Deep-sea palaeoceanographic evolution of the eastern Indian Ocean during the late Oligocene–Pleistocene: species diversity trends in benthic foraminifera

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Latest Oligocene–Pleistocene deep sea benthic foraminiferal species diversity parameters, including information function (*H*), equitability (*E*) and number of species (*S*) were analysed at Deep Sea Drilling Project sites 214 and 216 and Ocean Drilling Program holes 758A, 757B, 756B and 752A, presently located between 30.53°S and 5.23°N at lower bathyal to abyssal depths, in the eastern Indian Ocean. The values of these parameters have enabled us to understand deep-sea palaeoceanographic changes in the eastern Indian Ocean during the studied interval. The major changes in diversity parameters show close linkages to changes in the location of sites/holes, water mass stratification, productivity and high-latitude glaciations. Major Antarctic glaciations and intensification of the Indian Ocean oxygen minimum zone appear to have impacted deep-sea benthic foraminiferal diversity during the middle Miocene–early Pliocene. The water mass stratification in the eastern Indian Ocean appears to have intensified at ~17 Ma and peaked at ~12 Ma. The number of species, in general, is higher at low-latitude hole 758A and lower at high-latitude hole 756B, supporting the earlier hypothesis that *S* has an inverse relation with the latitudes.

Keywords: Benthic foraminifera, palaeoceanography, species diversity, water mass stratification.

Introduction

THERMOHALINE circulation plays an important role in global climate variability and evolution of deep-sea faunal provinces[1]. Climate proxies suggest that significant climatic and oceanographic changes have occurred during the Neogene resulting from changes in continental configuration[2,3]. The thermal isolation of Antarctica as well as shaping of the ocean basins during the late Oligocene–early Miocene led to the establishment of permanent temperature gradients between poles and tropics[2]. These turnovers in ocean–climate system brought major changes in surface ocean productivity and oxygenation of deep waters[3,4], impacting faunal regimes of the ocean. Deep-sea benthic foraminifera underwent important changes in both population of individual species and species assemblages in response to changes in the geometry of ocean basins and continents.

The decreasing pattern of species diversity with increasing latitude has been observed in numerous taxonomic groups on Earth[5,6], although exceptions exist[5,7]. The latitudinal species diversity gradients are increasingly well documented with their correlation with water temperature, water depth, surface productivity, seasonality of organic flux, salinity and ice cover[7–14]. Species diversity usually increases with temperature in the shallow-marine environments[7,8], at least when mean annual sea-surface temperature is < 25°C (ref. 9) and shows a positive relationship with water depth down to middle bathyal depth[15]. The diversity decreases at greater depths owing to the influence of deep water circulation and/or dissolution in the Indian Ocean. The benthic foraminiferal diversity is predominantly controlled by water depth in the Arctic[16], by seasonality in organic flux in the North Atlantic[11], by temperature in the North Pacific[16] and by glaciations at higher latitudes in the eastern Indian Ocean[10,14]. However, the ecological preferences of taxa and their relation with water mass stratification also play a significant role in controlling species diversity[16,17]. Heterogeneity of habitat and predation are other important factors bringing changes in deep-sea species diversity patterns[18]. Yasuhara *et al.*[13] suggested that a multiplicity of variables appears to be related to community structure in the system. The exact mechanism that controls these large-scale species diversity patterns is still not fully understood and is a matter of debate[5,11,13]. The comprehensive marine ecological and palaeoecological studies are very few in the Indian Ocean[10,14,17,19]. The productivity-related events 'biogenic bloom' and expansion of Oxygen Minimum Zone (OMZ) to large parts of the Intermediate Indian Ocean also brought significant changes in the faunal diversification of the region during the middle

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Miocene to the early Pliocene[4,20,21]. In this study we present the new and published species diversity records of benthic foraminifera from the Neogene sediments of the Deep Sea Drilling Project (DSDP) sites 214 and 216 and Ocean Drilling Program (ODP) holes 758A, 757B, 756B and 752A in the eastern (including southeastern) Indian Ocean. These sites/holes are presently located between 30.53°S and 5.23°N at lower bathyal to abyssal depths (~ 1100–2900 m), enabling us to understand the patterns of species diversity and oceanic circulation, which led to the understanding of deep sea palaeoceanographic evolution of the eastern Indian Ocean.

