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THE MIDDLE EOCENE CLIMATIC OPTIMUM (MECO) IMPACT ON THE BENTHIC AND PLANKTIC FORAMINIFERAL RESILIENCE FROM A SHALLOW-WATER SEDIMENTARY RECORD

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Abstract. We present here new quantitative analyses of planktic and benthic foraminifera to assess the impact of the Middle Eocene Climatic Optimum (MECO, ~40 Ma) on these biotic groups studied along a shallow-water succession rich in larger benthic foraminifera (Sealza, Liguria, NW Italy). The MECO is one of the major Eocene global warming events, characterized by ~4–6°C warming, shifts in the global carbon cycle, and rise in atmospheric pCO_2. The Sealza succession is interpreted as the product of a drowning ramp influenced by tectonic activity and provides an exceptional chance to compare biotic variations in shallow-water assemblages with deep-water communities across the MECO. In the section, the MECO interval is tentatively constrained by stable isotope oxygen data and calcareous plankton biostratigraphy. The marked decline in abundance of the epifaunal benthic *Cibicidoides* across the lower-middle part of the MECO suggests a decrease in oxygenation at the seafloor. Further evidence of oxygen depletion is the increase in organic matter content (TOC) of the sediment and the presence of infaunal genera *Uvigerina* and *Bolivina*. The planktic foraminiferal assemblages record the MECO warming in the upper water column as the mixed-layer warm index genera *Acarinina* and *Morozovelloides* markedly increase in abundance. In the post-MECO interval, here poorly exposed, cooler conditions are indicated by the dominance of the cold-water index genus *Subbotina*. Remarkably, *Acarinina* decline in abundance in the upper MECO interval and never recover. The MECO perturbance permanently impacted the benthic and planktic communities at Sealza that exceeded the tipping point to move to a new regime, thus proving the fauna to be not resilient, but also not recording any extinctions.

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Introduction

Marine calcifiers are threatened by the consequences of anthropogenic CO_2 emissions. The ongoing and future global climate changes such as global warming, ocean acidification, eutrophication and anoxia, are all phenomena which weaken their ecological resilience (e.g., Raven et al. 2005).

As highlighted in the most recent IPCC (Intergovernmental Panel on Climate Change 2018) reports, the evaluation of marine ecosystem health needs long-term observation data and studies on modern fauna only provide a limited time span. In contrast, the geological record allows us to evaluate long term responses to global climatic changes.

The Paleogene, being one of the most climatically dynamic periods of Earth's history, offers the opportunity to study the biotic effects. In particular, the early Paleogene is characterized by several short-term warming events (~50-200 kyr), known as hyperthermals (e.g., Zachos et al. 2001); the peak of temperature and pCO_2 were reached during the Early Eocene Climatic Optimum (EECO ~53-49 Ma). A long-term cooling trend (~49 to ~34 Ma) followed the EECO, eventually leading to the establishment of a continental Antarctic icesheet by the early Oligocene (e.g., Coxall et al. 2005). This climatic transition was interrupted by a prominent, though transient global warming event: the Middle Eocene Climatic Optimum (MECO). During the MECO the $\delta^{18}O$ values of marine carbonatic sediments and of benthic foraminifera shells declined by roughly 1‰ in over ~400 kyr, which is usually interpreted as 4–6 °C of global temperature rise, with a gradual onset and brief peak temperatures at ~40 Ma and followed by a rapid return to pre-event conditions (e.g., Bohaty & Zachos 2003; Jovane et al. 2007; Bohaty et al. 2009; Edgar et al. 2010; Luciani et al. 2010; Spofforth et al. 2010; Savian et al. 2013; Boscolo Galazzo et al. 2014; D'Onofrio et al. 2021). This event is particularly appealing to study as it records temperatures and pCO_2 (Boscolo Galazzo et al. 2014; Cramwinckel et al. 2019; Henehan et al. 2020) that Earth will reach in the next few centuries if anthropogenic emissions do not stop (IPCC, 2018). Several characteristics, such as a duration longer than the Eocene hyperthermals, the absence of a clear trigger mechanism, and the lack of a globally coherent negative $\delta^{13}C$ excursion in marine carbonates, make the MECO one of the most enigmatic events in the Cenozoic, dubbed a middle Eocene "carbon cycle conundrum" (Sluijs et al. 2013).

Even though the MECO is attracting high attention from the scientific community, studies on the paleoenvironmental changes and paleobiotic repercussions across the MECO are still limited. To improve the understanding of the impact of the MECO on the marine biotic communities and their resilience to global warming, here we present the analysis of the Sealza shallow-water succession outcropping in Liguria (NW Italy) (Fig. 1) that contains a very high diversity of both small benthic and planktic foraminifera, calcareous nannofossils, and larger benthic foraminifera (LBF) (Briguglio et al. 2023), thus making it a perfect study site to detect differential resilience among all taxa. Specifically, a multi-proxy study across the section is presented, including data from foraminiferal quantitative analysis, stable isotopes, and total organic carbon (TOC) to better understand the impact of the MECO on the taxa analyzed and on the environment. The data here presented provide for the first time, an analysis on the resilience of both benthic and planktic foraminifera in a shallow-water setting, consistently within the photic zone where mixed- and autotrophic organisms thrived, whereas most of the known literature focuses on deep-water environments (e.g., Luciani et al. 2010; Edgar et al. 2013; Boscolo Galazzo et al. 2013, 2014; D'Onofrio et al. 2021).

Geological setting

the study area is located close to the border between Italy and France, and the investigated section is exposed along a winding gravel-road starting from the hamlet of Sealza (Ventimiglia municipality, Imperia Province, Liguria, NW Italy) (Fig. 1).

The Sealza section is part of the Provençal Domain sedimentary succession, that form the sedimentary cover of the Argentera-Mercantour Crystalline Massif (European plate) (De Graciansky et al. 2010; Giammarino et al. 2010; Dallagiovanna et al. 2012; Decarlis et al. 2014; Marini et al. 2022). During the Eocene, the Provençal Domain was involved in the tectonic migration of the Alpine thrust front as the Western and Ligurian Alps' orogenic wedge was thrust onto this area of the European plate, forming the Western and Ligurian

Fig. 1 - A, B) Geographic maps showing the location of the studied area (Liguria, NW Italy); C) Map of the locality of Sealza (Ventimiglia) (red highlighted area). The red line represents the measured section. Image created using QGIS. (Modified from https://server.arcgisonline.com/ArcGIS/rest/services/World_Imagery/).

Alps' foreland-foredeep system (Lanteaume 1968; Varrone 2004; De Graciansky et al. 2010; Giammarino et al. 2010; Dallagiovanna et al. 2012; Marini et al. 2022). This tectonically controlled sedimentation is characterized by shallow-water limestones grading upward to marlstones capped by siliciclastic turbidite deposits, known as the Priabonian Trilogy (Boussac 1912) or Sinclair Trinity (Sinclair 1997). In the Sealza area, the Eocene "Priabonian Trilogy" unconformably overlies a thick marl and marly limestone succession (Trucco Formation, upper Cretaceous) and includes, bottom to top, coarse-grained siliciclastic, mixed and carbonate deposits of shallow-marine environments (Capo Mortola Calcarenite, also known as Nummulitic Limestone), deep-marine marls and silty marls (Olivetta San Michele Silty Marl, also known as *Globigerina* marls), and sandy silty turbiditic deposits (Ventimiglia Flysch). The lithostratigraphic section of Sealza perfectly fits with the schematized succession, although the "*Globigerina* marls" are very poorly exposed (Lanteaume 1968; Campredon 1977; Varrone 2004; Giammarino et al. 2009, 2010; Dallagiovanna et al. 2012; Perotti et al. 2012; Maino & Seno 2016; Mueller et al. 2020; Coletti et al. 2021; Marini et al. 2022; Briguglio et al. 2023).

This sector of the Provençal Domain exhibits a complex tectonic setting, which is the consequence of the superposition of Alpine (Paleogene-Neogene) and Provençal (Cretaceous-Paleocene) orogenic events, both of which are represented by ductile and brittle structures, that are subsequently involved in the Neotectonic deformations (Giammarino et al. 2009, 2010; Dallagiovanna et al. 2012; Perotti et al. 2012; Morelli et al. 2022).

Material and methods

Field sampling

The Sealza sedimentary succession here analyzed, rich in LBF, lies in disconformity on deep-water upper-Cretaceous deposits of the Trucco Formation and is overlain by the deep-water Olivetta San Michele Silty Marl Formation (Briguglio et al. 2023). In this study we selected the interval from 58 m to 124.3 m where the lithology shows alternations between biocalcirudites to biocalcisiltites and marls, thus suggesting potential deepening of depositional setting that may include calcareous plankton. We collected from this interval seventeen samples (SE-21, 23, SE25-SE41), all processed for foraminiferal and calcareous nannofossil analyses. The numerical order of samples is not sequential along the sedimentary sequence due to different sampling phases. In addition, samples SE-34 and SE-40 are missing (Fig. 2). The sample SE-33 was taken at 205 m in the Olivetta San Michele Silty Marl Formation, above an interval of approximately 81 m fully covered by vegetation, where a very little rocky exposure was visible underneath the ruins of an abandoned house.

In addition, 159 powder samples, spaced ~40 cm, were collected, from the 51 m to 124.3 m interval for carbon and oxygen stable isotopes analysis, directly on the outcrop surface using a pressure driller. Before collecting the powder samples, each surface point was carefully cleaned, subsequently initial holes of at least 2 cm were performed. A funnel has been used to collect the powder, which was immediately stored in numbered plastic vials. Additionally, nineteen of the total 159 powder samples collected were analyzed for the amount and type of organic matter by Rock-Eval pyrolysis.

Foraminiferal extraction

Planktic and benthic foraminifera were extracted from the marly-limestones and limestones using two different techniques. The less lithified lithotypes were treated through neo-steramina, a surface-active agent with the following chemical composition: alkyldimethylbenzylammonium chloride diluted at 10%, following the procedure by D'Onofrio & Luciani (2020). The seventeen samples collected for this study were crushed (size 1-2 cm) using a press and immersed in a neo-steramina bath for the time needed to obtain disaggregation (2-3 days). After that, all samples were washed through a 63 µm-mesh sieve and successively dried at 50°C. This procedure was effective for eleven of the total seventeen samples.

The most lithified samples (SE-35-39, 41) did not disaggregate using the neo-steramina method. Therefore, we adopted the acetic acid or "cold acetolyse" technique (Lirer 2000; D'Onofrio & Luciani 2020) that has been successfully applied for lithified rocks (e.g., Fornaciari et al. 2007; Luciani et al. 2007; Coccioni et al. 2012; Luciani & Giusberti 2014; D'Onofrio et al. 2016; Luciani et al. 2016). Specifically, the rock fragments were immersed in 80% diluted acetic acid for five hours, washed through a 63 µm-mesh sieve and dried at 50°C. However, this method also proved to be ineffective to appropriately disaggregate the most lithified samples and therefore, no data are available.

The obtained washed residues (≥ 63 µm fraction) from the successfully dissolved samples were then analyzed for planktic and benthic foraminifera content. Microfossils were identified under a binocular stereomicroscope (Optech GZ808

