Amplified seasonality in western Europe in a warmer world

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This is a non-peer reviewed pre-print. This manuscript has been submitted for publication in the journal Science Advances.

Abstract

Documenting the seasonal temperature cycle constitutes an essential step towards mitigating risks associated with extreme weather events in a future warmer world. The mid-Piacenzian Warm Period (mPWP), 3.3 – 3.0 million years ago, featured global temperatures approximately 3°C above pre-industrial levels. It represents an ideal period for directed paleoclimate reconstructions equivalent to model projections for 2100 under moderate Shared Socioeconomic Pathway SSP2-4.5. Here, seasonal clumped isotope analyses in fossil mollusc shells from the North Sea are presented to test Pliocene Model Intercomparison Project 2 outcomes. Joint data and model evidence reveals enhanced summer warming (+4.2 ± 2.6 °C) compared to winter (+2.2 ± 2.0°C) during the mPWP, equivalent to SSP2-4.5 outcomes for future climate. We show that Arctic Amplification of global warming weakens mid-latitude summer circulation while intensifying seasonal contrast in temperature and precipitation, leading to an increased risk of summer heatwaves and other extreme weather events in Europe's future.

Teaser: Seasonal scale climate reconstructions and models show that CO_2 increase warms up Europe's summers faster than its winters.

Introduction

The mid-Piacenzian Warm Period (mPWP) represents an interval with global temperatures estimated on average 3.2°C (1.7 – 5.2°C) higher than pre-industrial climate due predominantly to elevated atmospheric CO_2 concentrations (~400 ppmV)[1–3]. Temperatures during this period closely resemble the mean global temperatures projected for the year 2100 following the Shared Socioeconomic Pathway (SSP) 2-4.5[4–7], the SSP scenario most likely to occur given the current global climate policy[8]. The Pliocene Model Intercomparison Project 2 (PlioMIP2) consortium has targeted the mPWP using an ensemble of General Circulation Models[9]. This allows a detailed data-model comparison, which is essential for assessing the performance of climate models simulating climate scenarios with higher temperatures than represented in instrumental records, similar to conditions which will most likely define future climate on Earth[2,5].

One region under extreme threat in a global warming scenario is the Arctic region that is anticipated to warm up two to four times faster than the global average, a phenomenon called Arctic Amplification[10]. Model experiments using future CO_2 forcing scenarios imply that Arctic Amplification caused by global warming of mPWP magnitude might impact the storm-track affected regions of European climate by weakening atmospheric summer circulation[11], significantly reducing summer cloud cover[12] and leading to persistently elevated summer temperatures and droughts over Europe[13,14]. Considering these "dynamic" drivers of summer weather extremes, related to changes in atmospheric circulation, in future projections would result in more extreme weather variability than expected based on "thermodynamic" drivers based on temperature changes alone[14]. Given this season-specific response of weather patterns to warming, seasonal scale reconstructions of mPWP climate are crucial to validate climate model simulations and improve our understanding of the impact of higher atmospheric greenhouse gas concentrations on European climate.

Yet, climate proxy records from pelagic sediment cores, which form the predominant method of estimating mPWP temperatures[15–17], rarely resolve seasonal scale variability in the temperature cycle due to low temporal resolution. Furthermore, short-lived marine organisms that make up pelagic sediments preferentially grow only during specific seasons with favourable conditions. This seasonal bias places considerable uncertainty on marine climate reconstructions and data-model comparisons based on common temperature proxies, such as Mg/Ca and stable isotope ratios in foraminifera[18], TEX_{86} from membrane lipids in Crenarchaeota[19] and $U_{37}^{K'}$ based on ketones in haptophyte algae[20]. Likewise, previous studies have highlighted the challenge of reconciling seasonal-scale mPWP climate reconstructions and models of terrestrial seasonality[21].

One approach to facilitate seasonal data-model comparison is to use marine molluscs that record daily to decadal scale variability in the chemistry of their calcium carbonate shells[22–25], and preserve this high-resolution environmental variability on geological timescales[26–28]. Climate reconstructions from mid-latitude shelf seas, where these molluscs are common, are instrumental in assessing the impact of warming on the seasonal scale, because these regions experience high seasonal temperature contrast and their ecosystems are strongly impacted by climate change[29–32]. Going a step further, by using the clumped isotope composition of shell carbonate, it becomes possible to reconstruct seasonal temperature changes of the water in which molluscs grow without relying on uncertain assumptions of the isotopic composition of past ocean water, leading to accurate reconstructions of past seasonality [26,33,34].

We present seasonal sea surface temperature (SST) reconstructions based on clumped isotope analyses from well-preserved fossil mollusc shells originating from the Lillo Formation (northern Belgium; see

Methods). These sediments were deposited below fair-weather wave base (30 – 50 m water depth) in the southern North Sea (SNS) during the warm, high-sea level intervals during and slightly after the mPWP (2.7 – 3.3 Ma[35,36]; **Fig. 1**). These shells record marine temperatures in the mPWP southern North Sea[37], an important model ecosystem for temperate shelf seas worldwide[38]. Based on the observation of sedimentary structures indicative of strong tidal mixing[39], the absence of dysoxic fauna (see **Online Methods**) and the observation of high spring temperatures (see **Results**; **Fig. 2-3**), it seems likely that the shells used in this study record conservative summer temperatures close to the true summer SST during the mPWP.

