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CHAPTER 8 : PLANKTIC FORAMINIFERA THROUGHOUT THE PLEISTOCENE: FROM CELL TO POPULATIONS TO PAST MARINE HYDROLOGY

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ABSTRACT

Among microfossils currently extracted from Cenozoic sediments to reconstruct past environments are planktic foraminifers. These small calcareous organisms are furthermore probably ranked first in this set of tools when considering Paleocanography, a science that has grown up proportionally to their use since now more than half a century. Planktonic foraminifera (PF) actually constitute the key material for paleoceanographers as a basic tool for stratigraphical and paleoecological reconstructions, both often based on coupled geochemical and micropaleontological approaches. Since the late ninety's, the modern calibration of the PF proxy has taken growing importance, challenging the principle of uniformitarianism, especially in response to questions introduced by the molecular biology. This calibration can rely on two approaches: the first implies repetitive surveys of modern populations (throughout plankton tows or sediment traps) and the other one directly targets the analysis of recently fossilized populations in the topmost oceanic sediments in order to implement regional databases and develop the statistical approach of transfer functions *sensu lato*. This paper reviews the strengths and weaknesses of the latter approach, focusing on the North Atlantic Ocean (and its border seas), which up to now counts the largest existing set of data concerning planktonic foraminifera population.

Keywords: planktic foraminifera, paleoceanography, paleo-environmental transfer functions.

INTRODUCTION

The modern earth system cannot be considered anymore as a natural system since human imprints are detectable among each biotic or abiotic reservoir. This is the basic line which has contributed to the definition of the "Antropocene era" concept, with an anthropogenic bias dominating since at least 200 years (e.g., Crutzen 2002; Crutzen and Steffen 2003) or that could have begun as soon as 4000 years ago (Ruddiman 2003). In this context the retrospective approaches based on fossil archives constitute the unique way to define the initial (zero) state of our natural system, with additionally the recognition of what are natural ranges in environmental oscillations: "what has been possible in the past could be possible in the future…"

Few ways exist to provide robust evaluations of past environmental changes. Most of them firstly depend on the recovery of preserved (undisturbed) archives offering enough material to undertake statistically valid investigations and construct an adequate chronology. Among the existing ones, we can cite for instance the high resolution reconstructions obtained from geological rhythmites (corals, speleothems, varves in sediment…), but for marine environments the most popular tool is probably the micropaleontological record offered by planktic foraminifera. These calcareous protists are the basic material of paleoceanographical approaches (e.g., Emiliani 1955) and are used extensively as the support of both geochemical (^{14}AMS measurements, stable isotopes, elemental ratio) and (paleo)ecological studies. Geographically confined in bio-climatic provinces but also in specific water-depth windows (e.g. Hemleben et al. 1989), they represent precious (paleo)-bioindicators.

The present contribution focuses on their interest in quantitative approaches and is based on the reanalysis of the North Atlantic databases delivered in the frame of the MARGO project (Hayes et al. 2005; Kucera et al. 2005a, b; MARGO project members, 2009). A new database has been built from this set of data and is herein tested and used to perform quantification of Sea Surface Temperatures (SST) with the aid of an ecological transfer function (Guiot and de Vernal 2007) developed at the EPOC laboratory (Environnements et Paléoenvironnement OCéaniques, Bordeaux1 University, France). Several sequences from diversified places within the North Atlantic Ocean are furthermore tested to highlight the strengths and limitations of this approach.

QUANTITATIVE TOOLS IN PALEO-ENVIRONMENTAL RECONSTRUCTIONS: POTENTIALITIES AND WEAKNESSES OF PLANKTIC FORAMINIFERA

Since the discovery of planktic foraminifera (PF) and their first use as qualitative proxies of sea-surface conditions, researchers tried to overcome issues linked to the subjectivity in the interpretation of faunal assemblages. Patterns within the bioclimatic distribution of foraminifera have been established early in the history of oceanography (e.g. Brady 1884) and therefore many micropaleontologists derived observed changes in the assemblages especially for PF to environmental variables, such as sea-surface temperatures. The next step was to provide data beyond these qualitative pictures, and thus quantitative palaeoenvironmental reconstructions were developed based on statistical and mathematical methods (i.e., via transfer functions). This contribution does not aim at a review of the different methods which were applied to biotic assemblages, as many literature has been produced on the subject for PF or other microfossils (i.e., Imbrie and Kipp 1971; Hutson 1977; Birks 1995; Maslin et al. 1995; Pflauman et al. 1996: Waelbroeck et al. 1998; Kucera et al. 2005b; Telford and Birks 2011; see Guiot and de Vernal 2007; 2011a, b for a complete review). Focusing our summary on PF, the first major achievements were obtained with the Imbrie and Kipp (1971) approach (IK), which was rapidly replaced by the Modern Analogue Technique (MAT), which up to date remains the most applied and performing one in spite of the development of much complex approaches, such as the Artificial Neural Networks (ANN) (e.g. Kucera et al. 2005b, Hayes et al. 2005, Guiot and de Vernal 2007). Different versions of MAT have been successively developed and they are all derived from *k*-nearest-neighbour algorithms (see Guiot and de Vernal 2007 for a review). The most critical point is the construction of the database, which constitutes the original set of training compiling modern analogues, for each of the cited approaches. The most extended the set is, the most analogues it provides, but conversely regional extremes could bias quantifications (see discussions in Waelbroeck et al. 1998; Guiot and de Vernal 2011a, b). Using micropaleontological assemblages, modern samples are thus obtained from oceanic surface sediments for which the age control is of primary importance (see recommendations in Kucera et al. 2005a).