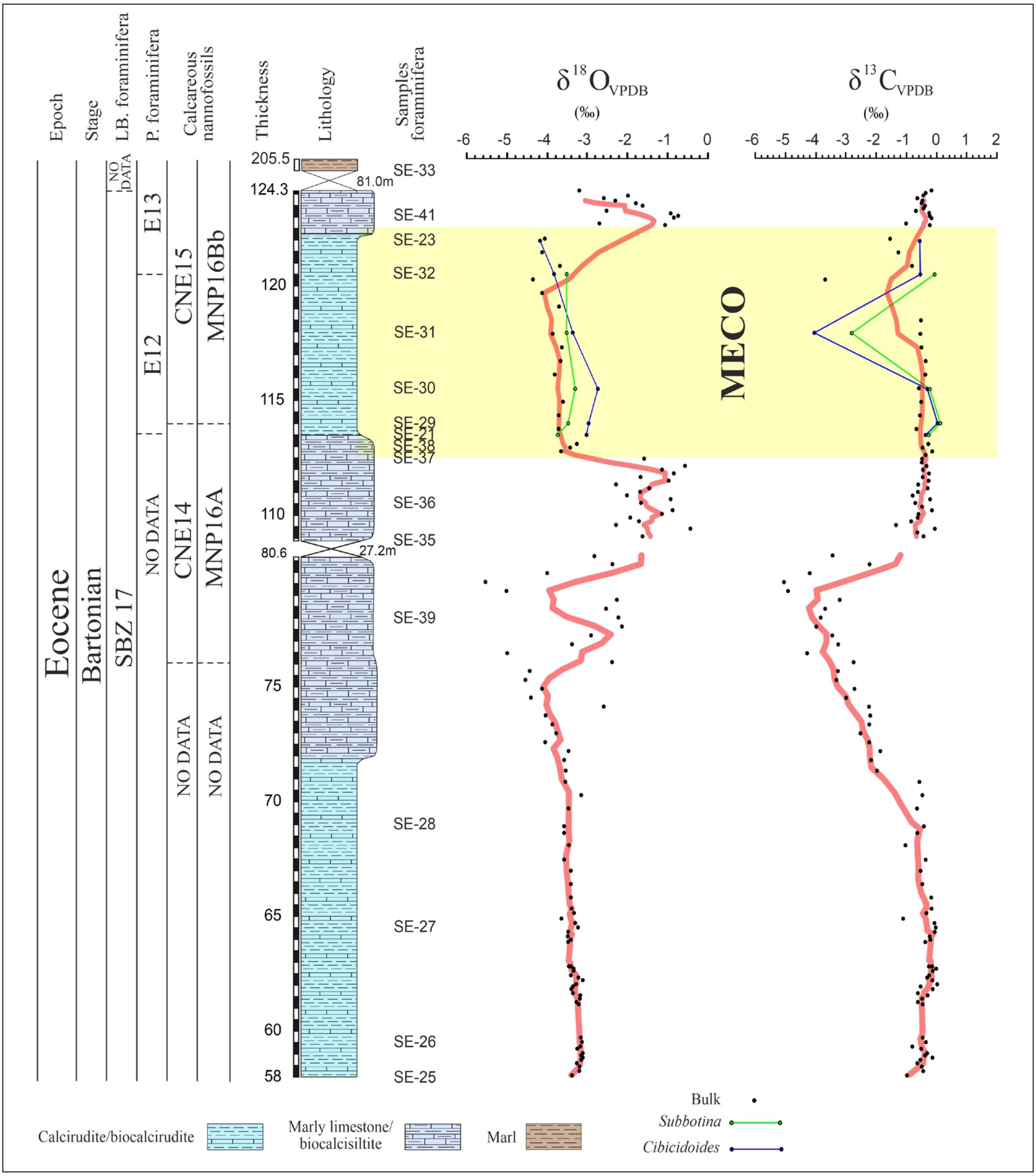

Fig. 2 - Carbon ($\delta^{13}C$) and oxygen ($\delta^{18}O$) isotope data from bulk organic matter (red curve: five-point movement average) plotted against the stratigraphic log of the Sealza section and biozones. Large benthic foraminiferal zones are from Serra-Kiel et al. (1998); planktic foraminiferal zones follow the zonation scheme by Wade et al. (2011); calcareous nannofossils zonation are according to Fornaciari et al. (2010) and Agnini et al. (2014). The yellow-shaded band outlines the Middle Eocene Climatic Optimum (MECO) interval. Blue curves represent carbon and oxygen stable isotopes measured on the benthic foraminifera genus *Cibicidoides*, while green curves represent stable isotopes measured on the planktic foraminifera genus *Subbotina*.

and Zeiss) equipped with on-board camera, picked, and isolated in microslides. The taxonomic criteria adopted in this work to identify the benthic foraminiferal genera follow Loeblich & Tappan (1988, 1994) and Holbourn et al. (2013), while for planktic foraminiferal taxa follow Pearson et al. (2006).

In addition, the most significant taxa retrieved in this study have been imaged by Scanning Electron Microscope (SEM, EVO 40 Zeiss), at University of Ferrara.

Quantitative analysis and data treatment

The abundance of foraminifera was counted on a population of ~300 specimens (when possible) in the ≥63 µm size fraction of washed residues, expressed as percentage as well as absolute abundance standardized to 1g of dried sediment (Supplementary data 1). The absolute abundance of benthic and planktic foraminifera is expressed as BFN and PFN respectively. The planktic and benthic ratio (P/B) was calculated as P/(P+B) *100 and expressed as percentages. Additionally, biodiversity parameters such as dominance D' and the Shannon–Weaver (H') index, calculated as proxies for diversity and heterogeneity of the assemblages (e.g., Murray 2006), were determined using the PAST software (Hammer et al. 2001).

Calcareous nannofossils

Nine samples (SE25-SE33) from the Sealza section, the same collected for the foraminiferal analysis, were prepared from unprocessed material as smear slides and examined using a light microscope at ~1250X magnification. Due to the scarcity of calcareous nannofossil content in all studied samples, we applied the semi-quantitative counting method developed by Gardin & Monechi (1998) assessing the presence or absence of index species in an area of ~6 mm^2 (three vertical traverses). This method allows a larger area to be scanned when the calcareous nannofossil content is too low for a statistically sound quantitative count. In addition, a qualitative estimate of the abundance of all nannofossil taxa detected was performed as reported in Rio et al. (1990) and modified following the abundance code outlined below: D (dominant) = taxon with frequencies greater than the 50% of assemblage; A (abundant) = usually more than 5 specimens occurring per field; C (common) = 1-5 specimens per field; F (few) = 1 specimen per 1-10 fields; R (rare) = 1 specimen per more than 10 fields (Supplementary data 2). Taxonomic concepts follow those of Perch-Nielsen (1985) and Nannotax (Young et al. 2017). We adopted the zonations of Fornaciari et al. (2010) and Agnini et al. (2014).

Stable isotopes

A first batch of 86 powder samples (SEP1 to SEP86) were analyzed for carbon and oxygen stable isotopes at the Laboratory of Paleoclimatology and Isotopic Stratigraphy of the Department of Physics and Earth Sciences of the University of Ferrara, using isoFLOW (Elementar©) operating in continuous flow with a PrecisION Isotopic Ratio Mass Spectrometer (IRMS; Elementar©). For each analysis, approximately 150 µg of homogenous powder of sample was weighed and placed into vials, which were flushed with pure He to replace the atmosphere. In each vial the powder reacted with hot viscous water-free orthophosphoric acid for 3 h at 50 °C, triggering the release of CO_2 from the samples. The released CO_2 sample gas was extracted through a needle and transferred to the IRMS for the simultaneous analysis of C and O. The $^{13}C/^{12}C$ and $^{18}O/^{16}O$ isotopic ratios were expressed with the δ notation (in ‰ units) relative to V-PDB. The in-house MAQ-1 standard was used for the single-point calibration and two control standards (IAEA 603 and Carrara Marble) were measured to monitor the quality of the analysis. Analytical uncertainties (1σ) for the isotope analyses were in the order of ± 0.1‰ for both $\delta^{13}C$ and $\delta^{18}O$.

The remaining 73 powdered samples (SEP87-SEP159) were analyzed for $\delta^{13}C$ and $\delta^{18}O$ in the stable isotope laboratory of University of Lausanne in Switzerland, with the additional measurements of selected planktic and benthic foraminiferal genera *Subbotina* and *Cibicidoides*, respectively (picked from the 11 washed residues). The analyses were done on a Gasbench II coupled to a Finnigan MAT Delta V mass spectrometer via reacting the samples with phosphoric acid at 70 °C (Spötl &Vennemann 2003). The generated CO_2 was introduced with a He-flow into the mass spectrometer. In-house Carrara Marble standards calibrated to NBS-19 were used to normalize the obtained data. The analytical precision for this method was better than ±0.1‰ standard deviation.

Rock-Eval analysis

The amount and type of organic matter of 19 powdered samples were determined by Rock-Eval pyrolysis at the Institute of Earth Sciences of the University of Lausanne, Switzerland, using Rock-Eval 6 following the procedure of Espitalié et al. (1985) and Behar et al. (2001). The total organic carbon (TOC) content is expressed in weight (wt%), the hydrogen index (HI = S2/TOC × 100) in mg hydrocarbons per gram of TOC and the oxygen index (OI = S3/TOC × 100) in mg CO_2 per gram of TOC. The calibration was performed with the IFP 160000 standard (French Institute of Petroleum), and the precision was better than 0.1%.

Results

Biostratigraphy

The stratigraphic column of the Sealza section with collected samples, isotopic records, and biozones is shown in figure 2. In this study, the biostratigraphy is based on planktic foraminifera and calcareous nannofossils; nevertheless, along the same section, previously published data on LBF are available in Briguglio et al. (2023). These authors identified several *Nummulites* species that correspond to the Shallow Benthic Zone 17 (SBZ17) (Serra-Kiel et al. 1998), that is in the lower Bartonian (Papazzoni et al. 2017). Specifically, the species *N. puschi*, *N. perforatus*, *N. biarritzensis*, and *N. beaumonti* are all restricted to SBZ17. The species *N. cyrenaicus* and *N. biedai*, also recorded from Sealza, were previously believed to occur only in SBZ18 (Serra-Kiel et al. 1998). However, these species have been observed by Papazzoni & Sirotti, (1995) in their "*N. lyelli* zone" (=SBZ17) from the Igualada (NE Spain) and Pradipaldo (NE Italy) sections, which allows excluding the occurrence of SBZ18 at Sealza. In our section, the absence of *Heterostegina,* which first appeared at the base of SBZ18 (Less et al. 2008; Less & Özcan 2012), supports the attribution of the entire larger foraminiferal assemblages to the lower Bartonian (SBZ17) in the studied succession.

As for planktic foraminifera, the occurrence of the species *Orbulinoides beckmanni,* even though represented by rare specimens, in the interval from 113.5 m to 120.5 m allowed us to identify the Total Range Zone E12 (Wade et al. 2011) that largely corresponds to the MECO interval (Sexton et al. 2006; Bohaty et al. 2009).

Calcareous nannofossils are generally poorly preserved, as expected from the rocks sampled. In the interval from 58 m to 69 m, the assemblages consist mainly of reworked Cretaceous taxa thus preventing detailed biostratigraphic attribution. The presence of very rare specimens of genus *Reticulofenestra* (1-2 specimens in samples SE-25 and SE-27; Supplementary data 2) allows us to ascribe them to the Eocene (e.g., Agnini et al. 2006; Agnini et al. 2014; Fig. 2). At 114 m (SE-29), the occurrence of *Sphenolithus furcatolithoides*, *Cribrocentrum reticulatum*, and *Reticulofenestra umbilicus* allows us to assign the sample to the upper part of Zone CNE14 of Agnini et al. (2014), which correlates to Zone MNP16A of Fornaciari et al. (2010). The absence of *Sphenolithus furcatolithoides,* the top occurrence of which marks the CNE14-CNE15 boundary, and the presence of a reliable specimen of *Dictyococcites bisectus* allow the attribution of sample SE-30 to Zone CNE 15 (=MNP16Bb) starting from 115.5 m. The single other productive sample at 205 m (SE-33) confirms, due to the concomitant presence of *D. bisectus*, few *Sphenolithus spiniger* and the absence of *Sphenolithus obtusus*, the attribution of this portion to the Zone CNE15 (Fig. 2; Supplementary data 2).

Benthic and planktic foraminifera

The preservation of benthic and planktic foraminiferal tests is generally poor but adequate to detect the diagnostic morphological features useful to correctly identify the species. The most significant taxa retrieved in this study are reported in Plate 1 and the raw quantitative data are shown in Supplementary data 1. Benthic foraminiferal specimens are generally better preserved than the planktic specimens; a total of 12 benthic foraminiferal genera were recognized (Fig. 3). The most abundant genus is *Cibicidoides* (*Cibicidoides* sp., *C. lobatulus*) that displays a marked abundance decrease of 2.59% from 113.5 m to 118 m (samples SE-21, SE-29 -31), followed by an increase of up to 42.1% in the upper part of the section. Another abundant genus is *Anomalinoides* (*Anomalinoides* sp.), which similarly to *Cibicidoides*, is very abundant in the lower part of the measured section (up to 43.1%) but records a decrease in the same interval, though less pronounced (mean value 14.7%). However, differently from *Cibicidoides*, the genus *Anomalinoides* did not recover in the upper part, becoming absent at the top of the section. The genus *Heterolepa* (*Heterolepa* sp., *H. dutemplei*) is very scarce in the lower part of the succession; it increases in abundance around 117 m, markedly decreases in sample SE-30, and finally increases in abundance up to 25.6% in the upper part of the section, from 113.5 m to 122 m. The genus *Uvigerina* (*Uvigerina* sp., *U. eocaena*) exhibits low abundance in the basal and uppermost portions of the section but becomes more abundant from 116 m to 121 m. The genus *Bolivina* is absent in most of the lower portion of the section, only sporadically occurring in samples SE-21, SE-29-31. This genus displays two abundance peaks of up to 30% at 116 m and at the top of the section. The genera *Lagena* and *Quinqueloculina* occur only in samples SE-21 and SE-29-30, constituting a minor component of the assemblages. In turn, *Lenticulina* (*Lenticulina* sp., *L. rotulata*), *Melonis affinis*, and *Dentalina* sp. do not show significant changes in abundance, and they are present approximately from the base up to the top of the interval analyzed.

The disaggregated samples contain planktic foraminiferal specimens, except for SE-27-28, and SE-23, which proved to be barren. However, where present, planktic foraminifera are scarce, as expected from a shallow-water succession. The identification of planktic foraminifera is more difficult in the lower part of the section due to the pronounced recrystallization of their tests, while specimens from the washed residues obtained from samples SE21-SE33 are better preserved. A total of 4 genera were identified from the 113.5 m to 120.5 m interval: *Acarinina* (*A. praetopilensis, Acarinina* sp.), *Morozovelloides* (*M. bandyi*), *Subbotina* (*S. hagni*, *S. eocaena*) and *Turborotalia* (*T. cerroazulensis*), together with the species *Orbulinoides beckmanni* (Fig. 4). The genus *Subbotina* shows the lowest abundances in the interval from 113.5 m to 122 m and reaches the highest abundance in SE-33 with a partial increase from 115 to 117 m. The genus *Acarinina* is very scarce in the lower part of the section, but its abundance significantly increases from 113.5 m to 122 m (6.98% on average). The genus *Morozovelloides* displays a similar trend: it increases from mean values in abundance of 2.90% to 6.38% in the same interval, but it is absent in the lower part of the section. The genus *Turborotalia* occurs in very low abundances, only in samples SE-29-30. The species *Orbulinoides beckmanni* is recorded in the samples SE-21 and SE-29-32.

