

Paleoceanography of the southern Agulhas Plateau during the last 150 ka: Inferences from benthic foraminiferal assemblages and multispecies epifaunal carbon isotopes

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Received 22 June 2007; accepted 27 August 2007; published 29 December 2007.

[1] Benthic foraminiferal assemblages and the carbon isotope composition of the epifaunal benthic foraminifera *Epistominella exigua* and *Fontbotia wuellerstorfi* have been investigated along core MD02-2589 located at the southern Agulhas Plateau (41°26.03'S, 25°15.30'E, 2660 m water depth). This study aims to evaluate changes in the benthic paleoenvironment and its influence on benthic $\delta^{13}\text{C}$ with a notable focus on *E. exigua*, a species associated with phytodetritus deposits and poorly studied in isotope paleoceanographic reconstructions. The benthic foraminiferal assemblages (>63 μm) show large fluctuations in species composition suggesting significant changes in the pattern of ocean surface productivity conceivably related to migrations of the Subtropical Convergence (STC) and Subantarctic Front (SAF). Low to moderate seasonality and relatively higher food supply to the seafloor are indicated during glacial marine isotope stages (MIS) 6, 4, and 2 and during MIS 3, probably associated with the northward migration of the SAF and confluence with the more stationary STC above the southern flank of the Agulhas Plateau. The lowest organic carbon supply to the seafloor is indicated from late MIS 5b to MIS 4 as a consequence of increased influence of the Agulhas Front (AF) and/or weakening of the influence of the STC over the region. Episodic delivery of fresh organic matter, similar to modern conditions at the core location, is indicated during MIS 5c–MIS 5e and at Termination I. Comparison of this paleoenvironmental information with the paired $\delta^{13}\text{C}$ records of *E. exigua* and *F. wuellerstorfi* suggests that organic carbon offsets $\delta^{13}\text{C}$ of *E. exigua* from ambient bottom water $\delta^{13}\text{C}_{\text{DIC}}$, while its $\delta^{13}\text{C}$ amplitude, on glacial-interglacial timescales, does not seem affected by changes of organic carbon supply to the seafloor. This suggests that this species calcifies preferentially during the short time span of the year when productivity peaks and phytodetritus is delivered to the seafloor. Therefore *E. exigua*, while offset from $\delta^{13}\text{C}_{\text{DIC}}$, potentially more faithfully records the amplitude of ambient bottom water $\delta^{13}\text{C}_{\text{DIC}}$ changes than *F. wuellerstorfi*, notably in settings such as the Southern Ocean that experienced substantial changes through time in the organic carbon supply to the seafloor.

Citation: Diz, P., I. R. Hall, R. Zahn, and E. G. Molyneux (2007), Paleoceanography of the southern Agulhas Plateau during the last 150 ka: Inferences from benthic foraminiferal assemblages and multispecies epifaunal carbon isotopes, *Paleoceanography*, 22, PA4218, doi:10.1029/2007PA001511.

1. Introduction

[2] The South Atlantic is involved in setting the state of global climate through its role in redistributing heat and salt through the world ocean and its control on atmospheric CO_2 . Over the past 10 years (a) or so efforts have been made to quantify the flux of biological export production to the deep Southern Ocean to unravel if and to what extent such changes may have contributed to the glacial-interglacial changes in atmospheric CO_2 seen in Antarctic ice cores [e.g., Kumar *et al.*, 1995; François *et al.*, 1997; Anderson *et al.*, 1998, 2002; Moore *et al.*, 2000; Chase *et al.*, 2001;

Schneider-Mor *et al.*, 2005; Kohfeld *et al.*, 2005; Abelmann *et al.*, 2006]. However, results are inconsistent [e.g., Anderson *et al.*, 2002; Anderson and Winckler, 2005] and past changes in export production have yet to be unequivocally characterized in the Southern Ocean. It has been suggested that it is the seasonality of primary production that determines the export flux of organic carbon (C_{org}) to the deep ocean. Initially it was assumed that export production is higher in strongly seasonal systems [Berger and Wefer, 1990], but this was not consistent with sediment trap data [Lampitt and Antia, 1997] and it rather appears now that a higher fraction of the exported organic matter sinks in regions with low seasonality [François *et al.*, 2002]. In areas characterized by high seasonality of primary production, organic particles rapidly sink and produce a fluffy layer of phytodetrital aggregates on the seafloor [Beaulieu, 2002] which provide a major source of high-quality food for benthic organisms, including benthic foraminifera. Therefore studies of the benthic foraminiferal community structure can provide useful environmental

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information because changes in the abundance and distribution of deep sea benthic foraminifera are mainly controlled by the oxygenation levels in the bottom and interstitial waters [e.g., *Bernhard and Sen Gupta*, 1999], the quantity, quality [*Loubere and Fariduddin*, 1999a] and seasonality of the C_{org} arriving at the seafloor [*Loubere*, 1998; *Loubere and Fariduddin*, 1999a, 1999b; *Sun et al.*, 2006]. Once it is defined which benthic foraminiferal species are physically associated with the deposition of phytodetritus [e.g., *Goody*, 1988, 1993; *Goody and Lambshead*, 1989], abundance variations of these species in the fossil record can be used to reconstruct seasonality in the geological past [*Thomas et al.*, 1995; *Thomas and Goody*, 1996; *Nees*, 1997; *King et al.*, 1998; *Bornmalm et al.*, 1999; *Ohkushi et al.*, 2000; *Kawagata*, 2001; *Rasmussen et al.*, 1996, 2002; *Gupta and Thomas*, 2003; *Ujiié*, 2003; *Hayward et al.*, 2004a, 2004b; *Wollenburg et al.*, 2001, 2004].

[3] Variable flux of C_{org} to the seafloor also influences the stable carbon isotope composition of calcareous benthic foraminifera ($\delta^{13}\text{C}$), particularly of shallow infaunal species that live in organic-rich environments such as *Uvigerina peregrina* [*Dunbar and Wefer*, 1984; *Zahn et al.*, 1986; *McCorkle et al.*, 1990, 1997; *Fontanier et al.*, 2006] or *Bulimina aculeata* [*Mackensen and Licari*, 2004]. For this reason, $\delta^{13}\text{C}$ of these taxa does not directly reflect the ambient deep water chemistry and its use in deepwater paleoceanography is limited. Epifaunal species such as *Fontbotia wuellerstorfi* (also named *Planulina*, *Cibicides* or *Cibicidoides*) which live on elevated substrates [*Linke and Lutze*, 1993], are widely used as carriers of deep water circulation signals since they are in direct contact with ambient bottom waters and variations of $\delta^{13}\text{C}$ in their shells is believed to more closely follow changes in $\delta^{13}\text{C}$ of dissolved inorganic carbon ($\delta^{13}\text{C}_{\text{DIC}}$) of ambient bottom waters [*Woodruff et al.*, 1980; *Belanger et al.*, 1981; *Graham et al.*, 1981; *Curry et al.*, 1988; *McCorkle and Keigwin*, 1994]. Carbon isotopes of epifaunal species may still become offset from ambient bottom water $\delta^{13}\text{C}_{\text{DIC}}$ if the supply of the organic matter to the seafloor is high and/or highly seasonal and leads to the deposition of a phytodetritus layer on the seafloor [*Mackensen et al.*, 1993a, 2001; *Bickert and Wefer*, 1999; *Corliss et al.*, 2002]. In such cases the influence of productivity-induced low- $\delta^{13}\text{C}$ overprint on epibenthic $\delta^{13}\text{C}$ values needs to be taken into consideration when reconstructing deep ocean nutrient inventories and water mass circulation [*Bickert and Mackensen*, 2004; *Rutberg and Peacock*, 2006]. Such influence may be constrained by $\delta^{13}\text{C}$ analysis of an epifaunal foraminiferal species that is physically associated with the presence of phytodetritus as a food source such as, for instance, *Epistominella exigua* (Brady) that is known to grow and reproduce rapidly when phytodetritus is available [*Goody*, 1988, 1993, 1996; *Goody and Lambshead*, 1989; *Goody and Malzone*, 2003; *Cornelius and Goody*, 2004]. However, little is known about the stable isotope fractionation of *E. exigua* during calcite precipitation as only few studies have focused on the isotopic composition of this species in recent sediments [*Woodruff et al.*, 1980; *Corliss et al.*, 2006]

and its use in paleoceanography [*Mackensen et al.*, 1989, 1994; *Labeyrie et al.*, 1996].

[4] We present millennial resolution records of benthic foraminiferal assemblages and stable isotopes in *E. exigua* from a sediment core from the southwestern flank of the Agulhas Plateau. The core is located close to the present-day position of the STC, within the Agulhas Current Retroflexion region and it is presently bathed by North Atlantic Deep Water (NADW). Its location is particularly promising to monitor variations in the C_{org} flux to the seafloor in relation to the position of the main oceanographic fronts as well as changes in the deep water chemistry related to the variable advection of NADW during the last climatic cycle. Paleoenvironmental information drawn from down-core changes of benthic foraminiferal assemblages is compared with the $\delta^{13}\text{C}$ profiles from *E. exigua* and *F. wuellerstorfi* [*Molyneux et al.*, 2007] to examine the significance of $\delta^{13}\text{C}$ in *E. exigua* and their relation to variable C_{org} supply to the seafloor versus ambient bottom water $\delta^{13}\text{C}_{\text{DIC}}$.

2. Modern Hydrography

[5] The Agulhas Current (AC) is the largest surface western boundary current in the global ocean transporting about 70 Sv of warm water along the southeast coast of Africa [*Bryden and Beal*, 2001]. Off the southern tip of South of Africa it undergoes a retroflexion returning back into the South Indian Ocean and flows east as the Agulhas Return Current (ARC). The regional pattern of the ARC is locked to the submarine morphologic high of the Agulhas Plateau that steers the ARC into a quasi-stationary northward meander (Figure 1) seen in hydrographic, kinematic and dynamical data [*Harris*, 1970; *Lutjeharms and van Ballegooyen*, 1984; *Gordon et al.*, 1987; *Lutjeharms and Anson*, 2001; *Boebel et al.*, 2003; *Kostianoy et al.*, 2004]. In the retroflexion area, warm water eddies, so-called Agulhas rings spin off from the main current (Figure 1) and drift westward into the South Atlantic Ocean contributing to the interbasin exchange of heat and salt between the Indian and the South Atlantic Ocean [*Gordon*, 1996, 2003; *Lutjeharms*, 1996].

