The character of mass extinctions can be assessed by studying extinction patterns of organisms, the "fabric" of the extinction, and assessing the environmental niche and mode of life of survivors. Deep-sea benthic foraminifera have been listed as little affected by the Cretaceous/Tertiary (K/T) mass extinction (1), but very few quantitative data are available. New data on deep-sea Late Maestrichtian-Eocene benthic foraminifera from Maud Rise (Antarctica) indicate that about 10% of the species living at depths of 2000-2500m had last appearances within 1 m.y. of the K/T boundary, versus about 25% of species at 1000-1500m. Many survivors from the Cretaceous became extinct in a period of global deep-sea benthic foraminiferal extinction at the end of the Paleocene (2), a time otherwise marked by very few extinctions (3). On Maud Rise the late Paleocene extinctions occurred over a period of less than 50,000 years, with diversity dropping by 50% and loss of dominant species. Thus mass extinctions in the deep oceans and at the Earth's surface are not necessarily correlated: even the collapse of the planktonic biota at the K/T boundary (1,4) did not strongly disturb the deep ocean biota. The minor changes in the deep-sea benthic foraminiferal faunas at the K/T boundary were probably a result of the collapse of surface water productivity and not of a disturbance of the deep oceans themselves. The extinction of the faunas at the end of the Paleocene might be related to a strong warming of the oceans and a concomitant decrease in dissolved oxygen. This warming of deep waters with a less pronounced effect in surface waters (5,6) might be related to reorganization of deep water circulation as a result of plate tectonic activity (7,8,9).

Reviews of the history of deep sea benthic foraminifera generally state that these organisms do not show a biotic crisis at the K/T boundary (10), as demonstrated by the fact that earlier workers did not recognize Paleocene faunas as Tertiary (11). Until recently there have been few quantitative reports; bathyal-abyssal faunas from the Rio Grande Rise were reported to have a species survival rate of 67% (12), shelf to upper slope faunas from the El Kef section in Tunisia 50% (13). Reports of extinction rates at other sites (12, 13) have ranged from 20 to 80%; these values are maximum estimates of extinction rates, however, because they were obtained by comparison of faunal lists for Cretaceous and Paleocene species and species that had last appearances long before and after the K/T boundary are included.

Extinction rates in deep-sea benthic foraminifera are difficult to establish because faunas are very diverse (60-70 species per sample of 300 specimens) and dominated by few species. Thus many species are rare (<1-2%) and have discontinuous ranges, so that the level of their last appearances cannot be determined precisely. Extinction of one dominant species has much more effect on the fauna than extinction of several rare species. There is no general agreement on taxonomy, especially for morphologically variable groups, and it is commonly impossible to decide from the literature whether a species becomes globally or locally extinct: benthic species can react on environmental disturbance by moving laterally or vertically.

New data on extinction and evolution patterns of deep-sea benthic foraminifera were collected at ODP Sites 689 and 690 on Maud Rise (689: 64°31.01'S, 03°05.99'E, water depth 2084m; 690: 65°09.63'S, 01°12.30'E, water depth 2920 m). These sites are well-suited for study of benthic faunas because of their close proximity and difference in depth. Benthic faunal reaction to the K/T mass extinction could be compared with the extinctions at the end of the Paleocene although the situation is somewhat complicated because of hiatuses at Site 689 (16). Late Maestrichtian faunas show considerable fluctuations in relative abundance of species, with a greater amplitude at the shallower site. In most samples trochospiral and planispiral ("spiral") species are dominant, but in some intervals triserial and biserial ("buliminid") species are abundant. If Cretaceous species are similar in environmental requirements to modern, morphologically similar species, then the samples with high relative abundances of "buliminid" species indicate periods of higher nutrient supply and/or lower dissolved oxygen than the samples with dominantly "spiral" species (17); such environmental
fluctuations are probably caused by changes in primary productivity. Thus benthic faunal patterns suggest that surface productivity at Maud Rise fluctuated strongly during the late Maestrichtian, and that benthic faunas routinely survived such fluctuations, reacting with changes in relative abundance. This tentative conclusion might explain the limited reaction of the deep-sea benthic species to the much stronger disruption of the nutrient supply at the K/T boundary: the species that disappeared are "high-productivity indicators"; the dominant spiral species survived. In the Paleocene fluctuations resumed, but with new genera and species of "high-productivity indicators". At the end of the Paleocene the dominant spiral species, probably indicating the presence of bottom waters that are well-oxygenated and poor in nutrients, became extinct. There was no coeval major disturbance of the planktonic community, thus the cause of this extinction is probably in the deep waters themselves. Oxygen isotope studies indicate a strong warming of bottom waters and a much smaller effect in surface waters at the end of the Paleocene (5,6). This warming might have resulted in availability of less dissolved oxygen to the bottom fauna because of the decreased solubility of oxygen at higher temperatures: this caused fast extinction of exactly those species that survived the collapse in productivity at the K/T boundary. The cause of the warming of the deep waters might be a change in ocean circulation resulting from a change in deep-water sources. In the Paleocene and Eocene there were no large polar ice caps and thus no sources of dense and cold polar deep water. The deep water probably originated in shallow marginal shallow seas at low latitudes, providing salty, dense water (7). Changes in plate tectonic arrangements, possibly resulting from the India-Asia collision (9), might result in changes in deep-water sources.

These conclusions are as yet preliminary, but they suggest that the deep oceanic environment is essentially decoupled from the shallow marine and terrestrial environment, and that even major disturbances of one of these will not greatly affect the other. This gives deep-sea benthic faunas a good opportunity to recolonize shallow environments from greater depths and vice versa after massive extinctions. The decoupling means that data on deep-sea benthic faunas are not of great help in deciding whether the collapse in surface productivity at the K/T boundary was caused by the environmental effects of asteroid impact (19) or excessive volcanism (20). The benthic foraminiferal data strongly suggest, however, that the environmental results were strongest at the Earth's surface, and that there was no major disturbance of the deep ocean; this pattern might result both from excessive volcanism and from an impact on land (20).

References