Anomalous shifts in tropical Pacific planktonic and benthic foraminiferal test size during the Paleocene–Eocene thermal maximum

Kunio Kaiho a,⁎, Kotaro Takeda a, Maria Rose Petrizzo b, James C. Zachos c

a Institute of Geology and Paleontology, Tohoku University, Sendai 980-8578, Japan
b Dipartimento di Scienze della Terra ‘Ardito Desio’, Universita' degli Studi di Milano, via Mangiagalli 34, Milano 20133, Italy
c Earth and Ocean Sciences Departments, University of California, Santa Cruz, CA 95064, United States

Received 24 May 2005; received in revised form 21 December 2005; accepted 23 December 2005

Abstract

Paleocene–Eocene warming and changes in oceanic hydrography should have significantly impacted the ecology of marine microorganisms, both at the surface and on the seafloor. We analyzed several key characteristics of foraminifera from two Shatsky Rise (ODP Leg 198) cores spanning the P/E boundary including the maximum test diameters of the largest calcareous trochospiral benthic foraminifera and largest shallow-dwelling planktonic foraminifera, and the stable carbon and oxygen isotope ratios of benthic foraminifera and bulk samples. We also qualitatively constrained changes in bottom water dissolved oxygen concentrations by quantifying changes in benthic species abundances. We find warming synchronous with an unusual increase in the size of surface-water planktonic in contrast to deep-water benthic foraminifera which decrease in size. We suggest that a decline in bottom water dissolved oxygen is the primary mechanism responsible for the size reduction of Pacific deep-sea benthic foraminifera, whereas the contemporaneous size increase of surface-water planktonic foraminifera is attributed to an increase in thermal stratification and decrease in local nutrient supply.

© 2006 Elsevier B.V. All rights reserved.

Keywords: Benthic foraminifera; Planktonic foraminifera; Size; Dissolved oxygen; Nutrient; Stable isotope; Paleocene; Eocene

1. Introduction

Stable isotope investigations of Ocean Drilling Program (ODP) Site 690 (Kennett and Barker, 1990; Kennett and Stott, 1991), South Atlantic ODP Sites 525 and 527 (Thomas and Shackleton, 1996; Thomas et al., 1999), and paleoequatorial Pacific ODP 865 (Bralower et al., 1995) document a rapid, nearly contemporaneous (<6 kyr) ~5 °C warming of deep water, and a reduction of vertical and latitudinal thermal gradients. Sea surface temperatures (SST) in the Antarctic increased by as much as 10 °C (Kennett and Stott, 1991), while tropical SST increased by 5 °C (Zachos et al., 2003). Often referred to as the Paleocene–Eocene thermal maximum (PETM, a.k.a., LPTM (Late Paleocene thermal maximum) and IETM (Initial Eocene Thermal Maximum)), this event also coincides with a ~2.5–3.0‰ drop in marine δ13C (CIE), presumably from massive dissociation of methane hydrate (~55.5 Ma; Dickens et al., 1995, 1997; Kaiho et al., 1996). The subsequent oxidation of
methane and solution into the ocean resulted in extensive
dissolution of seafloor carbonate, drop in ocean pH, and
carbonate ion content beneath the thermocline (Thomas
et al., 1999; Zachos et al., 2005).

The Paleocene/Eocene (P/E) boundary is also marked
by the largest benthic foraminiferal extinction event
(BEE) of the last 90 m.y. (Kaiho, 1988, 1989, 1991,
1994b; Kaiho et al., 1993, 1996; Kennett and Stott,
1991; Miller et al., 1987; Nomura, 1991; Ortiz, 1995;
Thomas, 1989, 1990; Tjalsma and Lohmann, 1983). The
extinction event was relatively abrupt occurring over a
couple of tens of thousands of years or less (Kennett and Stott,
1991; Pak and Miller, 1992; Thomas, 1992; Thomas and
Shackleton, 1996). The event is marked by extinction of
many intermediate- and deep-water benthic foraminiferal
species (more than one third of the taxa: 33–50% per
site and occasionally 65% per site) as well as some
shallow dwelling (50- to 150-m water depths) benthic
foraminifera (22%; Kaiho, 1994b).

