The PETM Extreme Climate Impact on the Benthic Foraminiferal Traits and Ecological Functioning in the Tropical Pacific Ocean

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Abstract Foraminifera are marine microorganisms which provide essential ecological functions in the oceans. They are very sensitive to the physio-chemical changes in the marine environment and tend to incorporate the changes in the environment they lived into their test during calcification. The records of the changes in their test serves as a black box for the changes in ocean ecology over time. In view of current changes in the global marine ecosystem as a result of anthropogenic and natural pressures, it is important to understand the reaction of foraminifera (both at the community level and individual attributes) to the late Palaeocene – early Eocene hyperthemal event [the Palaeocene-Eocene thermal maximum (PETM)]. The PETM was a global warming event that occurred 55 million years ago. It resulted in the acidification of the deep sea, shoaling of the lysocline and Carbon Compensation Depth (CCD), massive extinction of benthic foraminifera as well as diversification and migration of both marine and terrestrial organisms. This study used Biological Trait Analysis (BTA) to understand the changes in foraminiferal population and trait composition during the PETM. The results from this study demonstrated that BTA techniques could be used to detect ecological disturbance based on non-metric multi-dimensional scaling (nmMDS) ordination. The nmMDS ordination of all the studied sites showed wider separation during environmental disturbance [period of negative Carbon Isotopic Excursion (CIE)] compared to other intervals. Thirteen (13) foraminiferal traits and over 60 trait categories were perceived to be crucial for the foraminiferal ecological functioning in the marine environment. However, BTA recognised test composition, chamber arrangement/ shape, ornamentation, primary aperture position, perforations and living/feeding habit as the most important foraminiferal trait in the benthic ecosystem. Traits such infauna and sessile life habits; cylindrical elongate and bi-triserial test forms; complex terminal apertures and omnivorous feeding modes were the most resilient traits during the hyperthermal.

Keywords: PETM, benthic foraminifera, palaeooceanography, palaeocology, extreme climate, biological traits

Cite This Article: Celestine Nwojiji, Bryony Caswell, and Fabienne Marret, "The PETM Extreme Climate Impact on the Benthic Foraminiferal Traits and Ecological Functioning in the Tropical Pacific Ocean." *Journal of Ocean Research*, vol. 4, no. 1 (2019): 6-19. doi: 10.12691/jor-4-1-2.

1. Introduction

The rate at which species are disappearing in the biosphere due to the current climate change has made the scientific community propose that if mitigating circumstances are not put in place, the Earth will be approaching the sixth mass extinction before the end of the century [1]. The primary driver of current climate change is the emission of carbon dioxide (CO_2). The understanding of the impact of extreme climate on marine biodiversity resulting from increased greenhouse gas input into the oceans is critical to the understanding of how the Earth systems will function in the near future [2,3,4,5]. The estimated CO_2 concentration of the earth system for the next 100 – 500 years based on the assessments of fossil fuel reserves and other resources is 5000 pentagrams of carbon [6,7,8]. A Similar scenario of CO_2 in the Earth system was recorded during the Palaeocene – Eocene thermal maximum (PETM) 55.6 million years ago. The PETM is one of the most significant climatic events in the last 90 million years of Earth history [9]. The hyperthemal was caused by the release of enormous ^{13}C depleted carbon into the Earth system carbon pool. The source of this carbon included the greenhouse gases emitted from dissociation of methane clathrates from the sea floor [10,11], large igneous provinces e.g. during the opening of the North Atlantic basin [12], and thermogenic emissions of carbon dioxide from decaying organic matter [13]. The dissolution of these gases in the ocean and the increases in their atmospheric concentration raised the temperature of

the global surface oceans to 9°C and 5°C in the bottom water in a relatively short period of geological time ~10, 000 years [14,15]. In addition, the rise in temperature resulted in other major environmental and biological changes including acidification of the deep ocean, global expansion of oxygen minimum zones and local photic zone euxinia, sea-level rise, significant shoaling of the global ocean carbonate compensation depth (CCD), an accelerated hydrological cycle and most importantly, species biogeographic migrations and the disappearance of 30-50% of intermediate – deep-sea benthic foraminifera [16-21].

The principal expression of the PETM in the geological record is the benthic foraminiferal extinction (BEE), a large and rapid negative carbon isotopic excursion (CIE) from both the marine and terrestrial environments [22]. There has been a series of debates over which of the climatic feedbacks caused the extinction of benthic foraminifera: whether it was ocean acidification, rises in water temperature, changes to nutrient supply or deoxygenation of the bottom water. This study will contribute to this debate by investigating if trait changes in foraminifera during the event played a role in the benthic foraminiferal extinction.

Foraminifera are important in the functioning of marine ecosystems and ocean biogeochemical cycles such as organic carbon export as 60% of deep sea sediment compose of their test. They link the primary production from phytoplankton to the higher trophic levels – shrimps, fishes, mammals and seabirds hence are critical components of the trophodynamics of benthopelagic ecosystems [23].

Most of the micropalaeontological techniques used in understanding the impact of extreme climate on biotic turnover in deep-time were based on taxonomic assemblage, specific species analysis and geochemical data [18,19,24-29]. These have provided significant insight to the events nevertheless, faunal assemblage data are prone to error due to poor preservation that may result from the taphonomic processes [30]. Hence, this study explores the use of trait-based approach [Biological Trait Analysis (BTA) technique] in understanding how traits and ecological functioning of foraminifera changed across the Palaeocene – Eocene Thermal Maximum (PETM).

By definition, trait is the total constitution, physical appearance and behaviour of an organism while biological trait analysis is a multivariate statistical approach used to describe species distribution, their biological characteristics and how it is related to the running of their ecosystem [31]. This new approach was used to examine the benthic foraminiferal data generated from two different oceans in order to understand the biotic and functional turnover based on the trait composition of foraminifera. The ecological functioning of foraminifera have been inferred based on their traits changes during the hyperthermal.

The key questions answered by this study include;

1. Are there evidence of trait changes in foraminifera during the PETM

2. Does any pattern exist in the trait composition of benthic foraminifera during the PETM in the tropical Pacific?

3. Did changes in the traits of benthic foraminifera coincide with the changes in taxonomic composition?

4. How did the faunal turnover of benthic foraminifera and their traits affect the ecological functioning of the benthic system during the PETM?

