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MIOCENE DEEP-SEA BENTHIC FORAMINIFERA FROM THE ATLANTIC AND INDIAN OCEANS: DIVERSITY PATTERNS AND PALAEOCEANOGRAPHY

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ABSTRACT

During the early to middle Miocene of the Atlantic and Indian Oceans there were variations in species diversity of the lower bathyal to abyssal plain (3-4.4 km) benthic foraminiferal assemblages although, overall, diversity remained high and comparable with that of the modern environment. The early Miocene was a period of palaeoceanographic change and this has previously been documented both through studies of stable isotopes and the rate of appearances or disappearances of taxa (whether evolutionary or ecological). The diversity oscillations appear to represent shorter period change. The lowest diversities are associated with the peak abundance of bolivinids. Other variations cannot be correlated from one site to another and are thought to represent local environmental changes. During the early-middle Miocene, the diversity of the Atlantic abyssal plain was lower than that of the Indian and Pacific Oceans possibly indicating significant diversity differences between ocean basins. On the basis of limited data, it is possible to speculate that the species diversity of the Miocene was perhaps higher than that of today.

Keywords: Benthic foraminifera, Miocene, species diversity, palaeoceanography.

RESUMEN

Durante el Mioceno inferior y medio, en los océanos Atlántico e Índico, hubo variaciones en la diversidad específica de las asociaciones de foraminíferos bentónicos batiales, parte inferior, y abisales (3-4,4 Km), aunque en conjunto la diversidad permaneció alta y comparable con la actual. El Mioceno inferior fue un lapso de cambios paleoceanográficos, previamente documentados tanto por estudios sobre isótopos estables como por los de los índices de aparición y desaparición de los taxones (ya sean evolutivos o ecológicos). Las oscilaciones de la diversidad parecen representar cambios de período corto. Las diversidades más bajas están asociadas con los picos de abundancia de los bolivínidos. Sin embargo, otras variaciones no pueden correlacionarse de un lugar a otro y deben representar variaciones ambientales locales. Durante el Mioceno inferior y medio, la diversidad en la llanura abisal atlántica era menor que la de los Océanos Índico y Pacífico, indicando probablemente diferencias significativas en la diversidad entre los mismos. Sobre esta base limitada, se puede especular que la diversidad específica miocena fue quizás mayor que la de hoy día.

Palabras clave: Foraminíferos bentónicos, Mioceno, diversidad específica, paleoceanografía.

INTRODUCTION

Over the last decade there has been an increasing awareness of the importance of understanding the ecological and evolutionary significance of biodiversity. The modern deep-sea is proving to be a region of high species diversity for many groups of organisms (Gage and Tyler, 1991). The benthic foraminifera have the advantage that they posses a test which is preserved in the fossil record. It is therefore possible to document changes in species diversity through geological time. This is important because modern diversity patterns are not just the result of current environmental pressures on the living fauna; they are also influenced by the historical development of the habitats.

Previous studies have established that the diversity of deep-sea benthic foraminifera has varied throughout the Cenozoic (Gupta and Srinivasan, 1992; Thomas, 1985, 1986, 199(); Woodruff, 1985; Nomura, 1991). In relation to ocean size and differences of water depth, there are still very few data. In this study we examine the species diversity trends of benthic foraminifers at similar lower bathyal and abyssal water depths at different latitudes in the Atlantic and Indian Oceans during the early to middle Miocene. This was a period of faunal turnover (extinctions and speciations) in the deep-sea (Thomas, 1992; Miller, *et al.* 1992) and led to the development of the essentially modern fauna in the middle Miocene (Berggren, 1972). It is thus a period of particular interest in terms of benthic foraminiferal diversity.

METHODS

Early to middle Miocene deep-sea benthic foraminiferal faunas have been studied from six sites in the Atlantic Ocean and three sites in the Indian Ocean: DSDP Site 368 (17º30.04'N, 21º21.02'W; present water depth 3366m), DSDP Site 400A (47º22.90'N, 09º11.90'W; 4399m), DSDP Site 518 (29º58.42'S, 38º08'12'W; 3944m), DSDP Site 529 (28º55.83'S, 02º46.08'E; 305m), DSDP Site 563 (33º38.53'N, 43º46.04'W; 3786m), ODP Site 667A (04º34.15'N, 21º54.68'W; 3529m), ODP Site 709C (03º54.09'S, 60º33.01'E; 3041m), ODP Site 710A (04º18.07'S, 60º58.08'E; 3824m) and ODP Site 758A (05º23.04'N, 90º21.60'E; 2924m) (Fig. 1). These sites were chosen for their generally complete and continuous Miocene sections. Samples were collected from each core section at intervals of approximately 1.5m equivalent to 0.1 to 0.3 m.y. apart.

For each of the 191 samples studied, more than 200 benthic foraminifers were picked from the >63 µm size-fraction to ensure that the large number of small-sized specimens were included in the analysis (see comments by Schröder, *et al.*, 1987).

Species diversity was recorded in terms of the α index and information function [H(S)]. The α index, first described by Fisher *et al.* (1943), gives a measure of species richness. Values were read off the base graph in Williams (1964, p. 311) by plotting the number of species against the number of individuals in a sample. This index is an objective method as it takes the size of the assemblage into consideration although

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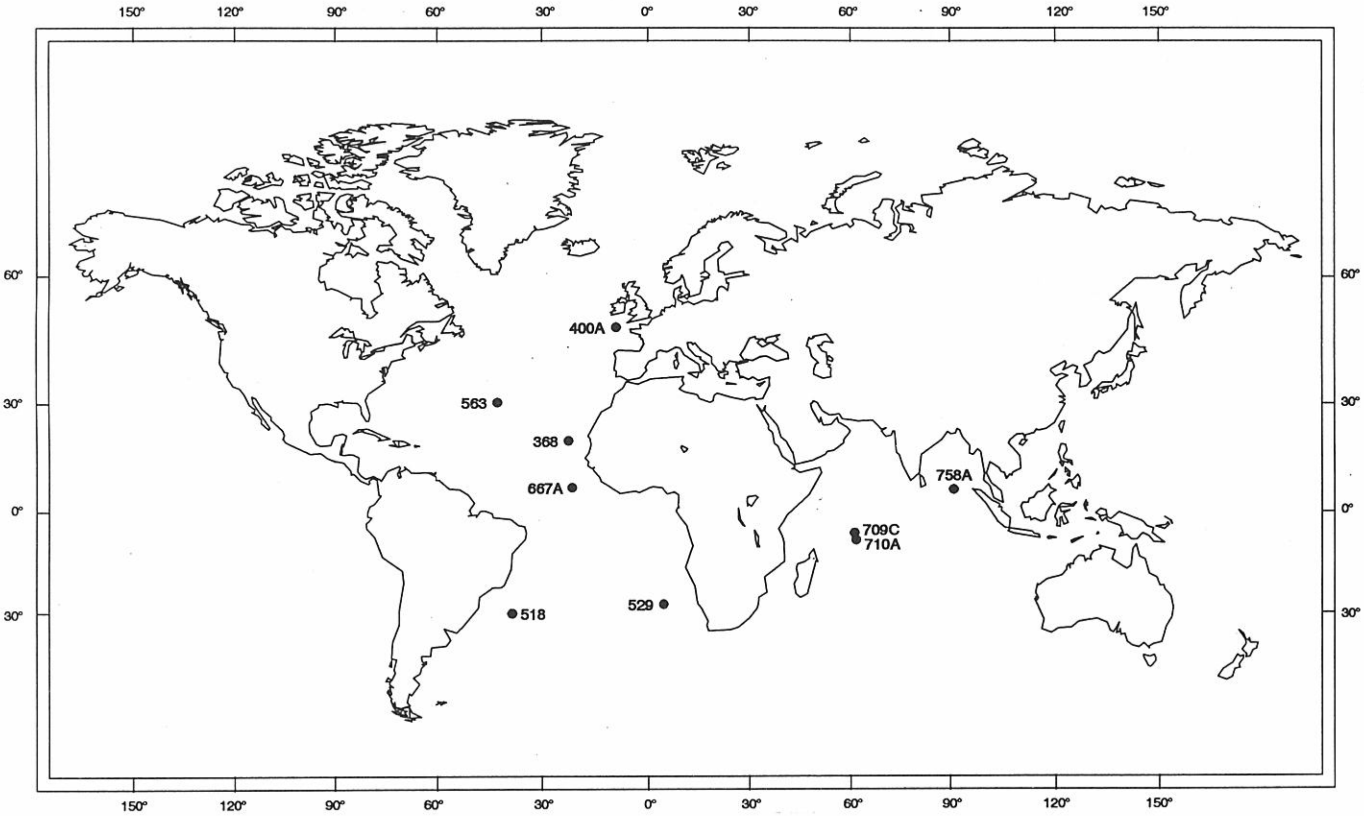

