The biostratigraphy and paleobiology of Oligocene planktonic foraminifera from the equatorial Pacific Ocean (ODP Site 1218)

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Abstract

Planktonic foraminifera from a continuous Oligocene succession with clear magnetostratigraphy and sediment cycles at Ocean Drilling Program Site 1218 (equatorial Pacific Ocean) were studied in the interval from 27 to 30 Ma. Paragloborotalia taxa are common and we examined their size, relative abundance, and stable isotopes. Multispecies stable isotope data indicate the depth habitats of Oligocene planktonic foraminifera and suggest that “Globoquadrina” venezuelana and Dentoglobigerina globularis were probably mixed-layer dwellers, with paragloborotaliids recording heavier δ18O signatures consistent with a thermocline habitat. Cyclic variations in the abundance of Paragloborotalia match eccentricity (100 kyr) variations in percent carbonate and δ13C, suggesting orbitally forced upwelling in the equatorial Pacific Ocean and that Paragloborotalia were responding directly to changes in surface water productivity. The high-resolution biostratigraphy calibrated to the magnetostratigraphy constrains the extinction of Paragloborotalia opima which marks the top of Planktonic Foraminifera Biozone O5 (P21b) at 27.456 Ma. The highest occurrence of P. opima is associated with a 50% size decrease in Paragloborotalia pseudocontinuosa taxa within Chron 9n. In addition, we find the extinction of Chiloguembelina cubensis is consistent with other deep-sea sections within Chron 10n at 28.426 Ma marking the O4/O5 (P21a/P21b) boundary.

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1. Introduction

The Oligocene was a time of dynamic climate change with orbitally paced variations in ice volume (Wade and Pälike, 2004). Planktonic foraminifera are highly sensitive to paleoceanographic conditions, yet the impact of these orbital variations on equatorial surface waters and marine biota has not been explored in detail. Ocean Drilling Program (ODP) Site 1218 (Fig. 1) located in the equatorial Pacific Ocean (8°53.38′ N, 135°22.00′ W, 4826 m present water depth), recovered an uninterrupted Oligocene succession of carbonate ooze with high sedimentation rates (15 m myr⁻¹), no unconformities and abundant calcareous microfossils (Shipboard Scientific Party, 2002). These features, coupled with a clearly defined magnetostratigraphy (Lanci et al., 2005), cyclostratigraphy (Pälike et al., 2005), and the high-resolution, orbitally tuned stable isotope record (Wade and Pälike, 2004, 2005) provide a strong age control.
Planktonic foraminifera preservation is best between magnetochrons C9n and C11n.1n (∼27.1–29.8 Ma).

Previous studies have documented the taxonomy and biostratigraphy of major Oligocene taxa (e.g., Jenkins and Orr, 1972; Douglas, 1973; Poore, 1984; Miller et al., 1985; Huber, 1991; Spezzaferri and Premoli Silva, 1991; Leckie et al., 1993; Spezzaferri, 1994). However, while the succession of Oligocene bioevents is well known, many biostratigraphic events are poorly constrained to the Geomagnetic Polarity Time Scale as sites have incomplete recovery or ambiguous magnetostratigraphy. The refinement and calibration of planktonic foraminiferal ages is important to developing a detailed chronology of the Oligocene. This permits the timing of biotic and oceanographic events to be determined and thus has the potential to significantly enhance our understanding of both evolutionary and paleoceanographic processes.

Modern planktonic foraminifera are vertically stratified through the upper portion of the water column. Stable isotope analysis ($\delta^{18}O$, $\delta^{13}C$) of planktonic foraminifera can reveal the paleo habitats of extinct forms as surface waters tend to be depleted in $\delta^{18}O$ and enriched in $\delta^{13}C$. Multispecies stable isotope analysis of Oligocene taxa has previously been conducted from deepsea sites (e.g., Boersma and Shackleton, 1977; Douglas and Savin, 1978; Poore and Matthews, 1984; van Eijden and Ganssen, 1995). We performed multispecies stable isotope analyses at Site 1218 to determine the relative paleo-depth habitats of Oligocene planktonic foraminifera within the upper water column.

Here we investigate the taxonomy, biostratigraphy and paleoecology of Oligocene planktonic foraminifera in the equatorial Pacific Ocean. Relative abundance changes in key taxa are used to identify the biotic response of planktonic foraminifera to the cyclic $\delta^{13}C$ signal (Wade and Pälike, 2004).

