

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

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

Keywords: benthic foraminifera; palaeoproductivity; seasonality; abyssal; phytodetritus

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

Evaluating the extent to which benthic foraminifera can be used to infer a particular set of past environmental conditions and

understanding the complicating factors and limitations of such reconstructions is fundamental to advancing the use of proxy methods based on these organisms. In this study we discuss palaeoenvironmental inferences based on benthic foraminiferal assemblage characteristics from an abyssal core located in the south of Cape Basin (South Atlantic). We examine the consistency of the most typical palaeoproductivity proxies by comparing information provided by our assemblages with environmental parameters from independent proxies obtained in the same core and other proxy archives.

Material and methods

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

Several previous micropalaeontological studies have been carried out on core TN057-21. The palaeoceanographic significance of planktonic foraminifera assemblages are discussed in Barker *et al.* (2009, 2010) and Barker & Diz (2014). The linkages between the

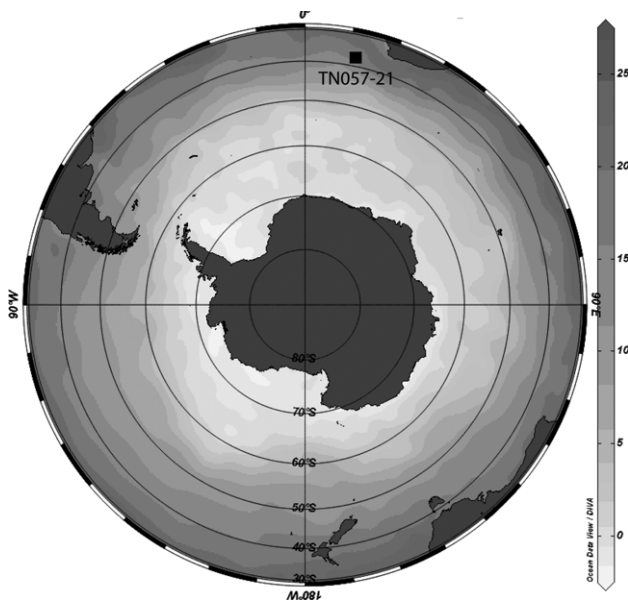


Fig. 1. Location of core TN057-21 in the South Atlantic Southern Ocean (map elaborated using Ocean Data View, Schlitzer, R., <http://odv.awi.de>, 2015). Detailed information about modern hydrography and primary productivity patterns can be found in Llido *et al.* (2004) and Machu *et al.* (2005).

record of the benthic foraminifera *Epistominella exigua* and millennial-scale climate variability during the last 95 ka are considered in Diz & Barker (2015). However, detailed information about benthic assemblage composition from *c.* 25 to 95 ka, and relevant additional palaeoenvironmental information, were beyond the scope of these earlier papers and are therefore addressed in the present study. The age model used in this study is described in Barker & Diz (2014) and the methods for the study of benthic fauna are indicated in Diz & Barker (2015). Briefly, foraminifera are picked from the >125 μm fraction, mounted on faunal slides and identified following the generic assignments of Loeblich & Tappan (1987) and published illustrations (see Table 1). The study of benthic foraminifera in the >125 μm size fraction potentially underestimates the abundance of small (63–125 μm) opportunistic taxa such as *Alabaminella weddellensis* (Earland) which are typically abundant in areas characterized by episodic phytoplankton blooms (e.g. Thomas *et al.* 1995; Diz *et al.* 2007; Smart *et al.* 2010). On the other hand, it allows for studying a feasible number of samples still showing major faunal patterns (e.g. Poli *et al.* 2012; Schönfeld *et al.* 2012). Raw counts can be found in Diz & Barker (2015) and the most characteristic species of benthic foraminifera are illustrated in this study (Fig. 2). The assemblages are largely dominated by *Epistominella exigua* (>40% on average), a phytodetritus-related species. In order to assess the ecological significance of the other relevant species we discuss the