[6] The Agulhas Current system is also involved in the carbon cycle by stimulating elevated levels of biological production and chlorophyll a along the oceanic frontal system formed by the ARC and the STC [*Weeks and Shillington*, 1994, 1996]. The ARC largely follows the STC but occasionally separates from this front between 13° and 25°E to form a double front, making up the Agulhas Front (AF) and the STC Front [*Lutjeharms and Valentine*, 1984]. *Weeks et al.* [1998] and *Machu et al.* [1999] demonstrated strong seasonality in the dynamics of the ARC in the Agulhas Plateau (AP) region, such that in the austral winter the AF skirts the northern boundary of the Agulhas Plateau and separates from the STC front to the South. This is contrasted by austral summer when the AF and the STC front merge into a single broad and intense front on the southern edge of the AP which is associated with particularly high chlorophyll pigment concentrations compared to winter conditions [see *Machu et al.*, 1999,

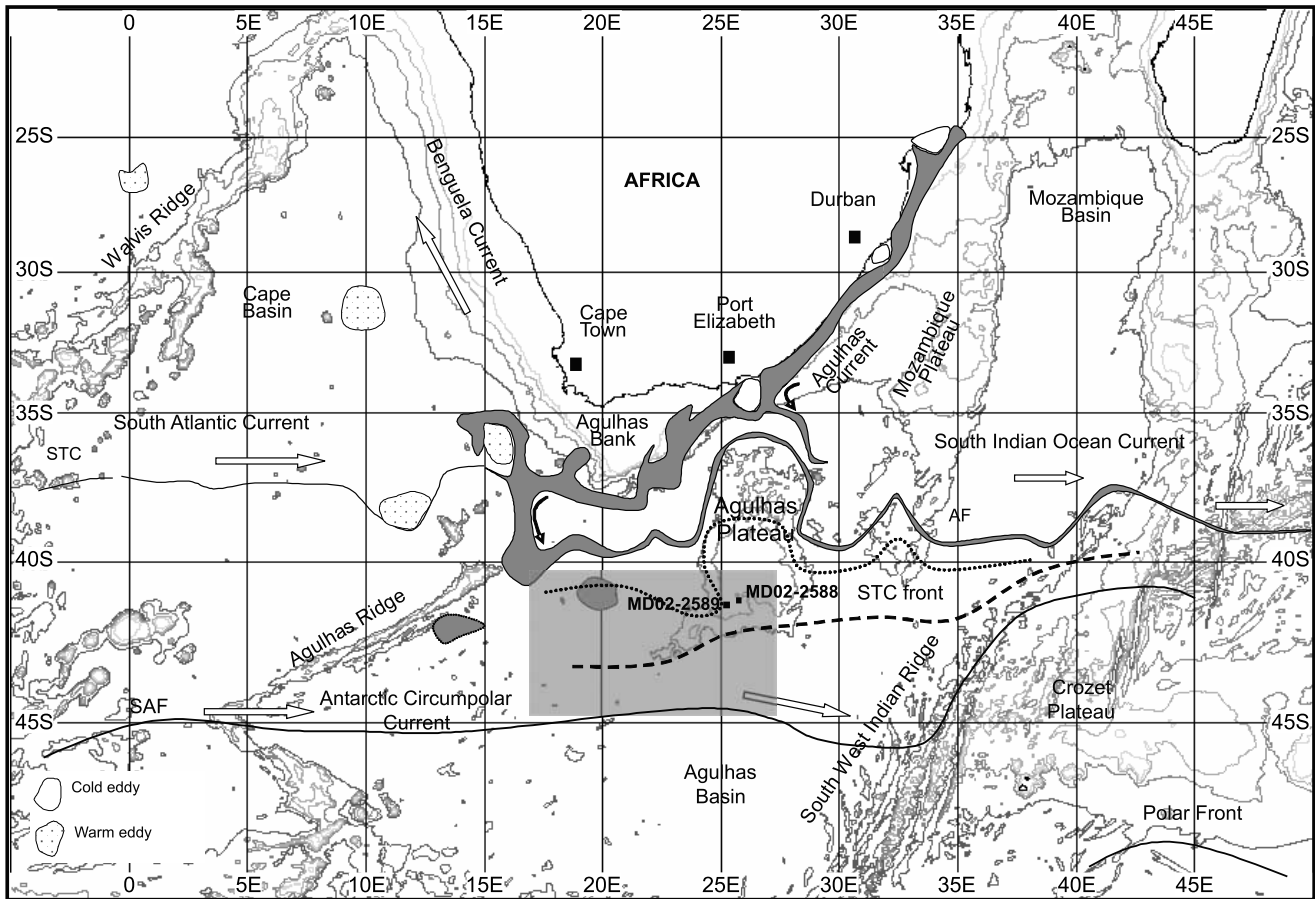


Figure 1. Map showing location of cores MD02-2589 ($41^{\circ}26.03'S$, $25^{\circ}15.30'E$, 2660 m water depth) and MD02-2588 ($41^{\circ}19.90'S$, $25^{\circ}49.7'E$, 2907 m water depth) and the main features of the bottom topography (isobaths after the General Bathymetric Chart of the Oceans) of the south Indian and South Atlantic oceans and main mesoscale and larger features of the circulation in the upper ocean layers of the Agulhas Current Retroflexion area [after Lutjeharms, 1996]. Major oceanographic fronts are indicated after Lutjeharms and Valentine [1984], Belkin and Gordon [1996], and Kostianoy *et al.* [2004]. The grey rectangle represents a large patch enriched in chlorophyll pigment during the present austral summer conditions [Machu *et al.*, 1999], and the dotted line indicates the variability of the Agulhas Return Current over the Agulhas Plateau [after Boebel *et al.*, 2003].

Figure 1]. Similarly, the occasional convergence of AF, STC front and SAF also causes enhanced pigment concentrations in the southern Agulhas Region [Llido *et al.*, 2004]. Satellite observations in this area indicate that primary productivity consists of intermittent bloom events occurring mainly in austral spring-summer [Llido *et al.*, 2005].

[7] The hydrography of the upper subsurface water column in the wider Agulhas Current region is defined by Antarctic Intermediate Water (AAIW) and Central Waters that constitute the main contributors to the water mass architecture of the upper 1500 meters water depth [Valentine *et al.*, 1993]. Deep waters are primarily derived from high-salinity, oxygen-rich and nutrient-depleted NADW that is bound above and below by nutrient-rich Upper and Lower Circumpolar Deep Water (CDW) [Gordon *et al.*, 1987]. The contribution of cold, low-salinity Antarctic Bottom Water

(AABW) in the Retroflexion region is very low [Valentine *et al.*, 1993].

3. Material and Methods

[8] Giant piston core MD02-2589 was retrieved in 2002 during R/V *Marion Dufresne* cruise MD128. The core is located at the southwestern flank of the Agulhas Plateau ($41^{\circ}26.03'S$, $25^{\circ}15.30'E$, Figure 1) in a sediment drift that closely follows the morphology of the plateau [Uenzelmann-Neben, 2001]. At 2660 m water depth core MD02-2589 is presently bathed by high-salinity, oxygen-rich and nutrient-poor NADW (see eWOCE hydrographic section I6 by Schlitzer [2000] and Figure 12 of Arhan *et al.* [2003]).

[9] For this study the upper 8.6 m of the core representing the last 150 ka (see below) were sampled at 4–8 cm intervals for the analysis of stable isotopes and benthic

foraminiferal assemblages. Samples were washed over a 63 μm sieve, dried at 40°C and weighed. A microsplitter was then used to obtain an aliquot containing a minimum of 270 benthic foraminifera specimens within the >63 μm fraction. All benthic specimens were picked under light microscope, mounted on faunal slides and identified using the generic classification of *Loeblich and Tappan* [1987]. The relative abundance and the benthic foraminiferal accumulation rates (BFARs) of the most characteristic benthic foraminiferal species along core MD02-2589 were calculated. BFAR was estimated from the number of benthic foraminifera/gram of dry sediment, the linear sedimentation rate (cm ka^{-1}) and the bulk density (g cm^{-3}). Diversities of the benthic foraminiferal assemblages were determined from the Information Function, *H*, calculated from the PAST software [Hammer *et al.*, 2001] (see at http://palaeo-electronica.org/2001_1/past/issue1_01.htm). The use of >63 μm size fraction in the benthic foraminifera analysis does not enable direct comparison with studies of Recent or late Quaternary records of benthic foraminifera from the southern Atlantic Ocean that are mostly based on the analysis of the >125 μm fraction [e.g., Mackensen *et al.*, 1990, 1993b, 1995; Schmiedl *et al.*, 1997; Schmiedl and Mackensen, 1997; Licari and Mackensen, 2005]. Studies that use >63 μm size fraction are mainly restricted to the Antarctic continental shelf [e.g., Ishman and Domack, 1994; Murray and Pudsey, 2004; Cornelius and Gooday, 2004]. However, including the finer component does enable significant additional information to be derived for example, the addition of small opportunistic taxa that are not common in the larger (>125 μm) fractions [Schroeder *et al.*, 1987] as has been recently demonstrated [e.g., Thomas *et al.*, 1995; Nees, 1997; Ohkushi *et al.*, 2000; Rasmussen *et al.*, 1996, 2002; Ujié, 2003; Hayward *et al.*, 2004a, 2004b; Wollenburg *et al.*, 2001, 2004].

