Abrupt deep-sea warming, palaeoceanographic changes and benthic extinctions at the end of the Palaeocene

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A remarkable oxygen and carbon isotope excursion occurred in Antarctic waters near the end of the Palaeocene (~57.33 Myr ago), indicating rapid global warming and oceanographic changes that caused one of the largest deep-sea benthic extinctions of the past 90 million years. In contrast, the oceanic plankton were largely unaffected, implying a decoupling of the deep and shallow ecosystems. The data suggest that for a few thousand years, ocean circulation underwent fundamental changes producing a transient state that, although brief, had long-term effects on environmental and biotic evolution.

WE describe foraminiferal oxygen and carbon isotope changes over the Palaeocene/Eocene transition at high stratigraphic resolution in an Antarctic sedimentary sequence. We infer palaeoenvironmental changes that caused major deep-sea benthic faunal extinctions at the end of the Palaeocene, perhaps the largest during the last 90 Myr (refs 1, 2). This event profoundly affected oceanic benthic communities deeper than the continental shelf (>100 m; neritic zone) [1-4] resulting in a 35-50% species reduction of benthic foraminiferal taxa[4,5]. The extinction level pre-dates the last appearance of *Morozovella velascoensis* (at the tropical P6a/P6b boundary[1,6,7]) and is close to other biostratigraphic levels at or close to the Palaeocene/Eocene boundary[1,8]. It is also located within one of the largest negative $\delta^{13}C$ changes of the Cenozoic, beginning in the late Palaeocene at ~60 Myr and continuing into the early Eocene[6,9-11]. The $\delta^{13}C$ values immediately preceding the event are the highest for the entire Cenozoic[9]. This event is also located within a long-term negative $\delta^{18}O$ trend of >1‰ (refs 6, 9, 12-15), interpreted[16] to reflect a warming of Antarctic surface waters by ~5 °C.

What could have caused such extensive changes in the ocean deeper than the continental shelf, an ecosystem that forms >90% by volume of the Earth's total habitable environments[17]? Before now, the extinction event has been studied at insufficient stratigraphic resolution to determine its speed and potential causes. During our earlier stable isotope investigations[12,16] of Antarctic Palaeogene sequences, we discovered a sudden, brief, striking negative isotope excursion in planktonic and benthic $\delta^{13}C$ and $\delta^{18}O$ coinciding with the major benthic foraminiferal extinctions[5] close to the Palaeocene/Eocene boundary. Our subsequent detailed studies reveal correlations in the timing of a number of isotopic changes and the extinctions (Figs 1, 2), thus providing a stronger basis for evaluation of the possible environmental changes that caused them.

The Palaeocene/Eocene transition has been examined in Ocean Drilling Project (ODP) hole 690B (65° 09′ S, water depth 2,914 m) on the flank of Maud Rise, Weddell Sea, Antarctica. Palaeodepths during the Palaeocene/Eocene transition were ~2,100 m (ref. 12). The Palaeogene sequence[18,19] consists of a nannofossil ooze with well-preserved planktonic and benthic foraminifera. There is a minor terrigenous sedimentary fraction (5-15% clay and ~10-15% mica)[18]. Colour photographs of the cores indicate a lack of bioturbation for several centimetres (core 19-3, 75-65 cm) encompassing the extinction level, whereas underlying and overlying sediments were clearly bioturbated. The cores show no drilling disturbance.

