Clim. Past Discuss., doi:10.5194/cp-2015-185, 2016
Manuscript under review for journal Clim. Past
Published: 18 January 2016

Detecting the onset and effects of major northern hemisphere glaciation in the abyssal tropical Atlantic Ocean

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Abstract

The cooling trend of the Neogene resulted in the diachronous development of glacial conditions, southern high latitudes glaciating before northern. This cooling culminated in the early Pleistocene (2.54 Ma) onset of major glaciation, during which large areas of high latitude land and sea in both hemispheres were periodically blanketed with ice. However, this onset and its impact at low latitude abyssal depths are elusive. This paper examines the abyssal benthic foraminiferal community in the Atlantic Ocean near the Northern Equatorial Countercurrent, in ODP Hole 926A (Ceara Rise), off the River Amazon. Using an assemblage turnover index (ATI), a related conditioned-on-boundary index (CoBI) and SHE analysis, we show how a change in mean assemblage turnover coincides with the early Pleistocene onset of northern hemisphere major glaciation. The community comprises primarily phytodetritivores (*Alabaminenella weddellensis, Epistominella exigua* and *Globocassidulina subglobosa*), the proportional abundances of which differ before and after 2.54 Ma. Coupled with changes in the abundances of *Nuttallides umbonifera*, *Bulimina* spp. and *Uvigerina* spp., alterations in the abundances of the phytodetritivores after 2.54 Ma show that the adjustment in biotic turnover at depth resulted from enhanced organic carbon flux from sea surface water. This was probably related to forced southward repositioning of the inter-tropical convergence zone (ITCZ) by the growth of the northern hemisphere ice caps. This was coupled with an increase in bottom current velocity, as shown by a change in the abundance of *Cibicidoides wuellerstorfi*.

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1. Introduction

The stratigraphic level coincident with the Early Pleistocene onset of major northern hemispheric glaciation at abyssal depths in the tropical Atlantic Ocean has so far proven elusive. There are no obvious sedimentological proxies coincident with that onset (Dobson et al., 1997). Nor is the subsequent impact of that onset clear. Biotic responses must therefore be sought, such as among benthic foraminifera away from slumped material along continental margins.

The Ceara Rise is an abyssal, aseismic ridge in the western tropical Atlantic Ocean off NE South America between 3 – 8°N and 38 – 45°W (Kumar and Embley, 1977). It lies beneath the eastward-flowing North Equatorial Countercurrent (NEC), which extends between ~3 – 10°N (Phialnder, 2001) and for some months each year carries low-salinity water derived from the Amazon (CERSAT, 2011). Thus, although the ridge is covered with muds of Andean origin delivered to the open ocean by the Amazon, the Ceara Rise lies beyond the limits of slumping within the Amazon deep-sea fan (Damuth and Kumar, 1975; Dobson et al., 1997; Manley and Flood, 1988). Ocean Drilling Program (ODP) Holes on the rise are ideally situated to examination of the impact of the Countercurrent and its associated Amazon water on the foraminifera of the western tropical Atlantic. We show here the impact of the alteration of the current by the onset of major glaciation in the northern hemisphere at ~2.4 Ma.

Primary productivity in the tropical Atlantic is usually examined with mean annual rates only (da Cunha and Buitenhuis, 2013; Foster and Sexton, 2014). The open western tropical Atlantic waters have been shown to be oligotrophic, with mean primary productivity rates (MPPR) in surface water of ~400 mgC/m^2/day (Foster and Sexton, 2014). In contrast, water immediately off the River Amazon is eutrophic, with a MPPR ~1200 mgC/m^2/day. However, Shipe et al.(2007) found that production of diatoms, the main phytoplankton within the Amazon plume between 2 – 14°N and 40 – 57°W, was markedly greater during the equatorial summer (July and August), coinciding with the maximum transport of Amazon water eastwards by the NEC; it follows that the Ceara Rise is subject to a seasonal phytodetrital flux. Yasuda (1997), using qualitative interpretations, found this seasonal flux to be reflected in the benthic foraminiferal fauna at the Ceara Rise ODP Site 926 (3°43.146′N, 43°44.884′W, water depth 3598.4 m; Figure 1). The three most common species (*Globocassidulina subglobosa*, *Epistominella exigua*, *Alabaminella weddellensis*) are phytodetrivores that respond opportunistically to a pulsed phytodetrital rain (Gooday, 1994, 2002; Gooday and Rathburn, 1999; Smart et al., 1994), although *G. subglobosa* has also been recorded as abundant in sediment associated with methane seeps (Panieri and Sen Gupta, 2008). The fourth most abundant species (*Nuttallides umbonifera*) is adapted to extreme oligotrophy (Gooday, 1993) and corrosive bottom waters (Corliss, 1979; Gupta et al., 2013). Of these four species, *A. weddellensis*, *E. exigua* and *N. umbonifera* are epifaunal, while *G. subglobosa* is infaunal.

