

Deep-Sea environments across the Cretaceous/Paleogene boundary in the eastern South Atlantic Ocean (ODP Leg 208, Walvis Ridge)

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Abstract

Sediments recovered at ODP Site 1262 on Walvis Ridge (eastern South Atlantic Ocean, paleodepth ~2500–3000 m) offer an opportunity to look into the nature and cause(s) of the benthic foraminiferal turnover across the Cretaceous/Paleogene (K/Pg) boundary at abyssal depths at a location relatively remote from the location of the asteroid impact on the Yucatan peninsula. Late Maastrichtian assemblages were diverse and heterogeneous, reflecting oligo- to mesotrophic conditions at the sea floor. As at other locations, there was no significant extinction of benthic foraminiferal species at the K/Pg boundary, but the diversity and heterogeneity of the assemblages decreased precipitously. The percentage of infaunal buliminid taxa decreased rapidly, but the total percentage of infaunal taxa remained essentially unchanged. Benthic foraminiferal accumulation rates (BFAR) dropped at the boundary itself, and fluctuated strongly later in the Danian. After the K/Pg boundary, opportunistic taxa increased in relative abundance, and diversity and heterogeneity strongly fluctuated. There thus is no clear agreement between three proxies which have been used to indicate a high food supply to the sea floor: percentage buliminids, percentage infaunal taxa, and BFAR. This discrepancy might indicate that the food supply changed in character (e.g., type of food, temporal variability in flux), but did not show a long-term, large net change in total amount. The strong fluctuations in BFAR, heterogeneity and diversity indicate that environmental instability started at the K/Pg boundary, and persisted through planktic foraminiferal zones P α and P1a. In lower planktic foraminiferal zone P1b, agglutinated species of the genera *Spiroplectammina* and *Clavulinoides*, thought to be infaunal and indicative of increasing levels of food supply, increased in relative abundance while the relative abundance of buliminids remained low. Possibly, agglutinated taxa took over at least part of the infaunal niche in the Paleocene, as a result of the rise in the calcium carbonate compensation depth. Towards the upper part of the studied interval (lower planktic foraminiferal Subzone 1c), benthic foraminiferal assemblages stabilized, with heterogeneity almost back to Maastrichtian values, although diversity and BFAR did not fully recover.

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1. Introduction

Benthic foraminifera did not suffer significant extinction across the Cretaceous/Paleogene (K/Pg) boundary (e.g., Thomas, 1990a,b; Alegret et al., 2001, 2003; Culver, 2003), one of the largest mass extinctions in the

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Phanerozoic. At this time planktic foraminifera and calcareous nannoplankton underwent severe extinction (e.g., Luterbacher and Premoli Silva, 1964; Smit, 1990; Gardin and Monechi, 1998; Molina et al., 1998). Whereas calcareous planktic microfossil groups were strongly affected by the extinction and show low diversity and abundance during the earliest Paleocene, benthic foraminifera show temporary changes in assemblage composition, true extinction of only very few species, and remained common after the K/Pg boundary. The temporary changes in the community structure of deep-sea benthic foraminiferal faunas as observed at many locations have been interpreted as resulting from the collapse of the pelagic food web and a subsequent drop in food supply to the benthos (e.g., Kuhnt and Kaminski, 1993; Thomas, 1990a,b; Alegret et al., 2001, 2002, 2003; Culver, 2003). At some locations, in contrast, the food supply apparently increased just after the K/Pg boundary (e.g., section Caravaca, Spain, Coccioni and Galeotti, 1994; section Agost, Spain, Alegret et al., 2003; Pacific DSDP Site 465, Alegret and Thomas, 2005). At some of these locations (Caravaca, Agost) sediments deposited just after the K/Pg boundary reflect anoxic conditions (laminated sediments) such as found under high-productivity zones in the present oceans. There thus are considerable regional differences in the effect of the K/Pg event on the flux of food to the sea floor (Culver, 2003; Alegret and Thomas, 2005).

The fact that only minor, largely reversible changes in benthic foraminiferal assemblages occurred at a time when oceanic primary productivity supposedly collapsed for hundreds of thousands of years (“Strangelove Ocean”; Hsü et al., 1982; Perch-Nielsen et al., 1982; Hsü and McKenzie, 1985), as evidenced by the collapse of the gradient between benthic and planktic (foraminiferal and/or bulk carbonate) carbon isotope values (e.g., Zachos and Arthur, 1986; Zachos et al., 1989; Kump, 1991), poses a major challenge (e.g., Thomas, in press; Thomas et al., 2006). Benthic foraminiferal assemblages in the present oceans show a correlation with events in the plankton, which serves as their food supply (benthopelagic coupling; e.g., Gooday, 2003). Even if Cretaceous–Paleogene benthic foraminiferal assemblages were characterized by less intense benthopelagic coupling (e.g., Thomas et al., 2000; Thomas, in press), they would be expected to suffer more severely than observed if their food supplies had remained extremely low for several hundred thousands of years. A deposit-feeding life style has been described as a possible exaptation to survive a productivity crash, but this hypothesis has been questioned because of the linkage

between surface ocean productivity and the organic carbon reservoir in the sediments (Levinton, 1996).

The hypothesis that oceanic productivity was severely reduced for several hundred thousand years has been questioned, and it has been argued that productivity of plankton in terms of biomass may have recovered as soon as light returned, although plankton diversity remained low (“Living Ocean Model” of d’Hondt et al., 1998; d’Hondt, 2005; Coxall et al., 2006). According to this model, gradients of benthic–planktic carbon isotope values remained low for several hundred thousands of years not because of a collapse of productivity, but because of a lack of transfer of organic matter from surface water to the sea floor as the result of ecosystem reorganization after the mass extinction, including loss of fecal pellet producers and a shift to smaller-celled, prokaryote primary producers (e.g., cyanobacteria). The carbon isotope gradients then recovered gradually over several more millions of years, while the diversity of calcareous species recovered (d’Hondt et al., 1998; Coxall et al., 2006).

There is considerable evidence that oceanic primary productivity did not collapse for several hundred thousands or millions of years. Calcareous nannoplankton suffered high rates of extinction, but after the extinction there were blooms of opportunistic survivor groups such as *Braarudosphaera* and *Biscutum* species (e.g., Perch-Nielsen et al., 1982; Gardin and Monechi, 1998; Bown, 2005). The magnitude of such blooms may have been underestimated from data on the percentage of CaCO₃ in the sediments, because the survivors may have been only weakly calcified (Gardin and Monechi, 1998). In addition, other primary producers such as diatoms did not suffer massive extinction (Kitchell et al., 1986; Hollis, 2003), cyanobacteria may not have been affected (d’Hondt et al., 1998), and the dinoflagellate producing the calcareous cyst *Thoracosphaera* bloomed opportunistically worldwide (e.g., Gardin and Monechi, 1998). Dinoflagellates with organic-walled cysts bloomed along the southern Tethys margin (El Kef section; Brinkhuis and Zachariasse, 1988; Brinkhuis et al., 1998). Surviving phytoplankton would be expected to bloom as soon as light conditions allowed, because the extinction of many calcareous nannoplankton taxa lessened competition for nutrients, and in addition nutrients may have been supplied from land after destruction of land biota (e.g., Brinkhuis and Zachariasse, 1988). Blooms of opportunistic phytoplankton may have occurred locally or regionally, leading to bottom-water anoxia, as observed, for instance, in sections at Caravaca and Agost (Southern Spain, Coccioni and Galeotti, 1994; Alegret et al.,

2003), as well as in Japan and New Zealand (Kaiho et al., 1999). The ‘Living Ocean Model’, however, does not solve the problem of the lack of extinction of benthic foraminifera nor that of the occurrence of anoxic conditions, since this model includes a lack of food transfer to the sea floor where the benthic foraminifera live and where the oxidized organic matter have caused anoxia.