[10] Total carbon and inorganic carbon contents of the sediment were determined with a FlashEA 1112 Elemental Analyser and expressed in percent per dry weight. Total carbon contents (TC) were measured on untreated samples and inorganic carbon (IC) concentrations on burnt samples (400°C for 3 h). Total organic carbon concentrations (TOC) were calculated from the formula: $\text{TOC (\%)} = \text{TC} - \text{IC}$ and carbonate concentrations were calculated from IC contents times (100/12). The TOC accumulation rate was estimated from TOC contents of the sediment, the linear sedimentation rate (cm ka^{-1}) and the bulk density (g cm^{-3}).

[11] Stable carbon and oxygen isotope measurements were performed on 20–30 specimens of *E. exigua* picked from the >125 μm fraction. Measurements were carried out at the stable isotope facilities at Cardiff University and the University of Barcelona both using Thermofinnigan MAT-252 mass spectrometers coupled online to an automated carbonate sample preparation device. Both spectrometers are intercalibrated through an internal laboratory standard (Solenhofen limestone). External reproducibility (1σ) of carbonate standards was better than $\pm 0.06\text{‰}$ and $\pm 0.03\text{‰}$ for $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ respectively. Results are calibrated against the international standard NBS-19 and reported on the Vienna Peedee belemnite (VPDB) scale. The $\delta^{13}\text{C}$ record of *E. exigua* was compared with the paired $\delta^{13}\text{C}$ record of *F. wuellerstorfi* in the same core. Oxygen and carbon isotope

measurements of *F. wuellerstorfi* in core MD02-2589 were performed on 8–10 specimens from the 150–250 μm size fraction using the same procedure described above for *E. exigua* [Molyneux *et al.*, 2007].

[12] The age model for core MD02-2589 is based on 14 monospecific planktonic foraminiferal AMS ^{14}C dates in the upper 192 cm core depth and on graphical correlation of the deeper section of the benthic $\delta^{18}\text{O}$ record of *F. wuellerstorfi* [Molyneux *et al.*, 2007] with the fine-scale benthic $\delta^{18}\text{O}$ record of core MD97-2120 [Pahnke and Zahn, 2005]. The AMS ^{14}C ages were reservoir corrected by 800 a [Bard, 1988] before being converted to calendar ages using the Fairbanks *et al.* [2005] calibration. The 800 a reservoir age is elevated over the mean mixed layer age of 400 a that is observed through most of the ocean and reflects the contribution of “old” i.e., ^{14}C deplete waters that mix into the upper layers from below at this high southern latitude site [e.g., Butzin *et al.*, 2005]. Two age reversals occur in the upper 60 cm of the core MD02-2589 that led us to discard the four uppermost AMS dates. Ages for this interval have been adjusted to a continuous age-depth function using a third-order polynomial fit [Molyneux *et al.*, 2007]. The fit derives an age estimate for the top of the core of 11.62 ka B.P. At our sampling resolution the age model implies a mean time step of ~ 660 a and ~ 1200 a between two successive samples of stable isotopes and benthic faunal assemblage data, respectively. Owing to the lack of Holocene recovery in core MD02-2589, and, in order to obtain the Recent isotopic signature of *E. exigua*, the uppermost section (2–23 cm) of the nearby core MD02-2588 was analyzed for stable oxygen and carbon isotopes in this species. CASQ core MD02-2588 (41°19.90'S, 25°49.7'E, Figure 1) was also retrieved in 2002 with R/V *Marion Dufresne* during cruise MD128 and at a water depth of 2907 m it is likewise presently bathed by NADW. The age model for the topmost part of this core is based on four monospecific planktonic foraminiferal AMS ^{14}C dates which were converted to calendar years following the procedure described above. The uppermost 23 cm of core MD02-2588 span the last 8.8 ka. Total counts, taxonomic references and illustrations of the most characteristic benthic foraminifera in core MD02-2589, stable oxygen and carbon isotope measurements in *E. exigua* in cores MD02-2589 and MD02-2589 and radiocarbon ages in core MD02-2588 are available as supporting auxiliary material.¹

4. Results

4.1. Benthic Foraminifera

[13] The recovered sediments consist of biogenic mud dominated by planktonic foraminifera. The carbonate content is high along the core with lower values (~ 80 wt %) during MIS 3, MIS 2, and substages MIS 5c and early MIS 5e (Figure 2a). Organic carbon concentrations are generally low ~ 0.2 wt %. Higher C_{org} contents (~ 0.3 – 0.4 wt %) are recorded for glacials MIS 6 and MIS 2 and low values during MIS 5e and Termination I. A similar pattern is shown by the C_{org} flux (Figure 2b).

¹Auxiliary material data sets are available at <ftp://ftp.agu.org/apend/pa/2007pa001511>. Other auxiliary material files are in the HTML.

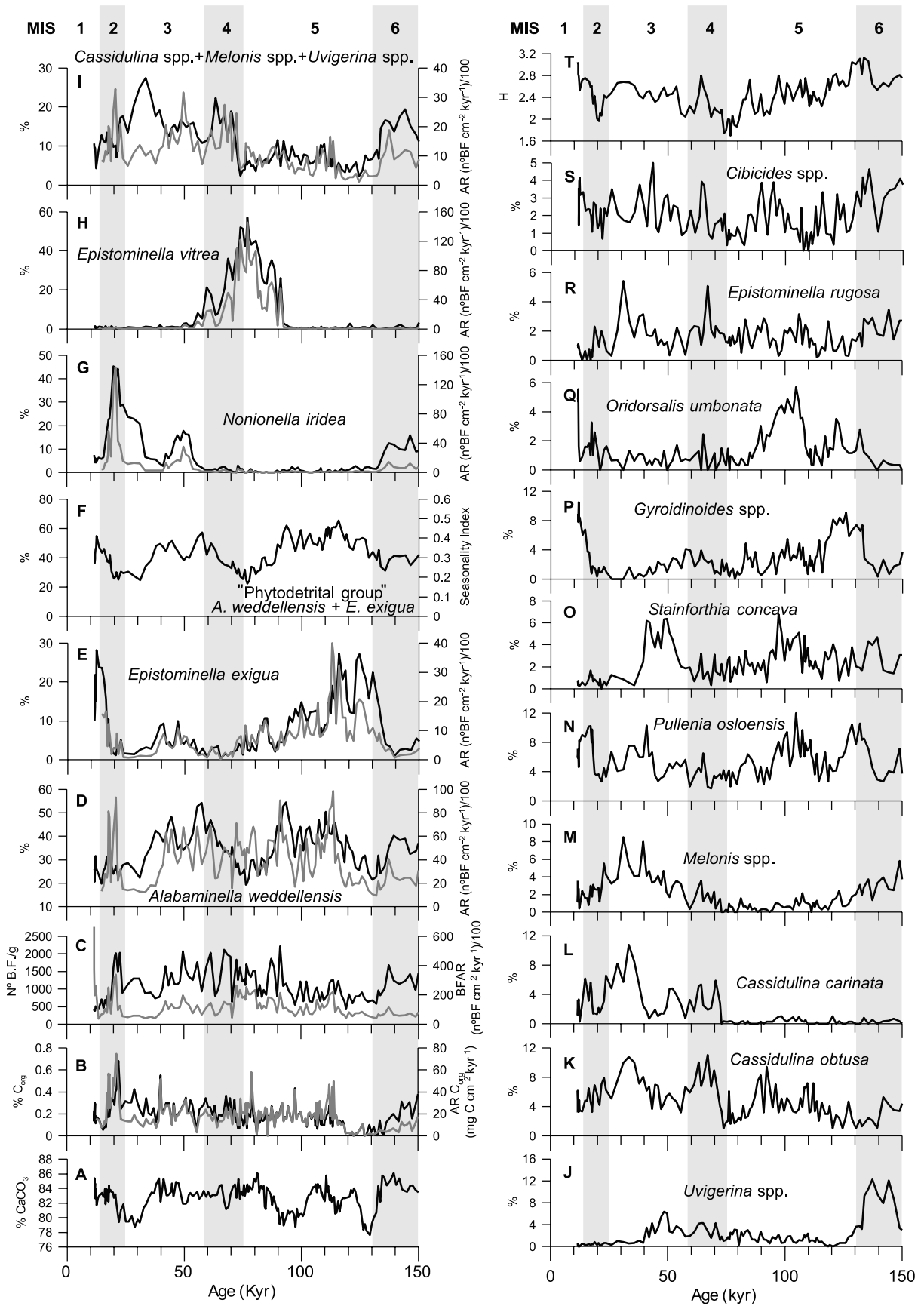


Figure 2

[14] There is no evidence of faunal composition being affected by carbonate dissolution [Molyneux *et al.*, 2007]. The concentration of benthic foraminifera (BF) expressed as n° BF ($>63 \mu\text{m}$) per gram of dry sediment fluctuates between 380 and 2200, with a mean abundance of 1085. There is no clear glacial interglacial trend in the total benthic foraminiferal abundance distribution (Figure 2c). The lowest concentration of benthic foraminifera occurred at Termination I and throughout MIS 5c–MIS 5e (Figure 2c). Conversely, high benthic foraminiferal accumulation rates (BFAR) are found at Termination I, MIS 2 and MIS 5a and low BFAR values occur at late MIS 3 and MIS 6 (Figure 2c). The extremely high BFAR at Termination I are likely an artifact resulting from sediment over sampling during piston coring processes [Skinner and McCave, 2003; Széréméta *et al.*, 2004] together with some inaccuracies in the age model in the upper 60 cm of the core.

