Palaeogeography, Palaeoclimatology, Palaeoecology 680 (2025) 113350

Contents lists available at ScienceDirect

Palaeogeography, Palaeoclimatology, Palaeoecology

journal homepage: www.elsevier.com/locate/palaeo

Intra-annually-resolved sea surface temperature variability at the onset of the Oligocene icehouse based on *Nummulites* geochemistry

Laura J. Cotton[a,*], David Evans[b,c], Max Fursman[c,d], Wolfgang Müller[c,d], Willem Renema[e], Paul N. Pearson[f,g]

[a] Natural History Museum Denmark, Gothersgade 130, 1123, Copenhagen K, Denmark
[b] School of Ocean and Earth Science, University of Southampton, Southampton, SO14 3ZH, UK
[c] Frankfurt Isotope and Element Research Center (FIERCE), Goethe University Frankfurt, Frankfurt am Main, Germany
[d] Institute of Geosciences, Goethe University Frankfurt, Frankfurt am Main, Germany
[e] Naturalis Biodiversity Center, Darwinweg 2, 2333, CR, Leiden, Netherlands
[f] School of Earth and Environmental Sciences, Cardiff University, Cardiff, CF10 3AT, UK
[g] Department of Earth Sciences, University College London, Gower Street, London WC1E 6BT, UK

ARTICLE INFO

Editor: Dr. Howard Falcon-Lang

Keywords:
foraminifera
subannual
climate change
Nummulites
Oligocene
inter-annual
Mg/Ca

ABSTRACT

Corals, otoliths, molluscs, and foraminifera all produce growth-banded shells, which can be subsampled to produce records of intra-annual variation in Earth's past, including seasonality. However, foraminifera remain under-utilised for this purpose, with only a handful of studies to date. In particular, the larger foraminifera, which live for several months or more, remain a largely untapped archive of past intra-annual changes. Here we use laser ablation ICPMS to generate continuous Mg/Ca records along the spiral whorl of *Nummulites* from the late Eocene and early Oligocene of Tanzania. Using in situ temperature logger data in a modern tropical setting, the intra and inter-test variability of this Mg/Ca palaeothermometer was calibrated utilising corresponding Mg/Ca profiles from the related modern species *Heterostegina depressa*. Eocene *Nummulites* proved affected by diagenesis and could not be used for reconstructions. However, nine Oligocene specimens showed excellent preservation enabling us to generate records of intra-test Mg/Ca variability, and transfer this to an estimate of intra/inter-annual palaeotemperature variability using the relationship between these parameters determined from our modern sample site. Our results constrain a mean annual temperature of 29.7 ± 3.9 °C, comparable with the oxygen isotope and TEX_{86} sea surface temperatures in previous studies from Tanzania, and intra/inter-annual temperature variability of ±2.3–3.0 °C. This is similar to both modern values for the region and sparse existing Oligocene seasonal data from the US. Our records thus contribute to unravelling Oligocene climate, and highlight the potential of larger foraminifera in filling the key seasonality gap in our understanding of past climates.

1. Introduction

Intra-annual temperature variation, including seasonality (intra-annual variability with clearly resolvable cyclicity), is a key parameter in the modern ocean, for example, exerting a primary control on species distributions, biological productivity, ocean currents (or vice versa), and the growth of sea ice (e.g. Eayrs et al., 2019; Stuart-Smith et al., 2017; Lisovski et al., 2017; Loubere and Fariduddin, 1999). It is therefore more than likely intra-annual fluctuations in temperature and the associated changes that they drive also had such an influence in the past. However, there remain relatively few studies that have successfully reconstructed intra-annual variation in the geological record. This is therefore a major gap in our understanding of the evolution of the Earth system, given the critical role that seasonality may play in abrupt climate change (Denton et al., 2005) as well as the processes mentioned above. Generating such records is key, not only to understanding the climate dynamics of intra-annual variation in a higher CO_2 world, but also for understanding patterns of past and present biotic responses to climatic change.

Over the last few decades, the advent and development of quantitative geochemical tools that potentially facilitate the reconstruction of

* Corresponding author.
E-mail addresses: laura.cotton@snm.ku.dk (L.J. Cotton), D.Evans@soton.ac.uk (D. Evans), w.muller@em.uni-frankfurt.de (W. Müller), willem.renema@naturalis.nl (W. Renema), pearsonp@cardiff.ac.uk (P.N. Pearson).

https://doi.org/10.1016/j.palaeo.2025.113350
Received 17 March 2025; Received in revised form 11 July 2025; Accepted 14 October 2025
Available online 16 October 2025
0031-0182/

intra-annual changes in temperature have led to a variety of fossil organisms being used for these purposes. In particular, molluscs, otoliths, foraminifera, and corals, all of which sequentially secrete growth-banded calcium carbonate, have been sub-sampled for their stable and clumped isotopes, and trace element composition. The heterogeneities in these analyses have been observed in terms of seasonality or intra-annual variation throughout the Cenozoic (e.g. Purton and Brasier, 1999; Ivany et al., 2004a; Evans et al., 2013; Warter et al., 2015; de Winter et al., 2017; Kniest et al., 2024; see Ivany and Judd, 2022 for a review). Many of these studies focus on individual or few specimens, partly due to the laborious nature of the work and the requirement of exceptional sample preservation for such studies, which means that few studies have been replicated and there is an overall sparsity of data (Ivany and Judd, 2022). In addition, calibration of quantitative geochemical tools in extinct organisms is frequently a source of uncertainty, although much work characterising molluscs has been undertaken (e.g. Jones, 1983; Warter et al., 2018; de Winter et al., 2021, 2023).

One potential source of intra-annual records that remains under-explored are the (larger) foraminifera (Purton and Brasier, 1999; Evans et al., 2013; Fehrenbacher et al., 2024). Larger foraminifera are an informal group of foraminifera based on complex internal structures linked to the hosting of symbionts, and, to some extent, size. The largest specimens have been known to reach over 10 cm in diameter and lived up to several years (Ferràndez-Cañadell, 2012), although many examples are just a few millimetres in size and presumably had shorter lifespans. Larger foraminifera occur throughout the Cenozoic and were especially abundant within the Eocene. Since there are extant close relatives to some of the most abundant Eocene larger foraminiferal genera (e.g. *Nummulites*), this has enabled the calibration and interpretation of geochemical data with a relatively low degree of uncertainty (e.g. Evans et al., 2013), and thus the reconstruction of near-surface ocean conditions deep in the geologic record. Observations of modern relatives of the Eocene *Nummulites* show that one species adds chambers at a rate of 2–3 chambers per week, thus implying that months or years of environmental variability may be recorded deep in the fossil record given the size of (e.g.) Eocene *Nummulites*.

Despite the importance of reconstructing past changes in seasonality and intra-annual variation, only ~750 specimens have been analysed for this purpose across all of Earth history (Ivany and Judd, 2022), a small fraction of which were benthic foraminifera (compared to ~50 % based on bivalve schlerochemistry/schlerochronology and ~ 75 % derived from molluscs). The small number of studies that do utilise foraminifera build on the work of Wefer and Berger (1980), who demonstrated the viability of shell chemistry-derived seasonal records by subsampling the annular rings of modern *Marginopora* and *Cycloclypeus* for their stable isotope composition, showing that intra-annual variability/seasonality are indeed recorded in larger foraminifera. Purton and Brasier (1999) applied this concept to the middle Eocene using *Nummulites laevingatus* from the south of the UK, taking samples with a microdrill every 5–10 chambers and interpreting the results to represent six seasonal cycles within the lifespan of the foraminifera. However, obtaining samples via microdrill is time consuming, has a spatial (and therefore temporal) resolution limited by the size of the drill bit, and is challenging in that it can be difficult to avoid accidental sampling of ontogenetically younger lamelli beneath the target area. To avoid these issues, Mg/Ca may be used as an alternative palaeotemperature proxy (e.g. Nürnberg et al., 1996), which is based on the thermodynamically-driven increasing substitution of Mg^{2+} for Ca^{2+} in the calcite lattice at higher temperature (Lea et al., 1999; Evans et al., 2015) and has the advantage of being only weakly sensitive to possible salinity changes (Hönisch et al., 2013; Hauzer et al., 2021). In the symbiont-bearing benthic nummulitid foraminifera, the proxy has the additional benefit of being incorporated to a degree that is very similar to inorganic calcite precipitated from seawater (Evans et al., 2018), that is, unlike their planktonic counterparts, these species do not appear to exert a strong biological control over shell chemistry (see Hauzer et al., 2025 and references therein). Utilising laser ablation ICPMS to produce a continuous profile along the marginal cord (the growth axis of these organisms, around the whorl) Evans et al. (2013) analysed 26 *Nummulites* specimens from the middle Eocene (Bartonian) of Java. By comparison to extant *Operculina*, enabling calibration of the Mg/Ca-temperature relationship in this group of foraminifera (Evans et al., 2015), the data demonstrated a greater-than-modern Eocene seasonal variation of 5–6 °C at this location.

Here we provide reconstructions of inter and intra-annual temperature variability for the earliest Oligocene based on LA-ICPMS Mg/Ca analysis of 20 specimens of *Nummulites* from Tanzania (Fig. 1). The Tanzania Drilling Project (TDP) recovered a series of cores with complete or near complete recovery of an approximately 2 million year interval across the Eocene-Oligocene transition (EOT) from the Kilwa region in coastal Tanzania (Nicholas et al., 2006; Pearson et al., 2008). The EOT is a major Earth system shift that was associated with a global decrease in temperature, increase in Antarctic ice cover and changes in ocean circulation, precipitation, weathering, and biotic overturning (e.g. Coxall and Pearson, 2007; Hutchinson et al., 2021). However, little is known about the changes in intra-annual temperature variation at that time, with early Oligocene reconstructions available from a handful of locations worldwide (Ivany et al., 2000; Eldrett et al., 2009). The micro and nannofossils from the TDP cores show exceptional preservation, and include small sized *Nummulites* from both before, during and after the transition (Cotton and Pearson, 2011; Koorapati et al., 2025). In addition, we pair and calibrate these palaeontological data with analyses of modern *Heterostegina* (Fig. 1) from the Spermonde Archipelago that grew in an area covered by temperature data loggers in order to ground-truth the transformation of intra-shell Mg/Ca heterogeneity to environmental variability. This modern-palaeo comparison allows us to assess the minor and major fluctuations in the Mg/Ca and interpret variations in temperature from a barely studied time interval, and highlights the potential of nummulitid larger foraminifera as archives capable of functioning as archives of past intra-annual temperature variability.