Although changes in deep-sea benthic foraminiferal
test size and an oxygen index have been established at
low resolution for the past 120 m.y. (Kaiho, 1994b, 1998,
1999a), these indices have yet to be applied at high-
resolution to the P/E boundary. One exception is the
section at Tawanui, New Zealand (Kaiho et al., 1996),
where application of the benthic foraminiferal oxygen
index (BFOI; Kaiho, 1994a) documented near anoxia of
intermediate water at the onset of the event. A similar
record has yet to be developed for the deeper pelagic
sections of the Pacific or Atlantic Oceans.

In contrast, planktonic foraminifera suffer no extinc-
tion (Kelly et al., 1996). Instead, there are significant
changes in both the distribution and diversification of
foraminifera virtually in all regions. In the tropics, ther-
mocline dwellers such as Subbotina disappear while
Morozovella diversify with the appearance of exotic
taxa (Kelly et al., 1996). In the polar regions, cooler
water species are displaced by warmer water taxa (Kelly,
2002; Stott et al., 1991).

A number of parameters control the composition and
size range of benthic foraminiferal assemblages. Food
resources and algal symbiosis are probably the main
controlling factors of test size of shallow-water benthic
foraminifera (Hallock, 1985). Test size of the deep-sea
benthic foraminifera, on the other hand, may be affected
by factors such as dissolved oxygen levels and food
supply (Perez-Cruz and Machain-Castillo, 1990; Phleger
and Soutar, 1973; Kaiho, 1994a, 1998, 1999a; Koutsou-
kos et al., 1990). Planktonic foraminifera abundances
and size are influenced by several factors including
nutrient fluxes and productivity. In highly oligotrophic
settings, for example, the populations tend to be diverse
and dominated by species bearing algal symbionts
(Hallock et al., 1991; Hemleben et al., 1989). Reduced
surface productivity during the PETM has been inferred
from assemblage shifts of calcareous nannoplankton at
Site 690 (Bralower, 2002) and Site 865 (Bralower et al.,
1995; Tremolada and Bralower, 2004), and by the
proliferation of photosymbiotic planktonic foraminifera
at Site 865 (Kelly, 2002; Kelly et al., 1998), which seem to
thrive under oligotrophic conditions.

Cores recovered from Shatsky Rise during ODP Leg
198 provide a unique opportunity to establish detailed
records of changes in water column chemistry during the
PETM in the low latitude Pacific Ocean. This includes
the carbon isotope and dissolved oxygen (BFOI) chem-
istry. The objective of this paper is to (1) document
variations in the test size of deep-water (1500–1700 m
water depth) calcareous trochospiral benthic and mixed-
layer planktonic foraminifera spanning the PETM, and
(2) evaluate potential causes of the variations on the
basis of the comparison of the test size with the benthic
foraminiferal oxygen index (BFOI; Kaiho, 1994a), δ18O
and δ13C data. We show here that minima in benthic
foraminiferal test size and maxima in mixed-layer
planktonic foraminiferal test size coincident with the
PETM and low BFOI values.

2. Materials and methods

We analyzed latest Paleocene to earliest Eocene
calcareous trochospiral benthic and planktonic forami-

nifera in 61 samples from two ODP Holes 1209B (Core
22H, Section 1, Interval 100–141 cm; 32°30.1081′N,
158°30.3564′E, water depth 2387 m) and 1210B (Core
20H, Section 3, Interval 90–120 cm; 32°13.4202′N,
158°15.5623′E, water depth 2573 m) (Bralower et al.,
2002). Paleodepths of 2000 and 2160 m, respectively,
were estimated using a simple thermal subsidence model
(Berger and Winterer, 1974; Sclater et al., 1971).
Lithologically, the Paleocene/Eocene boundary is rep-
resented by a sharp contact with light (pale yellowish
brown) calcareous ooze overlain by a thin (< 2 mm)
dark (dusky yellowish brown) calcareous ooze (Hallock et al.,
1991; Tremolada and Bralower, 2004), and by the
proliferation of photosymbiotic planktonic foraminifera
around Site 865 (Kelly, 2002; Kelly et al., 1998), which seem to
thrive under oligotrophic conditions.

