# Strategies in times of crisis – insights into the benthic foraminiferal record of the PETM

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Strategies in times of crisis – insights into the benthic foraminiferal record of the Paleocene Eocene Thermal Maximum

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Summary

Climate change is predicted to alter temperature, carbonate chemistry, and oxygen availability in the oceans, which will affect individuals, populations and ecosystems. We use the fossil record of benthic foraminifers to assess developmental impacts in response to environmental changes during the Paleocene Eocene Thermal Maximum (PETM). Using an unprecedented number of µ-Computer Tomography scans, we determine size of the proloculus (first chamber), number of chambers, and final size of two benthic foraminiferal species which survived the extinction at Sites 690 (Atlantic sector, Southern Ocean, paleodepth 1900m), 1210 (central equatorial Pacific, paleodepth 2100m), and 1135 (Indian Ocean sector, Southern Ocean, 600-1000m). The population at shallowest Site 1135 does not show a clear response to the PETM, whereas those at the other sites record reductions in diameter or proloculus size. Temperature was similar at all sites, thus not likely the reason for differences between sites. At Site 1210, small size coincided with higher chamber numbers during

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the peak event, and may have been caused by a combination of low carbonate ion concentrations and low food supply. Dwarfing at Site 690 occurred at lower chamber numbers, and may have been caused by decreasing carbonate saturation at sufficient food levels to reproduce. Proloculus size varied strongly between sites and through time, suggesting a large influence of environment on both microspheric and megalospheric forms without clear bimodality. The effect of the environmental changes during the PETM was more pronounced at deeper sites, possibly implicating carbonate saturation.

Introduction

The anthropogenic increase in atmospheric pCO$_2$ impacts the physical, chemical and biological properties of the ocean [1]. In high end scenarios, the rise in CO$_2$ is modelled to result in a further increase of global mean surface temperatures by 2.6 to 4.8°C [2], and a lowering of the pH by an additional 0.3 to 0.4 units by 2100 [3]. At depth, warming is projected to be largest in the Southern Ocean [2]. Changes in these environmental parameters are projected to impact marine species, as well as interaction with their environment and with other species [e.g., 1, 4]. Warming directly affects species by increasing the rate of metabolic processes such as feeding and growth, which are, however, limited by food availability. Species which cannot regulate their temperature may be more strongly impacted [5], though they show a wide range of species-specific responses [5]. The response to ocean acidification includes reduced fertilization, decreases in larval and adult growth rates, reduced calcification, and increased mortality [1]. However, some species are able to up-regulate their internal pH as adults, and may continue to grow [6]. Even during acidification, high food availability may provide sufficient energy to sustain physiological processes in juvenile bivalves [7], but the effects of multiple impactors need further studies.

Environmental factors influence an organism through developmental plasticity, thereby providing a target on which evolution can act to produce novel, potentially adaptive, phenotypes [8]. Multigenerational experiments

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assessing the potential for acclimatization [9, 10] suggest that adaptive evolution can help to maintain physiological processes otherwise strongly impacted by climate change. Such adaptation could facilitate survival during rapid climate change. Therefore, it is paramount to not just determine the effects of environmental change on the morphology of adult individuals, but across ontogeny.

The fossil record documents natural climate change and variability as well as preserving some species exposed to these environmental changes [11]. The Paleocene-Eocene Thermal Maximum (PETM), 56 Ma, is the best studied hyperthermal event in the geological record, with significant warming over a few thousand years [12], global changes in carbonate chemistry [13, 14], a reduction of oxygen concentrations in the oceans [15], in surface and deep waters [16] and resulting biotic responses [17, 18]. Foraminifers have an excellent ocean-wide distribution and preservation potential making it possible to quantify the impact of climate change in the geological record. Benthic foraminifers live in the dark, cold, deep ocean, at comparably stable physical environmental conditions, and, like metazoans in the same environment [19], display a high species diversity [20]. The impact of climate change on benthic deep-sea organisms is significantly less well understood than is the case for shallow water organisms, mainly due to the difficulties in collecting them from their habitat and successfully culturing them, where necessary at in situ pressures [21]. Traditionally, impacts of climate change in the fossil record have been assessed in terms of relative or absolute abundance of species, and their origination and extinction. Such data show that the PETM resulted in a significant extinction of benthic foraminifera [21] and a transient faunal turnover [25], as well as migration to higher latitudes in planktic species [22, 23]. Experimentally, it has been shown that foraminifers are able to control their calcification [24] and, using novel tomographic methodologies [25], unexpectedly increased calcification during the PETM at least at some locations [26].

