Global and Planetary Change 259 (2026) 105314

Contents lists available at ScienceDirect

Global and Planetary Change

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

Tropicalization and biodiversity restructuring of calcifying plankton in a rapidly warming Mediterranean Sea

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ARTICLE INFO

Editor: Dr. Fabienne Marret-Davies

Keywords:
Mediterranean Sea
Biodiversity change
Calcifying plankton
Coccolithophores
Planktonic foraminifera
Anthropogenic warming
Tropicalization

ABSTRACT

Climate-driven shifts in species diversity, community composition and phenology can disrupt ecosystem functioning and compromise marine ecosystem stability. The Mediterranean Sea, a global biodiversity hotspot, is particularly vulnerable to anthropogenic climate change and is experiencing a growing biodiversity crisis especially driven by warming, habitat degradation, pollution and the introduction of new species. Yet, current knowledge of biodiversity changes in this region is largely limited to shallow shelf benthic communities and macroorganisms. Calcifying phytoplankton and zooplankton, however, offer a unique lens into pelagic ecosystem dynamics, as their fossil record preserves signals of biodiversity change in deep-sea sediments spanning the Industrial Era and the current phase of rapid warming. This study focuses on the reconstruction of diversity change of two dominant calcifying plankton groups: coccolithophores and foraminifera (primary and secondary producers). We examine two selected sedimentary records of the western and central Mediterranean—Alboran Sea and the Strait of Sicily—spanning the last ~1700 and 200 years of modern climate, respectively. By quantifying abundance, diversity and turnover of species composition we evaluate the potential response of calcifying plankton assemblages to oceanographic changes under anthropogenic climate change. The results revealed contrasting changes in the diversity of the two dominant calcifying plankton groups, with a rapid increase in coccolithophore diversity alongside a decrease in planktonic foraminiferal diversity during the Industrial Era. We attribute these group-specific responses to ecological and physiological differences, particularly in relation to life cycles and water column distribution, under increasingly stratified, nutrient-depleted surface waters driven by rising sea surface temperatures. In addition, this study provides first indication of tropicalization of the western Mediterranean plankton derived from the increasing intrusion and eastward expansion of the coccolithophore *Gephyrocapsa oceanica* from the Strait of Gibraltar into the Mediterranean Sea. The highest abundances of this species are restricted to the Equatorial Atlantic Divergence Zone and only found in higher proportions in the Mediterranean during past warm periods. Although the temperate-productivity foraminiferal species of *Globigerina bulloides* and *Globorotalia inflata* remain the dominant foraminiferal species, previous minor dominant species are being replaced by warm-oligotrophic species, such as *Trilobatus sacculifer* and *Globigerinella* spp. These align with model projections of tropical species migrating into the area, previously documented among benthic organisms and point to a broader restructuring of planktonic life.

1. Introduction

Species diversity and biological interaction are fundamental drivers of ecosystem functioning and the regulation of global biogeochemical cycles. Consequently, changes in species composition, distribution, and phenology are expected to have important implications for ecological

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https://doi.org/10.1016/j.gloplacha.2026.105314
Received 5 August 2025; Received in revised form 17 December 2025; Accepted 14 January 2026

processes and the stability of marine ecosystems (Poloczanska et al., 2013). Yet, diversity changes among planktonic communities remain poorly characterized and understood. This represents a critical knowledge gap, as microscopic plankton (comprising both phytoplankton and small zooplankton) form the base of marine food webs and sustain biogeochemical cycles (Benedetti et al., 2021).

Biological monitoring programs provide valuable insights into present-day biodiversity patterns and species response to environmental variability. However, their limited temporal scope restricts our ability to detect long-term ecological trends. Moreover, the environmental fluctuations recorded during these periods are relatively minor compared to the magnitude of projected anthropogenic impacts. In this context, sedimentary records of calcifying plankton microfossils provide a unique opportunity to reconstruct biodiversity dynamics over extended timescales and serve as baselines for evaluating pre-industrial variability (Yasuhara et al., 2020). Analyses of marine sediment records have yielded unprecedented insights into how and why biodiversity has changed over millions of years, particularly in relation to major climatic and tectonic changes (Cermeño et al., 2013; De Vargas et al., 2007; Renema et al., 2008; Swain et al., 2024; Woodhouse et al., 2023). Yet, little is known about biodiversity responses to rapid changes in climate and environmental conditions over decades and centuries, which are important time scales relevant to ongoing and future human-induced climate change (Lewandowska et al., 2020). These intermediate timescales remain a persistent "blind spot" between the fine resolution of biological monitoring and the coarse scope of traditional paleoecological records. In regions with high sedimentation rates, however, high-resolution reconstructions can help bridge this gap (Yasuhara et al., 2020). Although soft-bodied plankton species, which constitute the majority of plankton biomass, are not preserved in the fossil record, the diversity of calcifying plankton is globally correlated with broader pelagic biodiversity patterns (Ibarbalz et al., 2019; Tittensor et al., 2010).

Among calcifying plankton groups, coccolithophores and foraminifera are the most abundant and well-preserved in marine sediments. Coccolithophores are unicellular haptophyte algae encased in calcite platelets (coccoliths) and are widely distributed in surface ocean waters. Planktonic foraminifera are single-celled ameboid protists that build calcite shells (tests) composed of one or more globular chambers. They occur globally and are especially abundant and diverse in the sunlit ocean layers, where many species host photosynthetic algal symbionts (photosymbionts), while others inhabit deeper waters below the photic zone. Their shells are relatively resistant to dissolution in the water column and their fossil record closely reflects surface-dwelling communities (Kucera et al., 2005). In contrast, coccolithophore fossil records are biased towards species that produce larger and more robust coccoliths, due to differential preservation and water column dissolution (Andruleit et al., 2004; Ziveri et al., 2023). Both groups play central roles in the marine carbon cycle by contributing to long-term carbon sequestration, from decades to millennia, and shaping ocean chemistry over geological timescales (Boudreau et al., 2018; Ridgwell and Zeebe, 2005; Zeebe and Westbroek, 2003). However, these vital functions are increasingly threatened by climate-driven physico-chemical stressors affecting calcifying plankton. Rapid ocean warming is reshaping planktonic community structure, metabolism and carbon export efficiency (Beaugrand et al., 2010; Benedetti et al., 2023; Ibarbalz et al., 2019), while ocean acidification disrupts calcification processes and alters morphology (Kroeker et al., 2013; Langer and Ziveri, 2025; Leung et al., 2022).

Recent studies have demonstrated the value of planktonic foraminifera as indicators of anthropogenic change. For example, Jonkers et al. (2019) compared global assemblages from surface sediments that provided a pre-industrial baseline with assemblages collected from sediment traps and found consistent shifts in species composition attributed to ocean warming. Similarly, studies using foraminiferal shell weight as a proxy for calcification have reported that modern specimens are lighter than those in surface sediments, consistent with acidification-driven reductions in calcification (Fox et al., 2020; Moy et al., 2009; Pallacks et al., 2023). In the Mediterranean Sea, the first microfossil-based evidence of planktonic responses to human-induced climate change was provided by Pallacks et al. (2021), showing that the pre-industrial variability in foraminiferal assemblages has been increasingly overprinted by anthropogenic warming. Their findings also revealed significant shifts in coccolithophore communities since the Industrial Era. More recently, Ferraro et al. (2024) linked a marked decline in planktonic foraminiferal productivity since the mid-20th century to the increasing frequency of persistent winter high-pressure systems—unprecedented in the last millennium—which limit vertical mixing and reduce nutrient supply to surface waters.

We hypothesize that accelerated warming and declining productivity may have already altered calcifying plankton diversity in the Mediterranean Sea. To test this, we analysed two high-resolution sediment records from the western and central Mediterranean, spanning the past ~1700 and 200 years to reconstruct whole-community composition and assess long-term diversity trends in coccolithophores and planktonic foraminifera. By examining shifts in taxonomic diversity and assemblage structure, we provide the first reconstruction of multi-centennial, decadal and interannual changes in the diversity of these key calcifying groups in the Mediterranean Sea. We further explore the implications of these changes into the ecosystem function and discuss the potential future trajectory in the context of ongoing environmental pressures.

While this study is conducted at a regional scale in the western and central Mediterranean Sea, its implications extend beyond the basin. The Mediterranean serves as a key natural laboratory for investigating the impacts of global climate change (Bethoux et al., 1999), as it exhibits amplified signals of global warming and oceanic change (Cramer et al., 2018; Marriner et al., 2022). Its hydrography is highly heterogenous, shaped by strong west-east gradients in temperature, salinity, and nutrient availability, and influenced by mesoscale gyres that generate patchy environmental conditions (Woodward, 2009). Within this complex oceanographic setting, the Mediterranean provides an exceptional context for assessing how anthropogenic warming drives diverse local and regional plankton responses. By comparing these two sites, our study explores whether consistent large-scale patterns, such as biogeographical shifts (Chaabane et al., 2024; O'Brien et al., 2016) and changes in calcifying plankton diversity, emerge despite pronounced local variability. In this sense, the Mediterranean functions as a microcosm for understanding how the pelagic ecosystems worldwide may respond to ongoing and future climate-driven environmental change.

2. The Mediterranean Sea: Oceanographic setting and climate system

The Mediterranean Sea is a semi-enclosed marine system bordered by the Eurasian, Arabian and African plates, situated between the monsoon system and the temperate westerlies, which makes it highly sensitivity to global climate variability (Ali et al., 2022). It connects to the Atlantic Ocean through the Strait of Gibraltar, to the Black Sea via the Dardanelles and the Sea of Marmara, and to the Red Sea and Indian Ocean through the Suez Canal. The Strait of Sicily divides the Mediterranean Sea into the western and eastern basin, further segmented into sub-basins due to complex geomorphology that influence the water mass circulation (Fig. 1).

The Mediterranean is a marine biodiversity hotspot, hosting high species richness and endemism (Coll et al., 2010; Giorgi, 2006). It is often considered a small-scale analogue of the global ocean due to the presence of most of its key oceanographic features (Bethoux et al., 1999), and serves as a model for predicting global ocean responses to various environmental pressures (Lejeusne et al., 2010). Its hydrographic regime is dominated by an anti-estuarine thermohaline circulation, driven by the net excess of evaporation over precipitation and

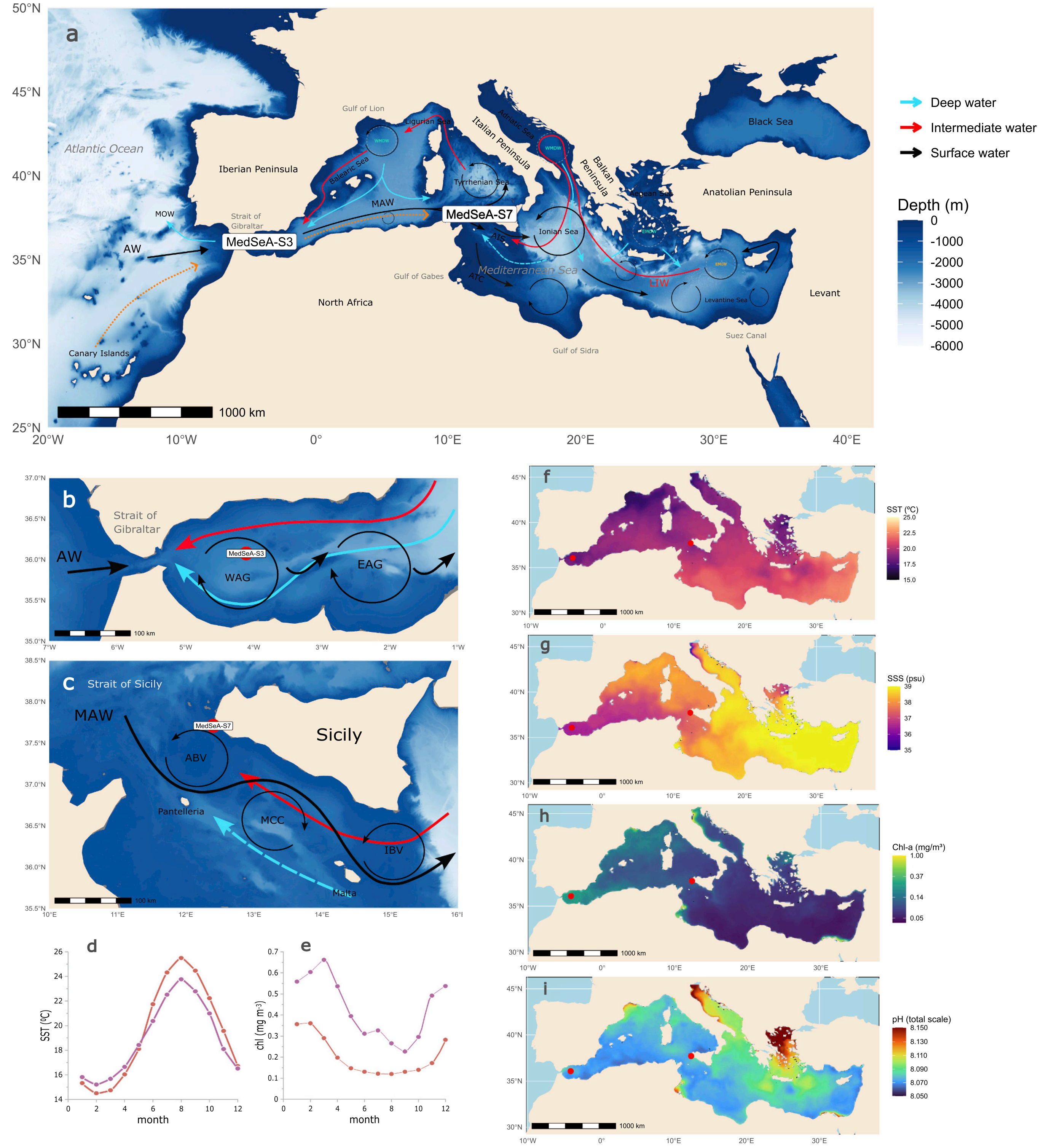

Fig. 1. The Mediterranean Sea a) The Mediterranean Sea, bathymetry (GEBCO 2024 Grid), thermohaline circulation, gyres, intermediate- and deep-water formation zones and labelled-location of analysed sedimentary records. Orange-doted arrows represent the dispersal pathway for West African species in the northern-east Atlantic and Mediterranean basin (Albano et al., 2024). AW: Atlantic Water. MAW: Modified Atlantic Water. AIS: Atlantic Ionian Stream. ATC: Atlantic Tunisian Current. LIW: Levantine Intermediate Water. EMIW: Eastern Mediterranean Intermediate Water formation zone. WMDW: Western Mediterranean Deep Water formation zones. MOW: Mediterranea Outflow Water. b) Station MedSeA-S3 in the Alboran Sea. WAG: Western Alboran Gyre. EAG: Eastern Alboran Gyre. c) Station MedSeA-S7 in the Strait of Sicily. Meandering surface current encircling two cyclonic vortices with a pronounced anticyclonic meandering in between. ABV: Adventure Bank Vortex. MCC: Maltes Channel Crest. IBV: Ionian Shelf Break Vortex. d) Monthly sea surface temperature (SST) and e) surface chlorophyll-a concentration from 2002 to 2020 CE at the Alboran Sea (purple line) and the Strait of Sicily (red line) core sites. Data was retrieved from AQUA-Modis, Level 3 sensor, and is centred at the exact core location, covering 16 km^2. f) SST and g) Sea Surface Salinity (SSS) from Mediterranean Sea Physics Reanalysis for the year 2000 (Escudier et al., 2020). h) Surface chlorophyll-a concentration and i) surface pH (total scale) from Mediterranean Sea Biogeochemistry Reanalysis for the year 2000 (Teruzzi et al., 2021). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

river discharge (Rohling and Abu-Zied, 2009). As a concentration basin, it receives relatively cool, less saline Atlantic water, which warms and becomes saltier as it flows eastward, eventually sinking in the Levantine Sea (Millot and Taupier-Letage, 2005). This process creates a strong west-east gradient in sea surface temperature (SST), salinity, alkalinity and nutrient concentration (Álvarez et al., 2014; Escudier et al., 2020; Tanhua et al., 2013; Teruzzi et al., 2021). Although largely oligotrophic due to extremely low inorganic phosphorous levels (Berland et al., 1980), certain regions benefit from enrichment via wind-driven mixing, river discharge and mesoscale circulation.

