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Ecological stasis and saltation: species richness change in planktic foraminifera during the late Paleocene to early Eocene, DSDP Site 577

G. Lu, G. Keller

Department of Geological and Geophysical Sciences, Princeton University, Princeton, NJ 08544, USA

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Abstract

A high resolution study of late Paleocene to early Eocene planktic foraminifera at DSDP Site 577 indicates the presence of three rapid faunal turnovers, or saltation events, with durations varying between 200–400 kyr and species turnover rates between 4–12 species/100 kyr. These saltation events are separated by slow faunal turnovers, or stasis intervals, with durations varying between 2.56–5.21 Myr and species turnover rates between 0.6–1.8 species/100 kyr. Each saltation event has different characteristics with disappearances equal to appearances in event T1, appearances dominate in event T2 that nearly double species richness, and primarily disappearances in event T3 that nearly halve species richness. Only event T2 near the P/E boundary is associated with major and sudden environmental changes, as marked by a rapid warming in the deep ocean and high-latitude surface ocean and a negative excursion in carbonate $\delta^{13}\text{C}$ values, that suggest a cause-effect relationship. The other two events occur during intervals of gradual environmental changes. We suggest that all three faunal events are triggered by the attainment of threshold conditions during the oceanic environmental changes. Threshold conditions may be attained through rapid environmental changes as in the case of event T2 near the P/E boundary, or by gradual though cumulative environmental changes as appears to be the case in events T1 and T3. It is unclear, however, which environmental factors (e.g., temperature, salinity, nutrients, water-mass stratification) force rapid faunal turnovers or what role intrinsic biotic factors play.

1. Introduction

Microplankton differs from other organisms in their passive life-style. This passive life-style affects geographic distributions, ecologic structures and evolutionary processes of planktic foraminifera, as well as other marine microplankton, in a way of closely following changes in ambient water masses (Lipps, 1970; Lazarus, 1983; Pearson, 1992). The biogeography of living planktic foraminifera is marked by latitudinal bands where water temperature is the major control factor (Berger, 1969; Bé, 1977; Hemleben et al., 1989). Fossil records show that these latitudinal bands expanded and

contracted associate with changes in meridional thermal gradients. For instance, the low-latitude band expanded following the proliferation of thermophilic species towards high latitudes during the polar warming across the Paleocene–Eocene transition (Stott and Kennett, 1990; Huber, 1991; Lu and Keller, 1993), whereas the high-latitude band expanded following the proliferation of cryophilic species towards low latitudes during the polar cooling across the Eocene–Oligocene transition (Corliss et al., 1984; Keller, 1986). Close relationships have been observed between changes in surface water structures and planktic foraminiferal ecology. Lipps (1970) showed that diversification

of planktic foraminifera was associated with sea-surface temperature changes in high latitudes which affect vertical and meridional thermal gradients. Boersma and Premoli-Silva (1986, 1988, 1989) demonstrated that the relative abundance of the Paleogene biserial planktic foraminifera was associated with the development of the subsurface oxygen minima. Many evolutionary processes of planktic foraminifera may also be affected by changes in surface water masses. Corfield and Shackleton (1988) suggested that the extinction and speciation rates of the early Paleogene planktic foraminifera might be controlled by surface productivity. Lipps (1970) and Bé (1977) argued that at least some morphologic changes during planktic foraminiferal evolution were the results of adaptation for changing surface water stratification. These tight relationships between planktic foraminiferal faunas and ambient water masses provide significant advantages in reconstruction of oceanic environments during the geological past.

As the result of these tight relationships, a simple correlation is usually assumed between planktic foraminiferal faunal changes and oceanic environmental fluctuations. For instance, rapid faunal changes are linked with catastrophic environmental events, whereas slow faunal changes are linked with gradual environmental variations. However, this simple assumption may not be valid in some cases. A high-resolution study at DSDP Site 577 spanning the late Paleocene to early Eocene suggests a more complex relationship between planktic foraminiferal faunas and the oceanic environment.

The late Paleocene to early Eocene was the warmest period of the Cenozoic (Shackleton and Kennett, 1975; Savin et al., 1975; Shackleton and Boersma, 1981; Boersma et al., 1987; Miller et al., 1987; Kennett and Stott, 1990, 1991; Stott et al., 1990; Barrera and Huber, 1991; Pak and Miller, 1992). Associated with this global warming were major changes in oceanic environments and marine biotic systems (Tjalsma and Lohmann, 1983; Miller et al., 1987; Thomas, 1990; Katz and Miller, 1991; Nomura, 1992; Pak and Miller, 1992; Lu and Keller, 1993; Canudo et al., in press). This period thus provides an ideal opportunity to examine the relationship between faunal changes in planktic foraminifera and environmental fluctua-

tions. During the late Paleocene to early Eocene, Site 577 was located between 15°N and 22°N in the central Pacific based on the back-tracked path of the Pacific Plate by Lancelot and Larson (1975). A continuous and well preserved sedimentary record of this interval was recovered. Magnetostratigraphy in conjunction with nannofossil and planktic foraminiferal biostratigraphies provide chronological control (Bleil, 1985; Monechi, 1985; Lu and Keller, in press). Major environmental indices for the surface ocean in this region are $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ values of planktic foraminifera and terrigenous grain size which provide information about sea-surface temperature, ocean chemistry and surface wind intensity (Shackleton et al., 1985; Miller et al., 1987; Corfield and Cartlidge, 1992). The planktic foraminiferal fauna at this site is characterized by high diversity and has a similar species composition to those recovered at other coeval low-latitude Pacific and Caribbean sites (Bolli, 1957; Blow, 1979; Toumarkine and Luterbacher, 1985; Corfield and Shackleton, 1988; Lu and Keller, in press). With these spatial and temporal restrictions, the results from Site 577 are considered to be representative of low latitude regions in general. In this study, we explore the nature and tempo of species richness changes during the late Paleocene to early Eocene in order to evaluate the relationship between planktic foraminiferal faunal changes and oceanic environmental fluctuations.

2. Methods

A total of 126 sedimentary samples spaced at 25 cm (averaging 81 kyr) intervals and spanning the biozones P3–P9 were analyzed for planktic foraminifera. Additional samples were analyzed for the intervals of rapid faunal changes (e.g. across zonal boundaries P6a/P6b and P8/P9). First and last appearances of species, species richness and relative abundances were based on counts in a random sample of 300 individuals from the >106 μm size fraction. Justifications for choosing this sample size and size fraction are given by Buzas (1990). Ages are computed from the magnetostratigraphy by Bleil (1985) and the geomagnetic

polarity time scale by Berggren et al. (1985). Paleocene/Eocene (P/E) boundary is assigned based on the revision of the time scale of Berggren et al. (1985) by Aubry et al. (1988). Polarity chrons are identified using nannofossil and planktic foraminiferal stratigraphies (Monechi, 1985; Lu and Keller, in press). The species turnover rate is computed by the number of first and last appearances within a 100 kyr interval. This is the minimum time unit imposed by the limits of the sample resolution.

A total of 107 planktic foraminiferal species were identified from Zone P3 through P9. Their ranges are illustrated in Fig. 1. The number of species within one sedimentary sample varies from 18 to 40 although some rare species (relative abundance <0.33%) might not be included. The classification of genera was based on the framework discussed by Loeblich and Tappan (1988). Species identification was based on the observations of Subbotina (1953), Bolli (1957), Loeblich and Tappan (1957), Jenkins (1971), Blow (1979), Toumarkine and Luterbacher (1985). Species ranges and their relative abundances are discussed in Lu and Keller (in press). Depth habitats of the species are based on Shackleton et al. (1985) and Lu and Keller (in prep.).

