Benthic foraminiferal turnover across the Dan-C2 event in the eastern South Atlantic Ocean (ODP Site 1262)

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Abstract

The Paleogene was punctuated by perturbations of the global carbon cycle, many associated with transient global warming events (hyperthermals). The Dan-C2 event (~160 kyr after Cretaceous/Paleogene boundary; K/Pg) was the oldest of these eccentricity-linked carbon cycle disturbances (ELCD). In contrast to other hyperthermals, the Dan-C2 event was not characterised by bottom water warming, and surface water warming probably was not global. Benthic foraminiferal assemblages across Dan-C2 at SE Atlantic Ocean Drilling Program (ODP) Site 1262 are diverse and strongly dominated by calcareous species.
Epifaunal and infaunal morphogroups are equally abundant, suggesting meso-oligotrophic seafloor conditions. Assemblages decreased in diversity gradually before Dan-C2, and *Nuttallides truempyi* decreased in relative abundance while *Stensioeina beccariiformis* and the agglutinant *Spiroplectammina spectabilis* increased, suggesting enhanced food supply to the seafloor. Benthic foraminifera were not highly affected by the Dan-C2 event. An increase in relative abundance of the opportunistic species *Bulimina kugleri* and *Seabrookia cretacea* after Dan-C2 points to a change in the type of organic matter arriving at the seafloor. These changes may have been caused by ongoing environmental and/or evolutionary instability following K/Pg mass extinction of oceanic plankton. Variability in composition of pelagic ecosystems, thus the type and/or amount of food arriving at the seafloor, may have been caused by the gradual recovery of pelagic ecosystems after that extinction, possibly affected by warming and pH changes due to Deccan volcanism.

**Keywords:** warming; benthic foraminifera; K/Pg extinction; plankton evolution; Paleocene; Paleogene.

1. **Introduction**

A series of perturbations of the global carbon cycle associated with global warming (hyperthermal events) punctuated the long-term warming trend of the early Paleogene (e.g., Thomas and Zachos, 2000; Cramer et al., 2003; Leon-Rodriguez and Dickens, 2010; Littler et al., 2014; Westerhold et al., 2018, 2020). The Paleocene-Eocene Thermal Maximum (PETM) was the largest of these events, while smaller hyperthermals occurred both before and after the PETM (e.g., Cramer et al., 2003; Dinarès-Turrèll et al., 2014; Galeotti et al., 2015; Westerhold et al., 2018, 2020). Hyperthermals generally are modulated at astronomical frequencies, specifically eccentricity (e.g., Lourens et al., 2005; Westerhold et al., 2017, 2020; Barnet et al., 2019; Zeebe and Lourens, 2019). Paleocene hyperthermals
include the Lower C29n event (Coccioni et al., 2010), the Latest Danian Event (LDE, also called Top C27n event, Westerhold et al., 2008, 2011; Bornemann et al., 2009; Alegret et al., 2016) and the Early Late Paleocene Event (ELPE, also called Mid Paleocene Biotic Event, MPBE; Petrizzo, 2005; Bralower et al., 2006; Bernaola et al., 2007). The earliest Paleocene perturbation of the global carbon cycle is known as the Dan-C2 event (duration ~100 kyr), identified by Quillévéré et al. (2008) at ~65.2 Ma (Gradstein et al., 2004). In an updated calibration of the Upper Cretaceous–lower Eocene time scale (Barnet et al., 2019), Dan-C2 occurred ~160 kyr after the K/Pg boundary (66.0225 Ma; Dinarès-Turell et al., 2014), i.e., at ~65.86 Ma, the first 405-kyr Paleocene eccentricity maximum (Pc405) (Westerhold et al., 2011, 2020; Barnet et al., 2019).

Dan-C2 resembles hyperthermal events: negative excursions in $\delta^{13}C$ and $\delta^{18}O$ values in bulk sediment and in planktic foraminifera, and lower CaCO$_3$ concentrations in marine carbonate. The Dan-C2 event as observed at a few sites in the Atlantic Ocean is characterised by double, fairly symmetrical negative excursions in carbon and oxygen isotopes ($\delta^{13}C$ and $\delta^{18}O$) in bulk sediment, an increase in sediment clay content and a decrease in carbonate content (Kroon et al., 2007; Quillévéré et al., 2008; Barnet et al., 2017, 2019). The Dan-C2 was shorter than the PETM (Quillévéré et al., 2008), similar to post-PETM Eocene hyperthermals (e.g., Eocene Thermal Maximum 2, ETM2, Stap et al., 2009, 2010; Jennions et al., 2015; and Eocene Thermal Maximum 3, ETM3, Thomas et al., 2018). However, the event might have been restricted to the Atlantic and surrounding areas, including the Tethys Ocean (e.g., Westerhold et al., 2011). A Dan-C2 negative Carbon Isotope Excursion (CIE) was identified at ODP Hole 1049C (NW Atlantic) in bulk sediment (~1.3‰), planktic (~0.7‰) and benthic foraminifera (~1‰), and in bulk sediment in Deep Sea Drilling Project (DSDP) Holes 527 and 528 (SE Atlantic; ~1.5‰ and ~0.8‰ respectively) (Quillévéré et al., 2008).

In the western Tethys (Gubbio section, Coccioni et al., 2010), Dan-C2 is observed in bulk $\delta^{13}C (~0.8‰)$ and $\delta^{18}O$ records, with a decline in CaCO$_3$ and in $\delta^{13}C$ data from a Ukrainian terrestrial setting (CIE of ~3‰; Gilmour et al., 2013). The event was not identified at Site
1209 in the Pacific Ocean (Westerhold et al., 2011; Hull et al., 2020), nor Newfoundland
Ridge Site U1403 (Hull et al., 2020). In contrast to other events, there was no deep-water
warming recorded at any of these locations. At ODP Hole 1049C, there was ~4°C surface
ocean warming as reconstructed from δ¹⁸O values of bulk and planktic foraminifera, but no
warming in the benthic record.

The event occurs at a 405-kyr eccentricity maximum, like later hyperthermal events
(e.g., Lourens et al., 2005; Zeebe and Lourens, 2019; Westerhold et al., 2020). CIEs are
generally related to the release of a large amount of ¹²C-enriched carbon compounds into
the ocean-atmosphere system, possibly through volcanic outgassing from Deccan Trap
volcanism, but a volcanic origin would not explain the orbital pacing, and volcanic CO₂ does
not have a sufficiently light isotopic signature (Barnet et al., 2017, 2019; Hull et al., 2020).