Recovery of the biotic pump as well as productivity might well have been faster than envisaged by d’Hondt et al. (1998), because fecal pellets are not the only method of fast transport of organic matter to the sea floor. Coagulation of organic particles by sticky diatoms and cyanobacteria may have assisted in forming large particles for rapid deposition (Armstrong et al., 2002), and various methods of ballasting particles with biogenic silica or terrigenous dust may have remained effective, even with less biogenic carbonate available. If atmospheric pCO₂ levels were very high after the impact (Beerling et al., 2002), calcification of the few surviving calcareous nannofossils may have decreased (e.g., Gardin and Monechi, 1998), but decreased calcification may have led to increased delivery of organic matter to the sea floor (Delille et al., 2005) because of increased formation of sticky polysaccharides (Engel et al., 2004).

If both productivity and food transfer to the deep sea floor recovered fast at least at some locations, the lack of extinction of benthic foraminifera would be explained and the recovery of marine ecosystems in terms of biomass would be similar to the rapid recovery postulated for terrestrial ecosystems (e.g., Beerling et al., 2001), but the persistent collapse of benthic–planktic carbon isotope gradients must be explained. More detailed stable isotope records are needed in order to understand the patterns of change in $\delta^{13}\text{C}$ values in benthos and plankton: a simple collapse of the food chain (as modelled by Kump, 1991 using data in Zachos et al., 1989) cannot explain the observations that surface-water values become not just equal to, but lighter than benthic values at many locations (e.g., Ivany and Salawitch, 1993). These authors argued for an influx of isotopically light carbon from biomass burning (Ivany and Salawitch, 1993), others argued for clathrate dissociation (Day and Maslin, 2005). A problem with any explanation involving addition of light carbon to the ocean-atmosphere system is the persistence of the reversed gradient for long periods of time (10^5 years), which would not occur unless stratification of the oceans was severe. Such severe stratification almost certainly did not occur, because it would have led to the development of global anoxic conditions and thus severe extinction of benthic foraminifera.

The carbon isotope record thus might be complex, and reflect a multitude of factors including diagenetic effects in low-carbonate sediment, as well as regionally variable effects such as post-extinction decrease or increase in productivity, changes in the biological pump and/or in the nature of the food supply to the deep sea, and circulation changes. In addition, at least part of the surface isotope signal may reflect ‘vital effects’. Surface water carbon isotope values must by necessity be measured on calcareous nannofossils (bulk records) and/or planktic foraminifera, both of which underwent severe extinction, so that post-extinction records are derived from different species than pre-extinction records. Post-extinction calcareous nannoplankton is dominated by bloom species including the calcareous dinocyst *Thoracosphaera*, and Recent (Zonneveld, 2004) as well as Cretaceous species (Friedrich and Meijer, 2003) of this genus have light carbon isotope signatures.

To conclude, there is at present no solid explanation of the observed carbon isotopic records across the K/Pg boundary. More high resolution records are needed in order to document reliably whether the negative gradient occurred globally (reflecting the global carbon cycle) or was more local or regional, reflecting productivity and/or transport of organic matter, or was more random, reflecting diagenesis.

Detailed study of benthic foraminiferal assemblages may provide information to elucidate changes in oceanic environments and the oceanic carbon cycle across the K/Pg boundary. We analysed benthic foraminifera from a continuous K–Pg transition recovered on ODP Leg 208 (Site 1262; Fig. 1), SE Atlantic Ocean (paleodepth ~ 2500–3000 m; Zachos et al., 2004). Previous low-resolution studies of the benthic foraminiferal turnover across the K/Pg boundary in this area were carried out at nearby Sites 525 (Walvis Ridge; paleodepth 1100 m; present depth 2467 m) and 527 in the Angola Basin, paleodepth 2700 m, present depth 4428 m (Widmark and Malmgren, 1992; Widmark, 1997).

2. Material and methods

A continuous, well-preserved K/Pg transition was recovered during Ocean Drilling Program Leg 208 in two holes at Site 1262 (27°11.15' S; 1°34.62' E; eastern South Atlantic Ocean; Fig. 1), on the northwestern end of Walvis Ridge in the Angola Basin, at a present water depth of 4755 m (paleodepth ~ 2500–3000 m, Zachos et al., 2004). At Site 1262, the boundary is at 216.72 mcd (meter composite depth; Bernaola and Monechi, in press), and marked by a sharp transition

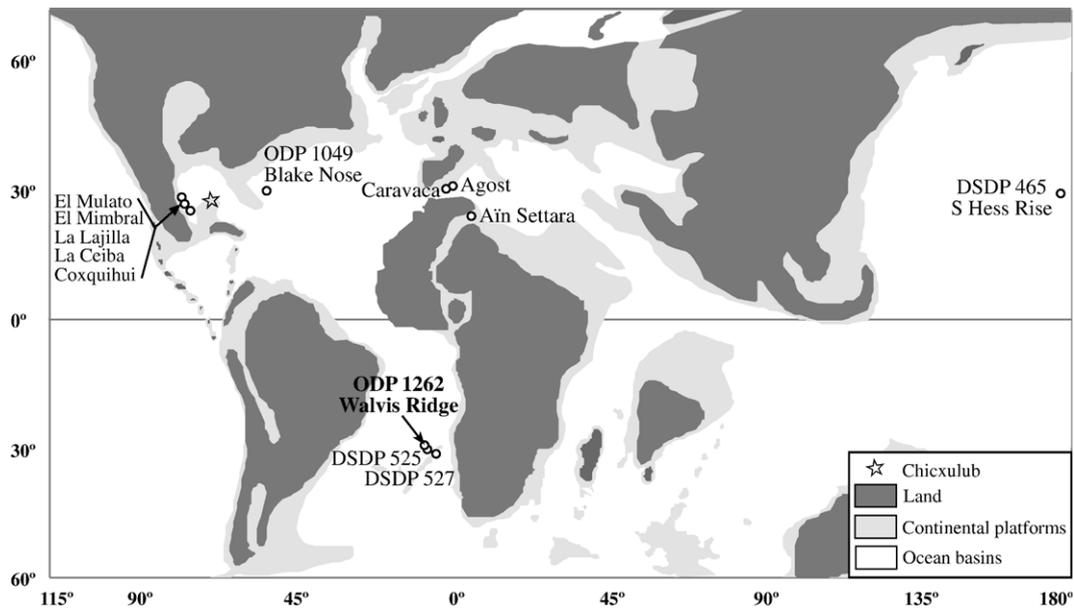


Fig. 1. Paleogeographical distribution of land masses, shallow seas and deep ocean basins at the end of the Cretaceous, showing the location of ODP Site 1262, the K/Pg Chicxulub structure (Yucatan peninsula, Mexico) and other K/Pg boundary sections and sites referred to in the text. Modified from Denham and Scotese (1987).

from yellowish Maastrichtian clay-bearing nannofossil ooze with abundant planktic foraminifera to Danian dark reddish to brown, clay-rich nannofossil–ooze and clay. The boundary coincides with a distinctive increase in magnetic susceptibility and a decrease in carbonate content (going up-section); microspherules occur in the lowermost cm of the Danian, where clays and mineral oxides are abundant (Zachos et al., 2004). Further up-section, sediments grade into brown clays with abundant nannofossils and planktic foraminifera, but the carbonate content of sediments did not return to Maastrichtian values for several million years. Foraminiferal preservation in the low-carbonate interval, however, is excellent, as is that of calcareous nannofossils (Bernaola and Monechi, in press).

We analyzed 33 samples from the ‘splice’, i.e., the complete stratigraphic record from the combined two holes (Zachos et al., 2004; Thomas et al., 2006), composed of material from sections 1262C-12H-6, 1262B-22H-1, 1262B-22H-3, and 1262C-13H-1 to 13H-5 (210.30–221.46 mcd), and comprising the upper 4.3 m of the Maastrichtian and the lower 6.4 m of the Danian (Fig. 2). This section encompasses the top of the Maastrichtian planktic foraminiferal *Abathomphalus mayaroensis* Zone through the lower part of Danian zone P1c (Zachos et al., 2004). Samples were spaced at 1 to a few cm directly after the K/Pg boundary, with decreasing resolution (to ~1 m) further away from

the boundary (electronic supplement Table A1). We used the planktic foraminiferal zonation in Zachos et al. (2004) and the calcareous nannofossil zonation in Bernaola and Monechi (in press).

