Dear editor and reviewer,

The letter addresses all reviewers remarks: main issues that needed clarifications as well as minor points (words or sentences corrected/re-written, typos..) that have easily been corrected in the revised manuscript.

Comments have been grouped when they addressed same issues. For the reader convenience, all our responses are in red in the following text.

We hope to have satisfied / clarified all remarks.

Sincerely yours,

Aurélie Penaud and co-authors
General comments Authors describe new dinocyst evidence obtained in the Gulf of Cadiz, which interpretation is based on a new chronology (tuned with the latest NGRIP time-scale) for the deepest part of the section studied. Then they contrast their results with other previous data in the region. Comparison between both sides of the Gibraltar Strait reveals interesting features that might be connected with the climatic changes and the reorganization of the marine currents. I found that the regional review, methods and argumentation are usually good. In general terms I am satisfied with the content of this manuscript, which in my opinion may be considered a notable piece of work.

Nevertheless, in order to improve some parts, I suggest punctual rephrasing and perhaps putting more emphasis in some points that I consider not entirely clear:

A) it should be noted somewhere in the text that in transferring the GICC05 chronology to SST event-based records in the North Atlantic is necessary to assume that the abrupt D/O warming events in both records are synchronous. Therefore, being rigorous it is not possible to evaluate properly any leads or lags in the climate system (Austin & Hibbert, 2012)

Also:

Page 9, Line 197: Do you mean you don’t have enough subsampling resolution for individualize every single short event? Clarify, please.

Page 9, Line 212: Nevertheless you have assumed above that chronologies of the main climatic shifts have been synchronous in Greenland and your site. Of course, such assumption prevents to establish any definitive conclusion about leads and lags. I can see a possible trouble here. You should be very clear about the possibilities/limitations of your new chronological approach along the text.

Page 20, Line 451: Synchronicity (which may be observed in Figure 8c but seems a bit imperfect between ca. 43-35 ka) may be (at least in part) a result of the previous tuning. Synchronization between both areas is reliable, but not well-demonstrated until two independent sets of chronological data were compared. Such point may be clear along the text.

Response: this is something we are definitely conscious about, see for instance the paper our team has published in 2012 (Eynaud et al., GRL 2012) where we stated:

(1) In the main text, regarding the age model: "...Taking advantages of the recent discussion cautioning "marine event-based chronostratigraphies" (Austin and Hibbert, 2012), especially regarding phasing issues, we thus prefer to avoid any artificial tuning to the Greenland ice-cores. This approach thus generated a fully independent chronology.

(2) In the Supplementary Figure 1 caption: "Stratigraphy of core MD95-2002, with the comparison of the initial published age model (in blue; see Ménot et al, 2006 and Eynaud et al., 2007) with the NGRIP (orange) tuned age model. Arguments to validate this tuning are not sufficiently strong to require a new age model. Furthermore, such tuning assumes synchronicity of abrupt millennial-scale air-temperature changes over Greenland with sea-surface temperature / planktonic foraminifera population events in the temperate North Atlantic and, thus by definition is unable to detect latitudinal intra-hemispheric propagation of climatic changes which have a direct impact on
the duration of the perturbation in the surface ocean and therefore on planktonic communities (see Eynaud et al., 2009 or Scourse et al., 2009 - Figure 5; for an illustration of this question regarding the expression of the regional impact of Heinrich Stadial on N. pachyderma s. records)"

Here we decided to adopt such a tuning based on $\delta^{18}$O stratigraphy thanks to the already published material on the MD99-2339 core and furthermore on proximal reference cores (e.g. MD95-2042) where this methodological choice was supported by complementary indicators (see Shackleton et al. 2000, for a review).

To avoid any ambiguity on our choice we have thus added in the text from line 156:

« Such an approach is validated by previous works conducted on the southern Iberian margin where the stratigraphy of paleoclimatological reference sites were constructed using a similar tuning to Greenland ice records (e.g. Shackleton et al., 2000; Bard et al., 2004). This event based stratigraphy (i.e., Austin and Hibbert, 2012), however, prevents establishing any definitive conclusion about latitudinal leads and lags, and evaluating intra-hemispheric propagation velocities of climatic perturbations. »

Also:

Page 54, Line 1260:

Here you are assuming that the chronologies were exactly the same in Greenland and the Subtropical North-Atlantic, which perhaps it is not completely true. A certain latitudinal variation is likely (line 204 in your text), but perhaps impossible to detect after discarding your independent radiocarbon chronology. Of course you can believe (and argue) that the alternative tuning chronology is more realistic, but in my opinion this point (the lack of chronological independence) should be clearly stayed in the text, in order to a better contextualization of your interpretations.

Response: Idem above

Furthermore, the model study by Charles et al. 1994 showed a strong linkage between the subtropical gyre and Greenland snow/ice in the form of the subtropical gyre being a significant moisture source for Greenland precipitation.


B) I wonder if could be possible to develop a more ambitious age-depth model (e.g. by combining radiocarbon dates and age-points inferred by tuning) in order to improve the calculation of flux rates.

This is already what was done with the age model revision. See lines 155-156 of the initial manuscript.

Also:

Page 9, Line 195:
I have some doubts about this. Apparently, with a limited set of age-points (radiocarbon or tuning), it seems possible that you could build a robust Age-Depth model able to attribute an age for each sample studied; and thus, to calculate the flux rates between each two samples. Why not?