Diversity and statistical data

The values of benthic and planktic foraminifera (BFN and PFN) and the P/B ratio are shown in figures 3 and 4. The P/B ratio varied from 0 to 35%; in particular, lower P/B ratio values occur in the lower and upper parts of the section (except for sample SE-33), while higher values are recorded in samples SE-21 and SE-29-32 (Fig. 4). The benthic foraminiferal Shannon–Weaver (H'b) index (1.23 on average) exhibits slightly high values in the interval from 113.5 m to 122 m, while Dominance D'b (0.35 on average) does not show changes, implying that no one genus dominates over the others (Fig. 3). The Shannon index (H'p) for planktic foraminifera (0.91 on average) exhibits lower values in the lower part of the section and increases from 113.5 m to 122 m as for H'b. Differently, the dominance D'p (0.44 on average) indicates that the genus *Subbotina* is dominant (Fig. 4).

Calcareous nannofossils

Data from calcareous nannofossils are ambiguous because the section is represented by rocks poorly suitable for calcareous nannofossil analysis and generally dominated by Cretaceous reworking. Pristine assemblages are rare to few, and only three samples (SE-29, SE-30, and SE-33) have a statistically significant content of calcareous nannofossils. Preservation ranges from poor to moderate, with variable degrees of overgrowth and recrystallization in most of the analyzed samples. Raw semi-quantitative data are shown in Supplementary data 2. From the 58 m to 69 m interval, just 1-2 specimens of the genus *Reticulofenestra* were found (samples SE-25 and SE-27). The pristine assemblages are dominated by the genera *Reticulofenestra*, *Cyclicargolithus*, *Sphenolithus*, and very small *Dictyoccocites*, while *Cribrocentrum reticulatum* is scarce to common. The genera *Coccolithus* and *Ericsonia* are rare, while the genus *Discoaster* is virtually absent.

Plate 1

Scanning electron micrograph (SEM) images of most significant taxa retrieved in the Sealza section (sample SE-21).

Figs. A, B, C - *Heterolepa dutemplei* (d'Orbigny 1846) A) umbilical view, B) spiral view, C) lateral view;

Figs. D, E, F - *Cibicidoides lobatulus* (Walker & Jacob 1798) D) umbilical view, E) spiral view, F) lateral view;

Fig. G - *Uvigerina* sp;

Figs. H, I - *Orbulinoides beckmanni* (Saito 1962);

Fig. J - *Subbotina eocaena* (Guembel 1868), umbilical view;

Figs. K, L - *Subbotina hagni* (Gohrbandt 1967), K) spiral view, L) umbilical view;

Figs. M, N, O - *Acarinina praetopilensis* (Blow 1979), M, O) umbilical view, N) spiral view. Scale bar = 100 μm.

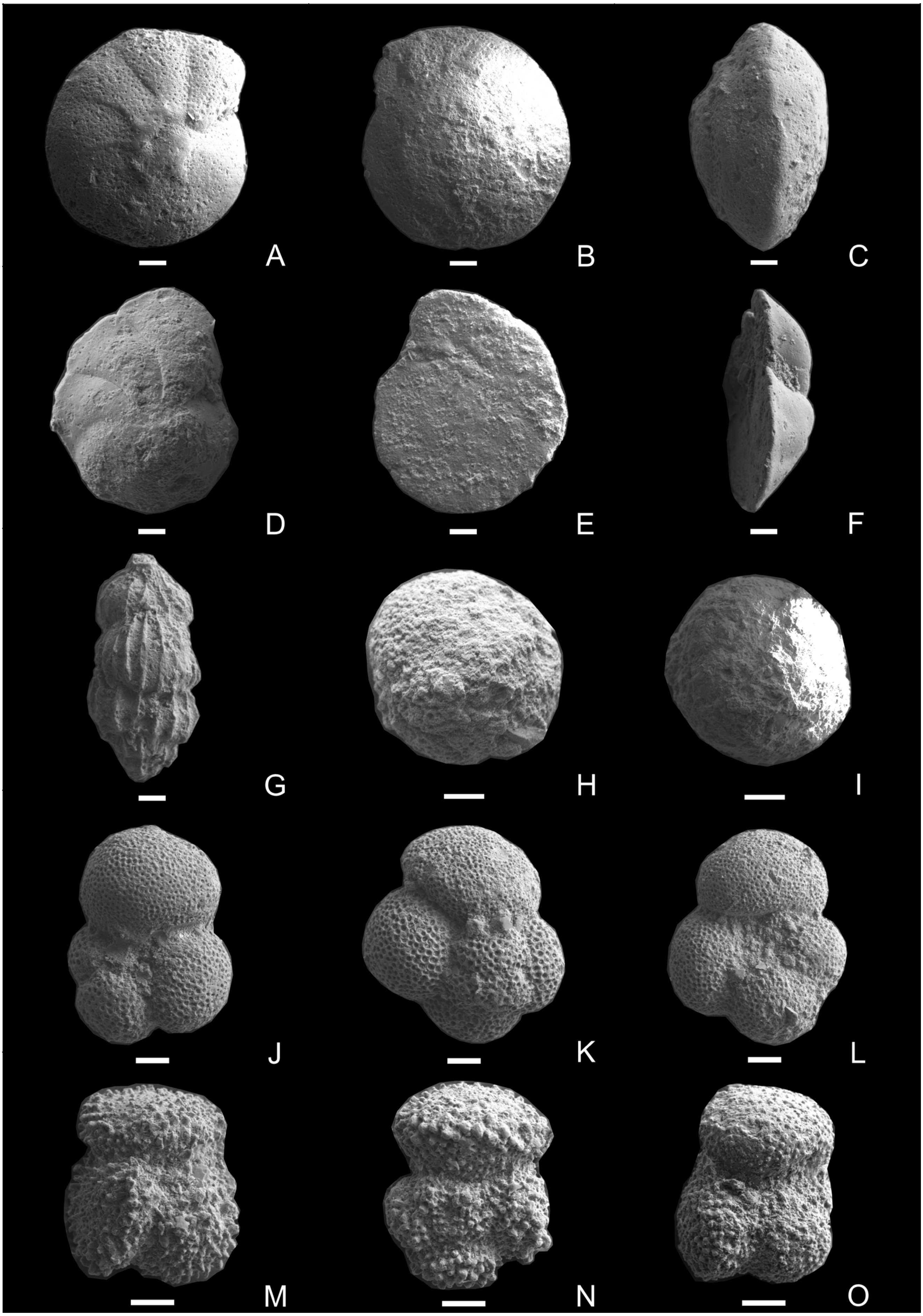

Plate 1

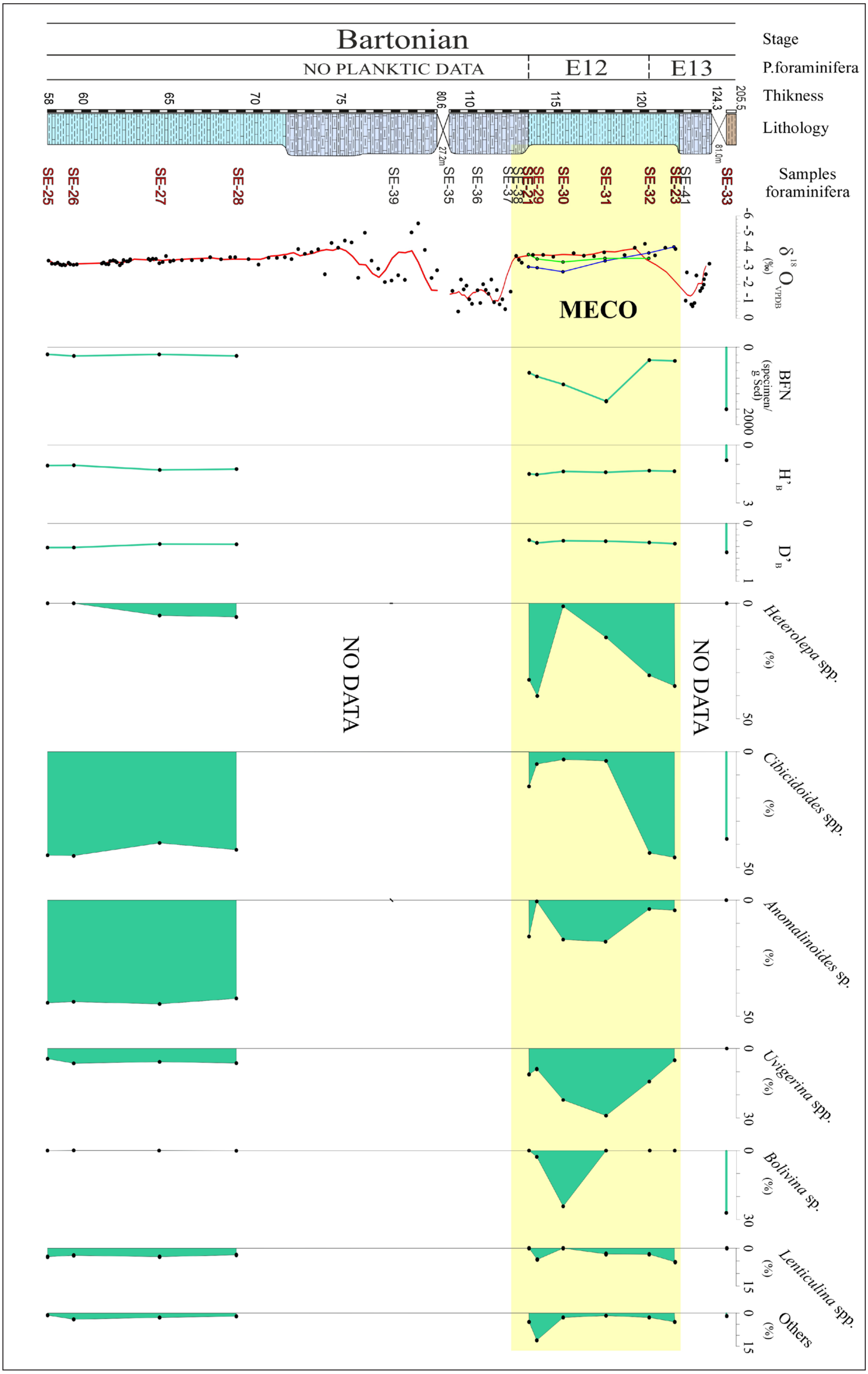

Fig. 3 - Abundance of benthic foraminiferal genera (>63 μm fraction) before, across, and after the MECO interval (yellow-shaded band) of the Sealza section plotted against lithology, oxygen isotope curve ($\delta^{18}O$) and benthic foraminiferal assemblage's parameters (H' and D'). BFN: benthic foraminiferal number (specimen/1g sediment); H': Shannon index; D: dominance. Others include the minor components of the assemblage. The green line at 205 m represents the abundance of genera in sample SE-33.

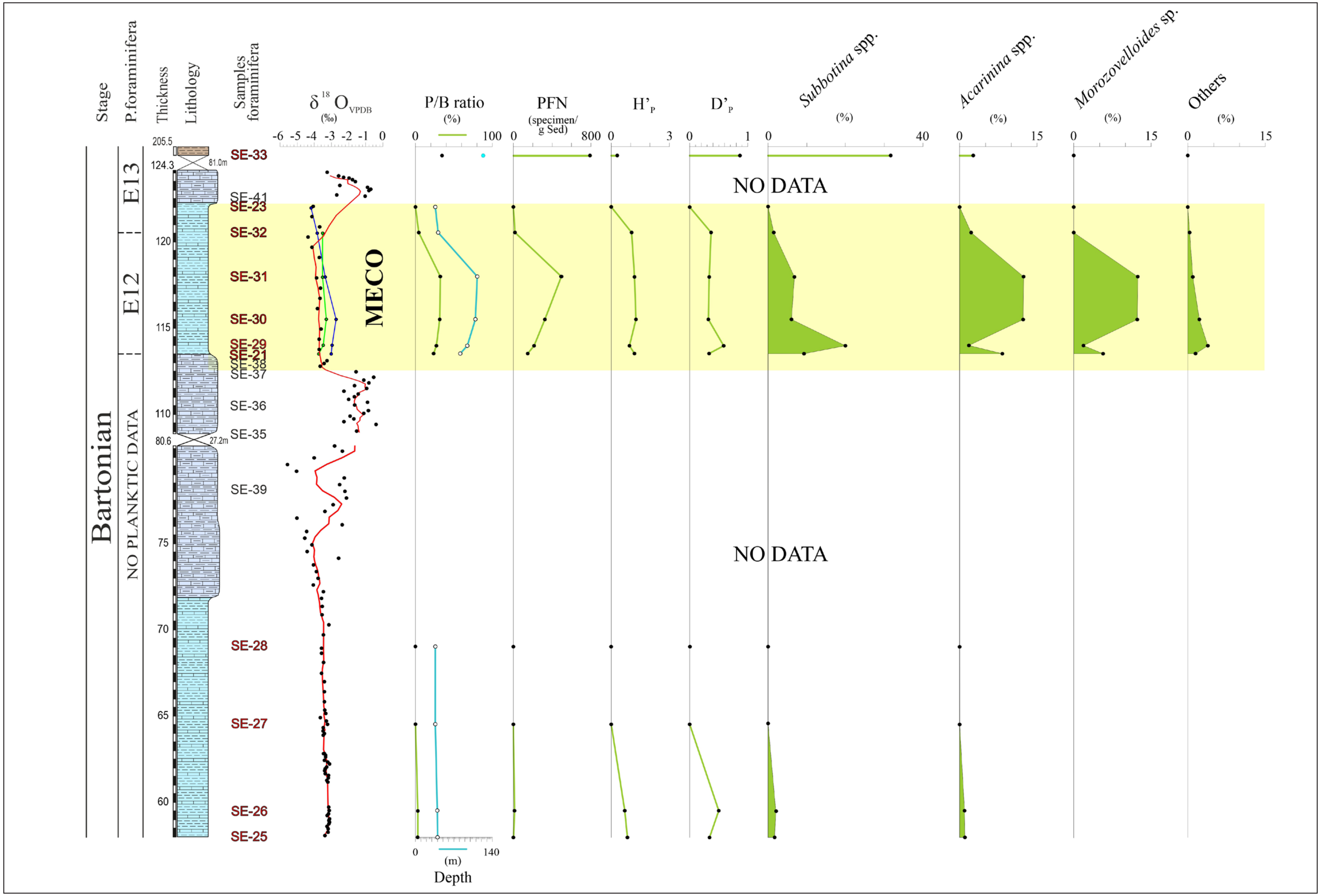

Fig. 4 - Abundance of planktic foraminiferal genera (> 63 µm fraction) before, across and after the MECO interval (yellow-shaded band) of the Sealza section plotted against lithology, oxygen isotope curve ($\delta^{18}O$) and planktic foraminiferal assemblage's parameters (H' and D'). PFN: planktic foraminiferal number (specimen/1g sediment); P/B: planktic to benthic (P/B) ratio calculated as P/(P+B) *100 expressed as percentages of planktonic foraminifera in the total foraminiferal assemblage; H': Shannon index; D: dominance. Others include the minor components of the assemblage. The green line at 205 m represents the abundance of genera in sample SE-33.