5. Which traits were resilient or susceptible to changes during the PETM?

2. Materials and Methods

2.1. Data Sources and Site Descriptions

The data for this study was derived from the previously published foraminiferal census of ODP leg 198 sites 1209B and 1212B by [32]. The foraminiferal census data as used to generate a new trait composition data of individual species (see the supplementary data). The cores from ODP 198 were located in the southern high area of the Shatsky Rise (Figure 1) along a prograding water depth transect of 500m [33]. Thirty (30) sediment samples each were analysed from a 30cm length of core across the PETM interval at sites 1209B and 1212B. The sediments consist largely of nannofossil ooze with a distinct dark brown clay-rich interval that marks the core of the PETM and the P/E boundary [32].
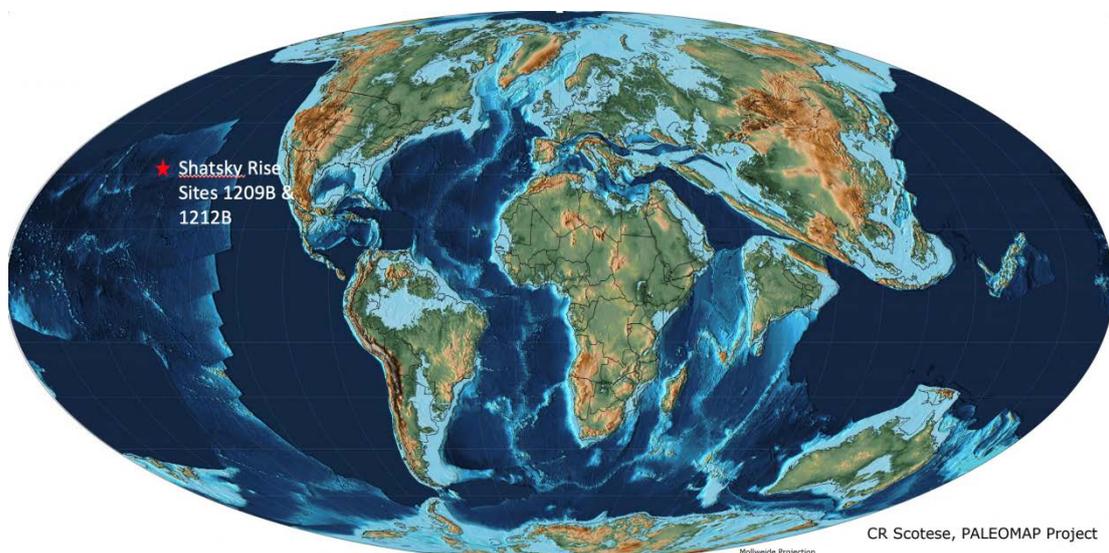

Figure 1. Late Eocene palaeogeographic map showing the studied sites. 1-ODP Leg 198 Shatsky rise (Sites1209B &1212B)

2.2. Trait Classifications and Analytical Procedures

The foraminifera species in the census data [25,32] were classified into thirteen different biological categories (Table 1). The traits selected were those considered to reference core ecosystem functions or processes in the ocean that may be provided by foraminifera. Important traits that can provide an index for some of these ecosystem functions include basic aspects of test composition, morphology such as the test shape, chamber arrangement, chamber shape, wall structure and living habit.

Foraminiferal test composition varies from agglutinated materials to secreted calcite and could indicate changes in the ambient environmental chemistry and composition [34]. Foraminiferal test composition functions as a protective tool and is known to reduce biological, physical and chemical stress in their environment [35]. The test shape could indicate ecological adaptation and preference by foraminifera. Spiral tests have been associated with epifaunal habitat [36], they are characterised by plano-convex – bi-convex trochospirally coiled test with large pores (e.g. *Gavelinella beccarriformis*). The shallow infaunal taxa are usually elongate, uniserial to triserial chambered or planispirally coiled (e.g. Dentallinid or Buliminid) while the deep infauna are ovate (globose) to triserial which are common in imperforate taxa such as *Oolina globosa; Tapanina selmensis*. The arrangement of the test chambers and their shape chamber could also indicate ecological stress, for instance, change from sinistral to dextral or evolute to involute coiling in trochospiral test has been related to change in water temperature and bathymetry [37]. Elements of test microstructure such as the test macro-ornamentation (e.g. spines) could also reflect the mode of living and adaptation to surrounding water condition. Spinose species of living foraminifera are known to be symbiotic, harbouring photosynthetic alga like dinoflagellates within their spines and gaining sufficient nutrient from them. In general ornamentation in foraminifera play a huge role in feeding, adaptation to extreme environmental condition, movement as well as prey -predation relationship. A study by [38] demonstrated that foraminifera (*Haynesina germanica*) use body ornamentation to sort food particles into different shapes and sizes thereby removing harmful substances as well as disaggregating larger particles into smaller pieces before ingestion [38]. It is a great adaption for escaping from predators. The form of apertures, the presence of accessory structures and their primary position vary with change in environmental condition. For instance, at ambient water chemistry, *Haynesina germanica* had a well-developed apertural face, teeth, tubercle and umbilical area but these features were difficult to identify in species found in extreme CO_2 and pH levels [38].

The perforation of foraminiferal test is a critical functional feature of the organism; they could be coarse exceeding 10µm or fine ranging from 1µm to a few tenths of micro-millimetres. Pores in foraminifera are used for gas exchange, osmoregulation, intake and release of nutrient and ecosymbiosis. Large pores are possessed by species in a well-oxygenated environment while species found in the low oxygen environment have smaller pores [39]. They allow the organism to attach to hard substrate by secreting some organic adhesives through them.

Characteristics of foraminiferal behaviour such as their life habit (whether they live infaunal or epifaunal), feeding habit and mobility may indicate their level of tolerant to prevailing water chemistry, nutrient and oxygen concentration and other hydrodynamic conditions.

These traits (mentioned above) were each classified into subcategories referred as modalities (Table 1), for instance, test shape is classified into spiral, elongate, globose, tubular, subquadrate, and others. This categorisation is not exhaustive but highlighted the modalities that are; common in the recovered species, quantifiable or those available in the accessed literature and databases.

Table 1. Example of traits and associated modalities used in biological traits classification of foraminiferal communities

Traits	Modalities				
A. Test Shape	A1. Spiral	A2. Elongate	A3. Globose	A4. Tubular	A5. Others
B. Test Composition	B1. Agglutinated	B2. Hyaline calcite	B3. Hyaline aragonite	B4. Secreted: Porcellanous	B5. Others
C. Chamber arrangement	C1. Unilocular	C2. Uniserial	C3. Bi/Tri-serial	C4. Planispiral	C5. Trochospiral	C6.Other
D. Chamber shape	D1. Spherical/Oval	D2. Tubular	D3. Triangular or trapezoidal	D4. Semi-circular	D5. Others
E. Test macro-ornamentation	E1. Depressed sutures	E2. Raised sutures	E3.Ponticuli	E4. Keeled	E5. Others
F. Test micro-ornamentation	F1. No ornament	F2. Spinose	F3. Striate	F4. Costae	F5. Others
G. Aperture form	G 1. Oval/reniform	G2. Arcuate	G3. Radiate	G4. Slit-like	G5. Others
H. Aperture accessory structures	H1. Lips	H2. Teeth	H3. Neck	H4. None	
I. primary aperture position	I1. Terminal	I2. Basal interiomarginal	I3. Umbilical	I4 Extra-umbilical	I5. Others
J. Test perforation	J1. Microperforation	J2. Fine perforation	J3. Coarse perforation	J4. no perforation	
K. Life habit	K1. Benthic epifaunal	K2. Benthic shallow-infaunal	K3. Benthic deep- infaunal	K4. Others	
L. Feeding habit	L1. Deposit feeder	L2. Herbivore	L3. Omnivore	L5.Others	
M. Mobility	M1. Stationary	M2. Mobile	M3. Clinging	M4. Others	

Table 2. Example list of eight foraminiferal taxa from site 1209B with the fuzzy trait coding for 2 (test shape and chamber arrangement) out of the 13 traits used for this study

Modality	A1. Spiral	A2. Elongate	A3. Globose	A4. Tubular	C1. Unilocular	C2. Uniserial	C3. Bi/Tri-serial	C4. Planispiral	C5. Trochospiral
Anomalinoides trinitatensis	1	0	0	0	0	0	0	0	1
Bolivina inconspicua	0	1	0	0	0	0	1	0	0
Quadrimorphina profunda	1	0	0	0	0	0	0	1	0
Oridorsalis umbonatus	1	0	0	0	0	0	0	0	1
Nuttallides truempyi	1	0	0	0	0	0	0	0	1
Gyroidinoides spp.	1	0	0	0	0	0	0	0	0.5
Laevidentalina spp.	0	0	0	1	0	1	0	0	0
Aragonia spp.	0	1	0	0	0	0	1	0	0

A fuzzy coding [40] technique was used to express the affinity of different species to the different trait modalities using a scale of 0.0–1.0. The absence of an affinity for a particular trait is denoted with 0 whereas 1 is used to code a species that exhibited a high affinity to a trait (Table 2). This coding technique allows species that exhibited more than one modality to be categorised according to their affinity (e.g. Table 2), however all the categories shall sum to one [5,41,42].

