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Late Cretaceous–early Eocene mass extinctions in the deep sea

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ABSTRACT

Upper Maastrichtian through lowermost Eocene deep-sea benthic foraminiferal records from Maud Rise (Weddell Sea, Antarctica) demonstrate that there was no mass extinction of these organisms at the end of the Cretaceous. There is no significant drop in diversity across the Cretaceous/Tertiary boundary, but just above this boundary there is a peak in relative abundance of species that may indicate low-nutrient conditions, probably reflecting the decrease in food supply to the ocean floor resulting from the large-scale extinction of surface-dwelling primary producers. In contrast, there was a global extinction of bathyal to abyssal benthic foraminifera at the end of the Paleocene, occurring in fewer than 25,000 yr at Maud Rise. Many benthic foraminiferal species that had originated during the Cretaceous became extinct, although there was no coeval mass extinction (of comparable importance) of terrestrial organisms and planktonic marine organisms. After this extinction the diversity of benthic faunas on Maud Rise was low for about 260,000 yr, and during the period of low diversity, the assemblages were dominated by species that may indicate the presence of abundant organic carbon, and possibly low concentrations of dissolved oxygen. The dominance suggests that the Paleocene/Eocene deep-sea benthic foraminiferal mass extinction was caused by a decrease in oxygen content of the waters bathing the lower bathyal reaches of the sea floor. Such a change could have been caused by a change in the circulation patterns of deep waters: these waters would become depleted in dissolved oxygen if there was a change from predominant formation of deep waters at high latitudes (cooling and sinking) to initiation of, or a strong increase of, formation at low latitudes (evaporation and sinking). Thus, one of the largest Phanerozoic extinctions at the Earth's surface is not reflected by the deep-water foraminifera, and the largest Cenozoic extinction event in the bathyal-abyssal realm of the oceans is of little importance to surface biota: even some of the largest extinction events that we know do not reach all environments of the Earth.

INTRODUCTION

At the end of the Cretaceous, land-dwellers and surface-dwelling organisms in the oceans underwent one of the largest extinction events of the Phanerozoic (e.g., Thierstein, 1982; Clemens, 1982; Russell, 1982), but extinction rates in deep-sea benthic organisms are not well known (Culver, 1987; Thierstein, 1982; Hsü, 1986). Benthic organisms in the deep oceans have been said to show little or no change across the Cretaceous/Tertiary boundary (Hsü, 1986); detritus feeding has been seen as a "buffer to extinction" (Sheehan and Hansen, 1986; Arthur and others, 1987), although some authors suggest that burrowing organisms underwent a mass extinction (Wright *in* Hsü and others, 1984, p. 335). Deep-water ostracodes have been reported to have had a "faunal crash" at the end of the Cretaceous (Benson and others, 1984), but few data are available for faunas living just after that "crash," so mass-mortality patterns for that group have not been well established (Steineck, personal communication, 1989; Benson and others, 1985, Fig. 1).

Benthic foraminifera, which supply the most abundant fos-

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sils of deep-water organisms, were reportedly little affected by the mass extinction at the end of the Cretaceous (Douglas and Woodruff, 1981; Thierstein, 1982; Culver, 1987), but this observation is based on few quantitative data sets. Many earlier workers on benthic foraminifera described the great similarity of Maastrichtian and Danian (lower Paleocene) faunas (e.g., Cushman, 1946). More recently, differences have been recognized, although estimates of extinction rates vary widely (18 to 67 percent species extinction; Beckmann, 1960; Webb, 1973; Beckmann and others, 1982; Dailey, 1983; Widmark and Malmgren, 1988; Keller, 1988b). Several of the estimates (Beckmann, 1960; Webb, 1973; Beckmann and others, 1982) must be seen as maximum estimates, simply because they were derived from comparisons of faunal lists for the Maastrichtian and Danian. Therefore, these estimates include last appearances that occurred a considerable time before the boundary.

Environmental conditions at the end of the Paleocene contrast with those at the end of the Cretaceous. At the end of the Paleocene there were no extinctions among shallow-water and surface dwellers comparable in size to the extinctions at the end of the Cretaceous: it was a period of below-average extinction rates (Raup and Sepkoski, 1986). The diversity of marine planktonic microorganisms such as dinoflagellates, calcareous nannoplankton, and foraminifera was increasing after the middle Paleocene (e.g., Oberhaensli and Hsü, 1986). At the same time, however, deep-sea benthic foraminifera underwent their largest known extinction of the Cenozoic (e.g., Beckmann, 1960; Braga and others,1975; Schnitker, 1979; Douglas and Woodruff, 1981; Tjalsma and Lohmann, 1984; Culver, 1987), and this extinction has remained unexplained. Some authors suggest that primary productivity decreased at the end of the Paleocene (Shackleton and others, 1985), and this could have caused the extinction of deep-water dwellers; the suggestion has not been widely accepted, however (Miller and others, 1987b; Katz and Miller, 1989).

One purpose of this study was to contribute to the knowledge of the "fabric" of the extinction at the end of the Cretaceous by collecting a quantitative data set on ranges and abundance patterns of deep-sea benthic foraminifera from Maud Rise (Weddell Sea, Antarctica). Another purpose was to compare the changes in faunal composition of deep-sea benthic foraminifera at the Cretaceous/Tertiary (K/T) boundary (a time of collapse of the primary productivity; Arthur and others, 1987) with faunal changes at the end of the Paleocene at the same location, to assess whether the patterns of faunal change were similar. This information should be important in evaluating whether mass extinctions reach all environments from the surface to the lower bathyal areas of the oceans, or whether these two environments (and thus their inhabitants) are largely decoupled.

MATERIAL AND METHODS

Sites and Stratigraphy

Ocean Drilling Program (ODP) Sites 689 (64°31.009′S, 03°05.996′E, present water depth 2,080 m) and 690 (65°9.629′S, 1°12.296′E, present water depth 2,914 m) were drilled on Leg 113 (January-March 1987) on Maud Rise, an aseismic ridge at the eastern end of the Weddell Sea (Barker and others, 1988; Fig. 1). Site 689 is on the northeastern side of the ridge near its crest, Site 690 is on the southwestern flank, 116 km to the southwest of Site 689. Lowermost Maastrichtian through Pleistocene biogenic sediments were recovered at both sites (Fig. 2). The Upper Cretaceous through lower Eocene consists of calcareous chalks and oozes; fine-grained terrigenous material is present in parts of the section at Site 690 (Barker and others, 1988, p. 190–191).

Paleodepths of the sites could not be estimated using simple thermal subsidence models because Maud Rise is an aseismic ridge; benthic foraminiferal faunas indicate latest Cretaceous–Paleocene depths of 1,000 to 1,500 m for Site 689, and 1,500 to 2,000 m for Site 690 (Thomas *in* Barker and others, 1988; Thomas, 1990). For several sites drilled on ODP Leg 114 (Sites 698–702; see Fig. 1 for locations), paleodepths could be estimated using simple thermal subsidence models; overall, these depths showed good agreement with depths derived from faunal data (Katz and Miller, 1990). Comparison of the Maud Rise faunas and the Leg 114 faunas confirms the depth estimate of 1,000 to 2,000 m for Sites 689 and 690 during the late Maastrichtian–early Eocene. In this study the following bathymetric divisions were recognized, in agreement with Berggren and Miller (1989): neritic—<200 m; upper bathyal—200 to 600 m; middle bathyal—600 to 1,000 m; lower bathyal—1,000 to 2,000 m; upper abyssal—2,000 to 3,000 m; lower abyssal > 3,000 m. Therefore, both sites can be placed in the lower bathyal interval for the time period studied.

The biostratigraphic information was obtained from calcareous nannofossils (Pospichal and Wise, 1990a, b, c); only a few datum levels of planktonic foraminifera were reliable age indicators at these high latitudes (Stott and Kennett, 1990a; Huber, 1990). In addition, data on the paleomagnetic record were provided by Hamilton (1990) for the Mesozoic, and Spiess (1990) for the Cenozoic. The stratigraphic information supplied by all these authors is compiled in Figure 2.