[15] The foraminiferal fauna of core MD02-2589 comprises 159 species predominantly of small calcareous benthic foraminifera. The most abundant species throughout the core is *Alabaminella weddellensis* (Earland) with percentages ranging between 20 and 55% (Figure 2d). *Epistominella exigua* (Brady), *Nonionella iridea* (Heron-Allen and Earland) and *Epistominella vitrea* (Parker) occur at highly fluctuating abundances along the core. *Epistominella exigua* (0–27%, Figure 2e) displays the clearest glacial-interglacial modulation with lowest abundances recorded during full glacial periods (MIS 6, MIS 4 and early MIS 2). *Nonionella iridea* (0–45%, Figure 2g) reaches abundance maxima during full glacial MIS 6, early MIS 3, early MIS 2 and across the MIS 3/2 transition, while *E. vitrea* (0–57%, Figure 2h) displays a single broad maximum between MIS 5b and MIS 4 with maximum percentage centered close to MIS 5/MIS 4 boundary. Several less common species occur in all samples at relative abundance of $<15\%$ such as *Pullenia osloensis* Feyling-Hanssen, *Cassidulina obtusa* Williamson, *Uvigerina* spp., *Cassidulina carinata* (Silvestri), *Melonis* spp., *Gyroidinoides* spp. and *Stainforthia concava* Höglund (Figures 2j–2p). These species present various degrees of variability. Whereas *C. carinata*, *C. obtusa* and *Melonis* spp. covary, and generally show higher relative abundance in glacial MIS 4 and late MIS 3 (Figures 2i and 2k–2m), *Uvigerina* spp. exhibits peak abundances at MIS 6 coinciding with high C_{org} contents in the sediment (Figure 2j) and *P. osloensis* does not show any clear temporal pattern (Figure 2n). *Oridorsalis umbonata* (Reuss), *Epistominella rugosa* (Phleger and Parker) and *Cibicides* spp. group occur at relative abundance of $<5\%$ (Figures 2q–2s). The diversity of the benthic foraminiferal

fauna ranges between $H(S) = 1.3$ and 3.3 (Figure 2t). There is a clear decreasing trend in the diversity values from MIS 6 to MIS 5/MIS 4 boundary. Subsequently, the diversity index increases to Termination I though there is a relative decrease in this parameter during MIS 2 coinciding with the dominance of *N. iridea*. An estimation of the BFARs for the most common species along the core (Figure 2, shaded lines) indicates that the outline of BFAR is almost identical to the relative abundance patterns, particularly for those species that fluctuate most along the core (*E. exigua*, *E. vitrea* and *N. iridea*).

4.2. Oxygen and Carbon Isotopes in *E. exigua*

[16] The $\delta^{18}\text{O}$ record of *E. exigua* in core MD02-2589 characterizes the main climate periods from late MIS 6 to Termination I, though MIS 4 is not clearly defined (Figure 3a, crosses). The inclusion of *E. exigua* $\delta^{18}\text{O}$ data from core MD02-2588 confirms the absence of Holocene sediments in core MD02-2589 (Figure 3a, squares). The global ice volume decrease and warming toward interglacial conditions of Stage MIS 5e exhibits a transient slowdown/reversal between 133 and 129 ka (Figure 3a). This “pause” has been recently interpreted as caused by a reversal in the rising sea level trend at Termination II [Siddall *et al.*, 2006].

[17] The modern (2–5 ka) value of $\delta^{13}\text{C}$ in *E. exigua* calculated from core MD02-2588 ($\sim -0.54\text{‰}$ VPDB, Figure 3b, squares, see also auxiliary material) is offset by some -1.1‰ from the $\delta^{13}\text{C}_{\text{DIC}}$ of modern ambient bottom waters at the core location (Table 1). Given the uncertainties in the values of $\delta^{13}\text{C}_{\text{DIC}}$ of bottom waters, this $\delta^{13}\text{C}$ offset ($\Delta\delta^{13}\text{C}_{E.exigua-DIC}$) compares well with offsets of between -0.77‰ and -0.93‰ calculated from three other locations in the Southern Ocean (Table 1) and with -1.28‰ from the eastern equatorial Pacific [Woodruff *et al.*, 1980]. The $\delta^{13}\text{C}$ record of *E. exigua* along core MD02-2589 displays negative values varying between -0.4‰ and -1.1‰ VPDB with lower values during glacial stages and higher values during interglacial periods (Figure 3b).

[18] The paired $\delta^{13}\text{C}$ records of coexisting *E. exigua* and *F. wuellerstorfi* along our core show several distinctive features (Figure 3b). *F. wuellerstorfi* exhibits more pronounced fine-scale $\delta^{13}\text{C}$ variability than *E. exigua* even though both records are sampled at the same temporal resolution. Glacial-interglacial $\delta^{13}\text{C}$ amplitudes recorded by *E. exigua* in cores MD02-2588 and MD02-2589 during glacial Termination I (0.41‰) and Termination II (0.37‰) are considerably lower than those recorded by *F. wuellerstorfi* (TII = 0.8‰ [Molyneux *et al.*, 2007]). The $\delta^{13}\text{C}$ offset between *E. exigua* and *F. wuellerstorfi* varies between -0.7

Figure 2. (a and b) Carbonate calcium and organic carbon contents of the sediments (percent, solid line) and estimated accumulation rate of C_{org} ($\text{mgC cm}^{-2} \text{ka}^{-1}$, shaded line) along core MD02-2589. (c) Time series plots of the absolute abundance of benthic foraminifera (number benthic foraminiferal (BF) ($>63 \mu\text{m}$) per gram of dry sediment, solid line) and estimated benthic foraminiferal accumulation rate (BFAR) (number BF $\text{cm}^{-2} \text{a}^{-1} 100^{-1}$, shaded line). (d–s) Relative abundance (solid lines) and accumulation rates of the most common benthic foraminiferal species and group of species (shaded lines) in core MD02-2589. (t) Diversity of the benthic foraminiferal faunas. The accumulation rates of benthic foraminiferal species and organic carbon were not plotted for the first 60 cm of the core (see text). The seasonality index (SI) in Figure 2f was estimated from the sum of the percentage of *A. weddellensis* and *E. exigua* referred as “phytodetrital group” (see text) and following Sun *et al.* [2006, see Figure 9b].

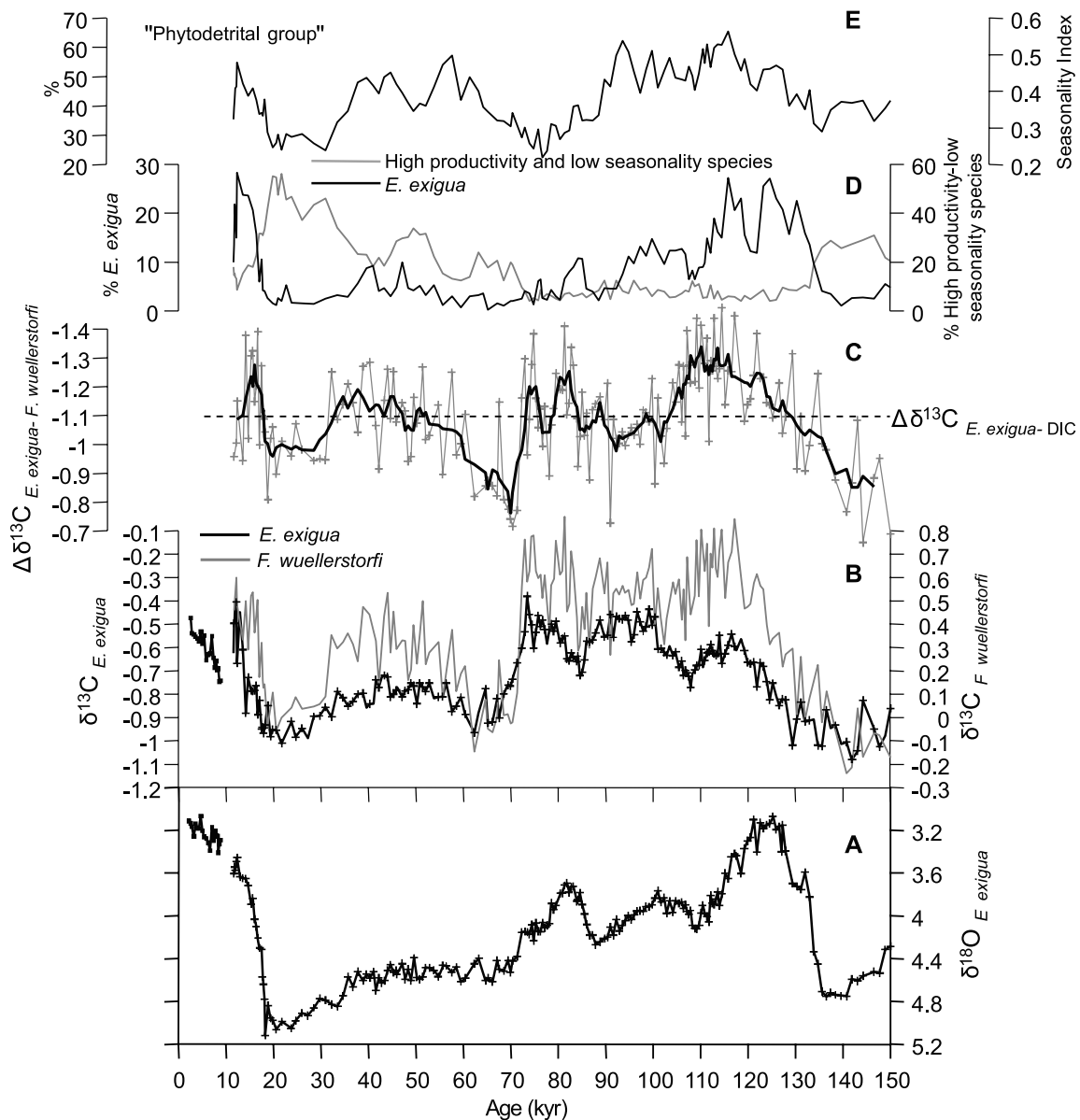


Figure 3. Time records of (a) $\delta^{18}\text{O}$ and (b) $\delta^{13}\text{C}$ in the benthic foraminifera *Epistominella exigua* in sediments cores MD02-2589 (crosses) and MD02-2588 (black squares). Paired $\delta^{13}\text{C}$ record of coexisting *E. exigua* (solid line) and *Fontbotia wuellerstorfi* (shaded line [Molyneux et al., 2007]) in core MD02-2589 are shown in Figure 3b. (c) The $\delta^{13}\text{C}$ difference between *E. exigua* and *F. wuellerstorfi* ($\Delta\delta^{13}\text{C}_{E. exigua-F. wuellerstorfi}$) in reversed scale (crosses) and five-point running average (solid line). The dashed horizontal line indicates the average value of the $\delta^{13}\text{C}$ difference between *E. exigua* and *F. wuellerstorfi* in core MD02-2589, which is also the difference between the $\delta^{13}\text{C}$ of Recent *E. exigua* in core MD02-2588 and the $\delta^{13}\text{C}_{\text{DIC}}$ of modern bottom water at the core location. (d and e) Percentage of *E. exigua*, high-productivity and low-seasonality proxy species (percent *Cassidulina* spp., *Uvigerina* spp., *Melonis* spp., and *N. iridea*) and “phytodetrital group.” The seasonality index was estimated from the percentage of “phytodetrital group” following Sun et al. [2006, see Figure 9b].