Recent studies have demonstrated that benthic foraminiferal species differ in their niche widths. Examining Middle Miocene foraminifera in the Cipero Formation of Trinidad, Wilson and Hayek (2015a) characterised *Cibicidoides wuellerstorfi* as a generalist and *E. exigua*, although an opportunist, as a relative specialist. Wilson and Hayek (2015b) used Late Quaternary benthic foraminifera to demonstrate that generalists such as *Bulimina aculeata* will range through a stratigraphic section showing no significant trends in proportional abundance, while relative specialists such as *Bulimina alazanensis* and *E. exigua* show trends, their proportional abundances fluctuating throughout the section. Thus, even congeneric species such as these can possess different niche widths. Here we re-examine the data published by Yasuda (1997) from ODP Hole 926A. We use a quantitative measurement approach with assemblage

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turnover and conditioned-on-boundary indices (Hayek and Wilson, 2013; Wilson and Hayek 2014a, 2014b) to (a) identify and explain the timing of a major regime shift within the later Neogene, and (b) compare niches of the phytodetritivore species *A. weddellensis*, *G. subglobosa* and *E. exigua*.

2. Materials and methods

Yasuda (1997, table 1) tabulated the benthic foraminifera in the >63 μm fraction in 115 samples from ODP Hole 926A taken between 0.8 – 164.27 meters below the seafloor (mbsf), with a mean sample spacing of 1.62 m (minimum spacing = 0.11 m, maximum = 5.94 m). He presented an age model based on the correlation between magnetic susceptibility records and previously published isotope records, which is accepted here. According to this model, the samples range in age from 0.027 – 6.598 Ma, which equates to the latest Miocene (Messinian) and younger, with 199 – 376 benthic foraminifera per sample (mean, 242 specimens), and a total yield of 27,542 specimens and 53 taxa. Some specimens were identified to species level, but some taxa were not split into species (*Gyroidina*, some *Uvigerina*, miliolids and unilocular specimens). A small number of rare specimens (mean ~3% per sample) were grouped as unidentified.

For this study, the proportional abundance of each taxon in each sample was calculated. The absolute values of the differences in these proportional abundances were summed between adjacent samples to give the sample-wise assemblage turnover index (ATI_s) (Hayek and Wilson, 2013). The series of values of ATI_s in ODP Hole 926A was examined for overall trend and sequenced into two subsections for which linear regression did not show any significant trend.

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Because ATI is the sum of random variables that are the differences of proportions, each component or random variable is Normally distributed for our large samples and can be tested with a normal deviate test. Then, the sum of Normal variates is known to be Normally distributed. Therefore, the index ATI will likewise be normally distributed by definition for our samples. However, because we include rare species we chose to include a normal quantile plot test to assess observed normality of ATI values. Hartley's Fmax test, the ratio of the maximal to minimal variance, was used was used to compare the variances between the subsections determined by sequencing. Subject to assumptions testing, Student's or Welch's *t*-test was used to compare subsection means.

The thorough ATI_t (Hayek and Wilson, 2013) objectively determines total assemblage turnover across any boundary, while the thorough conditioned-on-boundary index ($CoBI_t$) objectively determines the proportional contribution of each species to the ATI_t (Wilson and Hayek, 2014a). For our study, the ATI_t was calculated between the subsections determined from sequencing, while $CoBI_t$ was determined for each taxon across the subsection boundary. What is known of the ecologies of species with high $CoBI_t$ was used to check whether they showed distributions typical of specialist species and to infer palaeoenvironmental change.

Sample-wise diversity was quantified using Shannon's H index, dominance using the Berger-Parker index of max (p_i) and evenness by $E = e^H/S$, where S is species richness (for details see Hayek and Buzas, 2013). The values of H in the subsections identified using ATI_s were tested for similarity of variance, and compared using Student's t-test. SHE analysis (Buzas and Hayek, 1998; Hayek and Buzas, 1997; Hayek and Buzas, 2010) was used on the matrix of relative abundances accumulated over samples to determine abundance biozones.

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Jain and Collins (2007) and Jain et al. (2007) suggested that the joint abundances of *Cibicidoides wuellerstorfi* and *Globocassidulina subglobosa* per sample can be used as a proxy for palaeocurrent strength, these two species showing similar trends (Pearson's $r = 0.33$, $p = 0.03$) in the Neogene at ODP Site 999 (western Caribbean Sea), even though Jain and Collins (2007) listed them as being epifaunal and infaunal respectively. They are here used to assess variations in relative current strength in the later Neogene of ODP Hole 926A.