The n=1007 Database

The database herein discussed was built upon two of the geo-referenced databases which were developed and/ or revised for the MARGO exercise (e.g., Kucera et al. 2005a, b). It couples 1007 points respectively distributed in the North Atlantic Ocean (Kucera et al. 2005b, which is mainly derived from the one used in Pflauman et al. 1996) and in its adjacent sea, namely the Mediterranean basin (Hayes et al. 2005) (Figure 1).

The choice of this coupling was justified by the highest options it provides for the selection of modern analogues, especially for cores that are located in subtropical latitudes surrounding the Gibraltar strait. Ambiguous data points were excluded from the original MARGO databases by a mapping of the biogeographical distribution (under the ARCVIEW GIS) of the 38 selected species. Incoherent samples were deleted resulting in a final set of n=1007 data points. Modern hydrological parameters (exclusively sea-surface temperatures, namely SST for PF) were requested from the World Ocean Atlas (1998) using the "WOA sample tool" developed during the MARGO project, which allows the extraction at 10 m depths of annual SST and seasonal SST (average winter - January/February/March, spring - April/May/June, summer - July/August/September and fall - October/November/December) (Schäfer-Neth and Manschke 2002). Here again their coherency regarding the WOA ATLAS seasonal SST was tested by mapping their distribution with the ARCVIEW-GIS (see supplementary information online).

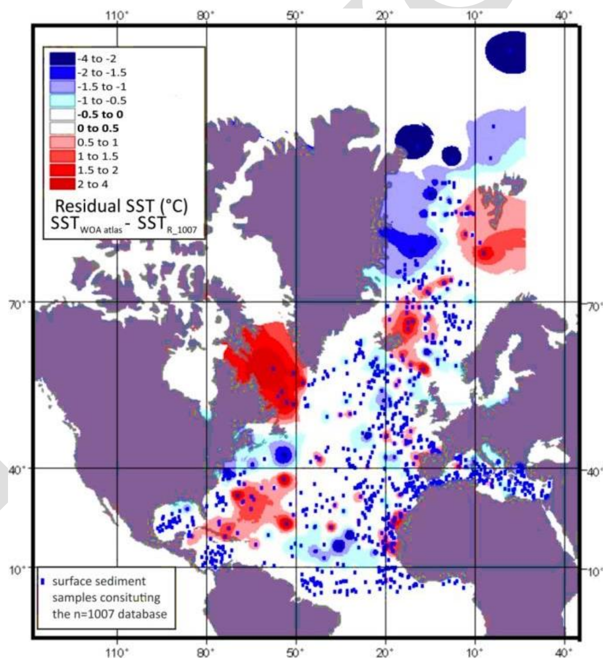

Figure 1. Geographical distribution of the n=1007 points (surface sediment samples) included in the North Atlantic database. The difference in this set of training when compared to the MARGO database (Kucera et al. 2005b) is related to the inclusion of the Mediterranean basin samples (Hayes et al. 2005). On this map are also plotted the residual differences (°C) obtained by the mathematical difference between the values extracted from the WOA ATLAS (with the WOA sample tool, Schäfer-Neth and Manschke 2002, http://www.geo.uni-bremen.de/geomod/staff/csn/woasample.html) and those obtained with the MAT$_{R}$_1007$_{PF}$ for the mean ANNUAL SST (autorun of the database with the exclusion of the tested sample). Contours were drawn with ARCVIEW.