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

Species	Microhabitat	Ecological significance
Low flux		
<i>Fontbotia wuellerstorfi</i> (Schwager)= <i>Anomalina wuellerstorfi</i> Schwager. See Phleger <i>et al.</i> (1953, pl. 11, figs 1–2) and this work, Fig 2:8.	Epifaunal/ Epibenthic	<i>Fontbotia 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 $2 \text{ g cm}^{-2} \text{ a}^{-1}$ (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 an 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 latter (Altenbach <i>et al.</i> 1999). This information suggests that <i>F. wuellerstorfi</i> is adapted to a wide range of environmental conditions, including a 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. See Smith (1964, pl. 4, fig. 8 as <i>Pseudoepionides umbonatus</i>) and this work (Fig. 2:15). Most of the individuals found in core TN057-21 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 & De Deckker (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) interprets the group of <i>O. umbonatus</i> , <i>Eggerella bradyi</i> and <i>Melonis pompilioides</i> as reflecting intermediate flux of relatively degraded organic matter and Kaiho (1999) considers <i>O. umbonatus</i> as an indicator of low-oxygen conditions.
Low flux		
<i>Pyrgo murrhina</i> (Schwager) = <i>Biloculina murrhina</i> Schwager. See Phleger <i>et al.</i> (1953, pl. 5, figs 22–24).	Epifaunal	<i>Pyrgo murrhina</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. murrhina</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. See Parker (1958, pl. 4, fig. 13) and this work (Fig. 2:10).	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 SE Atlantic, this species characterizes sandy sediments of the Walvis Ridge (South Atlantic) with low organic carbon and high calcium carbonate content and enhanced bottom current velocities (Schmiedl <i>et al.</i> 1997). However, <i>G. subglobosa</i> has been associated with deposition of phytodetritus in the NE Atlantic Abyssal Plain (Gooday 1988, 1993), NW Africa (Eberwein & Mackensen 2006) and the Antarctic shelf (Suhr <i>et al.</i> 2003).

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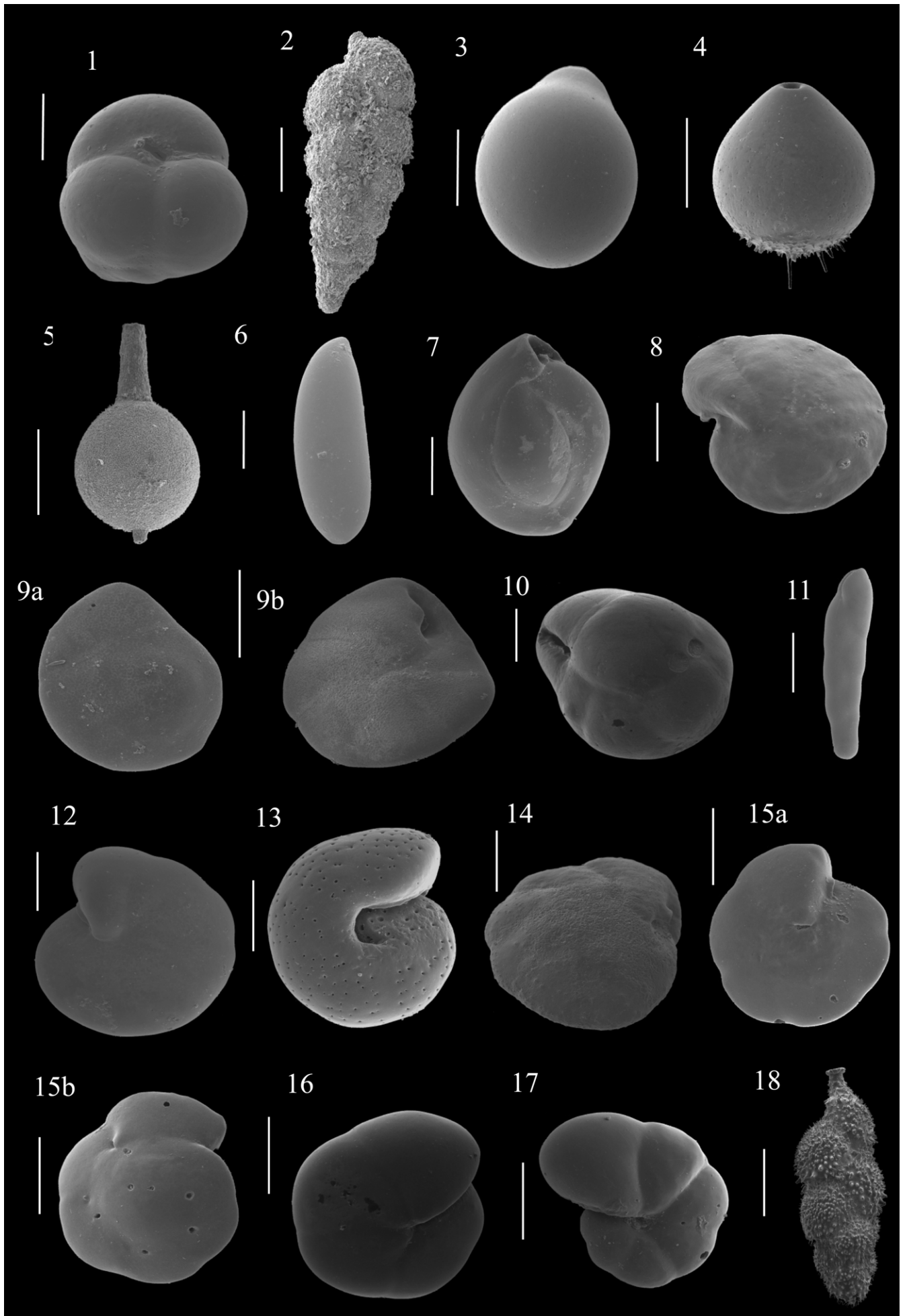
Table 1. (Continued)