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Many foraminifers grow by sequentially adding chambers and hence preserve their entire ontogeny in their morphology [27], which can be revealed by tomography [28, 29], a technique using X-rays to reveal internal features of objects. Some benthic foraminifers can alternate between sexual and asexual reproduction, as recorded in the size of the first chamber (proloculus) [30]: the asexually produced, haploid generation generally has a large proloculus and is called megalospheric, whereas the sexually produced diploid generation usually has a smaller proloculus and is called microspheric [31]. Little is known to date about morphological plasticity within the megalospheric and microspheric stages, and the potential link to environmental variability. Body size is a central feature of all organisms, reflecting their physiology, ecology and evolutionary history [32] including metabolism, respiration, calcification and - in the case of foraminifers - number of offspring, which is related to terminal size [33, 34]. In some deep-sea environments, foraminifera have a short life span (<1 year) because seasonal food flux triggers rapid reproduction, whereas species which do not access the fluctuating food supply have a life cycle of > 2 years [35].

Here we use 3-dimensional micro-CT imaging to collect information on proloculus size, number of chambers and final size of two species of benthic foraminifera which survived the extinction at the PETM, at three locations, to quantify response by benthic foraminifers to the climatic and environmental perturbation. Based on our understanding of climate change impacts, competing stressors can impact growth in foraminifers. For example, dwarfing is common physiological response to environmental stress (e.g., low oxygen, low carbonate saturation [36]). Alternatively, changes in development caused by delayed reproduction in challenging environments have been suggested to lead to larger individuals with more chambers [37]. Increased stress should favour sexual reproduction, but it is not clear whether this leads to earlier maturity and fewer chambers, or if indeed size and number of chambers are related at all.
Materials and Methods

2.1 Materials

Samples from three Ocean Drilling Program (ODP) sites were analysed to compare trends across the PETM in different environmental settings (Figure 1). Site 690 (Maud Rise) is in the Atlantic sector of the Southern Ocean, at a palaeodepth of 1900 m [38], Site 1210 (Shatsky Rise) in the central equatorial Pacific at a palaeodepth of 2100 m, Site 1209 at a palaeodepth of ~1900 m [39] and Site 1135 (Kerguelen Plateau) in the Indian Ocean sector of the Southern Ocean at a palaeodepth of 600-1000 m (Thomas, unpubl.). The age model for Site 690 follows Röhl et al. [40], for Site 1135 Jiang & Wise [41], for 1210 Westerhold et al. [42] and 1209 [43]. Samples were chosen relative to the Carbon Isotope Excursion (CIE) to represent Pre-CIE (before PETM), Core-CIE, Recovery, and Post-CIE (after PETM), influenced by the availability of benthic species, which is affected by the extinction event. At Site 690, Nuttallides truempyi is absent in the lowermost peak CIE.

Carbon isotopes for site 1135 were measured at the University of California Santa Cruz SIL facilities. From all samples, 10-15 Nuttallides truempyi specimens were measured. All values are reported relative to the VPDB standard. Analytical precision based on replicate analyses of in-house standard Carrara Marble and NBS-19 averages 0.04% (1s) for $\delta^{13}$C and 0.07% (1s) for $\delta^{18}$O. Carbon isotopes for 1210 are from [39] and for Site 690 from [38].

