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Key Points:

- Coccolith abundance and assemblage diversity increase during Marine Isotope Stage (MIS) 5e and Termination II (T-II)
- The heavily calcified species contribution to calcium carbonate production increased during T-II and MIS 5e
- Variations in coccolith abundances reflect changes in East Asian Monsoon circulation during MIS 6-3

Supporting Information:

Supporting Information may be found in the online version of this article.

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Tracking via Coccolith Assemblages the East Asian Monsoon and Carbonate Production in the South China Sea During Termination II and Marine Isotope Stage 5e

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Abstract Coccolith assemblages from the last 158 kyr, encompassing Marine Isotope Stage (MIS) 5e (130–116 kyr) and preceding deglaciation (Termination II; T-II), offer important insights about current and future climate changes. The South China Sea (SCS) represents a perfect area for reconstructing past East Asian Monsoon (EAM) dynamics thanks to its semi-enclosed location and high sensitivity to climate variability. Here, we investigated the coccolith assemblages at Site U1501 (northern SCS) deposited during MIS 6-3 (158–50 kyr). Coccolith abundances, community composition, and calcium carbonate (CaCO₃) production/accumulation were used to reconstruct past climate, EAM variations, and oceanographic conditions in SCS. Coccolith assemblages record a persistent oligotrophic regime with a shallow nutri-thermocline. Coccolith abundance variations align with changes in monsoon dynamics, showing that EAM strengthened during MIS 6, T-II, cold substages of MIS 5, and MIS 4/3 transition, and weakened during interglacials. The distinction adopted here for the first time between lightly and heavily calcified species revealed that the latter contributed significantly to CaCO₃ production during T-II and MIS 5e despite their general lower abundances. Comparison between MIS 5e and future predicted scenarios for the SCS shows a strong similarity in the evolution of EAM dynamics. The weakening of Winter EAM recorded for the past interglacial is also predicted for 2100. This suggests a possible similar coccolithophores' response to future climate conditions in the SCS, with an increase in their abundance and calcite production/accumulation. These findings confirm the potential of coccolithophores in climate reconstructions, opening interesting perspectives on their fate in future oceans.

Plain Language Summary Anthropogenic activities are driving a rapid increase in atmospheric carbon dioxide and global temperatures. Understanding how this may affect the oceans is essential for predicting future climate changes. An effective strategy is to examine past climate events that partially resemble current conditions. In this study, we focused on a past warming event—Marine Isotope Stage 5e (MIS 5e)—and its onset phase, Termination II (T-II), within an interval that spans both glacial (cold) and interglacial (warm) phases. We investigated how coccolithophores, calcifying marine microalgae, responded to this event in the South China Sea. By analyzing changes in coccolith abundance and assemblage diversity, we reconstructed their response to past warming and determined their contribution to calcium carbonate production. Our results show the need to consider both dominant and less abundant species, especially if heavily calcified, to accurately reconstruct carbonate production from coccoliths. Moreover, coccoliths fluctuated in response to changes in the East Asian Monsoon (EAM). These algae were less abundant during cooler periods (before and after MIS 5e and T-II) when EAM was stronger. In contrast, coccoliths were more numerous during warmer phases, when temperatures and water stratification increased, and the monsoon weakened (T-II and MIS 5e).

1. Introduction

The current rise in global mean temperatures and atmospheric carbon dioxide (pCO₂) largely due to anthropogenic activities, makes the need to predict oceans' response to climate change increasingly pressing. To do so, a deeper understanding of past climate events is fundamental to better comprehend the natural climate forcing's, and to develop more reliable future climate models. Global warming events, such as Pleistocene interglacials, can provide valuable insights into the evolution of current warming characterized by a trend of rapidly increasing

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and higher temperatures compared to pre-industrial period (+1.5°C; e.g., Tzedakis et al., 2009; Yin & Berger, 2012). Among them, the Marine Isotope Stage (MIS) 5, and particularly its substage 5e (~130–116 kyr; Lisiecki & Raymo, 2005), has long been considered a potential analog of current warming due to some similarities. In fact, recognized as one of the warmest interglacial intervals (Yin & Berger, 2012), MIS 5e recorded global mean temperatures 1°–2°C higher than current warming (Turney et al., 2020), global mean sea level ~6–9 m above the present (e.g., Kopp et al., 2009; Thompson et al., 2011) and reduced ice sheets (e.g., CAPE, 2006; Turney & Jones, 2010). However some key differences are known regarding astronomical configuration and atmospheric CO₂ content (e.g., Loutre & Berger, 2003; Yin & Berger, 2012; Yin & Berger, 2015). During MIS 5e, atmospheric CO₂ fluctuated between 260 and 285 parts per million (ppm; Colleoni et al., 2014); whereas in recent decades atmospheric CO₂ surpassed 400 ppm (Lan et al., 2023). While the leading cause of current warming is anthropogenic CO₂, the primary driving force for MIS 5e was high summer insolation in the Northern Hemisphere (Yin & Berger, 2015). Despite these caveats in considering MIS 5e as an analog for current and future warming, the comparison still offers important information into climate feedback, providing insights into the natural progression of the present-day interglacial. As such, the comparison could enhance our comprehension into the progression of the current period, MIS 1, what might be expected in the absence of anthropogenic driven climate change, and the extent of anthropogenic influence on the climate (Yin & Berger, 2015).

Coccolithophores are unicellular marine microalgae producing a calcite shell (coccosphere), consisting of a variable number of plates, called coccoliths (e.g., Young et al., 1997). Coccolithophores are particularly sensitive to environmental and climate variations, and their abundance and geographical distribution in the oceans are strictly dependent on many environmental factors (e.g., temperature, nutrient availability, light intensity, salinity, water mixing), directly modulated by climate (e.g., Balch, 2004; Balch et al., 2016; Giraudeau et al., 1993; Winter et al., 1994). Their responses to environmental and climate variations are quite rapid (e.g., Baumann et al., 2005; Winter et al., 1994), making their fossil remains in the deep-sea sediments, a useful tool to reconstruct past climate changes and oceanographic conditions (e.g., Monteiro et al., 2016; Winter et al., 1994), as proved by many works in the field (e.g., (Bolton & Stoll, 2024; Bordiga et al., 2014; Brand, 1994; Winter et al., 1994; Young, 1994). Coccolithophores play a significant role in the global carbon cycle through photosynthesis (organic carbon pump; CO₂ uptake) and calcification (carbonate pump; CO₂ release) and by exporting organic carbon and calcium carbonate (CaCO₃) into the deep-sea sediments (C stock; e.g., Balch, 2018; Hay, 2004; S. Li et al., 2024; Monteiro et al., 2016). Changes in their abundance, assemblage composition and, calcite production can directly influence their net contribution to carbon fluxes (e.g., Baumann et al., 2004; Hay, 2004; Robertson et al., 1994; Zeebe et al., 2001). Therefore, studying their fossil remains provides valuable insights also into coccolithophores contribution to the ocean carbon cycle over time.

Here, we analyze the coccolith assemblages collected from the International Ocean Discovery Program (IODP) Site U1501 in the South China Sea (SCS) spanning from ~158 to 50 kyr (MIS 6–MIS 3). Site U1501 represents a valuable opportunity to investigate the climatic and oceanographic evolution of SCS region which is a crucial paleoceanographic archive for the low latitude Pacific, due to its high sedimentation rates and exceptional carbonate preservation thanks to the strong bottom-water ventilation (e.g., Wang, 1999; Wang et al., 2014; Wang and Li, 2009). The SCS, due to its semi-enclosed location, is highly sensitive to climate changes, providing key information on primary productivity, oceanographic current dynamics, water column mixing and riverine input mechanisms (e.g., Wang, 1999; Wang et al., 1995, 2014). Moreover, since the monsoonal circulation strongly influences the area, numerous studies have been conducted to understand the past (e.g., Su et al., 2013 and references therein) and future (Dao & Yu, 2022; IPCC, 2023; Samanta et al., 2021; W. Sun et al., 2024) dynamics of East Asian Monsoons (EAM) in this densely populated area.

Our study on coccolithophore responses to the deglaciation (MIS 6/5e transition) and the subsequent onset of MIS 5e in the SCS in terms of assemblage composition and production/accumulation of CaCO₃ highlights the interaction between monsoon activity and water column structure, deepening our understanding of the effects of this climatic phase on primary production (PP) and calcification. We propose a simplified model of surface water structure and monsoon cell intensity for the studied interval in the SCS. Paleoclimatic data are then compared with already published climate projections for 2100 to shed light on the future of coccolithophores in the studied area.

