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Traits changes in Planktonic Foraminiferal during the Palaeocene-Eocene Thermal Maximum (PETM) at ODP Site 1265A, Walvis Ridge, SE Atlantic Ocean

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ABSTRACT

Microfossils from Ocean Drilling Program Leg 199, Site 1215A Cores H6-H8 have been analyzed for faunal assemblages and trait changes across the Paleocene-Eocene Thermal Maximum (PETM). The cores were collected from the Central Pacific Ocean at 5396 meters below sea level during the Paleogene Equatorial transect cruise aimed to study the evolution of the Paleogene Equatorial Pacific climate. The lithologic composition of the cores are mainly dark yellowish brown nannofossil clay with chert fragments in some sections. Microfossil extraction followed the conventional procedure of soaking, sieving and chemical treatment. Picking and trait analysis were done using the MEIJI phase contrast microscope and INFINITY analyser software. The foraminifera traits analyzed include; test composition, shape, chamber forms, ornamentation, living habit, aperture, sizes, and feeding habits. The result shows significant relationship between trait composition and environmental changes during the early Eocene warm event in the cores analysed.

Keywords: Foraminifera, Traits, Ordination, Ocean, Paleoecology.

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INTRODUCTION

Traits refer to well-defined and measurable attributes of an organism. Foraminiferal traits are closely related to the biological functions they perform in the marine ecosystem. For instance, test composition of foraminifera functions as a protective element and is known to reduce biological, physical and chemical stresses of foraminifera in their environment (Armstrong and Brasier, 2005; Dubicka et al. 2015).

Because of the significant role that foraminifera plays in the global carbon sequestration and food supply, it is very important to understand how they coped with this past climatic extreme and probably encourage the intervention that boasts their ecosystem services in order to understand how the current climate change may impact on the ecological function of marine environment in the future.

The main aim of this research is to examine the changes in trait composition of planktonic foraminifera across the Paleocene-Eocene Thermal Maximum PETM) at ODP site 1265A using a procedure known as the biological trait analysis (BTA) that allows the traits of organisms to be quantified. The samples for this study was sampled across the Paleocene-Eocene Thermal Maximum (PETM) interval at the Walvis Ridge.

The BTA has been previous used to examine the impact of ecological disturbance in the terrestrial plants (Olff et al., 1994; McIntyre et al., 1995), freshwater invertebrates (Townsend & Hildrew, 1994) and marine macrobenthic (Charvet et al., 1998; Bremner et al., 2006; 2008; Tyler et al. 2012; Frid et al 2009; Beauchard et al., 2017). The evidences from these studies show that the procedures is very strong in detecting the impact of anthropogenic disturbance in the ecosystem, this is because, the interaction between organisms with the environment as well as other organisms is controlled by the it's biological traits. Biological trait analysis has also been used to investigate the impact of extreme ecological condition on the on the ecological function of fossil macro benthos in deep time. For instance, Caswell and Frid, 2013 apply the techniques in the study of the impact of hypoxia (low oxygen) in the ecological functioning of fossil macro benthos (bivalve, molluscs, gastropods, brachiopods and echinoderms) from the Late Jurassic Kimmeridge Clay Formation (KCF; ~ 148 – 155 Ma) in the Wessex Basin, UK. Their study showed that extreme ecological pressures could lead to a collapse of functioning; nevertheless, change in the ecological functioning does not follow the same trend as species change.

BTA have not been previously applied in the study of microfossils, both in the continental and marine environment, but the results from previous studies enumerated above, motivated the use of the techniques in investigating the impact of the PETM on the ecological functioning of foraminifera (microfossil). The foraminifera turn-over during the PETM is well documented (Foster, et al. 2013, Jennions, et al. 2015, Giusberti, et al. 2016) based on faunal assemblage and geochemical data, but for the fact that foraminifera community interaction with the environment and with other marine fauna is driven by biological traits instead of taxonomic composition (McGill et al., 2006; Tyler et al. 2012), it becomes necessary to use the BTA in assessing the impact of the hyperthemal on the traits of foraminifera in the marine ecosystem.

METHODOLOGY

There are 35 cores samples used for this study. The sediments were weighed and transferred into the 250ml glass beaker and soaked with water overnight in a fume cupboard. This allows enough time for the sediment to disaggregate and the clays to be dissolved. The disaggregated sediment samples were washed with Endecotts stainless steel 63µ sieve under a running tap water. The recovered residues were transferred to a labeled filter paper placed in a funnel and dried in the laboratory oven. The dried residue was stored in vials for identification and counting.