Figure 1. Location of the 9 sites in the Atlantic and Indian Oceans.

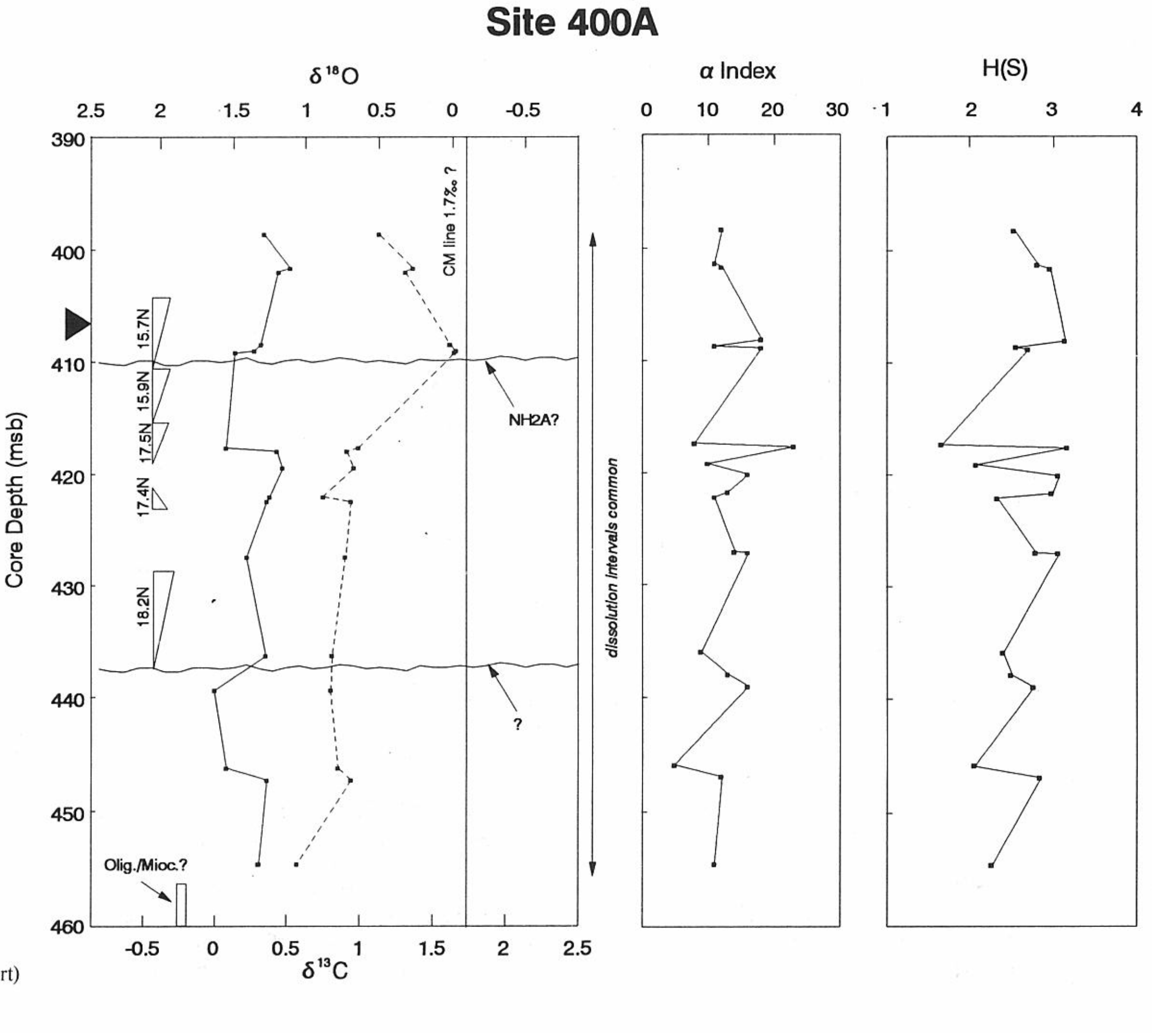

Figure 2 (part)

it takes no account of each species abundance. The information function [H(S)] takes into account both the number of species and the distribution of individuals between species but it ignores sample size. It is a measure of uncertainty and therefore of heterogeneity. Values were calculated using the Shannon-Weaver formulation based on information theory *(H)* as follows:

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

where S is the number of species and p_i the proportion of the ith species (p = per cent divided by 100). The maximum value of H [H(S) max.] for any given number of species is attained when all S species have equal abundances, i.e.:

$$H(S)_{\max} = \ln S$$

RESULTS

The early to middle Miocene deep-sea benthic foraminiferal fauna is very diverse and many species occur at all nine sites. Most of the taxa are rare, often are represented by very few individuals per assemblage and some occur at a single site only. The constant taxa throughout the interval include *Cibicidoides* spp., *Epistominella exigua* (Brady), *Gyroidinoides* spp., *Globocassidulina subglobosa* (Brady), *Nuttallides umboniferus* (Cushman), *Oridorsalis umbonatus* (Reuss), *Pullenia* spp., and unilocular forms. An interval of high abundances of smooth-walled bolivinids occurs in the early Miocene of the Atlantic Ocean (previously reported by Smart and Murray, 1994).

