Species diversity of Miocene deep-sea benthic foraminifera and watermass stratification in the northeastern Indian Ocean

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ABSTRACT: The Miocene species diversity of deep-sea benthic foraminifera (expressed as $\alpha$ index, information function $H(S)$, and Sanders’ rarefaction values) at DSDP Sites 214 (1671 m) and 216 (2262 m), and ODP Site 758 (2923 m) in the northeastern Indian Ocean was overall higher than the modern diversity, but with major variations. The $\alpha$ and $H(S)$ values were relatively low at the shallowest Site 214, medium at intermediate-depth Site 216, and highest at the deepest Site 758. Across the Oligocene/Miocene boundary, when the Antarctic Circumpolar Current (ACC) might have originated, diversity dropped at Sites 214 and 758. All diversity parameters decreased for a short time at 17 Ma at all sites (more prominent at Site 216), at which time production of Northern Component Water (NCW) may have peaked. At shallow Site 214 and deep Site 758, the $\alpha$ and Sanders’ values show an abrupt decrease at about 12.5 Ma, a time of major expansion of the East Antarctic Ice Sheet (EAIS) and increased production of Antarctic Bottom Water (AABW), Northern Component Water (NCW) and Indonesian Intermediate Water (IIW). These decreases in diversity are not seen in the records of Site 216. In the latest Miocene (about 7.15 to 6.5 Ma) the $\alpha$ and Sanders’ values at Sites 214 and 758 decreased further, during the Chron-6 global carbon shift and the Indo-Pacific biogenic bloom in productivity. The $H(S)$ values also show a decrease in this interval at Sites 214 and 758. We suggest that deep-ocean circulation played a significant role in shaping the long-term diversity trends in the northeastern Indian Ocean. Productivity, which might in turn have been influenced by the circulation changes, dominantly affected the diversity in the latest Miocene.

INTRODUCTION

The climate of the Earth has witnessed important changes during the Neocene, including the waning and waxing of the polar ice sheets, changes in ocean circulation, and tectonics, such as mountain building and the opening and closing of oceanic gateways (e.g., Kennett 1977; Ruddiman and Kutzbach 1989; Kennett and Barker 1990; Gupta and Srinivasan 1992a; Wright and Miller 1996). The circulation and chemistry of the deep ocean basins are closely linked to the Earth’s climate, and we must understand the interactions between the cryosphere, hydrosphere, atmosphere, and biosphere in order to understand the past, and predict possible future climate changes.

Understanding the climatic and biotic developments of the Miocene is of major importance for understanding these interactions. By the early Miocene (~22 Ma) the ocean basins had essentially assumed their modern shapes, and the Antarctic continent had formed (Ramstein et al. 1997; Cande et al. 2000). The East Antarctic Ice Sheet (EAIS) had become established in the earliest Oligocene (e.g., Ehrmann and Mackensen 1992; Diester-Haass and Zahn 1996; Zachos et al. 1999), when steep thermal gradients between polar and tropical regions were established (e.g., Zachos et al. 1993, 1994, 2001). Surface water productivity increased in the latest Eocene into the Oligocene (e.g., Diester-Haass and Zahn 1996), and the seasonality of ocean surface productivity also increased (Thomas and Gooday 1996).

The Earth cooled from the end of the early Eocene (Zachos et al. 2001), but long-term cooling was interrupted for a period of warming in the early Miocene. Locally, intermediate ocean waters may have held little oxygen in the early Miocene warm period (Thomas 1986a, 1986b; Smart and Murray 1995). Causes of this warming are not clear, especially because more and more evidence suggests that the Miocene atmospheric CO$_2$-levels were not higher than preindustrial levels (Flower 1999; Pagani et al. 1999a, 1999b). Cooling resumed in the middle Miocene, when Tethyan outflow into the Indian and Southern Oceans probably ended (Woodruff and Savin 1989). At this time, the rate of production of Northern Component Water (the Miocene equivalent of the modern North Atlantic Deep Water) may have increased substantially (Wright and Miller 1996). Global benthic foraminiferal faunas underwent major restructurings, including changes in diversity (e.g., Douglas and Woodruff 1981; Thomas 1985, 1986a, 1986b).