Response: This not really our point here as we have built an age model and thus have attributed an age for each studied sample. The referee seems precisely to not support this assumption “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…” Our aim here was to avoid miscalculations with fluxes rather forced by the number of tie points than by natural shifts.

C) I would appreciate a well-defined position about the possible influence of the deglaciation of North America in the regional context, especially during the MIS2 and Early Holocene

Response: This topic is outside of the scope of the current manuscript. The last deglaciation/ Last Glacial Interglacial Transition off western Iberia has been discussed in several previous publications. As such Skinner & Shackleton, 2003 (Rapid transient changes in northeast Atlantic deep water ventilation age across Termination I) discussed this in details and it was also the main topic of Bard et al., 1981; Rogerson et al., 2004; Rodrigues et al., 2010 and more recently the review by Naughton et al., in press. The studies of Turon et al., 2003 and of Penaud et al., 2010, 2011 focused on this transition with dinocyst proxies with Penaud et al. (2010 and 2011) covering the waters between southwestern Iberia and Morocco (including core MD99-2339).


Our choice was then to focus on the data from MIS3. We have added a sentence to overcome such a view for future readers between lines 87-89:

"For this paper, we focus on the paleohydrographical 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. Bard et al., 1981; Rogerson et al., 2004; Turon et al., 2003; Penaud et al., 2010)."

Also:

Page 17, Line 371:
Climatic changes affecting the regional freshwater inputs also may contribute to explain those similarities between last Glacial in the Gulf of Cadiz and mid-Holocene in the Bay of Biscay (e.g. Mikolajewicz, 2011). Might be this is another way for supporting a similar argument? Clarify, please.

Page 2, Line 32
After reading the MS, it is not completely clear for me if authors believe that those changes observed in their record during the Early Holocene might be (almost partially) associated to variations in the Eastern
North Atlantic circulation cells, perhaps promoted by the deglaciation in North America (i.e. 8.2 ka event) or other cold relapses described in the NGRIP record during the Early Holocene. I would appreciate a more clear position about this point somewhere along your text.

Response: Millennial-scale climate variations during the Holocene are not the topic of the current manuscript and cannot be resolved with the current resolution in the Holocene section of core MD99-2339. None of the western Iberian margin surface water records show a strong response to the 8.2 ka (see core compilations in Voelker and de Abreu, 2011; Salgueiro et al., 2014). The best impression of a 8.2 ka related surface water cooling is probably in core D13882 from the Tagus pro-delta (Rodrigues et al., 2009) and even here the cooling is just in the range of 1.0-1.5°C. Furthermore, in the Gulf of Cadiz, any climate change related to the 8.2 ka event is overprinted by the impact of the African monsoon signal / Sapropel 1 climate conditions. Such processes are not easy to discriminate from each other.


D) The existence of methane in the seafloor in the area, and their possible influence (e.g. C sequestration, productivity, evidence of sea-level changes, etc) could be also considered along the text.

Also:

Page 3, Line 54:
Suggestion: sequestration of C in form of methane (CH4) is another important component of the total C sequestration/emissions in marine environments, which also can affect the local productivity and biodiversity around the seepages (e.g. Judd & Hovland, 2007). Multiplicities of evidences exist in this area revealing the occurrence of CH4 in the seafloor (e.g. León & Somoza, 2011). Consider to include some references to this point in your text, please.

Response: Our discussion on methane is related to the atmospheric methane concentrations and the related climate forcing. Methane emissions from deep-sea floor source could contribute to the atmospheric methane levels, but such processes are outside of the scope of the current manuscript. Furthermore, we are discussing productivity and biodiversity in the surface ocean and not at the ocean floor. Methane sequestration/emission in the Gulf of Cadiz is related to particular features such as mud volcanoes and/or tectonic faults and core MD99-2339 was not retrieved from an area close to mud volcanoes (which would have been counterproductive for paleoceanographic/climatic studies as methane related diagenetic processes could alter proxy signals (such as of the foraminifer carbonate shells).

These CH4 seafloor emissions are actually important component of the bottom water chemistry and geology (e.g. Pinheiro et al., 2003, 2006; Maldonado & Nelson, 1999) but rather occur on the eastern Gulf of Cadiz, close to the horseshoes structure of the Gibraltar strait where a lot of mud volcanoes are actually sustained by CH4 releases. These phenomena however do not interact with climatic processes
at the scale of our study and furthermore do not impact surface marine proxies (which are the focus of our topic).


Other minor specific comments are listed below. Specific Comments:

Page 4. Line 73:
Also in form of CH4.
Response: done line 70.

Page 4, Line 89:
This sentence is a bit unclear for my taste. Some specific references could be useful here to illustrate your idea.
Response: We have added a reference line 91 (Bahr et al., 2015).

Page 4, Line 92:
Insert a spacebar between HYDROGRAPHY and OF, please
Response: done line 93.

Page 7, Line 151:
Figure 2 should be cited before Figure 3. May be you refer Figure 2 but not Figure 2? Reordered the references or rename the Figures, please.
Response: this has been corrected. The order of citation is now correct and old Figures 2 and 3 have been inverted and are now new Figures 3 and 2, respectively. lines 151 to 166.