The information on the biological traits were sourced from the biological database such as WORMS – World Register of Marine Species: http://www.marinespecies.org, The Palaeobiology database http://palaeodb.org; Fossilworks http://fossilworks.org/, Pangaea https://www.pangaea.de/and Atlas of Paleogene Cosmopolitan Deep-Water Agglutinated Foraminifera http://nhm2.uio.no/norges/full/atlas/pecol_text.htmp published literature (e.g. [43,44]). Review of these data resources as well as morphometric measurements of specimens, and personal communications with experts on a range of taxa informed the coding of traits selected for this analysis.

In some species, traits like mobility or feeding habit could not be directly established because they are already extinct with no record of the life history in the literature. In such cases, the indeterminate traits were extrapolated from the closest relative (at the genera or family level) or from the functional morphology of a known taxa. For instance, if the chamber form of a species was rounded trochospiral, Nagy's (1995) functional morphology principles were applied to indicate that the species was probably a superficial epifauna and may have been a deposit feeder (see http://nhm2.uio.no/norges/full/atlas/pecol_text.htm), though this was on a very rare cases.

The frequency of each trait modality in the dataset was determined by multiplying the trait modality scores by the relative abundance of each species exhibiting those modalities in each sample. This was achieved by matrix multiplication [42].

Statistical analyses of both taxonomic abundance and trait composition were performed with PRIMER v. 6 (PRIMER-e, Plymouth, UK). Prior to the statistical analysis, data were subdivided into three to reflect the stages in CIE (Pre-CIE, CIE and Recovery) event. The pre-analysis treatment of the samples required standardisation of the species data which were transformed with Log (x+1) to reduce the influence of dominant species on the overall result. The similarities of both species and biological traits between samples were calculated using Bray-Curtis index to create resemblance matrices. Non-metric multidimensional scaling (nmMDS) was used to visualise the similarities/differences in species and trait composition between the different sections of CIE. Species/taxa composition and biological trait composition were compared using Analysis of Similarity (ANOSIM), and subsequently, the similarity percentages (SIMPER) routine was used to identify which taxa or traits contributed the most to differences identified from the ANOSIM across the PETM.

3. Results

3.1. Changes in Taxonomic Composition at ODP Site 1209B

The majority of the benthic foraminiferal assemblages recovered from Site 1209B are dominated by calcareous taxa and very few agglutinated forms such as Bathysiphon spp., Spiroplectammina spp., and Tritaxia spp. [32]. Epifauna taxa accounted for about 14% of the total faunal abundance and are characterised by Anomalinoides, Cibicidoides, Oridosalis, Gavelinella and Gyroidinoides taxa. Infaunal morphogroup constituted over 80% of the total abundance and was dominated by the Buliminds with 50% of the total abundance [32]. The pre-CIE interval of the PETM at site1209B was characterised by a predominance of Bolivina inconspicua, Bulimina kugleri, Paralabamina spp., Gavelinella spp., Gyroidinoides spp., Lenticulina spp., Siphogenerinoides brevispinosa, Fursenkoina sp. and the Stilostomellids. Most of these taxa disappeared at the peak of the CIE [32]. The CIE interval was characterised by the acme of Bolivina gracilis, Anomalinoides trinitatensis, Buliminella cf. beaumonti, Globocassidulina subglobosa, Quadrimorphina halli, Q. pacifica, Q. profunda, Quadrimorphina sp. 1, Tappanina selmensis and Bulimina bradburyi. The recovery section recorded the highest relative abundance of foraminifera and was dominated by Bulimina spp., Nuttallides truempyi, Bulimina bradburyi and Pleurostomellid taxa. The detailed faunal composition has been discussed in [32] and the focus here is using the BTA to understand the changes in taxonomic composition in relation to changes in trait composition.
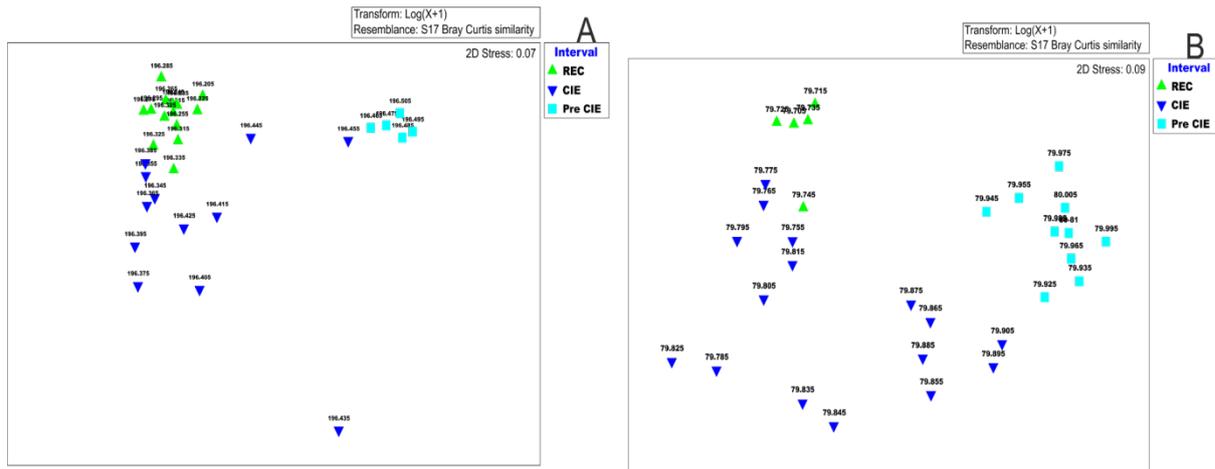
Figure 2. Non-Metric Multidimensional Scaling ordination of foraminiferal taxonomic composition (transformed with log x+1) of Bray-Curtis similarity. A- Samples from ODP Site 1209B Shatsky Rise, Pacific Ocean. B- Samples from ODP Site 1212B Shatsky Rise, Pacific Ocean. Colours indicates samples from the three intervals the PETM (Pre-CIE, CIE and Recovery)

Table 3. Mean abundance of species contributing to the most dissimilarity between the three PETM intervals at Site 1209B (50 % cut off).

Species	Mean abundance			% Contribution
	Pre-CIE	CIE	REC	
Quadrimorphina profunda	1.45	**27.66**	17.96	17.41
Bulimina kugleri	**20.27**	1.79	0.12	12.47
Bolivina gracilis	0.33	**11.87**	1.83	8.13
Bolivina inconspicua	**12.3**	2.08	0.07	7.63
Oridosallis spp.	**9.29**	1.92	4.98	5.31
Buliminids	12.5	14.92	**30.79**	13.63
Pleurostomellid spp.	1.14	3.1	**11.41**	7.52
Nuttallides sp.	5.99	4.59	**13.39**	7.61
Nuttallides truempyi	4.27	4.59	**13.39**	5.64

Non-metric multi-dimensional scaling (nmMDS) ordination of the recovered benthic foraminiferal assemblages (Figure 2) showed three clear taxonomic groupings during the pre-CIE, CIE and the recovery. ANOSIM values confirmed that the three groups significantly differed (global R= 0.693; p<0.01) and pairwise ANOSIM with p<0.01 also showed that all the three groups significantly differed from each other. However, the taxa from 196.455 mbsf (classified as CIE based on the carbon isotope) ordinated closely with the pre-CIE. Taxa in sample 196.445 mbsf ordinated at the centre of the three groupings while taxa in 196.435 mbsf was an outlier. The reason for the outlier was that foraminiferal specimens in sample 196.435 mbsf was lowest in number when compared to other samples and not up to 100 specimen. Also, the benthic foraminiferal extinction event (BEE) that marks the onset of the CIE occurred at this sample depth.