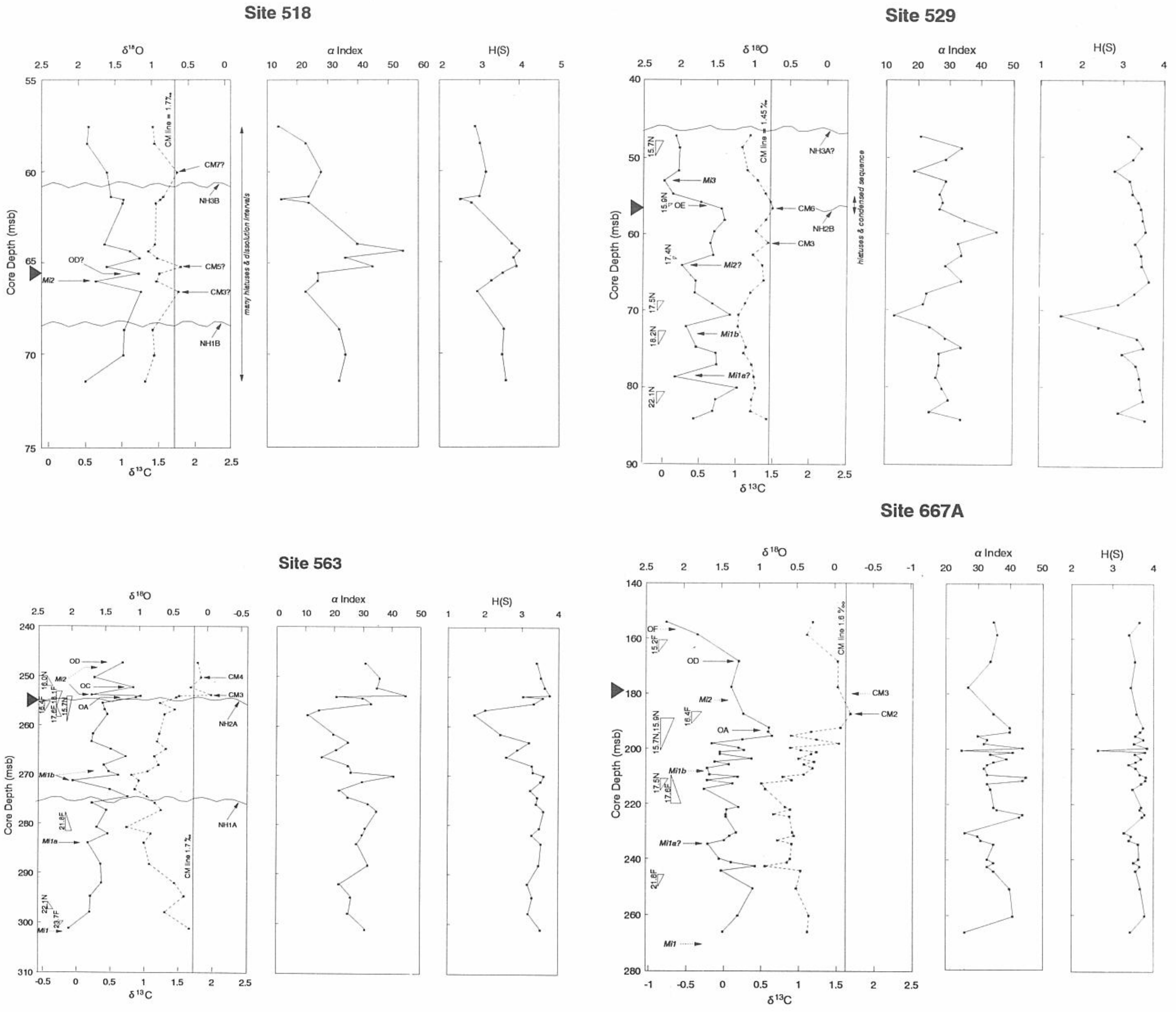

Figure 2. Logs of diversity at the 5 Atlantic sites. Biostratigraphy and benthic stable isotope curves from Smart and Murray, 1994. The left isotope curve (solid line) is the δ^{18}O record and the right isotope curve (dashed line) is the δ^{13}C record. The location of Miocene δ^{18}O events (Mi) of Miller, *et al.* (1991) and Wright, *et al.* (1992), δ^{18}O events *(O)* and δ^{13}C maxima *(CM)* of Woodruff and Savin (1991) are indicated. At Site 563, broken arrow lines indicate positions of events recognised by Miller, *et al.* (1991). At Site 667A, broken arrow lines indicate positions of events recognised by Woodruff and Savin (1991) and Wright, *et al.* (1992). Also shown is the CM line for each site estimated from Woodruff and Savin (1991). Wavy lines indicate locations of hiatuses and are labelled *NH* following Keller and Barron (1983). The open triangles represent the locations of biostratigraphic datums (bottom and top) and the age (in Ma) and fossil type of each: N = nannofossil, F = planktonic foraminifera. Ages are as in Smart and Murray (1994). The uncertainty of the location of the biostratigraphic datums (which is a function of sampling interval) is indicated by the length of the open triangles. The solid triangle indicates the approximate position of the Lower to Middle Miocene transition.

ATLANTIC OCEAN

Site	Latitude Longitude	Number of samples studied	Mean		Range	
			α index	H(S)	α index	H(S)
400A	47°22'N 09°11'W	20	13	2.64	5-23	1.67-3.18
563	33°38'N 43°46'W	29	28	3.23	11-45	1.73-3.66
368	17°30'N 21°21'W	6	20	2.93	14-33	2.70-3.35
667A	04°34'N 21°54'W	38	35	3.59	25-45	2.66-3.85
529	28°55'S 02°46'E	27	28	3.23	13-45	1.52-3.66
518	29°58'S 38°08'W	16	30	3.35	14-55	2.52-4.01

INDIAN OCEAN

Site	Latitude Longitude	Number of samples studied	Mean		Range	
			α index	H(S)	α index	H(S)
758A	05°23'N 90°21'E	21	39	3.67	22-60	3.07-4.03
709C	03°54'S 60°33'E	13	36	3.52	22-46	2.41-3.83
710A	04°18'S 60°58'E	21	28	3.32	15-47	2.81-3.89

Table 1. Location of Sites in the Atlantic and Indian Oceans and summary of species diversity data.

Atlantic Ocean

All the data are given in the Appendix Table and summarised in Table 1. For five of the six Atlantic sites, the α index and H(S) values are plotted versus sub-bottom depth (mbsf) and benthic stable isotope stratigraphy from Smart and Murray (1994) (Fig. 2). Site 368 was omitted from Fig. 2 because of the absence of an isotope stratigraphy. The benthic foraminiferal faunas are highly diverse and generally between 50 and 70 taxa are recognised in a sample of 200 individuals. Both the α index and H(S) show some fluctuations through time but the values are always high and there is no obvious latitudinal trend. However, maximum diversity is seen at Site 667A close to the area of equatorial upwelling. Postmortem dissolution is thought to be insignificant except at Site 400A where it may be responsible for the observed lower diversity. Site 400A has moderate $CaCO_3$ values (<60 % Montadert, Roberts, et al., 1979), P:B ratios are very low (typically $<1:1$) and fragmentary and corroded planktonic and benthic foraminifera are common.

At individual sites, the α index and H(S) all show very similar patterns, although, in general, there is no apparent correlation of peaks between different sites. The exception is a period of lowered α (<15) and H(S) values (<2.0) during the late early Miocene (NN4) at Sites 400A, 529, 563 and 667A. This equates with an interval of high abundances of smooth-walled bolivinids (>60 %) (Smart and Murray, 1994). Regardless of stratigraphic position, there appears to be no correlation between diversity and the benthic $\delta^{18}O$ and $\delta^{13}C$ values (Fig. 3).

