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Extinction and food at the seafloor: A high-resolution benthic foraminiferal record across the Initial Eocene Thermal Maximum, Southern Ocean Site 690

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ABSTRACT

A mass extinction of deep-sea benthic foraminifera has been documented globally, coeval with the negative carbon isotope excursion (CIE) at the Paleocene-Eocene boundary, which was probably caused by dissociation of methane hydrate. A detailed record of benthic foraminiferal faunal change over ~30 k.y. across the carbon isotopic excursion at Ocean Drilling Program Site 690 (Southern Ocean) shows that shortly before the CIE absolute benthic foraminiferal abundance at that site started to increase. “Doomed species” began to decrease in abundance at the CIE, and became smaller and more thin-walled. The main phase of extinction postdated the CIE by a few thousand years. After the extinction faunas were dominated by small species, which resemble opportunistic taxa under high-productivity regions in the present oceans. Calcareous nannofossils (primary producers), however, show a transition to more oligotrophic nannofloras exactly where the benthic faunas show the opposite. Plankton and benthos is thus decoupled. Possibly, a larger fraction of food particles reached the seafloor after the CIE, so that food for benthos increased although productivity declined. Enhanced organic preservation might have resulted from low-oxygen conditions caused by oxidation of methane. Alternatively, and speculatively, there was a food-source at the ocean-floor. Benthic foraminifera dominating the post-extinction fauna resemble living species that symbiotically use chemosynthetic bacteria at cold seeps. During increased, diffuse methane escape from hydrates, sulfate-reducing bacteria could have produced sulfide used by chemosynthetic bacteria, which in turn were used by the benthic foraminifera, causing extinction by a change in food supply.

INTRODUCTION

A major extinction of deep-sea benthic foraminifera in open ocean occurred at the Paleocene-Eocene boundary (as defined recently, Luterbacher et al., 2000), with 35%–50% of deep-sea species becoming extinct (e.g., Thomas, 1990, 1998; Pak and Miller, 1992; Coccioni et al., 1994; Katz et al., 1999). At this

time, many long-lived bathyal to upper abyssal species, which had been in existence from the Maastrichtian or Campanian, became extinct within ~10,000 yr, as observed at locations where precise correlation is available (e.g., Thomas, 1998). Rapid extinction of many deep-sea benthic foraminiferal species at the same time is very unusual in earth history, and most faunal changes of deep-sea faunas occur gradually, over hundreds of

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thousands to a few million years (e.g., Thomas, 1992). The Maastrichtian-Paleocene bathyal and abyssal benthic foraminiferal faunas were globally rather uniform although relative abundances varied geographically (e.g., Widmark and Speijer, 1997), and had such common constituent species as *Stensioeina beccariiformis*, *Pullenia coryelli*, *Alabamina creta*, *Clavulinoides paleocenica*, *Clavulinoides havanensis*, *Gyroidinoides globosus*, *Paralabamina hillebrandti* and *Paralabamina lunata*.

The extinction has been recognized at many bathyal through upper abyssal sites worldwide (see review in Thomas, 1998). At lower abyssal depths below the Calcium carbonate Compensation Depth (CCD), agglutinated foraminiferal faunas show a probably coeval change in faunal composition although no major faunal turnover occurred (e.g., Kaminski et al., 1996; Galeotti et al., 2003). In agglutinated assemblages, the counterpart of the post-extinction faunas in calcium carbonate foraminifera is the "*Glomospira* assemblage," which has been recognized in lower Eocene sediments over a large area in the North Atlantic and western Tethys. Lesser extinctions or temporary changes in benthic foraminiferal faunal composition occurred in marginal and epicontinental basins (e.g., Speijer and Schmitz, 1998; Stupin and Muzylöv, 2001; Speijer and Wagner, 2002).

The extinction was coeval with rapid global warming and a negative excursion of at least 2.5‰ in $\delta^{13}\text{C}$ values in the oceanic and atmospheric carbon reservoirs (Kennett and Stott, 1991; Pak and Miller, 1992; Kaiho et al., 1996; Thomas and Shackleton, 1996; Koch et al., 1992, 1995; Stott et al., 1996; Fricke et al., 1998; Bowen et al., 2001). This carbon isotope excursion started rapidly, over less and possibly considerably <10,000 yr, with carbon isotope values returning to background in several hundred thousand years (Katz et al., 1999; Norris and Röhl, 1999; Röhl et al., 2000, this volume; Cramer, 2001). These authors documented that the initiation of the carbon isotope excursion (CIE) occurred over a period shorter than one precessional cycle.

The cause of the CIE probably was a rapid dissociation of sedimentary methane hydrates (e.g., Dickens et al., 1995; Dickens, 2000, 2001a), possibly in several steps (Bains et al., 1999). The cause of the dissociation is not clear, and might have been rapid warming of the intermediate ocean waters as a result of changing oceanic circulation patterns (e.g., Kennett and Stott, 1991; Kaiho et al., 1996; Thomas et al., 2000; Zachos et al., 2001; Dickens, 2001a; Bice and Marotzke, 2002), continental slope failure as the result of increased current strength in the North Atlantic Ocean (Katz et al., 1999, 2001), sea-level lowering (Speijer and Morse, 2002), the impact of a comet (Kent et al., 2001) or other extraterrestrial body (Dolenec et al., 2000), or a combination of several of these factors.

In the deep-sea, post-extinction faunas of carbonate foraminifera are mainly dominated by small individuals, with thin walls, and carbonate-cemented agglutinants are absent (e.g., Thomas, 1998). These faunas are low-diversity as compared with pre-extinction assemblages, in species richness as well as in such measures as alpha-diversity and rarefied number of species, because they are strongly dominated by few species.

These post-extinction faunas were considerably more variable from site to site than the pre-extinction faunas, being at some sites (many in the South Atlantic) dominated by the oligotrophic indicator *Nuttallides truempyi* and possibly abyssaminids, at others by common eutrophic or low-oxygen indicators such as buliminid species (Thomas, 1998; Thomas and Röhl, 2002).

In marginal regions such as the Tethys and northeastern Peri-Tethys, faunal changes including extinction have been linked to low-oxygen conditions resulting from local high primary productivity of noncarbonate primary producers, as shown by the occurrence of the extinction at the base of laminated, dark-brown to black sediments with high concentrations of organic matter (Gavrilov et al., 1997, this volume; Stupin and Muzylöv, 2001; Speijer and Wagner, 2002). In these regions, faunal as well as geochemical evidence (Schmitz et al., 1997; Gavrilov et al., this volume) supports the theory that high productivity was the major cause of anoxia and extinction, possibly exacerbated by stratification of the water column and low ventilation. High productivity may also have occurred in shallow waters along the northeastern seaboard of America (Gibson et al., 1993). In an upper-middle bathyal section in New Zealand, laminated dark shales are slightly enriched in organic carbon; although surface productivity may have been high, benthic foraminiferal productivity dropped strongly at the extinction event, probably as the result of low-oxygen conditions (Kaiho et al., 1996).

In the open ocean, in contrast, the exact causes of the extinction are not so clear, although the extinction was more severe than in marginal basins. In land sections representing bathyal-abyssal depths (e.g., Spain, Coccioni et al., 1994; Ortiz, 1995) the benthic extinction commonly occurred in an interval with strong carbonate dissolution. Post-extinction faunas thus are enriched in agglutinated species, followed by faunas rich in thin-walled, small specimens of the oligotrophic indicator species *N. truempyi*. In some open-ocean sites (e.g., Site 999 in the Caribbean, and Sites 525 and 527 on Walvis Ridge, South Atlantic; site 929, Ceara Rise), there also is an interval of strong carbonate dissolution, where dark clays are not enriched in organic matter, and where neither benthic foraminifera nor planktonic organisms indicate high productivity (Thomas and Shackleton, 1996; D. Thomas et al., 1999; Thomas and Röhl, 2002).