Quantitative studies and species richness calculations were based on representative splits of approximately 300 specimens of benthic foraminifera larger than 63 μm , mounted on microslides for a permanent record and identification. The classification at the generic level follows Loeblich and Tappan (1987). When possible, benthic foraminifers were identified at the specific level (electronic supplement Table A2) largely following the taxonomy of Tjalsma and Lohmann (1983), Boltovskoy and Boltovskoy (1989), Widmark and Malmgren (1992), Widmark (1997), and Alegret and Thomas (2001). We calculated the relative abundances of foraminiferal species (electronic supplement Table A1), as well as the Fisher- α diversity index, and the H(S) Shannon-Weaver heterogeneity index (Murray, 1991) (Fig. 3). For an estimate of benthic foraminiferal accumulation rates (BFAR), a commonly used proxy for delivery of organic matter to the sea floor (Jorissen et al., in press) we used the published density values (Zachos et al., 2004), the weight percentage of material in the size fraction larger than 63 μm as recorded during sample processing, and preliminary estimates of sedimentation rates using orbital tuning of the magnetic susceptibility record (Roehl, U., 2006, personal communication).

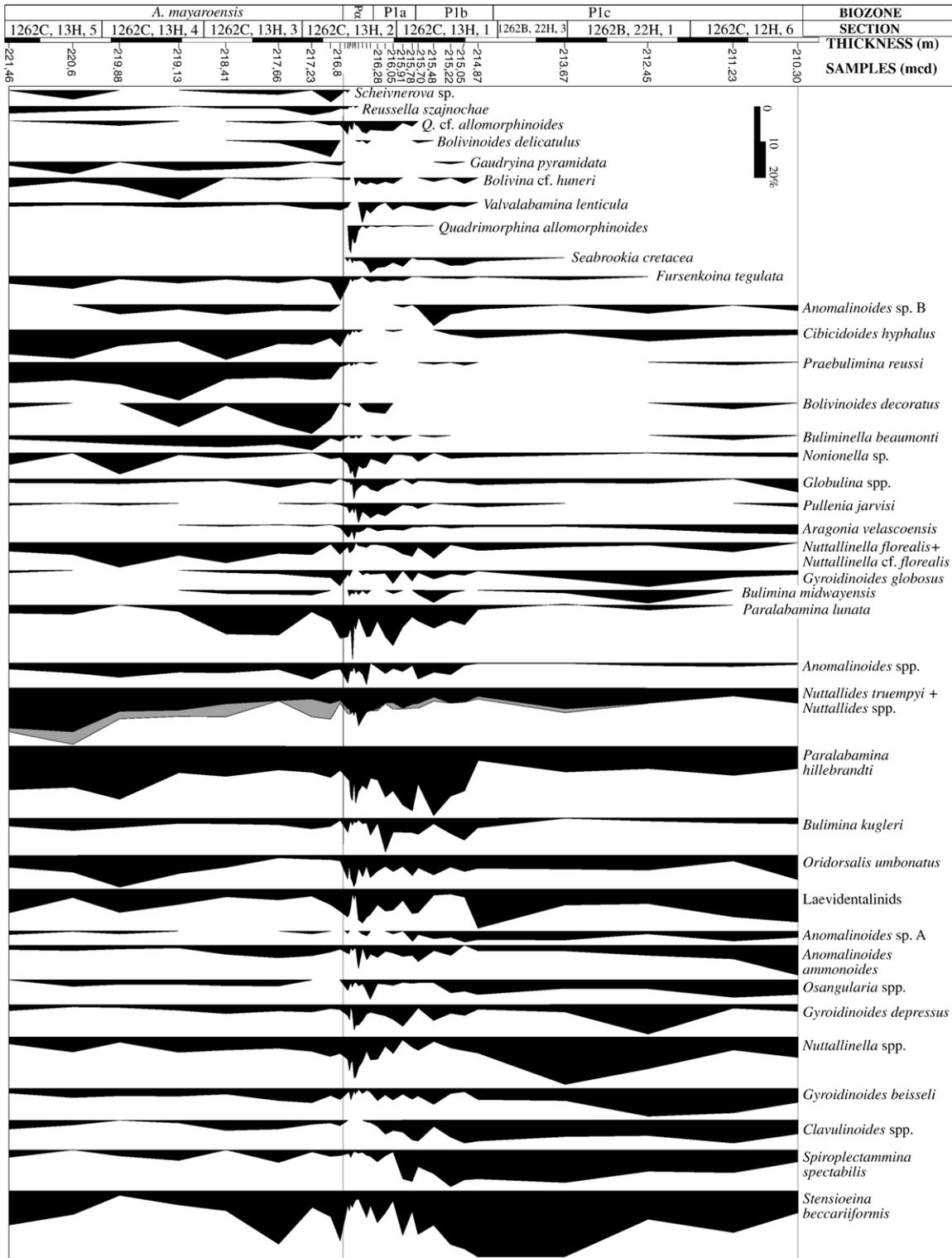
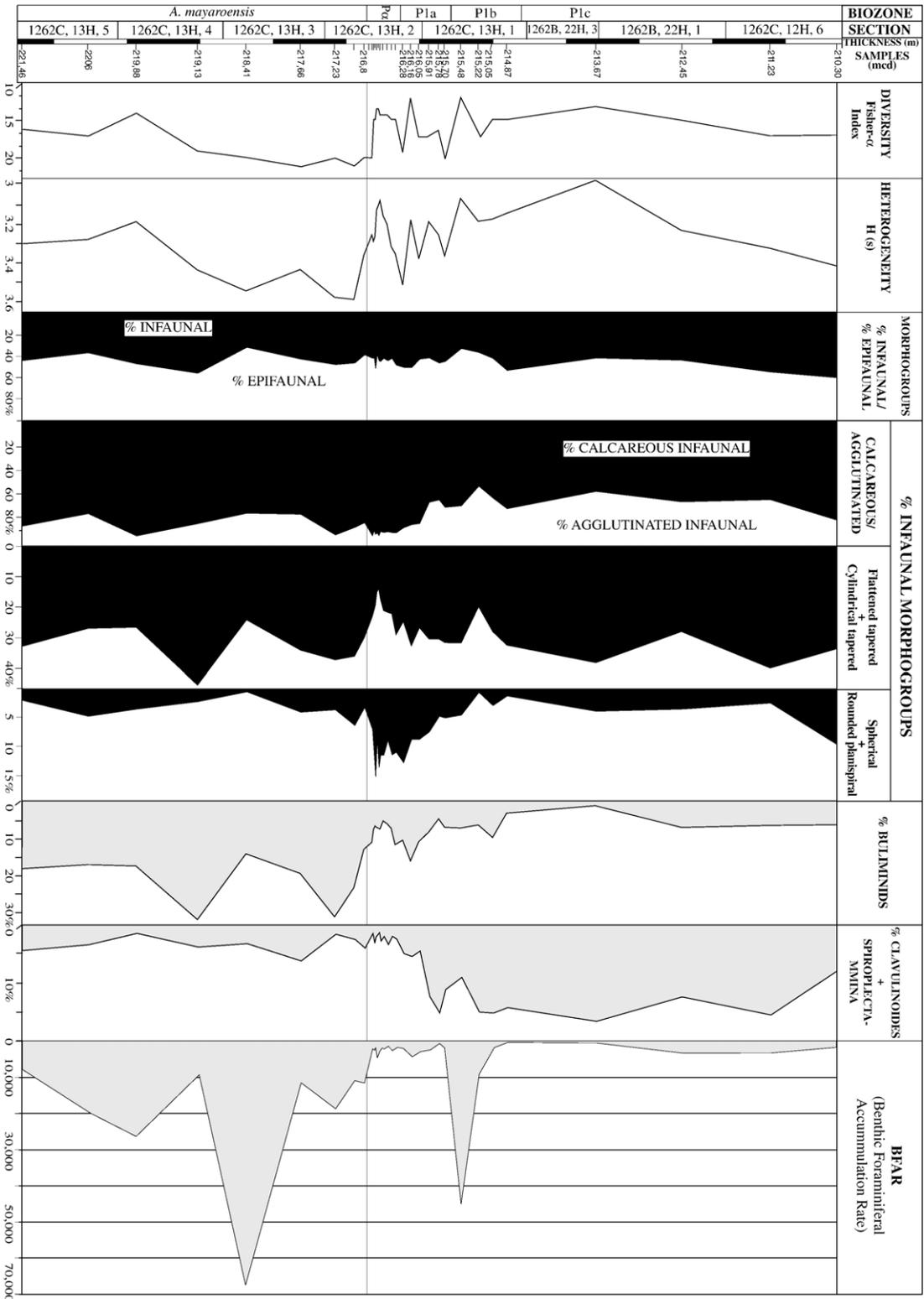