The MAT_R_1007_{PF} Protocol and Its Limitations

The MAT, which was run on the basis of the North Atlantic PF n= 1007 database (further named MAT_R_1007_{PF}), is a very intuitive tool. It relies on several statistical tests and different calculation steps (see Guiot & de Vernal 2007 for the complete explanation of the protocol) which, as a result of a necessity to homogenise and inter-calibrate transfer function *sensu lato* protocols, were lumped under the R software (http://www.r-project.org/) within the BIOINDIC package developed by J. Guiot (https://www.eccorev.fr/ spip.php?article389). The MAT_R_1007_{PF} is run with the ReconstMAT script. Quantifications are based on the selection of the five best modern analogues existing in the database. The selection relies on the calculation of dissimilarity indexes directly from relative percentages for which no further mathematical transformations have been applied. In fact, the root square or logarithmic transformations are commonly used in MAT for instance for other bioindicators, notably when it concerns assemblages where the species diversity is higher than 50 (i.e. dinocysts, pollen…, e.g., Guiot & de Vernal 2007). We will see in section 3 that these modifications which contribute to equalize the diversity structure (they artificially increase the equitability) are not necessary useful for PF (except in cases of very low diversity indexes, but quantitative methods have no interest for such assemblages).

Past hydrological parameter values are derived from a weighted average of the SST values of the five best analogues. The maximum weight is given for the closest analogue in terms of statistical distance / i.e. dissimilarity minimum (Guiot and de Vernal 2007). The ReconstMAT script furthermore includes the calculation of a threshold regarding the distance which prevents calculation in the case of poor- or no- analogous situations. The degree of confidence of this method allows reconstructing seasonal and annual SST with a root mean square error (RMSEP) of prediction of maximum 1.3°C (Table 1). These low RMSEP values mask internal disparity in the transfer function highly dependent on its geographical structure. This is illustrated in Figures 1 and 2, which compile differences obtained by comparing the "true"-ATLAS values to the "calculated" (i.e., MAT_{1007} derived) ones for the mean annual SST. This disparity is plotted as a mapping of the residual SST (mathematical difference) in Figure 1, whereas the Log ratio between true and calculated values is displayed in Figure 2 along the SST_{annual} and latitudinal ranges covered by the database.

Hydro-graphical parameters	Annual SST (°C)	Winter JFM SST (°C)	Spring AMJ SST (°C)	Summer JAS SST (°C)	Fall OND SST (°C)
RMSEP	1.1	1.2	1.1	1.3	1.2

Table 1. Prediction error (°C, RMSEP : root mean square error of prediction).
Values are calculated from the residual differences obtained by the mathematical difference between the values extracted from the WOA ATLAS (with the WOA sample tool, Schäfer-Neth and Manschke 2002, http://www.geo.uni-bremen.de/geomod/staff/csn/woasample.html) and those obtained with the MATR_1007_{PF} (autorun of the database with the exclusion of the tested sample). See also Figure 1.

These figures clearly underline the limitation of PF transfer functions (MAT in our case) for polar basins where is recorded the maximum disparity in the calculated ("modeled") values, when compared to the WOA ATLAS ones. This is precisely where the diversity of the PF assemblages is significantly low, with the taxon *Neogloboquadrina pachyderma* sinistral representing between 90 and 100 % of the PF assemblage (Ericson 1959; Kucera et al. 2005b; de Vernal et al. 2006; Eynaud et al. 2009a, b, 2011). This represents one of the most important limitations for transfer functions deriving from PF and should be considered for further studies. The MAT_R_1007_{PF} protocol has however successfully provided several paleoceanographical reconstructions that were used in a number of papers on this topic (Penaud et al. 2011; Matsuzaki et al. 2011; Sánchez Goñi et al. 2012, 2013). They document a large range in geographical and temporal case studies, which will be extended and discussed in the following sections.

