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Deep-Sea Benthic Foraminiferal Distribution in South West Indian Ocean: Implications to Paleoecology

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Abstract

Five grab samples from the southwestern part of the Indian ocean were collected by ORV *Sagar Kanya* during the third expedition to the southern Indian ocean in June 2009. The sediment samples have been analyzed and recorded 36 benthic foraminiferal species belonging to 21 genera and 3 suborders. All the species were taxonomically identified, SEM photographed and illustrated. Deep sea-benthic foraminiferal species at different locations of South of West India Ocean (3150-4125 m water depth) is examined in terms of number of species (n) and diversity (d). The observed depth ranges of benthic foraminifera have been documented to recognize their bathymetric distribution. The valves of these parameters reached their maximum at 3190 m water depth. Productivity continued in the Indo-Pacific Ocean (the biogenic boom) and the Oxygen minimum zone (OMZ) intensified over large parts of Indian Ocean continually. The diversity values show more abrupt trend as depth increases. Species like *Epistominella exigua* and *Pullenia bulloides* occur at both 3150 m & 3465 m depths indicating depth persistence. Further, *Oridorsalis umbonatus* and *Melonis sphaeroides* occur at both 3150 m & 3465 m depths. Species like *Gyroidina* sp an indicate of low oxygen environment and *Uvigerina hispida-costata* indicative of high organic carbon are found to occur at 3150 m & 3740 m respectively. Factor analysis and Pearson correlation matrix was performed on foraminiferal census data of 10 highest ranked species which are present in at least one sample. 3 factors were obtained accounting for 72.81% of the total variance. Thus the study suggests that fluctuations in species diversity at the locations of the present study were related to changes in productivity during the geological past. Further, the faunal data do indicate the early Holocene Indian Ocean was influenced by increased ventilation perhaps by North Atlantic deep water and or circumpolar deep waters.

Keywords: Paleoecology, Benthicforaminifera, Holocene, Indian Ocean

1. Introduction

Considerable amount of work has been done to understand Paleoecology, Paleoclimatic and Paleoocenographic evolution of the Indian Ocean during Pleistocene and Holocene using faunal data [1,2]. Benthic foraminifera have substantial scope in paleoecological studies because of their wide distribution in all marine environments and the high fossilization potential of their tests. During the last three decades, several hypotheses have been proposed to explain the distribution patterns and ecologic preferences of this group. For instance, benthic foraminifera have been used extensively to reconstruct the past variability in deep water properties in different ocean basins explained the relationship of various taxa with different levels of deep-sea oxygenation, whereas other studies have related benthic assemblages to the intensity of deep sea currents and ventilation [3]. The fact that benthic foraminifera occupy both epifaunal and infaunal microhabitats led some workers to suggest that sediment and pore water properties may be more important than bottom water conditions in controlling benthic foraminiferal distribution [4,5]. Other studies indicate that benthic foraminiferal assemblages are strongly correlated with productivity of the overlying surface waters and the flux of organic matter to the seafloor. Faunal proxy data suggests major changes in the Cenozoic Earths climate forms relatively warm and equable climate in the Paleocene to cold conditions with nearly frizzing temperatures at the poles in the Pliocene [6]. Other changes during this time include those in ocean circulation and productivity and opening and closing of different seaways, including the closure of Tethyan Seaways, including the closure of the Panamanian sea way in the Pliocene [7]. The changes in Antarctic climate during the middle Miocene brought significant changes in ocean surface productivity and oxygenation of deep waters as well [8], which had an impact on the oceans faunal regime. Productivity has increased significantly in all oceans since the late middle Miocene (~ 13 Ma). The increased glaciations on Antarctica may have intensified wind regimes, loading to widespread open-ocean as well as coastal upwelling over large parts of the Indian, Pacific and Atlantic oceans during the middle Miocene [8]. These productivity events are believed to have triggered the “biogenic bloom” and expansion of the oxygen minimum zone in large parts of the intermediate water of the Indian and Pacific Oceans in the late middle Miocene, about 15 Ma [9]. With these climatic and oceanic changes, deep-sea faunal diversity changed considerably [10].

