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Deep-sea environments on a warm earth: latest Paleocene–early Eocene

ELLEN THOMAS, JAMES C. ZACHOS, AND TIMOTHY J. BRALOWER

ABSTRACT

Latest Paleocene–early Eocene high-latitude surface and global deep-ocean waters were warmer than those of today by up to 15 °C; planktonic foraminiferal and nannofossil assemblages suggest that primary oceanic productivity was low. Low oceanic productivity is also indicated by geochemical evidence that the supply of nutrients to the oceans may have been low. Climate modeling suggests that oceanic and atmospheric circulation may have been sluggish at low temperature gradients, leading to low rates of upwelling of nutrients. Benthic foraminiferal data, by contrast, suggest that the food supply to the deep sea floor in open-ocean settings was larger than that in Recent oceans, in agreement with the speculation that a larger fraction of organic carbon was buried. The benthic foraminiferal evidence might be explained by more efficient food transfer to the bottom in poorly oxygenated, warm deep waters. Possibly the pelagic microbial loop was more active at the higher temperatures, leading to enhanced zooplankton productivity and thus enhanced food supply. Or possibly the benthic faunas do not indicate a high average food supply, but a more continuous and less seasonally pulsed supply than that today. Environmental interpretation of early Eocene benthic foraminiferal faunas is difficult not only because they differ substantially from Recent ones but also because the faunas had been decimated by a massive extinction during an episode of rapid warming, the Late Paleocene Thermal Maximum (LPTM), with a duration of between 25 and 200 000 ka. During the LPTM carbon isotope values of the atmospheric and oceanic carbon reservoir decreased by 2–3‰, a sign of major upset in the global carbon cycle. The carbon isotope excursion could be explained by dissociation of methane hydrates as a consequence of warming of deep water masses, which occurred when dominant formation of deep–intermediate waters shifted from high to low latitudes. Methane dissociation in combination with changes in ocean circulation offers a possible mechanism for climatic instability in the absence of polar ice caps. We lack the high-resolution, stratigraphically complete biostratigraphical and isotope data sets necessary to evaluate whether the early Eocene climate was unstable, but high average temperatures could reflect a warm background climate with superimposed 'hyperthermals': intervals of extremely high temperatures and

very low latitudinal sea surface temperature gradients, during which the deep–intermediate oceans were dominated by waters derived from subtropical latitudes.

INTRODUCTION

A time interval of about 5 million years in the latest Paleocene through early Eocene was the warmest part of the Cenozoic, and deep-ocean waters reached temperatures of up to 15 °C (see reviews by Zachos *et al.*, 1993; Seto, 1995; Oberhänsli, 1997; Fig. 5.1). Latitudinal temperature gradients in surface waters were low (e.g., Zachos *et al.*, 1994), warm-water pelagic marine organisms extended their geographic range into polar latitudes, and their associations indicate low productivity (see reviews by Aubry, 1992, 1998*b*). Thermophilic vertebrates occurred in the Arctic (e.g., Markwick, 1994). Vegetation and soil-types suggest warm high latitudes in both hemispheres (e.g., Askin, 1992; Basinger *et al.*, 1994; Wolfe, 1994), and clay mineral associations in oceanic sediments indicate high humidity and intense chemical weathering in the Antarctic (Robert and Kennett, 1992), on the New Jersey margin (Gibson *et al.*, 1993), in the North Sea region (Knox, 1996), and in New

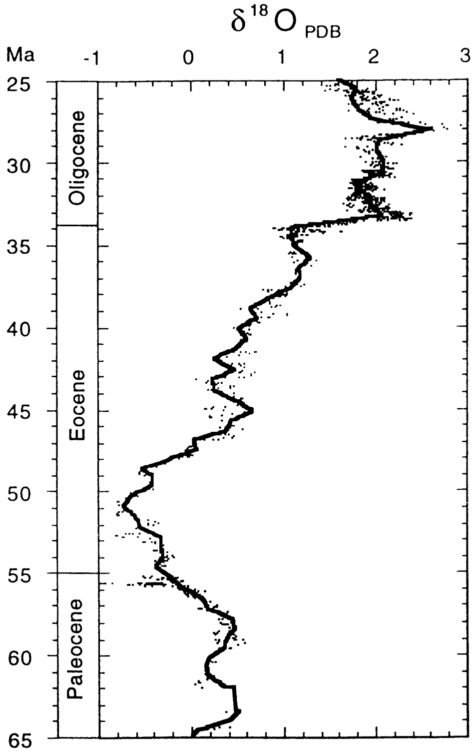

Figure 5.1. Smoothed compilation of deep-sea $\delta^{18}O$ data, modified after Zachos *et al.* (1993); numerical ages after Berggren *et al.* (1995). Note small dots indicating single data points.

Zealand (Kaiho *et al.*, 1996). The land regions around eastern Tethys were very warm and arid (Oberhänsli, 1992). It has been generally assumed that polar ice sheets were either small or absent (e.g., Zachos *et al.*, 1993), although there is some evidence that they existed for at least some time intervals (e.g., Leckie *et al.*, 1995).

The unusual warmth of this period has been commonly explained by high atmospheric CO_2 levels (e.g., Freeman and Hayes, 1992). Possible causes of these higher levels of atmospheric CO_2 include massive volcanism in the North Atlantic Igneous Province during the initial opening of the North Atlantic, decarbonation of limestone or oxidation of organic-rich sediments resulting from the India–Asia continental collision, and high hydrothermal activity along mid-oceanic ridges (see review by Thomas and Shackleton, 1996). Climate modeling indicates, however, that at high CO_2 levels tropical temperatures would be much higher than deduced from paleoceanographic data. Mechanisms for highly increased heat transport from low to high latitudes at the low latitudinal temperature gradients remain unexplained (Barron and Moore, 1994; Sloan and Rea, 1995; Sloan *et al.*, 1995).

The earth's climate during warm periods has been said to be more stable than that during cold periods such as the Plio-Pleistocene. Climate fluctuations on Milankovitch and sub-Milankovitch timescales during cold periods could have been amplified through feedback loops involving climatically sensitive factors (e.g., sea ice) which are absent in a 'greenhouse' world (e.g., Rind and Chandler, 1991). Rapid climate change, however, did occur when polar ice caps were small or absent during the Late Paleocene Thermal Maximum (LPTM: Zachos *et al.*, 1993), when intermediate to deep oceans globally warmed by 4–6 C over less than a few thousand years (Kennett and Stott, 1991; Pak and Miller, 1992; Thomas and Shackleton, 1996), while mid-latitude to tropical surface temperatures did not change much (Stott, 1992; Bralower *et al.*, 1995*a,b*; Lu and Keller, 1995*b*; Pardo *et al.*, 1996; Bralower *et al.*, 1997). Estimates of the duration of the LPTM range from 25 ka (Cramer *et al.*, 1997; Norris, 1997*b*) to 200 000 ka (Kennett and Stott, 1991; Lu *et al.*, 1996), but the transition into the LPTM is generally agreed to have occurred over less than 10 ka (e.g., Kennett and Stott, 1991; Lu *et al.*, 1996; Thomas and Shackleton, 1996).

During the LPTM carbon isotope values in the oceans and the atmosphere decreased globally by about 2–3‰ (Kennett and Stott, 1991; Koch *et al.*, 1992, 1995; Pak and Miller, 1992; Lu and Keller, 1993, 1995*a,b*; Canudo *et al.*, 1995; Aubry *et al.*, 1996; Kaiho *et al.*, 1996; Schmitz *et al.*, 1996; Stott *et al.*, 1996; Thomas and Shackleton, 1996; Bralower *et al.*, 1997). This rapid decrease is superimposed on a long-term decrease that started in the middle Paleocene (see review by Corfield, 1995). Mass-balance equations show that this carbon isotope excursion was so large that it could not have been caused by transfer of terrestrial biomass into the ocean–atmosphere system or by eruption of volcanogenic CO_2; it was so rapid that it probably could not have been caused by a change in deposition or erosion rates of carbon in carbonate as compared with carbon in organic matter (Thomas and Shackleton, 1996). Such large, rapid excursions in the isotopic composition of the global carbon reservoirs require causes that are not included in the commonly used models of the carbon cycle at various timescales (e.g., Walker and Kasting, 1992; Berner, 1995): the input rates of isotopically light carbon during the transition into the LPTM excursion are similar to rates of anthropogenic fossil fuel burning. Such an excursion could have been caused by massive dissociation of isotopically light methane hydrates in oceanic sediments as a result of the deep-ocean warming (Dickens *et al.*, 1995, 1997; Matsumoto, 1995; Kaiho *et al.*, 1996).

