

Contrasting response in test size and abundance of planktic foraminifera *Morozovella* and *Acarinina* to the EECO in the subtropical Pacific Ocean

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ABSTRACT

The EECO (~53–49 Ma) is characterized by the highest global average temperature and CO₂ levels of the Cenozoic, providing the opportunity to explore the interplay between prolonged warmth, potential physiological stress, and marine planktic ecosystems, of which planktic foraminifera are a component. Previous studies have documented a dramatic decline in the dominant planktic foraminiferal genus *Morozovella* and a concurrent increase in *Acarinina* abundances at the onset of the EECO in the Atlantic, Tethys and Pacific Oceans. This study aims to investigate how extreme climatic conditions during the EECO influenced the abundance, size, and ecological strategies of planktic foraminifera, focusing on the response of the symbiont-bearing mixed-layer dweller *Morozovella* and *Acarinina* at Ocean Drilling Program (ODP) sites 1209–1210 Shatsky Rise, in the subtropical Pacific Ocean. We present species abundances, test size and $\delta^{13}\text{C}$ data of *Morozovella*. *Acarinina* test size and $\delta^{13}\text{C}$ data were quantified to assess whether observed changes affected all mixed-layer dwellers or were specific to *Morozovella*.

Our results show a temporary increase in *Morozovella* test size at the EECO onset, partially linked to the dominance of larger species such as *M. crater* and *M. aragonensis*. In contrast, *Acarinina* displays a reduction in test size. The generally lower $\delta^{13}\text{C}$ values across the EECO in *Acarinina* suggest a deeper habitat in the mixed-layer and/or reduced symbiosis relative to *Morozovella*. We speculate that *Acarinina* evaded the high temperatures by moving deeper in the mixed layer. The reduced symbiosis relationship due to diminished light in the deeper water column might have led to a smaller test size. In contrast, *Morozovella* maintained a shallower position in the mixed layer allowing it to sustain efficient symbiosis and larger size. However, the limited ecological flexibility of this taxon may have impeded its ability to adapt and maintain high abundance across the EECO.

1. Introduction

The early Eocene represents an important time interval to study the response to global warmth and perturbations in the carbon cycle. During the Eocene (56–34 Ma), increased volcanic emissions released substantial amounts of greenhouse gases (Kender et al., 2021; Hönsch et al., 2023), leading to the highest global temperatures of the Cenozoic Era (Inglis et al., 2020). The prolonged expression of this warmth is known as the Early Eocene Climatic Optimum (EECO; ~53–49 Ma; Slotnick et al., 2015; Lauretano et al., 2016; Luciani et al., 2016; Westerhold et al., 2018; Hollis et al., 2019). Global mean surface temperature estimates for the EECO (27.0 °C) suggest temperatures ~10 to 16 °C warmer than the Holocene (Inglis et al., 2020) and may have led to

physiological stress due to high metabolic rates. The impacts of ongoing warming on marine ecosystems include reductions in species growth, reproduction rate and other physiological processes, migration towards higher latitudes and deeper waters, and local extinctions (e.g., Cooley et al., 2022). The increasing temperatures of the EECO were caused by the highest levels of atmospheric CO₂ of the whole Cenozoic, reaching values between 1170 and 2490 ppm (Anagnostou et al., 2020; Miller et al., 2020; Hönsch et al., 2023; CenCO2PIP, 2023). The high atmospheric CO₂ levels resulted in increased concentrations of dissolved CO₂ in the ocean and in turn lower pH (e.g., Pearson and Palmer, 2000; Anagnostou et al., 2020; Rae et al., 2021).

Superimposed on the early Eocene warming, several short-lived warming events (hyperthermals) are documented, of which the

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Paleocene Eocene Thermal Maximum (PETM, ~ 56 Ma) is the most prominent example, followed by a series of smaller events (e.g., Zachos et al., 2005, 2010; Kirtland-Turner et al., 2014; Littler et al., 2014). The J event represents the start of the EECO (Slotnick et al., 2012, 2015; Lauretano et al., 2016; Luciani et al., 2016). Beyond rapid rises in ocean temperature, these hyperthermals (Thomas, 1998) share several key characteristics, most notably negative carbon isotope ($\delta^{13}\text{C}$) excursions (CIEs) and evidence for dissolution of deep-sea carbonate (e.g., Zachos et al., 2005; Leon-Rodríguez and Dickens, 2010).

One of the primary effects of ocean surface warming is the increase in stratification, due to the greater heat retention in surface waters compared to deeper layers (Venegas et al., 2023). This stratification limits vertical mixing, reducing nutrient regeneration and in turn primary productivity (Lozier et al., 2011). The decrease in nutrient availability may have the potential to impact marine food webs, due to nutrient limitations of phytoplankton (Behrenfeld et al., 2006) and the zooplankton such as planktic foraminifera populations which depended on them. Given the higher food demand due to increased metabolic rates associated with warming, the increased stratification would have decreased food availability, potentially favouring species adapted to oligotrophy and supported by symbionts.

Predictive models suggest that future warming, stratification and acidification will have adverse ecological effects on calcifying plankton (Beaugrand et al., 2015; Roy et al., 2015; García Molinos et al., 2016). We therefore hypothesize that foraminiferal responses to the EECO may have led to shifts in species distribution, changes in abundance and size, and migration towards higher latitudes and deeper waters (Luciani et al., 2017a, 2017b; D'Onofrio et al., 2020; D'Onofrio et al., 2024). Evolutionary trends of planktic foraminifera and major drops in their abundance often appear to correlate with significant changes in oceanography, although causal relationships remain uncertain (e.g., Schmidt et al., 2004b; Wade and Pearson, 2008; Ezard et al., 2011; Fraass et al., 2015).

One of the key traits to assess stress responses in organisms is their body size (Martins et al., 2023; Sentis et al., 2024). The size of an organism influences its metabolic rate, its ability to coexist with other organisms, and its response to changes in ambient conditions (Brown et al., 2007; Hart et al., 2016; Violle et al., 2012), representing a functional trait related to population growth rate, competition, and reproduction (Arendt, 2007; Millien et al., 2006). The test size of planktic marine calcifiers can reveal important information on their physiological performance and is an important determinant of their functions in marine ecosystems (Kucera, 2007). Studies show that test size distribution can provide valuable insight into present and past oceanographic conditions (Møller et al., 2013; Schmidt et al., 2004a). For example, larger test sizes respond to temperatures and nutrient availability, while shifts towards smaller sizes can reflect environmental stressors like ocean acidification, warming, or reduced nutrient supply (Schmidt et al., 2004a; Reuman et al., 2014; D'Onofrio et al., 2024). Most modern foraminiferal species reach the largest size when food and temperature are advantageous (Spero et al., 1991; De Villiers, 2004; Schmidt et al., 2004b, 2006; Lombard et al., 2009) though patterns are different in different taxa (Rillo et al., 2020). While temperature is often considered a key factor influencing size variation in planktic foraminifera, with larger individuals found in warmer tropical waters (Schmidt et al., 2004a), other studies have linked size variation to salinity, carbonate saturation, nutrients, and oxygen availability (Bé et al., 1981; Caron et al., 1982; Hemleben et al., 1987; Bijma et al., 1990; Kuroyanagi et al., 2013; Weinkauf et al., 2016; Rillo et al., 2020; Adebayo et al., 2023; Moretti et al., 2024). In tropical oceans, where temperature variation is minimal, carbonate ion concentration may strongly influence size, although temperature and food availability are found to exert a main control on assemblage size variation (Adebayo et al., 2023 and references therein).

Over longer time scales, planktic foraminiferal test size can also be modified by evolutionary changes and shifts in species composition

within communities. These changes might be influenced by individuals' physiological functioning, which may be impacted by environmental stress as a potential consequence of extreme warmth (e.g., Cooley et al., 2022; Schmidt et al., 2006 and reference therein). The loss of symbionts (i.e. bleaching) is also a potential consequence of elevated sea surface temperature and decreased pH (e.g., Douglas, 2003; Dong et al., 2022), both of which may have occurred at the EECO (e.g., Anagnostou et al., 2016; Zachos et al., 2008). Bleaching may result in smaller size as symbiosis plays an important role in foraminiferal calcification and growth (Bé et al., 1982; Caron et al., 1982). Bleaching episodes have been hypothesized for several warming intervals, including the PETM (Si and Aubry, 2018; Shaw et al., 2021), the Early Eocene Climatic Optimum (Luciani et al., 2017a), and during the Middle Eocene Climatic Optimum (~40 Ma) (Edgar et al., 2013). However, some of these examples remain subject to debate (Hupp and Kelly, 2020), as separating bleaching signals from potential influence of diagenesis might be difficult.