The PETM and other hyperthermals are characterised by increased clay and Fe
concentrations in deep-sea sediments due to dissolution as a result of ocean acidification by
the release of carbon compounds (Kroon et al., 2007; Speed and Kroon, 2000; Westerhold
et al., 2008). However, low CaCO₃ levels in Dan-C2 may have been influenced by the fact that
pelagic calcifiers (calcareous nannoplankton and planktic foraminifera) were not yet fully
recovered from the K/Pg extinction (e.g., D'Hondt, 2005; Bernaola and Monechi, 2007; Birch
et al., 2012, 2016; Alvarez et al., 2019). Its low carbonate concentration could have been due
to low carbonate mass accumulation rates (Kroon et al., 2007) rather than to CaCO₃
dissolution (Barnet et al., 2019; Hull et al., 2020). The fine-grained carbonate in sediments
directly above the K/Pg may have been produced not by calcareous nannoplankton, but by
microbial 'whitings' (Bralower et al., 2020) and/or have an unknown, in part diagenetic
origin (Minoletti et al., 2005).

Biotic turnover across the largest hyperthermal event, the PETM, has been
extensively described, especially of deep-sea benthic foraminifera which underwent their
largest extinction of the Late Cretaceous-Cenozoic (Tjalsma and Lohmann, 1983; Miller et
al, 1987; Katz and Miller, 1991; Thomas, 1989, 1990a, b, 1998, 2007; Alegret et al., 2009a,
Other marine and terrestrial groups show diversification, evolution of short-lived taxa, and/or migration to higher latitudes (e.g., McInerney and Wing, 2011; Speijer et al., 2012).

Benthic foraminiferal turnover across the smaller Paleocene - Eocene hyperthermals has been documented at fewer locations than the PETM. Assemblage changes are similar to those recorded across the PETM (low diversity and high dominance post-event), but there were no significant extinctions (D’haenens et al., 2012; Jennions et al., 2015; Alegret et al., 2016; Arreguín-Rodríguez et al., 2016; Arreguín-Rodríguez and Alegret, 2016; Thomas et al., 2018).

The response of benthic foraminifera to the Dan-C2 event has not been studied at sufficient time resolution and information is predominantly drawn from low-resolution data from studies on the K/Pg event (e.g., Alegret and Thomas, 2004, 2013), including at Site 1262 (Alegret and Thomas, 2007; Alegret et al., 2012). A low-resolution study of benthic foraminifera of the western Tethys Contessa Highway section reported increased abundance of opportunistic taxa, suggesting enhanced food flux to the seafloor and decreased oxygenation across Dan-C2 (Coccioni et al., 2010). We evaluate the benthic foraminiferal turnover at SE Atlantic ODP Site 1262 to investigate the paleoenvironmental and faunal response to the Dan-C2 event, over a time interval extending from 10.59 to 563.23 kyr after the K/Pg boundary.

2. Location and setting

Paleocene sediments at Ocean Drilling Program (ODP) Site 1262 (27°11.15′S, 1°34′2E; 3600 m paleodepth) in the Angola Basin, near the base of the north-western flank of Walvis Ridge (Figure 1) consist of brown calcareous clays with abundant nannofossils and planktic foraminifera (Zachos et al., 2004). The Dan-C2 event was recognised by a prominent double-spiked negative CIE in bulk sediment δ¹³C values (Kroon et al., 2007;
Barnet al., 2019), superimposed on a gradually decreasing trend in δ¹³C between the K/Pg boundary and Dan-C2, with minimum values during the latter (~0.58 ‰; Figure 2).

Both Site 1262 and the shallower Walvis Ridge Site 1267 show the double-spiked negative excursion in δ¹³C_bulk values across Dan-C2 (Kroon et al., 2007; Hull et al., 2020; Figure 2), also seen at nearby DSDP Sites 527 and 528 (Quillévéré et al., 2008), and a gradual increase after the event, but no return to pre-excursion values in the studied interval. In contrast, δ¹³C_benthic values decrease above the K/Pg, then are stable across Dan-C2, followed by a slightly decreasing trend up to the upper part of the studied section (213.7 meters composite depth, mcd) (Barnet et al., 2017, 2019; Figure 2). The Δδ¹³C_(planktic-benthic) is reversed from normal (i.e., benthic values are heavier) from the K/Pg until ~100 kyr after Dan-C2.

The δ¹⁸O_bulk values do not show a negative excursion during Dan-C2, and δ¹⁸O_benthic values remain relatively stable, with a marked drop above it (215 mcd), reflecting similar values as in bulk sediment (Barnet et al., 2017, 2019; Figure 2). The CaCO₃ wt % shows the same pattern as bulk sediment δ¹³C values, i.e., a decreasing trend below the event, minimum values during Dan-C2 (~5%) and a slight overall increase towards the upper part.
of the studied interval (Alegret et al., 2012). The XRF-derived Fe intensity values mirror the %CaCO₃ trends, increasing from the lower part of the section up to Dan-C2, then slightly decreasing above the event, with two intervals of higher values coinciding with the two intervals with low CaCO₃% (Figure 2).

Figure 2. Stable isotope values (δ¹³C and δ¹⁸O) of benthic foraminifera (N. truempyi; Barnet et al., 2017, 2019), bulk sediment (Kroon et al., 2007) and planktic foraminifera (Birch et al., 2016) at ODP Site 1262, compared with CaCO₃ content (Alegret et al., 2012), XRF-Fe counts (Westerhold et al., 2008), coarse fraction > 63 µm (CF; Barnet et al., 2019), and mass accumulation rates (MAR bulk). Biomarker data (2MeHI% and S/H; Bralower et al., 2020) and calcareous nannofossil abundance (Bernaola and Monechi, 2007) are shown to illustrate primary producers. The 2-methyl hopane index (2MeHI%) is indicative of cyanobacteria, and Sterane/Hopane (S/H) indicates the relative contribution of bacteria (H) and algae (S). Calcareous nannofossils: Cretaceous vanishing species (C-vanishing), Cretaceous-persistent species (C-persistent), and new Paleocene species (n-Paleocene). spp./f.v. = specimens per field of view. Grey area indicates the Dan-C2 event.

3. Methods
Samples were oven-dried at 50°C for 2–3 days, then weighed to obtain a bulk dry sample weight, and soaked and disaggregated in a cold buffered sodium hexametaphosphate ((NaPO$_3$)$_6$) solution for 12–24 hours. Then samples were sieved through a 63 μm sieve to retain the coarse fraction and remove the fine clays and calcareous nannofossils. The sieved samples were put onto a shaker table in a buffered (NaPO$_3$)$_6$ solution for 2 hours, to remove any further fines, then sieved a final time through a 63 μm sieve. After a final rinse with ethanol to displace the water, samples were oven-dried at 50°C. The >63 μm sediment fraction was used for quantitative faunal analysis.

Benthic foraminifera were analysed in 39 samples from Cores 1262C-13H and 1262B-22H (216.55 – 214.03 mcd), 14 of which were studied by Alegret and Thomas (2007), which encompass 552.64 kyr of the early Paleocene. We adjusted taxonomic assignments following Arreguín-Rodríguez et al. (2018). The sampling resolution varies from ~5–12 cm close to the event to up to ~20 cm towards the upper part of the studied interval.