Availability of nutrients, heterogeneity of the habitat and predation are factors controlling diversity patterns in the deep-sea fauna [10]. It’s also observed, low values of species diversity during intervals of environmental instability in the South Indian Ocean in the middle – late Miocene. The high productivity and subsequent microbial decay of organic matter, as well as biotic respiration and other oceanographic factors, lead to extremely low oxygen concentrations in the water column, forming a pronounced oxygen minimum zone (OMZ). Underlying sediments thus contain a geological record of changes in the SW monsoon and OMZ variability [11]. Benthic foraminifera dominate modern ocean floor meiobenthic communities, and in many deep-sea areas, constitute a substantial proportion of the eukaryotic biomass [6]. Due to their high fossilization potential they area very useful in paleooceanograpgic studies. The factors controlling their distribution and abundance are complex and controversial [12], but it appears that two usually inversely related parameters, the flux of organic particulate matter to the sea floor and oxygen concentrations of bottom water and pore waters, are major controlling variables [5]. Other factors which have been suggested (and some of which are not independent of these two) include the type of food supply, bathymetry, sediment type, chemistry of bottom waters current flow intensity and hydrostatic pressure [13]. The supply of organic matter from the euphotic zone to the ocean floor exerts a strong influence on the abundance and biomass of deep-sea benthic foraminifera [12] as on other deep-sea organisms.

The composition of benthic foraminiferal assemblages is closely related to the amount and quality of organic matter. Assemblages dominated by the in faunal species *Bolivina, Bulimina, Melonis* and *Uvigerina* commonly occur in areas with high, continuous fluxes of organic matter to the sea floor, often associated with reduced bottom water oxygen concentrations. It has been shown, however, that *Uvigerina* spp are correlated to organic flux and not to low oxygen conditions. To understand the distribution and diversity of benthic foraminifera at different bathymetric levels, the present study was carried out. Benthic foraminiferal species used in the faunal study include, *Uvigerina hispida-costata* which was dominant during times of high productivity and /or low oxygen and *Oridorsalis umbonatus* and *Quinqueloculina parkeri* characteristic of well oxygenated, oligotrophic conditions. Changes in organic flux to the sea floor due to variations in surface productivity modulate deep-sea faunal composition [3]. The amount of organic flux to the sea floor not only depends on surface production but also on the nature of deep-sea column. Well oxygenated deep-sea circulation may cause remineralization of organic carbon resulting in little organic material reaching the sea floor [14]. To understand if the changes in the surface and deep-water column of the tropical condition ocean driven by the Indian ocean climate (monsoon) and deep-sea circulation, an attempt has been made to analyze deep-sea benthic foraminifera from varying depths from (3150 m, 3465 m and 4125 m) (**Figure 1**). The investigations of benthic foraminifera from south west Indian Ocean provided data on the species distribution and species-specific relations for different depths and areas. These data were later used to distinguish faunistive provinces with the implication to paleoecology. The study presented is aimed at the description of the biogeography and ecology of foraminifera communities based on the data about the dominant species in the tropical Indian Ocean and their occurrences in other areas of the world Ocean.