Page 8, Line 181:
If some non- Quaternary specimens in your record come from reworking, anyone might wonder if any other Quaternary specimens have been reworked too. Clarify, please.
Response: Few reworked specimens have been identified; we then have deleted the sentence.

Page 12, Line 268:
Insert a comma, please: just after HS5, during GI 12.
Response: the sentence has been modified lines 271-273.

Page 13, Line 273:
Perhaps be useful to indicate the MIS intervals also in Figure 4.
Response: done in revised Figure 4.

Page 15, Line 327:
This differentiation between MIS-2 and deglaciation may be confused. Please, indicate what exactly mean everyone in this context. Perhaps do you mean Late Glacial instead of deglaciation?
Response: yes, corrected line 335.

Page 15, Line 329:
Indicate its position in Fig. 1, please.

Response: we have added line 338 “was also previously discussed in 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)”. It is mentioned in the text that it is a nearby core. There are so close from each other that it would increase Figure 1 to also position this core on the Figure.

Page 16, Line 337:
Use lower case (gC/m2)
Response: done line 345.

Page 20, Line 456:
In relation to pollen representation and the associated interpretations, you might have in mind that the difference between Interglacials and Interstadials has been clearly established in the literature (e.g. Birks and Birks, 1980). Relative high tree pollen percentages observed during those interstadials (GI 12 and 8) might be considered increases but uncomplete ecological successions. Alternatively, it should be only a true tree expansion (complete forest succession) at the beginning of the Holocene. I suggest rephrasing consequently.
Response: we agree with your remark but this not requires modifying the text.

Figure 7. Might be % Grain size <0.063_m? Revise if necessary, please.
Response: corrected line 1321.
This paper presents a new high resolution dinoflagellate cyst record from the bay of Cadiz, covering the last 50 ka, with an emphasis on the Marine Isotopic Stage 3 and interstadials. The variations in dinocyst assemblages are explained as a complex interaction between orbital forcing (precession and obliquity) as well as land-ocean interactions. Overall, this study should be published as it highlights the complex answer of the ocean to environmental changes but the text would need some moderate revisions as it is not always well expressed or structured. Given that Reviewer#1 has highlighted mistakes that I have seen, my review is focused on some other aspects.

Lines 47-51: This introductory sentence gives the wrong information as it leads the reader to assume that this paper is about CO2 sequestration, but that is not the case. You may want to start to talk about marine regions in the world where productivity is at its highest (shelves, upwelling cells, river mouths, etc) and how they play an important role as a carbon sink. Restructure your introduction to be clearer where you are going.

Response: The introduction has been re-structured at the beginning: lines 47-52.

Line 64: include sea-ice cover duration
Response: done line 63

Line 70: This sentence could be better structured, please rephrase such as: “The central Gulf of Cadiz is a place of low present-day marine productivity, with a moderate responsibility for CO2 storage (REF). However, it may not have been the case in the past with the potential migration of proximal productive centers (e.g. Portugal and Moroccan upwellings) through time. In fact, it was demonstrated that productivity changes in this region involve: Our study aims to explore how these changes may have impacted dinoflagellates, here viewed as an:

Response: done lines 71-79

Line 93: replace focused with located
Response: done line 94

Lines 109-110. Give values of Chlor. and PP if possible.
Response: we re-phrased lines 109-110

Line 143: Start with: “Core MD99-2339 (35.89_N; 7.53_W; 1170m water depth; 18.54m length; Figure 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 146 (IMAGES V-GINNA) cruise (Labeyrie et al, 2003).

Response: done lines 143-146

Either Ky or Ka but not both
Response: both are used in the manuscript following Aubry et al. 2009 “the distinction between geohistorical date, in years before present expressed in ‘annus’, symbol ‘a’, with the multiples ‘ka’, ‘Ma’, and ‘Ga’ for thousands, millions and billions of years ago, according to a convention that has been very widely adopted during the last 30 years, and geohistorical duration, expressed in ‘year’, symbol ‘yr’, with multiples ‘kyr’, ‘Myr’ and ‘Gyr’, respectively” (Terminology of geological time: Establishment of a community standard; Stratigraphy vol. 6(2), pp.100-105)

Line 156: six instead of 6
Response: done line 162

Line 167: delete dinocyst, as already mentioned earlier in the text
Response: done

Lines: 169-171. Rephrase as suggested: 161 samples were analyzed for their dinocyst content (every 10 cm in average, representing a sample resolution of around 300 years [_̶210]) for the whole MD99-2339 core, using an Olympus BX50 microscope at 400X 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).
Line 176: cold HCl (10%) and cold HF (??%)
Line 180: following the taxonomy in Fensome and Williams (2004) and Fensome et al. (2008).
Percentages were calculated based on a total dinocyst sum that excludes reworked : : :
Response: done lines 175-176, 182, 186

Lines 206-209: rephrase as suggested: A qualitative thermic index “Warm/Cold” (W/C) that has previously been used (Turon and Londeix, 1988; Versteegh, 1994; Combourieu-Nebout et al., 1999; Eynaud et al., 2016) to qualitatively address SST change issues, was calculated for core MD99-2339 (cf. Table 1).
Response: done lines 211-214

Line 218: Protoperidinium in italics
Response: done line 223

Lines 221-22: correct Heterotrophics/Autotrophics
Response: done line 226-227

Line 226: Suggested rephrasing: Quantifying taxonomical diversity in study samples was carried out through a variety of statistical analyses using “Past version 1.75b” software (Hammer et al., 2001); most of these indices being explained in: : : :
Response: done lines 231-232

Line 241: replace 5 with five. You may want to explain this number, rather than 10 or less.
Response: we refer the reader, in the text, to Guiot and de Vernal (2007) for the complete methodology about the transfer function used in this study

Line 244. Give a source for the modern-day sea-surface conditions.
Response: done in the legend of Figure 6 since present-day conditions are highlighted in the Figure for comparison with reconstructed sea surface parameters via the dinocyst transfer function.

