

# Ocean bottom-water oxygenation across the Late Miocene–Early Pliocene biogenic bloom

Oxigenación de las aguas de fondo oceánicas durante el bloom biogénico del Mioceno Tardío–Plioceno Temprano

Maria Elena GASTALDELLO , Claudia AGNINI  & Laia ALEGRET 

**Abstract:** The Late Miocene–Early Pliocene biogenic bloom (ca. 9.0–3.5 millions of years ago, My) represents a period of globally heightened marine biological productivity. Palaeoenvironmental studies across this interval show alternating phases of low-oxygen eutrophic and well-oxygenated oligotrophic conditions. Here, we focus on the bottom water oxygenation changes during the biogenic bloom to assess the validity of the enhanced Benthic Foraminifera Oxygen Index (EBFOI). The index was calculated for three ocean drilling sites: Ocean Drilling Program Site 1085 (southeast Atlantic), and International Ocean Discovery Program sites U1506 (southwest Pacific) and U1488 (equatorial Pacific). The quantitative study of benthic foraminiferal assemblages from Site 1488 allowed us to infer the palaeoenvironmental evolution across the biogenic bloom. At this site, we document a shift from stable oxygen concentrations and seasonal input of phytodetritus (8.7–4.3 My) to short-term fluctuations between low oxygen eutrophic conditions and well-oxygenated oligotrophic conditions (4.3–3.0 My). The EBFOI calculated at sites 1085 and U1506 was cross-referenced with the published palaeoenvironmental conditions. While the EBFOI proves to be a valuable tool to infer palaeoenvironmental changes at the seafloor, it has limitations, as evidenced by comparisons with palaeoenvironmental interpretations of Site U1488, where it does not consistently align with inferred oxygen conditions.

**Resumen:** El bloom biogénico del Mioceno Tardío–Plioceno Temprano (aproximadamente 9.0–3.5 millones de años, My) se caracterizó por una intensa productividad biológica marina a nivel global. Los estudios paleoambientales de este intervalo muestran alternancia de condiciones eutróficas con bajo oxígeno y condiciones oligotróficas bien oxigenadas. Este trabajo evalúa la validez del índice mejorado de oxigenación en los foraminíferos bentónicos (EBFOI, por sus siglas en inglés) durante el bloom biogénico, calculándolo en tres sondeos oceánicos: el Sitio 1085 (Atlántico Sureste) del Ocean Drilling Program, y los sitios U1506 (Pacífico sudoccidental) y U1488 (Pacífico ecuatorial) del International Ocean Discovery Program. El estudio cuantitativo de las asociaciones de foraminíferos bentónicos del Sitio U1488 ha permitido inferir la evolución paleoambiental a través del bloom biogénico. Se documenta el paso de concentraciones estables de oxigenación de las aguas del fondo con llegada estacional de fitodetritos (8.7–4.3 My), a fluctuaciones a corto plazo entre condiciones eutróficas de baja oxigenación y condiciones oligotróficas bien oxigenadas (4.3–3.0 My). El EBFOI en los sitios 1085 y U1506 se comparó con reconstrucciones paleoambientales publicadas. Es una herramienta valiosa para inferir cambios paleoambientales en el lecho marino, pero la comparación con interpretaciones paleoambientales del Sitio U1488 muestra sus limitaciones.

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Índice de oxigenación

## INTRODUCTION

The Late Miocene–Early Pliocene transition witnessed significant transformations in global tectonics, climate, and oceanography (Steinthorsdottir *et al.*, 2021). The so-called “Late Miocene–Early Pliocene biogenic bloom” (Farrell *et al.*, 1995), between 9.0 millions of years ago (My) and 3.5 My (Farrell *et al.*, 1995; Dickens & Owen, 1999; Diester-Haass *et al.*, 2005), is one of the most notable palaeoceanographic events during this time interval. The biogenic bloom has been

primarily observed in upwelling regions of the Indian and Pacific Oceans, and it has been associated with increased supply of biogenic CaCO<sub>3</sub> to the seafloor, high abundance of diatoms related to high productivity, and suboxic and dysoxic bottom-waters as inferred from benthic foraminifera and decreased sedimentary redox conditions, overall indicating a substantial increase in marine primary productivity (Peterson *et al.*, 1992; Berger *et al.*, 1993; Dickens & Owen, 1994;

Farrell *et al.*, 1995; Nomura, 1995; Dickens & Owen, 1999; Gupta & Thomas, 1999; Grant & Dickens, 2002; Lyle *et al.*, 2019; Gastaldello *et al.*, 2023a). Despite the extensive documentation of the biogenic bloom globally, our understanding of its driving mechanisms, consequences, and biotic response remains limited.

Various environmental factors, such as the oxygenation levels or the type and quantity of organic matter reaching the seafloor, influence both the abundance of benthic foraminifera and the composition of their assemblages; these components, in turn, are controlled by local and regional changes in oceanographic and environmental factors (e.g., Erbacher *et al.*, 1999; Friedrich *et al.*, 2006; Jorissen *et al.*, 2007; Alegret *et al.*, 2021). The study of the benthic foraminiferal assemblages across the biogenic bloom provides useful information to interpret the palaeoenvironmental conditions at the seafloor, and to better understand the mechanisms behind this palaeoceanographic phenomenon.

Benthic foraminifera serve as a proxy of bottom water oxygenation and food supply to the seafloor, mostly based on morphological similarities with modern benthic foraminifera (Corliss, 1985; Jones & Charnock, 1985) and the strong relationship between their morphology and microhabitats (Corliss, 1985; Jorissen *et al.*, 1995). Palaeoenvironmental reconstructions across the biogenic bloom reveal variability in the seafloor conditions, switching from low oxygen eutrophic conditions with a fairly constant food supply, to well-oxygenated oligotrophic conditions associated with seasonal phytodetritus inputs (Gastaldello *et al.*, 2023a, 2024b).

The possible link between changes in benthic foraminiferal abundance taxa and bottom-water oxygenation was highlighted by Kaiho (1991, 1994), who defined oxic, suboxic, and dysoxic indicators and introduced the Benthic Foraminifera Oxygen Index (BFOI) to evaluate changes in bottom-water oxygenation. An enhanced version of the BFOI (EBFOI) was later introduced by Kranner *et al.* (2022), who incorporated the suboxic indicators in the original formula.

This study aims to investigate changes in bottom-water oxygenation during the biogenic bloom, and to test the validity of the EBFOI as a method to infer palaeoenvironmental changes at the seafloor. We carried out a quantitative analysis of Late Miocene and Early Pliocene benthic foraminiferal assemblages at International Ocean Discovery Program (IODP) Site U1488, in the western equatorial Pacific Ocean, we inferred the palaeoenvironmental changes across the biogenic bloom and calculated the EBFOI. This index was further calculated and tested at two other ocean drilling sites where the palaeoenvironmental conditions during the biogenic bloom have already been reconstructed, Ocean Drilling Program (ODP) Site 1085 from the southeast Atlantic Ocean, and IODP Site U1506 from the southwest Pacific Ocean.