Species	Microhabitat	Ecological significance
Episodic phytoplankton blooms		
<i>Epistominella exigua</i> (Brady) = <i>Pulvinulina exigua</i> Brady. See Lobegeier & Sen Gupta (2008, pl. I, fig. 18) and this work (Fig. 2:9).	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 (Schmiedl <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 SW Indian Ocean (Corliss 1983; Peterson 1983).
Intermediate flux		
<i>Pullenia osloensis</i> Feyling- Hanssen. See Diz <i>et al.</i> (2007, supplementary information, pl. II, fig. 5) and this work (Fig. 2:16).	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), SW 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 an 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 an 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 (Fig. 2:17) even though its relative contributions are lower than <i>P. osloensis</i> .
Intermediate flux		
<i>Melonis zaandamae</i> (Van Voorthuysen)= <i>Melonis barleeaanum</i> var. <i>zaandamae</i> van Voorthuysen. See Mackensen <i>et al.</i> (1993, pl. 3, figs 4–5) and this work (Fig. 2:13).	Shallow infaunal	<i>Melonis</i> spp. species (in this core mainly <i>M. zaandamae</i>) are intermediate infaunal foraminifera that tolerate moderate oxygen depletion (Fontanier <i>et al.</i> 2002). <i>Melonis</i> spp. is generally associated with 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 pompiloides</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. See Phleger <i>et al.</i> (1953, pl. 5, fig. 7) and this work (Fig. 2:2).	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 in Nees & Struck 1994), SW Pacific (Kurihara & Kennett 1986), South China Sea (Szarek <i>et al.</i> 2006) and the Indian Ocean (Corliss 1979, Nees 1997). Similarly, this species is reported as rare in South Atlantic superficial sediments by Mackensen <i>et al.</i> (1993, <i>Siphotextularia</i> sp.), Schmiedl <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 Sea 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).
Wide flux range?		
The so-called ‘Lagenina group’ is composed of several species belonging to the genus <i>Amphycorina</i> , <i>Bifarilaminella</i> , <i>Cushmanina</i> , <i>Fissurina</i> , <i>Homaloedra</i> , <i>Lagena</i> , <i>Oolina</i> , <i>Palliolatella</i> , <i>Parafissurina</i> and <i>Procerolagena</i>	Unknown	The species belonging to the so-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 the Lagenina group are illustrated in Figure 2: <i>Fissurina staphyllearia</i> (Fig. 2:3), <i>Lagena hispidula</i> (Fig. 2:5), <i>Oolina globosa</i> (Fig. 2:4); <i>Parafissurina felsinea</i> (Fig. 2:6).

assemblages after removing the contribution of *E. exigua* (i.e. the ‘phytodetritus-free assemblage’, see also Thomas *et al.* 1995). Additionally, we examined the record of benthic foraminiferal accumulation rate (BFAR, total number of foraminifera $\text{cm}^{-2} \text{ka}^{-1}$) and phytodetritus-free benthic foraminiferal accumulation rate (BFAR_{phfree}). BFARs are calculated as the number of individuals per gram of total dry bulk sediment ($\# \text{bf g}^{-1}$, Diz & Barker 2015) \times linear sedimentation rates (cm ka^{-1}) \times density (g cm^{-3}). Sedimentation rates are taken from the age model developed by Barker & Diz (2014) and vary from 8 to 16 cm ka^{-1} . It is considered that the age model is sufficiently robust as to assume that differences in BFAR are not mainly caused by inaccuracies in the calculation of sedimentation rates. In the absence of direct measurements of dry or wet bulk density, we used the algorithm developed by Sachs &

Anderson (2003) which is based on the percentage of calcium carbonate. To do this, the high resolution % CaCO_3 record of core TNO57-21 (Sachs & Anderson 2003) was re-sampled and values interpolated to the lower resolution record of benthic foraminiferal abundance using the program Analyseries (Paillard *et al.* 1996). Then, density values were calculated using the Sachs & Anderson formula. Calculated values vary between 0.5 and 0.7 g cm^{-3} .

The core TNO57-21 was recovered from deep waters that are currently undersaturated with respect to calcium carbonate (4891 m water depth, see Barker *et al.* 2010, supplementary information). Several episodes of increased carbonate dissolution have been identified in planktonic foraminiferal (Barker *et al.* 2009, 2010; Barker & Diz 2014) as well as benthic foraminiferal (Diz & Barker 2015) assemblages. By considering the information provided by



