

14. POPULATION DYNAMICS, PALEOGENE ABYSSAL BENTHIC FORAMINIFERS, EASTERN SOUTH ATLANTIC¹

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ABSTRACT

Benthic foraminifers from Holes 522, 523, and 524 of DSDP Leg 73 (eastern South Atlantic) were quantitatively analyzed by using three methods: analysis of local originations and extinctions, factor analysis of species relative abundances, and population structure analyses of species diversity and equitability. The results of all three forms of analysis are compatible and show a sharp faunal change in the late Eocene. This change involves an almost complete cessation of local originations, a small increase in local extinctions, a dramatic shift in species relative abundances, and a sharp increase in species equitability. Sporadic small-scale variations in the same parameters during the middle Eocene precede the major change. These results indicate initiation of the psychrosphere in the latest Eocene, with precursor events in the middle Eocene. The faunal evidence is consistent with a northeast Atlantic source for the cold bottom water.

INTRODUCTION

Knowledge of the faunal dynamics of abyssal microfossils represents an important tool for the analysis of ancient deep-ocean circulation patterns. This is no less true of the Paleogene benthic foraminiferal faunas retrieved from DSDP Sites 522, 523, and 524 in the eastern South Atlantic (Fig. 1). Sediments recovered from these sites cover a time range (Paleocene–Oligocene) that has been suggested by many to include the development of the psychrosphere and thermohaline circulation (Benson, 1975; Schnitker, 1979; Haq, 1981; Miller, et al., in press). Extinctions, originations, population structure, and migrations within the faunas from these periods may provide our best clues as to the nature and timing of circulation changes in the abyssal realm.

It is the purpose of this paper to analyze quantitative observations taken from Paleogene benthic foraminifers to document and test hypotheses about Paleogene abyssal hydrography. The data discussed here include the relative abundances of 112 species of benthic foraminifers (separated from the $> 125 \mu\text{m}$ size fraction) in each of 64 samples. The biostratigraphic age of each sample was determined from calcareous nannofossils, with supplemental dating from planktonic foraminifers in the Paleocene, middle Eocene, latest Eocene, and Oligocene (Wright et al., this vol.). The absolute age of each sample was determined by linear interpolation between magnetic reversal events in the sediments in each hole as established by Tauxe et al. (this vol.).

ANALYSIS

Before we could analyze the faunal dynamics preserved in these samples, we had to recalculate the data in

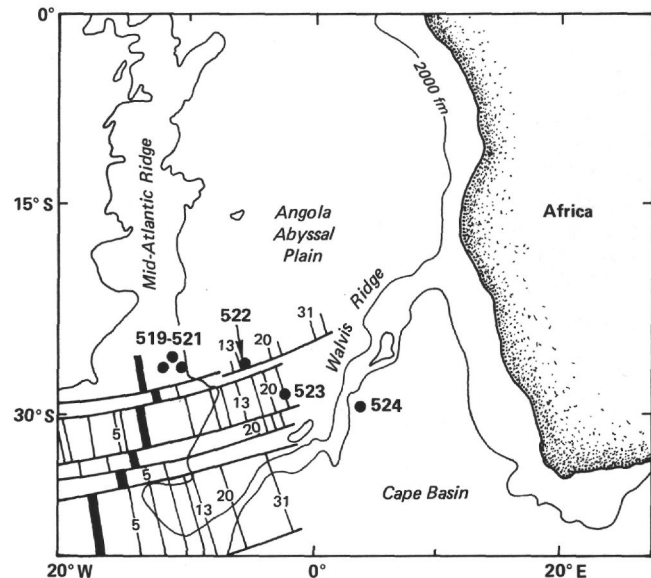


Figure 1. Location map showing positions of sites, marine magnetic anomalies, and the 2000-fm bathymetric contour.