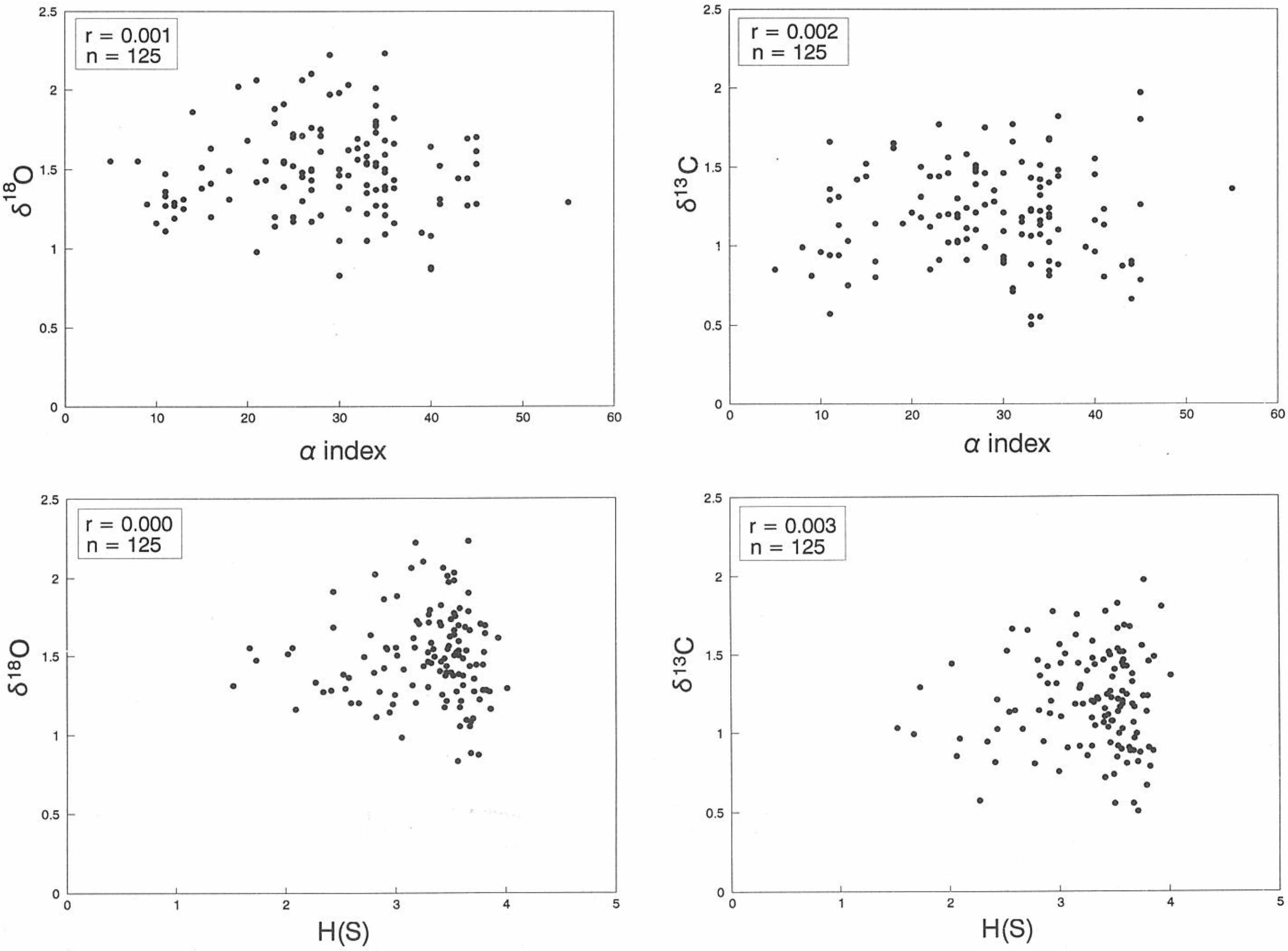

Figure 3. Scatter plots of stable isotopes and species diversity for Atlantic Ocean data.

Although the two indices measure slightly different aspects of diversity (alpha index = species richness, H(S) = heterogeneity), there is a good positive correlation between them (Fig. 4a). In addition, a clear exponential distribution can be seen.

Indian Ocean

The data are given in the Appendix Table and summarised in Table 1. The benthic foraminiferal faunas are highly diverse and generally between 60 and 80 taxa are recognised in assemblages of 250 individuals. Like that of the Atlantic Miocene, α and H(S) fluctuate and there are no latitudinal trends. Dissolution occurs at Site 710A which may account for the lower diversity values. At Site 710A, $CaCO_3$ values are moderate, fluctuating from 30 to 70 % (Backman, Duncan, *et al.*, 1988) and P:B ratios are generally low (~ 2:1).

In contrast to the Atlantic Ocean Miocene sites, α and H(S) values are generally higher in the Indian Ocean sites and the lowest values are not as low (Table 1). A peak in smooth-walled bolivinids (~ 53 %) occurs at ~ 17 Ma at Site 709C (Sample 709C-16H-7, 30-32 cm, 150.10 m sub-bottom) which is coeval with the main bolivinid phase recognised in the Atlantic Ocean (Thomas, 1986; Smart and Murray, 1994). No stable isotope analyses have yet been undertaken on the Indian Ocean samples discussed in this study.

DISCUSSION

Species diversity

The most up-to-date review of the theoretical background, discussion of some of the problems revealed by actual data, and a forward look to ways of establishing the controls on species diversity is that of Schluter and Ricklefs (in Ricklefs and Schluter, 1993). They conclude that at least seven processes influence species diversity (*op. cit.,* p. 10 summarised):

1. Local ecological interactions within small areas of uniform habitat are the population processes of classic diversity theory. Both competition and predation tend to reduce diversity through the elimination of taxa. Unless local communities are saturated, local ecological interactions are necessary, but not sufficient, to explain patterns of diversity.

2. The movement of individuals between patches of the same kind of habitat underscores the importance of regional (external) processes and the ephemeral nature of local populations, and hence the dynamic nature of the local community.

3. The dispersal of individuals between habitats reflects the mosaic nature of the ecological landscape and the interdependence of local and regional diversity due to migration between habitats. Local diversity may reflect the variety and size of habitat patches within the larger region.

4. The spread of taxa within regions according to their habitat of origin and their subsequent ecological diversification may be responsible in part for prevalent relationships between habitat and diversity. Taxa originate and diversify within certain habitat types and require evolutionary change to expand into other habitats. Thus, the relationships between diversity and habitat may depend upon the histories and sizes of habitats as well as upon ecological conditions within particular habitat types. These considerations recognise that community development, including the extinction of taxa, has a long evolutionary history constrained by ecological conservatism of taxa within clades.

5. Allopatric production of species within regions depends on the particular geographical configuration of habitats, which of course differ in their influence according to the dispersal abilities and other properties of taxa. Regions with different spatial arrangements of habitats and barriers to dispersal, as well as different climates, may vary markedly in rates of species production and consequent regional diversity. Speciation has not been studied systematically from ecological and biogeographical perspectives.

6. The exchange of taxa between regions often depends on unique events and geographical configurations, such as those that occur when barriers between major land masses or ocean basins break down or when habitats are displaced, global climate changes and glaciation. Because biotic exchange may elevate diversity within regions of mixing, instances of exchange may provide insights into the regulation of local diversity.

7. Many types of unique events (glaciation, bolide impacts) may lead to episodes of extinction that reduce diversity for periods long enough to require cladogenesis and biotic exchange for its recovery.

At a local level it is possible to recognise processes that allow numerous species to persistently coexist and others that limit diversity. The persistence of species is not understood because the theoretical models predict that "the number of species that can coexist can be no greater than the number of limiting resources" (Tilman and Pacal in Ricklefs and Schluter 1993) yet field data do not support this concept (there are more species than limiting resources). Species diversity may be limited by small population size and by fluctuations in environmental conditions, both of which increase the likelihood of local extinction of rare species. The heterogeneity of a habitat is inversely related to the size of individuals (Morse, *et al.* 1985) and this may account for the greater numbers of small species. In the deep-sea, slight differences of sea floor elevation, presence of different types of burrows and surface trails made by macrofaunal organisms and their different mucilaginous coatings, apart from variations in grain size may all be significant at the scale of a 63-500 µm foraminiferan.