At other locations (equatorial Pacific Site 865, Southern Ocean Sites 689, 690) there are sediment color variations (see Cramer, 2001), and variations in carbonate percentage (D. Thomas et al., 1999), but the percentage carbonate does not fall below ~65%. At these three sites, deep-sea benthic foraminiferal faunas suggestive of a high food supply or low oxygen levels cooccur with planktic foraminiferal and nannofossil assemblages indicative of low productivity (e.g., Thomas, 1998).

The benthic foraminiferal extinction occurred during a time characterized in general by decreasing oceanic productivity, after a high in productivity in the middle Paleocene (Aubry, 1998; Boersma et al., 1998; Corfield and Norris, 1998). Trace element (Ba) data from the Initial Eocene Thermal Maximum, however,

have been interpreted as indicative of increased productivity in open ocean at such locations as Site 690 (Bains et al., 2000).

Possible causes of the benthic extinction event (BEE) at bathyal-abyssal depths in open ocean thus include low oxygenation, either as a result of increased deep sea temperatures or as a result of oxidation of methane in the water column, increased corrosivity of the waters for CaCO_3 as a result of methane oxidation, increased temperatures, globally increased or decreased productivity, locally increased and/or decreased productivity as a result of an expansion of the trophic resource continuum, or a combination of several of these factors (e.g., Boersma et al., 1998; Thomas, 1998; Thomas et al., 2000).

In this paper, the question of the cause(s) of the benthic foraminiferal extinction is addressed by a high-resolution study of benthic foraminifera at Ocean Drilling Program Site 690, which has been intensively studied for many parameters (e.g., Kennett and Stott, 1991; Thomas, 1990; Thomas and Shackleton, 1996; Thomas et al., 2000; Bains et al., 1999, 2000; Norris and Röhl, 1999; Röhl et al., 2000; Cramer, 2001; Bralower, 2002; D. Thomas et al., 2002). I intend to document the relative abundances of benthic foraminiferal species across the extinction in detail, and compare the benthic foraminiferal data with data on calcareous nannoplankton (Bralower, 2002) and geochemical data (Bains et al., 1999, 2000). Comparison of data on surface primary producers and bottom dwellers might help in trying to understand whether we have sufficient information to deduce whether productivity changed, and if it changed, whether it decreased or increased.

METHODS

Site 690 was drilled on Maud Rise, an aseismic ridge at the eastern entrance of the Weddell Sea in the Atlantic sector of the Southern Ocean ($65^{\circ}9.629'S$, $1^{\circ}12.296'E$), at a present water depth of 2914 m, paleodepth during the Paleocene-Eocene $\sim 1900\text{--}2000$ m (Thomas, 1990). Site 690 is on the southwestern flank of this ridge. A continuous U-channel sample was collected from the archive half of Core 690B-19H, over the interval between 690B-19H-3, 50 cm to -121.5 cm (Bralower, 2002; D. Thomas et al., 2002). The U-channel was sectioned into 1 cm samples, which were processed (dried and sieved) at the University of North Carolina. The fraction $>63\ \mu$ was used for the benthic foraminiferal study, from the interval between 690B-19H-3, 51–52 cm, and 690B-19H-3, 84–85 cm (170.42 and 170.75 mbsf), corresponding to $\sim 31,000$ yr in the time scale of Röhl et al. (2000), but less so in that by Cramer (2001).

In the samples located above the level of the benthic foraminiferal extinction, many specimens are small. The abundant specimens of biserial and triserial, small taxa may be washed through the sieve with $63\ \mu$ (230 mesh) openings and thus may be lost (see, for example, Thomas, 1985). It is therefore possible that samples washed more vigorously than others could have fewer of such specimens than other samples. Washing of the samples was not standardized, but the sediments were not strongly in-

durated, and have a very similar degree of induration over the short studied interval, so that the washing process was similar for all samples. This thus probably did not have a major effect on the observations on benthic foraminifera, especially because the samples with dominant small specimens were much richer in numbers of foraminifera than samples with larger specimens, suggesting that these faunas were not largely lost in sieving.

Benthic foraminifera were picked from 24 samples, at 1- or 2-cm intervals (Table DR1¹). All samples contained sufficient specimens for study. Between 250 and 400 individuals were picked from a split of the samples (Table DR1). The weight of the sample split from which foraminifera were picked was determined, so that the number of foraminifera per gram of sediment ($>63\ \mu$) could be determined. Taxonomy follows Thomas (1990) and Thomas and Shackleton (1996), but modified in the use of generic names after Alegret and Thomas (2001) and as discussed in Appendix 1. In addition, species formerly classified in the genus *Stilostomella* now are placed in *Siphonodosaria* and *Mylostomella*, following Hayward (2002).

In order to estimate diversity, the species richness numbers were rarified following Sanders (1968), so that the number of species per 100 individuals was estimated.

RESULTS

The high-resolution data confirm that the benthic foraminiferal extinction event (BEE) occurred rapidly, over a few cm of sediment, with a rapid loss of diversity, extinction of species locally that also became extinct globally, and a change toward a strongly increased relative and absolute abundance of species from the Superfamily Buliminacea, generally thought to indicate a high food supply to the sediment and/or low-oxygen conditions (Figs. 1–4). At this high resolution, however, the BEE shows a more complex structure than earlier documented (Thomas, 1990; Thomas and Shackleton, 1996).

The sharp decline in species diversity occurred at 170.60 mbsf, slightly above the largest decrease in bulk sediment $\delta^{13}\text{C}$ at 170.63 mbsf (Bains et al., 1999). The species that became extinct at the event, however (e.g., *Stensioeina beccariiiformis*; several calcareous agglutinated species such as *Clavulinoides havanensis*, *C. aspera*, *Paralabamina hillebrandti*, *P. lunata*, *Pullenia coryelli*) drastically declined in abundance exactly at the level of the initiation of the CIE at 170.63 mbsf (Figs. 1A, B). At this level these “extinction species” or “doomed species” decreased in test size, and between 170.63 and 170.60 mbsf they are represented by unusually small, thin-walled specimens only. There are a few large specimens of the “extinction species” present higher in the section, but all these specimens (marked with * in Table DR1) show signs of reworking: They are badly pre-

¹GSA Data Repository item 2003051, Table DR1, is available on request from Documents Secretary, GSA, P.O. Box 9140, Boulder, CO 80301-9140, USA, editing@geosociety.org, or at www.geosociety.org/pubs/ft2003.htm.