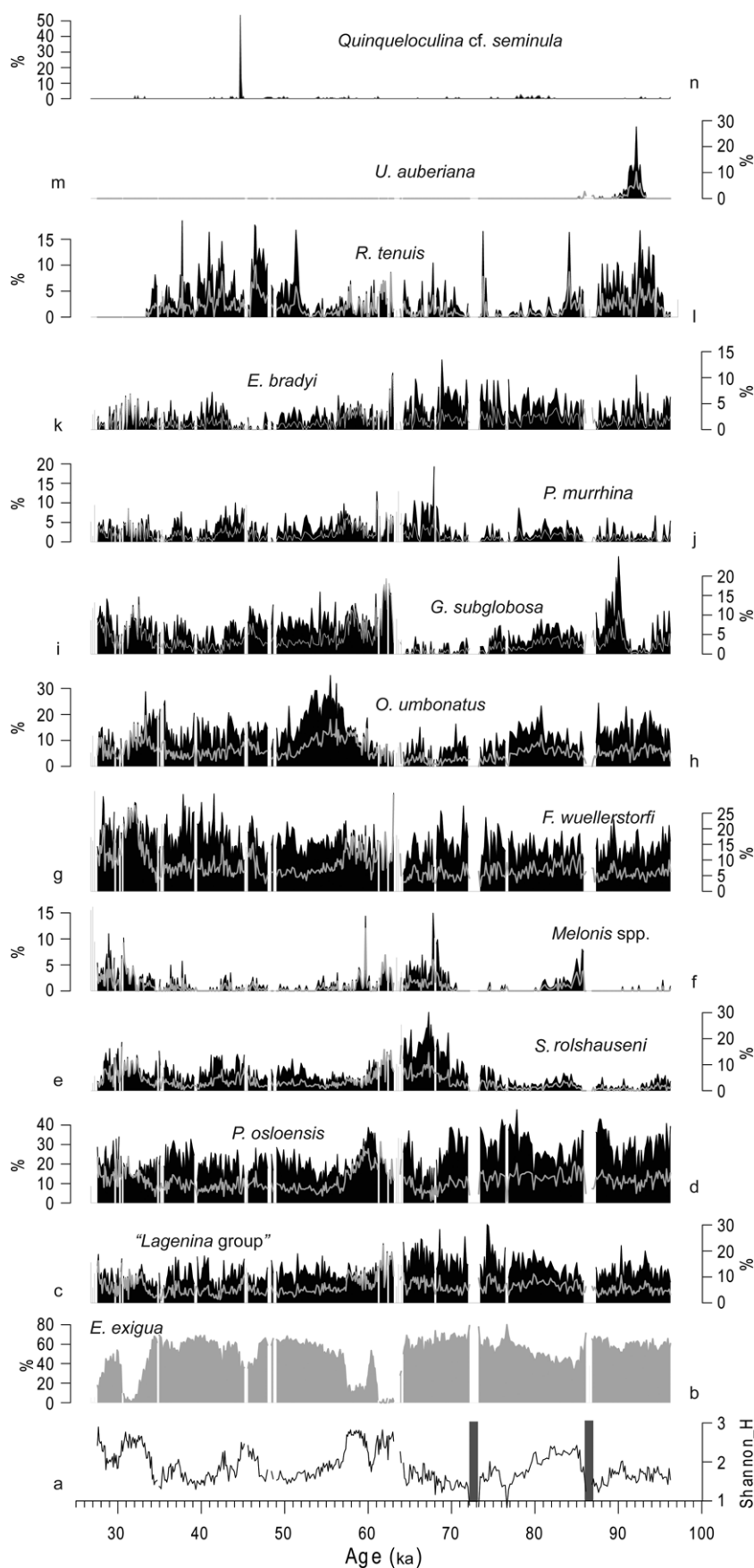
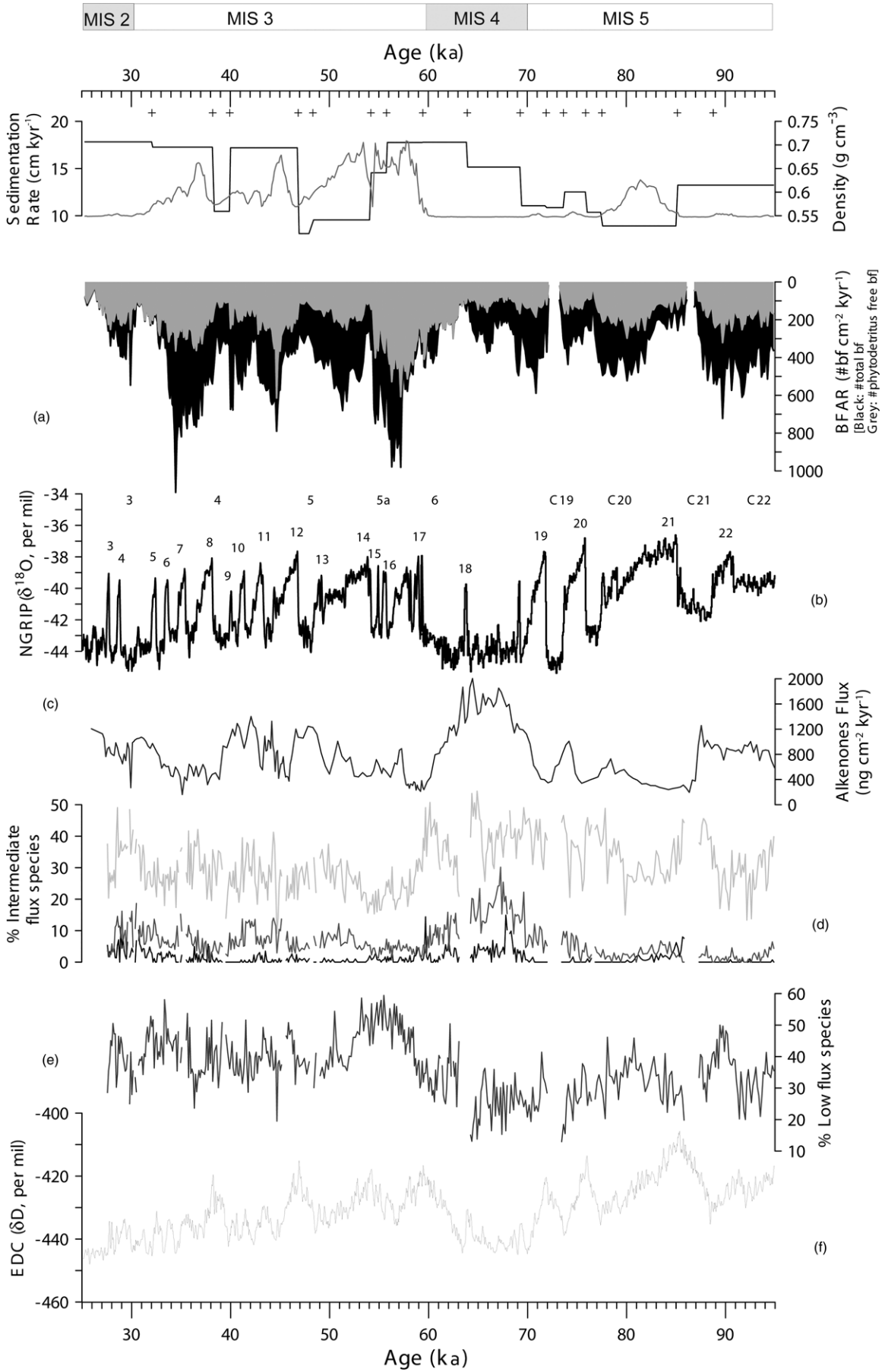


