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**Approaches and constraints to the reconstruction of palaeoproductivity
from Cape Basin abyssal benthic foraminifera (South Atlantic)**

Short title: Palaeoproductivity abyssal benthic foraminifera

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28 **ABSTRACT:**

29

30 The characteristics of benthic foraminiferal assemblages from well oxygenated deep-sea
31 settings have been used to reconstruct past productivity conditions. None of the different
32 approaches that have been developed are without complications or apply in all settings. In this
33 study we assess the use of benthic foraminifera (accumulation rates and assemblages
34 composition) as proxies for palaeoproductivity changes during the last glacial period (25-95
35 kyr) in an abyssal core located in the south of Cape Basin (41.1°S, 7.8°E, 4981 m water
36 depth). Assemblage characteristics indicate a generally food-limited environment receiving
37 episodic inputs of labile organic carbon of variable strength. High seasonality in the delivery
38 of organic material to the sea floor in the form of phytodetritus influences the assemblage
39 characteristics because the corresponding response does not involve the whole community.
40 Benefiting from this occasionally high organic input is the opportunistic species,
41 *Epistominella exigua*, that reproduces rapidly to build up large populations. In general, the
42 rest of the species (i.e., less opportunistic compared to *E. exigua*) show only subtle variations
43 in their population densities and fauna composition. Under those circumstances benthic
44 foraminiferal accumulation rates seem to be independent of the amount of organic flux
45 arriving at the sediment surface and respond instead to the strength of phytoplankton blooms.

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49 Key words: benthic foraminifera, palaeoproductivity, seasonality, abyssal, phytodetritus

50

51 **INTRODUCTION**

52 The fossil record of benthic foraminifera has been widely used as a proxy for past
53 environmental conditions (for reviews see Gooday 2003; Gooday & Jorissen 2012; Jorissen *et*
54 *al.* 2007; Murray 2006). Despite the complexity of factors playing a role in foraminiferal
55 distribution and the effect of post-depositional processes (Jorissen *et al.* 2007; Murray 2001),
56 there is a general agreement that benthic foraminifera from deep sea environments largely
57 respond to a few parameters: the organic carbon flux, bottom-water hydrodynamics (and
58 related grain size), bottom and pore-water oxygenation and carbonate saturation (see reviews
59 in Mackensen *et al.*, 1995; Jorissen *et al.* 2007). Within these parameters, the estimation of
60 past changes in the primary production (and organic carbon flux to the sea floor) from benthic
61 foraminifera has received major attention in palaeoceanographic studies because of the
62 implications of changes in the biological pump on past and future climate. Based on
63 knowledge of the ecology of benthic foraminifera, a number of studies have suggested the
64 abundance of benthic foraminifera (benthic foraminiferal accumulation rates, Herguera &
65 Berger 1991), the contribution of different foraminiferal morphotypes (Corliss & Chen 1988)
66 and species composition (e.g., Altenbach *et al.* 1999) as quantitative and qualitative proxies
67 for past organic carbon fluxes arriving at the seafloor. Faunal composition might also provide
68 information about the quality (refractory versus labile) of the organic carbon (e.g., Fontanier
69 *et al.* 2005). The input of labile organic carbon to the sea floor derived from seasonal or
70 episodic phytoplankton blooms at the surface also influences assemblage composition (e.g.,
71 Smart *et al.* 1994; Sun *et al.* 2006) and diversity (e.g., Corliss *et al.* 2009; Enge *et al.* 2011;
72 Gooday *et al.* 2010, 2012) so providing information about the periodicity of the organic
73 carbon flux.

74 Evaluating the extent to which benthic foraminifera can be used to infer a particular set of
75 past environmental conditions and understanding the complicating factors and limitations of
76 such reconstructions is fundamental to advancing the use of proxy methods based on these

77 organisms. In this study we discuss palaeoenvironmental inferences based on benthic
78 foraminiferal assemblage characteristics from an abyssal core located in the south of Cape
79 Basin (South Atlantic). We examine the consistency of the most typical palaeoproductivity
80 proxies by comparing information provided by our assemblages with environmental
81 parameters from independent proxies obtained in the same core and other proxy archives.

82

83 **MATERIAL AND METHODS**

84 The marine sediment core discussed in this study (TNO57-21) was recovered in the south
85 Cape Basin, slightly north of the Agulhas ridge in the southeast Atlantic Ocean (41.1°S, 7.8°E,
86 4981 m of water depth, 13.8 m long, Fig. 1) . It is presently bathed by the poorly ventilated,
87 cold and fresh Antarctic Bottom Water (AABW). The location lies below at the Subtropical
88 Convergence (STC) front that separates the cold low-salinity Subantarctic waters to the south
89 and warm saline Subtropical waters to the north. The complex interaction of physico-
90 chemical factors associated with cross-frontal mixing of subantarctic and subtropical waters
91 and the intense turbulence and eddy activity (Baker-Yeboah *et al.* 2010; Llido *et al.* 2004)
92 results in relatively elevated pulses or episodes of primary production in the surface waters of
93 the study area (Froneman *et al.* 1997; Machu *et al.* 2005).

94 Several previous micropalaeontological studies have been carried out on core TN057-21. The
95 palaeoceanographic significance of planktonic foraminifera assemblages are discussed in
96 Barker *et al.* (2009, 2010) and (Barker & Diz 2014). The linkages between the record of the
97 benthic foraminifera *Epistominella exigua* and millennial-scale climate variability during the
98 last 95 kyr are considered in Diz & Barker (2015). However, detailed information about
99 benthic assemblage composition from ~25 to 95 kyr, and relevant additional
100 palaeoenvironmental information, were beyond the scope of these earlier papers and are
101 therefore addressed in the present study. The age model used in this study is described in