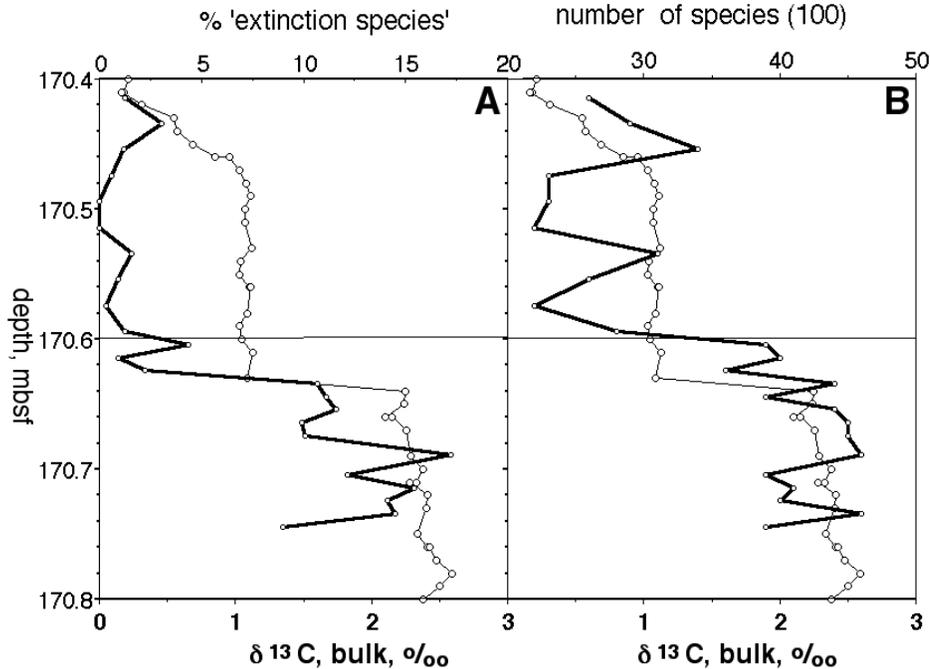


Figure 1. A: Percentage “extinction species” (*Stensioeina beccariformis*, *Paralabamina* spp., *Clavulinoides* spp., *Alabama creta*, *Pullenia coryelli*) shown by thick line, plotted over $\delta^{13}\text{C}$ in bulk sediment (Bains et al., 1999), shown in thin line with open circles. Horizontal line indicates the level of the main phase of benthic foraminiferal extinction. B: Number of species normalized to 100 specimens (rarefied, Sanders, 1968) shown by thick line, plotted over $\delta^{13}\text{C}$ in bulk sediment (Bains et al., 1999), shown in the thin line with open circles. Horizontal line indicates the level of the main phase of benthic foraminiferal extinction.

served, abraded, and riddled with fungal borings. Several were analyzed for carbon isotopes, and had pre-extinction values (Thomas and Shackleton, 1996).

At the BEE the species composition of the assemblages changed considerably at Site 690 (Thomas and Shackleton, 1996; Thomas, 1998), with a strong increase in relative abundance of species of the buliminid group (“infaunal species” in

Thomas, 1990). These species morphologically resemble species that presently live infaunally, and are common in regions with a high, continuous food supply to the sediment, and/or where low-oxygen conditions may prevail (e.g., Sen Gupta and Machain-Castillo, 1993; Alve, 1995; Bernhard, 1996; Bernhard and Sen Gupta, 1999; Gooday and Rathburn, 1999; van der Zwaan et al., 1999; Gooday, 2002).

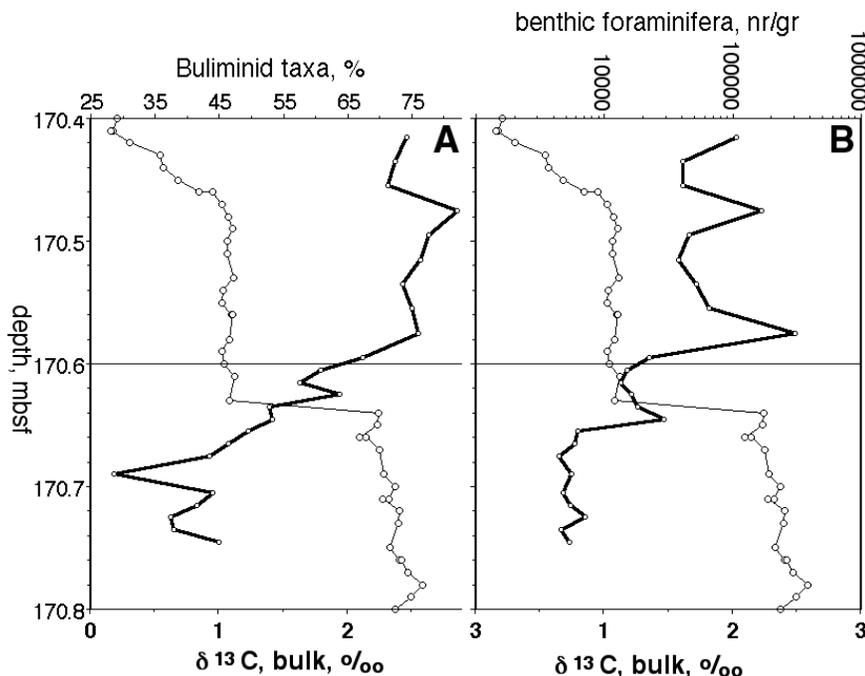


Figure 2. A: Percentage of buliminid taxa (*Bolivinoidea* spp., *Bulimina* spp., *Buliminella beaumonti*, *Fursenkoina* spp., *Rectobulimina carpentierae*, *Siphogenerinoides* spp., *Tappanina selmensis* and *Turrilina brevispira*) shown by the thick line, plotted over $\delta^{13}\text{C}$ in bulk sediment (Bains et al., 1999), shown in the thin line with open circles. Horizontal line indicates the level of the main phase of benthic foraminiferal extinction. B: Number of benthic foraminifera per gram of sediment $>63\ \mu$, shown in thick line, plotted over $\delta^{13}\text{C}$ in bulk sediment (Bains et al., 1999), shown in the thin line with open circles. Horizontal line indicates the level of the main phase of benthic foraminiferal extinction.

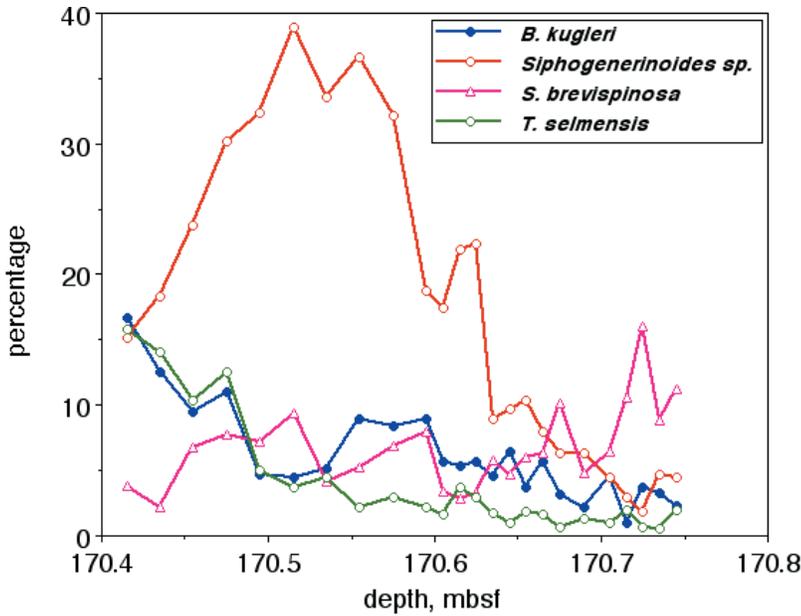


Figure 3. Relative abundances of common small, buliminid taxa.

This increased relative abundance of buliminid taxa after the BEE remains a feature in this high-resolution study (Fig. 2B), but the increase occurred gradually over the short distance between ~170.69 and 170.58 mbsf, and was not instantaneous. Another foraminiferal proxy that may indicate an increased supply of food to the benthic fauna is the absolute abundance of benthic foraminifera (nr/gr; Figure 2B) (Herguera and Berger, 1991; Jorissen et al., 1995), although this proxy may not be applicable under low-oxygen conditions (e.g., Den Dulk et al., 2000). This

parameter (plotted on a logarithmic scale) shows a first rapid increase at 170.65 mbsf, just below the CIE. At equatorial Pacific Site 865 the absolute abundance of benthic foraminifera also increased after the BEE, but total numbers of benthic foraminifera per gram are lower by an order of magnitude at that site as compared to Site 690 (Thomas, 1998). I cannot say whether the total benthic foraminiferal biomass increased, however, because the abundant benthic foraminifera after the extinction are so much smaller than the common pre-extinction species that the