Chronology and approaches

The Palaeocene/Eocene boundary in hole 690B is located in a long reversed-polarity zone identified[20,21] as Magnetochron 24R. As before[20], we place the boundary magnetostratigraphically at 57 Myr within Chron 24R[21,22] at 166 m below sea floor (mbsf). This is close to the first appearance of *Planorotalites australiformis* (which defines the AP4/AP5 boundary at 170.05 mbsf; core 19-3, 15-18 cm) and below the first appearance of *Acarinina wilcoxensis berggreni* (159.8 mbsf). The principal benthic extinction level (core 19-3, 70 cm) is ~40 kyr older, and is assigned an age of 57.33 Myr (Fig. 1). Our chronology is based on an age for the top of Chron 25N (185.2 mbsf) of 58.64 Myr and the bottom of Chron 24N (154.62 mbsf) of 56.14 Myr (ref. 21). This provides an average sedimentation rate of 1.23 cm per 1,000 yr (1 cm in ~800 yr). In low-latitude sequences, the Palaeocene/Eocene boundary has been correlated to the last appearance of *M. velascoensis*, marking the boundary between the P6a and P6b zones with an assigned age of 57.8 Myr (refs 6, 7, 22). More recent correlations[23] place the younger boundary at 57 Myr and within zone P6b, postdating the extinction of *M. velascoensis*. This species is not present in site 690 and the AP4/AP5 boundary remains to be accurately correlated with low-latitude biostratigraphy including the P6a/P6b boundary. We believe that the chief deep-sea extinction level near the end of the Palaeocene is synchronous in marine sequences, and that offsets between our age estimates (Fig. 1) and others[6,22] result either from biostratigraphic miscorrelations or the necessarily broad age interpolations between magnetochrons at site 690.

Foraminiferal samples were analysed for oxygen and carbon isotope composition between 174.00 mbsf (57.59 Myr) and 166.95 mbsf (57.06 Myr) at a maximum sampling interval of 10 cm, a stratigraphic resolution of ~4-7.5 kyr. We located the extinction horizon within a 4-cm interval between 170.62 mbsf (core 19-3, 72 cm) and 170.58 mbsf (core 19-3, 68 cm), estimated to represent ~3 kyr (57.334 and 57.331 Myr) (Fig. 2). This we sampled at 1-cm intervals, providing an age resolution of ~800 yr (Fig. 2).

Isotope analyses were conducted on monospecific samples of the planktonic foraminifers *Acarinina praepentacamerata*, *Subbotina patagonica* and *Subbotina varianta*, and the benthic foraminifer *Nuttallides truempyi*. This benthic species occurs throughout the record, except for a brief gap close to the extinction event. We used standard approaches to extract and prepare the foraminifera for faunal and isotopic analyses[12]. Oxygen isotopic palaeotemperatures were determined assuming an ice-free world (mean ocean water $\delta^{18}O = -1.2$‰ relative to present day[13]).

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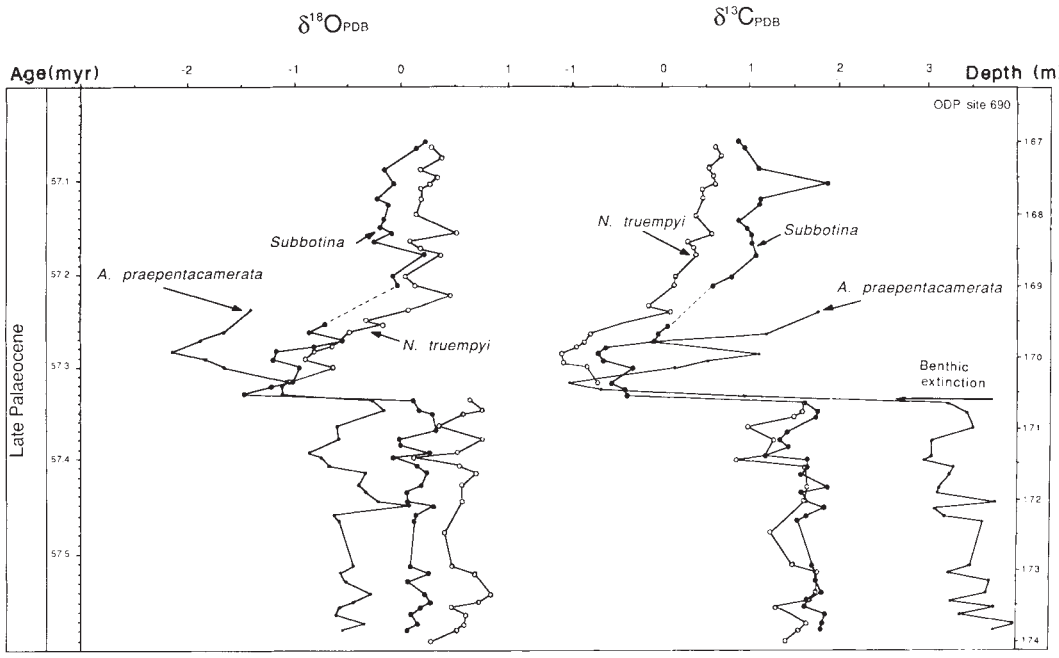