102 Barker & Diz (2014) and the methods for the study of benthic fauna are indicated in Diz &
103 Barker (2015). Briefly, foraminifera are picked from the > 125 μm fraction, mounted on
104 faunal slides and identified following the generic assignments of (Loeblich & Tappan 1987)
105 and published illustrations (see Table 1). The study of benthic foraminifera in the >125 μm
106 size fraction potentially underestimate the abundance of small (63-125 μm) opportunistic taxa
107 such as *Alabaminella weddellensis* which are typically abundant in areas characterized by
108 episodic phytoplankton blooms (e.g., Diz *et al.* 2007; Smart *et al.* 2010; Thomas *et al.* 1995).
109 On the other hand, it allows for studying a feasible number of samples still showing major
110 faunal patterns (e.g., Poli *et al.* 2012, Schönfeld *et al.* 2012). Raw counts can be found in Diz
111 & Barker (2015) and the most characteristic species of benthic foraminifera are illustrated in
112 this study (Plate I). The assemblages are largely dominated by *Epistominella exigua* (>40%
113 on average), a phytodetritus related species. In order to assess the ecological significance of
114 the other relevant species we discuss the assemblages after removing the contribution of *E.*
115 *exigua* (i.e., the "phytodetritus free assemblage", see also Thomas *et al.* 1995). Additionally,
116 we examined the record of benthic foraminiferal accumulation rate (BFAR, total number of
117 foraminifera $\times \text{cm}^{-2} \times \text{kyr}^{-1}$) and phytodetritus free benthic foraminiferal accumulation rate
118 (BFAR_{phfree}). BFARs are calculated as the number of individuals per gram of total dry bulk
119 sediment ($\#bf \times \text{g}^{-1}$, Diz & Barker 2015) \times linear sedimentation rates ($\text{cm} \times \text{kyr}^{-1}$) \times density (g
120 $\times \text{cm}^{-3}$). Sedimentation rates are taken from the age model developed by Barker & Diz (2014)
121 and vary from 8 to 16 cm kyr^{-1} . It is considered that the age model is sufficiently robust as to
122 assume that differences in BFAR are not mainly caused by inaccuracies in the calculation of
123 sedimentation rates. In the absence of direct measurements of dry or wet bulk density, we
124 used the algorithm developed by Sachs & Anderson (2003) for the calculation of, which is
125 based on the percentage of calcium carbonate in order to calculate densities in core TNO57-
126 21. To do this, the high resolution % CaCO_3 record of core TNO57-21 (Sachs & Anderson

127 2003) was re-sampled and values interpolated to the lower resolution record of benthic
128 foraminiferal abundance using the program Analyseries (Paillard *et al.* 1996). Then, density
129 values were calculated using Sachs and Anderson' formula. Calculated values vary between
130 0.5 to 0.7 g x cm⁻³.

131 The core TNO57-21 was recovered from deep waters that are currently undersaturated with
132 respect to calcium carbonate (4891 m water depth, see Supplementary Information by Barker
133 *et al.* 2010). Several episodes of increased carbonate dissolution have been identified in
134 planktonic foraminiferal (Barker & Diz 2014; Barker *et al.* 2009, 2010) as well as benthic
135 foraminiferal (Diz & Barker 2015) assemblages. By considering the information provided by
136 multiple proxies (e.g., % of coarse fraction, % CaCO₃, foraminiferal abundances, composition
137 of assemblages) it was indicated that carbonate dissolution does not seem to exert an overall
138 control on benthic abundance or species distribution with the exception of the Holocene (not
139 considered in this study) and Greenland Stadial (GS) events GS19 and 21. Those poorly
140 preserved periods (indicated in figure 2 by bars) are characterized by low percent of calcium
141 carbonate, very low foraminiferal abundances and low number of benthic taxa. They are not
142 used to infer palaeoenvironmental conditions (see detailed discussion in Diz & Barker 2015).
143 The comparison of the composition of the "dissolved assemblages" with modern samples
144 (Mackensen *et al.* 1993) indicates that *Nutallides umboniferus* is very rare along core TNO57-
145 21 (see Plate). *N. umboniferus* is generally related to corrosive bottom waters in the South
146 Atlantic (Mackensen *et al.* 1993; Harloff & Mackensen, 1997; Schmiel *et al.* 1997). It might
147 suggest that other factors more than carbonate undersaturated waters are playing a role in this
148 species distribution (i.e, oligotrophic conditions and absence of phytodetritus deposition,
149 Smart & Gooday, 1997; Kurbejeweit *et al.* 2000; Carman & Keigwin, 2004).

150

151 **RESULTS**

152 The foraminifera fauna of core TNO57-21 comprises 39 benthic species dominated by
153 calcareous forms. The Shannon H diversity Index averages 1.9 (Figure 2a). High diversity
154 values occur when the relative contribution of the dominant phytodetritus-related species
155 *Epistominella exigua* (Brady) are diminished. The averaged relative contribution of this
156 species is as high as 47% (Fig. 2b). Other, relatively common species are *Pullenia osloensis*
157 (Feyling-Hanssen) (average percentage 11.9%, Fig. 2d), *Oridorsalis umbonatus* (Reuss) (6%,
158 Fig. 2h), *Fontbotia wuellerstorfi* (Schwager) (7.9%, Fig. 2g) and the group of species
159 belonging to the suborder *Lagenina* called "Lagenina group" (see Table 1, 11.9%, Fig. 2c).
160 Secondary calcareous species (<10 % on average) showing high abundances at particular
161 intervals are *Pyrgo murrinha* (Schwager) (Fig. 2j), *Globocassidulina subglobosa* (Brady)
162 (Fig. 2i), *Melonis* spp. (comprised of *M. zaandamae* (Van Voothuysen), *Melonis pompilioides*
163 (Fichtel and Moll) and *Melonis* sp., Fig. 2f) and *Rutherfordoides tenuis* (Phleger and Parker)
164 (Fig. 2l). Calcareous species with short-lived peaks are *Uvigerina auberiana* (d'Orbigny)
165 (Fig. 2m) and *Quinqueloculina* cf. *seminula* (Fig. 2n). The most characteristic agglutinated
166 foraminifera is the calcareous agglutinated *Siphotextularia rolshauseni* (Phleger and Parker,
167 Fig.2e) with *Eggerella bradyi* (Cushman) as secondary species (Fig. 2k).

168 The BFAR values in core TNO57-21 show large fluctuations ranging from 30 to 1100
169 foraminifera ($> 125 \mu\text{m}$ fraction) $\text{cm}^{-2} \text{kyr}^{-1}$. On average, peak BFAR values are higher during
170 northern stadial events occurring during MIS 3 than over MIS 5 (Fig. 3a). The lowest BFAR
171 values occur during GS19 and GS21 (also the Holocene, not shown) when benthic
172 foraminiferal dissolution was inferred (Diz & Barker 2015) and thus they are excluded from
173 interpretation (Fig. 3a). In general, episodes of peak BFAR values are largely driven by the
174 phytodetritus-related species *Epistominella exigua* (Fig. 3a), and show a tight temporal
175 correspondence with abrupt climate changes occurring in the North Atlantic Ocean and
176 concomitant antiphase response in the South Atlantic (see Fig. 3 and Diz & Barker 2015).