Approximately 300 specimens of benthic foraminifera were picked from each sample (Table S1, Figures 3 and 4). For identification at the species and genus level we followed Tjalsma and Lohmann (1983), Van Morkhoven et al. (1986), Loeblich and Tappan (1988), and Alegret and Thomas (2001); for species that survive into the Eocene we followed Arreguín-Rodríguez et al. (2018) and Hayward et al. (2012) for uniserial species with complex apertures. A taxonomic reference list of common species (>2% of relative abundance), including taxa cited in the text, is given in Table S2. Relative abundance of taxa, diversity (Fisher-ɑ index) and heterogeneity (Shannon-Weaver index) indices, as well as the agglutinated-calcareous and infaunal-epifaunal ratios were calculated. The infaunal-epifaunal ratio is based on the relation between morphology and microhabitat, and can be used, with careful evaluation, as an approximate proxy for oxygenation and trophic conditions at the seafloor (Jorissen et al., 1995, 2007). Additionally, we calculated the
percentage of buliminids *sensu lato* (s.l.) (Alegret and Thomas, 2013), excluding the superfamily Stilostomellacea. This group tolerates reduced oxygen conditions (Sen Gupta and Machain-Castillo, 1993) and/or thrives under abundant food supply (Thomas, 1998; Fontanier et al., 2002; Gooday, 2003; Jorissen et al., 1995, 2007).

The number of foraminifera per gram of dry sediment was calculated considering the sample-split weight used to pick benthic foraminifera. Bulk sediment accumulation rates (MAR\textsubscript{bulk}) and benthic foraminiferal accumulation rates (BFAR) were calculated based on the average dry density for the studied interval (Zachos et al., 2004), and the age model in Barnet et al. (2019), which is orbitally tuned based on benthic $\delta^{13}$C record and grounded with detailed magnetostratigraphic and biostratigraphic data. We used the number of specimens in the $>$63 µm size fraction corrected to the weight of bulk sediment to estimate BFAR, which is a proxy to estimate the total organic matter flux to the seafloor (Herguera and Berger, 1991; Jorissen et al., 2007). The coarse fraction was determined as the weight ratio of $>$63 µm size fraction to the bulk dry sediment weight.

R-mode hierarchical cluster analyses were performed to identify groups of species with similar distribution patterns. We used the unweighted pair-group average algorithm (UPGMA) and the Pearson correlation, as similarity coefficient. We performed detrended correspondence analyses (DCA) on R- and Q-modes to identify potential ecological variables that may have controlled the distribution of benthic foraminifera. A dataset of species with a relative abundance $>$2% in at least one sample (32 species) was constructed to perform cluster and DCA analyses. Some groups of taxa such as *Abyssammina* spp., *Anomalinoidea* spp., *Chrysalogonium* spp., *Globulina* spp., *Gyroidinoides* spp., nodosariids, *Nuttallides* spp., *Nuttallinella* spp., *Osangularia* spp., *Paralabamina* spp., pleurostomellids and *Pyrulinoides* spp. were excluded from this dataset in order to compare exclusively single species.
Figure 3. SEM images of selected benthic foraminifera at ODP Site 1262. All scale bars represent 100 µm, unless otherwise indicated. 1 Spiroplectammina spectabilis, 215.27 mcd; 2 Spiroplectammina spectabilis, 215.27 mcd; 3 Clavulinoides sp., 215.53 mcd; 4 Seabrookia cretacea, 214.95 mcd; 5 Bolivina huneri, 216.34 mcd; 6 Tappanina eouvigeriniformis, 216.34 mcd; 7 Tappanina eouvigeriniformis, 215.66 mcd; 8 Aragonia ouezzanensis, 214.03 mcd; 9 Bulimina kugleri, 214.95 mcd; 10 Bulimina midwayensis, 215.41 mcd; 11 Paralabamina hillebrandti, 214.15 mcd; 12 Paralabamina hillebrandti, 214.15 mcd; 13 Paralabamina hillebrandti, 215.34 mcd; 14 Paralabamina hillebrandti, 214.15 mcd; 15 Nuttallinella ripleyensis, 215.84 mcd; 16 Nuttallinella ripleyensis, 215.84 mcd; 17 Nuttallinella florealis, 214.29 mcd; 18 Nuttallinella florealis, 214.29 mcd; 19 Nuttallinella florealis,

Statistical analyses based on the comparison of samples from distinct time intervals were performed in order to determine whether benthic foraminifera responded significantly to the Dan-C2 event. We applied the Fligner-Killeen test (T), a nonparametric test used to recognize equal coefficients of variation in two sample groups (Fligner and Killeen, 1976), assuming that this measure of dispersion may reflect the stability of the system (i.e., major variability points to unstable/perturbed systems and *vice versa*). The intervals of time employed for these analyses were selected considering three alternatives: the occurrence of the event (option A), a main change in diversity (option B), and a marked change in faunal clusters (option C). In option A, the pre-event interval includes samples from 216.55 to 215.66 mcd, and samples from 215.63 to 215.11 mcd correspond to Dan-C2. For option B, the studied interval was divided in two parts: a lower (216.55 to 214.95 mcd) and an upper part (214.87 to 214.03 mcd). In option C, the lower part includes samples from 216.55 to 215.81 mcd, and the upper part encompasses samples from 215.78 to 214.03 mcd. We compared diversity and heterogeneity indices, relative abundance of agglutinated and infaunal taxa, and the abundance of the faunal clusters. We used PAST software for the statistical analyses (Hammer et al., 2001).
Figure 4. SEM images of selected benthic foraminifera at ODP Site 1262. All scale bars represent 100 µm, unless otherwise is indicated. 1 Anomalinoides praeacutus, 215.73 mcd; 2 Anomalinoides praeacutus, 215.57 mcd; 3 Anomalinoides praeacutus, 215.57 mcd; 4 Abyssamina subplanispira, 216.34 mcd; 5 Abyssamina subplanispira, 216.34 mcd; 6 Abyssamina subplanispira, 216.34 mcd; 7 Cibicidoides hyphalus, 214.15 mcd; 8 Cibicidoides hyphalus, 214.15 mcd; 9 Cibicidoides hyphalus, 214.15 mcd; 10 Osangularia velascoensis, 214.7 mcd; 11 Osangularia velascoensis, 215.27 mcd; 12 Osangularia velascoensis, 215.27 mcd; 13 Gyroidinoides depressus, 214.29 mcd; 14 Gyroidinoides depressus, 214.29 mcd; 15 Gyroidinoides depressus, 214.29 mcd; 16 Gyroidinoides globosus, 215.96 mcd; 17 Gyroidinoides globosus, 215.96 mcd; 18 Gyroidinoides globosus, 215.96 mcd; 19 Gyroidinoides globosus, 215.96 mcd; 20 Gyroidinoides globosus, 215.96 mcd; 21 Gyroidinoides globosus, 215.96 mcd; 22 Gyroidinoides globosus, 215.96 mcd; 23 Gyroidinoides globosus, 215.96 mcd; 24 Gyroidinoides globosus, 215.96 mcd.
4. Results

