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► **To cite this version:**

Julia Gottschalk, Luke C. Skinner, Samuel L. Jaccard, Laurie C. Menviel, Christoph Nehrbass-Ahles, et al.. Southern Ocean link between changes in atmospheric CO₂ levels and northern-hemisphere climate anomalies during the last two glacial periods. *Quaternary Science Reviews*, 2020, 230, pp.106067. 10.1016/j.quascirev.2019.106067 . hal-02407224

HAL Id: hal-02407224

<https://hal.science/hal-02407224>

Submitted on 30 Nov 2021

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1 **Southern Ocean link between changes in atmospheric CO₂ levels and northern-hemisphere cli-**
2 **mate anomalies during the last two glacial periods**

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14
15 **Abstract**

16 Past millennial-scale changes in atmospheric CO₂ (CO_{2,atm}) levels have often been attributed to varia-
17 tions in the overturning timescale of the ocean that result in changes in the marine carbon inventory.
18 There remains a paucity of proxy evidence that documents changes in marine carbon storage globally,
19 and that links them to distinct abrupt climate variability in the northern hemisphere that involve per-
20 turbations of the Atlantic Meridional Overturning Circulation (AMOC). The last two glacial periods
21 were suggested to differ in the spatial extent of the AMOC and its sensitivity to perturbations. This
22 provides an opportunity to study the nature of marine carbon cycling during these two climate inter-
23 vals. Here, we reconstruct variations in respired carbon storage (via oxygenation) and the AMOC ‘ge-
24 ometry’ (via carbonate ion saturation) in the deep South Atlantic. We infer decreases in deep South
25 Atlantic respired carbon levels at times of weakened AMOC and rising CO_{2,atm} concentrations during
26 both glacial periods. These findings suggest a consistent pattern of increased Southern Ocean convec-
27 tion and/or air-sea CO₂ fluxes during northern-hemisphere stadials accompanying AMOC perturba-
28 tions and promoting a rise in CO_{2,atm} levels. We find that net ocean carbon loss, and hence the magni-
29 tude of CO_{2,atm} rise, during a glacial is largely determined by the stadial duration. North Atlantic cli-
30 mate anomalies may therefore significantly affect Southern Ocean carbon cycling through oceanic
31 (e.g., ‘ventilation’ seesaw) and/or atmospheric processes (e.g., Ekman pumping). (250 words)

32
33 **Keywords:** Glacials; Paleoclimatology; Southern Ocean; Redox-sensitive elements; Carbon cycle;
34 Foraminifera; Dansgaard-Oeschger cycles; Atmospheric CO₂ variations; Stadials; Interstadials

35
36 **1. Introduction**

37 Changes in the concentration of CO₂ in the atmosphere (CO_{2,atm}) recorded in Antarctic ice cores have
38 been found to be tightly linked with Antarctic temperature-proxies over the past eight glacial-
39 interglacial cycles (e.g., Fischer et al., 2010). This link can be partly explained by the radiative forcing
40 imparted by CO_{2,atm} (i.e., the greenhouse effect; e.g., Köhler et al., 2017), and by the temperature de-
41 pendence of processes governing global ocean- and land-atmosphere CO₂ exchange, such as the ocean
42 CO₂ solubility (Bacastow, 1996; Bereiter et al., 2018), metabolic rates of plants and phytoplankton
43 (Eppley, 1972; Policy et al., 1993; Matsumoto, 2007) and organic carbon respiration rates in the ocean
44 (Matsumoto, 2007; Matsumoto et al., 2007; Kwon et al., 2009). However, this link is also thought to
45 rely on a variety of biogeochemical and hydrographic feedback mechanisms that affect the deep- and
46 surface ocean's total carbon- and alkalinity levels (e.g., Sigman and Boyle, 2000; Hain et al., 2010;
47 Cartapanis et al., 2018). The ocean's sizeable carbon reservoir exchanges with the atmosphere on cen-
48 tennial- to millennial timescales, in particular through vertical mixing and Ekman pumping in the
49 Southern Ocean (Primeau, 2005; Marinov et al., 2006; Gebbie and Huybers, 2011). Other potential
50 carbon sources/sinks that may have influenced CO_{2,atm} concentrations on these timescales include the
51 terrestrial biosphere (Köhler et al., 2005; Menviel et al., 2008; Bozbiyik et al., 2011), Arctic perma-
52 frost (Zech, 2012; Köhler et al., 2014; Tesi et al., 2016) and the mantle/lithosphere (Huybers and
53 Langmuir, 2009; Broecker et al., 2015; Lund et al., 2016). The Southern Ocean bears a strong leverage
54 on the efficiency of ocean-atmosphere gas exchange (i.e., the "ocean CO₂ solubility pump") and on the
55 global-ocean pre-formed versus respired nutrient ratio (i.e., the "soft-tissue/organic carbon pump"),
56 while also influencing global-ocean alkalinity (i.e., the "hard-tissue/carbonate pump"). The Southern
57 Ocean is therefore assumed to play a dominant role in past CO_{2,atm} changes (Sarmiento and
58 Toggweiler, 1984; Volk and Hoffert, 1985; Broecker et al., 1999; Sigman and Boyle, 2000; Ito and
59 Follows, 2005; Fischer et al., 2010; Hain et al., 2010; Sigman et al., 2010).

60

61 Proxy evidence from the Southern Ocean covering the last glacial cycle strongly supports this view.
62 The glacial Antarctic Zone of the Southern Ocean, south of the Polar Front (Fig. 1), has yielded proxy
63 evidence for reduced vertical mixing and stronger water column density stratification during peak
64 glacial periods, suggesting increased carbon sequestration from the atmosphere (e.g., François et al.,
65 1997; Skinner et al., 2010; Jaccard et al., 2013; Roberts et al., 2015; Studer et al., 2015). In addition,
66 an extended seasonal Antarctic sea ice zone during these intervals may have curbed air-sea gas ex-
67 change (Stephens and Keeling, 2000; Gersonde et al., 2003; Benz et al., 2016) and may have stimulat-
68 ed increased export production of organic carbon (Abelmann et al., 2015), both acting to further de-
69 crease CO_{2,atm}. In the sub-Antarctic Zone between the sub-Antarctic and sub-Tropical Front (Fig. 1),
70 enhanced supply of aeolian dust that may have alleviated iron-limitation imposed on phytoplankton
71 growth (Martin, 1990; Shoenfelt et al., 2018) has been shown to have led to increased carbon export
72 and CO_{2,atm} drawdown during the last peak glacial (Kumar et al., 1995; Ziegler et al., 2013; Anderson
73 et al., 2014a; Lamy et al., 2014; Martínez-García et al., 2014; Gottschalk et al., 2016b; Jaccard et al.,

74 2016). These biological and hydrographic conditions were suggested to have relaxed over the last de-
75 glaciation and during Antarctic warming intervals, reducing the biological export of carbon to the deep
76 ocean, and exposing the deep-ocean carbon reservoir to the atmosphere through enhanced vertical
77 mixing and air-sea gas exchange in the Southern Ocean, causing a rise of $\text{CO}_{2,\text{atm}}$ (e.g., Anderson et al.,
78 2009; Skinner et al., 2010, 2014; Gottschalk et al., 2016b; Jaccard et al., 2016; Ronge et al., 2016;
79 Sikes et al., 2016; Basak et al., 2018). In addition, these processes are thought to be closely connected
80 to North Atlantic climate and parallel perturbations in the AMOC (Sigman et al., 2007; Anderson and
81 Carr, 2010; Charles et al., 2010; Denton et al., 2010; Lee et al., 2011; Chiang et al., 2018). Specifical-
82 ly, CO_2 evasion from the Southern Ocean may have been promoted through a poleward shift and/or
83 intensifications of the southern-hemisphere westerlies (SHW) and an associated increase in Ekman
84 pumping (Toggweiler et al., 2006; Anderson et al., 2009; Denton et al., 2010; Lee et al., 2011), surface
85 buoyancy variations in the Southern Ocean (Watson and Naveira Garabato, 2006; Watson et al.,
86 2015), Antarctic sea ice retreat and/or the rejuvenation of Southern Ocean deep waters (Skinner et al.,
87 2010, i.e., a “bi-polar ventilation seesaw”; 2014). These scenarios highlight separate atmospheric and
88 oceanic pathways (though not mutually exclusive), by which northern-hemisphere climate variability
89 might affect the respired carbon budgets and marine carbon cycling in the Southern Ocean. Their rela-
90 tive contributions to $\text{CO}_{2,\text{atm}}$ change remain, however, unclear.

91

92 An important test of the classical view of a primary role of Southern Ocean processes in driving mil-
93 lennial-scale $\text{CO}_{2,\text{atm}}$ variations and their connection to North Atlantic climate anomalies gained from
94 proxy records of the last 70 kyr can be made by extending the analyses to older millennial-scale cli-
95 mate events. The penultimate glacial period, i.e., Marine Isotope Stage (MIS) 6, may prove particular-
96 ly useful for this undertaking, because MIS 6 was characterised by slightly different climatic condi-
97 tions compared to the last glacial period (i.e., MIS 3), in particular with respect to the extent of north-
98 ern-hemisphere ice sheets (Svendsen et al., 2004) and the strength of the hydrological cycle (Margari
99 et al., 2010). These differences have likely led to a weaker AMOC during MIS 6 that may be associat-
100 ed with lower-amplitude changes in Antarctic temperature (Margari et al., 2010). We hypothesize that
101 the sensitivity of the ocean carbon system to perturbations was likely different during both glacial
102 periods, and a comparison between the two may therefore provide important insights into the depend-
103 ency of respired carbon changes in the deep South Atlantic and $\text{CO}_{2,\text{atm}}$ variations to the nature, timing
104 and duration of North Atlantic climate events and overall glacial conditions.

105

106 Here, we assess and compare changes in respired carbon content in the Atlantic sector of the Southern
107 Ocean and the AMOC ‘geometry’ during the last two glacial periods based on sub-Antarctic Atlantic
108 sediment cores MD07-3076Q (14.20°W, 44.10°S, 3777 m water depth) and MD07-3077 (14.23°W,
109 44.15°S, 3776 m water depth). Respired carbon changes are derived from qualitative and quantitative
110 estimates of bottom water oxygen concentrations ($[\text{O}_2]$) variations, which are reflected in the enrich-

111 ment of redox-sensitive elements in foraminiferal authigenic coatings and epibenthic-to-deep infaunal
112 foraminiferal $\delta^{13}\text{C}$ gradients. Reconstructions of AMOC changes are based on partial sedimentary
113 dissolution proxies that track variations in bottom water carbonate ion saturation. These proxies are
114 sensitive to the presence of northern-sourced (oversaturated) and southern-sourced (undersaturated)
115 water masses, as well as water mass end-member changes, at our study site (Gottschalk et al., 2015a).
116 Additional analyses of past changes in local productivity approximated by determinations of the sedi-
117 mentary opal content (e.g., Anderson et al., 2014a) and cryosphere dynamics based on the abundance
118 of ice-rafted debris (IRD; e.g., Kanfoush et al., 2000; Nielsen et al., 2007) help to assess the roles of
119 ocean biology and sea ice/icebergs in Southern Ocean carbon cycle dynamics, respectively.

120

121 **2. Study area**

122 Sediment cores MD07-3076Q and MD07-3077 were retrieved from the eastern flank of the Mid-
123 Atlantic Ocean Ridge and are located within the sub-Antarctic Zone of the Atlantic sector of the
124 Southern Ocean (Fig. 1). The cores were collected at the same site using different coring techniques,
125 i.e., by square kasten- and piston coring, respectively. With a length of 10.9 m, MD07-3076Q covers
126 the last ~ 100 kyr, while its sister core MD07-3077 has a length of 49.5 m and extends back to 450 kyr
127 before present (BP) (Vázquez Riveiros et al., 2010). Analyses for MIS 3 are therefore based on core
128 MD07-3076Q, while those for MIS 6 are based on MD07-3077.

129

130 The core sites are currently bathed in Lower Circumpolar Deep Water (LCDW), which is a mixture of
131 DIC-rich and $[\text{CO}_3^{2-}]$ -low Antarctic Bottom Water (AABW), derivatives of DIC-rich and low- $[\text{CO}_3^{2-}]$
132 Indian and Pacific Deep Water and DIC-low and high- $[\text{CO}_3^{2-}]$ North Atlantic Deep Water (NADW)
133 (Carter et al., 2009; Talley, 2013). Our site is characterised by slight carbonate (i.e. calcite) oversatura-
134 tion ($\Omega = [\text{CO}_3^{2-}]_{\text{in-situ}} / [\text{CO}_3^{2-}]_{\text{saturated}} = 1.09$), but is proximal to carbonate-undersaturated water masses
135 located deeper in the South Atlantic water column. It is therefore sensitive to changes in the prepon-
136 derance of high- $[\text{CO}_3^{2-}]$ NADW and low- $[\text{CO}_3^{2-}]$ AABW in the deep South Atlantic through associat-
137 ed changes in carbonate saturation at the core site (Gottschalk et al., 2015a). The modern $[\text{O}_2]$ at our
138 core site is $215 \mu\text{mol kg}^{-1}$ (Garcia et al., 2010).

139

140 **3. Methods**

141 **3.1. Respired carbon levels**

142 Respired carbon levels are directly linked to apparent oxygenation utilization (AOU) in the ocean,
143 which reflects the drawdown of O_2 due to the respiration of organic matter (Kroopnick, 1985; Jaccard
144 et al., 2014; Galbraith and Jaccard, 2015). AOU changes were suggested to be the main driver of deep-
145 ocean $[\text{O}_2]$ changes, because $[\text{O}_2]$ saturation in the surface- and deep ocean varied little over glacial-
146 interglacial timescales (Jaccard and Galbraith, 2012; Galbraith and Jaccard, 2015). We therefore re-
147 construct bottom water $[\text{O}_2]$ to assess respired carbon changes during the last two glacial periods using

148 the two following independent approaches in order to circumvent potential limitations and biases that
149 may come with the analysis of a single proxy.

150

151 **3.1.1. Uranium enrichment in foraminiferal coatings**

152 The enrichment of uranium (U) in marine sediments is mainly a result of reducing conditions in pore
153 waters of marine sub-surficial sediments (Anderson et al., 1989; Barnes and Cochran, 1990;
154 Klinkhammer and Palmer, 1991; Morford and Emerson, 1999; McManus et al., 2006; Tribovillard et
155 al., 2006). Most of the soluble uranyl (U^{VI}) carbonate ions that are reduced to insoluble uraninite (U^{IV}
156 or U^{III}) under oxygen-depleted conditions in pore waters diffuse from the water column into the sedi-
157 ment (Barnes and Cochran, 1990; Klinkhammer and Palmer, 1991; Morford and Emerson, 1999;
158 Zheng et al., 2002). Uraninite precipitates on any substrate within marine sediments, including detrital
159 material and carbonate shells of foraminiferal tests, resulting in a co-variation of authigenic U levels of
160 bulk sediments and foraminiferal coatings (Boiteau et al., 2012; Chen et al., 2017).

161

162 Owing to the very low U concentrations within the carbonate lattice of foraminiferal shells ($< \sim 20$
163 $nmol\ mol^{-1}$) (Russell et al., 2004; Yu and Elderfield, 2007; Yu et al., 2008; Raitzsch et al., 2011) com-
164 pared to those measured on non-reductively cleaned bulk (carbonate lattice and authigenic coating)
165 foraminiferal shells (up to $700\ nmol\ mol^{-1}$) (Boiteau et al., 2012; Gottschalk et al., 2016b; Lear et al.,
166 2016), the U/Ca ratio of bulk foraminifera obtained by inductively coupled plasma-mass spectrometry
167 (ICP-MS) are dominated by U/Ca ratios of authigenic coatings. As the thickness of the shells and the
168 size of the foraminifera may have varied over time (Barker and Elderfield, 2002) and may have had an
169 impact on foraminiferal U/Ca ratios, it was suggested that normalization to manganese (Mn) might
170 alleviate morphological biases (Gottschalk et al., 2016b). Under oxic conditions, Mn(II) is oxidised
171 and precipitates as insoluble Mn(IV) or Mn(III) oxyhydroxides (Calvert and Pedersen, 1996). Under
172 reducing conditions, these Mn oxides dissolve releasing Mn(II) that may be precipitated as Mn-
173 carbonates below the anoxic boundary, or diffuse upward to the oxic zone, where it can be recycled
174 (Froelich et al., 1979; Tribovillard et al., 2006). As foraminiferal tests in marine sediments act as a
175 nucleus for the accumulation of both solid U- and Mn-phases, they were found to accumulate as in
176 coatings inside and/or outside of the foraminiferal shell (Pena et al., 2005, 2008; Hasenfratz et al.,
177 2016; Detlef et al., 2019). Foraminiferal U/Mn ratios, along with U/Ca ratios (Boiteau et al., 2012),
178 were hence suggested to be sensitive to and indicative of changes in bottom water oxygenation in ma-
179 rine sediments (Gottschalk et al., 2016b; Chen et al., 2017; Detlef et al., 2019).

180

181 However, Chen et al. (2017) do not find a close relationship between core-top epibenthic foraminiferal
182 U/Mn ratios and bottom water $[O_2]$. This may not be surprising, because the redox-cycling of U was
183 suggested to be closely linked to that of Fe (Barnes and Cochran, 1990; Zheng et al., 2002), and hence
184 occurs a few centimeters below the sediment-water interface, and may thus not be recorded by core-

185 top foraminifera. This becomes evident in the tandem analyses of planktonic foraminiferal coatings
186 and pore-waters in multi-cores from a well-oxygenated setting performed by Skinner et al. (2019),
187 which show that foraminiferal Mn/Ca ratios track the pore-water Mn^{2+} concentration (with enrichment
188 of both below the anoxic boundary), while foraminiferal U/Ca ratios track the loss of U from pore-
189 waters through precipitation of U-compounds in oxygen-depleted sub-surface sediments (slightly low-
190 er than the zone of Mn accumulation). These findings emphasise a separation of early diagenetic reac-
191 tions involving U and Mn in sub-surface sediments (Froelich et al., 1979). This is consistent with find-
192 ings of Detlef et al. (2019), who observe a *correlation* of foraminiferal U/Ca and Mn/Ca ratios in the
193 Bering Sea, suggesting the accumulation of Mn in authigenic or recrystallized carbonate phases in
194 foraminiferal coatings, possibly under anoxic conditions. The authors suggest that the increase in U
195 accumulation over Mn accumulation in foraminiferal coatings in this setting is proportional to diage-
196 netic alteration, and hence possibly dependent on bottom water $[O_2]$ conditions. In contrast, Boiteau et
197 al. (2012) show an *anticorrelation* of foraminiferal U/Ca and Mn/Ca in foraminiferal samples from the
198 Southeast Atlantic, emphasising different oxic and anoxic pathways of diagenetic precipitation of solid
199 U- and Mn-phases. Further investigation is needed to fully understand the mechanisms driving the
200 U/Mn proxy. Nonetheless, despite the different processes driving U- and Mn precipitation on forami-
201 niferal shell, there is a strong connection to redox-chemical cycling in sub-marine sediments that is in
202 turn tightly coupled to the availability of oxygen in bottom waters (Boiteau et al., 2012; Gottschalk et
203 al., 2016b; Chen et al., 2017; Detlef et al., 2019; Skinner et al., 2019). In our study, we analyse the U
204 enrichment in authigenic coatings on several foraminiferal species, and report the associated U/Ca and
205 U/Mn ratios.

206

207 The foraminiferal record of redox-sensitive elements may be influenced by post-depositional deepening
208 of the anoxic boundary, which may cause precipitated U compounds to be oxidised leading to a
209 "burn-down" effect (Zheng et al., 2002; Kasten et al., 2003; McManus et al., 2005). As we find high
210 sedimentation rates of 10 to 15 cm kyr⁻¹ during MIS 3 and 6, we assume that the observed U/Ca and
211 U/Mn ratios represent signals that mostly formed in equilibrium with bottom waters, with little over-
212 prints from non-steady state processes. We argue that the temporal offset between our redox-sensitive
213 proxy changes and contemporaneous shifts in other foraminiferal proxies during past glacials is lim-
214 ited to a maximum of 500–1000 yr, assuming that oxygen penetration depths into sub-surface sedi-
215 ments were of the order of ~5–7 cm or lower during past glacials. This is supported by a good agree-
216 ment of foraminiferal U/Ca and U/Mn ratios with other bottom water oxygenation proxies and ventila-
217 tion age changes over the last glacial cycle at the core site (Gottschalk et al., 2016b; Skinner et al.,
218 2019).

