



Evidence for calcification depth change of *Globorotalia truncatulinoides* between deglaciation and Holocene in the Western Atlantic Ocean

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ABSTRACT

Measurements of the $\delta^{18}\text{O}$ in tests of planktonic and benthic foraminifera in the Florida Straits are used to reconstruct the properties of the water column through time over the last 12 ka (Lynch-Stieglitz et al., in press). The isotopic composition of the foraminifera largely reflects the vertical density gradient. We use this reconstruction and $\delta^{18}\text{O}$ measurements on *Globorotalia truncatulinoides* in a nearby core to track the depth habitat of this species from the last deglaciation to 1.6 ka B.P. Around 9 ka, *G. truncatulinoides* was calcifying in much shallower water than during the late Holocene. The downward migration toward its modern habitat is a regional phenomenon over the western tropical Atlantic continental slope. The cause is still unclear but we hypothesize that the shallower calcification depth may be a response to the presence of glacial melt water or to circulation changes. This study points to the value of further study of the ecology, life cycle and calcification depth for *G. truncatulinoides* and other planktonic foraminifera that are used to reconstruct the history of the thermocline and upper water column structure.

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1. Introduction

Planktonic foraminifera are commonly used in paleoceanographic studies to reconstruct sea surface conditions and upper ocean structure (Mulitza et al., 1997; Prell et al., 1976). The ecology, seasonality and depth habitat of the studied species must be well constrained to generate meaningful reconstructions. Although surface calcifying planktonic foraminifera have been well studied, less is known about subsurface species which are used to reconstruct conditions in the thermocline. This paper focuses on the depth habitat of *Globorotalia truncatulinoides* over the Holocene.

Early studies (Bé, 1960; Bé and Tolderlund, 1971; Emiliani, 1954) or in-situ observations (Deuser and Ross, 1989; Fairbanks et al., 1980) classified *G. truncatulinoides* as a deep-dwelling planktonic foraminifera. Living specimens below 1000 m have been observed in the Western Atlantic (Hemleben et al., 1985). *G. truncatulinoides* is also well known for its complex life cycle. Like most other foraminifer species, its life begins in the upper few hundred meters of the water column. However, unlike most other species, this species continues to grow and calcify new chambers deeper in the water column until it reaches the adult stage. The reproductive strategy of *G. truncatulinoides* seems to require an annual vertical migration of several hundred meters. In the Sargasso Sea, neanic and juvenile specimens

appear to develop during winter/spring months in relatively shallow water. Adult specimens then descend deeper in the water column but migrate upward again in late fall to reproduce (Deuser and Ross, 1989; Lohmann and Schweitzer, 1990). These vertical migrations are thought to be associated with the stability of the water column, as the upward and downward movements are synchronous with times of low stratification (Lohmann and Schweitzer, 1990; McKenna and Prell, 2004). Looking at different locations, Lohmann and Schweitzer (1990) showed that adults live and reproduce at different depths, possibly reflecting different water masses or thermocline depth. It is still unclear whether the movements in the water column are a passive response to changes in physical properties or an active migration of the organism themselves. This vertical displacement might also be governed by different dietary needs between the juveniles and adults.

Despite these displacements, comparison between the oxygen isotopic composition ($\delta^{18}\text{O}$) of modern foraminifera shells and the temperature and isotopic composition of modern seawater (Cléroux et al., 2007; Deuser and Ross, 1989; Ganssen and Kroon, 2000; LeGrande et al., 2004) lead to the general agreement that *G. truncatulinoides* builds most of its test in the main thermocline, around 200 m water depth in low latitude Atlantic regions. This depth represents the main calcification habitat, not the depth range of the life cycle. Based on these studies, geochemical analyses or abundance counts of *G. truncatulinoides* have been used to reconstruct paleo conditions in the deep subsurface (Martinez et al., 2007; Mulitza et al., 1997; Toledo et al., 2007). Such interpretations rely on the assumption that *G. truncatulinoides* did not change its depth habitat in the past.