In this chapter, data are presented for the interval between 140 and 260 meters below sea floor (mbsf) at Site 690 and 200 to 260 mbsf at Site 689, corresponding to upper Maastrichtian (*Nephrolithus frequens* Zone; Pospichal and Wise, 1990a) through lowermost Eocene (CP9; Pospichal and Wise, 1990c). Absolute ages were derived from cross correlation of the paleomagnetic and calcareous nannofossil data with the geomagnetic polarity time scale of Berggren and others (1985). At Site 689 there are unconformities at the K/T boundary (Zone CP1a, several hundred thousands of years), in the middle Paleocene (Zones CP4 through CP5), and in the topmost Paleocene through lower Eocene (at least Zones CP9 through CP11; about 6.6 m.y.; Fig. 2). There is no Ir anomaly at the stratigraphic K/T boundary in Hole 689B, confirming the presence of an unconformity (Michel and others, 1990). The upper Maastrichtian–lowermost Eocene record at Site 690 does not contain

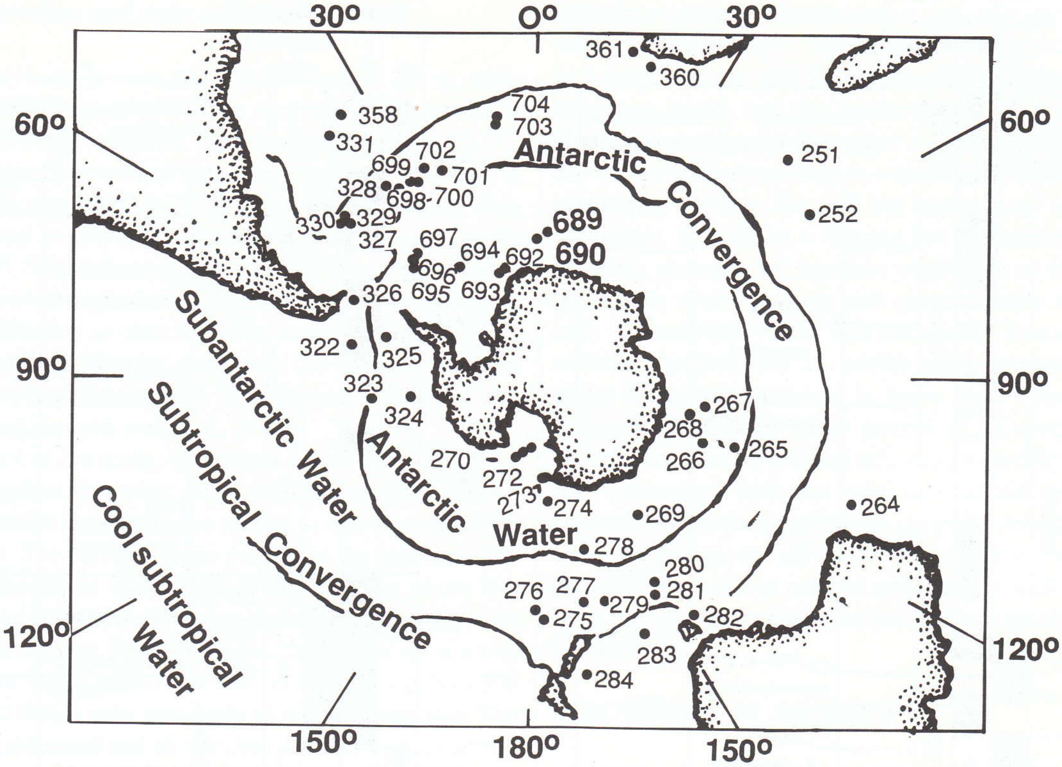

Figure 1. Location of Sites 689 and 690, and other sites at high southern latitudes drilled by the Deep Sea Drilling Project and the Ocean Drilling Program (ODP). Sites 698 through 704 were drilled during ODP Leg 114.

unconformities detectable at the present level of biostratigraphic precision, and an Ir anomaly was detected at the location of the calcareous nannofossil boundary (Michel and others, 1990; Pospichal and Wise, 1990b). The interval just above the K/T boundary was recognized by the presence of the lowermost Paleocene nannofossil zone CP1a (with the index form *Biscutum sparsum*; Pospichal and Wise, 1990b) and by an interval containing the lowermost Paleocene index species *Eoglobigerina fringa* and *E. eobulloides* combined with small heterohelicids (Stott and Kennett, 1990a). Sedimentation rates were estimated at Site 690 using paleomagnetic data, resulting in a sedimentation of 14.4 m/m.y. for the uppermost Paleocene (Chron 24R). Sedimentation rates for the uppermost Cretaceous are more difficult to derive, but Hamilton (1990) has suggested a sedimentation rate of about 7.5 m/m.y. at Site 690, and not much different for Site 689 (below the unconformity at the K/T boundary).

The location of the Paleocene/Eocene boundary with regard to biostratigraphic zonations is difficult and often discussed (Berggren and others, 1985; Aubry and others, 1988). The benthic extinction had been reported to occur at the boundary of planktonic foraminiferal zones P5 and P6a (i.e., in the late Paleocene, according to Berggren and others, 1985) by Tjalsma and Lohmann (1983), but Boersma (1984) and Miller and others (1987b) placed the event closer to the boundary, between zones P6a and P6b (the Paleocene/Eocene boundary as defined in Berggren and others, 1985, but late Paleocene in Aubry and others, 1988). At Site 690 the benthic faunal events occurred at the boundary between Antarctic foraminiferal Zones AP4 and AP5, thought to be equivalent to the P6a/P6b boundary (Stott and Kennett, 1990a). The benthic extinction also occurred in paleomagnetic Chron C24R and in calcareous nannofossil Zone CP8, almost exactly in the middle of the interval between the first appearance of *Discoaster multiradiatus,* the lower boundary of that zone, and the first appearance of *Tribrachiatus bramlettei,* the lower boundary of the subsequent zone CP9a (Pospichal and Wise, 1990a). This places the age of the benthic extinction at about 57.5 Ma, in the late Paleocene (in the time scale of Aubry and others, 1988), and at the Paleocene/Eocene boundary in the zonal scheme of Berggren and others (1985).

At the Maud Rise sites the benthic faunal event occurs at the same location in the section as a major change in $\delta^{13}C$ values in bulk carbonate (Stott and others, 1990) and in benthic foraminifera (Kennett and Stott, 1990). This isotopic event had been correlated with the Paleocene/Eocene boundary (Miller and others, 1987a, b; Shackleton, 1986), and at Site 690 it occurred at the Paleocene/Eocene boundary in the zonal scheme of Berggren and others (1985), but clearly before the Paleocene/Eocene boundary as defined in Aubry and others (1988); i.e., within Zone CP8, and precisely at the planktonic foraminiferal zonal boundary between Zones AP4 and AP5 (equivalent to the bound-