We directly compare our seasonal SST reconstructions with the results of PLIOMIP2 ensemble model simulations of seasonal temperature changes in the SNS during the mPWP as well as with instrumental temperature records in the region and Coupled Model Intercomparison Project Phase 6 (CMIP6) SSP2-4.5 projections of European climate for the year 2100. This approach offers a detailed glimpse of the potential future climate in Europe under a moderate emission scenario.

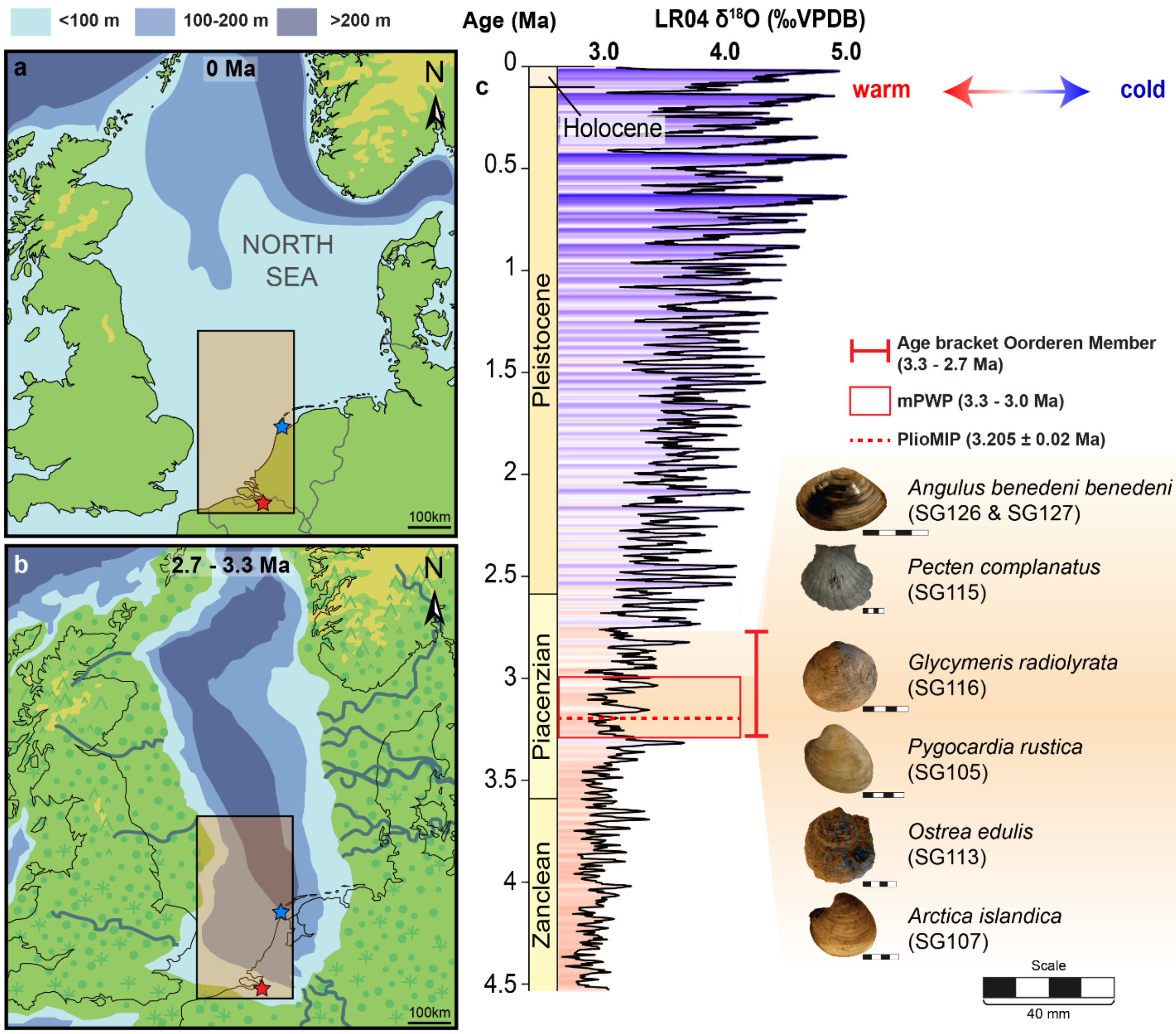

Figure 1: **Locality of the study site and long-term climate context**. Maps of northwestern Europe showing the present (**a**) and estimated mPWP (**b**; after[35,37,40]) SNS bathymetry. The locality of fossil shells (red star), the local temperature record (blue star) and the area containing the SNS data integrated from extended reconstructed SST (ERSSTv5), PlioMIP2 and CMIP6 models (black rectangle with orange filling; 51-55°N, 2-4°E; **Fig. 2-3**) is indicated. **(c)** Age bracket of the Oorderen Member (Lillo formation) containing the mollusc specimens[35] (orange shaded region) relative to the mPWP[41] (red box) and PlioMIP2[1] interval (dashed red line) and the global benthic foraminifera oxygen isotope stack[42] with relative temperature change indicated. Note that mollusc specimens likely originate from highstand (i.e., warmer) periods within the age bracket (see **Online Methods**).

