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Eocene–Oligocene
transition at ODP Site
1263, Atlantic Ocean

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The Eocene–Oligocene transition at ODP Site 1263, Atlantic Ocean: decreases in nanoplankton size and abundance and correlation with benthic foraminiferal assemblages

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Abstract

The biotic response of calcareous nannoplankton to environmental and climatic changes during the Eocene–Oligocene transition (~ 34.8–32.7 Ma) was investigated at high resolution at Ocean Drilling Program (ODP) Site 1263 (Walvis Ridge, South East Atlantic Ocean), and compared with a lower resolution benthic foraminiferal record. During this time interval, the global climate which had been warm during the Eocene, under high levels of atmospheric CO₂ ($p\text{CO}_2$), transitioned into the cooler climate of the Oligocene, with overall lower $p\text{CO}_2$. At Site 1263, the absolute nannofossil abundance (coccoliths per gram of sediment; N g^{-1}) and the mean coccolith size decreased distinctly across the E–O boundary (EOB; 33.89 Ma), mainly due to a sharp decline in abundance of large-sized *Reticulofenestra* and *Dictyococcites*, within ~ 53 kyr. Since carbonate dissolution did not vary much across the EOB, the decrease in abundance and size of nannofossils may highlight an overall decrease in their export production, which could have led to an increased ratio of organic to inorganic carbon (calcite) burial, as well as variations in the food availability for benthic foraminifers.

The benthic foraminiferal assemblage data show the global decline in abundance of rectilinear species with complex apertures in the latest Eocene (~ 34.5 Ma), potentially reflecting changes in the food source, thus phytoplankton, followed by transient increased abundance of species indicative of seasonal delivery of food to the sea floor (*Epistominella* spp.; ~ 34.04–33.54 Ma), with a short peak in overall food delivery at the EOB (buliminid taxa; ~ 33.9 Ma). After Oi-1 (starting at ~ 33.4 Ma), a high abundance of *Nuttallides umbonifera* indicates the presence of more corrosive bottom waters, possibly combined with less food arriving at the sea floor.

The most important signals in the planktonic and benthic communities, i.e. the marked decrease of large reticulofenestrids, extinctions of planktonic foraminifer species and more pronounced seasonal influx of organic matter, preceded the major expansion of the Antarctic ice sheet (Oi-1) by ~ 440 kyr. During Oi-1, our data show no major change in nannofossil abundance or assemblage composition occurred at

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Site 1263, although benthic foraminifera indicate more corrosive bottom waters following this event. Marine plankton thus showed high sensitivity to fast-changing conditions, possibly enhanced but pulsed nutrient supply, during the early onset of latest Eocene-earliest Oligocene climate change, or to a threshold in these changes (e.g. ρCO_2 decline, high-latitude cooling and ocean circulation).

1 Introduction

The late Eocene-early Oligocene was marked by a large change in global climate and oceanic environments, reflected in significant turnovers in marine and terrestrial biota. The climate was driven from a warm “greenhouse” with high ρCO_2 during the middle Eocene through a transitional period in the late Eocene to a cold “icehouse” with low ρCO_2 in the earliest Oligocene (e.g. Zachos et al., 2001; DeConto and Pollard, 2003; Pearson et al., 2009; Pagani et al., 2011; Zhang et al., 2013). During this climate shift, Antarctic ice sheets first reached sea level, sea level dropped, and changes occurred in ocean chemistry and plankton communities, while the calcite compensation depth (CCD) deepened rapidly, at least in the Pacific Ocean (e.g. Zachos et al., 2001; Coxall et al., 2005; Pälike et al., 2006; Coxall and Pearson, 2007). There is ongoing debate whether the overall cooling, starting at high latitudes in the middle Eocene while the low latitudes remained persistently warm until the end of the Eocene (Pearson et al., 2007), was mainly caused by changes in oceanic gateways (opening of Drake Passage and the Tasman gateway) leading to initiation of the Antarctic Circumpolar Current as proposed by e.g. Kennett (1977), or by declining atmospheric CO_2 levels as proposed by DeConto and Pollard (2003), Barker and Thomas (2004), Katz et al. (2008) and Goldner et al. (2014), or by some combination of both (Sijp et al., 2014). Recently, it has been proposed that the glaciation itself caused further oceanic circulation changes (Goldner et al., 2014; Rugenstein et al., 2014).

The Eocene–Oligocene boundary (EOB; ~ 33.89 Ma, Gradstein et al., 2012) is defined by the extinction of planktonic foraminifers (specifically, the genus *Hantkenina*),

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1999). Five samples along the studied sequence were also prepared with the filtration technique (Andrulleit, 1996) and spiked with microbeads to investigate the reproducibility of absolute abundances obtained with our technique. This resulted in similar temporal trends between the techniques (mean CV= 11 %). The estimates of absolute abundances (Ng^{-1}) allow us to better identify the real fluctuations in abundance of single species within the sediment. In contrast, the use of the relative abundances (%) could lead to loss of information and misinterpretation of the results through the closed-sum problem, as each percentage value refers to how common or rare a species is relative to other species without knowing whether a species truly increased or decreased in abundance. Sample set B was prepared with the standard smear slide technique (Bown and Young, 1998).

In both sets A and B, calcareous nannofossils were examined under crossed polarized light microscopy (LM) at 1000 \times magnification. Quantitative analyses were performed by counting at least 300 specimens in each slide. Additional observations were performed on the slide to detect the occurrence of rare species, especially biostratigraphical markers. All specimens were identified at species or genus level, depending on the coccolith preservation. We used *Cyclicargolithus* sp. to group the specimens with dissolved central area that can be associated to the genus *Cyclicargolithus* but not directly to the species *Cyclicargolithus floridanus* (Fig. S1 in the Supplement). Taxonomy of the calcareous nannofossils follows the reference contained in the web-site <http://ina.tmsoc.org/Nannotax3> (edited by Young et al., 2014). Additional taxonomic remarks are given in the Supplement. For dataset A, the number of fields of view (FOV) observed were also noted in order to calculate absolute abundances.

Both datasets were used to provide biostratigraphical information: dataset A with a more detailed resolution across the EOB, and dataset B covering a longer interval below the EOB. For quantitative description of the nannofossil assemblage, relative abundances (%) for all the identified species were calculated for both datasets A and B.

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Kucera and Malmgren, 1998; Bucciatti and Esposito, 2004), arcsine (e.g. Auer et al., 2014), etc.

We applied two transformations to the nannofossil species percentage abundances: (i) log-transformation by $\log(x + 1)$, which amplifies the importance of less abundant species, and minimizes the dominance of few abundant species (Mix et al., 1999), and (ii) centered log-ratio (clr) transformation (Aitchison, 1986; Hammer and Harper, 2006), which opens a closed data matrix and retains the true covariance structure of compositional data as well. The normal distribution of each species before and after the transformations was verified using SYSTAT 13.0 software. Datasets A and B were treated the same, but were analysed independently.