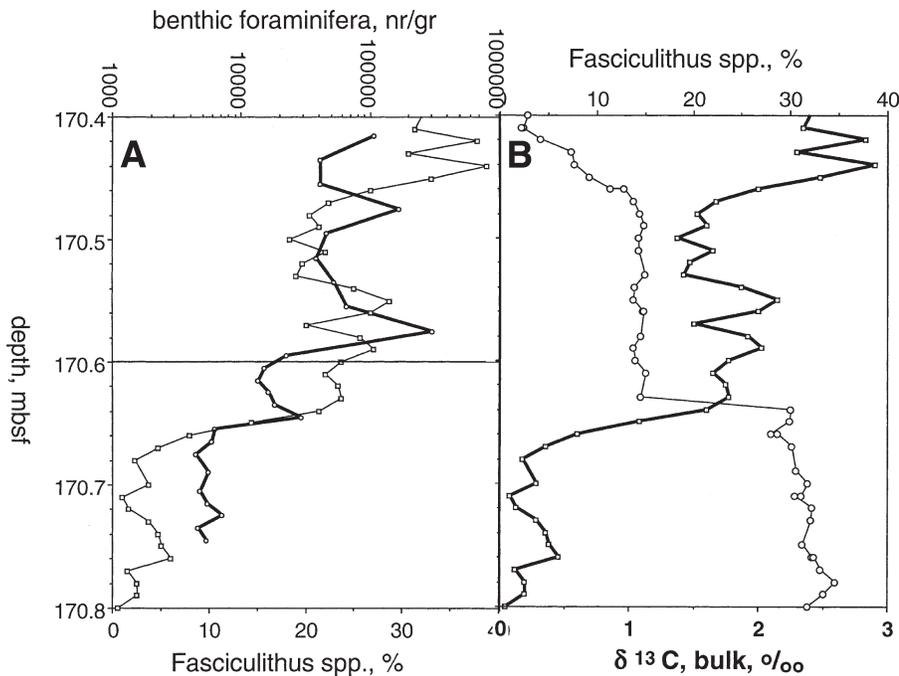


Figure 4. A: Number of benthic foraminifera per gram of sediment >63 μ, shown by the thick line, plotted over the percentage of *Fasciculithus* spp. in the calcareous nannofossil assemblage (Bralower, 2002), shown in the thin line with open circles. Horizontal line indicates the level of the main phase of benthic foraminiferal extinction. B: Percentage of *Fasciculithus* spp. in the calcareous nannofossil assemblage (Bralower, 2002), shown by the thick line, plotted over δ¹³C in bulk sediment (Bains et al., 1999), shown in the thin line with open circles.

increased numbers may be balanced by the decreased size per individual. Note that the overall increase in numbers of foraminifera per gram combined with the increased relative abundance of buliminid taxa means that buliminids increased in numbers very strongly.

The taxa that are responsible for this increase in relative abundance of buliminids as well as the increased numbers of benthic foraminifera are somewhat different in this high-resolution report (Table DR1) than was documented earlier (Thomas, 1990; Thomas and Shackleton, 1996). These authors documented that abundant post-extinction taxa were mainly *Tappanina selmensis* and several small *Bolivinoidea* and *Bulimina* species, including *Bulimina ovula* (now called *Bulimina kugleri*, see Appendix 1), followed by a short-lived increase in the relative abundance of *Aragonia aragonensis*. These species, however, begin their increase higher in the section, just above the interval studied here, as can be seen by their increasing abundance at the top of the studied interval (Fig. 3).

Between 170.63 mbsf and 170.45 mbsf, directly before and after the extinction, the faunas are dominated by a small taxon called *Siphogenerinoides* sp. (Plate 1; Appendix 1). This taxon is somewhat more flattened in overall test shape than the species *S. brevispinosa*. Both *S. brevispinosa* and *Siphogenerinoides* sp. are small species (diameter of ~20–40 μ , length ~100–150 μ), with *S. brevispinosa* in the lower part of that range in the post-extinction interval.

Siphogenerinoides sp. may be an ecophenotype present only in samples deposited during the unusual circumstances just before and after the extinction, similar to the occurrence of short-lived planktic taxa (Kelly et al., 1996). Other benthic foraminiferal species show similar morphological changes in populations after an extinction, such as across middle Cretaceous Oceanic Anoxic Event OAE1b (Holbourn et al., 2001).

At the BEE, the benthic foraminiferal faunas at Site 690 changed from highly diverse faunas with a rather equal distribution of specimens over species to a much less diverse fauna dominated by a few taxa (Figs. 1A, 1B). The pre-extinction faunas had common large, heavily calcified species with many chambered-tests. Such individuals were probably long-lived, and the assemblages can be interpreted as typical highly diversified faunas containing many specialist species (e.g., Valentine, 1973; Hallock, 1987). Such faunas, dominated by K-mode, specialist taxa, are common in oligotrophic regions (e.g., Boersma et al., 1998; Bralower, 2002).

In stark contrast, the post-extinction faunas are dominated by few species, for a short interval *Siphogenerinoides* sp., and all species are very small (<125 μ), consisting of few chambers (10–12 or fewer, in the case of *S. brevispinosa* and *Siphogenerinoides* sp.). Such faunas are usually common in regions with rapidly varying or disturbed environments, which are more eutrophic and more food is supplied to the benthos (e.g., Valentine, 1973; Hallock et al., 1991; Alve, 1995; Boersma et al., 1998; Bernhard and Sen Gupta, 1999). The overall appearance of the BEE at Site 690 is thus that of a diverse, oligotrophic community