177 Episodes of high $\text{BFAR}_{\text{phfree}}$ coincide with BFAR although they are of much lower magnitude
178 and sharpness (Fig. 3a, grey shaded area). The highest $\text{BFAR}_{\text{phfree}}$ values coincide with a
179 single peak in *Quinqueloculina cf. seminula* (Fig. 2n) at ~45 kyr and near the beginning of
180 MIS 3 (~56-58 kyr) with high relative abundances of *G. subglobosa*, *F. wuellerstorfi* and *O.*
181 *umbonatus* (see Figure 2).

182

183 **DISCUSSION**

184 **Reconstructing the flux of organic carbon to the seafloor from benthic foraminifera**

185 **Benthic foraminiferal accumulation rates.** The benthic foraminiferal accumulation rate
186 (BFAR, number of foraminifera $\times \text{cm}^{-2} \times \text{kyr}^{-1}$) has been suggested as a palaeoproductivity
187 proxy (Herguera 1992, 2000; Herguera & Berger 1991). However, several studies indicated
188 that obtaining a quantitative estimation of primary production or export production from
189 BFAR values might be limited by several factors, with the difficulty of obtaining reliable
190 calibrations, carbonate dissolution and taphonomical processes being the most important (see
191 review in Jorissen *et al.* 2007). In this study no attempts have been made to estimate absolute
192 palaeoproductivity or palaeo-carbon fluxes, but we evaluate the potential use of the calculated
193 BFAR as a semi-quantitative proxy for food supply to the ocean floor (e.g., Thomas *et al.*
194 1995; Alegret & Thomas 2009) in core TNO57-21.

195 The BFAR values during the Holocene and late deglaciation (not plotted but calculated on the
196 basis of Diz & Barker (2015) data; <100 foraminifera $\text{cm}^{-2} \text{kyr}^{-1}$) are within the range of
197 values for abyssal core tops from the Pacific open ocean at water depths > 4000 m likely
198 affected by carbonate dissolution (Herguera 1992; Herguera & Berger 1991). However, peak
199 BFAR values from MIS 3 to MIS 5 are four to eight times Holocene values (Figure 3). These
200 accumulation rates are substantially higher than maxima values recorded in core-top samples

201 from widely distributed open-ocean areas at various depths in the Pacific. Following the use
202 of BFAR as a palaeoproductivity proxy, these results might suggest past increases in the
203 organic carbon flux to the sea floor up to several times the present conditions. According to
204 modern primary production distributions (see Machu *et al.* 2005, their Fig. 5) this might be
205 equivalent to a change from oligotrophic subtropical open ocean areas to high productivity
206 upwelling centres (e.g., Benguela upwelling). In fact, peaks of BFAR reach values found in
207 continental shelf areas affected by seasonal upwelling such as Cape Blanc upwelling
208 (Guichard *et al.* 1999; Zarriess & Mackensen 2010) or the Southwest African upwelling
209 (Schmiedl & Mackensen 1997). Such a change in the palaeoenvironmental conditions, if it had
210 occurred, would have involved a large change in assemblage composition, i.e. from low
211 productivity faunas (low abundances) to a high productivity assemblage (high BFAR). This
212 seems to be unrealistic considering that assemblage changes are subtle in comparison to
213 BFAR fluctuations (see Figure 2-3) and they do not involve the appearance of species related
214 to eutrophic conditions (see next section). In fact, variations in BFAR are mainly driven by
215 the phytodetritus-related species *Epistominella exigua* (Table 1, Figure 3a). In the absence of
216 this species fluctuations in BFAR_{phfree} (BFAR phytodetritus free; "phfree") are of much lower
217 magnitude and suggest only subtle changes in organic carbon fluxes.

218 This could be explained by the fact of that when large quantities of fresh marine organic
219 matter (phytodetritus) are available, even for short periods of time, opportunistic species, such
220 as *Epistominella exigua*, reproduce rapidly and produce a large number of tests (see Thiel *et*
221 *al.* 1989). The accumulation of foraminifera is not related in a predictable manner to organic
222 flux and, in these circumstances, BFAR should not be used as a quantitative (or
223 semiquantitative) proxy (Thomas *et al.*, 1995; Diz *et al.*, 2007; Smart, 2008; Zarriess &
224 Mackensen, 2010) for the organic carbon flux reaching the sea floor. BFAR is rather related
225 to the strength of the phytoplankton blooms. The episodic and labile nature of the

226 phytodetritus aggregates reaching the sea floor (Beaulieu 2002; Smith *et al.*, 2008) could
227 explain the weak correlation ($r = -0.24$, $p = 0.000$, $n = 467$) between BFAR (also $\text{BFAR}_{\text{phfree}}$)
228 and the alkenones flux, a proxy for averaged organic carbon flux to the seafloor (Sachs &
229 Anderson 2003) obtained in the same core (Fig. 3c).

230

231 **Benthic foraminiferal assemblage composition.** The use of benthic foraminiferal
232 assemblages as palaeo-productivity proxies is based on the relation of faunal composition to
233 organic flux rates (e.g., Morigi *et al.* 2001). Again, the quantification of flux regimes from the
234 relative abundance of major species is complicated by ecological factors, broad adaptability of
235 some species to organic carbon fluxes and uncertainties related to estimations of carbon flux
236 (Altenbach *et al.* 1999; Gooday 2003; Jorissen *et al.* 2007). Thus, the information provided by
237 the faunal composition of core TNO57-21 is used here as qualitative proxy for the organic
238 carbon flux or its quality/periodicity.

239 The relative abundance of particular species or group of species is related qualitatively to the
240 predominance of a particular flux regime (i.e., high, intermediate, low-flux species), quality
241 (i.e., labile, refractory) or seasonality of the flux (i.e., seasonal, sustained). In this study,
242 groups are defined based on representative species with well-known ecology (see the
243 ecological attributions of characteristic species in Table 1). Because organic flux dependent
244 patterns should be best analysed within the environmental optimum of species (Altenbach *et al.*
245 1999) those species with percentages lower than 10% for most of the record (e.g.,
246 *Eggerella bradyi*, *Quinqueloculina cf. seminula*, *Rutherfordoides tenuis*, see Plate) and/or
247 those species for whom the ecology is not well-constrained are not included in any of the
248 groups. An example of the later is the high contribution to the assemblage of individuals
249 belonging to the "Lagenina group" (>10%, Fig. 2c, see Plate). Unfortunately their ecology is

250 poorly known (see Table 1) and consequently the contribution to the paleoenvironmental
251 understanding of the assemblage changes is limited.