219

220 U/Ca- and U/Mn analyses were performed on the planktonic foraminifer *Globigerina bulloides* (20-30
221 specimens; 250-300 μm size fraction) and *Globorotalia inflata* (20-30 specimens; >212 μm size frac-

222 tion) for MIS 6 and Termination (T) II, and on *G. bulloides* (20-30 specimens; 250-300 μm size frac-
223 tion) and the benthic foraminifer *Uvigerina* spp. (5-15 specimens; 250-300 μm size fraction) for MIS
224 3 and TI. Prior to ICP-MS analyses, the foraminiferal samples were cleaned by clay removal and sili-
225 cate picking (Barker et al., 2003; Boiteau et al., 2012). The reproducibility of U/Ca and U/Mn ratios of
226 replicate samples is within 30 nmol mol^{-1} and 0.08 mmol mol^{-1} ($n=6$) (1σ), respectively.

227

228 **3.1.2. Epibenthic-deep infaunal foraminiferal $\delta^{13}\text{C}$ gradients**

229 The benthic foraminifer *Globobulimina affinis* is thought to actively migrate towards the low-oxygen
230 microhabitat near or at the anoxic boundary within marine sub-surface sediments (Geslin et al., 2004),
231 and has therefore a deep infaunal habitat (Corliss and Emerson, 1990; McCorkle et al., 1990). The
232 $\delta^{13}\text{C}$ offset of *G. affinis* from bottom water (i.e., from the supposedly epibenthic foraminifer *Cibi-*
233 *cidoides kullenbergi*), $\Delta\delta^{13}\text{C}_{\text{Ck-Ga}}$, has been proposed to record the depletion of pore water $\delta^{13}\text{C}$ due to
234 organic carbon respiration. This is thought to be controlled by bottom water oxygen diffusion into the
235 sediment that is a function of bottom water $[\text{O}_2]$ itself (McCorkle and Emerson, 1988; McCorkle et al.,
236 1990; Hoogakker et al., 2015). We use the $\Delta\delta^{13}\text{C}$ -bottom water $[\text{O}_2]$ calibration of Hoogakker et al.
237 (2015) to obtain quantitative estimates of bottom water $[\text{O}_2]$ at our core sites during the past two gla-
238 cial periods.

239

240 We have performed stable isotopic analyses on *G. affinis* (*Ga*) and *C. kullenbergi* (*Ck*) on one to four
241 specimens of the $>150 \mu\text{m}$ size fraction. The analysed *Ck* specimens refer to the *sensu lato*-
242 morphotype as illustrated in Gottschalk et al. (2016a). The samples were measured on Finnigan $\Delta+$
243 and Elementar Isoprime mass spectrometers at the LSCE in Gif-sur-Yvette (France). Prior to the anal-
244 yses, foraminifera were rinsed with methanol, ultrasonicated for 10 s, dried at room temperature, and
245 finally roasted under vacuum at $\sim 380^\circ\text{C}$ for 45 min to remove contaminant organic phases or detritus.

246

247 The oxygen and carbon isotopic shell composition is expressed as $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ in ‰ versus Vienna
248 Pee Dee Belemnite (VPDB). VPDB is defined with respect to the National Bureau of Standards
249 (NBS)-19 calcite standard ($\delta^{18}\text{O} = -2.20$ ‰ and $\delta^{13}\text{C} = +1.95$ ‰) (Coplen, 1988). The mean external
250 reproducibility of our carbonate standards is $\sigma=0.05$ ‰ ($\delta^{18}\text{O}$) and $\sigma=0.03$ ‰ ($\delta^{13}\text{C}$), and the measured
251 NBS-18 $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ values are -23.2 ± 0.2 ‰ VPDB and -5.0 ± 0.1 ‰ VPDB, respectively.

252

253 **3.2. Deep South Atlantic carbonate ion saturation as an indicator of the Atlantic overturning** 254 **‘geometry’**

255 Partial sedimentary dissolution proxies, such as the benthic-to-planktonic (Be/Pl) foraminiferal ratio,
256 planktonic foraminifer abundances or the planktonic foraminiferal fragmentation, are sensitive to the
257 carbonate saturation (i.e., corrosiveness) of deep South Atlantic bottom waters (Barker and Diz, 2014;
258 Gottschalk et al., 2015a, 2018). We have normalised and averaged these three proxy records from our

259 study sites for each glacial period in order to obtain the ‘carbonate saturation index’ (Gottschalk et al.,
260 2015a). This index qualitatively reflects changes in carbonate saturation at our study site, which is
261 mainly driven by the southward advance of high-[CO₃²⁻] NADW (Gottschalk et al., 2015a). However,
262 given nonlinearities of processes affecting this proxy (such as changes in water mass end-members,
263 local sedimentation rate and sediment porosity) it does not reflect changes in the strength of the AM-
264 OC, in particular during different time intervals.

265
266 Be/Pl ratios, planktonic foraminifer abundances and the foraminifer fragmentation were determined by
267 sedimentary census counts of a sample aliquot of the >150 µm-fraction (CLIMAP project members,
268 1984). At least 300 planktonic foraminifera were counted for each sample, which also allowed an es-
269 timation of sea surface temperature (SST) changes at the core site based on planktonic foraminiferal
270 assemblages and the Southern Ocean calibration of Haddam et al. (2016). The abundance of plankton-
271 ic foraminifera is expressed as number per gram dry bulk sediment (>150 µm), while the fragmenta-
272 tion represents the percent fraction of planktonic foraminifer fragments (when larger than half a bro-
273 ken shell) of the total abundance of planktonic foraminifera and fragments. The reproducibility of
274 reported planktonic foraminifer abundances, planktonic foraminifer fragmentation and the Be/Pl ratio
275 has been inferred from 15 duplicate counts, and amounts to (1σ=) 6000 g⁻¹, 1.9% and 0.014, respec-
276 tively.

277

278 **3.3. Opal as an indicator for export production**

279 The sedimentary biogenic silica (opal) content in our study cores was quantified by Fourier Transform
280 Infrared Spectroscopy (FTIRS; Vogel et al., 2016) using a Vertex 70 FTIR-spectrometer (Bruker Op-
281 tics Inc.) at the University of Bern. Repeating the analyses of parts of the record in MIS 3 and MIS 6
282 indicate the robustness of relative changes in sedimentary opal. However, absolute values may differ
283 from wet-chemical opal analyses during MIS 3 (Gottschalk et al., 2016b) and by 4.5±1.6 % (n=55)
284 across different FTIRS sample batches during MIS 6 (Supplementary Fig. S1). This may be associated
285 with a bias related to increased water content of marine samples on FTIR spectra (Vogel et al., 2016)
286 that we were not able to eliminate entirely from the samples despite several precautionary measures.
287 Because absorbed water in the samples biases the opal content towards higher values, we have cor-
288 rected all individual datasets onto those opal records with the lowest absolute values (based on calcu-
289 lated offsets in overlapping sections, Supplementary Fig. S1).

290

291 **3.4. Ice-rafted detritus as an indicator of sea ice and/or iceberg export**

292 The abundance of IRD was assessed alongside the census counts of fragmented shells and planktonic
293 and benthic foraminifera (see section 3.2. above). It is reported as percentage with respect to the total
294 number of sediment grains (including foraminifera and fragments). The reproducibility of estimated
295 IRD percentages is within 1.5% (1σ, n=15).

296

297 3.5. Chronology

298 Chronological control of sediment core MD07-3076Q younger than 27 kyr BP is based on calibrated
299 radiocarbon ages of mono-specific planktonic foraminifera samples, which have been adjusted for
300 variations in surface ocean reservoir ages (Skinner et al., 2010). The age models of cores MD07-
301 3076Q (i.e., for MIS 3) and MD07-3077 (i.e., for TII and MIS 6) are based on a stratigraphic align-
302 ment of abundance peaks of *G. bulloides* with maxima in Antarctica air-temperature, represented by
303 peaks of the EPICA (European Project for Ice Coring in Antarctica) Dome C (EDC) δD Antarctic ice-
304 core record (Jouzel et al., 2007) (Fig. 2). This approach assumes that temperature-sensitive *G.*
305 *bulloides* abundance variations at our South Atlantic core site and Antarctic air-temperatures (at EDC)
306 co-vary. We therefore take the age model for >27 kyr BP for our core site from a previous study that
307 used this approach (Channell et al., 2017) with minor revision of three tiepoints during MIS 6 (encir-
308 cled symbols in Fig. 2a), in order to produce a better match of *G. bulloides* variations with Antarctica
309 air-temperature (The depths of two of these tiepoints (174.6 and 177.4 kyr) were shifted 20 cm to-
310 wards the top of the core, and the tiepoint at ~2490 cm was shifted by 1 kyr towards older ages). Our
311 simple approach is consistent with another age model approach that has been applied to study millen-
312 nial-scale variability at our core site based on the first time derivative of EDC δD , as demonstrated in
313 Gottschalk et al. (2015a). During Termination II, we use the age control points of Gottschalk et al.
314 (2016a) that are based on an alignment of abundance variations of *Neogloboquadrina pachyderma*
315 with EDC δD . Although this age model approach may deviate from one based on *G. bulloides* abun-
316 dance variations (cf. Fig. 2), these age uncertainties are not relevant for the objectives of this paper.

317

318 Resulting sedimentation rates range between 5 cm kyr⁻¹ during the last deglaciation and 15 cm kyr⁻¹
319 during MIS 3 and MIS 6 (Fig. 2). We apply a 700 yr ad-hoc-error for each of our planktonic abun-
320 dance-based tiepoints (not considering absolute age uncertainties of the EDC chronology of up to 2400
321 yr in MIS 3 and 3000 yr in MIS 6), which translates into a relative age uncertainty of 1700±500 yr
322 during MIS 3 and 1800±800 yr during MIS 6 and TII with respect to the Antarctic AICC2012 ice age
323 scale (Bazin et al., 2013; Veres et al., 2013). These age uncertainties were estimated based on Monte
324 Carlo simulations with the Bayesian software package Bchron (Haslett and Parnell, 2008), and consid-
325 er potential sedimentation rate changes in between our selected tiepoints. Although the millennial-
326 scale accuracy of our age model is limited, circumstantial support for our age model alignment comes
327 from benthic (*Cibicidoides* sp.) $\delta^{18}O$ analyses. During both MIS 3 and MIS 6, we observe a good
328 agreement on millennial time scales between the benthic $\delta^{18}O$ records at our sub-Antarctic Atlantic
329 site and sediment core MD01-2444 from the Iberian margin in the North Atlantic (Skinner et al., 2007;
330 Fig. 2; 2.6 km water depth, Margari et al., 2010), although both records are on entirely independent
331 agescales. Benthic $\delta^{18}O$ records are not per se expected to co-vary in the Atlantic (given the finite
332 timescale of transport/mixing in the ocean, e.g., Skinner and Shackleton, 2005). However, the fact that

333 they broadly parallel each other during *both* glacial intervals lends credibility to our chronostratigra-
334 phy.

335

336 **3.6. Antarctic ice core CO_{2,atm} data**

337 In order to evaluate the possible influence of changes in deep ocean respired carbon change at our
338 study sites on CO_{2,atm}, we compare available high-resolution CO_{2,atm} records (Bereiter et al., 2015) with
339 our marine proxy data on millennial timescales. The mean temporal resolution of the available ice core
340 CO_{2,atm} data covering MIS 3 (~160±130 yr, *n*=279) (Bereiter et al., 2012; Ahn and Brook, 2014) is
341 much higher than during MIS 6 (~1400±700 yr, *n*=45) (Petit et al., 1999; Schneider et al., 2013), ren-
342 dering a comparison of the CO_{2,atm} variability during MIS 6 to our centennially resolved (220±70 yr,
343 *n*=220) proxy data problematic. In order to circumvent this potential limitation, millennial-scale
344 CO_{2,atm} variations may be predicted by taking advantage of the tight relationship between the Antarctic
345 temperature proxy δD and CO_{2,atm} (Petit et al., 1999; Fischer et al., 2010). We obtain a linear regres-
346 sion between EDC δD (smoothed by a 500 yr-running average; Jouzel et al., 2007) and CO_{2,atm} during
347 MIS 3 (63-32 kyr BP) and MIS 6 (184-134.5 kyr BP) using the compilation of Bereiter et al. (2015)
348 (Fig. 3). Our MIS 3 regression shows a correlation coefficient of $R^2=0.64$ ($p<0.05$), whereas R^2 for the
349 MIS 6 regression is lower ($R^2=0.41$, $p<0.05$, excluding two outliers; Fig. 3). Both are statistically sig-
350 nificant. The resulting 2σ-uncertainty of the predicted CO_{2,atm} (hereafter referred to as CO_{2,atm}-PRED) is
351 10 ppm and 12 ppm, respectively (Fig. 3). Given the low resolution of CO_{2,atm} data during MIS 6 (Petit
352 et al., 1999; Bereiter et al., 2015), we consider our predicted MIS 6 CO_{2,atm} data as a reasonable first-
353 order approximation of true CO_{2,atm} variability during that time period. However, high-resolution
354 CO_{2,atm} data from Antarctic ice cores during MIS 6 are needed to test the reliability of this approach.

355

356 **4. Results**

357 **4.1. Changes in bottom water oxygenation**

358 We observe systematic change in the enrichment of uranium in authigenic coatings of foraminifera
359 with past variations in Antarctic temperature and CO_{2,atm} (Fig. 4). Bulk foraminifer U/Mn- and U/Ca
360 ratios closely resemble each other both during MIS 3 and MIS 6 (Supplementary Fig. S2). If forami-
361 niferal coating U and Mn enrichment is primarily driven by precipitation under anoxic versus oxic
362 conditions (uraninite and Mn-oxides), respectively, bulk foraminifer U/Ca- and Mn/Ca ratios are ex-
363 pected to anti-correlate (Boiteau et al., 2012). If their enrichment occurs below the anoxic boundary,
364 they are expected to correlate with one another (Detlef et al., 2019; Skinner et al., 2019). U/Ca- and
365 Mn/Ca ratios of our planktonic foraminifer samples show a statistically significant positive regression
366 slope (*G. bulloides*: *n*=96; *G. inflata*: *n*=237; Supplementary Fig. S2), suggesting that they were gov-
367 erned by similar processes. In contrast, *Uvigerina* spp. do not show a strong relationship between U
368 and Mn enrichment (if at all a slight anti-correlation), potentially highlighting the opposing redox-
369 behaviour of these two elements. However, irrespective of whether Mn/Ca and U/Ca are correlated or

370 anti-correlated, relative changes in the foraminiferal U/Ca- and U/Mn ratios agree (Supplementary Fig.
371 S2), suggesting that the redox-sensitive U precipitation is the main control of the observed changes in
372 foraminiferal U/Ca- and U/Mn ratios.

373

374 During MIS 3 and TI, *G. bulloides* and *Uvigerina* spp. U/Mn ratios and the $\delta^{13}\text{C}_{\text{Ck-Ga}}$ gradient show
375 marked variations during strong Antarctic warming events (AIM 8, 12, 14, 16/17), as well as during
376 the more subdued AIM 6 and 7 (*sensu* EPICA Community Members 2006; Fig. 4, 5). Both bottom
377 water oxygenation records parallel changes in $\text{CO}_{2,\text{atm}}$ levels, indicating oxygen-rich bottom waters in
378 the deep sub-Antarctic Atlantic during rising $\text{CO}_{2,\text{atm}}$, and vice versa (Fig. 4, 5). The relative change in
379 *G. bulloides* and *Uvigerina* spp. U/Mn levels correlates with the magnitude of parallel $\text{CO}_{2,\text{atm}}$ varia-
380 tions (Fig. 6a). During the penultimate glacial period (e.g., AIM 6vi to i), changes in *G. inflata* U/Mn
381 ratios are similar to Antarctic temperature variations (*sensu* Margari et al. 2010; Fig. 4, 5). Decreases
382 in *G. inflata* U/Mn levels during Antarctic warming events coincide with predicted increases in $\text{CO}_{2,\text{atm}}$
383 during MIS 6 (Fig. 4, 5).

384

385 To specify, we estimated the maximum magnitude of foraminiferal U/Mn change during intervals of
386 Antarctic warming as given in Margari et al. (2010) and link that with maximum parallel rise in
387 $\text{CO}_{2,\text{atm}}$ that we consider to be associated with it (Fig. 5). These intervals do not necessarily fully agree.
388 In fact, during intervals DO14, DO16/17, 6iv and 6ii, the U/Mn maximum occurs slightly later than
389 the onset of Antarctic warming (Fig. 5f). Similarly, intervals of rising $\text{CO}_{2,\text{atm}}$ levels during MIS 3
390 (e.g., DO14 and DO16/17) may last slightly longer than the period of rising temperatures over Antarc-
391 tica (Fig. 5g). We find that the relationship between the two agrees during both glacial periods (Fig.
392 6a).

393

394 Distinct excursions of *G. affinis* $\delta^{13}\text{C}$ from *C. kullenbergi* $\delta^{13}\text{C}$ during MIS 3 (Supplementary Fig. S3)
395 indicate that bottom water $[\text{O}_2]$ change in parallel with variations in foraminiferal U/Mn amounts to
396 $110\pm 50 \mu\text{mol kg}^{-1}$ on average (Fig. 4; Gottschalk et al., 2016b). Although the U/Mn proxy seems to
397 provide the most consistent pattern of variability between the two glacials, its agreement with $\Delta\delta^{13}\text{C}_{\text{Ck-}}$
398 Ga -based bottom water $[\text{O}_2]$ variations is poor (Fig. 4). As the $\Delta\delta^{13}\text{C}_{\text{Ck-Ga}}$ proxy is based on the *aerobic*
399 respiration of organic matter in marine sub-surface sediments, one can surmise that strong carbon
400 fluxes to the sea floor may have caused *anaerobic* organic matter degradation in sub-surface sediments
401 to severely bias the proxy. This might have been the case during MIS 6, but not during MIS 3. Fur-
402 thermore, the $\Delta\delta^{13}\text{C}_{\text{Ck-Ga}}$ proxy relies on an accurate representation of pore-water $\delta^{13}\text{C}$ at the anoxic
403 boundary in sub-surface sediments via the deep-infaunal benthic foraminifera *G. affinis*, and of bottom
404 water $\delta^{13}\text{C}$ levels in bottom waters by the benthic foraminifer *C. kullenbergi*. Either or both of these
405 conditions might not have been met during MIS 6: firstly, *Globobulimina* species and other deep in-
406 faunal benthic foraminifera were shown to be capable of denitrification, and can hence thrive signifi-

407 cantly below the anoxic boundary, where pore water $\delta^{13}\text{C}$ is reduced independently of $[\text{O}_2]$ (Risgaard-
408 Petersen et al., 2006; Piña-Ochoa et al., 2010; Glock et al., 2019); and secondly, *C. kullenbergi* was
409 suggested to thrive and possibly prefer slightly infaunal habitats with lower $\delta^{13}\text{C}$ than in bottom waters
410 (Gottschalk et al., 2016a). Along with large intra-species $\delta^{13}\text{C}$ variability and potential vital effects of
411 both benthic foraminifer species, as well as carbonate dissolution changing the pore-water $\delta^{13}\text{C}$ gradi-
412 ent, these processes may have conspired to cause an insensitivity of the $\Delta\delta^{13}\text{C}$ proxy to bottom water
413 $[\text{O}_2]$ changes during MIS 6. The discrepancy of our MIS 6 $\Delta\delta^{13}\text{C}_{Ck-Ga}$ data underlines possible differ-
414 ences in glacial climate background conditions but also emphasizes the need for further work investi-
415 gating the controls on both the $\Delta\delta^{13}\text{C}_{Ck-Ga}$ and U/Mn redox proxies under a wide range of depositional
416 and hydrographic settings.

417

418 **4.2. Changes in the carbonate saturation state of the deep sub-Antarctic Atlantic Ocean**

419 The carbonate saturation index (and all individual partial sedimentary dissolution proxies; Supplemen-
420 tary Fig. S4) exhibits several minima during MIS 3 and MIS 6 that indicate the presence of corrosive
421 bottom waters in the deep sub-Antarctic Atlantic, likely of southern origin (Fig. 5; Gottschalk et al.,
422 2015a). This is also consistent with quantitative bottom water $[\text{CO}_3^{2-}]$ variations at the study site dur-
423 ing MIS 3 (Supplementary Fig. S4; Gottschalk et al., 2015a). The saturation index minima are paral-
424 leled by gradually decreasing foraminiferal U/Mn ratios (Fig. 5), and coincides with minima in epiben-
425 thic foraminiferal $\delta^{13}\text{C}$ at the deep Iberian Margin (Fig. 7; Skinner et al., 2007; Margari et al., 2010).
426 The duration of northern-hemisphere stadials was suggested to be expressed in the length of parallel
427 Antarctic warming (Margari et al., 2010). By construction, SST at the core site closely varies with
428 Antarctic temperature, and we hence compare the duration of Antarctic warming, i.e. the length of
429 northern-hemisphere stadials, with the maximum amplitude of foraminiferal U/Mn change that we
430 consider to be associated with it (Fig. 5; Margari et al., 2010). We find that the magnitude of change in
431 foraminiferal U/Mn ratios during both glacial periods linearly correlates with the duration of northern-
432 hemisphere stadial conditions, in a similar fashion (Fig. 6b).