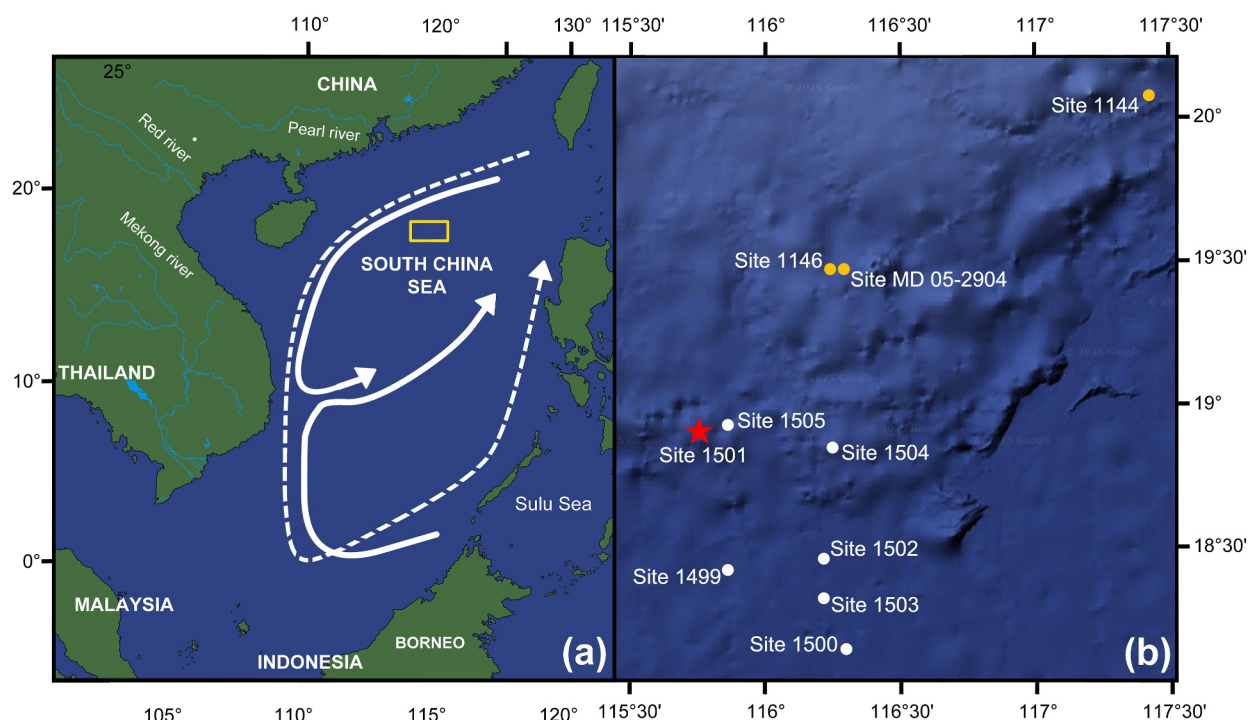


Figure 1. (a) Map of South China Sea (SCS). Yellow square: studied area; arrow (dashed line) winter, basin-wide cyclonic gyre; arrow (solid line) summer cyclonic (north) and anticyclonic (south) gyres in the south (modified from: SCS location map by NordNordWest, Wikimedia Commons, CC BY-SA 3.0 DE, base map: Nzeemin, own work, 2012). (b) Location of the sites drilled during International Ocean Discovery Program Expedition 367/368 (white dots), Site U1501 (red star) and other sites from other expeditions located in the Northern SCS (yellow dots; modified from Google Earth; Base map: ©2025 Google. Data: SIO, NOAA, U.S. Navy, NGA, GEBCO; Landsat/Copernicus; LDEO-Columbia, NSF, NOAA).

2. Materials and Methods

2.1. Oceanographic Setting

The northern margin of the SCS has been the subject of several oceanographic cruises including IODP Expedition 367/368, to which Site U1501—the site studied here—belongs (Figures 1a and 1b). The SCS is the largest marginal sea in the western Pacific (Wang & Li, 2009), with an average water depth above 2,000 m (Wang et al., 1995). This basin is bordered to the north and west by the South China coastline and the Indochina Peninsula, while to the east, a discontinuous chain of mountainous islands from Luzon down to Borneo which ensures a connection with the Pacific Ocean (Qu et al., 2000; Wang & Li, 2009). On the continental coastline there is a predominantly mountainous landscape and the extensive deltaic system of Pearl River, Mekong River, and Red River (Figure 1a). The general morphology of the SCS, in combination with atmospheric circulation, in particular monsoon activity, are the primary factors contributing to the basin's defining oceanographic characteristics (Table S1 in Supporting Information S1; Wang & Li, 2009). The EAM acts with different timing and intensity in northern and southern SCS, leading to different oceanographic conditions (e.g., different sea surface temperatures (SSTs), salinity, nutrient availability). The EAM exhibits varying circulation patterns, with a cyclonic gyre developing during winter in both the northern and southern SCS (see Table S1 in Supporting Information S1 for references). In summer, a weakened cyclonic gyre (north of 12°N) and a strong anticyclonic gyre dominate the northern and southern SCS, respectively. The winter component (EAWM) is more intense in the northern SCS, whereas the summer component (EASM) exerts a stronger influence on the southern area. Salinity is strongly related to seasonal variations, connected to river inputs, rainfall variability and EAM activity (Wang & Li, 2009). Although, in the area of Site U1501, salinity fluctuates between 32.8 and 34.2‰ through the year, the thermocline and the mixed layer depth vary seasonally, with a deeper mixed layer and a shallower thermocline in autumn and winter (see Table S1 in Supporting Information S1 for details and references).

SCS is optimal for paleoceanographic studies also for its high sedimentation rates and good carbonate preservation attributed to a generally deeper Carbonate Compensation Depth (CCD; ca. 3,500 m) compared to other nearby basins (Z. Sun et al., 2018; Wang & Li, 2009).

2.2. Sediment Core at IODP Site U1501

Site U1501 (18°53.0919'N, 115°45.9485'E, Hole C), drilled at 2845.8-meter (m) depth well above the modern CCD, with a 96.29% core recovery, spans from Pleistocene to late Eocene (Z. Sun et al., 2018). The interval studied here encompasses Sections 1H-4W to 2H-3W, that is, from 5 to 13.68-meter composite depth (mcd), with an average sampling interval of 10 cm, for a total of 89 samples studied in their coccolith content. The studied sequence is dominated by clay-rich nannofossil ooze and terrigenous minerals (i.e., quartz, plagioclase, authigenic halite, and clay minerals such as illite, kaolinite, and/or chlorite) and the CaCO₃ content represents on average 10%–23% (Z. Sun et al., 2018). Fossil remains of coccolithophores, and foraminifera are abundant and well preserved (Z. Sun et al., 2018).

2.3. Age Model of Site U1501

Oxygen stable isotopes at Site U1501 were obtained analyzing the tests of benthic foraminifera *Cibicidoides* spp., dominantly *Cibicidoides wuellerstorfi* (shell size: 250–500 μm; 2–6 specimens), with an average sampling resolution of 6 cm between 0.07 and 26.75 mcd (412 samples). The analysis was performed at the State Key Laboratory of Marine Geology, Tongji University, following the standard procedure described in Cheng et al. (2005). δ¹⁸O was measured using a Finnigan Modern Analog Technique 253 mass spectrometer equipped with an automatic carbonate preparation device (Kiel III). The results were converted to the international Vienna Pee Dee Belemnite (VPDB) scale using the international reference standards of the National Bureau of Standards 18 and 19. The standard deviation for δ¹⁸O is ±0.07‰.

To calibrate the age model, we compared the obtained isotope curve to the standard LR04 references stack (Lisiecki & Raymo, 2005) using the AnalySeries program (Paillard et al., 1996). This software allows calibrating the ages of a sequence through a linear interpolation between depth-age control points, in our case study are the site δ¹⁸O data and the data from LR04 (Lisiecki & Raymo, 2005; Figure 2). We identified 10 key points along the studied sequences, with the older samples dated 175 ka and the youngest 3.1 ka (Table S2 in Supporting Information S1). Linear sedimentation rate was derived directly from the age model. Partial sedimentation rate is calculated as the change in depth divided by the change in time between known key points (see Table S2 in Supporting Information S1).

The average sedimentation rate along the studied sequence is ~8.75 cm ka⁻¹. For the analyzed microfossil assemblage, the sequence is then dated ~159–50 ka, with an average sampling resolution of 1.2 kyr.

2.4. Sediment Carbonate Content

The bulk CaCO₃ content was measured in 40 samples along the studied interval with a sampling resolution of 20 cm (2.5 kyr), following the technique of Müller and Gastner (1971) and using a Dietrich Friling 48-D0570 gasometer. This technique measures the volume of gas produced during the reaction of CaCO₃ with hydrochloric acid in a closed vessel using a graduated burette. By comparing the standard data derived from pure CaCO₃ and the data from ca. 0.50 g of dry powdered sediment, it is possible to calculate the carbonate mass, expressed in percentage weight (wt%), following the formula (Equation 1):

$$\text{CaCO}_3(\text{bulk; wt\%}) = \left(\frac{\text{gasometer value sediment}}{\text{sample gasometer value standard sample}} \right) \times 100 \quad (1)$$

2.5. Coccolith Assemblage Analysis

All samples were prepared using the drop technique (Bordiga et al., 2015), that ensures an even particle distribution and allows calculation of coccolith absolute abundances (N. of coccoliths g⁻¹). The amount of material analyzed for coccolith analyses averaged 5 mg per sample. Samples were analyzed under a polarizing light microscope (Leica DMRBE) at 1000X magnification. More than 500 specimens were counted in each sample on a minimum of 10 fields of view. Coccoliths were identified at species level, or if not possible, at genus level

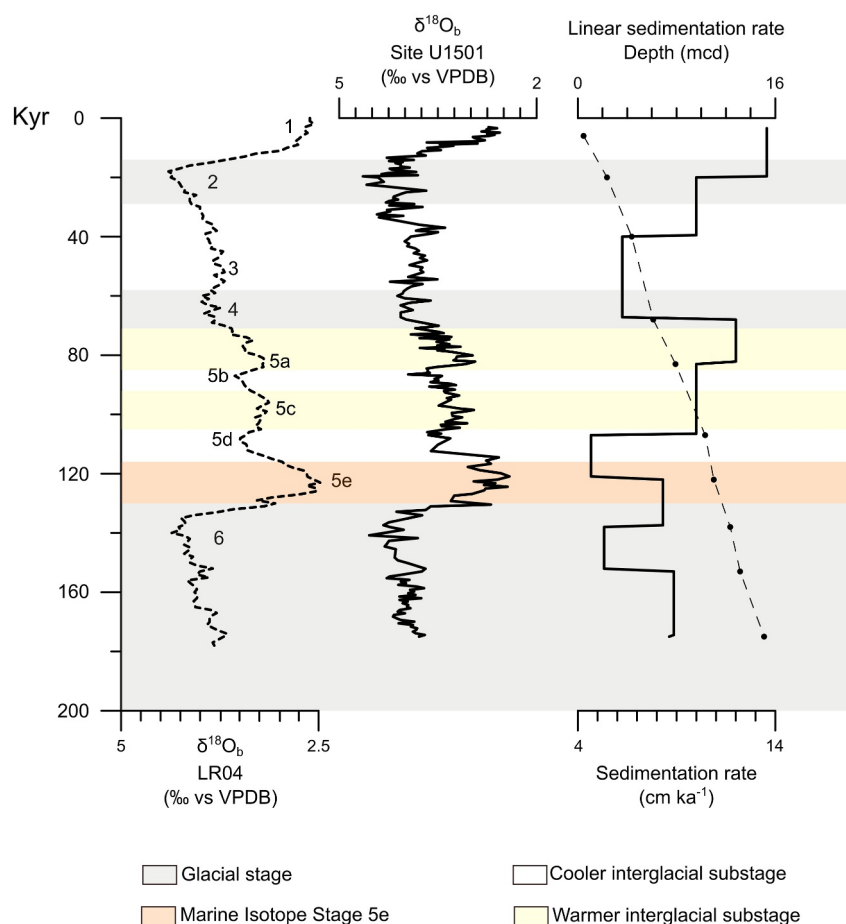


Figure 2. Age model for Site U1501. Benthic foraminifera $\delta^{18}\text{O}_b$ tuned to LR04 of Lisiecki and Raymo (2005). Linear and partial sedimentation rates and key points (black dots) are also reported. Numbers on LR04 indicate Marine Isotope Stage and substages.

following Young et al. (2022) and Bendif et al. (2019) for *Gephyrocapsa huxleyi* (formerly *Emiliania huxleyi*). We noted a few reworked species (e.g., *Discoaster* spp., *G. oceanica* >5.5 μm , average $\sim 0.12\%$), which were excluded from the final count. Coccoliths of *gephyrocapsids* were divided into two size-based morphogroups: small (coccolith size <4 μm) and medium (coccolith size >4 μm) (cf. Lupi et al., 2012; Raffi et al., 1993, 2006; Rio, 1982). From the raw count, both relative (%) and absolute (N g^{-1}) abundances were calculated. Assemblage raw counts are available at Zenodo (Bianco et al., 2026).