4.1 Benthic foraminiferal assemblages and mass accumulation rates

The preservation of benthic foraminifera is generally good throughout the studied section (Figures 3, 4). Calcareous (average ~89%) and epifaunal (average ~56%) taxa dominate the assemblages (Table S1). The most abundant epifaunal taxa include the trochospiral Stensioeina beccariiformis (average 10.8%), Paralabamina hillebrandti (average 6.3%) and Nuttallinella rippleyensis (average 5.7%). Spiroplectammina spectabilis (average 6.2%) is the most abundant infaunal species, which together with Clavulinoides spp. makes up the most abundant agglutinated taxa.

Diversity and heterogeneity are high at Site 1262, as expected for deep-sea faunas of the Late Cretaceous–Paleocene Velasco-type assemblage, but vary across the studied section. For a description of benthic foraminiferal assemblages, proxies and mass accumulation rates, the section was divided into three intervals, based on the recognition of Dan-C2 through the δ¹³C record (Table 1). The pre-event interval includes samples from 216.55 to 215.66 mcd, the Dan-C2 interval samples from 215.63 to 215.11 mcd, and the post-event interval samples from 215.05 to 214.03 mcd.

The pre-event interval is characterised by strong fluctuations superimposed on a slight overall decrease in diversity and heterogeneity indices (Figure 5). BFAR values remain stable throughout this interval, increasing in its uppermost part, and reaching maximum values immediately below Dan-C2. The gradual increase in % agglutinated taxa correlates with a gradual decrease in %CaCO₃. The absolute abundance of benthic
foraminifera (Nr/gr) remains low, whereas taxa such as uniserial lagenids and polymorphinids decrease in abundance across this interval. Bolivinids s.s. peak in abundance in the lower part of the pre-event interval. Among the epifaunal taxa, *N. ripleyensis* and *N. truempyi* decrease in abundance below Dan-C2, whereas *S. beccariiformis* increases. *Paralabamina hillebrandti* remains relatively stable, with a peak in abundance close to the base of Dan-C2. Bulk mass accumulation rates decrease markedly (from ~2 to 0.7 g cm⁻² kyr⁻¹) at 216.36–216.16 mcd, followed by a slight gradual decrease towards the upper part of the pre-event interval (Figure 2).

Table 1. Mean values of benthic foraminiferal indices, proxies and mass accumulation rates at pre-event, Dan-C2 and post-event intervals.

<table>
<thead>
<tr>
<th></th>
<th>Pre-event</th>
<th>Dan-C2</th>
<th>Post-event</th>
</tr>
</thead>
<tbody>
<tr>
<td>BFAR</td>
<td>2151.0</td>
<td>1052.5</td>
<td>564.8</td>
</tr>
<tr>
<td>Diversity (Fisher-α)</td>
<td>19.4</td>
<td>17.7</td>
<td>21.1</td>
</tr>
<tr>
<td>Heterogeneity (H(S))</td>
<td>3.4</td>
<td>3.3</td>
<td>3.4</td>
</tr>
<tr>
<td>Foraminiferal density (Nr/gr)</td>
<td>76276.9</td>
<td>481652.1</td>
<td>11680.0</td>
</tr>
<tr>
<td>Agglutinated taxa (%)</td>
<td>8.8</td>
<td>14.2</td>
<td>11.5</td>
</tr>
<tr>
<td>Infaunal taxa (%)</td>
<td>47.1</td>
<td>39.8</td>
<td>46.3</td>
</tr>
<tr>
<td>Buliminids s.l. (%)</td>
<td>13.0</td>
<td>11.5</td>
<td>14.4</td>
</tr>
<tr>
<td>Buliminids s.s. (%)</td>
<td>4.5</td>
<td>5.3</td>
<td>7.0</td>
</tr>
<tr>
<td>Bolivinids s.s. (%)</td>
<td>5.2</td>
<td>3.9</td>
<td>4.3</td>
</tr>
<tr>
<td>Uniserial lagenids (%)</td>
<td>4.5</td>
<td>1.4</td>
<td>3.7</td>
</tr>
<tr>
<td>Stilostomellids (%)</td>
<td>0.8</td>
<td>0.3</td>
<td>1.3</td>
</tr>
<tr>
<td>Polymorphinids (%)</td>
<td>2.2</td>
<td>1.1</td>
<td>3.0</td>
</tr>
<tr>
<td>Unilocular taxa (%)</td>
<td>1.2</td>
<td>0.9</td>
<td>1.6</td>
</tr>
<tr>
<td>MAR&lt;sub&gt;bulk&lt;/sub&gt;</td>
<td>1.1</td>
<td>0.5</td>
<td>0.6</td>
</tr>
</tbody>
</table>

The Dan-C2 interval includes the lowest diversity values (Fisher-α ~13 at 215.45 mcd) and the highest absolute abundance of benthic foraminifera (215.51 mcd; Figure 5) due to the low coarse fraction, occurring during the lowest of the two negative δ¹³C excursions. Diversity quickly recovers up-section, and a small peak in BFAR occurs in Dan-C2 (215.34 mcd). The increase in relative abundance of agglutinated species (up to ~22% of the assemblages) in the middle part of Dan-C2 is not coeval with the decrease in %CaCO₃,
and a linear regression analysis indicates that only 33% of the variability of agglutinated taxa is explained by variability of %CaCO$_3$ (Figure S1). Infaunal morphogroups, including uniserial lagenids, stilostomellids, polymorphinids and unilocular taxa, show their minimum in relative abundance across the event, whereas the epifaunal *S. beccariiformis* has its highest abundance in Dan-C2. Other taxa, such as *P. hillebrandti*, peak in abundance at the lowermost part of the event, and *N. rippleyensis* slightly increases towards the top of the event. Bulk mass accumulation rates, % calcium carbonate and coarse fraction reach their lowest values across Dan-C2 (Figure 2).