433

434 The presence of corrosive bottom waters at our core site (i.e., low saturation indices) also parallels
435 intervals of rising $\text{CO}_{2,\text{atm}}$ levels (Fig. 5). Relying on MIS 6 $\text{CO}_{2,\text{atm-PRED}}$ levels and ice core observa-
436 tions during MIS 3 (Bereiter et al., 2015), we observe a good correlation between the duration of these
437 stadials and the magnitude of concomitant $\text{CO}_{2,\text{atm}}$ increase (Fig. 6c). No significant difference in the
438 relationship between the two parameters during MIS 3 and MIS 6 can be identified (Fig. 6c).

439

440 **4.3. Changes in opal percentages**

441 During MIS 3 and TI, changes in sedimentary opal percentages in MD07-3076Q broadly co-vary with
442 EDC dust fluxes (Fig. 4; Gottschalk et al., 2016b). This relationship could suggest an influence of
443 aeolian dust-driven iron fertilization on nutrient utilization and export production in the sub-Antarctic

444 Zone during the last glacial period (Martin, 1990; Anderson et al., 2014b; Lamy et al., 2014; Martínez-
445 García et al., 2014; Gottschalk et al., 2016b). In contrast, during MIS 6 and TII, the link between opal
446 percentages and EDC dust variations is rather poor on millennial timescales, and significant offsets
447 exist between changes in the sedimentary opal content at our study site and the EDC dust flux record
448 (Fig. 4).

449

450 **4.4 Ice-rafted debris**

451 The abundance of IRD in our study core during the first half of MIS 3 is low but progressively in-
452 creases towards the end of MIS 3, with pronounced peaks during North Atlantic stadials, and periods
453 of Antarctic warming (Fig. 7). IRD percentages were generally higher during MIS 6 than during MIS
454 3, and show a more distinct response during stadials (Fig. 7). Kanfoush et al. (2000) interpreted IRD
455 peaks in the South Atlantic as indication of significant iceberg fluxes to the South Atlantic. In contrast,
456 Nielsen et al. (2007) highlighted that a large proportion of the IRD material in the South Atlantic iden-
457 tified by Kanfoush et al. (2000) was likely transported from the South Sandwich and Bouvet Islands
458 via sea ice.

459

460 **5. Discussion**

461 **5.1. Changes in deep South Atlantic carbon sequestration during the last two glacial periods**

462 Our foraminiferal U/Mn records spanning MIS 3 and MIS 6 indicate increases in bottom water oxy-
463 genation in the deep South Atlantic during North Atlantic stadials (only partly supported by the
464 $\Delta\delta^{13}\text{C}_{\text{Ga-Ck}}$ – bottom water $[\text{O}_2]$ proxy in MIS 6), which indicate changes in the respired carbon content
465 of the deep South Atlantic (Gottschalk et al., 2016b; this study). During MIS 3, these occur in parallel
466 to reductions in the sedimentary opal content, rising SSTs and increased ice-rafting/-export (Fig. 5;
467 Gottschalk et al., 2016b; this study). This also applies to MIS 6, with the exception of distinct offsets
468 between variations in opal, Antarctic dust fluxes and deep South Atlantic bottom water oxygen chang-
469 es (Fig. 4).

470

471 In MIS 3, variations in the degree of iron fertilization via aeolian dust supply were suggested to con-
472 trol export production, and hence opal fluxes, in the sub-Antarctic Atlantic (Anderson et al., 2014a;
473 Martínez-García et al., 2014), contributing to millennial-scale bottom water oxygen and respired car-
474 bon changes at depth (Gottschalk et al., 2016b). However, whether the same mechanism operated dur-
475 ing MIS 6 remains ambiguous (Fig. 4). The observed offsets may be caused by sediment winnowing
476 or -focussing, or sedimentary opal percentages may in fact poorly represent annually integrated export
477 production (of all taxonomic groups) in the sub-Antarctic Atlantic. Indeed, the opal content in marine
478 sediments was shown to be influenced by the availability of silicic acid, Antarctic sea ice extent, eco-
479 system structures and the degree of diatom silicification causing variable Si:C ratios of exported mate-
480 rial (Chase et al., 2015). Irrespective of whether our opal in MIS 6 faithfully records export produc-

481 tion, we argue based on our proxy records and earlier findings (Gottschalk et al., 2016b) that increased
482 oxygen levels and decreased respired carbon content in the deep South Atlantic during intervals of
483 Antarctic warming did not occur without the contribution from increased ventilation of the deep
484 Southern Ocean (e.g., Skinner et al., 2010, 2014; Gottschalk et al., 2015b, 2016b; Jaccard et al., 2016).
485 Southern Ocean ventilation was likely accompanied by increased air-sea CO₂ equilibration and adjust-
486 ed surface ocean buoyancy forcing in the Antarctic Divergence Zone of the Southern Ocean, driving
487 up both CO_{2,atm} levels and deep Southern Ocean oxygenation (Anderson et al., 2009; Skinner et al.,
488 2010, 2014; Gottschalk et al., 2015b, 2016b; Jaccard et al., 2016). These changes have likely also af-
489 fected deep-ocean respired carbon content in other ocean basins, such as the Atlantic and the Pacific
490 Ocean (e.g., Menviel et al., 2015b, 2018; Umling and Thunell, 2017; Chalk et al., 2019). Hence, we
491 suggest that similar mechanisms of (southern high-latitude) oceanic CO₂ release might have operated
492 during the last two glacial period, which is supported by similar patterns of reconstructed bottom water
493 oxygenation change at our study site and parallel CO_{2,atm} rise observed and predicted from Antarctic
494 ice core proxy data during MIS 3 and MIS 6, respectively (Fig. 6a). Our results therefore predict much
495 higher variability in CO_{2,atm} during MIS 6 than current observations from Antarctic ice cores convey.

496

497 The occurrence of saturation index minima in the deep South Atlantic during intervals of increasing
498 bottom water oxygenation (Fig. 6) indicates a shallower cell and/or reduced southward advection of
499 NADW, favouring the presence of southern-sourced (carbonate ion-undersaturated) water masses at
500 our core site, as suggested previously (Gottschalk et al., 2015a). This is supported by an agreement of
501 our saturation index with epibenthic δ¹³C- (Skinner et al., 2007; Margari et al., 2010) and SST changes
502 at the Iberian Margin (Martrat et al., 2007; Fig. 7), the high-resolution ²³¹Pa/²³⁰Th record from Bermu-
503 da Rise (Henry et al., 2016) and a carbonate saturation record from the deep Cape Basin (Gottschalk et
504 al., 2018), which reflect similar AMOC changes in the Atlantic basin. This agreement corroborates a
505 strong causal link between bottom water [O₂] changes in the deep South Atlantic and end-member
506 changes of southern-sourced water masses related to variations in air-sea gas exchange- and/or the
507 ventilation rate, which may be linked to variations in the southward extent of NADW.

508

509 However, this may be challenged by the observation of increasing bottom water oxygenation (i.e.,
510 decreasing respired carbon levels) in deep South Atlantic during periods of rising CO_{2,atm} levels, de-
511 spite low [CO₃²⁻] levels (i.e., saturation index minima) (Fig. 5), whereas a positive correlation between
512 bottom water [CO₃²⁻] and -oxygenation is expected. Our saturation index in fact shows an initial drop
513 at the stadial onset and a subsequent gradual increase towards the end of the stadial (Fig. 5). Changes
514 in bottom water [O₂] and [CO₃²⁻] may be affected by different processes operating on different time-
515 scales, involving not only changes in the amount of respired carbon, but also changing northern- and
516 southern-sourced end-member signatures and/or -contributions. A decrease in the contribution of
517 northern-sourced water masses might have strongly affected bottom water [CO₃²⁻] levels *at the onset*

518 of stadial conditions, when differences in bottom water [O₂] between northern- and southern-sourced
519 water masses might have been small, thus explaining the absence of abrupt changes in our U/Mn-
520 based bottom water [O₂] record. *During* North Atlantic stadials, however, increasing equilibration of
521 southern-sourced water masses with the atmosphere and increased AABW formation might have rap-
522 idly affected bottom water [O₂] but more slowly [CO₃²⁻], because the carbonate system has an order of
523 magnitude longer equilibration time as compared to non-dissociating gases. Further analyses are re-
524 quired to test this proposition.

525

526 **5.2. Inter-hemispheric climate variability and changes in deep-ocean carbon storage during the** 527 **last two glacial periods**

528 The exact mechanisms that connect the hemispheres over deglaciations or millennial-scale climate
529 events, and their implications for ocean respired carbon storage and CO_{2,atm} change, remain difficult to
530 unravel. However, insights into the controls on deep-ocean respired carbon storage in the deep South
531 Atlantic may evolve from a comparison of millennial events occurring under different background
532 climate states during MIS 3 and MIS 6 (sections 5.2.1. and 5.2.2 below) and from a comparison of our
533 proxy data with numerical model outputs (sections 5.2.3. and 5.2.4).

534

535 **5.2.1. Role of glacial background conditions**

536 We observe slightly higher foraminiferal U/Mn ratios (indicative of lower [O₂] and higher respired
537 carbon levels) during MIS 6 (mean U/Mn=1.12 mmol mol⁻¹, 183-143.5 kyr BP) than during MIS 3
538 (mean U/Mn=0.75 mmol mol⁻¹, 63-32 kyr BP) (Fig. 4). This may be associated with differences in the
539 foraminiferal species used for the U/Mn analyses, but a few *G. bulloides* and *Uvigerina* spp. analyses
540 during MIS 6 show agreement or slightly higher values than the *G. inflata* data (Fig. 4), which sup-
541 ports our notion. Although this observation needs to be tested with other proxy data, our data suggests
542 overall more intense respired carbon sequestration in the deep South Atlantic during MIS 6 compared
543 to MIS 3. In contrast, our Δδ¹³C-derived [O₂] data suggest similar bottom water oxygenation, and
544 hence respired carbon levels, during these two glacial periods (Fig. 4), but as mentioned above this
545 [O₂] proxy may be biased during MIS 6. On the basis of North Atlantic benthic δ¹³C data, Margari et
546 al. (2010) argued for a shallower Atlantic overturning cell during MIS 6 than during MIS 3. This may
547 have promoted an expansion of southern-sourced water masses, and may have hampered mid-depth
548 mixing with overlying (northern-sourced) water masses, more so during MIS 6 than during MIS 3,
549 owing to increased distance from rough topography (Adkins, 2013; Ferrari et al., 2014) or an increased
550 density difference between the two. This slightly different water mass structure in the Atlantic and
551 Southern Oceans during MIS 6 may have caused overall increased carbon sequestration in the deep
552 South Atlantic and the Southern Ocean compared to MIS 3, and hence lower CO_{2,atm} levels (Fig. 3).
553 This is supported by numerical model simulations that highlight an increased carbon sequestration

554 potential of the ocean through a combined weakening of the overturning rate of both NADW and
555 AABW (Menviel et al., 2017; Ödalen et al., 2018).

556

557 In addition, we find increased variability in IRD supply to the central South Atlantic and overall cooler
558 SST conditions during MIS 6 than during MIS 3 (Fig. 7). Our data are consistent with a more proximal
559 seasonal sea ice edge to the study site and/or an increased production of icebergs, which would sug-
560 gest more extensive sea ice cover and generally colder conditions in the Southern Ocean during MIS 6
561 (Fig. 7). Along with associated changes in Southern Ocean buoyancy forcing, more extended Antarctic
562 sea ice cover during MIS 6 may have contributed to stronger respired carbon storage during MIS 6
563 compared to MIS 3, as long as this reduced ocean-to-atmosphere CO₂ fluxes (Stephens and Keeling,
564 2000) more than it reduced atmosphere-to-ocean CO₂ fluxes due to diminished biological export pro-
565 duction (Kurahashi-Nakamura et al., 2007; Sun and Matsumoto, 2010). Overall, our findings suggest
566 that the difference in glacial boundary conditions, specifically through impacts on water mass geome-
567 tries in the Atlantic (as indicated by Iberian margin benthic $\delta^{13}\text{C}$ values) and Antarctic surface buoy-
568 ancy forcing (as shown by IRD abundances at our study site) likely accounted for differences in deep
569 ocean carbon storage and CO_{2,atm} background levels during MIS 3 and MIS 6 (Fig. 3).

570

571 **5.2.2. Stadial duration and atmospheric CO₂ rise**

572 Intervals of rising bottom water oxygenation, and hence decreasing respired carbon levels in the deep
573 South Atlantic, coincide with periods of weakened AMOC, i.e. stadials, during the last two glacial
574 periods (Fig. 4). The tight relationship between the duration of northern-hemisphere stadials and the
575 magnitude of concomitant bottom water oxygen increase at our core site (Fig. 6b) suggests that re-
576 respired carbon is gradually lost from the deep South Atlantic during AMOC perturbations. The associ-
577 ated millennial adjustment timescale may reflect the influence of Southern Ocean vertical mixing and
578 deep-ocean turnover rather than fast (centennial-scale) adjustments in the terrestrial biosphere for in-
579 stance. The observed link between deep South Atlantic oxygen/respired carbon changes and CO_{2,atm}
580 variations (Fig. 6c) suggests that the time the AMOC remains suppressed largely defines the net CO₂
581 flux from the ocean to the atmosphere, thus determining the magnitude of CO_{2,atm} increase during sta-
582 dials.

583

584 Our interpretation is supported by idealised numerical simulations of stadial periods and parallel
585 CO_{2,atm} change forced by freshwater fluxes to the North Atlantic (see crosses in Fig. 6c; Gottschalk et
586 al., 2019). Although these simulations have different experimental designs, background conditions and
587 forcing functions, the simulated CO_{2,atm} change at the end of stadials is broadly consistent with our
588 observations (Fig. 6c; Schmittner and Galbraith, 2008; Bouttes et al., 2012; Gottschalk et al., 2019),
589 and is largely driven by ocean carbon release (albeit from different ocean reservoirs) with compensato-
590 ry effects from carbon inventory changes in the terrestrial biosphere (e.g., Marchal et al., 1998;

591 Schmittner and Galbraith, 2008; Bouttes et al., 2012; Menviel et al., 2014). This emphasises that the
592 observed millennial adjustment timescale of $\text{CO}_{2,\text{atm}}$ in Fig. 6c is consistent with an influence from
593 deep-ocean ventilation (Schmittner and Galbraith, 2008).

594

595 However, during short stadials, rapid changes in the terrestrial biosphere such as the decline of boreal
596 forests and/or the expansion of southern-hemisphere land vegetation may dominate the atmospheric
597 carbon inventory (Köhler et al., 2005; Menviel et al., 2008; Bozbiyik et al., 2011; e.g., Bouttes et al.,
598 2012). This may also be influenced by fast upper-ocean carbon release through SHW strengthening
599 (Menviel et al., 2018) or rapid sea ice changes (Rae et al., 2018). Numerical simulations show that
600 modelled $\text{CO}_{2,\text{atm}}$ change during short stadials (<700 years) may range between slightly positive and
601 negative depending on the interplay between oceanic versus terrestrial processes (Fig. 6c; Gottschalk
602 et al., 2019), while $\text{CO}_{2,\text{atm}}$ changes observed in the Antarctic ice cores BYRD and Siple Dome were
603 suggested to be negligibly small during those intervals (Ahn and Brook, 2014). Two different modes
604 of $\text{CO}_{2,\text{atm}}$ change during stadials may thus be identified: the first dependent on a more sensitive and
605 fast responding terrestrial biosphere or another “reactive” reservoir such as the upper ocean; and the
606 second driven by slowly adjusting ocean processes (i.e., deep-ocean ventilation and -overturning).

607

608 The relationship between the duration of an AMOC perturbation (i.e., stadial) and deep South Atlantic
609 respired carbon/oxygen- and $\text{CO}_{2,\text{atm}}$ change is similar during MIS 3 and MIS 6 (Fig. 6b,c). The rate of
610 respired carbon loss from the deep (southern, high-latitude) ocean during northern-hemisphere stadials
611 was hence not discernibly different during MIS 3 and 6. However, this contrasts with suggested differ-
612 ences in the oceanic settings during the last two glacial periods: It has been suggested that the AMOC
613 was overall weaker during MIS 6, as shown by different baseline benthic $\delta^{13}\text{C}$ values at the Iberian
614 margin during MIS 3 and MIS 6 (Fig.7f; Margari et al., 2010). The generally weaker AMOC of MIS 6
615 may have resulted from a reduced density of northern-sourced water masses owing to a stronger hy-
616 drological cycle in the mid-latitude North Atlantic (Margari et al., 2010). Furthermore, the change in
617 Antarctic temperature and in SST at our core site (Fig. 7b) is much smaller in MIS 6 for a given stadial
618 duration than in MIS 3 (Margari et al., 2010), and may suggest weaker AMOC perturbations and less
619 intense Southern Ocean upwelling and deep-ocean ventilation during MIS 6. Additionally, increased
620 IRD abundances at our study site during North Atlantic stadials in MIS 6 imply stronger ice wasting
621 and/or -export during periods of Antarctic warming, when compared to MIS 3, which could have had
622 implications for the density structure of the Southern Ocean surface, and hence ocean-atmosphere CO_2
623 fluxes during MIS 3 and MIS 6. However, despite these dynamic and hydrographic differences, we do
624 not resolve any systematic differences in respired carbon loss from the deep sub-Antarctic Atlantic and
625 associated $\text{CO}_{2,\text{atm}}$ change during the last two glacial periods. Although uncertainties of our estimates
626 are large, in particular with respect to $\text{CO}_{2,\text{atm}}$ change during MIS 6, this suggests that the rate of
627 Southern Ocean CO_2 outgassing is similar during northern-hemisphere stadials of the last two glacial

628 periods (Fig. 7). However, the degree to which compensatory effects in MIS 6, such as when a larger
629 respired deep-ocean carbon pool and weaker AMOC/Southern Ocean perturbations are combined,
630 cause a similar $\text{CO}_{2,\text{atm}}$ rate of change as in MIS 3 remains unconstrained.

631

632 **5.2.3. Comparison with equilibrium climate model simulations**

633 Numerical simulations forced by freshwater hosing in the North Atlantic produce a weakened AMOC-
634 scenario (i.e., stadial conditions) that is qualitatively consistent with our observations (Gottschalk et
635 al., 2019). A subset of these freshwater hosing experiments find that changes in Southern Ocean verti-
636 cal mixing and -carbon release during AMOC perturbations are the main driver of simulated ocean
637 carbon loss and increase in $\text{CO}_{2,\text{atm}}$ at that time (Schmittner et al., 2007; Schmittner and Galbraith,
638 2008; Schmittner and Lund, 2015). This is supported by Menviel et al. (2008, 2014, 2015a, 2015b,
639 2018), who highlight that an agreement of simulated and observed $\text{CO}_{2,\text{atm}}$ changes during stadial peri-
640 ods can only be achieved through an increase in AABW formation and Southern Ocean convection.
641 Our proxy data support these model findings and highlight the operation of a bipolar seesaw in deep
642 ocean convection between the northern and southern hemispheres ("ventilation seesaw") during the
643 last two glacial periods, which extends the findings of Skinner et al. (2014) to the last two glacial peri-
644 ods.

645

646 Intensifications and/or poleward shifts of the SHW were also suggested to occur in parallel with AM-
647 OC perturbations and to increase ocean ventilation and ocean-to-atmosphere CO_2 fluxes, with implica-
648 tions for $\text{CO}_{2,\text{atm}}$ (Anderson et al., 2009; Lee et al., 2011; Jaccard et al., 2016; Chiang et al., 2018;
649 Pedro et al., 2018). This can be assessed based on numerical simulations that are forced by changes in
650 the SHW, taking advantage of the recent compilation of Gottschalk et al. (2019).

