Long-term hydrological changes in the northeastern Gulf of Mexico (ODP-625B) during the Holocene and late Pleistocene inferred from organic-walled dinoflagellate cysts

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A B S T R A C T

Palynological analyses are used in conjunction with oxygen isotopes and Mg/Ca ratios in foraminifers in order to document the response of dinoflagellate cysts (dinocysts) assemblages to changing climate conditions in the northeastern Gulf of Mexico over the Holocene and late Pleistocene. During MIS 6, but also during the cooler phases of MIS 5, *Impagidinium* species and *Opechocladum centrocarpum* were dominating the assemblages. By contrast, during the last interglacial (LIG) and the Holocene, assemblages were mainly composed of *Spiniferites* taxa and characterized by high relative abundance of *Spiniferites mirabilis-hyperacanthus, Opechocladum israelicum* and/or *Polypleuris zoharyi*. These two periods exhibit ~1-2 °C difference in temperature as inferred from Mg/Ca ratios and show significantly distinct assemblages, with higher percentages of *P. zoharyi* during the Holocene. This likely denotes important differences in the hydrogeographical conditions (e.g. surface circulation, bathymetric configuration) between the present and last interglacial. The importance of environmental parameters other than temperature and salinity for dinocyst assemblage dynamics is furthermore illustrated.

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1. Introduction

In the Gulf of Mexico, the interplay between the Mississippi River discharge, open ocean water masses and atmospheric circulation creates a complex dynamic system responsible for hydrological fluctuations on both annual and long-term timescales. To better understand the impact of these parameters on the regional climate, a number of marine sediment studies has focused on the hydrologic evolution of the basin during the Holocene (Poore et al., 2003; Lo Dico et al., 2006; Richey et al., 2007; Meckler et al., 2008; Montero-Serrano et al., 2010) and the last interglacial (LIG) interval (Joyce et al., 1990, 1993; Tripsanas et al., 2007; Nürnberg et al., 2008; Kujau et al., 2010; Montero-Serrano et al., 2011; Simms et al., 2013). The LIG, referred to as Marine Isotope Stage (MIS) 5e in marine sediments and spanning the interval between ~130 and 115 kyrs (Liesecki and Raymo, 2005), has experienced conditions warmer than those of the current interglacial in response to higher levels of insolation during boreal summer (e.g., CAPE, 2006; Otto-Bliesner et al., 2006; Hearty et al., 2007). Regional data from the Gulf of Mexico indicate that overall sea-surface temperatures were generally warmer by 1-2 °C (Nürnberg et al., 2008; Ziegler et al., 2008; Montero-Serrano et al., 2011) and relative sea-level was approximately 4-6, possibly 9 meters above the present limit (Simms et al., 2013, and references therein). Numerous paleoceanographic investigations therefore stem on the recognition that this interval may represents a possible analogue for future climate and could help infer potential changes in hydrographic conditions in the context of global warming.

Dinoflagellate cysts (dinocysts), which are the organic-walled remains of unicellular algae routinely recovered in palynological preparations, have proven to be a good proxy for paleoenvironmental changes in the upper water column (e.g. Rochon et al., 1999; de Vernal and Marret, 2007). Their assemblages are not only controlled by temperature, but also depend on other environmental parameters (e.g., productivity, salinity, sea-ice cover, seasonality, sea-level etc) as shown by multivariate analyses of distribution patterns in middle to high latitudes of the Northern Hemisphere (e.g., de Vernal et al., 1997; Devillers and de Vernal, 2000; Pospelova et al., 2008; Radi and de Vernal, 2008; Price and Pospelova, 2011; Bonnet et al., 2012) and in the Gulf of Mexico (Limoges et al., 2013). Therefore, the analysis of dinocyst assemblages has the potential to assess past hydrographic conditions in a fairly nuanced way. While dinocysts have been widely used in paleoceanographic reconstructions for the high latitudes (Mudie et al., 2001 and references therein; de Vernal et al., 2005),...
they remain a less-exploited tool for such reconstructions in the tropical areas, which is in part due to the lower availability of modern reference datapoints for these regions. For the Gulf of Mexico, the relationship between dinocyst assemblages and modern sea-surface parameters was documented by Limoges et al. (2013) allowing for a more comprehensive interpretation of their regional distribution.