2. Material and methods

2.1. Modern *Heterostegina* samples and preparation

Modern *Heterostegina depressa* were picked from surface sediment samples in 2010 from several islands within the Spermonde Archipelago, southwest Sulawesi: Pulau Langkadea, Pulau Lumulumu and Pulau Pajenekang situated between 4.58°S and 4.55°S (Girard et al., 2022). The *Heterostegina* were picked from the sediment based on test colour for

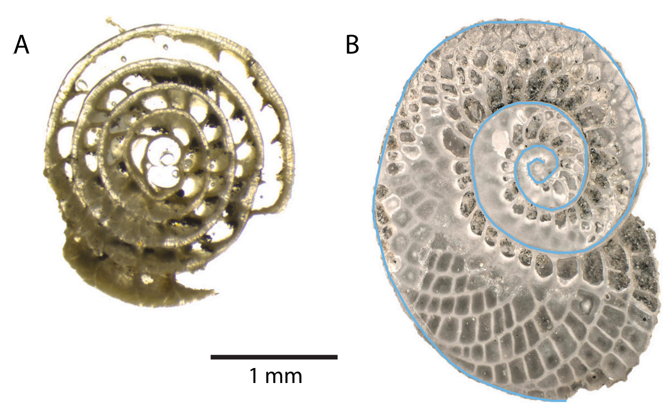

Fig. 1. Examples of foraminifera used in the study: A) fossil *Nummulites* from Tanzania, sample 17–16-2 (9); B) modern *Heterostegina depressa* from the Spermonde Archipelago, laser ablation path along the marginal cord is highlighted.

the work of Girard et al. (2022), and were therefore live or recently live at the time of collection. In order to compare shell geochemistry to in situ temperature, and to complement longer, lower resolution datasets (e.g. Teichberg et al., 2018) 20 dataloggers were placed across the collection areas (see Section 2.4). While we cannot unambiguously relate time-resolved shell geochemistry to specific monitored environmental change over the lifespan of the foraminifera, we note that the degree of inter and intra-annual temperature variability is likely to be broadly consistent between years. Given that we principally use these samples to validate the conversion of nummulitid foraminifera Mg/Ca heterogeneity to temperature variability, we consider the fact that we do not know the precise months in which these foraminifera calcified to be a minor source of uncertainty in our analysis.

Modern *H. depressa* were oxidatively cleaned to remove remnant organic material by placing the specimens into dilute (~1 %) H_2O_2 overnight, with a 1 min ultrasonication step at the start to ensure no air bubbles remained in the chambers. The oxidative cleaning solution was removed via four rinsing steps in ultrapure (18.2 MΩ cm) water, with at least ~30 s ultrasonication each time, following which the samples were dried in centrifuge tubes. Specimens were subsequently sectioned to expose the marginal cord by embedding in epoxy resin and polishing using successively finer-grained polishing papers.

2.2. Eocene-Oligocene *Nummulites* samples

Site 17 of the Tanzania Drilling Project was drilled in 2004 and is located at UTM 37 L; 560,539 8,984,483 close to the town of Pande on the Tanzanian coast (e.g. Nicholas et al., 2006; Cotton and Pearson, 2011). The Site recovered 125.9 m of sediments spanning approximately 2 million years from the Upper Eocene to Lower Oligocene and containing an apparently complete record of the EOT (Pearson et al., 2008; Wade and Pearson, 2008; Lear et al., 2008). The palaeolatitude is 18.4°S, calculated using paleolatitude.org with the palaeomagnetic reference frame of Vaes et al. (2023) and the modern site location of 8.85°S, 39.63°E.

Residues previously prepared for the studies of Pearson et al. (2008), Wade and Pearson (2008) and Lear et al. (2008) were used. These consisted of half round samples approximately 10 cm in length that were washed through a 63 μm sieve and dried in a low temperature oven. *Nummulites* are relatively common in these samples (see Cotton and Pearson, 2011) and were picked with a paintbrush under a stereomicroscope. The *Nummulites* were prepared as equatorial thin sections, by attaching to a slide using Lakeside 70 cement and grinding with fine polishing paper. A total of 20 specimens were analysed by laser-ablation ICPMS: Ten from the Oligocene, four from close to the Eocene/Oligocene boundary and six from the Eocene.

2.3. Laser-ablation ICPMS trace element analysis and data quality

Prior to analysis, the samples were subjected to a cleaning step to remove contamination from the sectioning/polishing procedure and possible remnant clays in the case of fossil material. All resin mounts were ultrasonicated for several minutes in ultrapure H_2O, with at least three water replacements and rinsing steps during this process, followed by a final ultrasonication step in trace metal-grade ethanol. Samples were subsequently left to dry overnight in a class 100 laminar flow hood.

Fossil *Nummulites* were analysed in the Department of Earth Sciences, Royal Holloway University of London (RHUL) using the RESOlution M-50 prototype laser ablation system (Müller et al., 2009) connected to an Agilent 7500ce ICPMS (Evans et al., 2013). Modern *H. depressa* were analysed at the Frankfurt Element and Isotope Research Center (FIERCE) in the Institute of Geosciences at Goethe University Frankfurt using a RESOlution S-155 laser ablation system connected to a ThermoFisher Scientific Element XR sector field mass spectrometer. We describe the instrumental analytical details for each system separately here (laser ablation parameters, data quality) and in the supplementary materials (gas flow rates, plasma power, etc.), whereas the data processing procedure is common to both laboratories.

In both cases, the marginal cord was analysed by tracking the laser across the sample surface, using a 34 μm diameter laser beam, 25 Hz laser repetition rate, 1 mm/min scan speed, and ~ 3 J/cm^2 fluence in the case of the fossil samples, and 33 μm, 15 Hz, 0.36 mm/min, and 6 J/cm^2 in the case of the modern samples. In both cases the sample surface was further pre-cleaned by scanning the laser over the path to be analysed before data acquisition, using 57 μm, 40 Hz, 3 mm/min, and 50 μm, 20 Hz, 3.6 mm/min, respectively.

In both laboratories, monitored masses included ^{11}B, ^{24}Mg, ^{25}Mg, ^{27}Al, ^{43}Ca, ^{55}Mn, ^{88}Sr, ^{89}Y, and ^{138}Ba, with Al, Mn, and Y analysed to assess potential μm-scale diagenesis and contamination (Evans et al., 2013; overall preservation is best assessed using textural information and the absolute Mg/Ca and Sr/Ca values, see Section 3). The internal standard was ^{43}Ca in both cases, primary standardisation was performed using the NIST SRM610/612 glasses, and trace element data quality was assessed using the MPI-DING glasses GOR132-G and GOR128-G, selected because they have a Mg/Ca broadly comparable to the high-Mg calcite samples analysed here. Data processing followed standard procedures (Heinrich et al., 2003) using an in-house Matlab script and is described in detail elsewhere (Evans and Müller, 2018). Briefly, sample analyses were corrected for background analyte counts, ratioed to ^{43}Ca, and standardised to molar ratios using the mean NIST glass count rate/M ratio data (Jochum et al., 2011) within each sequence. NIST SRM612 was used as the calibration for all trace elements with the exception of Mg/Ca, which was calibrated using GOR128-G because this standard is more homogeneous with respect to [Mg] (see detailed discussion in the supplementary materials of Evans et al., 2015).

At RHUL, data quality based on repeat analysis ($n = 27$) of the MPI-DING glasses, treated as unknowns and measured in the same analytical sessions as the samples and in an identical manner was: Mg/Ca −3 ± 3 %, Al/Ca +3 ± 2 %, Mn/Ca −0.5 ± 2 %, and Sr/Ca +1 ± 3 %, where these values give accuracy±precision. Accuracy is defined here as the percent deviation from the reported value and the precision is the 2 relative standard deviation (RSD) variability of repeat analysis. In all cases, these values represent the best data quality from the two standards on the assumption that poorer data are an artefact of uncertainties in the reported values (Evans and Müller, 2018).

In the FIERCE laboratories, data quality was based on 22 analyses of the same MPI-DING glasses as well as the nanopellet versions (Garbe-Schönberg and Müller, 2014) of three $CaCO_3$ reference materials (JCp, JCt, MACS-3), analysed in an identical manner to the samples. Averaged across all five standards, Mg/Ca, Al/Ca, Mn/Ca, and Sr/Ca accuracy was 0 %, +7 %, −1 %, and + 1 % respectively, while Mg/Ca accuracy based on the GOR glasses alone was −2.6 %. Precision (2RSD of all analyses) was <3.5 % for Mg/Ca in all standards, except JCt (10 %) and 2–3 % in the case of the GOR glasses, ≤5 % for Al/Ca, ≤6 % for Mn/Ca, and ≤4 % for Sr/Ca (except GOR-132G; 8 %). Note that in the case of the GOR glasses, the concentrations of Al and Mn are far higher than in the samples, such that these estimates of data quality are not necessarily representative of the sample analyses presented here, although we stress that we use Al/Ca and Mn/Ca only as qualitative indicators of preservation/contamination.

2.4. In situ temperature logging on the Spermonde reef

The magnitude of intra and inter-annual SST variability at several reef locations on the Spermonde Archipelago was determined by placing 20 in situ temperature loggers (HOBO MX2202) on a number of different islands across the archipelago (Langkadea, Gusung Khayangan, Samalona, Badi, Lankai, Kudingarengkeke) and at several different water depths. The locations spanned the deep and shallow parts of the reef slopes as well as three reef flats and cover a range of water depths from 1 to 22 m. Data were collected between 16th January 2021 and 9th November 2022 at 5 min resolution. No logger recorded continuously during this interval, with data retrieved from the loggers intermittently and several lost during the monitoring period. For this reason, of the 3.9 $\times 10^6$ possible data points across the 20 loggers, 1.9 $\times 10^6$ are presented here.