3. Results

Assemblages were dominated by *Globocassidulina subglobosa* (17.1% of total recovery), *Alabaminella weddellensis* (14.2%) and *Epistominella exigua* (12.1%), with lesser *Nuttallides umbonifera* (7.0%) and unilocular species (6.1%). *Uvigerina* spp. formed only 0.7% of the total recovery, while *Bulimina* spp. (principally *B. alazanensis*) formed 1.4%. *Cibicidoides* spp. formed 3.4% of the total recovery, while *C. wuellerstorfi* alone formed 0.6%. Unidentified specimens accounted for 3.1% of total recovery.

The minimum ATI_s was 0.33, between 143.8 – 145.3 mbsf, which equates to 5.627 – 5.560 Ma (Figure 2). In contrast, the maximum ATI_s of 1.28, between 18.39 – 19.89 mbsf, equates to 0.564 – 0.610 Ma. The mean ATI_s was 0.59. For determination of long-term trends, ATI_s values were assumed to reflect assemblage turnover at the mean of the ages of adjacent samples ($mean_{MA}$). Linear regression ($F_{(1,112)} = 25.310$, $p < 0.0001$) suggests that there is an overall long-term trend in turnover, with $ATI_s = 0.713 – 0.039(mean_{Ma})$. Over this time period the curve of ATI_s comprises two subsections, each with insignificant linear trends. In the 61 samples in the lower subsection (164.27–75.8 mbsf, 6.598 – 2.654 Ma, for which $F_{(1,\ 59)} = 2.235$, $p =$

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0.140), $ATI_s = 0.604 – 0.017(mean_{Ma})$. For the 53 samples in the upper subsection (74.3 – 0.8 mbsf, 2.605 – 0.027 Ma, for which $F_{(1,52)} = 1.639$, p = 0.206) $ATI_s = 0.732 – 0.048(mean_{Ma})$. Values of ATI_s in the lower subsection were normally distributed, as expected, though the variance for ATI_s in the lower subsection ($\sigma^2 = 0.01$) was significantly different from that for the upper ($\sigma^2 = 0.04$). Mean values of ATI_s (0.526 lower, 0.669 upper) were compared (Welch *t* = 4.62, p<0.0001, df = 72). Thus, mean assemblage turnover between samples was greater after ~2.625 Ma, at which time assemblage turnover fluctuated more widely.

SHE analysis found 21 abundance biozones (ABs) over the interval represented by the 115 samples. The lower subsection prior to 2.654 Ma contained most of the abundance biozones' change (14/21). Communities contained only 1 to 6 samples, and diversity increased in each. Beginning with AB15 (2.954 – 2.654 Ma) and continuing into AB16 (2.605 – 2.040 Ma), diversity decreased. Regression of H against lnN was insignificant in the lower subsection but significant in the upper. After AB15, diversity again increased. During AB15, evenness dropped from 0.562 to 0.415, then over the boundary, dominance increased sharply so that E reached 0.60, remaining high into time period 2.555 –2.506 Ma, then decreased to prior levels. Species richness S increased from 34 to 43. At the boundary time period S dropped approximately 30% to 31. This was the largest decrease in S over any of the AB boundaries in Hole 926A.

Shannon's H ranged from 2.403 – 3.039 ($\bar{x}$ = 2.773) in the lower subsection, and 2.141 – 2.940 ($\bar{x}$ = 2.605) in the upper (Figure 2B). Values of H were normally distributed in both subsections as expected, while the variances did not differ (lower, σ^2= 0.021; upper, σ^2= 0.029). However, mean H for the two sections differed significantly (Student's *t*= 5.693, df = 112, p< 0.0001). Mean evenness E for the lower subsection ($\bar{x} = 0.816$) was greater than for the upper

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($\bar{x} = 0.793$). Mean dominance ($\max(p_i)$)was smaller in the lower subsection ($\bar{x} = 0.215$) than in the upper subsection ($\bar{x} = 0.245$). Thus, there was an overall fall in diversity and evenness, and an increase in dominance, after ~2.625 Ma, as was likewise evidenced by the accumulated data in regression.

The boundary between the two subsections identified using ATI_s and the AB detection method SHE, was examined using ATI_t, with subsequent conditioned-on-boundary index ($CoBI_t$) applied to each of the taxa. The ATI_t between the two subsections was 0.402. $CoBI_t$ ranged between 0.0001 (*Bolivina pacifica*) and 0.263 (*Alabaminella weddellensis*). That is, *B. pacifica* was responsible for 0.01% of the turnover between the two subsections, while *A. weddellensis* was responsible for 26.3% of the approximate total 40% turnover during that time. Mean $CoBI_t$ among the 53 taxa was 0.019; 12 taxa had $CoBI_t$ greater than the mean (Table 1). Clearly, the most abundant species need not contribute the greatest amount to ATI_t at a boundary; the most frequently recovered species, *G. subglobosa* (17.1% of total recovery), contributed only 8% to the ATI_t, while the second most abundant species, *A. weddellensis* (14.2% of total recovery), contributed 26% to ATI_t. *Uvigerina peregrina* had a $CoBI_t$ of 0.018, which is just less than the mean.

