

Evidence of traits and faunal turnover in planktonic foraminifera during extreme climate: A biological Traits Analysis approach

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Abstract

The Palaeocene-Eocene Thermal Maximum (PETM) is a paleoclimatic event associated with massive radiation and the extinction of planktonic foraminifera. It is still unclear which planktonic foraminiferal attribute was responsible for its enormous turnover during the PETM event. It has been hypothesized that biotic interaction with the environment is driven by biological traits rather than faunal composition. This idea stimulated this research where a combination of faunal composition and biological traits of planktonic foraminifera from Ocean Drilling Program (ODP) Site 1265 (Walvis Ridge, SE Atlantic Ocean) were used to understand the planktonic foraminiferal attribute responsible for biotic turnover during the PETM. Our results show that the studied section cut across three planktonic foraminiferal (PF) zones namely *Morozovella valescoensis*, *Pseudohastigerina wilcoxensis*, and *Morozovella marginodentata* dated 54.5 – 55.5 Ma. The faunal occurrence showed high variability in abundance and diversity with the last appearance (local extinction) of nineteen (19) species and the first appearance of eight (8) species including *Globoturborotalita bassriverensis*. Statistical analyses showed that the faunal compositions of the recovered planktonic foraminifera differed across the three sections of the PETM. Multivariate analyses of the faunal and trait compositions suggest evidence of disturbance in planktonic foraminiferal ecology during the PETM. The key foraminiferal traits that increased in abundance during the extreme climate event were triangular/trapezoid chamber arrangement, muricate wall texture, presence of accessories like lip in the aperture, umbilical and extraumbilical apertures, perforations in the test wall, grazing and surface-dwelling habits. These traits are believed to characterize resilient types that enabled taxa to survive the PETM.

Keywords: Extreme climate; Extinction; Paleoclimate; Planktonic foraminifera; Traits

1. Introduction

With the rapid changes in global marine ecosystems resulting from anthropogenic interplay (e.g., excessive input of greenhouse gases; destruction of natural habitat; environmental pollution) and natural evolution, climate scientists have forecasted extreme climatic conditions for the next few millennia [1, 2]. The imminent extreme climate could lead to global mass extinction that will permanently alter the current climate system. To understand how this extreme climate will affect the oceans in the future and in particular one of the most important producers (foraminifera) in the marine ecosystem. This study has become necessary to investigate a similar paleoclimatic event known as the Palaeocene – Eocene Thermal Maximum (PETM) which is believed to be similar in magnitude and rate of greenhouse emission as present values. The PETM is a globally recognizable event that occurred 55 – 56 million years ago. The event is reported to have been caused by a massive injection of light carbon into the Earth's system [3] and coincided with

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eccentricity maxima [4]. The event is characterized by 2 - 3‰ carbon isotopic excursion (CIE), extensive acidification of the deep ocean that led to the burn down of existing calcite deposits in the ocean and a significant rise in the lysocline and carbon compensation depth (CCD) [5, 6]. The PETM also had a significant effect on marine ecosystem faunal turnover such as the massive extinction of benthonic foraminifera, diversification and migration of planktonic foraminifera [7].

Foraminifera are unicellular marine protozoans with calcareous shells usually subdivided into chambers. They are the most important calcifying zooplankton group [8] and provide crucial ecological functions in the oceans such as primary production, nutrient cycling, carbon sequestration, and a food source to numerous organisms in the higher trophic level of marine ecosystems. Foraminifera are divided into planktonic and benthonic taxa based on where they live in the water column. Benthonic foraminifera live either above (epifauna) or below (infauna) the sediment-water interface in water depths ranging from the intertidal zone to the deep ocean [9]. Planktonic foraminifera, which is the focus of the study, live in the euphotic zone while some live deeper down to approximately 2 km water depth in the oceans, during their lifetime [10]. The test of planktonic foraminifera are made of relatively globular chambers essential to buoyancy, which enables their distribution spatially and temporally across the water column [10].

Foraminifera are known to be very sensitive to the physio-chemical variability in the oceans. They tend to incorporate the physical and chemical signature of the seawater in which they have calcified their shells, thereby recording the prevailing environmental conditions. The chemical composition of foraminifera tests is used as a proxy for the interpretation of palaeoecological and palaeoclimatic conditions such as temperature, carbon saturation, salinity, palaeocirculation, oxygen concentration, and hydrodynamics during their lifetime [11,12, 13,14, 15, 16, 10]. The physiological makeup (traits) of foraminifera plays a huge role in the survival strategies they adopt while alive and has been demonstrated in fossil as well as modern species records to have a close relationship with environmental parameters [17].

Several palaeoecological studies have linked spatial and temporal variations in the ocean to the morphological stratification of foraminiferal ecosystems both at the pelagic and benthic zones [18, 19, 10]. In the modern oceans, the planktonic foraminifera found in the mixed layer of the surface water is dominated by rounded globular test, such as in Globigerinids with algal symbionts while the species found deeper below the thermocline are predominantly characterized by traits such as flattened discoidal, or conical forms representing Globorotalids morphologies with herbivorous feeding habits [20].

Traits are believed to have a stronger control on the organism's interaction within their ecological community than taxonomic composition. Foraminiferal traits are intrinsically linked to the ecological functions they perform in the ocean. For instance, test composition functions as a protective tool and is known to reduce biological, physical, and chemical stresses of foraminifera in their environment [21]. The test shape could also indicate ecological adaptation and preference by foraminifera. The arrangement of the test chambers and their shape could also indicate ecological stress. For instance, changes from sinistral to dextral or evolute to involute coiling in trochospiral tests have been related to changes in water temperature and bathymetry [22]. Elements of test microstructure such as the macro-ornamentation (e.g. spines or muricae) could also reflect the mode of living and adaptation to surrounding water conditions. Ornamentation in foraminifera plays a huge role in feeding, adaptation to extreme environmental conditions and movement as well as prey-predation relationship [23]. Pores in foraminifera are used for gas exchange, osmoregulation, intake and release of nutrients, and ecosymbiosis.

Because foraminifera play significant roles in the global carbon sequestration and food supply, it is important to understand their feedback to past climatic extremes. The response of foraminifera to past climatic changes will provide useful clues to the current and future climatic changes. To achieve this aim, we have selected a suitable location in the southeastern Atlantic Ocean drilled during the ODP campaign, Leg 208 site 1265 (Figure 1). This Site is located at an upper bathyal water depth of 3,083m [24] in a broad channel at the base of the westward trending slope of the Walvis Ridge. The channel contains a thick sequence of Palaeogene to Neogene sedimentary deposits and the section analyzed is composed of foraminifer-bearing nannofossil oozes with red clay layer recording the main CIE interval. ODP Leg 208 was the first site to recover an intact and undisturbed continuous sequence of Palaeocene – Eocene (P/E) boundary in the deep-sea drilling because of the drilling strategy that adopted advanced piston corer (APC) techniques. However, there was a poor recovery of the lower part of the PETM at site 1265A [24].

