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RESEARCH ARTICLE

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Key Points:

- Tropical nannofossil ecosystem change is concentrated at the start of the Eocene-Oligocene Transition
- Species biodiversity declined with time; it is most rapid across the latest Eocene rosette-shaped *Discoaster* extinction event at ~34.44 Ma
- No preferential loss of large coccoliths across the EOT suggests no limitation on lith size with declining atmospheric CO₂ concentrations at this time

Correspondence to:

A. P. Jones,
apj527@bham.ac.uk

Citation:

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Low-Latitude Calcareous Nannofossil Response in the Indo-Pacific Warm Pool Across the Eocene-Oligocene Transition of Java, Indonesia

Amy P. Jones¹ , Tom Dunkley Jones¹ , Helen Coxall², Paul N. Pearson³, Dominika Nala¹, and Murray Hoggett¹

¹School of Geography, Earth and Environmental Sciences, University of Birmingham, Birmingham, UK, ²Department of Geological Sciences, Stockholm University, Stockholm, Sweden, ³School of Earth and Ocean Sciences, Cardiff University, Cardiff, UK

Abstract We reconstruct the calcareous nannofossil response to the Eocene-Oligocene Transition (EOT)—the most significant climate transition of the Cenozoic—in the Indo-Pacific Warm Pool. Data from south central Java consist of species relative abundance counts of well-preserved nannofossil assemblages. From the late middle Eocene to early Oligocene species biodiversity declined, with the most rapid species loss occurring across the latest Eocene rosette-shaped discoaster extinction event (DEE; ~34.44–34.77 Ma). A decline in abundance of oligotrophic indicator taxa across the DEE indicates increased nutrient supply to the tropical surface ocean in the early stages of the EOT. The mean lith size of reticulofenestrids also increases across the DEE driven by a marked reduction in the abundance of small *Reticulofenestra* morphotypes (<3.5 μm). There is no preferential loss of larger *Reticulofenestra* cell sizes (coccoliths > 8 μm) across the EOT, indicating that coccolith size was apparently not limited by atmospheric CO₂ concentrations at this time. Overall, the main phase of tropical phytoplankton ecosystem change preceded the interval of rapid Antarctic ice sheet growth and is closely associated with the biotic perturbations that define the start of the EOT. This suggests that enhancement of Southern Ocean controls on tropical ocean biogeochemistry and nutrient pathways may have played a role in triggering the transition to an icehouse climate state.

1. Introduction

The geologically rapid step change in the global climate system across the Eocene-Oligocene Transition (EOT; ~34.5–33.5 Ma) (Coxall & Pearson, 2007) is the most significant of the Cenozoic (Zachos et al., 2008). It is closely associated with the major expansion of continental Antarctic ice sheets (Bohaty et al., 2012; Coxall et al., 2005; Lear et al., 2008; Scher et al., 2011), global cooling (Liu et al., 2009), a reorganization of ocean circulation (Coxall et al., 2018; Egan et al., 2013; Elsworth et al., 2017; Goldner et al., 2014; Hutchinson et al., 2018; McKinley et al., 2019), and an altered biogeochemical cycle (Egan et al., 2013; Lyle & Lyle, 2006). Due to the fundamental changes in climate and biogeochemistry across the EOT, it is an important target for determining how large magnitude global environmental change can restructure key ecosystems, niche construction, and the evolutionary adaptive landscapes. Environmental changes across these intervals are primarily attributed to high-latitude drivers, specifically, the continental-scale glaciation of Antarctica (Bohaty et al., 2012; Coxall et al., 2005; Lear et al., 2008; Scher et al., 2011) and an increased role for the Southern Ocean in global circulation in global ocean overturning systems and biogeochemistry (Egan et al., 2013; Goldner et al., 2014). Compilations of Cenozoic marine microplankton diversity shows the EOT is consistently identified as the interval of maximum change (Bown et al., 2004; Rabosky & Sorhannus, 2009), often with important restructuring of ecological groups (Ezard et al., 2011), and a large shift in dominance between clades (Bown et al., 2004; Egan et al., 2013; Falkowski & Oliver, 2007). Understanding the detailed climate drivers of this change remains largely unresolved (Ezard et al., 2011).

Coccoliths are the biocalcified plates produced by the phytoplanktonic coccolithophore algae, which post-mortem are often preserved in great abundances within marine sediments (Bown et al., 2004). The fossil record of the coccolithophores, and other associated calcareous nannofossils, is one of the most complete of any Cenozoic clade (Bown et al., 2004), exceeded only by the planktonic foraminifera (Ezard et al., 2011). Coccolithophore algae are a key component of modern pelagic ecosystems, especially in the tropical and midlatitude oceans, estimated to be responsible for up to ~10% of total phytoplankton primary

Figure 1. Paleoreconstruction of the Sunda region, southeast Asia during the late Eocene. Shades of gray represent Eurasian crust and red dot indicates the location of NKK1. Redrawn from Hall (2012).

