



Contents lists available at ScienceDirect

Marine Micropaleontology

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

Morphometric changes in *Watznaueria barnesiae* across the mid Cretaceous: Paleocological implications

Chiara Bettoni^{a,*}, Elisabetta Erba^a, Silvia Castiglione^b, Pasquale Raia^b, Cinzia Bottini^a

^a Università degli Studi di Milano, Dipartimento di Scienze della Terra "Ardito Desio", Via Mangiagalli 34, Milano 20133, Italy

^b Università degli studi di Napoli Federico II, Dipartimento di Scienze della Terra, dell'Ambiente e delle Risorse, Via Cintia 21, Napoli 80126, Italy

ARTICLE INFO

Keywords:

Cretaceous
Calcareous nannofossils
Morphometry
Oceanic Anoxic Events

ABSTRACT

This study reveals moderate yet important variations in *Watznaueria barnesiae* coccolith and central unit size throughout the Aptian–late Cenomanian (27 my) time interval in western Tethys. A new statistical approach was applied to determine whether non-random size trends apply to these metrics and to identify possible links between their variation and fertility or temperature. During OAE 1a, *W. barnesiae* coccoliths were the smallest and the most elliptical, with reduced central unit size. A further minor size decrease occurs during OAE 1b but not during OAE 1d. From the middle Albian to the middle Cenomanian, larger and less elliptical coccoliths are observed, with unchanged central unit dimensions. These results, together with concomitantly larger size changes in *Biscutum constans* confirm that *W. barnesiae* is a tolerant taxon. High-frequency, high-amplitude paleoenvironmental changes during the Aptian–early Albian indicate that temperature and fertility – either individually or in combination – had no direct impact on the mean coccolith size and potentially other factors affected coccolith size. Instead, lower nutrients with lower temperatures probably played a role in promoting larger *W. barnesiae* but smaller *B. constans* coccoliths during the middle Albian–Cenomanian. The size and ellipticity changes during OAE 1a and 1b were the strongest, likely resulting from ocean acidification and trace metal inputs, in addition to (or independently of) fertility and temperature variations.

1. Introduction

The morphometrics of coccoliths and nannoliths in the geological record have been the focus of several works aimed at highlighting size and/or shape variations in relation to past environmental perturbations (e.g. Mattioli et al., 2004; Bornemann and Mutterlose, 2006; Mattioli et al., 2009; Erba et al., 2010; Linnert and Mutterlose, 2012; Barbarin et al., 2012; Lübke et al., 2015; Lübke and Mutterlose, 2016; Peti and Thibault, 2017; Faucher et al., 2017; Ferreira et al., 2017; Erba et al., 2019; Gollain et al., 2019; Bottini and Faucher, 2020; Wulff et al., 2020; Möller et al., 2020; Faucher et al., 2022). Calcareous nannoplankton are known to be sensitive to chemical and physical ocean parameters such as nutrient and light availability, seawater temperature, trace metal and CO₂ concentrations. Most morphometric studies performed on Mesozoic coccoliths and nannoliths focused on relatively short-time intervals characterized by extreme and/or peculiar paleoenvironmental conditions such as those occurred during Ocean Anoxic Events (OAEs). These results show that the most sensitive coccolith-bearing species known is *Biscutum constans* followed by *Zeughrabdodus erectus* and *Discorhabdus*

rotatorius (e.g., Bornemann and Mutterlose, 2006; Erba et al., 2010; Lübke and Mutterlose, 2016; Faucher et al., 2017; Bottini and Faucher, 2020; Möller et al., 2020; Wulff et al., 2020). In contrast, *Watznaueria barnesiae* was a dominant and ubiquitous species in Lower Cretaceous sediments which were little affected by major environmental changes. Small or no size variation in *Watznaueria* occurs across the Valanginian Weissert-OAE (Gollain et al., 2019; Möller et al., 2020), the early Aptian OAE 1a (Erba et al., 2010; Lübke and Mutterlose, 2016), the late Albian OAE 1d (Bornemann and Mutterlose, 2006) and the latest Cenomanian OAE 2 (Linnert and Mutterlose, 2012; Faucher et al., 2017). A size increase in *W. barnesiae* coccoliths was nonetheless detected across the Barremian Hauptblättertun (Wulff et al., 2020) and in the aftermath of the Weissert-Event (Gollain et al., 2019; Möller et al., 2020). The presence of several smaller and more elliptical *W. barnesiae* coccolith was further reported during OAE 1a (Erba et al., 2010). Over longer periods, Linnert et al. (2014) found no robust evidence for significant size changes in *W. barnesiae* across the Cenomanian to Maastrichtian. Conversely, size variations were detected in *B. constans* coccoliths over the latest Barremian to Cenomanian interval (Bottini and Faucher,

* Corresponding author.

E-mail address: chiara.bettoni@unimi.it (C. Bettoni).

<https://doi.org/10.1016/j.marmicro.2024.102343>

Received 19 July 2023; Received in revised form 19 December 2023; Accepted 23 January 2024

Available online 6 February 2024

0377-8398/© 2024 The Authors. Published by Elsevier B.V. This is an open access article under the CC BY-NC-ND license (<http://creativecommons.org/licenses/by-nc-nd/4.0/>).

2020) although not unambiguously correlated with paleotemperature and/or paleofertility.

Thus, although many abiotic characteristics were found to be associated with size changes in Mesozoic calcareous nannofossils, their mutual effects and/or their significance are unknown. Species like *W. barnesiae* seem to defy simplistic models of reaction to environmental change. In this regard, the study of longer-time intervals may help shed light on the influence of these ecological/physical parameters on size and shape of coccoliths.

Herein, we studied coccolith size and shape of *W. barnesiae* and *B. constans* across a ca. 27 myr-long interval spanning the Aptian–late Cenomanian time interval, which includes OAE 1a, OAE 1b and OAE 1d. We selected samples from well-dated sections in the Umbria-Marche Basin (Piobbico Core and Monte Petrano section) and the Belluno Basin (Cismon Core) to gather a morphometric record of *W. barnesiae* coccoliths. The same sections were previously investigated for *B. constans* morphometries (Bottini and Faucher, 2020) and used to reconstruct a composite nannofossil record of paleotemperature and paleofertility (Bottini et al., 2015; Bottini and Erba, 2018).

The aims of this work are to: 1) test whether *W. barnesiae* shows any detectable size variation of the coccolith and the central unit through the Aptian–late Cenomanian time interval; 2) test whether *W. barnesiae* size displays different trends during OAEs compared to intervals not marked by extreme paleoenvironmental conditions; 3) identify any influence of temperature and nutrient on long-term size variations; 4) observe whether *W. barnesiae* and *B. constans* experienced similar size changes.

2. Material and methods

2.1. Studied sections

We investigated size variations of the total coccolith and the central unit in *W. barnesiae* by sampling specimens from the uppermost Barremian to the upper Cenomanian recorded in a composite section which includes three sedimentary successions: the Cismon Core in the Belluno Basin (Southern Alps, Italy), the Piobbico Core and the Monte Petrano section in the Umbria-Marche Basin (Fig. 1).

The Piobbico Core was drilled at “Le Breccie” (43°35′ 3.78″ N/12°29′10.09″ E) about 3 km west of the town Piobbico (Marche, Italy) in the central Apennines. The sedimentary sequence was deposited in a

portion of the southern Tethyan passive margin (Tiraboschi et al., 2009). The total core length is 84 m with an excellent recovery (98%). The drilling penetrated the entire Marne a Fuocidi Formation, including the upper transition to the Scaglia Bianca and the lower transition to the Maiolica (Erba, 1992). The total stratigraphic thickness of the studied interval of the Piobbico Core is 62.5 m (71.02 to 8.5 m) and includes the 113 Level (50.65–5.5 m), Kilian Level (45.13–44.8 m) and the Urbino Level (38.95–38.68 m).