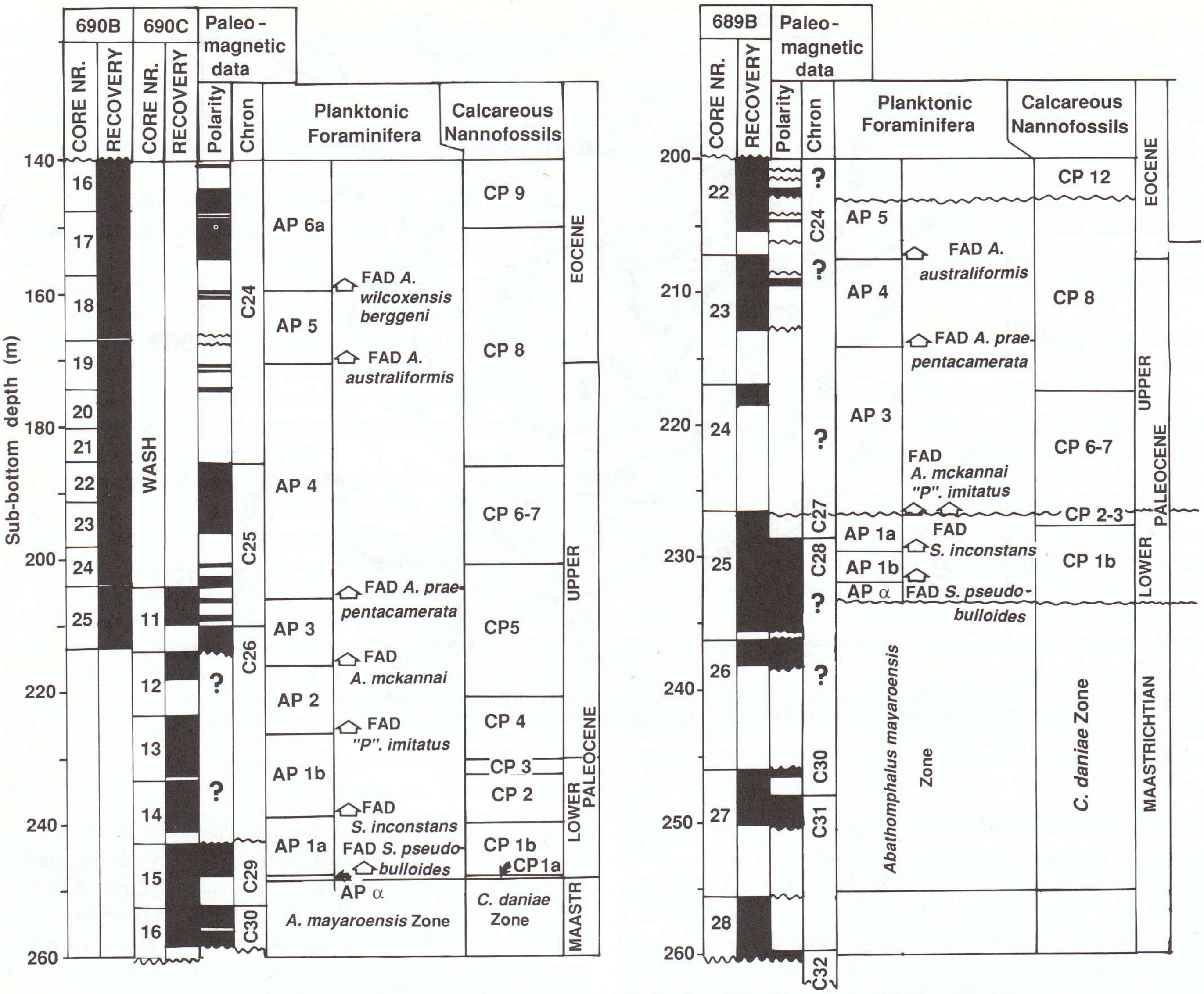

Figure 2. Core recovery, biostratigraphy, and magnetostratigraphy at Sites 689 and 690. The core recovery data are after Barker and others (1988); data on the magnetostratigraphy for the Cenozoic are after Spiess (1990), and for the Mesozoic are after Hamilton (1990). The nannofossil biostratigraphy is after Pospichal and Wise (1990a, 1990b, 1990c), the planktonic foraminiferal biostratigraphy for the Cenozoic is after Stott and Kennett (1990a), and for the Mesozoic is after Huber (1990). For planktonic foraminifera, Cenozoic datum levels are given in the figure, because the proposed zones are not yet widely known or accepted.

ary between Zones P6a and Pb6). It is difficult to judge whether sections across the Paleocene/Eocene boundary are complete, because so many sections contain unconformities in this interval and there is thus no obvious "standard complete section." The section at Site 690 appears to be the most complete section available from all Deep Sea Drilling Project (DSDP) and ODP sites, if judged on the distance between the boundary between nannofossil Zones CP8 and CP9, and the planktonic foraminiferal boundary between AP4 and AP5 (equivalent to P6a/P6b). These boundaries were thought to be coeval (Berggren and others, 1985), but later it was realized that there is an offset between the two in more complete sections (Aubry and others, 1988). This offset is almost 20 m at Site 690, more than at any other site. In addition, the thickness of Chron 24R is greater at Site 690 than at any other DSDP or ODP site, and comparison of the isotope records for Site 690 with those of the southern Atlantic sites (Shackleton, 1986) also suggests that the Site 690 record is the thickest section across this interval. In addition, the recovery was very good at that site (Fig. 2), and core disturbance was minimal, with the exception of the interval of overlap between Holes 690B and 690C (Barker and others, 1988). The record at Site 689 is of much lower quality, because of the presence of several hiatuses (Fig. 2) and poor recovery in some intervals.

Sample preparation and data collection

Samples (15 cm^3) were taken at intervals of 1.5 m; additional samples at distances of 0.35 m were taken in intervals in which major changes occurred. Samples were dried at 75 °C, soaked in Calgon, and washed through a sieve with openings of 63 μm; residues were dried at 75 °C. The size fraction larger than 63 μm was used to obtain good representation of small species (Thomas, 1985; Schroeder and others, 1987). The preservation of benthic foraminifera is good to excellent over the studied interval; there is no dissolution as observed from fragmentation and fluctuations in planktonic/benthic ratios, and the isotopic values do not indicate recrystallization (see also discussion in Stott and others, 1990 and Kennett and Stott, 1990).

At the start of the study, rarefaction curves were drawn for some samples (plots of number of species versus number of specimens) to determine the sample size needed to recover most of the species present. The curves became parallel to the specimen axis at about 270 specimens in the more diverse samples, about 200 specimens in the less diverse samples; about 300 specimens were picked from all samples. Part of each sample was spread in a tray to estimate how much material would be needed to collect 300 specimens, and then a split was made of the estimated size. The taxonomy was discussed and all raw data (counts) were presented together with range charts in Thomas (1990). The most used taxonomic references for the Cenozoic were Plummer (1926), Berggren and Aubert (1975), and Morkhoven and others (1986); for the Mesozoic, references were Cushman (1946), Dailey (1983), and Nyong and Olsson (1984).

Calcareous benthic foraminifera dominated in all samples, and calcareous taxa were placed in morphological groups. The three groups distinguished are: (1) the spiral group (including most trochospiral and some planispiral species); (2) the biserial-triserial group, including species that belong in the superfamily Buliminacea (to which the recent low-oxygen/high-nutrient indicators such as bolivinids and uvigerinids also belong); and (3) the cylindrical group (uniserial species with a cylindrical shape). These morphological groups were then compared with the classification of morphological groups as described by Corliss and Chen (1988). The spiral group agrees closely with the group of epifaunal species listed by these authors, and the triserial-biserial group with the infaunal species. There are few data on the environmental preference of the morphological group of cylindrical species, consisting of *Stilostomella* spp., *Pleurostomella* spp., and uniserial lagenids (Thomas, 1985), because these species are rare in the recent oceans. Therefore these specimens were not included in the counts of epifauna or infauna, but were plotted by themselves (see below). These cylindrical species might be placed in the group of infaunal species in the future (Corliss, written communication, 1989) if this placement is supported by additional data. There is a significant correlation ($p > 97.5$) between the relative abundances of the infaunal and the cylindrical group in the Maud Rise samples.

Faunal events in deep-sea benthic foraminiferal faunas are difficult to quantify. The faunas are generally very diverse (commonly >60 species per 300 specimens), with many rare species (<5 percent on the total fauna). The most common species have very long ranges, and the shorter-ranged species are rare; thus, ranges of many species that might be stratigraphically useful cannot be determined precisely in a statistically valid way, and precise timing of many first and last appearances is difficult if not impossible. In addition, a first or a last appearance of a species at a specific site may not represent origination or extinction: deep-sea benthic species migrate both geographically and bathymetrically (Woodruff, 1985; Kurihara and Kennett, 1988). In addition, the literature can not be easily interpreted because of major taxonomic confusion in many taxa. Therefore, a simple statement about how many percent of all species of deep-sea benthic foraminifera became extinct at a specific time is equivocal: "extinction" rates are rates of local last appearances, not necessarily of extinctions (which are global by definition). In this chapter I disregarded all species that occur in one sample only, and then counted first and last appearances in all samples. All of these first and last appearances (also of rare species) are included in Tables 1 and 2.

DISCUSSION OF RESULTS

The record of late Maastrichtian through Eocene deep-sea benthic faunal events from Site 690 is more complete than that at Site 689, so the record at the former site was used to determine the sequence of faunal events. The fragmented record of Site 689 was later correlated to the more complete Site 690 record. Faunal events (last appearances and first appearances) clearly were not spread out evenly over time, but were concentrated at a few times (Fig. 3). The extinction at the end of the Paleocene is the most significant event for benthic foraminifera in the period from late Maastrichtian through early Eocene, in contrast to planktonic taxa, where the extinction at the end of the Cretaceous is by far the most important (e.g., Smit, 1982; Thierstein, 1982; Keller, 1988a). At Site 690, very few species (8.3 percent) last appear close to the K/T boundary (Table 1), whereas at the shallower Site 689, the percentage of last appearances is higher, but still not indicative of a major catastrophe (12.7 percent; Table 1). Of the seven species with a last appearance near the K/T boundary at Site 690, only three have a coeval last appearance at Site 689: *Coryphostoma incrassata, Praebulimina reussi,* and *Spiroplectammina* aff. *spectabilis. Coryphostoma incrassata* became extinct worldwide at the end of the Cretaceous (Morkhoven and others, 1986); *P. reussi* had its last appearance close to the K/T boundary at lower bathyal Site 516 (Walvis Ridge, South Atlantic; Dailey, 1983) but survived the boundary at the upper bathyal El Kef section (Keller, 1988b). The Upper Cretaceous guide fossil *Bolivinoides draco draco* became extinct at the K/T boundary (Hiltermann and Koch, 1960; Morkhoven and others, 1986), but this is largely a neritic to upper bathyal species. The species occurs in a few samples just below the K/T boundary at Site 689, but there is only one specimen in one sample at Site 690. Only one

TABLE 1. FIRST APPEARANCES (FAs) AND LAST APPEARANCE (LAs) ACROSS THE CRETACEOUS/TERTIARY BOUNDARY AT SITES 689 AND 690*

Interval at 689	FAs	LAs	Interval at 690	FAs	LAs
0.5 m.y. after	2	5	0.5 m.y. after	6	3
Across K/T	2	3	Across K/T	5	0
0.5 m.y. before	6	3	0.5 m.y. before	2	4
Total	10	11		13	7

*Note that there is a short unconformity across the boundary at Site 689.