252 The most abundant species throughout the core is *Epistominella exigua*, an epifaunal/shallow
253 infaunal abyssal deep-sea opportunistic foraminifera that flourishes and rapidly reproduces in
254 the presence of phytodetritus aggregates (see ecological attributions in Table 1). Thus, high
255 relative abundance of *E. exigua* (Figure 2b) along core TNO57-21 indicates overall low
256 organic carbon fluxes punctuated by episodic phytoplankton blooms that resulted in the
257 deposition of phytodetrital inputs (i.e., labile organic carbon). This interpretation is supported
258 by the "phytodetritus free" assemblage which is composed by species typical of oligotrophic
259 ("low flux") to moderately mesotrophic ("intermediate") environmental conditions.

260 The "low-flux species" are the epifaunal *Fontbotia wuellerstorfi*, *Pyrgo murrinha* and the
261 shallow infaunal *Oridorsalis umbonatus* and *Globocassidulina subglobosa* (see Table 1). All
262 together these represent > 30% of the phytodetritus free assemblage (Fig. 3f) reaching up to
263 60% during early MIS3. For some of these species (i.e. *G. subglobosa*, *F. wuellerstorfi*, *P.*
264 *murrinha*) a relationship to phytodetritus input (See Table 1) has also been suspected.

265 However, their downcore relative abundance does not covary with BFAR or percentages of
266 phytodetritus-related species *E. exigua* (Figure 3). Instead, they must respond to a different
267 type of phytodetritus or, more likely, they prefer sustained (and low) organic carbon flux to
268 the sea floor rather than pulsed (see also Smart, 2008).

269 The group of species considered indicative of an "intermediate -flux" regime are mainly
270 represented by the relatively common shallow infaunal *Pullenia osloensis* together with
271 *Melonis* spp. and *Siphotextularia rolshauseni* (Figure 3e, Table 1). Those species show a
272 statistically significant negative correlation ($p < 0.000$) to the relative contribution of the
273 species belonging to low - flux group ($r_{O. umbonatus-S. rolshauseni} = -0.38$; $r_{P. osloensis-P. murrinha} = -0.39$; $r_{P.$
274 $osloensis-F. wuellerstorfi} = -0.28$; $r_{P. osloensis-G. subglobosa} = -0.23$; $r_{O. umbonatus-Melonis spp.} = -0.35$). The relative

275 contribution of the "intermediate-flux" group indicates slightly more eutrophic conditions
276 during MIS 5 and MIS 4 than during MIS 3. Peaks of the intermediate flux fauna occurring
277 over MIS 4 are mainly caused by noticeably increased contributions of *Melonis* spp. and *S.*
278 *rolshauseni* (Figure 2d-f, Figure 3e) occurring in coincidence with high relative contribution
279 of *Epistominella exigua* (Fig. 2-3) and the substantial increase in the alkenone flux measured
280 during glacial MIS 4 (Fig. 3c). These two species show affinity for degraded organic carbon
281 (Table 1) suggesting that during MIS 4 part of the sedimentary organic compounds are of low
282 nutritional value. This might be explained by a different type and/or fate of phytodetrital
283 material arriving to the seafloor which could promote the response of species that benefit
284 from the bloom indirectly (i.e., bacteria colonizing aggregates, Koho *et al.*, 2008). In fact, it
285 has been inferred (Diz & Barker 2015) that a slightly different physical conditions promoting
286 phytoplankton blooms in the surface waters occurred during MIS 4/MIS 5 transition and early
287 MIS 4 (seasonality and windiness) than during MIS 3 and late MIS 5 (mainly eddy activity).
288 Notably, that assemblage change does not trigger a parallel increase in the $\text{BFAR}_{\text{phfree}}$
289 indicating that a change in the food quality does not force a change in the absolute numbers of
290 benthic foraminiferal accumulation rate but only in the assemblage composition.

291

292

293 **CONSTRAINTS AND APPROACHES: OVERVIEW**

294

295 Benthic foraminifera (BFAR and assemblage composition) were analysed in abyssal core
296 TN057-21 . Episodic phytoplankton blooms represents the main source of "disturbance" to the
297 benthic environment and have important consequences for the structure and taxonomic
298 composition of the benthic foraminifera record. The inferred phytodetritus deposition does not

299 seem to trigger a response by the whole community but it is limited to a single species,
300 leading to a decrease in the diversity of the assemblages. The species benefiting from
301 phytodetritus input is the opportunistic (r-strategist) *Epistominella exigua* which reacts
302 quickly, producing high numbers of individuals and consequently high benthic foraminiferal
303 accumulation rates. The response of the remaining fauna (the so called "phytodetritus free
304 assemblage") to phytodetritus input is mainly constrained to a concomitant moderate increase
305 in the foraminiferal abundance ($\text{BFAR}_{\text{phfree}}$) with overall little variations in the assemblage
306 composition. This could be explained by the different ecological preferences of species with
307 lower reproductive potential (k-strategists) and likely benefiting from other type organic
308 carbon (less labile). All these data together suggest BFAR could not be a reliable proxy for
309 palaeoproductivity in abyssal (food limited) environments when benthic foraminifera are
310 highly dependent on the rate and nature of the input of labile organic material generated in the
311 euphotic zone. Under these circumstances fluctuations in BFAR do not reflect the flux of
312 organic carbon to the seafloor but rather the strength of phytoplankton blooms in the surface
313 waters. In this case, the assemblage composition is relevant for interpreting
314 palaeoenvironmental conditions.

315

316

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323

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566

567 **FIGURE CAPTIONS:**

568

569 **Figure 1:**

570 Location of core TN057-21 in the South Atlantic Southern Ocean (map elaborated using
571 Ocean Data View, Schlitzer, R., <http://odv.awi.de>, 2015). Detailed information about modern
572 hydrography and primary productivity patterns can be found in Llido *et al.* (2004) and Machu
573 *et al.* (2005).

574

575 **Figure 2: Benthic foraminiferal assemblages in core TN057-21**

576

577 Shannon-H diversity index (a) and the relative abundance of *Epistominella exigua* (b) and the
578 most characteristic species of benthic foraminifera in core TNO57-21 (c-n). Percentages are
579 shown in the total assemblage (grey line) and in the phytodetritus free assemblages (black
580 filled area). Percentages are calculated on the basis of samples containing > 50 specimens and
581 non affected by dissolution. Intensely dissolved intervals that correspond to Greenland
582 Stadials 19 and 21 are indicated by vertical bars. The ecological preferences for the most
583 characteristic benthic foraminiferal species or group of species are summarized in Table 1.