Fig. 2. Occurrence and relative abundance of the most characteristic benthic foraminiferal species across the K/Pg transition at Site 1262, Walvis Ridge. Biostratigraphy according to Zachos et al. (2004).



Benthic foraminifera are useful indicators in paleobathymetrical reconstructions. The comparison between fossil and recent assemblages, the occurrence and abundance of depth-related species, and their upper-depth limits (e.g., Van Morkhoven et al., 1986; Alegret and Thomas, 2001; Alegret et al., 2003) allowed us to infer the paleobathymetry.

We allocated all specimens to morphogroups (Fig. 3) following Corliss (1985), Jones and Charnock (1985) and Corliss and Chen (1988). The comparison of fossil and recent communities of benthic foraminifera, in addition to morphotype analysis, allows us to infer probable microhabitat preferences and environmental parameters such as the nutrient supply to the sea floor or sea water oxygenation (e.g., Bernhard, 1986; Jorissen et al., 1995; Fontanier et al., 2002; Jorissen et al., in press). However, caution must be taken with the interpretation of these comparisons, since we do not know to what extent the Cretaceous–early Paleogene faunas were analogous to Recent faunas (e.g., Thomas et al., 2000; Alegret et al., 2003), and even for present faunas we do not know the microhabitat for many deep-sea species with confidence (e.g., Buzas et al., 1993; Jorissen et al., in press).

3. Results

3.1. Benthic foraminiferal turnover

Benthic foraminiferal assemblages from the uppermost 4.3 m of the Maastrichtian and the lowermost 6.4 m of the Paleogene at Site 1262 contain abundant representatives of the cosmopolitan deep-water Velasco-type fauna such as *Cibicidoides hyphalus*, *Nuttallides truempyi*, *Nuttallinella florealis*, *Osangularia cordieriana*, *Osangularia velascoensis* and *Stensioeina beccariiiformis*, as well as other species that are common at deep bathyal to abyssal settings, such as *Aragonia velascoensis*, *Gyroidinoides globosus*, *Praebulimina reussi*, *Paralabamina hillebrandti*, *Paralabamina lunata*, *Oridorsalis umbonatus* and *Reussella szajnochae* (e.g., Berggren and Aubert, 1975; Tjalsma and Lohmann, 1983; Widmark and Malmgren, 1992; Widmark, 1997; Alegret and Thomas, 2001, 2004). They also contain relatively abundant (~25%) buliminid species such as *Bulimina kugleri*, *Bulimina velascoensis* and *Buliminella beaumonti*, which proliferate at deep

bathyal and abyssal depths (e.g., Tjalsma and Lohmann, 1983). These data suggest that Upper Cretaceous and lower Paleogene sediments at Site 1262 were deposited at upper abyssal paleodepths (2000–3000 m, Van Morkhoven et al., 1986), in agreement with paleodepths derived from backtracking of the site (Zachos et al., 2004).

Benthic foraminiferal assemblages are dominated by calcareous foraminifera (80–97% of the assemblages) throughout the studied interval, but agglutinated species were somewhat more abundant in the Danian. Both Maastrichtian and Danian assemblages consist of mixed infaunal and epifaunal morphogroups with about equal abundance (Fig. 3). There is no change in the percentage of infaunal taxa over the studied interval, including the K/Pg boundary. Directly above the K/Pg boundary, however, the abundance of spherical and rounded infaunal taxa increased, while that of flattened and cylindrical tapered taxa decreased. Below the K/Pg boundary infaunal morphotypes are strongly dominated by calcareous forms, but from upper Zone P1a upwards agglutinated morphotypes are more common (Fig. 3).

Diversity and heterogeneity indices overall increased during the latest Maastrichtian (*A. mayaroensis* Biozone), reaching maximum values just before the K/Pg boundary. Trochospiral taxa such as *P. hillebrandti*, *P. lunata*, *C. hyphalus*, *N. truempyi*, *O. umbonatus* and *S. beccariiiformis* dominated the epifaunal morphogroups during the latest Cretaceous (Fig. 2). Among infaunal taxa, buliminids such as *Bolivina* cf. *hunei*, *Bolivinoidea decoratus*, *B. delicatulus*, *B. kugleri*, *B. beaumonti* or *P. reussi* dominated, making up to 30% of the assemblages (Fig. 3); their abundance as well as the heterogeneity of the assemblages start to decrease a few cm below the K/Pg boundary.

Only two species of benthic foraminifera, *Scheibnerova* sp. and *R. szajnochae* last appear at the K/Pg boundary at Site 1262 (Fig. 2); these species have been documented to have their last appearance at the boundary at many locations (e.g., Thomas, 1990a,b; Culver, 2003). A total of four specimens of these species occur a few cm above the boundary, and we consider these to be reworked. At Site 1262 there is a 5 cm-thick mixing zone just at the K/Pg interval (Bernaola and Monechi, in press), which accounts for the presence of some reworked specimens above the boundary, increasing the apparent diversity and heterogeneity of the

Fig. 3. Fisher- α diversity index of benthic foraminiferal species; H(S) Shannon–Weaver heterogeneity index; relative abundance of infaunal and epifaunal morphogroups, and of infaunal calcareous and infaunal agglutinated taxa; percentages of infaunal elongated taxa and of rounded planispiral and spherical infaunal taxa; percentages of buliminids and of *Clavulinoides* and *Spiroplectammina*; and Benthic Foraminiferal Accumulation Rates (BFAR) across the K/Pg transition at Site 1262, Walvis Ridge. Biostratigraphy according to Zachos et al. (2004).

lowermost Danian assemblages. If we do not take into account this short interval, a dramatic decrease in diversity and heterogeneity of the assemblages occurred just above the K/Pg boundary, although there are no major changes in general morphogroup composition. The percentage of buliminid taxa, however, decreases across the boundary, and does not recover in the studied interval; infaunal morphotypes in the Danian consist of dominantly non-buliminid groups.

Assemblages from the lowermost Danian (2–3 cm above the K/Pg boundary) contain peaks in the relative abundance of *P. hillebrandti*, *P. lunata*, *Quadrimorphina allomorphinoides*, *Nonionella* sp. and *Nuttallinella* spp., among other species, and are marked by low abundances of laevidentaliniids (Fig. 2). This post-K/Pg assemblage is overlain by a 1.5-m-thick interval in which assemblages are dominated by the epifaunal paralabaminids (*P. hillebrandti*, *P. lunata*) and *S. beccariiiformis*. The agglutinated taxa *Clavulinoides* spp. and *Spiroplectammina spectabilis* increase in abundance, and diversity and heterogeneity of the assemblages strongly fluctuate in this interval. In addition to these changes in faunal composition, several species have a local last appearance, but did not become extinct (e.g., *Q. allomorphinoides*, *Q. cf. allomorphinoides* flat, *Bolivina cf. huneri*, *Bolivinoidea delicatulus*, *Gaudryina pyramidata*, *Valvalabamina lenticula*; Fig. 2).