The three samples that did not ordinate with their group could be evidence of the severe environmental changes that occurred at the beginning of the CIE [32].

Similarity percentage (SIMPER) between the pre-CIE and the CIE intervals (at 50% cut off) showed that only five taxa (Table 3) contributed to the most dissimilarities in site 1209B. The taxa contributing to the dissimilarity were *Quadrimorphia profunda* and *Bolivinia gracilis* which was 20-fold more during the CIE than at the pre-CIE. *Bulimia kugleri* was also 20-fold less during the CIE than at the pre-CIE while *Bolivinia inconspicua* and *Oridosallis spp* significantly decreased in abundance

during the CIE (Table 3). During the recovery period, half as many *Quadrimorphia profunda* and ten-fold less *Bolivina gracilis* occurred compared with the CIE period (Table 3). Whereas *Buliminids, Nuttalides truempyi* and *Pleurostomellid* spp increased. The recovery assemblage also differed from the pre-CIE in having less *B. kugleri* and *B. inconspicua,* Buliminids*, Quadrimorphina profunda*, *Pleurostomellid* spp. and *Nuttallides truempyi* than pre-CIE (Table 3).

3.2. Changes in Foraminiferal Trait Composition at ODP Site 1209B

Similar to the ordination for taxonomic composition, the trait composition (Figure 3) differed between the three intervals of the PETM as shown by the global R = 0.581 and *p*<0.01. Pairwise ANOSIM indicated that the composition present during the recovery period significantly differed (*p*<0.01) from both those preceding it. The trait assemblages present during the pre-CIE significantly differed from those present during the CIE although at lower significance (*p*>0.01). Overall trait composition during the recovery was more similar to the CIE than at the pre-CIE (Figure 3) as was the case for taxonomic composition. The trait composition of samples from depth 196.455, 196.435 and 196.445 mbsf ordinated away from the CIE group they belonged to. These are the first few samples at the beginning of the CIE and may be an evidence of biotic disturbance associated with the event.
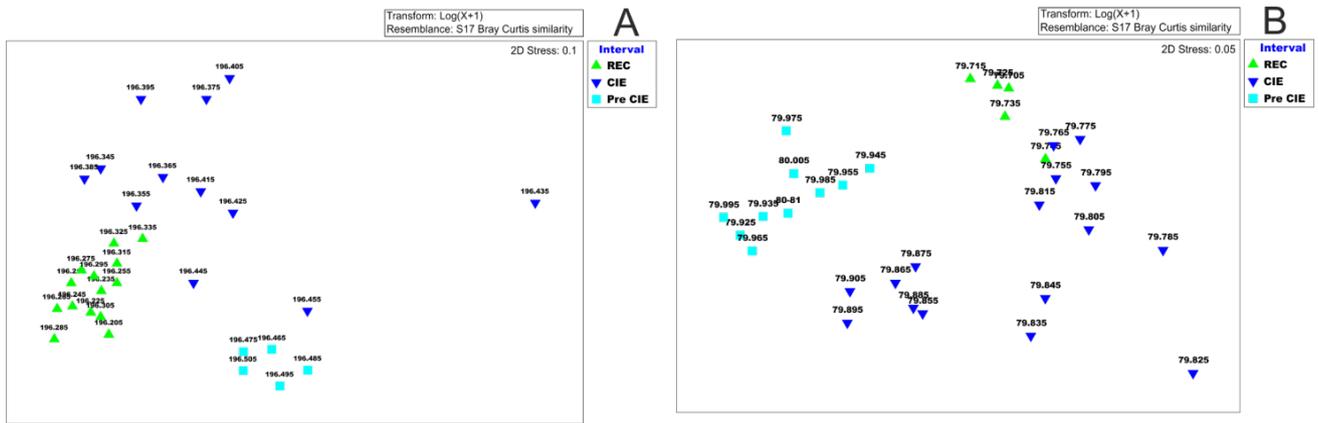
Figure 3. Non-metric Multidimensional Scaling ordination of foraminiferal traits composition (transformed with log x+1 and total resemblance) of Bray-Curtis similarity. A- Samples from ODP Site 1209B Shatsky Rise, Pacific Ocean. B- Samples from ODP Site 1212B Shatsky Rise, Pacific Ocean
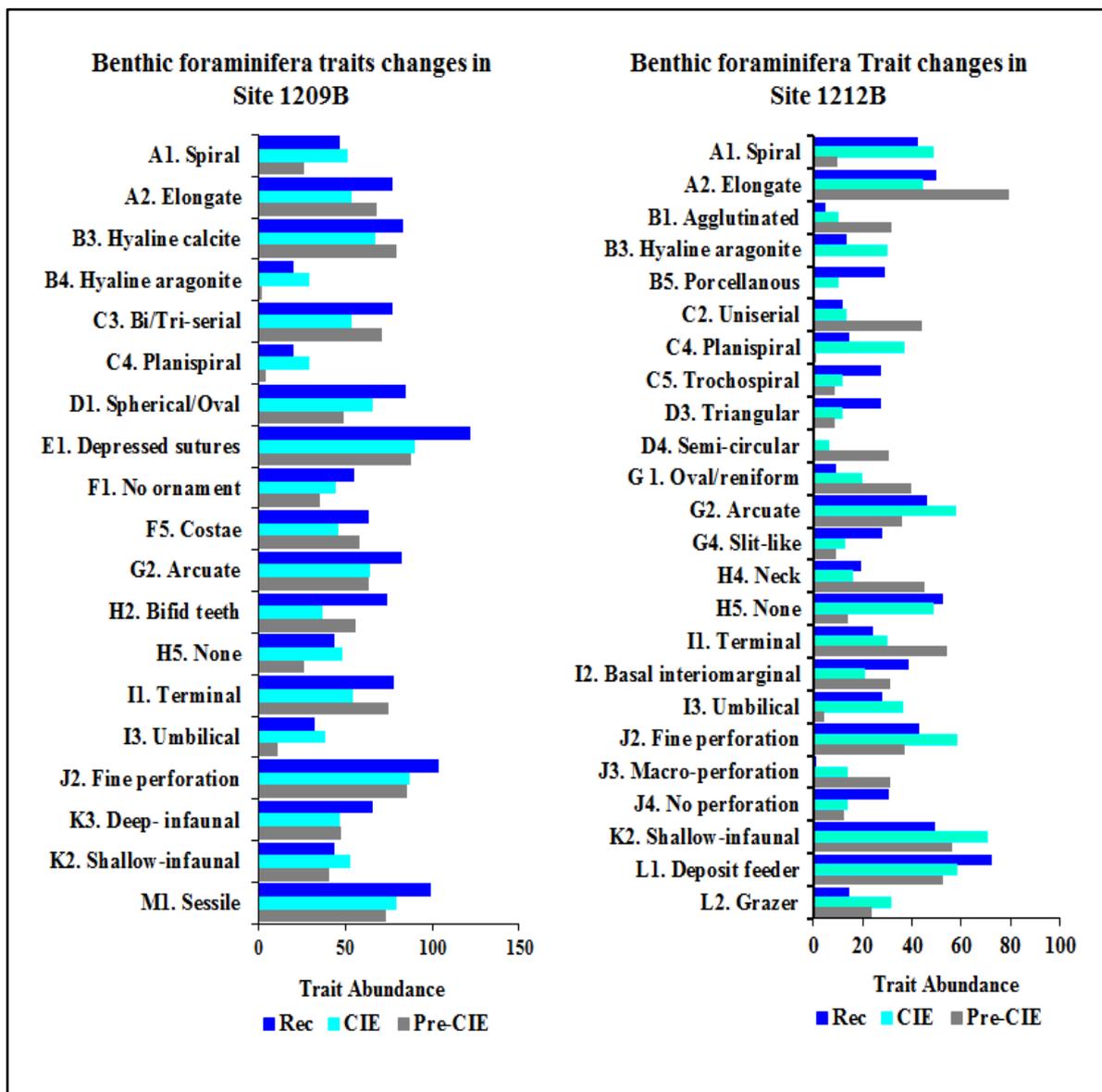
Figure 4. Similarity percentage (SIMPER) with traits that contributed to the differences in benthic foraminiferal trait composition across the PETM events in the studied sites (Data cut off 50%).. Grey bars = Pre-CIE; sky blue bars = CIE core; deep blue bars= Recovery