Here, we combine the analyses of stable isotopes (δ^{18}O and δ^{13}C) and trace elements (Mg/Ca) in planktic foraminiferal carbonate with palynological analyses from sediments collected at the Ocean Drilling Program (ODP) site 625B in the Gulf of Mexico (Fig. 1A), in order to document long-term changes in hydrological conditions over the MIS 1 (0 - 11 kyr), MIS 5 (b-e) (90 - 130 kyr) as well as the glacial-interglacial transition MIS 6/5 (130 - 160 kyr). Located in the northeastern part of the Gulf of Mexico, at the outer reaches of the seasonal influence of the Loop Current and near to the Mississippi River Mouth, site ODP-625B is ideally positioned to record changes in paleoproductivity and sea-surface conditions related to long-term hydroclimatic changes. Our study also evaluates the potential of dinocysts as paleoceanographic proxy in tropical areas.

2. Material and methods

2.1. Regional setting

The Gulf of Mexico is an oceanic basin located on the northwestern edge of the Atlantic Ocean. Its dominant surface current is the Loop Current: warm and salty waters originating from the Caribbean Sea enter into the Gulf via the Yucatán channel, loop northwest and exit through the Florida Strait as the Florida Current, eventually feeding the Gulf Stream (Fig. 1B) (Elliot, 1982; Blumberg and Mellor, 1985; Hofmann and Worley, 1986; Oey et al., 2005; Jochens and DiMarco, 2008; Auladell et al., 2010). The latitudinal extension of the Caribbean water inflow into the basin is seasonally modulated by the position of the Intertropical Convergence Zone (ITCZ) (Fig. 1B). A northward migration of the ITCZ during boreal summer causes the Loop Current to propagate farther north, influencing the hydrological properties of the entire basin (temperature, salinity). Consequently, in the modern climate system, the Atlantic Warm Pool reaches into the Gulf of Mexico during late summer, with temperatures above 28.5 °C in the entire basin during this...
period (Fig. 1C). Conversely, during boreal fall/winter, the tropical waters exit directly through the Florida Strait (Fig. 1D). Current mean annual sea-surface temperature is ~25.85 °C with a large seasonal amplitude (~8.5 °C), whereas salinity varies from about 34.38 to 35.97 (WOA, 2001). In addition to the Loop Current, the hydrology (salinity, stratification) of the northern Gulf is largely impacted by the freshwater input from the Mississippi River system, which has, at present, an annual mean discharge of over 13 000 m³s⁻¹ (Morey et al., 2003). Currently draining the continental U.S. from the Rockies to the Appalachians, the drainage area of the Mississippi River System intermittently included the meltwater inputs from the Laurentide Ice Sheet throughout the last glacial stages and Terminations (e.g., Teller, 1990; Aharon, 2006; Montero-Serrano et al., 2009; Sionneau et al., 2010, 2013), with potential consequences for the North Atlantic thermohaline circulation (e.g., Broecker et al., 1990; Bond, 1995; Manabe and Stouffer, 1995, 1997; Fanning and Weaver, 1997; Aharon, 2003; but see also Nürnberg et al., 2008). During interglacial phases, most of the Mississippi outflow is diverted westward (Nürnberg et al., 2008).

2.2. Core and stratigraphy

Core site ODP-625B was drilled in the northeastern Gulf of Mexico (28.83°N, 87.16°W) during the Ocean Drilling Program (ODP) Leg 100, in 1985 (Fig. 1A). The site is located at 889 m water

Table 1
Results from the radiocarbon analyses for core ODP-625B.