The proportions of selected taxa in each sample are shown in Figure 3. The variance in the proportional abundances of *A. weddellensis* in the lower subsection ($\sigma^2 = 0.003$) was significantly different and smaller than that in the upper ($\sigma^2 = 0.008$). The mean from the lower subsection as *A. weddellensis* ($\bar{x} = 0.093$) was significantly different and lower than the mean proportion as this species in the upper ($\bar{x} = 0.20$; by both Normal deviate test and Welch's $t = 7.43$, $p<0.0001$, df= 112). The variance for *E. exigua* in the two subsections (lower, $\sigma^2 = 0.004$; upper, $\sigma^2 = 0.005$) did not differ significantly and the mean from the lower as *E. exigua* ($\bar{x} =$

0.135) was significantly higher than that in the upper ($\bar{x}$ = 0.10; by both Normal deviate test and Welch's *t* = 2.77, p = 0007, df = 112). This difference between *A. weddellensis* and *E. exigua* would not have been detected if, as is usual, only the correlation between their proportional abundances over all samples had been examined, the correlation being statistically insignificant (r = –0149, p = 0.12). As with *E. exigua*, the proportional abundances of *G. subglobosa* were not normal in the lower subsection, but were in the upper. The variance of the proportional abundances of *G. subglobosa* in the two subsections did not differ, being 0.005 in both. The mean proportion from the lower subsection as *G. subglobosa* ($\bar{x}$ = 0.183) was significantly higher than that in the upper ($\bar{x}$ = 0.154; Welch's *t* = 2.04, p = 0.03, df = 112). As might be expected from these results, the proportional abundances as *G. subglobosa*, which was more abundant in the lower subsection, and *A. weddellensis*, which was more abundant in the upper subsection, were significantly negatively correlated (r = –0.472, p<0.0001). Intriguingly, however, the proportional abundances as *G. subglobosa* and *E. exigua*, both of which were more abundant in the lower subsection, were likewise significantly negatively correlated (r = –0.37, p = 0.0001). Overall, some proportion of the detritivores *E. exigua* and *G. subglobosa* was replaced by *A. weddellensis* in the upper subsection.

Wilson and Hayek (2015a) characterised *Cibicidoides wuellerstorfi* as showing relative generalist behaviour in the Middle Miocene Cipero Formation of Trinidad, while Wilson and Hayek (2015b) suggested that *Bulimina alazanensis* showed specialist behaviour in the Upper Quaternary offshore Trinidad. The distributions of both are examined here for comparison, although *C. wuellerstorfi* formed only 0.6% of the total recovery, and *B. alazanensis* only 1.4%. The proportional abundances of *C. wuellerstorfi* were not normally distributed in either of the subsections, while the variance was greater in the upper (σ^2 = 0.00007) than in the lower (σ^2 =

0.00003; $F_{max} = 2.14$). The mean of *C. wuellerstorfi* in the lower subsection ($\bar{x} = 0.40$) was smaller than in the upper subsection ($\bar{x} = 0.85$; Welch's $t = 3.20$, p = 0.002, df = 109). *Bulimina alazanensis* never formed >0.8% per sample, but was more frequently recovered from the lower subsection (6 of 61 samples) than the upper (2 of 53 samples).

Jain and Collins (2007) used the joint relative abundances of *Cibicidoides wuellerstorfi* and *Globocassidulina subglobosa* as a proxy for relative current strength. The proportional abundances of these two species are not significantly correlated at ODP Hole 926A (r = –0.162, p = 0.086). Whereas the mean proportional abundance of *G. subglobosa* was higher in the lower subsection, that of *C. wuellerstorfi* was lower in the lower subsection. The mean joint proportional abundance of these species did not differ between the lower ($\bar{x} = 0.176$) and upper ($\bar{x} = 0.162$) subsections (Welch's $t = 1.14$, p = 0.26, df = 103).

Wilson and Hayek (2015b); Wilson and Hayek (2015a) noted that congeneric species can have differing ecologies. Kaiho (1994) reported that species of *Cibicidoides* occupy oxic waters (>2 mL/L O_2), even though they prefer somewhat different rates of organic flux. Mean *Cibicidoides* in the lower ($\bar{x} = 3.2\%$) was significantly different and smaller than in the upper subsection ($\bar{x} = 4.7\%$; Welch's $t = 2.82$, p = 0.006, df = 102; Figure 3E). In contrast, Kaiho (1994) reported *Bulimina* spp. and *Uvigerina* spp. to be indicative of suboxic bottom water, perhaps due to a tolerance for a high organic flux (Altenbach et al., 1999). Variances of total *Bulimina spp* in the subsections differed significantly ($F_{max} = 5.3$; Figure 3D). Mean percentage as *Bulimina* spp. in the lower subsection ($\bar{x} = 0.4\%$) is significantly different and the value is smaller than in the upper subsection ($\bar{x} = 2.7\%$; Welch's $t = 12.25$, p = 0.0001, df = 102). Forty one of the 61 samples from the lower subsection did not yield *Bulimina* spp. at all, whereas only one sample in the upper subsection did not yield any. *Uvigerina* spp. (principally *U. peregrina*) showed similar distributions to *Bulimina* spp., with mean percentage in the lower subsection ($\bar{x}$ = 0.51%) significantly different and lower than in the upper ($\bar{x}$ = 1.0%; Welch's t = 2.202, p = 0.031, df = 102; Figure 3F).