Given our high-level understanding of the impacts of extreme temperatures on planktic foraminifera in the modern ocean, changes to assemblages documented during the EECO can be interpreted (Luciani et al., 2017a, 2017b, 2020, 2021; D'Onofrio et al., 2020). The symbiont-bearing mixed-layer genera, *Morozovella* and *Acarinina*, which dominated early Paleogene tropical and subtropical surface oceans (Boersma et al., 1987; Premoli Silva and Boersma, 1988; Pearson et al., 1993, 2006 and references therein), permanently switched their abundance in the Atlantic, Tethys, and Pacific Oceans close to the beginning of the EECO. *Morozovella* abundances and species diversity decreased while *Acarinina* increased and diversified from the onset of the EECO (Pearson et al., 2006; Aze et al., 2011; Fraass et al., 2015; Luciani et al., 2016, 2017a, 2017b; D'Onofrio et al., 2020; Filippi et al., 2024). Species diversity of planktic foraminifera was high during the Eocene (e.g., Fraass et al., 2015), but with generally small sizes which has been related to weaker vertical temperature gradients impacting niche availability, and the efficiency of the biological pump and hence food availability in the upper water column (e.g., John et al., 2013; Schmidt et al., 2004b). Smaller sizes may confer a competitive advantage by allowing more efficient resource allocation (Schmidt et al., 2004b; John et al., 2013; Reuman et al., 2014). Across the planktic foraminifera assemblages at subtropical Pacific Shatsky Rise a slight increase in the average sizes has been tentatively linked to increases in acarininids test size, the dominant group during this time (Filippi et al., 2024). Expanding on this work, we aim to investigate the driving causes behind the response of *Morozovella* during the EECO and explore its generality by contrasting with the response of *Acarinina*. We investigate adaptation sensu Laland et al. (2004), exploring the environment's role in directing evolutionary changes that enhance an organism's fitness within its habitat. In foraminifera, fitness is linked to size as the volume of the test is linked to the protoplasm volume which is converted into gametes during reproduction.

Morozovella biostratigraphic data have been previously published in Petrizzo et al. (2005). For this study, we recorded *Morozovella* species relative abundances (%) with a higher resolution and performed a cluster analysis. In addition, we analysed test size and stable isotope of *Morozovella* and *Acarinina* to evaluate potential responses in habitat preferences and symbiotic relationships. Drawing the data together, we aspired to better understand the ecological and evolutionary dynamics between the two main symbiont-bearing mixed-layer dwellers during the EECO.

2. Methods

2.1. Sites locations

We examined samples collected from Ocean Drilling Program (ODP) Leg 198, sites 1209 (paleodepth of ~2500 mbsf, current water depth = 2387 m; Dutton et al., 2005) and 1210 (paleodepth of 2700 mbsf,

current water depth = 2573 m; Larson et al., 1992) on Shatsky Rise (paleolatitude 15–20° N; Dutton et al., 2005) from the subtropical Pacific Ocean (Bralower et al., 2002a; Westerhold and Röhl, 2006; Fig. 1), consisting of nannofossil ooze with occasional intervals of nannofossil ooze with clay (Bralower et al., 2002a, 2002b). Fossil preservation at the sites is sufficiently good to ensure accurate identification of taxa (Bralower et al., 2002a). The availability of stable carbon and oxygen isotopic records, an excellent age model including identifiable hyperthermal events (Westerhold et al., 2017, 2018), and their location in the subtropical belt where temperatures have the potential to result in physical stress make these sites ideal. Additionally, data on planktic foraminiferal assemblages, fragmentation, test size and carbonate accumulation across the EECO are provided by Filippi et al. (2024), make these sites an optimal choice for detailed studies.

2.2. Sampling strategies

We analysed 29 samples from Site 1209, covering an age interval of 3.24 myr, from 53.14 to 49.93 Ma (Westerhold et al., 2018) and spanning from Core 21H 187.62 mbsf (meters below sea floor), i.e., 208.16 rmcd (revised composite depth) to Core 19H 172.50 mbsf, i.e., 189.70 rmcd (Table S1). The older part of the record was analysed at Site 1210 with an overlap timing with Site 1209 of ~1 My. We selected 40 samples from Site 1210 (Holes A and B) covering a time interval comprised between 55.61 and 52.26 Ma (Westerhold et al., 2018) and spanning from Core 20H 183.640 mbsf, i.e., 206.425 adj rmcd (adjusted rmcd accounting for samples outside the defined composite), to Core 19H 170.73 mbsf, i.e., 192.440 adj rmcd (Table S2). For genus-specific test size analyses, we selected the same samples analysed in Filippi et al. (2024).

We utilized different stratigraphic resolutions for various analyses, reflecting the specific requirements and constraints of each methodological approach. While the variation in stratigraphic resolution influences the comparability of results, the integration of data offers a comprehensive perspective on the evolutionary and dynamic behaviour of marine biota during the EECO. Cluster analysis of species abundance was performed at an approximate resolution of less than ~0.5 Ma while test size analysis was performed at an average higher resolution of ~0.07 Ma. To delineate hyperthermal events within the EECO, carbon isotope analyses were carried out at ~0.03 Ma, for temporal constraints

on these events.

2.3. *Morozovella* species abundance

The *Morozovella* species abundance was evaluated on more than 150 individuals in each sample, using a Zeiss stereomicroscope (Table S3 and Fig. 2) in 16 samples from 55.61 Ma to 52.71 Ma at Site 1210, and 12 samples from 52.99 Ma to 49.93 Ma at Site 1209 in the $\geq 150 \mu\text{m}$ fraction. The taxonomic criteria adopted to identify planktic foraminiferal *Morozovella* species follow Olsson et al. (1999) and Pearson et al. (2006).

To identify clusters of similar ecological signatures and how similarity might change through time, we performed hierarchical clustering, paired group (UPGMA) algorithm, Bray–Curtis similarity index on *Morozovella* species abundances across the studied interval (Fig. 3). We combined a non-metric multidimensional scaling (NMDS) ordination analysis using the Bray–Curtis similarity index to identify cluster robustness and recover similarities between faunal groups independently from the stratigraphic position, using the Software PAST 4.17 (Hammer et al., 2001) (Figs. 3 and 4). To differentiate the main phases, we used the major branching points in the lower part of the dendrogram, defined by similarity values <0.60. For the subphases, we applied a threshold below 0.675. The cluster analysis was conducted using a lower sampling resolution (species abundance across 28 samples, about ~0.75 mbsf) compared to other datasets in this study, such as the stable isotope curves, which were sampled every ~0.08 rmcd. While this limitation affects the precision with which the ecological phases are defined, it is driven by the available resolution of the planktic foraminifera abundance data.

2.4. *Morozovella* and *Acarinina* test sizes

We evaluated the variation in test size for the genera *Acarinina* and *Morozovella* in 29 Samples distributed from 208.16 to 189.70 rmcd (Site 1209), and in 40 samples from 192.440 to 201.790 adj rmcd (Site 1210) following the method in Schmidt et al. (2004a). Samples for test size analysis included those for *Morozovella* species abundance. Excluding samples at 51.20 Ma and 53.59 Ma, which contained only 53 and 25 morozovellids, respectively, we collected a minimum of 144 individuals, and a maximum of 571 individuals, for an average of 224 specimens per sample imaged at 160 $\times$ magnification. The morphological parameters of each specimen (i.e. maximum and minimum diameter, sphericity, and grey value of planktic foraminifera analysed tests) were analysed in Olympus Stream Motion. To remove juvenile specimens and fragments from analyses, the morphological parameters were set to exclude particles with a diameter < 150 μm , sphericity <0.5 and grey value below 80. The 95th percentile of the maximum diameter of all foraminiferal in the assemblage was calculated (Schmidt et al., 2004a) of which the average repeat measurement error is ~3 μm (Schmidt et al., 2003; Todd et al., 2020).