and -1.5‰ with lower differences during MIS 6, MIS 4 and MIS 2 and greatest dissimilarities during Termination I and MIS 5d. The average $\delta^{13}\text{C}$ difference between *E. exigua* and *F. wuellerstorfi* in core MD02-2589 of -1.1‰ (stdv < 0.2 , $n = 180$) is very close to the $\Delta\delta^{13}\text{C}_{E. exigua-\text{DIC}}$ observed at

the site of core MD02-2588 (Table 1) and compares well with published offsets of between -1.18‰ and -1.26‰ for Pleistocene and interglacial sediments from the Southern Ocean [Mackensen et al., 1994] and also with -0.85‰ determined from paired samples of living specimens from

Table 1. Comparison Between $\delta^{13}\text{C}_{\text{DIC}}$ of Bottom Waters and Modern $\delta^{13}\text{C}$ of *E. exigua* in Different Locations of the Southern Hemisphere^{a,b}

Core/Station	Age	Latitude	Longitude	Water Depth, m	$\delta^{13}\text{C}$ Holocene, ‰	$\delta^{13}\text{C}_{\text{DIC}}$, ‰	$\Delta\delta^{13}\text{C}_{E.exigua-\text{DIC}}$, ‰	Reference
PS1388-3	core top (Recent)	69°02'S	5°55'W	2526	-0.25 (n = 1)	0.52, ^{c,d} 0.58, ^c 0.56, ^d 0.53 ^d	-0.77, -0.83, -0.81, -0.78	<i>Mackensen et al.</i> [1989]
PS1506-1	core top (Recent)	68°45'S	5°53'W	2426	-0.33 (n = 2)	0.52, ^{c,d} 0.58, ^c 0.56, ^d 0.53 ^d	-0.85, -0.91, -0.89, -0.86	<i>Mackensen et al.</i> [1989]
MD88-770	late Holocene (4.6 ka)	46°01'S	96°28'E	3290	-0.53 (n = 1)	0.4 ^{e,f}	-0.93	<i>Labeyrie et al.</i> [1996]
MD88-770	early Holocene (7.4 ka)	46°01'S	96°28'E	3290	-0.52 (n = 1)	0.4 ^{e,f}	-0.92	<i>Labeyrie et al.</i> [1996]
MD02-2588	late Holocene (2.3–5 ka)	41°19.9'S	25°49'E	2907	-0.54 (n = 9)	0.58, ^{g,h} 0.68, ^h 0.52 ⁱ	-1.12, -1.22, -1.06	this work

^aHere n indicates the number of measurements used to calculate the modern value of $\delta^{13}\text{C}$ in *E. exigua*.

^bBottom water $\delta^{13}\text{C}_{\text{DIC}}$ values were selected according to the closest available data to core top locations, and for most sites more than one $\delta^{13}\text{C}_{\text{DIC}}$ value was used for the calculation $\Delta\delta^{13}\text{C}_{E.exigua-\text{DIC}}$.

^cStation PS16/201 (68.15°S, 7.19°W [*Mackensen et al.*, 1993a]).

^dPS16/197 (69.48°S, 8.22°W [*Mackensen et al.*, 1993a]).

^eGEOSECS 435 (39.952°S, 109.97° E [*Kroopnick*, 1985]).

^fGEOSECS 434 (45.637°S, 107.255° E [*Kroopnick*, 1985]).

^gStation 52 (44.01°S, 29.96°E [*Archambeau et al.*, 1998]).

^hStation PS1750-7 (42.69°S, 12.18°E [*Mackensen et al.*, 1993a]).

ⁱStation PS1751-1 (44.497°S, 10.48°E [*Mackensen et al.*, 1993a]).

surface sediments collected between 40° and 70°S [*Mackensen et al.*, 1994].

5. Discussion

5.1. Benthic Foraminifera and Paleoenvironmental Interpretation

[19] The factors exerting primary control on benthic foraminiferal distribution patterns are the availability of food and oxygen [*Jorissen et al.*, 1995, *Jorissen*, 1999] with redox gradients and the degree of competition for labile organic matter also playing a role [*van der Zwaan et al.*, 1999]. Deep-sea environments are often food limited, consequently C_{org} supply has a pervasive effect on the abundance, biomass and distribution patterns of benthic foraminiferal communities [e.g., *Altenbach et al.*, 1999; *Loubere and Fariduddin*, 1999a, *van der Zwaan et al.*, 1999; *De Rijk et al.*, 2000]. Pulsed fluxes of phytodetritus, usually reflecting seasonal primary production in the overlying surface waters, are a major vehicle for the delivery of C_{org} to the deep seafloor. Deep sea benthic foraminifera have the ability to grow rapidly and exploit this ephemeral food resource [*Goody*, 1988, 1993, 2003]. As such, the seasonality of the C_{org} arriving at the seafloor also has a major effect on abundance and assemblages composition as has been demonstrated in the North Atlantic [*Loubere and Fariduddin*, 1999a, 1999b; *Sun et al.*, 2006], Indian and Pacific [*Loubere*, 1998; *Loubere and Fariduddin*, 1999a, 1999b] oceans.

[20] Nonetheless, there is not a clear correlation between BFAR, which has been successfully used to estimate export

of organic matter to the seafloor [*Berger and Herguera*, 1992; *Herguera*, 1992, 2000], and accumulation rate (AR) of C_{org} in core MD02-2589 except for MIS 2 (Figures 2b and 2c). This suggests that one or both parameters are not reflecting the total signal of food delivery to the seafloor. On the one hand, BFAR seems to work adequately in well-oxygenated environments [e.g., *Schmiedl and Mackensen*, 1997] but it is compromised by severe dissolution of calcareous tests [*Wollenburg et al.*, 2001], in oxygen-depleted environments [*Naidu and Malmgren*, 1995] or in areas where the C_{org} is delivered to the seafloor in the form of phytodetritus aggregates [e.g., *Goody*, 2003]. In the latter case, sinking particles have a high food value and support a greater benthic biomass, mainly consisting of small (<150 μm) opportunistic foraminifera, than more refractory material sinking in steady rain areas. If small size opportunistic epifaunal species add dead shells to the sediments at a higher proportion than infaunal species, the incorporation of finer fractions (e.g., 63–150 μm fraction) into the calculation of BFAR could overestimate C_{org} fluxes [*Ohkushi et al.*, 2000] and so, the accumulation rates and concentrations of benthic foraminifera (n° B.F. >63 μm per gram of dry weight sediment) may not be related in a predictable manner to the C_{org} flux reaching the seafloor. Indeed, the benthic foraminiferal fauna in core MD02-2589 is dominated by small species: *A. weddellensis*, *N. iridea*, *E. exigua*, and *E. vitrea* which are typically present in the <125 μm size fraction [*Goody and Lambshead*, 1989; *Goody*, 1986, 2003; *Duchemin et al.*, 2007]. *Epistominella exigua* and *A. weddellensis* are also known to feed on, and reproduce in phase with seasonal pulses of fresh

phytodetritus [Goody, 1988, 1993, 1996; Goody and Lambhead, 1989; Turley et al., 1993; Smart and Goody, 1997; Cornelius and Goody, 2004]. This could explain why higher BFARs are strongly dominated by peaks in only one or two small sized species as occurs during MIS 2 (*A. weddellensis*, *N. iridea*) and between MIS 5b and MIS 4 (*E. vitrea*) while lower BFARs correspond to moderate abundance of both small and large size species, such as the combination of *N. iridea*, *A. weddellensis*, *Uvigerina* spp. at MIS 6 or *N. iridea*, *Melonis* spp., *C. carinata*, *C. obtusa* and *A. weddellensis* during MIS 3. On the other hand, the concentration of C_{org} in the sediments might not reflect the export of organic matter to the seafloor when the C_{org} supply is delivered in the form of short, seasonal pulses of phytodetritus. These deposited phytodetrital aggregates consist of very reactive organic matter which serves as a food source for foraminifera, bacteria and other organisms and they are easily resuspended by bottom currents and remineralized over an interval of several months [e.g., Beaulieu, 2002]. Therefore phytodetritus deposition does not necessarily result in enhanced C_{org} concentrations in the sediments [Thomas and Goody, 1996], so also explaining the lack of a general correlation between BFARs and C_{org} accumulation rates as it has likewise been observed in the northern Atlantic and Pacific [Thomas et al., 1995; Ohkushi et al., 2000].