Agglutinated taxa in the upper part of the studied section are dominated by *Clavulinoides* spp. and *S. spectabilis*, whereas calcareous groups are diverse and heterogeneous, with high percentages of *S. beccariiiformis*, *Nuttallinella* spp., *N. truempyi* and laevidentaliniids, among others (Fig. 2). The percentage of paralabaminids significantly decreases in this interval. Diversity and heterogeneity of the assemblages reach minimum values 3 m above the K/Pg boundary, and progressively increase towards the top of the section. The percentage of buliminids stays very low (Fig. 3).

BFAR values (Fig. 3) were high in the Maastrichtian (values > 10,000), and dropped at the K/Pg boundary to values between 1500 and 5000. The Danian record shows strong fluctuations, with one sample (215.48 mcd; within Zone P1b) giving a value similar to the high Maastrichtian values; this sample has a low diversity and heterogeneity and a low percentage of infaunal taxa. Overall, however, BFAR values do not return to Maastrichtian levels over the studied interval.

4. Discussion

No major extinctions affected benthic foraminiferal faunas at the K/Pg boundary at Site 1262, as at many

other sites and sections worldwide (Culver, 2003; Alegret and Thomas, 2005; Thomas, in press). Widmark and Malmgren (1992) estimated a higher percentage of last appearances at nearby Sites 525 and 527, but these last appearances include these of ‘Lazarus taxa’, which re-appear higher in the section than the interval studied by these authors, as also discussed by Culver (2003). For example, *Alabamina creta* is included in the species with a last appearance at the K/Pg boundary by Widmark and Malmgren (1992), but is in fact present higher in the section until its extinction at the end of the Paleocene (Zachos et al., 2004). In general, our data strongly resemble these presented by Widmark and Malmgren (1992) for Site 527, although these authors studied a larger size fraction (> 125 µm) than we did, had a somewhat lower sample resolution close to the boundary (~ 10 cm as compared to 1–2 cm), and Site 1262 is in waters that are presently several hundred meters deeper (although this difference was less at the end Cretaceous, Zachos et al., 2004).

A period of reduced organic flux to the sea floor, with a duration shorter than that of Zone P α , has been documented at the K/Pg boundary in sections from all over the world, and has been related to a decrease in primary productivity as the result of mass extinction of primary producers (e.g., Alegret et al., 2001; Peryt et al., 2002; Alegret and Thomas, 2004, 2005). At some locations, however, there is evidence for low-oxygen conditions just after the K/Pg extinction (e.g., Alegret et al., 2003; Alegret and Thomas, 2005), possibly caused by a high organic flux at these locations, and at equatorial Pacific Site 465 BFAR values increased just above the boundary (Alegret and Thomas, 2005).

At Site 1262 (as at many other sites) no evidence for low-oxygen conditions has been observed, and the common occurrence of *O. umbonatus* in the lower Danian probably indicates well-oxygenated pore-waters (Mackensen et al., 1995). At the K/Pg boundary, diversity and heterogeneity dropped dramatically, and BFAR as well as the percentage of buliminids decreased, although the total infaunal percentage did not decline.

Before the K/Pg boundary, conditions at the sea floor were oligotrophic to mesotrophic at Site 1262, as expected at abyssal depths, indicated by the morphogroup composition of the upper Maastrichtian assemblages, and the abundance of some low-food species such as *N. truempyi* or *Cibicidoides hyphalus* (Widmark and Malmgren, 1992; Nomura, 1995; Thomas et al., 2000). Calcareous nannofossil assemblages also indicate relatively oligotrophic conditions (Bernaola and Monechi, in press). Buliminids may have

increased somewhat in relative abundance in the uppermost Maastrichtian, although higher resolution studies are needed in order to document this convincingly: the relative abundance of buliminids fluctuated in the Maastrichtian (Fig. 3), and our data in this part of the section are not at high enough resolution to resolve the timing of these changes in abundance. Buliminids tolerate reduced oxygen concentrations, but a high relative abundance is thought to be mainly caused by an abundant food supply and a year-round or seasonally fluctuating high delivery of food to the sea floor (e.g., Widmark and Speijer, 1997; Fontanier et al., 2002; Jorissen et al., in press). Their increase in abundance thus suggests a slightly increased food supply to the sea floor. Increased nutrient supply to the sea floor during the latest Maastrichtian has also been documented from sections from NE and central-eastern Mexico (Alegret et al., 2001). The BFAR values for the Maastrichtian were much higher at Site 1262 than at equatorial Pacific Site 465 (Alegret and Thomas, 2005), but this might be due to uncertainty in the estimates for sediment accumulation rates. At Site 465 sedimentation rates are not well constrained, and the estimates for Site 1262 are only preliminary (Roehl, U., 2006, personal communication).

No significant changes in overall morphogroup composition occurred across the K/Pg boundary at Site 1262, as also reported for Site 527 by Widmark and Malmgren (1992), but this is in sharp contrast with the situation at many other sites (Culver, 2003; Alegret and Thomas, 2005). At both abyssal sites on Walvis Ridge (527, 1262), the increase in infaunal “rounded planispiral” and “spherical” morphotypes (e.g., *Pullenia*, *Globulina*, *Quadriformina*) compensates for the loss in infaunal “tapered and cylindrical” morphotypes (Fig. 3). In contrast, a decrease in the percentage of infaunal morphogroups has been documented for lower bathyal Site 525 on Walvis Ridge, suggesting that benthic foraminiferal assemblages may have been more affected in composition by the K/Pg boundary event at shallower sites, although there is no evidence for increased extinction rates at shallower sites (Culver, 2003).

Lowermost Danian assemblages contain peaks in the relative abundance of *Q. allomorhinooides*, *Nonionella* sp. and parabalaminids, which may have behaved as opportunistic taxa during the post-K/Pg boundary more oligotrophic and/or environmentally unstable conditions. Above this interval, there is a 1.5-m-thick interval where the percentage of calcareous infaunal morphogroups decreased in relative abundance, whereas the agglutinated taxa *S. spectabilis* and *Clavulinoides* spp. increased (Fig. 3). *S. spectabilis* bloomed after the K/Pg boundary at many locations in the deep oceans,

and is seen as a disaster taxon, which may indicate increased organic carbon flux (Kaminski and Gradstein, 2005).