3. Results

3.1. Intra-annual temperature variability on a modern tropical reef

The mean and range (2.5th and 97.5th percentiles) of SST averaged over all data loggers over the 21 month monitoring period was 29.5 $\pm$ 1.6 °C, in line with previous, lower-resolution measurements (e.g. 27–31 °C; Teichberg et al., 2018). The in situ temperature measurements show a high degree of coherence across the Spermonde Archipelago, with all data loggers recording similar degrees and equivalent timings of weekly to monthly scale temperature variability, irrespective of depth. Loggers placed closest to the surface are typically characterised by diurnal temperature fluctuations of ~1–1.5 °C (Fig. 2), which is not the case for those below ~10 m. Taken together, the combined dataset shows both weekly and monthly-scale excursions of 1–2 °C, with both short-term cooling (e.g. August–September 2021) and longer-term warming (November–December 2021) visible. Unsurprisingly for a tropical location, no clear seasonal trend is evident, although the yearly temperature minima occur towards the end of the dry season in both monitored years (Fig. 2). Overall, we observe intra-annual and inter-annual variability of a broadly similar magnitude (3.0 °C), and that this is approximately 2–3 times the diurnal range at water depths <10 m.

3.2. Modern Heterostegina Mg/ca variability

Fifteen specimens of *Heterostegina depressa* yielded marginal cord Mg/Ca profiles (Fig. 3), ranging in length from ~3–10 mm (~15–40 chambers), which likely reflects ~2–6 months of growth for each specimen assuming a chamber addition rate of 2–3/week (inferred from data on the closely-related nummulitid foraminifera *Operculina ammonoides*; Oron et al., 2020; Evans et al., 2013).

The mean Mg/Ca of the complete dataset, 159.0 $\pm$ 1.3 mmol/mol is within uncertainty of *Operculina ammonoides* from a nearby island on the same reef (153.1 $\pm$ 6.2 Evans et al., 2013). This adds to a body of evidence demonstrating that there are no resolvable species-specific vital effects in Mg incorporation in the nummulitid foraminifera, for example, *O. ammonoides*, *O. complanata* (Evans et al., 2015), and *H. depressa* (Raitzsch et al., 2010) all fall on the same Mg/Ca-temperature relationship, and Eocene fossil *Nummulites* sp. and *Operculina* sp. from the same interval are characterised by most proxy trace element concentrations within uncertainty (Evans et al., 2013). For this reason, we use the multi-species Mg/Ca-T slope of Evans et al. (2015) for the reconstruction of (relative) temperature changes in both Recent *H. depressa* and fossil *Nummulites*.

As previously observed in the case of *O. ammonoides* and as is well-known from many other species of low-Mg and high-Mg foraminifera, a large degree of fine-scale heterogeneity is visible that must result from physiological or biomineralisation-related processes rather than temperature (Eggins et al., 2003; Spero et al., 2015; Fehrenbacher et al., 2017; Evans et al., 2013). Specifically, we observe Mg/Ca variability on the order of $\pm$15 mmol/mol (~10 %) across distances of a few tens of micrometres around the marginal cord (Fig. 3), which is of a similar magnitude to the long-term changes that occur across several millimetres.

3.3. Fossil Nummulites Mg/ca variability

Of the 20 specimens that underwent marginal cord Mg/Ca analysis, 11 were found to be sufficiently well preserved for geochemical palaeoenvironmental analysis, of which nine were from the early Oligocene and two from the late Eocene. The remainder of the samples, all from the late Eocene were found to have recrystallised to low-Mg calcite (<30 mmol/mol) in contrast to their original high-Mg mineralogy (Cotton et al., 2020), and would yield impossible (negative) palaeotemperatures if we were to attempt to interpret these results. We stress that a continuum between well and poorly preserved samples is almost never observed when working with high-Mg calcite in exceptional preservational settings (Evans et al., 2018; Martens et al., 2022) such that it is extremely unlikely that the samples we consider to be well-preserved here fall some way along a diagenetic trend towards low-Mg calcite. Rather, in these settings, either the high-Mg primary mineralogy is preserved, or the samples quickly recrystallise to low-Mg calcite.

The small number of well-preserved samples from the Eocene means that we do not have a dataset on which we can base a statistically robust reconstruction and so, while we briefly explore the constraints that these data provide in the discussion, we caveat this with the requirement for further work before any robust conclusion can be drawn regarding late Eocene temperatures using samples such as these at this site.

The nine well-preserved Oligocene samples yield mean marginal cord Mg/Ca values of 69–86 mmol/mol, with an overall mean of 82 mmol/mol (Fig. 4). All specimens are characterised by substantial heterogeneity along the marginal cord profiles, far beyond that which can be explained via analytical noise. Specifically, we observe (multi-)millimetre-scale variability and, in some cases, quasi-periodicity with an amplitude of ~8–12 mmol/mol. We note that all specimens are also characterised by fine-scale (sub-mm) heterogeneity in the direction of the marginal cord profiles which must be related to biomineralisation processes rather than short-term environmental change, given that it is also present in specimens that experienced no external variability (see above; Evans et al., 2013, 2015).

The longer-scale variability is visible as both transient or repeating fluctuations across 1–2 mm distances (visible in the case of specimens 17–16-2 (13) and 17–16-2 (4); Fig. 4), and/or longer-term changes characterised by an overall upwards increase (17–24-3 (1) and 17–16-2

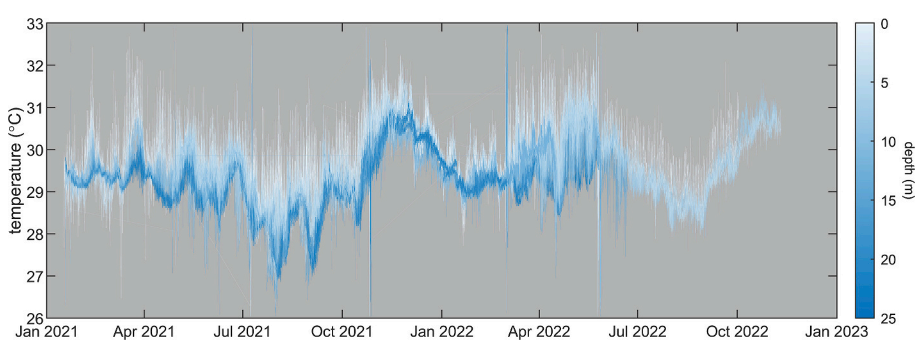

Fig. 2. Intra and inter-annual temperature variability measured using 20 individual in situ temperature loggers placed at different depths and on different islands within the Spermonde Archipelago (see Table S2 for details).

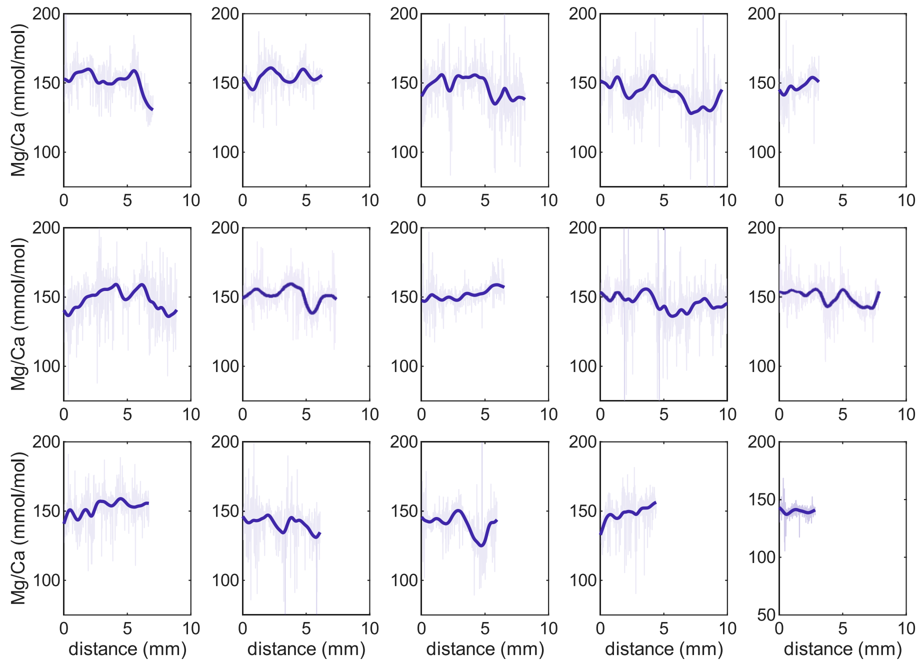

Fig. 3. Mg/Ca profiles of *H. depressa* sampled from the Spermonde archipelago, southwest Sulawesi. Light and dark lines display the measured values and smoothing spline fit, respectively.

