

What happens when the ocean is overheated?

The foraminiferal response across the Paleocene–Eocene Thermal Maximum at the Alamedilla section (Spain)

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ABSTRACT

The global warming and major perturbation of the global carbon cycle that occurred during the Paleocene–Eocene Thermal Maximum (PETM) have been investigated in the lower bathyal–upper abyssal Alamedilla section (Spain). Geochemical anomalies and dramatic faunal changes (including the globally recognized extinction event of deep-sea benthic foraminifera and the rapid evolutionary turnover of planktic foraminifera and calcareous nannofossils) are associated with the PETM at Alamedilla.

Biotic changes in the plankton and benthos indicate environmental instability ~11–14 k.y. before the onset of carbon isotope excursion that marks the Paleocene/Eocene boundary. The reorganization of the planktic ecosystem points to warm and oligotrophic conditions in surface waters during the earliest Eocene, whereas faunal and geochemical data indicate that the extinctions of benthic foraminifera occurred over an interval with a high CaCO₃ content and oxic conditions at the seafloor. The proliferation of disaster taxa (*Glomospira* spp.) after the extinctions has been related to a potential source of isotopically light carbon in the western Tethys and North Atlantic.

Significant changes in foraminiferal test size are documented across the PETM. We suggest that increased temperatures played an important role in benthic foraminiferal test size, increasing their metabolic rates and, consequently, their food requirements. Decreased planktic foraminiferal test size may be related to decreased nutrient availability or surface-water density. However, the differences in test size evolution among different species of both benthic and planktic forami-

nifera may be related to interspecific competition and ecological adaptations to direct or indirect consequences of the carbon addition during the PETM.

INTRODUCTION

A major perturbation of the global carbon cycle occurred ~55 million years ago, during the transition between the Paleocene and the Eocene epochs. During this interval of Earth's history, which is known as the Paleocene–Eocene Thermal Maximum (PETM; Zachos et al., 1993), temperatures increased globally by 5 to 9 °C (e.g., Zachos et al., 2006; Sluijs et al., 2008) within less than 10,000 years (e.g., Röhl et al., 2000; Thomas, 2007). More than 2000 gigatonnes of carbon as CO₂ entered the atmosphere and ocean, as inferred from the negative 2.5‰–6‰ carbon isotope excursion (CIE) in marine and terrestrial δ¹³C values of carbonate and organic carbon (e.g., Kennett and Stott, 1991; Thomas and Shackleton, 1996; Zachos et al., 2001; Bowen et al., 2006). The onset of the geochemical anomalies occurred during a time period <20 k.y., whereas subsequent recovery of δ¹³C values took 170–210 k.y. (Farley and Eltgroth, 2003; Röhl et al., 2007). The rapid input of isotopically light carbon into the ocean-atmosphere system caused acidification of the oceans and shoaling of the calcite compensation depth (CCD) and lysocline, resulting in widespread CaCO₃ dissolution in deep-sea sediments (e.g., Dickens et al., 1997; Zachos et al., 2005). In contrast to the modern deep-sea undersaturation gradient, CaCO₃ dissolution was not homogeneous among the different ocean basins during the PETM: while it was stronger in the Atlantic, only a small decrease in CaCO₃ content has been observed in the Southern Ocean and in the Pacific Ocean (e.g., Colosimo et al., 2006; Zeebe and Zachos, 2007).

Different hypotheses that have been postulated to be the driver of the CIE and warming include the massive dissociation of isotopically light oceanic methane hydrates (Dickens et al., 1995), burning of peat deposits (Kurtz et al., 2003), the impact of a comet on Earth (Kent et al., 2003), or the thermal liberation of methane from organic matter by igneous intrusions in the North Atlantic (Svensen et al., 2004). Evidence exists for massive volcanism close to the PETM (Storey et al., 2007), but it remains uncertain whether it could have produced CO₂ at a rate required for rapid global environmental change (Sluijs et al., 2007a). The dissociation of oceanic methane hydrates is the most popular hypothesis, although its triggering mechanism is still under debate (e.g., Katz et al., 2001; Cramer and Kent, 2005; Pagani et al., 2006; Sluijs et al., 2007b), while evidence for a pre-CIE warming suggests that warming and ocean acidification were caused by at least two sources of carbon (Sluijs et al., 2007a). Regardless of which cause ultimately affected temperature and carbon cycling, terrestrial and marine biota underwent rapid changes across the PETM.

Among marine organisms, planktic microfossils show a rapid evolutionary turnover (e.g., Kelly et al., 1998; Arenillas et al., 1999; Molina et al., 1999; Bralower, 2002; Stoll, 2005; Sluijs et al., 2007b), while deep-sea benthic foraminifera suffered the largest extinction recorded during the Cenozoic (35%–50% of the species; e.g., Tjalsma and Lohmann, 1983; Thomas, 2007). The benthic foraminiferal extinction event (BEE) was rapid, with an estimated duration of <10 k.y. (e.g., Thomas, 1990; Alegret et al., 2009a, 2009b), and it was more severe in the deep sea than in marginal regions (e.g., Thomas, 2003; Alegret et al., 2005). High productivity is considered as the main cause of anoxia and the extinctions in marginal settings (Thomas, 2003). In contrast, extinctions in the deep sea have been related to such causes as oxygen deficiency at

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the seafloor as a consequence of warming of the deep sea or as a result of methane oxidation in the water column, globally increased or decreased productivity, local changes in productivity due to the expansion of the trophic resource continuum, or increased water corrosivity for CaCO_3 (e.g., Thomas and Shackleton, 1996; Boersma et al., 1998; Thomas, 1998, 2003, 2007; Thomas et al., 2000). These prime causes, or a combination of them, can only explain some of the extinctions locally. In addition, data from open ocean sites do not support global hypoxia, and are inconsistent with regard to global productivity changes (e.g., Gibbs et al., 2006; Thomas, 2007). Oceanic warming was the only disturbing factor common to all latitudes and all ocean basins, and is considered as the only global feature of the PETM for which there was no refugia (Thomas, 2007; Alegret et al., 2009a, 2009b). However, the mechanisms through which warming caused the extinctions are not clear. Similarly, the causes of the shifts in benthic and planktic foraminiferal test size across the PETM are under debate (e.g., Thomas, 1998; Kaiho et al., 2006; Petrizzo, 2007), and more studies are needed to evaluate stratigraphic variations in detail.

