Planktonic foraminiferal response to the latest Maastrichtian abrupt warm event: a case study from South Atlantic DSDP Site 525A

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Abstract

An abrupt global warming of 3–4°C occurred near the end of the Maastrichtian at 65.45–65.10 Ma. The environmental effects of this warm event are here documented based on stable isotopes and quantitative analysis of planktonic foraminifera at the South Atlantic DSDP Site 525A. Stable isotopes of individual species mark a rapid increase in temperature and a reduction in the vertical water mass stratification that is accompanied by a decrease in niche habitats, reduced species diversity and/or abundance, smaller species morphologies or dwarfing, and reduced photosymbiotic activity. During the warm event, the relative abundance of a large number of species decreased, including tropical–subtropical affiliated species, whereas typical mid-latitude species retained high abundances. This indicates that climate warming did not create favorable conditions for all tropical–subtropical species at mid-latitudes and did not cause a massive retreat in the local mid-latitude population. A noticeable exception is the ecological generalist *Heterohelix dentata* Stenestad that dominated during the cool intervals, but significantly decreased during the warm event. However, dwarfing is the most striking response to the abrupt warming and occurred in various species of different morphologies and lineages (e.g. biserial, trochospiral, keeled globotruncanids). Dwarfing is a typical reaction to environmental stress conditions and was likely the result of increased reproduction rates. Similarly, photosymbiotic activity appears to have been reduced significantly during the maximum warming, as indicated by decreased $\delta^{13}C$ values. The foraminiferal response to climate change is thus multifaceted resulting in decreased species diversity, decreased species populations, increased competition due to reduced niche habitats, dwarfing and reduced photosymbiotic activity.

1. Introduction

The global cooling trend that began in the late Campanian and continued into the early Tertiary was temporarily interrupted by a short warm event between ∼65.45 and 65.1 Ma during which intermediate and surface waters warmed by 2–3°C (Li and Keller, 1998a,b; Barrera and Savin, 1999). This warm event is well-documented in the oxygen isotope records of various Atlantic, Pacific

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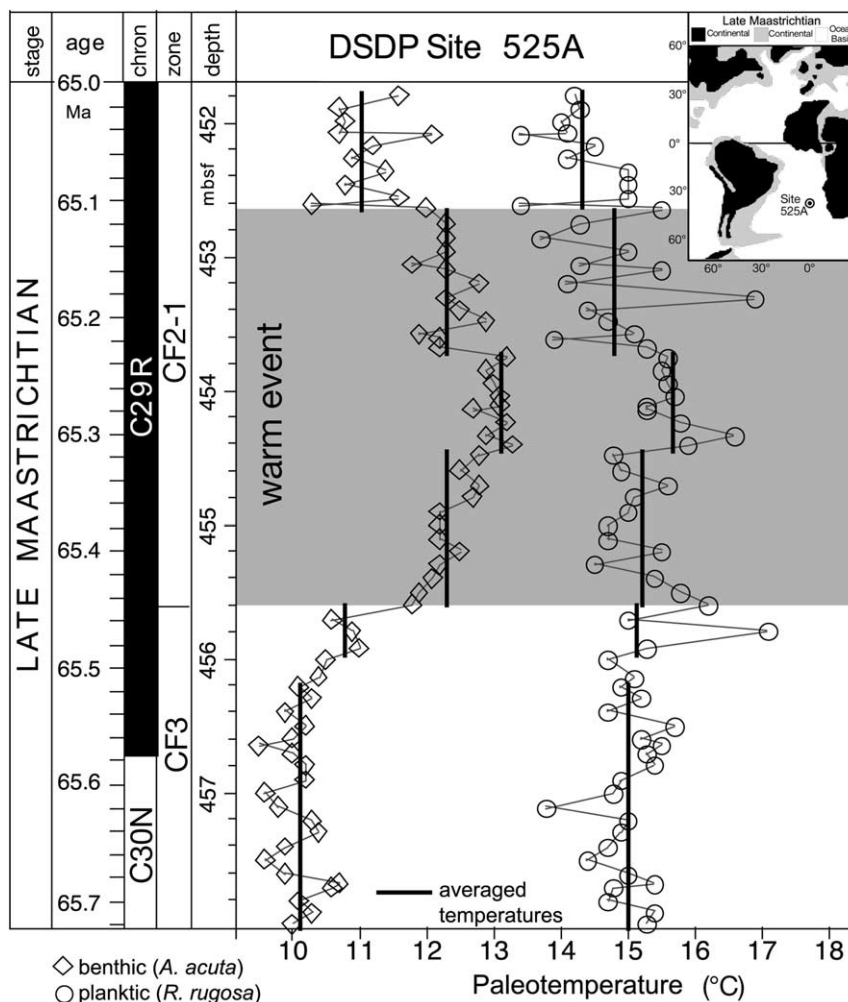 *E-mail address:* sigala@princeton.edu (S. Abramovich).

Fig. 1. High-resolution (10-kyr) paleotemperature records of surface (planktonic foraminifer *Rugoglobigerina rugosa*) and IWs (benthic foraminifer *Anomalinoides acuta*) during the last 720 kyr of the Maastrichtian at South Atlantic DSDP Site 525A. Note the fluctuating surface water temperatures and major warming (3–4°C) of IW between ∼65.45 and 65.11 Ma. During the last 100 kyr of the Maastrichtian temperatures decreased by 1–1.5°C (data from Li and Keller, 1998b). Inset map: Paleolocation of DSDP Site 525A during the late Maastrichtian.

and Indian ocean deep-sea localities including South Atlantic ODP Sites 690 and 689 (Stott and Kennett, 1990; Barrera and Huber, 1990; Barrera et al., 1997), DSDP Sites 528 and 525A (D'Hondt and Lindinger, 1994; Li and Keller, 1998a,b), North Atlantic DSDP Site 384 (Corfield and Norris, 1996), Indian Ocean ODP Site 761 (Barrera and Savin, 1999), tropical Pacific DSDP Site 577 (Zachos et al., 1985, 1989), and more recently at Elles, Tunisia (Stüben et al., in

press) and Bass River, New Jersey (Olsson et al., 2001).

The high-resolution study of the last 2 Myr at the South Atlantic DSDP Site 525A by Li and Keller (1998b) provides the most detailed record of this latest Maastrichtian warm event to date. Temperature records at this locality show that between 65.48 and 65. 46 Ma intermediate waters (IWs) gradually warmed by about 1°C while sea surface temperatures (SSTs) varied considerably

(Fig. 1). Thereafter, IWs rapidly warmed by 2.2°C, while SST slightly increased. Warming reached a maximum between 65.32 and 65.24 Ma when surface and intermediate waters warmed an additional 0.7 and 0.5°C, respectively. Between 65.24 and 65.11 Ma temperatures cooled to levels prior to the maximum warming, and then further decreased by 1–1.5°C during the last 100 kyr of the Maastrichtian (Fig. 1).

Climatic changes are generally expected to have a profound effect on unicellular plankton, which are known to be extremely sensitive to changes in the physical and chemical properties of their surrounding water environments (e.g. Lipps, 1979). The latest Maastrichtian warm event therefore provides a unique test case for understanding plankton population dynamics during climatic perturbations because of the exceptionally abrupt nature and brief duration of this event. In this study we examine the response of planktonic foraminiferal populations to rapid climatic changes during the late Maastrichtian (65.72–65.0 Ma), including the warm event and the preceding and succeeding cooling periods, in order to characterize the response to different climate modes. We chose the South Atlantic DSDP Site 525A for this study because of the availability of a high-resolution isotopic record for the late Maastrichtian (e.g. Li and Keller, 1998b), the continuous sedimentation record (up to the K–T boundary) and presence of an excellent paleomagnetic record that allows precise dating of climatic and faunal changes. Specific objectives of this study include: (1) documentation of planktonic foraminiferal species during the last 720 kyr of the Cretaceous; (2) evaluation of the response of morphologically small and large species groups to climate changes based on relative species abundances and diversity records; (3) probing the response of species to climate changes with respect to their affiliated habitats and biological activities.

2. Material and methods

This study is based on 47 sediment samples spanning the last 720 kyr (top 6.18 m, core 40) of the Maastrichtian from the South Atlantic,

DSDP Site 525A (Walvis Ridge). These samples are part of the sample set that was previously analyzed by Li and Keller (1998b) for stable isotopes (Fig. 1). Age and durations of magnetic polarities are based on Cande and Kent (1995). The planktonic foraminiferal zonation is based on the biostratigraphic scheme of Li and Keller (1998a) with the latest Maastrichtian represented by CF3 and CF2–1 zones (Fig. 1). Absolute age estimates of the 47 samples were determined based on average sedimentation rates within each CF biozone and magnetochron (Appendices A and B). Between 65.72 Ma (457.98 mbsf) and 65.34 Ma (454.6 mbsf) samples were analyzed at 20-cm intervals providing on average one sample every ∼20 kyr. From 65.32 (454.48 mbsf) to 65.01 Ma (451.8 mbsf) samples were analyzed at about 10-cm intervals providing on average one sample every ∼10 kyr.

During the Maastrichtian, DSDP Site 525A was located at 36°S (Fig. 1) at a paleodepth of about 1000 m (Moore et al., 1984), and hence above the foraminiferal lysocline (Kucera et al., 1997). Preservation of planktonic foraminifera in the latest Maastrichtian 720-kyr interval at DSDP Site 525A ranges from very good to moderate. Planktonic foraminiferal test surfaces are often recrystallized indicating early diagenesis, and minor dissolution is evident by less than 5% fragmented shells.

Samples for this study were disaggregated in tap water and washed through a >63-μm sieve until clean foraminiferal residues were recovered. The washed samples were oven-dried at 50°C, and sieved through a >150-μm sieve. From each sample, about 200–300 planktonic foraminifera were picked from random sample splits (using a microsplitter) of two size fractions (63–150 μm, and >150 μm) and mounted on cardboard slides and identified. The larger >150-μm size fraction was analyzed to evaluate the relative abundance of larger species (e.g. keeled globotruncanids, *Pseudotextularia*, *Planoglobulina*, *Racemiguembelina*), which are usually absent or rare in the smaller 63–150-μm size fraction. Relative percent abundances of picked specimens are listed in Appendices A and B. Taxonomic identification of planktonic foraminiferal species is based on Smith and Pessagno
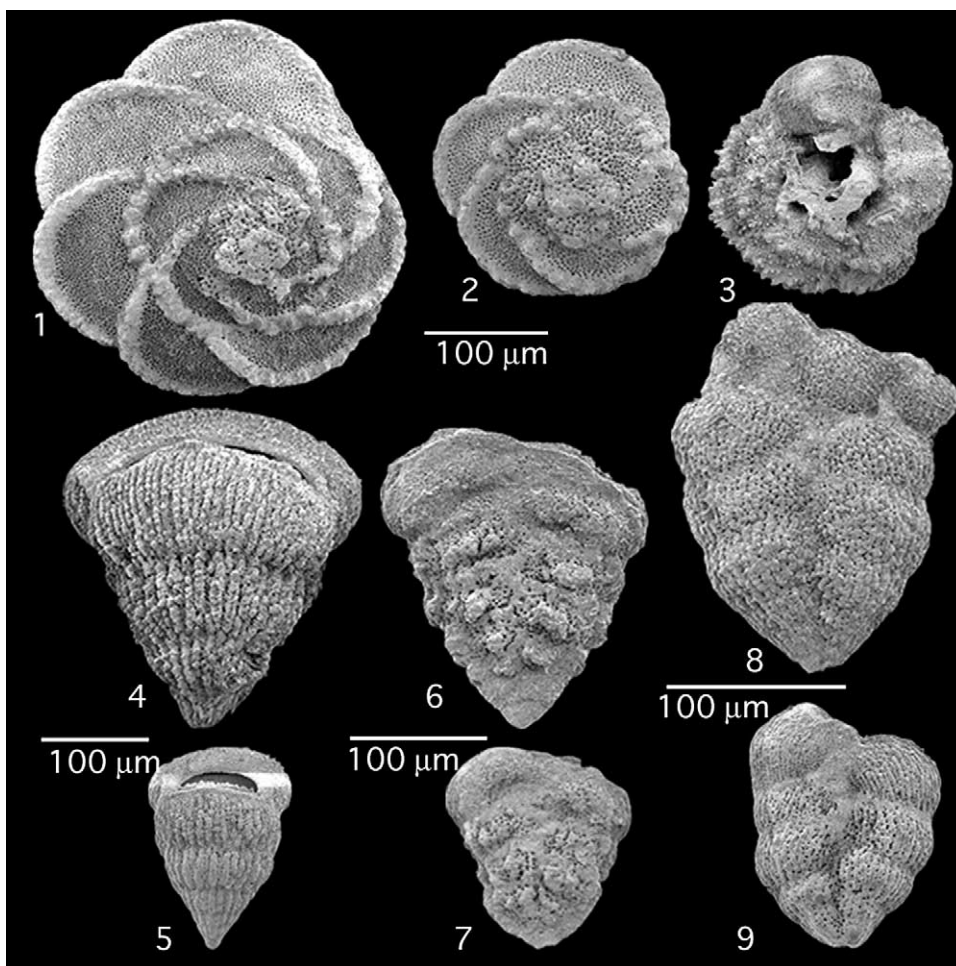
Plate I. Comparison between test sizes of normal-sized adult and dwarfed specimens of *Globotruncana arca* (Cushman) (1–3), *Pseudotextularia deformis* (Kikoine) (4, 5), *Heterohelix rajagopalani* (Govindan) (6, 7) and *Pseudoguembelina hariaensis* Nederbragt (8, 9).

