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# **RESEARCH ARTICLE**

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#### **Key Points:**

- Orbital forcing of global sea surface temperatures (SST) evolution
- Enhancement of the obliquity signal in the global SSTs at ~2.7 Ma is closely associated with the NH glaciation
- Changes in SST may drive processes of ocean-atmosphere carbon exchange that alter atmospheric CO<sub>2</sub> concentrations

#### Supporting Information:

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

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# Orbital-Scale Global Ocean Sea Surface Temperatures Coupling With Cryosphere-Carbon Cycle Changes Over the Past 4 Million Years

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**Abstract** Changes in the thermal conditions of the ocean surface, the interface for air-sea exchange, are critical for understanding global climate and environmental change. Here we explore the evolution of sea surface temperature (SST) and the meridional SST gradient (STG) at orbital timescales since 4 million years ago (Ma), along with interactions between SSTs, the cryosphere, and the global carbon cycle. We observe orbital eccentricity and obliquity influences on SST evolution and infer that SST changes may have played a key role in atmospheric CO<sub>2</sub> and cryosphere changes through key climate transitions in the past 4 Ma. We find a major equator-to-pole STG increase in the Northern Hemisphere (NH) close to the initiation of major NH glaciation (at ~2.7 Ma). In addition, we find substantial increases in the obliquity sensitivity (S<sub>obl</sub>) of NH STG at ~2.7 Ma and in Southern Hemisphere (SH) STG at ~1 Ma, which may be responses to important expansions of NH and SH ice sheets, respectively. Phase analysis shows that SST changes spice ~1.5 Ma, which indicates that SST changes either drove, or directly reflect, processes that changed ocean-atmosphere carbon exchange and, thus, atmospheric CO<sub>2</sub> concentrations. Overall, our study emphasizes that SST changes were a critical component of climate change throughout the last 4 Ma.

**Plain Language Summary** A compilation of global sea surface temperature (SST) records indicates that SST mainly fluctuated on orbital eccentricity and obliquity timescales during the last 4 million years. The compilation also reveals an important impact of meridional ocean circulation changes on global climate since 4 Ma, with a particularly notable change in the equator-to-pole SST gradient during the initiation of major Northern Hemisphere glaciations at ~2.7 Ma. Finally, we find that SST changes played a key role in the atmospheric CO<sub>2</sub> changes associated with global climate transformations.

### 1. Introduction

The oceans play a fundamental role in the climate system due to their enormous heat-storage capacity (Deser et al., 2010), and sea surface temperature (SST) changes since the early Pliocene are thought to have been a potential cause of the onset of NH glacial cycles (Fedorov et al., 2013). In addition, SST evolution profoundly affects at-mospheric circulation patterns (Brierley et al., 2009; Fedorov et al., 2013), as the ocean can transfer energy to the atmosphere through turbulence and radiative energy exchange at the sea surface (Deser et al., 2010). As such, SST assessment is crucial for understanding the evolution of Earth's climate system and the mechanisms of climate change. The emergence of increasing numbers of SST records based on geochemical proxies, such as the alkenone unsaturation index ( $U_{37}^{K'}$ ) and foraminiferal Mg/Ca ratios, has greatly improved understanding of global long-term SST evolution since the Pliocene (Lawrence et al., 2006, 2009; Liu & Herbert, 2004; Max et al., 2020; O'Brien et al., 2014). However, it remains unclear how SST affects other climate processes under changing geological boundary conditions, such as different atmospheric CO<sub>2</sub> concentrations (Fedorov et al., 2015).

The temperature of the ocean surface, the interface of air-sea exchange, is controlled by a combination of atmospheric and oceanic processes. The air-sea temperature contrast and wind velocity dominate air-sea heat exchange, mainly in the form of latent and sensible heat (Cayan, 1992). Ocean circulation (Dowsett et al., 2009),



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Figure 1. Map of sites (black dots) from which data were retrieved (data are from: Brierley et al., 2009; Dekens et al., 2007; Etourneau et al., 2009, 2010; Hasenfratz et al., 2019; Herbert et al., 2010; Karas et al., 2011; Lawrence et al., 2006, 2009, 2010; Liu & Herbert, 2004; Martínez-Garcia et al., 2010), superimposed on a map of modern annual mean sea surface temperature (contours and colors after Fedorov et al., 2013). Numbers indicate sites from the Deep Sea Drilling Project (DSDP), the Ocean Drilling Program (ODP), the Integrated ODP and International Ocean Discovery Program (both IODP), and the International Marine Global Change Study (IMAGES). Black arrows indicate modern global ocean circulation. Acronyms: Atlantic Drift (NAD), Gulf Stream (GS), North Equatorial Current (NEC), South Equatorial Current (SEC), Humboldt Current (HC), Labrador Current (LC), California Current (CC), Equatorial Courter Current (ECC), Thousand Islands Cold Current (TICC), Kuroshio (Kuro.), Canary Cold Stream (CCS), Benguela Current (BC), Somali Warm Current (SWC), and Western Australian Cold Stream (WACS).

vertical mixing (Hasenfratz et al., 2019), and thermocline depth (Wara et al., 2005) also significantly affect SST. SST records from different latitudes (Figure 1) show large-scale variations with time similar to those in records of the oxygen isotope composition of benthic foraminifera ( $\delta^{18}O_{benthic}$ ) and atmospheric CO<sub>2</sub> concentrations, but substantial differences exist at more detailed levels (Figure 2).  $\delta^{18}O_{benthic}$  is a well-established proxy for the evolution of deep-sea temperatures and seawater  $\delta^{18}O(\delta^{18}O_{sw})$ , the latter of which is related to global ice volume (De Vleeschouwer et al., 2020; Fedorov et al., 2013; Rohling et al., 2021). Hence, similarities between large-scale variations in  $\delta^{18}O_{benthic}$  and SST reflect the global nature of glacial-interglacial cycles, while differences reflect leads, lags, and amplitude response differences that may hold clues about the nature of the processes by which they are connected.