Lines 250-251: Consider rephrasing: A total of 40 taxa was identified, with an average diversity of 20 main species. Your diversity does not decrease; in fact, there is a slight increase from bottow to top.
Response: done lines 255-257

Line 256: suggestion: «thus probably indicating enhanced fluvial inflows“
Response: done line 260-261

Lines 261-265: I sort of understand what you mean but it is not well expressed. Suggestion: “Large increase of monospecific assemblages (when dominance is close to 1) will: : :”
Response: done line 265
Concentrations are generally low, with the exception of two large maxima, one centered around GIS 12 and another one around GIS8.

Response: done lines 271-273

L. machaerophorum is considered as mixotrophic, can you please explore this a bit further?

Response: This apparent conflict is discussed in our recent paper on the same margin but on longer time scales: see Eynaud et al., 2016. We suggest adding in the revised text: “Previous studies have revealed contrasted patterns between brown heterotrophic and L. machaerophorum cysts. Their apparent conflict is discussed at long time scales on the southern Iberian margin area in Eynaud et al. (2000; 2016).” lines 286-288.

Not sure that you can cite a paper in preparation. May be Pers. Comm. Would be more suitable.

Response: reference deleted and replaced by Pers. Comm. line 372

Correct spelling of Sanchez-Goni

Response: corrected throughout the text

replace “deduced” with “suggested”

Response: done line 466

replace “and” with “as well as”

Response: done line 467

occurrences of the thermophilic

Response: done line 468

replace “attest of” with “indicate”. Suggestion: warmer surface conditions at a time when bottom MOW velocity was reduced.

Response: done line 469

replace “are obviously related” with “seem to be related”

Response: done line 498

At the onset of the Holocene,

Response: done line 519

correct “contributes”

Response: done line 548

Conclusion: It is a bit weak. Your first sentence should refocus on the hypothesis from the introduction, i.e. change of primary productivity recorded by the dinocysts. The rest is a bit weak, more like a summary than a conclusion.

Response: the conclusion has been re-structured
Please note that all corrections should be applied to the corresponding references in the text in order to maintain consistency. The corrected references should be: Mertens et al., 2009b was a mistake in the reference list since it was not cited in the manuscript. There is only one reference of Mertens et al., 2009 in the text now and the « a » is then no longer useful.

Some references in the list are not in the right chronological order (Ambar and Howe, 1979; Bar-Matthews et al., 2000)

Response: corrected

Give all authors’ names for Barker et al. 2009; Magny et al., 2013; Rogerson et al, 2010

Response: corrected


Response: corrected

References not in the list:

Réponse : corrected
Paleohydrological changes over the last 50 ky in the central Gulf of Cadiz:

Complex forcing mechanisms mixing multi-scale processes

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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 to discuss paleohydrological changes over the last 50 ky in the subtropical NE Atlantic Ocean. Some index dinocyst taxa, according to their (paleo) 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 millennial time scale. Enhanced fluvial discharges occurred during Greenland Interstadials (GI) and 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 that we attributed to an advection of warm and nutrient-poor subtropical North Atlantic Central Waters. Over the last 50 ky, our study thus allows capturing and documenting the fine tuning existing between terrestrial and marine realms in North Atlantic subtropical latitudes, not only in response to the regional climate pattern, but also to 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.

KEYWORDS: Gulf of Cadiz; Dinoflagellate cysts; Dansgaard-Oeschger events; Lingulodinium machaerophorum; Obliquity and precession forcing; Paleoriver discharges; Upwelling.
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 then significantly contribute to CO$_2$ storage. In this context, the North Atlantic is the major contributor to atmospheric CO$_2$ sequestration (Sabine et al., 2004; Takahashi et al., 2009), especially in high latitudes, even if uncertainties remain on the calculated amount stored by coastal regions (e.g. Flecha et al., 2012). Disregarding abiotic processes, CO$_2$ 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 as well as in temperate and subpolar regions; these micro-organisms being extremely sensitive to climate changes at seasonal and interannual time scales. In this study, we targeted a major component of the modern phytoplanktonic biomass, the dinoflagellate group. About 15% of living dinoflagellate 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 to discuss qualitatively as well as quantitatively past surface environments; 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 responsibility for CO$_2$ and CH$_4$ storage (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 time scales (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 was demonstrated that productivity changes in this region involve complex hydrographical dynamics, including upwelling (Abrantes 1991, 1992), river inputs, 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 paleohydrological and paleoproductivity 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 paleohydrographical 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 paleoclimatological 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 oriental part of the North Atlantic’s subtropical gyre directly adjacent to the Gibraltar Strait (<14km width, <300m depth); the latter channelling water mass exchanges between Atlantic waters at the surface and saltier/denser Mediterranean Outflow Waters (MOW) at depth. This area thus associates 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 features which are: the Portuguese and Moroccan coastal currents, a branch of the Azores Current (AzC; Figure 1) flowing eastward at 35°N (Peliz et al., 2009), and the MOW also contributing to the generation of the AzC that feeds the Canary Current (CC; Figure 1) to the South. 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 both in terms of temperature gradients (about 4°C; Gould, 1985) and vertical structure of the water column (Fasham et al., 1985). This front is locally characterized by intense upwelling cells and thus higher sea-surface productivity (Rudnick, 1996; Alves and de Verdière, 1999; Alves et al., 2002). Nowadays, 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 CO₂ 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 Guadania, 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 influences 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, the evidence of extremely close paleohydrological patterns between the central Gulf of Cadiz and the NW Moroccan margin supported the idea of similar forcing acting on both these subtropical areas of the NE Atlantic margin (Penaud et al., 2011a).

