Paleoceanographic changes across the Latest Danian Event in the South Atlantic Ocean and planktic foraminiferal response

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Abstract

A number of short warming events occurred during Paleocene and Eocene, of which the “Paleocene-Eocene Thermal Maximum” (PETM, 56 Ma) is the most severe and most investigated event. The less known “Latest Danian Event” (LDE) at 62.2 Ma represents a 200 ky-lasting warming phase, superimposed on a long-term cooling trend after the Early Paleocene. South Atlantic ODP Site 1262 data, covering ~1 myr, indicate a warming of the entire water column by 1.5–2.6°C, accompanying a prominent negative carbon isotope excursion (~0.9–1.1 ‰) and a long-term re-organization of the planktic foraminiferal fauna associated with the LDE. This study unravels a different paleoceanographic evolution of the upper ocean structure compared to results from Pacific ODP Site 1210. Unlike the Pacific, the Atlantic site lacks an apparent change of stratification as well as an overall dominance of thermocline dwelling planktic foraminifera species and a low abundance of surface dwelling photosymbiotic foraminifera. Within the LDE, indications for a slightly enhanced stratification of the upper water column and transient warming was indicated when surface dwelling planktic foraminifera became temporarily more abundant. The long-term evolution in planktic foraminifera with the disappearance of *Praemurica* at the LDE onset and a contemporaneous rise in *Morozovella* is similar to the trends reported from Shatsky Rise ODP Site 1210.

Keywords: Paleocene, hyperthermal event, Latest Danian Event, negative CIE, planktic foraminifera assemblage, surface ocean stratification

1 Introduction

The early Paleogene is known for significant climate and carbon cycle perturbations (e.g. Kennett and Stott, 1991; Lourens et al., 2005; Zachos et al., 2008; Littler et al., 2014). It is characterized by a long-term global bottom water cooling trend between 66 and ~59 Ma by ~3°C, followed by a long-term temperature rise by ~4–5°C culminating at the Early Eocene Climatic Optimum (EECO, ~53 Ma; Zachos et al., 1994, 2008; Westerhold et al., 2011). These million-year-scale cooling and warming trends of Paleocene and Eocene are interrupted by

several short-term warming events of 100–200 ky duration (e.g., Kennett and Stott, 1991, Lourens et al., 2005; Quillévéré et al., 2008; Zachos et al., 2008; Westerhold et al., 2011). The warming events, also named hyperthermals, are accompanied by negative carbon isotope excursions (negative CIEs), indicating the injection of isotopically light carbon into the ocean-atmosphere system, and severe biotic responses such as extinctions and turnovers (e.g. Crouch et al., 2001; Lourens et al., 2005; Bernaola et al., 2007; Zachos et al., 2010).

The best studied and most severe hyperthermal event is the Paleocene-Eocene Thermal Maximum (PETM, ~56 Ma) with a duration of 170–220 ky (e.g. Kennett and Stott, 1991; Röhl et al., 2007). Characteristics of this event are: a negative CIE of at least -2.5 ‰, ocean warming by up to 6–7°C (Zachos et al., 2008) for the bottom water, and up to 10°C for the surface ocean (Sluijs et al., 2007), a drop in calcium carbonate (wt% CaCO₃) in deep-sea records, most likely due to lysocline shallowing as a consequence of ocean acidification (e.g. Zachos et al., 2005), a major extinction of deep-sea benthic foraminifera and assemblage changes in many other marine microfossil groups (e.g. Kelly et al., 1996; Crouch et al., 2001; Bralower, 2002; Thomas, 2003; Speijer et al., 2012; Yamaguchi and Norris, 2015).

Several similar events, albeit of smaller magnitude, were reported from the Paleocene and Eocene, like the “Latest Danian Event” (LDE = Top C27n Event, 62.2 Ma, Bornemann et al., 2009, Dinarès-Turell et al., 2012). So far, the LDE was described from the margins of the Tethys Ocean in Egypt (Speijer, 2003; Bornemann et al., 2009; Sprong et al., 2011), NW-Tunisia (Guasti, 2005; Sprong et al., 2013), Bjala in Bulgaria (Dinarès-Turell et al., 2012) and Caravaca, Spain (Alegret et al., 2016). The LDE also was unequivocally identified in the North Atlantic (Zumaia, Spain, e.g. Dinarès-Turell et al., 2012, 2014; off Newfoundland, Yamaguchi et al., 2017), the South Atlantic (Ocean Drilling Program [ODP] Site 1262; Westerhold et al., 2008; Monechi et al., 2013; Deprez et al., 2017a), and the Pacific at Shatsky Rise ODP Sites 1209 and 1210 (Westerhold et al., 2011; Jehle et al., 2015). Faunal changes amongst planktic foraminifera (Guasti, 2005; Jehle et al., 2015), mammals (Clyde et al., 2008) and calcareous nannofossils (Fuqua et al., 2008; Monechi et al., 2012) were observed as well as within benthic foraminifera in dysoxic shelf settings (Sprong et al., 2011, 2012; Schulte et al., 2013).

At several sites in the Pacific and South Atlantic, the LDE was identified by two remarkable XRF core scanning Fe peaks and decreasing CaCO₃ values, indicated as LDE1 and LDE2 beds (Westerhold et al., 2008, 2011; Deprez et al., 2017a). A 1.6–2°C ocean floor warming was derived from benthic foraminifera $\delta^{18}\text{O}$ variations (Westerhold et al., 2011; Jehle et al., 2015; Deprez et al. 2017a, 2017b) and 2.8°C from planktic surface-dwelling foraminifera (Jehle et al., 2015). Enhanced stratification of the upper water column at Shatsky Rise (ODP Site 1210) during the LDE was proposed, based on apparent isotope gradients ($\delta^{18}\text{O}$, $\delta^{13}\text{C}$) between surface and subsurface planktic foraminifera and an assemblage shift from high abundances of surface

dwelling to subsurface dwelling planktic foraminifera. Both observed changes started ~170 ky prior to the LDE. This increase in stratification was explained by the development of a Deep Chlorophyll Maximum formed under a permanent gyre system leading to high abundances of subsurface dwelling foraminifera, benefiting from high nutrient levels below this layer. Furthermore, the extinction of *Praemurica* species and the rise of morozovellids occurred simultaneously with the onset of the LDE (Jehle et al., 2015).

For this study, we analysed planktic foraminifera across the transient warming of the LDE from the South Atlantic deep-sea ODP Site 1262 (Fig. 1) in order to evaluate the impact of the event on the composition of planktic foraminiferal assemblages and to link this to paleoenvironmental changes as inferred from stable isotopes ($\delta^{18}\text{O}$, $\delta^{13}\text{C}$) of planktic and benthic foraminifera carbonate. Our new data provide insight into the upper ocean structure of the South Atlantic across the LDE. Further, we compare our results with those of Pacific ODP Site 1210 (Fig. 1, Jehle et al., 2015) to obtain more general patterns of paleoceanographic and paleoclimatic evolution based on planktic foraminifera across this event.

2 Material and Methods

2.1 Geological setting and deposition

ODP Site 1262 is positioned at the transition from the Angola Basin to Walvis Ridge (27°11.15'S, 1°34.62'E, 4755 mbsl, meters below sea level, Fig. 1). During the Paleocene, the Site was situated at a latitude of ~37°S (Zachos et al., 2004; van Hinsbergen et al., 2015). Walvis Ridge is a ~3000 km long SW-NE trending aseismic ridge and reaches up to 200 mbsl from an abyssal depth of ~5000 m. Paleocene sediments were deposited at a paleodepth of ~3300 mbsl (Zachos et al., 2005) and are predominantly composed of calcareous nannofossil ooze, though more clayey and ash-rich in the deeper parts. Cyclic changes in magnetic susceptibility, also visible in colour variation, reflect orbital forcing (Westerhold et al., 2008).

2.2 Stratigraphy

Site 1262 holds a continuous record between the Cretaceous-Paleogene boundary and PETM (Westerhold et al., 2008). The LDE is biostratigraphically positioned within the basal part of the planktic foraminifera Subzone P3b (Berggren and Pearson, 2005; see Fig. 2) and the upper part of calcareous nannofossil Zone NP4 (Martini, 1971). The first radiation of fasciculiths/*Lithoptychius* is pinpointed close to the base of the LDE (Monechi et al., 2012, 2013). Magnetostratigraphically, the LDE is situated in the topmost part of C27n and the basal part of C26r. Accordingly it was also referred to as “Top C27n Event” (Westerhold et al., 2008; Dinarès-Turell et al., 2012, 2014).

Age control of Site 1262 is based on magnetostratigraphy (Bowles, 2006), biostratigraphy (Monechi et al., 2003; this study) and astrochronology (Dinarès-Turell et al., 2014). The onset of the LDE is at 62.18 Ma (Dinarès-Turell et al., 2014), the total duration of the LDE is about 200 ky and the investigated interval spans ~950 ky. Top of magnetochron C27n was also pinpointed to 62.2 Ma in Zumaia, (Dinarès-Turell et al., 2014). Maxima of short-eccentricity cycles 38 (195.3 mcd, meters composite depth) and 39 (194.6 mcd) correspond to the two XRF Fe peaks during long eccentricity cycle $P_{c405}10$ (Dinarès-Turell et al., 2014). Site 1262 was stratigraphically correlated to ODP Sites 1209 and 1210 (Westerhold et al., 2008) as well as to Zumaia, Spain (Dinarès-Turell et al., 2014). The latter represents the Global boundary Stratotype Section and Point (GSSP) for the base of the Selandian Stage (Schmitz et al., 2011).

2.3 Methods

Nine meters of core (189.5 mcd–198.48 mcd) were sampled at a 2.5–45 cm spacing with highest sample density across the LDE. Sediment samples were washed over a 63 μm sieve and oven dried at 50°C for at least 48 hours.

Wt% CaCO_3 and coarse fraction (%CF) were measured on 84 and 86 samples, respectively, planktic foraminiferal fragmentation (%Fp), planktic foraminiferal number (PFN), planktic foraminiferal accumulation rate (PFAR) and planktic proportion (%P) as well as the faunal composition were analysed on 40 samples (Fig. 2). $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ were measured on *Morozovella angulata*, *M. praeangulata* (surface dwelling planktic foraminifera), *Parasubbotina pseudobulloides*, *P. variospira* (planktic subsurface dwellers) and *Nuttallides truempyi* (benthic foraminifera) to provide data for the different habitats of the surface ocean, subsurface thermocline and the deep-sea. For $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ measurements, *P. pseudobulloides* and *P. variospira* were lumped together due to their rather similar morphology (see for discussion Jehle et al., 2015) and extremely similar values. For each measurement, 3–6 planktic specimens were picked from 250–355 μm size, however, in samples without quantitatively sufficient material, specimens of the 180–250 μm fraction were added. Benthic foraminifera (Deprez et al., 2017a) were selected from the 125–180 μm fraction only with 5–7 specimens. The specimens were reacted with 100 % phosphoric acid at 75°C using a Kiel IV online carbonate preparation line connected to a MAT 253 mass spectrometer. Machine reproducibility was checked by replicate analysis of laboratory standards, which was better than 0.03 ‰ and 0.1 ‰ for $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$, respectively. In addition to the machine error other factors have an influence on the analytical variability of stable isotope values, specifically the number of analysed tests per measurement (see Fraass and Lowery, 2017, for a summary). Early studies proposed a robust reproducibility with only very high numbers of 30–50 tests per run (Killingley et al., 1981), which are hardly to achieve in high-resolution records. Such a larger number of tests corresponds to a 95% confidence limits between 0.01 ‰ and 0.02 ‰ (Fraass and Lowery,

2017), however, even five tests per run still show a 95% confidence limit of 0.03% (Fraass and Lowery, 2017). Thus, the summed analytical variability of the data is much smaller in magnitude than most signals usually interpreted in deep-time palaeoceanography. CaCO_3 values were analysed with a LECO CS 230 carbon-sulphur analyser, located at the BGR, Hannover.

Coarse fraction was calculated by:

$$\%CF = ((\text{dry weight of residue [g]} > 63\mu\text{m}) / (\text{dry weight of total sample [g]})) \times 100 [\%] \quad (\text{I}).$$

Planktic foraminiferal fragmentation (%Fp) was counted in the $>125\mu\text{m}$ size fraction during species quantification. Specimens with less than 50 % preserved were considered as a test fragment and %Fp was calculated by:

$$\%Fp = (\text{no. of fragments}) / (\text{no. of fragments} + \text{no. of complete tests}) \times 100 [\%] \quad (\text{II})$$

PFN is the number of planktic foraminifera per gram dry unwashed sediment. For PFAR, the age model of Dinarès-Turell et al. (2014), expressed in linear sedimentation rate (LSR , [cm kyr^{-1}]) between each short-term eccentricity maximum, and shipboard dry bulk density (DBD , [g cc^{-1}]) data were linearly interpolated and multiplied with PFN.

$$PFAR = DBD \times LSR \times PFN \quad [\# \text{ cm}^{-2} \text{ kyr}^{-1}] \quad (\text{III})$$

Forty samples were analysed for planktic foraminiferal assemblage composition under a Zeiss Stemi 2000-C binocular with $100\times$ magnification. Planktic foraminifera were counted from sample splits which yield between 300 and 400 specimens in the $>125\mu\text{m}$ size fraction (Fig. 3). On the one hand a cut-off at $125\mu\text{m}$ certainly results on an information loss on smaller taxa, but on the other hand the $<125\mu\text{m}$ fraction contains large numbers of juveniles, which increases the uncertainty in determinations on the species level. Therefore, we consider the $>125\mu\text{m}$ for more appropriate for species-level assemblage analyses. It bears high potential of failure to determine juvenile tests to the species level; therefore, assemblage census is usually based on larger sizes ($> 125\mu\text{m}$). Species identification follows almost exclusively Berggren and Norris (1997) and Olsson et al. (1999). The diversity of planktic foraminiferal assemblages was characterized by species richness (S), Shannon heterogeneity (H' , Shannon and Weaver, 1949) and evenness:

$$\text{Shannon heterogeneity:} \quad H' = - \sum_{i=1}^S p_i \ln p_i \quad (\text{IV})$$

$$\text{Evenness:} \quad E = H' / H_{\max}, \quad H_{\max} = \ln(S) \quad (\text{V})$$

- p_i as the proportion of individuals belonging to the i^{th} species in the dataset of interest,
- heterogeneity is $0 \leq H' \leq \ln S$,

172 - Evenness is $0 \leq E \leq 1.0$.