Many hypotheses have been proposed to explain global biodiversity patterns, including the stability-time hypothesis (Fischer 1960; Hessle and Sanders 1967; Sanders 1968), the spatial heterogeneity hypothesis (Simpson 1964), competition (Dobzhansky 1950; Williams 1964), predation or cropping (Paine 1966, Pianka 1966), productivity (Connell and Orias 1964), and dynamic equilibrium (Huston 1979). The relative importance of individual ecological and biologic factors influencing species diversity remains largely unresolved, however, and causes and effects of biodiversity are actively debated (e.g., Gaston 2000). The deep-sea diversity changed considerably during the major climatic changes of the Cenozoic (e.g., Thomas and Gooday 1996), and studies of Recent and modern faunas can thus help to narrow the debate regarding causes of high


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biodiversity, which typifies the deep ocean biota (e.g., Douglas and Woodruff 1981).

The deep-sea environment has been said to be more stable than the surface environments through geological time (e.g., Douglas and Woodruff 1981; Thieler et al. 1988; Gooday and Lambshead 1989). Recent studies, however, indicate that the deep-sea environment is dynamic and subject to short-term changes in diversity and standing stocks of deep-sea fauna (e.g., Huston 1979; Gooday and Lambshead 1989; Gupta 1990; Gupta and Srivinasa 1992a; Smith 1994; Smart and Murray 1995; Smart 1998). Documentation of deep-sea benthic foraminiferan faunas thus is useful within the debate of the stability-time hypothesis. This hypothesis is prominent, but widely discussed among marine scientists (see e.g., Smith 1994; McCann 2000, Stuart et al., in press, Rex et al., in press). The hypothesis asserts that high diversity in the deep sea and in the tropics results from long-term (geological) climatic stability. Under such physically stable conditions biological interactions may stabilize, resulting in an increase in species diversity through niche partitioning. Interruptions of the long-term stability are then predicted to lead to decreased diversity. As an example, Gupta and Srivinasa (1992a) related diversity changes in the northeastern Indian Ocean to variations in Antarctic Bottom Water (AABW) circulation in response to changes in Antarctic ice volume.

Cronin and Raymo (1997) demonstrated that Plioene ostracode diversity patterns dynamically responded to climatically induced change in ocean circulation, temperature, and food availability. They suggested that the deep sea is a temporally dynamic environment marked by orbitally induced climatic changes which affect the deep-sea benthic diversity on 10^-4 years time scales; such variability probably existed also in the Miocene (Zachos et al. 1997). Cronin and Raymo (1997) also argued that low diversity values correspond to glacial intervals, whereas diversity was higher during interglacials, when the food supply was greater. This is in contrast with the situation in benthic foraminiferal faunas in the North Atlantic, which were more diverse during the last glacial than they are at present (Thomas et al. 1995). In contrast, Valentine (1971) proposed that abundant and/or unstable food supply results in low diversity values whereas scarce and/or stable food resources lead to increased diversity, in agreement with Huston (1979) and Phleger and Soutar (1973). Thomas and Gooday (1996) docu-
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Observations on spatial variations of deep-sea species diversity are few, and the causes of species diversity patterns in various environments remain elusive (e.g., Stuart et al., in press). Two major spatial trends have been observed: (1) increasing species diversity with decreasing latitude (e.g., Fischer 1960; Valentine 1966; Thomas and Gooday 1996; Rex et al. 1997, in press; Culver and Buzas 2000), and (2) a general increase in species diversity with increasing water depth in the marine environment (Gibson 1966; Hessler and Sanders 1967; Buzas and Gibson 1969), possibly peaking at middle bathyal depths (e.g., Schmiedl 1995). In the Indian Ocean between about 1600 and 4500 m depth, Gupta (1990) observed that species diversity increases (with fluctuations) up to about 3000 m, then declines at greater depths owing to the influence of AABW circulation and/or dissolution. Smart (1998) also suggested that dissolution causes decreasing diversity values at the deeper Site 710 (3824 m) in the western Indian Ocean.