2. Materials and Methods

The study sites are located at different depths of 3150 m (N 10º E 65º); 3465 m (N 5º E 65º); 3790m (N 0º E 65º) and 4125 m (N 5º E 65º) in the South West Indian Ocean. The samples were collected from ORV *Sagar Kanya* during the third expedition to the southern Indian Ocean by National Center for Antarctica and Ocean Research, (NCAOR) Goa, India, in June, 2009. Sediment samples were transferred into plastic bags and frozen until analysis was carried out. The sediment samples were first washed over a sieve which is an average opening of 0.625 mm. This process helps to wash the sample free of sea water, fixatives, and the fine silt and clay size particles. Then a sample was air dried and a suitable sample weighing about 100 grams was obtained by coning and quartering. Samples were spilt using a micro splitter and all benthic foraminifera were picked and identified [15]. Quantitatively, foraminifera could not be separated easily with washing carbon tetra chloride only, so a mixture of Bromoform (specific gravity 2.8) and Acetone (specific gravity 2.4) were used to obtain about 15% crop from the sediment [16]. The residue was examined under a stereo binocular microscope for any left out fauna. Such tests were handpicked by a very fine pointed long haired welted Windsor Newton sable hair brush (“0”). The fauna thus obtained was sorted, counted and identified under a stereo binocular microscope using medium to high magnifications (6.3 × 2.5; 6.3 × 4.0). The sampling procedures especially sieving and drying reduce the number of the most fragile arenaceous foraminifera (**Table 2**). Statistical analysis was done by multivariate analysis, correlation analysis was applied to compare and correlate the data generated based on bathymetry [17]. Details of the hydrography, primary productivity and upper ocean mixed layer dynamics are given earlier [18].

To day, the depth of site 4125 m (S 10º E 65º) is close to the calcite Lysocline which, in this part of the Indian Ocean, has been considered to lie between 4000-4200 m and approaches calcite composition depth (CCD). This area was selected because it is a relatively flat area, far from continental shelf to the east and the mid-ocean ridge to the west and so is unlikely to be influenced by strong down slopes or adjective process. Recent sediments in the study area are calcareous oozes with rich biogenic carbonate with $CaCO_3$. In this study, the absolute abundance and species diversity of fauna in the sediment fraction of > 63 µm in weight % of total sediment. In addition, the state of preservation of foraminiferal tests was noted in the samples. Benthic foraminiferal species *Uvigerina hispida-costata, Oridorsalis umbonatus* and *Quinqueloculina* spp to understand changes in deep-sea organic carbon and oxygen content. Approximately 100-300 specimens of benthic foraminifera were picked from a suitable sample and their diversity and distribution were calculated (**Table 1**).

3. General Setting

Sampling stations are, at present located in subtropical waters. In the present-day locations, is bathed by low-oxygen and relatively productive deep waters of the northern Indian origin deep-sea benthic foraminife ra-provides useful information on the influence of various deep-water masses in the region. The physico-chemical properties of the surface waters in the western Indian Ocean are strongly influenced by African through flow water because of substantial export of freshwater and heat from the Pacific into the Indian Ocean through the Indian seas. At present, the area is influenced by the summer monsoon winds producing major divergence and an open-ocean upwelling. In the present-day ocean, the in situ primary production in the surface waters is between 200 and 300 mg during the summer monsoon, which is reduced during the winter monsoon.

Table 1. Benthic foraminiferal species number with depth (m).

S.No.	Species	Depth (m)			
		3150	3465	3790	4125
1	Marginopora vertibralis	164			
2	Sorites marginalis	131			
3	Borelis schlumbergeri	152			
4	Heterostegina depressa	140			
5	Elphidium crispum	131			
6	Ammonia tepida	129			
7	Quinqueloculina parkeri	153			
8	Spirillina decorata	146			
9	Textularia sagittula	133			
10	Eponides repandus	136			
11	Calcarina calcar	166			
12	Gyroidina sp.	156			
13	Pyrgo murrhina	145			
14	Bulimina alazanensis	135			
15	Pullenia subcarinata	148			
16	Discopulvinulina bertheloti	164			
17	Epistominella exigua	281	292		
18	Pullenia bulloides	136	156		
19	Gyroidina neosoldani		145		
20	Astrononion umbilicatulum		142		
21	Planulina wuellerstorfi			132	
22	Oolina apiculata			163	
23	Oolina desophora			155	
24	Laticarinina pauperata			145	
25	Fissurina sp.			165	
26	Fissurina alveolata			148	
27	Nummoloculina sp.			156	
28	Pullenia quinqueloba			148	
29	Lagena stelligera			158	
30	Oridorsalis umbonatus	286		278	
31	Melonis sphaeroides	279		214	
32	Chilostomella ovoidea				153
33	Uvigerina hispida				289
34	Uvigerina hispido-costata				163
35	Eggerella bradyi				180
36	Karreriella bradyi				163