Oxygen and carbon stable isotope trends

Results of bulk stable isotope analyses are shown in figure 2 (red curve – five-point movement average). The $\delta^{18}O$ bulk values vary between -5.6‰ and -0.4‰. The lower part of the section (58 to 73 m) is characterized by $\delta^{18}O_{bulk}$ values around -3.4‰. Several minor shifts toward major/minor negative values are recorded in the following interval up to 80.68 m. The interval from 109 m to 112.5 m records high values (between -1‰ and -2‰) with minor oscillations ranging between 0‰ and -2‰. An abrupt negative shift up to -3.7‰ occurs at 112.6 m. Following this shift, $\delta^{18}O_{bulk}$ values remain between -3.0‰ and -4.4‰ in the 113 m to 122.5 m interval. Following this interval, a sharp increase in $\delta^{18}O_{bulk}$ is recorded showing values varying between -0.7‰ and -3.0‰. A single negative peak of -5.2‰ occur at the top of the section analyzed.

The $\delta^{13}C_{bulk}$ values vary between -4.9‰ and 0.2‰ (Fig. 2). The interval from the base of the section to 74 m records roughly constant values around -0.4‰. The $\delta^{13}C_{bulk}$ curve show a negative trend up to 80.68 m reaching a minimum of -4.9 ‰ at 79.5 m. Above the covered interval of 27.25 m $\delta^{13}C_{bulk}$ data are similar to those recorded in the lower portion with mean values of -0.4‰. Three negative shifts occur at 109.4 m (-1.2‰), at 120.1 m (-3.6‰) and at 122 m (-1.4‰).

Carbon and oxygen stable isotopes measured on *Cibicidoides* (blue curve in figure 2), and *Subbotina* (green curve in figure 2) are constrained to the interval from 113.5 m to 122 m that provides the best foraminiferal preservation. Oxygen isotope values obtained from the *Cibicidoides* tests vary between -4.2‰ and -2.7‰ and exhibit a negative trend, while the *Subbotina* values are most constantly comprised from -3.7 ‰ and -3.3 ‰.

The $\delta^{13}C_{Cibicidoides}$ and $\delta^{13}C_{Subbotina}$ curves reveal similar trends consisting of a negative shift up to -3.9‰ for *Cibicidoides* and up to -2.7‰ for *Subbotina*. These shifts precede the negative peak recorded by the $\delta^{13}C_{bulk}$.

Organic matter

The total organic content (TOC) varies from 0.02% to 0.34% in the Sealza section. The TOC values increase in the marly limestone and decrease in the biocalcirudite (Fig. 5). The values of hydrogen index (HI) ranges between 63 mg and 367 mg HC/g TOC (Fig. 5) with the lowest values recorded in samples belong to the biocalcirudites (from 109 to 110 m). The oxygen index values (OI) varies from 73 to 636 mg CO_2/g TOC (Fig. 5) with maximum values in samples 109.00 m, 109.48 m, 111.08 m, and 120.14 m.

Discussion

MECO constrains at the Sealza section

The identification of MECO at the Sealza section though stable isotopes is not as straightforward as in most deep-water settings, and this was somehow expected due to the shallow- water setting of the depositional environment, which is largely controlled by runoff and local tectonics besides the climatic perturbations. The available data show a marked negative Oxygen Isotopic Excursion (OIE) of ~1‰ shown by the $\delta^{18}O_{bulk}$ record across the interval from 112.5 m to 122 m that is followed by rapid recovery to pre-excursion values. Similar OIEs have been documented in deep-sea cores from the Indian, Atlantic, Pacific, and Southern Oceans, as well as from land-exposing marine successions in China, Turkey, Italy, United Kingdom, and North America (e.g., Bohaty & Zachos 2003; Jovane et al. 2007; Villa et al. 2008; Luciani et al. 2010; Spofforth et al. 2010; Dawber & Tripati 2011; Toffanin et al. 2011; Boscolo Galazzo et al. 2013; Methner et al. 2016; Giorgioni et al. 2019; Shi et al. 2019). The recorded OIE has been interpreted mainly as a global temperature signal suggesting a transient global warming of 4–6 °C in both surface and deep waters (Bohaty & Zachos 2003; Bohaty et al. 2009; Bijl et al. 2010). The $\delta^{18}O$ record from Sealza shows more negative values with respect to those obtained from the oceanic sites (e.g., Bohaty et al. 2009) because the on-land successions may be affected by diagenetic or meteoric processes, which usually lower the $\delta^{18}O$ values (e.g., Marshall 1992; Schrag et al. 1995; Frank et al. 1999). Additionally, the isotope shift largely, yet not perfectly, correlates with a sudden shift in lithology, which might indicate differential diagenetic pathways for the lithotypes (e.g., Giraldo Gómez et al. 2017), thus revealing different isotopic signal. The isotopic values obtained for the isolated taxa seem coincident with the bulk, thus they neither give additional information on specific temperature differences on water column versus seafloor settings, nor exclude the lithological variation as a bias for the isotopic signal.

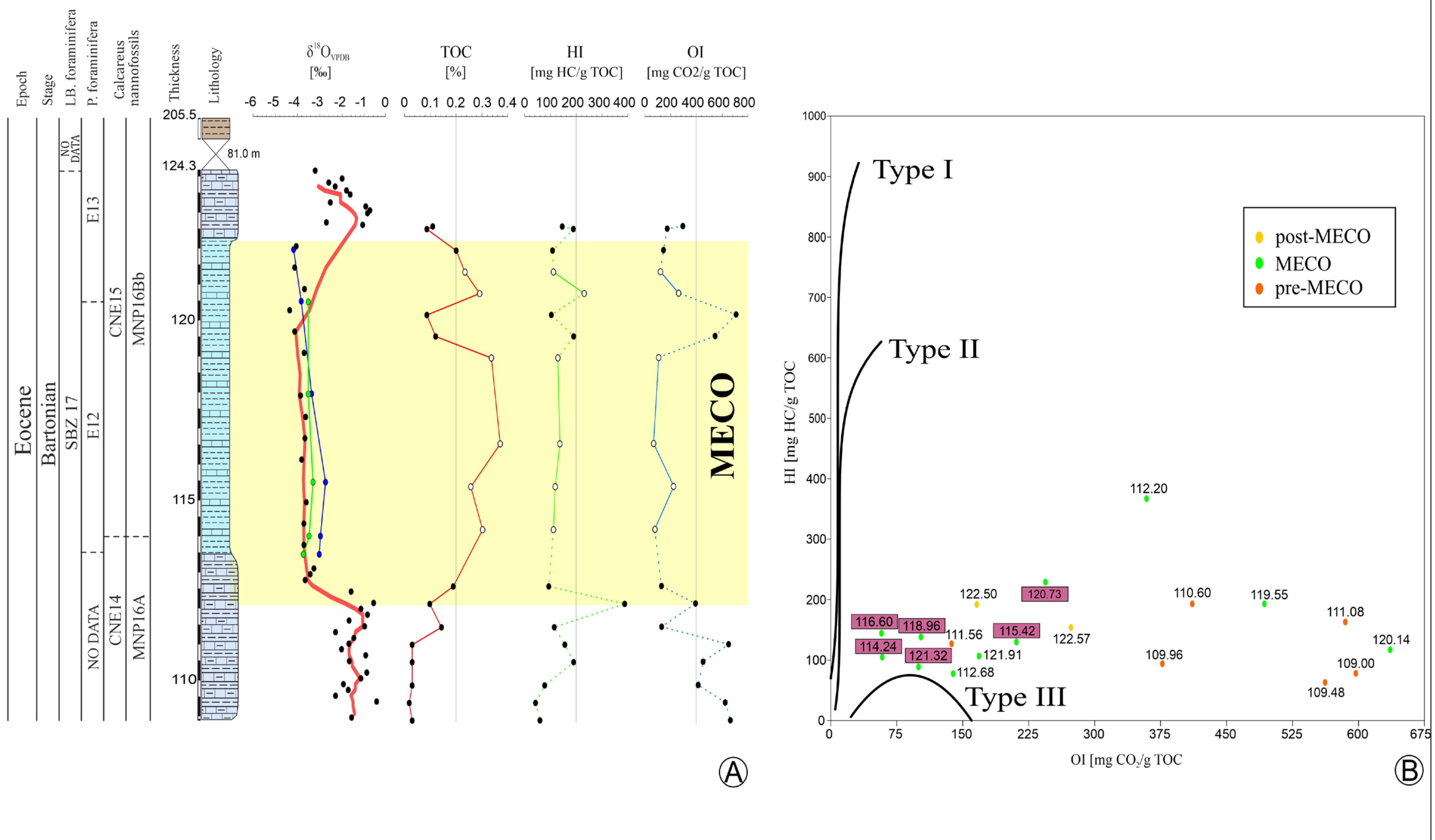

Fig. 5 - A) Total organic carbon (TOC), hydrogen, and oxygen indices (HI, OI) across the MECO interval (yellow-shaded band), plotted against lithology, biozones and oxygen isotope curve. Samples with TOC values lower than 0.2 wt% have been excluded for the interpretation of the HI and OI indices of this study; see dashed lines green and blue of the HI and OI indices, respectively; B) the scatter plot of hydrogen and oxygen indices (HI/OI) indicates organic matter origins. Type I indicates a strong marine component, while type III indicates a strong terrestrial component. Samples with TOC values higher than 0.2 wt% (rectangles in paleo-violet red) have been used for the interpretation of the HI and OI indices of this study.

Available $\delta^{13}C$ records show considerable geographic and bathymetric variability but are commonly characterized by rising rather than declining $\delta^{13}C$ values during the initial gradual warming (Bohaty & Zachos 2003; Bohaty et al. 2009; Boscolo Galazzo et al. 2014; Borelli et al. 2014). These records imply that there is no evidence for a sudden release of isotopically light carbon during the MECO warming phase. A transient ~0.5‰ negative Carbon Isotope Excursion (CIE) (~50 kyr) during the warming peak occurs at some but not all sites (Bohaty & Zachos 2003; Edgar et al. 2010; Boscolo Galazzo et al. 2014; Giorgioni et al. 2019). At the Sealza section, the $\delta^{13}C$ curve does not show the same trend recorded previously, except for a negative CIE corresponding to the OIE interval displayed by $\delta^{13}C_{bulk}$, $\delta^{13}C_{Subbotina}$ and $\delta^{13}C_{Cibicidoides}$. We cannot establish whether these shifts correspond to those previously recorded at this stage. It is known that in shallow-water environments, changes in $\delta^{13}C$ values may be controlled by the organic matter content (Oehlert & Swart 2014).

The MECO interval in our section could also be supported by the occurrence of Zone E12, marker *O. beckmanni*, which largely corresponds to the MECO interval (Sexton et al. 2006; Edgar et al. 2007; Bohaty et al. 2009), even though Edgar et al. (2010) demonstrated an earlier appearance (~500 kyr) in the equatorial Atlantic than in the subtropics (40.5 versus 41.0 Ma). This latitudinal diachroneity is attributed to the poleward expansion of warm surface-waters during the onset of the MECO, which created favorable conditions at higher latitudes for this potentially thermophilic species. At the Sealza section, the correct identification of *O. beckmanni* base and top is hampered by the scarce abundance and poor preservation of planktic foraminiferal assemblages. The species *O. beckmanni* first occurs just above the onset of the OIE at 113.5 m.

Biostratigraphic data from calcareous nannofossils at the Sealza section are in good agreement with the previous literature. Generally, the onset of the MECO is associated with the extinction of *Sphenolithus furcatolithoides* (Boscolo Galazzo et al. 2013; Toffanin et al. 2013; Messaoud et al. 2021), which in this section has been observed only just above the base of the OIE. At Sealza, the base of *O. beckmanni* seems to occur just below the top of *S. furcatolithoides*, while in other sections (e.g., Alano and Varignano, NE Italy), it is significantly above (Luciani et al. 2020). However, it must be remarked that at ODP Site 1051 (Blake Nose, Western North Atlantic), the base of *O. beckmanni* virtually coincides with the top of *S. furcatolithoides* (Edgard et al. 2010; Agnini et al. 2014; Luciani et al. 2020). Thus, at Sealza, the base of *O. beckmanni* appears to be comparable with the data from the western North Atlantic.