From absolute abundances, it was possible to calculate the coccolith-derived CaCO_3 (g) for almost all the identified species using the formula of Young and Ziveri (2000; Equation 2).

$$\text{Coccolith-derived CaCO}_3 = Cc \times \rho \times l^3 \times k_s \quad (2)$$

where Cc = coccolith absolute abundance (N g^{-1}), ρ = constant for calcite density (2.7 g cm^{-3}), l = species-specific mean coccolith length, and k_s = species-specific shape factor. For k_s and mean coccolith lengths see Table S3 in Supporting Information S1.

We divided the species used for coccolith-derived CaCO_3 estimation into two groups: the lightly and heavily calcified taxa considering the value of $1 \times 10^{-11} \text{ g}$ of calcite produced by a single coccolith as the discriminant threshold between the two groups. It is well known from literature that some coccolithophore species are more heavily calcified than others, as in the case of *Helicosphaera*, *Pontosphaera*, and *Calcidiscus* compared to *Gephyrocapsa huxleyi* (see e.g., Daniels et al., 2014; Ziveri et al., 2007). The distinction between heavily and

lightly calcified was based on this knowledge and on the species-specific average coccolith mass calculated following Young and Ziveri (2000). Species generally considered as heavily calcified shows indeed a coccolith mass higher than this value. This threshold was selected to highlight that an order of magnitude distinguishes the more heavily calcified species from the lighter ones and considers the subdivision within the same species based on coccolith size (e.g., Gephyrocapsids larger or smaller than 4 μm). Please note that, since the distinction is based on species morphology, different species belonging to the same genus (i.e., Gephyrocapsids) have been split into the two categories despite their similarity in physiology (see Table S3 in Supporting Information S1 for details on the subdivision). Data on coccolith-derived CaCO_3 were used to estimate the relative coccoliths' contribution to bulk CaCO_3 using the following Equations:

$$\text{Total CaCO}_3 \text{ (g)} = \frac{\text{g of sediment sample} \times \text{bulk CaCO}_3 \text{ \%}}{100} \quad (3)$$

$$\text{Coccolith carbonate (\%)} = \frac{100 \times \text{Total coccolith} - \text{derived CaCO}_3}{\text{Bulk CaCO}_3 \text{ (g)}} \quad (4)$$

Data of coccolith absolute abundances were also used to calculate the Nannofossil Accumulation Rate (NAR; $\text{N cm}^{-2} \text{ ka}^{-1}$) following Ziveri et al. (1999).

$$\text{NAR} = \text{Cc} \times \text{SR} \times \text{DBD} \quad (5)$$

where Cc = coccolith absolute abundance (N g^{-1}), SR = sedimentation rate (cm ka^{-1}) derived from the age model for Site 1501, DBD = Dry Bulk Density (g cm^{-3}) derived from the linear interpolation of the Gamma Ray Attenuation Bulk Density data collected onboard for Site U1501 (Larsen et al., 2018; online repository).

Data of coccolith-derived CaCO_3 were used to estimate the coccolith fluxes (CAR, $\text{g cm}^{-2} \text{ ka}^{-1}$) with the following Equation 6:

$$\text{CAR}_{\text{coccolith}} = N_{\text{carb}} \times \text{SR} \times \text{DBD} \quad (6)$$

The same data on SR and DBD were also used, together with bulk CaCO_3 content, to estimate the bulk carbonate accumulation rate CAR_{bulk} following Equation 7:

$$\text{CAR}_{\text{bulk}} = (\text{DBD} \times \text{SR} \times \text{CaCO}_3) / 100 \quad (7)$$

We assessed coccolith assemblage preservation with the Nannofossil-Dissolution Index (NDI; Marino et al., 2009) since NDI is unbiased by species-specific ecological preferences unlike other dissolution indices (e.g., CEX; Dittert et al., 1999; Jin et al., 2019). The reliability of NDI has been defined in Bordiga et al. (2013) by correlation with the well-established index derived from foraminifera, that is, Fragmentation Index (FI; J. Le & Shackleton, 1992, partly modified by Hayward et al., 2004). The usefulness of NDI compared to FI has also been reported in Cobianchi et al. (2015). The NDI considers the ratio between the entire and disarticulated coccoliths of *Calcidiscus* spp. (Marino et al., 2009; Matsuoka, 1990). High values indicate higher preservation.

$$\text{NDI} = (\% \text{ entire placoliths } C. \text{ leptoporus} / (\% \text{ entire} + \% \text{ distal} + \% \text{ proximal placoliths } C. \text{ leptoporus})) \quad (8)$$

For this index 50 specimens have been counted per sample following Matsuoka (1990). Unfortunately, *Calcidiscus* spp. is a minor component of coccolith assemblage at Site U1501 (average abundance 1.56%), thus it was not possible to calculate the NDI for all the samples. We also assessed the absence of partial dissolution through additional qualitative examination of coccoliths at Scanning Electron Microscope (SEM). Paleoproductivity was quantified using both *N* ratio (Flores et al., 2000) and *Npp* (Hernández-Almeida et al., 2019). The first considers the ratio between the abundances of small Noelaerhabdaceae (e.g., *G. ericsonii*, small *G. oceanica*, small *Gephyrocapsa* spp., small *G. caribbeanica*, *G. huxleyi*) and the species *Florisphaera profunda* (Equation 9).

$$N \text{ ratio} = \% \text{ small Noelaerhabdaceae} / (\% \text{ small Noelaerhabdaceae} + \% F. \text{ profunda}) \quad (9)$$

N ratio is based on the premise that, as a deep dweller, *F. profunda* has a strong dependence on nutricline and, thus, stratification depth (e.g., Boeckel et al., 2006; Molino & McIntyre, 1990a, 1990b; Saavedra-Pellitero et al., 2011; Table S4 in Supporting Information S1). In contrast, the small Noelaerhabdaceae has an affinity for upper photic zones and eutrophic conditions (see Table S4 in Supporting Information S1). Values closer to 1 indicate strong upwelling and shallower stratification, and those closer to 0 indicate weak upwelling and deeper stratification.

The Npp index is based on a calibration model that relies on the relative abundances of *F. profunda* and can be applied globally at all latitudes, though it is more reliable between 30°N and 30°S, especially when studying sediment cores (Hernandez-Almeida et al., 2019). At higher latitudes, the abundance of *F. profunda* is strongly influenced not only by variations in primary productivity but also by SSTs and the relative abundances of other dominant species, such as small coccoliths (Hernandez-Almeida et al., 2019). The location of Site U1501 allows the use of this index as a reliable proxy, and the following formula has been used for Npp:

$$\text{Log}_{10}\text{Npp} = 3.11 - 0.01 \times \% F. profunda \quad (10)$$

Assemblage diversity was calculated as the Shannon-Weiner diversity index (H') using the software Past, version 4 (Hammer et al., 2001). This index accounts for both the abundance and evenness of species. Based on the ecological preferences of some species toward warmer SSTs (e.g., Boeckel & Baumann, 2004; Skampa et al., 2020, 2024; Triantaphyllou, 2004); see also Table S4 in Supporting Information S1, a Warm Water Taxa (WWT) curve has been produced by summing the abundances of *Helicosphaera carteri*, *Syracosphaera pulchra*, *Umbilicosphaera*, *Umbellosphaera* spp., *Rhabdosphaera clavigera*.

Finally, to correlate different indices and data sets, we used Pearson's correlation on Past4 software (Hammer et al., 2001).

3. Results

3.1. Coccolith Assemblage

At Site U1501, the coccolith preservation along the studied sequence is overall good, as indicated by SEM observations and an average NDI of 0.7 (Figure 3). The preservation, mainly stable throughout the studied interval, records two distinct minima at ~119 ka (top of MIS 5e) and ~91.9 ka (MIS 5c/b boundary), with rapid changes in the dissolution index: NDI decreases from 0.7 to 0.46 and from 0.6 to 0.42 in only 2.14 and 1 kyr, respectively (Figure 3a). Due to the low abundances of *C. leptoporus* there are no NDI data between the top of MIS 5 and the base of MIS 4. However, available evidence shows that the modern CCD in the SCS is relatively deep (~3,500 m or deeper; Wang, 1999). Site U1501 is one of the few sites (ODP and IODP) in the SCS located well above both the modern CCD (Z. Sun et al., 2018) and the regional lysocline (~3,000 m), implying that carbonate dissolution is expected to be limited throughout the studied interval. Indeed, previous studies have shown that, at sites located above the lysocline in the SCS, carbonate cycles are predominantly controlled by dilution rather than dissolution, producing the so-called "Atlantic-type" carbonate cycles (Wang et al., 1986, 1995). Subsequent works demonstrated that the spatial variations in CaCO₃ accumulation, particularly enhanced carbonate production during warm stages, also play an important role (Huang et al., 1997; Wang, 1999). These observations further support the interpretation that carbonate dissolution at Site U1501 was limited during MIS 5e and that the CaCO₃ variations observed are unlikely to reflect significant shoaling of the CCD.

The *N* ratio exhibits higher values during MIS 6, up to T-II, and then decreases from MIS 5e until the beginning of MIS 5d (113 ka). From MIS 5d until the end of MIS 5, it remains relatively stable with average values of 0.2, like those values recorded during MIS 6. A decrease in *N* ratio characterizes the beginning of MIS 4; however, from ~65 ka onward the productivity index increases again, reaching its maximum value at ~56 ka (Figure 3a). The Npp curve shows a very similar trend compared to *N* ratio (Pearson correlation $r^2 = 0.93$), with higher values during glacial and cooler substages of the studied interval (Figure 3a). The similarity between these two proxies of paleo-productivity indicates a high reliability of the obtained data.

The H' index shows a similar trend to the *N* ratio (Pearson correlation $r^2 = 0.91$ p -value < 0.001), documenting a positive correspondence between paleoproductivity and coccolith assemblage diversity.