Rosenzweig and Abramsky (in Ricklefs and Schluter 1993) note that the number of species in a region shows a hump-shaped distribution pattern with respect to productivity; species diversity increases as productivity decreases. The authors are unable to satisfactorily account for this but they point out that the favoured theory at present is that environmental heterogeneity is increased by lower productivity.

On a regional scale, species diversity is higher than that of local communities; there is production of new species, and migration of species between habitats and between regions. Ricklefs and Schluter (1993, p. 362) conclude: "Biologists know so little about the generation and maintenance of diversity that it is possible to entertain hypotheses as opposed as local environmental determinism and age-and-area scenarios based on centers of origin".

The fossil record "can reveal patterns of association and change in community composition over time scales that are beyond the reach of neontology, and to which modern patterns cannot necessarily be extrapolated. Marine fossil data can usefully be brought to bear on some of the questions that are of interest in community ecology: for example, whether communities normally utilize all available resources to support a maximum number of species, and whether invasions create important effects among native populations" (Valentine and Jablonski in Ricklefs and Schluter, 1993, p. 341). From an examination of the Pleistocene record of the shallow water marine environment of west North America, they concluded that probably all the migrations of species into and out of communities were driven by climatic changes associated with glacial/interglacial cycles. The resultant associations often have no present-day analogues and, like those, were ephemeral. They suggest that communities contain unoccupied "adaptive space" into which immigrants can fit without totally disrupting the community and causing significant local extinction of pre-existing taxa.

The deep-sea

The bathyal and abyssal zones of modern oceans have high species diversity (Gage and Tyler, 1991). Theories previously put forward to account for this include the stability-time hypothesis of Sanders (1969) and the biological disturbance theory of Dayton and Hessler (1972). In the former, physical stability of the environment was thought to promote diversification, while in the latter biological disturbance such as cropping was thought to be responsible. But, as the recent review by Ricklefs and Schluter (1993) shows, the causes of species diversity patterns in all environments remain largely unresolved.

Recent research has shown that the deep-sea is subject to more short-term change than had previously been realised. For instance, benthic storms may rapidly disturb the sediment surface (Kaminski, 1985). There is seasonal input of food in the form of phytodetritus; this allows opportunistic species to bloom and generally promotes much benthic activity (see review by Gooday, 1994).

Living deep-sea foraminiferal faunas have high species diversity. Murray (1991) summarised the data for bathyal and abyssal environments from all the major oceans (including assemblages > 63, > 125 and > 150 µm) and found the ranges to be α 5-25 and H(S) 0.8-4.1. Individual species range in size from < 20 µm to > 5 cm. Many are soft-bodied with agglutinated or proteinaceous walls which do not survive the processes of fossilisation (Gooday, 1994). Some taxa are epifaunal (living on the sediment surface or on organisms which project above the substrate) but the majority are either shallow infaunal (0-1 cm) or deep infaunal (> 1 cm) in the sense of Buzas, *et al.* (1993).

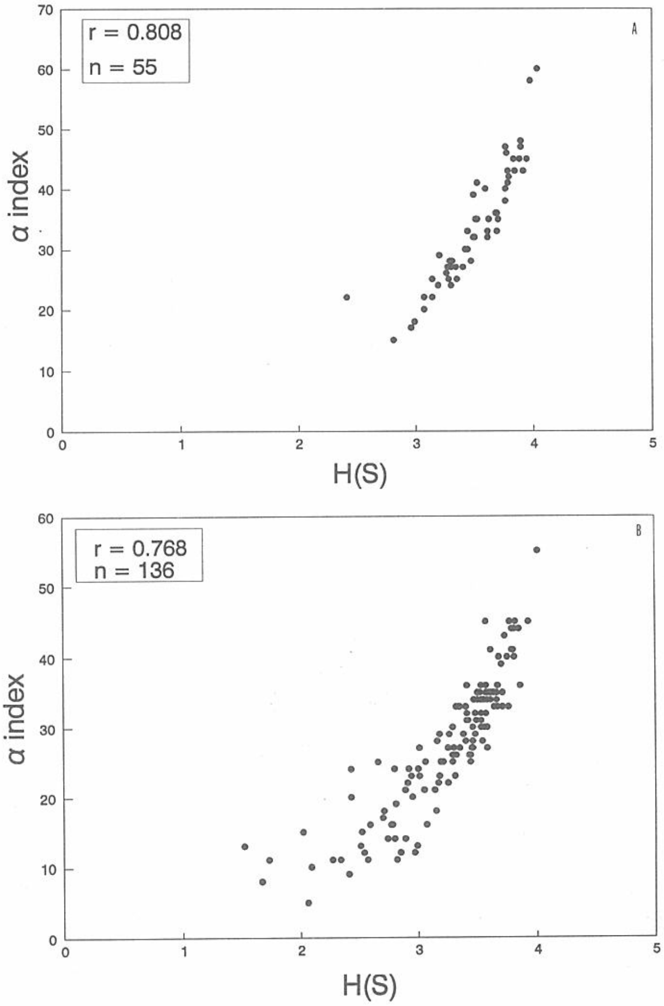

Figure 4. (a) Plot of α and H(S) for Atlantic Ocean data. Fig. 4 (b) Plot of α and H(S) for Indian Ocean data.

At depths of 4483-4539 m in the north Atlantic Porcupine Seabight, Gooday (1988) found that the H(S) of the superficial sediment assemblages was 2.83-3.62. The seasonal input of phytodetritus is an environmental disturbance to which certain opportunistic foraminifera (*Epistominella exigua* and *"Eponides" weddellensis* Earland) respond very rapidly and these assemblages had low diversity (H(S) 1.50-1.69). This is a good example of high productivity being associated with low species diversity.

According to Loubere, *et al.* (1993) the assemblage preserved in the fossil record "...depends on the vertical standing stock distribution of foraminiferal populations, the production rates of these populations, the rate of taphonomic processes and their vertical distribution in the sediments, and the mode and depth of bioturbation". The loss of tests through taphonomic processes includes dissolution of calcareous tests (which is usually obvious through breakage and loss of small individuals) and destruction of fragile agglutinated taxa. The latter invariably occurs so such forms are not normally seen in the fossil record.

From previous studies, possible explanations put forward to account for variations in species diversity throughout the Cenozoic include changes in the nature of the deep-sea environment caused by tectonics (gateways) (Woodruff, 1985) and/or climatically induced changes in ocean circulation, particularly in the nature of bottom water masses, (corrosiveness, i.e., dissolution effects; see Gupta and Srinivasan, 1992; Thomas, 1985, 1990), and intensity of surface water productivity. Gibson and Buzas (1973) have argued that each environment has its carrying capacity for species diversity and this is reached rather quickly on a geological timescale. Valentine and Jablonski (in Rickelfs and Schluter 1993) suggest that communities contain unoccupied adaptive space into which immigrants slot without disrupting the host community. Thus, communities are flexible and constantly changing without causing much local extinction.

Most of the species of modern and Neogene deep-sea assemblages are geologically long-ranging. Temporal changes in species diversity are not likely to be a measure of evolutionary appearances or extinctions but more an index of the Lazarus Effect, i.e, the short-term disappearance and reappearance of long-ranging taxa (see Flessa and Jablonski, 1983). This is comparable with species migration between habitat patches within larger regions.