Total faunal events at Site 689: 22 (27.8 percent).

Total last appearances over 1 m.y. around the K/T boundary: 11 (13.9 percent).

Total faunal events at Site 690: 20 (23.8 percent).

Total last appearances over 1 m.y. around the K/T boundary: 7 (8.3 percent).

TABLE 2. FIRST APPEARANCES (FAs) AND LAST APPEARANCES (LAs) ACROSS THE LATE PALEOCENE EXTINCTION INTERVAL*

Interval at 689	FAs	LAs	Interval at 690	FAs	LAs
After	?	?	0.5 m.y. after	10	6
Across event	0	18	Across event	0	12
Before	?	?	0.5 m.y. before	0	10
Total				10	28

*At Site 689 the length of a 1 m.y. interval across the boundary could not be estimated because of the presence of unconformities.

Total faunal events at Site 689: ?

Total last appearances over 1 m.y. around the event: >18 (35.2 percent).

Total faunal events at Site 690: 38 (50.1 percent).

Total last appearances over 1 m.y. around the event: 28 (37.3 percent).

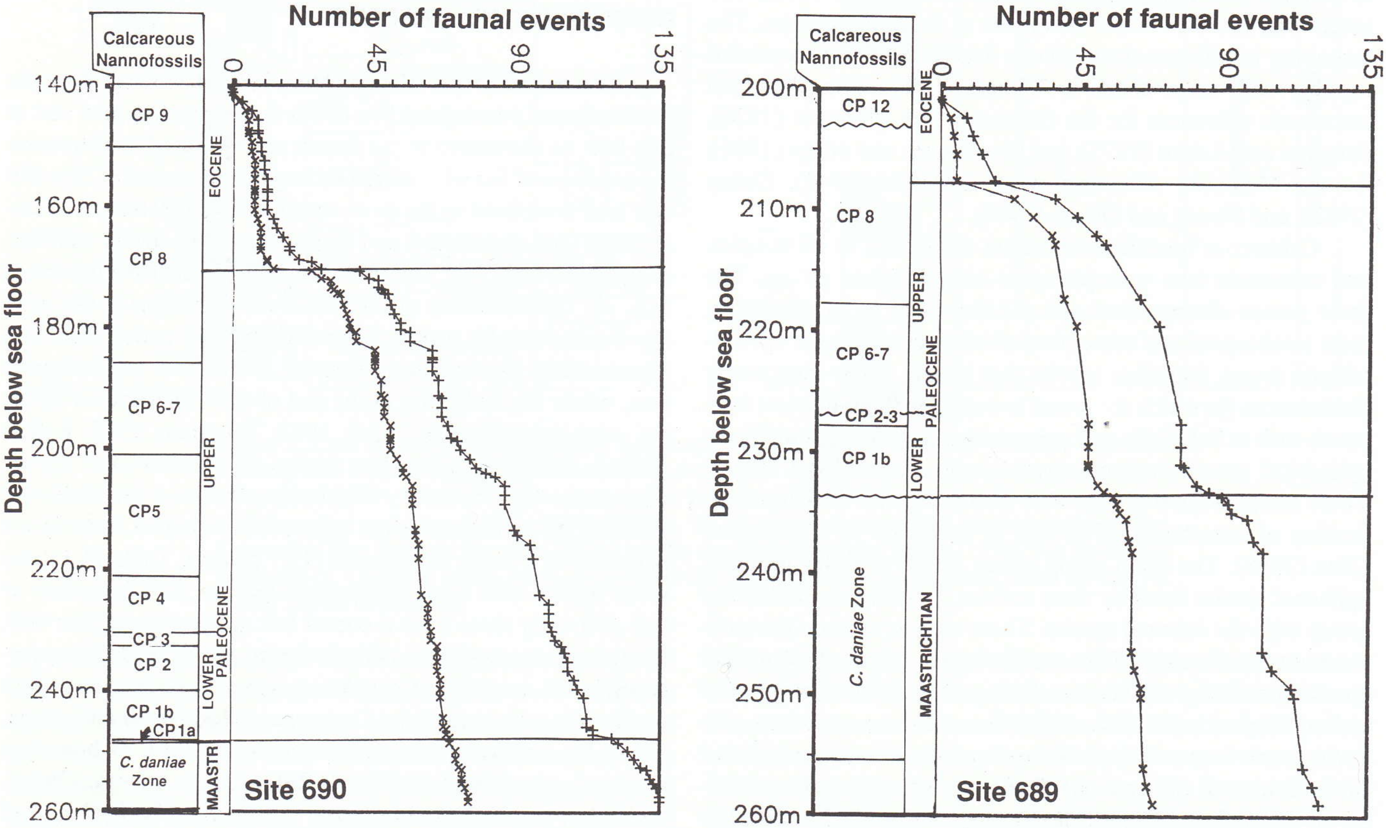

Figure 3. Number of faunal events plotted cumulatively versus sub-bottom depth for Sites 690 (left) and 689 (right). The horizontal lines mark the position of the Cretaceous/Tertiary (K/T) and Paleocene/Eocene (P/E) boundaries as established by calcareous nannofossil biostratigraphy (Pospichal and Wise, 1990a, 1990b, 1990c) and planktonic foraminiferal biostratigraphy (Stott and Kennett, 1990a). Note that the section of Site 689 is plotted at a different depth scale. The left curve (x) gives the number of last events per sample, plotted cumulatively from the first sample studied in this chapter; x marks a sample position. The right curve (+) gives the some of first and last appearances.

species (*Bulimina simplex*) had its first appearance at the K/T boundary at both sites.

This pattern of faunal events at the K/T boundary does not conform to the pattern during a large catastrophe (Table 1, Figs. 3 and 4); one would expect to see a record of a large number of last appearances, followed by a period of low diversity, and clustering of first appearances during a period of recovery. There is a small drop in diversity across the K/T boundary at both sites (Fig. 4), but this drop is not significantly larger than the normal fluctuations in diversity. There is no concentration of last appearances at the boundary, nor of first appearances just above it: rather, a few first and last appearances occur just below, across, and above the boundary (Table 1). Although there is an increase in the sum of first and last appearances in the interval close to the K/T boundary (especially at Site 689; Fig. 3), this period of increased faunal turnover started several hundreds of thousands of years before the boundary, similar to what has been described for planktonic foraminiferal extinctions (Keller, 1989). The lack of an interval with extinctions at the boundary, and of first appearances just above it, might be a result of strong bioturbation across the boundary (Barker and others, 1988). This is improbable, however, because the samples used in this study were selected from the least bioturbated intervals, and were taken several tens of centimeters away from the boundary itself, above and below the samples with high Ir contents (Michel and others, 1990). In addition, there was little or no reworking of planktonic foraminifera (which are much more common than benthics and easy to recognize as either Cretaceous or Tertiary) across the boundary.

In contrast to the events at the K/T boundary, the patterns of faunal events and of diversity of deep-sea benthic foraminifera in the latest Paleocene correspond closely to the pattern expected for a major catastrophe: a precipitous drop in diversity followed by a period of unusually low diversity (Fig. 4); many last appearances at and just below the faunal boundary, followed by a period of many first appearances (Fig. 3, Table 2). Many species (including *Gavelinella beccariiformis, Gavelinella hyphalus, Neoflabellina semireticulata, Neoflabellina jarvisi, Bolivinoides delicatulus, Pyramidina rudita, Pullenia coryelli, Aragonia velascoensis, Tritaxia paleocenica, Tritaxia havanensis, Gyroidinoides quadratus, Dorothia trochoides, Neoeponides hillebrandti,* and *Neoeponides lunata*) have a coeval last appearance at both sites, but also at many other locations over a wide range of paleodepths in the Atlantic Ocean (Tjalsma and Lohmann, 1983; Boersma, 1984), the equatorial Pacific (Miller and others, 1987b), and in the