651

652 Model simulations forced by increases in the *SHW wind intensity* show a $\text{CO}_{2,\text{atm}}$ rise owing to en-
653 hanced Ekman pumping and ocean carbon loss primarily, but not exclusively, from intermediate
654 depths (~500-2000 m) (Gottschalk et al., 2019). These simulations would be consistent with our ob-
655 servations, if ocean carbon loss from the deep South Atlantic was non-negligible. With the exception
656 of model simulations of Völker and Köhler (2013), numerical models forced by *southward shifts of the*
657 *SHW* show a reduction in the surface outcrop area of deep water masses in the Southern Ocean, which
658 decreases the ocean-atmosphere CO_2 flux and therefore lowers $\text{CO}_{2,\text{atm}}$ levels (Gottschalk et al., 2019).
659 These simulations predict increased deep-ocean carbon storage in the South Atlantic during North
660 Atlantic stadials, and would hence contradict our findings.

661

662 In summary, while equilibrium model simulations support our proxy data-based interpretation of an
663 oceanic driver of millennial-scale $\text{CO}_{2,\text{atm}}$ variations, the relative contributions from Southern Ocean

664 vertical mixing and/or wind-driven Ekman pumping, both potentially representing a Southern Ocean
665 response to North Atlantic climate anomalies (e.g., Anderson and Carr, 2010), cannot be unraveled.

666

667 **5.2.4. Comparison with transient model simulations**

668 To gain more insights into the possible drivers of our deep South Atlantic respired carbon changes, we
669 compare our proxy data with recent transient model simulations of the last early deglaciation (H1)
670 performed with LOVECLIM, an Earth system model of intermediate complexity (Menviel et al.,
671 2018). These simulations test the influence of a shutdown of the AMOC on $\text{CO}_{2,\text{atm}}$ levels (Fig. 8;
672 Menviel et al., 2018) through freshwater supply to the North Atlantic (0.04-0.07 Sv, 19 to 16.2 kyr)
673 and to the Southern Ocean (0.1 Sv, 19 to 15 kyr), as well as a 20%-weakening of the SHW (simulation
674 ‘LH1’). They also analyse the influence of a surface buoyancy-driven and wind-driven increase in
675 Southern Ocean convection stimulated through additionally prescribing salt fluxes in the Southern
676 Ocean (simulation ‘LH1-SO’; -1.5 Sv, 18-18 kyr) or intensifications of the SHW wind stress (simula-
677 tion ‘LH1-SHW’; 20%-increase, 18.3 to 15 kyr). Simulation ‘LH1-SO-SHW’ combines changes in
678 surface buoyancy and winds and applies both a SHW intensification and negative Southern Ocean
679 freshwater fluxes.

680

681 We derive depth-varying O_2 - and DIC anomalies for H 1 for the South Atlantic (60°W-20°E, 40-
682 70°S)- and the Southern Ocean (40-70°S) for each of these simulations by referencing the simulated
683 water column profiles from model year 15 ka to background levels at model year 18 ka (Fig. 8a,b),
684 and compare transient changes with our South Atlantic proxy data (Fig. 8c). The simulations show a 3
685 kyr-period of AMOC suppression, which is at the upper end of stadial durations considered here (Fig.
686 6c). Although these simulations apply transient changes in the orbital parameters and northern-
687 hemisphere ice sheet evolution that are appropriate for H1, we assume that the model results provide
688 insights into the dynamics during other North Atlantic stadial periods.

689

690 Simulations LH1-SO and LH1-SO-SHW are characterised by increased AABW formation, and the
691 upwelling of CO_2 -rich CDW, which leads to a carbon loss from the deep ocean, both from the South-
692 ern and Pacific Oceans, and a simulated $\text{CO}_{2,\text{atm}}$ rise of 10-20 ppm (see Fig. 3 in Menviel et al., 2018).
693 These findings are qualitatively consistent with our interpretation of the proxy data, although there are
694 offsets in absolute bottom water $[\text{O}_2]$ anomalies between the model and proxy data (Fig. 8a,b). How-
695 ever, transient changes in simulated bottom water $[\text{O}_2]$ in the South Atlantic closely resemble those
696 observed in our proxy analyses (Fig. 8c), and is hence consistent with a loss of (respired) carbon from
697 the South Atlantic (Fig. 8d).

698

699 In simulation LH1, Southern Ocean convection is suppressed due to parallel freshwater hosing in the
700 Southern Ocean and weakened SHW winds (Menviel et al., 2018). This leads to little change in simu-

701 lated $\text{CO}_{2,\text{atm}}$ levels owing to a balance between increased ventilation and release of carbon from North
702 Pacific intermediate depths and increased Atlantic carbon storage (Menviel et al., 2018). This is at
703 odds with our proxy data and observed $\text{CO}_{2,\text{atm}}$ change during long stadials (Fig. 8). In the SHW-
704 driven simulation, LH1-SHW simulated $\text{CO}_{2,\text{atm}}$ increases on a centennial timescale, because upper
705 Southern Ocean convection increases and oceanic carbon is rapidly lost primarily from the upper and
706 intermediate ocean (Menviel et al., 2018). Its impact on simulated deep-ocean $[\text{O}_2]$ and DIC was how-
707 ever minimal compared to what our observations suggest (Fig. 8). Although our deep-ocean proxy
708 data cannot rule out a SHW-driven mechanism, they suggest that changes in the SHW geometry have
709 likely not operated alone to change $\text{CO}_{2,\text{atm}}$.

710

711 Overall, simulated geochemical anomalies in the South Atlantic and the Southern Ocean strongly re-
712 semble each other (Fig. 8), which suggests that our deep South Atlantic core site may be representative
713 of a wider region of the Southern Ocean. Our proxy data comparison with the transient simulations of
714 Menviel et al. (2018) corroborates our proxy interpretations of a role of Southern Ocean vertical mix-
715 ing in changes of deep-ocean respired carbon storage, and hence millennial-scale $\text{CO}_{2,\text{atm}}$ variations,
716 during North Atlantic stadials.

717

718 **6. Conclusion**

719 We extend existing high-resolution proxy reconstruction of deep South Atlantic bottom water oxygen
720 changes, and by inference variations in respired carbon content, from the last glacial period to MIS 6.
721 Mainly based on sedimentary redox-proxies, we show that during both glacial periods respired carbon
722 levels in the deep South Atlantic changed in parallel with millennial-scale $\text{CO}_{2,\text{atm}}$ variations. Our ob-
723 servations support earlier findings of a contribution of increased Southern Ocean convection and
724 ocean-to-atmosphere CO_2 fluxes in the Southern Ocean to increases in millennial-scale $\text{CO}_{2,\text{atm}}$ con-
725 centrations, assuming a large enough area of the ocean was similarly affected and the associated ma-
726 rine carbon loss was not fully compensated by terrestrial carbon uptake.

727

728 Our foraminiferal U/Mn data suggest that respired carbon storage was overall slightly larger during
729 MIS 6 than during MIS 3 in the deep South Atlantic, possibly due to more expansive southern-sourced
730 water masses and a shallower AMOC cell, more expansive Antarctic sea ice cover and overall colder
731 conditions in the Southern Ocean. These glacial differences may have accounted for overall slightly
732 lower observed $\text{CO}_{2,\text{atm}}$ levels during MIS 6 than during MIS 3. Our findings suggest that glacial back-
733 ground climate conditions have an impact on marine carbon cycling in the Southern Ocean, for in-
734 stance by influencing the extent of Antarctic sea ice (and hence, surface ocean buoyancy forcing in the
735 Southern Ocean).

736

737 Our proxy data highlight that the magnitude of carbon release from the Southern Ocean was propor-
738 tional to the duration of the AMOC perturbation. This suggests that the rate of $\text{CO}_{2,\text{atm}}$ change during
739 long stadial periods was broadly constant, and was primarily set by the millennial timescale for deep
740 ocean adjustment (i.e., ocean mixing/ventilation, Southern Ocean-atmosphere CO_2 fluxes). During
741 long stadials, likely reflecting strong AMOC perturbations, the *duration* of the weakened AMOC may
742 have therefore primarily determined the magnitude of net ocean carbon release, and hence the $\text{CO}_{2,\text{atm}}$
743 rise. However, for shorter stadial periods, processes operating on centennial timescales such as ad-
744 justments of land carbon inventories, with contributions from SHW- or sea ice effects on Southern
745 Ocean upper-ocean convection and CO_2 outgassing, may have influenced $\text{CO}_{2,\text{atm}}$ levels, because they
746 would have overwhelmed the effects of much slower deep-ocean overturning.

747

748 Based on our proxy data and a comparison with existing numerical model simulations, we cannot dis-
749 criminate between possible oceanic and atmospheric mechanisms driving a teleconnection between
750 Southern Ocean carbon dynamics and North Atlantic climate anomalies, but contributions from both
751 seem likely. A comparison with recent transient model simulations performed with LOVECLIM
752 (Menviel et al., 2018) show the closest model-data agreement for scenarios with increased Southern
753 Ocean convection prescribed through Southern Ocean salt fluxes at the surface, rather than SHW-only
754 scenarios. However, whether the prescribed changes in Southern Ocean surface buoyancy forcing are
755 realistic and how they are mechanistically linked to North Atlantic climate anomalies remains yet elu-
756 sive and needs further study. A better understanding of the atmospheric and oceanic mechanisms by
757 which interhemispheric climate variability affect the Southern Ocean carbon cycle and $\text{CO}_{2,\text{atm}}$ (for
758 instance through buoyancy-driven Southern Ocean vertical mixing, SHW-driven Ekman pumping,
759 and/or Antarctic sea ice extent) may ultimately emerge from tandem reconstructions of respired car-
760 bon reconstruction at intermediate and deep sites throughout the global ocean, and through comparison
761 with existing and evolving climate model simulations.

762

763 **Acknowledgements**

764 This study was supported by the Gates Cambridge Trust, the German Research Foundation (through
765 grant GO 2294/2-1 to J.G.), the Royal Society, NERC grant NE/J010545/1, the Cambridge Newton
766 Trust (L.C.S.), the Swiss National Science Foundation (grants PP00P2_144811 and 200021_163003
767 to S.L.J.), the Australian Research Council (grant DE150100107 to L.M.), and the European Research
768 Council (grant 339108 to C.W.). We thank Jinhwa Shin and Jérôme Chappellaz (Institut des Géosci-
769 ences de l'Environnement, Grenoble, France) for fruitful discussions of $\text{CO}_{2,\text{atm}}$ variability in MIS 6,
770 and Sophie Hines and Jerry McManus for sharing views on inter-hemispheric climate variability. Alli-
771 son Jacobel and Babette Hoogakker are thanked for insightful discussions of the $\Delta\delta^{13}\text{C}-[\text{O}_2]$ proxy.
772 We are also grateful to Linda Booth, Adam Scrivner, Tim Setzkorn and Salima Souanef-Ureta for
773 laboratory support, and sincerely thank three anonymous reviewers for their thoughtful and construc-

774 tive feedback. Age models for the study cores and data presented in this study are available from the
775 PANGAEA website (<https://doi.pangaea.de/10.1594/PANGAEA.898193>).

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777 **References**

- 778 Abelman, A., Gersonde, R., Knorr, G., Zhang, X., Chaplignin, B., Maier, E., Esper, O., Friedrichsen, H.,
779 Lohmann, G., Meyer, H., Tiedemann, R., 2015. The seasonal sea-ice zone in the glacial Southern Ocean as
780 a carbon sink. *Nat. Commun.* 6, 8136. <https://doi.org/10.1038/ncomms9136>
- 781 Adkins, J.F., 2013. The role of deep ocean circulation in setting glacial climates. *Paleoceanography* 28, 539–561.
782 <https://doi.org/10.1002/palo.20046>
- 783 Ahn, J., Brook, E.J., 2014. Siple Dome ice reveals two modes of millennial CO₂ change during the last ice age.
784 *Nat. Commun.* 5, 3723. <https://doi.org/10.1038/ncomms4723>
- 785 Anderson, R.F., Ali, S., Bradtmiller, L.I., Nielsen, S.H.H., Fleisher, M.Q., Anderson, B.E., Burckle, L.H., 2009.
786 Wind-driven upwelling in the Southern Ocean and the deglacial rise in atmospheric CO₂. *Science* 323,
787 1443–1448. <https://doi.org/10.1126/science.1167441>
- 788 Anderson, R.F., Barker, S., Fleisher, M., Gersonde, R., Goldstein S. J. Kuhn, G., Mortyn, P.G., Pahnke, K.,
789 Sachs, J.P., 2014a. Biological response to millennial variability of dust supply in the Subantarctic South
790 Atlantic Ocean. *Philos. Trans. R. Soc.* 372, 20130054. <https://doi.org/10.1098/rsta.2013.0054>
- 791 Anderson, R.F., Barker, S., Fleisher, M., Gersonde, R., Steven, L., Kuhn, G., Mortyn, P.G., Pahnke, K., Julian,
792 P., Goldstein, S.L., Sachs, J.P., 2014b. Biological response to millennial variability of dust and nutrient
793 supply in the Subantarctic South Atlantic Ocean. *Philos. Trans. R. Soc.* 372, 20130054.
794 <https://doi.org/10.1098/rsta.2013.0054>
- 795 Anderson, R.F., Carr, M.-E., 2010. Uncorking the Southern Ocean’s Vintage CO₂. *Science* 328, 1117–1118.
796 <https://doi.org/10.1126/science.1190765>
- 797 Anderson, R.F., Fleisher, M.Q., LeHuray, A.P., 1989. Concentration, oxidation state, and particulate flux of
798 uranium in the Black Sea. *Geochim. Cosmochim. Acta* 53, 2215–2224. [https://doi.org/10.1016/0016-](https://doi.org/10.1016/0016-7037(89)90345-1)
799 [7037\(89\)90345-1](https://doi.org/10.1016/0016-7037(89)90345-1)
- 800 Bacastow, B., 1996. The effect of temperature change of the warm surface waters of the oceans on atmospheric
801 CO₂. *Global Biogeochem. Cycles* 10, 319–333. <https://doi.org/10.1029/96GB00039>
- 802 Barker, S., Diz, P., 2014. Timing of the descent into the last ice age determined by the bipolar seesaw.
803 *Paleoceanography* 29, 489–507. <https://doi.org/10.1002/2014PA002623>
- 804 Barker, S., Elderfield, H., 2002. Foraminiferal calcification response to glacial-interglacial changes in
805 atmospheric CO₂. *Science* 297, 833–836. <https://doi.org/10.1126/science.1072815>
- 806 Barker, S., Greaves, M., Elderfield, H., 2003. A study of cleaning procedures used for foraminiferal Mg/Ca
807 paleothermometry. *Geochemistry Geophys. Geosystems* 4, 8407. <https://doi.org/10.1029/2003GC000559>
- 808 Barker, S., Knorr, G., Edwards, R.L., Parrenin, F., Putnam, A.E., Skinner, L.C., Wolff, E., Ziegler, M., 2011.
809 800,000 Years of Abrupt Climate Variability. *Science* 334, 347–351.
810 <https://doi.org/10.1126/science.1203580>
- 811 Barnes, C.E., Cochran, J.K., 1990. Uranium removal in oceanic sediments and the oceanic U balance. *Earth*
812 *Planet. Sci. Lett.* 97, 94–101. [https://doi.org/10.1016/0012-821X\(90\)90101-3](https://doi.org/10.1016/0012-821X(90)90101-3)
- 813 Basak, C., Fröllje, H., Lamy, F., Gersonde, R., Benz, V., Anderson, R.F., Molina-kescher, M., Pahnke, K., 2018.
814 Breakup of last glacial deep stratification in the South Pacific. *Science* 359, 900–904.
815 <https://doi.org/10.1126/science.aao2473>
- 816 Bazin, L., Landais, A., Lemieux-Dudon, B., Toyé Mahamadou Kele, H., Veres, D., Parrenin, F., Martinerie, P.,
817 Ritz, C., Capron, E., Lipenkov, V., M.-F. Loutre, Raynaud, D., Vinther, B., Svensson, A., Rasmussen,
818 S.O., Severi, M., Blunier, T., Leuenberger, M., Fischer, H., Masson-Delmotte, V., Chappellaz, J., Wolff,
819 E., 2013. An optimized multi-proxy, multi-site Antarctic ice and gas orbital chronology (AICC2012): 120-
820 800 ka. *Clim. Past* 9, 1715–1721. <https://doi.org/10.5194/cp-9-1715-2013>
- 821 Benz, V., Esper, O., Gersonde, R., Lamy, F., Tiedemann, R., 2016. Last Glacial Maximum sea surface
822 temperature and sea-ice extent in the Pacific sector of the Southern Ocean. *Quat. Sci. Rev.* 146, 216–237.
823 <https://doi.org/10.1016/j.quascirev.2016.06.006>
- 824 Bereiter, B., Eggleston, S., Schmitt, J., Nehrbass-Ahles, C., Stocker, T.F., Fischer, H., Kipfstuhl, S., Chappellaz,
825 J., 2015. Revision of the EPICA Dome C CO₂ record from 800 to 600 kyr before present. *Geophys. Res.*
826 *Lett.* 42, 542–549. <https://doi.org/10.1002/2014GL061957>
- 827 Bereiter, B., Lüthi, D., Siegrist, M., Schüpbach, S., Stocker, T.F., Fischer, H., 2012. Mode change of millennial
828 CO₂ variability during the last glacial cycle associated with a bipolar marine carbon seesaw. *Proc. Natl.*
829 *Acad. Sci.* 109, 9755–9760. <https://doi.org/10.1073/pnas.1204069109>
- 830 Bereiter, B., Shackleton, S., Baggenstos, D., Kawamura, K., Severinghaus, J., 2018. Mean global ocean
831 temperatures during the last glacial transition. *Nature* 553, 39–44. <https://doi.org/10.1038/nature25152>
- 832 Boiteau, R., Greaves, M., Elderfield, H., 2012. Authigenic uranium in foraminiferal coatings: A proxy for ocean

833 redox chemistry. *Paleoceanography* 27, 1–8. <https://doi.org/10.1029/2012PA002335>

834 Bouttes, N., Roche, D.M., Paillard, D., 2012. Systematic study of the impact of fresh water fluxes on the glacial
835 carbon cycle. *Clim. Past* 8, 589–607. <https://doi.org/10.5194/cp-8-589-2012>

836 Bozbiyik, A., Steinacher, M., Joos, F., Stocker, T.F., Menviel, L., 2011. Fingerprints of changes in the terrestrial
837 carbon cycle in response to large reorganizations in ocean circulation. *Clim. Past* 7, 319–338.
838 <https://doi.org/10.5194/cp-7-319-2011>

839 Broecker, W.S., Lynch-Stieglitz, J., Archer, D., Hofmann, M., Maier-Reimer, E., Marchal, O., Stocker, T.F.,
840 Gruber, N., 1999. How strong is the Harvardton-Bear constraint? *Global Biogeochem. Cycles* 13, 817–
841 820. <https://doi.org/10.1029/1999GB900050>

842 Broecker, W.S., Yu, J., Putnam, A.E., 2015. Two contributors to the glacial CO₂ decline. *Earth Planet. Sci. Lett.*
843 429, 191–196. <https://doi.org/10.1016/j.epsl.2015.07.019>

844 Calvert, S.E., Pedersen, T.F., 1996. Sedimentary Geochemistry of Manganese: Implications for the Environment
845 of Formation of Manganiferous Black Shale. *Econ. Geol.* 91, 36–47.
846 <https://doi.org/10.2113/gsecongeo.91.1.36>

847 Cartapanis, O., Galbraith, E.D., Bianchi, D., Jaccard, S.L., 2018. Carbon burial in deep-sea sediment and
848 implications for oceanic inventories of carbon and alkalinity over the last glacial cycle. *Clim. Past* 14,
849 1819–1850. <https://doi.org/10.5194/cp-2018-49>

850 Carter, L., McCave, I.N., Williams, M.J.M., 2009. Circulation and water masses of the Southern Ocean: A
851 review. *Dev. Earth Environ. Sci.* 8, 85–114. [https://doi.org/10.1016/S1571-9197\(08\)00004-9](https://doi.org/10.1016/S1571-9197(08)00004-9)

852 Chalk, T.B., Foster, G.L., Wilson, P.A., 2019. Dynamic storage of glacial CO₂ in the Atlantic Ocean revealed by
853 boron [CO₃²⁻] and pH records. *Earth Planet. Sci. Lett.* 510, 1–11.
854 <https://doi.org/10.1016/j.epsl.2018.12.022>

855 Channell, J.E.T., Vázquez Riveiros, N., Gottschalk, J., Waelbroeck, C., Skinner, L.C., 2017. Age and duration of
856 Laschamp and Iceland Basin geomagnetic excursions in the South Atlantic Ocean. *Quat. Sci. Rev.* 167, 1–
857 13. <https://doi.org/10.1016/j.quascirev.2017.04.020>