Paleo-water depth reconstruction

A first approximation to estimate the paleodepth of the Sealza section derives from the P/B ratio data and the regression proposed by Van der Zwaan et al. (1990) for living foraminifera. The low values of the P/B ratio recorded, especially in the lower part of the section, are associated with paleodepths <50 m, while in the upper part (MECO interval), the increase of the P/B ratio values indicates paleodepths up to ~100 m (Fig. 4). The species *Uvigerina eocaena* and *U.* cf. *peregrina* are recorded in lower neritic environments (Lamb & Miller 1984; Barbin & Keller-Grünig 1991). The species *Cibicidoides lobatulus* thrives in shallow waters, closely linked to near-bottom currents useful for its nutritional needs (Barbin & Keller-Grünig 1991; Altenbach et al. 1999; Schweizer et al. 2009). Other species, such as *Heterolepa dutemplei* and *Melonis affinis*, inhabited in a wide bathymetric range but are specially recorded in shallow waters through the stratigraphic time here investigated (Barbin & Keller-Grünig, 1991; Szarek 2001).

According to Briguglio et al. (2023), the LBF recorded in Sealza are well in agreement with the bathymetric range here proposed. Most of the samples have a rich LBF fauna, pointing to shallow-water settings within the photic zone, as LBF lived in symbiosis with photosynthetic microalgae. Toward the uppermost part of the sections, the LBF assemblages indicate a deeper setting characterized by depths that get closer to the oligophotic range, thus around 50 to 80 meters water depth.

Bottom waters reconstruction based on benthic foraminiferal paleoecology

Benthic foraminifera represent one of the most widely applied groups in paleoceanographic and paleoenvironmental reconstructions in the geological record, as their assemblages can provide useful information on several environmental parameters at the sea floor, such as organic matter, oxygen availability, depth, salinity, and temperature (e.g., Van der Zwaan et al. 1999; Gooday 2003; Murray 2006; Jorissen et al. 2007). Previous investigations were done on paleoenvironmental reconstruction and biostratigraphy across the MECO from Tethyan successions but in deep-water settings (e.g., Boscolo Galazzo et al. 2013; Boscolo Galazzo et al. 2016; D'Onofrio et al. 2021). The investigation of the benthic foraminiferal assemblages at Sealza section, coupled with isotopic records and total organic carbon (TOC), provides, for the first time, evidence of the paleoenvironmental changes across the MECO in a shallow-water setting, and provides new insights on the resilience of both planktic and benthic communities in neritic environments.

The abundance of *Cibicidoides* in the pre-MECO interval (lower part of the measured section; Fig. 3) suggests a well-oxygenated seafloor because this genus is recognized as an epifaunal benthic foraminifera living in well-oxygenated environments (e.g., Speijer 1994; Speijer & Schmitz 1998; Giraldo-Gómez et al. 2018 a,b). These conditions are also supported by the rich LBF fauna (e.g., Briguglio et al. 2023).

The marked decrease of *Cibicidoides* across the MECO interval suggests oxygenation reduction and a rise in the organic flux, as confirmed by abundant infaunal taxa (*Uvigerina* and *Bolivina*), which suggest an enhanced nutrient supply (Fig. 3). Similar findings were reported for the initial MECO phase at the Alano section and interpreted as a shift from more oligotrophic to fully mesotrophic conditions (Boscolo Galazzo et al. 2013). In marginal continental basins, eutrophication and deposition of organic-rich sediments are commonly associated with the MECO warming and directly afterward (e.g., Spofforth et al. 2010). The decrease in oxygen content during the MECO caused an increase in organic matter preservation at the seafloor, providing environmental conditions favorable for *Uvigerina*, which is known as an infaunal genus, usually living in fine-grained sediments (Van der Zwaan et al. 1986) and considered an index of carbon-rich and oxygen-poor conditions (e.g., Sen Gupta & Machain-Castillo 1993; Kaiho 1994; Thomas & Gooday 1996; Schmied et al. 1997; Van der Zwaan et al. 1999; De Rijk et al. 2000; Hess & Kuhnt 2005; Kawagata et al. 2006). The slight increase in TOC content within the MECO (Fig. 5) supports this hypothesis.

The occurrence of the infaunal *Bolivina* exclusively across the MECO interval (Fig. 3), also supports an increase of organic matter at the seafloor together with lower oxygen concentrations (Kaiho 1994; Thomas 2007). The abundance of the epifaunal *Heterolepa* follows the same trend as that of *Cibicidoides* within the MECO, although it is rare in the pre-MECO, possibly due to a competition with *Cibicidoides*. *Heterolepa* is considered to inhabit oxygenated waters as well (e.g., Van der Zwaan 1982; Rögl & Spezzaferri 2002; Russo et al. 2022), and its decrease during the MECO supports weaker oxygenation at the seafloor.

The shift to meso-eutrophic conditions at the MECO is possibly related to an enhanced hydrological cycle and supply of terrigenous flux, which is plausible in the context of the active tectonic regime coupled by climatic perturbation, similar to what has been documented by geochemical proxies in different Tethyan sections (e.g., Luciani et al. 2010; Rego et al. 2018; Peris-Cabré et al. 2023). Our data from Rock-Eval analysis confirm the terrestrial origin and increase of organic matter deposited in the basin during the MECO (Fig. 5). It is reasonable to suppose that fluvial dynamics played an important role in the erosional and depositional regimes of the river mouths linked to the precipitation increment. Nonetheless, the presence of marly limestone suggests that the coastline was distally located, as indicated by the fine material deposited.

Our results indicate that the benthic foraminiferal communities from the shallow-water setting of Sealza were sensitive to the MECO perturbances that induced low oxygen conditions and high nutrient input, similarly to the communities of the deep-water settings of marginal continental basins.

Surface water conditions based on planktic foraminiferal paleoecology

Planktic foraminifera are highly sensitive to several environmental changes, such as variation in water column stratification, density, chemistry, temperature, and nutrient supply (e.g., Corfield & Norris 1998; Quillévéré & Norris 2003; Wade & Bown 2006; Luciani et al. 2007). Nonetheless, the impact of the MECO on planktic foraminiferal assemblages is still poorly investigated, although the climatic perturbations of the lower Paleogene have been extensively documented by geochemical, sedimentological, and isotopic data. As expected, the

Sealza shallow-water succession was dominated by LBF, and planktic foraminifera are not abundant, as confirmed by the PFN and the P/B ratio (Fig. 4).

The increase in the number of genera of planktic foraminifera, total abundance, and higher values of the P/B ratio detected across the MECO interval (Fig. 4) are related to the deepening of the environmental setting. Within this interval, the significant increment in abundance of *Acarinina* and the occurrence of *Morozovelloides* and *O. beckmanni* likely suggest an increase in surface water temperature. These taxa are indeed recognized as mixed-layer, oligotrophic warm-water indicators that dominated the tropical and subtropical assemblages in the late Paleocene to middle Eocene (with *Morozovella* preceding *Morozovelloides*) (e.g., Boersma et al. 1987; Pearson et al. 1993, 2001; Edgar et al. 2010). The absence of the genus *Globigerinatheka*, which is a common component of middle Eocene assemblages, appears unusual, especially considering that several species of this genus should co-occur with *O. beckmanni* which is considered the end member of the *Globigerinatheka curry-euganea* lineage (Proto Decima & Bolli 1970). The genus *Globigerinatheka* is regarded as a symbiont-bearing mixed layer dweller as recording depleted δ^{18}O and enriched δ^{13}C values (Boersma et al. 1987; Pearson et al. 1993; Premoli Silva & Jankins 1993; Pearson et al. 2001; Wade & Kroon 2002; Wade 2004), thus possibly comparable, for its ecological requirements and significance, with *Acarinina*. However, stable isotope values in *Globigerinatheka* commonly indicate calcification in deeper waters (Wade 2004; Premoli Silva et al. 2006; Sexton et al. 2006; Burgess et al. 2008; Boscolo Galazzo et al. 2014), suggesting that the genus had late-stage calcification, with $CaCO_3$ crusts forming deeper in the water column, possibly close to the thermocline (Pearson et al. 2001; Wade & Kroon 2002; Premoli Silva et al. 2006); that seems also supported by boron isotope data (Pearson & Palmer 1999). Unfortunately, stable isotope paleobiology is yet unknown for the species *G. curry, G. euganea*, and *O. beckmanni*. To explain the occurrence of *O. beckmanni*, though with very rare specimens, and the absence of *Globigerinatheka,* we hypothesize a differential response of gametogenesis with respect to the shallow-water character of the depositional environment here observed: *Orbulinoides beckmanni* probably completed its life cycle in shallower water, whereas *Globigerinatheka* might have preferred a deeper setting for gamete release. Test recrystallization and poor preservation of *O. beckmanni* in our samples prevent targeted stable isotope analysis to confirm this hypothesis. Nonetheless, this first record of planktic foraminifera in a shallow-water environment highlights such ecological requirements and calls for a better knowledge of *O. beckmanni* paleoecology. Across the MECO interval, the parallel decrease of the cold-water index genus *Subbotina* (e.g., Sexton et al. 2006) across the MECO interval reinforces the evidence of upper water column warming. The relative high abundance of *Subbotina* at the basal MECO despite the warming may be related to the meso-eutrophic conditions and elevated nutrient supply at the thermocline (D'Onofrio et al. 2021). This could also explain the absence, also in this portion of the section, of the oligotrophic *Globigerinatheka* and *Acarinina*. The dominance of *Subbotina* at the top of the section in the sample above the covered interval may be interpreted as a return to cooler conditions.

The decline in abundance of *Acarinina* in the upper MECO interval could have different explanations. Edgar et al. (2013) document that the symbiotic relationship of *Acarinina* was temporarily reduced for ~100 k.y. during the peak of the MECO at Sites 748 and 1051 (Southern Ocean and mid-latitude North Atlantic, respectively). The authors relate this bleaching episode as linked to the ecological stress induced by increased sea-surface temperatures. We cannot establish whether a bleaching episode caused the decrease in abundance of *Acarinina* at the Sealza section. However, a permanent middle Eocene decline in the abundance of acarininids, specifically of the species larger than 150 μm, well before their evolutionary extinction level occurred at the Bartonian-Priabonian boundary (Agnini et al. 2021) in the Tethyan realm (Luciani et al. 2010, 2020; D'Onofrio et al. 2021). Although only a single sample of the studied section is attributable to the post-MECO and cannot be considered conclusive to reconstruct foraminiferal resilience during the aftermath of the event, the very low abundance of *Acarinina* (Fig. 4) suggests that, even at the Sealza setting, this genus did not recover. The causes of this persisting decline in abundance are not yet established. However, a link to the climatic change and paleoceanographic variations that occurred during the MECO, or just following it, seems implied. Further analyses are needed to establish whether the permanent decrease in abundance of *Acarinina* is globally recorded.

The changes in planktic foraminiferal abundance recorded in the shallow-water setting of Sealza prove to be significantly different with respect to those analyzed from deeper environments. In the Tethyan Alano (northeastern Italy) and Baskil middle-bathyal sections (eastern Turkey), deposited in marginal continental basins (Luciani et al. 2010; D'Onofrio et al. 2021), planktic foraminiferal assemblages record a marked decline of acarininids and *Morozovelloides* within the MECO, coupled with an increase in subbotinids. Changes in salinity and a marked increase in eutrophic conditions related to freshwater input due to an enhanced hydrological cycle have been invoked as having impacted the habitat of the specialized, oligotrophic mixed-layer dweller acarininids. On the contrary, the eutrophic genus *Subbotina* may have benefitted from high food delivery to the thermocline, and this could explain the apparent inconsistency of the increase in this cold-water index genus at the Tethyan sections. In the Sealza assemblages, highly opportunistic and eutrophic taxa such as *Chiloguembelina*, *Jenkinsina*, and *Pseudoglobigerinella bolivariana*, do not occur, however they were recorded in high abundance across the MECO interval from the Alano section (Luciani et al. 2010; D'Onofrio et al. 2021). This evidence, together with the increase of warm, specialized index taxa, could attest to a minor degree of eutrophication in the Sealza setting. This scenario is also supported by the occurrence at Sealza by the LBF communities, which should have been heavily impacted by excess eutrophication.

Ecological resilience of the Sealza shallow-water communities across the MECO

Our results on benthic and planktic foraminifera highlight that the assemblages moved to a different state during the MECO perturbation. As detailed above, oxygenation at the sea floor probably decreased, as substantiated by a drop in abundance of *Cibicidoides* and *Anomalinoides*, paralleled by an increase in taxa tolerating deoxygenated conditions and high nutrient input, such as *Uvigerina* and *Bolivina* and by the increase in TOC values. However, in the upper part of the MECO interval, the benthic community recovered the genera abundance of the pre-MECO, except for *Anomalinoides.* In the upper water column, planktic foraminifera show marked changes in the assemblages, mainly related to the intense MECO warming. The decline of large acarininids, which started in the upper MECO interval, is also recorded above the MECO, even though we can provide just one sample from this interval. Remarkably, this permanent decline appears to coincide with the Tethyan deep-water record (Luciani et al. 2010; D'Onofrio et al. 2020). Considering that the benthic and planktic communities moved to a new state, they proved to be not resilient to the MECO perturbance. Interestingly, the LBF also show changes in assemblages across the MECO interval, moving from rich LBF communities to assemblages dominated by small nummulitids and operculinids (Briguglio et al. 2023). It is difficult to unravel the significance of these changes in LBF because they could be related to the deepening of the depositional setting (Briguglio et al. 2017; Eder et al. 2016, 2017, 2018) rather than to the MECO temperature and nutrient increase (Seddighi et al. 2015; Hohenegger et al. 2019, Roslim et al. 2019,).