This paper combines a review of the rapidly growing information on the LPTM and early Eocene warm period with new data. We will review latest Paleocene–early Eocene deep-ocean habitats as compared with those in the present deep oceans, discuss the nature and duration of the environmental changes during the LPTM, and consider the possibility that global climate during warm periods was highly unstable.

METHODS

Faunal data are presented from Ocean Drilling Program (ODP) Site 865 and isotope data from ODP Site 690 and Deep Sea Drilling Project (DSDP) Site 215 (Table 5.1); see Fig. 5.2 for location of sites. Samples for benthic foraminiferal faunal analysis were dried overnight at 50 °C and weighed, then soaked overnight in distilled water. Most samples disaggregated readily and could be washed over a 63-μm screen. Benthic foraminifera for faunal analysis were picked from the >63-μm size fraction, following Thomas (1990*a*,*b*). All specimens were picked and mounted in cardboard slides. All samples contained sufficient specimens (>250) for analysis. Taxonomy is as in Thomas (1990*a*) and Thomas and Shackleton (1996), and largely follows Van Morkhoven *et al.* (1986). In order to obtain a measure of diversity independent of the number of specimens counted, we calculated the number of species that would be present if only 100 specimens had been counted. We used the rarefaction method developed for Recent metazoan deep-sea faunas, which typically have high species diversity and many rare species, like deep-sea benthic foraminiferal faunas (Sanders, 1968).

Isotope measurements of benthic foraminifera were performed at the University of California at Santa Cruz. Samples were reacted in a common phosphoric acid bath at 90 °C. Average precision as determined from replicate analyses of the laboratory standards NBS-19 and Carrera marble was better than ±0.10‰ for both $\delta^{18}O$ and $\delta^{13}C$.

WARM DEEP-OCEAN ENVIRONMENTS

Discussions of links between climate and oceanic ecology and biota have characterized 'greenhouse' periods as having low average oceanic productivity coupled with high species diversity (Fischer and Arthur, 1977; Brasier, 1995*a*,*b*; Norris, 1997*a*). Low nutrient supply and slow oceanic circulation have been most widely discussed as causal factors for low productivity, but no explanation has been widely accepted. Nutrient supply from land to the oceans may have been low as a result of the low topographic relief, combined with high sea levels and thus relatively small continental area. Together these factors could have caused low weathering and erosion rates as deduced from the strontium isotopic record of marine carbonates

Table 5.1. *Isotope data for benthic foraminiferal taxa at Sites 690, 689, and 215*

Sample	Taxon	δ^{13}C	δ^{18}O
690B 19-3, 51-53	*B. ovula*	−1.55	−1.17
690B 19-3, 51-53	*N. truempyi*	1.29	−0.02
690B 19-3, 60-62	*B. ovula*	−1.10	−0.89
690B 19-3, 66-68	*B. ovula*	−1.05	−0.83
690B 19-3, 72-74	*N. truempyi*	1.57	−0.05
690B 19-3, 72-74	*B. ovula*	−1.15	−0.98
689B 23-1, 80-82	*B. thanetensis*	0.80	0.32
689B 23-1, 87-89	*Lenticulina* sp.	−1.10	−0.42
689B 23-1, 94-96	*B. thanetensis*	0.96	0.43
689B 23-1, 94-96	*N. truempyi*	1.30	0.17
689B 23-1, 94-96	*N. truempyi*	1.36	0.22
689B 23-1, 94-96	*Lenticulina* sp.	−0.84	−0.21
689B 23-1, 104-106	*B. thanetensis*	0.52	0.40
689B 23-1, 106-108	*Lenticulina* sp.	−0.84	−0.18
689B 23-1, 104-106	*N. truempyi*	1.24	0.27
215 11-6, 32-34	*N. truempyi*	0.98	−0.31
215 11-6, 32-34	*N. truempyi*	0.92	−0.27
215 11-6, 129-131	*N. truempyi*	0.74	−0.45
215 11-6, 129-131	*N. truempyi*	0.63	−0.53
215 11-7, 79-81	*N. truempyi*	0.97	−0.19
215 11-CC, 0-2	*N. truempyi*	0.77	−0.42
215 12-1, 10-12	*N. truempyi*	1.15	0.06
215 12-1, 12-14	*N. truempyi*	1.21	0.02
215 12-1, 38-40	*N. truempyi*	1.24	−0.09
215 12-1, 70-72	*N. truempyi*	1.32	−0.06
215 12-1, 94-96	*N. truempyi*	1.41	−0.01
215 12-1, 125-127	*N. truempyi*	1.27	−0.05
215 12-2, 6-8	*N. truempyi*	1.16	−0.07

(e.g., François and Walker, 1992) and the osmium isotope record from deep-sea clays (Turekian and Pegram, 1997). By contrast, higher temperatures, possibly higher atmospheric $p\mathrm{CO}_2$, higher humidity at high latitudes, and lack of ice cover on the Antarctic continent may have worked in an opposite direction, causing higher rates of weathering during 'greenhouse' periods (see review in Berner, 1995). In addition, the question of ocean nutrient supply involves more than just continental weathering rates. For instance, less oxygen dissolves in the warmer ocean waters, possibly leading to more efficient recycling of phosphorus in the oceans, and hence to higher productivity on long (10^6 years) timescales (Van Cappellen and Ingall, 1994). We therefore do not know whether the Paleogene supply of nutrients to the oceans was higher or lower than that today, or whether various differences with the present world canceled each other (see papers in Ruddiman, 1997).

Slow oceanic turnover rates caused by the low latitudinal thermal gradients have also been cited as a cause of the low average oceanic productivity during

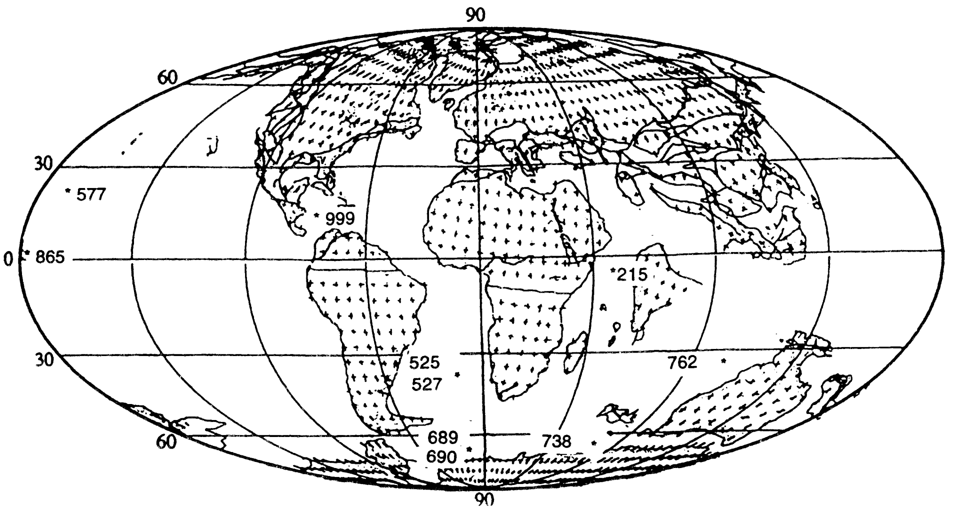

Figure 5.2. Location of drill sites mentioned in the text; figure modified after Zachos *et al.* (1994).

'greenhouse' periods, because such low rates of turnover would cause slow recycling of nutrients into the surface waters by upwelling (e.g., Fischer and Arthur, 1977). A possible corollary of sluggish ocean circulation might have been that large amounts of nutrients were sequestered in the deep oceans, resulting in low average productivity, but high productivity locally where these nutrient-rich waters welled up (Hallock, 1987; Hallock *et al.*, 1991).

It is not clear, however, whether oceanic circulation was indeed sluggish during greenhouse periods. During warm periods in the Cretaceous, sediments suggesting low oxygen conditions in the oceans ('black shales') were commonly deposited, and this deposition has been interpreted as resulting from sluggish circulation. But it has also been suggested that the low oxygenation resulted from high productivity during vigorous ocean overturn (see reviews by Hay, 1995; Parrish, 1995).