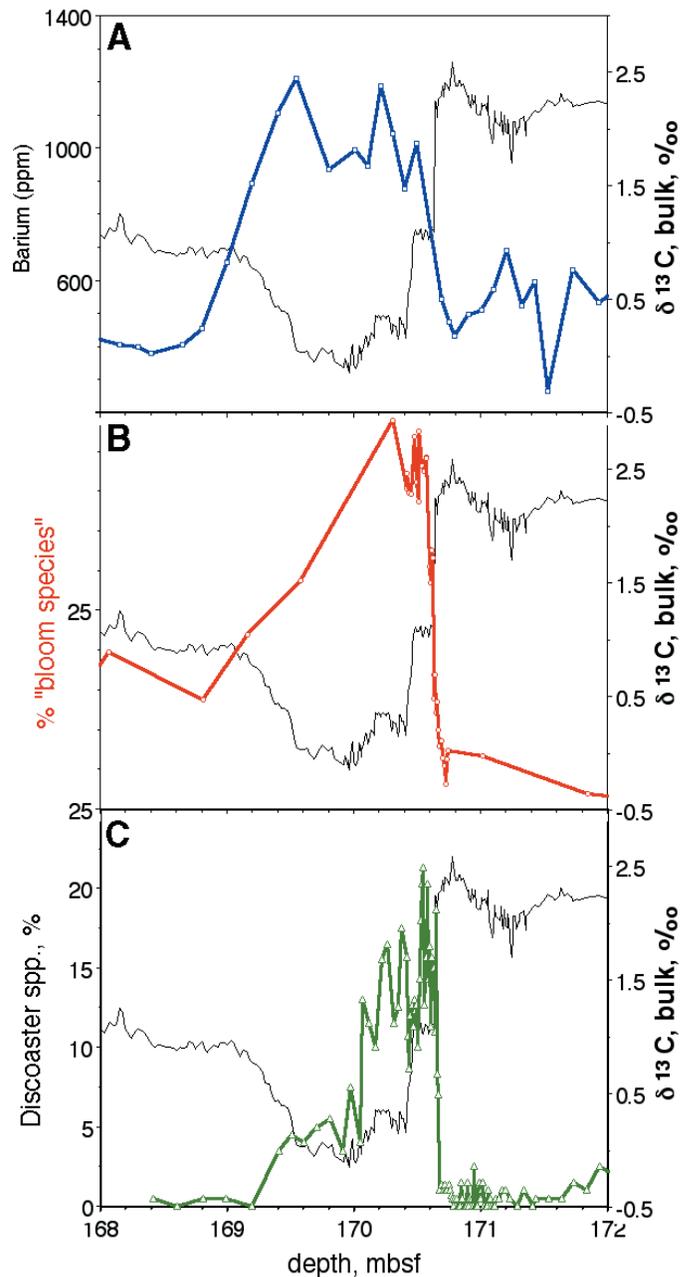


Figure 5. A: Ba content of the bulk sediment (in ppm) (Bains et al., 2000) shown in the thick line, plotted over the $\delta^{13}\text{C}$ in bulk sediment (Bains et al., 1999), shown in the thin line. B: Percentage of benthic foraminiferal opportunistic or "bloom" species (*Siphogenerinoides* spp., *Tappanina selmensis*) shown by the thick line (this paper; Thomas and Shackleton, 1996) plotted over the $\delta^{13}\text{C}$ in bulk sediment (Bains et al., 1999), shown in the thin line. C: Percentage of *Discoaster* spp. in the calcareous nannoplankton assemblage (Bralower, 2002) shown in the thick line, plotted over the $\delta^{13}\text{C}$ in bulk sediment (Bains et al., 1999), shown in the thin line. Note that the scale for this figure differs from that in Figures 1–4, and covers the full extent of the carbon isotope excursion.

with highly specialized, K-selected species, which was disturbed and replaced by an opportunistic group of r-selected taxa, reflecting a larger food input to the benthos, as documented by the increased percentage of buliminid taxa as well as by the increase of absolute abundance of benthic foraminifera (Figs. 2A, 2B).

The increase in numbers of benthic foraminifera per gram at 170.65 mbsf coincided with a change in the calcareous nannoplankton, as exemplified by the increased abundance of *Fasciculithus* spp. and *Discoaster* spp. (Figs. 4, 5). The relative abundances of these taxa are shown as an example of floral change involving the complete nannoplankton community (Bralower, 2002). These floral changes reflect a change from more eutrophic, cool-water floras with dominant r-selected taxa to more warm-water floras dominated by various more oligotrophic, K-selected taxa such as *Discoaster* spp. and *Fasciculithus* spp. (Bralower, 2002). In benthic foraminifera, faunas changed at the same time from dominated by K-selected taxa to dominated by r-selected taxa, the reverse pattern.

This change in nannoplankton floras occurred slightly below the CIE, and at the same depth as the increased abundance of benthic foraminifera (Figs. 4A, 4B). There is thus a major discrepancy between the environmental implications of the observed floral change in the pelagic primary producers (calcareous nannoplankton) which indicates decreased productivity after the CIE, and the deep-sea benthos, which presumably received its food from the primary producers, and indicates an increase in food supply. A similar discrepancy was observed at equatorial Pacific Site 865 (Kelly et al., 1996; Thomas et al., 2000).

The apparent increased productivity indicated by the benthic foraminiferal assemblage composition (specifically the relative abundance of the “bloom” species *Siphogenerinoides* spp., *Aragonia aragonensis* and *Tappanina selmensis*) lasted for longer than the interval studied here, and remained throughout the CIE interval estimated to last ~220 k.y. (Röhl et al., 2000), as did the enhanced Ba-levels interpreted as indicating enhanced productivity (Bains et al., 2000), and the nannoplankton indicating decreased surface primary productivity (Bralower, 2002) (Figs. 5A–C). There is no information available on the quantitative nannoplankton floral assemblage or trace element composition from longer sections at Site 690, but the relative abundance of the “bloom species” of benthic foraminifera shows strong fluctuations within the whole interval between ~61.5 and 49 Ma, roughly corresponding to the late Paleocene through early Eocene (Berggren et al., 1995) (Fig. 6). At equatorial Pacific Site 865 these species have a similar distribution in time.

DISCUSSION

Sequence of events

The benthic foraminiferal data, trace element data (Bains et al., 2000), nannofossil data (Bralower, 2002) and stable isotope data (D. Thomas et al., 2001) show considerable fluctuations at depth scales of a few cm. This is strong evidence that the record has not been fully homogenized by bioturbation on such scales,

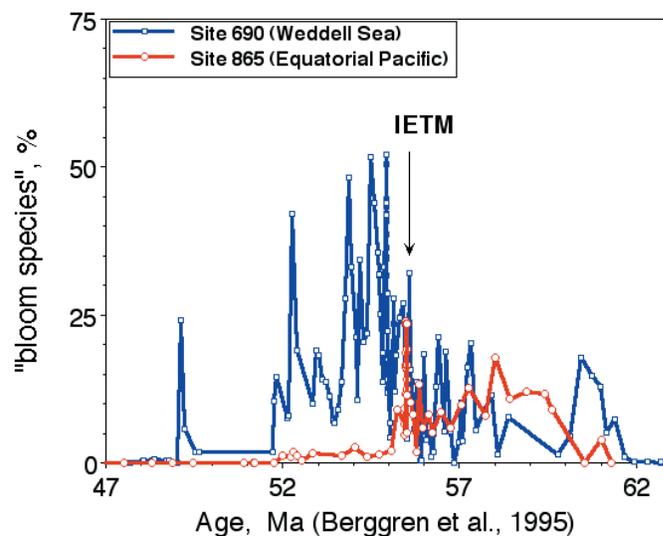


Figure 6. Percentage of bloom species (*Siphogenerinoides* spp., *Aragonia aragonensis*, and *Tappanina selmensis*) at Ocean Drilling Program Site 690 (Weddell Sea) and Site 865 (equatorial Pacific Ocean) plotted versus numerical time (Berggren et al., 1995). IETM—Initial Eocene Thermal Maximum.

although individual benthic foraminifera and their isotopic signatures indicate that reworking must have occurred (Table DR1). In Pleistocene-Holocene sediment, sediment components in the size range >150 μ (such as foraminifera) are bioturbated differently from fine (<5 μ) components such as calcareous nannoplankton, as seen in different radiocarbon dates of fine fraction and foraminifera while sedimentation rates derived from the two different data sets are the same (Thompson et al., 1995). High-resolution isotope data on planktic foraminifera in the same samples as studied for benthic foraminifera show the CIE in planktic foraminifera 8 cm below the CIE in bulk sediment (Bains et al., 1999; D. Thomas et al., 2002). This offset thus might at least in part be explained by differential bioturbation.

At Site 690, the comparison of the nannofossil and foraminiferal carbon isotope records becomes even more difficult because the nannofloras show such a large change in floral composition. Different species of nannoplankton vary in isotopic signature, and a change in bulk $\delta^{13}\text{C}$ composition due to changes in nannoplankton floral composition may thus be superimposed on the isotope excursion resulting from gas hydrate dissociation (Bralower, 2002). It is thus not so simple to compare global events in the carbon cycle with local events in benthic foraminifera, and with events in nannoplankton, which has a different size and thus a different pattern of bioturbation, even when all these are studied in the same samples. The pattern may become even more complex because many foraminiferal species, and especially buliminid taxa, live at least a few cm in the sediments (e.g., Jorissen et al., 1995). The increase in relative abundance of small buliminid taxa a few cm somewhat below the CIE may thus have resulted from this infaunal life style.

At exactly the level in the sediment where the rapid, large decrease in bulk $\delta^{13}\text{C}$ occurs (Bains et al., 1999), however, the relative abundance of the “doomed species,” as well as their size and wall thickness decreased, while there was a further increase in the relative abundance of small “bloom species,” especially *Siphogenerinoides* sp. (Figs. 1, 2). About 2.5 cm above the decrease in bulk $\delta^{13}\text{C}$ the final extinction of “doomed species” occurred (all specimens at higher levels that were analyzed showed pre-excursion carbon isotope values), as well as a drop in species richness and evenness of distribution. These data thus might be interpreted as suggesting that at the time of the large change in bulk $\delta^{13}\text{C}$, which probably indicates large-scale dissociation of methane hydrates (e.g., Dickens, 2000, 2001a), the benthic foraminiferal association underwent a first stage of change, with large individuals no longer being able to survive.