such a way as to remove, insofar as possible, any biasing due to variations in sample interval and sample size. For example, for various reasons, including uneven sample spacing, variations in sediment accumulation rate, and gaps in sediment recovery (notably a large gap in the latest early Eocene), the chronological spacing of the samples is not uniform. The temporal value of the sample intervals ranges from 0.01 m.y. to 10.15 m.y., with an average of 0.62 m.y.; thus, any attempt to tabulate the number of appearances and disappearance on a per sample basis would be biased in terms of time. Simple division of the number of "events" (number of appearances and disappearances) in a particular sample by the length of the preceding sampling interval would exaggerate the

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importance of isolated events in closely spaced samples. To offset this effect, events were retabulated at 1- and 2-m.y. intervals. These intervals were chosen to be compatible with the expected error for the sample ages and to ensure the presence of multiple samples per time interval (average: 1.97 per m.y.). Species with recorded durations less than one retabulation time interval were excluded from analysis, so that densely sampled intervals would not be overrepresented by short-lived species.

The number of specimens in each sample also varied considerably, ranging from 15 to 519 and averaging 135. A sample with few specimens is less representative than one with many, and the significance of a species event depends, at least to some extent, on the size of the sample in which the event occurs. Because of this effect of sample size, the species abundances were retabulated as percentages of the total number of specimens in the sample. A lower percentage cutoff, below which a species was considered absent, was then imposed. Thus, a species would formally appear in that time period during which its abundance first rose above the cutoff percentage and would disappear in the time interval during which its abundance last dropped below it.

Although such an abundance filter reduces the biasing effect of sample size, it results in the exclusion of some data. Therefore the choice of the value for the filter represents a compromise between sampling bias and sample size. In order to observe the effects of varying the filter, the analysis was carried out five times (at the 2-m.y. time interval), using filters of 0.1, 0.3, 0.5, 0.7, 1.0, 2.0, 3.0, and 5.0%. The results were similar for all these analyses. A 2.0% cutoff is preferred for the data discussed here because (1) 2.0% represents the minimum resolution capability of a sample with 50 specimens (and only 11% of the samples [7 of 64] have fewer than 50 specimens), and (2) only 20% of the species (22 of 112) fail to achieve a maximum abundance of at least 2.0%, and are therefore never recorded.

Once the aforementioned biases have been removed, the numbers of appearance and disappearance per time interval are as shown in Figures 2 and 3. The epoch and subepoch boundaries shown are taken from biostratigraphic evidence, and the time scale is interpreted from paleomagnetic data as mentioned above. The bold line represents the pattern of events using a 2-m.y. retabulation interval, and the fine line represents the pattern using a 1-m.y. interval. The lack of information within the 47- to 57-m.y. interval reflects an interval not recovered in the Leg 73 sediments. Because of the nature of the tabulations, the number of appearances in the first sample of the study (early Paleocene) and the sample immediately after the recovery gap (middle Eocene; 48 m.y.) appear inflated and must be ignored. The same is true for the number of disappearances in the last sample before the gap (early Eocene; 58 m.y.) and the last sample of the study (end of the Oligocene). The high number of appearances in NP16 (46 m.y.) is also suspect, but for a different reason; the two samples in the preceding 2-m.y. interval contained only 15 specimens each and are therefore poorly representative. Therefore, some of the events

at 46 m.y. represent true first appearances, while others are species that are in fact present below this level but were not observed because of sample size.

The pattern of appearances (Fig. 2) has two major peaks. The peak in the middle Eocene (46 m.y.) can be seen in both the 1- and 2-m.y. retabulations. The peak in the Paleocene (64 m.y.) could be dismissed as an artifact of the 2-m.y. analysis if the 1-m.y. analysis did not show that a large number of species appeared in the second sample interval as well as the first. These two peaks represent times when 8 to 10 new species appeared within a short (1- to 2-m.y.) timespan, in contrast to an average rate of species appearance of two to three during other similar timespans. Also shown in the diagram is a relative absence of new species appearances in the Oligocene (after 35 m.y.) for a period of 8 to 10 m.y. During this time only one species, *Cibicidoides kullenbergii*, makes its first appearance.