The Monte Petrano section (43° 30′16.14″ N / 12° 36′50.94″ E) is located north of the city of Cantiano, South-Est to the Piobbico Core drill site. The stratigraphic sequence consists of the Scaglia Bianca characterized by whitish limestones with black shales layers of the Pialli Level in the lower part of the OAE 1d carbon-isotope excursion (Schwarzacher, 1994; Giorgioni et al., 2012; Gambacorta et al., 2014). The lithological shift to organic-rich black shales and black chert bands alternated with whitish limestone corresponds to the Mid Cenomanian Event (MCE). Moreover, this section contains the Bonarelli Level (OAE 2) (Gambacorta et al., 2015). The thickness of the studied interval is 55.5 m (–8–63.5 m).

The Cismon Core was drilled in the Venetian Southern Alps of northern Italy, west of the town of Feltre. The drill site paleogeographically is located at the eastward deepening slope between the Trento Plateau and the Belluno Basin (Erba et al., 1999). The total stratigraphic thickness is 116.71 m with 100% recovery. The sedimentary succession includes the Selli Level (OAE 1a) a 5 m thick interval (23.67–18.64 m) characterized by marlstones alternating with black shales and radiolarian-rich beds (Erba et al., 1999). The studied interval covers 13.3 m, from 32.39 to 19.05 m.

2.2. Morphometry

A total of 105 samples were investigated as follows: 64 samples from the Piobbico Core, 30 from the Monte Petrano section and 11 from the Cismon Core. Morphometric analyses of *W. barnesiae* coccoliths were carried out in smear slides under polarized light microscope at 1250× magnification, prepared using the standard technique described by Bown and Young (1998).

For each sample, 30 pictures were digitally and randomly captured with an Olympus DS73 camera mounted on a Leica light-microscope. Length and width of the total coccolith and those of the central unit

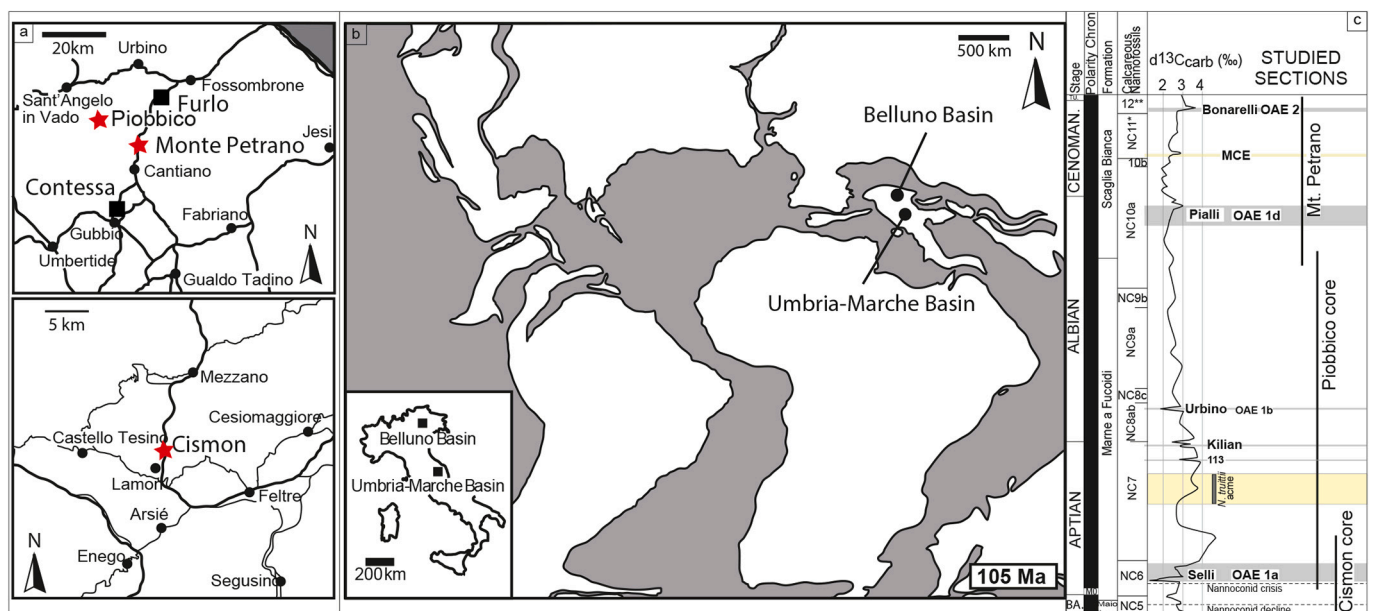


Fig. 1. a) Present-day and b) paleogeographic location of studied sections modified from Gambacorta et al. (2015), c) stratigraphic range of the studied sections across the Aptian–late Cenomanian interval (from Bottini and Faucher, 2020).

were measured with ImageJ using the macros by Young et al. (2014) (Fig. S1). The error of measurements is $\pm 0.08 \mu\text{m}$. Specimens of *W. barnesiae* previously measured by Erba et al. (2010) were analyzed here with this methodology and also for the central unit size.

2.3. Statistics

The morphometric results were elaborated to calculate the coccolith ellipticity (length to width ratio) and central unit (c.u.) ellipticity (c.u. length/c.u. width), total area, mean, median, maximum and minimum values, 95% confidence intervals, standard deviation and the linear regression between length and width.

Data were statistically analyzed within the R software to determine if there are significant differences between *W. barnesiae* size variations in the stratigraphic intervals. First, given the different sample size and distribution among intervals, we devised a bootstrap randomization test to evaluate the difference between stratigraphic intervals for each variable (length and ellipticity) and species. The advantage of this approach, as compared to parametric statistical tests (i.e. *t*-test), lays in the absence of any a-priori assumption about the distribution of sample variables and their relative abundance.

Furthermore, we compared variables per intervals by taking into account the effect of Nutrient Index (NI) and Temperature Index (TI) (from Bottini et al., 2015; Bottini and Erba, 2018), and which stratigraphic interval the measured specimens come from (inclusive of OAEs within major intervals) by means of generalized linear model regressions (glm). The same regression models were repeated within major stratigraphic intervals to test for the consistency between long-term (the whole sections) and short-term trends. Finally, marginal means of individual variables per interval were calculated and contrasted between intervals and OAEs using the package emmeans (Lenth, 2023).

3. Results

3.1. Calcareous nannofossil preservation

Calcareous nannofossils are generally common to abundant in the studied composite section. The nannofossil preservation was assessed under light polarizing microscope to ascertain the degree of etching and/or overgrowth according to the visual criteria of Roth (1983) and Roth and Thierstein (1972). As described in previous works (Erba and Larson, 1998; Erba et al., 2010; Bottini and Erba, 2018; Bottini and Faucher, 2020) the nannofossil preservation is moderate and the occurrence of dissolution-prone species (e.g., *D. rotatorious*, *B. constans*, *Z. erectus*) through the investigated interval suggests negligible influence of diagenesis on the original species assemblages. Moreover, the long-term morphometric analysis was conducted on the same lithologies (marly limestone and limy marlstones), yielding homogeneous and moderate preservation. The specimens photographed and measured are complete coccoliths with no signs of corrosion and/or overgrowth in the outline and in the central area. Therefore, differential preservation cannot be held responsible for any documented size change.

3.2. *Watznaueria barnesiae* size variations

W. barnesiae total coccolith and central unit lengths are linearly correlated with the width of the coccolith ($R^2_{\text{coccolith}}: 0.92$) (Fig. S2A) and the central unit ($R^2_{\text{central unit}}: 0.82$), respectively (Fig. S2B). Consequently, in this study we only discuss variations of the coccolith and the c. u. length (Fig. 2). Only during OAE 1a and OAE 1b the variations of the two parameters did not occur with the same amplitude producing more elliptical specimens.