<table>
<thead>
<tr>
<th>Sample</th>
<th>Depth</th>
<th>NOSAMS Lab #</th>
<th>Type</th>
<th>¹⁴C Age (yr)</th>
<th>¹⁴C Age error (yr)</th>
<th>Calibrated Age (yr)</th>
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<tr>
<td>100-625B-1H-01W-</td>
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<td>Foraminifera</td>
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<td>(50-51 cm)</td>
<td>OS-107193</td>
<td>Foraminifera</td>
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</table>

Fig. 2. A) Total concentration of dinoflagellate cysts (cyst · g⁻¹); B) Estimated SST on the basis of Mg/Ca ratios from G. ruber (white) (this study) and Mg/Ca SST from Ziegler et al. (2008); C) Stable carbon isotope (δ¹³C in ‰) records of U. peregrina, G. ruber (white) and G. ruber (pink) (this study) and average δ¹³C data from the benthic foraminifer Cibicidoides wuellerstorfi and Cibicidoides spp. from the northeast slope of Ceara Rise (Curry and Oppo, 1997); D) Stable oxygen isotope (δ¹⁸O in ‰) record of U. peregrina; E) Stable oxygen isotope (δ¹⁸O in ‰) records of G. ruber (white) and G. ruber (pink); F) Benthic stable oxygen isotopes (δ¹⁸O in ‰) from stack LR04 (Lisiecki and Raymo, 2005); G) Summer insolation at 30°N (Laskar et al., 2004). Shaded areas indicate the Holocene and last interglacial intervals. Black triangles represent calibrated radiocarbon dates.
depth on the western Florida continental slope, near the De Soto basin, and ~200 km from the current Mississippi River delta, whose position is thought to have remained the same since either MIS 5 or the beginning of the last glaciation (Coleman et al., 1983; Bouma and Coleman, 1985). The complete sequence of site 625B is 231 m long and provides a nearly complete stratigraphic record of the Quaternary and Pliocene, from which we studied the upper 98 cm of the studied sequence covering the last 10 600 14C years, which corresponds to the LIG, in order to parallel the number of samples recovered from the benthic foraminifera Uvigerina peregrina and the planktic Globigerinoides ruber (pink) and Globigerinoides ruber (white) (Fig. 2). Accordingly, the Pleistocene section we analyzed encompasses approximately 157 to 93 kyrs, thus spanning from late MIS 6 to MIS 5b.

### Table 2
Mean Mg/Ca values for each chamber of the analyzed foraminifers and resulting Mg/Ca corresponding to each sample.

<table>
<thead>
<tr>
<th>Samples</th>
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<th>100-625B-1H-01W</th>
<th>100-625B-1H-01W</th>
<th>100-625B-1H-01W</th>
<th>100-625B-1H-01W</th>
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<td>(40–42 cm)</td>
<td>(50–52 cm)</td>
<td>(58–60 cm)</td>
<td>(78–80 cm)</td>
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<td>5.03</td>
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<td>27.46</td>
<td>27.46</td>
<td>27.56</td>
<td>27.27</td>
<td>27.39</td>
<td>25.24</td>
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</table>

2.3. Isotopic analyses (δ18O and δ13C)

Isotopic analyses were conducted on 15–30 specimens (120 µg) of the shallow endo-benthic species *U. peregrina* (<1 cm sediment depth) and the surface-dwelling foraminifera *G. ruber* (white) and *G. ruber* (pink) picked from the 150 to 250 µm size fraction. In order to avoid possible organic matter contamination, benthic tests were burned under vacuum (residual pressure ~8 Pa) in an oven at 200 °C for one hour. The analyses were carried out using a Micromass Isoprime dual inlet isotope ratio mass spectrometer coupled to a Multicarb system. The δ13C and δ18O raw data were normalized to VSMOW-SLAP (δ18O) and NBS19-LSVEC (δ13C) using an inhouse reference calcium carbonate (δ18O: -1.40; δ13C: +2.25). Values are reported in δ notation in ‰ vs. Vienna-Pee Dee belemnite (VPDB). Analytical uncertainty is ±0.05 ‰ (1 σ) for both measurements.
2.4. Trace element determination (Mg/Ca)