3. Faunal changes

Examination of species ranges (Fig. 1) reveals intervals of rapid and slow faunal changes in planktic foraminifera at Site 577 during the late Paleocene to early Eocene. A clear view of the long-term pattern of these faunal changes is shown in Fig. 2 where species richness, first appearance datum (FAD) rates, last appearance datum (LAD) rates and species turnover rates are plotted. These faunal parameters reveal three long-term stasis intervals (S1–S3) as indicated by relatively stable species richness values and low species turnover rates. Separating the stasis intervals are short-term turnover or saltation events (T1–T3) that are characterized by rapid changes in species richness and high species turnover rates. This alternation between stasis and saltation forms the first order

pattern in faunal changes during this 12 Myr period.

3.1. Stasis intervals

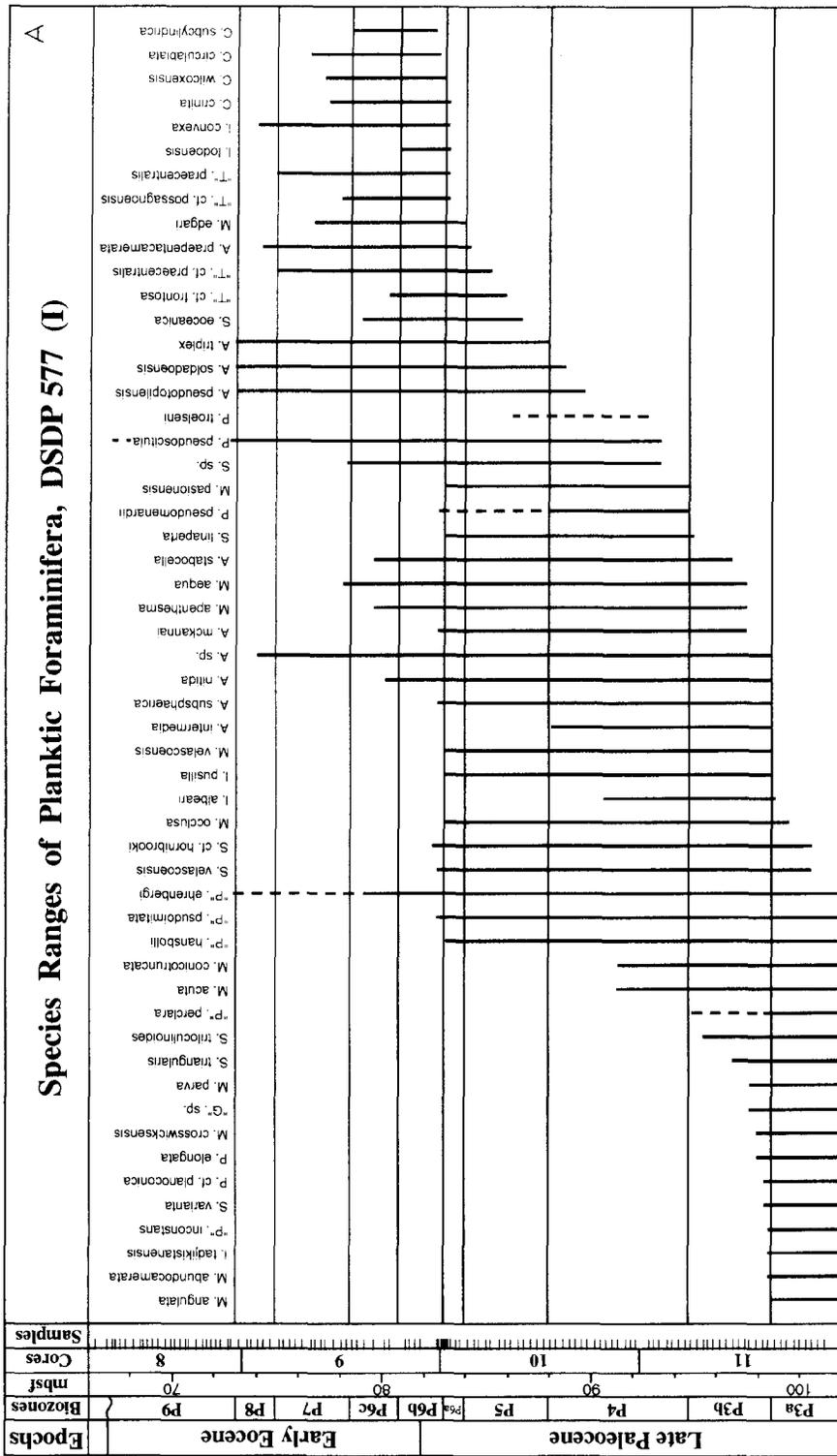
Major features of the three stasis intervals (S1–S3) are listed in Table 1 and include: (1) low species turnover rates (0.6–1.8 species/100 kyr), (2) relatively constant species richness (variation of ± 1.4 –3.3 species), and (3) long durations (2.56–5.21 Myr). Both S1 and S3 intervals have a mean species richness of 24 species which is here taken as the background value for species richness during the late Paleocene to early Eocene. In contrast, the S2 interval has a mean species richness that is nearly 50% higher than the S1 and S3 background value (Fig. 2). Associated with the higher species richness is an increase in the species turnover rate (Table 1).

Although faunal succession within stasis intervals is generally slow as indicated by low species turnover rates (Fig. 2), the cumulative effect over the entire interval can result in significant changes in species composition. This is demonstrated in Fig. 3 which shows a systematic change in the species ratios between *Morozovella* and *Acarinina*, the two dominant genera, within the S2 interval. In the early part of the S2 interval, the species ratio between the two genera is close to 1. After two million years of gradual faunal changes, *Acarinina* dominates over *Morozovella* in the number of species (Fig. 3). In fact, most changes at the species level during the late Paleocene to early Eocene is the result of slow cumulative species turnovers within stasis intervals. This is seen in the fact that gradual faunal changes