4. Ecological Preference of Foraminiferal Proxies Used

The study of benthic foraminifera is very useful in interpreting the changes in deep-sea environment. They are the longest biomass present at the lower (> 1000 m) and abyssal depths in the modern oceans and are the dominant carbonate tests to be preserved in the deep sea sediments. Many benthic species have separate stratographic ranges and their evolutionary and migratory patterns provide significant biostratigraphic and paleo-ecological information about the deep-sea environments [19].

Uvigerina hispido-costata preferentially occupies the uppermost surface centimeter of organic rich sediments feeding on sediment aggregates, algal remains, and bacteria having highest abundance in the lower part of the OMZ below upwelling areas reflecting a preference for suboxic or dysoxic conditions in the pore bottom water [20]. This species has highest population at water depths between ~300 and 800 m with *insitu* temperature 10-15°C and low oxygen. This species has been used as an indicator species for deepening/shoaling of the OMZ base in the northern Arabian Sea [21]. The large abundance of *U. perigrina* in the lower part of the OMZ or below indicate adaptation of this species to degraded organic matter [21]. *Oridorralis umbonatus* is a cosmopolitan taxon or lower bathyal and abyssal faunas in the Indian [22]. The Atlantic [23] and Antarctic oceans [24] and is often found associated with Antarctic bottom water (AABW) [22]. This species has been reported to indicate a well oxygenated and low organic carbon environment [25]. This species was probably of southern origin with a strongly pulsed food supply and carbonate preservation in an overall oligitrophic environment in the eastern Indian [26]. *O. umbonatus* reflects low organic carbon and higher carbonate saturation levels of bottom waters in the Sulu Sea [27]. *Quinqueloculina* is a cosmopolitan miliolid group found between 800-5000 m water depths in the Indian Ocean [28]. The persistence occurrence of milioliods in the Arabian sea indicates an overall better oxygenation of benthic environment and thus this group can be regarded as a sensitive oxygen marker and its population a toll for reconstructing past climatic changes in bottom water oxygenation [29]. Higher abundance of miliolid group in sediments deposited during glacial intervals under higher-salinity conditions in the northern Red Sea. Miliolids in general, are rare or absent oxygen deferent environments [13]. *Bulimina alzaninsis* is an intermediate to deep in faunal (> 2 cm) species in the Sulu sea and is dominant at bathyal depths (1500-2000 m) just below the Arabian sea OMZ [30].

5. Discussion

In the Indian Ocean, changes in benthic foraminiferal populations have occurred at orbital time scales and have been related to changes in the Indian monsoons [31]. More recently, [2] used environmental preferences of various benthic foraminiferal assemblages and related them to change in seasonality in the Indian Ocean monsoon during the Plio-Pleistocene. In the present study, we attempt to understand paleoceanographic changes in the southeastern Indian Ocean using multivariate analysis of deep-sea benthic foraminiferal census data from south western sampling stations (**Figure 1**). The interpretations are based on recent environmental preferences of various benthic foraminiferal taxa observed in the Indian as well as abroad.