production (Poulton et al., 2006, 2007, 2017) and similar proportions of particulate inorganic carbon flux from the surface to the deep ocean (Schiebel, 2002). Long-term diversity records indicate that nannofossils were an even more significant component of pelagic microplankton communities in the warm climates of the early Cenozoic (Bown et al., 2004). Strong evidence from the modern oceans (Beaufort et al., 2011; Rickaby et al., 2010; Rost & Riebesell, 2004), and paleoecological studies (Dunkley Jones et al., 2008; Gibbs et al., 2013; Stoll et al., 2007; Villa et al., 2008, 2013) show that nannoplankton assemblages are controlled by environmental conditions, including nutrient availability and euphotic zone depth (Baumann et al., 1999; Liu et al., 2018). The exceptional calcareous nannofossil record, their importance to marine ecosystems, and their sensitivity to environmental change make them ideal for the reconstruction of the coupling between oceanic microplankton ecosystems and global climate change.

Here, we seek to determine the nature and drivers of tropical calcareous phytoplankton restructuring through the global cooling of the EOT. Our study section, the NKK1 borehole, is located in the center of the Indo-Pacific Warm Pool (IPWP) within late Eocene paleogeographic reconstructions and so provides the only continuous EOT sedimentary record from the central IPWP known to date. NKK1 is one of few sites globally containing very well-preserved late Eocene and early Oligocene nannofossils, and we use this to analyze trends in coccolith size of the dominant placolith-forming reticulofenestrated coccolithophores, which is closely coupled to cell size (Henderiks & Pagani, 2008). The Neogene reduction in coccolith size and calcification has been linked to declining surface ocean dissolved inorganic carbon (DIC) concentrations with falling atmospheric carbon dioxide levels (CO_2) (Bolton et al., 2012, 2016; Bolton & Stoll, 2013). The timing of the onset of this coupling is unclear with isotopic evidence indicating carbon limitation from the late Miocene (Bolton et al., 2016; Bolton & Stoll, 2013), while others infer a CO_2 control on lith size across the EOT (Bordiga et al., 2015). The tropical oligotrophic surface waters of the IPWP have the lowest DIC in the modern oceans (Krumhardt et al., 2017). If a carbon uptake limitation exists across the EOT, this should be most clearly seen in IPWP coccolith size records.

2. Materials and Methods

We present new records of calcareous nannoplankton species assemblages and diversity from the EOT deriving from a sequence of hemipelagic, continental slope and clay-rich sediments from the Nanggulan Formation of Java situated within the IPWP (Plate 1). Today the IPWP—where surface water temperatures exceed 28°C throughout the year (De Deckker, 2016)—stretches across the western Pacific Ocean, through the Indonesian archipelago and into the eastern Indian Ocean, with climate models indicating it was much more extensive in the Eocene (Huber & Sloan, 2001; Lunt et al., 2012, 2016). This study focuses on the middle Eocene to lower Oligocene succession of the Nanggulan Formation, recovered from a single borehole, NKK1, drilled in 2006 in the province of Nanggulan, south central Java (-7.788555°S , 110.20578°E , Figure 1). Recovered strata consist of the middle Eocene upper Watu Puru Beds (88.02–99.98 meters below ground level [bgl]) and the upper Eocene to lower Oligocene Jetis Beds (86.85–41.04 m bgl). A total of 65 core samples were analyzed for calcareous nannofossil content, between core depths of 41.04 and 99.98 m bgl. All data are presented on an integrated calcareous nannofossil and planktonic foraminiferal biostratigraphy, based on the biostratigraphic schemes and calibrations of Wade et al. (2011) for planktonic foraminifera and Agnini et al. (2014) for calcareous nannofossils. All calibrated ages use the 2012 Geological Timescale (Gradstein et al., 2012), with the age-depth plot shown in Figure 8. Our study section spans ~ 8 Ma of time, from the late Bartonian (39.33 Ma) to the early Rupelian (31.23 Ma) and includes a stratigraphically continuous succession through the EOT. There is, however, a clear unconformity present between the Watu Puru and Jetis Beds within the interval ~ 86.85 to 88.02 m bgl, with an estimated time gap spanning ~ 38.59 to 36.05 Ma. The Nanggulan Formation was most likely deposited in an outer continental margin environment in proximity to a northward directed subduction zone, on the northern side of a relatively wide Indo-Pacific

Figure 2. Relative abundance (%) of ecologically important nannofossil species against age, throughout the NKK1 core. Black long dashed line indicates *Discoaster* extinction, and light gray dashed line signifies the Eocene-Oligocene boundary. Unconformity ranges from 38.59–36.05 Ma.

“gateway” (Hall, 2012). In this scenario, the paleolatitude of the site during the late Eocene would have been similar to today at $\sim -6.5^{\circ}\text{S}$ (Figure 1, redrawn after Hall, 2012).