The Mediterranean climate is characterized by warm, dry summers and mild, humid winters, with marked SST seasonality and regional contrasts. Large-scale atmospheric patterns influence interannual to multidecadal variability (Cortina-Guerra et al., 2021; Reale et al., 2020). The North Atlantic Oscillation (NAO) affects the western basin, modulating storm tracks and wet–dry cycles, while the Eastern Atlantic–West Russia (EA/WR) pattern shapes variability in the east, both modulating marine ecosystems. The Atlantic Multidecadal Oscillation (AMO) correlates with Mediterranean SST, though anthropogenic warming has increasingly dominated since the mid-20th century (Macias et al., 2013a, 2013b). Over the last two millennia, the Mediterranean climate has undergone several well-defined oscillations (Fig. 2) that have influenced its oceanographic dynamics (Luterbacher et al., 2012; Nieto-Moreno et al., 2013). The Dark Age (DA; ca. 300–800 CE) was marked by relatively cool conditions with pronounced interannual and decadal variability, likely driven by reduced solar irradiance and frequent volcanic activity (Nieto-Moreno et al., 2011). The Medieval Climate Anomaly (MCA; ca. 800–1300 CE) was a warm and stable interval associated with enhanced solar activity and prevailing positive NAO and AMO phases, strengthening ocean–atmosphere circulation and influencing surface stratification and productivity (Lüning et al., 2019). The Little Ice Age (LIA; ca. 1300–1800 CE) returned to cooler, more variable conditions, driven by diminished solar irradiance, negative NAO phases, and recurrent volcanic activity (Moreno et al., 2012; Wanner et al., 2022). Since the Industrial Era (IE; ca. 1800 CE), anthropogenic warming has progressively overridden the effects of natural NAO-AMO variability on Mediterranean SST, with this shift becoming especially pronounced in the second half of the 20th century (Macias et al., 2013a, 2013b).

Since the late 20th century, particularly from the 1980s onward, the Mediterranean Sea has undergone sustained and increasingly rapid physico-chemical changes, parallelling global patterns but often occurring at an amplified rate (Cramer et al., 2018; Cusack and Cox, 2025; García-Ibáñez et al., 2024; Hassoun et al., 2015; Marriner et al., 2022). The basin is warming approximately 20% faster than the global ocean, with SST increases of 0.6–1 °C over the past 30 years and projections of up to +5.8 °C by 2100 (López García, 2021; Parras-Berrocal et al., 2020). Seasonal extremes are intensifying, particularly in summer, with marine heatwaves becoming more frequent, prolonged, and severe (Garrabou et al., 2022). As of July 2025, the western Mediterranean experienced its most extreme marine heatwave on record, with anomalies of 5–6 °C relative to the 1982–2023 period (ICATMAR; Sever Weather EU). Concurrently, the poleward displacement of the jet stream has led to declining phytoplankton production in the northwestern Mediterranean (Crespin et al., 2025).

Compared to the global ocean, the Mediterranean exhibits higher alkalinity due to intense evaporation and the lateral influx from rivers and the Black Sea (Schneider et al., 2007). Combined with deep-water formation and relatively rapid overturning, this enhances CO_2 sequestration (Schneider et al., 2010; Lee et al., 2011; Palmiéri et al., 2015; Álvarez et al., 2014). However, rapid warming is disrupting oxygen and nutrient dynamics, with widespread consequences for marine productivity and biodiversity (Darmaraki et al., 2024). Increased stratification and reduced ventilation pose risks to both surface and deep ecosystems, although deep-water formation and rising surface salinity persist in some areas (Reale et al., 2022; Skliris et al., 2025).

Transitional regions such as the Alboran Sea and the Strait of Sicily are both influenced by North Atlantic atmospheric circulation patterns (Báez et al., 2013; Incarbona et al., 2008a, 2008b). During winter, the Intertropical Convergence Zone (ITCZ) is positioned near 10°N, allowing moist westerly winds to bring rainfall and lower temperatures to the region. In summer, the westerlies shift northward due to the strengthening of the Azores high-pressure cell, while the ITCZ advances to about 20°N, resulting in widespread drought conditions (Hurrel, 1995). Ongoing climatic shifts are reshaping regional productivity regimes, with potential cascading impacts on food webs and carbon export processes (Ciavatta et al., 2019). Persistent atmospheric high-pressure systems suppress vertical mixing and limit the replenishment of nutrients in surface waters, thereby disrupting the seasonal dynamics of primary production (Ferraro et al., 2024; Pallacks et al., 2021). Although the Alboran Sea and the Strait of Sicily exhibit different productivity regimes (D'Ortenzio and Ribera d'Alcalà, 2009), both areas are strongly influenced by the inflow of Atlantic surface water and belong to the same ecoregion (Ciavatta et al., 2019).

The Alboran Sea, the westernmost basin of the Mediterranean, is bounded by the Iberian Peninsula to the north and North Africa to the south (Fig. 1). Circulation is shaped by the interaction between the Atlantic Water (AW) from the west and the westward outflow of Levantine Intermediate Water (LIW) and West Mediterranean Deep Water (WMDW) from the east. The AW, which is warmer and fresher, dominates surface circulation down to 150–200 m depth. Beneath it, the colder, saltier LIW flows westward. Originating in the Eastern Mediterranean, the LIW crosses the Alboran Sea and exits into the Atlantic, contributing to the formation of the Mediterranean Outflow Water (MOW). The deeper WMDW, formed in the Gulf of Lion, flows below the LIW and also contributes to the MOW (Sánchez-Garrido and Nadal, 2022).

The interaction of Atlantic and Mediterranean waters, modulated by the regional geomorphology, sustains two semi-permanent anticyclonic gyres that support complex mesoscale dynamics and elevated biological productivity (Fig. 1b) (Sánchez-Garrido and Nadal, 2022). Internal diurnal waves further redistribute nutrients and biomass (van Haren, 2014). These processes upwell nutrient-rich waters into the euphotic zone, making the Alboran Sea one of the most productive Mediterranean regions (Uitz et al., 2012). Phytoplankton community composition has shifted in recent decades from small flagellates and diatoms (1994–2000) to coccolithophores and dinoflagellates, likely driven by nutrient changes in the upper water column (Mercado et al., 2005). Zooplankton is dominated by copepods, cladocerans and tunicates (Fernandez de Puelles et al., 2023).

The Strait of Sicily, a 145 km wide passage between Sicily and Tunisia, serves as a transition zone between the oligotrophic eastern and mesotrophic western Mediterranean (Fig. 1). The upper 100–200 m of the water column are occupied by the Modified Atlantic Water (MAW), where it splits into two distinct currents: the Atlantic Tunisian Current flowing along the African coast and the Atlantic Ionian Stream (AIS) flowing north-eastward. The AIS feeds the Mid-Mediterranean Jet, which continues eastward into the Levantine Basin, contributing to the LIW formation (Béranger et al., 2004).

Four recurring mesoscale summer features are associated with AIS meanders (Fig. 1c): the Adventure Bank Vortex (ABV), the Maltese Crest Channel (MCC) anticyclonic gyre, the Ionian Shelf Break Vortex (IBV) cyclonic gyre, shaped by bathymetry, internal dynamics and atmospheric forcing (Lermusiaux and Robinson, 2001). Primary productivity is higher in the western strait, where upwelling and frontal systems mix nutrient-rich waters. The phytoplankton community is dominated by nanophytoplankton (haptophytes and nanoflagellates) and picophytoplankton (cyanobacteria), with lower abundances of diatoms and dinoflagellates (Ciavatta et al., 2019). Zooplankton is dominated by copepods and ostracods (Di Lorenzo et al., 2018).

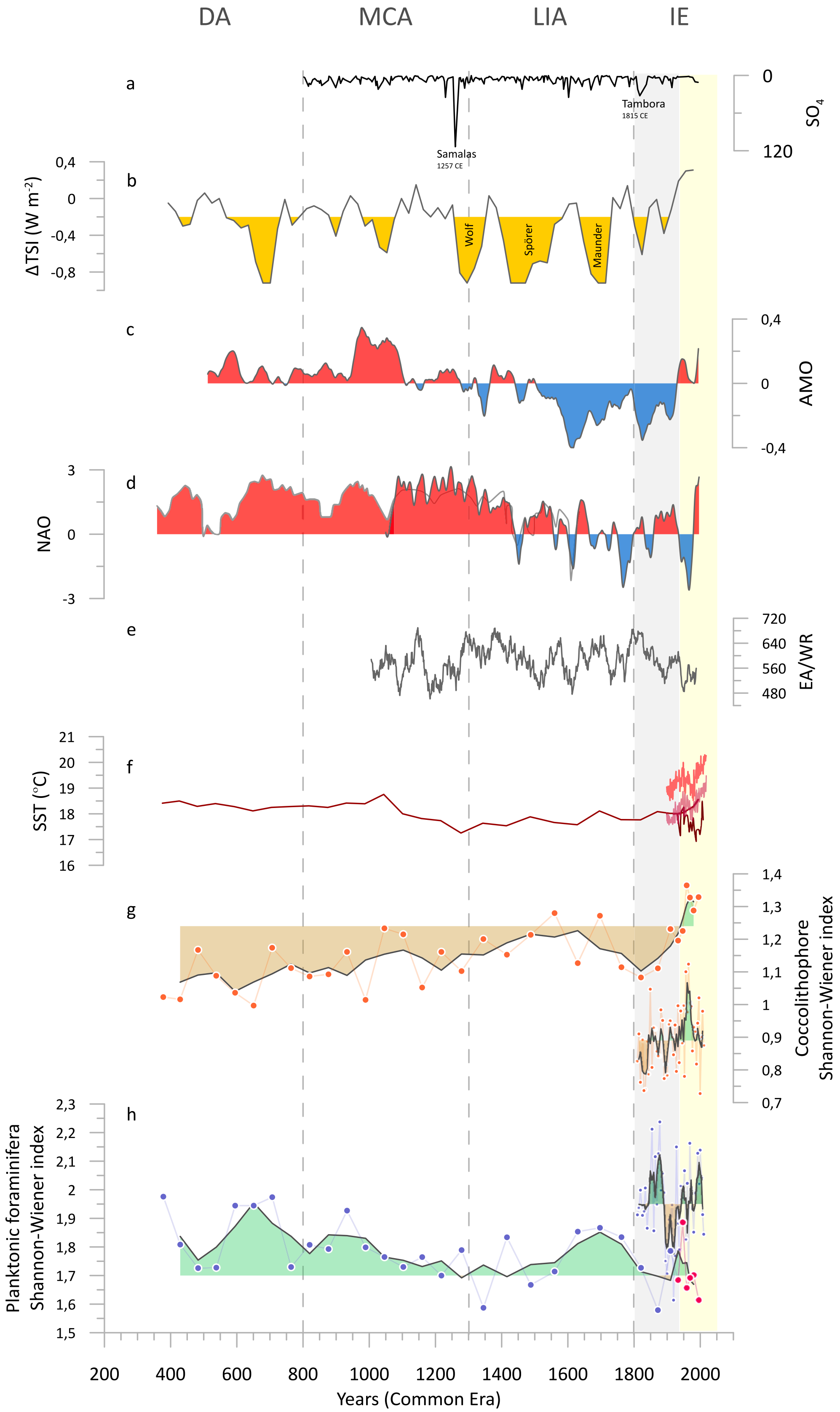

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Fig. 2. Coccolithophore and planktonic foraminiferal diversity over the past ~ 1700 years in the Alboran Sea and the last 200 years in the Strait of Sicily. a) Sulphate records in Antarctic and Greenland ice cores as a proxy for volcanic activity (Crowley and Unterman, 2013). b) Total solar irradiance (TSI) based on ^{10}Be and ^{14}C data (Steinhilber et al., 2012; Steinhilber et al., 2009). Yellow fillings indicate TSI periods below the mean (-0.2 W·m^{-2}). c) Atlantic Multidecadal Oscillation (AMO) reconstruction (Mann et al., 2009), shown as 29 point moving average (dark line). d) North Atlantic Oscillation (NAO) reconstruction through tree ring and speleothem-based records (dark line; Trouet et al., 2009) and a lake sediment record (grey line; Olsen et al., 2012). Positive and negative AMO and NAO phases are highlighted in red and blue, respectively, above and below the mean. e) East Atlantic-West Russia (EA/WR) atmospheric pattern reconstruction during the past 1000 years, derived from the projection of winter mean 500-mbar geopotential height fields onto the spatial pattern defined by winter upward heat flux gradients between the Aegean Basin and the Gulf of Lion (Cortina-Guerra et al., 2021). f) Sea surface temperature (SST) reconstruction based on alkenone derived SST for the Alboran Sea (ruby red) and the Strait of Sicily (dark red), combined with annual SST data from the HadISST dataset for the Alboran Sea (pink) and Strait of Sicily (salmon) sites. f) Coccolithophore diversity (Shannon-Wiener index) shown as 3-point moving average for the Alboran Sea (379–1995 CE) and the Strait of Sicily (1810–2010 CE) (both dark lines). g) Planktonic foraminiferal diversity (Shannon-Wiener index), shown as a 3-point moving average for the Alboran Sea (379–1980 CE) and the Strait of Sicily (1810–2010 CE) (both dark lines). Golden-filled areas indicate periods when coccolithophore and foraminiferal diversity fell below the Industrial Era mean (1800–2010 CE), while green-filled areas highlight periods above this mean. Orange points represent coccolithophore diversity values; twilight blue points indicate planktonic foraminiferal diversity. Neon red points denote the uppermost planktonic foraminiferal diversity values, dated using Pb^{210}. Shading denotes key intervals: the grey coloured band marks the first half of the Industrial Era (~1800 CE) and the chalk-coloured band the second half, where sustained changes of diversity trends are observed (1933–1959). Duration of the Dark Age (DA), Medieval Climate Anomaly (MCA), Little Ice Age (LIA) and Industrial Era (IE) based on estimates by Nieto-Moreno et al., 2011. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

3. Materials and methods

3.1. Sediment records

Marine sediment cores analysed in this study were collected during the MedSeA research cruise in 2013 on R/V Ángeles Alvariño using a MC400 Multi Corer. The age model and diversity analyses at MedSeA-Station 3 in the Alboran Sea were based on core 1 (MedSeA-S3-c1). At MedSeA Station 7 in the Strait of Sicily, the age model was developed from the twin core 2 (MedSeA-S7-c2), and diversity analyses were carried out on the twin core 4 (MedSeA-S7-c4).