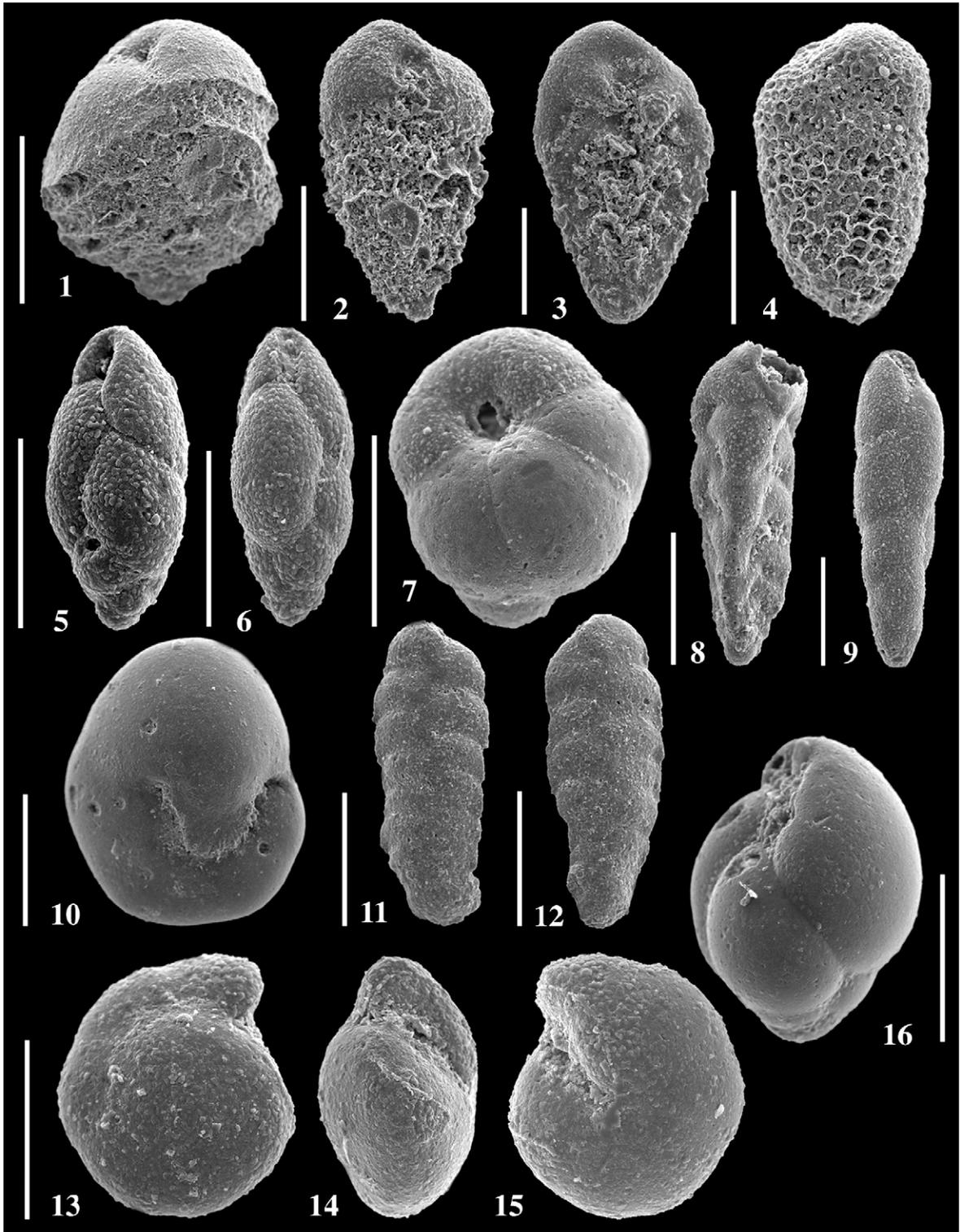
Diversity and heterogeneity of the assemblages fluctuate throughout the studied interval above the K/Pg boundary, as did BFAR. The drop in BFAR the K/Pg boundary and the decrease in relative abundance of buliminid taxa suggest a decrease in food supply, but the lack of a significant decrease in total percentage of infaunal taxa contradicts this suggestion. The increase in abundance of potentially opportunistic species, and the change in dominance of the specific infaunal morphotype present (calcareous tapered to calcareous spherical to agglutinated tapered) suggest that there was no persistent decrease in overall organic matter flux to the sea floor, but the change in infaunal morphology suggests that the type of organic material to the sea floor changed in its character or in the stability-variability of its supply. The increased abundance of opportunistic taxa, as well as the strongly fluctuating diversity, heterogeneity and BFAR suggest that the boundary was followed by a period of strong fluctuations in the food supply. Primary productivity in the interval of fluctuating diversity and heterogeneity may have been dominated by blooms of non-calcareous primary producers, which created a stressful environment for the benthos (Alegret and Thomas, 2004; see also Gardin and Monechi, 1998; Bernaola and Monechi, in press).

The increase in magnetic susceptibility at the K/Pg boundary (Zachos et al., 2004) reflects a decrease in calcium carbonate percentage, probably as the result of a prominent decrease in the delivery of carbonate due to the extinction of calcareous nannofossils, planktic foraminifera, resulting in a shallowing of the carbonate compensation depth (CCD) in the Danian. The decrease in calcium carbonate delivery might have influenced the benthic faunal composition (e.g., Kaminski et al., 1988; Alegret and Thomas, 2001), leading to the replacement of infaunal carbonate taxa (buliminids) by agglutinated groups when the food supply recovered stability (Fig. 3). Benthic foraminiferal assemblages stabilized towards the upper part of the studied Paleogene interval, suggesting the return to more stable mesotrophic conditions at the sea floor, although not to the Maastrichtian levels.

At sites and sections in the N Pacific (DSDP Site 465), NW Atlantic (ODP Site 1049) and Tethys (e.g., Caravaca, Agost, Aïn Settara sections), lowermost Danian assemblages also contain short-term (<Zone P α) peaks of opportunistic species that indicate instability in the environment and specifically in the food supply (Alegret, in press; Alegret and Thomas, 2004,

2005; Alegret et al., 2003). The question remains which paleoenvironmental changes caused the occurrence of these peaks of benthic foraminiferal species globally. At

many locations, the food flux to the benthos (according to benthic foraminiferal indices) decreased for at least several thousand years after the K/Pg boundary, but at



Site 465 the food supply appears to have increased; at some Tethyan sections an even more extreme increase in organic carbon flux is suggested by the development of low-oxygen conditions (Alegret and Thomas, 2005). The lack of deep-sea benthic foraminiferal extinction (Culver, 2003) suggests that there was no global anoxia following the K/Pg, and that not only the food supply to the deep sea recovered faster than commonly suggested (e.g., in the ‘Strangelove Ocean’ model; Hsü and McKenzie, 1985), but also its transport to the sea floor recovered faster than argued by Coxall et al. (2006). At Site 1262, a deep oceanic locality remote from continents as well as from the impact location, the overall food supply decreased as indicated by the BFAR and percentage buliminid values but the percentage of infaunal taxa did not change. BFAR strongly fluctuated in the Danian, and changes in benthic foraminiferal assemblages may have resulted at least in part from instability rather than collapse of the food supply.

The biomass of primary producers in the oceans as well as the flux of organic matter to the sea floor thus may have recovered much faster than the diversity of planktonic biota, probably through large blooms of opportunistic taxa, limited to specific regions, as shown by the geographically limited occurrence of laminated black clays. The short-term blooms of various phytoplankton groups may have resulted in food-transfer to the deep sea that varied strongly in quality and quantity depending on the location and the time, resulting in instability in the benthic assemblages. Environmental changes in the deep-sea thus varied geographically (as also argued by Coccioni and Galeotti, 1994), with strong variability in the degree and duration of the collapse in primary productivity as expressed in biomass rather than in diversity. Detailed investigations of carbon isotope records at different locations are needed in order to understand the collapse (and locally reversal) of the deep-surface gradients.

5. Conclusions

Analysis of upper Maastrichtian and lower Paleogene benthic foraminiferal assemblages from abyssal ODP Site 1262 on Walvis Ridge (eastern South Atlantic