Over the study interval, the total coccolith length of *W. barnesiae* displays great variability ranging from minimum mean value of $2.90 \mu\text{m}$ to maximum mean value of $8.96 \mu\text{m}$ with mean length of $6.53 \mu\text{m}$ (standard deviation = 0.92) (Fig. S3). The central unit length ranges

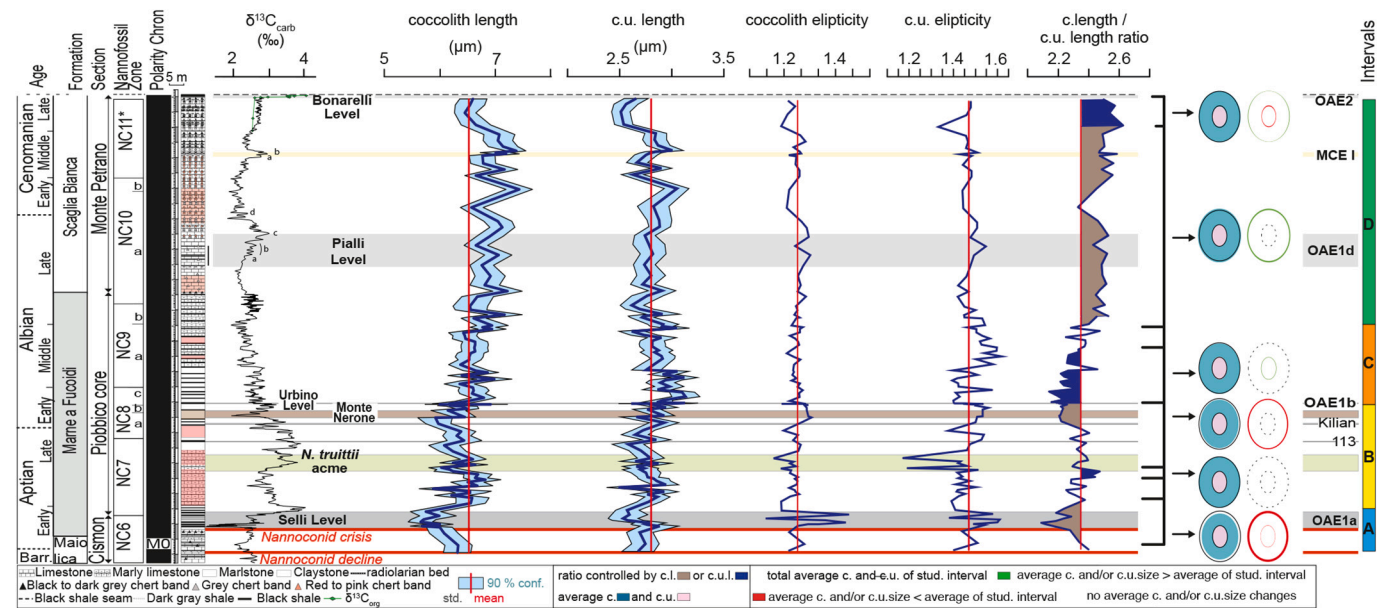


Fig. 2. Coccolith (c.) and central unit (c.u.) length record of *W. barnesiae* across the Aptian–late Cenomanian interval. Coccolith and central unit ellipticity (length/width) and the ratio between the coccolith and the central unit length. The drawing of coccolith and central unit shows the areal difference between coccolith and central unit average of the studied interval. The red area indicates how smaller the coccolith and/or the central unit average size are compared to the coccolith and the central unit average in the interval (A, B, C and D respectively). The green area indicates how larger the coccolith and/or the central unit average size are compared to the coccolith and the central unit average in the interval (A, B, C and D respectively). The composite section includes, from bottom to top: i) Cisoni Core, ii) Piobbico Core and iii) Monte Petrano section. Morphometric data are correlated with the $\delta^{13}\text{C}$ curve (5-point moving average) from Bottini and Erba (2018). Intervals A, B, C and D are defined in this work based on morphometries. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

from 1.27 to 5.49 μm with mean length of 2.80 μm (standard deviation = 0.45) (Table S1). Our dataset also shows that the central unit length did not change proportionally to the coccolith length causing a variable coccolith length/central unit length ratio (L/l) (Fig. 2).

The description of length fluctuations of *W. barnesiae* was made considering four consecutive stratigraphic intervals (A, B, C and D) identified based on a group of samples with coccolith length values lower, equal or higher than the overall mean of the coccolith length (Fig. 2).

The four intervals are described as follows:

Interval A includes 11 samples and extends for 13.34 m, from immediately below the Nannoconid decline to the top of the Selli Level thus encompassing OAE 1a. The interval is characterized by relatively smaller specimens (average length 5.90 μm) than the grand mean (Fig. 3a and S3). The central unit average length (mean = 2.69 μm) is also relatively smaller compared to the grand average (Fig. 3b and S4). The low L/l ratio is mostly controlled by the coccolith length which shows a more pronounced decrease compared to the central unit length (Fig. 2).

Interval B includes 29 samples and covers 32 m from the top of the Selli Level to the base of the Urbino Level, including the *N. truttii* acme, 113 Level and Kilian Level. The average coccolith length (6.37 μm) is slightly shorter than the grand mean, whereas the central unit length (average 2.78 μm) is close to the grand mean (Fig. S3 and S4). The L/l ratio is very close to the average L/l ratio of the total studied interval (Fig. 2).

Interval C comprises 37 samples and encompasses 29.79 m between the base of the Urbino Level and the end of nannofossil subzone NC9a (80.29 m). The coccolith length is almost the same as the grand mean (average 6.58 μm) (Fig. 3a and S3), while the average central unit length is larger (2.89 μm in average) than the grand mean (Fig. 3b and S4). The low L/l ratio in interval C is controlled by the central unit length, which shows a relative increase not paralleled by an increase in the coccolith length (Fig. 2). Interval D includes 37 samples and extends for 61.01 m from the top of the nannofossil subzone NC9a to the base of the Bonarelli Level.

Interval D is characterized by larger specimens (average length 6.88 μm) than the grand mean whereas the central unit length does not