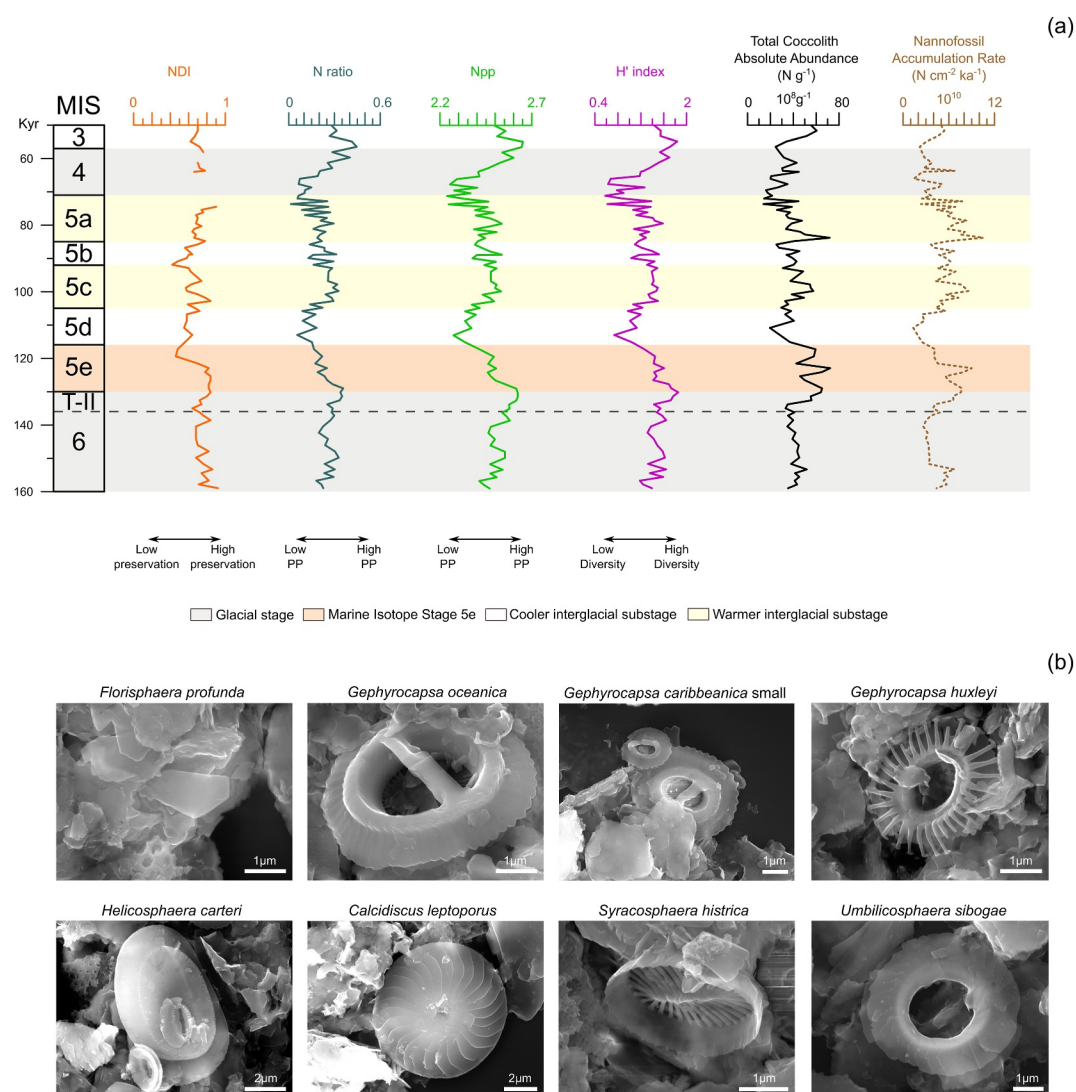


Figure 3. (a) Curves of coccolith assemblage preservation (NDI), paleoproductivity (N ratio and Npp) and diversity (H') indices, total coccolith absolute abundance and Nannofossil Accumulation Rate at Site U1501. Dotted black line delimits the bottom of Termination II. X axes have different scales. (b) Micrographs of coccoliths at Site U1501 collected via Scanning Electron Microscope (Tescan Mira3XMU of the CISRIC-Arvedi Laboratory at the Department of Earth and Environmental Sciences of University of Pavia).

The curve of total coccolith absolute abundance follows a similar pattern as the H' index (Pearson correlation $r^2 = 0.91$ p -value < 0.01). Throughout the entire sequence, the average absolute abundance is $40 \times 10^8 \text{ g}^{-1}$ with highest values recorded during MIS 5e (average $\sim 73 \times 10^8 \text{ g}^{-1}$) and at the base of MIS 5a. Significant minima are observed during MIS 5d (110 ka) and at the MIS 5a/4 transition (from 73.7 to 66.1 kyr), corresponding to minima in paleoproductivity and diversity (Figure 3a). The similarities indicate that coccolith abundances are closely related to productivity and that the increase in abundance is not always driven by a single dominant species (i.e., *F. profunda*), but rather reflects a diversification of the assemblage composition. Given this strong correlation, all three parameters will be considered in the present study.

Among the 40 different species and morphotypes distinguished in this study, the most abundant ones are reported in Figure 4. The assemblage is strongly dominated by *Florisphaera profunda* (mainly *F. profunda* subsp. *profunda*; Figure 3b), which contributes on average 64.21% to the assemblage. We record three main average variations in the abundance of *F. profunda*: between the bottom to the end of T-II (~ 159 – 130.2 ka; average 58.75%), from MIS 5e up to MIS 4/3 boundary (~ 129 – 58.1 ka; 67.22%), while in the uppermost part of the sequence (56.5–50.1 ka) is 52.96% (Figure 4).

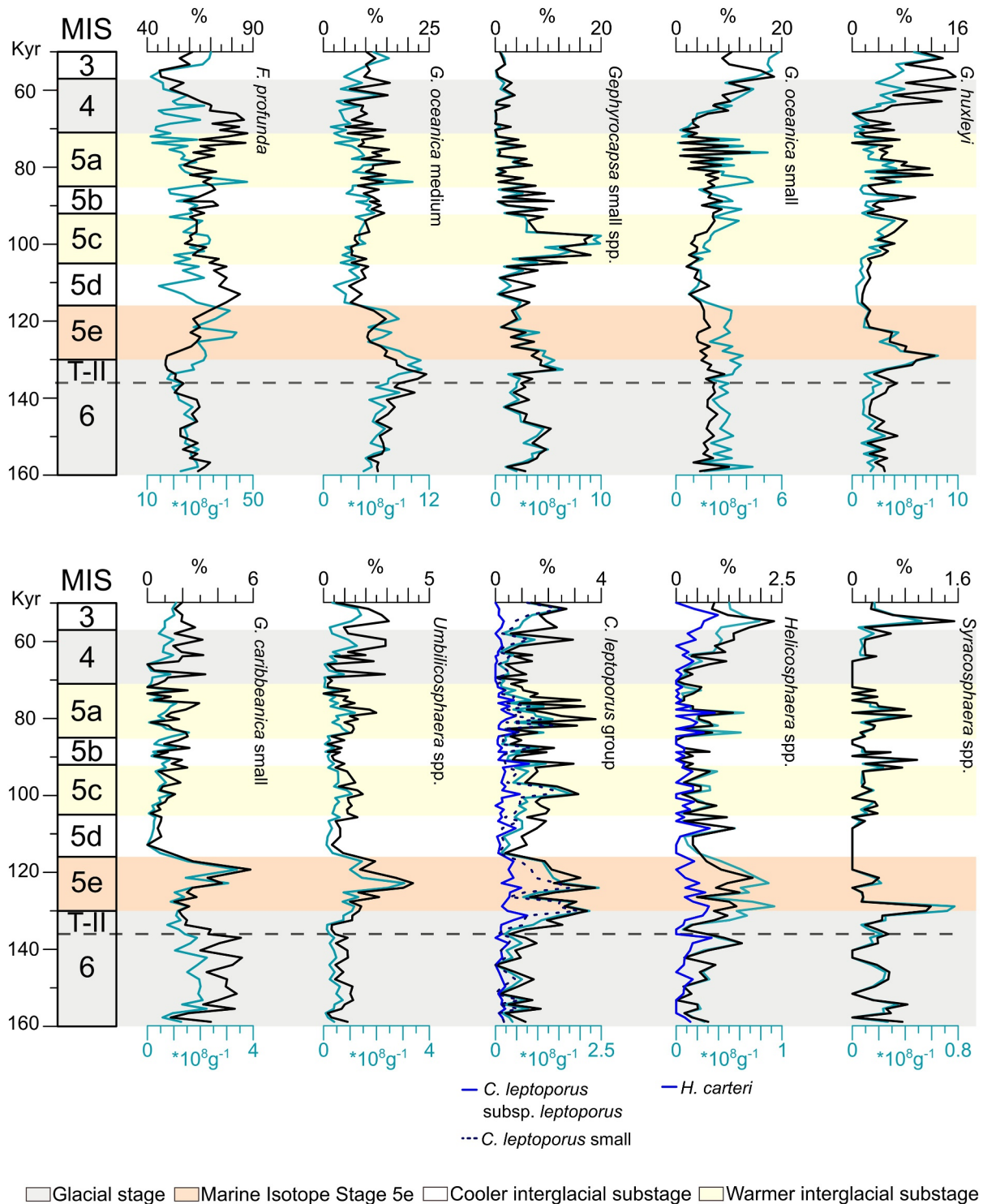


Figure 4. Relative (%) in black and absolute (Ng^{-1} , in teal green and blue) abundances of the most abundant coccolith species at Site U1501. Dotted black line delimits the bottom of Termination II. X axes have different scales.

The next most abundant species is the medium-sized *Gephyrocapsa oceanica* (Figure 3b). It is less than six times as abundant as *F. profunda* (average abundance ~12%) reaching its maximum percentage (24.3%) during T-II (133.8 ka). Another peak can be observed at the top of the MIS 5e. From MIS 5d afterward *G. oceanica* medium shows lower and stable abundances (average 10.26%; Figure 4).