2.2 Environmental background and model information

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Bottom water temperatures at all sites were comparable before the CIE, with similar warming in response to the carbon injection [44-46]. Paleo-productivity is notoriously difficult to quantify, but in general lowered productivity is expected in more stratified waters (preventing nutrient upwelling) during warmer climates [47]. Barium accumulation data are interpreted as indicating that export production was low at all our locations, with the lowest values in the Pacific gyre [48], and higher values in the Southern Ocean [52]. The data also suggest that export production increased at 690 during the CIE, but did not change in the Pacific gyre. The data on Ba accumulation, however, reflect not directly primary productivity, but remineralization at deeper levels [48]. Remineralization is projected to increase at higher temperatures, even at constant productivity [49, 50]. The general picture was corroborated by a recent review of combined data and modelling results [15], which suggested increased oligotrophy at Shatsky Rise, and generally oligotrophic conditions but with short-term increases in the food supply at the onset of the CIE for the Southern Ocean Sites.

Based on redox sensitive elements in the sediments, Kerguelen Plateau may have seen suboxic conditions during the PETM [51, 52] whereas at Site 690 suboxic conditions may have appeared 90-140kyrs after the onset of the CIE [51, 53]. The information for Shatsky Rise is ambiguous, with trace elements suggesting oxic conditions throughout [51]. There are no direct measurements of carbonate ion changes in the deep ocean published to date. Surface ocean pH reconstructions based on boron isotopes in the South [14] and North [54] Atlantic suggest changes around 0.3 pH units. Modelled changes in carbonate saturation in the deep ocean strongly depend on the rate and amount of carbon input [13], and suggest a global average pH change in the deep ocean below 2 km of 0.25 pH units.

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To provide a larger granularity we used cGENIE to estimate environmental change (Table 1, Figure 2). The model parameterisation and details of the model are as in Gutjahr et al. [54]. We used the early Eocene configuration [55] with the terrestrial weathering feedback. The time points are from the very start of the onset and peak $\delta^{13}C$ minimum time at 30 kyrs after the onset of the CIE. We first spun up the model under late Paleocene boundary conditions, choosing an open-system run time of 200 kyr in order to bring the $\delta^{13}C$ cycle into balance. The model temperatures and warming agree well with the proxy data. Carbonate ion concentrations at the onset and peak of the CIE are low and close to undersaturation at all sites, but especially Site 1210.

2.3 µ-Computer Tomography (µCT)

In total, we scanned and analysed 387 specimens. We focused on two species: the extant shallow-infaunal [45, 56, 57] Oridorsalis umbonatus and the extinct, probably epifaunal Nuttallides truempyi. The latter's descendent N. umbonifera lives epifaunally, and is adapted to deep-water environments with carbonate undersaturation [58] and highly oligotrophic conditions [59], thus is common at great depths. All N. truempyi and Oridorsalis umbonatus were picked form the >63 residue of the sample of each time slice, with the majority containing >10 individuals (min 6 to max 31 individuals). For some specimen, overall size or even chamber number could be determined, but measuring proloculus size was impossible due to internal dissolution. O. umbonatus was much less common in the studied samples (except for Site 1135), and specimens were commonly not sufficiently well preserved to determine the chamber number (or proloculus size) reliably at Site 1210.
The specimens were scanned using a Nikon XT H 225 ST CT scanner at 120kV, a 58µA current and an exposure time of 0.5s. Each scan project consisted of 3141 projections resulting in between 300 and 800 images (voxel size of 2.31 μm), which encompassed all the foraminifera of a single time slice. Slice data from the scans were imported into the 3D visualization software Avizo (Mercury Computer Systems Ltd, Chelmsford, MA, USA, www.tgs.com) to allow investigation of the internal features. As pixels are assigned a grey-scale value to represent the different X-ray attenuation properties of the materials making up the sample, the calcite test of the foraminiferal specimens could be isolated from the mount and any residual sediment infilling.