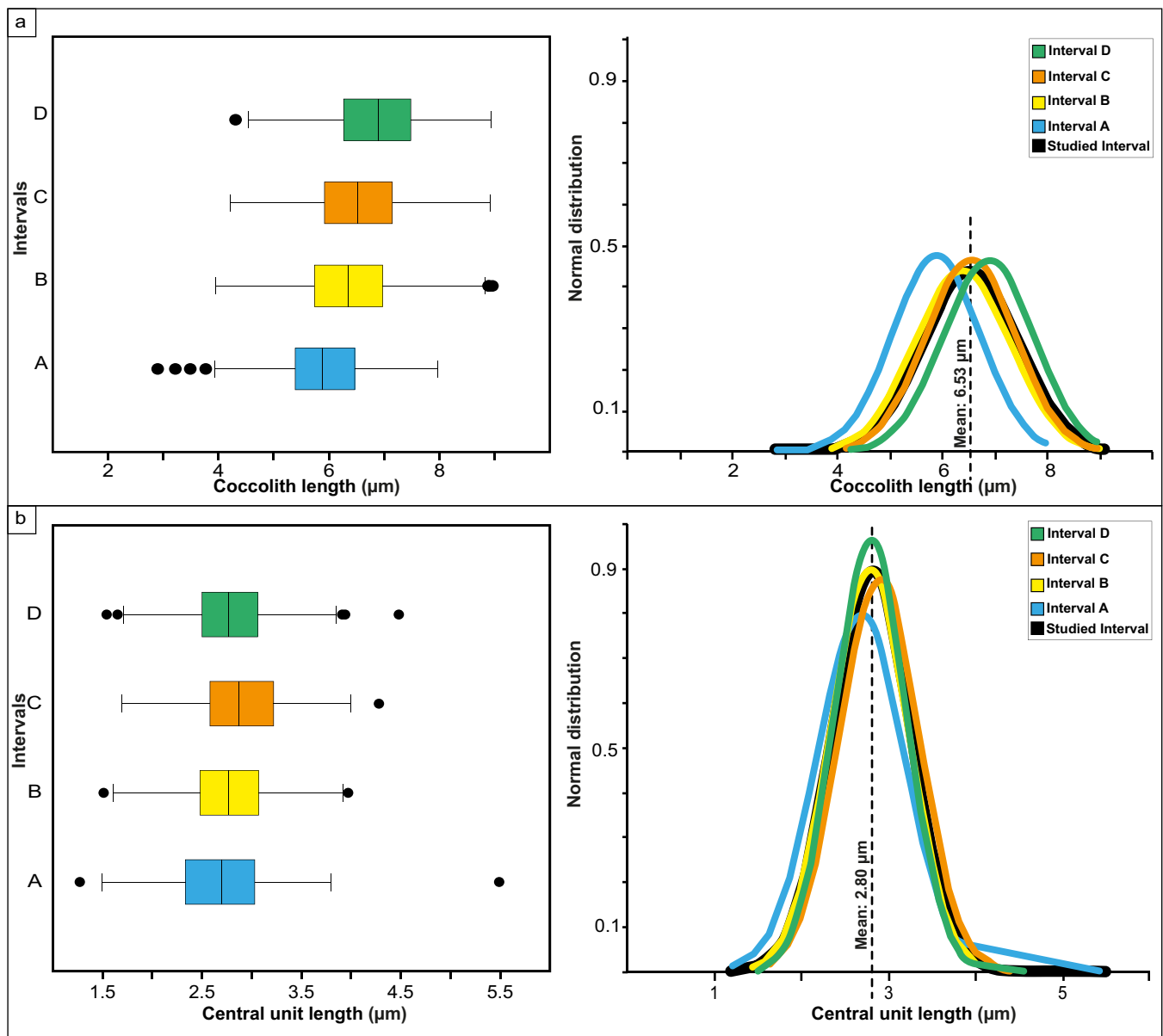


Fig. 3. Box plots and gaussians of the total *W. barnesiae* coccolith length (a) and central unit length (b) relative to the four intervals identified. The left and right limits of each box plot are the 25 and 75 percentiles. The line in the middle of the box plots is the median.

present any variations related to the total mean length of the central unit (2.79 μm) (Fig. 3b and S4). In interval D, the L/l ratio is higher than the total mean but for most of the interval this is controlled by coccolith length which shows a larger increase (Fig. 2). Close to the topmost part of interval D, the higher L/l ratio values are instead related to a more pronounced decrease of the central unit length with respect to the coccolith length (Fig. 2).

When compared, the four intervals exhibit significantly different mean values as follows.

In interval A the coccolith mean length (5.90 μm) is smaller than in the other intervals ($p = 0.033$). The mean length (6.37 μm) in interval B is smaller than in interval C ($p = 0.017$) and the mean length (6.58 μm) in interval C is smaller than in interval D ($p = 0.004$). Interval D is characterized by the largest coccoliths (mean length 6.88 μm) being ca. 0.3 μm larger than the total average length and also less elliptical (Fig. S5). At the end of interval D, from the middle Cenomanian (post Mid Cenomanian Event) to the OAE 2 onset, *W. barnesiae* coccoliths display a minor length decrease to average coccolith length of 6.57 μm (Fig. 2). In total, the dataset collected shows a neat trend towards larger *W. barnesiae* coccoliths from the bottom of the study section upward with a total delta of 1 μm .

The central unit does not show significant differences among intervals, except for interval C (2.91 μm) where it is statistically larger than in any other interval ($p < 0.001$).

No other statistically significant differences were found in coccolith ellipticity among intervals whereas the ellipticity of the central unit is statistically lower in interval B than in any other intervals ($p = 0.010$).

3.3. *W. barnesiae* size variations across OAEs

The studied interval encompasses three OAEs, namely OAE 1a, OAE 1b and OAE 1d. *W. barnesiae* shows smaller coccoliths during OAE 1a and OAE 1b but no significant size changes during OAE 1d (Fig. 4). Particularly, in OAE 1a the average coccolith length is 5.75 μm representing a decrease of 0.3 μm compared to the total average values, also the average ellipticity increases of 0.05. In this interval, coccoliths are also characterized by smaller (average length 2.63 μm) and more

elliptical central unit. During OAE 1b *W. barnesiae* also displays a temporary size decrease to average coccolith length of 6.30 μm (0.06 μm reduction) with specimens becoming less elliptical (average 1.21) than in pre-OAE 1b (Fig. 4).

Although the mean coccolith length in OAE 1a is the smallest (5.74 μm), it does not statistically differ from the mean total length in interval A ($p = 0.965$) (Fig. 4b and S6). The mean size in OAE 1b (6.30 μm) is not statistically different from the mean calculated over interval B ($p = 0.369$) (Fig. 4a and S6). Eventually, the mean size in OAE 1d (6.90 μm) does not statistically differ from the mean in D ($p = 0.505$) (Fig. S6). Intriguingly, the central unit length does not follow the same pattern except for OAE 1a characterized by a central unit length statistically smaller than in the rest of the study samples (mean in OAE 1a = 2.65 μm , $p = 0.002$) (Fig. 4b and S7).

An increase in total ellipticity is detected only during OAE 1a compared to the rest of the study samples ($p < 0.001$). In summary, there is the evidence of *W. barnesiae* coccolith size increase over time which is not followed by either the central unit size or the coccolith ellipticity and does not depend on OAEs.

3.4. *W. barnesiae* and *B. constans* size versus paleoenvironmental factors

We compared *W. barnesiae* size variations to the nannofossil-based Temperature Index (TI) and Nutrient Index (NI) (as provided in Bottini and Erba, 2018) by applying a generalized linear model (glm) regressions of total coccolith length against TI, NI, and both indices in interaction, and compared the likelihoods of the different regression models by means of Akaike Information Criterion (AIC). Although the AIC gain of the most complex model is modest (AIC_{TI} = 102.02, AIC_{NI} = 101.95, AIC_{TI-NI} = 101.16) it indicates a significant and positive effect of nutrients (surface-water fertility) on total length (slope = 0.007, $p = 0.037$) and a negative and marginally significant effect of temperature and nutrients in interaction (slope = -0.0003, $p = 0.079$). We calculated the marginal means of total coccolith length per interval while accounting for NI by using the function *emmeans* in the package *emmeans* (Lenth, 2023). The results indicate significantly smaller coccoliths in interval A compared to C ($p = 0.015$) and to D ($p < 0.001$), smaller