Fig. 3. Benthic foraminiferal assemblages in core TN057-21. (a) Shannon-H diversity index; (b) the relative abundance of *Epistominella exigua*; (c–n) the most characteristic species of benthic foraminifera in core TNO57-21. Percentages are shown in the total assemblage (grey line) and in the phytodetritus-free assemblages (black filled area). Percentages are calculated on the basis of samples containing >50 specimens and unaffected by dissolution. Intensely dissolved intervals that correspond to Greenland Stadials 19 and 21 are indicated by vertical bars in (a). The ecological preferences for the most characteristic benthic foraminiferal species or group of species are summarized in Table 1.

Fig. 2. 1. *Eggerella bradyi* (Cushman). 2. *Siphotextularia rolshauseni* Phleger & Parker. 3. *Fissurina staphyllearia* Schwager. 4. *Oolina globosa* (Montagu). 5. *Lagena hispidula* Cushman. 6. *Parafissurina felsinea* (Fornasini). 7. *Quinqueloculina cf. seminula* (Linnaeus). 8. *Fontbotia wuellerstorfi* (Schwager). 9. *Epistominella exigua* (Brady), (a) spiral side, (b) umbilical side. 10. *Globocassidulina subglobosa* (Brady), scale bar 200 μ m. 11. *Rutherfordoides tenuis* (Phleger & Parker), scale bar 200 μ m. 12. *Gyroidinoides cf. polius*. 13. *Melonis zaandamae* (Van Voorthuysen). 14. *Nutallides umbonifera* (Cushman). 15. *Oridorsalis umbonatus* (Reuss), (a) umbilical side, (b) spiral side. 16. *Pullenia osloensis* Feyling-Hanssen. 17. *Pullenia salisburyi* Stewart & Stewart. 18. *Uvigerina auberiana* d'Orbigny, scale bar 200 μ m. Scale bars 100 μ m unless noted otherwise.



multiple proxies (e.g. % of coarse fraction, % CaCO₃, foraminiferal abundances, composition of assemblages) it was indicated that carbonate dissolution does not seem to exert an overall control on benthic abundance or species distribution with the exception of the Holocene (not considered in this study) and Greenland Stadial (GS) events GS19 and 21. Those poorly preserved periods (indicated in Fig. 3 by bars) are characterized by a low percentage of calcium carbonate, very low foraminiferal abundances and a low number of benthic taxa. They are not used to infer palaeoenvironmental conditions (see detailed discussion in Diz & Barker 2015). The comparison of the composition of the ‘dissolved assemblages’ with modern samples (Mackensen *et al.* 1993) indicates that *Nutallides umbonifera* (Cushman) is very rare along core TNO57-21 (see Fig. 2). *Nutallides umbonifera* is generally related to corrosive bottom waters in the South Atlantic (Mackensen *et al.* 1993; Harloff & Mackensen 1997; Schmiedl *et al.* 1997). It might suggest that other factors more than carbonate undersaturated waters are playing a role in this species distribution (i.e. oligotrophic conditions and absence of phytodetritus deposition, Smart & Gooday 1997; Kurbjeweit *et al.* 2000; Carman & Keigwin 2004).