Benthic foraminiferal tests are comparatively resistant to post-mortem environmental changes, thus are suitable for species diversity studies among fossil populations. In this paper we present the species diversity record of benthic foraminifera from the Miocene of Deep Sea Drilling Project (DSDP) Sites 214 and 216, and Ocean Drilling Program (ODP) Site 758 in the northeastern Indian Ocean. The sites offer an opportunity to study the influence of long-term climate changes on species diversity at lower bathyal to abyssal depths, because they are in the equatorial region during the Miocene (e.g., Peirce et al. 1989; Nomura 1995). We examined the temporal relationship between diversity and environmental stability, as expressed in deep-ocean circulation, global ice-volume, productivity and...
dissolution. These may be the most important factors shaping the faunal diversity in the Indian Ocean.

**LOCATION**

DSDP Sites 214 (water depth 1671m, 11°20.21'S and 88°43.08'E), 216 (water depth 2262m, 01°27.72'N and 90°12.48'E), and ODP Site 758 (water depth 2923m, 5°22.049'N and 90°21.693'E) are located on the Ninetyeast Ridge (text-fig. 1). At present, the drift current of the southwest (SW) monsoon induces intense upwelling above these sites leading to seasonally high surface productivity.

Deeper water circulation patterns in the Indian Ocean are not well known. AABW is present below 3800 m (Kolla et al. 1976; Gupta and Srinivasan 1992b). North Atlantic Deep Water or Northern Component Water (NADW or NCW), flowing North into the Indian Ocean from the Antarctic Current component of the Global Ocean Conveyor (Broecker 1995) has been said to occur at intermediate depths, as argued by Tchernia (1980) and Corliss (1983). In contrast, Warren (1982), GEOSECS (1983) profiles and Johnson (1985) suggest that the water between 1200 and 3800m north of 30°S is of north Indian origin. More recently, You (1998) identified three sources of intermediate waters in the Indian Ocean: the Red Sea-Persian Gulf Intermediate Water, the Indonesian Intermediate Water (IW), and Antarctic Intermediate Water (AAIW). The role of AAIW is ambiguous north of the hydrographic front at 10°S (Tchernia 1980; You 1998). You (1998) suggested that the Indonesian Intermediate Water (IIW) contributes 50-60% of its water to the northeastern Indian Ocean including the Bay of Bengal.

**MATERIALS AND METHODS**

Miocene samples of 10cc volume at an interval of ~75-150cm from Site 758 (136 from 24.37-5.71 Ma), Site 214 (172 from 24.25-8.89 Ma), and Site 216 (70 from 20.38-7.10 Ma) have been examined. The samples were soaked in water with half a
spoon of baking soda for 8-12 hours. A few samples with high clay content were processed with hydrogen peroxide (5%). Samples were washed over a 63 μm sieve and oven-dried at about 60°C. The >125 μm-size fraction was used for benthic foraminiferal analysis at Site 758, and the >149 μm-size fraction at Sites 214 and 216. We could not analyze the >125 μm-size fraction from Sites 214 and 216 as the samples were pre-washed. The number of specimens analyzed in each sample varies from <100 to >1000. The specimens were counted, identified, and their percentages were calculated. Numerical ages are based on planktic foraminiferal (Vincent 1977; Srinivason and Gupta 1990 for Sites 214 and 216) and calcareous nanofossil (Petree et al. 1989 for Site 758) datum levels, and are after Berggren et al. (1995). Sites 214, 216, and 758 have well-preserved Neogene microfaunas and little to no reworking. In the Miocene, water depths at the sites were about 100 m shallower than at present (Sclater et al. 1977; Petree et al. 1989). In the early Miocene the sites were located about 5°S of their present position, in the latest Miocene about 2°S of their present location (Nomura 1995). At Sites 214 and 758A the sediment accumulation was low from 23 to 12.5 Ma and the time resolution therefore is low (text-figs. 2, 3 and 6). At Site 216A, however, the record is available only from 20.0 to 7.0 Ma with more or less uniform sample density (text-figs. 2, 3 and 6).