Here we focus on three issues that remain poorly explored within the past 4 million years, namely: (a) global-scale SST evolution at orbital time scales, (b) the evolution of the meridional SST gradient (STG) between the tropics, extra-tropics, and polar regions, and (c) the relationships between SST, global ice volume, and atmospheric CO<sub>2</sub>. We investigate the role of meridional ocean circulation changes in some of the major climate events of the last 4 Myr. The first event concerns the initiation of major NH glaciation (NHG) during the Late Pliocene-Early Pleistocene (LP/EP, ~3–2.7 Ma), when the NH transitioned from warm, virtually ice-free climatic conditions to a cold, persistent ice age climate, marked by an emerging dominance of 41-kyr obliquity cycles in  $\delta^{18}O_{\text{benthic}}$  records (Lisiecki & Raymo, 2005; Westerhold et al., 2020). The second event concerns the mid-Pleistocene transition (MPT, ~1.2–0.7 Ma), when dominant 41-kyr obliquity cycles gave way to high-amplitude 100-kyr eccentricity cycles in  $\delta^{18}O_{\text{benthic}}$  records (Lisiecki & Raymo, 2005; Raymo et al., 2006; Westerhold et al., 2020).

#### 2. Materials and Methods

#### 2.1. Data Sources

The International Ocean Discovery Program (IODP) and its predecessors have provided the high-quality sediment sequences used in the generation of a valuable set of Cenozoic climate and SST. We use alkenone





**Figure 2.** Sea surface temperature (SST) and  $CO_2$  concentration records shown with benthic foraminiferal  $\delta^{18}O$  and seawater  $\delta^{18}O_{sw}$  for the past 4,000 kyr (4 Myr). (a) Benthic foraminiferal  $\delta^{18}O$  (LR04 stack; Lisiecki & Raymo, 2005). (b) Seawater  $\delta^{18}O_{sw}$  (proxy for global ice volume; Rohling et al., 2021). The direction of the arrow indicates increasing ice volume. (c) SST of ocean drilling program (ODP) Sites 982 (North Atlantic; Lawrence et al., 2009). (d) SST of deep sea drilling project Site 607 (North Atlantic; Lawrence et al., 2010). (e) SST of ODP Site 1012 (North Pacific; Brierley et al., 2009). (f) SST of ODP Site 722 (Arabian Sea; Herbert et al., 2010). (g) SST of ODP Site 1239 (Eastern equatorial Pacific; Etourneau et al., 2010). (h) SST of ODP Site 662 (Equatorial Atlantic; Herbert et al., 2010). (i) SST of ODP Site 846 (Eastern equatorial Pacific; Lawrence et al., 2006; Liu & Herbert, 2004). (j) SST of ODP Site 709°C (Indian Ocean; Karas et al., 2011). (k) SST of ODP Site 1237 (South Pacific; Dekens et al., 2007). (l) SST of ODP Site 1082 (South Atlantic; Etourneau et al., 2009). (m) SST of ODP Site 1090 (Subantarctic; Martínez-Garcia et al., 2010). (n) SST of ODP Site 1094 (Antarctic; Hasenfratz et al., 2019). (o) Estimated atmospheric CO<sub>2</sub> concentrations (Bartoli et al., 2011; Hönisch et al., 2009; Martínez-Botí et al., 2015; Stap et al., 2016; Yamamoto et al., 2022).

unsaturation index ( $U^{K'}_{37}$ ) based SST records for Site 982 from the North Atlantic (58°N, 16°W; Lawrence et al., 2009), Site 607 from the North Atlantic (41°N, 33°W; Lawrence et al., 2010), Site 1012 from the North Pacific (32°N, 118°W; Brierley et al., 2009), Site 722 from the Arabian Sea (16.6°N, 59.8°W; Herbert et al., 2010), Site 846 (3°S, 91°W; Lawrence et al., 2006; Liu & Herbert, 2004), Site 1239 (1°S, 82°W; Etourneau et al., 2010) from the Equatorial Pacific, Site 662 from the Equatorial Atlantic (1°S, 12°W; Herbert et al., 2010), Site 709°C from the Indian Ocean (3°54.9′S, 60°33.1′E; Karas et al., 2011), Site 1237 from the South Pacific (16°S, 76°W; Dekens et al., 2007), Site 1082 (21°S, 12°E; Etourneau et al., 2009) from the Southern Ocean, Site 1090 (43°S, 9°E; Martínez-Garcia et al., 2010) from the Subantarctic, and Site 1094 (53.2°S, 5.1°E; Hasenfratz et al., 2019) from the Antarctic Zone. The age models for the sites used in this study, with exception of Site 1237, are based on orbital tuning of deep-sea oxygen isotope records (LR04 stack; Lisiecki & Raymo, 2005; see Table S1 in Supporting Information S1 for details). The  $U^{K'}_{37}$  index and foraminiferal Mg/Ca are widely used to reconstruct ocean temperatures. Use of the  $U^{K'}_{37}$  proxy is limited in warm tropical regions, where the  $U^{K'}_{37}$  index can saturate at temperatures >29°C (Fedorov et al., 2013; Li et al., 2011). We include  $U^{K'}_{37}$  based SSTs for three tropical sites (Sites 662, 846 and 1239; Figure S1 in Supporting Information S1), given that values remained below that 29°C limit (Figure S1 in Supporting Information S1).