Principal component analysis (PCA) was performed on the transformed data using the statistics software PAST (PAleontological STatistic; Hammer et al., 2001). Species with an abundance $< 1\%$ in all samples were not included in the PCA. The PCA (Q-mode) was performed to identify the major loading species and to evaluate the main factors affecting the changes on fossil coccolithophore assemblages.

The closed-sum problem, or constant-sum constraint, may obscure true relationships among variables as first noted by Pearson (1896) when performing statistical data analysis of compositional data. The clr transformation retains a major problem in carrying out the PCA on the covariance matrix, and the goal of keeping the most important data information with only few principal components (PCs) can fail using clr transformation in associations containing many outliers (e.g. Maronna et al., 2006) as is often the case in nannofossil assemblages. To minimize the presence of outliers we worked with abundant species and groups of nannofossils, instead of with single species.

The PAST software was used to calculate the Shannon Index, H , a diversity index taking into account the relative abundances as well as the number of taxa. High values indicate high diversity.

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3 Biostratigraphy

The EOB at Site 1263 was tentatively placed between 83 and 110 mcd by the Leg 208 Shipboard Scientific Party (Zachos et al., 2004). Riesselman et al. (2007) placed Oi-1 on the basis of an increase in the benthic $\delta^{18}\text{O}$ records from $\sim 1.5\%$ (94.49 mcd, uppermost Eocene) to $\sim 2.6\%$ (93.14 mcd, lowermost Oligocene). The $\delta^{18}\text{O}$ values remained high upsection, to 88.79 mcd. Steps 1 and 2 in the $\delta^{18}\text{O}$ increase were identified (Riesselman et al., 2007; Peck et al., 2010), although they are not clearly defined as at Site 1218 in the Pacific Ocean (Coxall et al., 2005).

Our high-resolution sampling allowed refining the position of the EOB by locating nannofossil and planktonic foraminifer bioevents (Fig. 2; Table 1), including some nannofossil bioevents not yet reported in Zachos et al. (2004). To avoid bias, sample sets A and B were analysed by two different operators for the occurrence of nannofossil marker species (Fig. 2).

The identified bioevents are delineated as Base (B, stratigraphic lowest occurrence of a taxon), Top (T, stratigraphic highest occurrence of a taxon), and Base common (Bc, first continuous and relatively common occurrence of a taxon) according to Agnini et al. (2014), and acme beginning (AB, base of the acme of a taxon) according to Raffi et al. (2006). No correlation with magnetochrons was possible because the soft nannofossil ooze at Site 1263 does not carry a clear signal (Zachos et al., 2004).

The depths of all identified nannofossil and foraminifer datums, together with the ages assigned to the most reliable datums in Gradstein et al. (2012) are displayed in Table 1. For bioevents which are diachronous or not reported in Gradstein et al. (2012), the most recent literature was selected, considering the datums recorded at latitudes as close as possible to the studied site. The succession spans from 32.7 Ma (HO of *Isthmolithus recurvus*, Lyle et al., 2002) to 34.76 Ma (HO of *Discoaster barbadien-sis*, Gradstein et al., 2012). The estimated average sedimentation rate is 9.8 m myr^{-1} , somewhat lower than the average value of 11.7 m myr^{-1} in Zachos et al. (2004). In

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3.2 Planktonic foraminifers

At Site 1263, the primary marker species for the EOB (the genera *Cribohantkenina* and *Hantkenina*) are not well preserved, and occur as fragments of variable size, including hantkeninid spines and partial specimens (several chambers). We primarily studied benthic foraminifera, so that we scanned through large samples, containing thousands of specimens of planktonic foraminifera. From 96.41 mcd up-section (the first higher sample being at 96.27 mcd) we did not find any fragments of hantkeninid tests and/or loose spines (*Cribohantkenina* and *Hantkenina alabamensis*), whereas these were consistently present in samples below that level (Fig. 2). The sample at 96.41 mcd contained rare spines, but no partial specimens (Fig. 2). We thus recorded the T of *H. alabamensis*, the traditional marker for the EOB (e.g. Coccioni, 1988; Premoli-Silva and Jenkins, 1993; Pearson et al., 2008), at 97.91 mcd, and placed the EOB above 96.41 mcd (1263A-10H-5-32-34cm, 96.27 mcd; Table 1; Fig. 2). The benthic foraminifera at Site 1263 show some evidence of reworking (Zachos et al., 2004), but this was limited to a few samples, so we consider that the uppermost sample with partial tests of hantkeninids marks the uppermost Eocene. This observation differs from that in Zachos et al. (2004), where only core catcher samples were studied and the partial specimens in Sample 1263A-10H-CC were not observed (Table 1). Samples from Core 1263A-11H and sample 1263A-10H-CC (99.97–109.79) contain strongly fragmented planktonic foraminifers, with non-broken specimens dominated by heavily calcified *Globigerinatheca* spp. (Zachos et al., 2004).

4 Biotic responses

4.1 Calcareous nannofossil preservation and assemblages

At ODP Site 1263 no consistent increase in carbonate content above the EOB was recorded (Riesselman et al., 2007), in contrast to other sites, specifically in the Pacific

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Ocean (e.g. Salamy and Zachos, 1999; Coxall et al., 2005; Coxall and Wilson, 2011), probably because this site was well above the lysocline since the late Eocene (Zachos et al., 2004). The carbonate accumulation was not strongly affected by potential CCD deepening, because the CaCO_3 (wt%) was and remained generally high (Fig. 3; Riesselman et al., 2007). The CaCO_3 (wt%) does not reflect the total coccolith absolute abundance (Fig. 3), suggesting that also other calcifying organisms (planktonic foraminifers) contributed consistently to the calcite accumulation in the sediments.

Although the site was above the lysocline during the studied time interval, the nannofossil and foraminiferal assemblages show signs of dissolution all along the sequence. Such dissolution may occur above the lysocline (e.g. Adler et al., 2001; de Villiers, 2005), leading to a reduction in species numbers and an increase of fragmentation with depth in both nannoplankton (e.g. Berger, 1973; Milliman et al., 1999; Gibbs et al., 2004) and planktonic foraminifer communities (e.g. Peterson and Prell, 1985).

At Site 1263 signs of dissolution were detected, in particular, on specimens of *Cycli-cargolithus* (Fig. S1 in the Supplement) – one of the least resistant species (Blaj et al., 2009), but also on more robust species like *Dictyococcites bisectus* (Fig. S1 in the Supplement). The absence of specimens $< 3 \mu\text{m}$ is indicative of dissolution, but does not prevent the identification of the main features in the assemblage. The coccolith dissolution index does not show large changes at the EOB, but during and after the Oi-1 nannofossil dissolution slightly intensified (Fig. 3). The correlation between the dissolution index and total coccolith abundance is positive and stronger in the upper interval of the studied sequence, but not significant across the EOB. In fact, from 90.5 mcd upward the correlation value, r , is 0.59 (p value = 0.002), instead for the entire interval $r = 0.32$ (p value = 0). This confirms that the total coccolith abundance and the nannofossil assemblage features are preserved in the fossil record, at least across the EOB, although nannofossil dissolution may be intense. From 90.5 mcd up-section, dissolution more strongly affected the assemblages.