Water masses from our study area are structured as follow: 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 1,200 m water depths, and also at 500 m in the continental shelf (Ambar and Howe, 1979; Ambar et al., 2002). North Atlantic Deep Waters are found below 1,500 m (Alvarez et al., 2005).
3. MATERIAL AND METHODOLOGY

3.1. Marine cores integrated within the study: chrono-stratigraphy

Core MD99-2339 (35.89°N; 7.53°W; 1170 m water depth; 18.54 m length; Figure 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 (IMAGES V-GINNA) cruise (Labeyrie et al., 2003). It covers the last 45 ky according to its published age model (Voelker et al., 2006) that is based on 20 AMS \(^{14}\)C dates and three \(^{18}\)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 1,400 years at 1500 cm; Voelker et al., 2006; Figure 2) and inconsistencies with the regional North Atlantic stratotype NGRIP GICC05 time scale (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; Figure 1). Such an approach is validated by previous works conducted on the southern Iberian margin where the stratigraphy of paleoclimatological reference sites were constructed using a similar tuning to Greenland ice records (e.g. Shackleton et al., 2000; Bard et al., 2004). This event based stratigraphy (i.e., Austin and Hibbert, 2012), however, prevents establishing any definitive conclusion about latitudinal leads and lags, and evaluating intra-hemispheric propagation velocities of climatic perturbations. To build the revised age-depth model (Figure 2), we chose to keep six radiocarbon dates (Voelker et al., 2006; Figures 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 \(^{18}\)O record (G. bulloides) of core MD99-2339 (thirteen pointers; Figures 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; Figure 2). Sedimentation rates show a general decreasing trend from 60-90 cm/ky around 40-45 ka BP to 10-40 cm/ky across the Holocene (Figure 3).

3.2 Dinoflagellate cyst analysis

3.2.1. Laboratory procedure and microscopic observation

161 samples were analysed for their dinocyst content every 10 cm in average, representing a sample resolution of around 300 years [σ=210] for the whole MD99-2339 core, using an Olympus BX50 microscope at 400X 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 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% and 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 fushin.

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 to obtain statistically robust dinocyst results (Fatela and Taborda, 2002). Dinocysts can be expressed in percentages and also in concentrations (number of specimens/cm³ of dry sediments), that are calculated through the marker grain method (Stockmarr, 1971; de Vernal et al., 1999; Mertens et al., 2009).
consists in adding aliquot volumes of *Lycopodium* spores before the palynological treatment in each sample; 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 versus 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/cm²/ky).

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 time scale, dinocyst fluxes may provide a better insight on dinocyst export to the seafloor, and perhaps also indirectly on 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 MD99-2339 core (cf. Table 1).

**Heterotrophic / Autotrophic ratio**
Most dinoflagellate species are mixotrophic, and strict autotrophic (phototrophic organisms) are rare. However, previous investigations 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 it 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; Bouimetarhan 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”; “coastal heterotrophics” being more specifically used for Selenopemphix species (S. quanta and S. nephroides; Table 1). Also a ratio “Heterotrophics / Autotrophics” (H/A) can be addressed that simply takes into account “strict” heterotrophic occurrences versus the other dinocyst taxa identified in fossil assemblages.

**Diversity statistics**

Quantifying taxonomical diversity in study samples was carried out through a variety of statistical analyses using the “Past version 1.75b” software (Hammer et al., 2001); most of these indexes being explained in Harper (1999). Here, we calculated the number of taxa per sample (S), the dominance (D) that 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 (paleoceanographic 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 1,492 stations from the North Atlantic, Arctic and North Pacific oceans and their adjacent seas, and is run under the “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; 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, leading then occasionally to non analogue configurations. Here, we discuss Winter/Summer SST with prediction errors of ±1.2°C/±1.6°C, respectively, Winter/Summer SSS, with prediction errors of ±2.1°C/±2.3°C, respectively, as well as primary productivity reconstructions with prediction error of 57 gC.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 was identified, with an average diversity of 20 main species. Considering the whole dinocyst assemblage, increased total diversity (Figure 4c) generally appears anti-correlated to decreased dominance (Figure 4d); this index being essentially explained by *Lingulodinium machaerophorum* percentages through time (Figure 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 if the paleoceanographical record has been disturbed by MOW plume hydrodynamics or advection by sedimentological processes (i.e. downslope transport). Large increase of 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 Figure 4 (diversity versus 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 cysts/cm³), with the exception of two large maxima, centred on GI 8 and GI 12, showing higher values (between 100,000 and 400,000 cysts/cm³) (Figure 4f). A general trend of decreasing concentrations is then observed throughout the record with lower values observed during the early to mid-Holocene (between 1,000 and 10,000 cysts/cm³) and especially at the very start of the Holocene (1,500 cysts/cm³; at 150-200 cm), following the cold interval of the Younger Dryas (YD) (Figure 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 (Figure 4h) and thus also accounts for extremely high dinocyst fluxes to the seafloor during MIS 3 (Figure 4j), compared to the last deglaciation and the Holocene. Total dinocyst concentrations are mainly explained by *L. machaerophorum* alone (Figure 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 (Figure 4g), it is interesting to note that both heterotrophic and *L. machaerophorum* concentrations / fluxes reveal the same decreasing trend along the record (Figure 4j). Previous studies have revealed contrasted patterns between brown heterotrophic and *L. machaerophorum* cysts. Their apparent conflict is discussed at long time scales on the southern Iberian margin area in Eynaud et al. (2000, 2016).