The pattern of disappearances (Fig. 3) is somewhat different from that of appearances. There is a peak in the number of disappearances at the Oligocene/Eocene boundary that is reflected in both scales of analysis. During this period the number of disappearances was approximately three times the average. Except for this peak, there is little agreement between the two scales of analysis, perhaps as a result of rapid small-scale variations in the number of disappearances per time interval. It is worth noting, however, that there is no cessation of disappearances in the Oligocene corresponding to a similar pattern among the originations.

Because an analysis of appearances and disappearances treats the data in a presence-absence fashion,

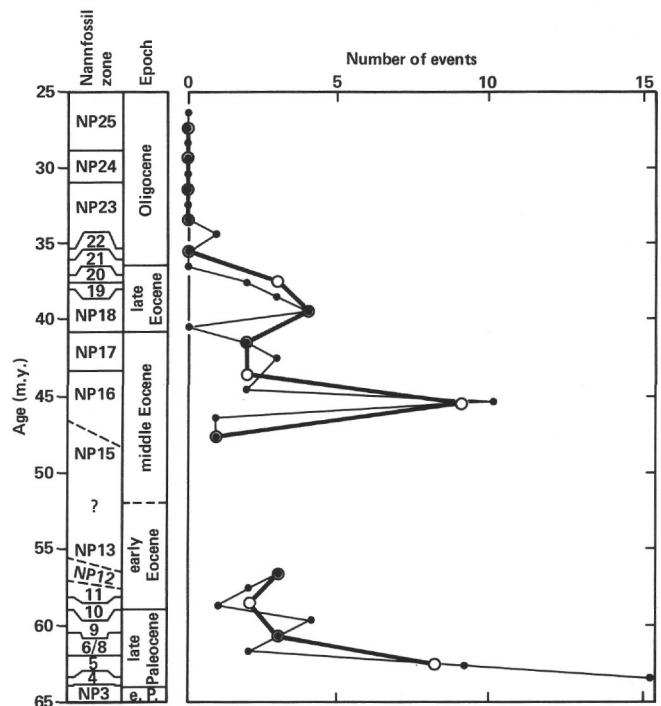


Figure 2. Pattern of local first appearances (local originations). Heavy line represents retabulation of data at 2-m.y. intervals. Thin line represents 1-m.y. intervals.

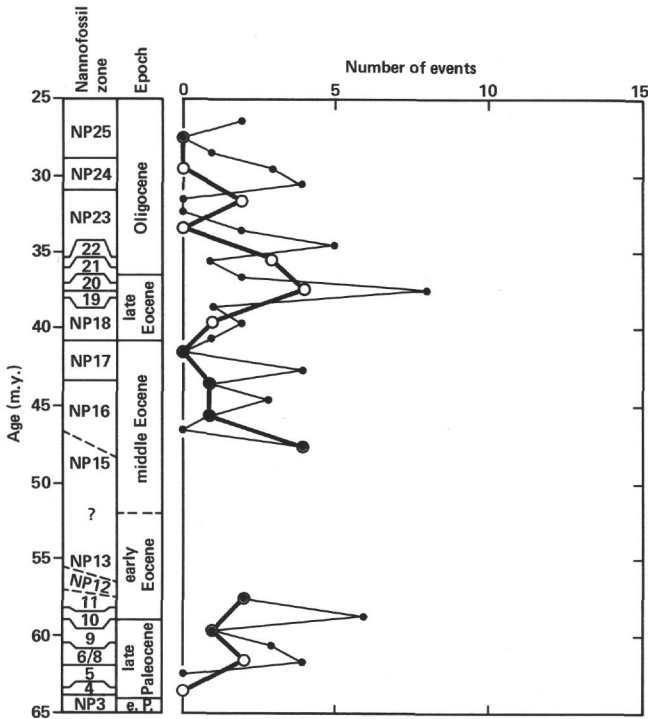


Figure 3. Pattern of local last appearances (disappearances or local extinctions). Heavy line represents retabulation of data at 2-m.y. intervals. Thin line represents 1-m.y. intervals.