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The total absolute coccolith abundance records a marked decrease across the EOB: within 60 cm (from 96.39 to 95.79 mcd) the abundance rapidly drops by 45 %, mainly driven by the loss of large-sized species, in particular of *D. bisectus* (Fig. 3).

Nannofossil diversity, based on the H index, does not record significant variations at the EOB. A more distinct step-wise decrease is recorded at 90 mcd (grey bar in Fig. 3), which could be explained by the increased dissolution in this interval, and by a community structure with fewer dominant species. Actually, in this interval *Cyclicargolithus* became more dominant in the assemblage, while large *Reticulofenestra* decreased in abundance significantly (Fig. 3). The calcareous nannofossil assemblage variations recorded in sample sets A and B are comparable despite the different sampling resolution (Figs. S2 and S3 in the Supplement).

The absolute abundances of all the large-sized species decreased markedly across the EOB (Fig. 3), including the species *D. bisectus*, *Dictyococcites stavensis*, *Reticulofenestra umbilicus*, *Reticulofenestra samodurovii*, *Reticulofenestra hillae*, *Reticulofenestra* sp.1 (see taxonomical remarks in the Supplement), and *Reticulofenestra daviesii*. Among these, *D. bisectus* and *D. stavensis* constitute a significant part (up to 28 %) of the assemblage.

The small-medium *Cyclicargolithus* sp. and *C. floridanus* are the most abundant species (up to 50 %), and the 5–7 µm size group is dominant. This group increases slightly from the bottom upwards, but at the EOB only a slight decrease in absolute abundance is recorded. Also, *C. pelagicus* is one of the most important components of the nannofossil assemblage, at a maximum abundance of 27 % (Fig. 3). This species increases its absolute abundance between 96.79–92.6 mcd, i.e. across and above the EOB, and then it decreases from 88 mcd upwards. *Sphenolithus* spp. also does not show marked variation at the EOB, even if this group is not very abundant. This lack of any species that increase in abundance above the EOB at Site 1263 suggests that the loss in large reticulofenestrids was not compensated for by other taxa, leading to a sustained decrease in total coccolith abundance (and export production) since the EOB.

Another component of the assemblage, *Lanternithus minutus*, is generally not abundant, but peaks between 89.6 and 87.12 mcd. *Zygralithus bijugatus* and *Discoaster* spp. both decreased in abundance before the EOB and, thereafter, never reached abundances as high as in the late Eocene.

4.1.1 Principal component analysis

The PCAs performed on datasets A and B give fairly comparable results, either using the log- or clr-transformation. For dataset A, the Pearson correlation value (r) between the components from the two transformations is 0.90 (p value = 0), confirming that the primary signals in the assemblage are revealed by the multivariate statistical analysis, as long as the normal distribution of the species is maintained. We also compared the PCA results with or without the presence of the marker species, because stratigraphically-controlled species are not distributed along the entire succession, thus affect PCA outcomes (e.g. Persico and Villa, 2004; Maiorano et al., 2013). Nonetheless, the results obtained with and without the marker species still provide similar trends because in the studied interval the marker species are not very abundant (Fig. 4; Table S1 in the Supplement).

In the following discussion, we will focus on the PCA results and the loading species using the log-transformation for datasets A and B (Fig. 4; Tables S1 and S2 in the Supplement). The only two significant principal components explain 50% of the total variance in dataset A, and respectively account for 36 and 14%. For dataset B the two components explain 35% (26 and 11% respectively).

Principal component 1 (PC1) of dataset A shows positive values below 96 mcd. A pronounced decrease occurs at the EOB, and from 96 mcd upwards the PC1 maintains mainly negative values (Fig. 4a). PC1 is negatively loaded by *C. obrutus*, *C. floridanus* small and medium size, and positively by *D. stavensis*, *D. bisectus*, *R. daviesii*, and *R. umbilicus* (Fig. 4a; Table S1 in the Supplement). The loadings of the other species are too low to be significant. The PC1 of dataset B does not record the same marked drop at the boundary, but rather a gradual decrease all along the sequence

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(Fig. 4a). Although the main loading species are the same for both datasets (i.e. *C. obrutus*, *Cyclicargolithus* vs. *D. bisectus* and *R. umbilicus*) some differences can be identified (Table S2 in the Supplement). In particular, the influence of *Cyclicargolithus* size groups on PC1 cannot be detected in dataset B because the size subdivision was not included in the count. As the distribution of large vs. small-medium sized species on the PCA seems to be important for both datasets and *Cyclicargolithus* is one of the most abundant species, it is possible that the lack of a detailed size grouping within this genus in dataset B could lead to the difference in the PC1 curves at the EOB. The higher abundances of *Discoaster* and *R. umbilicus* from the bottom up to 102 mcd in dataset B could also explain some differences in the loading species between the two datasets (Tables S1 and S2, and Fig. S3 in the Supplement).

Principal component 2 (PC2) of dataset A also records an abrupt variation across the EOB: the negative values at the bottom of the succession turn toward positive values above the boundary and remain positive up to 89.95 mcd. From 89 mcd upwards, PC2 displays mainly negative values again, except for a peak between 85.68–86.42 mcd (Fig. 4b). The most meaningful species loading on PC2 is *L. minutus* (negative loading). The PC2 is also loaded negatively by *D. stavensis* and *C. floridanus* (5–7 μm), and positively by *C. pelagicus* (3–7 μm and 7–11 μm), *I. recurvus* and *Sphenolithus* spp. (Fig. 4b; Table S1 in the Supplement). The PC2 for dataset B shows a similar trend as dataset A from 98 mcd upward (Fig. 4b), but it distinctly differs in the lower part of the succession. Again, the PC2 is resolved by the same main loading species *L. minutus* vs. *C. pelagicus* (but note that the relative direction (positive or negative) of the loadings is swapped between dataset A and B; Tables S1 and S2 in the Supplement). In particular, *L. minutus* has very strong loadings in both datasets. In dataset B *L. minutus* has its maximum abundance in the upper Eocene interval that was not sampled in dataset A (Fig. S3 in the Supplement), likely driving the differences between the two PC2 curves below the EOB (Fig. 4b). The distribution of *L. minutus* becomes more comparable between the datasets above 100 mcd, reaching a peak between 89.6 and

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87.12 mcd although not as high as during the upper Eocene (Figs. S2 and S3 in the Supplement).

In the following discussion, we used the PCA results for dataset A (without the markers) only, because of its more even sample distribution and direct comparison to the other available nannofossil proxies, i.e. dissolution index, coccolith size distribution and absolute abundance.