Table 1

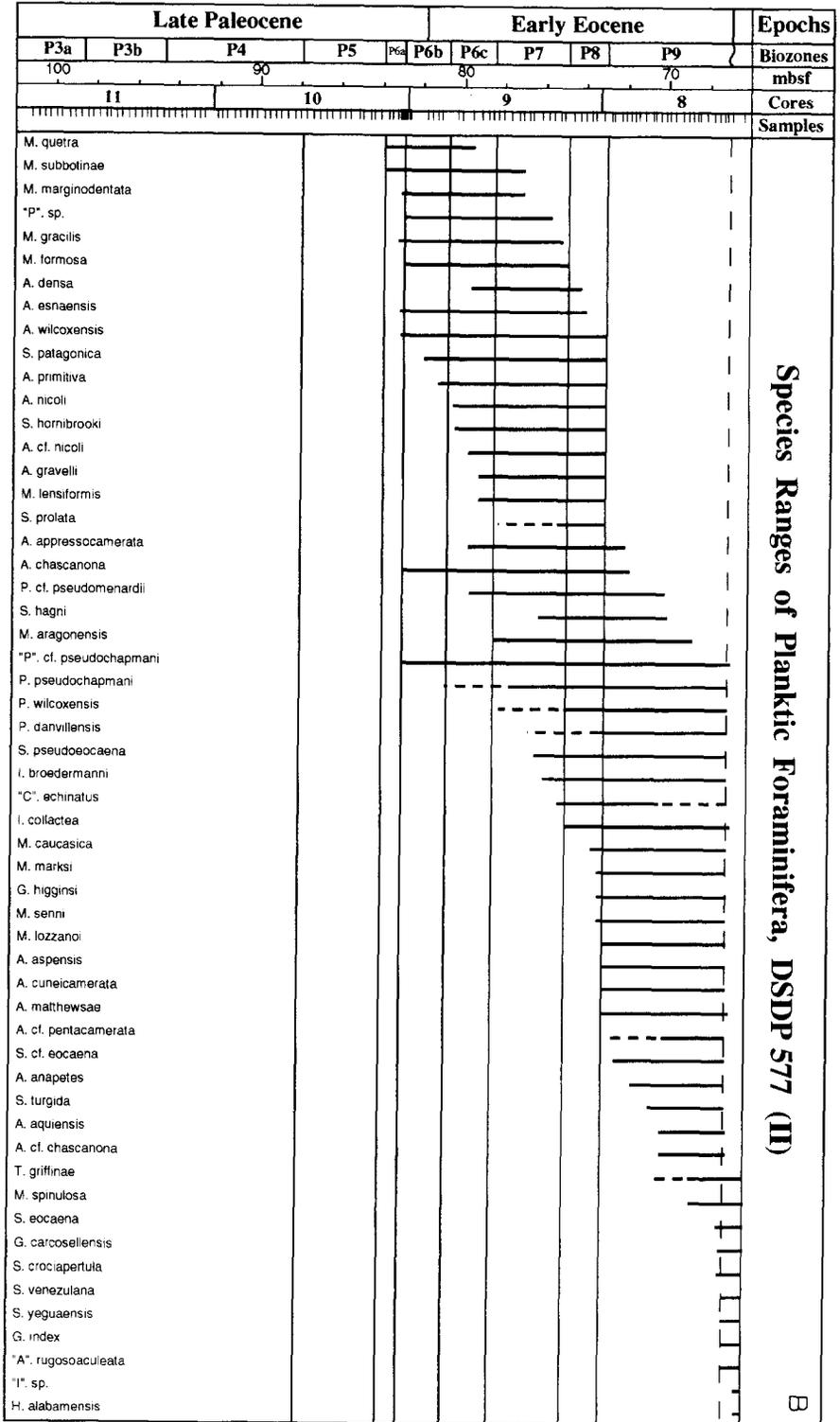
Major features of the planktic foraminiferal fauna in the stasis intervals (S1–S3) at Site 577 during the late Paleocene to early Eocene

Stasis interval	Duration (Myr)	Mean species richness (no. species)	Mean turnover rate (species/100 kyr)
S3	>2.56	241.4	0.7
S2	3.39	353.3	1.8
S1	5.21	242.4	0.6



1A Fig. 1. Species ranges of planktic foraminifera at Site 577. Dashed lines indicate appearances with very low relative abundance (<0.33%) which is beyond the confidence limit of the sample size.

Fig. 1. Continued.



B

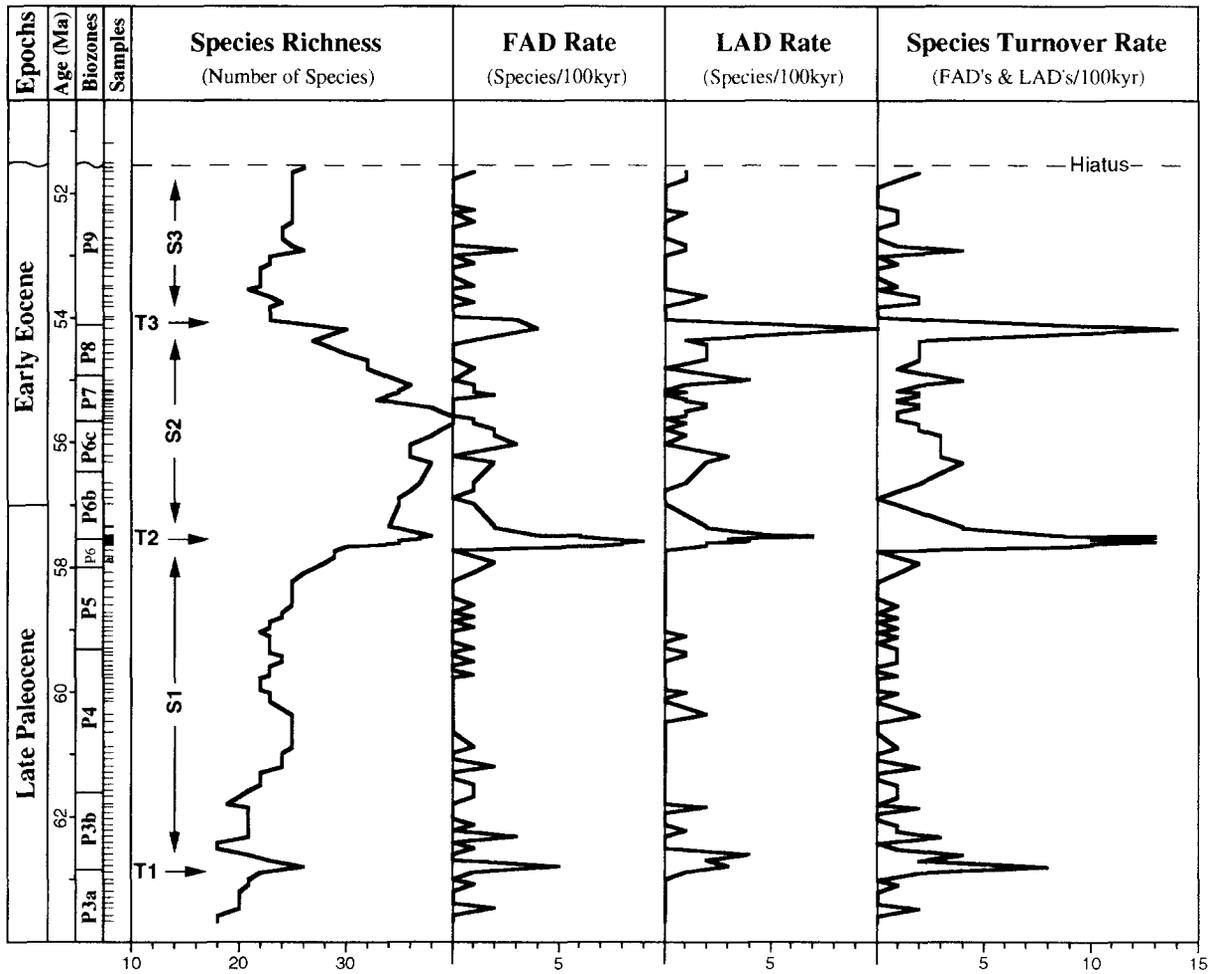


Fig. 2. Species richness, first appearance rate, last appearance rate and species turnover rate of planktic foraminifera at Site 577 during the late Paleocene to early Eocene. Data reveal three stasis intervals (S1–S3) and three turnover events (T1–T3).

occurring during the three stasis intervals account for 62% of the total first and last appearances of species and span 92% of the late Paleocene to early Eocene time interval.

S1 and S3 intervals are similar in both mean species richness (24 species) and mean species turnover rates (0.6–0.7 species/100 kyr) despite significant differences in species compositions (Fig. 1). These similarities suggest the existence of an equilibrium between species richness and species turnover rate where the fauna may be in its most stable situation. In S2 interval, mean species richness is nearly 50% higher than those in S1 and S3

intervals whereas mean species turnover rate is almost tripled (Table 1), indicative of increased instability. This instability in S2 interval is also evidenced by the presence of many opportunistic species, such as chiloguembelinids and “turborotaliids”, that have short ranges (Fig. 1) and highly variable relative abundances (Lu and Keller, in press).