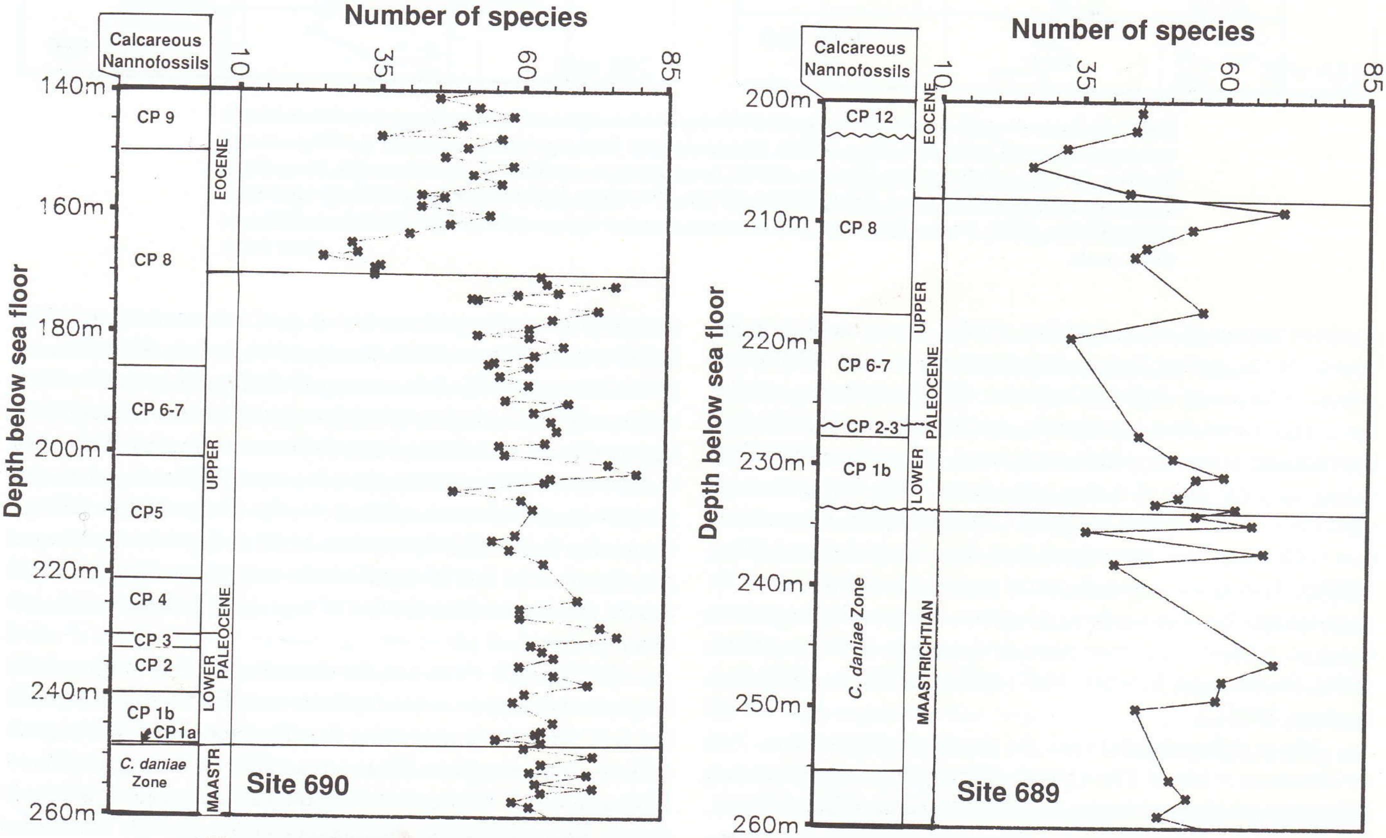

Figure 4. Diversity (expressed as number of species per 300 specimens) plotted versus sub-bottom depth for Sites 689 and 690. The horizontal lines mark the position of the Cretaceous/Tertiary (K/T) and Paleocene/Eocene (P/E) boundaries as established by calcareous nannofossil biostratigraphy (Pospichal and Wise, 1990a, 1990b, 1990c) and planktonic foraminiferal biostratigraphy (Huber, 1990; Stott and Kennett, 1990a); note that the section of Site 689 is plotted at a different depth scale.

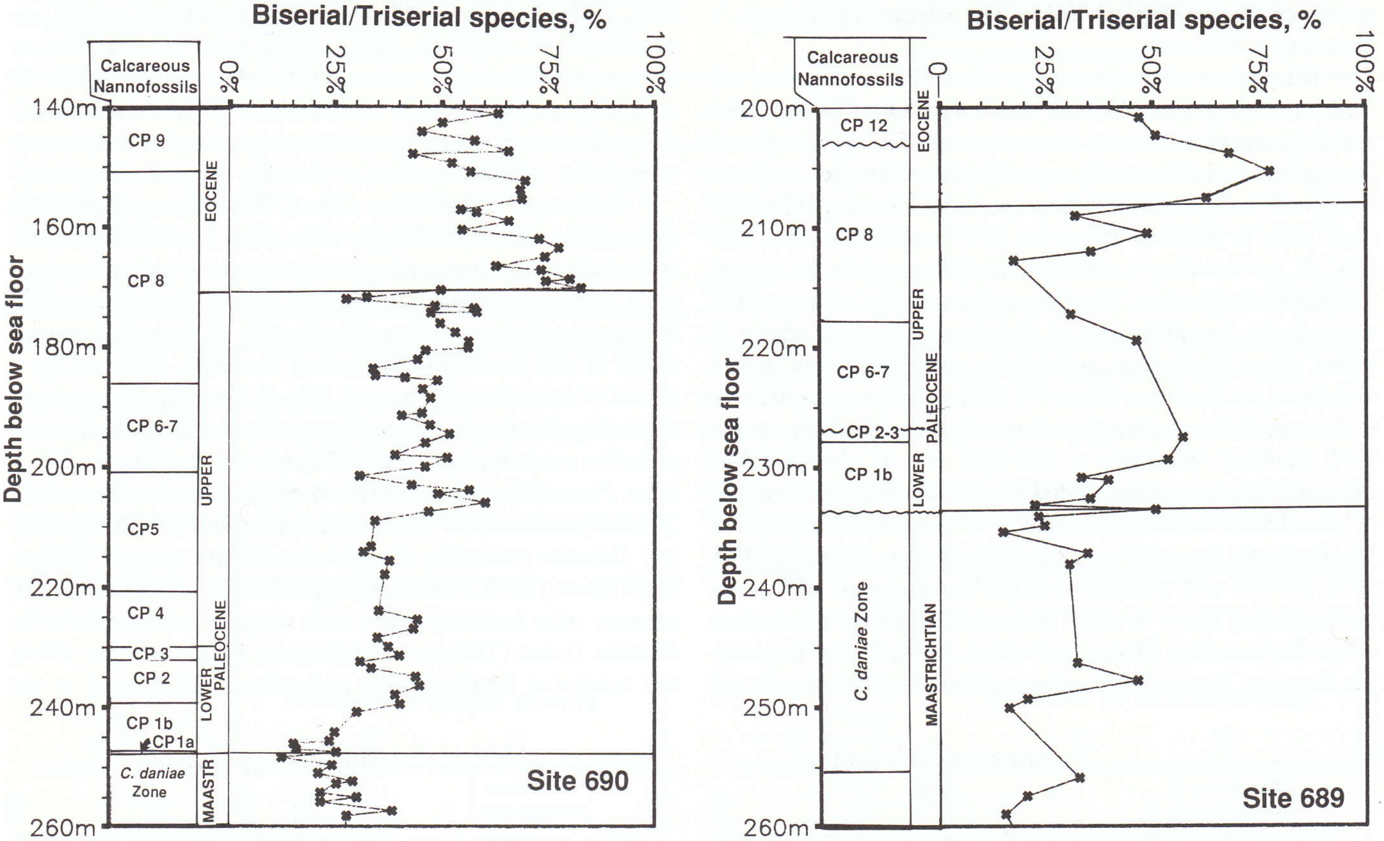

Figure 5. Percentage of specimens in the assemblage that belong to infaunal species, as estimated from test morphology (Corliss and Chen, 1988). The horizontal lines mark the position of the Cretaceous/Tertiary (K/T) and Paleocene/Eocene (P/E) boundaries as established by calcareous nannofossil biostratigraphy (Pospichal and Wise, 1990a, 1990b, 1990c) and planktonic foraminiferal biostratigraphy (Huber, 1990; Stott and Kennett, 1990a); note that the section at Site 689 is plotted at a different depth scale.

southern oceans (Katz and Miller, 1988). The same is true for several of the earliest Eocene first appearances, such as those of *Abyssamina poagi, Pullenia bulloides, Globocassidulina subglobosa,* and *Anomalina spissiformis.* At Site 690, most of the last appearances occurred within an interval of less than 25,000 yr (using the time scale of Aubry and others, 1988, and paleomagnetic data on the location of Chron C24 from Spiess, in combination with calcareous nannofossil data from Pospichal and Wise, 1990c). This is an unusually short period for faunal events in deep-sea benthic foraminifera, which are conservative organisms living in a (usually) conservative environment (Thomas, 1985, 1986; Thomas and Vincent, 1987; Miller and Katz, 1987; Boltovskoy, 1987).