INTERPRETATION OF BENTHIC FORAMINIFERAL FAUNAS

Recent faunas

Benthic foraminiferal faunas reflect combined effects of deep-water physicochemical parameters (dominantly oxygen content) and the flux of organic matter to the bottom. There is considerable controversy over which of these factors dominantly determines faunal composition (see reviews by Gooday, 1994; Schnitker, 1994; Murray, 1995; and modeling by Jorissen *et al.*, 1995). One of the reasons for this uncertainty is the fact that in the present oceans high productivity in the surface waters is usually the cause of low oxygenation of bottom waters so that it is difficult to deconvolve the influence of these two factors.

Presently regions of higher productivity are mostly along the continental margins (e.g., Berger, 1989). Species using the abundant food supply below oxygen minimum zones must be able to survive in relatively low oxygen conditions. They commonly migrate through the sediment vertically, following seasonally fluctuating oxygen gradients which result from seasonal fluctuations in productivity, and 'prefer' to stay away from extreme dysoxia to anoxia (Jorissen *et al.*, 1995; Kitazato and Ohga, 1995; Bernhard and Alve, 1996), even though some recent species have been documented to be facultative anaerobes (Bernhard and Reimers, 1991; Bernhard, 1993; Alve and Bernhard, 1995). Lack of oxygen could become a limiting factor to the faunas, or at least strongly influence faunal composition (e.g., Bernhard, 1992, 1996; Sen Gupta and Machain-Castillo, 1993).

The oligotrophic open-ocean deep-sea environment (away from hydrothermal vent systems) is in stark contrast to high-productivity regions, and populations of metazoan deep-sea organisms are strongly limited by the food supply (Gooday *et al.*, 1992). Under such conditions we expect that benthic foraminiferal faunas would be dominantly controlled by the food supply (e.g., Jorissen *et al.*, 1995), and we see clear evidence of benthic–pelagic coupling at many locations (e.g., Corliss and Chen, 1988; Gooday, 1993; Mackensen *et al.*, 1993; Rathburn and Corliss, 1994; Smart *et al.*, 1994; Thomas *et al.*, 1995). Some authors suggest that both present faunas (Kaiho, 1994*a*) and faunas throughout the last 100 million years of earth history have been strongly influenced by oxygen levels ($>44\,\mu M\ O_2$, or $>1\ ml\ l^{-1}\ O_2$) even in such overall oxygenated oceans (Thomas, 1989, 1990*a*; Kaiho, 1991, 1994*b*; Loubere, 1994), while others doubt this possibility (e.g., Rathburn and Corliss, 1994; Thomas *et al.*, 1995; Thomas, 1998).

Recent open-ocean calcareous benthic faunas living below shelf depth can be grouped, with much simplification, into three assemblages (Gooday, 1993): (1) relatively eutrophic faunas with high percentages of infaunally dwelling taxa (*Bolivina*, *Bulimina*, *Pullenia*, *Cassidulina*, *Melonis*), many of which belong to the superfamily Bolivinacea, and which are common in the bathyal reaches of continental margins; (2) faunas in open-ocean, oligotrophic regions with a seasonal high food supply (common *Epistominella exigua*, *Alabaminella weddellensis*; also called 'phytodetritus species'); these species react opportunistically to the pulsed food influx; (3) faunas in open-ocean, oligotrophic, $CaCO_3$-corrosive waters including abundant *Nuttallides umbonifera* (Bremer and Lohmann, 1982; Gooday, 1993; Loubere, 1994). The occurrence of these three assemblages is depth dependent, because less food arrives at greater depths: food supply at the ocean floor is a function of primary productivity, preservation, and depth (Herguera and Berger, 1991). Large agglutinated foraminifera in the abyssal oceans show a similar grouping, with Komokiacea in the most oligotrophic central oceanic regions, and astrorhizaceans and hippocrepinaceans in more eutrophic continental margin regions (Gooday, personal communication, 1998). This simplistic subdivision of calcareous benthic faunas into three large assemblages does not reflect the great variety and variability of living deep-sea benthic foraminiferal faunas. *Cibicidoides wuellerstorfi*, for instance, appears to be capable of suspension feeding, sometimes living on objects sticking out above the sediment–water interface. Common occurrence of this and similar taxa has been linked to active bottom currents, which can supply additional food (Lutze and Thiel, 1989; Linke and Lutze, 1993; Schnitker, 1994).

Late Paleocene–early Eocene faunas

We cannot interpret late Paleocene–early Eocene deep-sea faunas using these observations on Recent faunas, because two of the three groups of deep-sea calcareous benthic foraminifera have been common only since the latest Eocene (Fig. 5.3), when the psychrosphere (cold deep-ocean environment) was established (e.g., Benson, 1975). In addition, common Recent species such as *C. wuellerstorfi* and miliolids first occurred in the deep sea in the middle Miocene (Thomas and Vincent, 1987). The Paleogene counterpart of the three Recent groups listed above would read: (1) faunas with common taxa belonging to the superfamily Bolivinacea (e.g., *Brizalina, Bulimina, Coryphostoma, Tappanina, Bolivinoides, Uvigerina*), resembling the Recent faunas along continental margins; (2) faunas dominated by cylindrical taxa (e.g., *Pleurostomella* spp., *Stilostomella* spp., uniserial lagenids); (3) faunas dominated by *Nuttallides truempyi*. There is no early Paleogene counterpart of the faunas dominated by opportunistic, 'phytodetritus' species (Fig. 5.3).

In analogy with Recent faunas, we speculatively interpret faunas with common Bolivinacea as indicative of a continuous, fairly high food supply. Such faunas occurred in the Paleogene at deep open-ocean locations in the equatorial Pacific and Southern oceans, where they presently do not occur. This observation suggests that in the early Paleogene generally more food reached the ocean floor than after the establishment of the psychrosphere (Fig. 5.3). While we cannot be certain that early Paleogene taxa had the same trophic preferences and requirements as their Recent relatives, the early Paleogene Bolivinacea species were generally large, and had many-chambered, decorated tests, suggesting that they were fairly long-lived and non-opportunistic, requiring a fairly high food supply.

Faunas dominated by cylindrical taxa (e.g., *Pleurostomella* spp., *Stilostomella* spp., uniserial lagenids) have no modern analog (Fig. 5.3). These taxa declined strongly in abundance during the late Eocene–early Oligocene cooling, and further during the Miocene cooling (Thomas, 1987, 1992; Thomas and Vincent, 1987). *Stilostomella* spp. and possibly *Pleurostomella* spp. became extinct during the Pliocene in the Atlantic and Indian oceans, and their demise has been interpreted as resulting from increased ventilation of the oceans (Weinholz and Lutze, 1989; Gupta, 1993). Kaiho (1994*b*) tentatively classified such species as low-oxygen taxa. We cannot interpret these faunas with confidence, but we suggest that they might indicate a richer food source than what is common today on the open-ocean floor. This suggestion is supported by observations that lagenid taxa are presently much more common at shelf to upper bathyal depths (where the food supply is overall greater) than in deeper waters.

