Carbon isotope offsets between benthic foraminifer species of the genus Cibicides (Cibicidoides) in the glacial sub-Antarctic Atlantic

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Abstract

Epibenthic foraminifer δ13C measurements are valuable for reconstructing past bottom water dissolved inorganic carbon δ13C(DIC), which are used to infer global ocean circulation patterns. Epibenthic δ13C, however, may also reflect the influence of 13C-depleted phytodetritus, microhabitat changes, and/or variations in carbonate ion concentrations. Here we compare the δ13C of two benthic foraminifer species, Cibicides kullenbergi and Cibicides wuellerstorfi, and their morphotypes, in three sub-Antarctic Atlantic sediment cores over several glacial-interglacial transitions. These species are commonly assumed to be epibenthic, living above or directly below the sediment-water interface. While this might be consistent with the small δ13C offset that we observe between these species during late Pleistocene interglacial periods (Δδ13C = -0.19 ± 0.31‰, N=63), it is more difficult to reconcile with the significant δ13C offset that is found between these species during glacial periods (Δδ13C = -0.76 ± 0.44‰, N=44). We test possible scenarios by analyzing Uvigerina spp. δ13C and benthic foraminifer abundances: (1) C. kullenbergi δ13C is biased to light values either due to microhabitat shifts or phytodetritus effects and (2) C. wuellerstorfi δ13C is biased to heavy values, relative to long-term average conditions, for instance by recording the sporadic occurrence of less depleted deepwater δ13C(DIC). Neither of these scenarios can be ruled out unequivocally. However, our findings emphasize that supposedly epibenthic foraminifer δ13C in the sub-Antarctic Atlantic may reflect several factors rather than being solely a function of bottom water δ13C(DIC). This could have a direct bearing on the interpretation of extremely light South Atlantic δ13C values at the Last Glacial Maximum.

1. Introduction

Most species of the benthic foraminifer genera Cibicides and Cibicidoides are generally believed to dwell in an epibenthic habitat [Lutze and Thiel, 1989; Jorissen et al., 1995]. The term “epibenthic” denotes a habitat directly above the sediment (sometimes referred to as “real epibenthic”) and within the sediment near the sediment-water interface [Jorissen et al., 1995]. Despite ambiguities regarding the exact average living depth that is represented by an epibenthic habitat, the term is useful to make a distinction to (infaunal/endobenthic) species living within the sediment that may have a marked subsurface abundance maximum [Jorissen et al., 1995]. Epibenthic foraminifera are often assumed to record the δ13C of dissolved inorganic carbon (DIC) of the ambient (i.e., bottom) water in a roughly one-to-one relationship [Woodruff et al., 1980; Belanger et al., 1981; Graham et al., 1981; Duplessy et al., 1984; Zahn et al., 1986]. This assumption forms the basis for spatiotemporal reconstructions of DIC δ13C(DIC) of bottom waters that are used to infer past global ocean circulation [e.g., Duplessy et al., 1988; Sarneith et al., 1994; Ravelo and Andreassen, 2000; Bickert and Mackensen, 2003; Curry and Oppo, 2005; Gebhardt et al., 2008; Waelbroeck et al., 2011].

Past-ocean δ13C(DIC) reconstructions have shown much lower benthic δ13C in the deep sub-Antarctic Atlantic than in the deep Pacific Ocean during the last glacial period (Figure 1) [Curry et al., 1988; Charles et al., 1996; Mackensen et al., 2001; Ninemmann and Charles, 2002; Hodell et al., 2003a]. The modern ocean, however, is generally characterized by a progressive decrease of δ13C(DIC) and an increase of deepwater DIC concentrations from the North Atlantic toward the North Pacific related to the steady accumulation of respired organic carbon along the flow path of deep water [Kroopnick, 1985]. The very negative benthic δ13C values in the
Figure 1. Deglacial benthic $\delta^{13}C$ records: (a) Cibicides/Cibicidoides $\delta^{13}C$ records (circles: C. kullenbergi; triangles: C. wuellerstorfi; diamonds: mixed Cibicides/ Cibicidoides samples) from the North Atlantic (MD99-2334 [Skinner et al., 2007] and GeoB9526-5 [Zarriess and Mackensen, 2011]), the Indian Ocean (SK129-CR2 [Piotrowski et al., 2009]), the North Pacific (W8709A-13PC [Lund and Mix, 1998] and MD02-2489 [Gebhardt et al., 2008]), and the sub-Antarctic Atlantic (TN057-21 [Ninnemann et al., 1999], ODP site 1090 [Hodell et al., 2003a] [symbols only], MD07-3076Q [Waelbroeck et al., 2011], and MD02-2588 [Ziegler et al., 2013]). The numbers in the parentheses indicate the water depth at the core sites. The solid lines represent the 1000 year running averages. (b) Locations of sediment cores (Table S3 in the supporting information). The grey bars on the top indicate the Last Glacial Maximum (LGM), the deglaciation, and the Holocene periods. The benthic $\delta^{13}C$ records are shown on their previously published (14C-based) age scales, except for TN057-21 [Barker and Diz, 2014] and MD99-2334 (transferred to the GICC05 chronology [Svensson et al., 2008]).
deep South Atlantic during the Last Glacial Maximum (LGM) may thus imply much higher respired carbon levels [Kroopnick, 1985], if the processes governing seawater $\delta^{13}C_{DIC}$ remained the same over glacial-interglacial cycles. This observation is important because it would imply different glacial ocean circulation patterns and/or changes in ocean carbon sequestration [Curry et al., 1988; Michel et al., 1995; Charles et al., 1996; Ninnemann et al., 1999] that may be associated with glacial atmospheric CO2 minima [e.g., Toggweiler et al., 2006]. However, the interpretation of very high respired carbon levels in the deep Southern Ocean has proven difficult to reconcile with nutrient proxy data such as benthic Cd/Ca ratios, which show little or no change in nutrient concentrations compared to Holocene levels [Boyle, 1992; Martínez-Méndez et al., 2009]. Although benthic Cd/Ca ratios may also be affected by additional processes [e.g., McCorkle et al., 1995], the apparent discrepancy between benthic Cd/Ca and carbon isotope ratios in the deep Southern Ocean may suggest that the mechanisms influencing deep South Atlantic $\delta^{13}C_{DIC}$ and/or benthic $\delta^{13}C$ have changed over glacial-interglacial time scales [e.g., Martínez-Méndez et al., 2009; Mackensen, 2012]. However, the causes of low glacial South Atlantic benthic $\delta^{13}C$ values remain not fully understood.