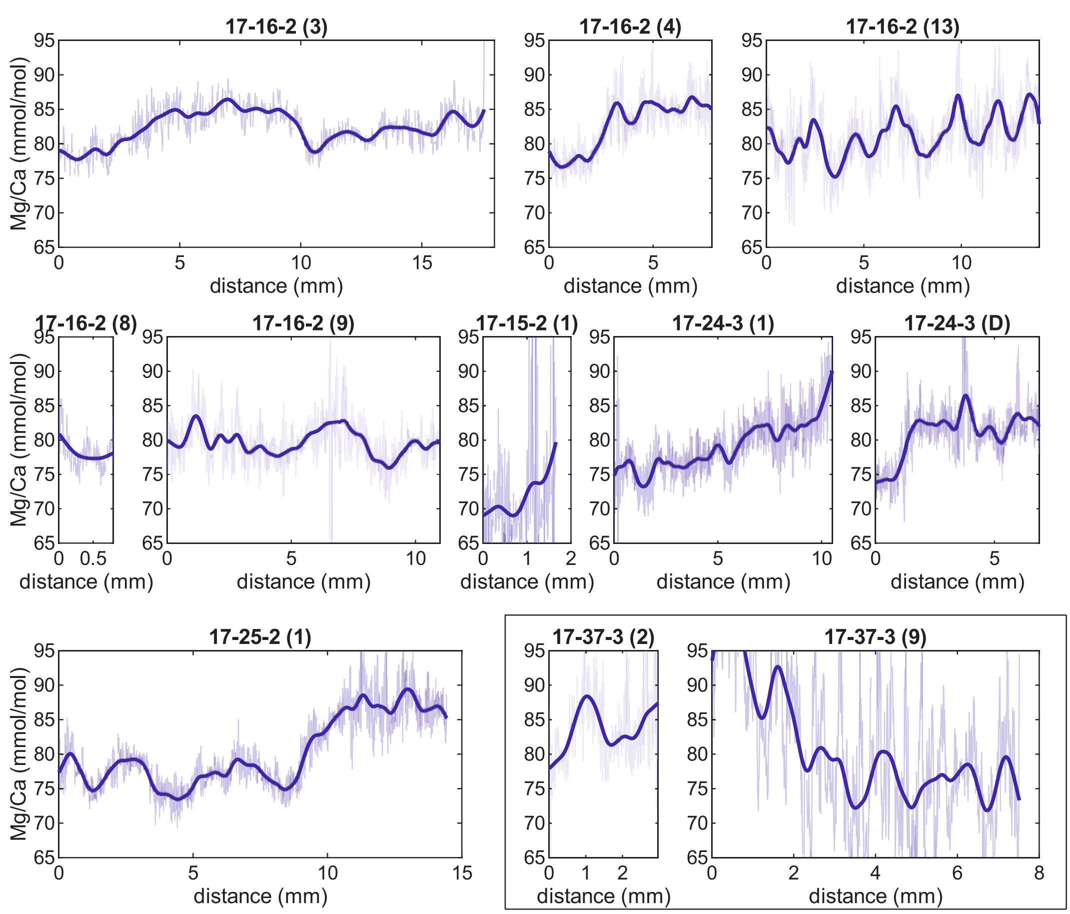

Fig. 4. Paleogene *Nummulites* Mg/Ca data. Sample names denote core interval (Site/core/m within core) followed by specimen number in parentheses. Eocene samples surrounded by a box in the lower-right corner. Note that the longest-lived specimen (17–16-2 (3)) shows the clearest seasonal trend, highlighting that the lack of clear seasonality in other specimens may be due to their sub-year lifespan. Light and dark lines display the measured values and smoothing spline fit, respectively.

(4)), while some specimens show step-like changes with an increase of ~8–10 mmol/mol over the course of a few millimetres (17–25-2 (1) and 17–24-3 (D)). The largest specimen presented here (17–16-2 (3), which has a total length of ~20 mm) has a quasi-sinusoidal Mg/Ca variability with a period of around 10 mm.

4. Discussion

4.1. Calibrating the relationship between Mg/Ca heterogeneity and SST variability

Within all *Heterostegina* specimens investigated no large sinusoidal seasonality signals are seen, which is to be expected for the tropics and is directly in line with the in situ monitoring data (Fig. 2) in which no clear seasonal signal is observed over a ~ 2 year interval, although large inter-annual temperature changes are visible. Given the magnitude of directly-measured SST variability on the Spermonde Archipelago (4 °C), we would expect medium to long-term Mg/Ca heterogeneity of ~ ± 4 % to be driven by this temperature change, using a Mg/Ca-temperature slope of 2 %/°C for this group of foraminifera (Evans et al., 2015). Taking the Mg/Ca marginal cord profiles at face value including all fine-scale (10s-μm) heterogeneity (Fig. 3) delineates a much larger Mg/Ca range and would consequently result in a much larger reconstructed intra/inter-annual temperature range, overestimating interannual variability by around 12 °C (Fig. 5A).

The simple analysis above provides clear evidence that much of this fine-scale variability cannot be attributed to environmental change. Using an average of 40 chambers/specimen for this sample, the fine-scale heterogeneity described in Section 3.2 represents calcification across a timescale of hours to around one day. The magnitude of the Mg/Ca variation in that interval is far too large to be attributed to the diurnal cycle, which is at most ~1.5 °C (Fig. 2) given the Mg/Ca-temperature slope of 2 %/°C for this group of foraminifera (i.e., a ± 15 % Mg/Ca change would require ~6 °C warming or cooling). Likewise, Hauzer et al. (2021) demonstrated a minor sensitivity of nummulitid foraminiferal Mg/Ca to salinity, with a slope of 0.75 mmol/mol per practical salinity unit, around 0.5 %/unit. The magnitude of daily or inter-annual salinity change required to explain the fine-scale Mg/Ca heterogeneity is beyond that which these foraminifera can tolerate and does not occur on this reef. Therefore, it is clear that the fine-scale (10s μm) variability should be smoothed out of the analysis before the interpretation of Mg/Ca variability in terms of temperature change. Evans et al. (2013) explored the impact of smoothing on reconstructed seasonality in detail, and ultimately concluded that a 40-point running mean represented the optimum trade-off between removing fine-scale heterogeneity and avoiding dampening of the longer-term temperature-driven information recorded in the Mg/Ca profiles. We revisit that analysis here in light of the multiple modern *H. depressa* marginal cord profiles we report, which we can compare to the in situ monitoring data from the same site. This information now allows us to empirically calibrate the degree to which Mg/Ca data like these should be smoothed before interpretation in terms of intra/inter-annual temperature variability. Specifically, we incrementally varied the smoothing parameter utilised within a smoothing spline fit to all marginal cord profiles (in Matlab: fit(x,y,'smoothingspline','SmoothingParam',smoothingFactor), where smoothingFactor is the empirically determined smoothing factor required to match the reconstructed and observed intra-annual temperature variability), and then calculated the reconstructed temperature range that would result from the smoothed data (Fig. 5), by collating all of the smoothing spline fits to the individual profiles and basing the range on the 16th and 84th percentiles (as in the modern sample calibration dataset, code available via Zenodo link in the Data Availability Statement). The smoothing parameter that resulted in a reconstructed seasonal temperature range that matches the in situ logger data (0.98) was then used in a smoothing spline fit to all fossil datasets. Applying a smoothing factor in this way assumes a broadly similar chamber addition rate between recent and fossil specimens, which we argue to be the case (Section 4.3). We note that while the methodology utilised here is quantitatively rooted in a modern dataset with comparative in situ temperature, in contrast to the approach of Evans et al. (2013) who applied a simple running mean to the marginal cord profiles reported in that publication, the resulting degree of smoothing on these samples is almost identical. As such, the analysis presented here also serves to increase the confidence of the findings of that study.

4.2. Quantitative *Nummulites* Mg/Ca-derived palaeotemperatures

The *Nummulites* Mg/Ca values were converted to temperature using the Mg/Ca-temperature and seawater-shell Mg/Ca relationships given in Evans et al. (2015; Eq. 10). In order to do so, we use an early Oligocene seawater Mg/Ca (Mg/Ca_{sw}) value of 2.45 ± 0.15 mol/mol, which is the average of the coral (Gothmann et al., 2015), ridge-flank $CaCO_3$ vein (Coggon et al., 2010), and foraminifera (Evans et al., 2018) derived estimates for the interval 34–42 Ma. Coupling this information with the mean Mg/Ca of all Oligocene specimens reported here (88.5 ± 3.7(1.2) mmol/mol; mean ± 2SD(2SE) where the average of each marginal cord

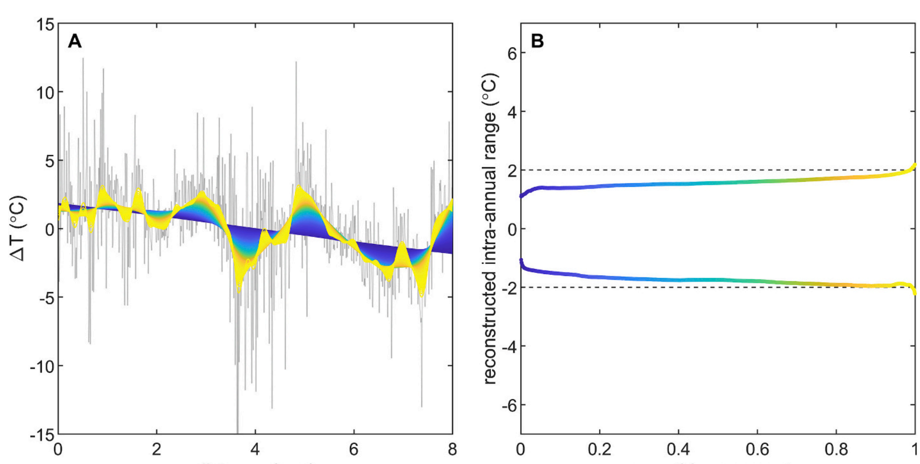

Fig. 5. Intra/interannual temperature variability smoothing parameter calibration based on 15 marginal cord profiles of *H. depressa* from the Spermonde Archipelago, compared to the known degree of variability. (A) Example marginal cord profile with smoothing spline fits, with different smoothing parameters shown as a function of colour (see panel B). (B) Reconstructed temperature variability based on all 15 profiles for a given smoothing parameter. The black dashed line shows the present day intra/interannual SST variability at the location these samples were collected.

profile was calculated before deriving the overall mean and statistics) yields an early Oligocene temperature of 29.7 ± 3.9 °C, with the uncertainty fully propagating the calibration and Mg/Ca_{sw} uncertainties as well as the 2SE variance in the measured mean Mg/Ca values. We do not include a correction for a possible differential early Oligocene versus modern salinity or seawater carbonate chemistry at this site because, in contrast to (some) planktonic and deep benthic foraminifera (e.g. Yu and Elderfield, 2008; Hönisch et al., 2013; Gray and Evans, 2019), there is no substantial salinity or (e.g.) pH effect on Mg/Ca incorporation into the nummulitid foraminifera (Hauzer et al., 2021; Hauzer et al., 2025).