Over 1000 species were counted for fraction and identified using the foraminifera albulm and other peer reviewed-publications. The trait analysis was done using the BTA . BTA is one of the statistical methods used by ecologists to study species distribution, the biological characteristics they exhibit and how it is related to the running of their ecosystem (e.g. Nwojiji et al., 2024; Bremner et al., 2006, Charvet et al., 2000; Elena et al., 2010; Paganelli et al., 2012; Caswell and Frid, 2017). BTA was initially designed to access terrestrial and fresh water biological community but has been recently modified and can be applied in all the ecosystems including the marine. The approach creates a meaningful connection between species, environments as well as processes within the trophic level. Biological trait analysis uses a series of life history, morphological and behavioural characteristics of species present in assemblages to indicate aspects of their ecological functioning. It has been successfully used to investigate anthropogenic influence in marine benthic ecosystem (Frid, 2000). Biological trait analysis has been widely applied in studying anthropogenic influence in modern ocean macro benthic communities and has successfully discriminated environmental disturbance. Due to the successes recorded on using the tool to study the functional ecology of marine benthos late Jurassic ocean anoxic event (see Caswell and Frid, 2013), we have deemed it necessary to deploy this approach in studying the traits of fossil foraminifera (zooplankton) across the Palaeocene- Eocene thermal maximum.

RESULTS

The key foraminifera traits identified include; Hyaline calcite test composition, Sprial, elongate, subquadrate, globose test shape, Trochospiral, planispiral, bispiral and trispiral chamber arrangement, keeled, deprtessed, muricae, ponticuli, hispid, and spinose ornamentation, arcuate, oval/reniform and slit-like aperture with lip as apertural accessory. Basal interiomargin, terminal, extra-umbilical, umbilical apertural position . performation include; fine, macro and microperforations and the feeding habit range from grazer, suspension feeding and symbiosis. Figure 1 below summarised the trait distribution across the studied section All the identified planktic foraminifera from the study site were composed of entirely hyaline calcite. This is the cause of collapse in trait richness at the beginning of the ocean anoxic event (OAE) resulting from carbonate dissolution that significantly reduced the faunal richness of the planktics taxa and traits during the period.