The proportional abundances of *N. umbonifera* were not normal in either of the subsections and lower ($\bar{x}$ = 0.08) and upper ($\bar{x}$ = 0.05) subsections were significantly different. The variances did not differ (lower, σ^2 = 0.002; upper, σ^2 = 0.003). There were no significant trends detected over time in the lower subsection. There was an overall decrease in *N. umbonifera* throughout the entire upper section from 6.598 – 0.027 Ma (0.021 + 0.027(age in Ma); $F_{(1, 52)}$ = 9.84, p= 0.003). However, as noted by Yasuda (1997), this decrease is modified by periods of relatively high and low proportional abundances.

4. Discussion

The sample-wise assemblage turnover index (ATI_s) of Hayek and Wilson (2013) is a measure of community stability, with lower values indicating more stable conditions. In ODP Hole 926A, ATI_s partitions the later Neogene into two subsections, each fluctuating around different mean values of ATI_s. The lower subsection (75.8 – 164.27 mbsf, 6.598 – 2.654 Ma) had a smaller mean value of ATI_s, or less community change, than did the upper subsection (74.3 – 0.8 mbsf, 2.605 – 0.027 Ma). Furthermore, the variance in ATI_s was greater in the upper subsection than the lower. The boundary between these subsections coincides with the onset of major Northern Hemisphere glaciations at ~2.64 Ma as modelled by Bailey et al. (2013). The impact on the benthic foraminiferal community is comparable to that noted by Veersteegh (1997), who found that dinoflagellate cyst and acritarch communities in the North Atlantic Ocean and Mediterranean Sea underwent reorganisation and relocation of species associations, coupled with enhanced species turnover, following the onset of northern hemispheric major glaciations. The higher value of mean ATI_s in the upper subsection shows that the benthic foraminiferal community was less stable during the Pleistocene after ~2.64 Ma than it was during the latest Miocene and Pliocene.

The impact of the onset of major glaciation is reflected in the diversity and dominance of the deep-sea foraminiferal assemblage in these samples. Mean sample-wise diversity, measured using the Shannon's H, was lower during deposition of the upper subsection, after the onset of major glaciations and at the time of increased mean ATI_s. This apparently suggests that times of higher stability (i.e., latest Miocene and Pliocene) were also times of higher diversity. However, that community stability engenders high diversity need not always be the case. Wilson et al. (2014) examined ATI_s among foraminifera and ostracods in an oxygen minimum zone in the Miocene Brasso Formation of Trinidad, where they found ATI_s to be low and stable within the zone, in a region with low values of H. In ODP Hole 926A, dominance was higher during the deposition of the upper, Pleistocene subsection. Hayek and Wilson (2013) suggested that peaks in benthic foraminiferal ATI_s coincide with the transgressions at glacial terminations. Due to wide and irregular sample spacing, peaks in ATI_s recorded by the present study cannot be used to invoke glacial terminations.

Wilson and Hayek (2015b) recorded that the changing position of the inter-tropical convergence zone (ITCZ) during the later Quaternary had a major impact on the bathyal benthic foraminiferal fauna off NE South America, around Trinidad. The impact of northern hemispheric glaciations on the tropical abyssal fauna may similarly have been related to a change in the location of the ITCZ. At present the mean position of the ITCZ is at about 5–7°N (Philander et al., 1996). During Late Miocene times, when South America lay approximately at