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Here we track the depth habitat of this species under past climatic conditions, which were significantly different from those of the present day. We analysed the $\delta^{18}\text{O}$ of *G. truncatulinoides* (right coiling) in three cores located on the continental slope from the SW Gulf of Mexico to Cape Hatteras. One of these cores is at immediate proximity to the cores used by Lynch-Stieglitz et al. (in press), in the Florida Straits. These authors published $\delta^{18}\text{O}$ measurements on the mixed-layer species *Globigerinoides sacculifer* and on benthic foraminifera species (*Cibicides pachyderma* and *Planulina ariminensis*) from cores taken at different water depths in the northern Florida Straits. By linear interpolation between the measured levels, they reconstructed the $\delta^{18}\text{O}$ of calcite for the entire water column during the last 12,500 calendar years. We determined *G. truncatulinoides* calcification depth by matching its $\delta^{18}\text{O}$ with the water column $\delta^{18}\text{O}$ reconstruction of Lynch-Stieglitz et al. (in press).

2. Materials and methods

2.1. Cores and oceanographic context

We measured the $\delta^{18}\text{O}$ of *G. truncatulinoides* in core KNR166-2 29JPC (24°16' N, 83°16' W, 648 m) and compare these values with the $\delta^{18}\text{O}$ of calcite reconstructed for the water column on the Florida Margin. We also analysed the $\delta^{18}\text{O}$ of *G. truncatulinoides* in core MD99-2203 (34°58' N, 75°12' W, 620 m) collected off Cape Hatteras and core RC12-10 (23°N, 95°53' W, 3054 m) raised from the southern Gulf of Mexico (Fig. 1). Age models for cores KNR166-2 29JPC and MD99-2203 are based on accelerator mass spectrometry ^{14}C dates on *Globigerinoides* species (Table 1). ^{14}C dates for core RC12-10 are from Poore et al. (2003). All ^{14}C dates were calibrated into calendar ages B.P. using the CALIB 5 program (Stuiver et al., 1998) using the standard marine reservoir correction.

Table 1
14C dates data and calendar ages for cores MD99-2203 and KNR166/2-29JPC.

Core	Depth, cm	Age ^{14}C , years	\pm	Age, cal. B.P. years, 1 σ
MD99-2203	60	820	40	440
	100	1065	25	618
	155	1360	40	893
	200	1880	25	1427
	245	2660	50	2349
	263	2800	45	2534
	265	2940	40	2731
	336	3950	40	3948
	476	7670	40	8126
	506	8260	60	8793
	579	9860	50	10,771
696 ^a			17,000	
KNR166/2-29JPC	0.75	1880	25	1424
	28.25	3660	50	3566
	40.25	6070	45	6494
	70.25	7320	40	7781
	88.25	10,200	70	11,195
	108.25	10,750	60	12,172
	120.25	11,250	70	12,849
	148.25	12,800	50	14,399
	156.25	13,650	60	15,695
	168.25	14,550	180	16,905
	182.25	16,150	60	18,955
224.25	20,300	160	23,832	

^a Age imposed from benthic $\delta^{18}\text{O}$ stratigraphy.

The northern part of the Florida Straits, the Gulf of Mexico and the Southeast American continental shelves have similar oceanographic features: a steep thermocline and a strong salinity maximum around 100–200 m water depth (Fig. 1B and 1C). This salinity maximum defines the Subtropical Under Water (SUW). This water mass, also called Salinity Maximum Water (SMW), is formed by excess