Atmospheric CO<sub>2</sub> concentrations are obtained from reconstructions based on leaf wax  $\delta^{13}$ C at IODP Site U1446 (0–1.46 Ma; Yamamoto et al., 2022) and foraminiferal  $\delta^{11}$ B (0–4 Ma; Figure 2o; Bartoli et al., 2011; Hönisch et al., 2009; Martínez-Botí et al., 2015; Stap et al., 2016). The IODP Site U1446 leaf wax  $\delta^{13}$ C record has a resolution of ~1.7 kyr, which we use for orbital-scale phase analysis. Its age model is derived from oxygen isotope tuning to the global  $\delta^{18}O_{\text{benthic}}$  (LR04) stack by Clemens et al. (2021). The  $\delta^{18}O_{\text{sw}}$  record in Figure 2b has been derived from the CENOGRID  $\delta^{18}O_{\text{benthic}}$  record of Westerhold et al. (2020) by Rohling et al. (2021), and has a 1 kyr resolution. The resolution of the collated data sets makes them suitable for analyzing changes in Earth's climate system at orbital time scales.

Meridional SST gradients (STG) are created by calculating the difference in SSTs between 2 ocean cores from different latitudes in the same ocean. For this study, we take these calculated STGs to be representative of the basin-wide situation as suggested by previous studies (Brierley et al., 2009; Wara et al., 2005). Due to differences between the temporal resolutions of the different SST records, we interpolated SST records from the different sites to 2 kyr spacing and then calculated the gradients. The North Atlantic STG is determined between ocean drilling program (ODP) sites 982 and 662; the North Pacific STG is that between ODP Sites 846 and 1012; the South Atlantic STG uses ODP sites 1082 and 1090; and the South Pacific STG is the difference between ODP Sites 1239 and 1237.

#### 2.2. Spectral Analysis

SST power spectra and sliding window spectrograms were calculated using Acycle 2.6 (Li et al., 2019). All records were detrended by fitting and removing LOESS functions (35%). SST power spectra were analyzed using the  $2\pi$ -MultiTaper Method (MTM) with robust red noise modeling to ascertain 95% confidence levels. Eccentricity and obliquity cycles in the SST records were extracted using Gaussian band-pass filtering in Acycle 2.6 (Li et al., 2019).

#### 2.3. Obliquity Sensitivity

Obliquity sensitivity (S<sub>obl</sub>) is calculated as  $\sigma^2_{STG}/\sigma^2_{La04}$ , where  $\sigma^2_{STG}$  is the temporal variance of obliquity in the STG in units of °C<sup>2</sup>, and  $\sigma^2_{La04}$  is the temporal variance of obliquity in units of degrees<sup>2</sup>, taken from the Laskar et al. (2004) orbital solution (La04). Obliquity variance was quantified using multitaper time-frequency power spectra by integrating the variance between 0.023 and 0.027 cycles/kyr (i.e., from ~43.5 to 37 kyr). All time-frequency analyses were performed using three  $2\pi$  prolate data tapers, with a 400-kyr window and a 10-kyr time step. The analysis was carried out in *R* and the *R* code was modified after Levy et al. (2019).

#### 2.4. Phase Analysis

SST- $\delta^{18}O_{sw}$  and SST-CO<sub>2</sub> phase relationships were calculated using cross-spectral analysis in the IRISSeismic package in *R* (Callahan et al., 2018). To visualize results, we invert  $\delta^{18}O_{sw}$  to make it positively correlated with sea level. Our study focuses on phase relationships between SST,  $\delta^{18}O_{sw}$ , and CO<sub>2</sub> on eccentricity scales. We calculated cross spectra using a 400-kyr sliding window and a 10-kyr step size in individual data sets. Phase analysis calculated at the ~100-kyr eccentricity scale was chosen for a 90–135 kyr period range with the highest



period coherence. The phase analysis was carried out in R and the R code was modified after De Vleeschouwer et al. (2020).

#### 2.5. Recurrence Analysis

Non-linear structure within proxy time series can help to reveal regime/system changes that cannot be validated otherwise by visual inspection or linear methods like spectral analysis (Han et al., 2020; Marwan et al., 2007). Recurrence analysis is used to identify transitions between different types of dynamics within a time series. Recurrence plots are matrix plots that visualize a fundamental property of dynamical systems–namely, when a system "repeats" itself, returning to a previous state (See Text S1 in Supporting Information S1 for a detailed description). Recurrence plots are a binary matrix where the coordinates of each entry mark the pair of time points with recurring states (Marwan et al., 2007). If climate dynamics have consistent patterns, they will show up as darker areas in the plot; if they have no common dynamics, the plot will remain white (Marwan et al., 2007; Westerhold et al., 2020). We conducted recurrence analyses of non-detrended SST data in Matlab's CRP Toolbox (Marwan, 2020).