3.2. Turnover events

Major features of the three turnover events (T1–T3) are listed in Table 2 and include: (1) high

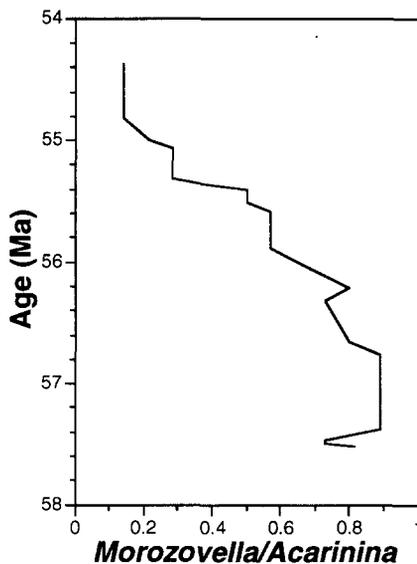


Fig. 3. Systematic change in species ratio between the two dominant genera *Morozovella* and *Acarinina* during the S2 interval as the result of slow turnovers.

Table 2

Major features of the faunal turnover events (T1–T3) in planktic foraminifera at Site 577 during the late Paleocene to early Eocene

Turnover event	Age (Ma)	Duration (kyt)	Mean turnover rate (species/100 kyr)	Species change (%)	Population change (%)
T3	54.15	300	7	49	78
T2	57.54	200	12	53	49
T1	62.75	400	4	56	63

species turnover rates (4–12 species/100 kyr), (2) major replacement of species (49–56%) and populations (49–78%), and (3) short durations (200–400 kyr). These three turnover events occur within 8% of the late Paleocene to early Eocene time interval and account for 38% of the total first and last appearances. Despite many similarities among the three turnover events, their FAD rates, LAD rates and the consequences on species richness are different (Fig. 2). More detailed patterns of the three turnover events are illustrated in Figs. 4–7.

Event T1 occurred at 62.75 Ma and is characterized by high species and population turnovers in 4 samples from a continuously recovered interval (Fig. 4). Although FAD and LAD rates across T1 are not significantly higher than some high background values during stasis intervals, their combined effects (species turnover rates) are much greater than background values and thus result in a major turnover event. Within Subzones P3a and P3b, the interval adjacent to T1, first and last appearances are approximately equal which results in little net-change in species richness (Figs. 2 and 4). Species and population compositions of this fauna, however, change drastically as 56% of the species have their first or last appearances and a total of 63% of the population are affected during this turnover (Fig. 4; Table 2). Examination of species ranges and relative abundances indicates that all existing genera are affected by event T1 with *Acarinina*, *Morozovella* and *Igorina* showing the most dramatic changes. Characteristic features of this turnover include: (1) first appearance of the genus *Acarinina* represented by conic taxa (e.g., *A. nitida*, *A. intermedia*, *A. subsphaerica*, *A. strabocella* and *A. mckannai*, Fig. 1); (2) decreased relative abundance in angulate and conic morozovellids (e.g., *M. angulata*, *M. parva*, *M. acuta*, *M. abundocamerata* and *M. conicotruncata*); (3) increased relative abundance in discoidal morozovellids (e.g., *M. occlusa* and *M. velascoensis*); (4) replacement of *Igorina tadjikistanensis* by *I. albeari* and *I. pusilla* which involved only three species but 30% of the total population; and (5) decreased relative abundance in *Subbotina*, *Planorotalites* and “*Planorotalites*”.

Event T2 occurred at 57.42 Ma and is characterized by high species and population changes in 8 samples (Fig. 5). Both FAD rates and LAD rates are high across T2 (Fig. 2). Within Subzone P6a to the lower part of Subzone P6b, the interval adjacent to T2, the number of first appearances is nearly twice the number of last appearances (Fig. 5) which results in a major increase in species richness (Fig. 2). T2 represents the most rapid faunal turnover in planktic foraminifera during the late Paleocene to early Eocene as indicated by the mean species turnover rate of 12 species/100 kyr. Nevertheless, the resulting population change

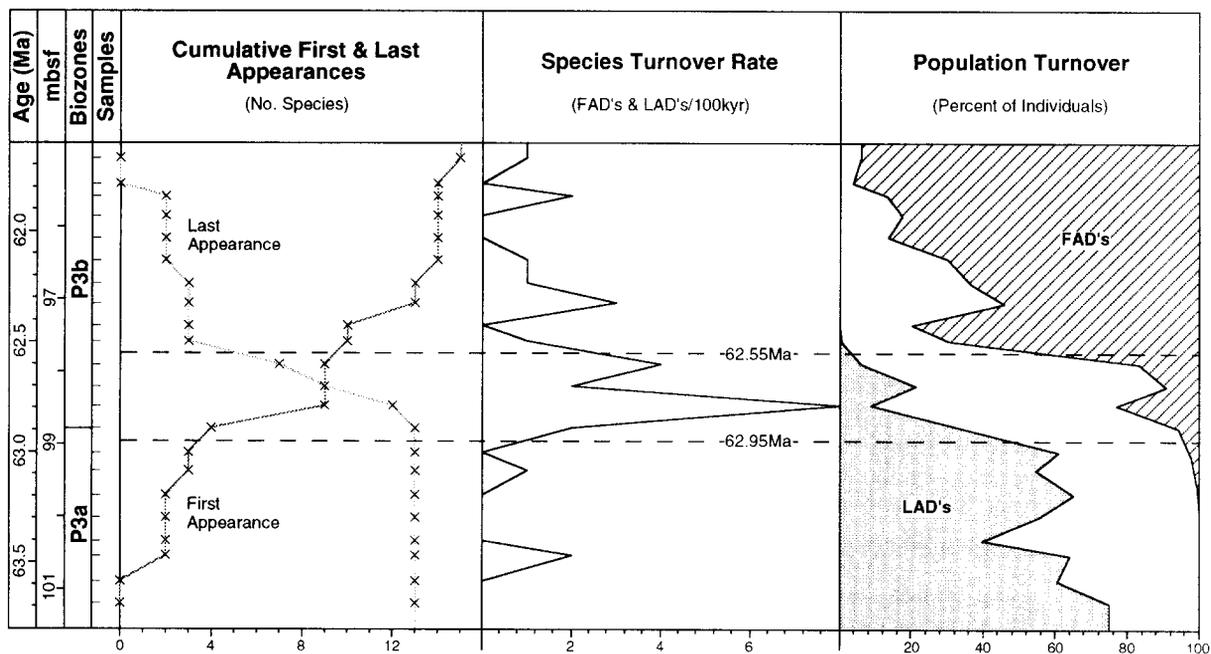


Fig. 4. Species and population turnovers during the faunal event T1 near the P3a/P3b zonal boundary at Site 577. FAD's and LAD's denote first appearance datums and last appearance datums respectively.

of 49% is relatively moderate compared with the slower T1 and T3 turnover events (Table 2). This is largely because (1) relative abundances of major taxa are more even near T2 than those near T1 and T3; (2) many opportunistic species appeared during T2, such as chiloguembelinids and "turborotaliids", have low relative abundances; and (3) some long-ranged, deep-dwelling taxa disappeared during T2, such as "planorotalitids", have low relative abundances. Examination of species ranges and relative abundances indicates that all existing genera are affected by T2. Characteristic features of this turnover are: (1) replacement of discoidal morozovellids (*M. oclusa* and *M. velascoensis*) by pustulate morozovellids (*M. aequa*, *M. quetra*, *M. subbotinae*, *M. marginodentata*, *M. gracilis* and *M. formosa*); (2) replacement of conic acarininids (*A. subsphaerica*, *A. mckannai*, *A. strabocella* and *A. nitida*) by rounded acarininids (*A. pseudotopilensis*, *A. soldadoensis*, *A. triplex*, *A. praepentacamerata*, *A. esnaensis* and *A. wilcoxensis*); (3) replacement of *Igorina pusilla* by *I. lodoensis* and *I. convexa*; (4) disappearance of major "planoro-

talitid" taxa ("*P.* *hansbolli*" and "*P.* *pseudoimitata*"); (5) disappearance of rounded and compressed subbotinids (*S. cf. hornibrooki*, *S. linaperta* and *S. velascoensis*); (6) appearance of the quadrate subbotinids (*S. patagonica*); (7) appearance of chiloguembelinids (*C. crinita*, *C. wilcoxensis*, *C. circumlabiata* and *C. subcylindrica*); and (8) appearance of "turborotaliids" ("*T.* *cf. frontosa*", "*T.* *cf. possagnoensis*", "*T.* *cf. praecentralis*" and "*T.* *praecentralis*").