FIG. 1 Changes in $\delta^{18}O$ and $\delta^{13}C$ ($[(^{18}O/^{16}O)_{sample}/(^{18}O/^{16}O)_{standard}-1]\times1{,}000$; $[(^{13}C/^{12}C)_{sample}/(^{13}C/^{12}C)_{standard}-1]\times1{,}000$) of the planktonic foraminifers *Acarinina praepentacamerata* and *Subbotina* and the benthic foraminifer *Nuttallides truempyi* in the latest Palaeocene (57.0 to 57.6 Myr) of Ocean Drilling Program (ODP) hole 690B, Maud Rise, Antarctica. Note the sharp negative shifts at 57.33 Myr coinciding with the main level of extinction in benthic foraminifera. Oxygen isotope values have been adjusted to account for non-equilibrium effects[6,12]. The gap in isotope records of *Subbotina* is between the last appearance of *S. patagonica* and the first appearance of *S. varianta*. The upper extent of isotope records of *A praepentacamerata* marks the disappearance of this species. Age framework is after ref. 23. The age assignments will change, however, because the age of the Palaeocene/Eocene boundary is being revised to 2 Myr younger[56]. Depth scale at right represents metres in section below sea floor. Samples were analysed with a Finnigan MAT 251 mass spectrometer linked to a Carousel-48 automatic carbonate preparation device. The laboratory gas standard is calibrated to PDB by cross-calibration using the standard NBS 20. Precision is 0.1‰ or better for both $\delta^{18}O$ and $\delta^{13}C$. We applied the standard $\delta^{18}O$ correction factor of +0.5‰ to *Nuttallides truempyi*[6,12]. No correction factor was made to $\delta^{13}C$ for this taxon.

The terminal Palaeocene isotopic excursion

The planktonic foraminifer *A. praepentacamerata* records the lowest oxygen and the highest carbon isotope values (Fig. 1). Such values are consistent with a near-surface habitat, possibly during the austral spring/summer months[12,16]. The species of *Subbotina* record higher $\delta^{18}O$ and lower $\delta^{13}C$ values (Fig. 1) than *A. praepentacamerata*, indicating a deeper-water planktonic habit and/or a preference for cooler months of the year[16]. As expected in a thermally stratified ocean with deep waters richer in nutrients, the highest $\delta^{18}O$ and lowest $\delta^{13}C$ values are shown by the benthic foraminifer *N. truempyi*.

Between 57.6 and 57.33 Myr, isotope values showed relatively little change (Fig. 1). Surface water isotopic temperatures are estimated to have been 13–14 °C and deep water temperatures ~10 °C. The oxygen and carbon isotopic composition of planktonic and benthic foraminifera (Fig. 1) show a considerable excursion between ~57.33 and 57.22 Myr. This excursion (the 'terminal Palaeocene isotopic excursion') began abruptly at ~57.33 Myr with a conspicuous decrease in $\delta^{18}O$ and $\delta^{13}C$ values, followed by a return to values only slightly lower than before the excursion (Fig. 1).

Oxygen isotopic changes. Between ~57.33 and 57.32 Myr, the marked decrease in $\delta^{18}O$ occurred in all three foraminiferal groups. The change was largest (2.0‰) in the benthic forms, intermediate (1.5‰) in deeper-dwelling planktonics and smallest (1.0‰) in shallow-dwelling planktonics. Surface water temperatures increased to ~18 °C. This isotopic shift coincided with the benthic extinctions (Figs 1 and 2). Isotope values in shallow surface water further decreased to ~ −2.2‰, suggesting temperatures of ~21 °C, between 57.31 and 57.28 Myr, probably the warmest of the Cenozoic[16]. In contrast, the isotope temperatures of *Subbotina* decreased after 57.32 Myr. The rapid warming is associated with an increase in warm subtropical planktonic microfossils in Antarctic waters, including discoasters[24] and morozovellids. Also, an associated peak in kaolinite suggests warm, humid climate on Antarctica, the inferred source of the clays[25].