#### 3. Results and Discussion

#### 3.1. Combined High- and Low-Latitude Forcing of Regional SSTs Since 4 Ma

There is a strong statistical relationship between  $U^{K'}_{37}$  and mean annual SST in many regions (Müller et al., 1998; Rosell-Melé, 1998); hence its use as an SST proxy. However, many studies have shown that coccolithophorid productivity (i.e., the main source of alkenone) is highest in subpolar ocean regions during the summer to autumn months (Lawrence et al., 2009; Max et al., 2020; Samtleben & Bickert, 1990). A study on coccolithophore fluxes in the Bering Sea and subpolar Pacific (Tsutsui et al., 2016) has further demonstrated that the main blooming season and export of coccolithophores is heavily biased to October–November. Despite the potential seasonal bias in the  $U^{K'}_{37}$  proxy implicit in these studies, other work has suggested that alkenone production may have been much less seasonal in the warm early Pliocene (Lawrence et al., 2009). Overall, there is potential for the SSTs reconstructed from the  $U^{K'}_{37}$  index to be biased. Our analyses provide some perspective on this, as follows.

Our analyses highlight prominent eccentricity (both 400-kyr and 100-kyr) cycles in SST records in both low and mid-latitude, and high-latitude oceans since 4 Ma (Figures 3–5; Figures S2, S3 in Supporting Information S1), and this strong eccentricity cycle is also present in SST records reconstructed using foraminiferal Mg/Ca (Site 709°C and 1094, Figures 4d and 5d). The eccentricity cycles in SST records are consistent with theoretical eccentricity cycles (Figure S3 in Supporting Information S1). Yet, annual mean insolation variability at the various sites is almost entirely dominated by obliquity, and the direct impact of eccentricity is very weak (Figure S4 in Supporting Information S1). This agrees with obliquity cycle influences on insolation (Laskar et al., 2004) and relatively negligible direct contributions of eccentricity to insolation changes (<0.1%) (Clemens & Tiedemann, 1997). However, eccentricity still modulates the amplitude of precession impacts, which controls the amount of summer insolation (e.g., equatorial Pacific planktonic foraminiferal Mg/Ca-based SSTs show dominant precession variability since 140 ka; Jian et al., 2020). This, with additional carbon cycle changes and icealbedo effects (Pälike et al., 2006), can drive major temperature responses at low latitudes (De Boer et al., 2014; Liebrand et al., 2017; Westerhold et al., 2020). Coupling between eccentricity pacing and carbon cycle variations has been inferred throughout the late Neogene based on carbon isotope variations (De Vleeschouwer et al., 2020), and is apparent also from orbital-scale covariation between global SST and atmospheric CO<sub>2</sub> concentrations (Figure 2) (also Liebrand et al., 2017; Pälike et al., 2006). We infer that whatever is measured by the  $U_{37}^{K}$  index (either annual mean SSTs, or summer and autumn SSTs) reflects predominantly precessionbased summer-insolation control, where persistence of insolation-driven summer and autumn warming affects winter SSTs due to the great thermal capacity of ocean water. Our observed prominence of eccentricity variability then reflects longer-term amplitude modulation of such precession influences.

Sliding window spectrograms of SSTs in the NH and equatorial regions reveal strong obliquity (41-kyr) variability between  $\sim$ 2.7 and  $\sim$ 0.7 Ma (except at Site 846; Figures 3 and 4; see also Figure S5 in Supporting Information S1). Although our collection of SST records from three Southern Hemisphere sites do not show a change in the obliquity signal during the Late Pliocene, a recent Southern Hemisphere SST stack that integrates additional records reveals substantial significant obliquity enhancement around 2.7 Ma (Clark et al., 2024). Our





**Figure 3.** Astronomical evolution of SSTs from ocean drilling sites at different latitudes in the Northern Hemisphere. Spectrograms with 600 kyr sliding windows with  $2\pi$  multi-taper (MTM) power spectra of (a) sea surface temperature (SST) of ocean drilling program (ODP) Site 982 since 4 Ma, (b) SST of deep sea drilling project Site 607 since 4 Ma, (c) SST of ODP Site 1012 since 4 Ma, (d) SST of ODP Site 722 since ~3.3 Ma. SSTs from these sites were reconstructed using  $U_{37}^{K'}$ . The red dotted lines on the power spectra are the 95% confidence levels. The arrows on the power *x*-axes indicate the enhancement of the periodic signal in the spectrogram. The colors in the sliding window spectrogram indicate the strength of the periodic signal, with blue-grayish blue-green indicating an increasingly strong periodic signal. The white shaded band indicates the enhancement of the obliquity signal at ~2.7 Ma.

spectral analysis of the global SST stack from the same publication shows that this enhancement of the obliquity signal at  $\sim$ 2.7 Ma is global in nature (Figure S6 in Supporting Information S1).