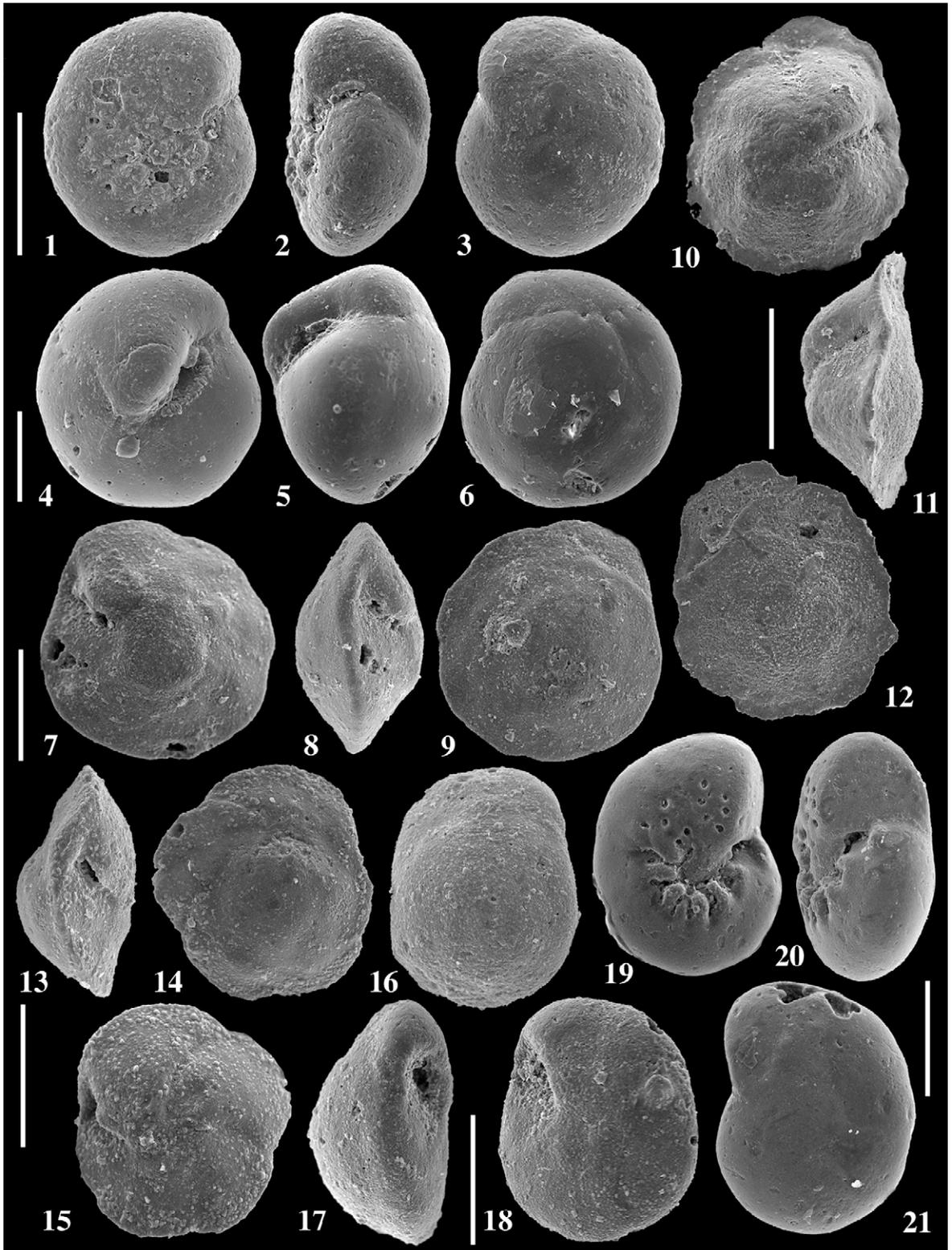
Ocean) allowed us to study the nature and cause/s of the benthic turnover across the K/Pg boundary in the deep-sea at a location relatively remote from the location of the asteroid impact and away from the continental margins.

Upper Maastrichtian assemblages are diverse and heterogeneous, and contain relatively abundant buliminids, suggesting mesotrophic conditions at the sea floor, as supported by high values of BFAR. As at other locations, there was no significant extinction of benthic foraminifera at the K/Pg boundary, but the drastic decrease in diversity and heterogeneity of the assemblages, in BFAR, and in the percentage of buliminids, together with the dominance of opportunistic taxa during the earliest Danian, suggest major environmental instability just after the K/Pg boundary event. This instability may have been expressed not in an overall, persistent decrease in the supply of food to the sea floor lasting a few millions of years, but in a change in stability of the supply and/or composition of the food.

The rise in the CCD, probably resulting from the drop in calcium carbonate delivery caused by the extinction of calcareous planktic groups, may have influenced the benthic faunal composition above this post-K/Pg interval, leading to the replacement of infaunal carbonate taxa (buliminids) by agglutinated groups when the food supply stabilized to some extent, about 1.5 m above the K/Pg boundary (zone P1b), and mesotrophic conditions returned, although not to the level of Maastrichtian productivity.

Benthic foraminiferal assemblages appear to have been affected by the collapse of nannoplankton productivity at the K/Pg boundary to a different extent in different regions, with the peaks in abundance of some benthic foraminiferal species indicating an increase in organic carbon flux directly above the boundary in some regions, as suggested by the development of low-oxygen conditions. The biomass of primary producers in the oceans thus may have recovered much faster than their diversity (e.g., d’Hondt, 2005; Coxall et al., 2006), probably through geographically variable and limited large blooms of opportunistic phytoplankton taxa. The

Plate 1. SEM illustrations of benthic foraminifera with an infaunal mode of life across the K/Pg transition at Site 1262, Walvis Ridge. Scale bar=100 μm . 1. *Aragonia velascoensis* (Cushman), sample 1226. 2. *Bolivinooides decoratus* (Jones), sample 1330. 3. *Bolivinooides delicatulus* Cushman, sample 1267. 4. *Bolivina* cf. *humeri* Howe, sample 1235. 5, 6. *Bulimina kugleri* Cushman and Renz, sample 1177. 7. *Buliminella beaumonti* Cushman and Renz, sample 1267. 8. *Bulimina paleocenica* Brotzen, sample 1355. 9. *Fursenkoina tegulata* (Reuss), sample 1250. 10. *Quadriformina allomorphinoides* (Reuss), sample 1234. 11, 12. *Spiroplectammina spectabilis* (Grzybowski), sample 1142. 13–15. *Oridorsalis umbonatus* (Reuss) — spiral (1), apertural (2), and umbilical (3) view, sample 1234. 16. *Praebulimina reussi* (Morrow), sample 1355.



benthic foraminiferal assemblages and BFAR values indicate that this food also reached the sea floor (at least in some areas), and suggest that the causes of the collapse or even reversal of vertical carbon-isotope gradients at the K/Pg boundary needs further investigation. If the speculations on the lack of extinction of benthic foraminifera at the K/Pg boundary are valid, and if Site 1262 is typical for larger parts of the ocean in indicating relatively little interruption of food supply to the deep sea, the oceanic ecosystems may have recovered on a timescale similar to that of terrestrial ecosystems (Beerling et al., 2001).

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Appendix A. Taxonomic notes

Aragonia velascoensis (Cushman)

1925 *Textularia velascoensis* Cushman, p. 18, pl. 3, figs. 1a–c.

Plate 1, fig. 1.

Our specimens are very similar to those identified and illustrated by Tjalsma and Lohmann (1983) as *Aragonia ouezzanensis* (Rey). According to these authors, the two species differ in the thickness of their shells, with *A. ouezzanensis* being thicker in transverse section, shorter in length and with a wide apical angle. However, we consider *A. ouezzanensis* a junior synonym of *A. velascoensis*, in agreement with Van Morkhoven et al. (1986).

Bolivina cf. huneri Howe

cf. 1939 *Bolivina huneri* Howe, p. 66, pl. 9, figs. 3–4. Plate 1, fig. 4.

The specimens found in Site 1262 differ somewhat from the holotype and from the specimens identified by Tjalsma and Lohmann (1983) as *Bolivina huneri* Howe in having nearly parallel sides in the adult forms, and being more heavily ornamented, even in the last few chambers. The test ornamentation in our specimens is more hexagonal, but resembles the ornamentation in the figure in Tjalsma and Lohmann (1983) in the semi-interruption of the ridges.

Bolivinooides decoratus (Jones)

1886 *Bolivina decorata* Jones, p. 330, pl. 27, figs. 7–8.

Plate 1, fig. 2.

Our material is very similar to the specimen identified by Widmark (1997) as *Bolivinooides cf. clavatus* Plotnikova at Sites 525 and 527, but we consider our specimens consistent with the original description of *B. decoratus*.

Bolivinooides delicatulus Cushman

1927 *Bolivinooides decorata* (Jones) var. *delicatula* Cushman, p. 90, pl. 12, fig. 8.

Plate 1, fig. 3.