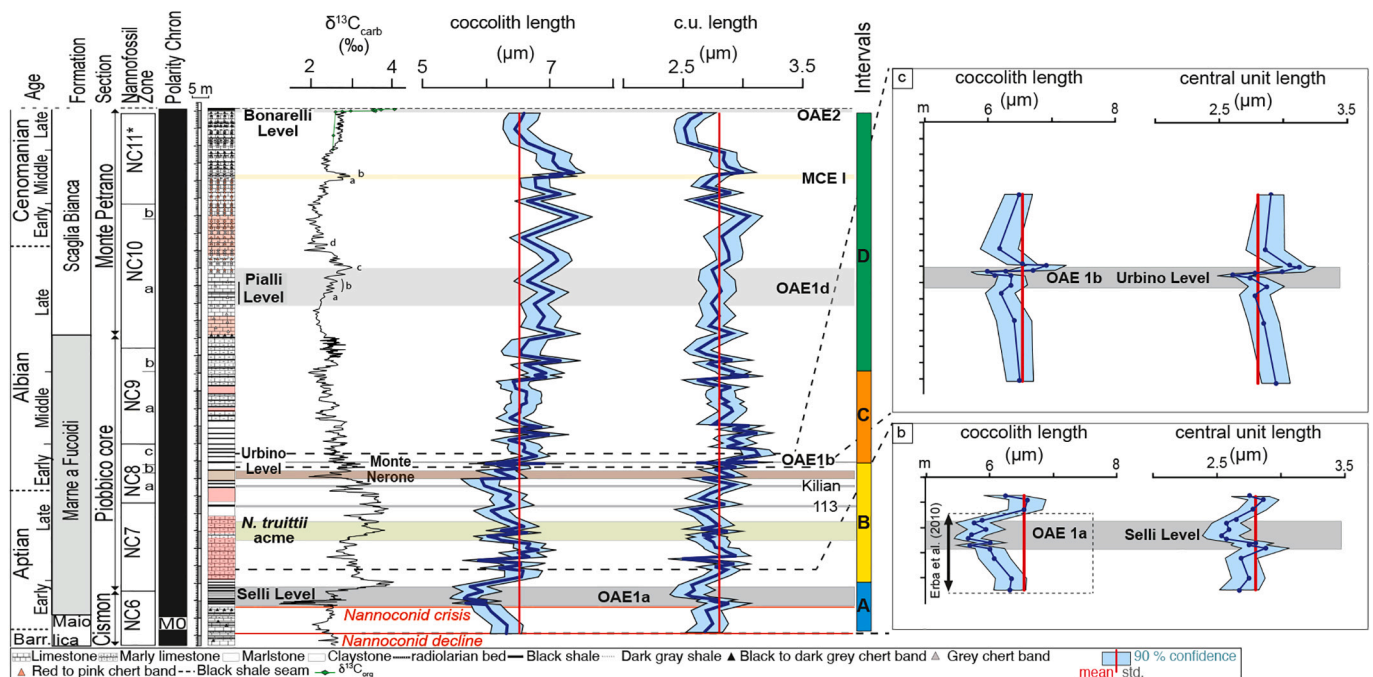


Fig. 4. a) *W. barnesiae* coccolith and central unit (c.u.) length record through the Aptian-late Cenomanian interval. Focus plot of coccolith and central unit length across b) OAE 1a and c) OAE 1b.

coccoliths in B compared to C ($p = 0.013$) and to D ($p < 0.001$), and no difference between coccolith length during the OAEs and intervals in which are included. The morphometric data show increasingly larger *W. barnesiae* coccoliths towards to the top of the study interval and that, in the long-term, nutrients have a positive effect on the total coccolith length when the interaction with temperature is considered. Such relationship disappears within intervals A, B and C (i.e. over the short time scale). In interval D, the best model is obtained considering temperature and nutrients in interaction ($AIC_{TI-NI} = 6.712$; $AIC_{NI} = 7.425$) and nutrients were found to exert a significant and negative effect on total coccolith length (slope = -0.009 ; $p = 0.021$). The coccolith and central unit ellipticity does not show any significant fluctuation although in interval A the coccoliths and the central units of *W. barnesiae* are more elliptical than in intervals B, C and D (Fig. 2). The average coccolith ellipticity is lower (1.24) than the average central unit ellipticity (1.47) and, in all intervals, there is no association between coccolith and central unit ellipticity and the coccolith and the central unit length (Fig. S8). We repeated glm regressions on both central unit length and on coccolith ellipticity. We found the statistically large central unit length in interval C to be entirely due to high nutrients and low temperature (Fig. 5). Significant and negative effects were found by temperature on central unit lengths in both intervals B and D. The glm models indicate that the large total ellipticity during OAE 1a is statistically linked to low NI and low TI (=warmer conditions). Size variation in *B. constans* shows that *B. constans* coccolith length is influenced by both nutrients and temperature, although the effect of the former plays the converse as with *W. barnesiae*. Irrespective of whether TI or NI is used as predictor, *B. constans* ellipticity is not significantly influenced by either temperature or nutrients or their interaction over the entire sample.

4. Discussion

4.1. Influence of paleoenvironmental changes on *W. barnesiae*

W. barnesiae is considered to be among the least sensitive nannofossils to paleoenvironmental changes. In fact, previous morphometric studies that focused on *Watznaueria* species (*W. barnesiae*, *W. fossacinta*, *W. manivittae*) did not identify consistent coccolith size and ellipticity

changes during either short-term (Lübke and Mutterlose, 2016; Bornemann and Mutterlose, 2006; Linnert and Mutterlose, 2012; Faucher et al., 2017; Bruno et al., 2022) or long-term intervals (Linnert et al., 2014), except for moderate size/shape changes detected by Erba et al. (2010), Gollain et al. (2019), Wulff et al. (2020) and Möller et al. (2020). Understanding the reason for such modest size variation is uneasy and still matter of debate. A possible dependence of *W. barnesiae* size on nutrient availability was suggested by Wulff et al. (2020) and Gollain et al. (2019) who detected larger coccoliths in correspondence of lower surface-water fertility in the Barremian Hauptblättern and in the aftermath of the Weissert Event, respectively. Möller et al. (2020) also identified a size increase in *W. barnesiae* specimens after the Weissert Event but associated this change with a nutrient increase from a double source, namely continental runoff and volcanic activity. Malformed coccoliths across OAE 1a (Erba et al., 2010) and the latest Aptian-middle Albian time interval (Bruno et al., 2022) were instead interpreted as the result of ocean acidification.

Our study highlights moderate and yet apparent variations in *W. barnesiae* size in the long-term. Specifically, coccolith average size is generally smaller across the Aptian (Intervals A, B, C), than during the middle Albian to upper Cenomanian (Interval D). The smallest (and elliptical in shape) coccoliths are detected during the early Aptian across OAE 1a. In order to detect and link such morphometric changes to environmental conditions, we used a new statistical approach never applied in this context which compares dimensional variation with temperature and fertility indices, as derived from Bottini and Erba (2018). Other environmental parameters (e.g., CO₂) were not included in the statistics due to the lack of long-term datasets with equivalent resolution.

We found evidence for a possible dependence of *W. barnesiae* size on lower surface-water fertility and, to a lesser extent, on lower surface-water temperature during the middle Albian to Cenomanian interval. This dependence does not apply to the Aptian-lower Albian period. Possibly, the absence of statistical dependence between *W. barnesiae* size and nutrient or fertility might depend on the highly variable paleoenvironmental conditions that characterized this period, whereas during the middle Albian-Cenomanian, the relative and prolonged stability might have promoted the evolution of larger coccoliths (Fig. 5).