A brief gap (20 kyr) exists in the range of *N. truempyi* during the excursion (Fig. 1). When *N. truempyi* reappeared at ~57.31 Myr, its oxygen isotope values were similar (−1.1‰) to the planktonic forms (Fig. 1). Thus, deep waters warmed to temperatures close to those at the ocean surface, temporarily eliminating the vertical temperature gradient at this location. This gradient was re-established ~30 kyr after the initial isotope decrease (Fig. 1). Following the warming peak, temperatures decreased, but remained ~1–2 °C higher than before the beginning of the excursion (Fig. 1).

Carbon isotopic changes. The pattern of $\delta^{13}C$ change during the excursion (Fig. 1) was similar to that of $\delta^{18}O$: a marked initial decrease in values at ~57.33 Myr followed by a more gradual increase. The change was very large (>4‰) in the surface-dwelling planktonic *A. praepentacamerata*. *Subbotina* showed a 2.0‰ decrease. The absence of benthic values during the shift prevents a detailed comparison, but values rapidly decreased by at least 2.6‰, from 1.5‰ at 57.33 Myr to −1.1‰ by 57.29 Myr. From ~57.33 to 57.31 Myr, $\delta^{13}C$ values of surface and deep planktonics are similar; *Subbotina* values are between ~ −0.5‰ and −0.8‰. Benthic $\delta^{13}C$ values at ~57.32 Myr are almost identical to surface-water planktonic values. The large $\delta^{13}C$ gradient (~2.0‰) that had existed between surface and deep waters before the excursion was virtually eliminated at ~57.32 Myr. After 57.30 Myr, surface-water $\delta^{13}C$ values began to increase again and a vertical gradient was re-established.

A decrease in benthic foraminiferal diversity (Fig. 2) coincided with the $\delta^{18}O$ and $\delta^{13}C$ changes in the deeper-dwelling planktonic *Subbotina* and the $\delta^{18}O$ changes in the shallow-dwelling planktonic *A. praepentacamerata*. Most of the reduction in benthic diversity had already occurred, however, before the initiation (~3 kyr later) of the principal $\delta^{13}C$ decrease in the surface-dwelling *A. praepentacamerata* (Fig. 2). Thus, the interval of rapid isotope change is not the result of a hiatus. Within ~3 kyr, surface water temperatures at hole 690B are estimated to have increased by 3–4 °C, with a total warming in subsurface waters of 6 °C in 6 kyr. The $\delta^{13}C$ shift (2.0‰) in *Subbotina* lasted 6 kyr. Most (3.5‰) of the $\delta^{13}C$ shift in *A. praepentacamerata*, which began slightly later (Fig. 2), occurred within 11 kyr,

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although the trend continued for more than 20 kyr. After the shift, the vertical $\delta^{18}O$ and $\delta^{13}C$ gradients were temporarily eliminated or even reversed.

Changes in carbon isotope gradients ($\Delta\delta^{13}C$) between shallow and deep forms (Fig. 2) indicate that characteristics of the vertical water column differed before, during and after the isotope excursion. A distinct $\delta^{13}C$ gradient between surface and deep waters existed before 57.33 Myr. Furthermore, at that time the similarity between the $\delta^{13}C$ composition of the benthic foraminifera and the subbotinids suggests the existence of a midwater zone with a strong minimum in oxygen concentration. During the $\delta^{13}C$ shift beginning at ~57.33 Myr, the gradient between all groups was eliminated (Fig. 2). After 57.29 Myr, the vertical $\delta^{13}C$ gradient was gradually re-established (Fig. 1). But after re-establishment, by ~57.28 Myr, a distinct isotope offset existed between benthic foraminifera and the subbotinids, suggesting a reduction in the strength of the oxygen minimum zone.