Very few locations are available where the sequence of events at the onset of the PETM can be studied, mainly because of the severe carbonate dissolution and thus incompleteness of records (Zachos et al., 2005). Recent studies on the lower bathyal–upper abyssal Alamedilla section (Subbetic Cordillera; southern Spain; Fig. 1) have pointed out the suitability of this section for micropaleontological and paleoenvironmental studies, mainly due to the abundance of microfossils, the high CaCO_3 content at the base of the CIE, and its relatively rapid recovery (Alegret et al., 2009b), thus preserving more of the record than at sites where the CaCO_3 recovery was slower. We document stratigraphic variations in test size of benthic and planktic foraminifera, and present a synthesis of faunal and geochemical patterns across the PETM at Alamedilla. These results may help to understand the potential direct effects of carbon input and warming on marine organisms.

METHODS

Shell diameters of benthic and planktic foraminifera were measured to evaluate stratigraphic variations in size. Among benthic foraminifera, we selected epifaunal (*Nuttallides truempyi*) and infaunal (*Globocassidulina subglobosa*) species; among planktic foraminifera, we measured surface-dwelling, photosymbiotic species (*Acarinina esnaensis*, *Morozovella velascoensis*, *M. subbotinae*) and the intermediate-dwelling,

asymbiotic species *Subbotina eocaenica* (Premoli-Silva and Boersma, 1988; d’Hondt et al., 1994; Olsson et al., 1999). Measurements across the PETM are expressed as mean values of the five largest specimens for each species in the $>63\text{-}\mu\text{m}$ size fraction (benthic foraminifera; GSA Data Repository Table DR1¹) and in the $>106\text{-}\mu\text{m}$ size fraction (planktic foraminifera; Table DR2 [see footnote 1]). Size measurements were based on the largest specimens from each sample in order to avoid the influence of juvenile specimens. For the measurements of benthic foraminifera, we used the same collection of foraminifera used by Alegret et al. (2009b), and for the planktic foraminifera, we used the specimens from the set published by Arenillas and Molina (1996).

To infer the paleoecological response of benthic foraminifera across the PETM, we grouped all the taxa identified by Alegret et al. (2009b) into four categories: (1) extinction taxa; (2) disaster taxa (taxa specifically adapted to stressed environmental conditions associated with mass extinction intervals, who develop short-lived, large populations immediately following crises, early in the survival phase); (3) opportunistic taxa (which quickly replace disaster taxa due to their capability of prolific population expansion and rapid bio-

¹GSA Data Repository item 2010098, Data repository items include size measurements of benthic and planktic foraminifera, and groups (extinction taxa, disaster taxa, opportunistic taxa and other taxa) of benthic foraminifera. The Ni, Co, V, Cr, and the CaCO_3 content of upper Paleocene and lower Eocene samples from the Alamedilla section are also shown, as well as several photographs of the outcrop, is available at <http://www.geosociety.org/pubs/ft2009.htm> or by request to editing@geosociety.org.

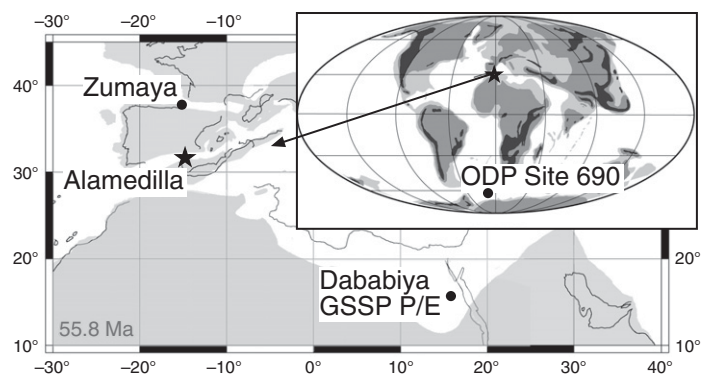


Figure 1. Paleogeographical reconstructions during the Paleocene–Eocene transition (modified from Hay et al. [1999] and Zachos et al. [2005]) and location of the Alamedilla section and other relevant sites and sections. Abbreviations: GSSP—Global Boundary Stratotype Section and Point; ODP—Ocean Drilling Program; P/E—Paleocene/Eocene boundary.

geographical dispersal into stressed environments; Kauffman et al., 1996); and (4) other taxa (Fig. 2 and Table DR3 [see footnote 1]). In addition, we analyzed the diversity of the assemblages from the same data set calculating the Fisher- α index (Fig. 2), which is based on the number of species and number of individuals per sample (e.g., Murray, 1991).