**Figure 5.** Benthic foraminiferal indices and proxies, including benthic foraminiferal accumulation rates (BFAR, including data from Alegret et al., 2012), diversity (Fisher-$\alpha$), heterogeneity (Shannon-Weaver), foraminiferal density (N$^\circ$ specimens/gr dry sed.), relative abundance of agglutinated taxa, infaunal morphogroups, buliminids *sensu lato* (s.l.), buliminids *sensu stricto* (s.s.), bolivinids s.s., and other infaunal taxa (uniserial lagenids, stilostomellids, polymorphinids and unilocular taxa), compared to CaCO$_3$ content (Alegret et al., 2012), $\delta^{13}$C values measured in *N. truempyi* (Barnet et al., 2017, 2019) and $\delta^{13}$C in bulk sediment (Kroon et al., 2007).
Diversity and heterogeneity gradually increase above Dan-C2, towards the upper part of the studied interval (Figure 5). The percentages of some infaunal taxa (buliminids s.s., uniserial lagenids, polymorphinids, stilostomellids and unilocular taxa) slightly increase above Dan-C2, whereas agglutinated taxa slightly decrease. Relative abundance of some epifaunal taxa gradually decreases above Dan-C2 (S. beccariiformis), and that of others increases towards the upper part of the studied section (e.g., N. truempyi, N. ripleyensis). BFAR and absolute abundance values decrease and are similar to pre-event values, and bulk mass accumulation rates remain low (Figure 2).

4.2 Faunal clusters and DCAs

The dendrogram of the R-mode cluster analysis shows two main clusters of benthic foraminiferal species (Figure 6). Cluster A is divided into subclusters A1 and A2, and it is composed of epifaunal and infaunal taxa. Subcluster A1 is dominated by Nuttallina ripleyensis, Nuttallides truempyi and Paralabamina lunata, and is most abundant in the pre-event interval (up to sample 215.81 mcd); its abundance decreases towards Dan-C2 and increases slightly above the event (Figure 6). Bulimina kugleri, Seabrookia cretacea and Oridorsalis umbonatus are the most abundant species of subcluster A2, which contains exclusively infaunal taxa that increase in abundance above Dan-C2 (214.60-215.05 mcd), remaining fairly stable in the interval below and across Dan-C2.

Cluster B, subdivided into subcluster B1 and subcluster B2, consists of mixed infaunal and epifaunal taxa, including species that dominate the assemblages (and/or increase in abundance) in Dan-C2. Subcluster B1 is mostly composed of epifaunal taxa, except for the infaunal agglutinated species Spiroplectammina spectabilis and Clavulinoides sp. This is the most abundant subcluster, and it gradually increases from the interval below the event towards Dan-C2 (Figure 6). Stensioeina beccariiformis, S. spectabilis and Paralabamina hillebrandti are the most abundant species. Less abundant subcluster B2
shows minor abundance peaks below and within Dan-C2 (215.41–215.81 mcd; Figure 6). The most abundant species of this subcluster are infaunal *Tappanina eouvieriniformis* and epifaunal-shallow infaunal *Gyroidinoides beisseli*.

Figure 6. R-mode dendrogram and relative abundances of selected benthic foraminiferal taxa and faunal clusters across the lower Paleocene at ODP Site 1262, plotted against $\delta^{13}$C values measured in *N. truempyi* (Barnet et al., 2017, 2019) and in bulk sediment (Kroon et al., 2007).

Cluster B species are located at lower values along axis 1 in the R-mode DCA plot (Figure 7A), whereas cluster A score middle-high values on this axis. Most species are placed at middle values along axis 2, but subclusters A1 and B2 include taxa at the lowermost values of this axis (*Bolivinoides decoratus*, *T. eouvieriniformis*). Species from subcluster A2, particularly infaunal *Fursenkoina tegulata* and *S. cretacea*, score the highest values along the vertical axis (axis 2).

Samples representing Dan-C2 are located towards the left of the Q-mode DCA plot (Figure 7B), i.e., at lowest values along axis 1, except for samples at 215.22 and 215.48 mcd,
which score middle values. Most samples above the event are at low-medium values along the horizontal axis (axis 1). Samples below the event show a wide range of values, with those corresponding to >216 mcd reaching higher values along axis 1.

Figure 7. Detrended correspondence analysis (DCA) results. A) R-mode (species) plot. The outlined groups represent faunal clusters (A1, A2, B1, B2) and the bars along the axes indicate the overall ecological preferences of the taxa. Full names are written in Table S2. B) Q-mode (samples) plot. The dashed line separates samples depending on their faunal content: samples to the right are dominated by species from cluster A1, and to the left by species from cluster B1.

4.3 Testing the coefficient of variation
We statistically compared several variables between intervals before and during Dan-C2 (Table 2). Neither diversity, heterogeneity nor faunal clusters (A1, A2 and B2) show significant differences in coefficient of variation among those intervals, but agglutinated species, infaunal taxa and cluster B1 show a statistically distinctive coefficient of variation (p-values <0.05). Coefficients of variation of agglutinated taxa and cluster B1 decrease in Dan-C2, indicating less variability thus more steady values during the event. In contrast, the coefficient of variation of infaunal taxa increases in Dan-C2, reflecting more fluctuating values (Figure 8).

Table 2. Results of Fligner-Killeen tests based on the Dan-C2 event (option A).

<table>
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We thus do not observe a clear response of benthic foraminifera to Dan-C2. We applied this test to other depth (thus time) intervals where we noted changes in diversity and heterogeneity (option B), and changes in relative abundance of clusters (option C; Figure 8). In option B, no variables show statistically significant differences (Table 3); whereas option C shows significant differences in coefficients of variation of the diversity
index, agglutinated taxa, and clusters B1 and B2. Such differences are associated with higher coefficients of variation of these variables (except for the diversity index) in the lower interval, which imply more variability, and thus more unstable conditions across this interval (Table 4, Figure 8).

Figure 8. Time intervals and variables used in the Fligner-Killeen test. Intervals are based on the occurrence of Dan-C2 (option A, orange), main change in diversity (option B, yellow) and change in dominance of faunal clusters (option C, pink). Coefficients of variation (CV) are indicated next to the variable, when comparison of such variable between intervals is statistically different.

Table 3. Results of Fligner-Killeen tests based on main changes in diversity (option B).

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Table 4. Results of Fligner-Killeen tests based on marked changes in faunal clusters (option C).

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<td>Lower</td>
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5. Discussion

5.1 Paleoecological inferences

We use the results of the multivariate analysis to infer changes in ecological conditions. Using the R-mode DCA plot and ecological preferences of taxa as derived from the literature, we interpret these axes as related to food availability (e.g., quantity, stability) to benthic foraminifera (Figure 7A). No evidence has been found to suggest other parameters (e.g., oxygenation, carbonate saturation or bottom current strength) as limiting
factors for benthic foraminiferal assemblages across the studied interval (see section 5.2 for further details).