Other ocean circulation proxies have been used to shed light on this conundrum and have highlighted the complexity of benthic $\delta^{13}C$ as a paleoceanographic proxy that incorporates the effects of ocean transport rates, biological export productivity, and air-sea gas exchange [e.g., Charles and Fairbanks, 1990; Lynch-Stieglitz et al., 1995]. For instance, despite general agreement of millennial-scale variations in benthic $\delta^{13}C$ and the water mass provenance indicator $\epsilon_{Nd}$ measured in sediment core TN057-21 from the Cape Basin, slight deviations between these proxies have been attributed to thermodynamic and kinetic fractionation effects on $\delta^{13}C$ during air-sea exchange of CO2 [Piotrowski et al., 2008]. These processes would have changed the preformed $\delta^{13}C$ signature of the water mass, producing changes in benthic $\delta^{13}C$ unrelated to respired carbon accumulation [Charles et al., 1993; Lynch-Stieglitz et al., 1995; Mackensen et al., 2001]. In addition, Mackensen et al. [1993] demonstrated negative deviations of epibenthic $\delta^{13}C$ from bottom water $\delta^{13}C_{DIC}$ in environments with strong seasonal phytodetrital organic carbon input as the result of the incorporation of $^{13}C$-depleted CO2 into foraminiferal carbonates. It has further been suggested that benthic $\delta^{13}C$ does not only reflect changes in $\delta^{13}C_{DIC}$ of bottom waters but also variations in carbonate ion concentrations [Rathburn et al., 1997; Mackensen and Licari, 2004]. Benthic foraminiferal $\delta^{13}C$ may also be biased if epibenthic foraminifera migrate from an elevated habitat above the sediment into the sediment and adopt a $^{13}C$-depleted infaunal habitat [Corliss, 1985; McCorkle et al., 1990; Rathburn et al., 1996; Tachikawa and Elderfield, 2002; Hodell et al., 2003a].

Here we present $\delta^{13}C$ and $\delta^{18}O$ records obtained from Cibicides kullenbergi and Cibicides wuellerstorfi during past glacial-interglacial transitions from sub-Antarctic Atlantic sediment core MD07-3076Q (44°9.19′S, 14°13.69′E; 3777m water depth) and the long piston core MD07-3077 retrieved at the same site (44°9.20′S, 14°13.69′W; 3776m water depth), as well as core TN057-6GC (42°52.7′S, 8°57.4′E; 3750m water depth). The core sites are currently bathed in Lower Circumpolar Deep Water, which is a transition zone between northern and southern sourced water masses. The goal of this study is to assess the consistency of stable isotope data for epibenthic foraminifer species and to test possible overprints. In our samples, we identify, analyze, and compare the records of distinct morphotypes of each of the species, and compare these with the $\delta^{13}C$ and $\delta^{18}O$ signature of Uvigerina spp., which we consider to consistently monitor $\delta^{13}C_{DIC}$ variations in an infaunal habitat. We discuss the general applicability of C. kullenbergi, C. wuellerstorfi, and Cibicides/ Cibicidoides spp. $\delta^{13}C$ analyses for ocean circulation reconstructions, in particular in the Atlantic sector of the Southern Ocean.

2. Modern Habitats and Morphologies

A variety of authors use different nomenclatures when referring to benthic species of the Cibicides and Cibicidoides genera. Although Cibicides and Cibicidoides species have been traditionally classified on the basis of their test convexity (planeconvex versus biconvex), along with wall structure and/or apertural shape [Mead, 1985; Loeblich and Tappan, 1988; Sen Gupta, 1989; Gupta, 1994], phylogenetic support for such placements is lacking [Schweizer et al., 2009]. Test shape is also believed to be the expression of intraspecies ecophenotypic variations [Gupta, 1994]. We follow this notion and group both species into the single genus Cibicides de Montfort 1808 [de Montfort, 1808], where they were first described [Sen Gupta, 1989; Schweizer, 2006]. However, we note that Cibicidoides is also a commonly used genus denomination (see Appendix A
Cibicides kullenbergi Parker is generally considered a synonym for Cibicidoides mundulus (Brady, Parker, and Jones) [Van Morkhoven et al., 1986; Holbourn et al., 2013]. Cibicides wuellerstorfi and C. kullenbergi may present different morphological varieties (“morphotypes”) [e.g., Van Morkhoven et al., 1986; Hayward et al., 2010; Rae et al., 2011], which is a common feature of benthic foraminifer species (Figure 2). The subtle differences among species and morphotypes, and the occurrence of anomalous features, challenge their identification, with specimens often presenting morphological characteristics that are “intermediate” between two species [Van Morkhoven et al., 1986]. Unequivocal identification of different species from the Cibicides and Cibicidoides groups is thus difficult and, in part, subjective. We summarize the most important morphological features of C. wuellerstorfi and C. kullenbergi and of the

![Figure 2. (left) Umbilical, (middle) lateral, and (right) spiral view of type specimens of (a) C. kullenbergi sensu stricto; (b) C. kullenbergi sensu lato; (c) C. wuellerstorfi sensu lato, referred to as C. cf. wuellerstorfi in this study; and (d) C. wuellerstorfi sensu stricto, photographed with the digital microscope ShuttlePix by Nikon®. These strongly resemble type specimens of C. wuellerstorfi and C. kullenbergi (called C. mundulus) and their morphotypes shown in Rae et al. [2011].]
morphotypes we have identified in our sub-Antarctic Atlantic sediment samples and outline their main habitats (although these are not exclusive to the individual benthic foraminifer species).

2.1. *Cibicides wuellerstorfi* (Schwager), 1866

The typical features of the morphology of *C. wuellerstorfi* are shown in Figure 2 and have been described in *Loeblich and Tappan* [1988]. Its most important features include a low trochospiral and planoconvex test, 8 to 12 chambers visible in the final whorl that curve back at the periphery, strongly arched sutures, and an interiomarginal aperture (see also Figure S1 in the supporting information).

We have identified a sensu lato morphtype of *C. wuellerstorfi* commonly found in Southern Ocean sediments (hereafter referred to as C. cf. *wuellerstorfi*), shown in Figure 2c. The test of *C. cf. wuellerstorfi* is subcircular and planoconvex with a flat spiral side and convex umbilical side. The last whorl shows 7 to 9 chambers, which are generally wider and slightly more inflated than those of *C. wuellerstorfi*. The intercameral sutures are curved and bending toward the periphery, although not as strongly as in *C. wuellerstorfi*, and are slightly depressed. The shell has a dull reflectance (that may be an effect of preservation) and little perforation on the umbilical and spiral sides but tends to have a coarser perforation on the spiral side. The aperture may extend on the spiral side along the base of the final chambers. The morphology of *C. cf. wuellerstorfi* resembles very closely that of one holotype figure of *Anomalina wuellerstorfi* Schwager, 1866 in *Ellis and Mssina* [1940].

*Cibicides wuellerstorfi* can live attached to benthic animals, plants, rocks, and hard substrates and is a “suspension feeder” [Lutze and Thiel, 1989]. This “real” epibenthic habitat makes *C. wuellerstorfi* a faithful recorder of bottom water δ¹³C_{DIC} [Belanger et al., 1981; Graham et al., 1981; Duplessy et al., 1984; Zahn et al., 1986; Lutze and Thiel, 1989; Mackensen and Licari, 2004]. However, live (Rose Bengal stained) *C. wuellerstorfi* have also been found within the topmost centimeters of the sediment, suggesting that its habitat may not be restricted to an above-seafloor habitat, but may also be within the sediment [Corliss, 1985; Corliss and Emerson, 1990; Rathburn and Corliss, 1994; Jorissen et al., 1998; Wollenburg and Mackensen, 1998b; Fontanier et al., 2002]. This species is often associated with strong bottom water currents [Linke and Lutze, 1993; Mackensen et al., 1995]. It prefers a low organic carbon flux to the seafloor but withstands seasonally pulsed phytodetrital (labile) food supply [Mackensen et al., 1993, 2001; Jorissen et al., 1998]. As such, it is considered an indicator of oligotrophic conditions [Wollenburg and Mackensen, 1998a, 1998b]. *Cibicides wuellerstorfi* does not generally withstand high and sustained annual fluxes of organic carbon or perennial oxygen depletion in bottom waters [Mackensen et al., 1995]. Although *C. wuellerstorfi* specimens can be found in association with the (episodic) arrival of young, well-oxygenated water masses, as observed in the South Atlantic [Mackensen et al., 1995; Schmiiedl and Mackensen, 1997], they have also been found in oxygen-poor seep environments [e.g., Rathburn et al., 2000; Burkett et al., 2015].