### 4.2. Dinocyst species reflecting qualitatively main paleohydrological changes

Present-day ecologies of major species found in MD99-2339 assemblages are listed in Table 1 with their major past occurrences in the fossil record. The detailed examination of the qualitative thermic index “Warm/Cold” (W/C) (Table 1; Figure 5; cf. subchapter 3.2.2 of this paper), compared with the planktonic δ^18O 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 then confirming the robustness of reconstructed surface environments through dinocyst assemblages in the central Gulf of Cadiz.

Specific percentages, calculated relatively to the total dinocyst assemblages but also *versus* a total that excludes *L. machaerophorum*, reveal that trends with or without *L. machaerophorum* are similar (Figure 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 (Figure 1) over the last 28 ky (Penaud et al., 2010; dotted lines in Figure 5). Obvious correlation between surface...
conditions recorded off the NW Moroccan coast (Marret and Turon, 1994; Penaud et al., 2010) and in the central part of the Gulf of Cadiz may be due to same dynamics governing paleohydrological changes in this sector (Penaud et al., 2011a). Considering more specifically heterotrophics, these are never dominant among studied assemblages (Figure 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 Brigantedinium percentages increased during GS (i.e. periods with relatively well-oxygenated bottom waters related to MOW dynamics) may argue for a negligible effect of oxidation processes on species-selective degradation after cyst deposition in our study site. Significant occurrences of some selected species (Table 1; Penaud et al., 2011a), and especially coastal heterotrophics (S. quanta and S. nephroides; Figure 5), will then indirectly reflect varying regimes of mesotrophic-oligotrophic conditions in the Gulf of Cadiz over the last 50 ky.
5. UNDERLYING MECHANISMS BEHIND DINOCYST CHANGES AT ORBITAL AND SUB-ORBITAL TIME SCALES 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 re-structuration of the water column. Understanding mechanisms underlying the complex pattern of paleoproductivity changes at orbital as well as millennial time scales 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 Gibraltar Strait, iceberg or fluvial discharges, and frontal upwelling cells; all of these being more or less inter-connected at different time scales.

5.1. Glacial fertilisation control on marine surface productivity

Annual productivity quantifications calculated from dinocyst transfer function (Figure 6), the qualitative ratio H/A, as well as 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 (Figure 6). Similar decreasing paleo-productivity at the end of the last glacial period (Voelker et al., 2009) was also previously discussed in 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 fertilisation effect caused by increasing aeolian dust supply to the ocean under stronger glacial winds (Moreno et al., 2002; Bout-Roumazeilles 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 are the highest (around 500 gC/m² compared to present-day values of about 90 gC/m²;
Figure 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 (Figure 7)
and total heterotrophic percentages (H/A; Figure 6) between 26 and 15 ka BP (Penaud et al., 2011a).

5.2. Orbital control on paleo-river discharges and nutrient availability

Furthermore, when considering L. machaerophorum percentages versus orbital parameters, a very close
relationship to the obliquity curve becomes obvious (Figure 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, the latter accounting 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) (Figure 7). The Mediterranean Basin being subject to interference of
northern and tropical latitudes, both obliquity and precession signals may be considered. They indeed
represent major influences for the East African and West Indian summer monsoon systems (Tuenter et
al., 2003) and can be evidenced, for instance, in Mediterranean paleorecords (Lourens et al., 1996,
2001). Furthermore, Tuenter et al. (2003) discussed the fact that the combination “obliquity maxima -
precession minima” (cf. MIS 1 in Figure 7) would have a weaker effect on the African monsoon,
compared to the combination “obliquity maxima - precession maxima” (cf. MIS 3 in Figure 7). This would
be consistent, during MIS 1, with our recorded enhanced stratification related to lower productivities
(Figure 6), especially between 10 and 6 ka BP, and our recorded enhanced stratification during periods of
higher productivities across the last glacial (Figure 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. PhD, Pers. Comm.). We can assume that high nutrient availability in the Gulf of Cadiz during
the last glacial may has been similarly high to modern nutrient availability in the northern latitudes of the
temperate NE Atlantic (Bay of Biscay). This northward migration of paleo-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 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
also may contribute to explain 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 preindustrial state (Le Mézo et al., EGU2015, unpublished data). It evidences the crucial
role of obliquity, i.e. glacial-interglacial conditions responsible for changing oceanic circulation, as a main
driver for phytoplanktonic productivities (Hardy et al., 2016).