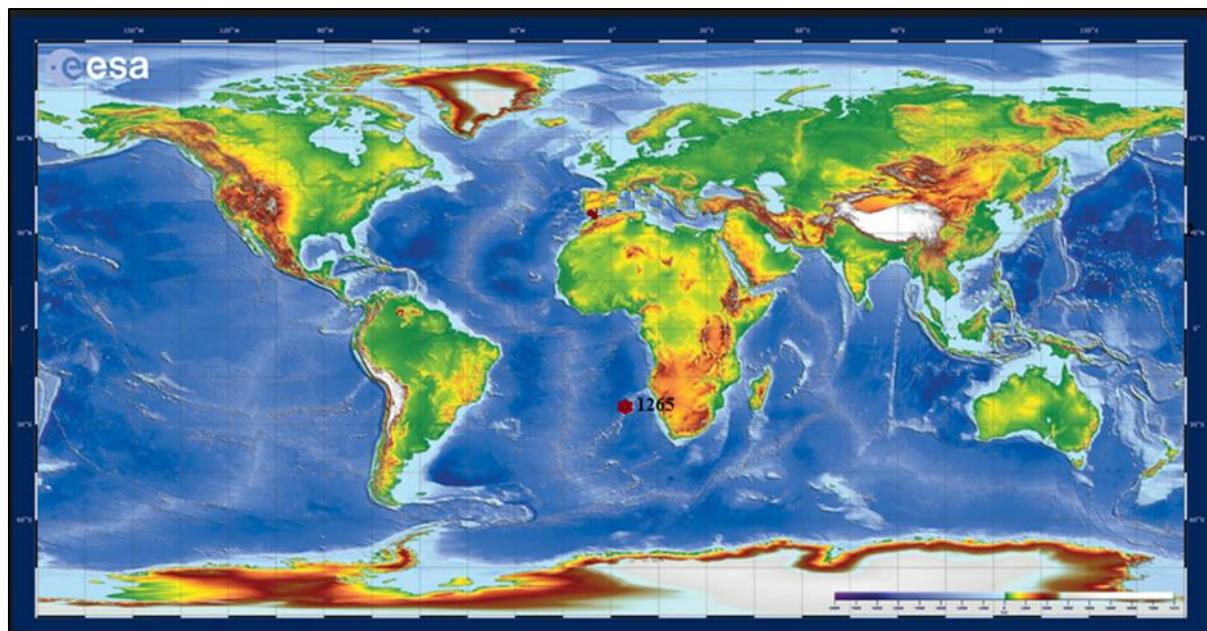


Figure 1 The site location of the study area as modified from the European Space Agency map archive

The objective of this paper is to investigate changes in faunal and trait composition across the PETM at ODP site 1265A using a procedure known as the Biological trait analysis (BTA) that allows the traits of organisms to be quantified. Here we generate foraminiferal population and trait data across the late Palaeocene-early Eocene section at ODP Site 1265A to examine the planktonic foraminiferal assemblages and trait composition across the hyperthermal event in the site. Use the data to understand foraminiferal sensitivity to extreme climatic conditions and integrate the planktonic faunal assemblage and trait compositions to interpret the ecological functioning of foraminifera in the SE Atlantic Ocean during the PETM.

The key focus of this research is to investigate the changes in trait and faunal composition of planktonic foraminifera during the Paleocene-Eocene Thermal Maximum (PETM) at ODP Site 1265 using the biological trait analysis (BTA); a technique that allows traits of organisms to be measured and quantified. The sediments used for this study were sampled from Hole 1265A of ODP Leg 208 at the Walvis Ridge in the South Atlantic Ocean.

The BTA was initially designed to study the impact of ecological disturbance in the terrestrial [25, 26, 27] and marine macrobenthic ecosystem [28, 29, 30, 31, 32, 33]. The technique tends to be good in detecting the impact of anthropogenic disturbance in these ecosystems. Biological trait analysis has also been applied in investigating the impact of extreme ecological conditions on the functioning of fossil macrobenthos in deep time. For instance, [34] applied the method in the study of the impact of hypoxia (low oxygen) in the ecological functioning of fossil macrobenthos (bivalve, mollusks, gastropods, brachiopods, and echinoderms) from the late Jurassic Kimmeridge Clay Formation in the Wessex Basin, United Kingdom. The results from this study showed that extreme climatic conditions could lead to a collapse of ecologic function in marine niches.

With results from previous studies using the BTA method, the authors deployed it in investigating the impact of the extreme PETM conditions on the traits and faunal composition of foraminifera (microfossil). The current method (BTA) has not been previously used in planktonic foraminiferal studies, also the taxonomic composition of Planktonic foraminifera during the PETM at Hole 1265A has not been previously studied, and this work documents this and investigates the impact of the hyperthermal event on their traits. The trait analysis is important because foraminifera interactions with other organisms in their community are driven by biological traits instead of faunal composition [35, 36].

2. Methodology

Thirty-five sediment samples from core depths 266.31 mbsf – 276.66 mbsf were selected at 5- 10 cm intervals and analyzed for foraminiferal abundance and distribution across the PETM section.

2.1. Foraminiferal Preparation

Foraminiferal sample preparation followed conventional protocols. Deep sea sediment samples from IODP were weighed using a weighing balance and were transferred into the 250ml glass beaker with sterilized water and soaked overnight in a fume cupboard. This is for the sediment to disaggregate and for the clays to be dissolved. The disaggregated sediments were washed with Endecotts stainless steel 63 μ sieve under running tap water. The recovered residues were transferred to a labelled filter paper placed in a funnel and dried in the laboratory oven. The dried residue was stored in vials for identification and counting.

2.1.1. Foraminiferal counting and identification

The recovered microfossils were sieved into three fractions, > 63 μ m (fine), > 125 μ m (medium), and > 250 μ m (coarse). Each size fraction was counted separately to prevent the larger microfossils from obstructing the smaller ones. Counting was done by sparingly spraying the microfossil on the observation tray. The observation tray is divided into forty –two equal-sized squares and 1-2 portions of microfossil-filled trays were counted for each sample by following systematically along a particular transect. Because the number of planktonic foraminifera in the sediment was large, over 1000 specimens were counted in one fraction. Counting the fine fraction (>63-125 μ) was useful because many species of *Chiloguembellina* and *Globanomalina*, which were scarce in the larger fraction were abundant in the fine fraction. Most of the taxa were identified at the species level using the systematic description and micrographs from [37, 38, 39, 40, 41] and other peer reviewed-publications cited herein.

2.2. Trait classification and analytical procedures

Biological trait analysis[BTA; 6, 34]) is the novel method used in this work. It uses multivariate ordination such as non-metric multi-dimensional scaling (nmMDS) and Similarity percentage analysis (SIMPER) to examine the patterns of biological trait composition across taxa assemblages(i.e. the types of trait present in assemblages and the relative frequency with which they occur). The approach was used to understand the dominant traits that sustained the planktonic foraminiferal species' existence or extinction in the Atlantic Ocean during the Palaeocene-Eocene thermal maximum. The planktonic foraminiferal traits such as composition, morphology, and life strategy were classified into thirteen biological characteristics based on ecological functions/ responses, and the availability of data on the traits. These foraminiferal traits were further classified into categories and referred to as modalities (Table 1). After categorizing the traits into modalities, the Fuzzy coding [42] technique was used in expressing the affinity of various species to the trait modalities using a scale of 0.0 – 1.0. The absence or no affinity of a particular trait in a species is denoted with 0 while 1 is used for a species that exhibited dominant/ high affinity to a trait (see supplementary data). This coding technique allows each species that exhibited more than one modality to be categorized according to their affinity to the trait under consideration, however, all the categories shall sum up to unity [34, 43]. The information on the biological traits was sourced from the biological database such as Mikrotax <https://www.mikrotax.org/pforams/>, WORMS – World Register of Marine Species: <http://www.marinespecies.org>, The Palaeobiology <http://palaeodb.org>; Fossilworks <http://fossilworks.org/> and published literature. The extensive review of these data sources as well as personal communications with experts in a range of taxa informed the choice of traits selected for this analysis.