Individual shells of the planktic *G. ruber* (white) were picked within a narrow range of size (specimens from 220 to 300 μm; foraminifers were measured), in order to minimize variations related to changes in calcification rate and/or depth habitat during their evolution from small to large individuals (Elderfield et al., 2002). Since *G. ruber* has a nearly uniform annual occurrence, it is a valuable species for reconstructing past temperature in tropical environments (Tedesco and Thunell, 2003). Prior to analysis, specimens were gently cleaned without crushing the tests: shells were repeatedly rinsed and sonicated for ~3 seconds with MilliQ water and methanol in order to release the silicate phases (clays) attached to the surface (Barker et al., 2003). Trace element analyses were conducted on selected samples from the Holocene, MIS 5e and MIS 6 using laser ablation inductively coupled plasma mass spectrometry (LA-ICP-MS: instrument used was a Photon Machine G2 with 193 nm wavelength laser, ran at low energy output (0.6 mJ) with elemental acquisition on a Nu Attom HR-ICP-MS). Laser ablation measurements were performed using spot size of 30 μm diameter at a pulse repetition rate of 2 Hz. Calibration was made against the international glass standard (NIST610). In order to avoid bias due to residual superficial and internal clay contamination and/or diagenetic coatings, the data integration interval was adjusted to exclude zones of manganese, iron and/or aluminum enrichments (see Philathearta et al., 2010).

Off-line data reduction was carried on as time resolved analysis using the lolite software (Paton et al., 2011). Four to ten foraminifer specimens were measured per sediment sample and six ablation spots were made on each foraminifer shell, two per chamber. This allowed the determination of single foraminifer test heterogeneity.

A bias linked to natural differences in composition between chambers of a single individual (Table 2) was eliminated by calculating an average for each chamber, and these values were then used to calculate an average Mg/Ca value for each foraminifer. In this way, equal weight was given to each chamber in the final foraminifer's Mg/Ca value. Temperature estimates from Mg/Ca ratios were calculated using the calibration curve based on a sediment trap from the Sargasso Sea: 

\[ T°C = \frac{\ln(Mg/Ca/0.38)}{0.09} \]  

(Anand et al., 2003). Absolute temperatures are differences between foraminifer (levels) are robust. Using analytical uncertainty budget for one single foraminifer Mg/Ca ratio relies on the analysis of a mineralogically different material (Anand et al., 2003). For almost all planktic foraminifers, culture and core top calibrations indicate a temperature dependence of Mg uptake into calcite of the order of 9.0 ± 0.3% per °C (Anand et al., 2003).
2.5. Organic-walled dinoflagellate cysts

Sample treatment was made according to standard laboratory procedures (e.g. de Vernal et al., 1999). One calibrated Lycopodium tablet (~18 584 spores) was added to every sample before sieving to allow estimation of the absolute dinocyst abundances (Stockmarr, 1971). A volume of 5 cm$^3$ of sediment was wet-sieved to eliminate fine silt and clay (mesh size of 10 μm) and coarse sand (mesh size of 106 μm). The fraction > 10 μm was treated with hydrochloric acid (HCl 10%) and hydrofluoric acid (HF 48%) to dissolve respectively carbonate and siliceous material. The remaining residue was re-sieved after chemical treatment in order to remove the fine fraction from the residue and subsequently mounted in glycerin jelly for microscopic observation. Cyst identification was made at magnifications ranging from 400 to 1000X and follows the most recent nomenclature (Fensome et al., 2008). Note that Operculodinium centrocarpum sensu Wall and Dale (1966) will be referred to simply as Operculodinium centrocarpum from here on. For most samples, 2 to 4 slides were analyzed. In order to insure statistical robustness, the palynological results of all samples with less than 100 dinocyst specimens counted were not used for percentage calculation and were omitted from Fig. 2 (see Appendix A for exhaustive data).

3. Results

3.1. Isotopic analyses (δ$^{18}$O and δ$^{13}$C)

On the whole, the oxygen isotopes series clearly reflect the Pleistocene and Holocene climate variations (Fig. 2; Table 3). The G. ruber (white) and G. ruber (pink) δ$^{18}$O profiles follow the same pattern during the different studied intervals, but the white variety show slightly lighter values than its pink counterpart. This divergence can be explained by the fact that G. ruber (pink) calcifies near-surface and is representative of summer temperatures, whereas G. ruber (white) habitat may extend deeper and records an average annual to summer temperature signal (Anand et al., 2003; Richey et al., 2012). In the section corresponding
to the Pleistocene, both benthic and planktic $\delta^{18}O$ profiles display a pronounced excursion from around 128 to 116 kyrs, the amplitude of the signal obviously being higher for the planktic species. When comparing our data to the standard LR04 reference stack (Lisiecki and Raymo, 2005), this interval is easily identified as the interglacial MIS 5e. These light values contrast with those from the preceding, isotopically heavy MIS 6, which is interrupted however, by a short excursion of isotopically lighter values in both planktic profiles, suggesting a brief hydrographic event centered around 144 kyrs. The MIS 5 b-d interval is characterized by a continual warming in its early phase and a subsequence increase at mid-Holocene and a gradual decrease towards the core top. Overall values range from 0.54 to 0.89‰ (G. ruber (white)), 0.49 to 1.18‰ (G. ruber (pink)) and -0.74 to -0.21‰ (U. peregrina).