858 Charles, C.D., Pahnke, K., Zahn, R., Mortyn, P.G., Ninnemann, U., Hodell, D.A., 2010. Millennial scale
859 evolution of the Southern Ocean chemical divide. *Quat. Sci. Rev.* 29, 399–409.
860 <https://doi.org/10.1016/j.quascirev.2009.09.021>

861 Chase, Z., Kohfeld, K.E., Matsumoto, K., 2015. Controls on biogenic silica burial in the Southern Ocean. *Global*
862 *Biogeochem. Cycles* 29, 1–18. <https://doi.org/10.1002/2015GB005186>

863 Chen, P., Yu, J., Jin, Z., 2017. An evaluation of benthic foraminiferal U/Ca and U/Mn proxies for deep ocean
864 conditions. *Geochemistry Geophys. Geosystems* 18, 617–630. <https://doi.org/10.1002/2016GC006730>

865 Chiang, J.C.H., Tokos, K.S., Lee, S.Y., Matsumoto, K., 2018. Contrasting Impacts of the South Pacific Split Jet
866 and the Southern Annular Mode Modulation on Southern Ocean Circulation and Biogeochemistry.
867 *Paleoceanogr. Paleoclimatology* 33, 2–20. <https://doi.org/10.1002/2017PA003229>

868 CLIMAP project members, 1984. The Last Interglacial Ocean. *Quat. Res.* 21, 123–224.
869 [https://doi.org/10.1016/0033-5894\(84\)90098-X](https://doi.org/10.1016/0033-5894(84)90098-X)

870 Coplen, B., 1988. Normalization of oxygen and hydrogen isotope data. *Chem. Geol.* 12, 293–297.
871 [https://doi.org/10.1016/0168-9622\(88\)90042-5](https://doi.org/10.1016/0168-9622(88)90042-5)

872 Corliss, B.H., Emerson, S., 1990. Distribution of rose bengal stained deep-sea benthic foraminifera from the
873 Nova Scotian continental margin and Gulf of Maine. *Deep Sea Res. Part A. Oceanogr. Res. Pap.* 37, 381–
874 400. [https://doi.org/10.1016/0198-0149\(90\)90015-N](https://doi.org/10.1016/0198-0149(90)90015-N)

875 Dansgaard, W., Johnsen, S.J., Clausen, H.B., Dahl-Jensen, D., Gundestrup, N.S., Hammer, C.U., Hvidberg, C.S.,
876 Steffensen, J.P., Sveinbjörnsdóttir, A.E., Jouzel, J., Bond, G.C., 1993. Evidence for general instability of
877 past climate from a 250-kyr ice-core record. *Nature* 364, 218–220. <https://doi.org/10.1038/364218a0>

878 de Abreu, L., Shackleton, N.J., Schönfeld, J., Hall, M., Chapman, M., 2003. Millennial-scale oceanic climate
879 variability off the Western Iberian margin during the last two glacial periods. *Mar. Geol.* 196, 1–20.
880 [https://doi.org/10.1016/S0025-3227\(03\)00046-X](https://doi.org/10.1016/S0025-3227(03)00046-X)

881 Denton, G.H., Anderson, R.F., Toggweiler, J.R., Edwards, R.L., Schaefer, J.M., Putnam, A.E., 2010. The last
882 glacial termination. *Science* 328, 1652–1656. <https://doi.org/10.1126/science.1184119>

883 Detlef, H., Sosdian, S.M., Kender, S., Lear, C.H., Hall, I.R., 2019. Multi-elemental composition of authigenic
884 carbonates in benthic foraminifera from the eastern Bering Sea continental margin (International Ocean
885 Discovery Program Site U1343). *Geochim. Cosmochim. Acta.* <https://doi.org/10.1016/j.gca.2019.09.025>

886 EPICA Community Members, 2006. One-to-one coupling of glacial climate variability in Greenland and
887 Antarctica. *Nature* 444, 195–198. <https://doi.org/10.1038/nature05301>

888 Eppley, R.W., 1972. Temperature and phytoplankton growth in the sea. *Fish. Bull.* 70, 1063–1085.

889 Ferrari, R., Jansen, M.F., Adkins, J.F., Burke, A., Stewart, A.L., Thompson, A.F., 2014. Antarctic sea ice control
890 on ocean circulation in present and glacial climates. *Proc. Natl. Acad. Sci.* 111, 8753–8758.
891 <https://doi.org/10.1073/pnas.1323922111>

892 Fischer, H., Schmitt, J., Lüthi, D., Stocker, T.F., Tschumi, T., Parekh, P., Joos, F., Köhler, P., Barbante, C., Le
893 Floch, M., Raynaud, D., Wolff, E., 2010. The role of Southern Ocean processes in orbital and millennial

894 CO₂ variations - A synthesis. *Quat. Sci. Rev.* 29, 193–205. <https://doi.org/10.1016/j.quascirev.2009.06.007>

895 François, R., Albaret, M.A., Yu, E.F., Sigman, D.M., Bacon, M.P., Frank, M., Bohrmann, G., Bareille, G.,
896 Labeyrie, L.D., 1997. Contribution of Southern Ocean surface-water stratification to low atmospheric CO₂
897 concentrations during the last glacial period. *Nature* 389, 929–936. <https://doi.org/10.1038/40073>

898 Froelich, P.N., Klinkhammer, G.P., Bender, M.L., Luedtke, N.A., Heath, G.R., Cullen, D., Dauphin, P.,
899 Hammond, D., Hartman, B., 1979. Early oxidation of organic matter in pelagic sediments of the eastern
900 equatorial Atlantic: suboxic diagenesis. *Geochim. Cosmochim. Acta* 43, 1075–1090.

901 Galbraith, E.D., Jaccard, S.L., 2015. Deglacial weakening of the oceanic soft tissue pump: global constraints
902 from sedimentary nitrogen isotopes and oxygenation proxies. *Quat. Sci. Rev.* 109, 38–48.
903 <https://doi.org/10.1016/j.quascirev.2014.11.012>

904 Garcia, H.E., Locarnini, R.A., Boyer, T.P., Antonov, J.I., Baranova, O.K., Zweng, M.M., Johnson, D.R., 2010.
905 World Ocean Atlas 2009, Volume 3: Dissolved Oxygen, Apparent Oxygen Utilization, and Oxygen
906 Saturation, NOAA Atlas NESDIS 70. National Oceanic and Atmospheric Administration, U.S.
907 Government Printing Office, Washington, D.C.

908 Garcia, H.E., Locarnini, R.A., Boyer, T.P., Antonov, J.I., Baranova, O.K., Zweng, M.M., Reagan, J.R., Johnson,
909 D.R., 2014. World Ocean Atlas 2013, Volume 3: Dissolved Oxygen, Apparent Oxygen Utilization, and
910 Oxygen Saturation., in: Levitus, S., Mishonov, A. V (Eds.), NOAA Atlas NESDIS 75. p. 27.

911 Gebbie, G., Huybers, P., 2011. How is the ocean filled? *Geophys. Res. Lett.* 38, L6604–L6604.
912 <https://doi.org/10.1029/2011GL046769>

913 Gersonde, R., Abelmann, A., Brathauer, U., Becquey, S., Bianchi, C., Cortese, G., Grobe, H., Kuhn, G., Niebler,
914 H.-S., Segl, M., Sieger, M., Zielinski, U., Fütterer, D.K., 2003. Last glacial sea surface temperatures and
915 sea-ice extent in the Southern Ocean (Atlantic-Indian sector): A multiproxy approach. *Paleoceanography*
916 18, 1–6. <https://doi.org/10.1029/2002PA000809>

917 Geslin, E., Heinz, P., Jorissen, F., Hemleben, C., 2004. Migratory responses of deep-sea benthic foraminifera to
918 variable oxygen conditions: laboratory investigations. *Mar. Micropaleontol.* 53, 227–243.
919 <https://doi.org/10.1016/j.marmicro.2004.05.010>

920 Glock, N., Roy, A.S., Romero, D., Wein, T., Weissenbach, J., Revsbech, N.P., Høglund, S., Clemens, D.,
921 Sommer, S., Dagan, T., 2019. Metabolic preference of nitrate over oxygen as an electron acceptor in
922 foraminifera from the Peruvian oxygen minimum zone. *Proc. Natl. Acad. Sci.* 116, 2860–2865.
923 <https://doi.org/10.1073/pnas.1813887116>

924 Gottschalk, J., Battaglia, G., Fischer, H., Frölicher, T., Jaccard, S.L., Jeltsch-Thömmes, A., Joos, F., Köhler, P.,
925 Meissner, K.J., Menviel, L., Nehrbass-Ahles, C., Schmitt, J., Schmittner, A., Skinner, L.C., Stocker, T.F.,
926 2019. Mechanisms of millennial-scale atmospheric CO₂ change in numerical model simulations. *Quat. Sci.*
927 *Rev.* 220, 30–74. <https://doi.org/10.1016/j.quascirev.2019.05.013>

928 Gottschalk, J., Hodell, D.A., Skinner, L.C., Crowhurst, S.J., Jaccard, S.L., Charles, C.D., 2018. Implications of
929 past carbonate preservation events in the deep Southeast Atlantic (Cape Basin) for Atlantic overturning
930 dynamics and the global carbon cycle. *Paleoceanogr. Paleoclimatology* 33, 1–21.
931 <https://doi.org/10.1029/2018PA003353>

932 Gottschalk, J., Riveiros, N.V., Waelbroeck, C., Skinner, L.C., Michel, E., Duplessy, J.-C., Hodell, D.,
933 Mackensen, A., 2016a. Carbon isotope offsets between species of the genus *Cibicides* (*Cibicidoides*) in the
934 glacial sub-Antarctic Atlantic Ocean. *Paleoceanography* 31, 1583–1602.
935 <https://doi.org/10.1002/2016PA003029>

936 Gottschalk, J., Skinner, L.C., Lippold, J., Vogel, H., Frank, N., Jaccard, S.L., Waelbroeck, C., 2016b. Biological
937 and physical controls in the Southern Ocean on past millennial-scale atmospheric CO₂ changes. *Nat.*
938 *Commun.* 7, 1–11. <https://doi.org/10.1038/ncomms11539>

939 Gottschalk, J., Skinner, L.C., Misra, S., Waelbroeck, C., Menviel, L., Timmermann, A., 2015a. Abrupt changes
940 in the southern extent of North Atlantic Deep Water during Dansgaard-Oeschger events. *Nat. Geosci.* 8,
941 950–955. <https://doi.org/10.1038/ngeo2558>

942 Gottschalk, J., Skinner, L.C., Waelbroeck, C., 2015b. Contribution of seasonal sub-Antarctic surface water
943 variability to millennial-scale changes in atmospheric CO₂ over the last deglaciation and Marine Isotope
944 Stage 3. *Earth Planet. Sci. Lett.* 411, 87–99. <https://doi.org/10.1016/j.epsl.2014.11.051>

945 Haddam, N.A., Michel, E., Siani, G., Cortese, G., Bostock, H.C., Duprat, J.M., Isguder, G., 2016. Improving
946 past sea surface temperature reconstructions from the Southern Hemisphere oceans using planktonic
947 foraminiferal census data. *Paleoceanography* 31, 822–837. <https://doi.org/10.1002/2016PA002946>

948 Hain, M.P., Sigman, D.M., Haug, G.H., 2010. Carbon dioxide effects of Antarctic stratification, North Atlantic
949 Intermediate Water formation, and subantarctic nutrient drawdown during the last ice age: Diagnosis and
950 synthesis in a geochemical box model. *Global Biogeochem. Cycles* 24, GB4023–GB4023.
951 <https://doi.org/10.1029/2010GB003790>

952 Hasenfratz, A.P., Martínez-García, A., Jaccard, S.L., Vance, D., Wälle, M., Greaves, M., Haug, G.H., 2016.
953 Determination of the Mg/Mn ratio in foraminiferal coatings: An approach to correct Mg/Ca temperatures
954 for Mn-rich contaminant phases. *Earth Planet. Sci. Lett.* 457, 335–347.

955 <https://doi.org/10.1016/j.epsl.2016.10.004>
 956 Haslett, J., Parnell, A., 2008. A simple monotone process with application to radiocarbon-dated depth
 957 chronologies. *J. R. Stat. Soc.* 57, 399–418. <https://doi.org/10.1111/j.1467-9876.2008.00623.x>
 958 Hemming, S.R., 2004. Heinrich events: Massive late Pleistocene detritus layers of the North Atlantic and their
 959 global climate imprint. *Rev. Geophys.* 42, RG1005. <https://doi.org/10.1029/2003RG000128>
 960 Henry, L.G., McManus, J.F., Curry, W.B., Roberts, N.L., Piotrowski, A.M., Keigwin, L.D., 2016. North Atlantic
 961 ocean circulation and abrupt climate change during the last glaciatiion. *Science* 353, 470–474.
 962 <https://doi.org/10.1126/science.aaf5529>
 963 Hoogakker, B.A.A., Elderfield, H., Schmiedl, G., McCave, I.N., Rickaby, R.E.M., 2015. Glacial-interglacial
 964 changes in bottom-water oxygen content on the Portuguese margin. *Nat. Geosci.* 8, 40–43.
 965 <https://doi.org/10.1038/ngeo2317>
 966 Huybers, P., Langmuir, C., 2009. Feedback between deglaciation, volcanism, and atmospheric CO₂. *Earth*
 967 *Planet. Sci. Lett.* 286, 479–491. <https://doi.org/10.1016/j.epsl.2009.07.014>
 968 Ito, T., Follows, M.J., 2005. Preformed phosphate, soft tissue pump and atmospheric CO₂. *J. Mar. Res.* 63, 813–
 969 839. <https://doi.org/10.1357/0022240054663231>
 970 Jaccard, S.L., Galbraith, E.D., 2012. Large climate-driven changes of oceanic oxygen concentrations during the
 971 last deglaciation. *Nat. Geosci.* 5, 151–156. <https://doi.org/10.1038/ngeo1352>
 972 Jaccard, S.L., Galbraith, E.D., Frölicher, T.L., Gruber, N., 2014. Ocean (de)oxygenation across the last
 973 deglaciation: Insights for the future. *Oceanography* 27, 26–35. <https://doi.org/10.5670/oceanog.2014.05>.
 974 Jaccard, S.L., Galbraith, E.D., Martínez-García, A., Anderson, R.F., 2016. Covariation of abyssal Southern
 975 Ocean oxygenation and pCO₂ throughout the last ice age. *Nature* 530, 207–210.
 976 <https://doi.org/10.1038/nature16514>
 977 Jaccard, S.L., Hayes, C.T., Martínez-García, A., Hodell, D.A., Anderson, R.F., Sigman, D.M., Haug, G.H., 2013.
 978 Two Modes of Change in Southern Ocean Productivity Over the Past Million Years. *Science* 339, 1419–
 979 1423. <https://doi.org/10.1126/science.1227545>
 980 Jouzel, J., Masson-Delmotte, V., Cattani, O., Dreyfus, G., Falourd, S., Hoffmann, G., Minster, B., Nouet, J.,
 981 Barnola, J.M., Chappellaz, J., Fischer, H., Gallet, J.C., Johnsen, S., Leuenberger, M., Loulergue, L.,
 982 Luethi, D., Oerter, H., Parrenin, F., Raisbeck, G., Raynaud, D., Schilt, A., Schwander, J., Selmo, E.,
 983 Souchez, R., Spahni, R., Stauffer, B., Steffensen, J.P., Stenni, B., Stocker, T.F., Tison, J.L., Werner, M.,
 984 Wolff, E.W., 2007. Orbital and millennial Antarctic climate variability over the past 800,000 years.
 985 *Science* 317, 793–796. <https://doi.org/10.1126/science.1141038>
 986 Kanfoush, S.L., Hodell, D.A., Charles, C.D., Guilderson, T.P., Mortyn, P.G., Ninnemann, U.S., 2000.
 987 Millennial-scale instability of the Antarctic ice sheet during the last glaciatiion. *Science* 288, 1815–1818.
 988 <https://doi.org/10.1126/science.288.5472.1815>
 989 Kasten, S., Zabel, M., Heuer, V., Hensen, C., 2003. Processes and signals of non-steady state diagenesis in deep-
 990 sea sediments and their pore waters, in: Wefer, G., Mulitza, S., Ratmeyer, V. (Eds.), *The South Atlantic in*
 991 *the Late Quaternary: Reconstruction of Material Budgets and Current Systems*. Springer-Verlag Berlin
 992 Heidelberg New York Tokyo, pp. 431–459.
 993 Key, R.M., Kozyr, A., Sabine, C.L., Lee, K., Wanninkhof, R., Bullister, J.L., Feely, R.A., Millero, F.J., Mordy,
 994 C., Peng, T.-H., 2004. A global ocean carbon climatology: Results from Global Data Analysis Project
 995 (GLODAP). *Global Biogeochem. Cycles* 18, GB4031–GB4031. <https://doi.org/10.1029/2004GB002247>
 996 Klinkhammer, G.P., Palmer, M.R., 1991. Uranium in the oceans: where it goes and why. *Geochim. Cosmochim.*
 997 *Acta* 55, 1799–1806. [https://doi.org/10.1016/0016-7037\(91\)90024-Y](https://doi.org/10.1016/0016-7037(91)90024-Y)
 998 Köhler, P., Joos, F., Gerber, S., Knutti, R., 2005. Simulated changes in vegetation distribution, land carbon
 999 storage, and atmospheric CO₂ in response to a collapse of the North Atlantic thermohaline circulation.
 1000 *Clim. Dyn.* 25, 689–708. <https://doi.org/10.1007/s00382-005-0058-8>
 1001 Köhler, P., Knorr, G., Bard, E., 2014. Permafrost thawing as a possible source of abrupt carbon release at the
 1002 onset of the Bølling/Allerød. *Nat. Commun.* 5. <https://doi.org/10.1038/ncomms6520>
 1003 Köhler, P., Nehrbass-Ahles, C., Schmitt, J., Stocker, T.F., Fischer, H., 2017. A 156 kyr smoothed history of the
 1004 atmospheric greenhouse gases CO₂, CH₄, and N₂O and their radiative forcing. *Earth Syst. Sci. Data* 9,
 1005 363–387. <https://doi.org/10.5194/essd-9-363-2017>
 1006 Kroopnick, P.M., 1985. The distribution of ¹³C of Sigma CO₂ in the world oceans. *Deep Sea Res.* 32, 57–84.
 1007 [https://doi.org/10.1016/0198-0149\(85\)90017-2](https://doi.org/10.1016/0198-0149(85)90017-2)
 1008 Kumar, N., Anderson, R.F., Mortlock, R.A., Froelich, P.N., Kubik, P., Dittrich-Hannen, B., Suter, M., 1995.
 1009 Increased biological productivity and export production in the glacial Southern Ocean. *Nature* 378, 675–
 1010 680. <https://doi.org/10.1038/378675a0>
 1011 Kurahashi-Nakamura, T., Abe-Ouchi, A., Yamanaka, Y., Misumi, K., 2007. Compound effects of Antarctic sea
 1012 ice on atmospheric pCO₂ change during glacial-interglacial cycle. *Geophys. Res. Lett.* 34, 1–5.
 1013 <https://doi.org/10.1029/2007GL030898>
 1014 Kwon, E.Y., Primeau, F., Sarmiento, J.L., 2009. The impact of remineralization depth on the air–sea carbon
 1015 balance. *Nat. Geosci.* 2, 630–635. <https://doi.org/10.1038/ngeo612>

1016 Lambert, F., Bigler, M., Steffensen, J.P., Hutterli, M., Fischer, H., 2012. Centennial mineral dust variability in
1017 high-resolution ice core data from Dome C, Antarctica. *Clim. Past* 8, 609–623. [https://doi.org/10.5194/cp-](https://doi.org/10.5194/cp-8-609-2012)
1018 8-609-2012

1019 Lamy, F., Gersonde, R., Winckler, G., Esper, O., Jaeschke, A., Kuhn, G., Ullermann, J., Martinez-Garcia, A.,
1020 Lambert, F., Kilian, R., 2014. Increased Dust Deposition in the Pacific Southern Ocean During Glacial
1021 Periods. *Science* 343, 403–407. <https://doi.org/10.1126/science.1245424>

1022 Lear, C.H., Billups, K., Rickaby, R.E.M., Diester-Haass, L., Mawbey, E.M., Sosdian, S.M., 2016. Breathing
1023 more deeply: Deep ocean carbon storage during the mid-Pleistocene climate transition. *Geology*
1024 G38636.1–G38636.1. <https://doi.org/10.1130/G38636.1>