2.5. Stable carbon and oxygen isotope analysis of *Morozovella* and *Acarinina*

Planktic foraminifera from the sites investigated exhibit “frosty” preservation (sensu Sexton et al., 2006), thus indicating recrystallization which may have influenced the oxygen stable isotope data (e.g., Pearson et al., 2001; Sexton et al., 2006). However, $\delta^{13}\text{C}$ values are less influenced by recrystallization (e.g., Frank et al., 1999; Edgar et al., 2013, 2015) and may be interpreted as revealing the position that the taxa occupied within the mixed-layer and photosymbiotic associations. We selected the best-preserved specimens and cleaned them in a gentle ultrasonic bath for a few minutes to remove potential particles on the surface. The carbonate infilling, where present, was carefully removed manually through a thin brush from each broken tests previously gently crushed between two small glasses.

Stable isotope analyses were performed on 5 samples from Site 1209,

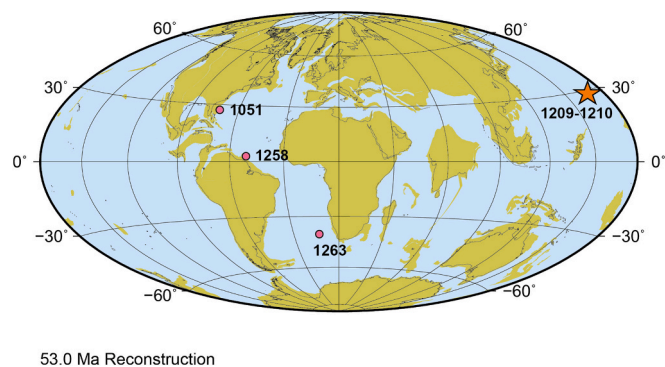


Fig. 1. Approximate location of the studied sites 1209 and 1210 during the early Eocene (orange star). Also shown are the locations of Ocean Drilling Program (ODP) Atlantic sites 1051, 1258 and 1263 (pink dots), where planktic foraminiferal records show a major change in genera across the EECO and $\delta^{13}\text{C}$ records are detailed (Luciani et al., 2017a, 2017b; D’Onofrio et al., 2020). The base map is from https://www.odsn.de/odsn/services/paleomap/adv_map.html with paleolatitudes modified for sites 1051, 1263, 1258, and 1209–1210 according to www.paleolatitude.org model version 1.2 (Van Hinsbergen et al., 2015). Note that locations might be adjusted to a different reference frame to account for changes in plate motion relative to the spin axis (Hollis et al., 2019) (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

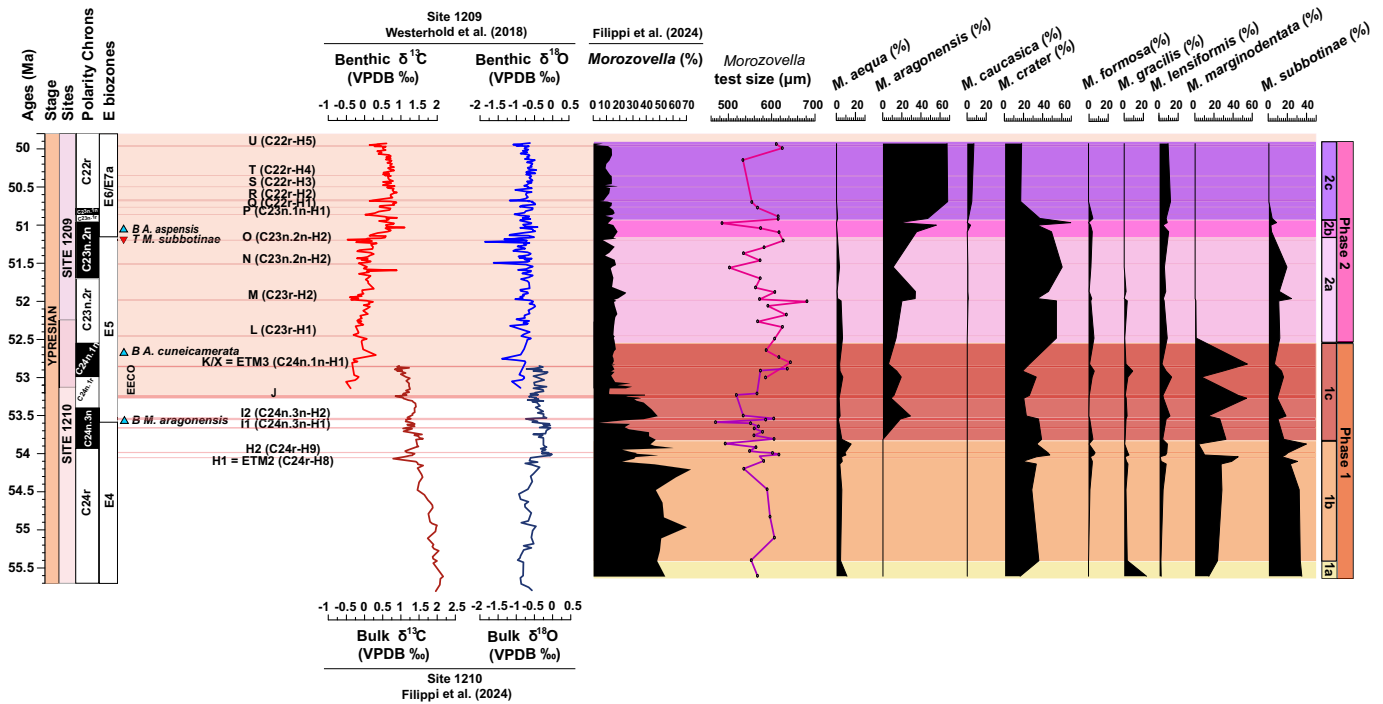


Fig. 2. Stable isotope records at ODP sites 1209 and 1210. The dark red bulk $\delta^{13}\text{C}$ and dark blue bulk $\delta^{18}\text{O}$ and curves are from Filippi et al. (2024) and referred to Site 1210. The benthic foraminifera red and blue curves are from Westerhold et al. (2018) and referred to Site 1209. The relative abundance (%) of the genus *Morozovella* is from Filippi et al. (2024), and the relative abundances of morozovellids species, and *Morozovella* test size are from this study. Phases are identified from the cluster analysis of this study, named and coloured as in Figs. 3 and 4: Phase 1 in orangish warm colours, Phase 2 in pinkish colours. The planktic foraminiferal *E*-zonation follows Wade et al. (2011) as partly modified by Luciani and Giusberti (2014). Main carbon isotope excursions (CIEs) are labelled according to Westerhold et al. (2017). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

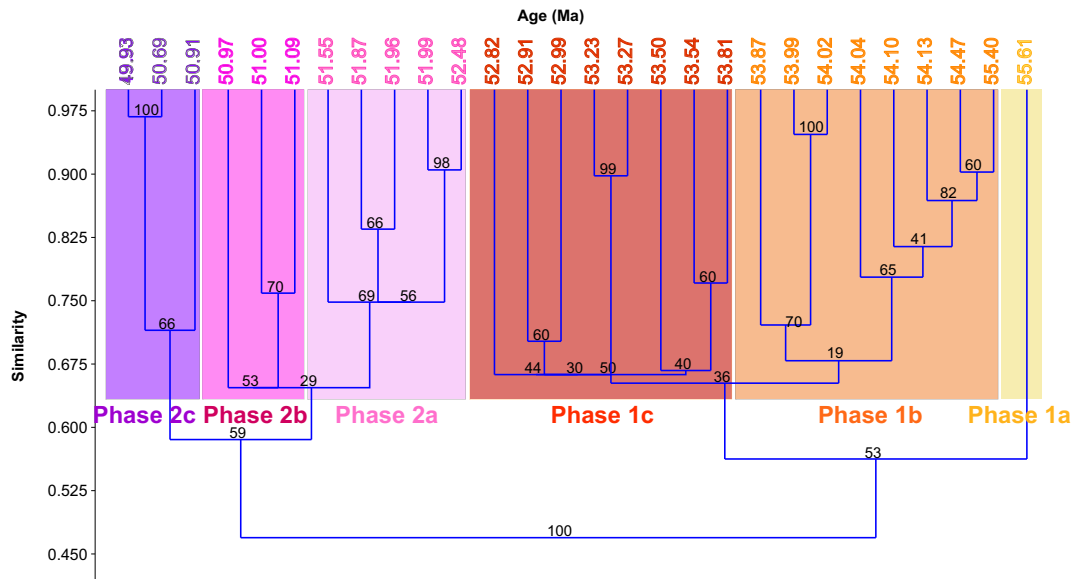


Fig. 3. Dendrogram of the stratigraphically-constrained multivariate classical clustering analysis performed on *Morozovella* species relative abundances (%) across the studied interval, using a Paired Group (UPGMA) algorithm and the Bray-Curtis similarity index, with the main clusters named (Phase 1a, 1b, 1c and Phase 2a, 2b, 2c) and highlighted. Node values are for 1000 bootstraps.