Biotic changes

Large changes in the taxonomic composition of benthic foraminifera clearly define the extinction event and the pattern of decreasing diversity[5]. Before the extinction event, the simple diversity of benthic foraminiferal assemblages (>150 μm) averaged ~55-60 species (Fig. 2) or higher[5]. Assemblages containing abundant benthic foraminifera include a wide range of morphotypes inferred to be of both infaunal and epifaunal habit[5,26], including trochospiral and other coiled forms. A considerable decrease in diversity (>150 μm) coincides with the $\delta^{18}O$ shift (Fig. 2). Simple diversity dropped by 72% from ~60 to 17 species (>150 μm) in <4 cm (<3 kyr). Many distinctive taxa such as *Stensioina beccariiformis* and *Neoflabellina* disappeared early and rapidly (<1.5 kyr) during the isotope shift marking the extinction event (Fig. 2). Most trochospiral forms such as *N. truempyi* had disappeared by the midpoint of the shift. Most lost taxa are not observed again even in the immediately overlying 1-cm sample interval, supporting sedimentary and isotope evidence for a lack of bioturbation over this interval. Benthic foraminifera (>150 μm) also became uncommon to rare (as low as ~30 specimens per sample) during the extinction event. Small specimens (<150 μm), however, remained abundant throughout this interval. Ostracods decreased markedly in diversity and abundance during the shift, leaving a rare assemblage composed almost exclusively of small, smooth, thin-walled forms. Both planktonic and benthic foraminiferal assemblages are well preserved throughout, showing no apparent increase in dissolution. During this episode, planktonic foraminifera and calcareous nannofossils, which remained abundant, increased in diversity in hole 690B (refs 20, 24) and elsewhere in the oceans[27], possibly as a result of ocean surface warming.

The 5-kyr interval immediately following the isotope shift (Fig. 2) is marked by low diversities and abundances of benthic foraminifera (>150 μm fraction). Coiled forms are almost completely absent, leaving an assemblage dominated by relatively small and thin-walled uniserial, triserial and other forms typical of an infaunal habitat[5,26]. The relative increase in abundances of small specimens of benthic foraminifera associated with a decrease in diversity suggests conditions low in oxygen and high in nutrients[5,28]. The diversity of benthic foraminiferal assemblages (>150 μm) increased thereafter (Fig. 2) to an average of ~30 species (>150 μm). This increase resulted, in part, from the reappearance of forms previously present, but a high proportion of species (~35%) in hole 690B became truly extinct at the beginning of the excursion[5].

Major, roughly coeval extinctions of benthic foraminifera have been recorded in other deep-sea sequences[1,7,29,30] and in upper bathyal marine sequences in Trinidad[3], the Reichenhall and Salzburg Basins, Austria[31] and northern Italy[32]. In contrast, benthic foraminiferal assemblages on the continental shelves were little affected. The loss of so many characteristic Late Cretaceous and Palaeocene deep-sea taxa produced a deep-sea benthic foraminiferal assemblage of Tertiary character[1]. The biotic crisis at the K/T boundary was opposite, in that elements of the oceanic plankton and shallow benthic communities were considerably reduced, whereas deep-sea benthic foraminiferal assemblages experienced little change[4,33-36].