1025 Lee, S.Y., Chiang, J.C.H., Matsumoto, K., Tokos, K.S., 2011. Southern Ocean wind response to North Atlantic
1026 cooling and the rise in atmospheric CO₂: Modeling perspective and paleoceanographic implications.
1027 *Paleoceanography* 26, 1214. <https://doi.org/10.1029/2010PA002004>

1028 Lund, D.C., Asimow, P.D., Farley, K.A., Rooney, T.O., Seeley, E., Jackson, E.W., Durham, Z.M., 2016.
1029 Enhanced East Pacific Rise hydrothermal activity during the last two glacial terminations. *Science* 351,
1030 478–482. <https://doi.org/10.1126/science.aad4296>

1031 Marchal, O., Stocker, T.F., Joos, F., 1998. Impact of oceanic reorganizations on the ocean carbon cycle and
1032 atmospheric carbon dioxide content. *Paleoceanography* 13, 225–244. <https://doi.org/10.1029/98PA00726>

1033 Margari, V., Skinner, L.C., Tzedakis, P.C., Ganopolski, A., Vautravers, M., Shackleton, N.J., 2010. The nature
1034 of millennial-scale climate variability during the past two glacial periods. *Nat. Geosci.* 3, 127–131.
1035 <https://doi.org/10.1038/ngeo740>

1036 Marinov, I., Gnanadesikan, A., Toggweiler, J.R., Sarmiento, J.L., 2006. The Southern Ocean biogeochemical
1037 divide. *Nature* 441, 964–967. <https://doi.org/10.1038/nature04883>

1038 Martin, J.H., 1990. Glacial-interglacial CO₂ change: The iron hypothesis. *Paleoceanography* 5, 1–13.
1039 <https://doi.org/10.1029/PA005i001p00001>

1040 Martínez-García, A., Sigman, D.M., Ren, H., Anderson, R.F., Straub, M., Hodell, D.A., Jaccard, S.L., Eglinton,
1041 T.I., Haug, G.H., 2014. Iron Fertilization of the Subantarctic Ocean During the Last Ice Age. *Science* 343,
1042 1347–1350. <https://doi.org/10.1126/science.1246848>

1043 Martrat, B., Grimalt, J.O., Shackleton, N.J., de Abreu, L., Hutterli, M.A., Stocker, T.F., 2007. Four climate
1044 cycles of recurring deep and surface water destabilizations on the Iberian margin. *Science* 317, 502–507.
1045 <https://doi.org/10.1126/science.1139994>

1046 Matsumoto, K., 2007. Biology-mediated temperature control on atmospheric pCO₂ and ocean biogeochemistry.
1047 *Geophys. Res. Lett.* 34, L20605–L20605. <https://doi.org/10.1029/2007GL031301>

1048 Matsumoto, K., Hashioka, T., Yamanaka, Y., 2007. Effect of temperature-dependent organic carbon decay on
1049 atmospheric pCO₂. *J. Geophys. Res.* 112, 1–9. <https://doi.org/10.1029/2006JG000187>

1050 McCorkle, D.C., Emerson, S.R., 1988. The relationship between pore water carbon isotopic composition and
1051 bottom water oxygen concentration. *Geochim. Cosmochim. Acta* 52, 1169–1178.
1052 [https://doi.org/10.1016/0016-7037\(88\)90270-0](https://doi.org/10.1016/0016-7037(88)90270-0)

1053 McCorkle, D.C., Keigwin, L.D., Corliss, B.H., Emerson, S.R., 1990. The influence of microhabitats on the
1054 carbon isotopic composition of deep-sea benthic foraminifera. *Paleoceanography* 5, 161–185.
1055 <https://doi.org/10.1029/PA005i002p00161>

1056 McManus, J., Berelson, W.M., Klinkhammer, G.P., Hammond, D.E., Holm, C., 2005. Authigenic uranium:
1057 relationship to oxygen penetration depth and organic carbon rain. *Geochim. Cosmochim. Acta* 69, 95–108.
1058 <https://doi.org/10.1016/j.gca.2004.06.023>

1059 McManus, J., Berelson, W.M., Severmann, S., Poulson, R.L., Hammond, D.E., Klinkhammer, G.P., Holm, C.,
1060 2006. Molybdenum and uranium geochemistry in continental margin sediments: Paleoproxy potential.
1061 *Geochim. Cosmochim. Acta* 70, 4643–4662. <https://doi.org/10.1016/j.gca.2006.06.1564>

1062 Menviel, L., England, M.H., Meissner, K.J., Mouchet, A., Yu, J., 2014. Atlantic-Pacific seesaw and its role in
1063 outgassing CO₂ during Heinrich events. *Paleoceanography* 29, 58–70.
1064 <https://doi.org/10.1002/2013PA002542>

1065 Menviel, L., Mouchet, A., Meissner, K.J., Joos, F., England, M.H., 2015a. Impact of oceanic circulation changes
1066 on atmospheric δ¹³CO₂. *Global Biogeochem. Cycles* 29, 1944–1961.
1067 <https://doi.org/10.1002/2015GB005207>

1068 Menviel, L., Spence, P., England, M.H., 2015b. Contribution of enhanced Antarctic Bottom Water formation to
1069 Antarctic warm events and millennial-scale atmospheric CO₂ increase. *Earth Planet. Sci. Lett.* 413, 37–50.
1070 <https://doi.org/10.1016/j.epsl.2014.12.050>

1071 Menviel, L., Spence, P., Yu, J., Chamberlain, M.A., Matear, R.J., Meissner, K.J., England, M.H., 2018. Southern
1072 Hemisphere westerlies as a driver of the early deglacial atmospheric CO₂ rise. *Nat. Commun.* 9, 2503.
1073 <https://doi.org/10.1038/s41467-018-04876-4>

1074 Menviel, L., Timmermann, A., Mouchet, A., Timm, O., 2008. Meridional reorganizations of marine and
1075 terrestrial productivity during Heinrich events. *Paleoceanography* 23, PA1203.
1076 <https://doi.org/10.1029/2007PA001445>

1077 Menviel, L., Yu, J., Joos, F., Mouchet, A., Meissner, K.J., England, M.H., 2017. Poorly ventilated deep ocean at
1078 the Last Glacial Maximum inferred from carbon isotopes: A data-model comparison study.
1079 *Paleoceanography* 32, 2–17. <https://doi.org/10.1002/2016PA003024>

1080 Morford, J.L., Emerson, S., 1999. The geochemistry of redox sensitive trace metals in sediments. *Geochim.*
1081 *Cosmochim. Acta* 63, 1735–1750. [https://doi.org/10.1016/S0016-7037\(99\)00126-X](https://doi.org/10.1016/S0016-7037(99)00126-X)

1082 NGRIP members, 2004. High-resolution record of Northern Hemisphere climate extending into the last
1083 interglacial period. *Nature* 431, 147–151. <https://doi.org/10.1038/nature02805>

1084 Nielsen, S.H.H., Hodell, D.A., Kamenov, G., Guilderson, T., Perfit, M.R., 2007. Origin and significance of ice-
1085 rafted detritus in the Atlantic sector of the Southern Ocean. *Geochemistry Geophys. Geosystems* 8,
1086 Q12005–Q12005. <https://doi.org/10.1029/2007GC001618>

1087 Ödalen, M., Nycander, J., Oliver, K.I.C., Brodeau, L., Ridgwell, A., 2018. The influence of the ocean circulation
1088 state on ocean carbon storage and CO₂ drawdown potential in an Earth system model. *Biogeosciences* 15,
1089 1367–1393. <https://doi.org/10.5194/bg-15-1367-2018>

1090 Orsi, A.H., Whitworth, T., Nowlin, W.D., 1995. On the meridional extent and fronts of the Antarctic
1091 Circumpolar Current. *Deep Sea Res.* 42, 641–673. [https://doi.org/10.1016/0967-0637\(95\)00021-W](https://doi.org/10.1016/0967-0637(95)00021-W)

1092 Pedro, J.B., Jochum, M., Buizert, C., He, F., Barker, S., Rasmussen, S.O., 2018. Beyond the bipolar seesaw:
1093 Toward a process understanding of interhemispheric coupling. *Quat. Sci. Rev.* 192, 27–46.
1094 <https://doi.org/10.1016/j.quascirev.2018.05.005>

1095 Pena, L.D., Cacho, I., Calvo, E., Pelejero, C., Eggins, S., Sadekov, A., 2008. Characterization of contaminant
1096 phases in foraminifera carbonates by electron microprobe mapping. *Geochemistry Geophys. Geosystems*
1097 1–12. <https://doi.org/10.1029/2008GC002018>

1098 Pena, L.D., Calvo, E., Cacho, I., Eggins, S., Pelejero, C., 2005. Identification and removal of Mn-Mg-rich
1099 contaminant phases on foraminiferal tests: Implications for Mg/Ca past temperature reconstructions.
1100 *Geochemistry Geophys. Geosystems* 6, Q09P02–Q09P02. <https://doi.org/10.1029/2005GC000930>

1101 Petit, J.-R., Jouzel, J., Raynaud, D., Barkov, N.I., Barnola, J.-M., Basile, I., Bender, M., Chappellaz, J., Davis,
1102 M., Delaygue, G., Delmotte, M., Kotlyakov, V.M., Legrand, M., Lipenkov, V.Y., Lorius, C., L. Pepin, L.,
1103 Ritz, C., Saltzman, E., Stievenard, M., 1999. Climate and atmospheric history of the past 420,000 years
1104 from the Vostok ice core, Antarctica. *Nature* 399, 429–436. <https://doi.org/10.1038/20859>

1105 Piña-Ochoa, E., Koho, K.A., Geslin, E., Risgaard-Petersen, N., 2010. Survival and life strategy of the
1106 foraminiferan *Globobulimina turgida* through nitrate storage and denitrification. *Mar. Ecol. Prog. Ser.* 417,
1107 39–49. <https://doi.org/10.3354/meps08805>

1108 Policy, H.W., Johnson, H.B., Marinot, B.D., Mayeux, H.S., 1993. Increase in C3 plant water-use efficiency and
1109 biomass over glacial to present CO₂ concentrations. *Nature* 361, 61. <https://doi.org/10.1038/361061a0>

1110 Primeau, F., 2005. Characterizing transport between the surface mixed layer and the ocean interior with a
1111 forward and adjoint global ocean transport model. *J. Phys. Oceanogr.* 35, 545–564.
1112 <https://doi.org/10.1175/JPO2699.1>

1113 Rae, J.W.B., Burke, A., Robinson, L.F., Adkins, J.F., Chen, T., Cole, C., Greenop, R., Li, T., Littley, E.F.M.,
1114 Nita, D.C., Stewart, J.A., Taylor, B.J., 2018. CO₂ storage and release in the deep Southern Ocean on
1115 millennial to centennial timescales. *Nature* 562, 569–573. <https://doi.org/10.1038/s41586-018-0614-0>

1116 Raitzsch, M., Kuhnert, H., Hathorne, C., Groeneveld, J., Bickert, T., 2011. U/Ca in benthic foraminifers: A
1117 proxy for the deep-sea carbonate saturation. *Geochemistry Geophys. Geosystems* 12, Q06019–Q06019.
1118 <https://doi.org/10.1029/2010GC003344>

1119 Risgaard-Petersen, N., Langezaal, A.M., Ingvarsdson, S., Schmid, M.C., Jetten, M.S.M., Op Den Camp, H.J.M.,
1120 Derksen, J.W.M., Piña-Ochoa, E., Eriksson, S.P., Nielsen, L.P., Revsbech, N.P., Cedhagen, T., Van Der
1121 Zwaan, G.J., 2006. Evidence for complete denitrification in a benthic foraminifer. *Nature* 443, 93–96.
1122 <https://doi.org/10.1038/nature05070>

1123 Roberts, J., Gottschalk, J., Skinner, L.C., Peck, V.L., Kender, S., Elderfield, H., Waelbroeck, C., Vázquez
1124 Riveiros, N., Hodell, D.A., 2015. Evolution of South Atlantic density and chemical stratification across the
1125 last deglaciation. *Proc. Natl. Acad. Sci.* 113, 514–519. <https://doi.org/10.1073/pnas.1511252113>

1126 Ronge, T.A., Tiedemann, R., Lamy, F., Köhler, P., Alloway, B. V, De Pol-Holz, R., Pahnke, K., Southon, J.,
1127 Wacker, L., 2016. Radiocarbon constraints on the extent and evolution of the South Pacific glacial carbon
1128 pool. *Nat. Commun.* 7, 11487. <https://doi.org/10.1038/ncomms11487>

1129 Russell, A.D., Hönisch, B., Spero, H.J., Lea, D.W., 2004. Effects of seawater carbonate ion concentration and
1130 temperature on shell U, Mg, and Sr in cultured planktonic foraminifera. *Geochim. Cosmochim. Acta* 68,
1131 4347–4361. <https://doi.org/10.1016/j.gca.2004.03.013>

1132 Sarmiento, J.L., Toggweiler, J.R., 1984. A new model for the role of the oceans in determining atmospheric
1133 pCO₂. *Nature* 308, 621–624. <https://doi.org/10.1038/308621a0>

1134 Schmittner, A., Brook, E.J., Ahn, J., 2007. Impact of the Ocean’s Overturning Circulation on Atmospheric CO₂,
1135 in: Schmittner, A., Chiang, J.C.H., Hemming, S.R. (Eds.), *Geophysical Monograph Series 173: Ocean
1136 Circulation: Mechanisms and Impacts*. American Geophysical Union, Washington, DC, USA, pp. 209–
1137 246. <https://doi.org/10.1029/173GM20>

- 1138 Schmittner, A., Galbraith, E.D., 2008. Glacial greenhouse-gas fluctuations controlled by ocean circulation
1139 changes. *Nature* 456, 373–376. <https://doi.org/10.1038/nature07531>
- 1140 Schmittner, A., Lund, D.C., 2015. Early deglacial Atlantic overturning decline and its role in atmospheric CO₂
1141 rise inferred from carbon isotopes ($\delta^{13}\text{C}$). *Clim. Past* 11, 135–152. <https://doi.org/10.5194/cp-11-135-2015>
- 1142 Schneider, R., Schmitt, J., Köhler, P., Joos, F., Fischer, H., 2013. A reconstruction of atmospheric carbon
1143 dioxide and its stable carbon isotopic composition from the penultimate glacial maximum to the last
1144 glacial inception. *Clim. Past* 9, 2507–2523. <https://doi.org/10.5194/cp-9-2507-2013>
- 1145 Shoenfelt, E.M., Winckler, G., Lamy, F., Anderson, R.F., Bostick, B.C., 2018. Highly bioavailable dust-borne
1146 iron delivered to the Southern Ocean during glacial periods. *Proc. Natl. Acad. Sci.* 115, 11180–11185.
1147 <https://doi.org/10.1073/pnas.1809755115>
- 1148 Sigman, D.M., Boyle, E.A., 2000. Glacial/interglacial variations in atmospheric carbon dioxide. *Nature* 407,
1149 859–869. <https://doi.org/10.1038/35038000>
- 1150 Sigman, D.M., De Boer, A.M., Haug, G.H., 2007. Antarctic stratification, atmospheric water vapor, and
1151 Heinrich events: A hypothesis for late Pleistocene deglaciations. *Ocean Circ. Mech. Impacts-Past Futur.*
1152 *Chang. Merid. Overturning* 335–349.
- 1153 Sigman, D.M., Hain, M.P., Haug, G.H., 2010. The polar ocean and glacial cycles in atmospheric CO₂
1154 concentration. *Nature* 466, 47–55. <https://doi.org/10.1038/nature09149>
- 1155 Sikes, E.L., Cook, M.S., Guilderson, T.P., 2016. Reduced deep ocean ventilation in the Southern Pacific Ocean
1156 during the last glaciation persisted into the deglaciation. *Earth Planet. Sci. Lett.* 438, 130–138.
1157 <https://doi.org/10.1016/j.epsl.2015.12.039>
- 1158 Skinner, L.C., Elderfield, H., Hall, M., 2007. Phasing of Millennial Climate Events and Northeast Atlantic Deep-
1159 Water Temperature Change Since 50 Ka BP, in: Schmittner, A., Chiang, J.C.H., Hemming, S.R. (Eds.),
1160 *Ocean Circulation: Mechanisms and Impacts*. American Geophysical Union, Geophysical Monograph
1161 Series, pp. 197–208. <https://doi.org/10.1029/173GM14>
- 1162 Skinner, L.C., Fallon, S., Waelbroeck, C., Michel, E., Barker, S., 2010. Ventilation of the deep Southern Ocean
1163 and deglacial CO₂ rise. *Science* 328, 1147–1151. <https://doi.org/10.1126/science.1183627>
- 1164 Skinner, L.C., Sadekov, A., Brandon, M., Greaves, M., Plancherel, Y., de la Fuente, M., Gottschalk, J., Souanef-
1165 Ureta, S., Sevilgen, D.S., Scrivner, A.E., 2019. Rare Earth Elements in early-diagenetic foraminifer
1166 ‘coatings’: pore-water controls and potential palaeoceanographic applications. *Geochim. Cosmochim. Acta*
1167 245, 118–132. <https://doi.org/10.1016/j.gca.2018.10.027>
- 1168 Skinner, L.C., Shackleton, N.J., 2005. An Atlantic lead over Pacific deep-water change across Termination I:
1169 implications for the application of the marine isotope stage stratigraphy. *Quat. Sci. Rev.* 24, 571–580.
1170 <https://doi.org/10.1016/j.quascirev.2004.11.008>
- 1171 Skinner, L.C., Waelbroeck, C., Scrivner, A.E., Fallon, S.J., 2014. Radiocarbon evidence for alternating northern
1172 and southern sources of ventilation of the deep Atlantic carbon pool during the last deglaciation. *Proc.*
1173 *Natl. Acad. Sci.* 111, 5480–5484. <https://doi.org/10.1073/pnas.1400668111>
- 1174 Sokolov, S., Rintoul, S.R., 2009. Circumpolar structure and distribution of the Antarctic Circumpolar Current
1175 fronts: 2. Variability and relationship to sea surface height. *J. Geophys. Res. Ocean.* 114.
1176 <https://doi.org/10.1029/2008JC005108>
- 1177 Stephens, B.B., Keeling, R.F., 2000. The influence of Antarctic sea ice on glacial-interglacial CO₂ variations.
1178 *Nature* 404, 171–174. <https://doi.org/10.1038/35004556>
- 1179 Studer, A.S., Sigman, D.M., Martínez-García, A., Benz, V., Winckler, G., Kuhn, G., Esper, O., Lamy, F.,
1180 Jaccard, S.L., Wacker, L., Oleynik, S., Gersonde, R., Haug, G.H., 2015. Antarctic Zone nutrient conditions
1181 during the last two glacial cycles. *Paleoceanography* 30, 845–862. <https://doi.org/10.1002/2014PA002745>
- 1182 Sun, X., Matsumoto, K., 2010. Effects of sea ice on atmospheric pCO₂: A revised view and implications for
1183 glacial and future climates. *J. Geophys. Res.* 115, 1–8. <https://doi.org/10.1029/2009JG001023>
- 1184 Svendsen, J.I., Alexanderson, H., Astakhov, V.I., Demidov, I., Dowdeswell, J.A., Funder, S., Gataullin, V.,
1185 Henriksen, M., Hjort, C., Houmark-Nielsen, M., Hubberten, H.W., Ingólfsson, Ó., Jakobsson, M., Kjær,
1186 K.H., Larsen, E., Lokrantz, H., Lunkka, J.P., Lyså, A., Mangerud, J., Matiouchkov, A., Murray, A.,
1187 Möller, P., Niessen, F., Nikolskaya, O., Polyak, L., Saarnisto, M., Siegert, C., Siegert, M.J., Spielhagen,
1188 R.F., Stein, R., 2004. Late Quaternary ice sheet history of northern Eurasia. *Quat. Sci. Rev.* 23, 1229–
1189 1271. <https://doi.org/10.1016/j.quascirev.2003.12.008>
- 1190 Takahashi, T., Sutherland, S.C., Sweeney, C., Poisson, A., Metzl, N., Tilbrook, B., Bates, N., Wanninkhof, R.,
1191 Feely, R.A., Sabine, C., Olafsson, J., Nojirih, Y., 2002. Global sea-air CO₂ flux based on climatological
1192 surface ocean pCO₂, and seasonal biological and temperature effects. *Deep Sea Res.* 49, 1601–1622.
1193 [https://doi.org/10.1016/S0967-0645\(02\)00003-6](https://doi.org/10.1016/S0967-0645(02)00003-6)
- 1194 Talley, L.D., 2013. Closure of the global overturning circulation through the Indian, Pacific, and Southern
1195 Oceans: Schematics and transports. *Oceanography* 26, 80–97. <https://doi.org/10.5670/oceanog.2013.07>
- 1196 Tesi, T., Muschitiello, F., Smittenberg, R.H., Jakobsson, M., Vonk, J.E., Hill, P., Andersson, A., Kirchner, N.,
1197 Noormets, R., Dudarev, O., Semiletov, I., Gustafsson, Ö., 2016. Massive remobilization of permafrost
1198 carbon during post-glacial warming. *Nat. Commun.* 7, 13653. <https://doi.org/10.1038/ncomms13653>

