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Research paper

Benthic foraminifera across the Cretaceous/Paleogene boundary in the Southern Ocean (ODP Site 690): Diversity, food and carbonate saturation

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ABSTRACT

The impact of an asteroid at the Cretaceous/Paleogene (K/Pg) boundary triggered dramatic biotic, biogeochemical and sedimentological changes in the oceans that have been intensively studied. Paleo-biogeographical differences in the biotic response to the impact and its environmental consequences, however, have been less well documented. We present a high-resolution analysis of benthic foraminiferal assemblages at Southern Ocean ODP Site 690 (Maud Rise, Weddell Sea, Antarctica).

At this high latitude site, late Maastrichtian environmental variability was high, but benthic foraminiferal assemblages were not less diverse than at lower latitudes, in contrast to those of planktic calcifiers. Also in contrast to planktic calcifiers, benthic foraminifera did not suffer significant extinction at the K/Pg boundary, but show transient assemblage changes and decreased diversity. At Site 690, the extinction rate was even lower (~3%) than at other sites. The benthic foraminiferal accumulation rate varied little across the K/Pg boundary, indicating that food supply to the sea floor was affected to a lesser extent than at lower latitude sites. Compared to Maastrichtian assemblages, Danian assemblages have a lower diversity and greater relative abundance of heavily calcified taxa such as *Stensioeina beccariiformis* and *Paralabamina lunata*. This change in benthic foraminiferal assemblages could reflect post-extinction proliferation of different photosynthesizers (thus food for the benthos) than those dominant during the Late Cretaceous, therefore changes in the nature rather than in the amount of the organic matter supplied to the seafloor. However, severe extinction of pelagic calcifiers caused carbonate supersaturation in the oceans, thus might have given competitive advantage to species with large, heavily calcified tests. This indirect effect of the K/Pg impact thus may have influenced the deep-sea dwellers, documenting the complexity of the effects of major environmental disturbance.

1. Introduction

The impact of an asteroid in the Yucatan Peninsula (Mexico) at the K/Pg boundary (Schulte et al., 2010) caused mass extinction of oceanic calcifying plankton (>90% of species), including planktic foraminifera (Smit, 1982; Stott and Kennett, 1990a; Liu and Olsson, 1992; Berggren and Norris, 1997; Molina et al., 1998) and calcareous nannoplankton (Pospichal and Wise, 1990; Bown, 2005; Fuqua et al., 2008). In contrast, non-calcifying pelagic organisms such as diatoms and radiolarians (Harwood, 1988; Hollis et al., 2003), dinoflagellates (Brinkhuis et al., 1998) and non-calcifying haptophytes (Medlin et al., 2008) suffered considerably less, and deep-sea bottom-dwelling calcifiers such as benthic foraminifera (e.g., Thomas, 1990a,b; Alegret and Thomas, 2005) and ostracodes (e.g., Majoran et al., 1997; Boomer, 1999; Elewa, 2002) did not suffer significant extinction over background levels (Culver, 2003).

Benthic foraminifera are one of the few groups of organisms to provide information on deep-sea ecosystems of the past. They underwent geographically variable, transient changes in assemblages, including declining diversity, across the K/Pg boundary. Causes of such changes may have included increased or decreased export productivity (flux of organic matter from the surface waters to the seafloor), dysoxic conditions, and other environmental stress factors, e.g., variability in the nature of the organic matter delivered to the sea floor (e.g., Alegret and Thomas, 2005; Alegret, 2007; Alegret and Thomas, 2009; Alegret et al., 2012).

The collapse of carbon isotope gradients between surface and deep-sea carbonates (as measured in bulk carbonate sediment/planktic foraminifera and benthic foraminifera, respectively) is a key feature of the sedimentary records of the K/Pg boundary, having been recognized globally in many sections and drill sites (e.g., d'Hondt, 2005; Alegret et al., 2012). This collapse has traditionally been interpreted as the result of a long-term (hundreds of thousands to millions of years) interruption of primary productivity or export productivity (Strangelove Ocean and Living Ocean models; Hsü and McKenzie, 1985; d'Hondt et al., 1998; d'Hondt, 2005; Coxall et al., 2006). The hypothesis that primary or

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export productivity collapsed for hundreds of thousands of years, however, conflicts with the lack of significant extinction amongst benthic foraminifera (Alegret et al., 2012): life on the deep-sea floor depends upon export of organic matter from surface ocean productivity (bentho-pelagic coupling) (Gooday, 2003; Jorissen et al., 2007). In addition, rapid resurgence of primary productivity in terms of biomass is indicated by organic biomarker data (Sepúlveda et al., 2009) and geochemical proxies for export productivity (Ba/Ti) (Hull and Norris, 2011). Oceanic primary productivity in terms of biomass thus probably recovered quickly after the K/Pg extinction. The collapse in carbon isotope values may at least in part have been caused by the effect of the extinction of the carriers of the isotope signal, calcareous nannoplankton and planktic foraminifera, because both were replaced by taxa with a much lighter carbon isotope signature than the Maastrichtian forms (Alegret et al., 2012; Birch et al., 2012).

Both benthic foraminiferal and geochemical proxies for export productivity indicate geographical heterogeneity in the post-extinction oceans, with increased export productivity in some areas (e.g., Pacific Ocean, New Zealand), decreased in others, including the Indian Ocean, Tethys, and some Atlantic sections (e.g., Hollis et al., 2003; Alegret and Thomas, 2005; Alegret, 2007; Alegret and Thomas, 2009; Hull and Norris, 2011; Alegret et al., 2012). Relatively eutrophic conditions in large parts of the surface oceans shortly after the extinction are also suggested by the fact that the few surviving species of pelagic calcifiers, from which the Cenozoic radiation of species started, were neritic, indicative of relatively eutrophic waters (Liu and Olsson, 1992; Berggren and Norris, 1997; Bown, 2005). Non-calcareous haptophytes did not suffer severe turnover, and also are dominantly neritic in the present oceans (Medlin et al., 2008).

Antarctic biota, including invertebrates, dinoflagellates, diatoms, and calcareous nannoplankton have been described as less severely affected by the K/Pg impact than their lower latitude counterparts (Zinsmeister et al., 1989; Elliot et al., 1994; Jiang et al., 2010). This lesser degree of extinction has been explained by arguing that high latitude biota are used to survive periods of darkness, thus assigning an important role to darkness as cause of extinction. These rates are, however, strongly influenced by the lower initial diversity of pelagic calcifiers at high latitudes.

We compare the biotic turnover of deep-sea benthic foraminifera at high southern latitudes with that at other sites, and increase the resolution of data on benthic foraminiferal assemblages at Southern Ocean ODP Site 690 on Maud Rise (Weddell Sea, Antarctica) (Thomas, 1990a, b). Study of deep-sea assemblages at high latitudes may provide insight in sources of diversity differences over time, because benthic foraminiferal assemblages in the Maastrichtian–Paleocene apparently lacked a significant latitudinal diversity gradient (Thomas and Gooday, 1996). The latitudinal diversity gradient in deep-sea benthic foraminiferal assemblages has been linked to the high seasonality in productivity at high latitudes (Culver and Buzas, 2000; Corliss et al., 2009). Seasonality may have increased with the high latitude cooling and formation of sea ice at the end of the Eocene, when the gradient may have become established (Thomas and Gooday, 1996), coeval with an increase in relative abundance of 'phytodetritus species' (Thomas and Gooday, 1996). These faunal changes might have been influenced by the increased abundance of diatoms, with ecosystem changes leading to changes in export particle productivity and organic matter transfer (Henson et al., 2012).