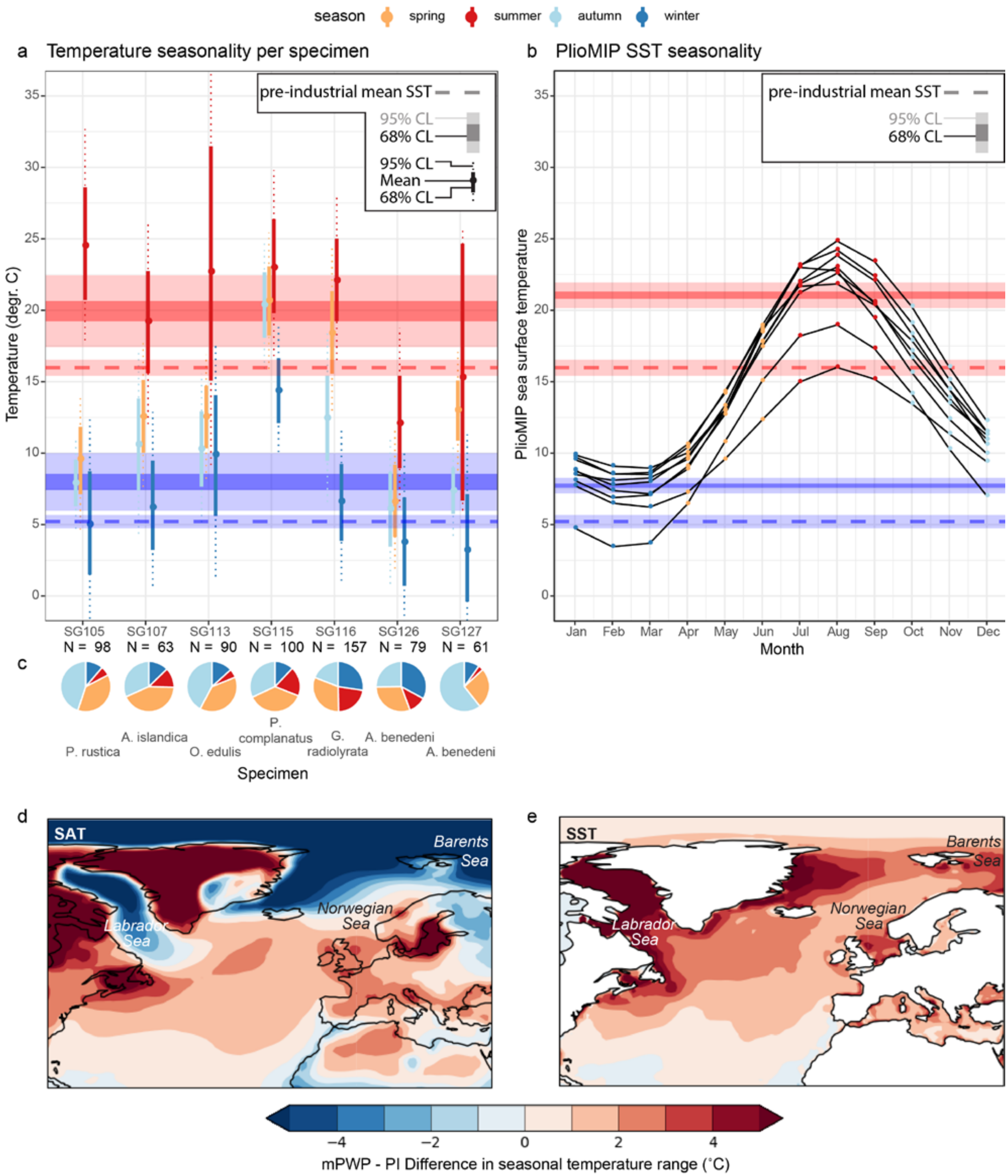

Figure 2: Data-model comparison. (**a**) Weighted mean seasonal temperatures per specimen (filled circles with solid and dotted vertical lines indicating 68% and 95% confidence levels, respectively) and summer and winter temperatures based on the complete dataset (horizontal shaded bars in red and blue, respectively) with propagated uncertainties (68% and 95% confidence level; see **Online Methods**). Dashed horizontal lines in the same colours indicate mean pre-industrial SNS SST. (**b**) Local monthly SST outcomes

of individual PLIOMIP2 models with winter (Jan-Mar; blue) and summer (Jul-Sep; red) temperature estimates (horizontal shaded bars showing 68% and 95% CL). Dashed lines in the same colours indicate mean SST outcomes (with uncertainty; 95% CL[9]) from pre-industrial control simulations using the same models. (**c**) Clumped isotope sample sizes and seasonal representation of samples per specimen. Panel **(d)** and **(e)** show spatial variability in the difference in seasonal contrast (July - January) in surface air temperature (SAT; **d**) and SST **(e)**, respectively, between PLIOMIP2 multi-model mean mPWP runs and PLIOMIP2 PI control runs of the same models.