Such a decrease in abundance of large, heavily calcified individuals occurred worldwide (Thomas, 1998), and could have been caused by increased solubility of calcite as a result of high total dissolved inorganic carbon levels resulting from oxidation of methane in the water column. At Site 690, dissolution of carbonate, as indicated by lower CaCO_3 values, started below the CIE and below this level of decrease in size of benthic foraminifera by several cm (D. Thomas et al., 1999), but this may well be the result of “burn-down,” dissolution reaching down into the sediment.

The actual extinction (i.e., drop in diversity, local disappearance of species that become extinct globally, and evenness of distribution of species over specimens) apparently occurred a few cm higher in the sediment than the CIE, which would mean about a few thousand years after the initiation of the CIE (chronology as in Röhl et al., 2000 [see also D. Thomas et al., 2002]). The faunal changes in benthic foraminifera started earlier, however, because the increase in absolute abundance started ~2 cm below the decrease in bulk $\delta^{13}\text{C}$ signaling the initiation of the CIE, at the same level as a drop in cool, higher productivity, r-mode nannoplankton species (Bralower, 2002). The change in floral assemblages, which was observed in the same size fraction as the bulk $\delta^{13}\text{C}$ values, thus must have predated the CIE, and might have been coeval with the initial gradual warming of the surface waters observed in the oxygen isotope values of *Acarinina* spp. (D. Thomas et al., 2002). The possibility of differential bioturbation, however, makes it impossible to precisely correlate these events in planktic foraminifera and nannoplankton, and possibly between benthic foraminifera and nannoplankton.

Changes in oceanic productivity

The benthic foraminiferal data at Site 690 appear to suggest increased productivity after the BEE (as argued by Thomas and Shackleton, 1996), in agreement with an interpretation of the Ba data as resulting from increased productivity (Bains et al., 2000). This interpretation conflicts with the nannofossil evidence for decreased productivity (Bralower, 2002; see also

Aubry, 1998). The Ba data, however, can be interpreted differently: During the dissociation of gas hydrates causing the CIE, significant dissolved Ba^{2+} was released to intermediate waters of the ocean. The dissolved Ba^{2+} concentrations in the deep ocean rose significantly, a smaller fraction of sinking barite particles dissolved, and “biogenic barite” accumulation increased (Dickens, 2001b; Dickens et al., this volume). In this model, no increased productivity is necessary to cause the increased Ba concentrations during the CIE.

In marginal oceans and epicontinental basins there is strong evidence for increasing productivity at the time of the Initial Eocene Thermal Maximum (IETM) (e.g., Gibson et al., 1993; Gavrillov et al., 1997, this volume; Speijer et al., 1997; Speijer and Schmitz, 1998; Egger et al., this volume), in some regions leading to local anoxic conditions and deposition of laminated “black shales” which are enriched in organic carbon (Crouch, 2001; Crouch et al., 2001; Speijer and Wagner, 2002; Gavrillov et al., this volume). The record for open ocean settings, however, is not so clear.

At many pelagic locations, post-extinction benthic foraminiferal assemblages may be interpreted as indicative of a high food supply and/or low oxygenation because of the abundant occurrence of buliminid foraminifera (see Thomas, 1998, for a review). At increased temperatures the metabolic food requirements of foraminifera increase rapidly, and the larger number of foraminifera at these higher temperatures thus mean a strongly increased food supply (Boersma et al., 1998). At other locations (e.g., many sites in the Atlantic Ocean such as Walvis Ridge Sites 525 and 527 and Ceara Rise site 929), productivity appears to have been lowered, although the same faunal effect might have occurred at rising temperatures and a stable food supply (Thomas and Shackleton, 1996; Boersma et al., 1998; Thomas and Röhl, 2002). Not only at Site 690, but also at equatorial Pacific Site 865 the nannoplankton and benthic foraminiferal evidence is contradictory, with surface records suggesting lowered productivity, benthic foraminiferal records increased productivity.

This discrepancy in data on productivity of benthic and planktic organisms is rather unexpected. In the present oceans, changes in surface primary productivity at various time scales are expressed in deep-sea, open ocean benthic faunas because of benthic-pelagic coupling (e.g., Smart et al., 1994; Jorissen et al., 1995; Loubere and Fariduddin, 1999; Gooday and Rathburn, 1999; Van der Zwaan et al., 1999), which is present even in the warm waters (>13 °C) of the eastern Mediterranean (Duineveld et al., 2000).

There are indications, however, that such benthic-pelagic coupling was less tight in the warmer oceans of the Greenhouse world (Thomas et al., 2000). For instance, the occurrence of benthic foraminiferal species that rely on the rapid deposition of fresh phytodetritus to the seafloor is limited to the late Cenozoic, after the establishment of the Antarctic ice sheet, when the diversity gradient from low to high latitudes may have developed (Thomas and Gooday, 1996; Culver and Buzas, 2000). The mass extinction at the end of the Cretaceous was devastat-

ing for planktic primary producers such as nannoplankton, but benthic foraminifera in the deep oceans showed minor assemblage fluctuations only and extinction was not above background levels (e.g., Alegret et al., 2001). In my opinion this was not the result of the fact that oligotrophic faunas were adapted to low food levels and thus not sensitive to a major drop in productivity: In oligotrophic regions food is severely limiting, and large changes in such a limiting factor are highly likely to affect faunas significantly.

How can we explain such a lack of benthic-pelagic coupling while deep-sea faunas must depend on food supplied from the surface, and the deep-sea is a strongly food-limited environment? A first interpretation could be that the lack of benthic-pelagic coupling might have resulted from a higher transfer rate of organic matter from the surface water to the seafloor in the warmer, and thus possibly less oxygenated waters of a greenhouse world. Presently, only a few percent of organic material produced in surface waters makes it to the deep sea environment (e.g., Murray et al., 1996). Obviously, only a small increase in this fraction could have a major impact on the total food arriving at the seafloor at constant or even decreasing primary productivity (Thomas et al., 2000).

There is, however, not much evidence in the present ocean that variation in oxygenation leads to variation in the preservation of organic matter in the water column (e.g., Hedges and Keil, 1995). Delivery of food particles to the seafloor in warm, oligotrophic regions such as the Red Sea is extremely low (Thiel et al., 1987). At the higher temperatures, one would surmise that the metabolic ratios of foraminifera as well as bacteria would be higher, so that organic matter descending through the water column would end up being more refractory after more intense bacterial degradation (Thomas et al., 2000).

Therefore, I want to present the highly speculative idea that benthic-pelagic coupling might have been less pronounced in Greenhouse Oceans in general than in the present ones because there may have been a larger supply of food generated directly at the ocean floor, by chemosynthetic bacteria. In recent years it has become clear that in the present oceans benthic foraminifera live in cold-seep areas, where methane hydrate is present close to the seafloor (Jones, 1993; Akimoto et al., 1994; Sen Gupta and Aharon, 1994; Rathburn et al., 2000; Bernhard et al., 2000, 2001). Not all these studies may have successfully distinguished actually living foraminifera in the seeps, because Rose Bengal staining of living specimens is not always reliable, but authors using various methods of assessment documented that the foraminifera actually lived in the seeps (Bernhard et al., 2001).

Such cold seep faunas are not characterized by endemic seep-species that occur nowhere else. To the contrary, these associations vary considerably on a regional as well as local, patchiness scale, but they all have abundant species that elsewhere occur in high-productivity regions, specifically small, few-chambered taxa from the superfamily Bulminacea. Such foraminifera may use the sulfur-reducing bacterial partner active in a consortium together with methane-consuming Archaea

(Boetius et al., 2000) symbiotically (Bernhard et al., 2000, 2001). The stable isotope signature of the cold seep faunas is not unequivocal, possibly because living individuals were not reliably distinguished, although at least in some cases specimens have unusually high values of $\delta^{18}\text{O}$ and low values of $\delta^{13}\text{C}$ (Rathburn et al., 2000).