We describe species diversity in terms of the a index, Sanders’ rarefaction number, and information function, H(S) for Site 758 (table 1; text-figs. 2 and 3). The a index is a measure of species richness and was first described by Fisher et al. (1943). This value is commonly used in foraminiferal studies (e.g., Murray 1991). We calculated a values following Williams (1964, p. 307-311). Sanders’ values are commonly used in studies of deep-sea faunas (e.g., Rex et al. 1997). We calculated these values by rarefying against 100 individuals at all the sites (Sanders 1968) (table 1; text-fig. 6). The values of H(S) were calculated using the Shannon-Wiener Diversity Index (Shannon and Wiener 1949) as follows:

\[ H(S) = - \sum_{i=1}^{S} p_i \ln p_i \]

Where S is the number of species in a given sample and p_i is the proportion of the ith species in the sample. H(S) takes into account both number of species and the abundance of individuals.
in each sample, thus $H(S)$ is a measure of both species richness and evenness. The $\alpha$, $H(S)$, and Sanders' values have been correlated using linear correlation (text-figs. 7 and 8).

Smart and Murray (1995) found a good correlation between $\alpha$ and $H(S)$ indices indicating that either is a satisfactory measure of species diversity. Alve and Murray (1994), however, suggested that $\alpha$ is a better discriminator in modern environments. We calculated the $\alpha$ values and re-plotted the $H(S)$ values from Sites 214 and 216 (table 1) based on the $>149\mu$m size fraction (Gupta and Srinivasan 1992a), and from the Somali Basin based on the $>63\mu$m size fraction (Smart 1998). All data were plotted on the Berggren et al. (1995) time scale for comparison with our values from the $>125\mu$m size fraction from Site 758A, in order to understand the diversity changes at various depths in the eastern and western sectors of the Indian Ocean. Since the size difference between fractions from Sites 214, 216 ($149\mu$m) and 758 ($125\mu$m) is very small, we presume that the comparison is realistic. However, our comparison with the Somali Basin sites may be less reliable because Smart (1998) used the $>63\mu$m size fraction.

RESULTS AND DISCUSSION

Our data show significant fluctuations in benthic foraminiferal diversity over the Miocene, but the changes differ by depth. Comparison of our data with published work shows that changes also differ by ocean basin. The $\alpha$, $H(S)$ and Sanders' values from Sites 214, 216, and 758 are given in table 1, and plotted against numerical ages in text-figures 2, 3, and 6. The $\alpha$ and Sanders' values show more changes than $H(S)$. In general, $\alpha$, $H(S)$ and Sanders’ values are lower at shallower Site 214, medium at the intermediate-depth Site 216, and higher at the deeper Site 758 (text-figs. 2, 3 and 6). This may indicate that environmental disturbances were more severe at intermediate depths than at abyssal depths, and that waters in the northeastern Indian Ocean became more stratified during the Miocene. Such increased stratification might be expected during cooling of the deeper waters while tropical surface waters did not change much in temperature.

The $\alpha$, $H(S)$, and Sanders' values are low and fluctuate across the Oligocene-Miocene boundary at Sites 214 and 758 (text-figs. 2, 3 and 6). From 23 to 12.5 Ma both $\alpha$ and $H(S)$ values remained high and fluctuated less (text-figs. 2 and 3), suggesting more stable conditions. The food supply was low and deep-sea oxygenation was moderate to high in the northeastern Indian Ocean during this time (Srinivasan and Gupta 1990; Joseph 1999). This interval of relative tranquility might have been interrupted at about 17 Ma by increased production of NCW (Wright and Miller 1996), which strengthened thermal gradients in the water column (Kennett 1986). Although there are not enough data points from this interval at the study sites, a short-lived decrease in all diversity parameters is visible. At this time, deep-sea benthic foraminiferal faunas in the Pacific Ocean also decreased in diversity (Thomas and Vincent 1987).
At 12.5 Ma the $\alpha$ values show a major and abrupt drop whereas the H(S) values do not show a significant decrease at Site 214 (text-figs. 2 and 3). The Sanders' values also show a major but stepwise decrease at Site 214 during this time (text-fig. 6). The correlation between $\alpha$ and H(S) is high at Site 214 (text-fig. 7), weak at Site 758 (text-fig. 8), and very weak at Site 216 (text-fig. 7). This contrasts with the observations by Smart and Murray (1995), indicating that the two functions may behave differently in different environmental setups. At Site 758 there is no shift at 12.5 Ma towards lower values in the parameters (text-figs. 2, 3 and 6), probably due to the coarse sampling interval.