Site 690 (Fig. 1) is a key location to study the paleoenvironmental turnover during the K/Pg transition at high southern latitudes because it is the only deep-sea site where $CaCO_3$-bearing sediments have been recovered containing an Iridium anomaly indicative of a relatively complete boundary section (Michel et al., 1990). Calcareous nannofossils at Site 690 have been studied by Pospichal and Wise (1990) and Jiang et al. (2010), planktic foraminifera by Stott and Kennett (1990a), and stable isotopes by Stott and Kennett (1989, 1990b), Kennett and Stott (1990) and Alegret et al. (2012).

2. Material and methods

A continuous, well-preserved K/Pg transition was recovered during Ocean Drilling Program (ODP) Leg 113 on Maud Rise, an aseismic ridge in the eastern Weddell Sea (Fig. 1). Site 690 is on its southwestern flank at 65°9.629′S, 1°12.30′E, at a present water depth of 2914 m (Thomas et al., 1990). The K/Pg boundary in Hole 690C is marked by a distinct change from white nannofossil ooze/chalk to brown clay-bearing nannofossil ooze (Barker et al., 1988; Figs. 2, 3). The color change does not exactly coincide with the horizon of maximum extinction of calcareous nannofossils and planktic foraminifera due to intense bioturbation (Pospichal and Wise, 1990; Stott and Kennett, 1990a), as also shown by the fact that Ir values >100 ppt (peak value 1566 ppt; Suppl. Table 1) occur over an interval of 76 cm, with a maximum value at 247.79 mbsf (Michel et al., 1990; Figs. 3, 4). Core photographs (Barker et al., 1988) show that bioturbation did not homogenize the sediment, but clearly delimited larger and smaller burrows of white Cretaceous that occur into dark brown Danian sediment and the reverse (Fig. 4). All calcareous nannofossil and planktonic foraminiferal zones were recognized, thus there are no detectable unconformities across the K/Pg transition.

We studied the top of the Maastrichtian planktic foraminiferal *Abathomphalus mayaroensis* Zone through the lower part of Danian Zone AP1b, equivalent to the top of the Maastrichtian calcareous nannofossil *C. daniae* Zone through Zone CP2 (Stott and Kennett, 1990a; Thomas et al., 1990; Pospichal and Wise, 1990; Figs. 2, 3). Calcareous chalks and oozes were deposited at upper abyssal to lower bathyal

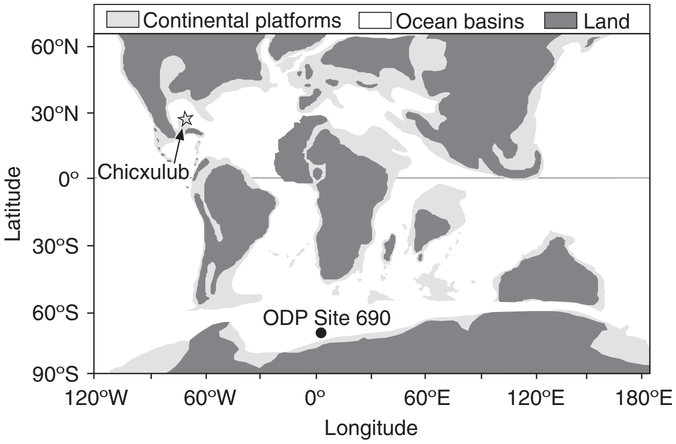


Fig. 1. Paleogeographic location of Southern Ocean Site 690 at the K/Pg boundary (modified from Scotese and Denham, 1988).

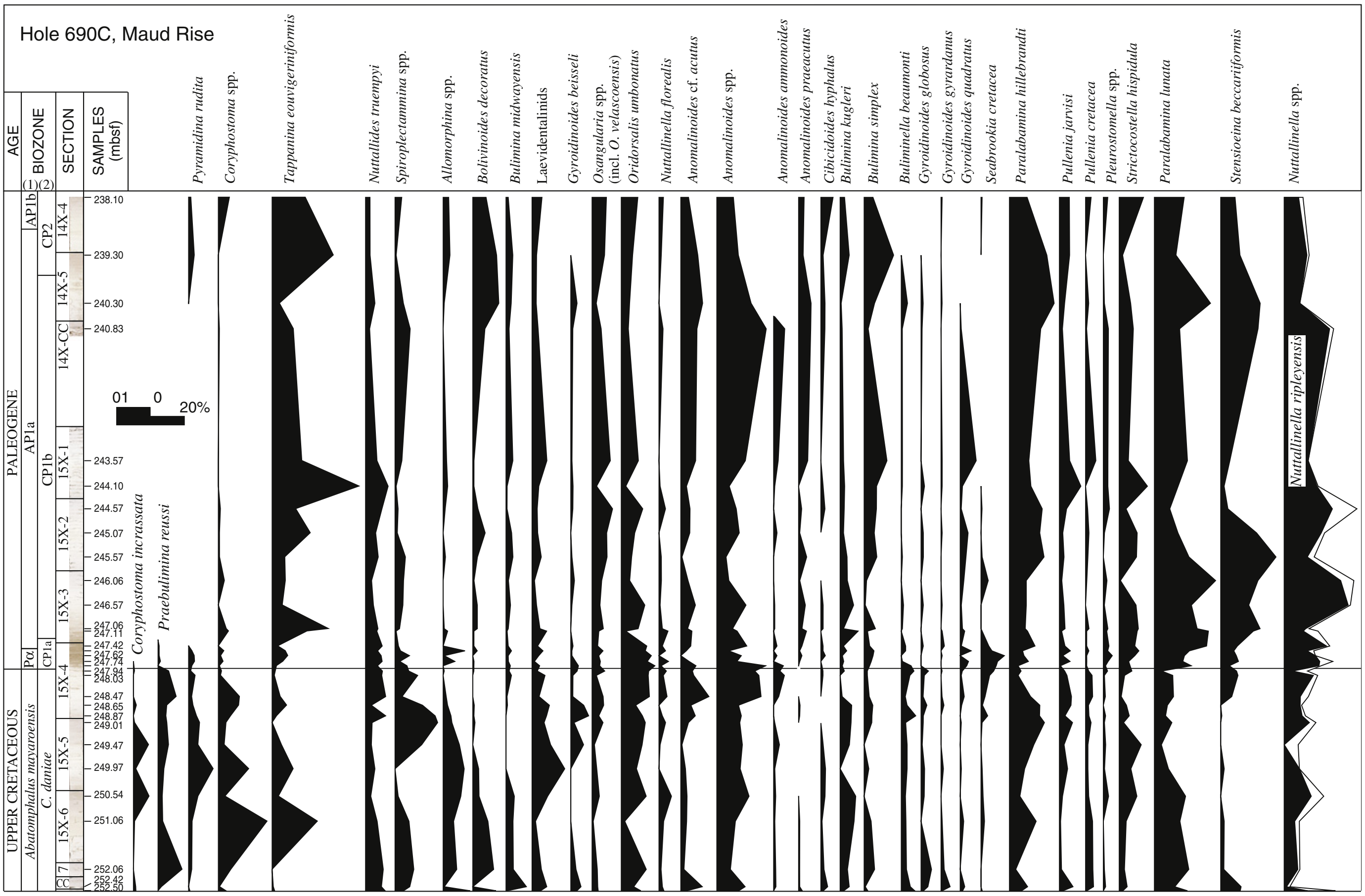


Fig. 2. Variations in the percentage of benthic foraminiferal taxa across the upper Maastrichtian and lower Danian at Hole 690C, Maud Rise. Horizontal line indicates the K/Pg boundary. Planktic foraminiferal (1) and calcareous nannofossils (2) biozones from Stott and Kennett (1990a), Thomas et al. (1990) and Pospichal and Wise (1990).

depths (Thomas, 1990a). The characteristic global collapse of the vertical carbon isotope gradient at the K/Pg boundary was documented by Stott and Kennett (1989, 1990b), and in more detail by Alegret et al. (2012). These authors modified the age model in Thomas et al. (1990) through correlation of the carbon isotope record with that at Site 1262 where an orbitally tuned record is available (Westerhold et al., 2008, 2012). We used the age model as in Alegret et al. (2012).