## MATERIALS AND METHODS

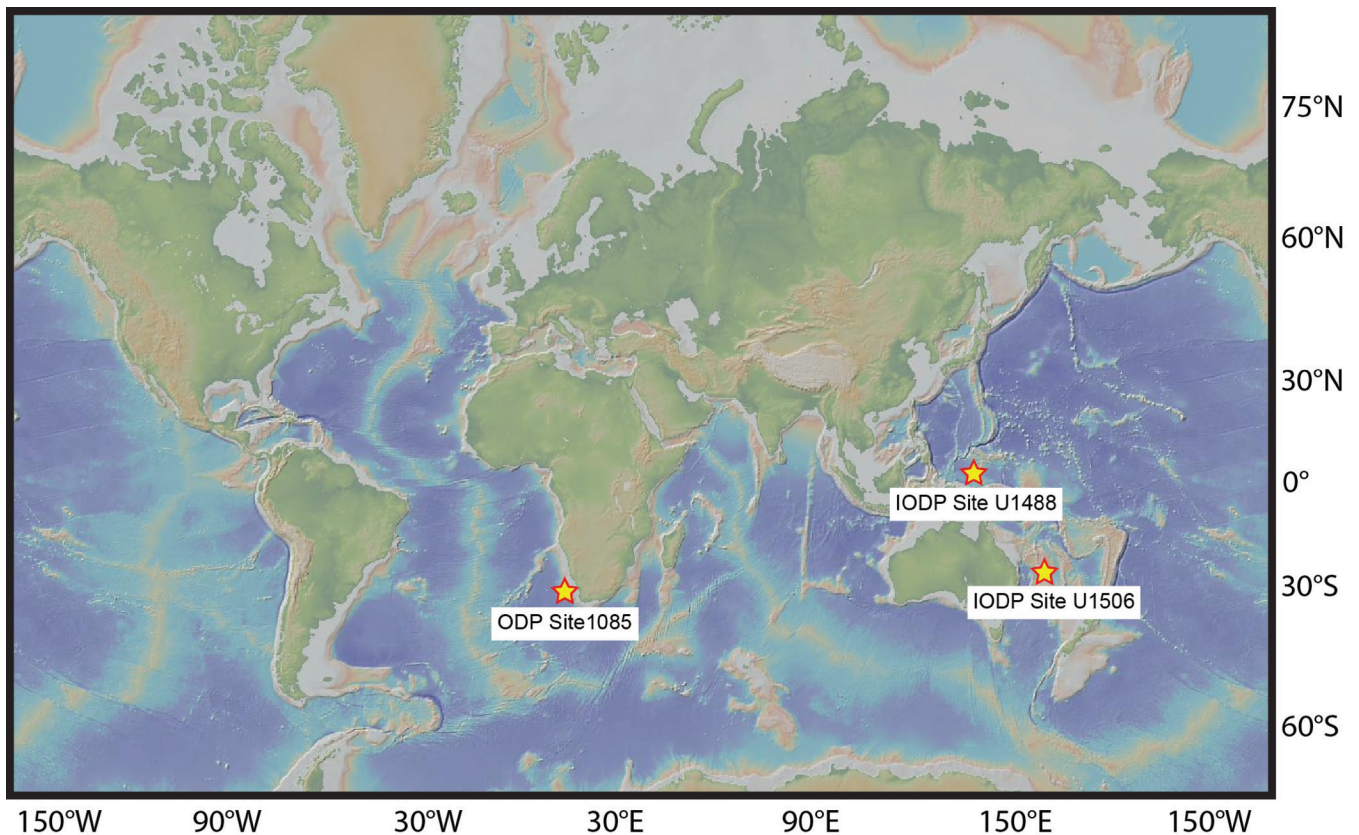
The Upper Miocene–Lower Pliocene interval was analysed at three ocean drilling sites from the Southern Hemisphere. Quantitative studies of benthic foraminiferal assemblages were carried out at IODP Site U1488 to infer the palaeoenvironmental turnover across the biogenic bloom. Bottom water oxygenation was inferred at this site and at two additional sites based on new and published palaeoenvironmental interpretations, and by means of the EBFOI.

IODP Site U1488 was drilled in the southern part of the Eauripik Rise at 2604 m water depth (02.02°N, 141.45°E; Fig. 1), in the western equatorial Pacific Ocean (Rosenthal *et al.*, 2018). This site is located in the Western Pacific Warm Pool (WPWP), the largest single expanse of warm water on the planet, which plays a fundamental role in the global climate (Siedler *et al.*, 2004). We focus on a ~210 m thick interval of foraminifera-nannofossil ooze from Holes U1488A, B, and C, Core 9H to Core 30H (85.02 to 297.86 revised m Core composite depth below sea floor “CCSF Top”, from here on referred to as m; Drury *et al.*, 2021), spanning the Upper Miocene–Lower Pliocene (Rosenthal *et al.*, 2018). The age model for Site U1488 is based on calcareous nannofossil datums available from the initial reports (Rosenthal *et al.*, 2018), recalibrated to the Geological Time Scale 2020 (Raffi *et al.*, 2020).

Ocean Drilling Program (ODP) Site 1085 was drilled during Leg 175 in the mid-Cape Basin at 1713 m water depth, in the southeast Atlantic Ocean (29.22°S, 13.59°E; Wefer *et al.*, 1998; Fig. 1). The site is located along the South African coast, close to the mouth of the Orange River, in the Benguela Current upwelling region (Rogers & Bremner, 1991; Berger *et al.*, 2002). A 400 m-thick Upper Miocene–Lower Pliocene interval spanning from 149.00 to 542.45 m (Hole 1085A and Hole 1085B) has been the focus of a study on the biogenic bloom, where the regional expression of this phenomenon has been investigated through the quantitative analysis of benthic foraminiferal assemblages (Gastaldello *et al.*, 2024b). Here we calculate the oxygenation index for Site 1085 and compare the results with the previously published palaeoenvironmental reconstructions.

International Ocean Discovery Program Site U1506 is located on the Lord Howe Rise in the northern part of Zealandia (28.66°S, 161.74°E; 1505 m water depth; Fig. 1). This site was drilled during IODP Expedition 371 in the Tasman Sea, southwest Pacific Ocean (Sutherland *et al.*, 2019). The Upper Miocene–Lower Pliocene interval consists of a 140 m thick interval of nannofossil ooze and chalk (from 82.01 to 221.75 m; Sutherland *et al.*, 2019). The biogenic bloom was identified across this interval, and the palaeoenvironmental turnover was documented through quantitative analyses of benthic foraminiferal assemblages, integrated with other independent proxies (Gastaldello *et al.*, 2023a,





**Figure 1.** Location map of ODP Site 1085, IODP Site U1506 and IODP Site U1488.

2024a). The palaeoenvironmental reconstruction in those publications is here compared with the EBFOI calculated for the first time at Site U1506.

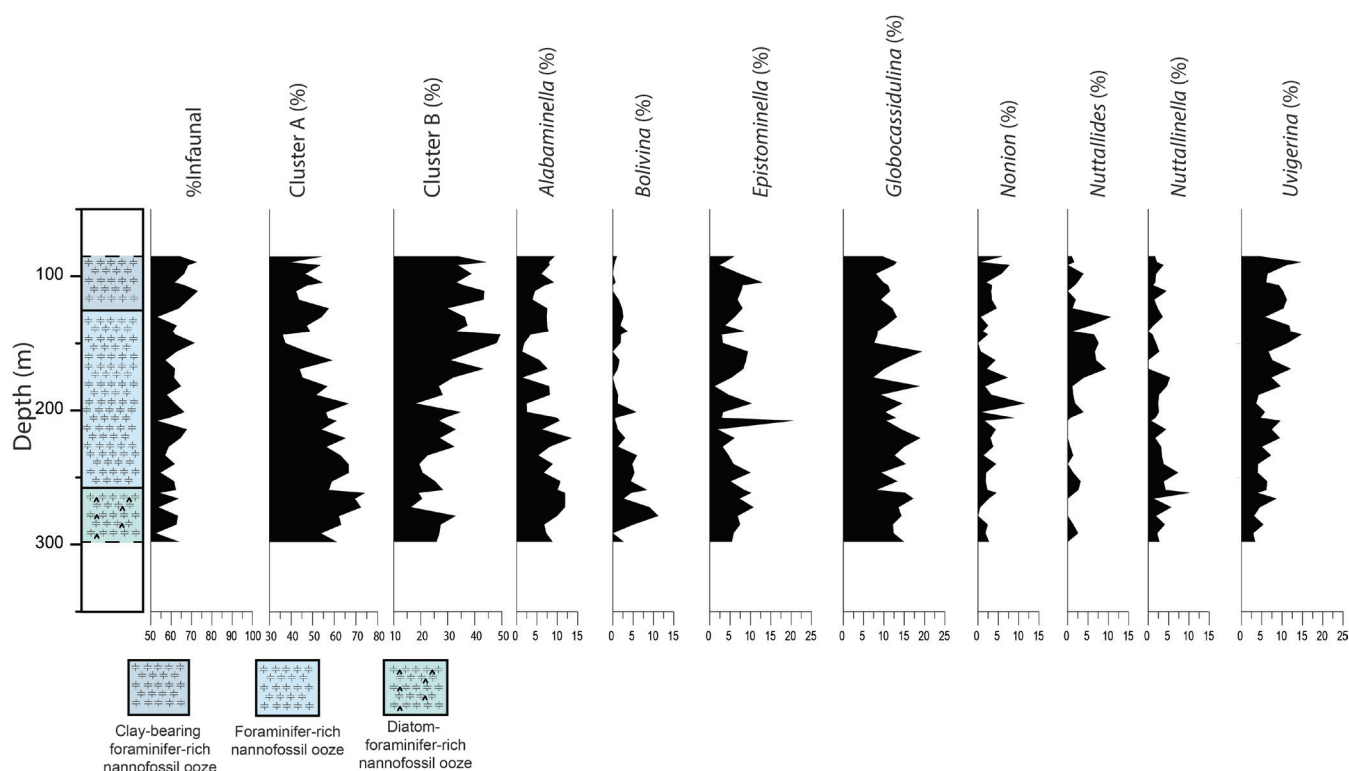
Here we analyse benthic foraminiferal assemblages on 39 samples from Site U1488 (Suppl. Tab. S1). Additionally, we selected 33 and 66 samples from Site 1085 and Site U1506, respectively, to calculate the oxygenation index based on published benthic foraminiferal datasets (assemblage counts) (Gastaldello *et al.*, 2024a, 2024b). The dataset from Site U1488 was collected using the same methodology and taxonomic concepts as in Gastaldello *et al.* (2023a).