2.2. *Cibicides kullenbergi* Parker, 1953

The sensu stricto morphology of *C. kullenbergi* is shown in Figure 2a and has been described by *Loeblich and Tappan* [1988]. Important characteristics are a trochospiral and biconvex test (2.5 to 3 whorls are generally visible), 10 to 11 chambers in the final whorl, arched sutures on the spiral side, almost straight and radial sutures on the umbilical side, and a low interiomarginal aperture (see also Figure S1 in the supporting information).

In most of our sub-Antarctic Atlantic sediment samples, the morphology of *C. kullenbergi* deviates from the sensu stricto morphtype. This sensu lato morphotype of *C. kullenbergi* appears mostly convex on the umbilical side but tends to be rather flat on the spiral side and has a more subcircular test compared to *C. kullenbergi* sensu stricto (Figure 2). The chamber length-to-width ratio is also slightly greater in comparison to *C. kullenbergi* sensu stricto (Figure 2b). The spiral side of *C. kullenbergi* sensu lato is coarsely perforated, whereas perforation on the umbilical side is sparse. Furthermore, the sutures of *C. kullenbergi* sensu lato may be slightly depressed and marginally arched toward the periphery both on the spiral and umbilical sides (Figure 2b).

*Cibicides kullenbergi* has been suggested to dwell at the sediment-water interface and has been considered a “mud dweller” [Corliss and Emerson, 1990; Schweizer, 2006]. Live (stained) specimens are generally found in the first centimeter of the sediment [Rathburn and Corliss, 1994; Jorissen et al., 1998] and have also been extensively used to reconstruct bottom water δ¹³C_{DIC} [e.g., Duplessy et al., 1984; Charles et al., 1996; Gebhardt et al., 2008]. In contrast to *C. wuellerstorfi*, *C. kullenbergi* is adapted to various modes of organic
carbon food supply [Lutze and Coulbourn, 1984; Jorissen et al., 1998; Eberwein and Mackensen, 2006]. Although it prefers oligotrophic conditions, similar to C. wuellerstorfi sensu stricto, it may withstand a much more continuous organic carbon supply to the seafloor [Eberwein and Mackensen, 2006].

3. Methods

3.1. Stable Isotope Measurements

Stable isotope analyses in sediment cores MD07-3076Q and MD07-3077 have been performed on 1 to 4 specimens of C. kullenbergi (212–500µm), C. wuellerstorfi (150–500µm), and C. cf. wuellerstorfi (150–500µm) as well as of Uvigerina spp. (mostly U. peregrina; 212–350µm) on Finnigan Delta+ and Elementar Isoprime mass spectrometers at the Laboratoire des Sciences du Climat et de l’Environnement (LSCE) in Gif-sur-Yvette.
France. Small size fractions (<212µm) were analyzed when benthic foraminifera (in particular, C. wuellerstorfi and C. cf. wuellerstorfi) were absent in the 212–500µm fraction. Stable isotope analyses of C. kullenbergi in MD07-3076Q and MD07-3077 were made on the sensu lato morphotype (Figure 2b) because of its predominant occurrence in these cores. Benthic foraminifer stable isotopes in sediment core TN057-6GC (same size fractions as above) have been measured on ThermoFisher MAT253 mass spectrometer with an automated Kiel Device at the Godwin Laboratory for Palaeoclimate Research at the University of Cambridge (UK). Both morphotypes of C. kullenbergi were identified in the 212–500µm size fraction and were measured separately.

In all cores, stable isotope analyses have been performed separately on C. wuellerstorfi and C. cf. wuellerstorfi (Figures 3–5). Paired stable isotope analyses on C. wuellerstorfi and C. cf. wuellerstorfi could not be performed, as they hardly coexist in exactly the same depth levels in our sediment cores. Cibicides cf. wuellerstorfi seems to be more common during glacial periods, whereas C. wuel- lerstorfi is abundant during interglacials. Although this needs to be verified by genetic characterization [e.g., Schweizer et al., 2009], we treat C. wuellerstorfi and C. cf. wuellerstorfi as the same species for our purposes, hereafter abbreviated as C. wuellerstorfi (in a sensu stricto; s.l.), owing to their close morphologies (section 2.1.) and the generally lower abundance of these foraminifera in sub-Antarctic Atlantic sediments. However, whether these two benthic foraminifera represent different species or different morphotypes does not matter for the conclusion of this study, because in practice they can be (and often are) considered as equivalents of the sensu stricto form.

Prior to stable isotope analyses, foraminifera were cleaned to remove organic matter and extraneous carbonates that are adsorbed or attached to the foraminiferal shells. Foraminifer samples from MD07-3076Q and MD07-3077 were rinsed with methanol, ultrasonicated for ~10s, dried at room temperature, and finally roasted under vacuum at ~380°C for 45min. Foraminifer samples from TN057-6GC were crushed, soaked in ~15% hydrogen peroxide for 30min at room temperature, rinsed in acetone, ultrasonicated for a
few seconds, and dried in an oven at 50°C. All foraminifer samples in each individual core were pretreated equally.

The mean external reproducibility of carbonate standards of LSCE Finnigan Δ+ and Elementar Isoprime mass spectrometers (Godwin Laboratory ThermoFisher MAT253 mass spectrometer) is σ=0.05‰ (0.08‰) for δ18O and σ=0.03‰ (0.06‰) for δ13C. The results are reported with reference to the international Vienna PeeDee Belemnite (VPDB) standard, defined with respect to the National Bureau of Standards (NBS)-19 calcite standard (δ18O=−2.20‰ and δ13C=+1.95‰) [Coplen, 1988]. Stable isotope analyses of the NBS-19 calcite standard and of an internal carbonate standard for the purpose of an interlaboratory comparison between GIF and Cambridge have indicated good reproducibility (GIF δ18O: −5.50±0.05‰, N=40; Cambridge δ18O: −5.52±0.07‰, N=20; GIF δ13C: 1.45±0.03‰, N=40; Cambridge δ13C: 1.44±0.02‰, N=20) and thus support consistency of stable isotope measurements between the laboratories.

Replicate measurements indicate an average intraspecies δ18O variability of 0.07±0.05‰ (N=87) for C. kullenbergi and 0.09±0.08‰ (N=21) for C. wuellerstorfi. Replicated stable isotope values are reported as mean values in our study.

Interspecies δ18O and δ13C offsets were estimated for interglacial periods (Holocene: last 10ka before present (B.P.), marine isotope stage (MIS) 11: 419–395ka B.P.) and for glacial periods (LGM: 25–18ka B.P., MIS 6: 149–132ka B.P., MIS 12: 448–425ka B.P.; Figures 3 and 4 and Table 1). Interspecies δ18O and δ13C offsets between C. kullenbergi and C. wuellerstorfi (s.l.) (Δδ18OCk-Cw and Δδ13CCk-Cw respectively) and between Uvigerina spp. and C. kullenbergi (Δδ18OUV-Ck and Δδ13CUV-Ck, respectively) were calculated based on paired measurements from the same sediment sample and in sediment core MD07-3076Q also from consecutive sediment samples within 2cm (or <400years) of each other. The benthic interspecies δ18O difference obtained from adjacent sediment samples from within 2cm in MD07-3076Q is −0.01±0.13‰ (N=11) on average, which is statistically indistinguishable from the average Δδ18OCk-Cw value of 0.03±0.12‰ (N=19) obtained from the same sediment samples. We argue that this correspondence justifies the calculation of Δδ13CCk-Cw from adjacent sediment samples within 2cm spacing that was necessary because of low benthic foraminifer abundances in MD07-3076Q.