Table 1 Foraminiferal traits and modalities used in Fuzzy coding

Traits	Modalities
A. Test Shape	A1. Spiral; A2. Elongate; A3. Globose; A4. Subquadrate; A5. Others
B. Test Composition	B1. Microgranular; B2. Hyaline calcite; B3. Hyaline aragonite; B4. Porcellanous; B5. Other
C. Chamber arrangement	C1. Uniserial; C2. Bi/Tri-serial; C3. Planispiral; C4. Trochospiral; C5. Other
D. Chamber shape	D1. Spherical/Oval; D2. Tubular; D3. Triangular or trapezoidal; D4. Semi-circular; D5. Others
E. Wall texture	E1. Depressed sutures; E2. Raised sutures; E3. Cancellate; E4. Muricate; E5. Spinose; E6 Smooth
F. Test micro-ornamentation	F1. No ornament; F2. Reticulate; F3. Limbate; F4. Striate; F5. Costae
G. Aperture form	G1. Oval/reniform; G2. Arcuate; G3. Radiate; G4. Slit-like

H. Aperture accessory structures	H1. Lips; H2. Bifid teeth; H3. Umbilical teeth; H4. Neck; H5. None
I. primary aperture position	I1. Terminal; I2. Basal interiomarginal; I3. Umbilical; I4. Extra-umbilical; I5. Areal
J. Test perforation	J1. Microperforation; J2. Fine perforation; J3. Macro-perforation; J4. No perforation
K. Life habit	K1. Surface dweller; K2. Intermediate dwellers; K3. Deep water dwellers; K4. Others
L. Feeding habit	L1. Grazer, L2; Suspension feeder; L3. Detrital feeder; L4. Symbiotic
M. Mobility	M1. Swimming; M2. Clinging; M3. Drifting; M4. Free-living

The frequency of each trait modality in the dataset was calculated by multiplying the category scores with the relative abundance of each species exhibiting those modalities. This was achieved by a simple matrix multiplication method [43, 44]. The result of this data treatment showed the relative abundance of all the biological traits recorded in all the species across the whole samples [6, 45].

Statistical analyses of both the species composition and biological trait datasets were performed with the software PRIMER ver. 6. [46]. All the counted foraminiferal taxa/traits were grouped into three PETM communities (Pre-CIE, CIE, and Recovery) according to their position in the sample relative to the hyperthermal based on $\delta^{13}\text{C}$ from [47].

The relative abundance of foraminiferal and trait similarities across the PETM was calculated using the Bray-Curtis index resemblance matrix. The resemblance data were transformed with $\text{Log}(x+1)$. A $\text{Log}(x+1)$ modified the relative abundance/traits of the species to reduce the influence of the dominant species on the data [46]. The taxa abundance data were standardized before any transformation (following the BTA procedure; [46]; however, trait data were not subjected to this procedure because it had been standardized during the fuzzy coding process [6, 34]. The transformed data were plotted with non-metric multidimensional scaling ordination (nmMDS) based on the Bray - Curtis similarity matrices [46]. The nmMDS is based on the rank similarities of samples and produced an ordination plot showing relative differences/ resemblance in biological trait or faunal composition across the PETM (see Figures 3 & 4).

To test for significant differences between various traits and faunal composition across the three PETM sections, analysis of similarity (ANOSIM) tests were performed on the data set. The similarity of percentages (SIMPER) analysis was also applied to the species abundance and biological traits to determine which species/traits accounted for the significant dissimilarities identified by the ANOSIM test.

3. Results

3.1. Planktonic foraminiferal distribution and changes through time

A total of 79,706 planktonic foraminifera specimens were counted from the core in Hole 1265A, across the PETM. These represent fifty-nine (59) species with Acarininidae, Morozovellidae, Subbotinidae, Chiloguembellinidae, and Globanomalinidae being the dominant taxa.

3.1.1. Planktonic foraminifera taxa across the Pre-CIE section

The faunal composition showed that the pre-CIE interval (276.66 - 275.19 mbsf; latest Palaeocene) was marked by the restricted occurrences of *Acarinina nitida*, *Acarinina strabocella*, *Chiloguembellina morsei*, *C. wilcoxensis*, *Globanomalina australiformis*, *G. compressa*, *G. pseudomenardii*, *Globanomalina planoconica*, *Morozovella pasionensis*, *M. velascoensis*, *M. angulata*, *Parasubbotina pseudobulloides*, *Parasubbotina varianta*, *Subbotina cancellata*, *Subbotina triangularis*, *S. triloculinooides* and *S. trivalis* (see Figure 3). The pre-CIE interval was characterized by high abundances of all the major taxa with relatively good preservation. The genera Acarinina, was the most abundant taxa in this interval; followed by Subbotina and Globanomalina, while Morozovella was the least abundant (Figure 3).

Table 2 Mean abundance of taxa dissimilarity between recovery and CIE (data was limited to 50% cumulative similarity)

Species	Foraminiferal mean abundance		Contribution to dissimilarity (%)
	REC	CIE	
<i>Morozovella spp.</i>	5.15	26.02	17.78
<i>Acarinina Spp</i>	1.28	12.27	8.50
<i>Chiloguembelina trinitatensis</i>	11.98	2.78	7.48
<i>Subbotina patagonica</i>	10.95	3.89	6.17
<i>Morozovella subbotinae</i>	10.58	5.09	6.10
<i>Globoturborotalita bassriverensis</i>	9.75	2.14	6.03

Table 3 Mean abundance of taxa dissimilarity between Recovery and Pre-CIE from Simper analysis.

Species	Foraminiferal mean abundance		Contribution to dissimilarity (%)
	REC	Pre CIE	
<i>Chiloguembelina trinitatensis</i>	11.98	2.93	7.72
<i>Globoturborotalita bassriverensis</i>	9.75	0.00	7.36
<i>Morozovellas ubbotinae</i>	10.58	2.78	6.18
<i>Subbotina Spp</i>	1.70	8.51	5.76
<i>Subbotina patagonica</i>	10.95	6.11	5.38
<i>Acarinina Spp</i>	1.28	7.71	5.13
<i>Acarinina interposita</i>	7.33	3.37	5.02
<i>Morozovella aequa</i>	0.00	6.25	4.72
<i>Chiloguembelina crinita</i>	6.10	3.73	3.97

Table 4 Mean abundance of taxa dissimilarity between pre-CIE and CIE from simper analysis.

Species	Foraminiferal mean abundance		Contribution to dissimilarity (%)
	CIE	Pre CIE	
<i>Morozovella spp.</i>	26.02	5.76	17.79
<i>Acarinina spp</i>	12.27	7.71	7.27
<i>Acarinina Soldadoensis</i>	14.58	6.71	6.46
<i>Subbotina Spp</i>	1.50	8.51	5.48
<i>Subbotina patagonica</i>	3.89	6.11	4.61
<i>Acarinina coalingensis</i>	2.86	6.84	4.34
<i>Acarinina nitida</i>	5.25	5.03	4.30

3.1.2. Planktonic foraminifera taxa across the CIE section

The CIE interval was marked by a significant reduction in the abundance and preservational quality of all the species present. The subbotinidae family (which included taxa like *Parasubbotina* and *Globoturborotalita*) decreased from 500,000 at the Pre-CIE to less than 100 at the CIE interval (foraminiferal abundance). Nineteen (19) planktonic foraminiferal species including *A. nitida*, *M. aequa*, *S. trivalis*, *G. chapmani*, *G. pseudomenardii*, *S. triangularis*, *S. cancellata*, *P. pseudobulloides*, *G. planoconica*, *M. occlusa*, *C. morsei*, *W. claytonensis*, *S. valescoensis*, *M. passionensis*, *S. triloculinoides*, *M. acuta*, *M. acutispira* and *A. strabocella* became locally extinct at Site 1265A (Figure 2). The First appearance of eight (8) taxa was recorded within the CIE interval (Figure 2). The interval was characterised by high abundances of *Morozovella acutispira*, *Morozovella aequa*, *Morozovella gracilis*, *Morozovella spp.*, *Acarinina spp.*, and *Subbotina spp.* No excursion taxa were recorded in the interval of main carbon isotopic excursion in this section as reported in the Pacific, Tethys, and continental seas[48, 49,12]. However, *Globoturborotalita bassriverensis* which has been reported as an excursion species in the PETM section of Bass River [51] made its first appearance at 275.19 mbsf. *Acarinina sibaiyaensis* widely reported as excursion taxon was found in the later part of the Recovery interval (Figure 2).