Final test diameter, number of chambers, and size of proloculus were measured for individual specimens following Foster et al. [26], in samples from before the CIE, in the core of the CIE, in the recovery interval and after the CIE (Table 2).

Results

Chamber number

Chamber numbers for *N. truempyi* are highly variable in all samples, though the averages in the populations are surprisingly stable (Table 2), ranging at Site 1135 from 19 to 23 with an average of 22; at Site 1210 between 20 to 25 with an average of 22; and at Site 690 19 to 23, with an average of 21 (Figure 3a). At the latter site, the population contains some specimen with fewer chambers (minimum 13). There is no clear trend in the number of chambers associated with the core CIE: chamber number increases at Site 1210, decreases at Site 690 (with trends starting in the sample prior to the CIE ~9kyrs) with a brief recovery followed by a second low, and shows no systematic change at the shallowest Site 1135. Average chamber number in the population of *O. umbonatus* ranges between 17 and 22.

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For N. truempyi, the ranges of test diameters are similar at all sites, from 192 to 474 µm with mean values highest at Site 1135 and lowest at Site 1210 (Figure 3b). Within the peak CIE, sizes at Sites 690 are lower than below or above the event with a reduction from 334 µm prior to the event to 222 µm 39.4 krys below the CIE; note that the size starts to decrease in the sample 9 kyrs before the large change in carbon isotopes. In contrast, at the shallower Site 1135 large sizes are present throughout.

Analogous to N. truempyi, O. umbonatus sizes are largest at the shallowest Site 1135 (mean of 348 µm with little variation) and smallest at Site 1210 (mean 278 µm, see SI). The average diameter in the population decreased by 100 µm at 1210, by 130 µm at 690 (see Table 2). These averages are based on very small specimen numbers and hence only informative.

Proloculus size

Average proloculus sizes for N. truempyi range from 150 µm³ to ~30,000 µm³ in all sites, which is equivalent to diameters of 7 to 40 µm. In a few specimens, the proloculus is larger (Figure SI1). At Site 1210, N. truempyi proloculus sizes are small below and in the peak CIE, with an increase 205kyrs after the event (Figure 3c). At Site 690, small values dominate. Populations at Site 1135 show the largest values below the onset of the CIE with a large drop within the CIE (Figure 3c). Above the CIE, the mean values for each population are within error of each other. None of the N. truempyi proloculus size distributions in any of the samples shows a clear bimodality which would allow a clear separation of microspheric and megalospheric forms (Figure 4).

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1. *O. umbonatus* proloculus are on average 2 to 3 times larger than those in *N. truempyi* (1183 µm$^3$ to ~76,000 µm$^3$ equivalent to 40 – 60 µm diameter), with a clear bimodality in before the CIE at Site 1135 (Figure 4).

Unfortunately, we lack data for this species due to dissolution.

Relationship between size, diameter

One might expect that a larger number of chambers leads to larger size, but the number of chambers is not necessarily a good predictor of the final size in any of the assessed populations, even within a species. Across all sites and time intervals mean proloculus size and final size chamber within the populations of *N. truempyi* are not significantly correlated, nor is chamber number and final size. In contrast, mean chamber number and proloculus size of *N. truempyi* are negatively correlated ($r^2 = 0.330$, $p = 0.008$).

In general, population proloculus size and diameter are statistically positively correlated, as small specimens have a small proloculus whereas large specimens have a proloculus volume above 10000 µm$^3$. At Site 1135, a large chamber number results in a large final diameter, though the statistical relationship is not significant due to the small number of specimens. The relation between number of chambers and final diameter appears more strongly controlled for specimens of both species below 250 µm (Figure 5). Above 250 µm, a wide range of final sizes can be found at similar chamber numbers, and the same final size can be reached with 15 or 26 chambers, for example. This is also the case for *N. truempyi* at Site 1210, whereas there is no clear trend at Site 690. The growth trajectories (chambers vs size, Figure 5) with time for *N. truempyi* are indistinguishable for all sites. *O. umbonatus* at Site 1135 adds fewer chambers (Figure SI3) than *N. truempyi* to reach the same size in the core CIE and the recovery, but not in the post CIE.