Samples were prepared using the “simple smear slide technique” after Bown and Young (1998). Examination of smear slides was completed using a transmitted-light microscope (Zeiss AxioScope at X1,250 magnification) under cross-polarized light and plane-polarized light. Digital imaging was undertaken with a QImaging camera and the QCapture Pro 7 imaging software. Nannofossil assemblages were recorded quantitatively using the extended count technique (Bown & Young, 1998) of 400 specimens. This technique was modified by incorporating an additional scan of two complete slide transects to record the presence of further rare species not observed during the extended count, which are included in total species diversity analyses. Morphometric data for reticulofenestrid coccoliths were recorded from 31 samples at roughly equal spacing through the succession. For each sample the maximum and minimum axes of more than 310 specimens of reticulofenestrid coccoliths were measured using the automated line measurement tool within the QCapture software. Due to the limitations of accurately identifying very small coccoliths with Light Microscope (LM) imaging, measurements were limited to specimens $>2\text{ }\mu\text{m}$.

3. Results

3.1. Relative Abundance

Calcareous nannofossils are abundant or common within sediments from the NKK1 cores, with preservation that is typically good in middle Eocene sediments and varies between good to excellent within the upper Eocene to lower Oligocene sediments. In the rare instances where samples have been taken from thin more sand-rich intervals, nannofossil preservation is moderate. Percent relative abundances for key taxa are shown in Figures 2 and 3 with key trends noted below.

A short succession of upper middle Eocene (Bartonian) sediments are recovered from NKK1, below the middle to upper Eocene unconformity commencing at 88.02 m bgl. Species within the *Reticulofenestra bisecta* group (*R. bisecta* $< 10\text{ }\mu\text{m}$; *Reticulofenestra stavensis* $> 10\text{ }\mu\text{m}$) dominate below the unconformity, but both decrease in abundance immediately above it (Figure 3). The *R. bisecta* group shows the most significant fall in abundance, decreasing to $<1\%$ throughout the early late Eocene, before recovering during the first stages of the EOT ($\sim 34.3\text{ Ma}$). The *Reticulofenestra reticulata* group (*Reticulofenestra isabellae*, *R. reticulata*, and *Reticulofenestra* sp. A) show differences in their abundance through the late middle Eocene to early late Eocene. *Reticulofenestra* sp. A is described as having a wide gridded central area similar to that of *R. reticulata* but is slightly smaller (medium to large placoliths) and lacks the distinct inner tube cycle present in *R. reticulata* and *R. isabellae*. *Reticulofenestra* sp. A is highest in abundance during the middle Eocene, and in this

Figure 3. Relative abundance (%) of ecologically significant nannofossil groups and species against age. Black long dashed line indicates point of *Discoaster* extinction, and light gray dashed line signifies the Eocene-Oligocene boundary.

succession is the first of the circular, gridded reticulofenestrids to appear, preceding both *R. reticulata* and *R. isabellae*. *Reticulofenestra reticulata* and *R. isabellae* are at their highest abundance within the late Eocene with *R. reticulata* being more abundant than *R. isabellae*. Immediately at the *Discoaster* extinction event (DEE), however, the group declines in abundance, and all but *Reticulofenestra* sp. A disappear, which has sporadic, potentially reworked, occurrences within lower Oligocene sediments.

Discoaster barbadiensis and *Discoaster saipanensis* show similar patterns of relative abundance (Figure 3) but with *D. barbadiensis* typically more common. In this record, both of these rosette discoaster species disappear together, although given the sample resolution there is the potential for some small offset between these extinctions—up to 6 ka, based on the age model. We assign this biohorizon to the calibrated age for the *D. saipanensis* extinction of ~34.44 Ma and use this coupled extinction as a marker for the initiation of nannoplankton diversity decline in NKK1 before the Eocene-Oligocene Boundary (EOB) which we term the DEE. Following Pearson et al. (2008), this characteristic coupled extinction of the rosette-shaped discoasters (end of biozone CNE20; Agnini et al., 2014) are used to mark the start of the EOT interval and associated biotic perturbations. This DEE coincides with a decline in the abundance of several significant species, including *Reticulofenestra isabellae* and *R. reticulata* as well as the sharp abundance decline and then loss of *D. barbadiensis* and *D. saipanensis* (Figure 2). These declines are matched by abundance increases in *R. bisecta* group, *Sphenolithus* spp., and *Sphenolithus tribulosus* through the same interval, with the *R. bisecta* group increasing back to abundances similar to those in the middle Eocene succession (~3–6%). *Cyclicargolithus floridianus* consistently dominates assemblages from both middle and upper Eocene sediments, with relative abundances typically greater than 40%. At the DEE, however, there is a sharp and sudden but transient drop in *C. floridianus* abundance, down to less than 15%. This fall in abundance appears to be compensated within the reticulofenestrids by a significant increase in the abundance of the *Reticulofenestra dictyoda* group (*R. dictyoda*, *Reticulofenestra minuta*, *Reticulofenestra moorei*, *Reticulofenestra umbilicus*, *Reticulofenestra wadeae*, and *Reticulofenestra westerholdii*), which reaches its highest values for the entire succession (Figure 3). At the DEE there is also a fall in abundance of the *Reticulofenestra lockeri* group (including *Reticulofenestra daviesii*, *Reticulofenestra filewiczii*, *R. lockeri*, and *Reticulofenestra macmillani*), with abundances that remain low until the later stages of the EOT (~33.8 Ma).