In order to improve the low-resolution study on benthic foraminifera (Thomas, 1990a), we quantitatively studied assemblages in 31 samples from sections 690C-15×-4, 39–41 cm through 690C-16×-1, 39–41 cm (238.15–252.50 mbsf), comprising the upper 4.6 m of the Maastrichtian and the lower 9.8 m of the Danian (Suppl. Table 2; Fig. 2). Samples were spaced at few cm immediately below and above the K/Pg boundary, with decreasing resolution (50 cm to ~1 m) further away from the boundary. Quantitative studies and species richness calculations were based on representative splits of approximately 300 specimens of benthic foraminifera larger than 63 μm. Quantitative changes in the assemblages and in their diversity are shown in Figs. 2 and 3, and some of the representative species are illustrated in Plates I and II. All the species that make up more than 2% of the assemblages in at least one sample have been plotted in Fig. 2. Our taxonomy follows Alegret and Thomas (2001), with taxonomy for uniserial forms with complex apertures following Hayward et al. (2012) (Suppl. Table 2).

We calculated benthic foraminiferal proxies (Figs. 3, 5) to infer the environmental turnover at Southern Ocean Site 690 across the K/Pg boundary. We combined the Benthic Foraminiferal Accumulation Rates (BFARs) in Alegret et al. (2012) with relative species abundances to interpret trophic conditions and export productivity. BFARs were calculated using the number of benthic foraminifera per gram of sediment >63 μm, the weight % of the sample >63 μm, the linear sedimentation rate as obtained from the age model, and the sediment density (Barker et al., 1988). The BFAR is commonly used as a qualitative proxy for delivery of organic matter to the sea floor (Jorissen et al., 2007). Changes in habitat-related benthic foraminiferal morphogroups (infaunal vs. epifaunal) were used as proxies for oxygenation and trophic conditions at the seafloor, with epifaunal morphogroups generally more abundant in oligotrophic environments (e.g., Jorissen et al., 2007). We followed the infaunal/epifaunal morphological concepts as in Corliss (1985, 1991) and Corliss and Chen (1988) for calcareous taxa, and as in Jones and Charnock (1985) and Murray et al. (2011) for agglutinated taxa, as documented in Alegret et al. (2003) and in Supplementary Table 2. These assignments from morphology must be used cautiously, because they have been found to be correct for living foraminifera only in about 75% of cases (Buzas et al., 1993). *Oridorsalis umbonatus* has a carbon isotope signature typical for shallow infaunal taxa (e.g. Thomas and Shackleton, 1996; Katz et al., 2003). Species belonging to biserial genera such as *Coryphostoma* and *Tappanina* are generally considered infaunal after analogy with the extant bolivinids (Corliss, 1985; Corliss and Chen, 1988; Corliss, 1991), and as far as known from a limited number of observations indeed show an infaunal carbon isotope signature (Thomas and Shackleton, 1996; Wendler et al., 2013). Many uniserial, rectilinear taxa, which were common in the Paleogene and Late Cretaceous, are now extinct so that we do not know their lifestyle from direct observations (Hayward et al., 2012). They have been considered infaunal because of correlations to the abundances of other infaunal taxa (Thomas, 1990a; Gupta, 1993; Hayward et al., 2007), as confirmed by carbon isotope analysis (Mancin et al., 2013). We consider trochospiral calcareous taxa as epifaunal (e.g., genera *Nuttallides*, *Nuttallinella*, *Paralabamina*) (Corliss and Chen, 1988).

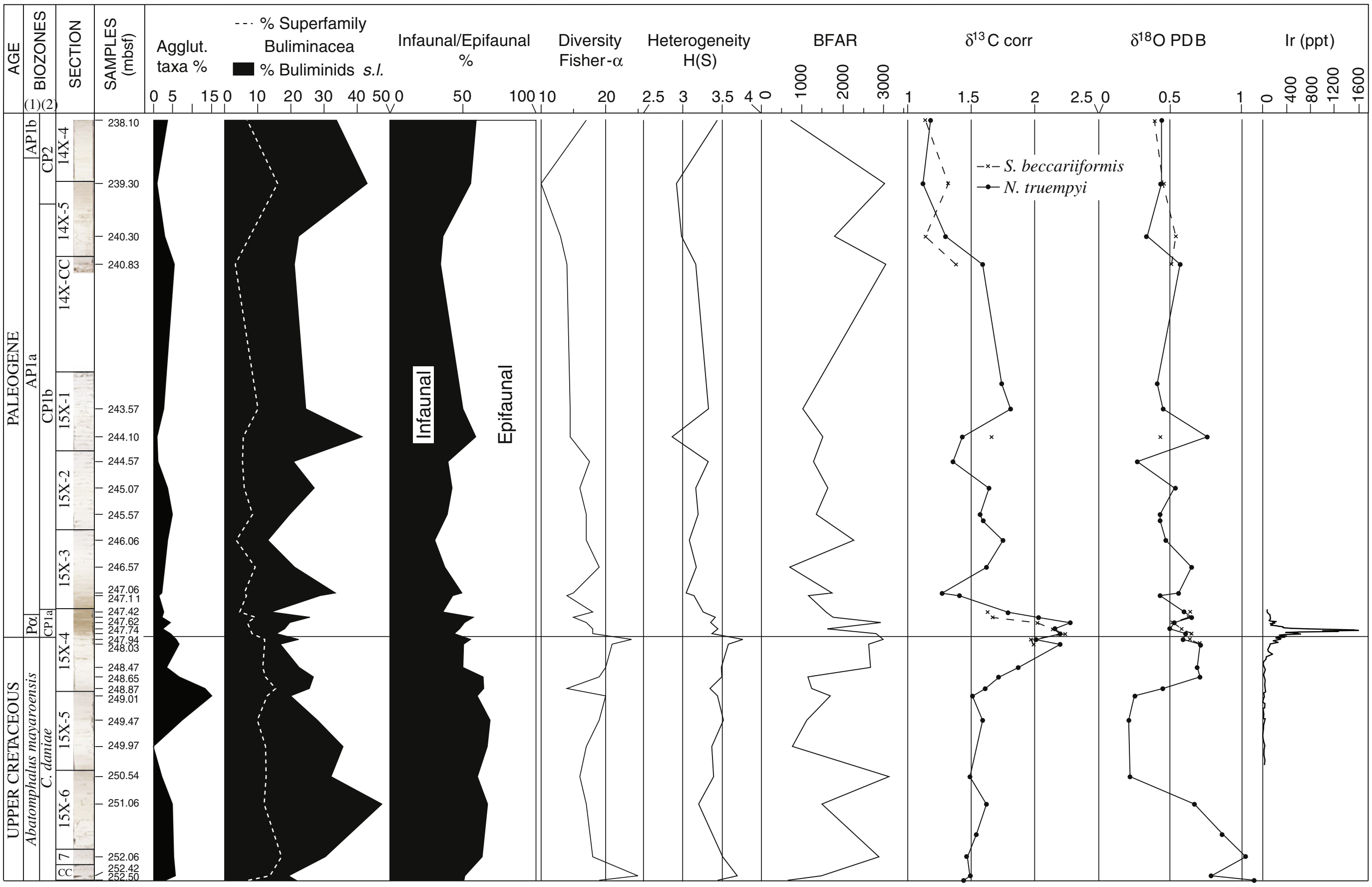


Fig. 3. Percentages of agglutinated benthic foraminiferal taxa, buliminids, and epifaunal/infaunal morphogroups; diversity (Fisher-α) index and heterogeneity H(S) Shannon–Weaver index of the benthic assemblages; benthic foraminiferal accumulation rates (BFAR); and $\delta^{13}C$ and $\delta^{18}O$ benthic foraminiferal records across the K/Pg boundary in Southern Ocean ODP Site 690. BFAR and $\delta^{13}C$ data after Alegret et al. (2012). Ir content from Michel et al. (1990). Horizontal line indicates the K/Pg boundary. Planktic foraminiferal (1) and calcareous nannofossils (2) biozones from Stott and Kennett (1990a), Thomas et al. (1990) and Pospichal and Wise (1990).