such an approach largely ignores changes in the relative abundances of species. So we could compare patterns of change in abundance with the event analysis, a Q-mode factor analysis was carried out by using the computer program CABFAC (Klovan and Imbrie, 1971). This form of analysis attempts to resolve each sample into a picture of some small number of uncorrelated end members. These end members are the "factors" and can be thought of as idealized samples. Each original sample is related to each factor by a "loading" which is the square root of the proportion of a factor in a sample. The composition of the factors is given by the "factor scores," which relate the relative importance of each variable in a factor. A solution involving a given number of factors may then be rotated (using a VARIMAX procedure) in order to maximize the variance in factor loadings. The data as submitted to this analysis consisted of the raw numbers of each species in each sample. A solution of three factors was found to account for 73% of the data. Figures 4 through 6 are bivariate plots of the factor loadings. (Factor scores reveal that each of these three factors are dominated by a few variables [species], as shown in Table 1.) The stratigraphic positions of the samples are also indicated in the factor loading diagrams. Samples poorly explained by the analysis (communalities less than 0.2) and samples with fewer than 50 specimens (11 samples in total) were omitted from the diagrams.

In addition to an examination of the patterns of local appearances and disappearances and the patterns of change in relative abundance with time, the species diversity of each sample was analyzed. An analysis of this

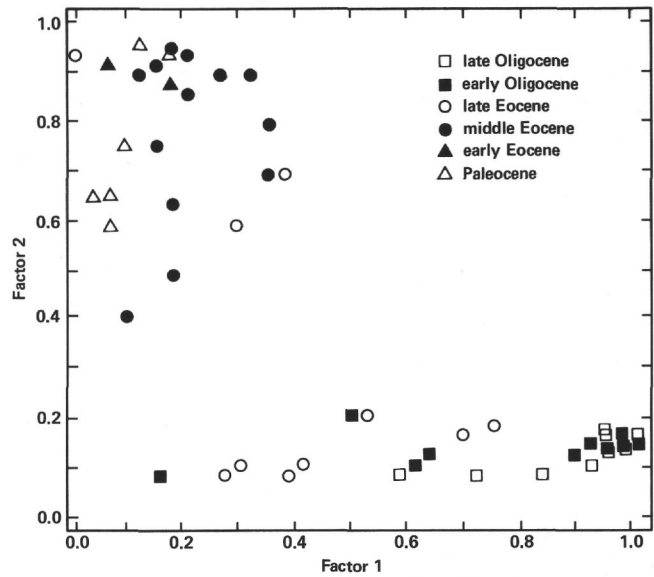


Figure 4. Bivariate plot of rotated factor loadings for Factors 1 and 2. Sample points are keyed to stratigraphic position.

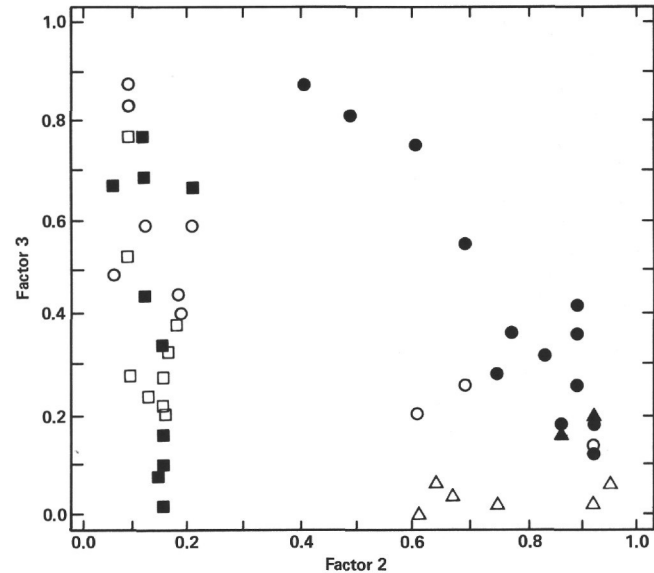


Figure 5. Bivariate plot of rotated factor loadings for Factors 2 and 3. Symbols as in Fig. 4.

type can yield two kinds of information. First, it can give information about the carrying capacity of the habitat from an analysis of rarefaction curves. Second, it can give information about the relative stability of environments from an analysis of the evenness of distribution of specimens among species (equitability).