Sediment samples were dried in an oven at 40°C, weighted, disaggregated in water, and sieved using a 63 µm mesh sieve. The residue was then dried in an oven at 40°C, and for each sample ca. 300 specimens of benthic foraminifera were picked from the dry > 63 µm sieved size fraction and placed on microslides. Specimens were identified at the genus level following Hayward and Buzas (1979), Van Morkhoven *et al.* (1986), Hermelin (1989), Kaminski and Gradstein (2005), Hayward *et al.* (2010, 2013), and Holbourn *et al.* (2013). The relative abundances of the genera present in each sample are reported in Supplementary Table S1. Based on a reduced dataset of genera that make up > 5% in at least one sample, we conducted a hierarchical cluster analysis using the PAST software, applying the unweighted pair-group average

algorithm (UPGMA) and Pearson correlation (Fig. 2), and a Detrended Correspondence Analysis (DCA) in R-mode (genera) (Hammer *et al.*, 2001; Hammer & Harper, 2005).

The taxonomic composition of benthic foraminiferal assemblages and their relative abundance are heavily influenced by the type and amount of food reaching the seafloor and the oxygen concentration of bottom waters (Corliss & Chen, 1988; Gage & Tyler, 1991; Jorissen *et al.*, 1995, 2007). For this reason, there is a well-recognized and close relationship between the test morphology of benthic foraminifera and the dissolved oxygen content (Bernhard, 1986; Kaiho, 1991, 1994). Following Corliss (1985, 1991), Jones and Charnock (1985), and Corliss and Chen (1988), each genus was assigned to epifaunal or infaunal morphogroups. The relative abundance of infaunal and epifaunal morphogroups (Suppl. Tab. S1) has been suggested as a proxy for trophic conditions and oxygen levels in deep sea following the TROX model (Jorissen *et al.*, 1995, 2007). A high relative abundance of deep infaunal species is considered to be indicative of eutrophic and/or low oxygen environments, while assemblages dominated by epifaunal morphogroups point to more oligotrophic conditions and/or higher oxygen availability (Jorissen *et al.*, 1995, 2007).

Using our new foraminiferal counts from Site U1488 and published datasets available from Sites 1085 and U1506, all genera were assigned to Dysoxic “D”,



**Figure 2.** Lithology (Rosenthal *et al.*, 2018), percentage of the infaunal morphogroup, and relative abundance of the most abundant genera (relative abundance >10% in at least one sample) at IODP Site U1488 plotted against depth.

Suboxic “S”, or Oxidic “O” groups following the criteria established by Bernhard (1986) and Kaiho (1991), and the benthic foraminifera oxygen preferences available in the literature (Loubere, 1994; Fariduddin & Loubere, 1997; Schmiedl *et al.*, 1997; Kaiho, 1994, 1999; Bernhard & Gupta, 1999; de Rijk *et al.*, 2000; Fontanier *et al.*, 2002; Jorissen *et al.*, 2007; Kranner *et al.*, 2022). The specimens of each group were imaged with a Scanning Electron Microscope at the University of Zaragoza (Zeiss Merlin) and the University of Padova (TESCAN SOLARIS) (Fig. 3). The specimens illustrated are deposited at the Natural Science Museum of the University of Zaragoza (Spain, repository numbers MPZ-2023/393 to MPZ-2023/404). The enhanced Benthic Foraminifera Oxygen Index (EBFOI, Kranner *et al.*, 2022) was calculated along the study succession of each investigated site. We used the EBFOI rather than the Benthic Foraminifera Oxygen Index (BFOI; Kaiho, 1991) because the former also takes into account the dysoxic group, which was not included in the original equation of BFOI. The EBFOI is a variation of the BFOI that has been developed to improve the assessment of dissolved oxygen concentrations within the sediment. In this study, we applied the equation “Eq. (3)” from Kranner *et al.* (2022):

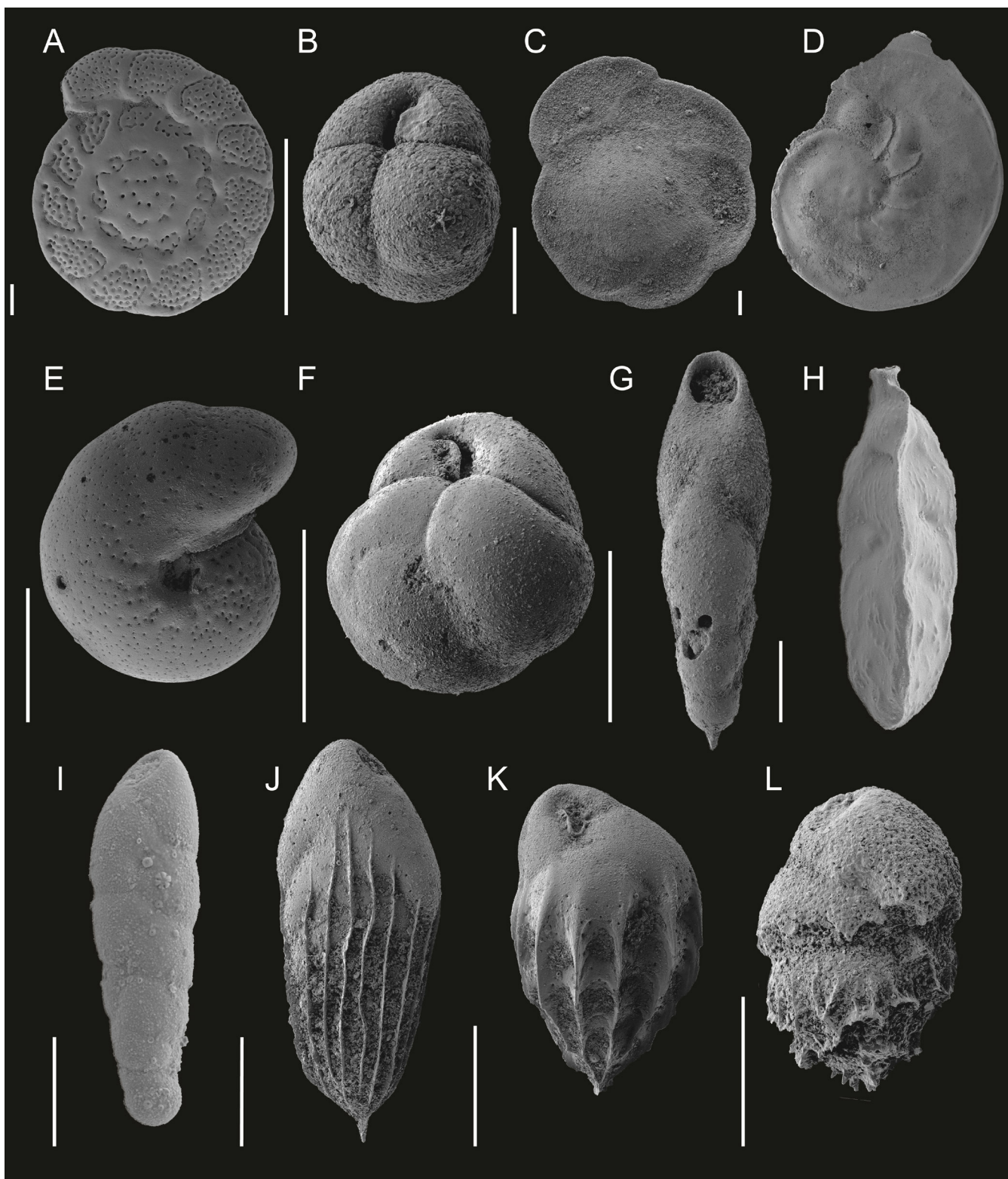
$$EBFOI = 100 * \left( \frac{O}{O + D + \frac{S}{2}} \right)$$