From 12.5 Ma onwards all three parameters show a continuous decrease at Site 214 and a moderate decrease at Site 758. At Site 216, however, the $\alpha$ values show a continuous increase, with fluctuations through the Miocene, and values show no correlation with those at the other sites. This difference in diversity trends at various depths in the northeastern Indian Ocean indicates that different water masses may have been present at the different depths of these sites, perhaps due to strengthened water mass stratification. Smart (1998) also did not see coherence in $\alpha$ and H(S) values between various sites in the Somali Basin (western Indian Ocean). At 12.5 Ma, $\alpha$ values decreased at bathyal to upper abyssal sites, although the data points are at low time resolution (text-figs. 4 and 5). At the deeper Site 710 (water depth 3824 m) the shift appears to occur at 12.0 Ma, possibly as a result of the wide sample spacing or a short unconformity.

The decrease in diversity values coincided with the middle Miocene positive oxygen isotope shift resulting from the expansion of the EAMS (e.g. Wright et al. 1992; Savin et al. 1981; Kennett 1986; Vincent et al. 1985), which was also observed at Site 758 (Joseph 1999; Gupta et al. 2000). At this time, increased production of NCW resumed in different ocean basins (Woodruff and Savin 1985; Nomura 1991; Wright and Miller 1996), and the thermal gradients in the water column increased (Kennett 1986). The supply of Tethyan outflow water into the Indian Ocean terminated (Woodruff and Savin 1989; Ramsay et al. 1998). The Indonesian Seaway may have closed about this time as well (ODP website), and this closure may have resulted in increased production of Indonesian Intermediate Water (I IW), influencing the intermediate waters in the northeastern Indian Ocean. In addition, a five-fold increase in terrigenous flux to the northern Indian Ocean started at approximately 12.5 Ma, possibly as a result of rapid uplift of the Himalayas (Rea 1992). Benthic foraminiferal faunas worldwide show major changes in the late middle Miocene at about 12.5 Ma in the time scale of Berggren et al. (1995), as documented by many authors (e.g., Douglas and Woodruff 1981; Woodruff 1985; Thomas 1985, 1986a, b, 1992). At this time, the Cibicides wuellerstorfi-Pyrgo murhina assemblage at Sites 758 and 754 (Nomura et al. 1992; Joseph 1999) occurred in the Atlantic, Indian and at least some parts of the Pacific Ocean (Woodruff 1985; Miller et al. 1987; Nomura 1991), although not in the abyssal eastern equatorial Pacific (Thomas 1985). The coeval increase in relative abundance of Nuttallides unisonifera at Indian Ocean Sites 237 and...
710 at about 12.5 Ma indicates a change in the Indian Ocean deep circulation at 2000 to 4000m water depths (Smart 1998).

What was the cause for the major and abrupt decrease in diversity parameters at 12.5 Ma? The fact that species diversity decreased at 12.5 Ma, during the increase of Antarctic ice volume, deep-sea cooling, increased thermal gradients, and increased production of NCW, AABW, and IIW, suggests that changes in deep ocean circulation influenced the species diversity of deep-sea benthic foraminifera in the northeastern Indian Ocean. The increased delivery of terrigenous material from the Himalayas (Rea 1992), however, may have caused increased productivity in the surface waters, and the increased productivity may have affected the diversity patterns, as suggested by an increase in high-productivity benthic faunas at ODP Site 758 (Gupta et al. 2000).

The $\alpha$, $H(S)$ and Sanders’ values decreased further between 7.15 and 6.5 Ma at Sites 214 and 758 (text-figs. 2, 3 and 6); at Site 216 there is no record from this interval. The lowest $\alpha$ and $H(S)$ values at Sites 214 and 758 in the uppermost Miocene coincide with the Chron-6 negative Carbon Shift (Vincent et al. 1985), a major expansion of western Antarctic ice volume (Kennett 1977, 1986; Kennett and Barker 1990; Woodruff and Savin 1985), a major regressive phase (Haq et al. 1987), and the occurrence of widespread deep-sea hiatuses (Keller et al. 1987). The surface productivity increased during the "Indo-Pacific biogenic bloom", and oxygen minimum zones (OMZs) expanded over large parts of the Indian Ocean (Berger and Stax 1994; Farrell et al. 1995; Pisias et al. 1995; Filipelli 1997). This was also a period of intense monsoon circulation, widespread upwelling, and increased flux of Himalayan sediment to the northern Indian Ocean (Kroon et al. 1991; Rea 1992; Gupta et al. 2000).