3.2. Trace element determination (Mg/Ca)

Significant differences were measured in the Mg/Ca ratios within one sample and between the different foraminiferal chambers (Table 2). Such differences between chambers have been reported from many studies (see Rosenthal, 2007, and references therein). They may be attributed to a number of different factors, amongst which vertical migration in the water column during calcification. They can result from temporal discrepancies (from a few weeks to a few months) recorded by each individual foraminiferal shell. Moreover, as mentioned by Rosenthal (2007), metabolic effects in symbiotic foraminifers such as G. ruber cannot be ruled out.

During the Pleistocene interval, Mg/Ca records from the monospecific G. ruber (white) are generally in phase with the corresponding $\delta^{18}O$ profile (Fig. 2). Raw Mg/Ca data range from 2.61 to 4.02 mmol/mol during the MIS 6 and are followed by a rapid transition to higher values (3.69 to 5.60 mmol/mol) during the MIS 5e, suggesting a sea-surface warming of approximately 6 °C during the glacial to interglacial transition. These records also show that SST culminated in the very beginning of MIS 5e. Besides, the peak in Mg/Ca ratios around 146 kyr appears to be somewhat concomitant with the excursion observed within the $\delta^{18}O$ values, reinforcing the hypothesis of a brief (sub)surface warming event shortly before the onset of the penultimate deglaciation. The Holocene interval is characterized by a continual warming in its early phase and a subsequent cooling towards the top of the section. These results agree with previous work which linked the change in the average position of the

![Fig. 3.](image-url)
ITCZ during the Holocene to increased summer insolation in the early phase of the interval and decreased summer insolation after ca. 6000 14C yrs B.P. (Hodell et al., 1991; Haug et al., 2001; Poore et al., 2005; Montero-Serrano et al., 2010, 2011). Conversion of the Mg/Ca ratios to temperature yields a mean SST of ~26 °C during the Holocene and ~28 °C during the last Interglacial. These values are therefore consistent with data from Ziegler et al. (2008) and previous Mg/Ca SST estimates for the Atlantic tropical regions, suggesting that the LIG was approximately 2 °C warmer than the Holocene (Schmidt et al., 2004; Nürnberg et al., 2008; Montero-Serrano et al., 2011; Bahr et al., 2013).

3.3. Palynology and organic-walled dinoflagellate cysts

Sediments from the studied sections are characterized by diverse palynological assemblages with abundant terrestrial palynomorphs (pollen grains of gymnosperms and angiosperms, spores of seedless plants), organic linings of foraminifers, and dinocysts (Fig. 3; Plates 1-2). Although they represent only a small proportion of the total palynomorphs, the dinocyst assemblages are characterized by high species diversity. Gonyaulacoid taxa, which usually correspond to phototrophic productivity, dominate the assemblages (60-100% of

and an increase of show high abundances of salinity stenohaline species during this period, and higher relative abundances of the high-\textit{spp.} In addition, \textit{Brigantedinium} with an abrupt rise in interval (MIS 5b-d). The peak in total concentrations is associated with changes in dinocyst associations and coincide with climate transitions during the last interglacial (MIS 5e), compared to generally low cyst numbers throughout MIS 6 and the remainder of the MIS 5. This is particularly well expressed by a major peak in cyst concentrations during the latter two intervals, that may in turn be related to the regional circulation shifts that coincide with the main climatic phases (Fig. 3). As such, the recurrence of cooler conditions after MIS 5e is evidenced by the increase of \textit{Impagidinium} spp. and \textit{O. centrocarpum} as well as \textit{Spiniferites} species have a wider tolerance for variation in salinity than \textit{Impagidinium} species do, these important changes in dominant species might further suggest strengthened seasonality during the interglacial intervals, that may in turn be related to the regional circulation (Loop Current and/or Mississippi discharge).