Through the EOT, key abundance trends that started at the DEE tend to continue, with further increases in *Sphenolithus* spp. and *R. bisecta* group abundances, while the *R. lockeri* group displays a full recovery during the latter part of the EOT. *Clausicoccus subdistichus* was present throughout the middle to late Eocene but increased significantly immediately after the start of the DEE. After this large spike, abundance dipped slightly before recovering and continuing to rise in the latter part of the EOT.

3.2. Principal Component Analysis and Diversity

To determine the dominant temporal trends in overall assemblage compositions, including groupings of species with similar responses to environmental forcing, a principal component analysis (PCA) was undertaken using the R software. Species of low abundance were excluded from the PCA, identified as those with a standard deviation of relative abundance across all samples of less than 0.5% (Dunkley Jones et al., 2008). Species relative abundances were then resummed to 100% and zero values replaced with nonnegative values (0.01%) prior to an additive log ratio transformation of the relative abundance data. Only the first two principal components, PC1 and PC2, are taken into consideration, representing the majority of the assemblage variability (eigenvalues of 39.8% and 19.2%, respectively, for PC1 and PC2). Taxa are ranked with respect to their PC1 and PC2 loadings in Figure 5. We identify subgroups of taxa with the greatest positive and negative loadings for PC1 and PC2: Groups 1A and 1B and Groups 2A and 2B (Figures 4 and 5). For each of these groups, we plot the summed total relative abundances of all the species within each group and show their variation through time in Figure 5, alongside PC1 and PC2 score for each sample. A cross-plot of PC1 and PC2 scores demonstrates a clear three-way separation of samples: middle Eocene (Bartonian) assemblages with strongly positive PC2 scores and slightly negative PC1 scores; late Eocene (Priabonian) assemblages with negative PC1 and PC2 scores; and early Oligocene assemblages with strongly positive PC1 scores and slightly negative PC2 scores (Figure 6). This analysis provides clear evidence for two major shifts in the calcareous nannofossil assemblages—one across the middle to upper Eocene unconformity and one at the DEE event, when PC1 scores shift from negative to positive values.

Strongly positive PC2 scores of middle Eocene assemblages reflect the presence of *Sphenolithus obtusus*, which is only present in the middle Eocene, and high abundances of *R. bisecta* and *Reticulofenestra* sp. A (Figures 4 and 5). Together these species make up Group 2A, which forms ~20% of assemblages within these late middle Eocene assemblages (Figure 5). Late Eocene assemblages are dominated (~15%) by the strongly positive PC1 scoring taxa (Group 1A) *Discoaster barbadiensis*, *D. saipanensis*, *R. isabellae*, *Umbilicosphaera protoannula*, and *Reticulofenestra reticulata* (Figures 4 and 5). Through the DEE, Group 1B taxa—*Reticulofenestra bisecta*, *Cl. subdistichus*, *S. akropodus*, and *Sphenolithus tribulosus*—increase in abundance (Figure 5). These assemblage shifts demonstrate a clear response within the entire calcareous phytoplankton community structure to the DEE event. In contrast to the shifts in assemblages coupled to the DEE, calcareous phytoplankton assemblages are relatively stable through the later, main phases of the EOT climate shift.

A total of 120 calcareous nannofossil species were observed within sediments recovered from the NKK1 borehole. To explore trends in both species and ecological diversity through the recovered succession, we plot the Shannon diversity (H) and the natural log of species richness ($\ln(S)$) in Figure 7. The difference between these two indexes is the natural log of evenness, such that when H diversity approaches $\ln(S)$ assemblages are more even, and when these two metrics diverge assemblages are more dominated by fewer taxa. The middle Eocene has the highest recorded species diversity, with relatively stable and high values of both H and $\ln(S)$. Through the late Eocene there is a steady decline in both H and $\ln(S)$ diversity, but with particular species diversity lows centered on ~35.6 and 35.3 Ma. Species and ecological diversity continue to fall following the DEE, with both metrics reaching their lowest values between the DEE and the EOB. Both metrics of diversity then recover slightly into the early Oligocene.

3.3. Nannofossil Coccolith Size

An interpolated heat map of the frequency distribution of reticulofenestrid coccolith size is shown in Figure 7, along with the mean and the 95th percentile (95%_{tile}) coccolith size—a metric which is less biased by outliers than maximum size (Chapelle & Peck, 1999). Middle Eocene assemblages have an average lith size around ~4 μm , with minimal variation, and include a high proportion (40–63%) of smaller reticulofenestrids (<3.5 μm) (Figure 7). There is a marked change in coccolith size across the middle to late Eocene unconformity, with an increase in mean coccolith size from ~4 to ~5 μm . This is mostly driven by a reduction in the abundance of very small coccoliths (<3.5 μm) in the late Eocene, from an average of 52% to <22%, although there is also an increase in the frequency of coccoliths larger than 8 μm , which is clearly visible in the heat map during intervals when the 95%_{tile} exceeds 10 μm . This trend away from small coccolith size continued from the late Eocene to the early Oligocene. The <3.5 μm coccoliths immediately preceding the DEE dominate with a percentage of >40%, but this falls to <5% after this event. The loss of this small size