Results

Data-model agreement on enhanced summer warming in the North Sea

Aggregated results from all bivalve specimens give weighted winter (8.0 ± 2.0°C), spring (13.1 ± 1.6°C), summer (19.9 ± 2.5°C) and autumn (10.0 ± 1.4°C) SST averages during the mPWP in the SNS (**Fig. 2a**). The reconstructed winter and summer temperatures agree with winter (January-March; 7.7 ± 0.5°C) and summer temperatures (July-September; 21.1 ± 0.9°C) from aggregated PLIOMIP2 model results (**Fig. 2b**). Both reconstructed and modelled winter and summer temperatures are significantly higher than winter (5.2 ± 0.9°C) and summer temperatures (16.0 ± 0.6°C) in pre-industrial (280 ppmV CO_2) PLIOMIP2 control runs and instrumental records (**Fig. 2a-b**). Our reconstructions yield 2.2 ± 2.0°C warmer winters and 4.2 ± 2.6°C warmer summers during the mPWP compared to mean winter (5.8 ± 0.3°C) and summer temperatures (15.7 ± 0.4°C) in the SNS over the period 1854-1900 CE (**Fig. 3a**; based on NOAA ERSSTv5[43]).

Locally elevated spring temperatures

Intriguingly, mollusc-based reconstructions yield significantly higher spring (April-June; 13.1 ± 1.6°C) than autumn (October-December; 10.0 ± 1.4°C) temperatures during the mPWP. This contrasts with regional SNS SST averages from both pre-industrial (spring: 9.4 ± 1.0°C; autumn: 10.3 ± 0.8°C) and mPWP (spring: 13.0 ± 1.2°C; autumn: 13.6 ± 1.1°C) PLIOMIP2 model runs as well as ERSST SNS SST averages (spring: 9.5 ± 0.3°C; autumn: 10.9 ± 0.3°C), which consistently yield higher temperatures in autumn compared to spring. Contrarily, local pre-industrial instrumental SST time series from the SNS coast (NIOZ monitoring station on the island of Texel, NW Netherlands[44]; see **Fig. 1a-b**; **Online Methods**) do exhibit significantly elevated spring temperatures (11.4 ± 0.5°C) compared to autumn (9.1 ± 0.5°C). Shallow coastal waters, such as the tidal flats of the Wadden Sea close to the NIOZ monitoring station, are highly responsive to air temperature, which leads to elevated sea surface temperatures in the spring season, while more offshore areas of the North Sea have higher thermal inertia, explaining elevated autumn temperatures[44]. The elevated spring and reduced autumn SST reconstructions thus highlight that the mollusc shells record detailed seasonal SST variability in the coastal SNS during the mPWP.

Inter-specimen variability

Reconstructed seasonal temperatures vary between fossil shell specimens, with some species recording warmer temperatures (e.g. *Pecten complanatus*; SG115; winter: 14.4 ± 4.3°C, summer: 23.0 ± 4.2°C) and others cooler temperatures (e.g. *Angulus benedeni benedeni*; SG126 & SG127; winter: 3.2 ± 6.7°C, summer: 13.0 ± 2.1°C; **Fig. 2a**). These inter-species differences probably occur due to the occurrence of growth stops, and variations in growth rates between seasons (**Fig. 2c**) and between consecutive growth years (see **Supplementary Information Figure S13-S26**), which dampen seasonality due to the averaging of samples around the seasonal extreme. In addition, variability between specimens may arise from differences in the seasonal temperature range within their age range (2.7 – 3.3 Ma; see **Fig. 1c**). Our weighed averages of summer and winter temperatures (**Fig. 2a**) ensures this inter-specimen variability does not bias the reconstructions.

PLIOMIP2 models reproduce SST seasonality in the modern North Sea

Transient simulations of SNS SST seasonality from before the Industrial Revolution (1850 CE) to present-day (2023 CE) by the CMIP6 model ensemble[6] mimic historical SST records from the region[43] (**Fig 3a**). Seasonal SNS SST simulations by the PlioMIP2 model ensemble under preindustrial radiative forcing[9] (winter: 5.2 ± 0.5°C; summer: 16.0 ± 0.6°C) closely resemble pre-industrial (1850 – 1900 CE) CMIP6 seasonal SNS SST simulations (winter: 5.5 ± 0.3°C; summer: 15.7 ± 0.7°C) and historical winter (5.8 ± 0.3°C) and summer SNS SST (15.7 ± 0.4°C) records[43] (**Fig. 3b**). Local SST records from the NIOZ monitoring station on Texel[44] reveal slightly higher seasonal SST ranges (winter: 4.0 ± 0.3°C; summer: 17.1 ± 0.2°C; **Fig. 3b**) which are well explained by their coastal location (see above). This agreement shows that PLIOMIP2 models successfully reproduce summer and winter SSTs in the SNS.

The mid- to high latitude seasonal temperature response to mPWP-like warming

Maps of PLIOMIP2 seasonal SST outcomes show that the enhanced seasonal contrast observed in our reconstructions is present throughout the mid to high latitudes in the North Atlantic (**Fig. 2e**). Enhanced SST seasonality is more pronounced in areas which are characterized by high seasonal contrast in surface air temperature and cold winters (e.g. Labrador Sea and Barents Sea) than in regions with milder winters (e.g. Norwegian Sea). Contrarily, surface air temperature (SAT) only shows enhanced seasonal contrast in the mid-latitudes under mPWP conditions (**Fig. 2d**). Areas with the strongest enhanced seasonal SST contrast (e.g. Labrador Sea and Barents Sea; **Fig. 2e**) show a reduced seasonal SAT contrast under mPWP conditions compared to the PI control runs (**Fig. 2d**). PLIOMIP2 model simulations of sea ice extent (**Supplementary Information Figure S33**) show that these regions where the SST and SAT seasonality respond differently to mPWP-scale warming are characterized by winter sea ice cover in PI runs. They lose much of their winter sea ice under mPWP conditions. A 53% decrease in mean annual sea ice extent during the mPWP compared to pre-industrial climate is simulated in PLIOMIP2 models[45]. Contrarily, areas with enhanced summer warming in both SST and SAT are sea-ice free year-round in both mPWP and PI model runs. SAT seasonality over land (both in North America and Europe; **Fig. 2d**) is enhanced in both mid and high latitudes, following the SST pattern. At the same time, PLIOMIP2 model outcomes show that summer cloud cover is severely reduced in the mid-latitudes of the North Atlantic, where both SST and SAT seasonality is enhanced (**Supplementary Information Figure S34-S35**).