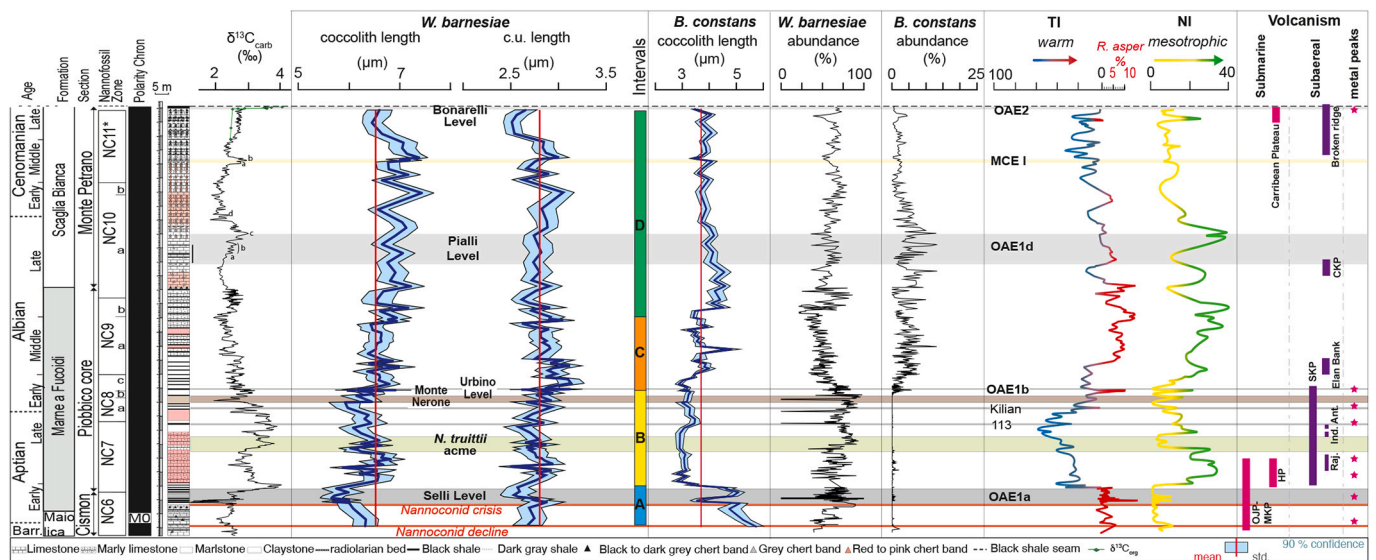


Fig. 5. *W. barnesiae* size variations through the Aptian-late Cenomanian time interval with *B. constans* morphometric data from Bottini and Faucher (2020). *W. barnesiae* abundance, Temperature and Nutrient Index from Bottini and Erba (2018). Large Igneous Province radiometric ages are based on Coffin et al. (2002), Duncan (2002), Hoernle et al. (2010), Timm et al. (2011), Chambers et al. (2004). Ontong Java Plateau (OJP), Manihiki Plateau (MP), Hikurangi Plateau (HP), Southern Kerguelen Plateau (SKP), Central Kerguelen Plateau (CKP), Rajmahal Traps (Raj.), Indian Lamprophyre (Ind.), Antarctic Lamprophyre (Ant.). Metal peaks are from Erba et al. (2015).

A different response in the long-term is detected in the size changes of the coccolith central unit length, with the largest values corresponding to interludes of cooler temperatures but higher nutrient availability, as observed for the middle Albian (Interval C).

The more pronounced size variations of *W. barnesiae* occurs during OAE 1a and OAE 1b (Fig. 4), marked by coccolith and central unit size reduction. Erba et al. (2010) already highlighted the presence of small and malformed *W. barnesiae* coccoliths across the negative $\delta^{13}\text{C}$ anomaly (nCIE) in the early phase of OAE 1a, albeit without significant variations in the mean dimension. In this work, results confirm that the coccoliths across OAE 1a do not show significant size changes. However, when compared to the morphometric record of the late Aptian–late Cenomanian, OAE 1a specimens are the smallest and the most elliptical. Therefore, OAE 1a is confirmed to have been characterized by extreme paleoenvironmental conditions – most extreme during the nCIE – that must have affected calcareous nanoplankton average size. Consequently, as already suggested by Erba et al. (2010, 2015), across OAE 1a nutrients and temperatures alone did not play a significant role in nanoplankton calcification. Rather ocean acidification and biolimiting/toxic metals linked to the volcanic activity of the Ontong Java Plateau were instrumental to recorded size and shape changes.

A considerable decrease in *W. barnesiae* size is also recorded during OAE 1b. Therefore, like during the nCIE of OAE 1a, the size reduction might be the result of an extreme disturbance caused by a variation in water chemistry following the volcanic activity of the Kerguelen Plateau responsible for the hyperthermal associated with OAE 1b (e.g., Bottini and Erba, 2018; Sabatino et al., 2018; Matsumoto et al., 2020).

Contrarily, across OAE 1d *W. barnesiae* coccoliths do not show noticeable changes in size, resembling observations made by Bornemann and Mutterlose (2006) in the Vocontian Basin. This unaffected size might mirror the nature of OAE 1d that, as highlighted by both nanofossil and geochemical data (Bornemann and Mutterlose, 2006; Gambacorta et al., 2020), was associated with minor paleoenvironmental changes, which is consistent with the moderately steady warm climates and low fertility levels.

4.2. *W. barnesiae* vs *B. constans* size variations

The morphometric data of *W. barnesiae* compared to *B. constans* size variations (Bottini and Faucher, 2020) confirms that, in keeping with earlier reports (Bornemann and Mutterlose, 2006; Erba et al., 2010; Lübke and Mutterlose, 2016; Faucher et al., 2017; Bottini and Faucher, 2020; Möller et al., 2020, this study) *W. barnesiae* is the least sensitive of the pair. Our results show that the long-term morphometric fluctuations of *W. barnesiae* are of the order of $\pm 5\%$, clearly much smaller than those of *B. constans* whose size fluctuated by $\pm 12\%$. This disparity can be attributed to the different species affinity, K-strategist for *W. barnesiae* and R-strategist for *B. constans*, which therefore adapted more rapidly when subjected to environmental stress conditions. The pronounced environmental instability during the Aptian might have influenced the average size of both species, albeit the effect is more evident in *B. constans*. However, the role played by temperature and fertility is unclear and the production of smaller coccoliths was probably mainly influenced by other factors. It is known that the Aptian was characterized by intense LIP activity, both submarine and subaerial, which was almost absent during the middle–late Albian.

The new statistical approach applied here highlights the combination of low nutrients and low temperature to produce larger *W. barnesiae* coccoliths in the middle Albian–Cenomanian, while the coccolith size of *B. constans* remained close to the average. This outcome underlines the distinct paleoecological affinities of the two species confirming previous reconstructions separating oligotrophic *W. barnesiae* from mesotrophic *B. constans*. The comparison of the long-term data with the record of short-lived events highlights two additional aspects: firstly, it indicates that during extreme paleoenvironmental conditions (namely during the nCIE of OAE 1a and during OAE 1b), both species exhibited a reduction

in size regardless of temperature and nutrient conditions, emphasizing the influence of third factors (e.g., ocean acidification); secondly, it confirms that *W. barnesiae* is more tolerant even under extreme conditions because it responded with minor variations compared to *B. constans*.

5. Conclusions

The morphometric study performed on *Watznaueria barnesiae* across the Aptian–late Cenomanian in the western Tethys region provides several key findings. Firstly, *W. barnesiae* evidence moderate but significant variations in coccolith and central unit size either in the long term and during extreme, short-lived events. The smallest and more elliptical coccoliths with reduced central units are observed in the initial phase of the early Aptian OAE 1a. In the late Aptian to early Albian, coccoliths exhibit sizes close to the overall mean. A minor decrease in size coincides with the early Albian OAE 1b. From the middle Albian to the Cenomanian, larger and less elliptical coccoliths are observed, with no significant changes in the central unit dimension.

Our study highlights the contrasting size variations between *W. barnesiae* and *B. constans* within the same time interval: *W. barnesiae* turned out to be more tolerant compared to *B. constans* which shows more pronounced, higher amplitude size variations and at different times compared to those of *W. barnesiae*.