Plotting the ratio between the dominant species (\textit{Impagidinium} spp. and \textit{O. centrocarpum} as colder and oligotrophic representatives over \textit{Spiniferites} spp. as more typical of productive environments) yields a semi-quantitative indicator that clearly illustrates the long-term assemblage shifts that coincide with the main climatic phases (Fig. 3). As such, productivity appears to have been reduced during cooler episodes. Assemblage changes from MIS 6 to MIS 5 reflect a shift from oligotrophic conditions to warm and more productive environments: while MIS 6 is characterized by high relative abundances of \textit{O. centrocarpum} and the typically fully-marine \textit{Impagidinium aculeatum}, MIS 5 shows an increase of \textit{Spiniferites} taxa as well as \textit{O. israelianum} (Fig. 4, Table 4). Furthermore, since \textit{Spiniferites} species have a wider tolerance for variation in salinity than \textit{Impagidinium} species, these important changes in dominant species might further suggest strengthened seasonality during the interglacial intervals, that may in turn be related to the regional circulation (Loop Current and/or Mississippi discharge).

The maximum in dinocyst concentrations during the LIG and at the base of the Holocene indicates high marine productivity during these warmer periods, which can also be inferred from the dinocyst/pollen grains ratio and coeval high amounts of foraminifer organic linings, especially during the Holocene. By contrast, productivity appears to have been reduced during cooler episodes. Assemblage changes from MIS 6 to MIS 5 reflect a shift from oligotrophic conditions to warm and more productive environments: while MIS 6 is characterized by high relative abundances of \textit{O. centrocarpum} and the typically fully-marine \textit{Impagidinium aculeatum}, MIS 5 shows an increase of \textit{Spiniferites} taxa as well as \textit{O. israelianum} (Fig. 4, Table 4). Furthermore, since \textit{Spiniferites} species have a wider tolerance for variation in salinity than \textit{Impagidinium} species, these important changes in dominant species might further suggest strengthened seasonality during the interglacial intervals, that may in turn be related to the regional circulation (Loop Current and/or Mississippi discharge).

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Plots of the ratio between the dominant species (\textit{Impagidinium} spp. and \textit{O. centrocarpum} as colder and oligotrophic representatives over \textit{Spiniferites} spp. as more typical of productive environments) yields a semi-quantitative indicator that clearly illustrates the long-term assemblage shifts that coincide with the main climatic phases (Fig. 3). As such, the recurrence of cooler conditions after MIS 5e is evidenced by the increase of \textit{Impagidinium} spp. and \textit{O. centrocarpum} as well as an important drop in absolute cyst concentrations. By contrast, “warmer” index values are shown for the Holocene, which furthermore shows high occurrences of \textit{Polysphaeridium zoharyi}, in line with the species’ common modern-day presence in subtropical to equatorial regions (Head and Westphal, 1999). The Holocene behavior of \textit{P. zoharyi} will be discussed in more detail in Section 4.2.
Table 4

Affinity to mean annual temperature (°C) and salinity (psu) for the dominant dinocyst species according to the global dataset (Zonneveld et al., 2013) and modern distribution in the Gulf of Mexico (Limoges et al., 2013).