## RESULTS

### Benthic foraminifera assemblages

A total of 53 genera of benthic foraminifera were recognised across the Upper Miocene–Lower Pliocene interval at Site U1488 (Suppl. Tab. S1). The assemblages are dominated by calcareous hyaline foraminifera, and agglutinated taxa constitute only a minor component (0.0–4.6%). The diversity of the assemblages is highest in the upper part of the study section, where a maximum of 38 genera have been identified (sample U1488C-10H-4W, 59–61 cm at 97.92 m). The lowest diversity (22 genera) has been recorded in the lowermost part of the study interval, in sample U1488B-28H-4W, 70–72 cm at 278.51 m. *Alabaminella*, *Bolivina*, *Epistominella*, *Globocassidulina*, *Nonion*, *Nuttallides*, *Nuttallinella* and *Uvigerina* are the most abundant genera, and they make up >10% of the assemblages in at least one sample (Fig. 2). *Alabaminella* is most abundant taxon in the lower part of the study interval (with a peak of 13.5% at 220.46 m), followed by a decreasing trend until ca. 155.95 m and an upward increasing trend towards the top of the section. The relative abundance of *Bolivina* (up to 11.2% at 278.51 m) decreases upwards, while *Uvigerina* increases towards the top of the study interval (from a minimum of 2.9% at 291.41 m to a maximum of 14.9% at 143.06 m). The genus *Epistominella* displays a constant abundance with only one marked peak at 207.53 m, where it reaches 20.5% of the assemblages. The relative abundance of





**Figure 3.** A–D, Benthic foraminifera belonging to the oxic group; A, *Cibicidoides* (sample 1085-15H5, 88–89 cm), MPZ 2023/393; B, *Globocassidulina* (sample U1488-20H1, 77–79 cm), MPZ 2023/394; C, *Gavelinopsis* (sample U1488-20H1, 77–79 cm), MPZ 2023/395; D, *Laticarinina* (sample U1488-16H7, 3–5 cm), MPZ 2023/396; E–H, benthic foraminifera belonging to the suboxic group; E, *Melonis* (sample U1488-18H2, 48–50 cm), MPZ 2023/397; F, *Cassidulina* (sample U1506-11R4, 80–82 cm), MPZ 2023/398; G, *Pleurostomella* (sample U1488-20H1, 77–79 cm), MPZ 2023/399; H, *Trifarina* (sample U1506-14R1, 126–128 cm), MPZ 2023/400; I–L, benthic foraminifera belonging to the dysoxic group; I, *Bolivina* (sample U1506-24R4, 64–66 cm), MPZ 2023/401; J, *Bolivina* (sample U1488-25H1, 121–123 cm), MPZ 2023/402; K, *Bulimina* (sample U1488-16H7, 3–5 cm), MPZ 2023/403; L, *Bulimina* (sample U1488-20H5, 123–125 cm), MPZ 2023/404; scale bars = 100 µm.

*Globocassidulina* ranges between 7.3% and 19.3%, displaying highest values in the middle of the study interval (between 220.46 and 155.95 m). The genus *Nonion* is most abundant in the middle (peak of 11.5% at 194.66 m) and in the uppermost part of the study interval (peak of 7.7% at 91.47 m), showing a low abundance (ca. 2.0%) in the rest of the study samples. *Nuttallides* ranges between 0.0–11.6%, reaching the higher values in the upper part of the study interval, between 181.75 and 91.47 m. The genus *Nuttallinella* shows overall low relative abundance throughout the study interval (ca. 2.0–3.0%), and it reaches a maximum of 10.2% at 261.31 m.

The hierarchical cluster analysis of genera ( $n=22$ ) shows two main clusters: the components of Cluster A ( $n=12$ ) are *Alabaminella*, *Anomalinoidea*, *Bolivina*, *Bulimina*, *Cibicidoides*, *Epistominella*, *Globocassidulina*, *Nodosaria*, *Nonion*, *Nuttallinella*, *Oridorsalis*, and *Stilostomella*. The relative abundance of taxa ascribed to this cluster is high in the lower part of the study interval (peak of 74.0% at 261.31 m) and gradually decreases towards the top. This cluster includes genera related to both oxic oligotrophic environments and suboxic-dysoxic eutrophic conditions. Cluster B ( $n=9$ ) includes *Cassidulina*, *Fissurina*, *Pleurostomella*, *Gyroidina*, *Nonionella*, *Nuttallides*, *Melonis*, *Pullenia*, and *Uvigerina*. The relative abundance of Cluster B increases in the upper part of the study interval, reaching a maximum of 49.5% at 143.06 m. The genera of this cluster are typically associated with suboxic-dysoxic environments and eutrophic conditions at the seafloor. In the DCA analysis in R-mode, genera from Cluster A fall within high values of Axis 1, while Cluster B shows lower values within Axis 1. The genera *Bolivina* and *Nuttallides* exhibit the highest and lowest values along Axis 1, but neither of these genera falls within the 95% confidence ellipse.

Genera with elongated, cylindrical, rounded planispiral, flattened, ovoid shapes, and those with a neck correspond to infaunal forms (e.g., *Uvigerina*, *Bulimina*, *Cassidulina*, *Pleurostomella*). Epifaunal morphogroups typically show trochospiral (planoconvex or biconvex) and planispiral shapes, with rounded and flat tests (e.g., *Cibicidoides*, *Epistominella*, *Gyroidinoides*, *Oridorsalis*). The infaunal to epifaunal ratio remains constant throughout the study interval, and the infaunal morphogroup (ca. 52.4–73.1%) dominates over the epifaunal one (Fig. 2).

The benthic foraminiferal assemblages from Site 1085 and Site U1506 have been previously described in detail in Gastaldello et al. (2023a, 2024a, 2024b). At ODP Site 1085, calcareous taxa (e.g., *Bolivina*, *Epistominella*, and *Globocassidulina*) dominate the assemblages. The relative abundance of infaunal and epifaunal morphogroups remains fairly constant throughout the study interval, with a slight prevalence of infaunal taxa. The most abundant genera (>10% in at least one sample) are *Alabaminella*, *Bolivina*, *Bulimina*, *Cibicidoides*, *Epistominella*, *Globocassidulina*,

*Nuttallides*, and *Uvigerina*. The benthic foraminiferal assemblages at IODP Site U1506 are dominated by calcareous hyaline taxa, and agglutinated taxa make up ca. 5.0–10.0% of the assemblages. Infaunal morphogroups dominate the assemblages with a relative abundance ranging from 57.5 to 86.4%. The most abundant genera (>10% in at least one sample) are *Abditodentrix*, *Anomalinoidea*, *Bulimina*, *Cibicidoides*, *Epistominella*, *Globocassidulina*, *Melonis*, *Nuttallinella*, *Osangularia*, *Spiroplectammina*, *Stilostomella*, and *Uvigerina*.