3.1.1. Age model development

Core MedSeA-S3-c1 (36.075° N, 4.110° W) was retrieved from the Alboran Sea, in the northern sector of the Western Alboran Gyre at 1137 m water depth, with a core length of 33 cm and sliced every centimetre (Fig. 1). The age model was reconstructed by combining radionuclide and radiocarbon analyses (Appleby and Oldfield, 1992; Bradley, 2015). Determination of ^{210}Pb activities was accomplished through the measurement of its alpha-emitter daughter nuclide ^{210}Po, following the methodology described in Sanchez-Cabeza et al., 1998 at the GRAB facility of Autonomous University of Barcelona. After addition of ^{209}Po as an internal tracer, sample aliquots of 200–300 mg were totally digested in acid media by using an analytical microwave oven and Po isotopes were subsequently counted using α-spectrometers equipped with low background silicon surface barrier (SSB) detectors (EG&G Ortec) for 4×10^5 seconds. The concentration of excess ^{210}Pb used to obtain the age model was determined as the difference between total ^{210}Pb and the uniform ^{210}Pb at depth. Maximum mean sediment accumulation rates and therefore the age-depth model over the last decades/century was estimated using the Constant Flux:Constant Sedimentation (CF:CS) model (Krishnaswamy et al., 1971; Robbins et al., 1978). Radiocarbon dating (^{14}C) was performed on the lower part of the core using planktonic foraminifera shells of *Globorotalia inflata* isolated from the 250–315 μm fraction from two different depths (15–16 and 30–31 cm). Analysis was performed by using accelerator mass spectrometry (AMS) at the NOSAMS facility of Woods Hole Oceanographic Institution. Taking the marine radiocarbon reservoir effect into account, with an offset of 400 years (Siani et al., 2000), radiocarbon ages were calibrated to calendar ages by using Marine13 calibration curve (Reimer et al., 2013) where ages were reported with a 2σ uncertainty. The core spans the interval 1995–378 CE. Sedimentation rates varied between the upper (~0.08 cm/yr; ^{210}Pb-based) and lower (~0.02 cm/yr;^{14}C-based) sections. The upper interval provides an average time resolution of ~12 years (back to 1933 CE), while the lower interval averages ~57 years (to 378 CE).

Core MedSeA-S7-c2 (37.708° N, 12.406° E) was obtained from the Adventure Bank continental shelf of the Strait of Sicily at 263 m water depth, with a core length of 46.5 cm, sliced every centimetre (Fig. 1). The age model was estimated through radionuclide analysis, determining total ^{210}Pb activity by measuring its alpha-emitter daughter nuclide ^{210}Po (Sanchez-Cabeza et al., 1998), at the GRAB facility of Autonomous University of Barcelona. ^{209}Po was added as an internal tracer, before sample aliquots of 200–300 mg were totally digested in acid media by using an analytical microwave oven and Po isotopes plated on silver discs in HCl 1 N at 70 °C while stirring for 8 h. Po emissions were subsequently counted through α-spectrometers equipped with low background silicon surface barrier (SSB) detectors (EG&G Ortec) for 4×10^5 seconds. The difference between total ^{210}Pb and the constant ^{210}Pb at depth describes the concentration of excess ^{210}Pb, which was used to estimate maximum mean sediment accumulation rates and the age-depth relation was determined by applying the Constant Flux:Constant Sedimentation (CF:CS) model (Robbins et al., 1978; Sanchez-Cabeza et al., 1998). The activities of ^{137}Cs (661 keV) were determined by γ spectrometry in a coaxial high-purity Ge detector (EG&G Ortec) calibrated with the SRM-4276 solution standard supplied by the National Institute of Standards and Technology (NIST). The quality of the results determined by gamma and alpha spectrometry was evaluated by participation in IAEA proficiency tests and continuous analysis of certified and replicate materials. The core covers the last 200 years (1810–2010 CE), with an average sedimentation rate of ~0.23 cm/yr. The resulting temporal resolution is approximately 4.3 years.

3.1.2. Identification of coccolithophores and planktonic foraminifera

Core MedSeA-S3-c1 was sliced at 1 cm intervals, whereas MedSeA-S7-c4 was sliced at 0.5 cm intervals but processed in combined 1 cm sections, consistent with the resolution of the developed age model. Samples were washed over a 63 μm sieve using distilled Elix water. The coarse size fraction (>63 μm) was used for quantitative analyses of planktonic foraminifera, while the fine fraction (<63 μm) was used for coccolithophore analyses.

Bulk sediment mass was obtained after drying samples at 60 °C for approximately 24 h. To facilitate clay disaggregation, dried sediment samples were soaked for 4 h in a saturated di-sodium tetraborate decahydrate (borax) solution (40 g L^{-1}), then washed again over a 63 μm sieve. The coarse fraction was dried at 40–60 °C for ~6 h, sieved, and split using a riffle splitter for foraminiferal quantification. A minimum of 300 specimens were counted and identified in the >125 μm fraction under a stereo microscope equipped with a ring illuminator, following the taxonomical guidelines of Schiebel and Hemleben (2017) and supplemented with the pforams@mikrotax website.

For coccolithophore analyses, standard procedures described by Bown and Young (1998) were followed. Smear slides were prepared from the <63 μm fraction and examined under a polarized microscope at 1000× magnification. At least 500 specimens were counted and identified following the taxonomical framework for extant coccolithophores established by Young et al. (2003) and Jordan et al. (2004). First results of coccolithophore assemblage from the Alboran Sea site were included in the supplementary material (Data Set S3) of Pallacks et al. (2021) to study productivity change. The complete dataset for studying biodiversity change is presented here and discussed in detail. The data are used to analyse trends in coccolithophore abundance, diversity, and species exchange ratio for ecological and paleoenvironmental interpretation (Figs. 2 and 3).

3.2. Analysis of temporal changes in calcifying plankton diversity

To evaluate the temporal dynamics in coccolithophore and planktonic foraminiferal diversity we combined different metrics. For each sediment sample, total and relative abundance of species were determined. Planktonic foraminiferal concentration and accumulation rate were also calculated. Diversity was quantified using the Shannon-Wiener index, as an abundance weighted measure, and Pielou's evenness index, expressed as the ratio of observed diversity to the theoretical maximum (Magurran, 2004; Pielou, 1969; Margalef, 1958). To evaluate the magnitude of co-occurring shifts in species identity and relative

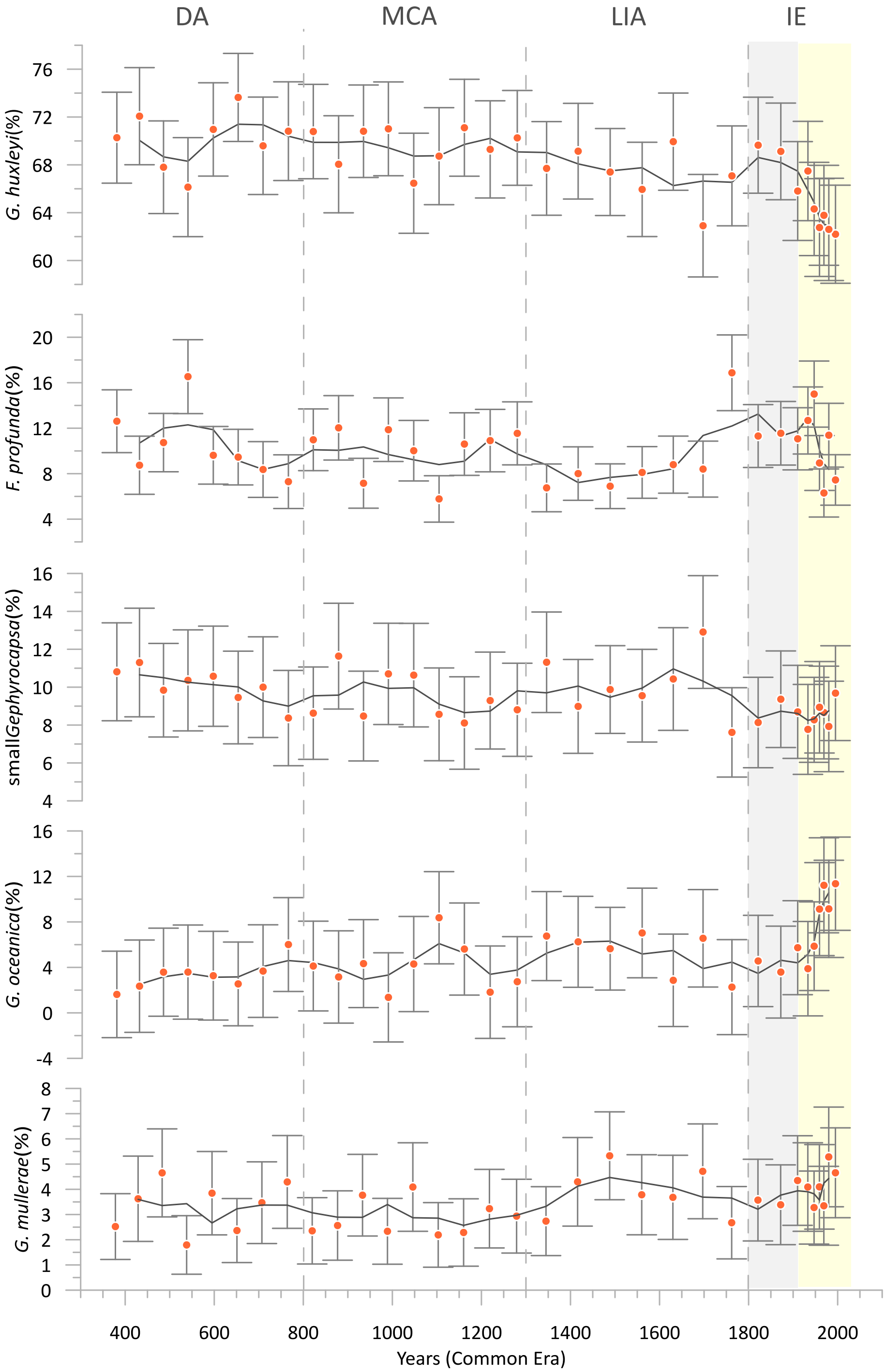

Fig. 3. Relative abundance of coccolithophore species in the Alboran Sea sedimentary record. The black line represents a 3-point moving average of the percentage value (orange). Error bars indicate the 95% confidence interval of the counts (Wald, 1939).

abundance, measures of richness-based and Simpson-based species exchange ratio (SER) were used to detect phases of strong compositional shifts (Hillebrand et al., 2018).

Stratigraphically constrained cluster analysis was conducted in R (version 4.5.1) with the "rioja" package (Juggins 2024 - version 1.0–7). A Bray-Curtis dissimilarity matrix was constructed based on the relative abundances of dominant taxa and ecologically significant grouping. Prior to analyses, data were standardized (z-score transformation) by subtracting the mean and dividing by the standard deviation (Wu et al., 2007). The dominant species were treated individually, while the rest were grouped into ecological categories based on shared functional or environmental affinities. Dominance was defined as species consistently ranking among the most abundant taxa in both sediment records, comprising 70–90% of the total assemblage and each contributing ≥5% of the total assemblage. An exception was *Gephyrocapsa oceanica*, which was preceded by small *Gephyrocapsa* and *Gephyrocapsa mullerae* in the Strait of Sicily record. In the coccolithophore assemblages, the dominant taxa in both sedimentary records were *Gephyrocapsa huxleyi*, *Florisphaera profunda* and *Gephyrocapsa oceanica*. The background taxa were grouped into three categories. Other *Gephyrocapsa* (OG) include small *Gephyrocapsa* spp., *Gephyrocapsa muellerae*. The other two categories were one containing the species that were characteristic of the upper photic zone (UPZ) and the other one containing species without a certain (known) depth preference and within a wide range of ecological preferences (Ms) (Bonomo et al., 2021; Di Stefano and Incarbona, 2004; Incarbona et al., 2010).For planktonic foraminifera, the dominant taxa were *Globigerina bulloides*, *Globorotalia inflata*, *Tenuitella* spp. and *Globigerinoides ruber* (white morphotype). Other species were grouped into three ecological categories based on thermal and trophic preferences (Ferraro et al., 2024; Béjard et al., 2024), temperate-productivity (TP), warm-oligotrophic (WO) and cold-transitional (CT). Non-identified species were also considered in the analysis.

4. Results

4.1. Coccolithophore assemblages

The sedimentary record from the Alboran Sea revealed a total of 18 coccolithophore taxa (Pallacks et al., 2021). Three species dominated the assemblage, accounting for 83.2% of the total: *Gephyrocapsa huxleyi* (68.1%), *Florisphaera profunda* (10.1%) and *Gephyrocapsa oceanica* (5%). These were followed by small *Gephyrocapsa* spp., which represented an average of 9.5% of the assemblage, and *Gephyrocapsa mullerae*, contributing 3.5% (Fig. 3). Other taxa consistently present throughout the record, though in lower abundances (<1% on average), included *Coronosphaera* spp. (0.9%), *Umbilicosphaera sibogae* (0.8%), *Calcidiscus leptosporus* (0.6%), *Umbellosphaera* spp. (0.5%) and *Syracosphaera histrica* (0.4%). Several additional species were detected sporadically, such as *Calciosolenia* spp., *Syracosphaera pulchra*, *Rhabdosphaera* spp., *Helicosphaera carteri*, *Helicosphaera pavimentum*, *Coccolithus pelagicus*, *Coccolithus pelagicus braarudii*, *Braarudosphaera bigelowi* and *Pontosphaera* spp. (Lucas et al., 2026).

The sedimentary record from the Strait of Sicily revealed a total of 23 coccolithophore taxa. Three species dominated the assemblage, accounting for 87.3% of the total: *Gephyrocapsa huxleyi* (72.3%), *Florisphaera profunda* (10.8%), and small *Gephyrocapsa* spp. (4.9%). These were followed by *Gephyrocapsa mullerae*, which represented an average of 1.8% of the assemblage, and *Gephyrocapsa oceanica*, contributing 1.2% (Fig. 5). Other taxa consistently present throughout the record, though in lower abundances (<1% on average), included *Umbilicosphaera sibogae* (0.7%), *Umbellosphaera* spp. (0.6%), *Syracosphaera pulchra* (0.5%), *Calcidiscus leptoporus* (0.3%) and *Syracosphaera histrica* (0.3%), *Helicosphaera carteri* (0.3%), *Coronosphaera* spp. (0.2%), *Gladiolithus flabellatus* (0.2%), *Calciosolenia* spp. (0.2%), *Rhabdosphaera* spp. (0.2%) and *Discosphaera tubifera* (0.1%). Several additional species were detected sporadically, such as *Oolithothus* spp., *Helicosphaera* spp., *Pontosphaera* spp., *Braarudosphaera bigelowi*, *Helicosphaera wallichii*, *Helicosphaera pavimentum* and *Coccolithus pelagicus*. Additionally, non-identified small placoliths, holococcoliths forms and other non-identified species were also consistently present, contributing 2%, 0.4% and 0.3% of the total assemblage, respectively (Lucas et al.,2026).

4.2. Planktonic foraminiferal assemblages

The sedimentary record from the Alboran Sea revealed a total of 25 planktonic foraminifera species. Four species dominated the assemblage, accounting for 84.4% of the total: *Globigerina bulloides* (37.4%), *Globorotalia inflata* (27.4%), *Tenuitella* spp. (11.2%) and *Globigerinoides ruber* (white morphotype) (7.8%). These were followed by *Globigerinita glutinata* (3%), *Turborotalita quinqueloba* (2.4%), *Globigerina falconensis* (1.5%), *Trilobatus sacculifer* (1.3%), *Globigerinoides ruber* (pink morphotype) (1.2%) and *Orbulina universa* (1.1%) (Fig. 4). Other taxa consistently present throughout the record, though in lower abundances (<1%), included *Neogloboquadrina incompta*, *Globorotalia truncatulinoides*, *Globigerinella* spp., *Globoturborotalita tenella*, *Globorotalia scitula*, *Beella digitata*, *Glovigerinita uvula* and *Globorotalia hirsuta*. Several additional species were detected sporadically, such as *Neogloboquadrina pachyderma*, *Neogloboquadrina dutertrei* and *Gallitellia vivans* (Lucas et al., 2026).