In order to address the issue of bottom-water oxygenation, several indices (Ni/Co and V/Cr) were obtained from X-ray fluorescence (XRF) analyses (Fig. 2 and Table DR4 [see footnote 1]). A total of 13 samples were previously powdered by hand in an agate mortar, and their Ni, Co, V, and Cr content was analyzed in the geochemical laboratories of the University of Zaragoza. According to Jones and Manning (1994), V-Cr and Ni-Co ratios are indicators of paleo-oxygen levels: a V/Cr ratio <2 corresponds to oxic conditions (values of ~ 2 correspond to the oxic-dysoxic transition, and values >4.25 are indicative of suboxic and/or anoxic conditions), whereas Ni/Co ratios <5 indicate oxic conditions, ratios ~ 5 show the transition between oxic and dysoxic, and values >7 indicate suboxic and/or anoxic environments. These authors point out that differentiation between oxic and dysoxic conditions is more successful than between the dysoxic and suboxic and/or anoxic environments. The CaCO_3 content of 21 samples (most of them close to the onset of the CIE) was also analyzed (white triangles in Figs. 2 and 3; Table DR5 [see footnote 1]).

For biochronological control (Figs. 2 and 3), we follow the planktic foraminiferal and calcareous nannofossil biostratigraphic data and zonations by Arenillas and Molina (1996), Molina et al. (1999), Monechi et al. (2000), and Berggren and Pearson (2005).

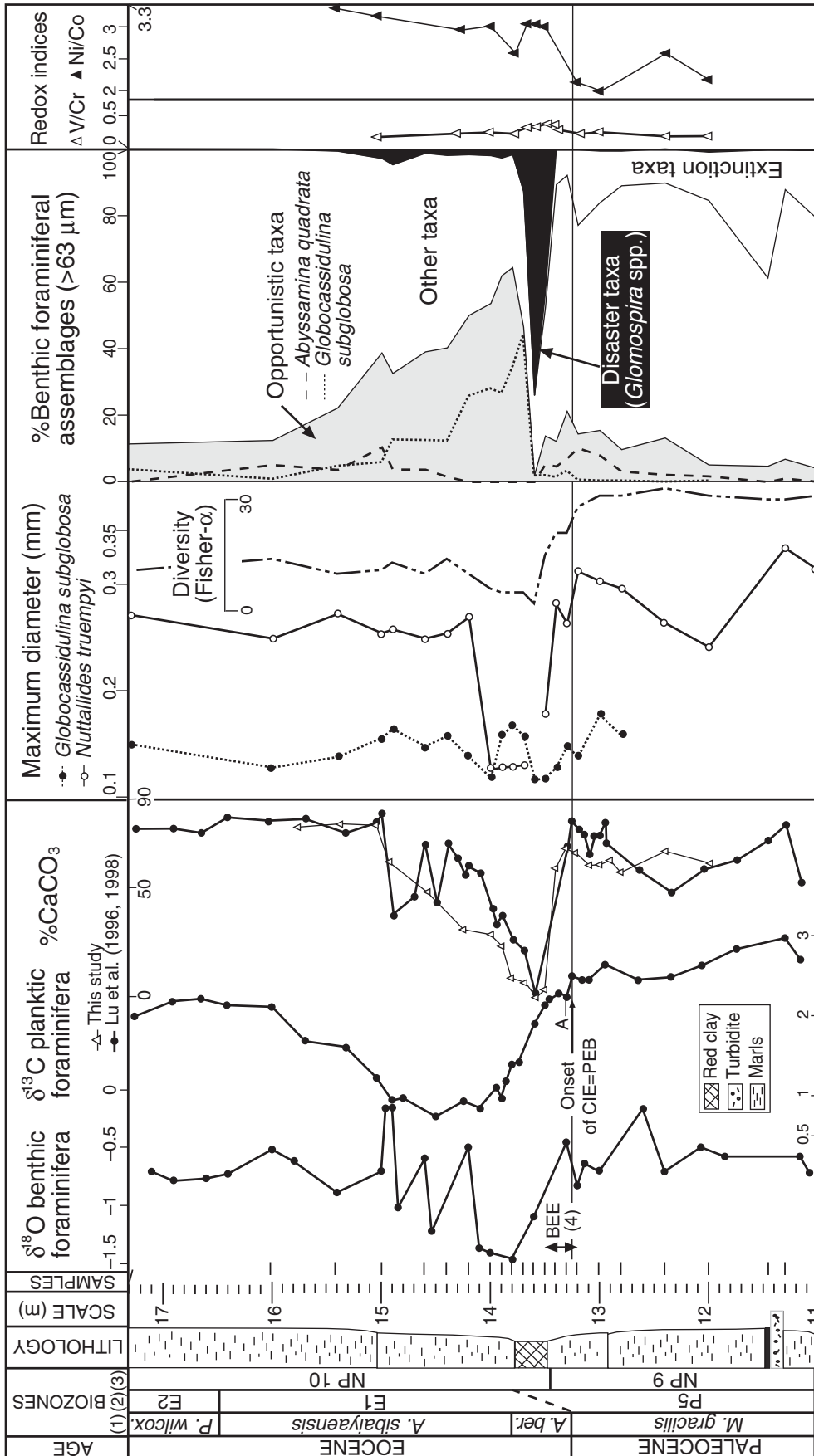


Figure 2. $\delta^{18}\text{O}$ isotopes (in benthic foraminifera), $\delta^{13}\text{C}$ isotopes (in planktic foraminifera), and percentages of CaCO_3 at Alamedilla, modified from Lu et al. (1996, 1998). White triangles—analyses of carbonate content carried out for this study. Maximum diameter of benthic foraminiferal tests, diversity of benthic foraminiferal assemblages, and their composition. Redox indices (Ni/Co and V/Cr) across the Paleocene/Eocene boundary. (1)—Arenillas and Molina (1996) and Molina et al. (1999); (2)—Berggren and Pearson (2005); (3)—Monechi et al. (2000). *M.*—*Morozovella*; *A. ber.*—*Acarina berggreni*; *P. wilcox.*—*Pseudohastigerina wilcoxensis*. (4)—The gradual but rapid BEE (benthic foraminiferal extinction event) spans 30 cm (~10 k.y.), from sample 13.20 to sample 13.50 (Alegret et al., 2009b). Abbreviations: CIE—Carbon Isotope Excursion; PEB—Paleocene/Eocene boundary.