2. Materials and methods

Planktonic foraminiferal analysis covers a splice from Holes 1218A, B and C, equivalent to 138 to 185 m composite depth (mcd). This interval represents the lower Oligocene (Chron C11n.2n) through upper Oligocene (Chron C9n), equivalent to 27.105 to 29.768 Ma. All data are calibrated to the Cande and Kent (1995) timescale (CK95 herein) using the magnetostratigraphy at Site 1218 (Shipboard Scientific Party, 2002; Lanci et al., 2005). To accurately determine planktonic foraminiferal biostratigraphic events, samples were examined every 10 cm between 138 and 185 mcd providing a temporal resolution of ∼6 kyr.

2.1. Relative abundance and size variations in planktonic foraminifera

Relative changes in foraminiferal abundance were determined through the cyclic climatic changes documented at Site 1218 in Wade and Pälike (2004). For quantitative analysis of planktonic foraminiferal assemblages, we counted 300 specimens of planktonic foraminifera from
the 250–355 μm size fraction from intervals of high (>1.2‰) and low (<0.9‰) δ^{13}C (Fig. 2) between 27.5 and 28.1 Ma.

To investigate the size variations and document the extinction of *Paragloborotalia opima*, we measured the diameter (marked α on Plate I) of paragloborotaliids from within Chron 9n (4 samples) and Chron 11n (1 sample). Measurements were recorded from 20 specimens per sample of *P. pseudocontinuosa* and the *nana-opima* plexus which was divided into four and five chambered forms to determine relationships between number of chambers and specimen size. The direction of coiling was also noted. Qualitative observations on size and coiling were recorded throughout the studied interval during biostratigraphic analysis.

### 2.2. Stable isotope analysis

Multispecies stable isotope analyses were conducted on four samples of Oligocene foraminifera from Site 1218. Selected specimens were free of carbonate infilling and sonicated prior to analysis. We analysed 10 species of planktonic foraminifera to provide first order details of the paleobiology of extinct Oligocene taxa. Analysis was performed on *Dentoglobigerina globularis*, “Globoquadrina” *venezuelana*, *Paragloborotalia pseudocontinuosa*, and *P. opima* from three samples between 29.62 and 27.69 Ma. In addition, *Catapsydrax dissimilis*, *Catapsydrax unicavus*, *Chiloquembelina cubensis*, “*Globoquadrina* euapertura,” *Dentoglobigerina cf. globularis* and *Subbotina eocaena* were analysed from selected samples. To minimize

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**Fig. 2.** Biostratigraphy, stable isotope, relative abundance and *Paragloborotalia* morphometric data at Site 1218. Magnetostratigraphy and planktonic foraminiferal biozones are shown on the left, a) last appearance datum (LAD) of *Paragloborotalia opima*, 143.82 mcd, 27.456 Ma, b) LAD of *Chiloquembelina cubensis*, 159.94 mcd, 28.426 Ma. The NP23/NP24 boundary is constrained by the lowest occurrence of *Sphenolithus ciperoensis* (Shipboard Scientific Party, 2002). Planktonic foraminiferal stable isotope data (δ^{18}O, δ^{13}C) from “*Globoquadrina* venezuelana” (Wade and Pälike, 2004, 2005). Increases in the relative abundance of the four chambered *P. nana-opima* plexus correspond to intervals of light δ^{13}C. A rapid decrease in paragloborotaliid size from 445 to 240 μm occurs at 27.456 Ma and marks the extinction of *Paragloborotalia opima*. 

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ontogenetic effects all specimens were selected from the 300–355 μm size fraction, except *C. cubensis* (125–250 μm size fraction), and *P. opima* (all specimens >390 μm). Paragloborotaliid taxa from sample 1218C-10H-2, 140 cm were separated into sinistral and dextral coiling forms.

Samples were analysed at the University of Edinburgh, Scotland using a VG Isogas Prism III mass spectrometer. Results of stable isotope measurements are expressed in ‰ relative to the Pee Dee Belemnite (PDB) standard. Analytical precision calculated from repeated analyses of standards was ±0.09‰ and ±0.05‰ for δ¹⁸O and δ¹³C respectively. These data are listed in Appendix A. Stable isotope analyses of “G.” *venezuelana* from Site 1218 are presented in Wade and Pälike (2004, 2005).