Major differences between the developments in the bathyal environment at Maud Rise at the K/T boundary and in the latest Paleocene are obvious not just in the frequencies of faunal events, but also in the character of the dominant species in the assemblages, especially of infaunal and epifaunal species (Figs. 5, 6, 7). Epifaunal species are dominant at locations where the oxygen content of deep waters is high and/or there is a low concentration of nutrients; infaunal species dominate in the presence of high concentrations of organic carbon (e.g., Corliss and Chen, 1988; Sen Gupta and others, 1981; Caralp, 1984; Lutze and Coulbourn, 1984; Bernard, 1988). It is not easy to distinguish between effects of low oxygen and high nutrients or organic carbon because there commonly is a correlation between these two factors. According to Corliss and Chen (1988), there is a strong correlation between percentage of Holocene infaunal species along a depth transect from a few hundreds of meters to 4,000 m depth in the Norwegian Sea and the flux of organic carbon to the sea floor; infaunal species dominate where the flux of organic carbon is more than 3 to 6 $g \cdot m^{-2} \cdot yr^{-1}$.

At Site 690 there are no changes in preservation of the faunas in the samples across the Paleocene/Eocene boundary and the K/T boundary, suggesting that the faunal changes are not artifacts of preservation. There are no data indicating that Maud Rise underwent strong vertical motions (except gradual subsidence); thus, changes in the epifaunal/infaunal ratio cannot be explained by depth fluctuations of the sites. Epifaunal species dominate in the Cretaceous part of the sections, although fluctuations in relative abundance of infaunal species occur, and are stronger at the shallower Site 689. Just above the K/T boundary

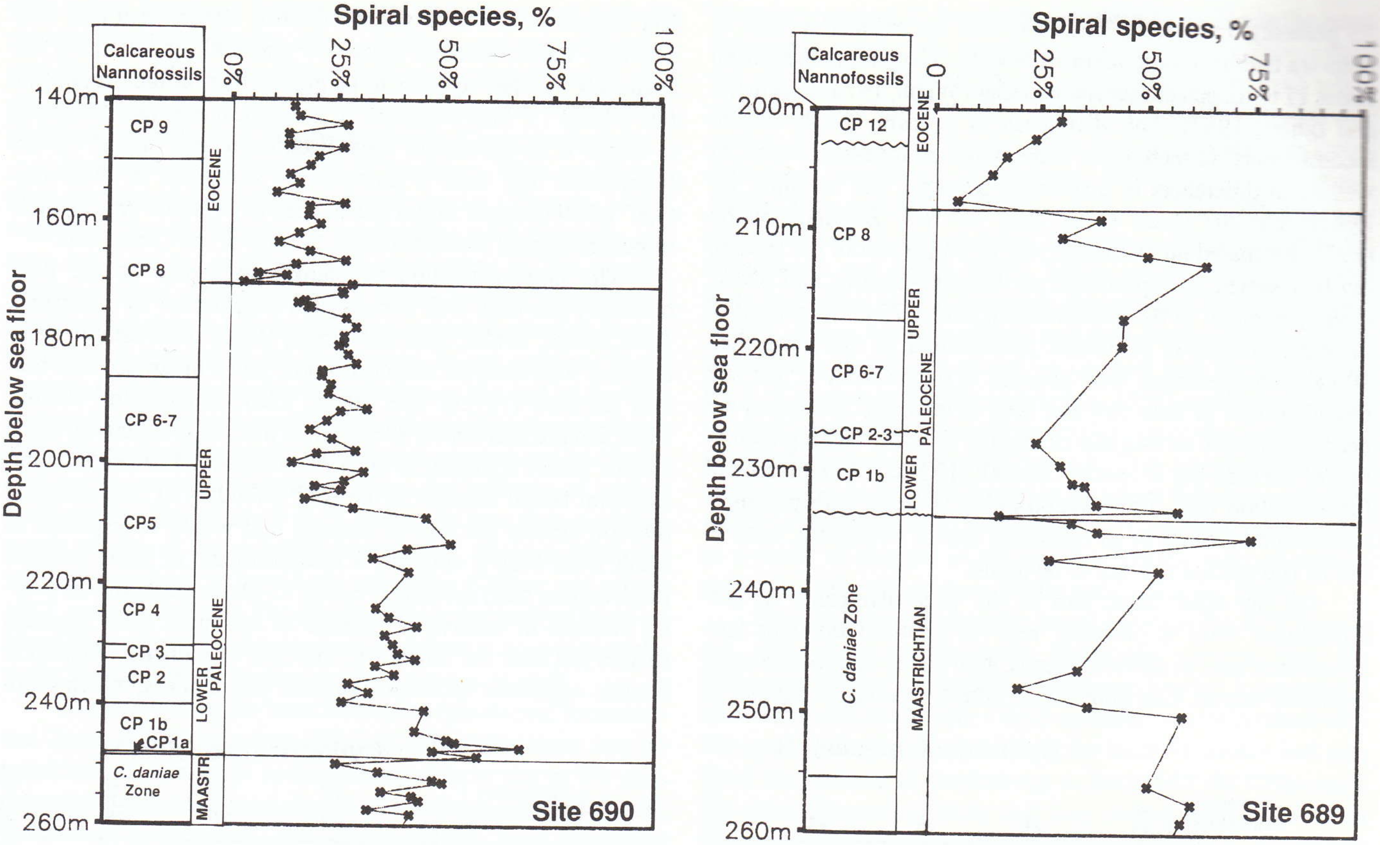

Figure 6. Percentage of specimens in the assemblage that belong to epifaunal species, as estimated from test morphology (Corliss and Chen, 1988). The horizontal lines mark the position of the Cretaceous/Tertiary (K/T) and Paleocene/Eocene (P/E) boundaries as established by calcareous nannofossil biostratigraphy (Pospichal and Wise, 1990a, 1990b, 1990c) and planktonic foraminiferal biostratigraphy (Huber, 1990; Stott and Kennett, 1990a); note that the section at Site 689 is plotted at a different depth scale.

there is a pronounced peak in relative abundance of epifaunal species at both sites and a concomitant decrease in relative abundance of infaunal species. The peak is less obvious at Site 689, possibly as a result of the unconformity across the K/T boundary. The relative abundance of infaunal species then recovers, and increases again slightly above the upper/lower Paleocene boundary (Fig. 4, 215 mbsf at Site 690; Pospichal and Wise, 1990). A large increase in the relative abundance of the infaunal species (to about 85 percent) occurs at the level of the latest Paleocene extinctions: during the period of very low diversity (Fig. 4) the fauna is dominated by infaunal species of the Superfamily Buliminacea (mainly the small species *Tappanina selmensis, Bulimina simplex, Siphogenerinoides brevispinosa,* and in a few samples *Aragonia aragonenis*; Fig. 5).

Such extreme dominance by buliminid species shortly after the benthic foraminiferal extinction has not been described before, but Tjalsma (1976) and Tjalsma and Lohmann (1983, Fig. 46) documented a much less extreme increase in relative abundance of buliminids at that time at Site 329 (paleodepth 1750 m, Falkland Plateau), and Boersma (1984) described a decrease in specimen size just after the extinction. Other authors (Tjalsma and Lohmann, 1983; Miller and others, 1987b; Katz and Miller, 1988) described high relative abundances of the epifaunal species *Nuttallides truempyi* just after the extinctions. At Site 690 the interval of extremely high relative abundances of infaunal species is very short (about 260,000 yr), and thus this interval might not have been sampled in sections with much lower sedimentation rates, or it might not be represented in the sediments in sections with unconformities or low recovery.

The relative abundance of infaunal species decreases higher in the section at the Maud Rise sites, but remains at higher levels than in the lower part of the section throughout the studied interval (uppermost Paleocene–lowermost Eocene). The diversity did not fully regain the high values of the late Maastrichtian and early Paleocene, and reached its peak for the Cenozoic during the early middle Eocene (Thomas, 1990).

The last-appearance rates at the K/T boundary at Sites 689 and 690 (remember that these are rates of local last appearances, and not necessarily extinctions) resemble rates published for Trinidad (18 percent extinction; Beckmann, 1960) and preliminary values for central Pacific Site 465 and Walvis Ridge Sites 525 and 527 (Widmark and Malmgren, 1988; extinction rate of 10 to

25 percent). In general, however, data on extinction rates of deep-sea benthic foraminifera are widely divergent, ranging from about 17 to 82 percent survivor species (Webb, 1973; Beckmann and others, 1982). This divergence is probably partly due to inconsistencies in methods of estimating last-appearance rates, as well as to differences in taxonomic concepts. For example, for DSDP Site 208 (Lord Howe Rise, off New Zealand), Webb (1973) estimated an extinction rate of 54 percent of the species, but he counted 300 specimens per sample—benthic and planktonic specimens. In the Maastrichtian, about 75 to 80 percent of the fauna consists of planktonic foraminifera, so that fewer than 100 benthic specimens were counted. If the diversity at Site 208 resembles that at Sites 689 and 690, at least 270 specimens are needed to obtain an estimate of the true diversity and representation of the majority of species (see METHODS). A reestimate of the extinction rates, using Webb's (1973) tables with presence-absence data, results in an extinction rate of 14 percent, with 40 out of 106 species too rare to be useful.