We do not know the environmental preferences of *N. truempyi*, which became extinct in the late–middle Eocene. We are not even certain about its Recent descendant species, *N. umbonifera*, which has been said to be an indicator of Antarctic Bottom Water in the present oceans, but has also been linked to corrosivity of bottom waters (Bremer and Lohmann, 1982), or to extreme oligotrophy

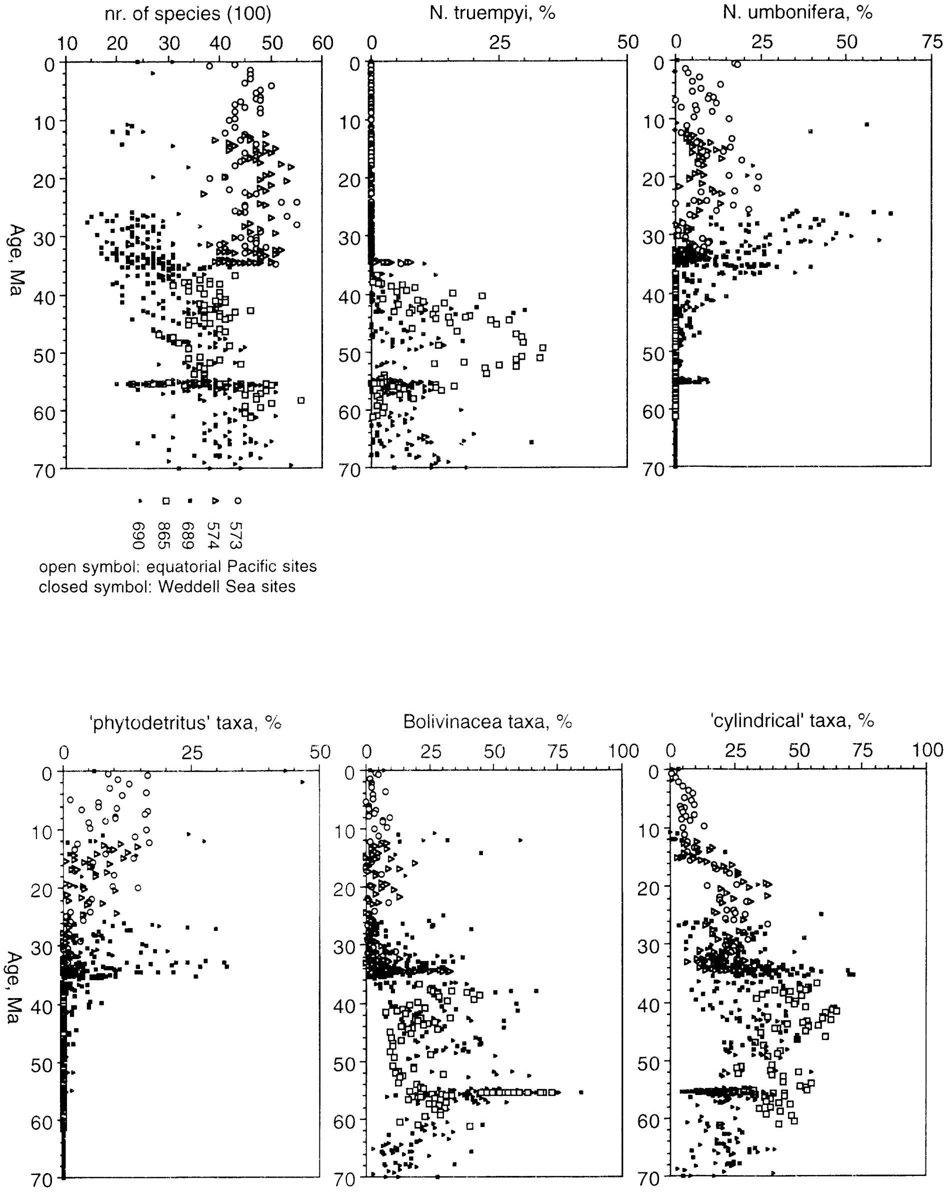

Figure 5.3. Benthic foraminiferal faunal data plotted vs. the timescales of Berggren *et al.* (1995). Sites 573 and 574: eastern equatorial Pacific (Thomas, 1985); Site 865: equatorial Pacific (Thomas, unpublished data); Sites 689 and 690: Maud Rise, Weddell Sea (Thomas, 1990*a*).

(Gooday, 1993; Loubere, 1994). We argue that *N. truempyi* may have been an oligotrophic species, as supported by its common occurrence at the deepest sites (Van Morkhoven *et al.*, 1986; Müller-Merz and Oberhänsli, 1991; Thomas, 1998). This species shows its highest Cenozoic abundance in the middle Eocene at many locations in various oceans (Fig. 5.3; Miller *et al.*, 1992; Oberhänsli, 1997), and became extinct during the period of gradual cooling of deep waters in the middle–late Eocene. We speculate that both *N. truempyi* and *N. umbonifera* indicate relatively oligotrophic conditions, but that *N. truempyi* could not survive in the more corrosive waters that filled the deep oceans from the late Eocene onwards.

We summarize tentatively that *N. truempyi* faunas may have been similar in food requirements to the present *N. umbonifera* faunas, and reflect the most oligotrophic conditions in open ocean (in the depth range where calcareous species occur). The cylindrical taxa might have had somewhat higher food preferences, and the species belonging to the Bolivinacea the highest. Both the Bolivinacea group and the cylindrical-species group were more common at southern high latitudes and in the tropical equatorial Pacific before the establishment of the psychrosphere, which suggests that overall more food reached the sea floor before the establishment of the psychrosphere than afterwards. This is amazing because there is strong evidence that oceanic productivity increased at the establishment of the Antarctic ice sheets (see reviews in Brasier, 1995*a*,*b*; Diester-Haass and Zahn, 1996). In addition, metabolic rates of foraminifera increase with increasing temperatures; therefore, an assemblage at higher temperatures should be more oligotrophic in character than an assemblage with the same food supply at lower temperatures (Hallock *et al.*, 1991).

We can suggest several reasons why lower surface water productivity in the early Paleogene resulted in increased food supply to the benthic faunas. The most obvious explanation is that lower overall oxygenation of the oceans resulting from the higher temperatures caused better preservation of organic matter. In the present oceans only about 1% of organic productivity reaches the sea floor (Jahnke, 1996), and relatively small changes in preservation could thus have a major effect on the total flux of organic matter to the bottom. There is evidence that preservation is linked to oxygenation through indirect links involving bacterial action (e.g., Kristensen *et al.*, 1995; Stigebrant and Djurfeldt, 1996). Better preservation of organic matter in the early Paleogene agrees with suggestions that the fraction of organic matter preserved in the sediments was larger in the early Paleogene (e.g., Kump and Arthur, 1997). There is, however, no clear correlation between oxygenation and organic matter preservation in the present-day oceans (e.g., Hedges and Keil, 1995), and delivery of food to the deep-sea floor in present environments with low productivity and warm waters (thus low oxygenation – Red Sea) is very low (Thiel *et al.*, 1987).

Bacterial action might have played a role in delivering more food to foraminiferal faunas at higher oceanic temperatures. At elevated temperatures the overall metabolic activity of the deep-sea bacteria would have been higher: even psychrophilic bacteria exhibit growth optima at temperatures between 8 and 16 °C (Jannasch, 1994). Higher rates of activity of the bacteria could have resulted in conversion of more dissolved organic carbon into particulate organic carbon

(Deming and Yager, 1992; Jannasch, 1994). Output from the 'bacterial loop' in the pelagic system would thus have resulted in an enhanced food supply for zooplankton, which in turn could result in more food for benthic foraminifera (e.g., through enhanced delivery of fecal pellets).

Possibly not just the quantity of food but also its quality and fluctuations in supply were important. Foraminifera consume their food in many different ways and from many different sources (e.g., Gooday *et al.*, 1992; Kitazato and Ohga, 1995), and species vary in their food preferences. The present 'phytodetritus species' – for which there was no early Paleogene counterpart – consume fresh, little-altered organic material, whereas infaunal taxa consume slightly more degraded material (Kitazato and Ohga, 1995). The mechanism for rapid delivery of little-degraded phytodetrital material might be dependent on high seasonal variability, which may not have existed in the warmer oceans of the early Paleogene (Thomas and Gooday, 1996). Early Paleogene deep-sea species thus may have depended dominantly on sedimentary organic material or on bacteria, rather than on non-degraded fresh phytodetrital material.

It might also be possible that the apparently high delivery of food to the sea floor during the early Paleogene is a sampling artifact. Hallock *et al.* (1991) proposed that sluggish ocean circulation resulted in higher concentrations of nutrients in the intermediate to deep ocean waters. In this model, oceanic productivity would have been low overall, but enhanced in the few regions with upwelling. Uneven site coverage in terms of geography and depth (Thomas, 1998) could thus cause an overestimate of the food supply to the sea floor. This does not appear to be the case for equatorial Pacific Site 865, which was probably located in an oligotrophic region for most of the Paleocene and early–middle Eocene (Bralower *et al.*, 1995*a*,*b*).