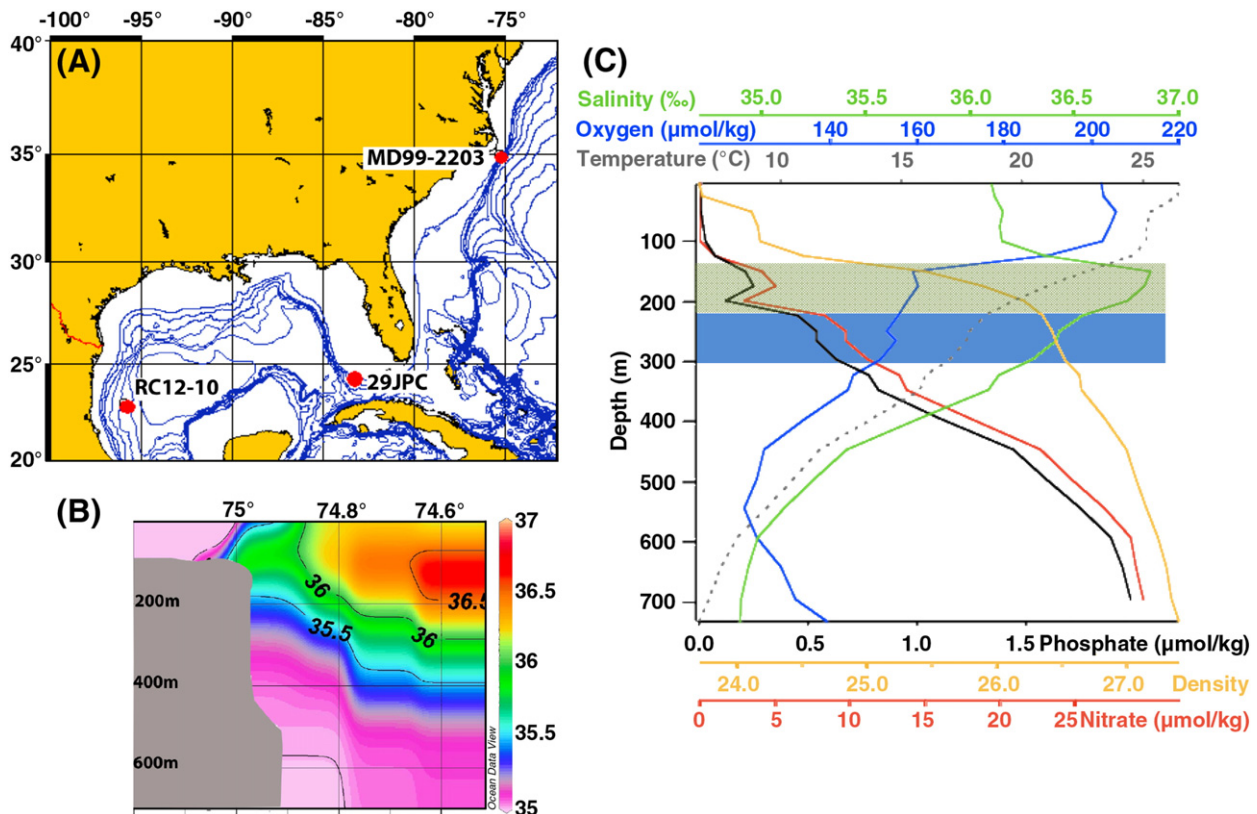


Fig. 1. Location of the cores (A) and oceanographic features. (B) Salinity section at 35°N off Cape Hatteras showing the subsurface salinity maximum (SUW) from WOCE database (Schlitzer, 2000). All core sites are at the western limit of SUW expansion. (C) Typical physical and chemical profiles above core sites (GLODAP Data, off Florida). SUW, characterized by the salinity maximum, is represented by the light green rectangle calcification depth of *G. truncatulinoides* is represented by the blue rectangle.

evaporation in the subtropical regions where it is subducted and transported northward via the Caribbean Sea and the Gulf of Mexico at around 150–300 m water depth (Blanke et al., 2002). The SUW is relatively nutrient rich but forms a strong density barrier that prevents nutrients and particles in deeper water masses from reaching surface water (Fig. 1C, Kameo et al., 2004).