Interpretations of biotic changes

An important question relates to the large-scale character of the oceanographic changes that caused these rapid biotic changes. The lack of major extinctions in oceanic plankton and in shallow-water benthic communities eliminates any possibility that the changes were caused by a bolide impact with the Earth, as has been suggested for the terminal Cretaceous extinctions[34]. A more plausible explanation would involve an oceanic cause. The extinctions were clearly driven by processes that preferentially affected the deep-sea biota below the thermocline or continental shelf. The process that caused the extinctions, although not instantaneous, was remarkably rapid (<3 kyr), and any proposed mechanism must have had the capacity to affect vast volumes of the deep ocean rapidly. The extinctions occurred at about the rate of the replacement time of the oceans (currently ~1 kyr (ref. 37), although possibly slower in the early Palaeogene). Also, the speed and magnitude of the associated temperature increase implies global, not solely oceanic, warming involving strong positive feedback mechanisms. The superposition of the rapid, negative $\delta^{13}C$ and $\delta^{18}O$ excursions upon similar, more gradual trends during the late Palaeocene to early Eocene[13,4] suggests a threshold event similar to the oxygen isotope shift near the Eocene/Oligocene boundary[28], although in the opposite sense. Our data indicate that an essentially isothermal water column developed, with deep waters in the Antarctic warming more than shallow waters. The rapidity of the initial changes and the gradual return (over ~100 kyr) to isotope values similar to those before the event suggest an ocean-climate system temporarily in disequilibrium[37]. As deep waters warmed, most benthic foraminiferal species (>150 μm) were eliminated at this location. The disappearance of many more inferred epifaunal than infaunal benthic species (>150 μm) indicates that species living in sediments were more likely to survive. Nevertheless, the disappearance of many infaunal forms indicates that the changes also affected the infaunal environment. Lack of bioturbation early in the excursion suggests that burrowing organisms were also severely affected.

Three main hypotheses have been proposed to account for the deep-sea benthic crisis at the end of the Palaeocene. They are: (1) a rapid warming of the deep ocean and a change in bottom water sources[6]; (2) a deep-sea oxygen deficiency due to the sudden warming and change in circulation of deep water[5,11,12,19,36]; and (3) a sharp drop in surface ocean productivity that reduced trophic resources available for deep-sea benthic organisms[10,39,40].

The benthic extinctions occurred at the same time as rapid warming of deep waters and before the shift in $\delta^{13}C$ in the surface planktonic foraminifera. They therefore occurred before any associated large change in surface water processes that might have affected primary production. Although no large changes are evident in calcareous nannofossils at this location (A. R. Edwards, personal communication), elsewhere an earliest Eocene peak in taxonomic turnover was interpreted as a response to decreasing primary production[41]. Substantial productivity reduction is generally accompanied by a decrease in biogenic calcium carbonate accumulation, which is not observed at the Palaeocene/Eocene boundary at site 690. Considerable reduction in delivery of organic matter to the deep sea during the faunal crisis is unlikely[4,11,12,36], although it could have occurred later during the isotope excursion.

It is more likely that the benthic extinctions were caused by the rapid temperature increase of deep waters and associated reduction of oxygen concentrations[4,16]. In the modern ocean,

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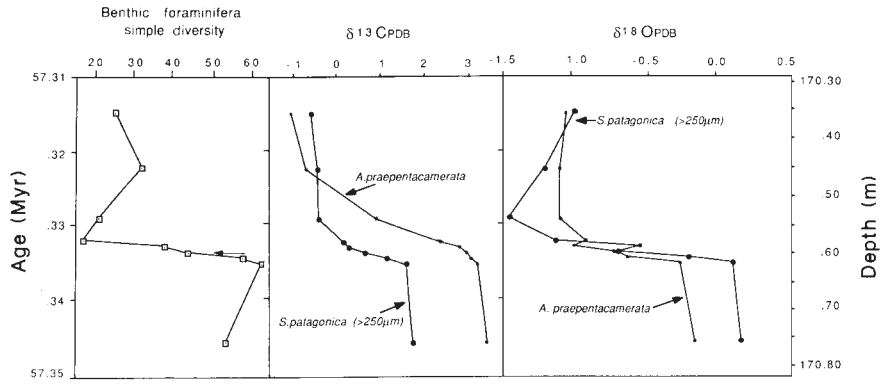