Location and oceanographic settings

The location and water depths of the studied holes/sites are given in Figure 1 and Table 1. DSDP sites 214 and 216 and ODP holes 758A, 757B and 756B are situated on the Ninetyeast Ridge, eastern Indian Ocean. Hole 758A lies in the north, whereas Hole 756B is located in the southern end of the Ninetyeast Ridge. ODP hole 752A is located at the crest of the Broken ridge. Except holes 752A and 756B, all the other holes/sites fall under the influence of the Indian monsoon system. Holes/sites 758A, 216, 214 and 757B are lying within the influence of both the southwest and northeast monsoon currents[22]. The southwest monsoon and trade winds develop major divergences (Figure 1), inducing strong upwelling[23] and thus high primary productivity[24,25] in the eastern Indian Ocean. Site 214 lies in the South Equatorial gyre and hole 757B is located south of the South Equatorial gyre. Surface water in this area records the conditions of the Indo-Pacific warm pool, whereas the subsurface waters belong to the cold and fresh Australasian Mediterranean water, which originates in the Indonesian seaway[26]. Indonesian Intermediate Water contributed 50–60% of its water to the northeastern Indian Ocean[27] at intermediate depths. Above holes 752A and 756B, the West Wind Drift, the South Equatorial Current and the Subtropical Convergence largely control the surface water circulation[28] (Figure 1). These holes have been under the influence of southern component deep water during the studied interval and might have been strongly influenced by the intermediate water of southern origin like Antarctic Intermediate Water (AAIW)[14].

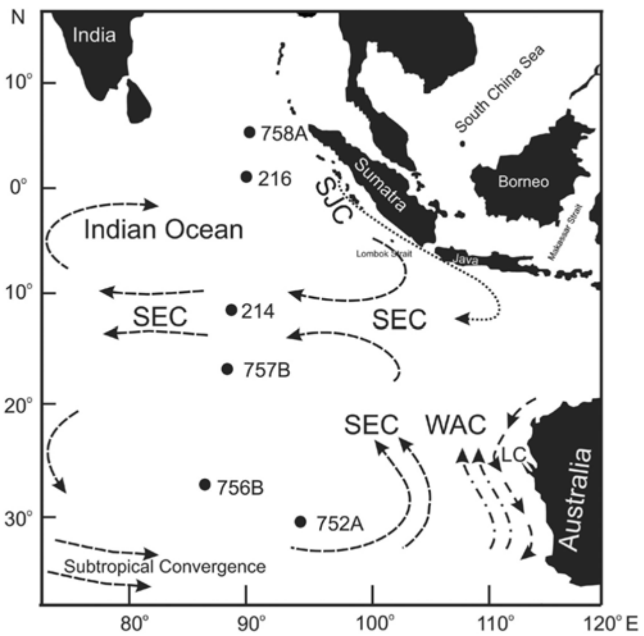

Figure 1. Location of DSDP sites 214 and 216 and ODP holes 758A, 757B, 756B and 752A with dotted arrow line showing different ocean currents. SEC, South Equatorial Current; SJC, South Java Current; LC, Leeuwin Current; WAC, West Australian Current (after Wijffels *et al.*[54]).