Variations in relative abundance of buliminids across the boundary were calculated. In the modern oceans, buliminid taxa tolerate reduced oxygen concentrations (Sen Gupta and Machain-Castillo, 1993; Bernhard et al., 1997) and are common at locations with an abundant, fairly continuous food supply (e.g., Fontanier et al., 2002). These two effects (food and oxygen) are generally correlated in the present oceans, so that they are difficult to deconvolve in the fossil record (Jorissen et al., 1995). At Site 690 there is no sedimentological evidence for low oxygenation in the studied interval (such as dark, organic-rich, laminated sediment), and the abundance of buliminids would have been interpreted as indicative of food availability at the seafloor. Recently, however, it has been suggested that infaunal taxa are also advantaged over epifaunal taxa when the carbonate saturation of bottom waters declines, because infaunal taxa are generally calcifying at the lower carbonate saturation levels characteristic in pore waters (Foster et al., 2013). At times of changes in carbonate saturation levels of bottom waters the percentage of infaunal taxa thus must be evaluated carefully. The K/Pg was such a time of changes in deep-sea carbonate saturation: deep-sea carbonate saturation may have increased because of the extinction of pelagic calcifiers in the absence of a decrease in weathering flux (Caldeira and Rampino, 1993; Zeebe and Westbroek, 2003; Ridgwell, 2005). We thus evaluate the benthic foraminiferal assemblages while including consideration of potential changes in organic flux as well as in carbonate saturation.

Stable isotope data for Site 690 (Figs. 3, 5) include data in Stott and Kennett (1990b) and Alegret et al. (2012), and new $\delta^{18}O$ data on benthic foraminifera (*N. truempyi*, *Stensioeina beccariiformis*; Suppl. Table 3) collected at the Earth Systems Center for Stable Isotopic Studies at Yale University, using a Thermo Gasbench II interfaced to a DeltaXP Stable Isotope Ratio mass spectrometer with a CTC Analytics GC-PAL autosampler, with analytical precision averages 0.07% for $\delta^{18}O$ and 0.04% for $\delta^{13}C$. Precision was monitored by analysis of National Bureau of Standards (NBS)-19 and NBS-18 every 10 samples. Results are reported in per mil (‰) relative to the Vienna Peedee belemnite (VPDB) standard. Temperature calculations based on $\delta^{18}O_{benthic}$ data, using O'Neil et al. (1969) as reformulated by Shackleton (1974), and assuming that no significant polar ice sheets were present are shown in Fig. 5.

3. Results: benthic foraminiferal turnover across the K/Pg boundary

Representatives of the cosmopolitan bathyal to abyssal Velasco-type fauna (Berggren and Aubert, 1975) such as *S. beccariiformis*, *Nuttallides truempyi*, *Cibicidoides hyphalus*, *Nuttallinella florealis* and *Osangularia velascoensis*, are common to abundant at Site 690. Taxa with an upper depth limit at upper to middle bathyal depths (500–700 m) include *N. truempyi*, *Spiroplectammina spectabilis* and *S. beccariiformis*. Species that are common at deep bathyal to abyssal settings, such as *Aragonia velascoensis*, *Gyroidinoides globosus*, *Paralabamina hillebrandti*, *Paralabamina lunata*, *Oridorsalis umbonatus*, and buliminid taxa such as *Bulimina kugleri*, *Buliminella beaumonti* and *Praebulimina reussi* (e.g., Tjalsma and Lohmann, 1983; Widmark and Malmgren, 1992; Widmark, 1997; Alegret and Thomas, 2001, 2004), are also present. Other buliminids such as *Pyramidina rudita*, show greatest abundances at sites of intermediate paleodepth (Tjalsma and Lohmann, 1983), and species with an upper depth limit at ~1000–1200 m depth (such as *Bulimina velascoensis* and *Pullenia coryelli*) are rare. These data indicate deposition in a lower bathyal environment (1000–2000 m) during the

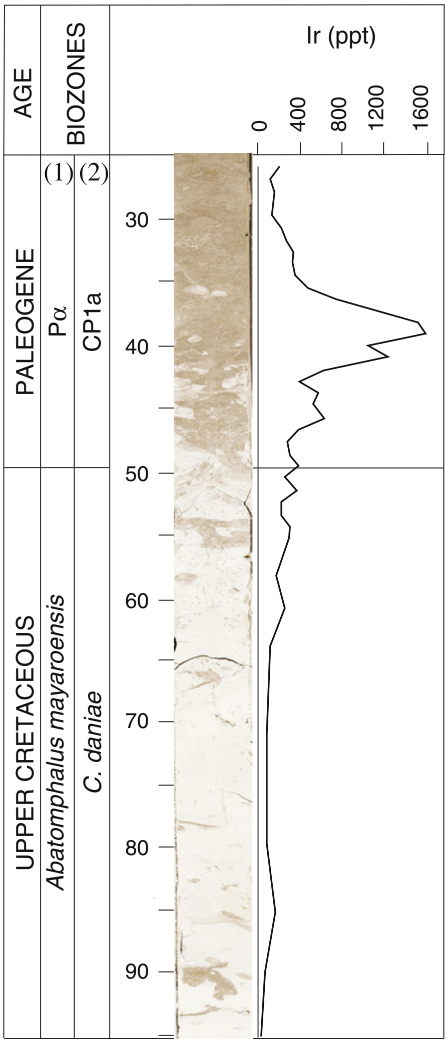


Fig. 4. Extent of bioturbation across the K/Pg boundary at ODP Site 690 (113-690C-15X-4, 25–95 cm). Burrows of white Cretaceous occur into dark brown Danian sediment and the reverse. Core photographs from Barker et al. (1988). Ir content from Michel et al. (1990). Planktic foraminiferal (1) and calcareous nannofossils (2) biozones from Stott and Kennett (1990a), Thomas et al. (1990) and Pospichal and Wise (1990).

K–Pg transition, probably at somewhat shallower depths (~1500–1600 m) than previously thought (Thomas, 1990a). Site 689, in waters 900 m shallower than Site 690 on Maud Rise, contained rare specimens of the outer neritic to upper bathyal species *Bolivinoides draco* which became extinct at the Cretaceous/Paleogene boundary (van Morkhoven et al., 1986), but this species is absent at Site 690 (Thomas, 1990b).

Assemblages show fluctuating relative abundances throughout the Maastrichtian and Danian. Upper Maastrichtian benthic foraminiferal assemblages from Site 690 are diverse and heterogeneous (Fig. 3). They contain abundant cylindrical and elongated tapered taxa, such as *Coryphostoma* spp., laevidentalinids, *Strictocostella hispidula*, *Spiroplectammina* spp. or *Tappanina eouvigeriniformis*, among others. These morphotypes, together with the trochospiral *O. umbonatus*, make up 50–69% of the assemblages in the upper Maastrichtian, and have an inferred infaunal mode of life.

Among taxa with an inferred epifaunal mode of life, trochospiral and planispiral species such as *Anomalinoides* spp., *Nuttallinella ripleyensis*, *P. hillebrandti* and *P. lunata* dominate (Fig. 2). Overall, Maastrichtian assemblages consist of mixed infaunal/epifaunal morphogroups, with slight dominance of infaunal taxa in most samples below the K/Pg boundary (Figs. 3, 5).