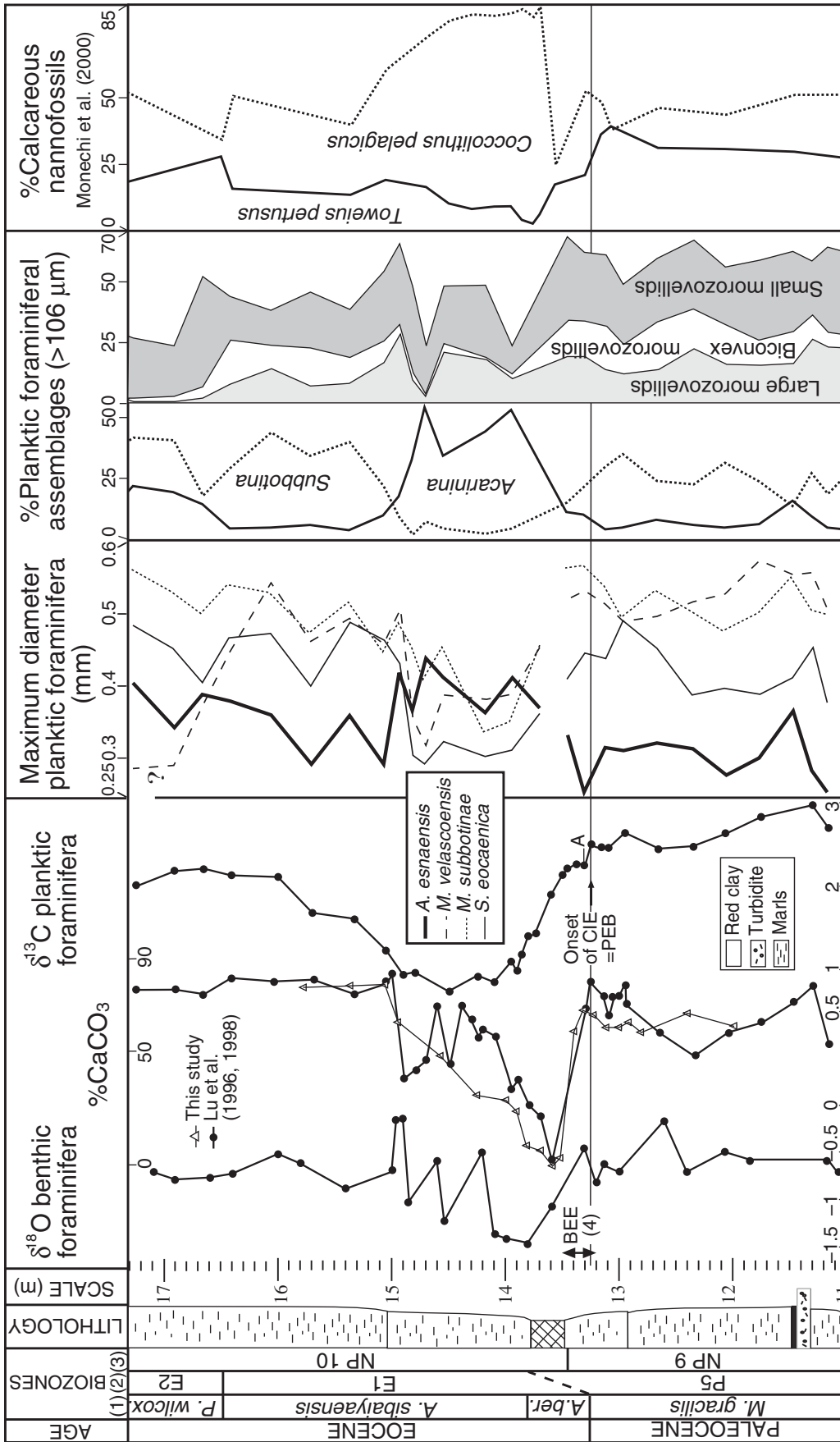


Figure 3. $\delta^{18}\text{O}$ isotopes (in benthic foraminifera), percentages of CaCO_3 and $\delta^{13}\text{C}$ isotopes (in planktic foraminifera) at Alamedilla, modified from Lu et al. (1996, 1998). White triangles—analyses of carbonate content carried out for this study. Maximum diameter of planktic foraminiferal tests and composition of the planktic foraminiferal and calcareous nannofossil assemblages. (1), (2), (3), (4), *M.*, *A. ber.*, *P. wilcox.*, BEE, and CIE as in Figure 2.