Rarefaction curves were constructed for each sample by using the probabilistic method of Hurlbert (1971) to calculate points on the curve. An attempt was made to predict (extrapolate) the asymptote (carrying capacity) of each curve by using the curve-fitting approach of de Caprariis et al. (1976). Unfortunately, the deviations between the predicted curves and the plotted ones were not randomly distributed and had a systematic bias. Conse-

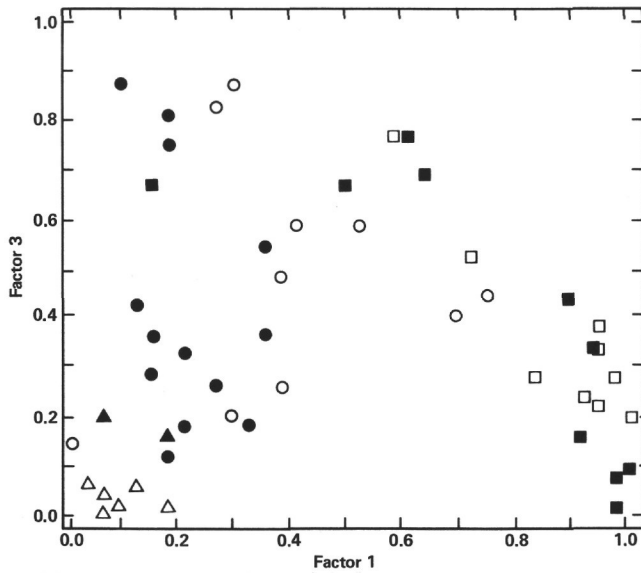


Figure 6. Bivariate plot of rotated factor loadings for Factors 1 and 3. Symbols as in Fig. 4.

Table 1. Taxa with highest rotated factor scores.

Taxon	Score
Factor 1	
<i>Oridorsalis umbonatus</i>	0.9524
<i>Nuttallides umboniferus</i>	0.2243
<i>Bolivina huneri</i>	0.1146
Factor 2	
<i>Nuttallides truempyi</i>	0.9409
<i>Gavelinella beccariiiformis</i>	0.1110
<i>Oridorsalis umbonatus</i>	0.1065
<i>Buliminella beaumonti-grata</i>	0.1033
<i>Gyroidinoides</i> spp.	0.1033
Factor 3	
<i>Globocassidulina subglobosa</i>	0.8207
<i>Gyroidinoides girardanus</i>	0.2687
<i>Cibicidoides</i> sp. 1	0.2007
<i>Plectofrondicularia lyrata</i>	0.1723
<i>Anomalina spissiformis</i>	0.1389
<i>Astrononion pusillum</i>	0.1346
<i>Cibicidoides</i> sp. aff.	0.1273
<i>C. ungerianus</i>	
<i>Stilostomella subspinosa</i>	0.1150

quently, the method was abandoned. A somewhat less satisfactory method was used to compare numbers of species. It is possible to "normalize" samples of unequal size by calculating the number of species that a sample would have if it were reduced to any given size (Hurlbert, 1971). For these calculations, a sample size of 75 was chosen. The results of this calculation are shown in Figure 7 as circles. The pattern is remarkably constant throughout the interval studied. Both mean values and deviations change little from subepoch to