584

585 **Figure 3: Paleoproductivity from benthic foraminiferal accumulation rates and**
586 **assemblage composition**

587

588 The Benthic Foraminiferal Accumulation Rate (BFAR, total number of foraminifera >125 μm
589 $\text{cm}^{-2} \text{ kyr}^{-1}$) is indicated as a shaded black areas and Benthic Foraminiferal Accumulation Rate
590 calculated on phytodetritus free basis (i.e., discounting the contribution of the phytodetritus-

591 related species *Epistominella exigua*, $\text{BFAR}_{\text{phfree}}$) is indicated by a grey shaded area (a).
592 Consequently, the difference between the two shaded areas is the BFAR of *E. exigua*
593 ($\text{BFAR}_{E.exigua}$). Figure c displays the flux of alkenones ($\text{ng cm}^{-2} \text{ kyr}^{-1}$) in core TNO57-21, a
594 proxy for organic carbon flux to the seafloor (Sachs & Anderson, 2005) plotted on Barker &
595 Diz (2014) age model. The group of "low flux" species (e) is composed by shallow infaunal
596 *O. umbonatus*, *G. subglobosa* and epifaunal *P. murrinha* and *F. wuellerstorfi*. Intermediate
597 flux species (light grey line, d) is constituted by individuals belonging to *P. osloensis*, *S.*
598 *rolhsauseni* (medium grey line) and *Melonis* spp. (dark grey line). Percentages are calculated
599 on the phytodetritus free assemblage basis. Records of Southern Hemisphere ice core
600 temperature (f, Antarctica Epica Dome C δD , Jouzel *et al.*, 2007, 3 points running average)
601 and Northern Hemisphere ice core temperature record (b, Greenland NGRIP $\delta^{18}\text{O}$; EPICA,
602 2006) are showed as reference. Figures b and f are plotted on GICC05/NALPS timescale
603 (Barker *et al.*, 2011). Black crosses on the top indicate tie points and sedimentation rates
604 respectively used in the age model construction and BFAR calculations. Grey line on the top
605 plot shows density values calculated using model proposed by Sachs & Anderson (2003).

606

607

608

609 **TABLE CAPTIONS:**

610

611 **Table 1:** Ecological attributions of the most characteristic benthic foraminiferal species in
612 core TNO57-21..

