophics (especially *Brigantedinium* spp.; Fig. 7) suggest primary productivity increases related to frontal system reorganizations within the Gulf of Cadiz (Rogerson et al., 2004, 2010; Voelker et al., 2009). This front was also discussed over the last 28 ky by the strong decreasing gradient of *N. pachyderma* (s.) percentages obvious during HS across a small north–south transect between southern Portugal and the sector Cadiz–Morocco (Penaud et al., 2011a). This configuration is similar to the one previously discussed for the LGM interval that recorded the highest productivities and *Brigantedinium* percentages in our Gulf of Cadiz fossil record (Figs. 6 and 7). Except for HS, other GS are not systematically marked by such features. Also, it is interesting to note that productivity drops were noted during GS in the same core with planktonic foraminiferal Cd/Ca values, thus suggesting low nutrient availability at that time (Patton et al., 2011). Our frontal upwelling conditions explaining higher productivities would thus be especially valid for HS climate extrema in the Gulf of Cadiz. In the northern North Atlantic, biomass decline has conversely been linked to abrupt climate changes (Schmittner, 2005; Mariotti et al., 2012) during AMOC disruption linked with massive iceberg calving (e.g. McManus et al., 2004; Gherardi et al., 2005).

5.3.3 The Greenland Interstadial (GI), especially GI 8 and GI 12: typical bipartite structure

In the Gulf of Cadiz, warmer surface conditions are generally recorded during GIs, as suggested from the W/C ratio (Fig. 5) as well as seasonal SST reconstructions with values close to modern ones (Fig. 6). Synchronous occurrences of the thermophilic species *S. mirabilis* on both sides of the Strait of Gibraltar (Fig. 8c) also indicate general warmer surface conditions at a time when bottom MOW velocity was reduced.

However, GI 12 and GI 8, immediately following HS 5 and HS 4, respectively, are characterized by very peculiar and unique features when compared to other GIs in the core. These two intervals show periods characterized by the longest and strongest expansions of mixed oak forest over MIS 3 (Alboran Sea; Fletcher and Sánchez-Goñi, 2008; Fig. 7), and, from a unique hydrological point of view, they can be described according to a bipartite structure in the Gulf of Cadiz (cf. “a” and “b”; Figs. 7 and 8), also previously described for the Alboran Sea (Penaud et al., 2011b; cf. Fig. 8). While the first part (“a”) is characterized by increasing coastal heterotrophics (Fig. 8o) and thermophilic species (Fig. 8c), paralleling higher polar air temperatures (Fig. 8j), the second part (“b”) is characterized by the highest total dinocyst concentrations (Fig. 8h) and *L. machaerophorum* percentages (Fig. 8k) ever recorded over the last 50 ky. This second part is also characterized by a strong *S. mirabilis* drop (Fig. 8c), and the lowest winter SST (10 °C colder than today; Fig. 6) and SSS (around 30 reconstructed at that time; Fig. 6). We therefore suggest a major atmospheric reorganization occurring at 37 ka BP within GI 8, and at 45.5 ka BP within GI 12, also detected in NGRIP with decreasing polar temperatures all along these long interstadials (Fig. 8j). Within both second phases (“b”, Fig. 8), synchronous high percentages of *L. machaerophorum* recorded in the subtropical NE Atlantic (quasi monospecific in the Gulf of Cadiz) and in the western Mediterranean Basin suggest extremely high fluvial discharges and well-stratified conditions. We therefore suggest an extreme southward shift of the winter westerlies belt, more pronounced during each part “b” than during each part “a”, that would also be responsible for huge advection of freshwater, especially during the winter season, and therefore reduced SST and SSS. This questions the feedbacks inherent to the atmospheric/oceanic reorganizations. Even if the precise mechanism underlying this shift is still questioned and deserved model simulations, our results argue for a fast response of the ocean in this millennial/sub-millennial timescale context of rapid climate change.

5.4 Dinocyst-specific pattern across MIS 1

Interestingly, during MIS 1, decreased dinocyst fluxes and increased *Impagidinium* percentages (Fig. 7) seem to be related to the humidity pattern as recorded in western (Fletcher

and Sánchez-Goñi, 2008; Fig. 7) and eastern (Bar-Matthews et al., 2000, 2003; Fig. 7) Mediterranean records. During the first half of the BA, *Impagidinium* species (especially *I. aculeatum*; Fig. 5) strongly expand (Fig. 7), arguing for the establishment of full oceanic and warm conditions, which may suggest oligotrophic conditions in this area (cf. dinocyst transfer function; Fig. 6) progressively replacing glacial eutrophic to mesotrophic ones (Behrenfeld et al., 2005; Wienberg et al., 2010). This shift is synchronous to widespread rainfall over the entire Mediterranean Sea (Toucanne et al., 2015). Increased vegetation cover at that time (Fletcher and Sánchez-Goñi, 2008; Fig. 7) and thus decreased river runoff on land may have also induced decreased nutrient supplies to the ocean. It is interesting to note that, in North Atlantic subtropical latitudes, each onset of warm conditions during climatic optima (i.e. MIS 1, MIS 5, MIS 11, and MIS 19) was associated with the expansion of *Impagidinium* species (Eynaud et al., 2016). This group thus marked post-glacial conditions instead of hypsithermal ones when competition with other thermophilous taxa such as *S. mirabilis* is observed (Turon and Londeix, 1988; Londeix et al., 2007; Eynaud et al., 2000, 2016; Penaud et al., 2008). It is worth noting that, and similar to GI 12 and GI 8, the BA is not homogeneous and is marked by a bipartite structure (cf. phases “a” and “b” in Fig. 7). The final BA (“b”) is indeed marked by a drastic drop of *Impagidinium* spp., a strong increase in *L. machaerophorum* percentages and high values of total dinocyst concentrations (Fig. 7). This may suggest slightly more productive conditions (cf. Fig. 6) that followed mean general Mediterranean aridity increases starting as soon as 14 ka BP and continuing during the following cold event of the YD (Figs. 6 and 7).