In conclusion, as recorded from the deep-water settings, the MECO event permanently impacted the benthic and planktic communities, although did not induce extinctions. The tipping point to undergo a permanent new regime shift was reached, thus preventing the recovery after the disturbance, wherein the communities proved to be highly unstable and finally not resilient.

Summary and conclusions

The identification of the MECO and its impact on both benthic and planktic faunas is still not fully understood, and most of the records and interpretations rely on deep-water successions. This study offers the remarkable opportunity to analyze the MECO from the shallow-water setting of the Sealza section (NW Italy), to evaluate the resilience of the studied groups to this environmental perturbance, and to compare shallow-water assemblages with those from deep-water settings.

We summarize below our main results:

The MECO interval was targeted by using the calcareous plankton biostratigraphy and the oxygen stable isotope signal that records a marked negative shift. The lithological expression of the MECO at the studied section is represented by variations from silty marls embedded within biocalcarenite to biocalcirudite beds rich in LBF, corals, and mollusks. The recorded lithological modifications evidence that a somewhat drastic change in the neritic inputs happened. However, correlating this evidence with the MECO event is not immediate, as the regional tectonic regime during the middle Bartonian was the main trigger of the ramp drowning, and therefore this must have played a role in the lithological variations. Nevertheless, the MECO negative shift in the isotopic signal synchronous with the lithological variations allows us to attribute mainly the silty marls deposition to enhanced hydrological cycles. This was enhanced by the temperature increase, that provided more carrying capacity of the riverine system to shed more material onto the offshore.

Our record on benthic and planktic foraminifera highlights that the communities moved to an unstable state during the MECO perturbation, as recorded de-oxygenation at the seafloor and an increase in the planktic foraminiferal warm-water index genus *Acarinina*. This genus significantly declined in abundance in the upper part of the MECO interval and did not recover in the post-MECO, as recorded in the deep-water Tethyan record. To explain the absence of *Globigerinatheka* in our record, we hypothesize a differential response of gametogenesis with respect to the shallow-water character of the depositional environment observed at Sealza. *Orbulinoides beckmanni* probably completed its life cycle in shallower water, whereas *Globigerinatheka* might have preferred a deeper setting for gamete release.

With the exception of the acarininid decline, changes in planktic foraminiferal assemblages are proved to be markedly different from those recorded from the bathyal Tethyan Alano succession, which documents a decrease in warm-water index taxa and a pronounced shift to eutrophic conditions, as proved by the marked increase of opportunistic and highly eutrophic taxa, that was not observed at Sealza. This dissimilarity suggests that the nutrient input and consequent eutrophication due to the enhanced hydrological cycle were less pronounced at the Sealza setting, as also substantiated by the occurrence of the oligotrophic LBF. These highlights suggest that the riverine system was rather far from the Sealza depositional setting.

The MECO perturbance at Sealza permanently impacted the benthic and planktic communities that exceeded the tipping point to move to a new regime, thus proving to be not only resilient but also not recording extinctions. In turn, the LBF demonstrate to be more resilient, as their changes in assemblages appear to be more related to the deepening of the depositional setting than to the MECO perturbation.

This study proved that only a multidisciplinary approach and a reliable stratigraphic constraint can tackle complex environmental interpretations during climatic crises, which is especially important when the focus is on the resilience of marine taxa. Our scenario on the impact on foraminiferal assemblages of the MECO warming event may offer a significant deep-time perspective to the IPCC or other policy-relevant organizations such as the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES) that still insufficiently consider the paleontological contribution to past biological changes (e.g., Kiessling et al. 2023).

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References

Agnini C., Muttoni G., Kent D.V. & Rio D. (2006) - Eocene biostratigraphy and magnetic stratigraphy from Possagno, Italy: the calcareous nannofossil response to climate variability. *Earth Planet Science Letters*, 241: 815-830. doi: 10.1016/j.epsl.2005.11.005.

Agnini C., Fornaciari E., Raffi I., Catanzariti R., Pälike H., Backman J. & Rio D. (2014) - Biozonation and biochronology of Paleogene calcareous nannofossils from low and middle latitudes. *Newsletters on stratigraphy*, 47(2):131-181.

Agnini C., Backman J., Boscolo-Galazzo F., Condon D. J., Fornaciari E., Galeotti S. & Wade B. S. (2021) - Proposal for the global boundary stratotype section and point (GSSP) for the Priabonian stage (Eocene) at the Alano section (Italy). *Episodes Journal of International Geoscience*, 44(2): 151-173.

Altenbach A.V., Pflaumann U., Schiebel R., Thies A., Timm S. & Trauth M. (1999) - Scaling percentages and distributional patterns of benthic foraminifera with flux rates of organic carbon. *Journal of Foraminiferal Research*, 29: 173-185.

Barbin V. & Keller-Grünig A. (1991) - Benthic foraminiferal assemblages from the Brendola section (Priabonian stage stratotype area, northern Italy): Distribution, palaeoenvironment and palaeoecology. *Marine Micropaleontology*, 17(3-4): 237-254.

Behar F., Beaumont V. & Penteado H.L.D. (2001) - Rock-Eval 6 technology: performances and developments. *Oil & Gas Science and Technology*, 56: 111-134. doi.org/10.2516/ogst:2001013.

Bijl P.K., Houben A.J.P., Schouten S., Bohaty S.M., Sluijs A., Reichart G.J., Sinninghe Damsté J.S. & Brinkhuis H. (2010) - Transient middle Eocene atmospheric CO_2 and temperature variations. *Science*, 330: 819-821. doi:10.1126/science.1193654.

Boersma A., Premoli Silva I. & Shackleton N.J. (1987) - Atlantic Eocene planktonic foraminiferal paleohydrographic indicators and stable isotope paleoceanography. *Paleoceanography*, 2: 287-331. doi:10.1029/PA002i003p00287.

Bohaty S.M. & Zachos J.C. (2003) - A significant Southern Ocean warming event in the late middle Eocene. *Geology,* 31: 1017-1020.

Bohaty S.M., Zachos J.C., Florindo F. & Delaney M.L. (2009) - Coupled greenhouse warming and deep-sea acidification in the Middle Eocene. *Paleoceanography,* 24: 2207. doi:10.1029/2008PA001676,2009.

Borelli C., Cramer B.S. & Katz M.E. (2014) - Bipolar Atlantic deep-water circulation in the middle late Eocene: Effects of Southern Ocean gateway openings. *Paleoceanography*, 29: 308-327. doi:10.1002/2012PA002444.

Boscolo Galazzo F., Giusberti L., Luciani V. & Thomas E. (2013) - Paleoenvironmental changes during the Middle Eocene Climatic Optimum (MECO) and its aftermath: The benthic foraminiferal record from the Alano section (NE Italy). *Palaeogeography, Palaeoclimatology, Palaeoecology*, 378: 22-35. doi: 10.1016/j.palaeo.2013.03.018.

Boscolo Galazzo F., Thomas E., Pagani M., Warren C. & Giusberti L. (2014) - The middle Eocene climatic optimum (MECO): A multi-proxy record of paleoceanographic changes in the southeast Atlantic (ODP Site 1263, Walvis Ridge). *Paleoceanography*, 29: 1143-1161.

Boscolo Galazzo F., Thomas E., Luciani V., Giusberti L, Frontalini F. & Coccioni R. (2016) - The planktic foraminifer *Planorotalites* in the Tethyan middle Eocene. *Journal of Micropaleontology*, 35: 79-89.

Boussac, J (1912) - Ètudes stratigraphique sur le Nummulitique alpin. *Mémoires pour servir à l'explication de la carte géologique détaillée de la France,* 662: 20.

Briguglio A., Seddighi M., Papazzoni C.A. & Hohenegger J. (2017) - Shear versus settling velocity of recent and fossil larger foraminifera: New insights on nummulite banks. *Palaios*, 32: 321-329.

Briguglio A., Giraldo-Gòmez V.M., Baucon A., Benedetti A., Papazzoni C.A., Pignatti J., Wolfgring E. & Piazza M. (2023) - A middle Eocene shallow-water drowning ramp in NW Italy: from shoreface conglomerates to distal marls. *Newsletter on Stratigraphy*. doi: 10.1127/nos/2023/0784.

Burgess C.E., Pearson P.N., Lear C.H., Morgans H.E., Handley L., Pancost R.D. & Schouten S. (2008) - Middle Eocene climate cyclicity in the southern Pacific: Implications for global ice volume. *Geology,* 36(8): 651-654.

Campredon R. (1977) - Les formations paléogènes des Alpes Maritimes franco-italiennes. *Mémoire hors-série de la Société géologique de France,* 9: 1-199.

Coccioni R., Bancalà G., Catanzariti R., Fornaciari E., Frontalini F., Giusberti L., Jovane L., Luciani V., Savian J. & Sprovieri M. (2012) - An integrated stratigraphic record of the Palaeocene-lower Eocene at Gubbio (Italy), new insights into the early Palaeogene hyperthermals and carbon isotope excursions. *Terra Nova,* 24: 380-386. doi.org/10.1111/j.1365-3121.2012.01076.x.

Coletti G., Mariani L., Garzanti E., Consani S., Bosio G., Vezzoli G., Hu X. & Basso D. (2021) - Skeletal assemblages and terrigenous input in the Eocene carbonate systems of the Nummulitic Limestone (NW Europe). *Sedimentary Geology*, 10: 6005. doi.org/10.1016/j.sedgeo.2021.106005.

Corfield R.M. & Norris R.D. (1998) - The oxygen and carbon isotopic context of the Paleocene–Eocene Epoch boundary. In: Aubry M.P., Lucas S. & Berggren W.A. (Eds.) - Late Paleocene - Early Eocene Climatic and Biotic Events in the Marine and Terrestrial Records: 124-137. Columbia University Press, New York.

Coxall H.K., Wilson P.A., Pälike H., Lear C.H. & Backman J. (2005) - Rapid stepwise onset of Antarctic glaciation and deeper calcite compensation in the Pacific Ocean. *Nature*, 433: 53-57. doi:10.1038/ nature03135.

Cramwinckel M. J., van der Ploeg R., Bijl P. K., Peterse F., Bohaty S. M., Röhl U., Schouten S., Middelburg J.J. & Sluijs A. (2019) - Harmful algae and export production collapse in the equatorial Atlantic during the zenith of Middle Eocene Climatic Optimum warmth. *Geology*, 47(3): 247-250.

Dallagiovanna G., Fanucci F., Pellegrini L., Seno S., Bonini L., Decarlis A., Maino M., Morelli D. & Toscani G. (2012) - Note illustrative della Carta Geologica Foglio 257-Dolceacqua e Foglio 270 - Ventimiglia. 75 pp. Regione Liguria. http://www.cartografia.regione.liguria.it/template-FogliaRC.asp.

Dawber C.F. & Tripati A.K. (2011) - Constraints on glaciation in the middle Eocene (46-37 Ma) from Ocean Drilling Program (ODP) Site 1209 in the tropical Pacific Ocean. *Paleoceanography*, 26: 2208. doi:10.1029/2010PA002037.

Decarlis A., Maino M., Dallagiovanna G., Lualdi A., Masini E., Seno S. & Toscani G. (2014) - Salt tectonics in the SW Alps (Italy–France): From rifting to the inversion of the European continental margin in a context of oblique convergence. *Tectonophysics*, 636: 293-314.

De Graciansky P.C., Roberts D.G. & Tricart P. (2010) - The Western Alps, from rift to passive margin to orogenic belt: an integrated geoscience overview. Developments in Earth Surface Processes 14. Elsevier, Amsterdam, 398 pp.

De Rijk S., Jorissen F.J., Rohling E.J. & Troelstra S.R. (2000) - Organic flux control on bathymetric zonation of Mediterranean benthic foraminifera. *Marine Micropaleontology*, 40(3): 151-166. doi.org/10.1016/S0377-8398(00)00037-2.

D'Onofrio R., Luciani V., Fornaciari E., Giusberti L., Boscolo Galazzo F., Dallanave E., Westerhold T., Sprovieri M. & Telch S. (2016) - Environmental perturbations at the early Eocene ETM2, H2, and I1 events as inferred by Tethyan calcareous plankton (Terche section, northeastern Italy). *Paleoceanography,* 31(9): 1225-1247. doi.org/10.1002/2016PA002940.

D'Onofrio R. & Luciani V. (2020) - Do different extraction techniques impact planktic foraminiferal assemblages? An early Eocene case study. *Marine Micropaleontology,* 155: 0377-8398. doi.org/10.1016/j.marmicro.2019.101795.

D'Onofrio R., Luciani V., Dickens G.R., Wade B.S. & Kirtland Turner S. (2020) - Demise of the planktic foraminifer genus *Morozovella* during the Early Eocene climatic optimum: new records from ODP Site 1258 (Demerara rise, Western Equatorial Atlantic) and site 1263 (Walvis Ridge, South Atlantic). *Geosciences*, 10(3): 88.

D'Onofrio R., Zaky A.S., Frontalini F., Luciani V., Catanzariti R., Francescangeli F. & Jovane L. (2021) - Impact of the Middle Eocene Climatic Optimum (MECO) on foraminiferal and calcareous nannofossil assemblages in the Neo-Tethyan Baskil Section (Eastern Turkey): Paleoenvironmental and paleoclimatic reconstructions. *Applied Sciences*, 11(23): 11339.