4.2 Mean coccolithophore cell size variations

The PC1 curve is mirrored ($r = 0.81$; p value = 0) by mean cell size estimates ($V : SA$ ratio) of all placolith-bearing coccolithophores within the assemblages (Fig. 5). Fluctuations in mean size are mainly driven by the relative abundance of the different placolith-bearing taxa and their respective size groups, rather than intra-specific size variations. The mean $V : SA$ ratios were higher (large cells were more abundant) during the late Eocene, and decreased by 8% across the EOB, within 60 cm above (from 96.39 to 95.79 mcd), or ~ 53 kyr.

Our coccolith dissolution index confirms that preferential dissolution of small species did not bias the $V : SA$ results, as intervals of increased dissolution did not generally correspond to large $V : SA$ ($r = -0.12$). The only exception is the top, 90–90.3 mcd, interval where a high dissolution peak corresponds to an increase in mean size.

4.3 Benthic foraminifer assemblage

The low resolution data on benthic foraminifera show that the diversity of the assemblages (see Fisher's alpha index curve; Fig. 6) started to decline in the late Eocene (~ 34.5 Ma; 102.79 mcd), reached its lowest values just below the EOB, then slowly recovered, but never to its Eocene values (Fenero et al., 2010). The decline in diversity was due in part to a decline in relative abundance of rectilinear species with complex apertures ("extinction group" species). Such a decline is observed globally at the end of the Eocene (Thomas, 2007; Hayward et al., 2012). The declining diversity was also

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due to a transient increase in abundance of species indicative of seasonal delivery of food to the sea floor (phytodetritus species, mainly *Epistominella* spp.; ~ 34.04–33.51 Ma; 97.91–91.91 mcd), with a short peak in overall, year-round food delivery at the E/O boundary (buliminid taxa; ~ 33.9 Ma; 96.41–96.27 mcd). After Oi-1 (starting at ~ 33.4 Ma; 90.41 mcd), the abundance of *N. umbonifera* increased. Due to evidence for dissolution, benthic foraminiferal accumulation rates can not be used to estimate food supply quantitatively and reliably.

5 Discussion

5.1 Nannoplankton abundance and cell size decrease at the EOB

The distinct variation in nannoplankton abundance and average coccolith size across the EOB at Site 1263 cannot be explained by dissolution or a change in species diversity, but is mainly linked changes in community structure (Fig. 3). The drop in total nanofossil abundance (Fig. 3) and mean cell size (Fig. 5) is mainly driven by the decrease in abundance of large *Reticulofenestra* and *Dictyococcites* across the EOB. The mean V : SA estimates for all ancient alkenone producers combined (i.e. *Cyclicargolithus*, *Reticulofenestra* and *Dictyococcites*; Plancq et al., 2012) tightly overlap (Fig. 5) with biometric data of the same group in the Equatorial Atlantic (Ceara Rise, ODP Sites 925 and 929; Pagani et al., 2011), while the mean size estimates for combined *Reticulofenestra* and *Dictyococcites* coincide with mean values measured at ODP Site 1090 in the Subantarctic Atlantic, where *Cyclicargolithus* spp. were not present and assemblages are likely severely affected by dissolution (Pea, 2010; Pagani et al., 2011).

The assemblage records illustrate the mid-latitude location of Site 1263, hosting both “subantarctic” and “equatorial” taxa. A striking correspondence with the mean V : SA of ancient alkenone producers at Site 1263 and Sites 929 and 925 (Fig. 5) would suggest more affinity with tropical assemblages than with high-latitude ones, south of the Subtropical Convergence (STF). The abundance patterns of the larger reticulofenestrids,

however, are strikingly similar to those at Southern Ocean sites (Persico and Villa, 2004; Villa et al., 2008). The mid-latitudinal Site 1263 thus probably records paleo-biogeographic patterns in the nannofossil assemblage intermediate between those in equatorial-tropical and subantarctic regions.

The coccolith size-shift and the decreased abundance of large reticulofenestrids across the EOB may be related to different bio-limiting factors. Under growth-limiting environmental conditions, phytoplankton (coccolithophores) with small cell volume-to-surface area ratios may outcompete larger cells due to lower resource requirements (lower C, P and N cell quota) and generally higher growth rates (e.g. Daniels et al., 2014). A change in overall nutrient regime, such as in coastal upwelling vs. oligotrophic, stratified gyre systems, may also cause a shift in opportunistic vs. specialist taxa (e.g. Falkowski et al., 2004; Dunkley Jones et al., 2008; Henderiks et al., 2012). The 16–37 % absolute abundance declines of the reticulofenestrid species *D. bisectus*, *R. umbilicus*, *R. hillae* and *R. daviesii* (Fig. 3), are strong indications that these large-celled coccolithophores were at a competitive disadvantage already during or shortly after the EOB. Earlier biometric studies of reticulofenestrid coccoliths point to a similar scenario (Fig. 5), postulating that the macroevolutionary size decrease reflects the long-term decline in $p\text{CO}_2$ (Henderiks and Pagani, 2008; Pagani et al., 2011). High CO_2 availability during the late Eocene could have supported high diffusive CO_2 -uptake rates and photosynthesis even in the largest cells, assuming that ancient coccolithophores had no or inefficient CO_2 -concentrating mechanism, similar to modern species today (Rost et al., 2003), and due to the fact that Rubisco's specificity for CO_2 increases at higher CO_2 levels (Giordano et al., 2005).

Available paleo- $p\text{CO}_2$ proxy reconstructions from Equatorial regions (Pearson et al., 2009; Pagani et al., 2011; Zhang et al., 2013) indicate a transient decrease in $p\text{CO}_2$ across the studied interval rather than a distinct drop in $p\text{CO}_2$ at the EOB, which would be suggested by our high-resolution assemblage (PC1) and mean V : SA time series (Fig. 5). Nevertheless, the paleo- $p\text{CO}_2$ proxy data are at much lower resolution, based on a range of geochemical proxies and assumptions (Pearson et al., 2009; Pagani

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PC2 of the calcareous nannoplankton analysis could be correlated with paleoproductivity and total water column stratification. The strongest negative loading on PC2 is the holococcolith *L. minutus* (Fig. 4b; Table S1 in the Supplement). In modern phytoplankton, the holococcolith-bearing life stages proliferate under oligotrophic conditions (e.g. Winter et al., 1994). Moreover, holococcoliths such as *L. minutus* and *Z. bijugatus* are quite robust (Dunkley Jones et al., 2008), so that dissolution is unlikely to affect their distribution which may be mainly linked to low nutrient availability.

The positive loadings on PC2 are the species *C. pelagicus*, *I. recurvus* and *Sphenolithus* spp. A high abundance of *C. pelagicus* has often been considered as indicative for warm-to-temperate temperatures (e.g. Wei and Wise, 1990; Persico and Villa, 2004; Villa et al., 2008). In the modern oceans, *C. pelagicus* seems to be restricted to cool-water, high-nutrient conditions (e.g. Cachao and Moita, 2000; Boeckel et al., 2006), but during the Paleogene it was cosmopolitan (Haq and Lohmann, 1976).