3.1.3. Foraminiferal Assemblages in the Recovery section

The Recovery interval occurs between 274.5–266.6 mbsf and is characterized by a remarkable increase in abundance of most species that survived the local extinction, e.g. *Acarinina soldadoensis*, *A. coalingensis*, *A. interposita*, *Chiloguembelina crinita*, *Chiloguembelina trinitatensis*, *Subbotina patagonica*, *Subbotina hornbrookii*, *Globoturborotalita bassriverensis*, and *Zeauvigerina spp.* (Figure 2). There is a significant increase in the abundance of *Morozovella* during the recovery stage of the PETM in this study, making it the most abundant taxon. The abundance of *Subbotina* and *Acarinina* species was relatively similar, while the genus *Chiloguembelina* replaced *Globanomalina* as the fourth most abundant taxon.

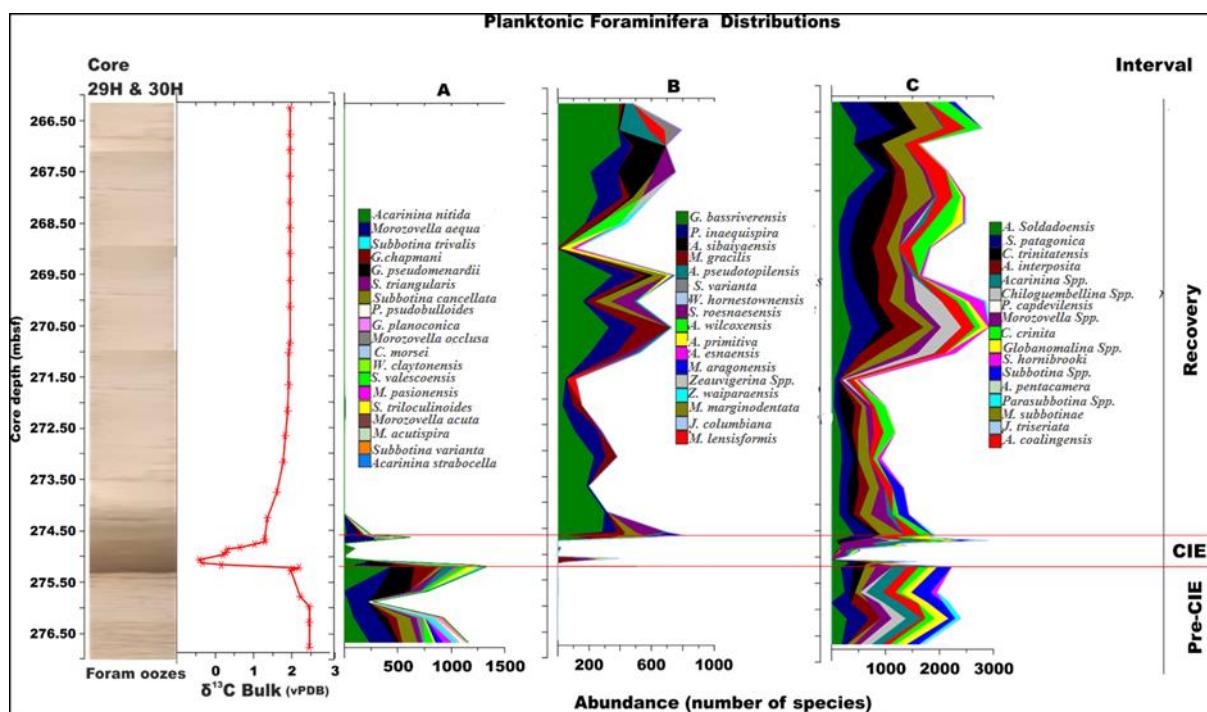


Figure 2 The distribution of planktonic foraminiferal species from core 29H and 30H (PETM interval) of Site 1265A. A - species that went extinct during or shortly after the CIE. B - Species that appeared during or after the CIE. C - Cosmopolitan species

The abundance and diversity of all the species were significantly affected by carbonate dissolution within the CIE interval. The bulk carbon isotope record and lithology were plotted with supplementary data from Zachos et al. [2005, 47].

3.1.4. Multivariate analyses

Based on the result from the ANOSIM, planktonic foraminiferal assemblage at Hole 1265A significantly differed between the Pre-CIE, CIE, and Recovery interval (global $R = 0.673, p < 0.01$), and the pairwise tests showed that all the three

intervals significantly differed from each other in terms of composition with $p<0.01$. The result also showed that each interval insignificantly differed from each other as follows: Recovery and CIE, $R= 0.632$ ($p< 0.01$); Recovery and Pre-CIE, $R= 0.918$, ($p< 0.02$); CIE and Pre-CIE ($R= 0.335$) ($p< 0.01$). The sample ordination during the pre-CIE was distinct and the Recovery samples were tightly grouped. However, the CIE was clearly different, because the grouping was more or less longitudinal, forming a transect between the Pre-CIE and the Recovery groups (Figure 3). The high dissimilarity ($R= 0.335$; $p< 0.01$) of planktonic foraminifera composition during the CIE suggests evidence of environmental disturbance (Figure 3) while the greater similarity ($R= 0.918, p< 0.01$) of the pre-CIE and the recovery imply a more stable ecosystem (Figure 3).