173 We used the “vegan package” for R for the statistical analysis of the non-metric
174 multidimensional scaling (NMDS, Fig. 4) with Bray-Curtis distance measure and CaCO_3 as
175 well as $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ of all three foraminifera groups. Relative abundance of all samples with
176 paired CaCO_3 , $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ results were used. All species with a relative abundance $>2\%$ in
177 at least one sample were included.

3 Results

3.1 Carbonate content and dissolution indicators

Background CaCO_3 values (Fig. 2) range between ~80 and 86 wt %, with two distinct minima of 69 and 71 wt % corresponding to LDE1 (195.4 mcd) and LDE2 (194.5 mcd).

Coarse fraction (%CF, Fig. 2) data show background values of 3–4 % below the LDE and a minimum of 0.6 % at the onset of LDE1, from where it rises up to 8 % from LDE2 to the upper part of the record, where it drops to 2 %. Fragmentation of planktic foraminifera (%Fp, >125 μm) shows maxima (~15 %) at the base of the sequence together with the lowest %CF during the onset of LDE1, relative to background values of 4–5 %.

The linear sedimentation rate (LSR, Fig. 2E) varies between 0.3 and 0.32 cm kyr^{-1} and, considering the uncertainties of this calculation, is seen as constant. Planktic foraminiferal numbers (PFN, >63 μm [$\# \text{g}^{-1}$]) decrease at the onset of LDE1, subsequently rise to peak values within LDE2 and show a long-term decrease after the LDE. PFN ranges between 15,000 and 219,000 g^{-1} . PFAR (>63 μm) ranges between ~17,000 and 250,000 $\text{cm}^{-2} \text{kyr}^{-1}$ with a similar trend like PFN. The percentage of planktic foraminifera, %P (>63 μm fraction; Fig. 2) shows a decrease to 97.9 % during LDE1 compared to a background of >99 %. The overall shape of the curve is similar to %CF.

3.2 Foraminiferal stable isotopes ($\delta^{13}\text{C}$, $\delta^{18}\text{O}$)

$\delta^{13}\text{C}$ of benthic foraminifera (*Nuttallides truempyi*) varies around 1.0 ‰ and displays two negative excursions (up to -0.9 ‰) contemporary to the Fe XRF core scanning peaks (Figs. 2; Deprez et al., 2017a). $\delta^{13}\text{C}$ values of subsurface dwelling *Parasubbotina pseudobulloides* and *P. variospira* show a slightly decreasing trend of -0.6 ‰ (2.3 to 1.7 ‰) within LDE1 and a sharper, more negative excursion of -0.8 ‰ (2.2 to 1.4 ‰) during LDE2. Surface dwelling *Morozovella angulata* shows a -1.1 ‰ excursion (3.7 to 2.6 ‰) and, thus, a more distinct response than *P. pseudobulloides* and *P. variospira* to the LDE. However, the variability in *M. angulata* is generally very high and may thus overestimate the amplitude. The positive excursion just below and above LDE1 show amplitudes of comparable heights to the negative CIEs.

The $\delta^{18}\text{O}$ values of *N. truempyi* show a high variability with two distinct negative excursions (up to -0.8 ‰) within the LDE. *Parasubbotina pseudobulloides* and *P. variospira* yield values between -0.7 and 0.2 ‰ and display a negative long-term trend from below LDE1. $\delta^{18}\text{O}$ of *M. angulata* decreases by -0.7 ‰ (-0.6 to -1.3 ‰) and rises directly above LDE2 to -0.7 ‰ before it slowly decreases to a steady level of -0.9 ‰. Surface and subsurface species display a rather

similar curve, whereas the benthic record shows a pattern with distinctly negative peaks in LDE1 and LDE2, resembling the negative excursions in the XRF Fe counts. The $\delta^{13}\text{C}$ gradient between surface and subsurface slightly increases below LDE1 (+0.3 ‰), but there is no clear trend for $\Delta\delta^{18}\text{O}$ (Fig. 2, Fig. 5).

3.3 Planktic foraminiferal assemblages

Planktic foraminiferal diversity remains relatively constant during the study interval. Shannon H' diversity varies between 2.2 and 2.6 and species richness (S) between 14 and 27 species. Both parameters show maxima during LDE1 and LDE2 and a high variability between the two phases (Fig. 6).

The ten most abundant species cover 92 % of all planktic foraminifera tests. Subsurface dwelling *Parasubbotina* and *Subbotina* make up almost 70 %, whereas surface dwelling *Morozovella* show an average abundance of 11 % (Fig. 3). Species can be grouped according to their abundance and appearance (Fig. 3): (1) species with highest abundances below the LDE, (2) species present with minor variations throughout the record or with slightly enhanced abundances during the LDE and (3) species with appearance or high abundances above the LDE.

Group (1) covers *Praemurica inconstans* and *P. uncinata* as they initially compose 4 % and 24 % of the assemblage and disappear just below or during the LDE, and *M. praeangulata* with a comparable pattern, starting with up to 17 % below the LDE.

Group (2) contains *Globanomalina ehrenbergi* with one peak of 4 % between LDE1 and LDE2, *Globanomalina imitata* varies between 0 and 5 % and is most common below the LDE. *Globanomalina chapmani* ranges from 1.5–10 %, *Parasubbotina varianta* appears between 7 and 18 % without distinct maxima, *Subbotina triloculinoides* occurs abundantly with peak values of 22 % just before the onset and after the termination of the LDE. *Subbotina cancellata* ranges from 10–21 % with a long-term decrease through the record. *Subbotina velascoensis* shows its highest abundance (7 %) below the LDE. *Parasubbotina pseudobulloides* shows a decreasing trend during our record from 9–2%. *Parasubbotina variospira* shows a similar pattern with peak values below the LDE (25 %). *Igorina pusilla* reaches highest abundances of up to 10 % during the LDE interval.

Generally higher abundances above the LDE (group 3) were observed for *M. conicotruncata*, *I. albeari* and *M. angulata*. *Morozovella conicotruncata* peaks (11 %) above the LDE, *I. albeari* shows peak abundances (12 %) during LDE1 and LDE2. *Morozovella angulata* initially also shows peak levels up to 12 % within LDE1 and LDE2 but becomes even more abundant (20 %) towards the top of the record.

This development is also shown in Fig. 3 (B), where species are summed up like described. In Fig. 3 (C), sums of mixed layer/surface species and thermocline/subsurface species are shown. Below the LDE, the abundance of surface dwellers decreases and goes up in two phases within each LDE1 and LDE2 phase and continuously increases upwards.

4 Discussion

4.1 Carbonate dissolution and preservation of foraminiferal calcite

4.1.1 Carbonate preservation

Deep-sea carbonate dissolution is predominantly controlled by depth changes of the lysocline/calcite compensation depth (CCD) as well as by oxidation of organic carbon. Dissolution causes enhanced test fragmentation of planktic foraminifera (%Fp: e.g. Berger, 1970; Dittert et al., 1999), which are up to three times more dissolution-susceptible than benthics (Berger, 1973). Consequently, carbonate dissolution leads not only to increased %Fp and lower CaCO₃, but also to lower %CF, %P, PFN and PFAR.

As indicated, carbonate background values are rather constant throughout the studied succession, whereas the LDE beds display CaCO₃ minima. CaCO₃ drops by 14 wt% (83–69 %) within LDE1 (195.4 mcd), and by 13 wt% (84–71 %) within LDE2 (194.5 mcd). We consider carbonate dissolution to be more severe during LDE1 than during LDE2 due to higher %Fp and lower %CF concurrent to lower values of %P, PFN and PFAR during LDE1. For LDE2, we speculate that other processes were involved such as enhanced dilution by clay or a decline of carbonate production. Enhanced dilution is assumed due to an accompanied increase in the sedimentation rate, starting during LDE2 (Fig. 2). However, absolute abundances of planktic foraminifera are rather constant, but changes within numbers of calcareous nannofossils were not taken into account. As the second benthic negative CIE (194.5 mcd) is smaller than the first peak, the amount of carbon injected into the ocean-atmosphere system might have been below the threshold for a substantial lysocline rise during LDE2. Clay-enriched horizons were also documented at the base of the entire LDE from deep-sea successions at Shatsky Rise (Westerhold et al., 2008, 2011; Jehle et al., 2015).

4.1.2 Foraminiferal preservation

Good preservation of foraminiferal carbonate is key for both reliable geochemical analyses and assemblage counts. Mechanisms controlling test preservation include dissolution, bacterial activity and recrystallization or overgrowth (e.g. Hancock et al., 2007; Nguyen et al., 2011). Foraminifera largely precipitate their carbonate from ambient seawater (e.g. Erez and Luz,

1983), and are, thus, considered to be excellent carriers of past seawater geochemistry signals. However, the geochemical composition of their calcite might be altered by diagenesis and recrystallization during and after burial (e.g. Stap et al., 2010; Edgar et al., 2013). $\delta^{13}\text{C}$ tends to be less influenced by diagenetic alterations while the effect on $\delta^{18}\text{O}$ is more substantial (Killingley, 1983; D'Hondt and Zachos, 1993; Pearson et al., 2001).

Light microscope observations of planktic foraminifera in Paleocene samples of Site 1262 reveal sparse overgrowth, but an overall moderate to good preservation (Birch et al., 2012 and observations of the current work). Slight yellow stains on the tests make them appear less white than seen in other Paleocene sequences like Shatsky Rise Site 1210 (Jehle et al., 2015). Specimens are free from infillings, show a milky, coarsely textured surface through light microscopy and indicate recrystallization under the SEM (Birch et al., 2012). It seems to be a typical, somewhat “frosty” preservation in deep-sea carbonate oozes (Pearson et al., 2001; Sexton et al., 2006). This state of planktic foraminiferal preservation usually leads to heavier $\delta^{18}\text{O}$ values, since the calcite carries an additional bottom water isotope signature due to recrystallization, and therefore reconstructed paleotemperatures are lower than for unaltered tests (Pearson et al., 2001; Sexton et al., 2006; Edgar et al., 2015). For benthic foraminifera, the impact of recrystallization on both $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ is considered to be much less severe than for planktic foraminifera (Edgar et al., 2013; Voigt et al., 2016).

In contrast to earlier studies (e.g. Thomas et al., 1999; Raffi and Bernardi, 2008), we suspect that diagenetic alteration has played a substantial role at Site 1262 for the planktic $\delta^{18}\text{O}$ signal. Besides ultrastructural observations by SEM (Birch et al., 2012), this is supported by the negligible vertical temperature gradient between $\delta^{18}\text{O}$ values of surface, subsurface and benthic dwellers and the complete lack of a $\delta^{18}\text{O}$ gradient between subsurface and benthic environment (Fig. 2). The temperature difference between surface ocean and seafloor of only $\sim 6.5^\circ\text{C}$ is unrealistically low. For comparison, the vertical temperature gradient at Pacific Shatsky Rise Site 1210 was estimated to be $\sim 9^\circ\text{C}$ during the LDE (Jehle et al., 2015) and up to 15°C at the tropical or equatorial North Pacific Ocean (Shatsky Rise Site 1209, Allison Guyot Site 865) during Late Paleocene, PETM and Early Eocene (Tripathi and Elderfield, 2005).

In certain intervals the subsurface dwellers have even lower $\delta^{18}\text{O}$ values than the benthics (Fig. 2, 195.05–195.98 rmcd). This would not be the case in well-preserved foraminiferal assemblages, even if we would consider the unlikely existence of warm saline bottom waters. Based on visually indicated recrystallization and overgrowth in these intervals (Birch et al., 2012), we conclude that surface and subsurface planktic foraminiferal tests were recrystallized during early burial, which shifted the recorded $\delta^{18}\text{O}$ towards more positive values. Nevertheless, assuming a more or less homogeneous diagenetic overprint during the studied

interval, the relative $\delta^{18}\text{O}$ changes might still represent the original trends (Sexton et al., 2006), with a modified magnitude of change.

Furthermore, species-specific dissolution susceptibility can change the assemblage composition (e.g. Berger, 1970; Pearson et al., 2001; Petrizzo, 2007; Nguyen et al. 2011; Nguyen and Speijer, 2014) and consequently bias the interpretation of faunal data. As some species are more dissolution susceptible than others, the planktic foraminiferal assemblage composition could, to some extent, be biased by carbonate dissolution. Dissolution and fragmentation occurs during settling, sedimentation or shortly after burial. As a consequence, the assemblage composition would shift to lower relative abundances of dissolution-susceptible taxa such as *Igorina* spp. and subsequently higher relative abundances of thick-walled *Acarinina* or *Morozovella* species (Petrizzo et al., 2008; Nguyen et al., 2011). However, both aforementioned taxa are not very abundant in the studied samples while *Igorina* spp. is present in moderate numbers and flourishes during the LDE. The species might prefer a warmer environment; therefore, the very high production rate might cover dissolution to some extent. Further indicators for partial dissolution are supposedly a combination of low relative abundance and increased fragmentation of *Subbotina* spp., low %P rate and PFN (e.g. Nguyen et al., 2009). Altogether, in contrast to the stable isotope signal, the planktic foraminiferal composition has presumably not been substantially affected by dissolution during or before sedimentation.