613

	SPECIES	MICROHABITAT	ECOLOGICAL SIGNIFICANCE
Low Flux	<i>Fombotia wuellerstorfi</i> (Schwager)= <i>Anomalina wuellerstorfi</i> Schwager, 1866. See Phleger <i>et al.</i> 1953, Pl. 11, Fig. 1-2. This work, Plate I, Fig. 8.	Epifaunal/ Epibenthic	<i>F. wuellerstorfi</i> is an epibenthic species (Linke & Lutze, 1993) that lives in well oxygenated and ventilated bottom waters away from high productivity coastal environments. Global distributional patterns indicate that it prefers organic fluxes below 2 gCm ⁻² yr ⁻¹ (Altenbach <i>et al.</i> 1999). In the South Atlantic, the distribution of this species coincides with relatively sustained food fluxes in areas where carbonate dissolution is not too severe (Mackensen <i>et al.</i> , 1995). In deep sea sediments of the Indian Ocean <i>F. wuellerstorfi</i> co-occurs with the phytodetritus species <i>E. exigua</i> . On ocean wide scale it co-occurs with <i>Uvigerina peregrina</i> (a typical high-flux species) on the lower range of organic carbon fluxes of the later (Altenbach <i>et al.</i> , 1999). This information suggest that <i>F. wuellerstorfi</i> is adapted to a wide range of environmental conditions, including strongly pulsed supply of organic carbon in the Indian Ocean (Gupta, 1997; De & Gupta, 2010).
Low Flux	<i>Oridorsalis umbonatus</i> (Reuss) = <i>Rotalina umbonata</i> Reuss 1851. See Smith, 1964, Pl. 4, Fig. 8 as <i>Pseudoepionides umbonatus</i> . This work, Plate I, Fig. 15. Most of the individuals found in core TNO57-21 are juvenile forms.	Shallow infaunal	On an ocean wide scale, <i>O. umbonatus</i> seems to be distributed in areas receiving low organic carbon fluxes (Altenbach <i>et al.</i> 1999). Mackensen <i>et al.</i> (1995) suggest that the distribution of <i>O. umbonatus</i> in the South Atlantic is related to relatively well-oxygenated pore waters receiving a relatively low but sustained food supply. It co-occurs with <i>E. exigua</i> in the carbonate supersaturated and low organic carbon areas of the Weddell sea continental Shelf (Mackensen <i>et al.</i> 1990). In the eastern Indian Ocean, Murgese & DeDecker (2005) found the assemblage composed by <i>O. umbonatus</i> - <i>E. exigua</i> and <i>P. murrhina</i> indicator of low organic carbon. In Sulu area, Miao & Thunell (1993) indicated <i>O. umbonatus</i> as a species inhabiting shallow infaunal low organic carbon, well oxygenated sediments in agreement with Rathburn & Corliss (1994). Likewise, Burke <i>et al.</i> (1993), include <i>O. umbonatus</i> together with <i>Eggerella bradyi</i> within the group of low productivity species in the central Pacific. Conversely Gupta (1997) interpret the group of <i>O. umbonatus</i> , <i>Eggerella bradyi</i> , and <i>Melonis pompilioides</i> as reflect intermediate flux of relatively degraded organic matter and Kaiho (1999) consider <i>O. umbonatus</i> as an indicator of low-oxygen conditions.
Low Flux	<i>Pyrgo murrhina</i> (Schwager)= <i>Biloculina murrhina</i> Schwager 1866. See Phleger <i>et al.</i> 1953, Pl. 5, Fig. 22-24.	Epifaunal	<i>Pyrgo murrinha</i> is an epifaunal species (Corliss & Chen, 1988) found in areas of low organic carbon fluxes (Altenbach <i>et al.</i> , 1999) and high oxygenation such as the South Central Indian Ocean (De & Gupta, 2010) or eastern Indian Ocean (Murgese & De Deckker, 2005). Conversely, Gupta & Thomas (2003) interpret the abundance of <i>P. murrinha</i> in Indian cores as related to pulsed food and good carbonate preservation.
Low Flux	<i>Globocassidulina subglobosa</i> (Brady)= <i>Cassidulina subglobosa</i> Brady, 1881. See Parker 1958, Pl. 4, Fig. 13. This work, Plate I, Fig. 10.	Epifaunal/ Infaunal	In the North Atlantic Sun <i>et al.</i> (2006) found an inverse correlation of the <i>G. subglobosa</i> - <i>N. umbonifera</i> assemblage with seasonality of the organic matter. In the Southeast Atlantic, this species characterize sandy sediments of the Walvis Ridge (South Atlantic) with low organic carbon and high calcium carbonate content and enhanced bottom current velocities (Schmiel <i>et al.</i> 1997). However, <i>G. subglobosa</i> has been associated with deposition of phytodetritus in the Northeast Atlantic Abyssal Plain Gooday (1988, 1993), North West Africa (Eberwein & Mackensen (2006) and the Antarctic shelf (Suh <i>et al.</i> 2003).
Episodic phytoplankton blooms	<i>Epistominella exigua</i> (Brady)= <i>Pulvinulina exigua</i> Brady, 1884. See Lobegeier & Sen Gupta, 2008, Pl. I, Fig. 18. This work, Plate I, Fig. 9.	Epifaunal/ Shallow infaunal	This is an opportunistic species that rapidly colonizes and feeds on aggregates of phytodetritus produced by episodic phytoplankton blooms (e.g., Gooday, 1988, 1993, Cornelius & Gooday, 2004; Sun <i>et al.</i> 2006; Gooday <i>et al.</i> 2010). <i>Epistominella exigua</i> is well adapted to oligotrophic conditions well away from areas where the productivity is high and the flux of organic matter is continuous (Mackensen <i>et al.</i> 1995). In the eastern South Atlantic <i>E. exigua</i> is found in association with <i>F. wuellerstorfi</i> in low organic carbon areas on the flanks of the Walvis Ridge (Schmiel <i>et al.</i> 1997). It is also abundant in the deep western South Atlantic (Harloff & Mackensen, 1997) the deep Weddell Sea continental slope (Anderson, 1975; Cornelius & Gooday, 2004) and South West Indian Ocean (Peterson, 1983; Corliss, 1983).
Intermediate Flux	<i>Pullenia osloensis</i> Feysling-Hanssen, 1954. See Diz <i>et al.</i> 2007-Supplementary information, Pl. II, Fig. 5. This work, Plate I, Fig. 16.	Not very well constrained Shallow to deep infaunal	The ecology of <i>Pullenia osloensis</i> is not well known. This species is described in deep and abyssal areas of the South Cape Basin (Boltovskoy & Boltovskoy, 1989), Southwest Indian Ocean (Corliss, 1979) and the Agulhas retroflection area (Diz <i>et al.</i> 2007). Most authors interpret the group of <i>Pullenia</i> spp. (mainly <i>Pullenia bulloides</i>) as indicator of areas of high organic supply (Rasmussen <i>et al.</i> 2003) or high but varying surface productivity (Mackensen <i>et al.</i> 1995). In the Indian Ocean, the assemblage dominated by <i>Epistominella exigua</i> with <i>Pullenia osloensis</i> and <i>Pullenia salisburyi</i> as secondary species is considered indicator of low to intermediate organic flux and high seasonality (Gupta & Thomas, 2003). <i>Pullenia osloensis</i> is common along core TNO57-21 suggesting that it is adapted to a wide range of carbon flux regimes (from low to intermediate) and organic carbon qualities (i.e., labile and refractory). <i>Pullenia salisburyi</i> is also present in core TNO57-21 (Plate, Fig. 17) even though its relative contributions are lower than <i>P. osloensis</i> .
Intermediate Flux	<i>Melonis zaandamae</i> (Van Voothuysen) = <i>Melonis barleeaanum</i> var. <i>zaandamae</i> van Voothuysen, 1952. See Mackensen <i>et al.</i> 1993, Pl.3, Fig. 4-5. This work, Plate I, Fig. 13.	Shallow infaunal	<i>Melonis</i> spp. species (in this core mainly <i>M. zaandamae</i>) are intermediate infaunal foraminifera that tolerates moderate oxygen depletion (Fontanier <i>et al.</i> , 2002). It is generally associated to intermediate organic carbon flux and refractory organic matter (Caralp, 1989; Alve, 2010). Mackensen <i>et al.</i> (1993, 1995) refer to the assemblage comprising <i>Melonis pompilioides</i> , <i>M. zaandamae</i> , and <i>O. umbonatus</i> as South Atlantic deep sea high productivity fauna.
Intermediate Flux	<i>Siphotextularia rolshauseni</i> Phleger and Parker, 1951. See Phleger <i>et al.</i> 1953, Pl. 5, Fig. 7. This work, Plate I, Fig. 2.	Not well constrained	<i>Siphotextularia rolshauseni</i> is an agglutinated species composed of calcareous fragments of various sizes and it is considered a junior synonym of <i>Siphotextularia catenata</i> Cushman (Corliss, 1979, Nees & Struck, 1994). There are a few references to this species in superficial sediments of the North Atlantic (see review Nees & Struck, 1994), Southwest Pacific (Kurihara & Kennett, 1986), South China Sea (Szarek <i>et al.</i> , 2006), the Indian Ocean (Corliss, 1979, Nees <i>et al.</i> 1997). Similarly, this species is reported as rare in South Atlantic superficial sediments by Mackensen <i>et al.</i> (1993, <i>Siphotextularia</i> sp.), Schmiel <i>et al.</i> (1997, <i>S. catenata</i>) as well as in Pleistocene and Miocene sediments of the Walvis Ridge (Boltovskoy & Boltovskoy, 1989). Nees & Struck (1994) and Struck (1995) relate the occurrence of <i>S. rolshauseni</i> in the Greenland-Norwegian Seas during MIS 2 with a period of low trophic quality. This interpretation is also suggested by the downcore distribution of <i>S. rolshauseni</i> in core TNO57-21 which peaks together with <i>Melonis</i> spp. during MIS 4 (see text).
Flux Range?	The called "Lagenina Group" is composed by several species belonging to genus <i>Amphycorina</i> , <i>Bifarilaminella</i> , <i>Cushmanina</i> , <i>Fissurina</i> , <i>Homaloedra</i> ;	Unknown	The species belonging to the called "Lagenina group" are found as rare representatives of the living and recently dead assemblages in different marine settings. Thus, the ecological significance of this group is not well constrained. Some of the species belonging to Lagenina group are illustrated in Plate I: <i>Fissurina staphyllearia</i> (Plate, Fig. 3).