2.2. Isotopic measurements

The $\delta^{18}\text{O}$ values of *G. ruber* (white) specimens in core KNR166-2 29JPC were used to constrain past sea surface conditions of the Florida Straits. *G. ruber* was picked from the 250–350 μm size fraction. The isotopic analyses of *G. truncatulinoides* were all performed on the dextral form. *G. truncatulinoides* specimens were selected from the 355–400 μm , 315–450 μm and 425–500 μm size fractions from KNR166-2 29JPC, MD99-2203 and RC12-10 cores respectively. $\delta^{18}\text{O}$ values can vary with the size of the analysed foraminifera, but this is not the case for *G. truncatulinoides* larger than 315 μm (Elderfield et al., 2002). $\delta^{18}\text{O}$ analyses of cores KNR166-2 JPC 29 and RC12-10 were made at Georgia Tech, on a GV Isoprime-Multiprep and on a MAT 253 equipped with an automated Kiel Carbonate device for CO_2 production respectively. Samples from core MD99-2203 were analysed on a Delta Plus with a Kiel Carbonate device at the LSCE. Both laboratories used NBS-19 and NBS-18 as reference standards to ensure calibration over a large range of $\delta^{18}\text{O}$ values and conversion to PDB scale. Long term reproducibilities are $<0.07\text{‰}$ for $\delta^{18}\text{O}$ on the GV and Delta Plus instruments. Replicate analyses of standards on a MAT 253 at Georgia Tech during the running of these samples reflected a precision of 0.1 ‰ .

2.3. *G. truncatulinoides* calcification depth estimate

We computed *G. truncatulinoides*, *G. ruber*, *G. sacculifer* and benthic foraminifera $\delta^{18}\text{O}$ signals on a common time scale from the 1.6 ka to 12.7 ka at intervals of 0.3 ka. As *G. ruber* is well known to represent summer surface conditions (Deuser and Ross, 1989), we fixed its calcification depth at 25 m. *G. sacculifer* was used to constrain the mixed-layer conditions and is assumed to represent conditions at 75 m water depth in accordance to modern observed mixed-layer depth. Benthic foraminifera data are from cores located at 198, 247, 358 and 445 m water depths. During the deglaciation, melting of the ice cap increased the sea level. Therefore these core depths were corrected for the past sea level changes before 6 ka (Lambeck and Chappell, 2001). These data are interpolated linearly to estimate the profiles of the $\delta^{18}\text{O}$ of calcite precipitated by foraminifera calcifying in the first 400 m water depth. The calcification depth of *G. truncatulinoides* was calculated by determining the depth in the profile that matched the $\delta^{18}\text{O}$ value of *G. truncatulinoides*.

Taking into account the measurable errors, i.e. error on ^{14}C dates, calendar age calibration uncertainties and corresponding impact on paleo core depth, the uncertainty on *G. truncatulinoides* depth habitat estimate is less than 20 meters from 11.5 to 0 ka. Around 12 ka, we estimate a maximum error of about 30 m.

3. Results

Fig. 2 illustrates the changing depth of calcification of *G. truncatulinoides* in the water column. It calcified at an intermediate depth (175 m) at the end of the deglaciation, moved to shallower depth during the early Holocene and finally reached its modern habitat (between 200 and 300 m water depth) during the mid to late Holocene. The reconstructed calcification depth is at its shallowest (125 m) around 9.4 ka, following a 50 m upward migration between 10.5 and 9.4 ka and preceding a downward displacement of 90 m from 9 to 6.7 ka.

Over the last 12.5 ka, isotope data suggests that the water column structure was relatively stable; the downward trend of the $\delta^{18}\text{O}$ isolines over the past 12,500 years reflects mainly the decrease on the global

oxygen isotopic composition of the ocean due to ice volume changes. This change impacted the $\delta^{18}\text{O}$ values of the *G. truncatulinoides* as well. Around 8.5 ka, the top 75 m water depth is homogenous and with a value of -1‰ . This period is synchronous with a freshening episode observed in the Gulf of Mexico (LoDico et al., 2006).