COMPLETENESS OF THE PALEOCENE–EOCENE RECORD

The studied section consists of a biostratigraphically continuous succession (Arenillas and Molina, 1996; Lu et al., 1996; Monechi et al., 2000) of upper Paleocene and lower Eocene pelagic sediments, and it includes the Paleocene/Eocene boundary as defined biostratigraphically and geochemically (Aubry et al., 2007). The onset of the CIE was identified by Lu et al. (1996, 1998) in sample 13.25, in a level of pink marls that grade into a 30-cm-thick, red clay interval (meters 13.50–13.80; Fig. 2). In coincidence with the onset of the CIE, these authors documented a decrease in the percentage of CaCO₃ (Figs. 2 and 3) and an increase in the percentage of silicate minerals. In order to document in detail the drop in CaCO₃ content, we analyzed several samples below and above the onset of the CIE, and found a dramatic decrease in the percentage of CaCO₃ between samples 13.40 and 13.50 (triangles plotted in Figs. 2 and 3), with lowest CaCO₃ content in samples 13.50 and 13.60. The fact that the basal part (lowermost 20 cm; samples 13.20, 13.30, and 13.40) of the CIE occurs in a short interval with high percentages of CaCO₃, together with the biostratigraphical completeness of the Paleocene–Eocene transition, make Alamedilla one of the most suitable sections to study the biotic and environmental evolution across the PETM in the deep sea. The red clay interval is overlain by red marls and, higher up in the section, by gray marls (Figure DR6 [see footnote 1]).

One may assume that the main peaks and plateaus of the bulk carbonate $\delta^{13}\text{C}$ curve may be related to changes in the input and removal of isotopically light carbon across the PETM. Following this assumption, an attempt can be made to compare the bulk carbonate $\delta^{13}\text{C}$ curve from Alamedilla (Lu et al., 1996, 1998) to the record from Ocean Drilling Program (ODP) Site 690, for which an orbitally calibrated age model has been developed (Röhl et al., 2007). However, the correlation of the bulk carbonate $\delta^{13}\text{C}$ curve is problematic because the onset of the excursion appears to be less abrupt at Alamedilla (Alegret et al., 2009b). This might result from a lower time resolution of the bulk carbonate record in Lu et al. (1996) than in the Bains et al. (1999) record for Site 690. Provided the small initial shift in bulk $\delta^{13}\text{C}$ at Alamedilla (tie point A in Figs. 2 and 3) is indeed coeval with the larger initial shift at Site 690, one could argue that the record is much more complete at Alamedilla, at least over the beginning of the CIE, making it one of the most complete marine records over that interval.

RESULTS

Benthic Turnover and Test Size

Although no major benthic foraminiferal turnover occurred before the onset of the CIE at Alamedilla (Fig. 2), a gradual decrease in diversity of the assemblages and an increase in the percentage of *Abyssamina quadrata* (a species that may have behaved opportunistically; Takeda and Kaiho, 2007) have been recorded ~14 k.y. (~25 cm) before the onset of the CIE (assuming a sedimentation rate of 1.8 cm/k.y. for the uppermost Paleocene; Alegret et al., 2009b).

Benthic foraminifera underwent severe extinction across the PETM at Alamedilla. The extinctions affected 44% of the species and were gradual but rapid (~10 k.y.), starting at the onset of the CIE (Alegret et al., 2009b). Our new data on % CaCO₃ confirm that the beginning of the extinctions occurred over an interval with a high CaCO₃ content (57%–67%; Fig. 2).

A decrease in the maximum diameter of the calcareous trochospiral species *Nuttallides truempyi* has been recorded in coincidence with the onset of the extinctions (and the onset of the CIE), whereas the decrease in size of the subglobular species *Globocassidulina subglobosa* may have started earlier (Fig. 2). Only three samples from the uppermost Paleocene contain *G. subglobosa*, making it difficult to assess the mean value and any changes in test size during the latest Paleocene.

Disaster taxa (*Glomospira* species) bloomed at the seafloor immediately after the BEE, in coincidence with the marked decrease in CaCO₃ content and the main drop in $\delta^{13}\text{C}_{\text{planktic}}$ values. No specimens of *N. truempyi* were found within this interval, whereas *G. subglobosa* shows minimum test-size values. Since *Glomospira* is an agglutinated genus and it peaks in an interval with a very low CaCO₃ content (lower half of the clay layer, samples 13.50 and 13.60), one might argue that the *Glomospira* peak is only the taphonomic result of strong CaCO₃ dissolution at the seafloor. In order to test this idea, we completely dissolved the CaCO₃ in the lowermost sample of the Eocene (sample 13.30) with HCl. The results of the dissolution experiment show that *Glomospira* is very scarce to absent in this sample, suggesting that, in addition to CaCO₃ dissolution (which accounts for the lack of calcareous taxa), there must have been an ecological contribution to the *Glomospira* peak.

The disaster fauna was rapidly replaced by opportunistic taxa (mainly *G. subglobosa*) coinciding with the lowest $\delta^{18}\text{O}_{\text{benthic}}$ values, a decrease in $\delta^{13}\text{C}_{\text{planktic}}$ values, a low CaCO₃ content, and minimum test size of *N. truempyi*

and *G. subglobosa*. Within this interval of generally decreased size of the tests, the later species shows an increase in test size in samples 13.70–13.90, in coincidence with its maximum abundance (Fig. 2), and goes back to minimum values in sample 14, whereas *N. truempyi* rapidly recovers in size shortly after. The size recovery of *G. subglobosa* probably occurred later (in sample 14.90, or even later), although it is difficult to know due to the scarce data on the “normal” size of the tests in the Paleocene.

The percentage of opportunistic taxa was high during the interval with a low CaCO₃ content, until sample 15, and it gradually decreased almost parallel to the recovery of $\delta^{13}\text{C}_{\text{planktic}}$ and $\delta^{18}\text{O}_{\text{benthic}}$ values, decreasing to almost pre-extinction values toward the upper part of planktic foraminiferal Zone E1 (Fig. 2).

Planktic Turnover and Test Size

In contrast to benthic foraminifera, planktic foraminifera did not suffer major extinction across the PETM. The most striking feature of the planktic foraminiferal turnover at Alamedilla is the sharp increase in abundance of the genus *Acarinina* (Fig. 3) above the interval with the minimum CaCO₃ values and up to sample 14.90. A decrease in the percentage of *Subbotina* and *Morozovella*—mainly deeper biconvex morozovellids such as *M. occlusa*—is recorded coeval with the acme of *Acarinina* (Fig. 3).