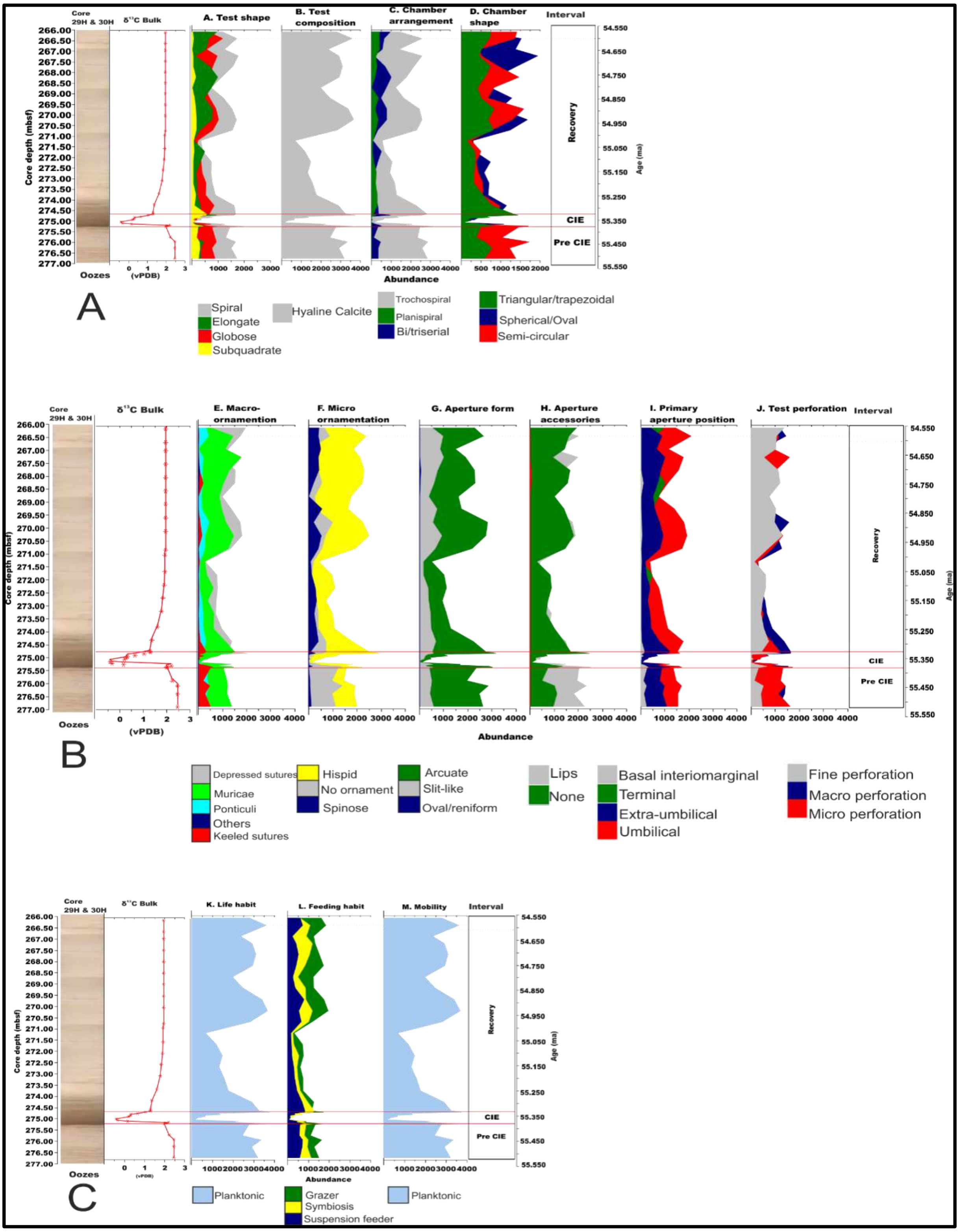

Figure 1: Planktonic foraminiferal traits distribution across the three intervals of PETM at ODP site 1265-South Atlantic Ocean shown with core depths (mbsf) on the left, bulk $\delta^{13}C$ record (extracted from Zachos et al., 2005) and age (ma) on the far right.

Biological Trait Analysis(BTA) was usd to check what trait is important. First the trait data was subjected to non-metric multidimentional ordination. The ordination of the planktonic foraminiferal traits composition grouped into three groups. The pre-CIE samples grouped nicely together, but the CIE samples stretched along a transact between the pre-CIE and recovery. The samples in the recovery grouped together but were more spread compared to the taxa nMDS especially at the upper part of the recovery (Figure 2). Sample depth 275.13mbsf classified as CIE based on carbon isotope record, ordinated with the pre-CIE and this could mean that trait changes did not start immediately with the negative carbon isotopic excursion (CIE). Samples from 274.68 mbsf and 274.58mbsf also classified as the upper part of the CIE were closer to the recovery than to the CIE and this could mean that the traits recovered earlier than the carbon isotope records. Or that the faunal turn over favoured the taxa that will enhance the ecosystem recovery from the OAE. Sample from 274.98mbsf identified as CIE lies quite outside the CIE group indicating the depth as the most affected part of the section during the OAE. The spread in the later part of the recovery samples could be a pointer to re-organization for the smaller hyperthermal that occurred during the early Eocene. The ANOSIM result showed that the three groups significantly differ at R=0.476 and p>0.1%.