THE LPTM EXTINCTION EVENT: FAUNAS AND ISOTOPES

Benthic foraminifera

During the LPTM, calcareous benthic foraminiferal faunas at middle bathyal and greater depths show high rates of extinction (30–50% of species; see Thomas (1998) for a review). At upper bathyal through neritic depths faunas exhibit significant, but temporary, changes in species composition, and extinction was less severe (Thomas, 1998). Abyssal agglutinated foraminiferal faunal change has not been described in much detail, but appears to have been less catastrophic (Kaminski *et al.*, 1996; Kuhnt *et al.*, 1996). After the extinction, low-diversity, high-dominance deep-sea benthic foraminiferal faunas, typical for perturbed communities, were ubiquitous (Thomas, 1998). Thin-walled benthic foraminifera and ostracodes were common (Steineck and Thomas, 1996). Organisms belonging to non-related phyla (foraminifera and ostracodes) were similarly affected, suggesting that the formation of thin-walled shells was probably caused by increasing corrosivity of the deep waters. Comparison of data on productivity and dissolution in open-ocean environments indicates that the high corrosivity was not caused by globally increased productivity (Thomas, 1998).

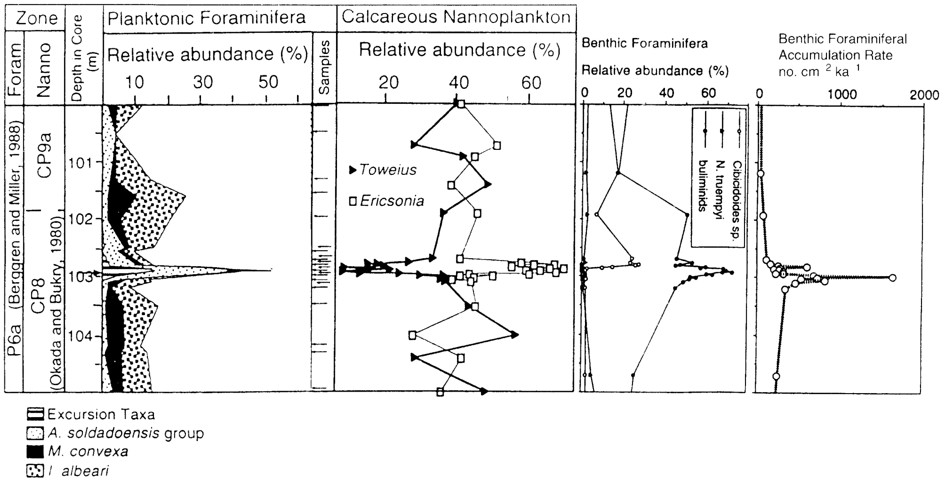

Figure 5.4. Data on the relative abundance of oligotrophic planktonic foraminiferal species and nannofossil species (Kelly *et al.*, 1996), combined with data on relative abundance of benthic foraminifera belonging to the superfamily Bolivinacea (bi/triserial taxa) and benthic foraminiferal accumulation rate (indicator of high food supply). Note co-occurrence of indicators of low productivity in surface water and high food-supply/low oxygenation indicators in the bottom waters just after the latest Paleocene benthic foraminiferal extinction. *A. soldadoensis*: *Acarinina soldadoensis*; *M. convexa*: *Morozovella convexa*; *I. albeari*: *Igorina albeari*.

Thomas and Shackleton (1998) argued that carbon isotopes as well as benthic faunal composition suggest increased upwelling and increased productivity during the LPTM in the Weddell Sea. Runoff, weathering, and possibly nutrient supply from the Antarctic continent probably could have increased during the LPTM (Robert and Kennett, 1994). Post-extinction ostracode faunas in this region had abundant opportunistic taxa, indicative of ephemeral, food-rich environments (Steineck and Thomas, 1996). By contrast, productivity during the LPTM was probably low in the Southern Atlantic (Thomas and Shackleton, 1996). At ODP Site 865 (tropical Pacific), planktonic foraminifera indicate decreased primary productivity during the LPTM (Kelly *et al.*, 1996), but benthic foraminiferal accumulation rates and the relative abundance of Bolivinacea taxa increased, suggesting that more food arrived at the sea floor (Fig. 5.4). A similar increase in Bolivinacea taxa was observed at equatorial Pacific Site 577 (Miller *et al.*, 1987). The abundant *Cibicidoides* species occurring just after the increased abundance of Bolivinacea at Site 865 resemble recent *C. wuellerstorfi* in shape (large and flat), and they may likewise indicate increased bottom-current activity, as also suggested by increased winnowing and very low sediment accumulation rates. At Caribbean Sea Site 999 (Bralower *et al.*, 1997), lower bathyal laminated LPTM sediments do not contain calcareous benthic foraminifera, but only tubular agglutinated benthic foraminifera, which are dominated by suspension feeders (Kaminski, personal communication, 1997). These faunas suggest enhanced bottom-water circulation and low productivity at that site. Both low oxygen conditions and high productivity during the LPTM may have occurred along many continental margins, as interpreted from benthic foraminiferal data (e.g., in the eastern Tethys, Speijer *et al.*, 1995, 1996; in Spanish sections, Ortiz, 1995, and Coccioni *et al.*, 1994; in the Bay of Biscay Site 401, Pardo *et al.*, 1996; in New Zealand sections, Kaiho *et al.*, 1996).

The occurrence of both oligotrophic and strongly eutrophic faunas during the LPTM after the extinction suggests that the trophic resource continuum may have expanded (Thomas, 1998). Globally, productivity decreased especially in open-ocean settings, but locally this effect was counteracted by lower oxygen levels in the water column, resulting in delivery of a larger fraction of organic matter to the sea floor (as at Site 865), or by increased productivity at locations where nutrient-enriched deep waters welled up to the surface (Sites 689 and 690).

Biogeographic differences in deep-sea benthic foraminifera persisted from the LPTM through the early Eocene (Fig. 5.3; Thomas, 1998). Throughout this interval *N. truempyi* was generally more common in the equatorial Pacific than at the Weddell Sea sites, whereas the species belonging to the Bolivinacea were less abundant; there were no clear differences in the abundance of the cylindrical species. This pattern can be interpreted as suggesting higher and/or more sustained delivery of food to the ocean floor in the Weddell Sea during the early Eocene, but not during the late Paleocene. This would suggest a different biogeographic pattern during the early Eocene than has been proposed by Widmark (1995) and Widmark and Speijer (1997) for the Late Cretaceous.

Isotope data

Isotope data on benthic foraminifera from several sites (Figs. 5.5–5.7) demonstrate the difficulties of working with records from short-lived events. The carbon isotope event is at most sites present in 10–20 cm of sediment (Fig. 5.5). *Nuttallides truempyi* is commonly used for isotope analysis, but is rare or absent at sites where Bolivinacea-dominated faunas occur after the extinction (Fig. 5.3). At Site 865, *Bulimina semicostata* specimens from the extinction interval show excursion values, whereas the few specimens of *N. truempyi* in the same samples do not, and thus appear to be reworked (Fig. 5.6). At Site 689 *N. truempyi* is rare in the upper Paleocene throughout lower Eocene, and rare specimens in the excursion interval gave non-excursion values; *Lenticulina* sp. specimens from the same samples gave excursion values (Table 5.1). At Site 690 *N. truempyi* is fairly common and specimens give a typical excursion signature about 20 cm above the last appearance of *Gavelinella beccariiformis*, indicator of the extinction (Kennett and Stott, 1991; Thomas and Shackleton, 1996). *Nuttallides truempyi* is rare or absent in the 20-cm-thick interval just above the extinction (690B-19-4, 51–53 cm through 690B-19H-4, 72–74 cm; Fig. 5.7). Rare *N. truempyi* from this interval gave non-excursion isotope values (Table 5.1), whereas *Bulimina ovula* specimens from these samples gave excursion values. Analyses from ODP Site 215 (Indian Ocean) demonstrated that the excursion is not represented in the recovered sediments, either because of an unconformity or because of non-recovery between Cores 215-11 and 215-12 (Fig. 5.6).