Materials and methods

We produced the Pliocene–Pleistocene record of deep-sea benthic foraminifera from hole 758A (134 samples) and Miocene record from hole 756B (73 samples) combined with published Neogene record from holes/sites 752A (142 samples), 757B (192 samples) and 214 (211 samples), and Miocene record from hole/site 216 (70 samples) and 758A (136 sample)[10,14,17,29]. Samples were processed by using standard procedures[17,30]. Benthic foraminiferal census data were generated from an aliquot of ~ 300 specimens from 125 μm + size fraction from holes 752A, 756B, 757B and 758A and 149 μm + size fraction from sites 214 and 216. We could not analyse 125 μm + size fraction from sites 214 and 216 as the samples were prewashed. Interpolated ages for each sample are based on the age model of Peirce *et al.*[31] and revised according to Berggren *et al.*[32] for the ODP holes 752A, 756B, 757B and 758A. For sites 214 and 216, numerical ages are based on planktic foraminifera[33,34]. Except for hole 758A, water depths at other holes were about ~ 100 m shallower than present in the Early Miocene, having well-preserved Neogene benthic microfauna with little to no reworking[31,35]. Across the Oligocene/Miocene boundary, the studied holes were located ~ 10–12°S of the present position[31,36,37].

We calculated the species diversity in terms of information function (H) and equitability (E; Figure 2). The number of species (S) was also counted from each sample (Figure 2). H was calculated using the Shannon–Wiener diversity index[38] given by the formula

$$H = -\sum_{i=1}^{S} p_i \ln p_i,$$

where S is the number of species in a given sample, p_i is the proportion of the ith species in the sample and ln is the

Table 1. Locations (latitude and longitude) and water depths of the studied ODP holes 752A, 756B, 757B and 758A and DSDP sites 214 and 216

Hole/site	Leg	Latitude	Longitude	Water depth (m)
758A	ODP 121	5°23.05′N	90°21.67′E	2924
216	DSDP 22	01°27.73′N	90°12.48′E	2262
214	DSDP 22	11°20.21′S	88°43.08′E	1671
757B	ODP 121	17°01.458′S	88°10.899′E	1652.1
756B	ODP 121	27°21.330′S	87°35.805′E	1518.1
752A	ODP 121	30°53.475′S	93°34.652′E	1086.3