1.   Normal-sized adult specimen (sample 40-5, 140–122 cm)
2, 3.   Dwarfed specimens with well-developed and widely separated peripheral keels (sample 40-3, 138–140 cm)
4.   Normal-sized adult specimen (sample 40-4, 80–82 cm)
5.   Dwarfed specimen with acute periphery in early chambers (sample 40-3, 95–97 cm)
6.   Normal-sized adult specimen (sample 40-5, 50–52 cm)
7.   Dwarfed specimens with test size ∼50% smaller than the adults
8.   Normal-sized adult specimen (sample 40-4, 80–82 cm)
9.   Dwarfed specimen with test size ∼40% smaller than the adults (sample 40-3, 65–67 cm)

(1983), Robaszynski et al. (1983–1984), and Nederbragt (1991). Scanning electron micrographs of selected species are shown in Plate I.

Species diversity measurements are expressed by the Shannon–Weaver index

$$H' = -\sum_{1}^{n} P_i \ln(P_i)$$

P_i is the proportion of each species, and n is the total number of species. This index takes into account both the number of species (i.e. species rich-
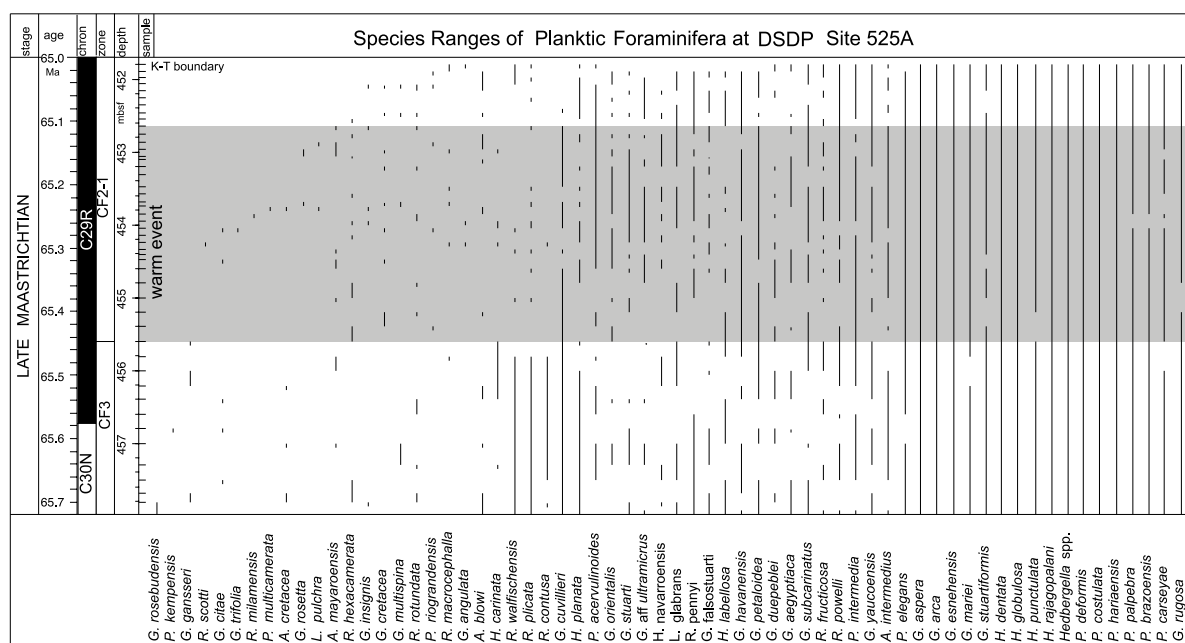
Fig. 2. Planktonic foraminiferal species ranges during the last 720 kyr of the Maastrichtian at DSDP Site 525A. Gray band marks the warm event between 65.45 and 65.1 Ma. Note that species census data do not reveal a specific affiliation with climate warming or cooling, except for *Rosita* species (e.g. *R. contusa, R. plicata, R. walfischensis*) that are sporadically present in the warm interval. Also note the last appearance of *Gansserina gansseri* at 65.45 Ma, which marks a global datum event and defines the base of Zone CF2.

ness) and the distribution of individuals among species (Buzas and Gibson, 1969). Evenness ($E = H'/\ln S$) is a measure of how similar the population of different species is, where S is the number of species in a sample. Evenness assumes a value between 0 and 1 where 1 represents complete evenness, and 0 the dominance of one species.

Determination of planktonic foraminiferal depth habitats and biological activities (e.g. photosymbiosis) is based on the discussion of previously analyzed stable isotopic results of species from sample intervals at 65.6 Ma (457.01 mbsf) and 65.1 Ma (452.63 mbsf, Abramovich et al., in press), and on isotopic measurements of species from sample interval 65.3 Ma (454.34 mbsf) analyzed for this study. Oxygen and carbon isotope analyses were conducted on 20–30 typical adult specimens of selected species from sample interval 65.3 Ma. Isotopic data were measured at the stable isotope laboratory of the Geochemistry Department at the University of Karlsruhe Germany

using a VG Prism II ratio mass spectrometer equipped with a common acid bath (H_3PO_4). Paleotemperature estimates were calculated using the equation of Erez and Luz (1983), with seawater $\delta^{18}O = -1.2\%o$ corresponding to a continental ice-free world (Shackleton and Kennett, 1975). Isotope results and paleotemperatures estimations are listed in Appendix C.

3. Species ranges and paleogeographic distribution

A total of 64 planktonic foraminiferal species are identified from the last 720-kyr interval of the late Maastrichtian at South Atlantic DSDP Site 525A (Fig. 2), though only 18 species are continuously present in all or most of the analyzed samples, and 24 species are intermittently present. This group includes 20 biserial or multiserial taxa of the Heterohelicidea (Cushman) family, 15 keeled globotruncanids, four planispiral taxa of the genus *Globigerinelloides* (Cushman and

Ten Dam), three trochospiral taxa of the *Rugoglobigerina* (Brönnimann) and *Hedbergella* (Brönnimann and Brown) genera (Fig. 2). Most of these species are geographically widespread spanning the tropics and warm transitional mid-latitudes, except for *Heterohelix rajagopalani* (Govindan) (Plate I), a species limited to the southern mid-latitudes of the Atlantic and Indian oceans (Malmgren, 1991; Nederbragt, 1992, 1998; Li and Keller, 1998a).

Twenty-two species are sporadically present in the 720-kyr interval of the late Maastrichtian at DSDP Site 525A (Fig. 2). Their sporadic presence suggests that they were rare or lived beyond the limits of their optimum geographic or biostratigraphic ranges. For example, the species *Planoglobulina multicamerata* (De Klasz) and *Pseudoguembelina kempensis* Esker are typical components of deep-sea tropical Tethyan planktonic foraminiferal assemblages (Malmgren, 1991; Nederbragt, 1992, 1998). In addition, most of the species with sporadic occurrences exhibit late appearances and early disappearances that do not generally reflect extinctions and evolutions, except for *Gansserina gansseri* (Bolli). The last appearance of this species marks a global datum event (Fig. 2) that defines the base of Zone CF2 (Li and Keller, 1998a) in late Maastrichtian strata of Tethyan and North Atlantic localities (e.g. Spain, Pardo et al., 1996, Tunisia, Li and Keller, 1998c; Abramovich and Keller, 2002, DSDP Site 605, and Bass River, New Jersey, Olsson et al., 2001).

There seems to be no clear signal in the species range data that points to specific preference for either warm or cool climate modes with the exception of the *Rosita* (Caron, Gonzalez, Donso and Robaszynski) group (e.g. *R. contusa*, *R. plicata*, *R. walfischensis*, Fig. 2). During the cool interval between 65.72 and 65.5 Ma *Rosita* species are almost continuously present, but during the warm event (65.48–65.1 Ma) they are sporadically present with the last *R. contusa* observed at 65.3 Ma (Fig. 2). After the warm event, both *R. plicata* (White) and *R. walfischensis* (Todd) exhibit sporadic occurrences, although the latter reappears during the last 40 kyr of the Maastrichtian. A similar pattern of *Rosita* occurrences was observed in Tethyan localities of Spain and Tunisia

(Pardo et al., 1996; Li and Keller, 1998c; Abramovich and Keller, 2002), and in four South Atlantic DSDP Sites (including DSDP Site 525A, Kucera and Malmgren, 1998).

4. Relative abundance changes

4.1. 63–150-μm size fraction

During the cool climatic intervals (both before and after the warm event) populations of small species at DSDP Site 525A are largely dominated by *Hedbergella* spp., *Pseudoguembelina costulata* (Cushman), *Heterohelix globulosa* (Ehrenberg), *Globigerinelloides aspera* (Ehrenberg) and *Heterohelix dentata* (all show abundances > 10%, Fig. 3). Within this group *H. dentata* is most abundant (33–66% at 65.72–65.5 Ma, and 23–50‰ at 65.1–65.01 Ma).

The most striking aspect of the faunal change during the warm event at Site 525A is the appearance of unusually small adult specimens (63–150-μm size fraction) of several planktonic foraminiferal species that are usually absent, or present only as juveniles in the < 63-μm size fraction. These species include *Globotruncana arca* (Cushman), *Globotruncana esnehensis* Nakkady, *Globigerinelloides subcarinatus* (Brönnimann), *Heterohelix rajagopalani*, *Pseudoguembelina hariaensis* Nederbragt, *Pseudotextularia elegans* (Rzehak), *Pseudotextularia deformis* (Kikoine) and *Rugoglobigerina rugosa* (Plummer) (Fig. 3). Their presence in the 63–150-μm size fraction therefore appears abnormal. An especially dramatic size reduction is observed in *P. hariaensis*, *P. deformis*, *P. elegans*, *G. arca* and *G. esnehensis*, which typically reach adult test sizes > 250 μm, with only juvenile forms < 150 μm. Test size reductions of 50% are common among these dwarfed species (Plate I). Similarly, normal adult test sizes of *R. rugosa*, *G. subcarinatus* and *H. rajagopalani* vary between 125 μm and 200 μm, whereas dwarfed specimens are generally smaller than 100 μm.