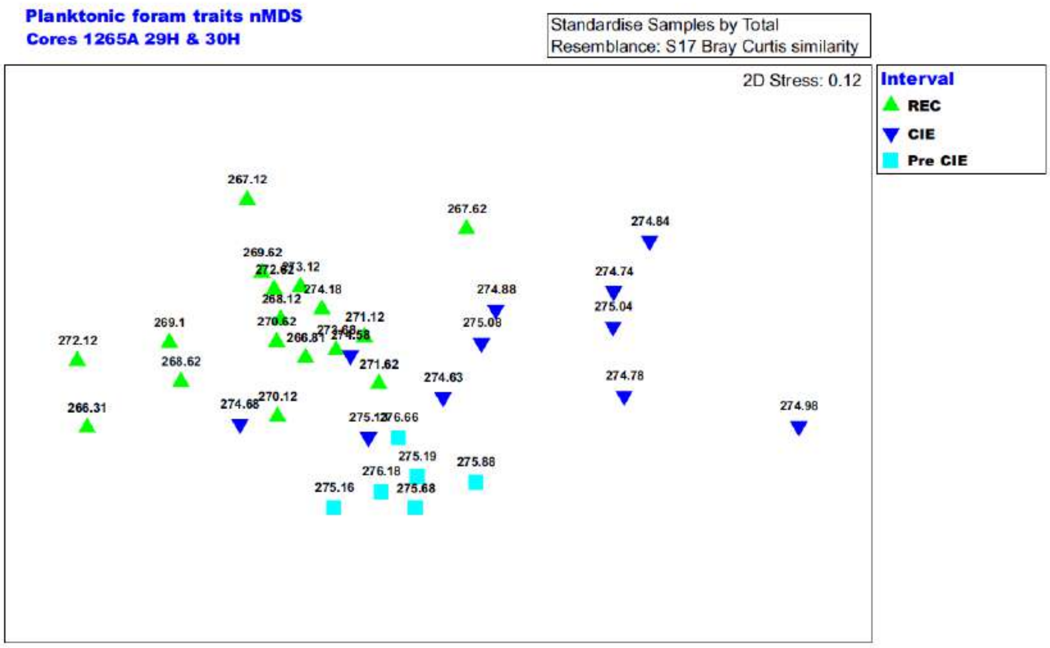

Figure 2 nMDS ordination of planktonic forams traits composition in site 1265. Pre CIE samples clustered at the base, CIE across the eastern axis and the recovery on western axis of the plot.

Moreso, the recovery interval differs from the CIE at R=0.493; p>0.1%; recovery and pre-CIE at R=0.545; p>0.1% and CIE and pre-CIE at R=0.322; p>0.8.

After ordination analysis, the data was subjected to similarity percentage analysis (SIMPER). The Simper result for planktonic foraminifera traits indicated that trochospiral trait was slightly more in relative abundance during the CIE than the recovery and about the same value before the CIE. A sequential decrease in the mean abundance of spherical/oval occurred from the pre-CIE to the recovery (Figure 3). Taxa with triangular/trapezoidal chamber were more abundant during the CIE than at the recovery and pre CIE but semi-circular chamber abundance was more during the pre-CIE than in the recovery and CIE intervals. The abundance of depressed sutures were more at the pre-CIE than during the recovery and CIE but less at the CIE than within the recovery interval.

There were more taxa with muricae structures during the CIE than the recovery and pre CIE. Muricate taxa are upper water colunm dwellers. This result shows that the relative increase in the abundance of Acrininids and Morozozovellids during the CIE was driven by trait changes other than taphonomic processes that was attributed to the reduction in the abundance of Subbotina during the same period. Keel ornamentation was more during the pre-CIE than CIE and recovery while taxa with no visible ornament were more before the CIE than at recovery and the main CIE interval. Hispid ornament was more during the CIE than at the recovery and before. The hispid ornament is peculiar to the Acaririnids and Morozovellids hence corroborating the increase of these taxa during the OAE. In addition, fewer taxa with apertural lip occurred during the recovery than at the CIE and pre-CIE. This result shows that the transformation before Simper analysis drastically reduced the influence of very high abundance taxa on the data. Taxa with no apertural accessories were more during the recovery than at the CIE and before. Mancini et al, 2013 reported that taxa with a complex apertural face (with neck, teeth lips) were known to be more competitive during the extreme ecological event as it provides strong support for feeding and defense. The reduction in the taxa with no apertural accessory supports this observation. The terminal apertures were more during the recovery than the CIE and pre CIE. However, the mean abundance of terminal aperture were higher before the CIE than in the main CIE section. Umbilical/extra-umbilical apertures were more during the CIE than the recovery and also more before the CIE than the recovery. Furthermore, the mean abundance of microperforation in foraminifera was about the same before and during the CIE but decreased during the recovery. Finely perforated taxa were more during the recovery than at the CIE and and before. Fine perforations are common in taxa like Globanomalids that dwell in the deeper part of the water column and this could mean that both the surface water and the meso pelagic ecosystem were both severely affected during the PETM. The mean abundance of taxa with grazing habit slightly reduced during the CIE than during the recovery and before pre-CIE (figure 3).