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its current location relative to the equator but glaciation was more extreme in the Antarctic than in the Arctic, the ITCZ was pushed north to about 30°N (Hay, 1993; Van Vliet-Lanoe, 2007). Billups et al. (1999) suggested that changes in thermohaline circulation, the density-driven part of global ocean circulation driven by regional variations in salinity and the flux of heat across the sea surface (Rahmstorf, 2006), around 4.4–4.3 Ma drove the ITCZ towards its modern location. This relocation was not especially marked by a peak in ATI_s in ODP Hole 926A, although changes in the thermohaline circulation system would be expected to have a large impact on global marine fauna and flora through associated climate change (Marotzke, 2000). Hoffmann et al. (2014) suggested that the mean annual position of the ITCZ in the Atlantic region during the Last Glacial Maximum was 2°S, with a shift to 10°–12°N during the early Holocene. It is possible that the arrival at this glacial-interglacial position at ~2.64 Ma, coincident with the onset of major glaciations in the northern hemisphere, caused the shift in mean ATI_s at ODP Site 926A, perhaps either by shifting the position of the NEC, which currently extends from ~3 – 10°N, or by changing the outflow from the Amazon. The marked increase in the variance of ATI_s within the Pleistocene post-2.64 Ma upper subsection might reflect the impact of the south-north, glacial-interglacial migration of the mean position of the ITCZ during Pleistocene times noted by Hoffmann et al. (2014).

The total recovery from ODP Hole 926A was dominated by opportunistic phytodetritivores adapted to a seasonal flux of phytodetritus: *G. subglobosa* (17.1% of total recovery), *A. weddellensis* (14.2%) and *E. exigua* (12.1%). However, the means of these species changed between the two subsections, *G. subglobosa* and *E. exigua* being more abundant in the lower subsection than in the upper, while *A. weddellensis* is the opposite. This suggests that these epifaunal species *A. weddellensis* and *E. exigua* have subtly different niches. This is supported by Suhr et al. (2003), who demonstrated that the different phytodetritivores selectively feed on different components of the deposited material. The epifaunal species *N. umbonifera* (7.0% of total recovery), which is indicative of extreme oligotrophy and corrosive bottom water, is more abundant in the lower subsection. This supports the contention that *G. subglobosa* is adapted to exploiting seasonal detrital inputs in oligotrophic areas (Singh and Gupta, 2004) and suggests that the same is true of *E. exigua*. *Uvigerina* spp. and *Bulimina* spp., which are indicative of an enhanced nutrient flux and diminished bottom-water oxygen concentrations, were never abundant (together they comprised 2.2% of total recovery), but were relatively more abundant in the upper subsection. Coupled with the change in the abundance of *N. umbonifera,* the change in *Uvigerina* spp. and *Bulimina* spp. indicates an enhanced flux of organic carbon during deposition of the upper subsection, which in turn suggests that *A. weddellensis* is indicative of an enhanced seasonal phytodetritus flux relative to *G. subglobosa* and *E. exigua*.

Jain and Collins (2007) suggested that the joint proportional abundance of *G. subglobosa* and *C. wuellerstorfi* can be used as a proxy for palaeocurrent strength. However, these species did not show similar distributions in ODP Hole 926A, the mean proportional abundance of *G. subglobosa* being higher in the lower subsection, where that of *C. wuellerstorfi* is lower. The mean joint proportional abundances of these species do not differ between the two subsections. This is not here taken to suggest that current strength did not differ between the subsections, but rather that this index might be unreliable. Whereas Jain and Collins (2007) characterised *C. wuellerstorfi* as being an epifaunal species, they classified *G. subglobosa* as having an infaunal habitat. It is challenging to imagine how a species living below the sediment-water interface can be influenced by current speed in the water above that interface unless there is frequent reworking of the sediment by current action. This is unlikely to be the case for the muddy sediment at Ceara Rise. The higher mean proportional abundance of *C. wuellerstorfi* in the upper subsection might, however, reflect higher current velocities after the onset of northern hemispheric glaciation.

Conclusions

The composition of the benthic foraminiferal community developed at depth is influenced by the organic matter flux from surface waters coupled with abiotic factors such as current strength, temperature and dissolved oxygen concentration at the sea floor. At the tropical, abyssal Ceara Rise, the onset of major northern hemispheric glaciations is marked by an increase in the mean value of benthic foraminiferal assemblage turnover, as measured using the assemblage turnover index. As indicated by the conditioned-on-boundary index, this change in large measure reflects restructuring of the phytodetritivore (*Alabaminella weddellensis*, *Epistominella exigua*, *Globocassidulina subglobosa*) community. This is coupled with an increase in the proportional abundances of dysoxic indicators associated with an enhanced flux of organic matter (*Uvigerina* spp., *Bulimina* spp.) and a decrease in the abundance of an oligotroph (*Nuttallides umbonifera*). Thus, much of the change in community was a function of events at the sea surface, perhaps being due to either a forced repositioning of the Northern Equatorial Countercurrent, a repositioning of the ITCZ causing an increase in the seasonal outflow of nutrient-rich water from the Amazon River, or both. This is coupled with an increase in bottom current strength, as indicated by enhanced levels of *Cibicidoides wuellerstorfi*. The changes demonstrate that the onset of Pleistocene glaciation had far flung effects on the deep-sea foraminiferal fauna in the Atlantic Ocean. Further work is needed to assess if this signal is present elsewhere in the Atlantic Ocean, especially far from major rivers, or in the tropical, abyssal realms of other oceans.