Among the small-sized taxa, small *G. oceanica* and small *Gephyrocapsa* spp. (including *G. ericsonii* and *G. muelleriae* and other undefined small-sized *Gephyrocapsa* spp.) contribute on average 6.2% and 5% to the assemblage, respectively. While small *G. oceanica* shows a peak in abundance during MIS 5a and another at MIS 3, the small-size *Gephyrocapsa* spp. shows peaks in abundance during T-II and MIS 5c (Figure 4). *Gephyrocapsa huxleyi* contributes on average 5.5% to the assemblage at Site U1501 during the studied interval. Peaks in relative abundance of this species occur at the base of MIS 5e, MIS 5c and 5a, reaching its maximum relative abundance of 15.6% at the beginning of MIS 3. Average relative abundance for the other displayed species (*C. leptoporus*, *Umbilicosphaera* spp. mainly *U. sibogae*, *Helicosphaera* spp., *G. caribbeanica* small and *Syracosphaera* spp.) are lower than 2%, but they are shown because, despite their general lower abundances, they record peculiar abundance variations during T-II and/or MIS 5e (Figure 4).

Excluding the species *F. profunda*, it is possible to highlight two major common patterns in the assemblage in both absolute and relative abundances. The first, during the T-II and at the T-II/MIS 5e boundary, when almost all the displayed species (i.e., *G. oceanica* medium, *Gephyrocapsa* small spp., *Umbilicosphaera* spp., *C. leptoporus* group, *Helicosphaera* spp. and *Syracosphaera* spp.) record a peak in both absolute and relative abundances. *Gephyrocapsa oceanica* small, however, shows an increase in absolute abundances only, reaching its highest values during MIS 5e (Figure 4). The second trend is documented at MIS 5e-5d boundary, during which a significant decrease in both absolute and relative abundances is recorded by most of the species, apart from *Gephyrocapsa* small spp. which maintains low relative abundances but shows higher absolute abundances, and *G. huxleyi* that anticipated this decrease by ~15 ka, that is, to the T-II/MIS 5e boundary. *Syracosphaera* spp. is absent (Figure 4). *Gephyrocapsa oceanica* small shows a decrease in absolute abundances only. This phase is also highlighted by a general decrease in the total absolute abundance which goes from an average of $47 \times 10^8 \text{ g}^{-1}$ until the MIS 5e-5d boundary to an average of $\sim 37 \times 10^8 \text{ g}^{-1}$ from ~115 ka upwards (Figures 3a and 4).

3.2. Calcium Carbonate Derived From Coccoliths

As shown in Figure 5, the average bulk CaCO_3 content in the entire studied sequence is 15.7 wt% (0.17g), well in accordance with literature (Z. Sun et al., 2018), but maxima up to 25 wt% are recorded from MIS 6/5e transition to the entire MIS 5e, MIS 5c and most of 5a. MIS 6 and cooler substages of MIS 5 (d and b) show a lower bulk CaCO_3 wt%. The transitions between glacial and interglacial stages, as well as among MIS 5 substages, are well marked by changes in bulk carbonate.

At Site U1501, the average total coccolith-derived CaCO_3 corresponds to 0.02 g, contributing around 23.6% to the total bulk CaCO_3 , with peaks of 33.4% and 31.9% during T-II and MIS 5e, respectively (Figure 5). It has to be noted that the coccolith-derived CaCO_3 can return an error of $\pm 50\%$ in the mass calculations (Young & Ziveri, 2000), thus, $\pm 0.01 \text{ g}$ for coccolith-derived CaCO_3 in this case-study. However, what is important to observe is that the general trends are reliable and representative of coccolith contribution to bulk CaCO_3 over time. Mirroring bulk CaCO_3 trend, minima are observed in the total coccolith-derived CaCO_3 during MIS 5d and b, whereas the maximum contribution of coccoliths is recorded during MIS 5e. The variations in the total coccolith-derived CaCO_3 also highlights the transitions between glacial and interglacial stages, as well as between MIS 5e and the upper substage MIS 5d (Figure 5). Although the average contribution of coccolith-derived carbonate to bulk CaCO_3 is lower during the studied time interval if compared to other calcifying organisms (i.e., foraminifera), the strong correlation between bulk and coccolith-derived CaCO_3 (Pearson correlation $r^2 = 0.83$; p -value < 0.001), confirms the role of coccolithophores as important carbonate producers at Site U1501. The CAR_{bulk} and the $\text{CAR}_{\text{coccolith}}$ show strong correlations with Bulk CaCO_3 (Pearson correlation $r^2 = 0.774$) and Total Coccolith-derived CaCO_3 (Pearson correlation $r^2 = 0.815$), respectively, indicating a weak influence of DBD and SR on CAR fluxes pattern.

Upon closer examination to the contribution to total coccolith-derived CaCO_3 of heavily and lightly calcifying species, we document the significant role of heavily calcified taxa that, despite representing on average only ~16% of the assemblage, contribute from 20% to 70% to the coccolith-derived CaCO_3 . In contrast, the lightly calcifying ones exhibit an average CaCO_3 contribution of 34% or 0.008 g even though reaching up to 94.1% of the

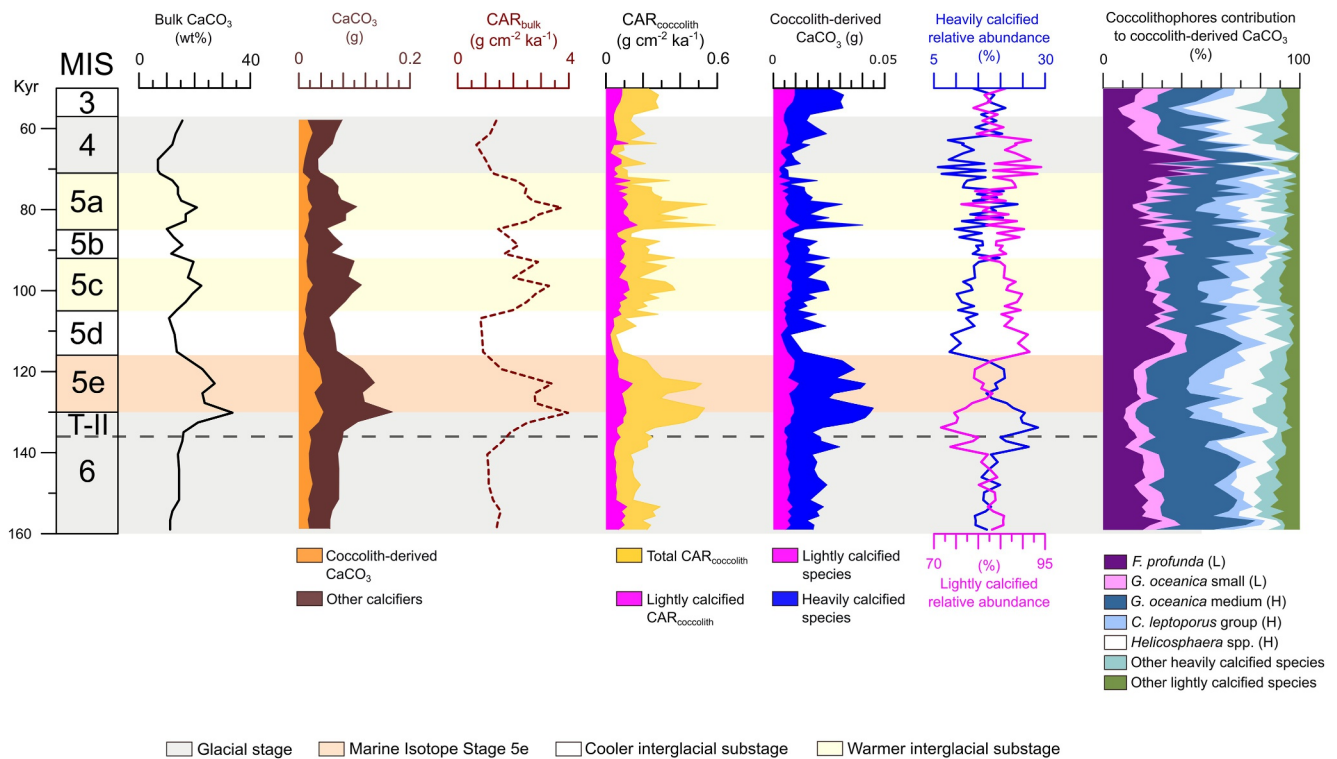


Figure 5. Calcium carbonate (CaCO_3) content at Site U1501: CaCO_3 measured in bulk (wt%); coccolith-derived CaCO_3 versus other calcifiers; carbonate in bulk (CAR_{bulk}) and coccolith ($\text{CAR}_{\text{coccolith}}$) fluxes; cumulative curve with the contribution of lightly and heavily calcified species to the coccolith-derived CaCO_3 ; relative abundances of heavily and lightly calcified species; species-specific relative (%) contribution to the coccolith-derived CaCO_3 reported to 100%; L: lightly calcifying taxa, H: heavily calcifying taxa. X axes have different scales.

entire assemblage (Figure 5). The interval when the heavily calcifiers contributed the most is at the base of the studied sequence, from 160 ka up to the end of MIS 5e.

Among the heavy calcifiers, *Gephyrocapsa oceanica* medium is on average the major contributor to the total coccolith-derived CaCO_3 (average of 30.15%) primarily due to its higher abundance ($\sim 12\%$) compared to other heavy calcifiers ($\sim 4.1\%$ in total) and not so much for its carbonate mass (1.49×10^{-11} g; Table S3 in Supporting Information S1). The second most important producer of CaCO_3 is the species *F. profunda* which, despite being a light calcifier, can contribute from 35 up to 52% to the coccolith-derived CaCO_3 . Other important CaCO_3 producers at Site U1501 are *C. leptoporus* (0.003 g on average being 1.6% in abundance) and *Helicosphaera* spp., mainly *H. carteri*, (0.002 g on average being 0.65% in abundance). Higher contributions of other light calcified taxa are observed during MIS 6 and from MIS 5d, until the end of MIS 4. On the contrary, the heavily calcified taxa show higher peaks starting from T-II up to the entire MIS 5e, accounting for more than half of the total CaCO_3 produced/accumulated by coccoliths, and during MIS 5c, 5a, and MIS 4/3. Among the heavily calcifying taxa, it is worth noting the significant CaCO_3 production of minor components of the assemblage such as *Helicosphaera carteri* that can reach 5.5% of the CaCO_3 contribution despite reaching only 0.24% in abundance (Figure 5). This peculiarity can be attributed to its massive coccolith calcite mass, that is around 1.35×10^{-10} g (Table S3 in Supporting Information S1).