Horizontal axis 1 may indicate the overall amount of food, with less food availability at higher values, where some oligotrophic species plot, such as *N. truempyi*, *N. rippleyensis*, *A. subplanispira* and *P. lunata* (subcluster A1; e.g., Alegret and Thomas, 2009; Deprez et al., 2015). Somewhat more eutrophic taxa (e.g., *S. beccariiformis*, *A. acutus*, *A. praecutus*, *Bulimina* spp.; e.g., Thomas, 1998; Jorissen et al., 2007; Alegret et al., 2021) are at lower values along the axis. We note that some taxa generally deemed oligotrophic (*C. hyphalus* and *N. florealis*; e.g., Widmark and Malmgren, 1992; Alegret and Thomas, 2005) occur at lower values on axis 1, and some species potentially linked to high food supply (*P. jarvisi*; e.g., Arreguín-Rodríguez and Alegret, 2016) at higher values, but these species are not abundant.

The distribution of species along the vertical axis (axis 2) may be related to the stability of the food supply, with high values representing a more pulsed or variable supply, and low values indicating stable conditions. *Seabrookia cretacea* and *B. kugleri* (subcluster A2) are at high values along axis 2 (Figure 7A), and may be opportunists responding to a pulsed food input (e.g., Alegret and Thomas, 2005; Sprong et al., 2013), possibly similar to *Seabrookia rugosa* (Thomas et al. 2018). *Paralabamina lunata* (high values along axis 2) is indicative of more oligotrophic conditions (e.g., Alegret and Thomas, 2005; Mello et al., 2017), and may have been able to feed on a specific type of food (Alegret and Thomas, 2013), e.g., more labile phytodetritus (Deprez et al., 2017). The position of *B. decoratus* at the lowermost values along axis 2 may support this interpretation, since buliminids are typically related to consistent trophic conditions (e.g., Jorissen et al., 1995, 2007; Gooday, 2003; Alegret and Thomas, 2009). *Bolivinoides crenulata* and *B. huneri*, which resemble *B. decoratus* in morphology (Arreguín-Rodríguez et al., 2018), might indicate a lower food flux than other buliminids, or a flux stabilised by a more refractory input (Fenero et al., 2012; Boscolo Galazzo et al., 2013, 2015; Arreguín-Rodríguez et al., 2018). *Tappanina*
eouvigeriniformis is indicative of higher organic flux to the seafloor (Alegret and Thomas, 2013), and plots at similarly low values along the vertical axis as B. decoratus, thus may indicate an overall higher food flux at similar stability.

In the Q-mode plot, samples from Dan-C2 and post-event interval plot at low values along axis 1 (Figure 7B), and are dominated by subcluster B1 (mainly S. beccariiformis and S. spectabilis). Dan-C2 samples reach the lowest values on axis 1, but two samples (215.22 and 215.48 mcd) are located at about the middle of this axis. These samples have small peaks in abundance of subcluster A1 species (N. rippleyensis or P. lunata), which have a lower abundance in other Dan-C2 samples.

Most samples from below Dan-C2 (pre-event interval) plot at higher values along axis 1, with a high percentage of subcluster A1 species (N. truempyi, N. rippleyensis). Benthic foraminiferal assemblages changed markedly ~117 kyr after the K/Pg (215.81 mcd), with lower samples (216.55 – 215.81 mcd) having common subcluster A1 species (oligotrophic). Subcluster B1 species are more abundant from 215.78 to 214.03 mcd (higher trophic conditions). We thus suggest that there was more extreme variability in food (thus stress) in the lower part of the studied interval (~117 kyr after the K/Pg, prior to Dan-C2), followed by more stable conditions, even in Dan-C2, although stressful environments persisted until at least ~368 kyr after the K/Pg (sample 214.95 mcd; Figure 5; Alegret and Thomas, 2007; Bralower et al., 2020). Factors associated to these unstable conditions are discussed on section 5.2.

5.2 Paleoenvironmental interpretation

The dominance of well-preserved calcareous benthic foraminiferal taxa indicates deposition well above the carbonate compensation depth. The lack of carbonate dissolution is also supported by linear regression analysis showing that only 33% of the variability of agglutinated taxa depends on %CaCO3 (Figure S1). The sediments deposited during the first
1–2 million years of the Paleocene are clay rich (60–80 wt % CaCO₃; Zachos et al., 2004), and have high XRF-derived Fe intensity at low sedimentation rates, indicating a lack of dilution by clays (Barnet et al., 2019). CaCO₃ wt. % declined precipitously at the K/Pg boundary with the mass extinction of pelagic calcifiers, then further declined gradually up-section to reach a minimum (~5%) at Dan-C2 (Figure 2). In Dan-C2 planktic foraminifera are rare, as shown by a low CaCO₃ wt% combined with minimum values of % coarse fraction (Thomas et al., 2007; Figure 2). The persistently low CaCO₃ wt. % over the studied interval at Site 1262 (Zachos et al., 2004) is probably due to a persistently low supply of carbonate produced by pelagic calcifiers after their extinction at the K/Pg mass extinction (e.g., D’Hondt, 2005; Alegret et al., 2012; Alvarez et al., 2019). The pattern of somewhat higher CaCO₃ wt. % just above the boundary followed by a decline is seen at several sites, and explained as due to microbial (not eukaryote) carbonate production directly after the asteroid impact (Sepulveda et al., 2019; Bralower et al., 2020). The organic matter produced by prokaryotes (e.g., similar to the extant *Synechococcus* and *Prochlorococcus*), however, may have been transported to the seafloor less efficiently than carbonate-ballasted organic matter (Bralower et al., 2020).

The benthic foraminiferal morphogroups point to meso-oligotrophic conditions, with a flux of organic matter to the seafloor sufficient to sustain both epifaunal and infaunal taxa (e.g., Jorissen et al., 1995). There is no organic enrichment or lamination in the sediments, and we see no high abundances of oxygen-tolerant taxa even in the samples with lowest diversity, so we conclude that oxygenation was not a limiting factor. Fluctuations in diversity and heterogeneity of the assemblages in the intervals before and during Dan-C2 (Figure 5) suggest environmental stress at the seafloor, possibly related to instability and heterogeneity of primary productivity after the K/Pg impact event (Hull and Norris, 2011; Alegret et al., 2012), as controlled by ecological processes and not by proximity to the impact site (Lowery et al., 2018; Bralower et al., 2020). Some argue for a fast recovery of primary productivity after the K/Pg, at least locally or regionally (e.g., Sepulveda et al., 2009;
Lowery et al., 2018; Henehan et al., 2019; Schaefer et al., 2020, though others indicate a more gradual and prolonged re-establishment of diverse ecosystems (e.g., Alvarez et al., 2019), and possibly increased roles for mixotrophic forms rather than photosynthesizers (Gibbs et al., 2020). It may well be that we see major regional heterogeneity in primary productivity after the K/Pg (e.g., Alegret et al., 2012; Esmeray-Senlet et al., 2015; Henehan et al., 2019), so that the tempo of recovery is not the same globally.