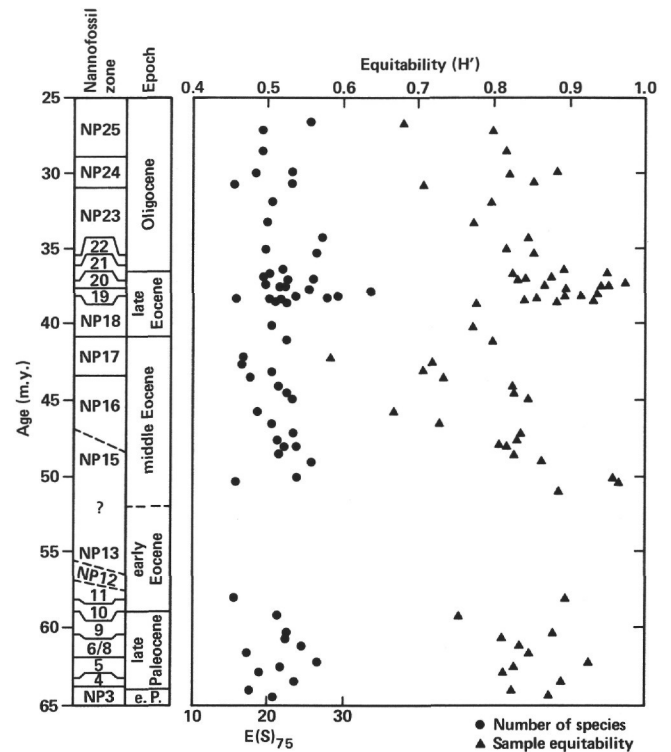


Figure 7. Normalized number of species, $E(S)_{75}$, and sample equitability, H' (see text).

subepoch. There is a brief and slight (but probably insignificant) increase in the number of species in the latest Eocene.

The equitability of species distribution within each sample was calculated by using the information function normalized for the number of species in a sample.

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

where p_i = proportion of the i^{th} species and S = number of species. These values are plotted on Figure 7 as triangles. Several time intervals in the plot show different patterns. The Paleocene to early Eocene values are higher and exhibit less variation than those of the middle Eocene; the values in the early late Eocene are comparable to those of the middle Eocene although less variable; the latest Eocene values are much higher than those seen earlier; and the Oligocene values show a decline in equitability and an increase in variance throughout the epoch.

DISCUSSION

The combined results of the event analysis, factor analysis, and population structure analysis allow us to compare patterns of local origination and extinction with changes in relative species abundance. Coincident patterns from the three analyses may then be used to

suggest a timetable of ocean circulation phenomena. It is important to remember that the appearances and disappearance of species as discussed here refer only to the assemblages in the cores under study. As such, they are probably related to occurrences within the eastern South Atlantic but probably do not reflect species originations and extinctions on a global scale. Because of this emphasis on local events, the most probable cause of local species origination is species migration, and the most probable cause of local extinction is a local unfavorable change in environment. The factor analysis results can be used as an index of a species' "success" between the time it enters and leaves the basin.

The present study begins in the Paleocene with the introduction of a large number of species. The Paleocene is dominated by the "Factor 2" fauna (primarily *Nuttallides truempyi*; see Figs. 4 and 5). Near the end of the Paleocene there is an increase in the number of local extinctions, an event followed by a small increase in the number of originations (although the latter is apparent in only the 1-m.y. interval analysis); however, the faunal dominants appear to be unaffected. Near the Eocene/Paleocene boundary an abrupt increase in extinctions is again followed by a rise in appearances. The dominant fauna loses one species (*Gavelinella beccariformis*), but it is otherwise remarkably unaffected.

The Paleocene and early Eocene apparently represent periods of relative faunal stability during which the appearance and disappearance of species did little to affect the dominant fauna. This dominant "Factor 2" fauna seems to represent a "core" fauna to which various predominantly low abundance exotics were added and subtracted.

The middle Eocene samples immediately following the recovery gap show a dramatic peak in originations and a relatively large number of extinctions. The faunal dominants reflect a mixture of the Factor 3 species (primarily *Globocassidulina subglobosa* and *Gyroidinoides girardanus*; see Table 1) with the Factor 2 core fauna of the older samples (Fig. 5). It is significant that the amount of admixture of Factor 3 species in the middle Eocene assemblages seems to be proportional to the number of originations that occur in the time period corresponding to the sample.

The middle Eocene appears to be a time of faunal instability, in contrast to the Paleocene-early Eocene. Equitability is not only less but also more variable. The core fauna was diluted various amounts by the Factor 3 fauna. This dilution was not a progressive process but rather a sporadic phenomenon that went furthest during major episodes of species origination in (or migration into) the basin. After each period of maximum dilution, the Factor 2 core fauna reasserted its dominance.