from 190.7 and 207.96 rmcd (after the EECO onset), and 5 from Site 1210, from 193.99 and 204.79 rmcd (before the EECO onset) (Table S4), spanning through a time interval from 55.1 to 50.08 Ma (Westerhold et al., 2018). $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values were obtained at the Ferrara University through the Elemental Mass Spectrometer[®] isoprime precisiON with a centrION system, isoFLOW Equilibration System, and ionOS[®] IRMS Software. Throughout the analyses, a laboratory standard (Carrara

Marble) MAQ 1 in the 80–150 μm fraction was utilized, weighing between 0.120 and 0.180 mg. The system demonstrated an analytical precision of ± 0.1 for $\delta^{13}\text{C}$ and ± 0.08 ‰ for $\delta^{18}\text{O}$ at 1 SD during the analysis period, assessed through systematic repetition of a quality control standard (GR 1). We collected from the fraction >250 μm (to avoid possible juvenile forms) ~ 30 – 40 specimens of *Morozovella* and *Acarinina* to reach the weight requested for the analysis, i.e., 120

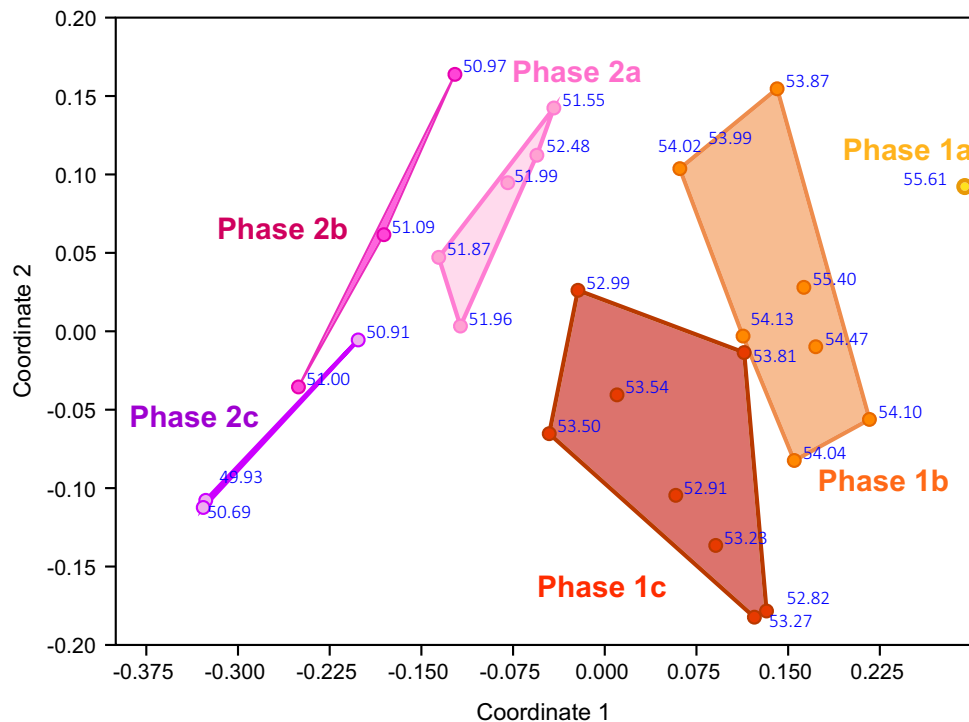


Fig. 4. Clusters recovered by non-metric multidimensional scaling ordination analysis, using the Bray-Curtis similarity index, with hulls and labels representing groups recovered in Fig. 3. Dots represents individual samples, with each dot corresponding to the phase it belongs to, as identified in the dendrogram in Fig. 3.

µg–180 µg.

3. Results

3.1. Morozovella species abundances and cluster analysis

Morozovella species identified across the studied interval according to Pearson et al. (2006) are *M. aequa*, *M. aragonensis*, *M. caucasica*, *M. crater*, *M. formosa*, *M. gracilis*, *M. lensiformis*, *M. marginodentata* and *M. subbotinae*. The dendrogram in Fig. 3 summarizes the clustering, while Fig. 4 shows the relationship between these phases based on their proximity and distribution within the NMDS plot. The average species abundances for each of the six phases are detailed in Table 1.

Across the studied interval, two main morozovellids species diversity phases could be identified (Phase 1 and 2) with three sub-clusters each (Phase 1a, 1b, 1c, 2a, 2b, 2c). It is important to note that the clusters identified in this study did not align with specific hyperthermal events such as the J event, start of the EECO, or other hyperthermals across the interval. Significant changes in the composition of *Morozovella* species occurred between Phase 1 and Phase 2 representing a transition from the dominance of *M. crater*, *M. subbotinae*, and *M. marginodentata* in Phase 1 to an increased dominance of *M. crater* and *M. aragonensis* in Phase 2. Additionally, there was a gradual decline and eventual disappearance of *M. marginodentata* and *M. gracilis* by the end of this interval (Table 1, Table S3, Figs. 2, 3, 4).

Phase 1a (55.61–55.40 Ma, Dark Yellow) is dominated by *M. subbotinae* (34.5 %) and *M. gracilis* (23 %; Tables 1, S3). Phase 1b (55.40–53.87, Orange) lightly overlaps with Phase 1c, while being spatially distinct from Phase 1a (Fig. 3) likely driven by a rise of *M. crater* (~34 %) and *M. marginodentata* (23 %), increases of *M. lensiformis* while *M. gracilis* decreased. Phase 1c (53.87–52.48, Red) overlap with 1b suggests that environmental conditions were similar between the two phases, leading to a shared region in the NMDS space (Fig. 4). Species in this phase show high fluctuations in abundance. *M. marginodentata* dominates (29 %) at samples within or close to hyperthermals, J, and K/ X (Table 1; Fig. 2).

Phase 2a (52.48–51.09, Pink) shows a marked difference from the preceding Phase 1 (Figs. 3, 4). *M. crater* dominates (~48 %), *M. aragonensis* and *M. subbotinae* become common. *M. marginodentata* disappears during this phase and *M. caucasica* appears (Table 1, Fig. 2). Phase 2b (51.09–50.91 Ma, Dark Pink) records a greater dominance of *M. crater* (~50 %) an increase in abundance of *M. aragonensis*. *M. gracilis* disappears in this phase (Table 1, Fig. 2). In Phase 2c (50.91–49.93 Ma, Violet) *M. aragonensis* is the dominant form (~61 %), *M. crater* registers a decrease in abundance. *M. subbotinae*, *M. formosa* and *M. aequa* are not found (Tables 1, S3).

3.2. Morozovella and Acarinina long-term test size variations

Test size variations are described across the six phases identified in

Table 1
Morozovella species relative abundance (%) mean values across the six subphases identified in the cluster analysis. Values of the most abundant species of each phase are in bold.