Obliquity signals at high latitudes are commonly interpreted in terms of annual mean solar radiation variations (Bosmans et al., 2015; Naish et al., 2009), but the reasons for weaker obliquity before ~2.7 Ma and after ~0.7 Ma are uncertain. At low latitudes, the proportional impact of obliquity on annual mean insolation is relatively small (cf. spatio-temporal illustrations in Loutre et al., 2004; Rohling et al., 2012), but we still observe a marked obliquity signal in tropical SST records between ~2.7 and ~0.7 Ma (Figure 4). Obliquity signals have also been found after ~2.7 Ma in other low latitude records (e.g., Lourens et al., 2001). Some studies have suggested ocean circulation as a possible mechanism for transfer of high-latitude obliquity influences to lower latitudes (Jouzel et al., 2007). Other studies have suggested that interhemispheric temperature gradients may be critical (Bosmans et al., 2015; Li et al., 2017; Raymo & Nisancioglu, 2003). Meridional temperature gradients drive both





**Figure 4.** Astronomical evolution of sea surface temperature (SST) from ocean drilling sites in the equatorial region. Spectrograms with 600 kyr sliding windows with  $2\pi$  multi-taper (MTM) power spectra of (a) SST of ocean drilling program (ODP) Site 662 since 4 Ma, (b) SST of ODP Site 1239 since 4 Ma, (c) SST of ODP Site 846 since ~3.9 Ma, (d) SST of ODP Site 709°C from ~4.9 to ~2.2 Ma. SST of ODP Sites 709°C were reconstructed using foraminiferal Mg/Ca, and the remaining SST temperatures were reconstructed using U<sup>K'</sup><sub>37</sub>. The red dotted line on the power spectra are the 95% confidence levels. The arrows on the power *x*-axes indicate the enhancement of the periodic signal in the spectrogram. The colors in the sliding window spectrogram indicate the strength of the periodic signal, with blue-grayish blue-green indicating an increasingly strong periodic signal. The white shaded band indicates the enhancement of the obliquity signal at ~2.7 Ma.

atmospheric heat and moisture transport toward the poles (Brierley & Fedorov, 2010; Fedorov et al., 2013; Raymo & Nisancioglu, 2003). However, the hemispheric insolation gradient has not changed significantly since 4 Ma, and no consensus explanation has yet been reached for the abrupt appearance of the obliquity signal at that time, for its strength across the LP/EP, or for its weakness after the MPT (especially at low latitudes) (Kender et al., 2018; Raymo et al., 2006; Yehudai et al., 2021). The explanation must include a mechanism that amplifies the Earth system response to obliquity variations, including especially its unexpected predominance at low latitudes.

To investigate this issue, we calculate meridional SST gradients (STG) in the North Pacific, North Atlantic, South Pacific and South Atlantic (Figure 6). We also present a new assessment of STG sensitivity to obliquity forcing  $(S_{obl})$ , which represents the ratio of obliquity-band variance in STG to the variance in obliquity (Figure 6; see Section 2). Given that previous studies have demonstrated that the influence of obliquity-driven ocean dynamics changes is amplified when Antarctic or Northern Hemisphere ice sheets expand into the marine environment (Cao





**Figure 5.** Astronomical evolution of sea surface temperature (SST) from ocean drilling sites at different latitudes in the Southern Hemisphere. Spectrograms with 600 kyr sliding windows with  $2\pi$  multi-taper (MTM) power spectra of (a) SST of ocean drilling program (ODP) Site 1237 since 4 Ma, (b) SST of ODP Site 1082 since ~3.5 Ma, (c) SST of ODP Site 1090 since ~3.6 Ma, (d) SST of ODP Site 1094 from 1.5 to 0.9 Ma. ODP Sites 1094 were reconstructed using foraminiferal Mg/Ca, and the remaining SST temperatures were reconstructed using U<sup>K</sup><sub>37</sub>. Note that the absence of an obliquity signal in the SST record at ODP Site 1237 is likely due to this record's lower temporal resolution (~14 kyr). The red dotted line on the power spectra are the 95% confidence levels. The arrows on the power *x*-axes indicate the enhancement of the periodic signal in the spectrogram. The colors in the sliding window spectrogram indicate the strength of the periodic signal, with blue-grayish blue-green indicating an increasingly strong periodic signal.

et al., 2021; Levy et al., 2019), variations in S<sub>obl</sub> may reflect major changes in terrestrial versus marine-based ice sheet responses to obliquity forcing (Levy et al., 2019).

We find substantial  $S_{obl}$  increases in NH STG records at ~2.7 Ma (Figures 6b and 6c), without noticeable  $S_{obl}$  changes in SH STG records (Figures 6d and 6e). At the same time, the STG in the NH also increased significantly at ~2.7 Ma (Figures 6b and 6c). The ~2.7 Ma time interval marks the intensification of Northern Hemisphere glaciation (iNHG), which is recognized in climate proxy data that include deep-sea oxygen isotopes (Lisiecki & Raymo, 2005; Westerhold et al., 2020), North Atlantic planktonic foraminiferal assemblages (Dowsett & Poore, 1990) and ice rafted debris records (Smith et al., 2018). This suggests that the strong global expression of obliquity in SST records at ~2.7 Ma likely resulted from  $S_{obl}$  increase associated with establishment of large-scale NH ice sheets. Conversely, a distinct  $S_{obl}$  increase in SH STG records at ~1 Ma may reflect expansion of the East Antarctic ice sheet (EAIS) margin into the ocean (Raymo et al., 2006), which would result in an enhanced

response to obliquity in the SH (Levy et al., 2019). EAIS expansion into the ocean at around this time agrees with drill core data that indicate widespread expansion of a marine-based ice sheet in the Ross Embayment at the MPT (McKay et al., 2012). A S<sub>obl</sub> decrease in the North Atlantic and North Pacific STGs at ~2.4 Ma (Figures 6b and 6c) corresponds to a negative  $\delta^{18}O_{sw}$  shift (Figure 6a), which suggests that a reduction in global ice volume led to a S<sub>obl</sub> decrease in the climate records.