4.2 Stable isotope patterns during the LDE at Walvis Ridge

In addition to literature data (Berggren and Norris, 1997; Olsson et al., 1999), the habitats of planktic foraminifera taxa were inferred from $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values. We distinguished between (photosymbiotic) surface dwelling and subsurface dwelling, thermocline species (e.g. Shackleton et al., 1985; Norris, 1996; Birch et al., 2012). Studied photosymbiont-bearing taxa are *M. angulata*, *M. praeangulata*, *P. uncinata* and *P. incontans*, while non-photosymbiotic are *P. variospira* and *P. pseudobulloides*. For the benthic habitat, *N. truempyi* was used.

4.2.1 $\delta^{13}\text{C}$ response to the LDE

The surface water signal is influenced by primary productivity and subsidence of ^{12}C -enriched organic particles to the seafloor, causing a carbon depth gradient. Due to preferred uptake of ^{12}C by symbiotic algae, photosymbiotic foraminiferal tests are ^{13}C enriched relative to ambient seawater and to deeper dwelling foraminifera without photosymbionts (e.g. Shackleton et al., 1985; Spero et al., 1991; Rohling and Cooke, 2003). Hence, $\delta^{13}\text{C}$ of seawater and foraminifera is depth-dependent.

Even though the ~1 ‰ CIE in planktic surface dwellers is quite large and distinct during the LDE, it also has a steady state below the LDE until ~ 62.25 Ma with about the same values as the peak and shows a quick positive excursion just below the event. For surface dwelling foraminifera, possible reasons might be (a) varying photosymbiotic activity or (b) surface ocean currents. Suboptimal living conditions might have led to smaller tests, inhabiting less algae symbionts (Schmidt et al., 2004). The average $\delta^{13}\text{C}$ values are more positive above the LDE than below, suggesting either a higher photosymbiotic activity for *M. angulata* than for *M. praeangulata*, or, more likely, they follow the secular trend to heavier $\delta^{13}\text{C}$ values above the LDE probably due to higher primary productivity and slightly more oxygenated surface water after the LDE.

The surface- to subsurface $\delta^{13}\text{C}$ gradient ($\Delta\delta^{13}\text{C}$) displays a rather constant offset (Fig. 2). Enhanced stratification as observed at Shatsky Rise (Jehle et al., 2015) is not visible here. The $\delta^{13}\text{C}$ value was probably very uniform in the different water layers due to a higher mixing rate and ocean currents, or because of diagenetic overprint, even though $\delta^{13}\text{C}$ is normally less affected.

4.2.2 $\delta^{18}\text{O}$ response to the LDE

Temperature is an important factor controlling $\delta^{18}\text{O}$ of foraminiferal calcite due to equilibrium fractionation between seawater and calcite. Because of their shallower habitat, $\delta^{18}\text{O}$ values are lower in photosymbiotic planktic foraminifera than in their non-symbiotic relatives. Changes in salinity, carbonate ion concentration or pH as well as waxing and waning of continental ice sheets (e.g. Shackleton, 1967; Railsback et al., 1989; Spero et al., 1997) are additional factors to influence foraminiferal $\delta^{18}\text{O}$. The ice-effect is not taken into consideration as the early Paleogene is generally suspected as an ice-free period (e.g. Zachos et al., 1994).

During the LDE, $\delta^{18}\text{O}$ records suggest a temperature rise of ~2.0°C (0.5 ‰) at the seafloor (*N. truempyi*), ~1.5°C (0.35 ‰) in the thermocline (*P. variospira* and *P. pseudobulloides*) and ~2.6°C (0.6 ‰) in surface water (*M. angulata*). This ocean warming is supported by the faunal data, which show an abundance increase of warm-water, low-latitude taxa such as *Morozovella*.

4.2.3 Implications on the stable isotope patterns for the LDE

The negative CIEs associated with the LDE could be explained by various scenarios as proposed for the PETM (e.g., Dickens et al., 1997). For the PETM, one scenario considers a sudden and massive release of methane from the seafloor, probably triggered by circulation changes in the deep ocean (Tripathi and Elderfield, 2005; Nunes and Norris, 2006) or large-scale continental slope failure (e.g. Katz et al., 2001). This methane was rapidly oxidized to CO_2 , contributing to stronger greenhouse forcing. On the other hand, the destabilization of methane

hydrates was seen as unlikely to be the sole source as the reservoir at the end of the Paleocene was probably not sufficient (e.g. Buffet and Archer, 2004; Kirtland Turner and Ridgwell, 2016), whereas the magnitude of warming and changes in the CCD are compatible with much greater carbon masses. Therefore, additional carbon sources were suggested, such as volcanic outgassing or thermal decomposition of organic matter or oxidation of terrestrial and marine organic carbon (Pagani et al., 2006; Dickens, 2011; DeConto et al., 2012; Gutjahr et al., 2017).

For the LDE, most of these explanations suggest amplifications by increased insolation due to temporal coincidence with short-term eccentricity maxima (Westerhold et al., 2008) contributing to global warming. In addition, the oxidation of a massive amount of organic carbon or enhanced CO₂ input to the ocean-atmosphere system resulting from the onset of the intense volcanic activity in the North Atlantic Igneous Province (NAIP) or southeastern Greenland margin (Sinton and Duncan, 1998; Pedersen et al., 2002; Larsen et al., 2016) might have contributed to the negative carbon isotope values during the LDE.

However, as the LDE is more comparable to ETM2 with regard to orbital pacing and magnitude than to the PETM, similar causes have been inferred for these two events (Deprez et al., 2017a, 2017b). As for the LDE, Eocene short-term hyperthermals like ETM2 and ETM3 mostly coincide with eccentricity maxima. Orbital pacing might have triggered changes in ocean ventilation, leading to oxidation of dissolved organic matter during transient Eocene warming events (Sexton et al., 2011; Stap et al., 2009).

4.3 Planktic foraminifera faunal changes

Surface mixed layer foraminifera were abundant below the LDE with a maximal abundance of *Praemurica uncinata*, *P. inconstans* (together up to 24 %) and *M. praeangulata* (up to 15 %). A turnover of photosymbiont-bearing taxa is well documented by the disappearance of the genus *Praemurica*, the long-term decline of *M. praeangulata* and the parallel emergence of other taxa (e.g. *Igorina albeari*, *Morozovella* spp.) with the onset of the LDE. The decline of *M. praeangulata* and *Praemurica* started ~170 ky before the event and *Praemurica* finally disappeared during LDE1. Simultaneously, the sum of all surface dwelling planktic foraminifera displays a minimum between 170 kyrs prior to the LDE and the LDE-onset. The surface ocean assemblage changed from a praemuricate to a muricate fauna as observed at other sites (Norris, 1996; Guasti et al., 2006), or more likely their different ability to adopt to the changing paleoenvironmental conditions. Other than *P. uncinata* and *P. inconstans*, *M. praeangulata* survived the LDE, albeit with decreasing abundances. The replacement of *Praemurica* by *Morozovella* could have had competitive reasons, since both genera are photosymbiotic surface dwellers and inhabited a similar ecological niche (Norris, 1996; Birch et al., 2012). The transition of a *Praemurica*- to *Morozovella*-dominated surface ocean fauna took place around the first occurrence of *Igorina albeari* (=P3a/P3b Subzone boundary),

whereas the final disappearance of *Praemurica* coincides with LDE1. In addition, the planktic turnover is characterised by the rise of *I. albeari* and *M. conicotruncata*.

$\delta^{18}\text{O}$ indicates slightly lower calcification temperatures for *Praemurica* than for *M. angulata* and *M. praeangulata*, suggesting either a somewhat deeper habitat or alternatively a flourishing of *Praemurica* during a colder season. *Morozovella praeangulata* is considered to have a closer relationship to *Praemurica* than the other morozovellid species (e.g. Berggren and Norris, 1997; Olsson et al., 1999). The ecological preferences of *M. praeangulata* as inferred from $\delta^{13}\text{C}$ suggest a similar photosymbiotic activity like *M. angulata* (Fig. 2).

Absolute and relative abundances of *M. angulata* increased within the LDE beds (Fig. 3), suggesting a relative benefit from temperature rise and paleoenvironmental changes. This development is compatible with a characterization as a warm water taxon showing higher numbers in the (sub-)tropical oceans (e.g. Quillévéré and Norris, 2003).

Similar to *M. angulata*, *I. albeari* showed enhanced abundances in both LDE beds, while *I. pusilla* only increased during LDE1. Therefore, *I. albeari* might have had a higher temperature sensitivity than *I. pusilla*. *Morozovella* and *Igorina* probably lived in different niches and were not direct competitors as the latter lived in slightly deeper water than *Morozovella* (e.g. Norris, 1996; Berggren and Norris, 1997; Pearson et al., 2001; Jehle et al., 2015). In contrast to *I. albeari*, which became more abundant towards the top of the record, *I. pusilla* then declined and might have had different ecological optima in terms of nutrient availability, temperature, water depth or flourishing during a somewhat colder season than *I. albeari*.

Over the long run, surface dwellers (*M. angulata*, *M. conicotruncata*) show a relative increase at the expense of *Parasubbotina* as also supported by absolute numbers. The change starts ~150 kyrs before the LDE onset and can be linked to the observed LDE warming.

Thermocline dwellers (*Parasubbotina* spp., *Subbotina* spp.) make up 46–86 % of all species (~70 % in average). Absolute abundance (cf. Appendix) of *Subbotina* and *Parasubbotina* show slightly enhanced numbers of *S. cancellata*, *S. triloculinoidea* and *P. variospira* during the LDE beds, however, as a short-term response only. We conclude that the thermocline habitat was constantly unstable and, thus, favourable for the two subsurface genera.

The above given interpretations are supported by non-metric dimensional scaling (NMDS). The strongest separation is between the samples below 196.63 mcd (before 62.30 Ma) by ~0.3 dissimilarity measure in the NMDS axis 1 (Fig. 4) and the samples during LDE1. Assemblage changes as demonstrated by the NMDS are expressed by two main sample groups, separating the samples “below the LDE” from those “during” and “above”. The samples during and above

the LDE show a very similar faunal assemblage opposed to the samples below the event. The start of major, but gradual changes are observed ~160 ky before the LDE (196.98 mcd at 62.34 Ma) as expressed by NMDS axis 1 loadings (Fig. 4), possibly caused by a decrease and subsequent disappearance of praemuricate species and the introduction of *I. albeari* and new *Morozovella* species.

Based on stable isotope and faunal data, the paleoceanographic scenario for Site 1262 might reflect a development from a “temperate” system to a more “subtropical” one, in which the zonal boundary shifted southwards during the LDE warmings. The subtropical system is generally warmer, more stable and better stratified, causing improved living conditions for surface dwelling photosymbiont-bearing foraminifera. Before the LDE, photosymbiotic species were rare, which can be explained by enhanced deep mixing of the upper water column. As surface dwellers mostly declined between the two LDE peaks and show higher abundances during both event levels, the somewhat colder and less stratified conditions in between probably inhibited proliferation. After the LDE, the situation became somewhat more favourable for photosymbiotic taxa, supporting a slightly better stratified upper ocean as indicated by the enhanced stable isotope gradients (Δ) and improved living conditions for subsurface taxa (Berggren and Norris, 1997; Fig. 3).

4.4 Comparison to Pacific ODP Site 1210

4.4.1 Paleogeography of ODP Sites 1210 and 1262

The opening of the South Atlantic Ocean started in the Early Cretaceous (Pérez-Díaz and Eagles, 2017), and so, the ocean was narrower in the Paleocene and more restricted than today, causing a different ocean current system compared to the recent South Atlantic. The Walvis Ridge Paleocene paleoceanographic reconstructions suggest strong vertical surface water mixing in the South Atlantic from south to north along the African coastline (e.g. Haq, 1981; Pak and Miller, 1992).

ODP Site 1210 (Shatsky Rise) was located at a subtropical paleolatitude of ~24°N (van Hinsbergen et al., 2015) and an estimated paleodepth of about 2700 m (Site 1262: ~3300 m). The plateau was positioned much closer to the equator than today and was, thus, subjected to higher insolation and a different circulation pattern from today (Bralower et al., 2002).

4.4.2 Geochemical data and preservation

Like for Site 1262, two distinct XRF core scanning Fe peaks identify the LDE horizons at Site 1210 (195.3 mcd, LDE1, and 194.6 mcd, LDE2). These Fe peaks serve as a key tool for stratigraphic correlation between the two sites (Westerhold et al., 2008).

The average wt% CaCO₃ content is high at both sites, but at Site 1210 with 84–95 % much higher than at Site 1262 (68–86 %). Both show two negative peaks contemporary to the event horizons.