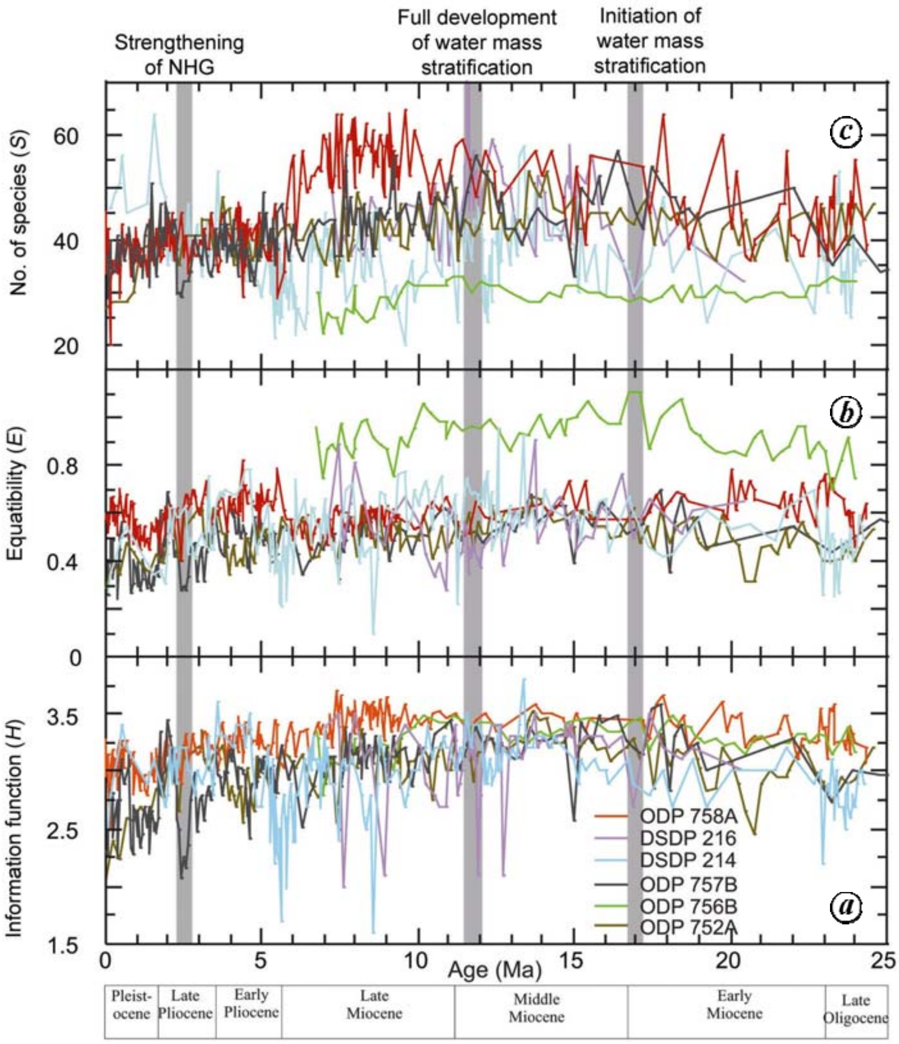

Figure 2. Species diversity parameters. (***a***) Information function (*H*), (***b***) equitability (*E*) and (*c*) number of species (*S*) at DSDP sites 214 and 216 and ODP holes 758A, 757B, 756B and 752A. Vertical bars mark the major events during the Miocene and Pliocene.

natural logarithm. To calculate *E*, we used the mathematical expression given by Buzas and Gibson[39] as below

$$E = e^H/S,$$

Combined oxygen (δ^{18}O) and carbon (δ^{13}C) isotope values of benthic foraminifera normalized to *Cibicides wuellerstorfi* are taken from Gupta *et al.*[21] (Figure 3). We have also plotted relative abundance of infaunal (high productivity) species *Uvigerina proboscidea*, epifaunal (low to intermediate and high oxygen, intermediate pulsed food supply preferring) species *C. wuellerstorfi* and epifaunal–corrosive bottom water species *Nuttallides umbonifera* (Figure 3).

Results and discussion

Information function, equitability and number of species from all the six holes/sites show significant changes during the Neogene, reflecting major turnovers in deep-sea environments of the eastern Indian Ocean (Figures 2–4). The values of *H* and *S* show high fluctuations with abrupt changes at site 214 and hole 757B, whereas at hole 756B the values are moderately fluctuating except in the late Miocene (Figures 2 and 4). *S* is lowest with highest *E* at hole 756B, in contrast to hole 758A where values of these parameters show opposite trends. During the latest Oligocene–earliest Miocene (ca. 25–20.5 Ma), *H*, *E* and *S* values at higher latitude holes 752A and 756B decreased coinciding with the establishment of the Antarctic Circumpolar Current (ACC) due to deep opening of the Drake Passage[40], whereas at lower latitude holes/sites 757B, 214 and 758A these values remain high during the same period. At the southernmost a hole 752A, the *H*, *E* and *S* values show an increase from ~20.5 to ~13.5 Ma and thereafter a gradual decrease from ~13.5 to 4.5 Ma coinciding with the major build-up of ice sheets in the Antarctic region[2]. The *H*, *E* and *S* values show an increase for brief period from ~4.5 to 3 Ma and thereafter abruptly decrease in the younger interval contemporaneous