Results

The foraminifera fauna of core TNO57-21 comprises 39 benthic species dominated by calcareous forms. The Shannon-H diversity index averages 1.9 (Fig. 3a). High diversity values occur when the relative contribution of the dominant phytodetritus-related species *Epistominella exigua* (Brady) is diminished. The averaged relative contribution of this species is as high as 47% (Fig. 3b). Other, relatively common species are *Pullenia osloensis* (Feyling-Hanssen) (average percentage 11.9%, Fig. 3d), *Oridorsalis umbonatus* (Reuss) (6%, Fig. 3h), *Fontbotia wuellerstorfi* (Schwager) (7.9%, Fig. 3g) and the group of species belonging to the suborder *Lagenina* called the ‘Lagenina group’ (see Table 1, 11.9%, Fig. 3c). Secondary calcareous species (<10% on average) showing high abundances at particular intervals are *Pyrgo murrhina* (Schwager) (Fig. 3j), *Globocassidulina subglobosa* (Brady) (Fig. 3i), *Melonis* spp. (comprising *M. zaandamae* (Van Voothuysen), *Melonis pompilioides* (Fichtel & Moll) and *Melonis* sp., Fig. 3f) and *Rutherfordoides tenuis* (Phleger & Parker) (Fig. 3l). Calcareous species with short-lived peaks are *Uvigerina auberiana* d’Orbigny (Fig. 3m) and *Quinqueloculina cf. seminula* (Linnaeus) (Fig. 3n). The most characteristic agglutinated foraminifera is the calcareous agglutinated *Siphotextularia rolshauseni* (Phleger & Parker, Fig. 3e) with *eggerella bradyi* (Cushman) as secondary species (Fig. 3k).

The BFAR values in core TNO57-21 show large fluctuations ranging from 30 to 1100 foraminifera (>125 µm fraction) cm⁻² ka⁻¹. On average, peak BFAR values are higher during northern stadial events occurring during MIS 3 than over MIS 5 (Fig. 4a). The lowest BFAR values occur during GS19 and GS21 (also the Holocene, not shown) when benthic foraminiferal dissolution was inferred (Diz & Barker 2015) and thus they are excluded from

interpretation (Fig. 4a). In general, episodes of peak BFAR values are largely driven by the phytodetritus-related species *Epistominella exigua* (Fig. 4a), and show a tight temporal correspondence with abrupt climate changes occurring in the North Atlantic Ocean and concomitant antiphase response in the South Atlantic (see Fig. 4 and Diz & Barker 2015). Episodes of high BFAR_{phfree} coincide with BFAR although they are of much lower magnitude and sharpness (Fig. 4a, grey shaded area). The highest BFAR_{phfree} values coincide with a single peak in *Quinqueloculina cf. seminula* (Fig. 3n) at c. 45 ka and near the beginning of MIS 3 (c. 56–58 ka) with high relative abundances of *G. subglobosa*, *F. wuellerstorfi* and *O. umbonatus* (see Fig. 3).

Discussion

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

Benthic foraminiferal accumulation rates

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

The BFAR values during the Holocene and late deglaciation (not plotted but calculated on the basis of Diz & Barker (2015) data; <100 foraminifera cm⁻² ka⁻¹) are within the range of values for abyssal core tops from the Pacific open ocean at water depths >4000 m likely affected by carbonate dissolution (Herguera & Berger 1991; Herguera 1992). However, peak BFAR values from MIS 3 to MIS 5 are four to eight times Holocene values (Fig. 4). These accumulation rates are substantially higher than maxima values recorded in core-top samples from widely distributed open-ocean areas at various depths in the Pacific. Following the use of BFAR as a palaeoproductivity proxy, these results might suggest past increases in the organic carbon flux to the seafloor up to several times the present conditions. According to modern primary production distributions (see Machu *et al.* 2005, fig. 5) this might be equivalent to a change from oligotrophic subtropical open ocean areas to high productivity upwelling centres (e.g. Benguela upwelling). In fact, peaks of BFAR reach values found in continental shelf areas affected by seasonal upwelling, such as Cape Blanc upwelling (Guichard *et al.* 1999; Zariess & Mackensen 2010) or the SW African upwelling (Schmiedl & Mackensen 1997). Such a change in the palaeoenvironmental conditions, if it had