Acknowledgements

BW would like to thank the Ministry of Energy and Energy Industries of Trinidad and Tobago for financial support for this project, and Andrew Jupiter in particular for helping arrange this support.

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Table Captions

Table 1. Values of CoBI_t for selected species of benthic foraminifera at the boundary between the lower and upper subsections, ODP Hole 926A, in rank order.

Thorough assemblage turnover index (ATI_t)	0.402
Alabaminella weddellensis	0.264
Globocassidulina subglobosa	0.080
Epistominella exigua	0.077
Pleurostomella sp.	0.065
Nuttallides umbonifera	0.063
Bulimina sp. A	0.057
Bolivina spp.	0.033
Ioanella tumidula	0.028
Pullenia osloensis	0.026
Unilocular species	0.025
Cibicidoides mundulus	0.022
Pullenia quinqueloba	0.020

Figure captions

Figure 1. ODP Hole 926A and ocean surface current systems in the western tropical Atlantic Ocean.

Figure 2. Statistical measures in the later Neogene of ODP Hole 926A. A. Between sample assemblage turnover index (ATI_s). B. Per sample Shannon diversity index, H. C. Per sample evenness index, E. D. Per sample dominance, $\max(p_i)$. Horizontal dashed line, onset of northern hemisphere glaciations. Vertical dashed lines, mean values of measure in lower and upper subsections.

Figure 3. Per sample proportional abundances of taxa in later Neogene of ODP Hole 926A. A. *Alabaminella weddellensis*. B. *Epistominella exigua*. C. *Globocassidulina subglobosa*. D. Total *Bulimina* spp. E. *Cibicidoides wuellerstorfi*. F. *Uvigerina* spp. Horizontal dashed line, onset of northern hemisphere glaciations. Vertical dashed lines, mean proportional abundances in lower and upper subsections.

Figure 1

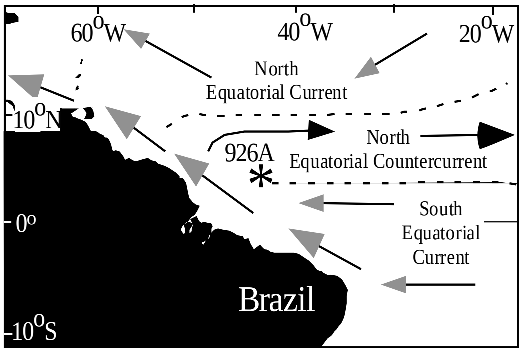

60°W
40°W
20°W
North Equatorial Current
10°N
926A
North Equatorial Countercurrent
0°
South Equatorial Current
Brazil
10°S