Cores recovered from Shatsky Rise during ODP Leg
198 provide a unique opportunity to establish detailed
records of changes in water column chemistry during the
PETM in the low latitude Pacific Ocean. This includes
the carbon isotope and dissolved oxygen (BFOI) chem-
istry. The objective of this paper is to (1) document
variations in the test size of deep-water (1500–1700 m
water depth) calcareous trochospiral benthic and mixed-
layer planktonic foraminifera spanning the PETM, and
(2) evaluate potential causes of the variations on the
basis of the comparison of the test size with the benthic
foraminiferal oxygen index (BFOI; Kaiho, 1994a), δ18O
and δ13C data. We show here that minima in benthic
foraminiferal test size and maxima in mixed-layer
planktonic foraminiferal test size coincident with the
PETM and low BFOI values.

2. Materials and methods

We analyzed latest Paleocene to earliest Eocene
calcareous trochospiral benthic and planktonic forami-

nifera in 61 samples from two ODP Holes 1209B (Core
22H, Section 1, Interval 100–141 cm; 32°30.1081′N,
158°30.3564′E, water depth 2387 m) and 1210B (Core
20H, Section 3, Interval 90–120 cm; 32°13.4202′N,
158°15.5623′E, water depth 2573 m) (Bralower et al.,
2002). Paleodepths of 2000 and 2160 m, respectively,
were estimated using a simple thermal subsidence model
(Berger and Winterer, 1974; Sclater et al., 1971).
Lithologically, the Paleocene/Eocene boundary is rep-
resented by a sharp contact with light (pale yellowish
brown) calcareous ooze overlain by a thin (∼ 2 mm) dark
(dusky yellowish brown) calcareous ooze (199.55 mbsf
in Hole 1209B and 184.31 mbsf in Hole 1210B; Figs. 1
and 2). Carbonate content declines from 95% to 80%
across this contact (Zachos et al., 2003).

A roughly one-meter long continuous U-channel was
collected across the Paleocene/Eocene boundary from
each core and continuously sampled at 1 cm intervals.
Each sample was freeze dried and soaked in a 3:1 solu-
tion of calgon and buffered water, and then sieved
through a 32 μm meshes with buffered deionized water.
The >63 μm fraction was used for the benthic
Fig. 1. Stratigraphic distribution of 1) stable carbon and oxygen isotope ratios of bulk sediment and benthic foraminifera, 2) percentages of oxic, suboxic, and dysoxic benthic indicators, 3) the benthic foraminiferal oxygen index (BFOI), and 4) maximum diameter of largest specimens among deep-sea calcareous trochospiral benthic foraminifera and trochospiral surface-dwelling planktonic foraminifera, during the latest Paleocene to earliest Eocene at ODP Hole 1209B, Core 22H, Section 1, Interval 100–141 cm (a; Present water depth is 2387 m and paleowater depth is ~2000 m) and ODP Hole 1210B, Core 20H, Section 3, Interval 90–120 cm (b; Present water depth is 2573 m and paleowater depth is ~2160 m). The sediment is calcareous nannofossil ooze. The interval can be divided into three parts: pre-event, anomaly, and recovery based on the above indices. The largest benthic specimens in each sample belong to five genera such as *Oridorsalis*, *Nuttallides*, *Stensioeina*, *Conorbinoides*, and *Quadrimorphina*. Largest trochospiral surface-dwelling planktonic foraminifera are composed of *Morozovella velascoensis*, *Morozovella subbotinae*, *Morozovella pasionensis*, and *Morozovella occlusa*. BEE: benthic extinction event. The four major carbon isotope events A to D were shown in Fig. 2. Anomalous values in one sample (199.48 mbsf) in Hole 1209B showing peaks in the dysoxic and oxic curves as well as BFOI are likely related to temporal beginning of recovery of dissolved oxygen conditions because of coincidence of temporal recovery of $\delta^{13}$C and $\delta^{18}$O of benthic foraminiferal test and the anomalous values.
foraminiferal assemblage and isotope work. We selected specimens of benthic foraminifera from the entire >250 μm fraction and a split of each >63 μm fraction and planktonic foraminifera from the entire >125 μm sample fraction.