Representatives of the superfamily Buliminacea (as defined by Sen Gupta, 1999) make up ~7–17% of the Cretaceous assemblages. However, the group "buliminids" *sensu lato (s.l.)*, including genera of the superfamilies Buliminacea, Bolivinacea (e.g., *Bolivina*, *Bolivinoides*, *Tappanina*), Loxostomatacea (e.g., *Aragonia*), Turrilinacea (e.g., *Praebulimina*, *Stainforthia*), Fursenkoinacea (e.g., *Fursenkoina*, *Coryphostoma*), Pleurostomellacea (*Pleurostomella*), and Stilostomellacea (*Siphonodosaria*, *Stilostomella*, *Strictocostella*), among others (Sen Gupta, 1999), makes up 16–47% of the assemblages, with a peak abundance ~230 kyr before the K/Pg boundary (Fig. 5), at 251.06 mbsf, 3.1 m below the boundary (Fig. 3). This peak abundance is mainly due to peak percentages of *Coryphostoma* spp. (incl. *C. incrassata*) and *T. eouvigeriniformis* (Fig. 2).

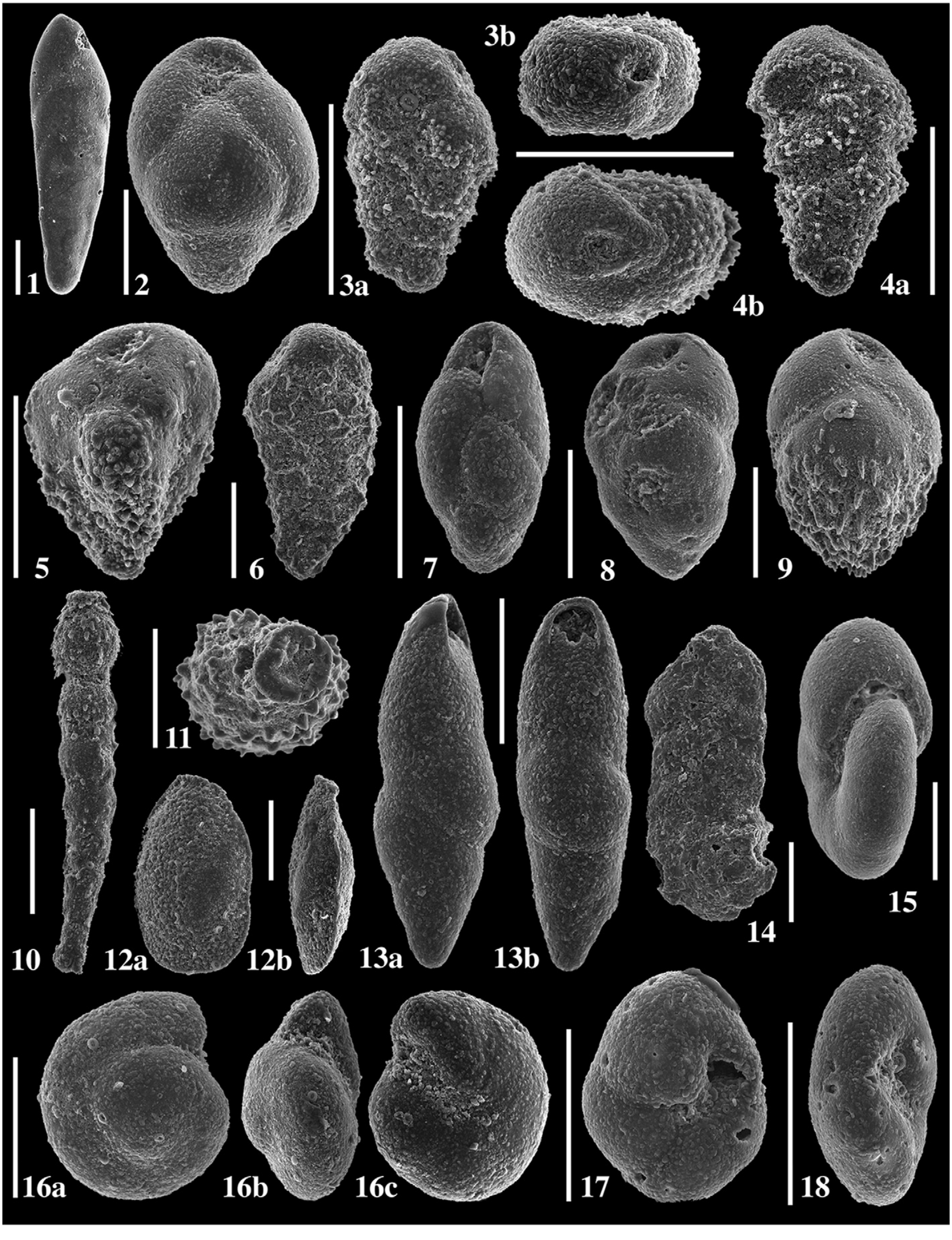
The relative abundance of the superfamily Buliminacea did not significantly change over the last 200 kyr of the Cretaceous, whereas that of buliminids *s.l.* decreased from 47% to 16–22% (Figs. 3, 5). Diversity and heterogeneity of the assemblages slightly increased toward the K/Pg boundary (except for one sample ~90 cm below the boundary). The peak in diversity indices just below the K/Pg boundary is probably related to intense bioturbation, which may have led to reworking of benthic foraminifera so that mixed Cretaceous/Paleogene assemblages are sampled, as previously documented for planktic foraminifera (Stott and Kennett, 1990a) and calcareous nannofossils (Pospichal and Wise, 1990). The Cretaceous and Paleogene assemblages are similar in species content, but the mixing caused increased evenness.

As a result of the decrease in relative abundance of buliminids *s.l.*, which have cylindrical tapered and flattened tapered tests, the percentage of infaunal morphogroups slightly decreased over this interval. BFARs fluctuate in the uppermost Cretaceous, with the lowest value at 249.97 mbsf, followed by a gradual recovery toward the K/Pg boundary (Figs. 3, 5).

A minor decrease in diversity (from 24 to 18) and heterogeneity of the assemblages (from 3.76 to 3.37), and in the percentage of infaunal morphogroups (from 55% to 44%), occurred across the K/Pg boundary (Fig. 3). BFARs fluctuate, but do not show significant changes across the boundary. BFARs show a moderate decrease later in the Danian, with minimum values recorded ~470 kyr after the boundary, but this value is not below the background values in the studied core interval, with similar BFARs recorded in the upper Maastrichtian (~340 kyr and 150 kyr before the K/Pg boundary) and the Danian (790 kyr and >1 Myr after the boundary; Fig. 5).

Assemblages show slight changes in species composition across the K/Pg (e.g., decrease in *Anomalinoides* spp. and *Spiroplectammina* spp., short-lived peaks in *Allomorphina* spp. and *Seabrookia cretacea*, and an increase in *N. ripleyensis* and *P. lunata*; Fig. 2, Suppl. Table 2). Two species, *Coryphostoma incrassata* and *P. reussi*, went extinct at or close to the K/Pg boundary globally (e.g., van Morkhoven et al., 1986; Alegret and Thomas, 2005). At Site 690, they have an uppermost occurrence within 50 cm above the K/Pg boundary, i.e., within the interval with above-background concentrations of Ir (Michel et al., 1990: Figs. 3, 4). These two species make up ~3% of the species identified in the uppermost Cretaceous (Fig. 2, Suppl. Table 2), which is a lower percentage than at other sites investigated (e.g. Alegret and