Both Sites 1262 and 1210 as well as 1209 (Westerhold et al., 2011) show two negative benthic CIEs, which are ~100 ky apart from each other, supporting the idea of a two-phase event coinciding with two short eccentricity maxima (Westerhold et al., 2008; Dinares-Turell et al., 2014) and Fe XRF peaks. A two-phase scenario was identified at several deep-sea sites (ODP Sites 1001, 1209, 1210, 1262, U1407; Westerhold et al. 2008; Jehle et al., 2015; Deprez et al., 2017a and b; Yamaguchi et al., 2017). At Site 1210, benthic foraminifera show a by 0.4 ‰ minor excursion of both $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ compared to Site 1262, indicating (a) slightly higher deep-water temperatures at 1210, which is plausible due to a shallower water depth, or (b) lighter $\delta^{13}\text{C}$ might result from aged water masses, transported from other ocean areas (e.g. Kroopnick, 1979; Quillévéré et al., 2002). As the Southern Ocean was an important place for deep-water formation (Pak and Miller, 1992, Kroopnick, 1980), the transport of bottom water masses to the central Pacific was longer than to the South Atlantic.

From comparing dissolution sensitive parameters of Site 1210 (Jehle et al., 2015) with Site 1262 such as CF, %PF or %Fp, we conclude more intense carbonate dissolution for Site 1262, like previously observed in the early Eocene (Stap et al., 2009). At both sites, LDE1 was more influenced by carbonate dissolution than LDE2. Slightly enhanced carbonate dissolution, caused by a lysocline/CCD rise, is assumed for LDE1, whereas terrigenous dilution could be more possible during LDE2 at Site 1262 than at Site 1210. Hints for that scenario are a stronger CaCO₃ drop, increased %Fp, low %CF and low %P, PFN and PFAR during LDE1 compared to a smaller CaCO₃ drop and a lack of these characteristic changes during LDE2 (Fig. 2).

In addition to that, recrystallization is higher at Walvis Ridge than at Shatsky Rise. This view is supported by a strongly muted temperature difference between planktic and benthic foraminifera at Site 1262. At Site 1210, the largest $\delta^{18}\text{O}$ temperature gradient (Δ) is ~9°C, which is already rather low and probably overprinted by early diagenesis. At Site 1262, however, this difference makes up only ~6.5°C, strongly suggesting an overprint of the pelagic signal through early diagenesis at the colder seafloor. Recrystallization of planktic foraminiferal calcite dampened the $\delta^{18}\text{O}$ warming signal (Pearson et al., 2001; Sexton et al., 2006; Jehle et al., 2015).

Jehle et al. (2015) observed at Shatsky Rise 1210 a rising gradient before and during the LDE, suggesting enhanced stratification of upper water masses, a change which is accompanied by higher abundance of thermocline dwelling *Parasubbotina*. It was proposed that a **Deep Chlorophyll Maximum** was developed under well-stratified conditions during and after the LDE.

Comparing the $\delta^{13}\text{C}/\delta^{18}\text{O}$ crossplots of the two sites, divergent signatures in the different habitats become apparent (Fig. 5). $\delta^{13}\text{C}$ results of surface dwelling *M. angulata* and *Praemurica* species are within the same range, but surface $\delta^{18}\text{O}$ values distinctly differ with higher values at Site 1210. Due to the tropical to subtropical setting at Site 1210, the observed $\delta^{18}\text{O}$ values seem realistic, although the different signals between the depth habitats might be reduced by stronger diagenetic alteration at Site 1262. Site 1262 subsurface dwellers isotope data cover a narrower range suggesting that (a) the thermocline habitat has been more stable through time in the South Atlantic or (b) diagenetic alterations made the signal more even.

Both sites show a wider spread in the $\delta^{18}\text{O}$ surface signal than in $\delta^{13}\text{C}$ and shows again the likelihood of biased 1262 results by poor preservation as indicated by a lack of $\Delta\delta^{18}\text{O}$ variation. These findings support our assumption that early diagenetic dissolution and recrystallization did probably not influence much the benthic foraminiferal $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ signals (Edgar et al., 2013; Voigt et al., 20156), but had a substantial impact on planktic foraminifera $\delta^{18}\text{O}$ (e.g. Pearson et al., 2001).

4.4.3 Planktic foraminiferal faunal response to the LDE

Both diversity (Shannon H') and evenness (Fig. 6) are generally higher at Walvis Ridge Site 1262 and show increased values at the onset of the LDE, in contrast to consistently lower parameter values at Shatsky Rise Site 1210 during the LDE. The diversity increase at the LDE onset is probably related to the introduction of several new *Morozovella* species right after the LDE potentially triggered by the warming associated with this event. The increase of Shannon H' and species richness at Walvis Ridge with the onset of the LDE might have also led to a more even distribution among taxa.

A striking similarity of the two sites is the pre-LDE shift in the assemblage starting 170–200 ky before the LDE **negative CIE shift** as indicated by an increase in *Morozovella angulata* and a contemporary decrease in *Praemurica uncinata*, *P. inconstans* and *M. praeangulata*. This prominent change represents a slow shift from praemuricate to muricate species, where *M. praeangulata* was replaced by *M. angulata* and *Praemurica* disappeared, starting each at ~62.35 Ma.

The most apparent compositional difference between the South Atlantic (Site 1262) and the Pacific (Site 1210) across the LDE is the dominance of subsurface dwellers at Site 1262 (79.9 % in average), whereas photosymbiotic planktic foraminifera are much more abundant at Site 1210 (74.9 % in average). Possible reasons for this are (a) the paleolatitude, as 1210 is situated closer to the equator and 1262 in a subtropical to temperate zone, which yield the highest diversity in modern oceans (e.g. Berger and Parker, 1970; Rutherford et al., 1999; Quillévéré and Norris, 2003), or (b) a closed-sum-effect, causing a bias due to much higher production of

Parasubbotina and *Subbotina* at 1262, diluting the less abundant surface-dwelling taxa, even though the total production of surface dwellers was unchanged. At Pacific Shatsky Rise Site 1210, environmental conditions resulting from a permanent gyre system might have been beneficial for higher abundances of surface dwellers (e.g. Ortiz et al., 1995; Birch et al., 2013).

There are other, more subtle differences between the faunal assemblages of the two sites, hinting towards the described scenario: At 1262, some surface water species vary highly in abundance, whilst subsurface species show more steady numbers during the LDE. This suggests that the surface ocean might have been more affected by environmental changes like enhanced vertical mixing and weaker stratification in contrast to the rather stable situation at Site 1210. The South Atlantic subsurface assemblage composition in turn seems to be more stable with less species variation compared to the Pacific fauna and less influenced by the environmental changes accompanying the LDE, even though the position of the thermocline was putatively shallower and seasonally more stirred up than in the tropical central Pacific. As outlined, at 1262 the abundance of subsurface dwellers was three times higher than surface specimens. A shoaling thermocline can indicate upwelling or high turbulence from deeper waters (Cullen, 1982; Herbland and Voituirez, 1979) resulting in higher abundances of subsurface dwellers. This fits well with the virtual lack of stratification at 1262 as indicated by the rather constant $\Delta\delta^{13}\text{C}$ offset.

5 Conclusions

The detailed study of planktic foraminifera and geochemistry revealed the following key results for the LDE at Walvis Ridge ODP Site 1262:

(a) The LDE occurs stratigraphically in P3b, 0.9 m above (200 ky after) the P3a/b Subzone boundary (see Fig. 2A).

- a. Both LDE beds are characterized by a substantial CaCO_3 drop of 15–17 wt%, of which LDE1 shows indications of dissolution, probably related to lysocline shallowing, and CaCO_3 decline LDE2 is interpreted as a result of terrigenous dilution.
- b. Two distinctly negative CIEs of about 0.9 ‰ are apparent in benthic (*Nuttallides truempyi*) and planktic surface foraminifera (*Morozovella angulata*), however, the subsurface planktic foraminifera (*Parasubbotina variospira/pseudobulloides*) $\delta^{13}\text{C}$ peak during LDE1 is only poorly developed.
- c. Ocean warming as reflected by $\delta^{18}\text{O}$ is rather uniform between the different habitats with 1.5–2.6°C. SST increases by 2.6°C, intermediate and bottom waters by 1.5°–2.2°C. A low temperature difference between the surface ocean and the seafloor as well as a lack of

gradient between the subsurface and benthic foraminifera $\delta^{18}\text{O}$, we suggest a substantial impact of recrystallization of planktic foraminiferal calcite.

d. Subsurface dwelling foraminifera are very dominant and decrease slightly over the studied interval in relative abundance. Surface-dwelling warm-water taxa *Morozovella* and *Igorina* significantly rise in their abundances within the LDE and become generally more abundant after the event hinting towards a shift from “temperate” to “subtropical” conditions.

A comparison between ODP Site 1262 and Shatsky Rise ODP Site 1210 (Jehle et al., 2015) revealed a number of striking similarities and differences:

~~(a) At both sites, the LDE occurs stratigraphically in Subzone P3b, however, the first occurrence datum of *Igorina albeari* is well below the LDE (62.76 Ma at Site 1210, 62.39 Ma at Site 1262).~~

a. Surface dwelling planktic and benthic foraminifera species show a stronger $\delta^{13}\text{C}$ response to the LDE by up to 0.4 ‰ at Site 1262.

b. Diagenetic alteration of planktic foraminiferal tests is more pronounced at Site 1262.

c. At both sites, faunal changes like a decrease of *Praemurica* occur about 170 kyrs before the LDE. Further, both sites show the extinction of *Praemurica* at the base of the LDE, followed by a long-term rise in *Morozovella* abundance.

d. Planktic foraminiferal assemblages of Site 1262 are dominated by subsurface taxa such as *Subbotina* and *Parasubbotina*, whereas warm surface water indicating *Morozovella* taxa are dominant in the Pacific (Site 1210). Overall assemblage changes within the event are stronger at Shatsky Rise Site 1210, probably due to stronger ecological changes like the development of a DCM.

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Figures

Fig. 1

Paleogeographic map (62 Ma) of the two studied ODP Sites 1262 (Walvis Ridge) and 1210 (Walvis Ridge). The map was generated using <https://www.odsn.de/odsn/services/paleomap/paleomap.html> (Hay et al., 1999).

Fig. 2

Stratigraphy, XRF core scanning Fe intensities, stable isotopes and other sedimentary parameters of samples from the LDE at Site 1262. (A) Stratigraphy, including magnetostratigraphy (Bowles, 2006) and biostratigraphy (own results). XRF core scanning Fe intensities (Westerhold et al., 2008) during the LDE are used for stratigraphic correlation. Sedimentary parameters are (B) carbonate (wt% CaCO₃) measurements, with (C) coarse fraction (%CF), (D) planktic foraminifera fragmentation index (%Fp) >125µm, (E) sedimentation rate (SR, Westerhold et al., 2008, used for planktic foraminifera accumulation rate (PFAR)), planktic foraminifera number (PFN) with PFAR and (F) the planktic foraminifera proportion (%P) in two different size fractions (>63µm, >125µm). (G) shows δ¹³C and (H) δ¹⁸O records of benthic (*N. truempyi*), planktic subsurface (*P. pseudobulloides* and *P. variospira*) and planktic surface dwellers (*M. praeangulata* and *M. angulata*) and (I) Δδ¹³C and Δδ¹⁸O gradients of surface to subsurface isotope values. Age model is based on Dinarès-Turell et al. (2014), La2011 solution.

Fig. 3

Species distribution of planktic foraminifera together with XRF core scanning Fe intensities (Westerhold et al., 2008) **and sum-plots of species.** (A) Species are coloured according to their habitats: surface mixed layer in red, subsurface thermocline in blue and green and *Igorina albeari* and *I. pusilla* in grey. The taxa also make three groups by their appearances, which is appearance mostly below the LDE, appearance over the entire record or enhanced during the LDE and appearance mostly after the LDE. Sum plots are showing (B) the appearances of species that are mainly abundant before, during or after the LDE and (C) summed up species which live in the surface (mixed layer) or subsurface (thermocline) water level. Age model is based on Dinarès-Turell et al. (2014), La2011 solution.

Fig. 4

Non-metric multidimensional scaling. Left panel: Results of NMDS (stress=0.15, Bray-Curtis distances) offer relative similarities and differences of the planktic foraminifera communities (species level) between the event stages (color-coded as indicated). Species are marked with cross symbols. Numbers of depth indicate the sample. Pre-LDE assemblages stand out from the rest of the record.

Vectors are considered to represent ecological control of the distribution and belong to the “species” coordinate system. Environmental parameters should be considered in aspects of direction, length again is arbitrarily scaled and should be compared in relation to each other (Hammer and Harper, 2012). Significant at the 95 % level are $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ of *Parasubbotina uncinata*, *P. inconstans* and *M. angulata*. Right panel: Loadings of NMDS Axis 1 and 2, as well as the XRF core scanning Fe variations (Westerhold et al., 2008) are shown. Age model is based on Dinarès-Turell et al. (2014), La2011 solution.

Fig. 5

The $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ crossplots indicate the preferred depth habitat of different foraminiferal taxa. In green: benthic foraminifera; blue: planktic subsurface foraminifera; red small triangles, dark red large triangles with blue frame (only 1262) as well as orange circles: planktic surface dwelling foraminifera.

(A) $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ crossplot of Site 1262. (B) $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ crossplot in a comparison between Sites 1262 (shaded areas) and Site 1210 (Shatsky Rise: open areas and symbols).

Fig. 6

Comparison of key results from ODP Sites 1210 and 1262: Shannon H' , simple diversity, evenness and benthic foraminifera $\delta^{13}\text{C}$. Age model is based on Dinarès-Turell et al. (2014), La2011 solution.