Our specimens are characterized by slender tests, ornamented with oblique lobes and have a smooth apertural end. They are very similar to those identified as *Bolivinooides cf. postulatus* Reiss by Widmark (1997). The name of this species has a typographical error: it should have been *B. pustulatus* Reiss. In our opinion these specimens better agree with the description of *Bolivinooides delicatulus* Cushman, with the variation within this species encompassing smaller specimens such as these named *B. cf. postulatus* by Widmark (1997).

Bulimina kugleri Cushman and Renz

1942 *Bulimina kugleri* Cushman and Renz, p. 9, pl. 2, fig. 9.

Plate 1, figs. 5, 6.

Our specimens closely resemble the holotype and paratypes of *B. kugleri*. All of these have elongate, fusiform tests about twice as long as broad, with distinct, slightly inflated and elongate chambers, distinct sutures

Plate 2. SEM illustrations of benthic foraminifera with an epifaunal mode of life across the K/Pg transition at Site 1262, Walvis Ridge. Scale bar=100 μm in all specimens but 10 to 12, where it corresponds to 300 μm. 1–3. *Cibicidoides hyphalus* (Fisher) — spiral (1), umbilical (2), and apertural (3) view, sample 1306. 4–6. *Gyroidinoides globosus* (Hagenow) — umbilical (1), apertural (2), and spiral (3) view, sample 1177. 7–9. *Nuttalides truempyi* (Nuttall) — umbilical (1), apertural (2), and spiral (3) view, sample 1409. 10–12. *Nuttallinella florealis* (White) — umbilical (1), apertural (2), and spiral (3) view, sample 1142. 13–15. *Paralabamina lunata* (Brotzen) — spiral (1), apertural (2), and umbilical (3) view, sample 1142. 16–18. *Paralabamina hillebrandti* (Fisher) — apertural (1), spiral (2), and umbilical (3) view, sample 1234. 19–21. *Stensioeina beccariiiformis* (White) — apertural (1), spiral (2), and umbilical (3) view, sample 1066.

and a highly arched aperture at the base of the last chamber.

Bulimina paleocenica Brotzen

1948 *Bulimina paleocenica* Brotzen, p. 61, pl. 6, figs. 5–6.

Plate 1, fig. 8

The specimens in our material fully agree with the original species description. *B. paleocenica* has an elongate test that slowly increases in breadth, is triangular in cross section, with rounded angles and numerous, high chambers and distinct sutures.

Buliminella beaumonti Cushman and Renz

1946 *Buliminella beaumonti* Cushman and Renz, p. 36, pl. 6, fig. 7.

Plate 1, fig. 7

The general morphology of the test, the broadly rounded apertural end, and the loop-shaped aperture at the base of the last chamber can be clearly observed in our specimens. The holotype shows backward-projecting lobes at the base of each chamber, which are not easy to recognise in all specimens in our material. We agree with Tjalsma and Lohmann (1983), who include in the species *B. beaumonti* specimens with few lobes, and specimens without lobes but otherwise similar in morphology.

Cibicidoides hyphalus (Fisher)

1969 *Anomalinoidea hyphalus* Fisher, p. 198, fig. 3a–c.

Plate 2, figs. 1–3.

This species has wide morphological variety, with two extreme morphotypes (Van Morkhoven et al., 1986; Alegret and Thomas, 2001). The plano-convex morphotype with a coarsely perforate flat side, involute to somewhat evolute, and a smoother convex, involute side dominates among our specimens from Site 1262. Widmark (1997) also found these two morphotypes of *C. hyphalus* in his material from Sites 525 and 527.

Fursenkoina tegulata (Reuss)

1845 *Virgulina tegulata* Reuss, p. 40, pl. 13, fig. 81.

Plate 1, fig. 9

Our specimens fully agree with the original description of the species.

Gyroidinoides globosus (Hagenow) emend. Alegret and Thomas 2001

1842 *Nonionina globosa* Hagenow, p. 574.

2001 *Gyroidinoides globosus* (Hagenow) emend. Alegret and Thomas, p. 288, pl. 8, figs. 1–5.

Plate 2, figs. 4–6.

G. globosus has a typical globular, unequally convex test, an interior marginal slit-like aperture, and a low and broad apertural face. The specimens found at Site 1262 fully agree with our concept of this species as described

in Alegret and Thomas (2001). Widmark (1997) also identified this species at Sites 525 and 527, where it is very rare.

Nuttallides truempyi (Nuttall)

1930 *Eponides truempyi* Nuttall, p. 287, pl. 24, figs. 9, 13, 14.

Plate 2, figs. 7–9.

This species is characterized by a biconvex trochospiral test, with a prominent boss on the ventral side and sinuous sutures near the umbilical boss. *N. truempyi* is abundant in our samples and in Sites 525 and 527 (Widmark, 1997).

Nuttallinella florealis (White)

1928 *Gyroidina florealis* White, p. 293, pl. 40, figs. 3a–c.

Plate 2, figs. 10–12.

Test planoconvex, with a flat and evolute dorsal side and a strongly convex, involute ventral side with a small depression in the umbilical area and thickened dorsal sutures around the umbilical depression. In some of our specimens, the broad hyaline keel, which is typical of this species, is exceptionally well preserved.

Oridorsalis umbonatus (Reuss)

1851 *Rotalina umbonata* Reuss, p. 75, pl. 5, fig. 35.

Plate 1, figs. 13–15.

Our material from Site 1262 agrees with the type description of the species. *O. umbonatus* has a biconvex, trochospiral test, characterized by the chamber sutures on the dorsal side, which are at right angles to the spiral suture. The slightly lobate outline can also be observed in our specimens from Site 1262.

Paralabamina hillebrandti (Fisher)

1969 *Neoepionides hillebrandti* nom. nov. Fisher, p. 196

Plate 2, figs. 16–18.

Widmark (1997) illustrated a highly planoconvex specimen of *P. hillebrandti* from Site 527. Although that morphotype is also present among our material, specimens with a less strongly convex umbilical side dominate.

Paralabamina lunata (Brotzen)

1948 *Eponides lunata* Brotzen, p. 77, pl. 10, figs. 17, 18.

Plate 2, figs. 13–15.

Our material close resembles the holotype figured by Brotzen, as well as the specimen from Site 527 figured by Widmark (1997).

Praebulimina reussi (Morrow)

1934 *Bulimina reussi* Morrow, p. 195, pl. 29, fig. 12.

Plate 1, fig. 16.

This species is characterized by its short, triserial test, and the comma-shaped aperture. It was also found by

Widmark (1997) in the Maastrichtian sediments from Sites 525 and 527.

Quadrimorphina allomorphinoides (Reuss)

1860 *Valvulina allomorphinoides* Reuss, p. 223, pl. 11, fig. 6.

Plate 1, fig. 10.

This species has an elongate, inflated last chamber and about four chambers in the last formed whorl. Our specimens strongly resemble those in the type description, and those described from Sites 525 and 527 by Widmark (1997).

Spiroplectamina spectabilis (Grzybowski)

1898 *Spiroplecta spectabilis* Grzybowski, p. 293, pl. 12, fig. 12.

Plate 1, figs. 11, 12.

Although *S. spectabilis* has a wide morphological variability, it can be distinguished from other species of *Spiroplectamina* by its elongate test, with a narrow and slender biserial part and parallel sides. Widmark (1997) identified this species at Sites 525 and 527.

Stensioeina beccariiiformis (White)

1928 *Rotalia beccariiiformis* White, p. 287, pl. 39, figs. 2a–4c.

Plate 2, figs. 19–21.

This species has a trochospiral, planoconvex to unequally biconvex test, with a broadly rounded periphery, and with flaps typically covering the umbilicus (present in well-preserved specimens), from which thread-like lines and depressions radiate. *S. beccariiiformis* is also abundant at Sites 525 and 527 (Widmark, 1997).

Appendix B. Supplementary data

Supplementary data associated with this article can be found, in the online version, at [doi:10.1016/j.marmicro.2006.12.003](https://doi.org/10.1016/j.marmicro.2006.12.003).

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