SIMPER results also showed that 19 traits (at 50% cut off) contributed to the dissimilarity between intervals (Figure 4) all of which were more abundant during the recovery than pre-CIE, these included spiral and elongate tests; hyaline calcite and hyaline aragonite tests; bi/triserial and planispiral chamber; spherically shaped chambers, depressed sutures, costate ornamentation, fine perforations and bifid teeth. Foraminifera with apertures at

the terminal and umbilical positions that lived a sessile lifestyle and shallow – deep infauna also contributed significantly to the dissimilarities. The mean abundance of taxa with spiral coiling, hyaline aragonite test, planispiral chamber arrangement, no apertural accessories, aperture at the umbilical position and lived shallow infauna were higher during the CIE than at any other interval of the PETM. After the CIE, the benthic communities seem to become more successful than before the CIE, as shown by the high abundance of most of the trait modalities at the recovery (Figure 4). The higher abundance of the traits at the recovery interval may be due to the bloom of foraminifera after the hyperthermal.

3.3. Changes in Taxonomic Composition at ODP Site 1212B

The recovered taxa from site 1212B were dominated by cosmopolitan foraminifera, mostly of calcareous test [32]. The foraminiferal census data [32] showed that *Siphogenerinoides brevispinosa,* Stilostomellids*, Bulimina kugleri and Bolivina inconspicua* were present at the pre-CIE section but disappeared during the PETM. However, *Quadrimorphina profunda, Tappanina selmensis, Bolivina gracilis, Anomalinoides trinitatensis* and *Laevidentalina* spp. recorded their highest abundance during the CIE while *Eponides elevata* was a local excursion taxon that appeared towards the end of CIE.

The ordination of samples from site 1212B in the nmMDS (Figure 2) showed three distinct groupings with global R =0.649, and that each group significantly differ from the other at $p<0.01$. The pairwise ANOSIM tests for the three intervals showed that the taxonomic composition of the assemblage significantly differs as follows: recovery and CIE R= 0.317, $p<0.02$; recovery and pre-CIE R= 1, $p< 0.02$; CIE and pre-CIE R= 0.683; $p<0.1$. During the CIE there was a wider separation between samples (SIMPER, 53% similarity) compared with the pre-CIE (SIMPER, 74% similarity) or the recovery (SIMPER, 76% similarity). This may be due to the high level of ecological stress recorded during the PETM warming

The nmMDS plot also showed six subgroupings: one each for the pre-CIE and the recovery, and four subgroups for the CIE. These subgroupings of samples during the CIE could imply that there may have been a number of distinct environmental changes during the PETM. Overall ordination shows a horseshoe (Figure 2) structure proceeding from the pre-CIE, through several substages of the CIE, and then the recovery. The recovery samples showed a clear separation from the pre-CIE and CIE groups.

Depth 79.745 mbsf which was classified within the recovery interval (using the carbon isotope curve) but ordinated with one of the CIE groups, meaning that it was similar in composition to this subgroup of the CIE than the recovery. The transitional nature of the sample from 79.745 mbsf suggests that even although δ^{13}C may have started to recover to the background levels, the benthic communities were yet to recover from the ecological stress caused by the hyperthermal.

Figure 5. Composite trait variations across the three studied sites. The figures show some trait similarities in trait composition across the two oceans. The colour used in a particular modality is uniform across all the sites. The trait abundance below each plot represents the absolute count of traits after standardization. Site location and core depths are plotted at the left-hand corner of the figure and the PETM events at the right

Table 4. Mean abundance of species contributing to the most dissimilarity between the three PETM intervals at Site 1212B (50 % cut off).

Species	Mean Abundance			%Contribution
	Pre-CIE	**CIE**	**Recovery**	
Quadrimorphina profunda	0.32	**26.89**	11.39	18.29
Nuttallides truempyi	4.34	5.68	**14.61**	8.81
Bolivina gracilis	4.2	**9.76**	1.32	8.5
Laevidentalina spp.	**6.18**	5.18	11.4	7.09
Bulimina bradburyi	0.35	1.5	**8.33**	6.73
Siphogenerinoides brevispinosa	**30.44**	6.39	0	6.2
Bulimina kugleri	**8.67**	3.18	0.07	6.72
Bulimina thanetensis	**10.75**	2.02	2.23	7.2

Results of the SIMPER showed that only five taxa accounted for 56% of the dissimilarity between the CIE and recovery interval (Table 4). During the CIE there were relatively higher abundances of *Q. profunda* and *Bolivina gracilis*, whereas, during the recovery Buliminids, Pleurostomellids and *N. truempyi* were two to four times more abundant (Table 4).

The four taxa that accounted for (50% cut off) of the dissimilarity between the pre-CIE and the CIE were *Bulimina thanetensis*, *Siphogenerinoides brevispinosa*, *Quadrimorpha profunda* and *Bolivinia gracilis*. *Bulimina thanetensis* and *Siphogenerinoides brevispinosa* were more abundant during the pre-CIE than in other sections while *Quadrimorpha profunda* and *Bolivinia gracilis* were more abundant during the CIE (Table 4). The differences in abundance of *Siphogenerinoides brevispinosa* and *Quadrimorpha profunda* together accounted for about 40% of the dissimilarity between the two intervals.

The taxonomic composition of the recovery interval differed from the pre-CIE by containing more Buliminids, Pleurostomellids, *Q. profunda* and *N. truempyii*. In contrast, pre-CIE had higher abundances of *B. kugleri* and *B. inconspicua* (Table 4) than the recovery.

3.4. Changes in Foraminiferal Trait Composition at ODP Site 1212B

The nmMDS ordination of trait composition showed that the pre-CIE, CIE and recovery intervals were clearly separate from each other (Figure 3) and ANOSIM showed that they significantly differed at global R = 0.542 and $p<0.01$. The section analysed during the recovery was short and did not show a significant change in the foraminiferal composition.

Pairwise ANOSIM showed that the trait composition of the assemblage present during the pre-CIE and the CIE differed significantly at $p<0.01$. The recovery and CIE also differed but at lower significance ($p<0.04$). During the CIE, samples were highly variable as shown by the lowest percentage (79%) in SIMPER group similarity, the pre-CIE samples were 88% similar, and the recovery sample similarity was 91%.

The nmMDS for trait composition was very similar to that of the taxonomic composition. The main CIE ordinates in three subgroups (Figure 3) with samples from depth 79.865 – 79.895 mbsf ordinating within one subgroup, samples from depth 79.755 – 79.815mbsf clustered fairly together, and depth 79.835mbsf -79.845 mbsf formed the third subgroup between the other two CIE subgroups. Samples from depth 79.785mbsf and 79.825mbsf lay separately from the rest (Figure 3). The clustering of the CIE samples into three groups could be evidence of environmental perturbation during the hyperthermal, and the outlier (sample 79.825mbsf) marks the BEE interval.