Deep-sea benthic foraminifera have been used to understand changes in deep water condition driven by climate forcing during the Pliocene and Pleistocene [29]. Several studies have been shown the relationship between benthic faunal composition, productivity of the overlying waters and organic flux to the sea floor [12]. Others suggested oxygen and food supply are the main factors controlling the spatial and in-sediment distribution of benthic foraminifera [29]. This group explains seasonal fluctuations in primary production [5]. Thus benthic foraminifera are considered useful for estimating paleoecology and they are also more resistant to digenetic change compared to planktic foraminifera. However, in oligotrophic areas deep-sea oxygenation plays an important role in controlling benthic foraminifera over different time scales. It is believed that changes in oxygenation are linked partially to productivity and partially to changes in deep-water ventilation [3]. Wind driven coastal and open-ocean surface productivity influences organic carbon flux and oxygenation of deep waters controlling benthic populations in the Arabian Sea. In the Northern part of the Indian Ocean, the wind regimes follow seasonal changes in circulation producing wide spread upwelling controlling surface productivity. Because of the sampling locations in oligotrophic areas

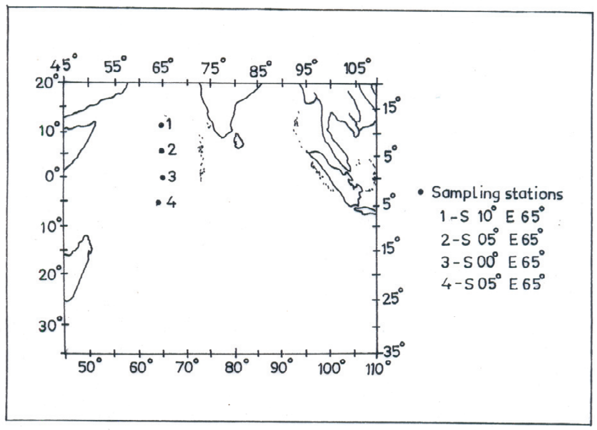

Figure 1. Map showing sampling locations in the tropical Indian Ocean.

with high dissolved oxygen content during the studies period, the changes in benthic foraminiferal population might have been linked to the supply of organic food.

6. Results

The absolute abundances (number of specimens per gram bulk sediment) of benthic foraminifera fluctuate largely. A total of 36 species of benthic foraminifera were recognized comprising predominantly of small calcareous species. In the samples (3150 m, 3465 m, 3790 m and 4125 m water depth) used in the benthic foraminiferal distribution, the abundant species occur in sample 3150 m are *Gyroidina* sp, *Pyrgo* murrhina, *Bulimina alazanensis Pullenia subcarinata, Discopulvinulina bertheloti, Epistominella exigua* and *Pullenie bulloides*; at sample 3465 m depth are *Epistominella exigua, Pullenia bulloides, Gyroidina neosoldani* and *Astrononion umbilicatalum*; at sample 3790 m depth are *Planulina wullerstorfi, Oolina apiculata, Oolina desophora, Laticarinina pauperata, Fissurina alveolata, Nummoloculina* sp, *Pullenia quinqueloba, Lagena stelligera, Oridorsalis umbonatus, Melonis sphaeroides* and *Chilostomella ovoidea* at sample 4125 m water depths are *Uvigerina hispido-costata, Eggerella bradyi and Karreriella bradyi.*

7. Factor Analysis

The foraminiferal data census of 10 species was subjected to the factor analysis. The analysis yield three factors namely Factor 1 (37.11%), Factor 2 (25.87%) and Factor 3 (10.83%) accounting for 72.81% (**Table 3**).

Factor 1

Factor 1 represented by *Uvigerina hispida* (0.827), *Eggerella bradyi* (0.827), *Epistominella exigua* (−0.796) and *Pullenia bulloides* (0.766). *Uvigerina hispida* relates continuous, high organic flux, low seasonality. *Eggerella bradyi* reflects cool, carbonate corrosive organic flux, variable and high oxygenation [8].

Factor 2

Factor 2 is dominated by *Gyroidina neosoldani* (−0.984), *Astrononion umbilicatulum* (−0.984); *Oridorsalis umbonatus* (0.713) and *Melonis sphaeroides* (0.700). This factor indicates intermediate organic flux, intermediate to high seasonality, high-moderate organic flux, intermediate high seasonality, refractory organic matter. However, *Oridorsalis umbonatus* tend to reflect relatively warm intermediate organic flux, intermediate seasonality, and moderate oxygenation [8].