The sedimentary record from the Strait of Sicily revealed a total 22 planktonic foraminiferal species. Four species dominated the assemblage, accounting for 72.5% of the total: *Globigerina bulloides* (32.5%), *Globorotalia inflata* (20.1%), *Globigerinoides ruber* (white morphotype) (11.4%), *Tenuitella* spp. (8.5%). These were followed by *Globorotalia truncatulinoides* (6%), *Globigerinita glutinata* (6%), *Tenuitella quinqueloba* (5.3%), *Globigerinella* spp. (2.6%), *Orbulina universa* (2.4%), *Globigerinoides ruber* (pink morphotype) (1.3%) and *Globigerina falconensis* (1.2%) (Fig. 6). Other taxa consistently present throughout the record, though in lower abundances (<1%), included *Trilobatus sacculifer*, *Globoturborotalita tenella* and *Neogloboquadrina incompta*. Several additional species were detected sporadically, such as *Globigerinoides uvula*, *Neogloquadrina dutertrei*, *Berggrenia pumillo*, *Neogloquadrina pachyderma* and *Dentigloborotalia anfracta* (Lucas et al., 2026).

4.3. Long-term variability in calcifying plankton diversity and composition

The sedimentary record from the Alboran Sea indicates a rapid increase in coccolithophore diversity at the onset of the Industrial Era (~1800 CE), culminating in peak diversity values during the second half of the 20th century ($R^2 = 0.7$; *p*-value <0.0001) (Fig. 2). In contrast, planktonic foraminiferal diversity displays greater variability, initially decreasing at the onset of the Industrial Era and subsequently shifting to a declining trend in the latter half of the 20th century ($R^2 = 0.5$; p-value = 0.004) (Fig. 2). Large-scale atmospheric patterns, such as North Atlantic Oscillation (NAO) and Atlantic Multidecadal Oscillation (AMO), which are closely associated with sea surface temperature (SST) variability in the western Mediterranean and influence species biogeography (Incarbona et al., 2019; Lirer et al., 2014; Margaritelli et al., 2016, 2018; Pallacks et al., 2021), do not exhibit a direct effect on calcifying plankton diversity. Anthropogenic warming since the industrialization is likely the primary driver of the observed diversity changes (Fig. 2).

Cluster analysis revealed four distinct coccolithophores assemblage groups (Fig. 7). The first group spans from the base of the core to ~900 CE; the second extends from ~900 to ~1730 CE; the third covers the period from ~1730 to 1950 CE; and the fourth the second half of the 20th century up to 1995 CE, marked by a shift in dominant species. This transition includes a decline in *Gephyrocapsa huxleyi* and *Florisphaera profunda*, along with an increase in *Gephyrocapsa oceanica* (Figs. 3). High values of richness-based species exchange ratio (SERr) and net species change (Δrichness = $S_{imm} - S_{ext}$) are observed near the cluster

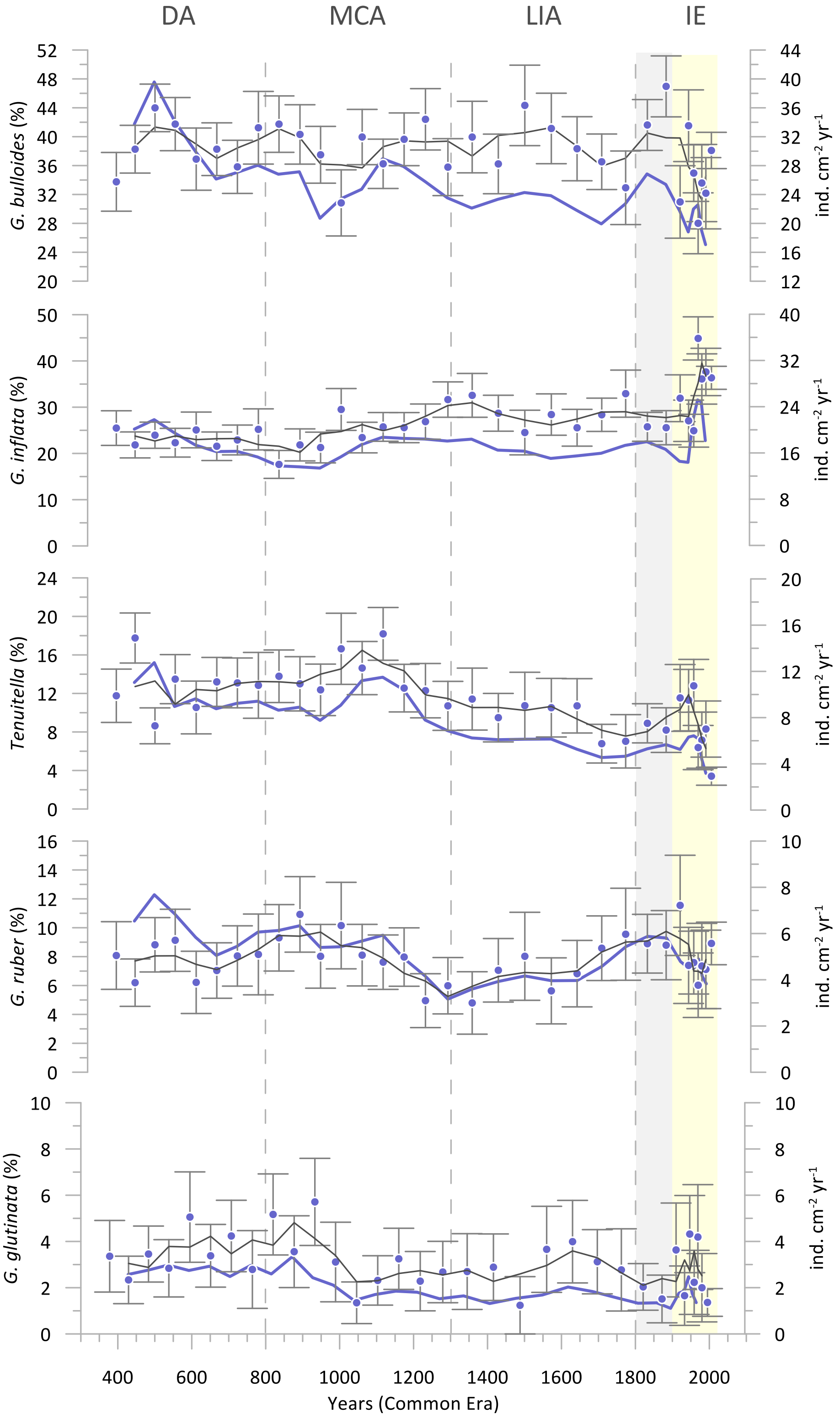

Fig. 4. Relative abundance of planktonic foraminiferal species and test accumulation rate in the Alboran Sea sedimentary record. The black line represents a 3-point moving average of the percentage values (twilight blue dot). Error bars indicate the 95% confidence intervals of the counts (Wald, 1939). The twilight blue line represents a 3-point moving average of standardized test accumulation rate based on a mean sedimentation rate upon Pb^{210} dating. Doted black line of total accumulation graph represent absolute values and twilight blue line represents a 3-point moving average of total accumulation. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

boundaries, indicating the proliferation of previously rare species (Table 1). However, these changes do not reflect a shift in species identity or overall community structure, as shown by relatively stable Simpson-based species exchange ratio (SERa) values.

Cluster analysis of planktonic foraminifera revealed four main assemblage groups (Fig. 7). The first group spans from the bottom of the

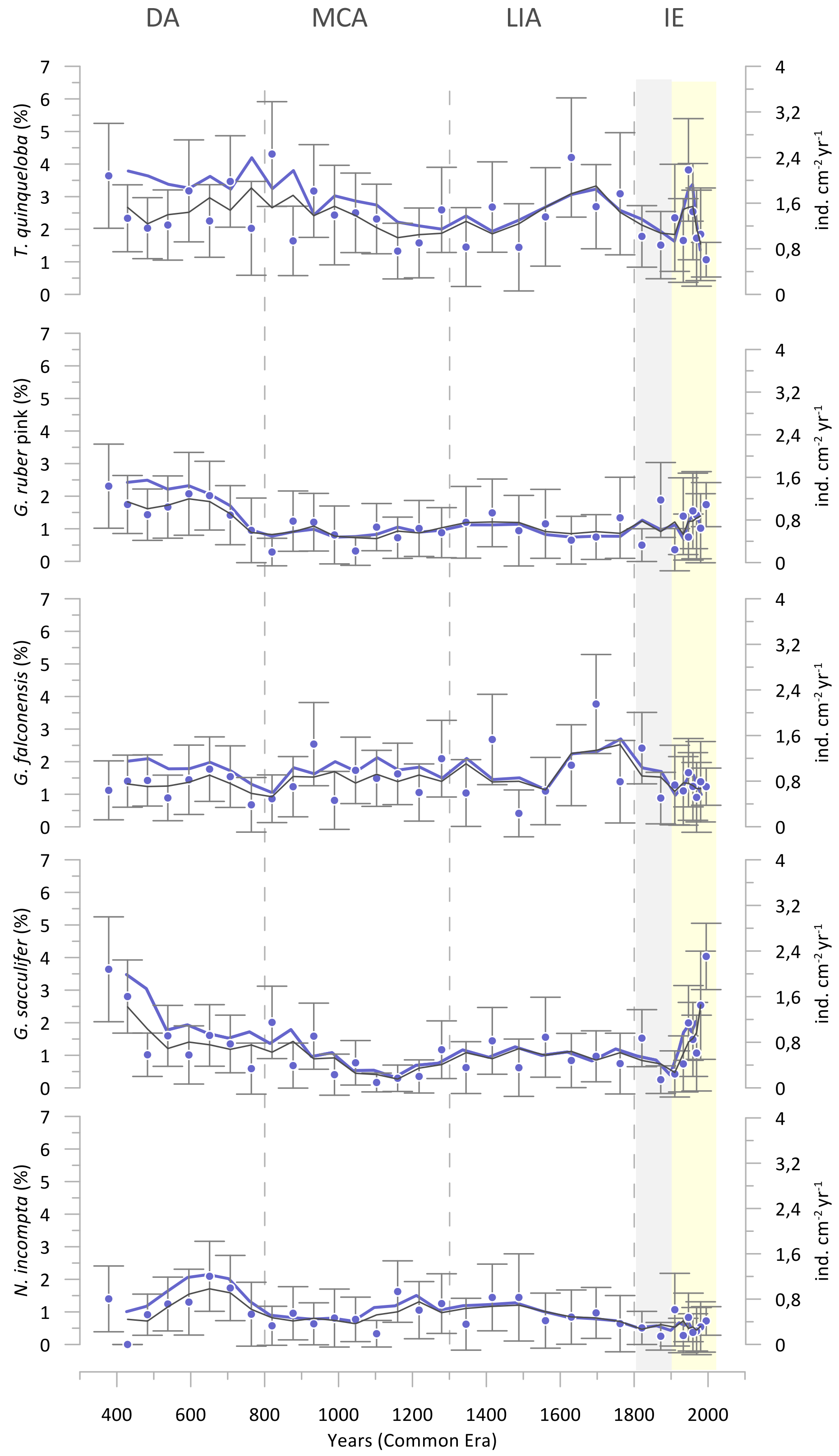

Fig. 4. (*continued*).

core to ~730 CE, preceding the onset of the Medieval Climate Anomaly (MCA), which corresponds to the second cluster (~730–1300 CE). The third cluster encompasses the Little Ice Age (LIA) and the first half of the Industrial Era up to ~1950, while the fourth group represents the second half of the 20th century up to 1995 CE. This most recent interval is characterized by a decline in *Globigerina bulloides* and *Tenuitella* spp., alongside an increase in *Globorotalia inflata* and *Globigerinoides ruber* (white morphotype). Additionally, it shows a shift from temperate-productivity and cold-transitional species towards more warm-oligotrophic taxa such as *Globigerinella* spp. and *Trilobatus sacculifer*

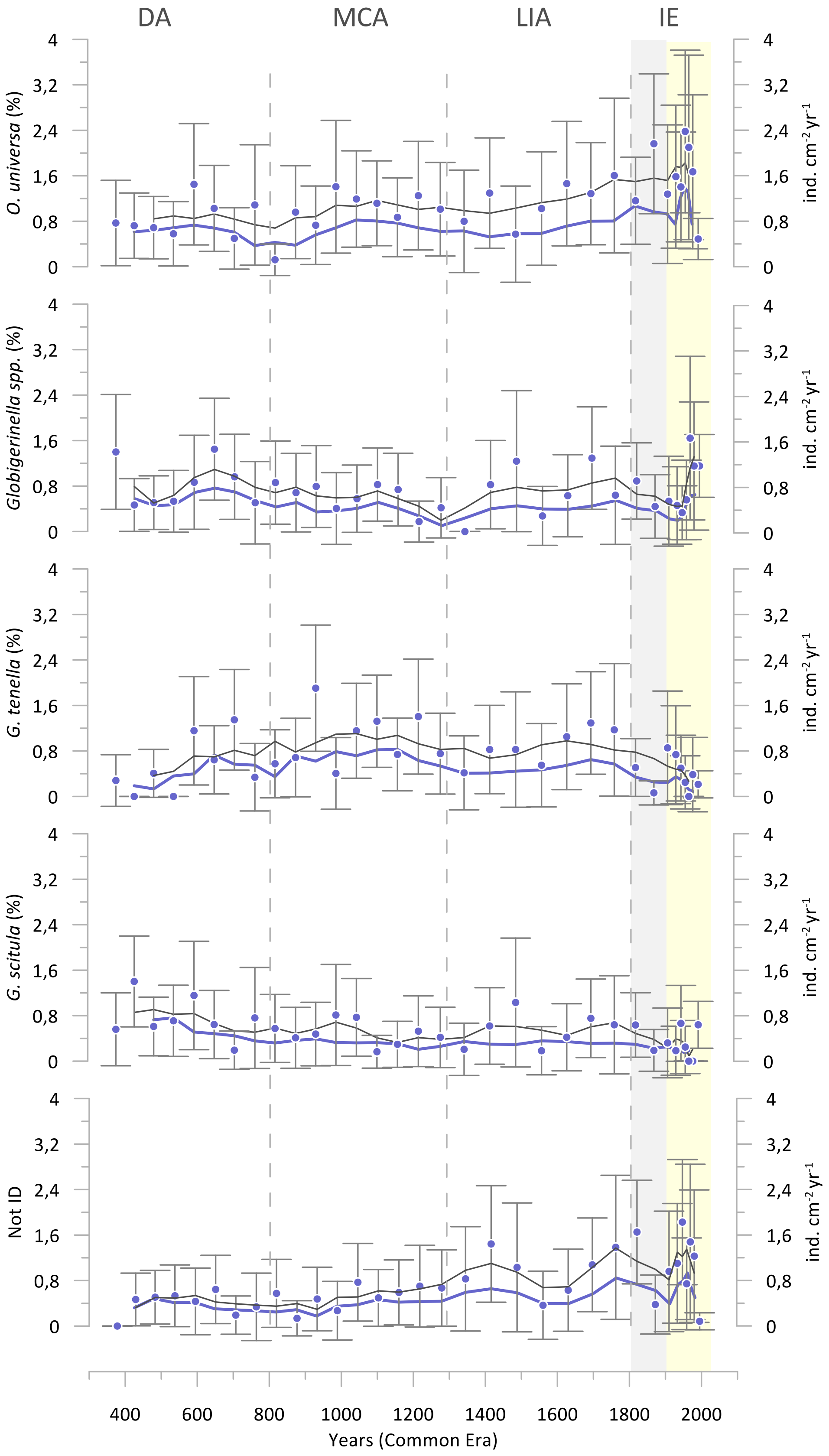

Fig. 4. (*continued*).

(Fig. 4). High turnover and net species change occur around the cluster boundaries (Table 1). Following the first cluster division (730 CE), net species change highly fluctuates. Similarly, after the second and the third divisions, high values of both net species change and SERr are observed, indicating substantial shifts in species composition without corresponding changes in community identity or structure (Table 1).