### Benthic foraminifera as oxygen indicators

The morphology, ornamentation, thickness, and size of benthic foraminiferal tests have been commonly related to the amount of oxygen dissolved in bottom waters. Under dysoxic conditions (0.1–0.3 ml/l of dissolved oxygen; Kaiho, 1994), assemblages commonly consist of small-shelled benthic foraminifera displaying elongated, flattened or cylindrical-conical unornamented morphologies, with abundant pores and thin-walled tests. The elevated pore density of the shells of anaerobic morphogroups has been correlated with enhanced oxygen absorption efficiency (Leutenegger & Hansen, 1979; Gupta & Machain-Castillo, 1993; Bernhard & Bowser, 1999). In suboxic environments (0.3–1.5 ml/l of dissolved oxygen; Kaiho, 1994) assemblages typically include small specimens of oxic species that can live in low oxygen conditions, as well as elongated taxa and small thin-walled species with planoconvex or biconvex trochospiral tests. In oxic environments, where the dissolved oxygen content in the waters exceeds 1.5 mL/L, assemblages are typically characterised by spherical, planoconvex, lenticular, and biumbilicate morphologies (Bernhard, 1986).

At Site U1488, dysoxic forms are represented by the genera *Allomorphina*, *Bolivina*, *Bulimina*, *Chilostomella*, *Eubuliminella*, *Fursenkoina*, and *Karrerella* (Fig. 3). Dysoxic forms make up 0.6 to 13.0% of the assemblages at Site U1488, with the highest values in the lower part of the record, between 291.41 and 252.71 m, and an upward decreasing trend. *Alabaminella*, *Epistominella*, *Nonion*, *Melonis*, *Nodosaria*, *Pleurostomella*, and *Uvigerina* are the most representative genera within the suboxic group (Fig. 3). This group is the most abundant at Site U1488, making up 46.4–72.2% of the assemblages. It displays high relative abundance in the middle of the studied interval, with a peak of 72.2% at 207.53 m. The minimum values are recorded at 233.36 m (46.4%) and at 130.18 m (51.1%). Lastly, the most representative genera of the oxic group include *Anomalinoidea*, *Cibicidoides*, *Globocassidulina*, *Laticarinina*, *Nuttallides*, *Osangularia*, and *Pyrgo* (Fig. 3). The relative abundance of the oxic group ranges from 21.8 to 45.7%, with several fluctuations from maximum to minimum values from the lowermost part of the record up to 110.82 m, where the relative



abundance drops and remains low towards the top of the studied interval (ca. 20.0–25.0%).

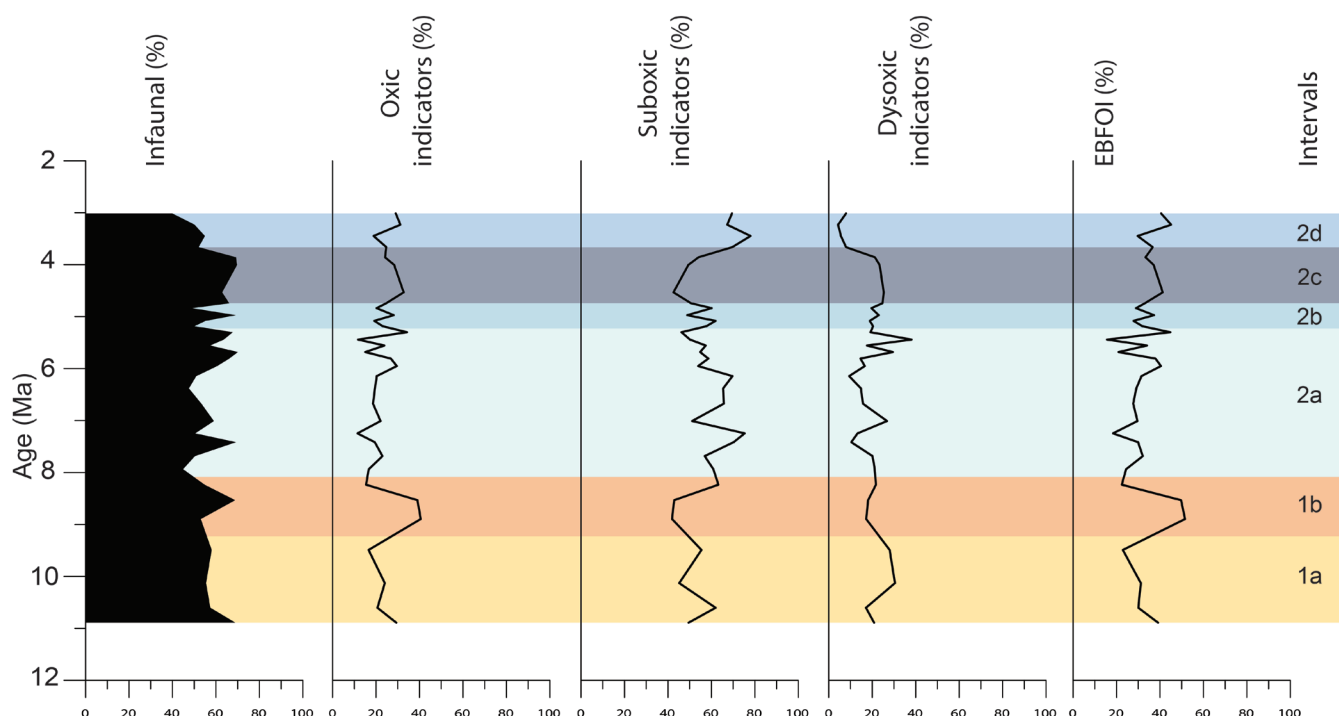
At Site 1085, dysoxic indicators include *Bolivina*, *Bulimina*, *Karreriella*, and *Globobulimina* (Fig. 3). The relative abundance of this group ranges between 4.3 and 38.1%, with overall consistent low values throughout the study interval, and only a slight increase between 314.34 and 265.66 m. *Alabaminella*, *Cassidulina*, *Epistominella*, *Melonis*, *Pullenia*, and *Uvigerina* are the most representative genera of the suboxic group (Fig. 3). This is the most abundant group at Site 1085, with values ranging from 41.9 and 78.0%. The suboxic group shows a consistent high relative abundance from the base of the study interval up to 214.37 m, where a sharp increase is recorded, reaching the maximum values of 78.0% at 157.13 m. The most abundant oxic indicators include *Anomalinoidea*, *Cibicoides*, *Gavelonopsis*, *Globocassidulina*, *Hanzawaia*, and *Nuttallides* (Fig. 3). This group makes up 11.5–40.6% of the assemblages, with the highest values in the lower part of the study interval, between 476.85 and 452 m. At Site U1506, the dysoxic indicators include *Allomorphina*, *Bolivina*, *Bulimina*, *Chilostomella*, *Fursenkoina*, and *Karreriella* (Fig. 3). The relative abundance of this group ranges between 2.8 and 26.1%, with high values in lower part of the study interval (between 192.91–164.77 m). The most representative genera of the suboxic group are *Abditodentrix*, *Epistominella*, *Melonis*, *Spiroplectammina*, and *Uvigerina* (Fig. 3). The relative abundance of this group is consistent throughout the study interval, with values ranging from 34.0 to 69.5%. A sharp 30.2%

decrease has been documented between 101.41 and 95.05 m. The oxic indicators include *Anomalinoidea*, *Cibicoides*, *Globocassidulina*, *Nuttallinella*, and *Osangularia* (Fig. 3). The relative abundance of the oxic group ranges between 20.7 and 58.2%, with peaks in relative abundance in the lower part (50.3% at 217.27 m) and in the upper part (58.2% at 95.05 m) of the study interval.