3. Results

The Oligocene planktonic foraminifera from Site 1218 are abundant and diverse. Dominant taxa included paragloborotaliids, *Catapsydrax* spp. and “G.” *venezuelana*, with common dentoglobeligerinids. *Tenuitella munda* is frequent in the smaller size fractions. Plates I and II illustrate typical taxa from this site. *Globoturborotalita angulisuturalis*, were rare to absent. All paragloborotaliids coil in both directions throughout the interval studied.

3.1. Biostratigraphy

The unequivocal magnetostratigraphy (Shipboard Scientific Party, 2002; Lanci et al., 2005), distinct sedimentary cycles (Shipboard Scientific Party, 2002; Pälike et al., 2005), and high-resolution stable isotope record (Wade and Pälike, 2004) have allowed the development of an orbital chronology for Site 1218 (Pälike et al., 2005). We have therefore been able to constrain the last appearance datum (LAD) of the paragloborotaliid taxon *Paragloborotalia nana-opima* (Plate In, o) at Site 1218 (Fig. 2). We find the occurrence (HO) of *C. cubensis* (Plate In, o) at Site 1218 (Fig. 2). We find the highest occurrence (HO) of *P. opima* at Site 1218, which calibrates to the magnetochronology of CK95 as 27.456 Ma (see discussion).

3.2. Relative abundance variations

Relative abundance counts of planktonic foraminifera from 14 samples between 28.05 and 27.52 Ma are given in Appendix B. *Catapsydrax unicavus* and *Paragloborotalia nana-opima* plexus dominate the samples and each account for approximately 30% of all specimens. *C. dissimilis* (Plate IIq), *D. globularis* (Plate III–h), “G.” *euapertura* (Plate IIIn,o), “G.” *venezuelana* and *P. pseudocontinuosa* (Plate III,m) vary between 1% and 13% of the assemblage. Fig. 2 shows the percentage distribution of *P. nana-opima* plexus.

3.3. Dwarfing of Paragloborotalia

From 185.16 to 143.82 mcd (29.768 to 27.456 Ma) paragloborotaliids at Site 1218 are large, average 450 μm in diameter, and are common in the >300 μm size fraction. There is an abrupt shift in mean specimen size from 445 μm to 240 μm during Chron 9n (Appendix C, Fig. 2), equivalent to 27.456 Ma per CK95. This reduction in size occurs within all paragloborotaliids. In the overlying intervals specimens of *Paragloborotalia* are rare in the >300 μm size fraction, but remain abundant in the <300 μm size fraction.

3.4. Multispecies stable isotope results

Multispecies stable isotope data are shown in Fig. 3 and Appendix A. Planktonic foraminifera δ¹⁸O values are between −0.03‰ and 1.68‰. Within sample 1218C-10H-2, 140–142 cm there is a 2% gradient between the lightest planktonic species and benthic foraminiferal values. All foraminifera are recrystallised and therefore the oxygen isotope values are considered artificially heavy (Schrag, 1999; Pearson et al., 2001); however, multispecies isotope data show a δ¹³C gradient through the water column and consistent offsets.

“G.” *venezuelana* was analysed in all samples and shows light δ¹⁸O values between 0.42‰ and −0.04‰.