Morphological features of the dwarfed specimens are similar or identical to normal-sized adults, as indicated by the fully developed shape of chambers and apertures, and the presence of a

Fig. 3. Planktonic foraminiferal species abundances in the smaller (63–150-μm) size fraction of the last 720 kyr of the Maastrichtian at DSDP Site 525A. Gray band marks the warm event between 65.45 and 65.1 Ma. Note the high relative abundance of *Heterohelix dentata* during the cool climatic intervals and the distinct decrease during the warm interval. Also associated with climate warming are the abnormal appearances of dwarfed specimens of eight species with a combined abundance that varies between 20 and 60%. The morphologies of most of these species are typically very large (> 250 μm) and normally only present as juveniles in the smaller size fraction.

complete set of chambers and surface ornamentation (e.g. costae, keels, pustules, Plate I, Appendix C). For example, dwarfed specimens of *Pseudotextularia deformis* bear thick costae, chambers are wide in apertural view and the aperture is broad and narrow as in normal adult forms (Plate I). Tests of dwarfed *Globotruncana arca* consist of five to six chambers in the last whorl, with distinct keels that are typically absent in juvenile specimens (Plate I). On the other hand, Kucera and Malmgren (1998) and Olsson et al. (2001) reported a significant increase in test size of *Rosita* and *P. deformis* during the warm interval. However, since they analyzed only the > 250-μm size fraction, the smaller dwarfed specimens would not have been present in their samples.

During the warm event the combined abundances of dwarfed specimens in the 63–150-μm size fraction varied between a low of 20% and a high of 60%, with *Heterohelix rajagopalani* (15%), *Pseudoguembelina hariaensis* (25%) and *Globotruncana arca* (22%) the major contributors (Fig. 3). Coincident with the appearance of dwarfed specimens is a sharp decrease in the relative abundance of *Heterohelix dentata* to 5–20%, though the relative abundances of other dominant species in the 63–150-μm size fraction show little change (Fig. 3). With the return of cooler conditions during the last 100 kyr of the Maastrichtian *H. dentata* returns to dominance and dwarfed specimens decrease to less than 10%.

4.2. > 150-μm size fraction

At DSDP Site 525A late Maastrichtian planktonic foraminiferal species populations in the > 150-μm size fraction are at least twice as diverse as those in the smaller < 150-μm size fraction (Fig. 4). At DSDP Site 525A, planktonic foraminiferal assemblages in the larger size fraction (> 150 μm) are dominated by *Globotruncana arca*, *Globotruncana esnehensis*, *Globotruncana*
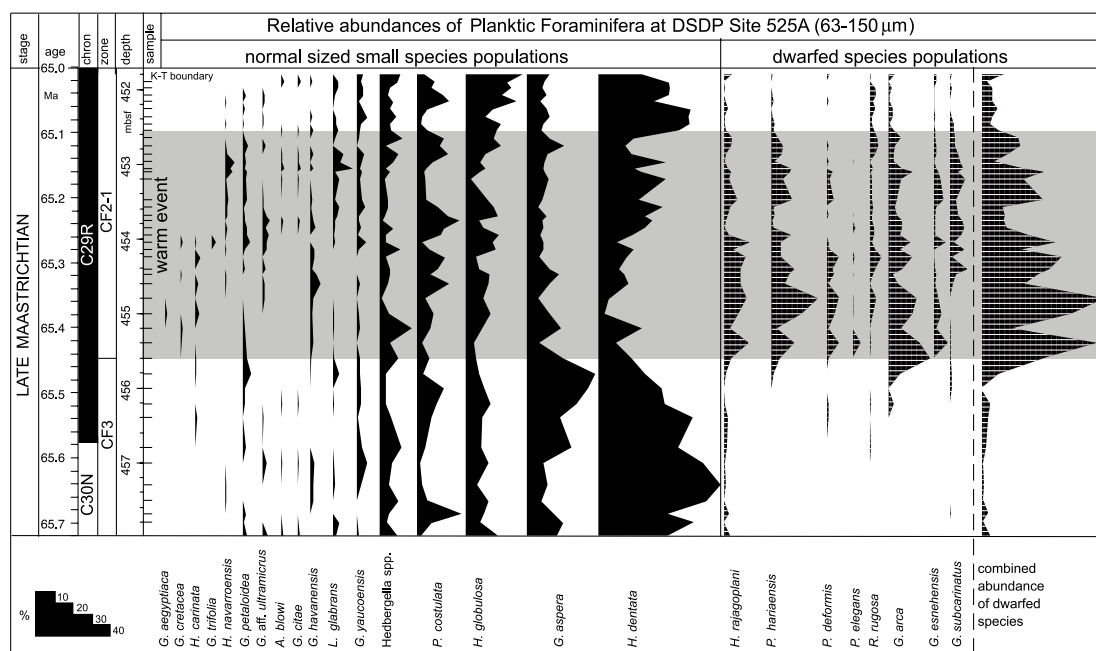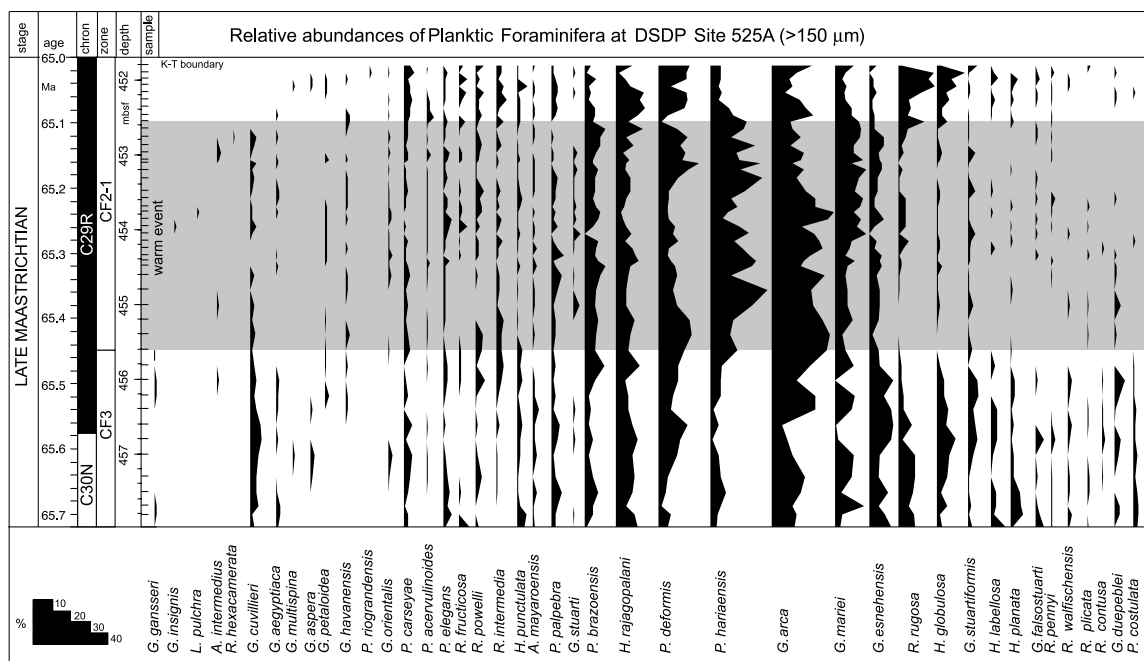
Fig. 4. Planktonic foraminiferal species abundances in the larger (>150-μm) size fraction of the last 720 kyr of the Maastrichtian at DSDP Site 525A. Gray band marks the warm event between 65.45 and 65.1 Ma. Note the marked increase of *Pseudoguembelina hariaensis* and high abundance of *Globotruncana arca*, *Globotruncana mariei* and *Pseudotextularia deformis* in the warm interval. An opposite trend is recorded by 13 species that decline in response to warming including the tropical affiliated *Pseudoguembelina costulata* and *Rugoglobigerina rugosa* and several keeled globotruncanids.

mariei Banner and Blow, *Heterohelix globulosa*, *Heterohelix rajagopalani*, *Planoglobulina brazoensis* Martin, *Pseudoguembelina hariaensis*, *Pseudotextularia deformis*, and *Rugoglobigerina rugosa*. Within this group the high abundance of *H. rajagopalani*, *P. hariaensis* and *G. arca* is a typical feature of mid-latitude South Atlantic planktonic foraminiferal assemblages (Nederbragt, 1998; Li and Keller, 1998a), whereas the other species are also common in tropical localities.

The most notable faunal changes during the warm event in the >150-μm size fraction at Site 525A include a marked increase in *Pseudoguembelina hariaensis* from ∼5% to >10% and occasionally to >30%, and the sharp decline of *Heterohelix globulosa*, *Globotruncana esnehensis* and *Rugoglobigerina rugosa* (Fig. 4). An additional 10 species decreased during the warm interval. These include *Globotruncana duepeblei* Caron, Gonzalez, Robaszynski and Wonders, *Globotruncana falsostuarti* Sigal, *Globotruncanita stuartiformis* (Dalbeis),

Heterohelix labellosa Nederbragt, *Heterohelix planata* (Cushman), *Pseudoguembelina costulata*, *Rugoglobigerina pennyi* (Brönnimann), *Rosita contusa*, *Rosita plicata* and *Rosita walfischensis*. *Globotruncana arca*, *Globotruncana mariei* and *Pseudotextularia deformis* continue to dominate at different intervals during the warm event.

The end Cretaceous climate cooling between 65 and 32 kyr before the K–T boundary (Fig. 1) is accompanied by major increases in the >150-μm populations of *Heterohelix globulosa* (15%) and *Rugoglobigerina rugosa* (19%), and minor increases in *Heterohelix labellosa*, *Heterohelix planata*, *Globotruncana falsostuarti*, *Globotruncana duepeblei*, and *Rosita plicata*. The opposite response is observed in *Pseudoguembelina hariaensis*, *Planoglobulina brazoensis*, *Globotruncana esnehensis*, and *Gublerina cuvillieri* (Kikoine) populations, which decreased during the last 100 kyr of the Maastrichtian (Fig. 4).
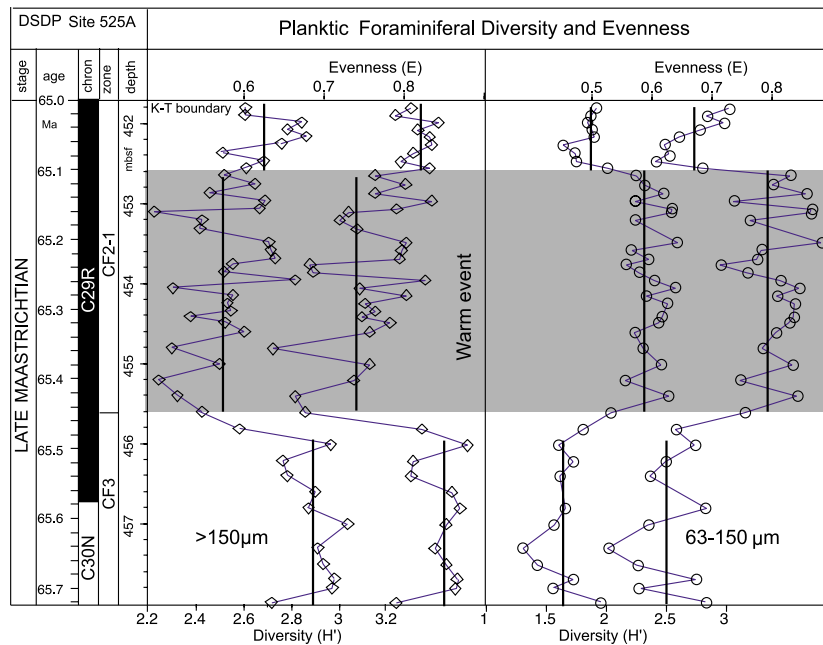
Fig. 5. Planktonic foraminiferal species diversity (*H′*) and evenness (*E*) in the small (63–150-μm) and large (>150-μm) size fractions measured by the Shannon–Weaver index. Gray band marks the warm event between 65.48 and 65.1 Ma. Note the increase in species diversity and evenness in the smaller size fraction during the warm interval is largely due to the presence of dwarfed specimens of species that are typically only found in the larger size fraction. Trends observed in the larger (>150-μm) size fraction indicate that during the warm event species diversity and evenness decreased significantly as result of the decline of 13 species. Vertical lines represent average values within interval.