We determined the maximum diameter of the single largest specimen of calcareous trochospiral benthic foraminifera (Oridorsalis, Nuttallides, Stensioeina, Conorbinioides, and Quadrimorphina) and the mean value of the five largest specimens of trochospiral surface-dwelling planktonic foraminifera (Morozovella spp.) in each sample. The total number of trochospiral benthic and planktonic specimens screened in each sample ranged from 66 to 463 benthics and 95 to 190 planktonics in Hole 1209B and 24 to 457 benthics and 72 to 170 planktonics in Hole 1210B. The reason for focusing on the test size of the largest specimen(s) in each sample rather than the mean of the entire population is that the latter would be strongly influenced by the number of and size of juvenile specimens counted. Because Morozovella are relatively abundant, we determined the mean of the 5 largest specimens (all adults). However, because the adult trochospiral benthic foraminifera are relatively scarce in some samples, we simply documented the largest specimen encountered in each sample. The coefficient of correlation between maximum test size and number of specimens counted is low (R² = 0.05 (benthic) and R² = 0.00 (planktonic)).

We also calculated BFOI values (Kaiho, 1994a,b) using the calcareous benthic foraminiferal assemblages (>63 μm; 500 to 1400 specimens in 1209B and 100 to 1600 specimens in 1210B). The BFOI was developed by Kaiho (1994a) using various morphologic and taxonomic parameters (Koutsoukos et al., 1990; Perez-Cruz and Machain-Castillo, 1990; Phleger and Soutar, 1973). Calcareous benthic foraminifera are divided into dysoxic (0.1–0.3 mL/L), suboxic (0.3–1.2 mL/L), and oxic (>1.2 mL/L) indicators on the basis of relations between specific morphologic characters (or species composition) and oxygen levels and calcareous benthic
foraminiferal microhabitat. Late Paleocene–early Eocene oxic, suboxic, and dysoxic indicators encountered in this study are as follows: Oxic indicators ($\geq 350$ μm, thick wall, epifaunal in high oxygen bottom water) consist of *Nuttallides truempyi*, *Stenioaeina beccariiformis*, and *Conorbinoiides hillebrandti*. Dysoxic indicators (thin wall, elongate, flattened, infaunal in high oxygen bottom water) consist of 1) non-ornamented Buliminids, 2) non-ornamented small *Nodosaria*, *Dentalina*, and *Stilostomella*, 3) *Bolivina* and *Coryphostoma* (flattened), 4) *Abyssamina* and *Quadrimorphina* (small, thin wall). The other calcareous benthic foraminifera are suboxic including small specimens of oxic species (<350 μm).

Stable isotope analyses were carried out on both bulk sediment (~100 μg) and benthic foraminifera (2 to 10 specimens of *N. truempyi*) with an Autocarb common acid bath (90 °C) coupled to a PRISM gas source mass spectrometer (Univ. of California, Santa Cruz). On the basis of replicate analyses ($n=40$) of a laboratory standard Carrera Marble (CM) precision was better than ±0.05‰ and ±0.10‰ (1 std dev) for δ$^{13}$C and δ$^{18}$O, respectively.