Figure 4. (a) Scatter plot to show species loading scores of the ecologically important nannofossil groups for PC1 and PC2. Groups 1A and 1B are indicated vertically by orange boxes, and Groups 2A and 2B are horizontal and in blue. (b) Line graph to show the loading scores of individual species in PC1 for Group 1. Vertical gray dashed lines separate the taxa defining Group 1. (c) Line graph to show the loading scores of individual species seen in PC2; vertical gray dashed lines indicate taxa comprising Group 2.

fraction will influence mean and 95%_{tile} coccolith size, but the reemergence of taxa such as *Reticulofenestra bisecta* group, with relative abundances going from <1% before the DEE to 3% after the DEE and then >6% (Figure 3) in the early Oligocene, indicates a genuine reemergence of larger reticulofenestrid morphotypes.

Figure 5. PC score with respect to their corresponding nanofossil groups (the summed total relative abundances of all the species within a group) against age, demonstrating the ecological effects on each group moving through time. PC1 and PC2 have differing group results; the different species composing each group react according to ecological changes. Biozonation scheme after Agnini et al. (2014).

4. Discussion

The succession recovered from the NKK1 borehole allows for the reconstruction of tropical calcareous phytoplankton dynamics through the critical EOT interval. It is one of few tropical sites with continuous and good calcareous nanoplankton preservation through this time period, enabling examination of environmental drivers associated with long-term tropical phytoplankton ecosystems. The NKK1 record provides information on three key components of middle-to-late Eocene biotic and oceanographic change: first, a distinguishable transition between late middle and early late Eocene tropical phytoplankton communities that can be associated with similar changes in the Southern Ocean; second, the presence of a major community restructuring and extinction event at the very start of the EOT; and finally, determining if there is any evidence for coccolithophore cell size limitation in response to declining global CO_2 across the EOT.

Figure 6. PCA scatter plot to depict the relationship between middle Eocene samples and samples occurring above and below the *Discoaster* extinction (DE). Yellow dots indicate Middle Eocene samples; blue dots and pink dots represent above and below the DE, respectively.

4.1. Tropical Phytoplankton Evolution Through the Middle to Late Eocene

The upper middle Eocene succession of NKK1 (~39.3 Ma to 38.5 Ma) recovers sediments deposited after the Middle Eocene Climatic Optimum (MECO) but before the Middle Late Eocene Turnover (Newsam et al., 2017). Therefore, assemblage changes between the middle and upper Eocene of NKK1 should be independent of perturbations associated with the MECO but, rather, record longer-term shifts associated with global cooling across the middle to late Eocene boundary (Cramwinckel et al., 2018). Across the middle to upper Eocene unconformity, which represents a time gap of ~2.5 Ma (~38.59 to 36.05 Ma), there is a marked change in assemblages including 10 species extinctions and seven inceptions. Although it is impossible to assess the rates and timing of assemblage change during the unconformity, this interval includes the marked transition from oligotrophic to eutrophic-favoring calcareous phytoplankton assemblages in the Southern Ocean at ~36.2 Ma (Villa et al., 2013). In NKK1, there is also a clear decline in the abundance of distinct warm-water/oligotrophic taxa, such as *Coccolithus formosus*, *Discoaster* spp., and *Sphenolithus obtusus* and an increase in known

Figure 7. Heatmap, nannofossil size (%), species diversity, PC score, and SHE analysis (Species richness, diversity (H) and Evenness) diversity plotted against age. Gray dashed line represents the *Discoaster* extinction. Age calibration after Agnini et al. (2014).

colder-water eutrophs within the *R. lockeri* group (Newsam et al., 2017; Villa et al., 2008) across the unconformity (Figures 2 and 3). This change in assemblage composition is also clearly shown in the shift from strongly positive to negative values in PC2 (Figure 5). The late Eocene increase in *R. reticulata* group abundance (Figure 3), interpreted as warm to temperate eurytopic and mesotrophic taxa (Newsam et al., 2017), also supports this shift from strongly oligotrophic conditions in the late middle Eocene to more mesotrophic conditions within the late Eocene.

This shift from warm-water and oligotrophic conditions to mesotrophic in the late Eocene seen in NKK1 nannoplankton assemblages reflects long-term changes in Southern Ocean ecosystems across the late middle to late Eocene, including an increased dominance of the siliceous microplankton (Baldauf, 1992; Diester-Haass, 1995; Diester-Haass & Zachos, 2003; Diester-Haass & Zahn, 2001). Southern Ocean cooling and enhanced circulation driven by the progressive opening of the Drake Passage and Tasman Gateway in the middle to late Eocene (Goldner et al., 2014) might be the ultimate cause of these ecosystem changes, but such changes in primary production can drive strong biogeochemical feedbacks that drawdown atmospheric CO₂ and accelerate global cooling (Egan et al., 2013; Goldner et al., 2014; Zachos & Kump, 2005). These changes are consistent with increased nutrient leakage from the Southern Ocean to lower latitudes (Egan et al., 2013), driven by a combination of enhanced deep-water mixing and nutrient supply to the surface Southern Ocean and then enhanced intermediate water advection of these waters toward the tropical ocean. This observed restructuring of far-field tropical phytoplankton communities in the IPWP, during the middle to late Eocene, seems to largely be driven by this process, which dominates nutrient supply to the modern tropical oceans (Sarmiento et al., 2004).