Re-establishment of diverse ecosystems of pelagic calcifiers may have been affected and/or delayed by ongoing CO\textsubscript{2} emissions from Deccan volcanism (e.g., Hull et al., 2020). At Walvis Ridge, evidence from calcareous nannofloras and planktic foraminifera as well as planktic $\delta^{13}$C records shows that high variability in pelagic ecosystems, thus probably in export of organic matter to the seafloor, persisted for more than 1 million years after the K/Pg, extending beyond our studied interval (Bernaola and Monechi, 2007; Schueth et al., 2015; Birch et al., 2016; Figure 2).

Low BFAR values prevailed throughout the studied section (Figure 5), pointing to low export productivity. Small peaks in BFAR (samples 215.66 and 215.34 mcd) indicate a transient increase in export productivity, possibly due to lateral terrigenous input with refractory organic matter, although we did not observe an increase in MAR\textsubscript{bulk}. A relatively low but variable input of organic matter to the seafloor is compatible with the common occurrence of oligotrophic species such as *N. truempyi*, *A. subplanispira* and *P. lunata* (subcluster A1), as well as with the scattered peaks in relative abundance of the more eutrophic buliminid group (Thomas et al., 2000; Alegret and Thomas, 2009; Deprez et al., 2015) in the interval below Dan-C2 (below 215.78 mcd, Figures 5, 6). Our data on fluctuations in the diversity and heterogeneity indices, and the abundance peaks of some taxa (e.g., buliminids *s.l.*) suggest that benthic foraminiferal assemblages remained disturbed until ~389 kyr after the KPg. Towards the upper part of the studied section (i.e., ~389 to ~563 kyr after the K/Pg, 214.87 to 214.03 mcd), the assemblages started to stabilise, diversity and heterogeneity indices gradually increased, and infaunal taxa other
than buliminids *s.l.* (such as uniserial lagenids, polymorphinids, stilostomellids and unilocular taxa) increased in relative abundance.

Towards the Dan-C2 event, *N. truempyi* decreased in abundance and *S. beccariiformis* (subcluster B1) increased. The species *S. beccariiformis* generally was more abundant at somewhat shallower depths than *N. truempyi* (e.g., Tjalsma and Lohmann, 1983; Widmark and Malmgren, 1992; Thomas, 1990a, b; Alegret et al., 2009a, b; Arregúin-Rodríguez et al., 2018), although *S. beccariiformis* extended its range into deeper waters at the K/Pg extinction (Alegret et al., 2012). This species has been found to thrive under oligotrophic, well-oxygenated conditions during the Late Cretaceous (e.g., Friedrich and Hemleben, 2007), but its negative correlation to the highly oligotrophic *N. truempyi* (e.g., Sites 1210 and 690; Alegret and Thomas, 2009, 2013) suggest that this species requires a higher food supply than *N. truempyi* (e.g., Widmark and Malmgren, 1992; Thomas et al., 2000). Thus, we interpret the increase in %*S. beccariiformis* and decrease in %*N. truempyi* towards Dan-C2 as the probable development of slightly more eutrophic conditions at the seafloor.

On the other hand, the increase in *S. beccariiformis*, a heavily calcified species which became extinct during the PETM whereas *N. truempyi* survived that ocean acidification event, has been linked to a higher carbonate saturation state after the K/Pg mass extinction of pelagic calcifiers (Alegret and Thomas, 2007), due to decreasing output of carbonate from the oceans while input did not decrease (e.g., Henehan et al., 2019; Bralower et al., 2020). Linear regression tests, however, indicate a significant but low correlation ($R^2 = \sim 40\%$ or less, Figure S1) between %CaCO$_3$ and diversity, heterogeneity, uniserial lagenids, polymorphinids and unilocular taxa, suggesting that perturbation of benthic foraminiferal assemblages was not exclusively associated with the recovery of calcareous plankton (thus declining deep ocean carbonate saturation state) and its potential influence on the efficiency of the biological pump, thus overall food supply.
The increased abundance of agglutinated taxa in Dan-C2 was largely due to the proliferation of infaunal *S. spectabilis*. This species agglutinates using carbonate (Kaminski and Gradstein, 2005), thus its proliferation was not caused by carbonate dissolution. In addition, we observed that CaCO$_3$ saturation increased, based on the dominance of calcareous benthic taxa across the low %CaCO$_3$ interval, and on the common occurrence of the heavily calcified *S. beccariiformis*. *Spiroplectammina spectabilis* is commonly regarded as a ‘disaster taxon’, blooming in the presence of an increased food supply (Kaminski and Gradstein, 2005; Alegret et al., 2003), and we note the decreased abundance of oligotrophic *N. truempyi* towards the Dan-C2 event, which supports this interpretation.

Other infaunal taxa such as buliminids *s.l.* (mainly *B. kugleri*) and *S. cretacea* (cluster A2) increased in abundance after Dan-C2 (214.95 mcd, Figure 6). *Bulimina kugleri*, like other buliminids and infaunal taxa, has been related to a high food supply (e.g., Alegret and Thomas, 2009) even in the absence of clear indicators of low-oxygen conditions at the seafloor (Sen Gupta and Machain-Castillo, 1993). The species bloomed after the K/Pg boundary in the NE Atlantic (Alegret and Thomas, 2004) and after the extinction event at the PETM in the Southern Ocean (e.g., Thomas, 2003), suggesting opportunistic behaviour.

The lack of a coeval increase in BFAR (Figure 5) points to a change in the nature of the food supply rather than to a net increase in the total amount of organic matter reaching the seafloor. We argue that the evolution of new species and varying productivity by different groups of primary producers during the early Paleogene may have caused variability in the type of food supply to the seafloor (Bralower et al., 2020; Figure 2), so that benthic opportunistic taxa (buliminids *s.l.*, *S. cretacea*) may have had an ecological advantage.

5.3 Dan-C2 event

Our results confirm that Dan-C2 differs materially from typical Paleogene hyperthermals (e.g., PETM, ETM2, ETM3; Littler et al., 2014; Barnet et al., 2019) in the minor
response of benthic foraminifera (even as compared to the smaller Eocene hyperthermals),
probably related to the lack of bottom water warming (Figure 2). There is considerable
evidence that bottom water warming caused a lower supply of food to the benthos due to
increased mineralization of organic matter (e.g., Jennions et al., 2015; Thomas et al., 2018;
Griffith et al., 2021).