Event T2 has also been observed at Caravaca and Zumaya sections in Spain where 51% of the planktic foraminiferal species are affected (Canudo et al., in press). Coincident with T2 is a mass extinction in benthic foraminifera which reduces species richness at ODP Sites 689 and 690 and Caravaca and Zumaya sections, Spain, by approximately 50% (Thomas, 1990; Ortiz and McDougall, 1992).

Event T3 is located between two cores and observed by only 2 samples in Hole 577 (Fig. 6). In order to examine whether this faunal turnover is real or an artifact of coring, this interval was

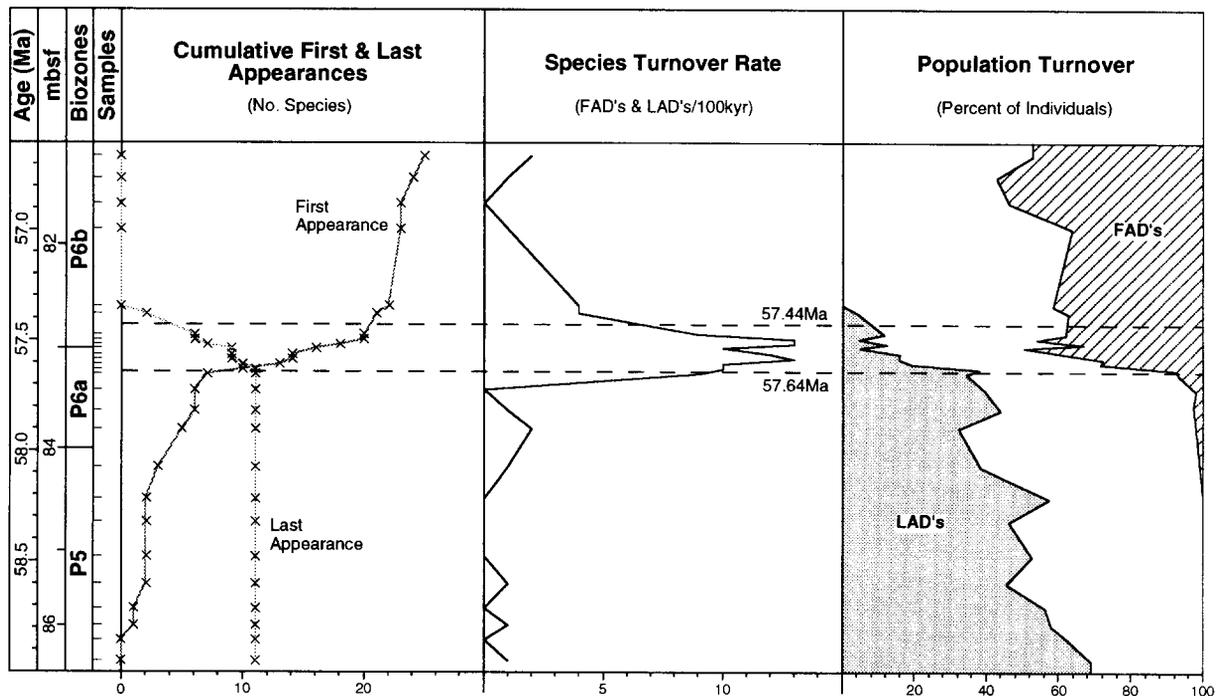


Fig. 5. Species and population turnovers during the faunal event T2 near the P6a/P6b zonal boundary at Site 577. Tighter samples were analyzed across this interval.

re-analyzed in the parallel Hole 577A where recovery is continuous within a core (Fig. 7). In Hole 577A, event T3 is also observed and represented by 7 samples. Moreover, species and population turnover patterns across this event are similar to those in Hole 577, indicating that this faunal event is real and not an artifact of sampling (Figs. 6 and 7). T3 is characterized by high LAD rates and low FAD rates (Fig. 2). Within Zones P8 and P9, the interval adjacent to T3, the number of last appearances is nearly twice the number of first appearances which results in a major decrease in species richness (Fig. 2). Event T3 affects 49% of the species but 78% of the population because most species who have their first or last appearances during T3, mainly acarininids and muricoglobigerinids, have high relative abundances. Examination of species ranges and relative abundances indicates that event T3 affects mainly *Acarinina*. Characteristic features of this turnover are: (1) replacement of rounded, angulate and early forms of muricate acarininids (e.g., *A. pseudotopilensis*,

A. soldadoensis, *A. triplex*, *A. praepentacamerata*, *A. esnaensis*, *A. gravelli*, *A. wilcoxensis*, *A. nicoli*, *A. cf. nicoli*, *A. densa*, *A. primitiva* and *A. appressocamerata*) by new forms of muricate acarininids (e.g., *A. matthewsae*, *A. cunicamerata*, *A. aspensis* and *A. anapetes*); and (2) first appearance of muricoglobigerinids (e.g., *M. senni* and *M. lozanoi*).

4. Correlation between faunal and environmental changes

As the net and combined effects of speciation, extinction and migration, local species richness and species turnover rates may be affected by regional and global environmental conditions. Correlation between faunal changes and environmental fluctuations should thus be considered in both regional and global contexts. Fig. 8 illustrates foraminiferal $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ values and eolian dust grain size changes which provide information