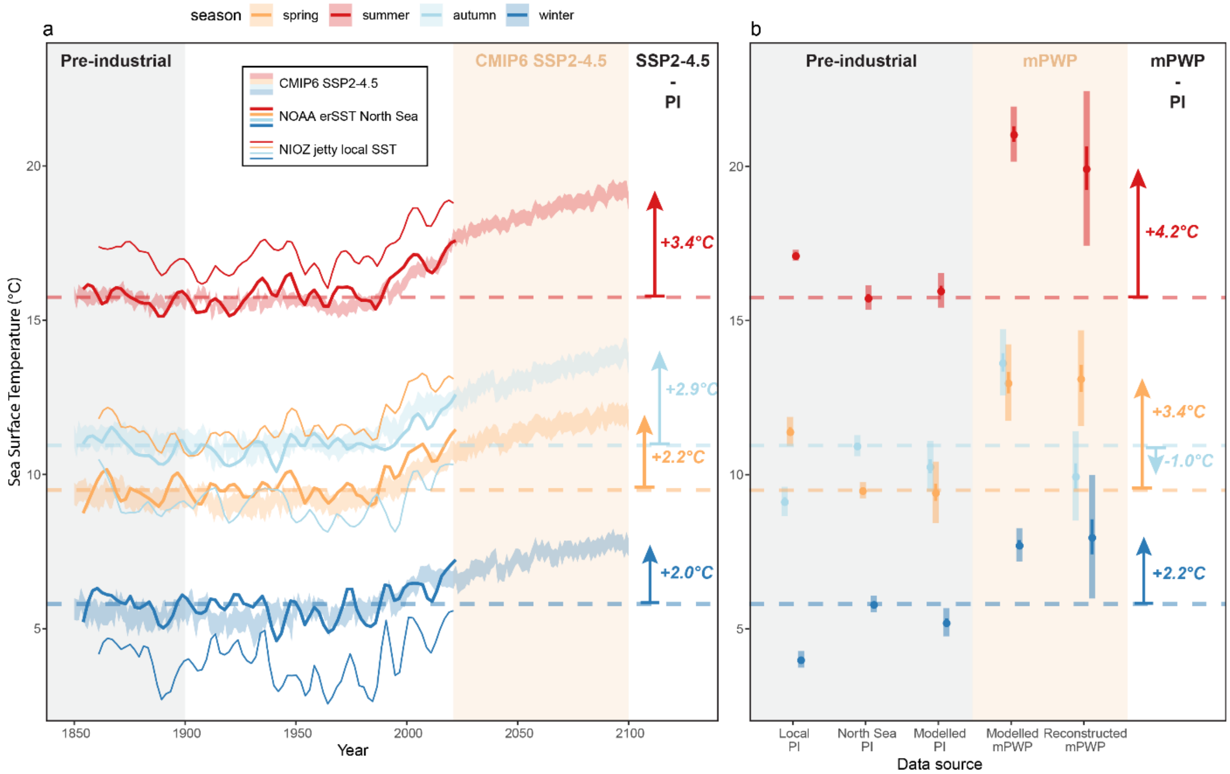

Figure 3: Pliocene reconstructions inform future climate projections (a) Seasonal local (NIOZ jetty, Texel, NL) SST measurements (thin solid lines; LOESS smoothed with span of 10% of the record), NOAA ERSSTv5 SNS SST averages (thick solid lines; LOESS smoothed with span of 10% of the record) and CMIP6 SSP2-4.5 scenario transient SNS SST simulations (shaded area) between 1850 and 2100. Arrows and figures on the right indicate temperature differences between CMIP6 SSP2-4.5 projections for 2100 CE and pre-industrial SNS SSTs (dashed lines) **(b)** Pre-industrial (PI; before 1900 CE) seasonal SST averages based on historical SST records (NOAA ERSSTv5[43] SNS averages and NIOZ jetty local record[44]) and PlioMIP2 pre-industrial model outcomes are compared with mPWP seasonality based on PlioMIP2 mPWP model simulations and mollusc-based reconstructions. Arrows and figures on the right indicate seasonal temperature differences between mollusc-based mPWP temperature reconstructions and pre-industrial SNS SST (dashed lines).