On the other hand, part of the wide divergence in last-appearance rates is probably real—a result of different last-appearance rates at different depths, with higher rates occurring at shallower depths. Last appearance rates for the upper bathyal El Kef section are about 50 percent (Keller, 1988b), and thus considerably higher than for Sites 689 and 690; extinction at the shallower Site 689 appears to be greater than at the deeper Site 690 (Table 1). This difference in last-appearance rate according to depth is in agreement with Beckmann and others' (1982) observation that there is more severe extinction in "Midway-type" (shelf to upper slope) faunas than in "Velasco-type" (lower slope and abyssal plain) faunas at the end of the Cretaceous.

The large extinction of planktonic species at the K/T boundary has been well documented (e.g, review by Thierstein, 1982; Keller, 1988b; Smit and others, 1988); these data, in combination with data on carbon isotopic ratios in surface and bottom dwellers (Arthur and others, 1987; Zachos and Arthur, 1986; Zachos and others, 1989), show that the productivity in the surface waters collapsed at the K/T boundary. The benthic foraminiferal faunal changes at the K/T boundary at Sites 689 and 690 are exactly the type of changes that would be expected to result from such a collapse: a disappearance of some infaunal (high carbon flux) species (*P. reussi, C. incrassata*), and an overall increase in relative abundance of epifaunal (low nutrient) species just after the boundary. The lack of a mass extinction in benthic organisms such as deep-water foraminifera, which prob-

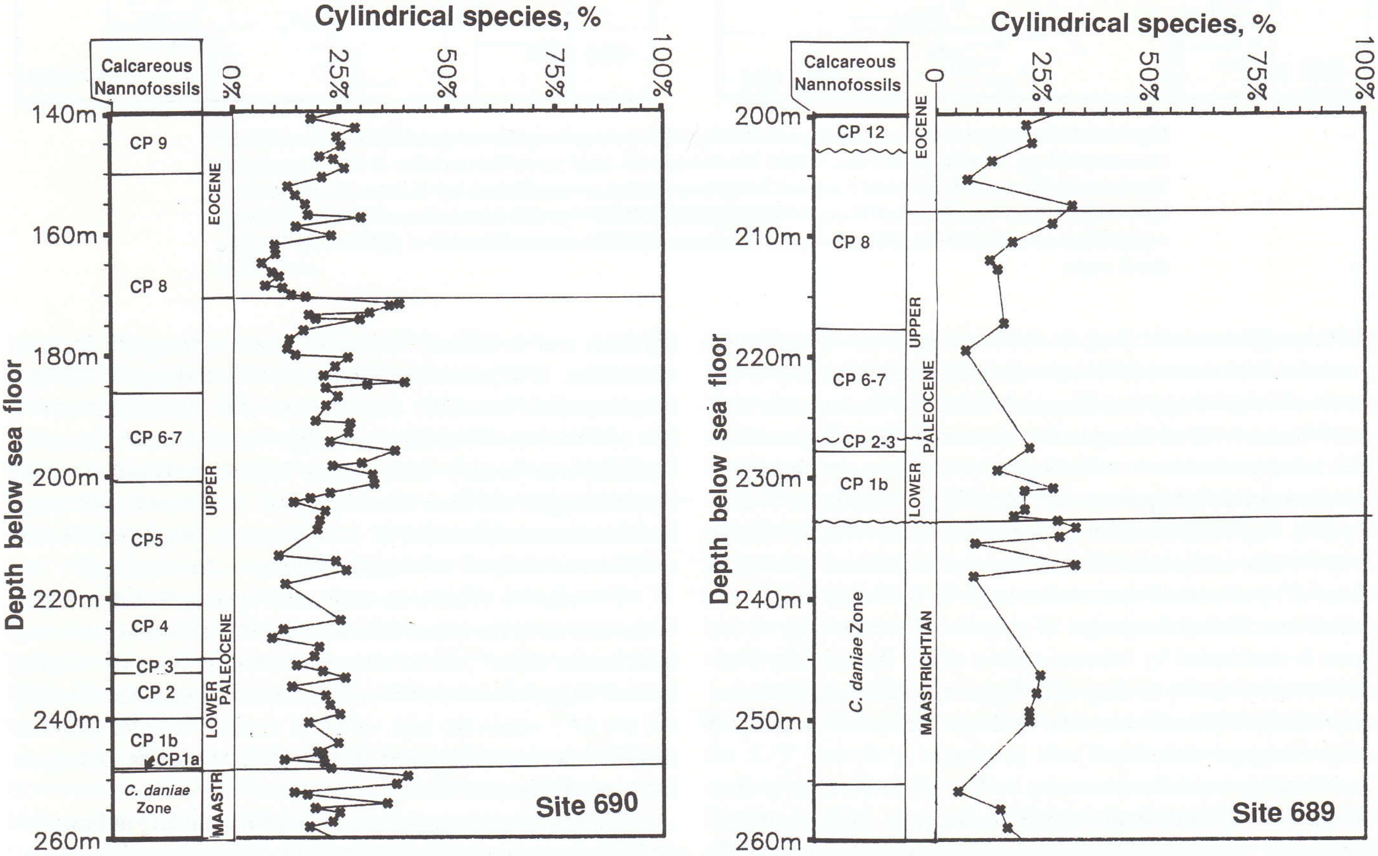

Figure 7. Percentage of specimens in the assemblage that belong to cylindrical species. The horizontal lines mark the position of the Cretaceous/Tertiary (K/T) and Paleocene/Eocene (P/E) boundaries as established by calcareous nannofossil biostratigraphy (Pospichal and Wise, 1989a, b, c) and planktonic foraminiferal biostratigraphy (Huber, 1990; Stott and Kennett, 1990a); note that the section of Site 689 is plotted at a different depth scale.

ably subsist largely as detritus feeders, is in agreement with the theory that detritus feeding offers a buffer to extinction (Sheehan and Hansen, 1986). In addition, bathyal to abyssal benthic species commonly live in an environment of very low food supply, and thus are well suited to survive periods of low productivity.

In the interval below the K/T boundary, there are fluctuations in ratio of infaunal to epifaunal species (Thomas, 1990), suggesting that fluctuations in productivity were common, and may have led to expansion and contraction of the oxygen-minimum zone. Therefore, many of the benthic foraminiferal species were able to survive the even greater fluctuation in productivity at the end of the Cretaceous. In my opinion, faunal changes of deep-sea benthic foraminifera at the end of the Cretaceous (small increase in relative abundance of epifaunal species, and minor extinction, mainly of infaunal species) can be considered to be secondary, resulting from the collapse of surface productivity. The cause of K/T extinction was thus a surface event, whether it was a bolide impact (e.g., Alvarez, 1986; this volume) or related to large-scale volcanism (Officer and others, 1987; and this volume). The effects on the lower bathyal fauna on Maud Rise appear to be secondary, and there is no evidence of a major disturbance of the deep-water environment itself.

The situation in the latest Paleocene (planktonic foraminiferal Zones P6a/b) was very different: at that time there was no extinction of planktonic species comparable in size to the end-Cretaceous extinction, and diversities of calcareous nannofossils, planktonic foraminifera, and dinoflagellates were increasing (Oberhaensli and Hsü, 1986). At Maud Rise, calcareous nannofossils indicated maximum surface-water temperatures at the same level as the benthic foraminiferal extinction (Pospichal, personal communication, 1989). The diversity of planktonic foraminiferal species at Maud Rise increased dramatically during the late Paleocene, and remained high during the early and early middle Eocene (Stott and Kennett, 1990a). Warm-water indicator species penetrated to high latitudes in the southern Atlantic Ocean (Oberhanesli and Hsü, 1986; Boersma and others, 1987), and oxygen isotopic records indicate the strongest increase in temperatures of the Cenozoic for bottom waters and surface water (Shackleton, 1986; Oberhaensli and Toumarkine, 1985; Oberhaensli, 1986; Corliss and Keigwin, 1986; Miller and others, 1987a; Prentice and Matthews, 1988). In addition, it was a period of least temperature difference between surface and bottom waters (Shackleton, 1986). These characteristics of the isotopic records are also present in the isotopic records from Maud Rise sites (Kennett and Stott, 1990; Stott and others, 1990), with the strongest increase in temperatures of deep and surface waters, and the lowest deep-to-surface temperature gradients at the time of the benthic faunal extinction.