Factor 3

Factor 3 comprises of *Calcarina calcar* (−0.465), *Oridorsalis umbonatus* (0.364) and are *Epistominella exigua* (−0.306). Three species indicate cool strongly pulsed, low to intermediate organic flux, high seasonality. In addition, relatively warm intermediate organic flux, intermediate seasonality, moderate oxygenation is also reflected.

A cross plot of Factors 1 & 2 and Factors 1& 3 gives district information of faunal assemblages a set clustered similar factor. Pearson correlation matrix of dominated species (**Table 2**) shows the distinct positive and negative correlation with a specific species. *Calcarina calcar* and *Gyroidina* sp shows high positive relation with *Melonis sphaeroides* (0.717), *Oridorsalis umbonatus* (0.594), *Epistominella exigua* (0.555). *Epistominella exigua* and *Pullenia bulloides* correlated positively with *Pullenia bulloides* (0.998), *Gyroidina neosoldani* (0.599) and *Astrononion umbilicatulum* (0.599). Where as *Gyroidina neosoldani*, *Astrononion umbilicatulum, Oridorsalis umbonatus, Melonis sphaeroides* shows negative correlation with other species (**Table 2**). The vertical distribution of living benthic foraminifera within the sediment is controlled largely by a combination of oxygen content and organic carbon levels [4,13]. In eutrophic regions, oxygen decreases close to the sediment surface and becomes a limiting factor, favouring low-

Table 2. Pearson correlation matrix of 10 dominant species.

Variables	Calcarina calcar	Gyroidina sp.	Epistominella exigua	Pullenia bulloides	Gyroidina neosoldani	Astrononion umbilicatulum	Oridorsalis umbonatus	Melonis sphaeroides	Uvigerina hispida	Eggerella bradyi
Calcarina calcar	**1**									
Gyroidina sp.	1.000	**1**								
Epistominella exigua	0.555	0.555	**1**							
Pullenia bulloides	0.496	0.496	0.998	**1**						
Gyroidina neosoldani	−0.333	−0.333	0.599	0.653	**1**					
Astrononion umbilicatulum	−0.333	−0.333	0.599	0.653	1.000	**1**				
Oridorsalis umbonatus	0.594	0.594	−0.005	−0.055	−0.577	−0.577	**1**			
Melonis sphaeroides	0.717	0.717	0.108	0.053	−0.568	−0.568	0.987	**1**		
Uvigerina hispida	−0.333	−0.333	−0.577	−0.575	−0.333	−0.333	−0.577	−0.568	**1**	
Eggerella bradyi	−0.333	−0.333	−0.577	−0.575	−0.333	−0.333	−0.577	−0.568	1.000	**1**

Table 3.Factor loading scores for 10 dominant species.

Species	F1	F2	F3
Calcarina calcar	**−0.786**	0.408	−0.465
Gyroidina sp.	**−0.786**	0.408	−0.465
Epistominella exigua	**−0.796**	−0.522	−0.306
Pullenia bulloides	**−0.766**	−0.579	−0.281
Gyroidina neosoldani	−0.146	**−0.984**	0.100
Astrononion umbilicatulum	−0.146	**−0.984**	0.100
Oridorsalis umbonatus	−0.600	**0.713**	0.364
Melonis sphaeroides	−0.679	**0.700**	0.220
Uvigerina hispida	**0.827**	0.161	−0.539
Eggerella bradyi	**0.827**	0.161	−0.539

oxygen species. In oligotrophic areas, most of the organic matter is remineralized near the sediment surface and the sediment is well oxygenated to a significant depth. Such environments are foodlimited and favour epifaunal species, which are intolerant of low oxygen concentrations. [5] suggested that the dynamics of foraminiferal populations can be explained by the interplay between food and oxygen availability. For example, in eutrophic environments population fluctuations will be driven mainly by changes in both food and oxygen availability whereas in food-limited (oligotrophic) systems the populations will be driven solely by changes in the food supply [14]. It has been found that some species of benthic foraminifera are opportunistic and prefer to feed on seasonal fluxes of organic matter in overall oligotrophic central oceanic areas or seasonally upwelling areas on continental margins [32]. The non-opportunists thrive during sustained supply of organic particles [6,32]. Besides, certain species have a preference to decayed organic matter that reaches the seafloor [4,21].