3.2. Benthic Foraminifer Abundances in MD07-3076Q

To quantify the abundance of C. wuellerstorfi, C. cf. wuellerstorfi, and C. kullenbergi during the last deglaciation in sediment core MD07-3076Q, we determined the number of specimens per gram of dry bulk sediment in discrete 8cm³ volume samples obtained from 1cm thick sediment slices. The benthic foraminifer accumulation rate (BFAR) was calculated as BFAR=#foraminifera×LSR×ρdry, where #foraminifera is the number of
benthic foraminifera per gram of dry bulk sediment, LSR is the linear sedimentation rate in cm ka⁻¹, and ρ_dry is the dry bulk sediment density in g cm⁻³ [Herguera and Berger, 1991]. The ρ_dry was calculated from the dry sediment weight of the discrete 8 cm³ samples.

### 3.3. Core Chronologies

The age model of sediment core MD07-3076Q is based on calibrated radiocarbon ages corrected for surface ocean reservoir age variations [Skinner et al., 2010]. Our deglacial age model applies a linear interpolation between the radiocarbon-derived age-depth tie points [Gottschalk et al., 2015] to be consistent with the age model approach used for core MD07-3077 [Vázquez Riveiros et al., 2010, 2013; this study]. However, the difference between the age models for the last 25 ka B.P. using a Monte Carlo-based approach [Skinner et al., 2010] and a piecewise linear interpolation [Gottschalk et al., 2015] is small (2 ± 38 years).

The chronology of sediment core MD07-3077 during MIS 12–11 is based on the stratigraphic alignment of abundance variations of the cold-water planktonic foraminifer Neogloboquadrina pachyderma (sinistral) with Antarctic temperature variations [Vázquez Riveiros et al., 2010, 2013] approximated by the δ¹³C record of the Antarctic Dome C ice core (European Project for Ice Coring in Antarctica) [Jouzel et al., 2007] on the newest Antarctic Ice Core Chronology (AICC) 2012 [Bazin et al., 2013]. Six additional age-depth markers were obtained using the same approach in the MIS 6–5 interval (Figure S2 and Table S1 in the supporting information). The final chronology is based on linear interpolation between tie points.

The age model of sediment core TN05-66G is based on the alignment of the benthic δ¹⁸O record of MD07-3076Q to that of TN05-66G (Figure S3 and Table S2 in the supporting information), justified because the cores are located in close proximity to each other. Although this provides only a rough age model, it is sufficient for comparing benthic δ¹³C and δ¹⁸O values between interglacial and glacial periods, which is the aim of our study.

### 4. Results

#### 4.1. Downcore δ¹³C and δ¹⁸O Variabilities

##### 4.1.1. MD07-3076Q/MD07-3077

We observe a δ¹³C offset between C. wuellerstorfi (s.l.) and C. kullenbergi in the sub-Antarctic Atlantic that is consistently larger during the glacial than during the succeeding interglacial periods (Figure 3 and Table 1). Also, the average Holocene C. wuellerstorfi (s.l.) δ¹³C value is higher than present-day δ¹³C_DIC at the core site, whereas the average C. kullenbergi δ¹³C value is lower (Figure 3).

The offset between C. wuellerstorfi (s.l.) δ¹³C and C. wuellerstorfi (s.l.) δ¹³C during MIS 12 (Δδ¹³C_Ck-Cw = −0.57 ± 0.37‰, N = 10) is significantly different from the MIS 11 offset within 95% uncertainties (p < 0.05). The scarcity of C. kullenbergi during MIS 5 does not permit an estimate of Δδ¹³C_Ck-Cw for this period. However, Δδ¹³C_Ck-Cw values during MIS 6 (−0.67 ± 0.22‰, N = 16) are similar to...
those observed during MIS 12. During the Holocene, the δ13C offset between C. wuellerstorfi (s.l.) and C. kullenbergi is Δδ13C_Ck-Cw = −0.72 ± 0.35‰ (N = 8) on average, which is lower than last glacial values in MD07-3076Q (Δδ13C_Ck-Cw = −1.21 ± 0.14‰, N = 10), but similar to those of MIS 6 and MIS 12 in MD07-3077 (Figure 3 and Table 1). Again, a statistical t test shows that the observed LGM Δδ13C_Ck-Cw values are significantly different from Holocene Δδ13C_Ck-Cw estimates within 95% uncertainties (p < 0.05). Despite the significant glacial δ13C offset, C. wuellerstorfi (s.l.) and C. kullenbergi δ18O values in the central sub-Antarctic Atlantic closely agree with each other throughout the studied time interval (Table 1 and Figure 3).

4.1.2. TN057-6GC

The distinct glacial-interglacial difference between C. kullenbergi δ13C and C. wuellerstorfi (s.l.) δ13C observed in MD07-3076Q/MD07-3077 agrees with results in Cape Basin sediment core TN057-6GC (Figure 4). The mean δ13C offset between C. kullenbergi and C. wuellerstorfi (s.l.) in TN057-6GC is Δδ13C_Ck-Cw = −0.61 ± 0.18‰ (N = 8) during the LGM and Δδ13C_Ck-Cw = −0.42 ± 0.43‰ (N = 3) during the Holocene. Because of the small number of observations during these two periods, the glacial-interglacial Δδ13C_Ck-Cw difference observed in TN057-6GC is not statistically significant and awaits confirmation in other Cape Basin sediment cores.

Mean Holocene C. wuellerstorfi (s.l.) and C. kullenbergi δ13C are higher than modern δ13C_CDIC at the core site (Figure 4).

The δ18O values of the different Cibicides species are in agreement, although the interspecies δ18O variability is slightly greater in TN057-6GC than in MD07-3076Q/MD07-3077 (Table 1 and Figure 4).

4.2. Comparison of C. kullenbergi δ13C and Uvigerina spp. δ13C

In sediment cores MD07-3076Q and MD07-3077, Uvigerina spp. and C. kullenbergi δ13C differences are larger during the interglacial periods than during the glacial periods we have investigated (Table 1 and Figure 3). Δδ13C_Uv-Ck values during MIS 11 (−0.83 ± 0.23‰, N = 16) and MIS 12 (−0.56 ± 0.12‰, N = 9) are statistically distinguishable from each other (p < 0.05). During MIS 6 (Table 1 and Figure 3), we observe Δδ13C_Uv-Ck values of −0.46 ± 0.19‰ (N = 13), consistent with values observed during MIS 12 (−0.56 ± 0.12‰, N = 9). During the Holocene (Table 1 and Figure 3), Δδ13C_Uv-Ck is −0.55 ± 0.26‰ (N = 19), which is slightly greater although not significantly different from the LGM offset (Δδ13C_Uv-Ck = −0.31 ± 0.20‰, N = 11; p < 0.05).