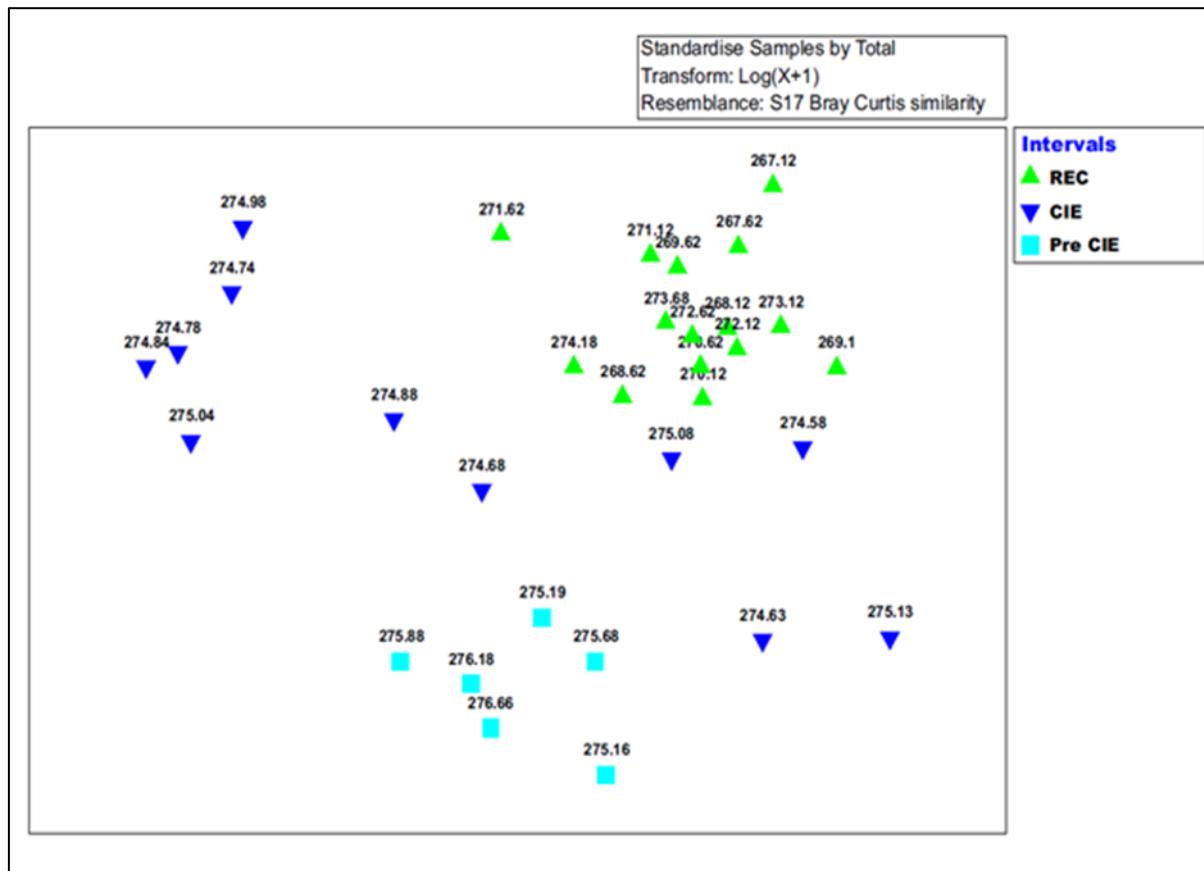


Figure 3 Non-Metric Multidimensional Scaling ordination of planktonic foraminiferal taxonomic composition (transformed with $\log x+1$) of Bray-Curtis similarity from Site 1265A

Similarity percentage routine (SIMPER) results showed that six(6) taxa contributed to 50% of the dissimilarity between the CIE and the recovery intervals, notably *Morozovella spp.* contributed about 17.78% of the dissimilarity being five-fold more abundant during the CIE. The high abundance of this taxon during the CIE was attributed to its increase during the PETM [52, 12]. Nevertheless, *Chiloguembelina trinitatensis*, *Subbotina patagonica*, *Morozovella subbotinae*, and *Globoturborotalita bassriverensis* were more in abundance (Table 2) during the Recovery interval than in the CIE interval.

Subbotina spp., *Acarinina spp.*, and *Morozovella Spp* were more abundant during the CIE interval than in the Recovery interval. The high abundance of *Subbotinaspp* and *Acarininaspp* during the CIE period (Tables 2 and 3) was due to the high level of dissolution witnessed within the interval. This made the identifications to species level difficult. *Chiloguembelina trinitatensis*, *C. Crinita*, *S. patagonica*, *M. subbotinae*, *G. bassriverensis*, and *A. interposita* maintained higher abundance during the recovery compared with during the CIE. *G. bassriverensis* appeared during the CIE. The absence of *M. aqua* at the same interval showed that the species went extinct before the Recovery period.

The dissimilarity between the CIE and pre-CIE indicated that *Morozovella spp.*, *Acarinina spp.*, *Acarinina soldadoensis*, and *Acarinina nitida* were more abundant during the CIE than during the Pre-CIE period. However, *Subbotina spp.*, *Subbotina patagonica*, and *Acarinina coalingensis* abundance were higher before the CIE event than in the main CIE

event. The abundance of *Subbotina* spp at the Pre-CIE interval indicated that the taxa test dissolution started before the CIE making the identification of the specimen to species level very difficult.

3.2. Planktonic foraminiferal trait composition and changes through time

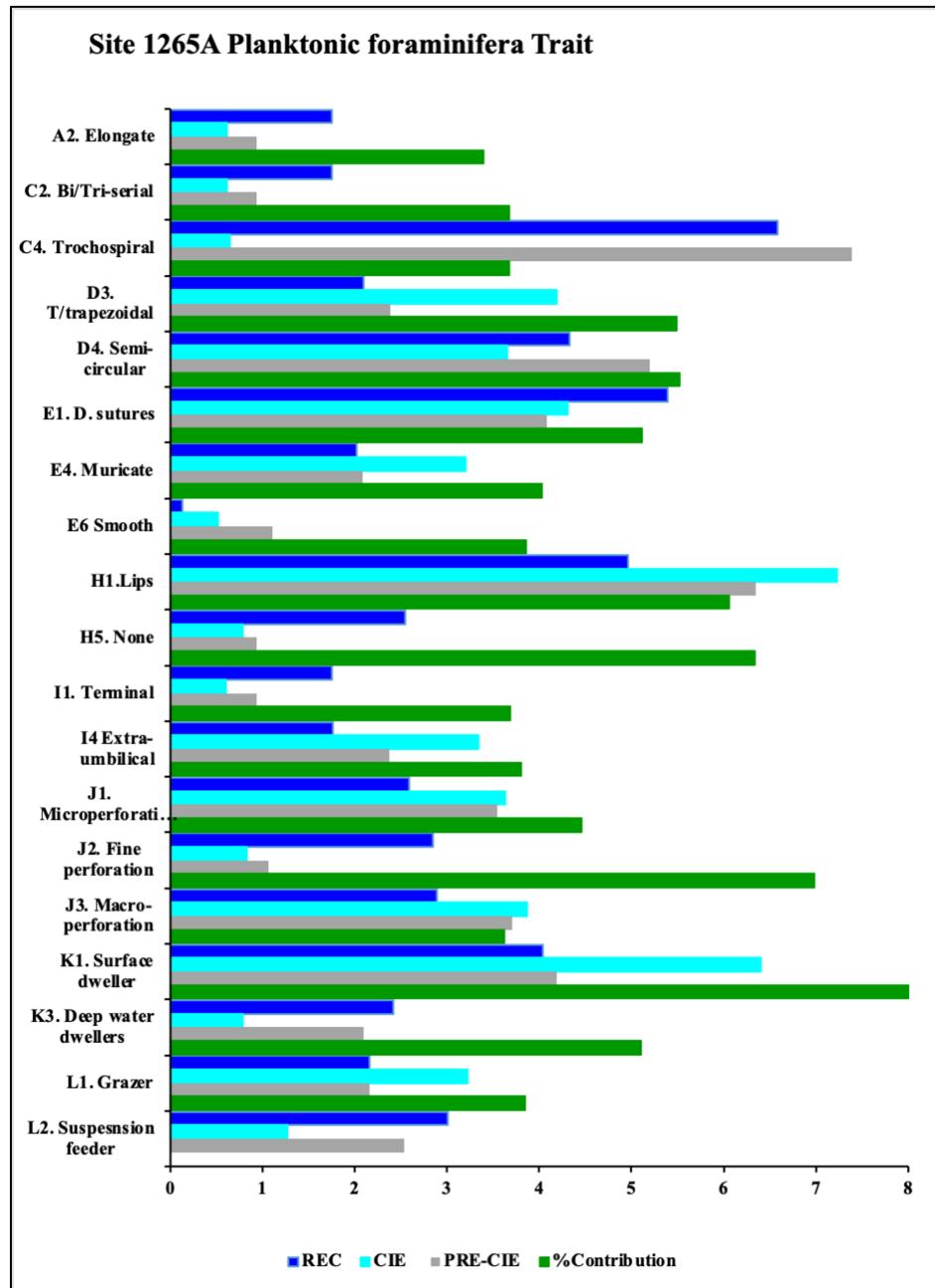


Figure 4 Mean abundance of planktonic foraminiferal traits driving the main differences in distribution across the PETM interval at Site 1265A (Data cut off 50%)