Discussion

Recent terrestrial mPWP data-model comparisons highlight that PLIOMIP2 models cannot reproduce the full extent of the mPWP warming that data suggest[2,21,46]. Likewise, in both the pelagic and terrestrial realm, reconstruction of the full seasonal cycle is challenging due to proxy limitations[2,21]. Detailed temperature monitoring studies show that shallow marine temperatures are strongly linked to air temperatures and local weather systems[47]. Together with the enhanced occurrence of summer stratification in warmer climates[24,48,49], a change in atmospheric circulation patterns may drive the summer increase in SST during the mPWP and in future climate observed in data and models (**Fig. 2-3**). Since the seasonal cycle is much more pronounced in the terrestrial realm, this limitation could explain part of the large seasonal data-model mismatch in terrestrial Northern Hemisphere high latitudes[21].

PLIOMIP2 models closely agree with mollusc-based reconstructions of SNS summer and winter SST during the mPWP (**Fig. 2 & 3b**). The summer warming observed in SST data and model outcomes is also reflected in PLIOMIP2 SAT seasonality in the SNS region (**Fig. 2d**; **Supplementary information Figure S37**). This highlights that PLIOMIP2 models can reconstruct seasonal SST variability in the North Atlantic, despite the difficulties with terrestrial data-model comparisons[21]. However, large inter-model variability in regions with poor data-model agreement suggests that structural model uncertainties also contribute to the mismatch[21].

The agreement between PLIOMIP2 pre-industrial control simulations and present-day climate (represented in CMIP6 models and instrumental records; **Fig. 3**)[1,9,50] lends confidence to the application of mPWP reconstructions and model simulations to better understand the seasonal impact of moderate global warming on future European climate. The seasonal-scale data-model agreement in the SNS, situated between the pelagic and terrestrial realms, both for present-day and mPWP climate, sheds new light on the seasonal response to warmer climate in the mid latitudes: The unique potential of marine molluscs to record seasonal-scale SST variability in coastal regions[28,51] in combination with the strong relationship between mid-latitude coastal SST and SAT[47,52] (see **Fig. 2d** and **Supplementary Information Figure S28-S32**) highlights the key role of seasonally resolved shallow marine climate archives for better understanding past and future climates.

Our mollusc-based data and PLIOMIP2 model estimates of mPWP SST seasonality resemble projections of future (2081 – 2100 CE) SNS winter (7.7 ± 0.3°C) and summer SST (19.1 ± 0.5°C; **Fig. 3a**) by transient CMIP6 model simulations of the “middle-of-the-road” SSP2-4.5 scenario[50] (**Fig. 3**). Note that these are two different climate scenarios: CMIP6 represents a transient climate disturbance, while the mPWP simulations and reconstructions sample an equilibrated climate under long-term atmospheric CO_2 forcing of 400 ppmV[9]. The difference is evident from atmospheric pCO_2 projections of ~600 ppmV in 2100 CE and ~580 ppmV on the long term (2500 CE) under SSP2-4.5, which significantly exceed the mPWP estimate of ~400 ppmV[3,5]. Notwithstanding this difference, the results of our data-model comparison and the similarity of the SSP2-4.5 scenario to the current global emission trajectory[4] show that the mPWP presents valuable lessons for climate in Europe by the end of this century and that models are able to project seasonal climate in this region in a warmer world.

The spatial variability in seasonal response to mPWP warming of SST and SAT reveals a clear signature of sea ice extent: SST and SAT respond in opposite directions to mPWP warming in the higher latitude areas that lose winter sea ice cover under mPWP conditions (**Fig. 2d-e**; e.g. Labrador Sea and Barents Sea; **Supplementary Information Figure S33**). The loss of winter sea ice in a mPWP-like climate scenario facilitates heat transfer from the upper ocean to the lower atmosphere in winter, cooling the upper ocean in winter (enhancing SST seasonality) and warming the lower atmosphere (reducing SAT seasonality)[45]. This effect explains why higher latitudes are more impacted by the sea ice-albedo feedback which changes due to a reduction in sea ice extent under the mPWP-like conditions[53,54] and in future climate scenarios[55]. In these regions, Arctic Amplification is expected to cause winter SAT to warm faster than other regions[10,56], while SST actually shows a summer warming effect in both the high and the mid latitudes.

This hypothesis is supported by climate models showing that Arctic Amplification reduces the latitudinal SAT gradient in warmer climates[10]. This weakens the mid-latitude atmospheric summer circulation, causing a weakening of storm tracks, with lower cyclone activity over Europe, more persistent weather and a reduction in summer cloud cover[11]. This reduction in cloud cover over temperate latitudes of the North Atlantic is also simulated in PlioMIP2 model outcomes (**Supplementary Information Figure S35**)[13]. Recent observations from various parts of the North Atlantic region suggest that circulation changes are already enhancing summer warming and prolonging heat waves through low cyclone activity, low cloud cover and more persistent weather[12,57,58]. In the winter months, zonal (westerly) wind increases, enhancing cloud cover and precipitation and suppressing winter warming[13]. Taken together, this change in the atmospheric circulation regime results in an increase in extreme weather conditions in Europe in both seasons, with more severe precipitation events in winter and more prolonged droughts in summer[13].