In Cape Basin core TN057-6GC, Δδ13C_Uv-Ck values during the Holocene (Δδ13C_Uv-Ck = −0.53 ± 0.39‰, N = 5) and during the LGM (Δδ13C_Uv-Ck = −0.59 ± 0.23‰, N = 4) are similar. A t test shows that these values are not significantly different from each other within the 95% confidence level.

Uvigerina spp. δ18O agrees with C. kullenbergi δ18O during interglacial (Δδ18O_Uv-Ck,mean = −0.13 ± 0.22‰, N = 40) and glacial periods (Δδ18O_Uv-Ck,mean = −0.02 ± 0.18‰, N = 37; Table 1), provided that an adjustment of 0.64‰ is applied to account for disequilibrium effects (Figures 3 and 4) [Shackleton and Opydyke, 1973; Duplessy et al., 1984]. Both mean interglacial and glacial Δδ18O_Uv-Ck values are statistically indistinguishable from zero within 95% confidence level (p < 0.05).

4.3. Benthic Foraminifer Accumulation Rates

Benthic census counts show that C. wuellerstorfi is very rare in MD07-3076Q sediments of the last 22ka B.P. (Figure 5). Cibicides cf. wuellerstorfi occurs very sporadically, with a mean accumulation rate of ±1 specimen cm−2 ka−1, primarily when C. wuellerstorfi is absent (Figure 5). Cibicides kullenbergi is the most abundant Cibicides species during the last deglaciation, with a mean accumulation rate of 7 ± 5 specimens cm−2 ka−1 (Figure 5).

5. Discussion

5.1. Benthic Foraminifer Interspecies δ13C Offsets

Our findings demonstrate a significant δ13C difference between C. kullenbergi and C. wuellerstorfi (s.l.) in the sub-Antarctic Atlantic. This difference is noticeable during glacial periods (Δδ13C_Ck-Cw,mean = −0.76 ± 0.44‰, N = 44), while it is smaller during interglacial periods (Δδ13C_Ck-Cw,mean = −0.19 ± 0.31‰, N = 63). In contrast, δ18O values agree between the species during both glacial and interglacial periods (Δδ18O_Ck-Cw,mean = 0.02 ± 0.12‰ (N = 44) and Δδ18O_Ck-Cw,mean = 0.01 ± 0.13‰ (N = 63), respectively; Table 1).
It has been previously shown that *C. kullenbergi* and *C. wuellerstorfi* δ¹³C values are nearly identical in globally distributed core tops or in down-core sediments [Graham et al., 1981; Duplessy et al., 1984], which agrees with paired *C. kullenbergi* and *C. wuellerstorfi* (s.l.) δ¹³C measurements in MIS 11 in core MD07-3077 (Figure 3). In contrast, core top studies from the upwelling region off the Moroccan margin show a significant δ¹³C offset between *C. kullenbergi* and *C. wuellerstorfi* [Eberwein and Mackensen, 2006] that has also been observed in a downcore record from the high-productivity coastal area off Chile over both glacial and interglacial intervals of the last 1 Myr (Δδ¹³C_Ck-Cw = −0.16 ± 0.16‰, N = 114; statistically significant within 95% confidence, p < 0.05) [Martínez-Mendoza et al., 2013]. The glacial offsets we have found are much larger and similar to glacial δ¹³C offsets in the deep, south Cape Basin [Hodell et al., 2003a] and in the Northeast Atlantic [Hodell et al., 2001].

Our comparison suggests that during interglacials, *C. wuellerstorfi* (s.l.) and *C. kullenbergi* δ¹³C generally reflect bottom water δ¹³CDIC with uncertainties of a few tenths of per mil, while during glacial periods *C. wuellerstorfi* (s.l.) δ¹³C and/or *C. kullenbergi* δ¹³C may be significantly shifted away from bottom water δ¹³CDIC.

The fact that specimens of *C. kullenbergi* and *C. wuellerstorfi* (s.l.) are neither consistently smaller nor larger during glacial periods compared to interglacials and that species of the genera *Cibicides* and *Cibicidoides* generally lack a significant δ¹³C response to varying respiration rates [Corliss et al., 2002; Franco-Fraguas et al., 2011; Theodor et al., 2016] rules out a bias of observed Δδ¹³C_Ck-Cw values due to ontogenetic isotope effects. We therefore explore two possible scenarios that could explain our data: (1) *C. kullenbergi* δ¹³C has been biased toward light values relative to average deepwater δ¹³CDIC, either due to a shift to a shallow infaunal microhabitat or due to phytodetritus effects that do not significantly affect *C. wuellerstorfi*, and/or (2) *C. wuellerstorfi* δ¹³C is biased to heavy values, relative to long-term average conditions, by recording the sporadic (seasonal to centennial) occurrence of less depleted deepwater δ¹³CDIC at our core sites or by reflecting δ¹³CDIC from a different location.

### 5.2. Potential Biases of *C. kullenbergi* δ¹³C from Bottom Water δ¹³CDIC

A significant negative offset of glacial *C. kullenbergi* δ¹³C from contemporaneous bottom water δ¹³CDIC may result from a microhabitat differentiation of *C. kullenbergi* and *C. wuellerstorfi*, which has been previously proposed [Hodell et al., 2001, 2003a], and/or from variations in the pore water δ¹³CDIC gradient. Even small microhabitat changes may have a significant influence on epibenthic foraminifer δ¹³C, because vertical pore water δ¹³CDIC gradients in marine sediments are large and vary depending on organic carbon rain rates and bottom water oxygen concentrations (Figure 6) [McCorkle and Emerson, 1988; McCorkle et al., 1997; Tachikawa and Elderfield, 2002]. These gradients may reach up to −1‰ cm⁻¹, in particular near the surface [McCorkle et al., 1985], and can be accompanied by pore water carbonate ion variations that may have an additional (potentially counteracting) influence on benthic δ¹³C [Spero et al., 1997; Bemis et al., 1998]; however, a carbonate ion-dependent carbon isotope effect on benthic foraminifera remains to be demonstrated and quantified. Small increases in the calcite precipitation depth of *C. kullenbergi* within the sediment may explain the observed glacial δ¹³C_Ck-Cw gradient, if the microhabitat of *C. wuellerstorfi* (s.l.) did not shift simultaneously in the same direction (or by a lesser amount) and remained epibenthic.

Benthic faunal analyses off West Africa have suggested that the microhabitat of (epi)benthic foraminifera may shift deeper into the sediment depending on the availability of food [Linke and Lutze, 1993; Licari and Mackensen, 2005; Licari, 2006]. These studies indicate that the average living depth of benthic foraminifera, i.e., *Cibicides pachyderma* and *Cibicides lobatus*, correlates with the δ¹³C offset from bottom water δ¹³CDIC, which ranges between −0.4% and 0‰ and may reach extremes of −0.8‰ owing to the effect of ¹³C-depleted pore waters. It is possible that this adaptable behavior also applies to *C. kullenbergi* in the glacial sub-Antarctic Atlantic.