The large isotopic shift seen in *G. truncatulinoides* in core KNR166-2 29JPC, which reflects the change in calcification depth, is also recorded in cores MD99-2203 and RC12-10 (Fig. 3). Given the depth of the first two cores and the fragmentation index calculated for the core RC12-10 (Poore et al., 2003), dissolution can be ruled out as a factor for the low $\delta^{18}\text{O}$ intervals. Despite small chronological uncertainties, the shallower depth habitat of *G. truncatulinoides* during the early Holocene is a common signal over the entire continental slope region. The reconstructed calcification depth during the late deglaciation was not the same in all of the slope cores. In cores MD99-2203 and RC12-10, *G. truncatulinoides* $\delta^{18}\text{O}$ are higher than in core KNR166-2 29JPC by about 0.7 ‰ . We therefore assume that *G. truncatulinoides* lived deeper than 200 m water depth in the southern Gulf of Mexico and off Cape Hatteras at the end of the deglaciation.

4. Discussion

The comparison between $\delta^{18}\text{O}$ in foraminifera with known calcification depths (benthic foraminifera and surface dwelling planktonic foraminifera) and the $\delta^{18}\text{O}$ values of *G. truncatulinoides* in the Florida Straits highlights how calcification depth changes in response to environmental variations during the last 12.5 ka. At the end of the deglaciation/early Holocene, the reconstructed *G. truncatulinoides* calcification habitat is remarkably shallow. This transitional period coincided with the collapse of the continental ice sheets and a large reorganization of ocean circulation. The exact cause for this migration is not well understood but we propose two hypotheses, based on the present understanding of *G. truncatulinoides* ecology and the paleoclimatic context of the region.

1) Migration caused by continental runoff.

These cores are located relatively close to the North American continent. Moreover, the Mississippi river, which was the main drainage system of North America during the deglaciation (Teller, 1990), flows into the Gulf of Mexico. Therefore, each core site might have been influenced by the large deglacial runoff associated with the ice sheet melting. Such large terrestrial runoff would have brought freshwater and particulate material into the ocean.

Several studies have been carried out on the influence of freshwater in the Gulf of Mexico (Flower et al., 2004; Kennett et al., 1985). Freshwater input is thought to have formed a 50 meter-thick lid (Aharon, 2003), changing the upper water column structure and creating a density barrier. Furthermore, the density barrier might have reduced the flux of organic carbon through the thermocline reducing food availability for deep subsurface organisms. We hypothesize that under highly stratified conditions, *G. truncatulinoides* was constrained to stay in the upper water column to feed. However the timing of the freshwater injections does not support this hypothesis. Surface salinity reconstructions show that the main freshwater discharge in the Gulf of Mexico occurred between 15.2 and 13 ka (Flower et al., 2004) and no melt water seems to have been released through the Mississippi after 9.5 ka (Aharon, 2003; Teller, 1990). This timing and the absence of a freshwater signal in *G. ruber* $\delta^{18}\text{O}$ records of core KNR166-2 29JPC (Fig. 1), RC12-10 (Poore et al., 2003) and MD99-2203 (Cl  roux, unpublished data) during the isotopic events recorded by *G. truncatulinoides* both suggest that the freshwater input was not responsible for the depth habitat change of this deep planktonic species.

The nutrient content and the turbidity of surface seawater are increased where large rivers discharge into the ocean. Food and light penetration are primary controls on the distribution of plankton (Corredor et al., 2003), including foraminifera (Ortiz et al., 1995). Little