The earliest three samples of the late Eocene are again dominated by the Factor 2 fauna (Fig. 5). However, the last eight samples are dominated primarily by Factor 3 faunas and are much more equitable (Figs. 5 and 7). The Oligocene samples are made up primarily of Factor 1 faunas (primarily *Oridorsalis umbonatus*; see Table 1), with various admixtures of Factor 3 fauna (Fig. 6). The amount of Factor 3 faunal admixture in a

sample is inversely related to the number of extinctions in the sample's time interval.

The data on the Paleocene-early Eocene core fauna and the Factor 3 fauna indicate that the late Eocene was a time of faunal turnover. This turnover was preceded by sporadic mixtures of the two faunas in the middle Eocene. The Oligocene record involved a shift in dominance from the Factor 3 fauna to the Factor 1 fauna and was characterized by periods of local extinction. Because of the paucity of local originations during the Oligocene and continuing local extinctions, the Oligocene fauna represents a reduced and relatively unstable remnant from the late Eocene.

If the initiation of the psychrosphere occurred near the Oligocene/Eocene boundary it would be reasonable to expect such an event to leave a dramatic signature in the abyssal microfossil record. The major faunal change indicated by the analyses described here would be compatible with the initiation of the psychrosphere in the latest Eocene. This change in ocean circulation was heralded by variation in the middle Eocene faunal dominances, possibly as a result of the sporadic introduction of cold bottom water into the basin. The Oligocene dominance shifts reflect the continued local extinction of warm-water species and the cessation of migration from other bathymetric realms.

The pattern of faunal change observed in this study is similar to that reported by Schnitker (1979), Tjalsma (1982), Tjalsma and Lohmann (1982), and Miller et al. (in press). However, the timing of the faunal events in most basins is complicated by numerous hiatuses in the interval of interest (Moore, et al., 1978; Miller, et al., in press). Authors who have used faunal information to address the psychrosphere problem have given its time of initiation as approximately the Eocene/Oligocene boundary (Schnitker, 1979; Benson, 1975; Haq, 1981). In contrast, our analyses and those of Miller et al. (in press) suggest that the initiation may have occurred in several steps and that the most dramatic of these occurred during the late Eocene.

The source of the cold deep water for the psychrosphere is somewhat speculative. It may have been a product of general climatic deterioration, as revealed by oxygen-isotope studies (cf. Savin et al., 1975; Boersma and Shackleton, 1977; Haq, 1981; Cavelier et al., 1981; Miller and Curry, 1981). Other investigators have suggested a high-latitude source for the water, either from the south as Antarctic Bottom Water (e.g., Schnitker, 1979, 1980) or from the north (e.g., Haq, 1981; Miller et al., in press). The distribution of some taxa, such as *Stetsonia* sp. 1 (Clark and Wright, this vol.), which occurs in the eastern South Atlantic and the Bay of Biscay (Schnitker, 1979) but not the western South Atlantic (Tjalsma, pers. comm., 1982) lends some support to the idea of a northern source for the water, which remained on the eastern side of the Mid-Atlantic Ridge. This source could have been tapped by the opening of the Greenland-Norwegian Sea, although the sporadic faunal shifts in the middle Eocene would seem to suggest that the passage was beginning to open as early as 45 m.y.

SUMMARY

In summary, the results of the three different types of faunal analysis (event analysis, factor analysis, and population structure analysis) indicate a major faunal change in the late Eocene benthic foraminifers of the eastern South Atlantic. This change involves a small increase in the number of local extinctions, an almost complete cessation of local originations, a dramatic shift in species relative abundances, and an abrupt increase in species equitability. This change was preceded in the middle Eocene by similar but smaller scale sporadic shifts in relative abundances and large fluctuations in both the number of local originations and species equitability. We suggest that these results mark the initiation in the latest Eocene of the psychrosphere in the eastern South Atlantic and that the changeover to thermohaline circulation may have involved the sporadic introduction of cold bottom water into this area as early as the middle Eocene. Faunal evidence seems most compatible with a northeastern Atlantic source for this cold water.

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