There is another possible pathway of food supply to benthic foraminifera, based on bacteria and not on photosynthesis in the surface waters. Bacterial oxidation of methane in hydrothermal plumes in the present oceans contributes an amount of organic carbon up to 150% that of organic matter reaching the depth of the plume (2200 m) from the surface in the northeast Pacific (de Angelis et al., 1993). There is no evidence of possible plume-bacteria based foraminiferal associations in the present oceans, but this may be because no one searched for them. Such methane plumes might have been generated during dissociation of methane hydrates, and if they indeed moved through the Paleocene-Eocene oceans, they may have supported benthic foraminifera living on bacteria (see also Dickens, 2000).

I therefore suggest that benthic foraminiferal communities supported by chemo-autotrophic primary producers were more important in the overall food supply in the oceans at times when deep-water temperatures were generally above $\sim 10^\circ\text{C}$, such as the late Paleocene and early Eocene (Zachos et al., 2001). At these temperatures the metabolic rates of the Archaea and Bacteria involved would have been considerably higher than at the present temperatures close to 0°C . Even in a warm ocean gas hydrates were probably commonly present along continental margins, wherever enough organic matter was deposited (Dickens et al., 1995). I speculate that under such conditions relatively small fluctuations in ocean temperatures could have led to relatively diffuse dissociation of gas hydrates, as occurs presently at the seafloor in regions where hydrates outcrop and downstream from hydrothermal areas. If the Paleogene climate fluctuated between warm and very warm intervals at Milankovich periodicity, as suggested by the occurrence of Milankovich periodicity in sediment parameters (Norris and Röhl, 1999; Röhl et al., 2000; Cramer, 2001), varying oceanic temperatures may have been expressed in varying, possibly diffuse, dissociation of methane hydrates (Dickens, 2001a).

If it is indeed true that the occurrence of common benthic foraminiferal "bloom" species indicates times of periodical, possibly diffuse dissociation of methane hydrates on the seafloor, then the warmest interval of the Cenozoic, the later part of the Paleocene through the early Eocene (Zachos et al., 2001) can possibly be seen as an interval during which such periodical dissociation occurred commonly (Fig. 6). During this entire interval the relative abundances of the bloom species varied strongly, and these species were present only in this time interval. The whole interval is characterized by overall low $\delta^{13}\text{C}$ values, although several short, more extreme excursions might, in fact, have occurred (Zachos et al., 2001). The isotope record has not been studied in sufficient detail to evaluate whether more than one large carbon isotope excursion (in contrast with more peri-

odic, smaller fluctuations) did, in fact, occur, although this is suggested by the benthic foraminiferal records as well as by a few isotope data points (Thomas and Zachos, 2000).

The sudden increase in sulfur isotope values at the end of the early Eocene (Paytan et al., 1998) can then be interpreted as resulting from the end of a period during which periodic dissociation of gas hydrates occurred (Dickens, 2001b), with associated elevated levels of bacterial activity by sulfate reducing bacteria as fueled by methane consuming Archaea (Boetius et al., 2000). The drop in sulfur isotope values at the initiation of the CIE in New Zealand sections (Kaiho et al., 1996) suggests that an effect on sulfur isotopes can indeed be perceived at times of gas hydrate dissociation.

It is an intriguing idea that the warmest Greenhouse intervals may have been characterized by an oceanic carbon cycle that had a larger contribution of chemosynthetic organic matter. One might, for instance, speculate that the middle Maastrichtian extinction of the deep-sea clams *Inoceramus*, suggested to have harbored chemosynthetic symbionts, might have resulted from cooling below the threshold needed to support such a food flux (MacLeod and Hoppe, 1992).

The scenario for the IETM can then be speculated to have been as follows: The Earth warmed globally and gradually, possibly as a result of CO₂ emissions from the North Atlantic Volcanic Province (e.g., Eldholm and Thomas, 1993). This warming was more extreme at high latitudes, and caused changes in the nannoplankton floras (Bralower, 2002), as well as in the benthic faunas. The former changed to floras more typical of warmer, more oligotrophic waters, whereas the latter increased in abundance because bacteria on the seafloor increased their metabolic activity. At a threshold level of surface water warming, ocean circulation changed suddenly, possibly as a reaction to changing precipitation/evaporation patterns, with a switch from southern to northern high latitudes (Bice and Marotzke, 2002), or from high southern to lower latitudes (e.g., Kennett and Stott, 1991).

The changing circulation resulted in sudden higher temperatures of oceanic water masses and thus rapid methane dissociation, possibly also because the changing current patterns caused margin collapse (Katz et al., 2001). Methane dissociation was probably a very complex and spatially variable process, with one or more large slumps (Katz et al., 1999) generating large and sudden releases, whereas at the same time the temperature increase might have caused a much more widespread, diffuse dissociation (Dickens, 2001a). The methane may have been partially oxidized in the oceans, as suggested by the possibility of widespread low-oxygen conditions, and partially in the atmosphere, depending upon the way in which the methane was liberated. One would assume that sudden release of large amounts of methane as the result of a major slump (Katz et al., 1999, 2001) would have resulted in bubble formation and release into the atmosphere, whereas more diffuse dissociation might lead to more oxidation within the oceans.

Methane dissociation in the oceans may have triggered increased chemosynthetic activity and thus increased food for the

benthos, even at a time of decreasing surface water primary productivity. Site 690 does not appear to be a prime candidate for vigorous local gas hydrate dissociation: At its paleodepth of 1900 m it was probably below the region of active dissociation (e.g., Dickens et al., 1995; Katz et al., 1999). These estimates are not very precise, however, and gas hydrate dissociation may have been a chaotic process, locally triggered by slumps or intense currents, or the presence of warmer currents than elsewhere. Interestingly, Kaminski et al. (1996) and Galeotti et al. (2003) mention that *Glomospira* spp., common in the early Eocene deep ocean basins, is an opportunistic taxon that in the Gulf of Mexico lives in areas of active petroleum seepage. In areas without methane dissociation and a chemosynthetic food supply the benthic foraminifera starved because their metabolic needs were not met at the suddenly increased temperatures.

Once the large-scale methane dissociation started, positive feedback would have been expected to cause a runaway greenhouse effect. How such an effect was prevented and why the Initial Eocene Thermal Maximum ended is not clear. I suggest that there is at present not sufficient evidence that primary production in open ocean surface waters increased, in contrast with Bains et al. (2000), and in agreement with Dickens et al. (this volume). There may, however, very well have been a large increase in carbon storage on land (Beerling, 2001), or in marginal ocean basins (Speijer and Wagner, 2002; Gavrillov et al., this volume) to take the added carbon dioxide produced from oxidized methane from gas hydrates out of the atmosphere-ocean system.

CONCLUSIONS

Detailed benthic foraminiferal records across the Paleocene-Eocene carbon isotope excursion suggest that highly diverse benthic foraminiferal faunas with an even distribution of specimens over species and with many specialized, large, K-selected taxa were rapidly replaced by low-diversity faunas, heavily dominated by small, opportunistic taxa, while the food supply to the benthos increased. The calcareous nannoplankton in the same samples, however, shows an exactly opposite trend, and suggests decreasing productivity (Bralower, 2002). I speculate that this contradiction might be solved if the benthic faunas in the Paleogene, warm oceans were less strictly coupled to surface water primary producers than benthos in the present oceans. Such coupling might have been much less efficient if a larger percentage of organic matter reached the ocean floor than does today, possibly because in warmer, less oxygenated waters less organic matter was oxidized.