#### 3.2. Coupling Between SST, Carbon Cycle, and Cryospheric Changes Since 4 Ma

The causes of the iNHG at ~2.7 Ma and subsequent frequency and amplitude changes of glacial cycles remain debated (Chalk et al., 2017; Kender et al., 2018; Willeit et al., 2019; Yehudai et al., 2021). Explanations for the LP/EP and MPT climate changes often invoke atmospheric CO<sub>2</sub> and ice volume variations as critical links between orbital forcing and the climate response (Willeit et al., 2019; Yehudai et al., 2021). Hence, we investigate relationships between SST, global ice volume ( $\delta^{18}O_{sw}$ ), and atmospheric CO<sub>2</sub> concentrations using time-evolutive SST- $\delta^{18}O_{sw}$  and SST-CO<sub>2</sub> phase analysis on 100-kyr eccentricity timescales (90–135 kyr period range). We use 400-kyr-wide sliding windows and 10-kyr steps to calculate leads and lags between SST,  $\delta^{18}O_{sw}$ , and CO<sub>2</sub> concentrations (see Methods). We find that SST led CO<sub>2</sub> concentrations for most of the time since ~1.5 Ma, with a lead of about 0–17 kyr (0–60°, Figure 7b) (ODP Sites 662, 709°C and 1237 were not used for phase analysis due to data discontinuities and their low temporal resolution). SST led global ice volume for most of the time since ~4 Ma, with a lead time of about 0–28 kyr (0–100°). However, some sites show that ice volume led SST between 2.2 and 1.5 Ma. The phase difference at these times is relatively large (50–180°; 14–50 kyr), which may suggest a decoupling between ice volume and SST between 2.2 and 1.5 Ma (Figure 7a).

The persistent lead of SSTs over global CO<sub>2</sub> concentrations (since 1.5 Ma) and ice volume (since 4 Ma, except for 2.2–1.5 Ma) suggests that SST changes played an important role in global climate cycles since 4 Ma. We find that the phase difference between CO<sub>2</sub> and ice volume is smaller and more stable  $(0-25^{\circ}; 0-7 \text{ kyr})$  than the phase difference between SST and ice volume  $(0-100^\circ; 0-28 \text{ kyr})$ , which suggests that CO<sub>2</sub> changes are more likely to be directly responsible for changes in global ice volume. This result could be informative also in the context of future climate change caused by anthropogenically forced increase in atmospheric CO<sub>2</sub>. Reconstructed CO<sub>2</sub> data suggest a significant decrease from  $\sim 2.7$  Ma (Figure 20), associated with the iNHG. Due to a lack of highresolution atmospheric CO<sub>2</sub> reconstructions before 1.5 Ma, we have no way to determine phase relationships between CO<sub>2</sub>, SST, and ice volume at  $\sim$ 2.7 Ma. However, we find that SST has continued to lead atmospheric CO<sub>2</sub> since ~1.5 Ma (Figure 7b; Figure S7 in Supporting Information S1). There is about 39,000 PgC of dissolved carbon stored in the oceans; more than 13 times the amount in the atmosphere and terrestrial biosphere combined (IPCC, 2007). Therefore, the mechanisms responsible for long-term changes in atmospheric CO<sub>2</sub> concentrations likely are ocean-related (Kohfeld & Ridgwell, 2009). Previous work has elucidated the importance of carbon redistribution between the atmosphere and ocean carbon reservoirs in driving atmospheric CO<sub>2</sub> changes, notably through CO<sub>2</sub> sequestration/release from the deep ocean (e.g., De Boer & Hogg, 2014; Hasenfratz et al., 2019; Kohfeld & Chase, 2017; Kohfeld & Ridgwell, 2009; Sigman et al., 2010; Yu, Anderson, & Rohling, 2014, Yu, Anderson, Jin, et al., 2014, 2016, 2019, 2020).