Phases	<i>M. aequa</i>	<i>M. aragonensis</i>	<i>M. caucasica</i>	<i>M. crater</i>	<i>M. formosa</i>	<i>M. gracilis</i>	<i>M. lensiformis</i>	<i>M. marginodentata</i>	<i>M. subbotinae</i>
2c	0.4	60.6	4.3	23.1	1.5	0.0	9.0	0.0	1.1
2b	0.2	35.7	1.1	49.7	2.0	0.0	7.0	0.0	4.3
2a	2.4	24.6	0.8	47.6	2.2	1.3	5.0	0.2	15.9
1c	4.1	13.3	0.0	29.7	2.7	2.7	6.5	29.1	11.9
1b	7.3	0.0	0.0	33.6	3.0	2.7	4.5	23.0	25.9
1a	10.9	0.0	0.0	15.5	0.0	23.1	1.7	14.3	34.5

the previous cluster.

analysis. **Before the EECO onset**, *Morozovella* dominated the assemblage abundance with a relatively stable test size (567 μm). In contrast, the less abundant *Acarinina* exhibited higher variability in test size (Fig. 5; Table 2). In **Phase 1a** *Morozovella* and *Acarinina* showed a mean test size of 566 and 504 μm , respectively. Standard deviation could not be calculated as this phase contains only one stratigraphic sample (Table 3). In **Phase 1b** *Morozovella* test size recorded a slight increase with some stabilization in the middle of the phase. *Acarinina*, despite an initial slight increase, quickly decreases in size. Towards the end of this phase, *Acarinina* exhibits a slight increase again, reaching its peak values (Tables 3, S2, Fig. 5). At the Phase 1b and 1c boundary (~ 54.2 Ma to ~ 53.5 Ma), a transitional phase is recorded, in which *Acarinina* and *Morozovella* test sizes fluctuate rapidly and converge on more similar size. During **Phase 1c**, *Morozovella* test size recorded a slight, stable decrease until the onset of the J CIE, marking the start of the EECO. From this point, *Morozovella* displayed a general increase in test size. *Acarinina* test size began to gradually decrease until the top of the succession (Tables 3, S1, S2, Fig. 5).

From the EECO onset, *Morozovella* showed a decline in abundance, coupled with a general slight increase in test size and slightly higher variability (Table 2). *Acarinina* test size decreased by $\sim 14\%$ with respect to the pre-EECO and became more stable (Table 2). To test for differences in variability between the two taxa test sizes before and during the EECO interval, Levene's test was applied (Levene, 1960). Two short-term negative peaks after H2 and before I1 were excluded due to their influence by CIEs and considered outliers from a long-term perspective for *Morozovella*. The p -values of ~ 0.003 and ~ 0.006 (< 0.05) for *Morozovella* and *Acarinina*, respectively, indicate statistically significant differences in the variability of the two taxa test size before and during the EECO.

In **Phase 2a**, *Morozovella* test size initially increased steadily, reaching the highest value of the entire interval (682 μm ; Table S1). *Acarinina* test size, after an initial peak, stabilized with moderate

Table 2

Average test size 95th percentile and standard deviation values of *Morozovella* and *Acarinina* respectively, across the entire interval, before the EECO Onset and during the EECO.

Genera Measure	Morozovella test size		Acarinina test size	
	Average (μm)	St. Dev (μm)	Average (μm)	St. Dev (μm)
Total interval	578	42	477	56
After EECO onset	587	44	445	26
Before EECO	567	35	519	51

Table 3

Test size 95th percentile average and standard deviation values of *Morozovella* and *Acarinina* respectively, across the six phases identified in the previous cluster analysis.

Genera Measure		Morozovella test size		Acarinina test size	
		Average (μm)	St. Dev (μm)	Average (μm)	St. Dev (μm)
Phase 2	2c	589	36	456	30
	2b	576	65	435	9
	2a	590	46	439	19
Phase 1	1c	574	43	475	46
	1b	571	34	538	51
	1a	566	–	504	–

fluctuations. **Phase 2b** exhibited high variations in test size for *Morozovella*, with a decrease in the mean test size of 14 μm . In contrast, *Acarinina* test size showed the lowest standard deviation (9), indicating more stable sizes.

Despite recording a gradual decrease in test size, *Morozovella* in **Phase 2c** achieved the second-highest mean size across the six phases. *Acarinina* test size, after an initial peak, declined slightly yet test sizes remained relatively high compared to earlier phases (Fig. 5, Tables 3, S1).

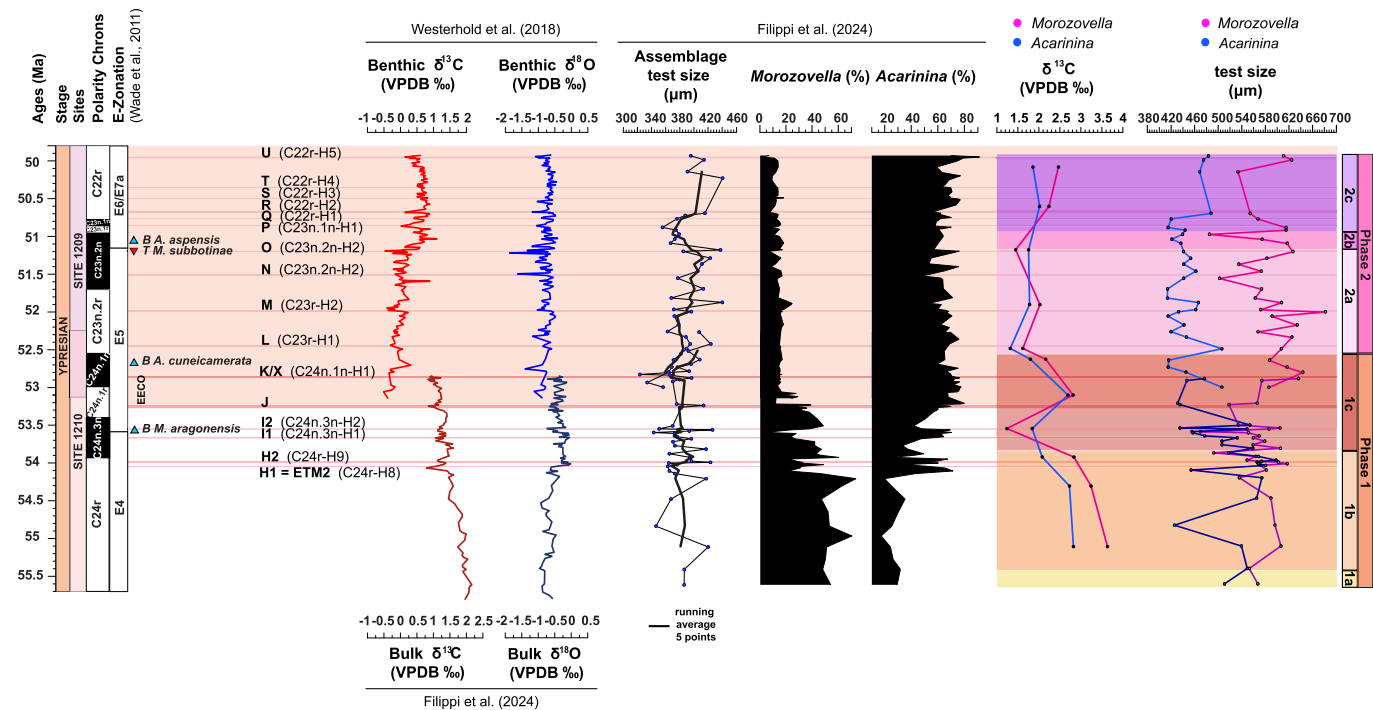


Fig. 5. Stable isotope records at ODP sites 1209 and 1210 plotted in age (Ma; according to the age model of Westerhold et al. (2018)) along with total assemblage test size and abundance of *Morozovella* and *Acarinina* (Filippi et al., 2024). *Acarinina* (blue curve) and *Morozovella* (violet, pink curves) $\delta^{13}\text{C}$ curves and test size 95th percentile (μm) are from this study. Phases are identified from the cluster analysis of this study and named and coloured as in Figs. 3 and 4. Other information is consistent with Fig. 2. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

3.3. *Morozovella* and *Acarinina* short-term test size variations

Acarinina and *Morozovella* showed short term size fluctuations, (Fig. 5, Tables S1, S2, S5).

Among the CIEs analysed, *Morozovella* increased in test size only at I2 and P while *Acarinina* concurrently decreased (Table 4). In other short-term variations there is no clear response. However, in these transient size fluctuations, the *Acarinina* increases in test size mainly corresponds to *Morozovella* size decrease (Fig. 5, Tables 4, S1, S2, S5).

3.4. $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ in *Morozovella* and *Acarinina*

In the pre-EECO interval, *Morozovella* and *Acarinina* recorded the highest $\delta^{13}\text{C}$ values, which decreased from 55.11 to 53.54 Ma (Tables 5, S4). Between 53.54 Ma until 53.10 Ma (Above the J CIE) *Morozovella* and *Acarinina* showed an abrupt increase in $\delta^{13}\text{C}$. Both taxa recorded a decrease in $\delta^{13}\text{C}$ between 53.10 and 52.48 Ma (L CIE), with *Acarinina* registering its lowest value, with a stabilization of the values upward.