Our data-model analysis reveals that a mPWP-scale SST increase in the SNS region causes more pronounced warming in summer (reconstructions: +4.2 ± 2.6 °C; PLIOMIP2 models: +5.1 ± 0.9 °C) than in winter (reconstructions: +2.2 ± 2.0°C; PLIOMIP2 models: +2.5 ± 0.5°C; **Fig. 3b**). Historical climate data (**Fig. 3a**) and recent climate attribution studies[59–61] reveal that this trend is already underway in Europe[62]. Therefore, reconstructions and model simulations of mPWP seasonality reveal the impact of our current climate trajectory: Due to the hypothesized mid-latitude circulation changes, global warming is likely to regionally shift the distribution of extreme weather events on top of the overall increase in frequency and severity of these events due to the thermodynamic effect of greenhouse warming[14]. The seasonally asymmetric change in mid-latitude zonal circulation, even under a relatively mild mPWP-like warming scenario, renders Europe particularly vulnerable to prolonged heat and drought in summer and intense precipitation events in winter[13]. Enhanced summer warming in coastal regions poses a serious risk for shallow marine communities, since it leads to more frequent and extreme weather events, such as marine heatwaves[29,30,59,61,63]. These marine heatwaves[64] have recently caused mass mortality events[65], mass coral bleaching[66] and toxic algae blooms[67], severely affecting marine biodiversity. They are among the major reasons for concern related to anthropogenic climate change[68]. Considering the high societal and ecological importance of mid-latitude coastal regions, local data-model comparison studies of short-term variability during past climates relevant for future warming scenarios play a fundamental role in honing model projections which inform climate adaptation strategies.

Materials and Methods

Specimen collection

Seven fossil mollusc specimens were collected by one of the authors (Stijn Goolaerts) for analysis from temporary exposures of the Oorderen Member of the Lillo Formation in the Antwerp area, (Belgium, see **Fig. 1**). These were specimens of *Angulus benedeni benedeni* (specimen ID: SG126 and SG127) from Deurganckdoksluis (51°16’49”N, 4°14’56”E; collected in 2013), *Pecten complanatus* (SG115) and *Glycymeris radiolyrata* (SG116) from Deurganckdok (51°17'24"N, 4°15'37"E; collected on Feb 2nd, 2001) *Pygocardia rustica* (SG105), *Ostrea edulis* (SG113), and *Arctica islandica* (SG107) from Verrebroekdok (51°16’16”N, 4°12’53”E; collected in 1999-2000). At these localities, the Oorderen Member, from bottom to top, is divided into: basal shell bed, *Atrina* level, *Cultellus* level (SG115 and SG116) and *benedeni* level (SG126 and SG127)[37]. Specimens SG105, SG113 and SG107 were collected *ex situ* within the Oorderen Member. The estimated age range for the Oorderen Member is 2.72 Ma – 3.3 Ma[35,40] (see **Supplementary Information Figure S2**).

Palaeoenvironmental context

Field observations and a detailed assessment of the composition of the invertebrate fauna reveal that the fossil-bearing sediments of the Oorderen Member were deposited between 30 m and 50 m water depth during warm, highstand intervals within this time window[35,36]. Previous studies have argued that the SNS undergoes summer stratification during the mPWP that would cause molluscan shell reconstructions to underestimate summer temperatures[49]. However, the lack of dysoxic faunas in the Oorderen Member suggests the absence of persistent stratification[35]. Furthermore, the presence of sedimentary structures indicative of tidal currents and strong vertical mixing during deposition of the Oorderen Member argues against a large surface to seafloor temperature gradient[39]. Therefore, it is likely that the molluscs recorded temperatures close to the sea surface temperatures year-round. This assessment is supported by the observation of warm spring and cool autumn temperatures, suggesting a direct response of the water temperature experienced by the molluscs to the seasonal cycle in surface air temperatures (see **Results**; **Fig. 3**). However, given this evidence, we cannot fully exclude that spatially and temporary restricted temperature stratification did occur during the lifetime of the studied specimens[49]. Note that, even if summer stratification occurred, the summer temperatures recorded by the molluscs would underestimate the true mPWP summer SST and the occurrence of enhanced summer warming during the mPWP would still be supported by the data.

Specimen preparation

Shells were partially embedded in epoxy resin before polished thick sections were prepared to expose a cross section through the axis of maximum shell growth (following [69]; see **Supplementary Information Figure S3**). Preservation of the original shell calcite and aragonite was verified using a combination of Scanning Electron Microscopy (SEM), cathodoluminescence microscopy (CL), Electron Backscatter Diffraction microscopy (EBSD), micro-X-ray fluorescence (µXRF) and X-ray Diffraction (XRD; see [40] and **Supplementary Information Figures S4-S12**). Only shells with excellent preservation as demonstrated by these methods were considered for clumped isotope analysis.

Geochemical analysis

Carbonate was sampled along transects in the direction of growth in transects on cross sections through the outer shell layers of all shells except *Pecten complanatus* (SG115) and *Angulus benedeni* (SG126 and SG127), whose thin outer shell layers necessitated sampling on the outside of the ventral margin. A combination of hand-held drilling (outside) and micromilling (in transects) was used to sample along the growth increments to minimize time averaging (**Supplementary Information**). The number of samples per specimen ranges from 61 to 157 (**Fig. 2**): SG105, n = 98; SG107, n = 63; SG113, n = 90; SG115, n = 100; SG116, n = 157; SG126, n = 79; SG127, n = 61). Small (70-160 µg) aliquots of each sample were digested in phosphoric acid for 600 seconds at 70°C in a Kiel IV carbonate preparation device, after which the resultant CO_2 gas was purified using two cold fingers and a Porapak trap[70] before the clumped isotope composition (Δ_{47}) was analysed using two Thermo MAT253 mass spectrometers. A Long-Integration Dual Inlet (LIDI) workflow[70,71] was used for all except 53 aliquots from *Pygocardia rustica* (SG105), the latter of which were measured using sample-standard measurement cycles ("click-clack" mode; e.g. [72]). Isotopic ratios were standardized using the ETH standards[73], which were run in approximately one-to-one ratio with the samples[74] and corrected for ^{17}O concentration following[75]. Long-term analytical precision was monitored using IAEA-C2 and Merck reference materials (typical standard deviation of 0.04‰; see **Supplementary Information Table S2**) after outlier removal based on metadata on instrument performance (see criteria in **Supplementary Information Section 3.2**).