Eder W., Briguglio A. & Hohenegger J. (2016) - Growth of *Heterostegina depressa* under natural and laboratory conditions. *Marine Micropaleontology*, 122: 22-43.

Eder W., Hohenegger J. & Briguglio A. (2017) - Depth-related morphoclines of megalospheric tests of *Heterostegina depressa* d'Orbigny: Biostratigraphic and paleobiological implications. *Palaios*, 32: 110-117.

Eder W., Hohenegger J. & Briguglio A. (2017) - Test flattening in the larger foraminifer *Heterostegina depressa:* Predicting bathymetry from axial sections. *Paleobiology*, 44: 76-88.

Edgar K.M., Wilson P.A., Sexton P.F. & Suganuma Y. (2007) - No extreme bipolar glaciation during the main Eocene calcite compensation shift. *Nature,* 448: 908-911.

Edgar K.M., Wilson P.A., Sexton P.F., Gibbs S.J., Roberts A.P. & Norris R.D. (2010) - New biostratigraphic, magnetostratigraphic and isotopic insights into the Middle Eocene Climatic Optimum in low latitudes. *Palaeogeography Palaeoclimatology Palaeoecology*, 297: 670-682. doi: 10.1016/j.palaeo.2010.09.016.

Edgar K.M., Bohaty S.M., Gibbs S.J., Sexton P.F., Norris R.D. & Wilson P.A. (2013) - Symbiont 'bleaching' in planktic foraminifera during the Middle Eocene Climatic Optimum. *Geology,* 41(1): 15-18.

Espitalié J., Deroo G. & Marquis F. (1985) - La pyrolyse Rock-Eval et ses applications. *Revue de l'Institut Français du Pétrole*, 40: 563-579. doi.org/10.2516/ogst:1985035.

Fornaciari E., Giusberti L., Luciani V., Tateo F., Agnini C., Backman J., Oddone M. & Rio D. (2007) - An expanded Cretaceous-Tertiary transition in a pelagic setting of the Southern Alps (central–western Tethys). *Paleogeography and Paleoclimatology*, 255: 98-131.

Fornaciari E., Agnini C., Catanzariti R., Rio D., Bolla E.M. & Valvasoni E. (2010) - Mid latitude calcareous nannofossil biostratigraphy and biochronology across the middle to late Eocene transition. *Stratigraphy,* 7: 229-264.

Frank T.D., Arthur M.A. & Dean W.E. (1999) - Diagenesis of Lower Cretaceous pelagic carbonates, North Atlantic: Paleoceanographic signals obscured. *Journal of Foraminiferal Research*, 29: 340-351.

Gardin S. & Monechi S. (1998) - Palaeoecological change in the middle to low latitude calcareous nannoplankton at the Cretaceous/Tertiary boundary. *Bulletin de la Societé Géologique de France*, 5: 709-723.

Giammarino S., Orezzi S., Piazza M. & Rosti D. (2009) - Evidence of syn-sedimentary tectonic activity in the "flysch di Ventimiglia" (Ligurian Alps foredeep basin). *Italian Journal of Geosciences*, 128(2): 467-472. doi: 10.3301/IJG.2009.128.2.467.

Giammarino S., Fanucci F., Orezzi S., Rosti D., Morelli D., Cobianchi M., De Stefanis A., Di Stefano A., Finocchiaro F., Fravega P., Piazza M. & Vannucci G. (2010) - Note Illustrative della Carta Geologica d'Italia alla scala 1:50.000 - Foglio "San Remo" n.258- 271. ISPRA - Regione Liguria. 130 pp. A.T.I. - SystemCart s.r.l. - L.A.C. s.r.l. - S.EL.CA., Firenze.

Giorgioni M., Jovane L., Rego E.S., Rodelli D., Frontalini F., Coccioni R., Catanzariti R. & Özcan E. (2019) - Carbon cycle instability and orbital forcing during the Middle Eocene Climatic Optimum. *Science*, 9: 9357.

Giraldo Gómez V. M., Beik I., Podlaha O. G. & Mutterlose J. (2017) - The micropaleontological record of marine early Eocene oil shales from Jordan. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 485: 723-739.

Giraldo-Gómez V. M., Mutterlose J., Podlaha O. G., Speijer R. P. & Stassen P. (2018a) - Benthic foraminifera and geochemistry across the Paleocene–Eocene Thermal Maximum interval in Jordan. *Journal of Foraminiferal Research,* 48(2): 100-120.

Giraldo-Gómez V. M., Beik I., Podlaha O. G. & Mutterlose J. (2018b) - A paleoenvironmental analyses of benthic foraminifera from Upper Cretaceous–lower Paleocene oil shales of Jordan. *Cretaceous Research*, 91: 1-13.

Gooday A.J. (2003) - Beyond methane: Towards a theory for the Paleocene-Eocene Thermal Maximum Benthic foraminifera (protista) as tools in deep-water palaeoceanography: Environmental influences on faunal characteristics. *Advances in Marine Biology*, 46: 1-90.

Hammer Ø., Harper D.A.T. & Ryan P.D. (2001) - PAST: paleontological statistics software package for education and data analysis. *Paleontologia Elettronica*, 4(1): 9.

Henehan M. J., Edgar K. M., Foster G.L., Penman D. E., Hull P. M., Greenop R., Anagnostou E. & Pearson P.N. (2020) - Revisiting the Middle Eocene Climatic Optimum "Carbon Cycle Conundrum" with new estimates of atmospheric pCO_2 from boron isotopes. *Paleoceanography and Paleoclimatology*, 35: e2019PA003713.

Hess S. & Kuhnt W. (2005) - Neogene and Quaternary paleoceanographic changes in the southern South China Sea (Site 1143): the benthic foraminiferal record. *Marine Micropaleontology*, 54(1-2): 63-87. doi.org/10.1016/j.marmicro.2004.09.004.

Hohenegger J., Kinoshita S., Briguglio A., Eder W. & Wöger J. (2019) - Lunar cycles and rainy seasons drive growth and reproduction in nummulitid foraminifera, important producers of carbonate buildups. *Scientific Reports*, 9(1): 8286.

Holbourn A., Henderson A.S., MacLeod N. & MacLeod N. (2013) - Atlas of benthic foraminifera. London, Wiley-Blackwell, vol. 654.

IPCC, Masson-Delmotte V., Zhai P., Pörtner H. O., Roberts D., Skea J. & Shukla P.R. (2018) - Global warming of 1.5°C. An IPCC Special Report on the impacts of global warming of 1.5°C above pre-industrial levels and related global greenhouse gas emission pathways, in the context of strengthening the global response to the threat of climate change, sustainable development, and efforts to eradicate poverty. IPCC Geneva, Switzerland, 2018.

Jorissen F.J., Fontanier C. & Thomas E. (2007) - Chapter seven: Paleoceanographical proxies based on Deep-Sea benthic foraminiferal assemblage characteristics. *Developments in Marine Geology*, 1: 263–325.

Jovane L., Florindo F., Coccioni R., Dinarès-Turell J., Marsili A., Monechi S., Roberts A.P. & Sprovieri M. (2007) - The middle Eocene climatic optimum event in the Contessa Highway section, Umbrian Apennines, Italy. *Geological Society of America Bulletin*, 119: 413-427.

Kawagata S., Hayward B.W. & Gupta A.K. (2006) - Benthic foraminiferal extinctions linked to late Pliocene–Pleistocene deep-sea circulation changes in the northern Indian Ocean (ODP Sites 722 and 758). *Marine Micropaleontology,* 58(3): 219-242. doi.org/10.1016/j.marmicro.2005.11.003.

Kaiho K. (1994) - Benthic foraminiferal dissolved-oxygen index and dissolved-oxygen levels in the modern ocean. *Geology,* 22(8): 719–722. doi: https://doi.org/10.1130/0091613(1994)022<0719: BFDOIA>2.3.CO;2.

Kiessling W., Smith J.A. & Raja N.B. (2023) - Improving the relevance of paleontology to climate change policy. *Proceedings of the National Academy of Sciences,* 120(7): e2201926119 https://doi.org/10.1073/pnas.2201926119.

Lamb J.L. & Miller T.L. (1984) - Stratigraphic Significance of Uvigerinid Foraminifers in the Western Hemisphere. University of Kansas Paleontological Institute, Lawrence, 100 p.

Lanteaume M. (1968) - Contribution à l'étude géologique des Alpes Maritimes franco-italiennes. *Mémoires puor servir à l'explication de la Carte Géologique détaillée de la France*, 1-405.

Less G., Özcan E., Papazzoni C.A. & Stockar R. (2008) - The middle to late Eocene evolution of nummulitid foraminifer *Heterostegina* in the Western Tethys: Acta Palaeontologica Polonica, 53: 317-350.

Less G. & Özcan E. (2012) - Bartonian-Priabonian larger benthic foraminiferal events in the Western Tethys. *Austrian Journal of Earth Sciences*, 105(1): 129-140.

Lirer F. (2000) - A new technique for retrieving calcareous microfossils from lithified lime deposits. *Micropaleontology,* 46: 365–369.

Loeblich Jr A.R. & Tappan H. (1988) - Foraminiferal genera and their classification. Springer, 2045 pp.

Loeblich A.R. & Tappan H. (1994) - Foraminifera of the Sahul shelf and Timor Sea. Cushman special publications, 661 pp.

Luciani V., Giusberti L., Agnini C., Backman J., Fornaciari E. & Rio D. (2007) - The Paleocene–Eocene Thermal Maximum as recorded by Tethyan planktonic foraminifera in the Forada section (northern Italy). *Marine Micropaleontology*, 64(3): 189-214. doi.org/10.1016/j.marmicro.2007.05.001.

Luciani V., Giusberti L., Agnini C., Fornaciari E., Rio D., Spofforth D.J.A. & Pälike H. (2010) - Ecological and evolutionary response of Tethyan planktonic foraminifera to the middle Eocene climatic optimum (MECO) from the Alano section (NE Italy). *Palaeogeography, Palaeoclimatology, Palaeoecology*, 292: 82-95. doi.org/10.1016/j. palaeo.2010.03.029.

Luciani V. & Giusberti L. (2014) - Reassessment of the early–middle Eocene planktic foraminiferal biomagnetochronology: new evidence from the Tethyan Possagno section (NE Italy) and Western North Atlantic Ocean ODP Site 1051. *Journal of Foraminiferal Research*, 44: 187-201.

Luciani V., Dickens G.R., Backman J., Fornaciari E., Giusberti L., Agnini C. & D'Onofrio R. (2016) - Major perturbations in the global carbon cycle and photosymbiont-bearing planktic foraminifera during the early Eocene. *Climate of the Past,* 12: 981-1007. doi. org/10.5194/cp-12-981-2016.

Luciani V., Fornaciari E., Papazzoni C.A., Dallanave E., Giusberti L., Stefani C. & Amante E. (2020) - Integrated stratigraphy at the Bartonian–Priabonian transition: Correlation between shallow benthic and calcareous plankton zones (Varignano section, northern Italy). *The Geological Society of America Bulletin*, 132: 495-520.

Maino M. & Seno S. (2016) - The thrust zone of the Ligurian Penninic basal contact (Monte Fronté, Ligurian Alps, Italy). *Journal of Maps*, 12: 341-351. doi.org/10.1080/17445647.2016.1213669.

Marini M., Patacci M., Felletti F., Decarlis A. & McCaffrey W. (2022) - The erosionally confined to emergent transition in a slope-derived blocky mass-transport deposit interacting with a turbidite substrate, Ventimiglia Flysch Formation (Grès d'Annot System, north-west Italy). *Sedimentology,* 69: 1675-1704.

Marshall J.D. (1992) - Climatic and oceanographic isotopic signals from the carbonate rock record and their preservation. *Geological magazine*, 129(2): 143-160.

Messaoud H.J., Thibault N., Bomou B., Adatte T., Monkenbusch J., Spangenberg J.E., Aljahdali H.M. & Yaich C. (2021) - Integrated stratigraphy of the middle-upper Eocene Souar Formation (Tunisian dorsal): implications for the middle eocene climatic optimum (MECO) in the SW Neo-Tethys. *Palaeogeography, Palaeoclimatology. Palaeoecology*, 581(10): 110639.

Methner K., Mulch A., Fiebig J., Wacker U., Gerdes A., Graham S.A. & Chamberlain C.P. (2016) - Rapid Middle Eocene temperature change in western North America. *Earth and Planetary Science Letters*, 450: 132-139. doi. org/10.1016/j.epsl.2016.05.053.

Morelli D., Locatelli M., Corradi N., Cianfarra P., Crispini L., Federico L. & Migeon S. (2022) - Morpho-structural setting of the Ligurian Sea: the role of structural heritage and neotectonic inversion. *Journal of Marine Science and Engineering*, 10(9): 1176.

Mueller P., Maino M. & Seno S. (2020) - Progressive deformation patterns from an accretionary prism (Helminthoid Flysch, Ligurian Alps, Italy). *Geosciences*, 10(1): 26 doi. org/10.3390/geosciences10010026.

Murray J.W. (2006) - Ecology and Applications of Benthic Foraminifera. Cambridge University Press, 426 pp.

Oehlert A.M. & Swart P.K. (2014) - Interpreting carbonate and organic carbon isotope covariance in the sedimentary record. *Nature Communications*, 5(1): 4672. doi: 10.1038/ncomms5672.