Mean values of *Morozovella* before the EECO onset were $\sim 2.74\text{‰}$ and dropped to $\sim 2.11\text{‰}$ from the EECO onset. Mean values of *Acarinina* before the EECO onset were $\sim 2.37\text{‰}$ and decreased to $\sim 1.89\text{‰}$ in the EECO interval (Fig. 6).

With exception of samples at 53.54 (above I1) and 51.18 (above O CIE) *Morozovella* recorded slightly higher values compared to *Acarinina* (Table 5, Figs. 6, S1 in Supporting Material). Oxygens isotope data of the two taxa record a generally slight increase in values, with the mean value of -1.20‰ for and -1.21‰ for *Morozovella* and *Acarinina* respectively in the pre-EECO, and -0.92‰ and -0.95‰ during the EECO (Table 5).

4. Discussions

Our understanding of foraminiferal ecology and physiology, allows to evaluate the impact of the EECO on test size, abundances, and stable isotopes for the symbiont-bearing mixed-layer dweller taxa, *Morozovella* and *Acarinina*. The genus *Morozovella* permanently declined in abundance and diversity at the EECO beginning, while *Acarinina* increased in abundance (Fig. 5). Although a truly accurate investigation on test size changes requires species-specific analysis, the long-term size variations recorded in both genera, coupled with the change in dominance in their abundance starting from the EECO, suggest the hypothesis of distinct responses to the changing environmental conditions of this interval. Their divergent evolutionary paths may have played a crucial role in determining their survival and ecological success or decline during the EECO. As discussed by Gibbs et al. (2005) for coccolithophores, evolutionary factors such as speciation and extinction may also play a key role in these variations. We explore the potential impact of extinction and speciation across the EECO and discuss the possible different strategies adopted by *Morozovella* and *Acarinina* to adapt to the extreme temperatures of the tropical ocean in the EECO.

Table 4

Ages (Ma) recording contrasting short-term size variations (μm) in *Morozovella* and *Acarinina*. Blue arrows indicate increase, and red arrows indicate decrease compared to the average values taxon size recorded in the pre-EECO (for data below the J event) and EECO intervals (for data above the J event) (Table 2).

Short-term <i>Morozovella</i> and <i>Acarinina</i> size variations			
Age (Ma)	<i>Morozovella</i> (μm)	<i>Acarinina</i> (μm)	CIEs
50.69	554 ↓	488 ↑	R
50.76	568 ↓	420 ↑	Q
50.88	615 ↑	415 ↓	P
53.21	565 ↑	425 ↓	above J
53.54	604 ↑	429 ↓	I2
53.67	559 ↓	526 ↑	I1

Table 5

Ages (Ma) with stable isotope $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ (‰) values for *Morozovella* and *Acarinina* across the studied interval.

Age (Ma)	<i>Morozovella</i> (‰)		<i>Acarinina</i> (‰)	
	$\delta^{13}\text{C}$	$\delta^{18}\text{O}$	$\delta^{13}\text{C}$	$\delta^{18}\text{O}$
50.08	2.47	−0.66	1.86	−1.05
50.60	2.24	−0.98	2.02	−0.71
51.18	1.45	−0.82	1.75	−0.68
51.90	2.02	−0.85	1.78	−1.04
52.48	1.62	−0.80	1.32	−0.79
52.63	2.43	−0.91	1.80	−1.15
53.10	2.82	−1.13	2.69	−1.26
53.54	1.24	−1.23	1.84	−1.03
53.92	2.83	−0.94	2.08	−0.98
54.30	3.24	−1.21	2.73	−1.34
55.11	3.63	−1.44	2.82	−1.51

4.1. Species replacement and *Morozovella* test size changes across the EECO

Based on the acquired records, we suggest that the changes in size and abundance observed in *Morozovella* were a combination of species replacement, evolutionary changes resulting in the appearance of new taxa, and physiological responses to the ocean conditions, such as rising temperatures and variations in the nutrient availability. Species replacement in *Morozovella* during the EECO (Phase 2 of Fig. 5) showed that this interval was marked by larger species such as *M. aragonensis* and *M. crater* replacing smaller ones such as *M. aequa*, *M. gracilis* and *M. subbotinae* (Petrizzo et al., 2005; Pearson et al., 2006; D'Onofrio et al., 2020) (Fig. 2, Tables 3, S3, S6). A similar switch in species composition has been recorded at Atlantic Ocean ODP Site 1051 (Black Nose), 1258 (Demerara Rise), and 1263 (Walvis Ridge) by D'Onofrio et al. (2020) despite lower abundances of both *M. crater* and *M. aragonensis* after the EECO onset compared to our sites. The finding suggests that these taxa were better adapted to the subtropical conditions of the Pacific Ocean than other Atlantic locations.

Morozovella aragonensis and *M. crater* are considered to derive from *M. lensiformis* (Blow, 1979) which was a smaller species than its descendants (Pearson et al., 2006). While being a classic example of Cope's rule (Cope, 1887), this evolutionary trend does not explain the size fluctuations linked to the short-term dominance of *M. marginodentata*, *M. aragonensis*, and *M. crater* (Fig. 2). For example, in Phase 1c the *Morozovella* test size increased when the 'small' *M. marginodentata* dominated the assemblages whereas in Phase 2c the size decreased when *M. aragonensis* was the most abundant species. (Figs. 2, 5). This dichotomy provides evidence that changes in species composition only partially influenced the genus size, and that size decreases or increases resulted from the environmental conditions of the EECO. It is important to note though that we are reporting the 95th percentile of the size distribution which will be strongly impacted by the species making the large part of the assemblage. Importantly, the cluster phases do not align with the start of EECO or CIEs. This suggest that while hyperthermal events influence foraminiferal assemblage composition, they did not evoke large shifts in the assemblages resulting in new clusters, even though our data suffer from different sampling resolution across the diverse hyperthermals.

The abundances of *Morozovella* species recorded at Shasky Rise (Fig. 2) display antiphase fluctuations between the species emerging as dominant across the EECO, *M. aragonensis* and *M. crater* and species becoming extinct, specifically *M. marginodentata*, *M. gracilis*, *M. formosa*. This pattern is especially evident during the hyperthermals and also recorded at the Atlantic Ocean (D'Onofrio et al., 2020). The ability of the different taxa, or vulnerability, to deal with the extreme warmth that may have played a role in the evolutionary replacement.