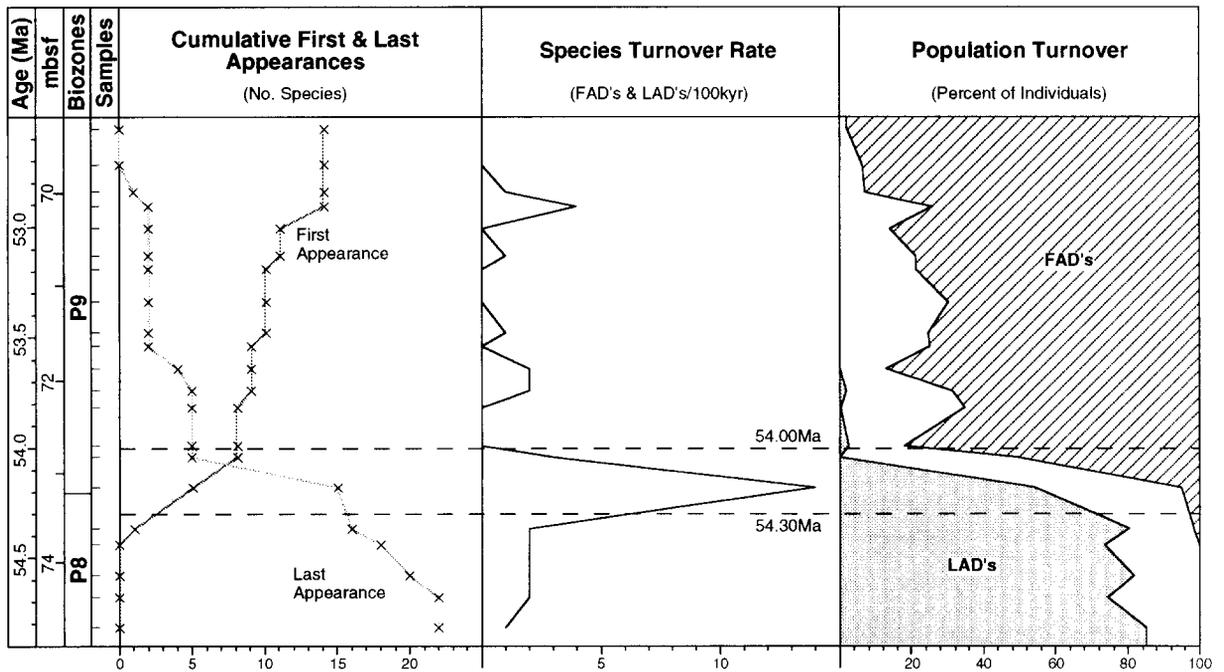


Fig. 6. Species and population turnovers during the faunal event T3 near the P8/P9 zonal boundary at Hole 577. Tighter sampling across this faunal event was prevented by a coring gap at this Hole but was possible at the parallel Hole 577A.

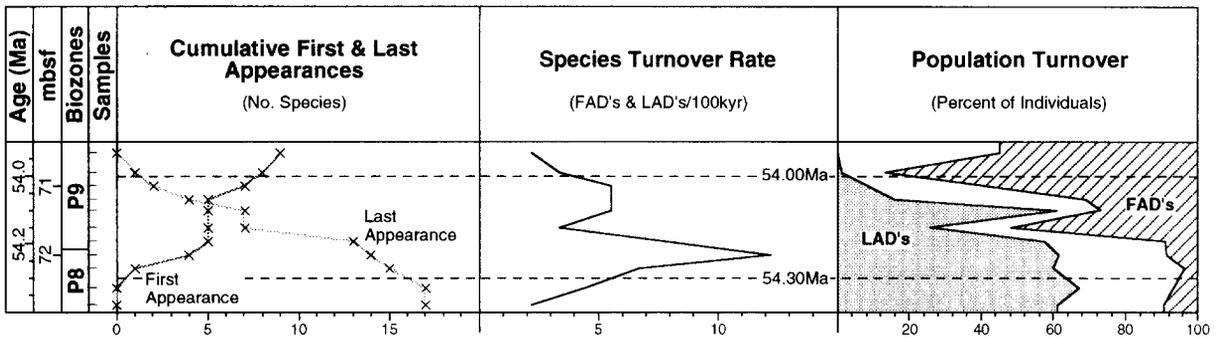


Fig. 7. Species and population turnovers during the faunal event T3 near the P8/P9 zonal boundary at Hole 577A. Tighter samples were analyzed across this faunal event.

about sea-surface temperature, ocean chemistry and surface wind intensity during the late Paleocene to early Eocene. These data show that the global oceanic environment changed profoundly across the Paleocene–Eocene transition (Miller et al., 1987; Kennett and Stott, 1990, 1991; Stott et al., 1990; Barrera and Huber, 1991; Stott, 1992; Corfield and Cartlidge, 1992; Lu and Keller, 1993).

Global foraminiferal $\delta^{13}\text{C}$ values show similar changes with depth and across latitudes (Fig. 8). Oceanic $\delta^{13}\text{C}$ values are generally heavy in the late Paleocene and light in the early Eocene which is characterized by a long-term $\delta^{13}\text{C}$ decrease of 2‰ (global average; Barrera and Huber, 1991; Pak and Miller, 1992; Lu and Keller, 1993) between 59 and 56 Ma. Superimposed upon this long-term decreasing trend in $\delta^{13}\text{C}$ is a major short-term

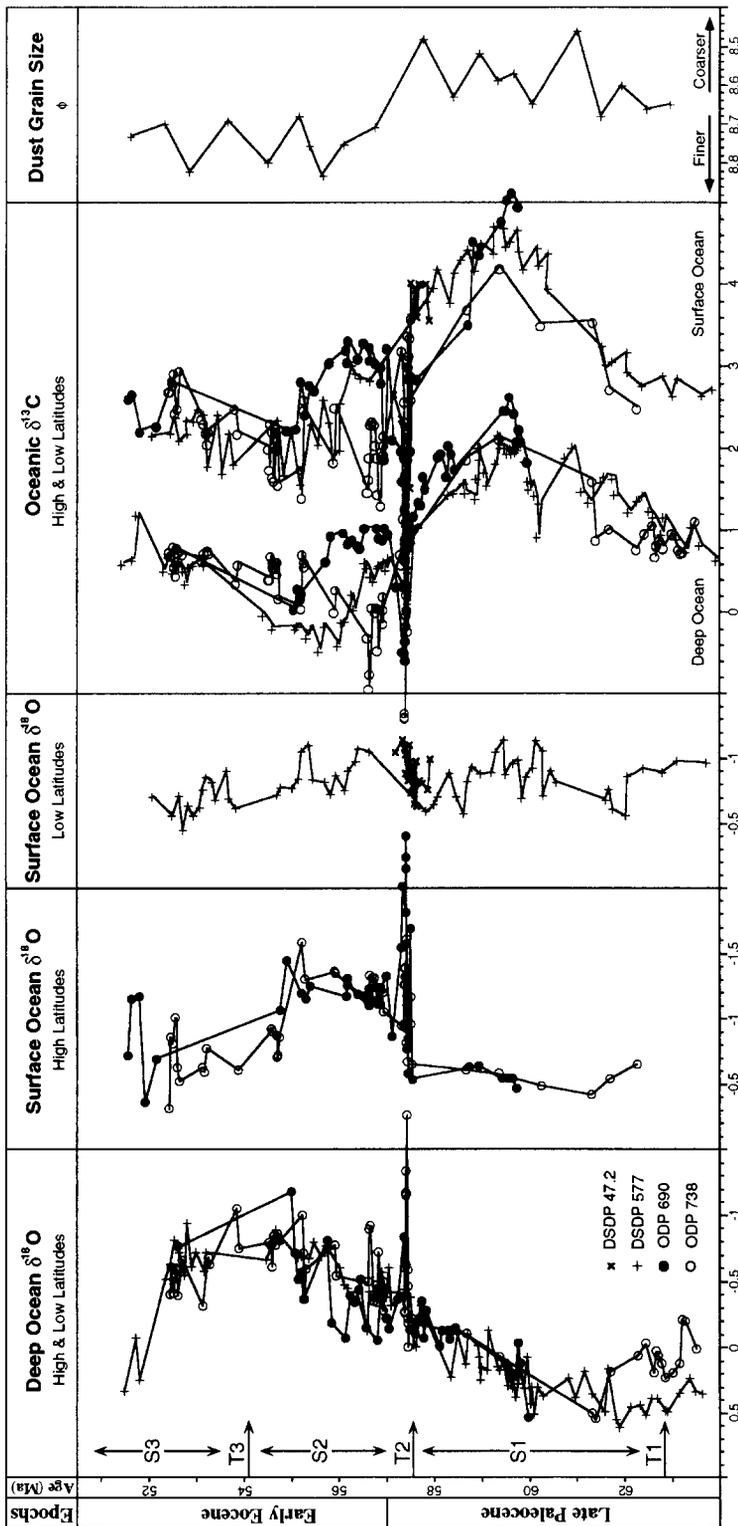


Fig. 8. Indices indicating climatic and oceanographic changes during the late Paleocene to early Eocene. $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ values: DSDP Site 47.2 (Stott, 1992), DSDP Site 577 (Pak and Miller, 1992; Corfield and Cartledge, 1992), ODP Site 690 (Kennett and Stott, 1990, 1991; Stott et al., 1990), ODP Site 738 (Barrera and Huber, 1991; Lu and Keller, 1993). Eolian dust grain sizes: DSDP Site 577 (Miller et al., 1987).