Plate I. SEM illustrations of some representative infaunal benthic foraminifera identified across the K/Pg transition at Southern Ocean Site 690. Scale bars = 100 µm. 1. *Coryphostoma incrassata* (Reuss), sample 250.54 mbsf. 2. *Praebulimina reussi* (Morrow), sample 248.03 mbsf. 3, 4. *Tappanina eouvigeriniformis* (Keller), samples 246.06 mbsf and 244.57 mbsf. 5. *Pyramidina rudita* (Cushman and Parker), sample 250.54 mbsf. 6. *Bolivinoides decoratus* (Jones), sample 240.83 mbsf. 7. *Bulimina kugleri* Cushman and Renz, sample 246.57 mbsf. 8. *Bulimina simplex* Terquem, sample 244.57 mbsf. 9. *Bulimina midwayensis* Cushman and Parker, sample 246.06 mbsf. 10, 11. *Strictocostella hispidula* (Cushman), samples 240.83 mbsf and 244.57 mbsf. 12. *Seabrookia cretacea* Pérébaskine, sample 246.06 mbsf. 13. *Pleurostomella acuta* Cushman, sample 252.42 mbsf. 14. *Spiroplectammina spectabilis* (Grzybowski), sample 246.57 mbsf. 15. *Pullenia jarvisi* Cushman, sample 244.57 mbsf. 16. *Oridorsalis umbonatus* (Reuss), sample 246.06 mbsf. 17, 18. *Allomorphina* sp., sample 251.06 mbsf.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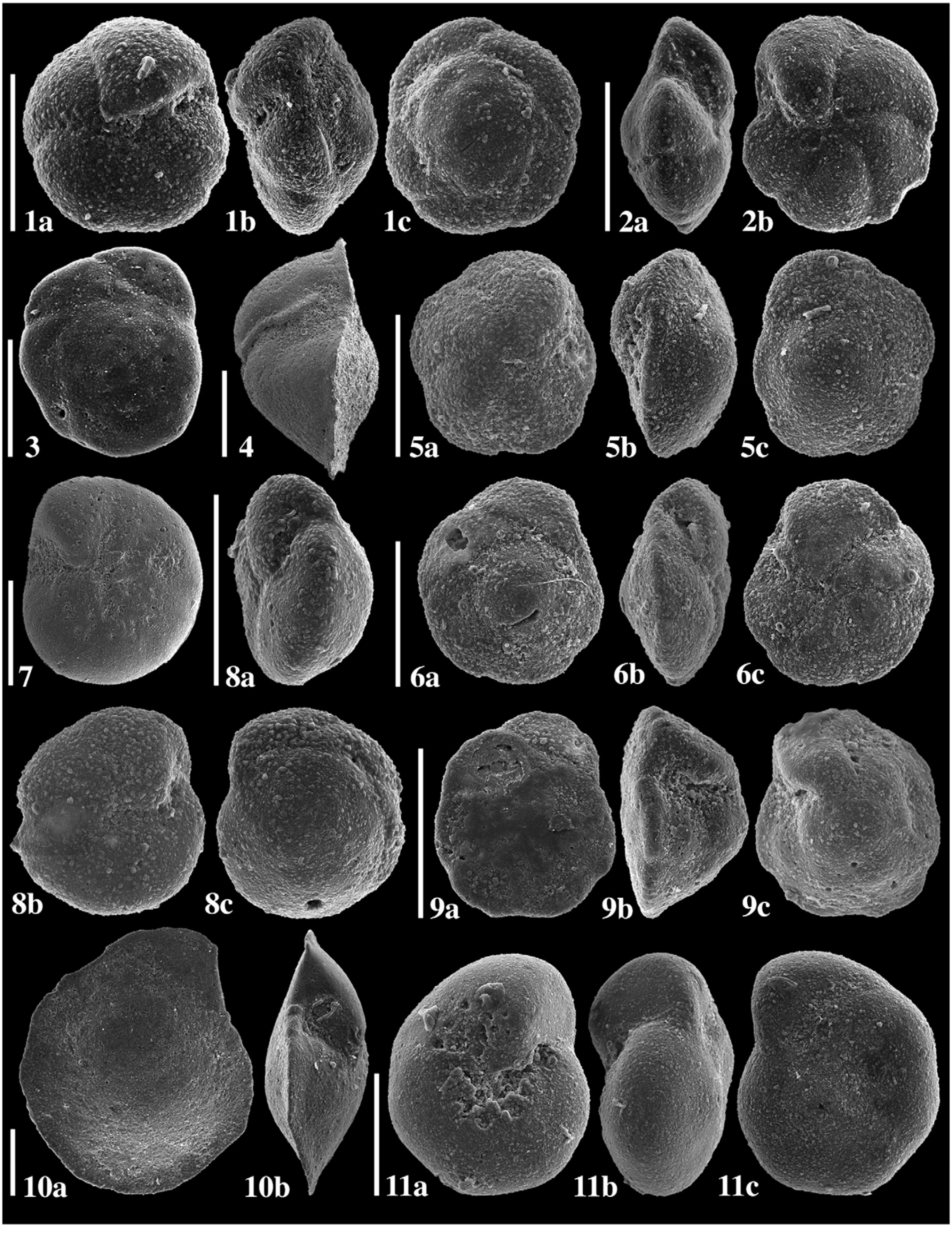
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Thomas, 2005), and lower than originally proposed by Thomas (1990a, b). For instance, *P. rudita* had been said to become extinct at the K/Pg boundary, but in our higher resolution samples we noted that it reappeared higher in the section (Lazarus taxon) (Fig. 2).

The relative abundance of several epifaunal (*N. truempyi*, *Gyroidinoides* spp., *Osangularia* spp., *N. florealis*, *C. hyphalus*, *P. hillebrandti*) and infaunal taxa (e.g., laevidentalinids, *S. hispidula*, *O. umbonatus*, *B. kugleri*, *B. simplex*, *Pleurostomella* spp.) did not change significantly across the boundary, and remained constant through the studied interval. *Anomalinoides praeacutus* was very rare in the Maastrichtian, and became common in the Danian. The relative abundance of *S. beccariiformis* and *P. lunata* is overall higher in the Danian than in the Maastrichtian, with an increase apparently starting just below the boundary, and broad peaks above. Overall, *P. lunata*, *P. hillebrandti*, *S. beccariiformis*, *N. ripleyensis*, *Anomalinoides* spp. and *T. eouvigeriniformis* dominate the lower Danian assemblages, with the latter species showing pronounced fluctuation in relative abundance. All these species except *T. eouvigeriniformis* are common in Danian sediments at many locations, including the North and South Atlantic (Alegret and Thomas, 2004, 2007) and the Pacific Ocean (Alegret and Thomas, 2005, 2009). In contrast, *T. eouvigeriniformis* has not been identified by these authors at other K–Pg boundary sites studied. This species was already present in the Cenomanian–Turonian and the Coniacian at middle latitudes of the North Atlantic (Bolli et al., 1994; Peryt and Lamolda, 1996) and Tethyan and Bohemian Cretaceous Basins (Gawor-Biedowa, 1980; Summesberger et al., 1999; Žítt et al., 2006), and may have migrated southwards to higher latitudes during Maastrichtian warming.

4. Results: stable isotope data

Benthic foraminiferal and bulk stable carbon isotope data have been discussed in Alegret et al. (2012). These two records show the widely documented collapse in δ^{13}C gradient across the K/Pg boundary, with a rapid decline in bulk data and a broad peak in benthic foraminiferal data across the boundary, the later starting about 100 kyr below the boundary, and ending about 250 kyr afterwards (Fig. 5). This broad peak in benthic foraminiferal carbon isotopes occurs globally (Westerhold et al., 2011; Alegret et al., 2012). Bulk stable carbon isotope values also increase in the uppermost Maastrichtian, so that both curves are parallel in that part of the section.