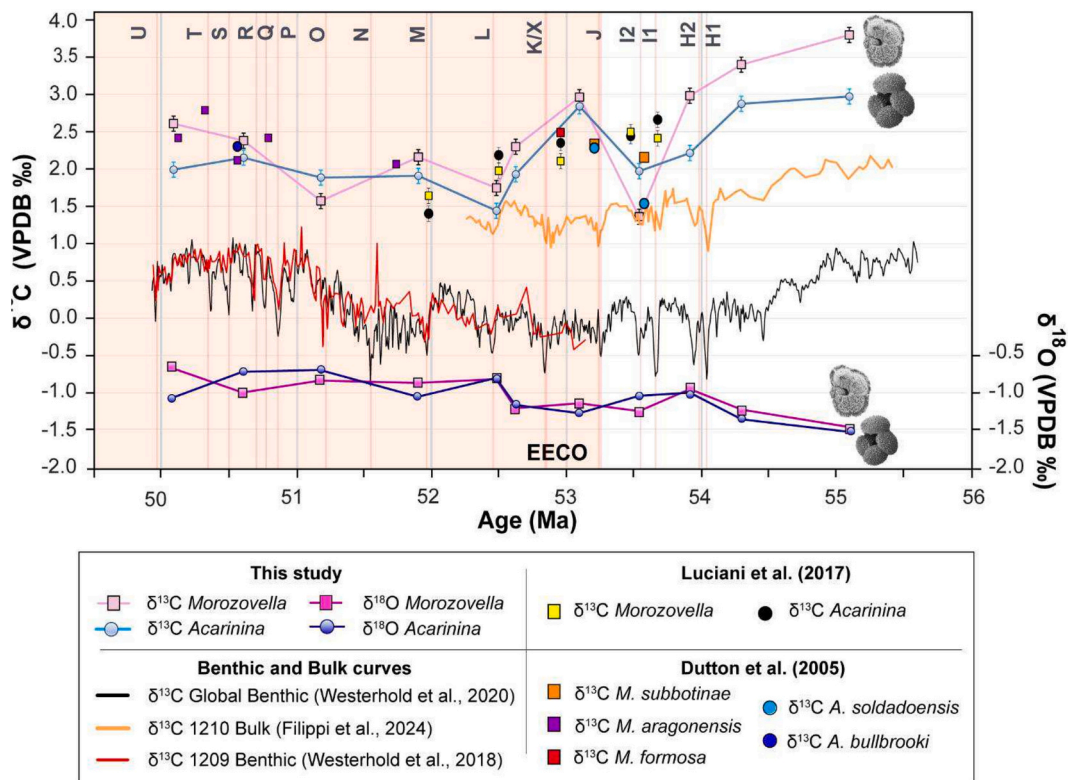


Fig. 6. $\delta^{13}\text{C}$ of *Morozovella* (pink curve) and *Acarinina* (light blue curve) before and during the EECO interval plotted against Age in (Ma). Benthic $\delta^{13}\text{C}$ curve (dark red curve) is from Westerhold et al. (2018) as well as Age in Ma. The Bulk $\delta^{13}\text{C}$ curve (light red) is from Filippi et al. (2024). CIEs are labelled and identified according to Westerhold et al. (2017). $\delta^{13}\text{C}$ of *Morozovella* (orange, violet and red square) and *Acarinina* (dark and light blue dots) picked from 300 to 355 μm size fraction by Dutton et al. (2005). Average $\delta^{13}\text{C}$ values of *Morozovella* (yellow square) and *Acarinina* (black dot) genera (size fraction $>250\ \mu\text{m}$) from Luciani et al. (2017a).

4.2. Evidence for acclimation to extreme warmth during the EECO

Our record demonstrates that *Acarinina*'s abundance increased during the EECO suggesting great adaptability to warmer conditions (Filippi et al., 2024). Still, test size decreased steadily, in contrast to *Morozovella* (Fig. 5). As discussed above, evolutionary changes alone cannot explain the observed patterns and therefore we are exploring the diverse acclimation to the environment as a potential cause.

Morozovella and *Acarinina* were symbiont-bearing genera living in the mixed layer as inferred by $\delta^{13}\text{C}$ values higher than thermocline dwellers (e.g., Pearson et al., 1993, 2006 and references therein). A characteristic increase in $\delta^{13}\text{C}$ with increasing test size occurs in tests of modern and fossil species because larger specimens support greater photosymbiont density and enhanced photosynthetic activity which removed from ^{12}C for the surrounding water providing a means to evidence photosymbiotic activity in fossil taxa such as *Morozovella* and *Acarinina* (e.g., Spero and Deniro, 1987; Norris, 1998; Luciani et al., 2017a).

Algal photosymbiosis is crucial for calcification in most surface-water dwelling planktic foraminifera and provides energy, allowing the host to succeed in low-nutrient environments (e.g., Bé et al., 1982; Hemleben et al., 1989; Takagi et al., 2019; LeKieffre et al., 2018). Symbionts, such as dinoflagellates, actively assimilate C during the day via photosynthesis and metabolize the fixed C through respiration and transfer to foraminiferal cells which receive lipid droplets for metabolic processes (LeKieffre et al., 2018). Reduction or loss in symbiotic relationships, indicated by $\delta^{13}\text{C}$ records, have been documented during warming events like the PETM (Shaw et al., 2021; Si and Aubry, 2018), the EECO (Luciani et al., 2016, 2017a, 2017b), and the Middle Eocene Climatic Optimum (~ 40 Ma) (Edgar et al., 2013), although some of them have been challenged (e.g., Hupp and Kelly, 2020).

In our record, both morozovellids and acarininids $\delta^{13}\text{C}$ values show a

general decreasing trend from the pre-EECO to the EECO (Fig. 6). Morozovellids and acarininids $\delta^{13}\text{C}$ values from this study are in general similar to the records of *M. subbotinae*, *M. formosa*, *M. aragonensis*, *A. soldadoensis* and *A. bullbrookii* documented at Shatsky Rise in the early Eocene (Dutton et al., 2005; Fig. 5) thereby facilitating our approach to analyse isotopes at the genus level, overcoming low species abundance in specific size fractions.

The observed decrease of the carbon isotopes in our samples could be interpreted as a slight deepening in the mixed layer to evade the extreme EECO warming. It is important to note, that the signal will also be impacted by the global stable carbon isotopes decrease recorded at the EECO in both bulk and benthic data and documented also at Shatsky Rise linked to variations in the global atmospheric CO_2 pool (e.g., Westerhold et al., 2018). The $\delta^{18}\text{O}$ can help in the habitat reconstruction of taxa examined (Figs. 6, S1) as temperatures are declining deeper in the water column. Yet, $\delta^{18}\text{O}$ appears more influenced than $\delta^{13}\text{C}$ by test recrystallization (e.g., Marshall, 1992; Schrag et al., 1995; Frank et al., 1999) as specimen from Shatsky Rise show 'frosty' preservation (Sexton et al., 2006). As a result, our $\delta^{18}\text{O}$ values result generally less negative (more than 2 ‰) than those recorded from 'glassy' preserved mixed-layer taxa of the same time interval and similar latitudes (e.g., Pearson et al., 2001) (Figs. 6, S1). In some cases, however, the $\delta^{18}\text{O}$ of morozovellids are more negative than those shown by acarininids, compatible with warmer thus shallower waters (e.g., d, i, l of Fig. S1).

The generally lower carbon isotopes exhibited by *Acarinina* may suggest a deeper habitat than those of *Morozovella*, resulting in a lower light availability thus impacting the performance of the photosymbiont. Moving deeper allows foraminifera to escape heat and UV stress (Rebotim et al., 2017; Luciani et al., 2017a, 2021; Si and Aubry, 2018; D'Onofrio et al., 2020). Deepening reduces light availability, which can lower symbiont activity and, in turn, energy production (D'Hondt et al., 1994; Birch et al., 2012; Si and Aubry, 2018). We cannot exclude that a

change in acarininids symbiotic microalgae with better tolerance to the EECO may have played a role, similar to interpretations by Davis et al. (2022) for the PETM and subsequent hyperthermals.

Modern oligotrophic tropical environments are typically characterized by low carbonate fluxes, high surface carbonate ion concentrations, and a high relative abundance of larger-sized species, such as *Orbulina universa*, *Trilobatus sacculifer*, and *Globigerinella siphonifera* (Peeters and Brummer, 2002; Schiebel and Hemleben, 2017; Adebayo et al., 2023). Following from this, we propose that the high temperatures and limited food during the EECO favoured smaller sizes in *Acarinina* as smaller sizes are advantageous for resource allocation in the oligotrophic conditions (Schmidt et al., 2004b; John et al., 2013; Reuman et al., 2014). *Acarinina* is interpreted as a more generalist taxon across the EECO than *Morozovella* as suggested by its wider latitudinal range compared than *Morozovella* (e.g., Boersma and Premoli Silva, 1983; Premoli Silva and Boersma, 1988; Pearson et al., 2006). Such a broad ecological niche may have allowed acarininids to respond plastically to the environmental change without losing fitness to the same degree as *Morozovella*. In contrast, *Morozovella*, maintaining an efficient symbiotic relationship was able to continue growing but suffered a decrease in fitness as indicated by a reduction in abundance (Fig. 7). A similar response of increasing size and population declined during the PETM at Shatsky Rise for *Morozovella velascoensis* was interpreted as resulting from reduced nutrient supply that may have delayed reproductive cycles, resulting in a large size with slower growth rates (Petrizzo, 2007).

Nannoplankton communities at Site 1209 provide evidence of a significant reduction in nutrient availability in surface waters during the PETM, linked to increased stratification and consequent expansion of oligotrophic regions (Gibbs et al., 2006). We speculate a similar scenario during the EECO impacted the size increase in *Morozovella* (Fig. 7). The Shatsky Rise setting is considered oligotrophic during the earliest Eocene (Petrizzo, 2007; Dutton et al., 2005), supported by high abundance of the coccolithophore genus *Discoaster*, a well-known as warm-index taxon adapted to oligotrophy (Aubry, 1992). Our planktic foraminiferal data do not record an increase in eutrophic taxa such as *Subbotina* across the EECO (Filippi et al., 2024) which would be needed to support other hypotheses of increased productivity.