The new statistical approach applied on long-term and Oceanic Anoxic Events (OAEs) data displays that during OAE 1a and OAE 1b, both *W. barnesiae* and *B. constans* were probably influenced by exceptional paleoenvironmental stress such as excess CO_2 and biolimiting trace metals rather than nutrients and temperature changes. Nevertheless, the two species responded differently in time and size deltas. *W. barnesiae* average size did not change significantly throughout OAE 1a but average values were smaller compared to younger record. During the n-CIE malformed and most elliptical *W. barnesiae* coccoliths were encountered. *B. constans* displayed instead a major size drop and ellipticity increase only during the n-CIE and returned to total average size values afterwards during OAE 1a.

Also in the Aptian, there was no clear primary control of temperature and fertility on average coccolith size, probably suggesting the high frequency and amplitude of the environmental perturbations which occurred in this period, involving the interplay of multiple factors such as ocean acidification and biolimiting trace metals related to LIP activity. Only during periods of greater stability, like the middle Albian to Cenomanian time interval, the combination of nutrients and temperature controlled the coccolith size, with larger *W. barnesiae* promoted by lower nutrients and lower temperature and the opposite for *B. constans*.

CRediT authorship contribution statement

Chiara Bettoni: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Software, Validation, Visualization, Writing – original draft. **Elisabetta Erba:** Funding acquisition, Resources, Supervision, Writing – review & editing. **Silvia Castiglione:** Data curation, Formal analysis, Methodology, Software, Validation, Writing – review & editing. **Pasquale Raia:** Data curation, Formal analysis, Methodology, Software, Validation, Writing – review & editing. **Cinzia Bottini:** Conceptualization, Data curation, Funding acquisition, Project administration, Resources, Supervision, Validation, 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.

Data availability

Data will be made available on request.

Acknowledgments

This research was funded through Seal of Excellence (SoE) SEED 2022 – Università degli Studi di Milano) “#OceansInShape” to C. Bottini and PRIN 2017RX9XXY to E. Erba. The work was also partly supported by the Italian Ministry for Universities and Research (MUR) through the project “Dipartimenti di Eccellenza 2023-27.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.marmicro.2024.102343>.