The result of statistical analysis indicated that taxa with smooth, trochospiral test and semi-circular chamber shape were higher at the Pre-CIE interval than at the main CIE and Recovery intervals (Figure 5). Taxa with muricae structures, triangular/trapezoidal chambers, micro- and macro-perforations, extra-umbilical apertures, surface-dwelling, and grazing habits were more abundant during the CIE than at the Pre-CIE and Recovery intervals. Whereas taxa with fine perforation, depressed sutures, elongate test, bi/triserial chambers, terminal aperture, no apertural accessories, deep-dwelling, and suspension feeding habit were more abundant during the Recovery than at the CIE and Pre-CIE intervals (Figure 4). The high abundance of the trochospiral chamber arrangement during the Pre-CIE period indicates that taxa such as *Acarinina*, *Morozovella*, *Subbotina*, and *Globanomalina* which are trochospiral in shape were predominant during this period. The high proportion of traits such as muricae, surface dwellers and triangular/trapezoid chamber, and

macro-perforation at the CIE interval is linked to the increase in the abundance of *Acarinina* and *Morozovella* taxa during the hyperthermal. Whereas the high preponderance of elongate, bi/triserial, terminal apertures, deep dwellers, and suspension feeding traits during the Recovery period is associated with the occurrence of *Chiloguembelina* species after the CIE.

The similarity of trait composition resulting from ANOSIM indicates that each of the three intervals slightly differ in terms of their trait composition at $R=0.45$ and $p<0.01$. The comparison of each interval with the other indicated that the Recovery interval significantly differed from the CIE at $R=0.564$; $p<0.01$; also, the Recovery interval significantly differed from the Pre-CIE at global $R=0.4$; $p<0.02$ signifying that the PETM significantly impacted on the trait composition of planktonic foraminifera across the studied intervals. However, there was a slight difference between the trait composition at the CIE and Pre-CIE with the $R = 0.206$ and $p>0.05$ (Figure 4).

The Non-metric Multidimensional Scaling (nmMDS) ordination of planktonic foraminiferal traits composition was entirely different from that of the faunal composition. Three groupings A, B, and C could be identified from the trait ordination (Figure 5).

Group A represented samples from the CIE interval, however some samples from the CIE interval such as samples 274.63, mbsf, 274.68 mbsf, 274.88 mbsf, and 275.00 plotted toward the field of the Pre-CIE interval (Figure 6). These samples mark periods that follow the initial perturbation when the organisms were trying to readjust to buffer the effect of the extreme climatic conditions. These species may be different from those of the CIE interval and closely related to the Pre-CIE species.

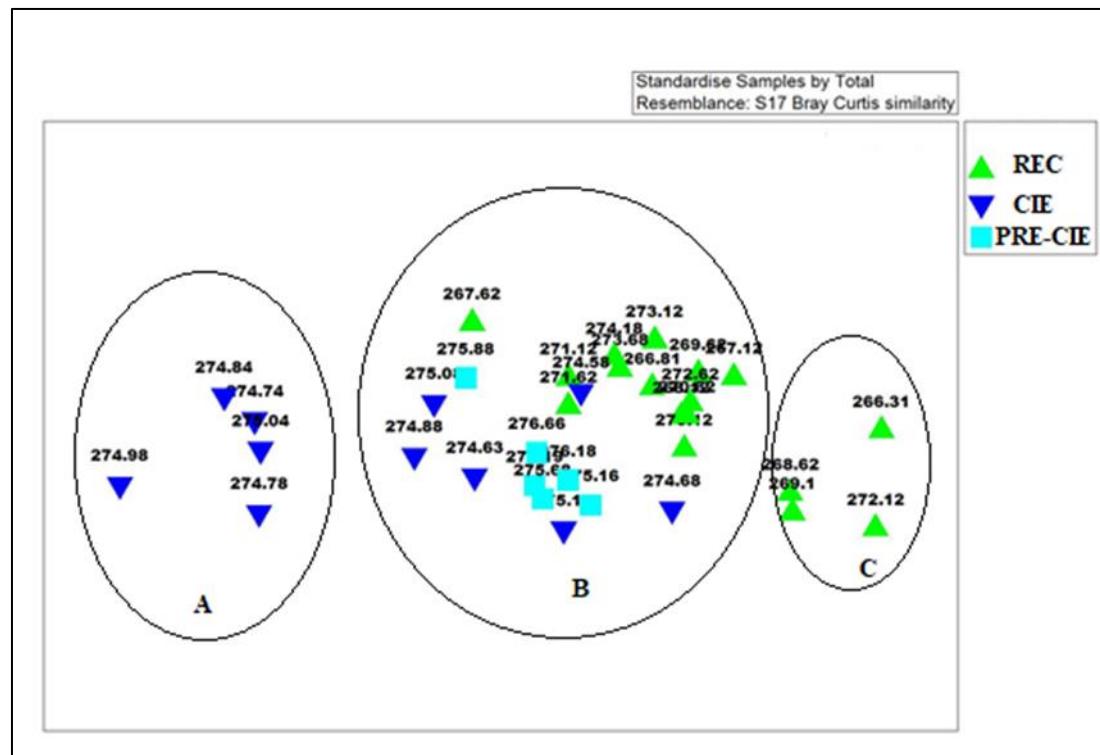


Figure 5 Non-metric Multidimensional Scaling ordination of planktonic foraminiferal trait composition from Site 1265A (transformed with total resemblance) of Bray-Curtis similarity indicating sample ordination across the CIE events

Samples 274.58 and 275.13 mbsf classified as CIE based on the $\delta^{13}\text{C}$, ordinated towards the Recovery species suggest that the traits were not affected by the change in the chemistry of the seawater. Alternatively, as the $\delta^{13}\text{C}$ was measured on the bulk carbonate, the record may have been affected by reworking or diagenesis.

Group B represents samples that are relatively less perturbed. Even though the samples came from different sections, nMDS classified them to be more similar than Groups A and C. This suggests that the extreme climatic conditions during the CIE had a significant impact on the trait composition of planktonic foraminifera.

Group C represents samples from the upper part of the Recovery interval. These samples suggest the onset of another warming event in the early Eocene such as Eocene Thermal Maximum - ETM 2 [1]. However, sufficient evidence is necessary to justify this claim.

Qualitatively, thirty-eight (38) trait modalities were identified in planktonic foraminifera identified. The trait composition indicates high variability from the Pre-CIE to the Recovery period (Figure 6). The trait distributions can be described as serrated, signifying the cyclical changes in palaeoecological conditions across the studied interval. The cyclical nature of the distribution of the traits suggests alternations of periods of rich supply of the needed ecological resources and conducive environment for the foraminifera to thrive and periods of ecological stress and resource scarcity. An overview of the trait distribution showed trait richness at the Pre-CIE as relatively high in diversity and stable except for spinose wall structure and circular/reniform apertures (Figure 6). The trait richness began to decrease in the later part of the Pre-CIE and early part of the CIE. The lowest trait abundance was recorded during the CIE period, while the highest trait diversity was recorded during the Recovery period. Most of the planktonic foraminiferal taxa (Figure 6) dropped to the minimum at the base of the CIE but later increased within the same interval.