5. Planktonic foraminiferal diversity trends

In the late Maastrichtian at DSDP Site 525A diversity (*H′*) and evenness (*E*) records of the two size fractions 63–150 μm and >150 μm show antithetical trends that are correlative with climatic trends and reflect the various aspects of the planktonic foraminiferal response to warming and cooling (Fig. 5). Highest species diversity and evenness values (averaged *H′* = 2.89, *E* = 0.85) are recorded in the >150-μm size fraction during the maximum cooling interval between 65.72 and 65.5 Ma (Fig. 5). These values reflect moderate dominance (∼10–20%) of six species and the common presence (∼5–10%) of 12 additional species. During the warm event, diversity and evenness in the >150-μm size fraction drop to averages of 2.51 and 0.76, respectively (Fig. 5). This decrease reflects the abundance decline of 13 key species and >30% dominance of *Pseudoguembelina hariaensis* and *Globotruncana arca* (Fig. 4). During the cool-

ing between 65.1 and 65 Ma diversity and evenness increased to 2.69 and 0.82. However, most of this increase corresponds to the interval between 65 and 32 kyr before the K–T boundary, and represents the temporary recovery of several planktonic foraminiferal species (Fig. 4), and decreased dominance of *P. hariaensis* and *G. arca*.

In the 63–150-μm size fraction, maximum diversity and evenness (averaged *H′* = 2.22, *E* = 0.79) correspond to the warm interval and reflect the appearances of dwarfed specimens of eight species but also the decreased dominance of *Heterohelix dentata* (Fig. 3). In contrast, in the cool interval preceding the warming (e.g. 65.72 and 65.5 Ma), average diversity and evenness record minimum values (*H′* = 1.62, *E* = 0.62) that correspond to peak abundance of *H. dentata* (35–66%, Fig. 4). Similarly, in the last 100 kyr of the Maastrichtian averaged diversity and evenness values (*H′* = 1.84, *E* = 0.67) are lower compared with the warm interval and reflect the recovery of

H. dentata and diminished presence of dwarf specimens.

6. Stable isotope analysis of species

6.1. Oxygen isotopes and paleotemperatures

At DSDP Site 525A, planktonic foraminifera are well preserved (Plate I), but presence of secondary calcite growths within shells indicates bottom deep-sea diagenesis (Pearson et al., 2001). Calculated temperatures for planktonic foraminiferal species at this site suggest that diagenesis slightly shifted the $\delta^{18}O$ signals towards heavier (cooler) values (Abramovich et al., in press). Despite the diagenetic alteration, global climatic and species vertical distribution trends are well preserved at site 525A. At the 65.6-Ma interval, cool temperatures and a well-stratified upper water column are indicated by the species oxygen isotope temperature records, which have been calculated from well-preserved adult tests of individual species (Abramovich et al., in press). Based on these $\delta^{18}O$ measurements and temperature calculations, the surface dweller *Pseudoguembelina hariaensis* averaged ∼16.7°C (−1.14‰), and the deep dweller (sub-thermocline) *Gublerina cuvillieri* averaged ∼13°C (−0.32‰). At the same time, *Globotruncana arca* and *Heterohelix globulosa* inhabited thermocline depths at ∼14.7°C (−0.7‰), whereas *Pseudotextularia deformis*, *Pseudotextularia elegans*, *Rugoglobigerina rugosa*, *Rosita walfischensis* and *Planoglobulina acervulinoides* Egger inhabited subsurface depths at ∼15.2–15.6°C (Fig. 6, Appendix C).

The late Maastrichtian warm event is reflected by the temperature signals of most species that peak in the 65.3-Ma interval (Fig. 6). During this interval upper water temperatures based on the surface dweller *Pseudoguembelina palpebra* Brönnimann and Brown averaged ∼18°C (−1.39‰), and the deep dweller *Abathomphalus mayaroensis* (Bolli) averaged ∼15.5°C (−0.86‰). This suggests that during the warm event surface and sub-thermocline temperatures at DSDP Site 525A increased by 1.2°C and 2.5°C (respectively), corresponding to a ∼1.3°C

decrease in the upper water temperature gradient. This estimation supports the notion that upper water temperatures warmed in a similar manner as deep-water masses (Stott and Kennett, 1990; Barrera, 1994; D'Hondt and Lindinger 1994; Li and Keller, 1998a,b; Barrera and Savin, 1999).

Temperature records of some species also point to significant changes in their relative depth stratification in response to the warming. Among the species affected, the response of *Pseudoguembelina hariaensis* and *Heterohelix globulosa* is the most distinct. The surface dweller *P. hariaensis* is the only species that does not record the temperature maximum in the 65.3-Ma interval exhibited by all other species. In fact, *P. hariaensis* records a ∼0.5°C (0.11‰) decrease compared with the 65.6-Ma interval, which suggests that this species migrated to deeper, subsurface depths in response to the warming (Fig. 6). The opposite trend is recorded by *H. globulosa*, which seems to migrate to subsurface depths during the warm event, as noticed by the change in its relative ranking compared with other species (Fig. 6). Most other species exhibit minor or no changes in their relative depth stratification during the warm event, although temperature differences between subthermocline, thermocline and subsurface dwellers are significantly reduced.

The return of cooler temperatures at DSDP Site 525A is indicated in the 65.1-Ma interval where most species exhibit decreased temperatures compared with the 65.3-Ma interval (Fig. 6). At 65.1 Ma, temperatures of the upper water column range between ∼17.1°C (−1.23‰), recorded by *Pseudoguembelina palpebra*, and ∼14.3°C (−0.59‰), recorded by *Heterohelix rajagopalani*. This range suggest ∼0.5°C and ∼1.2°C cooling of surface and deep plankton habitats (respectively), and a slight increase (∼0.4°C) in the subsurface temperature gradient. However, cooling at 65.1 Ma was not as intense as in the interval that preceded the warm event, as indicated by the temperature records of most species and also reported by Li and Keller (1998b) and Barrera and Savin (1999). For example, *Gublerina cuvillieri* exhibits a 1.4°C (0.32‰) difference between the 65.1-Ma and 65.6-Ma intervals. Similar trends, though smaller temperature differences, are recorded by

Fig. 6. Paleotemperature and δ¹³C records of selected planktonic foraminiferal species from intervals at 65.61, 65.3 and 65.11 Ma and the paleotemperature record of planktonic and benthic foraminifera during the last 720 kyr of the Maastrichtian at DSDP Site 525A (from Li and Keller, 1998b). Key to species: ace, *Planoglobulina acervulinoides*; arc, *Globotruncana arca*; cuv, *Gublerina cuvillieri*; def, *Pseudotextularia deformis*; ele, *Pseudotextularia elegans*; glo, *Heterohelix globulosa*; har, *Pseudoguembelina hariaensis*; may, *Abathomphalus mayaroensis*; pal, *Pseudoguembelina palpebra*; pow, *Racemiguembelina powelli*; rug, *Rugoglobigerina rugosa*; wal, *Rosita walfischensis*. For discussion of data, see text.

other species in the 65.1-Ma and 65.6-Ma intervals (Fig. 6, Appendix C). Despite the cooling at 65.1 Ma, *Heterohelix globulosa* remained a subsurface dweller in contrast to the earlier cooling noted above. On the other hand, *P. hariaensis* seems to have returned to surface depths as indicated by the ∼0.4°C increase in its temperature signal.

6.2. Carbon isotopes and photosymbiosis

Photosymbiotic activity has been recognized in several Maastrichtian taxa including species of the genera *Racemiguembelina* (strongest photosymbiotic signal), *Planoglobulina*, *Rosita*, *Pseudotextularia deformis* (weak photosymbiotic signal) and *Pseudoguembelina* (weakest photosymbiotic signal) based on size-related isotopic trends (D'Hondt and Zachos, 1998; Houston and Huber, 1998; Houston et al., 1999) and typically enriched δ¹³C compared with coexisting taxa

(D'Hondt and Arthur, 1995; Abramovich et al., in press). Such δ¹³C enrichment patterns of photosymbiotic taxa are observed in the 65.6-Ma interval at DSDP Site 525A (Fig. 6). In this interval, the difference in δ¹³C between photosymbiotic and the isotopically most enriched non-symbiotic species, *Globotruncana arca* ranges from 0.2‰ (*P. deformis*) to 0.6‰ (*Racemiguembelina powelli* Smith and Pessagno). These differences suggest that during the cool period at 65.6 Ma oligotrophic conditions that supported strong photosymbiotic activity were well established in the upper water column. In contrast, during the warm event at 65.3 Ma, δ¹³C values of most photosymbiotic species decreased significantly and are similar to δ¹³C values of some non-symbiotic species (Fig. 6). For example, δ¹³C values of *Rosita walfischensis* are ∼0.7‰ lower in the 65.3-Ma interval than at 65.6 Ma. Similarly, δ¹³C values of *P. deformis* and *Planoglobulina acervulinoides* dropped by ∼0.3‰ and 0.2‰ respectively, though δ¹³C

values of *Pseudoguembelina hariaensis* only slightly decreased (0.03‰) during the warm event. A $\delta^{13}C$ enrichment trend of photosymbiotic species is indicated in the cool interval at 65.1 Ma as exhibited by *P. acervulinoides* (0.2‰), *Pseudoguembelina palpebra* (0.6‰), *P. deformis* (0.15‰), and *P. hariaensis* (0.1‰).

7. Discussion

The global warming that took place just prior to the K–T boundary (e.g. ∼65.45–65.1 Ma) is a paradigm of naturally induced climatic perturbations with an immediate effect on marine environments. The cause is believed to be greenhouse warming due to a major pulse in Deccan volcanism between 65.4 and 65.2 Ma (Hoffmann et al., 2000). Stable isotope data indicate a global warming of 2–3°C in surface and intermediate water temperatures (Li and Keller, 1998b; Barrera and Savin, 1999; Olsson et al., 2001; Keller et al., 2002a).