The good correlation between the α and H(S) indices (Fig. 4) indicates that either is a satisfactory measure of species diversity. However, Alve and Murray (1994) have shown that α is the better discriminator of different modern environments. When the two diversity indices are plotted together (Fig. 5) it can be seen that an exponential relationship exists. This is because although α can increase to infinity, H(S) increases very slowly above about 100 species. Buzas *et al.* (1982) used the α index to determine that the number of species occurring at one, two, n localities conforms to a log series. Most species occur only once, a smaller number, twice, etc.; few species occur at many localities. On the modern Atlantic margin of North America ~ 25 % of the 878 species occur at only one locality (Buzas and Culver, 1991). The same situation applies to samples ("localities") from a stratigraphic succession. Thomas (1992, Fig. 1) showed that in a Palaeocene sample 36 species occurred once, 14 species twice, etc. to 1 with 79 individuals. She argued that to assess species richness, large assemblages should be studied and even then the stratigraphic ranges of rare species cannot be precisely determined.

Comparisons of diversity values between studies is dependent on the use of the same size fraction. Published data include the following size fractions: > 63, 74, 125, 149 µm. Small taxa are progressively "lost" as the size fraction is increased (Schröder, *et al.*, 1987). In addition, there may be different degrees of taxonomic splitting from one worker to another. It follows that the most reliable comparisons are on the same size fraction studied by the same author(s) as in this study.

The late Oligocene-early Miocene was a period of transitional faunas and the early to middle Miocene was a period of faunal turnover (Thomas, 1992; Miller, *et al.*, 1992). The change preceeded the oxygen isotopic increase. Thomas (1992) reviewed the stable isotope evidence for climatic change during this period and concluded that there was some correlation between faunal change and changes in surface water productivity. Thomas (1986) also plotted the number of faunal events (first and last events, whether evolutionary or migratory) at various deep-sea localities. At North Atlantic Sites 608 and 610 there were few events from the early Miocene to early middle Miocene (24-14.5 Ma) but somewhat more up to 11 Ma suggesting a faster rate of change. At Pacific Sites 573 and 574 the highest rate was between 18 and 13 Ma, so the faunal change started earlier there. In the Indian Ocean, a similar faunal change at 17.1 Ma was noted by Nomura (1991).

Whereas the faunal events discussed above signal long-term changes in the ocean environment, the variations in the α and H(S) curves presumably record changes of much shorter duration. Although there is no overall pattern of correlation of peaks from one site to another, the lowest values coincide with the peak abundances of smooth-walled bolivinids during the 20-17 Ma interval (see Smart and Murray, 1994). This was interpreted as representing a period of low oxygen conditions associated with sluggish circulation of the ocean bottom waters in the Atlantic Ocean. Other oscillations in species diversity may be due to localised rather than regional causes. In modern environments, localised habitats within the same region show variation in species diversity (Ricklefs and Schluter, 1993). It is perhaps for these reasons that peaks do not generally correlate from one site to another.

The species diversity values recorded here for the early-middle Miocene are comparable with those of assemblages in modern bathyal to abyssal environments. The Atlantic H(S) values are somewhat lower than those from the Indian Ocean. This is supported by Nomura (1991) who examined the > 149 µm size fraction from Indian Ocean Sites 754 and 756 (H' 3.1-5.0 and 3.7-5.0 respectively). The H(S) values are also higher in the Pacific Ocean (Boltovskoy and Watanabe, 1994; H(S) 3.7-4.8) compared with the Atlantic Ocean. This may indicate significant differences in deep-sea diversity between ocean basins or it could be an artefact resulting from the small data sets. Also, the range of α in the early-middle Miocene Atlantic and of H(S) in the Indian and Pacific Oceans is greater than that of modern oceans in general. It would be unwise to draw firm conclusions on these limited results but it is possible that in the past the species diversity of the oceans was greater than that of the modern ones. There is clearly a need to gather more comprehensive data on the modern oceans and the fossil record.

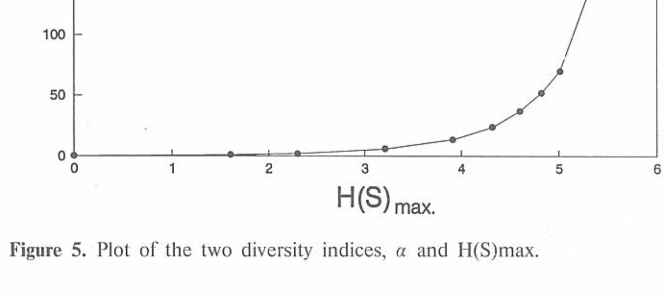

Figure 5. Plot of the two diversity indices, α and H(S)max.

CONCLUSIONS

The early to middle Miocene was a period of oceanic change. The species diversity of the benthic foraminiferal assemblages of the Atlantic and Indian Oceans at this time generally remained high (α 10-60, H(S) 2.0-4.0). Variability in species diversity may be a response to temporal variations in the carrying capacity of the abyssal environment or it may reflect localised environmental changes. There are limited data on the species diversity of modern oceans and much is based on size fractions greater than 63 µm (125 or 150 µm). Diversity values for modern bathyal and abyssal assemblages are α 5-25 and H(S) 0.8-4.1. The α values for the Atlantic and Indian Ocean Miocene range considerably higher (max. α 60). The Atlantic early-middle Miocene H(S) values are comparable with the modern ones but lower than those of the Indian and Pacific Oceans. It would be unwise to draw firm conclusions on these limited results but it is possible that in the past the species diversity of the oceans was greater than that of the modern ones.