Fig. 4. Palaeoproductivity from benthic foraminiferal accumulation rates and assemblage composition. (a) The Benthic Foraminiferal Accumulation Rate (BFAR, total number of foraminifera >125 µm cm⁻² ka⁻¹) is indicated as a shaded black area and Benthic Foraminiferal Accumulation Rate calculated on phytodetritus-free basis (i.e. discounting the contribution of the phytodetritus-related species *Epistominella exigua*, BFAR_{phfree}) is indicated by a grey shaded area. Consequently, the difference between the two shaded areas is the BFAR of *E. exigua* (BFAR_{E.exigua}). (b) Northern Hemisphere ice core temperature record (Greenland NGRIP δ¹⁸O; EPICA 2006) is shown as reference. (c) The flux of alkenones (ng cm⁻² ka⁻¹) in core TNO57-21, a proxy for organic carbon flux to the seafloor (Sachs & Anderson 2005), plotted on Barker & Diz (2014) age model. (d) Intermediate-flux species (light grey line) are composed of individuals belonging to *P. osloensis*, *S. rolshauseni* (medium grey line) and *Melonis* spp. (dark grey line). (e) The group of ‘low-flux’ species is composed of shallow infaunal *O. umbonatus*, *G. subglobosa* and epifaunal *P. murrhina* and *F. wuellerstorfi*. Percentages are calculated on the phytodetritus-free assemblage basis. (f) Record of Southern Hemisphere ice core temperature (Antarctica Epica Dome C δD, Jouzel *et al.* 2007, 3 points running average) is shown as reference. (b) and (f) are plotted on GICC05/NALPS timescale (Barker *et al.* 2011). Black crosses at the top of the figure indicate tie points and sedimentation rates, respectively, used in the age model construction and BFAR calculations. The grey line in the top plot shows density values calculated using the model proposed by Sachs & Anderson (2003).

occurred, would have involved a large change in assemblage composition, i.e. from low productivity faunas (low abundances) to a high productivity assemblage (high BFAR). This seems to be unrealistic considering that assemblage changes are subtle in comparison to BFAR fluctuations (see Figs 3 and 4) and they do not involve the appearance of species related to eutrophic conditions (see next section). In fact, variations in BFAR are mainly driven by the phytodetritus-related species *Epistominella exigua* (Table 1 and Fig. 4a). In the absence of this species, fluctuations in $\text{BFAR}_{\text{phfree}}$ (BFAR phytodetritus-free; 'phfree') are of much lower magnitude and suggest only subtle changes in organic carbon fluxes. This could be explained by the fact that when large quantities of fresh marine organic matter (phytodetritus) are available, even for short periods of time, opportunistic species, such as *Epistominella exigua*, reproduce rapidly and produce a large number of tests (see Thiel *et al.* 1989). The accumulation of foraminifera is not related in a predictable manner to organic flux and, in these circumstances, BFAR should not be used as a quantitative (or semi-quantitative) proxy (Thomas *et al.* 1995; Diz *et al.* 2007; Smart 2008; Zariess & Mackensen 2010) for the organic carbon flux reaching the seafloor. BFAR is rather related to the strength of the phytoplankton blooms. The episodic and labile nature of the phytodetritus aggregates reaching the seafloor (Beaulieu 2002; Smith *et al.* 2008) could explain the weak correlation ($r = -0.24$, $P = 0.000$, $n = 467$) between BFAR (also $\text{BFAR}_{\text{phfree}}$) and the alkenones flux, a proxy for averaged organic carbon flux to the seafloor (Sachs & Anderson 2003) obtained in the same core (Fig. 4c).

Benthic foraminiferal assemblage composition

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

The relative abundance of particular species or group of species is related qualitatively to the predominance of a particular flux regime (i.e. high, intermediate, low-flux species), quality (i.e. labile, refractory) or seasonality of the flux (i.e. seasonal, sustained). In this study, groups are defined based on representative species with well-known ecology (see the ecological attributions of characteristic species in Table 1). Because organic flux-dependent patterns should be best analysed within the environmental optimum of species (Altenbach *et al.* 1999), those species with percentages lower than 10% for most of the record (e.g. *Eggerella bradyi*, *Quinqueloculina* cf. *seminula*, *Rutherfordoides tenuis*, see Fig. 2 and 3) and/or those species for whom the ecology is not well constrained are not included in any of the groups. An example of the latter is the high contribution to the assemblage of individuals belonging to the 'Lagenina group' (>10%, Fig. 3c, see Fig. 2). Unfortunately their ecology is poorly known (see Table 1) and consequently the contribution to the palaeoenvironmental understanding of the assemblage changes is limited.