The benthic foraminiferal stable oxygen isotope record shows increasing temperatures from ~8.5 °C to 12 °C from about 400 kyr to about 200 kyr before the boundary (Fig. 5), in agreement with Kennett and Barker (1990), Stott and Kennett (1990b) and Wilf et al. (2003). Temperatures then declined over the last 200 kyr of the Maastrichtian, with strong variability possibly influenced by bioturbation, the vertical extent of which is reflected in the broad peak in the Ir concentrations (Michel et al., 1990; Figs. 3, 4). The variability occurs because the sediment has not been homogenized, but shows clearly delimited larger and smaller burrows of white Cretaceous into dark brown Danian sediment, with samples containing variable contributions (Fig. 4). Temperatures remain variable between 10 and 12 °C for the studied interval in the Danian. Bulk oxygen isotope data are generally not thought to be reliable for temperature reconstruction due to diagenetic effects, and we did not consider these.

5. Paleoenvironmental reconstruction

5.1. The uppermost Maastrichtian

Maastrichtian benthic foraminiferal assemblages consist of mixed infaunal/epifaunal morphogroups, with slight dominance of infaunal taxa in most samples (Figs. 3, 5), suggesting mesotrophic conditions at the seafloor, consistent with the high faunal density of ostracodes at nearby, shallower Site 689 (Majoran et al., 1997).

The relative abundance of the superfamily Buliminacea did not significantly change during the Maastrichtian, but buliminids *s.l.* (including *Coryphostoma* spp. and *T. eouvigeriniformis*, among others) peaked in abundance ~230 kyr before the K/Pg boundary, then declined gradually toward the boundary. The interpretation of the benthic foraminiferal turnover during the latest Maastrichtian is not straightforward, because buliminids *s.l.* and Buliminacea both have been argued to tolerate reduced oxygen concentrations, whereas a high relative abundance is thought to be mainly caused by an abundant food supply (e.g., Fontanier et al., 2002; Jorissen et al., 2007).

One might argue that the peak in relative abundance of buliminids *s.l.* (superfamilies Buliminacea, Bolivinacea, Loxostomatacea, Turrilinacea, Fursenkoinacea, Pleurostomellacea and Stilostomellacea, among others) ~230 kyr before the K/Pg boundary and their subsequent decrease indicates high trophic conditions followed by a decreased nutrient flux to the seafloor. The peak abundance, however, is not linked to a peak in BFAR, and agrees with the peak warming, whereas the decrease in buliminids occurred during a small rise in BFAR, paralleling the cooling trend of the latest Maastrichtian. We would expect that warming by itself should lead to higher food demands of benthic foraminifera due to higher metabolic rates, while remineralization of organic matter in the water column would rise due to more strongly increased metabolic rates of heterotrophs than autotrophs (O'Connor et al., 2009). In addition, increased stratification of the oceans might have led to less nutrient supply thus decreased primary productivity (e.g., Winguth et al., 2012). Overall, we thus would expect a lower food supply to the seafloor during warmer periods, everything else being equal (Norris et al., 2013).

We speculate therefore that the high abundance of buliminids may have been caused by decreased ventilation at peak warming rather than by an increased food supply, or by changing abundances of planktonic primary producers, with delivery of organic matter to the seafloor strongly dependent upon ecosystem structure (Henson et al., 2012). The genus *Chilostomella*, an indicator taxon for low oxygen conditions in the modern oceans (Jorissen et al., 2007), is very rare at Site 690, with the species *Chilostomella* cf. *oolina* present only in four samples close to 251.06 mbsf (230 kyr), coinciding with the peak in *T. eouvigeriniformis* and *Coryphostoma* spp. (Suppl. Table 2). The former species may also have been tolerant to oxygen deficiency and favored by high organic matter fluxes (Friedrich et al., 2009).

The positive shift in deep-sea benthic and planktic δ^{13}C (including bulk) values during the latest Cretaceous has been widely documented at low and high latitudes (e.g., Shackleton et al., 1984; Zachos and Arthur, 1986; Zachos et al., 1989; Westerhold et al., 2011; Alegret et al., 2012). Because this is a global change in both benthic and planktic values, it cannot have been caused by productivity changes directly, but there must have been increased storage of isotopically light carbon in the lithosphere. The increased carbon storage occurred during the period of cooling (Kennett and Stott, 1990). Such variability occurred at orbital periodicities during the Maastrichtian (Hussen et al., 2011; Westerhold et al., 2012), and a discussion is out of the range of the present paper. We argue that our data confirm evidence that there may have been orbitally-driven climatic variability in the later part of the Maastrichtian (Wilf et al., 2003), and that this variability influenced the benthic foraminiferal assemblage composition. The occurrence of such variability, however, does not necessarily imply that it must have influenced the occurrence or severity of the following mass extinction, in contrast to what has been argued by Renne et al. (2013). After all, climate variability did not increase toward the later Maastrichtian

Plate II. SEM illustrations of some representative epifaunal benthic foraminifera identified across the K/Pg transition at Southern Ocean Site 690. Scale bars = 100 μm. 1,2,3: *Nuttallinella ripleyensis* (Sandidge), samples 246.57 mbsf, 246.57 mbsf, and 240.83 mbsf. 4. *Nuttallinella florealis* (White), sample 249.47 mbsf. 5,6. *Paralabamina lunata* (Brotzen), sample 246.06 mbsf. 7,8. *Paralabamina hillebrandti* (Fisher), samples 240.83 and 244.57 mbsf. 9. *Nuttallides truempyi* (Nuttall), sample 246.06 mbsf. 10. *Osangularia velascoensis* (Cushman), sample 246.57 mbsf. 11. *Stensioeina beccariiformis* (White), sample 240.83 mbsf.

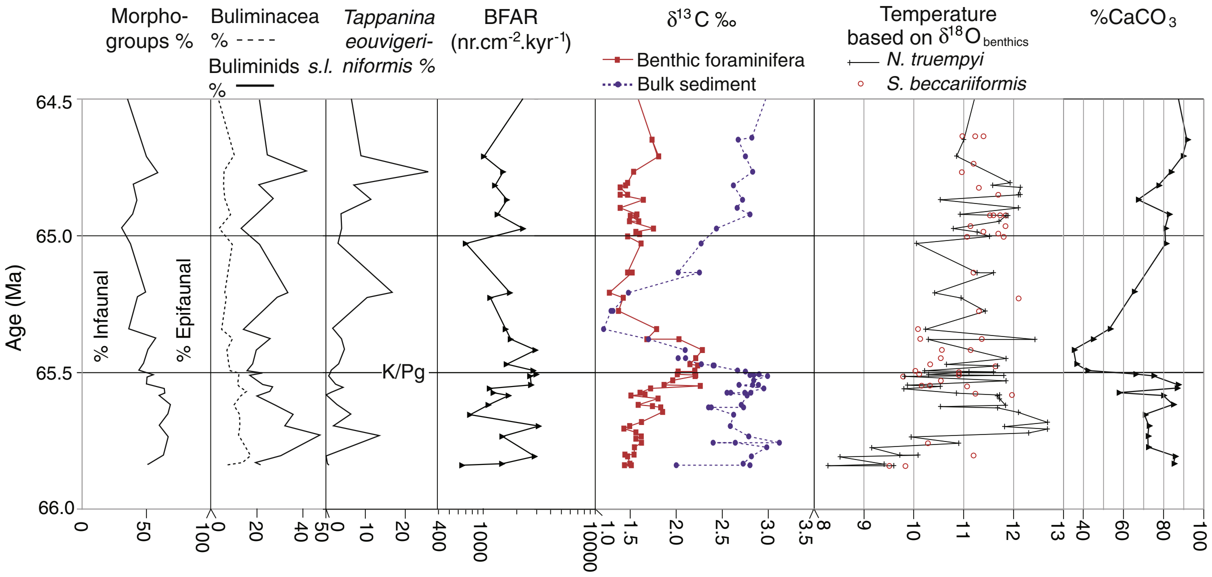

Fig. 5. Percentages of morphogroups, Superfamily Buliminacea and buliminids *s.l.*, and *Tappanina eouvigeriniformis*; benthic foraminiferal accumulation rates BFAR (nr cm^{-2} kyr^{-1}; note the logarithmic scale on the horizontal axis) as compared to benthic (*Stensioeina beccariiformis*, *Nuttallides truempyi*) and bulk δ^{13}C record, temperature based on $\delta^{18}O_{benthics}$ and %CaCO$_3$ at Hole 690C, plotted against age. BFAR and δ^{13}C data after Alegret et al. (2012). Horizontal line at 65.5 Ma indicates the K/Pg boundary.