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ATLANTIC OCEAN							
Sample	Sub-bottom depth (m)	Nannofossil Zone	No. of specimens	No. of species	Alpha index	H(S)	H(S) max.
368-11-2, 98-102	210.98	NN5	233	44	16	2.78	3.78
368-14-1, 119-121	238.19	NN5	220	68	33	3.35	4.22
368-14-2, 87-89	239.37	NN5	220	58	25	3.06	4.06
368-15-4, 61-63	251.61	NN3-NN4	223	45	17	2.70	3.81
368-16-2, 110-112	258.60	NN3-NN4	217	49	20	2.95	3.89
368-16-4, 32-34	260.82	NN3-NN4	242	40	14	2.74	3.69
400A-35-1, 84-86	398.34	NN5	302	40	12	2.54	3.69
400A-35-3, 84-86	401.34	NN5	261	36	11	2.82	3.58
400A-35-3, 119-121	401.69	NN5	214	35	12	2.97	3.56
400A-36-1, 112-114	408.12	NN5	204	45	18	3.15	3.81
400A-36-2, 20-22	408.70	NN5	228	34	11	2.57	3.53
400A-36-2, 38-40	408.88	NN5	206	44	18	2.71	3.78
400A-37-1, 86-88	417.36	NN4?	294	27	8	1.67	3.30
400A-37-1, 114-116	417.64	NN4?	205	53	23	3.18	3.97
400A-37-2, 114-116	419.14	NN4?	309	34	10	2.09	3.53
400A-37-3, 61-63	420.11	NN4?	249	46	16	3.07	3.83
400A-37-4, 73-75	421.73	NN4?	213	37	13	2.99	3.61
400A-37-4, 114-116	422.14	NN4?	424	39	11	2.34	3.66
400A-38-1, 105-107	427.05	NN2-NN3	219	40	14	2.80	3.69
400A-38-1, 114-116	427.14	NN2-NN3	354	50	16	3.07	3.91
400A-39-1, 48-50	435.98	NN2-NN3	241	29	9	2.41	3.37
400A-39-2, 97-99	437.97	NN2-NN1?	218	38	13	2.51	3.64
400A-39-3, 56-58	439.06	NN2-NN1?	227	44	16	2.77	3.78
400A-40-1, 94-96	445.94	NN2-NN1?	277	20	5	2.06	3.00
400A-40-2, 48-50	446.98	NN2-NN1?	261	39	12	2.85	3.66
400A-41-1, 9-11	454.59	NN2-NN1?	228	34	11	2.27	3.53
518-15-2, 133-135	57.53	NN7-NN9	371	46	14	2.89	3.83
518-15-3, 74-76	58.44	NN7-NN9	406	68	23	3.01	4.22
518-16-1, 91-93	60.01	NN7-NN9	505	83	28	3.16	4.42
518-16-2, 74-76	61.34	NN4-NN5	553	76	24	3.00	4.33
518-16-2, 90-92	61.50	NN4-NN5	356	47	15	2.52	3.85
518-16-2, 110-112	61.70	NN4-NN5	285	61	24	2.80	4.11
518-17-1, 46-48	63.96	NN4-NN5	213	72	40	3.81	4.28
518-17-1, 84-86	64.34	NN4-NN5	277	99	55	4.01	4.60
518-17-1, 122-124	64.72	NN4-NN5	330	85	36	3.86	4.44
518-17-2, 20-22	65.20	NN4-NN5	214	80	45	3.93	4.38
518-17-2, 56-58	65.56	NN4-NN5	259	65	27	3.58	4.17
518-17-2, 99-101	65.99	NN4-NN5	367	73	27	3.30	4.29
518-17-3, 8-10	66.58	NN4-NN5	542	73	23	2.94	4.29
518-18-1, 74-76	68.64	NN4-NN5	379	84	34	3.61	4.43
518-18-2, 64-66	70.04	NN4-NN5	473	94	36	3.57	4.54
518-18-3, 54-56	71.44	NN4-NN5	479	90	34	3.66	4.50
529-6-1, 75-77	47.25	NN6	268	55	21	3.14	4.01
529-6-2, 78-80	48.78	NN6	211	66	34	3.47	4.19
529-6-3, 77-79	50.27	NN6	236	63	29	3.26	4.14
529-6-4, 77-79	51.77	NN6	240	49	19	2.81	3.89
529-6-5, 60-62	53.10	NN6	226	63	29	3.18	4.14
529-6-6, 81-83	54.81	NN6	215	59	27	3.25	4.08
529-6-7, 39-41	55.89	NN5	246	64	28	3.40	4.16
529-7-1, 74-76	56.74	NN4	222	61	27	3.46	4.11
529-7-2, 75-77	58.25	NN4	233	69	35	3.50	4.23
529-7-3, 75-77	59.75	NN4	226	80	45	3.57	4.38
529-7-4, 79-81	61.29	NN4	217	67	33	3.32	4.20
529-7-5, 85-87	62.85	NN4	224	68	34	3.47	4.22
529-7-6, 74-76	64.24	"NN3"	231	64	29	3.48	4.16
529-8-1, 74-76	66.24	"NN3"	225	68	34	3.66	4.22
529-8-2, 84-86	67.84	NN4	210	54	23	3.31	3.99
529-8-3, 74-76	69.24	NN3	219	53	22	2.91	3.97
529-8-4, 72-74	70.72	NN3	229	36	13	1.52	3.58
529-8-5, 74-76	72.24	NN3	221	56	24	2.43	4.03
529-8-6, 74-76	73.74	NN2	219	62	29	3.38	4.13
529-8-7, 44-46	74.94	NN2	228	69	34	3.53	4.23
529-9-1, 74-76	75.74	NN2	291	68	27	3.01	4.22
529-9-2, 74-76	77.24	NN2	232	61	27	3.35	4.11
529-9-3, 84-86	78.84	NN2	222	59	26	3.43	4.08
529-9-4, 74-76	80.24	NN2	202	59	28	3.46	4.08
529-9-5, 74-76	81.74	NN1	238	65	30	3.53	4.17
529-9-6, 74-76	83.24	NN1	219	56	24	2.92	4.03
529-9-7, 23-25	84.23	NN1	230	68	34	3.58	4.22
563-10-4, 74-76	247.24	NN5	224	66	31	3.42	4.19
563-10-6, 75-77	250.25	NN5	219	72	36	3.53	4.28
563-11-1, 76-78	252.26	NN4	210	68	35	3.64	4.22
563-11-2, 76-78	253.76	NN4	242	83	45	3.77	4.42
563-11-2, 98-99	253.98	NN4	269	55	21	3.05	4.01
563-11-2, 128-130	254.28	NN4	226	65	30	3.58	4.17
563-11-3, 93-95	255.43	NN4	271	74	33	3.34	4.30
563-11-4, 74-76	256.74	NN4	214	41	15	2.02	3.71
563-11-5, 19-21	257.69	NN4	238	34	11	1.73	3.53
563-12-1, 65-67	261.65	NN4	259	53	20	2.43	3.97
563-12-2, 74-76	263.24	NN4	290	63	25	3.21	4.14
563-12-3, 74-76	264.74	NN4	209	50	21	2.89	3.91
563-12-4, 74-76	266.24	NN4	248	45	16	2.59	3.81
563-12-5, 99-101	267.99	NN4	220	57	25	3.29	4.04
563-12-6, 81-83	269.31	NN4	219	58	26	3.32	4.06
563-12-7, 4-6	270.04	NN4	223	76	41	3.61	4.33
563-13-1, 72-76	271.22	NN4	229	64	30	3.53	4.16
563-13-2, 99-101	272.99	NN4	260	55	22	3.25	4.01
563-13-3, 92-94	274.42	NN4	356	68	25	3.44	4.22
563-13-4, 74-76	275.74	NN2	261	72	32	3.41	4.28
563-13-5, 74-76	277.24	NN2	232	70	35	3.61	4.25
563-14-1, 71-73	280.71	NN2	216	64	31	3.49	4.16
563-14-2, 53-55	282.03	NN2	244	66	30	3.29	4.19
563-14-3, 86-88	283.86	NN2	215	62	28	3.54	4.13
563-14-6, 67-69	288.17	NN2	224	67	32	3.48	4.20
563-15-2, 100-102	292.00	NN2	208	52	22	3.17	3.95
563-15-4, 65-67	294.65	NN2	213	58	26	3.30	4.06
563-15-6, 86-88	297.86	NN1	219	56	25	3.19	4.03
563-16-2, 63-65	301.13	NP25/25	207	64	31	3.53	4.16
667A-18H-1, 68-70	153.98	NN6	232	69	35	3.66	4.23
667A-18H-4, 72-74	158.52	NN6	205	68	36	3.41	4.22
667A-19H-4, 90-92	168.20	NN5	229	68	34	3.55	4.22
667A-20H-4, 71-73	177.51	NN5	223	62	27	3.45	4.13
667A-21H-4, 84-86	187.14	NN5	225	68	35	3.59	4.22
667A-22H-1, 84-86	192.14	NN4-NN5	221	74	40	3.75	4.30
667A-22H-2, 89-91	193.69	NN4-NN5	228	77	40	3.68	4.34
667A-22H-3, 89-91	195.19	NN4-NN5	207	62	30	3.56	4.13
667A-22H-4, 69-71	196.49	NN4-NN5	205	65	33	3.76	4.17

Atlantic Ocean (cont.)