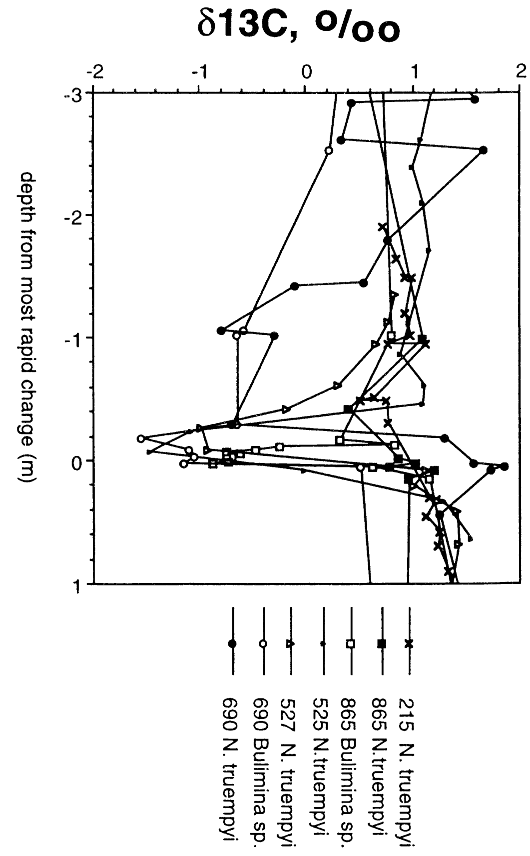

Figure 5.5. Benthic foraminiferal $\delta^{13}C$ record plotted vs. depth in meters above (negative values) or below (positive values) the benthic foraminiferal extinction. Data on *N. truempyi* from Sites 690, 525, and 527 (Thomas and Shackleton, 1996); data on *N. truempyi* and *Bulimina* sp. from Site 865 (Bralower *et al.*, 1995*a*,*b*); data on *N. truempyi* from Site 215 (Zachos *et al.*, 1994; see Table 5.1); data on *Bulimina* sp. from Site 690 (see Table 5.1).

It is therefore extremely difficult or impossible to shed light on possible paleoceanographic differences during the LPTM by comparing isotope records from different sites (e.g., temperature, salinity, productivity) (Figs. 5.5 and 5.8), even at two sites in close proximity such as 689 and 690 (Fig. 5.7). Isotope records can be fairly compared only if we can assume that the records have similar time resolution, which requires extremely detailed work (e.g., Kelly *et al.*, 1996). Work at lower resolution may easily lead to aliasing (e.g., compare Pak and Miller (1992) and Pardo *et al.* (1996) for Site 401). But high-resolution work suffers under the possibility that specimens of different sizes and shapes have been mixed to different depths by bioturbation (Thomson *et al.*, 1995), especially at sites with low sedimentation rates (Kelly *et al.*, 1996).

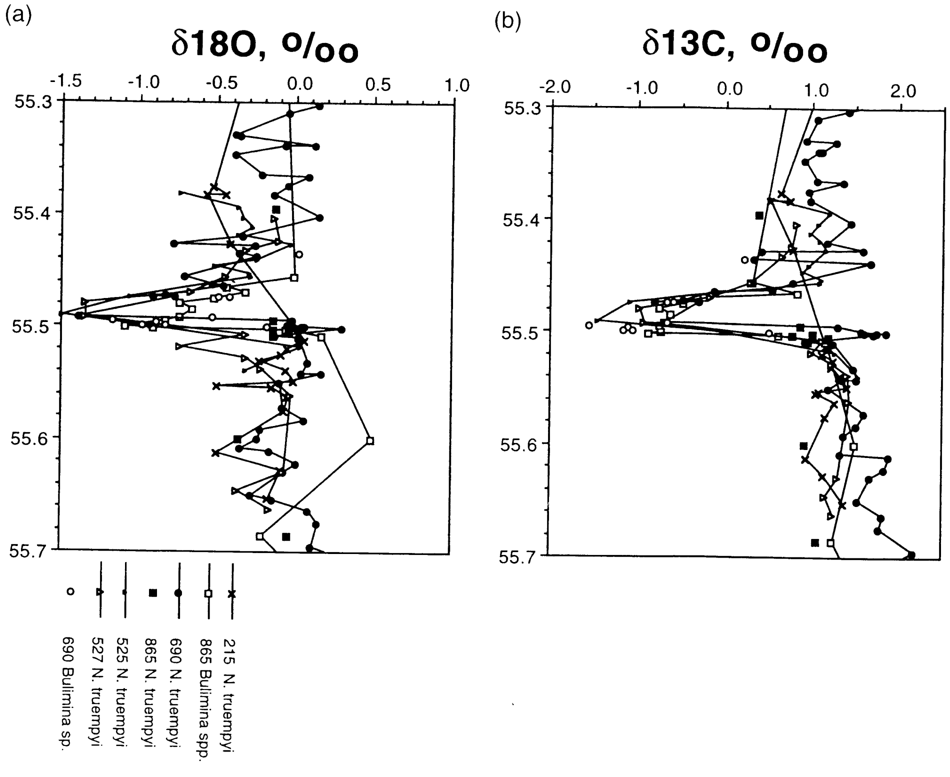

Figure 5.6. Benthic foraminiferal (a) $\delta^{18}O$ and (b) $\delta^{13}C$ data plotted vs. numerical age, using the age model in Thomas and Shackleton (1996). For data sources see Fig. 5.5.

In addition, at many sites different species must be used to capture the isotope excursion across an interval of severe extinction (Fig. 5.8), and for carbon isotopes we cannot simply adjust for the vital effects of different species because the difference in carbon isotope values of epifaunal species (e.g., *N. truempyi*) and infaunal species (e.g., *Bulimina* spp., *Lenticulina* spp.) has been demonstrated to vary according to productivity (e.g., Thomas and Shackleton, 1996).

At Site 690 we have sufficient planktonic and benthic foraminiferal isotope data to evaluate the timing of events (Fig. 5.9). In the interval lacking *N. truempyi* the planktonic faunas contain common *Morozovella aequa*, a shallow-dwelling species that is extremely rare at polar latitudes (Stott and Kennett, 1990; Stott *et al.*, 1990). The benthic foraminifera *Bulimina ovula* in these samples have a typical excursion isotope signature, as do *Acarinina* species (Table 5.1; Fig. 5.9). Specimens of *M. aequa*, however, have excursion $\delta^{18}O$ values but non-excursion $\delta^{13}C$ values, thus differing from specimens of *A. mckannai* in the same samples, which have excursion values for both isotopes (Thomas and Shackleton, 1996). The observation that the *Morozovella* specimens have excursion values for oxygen, but not for carbon, suggests that at some time the surface waters were unusually warm (as also

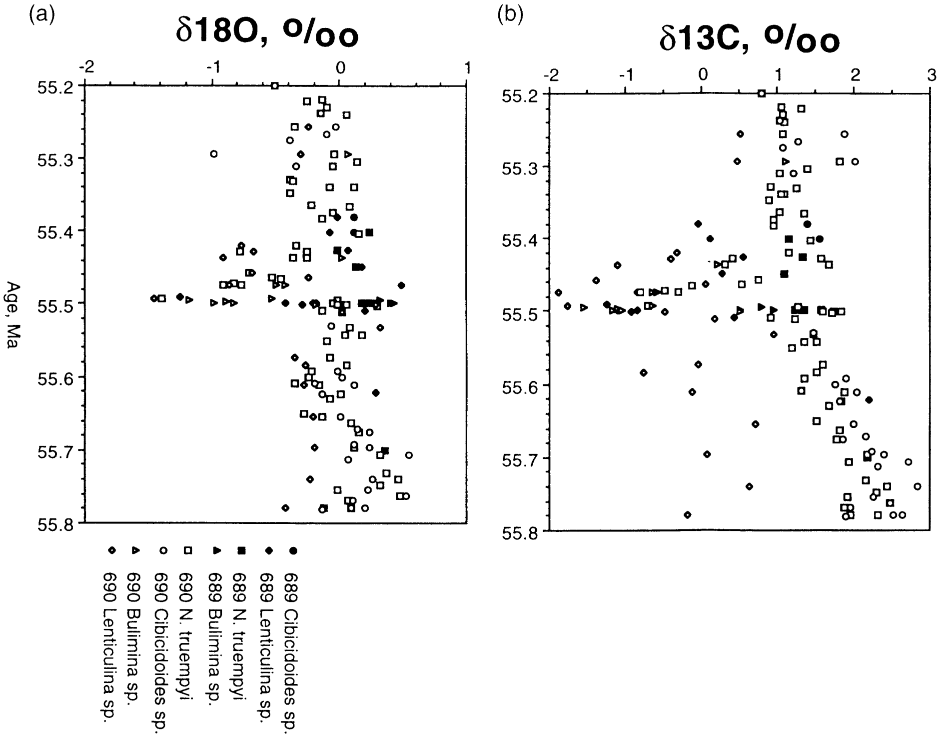

Figure 5.7. Benthic foraminiferal (a) $\delta^{18}O$ and (b) $\delta^{13}C$ data plotted vs. numerical age for Sites 689 (paleodepth 1100 m) and 690 (paleodepth 1900 m; Maud Rise, Weddell Sea). Data after Thomas and Shackleton (1996); see Table 5.1.

demonstrated by the presence of keeled planktonic foraminifera), but did not yet have the anomalous LPTM carbon isotope signature. The warming of surface waters at high latitudes thus started before the major change in carbon isotope values, but we cannot compare these data with those on other specimens (including benthics), because of the problems in mixing specimens by bioturbation (see Kelly *et al.*, 1996).