615

616 **PLATE I CAPTION:**

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618 1. *Eggerella bradyi* (Cushman), scale bar 100 μm .

619 2. *Siphotextularia rolshauseni* Phleger and Parker, scale bar 100 μm .

620 3. *Fissurina staphyllearia* Schwager, scale bar 100 μm .

621 4. *Oolina globosa* (Montagu), scale bar 100 μm .

622 5. *Lagena hispidula* Cushman, 1913, scale bar 100 μm .

623 6. *Parafissurina felsinea* (Fornasini), scale bar 100 μm .

624 7. *Quinqueloculina* cf. *seminula*, scale bar 100 μm .

625 8. *Fontbotia wuellerstorfi* (Schwager), scale bar 100 μm .

626 9. *Epistominella exigua* (Brady), 9a, spiral side, 9b umbilical side, scale bars 100 μm .

627 10. *Globocassidulina subglobosa* (Brady), scale bar 200 μm .

628 11. *Rutherfordoides tenuis* (Phleger and Parker), scale bar 200 μm .

629 12. *Gyroidinoides* cf. *polius*, scale bar 100 μm .

630 13. *Melonis zaandamae* (Van Voorthuysen), scale bar 100 μm .

631 14. *Nutallides umboniferus* (Cushman), scale bar 100 μm .

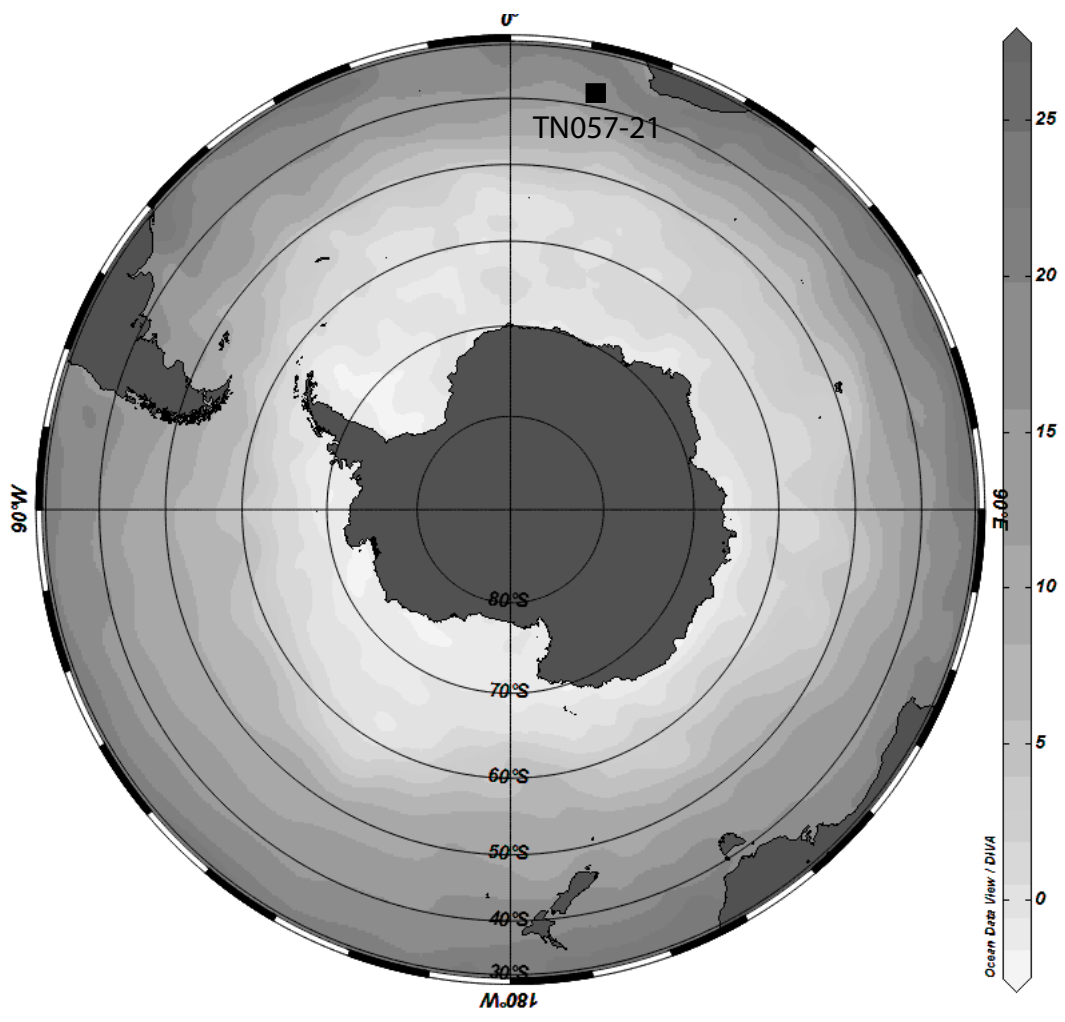
632 15. *Oridorsalis umbonatus* (Reuss), 4a, umbilical side, 4b spiral side, scale bars 100 μm .