In terms of individual traits, the most abundant modality in test shape was spiral, probably because all the three major planktonic taxa identified in Site 1265A were spirally coiled in the penultimate shells. Subquadrate and globose test shapes were equally high in abundance, while elongate test shapes were relatively low from the Pre-CIE till 271.0 mbsf, after which it increased remarkably.

All the identified planktonic foraminifera from the study site were composed of entirely hyaline calcite test based on the classification adopted for trait coding in this study. The collapse in trait richness in the planktonic at the beginning of the CIE was due to the carbonate dissolution that significantly reduced the faunal richness of the planktonic foraminifera during the period.

Chamber arrangement in planktonic traits recorded only two modalities with trochospiral constituting ~70% and bi/triserial (30%). The chamber shapes were predominantly semi-circular, triangular/trapezoid, spherical/oval, and a few tubular shapes in the order of decreasing abundance (Figure 7).

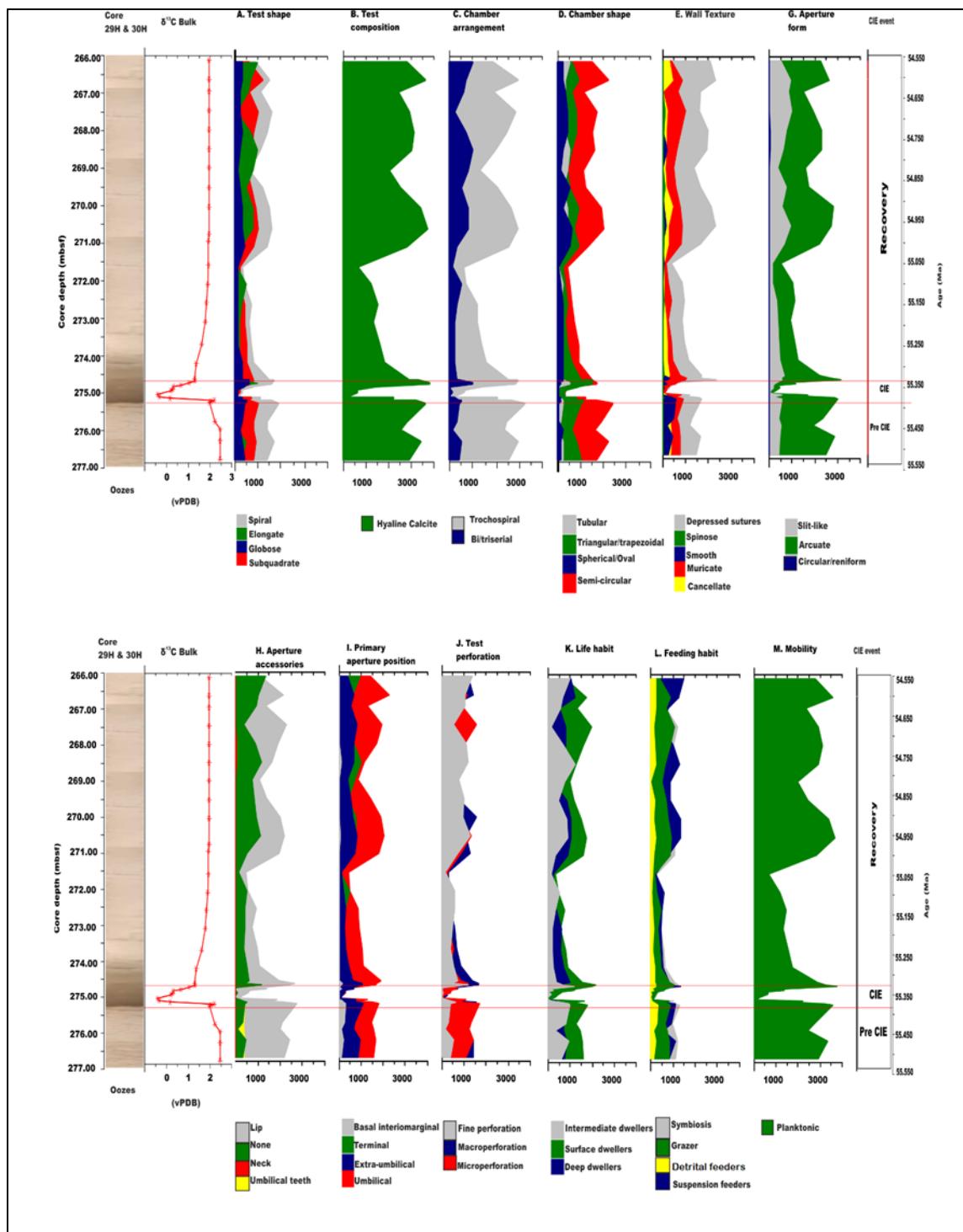
The wall texture of the recovered planktonic foraminifera was highly diverse. Depressed sutures were the most abundant; closely followed by muricate and much fewer cancellate structures. Taxa with smooth wall texture were common during the pre-CIE interval but disappeared after the CIE and occurred later at a few depths within the Recovery interval. Only an infinitesimal number of taxa with spinose wall texture was recorded across the studied section.

Aperture forms recorded approximately 70% arcuate and 28% slit-like apertures among the planktonic foraminifera. Circular/reniform apertures occurred in a very small number of foraminifera. The most abundant aperture accessories recorded were lip types. Umbilical teeth occurred sparingly across the studied section while the rest of the taxa lacked apertural accessories.

Umbilical - extra umbilical apertures recorded the highest abundance in terms of primary aperture positions over the interval studied. The abundance of terminal apertures was relatively moderate while basal interio-marginal aperture was the rarest and only occurred consistently before the CIE interval.

All the planktonic foraminifera identified in Site 1265 were perforated. Macro and micro perforation showed a similar trend across the studied interval. Fine perforations occurred in low abundance from Pre-CIE through the CIE intervals but increased during the Recovery period.

Surface dwellers were the most abundant planktonic foraminifera recovered in this study. This was followed by deep and intermediate water dwellers in decreasing order of abundance respectively. The highest abundance of surface dwellers reflected the preponderance of Acarinina and Morozovella across the studied sections; deep dwellers are represented by the subbotinids while the chiloguembelinids population represented the intermediate dwellers. Traits indicated in the planktonic foraminiferal mode of feeding were grazing, suspension feeding, symbiosis, and detrital feeding.



4. Discussion

4.1. Changes in pelagic ecology as indicated by planktonic foraminifera

The planktonic foraminiferal assemblages at ODP Site 1265A at Walvis Ridge were characterized by the typical late Palaeocene to early Eocene fauna [51]. They represent taxa from the full range of pelagic depth zones across the water

column [52, 53] e.g., the dominant taxa across the studied interval were *Morozovella* and *Acarinina* (Figure 3) which are symbiont-bearing taxa inhabiting the upper water column and classified as warm water / oligotrophic indicators [52]. *Chiloguembelina*, *Zeauvigerina*, and *Pseudohastigerina* dwell at intermediate depths and are tolerant of reduced oxygen [54, 55, 56, 57, 58, 59, 60]. Deep-water dwellers and colder-water indicators were represented by *Subbotina*, *Parasubbotina*, *Globanomalina*, and *Planorotalites*.