3. Results and discussion

3.1. Benthic foraminiferal extinction

The one prominent biostratigraphic horizon associated with the P/E boundary is the extinction of Paleocene benthic foraminiferal species such as *S. beccariiformis* that occurs at 199.56 mbsf in Hole 1209B and at 184.1 mbsf in Hole 1210B coinciding with the sharp lithologic change in both cores (Fig. 1). Based on the isotopic, biostratigraphic, and lithologic criteria, we correlate the P/E boundary to this level. Benthic foraminiferal assemblages and their stratigraphic variation will be reported by Takeda and Kaiho (in preparation).

3.2. Stable carbon isotope

Negative δ$^{13}$C excursions (CIE) in benthic and bulk carbonate were recorded in both sections. In Hole 1209B, bulk δ$^{13}$C decreased from 2.8‰ to 0.4‰ at 199.55 to 199.53 mbsf and increased to 1.5‰ at 199.43 to 199.33 mbsf; benthic δ$^{13}$C coincidently shifted from 1.2‰ to ~0.5‰ at 199.55 to 199.49 mbsf and increased to 0.2‰ at 199.42 to 199.33 mbsf (Fig. 1a). In Hole 1210B, bulk δ$^{13}$C decreased from 2.6‰ to 0.5‰ at 184.33 to 184.30 mbsf, and increased to 1.7‰ at 184.20 to 184.11 mbsf; benthic δ$^{13}$C coincidently shifted from 1.3‰ to −0.9‰ at 184.34 to 184.30 mbsf, and increased to 0.3‰ at 184.19 to 184.11 mbsf (Fig. 1b). The ~2‰ decrease and minima, which are observed globally, were used for correlation as discussed below (Fig. 2). The benthic and bulk carbonate δ$^{13}$C record shows a 2.5‰ decrease between 199.55 and 199.54 mbsf in Hole 1209B and between 184.33 and 184.30 mbsf in Hole 1210B, consistent with the P/E carbon isotope decrease documented in other locations (e.g., Katz et al., 1999; Kennett and Stott, 1991; Ortiz, 1995; Thomas and Shackleton, 1996).

3.3. Oxygen isotope and temperature

Minima in benthic and bulk carbonate δ$^{18}$O were recorded in both sections. At Hole 1209B, bulk δ$^{18}$O decreased from −1.1‰ to −1.8‰ at 199.55 to 199.54 mbsf and increased to −0.6‰ at 199.45 to 199.33 mbsf; benthic δ$^{18}$O coincidently shifted from −0.1‰ to −0.9‰ at 199.55 to 199.49 mbsf and increased to −0.4‰ from 199.42 to 199.33 mbsf (Fig. 1a). At Hole 1210B, bulk δ$^{18}$O decreased from −0.9‰ to −1.4‰ at 184.33 to 184.31 mbsf, and increased to −0.3‰ at 184.20 to 184.18 mbsf; benthic δ$^{18}$O shifted from −0.4‰ to −1.4‰ at 184.31 to 184.30 mbsf, and increased to −0.3‰ at 184.19 to 184.11 mbsf (Fig. 1b). The negative shifts of 0.5‰ to 0.7‰ in bulk carbonate δ$^{18}$O and 0.7‰ to 1.0‰ in benthic δ$^{18}$O, imply a 2 to 3 °C warming in the surface water and 3 to 4 °C warming of deep water in the central Pacific.

3.4. Isotopic correlation and age

Given the low sedimentation rates, evidence of dissolution at the boundary, and abrupt shift in the CIE, it appears the basal portion of the Eocene is condensed in Holes 1210B and 1209B of Shatsky Rise. Nonetheless, the general character of the remaining portion of the CIE as recorded by benthic foraminifera is similar to that recorded at Site 690 (Kennett and Stott, 1991) and other pelagic sites. As such, we correlated the Shatsky Rise bulk carbon isotope records to the Site 690 record which has a $^3$He-based age model (Farley and Eltgroth, 2003). We identified several correlation points, labeled A–E (Fig. 2). The assigned ages based on the 690 age model are as follows; A (55.000 Ma; 0 kyr), B (54.970 Ma; 72 kyr after A), C (54.915 Ma; 101 kyr after A), and D (54.890 Ma; 120 kyr after A) (Figs. 1 and 2). Based on this correlation, it appears that Hole 1210B is slightly more condensed than 1209B, most likely because of more intense/prolonged carbonate dissolution as the lysocline shoaled (see Zachos et al., 2005).
3.5. Dissolved oxygen levels