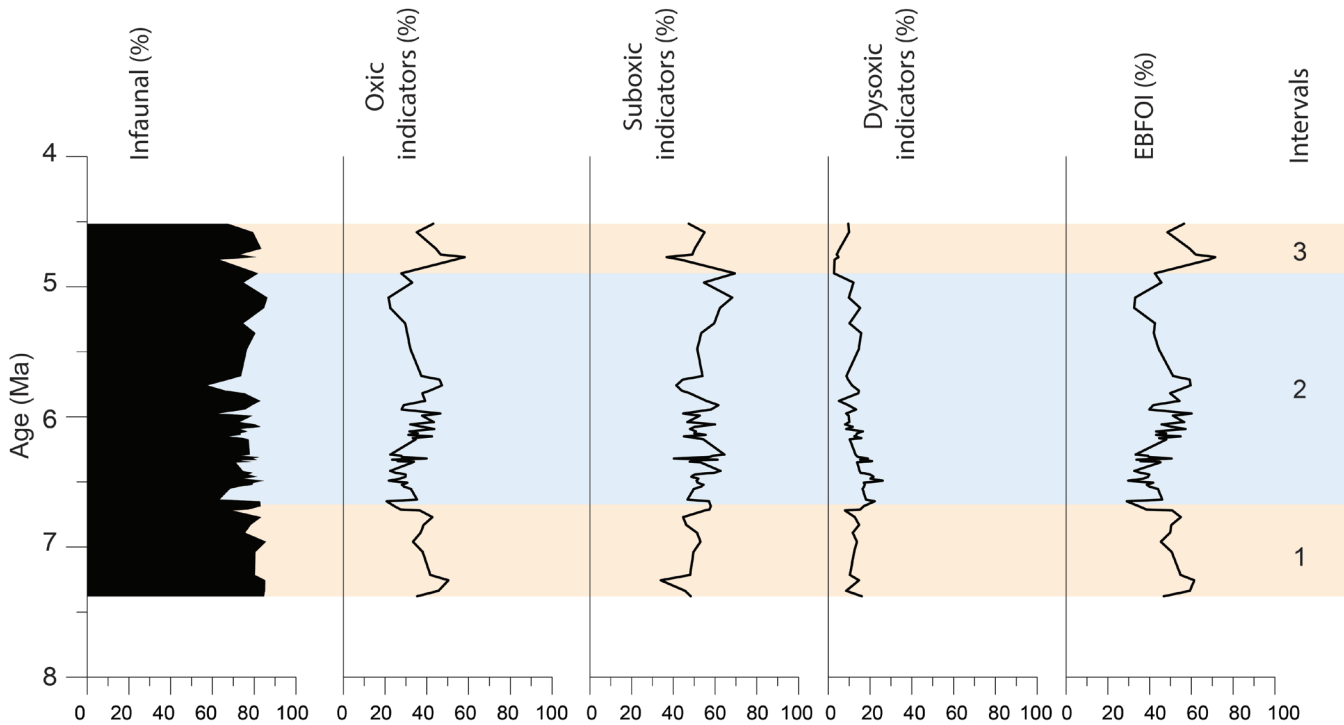
### Enhanced Benthic Foraminifera Oxygen Index (EBFOI)

The EBFOI at Site 1085 exhibits the lowest values of the three sites, ranging from a minimum of 15.66 (277.60 m) to a maximum of 51.55 (464.60 m) (Fig. 4). The record shows an initial peak between 470.73 and 432.33 m, where the highest EBFOI value has been recorded. A shift towards more positive values is shown in the middle of the study interval, between 387.40 and 277.66 m (with a maximum of 40.44 at 329.34 m). A sharp increase is recorded between 277.66 and 265.66 m, with a shift from 15.66 to 44.76 (an increase of 29.10 in 12 m). In the upper part of the study interval, the EBFOI fluctuates between 30 and 40.

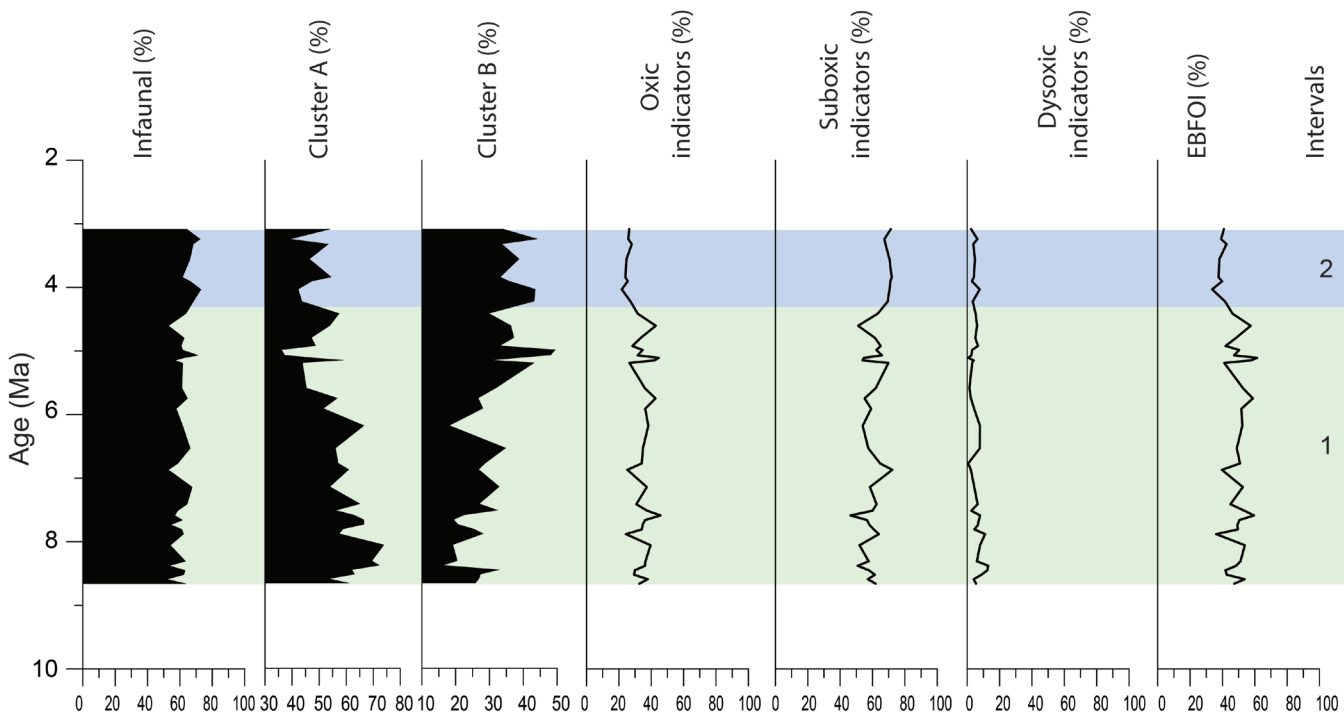
At Site U1506, the EBFOI values range from 29.01 at 188.41 m to 71.45 at 95.05 m (Fig. 5). From the bottom of the studied interval, the EBFOI shows an initial decrease of 32.37 between 217.27 and 188.41 m, followed by an increase towards the middle of the section (from 29.01 at 188.41 m to 59.61 at 142.81 m). A second major decrease has been documented between 142.81 and 110.81 m, where the EBFOI



**Figure 4.** Relative abundance of infaunal morphogroup, evolution of the morphogroups oxic, suboxic, dysoxic, enhanced Benthic Foraminifera Oxygen Index (EBFOI), and intervals at ODP Site 1085 plotted against age (Ma).



**Figure 5.** Relative abundance of infaunal morphogroup, evolution of the morphogroups oxitic, suboxic, dysoxic, enhanced Benthic Foraminifera Oxygen Index (EBFOI), and intervals at IODP Site U1506 plotted against age (Ma).