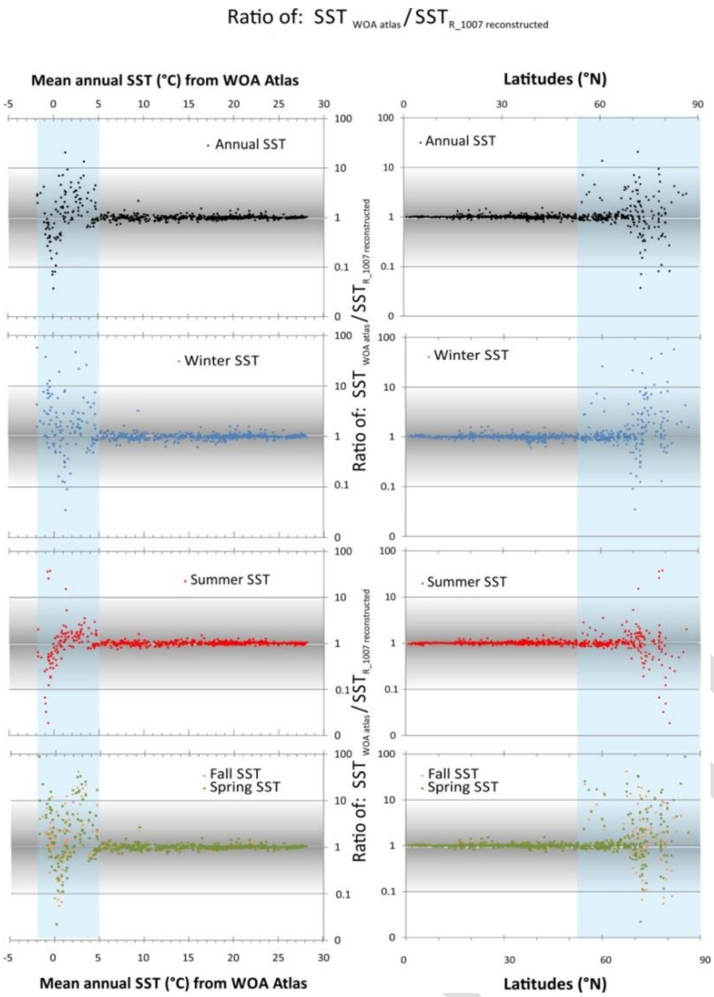

Figure 2. Logarithmic distribution of the ratio between values extracted from the WOA ATLAS and those derived from MAT_R_1007_{PF} for the mean ANNUAL SST plotted along the latitudinaland mean ANNUAL SST ranges covered by the n=1007 database. Values approaching one indicate that calculated values with the MAT_R_1007_{PF} protocol are close to those extracted from the WOA ATLAS. The blue vertical bands underline the ranges where the samples scattering indicate a limited confidence interval.

TESTING THE APPROACH OVER DIFFERENT TIME SCALES AND BASINS

Some MAT_R_1007_{PF} Reconstructions along the European Margin: A Focus on the Last Glacial Period

Six compiled reconstructions obtained for the summer season (the most discussed parameter in the literature) from MAT_R_1007_{PF} are shown in Figure 3. The selected cores have been chosen for their latitudinal and longitudinal distributions within the subtropical to temperate band (Table 2). They furthermore benefit from a robust age model and a high sedimentation rate for the considered time range, namely the last 20 ka (i.e., the last deglaciation). In Figure 3 are also plotted, when existing, the original reconstructions obtained with (comparable but not similar) transfer function *sensu lato* protocols applied to PF (from Sierro et al. 2005 on core MD95-2043, Voelker et al. 2006 on core MD99-2339 and Eynaud et al. 2012 on core MD95-2002 respectively), allowing us to test the coherency of the results throughout different databases and protocols. For cores located close to or within the Mediterranean basin, the geographical origin of the modern analogues used for the calculation is here also indicated. For each reconstructed series the low dissimilarity values allowed the systematic selection of 5 modern analogues, implying that the fossil assemblages were "realistic" enough to avoid one of the most critical issues related to transfer functions: the existence of non-analogous situations.

The obtained reconstructions provide a contrasted picture of the last glacial/interglacial transition with a high regional coherency. For instance, modern conditions are reached late in the Alboran sea, namely after 7.5 ka. This phenomenon occurred in this restricted basin with the installation of specific hydrological conditions, which were primarily forced by the sea-level rise and the associated inflow rate from the Atlantic waters (e.g., Rohling et al. 1995). This is also reflected in the localisation of the modern