No planktic foraminifera were found in the dissolution interval, and the specimens identified immediately above it (sample 13.70, upper part of the clay layer) show a decreased (*M. velascoensis*, *M. subbotinae*, *S. eoacnica*) or increased (*A. esnaensis*) maximum diameter of their tests (Fig. 3). The onset of these shifts coincides with the lowest percentages of CaCO₃ and a marked drop in $\delta^{13}\text{C}_{\text{planktic}}$ values and $\delta^{18}\text{O}_{\text{benthic}}$ values. Changes in test size are recorded until sample 15, where they go back to pre-PETM values.

From the data set published by Monechi et al. (2000), it may be inferred that the nannofossil turnover at Alamedilla started at 13.05 (~11 k.y. before the onset of the CIE, assuming a sedimentation rate of 1.8 cm/k.y. for the uppermost Paleocene; Alegret et al., 2009b), and that the last occurrence of at least six species (20% of the species, including *Prinsius bisulcus* and several species of *Fasciculithus*) is recorded between this level and the onset of the CIE. Some of these species have been reported to become extinct globally at the PETM (e.g., Tremolada and Bralower, 2004; Gibbs et al., 2006), while the exact stratigraphical distribution of the species at Alamedilla should be analyzed in more detail in future studies. A prominent abundance

decline in the nannofossil genus *Toweius* has been documented just at the onset of the CIE at Alamedilla (Monechi et al., 2000; Fig. 3). The abundance of *Toweius* remained low for the rest of the core of the CIE, whereas *Coccolithus pelagicus* dominated the assemblages.

The percentage of *C. pelagicus* decreased to pre-PETM values at around the same level where the maximum diameter of planktic foraminifera recovered, whereas the increase in percentage of *Toweius* was more gradual, and it occurred in sample 16.5 (~55.35 Ma, according to the first occurrence datum of *Pseudohastigerina wilcoxensis*; Berggren and Pearson, 2005) or even later (in sample 19.55; Monechi et al., 2000).

DISCUSSION

Environmental Turnover at the Seafloor

New data on redox indicators (Ni/Co and V/Cr ratios) point to oxic conditions at the seafloor during the PETM (including the extinction interval and the interval with the shifts in test size) at Alamedilla. The V/Cr ratio across the PETM interval shows values similar to those in the underlying, well-oxygenated Paleocene sediments (Fig. 2). The Ni/Co ratios vary within a narrow range, slightly increasing across the lowermost Eocene. However, the ratios of these elements remain within the oxic field, well below the transition between the oxic and dysoxic conditions (Jones and Manning, 1994), indicating well-oxygenated bottom waters at Alamedilla. Oxic conditions at the seafloor are corroborated by the abundance of benthic foraminifera and the composition of the assemblages, as well as by the reddish color of the sediments.

Disaster fauna (*Glomospira* peak) bloomed during the early Eocene just after the BEE, coinciding with an interval with a very low CaCO₃ content (Fig. 2). In addition to CaCO₃ dissolution triggered by the shoaling of the CCD (e.g., Zeebe and Zachos, 2007), and dilution of the carbonate compounds by silicate minerals (as inferred from the increased sedimentation rates; Alegret et al., 2009b), we argue that the *Glomospira* peak was also ecologically driven (as suggested by the scarcity of this genus in an artificially dissolved sample from the lowermost Eocene). After comparison with recent species of *Glomospira*, Alegret et al. (2009b) concluded that the common occurrence of the *Glomospira* peak in the North Atlantic might be related to areas with methane dissociation from gas hydrates (e.g., Katz et al., 2001) or from organic matter heated up by igneous intrusions (Svensen et al., 2004); or to regions associated with volcanic ash deposits from the North Atlantic

Volcanic Province (e.g., Egger et al., 2005). Our data corroborate the distribution of the early Eocene “*Glomospira* Acme” in deep-water settings of western Tethys and North Atlantic (e.g., Kaminski and Gradstein, 2005), but further studies are needed to determine whether the *Glomospira* peak was linked to any of these sources of isotopically light carbon.

Immediately above the prominent peak in disaster fauna, assemblages from the lower Eocene contain abundant opportunistic taxa (e.g., abyssaminids, *Globocassidulina subglobosa*, *Tappanina selmensis*, and *Aragonia aragonensis*) that point to oxic conditions at the seafloor (see references in Alegret et al., 2009b). Although some of these species might indicate oligotrophy, their abundance is more likely to be controlled by other variables such as pulsed food inputs, stressed seafloor conditions, and bottom waters undersaturated in calcium carbonate. Alternatively, these opportunistic taxa may not indicate specific environmental conditions, but may be simply opportunistic taxa colonizing a disturbed environment (Thomas, 2005). Since the current knowledge of the organic matter flux dependency of individual species or species groups needs better estimates and calibrations (Jorissen et al., 2007), we conclude that the benthic foraminiferal species composition does not provide strong interpretations as to increased or decreased food supply to the seafloor.

On the other hand, the depth of the foraminiferal microhabitat may help to infer the trophic conditions at the seafloor. In areas with low flux rates, most organic matter is consumed at the sediment-water interface, and deeper sediment layers are too poor in organic matter to be inhabited by deep infaunal taxa (Jorissen et al., 1995). This means that under oligotrophic conditions, benthic foraminiferal assemblages are dominated by epifaunal morphogroups, which live at the sediment-water interface and consume the scarce food particles available. In contrast, benthic assemblages at Alamedilla are dominated by infaunal morphogroups, which make up more than 60% of the assemblages in all the Eocene samples (Alegret et al., 2009b). Consequently, the morphogroup composition of the assemblages suggests mesotrophic rather than extreme oligotrophic conditions at the seafloor during the early Eocene.