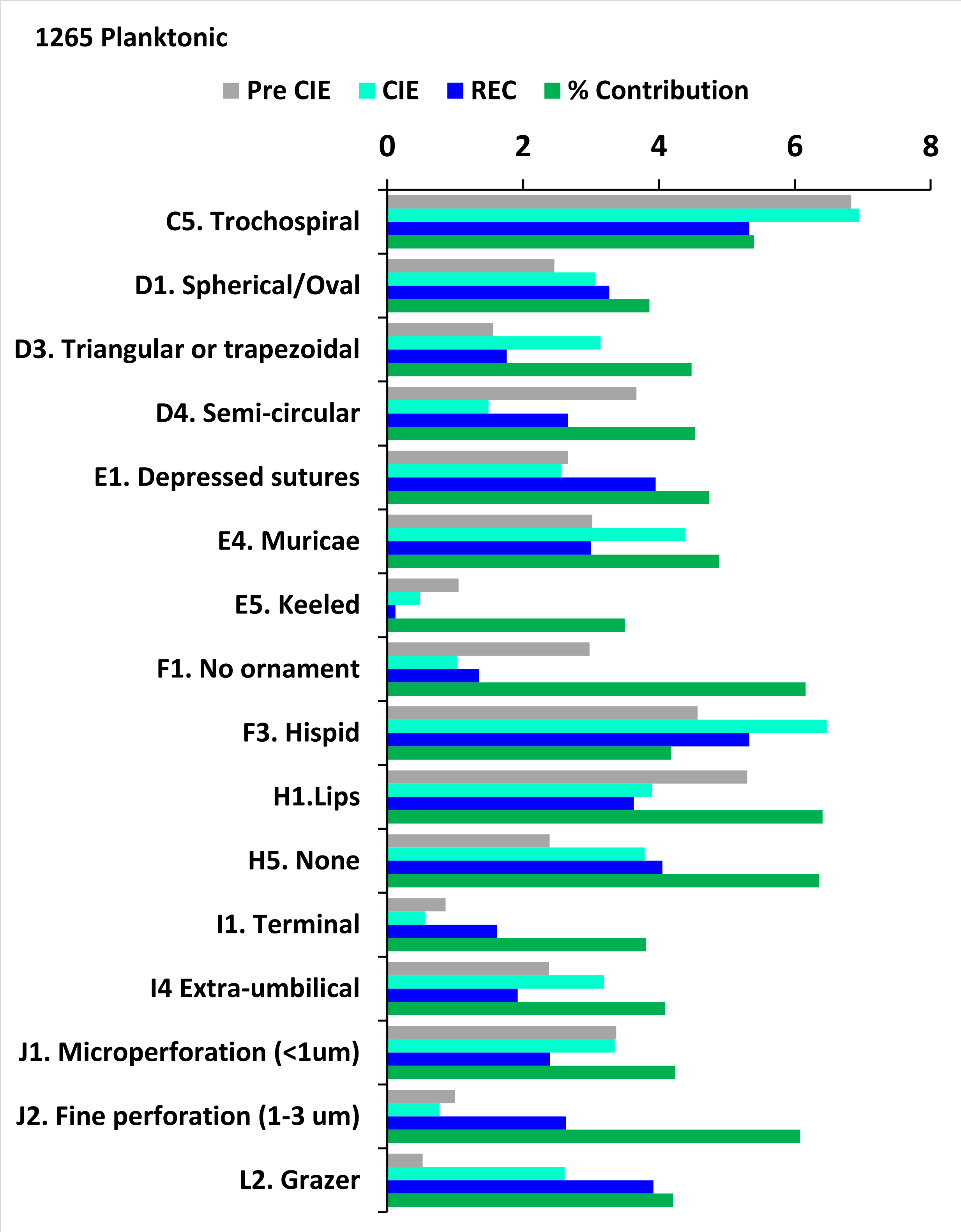

Figure 3: Mean abundance of planktonic foraminiferal traits driving the main differences in distribution across the PETM interval at site 1265A