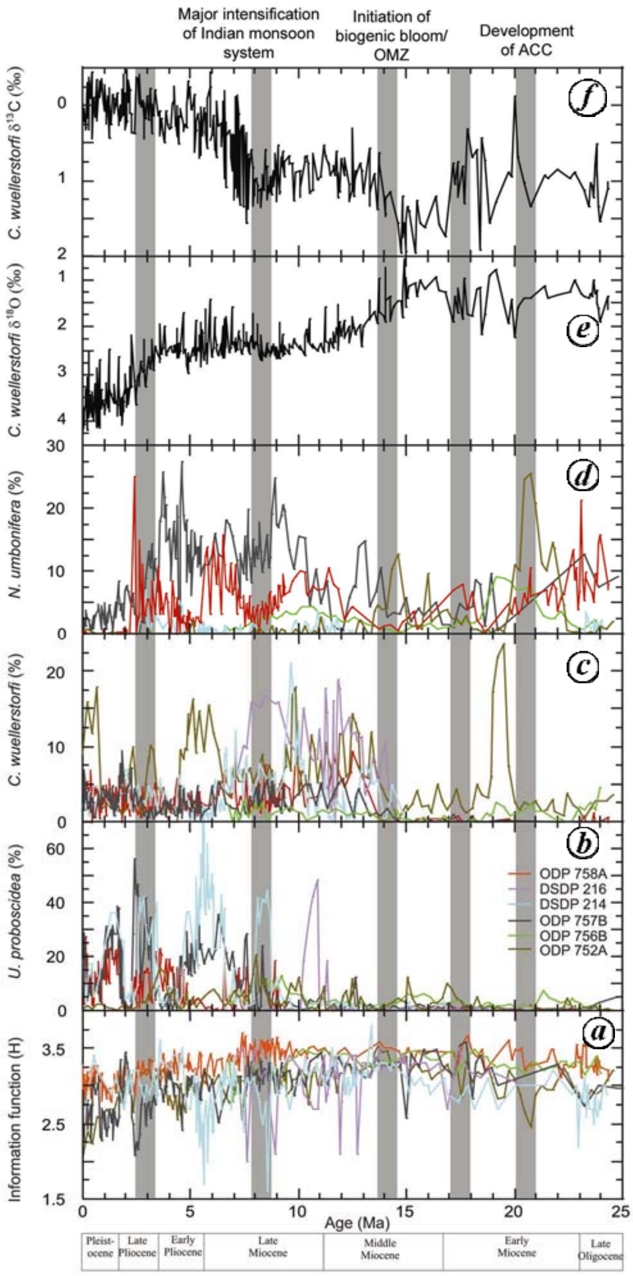

Figure 3. Information function (*H*) (***a***), along with population abundances benthic foraminifera *Uvigerina proboscidea* (***b***), *Cibicides wuellerstorfi* (***c***), and *Nuttallides umbonifera* (***d***) and combined δ^{18}O (***e***) and δ^{13}C (***f***) values of benthic formanifera normalized to *C. wuellerstorfi*[21]. For late Early Miocene and Late Pliocene vertical bars refer to Figure 2.