Trait distribution deduced from raw data before statistical analysis (Figure 5) indicated that species with spiral test shape, and planispirally test blossomed during the main period of the CIE when global temperature was highest. A coeval increase in species with tubular shape, arcuate apertures, fine perforations, shallow infaunal life habits as well as sessile lifestyle was also recorded at the CIE interval. While species with elongate tests, agglutinated forms, uniserial chamber arrangement, terminal apertures, and coarse-perforation increased in relative abundance at the pre-CIE, but their abundance plummeted drastically with further warming close to the CIE section.

The similarity percentage analysis (SIMPER) showed that 24 trait modalities accounted for (50% cut off) the dissimilarity between the three PETM subdivisions (Figure 4). Six traits predominated at the pre-CIE, these include elongate tests, uniserial chamber arrangements, terminal apertures with neck, agglutinated tests, fine perforation and semi-circular chamber shape. Taxa with spiral tests, fine perforation, planispiral coiling, umbilical apertures, no ornament, arcuate shaped apertures and grazers that live in the shallow infauna niche were more abundant during the CIE (Figure 4). The recovery interval recorded the highest abundance of trochospiral test shape, triangular/trapezoid chambers, slit-like apertures, and basal interiomarginal apertural position, non-perforated test and deposit feeders. During the period of recovery, almost all the species with coarse-perforations in their test and semi-circular chambers that was present during the pre-CIE had disappeared from the trait composition (Figure 4).

Other trait modalities that were predominant at the pre-CIE but decreased in abundance during the recovery include elongate shape, uniserial test arrangement, terminal apertures, and agglutinated tests (Figure 4). Nevertheless, there was an increase in taxa with deposit feeding habit, umbilical apertures and spiral test during the recovery.

The most affected traits at Site 1212B during the peak of the CIE were trochospirally coiled, semi-circular chamber shape, benthic epifauna and suspension feeding taxa as shown in Figure 4. However, species with sessile lifestyle, deposit-feeding habit and depressed sutures did not show any significant changes across the studied

interval, and these could be the traits that sustained ecological functioning during the hyperthermal (Figure 4 & Figure 5).

4. Discussion

Biological trait analysis of the benthic foraminiferal taxa and trait composition in the tropical Pacific Ocean have enabled us to understand faunal turn over and trait reorganization during the period of extreme climate conditions associated with the PETM. The changes in trait composition are consistent with foraminiferal turnover during the PETM in all the studied sites. However, our result showed that the disappearance of some taxa did not immediately affect the change in trait composition and hence the ecological functioning performed by them as seen in Site 1209B (Figure 5). Foraminifera reacted by either increase in the abundance of the taxa that shared similar traits or taxa with cosmopolitan behaviour that can tolerate a wide range of ecological changes. In addition, the extinction of some trochospiral and macro perforated taxa did not lead to the immediate disappearance of those traits (Figure 5) as other taxa reacted by increase in abundance [32] and thereby sustaining the ecological functioning. The changes in foraminiferal traits were found in most case to lag behind the taxonomic turnover (Figure 5).

4.1. Changes in Taxa and Trait Compositions in Relation to Palaeoecological Parameters

4.1.1. Nutrient Supply in the Pacific Ocean during the PETM

Nutrient supply to the benthic zone was inferred from the faunal composition, infaunal/epifaunal ratio, species and trait turnover from the statistical analyses. The faunal assemblages in the Pacific Ocean (Sites 1209B and 1212B) are dominated by calcareous infaunal taxa primarily by *Buliminids, Stilostomellids/Pleurostomellids* and *Bolivinids.* These taxa in the modern and ancient oceans thrive in the area of high and sustained food supply and low oxygen [25,39,45,46,47]. The relative dominance of infaunal morpho-groups with a coeval high abundance of *Buliminids* at the Pacific sites (Table 3 and Table 4; [32]) suggest a significant supply of nutrient to the seafloor during the PETM. The result from our SIMPER analyses between the pre-CIE and other intervals showed an increase in nutrient flux indicators such as *Bulimina kugleri* and *Bolivina inconspicua* (Table 3). The nutrient supply started to decrease within the CIE interval as shown by a decrease in the *Bulimina* taxa (Figure 6). The lowering in the number of *Buliminids* and *Stilostomellids* in the samples across this interval (Figure 6) was an indicator of oligotrophy. The abundance of these taxa may not have been extremely affected by carbonate dissolution since they live inside the sediment and also very low carbonate dissolution was recorded in the Pacific Ocean during the PETM [32].

There was an initial increase in the *Buliminid* abundance at the beginning of the CIE (Figure 6) which could be as a result of preliminary increase in the surface productivity encouraging more phytodetrital rain to the sea floor but when the further rise in temperature resulted to enhanced metabolic efficiency of pelagic phyto and zooplankton [24], they consumed more refractory organic particle in the upper water column and reduced the quantity and quality of food material reaching the bottom water. Food availability was made worse for the bottom-dwelling taxa as the rise in temperature resulted to increase in the opportunistic taxa (e.g *Quadrimorphina profunda* and *Nuttalides truempyi*) that out-competed the epifauna and shallow infauna by consuming the limited food supply ([48]; Table 4).

The faunal composition from the raw data at the recovery interval demonstrated a period of highest and most stable supply of quality nutrients to the sea floor. The highest abundance of the deep infaunal morphogroup, as well as other high organic carbon influx indicators across this interval (Figure 6), strongly supports this observation. The high nutrient supply during the recovery may be attributed to the enhanced continental weathering [49] supplying nutrients to the ocean and a smaller number of species competing for available resources after the PETM.

The evaluation of trait composition indicate that the prevailing conditions at the sea floor before the CIE favoured species with elongate and uniserial test; neck and bifid teeth as well as bi/triserial forms [36]. These species are well adapted to infaunal lifestyle and are predominantly *Stilostomellids, Pleurostomellids and Buliminids*. In general, the trait composition that constituted 50% similarities across the three PETM interval show that fine perforation, deep infauna, sessile, deposit feeder, terminal aperture, hyaline calcite test, bifid teeth, elongate, uniserial and shallow infauna and spherical aperture (Figure 5) were the most significant traits during the CIE across the studied section. These traits demonstrate high tolerance to high organic carbon influx to the bottom ocean and extreme environmental conditions [36].