Sea surface temperature records for Tanzania have been previously reported based on a variety of geochemical proxies. Specifically, the TDP 11,12, and 17 cores have yielded SST reconstructed using both stable isotopes ($\delta^{18}O$), planktonic foraminifera Mg/Ca, and at lower resolution with TEX_{86} (Lear et al., 2008; Pearson et al., 2008; Wade and Pearson, 2008). During the early Oligocene, when the *Nummulites* in this study were living, reported SST temperature values from $\delta^{18}O$ were approximately 31 °C, within uncertainty of the Mg/Ca and TEX_{86} estimates of ~29 °C (all three proxies are associated with uncertainties on the order of several °C). Our *Nummulites*-derived estimate of temperature represents near-surface conditions. While these are benthic foraminifera, modern nummulitids harbour photosymbionts and are not found beyond the base of the photic zone (Beavington-Penney and Racey, 2004), with typical peak abundance at <40 m (Renema, 2003) and the modern nearest living relative *Operculina ammonoides* found, for example, at 20 m in the northernmost Red Sea (Oron et al., 2018). This, coupled with the fact that mixed layer-dwelling planktonic foraminifera generally considered to be archives for surface conditions live at a similar depth (Schiebel and Hemleben, 2005), means that we consider the estimates presented here to approximate sea surface temperatures. Thus, SST based on exceptionally well-preserved *Nummulites*, suggests that, despite substantial cooling at this site across the EOT (Lear et al., 2008), (sub) tropical SST in the earliest Oligocene were substantially warmer than modern which is ~27 °C in this location (WOA 2018; although we note the northwards drift of Tanzania since the EOT). That this estimate is derived from an entirely different group of foraminifera, with a different shell mineralogy, compared to existing temperature records, increases the confidence in the SST estimates of the early Oligocene of Tanzania more broadly. We also note that this estimate is in good agreement with the global tropical data compilation of O'Brien et al. (2020) which yielded ~28 °C for this time interval, and the fact that, despite the transition into the icehouse world of the Oligocene, estimated atmospheric CO_2 was 2–3 times higher than pre-industrial (Pearson et al., 2009; Rae et al., 2021; CenCO2PIP, 2023)

4.3. Early Oligocene inter and intra-annual temperature variability

Comparison of the number of chambers in the analysed specimens to the chamber growth rate of closely related extant nummulitids (e.g. *Operculina* and *Heterostegina*, see above), indicates the *Nummulites* would have had a lifespan of around 10 to 30 weeks (~ 2–7 months) depending on the individual specimen. This is broadly consistent with the interpretation of the marginal cord Mg/Ca variability in terms of both weather events and longer-term intra-annual variability, and potentially explains why we observe a seasonal cycle in at least one specimen, and shorter-term heterogeneity in the majority of the rest (as in our modern sample set). We stress that this conversion is associated with considerable uncertainty (e.g. growth is nonlinear in many organisms, this is based on comparison to a different nearest living relative), such that this is only intended as an approximate assessment of the likely period of time represented in these marginal cord profiles. We also note that the structure of the marginal cord in these nummulitid foraminifera is complex, which means that a degree of time averaging is inherently present in any chemical analysis of these foraminifera. We avoid this issue by empirically calibrating the relationship between environmental variability and Mg/Ca heterogeneity (Section 4.1) but also note that this must be a minor source of complication in the interpretation of marginal cord Mg/Ca profiles, given that the slope of the Mg/Ca-temperature relationship derived from *individual* sub-sampled foraminifera from a location with in situ temperature data (coupled with the above growth rate calculation) is indistinguishable from that based on multiple whole specimens grown at different temperatures (Evans et al., 2013). This can only be the case if there is no substantial biomineralisation-related time averaging in the marginal cord on a length scale greater than that of a single whorl.

The fossil *Nummulites* specimens are characterised by fine-scale Mg/Ca variability that is similar in length scale and magnitude to modern *Heterostegina* (Figs. 3, 4) and *Operculina* (Evans et al., 2013). As discussed in the previous paragraph much of this small-scale variability (across distances of <100 μm) cannot represent environmental change and therefore must be due to internal physiological processes or those related to the effect of the biomineralisation process on the structure and composition of the test. However, like the modern samples presented here, all fossil *Nummulites* display Mg/Ca variability larger than that which can be explained by this phenomenon alone. We therefore explain these larger fluctuations as the response of shell chemistry to changes in the temperature of the seawater in which these foraminifera grew. These may be intra-annual and related to daily-monthly scale changes in shallow marine temperatures driven by wind, irradiance, and local currents, as is clearly visible in the in situ temperature logger data of a modern reef (Fig. 2) as well as in observational records from the Mozambique channel (Limbu and Kyewalyanga, 2015). However, in at least four of the *Nummulites* specimens there is a larger increase from values of around 70 mmol/mol to around 80 mmol/mol, equivalent to ±3 °C, after which Mg/Ca remains at this level until the end of the marginal cord (Fig. 4). We interpret this sustained temperature increase as a possible seasonal change in temperature. The estimate of 2–7 months lifespan, although not a full year, means that it is possible that the larger Mg/Ca shifts seen in specimens with the longer records may show part of a seasonal shift. As such, intra-annual but also possible seasonal SST variability are recorded in these samples. If seasonal, this contrasts to modern locations in the tropics, in which clear seasonal periodicity in temperature is absent (e.g. Fig. 2). This either suggests that the local/regional hydrodynamics of the region were such that seasonal changes in currents or upwelling were large enough off of the coast of Tanzania to result in substantial systematic differences in SST in different seasons (as opposed to the more transient events typical of the modern tropics) or that the study site has a palaeolatitude (18.4°S) sufficiently far south that regular seasonal changes in SST are present. In addition, we note that all four of the Oligocene specimens that show evidence of potential longer-term (seasonal) temperature changes in their marginal cord Mg/Ca profiles are characterised by a pattern of Mg/Ca increase from the ontogenetically younger to older parts of the shell. This suggests that all four specimens began growth under colder temperatures, and possibly that reproduction was aligned with, or influenced by, long-term temperature changes.

Using the calibrated relationship between the smoothing factor applied to the Mg/Ca profiles in order to remove biomineralisation/physiology-derived 'noise' and SST variability (Fig. 5), we reconstruct a total variability of ±2.3–3.0 °C during the earliest Oligocene in Tanzania. This uncertainty in the reconstructed SST variability is derived from the fact that foraminifera grown under identical conditions are typically characterised by mean shell Mg/Ca that vary on the order of a few to a few 10s percent (e.g. Sadekov et al., 2008; Evans et al., 2015). The fossil specimens presented here probably individually date to an interval spanning at least several centuries, yet we have no constraint regarding this and therefore cannot determine the degree to which the difference in mean shell Mg/Ca represents a difference in mean annual temperature between years compared to geochemical heterogeneity that would be present even if they all grew at the same temperature. To account for this, the above range of ±2.3–3.0 °C gives an estimate both with and without the inter-specimen differences in Mg/Ca subtracted out prior to the conversion of the overall dataset into SST heterogeneity (see Fig. 6C and D). The lower limit almost certainly underestimates the total range of intra plus inter-annual variability, as some of the difference in mean Mg/Ca between specimens will derive from inter-annual SST change. Conversely, the upper limit is almost certainly an overestimate because some of the pooled Mg/Ca variability will relate to inter-individual differences in Mg incorporation rather than environmental change. We cannot constrain where, within this range, the true value is most likely to lie, but note that the relatively small difference between these two endmember scenarios means that this is not a major complication in the use of nummulitid foraminiferal Mg/Ca datasets for the purposes of seasonality reconstruction.

Our reconstructed total degree of inter/intra-annual variability of ±2.3–3.0 °C is similar to that of the modern ocean in this region. For example, Muzuka et al. (2010) measured a daily variation of just under 0.5 °C and an overall increase of 1.5 °C across the month of September in Zanzibar's Chumbe and Bawe coral reefs. On the modern day Zanzibar coast, Limbu and Kyewalyanga (2015) measured a total seasonal (intrannual) variability of ±2.4 °C, while SST near the Tanzania coast is more broadly characterised by a ~ 4 °C seasonal range according to the World Ocean Atlas (Locarnini et al., 2024). In the context of these modern intra-annual temperature ranges, we find no resolvable difference between the modern and early Oligocene degree of SST variability in this region, despite the early Oligocene being characterised by an atmospheric CO_2 concentration ~ 2–3 times higher than pre-industrial (Pearson et al., 2009; Rae et al., 2021; CenCO2PIP, 2023).

Only a small number of studies reconstructing seasonal or intra-annual temperature variation have been carried out on *Nummulites*, and to our knowledge, we report the first Oligocene data derived from this archive. In the Eocene, Purton and Brasier (1999) used a microdrill to subsample a 1 cm diameter *Nummulites* specimen from the Lutetian of northwest Europe (Hampshire Basin, UK), with data collected at 5–10 chamber intervals interpreted to represent six seasonal cycles within the lifespan of the foraminifera. The analysis of Purton and Brasier (1999) showed heterogeneity in $\delta^{18}O$ of more than 2.5 ‰ in the early whorls of the *Nummulites*, which would equate to an approximately 10 °C seasonal change if interpreted purely in terms of temperature. This pioneering study demonstrated the potential of *Nummulites* for seasonality reconstruction and showed that they do record temperature variations on an intra-annual scale, however, it is now clear that these large amplitude changes typical of coastal settings likely reflect, at least in part, the seasonal influence of freshwater (e.g. Ivany et al., 2004a; Keating-Bitonti et al., 2011). Indeed, Kniest et al. (2024), applying clumped isotope analysis to molluscs samples from a broadly similar regions and time interval (working in the Paris Basin) demonstrated that around 1 ‰ (~4 °C) of this oxygen isotope variability could be attributed to freshwater flux. The similarities in environment between the shallow water, near coastal palaeoenvironments of the Bracklesham beds of southern UK and the Bartonian of the Paris Basin in France, mean that freshwater influence cannot be ruled out as an influence in the Bracklesham *Nummulites* and highlight the difficulty in interpreting $\delta^{18}O$ data alone (e.g. Judd et al., 2018). In contrast to the above studies, and using the same