After examining different ecological parameters across the PETM at Alamedilla, it may be concluded that oxygen deficiency and changes in food supply do not explain the extinction of benthic foraminifera. Similarly, CaCO₃ dissolution seems not to be the main cause of the extinctions, since these are recorded across an interval without strong evidence for bioturbation and with a high CaCO₃ content. According

to Lu et al. (1998), benthic foraminiferal $\delta^{18}\text{O}$ values show a 4 °C warming in bottom waters at Alamedilla. Warming is a common feature between Alamedilla and other PETM successions worldwide, and is thought to have been the main trigger of the paleoecological and paleoenvironmental changes that eventually led to the BEE (e.g., Thomas, 2007; Alegret et al., 2009a, 2009b). After the initial warming (e.g., Sluijs et al., 2007a) and destabilization of the assemblages during the late Paleocene (Fig. 2), benthic foraminiferal extinctions were perhaps associated with increased temperatures surpassing a threshold during the earliest Eocene.

Environmental Turnover in Surface Pelagic Ecosystems

Rapid changes in planktic assemblages at Alamedilla indicate a significant environmental turnover in surface waters across the PETM. A similar planktic foraminiferal turnover (dominance of the surface-dwelling, photosymbiotic genus *Acarinina* and decreased abundance of the intermediate-dwelling, asymbiotic genus *Subbotina*) has been documented globally (e.g., Kelly et al., 1998; Molina et al., 1999; Petrizzo, 2007). This turnover has been related to stressful conditions such as corrosiveness, increased surface temperature, low productivity, and oxygen deficiency (Kelly et al., 1998; Arenillas et al., 1999; Kelly, 2002; Kaiho et al., 2006), but the direct causes are still under debate.

Increased water corrosiveness due to the CCD shoaling does not account for the planktic foraminiferal turnover, since surface waters are usually beyond the range of CCD effects (Zachos et al., 2005). Even if the assemblage composition was an artifact of biostratigraphic dissolution processes (dissolution of the calcareous tests during the postmortem fall through the water column), morozovellid tests would have been the least affected since they are the thickest and most ornamented ones. In contrast, morozovellids decrease in test size across the PETM at Alamedilla (Fig. 3). On the other hand, increased surface-water temperatures and/or oligotrophy should have favored subtropical-tropical photosymbiotic taxa such as *Acarinina* and *Morozovella*, whereas only acarininid species bloomed and increased their test size at Alamedilla. The differences in behavior between these two planktic foraminiferal taxa, which occupied a similar ecological niche, remain to be explained.

According to the data set by Monechi et al. (2000), it may be concluded that the magnitude of the calcareous nannofossil extinctions at the onset of the PETM is comparable to that recently documented from the PETM at

Tanzania (Bown and Pearson, 2009), and that the nannofossil turnover was related to environmental perturbation at and just before the onset of the CIE. The prominent abundance decline in the nannofossil genus *Toweius* after rapid warming at the onset of the CIE suggests that cool-water taxa may have migrated to areas with cooler temperatures (e.g., higher latitudes, upwelling zones, or deeper in the water column), whereas the increase in *C. pelagicus* may be indicative of increased oligotrophy in surface waters (Bown and Pearson, 2009). A gradual increase in the percentage of *Toweius* higher up in the section indicates the return of cool-water taxa when temperatures cooled down, at 55.35 Ma or even later.

Causes of the Shifts in Foraminiferal Test Size

Body size is related to biological processes (metabolism, growth rate, resistance to starvation, and predation) and to environmental factors (Peters, 1983), but little is known about such relationships in the geological record. Significant changes in benthic and planktic foraminiferal test size have been documented across the PETM, although in some cases the stratigraphic variations are not described in detail.

The general decrease in benthic foraminiferal test size across the PETM (Thomas, 1998) has been interpreted in terms of oxygen deficiency at the seafloor (e.g., Kaiho et al., 2006), carbonate dissolution (Thomas, 2003), or changes in the food supply (Boltovskoy et al., 1991). At Alamedilla, the decrease in benthic foraminiferal test size during the lowermost Eocene is not related to oxygen deficiency, since geochemical redox indicators, the reddish color of the sediments, and the faunal composition indicate oxic conditions at the seafloor during the PETM. The decrease in benthic foraminiferal test size started at the onset of the CIE (*N. truempyi*) or possibly before (*G. subglobosa*), and it is recorded over an interval with a minimum CaCO₃ content, the lowest $\delta^{18}\text{O}_{\text{benthic}}$ values, and decreasing $\delta^{13}\text{C}$ values, suggesting that test size might be related to water corrosiveness for CaCO₃ and higher temperatures. Water corrosiveness for CaCO₃ may have controlled the growth of benthic foraminiferal tests, although Takeda and Kaiho (2007) argued that it does not explain the early Eocene dwarfism in Shatsky Rise (central Pacific), where the reduction in carbonate ion was not severe and enhanced the preservation of the tests.