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Plate I. Scanning Electron Microscope images of *Paragloborotalia* from Site 1218. Specimens (a–g) from Planktonic Foraminifera Biozone O6 (P22), specimens (h–p) are from Biozone O5 (P21b). Scale bars 100 μm. α represents the axis measured for morphometric investigation (Appendix C), the size of specimens belonging to the *P. opima/nana* plexus are given in brackets. (a–c) *Paragloborotalia nana*, ODP Site 1218A 14H2 80–82 cm (a = 0.20 mm; b = 0.20 mm; c = 0.22 mm; d = 0.19 mm; e = 0.24 mm), (f, g) *Paragloborotalia nana*, same specimen in umbilical and spiral views, ODP Site 1218A 14H4 140–142 cm (0.30 mm). (h, m) *Paragloborotalia nana-opima* transition, ODP Site 1218B 15H3 60–62 cm (h = 0.35 mm, m = 0.37 mm), (i–j, k–l) *Paragloborotalia nana-opima* transition, same specimens in umbilical and spiral views, ODP Site 1218B 15H4 50–52 cm (i–j = 0.35 mm, k–l = 0.36 mm), (n) *Paragloborotalia opima*, ODP Site 1218B 15H3 60–62 cm (0.40 mm), (o) *Paragloborotalia opima*, ODP Site 1218B 15H1 80–82 cm (0.46 mm), (p) *Paragloborotalia mayeri*, ODP Site 1218B 15H3 60–62 cm.
and carbon isotope values consistently heavier than those of dentoglobigerinids (Fig. 3). D. globularis (Plate II–h) has depleted oxygen isotope values (0.12‰ and 0.30‰) in 1218B-15H-2 and 18H-5, but δ¹⁸O values are heavier in 1218C-10H-2 (0.92‰). “G.” euapertura (Plate II-n, o) and Dentoglobigerina cf. globularis (Plate IIa–d) from 1218B-15H-2 indicate very similar oxygen and carbon isotope values as D. globularis. C. cubensis (Plate IIp)
analysed from 1218C-10H2, 140 cm indicates relatively enriched $\delta^{18}$O values (1.27‰) and $\delta^{13}$C values heavier than the rest of the assemblage by $\sim$0.3‰. C. unicavus and C. dissimilis (Plate IIq) record the heaviest oxygen isotope values (1.4‰) of all the planktonic foraminiferal species analysed.

$P. opima$ (Plate In–o) and $P. pseudocontinuosa$ (Plate III–m) record similar values in both $\delta^{18}$O and $\delta^{13}$C. Paragloborotaliid oxygen and carbon isotope values tend to cluster about $\sim$1‰ heavier in $\delta^{18}$O than “G.” venezuelana. Dextral and sinistral coiling forms of $P. pseudocontinuosa$ and $P. nana$ from sample 1218C-10H-2 140–142 cm show minor offsets in $\delta^{13}$C and $\delta^{18}$O ($\sim$0.2‰).

4. Discussion

High sedimentation rates and the clear magnetochrono-

ology at Site 1218 allows us to calibrate and re-assess the extinction of $C. cubensis$ as a marker for the zonal boundary O4/O5 (P21a/P21b) and the extinction of $P. opima$ (O5/O6, P21b/P22). As in Shipboard Scientific Party (2002) it was not possible to differentiate the Zone O3/O4 (P20/P21a) boundary due to the absence of $G. angulisuturalis$. We suggest that its absence here, but in oligotrophic sites (e.g. ODP Site 628, in the subtropical western North Atlantic Ocean, Leckie et al., 1993), is a reflection of elevated surface ocean productivity in the equatorial Pacific Ocean.

4.1. The extinction of $C. cubensis$

The highest (common) occurrence of $C. cubensis$ has been documented and calibrated by Berggren et al. (1995) to the top of Subzone P21a (Zone O4, Berggren and Pearson, 2005) corresponding to Chron 10n (28.5 Ma) and used as the biomarker for the early/late Oligocene boundary. The extinction of $C. cubensis$ as a reliable stratigraphic event has been questioned by van Simaeys et al. (2004). Indeed younger occurrences of $C. cubensis$ have been reported in Oligocene sections at ODP Site 628 and ODP Site 803 (Leckie et al., 1993), at and DSDP Site 593 (Hess et al., 1989). We examined the reliability of this event at Site 1218 at 10 cm resolution.

Identifying the highest (common) occurrence of $C. cubensis$ was difficult at Site 1218 due to the large amount of siliceous material (radiolarians) in the <125 μm size fraction. However, this species is very distinctive (Plate IIp) and we find the HO of $C. cubensis$, marking the top of Planktonic Foraminifer Biozone O4 (P21a) at 1218B, 16H-4, 159.94 mcd, within Chron 10n.1n, equivalent to 28.426 Ma (CK95) and 28.009 on the astronomical timescale (Pälike et al., 2005). In the upper Oligocene sediments $C. cubensis$ was completely absent. The synchronous extinction of $C. cubensis$ is documented from a number of sites and correlates either directly or indirectly with Chron 10n (e.g., Site 516, Pujol, 1983; Site 558, Miller et al., 1985; Site 529 and Site 77B, Hess et al., 1989; and ODP Site 1218, this study). This diminutive extinction is easily reworked. At DSDP Site 522, sporadic occurrences of $C. cubensis$ within the opima opima zone are considered by Poore et al. (1982) and Poore (1984) to be reworked. Contrary to van Simaeys et al. (2004) our results indicate that the $C. cubensis$ extinction is a robust bioevent for the O4/ O5 (P21a/P21b) boundary and correlates to within Chron 10n, consistent with many other deep-sea sections. Whilst the anomalously younger occurrences of $C. cubensis$ require further investigation, within the deep-sea tropical record this remains a useful marker for the mid-Oligocene.