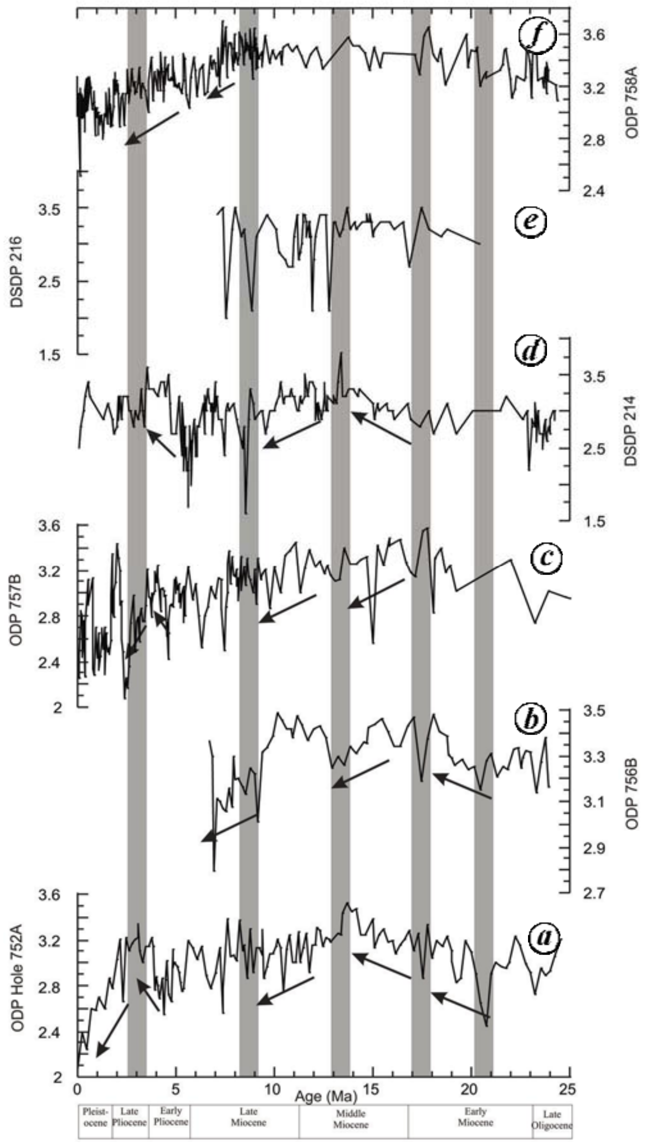

Figure 4. Information function (*H*) at ODP holes 752A (***a***), 756B (***b***), 757B (***c***), DSDP sites 214 (***d***) and 216 (***e***), and ODP Hole 758A (***f***). For details of vertical bars refer to Figures 2 and 3.

with the major build-up of Northern Hemisphere glaciations (NHG)[41]. The *H*, *E* and *S* values at hole 756B show a rough parallelism with those from hole 752A, having an increase from 20.5 to 17.5 Ma followed by a decrease until ~ 13 Ma. These values show a sudden drop during 10.5–7 Ma at hole 756B (Figures 2 and 4). Hole 757B shows high diversity values from 25 to 17 Ma and thereafter a continuous decrease until 3.5 Ma. Species diversity parameters at site 214 show an increase from 25 to 13 Ma followed by a decrease up to 8.5 Ma and thereafter the values show abrupt changes. It is important to note that hole 757B and site 214 are located in the Indian Ocean Hydrological Front, where chemical parameters remain constant through the water column[42]. Site 216 has only Miocene record of species diversity parameters which show no significant trend. At the northernmost hole 758A, the species diversity parameters show a stepwise increase from 24.5 to 7.5 Ma followed by a decrease until 1.7 Ma. Species diversity values at hole 758A increased in the Pleistocene with greater fluctuations.

During the latest Oligocene–earliest Miocene (25–20.5 Ma), deep-sea conditions were unstable in the eastern and southeastern Indian Ocean[14] marked by increased productivity (low δ^{13}C, Figure 3) and decreased species diversity at higher latitude holes 752A and 756B (Figure 3). The high abundance of *N. umbonifera* during this time indicates presence of carbonate corrosive deep/bottom water in the eastern Indian Ocean[43], coinciding with the opening of the Drake Passage and subsequent development of the ACC in the late Oligocene[40] (Figure 3).

The deep-sea conditions gradually changed between 20.5 and 17 Ma marked by increasing species diversity values at all the sites/holes with a decrease in surface productivity (high δ^{13}C), suggesting stable deep-sea conditions in the vicinity of the Ninetyeast Ridge (Figure 3). This was an interval of Early Miocene Climatic Optimum (EMCO) and decrease in Antarctic ice mass[3,44,45]. The EMCO was followed by rapid middle Miocene cooling, coinciding with narrowing of the eastern Tethys between 18 and 16 Ma that was finally closed during 15–14 Ma (ref. 46). The production of the Northern Component Water (NCW), the Miocene equivalent of the North Atlantic Deep Water, may have increased considerably, which strengthened the thermal gradients in the water column during this time[47,48]. We argue that this was a period when water mass stratification strengthened in the eastern Indian Ocean and species diversity values at each hole/site responded to the stratification at various depths (Figures 2 and 4). The *H* values at the shallower hole 752A show an increase; at intermediate depth holes 756B and 757B, the values show a decrease and at abyssal depth holes/sites 758A and 216 there was no significant change in *H* values. The water mass stratification in the eastern Indian Ocean reached its peak by ~ 12 Ma and species diversity values of northernmost hole 758A reached their maximum[17]. The largest changes in the assemblages of planktic foraminifera have been observed in the tropical Indian Ocean during this period[49].