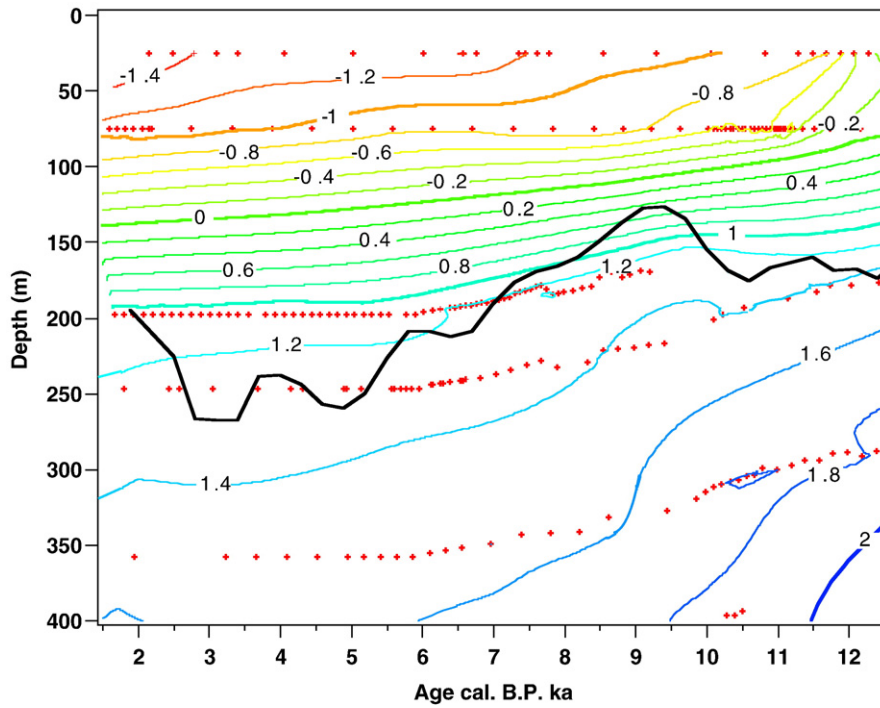


Fig. 2. *G. truncatulinoides* calcification depth change in the Florida Straits over the last 12.5 ka (in calendar age B.P.). Red points: pointer for $\delta^{18}\text{O}$ values at known water depth, from top to bottom: *G. ruber* (25 m), *G. sacculifer* (75 m), benthic foraminifera (modern depth 198, 247, 358 and 446 m). Thin colored lines: $\delta^{18}\text{O}$ isolines calculated by linear interpolation between $\delta^{18}\text{O}$ pointer values (red points). Thick black line: $\delta^{18}\text{O}$ and calcification depth of *G. truncatulinoides* from KNR166-2 29JPC measurements, $\delta^{18}\text{O}$ data smoothed on 3 points.

is known about the diet and feeding strategy of *G. truncatulinoides*, but it has been suggested that this species feeds at the deep chlorophyll maximum (Fairbanks et al., 1980). Enhanced sediment input during the deglaciation might have limited the penetration of light and thus concentrated productivity nearer to the surface, inducing a shallower deep chlorophyll maximum. Maximum clay and fine quartz ($2\ \mu\text{m}$) input in the Gulf of Mexico occurred between about 20 and 11 ka and from about 11.8 to 6.5 ka age cal B.P. respectively (Brown and Kennett, 1998). During these periods of high turbidity, superficial phytoplank-

ton live in a thin euphotic zone that may have forced *G. truncatulinoides* to live at a depth shallower than its late Holocene habitat.

2) Migration caused by changes in water masses.

Multiple plankton nets deployed in the Caribbean Sea showed that the distribution of *G. truncatulinoides* is highly related to the Subtropical Under Water (SUW) (Schmuker and Schiebel, 2002). These authors suggest that this species can be used as a tracer for SUW dynamics. Comparison between modern *G. truncatulinoides* $\delta^{18}\text{O}$ in