We provide the following speculative scenario to explain the available data. In the middle Paleocene a long-term period of warming started (e.g., Rea *et al.*, 1990; Corfield, 1995), possibly in response to massive CO_2 fluxes from North Atlantic flood basalts (e.g., Eldholm and Thomas, 1993). High latitudes warmed more than the tropics, resulting in very shallow latitudinal temperature gradients. When a threshold in warming (thus low density) at high latitudes was reached (Zachos *et al.*, 1994), waters could no longer sink to bathyal or abyssal depths, and the oceans at these depths were filled with relatively warm waters derived from subtropical latitudes (e.g., Thomas, 1989; Kennett and Stott, 1991). Alternatively, low density of surface waters at these latitudes may have been caused by increased precipitation and runoff at high latitudes (Bice *et al.*, 1997; Bice *et al.*, Chapter 4, this volume), or the deep-water circulation change might have been triggered by ephemeral low-latitude

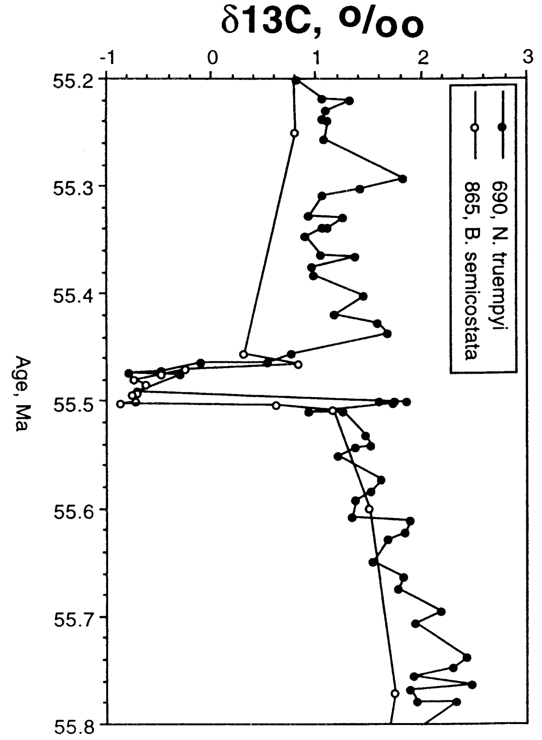

Figure 5.8. Benthic foraminiferal δ^{13}C data vs. numerical age for equatorial Pacific Site 865 (Bralower *et al.*, 1995*a*,*b*) and Weddell Sea Site 690 (Thomas and Shackleton, 1996).

cooling resulting from explosive volcanic eruptions in the Caribbean (Bralower *et al.*, 1997). The change in circulation resulted in rapid warming of the bathyal oceans, which caused dissociation of methane hydrate at depths of about 900–1500 m (Dickens *et al.*, 1995; Matsumoto, 1995; Kaiho *et al.*, 1996). This dissociation released a large amount of isotopically very light carbon in the oceans (Dickens *et al.*, 1997); the methane was oxidized, possibly leading to oceanic oxygen depletion and corrosivity for carbonate (Thomas, 1998).

The episode might have ended when greenhouse gas levels declined, or when heat transport to higher latitudes was no longer efficient at the very shallow temperature gradients, leading to high-latitude cooling and renewed formation of intermediate–deep waters at these latitudes. In this scenario, we would thus see an alternation between two modes of deep-sea circulation: in one mode, deep and intermediate waters would form dominantly at high latitudes; in another mode, deep–intermediate waters would dominantly form at subtropical latitudes, but the deepest ocean basins could still be ventilated from high-latitude regions, as proposed by Wilde and Berry (1982). Isotope data compilations suggest that deep–intermediate waters generally formed to at least some extent at high southern latitudes even

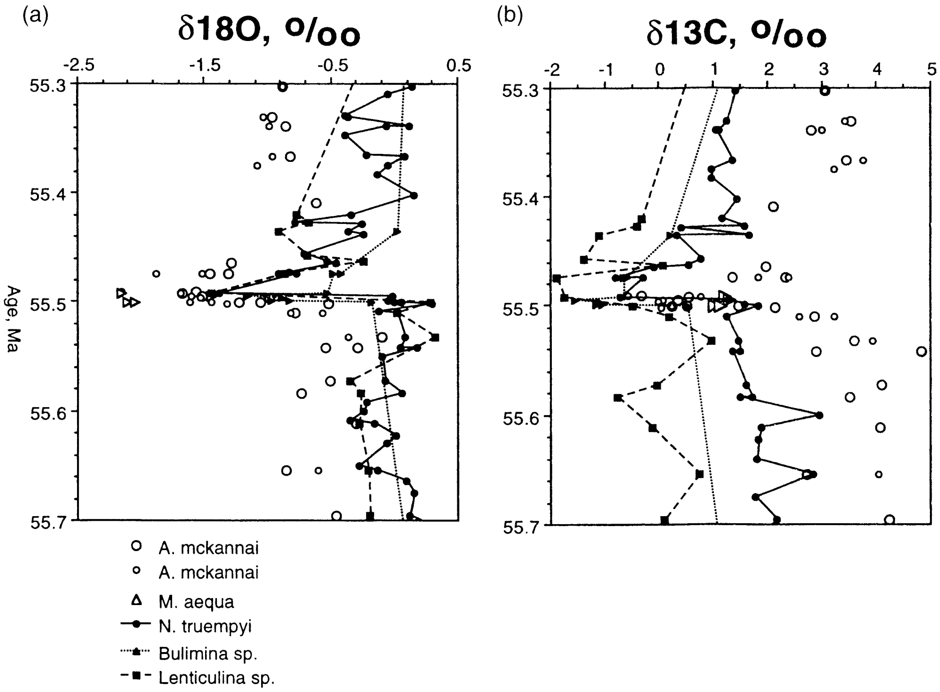

Figure 5.9. Benthic and planktonic foraminiferal (a) $\delta^{18}O$ and (b) $\delta^{13}C$ data for Site 690. Data after Stott *et al.* (1990) and Thomas and Shackleton (1996); see Table 5.1. The small circles indicate specimens of *A. mckannai* in the size range 212-250 mm; larger circles indicate specimens in the range 250-350 mm.

during the warm early Paleogene (e.g., Seto, 1995; Oberhänsli, 1997), and climate modeling indicates that deep convection occurs close to the Antarctic under most conditions (Bice *et al.*, Chapter 4, this volume). But information on the LPTM (e.g., Pak and Miller, 1992, 1995) suggests that relatively large volumes of deep–intermediate waters may have been derived from low latitudes for at least part of the latest Paleocene through early Eocene.

In such a scenario the benthic foraminiferal extinction was caused by multiple, geographically variable, factors. Methane oxidation in the oceans could have increased corrosivity while lowering oxygenation, and the degree of oxygen use could have been geographically variable (Dickens *et al.*, 1997). In some oceanic regions lowered productivity at a time of extreme warming and low windspeeds (Rea, 1994) could have been a factor, but at other locations increased preservation of organic matter counteracted the lowered productivity (e.g., equatorial Pacific Site 865). At yet other locations productivity might have increased because of increased weathering, precipitation, and nutrient runoff into the oceans (e.g., Tethys: Charisi and Schmitz, 1995; Speijer *et al.*, 1995, 1996; Speijer and Schmitz, 1998; New Zealand: Kaiho *et al.*, 1996). And at other locations productivity might have increased as a result of changing patterns of deep-oceanic circulation, causing increased upwelling of deeper waters with more nutrients (e.g., Maud Rise: Thomas and Shackleton, 1996).