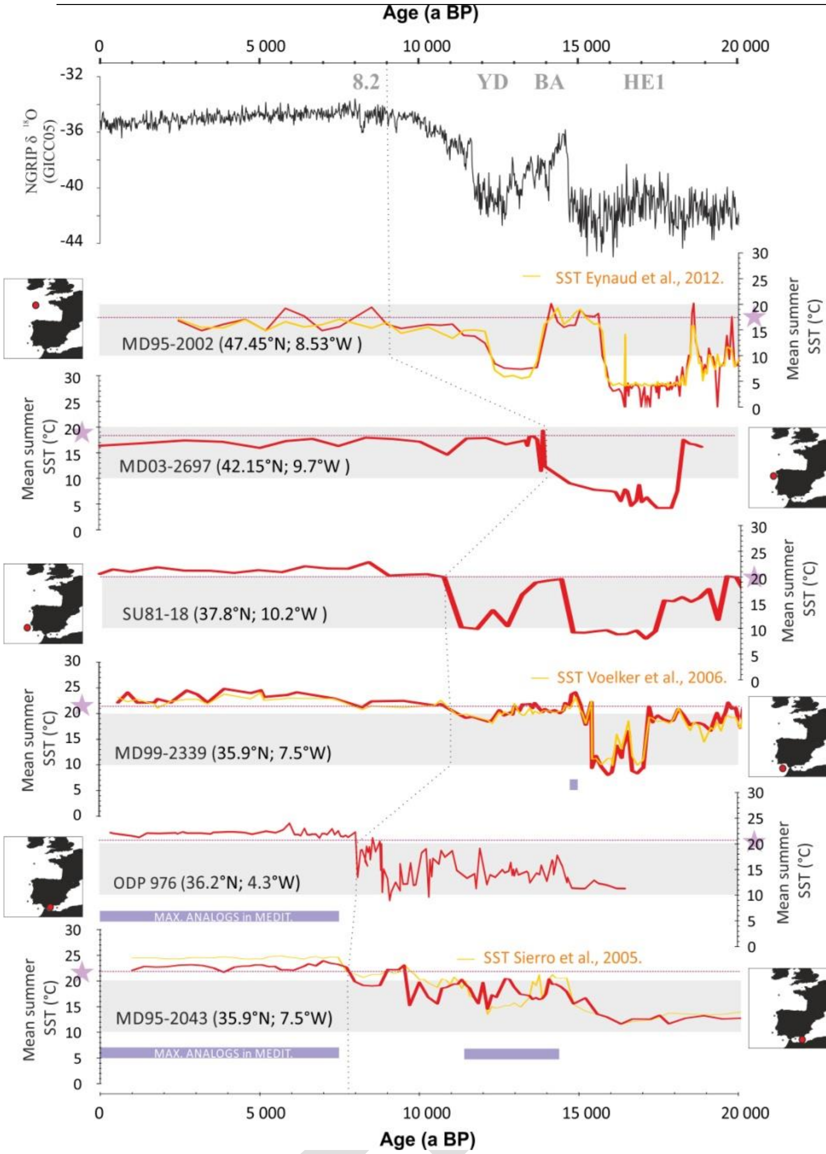

Figure 3. Latitudinal and basin scale compilation of summer SST reconstructions as derived from MAT_{R}_1007_{PF} during the last 20kyrs. Age scales of the selected cores conform to the original publications (MD95-2043 as in Sierro et al. 2005 also compared with their original calculations; ODP 976 as in Combourieu-Nebout et al. 2002; MD99-2339 as in Voelker et al. 2006 also compared with their original calculations; SU81-18 as in Turon et al. 2003; MD03-2697 as in Sánchez Goñi et al. 2008; MD95-2002 as in Eynaud et al. 2012 compared with their original calculations). The stars along the Y-axis indicate the modern SST values as extracted from WOA. Reconstructions are compared to the regional North-Atlantic stratotype (sensu Austin and Hibbert 2012; Austin et al. 2012) of the NGRIP-d^{18}O record (GICC05-1950 age scale after Svensson et al. 2008). The dotted vertical line limits the onset of modern SST stable conditions.

Core	**Latitude**	**Longitude**	**Water depth (m)**	**Annual (°C)**	**JFM (°C)**	**AMJ (°C)**	**JAS (°C)**	**OND (°C)**	**N**
MD95-2043	36.14	-2.62	1841	**18.2**	15.1	17.6	21.9	18.2	2
ODP976	36.20	-4.30	1108	**17.8**	15.4	17.3	20.6	18.0	2
MD99-2339	35.89	-7.53	1177	**18.5**	16.2	17.8	21.0	19.1	4
SU81-18	37.77	-10.18	3155	**17.7**	15.4	16.7	20.0	18.6	3
MD03-2697	42.15	-9.7	2164	**15.4**	13.2	14.7	17.7	16.0	4
MD95-2002	47.45	-8.53	2174	**13.9**	11.4	12.8	17.2	14.0	4

Table 2. Georeferences of the six selected cores including the mean annual and seasonal SST values (°C) over the respective sites as extracted from the WOA ATLAS (Schäfer-Neth and Manschke 2002).

analogues that are selected in the Mediterranean basin only after this major hydrological change (during the last glacial and up to 7 ka, all the best analogues are found within the North Atlantic). As a corollary, it implies that before this change calculations done with a limited Mediterranean set provide wrong or at least biased values. This could justify some revisions regarding the reconstructions that were made before within this basin, during or even after the MARGO exercises (e.g., Kallel et al. 1997; Hayes et al. 2005; Essallami et al. 2007; Rouis-Zargouni et al. 2010).