In the Atlantic Ocean across the EECO *Acarinina* exhibits slightly higher $\delta^{13}\text{C}$ values compared to most *Morozovella* species (Luciani et al., 2021), thus suggesting an inverse habitat distribution compared to the Pacific Ocean. These differences may be the result of more eutrophic

conditions at equatorial Atlantic Site 1051 (Luciani et al., 2017a) compared to Shatsky Rise. The $>250\text{ }\mu\text{m}$ size fraction used for $\delta^{13}\text{C}$ data at Site 1051 (Fig. 6) may also contribute to divergences in $\delta^{13}\text{C}$ between the two sites. Test size estimation for this Site shows a reduction of morozovellids size across the EECO (Luciani et al., 2017a) thus suggesting a similar acclimation strategy as evidenced by acarininids in the subtropical Pacific Ocean.

Morozovella and *Acarinina* exhibit also short-term test size fluctuations, with some of these fluctuations coinciding with or occurring close to major CIEs (Fig. 5, Table 4). This highlights different drivers and responses to long-term versus short-term extreme warmings. It is possible that extreme temperature changes may have led to a temporary loss of symbionts and stunted growth; a speculation which would demand $\delta^{13}\text{C}$ data to further investigate (Wade et al., 2008; Woodhouse et al., 2021; Davis et al., 2022). The antagonistic fluctuations in *Acarinina* and *Morozovella* test size and abundance played a crucial role in balancing the overall assemblage test size and ultimately resulted in a stable carbonate production (Filippi et al., 2024).

Our data highlight a crucial interval at the transition of Phase 1b to Phase 1c from $\sim 54.2\text{ Ma}$ to $\sim 53.5\text{ Ma}$, when acarininid and morozovellid test sizes fluctuate rapidly and converge on more similar sizes (Fig. 5). In the same interval, shifts in the relative abundance of morozovellids and acarininids mark a crucial transition from morozovellid dominance below to acarininids becoming the dominant genus at the EECO (Fig. 5). *Acarinina* peaks at the hyperthermals, when *Morozovella* significantly decrease whereas abundance rise of *Morozovella* occur outside the main CIEs (Fig. 5). Similar findings have been observed across the same interval in the Tethys (Agnini et al., 2009; D'Onofrio et al., 2016, 2024; Luciani et al., 2016) and in the Atlantic Ocean (Luciani et al., 2017a, 2017b; D'Onofrio et al., 2020). This points to the greater adaptability of *Acarinina* to extreme warmth which becomes permanent from the beginning of the EECO. In this time, the morozovellid-acarininid $\delta^{13}\text{C}$ gradient flips with morozovellid $\delta^{13}\text{C}$ dropping below that of the acarininids. All these observations suggest that the time interval after ETM2 but prior to the EECO corresponds to an important changeover phase between these two genera, perhaps representing a gradual adaptation to become the dominant mixed-layer genus at the EECO.

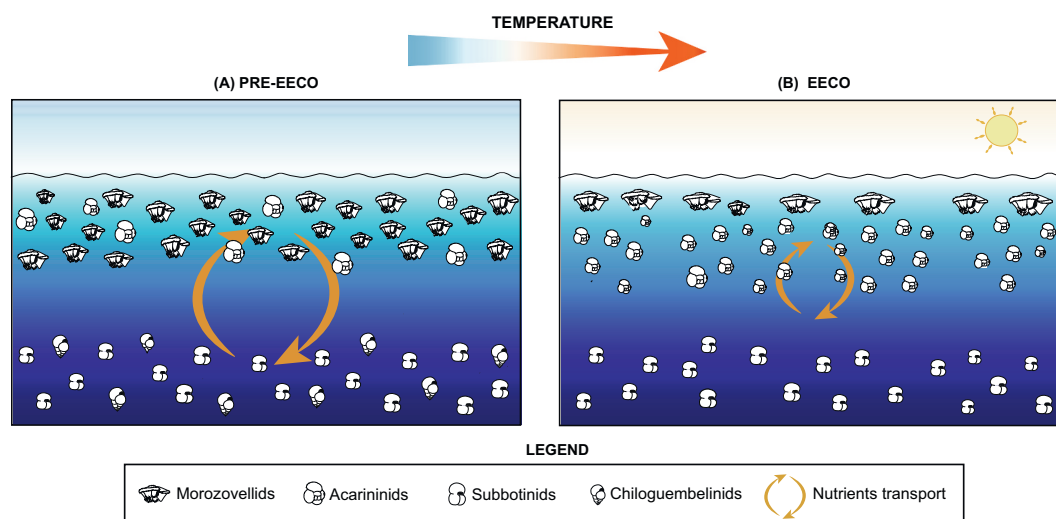


Fig. 7. Cartoons illustrating environmental changes in the upper water column across the EECO at Shatsky Rise as interpreted according to the record of changes in planktic foraminiferal assemblages and the new stable isotope data here achieved (modified from Luciani et al., 2017a). A) Pre-EECO environment showing the water column with abundant morozovellids and relatively stable nutrient supply. B) EECO scenario showing the reduction in size and increase in abundance of acarininids, which might have deepened in the mixed layer and/or changes the symbiosis relationship as a strategy to avoid the increasing temperature in a more stratified water column and oligotrophic environment. The 'eclipse' in abundance of chiloguembelinids at the EECO, related to contraction of the ODZ is also shown.

5. Conclusions

The recorded variations in *Morozovella* and *Acarinina* might then have been driven by a combination of increasing temperature, lower nutrient availability, acclimation and species replacement. Test size of *Morozovella* and *Acarinina* across the EECO at Shatsky Rise recorded prolonged size changes of the two genera which were not aligned with marked variations in abundance and higher frequency changes loosely associated with the CIEs. The dominance of larger species such as *M. aragonensis* and *M. crater* after the EECO onset combined with possible changes in their size might have contributed to the overall slight increase in the size of *Morozovella*. Morozovellid test size proves to increase even when ‘small’ taxa dominated the assemblages and vice versa. This record suggests that evolutionary replacements had limited impact, with fluctuations mainly driven by EECO impacts.

Our stable isotope data suggest that *Acarinina* may have had an advantage with respect to *Morozovella* by living in the deeper mixed layer and reducing symbiotic activity to cope with EECO warming. In contrast, $\delta^{13}\text{C}$ values of *Morozovella* suggest it continued to inhabit a shallower mixed-layer habitat maintaining its symbiotic relationships that allowed it to reach larger sizes. While a large size would generate large number of gametes, the abundance of the species dropped showing a loss of fitness. The recorded changes in size and abundance indicate that *Acarinina* was the ecologically more flexible taxon during the EECO. Size reduction may have allowed this taxon to optimize the energy use under warming and nutrient-limited environmental conditions. A deeper habitat may have enabled acarininids to exploit different thermal and nutrient niches, thereby enhancing their long-term survival chances compared to *Morozovella*. These more resilient species became dominant, maintaining ecosystem function despite environmental stress. Our records suggest that the time interval after ETM2 but prior to the EECO onset played a crucial role in the changeover between the two genera, when acarininids gradually adapted to substitute morozovellids as the most common mixed-layer group at the EECO.

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Morozovella aragonensis (Nuttall, 1930).
Morozovella caucasica (Glaessner, 1937).
Morozovella crater (Hornibrook, 1958).
Morozovella formosa (Bolli, 1957).
Morozovella gracilis (Bolli, 1957).
Morozovella lensiformis (Subbotina, 1953).
Morozovella marginodentata (Subbotina, 1953).
Morozovella subbotinae (Morozova, 1939).
Morozovella velascoensis (Cushman, 1925).
Orbulina universa D’Orbigny, 1839.
Subbotina Brotzen and Pozaryska, 1961.
Trilobatus sacculifer (Brady, 1877).

CRedit authorship contribution statement

Giulia Filippi: Writing – review & editing, Writing – original draft, Visualization, Validation, Resources, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Daniela N. Schmidt:** Writing – review & editing, Writing – original draft, Visualization, Validation, Supervision, Resources, Project administration, Methodology, Funding acquisition, Formal analysis, Conceptualization. **Silvia Sigismondi:** Writing – review & editing, Investigation, Data

curation. **Valeria Luciani:** Writing – review & editing, Writing – original draft, Visualization, Validation, Supervision, Resources, Project administration, Methodology, Funding acquisition, Formal analysis, Data curation, Conceptualization.

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.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.palaeo.2025.112840>.

Data availability

Data will be made available on request.

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