The Paleocene/Eocene benthic foraminiferal extinction was global (Beckmann, 1960; Braga and others, 1975; Schnitker, 1979; Tjalsma and Lohmann, 1983; Miller and others, 1987b; Katz and Miller, 1990), and represents the largest Cenozoic faunal turnover in deep-sea benthic foraminifera, larger than the K/T boundary event. Many species that had survived the K/T boundary (such as *G. beccariiformis*) became extinct in the latest Paleocene; many of the species that became extinct were epifaunal species. These extinctions, however, have remained unexplained (e.g., Culver, 1987). There is a major change in the carbon isotope record at the same time as the benthic faunal extinction (worldwide, Shackleton, 1987; Miller and others, 1987a; Katz and Miller, 1990), which had been interpreted as possibly resulting from a global decrease in surface productivity (Shackleton and others, 1985). Miller and others (1987b) and Katz and Miller (1990), however, documented that the gradient in $\delta^{13}C$ values between surface and deep waters did not change significantly during this period (in contrast with the situation at the K/T boundary; Zachos and Arthur, 1986), and thought that a decrease in productivity could not explain more than a part of the observed changes in the $\delta^{13}C$ records. They concluded that the large changes in the $\delta^{13}C$ record in the upper Paleocene probably reflect (at least partially) a change in $\delta^{13}C$ of mean ocean water as a result of changes in the input or output ratio of organic carbon to carbonate carbon (Miller and Fairbanks, 1985).

Comparison of the benthic faunal events at the K/T boundary with those in the latest Paleocene suggests that the Paleocene/Eocene extinction of deep-sea benthic foraminiferal species did not result from a drop in surface-water productivity. The species that became extinct in the latest Paleocene had survived the collapse of productivity at the end of the Cretaceous, and thus it appears unlikely that they would become extinct as the result of a much smaller drop in productivity in the late Paleocene: it has been well established that the extinction of planktonic taxa at the end of the Cretaceous was much more severe than any decrease in diversity during the Cenozoic. In addition, the Maud Rise faunal patterns of benthic foraminifera at the time of Paleocene extinction do not indicate a *decrease* in productivity: there is an *increase* in the relative abundance of infaunal (high organic carbon) species, such as might be expected from an *increase* in productivity, or a decrease in oxygen content of the deep waters, resulting in less oxidation of organic material. Thus it appears that the late Paleocene event was largely a deep-water event (affecting waters at lower bathyal depths or deeper), in contrast with the K/T boundary event, which was largely a surface-water event. This suggests that the cause of the late Paleocene extinction should be sought in changes in the deep oceanic environment, and such changes are most likely circulation changes, which occur in the right time range (less than 25,000 yr) for the late Paleocene extinction.

Many scientists, from Chamberlin (1906) through Hay (1988), have suggested that the deep waters of the oceans may in the past have formed differently from the way in which they form now, i.e., by sinking of dense, cold, well-oxygenated and nutrient-depleted waters at high latitudes in the northern Atlantic (Worthington, 1972) and at high southern latitudes in the Weddell Sea (Foster and Carmack, 1976). In the absence of large polar ice caps, deep waters might have formed by evaporation and formation of dense, warm, salty deep waters (Brass and others, 1982; Barron, 1987; Prentice and Matthews, 1988). Several lines of isotopic evidence, however, suggest that deep to intermediate waters formed at high latitudes during the Late Cretaceous (Barrera and others, 1987; Barrera and Huber, 1990) and the late Paleocene (Miller and others, 1987b), even in the absence of large ice caps. A major problem in evaluating the evidence for the existence of large deep-water masses of salty, warm water is the fact that the intermediate waters (down to depths of several kilometers) may have formed by sinking at high latitudes, while deeper waters formed by evaporation and sinking at low latitudes (e.g., Manabe and Bryan, 1985; Hay, 1988, Fig. 5B). Thus, data from sites at intermediate depths (such as lower bathyal Sites 689 and 690) might indicate formation of deep waters by sinking, while deeper basins were filled with saltier, warmer bottom waters.

Deep-sea benthic faunas at Sites 689 and 690 were dominated by epifaunal species during the late Maastrichtian and early Paleocene, suggesting the existence of well-oxygenated waters at lower bathyal depths in the Maud Rise area; preliminary data on the ostracode faunas from Maud Rise support the hypothesis that the bathyal waters were well oxygenated (P. Steineck, written communication, 1989). During the Paleocene, however, there were several episodes in which the relative abundance of infaunal species increased, especially during the late Paleocene (see e.g., Fig. 5, 210 mbsf at Site 690, corresponding to the middle part of the late Paleocene, about 61 Ma in the time scale of Berggren and others, 1985). These events culminated in the late Paleocene extinction event of deep-sea benthic foraminifera, when many epifaunal species that had survived since the Cretaceous became extinct. These episodes can best be explained by either the beginning of, or the strong increase in, formation of warm saline bottom waters, so that the volume of these warm and saline waters increased until their upper limit reached (at least) the levels of Sites 689 and 690. These waters would have a relatively high temperature at their formation, and thus a low oxygen content. In addition, cold oxygenated waters probably formed somewhere close to the Maud Rise sites, so that they would not have had time to become more depleted in oxygen during their short travel to the sites. Warm waters formed at low latitudes, however, had to travel a long distance before reaching Maud Rise, and thus became even more depleted in oxygen by the time they arrived there. The faunas dominated by the species *Tappanina selmensis* can be seen as the Paleocene/Eocene equivalent of more recent faunas dominated by bolivinids or uvigerinids. Preliminary data on the ostracode faunas from Maud Rise show the presence of non analog ostracode faunas during the short interval of low-diversity benthic foraminiferal faunas; these ostracode faunas resemble (on the generic level) much younger deep-thermospheric faunas from the Mediterranean (P. Steineck, written communication, 1989).

Oxygen and carbon isotope records from Maud Rise and the southern Oceans are in agreement with this interpretation of the benthic foraminiferal data. The benthic foraminiferal oxygen isotope record from the Maud Rise sites suggests that production of warm deep waters increased during the earliest part of the Eocene (Kennett and Stott, 1990). Miller and others (1987b) suggested that deep waters formed at high latitudes during the late Paleocene, and that circulation may have changed in the early Eocene or at the Paleocene/Eocene boundary. More recent data (Katz and Miller, 1990; Miller and Katz, 1988) on material recovered on ODP Leg 114 in the southernmost Atlantic indicate that during the late Paleocene and early Eocene the southern oceans were filled with nutrient-depleted (i.e., young) bottom water, which presumably formed by sinking at high southern latitudes. These authors also concluded, however, that the southern supply of "young" deep water was reduced or even eliminated near the Paleocene/Eocene boundary (58 to 57 Ma), and they agreed that this circulation change could have triggered worldwide benthic foraminiferal extinctions.

Maud Rise, however, is currently not in the path of newly formed Antarctic Bottom Water, because the site is too far toward the east, and is bathed with the relatively Warm Deep Water flowing into the Weddell Sea from the Indian Ocean (Seabrooke and others, 1971; Anderson, 1975; Pudsey and others, 1988). Therefore, data from the Maud Rise sites may not be indicative of conditions at the hypothetical Paleocene-Eocene sites of formation of high-latitude deep waters; recent deep waters rise up around Maud Rise from depths of 1,500 to 2,000 m to the surface, whereas bottom waters are formed in the northwestern end of the Weddell Sea (Comiso and Gordon, 1987). More data and precise stratigraphic correlations are needed before the exact extent of oxygen-poor deep waters can be evaluated. In my opinion, however, the large benthic faunal extinction in the late Paleocene is best explained by a major change in deep-water formational processes. Formation of warm, salty deep water can provide the circulation change necessary to cause the observed faunal changes.

CONCLUSIONS

1. The frequency of last appearances and first appearances of deep-sea benthic foraminifera from Maud Rise (Weddell Sea, Antarctica) and the diversity patterns indicate that there was no mass extinction of these organisms at the Cretaceous/Tertiary boundary. A short increase in relative abundance of epifaunal species just after the boundary can be explained as a secondary effect of the collapse of primary productivity.

2. The frequency of last appearances and first appearances, combined with the patterns of changes in diversity for the latest Paleocene, show that there was a mass extinction of deep-sea benthic foraminifera at that time (57.5 Ma). A large increase in relative abundance of infaunal species just after the extinction suggests that the extinction was caused by a change in deep-water circulation, and that more oxygenated deep waters at lower bathyal depths were replaced with warmer, less oxygenated waters. It is improbable that the extinctions were caused by decreased productivity, because the species that became extinct had survived the almost complete collapse of primary productivity at the end of the Cretaceous.

3. Comparison of the faunal records of deep-sea benthic foraminifera across the Cretaceous/Tertiary boundary (mass extinction at the surface, not in the deep sea) and the uppermost Paleocene (mass extinction in the deep sea, not at the surface) suggests that even the larger mass-extinction periods do not influence all the environments on Earth, from the surface to the deep waters. Mass extinctions, in these different environments are apparently not related.

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