1199 Toggweiler, J.R., Russell, J.L., Carson, S.R., 2006. Midlatitude westerlies, atmospheric CO₂, and climate change
1200 during the ice ages. *Paleoceanography* 21, 2005. <https://doi.org/10.1029/2005PA001154>

1201 Tribovillard, N., Algeo, T.J., Lyons, T., Riboulleau, A., 2006. Trace metals as paleoredox and paleoproductivity
1202 proxies: An update. *Chem. Geol.* 232, 12–32. <https://doi.org/j.chemgeo.2006.02.012>

1203 Umling, N.E., Thunell, R.C., 2017. Synchronous deglacial thermocline and deep-water ventilation in the eastern
1204 equatorial Pacific. *Nat. Commun.* 8, 1–10. <https://doi.org/10.1038/ncomms14203>

1205 Vázquez Riveiros, N., Waelbroeck, C., Skinner, L.C., Roche, D.M., Duplessy, J.C., Michel, E., 2010. Response
1206 of South Atlantic deep waters to deglacial warming during Terminations V and I. *Earth Planet. Sci. Lett.*
1207 298, 323–333. <https://doi.org/10.1016/j.epsl.2010.08.003>

1208 Veres, D., Bazin, L., Landais, A., Kele, H.T.M., Lemieux-Dudon, B., Parrenin, F., Martinerie, P., Blayo, E.,
1209 Blunier, T., Capron, E., Chappellaz, J., Rasmussen, S.O., Severi, M., Svensson, A., Vinther, B.M., Wolff,
1210 E., 2013. The Antarctic ice core chronology (AICC2012): an optimized multi-parameter and multi-site
1211 dating approach for the last 120 thousand years. *Clim. Past* 9, 1733–1748. <https://doi.org/10.5194/cpd-8-6011-2012>

1212

1213 Vogel, H., Meyer-Jacob, C., Thöle, L., Lippold, J., Jaccard, S.L., 2016. Quantification of biogenic silica by
1214 means of Fourier transform infrared spectroscopy (FTIRS) in marine sediments. *Limnol. Oceanogr.*
1215 *Methods* 14, 828–838. <https://doi.org/10.1002/lom3.10129>

1216 Volk, T., Hoffert, M.I., 1985. Ocean Carbon Pumps: Analysis of Relative Strengths and Efficiencies in Ocean-
1217 Driven Atmospheric CO₂ Changes, in: Sundquist, E.T., Broecker, W.S. (Eds.), *The Carbon Cycle and*
1218 *Atmospheric CO₂: Natural Variations Archean to Present*, Geophysical Monograph Series. pp. 99–110.
1219 <https://doi.org/10.1029/GM032p0099>

1220 Völker, C., Köhler, P., 2013. Responses of ocean circulation and carbon cycle to changes in the position of the
1221 Southern Hemisphere westerlies at Last Glacial Maximum. *Paleoceanography* 28, 726–739.
1222 <https://doi.org/10.1002/2013PA002556>

1223 Watson, A.J., Naveira Garabato, A.C., 2006. The role of Southern Ocean mixing and upwelling in glacial-
1224 interglacial atmospheric CO₂ change. *Tellus B* 58, 73–87. <https://doi.org/10.1111/j.1600-0889.2005.00167.x>

1225

1226 Watson, A.J., Vallis, G.K., Nikurashin, M., 2015. Southern Ocean buoyancy forcing of ocean ventilation and
1227 glacial atmospheric CO₂. *Nat. Geosci.* 8, 861–864. <https://doi.org/10.1038/ngeo2538>

1228 Yu, J., Elderfield, H., 2007. Benthic foraminiferal B/Ca ratios reflect deep water carbonate saturation state. *Earth*
1229 *Planet. Sci. Lett.* 258, 73–86. <https://doi.org/10.1016/j.epsl.2007.03.025>

1230 Yu, J., Elderfield, H., Jin, Z., Booth, L., 2008. A strong temperature effect on U/Ca in planktonic foraminiferal
1231 carbonates. *Geochim. Cosmochim. Acta* 72, 4988–5000. <https://doi.org/10.1016/j.gca.2008.07.011>

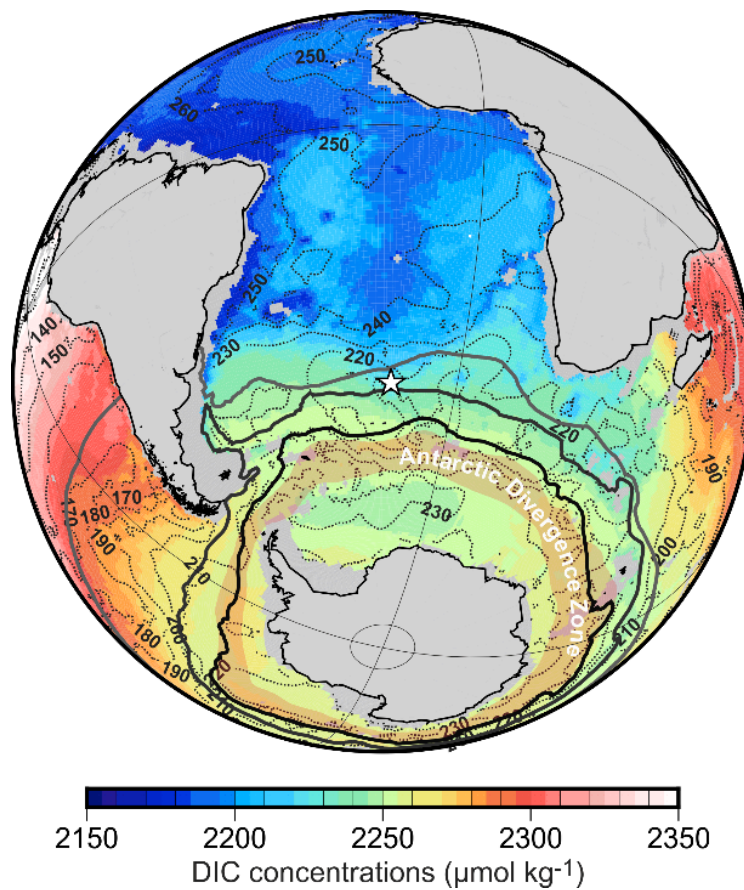
1232 Zech, R., 2012. A permafrost glacial hypothesis – Permafrost carbon might help explaining the Pleistocene ice
1233 ages. *Quat. Sci. J.* 61, 84–92. <https://doi.org/10.3285/eg.61.1.07>

1234 Zheng, Y., Anderson, R.F., van Geen, A., Fleisher, M.Q., 2002. Remobilization of authigenic uranium in marine
1235 sediments by bioturbation. *Geochim. Cosmochim. Acta* 66, 1759–1772. [https://doi.org/10.1016/S0016-7037\(01\)00886-9](https://doi.org/10.1016/S0016-7037(01)00886-9)

1236

1237 Ziegler, M., Diz, P., Hall, I.R., Zahn, R., 2013. Millennial-scale changes in atmospheric CO₂ levels linked to the
1238 Southern Ocean carbon isotope gradient and dust flux. *Nat. Geosci.* 6, 457–461.
1239 <https://doi.org/10.1038/ngeo1782>

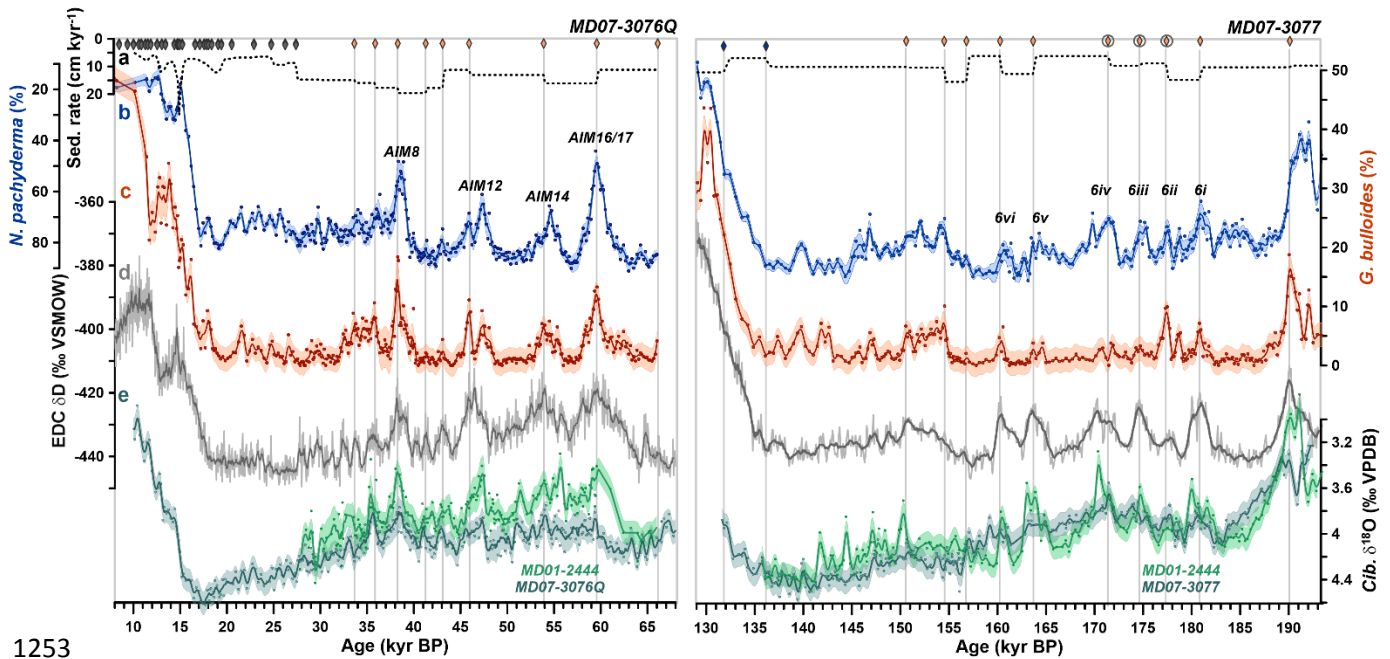
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1243 **Fig. 1. Location of study site.** Concentration of dissolved inorganic carbon (DIC, shaded; Key et al.,
 1244 2004) in the ocean averaged below 2.5 km water depth. Contours indicate the average seawater dis-
 1245 solved [O₂] below 2.5 km water depth (Garcia et al., 2014). The location of sediment cores MD07-
 1246 3076Q and MD07-3077 is indicated by a star. Major fronts are shown as stippled lines from south to
 1247 north: Polar Front (dark grey line), sub-Antarctic Front (grey line) and sub-Tropical Front (light grey
 1248 line) (Orsi et al., 1995; Sokolov and Rintoul, 2009). The Antarctic Divergence Zone is highlighted by
 1249 an orange circumpolar band, representing the region of strong positive air-sea CO₂ fluxes in austral
 1250 winter in the Southern Ocean at present-day (see maps in Takahashi et al., 2002).

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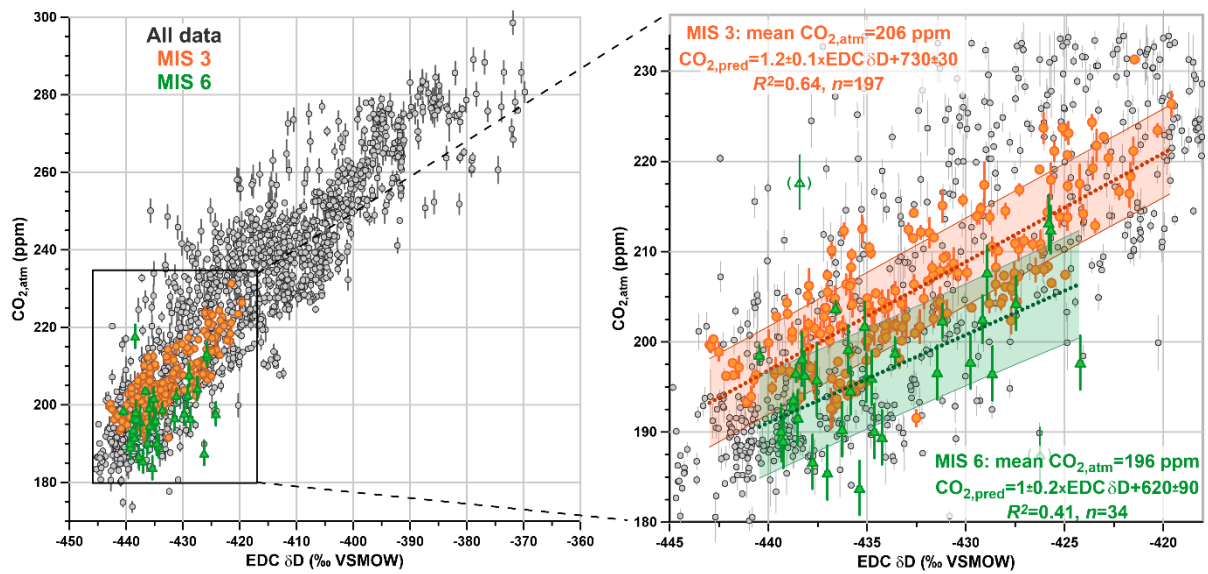


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1254 **Fig. 2. Chronologies of sediment cores MD07-3076Q (Termination (T) I and Marine Isotope**
 1255 **Stage (MIS) 3, left) and MD07-3077 (TII and MIS 6, right).** (a) Sedimentation rate (line) and tie-
 1256 points (grey: ^{14}C dates, alignment of abundance variations of *G. bulloides* (orange) and *N. pachyderma*
 1257 (blue) with EPICA Dome C (EDC) δD ; Gottschalk et al., 2016a; Channell et al., 2017), (b) abundance
 1258 changes of *N. pachyderma*, (c) abundance changes of *G. bulloides*, (d) EDC δD (Jouzel et al., 2007)
 1259 shown on the AICC2012 chronology (Bazin et al., 2013; Veres et al., 2013) and (e) *C. kullenbergi*
 1260 $\delta^{18}\text{O}$ records in comparison to mean benthic $\delta^{18}\text{O}$ records from the Iberian margin (Skinner et al.,
 1261 2007; MD01-2444; Margari et al., 2010). Lines and envelopes in (b), (c) and (e) show 500 years-
 1262 running averages and 2σ -uncertainties, respectively. Diamonds at the top of each panel show age
 1263 markers obtained by ^{14}C dating of planktic foraminifera (dark grey) and a stratigraphic alignment of
 1264 abundance variations of *G. bulloides* and *N. pachyderma* with EDC δD (light grey) (Channell et al.,
 1265 2017). Encircled symbols show adjusted age markers that differ from the chronology for this core
 1266 sequence published in Channell et al. (2017), as described in the text. The annotation of Antarctic
 1267 warming events (AIM – Antarctic Isotope Maxima) follows EPICA Community Members (2006) for
 1268 MIS 3 and Margari et al. (2010) for MIS 6.