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Paleoceanographic changes across the Latest Danian Event in the South Atlantic Ocean and planktic foraminiferal response

HIGHLIGHTS:

- Paleocene planktic foraminifera faunas from deep-sea ODP Site 1262 (Walvis Ridge)
- Some faunal changes and $\delta^{13}\text{C}$, $\delta^{18}\text{O}$ excursions can be directly linked to the LDE
- but other faunal changes are already initiated well below the LDE
- comparison to Pacific site revealed a different evolution of upper ocean structure

Paleoceanographic changes across the Latest Danian Event in the South Atlantic Ocean and planktic foraminiferal response

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Abstract

A number of short warming events occurred during Paleocene and Eocene, of which the “Paleocene-Eocene Thermal Maximum” (PETM, 56 Ma) is the most severe and most investigated event. The less known “Latest Danian Event” (LDE) at 62.2 Ma represents a 200 ky-lasting warming phase, superimposed on a long-term cooling trend after the Early Paleocene. South Atlantic ODP Site 1262 data, covering ~1 myr, indicate a warming of the entire water column by 1.5–2.6°C, accompanying a prominent negative carbon isotope excursion (~0.9–1.1 ‰) and a long-term re-organization of the planktic foraminiferal fauna associated with the LDE. This study unravels a different paleoceanographic evolution of the upper ocean structure compared to results from Pacific ODP Site 1210. Unlike the Pacific, the Atlantic site lacks an apparent change of stratification as well as an overall dominance of thermocline dwelling planktic foraminifera species and a low abundance of surface dwelling photosymbiotic foraminifera. Within the LDE, indications for a slightly enhanced stratification of the upper water column and transient warming was indicated when surface dwelling planktic foraminifera became temporarily more abundant. The long-term evolution in planktic foraminifera with the disappearance of *Praemurica* at the LDE onset and a contemporaneous rise in *Morozovella* is similar to the trends reported from Shatsky Rise ODP Site 1210.

Keywords: Paleocene, hyperthermal event, Latest Danian Event, negative CIE, planktic foraminifera assemblage, surface ocean stratification

1 Introduction

The early Paleogene is known for significant climate and carbon cycle perturbations (e.g. Kennett and Stott, 1991; Lourens et al., 2005; Zachos et al., 2008; Littler et al., 2014). It is characterized by a long-term global bottom water cooling trend between 66 and ~59 Ma by ~3°C, followed by a long-term temperature rise by ~4–5°C culminating at the Early Eocene Climatic Optimum (EECO, ~53 Ma; Zachos et al., 1994, 2008; Westerhold et al., 2011). These million-year-scale cooling and warming trends of Paleocene and Eocene are interrupted by

several short-term warming events of 100–200 ky duration (e.g., Kennett and Stott, 1991, Lourens et al., 2005; Quillévéré et al., 2008; Zachos et al., 2008; Westerhold et al., 2011). The warming events, also named hyperthermals, are accompanied by negative carbon isotope excursions (negative CIEs), indicating the injection of isotopically light carbon into the ocean-atmosphere system, and severe biotic responses such as extinctions and turnovers (e.g. Crouch et al., 2001; Lourens et al., 2005; Bernaola et al., 2007; Zachos et al., 2010).

The best studied and most severe hyperthermal event is the Paleocene-Eocene Thermal Maximum (PETM, ~56 Ma) with a duration of 170–220 ky (e.g. Kennett and Stott, 1991; Röhl et al., 2007). Characteristics of this event are: a negative CIE of at least -2.5 ‰, ocean warming by up to 6–7°C (Zachos et al., 2008) for the bottom water, and up to 10°C for the surface ocean (Sluijs et al., 2007), a drop in calcium carbonate (wt% CaCO₃) in deep-sea records, most likely due to lysocline shallowing as a consequence of ocean acidification (e.g. Zachos et al., 2005), a major extinction of deep-sea benthic foraminifera and assemblage changes in many other marine microfossil groups (e.g. Kelly et al., 1996; Crouch et al., 2001; Bralower, 2002; Thomas, 2003; Speijer et al., 2012; Yamaguchi and Norris, 2015).

Several similar events, albeit of smaller magnitude, were reported from the Paleocene and Eocene, like the “Latest Danian Event” (LDE = Top C27n Event, 62.2 Ma, Bornemann et al., 2009, Dinarès-Turell et al., 2012). So far, the LDE was described from the margins of the Tethys Ocean in Egypt (Speijer, 2003; Bornemann et al., 2009; Sprong et al., 2011), NW-Tunisia (Guasti, 2005; Sprong et al., 2013), Bjala in Bulgaria (Dinarès-Turell et al., 2012) and Caravaca, Spain (Alegret et al., 2016). The LDE also was unequivocally identified in the North Atlantic (Zumaia, Spain, e.g. Dinarès-Turell et al., 2012, 2014; off Newfoundland, Yamaguchi et al., 2017), the South Atlantic (Ocean Drilling Program [ODP] Site 1262; Westerhold et al., 2008; Monechi et al., 2013; Deprez et al., 2017a), and the Pacific at Shatsky Rise ODP Sites 1209 and 1210 (Westerhold et al., 2011; Jehle et al., 2015). Faunal changes amongst planktic foraminifera (Guasti, 2005; Jehle et al., 2015), mammals (Clyde et al., 2008) and calcareous nannofossils (Fuqua et al., 2008; Monechi et al., 2012) were observed as well as within benthic foraminifera in dysoxic shelf settings (Sprong et al., 2011, 2012; Schulte et al., 2013).

At several sites in the Pacific and South Atlantic, the LDE was identified by two remarkable XRF core scanning Fe peaks and decreasing CaCO₃ values, indicated as LDE1 and LDE2 beds (Westerhold et al., 2008, 2011; Deprez et al., 2017a). A 1.6–2°C ocean floor warming was derived from benthic foraminifera $\delta^{18}\text{O}$ variations (Westerhold et al., 2011; Jehle et al., 2015; Deprez et al. 2017a, 2017b) and 2.8°C from planktic surface-dwelling foraminifera (Jehle et al., 2015). Enhanced stratification of the upper water column at Shatsky Rise (ODP Site 1210) during the LDE was proposed, based on apparent isotope gradients ($\delta^{18}\text{O}$, $\delta^{13}\text{C}$) between surface and subsurface planktic foraminifera and an assemblage shift from high abundances of surface

dwelling to subsurface dwelling planktic foraminifera. Both observed changes started ~170 ky prior to the LDE. This increase in stratification was explained by the development of a Deep Chlorophyll Maximum formed under a permanent gyre system leading to high abundances of subsurface dwelling foraminifera, benefiting from high nutrient levels below this layer. Furthermore, the extinction of *Praemurica* species and the rise of morozovellids occurred simultaneously with the onset of the LDE (Jehle et al., 2015).

For this study, we analysed planktic foraminifera across the transient warming of the LDE from the South Atlantic deep-sea ODP Site 1262 (Fig. 1) in order to evaluate the impact of the event on the composition of planktic foraminiferal assemblages and to link this to paleoenvironmental changes as inferred from stable isotopes ($\delta^{18}\text{O}$, $\delta^{13}\text{C}$) of planktic and benthic foraminifera carbonate. Our new data provide insight into the upper ocean structure of the South Atlantic across the LDE. Further, we compare our results with those of Pacific ODP Site 1210 (Fig. 1, Jehle et al., 2015) to obtain more general patterns of paleoceanographic and paleoclimatic evolution based on planktic foraminifera across this event.

2 Material and Methods

2.1 Geological setting and deposition

ODP Site 1262 is positioned at the transition from the Angola Basin to Walvis Ridge (27°11.15'S, 1°34.62'E, 4755 mbsl, meters below sea level, Fig. 1). During the Paleocene, the Site was situated at a latitude of ~37°S (Zachos et al., 2004; van Hinsbergen et al., 2015). Walvis Ridge is a ~3000 km long SW-NE trending aseismic ridge and reaches up to 200 mbsl from an abyssal depth of ~5000 m. Paleocene sediments were deposited at a paleodepth of ~3300 mbsl (Zachos et al., 2005) and are predominantly composed of calcareous nannofossil ooze, though more clayey and ash-rich in the deeper parts. Cyclic changes in magnetic susceptibility, also visible in colour variation, reflect orbital forcing (Westerhold et al., 2008).

2.2 Stratigraphy

Site 1262 holds a continuous record between the Cretaceous-Paleogene boundary and PETM (Westerhold et al., 2008). The LDE is biostratigraphically positioned within the basal part of the planktic foraminifera Subzone P3b (Berggren and Pearson, 2005; see Fig. 2) and the upper part of calcareous nannofossil Zone NP4 (Martini, 1971). The first radiation of fasciculiths/*Lithoptychius* is pinpointed close to the base of the LDE (Monechi et al., 2012, 2013). Magnetostratigraphically, the LDE is situated in the topmost part of C27n and the basal part of C26r. Accordingly it was also referred to as “Top C27n Event” (Westerhold et al., 2008; Dinarès-Turell et al., 2012, 2014).

Age control of Site 1262 is based on magnetostratigraphy (Bowles, 2006), biostratigraphy (Monechi et al., 2003; this study) and astrochronology (Dinarès-Turell et al., 2014). The onset of the LDE is at 62.18 Ma (Dinarès-Turell et al., 2014), the total duration of the LDE is about 200 ky and the investigated interval spans ~950 ky. Top of magnetochron C27n was also pinpointed to 62.2 Ma in Zumaia, (Dinarès-Turell et al., 2014). Maxima of short-eccentricity cycles 38 (195.3 mcd, meters composite depth) and 39 (194.6 mcd) correspond to the two XRF Fe peaks during long eccentricity cycle $P_{c405}10$ (Dinarès-Turell et al., 2014). Site 1262 was stratigraphically correlated to ODP Sites 1209 and 1210 (Westerhold et al., 2008) as well as to Zumaia, Spain (Dinarès-Turell et al., 2014). The latter represents the Global boundary Stratotype Section and Point (GSSP) for the base of the Selandian Stage (Schmitz et al., 2011).

2.3 Methods

Nine meters of core (189.5 mcd–198.48 mcd) were sampled at a 2.5–45 cm spacing with highest sample density across the LDE. Sediment samples were washed over a 63 μm sieve and oven dried at 50°C for at least 48 hours.

Wt% CaCO_3 and coarse fraction (%CF) were measured on 84 and 86 samples, respectively, planktic foraminiferal fragmentation (%Fp), planktic foraminiferal number (PFN), planktic foraminiferal accumulation rate (PFAR) and planktic proportion (%P) as well as the faunal composition were analysed on 40 samples (Fig. 2). $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ were measured on *Morozovella angulata*, *M. praeangulata* (surface dwelling planktic foraminifera), *Parasubbotina pseudobulloides*, *P. variospira* (planktic subsurface dwellers) and *Nuttallides truempyi* (benthic foraminifera) to provide data for the different habitats of the surface ocean, subsurface thermocline and the deep-sea. For $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ measurements, *P. pseudobulloides* and *P. variospira* were lumped together due to their rather similar morphology (see for discussion Jehle et al., 2015) and extremely similar values. For each measurement, 3–6 planktic specimens were picked from 250–355 μm size, however, in samples without quantitatively sufficient material, specimens of the 180–250 μm fraction were added. Benthic foraminifera (Deprez et al., 2017a) were selected from the 125–180 μm fraction only with 5–7 specimens. The specimens were reacted with 100 % phosphoric acid at 75°C using a Kiel IV online carbonate preparation line connected to a MAT 253 mass spectrometer. Machine reproducibility was checked by replicate analysis of laboratory standards, which was better than 0.03 ‰ and 0.1 ‰ for $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$, respectively. In addition to the machine error other factors have an influence on the analytical variability of stable isotope values, specifically the number of analysed tests per measurement (see Fraass and Lowery, 2017, for a summary). Early studies proposed a robust reproducibility with only very high numbers of 30–50 tests per run (Killingley et al., 1981), which are hardly to achieve in high-resolution records. Such a larger number of tests corresponds to a 95% confidence limits between 0.01 ‰ and 0.02 ‰ (Fraass and Lowery,

2017), however, even five tests per run still show a 95% confidence limit of 0.03% (Fraass and Lowery, 2017). Thus, the summed analytical variability of the data is much smaller in magnitude than most signals usually interpreted in deep-time palaeoceanography. CaCO_3 values were analysed with a LECO CS 230 carbon-sulphur analyser, located at the BGR, Hannover.

Coarse fraction was calculated by:

$$\%CF = ((\text{dry weight of residue [g]} > 63\mu\text{m}) / (\text{dry weight of total sample [g]})) \times 100 [\%] \quad (\text{I}).$$

Planktic foraminiferal fragmentation (%Fp) was counted in the $>125\mu\text{m}$ size fraction during species quantification. Specimens with less than 50 % preserved were considered as a test fragment and %Fp was calculated by:

$$\%Fp = (\text{no. of fragments}) / (\text{no. of fragments} + \text{no. of complete tests}) \times 100 [\%] \quad (\text{II})$$

PFN is the number of planktic foraminifera per gram dry unwashed sediment. For PFAR, the age model of Dinarès-Turell et al. (2014), expressed in linear sedimentation rate (LSR , [cm kyr^{-1}]) between each short-term eccentricity maximum, and shipboard dry bulk density (DBD, [g cc^{-1}]) data were linearly interpolated and multiplied with PFN.

$$PFAR = DBD \times LSR \times PFN \quad [\# \text{ cm}^{-2} \text{ kyr}^{-1}] \quad (\text{III})$$

Forty samples were analysed for planktic foraminiferal assemblage composition under a Zeiss Stemi 2000-C binocular with $100\times$ magnification. Planktic foraminifera were counted from sample splits which yield between 300 and 400 specimens in the $>125\mu\text{m}$ size fraction (Fig. 3). On the one hand a cut-off at $125\mu\text{m}$ certainly results on an information loss on smaller taxa, but on the other hand the $<125\mu\text{m}$ fraction contains large numbers of juveniles, which increases the uncertainty in determinations on the species level. Therefore, we consider the $>125\mu\text{m}$ for more appropriate for species-level assemblage analyses. It bears high potential of failure to determine juvenile tests to the species level; therefore, assemblage census is usually based on larger sizes ($>125\mu\text{m}$). Species identification follows almost exclusively Berggren and Norris (1997) and Olsson et al. (1999). The diversity of planktic foraminiferal assemblages was characterized by species richness (S), Shannon heterogeneity (H' , Shannon and Weaver, 1949) and evenness:

$$\text{Shannon heterogeneity:} \quad H' = - \sum_{i=1}^S p_i \ln p_i \quad (\text{IV})$$

$$\text{Evenness:} \quad E = H' / H_{\max}, \quad H_{\max} = \ln(S) \quad (\text{V})$$

- p_i as the proportion of individuals belonging to the i^{th} species in the dataset of interest,
- heterogeneity is $0 \leq H' \leq \ln S$,

172 - Evenness is $0 \leq E \leq 1.0$.