Taxa with coarse perforations, trochospiral coiling and epifaunal habit (e.g. *G. beccariformis*) was extirpated during the PETM perhaps because they required high dissolved oxygen and lowered organic matter to thrive, but high organic matter influx that resulted in bottom water anoxia and acidification making the bottom water uninhabitable for them. Foraminifera with traits such as elongate cylindrical, flabelliform or biserial architecture were reported to have high surface to volume ratio that enables them to successfully adapt in the infaunal habitat with high organic matter inundation and anoxia [46]. Additionally, this form of chamber arrangement provides communication/exchange link at each end and this can reduce the rate of protoplasm mixing between the inside and outside of the test leading to decreased metabolic activity within the foraminiferal cell. This anatomy could reduce oxygen and nutrient requirement of the organism. Excessive organic carbon rain from the upper water column may have contributed to the decrease in some less competent epifaunal taxa because high abundance of organic matter in the sea floor hinders pseudopodia function as they are usually overwhelmed by algal growth [37,47].
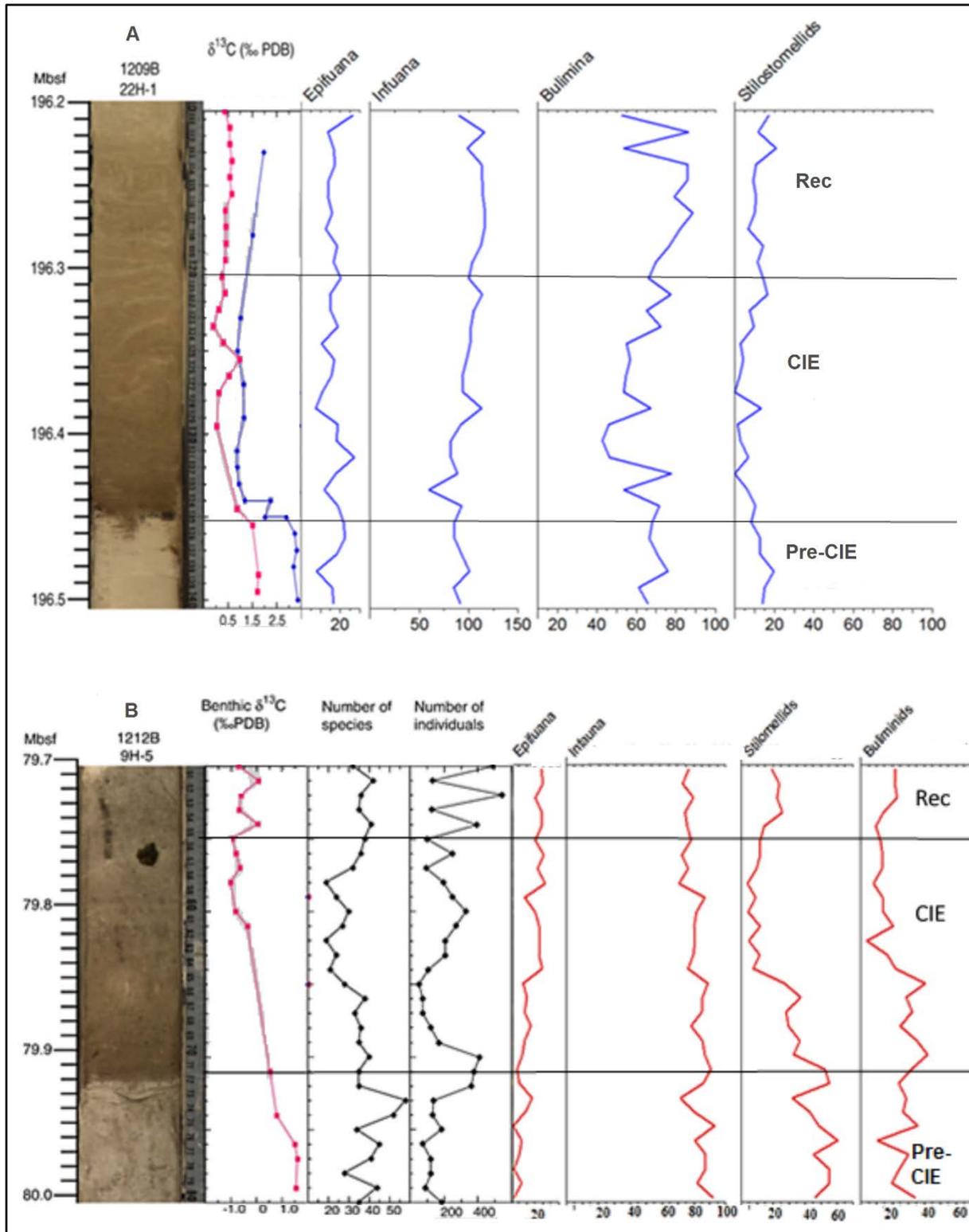
Figure 6. Changes in foraminiferal composition of major taxa in the Pacific Sites with core depth (mbsf) and foraminifera bound isotope records. The lithology is mainly foraminiferal oozes. The lithology and $\delta^{13}C$ record are those of Takeda and Kaiho (2007) while the morphogroups and taxa curves were created in this study

4.1.3. Productivity/global Carbon Cycle

4.1.3.1. Palaeoproductivity/global Carbon Cycle in the Pacific Ocean

Palaeoproductivity in the Pacific Ocean interpreted from fauna and trait results from sites 1209B and 1212B varied across the PETM intervals. The diversity and abundance of both the benthic and planktonic foraminifera [planktonic foraminiferal data in [50]) as well as the $\delta^{13}C$ signature of the biogenic carbonates supports this assertion. The carbon isotope record of the surface-dwelling planktonic foraminifera and bottom-dwelling taxa strongly suggests high primary productivity in the surface ocean and significant export production to the seafloor denoting

efficient benthopelagic coupling. The evidence of high export production in the Pacific Ocean was further supported by a notable abundance of taxa regarded as a good indicator of high export production such *Siphogenerinoides brevispinosa, Stilostomellids* and *Buliminids* ([47]; Table 3 and Table 4) at Sites 1209B and 1212B.

The productivity at the main CIE section was not very clear perhaps as a result of massive carbonate dissolution that led to shoaling of CCD globally during the PETM. All the proxies indicate a collapse in both pelagic (surface) and benthic productivity. The rise in temperature that resulted from the PETM must have increased the metabolic rate of the pelagic primary producers [19]. The high temperature recorded during the peak of the CIE must have caused encystment of many phytoplankton and reduced primary production (with episodic productivity when the environment is conducive to reproduce) while the zooplankton may have moved deeper into the water column and thoroughly foraged all the available organic matter and diminished the quality and quantity of organic carbon reaching the seafloor.

Enhanced foraging of the upper water column would mean that less phytodetritus will be reaching the ocean floor resulting in food scarcity and increased competition. In addition, increase in the solubility of calcium carbonate resulting from higher CO_2 concentration and lowered pH in the ocean will stimulate foraminifera to reduce calcification by building smaller and thinner test walls which are less likely to be preserved in the sediment record.

Palaeoproductivity picked up again after the BBE as indicated by the increase in the relative abundance of both planktonic and benthic foraminifera at Site 1209B [32,50], though this was not reflected on the $\delta^{13}C$ record as it remained relatively low throughout the rest of the studied interval in the Pacific. The lowering of $\delta^{13}C$ record in benthic foraminifera even when the abundance of biomass increased could be attributed to vital effect.

The connection between trait composition and productivity has not been well publicised in foraminiferal research. Reference [39] believed that cylindrical spherical and planispiral morphogroups usually with infaunal habit are common in the area of high productivity. In the PETM section at the Pacific Ocean, trait composition was dominated by the terminal apertures, fine perforation, grazers, infauna, planispiral, elongate test, sessile, biserial-triserial and complex apertures (Figure 4). These trait assemblages strongly support the [39] hypothesis. Another possible explanation for the increase in cylindrical and bi-triserial traits may be related to their response function towards environmental perturbation and not really to productivity increase. Increase in the abundance of oligotrophic taxa such *N. trumpyi, Q. profunda and G. subglobosa* may suggest lowered productivity or well-functioning bentho – pelagic coupling (Benthic – Pelagic coupling refers to the exchange of mass, nutrients/organic materials or energy between benthic and pelagic habitats of the ocean [51]. This is also in line with the deduction on the food supply that suggested sustained mesotrophy during the PETM in the Pacific Ocean. In addition, the topography of elevated platform like the Shatsky Rise [52,53], trophic focusing has been identified as the cause

of disparity between food supply and productivity. Trophic focusing involves winnowing of the fine organic particle by current and concentrating them on a particular part of the ridge [47,54].