At ~ 14 Ma, the Icehouse World was established which coincided with a period of prolonged Antarctic low summer insolation creating the boundary conditions needed for large-scale cooling[50]. This cooling event (high δ^{18}O values of *C. wuellerstorfi*) caused a drop in sea level and was marked by high population of *C. wuellerstorfi* at intermediate and abyssal depths (Figure 3). Cooling strengthened the meridional wind regimes that caused open ocean upwelling and increased productivity in the Indian Ocean leading to the initiation and intensification of the OMZ[14]. This coincides with the beginning of the 'biogenic bloom', which is marked by the dominance of *Bolivina pusilla* at site 752 and decrease in species diversity values at all the shallow and intermediate sites[14] (Figures 2 and 4). The species diversity at all the shallow and intermediate sites shows a decrease during this period of intense OMZ[12,14]. Hole 756B was out of influence of OMZ during this period, showing increase in the species diversity values. Productivity increased significantly in all the oceans in the middle Miocene and reached its maximum at ~ 8.5 Ma (ref. 4).

During the late Miocene (~ 8.5 Ma), OMZ intensified and expanded to large parts of the Indian Ocean at intermediate depths[4]. Productivity increased throughout the Indo-Pacific region and Indian monsoon intensified during this time[4,20,30] coinciding with the dominance of *U. proboscidea* – a high productivity species and decrease in species diversity in all the shallow and intermediate holes/sites (Figure 3). The δ^{13}C values of benthic foraminiferal species show significant decrease after this period (Figure 3). The species diversity values at the deeper site 758 also decreased as a combined effect of productivity and significant increase of water depth (water depth > 2500 m)[31].

The 'biogenic bloom' terminated during ~ 5.5–3.8 Ma marked by the disappearance of the OMZ species and increase in species diversity of the shallower site 752 (ref. 14) and a decrease in *C. wuellerstorfi* abundances at intermediate and abyssal depths coinciding with the early Pliocene climatic warmth[51]. This transition period of deep ocean environment is marked by increase in species diversity with fluctuation at shallower and intermediate depth holes. Karas *et al.*[26] reported that the $SST_{Mg/Ca}$ records of site 214 vary from 24°C to 26.5°C, showing a warming trend of 1.5°C during the early Pliocene from 5.5 to 3.8 Myr ago. After the closing of the Indonesian throughflow at ~ 4 Ma (ref. 52), site 214 was under the influence of the North Pacific water[26] and species diversity data do not show any significant rise or decline. The species diversity values at the abyssal depth hole 758A show decrease with increasing depth as observed in the Arctic Ocean[16].

The temporal changes in species diversity of shallow and intermediate holes during middle to late Miocene show significant fluctuations which were driven by a change in seasonality when low to intermediate organic carbon flux and high seasonality species (e.g. *Gavelinopsis lobatulus*) were common[14]. The sudden decrease in species diversity at shallow, intermediate and abyssal depth holes during ~2.6–2.2 Ma was probably due to vertical mixing of upper water column by increased monsoonal wind intensity[53] contemporaneous with the initiation and intensification of NHG[41]. The effect of NHG was more pronounced at high-latitude hole 752A, where benthic foraminiferal species diversity shows abrupt decrease at ~3.0 Ma (ref. 14; Figures 2 and 4). It is interesting to note that the number of species is higher at low-latitude hole 758A than the high southern latitude holes 752A or 756B throughout the studied interval (Figure 2). Our results are robust, which supports the hypothesis that species diversity increases with decreasing latitude[5,6].

Conclusions

The species diversity parameters in the eastern India Ocean fluctuated significantly during the Neogene and Quaternary, responding to changes in the location (northward movement of the studied holes/sites), and water mass stratification, productivity and high-latitude glaciations during the studied interval. During the early Miocene, species diversity increased with decreasing latitude[6]. Water mass stratification intensified at ~17 Ma and peaked by the middle Miocene (~12 Ma)[17]. Major changes in the species diversity parameters in the eastern Indian Ocean are correlated with the high-latitude glaciations, changes in the OMZ and productivity, while temporal changes are related with the seasonality of organic flux. During cold intervals, high productivity and decrease in species diversity have been observed at all the shallow and intermediate holes/sites, whereas high values of species diversity are observed during the warmer periods.

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