[21] As discussed above, both *A. weddellensis* and *E. exigua* have been described as species exploiting phytodetritus [e.g., Goody, 1988, 1993]. Even though these species are linked to phytodetritus deposition at the seafloor they display different down-core abundance patterns (Figures 2d and 2e). A similar lack of covariance between the percentages of both species has been observed in cores from the North Atlantic [Thomas et al., 1995] and Pacific [King et al., 1998; Ohkushi et al., 2000; Ujié, 2003] and has been suggested to reflect subtle differences in ecological preferences and/or microhabitats of both species [Loubere, 1998; Goody, 2003]. A conservative interpretation of the abundance of *A. weddellensis* and *E. exigua* is that these two species reflect intermittently high but strongly and unpredictably fluctuating primary productivity [Thomas et al., 1995; Ujié, 2003] and that each has preferences for different types of phytodetrital material [Ohkushi et al., 2000]. Another approach could be based on recent findings from the North Atlantic that suggest that the sum of the relative abundance of *A. weddellensis* and *E. exigua*, collectively referred as the “phytodetrital group”, may be used to reconstruct seasonality of productivity in paleoceanographic studies [Sun et al., 2006]. The relative abundance of the “phytodetrital group” along core MD02-2589 (Figure 2f) results in seasonality indices varying between ~ 0.2 (more constant primary production) and ~ 0.5 (more episodic primary production) (see definition of the seasonality index given by Sun et al. [2006] and Corliss et al. [2006]). However, as *A. weddellensis* is the most abundant species throughout the core, always occurring with percentages $>20\%$, and *E. exigua* shows high abundances only at particular intervals (e.g., Termination I and MIS 5c–MIS 5d), changes in the seasonality of the primary productivity estimated from the “phytodetrital group” are mainly driven

by changes in the relative abundance of *A. weddellensis* when *E. exigua* is nearly absent from the benthic assemblage. This diminishes the applicability of the “phytodetrital group” to reconstruct seasonality in MD02-2589 as the relative abundance of either single species (*E. exigua* or *A. weddellensis*) is not a strong indicator of either primary productivity or seasonality [Sun et al., 2006]. Consequently, we suggest that the inconsistent abundance patterns of *A. weddellensis* and *E. exigua* along core MD02-2589 are indicative of differing influences which exclude the possibility of considering their sum as a simple proxy of seasonality of primary productivity or seasonal flux of organic material to the seafloor. Studies in the Atlantic [Fariduddin and Loubere, 1997; Sun et al., 2006], Pacific [Loubere, 1996; Hayward et al., 2002] and Indian [Loubere, 1998] oceans assign *A. weddellensis* to the group of high-productivity species while *E. exigua* appears to be more directly dependent on phytodetritus input [Goody and Malzone, 2003]. Our benthic census counts support this observation in that increased abundance of *A. weddellensis* along core MD02-2589 occurs either with high abundance of *E. exigua* or with other benthic species that are related to more sustained primary productivity, such as *N. iridea*, *Uvigerina* spp. (*U. peregrina* and *U. proboscidea*), *Melonis* spp. (mainly *Melonis barleeanum*), *Cassidulina* spp. (*C. carinata* and *C. obtusa*) or opportunistic species adapted to low C_{org} supply combined with very short periods of pulsed food (*E. vitrea*) (Figure 2). From this we infer that *A. weddellensis* tolerates a wider range of C_{org} flux levels and sustainability regimes than *E. exigua* which is disadvantaged in regimes that sustain very high or low productivity for prolonged periods [Mackensen et al., 1995]. This suggests that maxima abundance of *E. exigua* indicates periods of relatively low but pulsed supply of labile organic matter to the seafloor (Termination I and MIS 5c–MIS 5e, Figure 2e), probably in the form of phytodetrital aggregates, similar to modern conditions at the core location with recurrent flux events in the course of 2 to 3 months per year (see section 2).

[22] *Cassidulina* spp., *Uvigerina* spp., *Melonis* spp. are large shallow infaunal species that have generally been linked to fairly high, continuous food supply with moderate oxygen depletions [Lutze and Coulbourn, 1984; Fariduddin and Loubere, 1997; Mackensen et al., 1993b, 1995; Schmiedl et al., 1997; Schönfeld and Altenbach, 2005; Licari and Mackensen, 2005; Hayward et al., 2002, 2006]. *Cassidulina* and *Uvigerina* species have been also reported as benefiting from phytoplankton blooms (e.g., *C. carinata*, *U. peregrina* [Duchemin et al., 2007]) or react quickly to phytodetritus (e.g., *C. crassa* [Suhr and Pond, 2006] and *U. akitaensis* [Nomaki et al., 2005]). *Melonis barleeanum* seems to prefer slightly altered organic matter [Caralp, 1989; Licari and Mackensen, 2005] or bacterial stocks [Fontanier et al., 2005]. All these species together show relatively high abundance ($\sim 20\%$, Figure 2i) during MIS 6, MIS 4, and late MIS 3 suggesting that these periods were characterized by low seasonality and year-round higher supply of organic material in comparison with periods dominated by pulsed deposition rates of food as indicated by high abundance of *E. exigua*. High abundances

of those species are coincident with elevated C_{org} concentrations during MIS 6 and with peaks of *N. iridea* during MIS 6 and early MIS 3 but not during early MIS 2 or across MIS3/MIS 2 transition. *N. iridea* occupies an infaunal microhabitat and commonly appears in the 63–125 μm fraction [Gooday, 1986] and it is easily dissolved after reproduction or death and therefore has an only low preservation potential [Mackensen et al., 1990; Alve and Murray, 1997]. Its presence in the benthic assemblage therefore is a good indication of conditions favorable for enhanced carbonate preservation. *Nonionella iridea* has been related to high-sediment C_{org} content [Mackensen et al., 1990], phytodetrital inputs (but it does not occur within the phytodetrital aggregates and probably benefits from bacterial densities beneath phytodetritus, [Gooday and Lambshead, 1989; Gooday and Hughes, 2002]), and episodic pulses of labile C_{org} flux to the seafloor [Duchemin et al., 2005, 2007]. The highest concentration of *N. iridea* is coincident with high C_{org} concentrations during early MIS 2. We interpret high abundance of *N. iridea* as indicating moderate seasonality and C_{org} supply to the seafloor during MIS 6, early MIS 3, early MIS 2 and across MIS 3/MIS 2 transition.

[23] Enhanced and more sustainable primary production at the southern edge of the Agulhas Plateau is most likely linked with shifts of the mobile SAF. In the Atlantic sector of the Southern Ocean, Brathauer and Abelmann [1999] and Gersonde et al. [2005] infer a northward migration of the SAF by between 2° and more than 5° in latitude, but a relative small displacement of the Subtropical Front [Gersonde et al., 2005] during MIS 2. Also, Howard and Prell [1992] in the Indian Ocean estimated a northernmost position of the Antarctic Polar Front at about 45°S during MIS 2, MIS 4 and MIS 6. Enhanced levels of chlorophyll concentrations are observed today where the AF, STF and SAF are in close proximity, such as around the southwest Indian Ridge, close to the northern edge of the Crozet Plateau [Machu et al., 1999; Read et al., 2000] and at the Crozet Basin [Fiala et al., 2003]. Confluence of the AF, STC and SAF and associated high chlorophyll *a* levels have been observed on occasion in the southern Agulhas region (20° – 25°E) [Llido et al., 2004].

[24] A further significant change in the benthic fauna occurs from late MIS 5b to early MIS 4 when *E. vitrea* increases in abundance and dominates the benthic assemblage (up to 57%; Figure 2h). The ecology of this species is not well known. Mackensen et al. [1995] related *E. vitrea* to coarse grain sizes and low carbonate contents of the sediment from the South Atlantic and Hayward et al. [2006] to the presence of terrigenous mud in shelf areas from New Zealand. It has been suggested that *E. vitrea* is tolerant to high accumulation rate settings [Blackwelder et al., 1996] and exhibits some tolerance to anoxia [Blackwelder et al., 1996; Gustafsson and Nordberg, 2000; Osterman, 2003; Platon et al., 2005]. Deposition of phytodetritus does not trigger increased reproduction of this species [Gustafsson and Nordberg, 2001; Gooday and Hughes, 2002] but rather an upward migration to shallower depths in the sediment [Ernst et al., 2005]. On the contrary, Rasmussen et al. [1996, 2002] suggest that *E. vitrea* in cores from the North Atlantic region is indicative of sporadic, i.e., seasonal food

supply under well-oxygenated ambient bottom water conditions, a habitat that could be intermediate between that of *E. exigua* and *Epistominella arctica*. *E. arctica* is a small thin-shelled species living in the Arctic and adapted to a lower and more irregular seasonal supply of C_{org} [Wollenburg and Kuhnt, 2000] and it seems that it is adapted to low surface productivity combined with extremely short periods of pulsed food input into the sediment [Thomas et al., 1995]. In core MD02-2589 the increase in *E. vitrea* abundance is neither accompanied by abundance increases of infaunal taxa related to high supply of organic matter and/or low-oxygenation conditions such as, *Cassidulina* spp., *Melonis* spp., *Uvigerina* spp., *N. iridea* nor to an increase in abundance of phytodetritus-related species such as *E. exigua*. We use this pattern as an indication that the dominance of this species during late MIS 5b to early MIS 4 relates to a combination of relatively persistent low C_{org} supply likely combined with extremely short pulses of phytodetritus to the seafloor (so extreme that phytodetritus-related species cannot bloom), both allowing *E. vitrea* to be the most successful colonizer of the sediment during this period. Such conditions could be linked with a weakening in the intensity of the STC front and/or enhanced influence of the AF over the southern Agulhas Plateau. Today greater photosynthetic pigment levels in the surface waters are a function of the intensity of the STC front rather than of the AF, which limits the spatial distribution of phytoplankton pigment concentrations [Weeks and Shillington, 1996].

[25] In summary, the dominance of extremely small, thin-shelled, largely epifaunal opportunistic species (e.g., *A. weddellensis*, *E. exigua*) suggest an overall low- to moderate-productivity regime affected by seasonal deposition of organic matter to the seafloor. Intervals characterized by a relatively more sustainable delivery of low (*E. vitrea*, MIS 5b–MIS 4) and high (*N. iridea*, *Uvigerina* spp., *Melonis* spp., *Cassidulina* spp., MIS 6, MIS 4, early MIS2, early MIS 3 and across MIS 3/MIS 2 transition) C_{org} supply are also identified. The near absence of infaunal taxa related to suboxic, dysoxic or anoxic conditions such as *Stainforthia*, *Bulimina*, *Globobulimina*, *Chilostomella* or *Brizalina* [Sen Gupta and Machain-Castillo, 1993; Kaiho, 1994] indicates that deficient oxygen conditions in bottom and interstitial waters were not present in the core. While a similar absence of epifaunal species with an attached mode of life, such as *F. wuellerstorfi* [Linke and Lutze, 1993] or *Cibicides*, *Cibicides* (Figure 2s) species also suggests the presence of generally low bottom current activity in the area.