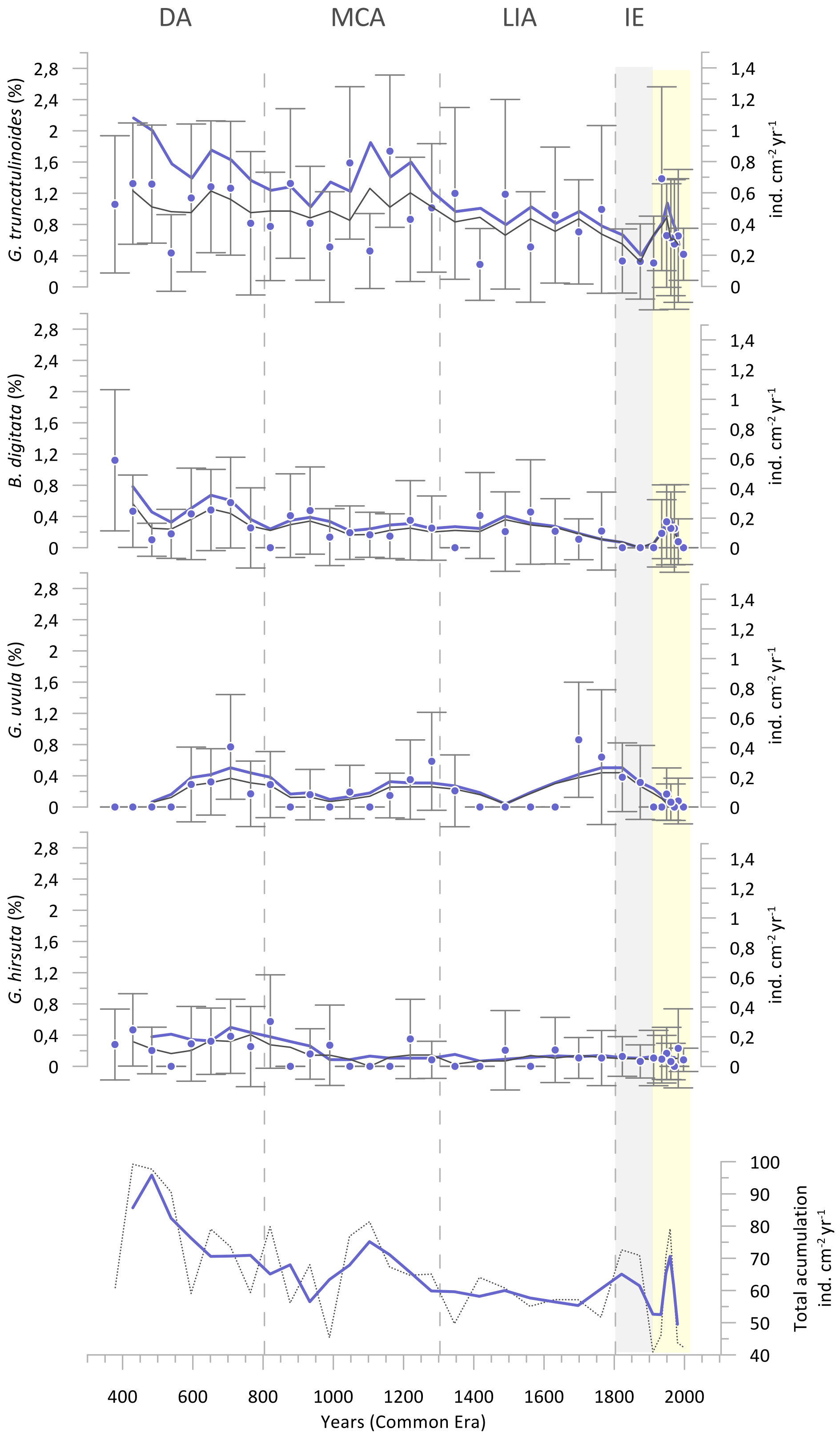

Fig. 4. (*continued*).

In the sedimentary record of the Strait of Sicily, reconstructions of coccolithophore and planktonic foraminifera diversity exhibit higher variability, likely reflecting the high temporal resolution of the sedimentary record (~4.3 years/cm) (Fig. 2). Coccolithophore diversity increases in general, interrupted by a decline during the second half of the Industrial Era ($R^2 = 0.3$; p-value = 0.02). Conversely, planktonic foraminiferal diversity does not exhibit a long-term decline; rather, it undergoes a temporary decrease between 1895 and 1950, followed by a recovery to earlier diversity levels ($R^2 = 0$; p-value = 1) (Fig. 2).

Cluster analysis of coccolithophores revealed two main groups. The

Table 1
Response of standing diversity metrics (richness and evenness) and species exchange ratio calculated based on presence-absence (SER_r) and Simpson's index (SER_a).

	Core depth (cm)	Years (CE)	Coccolithophores				Planktonic foraminifera			
			Δrichness	Δeveness	SERr	SERa	Δrichness	Δeveness	SERr	SERa
Alboran Sea	0–1	1995	0,03	0,02	0,17	0,01	-0,40	0,02	0,06	0,03
	1–2	1980	0,06	-0,03	0,17	0,01	-0,03	0,02	0,13	0,01
	2–3	1969	-0,07	-0,02	0,14	0,00	0,44	-0,07	0,31	0,04
	3–4	1959	0,14	-0,04	0,07	0,01	−1,29	0,09	0,05	0,25
	4–5	1947	0,15	−0,02	0,07	0,00	0,97	−0,07	0,00	0,02
	5–6	1933	-0,10	0,06	0,20	0,00	-0,64	0,03	0,00	0,07
	6–7	1910	0,19	-0,07	0,07	0,00	1,09	-0,07	0,00	0,09
	7–8	1872	0,02	0,05	0,25	0,00	-0,57	0,05	0,00	0,02
	8–9	1821	-0,09	-0,04	0,25	0,01	-0,39	0,02	0,05	0,06
	9–10	1762	-0,29	0,13	0,25	0,03	-0,07	0,04	0,11	0,02
	10–11	1697	0,39	-0,11	0,18	0,01	0,05	-0,01	0,00	0,02
	11–12	1630	-0,23	0,00	0,25	0,01	0,55	-0,06	0,06	0,01
	12–13	1560	0,08	0,03	0,27	0,00	0,12	0,01	0,11	0,02
	13–14	1488	0,10	-0,04	0,08	0,00	-0,70	0,06	0,00	0,05
	14–15	1416	-0,07	-0,01	0,13	0,00	0,79	-0,06	0,11	0,02
	15–16	1345	0,14	-0,01	0,13	0,01	-0,53	0,03	0,18	0,01
	16–17	1279	-0,05	0,01	0,07	0,00	0,38	-0,04	0,05	0,03
	17–18	1218	0,09	0,00	0,21	0,00	-0,36	0,03	0,05	0,01
	18–19	1160	-0,14	0,03	0,15	0,01	-0,15	0,01	0,11	0,02
	19–20	1103	-0,11	-0,02	0,14	0,01	0,10	0,00	0,06	0,02
	20–21	1046	0,26	-0,01	0,33	0,01	-0,41	0,00	0,05	0,06
	21–22	989	-0,05	-0,01	0,31	0,01	-0,18	0,05	0,00	0,07
	22–23	933	-0,10	0,02	0,21	0,01	0,54	-0,02	0,13	0,01
	23–24	877	0,12	-0,05	0,21	0,00	-0,06	-0,01	0,06	0,02
	24–25	820	-0,01	0,04	0,14	0,00	0,33	-0,05	0,12	0,03
	25–26	764	-0,06	-0,02	0,19	0,00	-0,92	0,08	0,00	0,02
	26–27	707	0,20	-0,06	0,06	0,00	0,22	0,00	0,05	0,01
	27–28	651	-0,12	0,06	0,23	0,00	0,00	0,00	0,00	0,01
	28–29	595	-0,20	0,02	0,00	0,02	0,61	-0,03	0,17	0,02
	29–30	538	0,03	0,00	0,15	0,01	0,23	-0,03	0,12	0,01
	30–31	483	0,22	-0,06	0,00	0,00	-0,58	0,06	0,12	0,06
	31–32	429	-0,07	0,04	0,15	0,00	-0,59	0,03	0,12	0,04
	32–33	378	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A
Strait of Sicily	0–1	2010	-0,24	0,07	0,13	0,01	-0,51	0,02	0,06	0,02
	1–2	2007	0,02	-0,03	0,00	0,00	-0,62	0,04	0,00	0,02
	2–3	2004	0,21	-0,04	0,14	0,01	-0,70	0,03	0,17	0,05
	3–4	2000	-0,11	0,04	0,41	0,01	1,05	-0,04	0,11	0,07
	4–5	1996	0,08	-0,02	0,06	0,00	-0,98	0,04	0,06	0,18
	5–6	1992	-0,07	0,02	0,40	0,01	0,83	-0,05	0,12	0,10
	6–7	1989	-0,01	-0,02	0,33	0,00	0,44	0,00	0,00	0,05
	7–8	1984	-0,08	0,02	0,06	0,00	0,56	-0,05	0,07	0,02
	8–9	1980	0,12	-0,01	0,13	0,00	−1,09	0,03	0,00	0,13
	9–10	1976	−0,24	0,01	0,27	0,01	−0,08	0,02	0,06	0,02
	10–11	1972	0,09	0,00	0,06	0,00	-1,30	0,06	0,00	0,16
	11–12	1968	−0,09	0,05	0,06	0,00	3,23	-0,16	0,06	0,15
	12–13	1965	0,06	-0,04	0,06	0,01	−2,09	0,11	0,12	0,22
	13–14	1961	−0,11	0,07	0,13	0,00	1,25	−0,07	0,19	0,04
	14–15	1957	0,31	−0,12	0,08	0,01	−1,95	0,08	0,13	0,17
	15–16	1952	−0,14	0,03	0,29	0,00	0,77	−0,02	0,00	0,13
	16–17	1950	0,04	−0,03	0,06	0,00	−0,15	−0,01	0,13	0,16
	17–18	1945	−0,05	0,03	0,06	0,00	0,23	0,01	0,07	0,04
	18–19	1941	0,13	−0,03	0,19	0,00	1,06	−0,08	0,00	0,02
	19–20	1937	−0,30	0,07	0,00	0,01	−0,48	0,03	0,07	0,03
	20–21	1933	0,35	−0,06	0,15	0,01	−1,97	0,09	0,06	0,30
	21–22	1928	−0,15	0,03	0,14	0,00	2,36	−0,13	0,12	0,11
	22–23	1924	0,18	−0,02	0,07	0,01	0,70	−0,05	0,23	0,03
	23–24	1919	−0,32	0,07	0,20	0,04	−1,78	0,12	0,23	0,15
	24–25	1915	0,17	−0,05	0,33	0,02	0,55	−0,02	0,07	0,05
	25–26	1909	−0,19	0,03	0,20	0,02	−0,07	0,00	0,07	0,08
	26–27	1905	0,35	−0,05	0,08	0,02	1,22	−0,07	0,08	0,19
	27–28	1900	−0,16	0,00	0,08	0,01	−0,13	0,02	0,14	0,01
	28–29	1895	−0,08	0,06	0,36	0,01	−1,55	0,08	0,06	0,20
	29–30	1891	−0,02	−0,03	0,46	0,01	−0,86	0,02	0,13	0,17
	30–31	1886	−0,08	−0,01	0,13	0,00	0,56	−0,02	0,19	0,05
	31–32	1881	0,31	−0,01	0,27	0,02	−2,13	0,08	0,00	0,17
	32–33	1878	−0,01	−0,02	0,14	0,00	0,91	−0,04	0,06	0,06
	33–34	1873	−0,10	0,03	0,14	0,00	1,92	−0,06	0,00	0,10
	34–35	1869	0,02	−0,02	0,24	0,00	−2,34	0,06	0,06	0,22
	35–36	1864	0,00	0,00	0,00	0,00	2,74	−0,09	0,00	0,13
	36–37	1860	0,01	−0,02	0,17	0,00	−2,91	0,12	0,18	0,31
	37–38	1854	−0,17	0,05	0,21	0,00	1,26	−0,06	0,29	0,04
	38–39	1849	0,21	−0,06	0,24	0,01	0,69	−0,03	0,08	0,12
	39–40	1844	−0,03	0,02	0,14	0,00	0,81	−0,03	0,08	0,10

(*continued on next page*)

Table 1 (*continued*)

Core depth (cm)	Years (CE)	Coccolithophores				Planktonic foraminifera			
		Δrichness	Δeveness	SERr	SERa	Δrichness	Δeveness	SERr	SERa
40–41	1840	0,21	−0,07	0,12	0,01	−1,09	0,05	0,14	0,11
41–42	1834	−0,16	0,03	0,22	0,01	0,66	−0,03	0,00	0,16
42–43	1830	−0,06	0,03	0,24	0,00	0,25	0,00	0,07	0,15
43–44	1825	0,14	−0,03	0,13	0,00	−0,68	0,03	0,13	0,23
44–45	1819	−0,15	0,05	0,06	0,00	0,57	−0,02	0,06	0,19
45–46	1815	0,10	−0,03	0,00	0,00	−0,12	−0,01	0,12	0,06
46–47	1810	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A

first group spans from 1810 up to 1974 CE and the second the most recent part up to 2010 (Fig. 8), coinciding with high turnover and net species change values (Table 1) The planktonic foraminiferal assemblage shows two main groups: the first spans from the base of the core to ~1920 CE, and the second from ~1920 to 2010 CE (Fig. 8). The uppermost cluster is characterized by an unexpected and sustained decline in *Globigerinoides ruber* (white morphotype). Each of the two main clusters can be further subdivided, with additional divisions around 1850 and 1960 CE. High species turnover values consistently follow these cluster boundaries, and in this case, changes in both community structure and species identity are observed close to the cluster boundaries (Table 1).

5. Discussion

5.1. Calcifying plankton diversity response in the Industrial Era

We found contrasting diversity trends in the two dominant calcifying plankton groups during the Industrial Era, driven in response to sea-surface changes linked to anthropogenically driven climate change. Coccolithophore diversity increases, while planktonic foraminiferal diversity shows an unstable decline. As SSTs rise and seasonal periods of water column stratification last longer, nutrient supply to surface waters declines, fostering increasingly oligotrophic conditions (Solidoro et al., 2022). Recent studies from the western and central Mediterranean Sea have similarly reported shifts in calcifying plankton communities in response to anthropogenic climate forcing (Ferraro et al., 2024; Pallacks et al., 2021). Contrasting diversity trends between coccolithophores and planktonic foraminifera over the last ~50 years (1933–1995 CE) in the Alboran Sea record (Fig. 1) are attributed to differences in water column niche distribution, life cycle, and population turnover rate (recombination-driven genetic diversity).

Coccolithophores, as photosynthetic organisms, are restricted to the photic zone. Their vertical distribution is shaped by light availability, nutrient concentrations, and water column stratification, with diversity being highest in the upper photic zone, moderate in the deep chlorophyll maximum (DCM) and negligible in the lower photic zone. Their haplo-diploid life cycle (alternating between a holococcolith-bearing and a heterococcolith-bearing phases) facilitates ecological resilience and promotes survival under fluctuating environmental conditions (Cros, 2001; Cros and Estrada, 2013; D'Amario et al., 2017; Oviedo et al., 2015; Šupraha et al., 2016). Unicellular coccolithophores reproduce rapidly via miotic division, leading to high turnover rates ranging from 0.6 to 10 days (Ziveri et al., 2025). Although loss factors such as grazing, viral infection, and sedimentation further shape population dynamics (Poulton et al., 2007). However, estimates of turnover rates primarily reflect asexual division and do not account for genetic renewal. On longer timescales, relatively stable environmental conditions, reduced seasonality amplitude, and warming provide the ecological opportunity for coccolithophore radiation, resulting in higher species diversity (Beaufort et al., 2022; Rigual Hernández et al., 2018).