The co-occurrence of abrupt changes in diversity parameters and enhanced production of intermediate or deep waters suggests that the change in deep ocean circulation significantly influenced the diversity of deep-sea benthic foraminifera in the early and middle Miocene Indian Ocean. In the late Miocene, however, changes in productivity became more important. Productivity increased in the Indo-Pacific region in the late Miocene (e.g. Berger and Stax 1994; Farrell et al. 1995; Pisias et al. 1995; Dickens and Owen 1999). The high productivity and low deep water temperatures increased the $CO_2$ levels and intensified the corrosiveness of the deep waters, as indicated by the presence of Nuttallides umbonifera across the Oligocene-Miocene boundary and in the uppermost Miocene at deeper Site 758. We agree with Gupta and Srinivasa (1992a) and Smart (1998), who suggested that long-term species diversity changes in the deep sea are linked to the environmental stability as expressed in deep-ocean circulation. Changes in productivity and deep-sea oxygenation, however, influenced the diversity patterns in deep-sea benthic faunas in the northeastern Indian Ocean between 7.15 and 6.5 Ma, in agreement with Thomas and Gooday (1996) and Smart (1998).
Average Miocene $\alpha$ and H(S) values in the Somali Basin (Smart 1998) are lower at deeper Site 710 (3824m) and higher at shallower sites in the Somali Basin. In contrast, in the northeastern Indian Ocean the average Miocene diversity values are higher at deeper Site 758 (2923m) than at the shallower sites. This suggests that different water masses were present in the two regions.

CONCLUSIONS

Species diversity of benthic foraminifera (as defined by $\alpha$, H(S) and Sanders' values) fluctuated significantly during the Miocene in northeastern Indian Ocean ODP Sites 214 (1671m), 216 (2262m), and 758 (2923m). The values of the diversity parameters are relatively low at the shallower Site 214, medium at the intermediate-depth Site 216, and high at the deepest Site 758. Fluctuations are more prominent and more abrupt at the shallower Site 214 than at the other sites. The average Miocene values are higher than those for the modern ocean (Gupta 1990) at all sites, as also observed by Thomas (1986a) for the Pacific and North Atlantic. Diversity decreased across the Oligocene-Miocene boundary (about 23 Ma) at Sites 214 and 758, but not at Site 216. A short-lived decrease in the diversity parameters (more conspicuous at Site 216) occurred at 17.0 Ma, coinciding with the peak production of NCW. Diversity further decreased at Sites 214 and 758 (but not at Site 216) in the middle Miocene (at about 12.5 Ma), a time of global change in deep-sea benthic foraminiferal faunas (e.g., Woodruff 1985; Thomas 1992). At this time, glacialion on the Antarctic continent increased, and production of Antarctic Bottom Water (AABW), Indonesian Intermediate Water (IIW) and Northern Component Water (NCW) may have intensified (Wright and Miller 1996), leading to the widespread formation of deep-sea unconformities (Keller et al. 1987). In the latest Miocene (7.15 to 6.50 Ma) diversity further decreased at Sites 214 and 758. During this time the carbon isotopic composition of total dissolved inorganic carbon in the oceans shifted to lower values (Chron-6 Carbon Shift), and surface productivity in the Indo-Pacific region strongly increased (Farrell et al. 1995).

We conclude that the changes in deep-ocean circulation and strengthened water mass stratification in the northeastern Indian Ocean can explain the long-term changes in species diversity at lower bathyal to abyssal depths during the early through middle Miocene, but productivity-related variations may have dominated during the late Miocene.

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TEXT-Figure 7
Linear Correlation between $E$ and H(S) values at DSDP Site 214 and 216. The correlation is high positive at Site 214 ($r=0.61$).


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