5.2. Stable Carbon Isotopes

[26] Variable flux of C_{org} to the seafloor may influence the $\delta^{13}\text{C}$ composition of the epifaunal *F. wuellerstorfi* and *E. exigua*. Both species are known to live on the sediment/water interface, *F. wuellerstorfi*, mainly attached to hard substrates protruding from the sediment [Linke and Lutze, 1993] while, *E. exigua*, prefers phytodetritus layers deposited on the seafloor as its primary habitat [Gooday, 1988, 1993; Cornelius and Gooday, 2004]. Carbon isotope ratios of *F. wuellerstorfi* is known to be close to bottom water $\delta^{13}\text{C}_{\text{DIC}}$ [Woodruff et al., 1980; Belanger et al., 1981; Graham et al., 1981; Zahn et al., 1986; Curry et al., 1988; McCorkle and

Keigwin, 1994], although data from the South Atlantic have demonstrated measurable deviations of $\delta^{13}\text{C}$ of *F. wuellerstorfi* from the bottom water $\delta^{13}\text{C}_{\text{DIC}}$ when collected from high-productivity regions that are prone to develop a phytodetritus layer on the seafloor [Mackensen et al., 1993a]. However, the relationship between the accumulation of organic material and the deviation from $\delta^{13}\text{C}_{\text{DIC}}$ is not straightforward. While some areas under high-productivity regimes show deviations [Bickert and Mackensen, 2004] in others the $\delta^{13}\text{C}$ of *F. wuellerstorfi* is not affected by primary production (e.g., under equatorial and coastal upwelling [Zahn et al., 1986; Eberwein and Mackensen, 2006]) or seasonality [e.g., Corliss et al., 2006]. Since data regarding the processes playing a role in the isotopic fractionation of *E. exigua* are limited, the carbon isotope record of *E. exigua* is initially discussed on the basis of two contrasting hypotheses. First, *E. exigua* digests algal cells derived from fresh phytodetritus [Turley et al., 1993] so that the $\delta^{13}\text{C}$ signal of this species may reflect varying carbon isotope composition of the phytodetritus it dwells on [DeNiro and Epstein, 1978]. As such this epifaunal species may also experience increasing ^{13}C depletion within its microenvironment as the microbial decomposition of the phytodetritus layer progresses, similar to the sensitivity of infaunal microenvironments to such process, as suggested by Turley and Lochte [1990] and Gooday [1994]. If so, $\delta^{13}\text{C}$ of *E. exigua* would be influenced strongly, but to a varying extent, by the local phytodetritus carbon isotope signals and would not reflect the variations in the ambient deepwater chemistry in a predictable manner. Second, the oxidation of the ^{12}C -rich organic matter at the seafloor causes a depletion of $\delta^{13}\text{C}$ in the pore waters in the phytodetritus layer, which results in lower $\delta^{13}\text{C}$ of *E. exigua*, an effect that is greatest with highest seasonality [Corliss et al., 2006]. If so, $\delta^{13}\text{C}$ of *E. exigua* in combination with $\delta^{13}\text{C}$ of *F. wuellerstorfi* that presumably records ambient bottom water $\delta^{13}\text{C}_{\text{DIC}}$ more directly may be used to reconstruct seasonality of the primary productivity in the geological record as suggested by Corliss et al. [2006] for the North Atlantic region.

[27] The strong depletion of the $\delta^{13}\text{C}$ of modern epifaunal *E. exigua* in excess of 1.1‰ relative to ambient bottom water $\delta^{13}\text{C}_{\text{DIC}}$, clearly demonstrates that this species does not directly record bottom water $\delta^{13}\text{C}_{\text{DIC}}$ but rather contains a distinctive $\delta^{13}\text{C}$ overprint from ^{13}C -depleted waters in the phytodetritus layer. The phytodetritus layer serves as a specific microhabitat with different geochemical characteristics than found in the overlying bottom waters [Corliss et al., 2006]. The “microhabitat effect” caused by the phytodetritus layer appears to be different from the microhabitats within the sediments, given that $\delta^{13}\text{C}$ of *E. exigua* remains more positive than the $\delta^{13}\text{C}$ signals of infaunal species that are directly influenced by sediment pore water gradients [see, e.g., Mackensen et al., 1994, Figure 15]. A plausible explanation of this pattern is that *E. exigua* rapidly colonizes freshly deposited phytodetritus layers that either have an only short residence time on the seafloor (since the extremely labile organic matter is quickly consumed by bacteria and foraminifera) or are irrigated rapidly by bottom waters so that strong $\delta^{13}\text{C}$ gradients do not develop.

[28] The relative homogeneity of $\Delta\delta^{13}\text{C}_{E.exigua-\text{DIC}}$ seen in different Southern Hemisphere locations (Table 1) contrast with the spatial variability observed at North Atlantic sites [Corliss et al., 2006]. These authors suggested that the change in $\Delta\delta^{13}\text{C}_{E.exigua-\text{DIC}}$ is mainly related to the effect of seasonality of the primary production on *E. exigua* $\delta^{13}\text{C}$ values, with more negative $\Delta\delta^{13}\text{C}_{E.exigua-\text{DIC}}$ values correlating with highest seasonality of primary production [see Corliss et al., 2006, Figure 3b]. We cannot quantitatively assess the influence of seasonality of the primary production on all the Southern Hemisphere locations displayed in Table 1, but it seems unlikely that core sites from the Weddell Sea continental shelf would experience episodic production events similar in structure to those occurring in northern areas from the Atlantic and Pacific oceans. From this we infer that the biologically induced offset observed between $\delta^{13}\text{C}$ of modern *E. exigua* and the ambient bottom water $\delta^{13}\text{C}_{\text{DIC}}$ from different locations of the South Atlantic and Pacific appears to be independent of the seasonality of the primary production in the surface waters and variations in the C_{org} flux to the seafloor.

[29] The $\delta^{13}\text{C}$ record of *F. wuellerstorfi* exhibits more pronounced variability than *E. exigua*, which is thus reflected in the fine-scale variability of $\delta^{13}\text{C}$ difference between *E. exigua* and *F. wuellerstorfi*. The number of specimens used for $\delta^{13}\text{C}$ measurements was lower for *F. wuellerstorfi* (8–10 individuals) compared to *E. exigua* (20–30 individuals) which may contribute to the smoother $\delta^{13}\text{C}$ record for *E. exigua*. However, it is also plausible that the apparent lack of variability in the *E. exigua* record reflects its dependence on the input of labile C_{org} [e.g., Gooday, 1993; Fontanier et al., 2003; Ernst and van der Zwaan, 2004] combined with a rather short time span in which this species calcifies and acquires its isotopic signal i.e., during the specific period of the year when conditions are most suitable for its growth and reproduction.

[30] Reduced $\delta^{13}\text{C}$ offsets between *E. exigua* and *F. wuellerstorfi* are recorded during glacial periods MIS 6, MIS 4 and MIS 2 when the organic supply was relatively higher and more sustained as indicated by the benthic foraminiferal assemblage composition and the C_{org} concentrations in the sediment (Figure 2b and Figures 3b–3d). The reduced $\delta^{13}\text{C}$ offset is caused by the larger $\delta^{13}\text{C}$ depletion in *F. wuellerstorfi* that is also reflected in the larger $\delta^{13}\text{C}$ amplitudes during the transitions into MIS 5, MIS 3 and the early Holocene. This pattern suggests that the magnitude of $\delta^{13}\text{C}$ amplitudes of *F. wuellerstorfi* along the record has been more directly affected by variations in primary productivity and concomitant carbon flux than in *E. exigua*. If this is the case then we can estimate from Figure 3c that the deviation of $\delta^{13}\text{C}$ of *F. wuellerstorfi* from $\delta^{13}\text{C}_{\text{DIC}}$ could be up to -0.3‰ (e.g., during MIS 4), a value that is close to the mean offset of -0.4‰ estimated by Bickert and Mackensen [2004] for the South Atlantic region. The corollary is that the $\delta^{13}\text{C}$ gradient between *E. exigua* and *F. wuellerstorfi* cannot easily be related to seasonality of the productivity because the bottom water $\delta^{13}\text{C}_{\text{DIC}}$ cannot be reliably estimated from the $\delta^{13}\text{C}$ of *F. wuellerstorfi* during glacial intervals. Likewise the $\delta^{13}\text{C}$ of *E. exigua* does not seem to be significantly affected by either increased sea-

sonality or primary productivity as we would expect more depleted $\delta^{13}\text{C}$ values of *E. exigua* and increased $\delta^{13}\text{C}$ differences between *E. exigua* and *F. wuellerstorfi* [see *Corliss et al.*, 2006, Figure 4] during the periods of higher pulsed supply of food to the seafloor (indicated by high abundances of *E. exigua*). Slightly depleted $\delta^{13}\text{C}$ values of *E. exigua* and therefore increased $\delta^{13}\text{C}$ offsets between *E. exigua* and *F. wuellerstorfi* coincide with abundance maxima of *E. exigua* during Termination I and MIS 5d but not during MIS 5e (Figures 3c and 3d). In addition, the offset differs in time from higher percentages of the “phytodetrital group” and the resultant higher seasonality indices (SI) of the primary production (Figures 3c and 3e) with similar $\delta^{13}\text{C}$ differences between *E. exigua* and *F. wuellerstorfi* for either high or low SI. Even though *E. exigua* prefers phytodetritus layers as its primary habitat, our data suggest that the $\delta^{13}\text{C}$ values of *E. exigua* in core MD02-2589 are not directly correlated with variations in seasonality of the primary production or affected by enhanced carbon fluxes to the seafloor. This suggests that the glacial-interglacial $\delta^{13}\text{C}$ amplitude of *E. exigua* is not dominated by variable ^{13}C -depleted microenvironments driven by surface productivity. If this is the case then *E. exigua* $\delta^{13}\text{C}$ would more reliably document the amplitude of changes in ambient bottom water $\delta^{13}\text{C}_{\text{DIC}}$ while its absolute $\delta^{13}\text{C}$ values remain offset from bottom water $\delta^{13}\text{C}_{\text{DIC}}$.