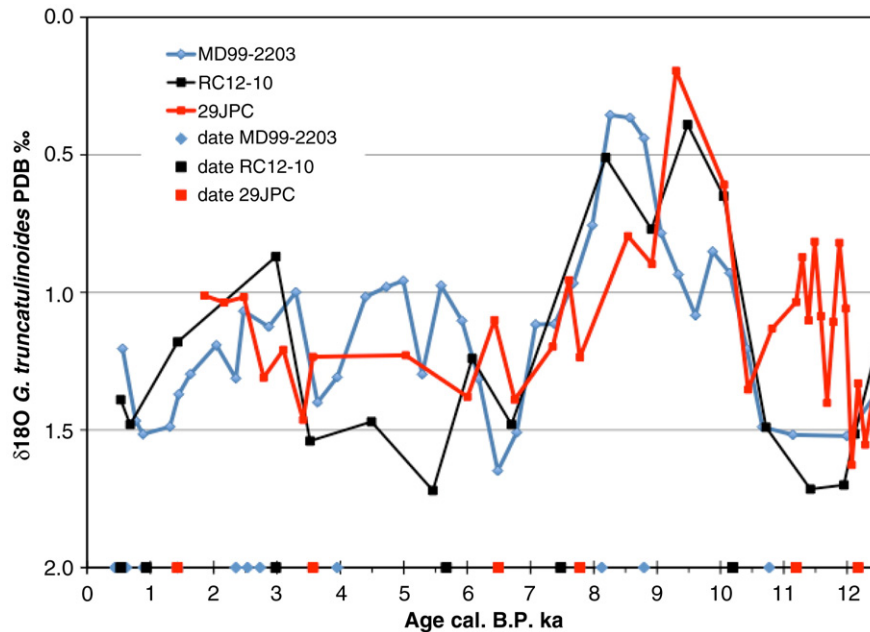


Fig. 3. Oxygen isotopic composition of *G. truncatulinoides* over the last 12.5 ka calendar age B.P. measured in cores KNR166-2 29JPC (Florida Straits, red), RC12-10 (South-west Gulf of Mexico, black) and MD99-2203 (off Cape Hatteras, blue). Also shown are calibrated ^{14}C ages performed in each core illustrated in the same color code. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

each core and present day oceanography shows that it calcifies just below the SUW (Fig. 1C). It is also worth noting that each core site is at the western limit of SUW water mass expansion and must have therefore been very sensitive to any SUW changes. This water mass has a salinity of up to 37.4 ‰ and is a strong density barrier corresponding to the nutricline. By analyzing the nannofossil assemblage, Kameo et al. (2004) reconstructed surface nutrient content and SUW history in the Caribbean Sea. They showed that glacial age surface waters were nutrient rich. In addition to the explanation already discussed here (runoff), they propose that SUW might have been shallower during glacial times. This is also in agreement with observations showing a deepening of SUW depth with increasing trade winds strength (Morell and Corredor, 2003). A deepening of SUW over the last 8 ka is therefore expected as ITCZ moved southward (Haug et al., 2001) and trade wind intensity was enhanced. While it is not clear why *G. truncatulinoides* follows SUW (presumably to find food or fill some other ecologic requirement), we can hypothesize that the depth habitat of *G. truncatulinoides* changed in response to the changes in the SUW.

5. Conclusions

Here we present a quantitative paleo calcification depth reconstruction of a deep-dwelling foraminifera species. We highlighted large calcification depth changes for *G. truncatulinoides* over the past 12 ka. The exact cause for this migration is still unclear but it occurred during a period of large environmental change, the melting of the continental ice sheets at the end of the last glaciation. This would have resulted in significant changes in freshwater runoff from the continent which would, in turn, affect ocean stratification, circulation and biology in near shore regions. The oxygen isotopic signal that results from the depth habitat change is seen over the entire Gulf of Mexico–SE United States continental margin region. The broad geographic extent of this signal shows its regional significance, but the hypothesized mechanisms behind the habitat change suggest that the shallower habitat depth might be restricted to the western margin of the North Atlantic. Our study clearly suggests caution when interpreting paleo proxy records based on *G. truncatulinoides*, or other planktonic foraminifera. Large environmental changes may well induce habitat shifts which invalidate assumptions about calcification depth that are derived from modern distributions. This study also calls attention to the need for better studies of the ecology of these deep-dwelling foraminifera which provide potentially vital information on the structure and properties of the upper ocean.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.marmicro.2009.07.001.

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