In order to test whether *C. kullenbergi* δ¹³C reflects the δ¹³CDIC of an infaunal habitat rather than that of bottom water, we compare *C. kullenbergi* δ¹³C with *Uvigerina* spp. δ¹³C. Most benthic foraminifera of the genus *Uvigerina*, including *Uvigerina peregrina*, are considered a shallow infaunal species [Zahn et al., 1986; Mackensen and Licari, 2004; Schweizer, 2006], as their highest abundance often occurs in the first two centimeters of the sediment [Corliss and Emerson, 1990; McCorkle et al., 1990, 1997; Jorissen et al., 1998; Fontanier et al., 2002; Mackensen and Licari, 2004]. These benthic foraminifera prefer moderate and perennial fluxes of organic matter [Lutze and Coulbourn, 1984; Zahn et al., 1986; Rathburn and Corliss, 1994] but have also been characterized as opportunistic species that may thrive under the supply of labile phytodetritus.
δ<sup>13</sup>C offsets despite a common microhabitat [Schmiedl et al., 2004; Theodor et al., 2016], a significant glacial Δδ<sup>13</sup>C<sub>Uv-Ck</sub> value is consistent among our core sites and over several past glacial periods (Figures 3 and 4).

We therefore conclude that if *C. kullenbergi* had an endobenthic habitat during glacials, it would have been shallower than that of *Uvigerina* spp., limiting the possible microhabitat effect, and thus the offset from δ<sup>13</sup>C<sub>DIC</sub> of the overlying bottom water during these time intervals. A negative bias due to <sup>13</sup>C-depleted pore water is supported by the observation of lower Holocene *C. kullenbergi* δ<sup>13</sup>C than modern δ<sup>13</sup>C<sub>DIC</sub> at the MD07-3076Q core site (Figure 3), which may have been larger during last glacial periods, for instance as a response to enhanced glacial organic carbon fluxes [Anderson et al., 2014; Gottschalk et al., 2016]. However, a close match of *C. kullenbergi* and *C. wuellerstorfi* δ<sup>13</sup>C during MIS11 (~0.09±0.19, N=52) suggest that this bias was negligible during some interglacials.

*Cibicides kullenbergi* δ<sup>13</sup>C may also significantly deviate from bottom water δ<sup>13</sup>C<sub>DIC</sub> during glacials if it calcified in a <sup>13</sup>C-depleted phyodetritus layer forming at the seafloor [Mackensen et al., 1993]. This would explain observed glacial Δδ<sup>13</sup>C<sub>Ck-Cw</sub> provided that *C. wuellerstorfi* (s.l.) was not affected by it (for instance owing to having an habitat above the phyodetritus layer and/or living at a time different from *C. kullenbergi* within the ~200–400 year time span that one sediment sample represents). The overprint of epibenthic foraminifer
δ¹³C caused by the incorporation of ¹³C-depleted CO₂ that accumulates in these phytodetritus layers is suggested to be 0.4‰ on average, but negative deviations of up to 0.9‰ have also been observed [Mackensen et al., 1993; Mackensen and Bickert, 1999]. Although the average phytodetritus effect of 0.4‰ is smaller than the mean glacial difference between C. kullenbergi and C. wuellerstorfi (s.l.) δ¹³C and was primarily shown for C. wuellerstorfi in the South Atlantic [e.g., Mackensen et al., 1993], we cannot rule out that it was not exceptionally strong (unprecedented) for C. kullenbergi at our core sites during past glacial intervals, explaining deviations of up to −1.21±0.14‰ (Table 1).

5.3. Potential Bias of C. wuellerstorfi (s.l.) δ¹³C from Bottom Water δ¹³CDIC

We now assess the possibility that glacial C. wuellerstorfi (s.l.) δ¹³C is positively offset from average bottom water δ¹³CDIC due to an allochthonous nature of C. wuellerstorfi (s.l.) specimens or due to calcification in a short-term ¹³C-enriched environment. We make use of benthic foraminifer abundance variations to discuss these two effects.

As Figure 5 shows, C. wuellerstorfi (s.l.) is scarce in MD07-3076Q, which may be an indication that specimens found in this core are allochthonous, being transported post mortem to our study site via bottom water currents or nepheloid layers along the mid-ocean ridge from shallower water levels. If C. wuellerstorfi (s.l.) lives elevated above the sediment [Lutze and Thiel, 1989], it may be particularly sensitive to these processes. This scenario is in line with similar benthic foraminifer δ¹⁸O and higher δ¹³C found at the crest of the sub-Antarctic mid-ocean ridge (~2.7km water depth) [Mackensen et al., 2001], from where we would expect allochthonous C. wuellerstorfi (s.l.) in MD07-3076Q and MD07-3077 to originate. However, this explanation requires a very fortuitous situation both in the central and southeast sub-Antarctic Atlantic, i.e., net volume transport by bottom currents toward our core sites, very high current velocities, and a sufficient number of specimens with elevated habitat to be transported downslope. Although the impact of this scenario on observed Δδ¹³C_{Ck-Cw} during past glacial is therefore likely small, it may be relevant for other study sites, in particular near or at continental slopes [e.g., Duros et al., 2012].

Abundances of benthic foraminifera in marine sediments also reflect the extent to what they are adapted to the prevailing ecological and hydrographic conditions [Loubere and Fariduddin, 2003]. High accumulation rates of C. kullenbergi in MD07-3076Q imply that this species may cope best with the prevailing seasonal to multidecadal ecological conditions, e.g., higher export production rates during glacial periods, which may have been unfavorable for C. wuellerstorfi (s.l.) at our core sites (Figure 5). The sparse occurrence of C. wuellerstorfi and C. cf. wuellerstorfi in core MD07-3076Q (Figure 5) might therefore indicate that its δ¹³C reflects only short-term (annual or seasonal) environmental conditions that deviate from average (long-term) bottom water δ¹³CDIC. Such temporaly constrained conditions may be related to short-term (seasonal) changes in the amount or quality of carbon exported [Diz and Barker, 2016] and with higher bottom water oxygen levels, for instance during the incursion of well-ventilated water masses, such as North Atlantic Deep Water (NADW) or unmixed Antarctic Bottom Water [e.g., Mackensen and Bickert, 1999], induced by turbulent mixing or frontal instabilities in this region [e.g., Naveira Garabato et al., 2004; Sheen et al., 2012, 2014]. The latter is only suitable to explain Δδ¹³C_{Ck-Cw} if the δ¹⁸O of the sporadically admixed waters was not very different from the waters that bathed our core sites in the long-term (Figures 3 and 4), making temporal changes in the carbon export explaining our data more likely. These effects may also explain the deviation of Holocene C. wuellerstorfi (s.l.) δ¹³C from modern δ¹³CDIC at the MD07-3076Q core site (Figure 3) and may have been more pronounced during glacial intervals. However, as short-term environments are difficult to reconstruct from the available sedimentary records, their impact on sub-Antarctic Atlantic glacial Δδ¹³C_{Ck-Cw} values remains to be shown.