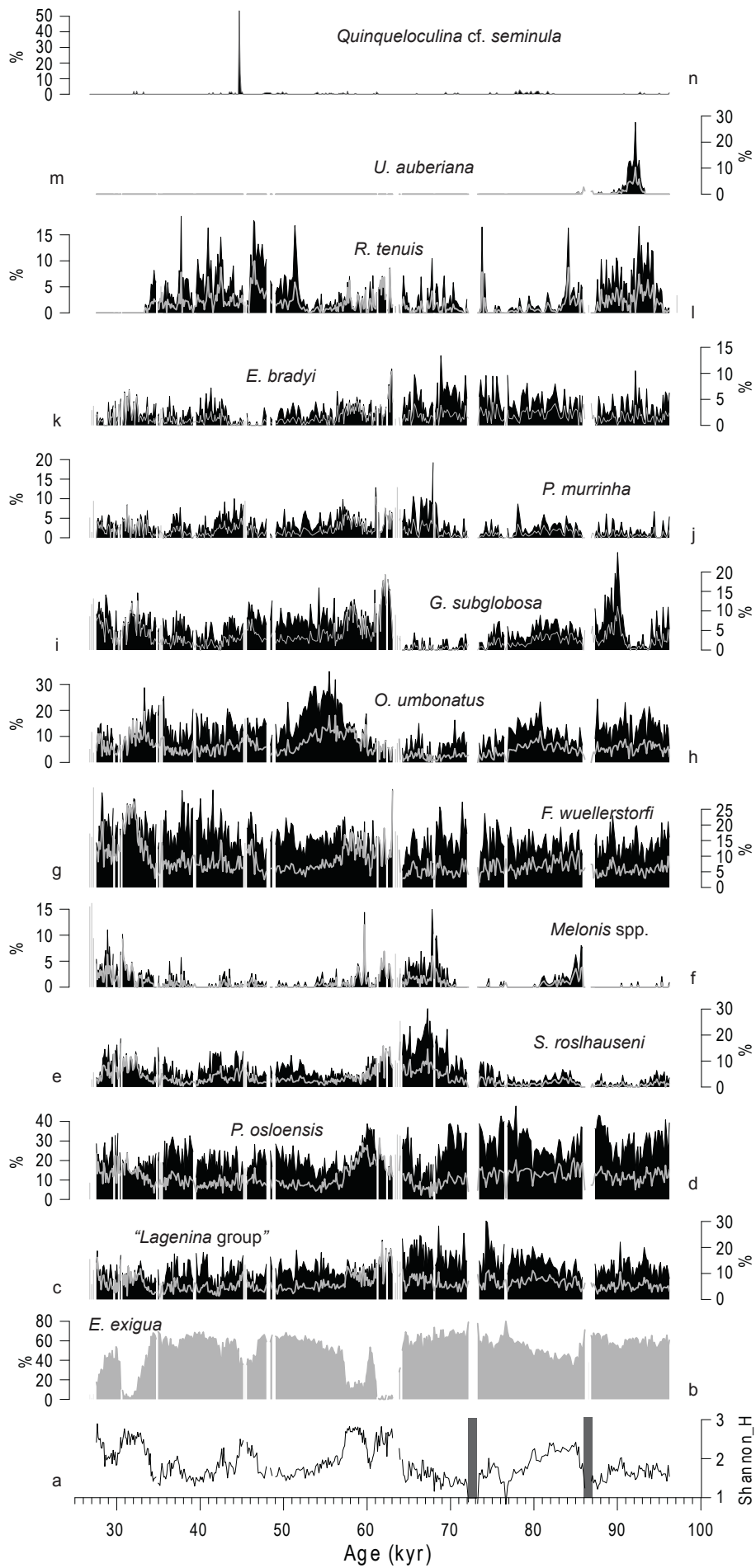
633 16. *Pullenia osloensis* Feyling-Hanssen, scale bar 100 μm .

634 17. *Pullenia salisburyi* Stewart and Stewart, scale bar 100 μm .

635 18. *Uvigerina auberiana* d'Orbigny, scale bar 200 μm .

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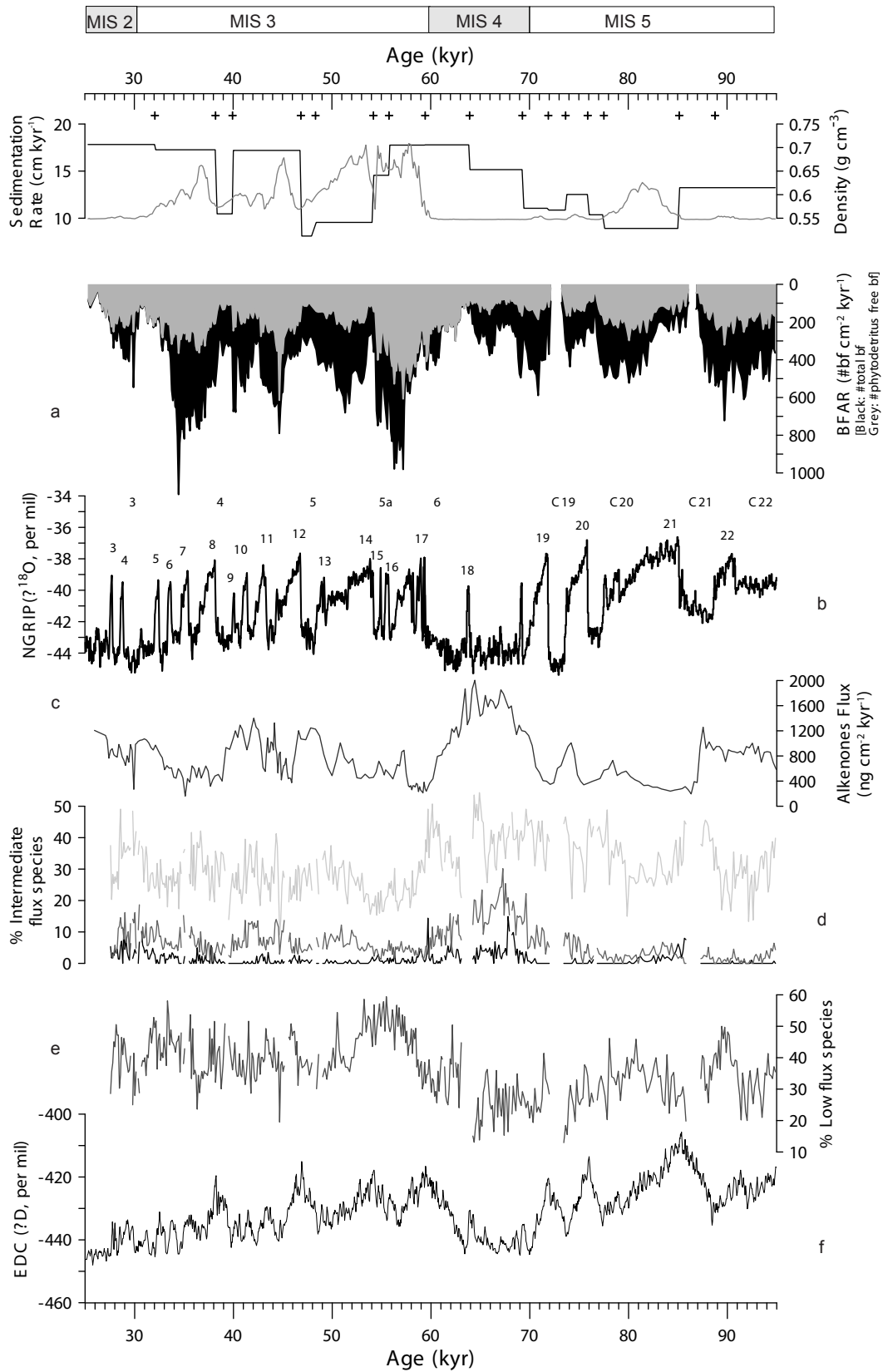


Plate I