Although there is no evidence for global increased or decreased food supply to the seafloor at the PETM, the increase in temperature has been observed in all oceans and on land, as well

as in all latitudes. Increased temperatures may also be related to nutrition: even if food supply did not change at the PETM, the increased temperatures would increase the metabolic rates of benthic foraminifera, which would require more food. These assemblages would then indicate more oligotrophic conditions, even if the total amount of food supply to the seafloor did not change. For example, if deep-water temperatures were ~10 °C higher than today, metabolic rates of foraminifera would be higher by as much as a factor of 2 (e.g., Hallock et al., 1991; Gillooly et al., 2001), thus requiring twice as much food in order to keep the same faunal structure (Thomas, 2007). In addition, it has been suggested that insufficient food creates a larger number of undersized benthic foraminifera, including *G. subglobosa* (e.g., Corliss, 1979; Boltovskoy et al., 1991).

Proxies for temperature and corrosiveness recover gradually across the PETM at Alamedilla, whereas the maximum diameter of *N. truempyi* increases sharply. Such a rapid size increase correlates to an increase in relative abundance of *N. truempyi*, suggesting that test size might also be modulated by interspecific competition. The variations in test size of *G. subglobosa* are more complex. The occurrence of larger tests of *G. subglobosa* within the “minimum size interval” might be related to the increased abundance of this opportunistic species, which took over the infaunal niche that was previously occupied by the disaster *Glomospira* species. We suggest that the increase in test size of *G. subglobosa* was the result of reduced interspecific competition for habitat and food resources following the decreased abundance of competitors.

These data suggest that the shifts in test size during the early Eocene were probably triggered by more than one parameter. We conclude that increased temperatures (which in turn controlled nutrition processes mainly increasing benthic foraminiferal metabolic rates and, consequently, their food requirements), as well as interspecific competition for habitat and food resources, were probably the main triggers of the shifts in postextinction benthic foraminiferal size. Water corrosiveness for CaCO₃ may have controlled the growth of benthic foraminiferal tests at Alamedilla, but not globally (e.g., Takeda and Kaiho, 2007). In the planktic ecosystem, Bown and Pearson (2009) recently argued that if surface-water acidification was a global phenomenon, and provided it had a negative pressure on calcification and growth of calcareous nannofossils, these should show a much greater evolutionary response.

Among planktic foraminifera, the increase in maximum diameter of *Morozovella* species in the Pacific and Southern Oceans has been

related to depleted surface nutrient levels and salinity (Kaiho et al., 2006; Petrizzo, 2007). At Alamedilla, the onset of the shifts in planktic foraminiferal test size coincides with the lowest percentages of CaCO₃, decreased $\delta^{13}\text{C}_{\text{planktic}}$ values, and low $\delta^{18}\text{O}_{\text{benthic}}$ values. Test sizes of planktic foraminifera recovered to pre-PETM values ~170 cm above the onset of the CIE, parallel to the recovery of the planktic foraminiferal and calcareous nannofossil assemblages, $\delta^{18}\text{O}_{\text{benthic}}$ values, and CaCO₃ content. These data suggest a possible correlation between test size of planktic foraminifera and such aspects of environmental change as increased temperatures or oligotrophic conditions.

Lower nutrient levels might also be related to the smaller size of the tests, whereas the symbiotic *A. esnaensis* might have attained unusually large sizes during the early stages of the PETM due to enhanced calcification through the photosynthetic activity of algal symbionts (Bé et al., 1982; Hallock, 1999), gaining energetic advantage in the adaptation to low-nutrient environments (Hallock et al., 1991). In contrast, *M. velascoensis* and *M. subbotinae*, which are also surface-dwelling photosymbiotic species (d'Hondt et al., 1994), decreased in size. Since morozovellid tests are denser and more robust than those of acarininids, a decrease in surface-water density (induced by warming) could have affected the depth habitat of morozovellids within the water column. As a response to decreased surface-water density, morozovellids would then decrease in size to maintain buoyancy.

The discrepancy in the planktic foraminiferal species responses (*M. velascoensis*, *M. subbotinae*, and *S. eoacena* decreased in size, and *A. esnaensis* increased) suggests a high degree of complexity in the ocean structure, possibly with differences in biotic responses. The different ecological adaptations of the planktic foraminiferal species to direct (elevated $p\text{CO}_2$) or indirect (rising temperatures, changes in nutrient supply and in surface-water stratification, decreased surface-water density, etc.) consequences of the carbon addition may have resulted in competitive advantages, driving the reorganization of planktic assemblages.

CONCLUSIONS

The micropaleontological and paleoenvironmental turnover across the Paleocene–Eocene Thermal Maximum has been analyzed in the lower bathyal–upper abyssal Alamedilla section (southern Spain). The Paleocene–Eocene transition at Alamedilla is biostratigraphically complete, and it displays the mass extinction event of benthic foraminifera at the base of the

CIE, in an interval with a high CaCO₃ content. However, changes in benthic assemblages and in calcareous nannofossils are recorded in the uppermost Paleocene, suggesting that environmental instability probably started ~11–14 k.y. before the onset of the CIE.

Changes in planktic foraminiferal and calcareous nannofossil assemblages indicate an extremely warm and oligotrophic scenario for the planktic ecosystem during the PETM, while multiple proxies indicate oxic conditions at the seafloor. The occurrence of the benthic foraminiferal *Glomospira* peak after the extinction event has been related to a possible addition of isotopically light carbon in the western Tethys and North Atlantic, although the source of the carbon remains unknown.

Significant changes in benthic and planktic foraminiferal test size have also been observed across the PETM. After considering several interpretations for the changes in test size (oxygen deficiency, carbonate dissolution, etc.), we conclude that benthic foraminiferal size was probably related to more than one parameter, mainly increased temperatures, nutrition (increased food requirements related to enhanced metabolic rates under warm temperatures) and interspecific competition.

The overall decrease in planktic foraminiferal test size may be related to lower nutrient levels or decreased surface-water density, while the discrepancy among species suggests interspecific competition and a high degree of complexity in the ocean structure.

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