negative excursion of more than 2‰ (global average; Lu and Keller, 1993; Thomas and Shackleton, in press) near the P/E boundary coincident with the faunal event T2. This short-term $\delta^{13}\text{C}$ excursion occurred in less than 10 kyr and lasted 100–200 kyr (Kennett and Stott, 1991; Pak and Miller, 1992; Lu and Keller, 1993; Thomas and Shackleton, in press). The amplitudes of both the long-term and short-term $\delta^{13}\text{C}$ changes are so large that transports of organic carbon from sedimentary reservoirs to the atmosphere, biosphere and ocean must have been involved (Lu and Keller, 1993; Thomas and Shackleton, in press). Increased tectonic and hydrothermal activities across the P–E transition, such as the India–Asia collision, the plate boundary reorganization in the Pacific and the formation of the volcanic margins in the North Atlantic, are generally considered the causes of the possible organic carbon transport associated with the long-term $\delta^{13}\text{C}$ decrease (Rea et al., 1990; Edhome and Thomas, 1993). However, it is not clear what mechanisms have resulted in the rapid organic carbon transport during the short-term event because the timing and amplitude of the $\delta^{13}\text{C}$ excursion suggest a rate comparable to the fossil fuel burning today (Kennett and Stott, 1991; Lu and Keller, 1993; Thomas and Shackleton, in press).

In contrast to $\delta^{13}\text{C}$ values, foraminiferal $\delta^{18}\text{O}$ values differ from surface to deep ocean and from high to low latitudes (Fig. 8). Benthic foraminiferal $\delta^{18}\text{O}$ values are uniform across latitudes with a heavier late Paleocene and a lighter early Eocene that is marked by a long-term decrease of 1.5‰ between 61 and 55 Ma, indicative of a long-term deep water warming of nearly 6°C (Kennett and Stott, 1990; Barrera and Huber, 1991; Katz and Miller, 1991; Pak and Miller, 1992; Lu and Keller, 1993). Superimposed upon this long-term decrease trend in benthic foraminiferal $\delta^{18}\text{O}$ values is a short-term negative excursion of 1–1.5‰ near the P/E boundary coincident with faunal event T2, indicative of a rapid deep ocean warming of 4–6°C (Kennett and Stott, 1991; Lu and Keller, 1993; Bralower et al., in press; Thomas and Shackleton, in press). High-latitude planktic foraminiferal $\delta^{18}\text{O}$ values follow benthic foraminiferal $\delta^{18}\text{O}$ trends, including the short-term negative excursion of

1.5–2‰. They differ in (1) the absence of a gradual decrease immediately preceding the short-term excursion in the high-latitude surface ocean, suggesting the high-latitude surface ocean warming lagged the deep ocean warming; and (2) the onset of the early Eocene gradual increase which started earlier in the high-latitude surface ocean, suggesting that the high-latitude surface ocean cooling led the deep ocean cooling (Stott et al., 1990; Barrea and Huber, 1991; Lu and Keller, 1993). In contrast to the profound changes in the benthic and the high-latitude planktic foraminiferal $\delta^{18}\text{O}$ values, low-latitude planktic foraminiferal $\delta^{18}\text{O}$ values show little change during the late Paleocene to early Eocene, indicating relative steady water temperatures in the low-latitude surface ocean (Miller et al., 1987; Corfield and Cartlidge, 1992; Stott, 1992; Bralower et al., in press).

A major decrease in eolian dust grain sizes has been observed at Site 577 across the P–E transition which are interpreted as a decrease in surface wind intensity as the result of decreased meridional thermal gradients during the high-latitude warming (Fig. 8; Miller et al., 1987). Similar shifts in eolian dust grain sizes have also been observed in other Pacific and Indian ocean sites (Miller et al., 1987; Rea et al., 1990; Hovan and Rea, 1992). However, it is not clear that this shift in eolian dust grain size is associated with the long-term or the short-term changes because of the low sample resolutions (Fig. 8).

Plate motion across latitudes has also been suggested as a possible cause of changing environment for Site 577 (Miller et al., 1987). Within the 12 Myr interval examined, Site 577 moved from 15°N to 22°N based on the back-tracked path of the Pacific Plate by Lancelot and Larson (1975). This latitudinal band is included in the subtropical gyre region without encountering major surface water mass boundaries (Levitus, 1982). Biogeographic studies of living and recent species indicate that planktic foraminiferal faunas in this latitudinal band are well contained within the tropical-subtropical province (Bé, 1977). It is thus unlikely that the plate motion during this time interval has affected planktic foraminiferal faunas at Site 577 (Miller et al., 1987; Lu and Keller, in press).

Chronologic correlation between faunal and environmental changes suggests possible causal effects (Fig. 8). Of the three stasis intervals (S1–S3), S1 and S3 have similar mean species richness and mean species turnover rates (Table 1). They are also correlated with similar and relatively stable sea-surface temperature as indicated by planktic foraminiferal $\delta^{18}\text{O}$ values, despite major long-term changes in deep water temperatures and fluctuations in global oceanic $\delta^{13}\text{C}$ values (Fig. 8). Within S2 interval, species richness was nearly 50% higher than those in S1 and S3 intervals (Table 1). This high species richness at Site 577 is correlated with 2–4°C warming in the high-latitude surface ocean, although little sea-surface temperature change occurred in low latitudes (Fig. 8). The differential warming across latitudes during the early Eocene resulted in a drastic reduction in meridional thermal gradients which affected surface water mass boundaries and surface water column stratification (Shackleton and Boersma, 1981; Miller et al., 1987; Boersma et al., 1987; Stott et al., 1990; Barrera and Huber, 1991; Corfield and Cartlidge, 1992; Lu and Keller, 1993). These changes in water mass boundaries and water column stratification might change niches and biogeography of planktic foraminifera that, in turn, caused changes in migration, speciation and extinction, as argued by Lipps (1970). Changes in planktic foraminiferal biogeography are evidenced by the proliferation of thermophilic species (e.g. morozovellids) towards high latitudes in the early Eocene (Stott and Kennett, 1990; Huber, 1991; Lu and Keller, 1993). Deep water temperatures and global oceanic $\delta^{13}\text{C}$ values also changed gradually during S2 interval (Fig. 8). However, it seems that sea-surface temperature and meridional thermal gradient are major factor affecting the species richness of planktic foraminifera at Site 577 during the three stasis intervals.

Of the three turnover events examined (T1–T3), only T2 can be chronologically correlated with major rapid changes in the oceanic environment, suggesting a causal relationship (Fig. 8). Faunal event T2 coincides with the short-term global change near the P/E boundary as marked by rapid warming of 4–8°C in the deep ocean and high-latitude surface ocean and a negative excursion of

more than 2‰ in oceanic $\delta^{13}\text{C}$ values (Kennett and Stott, 1991; Pak and Miller, 1992; Stott, 1992; Lu and Keller, 1993; Bralower et al., in press; Thomas and Shackleton, in press; Lu and Keller, in press). A major reduction in eolian dust grain size may also be correlated with the short-term global change (Fig. 8). During this short-term global change, vertical and meridional $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ gradients were essentially eliminated and thermohaline circulation might have changed profoundly (Kennett and Stott, 1991; Pak and Miller, 1992; Thomas, 1992; Lu and Keller, 1993; Thomas and Shackleton, in press). The biotic responses to this rapid, short-term global change are different among organisms. Benthic foraminifera suffered a mass extinction which reduced species richness at deep-sea Sites 689 and 690 and near-shore Caravaca and Zumaya sections, Spain, by nearly 50% (Thomas, 1990, 1992; Ortiz and McDougall, 1992). In contrast, the planktic foraminiferal faunal turnover at Site 577 (T2) is dominated by first appearances which increased species richness by nearly 50% (Figs. 2 and 5). However, the present data provides no clue as to what specific environmental factors fostered this faunal turnover.