Explaining the large (>100 ppm) atmospheric  $CO_2$  drops associated with glacials requires a complex set of interconnected oceanic processes, including: (a) direct dissolution of atmospheric CO2 into seawater (Kohfeld & Ridgwell, 2009; Martin et al., 2005; Yu, Anderson, & Rohling, 2014); (b) enhanced ocean biological pump activity (Hain et al., 2014; Martínez-Garcia et al., 2011); (c) weakened deep-ocean circulation (Farmer et al., 2019; Pena & Goldstein, 2014); and (d) reduced CO<sub>2</sub> exchange between the deep sea and the surface ocean ("stratification"; Martin et al., 2005; Hasenfratz et al., 2019). Sequestered CO<sub>2</sub> becomes "trapped" in the deep sea, as confirmed by deep-sea  $[CO_3^2]$  reconstructions (Anderson et al., 2008; Ridgwell & Zeebe, 2005; Yu et al., 2016, 2019, 2020). Air-sea disequilibrium can also enhance ocean carbon storage (Eggleston & Galbraith, 2018; Ito & Follows, 2013; Khatiwala et al., 2019; Odalen et al., 2018). In fact, previous studies in the Southern Ocean and the subarctic North Pacific based on biogenic opal accumulation and nitrogen isotope records indicate that a transition toward permanent polar ocean water-column stratification at ~2.7 Ma may have been a key driver of the atmospheric CO<sub>2</sub> decline (Haug et al., 1999; Sigman et al., 2010). This polar ocean stratification is thought to have been controlled by both temperature and salinity changes (Sigman et al., 2004). Our compiled data set indicates that North Atlantic and North Pacific SSTs decreased markedly from 4 to ~2.7 Ma (ODP Sites 982 and 607; Figures 2c and 2d), while the corresponding STG increased (Figures 6b and 6c). NH high latitude cooling (ODP Sites 982 and 1012, Figures 2c and 2e) would increase the equatorial-to-polar meridional





**Figure 6.** Meridional SST gradients (STG) and STG obliquity sensitivity ( $S_{obl}$ ) for the North Atlantic, North Pacific, South Atlantic and South Pacific since 4 Ma. (a) Seawater  $\delta^{18}O_{sw}$  (proxy for global ice volume; Rohling et al., 2021). The black arrow indicates increasing ice volume. (b) Meridional SST gradients between ocean drilling program (ODP) Sites 846 (3°S, 91°W; Lawrence et al., 2006; Liu & Herbert, 2004) and 1012 (32°N, 118°W; Brierley et al., 2009) for North Pacific and obliquity sensitivity ( $S_{obl}$ ). (c) Meridional SST gradients between ODP Site 662 (1°S, 12°W; Herbert et al., 2010) and 982 (58°N, 16°W; Lawrence et al., 2009) for North Atlantic and obliquity sensitivity ( $S_{obl}$ ). (c) Meridional SST gradients between ODP Site 662 (1°S, 12°W; Herbert et al., 2010) and 982 (58°N, 16°W; Lawrence et al., 2009) for North Atlantic and obliquity sensitivity ( $S_{obl}$ ). (c) Meridional SST gradients between ODP Site 662 (1°S, 12°W; Herbert et al., 2010) and 982 (58°N, 16°W; Lawrence et al., 2009) for North Atlantic and obliquity sensitivity ( $S_{obl}$ ). (c) Meridional SST gradients between ODP Site 562 (1°S, 12°W; Herbert et al., 2010) and 982 (58°N, 16°W; Lawrence et al., 2009) for North Atlantic and obliquity sensitivity ( $S_{obl}$ ). (c) Meridional SST gradients between ODP Sites 1239 (1°S, 82°W; Etourneau et al., 2010) and 1237 (16°S, 76°W; Dekens et al., 2007) for South Pacific and obliquity sensitivity ( $S_{obl}$ ). (e) Meridional SST gradients between ODP Sites 1082 (21°S, 12°E; Etourneau et al., 2009) and 1090 (43°S, 9°E; Martínez-Garcia et al., 2010) for South Atlantic and obliquity sensitivity ( $S_{obl}$ ). The thick black lines are  $S_{obl}$ .



# **Paleoceanography and Paleoclimatology**



**Figure 7.** Phase analysis of SST- $\delta^{18}O_{sw}$  and SST-CO<sub>2</sub> concentrations at the 100-kyr eccentricity scale over the past 4 Ma. A typical confidence interval is  $\pm 6^{\circ}$ . The  $\delta^{18}O_{sw}$  data are from Rohling et al. (2021), atmospheric CO<sub>2</sub> concentrations are obtained from reconstruction based on leaf wax  $\delta^{13}C$  at IODP Site U1446 (0–1.46 Ma; Yamamoto et al., 2022). Note that the red symbols and lines indicate SSTs in the NH, the green symbols and lines indicate SSTs in the equatorial regions, and the blue symbols and lines indicate SSTs in the SH. The time is based on the center of the window.

temperature gradient (Figures 6b and 6c), strengthening water vapor transport from the tropics (tropical Pacific and tropical Atlantic) to the Arctic (Brierley & Fedorov, 2010; Loutre et al., 2004) through the temperature-moisture feedback (Källén et al., 1979; Raymo & Nisancioglu, 2003). At the same time, NH high latitude cooling promotes Northern Hemisphere ice sheet development (Brierley & Fedorov, 2010; Lunt et al., 2008).

High latitude cooling and increased sea ice cover cause intensification of water-column stratification (Sigman et al., 2004) and, thus, favor enhanced carbon accumulation in the deep-sea (Eggleston & Galbraith, 2018; Marinov et al., 2008; Odalen et al., 2018). In sum, oceanic processes associated with high-latitude SST reduction were crucial to atmospheric  $CO_2$  reduction and NH glacial intensification during the Late Pliocene. This is supported by a substantial  $S_{obl}$  increase for NH STG at ~2.7 Ma (Figures 6b and 6c). Several studies have proposed a simple inverse correlation between global mean surface temperature and STG measures, indicating a robust and fairly universal relationship through the past 10 million years (at low resolution) and the Eocene (on eccentricity time scales; Fokkema et al., 2024; Gaskell et al., 2022; Liu et al., 2022). Similarly, we find both a notable STG increase (Figures 6b–6d) and a distinct global SST decrease at ~2.7 Ma (Figures 2c–2m). The predictability of this relationship between global (sea) surface temperature and STG may be relevant to future climate change.