At first sight, lower productivity appears unlikely to have played a role in the late Paleocene benthic extinction, because deep-sea benthic foraminifera did not suffer major extinction during the collapse of surface-ocean productivity at the end of the Cretaceous (Thomas, 1990*b*). We suggest that the end-Cretaceous collapse had less effect because it probably occurred on such a short term that detritus feeders were not affected. Comparatively, the decrease in productivity during the latest Paleocene and earliest Eocene was a long-term effect (e.g., Corfield, 1995; Aubry, 1998*b*). In the benthic foraminiferal faunas this long-term decline manifests itself in the gradually decreasing upper depth limit of the (inferred oligotrophic) *N. truempyi* assemblages (Tjalsma and Lohmann, 1983).

HOW MANY WARM EVENTS (HYPERTHERMALS)?

The occurrence of the LPTM demonstrates that short-term, rapid climate change is possible during a period of greenhouse climate in the absence of climate feedbacks that depend on the presence of polar ice. An obvious question is whether such rapid climate change occurred only once, or whether it occurred more often, possibly modulated by Milankovitch forcing. This question is of major importance for the use of paleoceanographic data to set boundary conditions for climate models: if short-term climate fluctuations between very warm periods (which we will call 'hyperthermals') and background warm climate were common, we must be extremely careful in data selection and time correlation to prevent aliasing.

There are some indications in isotope records that there may have been more than one hyperthermal (Kennett and Stott, 1990; Lu and Keller, 1993; Seto, 1995; Fig. 5.10; see also Fig. 5.1). In all these records, however, the possible 'events' are documented by one data point only, in some cases next to unconformities. For several reasons it remains difficult to obtain records with the resolution required to document events of such short duration. Firstly, the thickness of the sediments of the LPTM is in many sites on the order of 10–20 cm (Fig. 5.5). Such a small amount of material may not be recovered in deep-sea drilling sites, even at good recovery rates (e.g., Site 577, Aubry, 1998*a*; Site 215, this paper). Secondly, the lower Eocene record has proven to be less complete and more commonly riddled with short-term unconformities than had been assumed (Aubry, 1995, 1998*a*). We thus need high-resolution biostratigraphy in order to ascertain the completeness of each record. Thirdly, we cannot use benthic foraminiferal events to indicate at which level we will find an isotopic event even if the record is complete and we sample at high resolution, because the benthic faunas after the extinction show major fluctuations, probably resulting from the fluctuating abundances of 'disaster' or 'opportunistic' taxa (Thomas, 1998). In short, we must obtain highly detailed records from sites with excellent recovery and high-quality biostratigraphic data, where we can demonstrate the absence of unconformities. The highly detailed records would have to be obtained on some parameter that is quick, easy, and cheap to measure, because hundreds of observations are required. Possibly bulk isotopic records might be used (Shackleton and Hall, 1990), and downhole logging information on recently

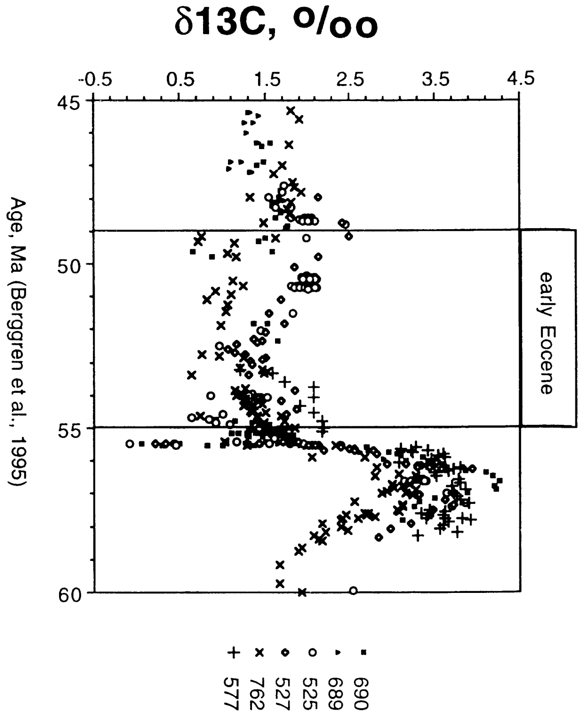

Figure 5.10. Bulk carbon isotope records from several sites, with numerical ages adjusted to Berggren *et al.* (1995). Sites 689 and 690: Shackleton and Hall (1990); Site 762: Thomas *et al.* (1991); Sites 525 and 527: Shackleton and Hall (1984); Site 577: Shackleton *et al.* (1985).

drilled ODP holes has great promise because recovery problems are circumvented (Norris, 1997*b*). Until we have such records, we cannot know whether the LPTM event was unique, or one of a series of events (Fig. 5.11).

CONCLUSIONS

1. Late Paleocene–early Eocene deep-sea environments cannot easily be characterized using deep-sea benthic foraminiferal faunas, because the most common Recent deep-sea faunal assemblages in open ocean originated in the late Eocene. There was no early Paleogene analog for faunas dominated by 'phytodetritus' species, i.e., opportunistic taxa, which in the present oceans are common in regions with a fluctuating primary productivity and supply of little-altered organic matter to the sea floor.
2. Early Paleogene benthic foraminiferal faunas may be indicative of overall higher supply to the ocean floor, even at lower primary productivity. The higher supply might have resulted from increased preservation of organic matter at lower oxygenation.
3. At least one short-term climate upheaval occurred during the late Paleocene–early Eocene 'greenhouse': the Late Paleocene Thermal

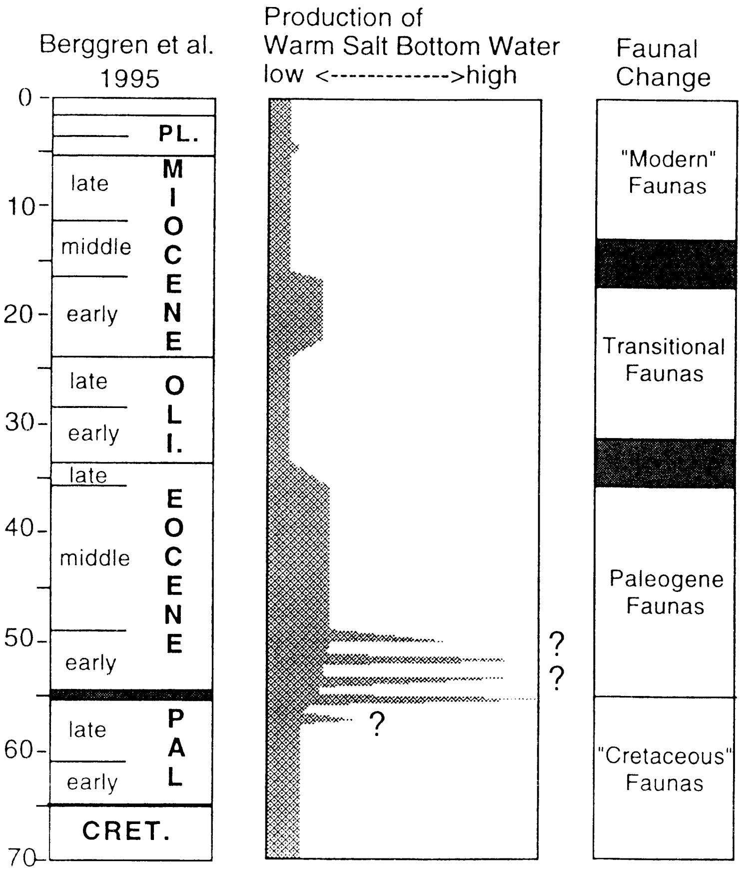

Figure 5.11. Speculation on possible occurrence of hyperthermal events in the early Eocene. During hyperthermals, deep-intermediate oceans were dominated by warm, high-salinity waters derived from subtropical sources, and climate was very warm, with extremely low latitudinal temperature gradients.

Maximum. We speculate that long-term high-latitude warming resulted in reversal of deep-ocean circulation so that waters at bathyal depths were derived from subtropical latitudes, resulting in increased deep-sea temperatures, leading to methane hydrate dissociation.

4. The benthic foraminiferal extinction was a complex event. Global productivity may have declined, while oxygenation decreased as a result of methane dissociation and warming of deep waters. Productivity increased locally as a result of increased runoff and nutrient supply, or upwelling; locally more food reached the ocean floor even as productivity declined.
5. We do not know whether other similar warm periods ('hyperthermals') occurred or were common in the early Paleogene; we thus do not know whether a warm climate would be inherently stable or unstable.

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