<table>
<thead>
<tr>
<th>Dominant dinocyst species</th>
<th>Complete range</th>
<th>Optimum global dataset</th>
<th>Complete range</th>
<th>Optimum global dataset</th>
<th>Comments and regional modern distribution</th>
</tr>
</thead>
<tbody>
<tr>
<td>Impagidinium aculeatum</td>
<td>-1.6 - 29.6</td>
<td>18 - 21</td>
<td>31.0 - 39.4</td>
<td>35 - 39</td>
<td>Highest relative abundances in oligotrophic environments. Offshore regions of the Gulf of Mexico.</td>
</tr>
<tr>
<td>Operculodinium centrocarpum</td>
<td>-2.1 - 29.8</td>
<td>-2 - 23</td>
<td>9.8 - 39.4</td>
<td>32 - 36</td>
<td>Cosmopolitan</td>
</tr>
<tr>
<td>Polysphaeridium zoharyi</td>
<td>8.9 - 29.8</td>
<td>24 - 27</td>
<td>28.4 - 39.4</td>
<td>33 - 36</td>
<td>Typical for tropical shallow and productive coastal environments.</td>
</tr>
<tr>
<td>Spiniferites mirabilis sensu stricto</td>
<td>-0.8 - 29.8</td>
<td>18 - 19 &amp; 27 - 29</td>
<td>17.5 - 39.4</td>
<td>35 - 37</td>
<td>Dominant in warm productive coastal environments of the Gulf of Mexico.</td>
</tr>
<tr>
<td>Operculodinium israelianum</td>
<td>1.8 - 29.8</td>
<td>18 - 27</td>
<td>30.3 - 39.4</td>
<td>37 - 39</td>
<td>Warm-water and high salinity species.</td>
</tr>
<tr>
<td>Lingulodinium maedaerophorum</td>
<td>0 - 29.8</td>
<td>17 - 20</td>
<td>8.5 - 39.4</td>
<td>35 - 37</td>
<td>Highest relative abundances close to river mouths.</td>
</tr>
</tbody>
</table>

Thus, sharp changes in the relative abundance of the dominant index species in the studied core clearly reflect shifts from glacial to interglacial periods, an observation that is further corroborated by synchronous changes in the dinocyst total concentrations. This demonstrates that dinocyst assemblages from the Gulf of Mexico provide a good proxy for long-term changes in hydrological conditions.

4.2. Comparison between Holocene and last interglacial records

In spite of the general dominance of Spiniferites species in the Holocene and last interglacial sediments, the overall species composition of the assemblages shows features that distinguish the two interglacial episodes and point to differences in surface water properties in the Gulf of Mexico. The LIG assemblages are marked by higher percentages of Spiniferites mirabilis sensu lato than during the Holocene. Interestingly, increased abundances of this species, whose highest occurrences at present are observed in the warm temperate to temperate regions of the eastern North Atlantic (Rochon et al., 1999; Penaud et al., 2008), have also been associated with the LIG climatic optimum in the high latitudes of the northern North Atlantic (Eynaud et al., 2004; Van Nieuwenhove et al., 2011, 2013). However, since Holocene temperatures (Mg/Ca SST: ~24-28 °C) are always higher in the Gulf of Mexico than in the present thriving area for this species in the North Atlantic, its high percentages during the LIG may not exclusively reflect temperature. These records imply that other parameters associated with warmer conditions may also have played a significant role on its distribution.

Another important observation is the increase in the relative abundance O. israelianum prior to the onset of the last interglacial maximum (~135 kyr) and its absence during the Holocene. Generally associated with fully marine equatorial environments, this species shows its highest concentrations in regions characterized by rather elevated salinity (Fig. 4, Table 4) (Zonneveld et al., 2013). Although it has been shown that the volume of freshwater discharged by the Mississippi river was not higher during the LIG than during the Holocene (Nürnberg et al., 2008; Montero-Serrano et al., 2010), the occurrence of O. israelianum exclusive to the LIG may highlight differences in sea-surface salinity between the present and last interglacial. It has been suggested that during the LIG, the higher insolation during boreal summer caused a northern shift of the ITCZ as compared to the early Holocene (Ziegler et al., 2008; Montero-Serrano et al., 2011; Nikolova et al., 2013). This would have fostered the warm and salty water from the Caribbean to penetrate further into the Gulf of Mexico during the last interglacial (Nürnberg et al., 2008; Ziegler et al., 2008; Montero-Serrano et al., 2011), heating up the entire basin and leading to saltier conditions, especially during the warm season. In this respect, the paired highest occurrence of S. mirabilis and O. israelianum during the LIG, as opposed to higher relative abundances of P. zoharyi and L. maedaerophorum during the Holocene are in line with the hypothesis of a farther-north propagation of the Loop Current during LIG (see scenarios in Montero-Serrano et al., 2011). Furthermore, it is interesting to note that both the high-salinity O. israelianum and dinocyst concentrations increase before the onset of optimal condition during the last interglacial (Fig. 3). This would denote a rapid regional response to changes in insolation, likely through the changing impact of the Loop Current in relation with the average position of the ITCZ. Such rapid response of dinocysts to insolation contrasts with observations from the high latitudes of the Atlantic Ocean, where other boundary conditions related to the deglaciation (e.g., surface ocean freshening) also may have played a major role in the development of optimal conditions during the LIG (Van Nieuwenhove et al., 2011; Govin et al., 2012).