6. Implications for Paleoceanographic Reconstructions

6.1. Bottom Water δ¹³CDIC Reconstructions Based on Cibicidoides spp. δ¹³C

Many paleoceanographic reconstructions rely on a combination of different species of the Cibicidoides and Cibicides genera (e.g., “Cibicides spp.”) to compensate for the scarcity of each species in marine sediment cores (Figure 7) [e.g., Mackensen et al., 2001; Hodell et al., 2003a; Gebhardt et al., 2008; Hoffman and Lund, 2012]. For example, Cibicidoides spp. δ¹³C data from the Brazil margin (~30°S) below 3.5km water depth [Hoffman and Lund, 2012] show a mean 1σ standard deviation of replicate measurements
(KNR159-5-22GGC: 0.31±0.19‰, N=12; KNR159-5-54GGC: 0.35±0.24‰, N=11) that exceeds the intraspecies $C. \text{kullenbergi}$ (0.15±0.13‰, N=129) and $C. \text{wuellerstorfi}$ δ13C variability (0.09±0.08‰, N=21) observed in MD07-3076Q and MD07-3077 by more than a factor of 2 (Figure 7b). The upper limit of these Brazil margin δ13C data broadly coincides with the composite $C. \text{wuellerstorfi}$ (s.l.) δ13C record of the deep sub-Antarctic Atlantic, whereas the lower limit broadly matches $C. \text{kullenbergi}$ δ13C from the deep sub-Antarctic Atlantic (Figure 7b). The large spread of Brazil margin δ13C values may be significantly influenced by mixed analyses of “low-δ13C” $C. \text{kullenbergi}$ and/or “high-δ13C” $C. \text{wuellerstorfi}$ (s.l.), as well as by bioturbational sediment mixing and variations in bottom water δ13CDIC. Marked interspecies offsets may increase the uncertainty of Atlantic seawater δ13CDIC reconstructions based on benthic δ13C compilations that incorporate mixed-species ($Cibicides/Cibicidoides$ spp.) δ13C [e.g., Duplessy et al., 1988; Sarnthein et al., 1994; Curry and Oppo, 2005; Oliver et al., 2010; Hesse et al., 2011; Peterson et al., 2014].

6.2. Bottom Water δ13CDIC Reconstructions Based on $C. \text{wuellerstorfi}$ and C. cf. $C. \text{wuellerstorfi}$ δ13C

High glacial $C. \text{wuellerstorfi}$ (s.l.) δ13C values of a deep sub-Antarctic Atlantic composite record combining MD07-3076Q and TN057-66GC records are broadly consistent with data from the deep Brazil Margin (not shown) [Oppo and Horowitz, 2000; Lund et al., 2015], the central South Atlantic (not shown) [Jonkers et al., 2015], the deep northern Cape Basin (not shown) [Bickert and Wefer, 1999; Wei et al., 2015], the deep Iberian Margin [Shackleton et al., 2000; Skinner et al., 2007], and the Agulhas Plateau [Ziegler et al., 2013] (Figure 7a). The similarity of the deep sub-Antarctic Atlantic $C. \text{wuellerstorfi}$ (s.l.) δ13C and data from north of the sub-Antarctic Front, in particular from the Iberian Margin, may support the notion that occasional southward incursions of well-ventilated and 13C-rich water masses, such as NADW from just north of the core sites, may influence the $C. \text{wuellerstorfi}$ (s.l.) δ13C records, although it falls short of proving it. The assumption that $C. \text{wuellerstorfi}$ (s.l.) may respond to a particular (seasonal) flux or quality of carbon exported and/or to a
particular oceanographic setting may be an explanation for its relative low abundance in the sediment during the last deglaciation and calls for caution in interpreting δ13C of very low abundant benthic foraminifer species in general.

### 6.3. Bottom Water δ13C Reconstructions Based on *C. kullenbergi* δ13C

Negative “Cibicidoides” spp. δ13C values similar to *C. kullenbergi* δ13C in our study cores have been observed in last glacial sediments throughout the sub-Antarctic zone (between the sub-Antarctic and sub-Tropical Fronts; Figure S4 in the supporting information) [e.g., Charles et al., 1996; Ninnemann et al., 1999; Mackensen et al., 2001]. These values remain among the most negative values observed in the entire last glacial ocean [e.g., Hesse et al., 2011; Peterson et al., 2014]. Possible explanations for lower δ13C_CDIC reconstructed in the deep sub-Antarctic Atlantic than in the North Pacific include (i) glacial changes in ocean circulation and in deep-water formation sites [Michel et al., 1995; Ninnemann and Charles, 2002; Toggweiler et al., 2006], (ii) a strong glacial density stratification of the ocean interior in the southern high-latitude Atlantic [Adkins et al., 2002; Bouttes et al., 2011], (iii) significant preformed bottom water δ13C variations due to alternating modes of formation of Southern Ocean deep waters [Mackensen et al., 2001; Martínez-Méndez et al., 2009; Mackensen, 2012] or different source regions of southern sourced deep waters along the Antarctic coast [McCave et al., 2008], and (iv) a large interbasin redistribution of DIC from the Pacific to the Atlantic Ocean over glacial-interglacial transitions [Schmittner et al., 2007]. However, these explanations assume a reliable representation of bottom water δ13C_CDIC by Cibicidoides spp. and *C. kullenbergi* δ13C. Above we have discussed some hypotheses why this one-to-one representation may be flawed—some of which have been discussed earlier [Ninnemann and Charles, 2002]. We conclude that the magnitude and significance of a bias of *C. kullenbergi* δ13C and/or *C. wuellerstorfi* (s.l.) δ13C from bottom water δ13C_CDIC cannot be unambiguously resolved based on presented data from our study cores.

Two arguments have been previously advanced to emphasize the validity of South Atlantic *C. kullenbergi* (or synonymously, *C. mundulus*) and Cibicides/Cibicidoides spp. δ13C as an indicator of low glacial bottom water δ13C_CDIC [Ninnemann and Charles, 2002], although other influences have been acknowledged [Charles et al., 1996]. First, low last glacial benthic δ13C values can be reproduced spatially (Figure S4 in the supporting information) and also temporally during older glacial Pleistocene periods [e.g., Oppo et al., 1990; Hodell et al., 2003a]. Second, the characteristic low glacial *C. kullenbergi* δ13C is also mirrored in planktonic (*N. pachyderma* s.l.) δ13C in the Cape Basin [Hodell et al., 2003a], suggesting that the planktonic record reflects bottom water δ13C_CDIC that is recorded in benthic foraminifer δ13C [Ninnemann and Charles, 2002]. We discuss these arguments below.

Most core sites with low benthic δ13C during the last glacial period are located near or within the sub-Antarctic zone (Figure S4 in the supporting information). North of this zone, higher glacial benthic δ13C values (>−0.6‰) are observed [e.g., Oppo et al., 1990; Bickert and Wefer, 1999; Hodell et al., 2003a; Martínez-Méndez et al., 2009; Hoffman and Lund, 2012]. Proxy data indicate that increases in aeolian dust supply caused an increase in organic carbon fluxes throughout the sub-Antarctic Atlantic during the LGM [e.g., Anderson et al., 2014], and bottom water oxygen levels have declined in the southern high-latitude Atlantic during this interval [Gottschalk et al., 2016]. If active shifts of the microhabitat or changes within the (infaunal) microhabitat of *C. kullenbergi* are ecologically motivated (for instance, as a response to increased organic carbon fluxes or the seasonal supply of labile food sources) [e.g., Licari, 2006] and *C. kullenbergi* dominates the Cibicides/Cibicidoides population, a bias of *C. kullenbergi* and Cibicides/Cibicidoides spp. δ13C may be possible during glacial periods throughout the (sub-)Antarctic zone. This contention, however, remains to be tested.