Seasonality reconstructions

For each mollusk specimen, samples were internally dated relative to the seasonal cycle using ShellChron[76], after which measurements within a specimen were grouped in four three-monthly bins ("seasons"). Summer and winter seasons were defined as consecutive three-month periods with lowest and highest Δ_{47} values, respectively, calculated separately for each specimen (see **Supplementary Information Section 3.2** and **Figures S20-S32**). Mean seasonal Δ_{47} values were obtained through weighted averages of seasonal means and uncertainties considering uncertainty within and variability between specimens. Seasonal temperatures during the mPWP were reconstructed from Δ_{47} for each seasonal group using the clumped isotope calibration by [77], propagating uncertainty on Δ_{47} values following the procedure described in the supplement of [78].

Climate model output

Seasonal SST from the SNS was extracted from the corresponding local ocean grid cells (51-55°N, 2-4°E) in the PlioMIP2 model ensemble (see **Fig. 2**). SNS SST records were obtained from the same area within the ERSSTv5 product[43] and supplemented with local SST observations from the NIOZ monitoring station[44]. Future projections matching the SSP2-4.5 scenario[50] were produced for CMIP6 and the regional SST outcomes were exported from the IPCC WG1 Interactive Atlas[79]. Seasons were defined as weighted means of the three months containing the largest number of days in the season according to the astronomical definition: Winter: January-March, spring: April-June, summer: July-September, Autumn: October-December. Data processing was carried out using the open-source computational software R[80] and scripts are provided in [81].

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Acknowledgements

This research would not have been possible without the dedicated lab assistance from Arnold van Dijk, Desmond Eefting, Ilja Kocken and Inigo Müller in the Utrecht University clumped isotope lab. The authors would like to thank Leonard Bik (UU), Bart Lippens (VUB) and Bauke Lacet (VU Amsterdam) for their help with sample preparation and Maarten Zeilmans (UU) for his assistance with high-resolution colour scans of the shell specimens. We thank Tilly Bouten (UU) for help with the SEM analyses, Maartje Hamer (UU) for assistance with EBSD, João Trabucho Alexandre (UU) and Anita van Leeuwen (UU) for assistance with XRD analyses, Andre Niemeyer (UU) for his help with cathodoluminescence microscopy and Roald Tagle (Bruker Nano GmbH), Steven Goderis and Luc Deriemaker (VUB) for their assistance in the AMGC-VUB XRF lab. NJW thanks Lenette de Gier (UU), Jennifer Franke (UU), and Bram Verhage (UU) for their assistance with sampling, diagenetic screening and lab analysis. This manuscript benefitted from discussions with Paolo Scussolini (VU Amsterdam). Stijn Goolaerts is grateful to Veerle Schelfhout, Freddy Aerts, Murielle Reyns, Roger Sieckelink, and Nouredine Ouifak of “Mobiliteit en Openbare Werken (MOW)” for granting access to the Verrebroekdok (1999-2000), Deurganckdok (2001-2002) and Deurganckdoksluis (2012–2014) construction sites, allowing the collection of the study material.

This work was funded through a Marie Curie Individual Fellowship (grant no. H2020-MSCA-IF-2018 - UNBIAS, 843011) and Flemish research Council (FWO) postdoctoral fellowship (grant no. 12ZB220N), both awarded to NJW. BG is supported by an UU-NIOZ collaboration grant. AJ is supported by a grant from the Leverhulme Trust (RPG-2021-090). PK was supported by FWO PhD fellowship 11E6621N. PC thanks the VUB Strategic Research Program for support, as well as the FWO - Hercules Program for financing the µXRF instrument at AMGC.

Below is an overview of author contributions according to the CRediT framework: This study was conceptualized by NJW, PC and MZ. Data curation was done by NJW, JT, BG, NW, SL, BM and MZ. Formal analysis was carried out by NJW. Funding for the project was acquired by NJW, PC and MZ. Investigation and experimental work were done by NJW, BG, NW, PK, FH and MZ. NJW, JT and MZ were responsible for development of the methodology. The project was managed by NJW under supervision by PC and MZ. Resources were provided by SG and FW. Development of software for formal analysis was by NJW. NJW, AJ, PC and MZ supervised the project. Validation of the reproducibility of the results was by NJW, JT, BG, PK, FH, SL, BM, PB, FW and MZ. Visualization of the results was initiated by NJW, JT, NW and FW and improved through contributions from AJ, BG, BM, PB and MZ. The original draft was written by NJW. All authors contributed to reviewing and editing subsequent versions of the manuscript.

The authors declare that they have no competing interests. All data on which this study is based are made available through the open-access database Zenodo: https://doi.org/10.5281/zenodo.8378900.