No major shift is recorded in the stable isotope records of planktonic or benthic foraminifera at the extinction; however, the event is 100 kyr prior to an interval of $\delta^{18}$O lows associated with Oi2a (Wade and Pälike, 2004), suggesting that global cooling and ice volume increase may be involved.

4.2. Size variations in paragloborotaliids

Paragloborotaliids are diagnostic taxa of the Oligo-
cene and particularly abundant at Site 1218 (Plate I). Paragloborotalia nana was originally described by

Plate II. Scanning Electron Microscope images of common planktonic foraminifera from Site 1218. All images are from Planktonic Foraminifera Biozone O5 and scale bars 100 μm unless indicated otherwise. (a–d) Dentoglobigerina cf. globalisaur, ODP Site 1218B 15H4 50–52 cm (same specimen). This species is morphologically similar to D. globalisaur (Plate II f–h), but we have separated the forms which possess an elongate tooth. Scale bar (c) 50 μm (d) 10 μm. (e) Tenuitella angustumbillicata, ODP Site 1218B 17H3 90–92 cm, zone O3/O4, (f) Dentoglobigerina globalisaur, ODP Site 1218B 15H2 60–62 cm, (g–h) Dentoglobigerina globalisaur, ODP Site 1218B 15H3 60–62 cm, (i) Paragloborotalia spp., ODP Site 1218B 15H3 60–62 cm. This form has five chambers in the final whorl, thin lip and lobate outline. It is morphologically similar but is inconsistent with P. pseudocontinuosa (Plate III–m), (j–k) Tenuitella mund, ODP Site 1218B 15H3 60–62 cm, (k) scale bar 50 μm, (l–m) Paragloborotalia pseudocontinuosa, ODP Site 1218B 15H3 60–62 cm, (n) “Globoquadrina” euapertura ODP Site 1218A 14H1 120–122 cm, zone O6, (o) “Globoquadrina” euapertura ODP Site 1218B 15H3 60–62 cm, (p) Chilonguembelina cubensis ODP Site 1218C 11H3 130–132 cm, zone O3/O4, (q) Catapsydrax dissimilis, ODP Site 1218B 15H3 60–62 cm.

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Bolli (1957) as a subspecies of *P. opima*. There is a large degree of variation within the *opima-nana* plexus in terms of specimen size and number of chambers in the final whorl. The criterion to differentiate between *P. nana* and *P. opima* has been considered in Spezzaferri (1994). For taxonomic and biostratigraphic clarity we follow Bolli and Saunders (1985) and distinguish *P. opima* and *P. nana* on size, with *P. opima* ranging from 0.39 to 0.55 mm (Plate In, o), and smaller specimens (<0.32 mm) assigned to *P. nana* (Plate Ia–g), specimens between 0.32 and 0.38 mm (Plate Ih–l) are referred to as “opima-nana transition” as per Bolli and Saunders (1985). *P. nana* is commonly found in the <300 μm size fraction at Site 1218 and *P. opima* is present in the larger size fractions to 143.82 mcd. *P. pseudocontinuosa* was also very common at Site 1218, this species usually has four chambers in the final whorl (Plate Ill–m). Unlike *P. nana*, chambers increase more rapidly in size resulting in a larger final chamber size.
Paragloborotalia are common in the disappearance of the Essentially for biostratigraphic purposes it is the boundary 4.3. Recalibration of the O5/O6 (P21b/P22) zonal interval and from the base of the studied section (29.8 Ma) of paragloborotaliids that takes place at 143.82 mcd equivalent to 27.456 Ma as per CK95 (26.889 Ma astronomical timescale) within Chron 9n, which marks the extinction of P. opima. Paragloborotaliids decrease here by almost 50% from 445±27 to 240±28 μm (Fig. 2). Prior to this interval and from the base of the studied section (29.8 Ma) Paragloborotalia are common in the >300 μm size fraction, and range up to (and greater than) 462 μm in size (Appendix C). Above 143.82 mcd paragloborotaliids are only found in the <300 μm size fraction. P. nana and P. pseudocontinuosa, (less than 300 μm in size), are abundant and persist to the top of the section (27.1 Ma). These results are constrained by qualitative observations of paragloborotaliid size throughout the section.