There are no major differences in the structure or composition of the assemblages
before and during Dan-C2, and the minor changes do not support the occurrence of a major
ecological perturbation in the deep-sea. This lack of response is documented by the results
of the Fligner-Killeen test (option A, Table 2), which indicates that samples from the Dan-
C2 interval do not show significant evidence of perturbation. The relative abundance of
agglutinated taxa and cluster B1 show statistically significant differences between
assemblages before and during the event, with higher values of the coefficient of variation
before the event indicating more instability of the assemblages. Similarly, a comparison of
time intervals based on the main change in faunal clusters (option C), also shows that the
diversity index and the relative abundance of agglutinated taxa, clusters B1 and B2 have
significantly higher coefficients of variation in the lower interval (i.e., before Dan-C2; Figure
8). Only infaunal taxa show a higher coefficient of variation during the Dan-C2 event (Figure
8), possibly related to changing trophic conditions at the seafloor (i.e., an increase in input
of food during Dan-C2). Our data indicate that benthic foraminifera underwent more
environmental stress before the Dan-C2 event than during the event, in agreement with
Alegret and Thomas (2007). Possibly, the food supply increased during Dan-C2 because of
surface (though not deep-sea) warming, which caused intensification of the hydrological
cycle as during the PETM (e.g., McInerney and Wing, 2011), thus more intense weathering
on land, delivering more nutrients and resulting in increased primary productivity, while
the lack of warming deeper in the water column meant that the food was delivered to the
benthal, and not remineralized (Griffith et al., 2021).
Benthic foraminifera across Dan-C2 have been scarcely studied so far, with information available from the Italian Gubbio section only (Coccioni et al., 2010). This record, and our results, both show minor changes in benthic assemblages during the event, with agglutinated taxa slightly increasing in relative abundance. Coccioni et al. (2010) linked the faunal turnover to carbonate dissolution, because of higher values of the planktic fragmentation index, whereas we see no such evidence at Site 1262. These authors noted an increase in the absolute abundance of benthic foraminifera across Dan-C2, which they interpreted as a recovery of the food web and/or enhanced eutrophication, similar to what we observed, and possibly likewise the result on an increased hydrological cycle due to surface warming.

The occurrence of Dan-C2 during an eccentricity maximum strongly suggests that this event, though fundamentally different from later hyperthermal events in environmental and ecological expression (e.g., a lack of deep-sea warming, geographically different bulk δ¹³C records), had similar causal mechanisms. All Paleogene hyperthermals, occurred at specific orbital configurations, i.e., at maxima in the 405 kyr eccentricity (e.g., Lourens et al., 2005; Zeebe and Lourens, 2019; Westerhold et al., 2020).

The precise causal mechanisms of the orbital triggering are not known and strongly debated: e.g., an orbitally-triggered process of release of isotopically light carbon from the lithosphere into the ocean-atmosphere system through dissociation of gas hydrates (e.g., Dickens, 2011) or decomposition of soil organic carbon in circum-Arctic and Antarctic terrestrial permafrost, as proposed by DeConto et al. (2012). The environmental (thus isotopic) expression of the Dan-C2 event may have differed from that of typical hyperthermals, because a release of carbon compounds occurred at a time when the global carbon cycle functioned very differently than later in the Paleogene (e.g., Barnet et al., 2019), due to its major disruption by the loss of functional pelagic calcifiers. This extinction changed the oceans from a so-called 'Cretan' state of low saturation dominated by biogenic pelagic CaCO₃ precipitation, back to a 'Neritan' state of indefinite saturation with only
shallow-water biogenic CaCO₃ precipitation (Zeebe and Westbroek, 2003; Ridgwell, 2005; Ridgwell and Zeebe, 2005). If the oceans were carbonate-oversaturated at the time of Dan-C2 because pelagic calcifiers had not fully recovered from the K/Pg extinction, even a large CO₂ release (from the Deccan Traps, e.g., Henehan et al., 2019; Hull et al., 2020, or another source releasing carbon at orbital periodicity) may not have had a major effect on deep-sea carbonate saturation.

Dan-C2 represents a carbon cycle perturbation at the same orbital configuration as Paleogene hyperthermals, but we think that it cannot be considered a true hyperthermal event because it was not global in extent, there was no deep-sea warming or carbonate dissolution, and a lack of response in deep-sea benthic foraminifera. Therefore, we suggest that Dan-C2 for now should be considered as an eccentricity-linked carbon cycle disturbance (ELCD). Possibly, negative excursions in planktic and bulk δ¹⁸O do not indicate surface warming, because they can have been affected by differences in diagenesis during and outside the event, or by changes in surface ocean salinity, e.g., due to alterations in the evaporation/precipitation balance. We thus need to confirm whether there was surface ocean warming during Dan-C2, and if so, how much, using independent temperature proxies such as Mg/Ca in carbonate or organic biomarker-derived proxies. Alternatively, the nature of the Dan-C2 event was modified because of its occurrence in a world in which the oceanic carbon cycle was affected by a lack of abundant oceanic calcifiers.

6. Conclusions

Analysis of benthic foraminifera at Walvis Ridge ODP Site 1262 (SE Atlantic) reveals unstable environmental deep-sea floor conditions during the early Paleogene, probably related to changes in calcareous and non-calcifying primary producers as a long–term effect of the K/Pg mass extinction, potentially affected by CO₂-release from continuing Deccan volcanism. Such volcanic activity could have affected sea-surface biota which had not yet
recovered from the K/Pg extinction. We suggest that these changes triggered variability in
the quantity, stability and type of food arriving at the seafloor. Benthic foraminiferal
assemblages indicate a gradual improvement in trophic conditions towards the upper part
of the studied interval: environmental stress was most significant up to ~117 kyr after the
K/Pg (215.81 mcd), when assemblages were dominated by species from cluster A1,
followed by less perturbed conditions (dominance of cluster B1; up to ~368 kyr after the
K/Pg; 214.95 mcd), and finally stabilization of the food supply at ~65.633 Ma (~389 kyr
after the K/Pg; 214.87 mcd).

The Dan-C2 event, an eccentricity-linked carbon cycle disturbance, cannot be
considered as a hyperthermal event because of the lack of bottom water warming, a lack of
evidence of surface water warming on a global scale, a lack of evidence for widespread deep-
sea dissolution, and a lack of significant changes in benthic foraminiferal assemblages. More
evidence is needed, however, to define how widespread surface warming was. We agree
with earlier suggestions that Dan-C2, though it occurred at a similar orbital configuration
as later hyperthermals, may have had a very different expression (isotopically and
environmentally) because of the fundamentally different carbonate saturation state of the
oceans caused by long-term effects of the mass extinction of pelagic calcifiers at the K/Pg
boundary.

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References


Supplementary material captions:

Figure S1. Correlation plots and regression lines between %CaCO3 (Alegret et al, 2012) and distinct variables: relative abundance of agglutinated taxa (a), diversity index (b),
heterogeneity index (c), as well as percentages of polymorphinids (d), unilocular taxa (e), uniserial lagenids (f), and stilostomellids (g).

Table S1. Quantitative data of benthic foraminifera and MAR$_{bulk}$ data from ODP Site 1262.

Table S2. Taxonomic list and original references of common benthic foraminiferal species at ODP Site 1262 in the lower Paleocene.