Planktonic foraminifera are primary consumers, thus higher in the trophic chain compared to primary producer coccolithophores. They occupy a broader depth range with species-specific preferences shaped by temperature, food availability, oxygen concentration and hydrography. Most planktonic foraminiferal species inhabit the surface mixed layer or upper thermocline, where their photosymbionts benefit from light and food supply. But, some others dwell deeper, feeding on sinking organic matter and mesopelagic prey such as copepods (Schiebel and Hemleben, 2005). Their life cycle begins with the development of a diploid zygote into a juvenile that constructs calcareous test and sequentially adds chambers as it matures. Reproduction involves meiosis and the release of haploid gametes, which fuse in the water column to form a new diploid zygote, which is often coupled by ontogenetic vertical migration and synchronized with seasonal or lunar cycles (Jonkers et al., 2015; Schiebel and Hemleben, 2005). However, non-spinose planktonic species deviate from this pattern exhibiting a biphasic life cycle where an asexual phase produces offspring (Darling et al., 2023). As a result, planktonic foraminifera exhibit more variable and generally slower population turnover rates than coccolithophores (Schiebel and Hemleben, 2005). Growth rates are influenced by food availability, temperature, and carbonate chemistry, leading to turnover rates that range from monthly or bimonthly cycles to more extended seasonal cycles (Schiebel and Hemleben, 2017a; Ziveri et al., 2025).

Our results demonstrate that over the past century anthropogenic climate change can enhance coccolithophore diversity in the western Mediterranean Sea. The rapid warming of Mediterranean surface waters enhances water column stratification, leading to a decline in nutrient availability and productivity—conditions that tend to favour increased coccolithophore diversity and dominance over other phytoplankton groups (Vuković and Godrijan, 2025). Additionally, the increasing influence of subtropical and tropical influx waters from the Atlantic Ocean—regions characterized by high coccolithophore diversity (Brand, 1994; Winter et al., 1994)—contribute to the observed rise. Supporting this, previous modelling efforts have demonstrated a negative correlation between coccolithophore diversity and chlorophyll concentration (O'Brien et al., 2016). We hypothesize that rising SST and prolonged water column stratification have reshaped the community structure by suppressing dominant coccolithophore taxa that typically flourish in winter, nutrient-rich, mixed surface waters. And that community persistence is linked to their life cycle and rapid turnover rates, allowing to expand species that were previously rare and more adapted to oligotrophic conditions. In contrast, deeper-dwelling planktonic foraminifera, with inherently slower turnover rates appear more vulnerable to disrupted nutrient fluxes, limiting their capacity to maintain diversity under increasingly stratified conditions (Boscolo-Galazzo et al., 2021). Enhanced stratification further constrains vertical mixing, reducing nutrient availability across depth layers and thereby limiting the range of viable niches for planktonic foraminifera. In contrast, well-stratified but structured vertical water column can enhance diversity by promoting distinct ecological layers, allowing species to occupy specialized depth habitat (Yasuhara and Deutsch, 2023). However, under intensified stratification, this vertical niche partitioning is weakened, contributing to the observed declines in foraminiferal diversity.

Mediterranean calcifying plankton, including coccolithophores and planktonic foraminifera, are affected by ocean acidification (Béjard et al., 2023; Johnson et al., 2022; Pallacks et al., 2023; Ziveri et al., 2014). However, there is currently no evidence that plankton diversity has been significantly impacted by acidification (Ziveri et al., 2014) and ocean warming, decreasing nutrient and food supply appear to be more relevant drivers of recent diversity changes since ocean acidification remains above critical thresholds for major shifts (Hassoun et al., 2015; Mallo et al., 2017; Oviedo et al., 2015a, 2015b, 2017).

Two other potential factors lack direct evidence in this context. Changes in planktonic foraminifera abundances or distribution could stem from planktonic food web alterations, such as shift in predator-prey dynamics or resource competition with other zooplankton. Further research is needed to quantify these trophic influences alongside physico-chemical drivers.

5.2. First indication of tropicalization of the western Mediterranean plankton

This study provides the first evidence of incipient plankton tropicalization in the western Mediterranean. As previously suggested by Albano et al. (2024) for benthic molluscs, our results indicate that calcifying plankton communities in the Mediterranean Sea are undergoing directional biogeographic shifts, mediated through the Strait of Gibraltar. By examining species-specific trends in abundance and ecological preferences, we infer changes in the composition of coccolithophores and planktonic foraminiferal assemblages.

In the Alboran Sea, dominant coccolithophore species have undergone considerable shifts in abundance over the past two centuries, coinciding with the onset of the Industrial Era (Fig. 3). The observed decline in *Gephyrocapsa huxleyi* and *Florisphaera profunda* likely reflect an overarching reduction in productivity. *Gephyrocapsa huxleyi* responds to variations in upper-ocean nutrient availability, which is closely linked to seasonal water column mixing during autumn and winter (Cros, 2001). In contrast, *Florisphaera profunda*, which resides in the lower photic zone, serves as a proxy for a well-developed DCM, typically associated with summer stratification and nutrient-depleted conditions in the upper layers (Grelaud et al., 2012; Incarbona et al., 2008a; Malinverno et al., 2009). However, with warming emerging as the dominant driver superseding the previously prevailing influence of the NAO in the Industrial Era, the link between deep-water formation in the Gulf of Lion and surface productivity in the Alboran Sea have weakened (Pallacks et al., 2021). For this reason, we hypothesize that the reduced winter nutrient supply to the upper water column, followed by spring and summer seasons marked by higher metabolic and remineralization rates, have undermined the conditions necessary for the stability of *Florisphaera profunda* populations.

Gephyrocapsa huxleyi and *Gephyrocapsa oceanica* are among the most common coccolithophore species in the modern ocean. *Gephyrocapsa huxleyi* exhibits a broad ecological range, occurring from polar to equatorial regions and inhabiting both oligotrophic ocean gyres and nutrient-rich upwelling systems. It can be found from the sea surface down to depths of approximately 200 m (Boeckel and Baumann, 2008; Henderiks et al., 2012). *Gephyrocapsa oceanica* also has a wide distribution but shows stronger affinity for warmer waters (Flores et al., 1999), with very few specimens recorded at temperatures below 13 °C (Eynaud et al., 1999; Hagino et al., 2005; McIntyre and Bé, 1967). In the Atlantic Ocean, *Gephyrocapsa oceanica* reaches its highest abundances primarily within the Equatorial Divergence Zone (Ziveri et al., 2004).

Hydrographically, the mean Atlantic inflow into the Mediterranean has been relatively stable, with seasonal peaks occurring in September. However, recent observations have reported significant changes in the properties of these inflowing waters near the Strait of Gibraltar (Flecha et al., 2019; Soto-Navarro et al., 2012). Over the past few decades, a notable trend of increasing salinity, accompanied by a more moderate rise in temperature, has been reported (Soto-Navarro et al., 2012). This is attributed to the intrinsic warming and salinification of Atlantic surface waters rather than vertical mixing with the Mediterranean waters and linked to climate change and alterations in regional water circulation patterns. Under these evolving new oceanographic conditions, *Gephyrocapsa oceanica* may be expanding its range into the Mediterranean Sea, consistent with projections under the intermediate climate scenario (RCP 4.5), which forecasts a northward migration of marine species from West Africa by 2050 CE (Albano et al., 2024). However, as CO_2 concentrations continue to rise, *Gephyrocapsa oceanica* may be negatively affected in the future due to its higher sensitivity to elevated CO_2 compared to *Gephyrocapsa huxleyi* (Gafar and Schulz, 2018).

Shifts in planktonic foraminifera species abundance and test accumulation rates are also evident, especially during the second half of the Industrial Era (Fig. 4). As previously reported by Pallacks et al. (2021), the decline of *Globigerina bulloides* relative to the increase of *Globorotalia inflata* indicates a reduction in surface primary productivity, and is linked to unprecedented SST rise and prevalent positive phase of the AMO. In the Alboran Sea, *Globigerina bulloides* typically dominates during periods of high productivity in spring and autumn, whereas *Globorotalia inflata* reaches its highest abundances during winter and summer, periods marked by strong stratification, reduced upwelling and lower productivity (Bárcena et al., 2004; Kontakiotis et al., 2016). Secondary taxa such as *Tenuitella* spp., *Globigerinoides ruber* and *Globigerinita glutinata* also exhibit declining abundances and accumulation rates (Fig. 3). *Tenuitella* spp., includes *T. fleisheri*, *T. iota* and *T. parkerea* due to their morphological similarities and because their differentiation is only possible in mature tests under the incident light microscope (Schiebel and Hemleben, 2017). These species are rare and generally associated with intermediate to deep waters, though they remain poorly documented in the literature and particularly in modern contexts. *Globigerinoides ruber* is commonly associated with warm, stratified waters (Azibeiro et al., 2023; Pujol and Grazzini, 1995), yet multiple studies have also reported declining trends throughout the Industrial Era (Ferraro et al., 2024; Lirer et al., 2014; Margaritelli et al., 2016; Pallacks et al., 2021). *Globigerinita glutinata* is considered opportunistic, often peaking after enhanced phytoplankton production in the NE Atlantic (Schiebel and Hemleben, 2017), but in the Mediterranean Sea its major concentrations are recorded during winter, particularly in the northwest (Pujol and Grazzini, 1995).

Less abundant species also exhibit declining trends and accumulation rates, such as *Turborotalita quinqueloba*, *Globigerina falconensis*, *Neogloboquadrina incompta* and *Orbulina universa* (Fig. 3). *T. quinqueloba* dominates the small-sized cold-water assemblages (co-occurring with *Neogloboquadrina pachyderma*) (Schiebel and Hemleben, 2017) and in the Mediterranean Sea is considered rare, except for the Alboran Sea (Avnaim-Katav et al., 2020; Hernández-Almeida et al., 2011; Pujol and Grazzini, 1995; Rigual-Hernández et al., 2012). *Globigerina falconensis* is less opportunistic than its "sister taxon" *Globigerina bulloides*, which is adapted to higher food availability in surface waters. Although they share similar ecological preferences, *Globigerina falconensis* typically occurs in lower abundances (Kontakiotis et al., 2016). *Neogloboquadrina incompta* is found from subpolar to subtropical latitudes (Schiebel and Hemleben, 2017) and in the Mediterranean is limited to regions where surface water temperatures remain below 13 °C, explaining its absence in the Eastern Basin (Pujol and Grazzini, 1995). *Orbulina universa* is a cosmopolitan species, tolerating wide ranges of water salinity and temperature, and is abundant from tropical to temperate waters. The Mediterranean genotypes are mostly correlated with nutrient rich waters of the western basin (Schiebel and Hemleben, 2017).

In contrast, symbiont-bearing, warm-water species such as *Trilobatus sacculifer* and *Globigerinella* spp., *Globigerinoides ruber* (pink morphotype) display increasing trends (Fig. 3), suggesting that these taxa are resilient to ongoing oceanographic changes. *Trilobatus sacculifer* is one of the most frequent species in oligotrophic surface waters, reaching their maximum abundances after the strong summer stratification, and particularly abundant in the Eastern Mediterranean (Avnaim-Katav et al., 2020; Béjard, 2024; Pujol and Grazzini, 1995; Rigual-Hernández et al., 2012). Within *Globigerinella* spp., *Globigerinella calida* and *Globigerinella siphoniphera* differ in seasonality in the Mediterranean but were grouped in this study because in their pre-adult stages are virtually indistinguishable in incident light microscopy (Schiebel and Hemleben, 2017). *Globigerinella calida* is typically associated with mesotrophic waters, potentially reflecting emerging winter conditions, whereas *Globigerinella siphoniphera* prefers oligotrophic conditions, characteristic of late summer (Pujol and Grazzini, 1995). *Globigerinoides ruber* (pink morphotype), occurring only in the Atlantic and the Mediterranean Sea is considered a summer species (Béjard, 2024; Rigual-Hernández et al., 2012).

Although symbiont-hosting is generally considered an adaptation to nutrient-poor, sunlit surface waters, fundamental gaps remain in our understanding of symbiotic relationships in planktonic foraminifera. It is still unclear which symbionts are hosted by different species, which environmental or physiological factors regulate symbiont activity and symbiosis mode, the extent of energetic contribution symbionts provides to their host, and whether symbionts may also serve as prey (Edgar et al., 2025). Recent evidence suggests that biodiversity loss at low latitudes appears to be unrelated to the trophic preferences of planktonic foraminifera. Species with or without symbionts, whether spinose or non-spinose, tropical or subtropical, are all shifting towards higher latitudes tracking their optimal habitats (Chaabane et al., 2024). This suggests that the presence of symbionts does not necessarily confer resilience to planktonic foraminiferal species under modern

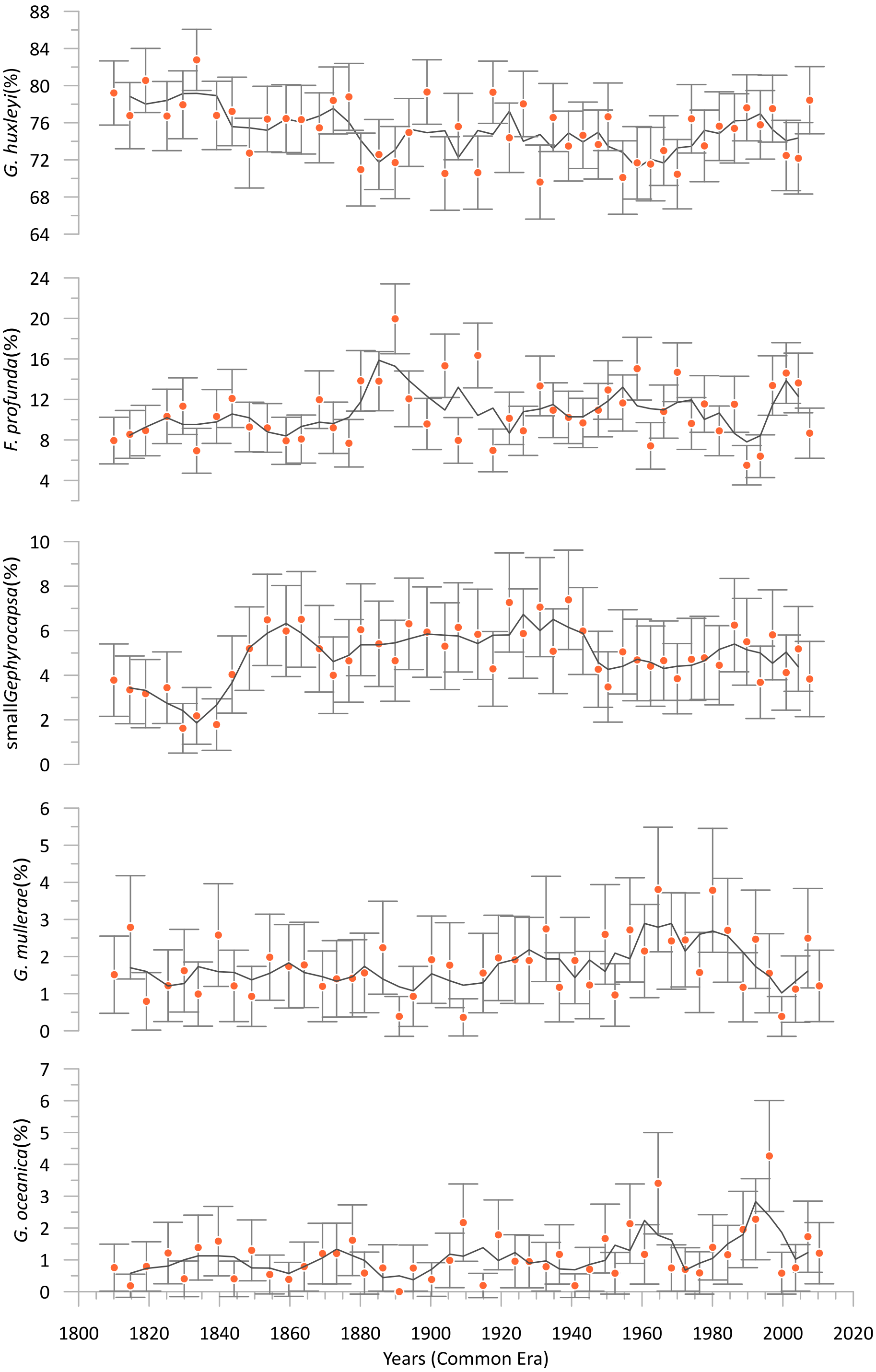

Fig. 5. Relative abundance of coccolithophore species in the Strait of Sicily sedimentary record. The black line represents as 3-point moving average of the percentage value (orange). Error bars indicate the 95% confidence interval of the counts (Wald, 1939).

anthropogenic environmental change.