[31] Clearly, in the absence of an additional independent water mass tracer it is very difficult to definitively assess which benthic species are tracking the amplitude of the $\delta^{13}\text{C}$ changes in ambient bottom water. Indeed, we do not say that *F. wuellerstorfi* does not record ambient bottom water $\delta^{13}\text{C}_{\text{DIC}}$ during most of the record, but the $\delta^{13}\text{C}$ signature of *F. wuellerstorfi* has been directly affected by a productivity-induced low- $\delta^{13}\text{C}$ overprint caused by enhanced primary productivity and concomitant carbon flux during glacial periods MIS 6, MIS 4 and MIS 2, resulting in larger (up to 60%) glacial-interglacial $\delta^{13}\text{C}$ amplitudes than recorded in *E. exigua*. Even if $\delta^{13}\text{C}_{E. exigua}$ is slightly depleted in comparison with $\delta^{13}\text{C}_{F. wuellerstorfi}$ during termination I and MIS 5d, the magnitude of the offset between *E. exigua* and *F. wuellerstorfi* is much lower than expected given the large variations in the sustainability of the exported production in core MD02-2589. Besides, depleted offsets are not fully correlated with the percentage of *E. exigua* that according to our interpretation indicates periods of seasonal and pulsed C_{org} flux to the seafloor. This could reflect the different modulation on glacial-interglacial scales of benthic foraminiferal assemblages and thus the mode of delivery of C_{org} to the seafloor and the $\delta^{13}\text{C}$ in the epifaunal foraminifera *E. exigua*. Whereas most of the benthic foraminiferal assemblage changes coincide with glacial-interglacial transitions, the $\delta^{13}\text{C}$ of *E. exigua* is considerably lagged over $\delta^{18}\text{O}$ (Figures 3a and 3b) especially during the transition from MIS 6 to MIS 5. This suggests that the glacial-interglacial $\delta^{13}\text{C}$ amplitude changes recorded by *E. exigua* cannot be related to changes in the C_{org} flux to the seafloor, which occur much earlier, but most likely change with glacial-interglacial variations in the nutrient inventory of bottom water masses. Indeed, the glacial-interglacial $\delta^{13}\text{C}$ amplitudes recorded by *E. exigua*

in cores MD02-2589 and MD02-2588 during glacial Terminations I and II of 0.34‰ and 0.41‰ compare well with the estimated mean ocean $\delta^{13}\text{C}$ change of 0.32‰ [Matsumoto and Lynch-Stieglitz, 1999]. Taken at face value, consistency of $\delta^{13}\text{C}$ amplitudes along the *E. exigua* isotope record with mean ocean $\delta^{13}\text{C}$ change would suggest that during glacial periods (MIS 2 and MIS 6) there was a persistent contribution of a well-ventilated water mass at intermediate depths at the Agulhas Plateau with a $\delta^{13}\text{C}$ signature similar to present-day NADW. A possible continued northern component water influence is in line with inferences from $^{213}\text{Pa}/^{230}\text{Th}$ [Yu et al., 1996], paired benthic-planktonic $\delta^{18}\text{O}$ [Matsumoto and Lynch-Stieglitz, 1999; Matsumoto et al., 2001] and detrital Nd isotopic records [Bayon et al., 2003] that all suggest only minor changes in water mass structure and circulation in the area on glacial-interglacial timescales. As well as the suggestion of only little change in the nutrient inventory for deep waters in the Southern Ocean derived from nearly constant glacial and interglacial foraminiferal Cd/Ca values in the region [Boyle, 1992; Oppo and Rosenthal, 1994; Boyle and Rosenthal, 1996]. Alternatively, our site could also have received a contribution of a Southern Ocean water mass during glacial times with a ventilation signature influenced by air-sea gas exchange [Molyneux et al., 2007], similar to that seen in modern Antarctic Intermediate Waters.

[32] Our data suggest that the large-amplitude glacial-interglacial changes, in the range of 1‰, that is observed in epibenthic $\delta^{13}\text{C}$ records from high southern latitudes can be at least partially attributed to productivity induced $\delta^{13}\text{C}$ changes within the immediate benthic boundary layer as suggested by Bickert and Mackensen [2004] and Rutberg and Peacock [2006]. Unlike *F. wuellerstorfi* such effects are not seen in the $\delta^{13}\text{C}$ of *E. exigua* possibly because this species consistently calcifies during the short time span of the year when phytodetritus is delivered and thereby is not exposed to changing environments of sequential appearance and disappearance of productivity signals.

6. Conclusions

[33] The record of benthic foraminifera ($>63\ \mu\text{m}$) in core MD02-2589 located in the southern flank of the Agulhas Plateau shows considerable fluctuations in the benthic foraminiferal assemblage composition over the last 150 ka that are indicative of variations in the C_{org} supply to the seafloor in relation with changes in productivity and its seasonality. Periods of reduced but seasonally paced delivery of labile organic matter to the seafloor are indicated during Termination I and MIS 5c–MIS 5e. These suggest an oceanographic configuration similar to modern conditions at the core location with intermittent bloom events occurring mainly in the austral-summer period. Periods of higher surface productivity and moderate to low seasonality of the food supply are suggested during MIS 6, MIS 4, MIS 3 and early MIS 2. In accordance with the modern surface productivity distribution, such pattern indicates a northward migration of the SAF and confluence with the more stationary STF and AF. Productivity was strongly reduced and

characterized by extremely short pulses of phytodetritus from late MIS 5b to early MIS 4 suggesting a decreased intensity of the STC and/or greater influence of the AF in the region.

[34] The significance of $\delta^{13}\text{C}$ in *E. exigua* as an epifaunal species that is physically associated with the deposition of a phytodetritus layer at the seafloor is evaluated. A primary conclusion is that *E. exigua* contains a distinctive $\delta^{13}\text{C}$ overprint from ^{13}C -depleted phytodetritus that offsets its carbon isotope signal by $\sim 1.1\text{‰}$ from the $\delta^{13}\text{C}_{\text{DIC}}$ of ambient bottom waters. However, the $\delta^{13}\text{C}$ amplitude of *E. exigua*, on glacial-interglacial timescales, does not seem affected by the variable C_{org} supply to the seafloor or by variable ^{13}C -depleted microenvironments generated in the course of C_{org} decomposition within the phytodetrital layer. From this we conclude that while absolute $\delta^{13}\text{C}$ values of *E. exigua* are offset from ambient bottom water $\delta^{13}\text{C}_{\text{DIC}}$, the amplitude of $\delta^{13}\text{C}$ changes recorded by this species in high-productivity environments more reliably document changes in bottom water $\delta^{13}\text{C}_{\text{DIC}}$ than epibenthic species such as *F. wuellerstorfi*. A great advantage of *E. exigua* appears to be that this species rapidly colonizes freshly deposited phytodetritus on the seafloor and restricts calcification, and acquisition of its carbon isotope signal, to an only short time span of the year when phytodetritus is present and thereby is not exposed to changing environments of sequential appearance and disappearance of productivity signals. In comparison, *F. wuellerstorfi*, appears more affected by variable $\delta^{13}\text{C}$ overprints depending on the presence or absence of productivity induced influences on $\delta^{13}\text{C}_{\text{DIC}}$.

[35] Glacial-interglacial $\delta^{13}\text{C}$ amplitudes of 0.3–0.4‰ are recorded by *E. exigua* along core MD02-2589 and compare

well with the estimated mean ocean $\delta^{13}\text{C}$ change. Such a signal is consistent with a continued influence of a well-ventilated water mass, either of Northern Hemisphere origin or one that is formed regionally in the Southern Ocean with a $\delta^{13}\text{C}_{\text{DIC}}$ signal shifted to positive levels by air-sea gas exchange. If confirmed, the results of this study suggest that *E. exigua* may provide a reliable reference in stable isotope paleoceanography against which the productivity-driven $\delta^{13}\text{C}$ modulation of the more widely used epibenthic species, *F. wuellerstorfi*, can be evaluated. This will notably aid the reconstruction of past $\delta^{13}\text{C}_{\text{DIC}}$ variations at high southern latitudes, and plausibly in other ocean regimes, that experienced major changes in biological productivity during the past.

[36] **Acknowledgments.** The authors are grateful to G. G. Bianchi, J. Becker, R. M. Marimón, and I. Cacho for their assistance in the stable isotope analysis. We thank H. Medley for assistance with sample preparation. Comments from E. Rohling, B. H. Corliss, and an anonymous reviewer significantly improved this manuscript and are gratefully acknowledged. We thank the Institut Polaire Français Paul Emile Victor (IPEV) for making the research vessel *Marion Dufresne* available and for technical support for retrieving the sediment cores used in this study. We are indebted to Gabriele Uenzelmann-Neben from the Alfred Wegener Institute for Polar and Marine Research, Bremerhaven, Germany, for providing her multi-channel seismics that helped positioning and retrieval of cores MD02-2588 and -2589. P.D. was financially supported by the postdoctoral research grant EX-2004-0918 funded by the Spanish Ministerio de Educación y Ciencia (MEC). I.H. and E.M. acknowledge funding from the U.K. Natural Environment Research Council; R.Z. acknowledges funding from the MEC through grant 1040 REN2002-0195 and the Comer Science and Education Foundation, USA.

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