**Figure 6.** Relative abundance of infaunal morphogroup, Cluster A, Cluster B, evolution of the morphogroups oxitic, suboxic, dysoxic, enhanced Benthic Foraminifera Oxygen Index (EBFOI), and intervals at IODP Site U1488 plotted against age (Ma).

drops from 59.61 to 33.07. This decline is followed by a sharp increase recorded in the upper part of the study interval, where the maximum value of 71.45 is reached at 95.05 m.

The EBFOI values at Site U1488 span from a minimum of 33.66 at 110.82 m, to a maximum of 61.47 at 155.95

m (Suppl. Tab. S1; Fig. 6). The EBFOI shows the same trend as the oxitic group, with several fluctuations in the lower and middle part of the studied interval from maximum (50–60) to minimum values (35–40). Constant low values (around 33–40) are observed from 110.82 m towards the top.



## DISCUSSION

The Upper Miocene–Lower Pliocene interval at sites 1085 and U1506 has been the focus of previous studies to investigate the palaeoenvironmental and palaeoceanographic changes across the biogenic bloom, and to assess the local, regional and global imprints of this phenomenon (Gastaldello *et al.*, 2023a, 2024a, 2024b). In this study we present the first palaeoenvironmental study based on benthic foraminifera at Site U1488 during the biogenic bloom. At Site 1085, Gastaldello *et al.* (2024b) documented six intervals with palaeoenvironmental significance during the Upper Miocene–Lower Pliocene (10.9–3.0 My), four of which span the biogenic bloom (from 8.1 to 3.0 My). These intervals are characterised by changes in nutrient supply to the seafloor, seasonality, and bottom water oxygenation. Overall, the EBFOI at Site 1085 is fairly consistent with the palaeoenvironmental interpretation in Gastaldello *et al.* (2024b) (Fig. 3). These authors identified two intervals previous to the biogenic bloom. Their interpretation of low oxygen conditions between 10.9 and 9.2 My (Interval 1a, 542.45 to 498.46 m; Gastaldello *et al.* 2024b) agrees with the decreasing EBFOI in this interval, which points to decreased oxygen levels and suboxic-dysoxic conditions. In the interval between 9.2 and 8.1 My (498.46 to 459.80 m), Gastaldello *et al.* (2024b) reported low food supply, oxic conditions, and the vertical expansion of the corrosive Upper Circumpolar Deep Water at the expense of the Antarctic Intermediate Water, mainly related to high relative abundance of agglutinated species and a peak in *Nuttallides umbonifera*. The increase in bottom water oxygenation is also supported by our results, which show increased EBFOI (up to 50) in this interval. During the biogenic bloom, the EBFOI is particularly consistent with intervals 2b and 2d of Gastaldello *et al.* (2024b) (Fig. 4). The short-term alternation between oligotrophic/oxic conditions and eutrophic/suboxic-dysoxic conditions documented during Interval 2b (287.73 to 245.13 m; 5.2 to 4.8 My) can also be inferred from the EBFOI, which shows short-term oscillations during this interval. The increase in EBFOI in the upper Interval 2d points to a shift towards more oxic conditions, which is consistent with the almost disappearance of suboxic-dysoxic taxa and with the increase in phytodetritus exploiting taxa (PET), related to the enhanced regional upwelling (Gastaldello *et al.*, 2024b).

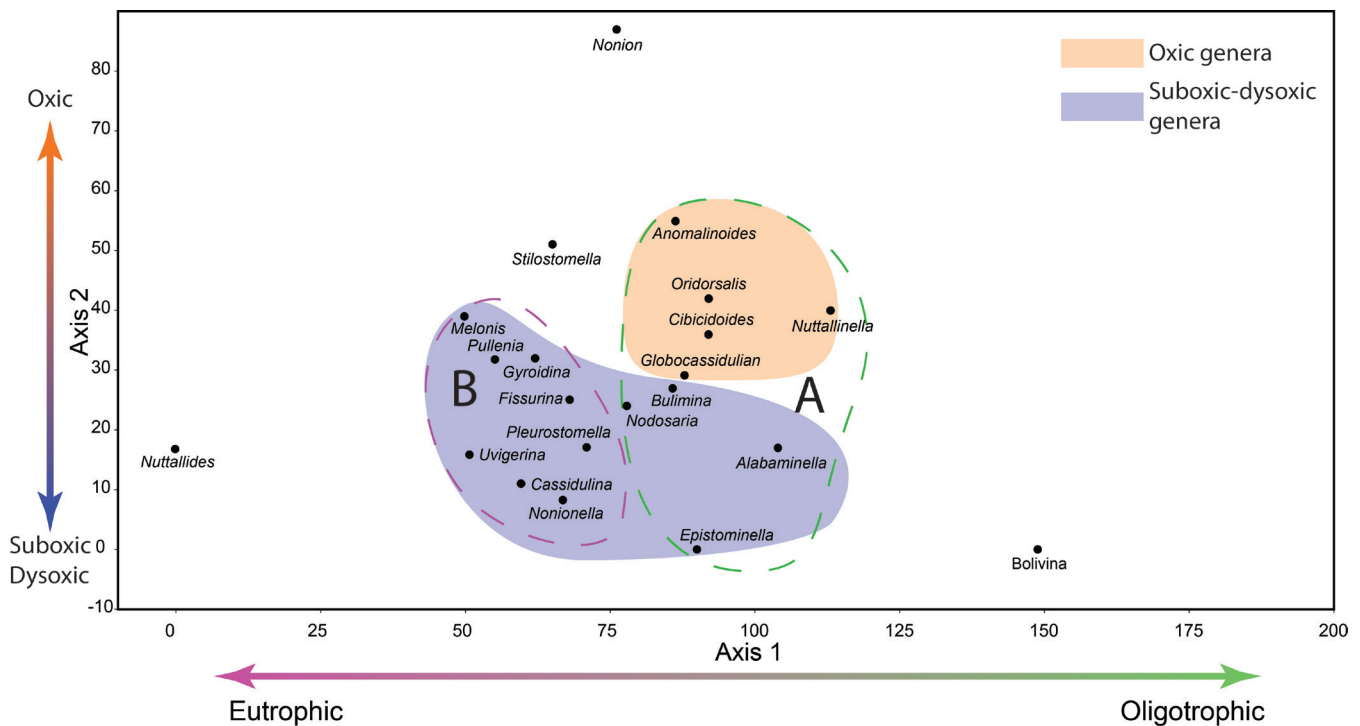
We observed some inconsistencies between the EBFOI and the palaeoenvironmental interpretation of Intervals 2a and 2c. The benthic foraminiferal assemblage during Interval 2a (459.90 to 287.73 m; 8.1 to 5.2 My) points to oligotrophic conditions at the seafloor and well oxygenated bottom waters, but the EBFOI values are relatively lower than in the underlying interval, suggesting more suboxic conditions. No significant changes in bottom-water oxygenation were reported from Interval 2c (245.13 to 191.00 m; 4.8 to 3.8 My)

by Gastaldello *et al.* (2024b), but the EBFOI displays a trend towards more positive values, indicating a prevalence of oxic conditions.

The palaeoenvironmental changes across the biogenic bloom at Site U1506 were documented by Gastaldello *et al.* (2023a, 2024a). Three intervals with palaeoenvironmental significance were identified: Interval 1 (from 221.75 to 194.75 m; 7.4 to 6.7 My) and Interval 3 (103.21 and 82.01 m; 4.9 to 4.5 My) are characterised by the high relative abundance of phytodetritus exploiting taxa, low diversity, and low relative abundance of *Bolivina*, *Bulimina*, and *Uvigerina*, pointing to seasonal phytoplankton blooms in surface waters, a high seasonal input of food to the seafloor and well oxygenated bottom waters. In contrast, Interval 2 (from 194.75 to 82.01 m; 6.7 to 4.9 My) is characterised by a stable food supply and low oxygen conditions, as suggested by the increase in infaunal morphogroups and in suboxic-dysoxic taxa. The limits between the intervals are easily recognisable in the EBFOI (Fig. 5). The EBFOI drops (from ca. 50–60 to 30) at the boundary between Intervals 1 and 2 (at 6.7 My), and it increases from Interval 2 to Interval 3 showing a peak of 71.45 at 4.8 My. In addition, the EBFOI is not constant across interval 2, and it shows an increase towards more oxic conditions between 6.7 and 5.8 My followed by a decrease between 5.8 and 5.0 My.