The percentage of “oxic” benthic foraminifera dramatically declines at the benthic foraminiferal extinction horizon or event (BEE): from 0.5–1.2% to 0–0.1% and from 0.4–1.5% to 0%, and at Holes 1209B and 1210B, respectively. When bottom waters are oxic, suboxic and disoxic forms are still present, but primarily living several cm below the sediment/water interface as infauna (Kaiho, 1994a). This explains why the percentages of the suboxic and disoxic indicators do not change significantly in the lower portion of the PETM. However, in the upper portion of the PETM the ratio of suboxic/disoxic indicators increased from 0.5 to 1 coincident with the δ13C recovery, indicating partial recovery of dissolved oxygen. During the interval when oxic species were absent, suboxic forms probably changed habitat and became more epifaunal, and thus more sensitive to bottom water oxygen conditions (Kaiho, 1994a). As a consequence, the suboxic % or ratio of suboxic/disoxic (similar to BFOI) becomes a sensitive indicator of dissolved oxygen levels when oxic species were absent. The gradually increasing BFOI values from −35 to −25 following the BEE reflects a gradual increase in ratio of suboxic/disoxic indicators. The fluctuations in BFOI values, oxic indicator (%), and suboxic indicator (%) in the absence of oxic indicators mainly reflects first-order changes of global deep-ocean ventilation and stagnation. The decrease in BFOI (%), oxic indicator (%), and suboxic indicator (%) in the absence of oxic indicators but remained within suboxic conditions.

3.6. Test size of benthic foraminifera

At both sites, the maximum diameter of calcareous trochospiral benthic foraminifera decreases sharply coincident with the benthic extinction event (BEE), reaching a minima during the peak of the PETM. Test sizes begin to increase almost immediately as temperature drops (Fig. 1).

Kennett and Stott (1991) suggested that during periods of warmth, deep-water convection was reduced thereby limiting ventilation of the deep sea. The reduced test size of benthic foraminifera is inferred to represent a rapid drop in bottom water dissolved oxygen during the initial phases of the PETM, an event that likely contributed to the deep-sea benthic faunal extinctions and turnover.

3.7. Test size of planktonic foraminifera

During the CIE, the maximum diameter of the surface-dwelling planktonic foraminifera increases from 600 to 750 μm before returning to pre-excursion values (Figs. 1, 2). The maximum coincides with the maxima in SST as recorded at Hole 1209B (Zachos et al., 2003) and is slightly higher than the size minima in benthic foraminifera. Such large test sizes are truly anomalous with the diameters of several specimens of Morozovella velascoensis nearing 800 μm. This is the first such documentation of this maxima of planktonic foraminiferal test size during the PETM, though it should have occurred in other tropical sites (i.e., Site 865) as well.

The changes in test size do not appear to be an artifact of preservation. With increased dissolution the largest specimens are often broken and/or not preserved. The drop in CaCO3 content and an increase in fragmentation of planktonic foraminifera in Hole 1209B (Zachos et al., 2003) indicate that dissolution was most intense just at the boundary layer, below the test size maximum. Carbonate content gradually recovered peaking well above the peak in maximum test size indicating that this anomaly is not an artifact of preservation.