We compared PC2 with the proxy for paleoproductivity $\Delta\delta^{13}\text{C}_{\text{P-B}}$ (Fig. 6), with lower values corresponding to lower productivity or higher stratification. The $\Delta\delta^{13}\text{C}_{\text{P-B}}$ data are not available for the interval below 96 mcd (upper Eocene), but lower paleoproductivity in general corresponds to negative loadings on PC2, and vice versa. The correlation coefficient between the two curves is 0.33 (p value = 0.05), i.e. a significant but not a very strong correlation, possibly due to the lower number of stable isotope data points. We infer that PC2 probably reflects lower productivity during the latest Eocene, and both PC2 and $\Delta\delta^{13}\text{C}_{\text{P-B}}$ curves show a higher productivity signal at the onset of Oi-1 (Fig. 6). In particular, PC2 records a longer interval of higher productivity above the EOB, and an initial decrease before the highest peak in $\delta^{18}\text{O}$ (at ~ 93 mcd; ~ 33.6 Ma), as recorded also by $\Delta\delta^{13}\text{C}_{\text{P-B}}$. Paleoproductivity subsequently remained lower from the end of Oi-1 upward. The PC2 and $\Delta\delta^{13}\text{C}_{\text{P-B}}$ curves differ from 90.5 mcd upward, possibly related to increased nannofossil dissolution. The increase of dissolution is confirmed by the increased abundance of the benthic foraminifer species *N. umbonifera* (Fig. 6), indicative of more corrosive bottom waters or possibly a lower food

supply. This is thus in agreement with the intensified dissolution interval recorded by the coccolith dissolution index (compare Figs. 3 and 6).

The benthic foraminifer assemblage confirms the interpretation of the PC2, adding information on the nature of the nutrient supply (Fig. 6). The increase across the EOB of the phytodetritus species indicates an increase in seasonal delivery of food to the seafloor, correlated to the interval with positive scores in PC2 (Fig. 6), though interrupted by a short interval of increased productivity across the EOB (as showed by the peak in the buliminid species curve at 96.27 mcd; Fig. 6). After the Oi-1, the high abundance of *N. umbonifera* and the decrease of phytodetritus and buliminid species are indicative of more corrosive bottom waters, possibly combined with less food arriving at the sea floor and/or a less pronounced seasonality (Fig. 6).

The variations in nutrient supply, as reflected in both nannofossil and benthic foraminifer assemblages, could possibly have driven the mean coccolith size decrease across the EOB. In fact, the transient higher availability of nutrients at the onset of Oi-1, may have made it possibly for small opportunistic species above the EOB to out-compete large specialist species. The decrease of mean cell size (less biomass per individual) and, also, of total nannofossil abundance could have led to less available organic matter and, thus, less food for the benthic foraminifers, and smaller nannoplankton could have caused a decrease in delivery of organic matter to the seafloor (and/or higher remineralization).

Possibly, major instability of the water column during the onset of Oi-1 favoured seasonal or episodic upwelling, thus primary productivity in this area, but an increase in productivity at the Oi-1 onset is not reflected in the absolute coccolith abundance (Fig. 3). After the major peak in $\delta^{18}\text{O}$ (Oi-1) a more stable system, related also to the onset of North Atlantic Deep Water (NADW) production in the early Oligocene (Via and Thomas, 2006), may have allowed the proliferation of more oligotrophic taxa, including holococcoliths, and the establishment of more oligotrophic environmental conditions (Fig. 6).

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Previous studies have documented an increase in primary productivity during the late Eocene-early Oligocene, in particular in the Southern Ocean (e.g. Salamy and Zachos, 1999; Persico and Villa, 2004; Schumacher and Lazarus, 2004; Anderson and Delaney, 2005). At tropical latitudes, both transient increases (equatorial Atlantic; Diester-Haass and Zachos, 2003) and decreases (e.g. Griffith et al., 2010; Moore et al., 2014) in paleoproductivity have been recorded during the early Oligocene, with a sharp drop in the export productivity in the early Oligocene at ~ 33.7 Ma (Moore et al., 2014), similar to what we observed in the southeastern Atlantic. Schumacher and Lazarus (2004) did not record a significant shift of paleoproductivity at the EOB in equatorial oceans, but noted a decrease in the early Oligocene (after 31 Ma). An increase in seasonality at the EOB, similar to the one we recorded at mid-latitudinal Site 1263, was documented at Site 689 in Southern Ocean (Schumacher and Lazarus, 2004), and seasonality increased just before Oi-1 in the northern high latitudes as well (Eldrett et al., 2009).

5.3 Timing and possible causes of the biotic response at the EOB

Marine faunal and floral species extinctions and community changes were coeval with the climatic deterioration during the late Eocene-early Oligocene (e.g. Adams et al., 1986; Coccioni, 1988; Berggren and Pearson, 2005; Dunkley Jones et al., 2008; Pearson et al., 2008; Tori, 2008; Villa et al., 2008, 2014). At ODP Site 1263, we also see close correspondence between marked changes in the nannoplankton assemblages (i.e. nannofossil abundance and coccolith size decrease) and the extinction of the hantkeninid planktic foraminifers. Both events occurred at the EOB, pre-dating the onset of Oi-1, i.e. the first major ice sheet expansion on Antarctica. Extinction events are usually rapid (10–100 kyr; Gibbs et al., 2005; Raffi et al., 2006). The nannoplankton did not suffer significant extinctions at the same boundary, but the change in the community was relatively fast, taking place within ~ 53 kyr.

The timing of the main shifts in the planktonic community was relatively early during the transient climate change across the EOB, and pre-dated significant cooling and

increase in Antarctic ice sheet volume by about 440 kyrs (i.e. Oi-1). Therefore, fossil planktonic assemblages are fundamentally important and accurate tools to investigate early impacts or crossing of threshold levels during climate change on biotic systems.

Benthic foraminiferal changes at Site 1263 likewise started before the EOB (Thomas, 1990, 2007), and the faunal turnover persisted into the early Oligocene. The benthic faunas in general show a decline in rectilinear species, possibly linked to the decline in nannoplankton species which may have been used by the rectilinear benthics (as e.g. hypothesized by Hayward et al., 2012; Mancin et al., 2013). The increase in phytodetritus-using species was possibly linked to more episodic upwelling and thus productivity, and potentially blooming of more opportunistic nannoplankton species. Unfortunately, the lower resolution of the benthic foraminifer data compared to the nanofossil data does not allow to unravel the exact timing of the benthic fauna response across the EOB.

At Site 1263 and in Southern Ocean records (Persico and Villa, 2004; Villa et al., 2008) the large reticulofenestrads declined in abundance rapidly at the EOB. Persico and Villa (2004) and Villa et al. (2008, 2014) inferred a strong influence of SST cooling on coccolithophores, and the drop in SST across the EOB at high-latitudes is also confirmed by a decrease of 5 °C in $U_{37}^{K'}$ -based SST (Liu et al., 2009). In contrast, at Site 1263 planktonic foraminifer Mg/Ca data record no significant change in SST at that time (Peck et al., 2010; Fig. 5), as at ODP Sites 925 and 929 (tropical western Atlantic) where $U_{37}^{K'}$ -based SSTs also show no relevant cooling (Liu et al., 2009; Fig. 5). Fairly stable SSTs were also documented in the tropics using Mg/Ca-based SST reconstructions (Lear et al., 2008). The temperatures at mid-latitude Site 1263 thus may have been stable, like those in the tropics, rather than cooling, as inferred for high latitudes in the Southern Ocean (e.g. Persico and Villa, 2004; Villa et al., 2008, 2014; Liu et al., 2009).