The size reduction of all paragloborotaliids taxa in Chron 9n suggests a strong ecological control of test size. However, the mechanism of this distinct morphological change cannot be easily verified, as this event lacks any significant variability in the stable isotope record (Fig. 2). The decrease in size of paragloborotaliids takes place within an interval of enriched δ18O in planktonic foraminifera values (Fig. 2) but 174 kyr prior to O2b, and 432 kyr post the surface water cooling event documented in Wade and Pälike (2004).

Bolli and Saunders (1985) suggested that further population studies were necessary to determine if the transitional forms of the P. nana-opima plexus in the 0.32–0.38 mm size range (Plate I–h I) belonged within the P. opima group (Bolli and Saunders, 1985, p. 202). In our morphometric analysis (Appendix C, Fig. 2) only forms less than 300 μm continue beyond 27.456 Ma, (143.82 mcd) suggesting that the “transitional” forms are consistent with P. opima and restricted to P21b (O5). Essentially for biostratigraphic purposes it is the disappearance of the P. opima-nana plexus from the >300 μm size fraction that marks the zonal boundary between P21b and P22 (O5/O6).

4.3. Recalibration of the O5/O6 (P21b/P22) zonal boundary

In current planktonic foraminifera zonations (e.g., Berggren and Pearson, 2005), the HO of P. opima marks the top of Biozone P21b (O5). Previous calibrations of the HO of P. opima have been hindered by rare planktonic foraminifera, inadequate recovery or poor magnetostratigraphy. Detailed biostratigraphic studies have been conducted at numerous DSDP and ODP sites, including Site 526, 588, 628, 709, 803 (e.g., Leckie et al., 1993; Spezzaferri, 1994), all of which lack paleomagnetics or the record is ambiguous during this interval. At DSDP Hole 516F P. opima was not recognised in frequencies greater than rare in subzones P21a or P21b (Pujol, 1983). The top of P opima at Hole 516F was placed by Pujol (1983) between cores 14 cc and 15–1 at 302 m and based on an identification of “cf. opima”. Therefore the estimated extinction in Pujol (1983) and Berggren et al. (1995) is not precise. A more detailed biostratigraphy of hole 516F was conducted by Spezzaferri (1994) who placed the HO of P. opima between 15–7, 14–16 cm and 16–1, 8–10 cm (311.6 m), however the magnetostratigraphy here is too indistinct for direct calibration. At Sites 558 and 563, Echols (1985) identified the HO of P. opima which corresponded to a concatenated normal interval identified as Chron 8/9 (Kahn et al., 1985; Miller et al., 1985). Direct calibrations between planktonic foraminifera biostratigraphy and magnetostratigraphy for the Oligocene are possible from DSDP Site 522 (Poore et al., 1982, 1983; Tauxe et al., 1983) and the Contessa Quarry Section, Italy (Lowrie et al., 1982). At Site 522, the HO of “typical” P. opima occurs at the top of core 21, corresponding to 82 mbsf and mid Chron 9n (Poore et al., 1982, 1983, Tauxe et al., 1983; Poore, 1984). Based on the magnetostratigraphy at Site 522 (Lauxe et al., 1983) we can recalibrate the opima extinction at Site 522, resulting in an age of 27.440 Ma, as per CK95.