In the Strait of Sicily, coccolithophore species trends during the Industrial Era appear relatively stable but highly variable, likely due to the high-temporal resolution of the sedimentary record (Fig. 5). However, pulses of *Gephyrocapsa oceanica*, particularly from the early 20th century onward, mirror patterns observed in the Alboran Sea. The composition of planktonic foraminiferal assemblages reflects the complex hydrographic configuration of the Strait of Sicily and the higher influence of

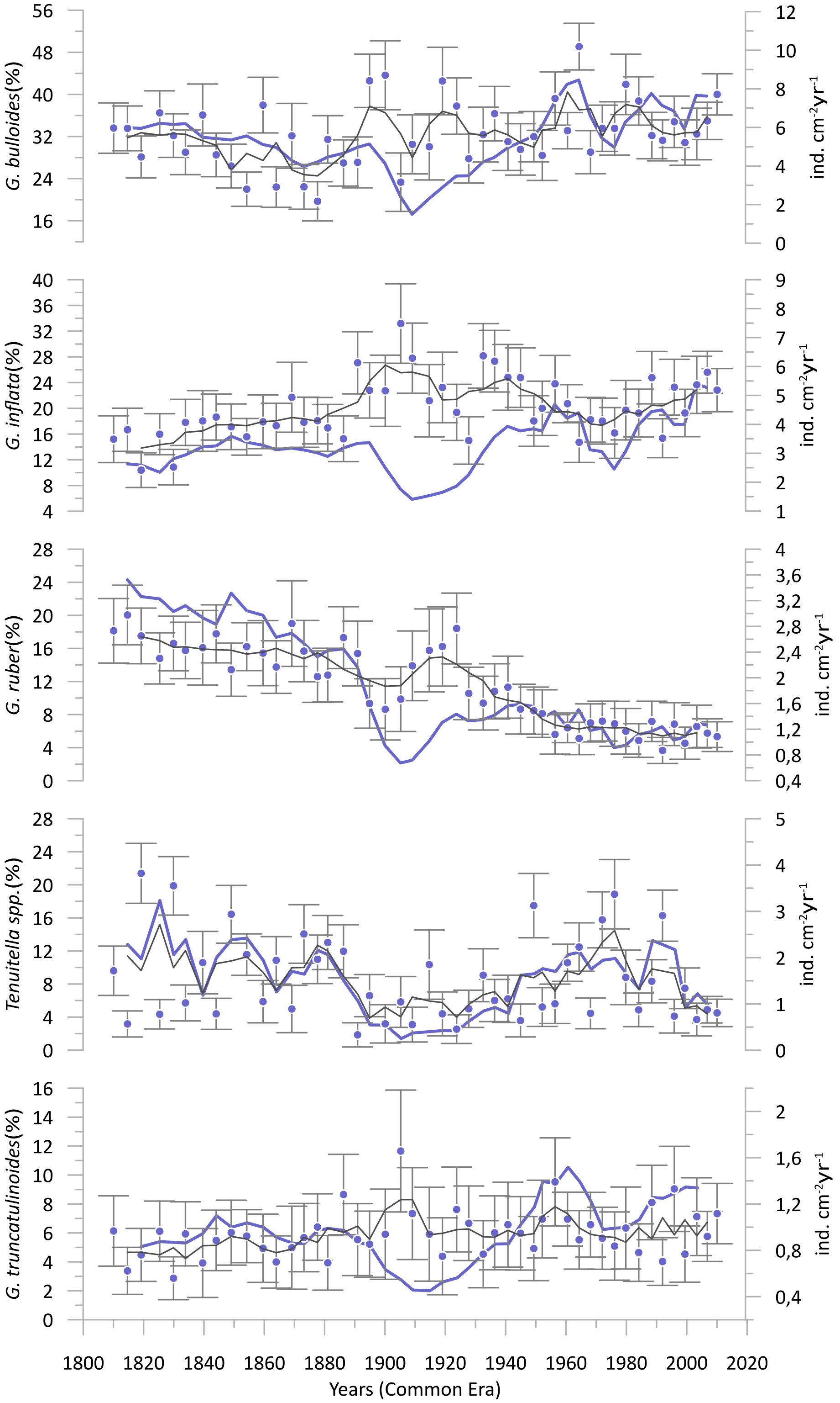

Fig. 6. Relative abundance of planktonic foraminiferal species and test accumulation rate in the Strait of Sicily sedimentary record. The black line represents a 3-point moving average of the percentage values (twilight blue dot). Error bars indicate the 95% confidence intervals of the counts (Wald, 1939). The twilight blue line represents a 3-point moving average of standardized test accumulation rate based on sedimentation rate upon Pb^{210} dating. Doted black line of total accumulation graph represent absolute values and twilight blue line represents a 3-point moving average of total accumulation. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

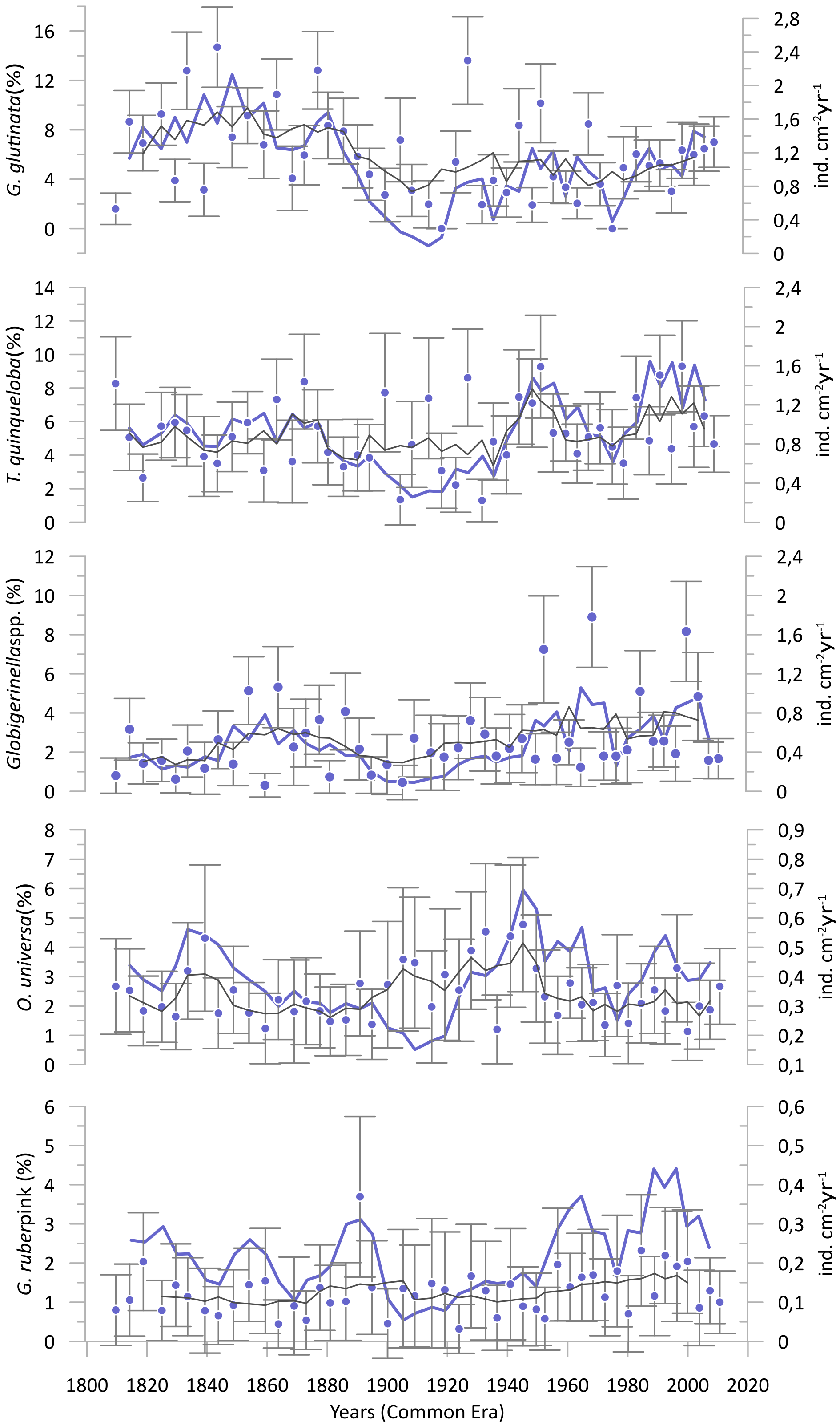

Fig. 6. (*continued*).

the western Mediterranean basin. Our findings align with the MARGO database (Béjard et al., 2024), though they diverge from assemblages reported in box cores from sites 342 and 407 (Incarbona et al., 2019) and sediment trap C01(Béjard et al., 2024), underscoring regional variability. The sharp decline in the relative abundance of *Globigerinoides ruber* (white morphotype) from 20% to 5% since 1930 may once again reflect an anthropogenic signal, linked to changes in nutrient cycling in coastal zones (Margaritelli et al., 2016). Meanwhile, *Globigerinella* spp., and to a lesser extent, *Trilobatus sacculifer,* show increasing trends consistent with observations from the Alboran Sea (Fig. 6).

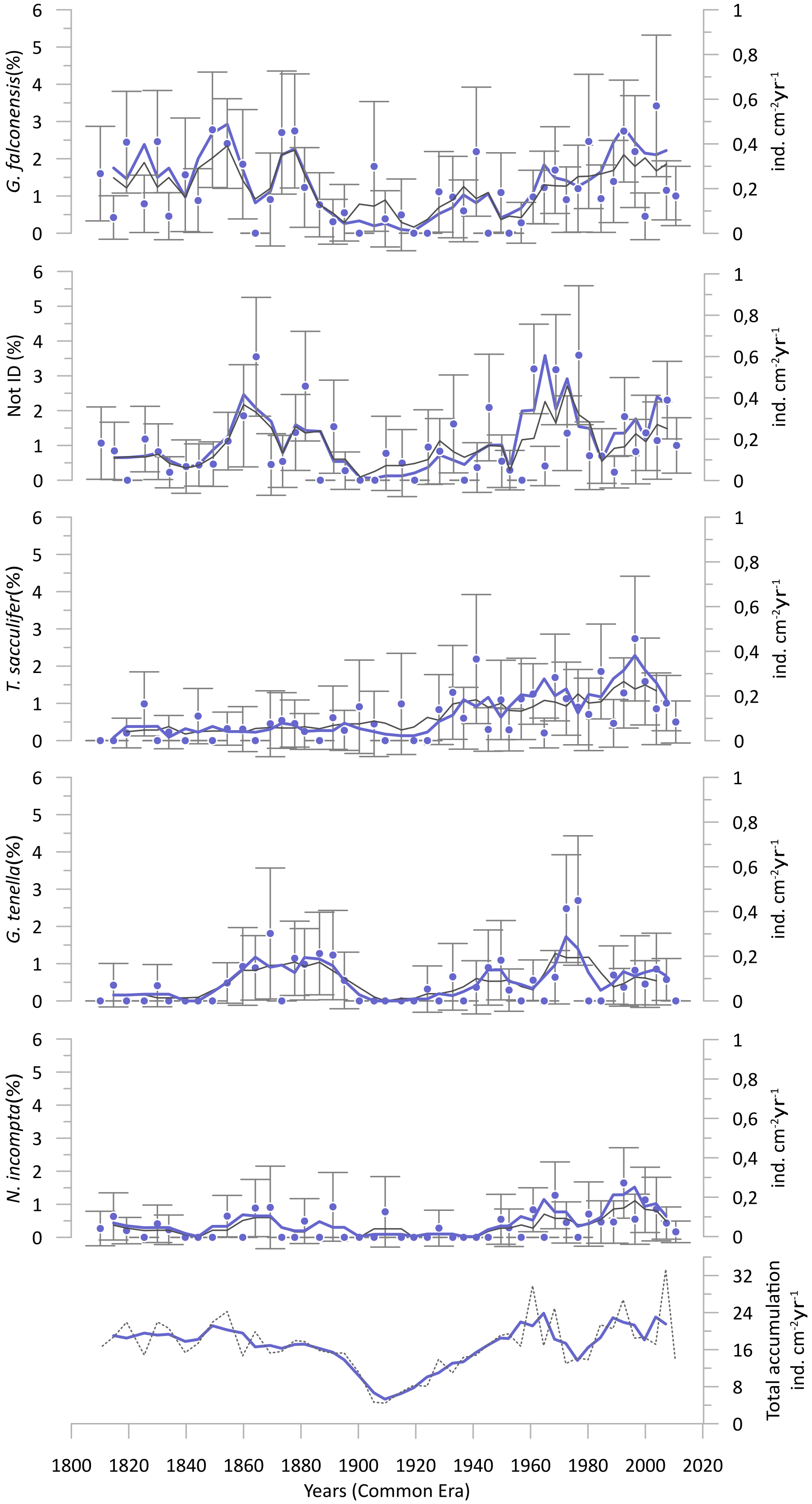

Fig. 6. (*continued*).