Site U1488 shows overall high values compared to the other sites, ranging between ca. 40 and 60. We identified two intervals based on the EBFOI values, and confirmed by the statistical analysis (Fig. 6). In the DCA analysis (Fig. 7), we interpret Axis 1 as controlled by trophic conditions, with eutrophic genera limited to low values along this axis and oligotrophic genera showing high values. Axis 2 seems to be controlled by oxygenation, as oxic genera (e.g., *Anomalinoidea*, *Cibicides*, *Globocassidulina*) show high values along this axis, and suboxic-dysoxic genera (e.g., *Epistominella*, *Pleurostomella*, *Uvigerina*) are located at low values along this axis, confirming the separation of the genera in the oxic, suboxic, and dysoxic groups. Interval 1 spans from 8.7 to 4.3 My (297.86 to 120.50 m), the EBFOI oscillates between high (ca. 55–60) and low values (ca. 35–40) but overall shows a generally stable trend around 50. A similar trend is observed in the infaunal/epifaunal ratio, which shows overall stable values (ca. 50.0%). Cluster A dominates in this interval, with high percentages of *Alabaminella*, *Epistominella*, and *Nuttallinella*. In the DCA analysis, this cluster falls at high values along Axis 1, indicating oligotrophic conditions at the seafloor.

Genera that are tolerant to low-oxygen conditions, such as *Bolivina*, *Bulimina*, or *Uvigerina*, are present but show low relative abundance, suggesting that oxygen levels did not significantly change across this interval. Since benthic foraminiferal assemblages are primarily related to such environmental factors as water depth, availability of organic matter and oxygen levels (e.g., Van der Zwaan *et al.*, 1999; Gooday, 2003; Murray,



**Figure 7.** R-mode DCA analysis of genera from Site U1488. Dashed ellipses indicate Cluster A (green) and Cluster B (purple). Coloured ellipses group together oxic (orange) and suboxic-dysoxic (blue) indicators. Low values along Axis 1 (Cluster B) indicate high food supply, high values (Cluster A) are linked to a low food supply. Low values along Axis 2 indicate low oxygen conditions, high values are linked to high oxygen conditions.

2006), we suggest that assemblages were likely controlled by the amount and/or type of food reaching the seafloor. Phytodetritus exploiting taxa (PET) such as *Alabaminella*, *Epistominella*, or *Globocassidulina*, are abundant in Interval 1. This group has a preference for phytodetritus, a type of organic matter that reaches the seafloor following massive phytoplankton blooms in surface waters, suggesting increased seasonal primary production (Gooday, 1988, 2003; Jorissen *et al.*, 2007; Boscolo-Galazzo *et al.*, 2015). In line with our findings, between 8.6 and 6.5 My, Nathan and Leckie (2009) documented an increase in relative abundance of *Neoglobobadrina* and a reduced  $\delta^{13}\text{C}$  gradient between upper thermocline and mixed layer taxa at ODP Site 806, located in the western equatorial Pacific Ocean on the Ontong Java Plateau, indicating increased seasonal productivity in this area.

Phytoplankton blooms, high surface productivity and high relative abundance of PET have been previously documented during the biogenic bloom at Sites 1085 and U1506 (Gastaldello *et al.*, 2023a, 2024b), and have been related to changes in water currents, wind and upwelling intensification. Site U1488, however, is not situated in close proximity to an upwelling zone (Rosenthal *et al.*, 2018). The biogenic bloom at Site U1488 could have been influenced by regional changes in the palaeoceanography probably influenced by the gradual closure of the Indonesian Seaway and the development of the Western Pacific Warm Pool during the Late Miocene (Van Andel *et al.*, 1975; Kennett *et al.*, 1985; Savin *et al.*, 1985; Kuhnt *et al.*, 2004).

Between intervals 1 and 2, the EBFOI drops from ca. 60 to 30, and it remains stable with lower values (35–40) throughout Interval 2 (from 4.3 to 3.0 My; 120.50 to 85.02 m). This drop in EBFOI values is reflected in the epifaunal/infaunal ratio, which shows a high relative abundance of the infaunal morphogroup (70.0%) during Interval 2. The EBFOI points to suboxic-dysoxic conditions, but changes in the relative abundance pattern of the genera suggest that the palaeoenvironmental conditions were not stable during Interval 2. The genera tolerant to low-oxygen conditions show different trends, *Bolivina* and *Bulimina* are almost absent and *Uvigerina* increases up to 14.7% at 3.2 My. *Epistominella* peaks at 3.8 My, indicating abundant phytodetritus at the seafloor. The high abundance of Cluster A during this interval confirms the suboxic-dysoxic conditions inferred from the EBFOI. This cluster is located at low values in the DCA analysis, suggesting high food supply and eutrophic conditions at the seafloor, which are typically related to a decrease in the oxygen levels (Jorissen *et al.*, 2007).

In conclusion, the EBFOI suggests a stable interval of low oxygen conditions, but the assemblages point to a switch from a high food supply, low oxygen levels (e.g., coinciding with the peak in *Uvigerina*) and phytoplankton blooms in surface waters, to a seasonal food supply and high oxygenation at the seafloor (e.g., coinciding with the peak in *Epistominella*).

The EBFOI reveals as a useful tool to differentiate phases within the biogenic bloom but it shows some limitations. The comparison of this index with palaeoenvironmental

interpretations based on several proxies shows that the EBFOI is not always consistent with the inferred oxygen conditions at the seafloor, particularly at Site U1488. Further studies of this site, including more detailed quantitative analyses of benthic foraminiferal assemblages as well as independent proxies, will be fundamental to understand the palaeoenvironmental changes at Site U1488 and to delve deeper into the impact of palaeoceanographic changes during the Late Miocene–Early Pliocene biogenic bloom.

## CONCLUSIONS

The comparison between the EBFOI and the palaeoenvironmental reconstructions available for Site 1085 and Site U1506, confirms the reliability of this index in the investigation of bottom-water oxygenation, but it shows some limitations at Site U1488. Based on the EBFOI values, we distinguished two intervals across the Late Miocene–Early Pliocene at Site 1488. Stable EBFOI values during Interval 1 (8.7 to 4.3 My) indicate constant oxygen conditions, but the abundance of phytodetritus exploiting taxa suggests highly seasonal phytoplankton blooms in surface waters, probably related to oceanographic changes due to the development of the Western Pacific Warm Pool. Stable but lower EBFOI values in Interval 2 (4.3 to 3.0 My) point to stable suboxic-dysoxic conditions, but benthic foraminiferal assemblages indicate periods of high food availability and reduced oxygen levels, and episodes characterised by seasonal food supply and increased seafloor oxygenation. The Upper Miocene–Lower Pliocene interval at Site U1488 supports the premise that the biogenic bloom was a multiphase, complex phenomenon, with shifts in productivity regimes related to regional and global oceanographic changes. Our research findings at Site U1488 are a first step to investigate the palaeoenvironmental changes, in terms of nutrient type and availability at the seafloor and oxygen conditions, across the biogenic bloom. A precise age model and a detailed quantitative analysis of benthic foraminifera, integrated with other independent proxies such as carbonate mass accumulation rates and stable carbon and oxygen records, will be fundamental to reveal the precise timing and expression of the biogenic bloom in the western equatorial Pacific Ocean, and to speculate about the regional and global mechanisms behind this phenomenon.

**Supplementary information.** Data generated in this study are available in the Supplementary Information S1 and archived in PANGAEA database (Gastaldello *et al.*, 2023b).

**Author contributions.** Conceptualization: GME, AC, AL; Data curation: GME; Investigation: GME; Supervision: AC and AL; Writing – original draft: GME.

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