Along the subtropical to temperate European margin, modern conditions were first recorded with the Bölling-Allërod (BA) warm pulse, and became stabilized after the Younger Dryas (YD) event, namely between 11 to 10 ka BP. After this date the summer temperatures follow a linear trend with some small amplitude changes that are hardly connectable from one site to another. The values are very close from the modern ones and with, at least for the southern sites, a discrete and constant overestimation during the whole Holocene period that could not be reasonably related to a climatic signal considering the error bars in the quantifications of our study (±1.3 °C, see Table 1). The MD99-2339 site is the only one depicting a clear middle Holocene hypsithermal.

Few temperature oscillations marked the Holocene period when compared to the late glacial during which marked excursions were recorded, especially during the Heinrich 1 (e.g., Heinrich 1988) and Younger Dryas events (HE1 and YD respectively). Summer SST dropped with up to 15 °C when compared to the modern values during HE1 for the whole North Atlantic Ocean. This is in accordance with the previous works that established that nearly freezing conditions, and even the development of sea-ice cover (Eynaud et al. 2012), characterized these major collapse episodes of boreal ice-sheets within the temperate North Atlantic Ocean (e.g., Bond et al. 1993; Chapman and Maslin 1999). By considering the coherency of the obtained reconstructions, the exercise made with the multi-core compilation demonstrates the robustness of the $MAT_R\_1007_{PF}$ method. The confrontation of our results to the previous ones obtained on the same cores furthermore underlines the exceptional reproducibility of the transfer function method derived from PF. However, we should keep in mind that this response is restricted to one organism community (i.e., PF) and therefore it provides only a partial view of the ecological response to environmental changes. In fact multi-proxy compilations derived from biogeochemistry and/or paleo-ecological techniques as well have often challenged the sea-surface character of the message empirically (and therefore restrictively) considered in Paleoceanography (e.g., Marchal et al. 2002; Penaud et al. 2011). This is especially true with PF as the representatives of this group are related to differential depth habitats (e.g., Hemleben et al. 1989).

About Regionalism: A Test in the Gulf of Cadix

Among the most severe criticisms recurrently addressed to MAT derived approaches is the question of regionalism ("spatial autocorrelation", see Telford and Birks 2011 and the reply of Guiot and de Vernal 2011b). To test this issue with the $MAT_R\_1007_{PF}$ method we have taken advantage from a regional database compiled by Salgueiro et al. (2008) off Iberia (n=131 points after removing 3 points for which no WOA sampling extraction was possible) by recalculating SST reconstructions on the basis of our protocol. We therefore generate additional reconstructions for core MD99-2339 (included in the geographical limits of the Salgueiro et al. database), calculating SST on the basis of their own dataset (data available at http://doi.pangaea.de/10.1594/ PANGAEA.743256) and also by merging the two databases (n= 1007+ 131 = 1138 points). These calculations are compared with the initial results obtained with the $MAT_R\_1007_{PF}$ method (Figure 4).

The obtained reconstructions with the n=131 database provide a non-continuous record as many fossil samples due to the too large dissimilarity do not find correct analogues in the regional Iberian margin set.