5.3. The future of the Mediterranean Sea and calcifying plankton

Model projections indicate that the Mediterranean Sea will continue to experience rising SST and increasingly frequent and intense marine heatwaves (Galli et al., 2017; Soto-Navarro et al., 2020). Enhanced stratification and reduced vertical mixing are anticipated to lower

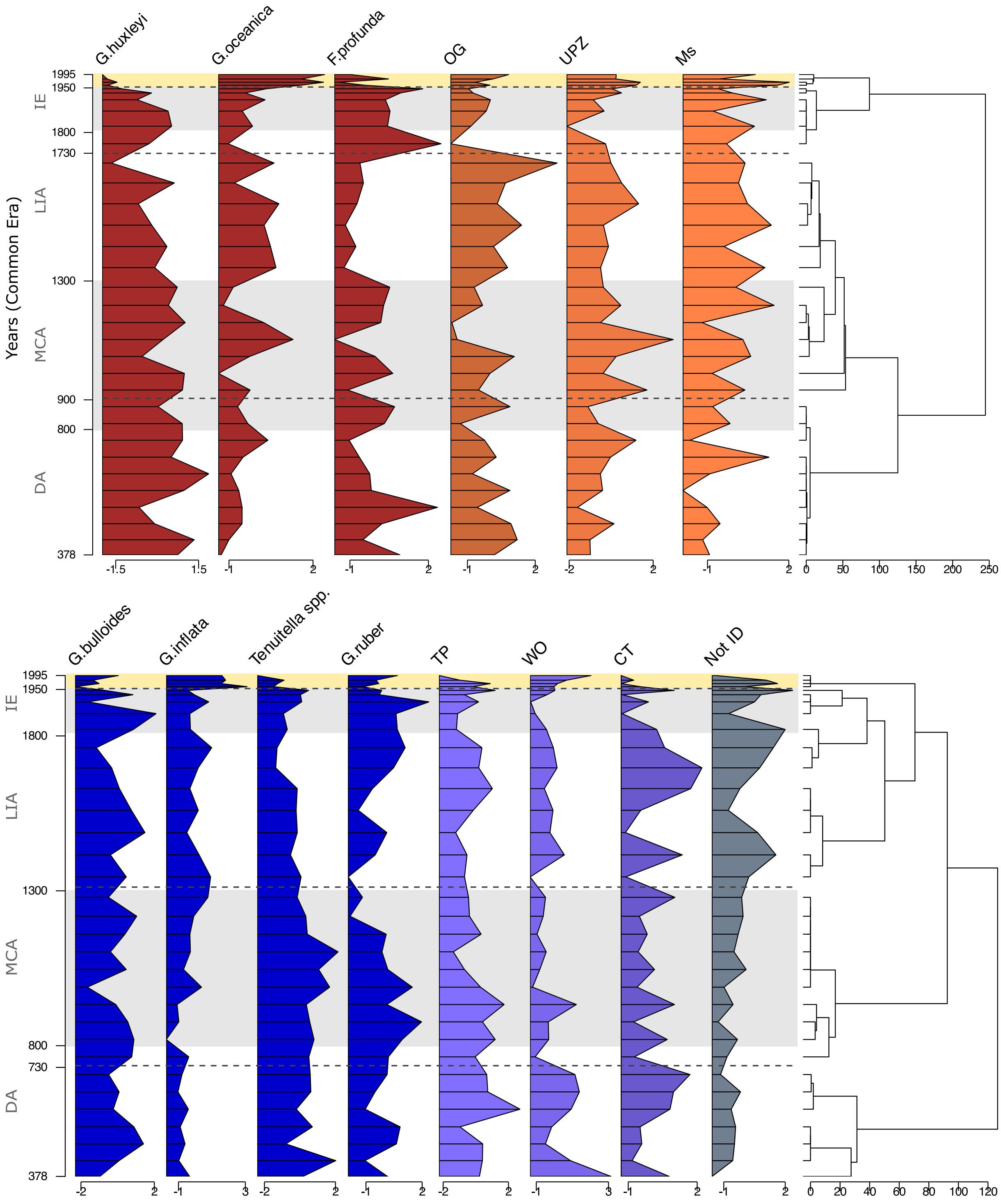

Fig. 7. Stratigraphic diagrams and cluster analysis of coccolithophores (above) and planktonic foraminifera (below) from the Alboran Sea. OG = Other *Gephyrocapsa* spp.; UPZ = Upper Photic Zone; Ms. = Miscellaneous. TP = temperate-productivity; WO = warm-oligotrophic; CT = cold-transitional, and Not ID = non-identified specimens.

surface nutrient concentrations, thereby constraining primary productivity and impairing biological carbon export (Solidoro et al., 2022), a key process in sequestering atmospheric CO_2 into the deep ocean (De La Rocha and Passow, 2014; Mouw et al., 2016). Carbonate production, export and sedimentation represents a major sink for alkalinity in the Mediterranean (Schneider et al., 2007; Tsiaras et al., 2024). However, even though alkalinity levels are higher than in most open ocean regions, a clear basin-wide acidification is predicted (Solidoro et al., 2022) and current acidification rates are similar to those observed in the global ocean (García-Ibáñez et al., 2024; Kapsenberg et al., 2017). Ocean acidification poses significant challenges to calcifying organisms (Kroeker et al., 2013; Leung et al., 2022), while projected declines in dissolved oxygen represents an additional stressor, particularly for planktonic foraminifera (Ziveri et al., 2025). Although the Alboran Sea and southwestern Mediterranean are partially buffered by oxygen exchanges at the Atlantic boundary, widespread deoxygenation is expected, primarily driven by surface warming and enhanced respiration rates (Bindoff et al., 2019; Reale et al., 2022). Synergistically, these

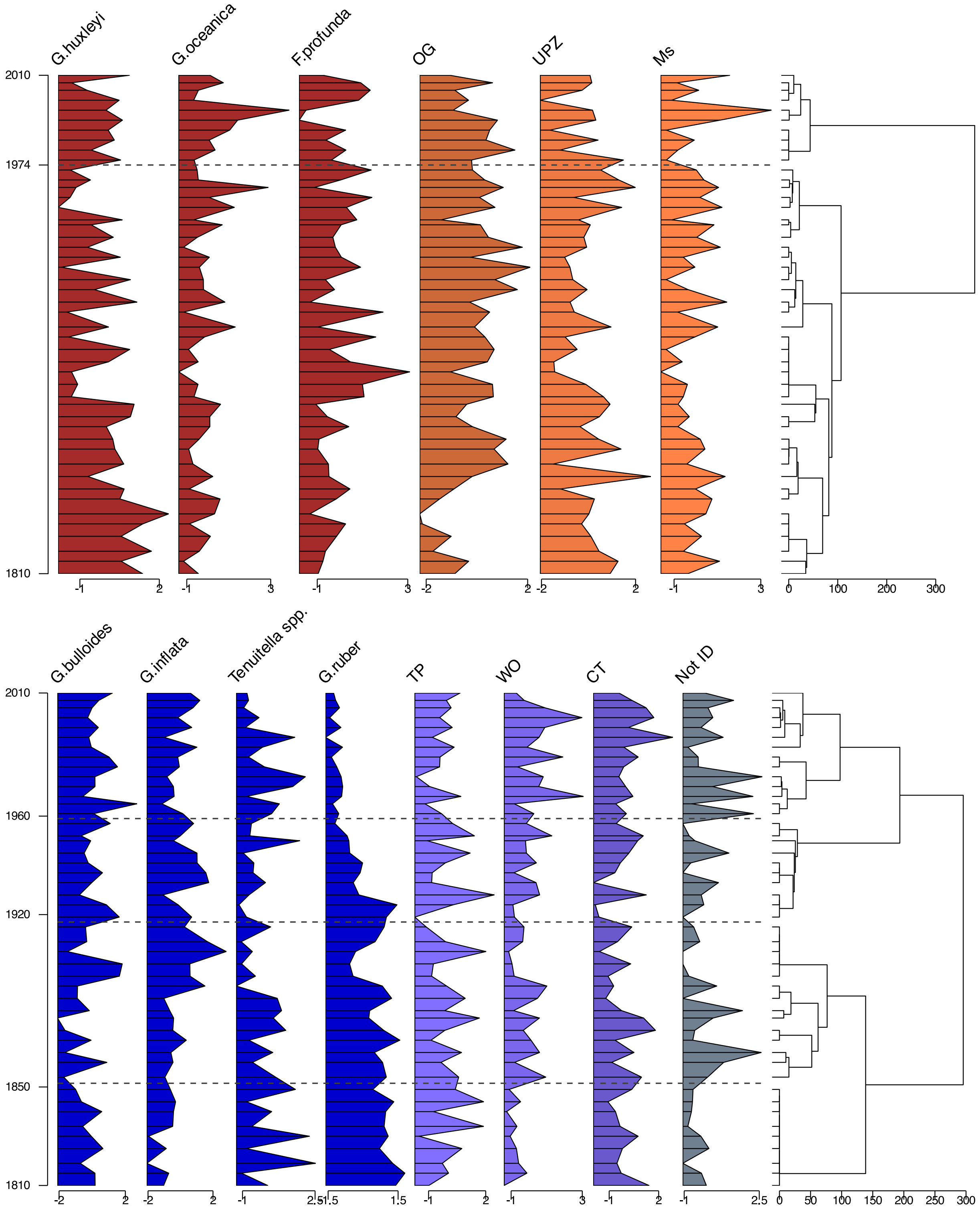

Fig. 8. Stratigraphic diagrams and cluster analysis of coccolithophores (above) and planktonic foraminifera (below) from the Strait of Sicily. OG = Other *Gephyrocapsa* spp.; UPZ = Upper Photic Zone; Ms. = Miscellaneous. TP = temperate-productivity; WO = warm-oligotrophic; CT = cold-transitional, and Not ID = non-identified specimens.

ongoing and projected environmental changes are likely to disrupt the structure and functioning of local marine ecosystems.

Globally, coccolithophore diversity is projected to increase due to warming and expanded stable conditions by the end of the century (O'Brien et al., 2016). However, as high-latitude oceans with lower natural buffering capacity absorb more CO_2, uncertainties remain regarding coccolithophore calcification physiology. Their intracellular calcification and passive proton removal mechanisms may limit their adaptability compared to foraminifera, which calcify extracellularly (Kottmeier et al., 2022; Nagai et al., 2018). Evidence from sediment traps and high-CO_2 environments generally shows negative effects on coccolith mass and diversity (Meier et al., 2014; Triantaphyllou et al., 2010; Ziveri et al., 2014), though occasional increases in diversity have been reported under certain conditions (Triantaphyllou et al., 2018).

Although coccolithophore diversity in the Mediterranean appears to be increasing, this trend is likely bounded by a physiological threshold. A mesocosm experiment from the Eastern Mediterranean showed that warming had a clearly negative impact on coccolithophore cell production and calcification, albeit with species-specific responses (D'Amario et al., 2020). Notably, many coccolithophore species show lower CO_2 optima for growth compared to picoeukaryotes or certain diatoms (Schulz et al., 2017). Biogeochemically, coccolithophores play a central role by contributing to carbonate ballast, enhancing the sinking of otherwise neutrally buoyant organic matter (Francois et al., 2002; Klaas and Archer, 2002; Ziveri et al., 2007). Conversely, picoeukaryotes, key players in the microbial loop, primarily facilitate carbon recycling within the euphotic zone, rather than contributing to deep carbon export. A decline in export production, combined with increased remineralization in the upper mixed layer, could thus create a feedback loop that diminishes the Mediterranean's capacity to absorb atmospheric CO_2.

Global foraminiferal assemblages and diversity are strongly influenced by temperature (Fenton et al., 2016; Morey et al., 2005; Rillo et al., 2022). Morey et al. (2005) found that secondary drivers, such as ocean fertility, also play a role, albeit indirectly. Fenton et al. (2016) suggested that diversity patterns result from multiple processes acting in concert, while Rillo et al. (2022) observed a consistent species turnover rate across SST gradients up to 25 °C, with temperature becoming less predictive in warmer waters. Recent work by Rufino et al. (2022) statistically demonstrated that temperature, food supply, and ocean currents are the primary environmental drivers of foraminiferal diversity, defining thresholds for species changes associated with these variables. Additionally, Richter et al. (2022) emphasized the role of large-scale ocean circulation in shaping foraminiferal communities. Aside from all this complexity in defining diversity patterns, the insights of Chaabane et al. (2024) into adaptation of foraminifera during the current Industrial Era suggest that migration will not be enough to ensure planktonic foraminifera survival. In the Mediterranean Sea, studies tend to focus on specific regions (Bárcena et al., 2004; Béjard et al., 2024; De Castro Coppa, 1980; Ferraro et al., 2024; Hernández-Almeida et al., 2011; Incarbona et al., 2019; Kontakiotis et al., 2021; Pallacks et al., 2021; Rigual-Hernández et al., 2012; van Raden et al., 2011; Zarkogiannis et al., 2020), while fewer address basin-wide or seasonal variability (e.g., Azibeiro et al., 2023; Cifelli, 1974; Mallo et al., 2017; Pujol and Grazzini, 1995). Nevertheless, research consistently identifies temperature and food availability as the primary factors influencing spatial and temporal distributions, with additional contributions from regional hydrographic conditions and atmospheric phenomena (Azibeiro et al., 2023; Ferraro et al., 2024). Thus, as Mediterranean SST rises and primary productivity decreases, foraminiferal assemblages will remain under stressful conditions. For symbiont-bearing foraminifera, increasing temperatures and decreasing nutrient availability are known to impact their distribution depending on their level of phagotrophy in alleviating nutrient limitation (Edwards, 2019). For symbiont-barren foraminifera, nutrients primarily impact their distributions of abundance and diversity indirectly by influencing the availability of essential food sources (Azibeiro et al., 2023; Schiebel et al., 1997; Tolderlund and Bé, 1971). However, as previously mentioned, current biogeographical shifts appear to be unrelated to the feeding strategies and trophic preferences (Chaabane et al., 2024).

Our analysis reveals that calcifying plankton diversity during the Industrial Era in the Mediterranean Sea exhibits group-specific responses to environmental change. Analysis of additional long-term sedimentary archives remains crucial to contextualize ongoing observations and disentangle anthropogenic signals from natural variability, thereby improving our understanding of pelagic biodiversity change. Furthermore, genetic analyses would provide valuable insights into the biogeographical shifts observed. Our results align with Hillebrand et al. (2023), who cautioned that biodiversity responses to human impacts are often decoupled from environmental changes due to complex interactions among species, population dynamics and system inertia. Such mechanisms may explain why anthropogenic effects are clearly detected by some analytical approaches (e.g., Béjard et al., 2023; Jonkers et al., 2019; Pallacks et al., 2021, 2023) but not reflected in major shifts in plankton community structure in our records. Nevertheless, the continued intensification of physico-chemical changes in the Mediterranean Sea is expected to accelerate structural reorganization within calcifying plankton communities, potentially reversing the current trends in coccolithophore diversity, as indicated by mesocosm experiments (D'Amario et al., 2020). A key challenge for future work will be to resolve these emerging trajectories across spatial and temporal scales, in order to better anticipate thresholds and tipping point in calcifying plankton diversity under continued climate change.

CRediT authorship contribution statement

Arturo Lucas: Visualization, Software, Methodology, Investigation, Formal analysis, Data curation, Conceptualization, Writing – original draft. **Sven Pallacks:** Methodology, Investigation, Conceptualization, Writing – review & editing. **Alessandro Incarbona:** Methodology, Investigation, Conceptualization, Writing – review & editing. **P. Graham Mortyn:** Validation, Supervision, Resources, Project administration, Funding acquisition, Conceptualization, Writing – review & editing. **Patrizia Ziveri:** Supervision, Resources, Project administration, Funding acquisition, Conceptualization, Writing – review & editing.

Funding sources

Financial support was provided by the Spanish Ministry of Science, Innovation and Universities through the research project BIOCAL (PID2020-113526RB-I00) and the European Union (ERDF, “A way of making Europe”). A.L. acknowledges a PID PhD contract funded by the Spanish State Research Agency (AEI). This work contributes to ICTA-UAB “María de Maeztu” Programme for Units of Excellence of the Spanish Ministry of Science, Innovation and Universities (CEX2024–001506-M funded by MICIU/AEI/10.13039/501100011033). It is also part of the Marine and Environmental Biogeosciences Research Group (Grant2021SGR00640) from the Generalitat de Catalunya. Additional support was provided by the BONITOS Project (International program DFG-AEI 2023—Grant PCI2025-163190) and PU-REEF-y Twinning project (GA 101158830).

Declaration of competing interest

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

Acknowledgments

Arturo Lucas acknowledges fruitful discussions with Richard. D. Norris for his expert guidance in the taxonomic identification of planktonic foraminifera, and Thibault de Garidel-Thoron for the opportunity to test the automated Microfossil Sorter (MiSo). We gratefully acknowledge Aleix Cortina-Guerra for providing the EA/WR atmospheric pattern reconstruction data, and the reviewers for their constructive comments, which helped improve the quality and clarity of the manuscript.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.gloplacha.2026.105314.

Data availability

Data of this article can be found online at PANGAEA (Felden et al., 2023).

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