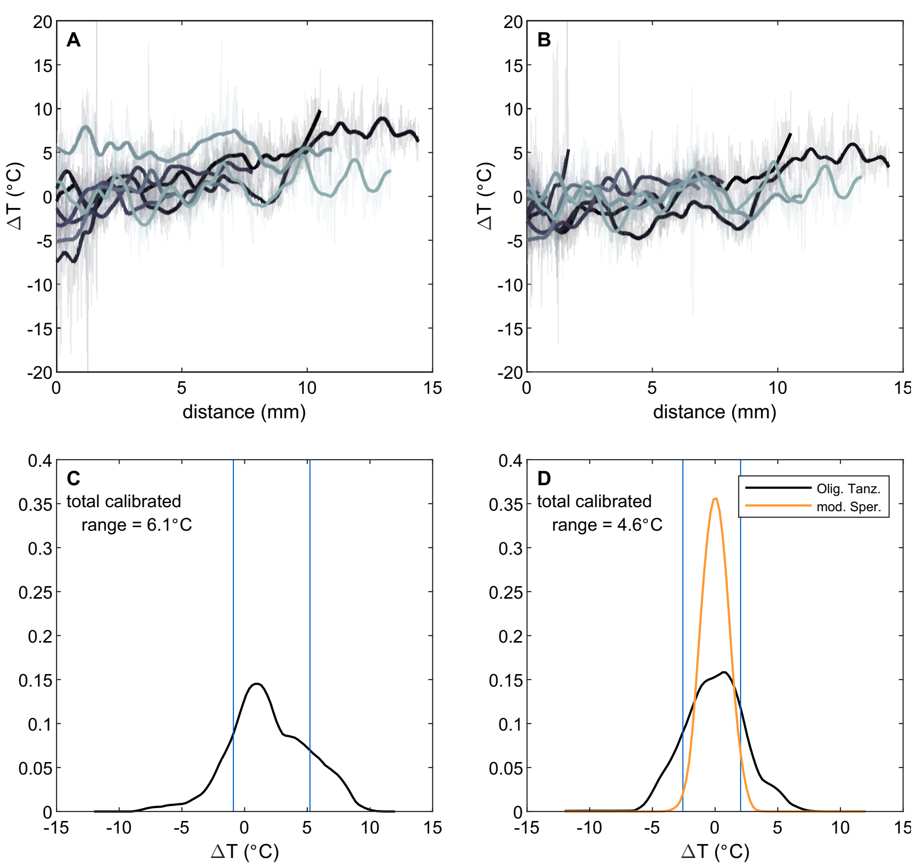

Fig. 6. Mg/Ca converted to relative temperature change for all specimens, both without (A) and with (B) normalisation of each specimen to its mean Mg/Ca value. (C,D) Probability distributions for data from all samples combined, both without and with normalisation of each specimen to its mean value. The 16th and 84th percentiles (blue lines) show the reconstructed degree of SST variability in both cases, based on the calibration of the required smoothing factor in order to accurately reconstruct modern variability using live-collected specimens shown in Fig. 5 (note that we use these percentiles as the calibration was also performed using the 1SD variance in the data). The total degree of variability (panel C) gives an upper estimate of the combined inter and intra-annual SST variability (see text for details), whereas the variability calculated relative to the mean on a sample by sample basis gives an estimate of the intra-annual variability only. The modern intra-annual variability in a tropical setting is shown for comparison in panel D, based on the in situ logger data shown in Fig. 2. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

methodology as reported here, Evans et al. (2013) applied LA-ICPMS analysis of the marginal cord Mg/Ca of *Nummulites* from the middle Eocene of Java. These mid-Eocene (39 Ma) equatorial specimens lived in a region with a higher MAT (Evans et al., 2018) and were characterised by a greater degree of intra-annual temperature change (5–6 °C) than both the Oligocene specimens reported here and the modern degree of inter/intra-annual variability in the tropics (e.g. Fig. 2). These higher-than-modern seasonality values are broadly in line with those derived from mollusc $\delta^{18}O$ from the mid-Eocene of Panama (Tripati and Zachos, 2002), while, in contrast, a similar degree of modern/Eocene seasonality has been reported from the west coast of Africa (southern Nigeria; Andreasson and Schmitz, 1998), and a lower than modern seasonality on the early Eocene US Gulf Coast (Ivany et al., 2004a). Overall, these sparse seasonality reconstructions point to a complex picture of Eocene versus modern inter-annual SST variability and, coupled with the overall sparsity of data, means that the relationship between global warmth and SST variability is not well constrained. Several studies, including two conducted in the tropics indicate a substantially increased seasonal temperature range, while other regions were seemingly characterised by a mixed response to CO_2 and/or palaeogeographic forcing.

While little is known about Eocene intra-annual temperature variation, even less work has been conducted in the Oligocene. Indeed, Oligocene climate more broadly has also been studied to a far lower degree, while existing studies have shown important discrepancies between Oligocene climate models and proxy records as well as uncertainties about the potential root cause(s) (O'Brien et al., 2020). Intra-annually -resolved records have focused almost exclusively on the Eocene-Oligocene transition (EOT), which therefore do include records from the earliest Oligocene which are broadly contemporaneous with our record Tanzanian *Nummulites* records. Specifically, oxygen isotope records derived from otoliths from the US Gulf Coast showed an increase in seasonality across the EOT driven by differential winter versus summer cooling, specifically, with winter SST in this region becoming ~4 °C cooler than in the Eocene (Ivany et al., 2000), a finding which is concordant with an assemblage-based approach in the northern high latitude (Eldrett et al., 2009), while a possible small seasonality increase was reported in central North America (Zanazzi et al., 2007). The well-preserved samples in our dataset are limited to the earliest Oligocene such that we cannot assess Tanzanian seasonality change across the Eocene-Oligocene transition. However, our results are in-line with those of Ivany et al. (2000, 2004b) which reconstruct similar early Oligocene compared to modern seasonal temperature ranges. We also note that the fact that we record no resolvable difference at our site between today and the earliest Oligocene means that if seasonality also increased in this region across the EOT, then it would add to the complex picture of the response of SST variability to both CO_2 and non-CO_2 forcing, with this, together with the evidence listed above, painting a picture of a strong regional dependence on the difference in seasonality between today and past intervals with higher CO_2 (also see de Winter et al., 2024).

5. Conclusion

Seasonal and intra-annual changes in temperature are a key climate parameter, controlling, for example, the growth, survival, and distribution of species globally, yet the relationship between seasonality and global and regional climate change is poorly known. The data presented here add to the sparse amount of intra-annually-resolved temperature information available from the Oligocene greenhouse-icehouse transitional interval, based on the spatially-resolved measurement of Mg/Ca along the growth axis of the long-lived large benthic foraminifera genus *Nummulites*.

To present the most accurate estimates of intra-annual variation to-date using this approach, we calibrated the relationship between intra/inter-test variability and intra-annual surface ocean temperature variability using a very closely related foraminifera collected in a modern tropical setting for which high-resolution in situ temperature logger data is also available. This is necessary because Mg incorporation in foraminifera is controlled by both environmental and biological factors, which we were able to fully disentangle. Specifically, we quantitatively determined the degree to which the observed fine-scale (sub-mm) Mg/Ca heterogeneity that is observed in this family of foraminifera must be removed, which nonetheless leaves a high degree of small scale fluctuation in Mg/Ca values through test growth which must reflect temperature changes in the organisms' environment.

Applying this knowledge to fossil *Nummulites* from the latest Eocene and earliest Oligocene of Tanzania provides a method of reconstructing intra-annual variation at the onset of the Oligocene icehouse that cannot be biased by seasonal changes in seawater chemistry (i.e. $\delta^{18}O_{sw}$) in nearshore environments. Nine Oligocene specimens were characterised by excellent preservation and the Mg/Ca records from these displayed heterogeneity indicative of both seasonal and shorter-scale near-surface ocean temperature changes. However, despite excellent preservation in other microfossil groups (e.g. Pearson et al., 2008) the majority of the Eocene specimens showed likely diagenetic alteration such that we were unable to determine late Eocene variability using this approach.

Quantitatively, our results constrain a greater-than-modern average temperature of 29.7 ± 3.9 °C in this region in good agreement with previous SST reconstructions for Tanzania, as well as broader global temperature reconstructions (O'Brien et al., 2020). Moreover, we constrain minimum intra-annual variability of ±2.3 °C and a maximum intra plus inter-annual variability of ±3.0 °C. This is similar to the present day variability, indicating no relationship between CO_2 and seasonality in this region, given that the icehouse conditions of the early Oligocene were nonetheless characterised by CO_2 2–3 times higher than pre-industrial, or highlighting that any CO_2 effect was masked by other factors such as palaeogeographic or circulation forcings. However, we stress that further work will be required to determine whether this is a consistent feature of the region through time, with insufficient data currently available to disentangle (e.g.) the complex interaction between seasonality, atmospheric CO_2, and the northwards drift of the African continent through time.

Previous seasonality reconstructions that are approximately coeval with that reported here based on corals and otoliths from the US Gulf region (Ivany et al., 2000, 2004b) are similarly characterised by a similar degree of seasonality to today, while a broader modern versus Oligocene comparison with mid and high latitude estimates is more complex given (e.g.) palaeogeographic changes. Moreover, the extremely small number of estimates globally means that any broader inference would be premature, although we note that there is currently no evidence for a strongly differential Oligocene versus modern seasonality. If this was indeed the case, it indicates that the atmospheric CO_2 concentration required to drive global changes in coastal seasonality is greater than that of the early Oligocene (~2–3 times pre-industrial). However, many more records across different geographic areas are needed to confirm whether this holds true.

Determining intra-annual variation from the geochemistry of organisms with incremental growth is time consuming, and exceptionally well-preserved archives are relatively rare. Here, we have shown that larger foraminifera are a potential, yet largely untapped resource that can contribute to intra-annual temperature reconstructions, and improve our understanding of palaeoclimate dynamics, particularly within the Oligocene. That these reconstructions can be based on trace element rather than stable isotope composition offers the advantage of avoiding the bias associated with temporal changes in freshwater flux in proximal locations without the need for sample and labour intensive analyses such as clumped isotope analysis.