Finally, a more coastal character typifies early Holocene dinocyst assemblages compared to those of the last interglacial. This is notably evidenced by the occurrence of P. zoharyi, which is nearly absent in...
the LIG sediments. Since this species is presently associated with warm shallow and nearshore environments (Wall and Dale, 1969; Limoges et al., 2013; Zonneveld et al., 2013), its high relative abundance in the early part of the Holocene and its subsequent decline toward the top of the core may reflect the paired impact of 1) a slight decrease in temperature from early to late Holocene, as also indicated by Mg/Ca SST and, 2) the gradually rising sea-level associated with the reduction of global land-based ice during the early Holocene. Indeed, following the Last Glacial Maximum (LGM), the eustatic sea-level has steadily increased from 20–19 kyrs ago until approximately 6 kyrs ago, when it attained its present-day level (Clark et al., 2004, 2009, 2012). For the Gulf of Mexico, taking into account the subsidence process, the minimum LGM sea level has been estimated to have stood about 90 m below present level (Bart and Ghoshal, 2003; Simms et al., 2007) leading to an important migration of the shoreline towards the outer shelf (see Fig. 5) and thus reducing the distance between the site location and the paleo-shoreline. During the early Holocene transgression, shallow environments (i.e. lagoons) may have developed on the continental shelf and fostered P. zoharyi. Conversely, it has been recognized that a more rapid eustatic sea-level rise, due to a more rapid increase in insolation, has occurred during the penultimate deglaciation (e.g., Otto-Bliesner, 2006; Hearty et al. 2007). The establishment of a high interglacial sea level stand (4–9 m above present) may therefore account for very limited abundance of P. zoharyi during the LIG, as ODP site 625 is located further away from the preferred shallow near-shore environment of the species. Such interpretations are in line with the observations of Wall and Dale (1969) from a marine sequence from the Bermudas, showing that sea level changes were associated with alternations between littoral and neritic facies, with Pyrodinium (i.e. P. zoharyi) likely associated with the former and Gonyaulax (i.e. Spiniferites) with the latter. Similarly, a reduced area of shallow habitats during glacial sea level lowstands might explain the dominance of oceanic Impagidinium species over more shelf-dwelling dinoflagellate species during MIS 6.

5. Conclusions

Phytoplanktonic records from the Gulf of Mexico have shown to document long-term oscillations in climatic conditions over the late Quaternary and to respond to differences in hydrological conditions that existed during the present and last interglacial. Changes from glacial to interglacial stages are marked by shifts from dinocyst assemblages dominated by Impagidinium and O. centrocarpum to assemblages largely dominated by Spiniferites taxa, high abundances of S. mirabilis-hyperacanthus, O. israelianum and/or P. zoharyi. Furthermore, the composition of the dinocyst assemblages indicates distinct phytoplanktonic signatures for the two interstadial stages, which likely underline differences in the hydrological settings of the northeastern Gulf of Mexico during the present and last interglacial intervals:

• The peak in the relative abundance of the coastal P. zoharyi shortly after the onset of the Holocene matches with the culminating Mg/Ca SSTs and may indicate the phase when sea-level was still rising, allowing the development of very shallow habitats on the continental shelf during the early part of the Holocene. Moreover, the absence of this coastal taxon in the LIG assemblages agrees with the rapid establishment of high sea-level stand.

• The relatively high occurrences of S. mirabilis-hyperacanthus and O. israelianum during the LIG suggest that summer sea-surface salinity was higher during the LIG than during the Holocene. This is in line with the hypothesis of a further-northward extension of the ITCZ during the LIG that would have fostered enhanced penetration of Caribbean water into the northern part of Gulf of Mexico.

Finally, this study shows that despite small differences in temperature between interglacial phases in low latitudes such as the Gulf of Mexico, dinocyst assemblages may still provide clues on the disparities in hydrographic conditions that characterize these late Quaternary major climatic phases.

Supplementary data to this article can be found online at http://dx.doi.org/10.1611/j.palaeo.2014.08.019.

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