If this is true, SST may not have been the main environmental factor affecting the nannoplankton assemblages at Site 1263 across the EOB. Andrleit et al. (2003) documented that for modern coccolithophores in tropical–subtropical regions temperature

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changes may be of less importance, but the lower temperature at high latitudes can approach the vital limits for coccolithophores (Baumann et al., 1997), and become important as a bio-limiting factor.

Changes in the phytoplankton community could be related to a global influence of declining $p\text{CO}_2$. Unfortunately the estimates available from alkenone- and boron isotopes lack the resolution to unravel the variation at the EOB (Fig. 5), but leave open the possibility that falling $p\text{CO}_2$ below a certain threshold-level could have played a role in driving the reorganization in the nannoplankton community. Alternatively, our combined biotic and geochemical proxy data (i.e. nannofossil and benthic foraminifer assemblages, and $\Delta\delta^{13}\text{C}_{\text{P-B}}$) suggest an increase in nutrient and food supply just after the EOB (Fig. 6), which would have favored opportunistic taxa over low-nutrient selected, specialist species. We conclude that the large reticulofenestrads were clearly at an ecological disadvantage, either due to changes in nutrient supply and/or $p\text{CO}_2$, whereas *Cyclicargolithus* and *Coccolithus* remained unaffected, or slightly increased in absolute abundance. Most large reticulofenestrads (except *R. hillae* and *Reticulofenestra* sp.1) never recovered to pre-EOB abundances, despite a return to more stratified conditions after the Oi-1 event. Increased dissolution after the Oi-1 event unlikely explains the loss of large, heavily calcified taxa, but may also have led to enhanced remineralization of organic matter and less food supply to the benthic communities.

A regional increase in nutrients after the EOB was also postulated to have occurred at low latitudes, based on a decrease in nannofossil species diversity at Tanzanian sites (Dunkley Jones et al., 2008). At Site 1263, no marked change in diversity was recorded at the EOB (Fig. 3). The diversity and species richness of fossil assemblages, however, are strongly affected by dissolution, or by reworking and taxonomic errors (Lazarus, 2011; Lloyd et al., 2012). The Tanzanian sites indeed reveal remarkable and pristine marine microfossil preservation (Dunkley-Jones et al., 2008; Pearson et al., 2008), rarely matched by other Eocene–Oligocene deep-sea records.

There appears to be a latitudinal gradient in the timing of nannofossil abundance decreases. The abundance decreases were first detected in the Southern Ocean (late

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Eocene; Persico and Villa, 2004), then at mid-latitude (at the EOB; this study), and finally at the equator (after the Oi-1; Dunkley Jones et al., 2008). So that may suggest a direct temperature effect on nannoplankton abundance since the cooling started and was most pronounced at high latitudes, or indirect high-latitude cooling impacts on global nutrient regimes and ocean circulation. Since regional dissolution bias may also affect the comparison of absolute coccolith abundance, additional studies on well-preserved material will be necessary to confirm the timing and character of the response at different latitudes and in different ocean basins. Nevertheless, a meridional gradient in biotic response is expected, given the different environmental sensitivities and biogeographic ranges of different phytoplankton species (e.g. Wei and Wise, 1990; Monechi et al., 2000; Persico and Villa, 2004; Villa et al., 2008), and the diachroneity of the onset of cooling (Pearson et al., 2008).

6 Conclusions

High-resolution analyses of the calcareous nannofossil and foraminifer assemblages refine the biostratigraphy at ODP Site 1263 (Walvis Ridge), and demonstrate distinct assemblage and abundance changes in marine biota at the Eocene–Oligocene boundary. The biotic response of calcareous nannoplankton was very rapid (~ 53 kyr), similar to the hantkenid extinction event, and pre-dated the Oi-1 event by 440 kyr.

The ecological success of the small-sized coccolithophore species vs. the drastic decrease of large ones, and the overall decrease of nannoplankton productivity across the EOB may have affected the benthic foraminiferal community (e.g. decrease in recitilinear species due to changes in nannoplankton floras), with increased seasonality driving the transient increased abundance of phytodetritus-using species. After Oi-1, both nannoplankton and benthic records are affected by intensified dissolution and corrosivity of bottom waters.

We conclude that the planktonic community reacted to some fast-changing environmental conditions, possibly seasonally increased nutrient supply to the photic zone,

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Table 1. Calcareous nannofossil and planktonic foraminifer bioevents as identified in this study (at meter composite depth, mcd), and the mcd reported by the Shipboard Scientific Party (Zachos et al., 2004). For each bioevent, the ages available in the most recent literature are given, as well as the location of the reference sites. N.A.: not available datum; *: ages not included in the sedimentation rate estimate.

Datum	This study		Shipboard Scientific Party (Zachos et al., 2004)		Ages	
	Interval (hole-core-section, cm)	Depth (mcd)	Average Depth (mcd)	Age (Ma)	Site/Area	References
T <i>Isthmolithus recurvus</i>	B-3H-5, 115–116	83.19	86	32.7	Leg 199	Lyle et al. (2002)
T <i>Coccolithus formosus</i>	A-9H-4, 9–10	85.16	86	32.92	Site 1218	Gradstein et al. (2012)
Bc <i>Sphenolithus akropodus</i>	A-9H-4, 100–102	86.34	N.A.			
B <i>Chiasmolithus altus</i>	B-4H-2, 131–132	89.4	N.A.	33.31*	Site 1218	Pälike et al. (2006)
B <i>Sphenolithus akropodus</i>	B-4H-3, 50–52	90.09	N.A.			
AB <i>Clausicoccus obrutus</i>	A-10H-4, 141–142	96	94.77	33.85*	Massignan GSSP	Brown et al. (2009)
T <i>Hantkenina</i> spp.	A-10H-5, 32–34	96.27	104.5	33.89	Mediterranean	Gradstein et al. (2012)
T <i>Discoaster saipanensis</i>	B-5H-3, 50–52	102.27	104.1	34.44	Site 1218	Gradstein et al. (2012)
T <i>Discoaster barbadiensis</i>	B-5H-4, 0–2	103.27	N.A.	34.76	Site 1218	Gradstein et al. (2012)
B <i>Sphenolithus tribulosus</i>	B-5H-4, 50–52	103.77	N.A.			