Discussion

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The main response in morphology during ontogeny of these benthic foraminiferal populations to the environmental changes at the PETM are 1) dwarfing during peak CIE at Site 690 to values as low as Site 1210, 2) site specific decreases (690), increases (1210) or no directional changes in chamber number associated with peak CIE, 3) low proloculus values at Sites 690 and 1210 at peak CIE, associated with a large variability, but no bimodality in the size distribution of the proloculus, and a 4) lack of relationship between size of the first chamber, number of chambers and final size of the organism across sites and time.

Size is the product of life history of a specimen, including factors such as growth rate (at specific food supply), reproduction and death [60]. Amongst the physiological factors are metabolic processes such as respiration, ingestion or resistance to starvation, allocation of energy to growth, reproduction or maintenance. As such, dwarfing in benthic foraminifers can be an ecophenotypic response to changes in temperature, oxygen, carbonate ion and food [36]. Within the food web, predator – prey relationships, such as the ability to gather and process prey become important [61].

Both the absolute temperature and the warming associated with the PETM was similar at our three study sites (Figure 2), thus warming per se is an unlikely cause for the dwarfism seen at the two deeper sites, but not at the shallowest Site 1135. Increased temperatures lead to an increase in food demand, to support the higher metabolic rates. Food probably was most limited in the Pacific gyre (Site 1210), where sizes were already small before the CIE, and where some authors suggested (though not quantified) dwarfing in other benthic foraminiferal species than the ones we investigated [39]. This ‘dwarfing’ was largely due to increased abundance of small taxa, not of size changes within survivor taxa. The temporal record of export production for Site 690 suggest enhanced remineralization as seen, for example, in the Ba-accumulation rate [48] up to 60kyrs after the onset of the CIE [62], but we do not know whether primary productivity changed, thus whether Phil. Trans. R. Soc. A.
more or less food reached the benthos. The reduction of size at this site can be interpreted as resource
limitation. Small specimens need fewer resources, thus can survive on a smaller amount of food during
environmental perturbations impacting food supply. On the other hand, larger size in foraminifers has also
been linked to food limitations, i.e., as individuals do not have enough food to reproduce, they keep growing
[37]. At Site 1210, smaller test size is associated with more chambers (thus a slower rate of increase in test
volume if chamber formation occurred at a fixed rate) during the peak CIE, but with fewer chambers at Site
690. This observation indicates that the population at Site 1210 lived longer while growing more slowly, thus
resulting in small size. The other process leading to smaller adult size is accelerated reproduction under
optimal conditions (i.e. opportunistic behaviour) as e.g. seen in the short-lived phytodetritus-using living
species *Epistominella exigua* [e.g. 59, 63]. We would postulate that faster reproduction would lead to a smaller
number of chambers, as seen at Site 690. A more seasonal food supply (due to its high latitude thus seasonal
darkness), with a temporarily increased food supply resulting in more rapid growth would result in reproduction
at a smaller final test size [38]. Consequently, changes in foraminiferal body size can be the response to both
good environmental conditions and stress events.

In our model results, the location of Site 690 records the lowest oxygen concentrations of all investigated sites,
whereas values at 1135 and 1210 were high enough to make physiological responses unlikely. We therefore
postulate that the small test size at Site 1210 is a combination of low carbonate ion concentrations (Figure 2)
and low food supply, whereas at Site 690 low oxygen availability, possibly in combination with a low food
supply, could have resulted in physiological stress.