References

- Barbarin, N., Bonin, A., Mattioli, E., Puc at, E., Cappetta, H., Gr eselle, B., Pittet, B., Vennin, E., Joachimski, M., 2012. Evidence for a complex Valanginian nannoconid decline in the Vocontian basin (South East France). *Mar. Micropaleontol.* 84, 37–53. <https://doi.org/10.1016/j.marmicro.2011.11.005>.
- Bornemann, A., Mutterlose, J., 2006. Size analyses of the coccolith species *Biscutum constans* and *Watznaueria barnesiae* from the Late Albian “Niveau Breistroffer” (SE France): taxonomic and palaeoecological implications. *Geobios* 39 (5), 599–615. ISSN 0016-6995, <https://doi.org/10.1016/j.geobios.2005.05.005>.
- Bottini, C., Erba, E., 2018. Mid-Cretaceous paleoenvironmental changes in the western Tethys. *Clim. Past* 14, 1147–1163. <https://doi.org/10.5194/cp-14-1147-2018>.
- Bottini, C., Faucher, G., 2020. *Biscutum constans* coccolith size patterns across the mid Cretaceous in the western Tethys: Paleoecological implications. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 555, 109852. ISSN 0031-0182.
- Bottini, C., Erba, E., Tiraboschi, D., Jenkyns, H.C., Schouten, S., Sinninghe Damst e, J.S., 2015. Climate variability and ocean fertility during the Aptian Stage. *Clim. Past* 11, 3. <https://doi.org/10.5194/cp-11-383-2015>.
- Bown, P.R., Young, J.R., 1998. Introduction. In: Bown, P.R. (Ed.), *Calcareous Nannofossil Biostratigraphy*. British Micropaleontol. Soc. Publ. Series. Kluwer Academic Publ. University Press, Cambridge, UK, pp. 1–15.
- Bruno, M.D.R., Fauth, G., Watkins, D.K., da Silva, Goulart, Caramze, M., Nauter-Alves, A., Savian, J.F., 2022. Paleooceanographic evolution in the South Atlantic Ocean (Kwanza Basin, Angola) during its post-salt foundering. *Mar. Pet. Geol.* 144, 105852. ISSN 0264-8172. <https://doi.org/10.1016/j.marpetgeo.2022.105852>.
- Chambers, L.M., Pringle, M.S., Fitton, J.G., 2004. Phreatomagmatic eruptions on the Ontong Java Plateau: an Aptian 40Ar/39Ar age for volcanoclastic rocks at ODP Site 1184. In: Fitton, J.G., Mahoney, J.J., Wallace, P.J., Saunders, A.D. (Eds.), *Origin and Evolution of the Ontong Java Plateau*, 229. Geological Society of London Special Publication, pp. 325–331. <https://doi.org/10.1144/GSL.SP.2004.229.01.18>.
- Coffin, M.F., Pringle, M.S., Duncan, R.A., Gladchenko, T.P., Storey, M., M uller, R.D., Gahagan, L.A., 2002. Kerguelen hotspot magma output since 130 Ma. *J. Petrol.* 43, 1121–1137. <https://doi.org/10.1093/petrology/43.7.1121>.
- Duncan, R.A., 2002. A time for construction of the Kerguelen Plateau and Broken Ridge. *J. Petrol.* 43, 1109–1119. <https://doi.org/10.1093/petrology/43.7.1109>.
- Erba, E., 1992. Calcareous nannofossil distribution in pelagic rhythmic sediments (Aptian-Albian Piobbico core, Central Italy). *Riv. Ital. Paleontol. S.* 97, 455–484.
- Erba, E., Larson, R., 1998. The Cisonon Apticore (Southern Alps, Italy): a “reference section” for the lower cretaceous at low latitudes. *Riv. Ital. Paleontol. S.* 104, 181–182.
- Erba, E., Channell, J.E.T., Claps, M., Jones, C., Larson, R., Bradley, O., Premoli Silva, L., Riva, A., Salvini, G., Torricelli, S., 1999. Integrated stratigraphy of the Cisonon Apticore (southern Alps, Italy): a “reference section” for the Barremian-Aptian interval at low latitudes. *J. Foramin. Res.* 29 (4), 371–391.
- Erba, E., Bottini, C., Weissert, H.J., Keller, C.E., 2010. Calcareous nannoplankton response to surface-water acidification around Oceanic Anoxic Event 1a. *Science* 329 (5990), 428–432. <https://doi.org/10.1126/science.1188886>.
- Erba, E., Duncan, R.A., Bottini, C., Tiraboschi, D., Weissert, H., Jenkyns, H.C., Malinverno, A., 2015. Environmental Consequences of Ontong Java Plateau and Kerguelen Plateau Volcanism. *GSA Spe. Paper* 511. <https://doi.org/10.1130/2015.2511>.
- Erba, E., Bottini, C., Faucher, G., Gambacorta, G., Visentin, S., 2019. The response of calcareous nannoplankton to Oceanic Anoxic events: the Italian pelagic record. *Boll. Soc. Paleontol. Ital.* 58 (1), 51–71.
- Faucher, G., Erba, E., Bottini, C., Gambacorta, G., 2017. Calcareous nannoplankton response to the latest Cenomanian Oceanic Anoxic Event 2 perturbation. *Riv. Ital. Paleontol. Stratigr.* 123, 159–176 (/2039-4942/8092).
- Faucher, G., Visentin, S., Gambacorta, G., Erba, E., 2022. *Schizosphaerella* size and abundance variations across the Toarcian Oceanic Anoxic Event in the Sogno Core (Lombardy Basin, Southern Alps). *Paleogeogr. Paleoclimatol. Paleoecol.* 595, 110969. ISSN 0031-0182, <https://doi.org/10.1016/j.palaeo.2022.110969>.
- Ferreira, J., Mattioli, E., van de Schootbrugge, B., 2017. Palaeoenvironmental vs. evolutionary control on size variation of coccoliths across the Lower-Middle Jurassic? *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 465, 177–192. <https://doi.org/10.1016/j.palaeo.2016.10.029>.
- Gambacorta, G., Bersezio, R., Erba, E., 2014. Sedimentation in the Tethyan pelagic realm during the Cenomanian: monotonous settling or active redistribution? *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 409, 301–319.
- Gambacorta, G., Jenkyns, H.C., Russo, F., Tsikos, H., Wilson, P.A., Faucher, G., Erba, E., 2015. Carbon-and oxygen-isotope records of mid-cretaceous Tethyan pelagic sequence from the Umbria–Marche and Belluno Basins (Italy). *Newsl. Stratigr.* 48 (3), 299–323. <https://doi.org/10.1127/nos/2015/0066>.
- Gambacorta, G., Bottini, C., Brumsack, H.J., Schnetger, B., Erba, E., 2020. Major and trace element characterization of Oceanic Anoxic Event 1d (OAE 1d): insight from the Umbria–Marche Basin, Central Italy. *Chem. Geol.* 557, 119834.
- Giorgioni, M., Weissert, H., Bernasconi, S.M., Hochuli, P.A., Coccioni, R., Keller, C.E., 2012. Orbital control on carbon cycle and oceanography in the mid-cretaceous greenhouse. *Paleoceanogr. Paleoclimatol.* 27 <https://doi.org/10.1029/2011PA002163>. PA1204.
- Gollain, B., Mattioli, E., Kenjo, S., Bartolini, A., Reboulet, S., 2019. Size patterns of the coccolith *Watznaueria barnesiae* in the lower Cretaceous: Biotic versus abiotic forcing. *Mar. Micropaleontol.* 152, 101740 <https://doi.org/10.1016/j.marmicro.2019.03.012>.
- Hoernle, K., Hauff, F., van den Bogaard, P., Werner, R., Mortimer, N., Geldmacher, J., Garbe-Sch onberg, D., Davy, B., 2010. Age and geochemistry of volcanic rocks from the Hikurangi and Manihiki oceanic Plateaus. *Geochim. Cosmochim. Acta* 74, 7196–7219. <https://doi.org/10.1016/j.gca.2010.09.030>.
- Lenth, R., 2023. emmeans: Estimated Marginal Means, Aka Least-Squares Means. R package version 1.8.6. <https://CRAN.R-project.org/package=emmeans>.
- Linnert, C., Mutterlose, J., 2012. Biometry of Cenomanian–Turonian palcoliths: a proxy for changes of fertility and surface-water temperature? *Lethaia* 46 (1), 82–97. <https://doi.org/10.1111/j.1502-3931.2012.00323.x>.
- Linnert, C., Mutterlose, J., Bown, P.R., 2014. Biometry of Upper Cretaceous (Cenomanian–Maastrichtian) coccoliths – a record of long-term stability and interspecies size shifts. *Rev. Micropaleontol.* 57 (4), 125–140. ISSN 0035-1598, <https://doi.org/10.1016/j.revmic.2014.09.001>.
- L ubke, N., Mutterlose, J., 2016. The impact of OAE 1a on marine biota deciphered by size variations of coccoliths. *Cretac. Res.* 61, 169–179. <https://doi.org/10.1016/j.cretres.2016.01.006>.
- L ubke, N., Mutterlose, J., Bottini, C., 2015. Size variations of coccoliths in Cretaceous oceans – a result of preservation, genetics and ecology? *Mar. Micropaleontol.* 117, 25–39. <https://doi.org/10.1016/j.marmicro.2015.03.002>.
- Mattioli, E., Pittet, B., Young, J.R., Bown, P.R., 2004. Biometric analysis of Pliensbachian–Toarcian (Lower Jurassic) coccoliths of the family Biscutaceae: intra- and inter-specific variability versus palaeoenvironmental influence. *Mar. Micropaleontol.* 52, 5–27. <https://doi.org/10.1016/j.marmicro.2004.04.004>.
- Matsumoto, H., Kuroda, J., Coccioni, R., Frontalini, F., Sakai, S., Ogawa, N.O., Ohkouchi, N., 2020. Marine Os isotopic evidence for multiple volcanic episodes during Cretaceous Oceanic Anoxic Event 1b. *Sci Rep* 10, 12601. <https://doi.org/10.1038/s41598-020-69505-x>.
- Mattioli, E., Pittet, B., Petitpierre, L., Mailliot, S., 2009. Dramatic decrease of pelagic carbonate production by nannoplankton across the early Toarcian anoxic event (T-OAE). *Glob. Planet. Chang.* 65, 134–145. <https://doi.org/10.1016/j.gloplacha.2008.10.018>.
- M oller, C., Bornemann, A., Mutterlose, J., 2020. Climate and paleoceanography controlling size variations of calcareous nannofossils during the Valanginian Weissert Event (early cretaceous). *Mar. Micropaleontol.* 157, 101875 <https://doi.org/10.1016/j.marmicro.2020.101875>.
- Peti, L., Thibault, N., 2017. Abundance and size changes in the calcareous nannofossil *Schizosphaerella* – Relation to sea-level, the carbonate factory and palaeoenvironmental change from the Sinemurian to earliest Toarcian of the Paris Basin. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 485, 271–282. <https://doi.org/10.1016/j.palaeo.2017.06.019>.
- Roth, P.H., 1983. Jurassic and lower cretaceous calcareous nannofossils in the Western North Atlantic (Site 534): Biostratigraphy, preservation, and some observations on biogeography and paleoceanography. *Initial Rep. Deep Sea Drill. Proj.* 517–546.
- Roth, P.H., Thierstein, H.R., 1972. Calcareous Nannoplankton: Leg 14 of the Deep Sea Drilling Project. *Initial Rep. Deep Sea Drill. Proj.* 14, 421–485.
- Sabatino, N., Ferraro, S., Coccioni, R., Bonsignore, M., Del Core, M., Tancredi, V., Sprovieri, M., 2018. Mercury anomalies in upper Aptian-lower Albian sediments from the Tethys realm. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 495, 163–170.
- Schwarzacher, W., 1994. Cyclostratigraphy of the Cenomanian in the Gubbio district, Italy: A field study. In: de Boer, P.L., Smith, D.G. (Eds.), *Orbital Forcing and Cyclic Sequences*. Special Publications International Association of Sedimentologists 19, pp. 99–107. Tulsa, Oklahoma.
- Timm, C., Hoernle, K., Werner, R., Hauff, F., van den Bogaard, P., Michael, P., Coffin, M.F., Koppers, A., 2011. Age and geochemistry of the oceanic Manihiki Plateau, SW

- Pacific: new evidence for a plume origin. *Earth Planet. Sci. Lett.* 304, 135–146. <https://doi.org/10.1016/j.epsl.2011.01.025>.
- Tiraboschi, D., Erba, E., Jenkyns, H.J., 2009. Origin of rhythmic Albian black shales (Piobbico core, Central Italy) Calcareous nannofossil quantitative and statistical analyses and paleoceanographic reconstructions. *Paleoceanogr. Paleoclimatol.* 24, PA2222. <https://doi.org/10.1029/2008PA001670>.
- Wulff, L., Mutterlose, J., Bornemann, A., 2020. Size variations and abundance patterns of calcareous nannofossils in mid Barremian black shales of the Boreal Realm (Lower Saxony Basin). *Mar. Micropaleontol.* 156, 101853 <https://doi.org/10.1016/j.marmicro.2020.101853>.
- Young, J.R., Poulton, A.J., Tyrrell, T., 2014. Morphology of *Emiliana huxleyi* coccoliths northwestern European shelf - is there an influence of carbonate chemistry? *Biogeosciences* 11, 4771–4782.