CRediT authorship contribution statement

Laura J. Cotton: Visualization, Validation, Resources, Project administration, Methodology, Investigation, Formal analysis, Conceptualization, Writing – review & editing, Writing – original draft. **David**

Evans: Visualization, Validation, Supervision, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Conceptualization, Writing – review & editing, Writing – original draft. **Max Fursman:** Resources, Methodology, Formal analysis, Writing – review & editing. **Wolfgang Müller:** Supervision, Resources, Funding acquisition, Writing – review & editing. **Willem Renema:** Resources, Funding acquisition, Writing – review & editing. **Paul N. Pearson:** Supervision, Resources, Writing – review & editing.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

We are grateful for funding of the European Union's Horizon 2020 Marie Skłodowska-Curie grant agreement (4D-REEF, No 813360). We thank Masdar for assistance and monitoring of the data loggers in the Spermonde Archipelago. The Tanzania Drilling Project was funded by UK Natural Environment Research Council grants NE/X509345/1 and NE/B503225/1 directed by Paul N. Pearson and supported by the Tanzania Commission for Science and Technology and Tanzania Petroleum Development Corporation. LA-ICPMS instrumentation at RHUL was funded by SRIF3 (HEFCE, 2008) and NERC (NERC CC073; 2014) equipment grants. FIERCE is financially supported by the Wilhelm and Else Heraeus Foundation and by the Deutsche Forschungsgemeinschaft (DFG: INST 161/921-1 FUGG, INST 161/923-1 FUGG and INST 161/1073-1 FUGG). This is FIERCE contribution number 212.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.palaeo.2025.113350.

Data availability

All dataset and the Matlab code used to perform the data analysis and produce all data figures is available in the following Zenodo repository: 10.5281/zenodo.17384982.

References

Andreasson, F.P., Schmitz, B., 1998. Tropical Atlantic seasonal dynamics in the early middle Eocene from stable oxygen and carbon isotope profiles of mollusk shells. Paleoceanography 13 (2), 183–192.
Beavington-Penney, S.J., Racey, A., 2004. Ecology of extant nummulitids and other larger benthic foraminifera: applications in palaeoenvironmental analysis. Earth-Science Reviews 67 (3–4), 219–265.
Cenozoic CO2 Proxy Integration Project (CenCO2PIP) Consortium, Hönisch, B., Royer, D. L., Breecker, D.O., Polissar, P.J., Bowen, G.J., Zhang, L., 2023. Toward a Cenozoic history of atmospheric CO_2. Science 382 (6675) eadi5177.
Coggon, R.M., Teagle, D.A., Smith-Duque, C.E., Alt, J.C., Cooper, M.J., 2010. Reconstructing past seawater Mg/Ca and Sr/Ca from mid-ocean ridge flank calcium carbonate veins. Science 327 (5969), 1114–1117.
Cotton, L.J., Pearson, P.N., 2011. Extinction of larger benthic foraminifera at the Eocene/Oligocene boundary. Palaeogeography, Palaeoclimatology, Palaeoecology 311 (3–4), 281–296.
Cotton, L.J., Evans, D., Beavington-Penney, S.J., 2020. The high-magnesium calcite origin of nummulitid foraminifera and implications for the identification of calcite diagenesis. Palaios 35 (10), 421–431.
Coxall, H.K., Pearson, P.N., 2007. In: Williams, M., Haywood, A.M., Gregory, F.J., Schmidt, D.N. (Eds.), The Eocene–oligocene transition. The Micropalaeontological Society, Special Publications: Deep-Time Perspectives on Climate Change: Marrying the Signal from Computer Models and Biological Proxies, 2, pp. 351–387.
de Winter, N.J., Goderis, S., Dehairs, F., Jagt, J.W., Fraaije, R.H., Van Malderen, S.J., Claeys, P., 2017. Tropical seasonality in the late Campanian (late cretaceous): Comparison between multiproxy records from three bivalve taxa from Oman. Palaeogeogr. Palaeoclimatol. Palaeoecol. 485, 740–760.
de Winter, N.J., Müller, I.A., Kocken, I.J., et al., 2021. Absolute seasonal temperature estimates from clumped isotopes in bivalve shells suggest warm and variable greenhouse climate. Commun Earth Environ 2, 121. https://doi.org/10.1038/s43247-021-00193-9.
de Winter, N.J., van Sikkeleras, S., Goudsmit-Harzevoort, B., Boer, W., de Nooijer, L., Reichart, G.J., Claeys, P., Witbaard, R., 2023. Tracing timing of growth in cultured molluscs using strontium spiking. Front. Mar. Sci. 10, 1157929.
de Winter, N.J., Tindall, J., Johnson, A.L., Goudsmit-Harzevoort, B., Wichern, N., Kaskes, P., Ziegler, M., 2024. Amplified seasonality in western Europe in a warmer world. Sci. Adv. 10 (20), eadl6717.
Denton, G.H., Alley, R.B., Comer, G.C., Broecker, W.S., 2005. The role of seasonality in abrupt climate change. Quat. Sci. Rev. 24 (10–11), 1159–1182.
Eayrs, C., Holland, D., Francis, D., Wagner, T., Kumar, R., Li, X., 2019. Understanding the seasonal cycle of Antarctic Sea ice extent in the context of longer-term variability. Rev. Geophys. 57 (3), 1037–1064.
Eggins, S., De Deckker, P., Marshall, J., 2003. Mg/ca variation in planktonic foraminifera tests: implications for reconstructing palaeo-seawater temperature and habitat migration. Earth Planet. Sci. Lett. 212 (3–4), 291–306.
Eldrett, J.S., Greenwood, D.R., Harding, I.C., Huber, M., 2009. Increased seasonality through the Eocene to Oligocene transition in northern high latitudes. Nature 459 (7249), 969–973.
Evans, D., Müller, W., 2018. Automated extraction of a five-year LA-ICP-MS trace element data set of ten common glass and carbonate reference materials: long-term data quality, optimisation and laser cell homogeneity. Geostand. Geoanal. Res. 42 (2), 159–188.
Evans, D., Müller, W., Oron, S., Renema, W., 2013. Eocene seasonality and seawater alkaline earth reconstruction using shallow-dwelling large benthic foraminifera. Earth Planet. Sci. Lett. 381, 104–115.
Evans, D., Erez, J., Oron, S., Müller, W., 2015. Mg/Ca-temperature and seawater-test chemistry relationships in the shallow-dwelling large benthic foraminifera *Operculina ammonoides*. Geochim. Cosmochim. Acta 148, 325–342.
Evans, D., Sagoo, N., Renema, W., Cotton, L.J., Müller, W., Todd, J.A., Affek, H.P., 2018. Eocene greenhouse climate revealed by coupled clumped isotope-Mg/ca thermometry. Proc. Natl. Acad. Sci. 115 (6), 1174–1179.
Fehrenbacher, J.S., Russell, A.D., Davis, C.V., Gagnon, A.C., Spero, H.J., Cliff, J.B., Martin, P., 2017. Link between light-triggered Mg-banding and chamber formation in the planktic foraminifera *Neogloboquadrina dutertrei*. Nat. Commun. 8 (1), 15441.
Fehrenbacher, Jennifer S., Hupp, Brittany N., Branson, Oscar, Evans, David, Foster, Gavin L., Glock, Nicolaas, Thirumalai, Kaustubh, Wycech, Jody, 2024. Individual Foraminiferal analyses: a Review of current and emerging Geochemical Techniques. J. Foraminifer. Res. 54 (4), 312–331.
Ferràndez-Cañadell, C., 2012. Multispiral growth in *Nummulites*: paleobiological implications. Mar. Micropaleontol. 96, 105–122.
Garbe-Schönberg, D., Müller, S., 2014. Nano-particulate pressed powder tablets for LA-ICP-MS. J. Anal. At. Spectrom 29 (6), 990–1000.
Girard, E.B., Ferse, S., Ambo-Rappe, R., Jompa, J., Renema, W., 2022. Dynamics of large benthic foraminiferal assemblages: a tool to foreshadow reef degradation? Sci. Total Environ. 811, 151396.
Gothmann, A.M., Stolarski, J., Adkins, J.F., Schoene, B., Dennis, K.J., Schrag, D.P., Bender, M.L., 2015. Fossil corals as an archive of secular variations in seawater chemistry since the Mesozoic. Geochim. Cosmochim. Acta 160, 188–208.
Gray, W.R., Evans, D., 2019. Nonthermal influences on Mg/Ca in planktonic foraminifera: a review of culture studies and application to the last glacial maximum. Paleoceanography and Paleoclimatology 34 (3), 306–315.
Hauzer, H., Evans, D., Müller, W., Rosenthal, Y., Erez, J., 2021. Salinity effect on trace element incorporation in cultured shells of the large benthic foraminifer *Operculina ammonoides*. Paleoceanography and Paleoclimatology 36 (6), e2021PA004218.
Hauzer, H., Evans, D., Müller, W., Rosenthal, Y., Erez, J., 2025. The effect of carbonate chemistry on trace element incorporation in high-Mg calcitic foraminifera. Geochim. Cosmochim. Acta 390, 105–116.
Heinrich, C.A., Pettke, T., Halter, W.E., Aigner-Torres, M., Audétat, A., Günther, D., Horn, I., 2003. Quantitative multi-element analysis of minerals, fluid and melt inclusions by laser-ablation inductively-coupled-plasma mass-spectrometry. Geochim. Cosmochim. Acta 67 (18), 3473–3497.
Hönisch, B., Allen, K.A., Lea, D.W., Spero, H.J., Eggins, S.M., Arbuszewski, J., Elderfield, H., 2013. The influence of salinity on Mg/Ca in planktic foraminifers–evidence from cultures, core-top sediments and complementary $\delta^{18}O$. Geochim. Cosmochim. Acta 121, 196–213.
Hutchinson, D.K., Coxall, H.K., Lunt, D.J., Steinthorsdottir, M., De Boer, A.M., Baatsen, M., Zhang, Z., 2021. The Eocene–Oligocene transition: a review of marine and terrestrial proxy data, models and model–data comparisons. Clim. Past 17 (1), 269–315.
Ivany, L.C., Judd, E.J., 2022. Deciphering temperature seasonality in Earth's ancient oceans. Annu. Rev. Earth Planet. Sci. 50 (1), 123–152.
Ivany, L.C., Patterson, W.P., Lohmann, K.C., 2000. Cooler winters as a possible cause of mass extinctions at the Eocene/Oligocene boundary. Nature 407 (6806), 887–890.
Ivany, L.C., Wilkinson, B.H., Lohmann, K.C., Johnson, E.R., McElroy, B.J., Cohen, G.J., 2004a. Intra-annual isotopic variation in *Venericardia* bivalves: implications for early Eocene temperature, seasonality, and salinity on the US Gulf Coast. J. Sediment. Res. 74 (1), 7–19.
Ivany, L.C., Peters, S.C., Wilkinson, B.H., Lohmann, K.C., Reimer, B.A., 2004b. Composition of the early Oligocene Ocean from coral stable isotope and elemental chemistry. Geobiology 2 (2), 97–106.
Jochum, K.P., Weis, U., Stoll, B., Kuzmin, D., Yang, Q., Raczek, I., Enzweiler, J., 2011. Determination of reference values for NIST SRM 610–617 glasses following ISO guidelines. Geostand. Geoanal. Res. 35 (4), 397–429.