At Site 1218, the high sedimentation rates, clear magnetostratigraphy (Lanci et al., 2005), orbitally-tuned isotopic record (Wade and Pälike, 2004) and high resolution biostratigraphic sampling (this study) at Site 1218, have allowed us to accurately constrain the HO of P. opima and to directly calibrate the O5/O6 zonal boundary. We find the HO P. opima marking the O5/O6 (P21b/P22) boundary at 143.82 mcd, within Chron 9n. This corresponds to 27.456 Ma as per CK95 or (26.889 Ma astronomical timescale as per Pälike et al., 2005). The extinction of P. opima at 27.456 Ma is 356 kyr older than the LAD of P. opima identified in the Berggren et al. (1995) timescale (27.1 Ma). However, considering the limitations of previous calibrations (e.g. Site 516 and 558, discussed above) we conclude that the LAD of P. opima at Site 1218 and recalibration to 27.456 Ma within Chron 9n, is robust and to a much
greater resolution than previous records. The difference between the recalibrated age of 27.440 Ma at Site 522 and 27.456 Ma at Site 1218, is minimal (only 16 kyr) and can be accounted for by the lower resolution biostratigraphic analysis at Site 522. Poore et al. (1982) report the isochronous extinction of *P. opima* between South Atlantic Site 522 and the Contessa Quarry Section, Italy. Our results further suggest that the extinction of *P. opima* is globally synchronous between the equatorial Pacific, Mediterranean and Atlantic.

### 4.4. Relative abundance variations in *Paragloborotalia*

During the Oligocene, Site 1218 was situated in the equatorial high-productivity belt (4°N, *Shipboard Scientific Party*, 2002). The sediments are rich in biogenic silica, principally radiolarians. Four chambered forms of the *P. nana-opima* plexus account for ~30% of the 250–355 μm assemblage at Site 1218. The relative abundance data indicates swings in the abundance of *P. nana-opima* between 25% and 37% (Fig. 2, Appendix B), these changes are small (12%) but appear to be meaningful in paleoceanographic analysis and relate to properties of the water mass. Intervals of high abundance correspond with $\delta^{13}C$ lows (Fig. 2) and the relative abundance data track cyclic changes in the $\delta^{13}C$ record at Site 1218 (Wade and Pälike, 2004). This suggests that changes in the water column on Milankovitch timescales are reflected in the assemblages of planktonic foraminifera. The carbon isotope values of planktonic foraminifera are strongly influenced by productivity in the surface waters and the shifts in $\delta^{13}C$ suggest large swings in equatorial productivity at this site. Upwelling has also been shown to bring nutrient-rich, $\delta^{13}C$-depleted thermocline waters into the photic zone, resulting in lower or lighter $\delta^{13}C$ values of planktonic foraminifera (e.g., Pak and Kennett, 2002). We interpret the $\delta^{13}C$ lows to be intervals of pronounced orbitally forced (100 kyr) upwelling or the latitudinal movement of the equatorial upwelling belt. Modern and ancient planktonic foraminiferal assemblages have been shown to be significantly influenced by upwelling variability. The covariation between *P. nana-opima* abundance and the stable isotope record, suggests that this group was sensitive to productivity fluctuations.

### 4.5. The paleobiology of Oligocene planktonic foraminifera

Understanding the paleoecology of planktonic foraminifera is key to determining SSTs, the structure of the water column, and paleoceanographic evolution. Significant information on the paleobiology of Oligocene planktonic foraminifera can be gained by comparing the stable isotope results of multiple species of planktonic foraminifera. The multispecies stable isotope data at Site 1218 (Fig. 3) indicate a marked offsets in $\delta^{18}O$ between species.

"G." venezuelana consistently records depleted oxygen isotope values in comparison to the rest of the assemblage (Fig. 3). The corresponding light isotopes in "G." venezuelana and *D. globularis* and the 1.5‰ offset in $\delta^{18}O$ to *C. dissimilis* is comparable with results from Biolzi (1983). These data suggest that "G." venezuelana and *D. globularis* occupied a mixed-layer dwelling habitat.

*P. opima* and *P. pseudocontinuosa* yield very similar stable isotope values at Site 1218. Paragloborotalid oxygen isotope values fall between 0.75‰ and 1.27‰ and are consistently heavier than "G." venezuelana by 0.97‰ ±0.14‰. The enriched $\delta^{18}O$ results in comparison to "G." venezuelana suggest that the paragloborotaliids occupied a deeper pelagic habitat, typical of thermocline dwellers.

*C. unicavus* and *C. dissimilis* record the heaviest oxygen isotope values of the assemblage and results are consistent with previous studies of the Eocene, Oligocene and Miocene that have suggested that these taxa occupy a deep-dwelling (sub-thermocline) habitat (Boersma and Shackleton, 1977; Biolzi, 1983; Poore and Matthews, 1984; Wade et al., 2000; Wade, 2004).