173 We used the “vegan package” for R for the statistical analysis of the non-metric
174 multidimensional scaling (NMDS, Fig. 4) with Bray-Curtis distance measure and CaCO_3 as
175 well as $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ of all three foraminifera groups. Relative abundance of all samples with
176 paired CaCO_3 , $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ results were used. All species with a relative abundance $>2\%$ in
177 at least one sample were included.

3 Results

3.1 Carbonate content and dissolution indicators

Background CaCO_3 values (Fig. 2) range between ~80 and 86 wt %, with two distinct minima of 69 and 71 wt % corresponding to LDE1 (195.4 mcd) and LDE2 (194.5 mcd).

Coarse fraction (%CF, Fig. 2) data show background values of 3–4 % below the LDE and a minimum of 0.6 % at the onset of LDE1, from where it rises up to 8 % from LDE2 to the upper part of the record, where it drops to 2 %. Fragmentation of planktic foraminifera (%Fp, >125 μm) shows maxima (~15 %) at the base of the sequence together with the lowest %CF during the onset of LDE1, relative to background values of 4–5 %.

The linear sedimentation rate (LSR, Fig. 2E) varies between 0.3 and 0.32 cm kyr^{-1} and, considering the uncertainties of this calculation, is seen as constant. Planktic foraminiferal numbers (PFN, >63 μm [$\# \text{g}^{-1}$]) decrease at the onset of LDE1, subsequently rise to peak values within LDE2 and show a long-term decrease after the LDE. PFN ranges between 15,000 and 219,000 g^{-1} . PFAR (>63 μm) ranges between ~17,000 and 250,000 $\text{cm}^{-2} \text{kyr}^{-1}$ with a similar trend like PFN. The percentage of planktic foraminifera, %P (>63 μm fraction; Fig. 2) shows a decrease to 97.9 % during LDE1 compared to a background of >99 %. The overall shape of the curve is similar to %CF.

3.2 Foraminiferal stable isotopes ($\delta^{13}\text{C}$, $\delta^{18}\text{O}$)

$\delta^{13}\text{C}$ of benthic foraminifera (*Nuttallides truempyi*) varies around 1.0 ‰ and displays two negative excursions (up to -0.9 ‰) contemporary to the Fe XRF core scanning peaks (Figs. 2; Deprez et al., 2017a). $\delta^{13}\text{C}$ values of subsurface dwelling *Parasubbotina pseudobulloides* and *P. variospira* show a slightly decreasing trend of -0.6 ‰ (2.3 to 1.7 ‰) within LDE1 and a sharper, more negative excursion of -0.8 ‰ (2.2 to 1.4 ‰) during LDE2. Surface dwelling *Morozovella angulata* shows a -1.1 ‰ excursion (3.7 to 2.6 ‰) and, thus, a more distinct response than *P. pseudobulloides* and *P. variospira* to the LDE. However, the variability in *M. angulata* is generally very high and may thus overestimate the amplitude. The positive excursion just below and above LDE1 show amplitudes of comparable heights to the negative CIEs.

The $\delta^{18}\text{O}$ values of *N. truempyi* show a high variability with two distinct negative excursions (up to -0.8 ‰) within the LDE. *Parasubbotina pseudobulloides* and *P. variospira* yield values between -0.7 and 0.2 ‰ and display a negative long-term trend from below LDE1. $\delta^{18}\text{O}$ of *M. angulata* decreases by -0.7 ‰ (-0.6 to -1.3 ‰) and rises directly above LDE2 to -0.7 ‰ before it slowly decreases to a steady level of -0.9 ‰. Surface and subsurface species display a rather

similar curve, whereas the benthic record shows a pattern with distinctly negative peaks in LDE1 and LDE2, resembling the negative excursions in the XRF Fe counts. The $\delta^{13}\text{C}$ gradient between surface and subsurface slightly increases below LDE1 (+0.3 ‰), but there is no clear trend for $\Delta\delta^{18}\text{O}$ (Fig. 2, Fig. 5).

3.3 Planktic foraminiferal assemblages

Planktic foraminiferal diversity remains relatively constant during the study interval. Shannon H' diversity varies between 2.2 and 2.6 and species richness (S) between 14 and 27 species. Both parameters show maxima during LDE1 and LDE2 and a high variability between the two phases (Fig. 6).

The ten most abundant species cover 92 % of all planktic foraminifera tests. Subsurface dwelling *Parasubbotina* and *Subbotina* make up almost 70 %, whereas surface dwelling *Morozovella* show an average abundance of 11 % (Fig. 3). Species can be grouped according to their abundance and appearance (Fig. 3): (1) species with highest abundances below the LDE, (2) species present with minor variations throughout the record or with slightly enhanced abundances during the LDE and (3) species with appearance or high abundances above the LDE.

Group (1) covers *Praemurica inconstans* and *P. uncinata* as they initially compose 4 % and 24 % of the assemblage and disappear just below or during the LDE, and *M. praeangulata* with a comparable pattern, starting with up to 17 % below the LDE.

Group (2) contains *Globanomalina ehrenbergi* with one peak of 4 % between LDE1 and LDE2, *Globanomalina imitata* varies between 0 and 5 % and is most common below the LDE. *Globanomalina chapmani* ranges from 1.5–10 %, *Parasubbotina varianta* appears between 7 and 18 % without distinct maxima, *Subbotina triloculinoides* occurs abundantly with peak values of 22 % just before the onset and after the termination of the LDE. *Subbotina cancellata* ranges from 10–21 % with a long-term decrease through the record. *Subbotina velascoensis* shows its highest abundance (7 %) below the LDE. *Parasubbotina pseudobulloides* shows a decreasing trend during our record from 9–2%. *Parasubbotina variospira* shows a similar pattern with peak values below the LDE (25 %). *Igorina pusilla* reaches highest abundances of up to 10 % during the LDE interval.

Generally higher abundances above the LDE (group 3) were observed for *M. conicotruncata*, *I. albeari* and *M. angulata*. *Morozovella conicotruncata* peaks (11 %) above the LDE, *I. albeari* shows peak abundances (12 %) during LDE1 and LDE2. *Morozovella angulata* initially also shows peak levels up to 12 % within LDE1 and LDE2 but becomes even more abundant (20 %) towards the top of the record.

This development is also shown in Fig. 3 (B), where species are summed up like described. In Fig. 3 (C), sums of mixed layer/surface species and thermocline/subsurface species are shown. Below the LDE, the abundance of surface dwellers decreases and goes up in two phases within each LDE1 and LDE2 phase and continuously increases upwards.

4 Discussion

4.1 Carbonate dissolution and preservation of foraminiferal calcite

4.1.1 Carbonate preservation

Deep-sea carbonate dissolution is predominantly controlled by depth changes of the lysocline/calcite compensation depth (CCD) as well as by oxidation of organic carbon. Dissolution causes enhanced test fragmentation of planktic foraminifera (%Fp: e.g. Berger, 1970; Dittert et al., 1999), which are up to three times more dissolution-susceptible than benthics (Berger, 1973). Consequently, carbonate dissolution leads not only to increased %Fp and lower CaCO₃, but also to lower %CF, %P, PFN and PFAR.

As indicated, carbonate background values are rather constant throughout the studied succession, whereas the LDE beds display CaCO₃ minima. CaCO₃ drops by 14 wt% (83–69 %) within LDE1 (195.4 mcd), and by 13 wt% (84–71 %) within LDE2 (194.5 mcd). We consider carbonate dissolution to be more severe during LDE1 than during LDE2 due to higher %Fp and lower %CF concurrent to lower values of %P, PFN and PFAR during LDE1. For LDE2, we speculate that other processes were involved such as enhanced dilution by clay or a decline of carbonate production. Enhanced dilution is assumed due to an accompanied increase in the sedimentation rate, starting during LDE2 (Fig. 2). However, absolute abundances of planktic foraminifera are rather constant, but changes within numbers of calcareous nannofossils were not taken into account. As the second benthic negative CIE (194.5 mcd) is smaller than the first peak, the amount of carbon injected into the ocean-atmosphere system might have been below the threshold for a substantial lysocline rise during LDE2. Clay-enriched horizons were also documented at the base of the entire LDE from deep-sea successions at Shatsky Rise (Westerhold et al., 2008, 2011; Jehle et al., 2015).

4.1.2 Foraminiferal preservation

Good preservation of foraminiferal carbonate is key for both reliable geochemical analyses and assemblage counts. Mechanisms controlling test preservation include dissolution, bacterial activity and recrystallization or overgrowth (e.g. Hancock et al., 2007; Nguyen et al., 2011). Foraminifera largely precipitate their carbonate from ambient seawater (e.g. Erez and Luz,

1983), and are, thus, considered to be excellent carriers of past seawater geochemistry signals. However, the geochemical composition of their calcite might be altered by diagenesis and recrystallization during and after burial (e.g. Stap et al., 2010; Edgar et al., 2013). $\delta^{13}\text{C}$ tends to be less influenced by diagenetic alterations while the effect on $\delta^{18}\text{O}$ is more substantial (Killingley, 1983; D'Hondt and Zachos, 1993; Pearson et al., 2001).

Light microscope observations of planktic foraminifera in Paleocene samples of Site 1262 reveal sparse overgrowth, but an overall moderate to good preservation (Birch et al., 2012 and observations of the current work). Slight yellow stains on the tests make them appear less white than seen in other Paleocene sequences like Shatsky Rise Site 1210 (Jehle et al., 2015). Specimens are free from infillings, show a milky, coarsely textured surface through light microscopy and indicate recrystallization under the SEM (Birch et al., 2012). It seems to be a typical, somewhat “frosty” preservation in deep-sea carbonate oozes (Pearson et al., 2001; Sexton et al., 2006). This state of planktic foraminiferal preservation usually leads to heavier $\delta^{18}\text{O}$ values, since the calcite carries an additional bottom water isotope signature due to recrystallization, and therefore reconstructed paleotemperatures are lower than for unaltered tests (Pearson et al., 2001; Sexton et al., 2006; Edgar et al., 2015). For benthic foraminifera, the impact of recrystallization on both $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ is considered to be much less severe than for planktic foraminifera (Edgar et al., 2013; Voigt et al., 2016).

In contrast to earlier studies (e.g. Thomas et al., 1999; Raffi and Bernardi, 2008), we suspect that diagenetic alteration has played a substantial role at Site 1262 for the planktic $\delta^{18}\text{O}$ signal. Besides ultrastructural observations by SEM (Birch et al., 2012), this is supported by the negligible vertical temperature gradient between $\delta^{18}\text{O}$ values of surface, subsurface and benthic dwellers and the complete lack of a $\delta^{18}\text{O}$ gradient between subsurface and benthic environment (Fig. 2). The temperature difference between surface ocean and seafloor of only $\sim 6.5^\circ\text{C}$ is unrealistically low. For comparison, the vertical temperature gradient at Pacific Shatsky Rise Site 1210 was estimated to be $\sim 9^\circ\text{C}$ during the LDE (Jehle et al., 2015) and up to 15°C at the tropical or equatorial North Pacific Ocean (Shatsky Rise Site 1209, Allison Guyot Site 865) during Late Paleocene, PETM and Early Eocene (Tripathi and Elderfield, 2005).

In certain intervals the subsurface dwellers have even lower $\delta^{18}\text{O}$ values than the benthics (Fig. 2, 195.05–195.98 rmcd). This would not be the case in well-preserved foraminiferal assemblages, even if we would consider the unlikely existence of warm saline bottom waters. Based on visually indicated recrystallization and overgrowth in these intervals (Birch et al., 2012), we conclude that surface and subsurface planktic foraminiferal tests were recrystallized during early burial, which shifted the recorded $\delta^{18}\text{O}$ towards more positive values. Nevertheless, assuming a more or less homogeneous diagenetic overprint during the studied

interval, the relative $\delta^{18}\text{O}$ changes might still represent the original trends (Sexton et al., 2006), with a modified magnitude of change.