Papazzoni C.A. & Sirotti A. (1995) - Nummulite biostratigraphy at the Middle/Upper Eocene boundary in the Northern Mediterranean area. *Rivista Italiana di Paleontologia e Stratigrafia*, 101: 63-80.

Papazzoni C.A., Cosovic V., Briguglio A. & Drobne K. (2017) - Towards a calibrated larger foraminifera biostratigraphic zonation: Celebrating 18 years of the application of shallow benthic zones. *Palaios*, 21: 1-5.

Pearson P.N., Shackleton N.J. & Hall M.A. (1993) - Stable isotope paleoecology of middle Eocene planktonic foraminifera and multispecies isotope stratigraphy, DSDP Site 523, South Atlantic. *Journal of Foraminiferal Research*, 23: 123-140.

Pearson P.N. & Palmer M.R. (1999) - Middle Eocene seawater pH and atmospheric carbon dioxide concentrations. *Science*, 284(5421): 1824-1826.

Pearson P.N., Ditchfield P.W., Singano J., Harcourt-Brown K.G., Nicholas C. J., Olsson R.K., Shackleton N. J. & Hallk M.A. (2001) - Warm tropical sea surface temperatures in the Late Cretaceous and Eocene epochs, *Nature*, 413, 481-488, doi:10.1038/35097000.

Pearson P.N., Olsson R.K., Hemblen C., Huber B.T. & Berggren W.A. (2006) - Atlas of Eocene Planktonic Foraminifera. Cushman Special Publication, Department of Geology East Carolina University, Greenville, 513 pp.

Perch-Nielsen K. (1985) - Cenozoic calcareous nannofossils. In: Bolli H.M., Saunders J.B., Perch-Nielsen K. (Eds.) - Plankton Stratigraphy: 427-554. Cambridge University Press, Cambridge.

Peris-Cabré S., Valero L., Spangenberg J. E., Vinyoles A., Verité J., Adatte T., Maxime Tremblin M., Watkins S., Sharma N., Garcés M., Puigdefàbregas C. & Castelltort S. (2023) - Fluvio-deltaic record of increased sediment transport during the Middle Eocene Climatic Optimum (MECO), Southern Pyrenees, Spain. *Climate of the Past*, 19(3): 533–554. doi.org/10.5194/cp-19-533-2023.

Perotti E., Bertok C., D'Atri A., Martire L., Piana F. & Catanzariti R. (2012) - A tectonically induced Eocene sedimentary mélange in the West Ligurian Alps, Italy. *Tectonophysics*, 568: 200-214. doi.org/10.1016/j.tecto.2011.09.005.

Premoli-Silva I. & Jenkins D.G. (1993) - Decision on the Eocene-Oligocene boundary stratotype. *Episodes Journal of International Geoscience*, 16(3): 379-382.

Premoli-Silva I., Wade B.S. & Pearson P.N. (2006) - Taxonomy, biostratigraphy, and phylogeny of *Globigerinatheka* and *Orbulinoides*. In: Pearson P.N., Olsson R.K., Huber B.T., Hemleben C. & Berggren W.A. (Eds.) - Atlas of Eocene Planktonic Foraminifera: 169-212. Cushman Foundation.

Proto Decima F. & Bolli M.H. (1970) - Evolution and variability of *Orbulinoides beckmanni* (Saito). *Eclogae Geologicae Helvetiae*, 63: 883-905.

Quillévéré F. & Norris R. (2003) - Ecological development of acarininids (planktonic foraminifera) and hydrographic evolution of Paleocene surface waters. In: Wing S.L., Gingerich P.D., Schmitz B., Thomas E. (Eds.) - Causes and consequences of globally warm climates in the Early Paleogene: 223-238. Geological Society of America Special Paper.

Raven J., Caldeira K., Elderfield H., Hoegh-Guldberg O., Liss P., Riebesell U. & Watson A. (2005) - Ocean acidification due to increasing atmospheric carbon dioxide. The Royal Society, 60 pp.

Rego E.S., Jovane L., Hein J.R., Sant'Anna L.G., Giorgioni M., Rodelli D. & Özcan E. (2018) - Mineralogical evidence for warm and dry climatic conditions in the Neo-Tethys (eastern Turkey) during the middle Eocene. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 501: 45-57.

Rio D., Fornaciari E. & Raffi I. (1990) - Late Oligocene through early Pleistocene calcareous nannofossils from western equatorial Indian Ocean (Leg 115). In: Duncan R.A., Backman J., Peterson L.C. et al. (Eds.) - Proceedings of the ODP, Scientific Results: 175-235. Ocean Drilling Program, College Station.

Rögl F & Spezzaferri S. (2002) - Foraminiferal paleoecology and biostratigraphy of the Mühlbach section (Gaindorf Formation, lower Badenian), Lower Austria. In: Weinmann A., Krapf A. & Kroh A. (Eds.) - Serie A für Mineralogie und Petrographie, Geologie und Paläontologie, Anthropologie und Prähistorie: 23-75. Annalen des Naturhistorischen Museums in Wien.

Roslim A., Briguglio A., Kocsis L., Ćorić S. & Gebhardt H. (2019) - Large rotaliid foraminifera as biostratigraphic and palaeoenvironmental indicators in northwest Borneo: An example from a late Miocene section in Brunei Darussalam. *Journal of Asian Earth Sciences*, 170: 20-28.

Russo B., Ferraro L., Correggia C., Alberico I., Foresi L.M., Vallefuoco M. & Lirer F. (2022) - Deep-water paleoenvironmental changes based on early-middle Miocene benthic foraminifera from Malta Island (Central Mediterranean). *Palaeogeography, Palaeoclimatology, Palaeoecology*, 586: 110722.

Savian J. F., Jovane L., Trindade R.I.F., Frontalini F., Coccioni R., Bohaty S.M., Wilson P.A., Florindo F. & Roberts A. (2013) - Middle Eocene Climatic Optimum (MECO) in the Monte Cagnero Section, Central Italy. *Latinmag Letters, Special Issue*, (3): 1-8.

Schmiedl G., Mackensen A. & Müller P.J. (1997) - Recent benthic foraminifera from the eastern South Atlantic Ocean: dependence on food supply and water masses. *Marine micropaleontology*, 32(3-4): 249-287.

Schrag D.P., Depaolo D.J. & Richter F.M. (1995) - Reconstructing past sea surface temperatures: Correcting for diagenesis of bulk marine carbonate. *Geochimica et Cosmochimica Acta*, 59: 2265-2278. doi:10.1016/0016-7037(95)00105-9.

Schweizer M., Pawlowski J., Kouwenhoven T. & Van Der Zwaan B. (2009) - Molecular phylogeny of common cibicidids and related Rotaliida (Foraminifera) based on small subunit rDNA sequences. *Journal of Foraminiferal Research*, 39(4): 300-315.

Seddighi M., Briguglio A., Hohenegger J. & Papazzoni C.A. (2015) - New results on the hydrodynamic behaviour of fossil Nummulites tests from two nummulite banks from the Bartonian and Priabonian of northern Italy. *Bollettino della società paleontologica italiana,* 54(2): 103.

Sen Gupta B.K. & Machain-Castillo M.L. (1993) - Benthic foraminifera in oxygen-poor habitats. *Marine Micropaleontology,* 20: 3-4.

Serra-Kiel J., Hottinger L., Caus E., Drobne K., Ferrández C., Jauhri A.K., Less Gy., Pavlovec R., Pignatti J.S., Samsó J.M., Schaub H., Sirel E., Strougo A., Tambareau Y., Tosquella J. & Zakrevskaya E. (1998) - Larger Foraminiferal Biostratigraphy of the Tethyan Paleocene and Eocene. *Bulletin de la Société Géologique de France*, 169: 281-299.

Sexton P.F., Wilson P.A. & Norris R.D. (2006) - Testing the Cenozoic multisite composite $\delta^{18}O$ and $\delta^{13}C$ curves: new monospecific Eocene records from a single locality, Demerara Rise (Ocean Drilling Program Leg 207). *Paleoceanography*, 21: 2019. doi:10.1029/2005PA001253.

Shi J., Jin Z., Liu Q., Zhang R. & Huang Z. (2019) - Cyclostratigraphy and astronomical tuning of the middle Eocene terrestrial successions in the Bohai Bay Basin, Eastern China. *Global and Planetary Change*, 174: 115-126.

Sinclair H.D. (1997) - Tectonostratigraphic model for underfilled peripheral foreland basins: An Alpine perspective. *The Geological Society of America Bulletin*, 109: 324-346.

Sluijs A., Zeebe R.E., Bijl P.K. & Bohaty S.M. (2013) - A middle Eocene carbon cycle conundrum, *Nature Geoscience*, 6(6): 429–434. doi:10.1038/NGEO1807.

Speijer R.P. (1994) - Extinction and recovery patterns in benthic foraminiferal paleocommunities across the Cretaceous/Paleogene and Paleocene/Eocene boundaries. Utrecht University Repository, 1-191 pp.

Speijer R.P. & Schmitz B. (1998) - A benthic foraminiferal record of Paleocene Sea level and trophic/redox conditions at Gebel Aweina, Egypt. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 137(1-2): 79-101.

Spofforth D.J.A., Agnini C., Pälike H., Rio D., Fornaciari E. & Giusberti L. (2010) - Organic carbon burial following the middle Eocene climatic optimum in the central western Tethys. *Paleoceanography,* 25: A3210. doi: 10.1029/2009PA001738.

Spötl C. & Vennemann T.W. (2003) - Continuous-flow IRMS analysis of carbonate minerals. *Rapid Communications in Mass Spectrometry*, 17: 1004-1006.

Szarek R. (2001) - Biodiversity and biogeography of recent benthic foraminiferal assemblages in the south-western South China Sea (Sunda Shelf). PhD thesis, Christian-Albrechts Universität Kiel, Germany, 273 pp.

Thomas E. (2007) - Cenozoic mass extinctions in the deep sea: What perturbs the largest habitat on Earth? In: Monechi S., Coccioni R. & Rampino M.R. (Eds.) - Large Ecosystem Perturbations: Causes and Consequences: 424: 1-23. Geological Society of America Special Paper. doi: 10.1130/2007.2424(01).

Thomas E. & Gooday A.J. (1996) - Cenozoic deep-sea benthic foraminifers: tracers for changes in oceanic productivity? *Geology*, 24(4): 355-358.

Toffanin F., Agnini C., Fornaciari E., Rio D., Giusberti L., Luciani V., Spofforth D.J.A. & Pälike H. (2011) - Changes in calcareous nannofossil assemblages during the Middle Eocene Climatic Optimum: clues from the central-western Tethys (Alano section, NE Italy). *Marine Micropaleontology,* 81: 22-31.

Toffanin F., Agnini C., Rio D., Acton G. & Westerhold T. (2013) - Middle Eocene to Early Oligocene calcareous nannofossil biostratigraphy at IODP Site U1333 (equatorial Pacific). *Micropaleontology,* 59: 69-82.

Van der Zwaan G.J. (1982) - Paleoecology of late Miocene Mediterranean foraminifera. PhD Thesis, Utrecht University, Netherland, 199 pp.

Van der Zwaan G. J., Jorissen F.J., Verhallen P.J.J.M. & Von Daniels C.H. (1986) - Atlantic-European Oligocene to recent *Uvigerina*: taxonomy, paleoecology, and paleobiogeography. Utrecht University Repository, 35: 7-20.

Van der Zwaan G.J., Jorissen F. J. & De Stigter H.C. (1990) - The depth dependency of planktonic/benthic foraminiferal ratios: constraints and applications. *Marine Geology*, 95(1): 1-16.

Van der Zwaan G.J., Duijnstee A.I., Den Dulk M., Ernst S.R., Jannink N. T. & Kouwenhoven T.J. (1999) - Benthic foraminifers: proxies or problems? A review of paleocological concepts. *Earth-Science Reviews*, 46(1-4): 213-236.

Varrone D. (2004) - Le prime fasi di evoluzione del bacino di avanfossa alpino: la successione delfinese cretacio-eocenica, Alpi marittime. PhD Thesis (unpublished), University of Torino.

Villa G., Fioroni C., Pea L., Bohaty S. & Persico D. (2008) - Eocene–late Oligocene climate variability: calcareous nannofossil response at Kerguelen Plateau, Site 748. *Marine Microplaeontology,* 69: 173-192.

Wade B. S. (2004) - Planktonic foraminiferal biostratigraphy and mechanisms in the extinction of *Morozovella* in the late middle Eocene. *Marine Micropaleontology*, 51(1-2): 23-38.

Wade B. S., & Kroon D. (2002) - Middle Eocene regional climate instability: Evidence from the western North Atlantic. *Geology,* 30(11): 1011-1014.

Wade B.S. & Bown P.R. (2006) - Calcareous nannofossils in extreme environments: the Messinian salinity crisis, Polemi Basin, Cyprus. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 233(3-4): 271-286.

Wade B., Pearson P.N., Berggren W.A. & Pälike H. (2011) - Review and revision of Cenozoic tropical planktonic foraminiferal biostratigraphy and calibration to the geomagnetic polarity and astronomical time scale. *Earth Science Reviews*, 104: 111-142. doi: 10.1016/j.earscirev.2010.09.003.

Young J.R., Bown P.R. & Lees J.A. (2017) - Nannotax3 Website. International Nannoplankton Association, available at: www.mikrotax.org/Nannotax3, accessed 21st Apr 2017.

Zachos J.C., Pagani M., Sloan L.C., Thomas E. & Billups K. (2001) - Trends, rhythms, and aberrations in global climate 65 Ma to present. *Science,* 292: 686-693.