Interestingly, whilst the oxygen isotope gradient between the lightest and heaviest species is ~1.5‰, there is surprisingly little gradient in $\delta^{13}C$ (0.18‰). All planktonic $\delta^{13}C$ values are clustered around 1‰. The light $\delta^{13}C$ values would suggest that none of these species had a symbiotic relationship with photosynthetic algae. From the multispecies stable isotope data at Site 1218 (Fig. 3), we infer the following depth-habitats for Oligocene planktonic foraminifera:

- **Mixed-layer dwellers**
  - "Globoquadrina" venezuelana
  - *Dentoglobigerina globularis*
  - *Globoquadrina euapertura*

- **Thermocline dwellers**
  - *Paragloborotalia opima*
  - *Paragloborotalia pseudocontinuosa*
  - *Chiloguembelina cubensis*
  - *Subbotina eocaena*

- **Sub-thermocline dwellers**
  - *Catapsydrax dissimilis*
  - *Catapsydrax unicavus*

However, our stable isotope results and inferred depth habitats are inconsistent with previous studies. Paragloborotaliids have previously been documented as sub-
thermocline dwellers by Douglas and Savin (1978), and as surface dwellers by Boersma and Shackleton (1977), Poore and Matthews (1984), and van Eijden and Ganssen (1995). Douglas and Savin (1978) and Biolzi (1983) suggested that “G.” venezuelana was an intermediate dwelling form, and it is documented as a deep dwelling species in the Miocene (Gasperi and Kennett, 1993). This therefore questions whether these groups changed their depth habitat through time and whether disparate authors are unified in their taxonomic approach. Through their life cycle certain species of modern planktonic foraminifera are known to alter their habitat, with adult stages and gametogensis at a greater depth within the water column, than juvenile stages (Hemleben et al., 1989). Our relatively depleted δ18O signatures for “G”. venezuelana may relate to the restricted size interval for stable isotope analysis (300–355 μm). Specimens from larger size fractions (>355 μm) may result in more enriched δ18O results consistent with previous studies. Further work from multiple size fractions is clearly required to determine the paleobiology of planktonic foraminifera through the Oligocene.

5. Conclusions

Multispecies planktonic foraminiferal stable isotope data suggest that “G.” venezuelana and D. globularis were mixed-layer dwellers and Paragloborotalia occupied a deeper habitat within the thermocline. Orbitally driven upwelling in the equatorial Pacific resulted in prominent (1‰) shifts in δ13C that significantly impacted on planktonic foraminiferal assemblages. There is close correspondence between carbon isotope variations in “G.” venezuelana and the relative abundance of the thermocline dwelling species Paragloborotalia, suggesting that this group responded directly to changes in productivity. Size analysis of Paragloborotalia from Site 1218 indicates a significant decrease in test size from 445 to 240 μm within Chron 9n, corresponding to the extinction of P. opima and marking the upper boundary of Planktonic Foraminifera Biozone O5. Recalibration of high-resolution biostratigraphy to the magnetochronology at Site 1218 constrains the top of Planktonic Foraminifera Biozones O4 (P21a) and O5 (P21b) to 28.426 Ma and 27.456 Ma, respectively.

6. List of species

Catapsydrax dissimilis (Cushman and Bermudez), Plate Iip
Catapsydrax riverae (Bolli and Bermudez)
Catapsydrax unicusus Bolli, Loeblich and Tappan
Chilognemelina cubensis (Palmer), Plate Iip
Dentoglobigerina barroisoides (Le Roy)
Dentoglobigerina globularis (Bermudez), Plate IIa–h
Globigerina bulloides d’Orbigny
“Globoquadrina” euapertura (Jenkins), Plate II–o
“Globoquadrina” venezuelana (Hedberg)
Globoturborotalita angulissuturalis Bolli
Paragloborotalia mayeri (Cushman and Elliot), Plate I
Paragloborotalia nana (Bolli), Plate Ia–f
Paragloborotalia opima (Bolli), Plate In–o
Paragloborotalia pseudocontinuosa (Jenkins), Plate III–m
Subbotina eocaena (Guembel)
Tenuitella munda (Jenkins) Plate Ij–k
Tenuitellinata angustiumbilicata (Bolli) Plate IIc

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.marmicro.2006.08.005.

References