Furthermore, species-specific dissolution susceptibility can change the assemblage composition (e.g. Berger, 1970; Pearson et al., 2001; Petrizzo, 2007; Nguyen et al. 2011; Nguyen and Speijer, 2014) and consequently bias the interpretation of faunal data. As some species are more dissolution susceptible than others, the planktic foraminiferal assemblage composition could, to some extent, be biased by carbonate dissolution. Dissolution and fragmentation occurs during settling, sedimentation or shortly after burial. As a consequence, the assemblage composition would shift to lower relative abundances of dissolution-susceptible taxa such as *Igorina* spp. and subsequently higher relative abundances of thick-walled *Acarinina* or *Morozovella* species (Petrizzo et al., 2008; Nguyen et al., 2011). However, both aforementioned taxa are not very abundant in the studied samples while *Igorina* spp. is present in moderate numbers and flourishes during the LDE. The species might prefer a warmer environment; therefore, the very high production rate might cover dissolution to some extent. Further indicators for partial dissolution are supposedly a combination of low relative abundance and increased fragmentation of *Subbotina* spp., low %P rate and PFN (e.g. Nguyen et al., 2009). Altogether, in contrast to the stable isotope signal, the planktic foraminiferal composition has presumably not been substantially affected by dissolution during or before sedimentation.

4.2 Stable isotope patterns during the LDE at Walvis Ridge

In addition to literature data (Berggren and Norris, 1997; Olsson et al., 1999), the habitats of planktic foraminifera taxa were inferred from $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values. We distinguished between (photosymbiotic) surface dwelling and subsurface dwelling, thermocline species (e.g. Shackleton et al., 1985; Norris, 1996; Birch et al., 2012). Studied photosymbiont-bearing taxa are *M. angulata*, *M. praeangulata*, *P. uncinata* and *P. incontinans*, while non-photosymbiotic are *P. variospira* and *P. pseudobulloides*. For the benthic habitat, *N. truempyi* was used.

4.2.1 $\delta^{13}\text{C}$ response to the LDE

The surface water signal is influenced by primary productivity and subsidence of ^{12}C -enriched organic particles to the seafloor, causing a carbon depth gradient. Due to preferred uptake of ^{12}C by symbiotic algae, photosymbiotic foraminiferal tests are ^{13}C enriched relative to ambient seawater and to deeper dwelling foraminifera without photosymbionts (e.g. Shackleton et al., 1985; Spero et al., 1991; Rohling and Cooke, 2003). Hence, $\delta^{13}\text{C}$ of seawater and foraminifera is depth-dependent.

Even though the ~1 ‰ CIE in planktic surface dwellers is quite large and distinct during the LDE, it also has a steady state below the LDE until ~ 62.25 Ma with about the same values as the peak and shows a quick positive excursion just below the event. For surface dwelling foraminifera, possible reasons might be (a) varying photosymbiotic activity or (b) surface ocean currents. Suboptimal living conditions might have led to smaller tests, inhabiting less algae symbionts (Schmidt et al., 2004). The average $\delta^{13}\text{C}$ values are more positive above the LDE than below, suggesting either a higher photosymbiotic activity for *M. angulata* than for *M. praeangulata*, or, more likely, they follow the secular trend to heavier $\delta^{13}\text{C}$ values above the LDE probably due to higher primary productivity and slightly more oxygenated surface water after the LDE.

The surface- to subsurface $\delta^{13}\text{C}$ gradient ($\Delta\delta^{13}\text{C}$) displays a rather constant offset (Fig. 2). Enhanced stratification as observed at Shatsky Rise (Jehle et al., 2015) is not visible here. The $\delta^{13}\text{C}$ value was probably very uniform in the different water layers due to a higher mixing rate and ocean currents, or because of diagenetic overprint, even though $\delta^{13}\text{C}$ is normally less affected.

4.2.2 $\delta^{18}\text{O}$ response to the LDE

Temperature is an important factor controlling $\delta^{18}\text{O}$ of foraminiferal calcite due to equilibrium fractionation between seawater and calcite. Because of their shallower habitat, $\delta^{18}\text{O}$ values are lower in photosymbiotic planktic foraminifera than in their non-symbiotic relatives. Changes in salinity, carbonate ion concentration or pH as well as waxing and waning of continental ice sheets (e.g. Shackleton, 1967; Railsback et al., 1989; Spero et al., 1997) are additional factors to influence foraminiferal $\delta^{18}\text{O}$. The ice-effect is not taken into consideration as the early Paleogene is generally suspected as an ice-free period (e.g. Zachos et al., 1994).

During the LDE, $\delta^{18}\text{O}$ records suggest a temperature rise of ~2.0°C (0.5 ‰) at the seafloor (*N. truempyi*), ~1.5°C (0.35 ‰) in the thermocline (*P. variospira* and *P. pseudobulloides*) and ~2.6°C (0.6 ‰) in surface water (*M. angulata*). This ocean warming is supported by the faunal data, which show an abundance increase of warm-water, low-latitude taxa such as *Morozovella*.

4.2.3 Implications on the stable isotope patterns for the LDE

The negative CIEs associated with the LDE could be explained by various scenarios as proposed for the PETM (e.g., Dickens et al., 1997). For the PETM, one scenario considers a sudden and massive release of methane from the seafloor, probably triggered by circulation changes in the deep ocean (Tripathi and Elderfield, 2005; Nunes and Norris, 2006) or large-scale continental slope failure (e.g. Katz et al., 2001). This methane was rapidly oxidized to CO_2 , contributing to stronger greenhouse forcing. On the other hand, the destabilization of methane

hydrates was seen as unlikely to be the sole source as the reservoir at the end of the Paleocene was probably not sufficient (e.g. Buffet and Archer, 2004; Kirtland Turner and Ridgwell, 2016), whereas the magnitude of warming and changes in the CCD are compatible with much greater carbon masses. Therefore, additional carbon sources were suggested, such as volcanic outgassing or thermal decomposition of organic matter or oxidation of terrestrial and marine organic carbon (Pagani et al., 2006; Dickens, 2011; DeConto et al., 2012; Gutjahr et al., 2017).

For the LDE, most of these explanations suggest amplifications by increased insolation due to temporal coincidence with short-term eccentricity maxima (Westerhold et al., 2008) contributing to global warming. In addition, the oxidation of a massive amount of organic carbon or enhanced CO₂ input to the ocean-atmosphere system resulting from the onset of the intense volcanic activity in the North Atlantic Igneous Province (NAIP) or southeastern Greenland margin (Sinton and Duncan, 1998; Pedersen et al., 2002; Larsen et al., 2016) might have contributed to the negative carbon isotope values during the LDE.

However, as the LDE is more comparable to ETM2 with regard to orbital pacing and magnitude than to the PETM, similar causes have been inferred for these two events (Deprez et al., 2017a, 2017b). As for the LDE, Eocene short-term hyperthermals like ETM2 and ETM3 mostly coincide with eccentricity maxima. Orbital pacing might have triggered changes in ocean ventilation, leading to oxidation of dissolved organic matter during transient Eocene warming events (Sexton et al., 2011; Stap et al., 2009).

4.3 Planktic foraminifera faunal changes

Surface mixed layer foraminifera were abundant below the LDE with a maximal abundance of *Praemurica uncinata*, *P. inconstans* (together up to 24 %) and *M. praeangulata* (up to 15 %). A turnover of photosymbiont-bearing taxa is well documented by the disappearance of the genus *Praemurica*, the long-term decline of *M. praeangulata* and the parallel emergence of other taxa (e.g. *Igorina albeari*, *Morozovella* spp.) with the onset of the LDE. The decline of *M. praeangulata* and *Praemurica* started ~170 ky before the event and *Praemurica* finally disappeared during LDE1. Simultaneously, the sum of all surface dwelling planktic foraminifera displays a minimum between 170 kyrs prior to the LDE and the LDE-onset. The surface ocean assemblage changed from a praemuricate to a muricate fauna as observed at other sites (Norris, 1996; Guasti et al., 2006), or more likely their different ability to adopt to the changing paleoenvironmental conditions. Other than *P. uncinata* and *P. inconstans*, *M. praeangulata* survived the LDE, albeit with decreasing abundances. The replacement of *Praemurica* by *Morozovella* could have had competitive reasons, since both genera are photosymbiotic surface dwellers and inhabited a similar ecological niche (Norris, 1996; Birch et al., 2012). The transition of a *Praemurica*- to *Morozovella*-dominated surface ocean fauna took place around the first occurrence of *Igorina albeari* (=P3a/P3b Subzone boundary),

whereas the final disappearance of *Praemurica* coincides with LDE1. In addition, the planktic turnover is characterised by the rise of *I. albeari* and *M. conicotruncata*.

$\delta^{18}\text{O}$ indicates slightly lower calcification temperatures for *Praemurica* than for *M. angulata* and *M. praeangulata*, suggesting either a somewhat deeper habitat or alternatively a flourishing of *Praemurica* during a colder season. *Morozovella praeangulata* is considered to have a closer relationship to *Praemurica* than the other morozovellid species (e.g. Berggren and Norris, 1997; Olsson et al., 1999). The ecological preferences of *M. praeangulata* as inferred from $\delta^{13}\text{C}$ suggest a similar photosymbiotic activity like *M. angulata* (Fig. 2).

Absolute and relative abundances of *M. angulata* increased within the LDE beds (Fig. 3), suggesting a relative benefit from temperature rise and paleoenvironmental changes. This development is compatible with a characterization as a warm water taxon showing higher numbers in the (sub-)tropical oceans (e.g. Quillévéré and Norris, 2003).

Similar to *M. angulata*, *I. albeari* showed enhanced abundances in both LDE beds, while *I. pusilla* only increased during LDE1. Therefore, *I. albeari* might have had a higher temperature sensitivity than *I. pusilla*. *Morozovella* and *Igorina* probably lived in different niches and were not direct competitors as the latter lived in slightly deeper water than *Morozovella* (e.g. Norris, 1996; Berggren and Norris, 1997; Pearson et al., 2001; Jehle et al., 2015). In contrast to *I. albeari*, which became more abundant towards the top of the record, *I. pusilla* then declined and might have had different ecological optima in terms of nutrient availability, temperature, water depth or flourishing during a somewhat colder season than *I. albeari*.

Over the long run, surface dwellers (*M. angulata*, *M. conicotruncata*) show a relative increase at the expense of *Parasubbotina* as also supported by absolute numbers. The change starts ~150 kyrs before the LDE onset and can be linked to the observed LDE warming.

Thermocline dwellers (*Parasubbotina* spp., *Subbotina* spp.) make up 46–86 % of all species (~70 % in average). Absolute abundance (cf. Appendix) of *Subbotina* and *Parasubbotina* show slightly enhanced numbers of *S. cancellata*, *S. triloculinoidea* and *P. variospira* during the LDE beds, however, as a short-term response only. We conclude that the thermocline habitat was constantly unstable and, thus, favourable for the two subsurface genera.

The above given interpretations are supported by non-metric dimensional scaling (NMDS). The strongest separation is between the samples below 196.63 mcd (before 62.30 Ma) by ~0.3 dissimilarity measure in the NMDS axis 1 (Fig. 4) and the samples during LDE1. Assemblage changes as demonstrated by the NMDS are expressed by two main sample groups, separating the samples “below the LDE” from those “during” and “above”. The samples during and above

the LDE show a very similar faunal assemblage opposed to the samples below the event. The start of major, but gradual changes are observed ~160 ky before the LDE (196.98 mcd at 62.34 Ma) as expressed by NMDS axis 1 loadings (Fig. 4), possibly caused by a decrease and subsequent disappearance of praemuricate species and the introduction of *I. albeari* and new *Morozovella* species.

Based on stable isotope and faunal data, the paleoceanographic scenario for Site 1262 might reflect a development from a “temperate” system to a more “subtropical” one, in which the zonal boundary shifted southwards during the LDE warmings. The subtropical system is generally warmer, more stable and better stratified, causing improved living conditions for surface dwelling photosymbiont-bearing foraminifera. Before the LDE, photosymbiotic species were rare, which can be explained by enhanced deep mixing of the upper water column. As surface dwellers mostly declined between the two LDE peaks and show higher abundances during both event levels, the somewhat colder and less stratified conditions in between probably inhibited proliferation. After the LDE, the situation became somewhat more favourable for photosymbiotic taxa, supporting a slightly better stratified upper ocean as indicated by the enhanced stable isotope gradients (Δ) and improved living conditions for subsurface taxa (Berggren and Norris, 1997; Fig. 3).

4.4 Comparison to Pacific ODP Site 1210

4.4.1 Paleogeography of ODP Sites 1210 and 1262

The opening of the South Atlantic Ocean started in the Early Cretaceous (Pérez-Díaz and Eagles, 2017), and so, the ocean was narrower in the Paleocene and more restricted than today, causing a different ocean current system compared to the recent South Atlantic. The Walvis Ridge Paleocene paleoceanographic reconstructions suggest strong vertical surface water mixing in the South Atlantic from south to north along the African coastline (e.g. Haq, 1981; Pak and Miller, 1992).

ODP Site 1210 (Shatsky Rise) was located at a subtropical paleolatitude of ~24°N (van Hinsbergen et al., 2015) and an estimated paleodepth of about 2700 m (Site 1262: ~3300 m). The plateau was positioned much closer to the equator than today and was, thus, subjected to higher insolation and a different circulation pattern from today (Bralower et al., 2002).

4.4.2 Geochemical data and preservation

Like for Site 1262, two distinct XRF core scanning Fe peaks identify the LDE horizons at Site 1210 (195.3 mcd, LDE1, and 194.6 mcd, LDE2). These Fe peaks serve as a key tool for stratigraphic correlation between the two sites (Westerhold et al., 2008).

The average wt% CaCO₃ content is high at both sites, but at Site 1210 with 84–95 % much higher than at Site 1262 (68–86 %). Both show two negative peaks contemporary to the event horizons.