4. Discussion

4.1. Coccolith Evidence for MIS 6-3 Climate Variability in a Multiproxy Context

Caution is needed when interpreting the ecology of coccolithophores by linking each species to a specific environmental parameter. In fact, their abundance and distribution are affected by a complex and multiple combination of many factors, such as salinity, SST, light intensity, and nutrient availability (e.g., Winter et al., 1994), more than by a single environmental driver. For this reason, it is fundamental to compare the

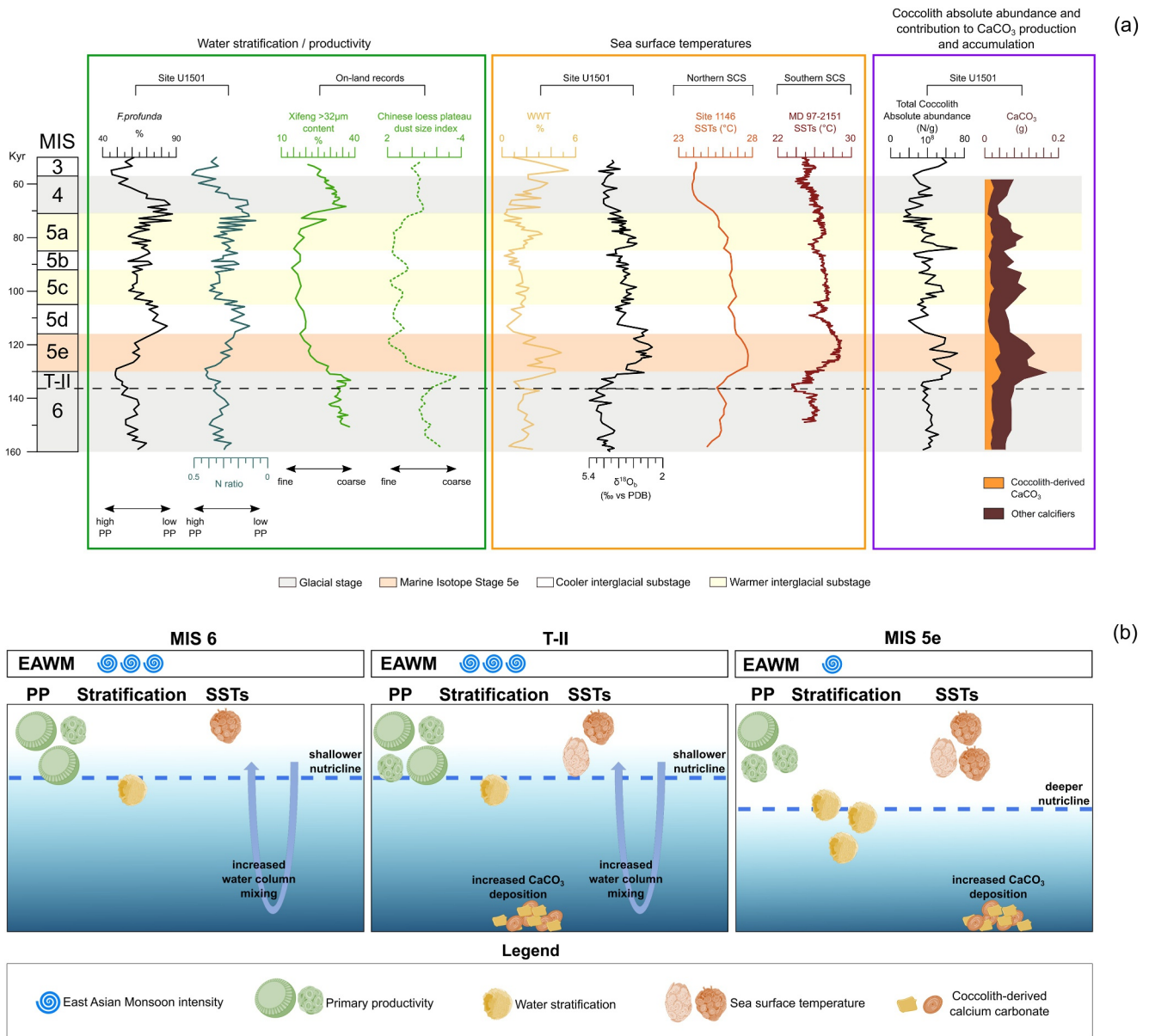


Figure 6. (a) Main environmental proxies at Site U1501 compared to other sites from South China Sea (SCS) or nearby regions. *Florisphaera profunda* relative abundances (%); productivity index (*N* ratio); relative content of >32 μm loess size-fraction at Xifeng (Z. T. Guo et al., 2009); Chinese Loess dust size index from Chinese Loess Plateau (Barth et al., 2018); Warm Water Taxa curve and benthic oxygen isotopes from Site U1501; reconstructed sea surface temperatures at Site 1146 (Herbert et al., 2010) from Northern SCS and MD97-2151 from Southern SCS (Zhao et al., 2006); total coccolith absolute abundance and coccolith-derived CaCO₃ versus other calcifiers (e.g., foraminifera). X axes have different scales. (b) Schematic representation of the Eastern Asian Winter Monsoons (EAWM) intensity and water column conditions during Marine Isotope Stage (MIS) 6, Termination II, and MIS 5e in northern SCS. The number of elements represents a gradient, with higher numbers indicating a stronger expression of the respective parameter.

coccolithophore variations with other independent proxies (e.g., oxygen and carbon isotopes, other planktonic groups such as foraminifera or diatoms, alkenones, dust inputs...). Based on the coccolithophore ecological preferences reported in literature (see Table S4 in Supporting Information S1) and by comparing species abundance variations with independent parameters (Figure 6a), it was possible to reconstruct water column stratification, nutrient supply, and SSTs at Site U1501.

Our data on the dominance of the oligotrophic species *F. profunda* at Site U1501 are in agreement with previous studies (e.g., Fernando et al., 2007; Wilcox et al., 2015). The presence of this species has been widely documented in the SCS region in the last 150 kyr until nowadays (e.g., Hernández-Almeida et al., 2019; Jin et al., 2016; Su

et al., 2013; Wang et al., 2014). Despite the overall oligotrophic nature of this area, during MIS 6 and 4 and the deglaciations (MIS 6/5 and MIS 4/3), we recorded intervals of higher PP at Site U1501 (Figure 6a), highlighting a relationship between PP and glacial-interglacial cycles. Previous works documented a similar relationship in the SCS (e.g., D. Li et al., 2014 and references therein). More specifically, higher PP during glacial intervals in the northern SCS has been detected thanks to variations in coccolithophore and foraminiferal assemblages, opal and Total Organic Carbon content in the sediments (D. Li et al., 2014 and references therein; Su et al., 2013; Wang et al., 2014), and organic biomarkers (He et al., 2008, 2013; D. Li et al., 2014).

At Site 1501 the fluctuations in the water column stratification and productivity documented by changes in *F. profunda* abundances, and consequently by N ratio and Npp, can be also associated with the activity of the EAM (Figure 6b), as already reported for the same area (e.g., He et al., 2013; Su et al., 2013). Indeed, despite other factors such as variations in eolian and fluvial inputs that can influence PP during glacial intervals, the EAM circulation is the most influential parameter in this region (He et al., 2013 and references therein; D. Li et al., 2014). As East Asian Winter Monsoon (EAWM) intensifies, wind strengthening leads to increased upper water mixing, which lessens stratification (D. Li et al., 2014; Su et al., 2013) and increases the availability of nutrients, particularly nitrogen, the main limiting factor of phytoplankton productivity in this area (Lee Chen, 2005). Glacial intervals are those that experienced stronger EAWM, favoring water column mixing as well as coastal upwelling (e.g., Chen et al., 2006; S. Li et al., 2024; Ning et al., 2004; Figure 6b). Higher PP values at Site U1501 confirm periods of intense upwelling and shallow water column stratification, conditions correlated with higher relative monsoonal intensity (Figure 6b), as previously observed also by Su et al. (2013) at the nearby Site MD05-2904 through the correlation between *F. profunda* abundances and EAM dynamics.

To verify the relationship between PP and EAWM, we also compared our PP data with the percentage of coarse grain sediment fraction ($>32\ \mu\text{m}$) derived from the Chinese Plateau from Z. T. Guo et al. (2009). Loess grain-size, especially the contents of the coarse fractions, is indeed a reliable proxy of EAWM intensity (e.g., Ding et al., 1995; Z. Guo, 2004; Porter & Zhisheng, 1995), with stronger winds transporting coarser dust. Data from Z. T. Guo et al. (2009) document a stronger EAWM during glacials corresponding to higher N ratio values, and weaker EAWM during the warmer MIS 5 associated with reduced PP, validating our hypothesis (Figure 6a). The assumption of a strong influence of EAWM in the northern area compared to the other sectors of SCS is also supported by modern winter wind speed patterns of the region.

Previous studies on the northern SCS showed how cooler intervals were characterized by higher abundance of diatoms, favored by enhanced water column mixing and dust nutrient-enriched supply derived from Chinese loess and associated with stronger EAWM (He et al., 2013; D. Li et al., 2014; Shiao et al., 2008). Coccolithophores and other phytoplanktonic organisms (e.g., dinoflagellates) were also present but in much lower proportions. These observations are consistent with the data collected from Site U1501. In contrast, as shown by He et al. (2013), during the warmer substages of MIS 5, despite the persistence of diatoms as the dominant group within the phytoplankton community, the total coccolith abundance increased. Despite being based on different proxies - i.e., algae biomarker abundances (He et al., 2013) and calcareous nannofossil counting (this work) - the same phenomena have been observed at Site U1501, particularly during the warmest and most oligotrophic MIS 5e (Figure 6). A possible explanation of this increase in coccolith abundances is the weakening of the monsoon winds recorded during the interglacial MIS 5 (e.g., Su et al., 2013). Indeed, coccolithophores' preference for less dynamic and turbulent conditions and nutrient-depleted waters could have allowed this group to proliferate (e.g., Werne et al., 2000; Winter et al., 1994; Young, 1994).