Planktonic δ13C records have been used to suggest that the benthic δ13C signal in the sub-Antarctic Atlantic is not spurious [Ninnemann and Charles, 2002; Hodell et al., 2003a], although vital effects render a direct comparison of planktonic δ13C and benthic δ13C difficult [Kohfeld et al., 2000; Gottschalk et al., 2015]. However, two observations may support this suggestion: (1) benthic and planktonic δ13C values in the Cape Basin resemble each other, reflecting the influence of bottom water δ13C_CDIC, and (2) the relative magnitude of glacial-interglacial changes in planktonic δ13C south of the Polar Front in the Antarctic divergence zone, where vertical mixing of the water column is expected and deep waters may reach the surface [Mackensen et al., 1994; Hodell et al., 2003b], is close to glacial-interglacial *C. kullenbergi* (or Cibicides spp.) δ13C changes in the sub-Antarctic [Ninnemann and Charles, 2002; this study]. However, planktonic δ13C records do not reproduce the low benthic δ13C values at all sites [e.g., Michel et al., 1995; Charles et al., 1996; Gottschalk et al., 2015].
and in MD07-3076Q, *N. pachyderma* (s.) $\delta^{13}C$ closely resembles high *C. wuellerstorfi* (s.l.) $\delta^{13}C$ rather than the low *C. kullenbergi* $\delta^{13}C$ record [Gottschalk et al., 2015]. This shows that a better understanding of the controls governing sub-Antarctic Atlantic planktonic foraminifer $\delta^{13}C$ (e.g., export production, air-sea gas exchange, and vertical mixing) is required to reconcile the observed benthic $\delta^{13}C$ patterns and to validate low glacial sub-Antarctic bottom water $\delta^{13}CDIC$.

### 7. Conclusions

Paired *C. kullenbergi* and *C. wuellerstorfi* (s.l.) $\delta^{13}C$ analyses in several sub-Antarctic Atlantic sediment cores over three glacial-interglacial cycles show a significant $\delta^{13}C$ difference during glacial periods of $\Delta\delta^{13}C_{Ck-Cw} = -0.76\pm0.44\%o$, despite a very close agreement of their $\delta^{18}O$ values. This offset is significantly higher than the average interglacial offset ($\Delta\delta^{13}C_{Ck-Cw} = -0.19\pm0.31\%o$). We have ruled out ontogenetic effects as cause of our observations and have subsequently discussed several possible scenarios: (1) *C. kullenbergi* $\delta^{13}C$ is biased toward lighter values owing to the influence of low $\delta^{13}CDIC$ in an infaunal microhabitat or in a benthic phytodetritus layer, while *C. wuellerstorfi* (s.l.) is not affected, and (2) *C. wuellerstorfi* (s.l.) $\delta^{13}C$ is biased to heavy values, by being transported from elsewhere (downslope) or by recording the sporadic occurrence of a microenvironment with higher $\delta^{13}CDIC$, while *C. kullenbergi* is not affected. We found that neither of these explanations can be ruled out unequivocally. However, our observations are important for glacial $\delta^{13}C$ interpretations and raise important questions on the universal consistency of benthic $\delta^{13}C$ as indicator of long-term average bottom water $\delta^{13}CDIC$.

Due to the complexity of *Cibicides* morphotypes presented here, and the inherent subjectivity of the process of picking foraminifera, we recommend the careful documentation of selected specimens of a given species or morphotype, when possible, for example by supplying photographs together with the respective $\delta^{13}C$ data or a detailed taxonomic list. The observed divergence of $\delta^{13}C$ measured in apparently epibenthic foraminifera in the sub-Antarctic Atlantic underscores the need for multiproxy approaches for the reconstruction of ocean circulation changes in the past. In order to avoid adding different biases, stable $\delta^{18}O$ and $\delta^{13}C$ measurements should be performed on monospecific benthic foraminifera samples only, whenever possible. This will allow a clearer picture of the reconstructed benthic and/or bottom water $\delta^{13}C$ variability.

Notwithstanding the possible caveats of benthic $\delta^{13}C$ in the cores we have studied, we suggest that benthic $\delta^{13}C$ of abundant *Cibicides* species likely remains a good proxy for bottom water $\delta^{13}CDIC$ in the deep sub-Antarctic Atlantic, although it may be associated with a larger uncertainty than previously assumed. It remains to be shown which benthic foraminifer species is the most trustworthy in representing bottom water $\delta^{13}CDIC$ in particular in the sub-Antarctic Atlantic.

### Appendix A

*Cibicides wuellerstorfi* (Schwager), 1866

- *Anomalina wuellerstorfi* Schwager, 1866, p. 258, pl. 7, Figures 105 and 107.
- *Truncatulina wuellerstorfi* (Schwager) [Brady, 1884], p. 662, pl. 93, Figure 9.
- *Planulina wuellerstorfi* (Schwager) [Phleger and Parker, 1951], p. 33, pl. 18, Figure 11.
- *Planulina wuellerstorfi* (Schwager) [Phleger et al., 1953], p. 49, pl. 11, Figures 1 and 2.
- *Cibicides wuellerstorfi* (Schwager) [Parker, 1958], p. 275, pl. 4, Figures 41 and 42.
- *Cibicidoides wuellerstorfi* (Schwager) [Parker, 1964], pp. 624–625, pl. 100, Figure 29.
- *Cibicides wuellerstorfi* (Schwager) [Boltovskoy, 1978], pl. 3, Figures 19–21.
- *Planulina wuellerstorfi* (Schwager) [Corliss, 1979], pp. 7–8, pl. 2, Figures 13–16.
- *Cibicidoides wuellerstorfi* (Schwager) [Mead, 1985], pl. 6, Figures 1 and 2.
- *Planulina wuellerstorfi* (Schwager) [Van Morkhoven et al., 1986], pp. 48, 50, pl. 14, Figures 1 and 2.
- *Fontbotia wuellerstorfi* (Schwager) [Loeblich and Tappan, 1988], p. 583, pl. 634, Figures 10–12; pl. 635, Figures 1–3.
- *Planulina wuellerstorfi* (Schwager) [Corliss, 1991], pl. 1, Figures 1, 2, and 5.
- *Cibicides wuellerstorfi* (Schwager) [Gupta, 1994], pl. 5, Figures 8 and 9.
- *Cibicides wuellerstorfi* (Schwager) [Schweizer, 2006], pl. 11a–11l.
Cibicides kullenbergi Parker, 1953

- **Cibicides kullenbergi** Parker [Pfleger and Freirichs, 1953], p. 49, pl. 11, Figures 7 and 8.
- **Cibicides kullenbergi** Parker [Pfleger and Freirichs, 1976], pl. 2, Figures 6–8.
- **Cibicoides kullenbergi** (Parker) [Lohmann, 1978], p. 29, pl. 2, Figures 5–7.
- **Cibicoides kullenbergi** (Parker) [Corliss, 1979], p. 10, pl. 3, Figures 4–6.
- **Cibicoides cf. kullenbergi** (Parker) [Mead, 1985], p. 242, pl. 6, Figures 6a and 6b.
- **Cibicoides mundulus** (Brady, Parker, and Jones) [Loeblich and Tappan, 1988], p. 572, pl. 626, Figures 1–3.
- **Cibicoides kullenbergi** (Parker) [Corliss, 1991], pl. 1, Figures 6, 8, and 9.
- **Cibicides kullenbergi** Parker [Gupta, 1994], pl. 1, Figures 6, 8, and 9.
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Cipollini, L., and L. Booth for allowing access to a digital microscope for photographic purposes. This study greatly benefited from discussions with Lloyd Keigwin and participants of the rst meeting of the international Ocean Circulation and Carbon Cycling (OCC) project in Bern, Switzerland, in September 2014, which gave the inspiration for this paper. We are grateful to comments from three reviewers and the Editor Ellen Thomas that helped to improve the manuscript. This is LICE contribution 5597. All data accompanying this study are available from PANGAEA (doi.pangaea.de/10.1594/PANGAEA.861823).


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Paleoceanography 10.1002/2016PA003029