What effects did the global warming have on planktonic foraminiferal populations? Previous studies that addressed this issue suggested that the main planktonic foraminiferal response to the late Maastrichtian climate warming was a poleward migration of tropical–subtropical species. For example, Kucera and Malmgren (1998) observed an increase in test size and test conicity of *Rosita* during the warm interval in several South Atlantic localities and concluded that warming provided optimum conditions for tropical morphotypes (e.g. large test) to inhabit mid-latitudes. Similarly, Olsson et al. (2001) reported an increase in abundance and test size of populations of *Pseudotextularia deformis* within the larger (>250-μm) size fraction at DSDP Site 525A, 609 and Bass River, New Jersey, that suggested the same poleward migration pattern as recorded by the *Rosita* group. These studies imply that climate warming mimics the tropics in mid-latitudes and results in migration of tropical species.

If this is the case, there should also be a distinct increase in plankton diversity that reflects increased water mass stratification, incursion of restricted tropical species and a decline in the rela-

tive abundance of mid-latitude species, all expected consequences of climate warming. The present study suggests that latitudinal migration may be only one of several factors affecting marine plankton during climate change. Other factors, such as changes in water mass stratification, vertical migration, changes in photosymbiotic activity, and dwarfing, may all have contributed to the observed assemblage changes associated with climate warming. This study provides insights into each of these factors.

7.1. Latitudinal migration

Migration of species into higher latitudes at times of warming implies the export and establishment of tropical–subtropical faunas at mid-latitudes. At the same time, the abundance of native species is expected to decrease due to the influx of competitor species and the effect of increased temperatures. However, the faunal data of DSDP Site 525A for the most part do not support the predicted pattern at mid-latitudes. Instead, the observed changes in the relative abundances of species suggest a more complex and variable species response to climate warming.

Thirteen species, which are typically of large size (>150 μm), show significant relative abundance changes during the climate warming (Fig. 4). Species with decreased abundances include the tropical–subtropical *Pseudoguembelina costulata*, *Rugoglobigerina rugosa* and several keeled globotruncanids (including *Rosita* species, Figs. 4 and 7). Their decline suggests unfavorable, rather than favorable, environmental conditions for tropical–subtropical affiliated species during climate warming in mid-latitudes. In addition, the absence of tropical species such as *Pseudoguembelina kempensis* or *Planoglobulina multicamerata* in the warm interval at DSDP Site 525A further indicates that warming does not necessarily create suitable conditions for tropical species in mid-latitudes (Fig. 2). Nor does the return of a cooler climate during the last 100 kyr of the Maastrichtian necessarily restore species to their former dominance. For example, although *R. rugosa* shows a marked recovery, keeled globotruncanids (particularly *Globotruncana esnehensis*, Fig. 4) de-
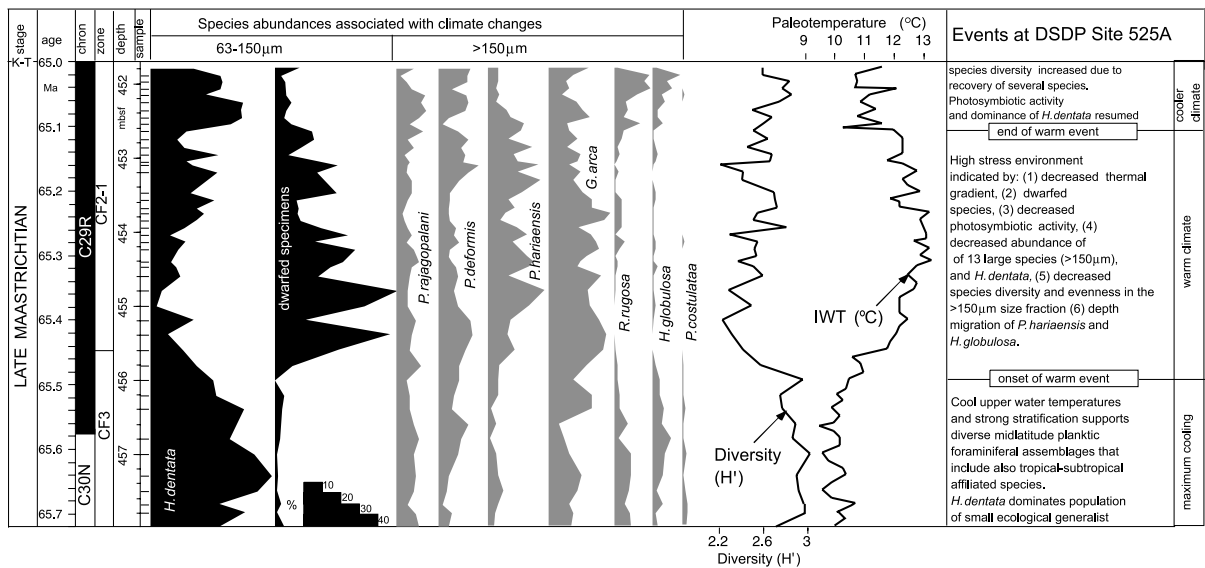
Fig. 7. Summary of faunal and environmental events during the last 720 kyr of the Maastrichtian at South Atlantic DSDP Site 525A. Note the exceptional concurrence between faunal and climate changes indicates a causative relationship.

creased further and *P. costulata* failed to recover (Fig. 7). These species abundance patterns suggest that plankton habitats were not fully restored to pre-warming conditions during the last 100 kyr of the Maastrichtian.

In contrast, some species populations remained apparently unaffected by the warm event as indicated by their continuous dominance (e.g. *Pseudoguembelina hariaensis*, *Globotruncana arca*, *Globotruncana mariei*, *Pseudotextularia deformis*, and *Heterohelix rajagopalani*, Fig. 7). These species are typical components of mid-latitude planktonic foraminiferal assemblages (Li and Keller, 1998a) and *H. rajagopalani* was endemic to mid-latitude South Atlantic localities (Nederbragt, 1998). The dominant presence of these species during the warm event at DSDP Site 525A indicates that warming did not cause a massive retreat of the local mid-latitude population. A different response is recorded by *Heterohelix dentata*, which is the most dominant component of the population of ecological generalists in the Maastrichtian at South Atlantic DSDP Site 525A (Fig. 7). During the warm event, this species decreased sharply reflecting a distinct negative response to warming. A similar trend was recorded at El Kef and Elles, Tunisia, and in central Egypt where *H. dentata*

decreased during the warm interval (Li and Keller, 1998c; Abramovich and Keller, 2002; Keller, 2002).

7.2. Water mass stratification and species diversity

A well-stratified upper water mass is a key factor for the existence of diverse plankton communities. Such conditions generally exist at low latitudes where a warm mixed layer overlies distinct cooler/denser thermocline waters that differentiate niches for surface and deeper plankton dwellers. In contrast, at higher latitudes the density gradient is much weaker and hence species diversity is markedly lower compared with lower latitudes. Warming of surface waters during the late Maastrichtian is expected to have increased the water mass stratification at mid-latitudes and created similar conditions as in the tropics. However, oxygen isotope data from DSDP Site 525A do not support the notion that the vertical thermal gradient at mid-latitudes resembled the tropics.

The oxygen isotope record of DSDP Site 525A indicates that water mass stratification was significantly reduced during the warm event (Li and Keller, 1998b; Barrera and Savin, 1999). This is also indicated by the oxygen isotope results of

individual species in the 65.3-Ma interval, which reveal that the upper water thermal gradient decreased by about 1.3°C compared with the cooler interval at 65.6 Ma (Fig. 6). This decrease is attributed to warming of sub-thermocline waters, which is indicated by the distinct increase in temperature records (∼2.5°C) of deeper-dwelling species (Fig. 6). Particularly noticeable is the decrease in the temperature difference between deep and subsurface species in the warm interval, which implies that ecological niches that required a strong temperature/density contrast in the upper water were eliminated.

The reduction in upper water mass stratification is probably also in part responsible for the sharp drop in the diversity of large planktonic foraminiferal populations that coincide with the climate warming (Fig. 7), and suggests a reduction of available habitats. The disruptive effect of climate warming on planktonic foraminiferal communities is further demonstrated by the marked decrease in species evenness (Fig. 5). This decrease reflects the dominance of only a few local species (e.g. *Globotruncana arca*, *Globotruncana mariei*, *Pseudotextularia deformis*, *Pseudoguembelina hariaensis*, Fig. 7) and indicates a significant reduction in the complexity of the planktonic foraminiferal communities, which is a typical trend during periods of environmental perturbation.

7.3. Vertical migration

The relative oxygen isotope ordering of planktonic foraminiferal species is a primary tool for determining their depth habitats. A repeated pattern of the isotopic ordering of species over time indicates stability in water mass stratification and hence adaptations to specific niches. Climate changes are expected to have an effect on the depth habitats of species that are more sensitive to temperature variations. Such an effect is recorded at DSDP Site 525A by the oxygen isotopes of some planktonic foraminiferal species that indicate vertical migration as adjustment to climate change. For example, *Pseudoguembelina hariaensis* normally inhabited the surface mixed layer during the cool Maastrichtian, as well as all other mem-

bers of this lineage, and therefore was likely particularly sensitive to climate change (Douglas and Savin, 1978; Boersma and Shackleton, 1981; Abramovich et al., in press). This species responded to the climate warming at 65.3 Ma by temporary migration to deep subsurface depths, as indicated by the increase in oxygen isotopes of its shells that reflect lower temperatures compared with the cold climate interval at 65.6 Ma (Fig. 6). During the subsequent cool interval at 65.1 Ma this species returned to inhabit the surface mixed layer.

The acme of *Pseudoguembelina hariaensis* during the warm event implies that the change in its depth habitat reflects an alternative strategy (vertical migration) for sustaining high population size during climate warming. Vertical migration is also demonstrated by *Heterohelix globulosa* which normally inhabited thermocline depths at South Atlantic DSDP Site 525A and shallower subsurface depths in the tropics (Fig. 6, Abramovich et al., in press). *Heterohelix globulosa* responded to the climate warming at DSDP Site 525A by upward migration to surface depths, as indicated by the change in temperature ranking relative to other species (Fig. 6). However, in contrast to *P. hariaensis*, *H. globulosa* remained a shallow dweller during the cooler interval at 65.1 Ma, which suggests that the migration response of this species does not necessarily reflect sensitivity to temperature changes. Other factors, such as competition with other species, may have been the source of these species' migratory response.

7.4. Species dwarfism

The most striking planktonic foraminiferal response to the warm event at DSDP Site 525A is revealed in the smaller 63–150-μm size fraction, which records an abnormal presence of dwarfed adult forms of normally larger sized (>150 μm) species. A number of different morphologies and lineages are affected by dwarfing (e.g. *Heterohelix rajagopalani*, *Pseudoguembelina hariaensis*, *Pseudotextularia deformis*, *Pseudotextularia elegans*, *Rugoglobigerina rugosa*, *Globotruncana arca*, *Globotruncana esnehensis*, and *Globigerinelloides sub-*

carinatus Fig. 7, Plate I). Their appearance in the warm interval accounts for the increase in species diversity in the smaller size fraction (Fig. 5). Dwarfed specimens thrived throughout most of the warm event but decreased during the subsequent cooling (e.g. 65.1–65 Ma, Fig. 7).

Reports of planktonic foraminiferal dwarfing in the Cretaceous and particularly in the Maastrichtian are scarce. This may reflect the infrequent use of the smaller 63–150-μm size fraction in population studies, or a tendency to clump dwarfed specimens with juveniles. Reports of Maastrichtian dwarfing events include qualitative and quantitative observations at Brazos River, Texas (Keller, 1989), South Atlantic ODP Site 738 (Keller et al., 1993), and Central Egypt (Keller, 2002). A morphometric study by MacLeod et al. (2000) quantified a significant test size reduction among the species *Heterohelix globulosa*, *Heterohelix navarroensis* (Loeblich) and *Guembelitria cretacea* Cushman in the latest Maastrichtian and early Danian sediments at Brazos River, Texas. Dwarfing of species during the latest Maastrichtian and earliest Danian is not unique to planktonic and benthic foraminifera, but has also been observed by Gardin and Monechi (1998) in calcareous nannoplankton assemblages of several low- and mid-latitude localities including DSDP Site 525A.