Jones, D.S., 1983. Sclerochronology: reading the record of the molluscan shell: annual growth increments in the shells of bivalve molluscs record marine climatic changes and reveal surprising longevity. Am. Sci. 71 (4), 384–391.
Judd, E.J., Wilkinson, B.H., Ivany, L.C., 2018. The life and time of clams: Derivation of intra-annual growth rates from high-resolution oxygen isotope profiles. Palaeogeography, Palaeoclimatology, Palaeoecology 490, 70–83.
Keating-Bitonti, C.R., Ivany, L.C., Affek, H.P., Douglas, P., Samson, S.D., 2011. Warm, not super-hot, temperatures in the early Eocene subtropics. Geology 39 (8), 771–774.
Kniest, J.F., Evans, D., Gerdes, A., Cantine, M., Todd, J.A., Sigwart, J.D., Vellekoop, J., Müller, W., Voigt, S., Raddatz, J., 2024. Spatiotemporal changes in riverine input into the Eocene North Sea revealed by strontium isotope and barium analysis of bivalve shells. Sci. Rep. 14 (1), 28806.
Koorapati, R.K., Moon, B.C., Cotton, L.J., 2025. Morphological trends in reticulate *Nummulites* across the Eocene–Oligocene transition. Palaeontology 68 (2), e70003.
Lea, D.W., Mashiotta, T.A., Spero, H.J., 1999. Controls on magnesium and strontium uptake in planktonic foraminifera determined by live culturing. Geochimica et Cosmochimica Acta 63 (16), 2369–2379.
Lear, C.H., Bailey, T.R., Pearson, P.N., Coxall, H.K., Rosenthal, Y., 2008. Cooling and ice growth across the Eocene-Oligocene transition. Geology 36 (3), 251–254.
Limbu, S.M., Kyewalyanga, M.S., 2015. Spatial and temporal variations in environmental variables in relation to phytoplankton composition and biomass in coral reef areas around Unguja, Zanzibar, Tanzania. SpringerPlus 4, 1–18.
Lisovski, S., Ramenofsky, M., Wingfield, J.C., 2017. Defining the degree of seasonality and its significance for future research. Integr. Comp. Biol. 57 (5), 934–942.
Locarnini, R.A., Mishonov, A.V., Baranova, O.K., Reagan, J.R., Boyer, T.P., Seidov, D., Wang, Z., Garcia, H.E., Bouchard, C., Cross, S.L., Paver, C.R., Dukhovskoy, D., 2024. World Ocean Atlas 2023, Volume 1: Temperature. A. Mishonov Technical Editor, NOAA Atlas NESDIS 89.
Loubere, P., Fariduddin, M., 1999. Quantitative estimation of global patterns of surface ocean biological productivity and its seasonal variation on timescales from centuries to millennia. Global Biogeochem. Cycles 13 (1), 115–133.
Martens, L., Stassen, P., Steurbaut, E., Speijer, R.P., 2022. Assessing *Nummulites* geochemistry as a proxy for early Eocene palaeotemperature evolution in the North Sea Basin. J. Geol. Soc. London 179 (4) jgs2021-102.
Müller, W., Shelley, M., Miller, P., Broude, S., 2009. Initial performance metrics of a new custom-designed ArF excimer LA-ICPMS system coupled to a two-volume laser-ablation cell. J. Anal. At. Spectrom 24 (2), 209–214.
Muzuka, A.N., Dubi, A.M., Muhando, C.A., Shaghude, Y.W., 2010. Impact of hydrographic parameters and seasonal variation in sediment fluxes on coral status at Chumbe and Bawe reefs, Zanzibar, Tanzania. Estuar. Coast. Shelf Sci. 89 (2), 137–144.
Nicholas, C.J., Pearson, P.N., Bown, P.R., Jones, T.D., Huber, B.T., Karega, A., Wade, B. S., 2006. Stratigraphy and sedimentology of the Upper Cretaceous to Paleogene Kilwa Group, southern coastal Tanzania. J. Afr. Earth Sci. 45 (4–5), 431–466.
Nürnberg, D., Bijma, J., Hemleben, C., 1996. Assessing the reliability of magnesium in foraminiferal calcite as a proxy for water mass temperatures. Geochim. Cosmochim. Acta 60 (5), 803–814.
O'Brien, C.L., Huber, M., Thomas, E., Pagani, M., Super, J.R., Elder, L.E., Hull, P.M., 2020. The enigma of Oligocene climate and global surface temperature evolution. Proc. Natl. Acad. Sci. 117 (41), 25302–25309.
Oron, S., Abramovich, S., Almogi-Labin, A., Woeger, J., Erez, J., 2018. Depth related adaptations in symbiont bearing benthic foraminifera: New insights from a field experiment on *Operculina ammonoides*. Sci. Rep. 8 (1), 9560.
Pearson, P.N., McMillan, I.K., Wade, B.S., Jones, T.D., Coxall, H.K., Bown, P.R., Lear, C. H., 2008. Extinction and environmental change across the Eocene-Oligocene boundary in Tanzania. Geology 36 (2), 179–182.
Oron, S., Evans, D., Abramovich, S., Almogi-Labin, A., Erez, J., 2020. Differential sensitivity of a symbiont-bearing foraminifer to seawater carbonate chemistry in a decoupled DIC-pH experiment. J. Geophys. Res. Biogeosci. 125 (9), e2020JG005726.
Pearson, P.N., Foster, G.L., Wade, B.S., 2009. Atmospheric carbon dioxide through the Eocene–Oligocene climate transition. Nature 461 (7267), 1110–1113.
Purton, L.M., Brasier, M.D., 1999. Giant protist *Nummulites* and its Eocene environment: Life span and habitat insights from $\delta^{18}O$ and $\delta^{13}C$ data from Nummulites and Venericardia, Hampshire basin, UK. Geology 27 (8), 711–714.
Rae, J.W., Zhang, Y.G., Liu, X., Foster, G.L., Stoll, H.M., Whiteford, R.D., 2021. Atmospheric CO2 over the past 66 million years from marine archives. Annu. Rev. Earth Planet. Sci. 49 (1), 609–641.
Raitzsch, M., Dueñas-Bohórquez, A., Reichart, G.J., de Nooijer, L.J., Bickert, T., 2010. Incorporation of Mg and Sr in calcite of cultured benthic foraminifera: impact of calcium concentration and associated calcite saturation state. Biogeosciences 7 (3), 869–881.
Renema, W., 2003. Larger foraminifera on reefs around Bali (Indonesia). Zoologische Verhandelingen 345, 337–366.
Sadekov, A., Eggins, S.M., De Deckker, P., Kroon, D., 2008. Uncertainties in seawater thermometry deriving from intratest and intertest Mg/Ca variability in Globigerinoides ruber. Paleoceanography 23 (1).
Schiebel, R., Hemleben, C., 2005. Modern planktic foraminifera. Paläontol. Z. 79, 135–148.
Spero, H.J., Eggins, S.M., Russell, A.D., Vetter, L., Kilburn, M.R., Hönisch, B., 2015. Timing and mechanism for intratest Mg/Ca variability in a living planktic foraminifer. Earth Planet. Sci. Lett. 409, 32–42.
Stuart-Smith, R.D., Edgar, G.J., Bates, A.E., 2017. Thermal limits to the geographic distributions of shallow-water marine species. Nature Ecology & Evolution 1 (12), 1846–1852.
Teichberg, M., Wild, C., Bednarz, V.N., Kegler, H.F., Lukman, M., Gärdes, A.A., Plass-Johnson, J.G., 2018. Spatio-temporal patterns in coral reef communities of the Spermonde Archipelago, 2012–2014, I: comprehensive reef monitoring of water and benthic indicators reflect changes in reef health. Front. Mar. Sci. 5, 33.
Tripati, A., Zachos, J., 2002. Late Eocene tropical sea surface temperatures: a perspective from Panama. Paleoceanography 17 (3), 4–1.
Vaes, B., van Hinsbergen, D.J., van de Lagemaat, S.H., van der Wiel, E., Lom, N., Advokaat, E.L., Langereis, C.G., 2023. A global apparent polar wander path for the last 320 Ma calculated from site-level paleomagnetic data. Earth Sci. Rev. 245, 104547.
Wade, B.S., Pearson, P.N., 2008. Planktonic foraminiferal turnover, diversity fluctuations and geochemical signals across the Eocene/Oligocene boundary in Tanzania. Marine Micropaleontology 68 (3–4), 244–255.
Warter, V., Mueller, W., Wesselingh, F.P., Todd, J.A., Renema, W., 2015. Late Miocene seasonal to subdecadal climate variability in the Indo-West Pacific (East Kalimantan, Indonesia) preserved in giant clams. Palaios 30 (1), 66–82.
Warter, V., Erez, J., Müller, W., 2018. Environmental and physiological controls on daily trace element incorporation in *Tridacna crocea* from combined laboratory culturing and ultra-high resolution LA-ICP-MS analysis. Palaeogeography, Palaeoclimatology, Palaeoecology 496, 32–47.
Wefer, G., Berger, W.H., 1980. Stable isotopes in benthic foraminifera: seasonal variation in large tropical species. Science 209 (4458), 803–805.
Yu, J., Elderfield, H., 2008. Mg/Ca in the benthic foraminifera *Cibicidoides wuellerstorfi* and *Cibicidoides mundulus*: Temperature versus carbonate ion saturation. Earth Planet. Sci. Lett. 276 (1–2), 129–139.
Zanazzi, A., Kohn, M.J., MacFadden, B.J., Terry, D.O., 2007. Large temperature drop across the Eocene–Oligocene transition in central North America. nature 445 (7128), 639–642.