He et al. (2013) attributed the increased abundance of coccolithophores not only to water stratification but also to increased SSTs in the SCS. At Site U1501, the increased abundance of WWT confirms this hypothesis (Figure 6a). Higher WWT percentages fit well with deglaciation events at MIS 6/5 and all the warmer substages of MIS 5 (Figure 6a), during which an increase in total coccolith abundances is recorded. The WWT curve shows a progressive increase during the MIS 4, and higher values at the MIS 4-3 transition and the base of MIS 3. This increase can be mostly related to the higher abundances of *Umbilicosphaera* spp. and *Helicosphaera* spp. These species prefer both warm/temperate waters and low nutrient concentrations (Table S4 in Supporting Information S1). Therefore, the SSTs characterizing MIS 4 (23.8°C; He et al., 2008) and the MIS 4/3 transition, combined with a weakened EAWM, could have been favorable for their proliferation. A similarity between WWT curve at Site U1501 and SST trends can be observed at sites 1146 (Herbert et al., 2010) and MD05-2904 (He et al., 2008), where SSTs have been calculated from the alkenone U_k^{37} (Figure 6a) and also at Site 1144, where the SST is

reconstructed from the Mg/Ca ratio of *Globigerinoides sacculifer* (Wei et al., 2007). A comparable pattern in SST during MIS 6–5 can also be observed in the southern SCS, as shown by the SST curve from Site MD97-2151 reconstructed using alkenone U_k^{37} (Zhao et al., 2006; Figure 6a), indicating similarities between the two areas. These observations suggest that the WWT index reliably reflects SST variations in the northern SCS. Higher SSTs can also be related to a major influence of the warm and oligotrophic Kuroshio current, entering the Luzon Strait and affecting the SSTs and water chemistry in the SCS downwards to the West Philippine Sea (Roberts et al., 2021 and reference therein; C.-R. Wu et al., 2017). Variations in the intensity and influence of the Kuroshio current from the last 500 kyr up to nowadays have been documented both in the Pacific Ocean (Bordiga et al., 2014; Qiu, 2000) and SCS (e.g., Roberts et al., 2021) areas.

At Site U1501, glacial and cooler intervals are associated with lower percentages of bulk CaCO_3 , indicating the concurrent presence of other biogenic (siliceous) or terrigenous components in the sediment accumulation, rather than coccoliths (Figure 6a). In this area, a lower CaCO_3 content due to increased dilution resulting from terrigenous inputs coming from land during glacials is known (Higginson et al., 2003; Pelejero, 2003; Wang, 1999; Wang et al., 1995). However, dilution is not the only factor affecting the carbonate percentages. The higher phytoplankton PP (e.g., He et al., 2013) occurring during glacials in parallel with lower coccolith absolute abundances (this work) is indicative of the biogenic contribution of other phytoplanktonic groups, such as diatoms, to the accumulation rate besides coccolithophores. On the contrary, climate and oceanographic conditions during T-II and the following MIS 5e appear to favor the coccolithophores, and consequently their CaCO_3 production (Figures 6a and 6b).

4.2. Coccolithophore Contribution to CaCO_3 Production/Accumulation at Site U1501

Focusing on the species-specific contribution to CaCO_3 production at Site U1501, it is clear that despite their low relative abundances (<4%; Figure 4) the heavily calcified species are the most important contributor to the coccolith-derived CaCO_3 production during T-II and MIS 5e, representing 75.44% of the total coccolith-derived CaCO_3 (Figure 5). This evidence confirms the important role of more calcified species to the calcite production and, consequently, to the carbonate pump as previously documented (e.g., Balch, 2018; Rost & Riebesell, 2004; Smith & Gattuso, 2011; Ziveri et al., 2007). It also highlights the importance of studying more in detail the less abundant species, since even small increases in their abundance can have a substantial impact on carbon production and export (e.g., Ziveri et al., 2007). During T-II and most of MIS 5e, the higher abundance of heavily calcified species may have strongly influenced atmosphere/ocean CO_2 exchanges, favoring on one side an increase in the carbon export and sequestration, and on the other side a rise in seawater CO_2 concentration due to the intensified calcification process (e.g., S. Li et al., 2024; Riebesell et al., 2009; Zeebe et al., 2001). However, a more precise estimate of coccolithophores' contribution to both the biological and carbonate pumps is needed for improved quantification of their impact on CO_2 during the studied interval.

Notably, among the heavy calcifiers at Site U1501, *G. oceanica* medium strongly contributes to the total coccolith-derived CaCO_3 due to its higher abundance compared to other species of this group (Figure 5). A recent analysis of Noelaerhabdaceae coccolith mass and calcification rate over the past 200 kyr in the SCS, at the nearby Site MD05-2904, documented an increase in the weight of medium-sized *Gephyrocapsa oceanica* during T-II and part of MIS 5e (from 153 to 125 kyr), in parallel with a decrease in the weight of small placoliths such as *Gephyrocapsa* small spp. and *G. huxleyi* (Su et al., 2020). They also observed a significantly larger size for *G. oceanica* medium, approximately 5–5.3 μm , compared to the average size of 4.5 μm reported in literature (Young & Ziveri, 2000).

A similar trend in *gephyrocapsids* mass variation during T-II was observed by McClelland et al. (2016) at ODP Site 1133 in Southernmost Pacific Ocean and by Meier et al. (2014), at site ODP 980 and Piston Core SO164-17-2 in North Atlantic Ocean and Southern Florida Strait. McClelland et al. (2016) recorded an increase in *G. oceanica* mean coccolith weight from ~3 to 5.5 pg moving from MIS 6 to the end of T-II, parallel to a slight decrease in *G. huxleyi* coccolith mass. During the same interval, Meier et al. (2014) observed a rise in Noelaerhabdaceae average weight from 5 to 6 pg, followed by another increase up to 7.7 pg during MIS 5e, in the North Atlantic. At the site located in the Florida Strait, the mean coccolith weight increased from 5.5 to 12 pg from MIS 6 to the deglaciation (T-II), reaching a peak of 13 pg during MIS 5e, due to an increase of both relative abundance of larger *gephyrocapsids* (from 2% to 12%) and heavier calcifying morphotypes. This documented increase of *gephyrocapsids* mass in different oceanographic settings could be indicative of a more global event. Unfortunately, the

observations regarding increased calcification are limited to Noelaerhabdaceae species and cannot be confirmed or extended to other heavily calcified taxa in this study because of the lack of species-specific coccolith mass measurements from Site U1501. Identifying comparable trends for other heavily calcified species will be crucial to improve our understanding of species-specific responses to past and future climate variability and carbon export, at least within the SCS.

Finally, another noteworthy aspect to remark is the significant and continuous contribution to CaCO_3 production of the lightly calcified species *F. profunda*, strictly related to its high abundance along the studied interval (Figure 5). Even when the heavily calcified species such as *S. pulchra* and *H. carteri* are more abundant, their contribution to coccolith calcite production never exceeds 30%. All this evidence underscores the importance of considering both heavily and lightly calcified species, as well as rare and abundant taxa, when evaluating coccolith-derived CaCO_3 production.

4.3. Comparison Between MIS 5e and Future Climate Model: Investigating Coccolithophores Behavior in the SCS Area

Understanding the future evolution of monsoon dynamics is essential for predicting the impact of this changing system on human populations residing in the monsoon regions. It is also crucial for assessing changes to the ecosystem components for which this circulation system exerts a strong influence. The EAWM is the most influential component of EAM in the northern SCS and it plays an important role in the global-scale cycling and transport of matter and energy (e.g., water vapor, water, dust; Ma & Chen, 2021), impacting climate conditions in East Asia, as well as the tropical regions of Indonesia and the western Pacific. A recent analysis of future variations (from ~2050 to 2080) of the EAWM under a warmer scenario (Shared Socio-economic Pathways (SSP) 3-7.0 of IPCC, 2023) identified a weakening of the EAWM, a reduction in its interannual variability, and a shift in its circulation patterns (C.-H. Wu et al., 2023). These projections indicate the development of warmer winters, alterations in regional climate dynamics, and a reduction in the predictability of future monsoon patterns (Table S5 in Supporting Information S1; Figure 7). A similar scenario is reconstructed here for T-II and MIS 5e, when a weakening of the EAWM led to enhanced water column stratification, due to reduced mixing. This in turn, resulted in lower total primary productivity (e.g., this work; He et al., 2013; Su et al., 2013). Under these conditions during the late Pleistocene, coccolithophores were favored, leading to an increase in their abundance, diversity, and contribution to CaCO_3 production/accumulation (Figure 7).

Drawing on similarities between reconstructions for MIS 5e in the northern SCS and future trends (Figure 7; Table S5 in Supporting Information S1), we can hypothesize the fate of coccolithophores in this region. Using the paleo data from Site U1501 as reference, we can expect an increase in coccolithophore abundance and diversity associated with the dominance of *F. profunda*, and heavily calcified species (Figure 7). The hypothesis of a positive response of coccolithophores with respect to the future EWAM weakening and the parallel increase in SST, is supported also by the variations recorded during the other warmer substages of MIS 5 (c and a), indicating that the transition from a cooler to a warmer stage, seems to favoring this group of calcifying phytoplankton.

Although coccolithophores represent a minor component of the whole phytoplankton community in the SCS, with diatoms comprising the dominant phytoplankton group (e.g., Ke et al., 2011; F. F. Le et al., 2006; T. Li et al., 2010; Y. Li, 2012; Ning et al., 2004; J. Sun et al., 2007; Xu et al., 2011), they still play a significant role in the global C cycle. Thus, it is interesting to consider how changes in their abundance and assemblage composition might influence their future contribution to CO_2 uptake and carbon storage in the studied area. The reported increase in coccolith-derived CaCO_3 production and shift toward more calcified species during T-II and MIS 5e (Figures 5 and 7), together with the combined increase in abundance of the highly calcified *G. oceanica* medium, lead us to infer a similar variation in the next global warming (Figure 7), with a consequent increase in their contribution to the production of CaCO_3 , and a strong impact on the carbonate chemistry of SCS.