One of the most notable signals within the NKK1 record is the near-complete loss of *R. bisecta* (abundances <1%; Figure 2) within the late Eocene, when this species is abundant in both the upper middle Eocene and recovers to high abundances in lower Oligocene sediments. Such a pattern of partial abundance decline is not easily related to the dominant trend of global cooling from the late middle Eocene to early Oligocene. A reduction in *R. bisecta* abundance is recorded from midlatitude sites in the western (DSDP [Deep Sea Drilling Project] Site 516) and eastern (DSDP Site 360) South Atlantic through the middle to late Eocene transition (Wei & Wise, 1990), but at these locations abundances remain low into the early Oligocene. Although without a complete record through the late Eocene, *R. bisecta* relative abundances reach over 30% in the earliest Oligocene of DSDP Site 366 in the western tropical Atlantic and first appear and then peak in abundance during the early Oligocene at equatorial Indian Ocean ODP (Ocean Drilling Program) Site 711 (Fioroni et al., 2015). The pattern of long-term declining *R. bisecta* abundance in middle to high latitudes through the late middle to late Eocene, followed by increased abundances in the tropics in the earliest

Figure 8. Age model for NKK1, displaying nannofossil and planktic foraminifera biostratigraphic datums with accompanying lithostratigraphic log. Bioevents after Agnini et al. (2014); datums and timescale recalibrated to GTS2012 (Gradstein et al., 2012).

Oligocene, is consistent with a “temperate-warm water” affinity (Wei & Wise, 1990; Persico & Villa, 2004), a niche which gradually shifts toward tropical locations through the middle Eocene to early Oligocene cooling. The anomaly in this pattern is the relatively high abundances of *R. bisecta* morphotypes in the late middle Eocene of the NKK1 core. This pattern could either represent a transient post-MECO response of *R. bisecta* (Fioroni et al., 2015; Wei & Wise, 1990) or imply the presence of two ecotypes—a tropical middle Eocene form and a more temperate late middle Eocene to Oligocene form—with different ecological and biogeographic ranges.

4.2. Late Eocene Impact Events and Phytoplankton Diversity

Calcareous nannofossil species diversity is variable within the late Eocene with two particular lows at 35.8 and 35.4 Ma (Figure 7). These changes in species diversity are broadly contemporaneous with the onset of the late Eocene “climate instability” in the Southern Ocean between 35.8 and 34.1 Ma (Passchier et al., 2017; Scher et al., 2014). The late Eocene also witnessed two of the Cenozoic’s largest impact events, the Popigai impact situated in the Anabar Shield of central Siberia, which generated a widely distributed microspherule strewn fields at $\sim 35.7 \pm 0.2$ Ma (Bottomley et al., 1997; Rampino & Calderia 2017), and the Chesapeake Bay impact at $\sim 35.3 \pm 0.1$ Ma that produced a tektite/microtektite strewn field across south eastern North America (Liu et al., 2009; Rampino & Caldeira, 2017). The far-field effects of the Popigai impact are recorded in the Southern Ocean ODP Sites 689 and 1090, with a clinopyroxene spherule layer and an iridium spike at circa 35.8 Ma coinciding with a decrease in benthic and bulk carbonate $\delta^{13}\text{C}$ ($\sim 0.5\%$) (Passchier et al., 2017), which is interpreted as an enhanced phase of cooling and increased productivity. In the northern midlatitudes, there is evidence for persistent postimpact environmental change within dinoflagellate and calcareous nannofossil assemblages (Coccioni et al., 2000; Vonhof et al., 2000), consistent with enhanced productivity and/or transient cooling. Although a tight correlation between the notable late Eocene minima in species diversity and these impact events is not yet possible, they are closely associated in time based on the current age model (Figure 8).