At the onset of the Holocene, during the 9.5–6.5 ka BP interval, the proportion of clay cohesive sediments (cf. grain-size < 63 µm; Fig. 7) observed in core MD99-2339 is the largest of the record, thus suggesting a strong reduction of MOW flow strength (Voelker et al., 2006), as also evidenced in western Mediterranean Sea contourites from the Corsica Trough (Toucanne et al., 2012). This early Holocene interval is coeval with enhanced summer precipitation over the northern borderlands of the eastern Mediterranean (i.e. North African summer monsoon forcing; Rossignol-Strick, 1983; Rohling and Hilgen, 1991; Bar-Matthews et al., 2000, 2003; Fig. 7) and thus increasing summer/autumn fluvial discharges mainly from the Nile (deMenocal et al., 2000; Gasse, 2000). This leads, in the eastern Mediterranean Sea, to important water column stratification, a cessation of the deep convection, an anoxic phase of bottom waters, and high surface productivity and thus to the organic-rich Sapropel 1 formation (e.g. Kallel et al., 1997; Mercone et al., 2000). Also, the western Mediterranean Basin was subject to enhanced rainfalls (Aritzegui et al., 2000; Zanchetta et al., 2007; Magny et al., 2013), and this has been recently connected to seasonal Mediterranean autumn/winter rainfalls sustaining high fluxes of nutrients and organic matter to the

seafloor (Toucanne et al., 2015). Conversely, in our study, the period between 9.5 and 6.5 ka BP is characterized by low quantified productivities (Fig. 6), the lowest dinocyst fluxes (Fig. 6) and by the highest percentages of *Impagidinium* spp. ever recorded over the last 50 ky (Fig. 7). Full-oceanic oligotrophic conditions have prevailed in the central Gulf of Cadiz, and this can be attributed to significantly lower amounts of Saharan dust inputs at that time (Wienberg et al., 2010) in a context where Mediterranean forest strongly expanded (Fletcher and Sánchez-Goñi, 2008; Fig. 7), preventing dust remobilization and run-off. Furthermore, at the time of Sapropel 1 formation (Toucanne et al., 2015), a displacement of the autumn/winter storm track along the northern Mediterranean borderlands (i.e. atmospheric configuration extremely close to a persistence of negative NAO conditions) could have been favourable to a southward winter displacement of the Azores High reinforcing the Azores Current influence towards the Gulf of Cadiz and therefore probably also the advection of nutrient-poor subtropical North Atlantic Central Water during winter. This would also be consistent with the occurrence of thermophilous *Impagidinium* species, mainly encountered today in fully marine tropical environments (Bouimetarhan et al., 2009). Also, in the Gulf of Cadiz, the Levantine Intermediate Water (LIW) directly contributes to the upper MOW export during interglacials, while a downslope shift of the denser MOW plume is noted during glacials/lowstands (Voelker et al., 2006; Toucanne et al., 2012; Kabeth et al., 2016). We can then hypothesize that, during the Holocene, the cessation of LIW formation in the eastern Mediterranean Basin may have impacted the remobilization of sediments/nutrients through the lack of mixing at the subsurface between surface and deep currents across the Strait of Gibraltar (Gomez et al., 2000), also additionally contributing to the decreased dinocyst fluxes recorded in the central Gulf of Cadiz (Fig. 7).

6 Conclusions

Marine regions characterized by high primary productivity conditions play an important role as a carbon sink and thus significantly contribute to CO₂ storage, and subtropical latitudes could play a crucial role in the carbon pump at a global scale. Here, new palynological investigations carried out in the central part of the Gulf of Cadiz over MIS 3 (25–50 ka BP) allow for consideration of dinocyst population shifts over the last 50 ky in the subtropical northeastern Atlantic Ocean. This study provides important evidences of migrating palaeo-productivity centres from the last glacial period to the Holocene, and can therefore also be of crucial importance for our understanding of long-term and abrupt climate changes in primary productivity regimes and organic matter export to the seafloor.

We especially focus on the dinocyst species *L. machaerophorum*, which we interpret as a powerful

tool to discuss surface hydrological changes through time in the northeastern Atlantic, and especially water column stratification under varying regimes of palaeo-precipitations, primarily forced by obliquity maxima at orbital timescales. Dinocyst fluxes, and perhaps also dinoflagellate productive conditions, in the Gulf of Cadiz were the highest during the last glacial (especially between GI8 and GI12), and a clear imprint of millennial-scale abrupt climate changes was detected on palaeohydrological changes all over the investigated period. During the Holocene, precessional forcing is also suggested through the probable impact of Sapropel 1 formation in the eastern Mediterranean on decreasing dinocyst fluxes and perhaps also on dinoflagellate productivity in the Gulf of Cadiz.

7 Data availability

Underlying research data can be accessed as a supplement to this article in Excel format.

The Supplement related to this article is available online at doi:10.5194/bg-13-5357-2016-supplement.

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