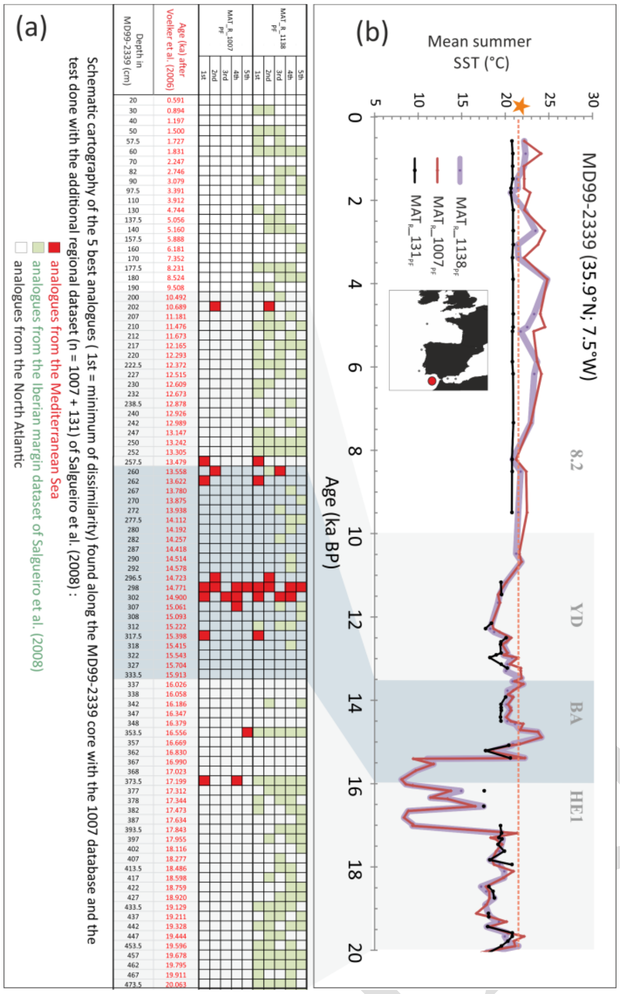

Figure 4. Illustration of the calculation tests done considering the Iberian margin regional database of Salgueiro et al (2008). **(a)**: sample per sample "map" of the five best analogues selected with their geographical origin (color code). Star=modern summer SST as extracted from WOA. **(b):** comparison of the MAT_R derived results for the summer months obtained on core MD99-2339; in red are given the reconstructions with the n=1007 database; in black, are marked those reconstructed with the n=131 restricted database of Salgueiro et al. (2008); in purple those realized with the enlarged database (n=1007+131=1138).

As previously seen for the Mediterranean database, this demonstrates again that a too geographically restricted set limits the reconstructions, especially when hydrological conditions were drastically divergent from the modern ones (glacial extremes for instance). At the opposite pole, the test realized with the enlarged dataset (n=1007+13=1138 points) offers a very interesting result. In fact, as seen in Figure 4a, no marked differences are recorded in absolute SST values in comparison with those provided by the MAT_R_1007_{PF}.

However, when considering the list of the selected analogues, a very sharp difference is obvious (see Figure 4a) with an especially high degree of mixing between the original 1007 database and the modern samples newly added with the Iberian margin dataset. In spite of this mixing the comparable SST values demonstrate the high stability of the MAT_R protocol. It specially underlines that the geographical structure of the database is not so critical if sufficient analogues are provided in the modern training set. The introduction of a very patchy set of data (Salgueiro et al. 2008) did not affect the final quantifications. The two reconstructions pointed out in the MD99-2339 record the beginning of the BA/termination of HE1 as displaying highest similarity with the Mediterranean assemblages rather than in the North Atlantic or regional databases. It suggests a peculiar intense warming at this transition and/or the transiently installation of hydrological conditions in the Gulf of Cadiz, which were comparable to those of the modern Mediterranean basin.

Some MAT_R_1007_{PF} Reconstructions along the European Margin: What about Previous Time Windows?

This section aims at challenging the robustness of the MAT_R_1007_{PF} approach when applied to long term past windows for which uniformitarianism principles (e.g., Gould 1965) could be questioned (e.g., de Vargas et al. 2001). Some already published quantifications on the basis of this protocol and covering up to two last climatic cycles can be found in the recent papers of

Matsuzaki et al. (2011) and Sánchez Goñi et al. (2012, 2013). For the present paper we selected two cores that allowed a high resolution analysis (Figure 5) over the last interglacial complex (Marine Isotopic Stage -MIS- 5 and its substages), such as the core MD95-2001 (46.8° N, 8.67°E, at a 3788 m water depth) and MD99-2331 (42.15°N, 9.68°E, which is the twin core of MD03-2697). Core MD95-2001 was retrieved on the Trevelyan Escarpment off Brest and PF assemblages were analyzed by Morvan (2001, unpublished). The Core MD99-2331 PF data were partially published by Sánchez Goñi et al. (2008). The age models of these two cores conform to the previously published ones for the last interglacial interval (Eynaud et al. 2007; Sánchez Goñi et al. 2008). They were basically tied on the chronological framework of existing regional references for this period, such as the δ^{8}O stacks of SPECMAP (Martinson et al. 1987) and of LR04 (Lisiecki & Raymo 2005) and the high resolution NGRIP SS09 δ^{18}O record (North Greenland Ice Core Project members, 2004), which are herein compared to the annual SST data obtained from off Iberia by Martrat et al. (2007).

The quantifications obtained over MIS5 were all supported by a weighted average of systematically five best analogues, therefore with no occurrence of a too large dissimilarity between the modern and MIS5 assemblages. This indicates that at least for the last climatic cycle no major changes or innovations were observed in the PF biogeographical distribution and populations. The $MAT_R\_1007_{PF}$ protocol can therefore been applied with no limitation up to 150 ka BP (and even up to 220 ka after Matsuzaki et al. 2011). The results reveal that the summer hydrological conditions are comparable or slightly warmer to the present ones during the limited portion of the basal MIS5, such as the Eemian climatic optima (Sánchez Goñi et al. 1999). The whole complex recorded mild conditions, very close to the modern ones, except during cold climatic excursions that progressively become more and more severe up to the definitive glacial inception of MIS 4 (also coinciding with HE 6 around 60 ka).