667A-22H-5, 69-71	197.99	NN4-NN5	215	64	32	3.53	4.16
667A-22H-6, 68-70	199.48	NN4-NN5	227	79	44	3.85	4.37
667A-22H-7, 6-8	200.36	NN4-NN5	239	58	25	2.66	4.06
667A-23H-1, 23-25	201.03	NN4	207	74	41	3.80	4.30
667A-23H-2, 55-57	201.75	NN4	218	67	34	3.55	4.20
667A-23H-3, 92-94	203.42	NN4	223	73	39	3.70	4.29
667A-23H-4, 40-42	204.60	NN4	211	67	35	3.57	4.20
667A-23H-5, 48-50	205.53	NN4	223	66	33	3.40	4.19
667A-23H-6, 87-89	206.82	NN4	214	65	32	3.57	4.17
667A-23H-8, 86-88	209.16	NN4	214	67	33	3.67	4.20
667A-23H-9, 26-28	210.06	NN4	219	81	45	3.82	4.39
667A-24X-1, 93-95	211.23	NN3-NN4	218	78	44	3.81	4.36
667A-24X-2, 63-65	212.43	NN3-NN4	210	65	33	3.71	4.17
667A-24X-3, 114-116	214.44	NN3-NN4	209	66	34	3.50	4.19
667A-25X-1, 118-120	220.98	NN1-NN3	220	70	35	3.71	4.25
667A-25X-2, 55-57	221.85	NN1-NN3	204	67	36	3.67	4.20
667A-25X-3, 81-83	223.61	NN1-NN3	265	86	44	3.79	4.45
667A-25X-4, 19-21	224.49	NN1-NN3	222	77	43	3.73	4.34
667A-26X-1, 94-96	230.24	NN1-NN2	219	59	26	3.29	4.08
667A-26X-2, 62-64	231.42	NN1-NN2	214	64	30	3.46	4.16
667A-26X-3, 65-67	232.95	NN1-NN2	220	65	31	3.41	4.17
667A-26X-4, 49-51	234.29	NN1-NN2	216	68	35	3.63	4.22
667A-27X-1, 90-92	239.70	NN1-NN2	209	65	33	3.64	4.17
667A-27X-2, 71-73	241.01	NN1-NN2	227	70	35	3.52	4.25
667A-27X-3, 53-55	242.33	NN1-NN2	209	66	33	3.67	4.19
667A-27X-4, 70-72	244.00	NN1-NN2	215	68	35	3.57	4.22
667A-28X-2, 56-58	250.36	NN1-NN2	203	71	40	3.68	4.26
667A-29X-2, 87-89	260.17	NN1-NN2	205	73	41	3.79	4.29
667A-29X-6, 59-61	265.89	NN1-NN2	250	61	26	3.44	4.11

INDIAN OCEAN							
Sample	Sub-bottom depth (m)	Nannofossil Zone	No. of specimens	No. of species	Alpha index	H(S)	H(S)max.
709C-16H-5, 75-77	147.55	NN4	275	87	45	3.83	4.47
709C-16H-6, 74-76	149.04	NN4	262	65	28	3.47	4.17
709C-16H-7, 30-32	150.10	NN4	293	58	22	2.41	4.06
709C-17H-1, 75-77	151.25	NN4	260	79	40	3.59	4.37
709C-17H-2, 74-76	152.74	NN4	270	73	33	3.61	4.29

Appendix Table. Data from the Atlantic and Indian Oceans.

Indian Ocean (cont.)

709C-17H-3, 75-77	154.25	NN4	340	94	42	3.79	4.54
709C-17H-4, 74-76	155.74	NN4	265	81	41	3.78	4.39
709C-17H-5, 75-77	157.25	NN4	276	80	39	3.49	4.38
709C-17H-6, 74-76	158.74	NN4	280	77	35	3.51	4.34
709C-17H-7, 30-32	159.80	NN4	282	72	32	3.61	4.28
709C-18H-3, 75-77	163.95	NN4	265	78	38	3.76	4.36
709C-18H-4, 74-76	165.44	NN4	258	88	46	3.77	4.48
709C-18H-7, 30-32	169.50	NN4	281	69	29	3.20	4.23
710A-10H-5, 74-76	92.94	NN7	287	85	41	3.52	4.44
710A-11H-1, 73-75	96.53	NN5	259	67	30	3.42	4.20
710A-11H-4, 77-79	101.07	NN5	258	57	24	3.30	4.04
710A-11H-5, 72-74	102.52	NN5	264	60	25	3.35	4.09
710A-11H-6, 68-70	103.98	NN5	345	72	27	3.27	4.28
710A-11H-7, 29-31	105.09	NN5	307	66	25	3.14	4.19
710A-12H-1, 71-73	106.21	NN5	276	71	32	3.50	4.26
710A-12H-2, 78-80	107.78	NN5	337	72	27	3.34	4.28
710A-12H-3, 73-75	109.23	NN4	292	68	28	3.29	4.22
710A-12H-4, 78-80	110.78	NN4	404	80	30	3.44	4.38
710A-12H-5, 73-75	112.23	NN4	462	72	24	3.19	4.28
710A-12H-6, 77-79	113.77	NN4	309	69	26	3.26	4.23
710A-12H-7, 34-36	114.84	NN2	415	65	22	3.14	4.17
710A-13H-1, 72-74	115.92	NN2	288	50	18	2.99	3.91
710A-13H-2, 68-70	117.38	NN2	270	53	20	3.07	3.97
710A-13H-3, 73-75	118.93	NN2	311	66	25	3.28	4.19
710A-13H-6, 78-80	123.48	NN2	311	50	17	2.96	3.91
710A-14X-2, 97-99	127.37	NN2	357	48	15	2.81	3.87
710A-14X-5, 76-78	131.66	NN2	272	89	45	3.88	4.49
710A-15X-2, 78-80	134.68	NN1	269	90	47	3.89	4.50
710A-15X-5, 73-75	139.13	NN1	416	90	35	3.70	4.50
758A-14X-1, 80-82	122.50	NN6-8	381	73	27	3.30	4.29
758A-14X-2, 83-85	124.03	NN6-8	333	61	22	3.07	4.11
758A-14X-3, 81-83	125.51	NN6-8	292	74	32	3.49	4.30
758A-14X-4, 67-69	126.87	NN6-8	298	77	33	3.44	4.34
758A-14X-5, 14-16	127.84	NN6-8	314	71	28	3.31	4.26
758A-15X-1, 80-82	132.20	NN4-5	262	74	35	3.62	4.30
758A-15X-2, 92-94	133.82	NN4-5	279	86	43	3.78	4.45
758A-15X-3, 81-83	135.21	NN4-5	258	76	36	3.68	4.33
758A-15X-4, 19-21	136.09	NN4-5	271	74	35	3.52	4.30
758A-16X-1, 80-82	141.80	NN4-5	312	71	27	3.40	4.26
758A-16X-2, 82-84	143.32	NN4-5	303	78	33	3.69	4.36
758A-16X-3, 80-82	144.80	NN4-5	277	84	43	3.84	4.43
758A-16X-4, 78-80	146.28	NN3	265	88	47	3.89	4.48
758A-17X-1, 71-73	151.41	NN1-2	276	75	36	3.69	4.32
758A-17X-2, 82-84	153.02	NN1-2	258	80	40	3.76	4.38
758A-17X-3, 70-72	154.40	NN1-2	279	99	58	3.97	4.60
758A-17X-4, 41-43	155.61	NN1-2	274	89	47	3.76	4.49
758A-18X-3, 68-70	164.08	NN1-2	263	86	45	3.94	4.45
758A-19X-2, 67-69	172.17	NN1-2	264	83	43	3.91	4.42
758A-19X-5, 19-21	176.19	NN1-2	262	99	60	4.03	4.60
758A-20X-3, 81-83	183.51	NN1-2	259	89	48	3.89	4.49

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