(Hussen et al., 2011), and it seems improbable that variability that did not cause extinction during the last ~6.75 myr of the Maastrichtian did do so at the end of that stage.

5.2. Post-impact continuity of export productivity at high southern latitudes

As we argued before (Alegret et al., 2012), the lack of extinction of benthic foraminifera argues very strongly against a collapse of the food supply to the seafloor as postulated by the Strangelove Ocean and Living Ocean models (Hsü and McKenzie, 1985; d'Hondt et al., 1998), which would have caused starvation, thus significant extinction. The collapse in carbon isotope gradient thus cannot have been caused by a collapse of export productivity, and was most likely strongly influenced by the extinction of the carriers of the isotope signal, which were replaced by taxa with a lighter carbon isotope signature (Alegret et al., 2012). The severe extinction of pelagic calcifiers may have been influenced by a rapid and short acidification event linked to the asteroid impact, which was buffered before it could extend to the sea floor (Alegret et al., 2012; Hoenisch et al., 2012).

The lack of significant changes in diversity indices and in the benthic foraminiferal assemblage composition suggests a continuous food supply to the seafloor in Southern Ocean Site 690 across the K/Pg event. Low extinction rates of benthic foraminifera are characteristic for the K/Pg boundary (less than 10% of the species; Culver, 2003; Alegret and Thomas, 2005; Alegret, 2007), but at Site 690 we document the lowest extinction rates so far (3% of species).

Diversity and heterogeneity of benthic assemblages decreased globally at the K/Pg boundary, coeval with the severe extinction of many groups of calcareous plankton (e.g., Alegret and Thomas, 2005; Alegret, 2007; Alegret et al., 2012), thus showing that the deep-sea habitats were perturbed. The drop in benthic foraminiferal diversity indices and in BFAR was however, less dramatic at Southern Ocean Site 690 than at lower latitude locations (Alegret et al., 2012). This lesser disturbance of export productivity at high southern latitudes is in agreement with geochemical evidence (Hull and Norris, 2011), and evidence that export productivity may have increased in New Zealand (Hollis et al., 2003).

At Site 690, *S. beccariiformis* was rare in the Maastrichtian, then gradually became more abundant in the lower Danian, with the apparent increase in the top of the Maastrichtian probably caused by bioturbation. This species is in general more common at somewhat shallower paleodepths, including Site 689 on Maud Rise (Tjalsma and Lohmann, 1983; Thomas, 1990a,b). It may have become more abundant at greater depths after the K/Pg because a persistent high food influx allowed it to thrive at deeper, more oligotrophic sites (similar to the modern 'delta effect'; Jorissen et al., 2007), as argued by Alegret and Thomas (2009) for Pacific Ocean Site 1210. This explanation, however, does not agree with the observation that BFARs do not change significantly. One could speculate that *S. beccariiformis* may have become more abundant because of a higher input of a different type of food rather than a net increase in overall export productivity, and the same might be true for *A. praeacutus*, which is also more common at shallower depths and ranges from very scarce in the Maastrichtian to common in the Danian at Site 690.

Alternatively, however, the abundance of these taxa might have been influenced by increasing carbonate saturation in the deep oceans. The severe extinction of pelagic calcifiers resulted in a strong decline of carbonate deposition in the deep sea, as seen in the widespread occurrence of clay-rich layers, including the lowermost Danian brown clays at Site 690 with lower CaCO$_3$ wt.% (Fig. 5; Suppl. Table 3). This rapid decline of carbonate deposition was probably not balanced by declining influx in the oceans due to declining weathering rates, since the Sr and Li isotope records indicate a massive increase in influx (Martin and Macdougall, 1991; Mishra and Froelich, 2012). Such a change would have led to a strong increase in carbonate saturation of the oceans (Caldeira and Rampino, 1993; Zeebe and Westbroek, 2003; Ridgwell, 2005). That such an oversaturation indeed occurred is shown by the excellent preservation of delicate foraminifera in the lowermost Danian clay layers (as e.g. at Site 1262; Alegret and Thomas, 2007). We argue that the increased abundance of *S. beccariiformis* and other thick-walled taxa (e.g., *P. hillebrandti*, *P. lunata*) might have been caused by such changes in saturation, allowing these foraminifera to thrive at greater depths than in the Maastrichtian, as e.g., at Site 1210 (Alegret and Thomas, 2009). That these taxa were indeed sensitive to carbonate saturation is shown by their extinction during the Paleocene–Eocene Thermal Maximum (Thomas, 1990a,b; Thomas and Shackleton, 1996; Thomas, 1998; Alegret et al., 2009a,b), a time of deep-sea acidification (Zachos et al., 2005; Hoenisch et al., 2012; Foster et al., 2013).

Open-ocean nannoplankton assemblages showed lower extinction rates across the K/Pg boundary in the Southern Oceans than at lower latitudes (Jiang et al., 2010). The global extinction rate of calcareous nannoplankton, however, was >90% of species, and the higher relative survival rates of species at high southern latitudes are caused by the lower overall Maastrichtian diversity. Species common at higher latitudes (thus lower temperatures) as well as neritic species may have been more adapted to environmental variability, including variability in pH.

The post-extinction proliferation of non-carbonate photosynthesizers may account for the continuity in marine export productivity during the earliest Danian, and for the occurrence of peaks in abundance of benthic foraminiferal species (e.g., *Allomorphina* spp., *S. cretacea*, *P. lunata*) that could possibly feed on a different type of food. The occurrence of extensive plankton blooms highly variable in time and space (as e.g. seen in diatom blooms in New Zealand; Hollis et al., 2003) may explain the global variability of the benthic foraminiferal turnover after the K/Pg boundary (Alegret et al., 2012).

A discussion of the longer-term (several 10^5 years) evolution of the biota, as potentially modulated by orbital scale environmental variability as seen expressed in carbon isotope values (Westerhold et al., 2008, 2011) is outside the range of this paper, but we note that prominent peaks in the species *T. eouvigeriniformis* occurred through the studied interval in the Maastrichtian and Danian. Its highest percentages coincided with lowest δ^{13}C values in benthic foraminifera, supporting the idea that this species may have proliferated during periods of high organic matter flux to the seafloor. Specifically, the interval of lowest δ^{13}C in both bulk and benthic foraminifera occurred at about 250 kyr after the K/Pg boundary, the time of a potential hyperthermal event (Dan C2; Quillevere et al., 2008; Coccioni et al., 2010), although interpretation of this event as a hyperthermal is still debated (Westerhold et al., 2011).

6. Conclusions

1. Deep-sea benthic foraminifera at Southern Ocean Site 690 show the lowest rates of extinction globally (<3% as compared to <~10%) across the K/Pg boundary, and also the lowest rate of environmental disturbance in terms of food flux to the sea floor.
2. Benthic foraminiferal assemblages fluctuated in composition during Maastrichtian climate fluctuations, but assemblage fluctuations do not appear to be forerunner events of the end Cretaceous benthic faunal turnover coeval with the mass extinction of planktic foraminifera.
3. Faunal composition during the Danian may have been influenced by a combination of changes in food flux and increasing carbonate saturation due to extinction of pelagic calcifiers, with some heavily calcified benthic species increasing in abundance as well as moving into deeper waters. These species (e.g. *S. beccariiformis*, *P. lunata*) became extinct during the deep-sea acidification at the end of the Paleocene 10 million years later.

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