The congruence between the appearance of dwarfed specimens and climate warming in the late Maastrichtian suggests that test reduction was triggered by environmental instability. This premise is based on the notion that during high stress conditions the energy trade-off of planktonic organisms favored high reproduction rates over growth (MacLeod et al., 2000) and hence resulted in decreased test size. The early Danian is a case study for this type of high-stress reproduction mode, favoring a strategy of high turnover and small species size for both Cretaceous survivors and new evolving species (for a recent summary see Keller, 2001 and Keller et al., 2002b). It is reasonable to assume that the climatic instability during the late Maastrichtian also inflicted a change in the reproduction/growth strategy of at least some species, leading to smaller-sized specimens.

7.5. Photosymbiotic activity

During the maximum warming at 65.3 Ma, photosymbiotic activity was significantly reduced as evident by the decrease in the $\delta^{13}C$ differences between symbiotic species *Planoglobulina*, *Rosita* and *Pseudotextularia deformis* and non-symbiotic species (Fig. 6). Photosymbiotic activity was resumed during the subsequent cooler interval at 65.1 Ma, which suggests a specific reaction to the warm event. The source of the decrease in photosymbiotic activity during the warming is still unclear. Eutrophication of the upper water column during the last 300 kyr of the Maastrichtian may have been in part responsible for the reduction in photosymbiotic activity (Li and Keller, 1998b; Barrera and Savin, 1999; Keller, 2002; Keller et al., 2002b). Nutrient enrichment is expected to advance host-free photosynthesis at the expense of endosymbiosis. Temperature increase is also a possible source for the decrease in photosymbiotic activity, particularly if temperature was raised beyond the threshold of photosymbiotic planktonic foraminifera. Additional studies are needed to explore variations in photosymbiotic activity related to climate changes.

8. Summary

Planktonic foraminiferal and stable isotope records of the late Maastrichtian at South Atlantic DSDP Site 525A indicate that the global climate warming between 65.45 and 65.1 Ma elicited complex and variable responses in planktonic foraminiferal species populations, which are indicative of high-stress environmental conditions. A number of environmental and biotic factors have been identified that appear to be specific responses to rapid climate changes.

(1) Climate warming decreased the upper water mass stratification, which resulted in elimination of habitat niches, decreased diversity and complexity of planktonic foraminiferal assemblages, and vertical migration of some species.

(2) The unique aspect of the planktonic foraminiferal response to the warm event is the appearance of dwarfed forms of eight species with differ-

ent morphologies and taxonomic origins. Dwarfism reflects an opportunistic reproduction mode favoring a strategy of high turnover and small species size, which has been similarly employed by early Danian and K–T survivor species.

(3) Photosymbiotic activity was significantly reduced during the maximum climate warming. Eutrophication or temperature increase may have been the twin sources of this reduction.

(4) Thirteen larger-sized (>150 μm) species show significantly decreased relative population abundances that coincide with the warm event, including tropical–subtropical *Pseudoguembelina costulata*, *Rugoglobigerina rugosa* and several keeled globotruncanids (including *Rosita* species). Their decline suggests unfavorable environmental conditions for tropical–subtropical affiliated species accompanied climate warming in mid-latitudes.

(5) The local species *Globotruncana arca*, *Globotruncana mariei*, *Pseudotextularia deformis*, *Heterohelix rajagopalani* and *Pseudoguembelina hariaensis* retained their high presence through most of the warm event, which indicates that climate warming did not result in the massive retreat of the local mid-latitude population as a result of in-migration of low-latitude species. In contrast, the dominant local ecological generalist species, *Heterohelix dentata*, decreased during the warm event and recovered in the subsequent cooling.

Acknowledgements

Appendix A. Relative percent abundances of planktonic foraminifera in the 63–150-μm size fraction at DSDP Site 525A

Core	40cc	40cc	40-6	40-5	40-5	40-5	40-5	40-5	40-5	40-4	40-4	40-4	40-4	40-4	40-4
Interval (cm)	28–30	28–31	8–10	140–142	120–122	90–92	70–72	30–32	11–13	141–143	121–123	100–102	80–82	60–62	40–42
Depth (mbsf)	457.98	457.8	457.68	457.5	457.3	457	456.8	456.4	456.21	456.01	455.81	455.6	455.4	455.2	455
Age (Ma)	65.721	65.701	65.688	65.668	65.646	65.613	65.591	65.546	65.523	65.5	65.477	65.453	65.429	65.406	65.383
Abathomphalus intermedius (Bolli)	X														
Archaeoglobigerina blowi Pessagno	1	1	X			1		X	1					X	
Archaeoglobigerina cretacea (d'Orbigny)		X	X			X			X						
Globigerinelloides aspera (Ehrenberg)	16	20	15	8	11	9	24	18	27	33	37	20	7	19	12
Gobigerinelloides multispina (Lalicker)															
Gobigerinelloides rosebudensis Smith and Pessagno	X	X													
Globigerinelloides subcarinatus (Brönnimann)	X	X	1	X		X				1	1	1	1	1	
Globotruncanella aff. *ultamicrus*	3				1	2		1							
Globotruncanella yaucoensis (Pessagno)	1	1	X		2	6	3	1	2	2	2	2		2	1
Globotruncana aegyptiaca Nakkady													1		
Globotruncana arca (Cushman)			X						2		6	22	16	6	13
Globotruncana esnehensis Nakkady								X					8	1	4
Globotruncanella citae (Keller)				2	2	2		X			1	1	2	1	1
Globotruncanella havanensis (Voorwijk)				X			1		1						
Globotruncanella petaloidea (Gandolfi)	3	1	2				2	X	1	1	5	3	2	1	X
Guembelitria cretacea Cushman															
Guembelitria trifolia (Morozova)															
Hedbergella spp.	9	4	5	10	5	7	12	6	3	3	3	10	5	18	5
Heterohelix carinata (Cushman)					X			1	X	X	1			0	2
Heterohelix dentata Stenestad	38	52	37	58	66	56	42	51	35	33	25	18	9	23	3
Heterohelix globulosa (Ehrenberg)	17	8	10	13	6	12	9	9	13	10	8	6	5	9	14
Heterohelix navarroensis Loeblich		X		1	1				X	X	X				
Heterohelix planata (Cushman)				X											
Heterohelix punctulata (Cushman)	1														
Heterohelix rajagopalani (Govindan)	4	X	3		1	1	2	3	1		1	4	14	4	8
Laeviheterohelix glabrans (Cushman)	2	3		X	1	1			1	X	3	1		1	X
Planoglobulina carseyae (Plummer)													1		
Pseudoguembelina costulata (Cushman)	3	8	24	6	3	2	5	8	11	15	3	7	3	7	9
Pseudoguembelina hariaensis Nederbragt	X										1	5	12	3	16
Pseudoguembelina kempensis Esker							1								
Pseudoguembelina palpebra Brönnimann and Brown															X
Pseudotextularia deformis (Kikoine)	X							1	1				2	7	5
Pseudotextularia elegans (Rzehak)														5	1
Pseudotextularia intermedia De Klasz											X			1	
Rugoglobigerina hexacamerata Brönnimann			X											1	
Rugoglobigerina macrocephala Brönnimann											X				
Rugoglobigerina pennyi Brönnimann															
Rugoglobigerina rugosa (Plummer)		X		X		X	1		1					1	2
Rugoglobigerina scotti (Brönnimann)															
Total number counted	237	293	242	207	291	302	196	269	372	264	212	192	155	227	203

Appendix A (Continued).

Core	40-4	40-4	40-3	40-3	40-3	40-3	40-3	40-3	40-3	40-3	40-3	40-3	40-3	40-3	40-3
Interval (cm)	20–22	0–2	138–140	131–133	114–116	104–106	95–97	85–87	75–77	65–67	58–60	48–50	38–40	10–12	0–2
Depth (mbsf)	454.8	454.6	454.48	454.41	454.24	454.14	454.05	453.95	453.85	453.75	453.68	453.58	453.48	453.2	453.1
Age (Ma)	65.36	65.337	65.323	65.315	65.295	65.283	65.273	65.261	65.25	65.238	65.23	65.218	65.207	65.174	65.162
Abathomphalus intermedius (Bolli)										1					
Archaeoglobigerina blowi Pessagno			1						1	X					
Archaeoglobigerina cretacea (d'Orbigny)														1	
Globigerinelloides aspera (Ehrenberg)	7	12	18	13	7	9	10	7	9	8	11	6	8	12	10
Globigerinelloides multispina (Lalicker)										X	X				
Globigerinelloides rosebudensis Smith and Pessagno															
Globigerinelloides subcarinatus (Brönnimann)	X	2	4	10	1	8	2	6	8	7	5	4	4	9	4
Globotruncanella aff. *ulunienrus*	1	1	1	2	X	3	2	4	2	4	2	1	1	X	X
Globotruncanella yaucoensis (Pessagno)		2		X	X	1	5	1	2	1	1	5	3	2	3
Globotruncana aegyptiaca Nakkady				X										X	X
Globotruncana arca (Cushman)	15	5	2	7	12	6	11	6	7	7	4	3	4	7	12
Globotruncana esnehensis Nakkady	3	1	1	1			7	1	1	1	1	1	5	4	3
Globotruncanella havanensis (Voorwijk)	2	6	4	1	2	3		X	3	2	2	1	1		X
Globotruncanella citae (Keller)	X		1				1								
Globotruncanella petaloidea (Gandolfi)	X		1	1	1	1	4	2	2	1	2	1	2	2	2
Guembelitria cretacea Cushman							1				X			X	
Guembelitria trifolia (Morozova)							2								
Hedbergella spp.	1	4	6	6	4	11	3	3	8	2	3	5	5	3	5
Heterohelix carinata (Cushman)	1	2			3		1	X							
Heterohelix dentata Stenestad	6	16	14	11	15	19	10	18	25	29	24	35	21	36	23
Heterohelix globulosa (Ehrenberg)	10	12	14	8	6	16	15	18	10	7	17	15	12	3	8
Heterohelix navarroensis Loeblich		1	1		X	1		1	1		1	2	2	1	4
Heterohelix planata (Cushman)															
Heterohelix punctulata (Cushman)							1								
Heterohelix rajagopalani (Govindan)	12	9	10	9	12	5	15	3	1	1	2	3	8	3	4
Laeviheterohelix glabrans (Cushman)	X						1	1	1	1	2	4	2	4	1
Planoglobulina carseyae (Plummer)															
Pseudoguembelina costulata (Cushman)	4	18	8	11	15	7	3	13	15	23	17	11	5	5	4
Pseudoguembelina hariaensis Nederbragt	25	8	10	13	5	5	5	11	1	1	2	2	12	6	10
Pseudoguembelina kempensis Esker															
Pseudoguembelina palpebra Brönnimann and Brown															
Pseudotextularia deformis (Kikoine)	7	1	4	3	7	1	1	1	X	X	1		4	1	4
Pseudotextularia elegans (Rzehak)	1		1	X	1	X			1	X	1				
Pseudotextularia intermedia De Klasz						X									
Rugoglobigerina hexacamerata Brönnimann															
Rugoglobigerina macrocephala Brönnimann													X		
Rugoglobigerina pennyi Brönnimann				X	X										
Rugoglobigerina rugosa (Plummer)	4	2	2	3	6	3	1	2	3	1	2	2	2	1	
Rugoglobigerina scotti (Brönnimann)					X										1
Total number counted	227	290	167	213	215	238	184	296	278	274	321	331	252	285	226

Appendix A (Continued).