The tight relation between size and number of chambers in smaller specimens resembles developmental data
of planktic foraminifers, which show similar growth trajectories in earlier development, and an increase in
plasticity in specimens larger than 100 µm [64]. Increased morphological variability between juveniles and
adults has been also documented in other groups such as ammonites, as related to sexual dimorphism in the adult stage [65]. At small sizes, the surface area-to-volume ratio is higher than at larger sizes, facilitating nutrient uptake and diffusion of nutrients, oxygen and carbonate ions. Therefore, small size is preferential during times of reduced oxygen and carbonate ion availability, because of the lower metabolic requirements. The disadvantage of being small in specimens with asexual reproduction is the lower number of produced offspring. Benthic foraminifers can alternate between sexual and asexual reproduction, thus they could counteract the smaller cytoplasm volume at smaller size by increasing sexual reproduction, if sufficient energy would be available. The use of both reproductive styles would allow the population to respond to environmental conditions by optimising both energy use and number of offspring. Experiments in larger benthic foraminifers [66] suggest that homeostasis and growth, rather than reproduction, is favoured under stress conditions. Foraminifers mainly die at reproduction, thus continued growth without reproduction may lead to larger sizes. It is generally asserted that sexual reproduction is indicated by small proloculus sizes at large test diameter, asexual reproduction by large proloculus size, though there are no clear cut-off values for smaller benthic foraminifera in the literature. Analysis of proloculus sizes in *Uvigerina* species could not corroborate bimodality, but found a correlation between proloculus size and test size [67]. Absolute lower and upper boundaries for proloculus diameter in foraminifera are said to be 4 $\mu$m and 1 mm [68]. Given the potential of this method to assess reproductive strategies in the fossil record, it is astonishing how few quantitative data are available on a species level for smaller benthic foraminifera (in contrast to larger benthic foraminifera), and how little is known about environmental drivers of plasticity in both modes of reproduction.
Unexpected outcomes of our study on proloculus sizes are the lack of clear separation between microspheric and megalospheric populations, and the large plasticity in size across the spectrum (see SI1) making our interpretation speculative. The data from the populations at the three sites show different proloculus size changes. Sexual reproduction appears to be favoured at Sites 1210 up to 63kyrs after the CIE and 690, whereas Site 1135 shows a wide range of proloculus sizes. During the recovery phase of the CIE both modes of reproduction may have been used at Sites 1210 and 690.

The increased complexity of sexual reproduction imposes inherent costs: mates have to be found at low standing stocks, special cell types formed, and diploid genomes maintained [69]. In asexual reproduction, every individual has one parent, thus there is no genetic exchange, so that there can be no selection against deleterious mutations [70]. Foraminifers could rapidly change to obligate asexual reproduction if there were no advantage of sexual reproduction. Kondrashov [70] suggested that there is an evolutionary advantage to sexual reproduction in response to ecological changes, by maintaining a better genotype-environment match than possible with asexual reproduction; planktonic foraminifera are escribed as obligate sexual reproducers [71]. The cost-benefit ratio of sexual vs asexual reproduction may differ radically in different circumstances; for instance, in microorganisms, massive population sizes might be sufficient to avoid the irreversible accumulation of deleterious mutations [72]. The ecological stress, low food, warming, low oxygen and carbonate ion (Figure 2) during the PETM might have limited the energy available for sexual reproduction at Sites 1210 and 690, thereby increasing the relative proportion of asexual reproduction. In addition, the higher production of offspring by asexual reproduction might be beneficial in seasonal habitats such as the Southern Ocean.

In some samples, two modes of size distribution are tentatively identifiable, but the large range in size, most clearly at Site 1135, suggests that other factors than reproductive mode influence proloculus size. Proloculus
size has been linked to environmental factors, e.g., a large proloculus at organic pollution (i.e. high food supply) [73], optimal growth and high food availability [74], and temperature and salinity [75, 76]. As such, an extensive study of the plasticity of proloculus sizes in modern foraminifers would be timely.