FIG. 2 Changes in oxygen and carbon isotope composition of the planktonic foraminifers *A. praepentacamerata* (>63 μm fraction) and *Subbotina patagonica* (>250 μm fraction) and in simple diversity of benthic foraminiferal assemblages at high stratigraphic resolution during the negative isotope excursion in the latest Palaeocene shown at 57.33 in Fig. 1 (ODP hole 690B). Note the large, rapid decrease in diversity coinciding with the negative oxygen isotope shift, followed by a return to higher diversities. The large latest-Palaeocene extinction in benthic foraminifera coincides with the drop in diversity. Arrow at left indicates the last appearance of a distinctive Palaeocene benthic foraminifer *Stensioina beccariiformis*. All benthic foraminifera (>150 μm) were picked from samples in the early part of the excursion to determine simple diversity. Because specimens were abundant before the excursion, simple diversity was determined by partial picking and thorough scanning of sample residues (>150 μm). No relationship is apparent between the original dried weight of samples and the simple diversity and abundances of benthic foraminifera. Depth scale at right represents metres in section below sea floor.

cold (<6 °C) deep waters contain sufficient oxygen to oxidize organic matter fully and to maintain diverse benthic communities in most areas. At the same nutrient levels and Redfield ratios, however, deep waters of 10 °C would not contain sufficient preformed oxygen to avoid anoxia unless atmospheric oxygen levels were considerably higher or primary production lower than at present. Modelling studies suggest that atmospheric oxygen levels were possibly 10% higher in the early Palaeogene[42], in which case deep waters of 10 °C could have remained aerobic if overall nutrient levels were no higher than in the modern ocean. But at temperatures higher than 15 °C, as at the Palaeocene/Eocene boundary, deep waters would almost certainly have been depleted in oxygen. Deep waters are unlikely to have become completely anoxic during the excursion because there is no increase in organic carbon accumulation at hole 690B and possibly elsewhere[43]. Therefore a balance must have been maintained between deep-sea oxygen levels and the supply of organic carbon from surface waters and of preformed nutrients in deep waters[44]. The decrease in $\delta^{13}C$ gradients suggests reduced primary production, contrary to benthic foraminiferal trends.

Interpretations of oceanographic changes

What process could have triggered the rapid oceanic warming and inferred reduction in deep-sea oxygen concentrations that produced the extinctions? It has been proposed[4-6,11,12] that the rapid warming resulted from the concurrence of an almost total dominance in the oceans of warm saline deep waters produced at mid-latitudes, and a reduction of high-latitude deep water sources, in an extreme example of the Proteus ocean model[12]. Modelling studies[45] suggest that deep-ocean oxygen concentrations are primarily controlled by deep-water formation processes. The relative importance of high- and mid-latitude sources of deep ocean waters during the early to middle Palaeogene is controversial (G. Mead and D. Hodell, manuscript in preparation; and refs 5, 6, 12). In the modern ocean, almost all dense, oxygen-rich waters are produced at high latitudes as a result of cold temperatures in combination with moderately high salinities[37]. Saline, dense waters also form in the Mediterranean and Red Seas because of high net evaporation. Because of low buoyancy fluxes, however, they sink only to thermocline depths[37].

During the early Palaeogene, different global geography and climate[46-48] combined to make the ocean circulation very different from that of the modern ocean[12,46,49]. Significant Antarctic warmth[6,19,20,22] coupled with inferred higher precipitation[25,50-52] may have caused a large reduction in deep waters derived from the high latitudes[6,12]. At the same time, the mid-latitude Tethys Seaway would have produced warm, saline deep waters[12], probably in sufficient volume[45] to alter the density distributions in the oceans considerably. We suggest that during the excursion these factors combined to form, through positive feed-back responses, an extreme case of such an ocean, because a global climate threshold was temporarily penetrated. The nature of the triggering remains unknown.