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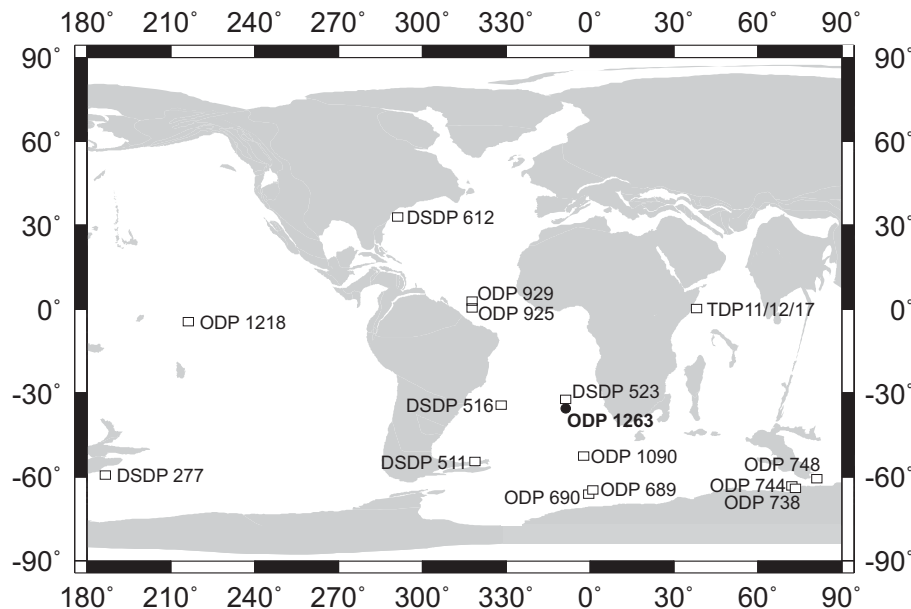


Figure 1. Paleogeographic reconstruction at 33 Ma (modified from Ocean Drilling Stratigraphic Network, Plate Tectonic Reconstruction Service, www.odsn.de/odsn/services/paleomap/paleomap.html) showing location of ODP Site 1263 (black dot) on Walvis Ridge. The positions of the other sites (white squares) used for comparison and cited in the text are also given.

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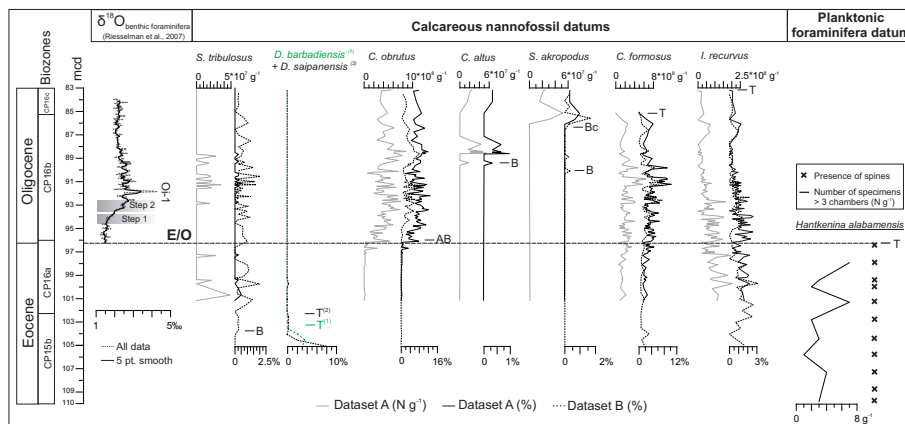


Figure 2. Eocene–Oligocene stratigraphy of Site 1263. Plotted against depth (mcd) are: benthic foraminifer stable isotope data (Riesselman et al., 2007), nannofossil marker species absolute abundances (N g^{-1} ; note 10^7 – 10^8 change in scale among curves) for dataset A (grey line) and their relative percentages (%) for datasets A (black line) and B (black dashed), number of specimens > 3 chambers per gram of sediment and presence of spines of the planktonic foraminifer *Hantkenina alabamensis*. Note the changes in scales among curves. Calcareous nannofossil and planktonic foraminifer datums are highlighted. B: Base occurrence; T: Top occurrence; Bc: Base common occurrence.

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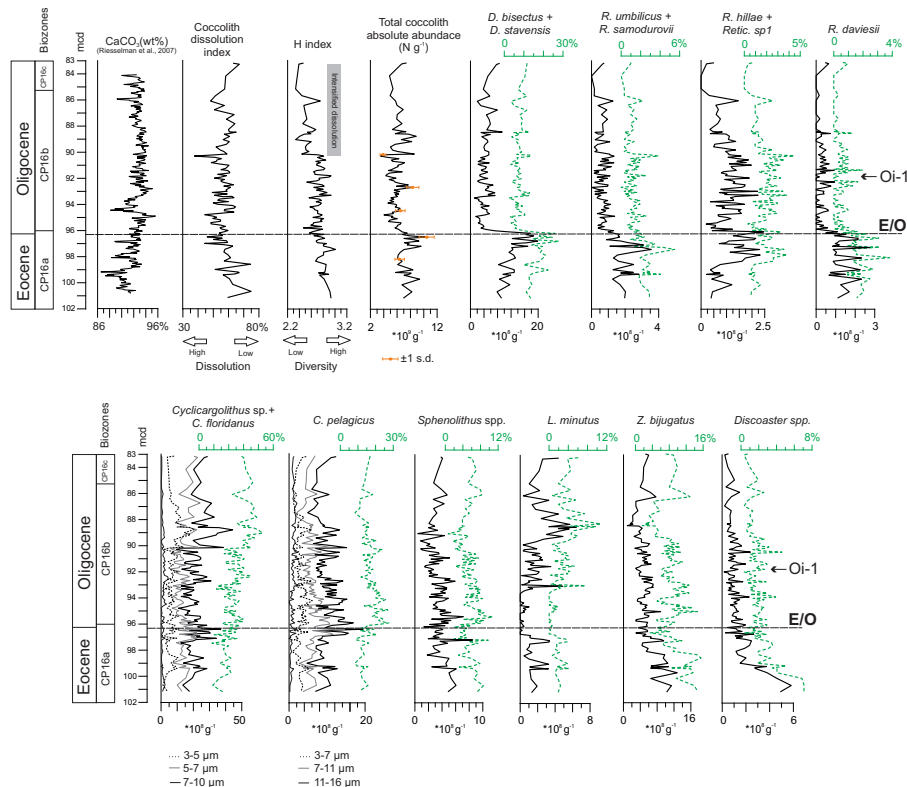


Figure 3. Calcareous nanofossil abundance and distribution at Site 1263. CaCO_3 (wt%; Rieselsman et al., 2007), coccolith dissolution index (%), H index, and the total absolute coccolith abundance (N g^{-1}) and the mean SD percentage on 5 samples are plotted against depth. The absolute (N g^{-1} , black solid line) and relative (% , grey dotted line) abundances of the main species which constitute the assemblage are displayed. For *Cyclicargolithus* sp. and *C. pelagicus* also the absolute abundances of the size groups are shown. The grey bar close to the dissolution index identifies an interval of major dissolution.