In contrast to the atmospheric CO<sub>2</sub> decrease from ~2.7 Ma, there is no notable long-term (>100 kyr) atmospheric CO<sub>2</sub> decrease after 1 Ma (Figure 2o), even though SST near Antarctica continued to decrease (ODP Site 1094). We note that Arctic SST (ODP Site 982) does not show this SST decrease. Inconsistent evolution of SST changes for the two poles gives a strong indication that global ice volume increases after 1 Ma had an important Antarctic component (Figure 2b). Mid-Pleistocene high latitude cooling may have caused persistent East Antarctic ice sheet expansion into the ocean so that it no longer contained an extensive terrestrial margin, which would favor in-phase variability of NH and SH ice sheets (Raymo et al., 2006). Ocean temperature plays an important role in controlling long-term fluctuations in ice sheet margins (Joughin et al., 2012), with marinebased ice particularly susceptible to rapid changes in ocean heat supply (Mengel & Levermann, 2014). Such mass balance sensitivity to ocean temperature has been emphasized for the EAIS (Hansen et al., 2015; Hasenfratz et al., 2019; McKay et al., 2012; Pollard & DeConto, 2009). Overall, therefore, we infer that EAIS variability may have become amplified from ~1 Ma by the development of an extensive marine ice sheet margin.

To test our argument about fundamental transitions in the relationships between SST, STG, and high-latitude ice sheets, we performed recurrence analyses of the NH and SH STG, as well as global ice volume ( $\delta^{18}O_{sw}$ ). Results highlight major global ice volume shifts at ~2.7 and ~1 Ma (Figure 8a), consistent with previous studies that suggest a major global climate transition associated with high-latitude ice sheet development (Westerhold et al., 2020). Recurrence analyses of STG in the North Atlantic and North Pacific (ODP Sites 662–982 and 846–1012; Figures 8b and 8c) show a major shift at ~2.7 Ma, suggesting a link between NH STG and iNHG. Conversely, recurrence analyses of STG in the South Atlantic and South Pacific (Sites 1082–1090 and 1239–1237; Figures 8d and 8e) show a major transition at ~1 Ma, in agreement with the aforementioned concept of widespread marine EAIS margin development. The recurrence analyses, therefore, support our previous interpretations that there were two key climate transitions since 4 Ma (LP/EP and MPT) that contained critical involvement of SST and STG changes with distinctly different expressions (and, hence, governing processes) between the two hemispheres.

#### 4. Conclusions

We compiled globally distributed SST records to investigate the involvement of orbital-scale SST trends and oceanic meridional temperature gradient changes in key climate transitions during the last 4 million years. We observe important orbital eccentricity and obliquity influences in the SST evolution, and infer both summer insolation and high-latitude ice volume (feedback) impacts on global SST. We find that the SST in the NH and the equatorial region shows a significant enhancement of the obliquity signal at ~2.7 Ma, and at the same time, the NH meridional SST gradient as well as its obliquity sensitivity also increases sharply at ~2.7 Ma. We infer that the enhancement of the obliquity signal in the NH and equatorial region during this period originates from large-scale NH ice sheet expansion. In addition, the increase in obliquity sensitivity of the southern hemisphere meridional SST gradient at ~1 Ma may be attributed to oceanward expansion of the Antarctic ice sheet margin. Phase analysis revealed key links between variations in SST, global ice volume, and atmospheric CO<sub>2</sub> levels, which underpinned the major climate shifts. Changes in SST can directly affect not only the formation and development of high-latitude ice sheets, but also global temperatures and thus ice volume by controlling changes in the atmospheric CO<sub>2</sub> concentration.





**Figure 8.** Recurrence plots of Global ice volume ( $\delta^{18}O_{sw}$ ) and surface temperature gradients (STG) in the NH and SH. (a–e) Show recurrence plots of  $\delta^{18}O_{sw}$  (global ice volume), STG in the North Atlantic, STG in the North Pacific, STG in the South Atlantic and STG in the South Pacific, respectively. The red arrows on top of the recurrence plots indicate points in time when transitions occurred. Transitions in these recurrence plots from darker areas to white areas indicate prominent systems changes (Marwan et al., 2007), see also Section 2.5 for further details. Global ice volume shows changes at ~2.7 and ~1 Ma. NH STG (ocean drilling program (ODP) 662–982; ODP 846–1012) show a change at ~2.7 Ma; SH STG (ODP 1239–1237; ODP 1082–1090) show a change at ~1 Ma. Note that subplot b has a different time axis than all the other subplots due to the lack of sea surface temperature data between ~1.5–0.5 Ma of ODP 662 in the North Atlantic.

### Data Availability Statement

The SST data are available at Zhang (2024a). The data analysis was carried out in *R*. The complete codes reported in this study are available at Zhang (2024b).

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