DISCUSSIONS

Biological trait analysis (BTA) is well suited for the understanding of functional diversity in palaeoecological data (Caswell and Frid, 2013) as it can be used to compare spatially and temporally separated communities with different taxonomic composition. The result from this study has confirmed some striking similarities in both planktonic and benthic traits during the analysed section of the PETM. The functional richness in the benthic foraminifera are much higher compared with planktonic assemblage and this is a clear reflection of the taxonomic richness of the two group. Planktonic fauna composition has about 57 species while the benthic fauna has 134 species. Because of the dissimilarities in the faunal composition in these two groups of foraminifera, their trait composition significantly differ as well. Despite the differences in species richness and trait composition, there is a positive correlation between some trait modalities. The relative increase in this trait could be interpreted as the increase in opportunist taxa during the OAE. In the modern ocean, there have been wide reports of an increase in cosmopolitan lifestyle during environmental disturbance (Culver and Lipps, 2003; Bremner et al., 2006). In term of the planktonic community, we think it is linked to increasing temperature and oligotrophy as most of the trochospiral fauna were mostly Acarinina and Morozovella while Subbotina was rare. Trochospiral coiling is also argued to be advantageous for floating and attachment at the sediment-water interface during the times of disturbance in the bottom water (D'haenens et al., 2012). The Simper result also demonstrates that spherical/oval chamber shape are important foraminifera trait, it occurred in both planktonic and benthic trait composition and showed a strong correlation in the occurrence across the studied PETM section. The trait shares many characteristics with the trochospiral trait described above and it further supports all the theories discussed above.

Ornamentation is a very crucial ecological function parameter in the planktonic community, more than seven (7) trait indicating ornamentation contributed to the most dissimilarity recorded in the planktonic trait Simper result. Muricae and hispid ornamentations are the most successful/ resilient trait while keel ornament is the most fragile. Taxa with large positive ornamentation tend to be more successful because they have low surface to volume ratio compared to the keeled and cancellate taxa that are strongly perforated and perforation create access for fluid to enter the test and dissolve the walls. In the benthic community, taxa with no ornamentation are the most successful and this corroborates Dubicka et al., (2015) observation that extreme ecological condition leads to loss of ornamentation in some species of foraminifera.

Test composition also come out as a very crucial functional trait from biological trait analysis, the result shows that $CaCO_3$ concentration at the Walvis Ridge was highest before the onset of the CIE. The period of OAE recorded the lowest number of taxa with hyaline calcite test indicating a fall in the $CaCO_3$, more so the mean value of the hyaline calcite test increased during the recovery but did not reach the pre CIE value and this trend corroborates with the $\delta^{13}C$ carbon isotope record. A similar circumstance has been documented in other PETM section such as the Shatsky Rise, Alamedilla and Bass River (Alegret et al. 2009; Petrizzo, 2007; Aze et al 2014; Stassen et al., 2015). The increase in a porcelaneous trait in the benthic ecosystem during the CIE and the recovery raises the question of the solubility high magnesium calcite test during ocean acidification.

CONCLUSIONS

The primary aim of this study was to understand the sensitivity of foraminifera trait to the ecological changes associated with the PETM. The results from BTA have provided good insight into this objective. The nMDS clearly demonstrated the reaction of foraminifera to the ecological disturbance, the planktonic community was relatively stable before and after PETM but experience a high level of ecological perturbation during the CIE. The planktonic trait distribution also indicated a relatively calm pre-CIE and recovery and evidence of disturbance during the PETM. We noticed that two samples classified as the upper part of the CIE were closer to the recovery than to the CIE and this could mean that the traits started to recover earlier than the carbon isotope records in the surface ocean. Planktonic fauna may have adjusted in such a way to favour taxa with traits that could enhance the recovery of the ecosystem. The BTA has also enabled us to identify some critical trait that controls the function of foraminifera in their ecosystem, these include: test composition, chamber arrangement/ shape ornamentation, primary aperture position, perforations and living/feeding habit. In the beginning of this study we were contemplating which trait was crucial and which one was not but this study has identified the important traits that should be focussed in the future studies of foraminiferal trait. The biotic and trait records from our study suggest massive carbonate dissolution and relatively normal oceanic productivity at the Walvis Ridge during the PETM and except for the decline in the amount of nutrient reaching the mesopelagic zone, however, it is hard to interpret the amount of oxygen concentration probably because of the ridge topography with enhanced current activities including eddies and circular current that prevail around the seamount and transport nutrient and oxygen from the surface to the sea floor. This is also made more complicated by the behaviour of some foraminifera in the low oxygen environment, if they have an alternative method of respiring nitrate in the absence of oxygen.

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