Although faunal events T1 and T3 have similar amplitudes and rapidity as those of T2, they do not coincide with any major and sudden changes in the oceanic environment (Fig. 8). Faunal event T1 seems to occur near the end of a deep ocean cooling as indicated by benthic foraminiferal $\delta^{18}\text{O}$ values. Global oceanic $\delta^{13}\text{C}$ values increased gradually across this interval. During this faunal event, species disappearances were rapidly replaced by as many appearances and the appearing species rapidly dominated (>80% of the population) the faunal assemblage (Fig. 4). These appearing taxa are generally warm water surface dwellers, such as discoidal morozovellids (e.g., *M. occlusa* and *M. velascoensis*), conic acarininids (e.g., *A. nitida*, *A. intermedia*, *A. subsphaerica*, *A. strabocella* and *A. mckannai*) and igorinids (*I. albeari* and *I. pusilla*), which thrived until faunal event T2.

Faunal event T3 occurs within an interval of gradually cooling in the high-latitude surface ocean (Fig. 8). Minor cooling also occurred in the low-latitude surface ocean whereas deep water temper-

atures remained high. Global oceanic $\delta^{13}\text{C}$ values increased gradually over this interval. There is, however, no major short-term environmental change can be correlated chronologically with faunal event T3 (Fig. 8). Examining the nature of faunal event T3 suggests that this faunal turnover is likely related to the gradual, long-term climate cooling in the surface ocean. This is evidenced that T3 is characterized by last appearances which reduces species richness by nearly 50%. Most of the taxa disappeared at T3 are warm, surface water dwellers, such as rounded, angulate and early forms of muricate acarininids (e.g., *A. pseudotopilensis*, *A. soldadoensis*, *A. triplex*, *A. praepentacamerata*, *A. esnaensis*, *A. gravelli*, *A. wilcoxensis*, *A. nicoli*, *A. cf. nicoli*, *A. densa*, *A. primitiva* and *A. appressocamerata*), which are the dominant species during the early Eocene warming in the S2 interval. The few appearing taxa, as represented by muricate acarininids (e.g., *A. matthewsae*, *A. cuneicamerata*, *A. aspensis* and *A. anapetes*) and muricoglobigerinids (e.g., *M. senni* and *M. lozanoi*), are generally more tolerant of temperate conditions.

5. Threshold effects

Despite the similar temporal patterns, the three rapid faunal turnover (saltation) events in planktic foraminifera at Site 577 during the late Paleocene to early Eocene period are very different in nature as indicated by the differences in species richness changes, first and last appearances rates and species compositions. Correlation between faunal and oceanic environmental changes suggests that, among other factors, sea-surface temperature and meridional thermal gradient were major factors affecting species richness. However, the tempos of faunal and environmental changes are not always correlative. Strong temporal correlation only exists during faunal event T2 which coincides with a rapid, short-term change in global oceanic environments (Fig. 8). Other two faunal events (T1 and T3) occurred in the interval of gradual, long-term environmental changes. This temporal discrepancy between faunal and environmental changes suggests threshold effects during faunal turnovers (saltation).

Threshold conditions for a particular fauna can be reached by the cumulative effect of gradual environmental changes as in the cases of faunal events T3 and, possibly, T1. The early Eocene high-latitude surface ocean cooling, which is likely the major cause of the faunal event T3 in planktic foraminifera, started within the faunal stasis interval T2, about 1 Myr prior to T3. Instead of immediately following the onset of the cooling, major increase in species turnover rate occurred about 1 Myr later that marks faunal event T3 and is correlated with only gradual changes in sea-surface temperatures and other oceanic environmental indices (Fig. 8). For faunal event T1, although insufficient data are available to evaluate the long-term trends of major oceanic environmental indices prior to this faunal event, it seems that this rapid faunal turnover occurred also within a interval of gradual environmental changes (Fig. 8). Unless other rapid changes in oceanic environments are discovered, the most likely explanation for these temporal discrepancy between faunal events T1 and T3 and oceanic environmental changes is threshold effects.

Like other marine organisms, planktic foraminifera can tolerate, to some extents, gradual changes in their ambient water masses (Berger, 1969; Bé, 1977; Hemleben et al., 1989). The extent of this tolerance determines the threshold condition of a planktic foraminiferal fauna to a certain environmental factor. Faunas will stay at stasis before threshold conditions are reached despite ongoing gradual environmental changes, as in the cases of the three stasis intervals examined at Site 577 (Figs. 2 and 8). When threshold conditions are reached by the cumulative effects of gradual environmental changes, rapid faunal turnovers will be triggered, as in the cases of faunal events T1 and T3. In such cases, the tempos of faunal and environmental changes are not correlative.

Threshold conditions may also be reached by sudden, large amplitude environmental changes where strong temporal correlations exist between faunal and environmental changes. This might have been the case in faunal event T2 when the global oceanic environment changed profoundly in less than 10 kyr and planktic foraminiferal faunas responded in a dramatic way (Fig. 8). In

such cases, threshold effects are usually ignored because of the seemingly instantaneous changes between faunas and environments. High resolution studies on expanded records may, therefore, help to elucidate the causes and mechanisms of this type of rapid faunal changes.

This study reveals only phenomena of threshold effects in planktic foraminiferal faunal turnovers that were possibly induced by environmental changes. It is not clear at this time what specific environmental factors may have forced these turnovers and what specific role intrinsic biotic factors may have played. Further investigations of threshold effects are important not only for paleobiological and paleoecological studies, but also for paleo-environmental reconstructions using fossil records. Because of threshold effects, temporal patterns of faunal changes do not always reproduce precisely temporal patterns of environmental changes. In particular, a rapid faunal turnover in planktic foraminifera may or may not correlate with a rapid change in the oceanic environment.

6. Conclusions

The 12 Myr record from DSDP Site 577 spanning the late Paleocene to early Eocene shows that species turnovers of planktic foraminifera are characterized by an alternation between stasis (slow turnovers) and saltation (rapid turnovers). Slow turnovers in three stasis intervals account for 62% of the total first and last appearances spread over 92% of the studied interval (11.1 Myr). No direct correlation is apparent between slow turnovers and gradual environmental changes. Rapid turnovers during three saltation events account for 38% of the total first and last appearances which, however, occur within only 8% of the studied interval (0.9 Myr). Among the three rapid faunal turnover events, a strong correlation exists only between faunal event T2 and the short-term change in the global oceanic environment as marked by a rapid warming in the deep ocean and high-latitude surface ocean and a negative shift in global oceanic $\delta^{13}\text{C}$ values near the P/E boundary. No sudden environmental changes are associated with the other two turnover events (late Paleocene event

T1 and early Eocene event T3), although they occur over a similarly short time interval of between 200–400 Kyr. We suggest that the attainment of threshold conditions for planktic foraminiferal faunas, whether due to sudden environmental changes or the cumulative effects of gradual changes, is largely responsible for triggering rapid faunal turnovers.

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