5.3. MIS 3 and the atypical pattern of Greenland Interstadials 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; Figure 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 (MD95-2043 core; Penaud et al., 2011b; Figure 1), have been compared so as to qualify Mediterranean-Atlantic surface exchanges at times when MOW experienced strongest/weakest bottom current velocities (Figure 8).

A first look on dinocyst concentrations for selected individual species (Figure 8d,e,f) reveals extremely close patterns from either side of the Strait of Gibraltar, however, with 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 (Figure 8d). Total dinocyst concentrations are also characterized by similar temporal fluctuations but different reconstructed values; these marked value differences being only explained by *L. machaerophorum* concentrations since other “autotrophic” species show generally comparable orders of concentrations (Figure 8g).

It is interesting to note that even if individual species concentrations follow obvious identical oscillations, they are not as clear when considering their relative abundances (Figure 8k, l, m). *L. machaerophorum* percentages generally dominate whole cyst assemblages all over MIS 3 in the Gulf of Cadiz, such as today (Rochon et al., 1999; Marret and Zonneveld, 2003; Zonneveld et al., 2013; Table 1; Figure 8k). In the Alboran Sea, *N. labyrinthus* (cool-temperate, outer neritic) percentages mirror *L. machaerophorum* (temperate, inner-neritic) ones in the Gulf of Cadiz (Figure 8l); 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 marshes 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 MD99-2339 core while *N.*
*labyrinthus* will preferentially characterize MD95-2043 one. When these two species are summed, their percentages show obvious similar patterns both in terms of values and timing of the different recorded peaks (Figure 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 (Figure 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 (Figure 6); dry and cold winter conditions being also previously recorded in these latitudes (Sánchez-Goñi et al., 2002; Combourieu-Nebout et al., 2002; Moreno et al., 2002, 2005; Bout-Roumazeilles et al., 2007). *B. tepikiense* combined with the polar foraminifera *N. pachyderma* s. attest, respectively, to enhanced seasonality (large offset between summer and winter temperatures as confirmed by dinocyst transfer function; Figure 6) and important coolings in the interval 25-50 ka BP (Figure 6). "*N. pachyderma* s. - *B. tepikiense*” thus evidence 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 (Figure 8). During HS, this occurs in a context when 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.,
In the Gulf of Cadiz, during HS, increased annual productivity reconstructions (Figure 6) together with increased heterotrophics (especially *Brigantedinium* spp.; Figure 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 BP by the strong decreasing gradient of *N. pachyderma* s. percentages obvious during HS across a small N-S 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 (Figures 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. Greenland Interstadial (GI) and 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 (Figure 5) as well as seasonal SST reconstructions with values close to modern ones (Figure 6). Synchronous occurrences of the thermophilic species *S. mirabilis* on both sides of the Gibraltar Strait (Figure 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; Figure 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”; Figures 7 and 8), also previously described for the Alboran Sea (Penaud et al., 2011b; cf. Figure 8). While the first part (“a”) is characterized by increasing coastal heterotrophics (Figure 8o) and thermophilic species (Figure 8c), paralleling higher polar air temperatures (Figure 8j); the second part (“b”) is characterized by the highest total dinocyst concentrations (Figure 8h) and L. machaerophorum percentages (Figure 8k) ever recorded over the last 50 ky. This second part is also characterized by a strong S. mirabilis drop (Figure 8c), and the lowest winter SST (10°C colder than today; Figure 6) and SSS (around 30 reconstructed at that time; Figure 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 (Figure 8j). Within both second phases (“b”, Figure 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 would deserve model simulations, our results argue for a fast response of the ocean in this millennial / infra-millennial time scale context of rapid climate change.

5.4. Dinocyst specific pattern across MIS 1
Interestingly, during MIS 1, decreased dinocyst fluxes and increased *Impagidinium* percentages (Figure 7) seem to be related to the humidity pattern as recorded in Western (Fletcher and Sánchez-Goñi, 2008; Figure 7) and Eastern (Bar-Matthews et al., 2000, 2003; Figure 7) Mediterranean records. During the first half of the Bölling-Alleröd (BA), *Impagidinium* species (especially *I. aculeatum*; Figure 5) strongly expand (Figure 7), arguing for the establishment of full oceanic and warm conditions, that may suggest oligotrophic conditions in this area (cf. dinocyst transfer function; Figure 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; Figure 7) and thus decreased river runoff onland 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 a 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). Noteworthy, 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 Figure 7). The final BA (“b”) is indeed marked by a drastic drop of *Impagidinium* spp., a strong increase of *L. machaerophorum* percentages and high values of total dinocyst concentrations (Figure 7). This may suggest slightly more productive conditions (cf. Figure 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 (Figures 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; Figure 7) observed in core MD99-2339 is the largest of the record, then suggesting a strong reduction of MOW flow strength (Voelker et al., 2006), as also evidenced in Western Mediterranean Sea contourites from the Corsica through (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; Figure 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, 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 (Figure 6), the lowest dinocyst fluxes (Figure 6) and by the highest percentages of Impagidinium spp. ever recorded over the last 50 ky BP (Figure 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 when Mediterranean forest strongly expanded (Fletcher and Sánchez-Goñi, 2008; Figure 7) preventing dust re-mobilization 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 also probably 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; Kaboth et al., 2015). 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 (Figure 7).