Core	40-2	40-2	40-2	40-2	40-2	40-2	40-2	40-2	40-2	40-2	40-2	40-2	40-2	40-2
Interval (cm)	146-148	136-138	126-128	115-117	104-106	95-97	87-89	76-78	66-68	56-58	47-49	38-40	29-31	20-22
Depth (mbsf)	453.06	452.96	452.86	452.75	452.64	452.55	452.47	452.36	452.26	452.16	452.07	451.98	451.89	451.8
Age (Ma)	65.158	65.146	65.135	65.122	65.109	65.099	65.089	65.077	65.065	65.053	65.043	65.032	65.022	65.012
Abathomphalus intermedius (Bolli)													2	
Archaeoglobigerina blowi Pessagno	2	1	1							X		X		
Archaeoglobigerina cretacea (d'Orbigny)	9	10	11	21	12	8	9	12	11	7	11	9	9	13
Globigerinelloides aspera (Ehrenberg)							X							
Globigerinelloides multispina (Lalicker)						1								
Globigerinelloides rosebudensis Smith and Pessagno														
Globigerinelloides subcarinatus (Brönnimann)	7	6	5	3	3	2	2	1		1	1	1	X	1
Globotruncanella aff. *ultamicrus*				2		X	1	1	X		1			
Globotruncanella yaucoensis (Pessagno)	2	3	4	X	1	2							2	4
Globotruncana aegyptiaca Nakkady						2	2	6	4	1	4	4		
Globotruncana arca (Cushman)	7	2	3	3	6	3	X	2	2	X	X			4
Globotruncana esnehensis Nakkady	1		1	1	1	1		1		X			1	1
Globotruncanella havanensis (Voorwijk)	1	2	2			1		1	X	X			1	
Globotruncanella citae (Keller)														
Globotruncanella petaloidea (Gandolfi)	1	2	2	3	1		1		1	X	1	X	X	
Guembelitria cretacea Cushman		X					X				X			
Guembelitria trifolia (Morozova)														
Hedbergella spp.	4	7	10	3	12	6	6	9	6	7	4	6	9	11
Hedbergella carinata (Cushman)	X	X												
Heterohelix dentata Stenestad	19	37	18	14	19	43	49	49	50	30	38	38	38	23
Heterohelix globulosa (Ehrenberg)	11	8	11	19	15	17	19	11	15	28	19	25	22	31
Heterohelix navarroensis Loeblich	3	5	1	1		X	1			1				
Heterohelix planata (Cushman)					1									
Heterohelix punctulata (Cushman)														
Heterohelix rajagopalani (Govindan)	2	1	1	4	5	1	1	1	2	1	X	1	X	
Laeviheterohelix glabrans (Cushman)	12	4	6	X	1	3	2	2		1	1	3	3	5
Planoglobulina carseyae (Plummer)										X				
Pseudoguembelina costulata (Cushman)	5	9	17	13	15	6	3	3	6	18	14	8	9	4
Pseudoguembelina hariaensis Nederbragt	11	2	6	6	4	2	2	1	X	1	1	X	X	1
Pseudoguembelina kempensis Esker														
Pseudoguembelina palpebra Brönnimann and Brown														
Pseudotextularia deformis (Kikoine)	X	1		1		X	X	X			X			1
Pseudotextularia elegans (Rzehak)		1		X									X	
Pseudotextularia intermedia De Klasz	X													
Rugoglobigerina hexacamerata Brönnimann		X												
Rugoglobigerina macrocephala Brönnimann													X	
Rugoglobigerina pennyi Brönnimann						1								1
Rugoglobigerina rugosa (Plummer)	2	X	3	4	4	2	2	2	3	2	4	3		1
Rugoglobigerina scotti (Brönnimann)														
Total number counted	216	307	190	224	164	258	302	328	254	334	274	336	213	138

X = < 1%.

Appendix B. Relative percent abundances of planktonic foraminifera in the size fraction > 150-μm at DSDP Site 525A

Core section	40cc	40cc	40-6	40-5	40-5	40-5	40-5	40-5	40-5	40-5	40-4	40-4	40-4	40-4	40-4	40-4
Interval (cm)	28–30	10–12	8–10	140–142	120–122	90–92	70–72	50–52	30–32	11–13	141–143	121–123	100–102	80–82	60–62	40–42
Depth (mbsf)	457.98	457.8	457.68	457.5	457.3	457	456.8	456.6	456.4	456.21	456.01	455.81	455.6	455.4	455.2	455
Age (Ma)	65.721	65.701	65.688	65.668	65.646	65.613	65.591	65.569	65.546	65.523	65.5	65.477	65.453	65.429	65.406	65.383
Abathomphalus intermedius (Bolli)											1	X				1
Abathomphalus mayaroensis (Bolli)	1		2	X	2	1	1	3	1	1				1		1
Archaeoglobigerina blowi Pessagno															X	
Archaeoglobigerina cretacea (d'Orbigny)																
Gansserina gansseri (Bolli)		1	1							1	1		X			
Globigerinelloides aspera (Ehrenberg)		X	X		1	2			1							
Globigerinelloides multispina (Lalicker)					X	1										
Globigerinelloides subcarinatus (Brönnimann)						X										
Globigerinelloides aff. *ultramicrus*																
Globotruncana aegyptiaca Nakkady	1	2	2	1			1		1	1	2					
Globotruncana arca (Cushman)	12	13	11	15	18	11	8	6	23	23	13	20	29	31	27	22
Globotruncana esnehensis Nakkady	12	8	5	10	5	6	12	13	12	8	13	6	5	2	5	6
Globotruncana duepeblei Caron, Gonz., Rob., and Wond.		3	3		2	3			1	3	5		X	1		3
Globotruncana falsostuarti Sigal	4	2	1		1	X	4				1		X			
Globotruncana insignis Gandolfi		X														
Globotruncana mariei Banner and Blow	3	4	16	3	9	10	2	1	9	11		10	6	4	9	7
Globotruncana orientalis El Naggar				1	2				X				1	X		X
Globotruncana rosetta (Carsey)																
Globotruncanella citae (Keller)	X		X	X					1	1		1	X	2	X	
Globotruncanella havanensis (Voorwijk)																
Globotruncanella petaloidea (Gandolfi)	X		X	X		X				2	X	1	1		1	
Globotruncanita angulata (Tiley)																
Globotruncanita stuarti (de Lapparent)	X	1			X	X	1		1						X	3
Globotruncanita stuartiformis (Dalbiez)	2	1	2	1	1	3	5	4	3	6	5	X	2	1		3
Gublerina cuvillieri (Kikoine)	2	1	4	3	3	4	6	5	3	2	3	2	1	2	1	2
Heterohelix dentata Stenestad	X		X			X		X		X						
Heterohelix globulosa (Ehrenberg)	3	2	6	2	6	7	10	5	6	4	4	2		X	1	2
Heterohelix labellosa Nederbragt	8	2	3	3		1	3	3	3			2	X	X	X	
Heterohelix planata (Cushman)	1	7	6	5	2	2	1	2	1	2	2		1			
Heterohelix punctulata (Cushman)	4	5	2	1	1	2	2	3	2	1	3	2	3		1	X
Heterohelix rajagopalani (Govindan)	12	10	6	9	10	9	12	9	7	7	5	13	7	8	10	6
Laeviheterohelix glabrans (Cushman)																
Laeviheterohelix pulchra (Brotzen)																
Planoglobulina acervulinoides Egger				X	1	1		1	X	X		1		1	1	
Planoglobulina brazoensis Martin	1	4	4	7	4	2	4	2	3	2	5	10	5	6	7	5
Planoglobulina carseyae Plummer	2	2	1	2	3	4	1	4	X	2	1		3	2	1	2
Planoglobulina multicamerata (de Klasz)																
Planoglobulina riograndensis Martin														X		X
Pseudoguembelina costulata (Cushman)	2	3	3	2	1	2	1		2	1	1	1	X			
Pseudoguembelina hariaensis Nederbragt	3	4	5	8	5	4	1	4	2	5	5	6	14	11	12	22
Pseudoguembelina palpebra Brönnimann and Brown	2	2	3	5	2	1	3	4	1	2	1	2	1	2	2	1
Pseudotextularia deformis (Kikoine)	5	7	2	4	5	10	12		16	7	8	11	11	14	17	10
Pseudotextularia elegans (Rzehak)	1	4	2	3	2	1		1	X	1	2	2	1		1	1
Racemiguembelina fructicosa Egger	5		1	X				X	X		1	1	1			X
Racemiguembelina intermedia de Klasz	X		1	1	1	X	2		1		3	4	3	3	4	1
Racemiguembelina powelli Smith and Pessagno	2		2	3	1		1		1		1	5	1	3	4	
Rosita contusa (Cushman)		X		X	1	X	2	1	1	X	1	X				
Rosita plicata (White)	1	X	X	1	1	X	X	1	1	X	X	X		1		1
Rosita walfischensis (Todd)	1	2	X	1	1	X	1	2	X	1	2	X				1
Rugoglobigerina hexacamerata Brönnimann		X	X	X									X	X		X
Rugoglobigerina macrocephala Brönnimann																
Rugoglobigerina milamensis Smith and Pessagno																
Rugoglobigerina pennyi Brönnimann	1	1	1	1	1	X	2		1							X
Rugoglobigerina rotundata Brönnimann		X	X		X			X	X						X	
Rugoglobigerina rugosa (Plummer)	9	8	6	8	9	9	2	7	3	3	2	2	1			X
Total number counted	337	312	297	314	340	314	301	311	291	329	340	308	353	341	304	318

Appendix B (Continued).