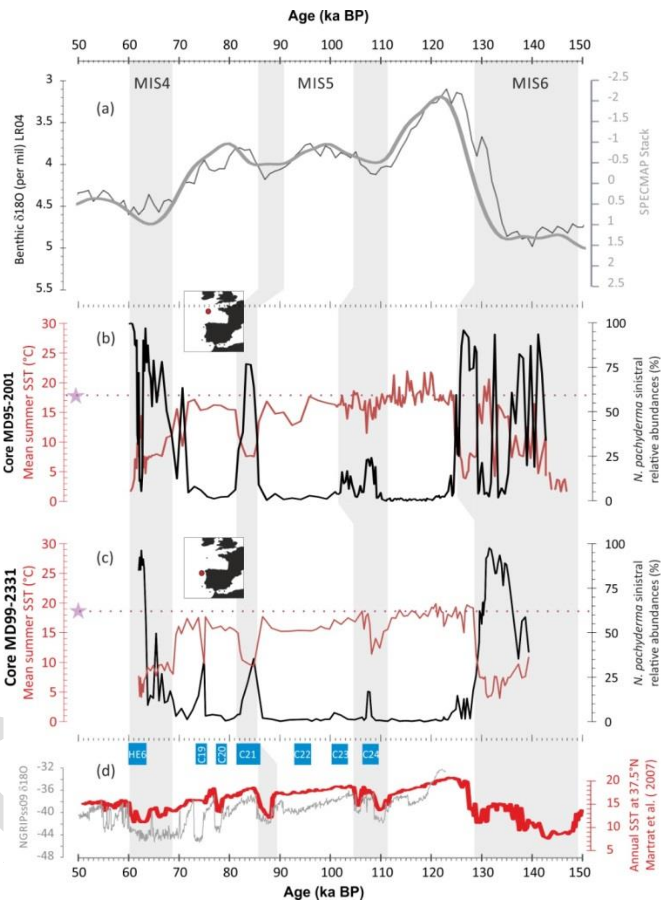

Figure 5. (a) Chronostratigraphic references of the SPECMAP (Martinson et al. 1987) and LR04 (Lisiecki and Raymo 2005) marine δ^{18}O stacks plotted along the last interglacial complex (MIS 5) compared to: **(b)** core MD95-2001 (46.8° N, 8.67° E), **(c)** core MD99-2331 (42.15° N, 9.68° E) summer SSTs obtained with $MAT_R\_1007_{PF}$ (stars = modern summer SST as extracted from WOA) and **(d)** high resolution NGRIP SS09 δ^{18}O versus annual SST data obtained by Martrat et al. (2007) off the Iberian margin for the same time interval. Grey vertical bands underline major cold episodes within MIS 6 to 4. Blue squares define the high frequency cold events as defined by Sánchez Goñi et al. (2008). The ages models of the respective cores conform to the previously published ones (Eynaud et al. 2007 for core MD95-2001 and Sánchez Goñi et al. 2008 for core MD99-2331).

This observation is consistently seen also in the relative abundances of the polar taxon *N. pachyderma* sinistral, which progressively increases to reach monospecific values at the transition with MIS4. The amplitude of the cold event detected within MIS5 varied from minus 5 °C to 10°C. They reached up to 15 °C during MIS4/HE6 and the penultimate glacial MIS6. These high values are in accordance with those obtained for HE1 (Figure 3) and therefore typifying the characteristic conditions of these major climatic shifts.

CONCLUSION

This work compiles paleoceanographical (SST) reconstructions obtained with the Modern Analog Technique. It is based on the re-analysis of planktic foraminifera assemblages of several marine sequences covering up to 150 ka and distributed along the eastern North Atlantic (including the occidental Mediterranean basin) with the $MAT_R\_1007_{PF}$ protocol. The obtained sets of

SST data shows that the method offers a high degree of accuracy, with no major incidence of the internal database structure (i.e. geographical distribution of the modern analogues) as long as a reasonable number of analogues exists in the training set. Even if the absolute hydrological values derived from past archives are still disputable, regarding the arbitrary choice done on the variable to reconstruct (i.e., here limited to SST), and considering the complex ecology of PF, this work demonstrates that past quantifications derived from PF could be considered as probably “the best” existing ones up to date (at least for the investigated region, i.e. the North Atlantic). Taken solely, these data however do not represent a comprehensive picture of the past hydrology. Quantifications should be confronted systematically to other proxies on the same record whenever possible, or either to proximal or regional records, to be validated. With the emergence of new analytical techniques, especially deriving from geochemical approaches (which are often less time consuming than the determination of species in a complete assemblage), the recent literature often gives greatest credits (when it is not a priority) to this kind of innovative results. Our study demonstrates that, if not revolutionary, classical paleoecological and micropaleontological approaches still remain powerful enough to represent the backbone of Paleoceanographical reconstructions.

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