In summary, it may be possible that the initial increase in the ocean-atmospheric CO_2 and the coeval rise in temperature before the CIE resulted in an increase in productivity with enhanced organic matter rain to the seafloor but with further rise in temperature, phytoplankton productivity optimum was exceeded in the surface ocean leading to lowered export production. More so, the increased ocean acidification resulted in reduced calcification in form of smaller and thinner test walls in benthic foraminifera and increase in bacterial activity in the sea floor. Increase in the opportunistic and resilient taxa utilised more bicarbonate in the upper water column and acted as a sink to the CO_2. The increase in silicate weathering from the continents enhanced this process and triggered the recovery of PETM. However, export production to the benthic realm never returned to the pre-CIE scenario as suggested by bulk carbonate and foraminiferal $\delta^{13}C$ records in Figure 6.

4.1.3. Oxygen Concentration in the Seafloor in the Equatorial Pacific Ocean

Estimating the amount of dissolved oxygen in the sea floor using faunal association is complicated but has been successfully demonstrated by [55]. This is because oxygen concentration in the bottom water also depends on the interaction between the quantity of organic matter reaching the seafloor, deep water circulation pattern, temperature and faunal composition. Another difficulty lies in the fact that some taxa (especially epifauna) considered to be abundant at a particular amount of oxygen concentration does not spend their whole lifetime in a single niche but migrate within a wide range of variable oxygen concentration environment during their life [39]. Nevertheless, the study by [55] identified critical dissolved oxygen concentration markers for estimating the amount of oxygen available in the benthic ecosystem.

Foraminiferal composition in the Pacific Ocean (Sites 1209B and 1212B) indicates low oxygen concentrations throughout the PETM. Prior to the initiation of the CIE, the faunal assemblage was composed of dysoxic (moderate oxygen concentration) indicators characterised by a mixture of low oxygen taxa such as *Bolivina inconspicua, Buliminids* and *stilostomellids* (Table 3) and oxic fauna like *Gavelinella spp., Anomalinoides* and *Gyroidinoides* species occurring together in the sediment.

The high abundance of deep infauna, in association with a few number of epifaunal taxa reveals that oxygen level was already low in the benthic environment, but just slightly enough to keep the species that needed higher oxygen concentration on life support. The threshold of taxa that require high oxygen concentration was probably reached at the onset of the CIE that resulted in the benthic foraminiferal extinction (BEE). The BEE may largely have been caused by low oxygen concentration because high porosity epifaunal taxa like *Gavelinella beccariformis* needed high dissolved oxygen for their metabolic requirements but could not get enough. Low amount of dissolved oxygen accompanied by high organic carbon influx to the sea floor plus water column

stratification combined to exterminate the susceptible (highly perforated) epifaunal species. Other epifaunal species that survived this hypoxia are well adapted to low oxygen concentration and had the ability to tolerate high organic carbon influx or are able to move up and down the sediment column.

The acme of *Bolivina gracilis* as well as a significant increase in the abundance of opportunistic taxa (*Q. profunda)* have been interpreted as a marker for low oxygen concentration at the peak of the CIE [32]. The amount of dissolved oxygen slightly increased after the peak of the CIE and at the beginning of the PETM recovery as suggested by high abundance of infaunal taxa (*Buliminids*) and the reduction in the opportunistic taxa ([32]; Table 3) because more oxygen was available in the sediment and the infauna could favourably compete with the opportunistic taxa for the accessible nutrients.

The trait composition from SIMPER results revealed that the dominant traits driving ecological changes in Sites 1209B and 1212B during the PETM are deep infauna, sessile, elongate, no ornamentation, fine perforation, terminal apertures, planispiral and bi/trispiral test shape (Figure 4). These trait assemblages strongly suggest adaptation to low oxygen condition, [55] describes the morphological characteristics of low oxygen taxa as thin wall, elongate, spiral and multi-serial. These attributes help them to maximise available oxygen to continue their metabolic activities in the face of hypoxia. Elongate and biserial taxa such as *Bolivina* have been reported to respiring nitrate in the absence of oxygen [56]. Some species of foraminifera found in the oxygen minimum zone have also been reported to lack ornamentation [37] and no ornamentation trait was relatively high in the SIMPER result as shown in Figure 4. There was a mixture of traits like basal interiomarginal, trochospiral, and species with umbilical apertures. Such traits are indicating an increase in the abundance of opportunistic taxa across PETM events and suggest environmental disturbance or periods of episodic bloom as a result of a seasonal increase in oxygen concentration.

5. Conclusions

This study is a novel one, and it pioneered the utilisation of trait changes in fossil foraminifera as indices for paleoecological changes in the benthic system. We have shown that trait composition in conjunction with faunal assemblages can be used as indices for palaeoecological changes and to detect ecological disturbance in the marine ecosystem. Detail examination of foraminiferal traits across the PETM sections at Northeastern Pacific indicated that mostly heavily calcified and perforated benthic foraminiferal taxa went into extinction during the PETM but a significant number survived. This suggests that foraminifera could tolerate a wide range of ecological changes and withstand extreme ecological conditions through various trait manoeuvring such as increasing the abundance of taxa with resilient traits during environmental perturbation.

The results from this study also showed that changes in foraminiferal traits do not occur at the same time as the faunal turn-over in foraminiferal taxa, implying that traits of foraminifera are conserved. Careful examination of

foraminiferal census data from [32] revealed a very dynamic changes in foraminiferal events across the studied sites. However, the foraminiferal trait diagrams in Figure 6 showed a more uniform and predictable bioevents. The similarities in trait events in Figure 6 indicate that some foraminiferal traits are redundant meaning that different species share similar traits and when one goes into extinction similar species sharing the same trait can still maintain ecological functioning in the ecosystem.

Our results also have shown strong evidence that the trait composition of foraminifera can be used to characterised climatic events across basins as exemplified by trait similarities during the hyperthermal in both basins (Figure 6).

The biological traits analysis of foraminiferal turnover from the Shatsky Rise (Pacific Ocean) across the PETM has revealed the ecophenotypic responses of benthic foraminiferal community to the environmental perturbations. The increase in temperatures and dissolved inorganic carbon associated with the event resulted in enhanced food supply, decreased the amount of dissolved oxygen and palaeoproductivity in the Pacific Ocean. The excessive supply of organic material to the seafloor and lowered oxygen concentration resulted in the extirpation of the highly porous trochospirally coiled epifaunal taxa (Figure 6).

The trait distribution partly conforms to the taxonomic composition of foraminifera from which they were derived (section 4.1), however, the biological trait analysis demonstrated how foraminifera maintained benthic functioning in the face of an extreme climate event that led to the extinction of numerous benthic foraminifera. For instance, the extinction of taxa with highly calcified and mega perforated taxa like Gavellinidae at the Shatsky Rise was followed by an increase in smaller-sized opportunistic taxa such as *Q. profunda*; (Table 3) with micro-perforated tests that require less dissolved oxygen and well adapted to high organic rain.

The result from statistical analyses showed that infaunal, sessile life habits, cylindrical elongate and bi-triserial test forms, complex terminal apertures and omnivorous feeding modes were the most resilient traits during the hyperthermal (Figure 5).

Along with other opportunistic taxa the *Buliminids, Bolivinids, Pleurostomellids* and *Stilostomellids* may have utilised their facultative anaerobic metabolism enhanced by cytoplasmic streaming to sustain calcification and drew down the excess dissolved inorganic carbon in the water column. Increase in populations of foraminifera during the recovery intervals in all the studied sites together with high-temperature feedbacks such as increase in precipitation and silicate weathering would have eventually returned the ocean to its normal state.

Acknowledgements

of Environmental Sciences, UOL provided parts of the funding for this study.

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