Both Sites 1262 and 1210 as well as 1209 (Westerhold et al., 2011) show two negative benthic CIEs, which are ~100 ky apart from each other, supporting the idea of a two-phase event coinciding with two short eccentricity maxima (Westerhold et al., 2008; Dinares-Turell et al., 2014) and Fe XRF peaks. A two-phase scenario was identified at several deep-sea sites (ODP Sites 1001, 1209, 1210, 1262, U1407; Westerhold et al. 2008; Jehle et al., 2015; Deprez et al., 2017a and b; Yamaguchi et al., 2017). At Site 1210, benthic foraminifera show a by 0.4 ‰ minor excursion of both $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ compared to Site 1262, indicating (a) slightly higher deep-water temperatures at 1210, which is plausible due to a shallower water depth, or (b) lighter $\delta^{13}\text{C}$ might result from aged water masses, transported from other ocean areas (e.g. Kroopnick, 1979; Quillévéré et al., 2002). As the Southern Ocean was an important place for deep-water formation (Pak and Miller, 1992, Kroopnick, 1980), the transport of bottom water masses to the central Pacific was longer than to the South Atlantic.

From comparing dissolution sensitive parameters of Site 1210 (Jehle et al., 2015) with Site 1262 such as CF, %PF or %Fp, we conclude more intense carbonate dissolution for Site 1262, like previously observed in the early Eocene (Stap et al., 2009). At both sites, LDE1 was more influenced by carbonate dissolution than LDE2. Slightly enhanced carbonate dissolution, caused by a lysocline/CCD rise, is assumed for LDE1, whereas terrigenous dilution could be more possible during LDE2 at Site 1262 than at Site 1210. Hints for that scenario are a stronger CaCO₃ drop, increased %Fp, low %CF and low %P, PFN and PFAR during LDE1 compared to a smaller CaCO₃ drop and a lack of these characteristic changes during LDE2 (Fig. 2).

In addition to that, recrystallization is higher at Walvis Ridge than at Shatsky Rise. This view is supported by a strongly muted temperature difference between planktic and benthic foraminifera at Site 1262. At Site 1210, the largest $\delta^{18}\text{O}$ temperature gradient (Δ) is ~9°C, which is already rather low and probably overprinted by early diagenesis. At Site 1262, however, this difference makes up only ~6.5°C, strongly suggesting an overprint of the pelagic signal through early diagenesis at the colder seafloor. Recrystallization of planktic foraminiferal calcite dampened the $\delta^{18}\text{O}$ warming signal (Pearson et al., 2001; Sexton et al., 2006; Jehle et al., 2015).

Jehle et al. (2015) observed at Shatsky Rise 1210 a rising gradient before and during the LDE, suggesting enhanced stratification of upper water masses, a change which is accompanied by higher abundance of thermocline dwelling *Parasubbotina*. It was proposed that a Deep Chlorophyll Maximum was developed under well-stratified conditions during and after the LDE.

Comparing the $\delta^{13}\text{C}/\delta^{18}\text{O}$ crossplots of the two sites, divergent signatures in the different habitats become apparent (Fig. 5). $\delta^{13}\text{C}$ results of surface dwelling *M. angulata* and *Praemurica* species are within the same range, but surface $\delta^{18}\text{O}$ values distinctly differ with higher values at Site 1210. Due to the tropical to subtropical setting at Site 1210, the observed $\delta^{18}\text{O}$ values seem realistic, although the different signals between the depth habitats might be reduced by stronger diagenetic alteration at Site 1262. Site 1262 subsurface dwellers isotope data cover a narrower range suggesting that (a) the thermocline habitat has been more stable through time in the South Atlantic or (b) diagenetic alterations made the signal more even.

Both sites show a wider spread in the $\delta^{18}\text{O}$ surface signal than in $\delta^{13}\text{C}$ and shows again the likelihood of biased 1262 results by poor preservation as indicated by a lack of $\Delta\delta^{18}\text{O}$ variation. These findings support our assumption that early diagenetic dissolution and recrystallization did probably not influence much the benthic foraminiferal $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ signals (Edgar et al., 2013; Voigt et al., 20156), but had a substantial impact on planktic foraminifera $\delta^{18}\text{O}$ (e.g. Pearson et al., 2001).

4.4.3 Planktic foraminiferal faunal response to the LDE

Both diversity (Shannon H') and evenness (Fig. 6) are generally higher at Walvis Ridge Site 1262 and show increased values at the onset of the LDE, in contrast to consistently lower parameter values at Shatsky Rise Site 1210 during the LDE. The diversity increase at the LDE onset is probably related to the introduction of several new *Morozovella* species right after the LDE potentially triggered by the warming associated with this event. The increase of Shannon H' and species richness at Walvis Ridge with the onset of the LDE might have also led to a more even distribution among taxa.

A striking similarity of the two sites is the pre-LDE shift in the assemblage starting 170–200 ky before the LDE negative CIE shift as indicated by an increase in *Morozovella angulata* and a contemporary decrease in *Praemurica uncinata*, *P. inconstans* and *M. praeangulata*. This prominent change represents a slow shift from praemuricate to muricate species, where *M. praeangulata* was replaced by *M. angulata* and *Praemurica* disappeared, starting each at ~62.35 Ma.

The most apparent compositional difference between the South Atlantic (Site 1262) and the Pacific (Site 1210) across the LDE is the dominance of subsurface dwellers at Site 1262 (79.9 % in average), whereas photosymbiotic planktic foraminifera are much more abundant at Site 1210 (74.9 % in average). Possible reasons for this are (a) the paleolatitude, as 1210 is situated closer to the equator and 1262 in a subtropical to temperate zone, which yield the highest diversity in modern oceans (e.g. Berger and Parker, 1970; Rutherford et al., 1999; Quillévéré and Norris, 2003), or (b) a closed-sum-effect, causing a bias due to much higher production of

Parasubbotina and *Subbotina* at 1262, diluting the less abundant surface-dwelling taxa, even though the total production of surface dwellers was unchanged. At Pacific Shatsky Rise Site 1210, environmental conditions resulting from a permanent gyre system might have been beneficial for higher abundances of surface dwellers (e.g. Ortiz et al., 1995; Birch et al., 2013).

There are other, more subtle differences between the faunal assemblages of the two sites, hinting towards the described scenario: At 1262, some surface water species vary highly in abundance, whilst subsurface species show more steady numbers during the LDE. This suggests that the surface ocean might have been more affected by environmental changes like enhanced vertical mixing and weaker stratification in contrast to the rather stable situation at Site 1210. The South Atlantic subsurface assemblage composition in turn seems to be more stable with less species variation compared to the Pacific fauna and less influenced by the environmental changes accompanying the LDE, even though the position of the thermocline was putatively shallower and seasonally more stirred up than in the tropical central Pacific. As outlined, at 1262 the abundance of subsurface dwellers was three times higher than surface specimens. A shoaling thermocline can indicate upwelling or high turbulence from deeper waters (Cullen, 1982; Herbland and Voituirez, 1979) resulting in higher abundances of subsurface dwellers. This fits well with the virtual lack of stratification at 1262 as indicated by the rather constant $\Delta\delta^{13}\text{C}$ offset.

5 Conclusions

The detailed study of planktic foraminifera and geochemistry revealed the following key results for the LDE at Walvis Ridge ODP Site 1262:

- ~~(a) The LDE occurs stratigraphically in P3b, 0.9 m above (200 ky after) the P3a/b Subzone boundary (see Fig. 2A).~~
- a. Both LDE beds are characterized by a substantial CaCO_3 drop of 15–17 wt%, of which LDE1 shows indications of dissolution, probably related to lysocline shallowing, and CaCO_3 decline LDE2 is interpreted as a result of terrigenous dilution.
- b. Two distinctly negative CIEs of about 0.9 ‰ are apparent in benthic (*Nuttallides truempyi*) and planktic surface foraminifera (*Morozovella angulata*), however, the subsurface planktic foraminifera (*Parasubbotina variospira/pseudobulloides*) $\delta^{13}\text{C}$ peak during LDE1 is only poorly developed.
- c. Ocean warming as reflected by $\delta^{18}\text{O}$ is rather uniform between the different habitats with 1.5–2.6°C. SST increases by 2.6°C, intermediate and bottom waters by 1.5–2.2°C. A low temperature difference between the surface ocean and the seafloor as well as a lack of

gradient between the subsurface and benthic foraminifera $\delta^{18}\text{O}$, we suggest a substantial impact of recrystallization of planktic foraminiferal calcite.

- d. Subsurface dwelling foraminifera are very dominant and decrease slightly over the studied interval in relative abundance. Surface-dwelling warm-water taxa *Morozovella* and *Igorina* significantly rise in their abundances within the LDE and become generally more abundant after the event hinting towards a shift from “temperate” to “subtropical” conditions.

A comparison between ODP Site 1262 and Shatsky Rise ODP Site 1210 (Jehle et al., 2015) revealed a number of striking similarities and differences:

~~(a) At both sites, the LDE occurs stratigraphically in Subzone P3b, however, the first occurrence datum of *Igorina albeari* is well below the LDE (62.76 Ma at Site 1210, 62.39 Ma at Site 1262).~~

- a. Surface dwelling planktic and benthic foraminifera species show a stronger $\delta^{13}\text{C}$ response to the LDE by up to 0.4 ‰ at Site 1262.
- b. Diagenetic alteration of planktic foraminiferal tests is more pronounced at Site 1262.
- c. At both sites, faunal changes like a decrease of *Praemurica* occur about 170 kyrs before the LDE. Further, both sites show the extinction of *Praemurica* at the base of the LDE, followed by a long-term rise in *Morozovella* abundance.
- d. Planktic foraminiferal assemblages of Site 1262 are dominated by subsurface taxa such as *Subbotina* and *Parasubbotina*, whereas warm surface water indicating *Morozovella* taxa are dominant in the Pacific (Site 1210). Overall assemblage changes within the event are stronger at Shatsky Rise Site 1210, probably due to stronger ecological changes like the development of a DCM.

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Figures

Fig. 1

Paleogeographic map (62 Ma) of the two studied ODP Sites 1262 (Walvis Ridge) and 1210 (Walvis Ridge). The map was generated using <https://www.odsn.de/odsn/services/paleomap/paleomap.html> (Hay et al., 1999).

Fig. 2

Stratigraphy, XRF core scanning Fe intensities, stable isotopes and other sedimentary parameters of samples from the LDE at Site 1262. (A) Stratigraphy, including magnetostratigraphy (Bowles, 2006) and biostratigraphy (own results). XRF core scanning Fe intensities (Westerhold et al., 2008) during the LDE are used for stratigraphic correlation. Sedimentary parameters are (B) carbonate (wt% CaCO₃) measurements, with (C) coarse fraction (%CF), (D) planktic foraminifera fragmentation index (%Fp) >125µm, (E) sedimentation rate (SR, Westerhold et al., 2008, used for planktic foraminifera accumulation rate (PFAR)), planktic foraminifera number (PFN) with PFAR and (F) the planktic foraminifera proportion (%P) in two different size fractions (>63µm, >125µm). (G) shows $\delta^{13}\text{C}$ and (H) $\delta^{18}\text{O}$ records of benthic (*N. truempyi*), planktic subsurface (*P. pseudobulloides* and *P. variospira*) and planktic surface dwellers (*M. praeangulata* and *M. angulata*) and (I) $\Delta\delta^{13}\text{C}$ and $\Delta\delta^{18}\text{O}$ gradients of surface to subsurface isotope values. Age model is based on Dinarès-Turell et al. (2014), La2011 solution.

Fig. 3

Species distribution of planktic foraminifera together with XRF core scanning Fe intensities (Westerhold et al., 2008) **and sum-plots of species.** (A) Species are coloured according to their habitats: surface mixed layer in red, subsurface thermocline in blue and green and *Igorina albeari* and *I. pusilla* in grey. The taxa also make three groups by their appearances, which is appearance mostly below the LDE, appearance over the entire record or enhanced during the LDE and appearance mostly after the LDE. Sum plots are showing (B) the appearances of species that are mainly abundant before, during or after the LDE and (C) summed up species which live in the surface (mixed layer) or subsurface (thermocline) water level. Age model is based on Dinarès-Turell et al. (2014), La2011 solution.

Fig. 4

Non-metric multidimensional scaling. Left panel: Results of NMDS (stress=0.15, Bray-Curtis distances) offer relative similarities and differences of the planktic foraminifera communities (species level) between the event stages (color-coded as indicated). Species are marked with cross symbols. Numbers of depth indicate the sample. Pre-LDE assemblages stand out from the rest of the record.

Vectors are considered to represent ecological control of the distribution and belong to the “species” coordinate system. Environmental parameters should be considered in aspects of direction, length again is arbitrarily scaled and should be compared in relation to each other (Hammer and Harper, 2012). Significant at the 95 % level are $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ of *Parasubbotina uncinata*, *P. inconstans* and *M. angulata*. Right panel: Loadings of NMDS Axis 1 and 2, as well as the XRF core scanning Fe variations (Westerhold et al., 2008) are shown. Age model is based on Dinarès-Turell et al. (2014), La2011 solution.

Fig. 5

The $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ crossplots indicate the preferred depth habitat of different foraminiferal taxa. In green: benthic foraminifera; blue: planktic subsurface foraminifera; red small triangles, dark red large triangles with blue frame (only 1262) as well as orange circles: planktic surface dwelling foraminifera.

(A) $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ crossplot of Site 1262. (B) $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ crossplot in a comparison between Sites 1262 (shaded areas) and Site 1210 (Shatsky Rise: open areas and symbols).

Fig. 6

Comparison of key results from ODP Sites 1210 and 1262: Shannon H' , simple diversity, evenness and benthic foraminifera $\delta^{13}\text{C}$. Age model is based on Dinarès-Turell et al. (2014), La2011 solution.

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