But one could also speculate that in such oceans at least part of the faunas used food produced at the ocean floor by chemosynthetic bacteria. The benthic foraminiferal extinction might thus have been caused by decreasing oxygen levels or increasing CaCO₃ corrosivity of the deep waters, but a change in food supply may have been an important contributing factor. In locations where methane dissociation could occur, the benthos received considerably more food during the Initial Eocene Ther-

mal Maximum, whereas in other regions (e.g., Walvis Ridge), the food supply to the benthos diminished as a result of decreasing surface water productivity, and starvation was exacerbated because foraminifera need more food to sustain life at higher temperatures. The increased overall patchiness of the deep ocean environments, resulting from the difference between regions with and without gas hydrates dissociation, may have been at least a contributing cause of the occurrence of biogeographically much more varied deep-sea faunas after the extinction (Thomas, 1998). Varying dependence upon chemosynthetic food supply by benthic foraminifera, with the supply depending on times of warming and/or cooling of the deep oceans may have been typical for the warmest period of the Cenozoic, the latest Paleocene through the early Eocene. We need to obtain detailed records of oxygen, carbon and sulfur isotopes over this whole time period in order to decipher the possible role of chemosynthesis in supporting ocean floor life, resulting in an oceanic carbon cycle very different from that in the present oceans.

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APPENDIX 1. TAXONOMIC NOTES

Siphogenerinoides sp.

Siphogenerinoides sp. has a strong resemblance to *Siphogenerinoides brevispinosa* (Plate 1), a species common in the upper Paleocene and lower Eocene at the Maud Rise drill sites (Thomas, 1990) as well as at equatorial Pacific Site 865 (Thomas, 1998). Both taxa have a test covered with fine spines and a short apertural neck. In contrast to *S. brevispinosa*, however, *Siphogenerinoides* sp. has a flattened rather than rounded early part of the test, with more chambers arranged biserially, and flattened rather than inflated in cross section. I have not noticed this morphotype in low-resolution samples from Site 689 (Maud Rise) and Sites 525 and 527 (Walvis Ridge, southeastern Atlantic Ocean), nor in high-resolution samples from Site 865 (equatorial Pacific). Both taxa cooccur just after the benthic

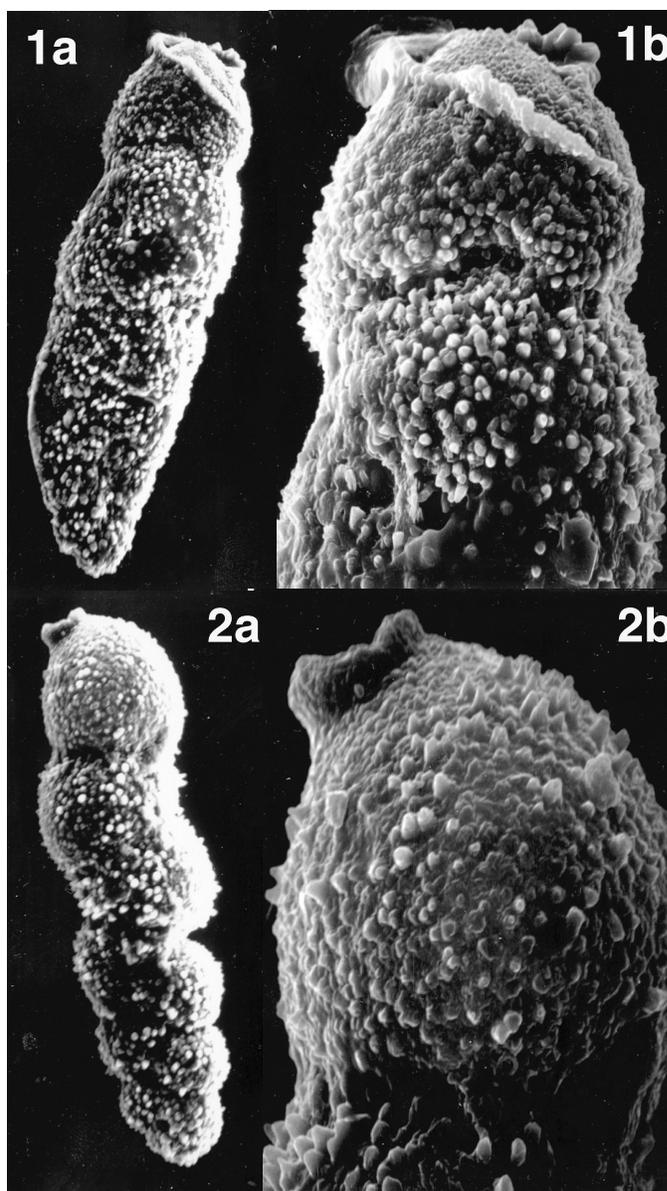


Plate 1. Figure 1: *Siphogenerinoides* sp. (a) Whole specimen; overall length 105 μ . (b) Last chamber (with later chamber broken off). Figure 2: *Siphogenerinoides brevispinosa* Cushman, overall length 125 μ . (a) Whole specimen. (b) Last chamber of 2a. Both specimens from Sample 690B-19H-3, 61–62 cm.

foraminiferal extinction at Site 690, but *Siphogenerinoides* sp. is not present over the rest of the section in Site 690. *Siphogenerinoides* sp. occurs in a very thin section of sediment only; higher-resolution studies are needed to document its biogeographic and stratigraphic range.

Bulimina kugleri Cushman and Renz, 1942

Bulimina kugleri Cushman and Renz, 1942, Cushman Laboratory for Foraminiferal Research, Contributions, v. 18, p. 9, Plate 2, Figure 9.

Bulimina ovula Reuss, Thomas, Thomas, E., 1990, Late Cretaceous through Neogene deep-sea benthic foraminifers (Maud Rise, Weddell Sea, Antarctica): Proceedings of the Ocean Drilling Program, Scientific Results: Texas A&M University, College Station, Texas, USA, v. 113, p. 571–594.

Bulimina ovula Reuss, Thomas, E., Zachos, J.C., and Bralower, T.J., 2000, Deep-sea environments on a warm earth: Latest Paleocene–early Eocene, in Huber, B., et al., eds., Warm climates in Earth history, Cambridge University Press, p. 32–160.

This is a small, fusiform species of *Bulimina*, about twice as long as wide, greatest breadth at about its middle. The chambers are distinct and slightly inflated, with slightly depressed sutures. The wall is smooth, and the aperture a high and arched, curved opening at the base of the inner margin of the last chamber. I compared the material from Sites 689 and 690 with the holotype (collection number 38199) and several paratypes (collection number 38257) at the Smithsonian Institution. The Weddell Sea specimens are smaller, but very similar in shape and proportions to the type specimens.

I called this species *B. ovula* in the past (Thomas, 1990; Thomas et al., 2000), because its fusiform shape was very similar to that figured in White (1928). In a recent restudy of White's original collection (Alegret and Thomas, 2001), however, it became clear that White's rather unclear figure represented the large and fusiform *Praebulimina reussi* (Morrow), the *nomen novum* for *Bulimina ovula* Reuss, and thus was not conspecific with the small fusiform *Bulimina* specimens. There is considerable confusion as to the use of the name *Bulimina ovula*, which has been used for forms now called *Praebulimina reussi*, for *Bulimina ovula* d'Orbigny, with which *B. ovula* Reuss was homonymic, and which is a much more inflated, Recent form, and also with *Bulimina ovula* Terquem, which is now placed in the genus *Buliminella*. All three species are fusiform to some degree.

The specimens from Sites 689 and 690 closely resemble *B. kugleri* Cushman and Renz in overall fusiform shape of the test, shape and placement of aperture, smooth wall and slightly depressed sutures, but they are in general smaller than the type specimens. Some of the paratypes but not the holotype have a smaller breadth-to-length ratio than my specimens.

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