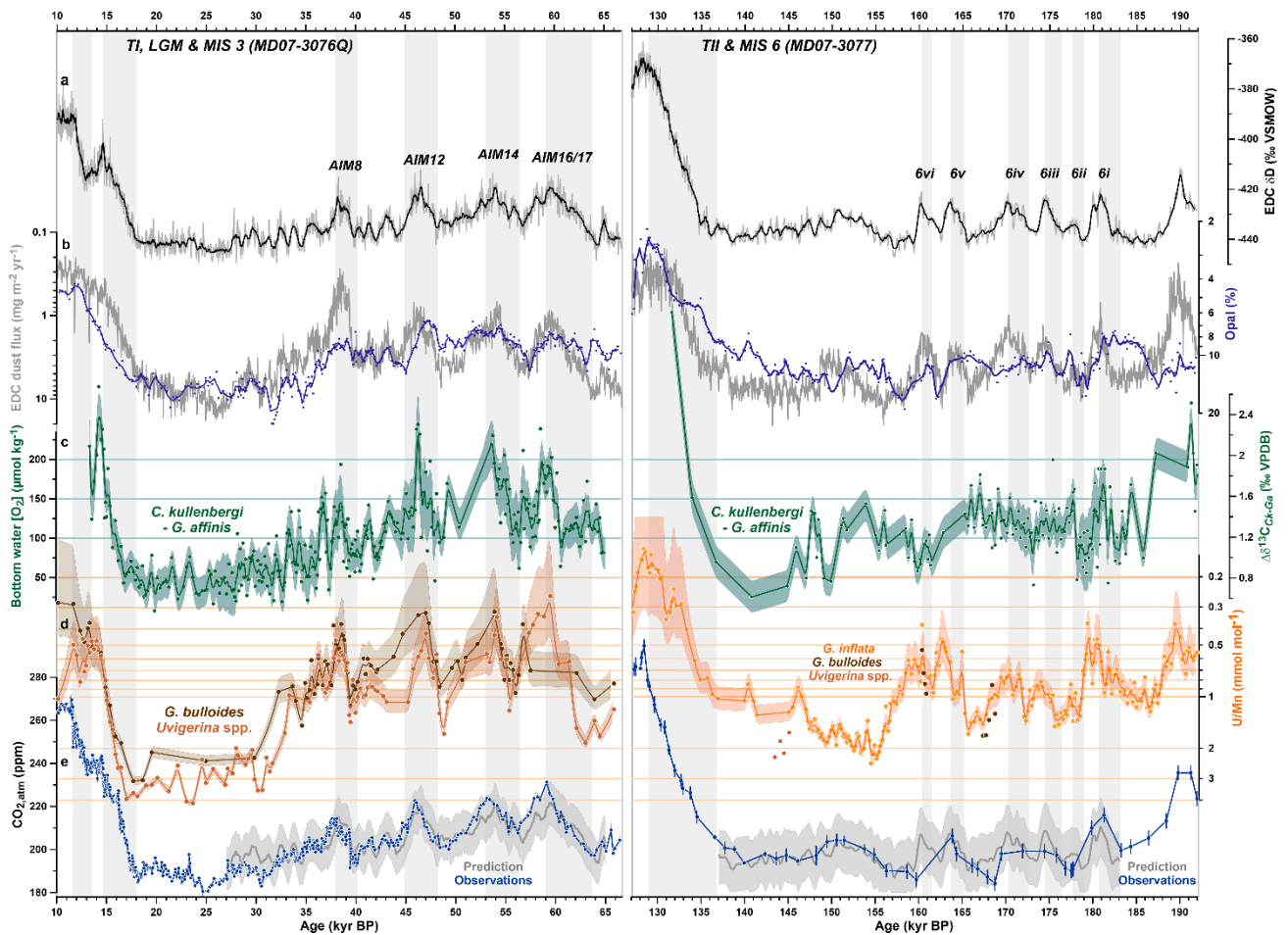
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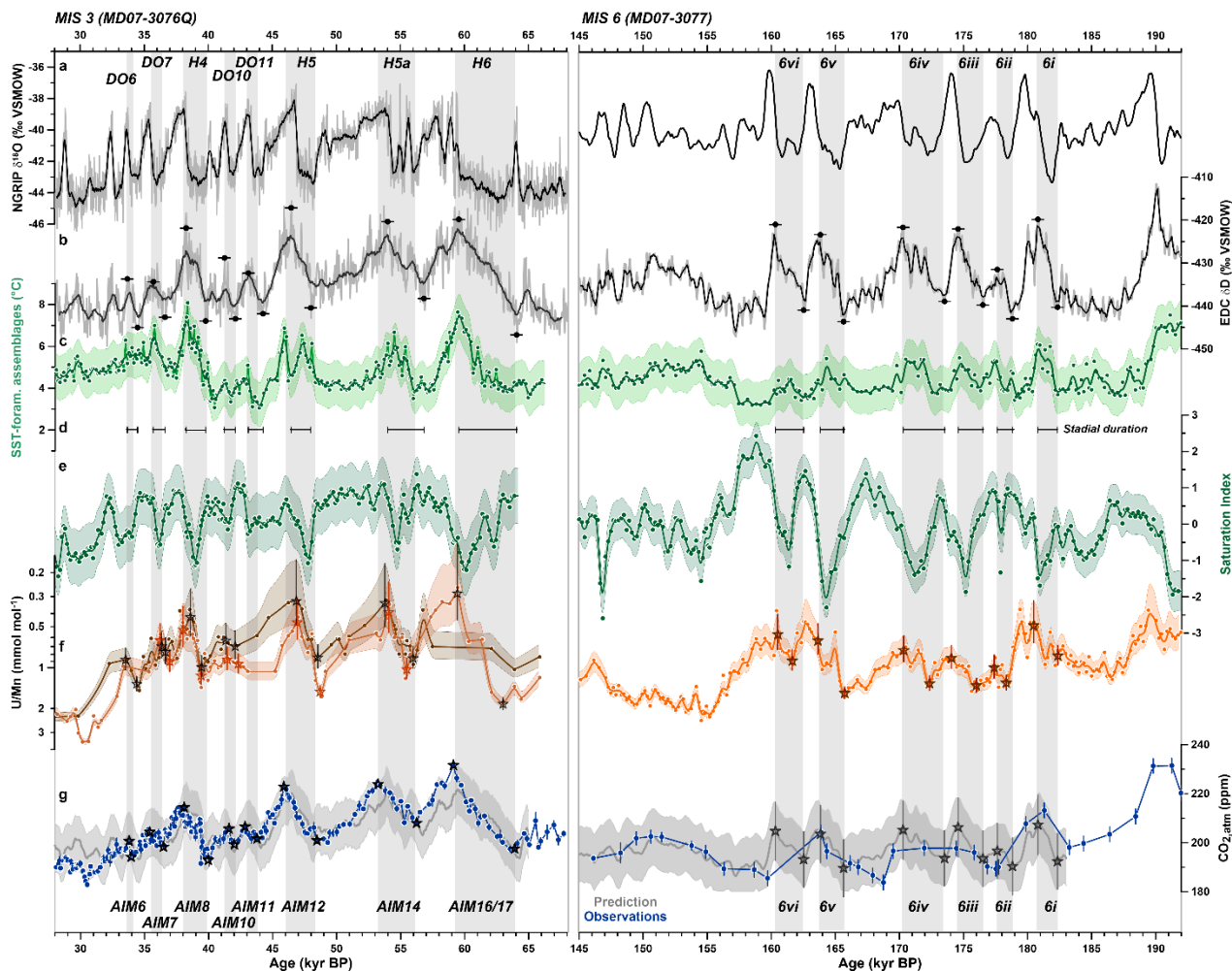
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1272 **Fig. 3. Prediction of atmospheric CO₂ levels (CO_{2,atm-PRED}) during MIS 6 based on δD variations**
1273 **in the EPICA Dome C (EDC) ice core.** Linear regression model between EDC δD (Jouzel et al.,
1274 2007) and CO_{2,atm} concentrations (Bereiter et al., 2015) for 63-32 kyr BP (MIS 3, orange: CO_{2,atm-PRED}=
1275 $1.2 \pm 0.1 \times (\text{EDC } \delta D) + 730 \pm 30$) and for 183-134.5 kyr BP (MIS 6, green: CO_{2,atm-PRED}= $1 \pm 0.2 \times (\text{EDC}$
1276 $\delta D) + 620 \pm 90$), excluding two bracketed outliers), used as a transfer function to predict CO_{2,atm} during
1277 MIS 3 and MIS 6, respectively. Gray symbols show all ice core data from 800-2 kyr BP. Envelopes
1278 (right) show the 1σ -uncertainties of the regression models.
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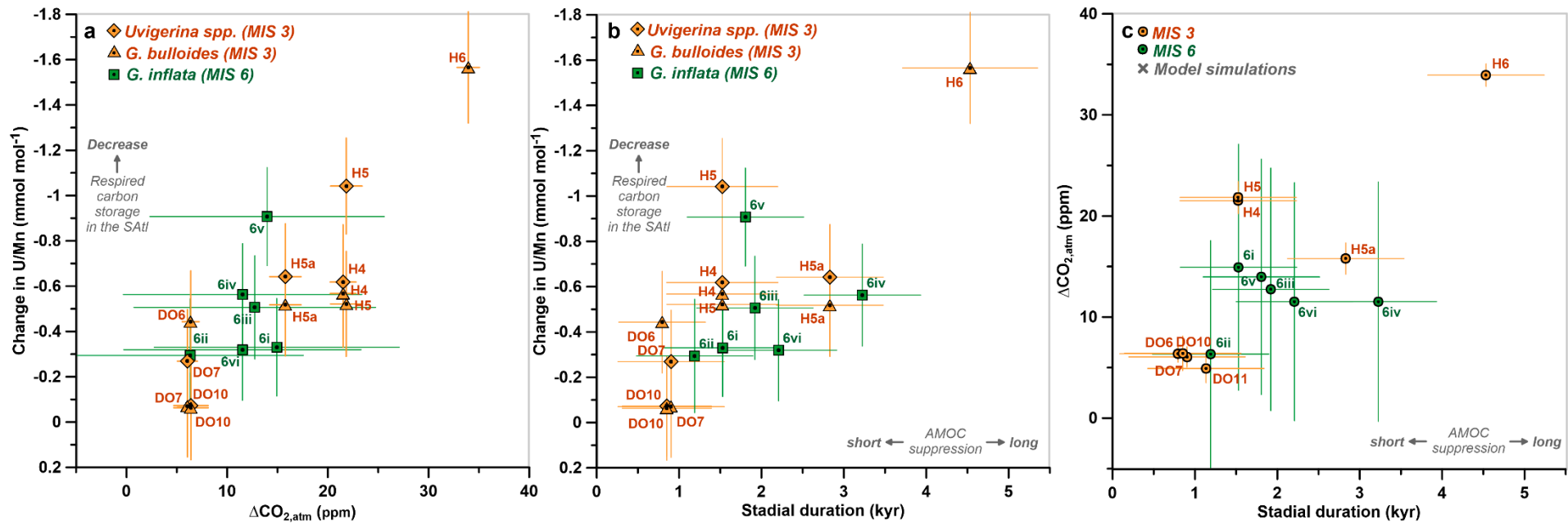
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1282 **Fig. 4. Deep-ocean oxygenation- and productivity changes in the South Atlantic during TI and**
 1283 **MIS 3 (left, MD07-3076Q), and TII and MIS 6 (right, MD07-3077).** (a) EDC δD (Jouzel et al.,
 1284 2007), (b) EDC dust fluxes (grey; Lambert et al., 2012) and sedimentary opal content at our study site
 1285 (purple, corrected for incomplete water removal as in Supplementary Fig. S1), (c) difference between
 1286 *C. kullenbergi* $\delta^{13}C$ (*Ck*) and *G. affinis* $\delta^{13}C$ (*Ga*), $\Delta\delta^{13}C_{Ck-Ga}$, and corresponding bottom water $[O_2]$
 1287 after Hoogakker et al. (2015), see Supplementary Fig. S3 for individual benthic foraminifer $\delta^{13}C$
 1288 records, (d) U/Mn ratios of *G. bulloides* (dark brown), *Uvigerina* spp. (light brown) and *G. inflata* (or-
 1289 ange) (cf. foraminiferal U/Ca ratios in Supplementary Fig. S2), (e) observed $CO_{2,atm}$ variations (dark
 1290 blue; Bereiter et al., 2015) and $CO_{2,atm}$ variations predicted from EDC δD (grey line with 1σ -envelope;
 1291 cf. Fig.3) for MIS 3 (left) and MIS 6 (right). Lines and envelopes in (b) to (d) represent 500 yr-running
 1292 averages and 1σ -uncertainties, respectively. The lower uncertainty range of *G. inflata* U/Mn is truncated
 1293 at $0.08 \text{ mmol mol}^{-1}$. Grey bars indicate intervals of rising $CO_{2,atm}$.
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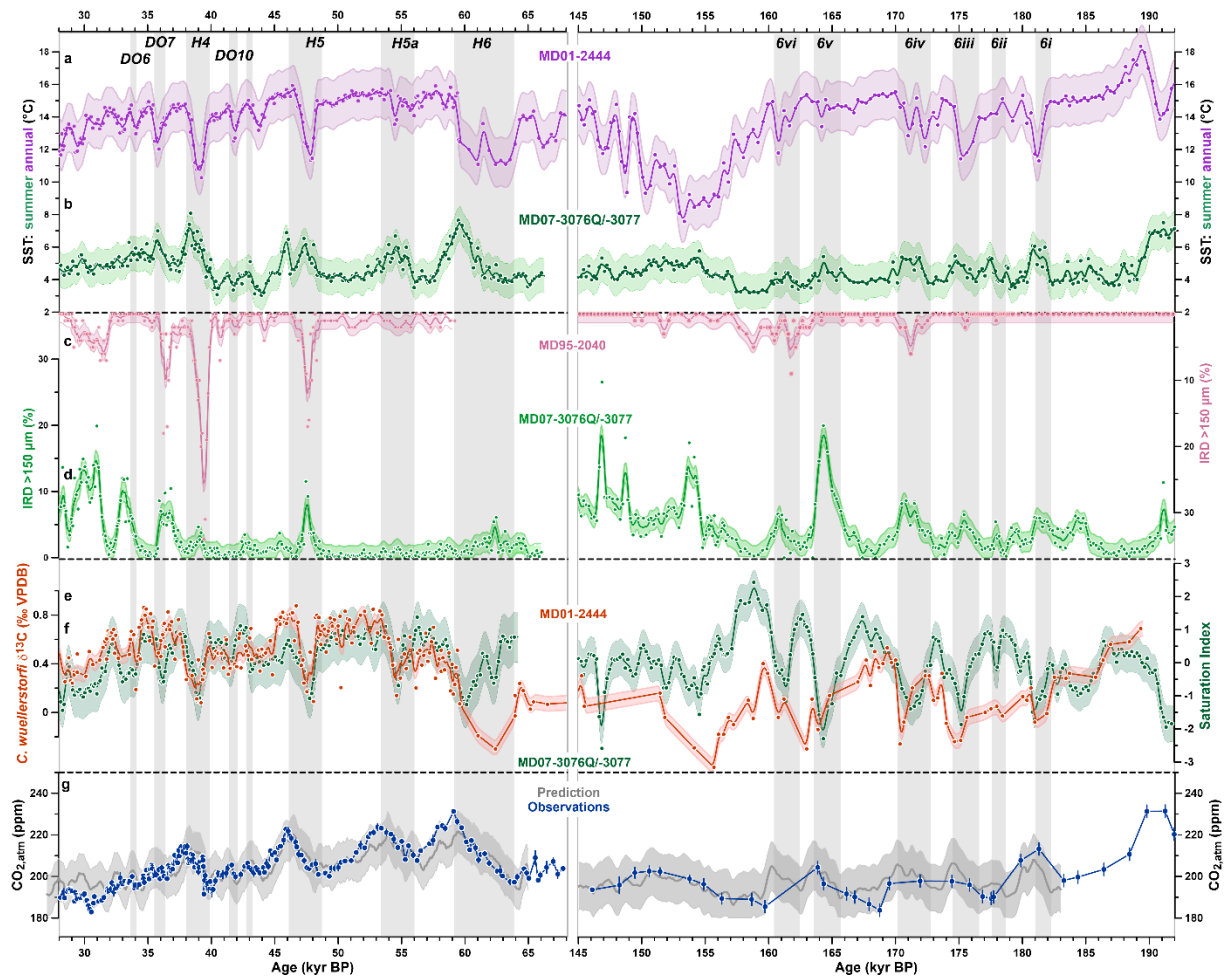
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1297 **Fig. 5. Millennial-scale CO_{2,atm} variations compared to changes in carbonate saturation and bot-**
 1298 **tom water oxygenation in the deep sub-Antarctic Atlantic during MIS 3 (left, MD07-3076Q) and**
 1299 **MIS 6 (right, MD07-3077).** (a) Observed (MIS 3: NGRIP members, 2004) and predicted NGRIP
 1300 δ¹⁸O variations (MIS 6: Barker et al., 2011), (b) EDC δD (grey; Jouzel et al., 2007) and symbols high-
 1301 lighting the onset and ends of northern-hemisphere stadials according to Margari et al. (2010) (black),
 1302 (c) summer sea surface temperatures (green; SST) derived from planktic foraminiferal assemblage
 1303 counts in the study cores and the calibration of Haddam et al. (2016), (d) stadal durations (i.e., dura-
 1304 tion of Antarctic warming) according to Margari et al. (2010), (e) saturation index as defined in
 1305 Gottschalk et al., (2015a) and shown in Supplementary Fig. S4, (f) authigenic-coating U/Mn ratios of
 1306 *G. bulloides* (dark brown), *Uvigerina* spp. (light brown) and *G. inflata* (orange), stars indicate onsets
 1307 and ends of gradual U/Mn change associated with northern-hemisphere stadials, (g) observed CO_{2,atm}
 1308 concentrations (dark blue; Bereiter et al., 2015) and CO_{2,atm}-PRED (grey) for MIS 3 (left) and MIS 6
 1309 (right), stars indicate onsets and ends of CO_{2,atm} change associated with northern-hemisphere stadials.
 1310 Grey bars indicate intervals of rising CO_{2,atm}. Annotations of Dansgaard-Oeschger (DO)-, Heinrich
 1311 (H) events and AIMs follow Dansgaard et al. (1993), Hemming (2004), EPICA Community Members
 1312 (2006) and Margari et al. (2010), respectively.
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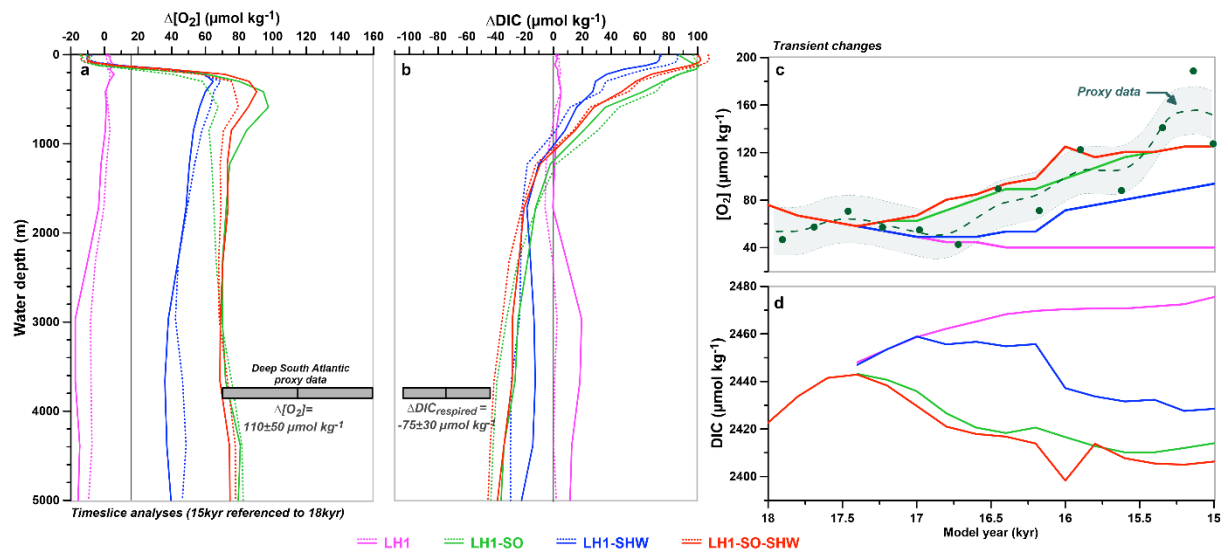
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Fig. 6. Variations in CO_{2,atm} levels during stadials and associated changes in respired carbon content at our study site. (a) Change in foraminiferal U/Mn versus parallel change in CO_{2,atm} (i.e., based on observations in MIS 3 and our MIS 6 prediction), (b) change in foraminiferal U/Mn ratios versus the duration of northern hemisphere stadials following Margari et al. (2010) and (c) change in CO_{2,atm} (i.e., based on observations in MIS 3 and our MIS 6 prediction) versus the duration of stadial conditions (circles). In (c) we also compare our proxy data with simulated CO_{2,atm} changes during stadials in freshwater hosing experiments in the North Atlantic (crosses; see review of Gottschalk et al., 2019). Data based on *G. inflata*, *Uvigerina* spp. and *G. bulloides* are shown as squares, diamonds and triangles, respectively. Time intervals are annotated as in Fig. 5. AMOC – Atlantic Meridional Overturning Circulation; SATl – South Atlantic.



1321

1322 **Fig. 7. Comparison of climate variability in the South Atlantic and the North Atlantic Ocean**
 1323 **(Iberian margin) during MIS 3 (left) and MIS 6 (right).** Sea surface temperature (SST) variability
 1324 reconstructed in (a) sediment core MD01-2444 based on alkenone unsaturation indices (annual mean
 1325 SST, purple; Martrat et al., 2007) and (b) MD07-3076Q/-3077 based on planktic foraminiferal assem-
 1326 blage counts (summer SST, green; this study), changes in the abundance of ice-rafted debris (IRD) in
 1327 (c) MD95-2040 (de Abreu et al., 2003; age model based on Margari et al. 2010) and (d) MD07-
 1328 3076Q/-3077 (this study), changes in the variability of the Atlantic Meridional Overturning Circula-
 1329 tion (AMOC) recorded in (e) epibenthic foraminiferal (*C. wuellerstorfi*) $\delta^{13}\text{C}$ changes in core MD01-
 1330 2444 (2.6 km water depth) (brown; Skinner et al., 2007; Margari et al., 2010), (f) carbonate saturation
 1331 indices in core MD07-3076Q/-3077 (green; Gottschalk et al., 2015a; this study), and (g) observed
 1332 (dark blue; Bereiter et al., 2015) and predicted $\text{CO}_{2,\text{atm}}$ levels (grey; this study). Vertical bars highlight
 1333 intervals of rising $\text{CO}_{2,\text{atm}}$ concentrations. Solid lines and error envelopes show 500 year-running aver-
 1334 ages. The error envelopes refer to 1σ -calibration uncertainties: (a) 1.5°C (Martrat et al., 2007), (b)
 1335 $\sim 1^\circ\text{C}$ (this study), 1σ -uncertainties of the IRD counts, i.e., (c) 1.5% (conservative estimate; de Abreu
 1336 et al., 2003) and (d) 1.5% (this study), (e) the external $\delta^{13}\text{C}$ reproducibility of carbonate standards
 1337 ($1\sigma=0.06\text{‰}$), (f) the 1σ -uncertainties of the saturation index, and (g) the 1σ -uncertainties of predicted
 1338 $\text{CO}_{2,\text{atm}}$ ($\sim 12\text{ ppm}$, cf. Fig. 3). All data are shown on the GICC05 or equivalent AICC2012 age scales.
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1342 **Fig. 8. Geochemical fingerprints of different forcings of millennial-scale $\text{CO}_{2,\text{atm}}$ variations in**
 1343 **transient climate model simulations with LOVECLIM (Menviel et al., 2018).** Water column pro-
 1344 files of (a) $[\text{O}_2]$ - and (b) DIC-anomalies averaged over the South Atlantic (solid lines; 60°W - 20°E , 40 -
 1345 70°S) and the Southern Ocean (stippled lines; 40 - 70°S). Simulated transient changes of (c) $[\text{O}_2]$ - and
 1346 (d) DIC-anomalies at our South Atlantic core site (lines) compared to reconstructed bottom water $[\text{O}_2]$
 1347 in core MD07-3076Q (see Fig. 4). The depth profiles show anomalies at model year 15 ka referenced
 1348 to background levels at model year 18 ka, and represent a H1 anomaly. The simulations apply transi-
 1349 ent changes in orbital parameters and in northern-hemisphere ice sheet characteristics for H1, and
 1350 force a shutdown of the AMOC through time-varying freshwater supply in the North Atlantic (simula-
 1351 tion ‘LH1’). They additionally stimulate increased Southern Ocean convection through prescribed
 1352 changes in the surface buoyancy fluxes without (simulation ‘LH1-SO’) or with intensification of the
 1353 SHW wind stress (simulation ‘LH1-SO-SHW’), or in fact with stronger SHW winds only (simulation
 1354 ‘LH1-SHW’). Gray bars indicate mean changes and 1σ -uncertainties of bottom water $[\text{O}_2]$ and respired
 1355 DIC levels at depth during millennial-scale rises in $\text{CO}_{2,\text{atm}}$ during MIS 3 derived from proxy recon-
 1356 structions in core MD07-3076Q (Fig. 4; Gottschalk et al., 2016b).