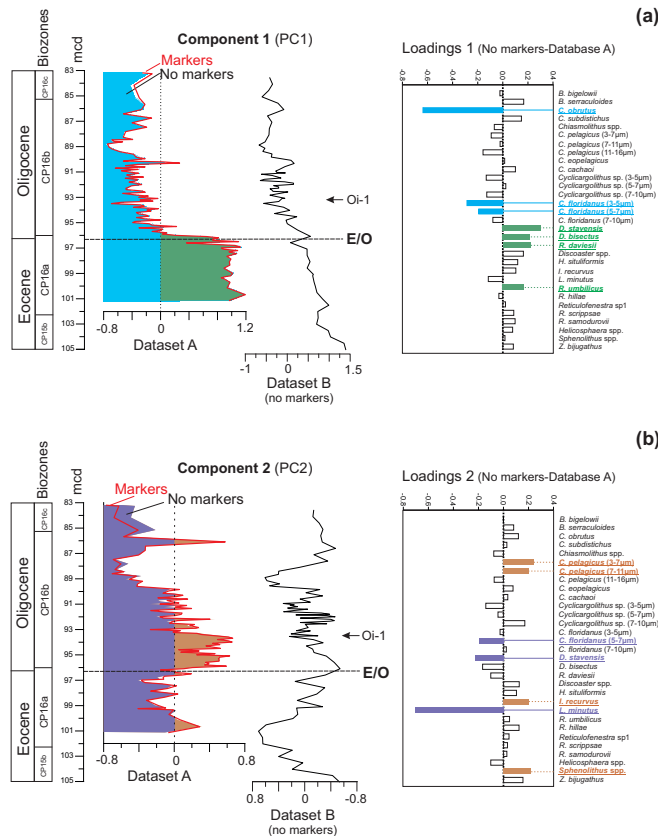


Figure 4. Distribution patterns of PC1 (a) and PC2 (b) obtained from the PCA for the datasets A and B (light green curves). Loadings of calcareous nannofossil taxa on the two principal components of the whole studied succession for dataset A are reported. The shaded boxes represent the most relevant loaded species. Shaded area: PCs (dataset A) obtained omitting the marker species in the dataset. Red line: PCs (dataset A) obtained inserting also the marker species.

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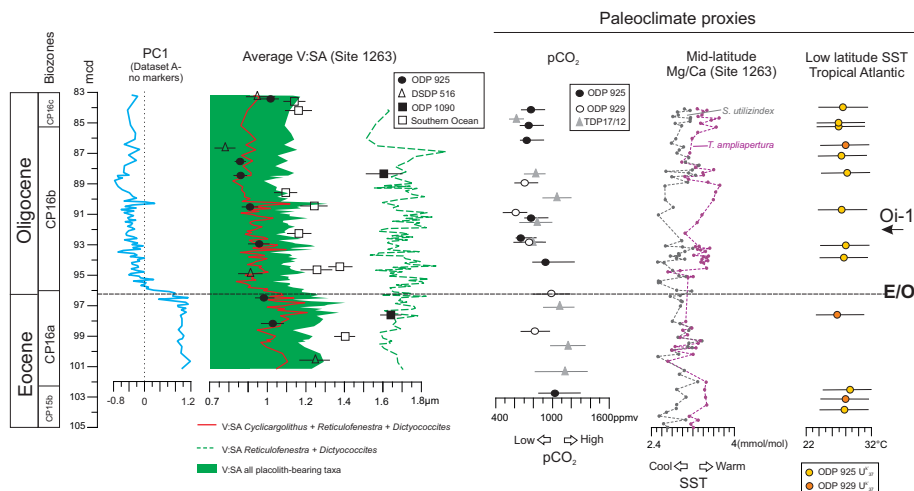


Figure 5. Coccolith total abundance (Ng^{-1}), PC1 and cell-size trends during the Eocene–Oligocene at Site 1263. The average cell V:SA (μm) of all placolith-bearing species (green area), *Reticulofenestra–Dictyococcites–Cyclocargolithus* (red solid line) and *Reticulofenestra–Dictyococcites* (green dotted line) are reported. The average cell V:SA of ODP 925 (black circles; Pagani et al., 2011), DSDP 516 (white triangles; Henderiks and Pagani, 2008), DSDP 511-277 (white squares) and ODP 1090 (black squares) from the southern ocean (Pagani et al., 2011), and $p\text{CO}_2$ (ppm) alkenone-based from ODP 925 (black circles; Zhang et al., 2013), ODP 929 (white circles; Pagani et al., 2011), and $p\text{CO}_2$ boron isotope-based from TDP12/17 (grey triangles; Pearson et al., 2009) are also shown. For comparison with sea surface temperature (SST) proxies, the Mg/Ca (mmol mol^{-1} ; Peck et al., 2010) at Site 1263 and the SST from $U_{37}^{K'}$ at low latitude in the Atlantic Ocean (Liu et al., 2009) are also displayed.

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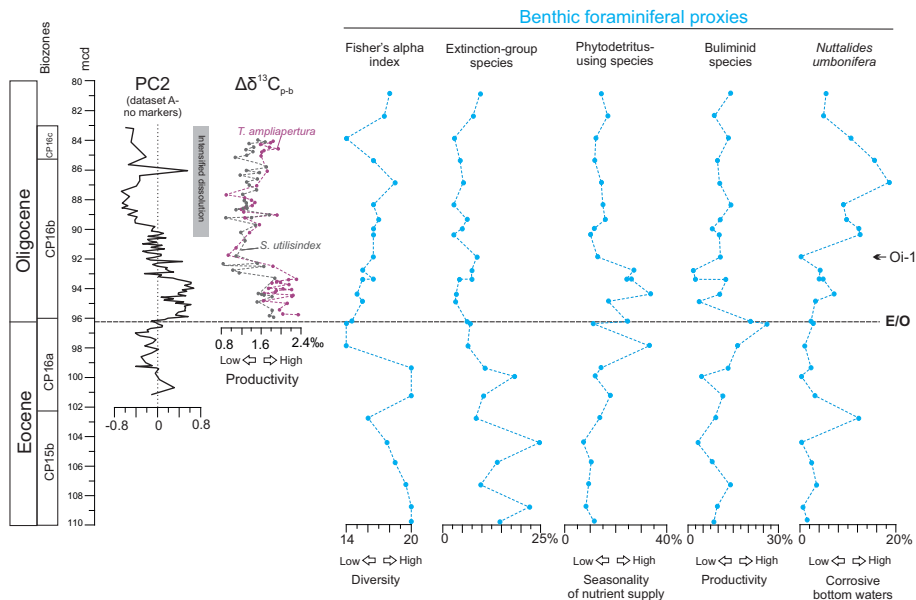


Figure 6. Paleoproductivity indices from nannofossil (PC2) and benthic foraminifer ($\Delta\delta^{13}C_{P-B}$) calculated from data in Riesselman et al. (2007) and Peck et al. (2010); Fisher's alpha index-diversity proxy, extinction group species, phytodetritus using species, buliminid species and the species *Nuttallides umbonifera*) datums are plotted against depth.