The most abundant species throughout the core is *Epistominella exigua*, an epifaunal/shallow infaunal abyssal deep-sea opportunistic foraminifera that flourishes and rapidly reproduces in the presence of phytodetritus aggregates (see ecological attributions in Table 1). Thus, high relative abundance of *E. exigua* (Fig. 3b) along core TNO57-21 indicates overall low organic carbon fluxes punctuated by episodic phytoplankton blooms that resulted in the

deposition of phytodetrital inputs (i.e. labile organic carbon). This interpretation is supported by the 'phytodetritus-free' assemblage which is composed of species typical of oligotrophic ('low flux') to moderately mesotrophic ('intermediate') environmental conditions.

The 'low-flux species' are the epifaunal *Fontbotia wuellerstorfi*, *Pyrgo murrhina* and the shallow infaunal *Oridorsalis umbonatus* and *Globocassidulina subglobosa* (see Table 1). All together these represent >30% of the phytodetritus-free assemblage (Fig. 4e) reaching up to 60% during early MIS 3. For some of these species (i.e. *G. subglobosa*, *F. wuellerstorfi*, *P. murrhina*) a relationship to phytodetritus input (see Table 1) has also been suspected. However, their downcore relative abundance does not covary with BFAR or percentages of the phytodetritus-related species *E. exigua* (Figs 3b and 4a, e). Instead, they must respond to a different type of phytodetritus or, more likely, they prefer sustained (and low) organic carbon flux to the seafloor rather than pulsed (see also Smart 2008).

The group of species considered indicative of an 'intermediate-flux' regime are mainly represented by the relatively common shallow infaunal *Pullenia osloensis* together with *Melonis* spp. and *Siphotextularia rolshauseni* (Fig. 4d and Table 1). Those species show a statistically significant negative correlation ($P < 0.000$) to the relative contribution of the species belonging to the low-flux group ($r_{O. umbon-S. rolshauseni} = -0.38$; $r_{P. osloensis-P. murrhina} = -0.39$; $r_{P. osloensis-F. wuellerstorfi} = -0.28$; $r_{P. osloensis-G. subglobosa} = -0.23$; $r_{O. umbonatus-Melonis spp.} = -0.35$). The relative contribution of the 'intermediate-flux' group indicates slightly more eutrophic conditions during MIS 5 and MIS 4 than during MIS 3. Peaks of the intermediate-flux fauna occurring over MIS 4 are mainly caused by noticeably increased contributions of *Melonis* spp. and *S. rolshauseni* (Figs 3e, f and 4d) occurring in coincidence with high relative contribution of *Epistominella exigua* (Fig. 3b) and the substantial increase in the alkenone flux measured during glacial MIS 4 (Fig. 4c). These two species show affinity for degraded organic carbon (Table 1) suggesting that during MIS 4 part of the sedimentary organic compounds are of low nutritional value. This might be explained by a different type and/or fate of phytodetrital material arriving to the seafloor which could promote the response of species that benefit from the bloom indirectly (i.e. bacteria colonizing aggregates, Koho *et al.* 2008). In fact, it has been inferred (Diz & Barker 2015) that slightly different physical conditions promoting phytoplankton blooms in the surface waters occurred during MIS 4/MIS 5 transition and early MIS 4 (seasonality and windiness) than during MIS 3 and late MIS 5 (mainly eddy activity). Notably, that assemblage change does not trigger a parallel increase in the $\text{BFAR}_{\text{phfree}}$ indicating that a change in the food quality does not force a change in the absolute numbers of benthic foraminiferal accumulation rate but only in the assemblage composition.

Constraints and approaches: overview

Benthic foraminifera (BFAR and assemblage composition) were analysed in abyssal core TN057-21. Episodic phytoplankton blooms represent the main source of 'disturbance' to the benthic environment and have important consequences for the structure and taxonomic composition of the benthic foraminifera record. The inferred phytodetritus deposition does not seem to trigger a response by the whole community but it is limited to a single species, leading to a decrease in the diversity of the assemblages. The species benefiting from phytodetritus input is the opportunistic (r-strategist) *Epistominella exigua* which reacts quickly, producing high numbers of individuals and consequently high benthic foraminiferal accumulation rates. The response of the remaining fauna (the so-called 'phytodetritus-free assemblage') to phytodetritus input is mainly constrained to a concomitant moderate increase in the

foraminiferal abundance (BFAR_{phfree}) with overall little variation in the assemblage composition. This could be explained by the different ecological preferences of species with lower reproductive potential (k-strategists) and likely benefiting from other types of organic carbon (less labile). All these data together suggest BFAR could not be a reliable proxy for palaeoproductivity in abyssal (food-limited) environments when benthic foraminifera are highly dependent on the rate and nature of the input of labile organic material generated in the euphotic zone. Under these circumstances fluctuations in BFAR do not reflect the flux of organic carbon to the seafloor but rather the strength of phytoplankton blooms in the surface waters. In this case, the assemblage composition is relevant for interpreting palaeoenvironmental conditions.

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