Conclusions

Our analysis of final size, number of chamber and size of the proloculus of deep-sea benthic foraminifera at three sites show a highly variable response of morphology to the environmental changes across the PETM. The population at shallowest Site 1135 does not show a directional response to the environmental impacts of the PETM, whereas the two other sites record reductions in proloculus size, and at 690 in overall diameter. Some populations suggest resource limitations, at least seasonally, resulting in small sizes. The driver of this change was not temperature *per se*, nor the increase in temperature, as these were the same at all three Sites. We speculate that it was driven by a site-specific combination of food limitations and oxygen changes.

Proloculus sizes vary strongly between sites and through time, suggesting a large influence of environment on both microspheric and megalospheric forms without clear bimodality.

Additional Information

**Data Accessibility**

The datasets supporting this article have been uploaded onto the web portal www.pangaea.de

**Authors' Contributions**

DNS conceived and designed the study; DS and EA carried out the lab work; EA and DNS conducted the data analysis; AR carried out the modelling; DNS and ET interpreted the data and wrote the manuscript. All authors gave final approval for publication.

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Competing Interests
The author(s) declare that they have no competing interests.

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Tables

Table 1: Reconstructed environmental changes using cGENIE for bottom water conditions at each location representing start of the carbon isotope excursion (CIE) and below 30kyrs after the onset of the event. Dcarb is the carbonate ion concentration relative to saturation with positive values indicating locally saturated conditions.

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Table 2: Mean values and standard error (SE) for proloculus volume, number (#) of chambers and diameter for *Nuttalides truempyi* (NT) and *Oridorsalis umbonatus* (OU). Ages [kyrs] are relative to onset of CIE, see methods for references for the age models.

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Figure captions
Figure 1: Paleogeographic map of the locations of the study and the study site of Foster et al. [26]. Map generated using ODSN Paleomap http://www.odsn.de/odsn/services/paleomap/paleomap.html

Figure 2: Environmental reconstructions derived from cGENIE for bottom water conditions at each location. From top to bottom carbonate ion concentration [µmol/kg], carbonate ion concentration relative to saturation with positive values indicating locally saturated conditions, temperature [°C] and oxygen concentration [µmol/kg]. Left onset of the Carbon Isotope Excursion (CIE), right 30kyrs into the CIE.
Figure 3: Mean population values for number of chambers (top), final diameter (middle) and proloculus size. The error bars represent the SE of the mean. The carbon isotope excursion is for reference at the bottom. For references for the carbon isotopes see material and methods.

Figure 4: Histogram of proloculus distributions for Sites 690, 1210 and 1135 for *N. truempyi* (left) and *O. umbonatus* at Site 1135 (right). Note the difference in scale of the x axis.

Figure 5: Relationship between final adult diameter and number of chamber for *N. truempyi* for all time slices. Site 690 circles, Site 1135 x and Site 1210 crosses.
*Nuttallides truempyi*  

**ODP Site 690B**  

- Age rel to CIE [kyrs]  
- Diameter [µm]  
- Proloculus volume [mm³]  
- δ¹³C_benthic [‰]  

**ODP Site 1209/2010**  

- Age rel to CIE [kyrs]  
- Diameter [µm]  
- Proloculus volume [mm³]  
- δ¹³C_benthic [‰]  

**ODP Site 1135**  

- Age rel to CIE [kyrs]  
- Diameter [µm]  
- Proloculus volume [mm³]  
- δ¹³C_benthic [‰]  

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**Oridorsalis umbonatus**  

**ODP Site 1135**  

- Age rel to CIE [kyrs]  
- Diameter [µm]  
- Proloculus volume [mm³]  
- δ¹³C_benthic [‰]
Nuttallides truempyi

Site 690

Site 1210

Site 1135

Oridorsalis umbonatus

Site 1135

Proloculus volume [µm³]

Before CIE

After CIE

Recovery CIE

Peak CIE

Proloculus volume [µm³]