The increase in planktonic foraminiferal test size is clearly associated with SST. It is possible that warmer temperatures enhanced stratification reducing vertical mixing and lowering productivity. In modern settings, there is a strong relationship between foraminiferal ecology and size and productivity. Schiebel et al. (2004) showed that modern planktonic foraminiferal and coccolithophore abundances are low in high NO3 and PO4 and high in low NO3 and PO4. Moreover, the largest planktonic foraminifera in areas of seasonal upwelling actually occur during the non-upwelling season (Peeters et al., 1999, Appendix B). High nutrient levels may inhibit calcification (Brown, 1997) or, low nutrient supply may delay reproduction. For mixed layer morozovellid foraminifera, the presence of algal symbionts probably gives them a distinct advantage in oligotrophic conditions (Berggren and Norris, 1997; D’Hondt et al., 1994). Symbiosis aids calcification and provides an important energetic advantage in the adaptation of the symbiont-bearing foraminifera to low nutrient environments, especially in subtropical and tropical oceanic environment (Hallock et al., 1991). Schmidt et al. (2004) argue that gradual increase of test size of planktonic
foraminifera through the Cenozoic was an adaptive response to intensifying surface water stratification in low latitudes, which was driven by polar cooling, whereas factors such as temperature and carbonate saturation had little influence. Similarly, our data imply that low nutrient supply by enhanced stratification by warming caused the increase in test size of planktonic foraminifera during the PETM.

3.8. Paleoenvironmental changes at the PETM

Seven variables ($\delta^{13}C_{\text{bulk}}$, $\delta^{13}C_{\text{benthic}}$, $\delta^{18}O_{\text{bulk}}$, $\delta^{18}O_{\text{benthic}}$, BFOI, test size of benthic foraminifera, and test size of shallow-dwelling planktonic foraminifera) show significant anomalies across the P/E boundary at both sites. The signals are highly coherent, with all exhibiting an abrupt change at the boundary followed by a more gradual recovery. The anomalies in several of the variables persist for up to ∼100 kyr, while others (i.e., planktonic test size) are more short-lived (Fig. 1).

These data imply warm, low oxygen conditions in deep water and warm, low nutrient conditions in surface water during the initial phases of the PETM in the central Pacific Ocean. The carbonate dissolution event caused by a CO₂-induced drop in ocean pH and carbonate ion concentration (Dickens et al., 1997; Zachos et al., 2004) does not appear to be as intense in these sections as elsewhere (i.e., the Atlantic; Zachos et al., 2005) Thus, we suggest that warming slowed thermohaline overturn which resulted in lower dissolved oxygen levels at depth, and triggered a reduction in test size of benthic foraminifera in deep and intermediate waters. In the sub-tropical Pacific, the sluggish circulation was accompanied by enhanced stratification and a weakening of vertical mixing, thus lowering nutrient supply and productivity, contributing to increased test size of photosymbiont bearing planktonic foraminifera.

4. Conclusion

The global warming and the CIE at the P/E boundary were accompanied by (1) a significant reduction in the test size of deep-water benthic foraminifera and BFOI, and (2) an increase in the maximum test size of mixed-layer planktonic foraminifera. The reduction in test size of deep-water benthic foraminifera as well as the extinction event appears to be related to a drop in dissolved oxygen levels. In contrast, the increase in test size of surface-water planktonic foraminifera may have been caused by a reduction in nutrient supply. Therefore, in addition to the benthic extinction event, it appears that this global warming event also triggered significant changes in the test sizes of both planktonic and deep-sea benthic protists.

Acknowledgments

We thank the Ocean Drilling Program for providing samples used in this study and all Leg 198 ship board members for assistance. We also thank Susan Keller, Robert Becker for technical assistance. This research was supported by grants from the Japan Society for the Promotion of Science to Kaiho and NSF Grant EAR-0120727 to Zachos. We especially thank two anonymous referees for reviewing and comments.

References

Hallock, P., Premoli Silva, I., Boersma, A., 1991. Similarities between planktonic and larger foraminiferal evolutionary trends through


Kaiho, K., 1994b. Planktonic and benthic foraminiferal extinction events during the last 100 m.y. Palaeogeogr. Palaeoclimatol. Palaeoecol. 111, 45–71.