The vertical distribution of benthic foraminifera in Indian Ocean is given in **Table 2**. A total of 36 species of benthic foraminifera were recognized comprising predominantly of small calcareous species from western Indian Ocean and 11 larger benthic species from Mauritius. The table shows that species like *Epistominella exigua* and *Pullenia bulloides* occur at both 3150 m and 3465 m depths indicating depth persistence. *Epistominella exigua* is an epibenthic, cosmopolitan, abyssal species, which feeds opportunistically on phytodetritus deposited seasonally on the sea floor [11]. It is suggested that this species is most abundant at highly seasonal food fluxes that occur more than once a year (e.g., spring and fall blooms; [14]). Futhermore, *Oridorsalis umbonatus* and *Melonis sphaeroides* occur at both 3150 and 3740 m depths indicating shelf fauna. species like *Gyroidina* spp an indicative of low oxygen environment and *Uvigerina hispido-costata* indicate high organic carbon are found to occur at 3150 m and 4125 m respectively. Changes in open-ocean surface productivity, linked to the wind regimes and major surface currents, influence the organic carbon fluxes and oxygenation of deep waters and thus benthic populations. Samplings Sites has moved from a temperate to subtropical position through the Miocene and is suitable to understand the effect of this northward movement on deep-sea fauna. The benthic foraminiferal vertical distributional pattern indicates important shifts in the character and amount of organic carbon flux and in oxygenation of deep waters at stations. This study suggests that benthic ecosystem variability in the deep Indian Ocean is not only driven by variations in monsoonal upwelling and related organic matter flux but also by changes in deeper water ventilation; increased summer monsoon circulation may not always result in an oxygen poor deep ocean with increased to total organic carbon (TOC) accumulation.

8. Conclusions

1) Benthic foraminiferal faunal distribution and species is erratic and appears to be influenced by availability of nutrients and oxygen content during seasonal upwelling (**Table 4**).

2) Changes in the abundance and diversity of benthic foraminiferal fauna are likely caused by variations in seasonal upwelling on the ocean floor at the sampling site.

3) The foraminiferal data show that it's relatively well oxygenated OMZ where the influence of intense monsoon-related production was migrated.

4) The high variability in the tropical deep-sea environments occurred at a time when the earth's climate was exploring large scale turnovers due to the increased intensity of glacial-interglacial cycles (**Table 4**).

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Table 4. Benthic foraminiferal species and bio faces.

Factors	Environment
Factor I *Uvigerina hispida* (0.827) *Eggerella bradyi* (0.827) *Epistominella exigua* (−0.796) *Calcarina calcar* (−0.786)	Continuous High organic flux Low seasonality, Cool Carbonate, Corrosive organic flux variable, high oxygenation.
Factor II *Gyroidina neosoldani* (−0.984) *Astrononion umbilicatalum* (−0.984) *Oridorsalis umbonatus* (0.713) *Melonis spharoides* (0.700)	Intermediate organic flux, Intermediate to high seasonality High-moderate organic flux intermediate seasonality
Factor III *Calcarina calcar* (−0.465) *Oridorsalis umbonatus* (0.364) *Epistominella exigua* (−0.306)	Cool, Strong by pulsed organic flux, high oxygenation, high seasonality, Relative warm, intermediate seasonality, Moderate oxygenation

*Values in parenthesis indicate factor scores for species.

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