Core section	40-4	40-4	40-3	40-3	40-3	40-3	40-3	40-3	40-3	40-3	40-3	40-3	40-3	40-3	40-3	40-3
Interval (cm)	20-22	0-2	138-140	131-133	124-126	114-116	104-106	95-97	85-87	75-77	65-67	58-60	48-50	38-40	21-23	10-12
Depth (mbsf)	454.8	454.6	454.48	454.41	454.34	454.24	454.14	454.05	453.95	453.85	453.75	453.68	453.58	453.48	453.31	453.2
Age (Ma)	65.36	65.337	65.323	65.315	65.306	65.295	65.283	65.273	65.261	65.25	65.238	65.23	65.218	65.207	65.187	65.174
Abathomphalus intermedius (Bolli)	1															1
Abathomphalus mayaroensis (Bolli)				1	X	2	1	1	X	1	X	X	1	1	1	1
Archaeoglobigerina cretacea (d'Orbigny)											X					
Gansserina gansseri (Bolli)																
Globigerinelloides aspera (Ehrenberg)			X													
Globigerinelloides multispina (Lalicker)																
Globigerinelloides subcarinatus (Brönnimann)																
Globigerinelloides aff. *ultramicrus*																
Globotruncana aegyptiaca Nakkady	X	X	1	X	1	1	1	1	1	1	1	X	2	2	X	X
Globotruncana arca (Cushman)	21	28	15	17	20	27	25	23	16	30	33	23	23	18	13	17
Globotruncana esnehensis Nakkady	6	4	7	6	7	3	4		3	8	5	3	3	4	4	7
Globotruncana duepeblei Caron, Gonz., Rob., and Wond.	X	1	1		1	X			X	X			1			X
Globotruncana falsostuarti Sigal	X	X	X	X	X	X	1	1	X	1	X		1		1	X
Globotruncana insignis Gandolfi									1		X					
Globotruncana mariei Banner and Blow	7	6	7	11	6	8	9	17	12	14	10	13	15	11	13	17
Globotruncana orientalis El Naggar		2	1	1	2	1	1	1		2	2	X	1	1	X	1
Globotruncana rosetta (Carsey)	1	1								1	X	1				
Globotruncanella havanensis (Voorwijk)			X	X	X	1					X	1			1	X
Globotruncanella citae (Keller)	X		X	1	1	1	1	1	1	1	1	1	X	X	X	X
Globotruncanella petaloidea (Gandolfi)				X	X											
Globotruncanita angulata (Tiley)	1	1		X	1	1	1	1	X	2	1	2	1	1	1	2
Globotruncanita stuarti (de Lapparent)	1	1		1	1	1	2	4	2	1	1	1	4	4	2	X
Globotruncanita stuartiformis (Dalbiez)	X	2			X			1	3	1	1		1	1		1
Gublerina cuvillieri (Kikoine)									X							
Heterohelix dentata Stenestad			3	1	1	2	2	1	1		1	1	2	2	X	X
Heterohelix globulosa (Ehrenberg)	X	X	X			2					1		X	1		1
Heterohelix labellosa Nederbragt	1	X	X			X	1	X	1		X			X		
Heterohelix planata (Cushman)		1	2	1	1	1	1	1	1	1	1	2	3	2	1	1
Heterohelix punctulata (Cushman)	6	7	8	12	11	9	5	8	6	4	3	4	6	8	8	5
Heterohelix rajagopalani (Govindan)									X	X						
Laeviheterohelix glabrans (Cushman)																
Laeviheterohelix pulchra (Brotzen)	1	1	1	2	1	1	1	1	1	1	1	1	1	1	1	1
Planoglobulina acervulinoides Egger	6	8	11	7	5	6	7	4	4	7	8	6	4	5	5	7
Planoglobulina brazoensis Martin	1	3	2	1	1	1	2	1	1		1	1	1	2	1	1
Planoglobulina carseyae Plummer											X					
Planoglobulina multicamerata (de Klasz)								X								
Planoglobulina riograndensis Martin													X			
Pseudoguembelina costulata (Cushman)	30	11	22	24	21	17	13	21	15	7	9	14	11	18	28	16
Pseudoguembelina hariaensis Nederbragt	3	5	2	1	7	3	1	3	3	1	2	1	2	2	3	1
Pseudoguembelina palpebra Brönnimann and Brown	8	10	9	7	5	6	11	9	9	6	5	5	6	6	11	16
Pseudotextularia deformis (Kikoine)	1	1	1	3	X	1		8	3	4	2	2	X	X	2	1
Pseudotextularia elegans (Rzehak)	X	X	X		X	1			4	1	2	2	X	X		X
Racemiguembelina fructicosa Egger	2	2	1	X	1	1	3		4	3	2	2	1	2	X	X
Racemiguembelina intermedia de Klasz	X	1	X		2	2	2		2	3	3	3	2	2	1	1
Racemiguembelina powelli Smith and Pessagno					1	1				1				4		
Rosita contusa (Cushman)								X	1		X					
Rosita plicata (White)	X	X						1				1		X	X	
Rosita walfischensis (Todd)									X							
Rugoglobigerina hexacamerata Brönnimann					X					X		X	X			
Rugoglobigerina macrocephala Brönnimann	X	1		1	X	X	X	1		X	1	1	2	X	X	X
Rugoglobigerina milamensis Smith and Pessagno	X		1						X	X						X
Rugoglobigerina pennyi Brönnimann	1	1	2	2	1	3	5	1	4	4	4	4	4	1	1	2
Rugoglobigerina rotundata Brönnimann																
Rugoglobigerina rugosa (Plummer)																
Total number counted	354	301	311	315	280	359	329	237	292	397	425	356	293	283	264	317

Appendix B (*Continued*).

Core section / Interval (cm)	40-3 0–2	40-2 146–148	40-2 136–138	40-2 126–128	40-2 115–117	40-2 104–106	40-2 95–97	40-2 87–89	40-2 76–78	40-2 66–68	40-2 56–58	40-2 47–49	40-2 38–40	40-2 29–31	40-2 20–22
Depth (mbsf)	453.1	453.06	452.96	452.86	452.75	452.64	452.55	452.47	452.36	452.26	452.16	452.07	451.98	451.89	451.8
Age (Ma)	65.162	65.158	65.146	65.135	65.122	65.109	65.099	65.089	65.077	65.065	65.053	65.043	65.032	65.022	65.012
Abathomphalus intermedius (Bolli)	1		2	1			1	1			1	X			
Abathomphalus mayaroensis (Bolli)		X	X	1						1	1	X		1	
Archaeoglobigerina blowi Pessagno					1							X			
Archaeoglobigerina cretacea (d'Orbigny)												X			X
Gansserina gansseri (Bolli)															
Globigerinelloides aspera (Ehrenberg)								X			X	1	1		
Globigerinelloides multispina (Lalicker)												1			
Globigerinelloides subcarinatus (Brönnimann)													1		
Globigerinelloides aff. *ultramicrus*													X		
Globotruncana aegyptiaca Nakkady	1	1				X		1						X	X
Globotruncana arca (Cushman)	11	15	17	10	15	11	10	22	18	15	7	11	9	13	22
Globotruncana esnehensis Nakkady	7	6	5	8	8	3	3	3	2	2	4	2	2	X	4
Globotruncana duepublei Caron, Gonz., Rob., and Wond.										1				1	X
Globotruncana falsostuarti Sigal		X		X	1	1		X	X	1	1				
Globotruncana insignis Gandolfi						X							2	1	
Globotruncana mariei Banner and Blow	9	15	10	10	13	14	13	9	9	6	5	6	4	6	10
Globotruncana orientalis El Naggar		X	1		1			1		1		X	X	1	
Globotruncana rosetta (Carsey)		X	X												
Globotruncanella havanensis (Voorwijk)	X	1	X	1		1	2	2		X	X	X	1		
Globotruncanella citae (Keller)														X	
Globotruncanella petaloidea (Gandolfi)				X	X	X				X					X
Globotruncanita angulata (Tiley)	1	2	2			X					1	1	1		
Globotruncanita stuarti (de Lapparent)	1	1	4		1						1			1	
Globotruncanita stuartiformis (Dalbiez)		2	1		3		1				1	1	X	1	5
Gublerina cuvillieri (Kikoine)	3	X		X				X							
Heterohelix dentata Stenestad	1							X							
Heterohelix globulosa (Ehrenberg)		2	3	2	1	1	6	3	3	7	5	11	8	15	2
Heterohelix labellosa Nederbragt						X	X	1	1	2			4	2	
Heterohelix planata (Cushman)				X	X		2	1	X	2	1	2	4		X
Heterohelix punctulata (Cushman)	1	2	1	X	X	1	2	2	2	2	1	6	1	1	1
Heterohelix rajagopalani (Govindan)	6	7	4	9	6	14	7	12	16	13	15	8	5	2	9
Laeviheterohelix glabrans (Cushman)				X							X				
Laeviheterohelix pulchra (Brotzen)				X											
Planoglobulina acervulinoides Egger	X	X	2	X	1	X	1	4	2	2	1	X	1	1	1
Planoglobulina brazoensis Martin	4	4	6	8	8	11	4	5	5	2	3	2	6	3	3
Planoglobulina carseyae Plummer		2	2	1	2	2	2	3	3	4	3	3	2	5	3
Planoglobulina multicamerata (de Klasz)															
Planoglobulina riograndensis Martin			X								1	X		1	
Pseudoguembelina costulata (Cushman)	27	16	14	24	11	18	19	12	10	4	6	4	5	5	5
Pseudoguembelina hariaensis Nederbragt	X	1	1	X	1	X	X	2	3	2	3	3	2	1	1
Pseudoguembelina palpebra Brönnimann and Brown	22	13	14	12	16	10	2	5	14	16	15	7	15	15	17
Pseudotextularia deformis (Kikoine)	1	14	3	X	1	1	2	1	X	1	1	1	1	2	
Pseudotextularia elegans (Rzehak)		2	2	X			3				4		1		
Racemiguembelina fructicosa Egger	1	2	2	X	1	X	4	1	2	2	3	4	4	X	2
Racemiguembelina intermedia de Klasz		1			1		2		2	6		1	1	3	3
Racemiguembelina powelli Smith and Pessagno	1	2	2	3	2	X	2	3		2	4	1	2	1	4
Rosita contusa (Cushman)				3											
Rosita plicata (White)						X							X		2
Rosita walfischensis (Todd)							X			X		1	1	X	X
Rugoglobigerina hexacamerata Brönnimann															
Rugoglobigerina macrocephala Brönnimann															
Rugoglobigerina milamensis Smith and Pessagno															
Rugoglobigerina penyui Brönnimann	X	1	1	X	1	X	1	1	X	1		1	X	2	
Rugoglobigerina rotundata Brönnimann						X		X			X	X			
Rugoglobigerina rugosa (Plummer)	1	1	3	2	4	5	14	5	7	6	12	19	16	19	2
Total number counted	280	301	327	268	351	219	327	319	261	327	300	245	220	286	245

X = <1%.

Appendix C. Stable isotope (‰) and paleotemperature data of selected planktonic foraminiferal species in the 65.6-, 65.3- and 65.11-Ma intervals at Site DSDP 525A

Core	40-2			40-3			40-5		
Interval (cm)	104–106			124–126			90–92		
Age (Ma)	65.11			65.3			65.6		
	$\delta^{13}C$ (‰)	$\delta^{18}O$ (‰)	Temp. (°C)	$\delta^{13}C$ (‰)	$\delta^{18}O$ (‰)	Temp. (°C)	$\delta^{13}C$ (‰)	$\delta^{18}O$ (‰)	Temp. (°C)
Abathomphalus mayaroensis (Bolli)	1.88	−0.66	14.6	1.76	−0.86	15.5	1.70	−0.58	14.2
Globotruncana arca (Cushman)	2.32	−0.75	15.0	2.13	−0.87	15.5	2.47	−0.70	14.7
Globotruncana mariei Banner and Blow	2.58	−0.94	15.8	2.40	−1.13	16.7			
Gublerina cuvillieri (Kikoine)	2.32	−0.64	14.5	2.06	−0.32	13.0			
Heterohelix globulosa (Ehrenberg)	2.44	−1.02	16.2	2.31	−1.09	16.5	2.19	−0.68	14.6
Heterohelix rajagopalani (Govindan)	2.15	−0.59	14.3	1.90	−0.50	13.8			
Planoglobulina acervulinoides Egger	2.89	−1.04	16.3	2.55	−0.94	15.8	2.71	−0.91	15.7
Pseudoguembelina hariaensis Nederbragt	2.79	−1.11	16.6	2.67	−1.03	16.2	2.70	−1.14	16.7
Pseudoguembelina palpebra Brönnimann and Brown	2.95	−1.23	17.1	2.40	−1.39	17.9			
Pseudotextularia deformis (Kikoine)	2.53	−0.81	15.3	2.38	−0.90	15.7	2.69	−0.82	15.3
Pseudotextularia elegans (Rzehak)	2.62	−0.96	15.9	2.39	−1.02	16.2	2.42	−0.90	15.6
Racemiguembelina powelli Smith and Pessagno	2.92	−0.91	15.7	3.06	−1.17	16.9			
Rosita walfischensis (Todd)	2.31	−0.90	15.6	3.00	−0.79	15.2			
Rugoglobigerina rugosa (Plummer)	2.63	−0.93	15.8		−1.10	16.6	2.56	−0.81	15.2

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