The character of the $\delta^{13}C$ changes constrains hypotheses for the cause of the extinctions. Of particular importance is that the negative carbon isotope shift occurred throughout the water column (Fig. 2) and was smaller (~2.5‰) in deep waters than in surface waters (~4.0‰). This trend is opposite to that of the $\delta^{18}O$ record. Furthermore, the shift in $\delta^{13}C$ in waters at thermoclinal and greater depths coincided with warming of these waters, but most of the $\delta^{13}C$ shift occurred later in surface waters. A negative $\delta^{13}C$ shift of this magnitude[39] might be interpreted as indicating a transfer of light $\delta^{13}C$ organic carbon from the continents to the oceans[43,53], but this is unlikely because there is no evidence of any significant and rapid drop in global sea level at that time[40,54]. Moreover, the diachronism shown in the carbon isotope changes between surface and deeper-dwelling planktonic forms does not support this hypothesis. It has been suggested[40] that plate-tectonic reorganization at this time increased oceanic volcanism and deep-sea hydrothermal activity, triggering warming of deep waters and global greenhouse warming by release of carbon dioxide. The speed of the palaeoenvironmental changes and brevity of the excursion lend little support to this hypothesis.

Summary

The rapid (<6,000 yr) negative oxygen and carbon isotope shifts in Antarctic waters near the end of the Palaeocene reflect oceanographic changes associated with global warming that caused considerable deep-sea extinctions. These observations show that for at least the early Cenozoic, short (1,000 yr) events can strongly affect the course of environmental and biotic evolution. Furthermore, such change can be effectively decoupled between different parts of the biosphere, in this case the deep and shallow marine ecosystems. The oceanographic changes associated with the excursion were clearly broad and complex, and seem to reflect a transient state between fundamentally different modes of ocean circulation. Brief elimination of the vertical $\delta^{18}O$ and $\delta^{13}C$ gradients indicates vertical ocean mixing and homogenization of nutrient distributions, presumably related to vertical instability of the Antarctic Ocean. The slightly delayed shift, during the excursion, to highly negative $\delta^{13}C$ values in Antarctic surface waters is difficult to explain but suggests higher concentrations of nutrients and total carbon dioxide, partial pressure of carbon dioxide[55]. This would have contributed to greenhouse warming. Detailed examination of the excursion is required elsewhere, especially at low latitudes, for better definition of the character and magnitude of the oceanographic and biotic changes associated with this remarkable event. □

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Primary structure and expression of bovine poly(A) polymerase

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Poly(A) polymerase has a critical role in the synthesis of messenger RNA in eukaryotic cells. The isolation and characterization of complementary DNAs encoding bovine poly(A) polymerase is described here. The predicted sequences of the mRNA and protein reveal features that provide insights into how the enzyme functions and how it might be regulated. Poly(A) polymerase expressed from a cloned cDNA is fully functional in *in vitro* assays, and mutational analyses have identified a putative regulatory domain that enhances, but is not essential for, activity.

AN enzyme activity able to polymerize AMP residues onto an RNA primer was first described over 30 years ago[1]. Subsequent studies have described the purification and characterization of poly(A) polymerases from many different organisms (reviewed in refs 2, 3). Although all these enzymes share a requirement for an RNA primer and are specific for ATP as substrate, significant differences in several properties, such as subcellular localization during fractionation (nuclear versus cytoplasmic) and apparent relative molecular mass (~40–80,000; M_r, ~40–80K), were observed. Although interest in these enzymes was heightened by the discovery of poly(A) tails on mammalian mRNAs[4–6], the involvement of the characterized enzymes in polyadenylation of mRNA precursors was clouded by the almost complete lack of primer specificity displayed by purified poly(A) polymerases.

The discovery of the highly conserved AAUAAA sequence in mRNA (ref. 7), the demonstration that this sequence is critical for polyadenylation (for example ref. 8, and reviewed in refs 9, 10), and the development of soluble *in vitro* systems capable of AAUAAA-dependent polyadenylation[11–14] have allowed progress in the identification and characterization of factors required for authentic pre-mRNA polyadenylation (reviewed in ref. 15). Cleavage and polyadenylation of mRNA precursors require multiple protein factors including a poly(A) polymerase (PAP)[16–20]. Initial experiments demonstrated that a nonspecific PAP activity could be separated from a cleavage-specificity factor, but that the PAP became specific for AAUAAA-containing RNAs when the fractions were combined[16]. Subsequently, it was shown that several highly purified PAPs that were nonspecific by themselves became AAUAAA-dependent when mixed with such a specificity factor[21–24]. These findings

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