6. CONCLUSION

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 deserve 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) enable to consider dinocyst population shifts over the last 50 ky in the subtropical northeastern Atlantic Ocean. This study provides important evidences of migrating paleoproductivity centres from the last glacial period to the Holocene, and can be therefore also 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* that 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 paleo-precipitations, primarily forced by obliquity maxima at orbital time scales. 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 paleohydrological 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. ACKNOWLEDGMENTS

Thanks to the French polar institute IPEV (*Institut Paul Emile Victor*), the captain and the crew of the Marion Dufresne and the scientific team of the 1995 IMAGES cruise. We wish to thank M. Castera, M. Georget and O. Ther for invaluable technical assistance at the laboratory. This study was supported by the French CNRS and contributes to the 2013 INSU project: « ICE-BIO-RAM : Impact des Changements Environnementaux sur la BIOdiversité marine lors des Réchauffements Abrupts du cliMat » (http://www.insu.cnrs.fr/files/ao_2013_--_eynaud_validee.pdf). This work was supported by the «Laboratoire d'Excellence» LabexMER (ANR-10-LABX-19) and co-funded by a grant from the French government under the program «Investissements d’Avenir». AV acknowledges her Investigador FCT (IF) Development Grant.
8. REFERENCES


9. TABLE CAPTION

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

10. FIGURE CAPTION

Figure 1: Area of interest with major sea-surface features. Study core MD99-2339, as well as other cores discussed in the paper, are located on the large map, depicting also 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 present large scale North Atlantic currents with: the North Atlantic Drift (NAD), the Portugal Current (PC) flowing southward from 45°N 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.

Figure 2: a) Age-depth model for core MD99-2339 (all symbols are explained in the Figure), allowing to compare: b) the new age model (this study: planktonic δ¹⁸O monospecific record in black) with the first published one (Voelker et al., 2006: planktonic δ¹⁸O record in red).

Figure 3: Comparison, against age (new age model from this study), between the planktonic δ¹⁸O monospecific record of core MD99-2339 (red curve, Voelker et al., 2006) and the NGRIP δ¹⁸O according to the GICC05 time scale (Svensson et al., 2008). a) Red stars locate the 6 radiocarbon dates retained for the chronology of core MD99-2339, and dark arrows locate the 13 pointers used to tune the δ¹⁸O data of core MD99-2339 to the NGRIP chronology, by considering GI onsets (numbers 1 to 12 on the Figure) according to Wolff et al. (2010). Sedimentation rates, calculated between different pointers of core MD99-2339, are also highlighted with the dark histogram. YD: Younger Dryas, BA: Bölling-Alleröd. b) A zoom on the interval 25 - 50 ka BP enables to better consider the pointers selected (dotted vertical lines) for this new age model.

Figure 4: Data from core MD99-2339 against depth (cm). δ¹⁸O 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 in linear scale, while h) illustrates total dinocyst and L. machaerophorum concentrations in 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).
Figure 5: Data from core MD99-2339 against age (cal ka BP): major taxa occurring with values higher than 2% in dinocyst assemblages from MD99-2339 core (0 - 48 ka BP; 0 - 1,854 cm). Red, blue and green colours respectively indicate the “Warm”, “Cold”, and “Heterotrophic” groups. W/C: Warm-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 ky 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, GI: Greenland Interstadial) and blue bands indicate colder events (HS: Heinrich Stadials and YD: Younger Dryas).

Figure 6: Data from core MD99-2339 against age (cal ka BP). δ¹⁸O 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 paleo-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 gC.m⁻², percentages of L. machaerophorum of 65.27% and B. tepikiense of 0%.

Figure 7: Greenland δ¹⁸O data (a) in parallel with data from core MD99-2339: planktonic δ¹⁸O (b) and mean grain-size <63 µm (c), over the last 50 ky. Dinocyst data (f, h, i, j) from core MD99-2339 are also depicted versus Western (pollen, Alboran Sea, g) and Eastern (δ¹⁸O, 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). 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. Full blue / blue curves represent MD99-2339 data (Gulf of Cadiz, this study) while full red / 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).
See Supplement Material for Table 1

Figure 1
Figure 2

Radiocarbon dates kept for the new age model
Stratigraphic pointers tuned with NGRIP GICC05
Radiocarbon dates not used for the new age model with their error bars

New age model (this study)
Age model from Voelker et al. (2006)
Figure 3
Figure 4

- a) $\delta^{18}$O planktonic (G. bulloides) (Voelker et al., 2006)
- b) WC ratio
- c) Margalef richness index (dotted line)
- d) Dominance index (straight line)
- e) L. machaerophorum Linuc (%)
- f) Dinocyst concentrations (10$^6$ cysts/cm$^2$)
- g) Heterotrophic concentrations (10$^6$ cysts/cm$^2$)
- h) Dinocyst concentrations (10$^6$ cysts/cm$^2$) - Lag scale
- i) Sedimentation Rates (cm/ky)
- j) Total dinocyst fluxes (straight line) (10$^5$ cysts/cm²/ky)

*C*: B. teyshiense, N. lathyruthus, S. elongatus, S. kezer, cysts of P. steiet
Figure 6
Figure 7