4.3. Extinction and Community Restructuring at the Start of the EOT

The most prominent ecological transition seen in NKK1 tropical calcareous phytoplankton assemblages is directly associated with the extinction of the rosette-shaped discoasters at ~ 34.4 Ma (Agnini et al., 2014; Fioroni et al., 2015). At the DEE level in the NKK1 core, extinctions of several species are coupled with a systematic shift in species dominance. Documenting this change is important because it occurs at the onset of the EOT, preceding the proposed onset of Antarctic glaciation at the first $\delta^{18}\text{O}$ step by ~ 300 kyr (Westerhold et al., 2014) and clearly indicates a major perturbation in the global surface ocean. The extinction of the rosette discoasters has long been known as one of the most important of the Cenozoic (Martini, 1971) and led the characteristic EOB extinctions of the hantkeninid planktonic foraminifera (Berggren et al., 1995) but have only recently been correlated in detail with the climate evolution of the EOT (Pearson et al., 2008). Our PCA clearly demonstrates the distinction between phytoplankton communities above and below the DEE (Figure 5), with a decrease in Group 1A (*Reticulofenestra reticulata*, *R. isabellae*, *Reticulofenestra* sp. A, *D. saipanensis*, *D. barbadiensis*, and *U. protoannula*) and increase in Group 1B (*R. bisecta*, *S. akropodus*, and *S. tribulosus*) taxa across this event (Figures 2 and 3). Given the ecological associations of these taxa, we argue that this change in PC1 is primarily driven by a shift from strongly oligotrophic to more mesotrophic conditions. The most rapid fall in species diversity is directly associated with the DEE, including the loss of several ecologically important taxa (Figure 7) (*D. barbadiensis*, *D. saipanensis*, *Reticulofenestra* sp. A, *R. reticulata*, *R. isabellae*, and *R. reticulata*). Almost all of these abundance shifts are remarkably similar, in timing and nature, to those recorded at ODP Site 711 in the equatorial Indian Ocean (Fioroni et al., 2015), indicating a regional, basin-wide response. This is supported by the timing of the major assemblage shifts in the western tropical Indian Ocean, which are also focused on the DEE and substantially lead the “first step” of the EOT climate transition (Dunkley Jones et al., 2008). The nature of these assemblage shifts

and the DEE event points toward a global-scale increase in nutrient supply to the tropical and subtropical surface ocean at the onset of the EOT.

The last occurrence of *R. reticulata* in NKK1 occurs just before the DEE at ~34.5 Ma, in a similar position to that recorded in equatorial Indian Ocean ODP Site 711 (Fioroni et al., 2015). This event is known to be diachronous across latitudes (Berggren et al., 1995), with calibrated ages of 35.29 Ma in the subtropics (Agnini et al., 2014; updated to GTS 2012, Gradstein et al., 2012) and between 36.5 and 36.3 Ma in the high latitudes (Persico et al., 2012; Villa et al., 2008). The last occurrence of *R. isabellae* (or *Cribrocentrum isabellae*), is coincident with the last occurrence of *R. reticulata* in NKK1, and both forms show parallel fluctuations in abundance through the late Eocene. Both species are absent across a short interval just below the DEE, between 64.55 and 61.75 m bgl, with their final occurrence recorded at 61.57 m bgl, or ~10 kyr before the DEE (biozone CNE20; Agnini et al., 2014). These trends strongly suggest that, in the NKK1 assemblages at least, *R. isabellae* are simply large morphotypes of *R. reticulata*. These findings are similar to the abundance variations of these two taxa, including a coincident last occurrence, found by Fornaciari et al. (2010). There are two potential interpretations of the proximity of top *R. reticulata* to top *D. saipanensis* in NKK1; either there is a substantial slowdown or cessation of sedimentation at this level or the known latitudinal diachroneity of the top *R. reticulata* between the high and midlatitudes continues to the low latitude oceans, where this species persists the longest. This event is calibrated to occur at 36.3 and 36.5 Ma at Southern Ocean ODP Holes 784B (Villa et al., 2008) and 689D (Persico et al., 2012), respectively. At middle and low latitudes (IODP Sites: 1218, 1051, 1052, and 1262; DSDP Site 522 and Cicogna and Possagno sections), Agnini et al. (2014) calibrate the bioevent at 35.29 Ma, making it clearly diachronous across latitudes. Given the coherency of the independently derived planktonic foraminiferal and calcareous nannofossil biostratigraphies (Figure 8), most consistent with continuous sedimentation through upper Eocene successions of NKK1, we suggest the most likely resolution of the clear offset of the top *R. reticulata* biohorizon is latitudinal diachroneity in this bioevent.

The peak in the abundance of the *R. dictyoda* group at the DEE, to over 60% of the assemblage, with a simultaneous decrease in the otherwise abundant *Cyclacargolithus floridianus*, indicates a transient change in communities associated with this event. *Reticulofenestra minuta*, a major component of this *R. dictyoda* group excursion, is suggested to be a cooler-water eutroph and an opportunist (Newsam et al., 2017; Wade & Bown, 2006) unlike *C. floridianus* which dominates in late Eocene and Oligocene low- and middle-latitude assemblages (Dunkley Jones et al., 2008; Wei & Wise, 1990). The switch in dominance between these two taxa is consistent with a significant but transient eutrophication of tropical surface waters, accounting for the final demise of the Paleogene rosette-shaped discoasters. We argue for a nutrient rather than temperature control on these assemblage changes because there is no evidence for global or regional surface water cooling at this time. For example, planktonic foraminiferal Mg/Ca records from the western Indian Ocean show no sea surface cooling associated with the nannofossil species turnover of the DEE at 34.44 Ma, with any cooling linked to the first step of the EOT at ~34 Ma (Lear et al., 2008). The cause of increased nutrient supply to the tropical oceans at ~34.4 Ma is uncertain, but new data from the continental margin of East Antarctica indicate the development of ephemeral mountain glaciers from 35.9 Ma with a major ice sheet advance at 34.44 Ma (Passchier et al., 2017). Silicon isotopes also show increased nutrient leakage out of the Southern Ocean during the late Eocene (Egan et al., 2013), a process which may have increased with the cooling of Southern Ocean waters once the East Antarctic Ice Sheet (EAIS) reached the continental margin (Passchier et al., 2017).