Prior to the CIE interval, the planktonic assemblages contained high abundances of *Subbotina*, a moderate abundance of *Acarinina*, and, relatively lower abundances of *Morozovella* and *Globanomalina* (Figure 2). The pre-CIE assemblages were indicative of eutrophic conditions and relatively mild temperatures [60]; [61]. Similar increases in *Subbotina* were found before the CIE at the PETM section in Forada section in Italy [61]. In another study, [59] reported a decrease in the abundance of the *Subbotina* at the Shatsky Rise during the PETM. However, the core analyzed was relatively thin compared to this study and the Forada section; and also, closer to the onset of CIE. Furthermore, the low abundances of biserial forms were indicative of a weakly developed oxygen minimum zone [60]. The co-occurrence of warm and cold-water planktonic taxa was an indication that the ocean was beginning to warm in the late Palaeocene.

Increasing global temperatures during the CIE coincided with decreases in the abundance of the cold-water indicators (*Subbotina* and *Globanomalina*), and corresponding increases in the warm water and nutrient-deficient indicators (*Acarinina* and *Morozovella*; Tables 2-4). A similar scenario was reported in the Forada section in the Tethys Sea [60]; and in the equatorial Pacific Ocean and Weddell Sea [62, 59]. The main excursion (CIE) interval was also marked by considerable dissolution of the tests of all three dominant taxa. *Subbotina* seemed to be most affected as shown by its low abundance and diversity among the major taxa. Also recorded in this study is the high abundance of *Acarinina* during the CIE which has been widely reported for the equatorial Pacific [59], Southern Ocean [63], and the Tethys Sea [60]. This could be related to temperature increases and nutrient depletion.

The high relative abundance of photosymbiotic taxa (*Acarinina* and *Morozovella*) at Site 1265A during the CIE and the decrease in *Subbotina* could be linked to the susceptibility of the later to carbonate dissolution because *Acarinina* and *Morozovella* are more heavily calcified. The depressed cancellate nature of *Subbotina* ornamentation makes them more susceptible to dissolution. Many studies e.g., [64, 54, 39] of modern low-latitude tropical planktonic foraminifera showed that the spinose taxa are more susceptible to dissolution than the non-spinose taxa. Again, the size of the test also determines the sinking speed [10] and susceptibility to dissolution. *Subbotina*, being smaller than the other taxa, spends longer travel time in the water column and is more likely to be destroyed by predation and carbonate dissolution. High proportions of unidentified *Subbotina* species in the samples within the CIE interval suggest a high level of alteration among the specimens before and after deposition.

During the recovery interval, high abundance and diversity of *Acarinina*, *Morozovella*, *Subbotina*, and *Chiloguembelina* occurred. When the populations of *Subbotina*, *Parasubbotina*, and *Globoturborotalita* were combined, they constituted the greatest proportion of the population from this section. The pelagic environment may have cooled down and must have been less stratified in order for the cold-water indicator *Subbotina* to proliferate. The high abundance of all major taxa *Acarinina*, *Morozovella*, and *Subbotina*, (Figure 2) during the recovery interval indicates that the pelagic zone experienced high seasonal variation, well stratified and highly productive surface water.

4.2. Linking trait changes in planktonic foraminifera with ecological disturbance

Evidence of ecological disturbance is indicated based on changes in foraminiferal traits in Site 1265A. The Planktonic foraminiferal trait composition is significantly different in all three CIE (pre-CIE, CIE, and Recovery) intervals. For the pre-CIE interval, the trait composition indicates an environment that was cooler than the CIE and the recovery intervals because taxa with smooth, trochospiral, and semi-circular chamber arrangements were higher in abundance (Figure 4). Only *Globanomalina* has a combination of these traits and the species is regarded as a cool-water indicator [60]. The traits that increased during the CIE interval are warm water indicators relating to taxa such as *Acarinina* and *Morozovella* [60]. This suggests that temperature increased during the period. The planktonic foraminiferal traits that increased in relative abundance during the recovery interval suggest that the SE Atlantic Ocean has relatively cooled because the increase in traits such as elongate tests, bi/tri serial chamber arrangement, and terminal apertures are related to deep water dwellers which are associated with intermediate and cold waters taxa such as *Subbotina*, *Chiloguembelina*, *Zeauvigerina*, *Jenkinsina* and *Woodringina* (Figures 2; 6).

Taxa with perforations increased during the CIE (Figure 6). This trait is associated with enhanced ventilation in their test during the hyperthermal and it implies that taxa with test perforations could be more resilient to extreme climate in the surface ocean.

An increase in traits such as lips and umbilical-extra umbilical apertures during the CIE (see Figure 6) was an indication of good adaptation for grazing habit that thrived during the CIE in planktonic foraminiferal community.

Planktonic trait ordination (see Figure 5) demonstrated a high level of disorderliness, especially during the CIE. The CIE ordination is interpreted to portray the efforts made by species to counteract the ecological crisis during the PETM by occasionally utilizing episodic seasonal bloom of opportunistic taxa to make up for the disappeared taxa. The samples before the CIE (pre-CIE) were tightly clustered indicating ecological stability.

5. Conclusions

- The PETM interval at ODP Site 1265 (Hole A), Walvis Ridge in the Atlantic Ocean, is marked by a significant reduction in the population of some planktonic foraminifera from 500,000 at the pre-CIE to less than 100 at the main CIE interval. *A. nitida*, *M. aequa*, *S. trivalis*, *G. chapmani*, *G. pseudomenardii*, *S. triangularis*, *S. cancellata*, *P. pseudobulloides*, *G. planoconica*, *M. occlusa*, *C. morsei*, *W. claytonensis*, *S. valescoensis*, *M. pasionensis*, *S. triloculinoides*, *M. acuta*, *M. acutispira* and *A. strabocella* went into extinction at the interval, while *Globoturborotalita bassriverensis* was recorded as an excursion taxa. This corroborates other studies that the PETM resulted in a radical biotic turnover in the Atlantic Ocean.
- Evidence from BTA has shown that statistical tools could be used to categorize planktonic foraminiferal fauna and trait compositions and successfully distinguish the degree of disorderliness in foraminiferal paleoecology (Figures 3 and 5).
- BTA also showed that traits such as triangular/trapezoid chamber arrangement, muricae wall texture, appertural accessories (like lip in the umbilical and extraumbilical apertures), and perforations in the test wall, grazing and surface-dwelling habits were identified as resilient traits in extreme warm climate conditions (Figure 4)
- There is a strong correlation between foraminiferal faunal/trait assemblages and water column stratification during the PETM event. Warm-water and non-spinose taxa such as *Acarinina* and *Morozovella* increased in abundance during the peak of the extreme warming event while spinose / cold-water indicators like *Subbotina* and *Globanomalina* taxa decreased in abundance at the same period. It can also be concluded that non-spinose taxa (*Acarinina* and *Morozovella*) are more resistant to dissolution than *Subbotina* which has spines. This is because non-spinose is more calcified, denser, and with a thicker test that allows them to sink faster in the water column after death than their spinose counterpart.

Compliance with ethical standards

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Disclosure of conflict of interest

This research is part of the Ph.D work of the corresponding author. It has not been sent for publication in any journal. The authors Dr. Celestine Nwite Nwojiji, Dr. Fabienne Marret, Dr. Godwin Nwonumara Nkwuda and Dr. Norbert I. Nnakenyi hereby declare no conflict of interest in this publication.

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