Figure 2

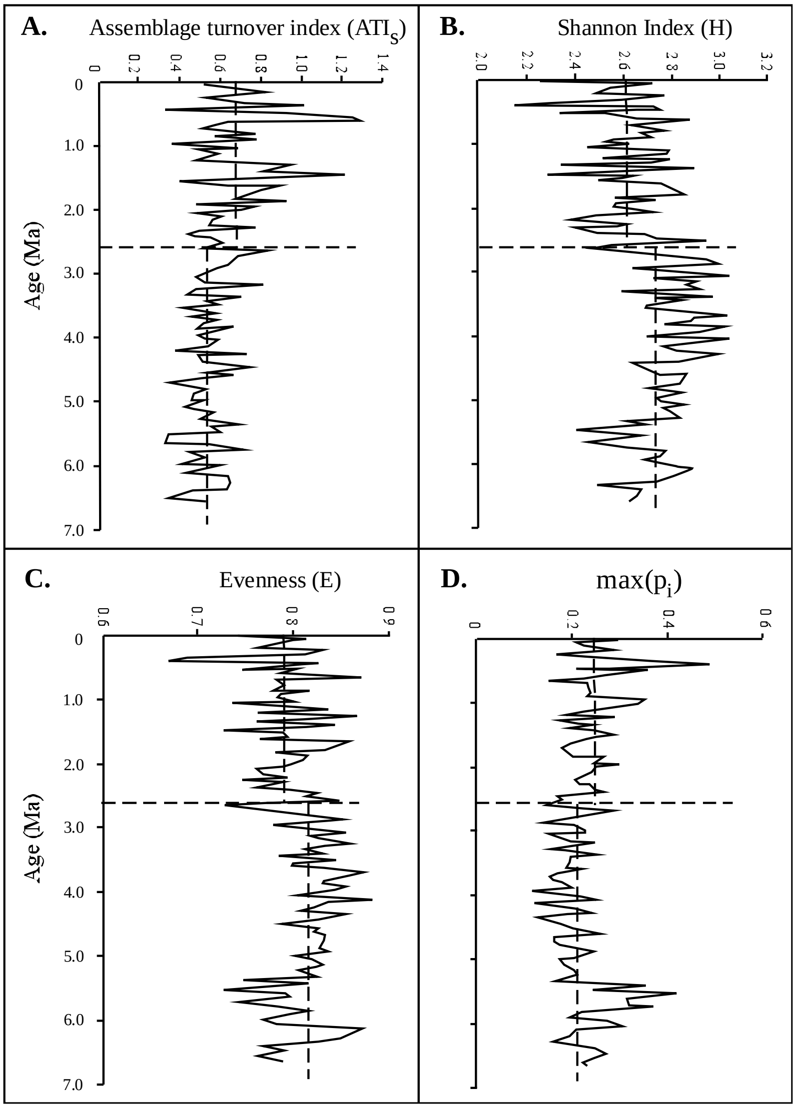
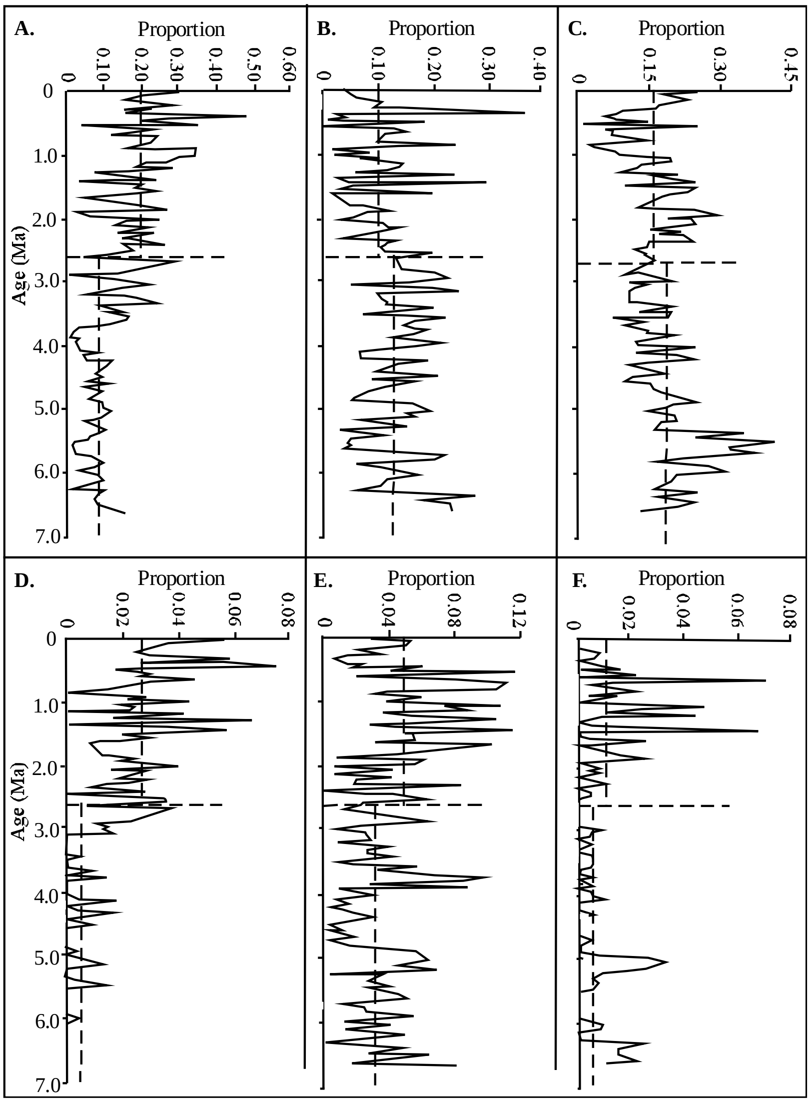

A.
Assemblage turnover index (ATI_S)
0
0.2
0.4
0.6
0.8
1.0
1.2
1.4
B.
Shannon Index (H)
2.0
2.2
2.4
2.6
2.8
3.0
3.2
Age (Ma)
0
1.0
2.0
3.0
4.0
5.0
6.0
7.0
C.
Evenness (E)
0.6
0.7
0.8
0.9
D.
max(p_i)
0
0.2
0.4
0.6
Age (Ma)
0
1.0
2.0
3.0
4.0
5.0
6.0
7.0

Figure 3


A.
Proportion
0
0.10
0.20
0.30
0.40
0.50
0.60
Age (Ma)
0
1.0
2.0
3.0
4.0
5.0
6.0
7.0
B.
Proportion
0
0.10
0.20
0.30
0.40
C.
Proportion
0
0.15
0.30
0.45
D.
Proportion
0
0.02
0.04
0.06
0.08
Age (Ma)
0
1.0
2.0
3.0
4.0
5.0
6.0
7.0
E.
Proportion
0
0.04
0.08
0.12
F.
Proportion
0
0.02
0.04
0.06
0.08