4.4. CO₂ Control on Phytoplankton Size Across the EOT

There is increasing evidence that the long-term decline in atmospheric CO₂ concentrations through the Cenozoic is a significant driver of calcareous nannoplankton macroevolution and cell physiology (Bolton & Stoll, 2013; Bolton et al., 2012, 2016). Within the Neogene, declining atmospheric *p*CO₂ reduced aqueous [CO₂] within the surface ocean (Bolton & Stoll, 2013) and caused a reallocation of bicarbonate ions (HCO₃[−]) from coccolithophore calcification to photosynthesis (Bolton & Stoll, 2013). Two robust lines of evidence exist: first, the onset of large size-dependent coccolith $\delta^{13}\text{C}$ vital effects (Bolton & Stoll, 2013) and second, a systematic reduction in coccolith size and mass (Bolton et al., 2016; Suchéras-Marx & Henderiks, 2014). Both strongly support this change in cellular carbon allocation from the late Miocene onward. On longer timescales, the presence of very large coccolith taxa during the high *p*CO₂ and warm climates of the early

Plate 1. A selection of middle Eocene to lower Oligocene calcareous nannofossils from borehole NKK1.

to middle Eocene (Hendriks & Pagani, 2008), together with the clear patterns of Eocene to Oligocene cooling (Cramer et al., 2011; Lear et al., 2004; Liu et al., 2009; Zachos et al., 2001, 2008) and declining $p\text{CO}_2$, poses the question of whether Paleogene nannofossil macroevolution was also strongly controlled by $p\text{CO}_2$. Some studies of coccolith size do indicate a loss of large coccoliths across the EOT and infer this to be driven by cell size limitation with declining $p\text{CO}_2$ (Bordiga et al., 2015) Plate 1.

The new reticulofenestrid size records presented here show no increased dominance of smaller coccoliths with declining $p\text{CO}_2$ across the EOT (Pagani et al., 2011; Pearson et al., 2009). These records come from the tropical IPWP, a region with the lowest DIC concentrations in the modern system and where algal communities experience the strongest carbon uptake limitation. In the NKK1 record we observe an *increase* in both the mean and 95%_{tile} reticulofenestrid coccolith size across the EOT with a shift toward the dominance of larger species such as *Reticulofenestra umbilicus*, *R. bisecta*, and *R. stavensis* and a notable loss of small reticulofenestrids ($<3.5\ \mu\text{m}$; Figure 7). These coccolith size records provide no evidence for a significant $p\text{CO}_2$ limitation on cell size across the immediate EOT. This is not to say that there is no longer-term $p\text{CO}_2$ control on coccolithophore cell size through the Paleogene, as by the late Eocene the very large early to middle Eocene taxa are mostly absent. In other words, the cell size distribution present during the late Eocene appears to have been insensitive to $p\text{CO}_2$, but this cell size distribution might have already been strongly selected by earlier cooling and $p\text{CO}_2$ declines between the middle and late Eocene (Gibbs et al., 2018; Hendriks & Pagani 2008).

5. Conclusion

Our data provide the first recorded response of IPWP calcareous phytoplankton communities to global cooling from the late middle Eocene to early Oligocene. We interpret assemblage changes and the progressive loss of species through this interval to be a direct response to enhanced nutrient supply to tropical surface waters from Southern Ocean-sourced subthermocline waters. Community restructuring and extinctions were most intense across the extinction of the rosette-shaped discoasters, *D. barbadiensis*, and *D. saipanensis* at ~34.4 Ma. The nature and timing of these assemblage changes are shown to have consistent features between globally distributed locations, including the extinction of warm-water oligotrophs and the increased dominance of eutrophic and/or those with temperate- and cool-water affinities. The DEE event is also the earliest biotic response to the large-scale environmental changes of the EOT, occurring substantially before the planktonic and benthic foraminiferal extinctions at the EOB. In contrast, there is relatively little change in calcareous phytoplankton communities across the EOB. Overall, our results indicate a substantial increase in nutrient supply to the tropical oceans at the very start of the EOT, potentially associated with either increased continental weathering or nutrient leakage from the Southern Ocean. Whether these perturbations at the start of the EOT are a result of the early stages of Antarctic ice sheet expansion or a potential biogeochemical trigger for CO_2 drawdown and ice sheet growth is yet to be determined. We show that coccolith size (mean and 95%_{tile}) increases through the EOT interval, with the pronounced loss of smaller reticulofenestrid morphotypes. Over the DEE the switch in dominance of smaller to larger cell size is rapid. As a result, we interpret that there is no obvious or significant $p\text{CO}_2$ limitation on cell size in NKK1 through the EOT but perhaps instead a longer-term $p\text{CO}_2$ control on coccolithophore cell size exists through the Paleogene.

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