The SCS can currently be considered a weak/moderate source of CO_2 (e.g., Zhai et al., 2013), but a possible future increase in CaCO_3 production due to the higher abundance of heavily calcified coccolithophores could influence CO_2 fluxes in the area, shifting the balance toward a positive flux of CO_2 atm-ocean. The importance of coccolithophores in regulating the carbonate equilibrium in SCS has been previously highlighted by Luo and Boudreau (2016). These authors simulated the future evolution of SCS and Japan Sea (JS) from preindustrial time to ~4,000, observing a slower acidification in the SCS compared to JS, associated with a higher CaCO_3 export characterizing the SCS. Moreover, Luo and Boudreau (2016) tested the effects of potential future reductions in

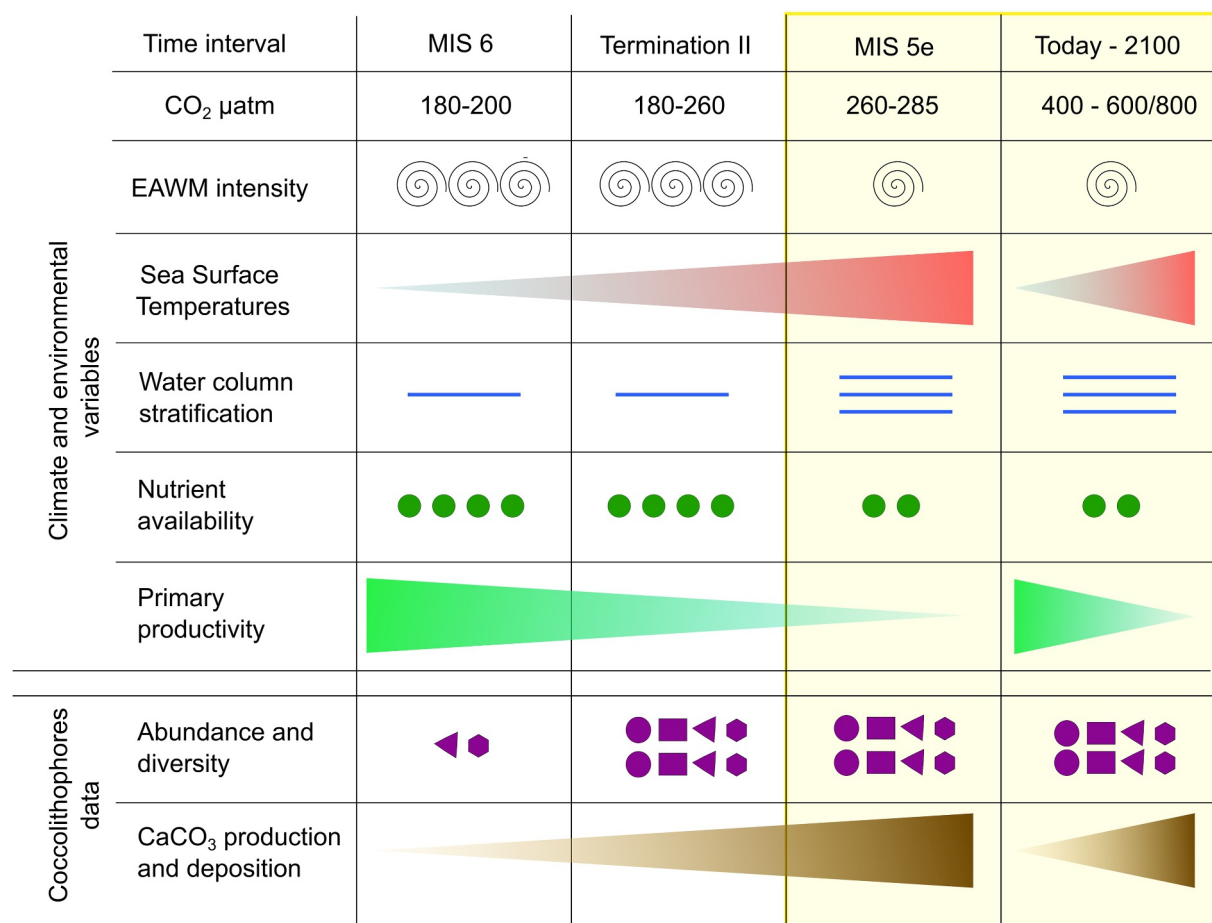


Figure 7. Schematic representation of climatic and environmental evidence and coccolithophore responses during Marine Isotope Stage 6-5e in South China Sea and their possible future evolution according to IPCC (2023), C.-H. Wu et al. (2023), Z. Li et al. (2019) and Krumhardt et al. (2019). An increase in the number of elements or in color intensity indicates a rise in the parameter. See Table S5 in Supporting Information S1 for more details.

CaCO₃ production by 33%, 50% and 67% in the SCS, documenting a progressive acceleration of acidification corresponding to the decrease in calcite export. However, when comparing past and future scenarios, it is important to consider similarities and differences between the two-time intervals. Between the 2100 scenario and MIS 5e a key difference is the concentration of CO₂ (e.g., Yin & Berger, 2015). The future projections discussed here are from models for SSP 2-4.5 and 3-7.0 scenarios from the latest Intergovernmental Panel for Climate Change (IPCC) report (IPCC, 2023), with CO₂ contents of 600 and 800 ppm, respectively (Figure 7). These values are significantly higher than those recorded during MIS 5e (up to 285 ppm; Bereiter et al., 2015; Lüthi et al., 2008; summarized in Past Interglacials Working Group of PAGES, 2016) and CO₂ content could have a significant impact on the coccolithophore communities which are sensitive to CO₂ variations (e.g., Chauhan & Rickaby, 2024; Langer et al., 2006; S. Li et al., 2024; Walker et al., 2018). Some information about the relationships between coccolithophores and high CO₂ contents is provided by the recent work of Krumhardt et al. (2019). The authors isolated the effects of CO₂ increase on coccolithophores using the Community Earth System Model (CESM2.0 with a modified version of MARBL that contains explicit coccolithophores). Their results show that increasing CO₂ levels return a reduction in CaCO₃ production by coccolithophores rather than a reduction in growth, only when CO₂ levels reach the critical threshold of 600 μatm. Today, global annual calcification is on average 6% higher than during pre-industrial times (CO₂ at ~280 ppm; Krumhardt et al., 2019). This increase is the result of both regional decreases and increases in calcification, with the latter occurring in the North Atlantic, the Patagonian Shelf, and the North Pacific and associated with increased growth and abundance. Krumhardt et al. (2019) further predict a progressive decrease in calcification from 600 ppm CO₂ upwards, reaching values of 11% at 900 ppm. However, these high concentrations in long-term projections do not seem to

have the same effects at different latitudes and in different oceans. No decreases in calcification are expected in the North Atlantic, Southern Ocean and the North Pacific, the latter including the SCS. In these regions, a possible increase in coccolithophores abundance, but also a shift in the phytoplankton community (with a decrease in diatom abundances) is predicted. As such, in the presence of CO₂ concentrations not higher than 900 ppm, or better below 600 ppm, the response of coccolithophores to future climate conditions may be more positive than in other areas. The observed increase in calcification (until 400 ppm of CO₂) and abundance (up to 900 ppm of CO₂) in Pacific Ocean from Krumhardt et al. (2019) aligns with what we document for the transition from T-II to MIS 5e, where a decrease in nutrient availability is associated with higher coccolithophores absolute abundances and contribution to CaCO₃ production/accumulation (Figure 7). However, it is important to consider that a change in coccolithophore assemblage composition is expected too. An increase in more lightly calcified (or even naked) species is predicted under increasing CO₂ levels (Krumhardt et al., 2019), with an expansion of coccolithophores species with a ratio between calcification and photosynthesis (PIC:POC ratio) lower than 0.1, especially at 900 ppm of CO₂ (Krumhardt et al., 2019).

Another critical parameter to consider in future responses of coccolithophores is their species-specific sensitivity to ocean acidification (OA). Over the last three decades, numerous experiments have demonstrated that not only species but also different strains can exhibit varying sensitivities to pH decreases and CO₂ increases (e.g., Bianco et al., 2025a, 2025b; Chauhan & Rickaby, 2024; G. Langer et al., 2009, 2011). Species such as *Coccolithus braarudii* or *Calcidiscus leptoporus* subsp. *quadriperforatus* (e.g., Gafar et al., 2019a, 2019b; Walker et al., 2018) could be more negatively affected by OA compared to other species that are less sensitive under controlled experimental conditions, such as *G. huxleyi* or *H. carteri* (e.g., Bianco et al., 2025a, 2025b; Walker et al., 2018). This different capacity to face future changes in carbonate system by coccolithophores will likely determine a shift in their assemblage composition and, consequently, in their contribution to CaCO₃ production/accumulation, inevitably affecting the carbon pump efficiency.

Finally, the increase in coccolith diversity, abundance, and calcification in the SCS during MIS 5e suggests a potential adaptability of these organisms to future rises in atmospheric CO₂ (Figure 7), below the threshold of 900 ppm. However, the rate of CO₂ increase during MIS 5e was significantly slower than the rise observed today. Moreover, the coccolithophores' species-specific sensitivity to OA is expected to vary. Therefore, these differences may limit the extent to which past responses can be directly applied to predict future coccolithophore behavior. For this reason, detailed information is needed to better understand the adaptation of coccolithophores to drastic and rapid environmental changes, to reduce the uncertainty in future predictions.

5. Conclusions

The evidence collected at Site U1501 of the SCS confirms the utility of coccolithophores for paleoclimatic reconstructions, particularly in relation to monsoon variations and associated oceanographic conditions. The conditions highlighted for MIS 5e, in terms of surface water stratification, SSTs, coccolithophore abundance, diversity and degree of calcification, show interesting similarities with future EAM scenarios that predict a weakening of the monsoon intensity. These results underscore the potential of coccolithophores as sensitive indicators of past climate dynamics and provide a valuable reference for anticipating their responses under future climatic changes. In this study, we documented:

- The predominance of *Florisphaera profunda*, indicative of sustained oligotrophic conditions and shallow nutri/thermocline, typical of this region.
- The relationship between coccolith abundances and changes in the EAM dynamics over the studied interval, reinforcing the reliability of coccolithophores remains as a proxy for paleoclimate reconstructions also in this region. Variations in PP correlated to changes in the strength of EAWM: more intense during MIS 6, T-II, colder substages of MIS 5 and MIS 4/3 transition, leading to an enhanced water column mixing; weaker toward the end of MIS 5e in relation to a more stratified water column.
- A significant contribution of heavily calcified species along crucial climate events such as T-II/MIS 5e and MIS 5e, despite their generally considerably lower abundances. This observation underscores the importance of considering less abundant species, which are often overlooked in climate reconstructions and carbon dynamics yet play a crucial role in CO₂ feedback and carbon export/production.
- A good correlation among our data from fossil assemblages during MIS 5e and future scenarios highlighting the relevance of using MIS 5e as a paleo-analog for improving future models.

Overall, these results highlight a general positive response of coccolithophores to increased SST and enhanced stratification in the SCS in the past 170 kyr. When considered, alongside future predictions, this evidence suggests a possible positive response of these calcifying microalgae under future climate conditions in the area, with CO₂ concentrations reaching up to 800 ppm. This positive signal in the geological record has been documented in the semi-enclosed SCS; however, further studies across additional regions are required to obtain a more comprehensive understanding of coccolithophore dynamics during T-II and MIS 5e. A more thorough and detailed assessment of their behavior, both in the past and present, is crucial for improving predictions of their responses to future global climate change.

Inclusion in Global Research Statement

Samples from Site U1501 were provided by the International Ocean Discovery Program (IODP) following the established procedures and permissions. The study complies with ethical standards for international research collaboration and aims to contribute to the shared scientific understanding of the South China Sea region.

Conflict of Interest

The authors declare no conflicts of interest relevant to this study.

Availability Statement

The full data set has been archived at Zenodo (Bianco et al., 2026).

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